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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 semi-arid rangelands; ecological threshold; grazing gradient;

grazing history; plant functional types; species coexistence; species diversity; Mongolia;

rangeland management

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 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 National 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 is 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 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 semi-nomadic patterns of

land use. Vegetation within these areas is characterized as low biomass (approximate

aboveground biomass at its peak time ranges from 20 g/m^2 to 130 g/m^2 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 around 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 (m) from each survey transect (see below) 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-m^2 (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 & 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 colinearity, the overall variances 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:

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

where p_i is the proportional cover value represented by the ith 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:

model 1: $d = a + bD$ (2)

model 2: $d = a + bD + cD^2$ (3)

model 3: $d = a + b \ln D$ (4)

model 4: $d = a + b \ln D + c(\ln D)^2,$ (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 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 above analysis for the

data matrices in which species diversity was calculated without species that were

considered rare (less than 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, total N, 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, 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 versus 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 versus 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, surbordinate 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 modification 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, 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 have

explicit potential of management significance, while ecological threshold can extend its

utility in rangeland management because it also has the 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.

Literature cited

Adler, P. B., D. G. Milchunas, O. E. Sala, I. C. Burke, and W. K. Lauenroth. 2005. Plant traits and ecosystem grazing effects: comparison of US sagebrush steppe and Patagonian steppe. Ecological Applications 15:774–792.

Andrew, M. H. 1988. Grazing impact in relation to livestock watering points. Trends in Ecology and Evolution 3:336–339.

Bestelmeyer, B. T. 2006. Threshold concepts and their use in rangeland management and restoration: the good, the bad, and the insidious. Restoration Ecology 14:325–329.

Bestelmeyer, B. T., J. R. Brown, K. M. Havstad, R. Alexander, G. Chavez, and J. E. Herrick. 2003a. Development and use of state-and-transition models for rangelands. Journal of Range Management 56:114–126.

Bestelmeyer B. T., J. R. Miller, and J. A. Wiens. 2003b. Applying species diversity theory to land management. Ecological Applications 13:1750–1761.

Cadotte, M. W. 2007. Competition-colonization trade-offs and disturbance effects at multiple scales. Ecology 88:823–829.

Chase, J. M., and M. A. Leibold. 2002. Spatial scale dictates the productivity-biodiversity relationship. Nature 416:427–430.

Chase, J. M., and W. A. Ryberg. 2004. Connectivity, scale-dependence, and the productivity-diversity relationship. Ecology Letters 7:676–683.

Cingolani, A. M., M. R. Cabido, D. Renison, and V. N. Solis. 2003. Combined effects of environment and grazing on vegetation structure in Argentinean granitic grasslands. Journal of Vegetation Science 14:223–232.

Cingolani, A. M., I. Noy-Meir, and S. Diaz. 2005. Grazing effects on rangeland diversity: a synthesis of contemporary models. Ecological Applications 15:757–773.

Collins, S. L. 1987. Interaction of disturbances in tallgrass prairie: a field experiment. Ecology 68:1243–1250.

Collins, S. L., and S. C. Barber. 1985. Effects of disturbance on diversity in mixed-grass prairie. Vegetatio 64:87–94.

Collins, S. L., and S. M. Glenn. 1997. Intermediate disturbance and its relationship to within- and between-patch dynamics. New Zealand Journal of Ecology 21:103–110.

Collins, S. L., S. M. Glenn, and D. J. Gibson. 1995. Experimental analysis of intermediate disturbance and initial floristic composition: decoupling cause and effect. Ecology 76:486-492.

Collins, S. L., A. K. Knapp, J. M. Briggs, J. M. Blair, and E. M. Steinauer. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. Science 280:745–747.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302–1309.

Dial, R., and J. Roughgarden. 1998. Theory of marine communities: the intermediate disturbance hypothesis. Ecology 79:1412–1424.

Didham, R. K., C. H. Watts, and D. A. Norton. 2005. Are systems with strong underlying abiotic regimes more likely to exhibit alternative stable states? Oikos 110:409–416.

De Bello, F., J. Leps, and M. T. Sebastia. 2006. Variations in species and functional

plant diversity along climatic and grazing gradients. Ecography 29:801–810.

del Pozo, A., C. Ovalle, M. A. Casado, B. Acosta, and J. M. de Miguel. 2006. Effects of

grazing intensity in grasslands of the Espinal of central Chile. Journal of Vegetation

Science 17:791–798.

Fernandez-Gimenez, M. E., and B. Batbuyan. 2004. Law and disorder: local

implementation of Mongolia's land law. Development and Change 35:141–165.

Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. Nature

242:344–347.

Guo, Q. F. 1996. Effects of bannertail kangaroo rat mounds on small-scale plant

community structure. Oecologia 106:247–256.

Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion:

implications for conservation. Conservation Biology 6:324–337.

Huston, M. A. 1979. A general hypothesis of species diversity. American Naturalist

113:81–101.

Huston, M. A. 1994. Biological diversity: the coexistence of species. Cambridge

University Press, Cambridge, UK.

International Society for Soil Science (ISSS), International Soil Reference and

Information Centre (ISRIC) and Food and Agriculture Organization of the United

Nations (FAO) 1994. World Reference Base for Soil Resources (ed. OC

Spaargaren). ISSS, ISRIC, FAO, Rome, Italy.

Johnson, J. B., and K. S. Omland. 2004. Model selection in ecology and evolution. Trends in Ecology and Evolution 19:101–108.

Johst, K., and A. Huth. 2005. Testing the intermediate disturbance hypothesis: when will there be two peaks of diversity? Diversity and Distributions 11:111–120.

Landsberg, J., C. D. James, S. R. Morton, W. J. Muller, and J. Stol. 2003. Abundance and composition of plant species along grazing gradients in Australian rangelands. Journal of Applied Ecology 40:1008–1024.

Lange, R.T. 1969. The piosphere: sheep track and dung patterns. Journal of Range Management 22:396–400.

Legendre, P., and L. Legendre. 1998. Numerical ecology. 2nd English edn. Elsevier Science, Amsterdam.

Lepori, F., and N. Hjerdt. 2006. Disturbance and aquatic biodiversity: reconciling contrasting views. Bioscience 56:809–818.

Mackey, R. L., and D. J. Currie. 2000. A re-examination of the expected effects of disturbance on diversity. Oikos 88:483–493.

Mackey, R. L., and D. J. Currie. 2001. The diversity-disturbance relationship: is it generally strong and peaked? Ecology 82:3479–3492.

Magurran, A. E. 2004. Measuring Biological Diversity. Blackwell Science, Oxford, UK.

McIntyre, S., and S. Lavorel. 1994. Predicting richness of native, rare, and exotic plants

in response to habitat and disturbance variables across a variegated landscape. Conservation Biology 8:521–531.

McIntyre, S., and S. Lavorel. 2001. Livestock grazing in subtropical pastures: steps in the analysis of attribute response and plant functional types. Journal of Ecology 89:209–226.

Milchunas, D. G., O. E. Sala, and W. K. Lauenroth. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. American Naturalist 132:87–106.

Mitchell-Olds, T., and R. G. Shaw. 1987. Regression analysis of natural selection: statistical inference and biological interpretation. Evolution 41:1149–1161.

Oba, G., O. R. Vetaas, and N. C. Stenseth. 2001. Relationships between biomass and plant species richness in arid-zone grazing lands. Journal of Applied Ecology 38:836–845.

Pierce, S., A. Luzzaro, M. Caccianiga, R. M. Ceriani, and B. Cerabolini. 2007. Disturbance is the principal α-scale filter determining niche differentiation, coexistence and biodiversity in an alpine community. Journal of Ecology 95:698–706.

R Development Core Team. 2006. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Radford, J. Q., A. F. Bennett, and G. J. Cheers. 2005. Landscape-level thresholds of

habitat cover for woodland-dependent birds. Biological Conservation 124:317–337.

Riginos, C., and M. T. Hoffman. 2003. Changes in population biology of two succulent shrubs along a grazing gradient. Journal of Applied Ecology 40:615–625.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, UK.

Roxburgh S. H., K. Shea, and J. B. Wilson 2004. The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. Ecology 85:359–371.

Sasaki, T., T. Okayasu, K. Takeuchi, U. Jamsran, and S. Jadambaa. 2005. Patterns of floristic composition under different grazing intensities in Bulgan, South Gobi, Mongolia. Grassland Science 51:235–242.

Sasaki, T., T. Okayasu, U. Jamsran, and K. Takeuchi. 2008a. Threshold changes in vegetation along a grazing gradient in Mongolian rangelands. Journal of Ecology 96:145–154.

Sasaki, T., T. Okayasu, Y. Shirato, U. Jamsran, S. Okubo, and K. Takeuchi. 2008b. Can edaphic factors demonstrate landscape-scale differences in vegetation responses to grazing? Plant Ecology 194:51–66.

Shachak, M., M. Sachs, and I. Moshe. 1998. Ecosystem management of desertified shrublands in Israel. Ecosystems 1:475–483.

