ORIGINAL ARTICLE

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Relationship between plant species diversity and soil microbial functional diversity along a longitudinal gradient in temperate grasslands of Hulunbeir, Inner Mongolia, China

Abstract Numerous experiments have been established to examine the effect of plant diversity on the soil microbial community. However, the relationship between plant diversity and microbial functional diversity along broad spatial gradients at a large scale is still unexplored. In this paper, we examined the relationship of plant species diversity with soil microbial biomass C, microbial catabolic activity, catabolic diversity and catabolic richness along a longitudinal gradient in temperate grasslands of Hulunbeir, Inner Mongolia, China. Preliminary detrended correspondence analysis (DCA) indicated that plant composition showed a significant separation along the axis 1, and axis 1 explained the main portion of variability in the data set. Moreover, DCA-axis 1 was significantly correlated with soil microbial biomass C ($r = 0.735$, $P = 0.001$), microbial catabolic activity (average well color development; $r = 0.775$, $P < 0.001$) and microbial functional diversity (catabolic diversity: $r = 0.791$, $P < 0.001$ and catabolic richness: $r = 0.812$, $P < 0.001$), which suggested that some relationship existed between plant composition and the soil microbial community along the spatial gradient at a large scale. Soil microbial biomass C, microbial catabolic activity, catabolic diversity and catabolic richness showed a significant, linear increase with greater plant species richness. However, many responses that we observed could be explained by greater aboveground plant biomass associated with higher levels of plant diversity, which suggested that plant diversity impacted the soil microbial community mainly through increases in plant production.

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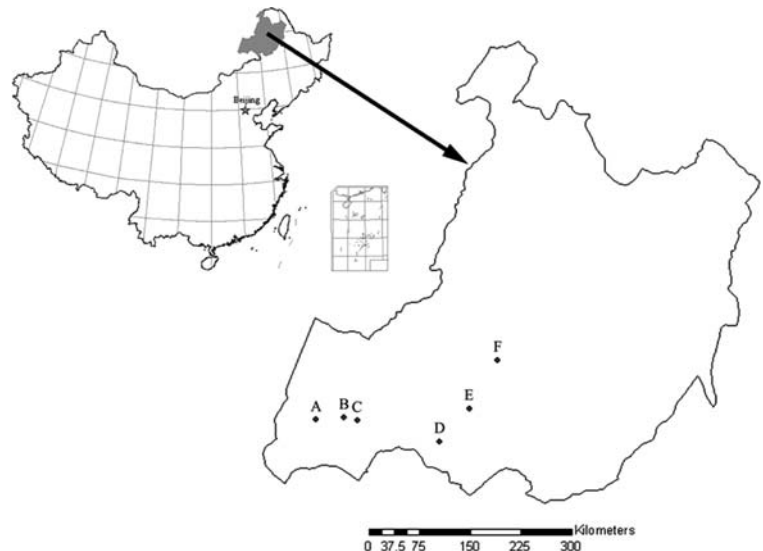Tel.: +86-10-68597542
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Introduction

Changes in plant diversity are known to affect aboveground ecosystem functioning (Tilman et al. 1997, 2001; Hector et al. 1999), but it is increasingly recognized that changes in plant diversity also have an impact on belowground ecosystem functioning, including soil processes, soil structure and soil biota (Hooper et al. 2001; Wardle et al. 2002; Zak et al. 2003; Heemsbergen et al. 2004; Bardgett and Shine 1999). Despite continued focus on the interaction between plant diversity and ecosystem processes, relatively little is known about the relationship between plant diversity and soil microbial diversity or whether plant-mediated changes in soil microorganisms influence ecosystem functioning (Carney and Matson 2005).

