

Threshold changes in vegetation along a grazing gradient in Mongolian rangelands

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Summary

1. The concept of threshold has become important in ecology, but the nature of potential threshold responses of vegetation to grazing in rangeland ecosystems remains poorly understood. We aimed to identify ecological thresholds in vegetation changes along a grazing gradient and to examine whether threshold changes were expressed similarly at a variety of ecological sites.
2. To accomplish this, we surveyed the vegetation along grazing gradients at 10 ecological sites, each located at different landscape positions in Mongolia's central and southern rangelands. Evidence for a threshold in changes in floristic composition along the grazing gradient was examined by comparing linear models of the data with nonlinear models fitted using an exponential curve, an inverse curve, a piecewise regression and a sigmoid logistic curve.
3. Three nonlinear models (piecewise, exponential and sigmoid) provided a much better fit to the data than the linear models, highlighting the presence of a discontinuity in vegetation changes along the grazing gradient. The shapes of the best-fit models and their fit to the data were generally similar across sites, indicating that the changes in floristic composition were relatively constant below a threshold level of grazing, after which the curve changed sharply.
4. Except for two sites, the best-fit models had relatively narrow bootstrap confidence intervals (95% CI), especially around threshold points or zones where the rate of change accelerated, emphasizing that our results were robust and conclusive.
5. *Synthesis.* Our study provided strong evidence for the existence of ecological thresholds in vegetation change along a grazing gradient across all ecological sites. This suggests that vegetation responses to grazing in the study areas are essentially nonlinear. The recognition that real threshold changes exist in real grazing gradients will help land managers to prevent the occurrence of undesirable states and promote the occurrence of desirable states, and will therefore permit a major step forward in the sustainable management of rangeland ecosystems.

Key-words: arid and semi-arid rangelands, bootstrap confidence interval, ecological threshold, land degradation, Mongolia, ordination, piecewise regression model, plant functional types, rangeland management

Introduction

The concept of a threshold has become important in ecology and natural resources management (Lindenmayer & Luck 2005; Briske *et al.* 2006; Groffman *et al.* 2006). Critical thresholds occur when the response of a species or ecological process to disturbance is not linear, but instead changes abruptly at some threshold level. Exceeding this threshold leads to a loss of ecosystem functions and biodiversity;

change in the opposite direction can instead lead to recovery if the threshold change can be reversed. Typical examples include observations that the loss of native vegetation cover to levels below a threshold leads to increased loss of species that depend on that native vegetation (Fahrig 2003; Radford *et al.* 2005) and that floristic composition changes abruptly at a threshold distance from habitat edges (Toms & Lesperance 2003). A comprehensive understanding of whether such threshold changes exist in rangeland ecosystems may be achieved through a grazing gradient approach (Lange 1969; Andrew 1988).

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A number of definitions of ecological thresholds have been proposed in the literature. Thus, it is essential to clarify which type of ecological threshold is being addressed and its potential roles in land management (Bestelmeyer 2006; Groffman *et al.* 2006). Bestelmeyer (2006) proposed two broad categories of threshold. Preventive thresholds can be defined using a pattern threshold generated by a prevailing disturbance regime, and represent the point at which disturbance should be limited to prevent drastic changes in ecological conditions (Toms & Lesperance 2003; Radford & Bennett 2004; Radford *et al.* 2005). In contrast, a restoration threshold can be defined using a degradation threshold, the point at which an ecological condition degrades so much that it can no longer recover on its own to its initial state. A restoration threshold must also address a pattern and a process threshold. A process threshold describes the point at which an environmental condition changes in response to an altered process rate (Bestelmeyer *et al.* 2003, 2004). Once a sufficient level of change has occurred under a given set of ecological conditions, a degradation threshold is reached in which subsequent changes in state become impossible to reverse (Bestelmeyer 2006).

The concepts of preventive and restoration thresholds can be useful tools for preventive management and attempts to restore an ecosystem, respectively. However, previous studies (Radford *et al.* 2005; Bestelmeyer 2006) have suggested that locating a degradation threshold as distinct points or zones of change remains a considerable methodological challenge, and therefore applying a restoration threshold to environmental management has had limited success. In contrast, a preventive threshold corresponding to abrupt changes in ecological responses will more readily translate into management guidelines (Huggett 2005; Radford *et al.* 2005). Moreover, evaluating thresholds on the basis of the prevailing disturbance regimes will more explicitly identify the driving force (Holling 1973; Peterson *et al.* 1998) and will provide additional insights into the underlying ecological processes (Briske *et al.* 2003). Thus, in the present study, we focused on the preventive threshold (*sensu* Bestelmeyer 2006). We have therefore defined ecological thresholds as points or zones at which relatively rapid change occurs from one ecological condition to another along a gradient in a prevailing disturbance regime (Radford & Bennett 2004; Radford *et al.* 2005).

Theory suggests that rapid changes in ecological conditions can occur in rangeland ecosystems (van de Koppel *et al.* 1997; Scheffer & Carpenter 2003). The threshold behaviour of vegetation in response to grazing may be a product of interactions between diverse ecological factors (e.g. the life span of woody species, competition among species or plant functional types), human activities (e.g. overgrazing and fire) and climate (Bestelmeyer *et al.* 2003, 2004; Groffman *et al.* 2006). Pattern thresholds in rangeland ecosystems appear to be based on changes in the multivariate characterization of community composition, plant growth form and the occurrence of invasive species (Scheffer *et al.* 2001; Stringham *et al.* 2003; Briske *et al.* 2005, 2006). These thresholds originally became a focal point in rangeland management through their relationship to state-and-transition models because the identification of

thresholds is necessary to recognize the various quasi-stable states that can potentially exist at a given ecological site (Briske *et al.* 2003, 2005). Threshold identification and prediction are also necessary to enable rangeland managers to prevent the occurrence of undesirable states and to promote the occurrence of desirable states (Bestelmeyer *et al.* 2003). A limited understanding of threshold behaviour frequently results in the identification of ecological thresholds after, rather than prior to, the threshold has been reached, thereby limiting the land manager's ability to prevent adverse changes in state (Briske *et al.* 2006).

