

Revegetated shrub species recruit different soil fungal assemblages in a desert ecosystem

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Abstract

Background and aims Revegetation with xeric shrubs is a widely applied measure for restoring degraded ecosystems in the deserts of northern China. However, knowledge on the soil fungal assemblages in revegetated shrubs still remains veiled. This study aimed to evaluate how soil fungal diversity and composition respond to shrub species. **Methods** We characterized soil fungal communities in three different shrublands (*Artemisia ordosica*, *Salix psammophila*, and *Caragana microphylla*), which had been planted on bare sandland for about 20 years, in the Mu Us Desert in northern China, using high-throughput 18S rRNA gene sequencing. The relationships of fungal community diversity and composition with environmental variables were explored by regression analysis and Mantel test, respectively.

Results The dominant phyla across the studied samples were Ascomycota and Basidiomycota. Compared to bare sandland, fungal diversity was significantly greater in *A. ordosica* and *C. microphylla* but not in *S. psammophila*. There was a positive linear relationship between soil

fungal and understory plant diversity. *A. ordosica* and *C. microphylla* shrublands showed the greatest relative abundance of Ascomycota; *S. psammophila* shrubland showed the greatest relative abundance of Basidiomycota. In terms of functional groups, the highest relative abundance of ectomycorrhizal fungi and the lowest relative abundance of pathogenic fungi were found in *S. psammophila* shrubland. Soil collected from *A. ordosica* shrubland showed the highest relative abundance of arbuscular mycorrhizal fungi.

Conclusions Variations in fungal diversity and assemblages were directly affected by the revegetated shrub species. The strong correlation of the fungal community and shrubs provides a better understanding of soil organic carbon sequestration and plant–soil interaction in different revegetated shrublands.

Keywords Semi-arid ecosystem · Shrub species · Soil fungal community composition · Soil fungal diversity · Revegetation

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Introduction

Fungi participate in a range of important ecological functions, such as decomposition, symbiosis, parasitism, and pathogenesis (Tedersoo et al. 2014). Soil fungi form intimate relationships with plant communities, whereby they increase soil nutrient availability, decrease water consumption, and mediate plant diversity and productivity (Li et al. 2006; Bever et al. 2015). In comparison to bacteria, fungi are more dependent on the presence of organic matter or on living organisms in the case of obligate parasites or symbionts (Urbanová et al. 2015). Despite their critical ecological and economic role, soil fungal assemblages recruited by plants are still poorly understood compared to soil bacterial communities (Öpik et al. 2006), especially in desert ecosystems.

In drylands, revegetation using xerophytic plants is regarded as an effective means of rehabilitating the ecological environment and improving biological diversity (Wang et al. 2012), which may help to maintain multiple ecological functions and ecosystem stability, particularly the diversity of aboveground plant communities (Zavaleta et al. 2010). However, the function of belowground biodiversity is not well understood (Hector and Bagchi 2007). Soil fungal communities, as a key component of total terrestrial biodiversity, play an important role in biodiversity conservation and help retain the functionality of desert ecosystems (Wardle and Lindahl 2014; Delgado-Baquerizo et al. 2016). As stress-tolerant life forms, soil fungi in drylands exhibit a high level of diversity (Makhalanyane et al. 2015). However, their contribution to biodiversity restoration in desert ecosystems has not been studied. Therefore, assessment of fungal diversity after revegetation with xerophytic shrubs will contribute to a better understanding of the importance of belowground diversity during the process of ecosystem rehabilitation in drylands.

Biotic and abiotic factors significantly affect soil fungal composition and diversity at local and regional scales (LeBlanc et al. 2015; Gao et al. 2016). Plants influence soil fungal communities through host specificity and by generating diverse organic substrates (Peay et al. 2013). Soil fungi acquire plant-derived carbon (C), which is ultimately derived from plant photosynthesis, through floor litter, root litter, and exudates (Herman et al. 2012). Precipitation and temperature are important climate factors influencing soil fungal communities (Vargas-Gastélum et al. 2015), as they have direct

effects on the primary production and photosynthetic processes, thus increasing litter production and input of C into both forest and desert ecosystems (Belnap et al. 2005; Boisvenue and Running 2006). Concurrently, soil fungal diversity and composition are strongly dependent on soil properties, such as soil water, nutrients, and pH (Liu et al. 2015; Wang et al. 2015). On a local scale, without considering any external factors, variation in soil properties is mainly caused by litter quality and root exudates provided by different plant species (Merilä et al. 2010). Because of their close associations with plants, especially in the case of symbionts and pathogens, fungal communities are particularly sensitive to shifts in vegetation (Goldmann et al. 2015). However, the knowledge on whether specific soil fungal assemblages exist under different shrub species in desert regions is limited.

