

Indicator species and functional groups as predictors of proximity to ecological thresholds in Mongolian rangelands

Takehiro Sasaki · Satoru Okubo ·
Tomoo Okayasu · Undarmaa Jamsran ·
Toshiya Ohkuro · Kazuhiko Takeuchi

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Abstract We focused on responses to grazing by individual species and functional groups in relation to ecological thresholds in Mongolian rangelands, with repeated measures from the same ecological sites to account for rainfall variability. At all sites, even under rainfall fluctuations, there were robust combinations of indicator species that could be used to forewarn managers to take action to minimize the probability of crossing ecological thresholds. Depending on the landscape condition of each site, the cover of functional groups, which shared traits of perennial life history, grass or forb growth form, linear leaf shape, and alternate leaf attachment, or the cover of functional groups of woody shrubs dramatically decreased before an ecological threshold was crossed.

Thus, across all sites, the responses of certain functional groups to grazing appeared to predict the crossing of an ecological threshold. The ecological indicators derived in this study should help to improve land managers' ability to prevent adverse changes in states before ecological thresholds are reached.

Keywords Arid and semi-arid rangelands · Ecological threshold · Mongolia · Non-equilibrium dynamics · Plant traits · Sustainable management

Introduction

The development and application of operational procedures for sustainable management of rangeland ecosystems need to be linked closely with a broader body of ecological theories (Bestelmeyer et al. 2003; Briske et al. 2003, 2005, 2006). Two major concepts describe the processes involved in applied ecological research in rangeland ecosystems: equilibrium and non-equilibrium concepts. The former idea posits that communities will respond in a sequential and predictable manner to the environment and to disturbance regimes (Dyksterhuis 1949). The latter idea minimizes ecosystem regulation and stability, and places greater emphasis on eventual drivers such as climatic variability and other episodic events, implying that ecosystems are less predictable than indicated by the equilibrium concept (De Angelis and Waterhouse 1987; Ellis and Swift 1988; Westoby

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T. Sasaki (✉)
Graduate School of Life Sciences, Tohoku University, 6-3
Aoba, Aramaki, Aoba-ku, Sendai 980-8578, Japan
e-mail: sasa@m.tohoku.ac.jp; sasa67123@gmail.com

S. Okubo · T. Okayasu · T. Ohkuro · K. Takeuchi
Graduate School of Agricultural and Life Sciences,
The University of Tokyo, 1-1-1 Yayoi, Bunkyo-ku,
Tokyo 113-8657, Japan

U. Jamsran
Center for Ecosystem Study, Mongolian State University
of Agriculture, Ulaanbaatar 210153, Mongolia

et al. 1989). Briske et al. (2003) proposed that both equilibrium and non-equilibrium concepts must be incorporated into rangeland management perspectives if rangeland ecology is to continue to underpin rangeland management. However, the current state of the art in rangeland management appears to be progressing at the extremes of the equilibrium–non-equilibrium continuum (Briske et al. 2003).

The most traditional approach to rangeland management has been to assess the position of rangelands along a condition spectrum by characterizing the relative abundances of “increaser” and “decreaser” species (*sensu* Dyksterhuis 1949). Recently, major progress has been made in identifying simple plant traits to predict the responses of these increaser or decreaser species and in generalizing them across landscapes or regions (Bullock et al. 2001; Diaz et al. 2001; Pakeman 2004; Vesk et al. 2004; De Bello et al. 2005). Although a synthesis between equilibrium and non-equilibrium concepts has been the subject of recent reviews (Briske et al. 2003; Vetter 2005; Gillson and Hoffman 2007), these applied approaches with highly management relevance are generally still based around the equilibrium concept (Dyksterhuis 1949), with assumptions of high stability, continuous change, and a single equilibrium point in rangeland ecosystems.

However, species and trait attributes do not always respond to grazing in a linear way. Theory and empirical evidence suggest that nonlinearity of vegetation responses to grazing can exist in some rangeland ecosystems (Friedel 1991; van de Koppel et al. 1997; Scheffer and Carpenter 2003). This is the case for Mongolian rangeland ecosystems; Sasaki et al. (2008a) suggested that ecological thresholds exist in vegetation changes along a grazing gradient, and that vegetation responses to grazing are nonlinear across the systems. This nonlinear behavior can be indicative of alternative stable states, and adverse changes in state beyond the ecological threshold might essentially be irreversible (Scheffer and Carpenter 2003). One potential explanation for the nonlinear responses of vegetation to grazing is that vegetation in arid regions with a long evolutionary history of grazing is relatively resistant to grazing (Milchunas et al. 1988; Cingolani et al. 2005). The rates of change in community composition are constant below threshold levels of grazing, even at moderate or light grazing intensities, and abrupt

changes can subsequently occur when grazing intensity surpasses a certain threshold (Sasaki et al. 2008a). In such systems, management applications of species’ and traits’ responses to grazing by assuming a single linear condition spectrum in vegetation dynamics could limit the land manager’s ability to prevent adverse changes in state before the ecological threshold has been reached (Briske et al. 2006). On the other hand, recognition of nonlinear vegetation dynamics (Briske et al. 2005) provides a strong incentive for an alternative or substantially modified evaluation procedure that would accommodate a broader spectrum of vegetation dynamics than the classical equilibrium model (Bestelmeyer et al. 2003; Stringham et al. 2003; Briske et al. 2005). This is because continuous and reversible vegetation dynamics prevail within quasi-stable vegetation states, whereas discontinuous and irreversible dynamics can occur when ecological thresholds are surpassed and one quasi-stable state replaces another.

Another important aspect of applied ecological research in rangeland ecosystems is that we need robust and repeatable predictions of species’ and traits’ responses to grazing under external perturbations such as rainfall variability (Westoby et al. 1989; Briske et al. 2003, 2005; Stringham et al. 2003). In this context, some rangeland ecosystems are reported to be driven by such external perturbations, i.e., non-equilibrium dynamics (Fernandez-Gimenez and Allen-Diaz 1999; Jackson and Bartolome 2002; Walker and Wilson 2002) and the others are not (Fernandez-Gimenez and Allen-Diaz 1999; Diaz et al. 2001; Walker and Wilson 2002). However, much of the prevailing rhetoric in rangeland ecology today emphasizes the stochastically driven nature of most rangelands and the inappropriateness of the equilibrium concept as a basis for management (Briske et al. 2003). The perception that vegetation dynamics are driven entirely by rainfall variability (i.e., grazing has a negligible impact) reduces the opportunity for observation and experience to be incorporated into management models and decreases incentives for adaptive management (Fernandez-Gimenez and Allen-Diaz 1999; Illius and O’Connor 1999; Briske et al. 2003). Hence, the debate has forced a more comprehensive interpretation of vegetation dynamics along the entirety of the equilibrium–non-equilibrium continuum (Fernandez-Gimenez and Allen-Diaz 1999; Illius and O’Connor 1999; Walker and Wilson 2002; Buttolph and Coppock

2004). In real ecosystems, a continuum of systems probably exists, rather than a stark dichotomy between equilibrium and non-equilibrium rangelands (Fernandez-Gimenez and Allen-Diaz 1999; Illius and O'Connor 1999; Walker and Wilson 2002).

In order to overcome these issues, we examined species' and traits' responses along a grazing gradient from livestock camps or sources of water, representing a spatial gradient in the accumulated impact of long-term exposure to livestock (Andrew 1988) across Mongolian rangeland ecosystems. We used a data-driven approach, making no a priori assumptions of the linearity of responses and using repeated measures from the same ecological sites to account for rainfall variability. Across the observation years, we contrasted these responses in relation to ecological thresholds, defined as the points or zones at which disturbance should be limited to prevent drastic changes in ecological conditions (for detailed definitions, see Bestelmeyer 2006 and Sasaki et al. 2008a), to extract important signs that would forewarn of the occurrence of threshold changes in vegetation state. We could therefore explicitly detect ecological indicators that would forewarn land managers that actions must be taken to stabilize resilience and minimize the probability of crossing an ecological threshold (Briske et al. 2008). Our expectations were that, even under climatic perturbations, the real accumulated damage caused by livestock grazing on rangeland ecosystems remains unchanged and can be recognized (i.e., the repeatability of an ecological threshold exists), and that predictable aspects of vegetation dynamics that are easily applicable to sustainable management might exist. We did not intend to definitively test the non-equilibrium concept; in fact, we based this study on an understanding that ecosystems need not be classified exclusively as either equilibrium or non-equilibrium from a management perspective (Fernandez-Gimenez and Allen-Diaz 1999; Walker and Wilson 2002; Briske et al. 2003).

