

Management applicability of the intermediate disturbance hypothesis across Mongolian rangeland ecosystems

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Abstract. The current growing body of evidence for diversity–disturbance relationships suggests that the peaked pattern predicted by the intermediate disturbance hypothesis (IDH) may not be the rule. Even if ecologists could quantify the diversity–disturbance relationship consistent with the IDH, the applicability of the IDH to land management has rarely been addressed. We examined two hypotheses related to the generality and management applicability of the IDH to Mongolian rangeland ecosystems: that the diversity–disturbance relationship varies as a function of landscape condition and that some intermediate scales of grazing can play an important role in terms of sustainable rangeland management through a grazing gradient approach. We quantified the landscape condition of each ecological site using an ordination technique and determined two types of landscape conditions: relatively benign and harsh environmental conditions. At the ecological sites characterized by relatively benign environmental conditions, diversity–disturbance relationships were generally consistent with the IDH, and maximum diversity was observed at some intermediate distance from the source of the grazing gradient. In contrast, the IDH was not supported at most (but not all) sites characterized by relatively harsh environmental conditions. The intermediate levels of grazing were generally located below the ecological threshold representing the points or zones at which disturbance should be limited to prevent drastic changes in ecological conditions, suggesting that there is little “conundrum” with regard to intermediate disturbance in the studied systems in terms of land management. We suggest that the landscape condition is one of the primary factors that cause inconsistencies in diversity–disturbance relationships. The ecological threshold can extend its utility in rangeland management because it also has the compatibility with the maintenance of species diversity. This study thus suggests that some intermediate scales of grazing and ecological thresholds are mutually supportive tools for sustainable management of Mongolian rangelands.

Key words: arid and semiarid rangelands; ecological threshold; grazing gradient; grazing history; Mongolia; plant functional types; rangeland management; species coexistence; species diversity.

INTRODUCTION

Factors driving patterns of species diversity at a variety of spatial and temporal scales and the mechanisms underlying those patterns have long been a central theme in community ecology (Huston 1994, Rosenzweig 1995). Historically, studies on species diversity were largely of academic interest, but growing concerns over the adverse effects of human activities on diversity and the services that it provides have broadened their scope considerably. Linking ecological theory of species diversity to land management has become a regional and global research and management priority for promoting species diversity and sustainable use of natural systems (Bestelmeyer et al. 2003b).

Disturbance is widely believed to be one of the main factors influencing variations in species diversity (e.g., Connell 1978, Huston 1979, 1994, Collins et al. 1998). The intermediate disturbance hypothesis (IDH; Grime 1973, Connell 1978, Huston 1979, 1994) is a model of species diversity that has postulated that disturbance prevents competitively dominant species from excluding other species from the community and that there is a trade-off between species' ability to compete and their ability to tolerate disturbance. If disturbances are too rare, the competitive dominants will eliminate other species and reduce diversity as equilibrium conditions develop. If disturbances are too frequent, most species will go locally extinct because they cannot tolerate repeated disturbances, which lowers diversity. Under intermediate levels of disturbance, diversity is maximized because disturbance-tolerant species and competitively dominant species coexist (Connell 1978, Sousa 1979). In this study, we used the term IDH solely to refer

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to the unimodal pattern of species diversity supported by any possible mechanism of species coexistence along a gradient in a disturbance regime (Roxburgh et al. 2004).

Mackey and Currie (2001), however, have expressed doubts about the generality of the IDH to describe diversity–disturbance relationships. They concluded that the relationships are neither consistently strong nor consistently peaked. This is also the case for rangeland ecosystems; empirical evidence supports positive monotonic (McIntyre and Lavorel 2001), negative monotonic (Collins et al. 1995, Todd 2006), unimodal (McIntyre and Lavorel 1994, Collins et al. 1995, Oba et al. 2001, del Pozo et al. 2006), and no significant relationships (Riginos and Hoffman 2003, Adler et al. 2005) between plant species diversity and disturbance, such as grazing or fire. One potential explanation for the lack of consensus is that the effect of disturbance on diversity may change according to environmental contexts (Milchunas et al. 1988, Shea et al. 2004, Cingolani et al. 2005, Lepori and Hjerdt 2006). The conceptual model in rangeland ecosystems (Milchunas et al. 1988, Cingolani et al. 2005) has focused on generalizing the regional-scale responses of plant species diversity to disturbance (grazing intensity) along gradients of climate and an evolutionary history of grazing. However, these responses are filtered to varying degrees by a combination of local biotic and abiotic factors (Zobel 1997) to create variation in diversity among local communities within a region (Wiens 1989).