Most soil microorganisms are heterotrophic and use plant exudates or decomposing plant material for food. As the main input of organic matter in terrestrial ecosystems, plants are thought to have a profound effect in steering soil communities and processes, especially in the rhizosphere. Consequently, changes in food quality and quantity caused by changes in plant diversity should alter the amount, activity and diversity of soil microorganisms (Hooper et al. 2001). A coupling of aboveground plant diversity and belowground microbial diversity has been implied in the studies dedicated to assessing the role of macrophyte diversity on the stability, resilience and functioning of ecosystems (Kowalchuk et al. 2002). Other previous experiments have examined how microbial communities vary with plant diversity. The results from these studies are equivocal; the soil microbial community shows either a positive relationship (Wardle and Nicholson 1996; Bardgett and Shine 1999; Wardle et al. 1999; Broughton and Gross

Fig. 1 Location of study sites along a longitudinal gradient in temperate grasslands of Hulunbeir, Inner Mongolia, China

2000) or no response (Wardle et al. 1997) to diversity and productivity of the plant community.

Previous studies offer some insight into how plant diversity affects the structure and function of microbial communities at a local scale. However, few of these studies have systematically investigated the relationship between aboveground plant diversity and the soil microbial functional diversity along broad spatial gradients of temperature, precipitation and plant production in the natural environment at a large scale (Zak et al. 1994a). Studies focusing on how plant species richness varies with productivity have been examined across spatial scales ranging from within communities to across entire continents. These studies demonstrate the importance of scale in determining the relationship between productivity and plant species diversity, and their results provide insights into how diversity influences ecosystem functioning at larger scale (Symstad et al. 2003). The same concepts, including competitive exclusion and niche packing, have been invoked to explain both productivity–diversity and diversity–ecosystem functioning relationships. These concepts are more applicable at the local scale and therefore have been generally successful at explaining results of small-scale biodiversity–ecosystem functioning experiments (Faber and Joose 1993; Tilman et al. 2001; Wardle 2002). However, larger scale properties, such as differences in soil fertility and climate, also influence productivity–diversity relationships. At scales larger than the experimental plot, these properties may have a more profound effect on ecosystem functioning than diversity. Similarly, numerous studies have shown that plant diversity has a significant positive effect or no effect on diversity of soil microbial communities in relatively small experimental plots. However, it is unknown how these effects scale up to larger ecosystems. In this study, we examined the relationship between plant species diversity and the soil microbial community along a longitudinal gradient in temperate grass-lands. We hypothesized that: (1) soil microbial biomass C would increase with the increases in plant species diversity and aboveground plant biomass along the spatial gradient and (2) catabolic activity and catabolic diversity would also increase correspondingly with plant diversity and aboveground plant biomass along the spatial gradient.

Materials and methods

Study area

The study area is located at the western part of Daxing'anling mountains, Hulunbeir (115°31′∼126°04′E, 47°05′∼53°20′N), Inner Mongolia, China (Fig. 1). The area is characterized by strong climatic gradients (in both mean annual precipitation and temperature) that are highly associated with trends in plant community composition and structure. Approximately 8.3×10^5 hm^2 of grasslands make this area very suitable for research at a large spatial scale. Floristically distinct plant communities in this region include western arid steppe, central semiarid steppe and eastern meadow steppe.

Study design and sample collection

We established six grassland sites spanning a 284-km longitudinal gradient from west to east within the Hulunbeir grasslands (Fig. 1). Aboveground plant biomass, soil moisture and mean precipitation (from May to September) increased from west to east across the spatial gradient. However, there were no significant site differences in mean temperature (from May to September) (Table 1). All the sites were selected for similar topography (flat), uniform soil type (chestnut soil) and land use type (grassland fenced for about 5 years) to minimum site differences.

