Land use affects the relationship between species diversity and productivity at the local scale in a semi-arid steppe ecosystem

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Summary

1. The accelerating extinction rate of plant species and its effect on ecosystem functioning is a hotly debated topic in ecological research. Most research projects concerning the relationship between species diversity and productivity have been conducted in artificial plant communities, with only a few in natural ecosystems. In this study we examined the relationship between species diversity and above-ground net primary productivity (ANPP) over two consecutive growth seasons (2004 and 2005) in a semi-arid steppe ecosystem of northern China, that were subjected to different land uses.

2. Land use affected the relationship between species diversity and ANPP in this semi-arid steppe ecosystem. Exclusion of grazing without or with biomass removal by mowing increased ANPP, species richness and species diversity compared with free grazing; the effect was reflected mainly as enhanced importance of the perennial forbs functional group in terms of their relative contributions to ANPP, plant cover and plant abundance.

3. Many mechanisms regulate the relationship between species diversity and productivity. Differential effects of anthropogenic activities on biodiversity and ecosystem functioning greatly complicate the analysis of such relationships. On grazing-exclusion sites the relationship between ANPP and species richness can be best described as an exponential growth function ($R^2 = 0.99$, $P < 0.001$, $n = 24$); whereas on the free-grazing site the relationship takes the form of exponential decay ($R^2 = 0.96$, $P < 0.001$, $n = 24$).

Our study concludes that the mode and severity of disturbance are important factors for interpreting the relationship between species diversity and productivity in semi-arid steppe ecosystems.

Key-words: biodiversity, land use, local scale, productivity, steppe ecosystem

Introduction

Worldwide loss of biodiversity and its consequences for ecosystem functioning have emerged recently as a hotly debated topic in ecological research (Troumbis 2001; Wardle 2001; Loreau, Naeem & Inchausti 2002). In past decades losses of biodiversity have occurred at an unprecedented scale, with the current global extinction rate estimated at 100–1000 times greater than prehuman levels (Pimm et al. 1995). Widespread stressors, such as land-use change, fragmentation, biotic invasions and climate change, are considered to be the major drivers of biodiversity losses (Chapin et al. 1997).

Interest in the effects of biodiversity on ecosystem stability and functioning has been heightened by the rapidly accelerating rate of species extinctions. A loss of biodiversity could significantly affect the functioning of many terrestrial ecosystems (Ehrlich & Ehrlich 1981; Schlapfer & Schmid 1999). Manipulation experiments on the relationship between plant diversity and ecosystem functioning (productivity, nutrient cycling, decomposition, nitrogen mineralization rate, nitrate leaching) have indicated that (i) more diverse plant communities are more productive; and (ii) more diverse ecosystems could make full use of the most limiting nutrient, soil mineral nitrogen, and lead to reduced leaching losses of this vital nutrient (Naeem et al. 1995; Naeem et al. 1996).

Although there have been extensive research efforts, controversy over the diversity–productivity relationship
in natural communities still looms large. Positive relationships between plant species (or functional group diversity) and productivity (or other ecosystem processes) have been reported in a number of experimental studies (Tilman & Downing 1994; Symstad et al. 1998; Loreau et al. 2002). Detailed evidence from terrestrial habitats, particularly grasslands, suggests that productivity is often a non-linear, concave function of the richness of species or functional groups (Waid et al. 1999). Mittelbach et al. (2001) found that, in 65% of the studies they examined, the relationship between biodiversity and productivity was described by a concave down function. In most recent laboratory and field experiments the effect of biodiversity on productivity was tested using artificial plant communities, where different diversity levels were established by drawing plant species from a random species pool (Kahmen et al. 2005). These experiments under artificial conditions are, by and large, constrained in their capacity for extrapolation to natural ecosystems. Cardinale, Nelson & Palmer (2000) noted that the cause of the diversity–productivity relationship could change with environmental context. In many manipulative experiments, the simplification of environmental conditions for testing specific hypotheses could unknowingly eliminate the very factors regulating the diversity–productivity relationship that exists in natural ecosystems. For example, the relatively homogenized soils in artificial grassland ecosystems could result in underestimation of the role of niche differentiation at a smaller spatial and/or temporal scale (He et al. 2003).

