

Running head: Two-phase functional redundancy in rangelands

Two-phase functional redundancy in plant communities along a grazing gradient in  
Mongolian rangelands

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**Abstract**

The concept of functional redundancy is at the core of theory relating changes in ecosystem functioning to species loss. However, few empirical studies have investigated the strength and form of the relationship between species and functional diversity (i.e., the presence of functional redundancy in ecological communities) in this context. In particular, we know little about how local extinctions in real communities might impact functional diversity. Here, we examined the relationship between species and functional diversity in plant communities along a grazing gradient across Mongolian rangeland ecosystems. We applied a recently described measure of functional diversity that incorporates species' dissimilarities defined from plant functional traits and tested several hypothesized forms of the relationship between species and functional diversity using linear and nonlinear modeling techniques. We found a significant sigmoid logistic relationship between species richness and functional diversity in relatively benign environmental conditions. This indicates high functional redundancy at low levels of species richness followed by a rapid increase at intermediate levels, until functional diversity reaches an asymptote at high levels (i.e., two-phase functional redundancy). In contrast, we generally observed a positive linear relationship between these parameters in relatively harsh environmental conditions, indicating low functional redundancy. Observed functional redundancy probably resulted from two factors, intrinsic redundancy in species' functional traits and extrinsic redundancy caused by nonrandom compositional change that is nonrandom with respect to functional traits. Lack of either intrinsic or extrinsic redundancy may result in low functional redundancy. Two-phase functional redundancy suggests that functional traits are abruptly lost from a community below a certain level of species richness, and a community then shifts into a contrasting state that has a few limited functional groups characterized by disturbance-resistant traits, as a consequence of disturbances such as

livestock grazing. This study represents a major step forward in predicting the consequences of livestock grazing on the functioning of Mongolian rangeland ecosystems.

**Key words:** arid and semi-arid rangelands; ecosystem functioning; functional diversity; functional redundancy; grazing history; intermediate disturbance hypothesis; Mongolia; plant functional trait; sigmoid logistic curve; species richness

## Introduction

The potential effects of biodiversity loss on ecosystem functioning and services have been a primary concern of ecologists during the last decade (Loreau et al. 2001, Hooper et al. 2005). Functional diversity, the value and range of functional traits of the organisms present in a given ecosystem (Diaz and Cabido 2001, Tilman 2001, Diaz et al. 2007a), is considered an important determinant of ecosystem functioning (Tilman et al. 1997, Chapin et al. 2000, Tilman 2000, Loreau et al. 2001).

The concept of functional redundancy is important to theories relating changes in ecosystem functioning to species loss (Lawton and Brown 1993, Rosenfeld 2002, Loreau 2004). There is a basic assumption that some species perform similar roles in communities and ecosystems, and redundant species can therefore be lost with minimal impact on ecosystem processes (Lawton and Brown 1993). In other words, redundant species are considered necessary to ensure ecosystem resilience to perturbation (Walker 1992, 1995). Determining the relationships between species diversity and functional diversity therefore has important implications for predicting the consequences of disturbance or management regimes on the functioning of a given ecosystem. However, our knowledge of the strength and the form of the relationship between species diversity and functional diversity (i.e., the presence of functional redundancy in ecological communities) is limited to a few studies (Naeem 2002, Flynn et al. 2009).

We would expect several hypothesized forms of the relationship between species and functional diversity (Fig. 1), depending on the extent of functional redundancy within the range of observed assemblages (Walker 1992, Naeem 1998, Micheli and Halpern 2005). Form A occurs when each species has a relatively unique trait, resulting in a positive linear relationship between species and functional diversity. This relationship indicates low

functional redundancy and that functional traits are accordingly lost or the dimensionality of trait space decreases from a system as species diversity declines (Micheli and Halpern 2005, Petchey et al. 2007). Alternatively, if new species have functional traits not already represented in the community, functional diversity may increase rapidly at lower diversity levels and subsequently increase at declining rates as functional redundancy increases (Fig. 1, form B). This high functional redundancy would indicate that the ecosystem functioning is robust with respect to changes in diversity (for the trait associated with pollination mechanism, see Mayfield et al. 2005). Another biological possibility is form C, which depicts functional redundancy at low levels of species diversity followed by a rapid increase at intermediate levels, until functional diversity reaches an asymptote at high levels (Fig. 1, form C). We would predict this form to occur when severe disturbance leads to the persistence of a subset of species having a limited number of shared functional traits. Species addition then leads to the addition of unique functions represented only at higher diversity levels. This form would indicate two-phase functional redundancy and that the functioning of the system is relatively stable with respect to perturbations above a certain level of species diversity, but that functional traits would be abruptly lost from a community below a certain level, and subsequently a community shifts into a contrasting state that has a few limited functional groups characterized by disturbance-resistant traits. No studies have provided empirical demonstrations of two-phase functional redundancy.

