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Precipitation drives the biogeographic distribution of soil fungal community in Inner Mongolian temperate grasslands

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Abstract
Purpose Understanding the biogeographic distribution of soil fungal communities is crucial for assessing the impacts of environmental factors on terrestrial biodiversity and ecosystem functioning. Here, we investigated spatial variations of fungal communities across three different types of temperate grasslands along a transect in the Inner Mongolia, China. The aims were to understand the biogeographic patterns of fungi and key drivers shaping soil fungal communities in temperate grasslands.
Materials and methods The composition and diversity of soil fungal community across 30 sites of the meadow steppe, typical steppe, and desert steppe along a 1200-km transect were studied through pyrosequencing. The relationships between fungal communities and environmental and biotic factors were assessed.
Results and discussion The results showed that the fungal community along this transect exhibited strong dependence on soil moisture content and nitrate concentration, while the fungal alpha diversity was positively correlated with precipitation and below-ground biomass. Drier environment has resulted in a shift towards an Ascomycota-dominating fungal community.
Conclusions Our findings suggest that the distribution and community structure of soil fungal communities are primarily driven by precipitation. Plant biomass and soil nutrient status which are also influenced by precipitation are also predictors of fungal community. Our results provide important implications for understanding the linkages among environmental factors and soil fungal communities in Eurasian steppe ecosystems.

Keywords Precipitation · Soil fungi · Soil properties · Temperate steppe

Di Wang and Yichao Rui contributed equally to this study.

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1 Introduction

Understanding the biogeographic distribution of soil microbial communities is crucial for studying terrestrial biodiversity and ecosystem functioning. Soil microbial communities play a key role in the soil carbon (C) and nutrient cycling (Zak et al. 2003), and the variations in microbial composition structure and abundance reflect variable ecosystem functioning and have implications for proper management practices to be adopted accordingly. Among eukaryotic microorganisms, fungi play a fundamental role in ecosystem processes through the decomposition of dead organic material and through mineral nutrition of plants via mycorrhizal symbiosis (Zeilinger et al. 2016). Although the drivers of the soil microbial community structure have been extensively studied in terrestrial

ecosystems, studies of fungal communities' patterns and drivers at regional scale remain few.

It has been suggested that microbial biogeographic patterns are shaped by environmental factors (Fierer and Ladau 2012), including climate, soil physical and chemical properties, and plant properties (Fierer and Jackson 2006; Prober et al. 2015). Abiotic factors, such as soil moisture, pH, and soil organic C (SOC), may result in predictable shifts in the soil microbial composition (Fierer et al. 2007) and could potentially be the primary driving forces changing microbial diversity and community (Fierer et al. 2012). Soil environments also strongly affect the diversity and community composition of fungi at the local scale (Taylor et al. 2008). Soil physicochemical properties including SOC, nutrient, and electrical conductivity all have an impact on soil fungal communities (Wakelin et al. 2016). It has been reported that arbuscular mycorrhizal fungal (AMF) taxa were significantly correlated with soil N-P ratio (Verbruggen et al. 2015). However, larger scale determinants of fungal species richness and community composition remain unknown.

Spatial scale is important in determining the variation pattern in a microbial community structure because environmental conditions are often scale-dependent (Bardgett and van der Putten 2014). More and more evidences indicate that microbial assembly displays non-random environmental distributions (Fierer and Ladau 2012; Prober et al. 2015) and in particular, soil pH is a key driver in shaping the distribution of soil bacterial communities at regional scales (Fierer and Jackson 2006; Lauber et al. 2009). Whereas, the regional-scale biogeographic distribution patterns of soil fungal communities have been rarely investigated and are less known compared with bacteria. It is likely that there is a close relationship of plant-fungal distribution patterns at regional scales given the fact that fungi depend more on plant products (Millard and Singh 2010). Meanwhile, climatic factors including precipitation and temperature influence plant community composition, biomass, and plant richness (Bai et al. 2007) and may exert indirect effects on the fungal community through changing plant properties. Therefore, it is expected that biogeographic patterns of fungal communities may be driven by not just soil properties but also climate and plant factors. However, there is a need for more evidences examining fungal composition at regional scale.