Table 1 Site characteristics with all soil parameters taken from top 20 cm soil

	Site					
	A	B	C	D	E	F
Latitude	48°29′24.8″	48°29′25″	48°26′14.9″	48°4′0.2″	48°28′0″	49°4′25″
Longitude	116°35′6.1″	117°9′17″	117°25′11.6″	118°59′35″	119°39′20″	120°18′29″
Mean rainfall, mm[a]	207.82	207.82	224.93	224.93	276.34	276.34
Mean temperature, °C[a]	19.10	19.10	19.12	19.12	17.13	17.13
Vegetation type	Arid steppe	Arid steppe	Semiarid steppe	Semiarid steppe	Meadow steppe	Meadow steppe
Aboveground biomass(g m^{-2})	16.4 ± 3.65	61.44 ± 13.53	51.75 ± 7.93	118.94 ± 18.98	102.46 ± 27.1	121.9 ± 17.39
Bulk density(g cm^{-3})	1.58 ± 0.07	1.50 ± 0.05	1.44 ± 0.05	1.23 ± 0.01	1.18 ± 0.01	0.95 ± 0.09
SMC (%)	4.54 ± 1.37	0.90 ± 0.61	1.64 ± 0.49	10.71 ± 2.09	17.03 ± 4.62	27.51 ± 2.01
SOC(g kg^{-1})	18.66 ± 4.17	7.45 ± 1.27	7.78 ± 1.41	24.58 ± 4.18	32.98 ± 5.66	29.66 ± 1.60

SMC Soil moisture content, *SOC* soil organic carbon

[a] Mean value (May to September) from 1992 to 2005

Vegetation survey and soil sampling were carried out in August 2006, at the peak of vegetative cover and species richness. At each site, a 50-m transect was set, and homogenous sample plots (1 m × 1 m) were established at 10-m intervals. In each plot, all species were identified and measured for cover, height and density. Aboveground plant biomass was also determined by clipping the plants at ground level, sorting by species, drying at 60°C for 48 h, and weighing. Soil samples were collected from the top 20 cm of soil for each of the five replicate sample plots at each site. These plots were considered to be true replicates as the distances among them exceeded the spatial dependence of most soil chemical and microbial variables (Mariotte et al. 1997). In each plot, the soil samples were collected from five randomly selected points and mixed into one sample. After carefully removing the surface organic materials and fine roots, each mixed sample was divided into two parts. One part was air-dried for the analysis of soil physicochemical properties. The other was sifted through a 2-mm sieve, sealed in plastic bags, kept on ice for transport to the laboratory and stored at 4°C for microbial assays.

Soil sample analyses

Soil moisture content of each sample was determined gravimetrically by weighing, drying in an oven at 105°C for 12 h and reweighing. Bulk density of the soils was determined from an undisturbed soil sample by the core method (Lu 1999). Soil organic carbon was determined by the $K_2Cr_2O_7$ titration method after digestion (Lu 1999).

Soil microbial biomass C was determined by the chloroform fumigation method (Vance et al. 1987), using a K_c = 0.45. The functional diversity of the soil microbial community was measured using BIOLOG® GN₂ plates (Biolog Inc., Hayward, CA). The method used for inoculum preparation was adopted from Zak et al. (1994b) and Staddon et al. (1998). To minimize the influence of cell density in comparisons among samples, results can be analyzed at constant average well color development (AWCD). The AWCD for each microplate was calculated by subtracting the control well optical density (OD) from the substrate well OD (blanked substrate wells), setting any resultant blanked substrate wells with negative values to 0 and taking the mean of the 95 blanked substrate wells (Garland 1996). BIOLOG data incubated for 72 h were analyzed to give the Shannon diversity index (the relative contribution of the optical density of positive wells on BIOLOG plates) and Shannon richness index (the number of positive wells identified by the analysis of metabolic profiles on BIO-LOG plates for the microbial communities) as measures of catabolic diversity and catabolic richness, respectively (Begon et al. 1990).

Data analysis methods

The importance value of each plant species was calculated by the combination of relative cover, height and density. Thus, a floristic data matrix of 83 species (30 × 83) was made for the diversity indices calculation and multivariate analyses. A preliminary detrended correspondence analysis (DCA) was carried out to examine variations in species composition among vegetation data and to investigate possible floristic gradients. Furthermore, to detect whether there was a linkage between plant species composition and the soil microbial community, sample scores of the DCA axis were selected as an integrated index reflecting similarities in plant species composition between sites and were used in correlation analysis to examine the relationship between plant species composition and the soil microbial community.