Various types of disturbance or stress, other than grazing, can be operating at a landscape scale in rangeland ecosystems (Collins 1987, Hobbs and Huenneke 1992). Fire regimes (Collins 1987), wind erosion (Wright et al. 2006), or other physical disturbances (Collins and Barber 1985) may interact with grazing to maintain a plant community at its potentially peak diversity through associated facilitation effects. Combined effects of aridity and an increased salinity in the soil (high-stress environment) may result in an edaphically controlled, sparsely populated community in which competitive exclusion can be weak, even in the absence of disturbance (Didham et al. 2005). When these criteria are met, unimodal patterns of species diversity predicted by IDH would be modified. Consequently, diversity may exhibit patterning that is the focus of a great deal of management activity between the scales of regional and local communities (i.e., a landscape scale; Bestelmeyer et al. 2003b). Nevertheless, we lack a generalization of the IDH at a landscape scale and a direct assessment of whether the IDH applies in such interactions (Shea et al. 2004). Despite the methodological difficulty of such a comprehensive study (Bestelmeyer et al. 2003b, Shea et al. 2004), the grazing gradient approach (Lange 1969, Andrew 1988) at a variety of ecological sites (as defined by the USDA Natural Resources Conservation Service 1997; see also Bestelmeyer et al. 2003a) would provide a comprehensive

insight into whether the shapes of diversity–disturbance relationships vary as a function of the landscape condition. Therefore, we used the distance from the source of the grazing gradient, such as livestock camps or sources of water, to represent a spatial gradient in the accumulated impact of long-term exposure to livestock at multiple ecological sites. In this study, we focused on livestock grazing as a primary disturbance that shapes plant species diversity and defined potential physical disturbance or environmental stress occurring at the ecological site as a landscape condition.

Another critique of the studies of the IDH is that many authors focused on merely quantifying the pattern of higher diversity at intermediate disturbance and presented little supplemental information to explain possible mechanism(s) that underlie the diversity–disturbance relationships (Shea et al. 2004). Understanding the responses of the life-history attributes of the component species (e.g., plant functional types, PFTs) to disturbance will facilitate identification of the possible mechanism(s) (Roxburgh et al. 2004, Shea et al. 2004). This is because life-history differences differentiate the species in their response to disturbance and, therefore, are key components in defining the spatio-temporal niches required for coexistence (Shea et al. 2004). More precisely, given the classical principle of the IDH, we suggest that the paucity of studies reporting a possible mechanism results from the fact that disturbance often presents a conundrum in terms of land management (Hobbs and Huenneke 1992). Disturbance may play an important role in the continued existence of particular species or communities, and therefore disturbance regimes must be integrated with management strategy; however, disturbance simultaneously promotes invasions by disturbance-tolerant, weedy plant species (Hobbs and Huenneke 1992). If higher species diversity at intermediate disturbance levels was supported by the coexistence of perennial species with weedy annual species that are often of little forage value, striking a balance between maintenance of species diversity and rangeland management would be difficult. In this context, we argue that it is necessary to examine the applicability of the IDH to land management.

To accomplish this, we contrast the intermediate levels of grazing with threshold levels (i.e., ecological threshold; Sasaki et al. 2008a) defined as the points or zones at which disturbance should be limited to prevent drastic changes in ecological conditions (Radford et al. 2005, Bestelmeyer 2006, Sasaki et al. 2008a). Sasaki et al. (2008a) showed that threshold responses of vegetation to grazing generally reflect the nonlinear rapid replacement between perennial grasses or forbs and weedy annual forbs. That is, the appearance of weedy annuals nearly corresponds to the points or zones at which threshold changes occur. When maximum species diversity is supported by the coexistence with weedy annuals, the intermediate levels of grazing would occur beyond the ecological threshold, while the opposite would be

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

Study area and site code	Landscape position	Location	Gradient source	Vegetation physiognomy	Soil texture	Reference distance (m)†
Kherlen Bayan Ulaan						
KH	hill	47°09' N, 109°17' E	livestock camp	grassland	loam	500
KP	pediment	47°14' N, 108°50' E	livestock camp	grassland	loam	1000
KD	depression	47°04' N, 108°46' E	livestock camp	grassland	sandy loam	500
Mandalgobi						
MH	hill	45°47' N, 106°11' E	livestock camp	shrubland	sand	2000
MT	tableland	45°41' N, 106°27' E	livestock camp	grassland	sandy clay loam	1000
MP	pediment	45°41' N, 106°10' E	livestock camp	grassland	sandy loam	1000
MD	depression	45°38' N, 106°16' E	livestock camp	halophytic shrubland	sandy loam	1000
Bulgan						
BUP	upper pediment	43°54' N, 103°30' E	source of water	grassland	sandy clay loam	2000
BLP	lower pediment	44°14' N, 103°38' E	livestock camp	shrubland	sand	1000
BD	depression	44°18' N, 103°35' E	livestock camp	halophytic shrubland	sandy loam	1000

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

predicted when maximum species diversity is supported by the coexistence with some subordinate perennials that are often of medium to high forage value. We can thus explicitly and simply demonstrate the applicability of the IDH to land management by locating the intermediate levels of grazing in light of the position of ecological threshold along a grazing gradient.