Grasslands cover 40% of the earth's terrestrial surface, which play an important role in the global C cycle (Glenn et al. 1993). The Inner Mongolian steppe lies in the eastern part of the Eurasian steppe and represents typical arid and semiarid ecosystems. Precipitation is recognized as the most important factor to influence C flux and plant productivity in this region (Niu et al. 2008). A higher frequency of extreme climatic events (e.g., increased drought and precipitation) has been projected in these ecosystems which have been considered fragile and sensitive to climate change (Ni and Zhang 2000). Further, it has been suggested that the area of arid and semiarid grasslands will expand due to global warming (Dai 2013) while irregular precipitation events are predicted to occur (Easterling 2000). All these factors may result in fundamental changes on the richness and community structure of soil fungi (Vargas-Gastélum et al. 2015). As a result, a better understanding of the driving forces and distribution patterns of soil fungi on a regional scale is essential to adopting better management of these arid and semiarid ecosystems.

Here, a regional-scale field study across 30 sites in temperate grasslands in Inner Mongolia, China, was conducted to elucidate the driving factors and distribution patterns of soil fungal communities through high-throughput sequencing technologies. The selected study region is characterized by a decreasing precipitation gradient from the east to the west and encompasses a wide variety of climatic, edaphic, and vegetational conditions (Wang et al. 2015). The main objectives of this study were to (1) determine the biogeographic patterns of soil fungal communities across three different types of temperate grasslands along a transect and (2) identify microclimatic and edaphic and vegetational characteristics driving fungal community composition and structure at regional scale. In particular, we hypothesized that soil fungal community composition was predominantly driven by precipitation at regional scale in temperate grasslands.

2 Materials and methods

2.1 Study area and sampling sites

The study area was in Inner Mongolia, China, spanning from Hailaer (119° 55′ E, 49° 19′ N) to Siziwang (111° 53′ E, 41° 47′ N), with an altitude from 600 to 1456 m, covering three main grassland vegetation types: meadow steppe (Stipa baicalansis and *Achnatherum splendens* account for 13% of the total area as the dominant species), typical steppe (*Stipa grandis* and *Leymus chinensis* account for 28% of the total area as the dominant species), and desert steppe (*Stipa klemenzii*, sheep fescue, and *Seriphidium gracilescens* account for 12% of the total area as the dominant species). Along the 1200-km transect, a total of 30 sites, including 15 for meadow steppe, 11 for typical steppe, 4 for desert steppe, were chosen for sampling. Figure 1 shows the geographical distribution of the study area and GPS coordinates of sites.

Mean annual precipitation (MAP) and mean annual temperature (MAT) from 1981 to 2012 for each site were obtained from the China Meteorological Administration database and were used as climate factors. The total rainfall of 2011 was 317, 227, and 242 mm in meadow steppe, typical steppe, and desert steppe, respectively, with rainfall amount being lower than long-term MAP of the three grassland types (341, 290, and 249 mm,