Petchey et al. (2007) suggested that two factors are particularly important in determining the extent of functional redundancy. First, intrinsic redundancy results from the patterns of functional similarity among species (Petchey et al. 2007). In rangeland ecosystems, theory and empirical evidence suggest that grazing resistance traits evolve in response to convergent selection by a long evolutionary history of grazing and arid climate (Milchunas et

al. 1988, Adler et al. 2004, 2005, Cingolani et al. 2005). Under such selective pressures, many species may have high intrinsic redundancy. Here, changes in species diversity will have little effect on functional diversity. In contrast, vegetation in which all species are rather unique will have low intrinsic redundancy, and changes in species diversity will cause changes in functional diversity. Second, extrinsic redundancy (or lack thereof) can result from nonrandom compositional change that is nonrandom with respect to functional traits (Petchey et al. 2007). In general, livestock grazing selectively affects particular species that have relatively high palatability to livestock (Pakeman 2004, Sasaki et al. 2005, Diaz et al. 2007b; but see Diaz et al. 2001). A typical example of extrinsic redundancy in rangeland ecosystems is that grazing often, but not always (see Milchunas et al. 1988, Olf and Ritchie 1998, Cingolani et al. 2005), suppresses potentially competitive-dominant species and favors diversity, with the additional increase of subordinate species (Collins et al. 1998, Bakker and Olf 2003, Sasaki et al. 2009) which may have high overlap in their functional traits resulted from abovementioned intrinsic redundancy; in this case, we would expect less change in functional diversity than if local extinctions occur randomly with respect to functional traits (but see Fonseca and Ganade 2001). In contrast, even in the context of intrinsic redundancy, loss of functionally important species (e.g., shrubs that have ecosystem engineering effects; Wright et al. 2006) may cause greater functional changes. Intrinsic and extrinsic redundancy might be mutually supportive components of the observed functional redundancy.

Most studies evaluating how changes in species diversity affect functional diversity have used removal experiments that target particular species thought to provide a key function, or simulation experiments that artificially or randomly assemble communities (Diaz et al. 2003). Although these studies provide useful insights into the functional role of particular species, they are necessarily artificial. Consequently, we know little about how local

extinctions in real communities might impact functional diversity (Petchey and Gaston 2002a, Rosenfeld 2002, Loreau 2004). It is therefore important to complement empirical analyses with studies that address the relationship between species and functional diversity in naturally assembling communities under a prevailing disturbance regime (Naeem and Wright 2003, Micheli and Halpern 2005, Petchey and Gaston 2006). In particular, possible significant nonlinearities in the response of functional diversity to changes in species diversity (represented by forms B and C in Fig. 1) would not be readily observed without using data that ensure a high sampling resolution and variation in species diversity along a full range of disturbance regimes.

Here, we examined the relationship between species and functional diversity in plant communities along a grazing gradient from livestock camps or sources of water, representing a spatial gradient in the accumulated impact of long-term livestock exposure (Andrew 1988), across Mongolian rangeland ecosystems. The data were collected expressly to identify ecological thresholds in vegetation changes along a grazing gradient (see Sasaki et al. 2008a), and as a result, the sampling resolution is high. We applied a recently described measure of functional diversity (Bady et al. 2005, Botta-Dukat 2005, De Bello et al. 2006, Lavorel et al. 2008) that incorporates species' dissimilarities defined from plant functional traits and tested for the above hypothesized forms of relationships between species and functional diversity (Fig. 1). By comparing the results from multiple ecological sites ("a distinctive kind of land with specific physical characteristics that differs from other kinds of land in its ability to produce a distinctive kind and amount of vegetation", as defined by the USDA National Resources Conservation Service 1997) that cover climatically and edaphically diverse environments, we can also examine which of the forms of diversity holds for different landscape positions to seek a general relationship between species and functional diversity

(Wellnitz and Poff 2001). This study complements the finding that some intermediate scales of grazing can play an important role in the maintenance of species diversity (Sasaki et al. 2009).

## **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. Based on meteorological data provided by Mongolia's Institute of Meteorology and Hydrology, Ministry of Nature and Environment, between 1993 and 2003 annual rainfall averaged around 210 mm (CV = 21%) at Kherlen Bayan Ulaan, 170 mm (28%) at Mandalgobi, and 140 mm (26%) at Bulgan. 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 types (Table 1; for more detailed characteristics of each site, see Sasaki et al. 2008a). Although livestock types differ somewhat among these landscapes, most livestock grazed across landscapes are sheep and goats. Detailed criteria and methods for selecting the ecological sites were described by Sasaki et al. (2008b). 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. (2009) quantified the landscape condition of each ecological site using an ordination technique (for the detailed result, see Sasaki et al. 2009) with the consideration of vegetation physiognomy and soil texture, and determined two types of landscape conditions (Table 1): (1) more benign environmental conditions typified by less erodible soil texture or lower pH (indicative of less potential wind erosion or environmental stress), and (2) more harsh environmental conditions typified by more erodible soil texture or higher pH (indicative of more potential wind erosion or environmental stress). As a consequence, the relative importance of grazing in creating species diversity varies as a function of landscape condition (Sasaki et al. 2009; see Discussion for the effect of this variation on our results); the relationships between species diversity and grazing were unimodal as predicted by the intermediate disturbance hypothesis (IDH) in more benign environmental conditions, whereas the IDH was not generally supported in more harsh environmental conditions. 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 form of the relationships between species and functional diversity.