While several researchers have suggested that causal relationships exist between diversity and ecosystem functioning, particularly between species diversity and above-ground productivity (Naeem et al. 1994, 1995), others believe that the key functional attributes or traits of dominant species in plant communities and the composition of functional types play a more prominent role than simply species richness in driving ecosystem properties (Hooper & Vitousek 1997; Berendse 1998; Grime 1998). Based on data from a 24-year grazing-exclusion study, Bai et al. (2004) reported a causal relationship between species diversity and productivity in a typical steppe of the Inner Mongolian Plateau, northern China. This finding, however, was questioned by Wang et al. (2005) and Guo (2005), who argued that the roles of spatial heterogeneity and functional groups were not sufficiently reflected in the analyses of Bai et al. (2004). In natural environments, spatio-temporal heterogeneities of resources are ubiquitous features that regulate both richness and the distribution of biomass among taxa (Petratius, Latham & Niesenbaum 1989). Stochastic environmental fluctuation and disturbance have been found to affect grassland biodiversity (McNaughton 1983; Collins 1987) and the spatial structure of communities (Seabloom & Richards 2003).

Research in the semi-arid Mediterranean region has provided rich information regarding the effects of land use on plant diversity in semi-arid grassland ecosystems (Osem, Perevolotsky & Kigel 2002; Bonet 2004; Armas & Pugnaire 2005). Bonet (2004) found that land-use history played an important role in determining the ordination of communities, and that previous cropping influenced the pathway of succession in a semi-arid Mediterranean region. In arid and semi-arid environments, competition and facilitation can both affect the composition and structure of plant communities (Armas & Pugnaire 2005; Michalet 2006), and spatial variation in the balance of the two factors may, to a large extent, determine diversity–productivity relationships at a local scale. Osem et al. (2002) showed that diversity of annual plant community could be determined by interactions between grazing and small-scale spatial and temporal variation in primary productivity. Despite the spatially wide occurrence and significant regional importance, the Eurasian steppe ecosystems have been largely under-represented in the global analysis of diversity–productivity relationships.

Steppe ecosystems under natural conditions are constantly subjected to disturbance and environmental perturbation. The intensified anthropogenic activities in recent history have had a great impact on both the structure and functioning of the semi-arid steppe ecosystems of northern China. Some land-use practices, such as hay harvesting by mowing, have been demonstrated to cause shifts in the composition of plant functional groups and consequently to lead to changes in ecosystem functioning (Bao, Li & Zhong 2004). To determine further how land use affects the diversity–productivity relationship in semi-arid steppe ecosystems, we conducted surveys on plant species diversity and community productivity over two growth seasons (2004–05) on sites of free grazing and grazing exclusion, with and without hay harvesting, in Inner Mongolia, northern China. We hypothesized that the mode and intensity of disturbance due to anthropogenic activities contributed to the relationship between species diversity and community productivity.

Materials and methods

STUDY SITES AND EXPERIMENTAL DESIGN

This study was conducted in Duolun County of Inner Mongolia (latitude 41°46’–42°39’ N, longitude 115°50’–116°55’ E, elevation 1150–1800 m a.s.l.), northern China. The long-term mean annual, minimum and maximum air temperatures for the area are 1·6, −18·3 and 18·7 °C. Mean annual precipitation is 385 mm (67% falls between June and August). The soil in the top 40-cm layer is classified as chestnut (FAO-UNESCO 1974), below 40 cm a mixture of sandy soil and gravels. Vegetation of the region consists predominantly of common grassland plants of the steppe zone including Stipa krylovii Roshev., Agropyron cristatum (L.) Gaertner, Allium bidentatum Fisch. ex Prokh. & Ikon. -Gal., Artemisia frigida Willd., etc.
Traditional land uses in the study area have been a mixture of livestock grazing and farming. From the late 1950s to the late 1970s, the land uses of the region were managed under communal systems subject to strict government regulations. During the period 1970–77, Duolun County experienced rapid expansion of farmlands at the expense of grasslands (Baoyin & Liu 2001). The economic reforms and open policy since 1978 have resulted in private ownership of lands and free land-use practices by the locals. Consequently, the area was subjected to intensive farming, grazing and land-use changes that reduced the areas of grasslands (Liu & Tong 2003; Zhan et al. 2004). The extremely intensified land uses placed tremendous pressure on the regional grasslands, causing severe land degradation and extreme levels of desertification (Liu & Tong 2003; You et al. 2003; Zhan et al. 2004). In recognition of the environmental problems caused by overexploitation of the lands in this agro-pastoral ecotone, in 2000 the local government imposed a policy banning livestock grazing, and sought alternative land uses that could help sustain the regional land productivity and economy. Hay production has been experimented with as one of the land-use types potentially suitable for the region. However, some areas are still used for sheep and cattle grazing.