Many rangeland studies have reported that the impacts of concentrated grazing on vegetation dynamics generally lead to marked reductions in forage resources, mainly due to shifts in the community composition from dominance by perennial grasses and forbs toward dominance by unpalatable forbs and weedy annuals (e.g. Fernandez-Gimenez & Allen-Diaz 2001; McIntyre & Lavorel 2001; Todd 2006). However, fewer studies (e.g. Friedel 1991, 1997; Bestelmeyer *et al.* 2004) have actually attempted to determine whether these compositional shifts exhibit a continuous or a discontinuous (threshold) response. In particular, the nature (i.e. the form and shape) of potential threshold responses of vegetation to grazing remains poorly understood. This lack of understanding stems from absent or inadequate data on the response of natural systems to changes in the rates and types of ecological processes, especially under different disturbance regimes (With & King 1999; Del-val & Crawley 2005). Moreover, identifying the threshold behaviour is difficult in terrestrial ecosystems because the main components of the system change slowly (Groffman *et al.* 2006). Finally, ecologists should consider whether the nature of threshold responses observed for one site can be generalized to other sites.

Studies of grazing gradients (Lange 1969; Andrew 1988) that reflect a realistic range of long-term grazing impacts may provide an ideal opportunity to overcome the aforementioned problems and test the nature of potential threshold responses in rangeland ecosystems. Livestock density and grazing intensity are usually highest close to livestock camps or sources of water. Many rangeland studies have sampled vegetation and soils along grazing gradients based on distance from a source of water (Fernandez-Gimenez & Allen-Diaz 1999, 2001; Landsberg *et al.* 2003; Todd 2006), from human settlements or from livestock camps (Turner 1998; Riginos & Hoffman 2003) to determine the impact of grazing on rangeland structure and function. In the present study, we therefore used the distance from livestock camps or sources of water to represent a spatial gradient in the accumulated impact of long-term exposure to livestock. We can explicitly detect abrupt changes in vegetation using statistical models by setting a high sampling resolution around the zones in which the rate of change is assumed to accelerate. We can also attempt to generalize our insights into the threshold responses by establishing grazing gradients at multiple ecological sites (Bestelmeyer *et al.* 2003).

Specifically, the present study addressed two main questions. (i) Can ecological thresholds in vegetation changes be identified

along a grazing gradient? (ii) Are threshold changes expressed similarly at a range of ecological sites (as defined by USDA National Resources Conservation Service 1997; see also Bestelmeyer *et al.* 2003) that differ in terms of edaphic and climatic conditions, and in landscape position?

Methods

STUDY AREAS

Research was conducted at 10 ecological sites widely spaced across three study areas which were located near Kherlen Bayan Ulaan (47°12' N, 108°44' E), Mandalgobi (45°46' N, 106°16' E) and Bulgan (44°05' N, 103°32' E) in Mongolia's Khenti, Dundgobi and South Gobi provinces, respectively (Table 1). Kherlen Bayan Ulaan and Mandalgobi are located in steppe ecological zones, and Bulgan is found in a desert–steppe ecological zone. These two ecological zones cover more than half of Mongolia. Both ecological zones are generally dominated by perennial grasses or forbs, but the dominant species vary as a function of the landscape positions and climatic conditions. Table 1 summarizes the dominant plant species at each ecological site. Taxonomic nomenclature follows Grubov (1982). The three study areas have a long history (centuries) of grazing by domestic livestock under nomadic or semi-nomadic patterns of land use. The main livestock are cattle and sheep in Kherlen Bayan Ulaan; sheep, goats and cattle in Mandalgobi; and sheep, goats and camels in Bulgan. Livestock type also differs among landscapes within these areas.

The region's climate is arid and cold, with a short summer. Based on meteorological data provided by Mongolia's Institute of Meteorology and Hydrology, Ministry of Nature and Environment, annual rainfall averaged around 210 mm (CV = 21%) at Kherlen Bayan Ulaan, 170 mm (CV = 28%) at Mandalgobi and 140 mm (CV = 26%) at Bulgan between 1993 and 2003. In all areas, peak rainfall occurred in July. Summer and winter temperatures averaged around 15 °C and –22 °C, respectively, at Kherlen Bayan Ulaan, 19 °C and –14 °C at Mandalgobi, and 21 °C and –11 °C at Bulgan.

SURVEY DESIGN AND VEGETATION SAMPLING

Our study was based on field surveys of the standing vegetation along grazing gradients at 10 ecological sites, each located at different landscape positions in a grassland, shrubland or halophytic-shrubland vegetation type in Mongolia's central and southern rangelands (Table 1). Ecological sites in each study area were located on the sequence of denudation planes (i.e. a land catena): hill (KH), pediment (KP) and depression (KD) in Kherlen Bayan Ulaan, and hill (MH), tableland (MT), pediment (MP) and depression (MD) in Mandalgobi, and upper-pediment (BUP), lower-pediment (BLP) and depression (BD) in Bulgan. Because potential correlations between the grazing gradient and other environmental factors (especially microtopography) often create confounding effects due to sampling across different vegetation types and soil textures (Landsberg *et al.* 2003; Sasaki *et al.* 2005; Todd 2006), we selected sites where these confounding effects appeared to be smallest. More detailed methods for selecting the ecological sites were described by Sasaki *et al.* (2007). In selecting these sites, we aimed to ensure that we had covered a range of the climatic, geomorphic, edaphic and vegetation variation found within Mongolian rangeland ecosystems. The ecological sites were not selected to be statistical replicates within each landscape; rather, each site was intended to provide an independent test for the existence of ecological thresholds.

In the present study, we used the distance (m) from each survey transect (see below) to a livestock camp or source of water to represent relative grazing intensity. Variation in the relative grazing intensities along the grazing gradient may differ due to the actual number and type of livestock at the site (see Discussion for the effect of this variation on our results). In this paper, we defined a 'reference distance' (Table 1), which represents the point at which livestock impacts were minimal, and this distance was chosen at a position located outside the normal grazing range of the livestock from a camp or source of water (hereafter, the 'gradient source'). Because of differences in the number of livestock involved in the site, not all the reference distances could be sampled to the same distance due to logistical considerations. According to our preliminary survey, dung frequency decreased with increasing distance from the source (T. Okayasu, unpublished data). However, even at the reference distance, various amounts of dung and plants damaged by grazing were sometimes found (T. Sasaki, personal observation), indicating the existence of slight grazing impacts.