### *Datasets*

We based this study on the data from Sasaki et al. (2008a, 2009). In our previous studies, we used a grazing gradient approach (Andrew 1988) and performed systematic sampling of vegetation by identifying and estimating the aerial cover of all species present within each quadrat on transects (five  $1 \times 1$  m subsample quadrats on each transect) placed at set distances along the grazing gradients (five gradient replicates were created in different directions) at each ecological site (for more detailed sampling procedures, see Sasaki et al. 2008a). Each plant species generally possesses a small stature (i.e., low aboveground biomass at its peak

time ranges from 20 to 130 g/m<sup>2</sup> across the areas; T. Sasaki, unpublished data), and sample units that consisted of five 1 m<sup>2</sup> subsample quadrats uniformly distributed along a transect could capture the variation in species diversity along a full range of grazing gradients (Sasaki et al. 2009). 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 gradient source; exceptions were the KH and KD ecological sites where transects were placed only up to 500 m from the gradient source, and the MH and BUP sites, where transects were also placed at 1500 and 2000 m from the gradient source. 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. The datasets consisted of a total of 3500 quadrats along 700 transects sampled at 12 to 16 sampling distances around 10 gradient sources, such as livestock camps or sources of water. From the survey, we recorded a total of 79 species, of which 9 were annual forbs, 46 were perennial forbs, 9 were grasses, and 15 were shrubs. Following analyses were based on these species.

### *Plant functional traits*

In analyses of functional diversity, traits must be linked to the function of interest (Petchey and Gaston 2002b, Petchey et al. 2004, 2007). We aimed to assess the integrated function of plant communities in rangeland ecosystems. We therefore selected functional traits of species that are considered key to determining their role within rangeland ecosystems, as well as their responses to livestock grazing, based on previous rangeland studies of trait responses to grazing over a range of environments (Pakeman 2004, De Bello et al. 2005, Diaz et al. 2007b). These included traits such as growth form, life history, shoot height, and leaf characteristics, for a total of 57 categories of 17 plant functional traits (Table 2). We compiled trait data from an existing Mongolian flora (Grubov 1982) and the information provided by Jigjidsuren and

Johnson (2003), and validated these data with field observations. Therefore the analysis was restricted to the range of information that was available for all the species found in this study.

Each option for the traits was recorded as a separate column of their category data (i.e., basically, with a value of 0 or 1 in a separate column of the trait's category). A “fuzzy coding approach” (Pakeman 2004, Bady et al. 2005, De Bello et al. 2005) was applied when species showed multiple membership in the different categories in which a trait is divided, and the sum of the scores for a species across that trait was set to 1. For example, a plant with a linear-lanceolate leaf shape would have a score of 0.5 as linear and 0.5 as lanceolate for the trait associated with leaf shape.

### *Numerical analyses*

Species richness has been used as the main measure in most studies linking species diversity to functional diversity (e.g., Petchey and Gaston 2002b, Mayfield et al. 2005, Micheli and Halpern 2005, Petchey and Gaston 2006, Petchey et al. 2007). However, the form of the relationship between species and functional diversity may vary among measures of species diversity. To assess the relative significance of variation in species richness and variation in species evenness for functional diversity within the concept of functional redundancy in the studied systems, we used both Simpson's diversity index (Magurran 2004) and species richness (*SR*) as a measure of species diversity. The results were consistent when we used the Shannon-Wiener index (Magurran 2004) for the index of species diversity. Thus, results are reported only for Simpson's diversity index (*SD*), which was calculated as follows for each transect:

$$SD = 1 - \sum_{i=1}^N P_i^2 \quad (1),$$

where  $N$  is the number of species found in each transect, and  $P_i$  is the proportional cover represented by the  $i$ th species (using pooled data from five subsample quadrats). The pairwise dissimilarity between species  $i$  and  $j$  ( $d_{ij}$ ) is numerically given as the species Euclidean distance:

$$d_{ij} = \sqrt{\sum_{k=1}^h (q_{ik} - q_{jk})^2} \quad (2),$$

where  $q_{ik}$  and  $q_{jk}$  are the scores for trait category  $k$  ( $1 \leq k \leq h$ ) for species  $i$  and  $j$ , respectively. Because previous studies (Petchey and Gaston 2002b, De Bello et al. 2006) suggested that non-orthogonality of traits affects the calculation of species distance, we excluded the trait of phanerophyte phenology from the analyses (i.e., a total of 16 traits were used) by checking the correlation matrix between the traits and calculating a principal component analysis (results not shown) on the base of a species  $\times$  trait matrix. We then calculated functional diversity ( $FD$ ) for each transect based on the adaptation of an index of species dissimilarity (Rao 1982, Bady et al. 2005, Botta-Dukat 2005, De Bello et al. 2006, Lavorel et al. 2008):

$$FD = \sum_{i=1}^N \sum_{j=1}^N d_{ij} P_i P_j \quad (3).$$

Thus,  $FD$  is the sum of the dissimilarity in the trait space among all possible pairs of species, weighted by the product of the species' relative abundance. We can better link changes in

ecosystem functioning with species loss by incorporating species' abundances into the index of functional diversity such as the one used in this study (Petchey and Gaston 2006). The calculated functional diversity is always one of many possible values (Petchey and Gaston 2006) because the number of traits used to calculate the index of functional diversity can affect the values of the index, and perception of functional redundancy changes accordingly (Petchey and Gaston 2002b). To confirm how robust our results were with respect to trait selection, we also calculated the *FD* with 4, 8, or 12 traits, with 10 randomized sets of traits at each of these numbers, and repeated the following model selection.