Thus, in this study, we examine two hypotheses related to the generality and management applicability of the IDH to Mongolian rangeland ecosystems: that the diversity–disturbance relationship varies as a function of landscape condition and that some intermediate scales of grazing can play an important role in terms of sustainable rangeland management through a grazing gradient approach. We also discuss the possible mechanisms of species coexistence under the IDH by assessing the results from this study with key information (i.e., the responses of floristic composition and PFTs to grazing) provided by Sasaki et al. (2008a).

MATERIALS AND METHODS

Study areas and ecological sites

Three study areas were situated 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). The region's climate is arid and cold, with a short summer. The study areas have a long evolutionary history of grazing by domestic livestock under nomadic or seminomadic patterns of land use. 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). The types of livestock are sheep, goats, and cattle in Kherlen Bayan Ulaan and Mandalgobi; and sheep, goats, and camels in

Bulgan. Although livestock types also differ somewhat among landscapes within these areas, most livestock grazed across landscapes are sheep and goats. Based on meteorological data provided by Mongolia's Institute of Meteorology and Hydrology, Ministry of Nature and Environment, annual rainfall averaged ~210 mm (coefficient of variation = 21%) at Kherlen Bayan Ulaan, 170 mm (28%) at Mandalgobi, and 140 mm (26%) at Bulgan, between 1993 and 2003. In all areas, peak rainfall occurred in July. Summer and winter temperatures averaged around 15° and –22°C, respectively, at Kherlen Bayan Ulaan; 19° and –14°C at Mandalgobi; and 21° and –11°C at Bulgan.

Ten ecological sites were located across the three study areas at different landscape positions in grassland, shrubland, or halophytic shrubland vegetation physiognomies (Table 1; for more detailed characteristics of each site, see Sasaki et al. 2008a). 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; hill (MH), tableland (MT), pediment (MP), and depression (MD) in Mandalgobi; and upper-pediment (BUP), lower-pediment (BLP), and depression (BD) in Bulgan. Detailed criteria and methods for selecting the ecological sites were described by Sasaki et al. (2008b). Although it was not possible to quantify grazing intensity precisely, our previous work suggested that the variation in the relative grazing intensities along the grazing gradient may differ due to the actual number of livestock involved in each site (Sasaki et al. 2008a; see *Discussion* for the effect of this variation on our results). In selecting these sites, we aimed to ensure that we had covered a range of the climatic, geomorphic, edaphic, and vegetation variations 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 prediction of the IDH.

Sampling

We used the distance (meters) from each survey transect to a livestock camp or source of water to represent relative grazing intensity. According to our preliminary survey (T. Okayasu, *unpublished data*), dung frequency decreased with increasing distance from a camp or source of water (hereafter, the “gradient source”). We defined a reference distance (Table 1), which represents the point at which livestock impacts were minimal (only very small amounts of dung could be found), and this distance was chosen at a position located beyond the normal grazing range of the livestock from the gradient source. Because of differences in the number of livestock between sites, not all the reference distances could be sampled to the same distance due to logistical considerations (for more detailed sampling procedures, see Sasaki et al. 2008a).

Between June and August 2006, we sampled vegetation at each ecological site using transects placed at set distances along the grazing gradients (five replicates of the gradient were created in different directions). 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 from the source; 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 to 50 m from the source and at intervals of 5 m thereafter.

Three soil samples at 0–5 cm depth were also collected and combined into one composite plot sample along the same vegetation transects at 10, 50, 100, 200, 500, and 1000 m from the source; exceptions were the KH and KD ecological sites (up to 500 m from the source) and the MH and BUP sites (additionally, at 1500 and 2000 m from the source). Sampling resolution of soil was thus lower than that of vegetation, but this was done to optimize the sampling effort. Each soil sampling point on a transect was laid out at intervals of 5 m for the transects located 10 and 50 m from the source and at intervals of 10 m thereafter. The samples were subjected to the following chemical analyses (Sparks 1996): pH in water (soil:solution = 1:2.5, using deionized water); organic C (Walkley-Black); total N (Kjeldahl); Ca⁺⁺, Mg⁺⁺, K⁺, and total P (Bray and Kurtz). Soil texture was determined following the criteria of ISSS et al. (1994).