Between June and August 2006, vegetation was sampled at each ecological site using transects placed at set distances along the grazing gradients (five replicates of the gradient were created in different directions). Because we anticipated that vegetation changes would be more rapid in the zone immediately adjacent to the gradient sources than at a greater distance from them, the sampling resolution consequently increased toward the gradient source. Transects were placed at intervals of 10 m from 10 to 50 m, then at 75, 100, 150, 200, 300, 400, 500, 750 and 1000 m; exceptions were the KH and KD ecological sites, where transects were placed only up to 500 m from the source, and the MH and BUP sites, where transects were also placed at 1500 and 2000 m from the source.

In each transect, vegetation was sampled by identifying and estimating the aerial cover of all species present within five 1-m² (1 × 1 m) quadrats. Each quadrat on a transect was laid out at intervals of 1 m for the quadrats located 10–50 m from the source and at intervals of 5 m thereafter. The resulting data matrices used in this study thus consisted of a total of 3500 quadrats along 700 transects, sampled at 12–16 sampling distances around 10 gradient sources.

DATA ANALYSIS

The floristic composition data for each transect (using pooled data from the five subsamples) were simplified separately for each site using two ordination techniques: correspondence analysis (CA) and detrended correspondence analysis (DCA; Legendre & Legendre 1998). Plant cover data for each species (not transformed) were used in these analyses. Because the results were consistent between the two techniques, we have only reported the DCA results. Through our survey design (which attempted to eliminate extraneous influences other than grazing impacts as far as possible), only the first axis showed any relationship with the distance from the gradient source (T. Sasaki, unpublished data); therefore, only results from this axis are reported. DCA has been shown to provide an accurate output when the first environmental factor (in our study, the grazing impacts) has a dominant effect (Kenkel & Orloci 1986), and can be a useful tool for gradient extraction and the reduction of dimensionality (Ejrnæs 2000).

We fitted a locally weighted, nonparametric regression (lowess) model (Cleveland 1979) to each scatterplot of the relationship between distance from the source and floristic composition (i.e. the scores of DCA axis 1) to check whether a nonlinear relationship existed. Ideal response patterns along grazing gradients tend to follow a sigmoid logistic curve (Graetz & Ludwig 1978; Andrew

Table 1. Characteristics of each ecological site and the reference distance along each gradient from a livestock camp or source of water

Study area	Ecological Site code	Landscape position	Location	Gradient source	Vegetation type	Soil texture*	Dominant plant species	Reference distance (m)†
Kherlen Bayan Ulaan	KH	Hill	47°09' N, 109°17' E	Livestock camp	Grassland	Loam	Grasses: <i>Stipa krylovii</i> , <i>Agropyron cristatum</i> , <i>Carex duriuscula</i>	500
	KP	Pediment	47°14' N, 108°50' E	Livestock camp	Grassland	Loam	Grasses: <i>S. krylovii</i> , <i>Cleistogenes squarrosa</i> , <i>C. duriuscula</i> Forbs: <i>Comvolvulus ammannii</i>	1000
Mandalgobi	KD	Depression	47°04' N, 108°46' E	Livestock camp	Grassland	Sandy loam	Grasses: <i>Achnatherum splendens</i> , <i>S. krylovii</i> , <i>C. squarrosa</i>	500
	MH	Hill	45°47' N, 106°11' E	Livestock camp	Shrubland	Sand	Shrubs: <i>Caragana microphylla</i> Forbs: <i>Artemisia adamsii</i>	2000
	MT	Tableland	45°41' N, 106°27' E	Livestock camp	Grassland	Sandy clay loam	Forbs: <i>Allium polyrrhizum</i> , <i>Allium anisopodium</i> , <i>Arenaria capillaris</i>	1000
	MP	Pediment	45°41' N, 106°10' E	Livestock camp	Grassland	Sandy loam	Forbs: <i>A. polyrrhizum</i> , <i>Allium mongolicum</i> , <i>A. anisopodium</i>	1000
	MD	Depression	45°38' N, 106°16' E	Livestock camp	Halophytic shrubland	Sandy loam	Shrubs: <i>Reaumuria soongorica</i> , <i>Salsola passerina</i>	1000
Bulgan	BUP	Upper pediment	43°54' N, 103°30' E	Source of water	Grassland	Sandy clay loam	Forbs: <i>A. polyrrhizum</i> Grasses: <i>Stipa gobica</i>	2000
	BLP	Lower pediment	44°14' N, 103°38' E	Livestock camp	Shrubland	Sand	Forbs: <i>Artemisia pectinata</i> , <i>A. polyrrhizum</i> Shrubs: <i>Caragana korshinskii</i> , <i>Brachanthemum gobicum</i>	1000
	BD	Depression	44°18' N, 103°35' E	Livestock camp	Halophytic shrubland	Sandy loam	Grasses: <i>S. gobica</i> Shrubs: <i>Zygophyllum xanthoxylon</i> , <i>Haloxylon ammodendron</i> , <i>Anabasis brevifolia</i>	1000

*Source: T. Sasaki, unpublished data.

†The reference distance at each ecological site represents the point at which livestock impacts were minimal, and was located outside the normal grazing range of the livestock that were using the camp or source of water.

1988), but our lowess fitting suggested threshold changes with a single breakpoint in all ecological sites except BUP, where the response pattern appeared to follow a sigmoid logistic curve. Evidence for a threshold in the changes in floristic composition along the grazing gradient was then examined by comparing two linear regression models (distance untransformed and \log_{10} transformed) with models fitted to the data using an exponential curve [Score of DCA axis 1 = $a + b \exp(-c \times \text{Distance})$], an inverse curve [Score of DCA axis 1 = $a + (b/\text{Distance})$], piecewise regression models (*sensu* Toms & Lesperance 2003) of the form [Score of DCA axis 1 = $a + b \times \text{Distance}$, if $\text{Distance} \leq D$; Score of DCA axis 1 = $a + b \times \text{Distance} + c \times (\text{Distance} - D)$, if $\text{Distance} > D$], where D is the distance at the designated discontinuity, and a sigmoid logistic curve [Score of DCA axis 1 = $a - b \exp\{-\exp[c + d \log(\text{Distance})]\}$]. [Correction added after publication 2 November 2007: the form of the piecewise regression models stated above was corrected from [Score of DCA axis 1 = $a + b \times \text{Distance} + c \times (\text{Distance} - D)$, if $\text{Distance} = D$; Score of DCA axis 1 = $a + bD + c \times \text{Distance}$, if $\text{Distance} > D$].