We examined the relationship between species diversity (Simpson's diversity or species richness) and functional diversity by fitting data to the following models:

$$FD = a + bS \quad (4),$$

$$FD = a + b \ln S \quad (5),$$

$$FD = a + b \exp(-c \times S) \quad (6),$$

$$FD = a + \frac{(b-a)}{1 + \exp(c-S)d} \quad (7),$$

where *S* is Simpson's diversity (*SD*) or species richness (*SR*), and *a*, *b*, *c*, and *d* are regression parameters. Constraints on the data from our sampling design (i.e., the potential correlation between sample transects) were controlled by adding the distance and gradient identity as random effects in these models (i.e., mixed-effect models; Pinheiro and Bates 2000).

Equations 4 and 5 linearly relate functional diversity to Simpson's diversity or species richness and to ln-transformed diversity or richness, and these models describe form A in Figure 1. Equation 6 is fitted to data using an exponential curve, and this model describes

form B in Figure 1. Equation 7 is fitted to data using a general sigmoid logistic curve, and this model describes form C in Figure 1. Models with the smallest Akaike's Information Criterion (AIC) were considered to provide the best fit (Johnson and Omland 2004). All statistical analyses were performed with the R software (version 2.7.0, R Development Core Team 2008).

## Results

The relationship between Simpson's diversity and functional diversity was best described as a positive linear (Eq. 4) or log-linear relationship (Eq. 5) in all ecological sites (Fig. 2), indicating low redundancy in the response of functional diversity to changes in Simpson's diversity. However, the form of the relationship between species richness and functional diversity differed among the sites (Fig. 3). The sigmoid logistic model (Eq. 7) provided the best fit for the data from the KH, KP, KD, MH, MT, MP, and BUP sites; the log-linear model (Eq. 5) provided the best fit for the BD site; and the linear model (Eq. 4) provided the best fit for the MD and BLP sites. The contrasting relationships among the sites probably reflected the differences in the relative importance of livestock grazing in creating species diversity as a function of relative landscape condition (see Table 1). The sigmoid logistic relationship generally can be observed under relatively benign environmental conditions and indicates a two-phase functional redundancy in the response of functional diversity to changes in species richness, whereas the positive linear relationship generally can be observed under relatively harsh environmental conditions and indicates low redundancy. These results were generally consistent when different numbers of traits were used to calculate functional diversity (results not shown), indicating that the observed relationships are robust despite considerable variation in the number of traits.

## Discussion

We showed that Simpson's diversity is positively and linearly related to functional diversity across all ecological sites (Fig. 2). The general interpretation for this relationship is that functional traits are lost accordingly from a system as Simpson's diversity declines (Fig. 1, form A). We suggest, however, that functional diversity may be a component of biodiversity captured by the variation of an index of species diversity that combines the measures of species richness and evenness (i.e., Simpson's diversity index, the Shannon-Wiener index) in the studied systems. Moreover, the theoretical model and empirical evidence (Nijs and Roy 2000, Polley et al. 2003) suggest that evenness of species' abundances influences ecosystem functioning independently of species richness. Our key finding highlights that species richness is a critical variable for the interpretation of functional redundancy (Petchey and Gaston 2002b). Under relatively benign environmental conditions, we found a sigmoidal logistic relationship between species richness and functional diversity, indicating functional redundancy at low levels of species richness followed by a rapid increase, until functional diversity reaches an asymptote at high levels (Table 1; Fig. 3). This suggests that functional traits are abruptly lost from a community below a certain level of species richness, and subsequently a community shifts into a contrasting state that has a few limited functional groups characterized by disturbance-resistant traits as a consequence of livestock grazing (Fig. 1, form C). In the following discussion, we primarily focus on the relationship between species richness and functional diversity within the concept of functional redundancy.