The objectives of this study were to examine how soil fungal communities respond to shrub species after revegetation and to identify which shrub species are most suitable for rebuilding degraded sandland ecosystems in terms of the structure and function of fungal communities. We investigated the soil fungal communities under the canopies of three shrub species (*Artemisia ordosica*, *Salix psammophila*, and *Caragana microphylla*) and in a nearby bare sandland (as a control), in the Mu Us Desert in northern China. We speculated that the shrublands would have higher fungal diversity than the bare sandland, and that different shrub species would have their own fungal assemblages. To test the above hypotheses, we applied high-throughput 18S ribosomal RNA (rRNA) gene sequencing to analyse the soil fungal communities in the three shrublands and bare sandland.

Materials and methods

Study site and soil sampling

This study was conducted at the Yanchi Research Station, Ningxia province, northwestern China (37°04'–38°10' N and 106°30'–107°47' E, 1550 m above sea level), on the southwestern fringe of the Mu Us Desert. The site is characterized by a semi-arid continental monsoon climate with an average annual temperature of 8.1 °C and a mean annual precipitation of 287 mm. Approximately 62% of the rainfall occurs from July to September (Jia et al. 2014). The soil texture of the study area was sandy in the 0- to 1-m profile. Before

revegetation, due to land degradation, the landscape of the research area has been composed of widespread sand dunes and sparse xeric island vegetation for over decade. Beginning in 1998, *A. ordosica*, *S. psammophila*, and *C. microphylla* were simultaneously established on stabilized sand dunes without vegetation via aerial seeding, cutting propagation, and seedling planting, respectively. After revegetation, the shrublands were fenced, grazing was prohibited, and no fertilizer was applied. Currently, the area is dominated by *A. ordosica*, *S. psammophila*, and *C. microphylla* shrublands, while some bare sandlands were reserved for scientific research outside the plantation area. In these shrublands, sparse herbaceous species (e.g., *Leymus secalinus*, *Setaria viridis*, *Ixeridium gracile*, and *Corispermum mongolicum*) are distributed beneath the shrubs.

Within the 2 × 2 km area of the study site, three shrublands (*A. ordosica*, *S. psammophila*, and *C. microphylla*) were selected for the study, as well as a bare sandland, used as the control. Their distribution on the study site is illustrated in Fig. S1. In July 2015, three 20 × 20 m sampling plots were randomly selected in each shrubland and the bare sandland, separated by a distance of 20 m from each other. Basic information on the sampled shrublands is shown in Table 1. For each shrubland, five shrubs were randomly chosen in each plot for soil sample collection. Five 10-cm deep soil core samples were collected under the canopy of each shrub at an intermediate distance between the trunk and the edge of the canopy using a 4.5-cm diameter soil cylinder after removing the litter layer. The five samples collected in each plot were mixed to create one composite sample. Furthermore, three sites 1 × 1 m in size were randomly established around the sampling cores in each plot, at which the understory herbaceous plants were investigated after soil sampling. For the bare sandland, an S-shaped route was designed in each plot to ensure the sample representativity. Five samples were then collected along this line (Fig. S2) and mixed into a composite sample. Twelve composite samples were collected in total: 4 treatments × 3 replicates. The samples were sieved through a 2-mm mesh to thoroughly homogenize and remove the roots, plant residues, and stones. Each soil sample was separated into two portions, one of which was stored at -20 °C for molecular analyses, while the other was air-dried for physicochemical analysis.