Three study sites were selected based on major land-use types and pre-existing experimental setups in the area, which included uncontrolled or free-range grazing (FG); grazing exclusion without biomass removal (GE); or grazing exclusion with biomass removal by mowing ≈ 6 cm above the ground surface (MW). The FG site had been heavily grazed since 1979, with an estimated 75% of above-ground biomass consumed by livestock (mainly cattle and sheep) each year (Wang, Wang & Chen 2003). The GE site was established in 2001 by constructing a fence around 21 ha of previously grazed grassland. The MW site, which also was previously grazed grassland, had been subjected to mechanical mowing in late August each year since 2001, with ≈80% of above-ground biomass harvested as forage. Before 1978 the study area was not utilized/managed and the major disturbance resulted mainly from antelope and rabbit (occasionally sheep) grazing, or wildfire.

Our study area is in an agro-pastoral zone, where interannual variation of climate is relatively small. For the past 10 years annual precipitation typically varied between 350 and 450 mm, and mean temperatures varied from around −15 °C in January (minimum) to ≈20 °C in July (maximum). The climatic conditions in both 2004 and 2005 at our study sites were close to the long-term average (data not shown).

MEASUREMENTS

Four 30 x 30-m plots were established on each site, representative of a land-use type for measurements of above-ground biomass, plant abundance, species composition and richness, and cover by plant functional groups. Those plots were located systematically along the north–south transect, taking into consideration the topography and spatial coverage of the given land-use type at our study sites. Most studies concerning productivity in the steppe ecosystems of the region have been based on a plot size of 10 x 10 m. In this study we increased our plot size to 30 x 30 m, necessary to account for the potential spatial heterogeneity of vegetation pattern and resources based on our knowledge of the study area. The plant functional group was defined as by Bai et al. (2004) on the basis of life form: annuals and biennials (AB); shrubs and semishrubs (SS); perennial rhizome grass (PR); perennial bunchgrass (PR); perennial forbs (PF).

We determined the above-ground net primary production (ANPP) by measuring the peak biomass, as our study sites contained mostly herbaceous plants with above-ground tissues that die back annually. All living tissues were clip-harvested by species in three replicated 1 x 1-m quadrats on each plot between 15 and 25 August in 2004 and 2005, respectively, and oven-dried at 65 °C to constant weight (≈48 h). The above-ground biomass was measured by individual species, and grouped into categories of total community productivity in the steppe ecosystems of the region. The ANPP of shrubs and semishrubs (such as Artemisia frigida and Thymus serphyllum) was determined by clip-harvesting subsamples at beginning (late April) and peak growth seasons (mid-August) and taken as the difference between the two harvests.

Several terms were used for describing the biodiversity traits of plant communities: plant abundance, diversity (species richness), evenness (Pielou index), and Shannon–Wiener index of species. The Pielou Evenness index (E) was calculated as:

\[
E = \left(-\sum P_i \ln P_i\right)/\ln S
\]

(eqn 1)

where \(P_i\) is the relative importance value of species \(i\), and \(S\) the total number of species. The Shannon–Wiener index was calculated as:

\[
H = -\sum_{i=1}^{S} P_i \ln P_i
\]

(eqn 2)

On each site, species frequencies were measured from 25 randomly placed quadrats (0.5 x 0.5 m) by recording the presence of species within each quadrat. Species frequency was expressed as the proportion of quadrats containing a given species (Duncan et al. 1997).