Specifically, we briefly described the temporal dynamics of floristic composition along a grazing gradient and examined the repeatability of ecological threshold across observation years. On the basis of the positions of the ecological threshold across the observation years, we defined a reliable ecological threshold (hereafter, RET). We then quantified species' responses to grazing to identify indicator species that could be used to forewarn of proximity to the

ecological threshold. Finally, to generalize ecological knowledge and management applications across Mongolian rangeland ecosystems, we examined the capacity of trait combinations to forewarn of proximity to ecological thresholds over a range of ecological sites (sensu USDA Natural Resources Conservation Service 1997) covering climatically and edaphically diverse environments.

Materials and methods

Study areas and ecological sites

The study was conducted from 2006 to 2008 across three study areas situated near Kherlen Bayan Ulaan, Mandalgobi, and Bulgan in Mongolia's Khenti, Dundgobi, and South Gobi provinces, respectively (see supplementary material Table S1). The region's climate is arid and cold, with a short summer. Vegetation within these areas is characterized as low biomass (approximate aboveground biomass at its peak time ranges from 20 to 130 g/m² across the areas; T. Sasaki, unpublished data). Taxonomic nomenclature follows that of Grubov (1982). In Bulgan, the grasses, *Stipa gobica* and *S. glareosa*, and the sedges, *Carex stenophylloides* and *C. duriuscula*, were lumped in the analyses because they were difficult to distinguish in the field after seed set. Most livestock grazed across landscapes within these areas are sheep and goats. Meteorological data provided by the National Climatic Data Center indicate that annual rainfall averaged about 200 mm at Kherlen Bayan Ulaan, 130 mm at Mandalgobi, and 110 mm at Bulgan between 2000 and 2008. Thus, there is a rainfall gradient from the north (Kherlen Bayan Ulaan) to the south (Bulgan). These differences in the climatic condition correspond to vegetation types in each area; Kherlen Bayan Ulaan and Mandalgobi are located in steppe ecological zones, and Bulgan is found in a desert-steppe ecological zone. Across the observation years, all areas received strong fluctuations in rainfall in the late spring/early summer (from April to May) and growing season (from June to August) (Table 1), which are considered a more important determinant of peak biomass than total annual rainfall. The existence of high interannual variability in rainfall drew our attention to the need to establish robust and repeatable predictions and

management applications of species' and traits' responses to grazing to account for uncertainty in the systems (Sasaki et al. 2009a).

Ten ecological sites were located across the three study areas at different landscape positions (see supplementary material Table S1). Ecological sites in each study area were located on a land catena (Sasaki et al. 2008b): hill (KH), pediment (KP), and depression (KD) at Kherlen Bayan Ulaan; hill (MH), tableland (MT), pediment (MP), and depression (MD) at Mandalgobi; and upper pediment (BUP), lower pediment (BLP), and depression (BD) at Bulgan. In selecting these sites, we tried to ensure that we had covered a range of the climatic, geomorphic, edaphic, and vegetation variations found within Mongolian rangeland ecosystems. Sasaki et al. (2009b) quantified relatively the landscape condition at each ecological site by using an ordination technique (for detailed results, see Sasaki et al. 2009b) that took into consideration vegetation physiognomy and soil texture, and they found two types of landscape condition, relatively benign and harsh environmental conditions (see supplementary material Table S1). The landscape conditions at each site were responsible for the dominant vegetation physiognomy there (Sasaki et al. 2008b; see supplementary material Table S1). The ecological sites were not selected to be statistical replicates within each landscape; rather, each site was intended to provide robust and repeatable predictions and management applications of species' and traits' responses to grazing.

Sampling

We used the distance (m) from each permanent transect to a livestock camp or source of water (hereafter, the “gradient source”) to represent relative

grazing intensity. We defined a “reference distance” (see supplementary material Table S1), which represented the point at which livestock impacts were minimal (only small amounts of dung could be found), and this distance was chosen at a position located outside the normal grazing range of the livestock from a camp or source of water according to the interview to local herders. Because of logistical considerations associated with the differences in the numbers of livestock at each site, not all the reference distances could be sampled to the same distance. Although it was not possible to quantify grazing intensities precisely, our previous work suggested that the relative grazing intensity along the grazing gradient differed with the number of livestock at each site (Sasaki et al. 2008a).

Between June and August 2006, we systematically sampled the vegetation by identifying and estimating the cover of all species present within each quadrat along a transect (five 1 × 1 m subsample quadrats on each transect) placed at set distances along the grazing gradients (five gradient replicates in different directions) at each site. Between June and August 2007 and 2008, we repeated vegetation sampling, but we set a lower sampling resolution in 2007 and 2008 than in 2006 to optimize the sampling effort. In 2006, we sampled transects placed at intervals of 10 m from 10 to 50 m, then at 75, 100, 150, 200, 300, 400, 500, 750, and 1000 m, from the gradient source; exceptions were the KH and KD sites (up to 500 m from the source) and the MH and BUP sites (additionally, at 1500 and 2000 m from the source). In 2007 and 2008, we sampled the same transects placed in 2006 (i.e., permanent transects) at 10, 50, 100, 200, 500, and 1000 m from the source; exceptions were the KH and KD sites (up to 500 m from the source) and the MH and BUP sites (additionally,

Table 1 Rainfall (mm) in the late spring/early summer (from April to May; AM) and growing season (from June to August; JJA) between 2006 and 2008

| Study area | 2006 AM rainfall | 2006 JJA rainfall | 2007 AM rainfall | 2007 JJA rainfall | 2008 AM rainfall | 2008 JJA rainfall | Long-term CV |
|---------------------|------------------|-------------------|------------------|-------------------|------------------|-------------------|--------------|
| Kherlen Bayan Ulaan | 29.5 | 120.1 | 22.1 | 102.1 | 3.56 | 238.3 | 21 |
| Mandalgobi | 4.3 | 83.3 | 3.6 | 52.1 | 7.1 | 79.0 | 28 |
| Bulgan | 7.9 | 51.8 | 7.4 | 120.7 | 11.4 | 82.8 | 26 |

Data were provided by the National Climatic Data Center. Long-term CV (%) of annual rainfall between 1993 and 2003 (provided by the Institute of Meteorology and Hydrology, Ministry of Nature and Environment in Mongolia) is also shown

at 1500 and 2000 m from the source). We used a GPS unit to fix the geographical positions of all permanent transect startpoint and endpoint nails. Each permanent 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. Basically, we used data sets from a total of 4,650 permanent quadrats along 310 permanent transects sampled at five to eight sampling distances around 10 gradient sources surveyed from 2006 to 2008.

Since potential correlations between the grazing gradient and other environmental factors (especially micro-topography) often pose confounding effects of sampling across different vegetation types and soil textures (Landsberg et al. 2003; Sasaki et al. 2005; Todd 2006; Sasaki et al. 2008b), we selected the sites where these confounding effects appeared to be minor. This allowed us to control the variation in soil moisture along a grazing gradient (Sasaki et al. 2005), but soil organic carbon and total nitrogen increased toward the gradient source (Sasaki et al. 2008b) probably due to the redistribution of nutrients near the gradient source through urine and dung of livestock. In order to solve this problem, some studies arbitrarily excluded samples at shorter distances from data analyses to minimize such confounding factors other than direct consumption of biomass by livestock (i.e., nutrient redistribution, trampling) (Stump et al. 2005; Strauss and Schickhoff 2007; Zemmrich 2007). However, the grazing impacts in situ on vegetation can include all of these factors. Although we may not be able to distinguish these factors clearly, we decided to capture the variation in plant community composition along a full range of grazing gradients for comprehensive understanding of the grazing impacts on vegetation dynamics in Mongolian rangelands, in accordance with most grazing gradient studies (e.g., Nash et al. 1999; Fernandez-Gimenez and Allen-Diaz 1999, 2001; Adler et al. 2005; Todd 2006; Fensham et al. 2010).