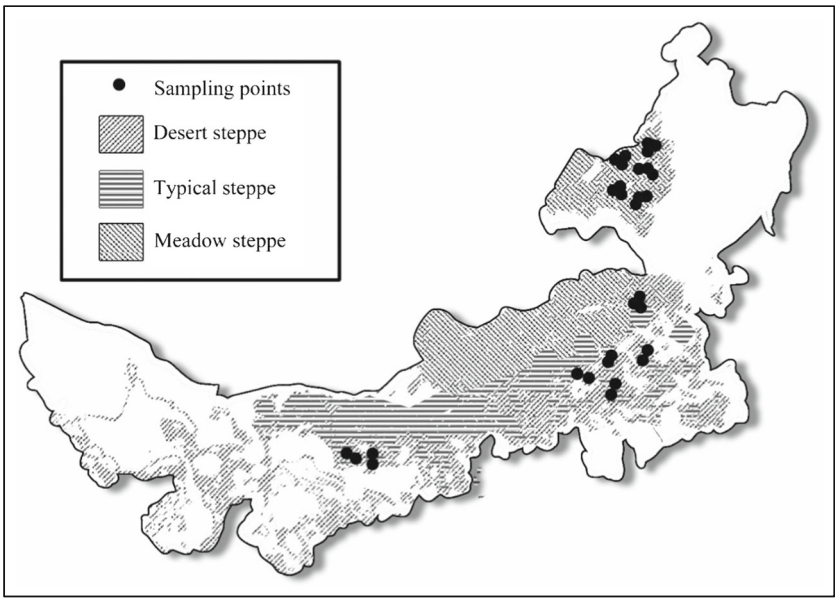

Fig. 1 The 30 sampling sites along a 1200-km transect in Inner Mongolian temperate grasslands. The three different types of temperate grasslands (meadow steppe, typical steppe, and desert steppe) were highlighted in the legend (see also Electronic Supplementary Material, Table S1)

respectively). The MAT was similar in the three grassland types, which was the highest from June to August and the lowest in January.

2.2 Field sampling and soil and plant property analyses

Soil and plant samples were collected along this transect in July 2011. Five soil cores with a diameter of 5 cm were taken from a depth of 0–10 cm of 1 × 1 m plot and mixed into one sample. Three replicates were sampled at each site. Soil samples were passed through a 2-mm sieve and stored at −20 °C for molecular analysis. Sub-samples were stored and air-dried for physicochemical analyses. The pH of air-dried soil sample was measured by a pH meter method whose calibration is Thermo® pH Buffer. Soil moisture content was measured after 24 h oven drying at 105 °C to a constant weight. Soil organic C was measured by potassium dichromate oxidation and heating (Lu 2000) and total soil nitrogen (TN) was measured by the Kjeldahl method (Bremner 1960). Soil ammonium and (NH_4^+-N) and nitrate (NO_3^--N) concentrations were determined by extraction with 2 M KCl on an Alpkem Flow Solution III.

Coverage of plants was measured by visual estimation method by one person. The standing above-ground biomass (AGB) of herbaceous plants was cut by species from the same size of plots as soil without the dead above-ground plants. Plant materials collected in each quadrat were oven-dried at 65 °C for 48 h and weighed. Roots were rinsed from the soil cores under running water and dried at 65 °C until constant weight as the below-ground biomass (UGB). In this study, the α-diversity was defined as the species richness of the single 1 × 1-m sample. The diversity of plant community was estimated by the Shannon-Wiener index to calculate H′ with the following equation:

$$H' = -\sum_{i=1}^{s} p_i \mathrm{In} p_i$$

where S is species number and p_i is the proportion of individuals belonging to the ith (the first i species) species in the dataset collected, such as the total number of samples is N and the number of ith individuals is N_i, then $p_i = N_i/N$.

2.3 DNA extraction, PCR, and pyrosequencing

Soil DNA was extracted using the PowerLyser™ PowerSoil® DNA Isolation Kit (MoBio Laboratories Inc., USA) according to manufacturer's protocol. Raw DNA excised from 1% agarose gel using an Agarose Gel DNA purification kit (TaKaRa) was quantified with a NanoDrop ND-1000 spectrophotometer (NanoDrop Technologies, Wilmington, DE, USA). The rDNA internal transcribed spacer (ITS) region was amplified using primer pairs ITSOF-T (5′-acttggtcatttagaggaagt-3′), LR5-Tom (5′-ctaccgtagaaccgtctcc-3′) (Tedersoo et al. 2010). PCR products from each sample were combined in equimolar ratio in a single tube and run on a Roche FLX 454 pyrosequencing machine (Roche Diagnostics Corporation, Branford, CT, USA). Tags were extracted from the FASTA file into individual sample-specific files based on the tag sequence. All sequences were clustered into operational taxonomic units (OTUs) at a 97% sequence threshold using UCLUST. Representative sequences from each phylotype were aligned using PyNAST for system development, then for the calculation of fungal diversity and fungal community structure difference comparison. Taxonomic identity of each phylotype