Data analysis

To determine the landscape condition of each ecological site, we used canonical correspondence

analysis (CCA; Legendre and Legendre 1998) for the floristic composition data of each transect (using pooled data from five subsamples at the distances where soils were also sampled) across the sites using plant cover data for each species. After testing for collinearity, the overall variance of floristic composition was analyzed by means of CCA using all soil variables and the distance from the sources (all variables were ln-transformed before analyses). We used permutation tests (1000 permutations) to test the significance of the constrained eigenvalue (Legendre and Legendre 1998). Based on the result of the CCA with the consideration of vegetation physiognomy and soil texture in each site (Table 1), we interpreted relatively the landscape condition of ecological sites that corresponded to particular environmental factors in the ordination space. This procedure has been shown to be valid in our study areas and can be a useful tool for identifying across-landscape (i.e., landscape condition) and within-landscape factors influencing variation in vegetation (Sasaki et al. 2008b).

For the following analyses, we calculated species richness and the index of species diversity (Shannon-Wiener index, H' ; Magurran 2004) as a measure of species diversity. In this study, the following results were consistent between measures, so results are reported only for the index of species diversity (hereafter, “species diversity”). Species diversity (H') for each transect was calculated as

$$H' = -\sum p_i \ln p_i \quad (1)$$

where p_i is the proportional cover value represented by the i th species (using pooled data from five subsamples). Consequently, the data matrices used in the following analysis consisted of a total of 3500 quadrats along 700 transects sampled at 12 to 16 sampling distances around 10 gradient sources. We examined the relationship between diversity and grazing (distance from the sources) by fitting data to the following models:

$$\text{model 1: } d = a + bD \quad (2)$$

$$\text{model 2: } d = a + bD + cD^2 \quad (3)$$

$$\text{model 3: } d = a + b \ln D \quad (4)$$

$$\text{model 4: } d = a + b \ln D + c(\ln D)^2 \quad (5)$$

where d is species diversity (H'), D is distance from the source, and a , b , and c are regression parameters. Models 1 and 3 linearly relate species richness and diversity to distance and to ln-transformed distance, respectively. A quadratic term is added to models 1 and 3 to form models 2 and 4, respectively, to test for curvilinearity. If more than two models revealed a significant relationship, they were compared using Akaike's Information Criterion (AIC). Models with the smallest AIC were considered the best fit (Johnson and Omland 2004). Confirmation of a unimodal relationship was done with the Mitchell-Olds and Shaw (MOS) test (Mitchell-Olds and Shaw 1987). The MOS