Data analysis

In the following analyses, we basically focused on the data for each site (the data from subsamples on each transect were pooled) within each year (within-year data) and the combined data for each site across observation years (across-year data), except for the identification of ecological thresholds.

In order to assess the general patterns of temporal change in floristic composition for each permanent transect at each site among observation years, we performed a detrended correspondence analysis (DCA; Legendre and Legendre 1998), using the cover value for each species in the across-year data (because the patterns of temporal change in floristic composition were generally consistent when we used the presence–absence data, we have only reported the results using the abundance data).

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. For the confirmation of the existence of nonlinearity, however, we need to be careful about inherently nonlinear livestock density patterns along a grazing gradient. Previous studies generally suggested that livestock densities along a grazing gradient are distributed exponentially (e.g., Riginos and Hoffman 2003; Pringle and Landsberg 2004; Fensham et al. 2010). Even if we used the ln-transformed distance in the lowess fitting, the nature of nonlinearity in our data essentially remained. Our lowess fitting suggested threshold changes with a single breakpoint in all ecological sites in the within-year and across-year data except BUP, where the response pattern appeared to follow a sigmoid logistic curve. We then aimed to identify the definitive distance corresponding to the ecological threshold at each site for the within-year and across-year data to set a “RET” based on each calculated breakpoint. However, an insufficiency of data around the designated discontinuity sometimes prevented the breakpoint estimates in the model from converging on a stable value (see Table 2). We therefore also made breakpoint estimates for the pooled floristic composition data at each site across observation years to complement any insufficient data around the discontinuity in the across-year data. We fitted a piecewise regression model (sensu Toms and Lesperance 2003) to a series of floristic composition data for each permanent transect (i.e., those scores on DCA axis 1 that showed any relationship with distance from the gradient source; see Results section):

$$\text{Score of DCA axis 1} = a + b \times \text{Distance},$$

if Distance $\leq D$,

Table 2 Ecological thresholds (estimated breakpoints) at the 10 ecological sites for the within-year data (2006, 2007, 2008 only) and across-year data (2006–2008 combined)

| Site | Estimated breakpoint (m) | | | | | RET (m) ^d |
|------------------|--------------------------|-----------|-----------------|--------------------|---|----------------------|
| | 2006 only | 2007 only | 2008 only | 2006–2008 combined | 2006–2008 combined (but pooled ^c) | |
| KH | 115.6 | 187.7 | NA ^b | 195.1 | 194.9 | 200 |
| KP | 80.4 | 90.92 | 83.5 | 84.83 | 83.65 | 100 |
| KD | 54.72 | 58.87 | NA | 60.11 | 63.68 | 100 |
| MH | 444.1 | 372.6 | 403.6 | 294.4 | 417.6 | 500 |
| MT | 170.1 | 151.1 | 115.3 | 139.2 | 157.7 | 200 |
| MP | 54.74 | NA | 51.1 | 54.22 | 54.48 | 100 |
| MD | 28.15 | NA | 54.79 | 54.49 | 43.27 | 100 |
| BUP ^a | 484.1, 906.0 | NA | NA | NA | 408.5, 924.2 | 1000 |
| BLP | 217 | 224.7 | 78.41 | 447.8 | 298.2 | 500 |
| BD | 44.87 | 55.47 | NA | NA | 42.16 | 100 |

^a At BUP, there were two breakpoints in compositional changes along the grazing gradient

^b The breakpoint estimates in the model did not converge on a stable value because of an insufficiency of data around the designated discontinuity

^c Any insufficient data around the discontinuity in the across-year data were complemented by pooling the high-sampling resolution data from 2006

^d “Reliable ecological threshold (RET)” was set at the nearest sampling distance located outside all the breakpoints calculated at each site

$$\text{Score of DCA axis 1} = a + b \times \text{Distance} + c \times (\text{Distance} - D), \quad \text{if Distance} > D, \quad (1)$$

where D is the distance at the designated discontinuity (for BUP, we set two designated discontinuities; Sasaki et al. 2008a); a , b , and c are regression parameters. From the results, we defined a “RET.” This was set as the nearest sampling distance located outside all the calculated breakpoints at each site.

In order to determine the species’ and functional groups’ (see below) responses along a grazing gradient at each site within each year, with no a priori assumption for a given response’s exact form and shape, we used a cubic smooth spline within the framework of generalized additive models (GAM; Hastie and Tibshirani 1990):

$$C = s(\text{Distance}), \quad (2)$$

where C is the cover of each species or functional group for each permanent transect in the within-year data and $s(x)$ is a function of the predictor variable (here, distance from the gradient source), which is defined locally by a cubic smooth spline function. The degree of smoothing for the predictor was determined by general cross-validation (Wood 2006). We then

contrasted the only significant and similar species’ response patterns across observation years with RETs to extract important and robust signs for predicting the occurrence of ecological thresholds.

We used a regression tree approach to detect potential predictive traits for the responses of species to grazing, as suggested by De Bello et al. (2005). Predictions were calculated separately for each site across observation years. Traits were used as independent variables and the species score on DCA axis 1, which is considered to predominantly represent the species’ responses to grazing (see Results section), as the dependent variable. We used the traits in the work of Sasaki et al. (2009c)—such as growth form, life history, shoot height, and leaf characteristics—for a total of 57 categories of 17 plant traits (for full descriptions, see supplementary material Table S2).

All combinations of potential predictive traits detected by a regression tree were categorized as functional response groups (sensu Lavorel and Garnier 2002). As in the processes used to determine species’ responses along a grazing gradient, we determined these functional groups’ responses along a grazing gradient at each site within each year. We also contrasted the responses of the significant and

similar functional groups across observation years with RETs to extract important and robust signs for predicting the occurrence of ecological thresholds. All statistical analyses were performed with the R software (version 2.7.0, R Development Core Team 2008).

Results

Community dynamics

The DCA ordination for the floristic composition of permanent transects at all sites indicated that changes in floristic composition along grazing gradients were generally represented predominantly by DCA axis 1 (Fig. 1; Pearson's correlation coefficients between the scores of permanent transects on DCA axis 1 and the distance from the gradient source were significant at all sites). Although the floristic composition of the permanent transects varied to a greater or lesser extent in an ordination space among observation years at all sites, the order of permanent transects (from permanent transects in proximity to the gradient source to those at the reference distance) along a grazing gradient represented by DCA axis 1 generally remained unchanged. Although the first ordination axis could be regarded as a grazing gradient, temporal variations in floristic composition across observation years at each distance could also be recognized in the ordination space. In addition, the contrasts in the gradient length indicated that changes in floristic composition were less pronounced at the sites in the desert-steppe region than at those in the steppe region.