was determined using the UNITE 7.1 database via the RDP classifier. To correct unequal sampling effort, we used a randomly selected subset of 3271 sequences per sample, resulting in the removal of some singletons. Shannon–Wiener index of fungal community was estimated by calculating the OTU richness at 97% sequence identity. Fungal diversity and community distances were calculated using the mean of the rarefying procedure repeated 20× subsampling. Relative abundance of the fungal phyla sequences, chao1 index (estimators of the total number of species), PD_whole_tree (Faith's Phylogenetic Diversity based on the phylogenetic tree), OTU (operational taxonomic unit) numbers were calculated by Sequence data with QIIME, v1.9.1.

2.4 Statistical analyses

One-way analysis of variance (ANOVA) was used to analyze the differences in the edaphic, topographical, and vegetational variables among the three different ecosystems. Means were contrasted post hoc by Tukey's studentized range (HSD) for comparing the samples from three types of grasslands. And, model was made based on stepwise regression to predict the relationship between environmental variables, such as edaphic, topographical, and vegetational variables, and the fungal Shannon-Wiener diversity. All the analyses were used the software IBM SPSS Statistics 22 (IBM Corporation, Armonk, NY). Correlations of fungal beta diversity with plant biomass and environment factors were calculated by Mantel test with the "ecodist" and "vegan" packages in R. To make the result more precise, partial Mantel tests were used with each of the significant independent variables according to the results of Mantel test to check the abiotic factors. Nonmetric multidimensional scaling (NMDS) was used to examine whether there was significant difference in fungal community composition among different ecosystems. Bray Curtis site distance table which was calculated from the primary data of fungal OTUs was applied with the "vegan" package in R. All statistical analyses were done with R 3.3.1 (R Development Core Team 2016).

3 Results and discussion

3.1 Soil and plant properties in three types of temperate grasslands along the transect

Along the 1200-km transect, the desert steppe was characterized by low-nutrient soils (as indicated by lowest NH_4^+-N, NO_3^--N, TN, and SOC) and a harsh climate (as indicated by low MAP and high MAT), while the typical steppe and meadow steppe had high-nutrient soils and a more benign climate (Table 1). Total biomass, AGB, and UGB of plants are the highest in the meadow steppe (993, 191, and 802 g m^{-2}, respectively) and the lowest in the desert steppe (705, 177, and 528 g m^{-2}, respectively; Table 1). Although the long-term precipitation was meadow steppe > typical steppe > desert steppe, higher soil moisture, and higher precipitation in 2011 in desert steppe compared with meadow steppe reflected the fact that the desert steppe had received more temporal rainfall than the meadow steppe before sampling (Table 1). Interestingly, the plant diversity was higher in the desert steppe than the meadow steppe and typical steppe ($P < 0.05$; Table 1). This was contrary to some studies which suggested that plant diversity was positively correlated with primary productivity in grassland ecosystems (Bai et al. 2007; Ma et al. 2010). This may be attributed to the short-term fluctuation of climate factors (mainly precipitation) before sampling. In 2011, the desert steppe had similar precipitation (242 mm)

Table 1 Summaries of the climatic, edaphic, and vegetational variables of three types of grasslands in this study