Shea, K., S. H. Roxburgh, and E. S. J. Rauschert. 2004. Moving from pattern to process:

coexistence mechanisms under intermediate disturbance regimes. Ecology Letters 7:491-508.

Shumway, S.W. 2000. Facilitative effects of a sand dune shrub on species growing beneath the shrub canopy. Oecologia 124:138–148.

Sousa, W. P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. Ecology 60:1225–1239.

Sparks, D. L. (ed.). 1996. Methods of soil analysis. Part 3 - Chemical methods. ASA, SSSA, CSSA, Madison WI.

Todd, S. W. 2006. Gradients in vegetation cover, structure and species richness of Nama-Karoo shrublands in relation to distance from livestock watering points. Journal of Applied Ecology 43:293–304.

USDA Natural Resources Conservation Service. 1997. National Range and Pasture Handbook. US Department of Agriculture, Washington, DC.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

Wilson, S. D., and D. Tilman. 2002. Quadratic variation in old-field species richness along gradients of disturbance and nitrogen. Ecology 83:492–504.

Wright, J. P., C. G. Jones, B. Boeken, and M. Shachak. 2006. Predictability of ecosystem engineering effects on species richness across environmental variability and spatial scales. Journal of Ecology 94:815–824.

Zobel, M. 1997. The relative role of species pools in determining plant species richness:

an alternative explanation of species coexistence? Trends in Ecology and Evolution

12:266–269.

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

Study area	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

† Source: this study.

‡ 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.

Figure legends

Fig. 1. Canonical correspondence analysis (CCA) biplots for floristic composition of each transect in 10 ecological sites and environmental vectors. Centroids (±SE) of scores for the transects in each ecological site are shown; KH(□), KP (×), KD (+), MH (◇), MT (■), MP (○), MD (△), BUP (●), BLP (◆), BD (▲). 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.