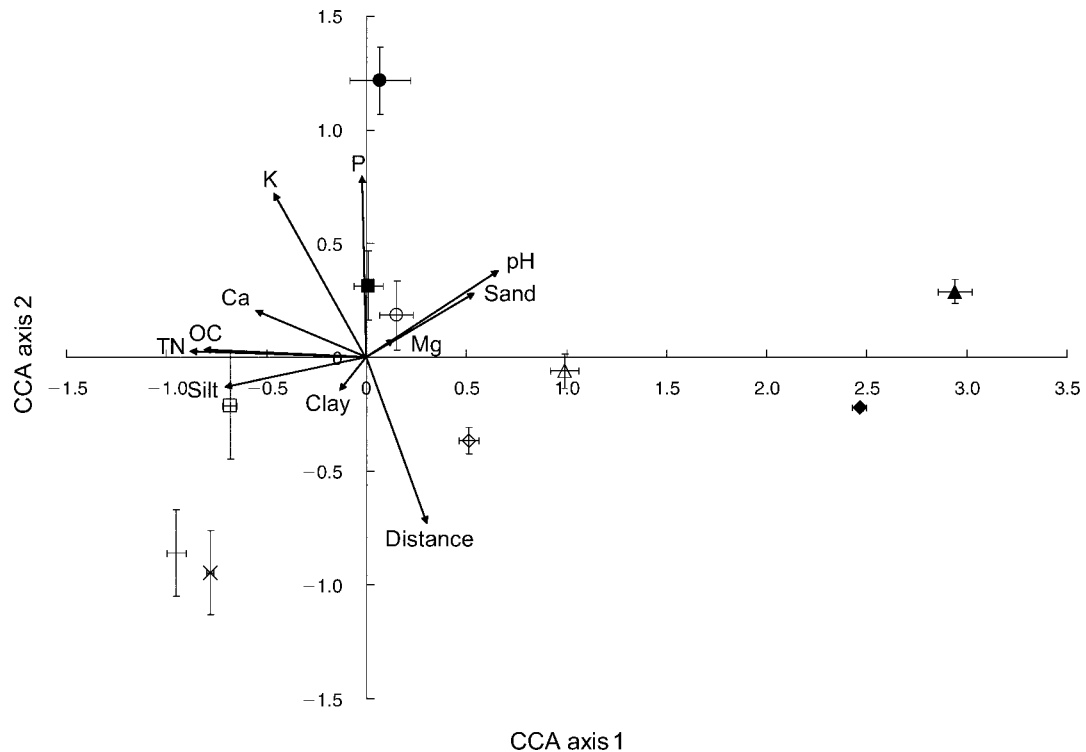


FIG. 1. Canonical correspondence analysis (CCA) biplots for floristic composition of each transect in 10 ecological sites and environmental vectors. Centroids (\pm SE) of scores for the transects in each ecological site are shown; KH (open square), KP (\times), KD (+), MH (open diamond), MT (solid square), MP (open circle), MD (open triangle), BUP (solid circle), BLP (solid diamond), BD (solid triangle). Note that potential wind erosion or environmental stress typified by sand content (indicative of high erodibility) or pH increased along axis 1. The result of the CCA with the consideration of vegetation physiognomy and soil texture in each site (Table 1) allows the relative interpretation of landscape conditions of the sites along axis 1; KH, KP, KD, MT, MP, and BUP sites were in more benign environmental conditions, whereas MH, MD, BLP, and BD sites were in more harsh environmental conditions.

test has been widely used and often shown to be more rigorous than simply looking for a significant quadratic regression (e.g., Mackey and Currie 2001, Chase and Leibold 2002, Chase and Ryberg 2004). To assess the relative rareness of the species contributing to variations in diversity along a grazing gradient, we repeated the previous analysis for the data matrices in which species diversity was calculated without species that were considered rare (<1% of total cumulative cover) according to their relative abundance in the vegetation of grazing gradients at each site.

Finally, we contrasted the distances at which the peaked species diversity occurred with the distances corresponding to the ecological threshold (from Sasaki et al. 2008a), defined as the points or zones at which disturbance should be limited to prevent drastic changes in floristic composition, to examine the significance of some intermediate scales of grazing in terms of rangeland management. In the search for the ecological threshold, Sasaki et al. (2008a) used nonlinear regression models such as a piecewise or an exponential regression model fitted to the floristic composition data for each transect simplified separately for each site using an ordination technique. Based on our prediction, the

intermediate levels of grazing would occur beyond the ecological threshold when the maximum diversity is supported by the coexistence with disturbance-tolerant annual forbs, while the opposite would be predicted when the maximum diversity is supported by the coexistence with some subordinate perennial grasses or forbs. All statistical analyses were performed with R software version 2.4.1 (R Development Core Team 2006).

RESULTS

Landscape conditions of the ecological sites

The CCA ordination identified the environmental factors influencing variation in vegetation across 10 ecological sites (Fig. 1; a permutation test for the constrained eigenvalue is significant, $P < 0.05$). Axis 1 shows a gradient of increasing pH and sand content and decreasing organic C (OC), total N (TN), Ca^{++} , and silt content. Axis 2 shows a gradient of increasing K^+ , P, and decreasing distance. Overall, axis 1 can be interpreted as the across-landscape indicators associated with potential wind erosion or environmental stress typified by higher sand content (indicative of higher

erodibility) or pH, and axis 2 as the within-landscape indicators associated with grazing impacts typified by increasing K^+ , P, and decreasing distance. The CCA ordination with the consideration of vegetation physiognomy and soil texture in each site (Table 1) thus allows the relative interpretation of landscape conditions of the sites along axis 1; KH, KP, KD, MT, MP, and BUP sites were in more benign environmental conditions whereas MH, MD, BLP, and BD sites were in more harsh environmental conditions (Fig. 1). In the following analysis, we examined whether the presence of a unimodal relationship between species diversity and distance from the gradient source depends on the relative landscape condition of a given ecological site based on this interpretation.

Diversity–disturbance relationships

The relationship between species diversity (H') and distance from the gradient source was best described as a unimodal relationship in KH, KP, KD, MT, MP, BUP, and BD sites (Fig. 2; MOS tests for the unimodality of all these relationships are significant, $P < 0.05$). These sites, except for BD, were in relatively benign environmental conditions (Fig. 1). In the MD and MH sites, the relationship was better fit by a quadratic regression, but this relationship failed the MOS test ($P > 0.05$). In the BLP site, the negative linear model (distance \ln -transformed) provided the best fit for the relationship. These three sites were in areas of relatively harsh environmental conditions (Fig. 1). We also obtained the same results for the data matrices in which species diversity was calculated without rare species (results not shown). Observed unimodal shapes of relationships between diversity and distance are almost similar (the distances at which the peaked species diversity occurred were almost the same), but the unimodality is generally slightly weaker (i.e., slightly higher P value for a MOS test) than for the data matrices in which species diversity was calculated including all species, indicating that the contribution of the rare species to the observed unimodal relationships cannot be ignored.

Peaks of species diversity in relation to ecological thresholds

At six of the seven sites at which we determined a unimodal relationship between species diversity and distance, the peaked species diversity along the grazing gradients (determined in this study) occurred at lower levels of grazing than the levels at which the threshold changes in floristic composition occurred (Fig. 2; Sasaki et al. 2008a).