In an attempt to understand the patterns in the variations of diversity for vegetation and the microbial community, plant species richness, which corresponded to the number of species in vegetation, was selected as an index to reflect plant diversity, and linear regression was used to explore the relationships between plant species diversity and the aforementioned attributes of the soil microbial community. Aboveground plant biomass was subsequently added as a covariate and analysis

of covariance (ANCOVA) was used to determine the influence of plant species diversity on the soil microbial variables without interferences from aboveground plant biomass. Type III sums of squares (SS) were used to calculate F-values and to determine the significance of plant diversity and biomass on each measure of microbial community biomass, catabolic activity and functional diversity. Analyses of one-way ANOVA and correlation test were applied using SPSS 11.5 for Windows. When significance was observed at the $P < 0.05$ level, Tukey's post hoc test was used to carry out multiple comparison.

Results

Effect of plant composition on the soil microbial community

A total of 83 plant species were identified along the spatial gradient. An overall DCA of the plant composition pattern was obtained by pooling the vegetation data (Fig. 2). Analysis results suggested that the plant composition patterns showed a significant separation along axis 1 (ANOVA; $F = 651.248$; $P < 0.001$), but not along axis 2 (ANOVA; $F = 1.075$; $P = 0.395$). Axis 1 mainly separated site A from sites B, C, D, E and F. The three grassland types along the spatial gradient each contained two sites: arid steppe (sites A and B), semiarid steppe (sites C and D) and meadow steppe (sites E and F). For arid steppe, *Allium polyrrhizum* and *Carex korshinskyi* dominated site A, and *Serratula centauroides* and *Aneurolepidium chinense* dominated site B. For semiarid steppe, *Aneurolepidium chinense*, *Serratula centauroides* and *Stipa krylovii* were most prevalent on site C, and *Stipa baicalensis* and *Aneurolepidium chinense* dominated site D. For meadow steppe, both sites E and F were dominated by *C. pediformis* and *Aneurolepidium chinense*.
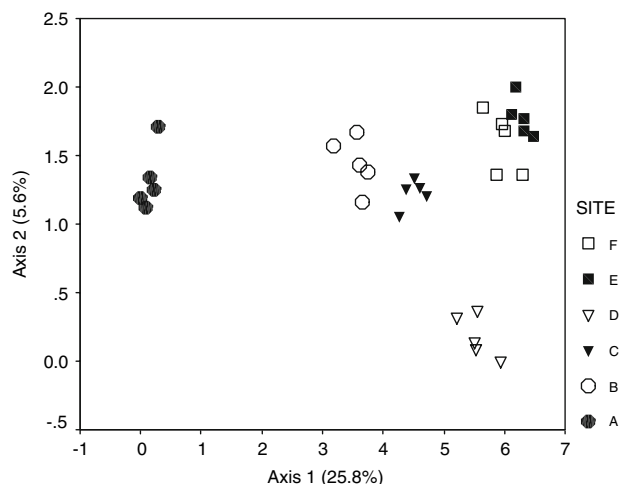
Eigen values for the first, second, third and fourth axes were 0.893, 0.193, 0.120 and 0.088, respectively, with the eigen value for the first axis being much higher than that for the other three axes. As axis 1 explained most of the variation in the species data sets, only the first axis of the DCA ordination was considered for further analysis. The length of the gradient along the first axis was 6.491, indicating a variation in the species data set that is significantly high for the purpose of the analysis. Correlation analysis showed that DCA-axis 1 had a significant positive correlation with soil microbial biomass C ($r = 0.735$, $P = 0.001$), microbial catabolic activity (AWCD; $r = 0.775$, $P < 0.001$) and microbial functional diversity [catabolic diversity (Shannon diversity index): $r = 0.791$, $P < 0.001$ and catabolic richness: $r = 0.812$, $P < 0.001$]. The results showed that differences in plant composition were significantly correlated with soil microbial biomass C, catabolic activity and functional diversity along the spatial gradient.