**Statistical Analysis**

ANOVA was used to analyse different treatment effects (land-use types). Means of the main effects were compared using Duncan’s multirange test at \(P < 0.05\). The relationships of ANPP with all variables of biodiversity were examined using Pearson’s correlation analysis. All statistical analyses were performed using SPSS (ver. 11.0) software.
Results

Land use affected both biodiversity and ANPP in the semi-arid steppe ecosystem studied. The values of Pielou and Shannon–Wiener indices and species richness were significantly higher on both types of grazing-exclusion plot (GE and MW) than on the FG plots, while the MW site had a markedly higher ($P < 0.05$) level of plant abundance than the other two land-use types (GE and FG) (Table 1). The ANPP averaged (in g m$^{-2}$ year$^{-1}$) 199 ± 9 on the GE site, 144 ± 6 on the MW site, and 96 ± 5 on the FG site.

Pearson’s correlation analysis revealed a significant ($P < 0.05$) and positive correlation between ANPP and Shannon–Wiener index on the MW site, and a significant ($P < 0.05$) but negative correlation on the FG site (Table 2). The correlation between ANPP and species richness was significant ($P < 0.01$) across all three land-use types, with a positive correlation on the GE and MW plots, but a negative correlation on the FG plots. As illustrated in Fig. 1, the relationship between ANPP and species richness can be best described as an exponential growth function on the GE and MW plots, and as an exponential decay function on the FG plots.

The species composition of plant communities varied with land-use type. In total 31 and 34 species were found on the GE and MW plots, and 27 species on the FG plots (Table 3). Most of these species belonged to the PF functional group.

Compared with FG plots, the GE and MW plots were characterized by significantly ($P < 0.05$) greater frequency of Liliaceae species (Allium bidentatum, Allium tenuissimum, Allium neriiflorum, Allium ramosum, Allium senescens), most of which grow close to the ground surface with low productivity. The FG plots had significantly ($P < 0.05$) greater numbers of legume species.
species (Oxypolis glabra, Melisitus ruthenica, Astragalus scaberrimus, Astragalus galactites), and a higher frequency of the rhizomatous species, especially Carex duriuscula, than the other two sites. Two plant species, Setaria viridis and Koeleria cristata, were found exclusively on the FG plots with relatively high frequencies, whereas Oroystachys fimbriatus, Echinops latifolius and Phloxon mungolica were exclusive to the MW plots with low frequencies (Table 3). Within the AB functional group, species numbers were, on average, 75 and 40% higher, respectively, on MW plots than on GE and FG plots.

The GE and MW plots differed from the FG plots by displaying greater importance of PF species and lesser importance of SS species in terms of relative contributions to ANPP, plant abundance and cover. On both GE and MW plots, above-ground production was comprised mainly of the PB, PF and SS functional groups, PF being the most dominant; whereas on the FG plots, above-ground production was predominantly and equally comprised of the PB and SS functional groups (Fig. 2). On the FG plots, above-ground production of the PB functional group increased with species richness, whereas above-ground production of the SS functional group decreased with species richness (Fig. 3). The AB functional group contributed a meaningful fraction of total ANPP only on GE plots. For plant abundance, the PF functional group was the next to highest, followed by the PR and PB functional groups (Fig. 4). On the FG plots, the PR functional group ranked highest and PB next to highest, followed by PF. The PF functional