DISCUSSION

At the ecological sites that had relatively benign environmental conditions (KH, KP, KD, MT, MP, and BUP), diversity–disturbance relationships were generally consistent with the IDH (Figs. 1 and 2). This suggests a tight coupling between biological interactions and

grazing in these sites (Sasaki et al. 2008b). Traditional prediction of the IDH assumes that a uniform trade-off between competition and disturbance tolerance can explain species coexistence at intermediate disturbance levels (Connell 1978, Sousa 1979). Previous studies of the IDH in plant communities of terrestrial ecosystems (e.g., Guo 1996, Wilson and Tilman 2002) have also shown that maximum species diversity at intermediate disturbance levels reflects the coexistence of annual (disturbance tolerator) and perennial species (superior competitor).

However, species coexistence that gave maximal diversity in this study probably diverged somewhat from a previously reported rule of coexistence. Although the rates of change in floristic composition were relatively constant below threshold levels of grazing, species diversity varied and reached the maximum below this threshold except for BUP (Fig. 2; Sasaki et al. 2008a). Turnover between PFTs (the cover by perennial grasses or forbs vs. annual forbs; Sasaki et al. 2008a) along a grazing gradient at these sites indicates the existence of a trade-off between disturbance tolerance and competitive ability. However, the cover by these PFTs exhibited a threshold response to grazing (a piecewise or exponential asymptotic increase vs. decrease), that is, the appearances of annual forbs nearly corresponded to the points or zones at which threshold changes occurred (Sasaki et al. 2008a). In addition, the relatively abundant and common species were probably the main contributor to the variation in species diversity along a grazing gradient.

These results suggest that grazing suppresses potentially competitive-dominant perennial grasses or forbs and favors diversity, with the additional increase of subordinate perennial grasses or forbs, resulting in the maximal diversity. Therefore, subordinate perennial grasses or forbs may also have a ruderal strategy (i.e., competitive ruderals; Pierce et al. 2007) for coexistence with a potentially competitive dominant. The appearance of rare species at some intermediate levels of grazing may also contribute to the maximal diversity. Species diversity then decreased drastically with the appearance of disturbance-tolerant annual forbs.

There is assumed to be a more intricate trade-off continuum between disturbance tolerance and competitive ability that cannot be explained simply by the traditional verbal model of the IDH (Cadotte 2007). The present results highlight that the basis of coexistence is the underlying differences in the species' responses to disturbance (Roxburgh et al. 2004). An exceptional result at BUP probably reflected the existence of two contrasting states in vegetation along the gradient (Fig. 2; Sasaki et al. 2008a). This case may refer to a specific condition under which Johst and Huth (2005) predicted that a diversity–disturbance relationship may follow a bimodal curve. How the concept of the IDH can apply to such a condition is beyond the scope of this study and remains unclear, but awareness of this possible modifi-