Model selection was based on Akaike's information criterion (AIC = $-2 \times \log\text{-likelihood} + 2 \times \text{the number of parameters}$). AIC is an information theoretic optimality criterion that trades off bias (decreasing with the number of parameters in a model) with variance (increasing with the number of parameters in a model) to identify the most parsimonious model, which is the one with a minimal value of AIC. Therefore models with the smallest AIC are considered best-fit (Johnson & Omland 2004). Sound evidence for a threshold response (i.e. a discontinuity) requires that one of the piecewise regression models provides the best fit to the data, followed by the exponential, inverse, \log_{10} -transformed, and untransformed linear models (Radford *et al.* 2005). Sigmoid logistic models also strongly indicate a threshold response (e.g. Fahrig 2002).

We calculated the bootstrap confidence intervals for the parameter estimates for each best-fit model. The type of bootstrap confidence interval that we computed was the widely used bias-corrected and accelerated (BCa) interval (Efron & Tibshirani 1993). This process is repeated a large number of times (here, $B = 1000$ times), and a 95% bootstrap confidence interval is calculated from the set of B bootstrapped estimates.

We assumed that a given form and shape of vegetation responses at the community level may reflect the responses of most species, but this assumption risks masking other important responses because some species will respond differently to the grazing gradient (i.e. not in the nonlinear way that would indicate the presence of a threshold). In this context, it is useful to understand the response of plant functional types (PFTs), in which species with similar biological traits exhibit similar responses to grazing and can thus be grouped together (Gitay & Noble 1997). In addition, responses of PFTs to grazing have been used as a surrogate for the ecological processes underlying the grazing impacts in arid and semi-arid areas; for example, previous rangeland studies have suggested that community responses to grazing are strongly associated with plant life history and growth form (e.g. Fernandez-Gimenez & Allen-Diaz 2001; McIntyre & Lavorel 2001; Pakeman 2004; Sasaki *et al.* 2007). Hence, we also sought a best-fit regression model for each PFT to examine how the cover of PFTs classified as shrubs, grasses (including sedges; all grasses found in our study were perennial), perennial forbs and annual forbs responded to the grazing gradient. These PFTs are generally correlated with the relative palatability in the study areas (e.g. grasses are palatable, whereas annual forbs are unpalatable) according to Jigjidsuren & Johnson (2003). The processes used for model selection were the same as those used to identify threshold changes in floristic composition. This approach resulted in all PFTs

being classified into eight possible patterns, five of which could be considered elements of threshold changes in vegetation along grazing gradients. All statistical analyses were performed with the R software (version 2.4.1, R Development Core Team 2006).

Results

We recorded a total of 79 species in our study, of which 9 were annual forbs, 46 were perennial forbs, 9 were grasses and 15 were shrubs. The biplots of DCA for floristic composition along grazing gradients at all sites suggested that changes in floristic composition occurred along environmental gradients indicated predominantly by DCA axis 1 (T. Sasaki, unpublished data). In the following analyses to identify threshold changes in floristic composition along the grazing gradient, we used the score along DCA axis 1 as the dependent variable and the distance from the gradient source as the independent variable.

TEST FOR THRESHOLD CHANGES IN FLORISTIC COMPOSITION ALONG A GRAZING GRADIENT

The scatterplots of the data fitted with a locally weighted, nonparametric regression (lowess) model indicated that a nonlinear relationship existed between distance and floristic composition. Of the six models that we compared in this study, three nonlinear models (piecewise, exponential or sigmoid) provided a much better fit to the data than the linear models and highlighted the discontinuity in vegetation changes along the grazing gradient (Table 2); the inverse model did not provide the best fit for any of the sites. The piecewise regression model had the smallest AIC (i.e. provided the best fit for the data) at the KH, KP, KD, MT, MD and BD ecological sites; the exponential model had the smallest AIC at the MH, MP and BLP sites; and the sigmoid logistic model had the smallest AIC at the BUP site (Fig. 1; Table 2).

The shapes of most of the best-fit models and their fit to the data (Fig. 1) were generally similar and indicated that changes in floristic composition were relatively constant below a threshold level of grazing, and then changed sharply when the threshold levels were exceeded. However, at BUP, the sigmoid logistic model revealed the existence of two contrasting states along the grazing gradient.

Except for MH and BLP, the models had relatively narrow bootstrap confidence intervals (95% CI), especially around the threshold points or zones where the rate of change in floristic composition changed sharply. There was more variability in the score along DCA axis 1 for sites MH and BLP at distances near the threshold zones, and this was reflected in the broader confidence intervals for these sites than for the other sites.

RESPONSE PATTERNS OF THE COVER BY DIFFERENT PLANT FUNCTIONAL TYPES TO THE GRAZING GRADIENT

We identified eight response patterns for the cover by different PFTs in response to the grazing gradient (Fig. 2). More than

Table 2. Values of AIC (Akaike's information criterion) for the models used to identify threshold changes in the floristic composition along a grazing gradient at 10 ecological sites. Site classifications are presented in Table 1. Values in bold indicate the smallest AIC (i.e. the best fit)

Ecological site	Model					
	Linear	Logarithmic	Inverse	Exponential*	Piecewise	Sigmoid*
KH	92.26	63.50	148.13	31.45	27.19	DNC
KP	188.46	132.89	138.39	80.31	57.84	DNC
KD	108.88	63.59	28.77	3.96	3.18	DNC
MH	119.56	54.83	107.12	48.37	50.70	DNC
MT	201.83	130.66	178.95	99.55	97.67	DNC
MP	185.82	129.30	75.48	35.85	36.63	DNC
MD	97.70	78.28	62.58	67.93	52.88	DNC
BUP	59.49	174.47	237.60	DNC	58.57	-49.30
BLP	-22.79	-55.52	-12.16	-61.21	-60.19	DNC
BD	92.02	64.59	71.38	65.93	48.75	DNC

*DNC, Did not converge. The parameter estimates in the model did not converge on a stable value.