| Plant functional group          | Species                  | Land-use type* |
|--------------------------------|--------------------------|----------------|
|                               |                          | GE  | MW  | FG  |
| Annual and biennial            | Setaria viridis          | 0 a | 0 a | 24 ± 3 b |
|                                | Dactylodon micranthus    | 3 ± 2 a | 8 ± 3 a | 3 ± 2 a |
|                                | Salsola collina          | 60 ± 7 b | 4 ± 2 a | 8 ± 3 a |
|                                | Chenopodium aristatum    | 9 ± 3 a | 25 ± 4 b | 12 ± 3 a |
|                                | Chenopodium glaucum      | 0 a | 1 ± 1 a | 3 ± 2 a |
|                                | Fagopyrum tataricum      | 0 a | 1 ± 1 a | 0 a |
|                                | Gentiana squarrosa       | 4 ± 2 a | 11 ± 3 b | 0 a |
|                                | Orostachys fimbriatus     | 0 a | 4 ± 2 b | 0 a |
| Perennial rhizome grass        | Agropyron microsorum     | 66 ± 5 b | 39 ± 5 a | 57 ± 4 b |
|                                | Leymus chinensis         | 11 ± 3 b | 3 ± 2 a | 3 ± 3 a |
|                                | Aneurolepidium secalinum | 0 a | 0 ± 2 a | 1 ± 1 a |
| Perennial bunchgrass           | Cleistogenes squarrosa   | 91 ± 3 ab | 98 ± 2 b | 83 ± 4 a |
|                                | Stipa krylovii           | 100 a | 100 a | 100 a |
|                                | Poa angustifolia         | 1 ± 1 a | 2 ± 2 a | 0 a |
|                                | Koeleria cristata        | 0 a | 0 a | 30 ± 5 b |
| Perennial forb                 | Oxypolis glabra          | 3 ± 2 a | 5 ± 2 a | 30 ± 3 b |
|                                | Carex duriuscula         | 46 ± 4 a | 82 ± 4 b | 96 ± 2 c |
|                                | Melisitus ruthenica      | 10 ± 3 a | 7 ± 2 a | 36 ± 4 b |
|                                | Astragalus scaberrimus   | 36 ± 6 b | 8 ± 2 a | 65 ± 3 c |
|                                | Astragalus galactites    | 0 a | 1 ± 1 a | 23 ± 2 b |
|                                | Heteropappus alatusius   | 47 ± 5 b | 31 ± 5 a | 41 ± 5 ab |
|                                | Echinops latifolius      | 0 a | 3 ± 3 a | 0 a |
|                                | Potentilla acauli        | 6·7 ± 0·6 b | 7·9 ± 0·5 b | 4·8 ± 0·6 a |
|                                | Potentilla bifurca       | 20 ± 4 b | 27 ± 3 b | 0 a |
|                                | Potentilla tanacetifolia | 1 ± 1 a | 1 ± 1 a | 12 ± 3 b |
|                                | Potentilla betoniccefolia| 1 ± 1 a | 0 a | 0 a |
|                                | Allium bidentatum        | 98 ± 1 b | 99 ± 1 b | 2 ± 1 a |
|                                | Allium tenuissimum       | 82 ± 3 b | 93 ± 3 c | 8 ± 2 a |
|                                | Allium eriniflorum      | 34 ± 6 b | 30 ± 5 b | 9 ± 2 a |
|                                | Allium ramosum           | 4 ± 2 a | 44 ± 2 b | 0 a |
|                                | Allium senescens         | 10 ± 3 b | 54 ± 2 c | 0 a |
|                                | Phloxon mungolica        | 0 a | 4 ± 2 b | 0 a |
|                                | Iris tenfolia            | 19 ± 4 b | 17 ± 2 b | 0 a |
|                                | Thalictrum petaloidem    | 7 ± 3 a | 7 ± 2 a | 2 ± 1 a |
|                                | Silene jenitenssis      | 1 ± 1 a | 2 ± 1 a | 1 ± 1 a |
|                                | Dianthus chinensis       | 1 ± 1 a | 5 ± 3 a | 0 a |
|                                | Stellera chamaejasme     | 1 ± 1 a | 2 ± 1 a | 2 ± 1 a |
| Shrub and semishrub            | Artemisia frigida        | 100 a | 100 a | 100 a |
|                                | Thymus serphyllum        | 1 ± 1 a | 0 a | 6 ± 2 b |

*GE, grazing exclusion without biomass removal; MW, grazing exclusion with biomass removal by mowing in August; FG, free grazing.

Values designated by the same letter are not significantly different at $P = 0.05$. 
group on the MW plots had much higher abundance than on plots of the other two land-use types (Fig. 4).

Plant cover was almost the same for the PB, PF and SS functional groups on the GE plots, and about equal for the PF and SS functional groups on the MW plots, but was dominated mainly by the SS functional group on the FG plots (Fig. 5).