Fig. 2. The relationships between species diversity (Shannon-Wiener index $H′$) and distance (m) from the gradient sources (black curve). Observed quadratic relationships are considered significant for unimodality only when the MOS test is significant ($P <$ 0.05). Landscape conditions of the ecological sites were also indicated (relatively benign and harsh environmental conditions, respectively; see also Fig. 1). Gray curve indicates the changes in compositional similarity (represented predominantly by scores of DCA axis 1) as a function of distance from the source (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) occurred at lower levels of grazing than the levels at which the threshold changes occurred (ecological threshold; from Sasaki et al. 2008a).
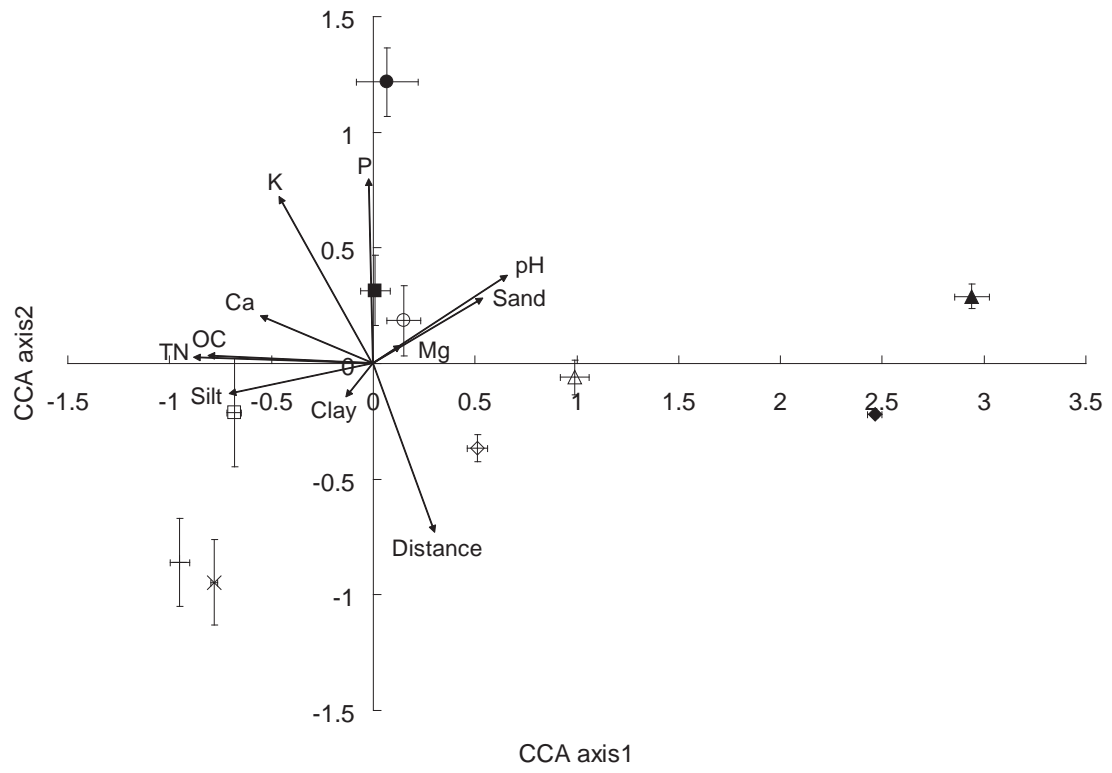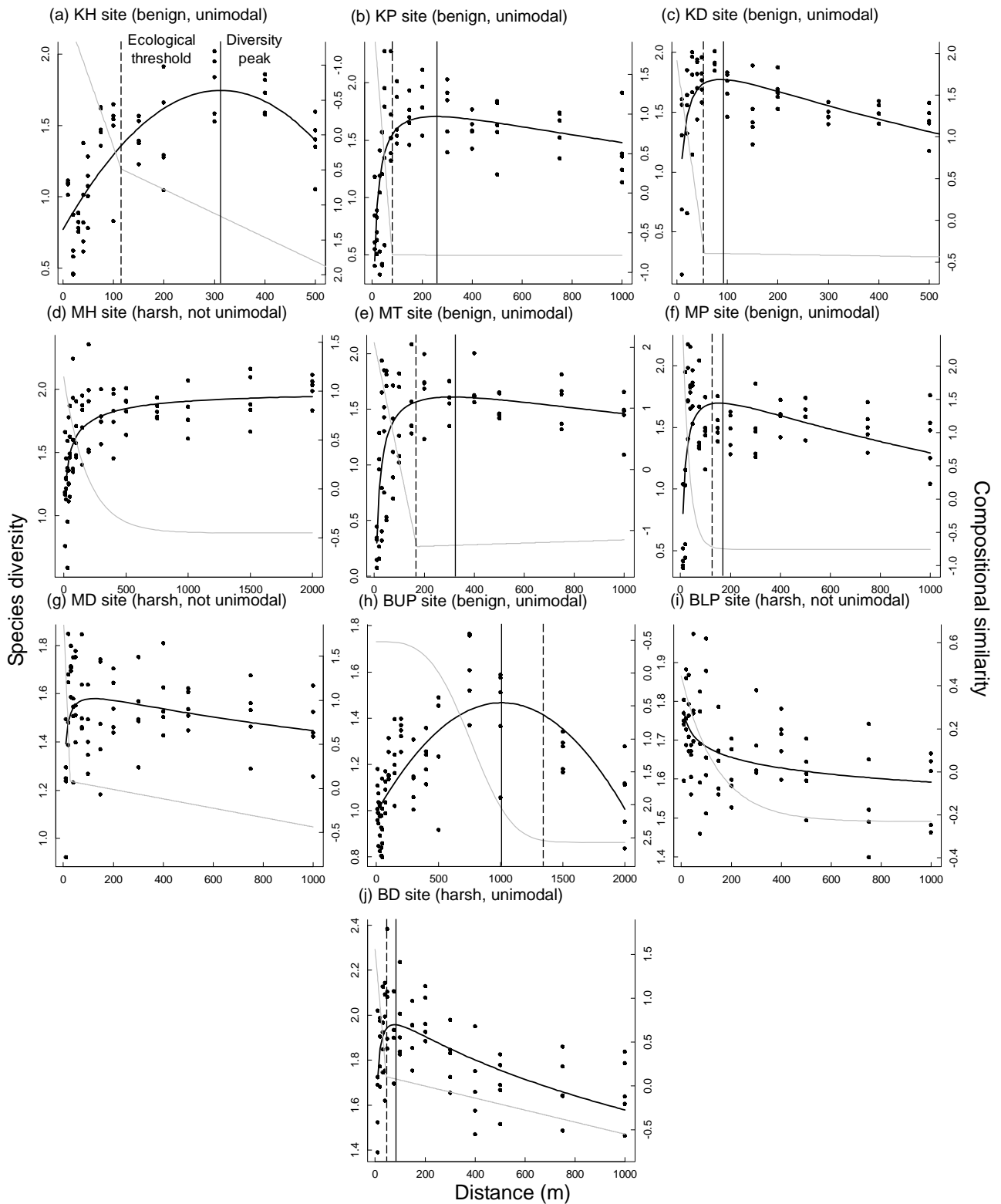
Fig. 1. (T. Sasaki et al.)

Fig. 2. (T. Sasaki et al.)