Variables	Meadow steppe (n = 15) Mean ± SE	Typical steppe (n = 11) Mean ± SE	Desert steppe (n = 4) Mean ± SE
MAP (mm)	341 ± 8.8	290 ± 38	249 ± 67
MAT (°C)	−1.56 ± 0.61	0.50 ± 1.42	3.75 ± 0.25
Soil moisture content (%)	7.2 ± 0.66	11.8 ± 1.58	10.1 ± 3.12
pH	6.4 ± 0.04	7.1 ± 0.11	7.1 ± 0.03
TN (%)	0.30 ± 0 .03	0.19 ± 0.01	0.15 ± 0.06
SOC (%)	3.46 ± 0.36	2.00 ± 0.17	1.45 ± 0.63
NH_4^+-N (mg kg^{-1})	10.9 ± 0.83	9.5 ± 1.10	3.8 ± 0.49
NO_3^--N (mg $kg^{-1)}$	5.0 ± 0.54	10.3 ± 0.95	4.3 ± 0.71
Total biomass (g m^{-2})	993 ± 40	942 ± 52	705 ± 259
AGB (g m^{-2})	191 ± 9.6	181 ± 10.4	177 ± 40
UGB (g m^{-2})	802 ± 32	761 ± 43	528 ± 221

MAP mean manual precipitation, *MAT* mean manual temperature, *TN* total nitrogen, *SOC* soil organic carbon, NH_4^+ *-N* ammonium-N concentration, NO_3^- *-N* nitrate-N concentration, *AGB* above-ground biomass, *UGB* below-ground biomass

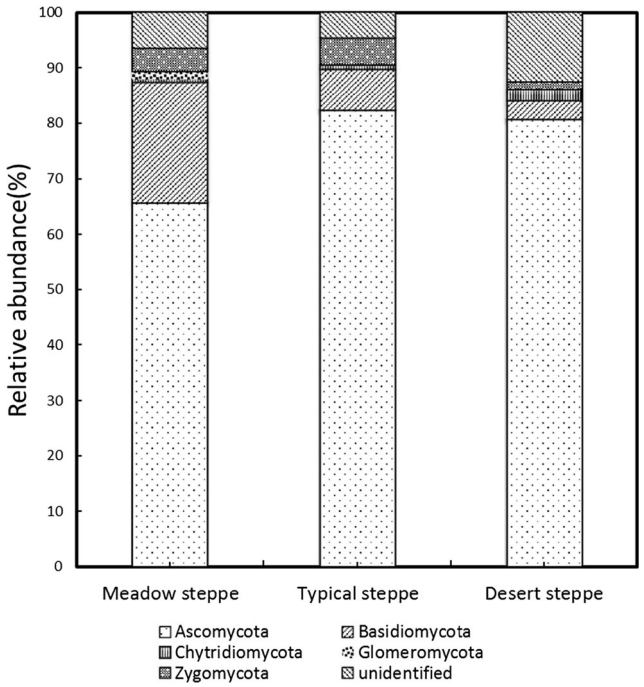

Fig. 2 Relative abundance of the fungal phyla sequences in three different types of temperate grasslands (meadow steppe, typical steppe, and desert steppe) along a 1200-km transect in Inner Mongolia, China

compared with long-term MAP (249 mm), while the meadow steppe and typical steppe had markedly lower precipitation (317 and 227 mm, respectively) than long-term MAP (341 and 290 mm, respectively). Bai et al. (2007) suggested that precipitation had a large control on the productivity–diversity relationship in the Eurasian Steppe. Therefore, the temporal shift in precipitation may have profound influence in plant diversity. Considering that increased drought has been projected in some part of the Eurasian Steppe (Ni and Zhang 2000), and the area of arid and semiarid grasslands is likely to expand (Dai 2013), a loss of plant diversity may pose a challenge for the Inner Mongolian temperate grasslands.