Effect of plant diversity on soil microbial community

Soil microbial biomass C (SMBC) ranged from 325.39 to 1265.12 mg kg^{-1} (Fig. 3). The value at sites D, E and F was significantly higher than that of sites A, B and C. SMBC was strongly influenced by plant species richness and aboveground plant biomass. A positive linear relationship was found between SMBC and plant species richness ($r = 0.7296$, $P = 0.001$, Fig. 4a) and aboveground plant biomass ($r = 0.6119$, $P = 0.009$, Fig. 4b). Microbial catabolic activity as measured by AWCD increased linearly with plant species richness (Fig. 5a) and aboveground plant biomass (Fig. 5b). Correlation analysis indicated that microbial catabolic activity was positively related to plant species richness ($r = 0.722$, $P = 0.001$) and aboveground plant biomass ($r = 0.529$, $P = 0.029$). The catabolic diversity measured by the
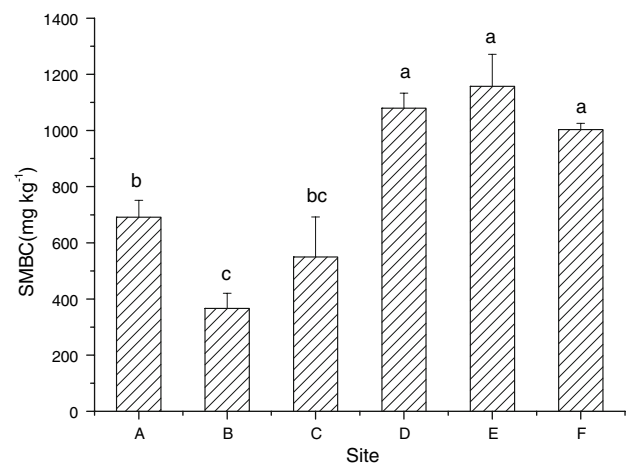

Fig. 2 Ordination of vegetation records ($n = 30$) by DCA analysis along the spatial gradient

Fig. 3 Variation of soil microbial biomass C (SMBC) along a longitudinal gradient (west to east). Within each series, *columns* marked by the same *letter* are not significantly different at $P < 0.05$

Fig. 4 Relationship of plant species richness (**a**) and aboveground plant biomass (**b**) with soil microbial biomass C (SMBC). The equation describes the linear fit line through sampling sites
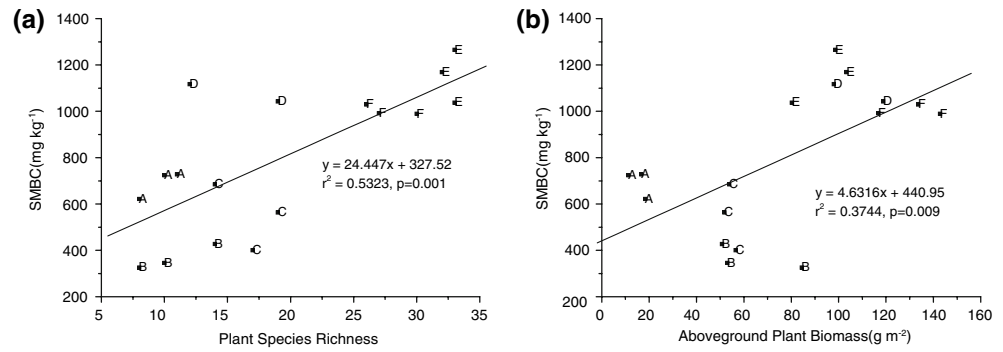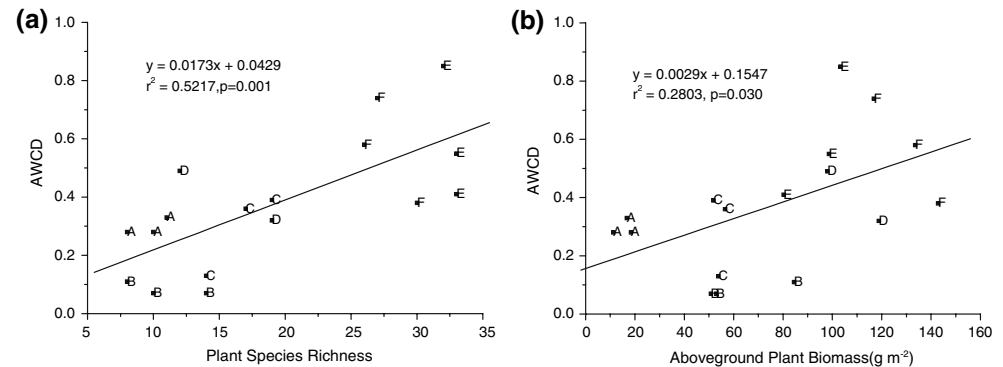