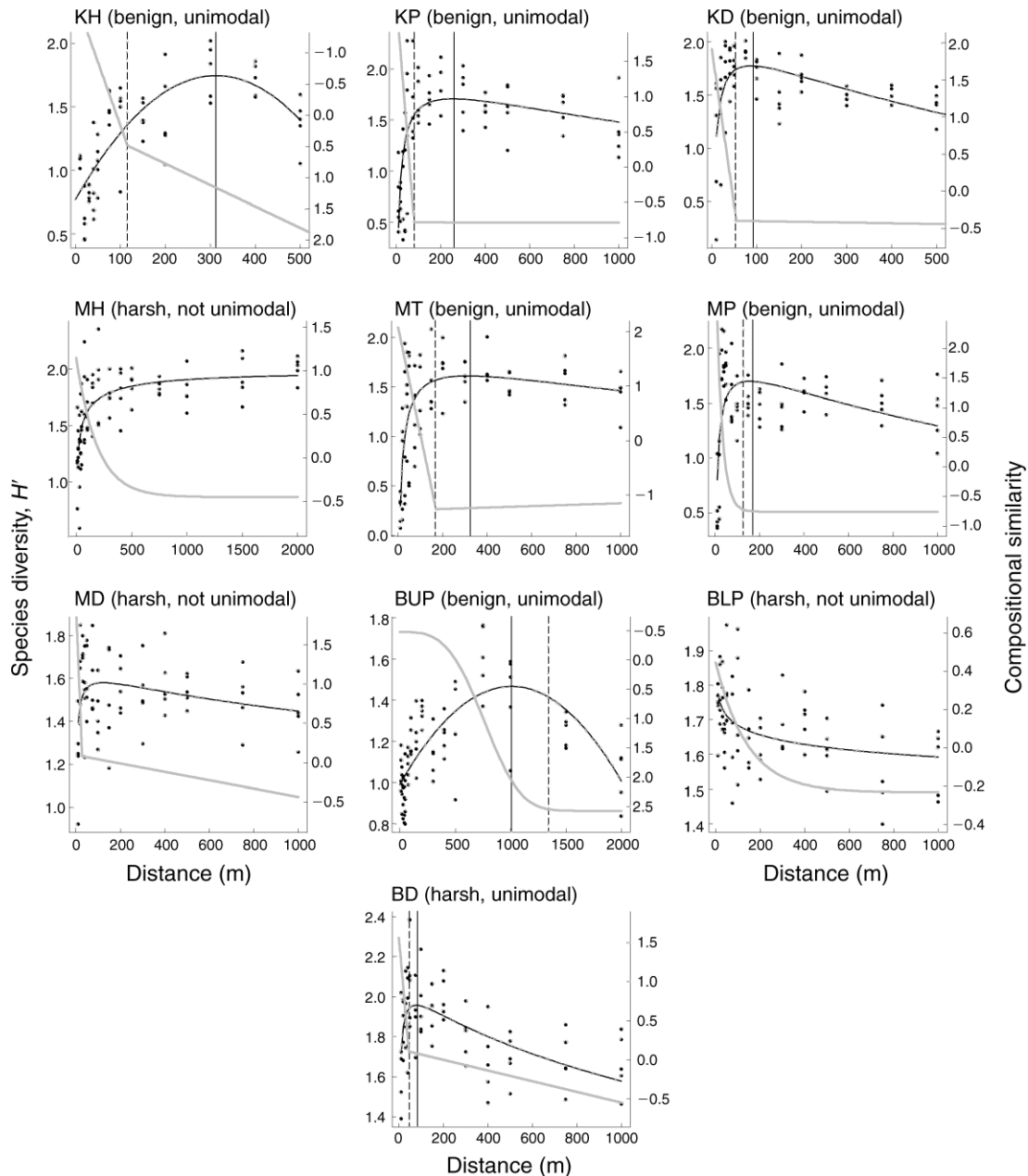


FIG. 2. The relationships between species diversity (Shannon-Wiener index H' , left-hand axes) and distance (m) from the gradient sources (black curve) for each of 10 sites. Observed quadratic relationships are considered significant for unimodality only when the MOS test (Mitchell-Olds and Shaw 1987) is significant ($P < 0.05$). Landscape conditions of the ecological sites are also indicated (relatively benign and harsh environmental conditions, respectively; see also Fig. 1). The gray curve indicates the changes in compositional similarity (represented predominantly by scores of DCA axis 1; right-hand axes) as a function of distance from the source for each of 10 sites (from Sasaki et al. 2008a). At six of the seven sites at which we determined a unimodal relationship, the diversity peak (determined in this study; solid vertical line) occurred at lower levels of grazing than the levels at which the threshold changes occurred (ecological threshold; dashed vertical line [from Sasaki et al. 2008a]).

cation of the IDH is important when studying diversity–disturbance relationships (Johst and Huth 2005).

In contrast, the IDH is not supported at sites, except for BD, that have relatively harsh environmental conditions typified by a higher sand content or pH (Figs. 1 and 2). Prediction by the IDH was probably

confounded by the interaction between grazing and potential wind erosion or environmental stress, suggesting that the relative importance of grazing in creating diversity is low. At MH and BLP sites that were characterized by sandy soils and high erodibility (Table 1; Fig. 1), the modification of the abiotic environment by

shrub mounds (Shachak et al. 1998, Shumway 2000, Wright et al. 2006) may favor the establishment of both perennial and annual herbaceous species. In addition, there are probably no clear trade-offs between disturbance tolerance and competitive ability and no competitive exclusion indicated by the response patterns of PFTs to grazing (Sasaki et al. 2008a). Thus, an underlying mechanism of species diversity could not be explained solely by biological interactions at these sites. MD and BD sites were characterized by salinized soils (Fig. 1), which were responsible for the establishment of halophytic shrubland (Table 1). In these sites, strong abiotic stress probably determines an edaphically controlled, sparsely populated community in which there can be weak competitive exclusion even in the absence of disturbance, resulting in many species that are functionally similar (Didham et al. 2005), and shifts in composition may be lessened (Cingolani et al. 2003). At the BD site, however, the diversity–disturbance relationship is best described as a unimodal relationship. The variation in the shape of the diversity–disturbance relationship at the sites with relatively harsh environmental conditions thus limited our understanding of a causal relationship between multiple interacting disturbances and species diversity. The underlying mechanisms of species diversity at these sites should be clarified in future studies.