Ecological thresholds under fluctuations in annual rainfall

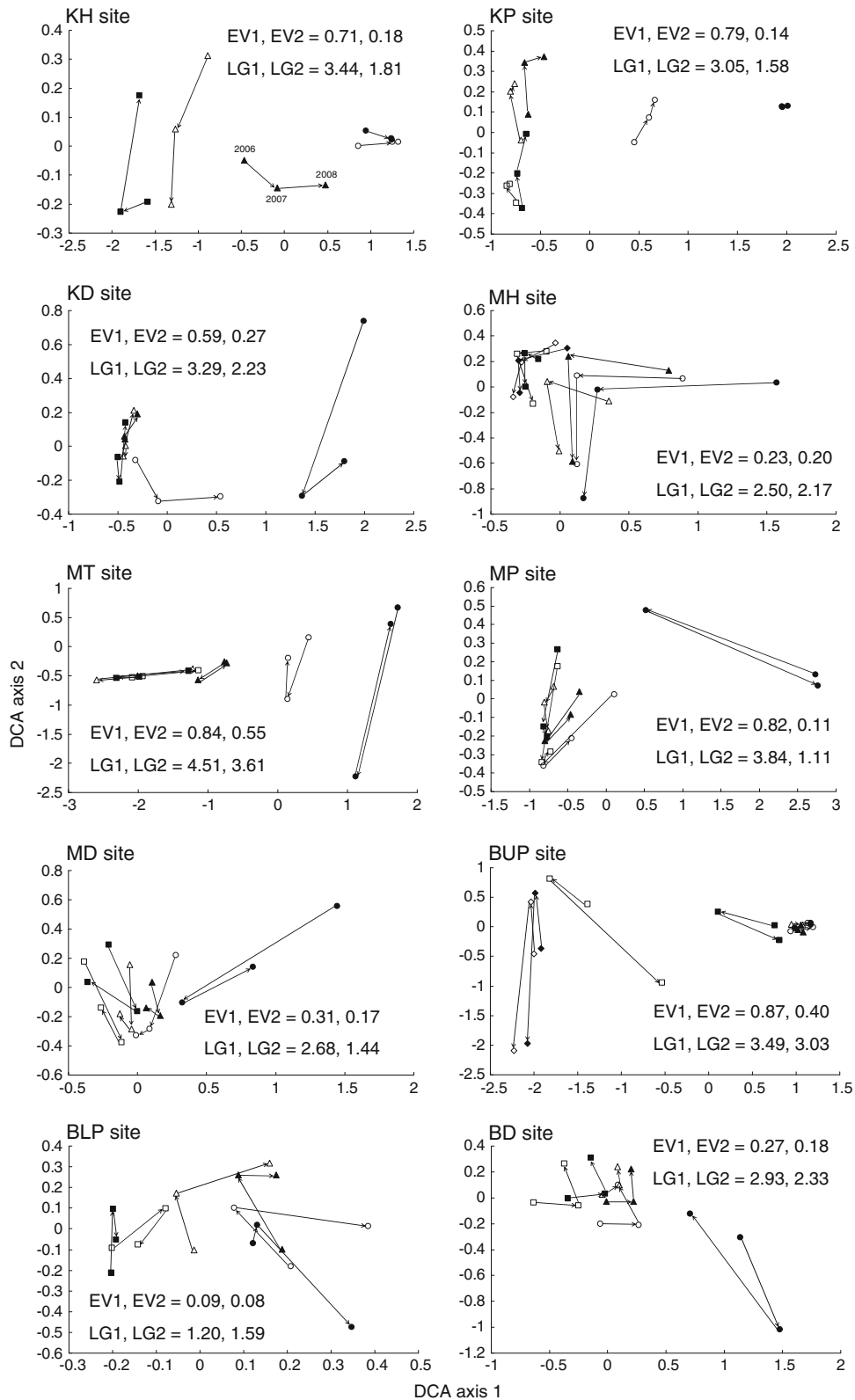
Fitting of the piecewise regression model to a series of floristic composition data clearly revealed the existence of ecological thresholds along the grazing gradients (Table 2). The position of the ecological threshold generally remained constant, except at MH and BLP, where movement of the ecological threshold was relatively large. At BUP, there were two breakpoints in compositional changes along the grazing gradient. These results allowed us to define the "RET" (Table 2) to use in deriving ecological indicators in the following analyses.

Individual species responses in relation to ecological thresholds

Of the 81 species recorded, only a subset of species showed significant (approximate $P < 0.05$ in all years in the GAM) and similar relationships between their cover in each permanent transect and the distance from the gradient source at each site across observation years. In addition, the number of species which showed significant and similar responses to grazing over the observation years tended to decrease toward the sites in the desert-steppe region. We identified four important and robust signs of species behavior as the RET was approached in the direction of the gradient source (Fig. 2a–d; not all results are shown): a drastically decreasing pattern (the responses of *Allium anisopodium* at KH; of *Stipa krylovii* and *Allium bidentatum* at KP; of *S. krylovii* and *A. anisopodium* at KD; of *S. krylovii* and *Caragana microphylla* at MH; of *A. anisopodium*, *Caragana leucophloea*, and *Orostachys spinosa* at MT; of *Allium polyrrhizum* and *Heteropappus hispidus* at MP; of *Salsola passerina* and *Achnatherum splendens* at MD; of *Haplophyllum dauricum* and *Sibbaldianthe sericea* at BUP; of *Caragana korshinskii* at BLP; and of *Nitraria sibirica* at BD); a decreasing pattern (the responses of *S. krylovii* and *Cleistogenes squarrosa* at KH; of *A. splendens* at KD; of *Agropyron cristatum* and *C. squarrosa* at MH; of *Reaumuria soongorica* at MD; of *Stipa gobica* at BUP; and of *Anabasis brevifolia* and *Zygophyllum xanthoxylon* at BD); a drastically increasing pattern (the responses of *Carex duriuscula* at KP; and of *Carex stenophylloides* at BUP); and an increasing pattern (the response of *A. splendens* at MT). This contrast also allowed us to identify good indicators for the assessment of degradation, which was probably a post-threshold state (Fig. 2e); some species appeared and increased after the RET had been passed (the responses of *Chenopodium album* at KH and KP; of *Chenopodium acuminatum* at KP and KD; and of *Peganum nigellastrum* at MT and BUP).

Visualization of trait combinations for predicting vegetation responses to grazing

The first trait selected by regression trees at most sites was life history, except at MH, BUP, and BLP; after the first node, annual species were not further discriminated, whereas several traits were subsequently



◀ **Fig. 1** Detrended correspondence analysis (DCA) ordination of vegetation data at 10 ecological sites (centroids of all permanent transects at each distance are shown): 10 m (*filled circle*), 50 m (*circle*), 100 m (*filled triangle*), 200 m (*triangle*), 500 m (*filled square*), 1000 m (*square*), 1500 m (*filled diamond*), and 2000 m (*diamond*). *Arrows* indicate trends in floristic composition through time (from 2006 to 2008). The first and second axes eigenvalue (EV1, EV2) and length of gradient (LG1, LG2) of each ordination are also shown. Although the floristic composition of permanent transects varied to a greater or lesser extent in an ordination space among observation years at all sites, the arrangement of floristic composition along a grazing gradient represented by DCA axis 1 remained almost unchanged

selected in a hierarchical way within subgroups defined by the perennial life history (Fig. 3). At MH, BUP, and BLP, the first traits selected were moderate palatability, forb growth form, and alternate leaf attachment, respectively. Among all selected plant traits, life history, growth form, leaf shape, and leaf attachment were considered the traits showing the greatest effects on species' responses to grazing in most sites.

Functional group responses in relation to ecological thresholds

There were some significant (approximate $P < 0.05$ in all years in the GAM) and similar responses in functional groups to grazing at each site across all years. We contrasted these responses with RETs to extract important signs predicting the occurrence of ecological thresholds (Fig. 4a–c; not all results are shown). Perennial grasses showed a drastically decreasing pattern at KH, KP, and KD and a decreasing pattern at BUP; perennial forbs with alternate leaf attachment showed a drastically decreasing pattern at KH and MP, and woody shrub species showed a drastically decreasing pattern at MH, MD, and BD. Annual forbs were probably good indicators of a post-threshold state, as they appeared and their cover increased drastically after the RET had been passed, or in close correspondence to the RET at KH, KP, and KD.