Measurement of soil and plant properties

The soil water content (SWC) was determined gravimetrically after drying the samples in an oven at 105 °C for 24 h. Soil pH was measured in a soil/water (1:1) suspension. The total soil organic C (SOC) was determined by the K₂Cr₂O₇-H₂SO₄ oxidation method. The total nitrogen (TN) content was analysed using a Kjeldahl Apparatus Nitrogen Analyzer (Kjeltec 2200; Foss, Hillerød, Denmark). The total phosphorus (TP) content was measured by an ultraviolet spectrophotometer (UV-2550; Shimadzu, Kyoto, Japan). The number of understory herbaceous plant species, the height of each specimen, and the cover per species were recorded. The diversity of understory plants was measured using the Shannon–Wiener index.

DNA extraction, PCR amplification, and sequencing

DNA was isolated from 0.2 g of homogenized soil sample with an E.Z.N.A.® Soil DNA Kit (D5625–01; Omega Bio-tek, USA), according to the manufacturer's instructions. An 18S rRNA gene fragment, corresponding to the NS1 and FUNG regions, was amplified. The forward primer (5'-CCTA CACGACGCTCTTCCGATCTN (barcode) GTAGTCATATGCTTGTCTC-3') contained a 7-bp barcode sequence unique to each sample and the fungal primer NS1. The reverse primer (5'-GACT GGAGTTCCTTGGCACCCGAGAATTCCAA TTCCCGTTACCCGTTG-3') contained the primer Fung. PCR amplifications were performed in 50-μL reaction mixture containing 10× PCR buffer, 0.5 μL dNTP, 0.5 μL of each primer, 5 μL Platinum Taq (5 U/μL), 10 ng of template DNA, and ultrapure H₂O filled up to the total volume. Thermal cycling consisted of an initial denaturation at 94 °C for 3 min; 5 cycles of denaturation at 94 °C for 30 s, annealing at 45 °C for 20 s, and extension at 65 °C for 30 s; 20 cycles of denaturation at 94 °C for 20 s, annealing at 55 °C for 20 s, and extension at 72 °C for 30 s; and a final extension at 72 °C for 5 min. Each sample was amplified in triplicate, combined, and purified using a DNA purification kit (Gel Purification Kits, Sangon, China). Amplicons of different samples were then pooled in equimolar concentrations. Primer and primer dimers were separated out by electrophoresis on a 1% agarose gel, and final PCR products were recovered. Sequencing was conducted on the Illumina MiSeq

Table 1 Basic information on the sampled shrublands

| Shrublands | Vegetation coverage (%) | Shrub type | Mean shrub height (m) | Mean shrub canopy area (m ²) | Main associated herbaceous plants |
|---------------|-------------------------|-----------------------------|-----------------------|--|--|
| Aro shrubland | 58 | <i>Artemisia ordosica</i> | 0.61 | 0.85 | <i>Leymus secalinus</i> <i>Setaria viridis</i> <i>Cynanchum thesioides</i> <i>Heteropappus altaicus</i> <i>Ixeridium gracile</i> |
| Sap shrubland | 65 | <i>Salix psammophila</i> | 2.60 | 6.41 | <i>Ixeridium gracile</i> <i>Lespedeza davurica</i> <i>Calamagrostis epigeios</i> |
| Cam shrubland | 62 | <i>Caragana microphylla</i> | 2.99 | 6.19 | <i>Corispermum mongolicum</i> <i>Calamagrostis epigeios</i> <i>Salsola collina</i> <i>Setaria viridis</i> |

Aro, *Artemisia ordosica*; Sap, *Salix psammophila*; Cam, *Caragana microphylla*

sequencing system (Illumina, USA) at Sangon Biotech Co., Ltd. (China).

Bioinformatics analyses

Paired-end reads were assigned to samples based on their unique barcode and truncated by cutting off the barcode and primer sequence. Paired-end reads from the original amplicons were merged into full length sequences by Flash software (v1.2.7; Magoč and Salzberg 2011). Sequences were then trimmed for primers, filtered, and assigned to their respective samples according to the unique barcodes. At the same time, sequence reads with a quality score lower than 20 or a read length of less than 200 bp were removed, as were sequences containing any unresolved nucleotides. The presence of chimeric sequences was assessed by the UCHIME algorithm (Edgar et al. 2011) implemented in Mothur (v1.30.1; Kozich et al. 2013). The remaining non-chimeric sequences were clustered into operational taxonomic units (OTUs) using Uclust (v1.1.579; Edgar 2010) at the $\geq 97\%$ identity threshold; singleton OTUs were removed. To eliminate the effects of different sequence numbers among the samples on the fungal community analysis, OTU abundance tables were rarefied at the minimum number of sequences (2961 sequences in this study) for each soil sample. Further analysis of composition and diversity was performed based on the rarefied OTU tables. Taxonomic assignment was carried out with the Ribosomal Database Project (RDP) classifier. The relative abundances of