Mackey and Currie (2000, 2001) suggested that the observed diversity–disturbance relationships may reflect sampling artifacts. It may be possible that we could not observe the variation in species diversity along a full range of grazing gradients, especially when the pattern was inconsistent with the IDH. However, the landscape condition–dependent generality of the IDH was generally clear even though the reference distances were a priori defined and systematic sampling procedures performed, indicating only a small possibility of this artifact. In addition, our decision to use sample units that consisted of five quadrats uniformly distributed along a transect could minimize the procedural artifact from missing rarer species (Mackey and Currie 2000). Because the levels of the disturbance regime are often laid out discretely in space in natural systems, a number of possible extraneous factors can influence the variation in species diversity (Lepori and Hjerdt 2006). In this study, we could control these extraneous factors by using a grazing gradient approach (see Landsberg et al. 2003, Sasaki et al. 2005, Todd 2006).

Although the diversity–disturbance relationship might be modified by the level of productivity (Huston 1979, 1994, Milchunas et al. 1988, Cingolani et al. 2005, De Bello et al. 2006) and there is a potential productivity gradient along the study areas, we generally observed the unimodal diversity–disturbance relationship at the sites that had relatively benign environmental conditions. Huston (1979, 1994) predicted that maximum diversity is observed at lower intensities of disturbance when productivity is low compared to when productivity

is high. Rather, the variation in the relative grazing intensities along the grazing gradient in each site (Sasaki et al. 2008a) probably reflected the differences in the distance at which peak diversity occurred (Fig. 2).

Several authors have suggested that the predictions of the IDH rely on several prerequisites, such as competitive exclusion (Connell 1978, Sousa 1979), multiple stages in succession (Collins and Glenn 1997), and trade-off between competition and tolerance (Connell 1978, Sousa 1979, Dial and Roughgarden 1998). We could not observe a unimodal relationship at most sites with relatively harsh environmental conditions, also suggesting that observational studies in the systems where these prerequisites are not fulfilled tend to reject the IDH. However, our study simultaneously suggests that there can be a somewhat different type of possible mechanism of species coexistence to support the IDH. As a promoter of species coexistence, the IDH may be both broader in scope and richer in detail than has previously been recognized (Roxburgh et al. 2004).

Milchunas et al. (1988) predicted that vegetation in arid regions with a long evolutionary history of grazing, such as Mongolia, is relatively resistant to grazing (i.e., convergent selection), and therefore responses of species diversity to grazing at a regional scale could remain constant. Overall, our data at a local (site) scale did not support this prediction. We suggest that the prediction by Milchunas et al. (1988) can be modified when grazing intensity surpasses an ecological threshold (Cingolani et al. 2005). In diversity terms, convergent selection pressure may not necessarily prevail at a local scale because there can be a possible mechanism of species coexistence that contributes to the highest diversity in plant communities along a grazing gradient. Rather, due to the strong resistance of vegetation to grazing, variations in species diversity may not be easily detected without using a sufficiently broad range of grazing gradients, especially including severe grazing impacts.

The peaked species diversity generally occurred at lower levels of grazing than the levels at which the threshold changes occurred (Fig. 2; Sasaki et al. 2008a), suggesting that there is little conundrum (*sensu* Hobbs and Huenneke 1992) with regard to intermediate disturbance in the studied systems in terms of land management. Management strategies that include the concept of intermediate disturbance to promote species diversity on rangelands do not conflict with the sustainable use of rangelands. Plant communities that have highest diversity under some intermediate levels of grazing are considered to remain a desirable state for the sustainable management of rangelands, in light of the definition of ecological thresholds (Radford et al. 2005, Bestelmeyer 2006, Sasaki et al. 2008a) as points or zones at which relatively rapid change occurs from one ecological condition to another along a disturbance gradient. In addition, previous studies suggested that plant communities with areas distant from the gradient source would provide a potential refuge for grazing-

sensitive species (Landsberg et al. 2003, Todd 2006). Therefore, for land managers to retain plant species diversity and ecosystem function on rangelands, it would be desirable to provide various levels of grazing across the landscapes that have benign environmental conditions, which is responsible for the establishment of grassland physiognomy (Table 1; Fig. 1), in so far as the levels of grazing do not exceed the ecological threshold. This recognition is important for rangeland management because extensive areas supporting grassland physiognomy are probably of greater value for providing forage resources, especially under 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). Thus, disturbance by domestic livestock grazing primarily plays an essential and sustainable role in enhancing plant species diversity on Mongolian rangelands.

CONCLUSIONS

Our study demonstrated that a diversity–disturbance relationship varies as a function of landscape condition. We suggest that the landscape condition (i.e., potential wind erosion or environmental stress occurring in the landscape) should be considered in the study of diversity–disturbance relationships and may be one of the primary factors that cause the current inconsistencies in this relationship in rangeland ecosystems. We also showed that some intermediate levels of grazing can play an important role in terms of sustainable rangeland management by contrasting with ecological threshold that has explicit potential of management significance, while ecological threshold can extend its utility in rangeland management because it also has compatibility with the maintenance of species diversity. We thus suggest that some intermediate scales of grazing and ecological threshold are mutually supportive tools for sustainable management of Mongolian rangeland ecosystems.

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