Fig. 5 Relationship of plant species richness (**a**) and aboveground plant biomass (**b**) with catabolic activity (AWCD). The equation describes the linear fit line through sampling sites

Shannon diversity index and richness increased linearly with plant species richness ($r = 0.690$, $P = 0.002$, Fig. 6a; $r = 0.705$, $P = 0.002$, Fig. 6b). Catabolic richness significantly increased with aboveground plant biomass ($r = 0.537$, $P = 0.026$, Fig. 6d), but for catabolic diversity did not ($r = 0.479$, $P = 0.051$, Fig. 6c).

Effect of aboveground plant biomass on the relationship between plant diversity and soil microbial community

Since increased plant species richness was associated with an increase of aboveground plant biomass across the spatial gradient in our study (Table 1), ANCOVA was used to determine the influence of plant diversity on the soil microbial variables without interferences from aboveground plant biomass. The effect of plant species richness on SMBC became not significant (ANCOVA; Type III SS; $F = 0.844$; $P = 0.630$) when we included aboveground plant biomass as a covariate. Similarly, the effect of plant species richness on catabolic richness was not significant (ANCOVA; type III SS; $F = 2.372$; $P = 0.210$) when aboveground plant biomass was included as a covariate in our analysis. However, the effect of plant species richness on microbial catabolic activity was still significant (ANCOVA; type III SS; $F = 6.869$; $P = 0.039$) when aboveground plant biomass was included as a covariate, which suggested that plant diversity played an important role in increasing microbial catabolic activity in temperate grasslands.

Discussion

The six grassland sites we studied exist across a 68-mm mean precipitation gradient. Since plant species are tightly constrained by the climatic regime and the soil condition under which they grow, they often reflect an integrated environmental condition. Aboveground plant biomass, soil water moisture and rates of soil biogeochemical processes increased concomitantly from western arid steppe to eastern meadow steppe along the gradient. Vegetation ordination revealed variation in plant composition well across this gradient of decreasing climatic limitations and increasing substrate availability. Since the spatial arrangements of sample scores reflect the similarities between sites and DCA-axis 1 was sufficient to explain the main portion of variability in the data set, DCA-axis 1 can reflect the variations in plant composition well between sites across the spatial gradient. Correlation analysis indicated that DCA-axis 1 had a significant positive relationship with soil microbial properties, so plant composition was significantly related to soil microbial community along the spatial gradient.