Two-phase functional redundancy under more benign environmental conditions (Table 1; Fig. 3) deviates from previous studies that reported low or no functional redundancy in coastal marine communities (Micheli and Halpern 2005) and in British avian communities

(Petchey et al. 2007). Although we cannot identify specific mechanisms underlying the observed relationships, two factors, intrinsic and extrinsic redundancy (*sensu* Petchey et al. 2007), appear to cause the observed functional redundancy. Theory and empirical evidence suggest that grazing resistance traits are well developed and common among plant species in arid regions with a long evolutionary history of grazing (Milchunas et al. 1988, Adler et al. 2004, 2005, Cingolani et al. 2005), such as Mongolia. Functional traits of species therefore may have converged and have high overlap; that is, intrinsic redundancy may exist in the vegetation. There may also be extrinsic redundancy because livestock grazing generally selectively impacts particular species that have relatively high palatability to livestock (Pakeman 2004, Sasaki et al. 2005, Diaz et al. 2007b; but see Diaz et al. 2001). Selective losses of competitive-dominant perennial grasses or forbs that are highly palatable with the additional increase of subordinate perennial grasses or forbs (Sasaki et al. 2009) that have high overlap in their functional traits probably explain high functional redundancy above a certain level of species richness. Below this level, functional complementarity may abruptly collapse and severe grazing impacts will then lead to the persistence of disturbance-tolerant annual forbs (Sasaki et al. 2008a) that share a limited number of functional traits, also resulting in functional redundancy.

In contrast, Micheli and Halpern (2005) suggested that resource partitioning among component species and low overlap in their functional traits (a lack of intrinsic redundancy), combined with fisheries selectivity for species in functional groups that are not species rich (a lack of extrinsic redundancy), may result in low redundancy. Petchey et al. (2007) also suggested that little redundancy intrinsic to the bird species' functional relationships (a lack of intrinsic redundancy) and the randomness of extinctions and colonizations with respect to functional traits among bird assemblages (a lack of extrinsic redundancy) may contribute to

the presence of no redundancy. We also found low redundancy under harsher environmental conditions (Table 1; Fig. 3). At the sites characterized by sandy soils and high erodibility (i.e., potential wind erosion in MH and BLP sites; Table 1), losses of shrubs that are preferred by livestock and of their associated ecosystem engineering effects (Wright et al. 2006) that may favor the establishment of both perennial and annual herbaceous species (Sasaki et al. 2009) probably cause greater changes in functional diversity (a lack of extrinsic redundancy), even in the context of the abovementioned intrinsic redundancy. Sasaki et al. (2009) suggested that species occurring at the sites characterized by higher pH (MD and BD sites; Table 1) are particularly suited to strong abiotic stress. These species generally have low palatability (Sasaki et al. 2008b) and there may be few differences among species with regard to preference by livestock, and thereby the patterns of species loss appear to be rather random (a lack of extrinsic redundancy), probably resulting in low redundancy. However, our result at the MH site provided a notable exception to this pattern: the relationship between species richness and functional diversity was best described as a sigmoid logistic relationship. There is assumed to be a finer continuum along the extent of functional redundancy in plant communities along a grazing gradient within a broad range of changing landscape conditions. Overall, the arguments presented here suggest that intrinsic and extrinsic redundancy may mutually contribute to the extent of functional redundancy in ecological communities.

Previous studies (Fonseca and Ganade 2001, Petchey and Gaston 2002b, Micheli and Halpern 2005, Petchey et al. 2007) suggested that functional redundancy decreases with increasing numbers of functional traits considered. Although it is possible that other traits that we cannot include due to lack of information are important, a well-informed pragmatic *a priori* decision must be made in order to make progress (Petchey et al. 2007). Our results were based on functional traits known to be directly related to functional roles of plant species

within rangeland ecosystems as well as their responses to livestock grazing (Pakeman 2004, De Bello et al. 2005, Diaz et al. 2007b), and they were robust with respect to considerable variation in the number of traits used to calculate functional diversity.

Several caveats are associated with our sampling design. It may be possible that we could not observe the two ends of two-phase functional redundancy if we could not sample vegetation efficiently (i.e., linear relationships would artificially be observed). However, our datasets ensured a high sampling resolution (Sasaki et al. 2008a) and variation in species diversity along a full range of grazing gradients (Sasaki et al. 2009). Moreover, the landscape condition–dependent generality of the observed functional redundancy was generally clear even though the reference distances were *a priori* defined and systematic sampling procedures performed, indicating only a small possibility of sampling artifact. Our results are also limited by a snapshot sampling design (i.e., sampling each quadrat only once), which was used to allocate a much greater sampling effort to a larger number of widely spaced ecological sites. Although this limitation is also largely supported by some generality, more prolonged observations are needed to address temporal changes in functional diversity caused by temporal changes in species richness and composition in a changing climate.

Evidence for strong nonlinearities in the response of functional diversity to changes in species richness may closely be linked with the threshold behavior of vegetation in response to grazing (i.e., the existence of ecological threshold; Friedel 1991, Laycock 1991, van de Koppel et al. 1997, Sasaki et al. 2008a). Empirical demonstrations of a direct linkage between the catastrophic collapse in functional diversity and the ecological threshold as well as ecological mechanisms underlying these nonlinearities remain a future challenge, but they should be an ecological research and management priority for comprehensive understanding of ecosystem functioning and sustainable use of ecosystem services (Hooper et al. 2005).