different phyla or other taxonomic categories in each sample were calculated. Alpha diversity indices were calculated using Mothur (v1.30.1; Kozich et al. 2013). Functional groups of fungi, i.e., saprotrophic, plant pathogenic, animal parasitic, mycoparasitic, ectomycorrhizal (EcM), and arbuscular mycorrhizal (AM), were identified following the criteria by Tedersoo et al. (2014) (detail in Table S1).

Statistical analyses

In this study, significant differences were determined using statistical tests at a significance level of 0.05. Bonferroni correction was used to correct for all multiple comparisons. Before statistical analyses, the data were subjected to the Kolmogorov-Smirnov test for normality and to the Levene test for homogeneity of variance. Differences between treatments in soil properties (SWC, pH, SOC, TN, and TP), understory plant diversity, fungal diversity index, and relative abundances of all fungal and functional groups were tested by one-way analysis of variance (ANOVA) with least significant difference tests. Results are presented as mean values \pm standard error (SE). Regression analyses were performed to evaluate the relationships between the environmental variables and the fungal community diversity. Correlations between the relative abundance of functional fungi and soil properties and between the relative abundance of functional fungi and understory plant traits were evaluated using the Pearson method. All statistical analyses were performed using SPSS 20.0

(SPSS Inc., Chicago, IL, USA). Similarity in OTU composition between treatments was analysed with non-metric multidimensional scaling (NMDS), using the Bray–Curtis similarity index and one-way analysis of similarity (ANOSIM) with 9999 permutations. For the Mantel test, the Bray–Curtis coefficient and Euclidean distance were used to construct dissimilarity matrices of fungal community and soil variables, respectively. NMDS, ANOSIM, and Mantel test were performed with the Vegan package in the R 3.3.1 software.

Results

Soil and understory plant properties

Compared to the bare sandland, significantly higher SOC, TN, and TP contents were observed in the *A. ordosica* and *S. psammophila* shrublands, while, in the *C. microphylla* shrubland, only the SOC content was markedly higher (Table 2; $P < 0.05$). The SOC and TN contents differed significantly among the three shrublands ($P < 0.05$), with highest values observed in the *A. ordosica* shrubland, followed by the *S. psammophila* shrubland, and the lowest values being observed in the *C. microphylla* shrubland. The SWC was also highest in the *A. ordosica* shrubland, as was the herbaceous plant diversity (Table 2).

Fungal community α -diversity

A total of 17,521 OTUs was obtained from 12 soil samples. Among these, 2795 non-fungal OTUs identified as Alveolata, Amoebozoa, and Animalia were removed from the dataset, leaving 14,726 OTUs that were identified as fungi. After normalization of sequence numbers, 193 fungal OTUs (35,532 sequences) were taken for subsequent analyses. Taxonomic richness was estimated by the Chao1 index, and diversity of the fungal community was analysed using the Shannon index. The results showed that taxonomic richness and diversity were significantly greater in the *A. ordosica* and *C. microphylla* shrublands than in the bare sandland ($P < 0.05$; Fig. 1). However, no significant difference was observed between the *S. psammophila* shrubland and the bare sandland. Additionally, based on regression analyses, there was a significantly positive linear relationship between the Chao 1 and Shannon indices of soil fungi and the understory plant diversity ($R^2 = 0.548$,

$P = 0.006$ and $R^2 = 0.397$, $P = 0.028$, respectively; Fig. 2b and c).