Discussion

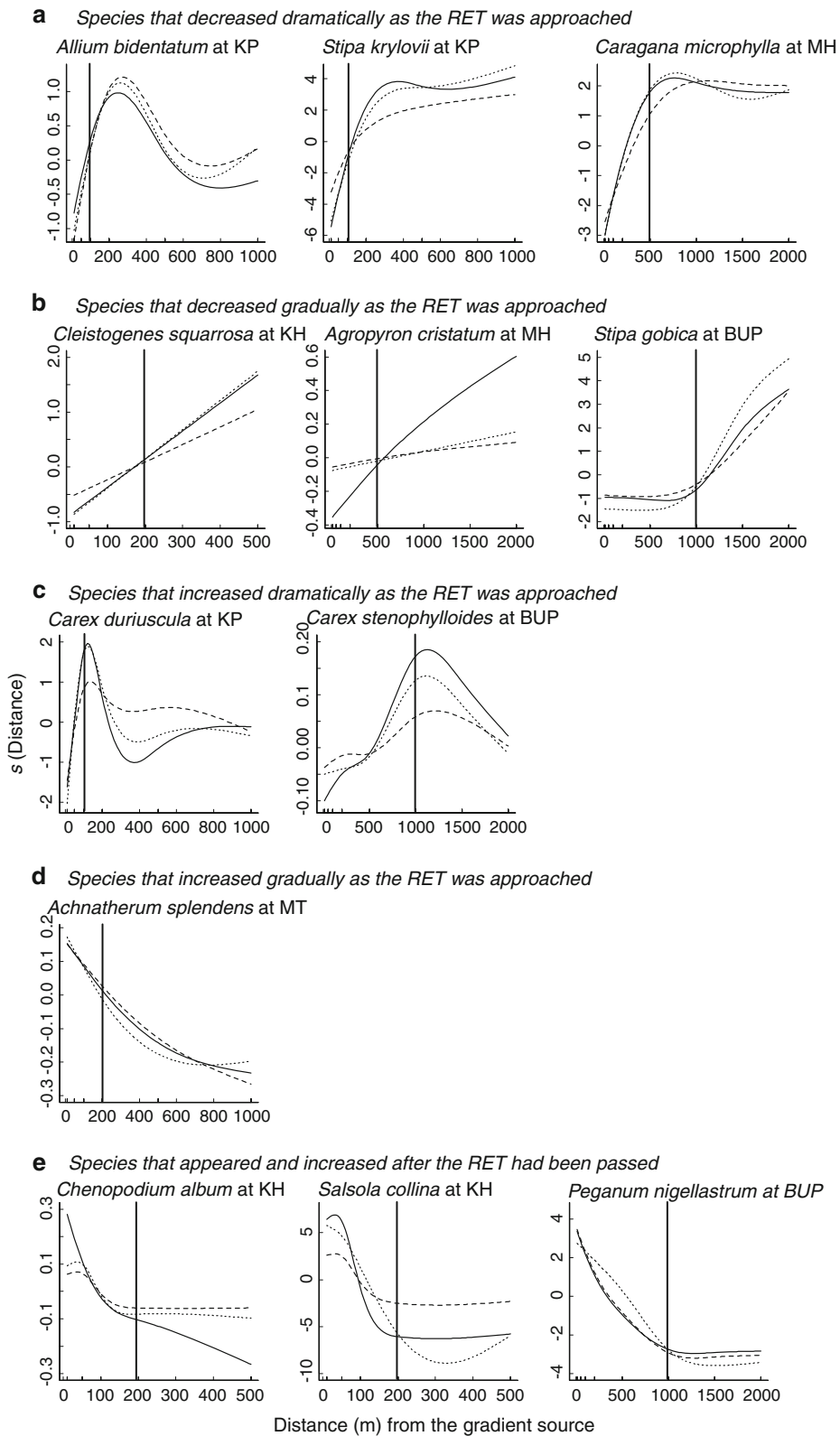
Repeatability of an ecological threshold from a rangeland management perspective

At all sites over the observation years, changes in floristic composition occurred along a grazing

gradient (Fig. 1), and at most sites there was repeatability in the ecological threshold (Table 2). This lends strong credence to the hypothesis that the accumulated damage done by livestock grazing in rangeland ecosystems remains unchanged and can be recognized even under fluctuations in rainfall. The occurrence of rainfall variability therefore does not justify the assumption that grazing has a negligible impact on vegetation dynamics in rangeland ecosystems (Fernandez-Gimenez and Allen-Diaz 1999; Illius and O'Connor 1999; Walker and Wilson 2002). In the following discussion, we focus primarily on management strategies that can use robust and repeatable ecological indicators to forewarn land managers of approaching thresholds, even under fluctuations in rainfall, thereby maximizing incentives for management under the uncertainty of rangeland ecosystems (Watson et al. 1996; Briske et al. 2003).

Indicator species as predictors of proximity to ecological thresholds

Overall, at all sites, even under fluctuating rainfall, there were some combinations of robust and repeatable indicator species that could be used to forewarn managers of the need to take action to minimize the probability of crossing ecological thresholds (Fig. 2a–d; see also Results section). The cover of the most dominant species at each site (see supplementary material Table S1) tended to decrease dramatically as the threshold was approached (e.g., *S. krylovii* at KP and KD, *C. microphylla* at MH, *Allium polyrrhizum* at MP, and *S. passerina* at MD). These species might be not only competitive, but basically tolerant of grazing, because the rates of change in their cover were relatively constant even at moderate or light grazing intensities. These results were generally consistent with previous studies conducted in Mongolia (Hilbig 1995; Fernandez-Gimenez and Allen-Diaz 2001; Gunin et al. 1999; Hoshino et al. 2009). Species with cover patterns that peaked at some intermediate distance from the gradient source and then decreased dramatically as the threshold was approached (e.g., *A. anisopodium* at KH, KD, and MT; and *A. bidentatum* at KP), or with patterns that exhibited a dramatic increase as the threshold was approached (*C. duriuscula* at KP and *C. stenophylloides* at BUP) might have a more ruderal strategy than the most dominant species at each site. The increase of these disturbance-



◀ **Fig. 2** Trends in covers of individual species as a function of distance from the source of the grazing gradient. Of the significant (approximate $P < 0.05$) and similar response patterns of species, representative responses to the grazing gradient across years of observation are shown (not all results are shown; for full results, see text); *solid lines* are responses in 2006, *dashed lines* in 2007, and *dotted lines* in 2008. Values on the y-axis are residuals, the smooth-term coefficients (s) fitted from a GAM, and scaled to have a mean of 0 across all permanent transects within each year, where the distance is the smoothed explanatory variable. We identified four important and robust signs of species behavior as the RET (*solid vertical line*; Table 2) was approached in the direction of the gradient source (a–d). We also identified good indicators for the assessment of degradation, which was probably a post-threshold state; some species appeared and increased after the RET had been passed (e). At BUP, *Stipa gobica* included *S. glareosa*, and *Carex stenophylloides* included *C. duriuscula*, because these species were indistinguishable in the field after seed set

associated species with intense grazing has often been reported in Mongolia (Fernandez-Gimenez and Allen-Diaz 2001; Gunin et al. 1999; van Staaldunin et al. 2007; Hoshino et al. 2009). Previous studies (Bullock et al. 2001; Grime 2001) have suggested that differences in species' responses to disturbance reflect the distribution of ruderal and competitive strategists along a gradient in disturbance regimes. In diversity terms, our previous work (Sasaki et al. 2009b) also suggested that there is an intricate trade-off continuum between disturbance tolerance and competitive ability. However, the indicator species that forewarned of proximity to ecological thresholds did not necessarily overlap among sites, even when the sites had similar vegetation physiognomies. This suggests that the behavior of many species is site-specific: their responses to grazing probably depend on contextual features such as the identity of their neighbors (Vesk and Westoby 2001; Pakeman 2004) and the landscape condition at a given site (Vesk and Westoby 2001).

From a rangeland management perspective, those species that showed a pattern of drastically decreasing cover or drastically increasing cover as the threshold was approached were of primary concern. As species cover is generally sensitive to yearly changes in rainfall, annual management under the uncertainty of systems will be accomplished by the initial identification of sharp decreases or increases in the cover of these species—definitive signs that the grazing intensity will soon cross the threshold level—in comparison with their cover at control sites where the impacts of livestock grazing are considered minimal.

Capacity of trait combinations to predict proximity to ecological thresholds

At most sites, the first traits selected were life history and the responses of annual species were not further discriminated in the regression trees (Fig. 3), probably reflecting the nonlinear fashion of annual species' responses to grazing. At KH, KP, and KD, the appearance of annual species corresponded fairly closely to the occurrence of the ecological threshold (Fig. 4c; see also Results section). At MT, MP, MD, and BD, although annual species did not show significant responses across observation years, because these species could not colonize areas close to the gradient source in relatively dry years (Fernandez-Gimenez and Allen-Diaz 1999), the first trait selected was also life history, suggesting that replacement of perennial species by annual species in association with a grazing impact essentially contributes to the occurrence of the ecological threshold (Sasaki et al. 2008a). Previous studies in Mongolia have also reported the appearance of annual species at disturbed or heavily grazed areas (Hilbig 1995; Fernandez-Gimenez and Allen-Diaz 1999; Gunin et al. 1999; Hoshino et al. 2009). At MH and BLP, annual species could not colonize areas close to the gradient source because of potential wind erosion (Sasaki et al. 2008a, b); this was why the traits selected first were different. At BUP, the cover of a perennial, but toxic and weedy forb, *Peganum nigellastrum*, increased drastically and consistently after the threshold was crossed in all years (Fig. 2e); the forb form was therefore selected first. Diaz et al. (2001) showed that plant height could be the best single predictor of species response to grazing in temperate climates, whereas Vesk et al. (2004) could not find robust proof that height predicted a species' response to grazing in arid climates; instead, they gave differences in vertical vegetation structure as an explanation. In the study areas, plant species also generally had a small stature, which is considered to a resistance trait developed under a long evolutionary history of grazing in an arid climate (Milchunas et al. 1988; Cingolani et al. 2005); consequently, the effect of plant height was less pronounced. The general importance of life history, growth form, leaf shape, and leaf attachment to species' responses to grazing was consistent with the results of previous studies on trait responses to grazing (Diaz et al. 2001; Pakeman 2004; Vesk et al. 2004; De Bello et al. 2005).