3.2 Composition and alpha diversity of fungal community in three types of temperate grasslands

The fungal communities along this 1200-km transect were mainly composed of Ascomycota, Basidiomycota, Zygomycota, Chytridiomycota, and Glomeromycota (Fig. 2). Ascomycota was the most dominant phylum and the Ascomycota, the Basidiomycota, and the Zygomycota accounted for 74, 13, and 5% of all fungal reads, respectively (Fig. 2). The relative abundance of Ascomycota in typical steppe and desert steppe was significantly higher than in meadow steppe (Fig. 2). It has been reported that Ascomycota were found to dominate the fungal phylum in semiarid grasslands (Porras-Alfaro et al. 2011; Vargas-Gastélum et al. 2015) and drylands (Maestre et al. 2015). As a result, the dominance of Ascomycota may reflect the distribution pattern of fungi in arid and semiarid ecosystems. Our result was also in agreement with some studies (Clemmensen et al. 2015; Sterkenburg et al. 2015) suggesting that Ascomyceta had the ability to tolerate stressful conditions (e.g., low C and nutrient availability, drought stress). Therefore, a shift to an Ascomycota-dominating fungal community may suggest its self-regulation in harsh environments to achieve a higher resource use efficiency.

The alpha diversity of fungi, measured as fungal OTU richness at 97% sequence identity, demonstrated significant difference across three different grassland types ($P < 0.01$). Despite the Shannon–Wiener index was the highest in the desert steppe, the chao1 index (number of rare classes) and the PD_whole_tree index (Faith's Phylogenetic Diversity) were the highest in the meadow steppe and the lowest in the desert steppe (Fig. 3). Pearson's correlation analysis showed a positive correlation between chao1 index and MAP ($r = 0.727$, $P < 0.001$), and PD_whole_tree index and MAP ($r = 0.817$, $P < 0.001$). Positive correlation was also detected between chao1 index and UGB ($r = 0.393$, $P = 0.03$), and

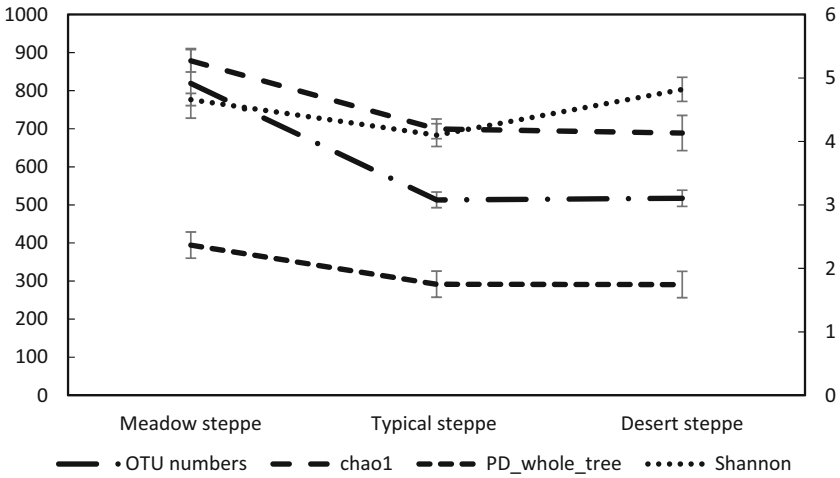

Fig. 3 The changing trends of OTU (operational taxonomic unit) numbers, chao1 (estimators of the total number of species), PD_whole_tree (Faith's Phylogenetic Diversity based on the phylogenetic tree), and fungal Shannon–Wiener index in the three grassland ecosystems along a 1200-km transect in Inner Mongolia. The fungal Shannon–Wiener index is explained by the right *y*-axis, while the others use the left *y*-axis (mean ± SE are showed by *error bars*)

PD_whole_tree index and UGB (r = 0.393, P = 0.03). This correlation demonstrated close relationships between fungal alpha diversity and precipitation and productivity in Inner Mongolian temperate grasslands. Despite the predominant role of precipitation in driving fungal alpha diversity, plant communities also represent the most influential predictor of fungal community (Johnson et al. 2004). A decline in productivity may limit the diversity and availability of resources that were available to microorganisms (Broeckling et al. 2008). Therefore, our results suggested that the composition and alpha diversity of fungal community in three types of temperate grasslands were controlled predominantly by precipitation.