For the application of functional redundancy to land management, as advocated by Walker (1992), it is a crucial step to address explicitly how species diversity itself is maintained in the systems (Petchey and Gaston 2002a, Rosenfeld 2002, Loreau 2004). Our previous work showed that the relationships between species diversity and grazing were consistent with the intermediate disturbance hypothesis (IDH), and maximum diversity was observed at some intermediate scales of grazing under benign environmental conditions, whereas the IDH generally was not supported under harsh environmental conditions (Sasaki et al. 2009). Our findings complement management strategies that incorporate the concept of IDH (Sasaki et al. 2009) in the context of retaining functional complementarities and possibly ecosystem functioning in rangelands across landscapes that have benign environmental conditions, which support extensive areas of grassland physiognomy (Table 1) that are probably of greater value for providing forage resources. Although the confounding causal relationship between multiple interacting disturbances and species diversity under harsh environmental conditions (Sasaki et al. 2009) limits the practical management implications, it can be advised for land managers to recognize that the significant loss of dominant shrubs preferred by livestock and their associated ecosystem engineering effects (Wright et al. 2006) may cause greater functional change under potential wind erosion (Rietkerk et al. 2004, Kefi et al. 2007). Even if the relative importance of grazing in creating species diversity is low under strong abiotic stress, severe grazing impacts still lead to the drastic decrease in species diversity (Sasaki et al. 2009), resulting in the loss of functional traits. Thus, our study provides critical insights into bridging the gap between ecological theory of functional redundancy and sustainable management of rangeland ecosystems.

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**Table 1.** Characteristics of each ecological site in Mongolia and the relative landscape condition of each site.

Study area, site code	Landscape position	Location	Vegetation physiognomy	Soil texture†	pH†	Relative landscape condition‡
Kherlen Bayan Ulaan						
KH	Hill	47°09'N, 109°17'E	Grassland	Loam	6.91	Benign
KP	Pediment	47°14'N, 108°50'E	Grassland	Loam	6.53	Benign
KD	Depression	47°04'N, 108°46'E	Grassland	Sandy loam	7.00	Benign
Mandalgobi						
MH	Hill	45°47'N, 106°11'E	Shrubland	Sand	7.67	Harsh (potential wind erosion)
MT	Tableland	45°41'N, 106°27'E	Grassland	Sandy clay loam	7.86	Benign
MP	Pediment	45°41'N, 106°10'E	Grassland	Sandy loam	7.53	Benign
MD	Depression	45°38'N, 106°16'E	Halophytic shrubland	Sandy loam	8.79	Harsh (salinized)
Bulgan						
BUP	Upper pediment	43°54'N, 103°30'E	Grassland	Sandy clay loam	7.83	Benign
BLP	Lower pediment	44°14'N, 103°38'E	Shrubland	Sand	7.94	Harsh (potential wind erosion)
BD	Depression	44°18'N, 103°35'E	Halophytic shrubland	Sandy loam	8.21	Harsh (salinized)

† The data are based on mean values from soil samples along grazing gradients at each site (source for the data: Sasaki et al. 2009).

‡ Sasaki et al. (2009) quantified the landscape condition of each ecological site using an

ordination technique (for the detailed result, see Sasaki et al. 2009) with the consideration of vegetation physiognomy and soil texture, and determined two types of landscape conditions: (1) more benign environmental conditions typified by less erodible soil texture or lower pH (indicative of less potential wind erosion or environmental stress), and (2) more harsh environmental conditions typified by more erodible soil texture or higher pH (indicative of more potential wind erosion or environmental stress).

**Table 2.** Plant functional traits and their categories used in the analyses

Plant functional trait	Trait categories	Multiple membership†
1. Growth form	Grasses; Forbs; Subshrubs (woody just at the base); Shrubs	No
2. Life history	Annual; Biennial; Herbaceous perennial; Woody	Yes
3. Leguminosae	Legume; Not legume	No
4. Lateral spread	Erect (solitary); Tussock; Branched; Prostrate	Yes
5. Shoot height	height < 5 cm; height 5–10 cm; height 10–20 cm; height 20–50 cm; height > 50 cm	No
6. Thorns	With thorns; No thorns	No
7. Leaf distribution	Regularly distributed; Rosette; Scarcely foliated	No
8. Photosynthetic pathway	C3 plants; C4 plants	No
9. Relative preference by livestock	High; Medium; Low	No
10. Phylogenetic group	Monocotyledon; Dicotyledon	No
11. Phanerophyte phenology	Evergreen; Deciduous; Not phanerophyte	No
12. Leaf hairs	With hairs; No hairs	No
13. Leaf succulence	Succulent; Not succulent	No
14. Leaf margin	Entire margin; Toothy margin; Revolute margin; Thorn margin	Yes
15. Leaf shape	Linear; Lanceolate; Elliptic; Ovate or obovate; Oblong; Round	Yes
16. Leaf form	Entire; Lobed; Pinnatisect; Pinnate; Multipinnate	Yes
17. Leaf attachment	Opposite; Alternate; Decussate; Fasciculate	Yes