Table 3. Summary of the responses of the cover of different plant functional types (PFTs) to the grazing gradient associated with distance from a livestock camp or a source of water at the 10 ecological sites. (Fig. 2 illustrates the form of the response curves). Entries in bold indicate nonlinear responses. + indicates increasing patterns; - indicates decreasing patterns

Ecological site	Cover of plant functional types					
	Shrub cover	Grass cover	Perennial forb cover	Annual forb cover		
KH	No obvious pattern	Piecewise	+	Linear	+	Piecewise
KP	No obvious pattern	Exponential	+	No obvious pattern	+	Piecewise
KD	-	Exponential	+	Logarithmic	-	Piecewise
MH	Exponential	+	Piecewise	+	Linear	+
MT	Linear	+	No obvious pattern	Exponential	+	Exponential
MP	No obvious pattern	No obvious pattern	No obvious pattern	Piecewise	+	Piecewise
MD	Piecewise	+	No obvious pattern	Linear	+	Piecewise
BUP	-	Piecewise*	+	Piecewise	-	Piecewise
BLP	Piecewise	+	Piecewise	+	Linear	+
BD	Exponential	+	No obvious pattern	Linear	+	No obvious pattern

*All the patterns indicated in bold were asymptotic, but only the pattern for BUP resembled that in graph 2 in Fig. 2.

half of the responses were nonlinear (Table 3). The cover of shrubs showed a piecewise or exponential asymptotic increase with increasing distance from the gradient source at sites with a shrubland vegetation type (MH, MD, BLP and BD). At the other sites, the appearance of shrubs was too rare to reveal a significant pattern, with the exception of MT (which showed a slight linear increase). Grass cover showed a piecewise or exponential rapid increase, and reached an asymptote at sites KH, KP, KD, MH and BLP, but only the pattern for BUP resembled that in graph 2 in Fig. 2. At the other sites, grasses were rare and showed no obvious response. Perennial forb cover generally did not exhibit a nonlinear response to the grazing gradient, and thus does not appear to be an element involved in the threshold changes in vegetation; however, perennial forbs were dominant in the grassland at MT and MP, and perennial forb cover at these sites showed exponential and piecewise asymptotic increases, respectively. Exceptionally, perennial forb cover showed a piecewise asymptotic decrease at BUP. Annual forb cover generally showed a piecewise or exponential rapid decrease, and reached an asymptote, but showed a piecewise increase at MH, an exponential increase

at BLP, and no obvious response at BD, where annual forbs were too rare to reveal a significant pattern.

Discussion

Our study provided strong evidence for the existence of threshold changes in vegetation along a grazing gradient across all ecological sites, even though the vegetation type, edaphic conditions, landscape position and climatic conditions differed between the sites. This suggested that vegetation responses to grazing in the study areas were essentially nonlinear and that the results were biologically realistic rather than an artefact of the statistical techniques that we used. Critical use of the threshold concept can thus shed additional light on rangeland management.

THE NATURE OF THRESHOLD CHANGES IN VEGETATION ALONG A GRAZING GRADIENT

The threshold changes in floristic composition along a grazing gradient (Fig. 1) suggest that the underlying response of

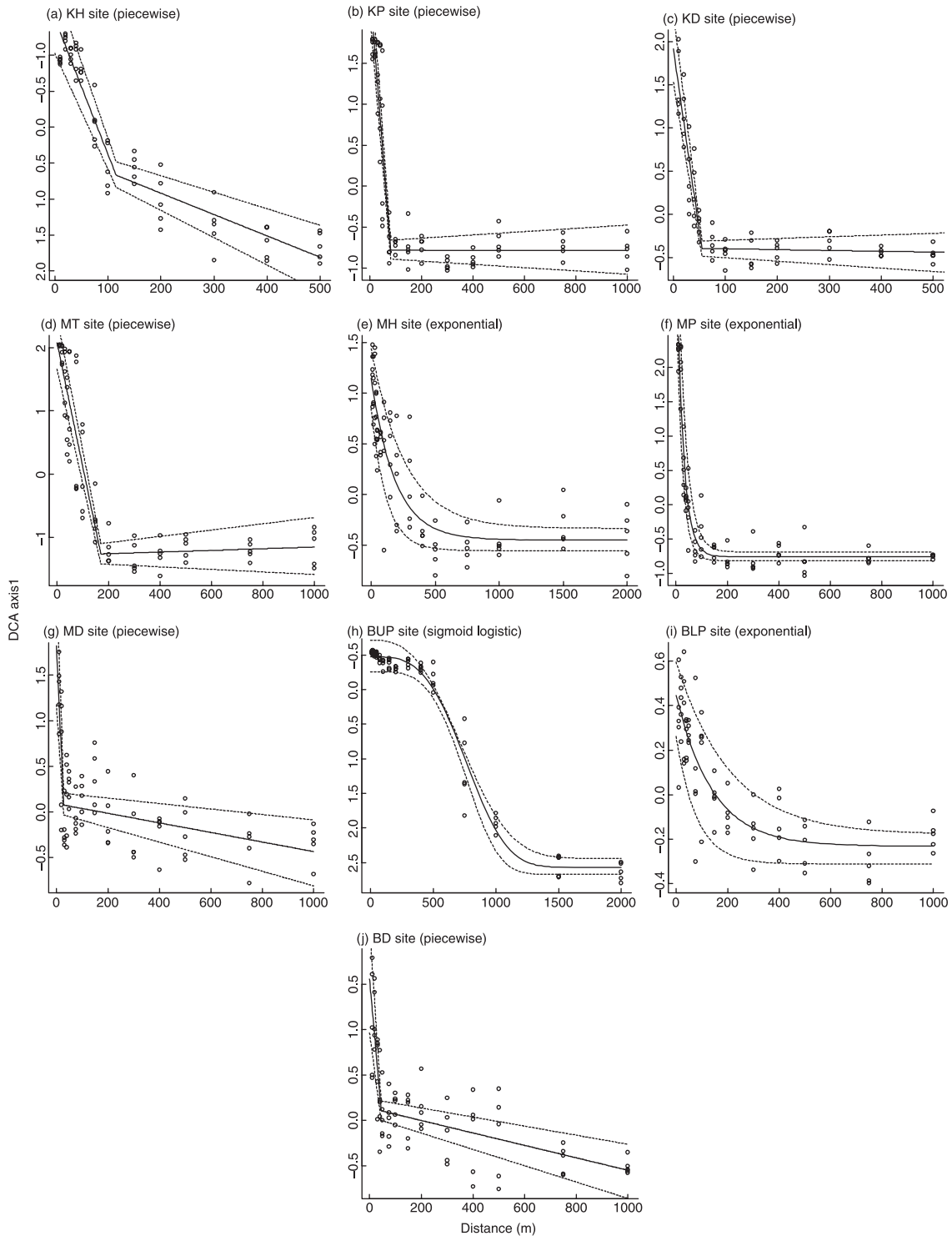


Fig. 1. Best-fit models of floristic composition for each transect (scores along DCA axis 1) as a function of distance from the gradient source (Distance). Note that the nonlinear models fitted the data well, highlighting the discontinuity in vegetation changes along the grazing gradient. Dashed lines indicate the 95% bootstrap CI. The values on the y-axes in KH and BUP have been reversed to avoid visual confusion.