**Discussion**

The current study demonstrated that, at the local scale, the relationship between biodiversity and productivity could be strongly affected by the mode and severity of disturbance reflected in different land-use types in the semi-arid steppe ecosystems. The three land-use types in this study represented three different modes and levels of disturbance: (1) minimal disturbance on the site of grazing exclusion without biomass removal (GE); (2) moderate disturbance on the site of grazing exclusion with biomass removal by mowing at ≈6 cm above the ground surface (MW); (3) severe disturbance on the site of free-range grazing (FG). A positive relationship was found between species diversity and productivity at the community level on the minimally and moderately disturbed GE and MW plots, in line with generally recognized patterns (Tilman, Wedin & Knops 1996; Loreau et al. 2002). On the severely disturbed FG plots, however, this pervasive pattern between biodiversity and productivity was altered in such a way that a negative correlation was displayed between ANPP and species diversity.
A previous study by Osem et al. (2002) indicates that increase in species richness is related to increasing availability of soil resources in the low productivity range, and that primary productivity can reflect spatial and temporal variation in resource availability across plant communities in semi-arid Mediterranean grassland ecosystems. In this study, the better restored soil resources may have contributed to the higher diversity and productivity on the GE and MW plots compared with the FG plots. Experimental studies on biodiversity have shown that productivity is often a decelerating monotonic function of biodiversity (Benedetti-Cecchi 2005). At diversity levels typically found in natural plant communities, there has been no strong evidence for a direct relationship between plant diversity and productivity (Kahmen et al. 2005a; Kahmen, Perner & Buchmann 2005b). In a climate perturbation experiment, Kahmen et al. (2005b) found that increasing diversity enhanced below-ground productivity during drought, but above-ground productivity was reduced. In this study, we found that the relationship between ANPP and species richness was best described by an exponential growth function ($n^{0.99}$, $P < 0.001$, $n = 24$) on the GE and MW plots, and by an exponential decay function ($R^2 = 0.96$, $P < 0.001$, $n = 24$) on the FG plots. Our results provide further evidence that the precise mechanisms underlying the relationship between species diversity and productivity can be very complex (Huston 1997; Wardle et al. 1999; Aarssen, Laird & Pither 2003), and that the mode and severity of disturbance are critical in regulating such a relationship.

Changes in biodiversity can affect ecosystem processes through a variety of pathways, such as changes in community structure, loss of a keystone species or changes in resource-use patterns among species (Huston 1997; Tilman 2000; Kinzig, Pacala & Tilman 2001; Hector et al. 2002). The positive diversity–productivity relationship has been largely based on the so-called ‘insurance hypothesis’, that more diverse ecosystems are more likely to contain species that can thrive during a given environmental perturbation and compensate for declining competitors caused by that disturbance (Pimm 1984). In the semi-arid Mediterranean rangeland, it was found that diversity of the annual plant community was determined mainly by the less abundant species (Osem et al. 2002), suggesting that higher species richness does not necessarily support higher productivity. On the less disturbed GE and MW plots, the positive relationship between species diversity and productivity may reflect the spatial variation in the relative balance between interspecific competition and facilitation among species in different functional groups.

In natural ecosystems, biodiversity can be insignificant in comparison with the overwhelming influences of environmental and anthropogenic factors on ecosystem functioning (Huston & McBride 2002). The mode and extent of disturbance could therefore dominate over the effects of biodiversity on productivity. For example, habitat conversion tends to exert a positive effect on NPP while having a negative effect on species richness (Williams et al. 2005). The pervasive effects of anthropogenic activities on both ecosystem functioning and biodiversity thus complicate the analysis of diversity–productivity relationship (Williams et al. 2005). One implication of this relationship is that an increase in the spatial variability of biodiversity can cause dramatic decreases in the mean productivity of the system (Benedetti-Cecchi 2005). In this study, free-range grazing represented a land-use type with severe disturbance by grazers that intensifies the spatial variability of habitats at smaller spatial scales, creating a range of niches suitable only for specialist plant species, in addition to the regular habitats in the ecosystem. The localized patches of high species diversity on severely disturbed plots could simply reflect the greater habitat or resource heterogeneity, rather than a strategy for maintaining the integrity of ecosystem functioning when under repeated disturbance, such as free-range grazing. On the FG plots, it was apparent that the SS functional group dominated above-ground production, and this dominance decreased with species diversity (Fig. 3). This could further explain the negative relationship between species diversity and productivity on the severely grazed site.