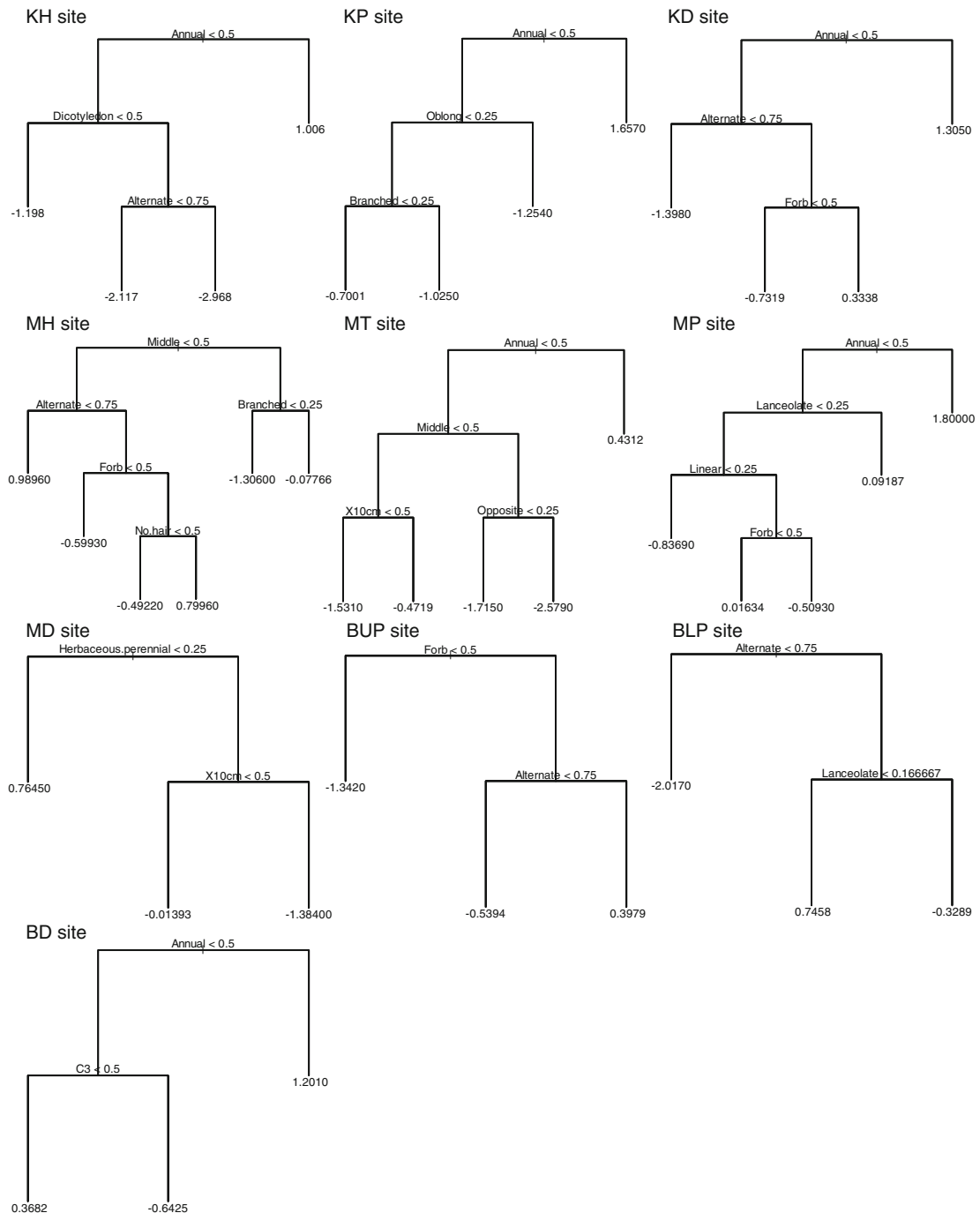
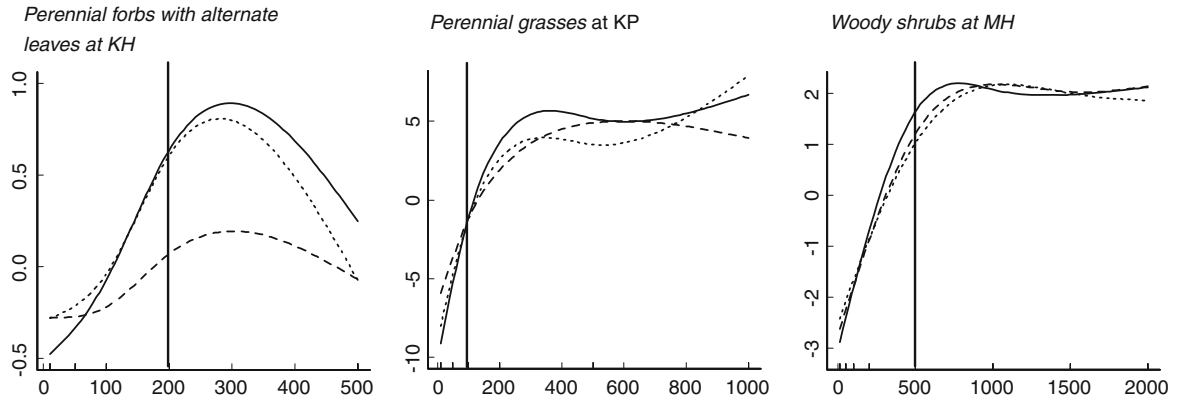


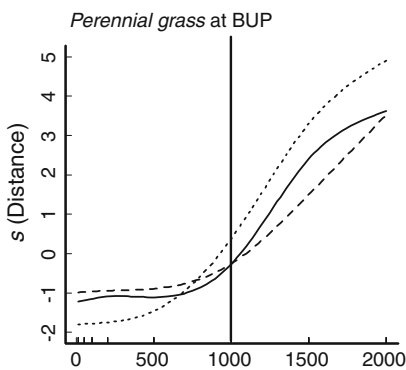
Fig. 3 Use of regression trees to visualize trait combinations to predict species' responses to grazing. Trees are shown corresponding to each ecological site across observation years. In this analysis, traits were used as independent variables and the score of species on DCA axis 1 as the dependent variable. In all graphs, the right branch should be followed downwards if

a species possesses the trait at any splitting node (indicated by a “yes” for the first nodes). Values at the ends of the branches are mean ordination scores of species sharing the set of traits defined by the upper nodes. See supplementary material Table S2 for a full description of the traits and their categories