ecological processes to grazing impacts is nonlinear for the species or PFTs that are most sensitive to the grazing gradient at each ecological site. When biotic structures and interactions are modified by grazing impacts, they are assumed to exhibit the presence of thresholds (Briske *et al.* 2005, 2006). Complete

replacement (a nonlinear rapid increase vs. a nonlinear rapid decrease) in the cover of PFTs may be the consequence of the biotic mechanisms underlying the grazing impacts (mainly foraging impacts by livestock in this study); this was the case for grasses vs. annual forbs at KH, KP and KD; for perennial

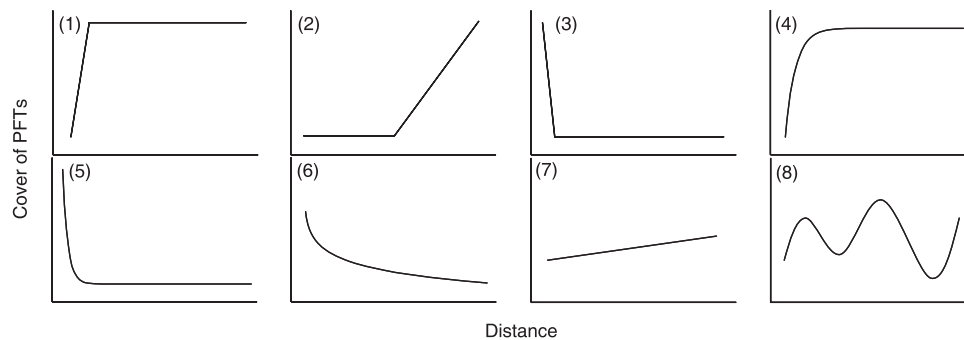


Fig. 2. Schematic diagrams representing the possible response patterns of the cover of different plant functional types (PFTs) to the grazing gradient at 10 ecological sites (see Table 3 for a summary of the actual results). Graphs 1–3 exhibit patterns that best fit a piecewise regression model. Graph 2 was observed only for the response of grass cover at the BUP site. Graphs 4 and 5 exhibit patterns that best fit an exponential model. Graphs 6 and 7 exhibit patterns that best fit a logarithmic and linear model, respectively. Graph 8 exhibits no obvious pattern.

forbs vs. annual forbs at MT and MP; for shrubs vs. annual forbs at MD; and for grasses vs. perennial and annual forbs at BUP (Table 3). One possible mechanism to explain these results is that the dynamic equilibrium among PFTs can switch rapidly as a result of increased interspecific competition (Milchunas *et al.* 1988); previous studies (McIntyre & Lavorel 2001; Pakeman 2004; Diaz *et al.* 2007) suggested that increased grazing favoured a suite of attributes associated with fast regeneration and growth, including annual life history and a ruderal strategy, whereas decreased grazing favoured perennial species, regeneration from a buried seed bank, and species that were relatively palatable. Exceptionally, perennial forb cover showed a nonlinear decrease at BUP. This resulted from the unusually high abundance of a perennial but toxic and weedy forb, *Peganum nigellastrum*, near the gradient sources (Sasaki *et al.* 2005). However, at MH and BLP, where annual forb cover showed a nonlinear rapid increase (Table 3), the underlying mechanisms are probably somewhat different. Because the MH and BLP sites were characterized by sandy soils and high erodibility (Table 1; Sasaki *et al.* 2007), decreased grazing may have favoured both annual and perennial herbs as a result of an ‘ecosystem engineering’ effect associated with wind erosion that is created by the shrubs (Wright *et al.* 2006). At these sites, shrub species gather sand around them, forming mounds, and the resulting modification of the abiotic environment (especially soil nutrients) by these mounds (Shachak *et al.* 1998; Shumway 2000) may favour the establishment of both perennial and annual herbaceous species. Thus, it is likely that abiotic mechanisms as well as biotic mechanisms contribute to the occurrence of a threshold, and therefore the sharp changes at the threshold zones cannot be derived only from the floristic composition data.

The distance at which the threshold changes occurred differed among the sites (Fig. 1). This originates as a result of what Andrew (1988) predicted as the range of the ‘sacrifice zone’, in which the severity of the grazing impact may differ according to the actual number of livestock at the site. In this context, the actual shape of the threshold responses (i.e. piecewise or exponential vs. sigmoid) may also depend on the magnitude or concentration of the grazing impact within the

sacrifice zone. Theory predicts that the response of ecological variables to the distance from a gradient source follows a sigmoid logistic curve (Graetz & Ludwig 1978; Andrew 1988), but the present results only followed this pattern at BUP. The shapes of the best-fit models showed that abrupt changes in floristic composition occurred within highly impacted zones relatively close to the gradient sources and that the rates of change were constant below threshold levels of grazing, even at moderate or light grazing intensities. This suggests that vegetation in regions such as Mongolia that has a long history of grazing domestic livestock is relatively resistant to grazing. However, if concentrated grazing impacts exceed the threshold level, the vegetation could change into a contrasting state (i.e. a ‘regime shift’; Scheffer *et al.* 2001). A sigmoid logistic response along a grazing gradient would be rarely observed in vegetation that has a relatively high resistance to grazing.