Analysis of soil microbial biomass provides an alternative for examining the impact of plant diversity on soil ecosystem functions regulated by the soil microbial community, such as the cycling of C, N, S and P (O'Donnell et al. 2001). Soil microbial biomass drives the turnover of organic matter and the immobilization and mineralization reactions to regulate plant nutrient

Fig. 6 Relationship of plant
species richness (**a, b**) and
aboveground plant biomass(**c,
d**) with the functional diversity
of soil microbial community.
The equation describes the
linear fit line through sampling
sites
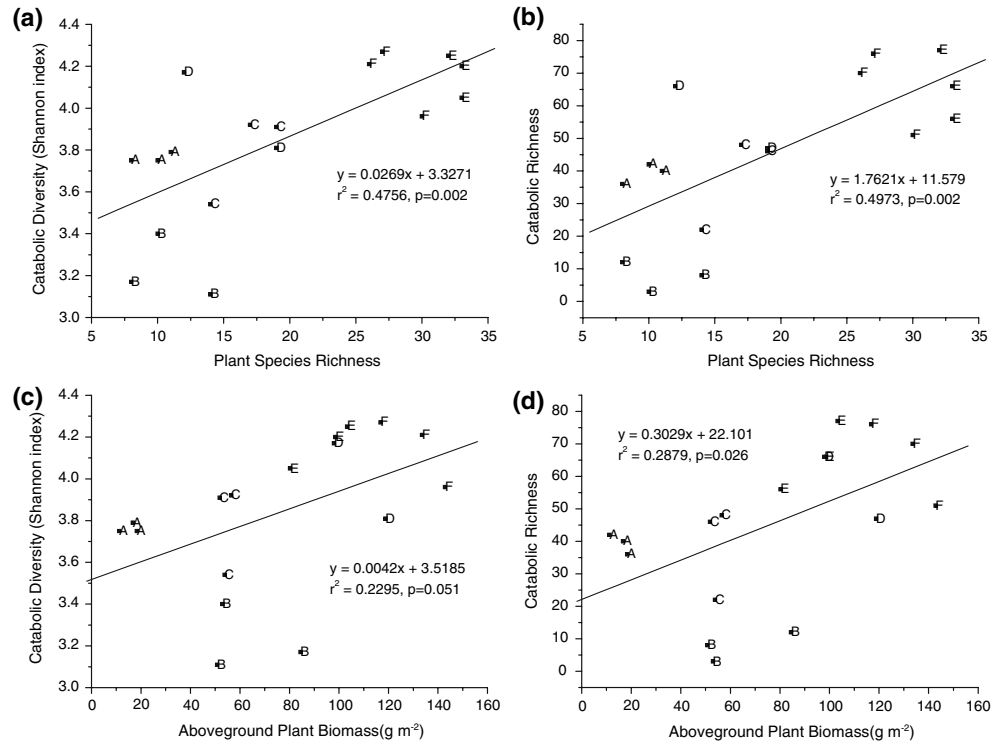
supply, making it the center of nutrient flux in soil. Our
data supported that both plant species richness and
aboveground plant biomass were positively and linearly
correlated with SMBC. Previous studies also showed
that plant species richness had a positive effect on soil
microbial biomass (Spehn et al. 2000a; Stephan et al.
2000). However, numerous studies also reported that
soil microbial biomass showed either an idiosyncratic
response or no response to increasing plant species
diversity (Gastine et al. 2003; Bardgett and Shine 1999).
In our study, increased plant species richness was asso-
ciated with an increase of aboveground plant biomass.
Moreover, the relationship between plant species rich-
ness and soil microbial biomass was no longer significant
when aboveground plant biomass was included as a
covariate in ANCOVA analysis, suggesting that plant
diversity impacted soil microbial biomass mainly
through increases in plant production. Our observations
agreed with those made in several other studies that have
demonstrated the linkage between plant productivity
and soil microbial biomass. For example, Zak et al.
(1994a) quantified the relationship between above-
ground net primary production (ANPP) and soil
microbial biomass in late-successional ecosystems along
a continent-wide gradient in North America and found
that soil microbial biomass C displayed a positive, linear
relationship with ANPP at the ecosystem level, which
supported the idea that substrate availability constrains
the soil microbial biomass at large spatial scales. Wardle
and Nicholson (1996) showed that soil microbial bio-
mass was primarily controlled by plant biomass pro-
duction, but it was also influenced by the type and

number of plant species present. Plant species richness
may therefore affect microbes directly, possibly through
resource heterogeneity. Another way in which diversity
could directly affect decomposers is through the spatial
and temporal provision of substrate. Low species
diversity creates a much patchier substrate when com-
pared to high species diversity and therefore could have
contributed to the lower microbial biomass per unit of
soil (Holland and Coleman 1987). Besides the effect of
plant species richness on soil microbial community, soil
fertility conditions also had an impact on soil microbial
biomass (Marschner et al. 2004).