a Functional groups that decreased dramatically as the RET was approached



b Functional groups that decreased gradually as the RET was approached



c Functional groups that increased dramatically after the RET had been passed

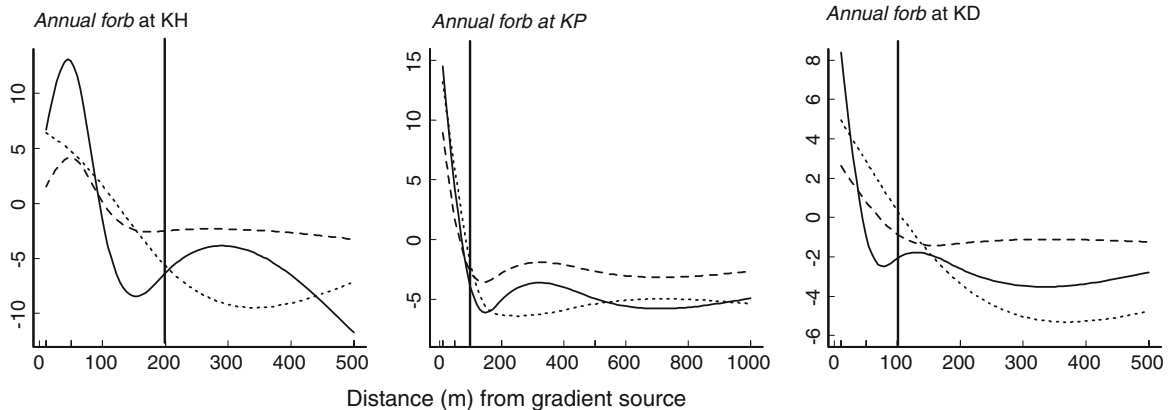


Fig. 4 Trends in the covers of functional plant groups that share the traits of life history, growth form, leaf shape, and leaf attachment, plotted against distance from the gradient source. Of the significant (approximate $P < 0.05$) and similar response patterns of functional groups, representative responses to the grazing gradient across years of observation are shown (not all results are shown); *solid lines* are the responses in 2006, *dashed lines* in 2007, and *dotted lines* in 2008. Values on the y-axis are residuals, the smooth-term coefficients (s) fitted from

a GAM, and scaled to have a mean of 0 across all permanent transects within each year, where the distance is the smoothed explanatory variable. We contrasted these functional groups' responses with the RET (*solid vertical line*; Table 2) to extract robust and repeatable predictors of occurrence of the ecological threshold (a–c). See supplementary material Table S2 and Fig. 2 for confirmation of the trait combinations used in the analyses here

Among the functional groups defined by all of these trait combinations, functional groups such as perennial grasses, or perennial forbs with alternate leaf attachment, showed drastically decreased cover as the threshold was approached (Fig. 4a; see also [Results](#) section) at ecological sites with relatively benign environmental conditions (except for MT and BUP); grasses or forbs dominated the vegetation at these sites (see supplementary material Table S1). These results were generally consistent with previous literature (Fernandez-Gimenez and Allen-Diaz 1999; Gunin et al. 1999; Hoshino et al. 2009). At MT, although the cover of perennial forbs with alternate leaf attachment also generally drastically decreased as the threshold was approached, the response was not significant in 2007, a relatively dry year. The severity of the grazing impact associated with the number of livestock at BUP was relatively large (Sasaki et al. 2008a), and the area surrounding the site may have been affected by moderate or light grazing, because the source of water here is a large spring from which a flat pediment spreads out. We therefore observed no drastic decrease in the response of perennial grasses at this site across all years. In contrast, at the ecological sites that had relatively harsh environmental conditions (except for BLP) and were dominated by shrubs or halophytic shrubs (see supplementary material Table S1), the cover of functional groups such as woody shrubs drastically decreased as the threshold was approached (Fig. 4a; see also [Results](#) section). Thus, differences in the landscape condition at each site (see supplementary material Table S1), which was responsible for the dominant vegetation physiognomy (Sasaki et al. 2008b), probably resulted in differences among sites in the responses of functional groups as predictors of an approaching threshold. Again, the theoretical prediction that vegetation in the Mongolian rangelands should be relatively resistant to grazing holds true in the sense that the landscape condition-dependent responses of functional groups to grazing were relatively constant at a certain level of grazing and then exhibited a sharp decrease in approaching the ecological threshold (Milchunas et al. 1988; Cingolani et al. 2005). Moreover, although not all species within the same functional group necessarily responded to grazing in strictly similar ways, important signs forewarning of approach to the threshold were revealed when the response of these species were combined. This suggests that vegetation responses to grazing at

the community level might reflect the behavior of functional response groups in the systems studied (Sasaki et al. 2008a). However, these community-level responses sometimes masked important signs of species responses as the threshold was approached or were confounded by complicated species responses. We therefore suggest that finer assessment of rangeland states in relation to ecological thresholds could better be based on plant species' responses to grazing at an ecological-site scale. Nonetheless, the plant trait approach allows the prediction of vegetation responses to grazing in a given locality where the flora is poorly described or where taxonomic knowledge is limited (Diaz et al. 2001; Pakeman 2004; Vesik et al. 2004).

Overall, the responses of some functional groups to grazing appear predictable and generalizable as predictors of threshold occurrence, taking landscape conditions into account, across Mongolian rangeland ecosystems. Annual management under the uncertainty of systems will be accomplished by a process similar to those used to monitor the responses of species cover to grazing. The ecological indicators derived here should therefore help to improve land managers' ability to prevent adverse changes in states before ecological thresholds are reached (Watson et al. 1996; Bestelmeyer et al. 2003).

Conclusions

Although our aims were not to test the non-equilibrium concept, temporal variations in floristic composition along a grazing gradient could be recognized, and only a subset of species showed significant and similar responses to grazing over the observation years, and the number of such species tended to decrease toward the sites in the drier, desert-steppe region. This suggests that there are non-equilibrium aspects to the vegetation dynamics of Mongolian rangelands (Fernandez-Gimenez and Allen-Diaz 1999). However, we demonstrated that the real damage accumulated by grazing in rangelands remains unchanged and can be recognized, and that the predictable aspects of vegetation dynamics that are easily applicable to sustainable rangeland management exist even under climatic perturbations. The clear implication from this study is that both equilibrium and non-equilibrium concepts must be incorporated into vegetation management across Mongolian rangeland ecosystems (Briske et al. 2003).

Ecological indicators related to the ecological threshold emphasized the importance of early warnings of the potential risk of land degradation caused by ongoing shifts in disturbance regimes due to the transition from nomadic to sedentary livestock grazing that has occurred since the demise of socialism in Mongolia in 1990 (Fernandez-Gimenez and Batbuyan 2004). Moreover, our data from recovery experiments established along the grazing gradients suggested that adverse changes in vegetation state beyond the ecological threshold cannot be reversed after short-term livestock exclusion in Mongolian rangelands (Sasaki et al., unpublished manuscript). Application of ecological indicators in this study would thus permit the use of practical management strategies for the sustainable use of Mongolian rangeland ecosystems.