3.3 Driving factors of fungal communities at regional scale in Inner Mongolian temperate steppe

Mantel and partial Mantel test assessed the relationships between fungal beta diversity with plant community and abiotic factors. Among all variables, NO_3^--N and soil moisture content had the strongest correlation with fungal community composition ($P < 0.01$; Table 2). There were also significant correlations of fungal community composition with plant diversity and abiotic factors such as MAP, soil pH, TN, SOC, AGB, and NH_4^+-N ($P < 0.05$; Table 2). This result was further supported by NMDS demonstrating that the fungal communities clustered according to different steppes (Fig. 4) which were divided by precipitation and soil moisture availability. Our study confirms the important influence of precipitation, as well as soil nutrient, on soil fungal communities and is in line with studies reporting that fungal community structure could be predicted by climatic factors (Tedersoo et al. 2014; Timling et al. 2014). Importantly, among all environmental factors, MAP was the strongest predictor of total fungal diversity at the global scale (Tedersoo et al. 2014). Precipitation or water availability plays key roles in regulating ecosystem functioning, especially in arid and semiarid areas like temperate grasslands (Niu et al. 2008). The correlation between soil fungi and other soil properties implied that precipitation might not only influence fungal community directly, but also had indirect influences through its impact on plant communities and soil properties. Our results suggested that the "soil-plant-fungi" interaction was primarily driven by precipitation (both long-term history and short-term tendency) in the temperate grasslands of Inner Mongolia.

Table 2 Correlations of fungal beta diversity with plant biomass and environment factors by Mantel test

Explanatory	Fungi	
	r_M	P
MAP (mm)	0.16	*0.011*
Soil moisture content (%)	0.26	*0.002*
pH	0.06	0.170
NH_4^+-N (mg kg^{-1})	0.04	0.297
NO_3^--N (mg kg^{-1})	0.30	*0.001*
TN (%)	0.13	*0.032*
SOC (%)	0.13	*0.034*
AGB (g m^{-2})	0.15	*0.018*
UGB (g m^{-2})	0.10	0.119
Total biomass (g m^{-2})	0.11	*0.080*
Plant diversity index	0.20	*0.019*

Values in italic indicate significant correlations ($P < 0.05$)

MAP mean manual precipitation, *NH_4^+-N* ammonium-N concentration, *NO_3^--N* nitrate-N concentration, *TN* total nitrogen, *SOC* soil organic carbon, *AGB* above-ground biomass, *UGB* below-ground biomass

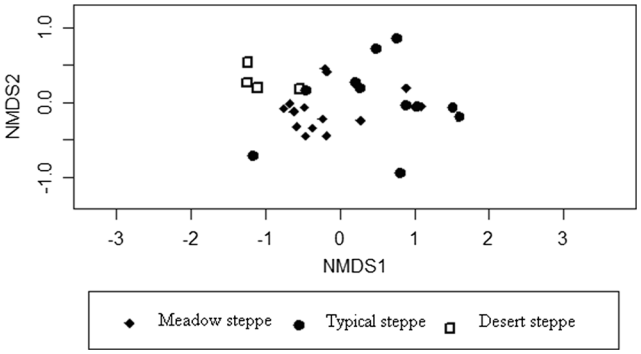

Fig. 4 Nonmetric multidimensional scaling (NMDS) of fungal community structure in three different types of temperate grasslands (meadow steppe, typical steppe, and desert steppe) along a 1200-km transect in Inner Mongolia, China

4 Conclusions

In conclusion, our results suggest that precipitation plays a key role in shaping plant and fungal community across meadow steppe, typical steppe, and desert steppe along the 1200-km transect in temperate grasslands in Inner Mongolia, China. Plant biomass and soil nutrient status which are also influenced by precipitation are also predictors of fungal community. Future changes in the arid and semiarid grasslands towards a drier climate may result in a shift to an Ascomycota-dominating fungal community.

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