CAVEATS

Several caveats and assumptions are associated with our study. We did not measure grazing intensity directly, and sampled vegetation only once per site. Our decision to sample vegetation only once allowed us to allocate a much greater sampling effort to a larger number of widely spaced ecological sites, which was necessary to test our hypothesis about the wide applicability of the observed patterns. We also chose distance from a livestock camp or source of water as a surrogate for long-term grazing because of its demonstrated reliability and generalizability in previous studies (Andrew 1988; Fernandez-Gimenez & Allen-Diaz 1999, 2001; Landsberg *et al.* 2003; Todd 2006). Other rangeland studies have attempted to interpret changes in vegetation along such grazing gradients and to develop the logistics of obtaining representative data for broad-scale areas (e.g. Pickup *et al.* 1994, 1998), but these scaling-up issues have not yet been resolved and remain future challenges. Moreover, it is desirable to use a range of grazing intensities so as to obtain an accurate response curve for identifying threshold changes rather than simply testing the significance of the differences in vegetation between a few grazing intensities replicated in a designed experiment. In

future studies, however, independent measures of grazing intensity at the same data resolution used in this study, using parameters such as dung frequency (Riginos & Hoffman 2003; Tadey 2006) and actual stocking densities along the grazing gradient predicted by means of spatial modelling (Pringle & Landsberg 2004) should be used to validate our results directly and confirm their applicability to rangeland management. We also recognize another study limitation: the nature of the threshold changes was explicitly determined, but the underlying ecological processes were only inferred from the observed patterns. Mechanistic linkages between patterns and processes related to threshold changes must also be developed. Measurement of variables that relate more directly to the underlying processes of threshold change may help to develop a pattern–process coupling.

IMPLICATIONS OF THRESHOLD CHANGES FOR ECOLOGICAL THEORY AND RANGELAND MANAGEMENT

Thresholds lie at the heart of non-equilibrium concepts (DeAngelis & Waterhouse 1987) in ecological theory. In ecological theory, thresholds were originally believed to represent boundaries between alternative stable states (Holling 1973), but more recent research has interpreted the same patterns as a degradation threshold (Stringham *et al.* 2003). The nonlinear behaviour of vegetation in response to grazing that we found can be indicative of alternative stable states (Scheffer & Carpenter 2003). However, a full demonstration of the existence of alternative stable states would require long-term data from recovery experiments established along grazing gradients. Further work is required to test which aspects of the theory are most important and what system characteristics indicate the presence or absence of alternative stable states.

From a rangeland management perspective, providing preventive indicators may be important because they permit the identification of critical threshold changes before damage becomes severe and may thus help management efforts in the study area. In this context, most species that are abundant in the proximity of gradient sources are good indicators for the assessment of degradation, but plant species in communities with a relatively high resistance to grazing may represent much better indicators for use in preventing the occurrence of threshold changes; when these species begin to disappear from a community, this is a sign that the grazing intensity may soon cross the threshold level. These communities would also provide a potential refuge for grazing-sensitive species (Landsberg *et al.* 2003; Todd 2006), so retaining these communities in the landscape may be a possible option for rangeland management.

Ecologists tend to focus on the consequences of catastrophic shifts that exhibit irreversible changes to structural attributes and that are recognized too late to prevent degradation rather than attempting to identify the abrupt changes in ecological response that would indicate the initial stages of such shifts and using this information to mitigate degradation (Bestelmeyer 2006). Our findings demonstrate the management significance of using preventive thresholds as an early warning

of possible catastrophic shifts. In future studies, the preventive threshold should be quantified using more direct indicators such as dung frequency or predicted stocking densities. Our study design therefore lends itself to identifying potential solutions capable of establishing a rigorous ecological benchmark related to the preventive thresholds. The recognition that real threshold changes exist along real grazing gradients is a major step forward in providing tools for the sustainable management of rangeland ecosystems.

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References

- Andrew, M.H. (1988) Grazing impact in relation to livestock watering points. *Trends in Ecology and Evolution*, **3**, 336–339.
- Bestelmeyer, B.T. (2006) Threshold concepts and their use in rangeland management and restoration: the good, the bad, and the insidious. *Restoration Ecology*, **14**, 325–329.
- 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., Herrick, J.E., Brown, J.R., Trujillo, D.A. & Havstad, K.M. (2004) Land management in the American Southwest: a state-and-transition approach to ecosystem complexity. *Environmental Management*, **34**, 38–51.
- 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.
- Briske, D.D., Fuhlendorf, S.D. & Smeins, F.E. (2006) A unified framework for assessment and application of ecological thresholds. *Rangeland Ecology and Management*, **59**, 225–236.
- Cleveland, W.S. (1979) Robust locally weighted regression and smoothing scatterplots. *Journal of the American Statistical Association*, **74**, 829–836.
- DeAngelis, D.L. & Waterhouse, J.C. (1987) Equilibrium and nonequilibrium concepts in ecological models. *Ecological Monographs*, **57**, 1–21.
- Del-val, E.K. & Crawley, M.J. (2005) Are grazing increaser species better tolerators than decreasers? An experimental assessment of defoliation tolerance in eight British grassland species. *Journal of Ecology*, **93**, 1005–1016.
- Diaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D.G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W., Clark, H. & Campbell, B.D. (2007) Plant trait responses to grazing – a global synthesis. *Global Change Biology*, **13**, 313–341.
- Efron, B. & Tibshirani, R. (1993) *An Introduction to the Bootstrap*. Chapman & Hall, New York, USA.
- Ejrnæs, R. (2000) Can we trust gradients extracted by Detrended Correspondence Analysis? *Journal of Vegetation Science*, **11**, 565–572.
- Fahrig, L. (2002) Effect of habitat fragmentation on the extinction threshold: a synthesis. *Ecological Applications*, **12**, 346–353.
- Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics*, **34**, 487–515.
- Fernandez-Gimenez, M.E. & Allen-Diaz, B. (1999) Testing a non-equilibrium model of rangeland vegetation dynamics in Mongolia. *Journal of Applied Ecology*, **36**, 871–885.
- Fernandez-Gimenez, M.E. & Allen-Diaz, B. (2001) Vegetation change along gradients from water sources in three grazed Mongolian ecosystems. *Plant Ecology*, **157**, 101–118.