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References

- Adler PB, Milchunas DG, Sala OE, Burke IC, Lauenroth WK (2005) Plant traits and ecosystem grazing effects: comparison of U.S. sagebrush steppe and Patagonian steppe. *Ecol Appl* 15:774–792
- Andrew MH (1988) Grazing impact in relation to livestock watering points. *Trends Ecol Evol* 3:336–339
- Bestelmeyer BT (2006) Threshold concepts and their use in rangeland management and restoration: the good, the bad, and the insidious. *Restor Ecol* 14:325–329
- Bestelmeyer BT, Brown JR, Havstad KM, Alexander R, Chavez G, Herrick JE (2003) Development and use of state-and-transition models for rangelands. *J Range Manag* 56:114–126
- Briske DD, Fuhlendorf SD, Smeins FE (2003) Vegetation dynamics on rangelands: a critique of the current paradigms. *J Appl Ecol* 40:601–614
- Briske DD, Fuhlendorf SD, Smeins FE (2005) State and transition models, thresholds, and rangeland health: a synthesis of ecological concepts and perspectives. *Range Ecol Manag* 58:1–10
- Briske DD, Fuhlendorf SD, Smeins FE (2006) A unified framework for assessment and application of ecological thresholds. *Range Ecol Manag* 59:225–236
- Briske DD, Bestelmeyer BT, Stringham TK, Shaver PL (2008) Recommendations for development of resilience-based state-and-transition models. *Range Ecol Manag* 61:359–367
- Bullock JM, Franklin J, Stevenson MJ, Silvertown J, Coulson SJ, Gregory SJ, Tofts R (2001) A plant trait analysis of responses to grazing in a long-term experiment. *J Appl Ecol* 38:253–267
- Buttolph LP, Coppock DL (2004) Influence of deferred grazing on vegetation dynamics and livestock productivity in an Andean pastoral system. *J Appl Ecol* 41:664–674
- Cingolani AM, Noy-Meir I, Diaz S (2005) Grazing effects on rangeland diversity: a synthesis of contemporary models. *Ecol Appl* 15:757–773
- Cleveland WS (1979) Robust locally weighted regression and smoothing scatterplots. *J Am Stat Assoc* 74:829–836
- De Angelis DL, Waterhouse J (1987) Equilibrium and non-equilibrium concepts in ecological models. *Ecol Monogr* 57:1–21
- De Bello F, Leps J, Sebastia MT (2005) Predictive value of plant traits to grazing along a climatic gradient in the Mediterranean. *J Appl Ecol* 42:824–833
- Diaz S, Noy-Meir I, Cabido M (2001) Can grazing response of herbaceous plants be predicted from simple vegetative traits? *J Appl Ecol* 38:497–508
- Dyksterhuis EJ (1949) Condition and management of rangeland based on quantitative ecology. *J Range Manag* 2:104–105
- Ellis JE, Swift DM (1988) Stability of African pastoral systems: alternate paradigms and implications for development. *J Range Manag* 41:450–459
- Fensham RJ, Fairfax RJ, Dwyer JM (2010) Vegetation responses to the first 20 years of cattle grazing in an Australian desert. *Ecology* 91:681–692
- Fernandez-Gimenez ME, Allen-Diaz B (1999) Testing a non-equilibrium model of rangeland vegetation dynamics in Mongolia. *J Appl Ecol* 36:871–885
- Fernandez-Gimenez ME, Allen-Diaz B (2001) Vegetation change along gradients from water sources in three grazed Mongolian ecosystems. *Plant Ecol* 157:101–118
- Fernandez-Gimenez ME, Batbuyan B (2004) Law and disorder: local implementation of Mongolia's land law. *Dev Change* 35:141–165
- Friedel MH (1991) Range condition assessment and the concept of thresholds: a viewpoint. *J Range Manag* 44:422–426
- Gillson L, Hoffman MT (2007) Rangeland ecology in a changing world. *Science* 315:53–54
- Grime JP (2001) Plant strategies, vegetation processes, and ecosystem properties, 2nd edn. John Wiley and Sons, Chichester
- Grubov VI (1982) Key to the vascular plants of Mongolia. Science Publishers, Enfield, NH
- Gunin PD, Vostokova EA, Dorefeyuk NI, Tarasov PE, Black CC (1999) Vegetation dynamics of Mongolia. Kluwer Academic Publishers, Boston
- Hastie T, Tibshirani R (1990) Generalised additive models. Chapman & Hall, London
- Hilbig W (1995) The vegetation of Mongolia. SPB Academic Publishing, Amsterdam
- Hoshino A, Yoshihara Y, Sasaki T, Okayasu T, Jamsran U, Okuro T, Takeuchi K (2009) Comparison of vegetation changes along grazing gradients with different numbers of livestock. *J Arid Environ* 73:687–690

- Illius AW, O'Connor TG (1999) On the relevance of non-equilibrium concepts to arid and semiarid grazing systems. *Ecol Appl* 9:798–813
- Jackson RD, Bartolome JW (2002) A state-transition approach to understanding nonequilibrium plant community dynamics of California grasslands. *Plant Ecol* 162:49–65
- Landsberg J, James CD, Morton SR, Muller WJ, Stol J (2003) Abundance and composition of plant species along grazing gradients in Australian rangelands. *J Appl Ecol* 40:1008–1024
- Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revising the Holy Grail. *Funct Ecol* 16:545–556
- Legendre P, Legendre L (1998) Numerical ecology, 2nd English edn. Elsevier Science, Amsterdam
- Milchunas DG, Sala OE, Lauenroth WK (1988) A generalized model of the effects of grazing by large herbivores on grassland community structure. *Am Nat* 132:87–106
- Nash MS, Whitford WG, de Soyza AG, Van Zee JW, Havstad KM (1999) Livestock activity and Chihuahuan desert annual-plant communities: boundary analysis of disturbance gradients. *Ecol Appl* 9:814–823
- Pakeman RJ (2004) Consistency of plant species and trait responses to grazing along a productivity gradient: a multi-site analysis. *J Ecol* 92:893–905
- Pringle H, Landsberg J (2004) Predicting the distribution of livestock grazing pressure in rangelands. *Austral Ecol* 29:31–39
- R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Riginos C, Hoffman MT (2003) Changes in population biology of two succulent shrubs along a grazing gradient. *J Appl Ecol* 40:615–625
- Sasaki T, Okayasu T, Takeuchi K, Jamsran U, Jadambaa S (2005) Patterns of floristic composition under different grazing intensities in Bulgan, South Gobi, Mongolia. *Grassl Sci* 51:235–242
- Sasaki T, Okayasu T, Jamsran U, Takeuchi K (2008a) Threshold changes in vegetation along a grazing gradient in Mongolian rangelands. *J Ecol* 96:145–154
- Sasaki T, Okayasu T, Shirato Y, Jamsran U, Okubo S, Takeuchi K (2008b) Can edaphic factors demonstrate landscape-scale differences in vegetation responses to grazing? *Plant Ecol* 194:51–66
- Sasaki T, Okayasu T, Ohkuro T, Shirato Y, Jamsran U, Takeuchi K (2009a) Rainfall variability may modify the effects of long-term enclosure on vegetation in Mandalgobi, Mongolia. *J Arid Environ* 73:949–954
- Sasaki T, Okubo S, Okayasu T, Jamsran U, Ohkuro T, Takeuchi K (2009b) Management applicability of the intermediate disturbance hypothesis across Mongolian rangeland ecosystems. *Ecol Appl* 19:423–432
- Sasaki T, Okubo S, Okayasu T, Jamsran U, Ohkuro T, Takeuchi K (2009c) Two-phase functional redundancy in plant communities along a grazing gradient in Mongolian rangelands. *Ecology* 90:2598–2608
- Scheffer M, Carpenter S (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends Ecol Evol* 18:648–656
- Strauss A, Schickhoff U (2007) Influence of soil ecological conditions on vegetation zonation in a western Mongolian lake shore—semi-desert ecotone. *Erdkunde* 61:72–92
- Stringham TK, Krueger WC, Shaver PL (2003) State and transition modeling: an ecological process approach. *J Range Manag* 56:106–113
- Stumpp M, Wesche K, Retzer V, Miede G (2005) Impacts of grazing livestock and distance from water sources on soil fertility in southern Mongolia. *Mt Res Dev* 25:244–251
- Todd SW (2006) Gradients in vegetation cover, structure and species richness of Nama-Karoo shrublands in relation to distance from watering points. *J Appl Ecol* 43:293–304
- Toms JD, Lesperance ML (2003) Piecewise regression: a tool for identifying ecological thresholds. *Ecology* 84:2034–2041
- USDA Natural Resources Conservation Service (1997) National range and pasture handbook. United States Department of Agriculture, Washington, DC
- van de Koppel J, Rietkerk M, Weissing FJ (1997) Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. *Trends Ecol Evol* 12:352–356
- van Staaldunin MA, Daring H, Werger MJA (2007) Impact of grazing regime on a Mongolian forest steppe. *Appl Veg Sci* 10:299–306
- Vesk PA, Westoby M (2001) Predicting plant species' responses to grazing. *J Appl Ecol* 38:897–909
- Vesk PA, Leishman MR, Westoby M (2004) Simple traits do not predict grazing response in Australian dry shrublands and woodlands. *J Appl Ecol* 41:22–31
- Vetter S (2005) Rangelands at equilibrium and non-equilibrium: recent developments in the debate. *J Arid Environ* 62:321–341
- Walker S, Wilson JB (2002) Tests for nonequilibrium, instability, and stabilizing processes in semiarid plant communities. *Ecology* 83:809–822
- Watson IW, Burnside DG, Holm AMR (1996) Event-driven or continuous; which is the better model for managers? *Rangel J* 18:351–369
- Westoby M, Walker BH, Noy-Meir I (1989) Opportunistic management for rangelands not at equilibrium. *J Range Manag* 42:266–274
- Wood SN (2006) Generalized additive models: an introduction with R. Chapman & Hall/CRC Press, Boca Raton, FL
- Zemlich A (2007) Equilibrium or non-equilibrium ecosystems? Scaling effects in rangeland ecosystems of western Mongolia. *Erdkunde* 61:335–343

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