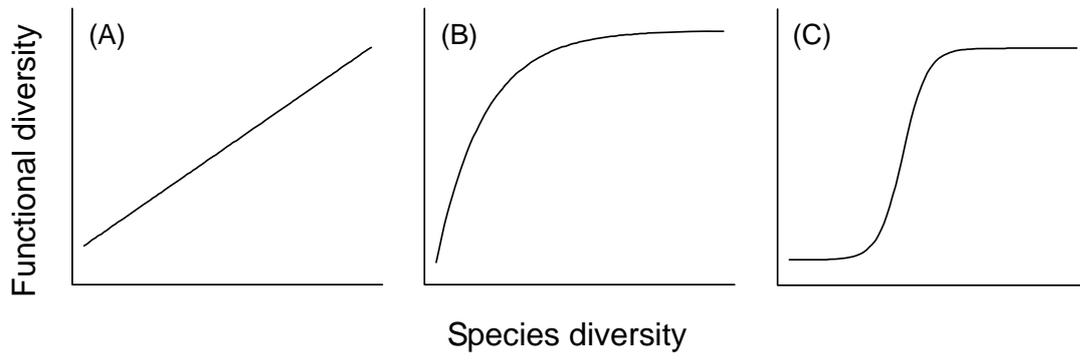
† Multiple membership means that some species belong to more than one trait category.

**Figure legends**

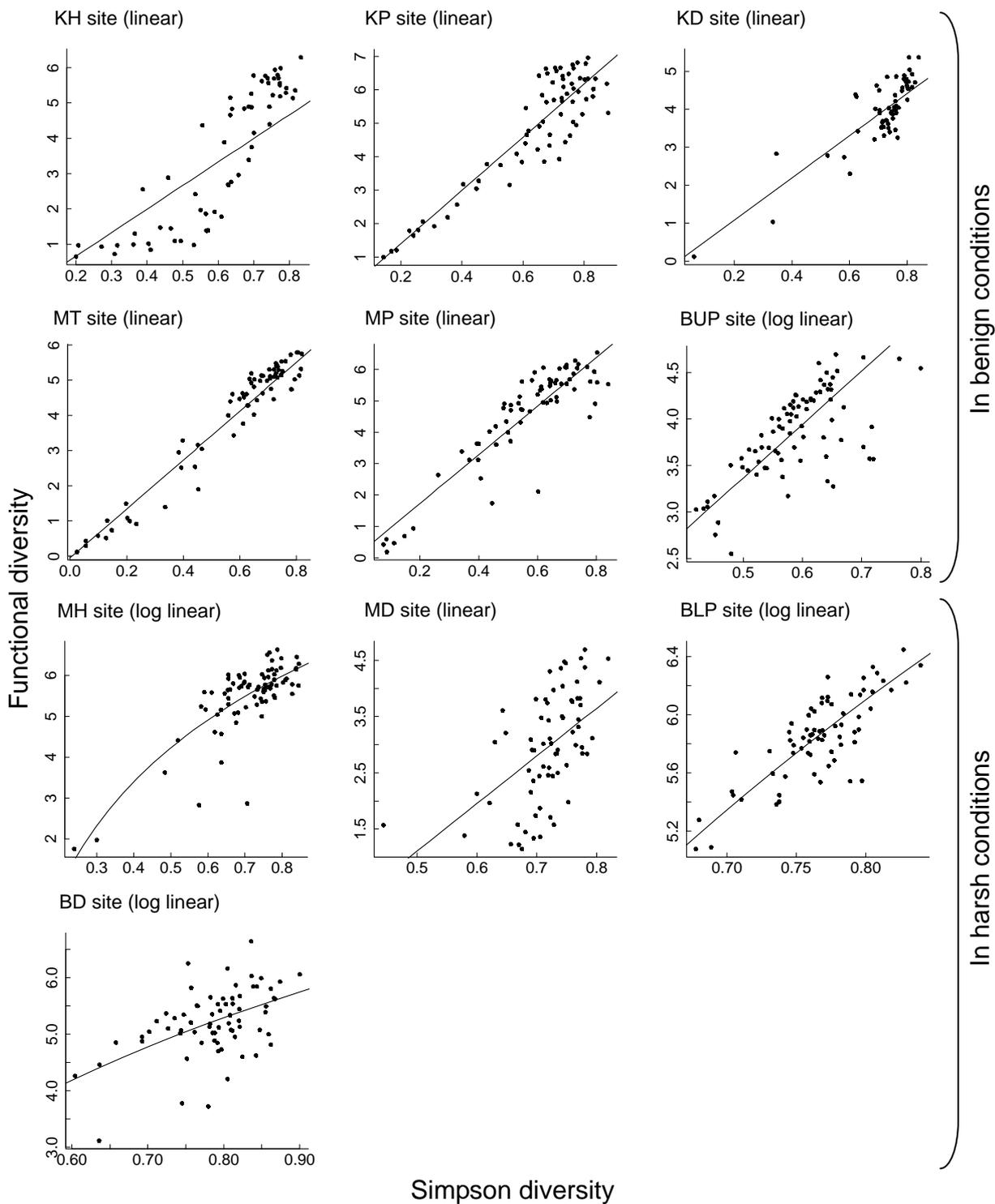
**Fig. 1.** The possible relationships between species and functional diversity. In form A, functional diversity increases linearly with increasing species diversity, regardless of diversity level. In form B, functional diversity increases at declining rates with increased species diversity and reaches an asymptote at high diversity levels. In form C, functional redundancy at low levels of species diversity is followed by rapid increase at intermediate levels, until functional diversity reaches an asymptote at high levels.