Although a general decline in biodiversity occurs at a global scale, fragmentation, transformation of land and a variety of other anthropogenic disturbances may have contrasting effects on the number of species at regional or local scales (Sax, Gaines & Brown 2002; Sax & Gaines 2003). We found that, at the local scale, different land-use practices, or severities of disturbance, caused shifts in species composition and plant functional group in the semi-arid steppe ecosystem. The minimally disturbed GE site or moderately disturbed MW site facilitated greater species richness and plant species frequency, compared with the severely disturbed FG site, while the latter seemed to favour legume species.

Competition and facilitation for resources are two of the most decisive factors determining vegetation pattern (Armas & Pugnaire 2005; Michalel 2006). Under harsh environmental conditions, interspecific interactions, instead of facilitation, are expected to play a vital role in determining the community structure and species composition (Bellot et al. 2004; Maestre & Cortina 2004). On the FG plots, heavy grazing by sheep and cattle greatly suppressed the growth of dominant S. krylovii, and promoted the occurrence for less competitive plants such as S. viridis and K. cristata, which were completely absent on minimally or moderately disturbed GE and MW plots. Their specific biological characteristics may explain the occurrence of those species exclusively on the FG plots. Setaria viridis is an annual opportunistic species and propagates by seed (Li & Yan 2006). It can grow on bare ground created by sheep grazing and trampling. Koeleria cristata is a turfed bunchgrass that reproduces from seeds and tillers, and is primarily found in sandy
or coarse-textured soils (Wang et al. 1999). The leaf layer of *K. cristata* extends to only 10–15 cm above the ground surface, making the species poorly competitive on less disturbed sites where high grasses are abundant (Wang et al. 1999). Three species, *O. fimbriatus*, *P. mongolica* and *E. latifolius*, were found exclusively on the MW plots at relatively low frequencies. While a comprehensive explanation is not readily available for the exclusive occurrence of these species on MW plots, the activities associated with mowing may play a part in facilitating their spread under this land-use type.

Some leguminous species, for example *O. glabra*, *M. ruthenica*, *A. seaberrimus* and *A. galactites*, had a higher frequency on the FG plots than on the GE and MW plots. These species could play important roles in maintaining site fertility by fixing atmospheric nitrogen and improving pastoral value (Bonet 2004). However, *O. glabra* is known to be poisonous to sheep. Several highly palatable species, including *A. bidentatum*, *A. tenuissimum*, *A. neriniflorum*, *A. ramosum* and *A. senescens*, were found to be better preserved in the absence of grazing on the GE and MW plots.

Anthropogenic pressure has produced quantifiable changes in the numbers, identities and abundances of species and functional groups in many habitats (Tilman & Lehman 2001). Species composition and diversity have proven to be significant determinants of ecosystem processes in grassland ecosystems (Tilman, Lehman & Thomson 1997). We found that, under the minimal or moderate disturbances such as on the GE and MW plots, there were greater contributions by perennial forbs to community ANPP, total abundance and plant cover than under severe disturbance, such as on the FG plots. Previous studies by others have shown increased diversity of native perennial plants after grazing exclusion in a grassland ecosystem in Australia (Conway 2000). On the MW plots, the improved light conditions by repeated harvesting of above-ground biomass might be one of the major mechanisms through which species richness was maintained, as mowing decreased the cover of perennials and favoured the recruitment of short-lived species. Bao *et al.* (2004) showed that, on a similar steppe ecosystem, repeated mowing resulted in replacement of the dominant rhizomatous species by short bunchgrasses after 17 years. This could account for the higher number of plant species found on the MW plots than on the GE plots.

There are many mechanisms underlying the changes in biodiversity and the relationship between diversity and productivity. Several studies have demonstrated that this relationship can arise from covariation of productivity with other abiotic or management factors, illustrating the complexity of environmental regulation of species diversity in natural communities (Gough, Grace & Taylor 1994; Schaffers 2002; Rajaniemi 2003). Moreover, the species-redundancy hypothesis asserts that many species are so similar that ecosystem functioning is independent of diversity if major functional groups are present (Vitousek & Hooper 1993). Indeed, many factors will coexist in natural grassland ecosystems, and the relationship between biodiversity and productivity will depend largely on which driver plays a dominant role during the process. Based on the results of this study, we conclude that the mode and severity of disturbance are important factors for interpreting the relationship between species diversity and productivity in semi-arid steppe ecosystems.

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