- Friedel, M.H. (1991) Range condition assessment and the concept of thresholds: a viewpoint. *Journal of Range Management*, **44**, 422–426.
- Friedel, M.H. (1997) Discontinuous change in arid woodland and grassland vegetation along gradients of cattle grazing in central Australia. *Journal of Arid Environments*, **37**, 145–164.
- Gitay, H. & Noble, I.R. (1997) What are functional types and how should we seek them? *Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change* (eds T.M. Smith, H.H. Shugart & F.I. Woodward), pp. 3–19. Cambridge University Press, Cambridge, UK.
- Graetz, R.D. & Ludwig, J.A. (1978) A method for the analysis of piosphere data applicable to range assessment. *Australian Rangeland Journal*, **1**, 126–136.
- Groffman, P., Baron, J., Blett, T., Gold, A., Goodman, I., Gunderson, L., Levinson, B., Palmer, M., Paerl, H., Peterson, G., Poff, N., Rejeski, D., Reynolds, J., Turner, M., Weathers, K. & Wiens, J. (2006) Ecological thresholds: the key to successful environmental management or an important concept with no practical application? *Ecosystems*, **9**, 1–13.
- Grubov, V.I. (1982) *Key to the Vascular Plants of Mongolia*. Science Publishers, Enfield, New Hampshire, USA.
- Holling, C.S. (1973) Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, **4**, 1–23.
- Huggett, A.J. (2005) The concept and utility of 'ecological thresholds' in biodiversity conservation. *Biological Conservation*, **124**, 301–310.
- Jigjidsuren, S. & Johnson, D.A. (2003) *Forage Plants of Mongolia*. Admon Publishing Co, Ulaanbaatar, Mongolia.
- Johnson, J.B. & Omland, K.S. (2004) Model selection in ecology and evolution. *Trends in Ecology and Evolution*, **19**, 101–108.
- Kenkel, N.C. & Orloci, L. (1986) Applying metric and nonmetric multidimensional scaling to ecological studies, some new results. *Ecology*, **67**, 919–928.
- van de Koppel, J., Rietkerk, M. & Weissing, F.J. (1997) Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. *Trends in Ecology and Evolution*, **12**, 352–356.
- Landsberg, J., James, C.D., Morton, S.R., Muller, W.J. & Stol, J. (2003) Abundance and composition of plant species along grazing gradients in Australian rangelands. *Journal of Applied Ecology*, **40**, 1008–1024.
- Lange, R.T. (1969) The piosphere: sheep track and dung patterns. *Journal of Range Management*, **22**, 396–400.
- Legendre, P. & Legendre, L. (1998) *Numerical Ecology*. 2nd English edn. Elsevier Science, Amsterdam.
- Lindenmayer, D.B. & Luck, G. (2005) Synthesis: thresholds in conservation and management. *Biological Conservation*, **124**, 351–354.
- McIntyre, S. & Lavorel, S. (2001) Livestock grazing in subtropical pastures: steps in the analysis of attribute response and plant functional types. *Journal of Ecology*, **89**, 209–226.
- 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. *American Naturalist*, **132**, 87–106.
- Pakeman, R.J. (2004) Consistency of plant species and trait responses to grazing along a productivity gradient: a multi-site analysis. *Journal of Ecology*, **92**, 893–905.
- Peterson, G., Allen, C.R. & Holling, C.S. (1998) Ecological resilience, biodiversity, and scale. *Ecosystems*, **1**, 6–18.
- Pickup, G., Bastin, G.N. & Chewings, V.H. (1994) Remote-sensing-based condition assessment for nonequilibrium rangelands under large-scale commercial grazing. *Ecological Applications*, **4**, 497–517.
- Pickup, G., Bastin, G.N. & Chewings, V.H. (1998) Identifying trends in land degradation in non-equilibrium rangelands. *Journal of Applied Ecology*, **35**, 365–377.
- Pringle, H. & Landsberg, J. (2004) Predicting the distribution of livestock grazing pressure in rangelands. *Austral Ecology*, **29**, 31–39.
- R Development Core Team (2006) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Radford, J.Q. & Bennett, A.F. (2004) Thresholds in landscape parameters: occurrence of the white-browed treecreeper *Climacteris affinis* in Victoria, Australia. *Biological Conservation*, **117**, 375–391.
- Radford, J.Q., Bennett, A.F. & Cheers, G.J. (2005) Landscape-level thresholds of habitat cover for woodland-dependent birds. *Biological Conservation*, **124**, 317–337.
- Riginos, C. & Hoffman, M.T. (2003) Changes in population biology of two succulent shrubs along a grazing gradient. *Journal of Applied Ecology*, **40**, 615–625.
- Sasaki, T., Okayasu, T., Shirato, Y., Jamsran, U., Okubo, S. & Takeuchi, K. (2007) Can edaphic factors demonstrate landscape-scale differences in vegetation responses to grazing? *Plant Ecology*. DOI: 10.1007/s11258-007-9274-0.
- Sasaki, T., Okayasu, T., Takeuchi, K., Jamsran, U. & Jadambaa, S. (2005) Patterns of floristic composition under different grazing intensities in Bulgan, South Gobi, Mongolia. *Grassland Science*, **51**, 235–242.
- Scheffer, M. & Carpenter, S. (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology and Evolution*, **18**, 648–656.
- Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. & Walker, B. (2001) Catastrophic shifts in ecosystems. *Nature*, **413**, 591–596.
- Shachak, M., Sachs, M. & Moshe, I. (1998) Ecosystem management of desertified shrublands in Israel. *Ecosystems*, **1**, 475–483.
- Shumway, S.W. (2000) Facilitative effects of a sand dune shrub on species growing beneath the shrub canopy. *Oecologia*, **124**, 138–148.
- Stringham, T.K., Krueger, W.C. & Shaver, P.L. (2003) State and transition modeling: an ecological process approach. *Journal of Range Management*, **56**, 106–113.
- Tadey, M. (2006) Grazing without grasses: Effects of introduced livestock on plant community composition in an arid environment in northern Patagonia. *Applied Vegetation Science*, **9**, 109–116.
- Todd, S.W. (2006) Gradients in vegetation cover, structure and species richness of Nama-Karoo shrublands in relation to distance from watering points. *Journal of Applied Ecology*, **43**, 293–304.
- Toms, J.D. & Lesperance, M.L. (2003) Piecewise regression: a tool for identifying ecological thresholds. *Ecology*, **84**, 2034–2041.
- Turner, M.D. (1998) Long-term effects of daily grazing orbits on nutrient availability in Sahelian West Africa. I. Gradients in the chemical composition of rangeland soils and vegetation. *Journal of Biogeography*, **5**, 669–682.
- USDA Natural Resources Conservation Service (1997) *National Range and Pasture Handbook*. US Department of Agriculture, Washington, DC.
- With, K.A. & King, A.W. (1999) Extinction thresholds for species in fractal landscapes. *Conservation Biology*, **13**, 314–326.
- Wright, J.P., Jones, C.G., Boeken, B. & Shachak, M. (2006) Predictability of ecosystem engineering effects on species richness across environmental variability and spatial scales. *Journal of Ecology*, **94**, 815–824.

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