**Fig. 2.** The relationships between Simpson's diversity index and functional diversity in plant communities along a grazing gradient at 10 ecological sites. The relationship was best described as a positive linear relationship (Eqs. 4 or 5) in all ecological sites. Landscape conditions of the ecological sites were also indicated (relatively benign and harsh environmental conditions, respectively; Table 1).

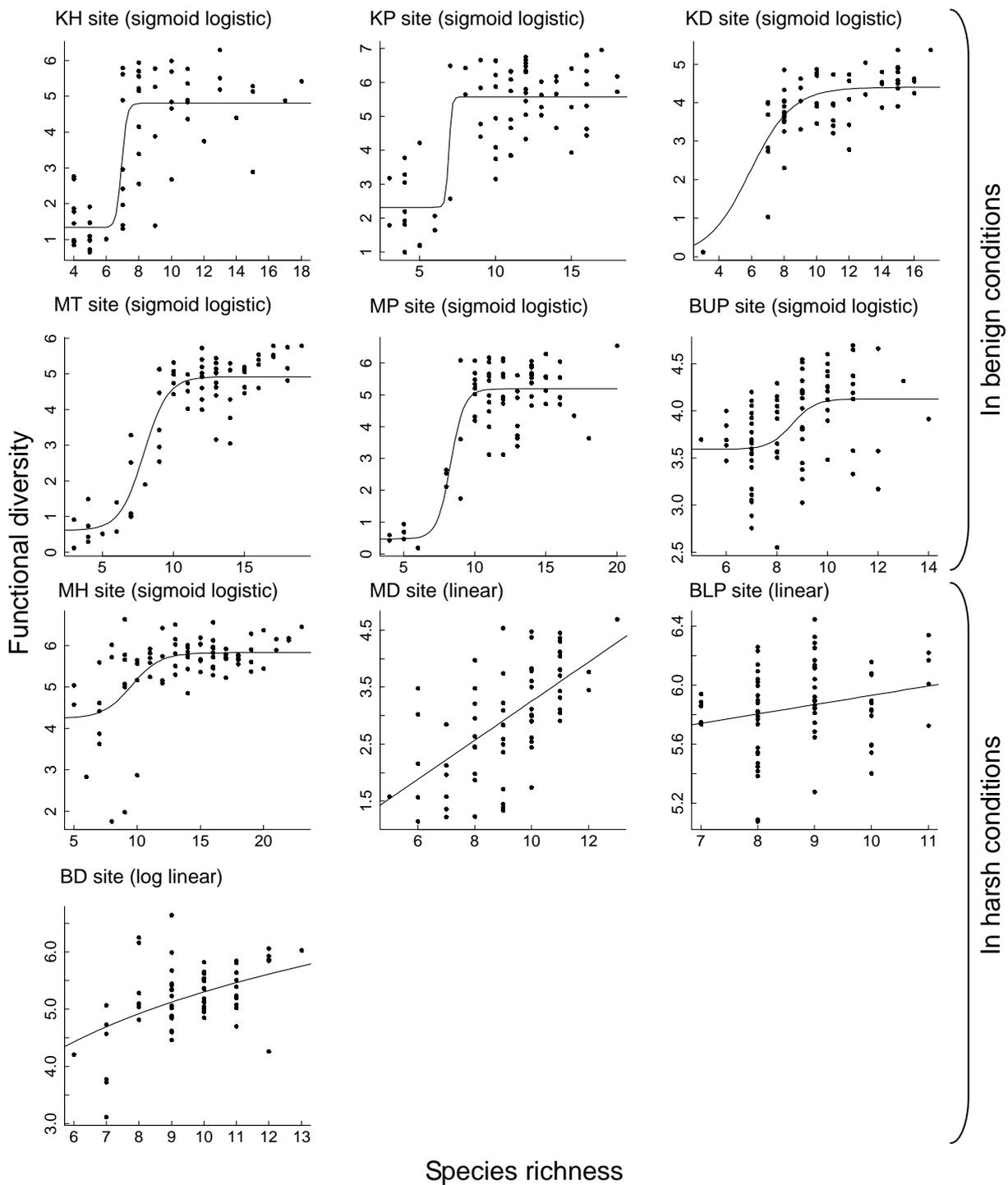
**Fig. 3.** The relationships between species richness and functional diversity in plant communities along a grazing gradient at 10 ecological sites. The sigmoid logistic relationship (Eq. 7) generally can be observed under relatively benign environmental conditions and indicates a two-phase functional redundancy, whereas the positive linear relationship (Eqs. 4 or 5) generally can be observed under relatively harsh environmental conditions and indicates low redundancy. Landscape conditions of the ecological sites were also indicated (relatively benign and harsh environmental conditions, respectively; Table 1). The contrasting relationships among the sites probably reflected the differences in the relative importance of livestock grazing in creating species diversity as a function of relative landscape condition of each site (Sasaki et al. 2009).



**Fig. 1 (T. Sasaki et al.)**



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



**Fig. 3. (T. Sasaki et al.)**