We used commercial microtiter plates with multiple
carbon sources (BIOLOG GN_2 plate) as a sensitive, but
rapid screening method to measure the catabolic activity
and functional diversity of a particular group of soil
bacteria (Garland 1996). Although these bacteria rep-
resent only a small fraction of the taxa present in the
soil, we consider them to be a useful indicator for
measuring the effects of plant diversity on the soil
microbial community in such a system. Our results
showed that plant species richness had a positive influ-
ence on microbial catabolic activity, catabolic diversity
and catabolic richness of the soil microbial community
along a longitudinal gradient in a temperate grassland
ecosystem, which accorded with Stephan et al. (2000).
The increase in catabolic activity reflects an increase in
the oxidation of the carbon sources supplied (Haack
et al. 1995), while the increase in catabolic diversity re-
flects the use of different carbon-oxidation pathways and
therefore functional diversity (Sharma et al. 1998;
Staddon et al. 1998). It is unlikely that a single genotype

or low-level taxonomic unit could express so much plasticity in carbon source utilization, and this functional diversity is therefore probably related to taxonomic diversity (Haack et al. 1995). However, plants show redundancy among taxa within functional groups, and a similar situation may exist within bacterial communities, so that functional diversity would provide a minimum estimate of taxonomic diversity. We therefore concluded that both catabolic activity and functional diversity of the soil microbial community increased with increasing plant diversity.

In our study, higher plant diversity may have influenced soil microbial functional diversity by increasing the aboveground plant biomass, since the relationship of plant species richness with microbial catabolic diversity and richness was no longer significant when aboveground plant biomass was included as a covariate in our analysis. Aboveground plant biomass increased with increasing plant species richness, and the resulting enhanced nutrient flow to the soil may also have contributed to the positive effect on the soil microbial community (Spehn et al. 2000b). Carney and Matson (2005) found that plant diversity had a significant effect on microbial community composition through alterations in microbial abundance rather than community composition. Other studies also reported that aboveground net primary productivity was expected to increase soil carbon input through enhancing the turnover of plant biomass and enhancing root exudation and may therefore influence carbon-limited microbial communities in the soil (Niklaus et al. 2003; Zak et al. 2003).

Apart from aboveground plant biomass, site features such as precipitation and soil moisture content might also influence the relationship between plant species diversity and soil microbial functional diversity. In arid and semiarid areas, soil water condition was an important factor limiting plant growth, and variation in precipitation could significantly affect aboveground plant biomass in grassland ecosystems (Bai 1999). The study in Xilin river basin also indicated that plant species richness, diversity and ANPP decreased with a decrease in precipitation (Bai et al. 2000). Consequently, variation in soil moisture across the spatial gradient might affect the relationship between plant diversity and microbial functional diversity through alerting plant biomass and diversity directly or indirectly. The relative role of soil moisture in determining the relationship between plant diversity and soil microbial community needed to be explored in future study.

Although our study has provided some insight into the effects of plant diversity on microbial communities along a longitudinal gradient at a large scale, there remain serious gaps in our understanding of the linkage between plant and microbial diversity. Moreover, there is still much work to be done to examine the relationship between plant diversity and the soil microbial diversity along broad spatial and temporal gradients at a large scale. Subsequent research might then focus on comparing the mechanisms behind observed relationships

between plant diversity and the soil microbial community at a large scale vs. those behind the effects of experimental manipulations of plant diversity on soil microbial diversity at a local scale. Differences in the influence of plant diversity on soil microbial diversity between short-term and long-term time spans, as well as small and large scales, need to be explored in future research.

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