Fungal community composition and taxonomic structure

The dominant fungal phyla across the 12 soil samples were Ascomycota and Basidiomycota, accounting for more than 90% of the fungal sequences. In addition, Chytridiomycota, Glomeromycota, Cryptomycota, and Blastocladiomycota were found at low relative abundances in all samples (Fig. 3). Compared to the bare sandland, there was a significantly lower relative abundance of Ascomycota and a markedly higher relative abundance of Basidiomycota in the *S. psammophila* shrubland ($P < 0.05$). In contrast, no significant differences in the relative abundances of Ascomycota or Basidiomycota were detected between the *A. ordosica* or *C. microphylla* shrublands and the bare sandland. In addition, the *A. ordosica* shrubland had higher relative abundances of Glomeromycota, Cryptomycota, and Blastocladiomycota than the bare sandland. Among the four treatments, the relative abundance of Glomeromycota was greatest in the *A. ordosica* shrubland ($P < 0.05$).

Further taxonomical classification at the genus level revealed that only 61 fungal genera were detected in this study. Among them, 16 genera with relative abundances greater than 1% were detected in all samples (Fig. 4). The genera *Hanseniaspora*, *Fusarium*, and *Penicillium*, belonging to Ascomycota, were dominant (Table S2). Furthermore, approximately 57% of the fungal sequences across all samples could not be classified into a definite genus. The three shrublands had markedly higher relative abundances of *Hanseniaspora* and *Penicillium* than the bare sandland ($P < 0.05$). *Fusarium* showed a higher relative abundance in the *A. ordosica* and *C. microphylla* shrublands ($P < 0.05$). Moreover, the highest relative abundance of *Ramicandelaber* was in the *A. ordosica* shrubland, while the *S. psammophila* shrubland had the highest relative abundances of *Geopora* and *Marcelleina* ($P < 0.05$).

In the sample ordination results, samples from the same shrub species tended to cluster together. Meanwhile, a clear separation was associated with revegetation along the NMDS axis (Fig. 5). The ANOSIM results indicated significant effects of different treatments on the fungal community structure ($R = 0.806$, $P < 0.001$). All pairwise comparisons were significantly

Table 2 Soil and understory plant properties as compared with ANOVA (mean values \pm S.E., $n = 3$)

| Properties | Bare sandland | Aro shrubland | Sap shrubland | Cam shrubland |
|-----------------|-------------------|-------------------|-------------------|-------------------|
| SWC (%) | 1.42 \pm 0.41 A | 2.40 \pm 0.06 B | 1.50 \pm 0.04 A | 1.47 \pm 0.22 A |
| pH | 8.58 \pm 0.03 A | 8.50 \pm 0.03 A | 8.54 \pm 0.06 A | 8.46 \pm 0.06 A |
| SOC (g/kg) | 0.47 \pm 0.06 A | 3.01 \pm 0.14 B | 2.07 \pm 0.05 C | 1.12 \pm 0.14 D |
| TN (g/kg) | 0.03 \pm 0.01 A | 0.26 \pm 0.02 B | 0.18 \pm 0.02 C | 0.07 \pm 0.01 A |
| TP (g/kg) | 0.16 \pm 0.01 A | 0.30 \pm 0.02 B | 0.26 \pm 0.01 B | 0.13 \pm 0.02 A |
| Plant diversity | – | 1.00 \pm 0.10 A | 0.58 \pm 0.03 B | 0.70 \pm 0.08 B |

Different capital letters indicate significant differences among the treatments tested by One-Way ANOVA ($P < 0.05$). SWC soil water content, SOC soil organic carbon, TN total nitrogen, TP total phosphorus. Plant diversity indicates understory plant diversity. Aro, *Artemisia ordosica*; Sap, *Salix psammophila*; Cam, *Caragana microphylla*

different, except for the bare sandland–*S. psammophila* shrubland and the *A. ordosica*–*C. microphylla* shrublands (Table S3). Based on the Mantel test, SOC content and understory plant diversity were significantly correlated with fungal community composition ($P = 0.038$ and $P = 0.031$, respectively; Table 3).

All fungal OTUs were further analysed in terms of their potential functional classification (Fig. 6 a–e). The

fungal OTUs, approximately 35%, were classified as saprotrophic, plant pathogenic, and EcM fungi. Compared to the bare sandland, the relative abundances of saprotrophic and parasitic fungi were higher in the *A. ordosica* and *C. microphylla* shrublands, but not in the *S. psammophila* shrubland (Fig. 6a and c). The relative abundance of plant pathogenic fungi was significantly lower in the *S. psammophila* shrubland ($P < 0.05$). The greatest relative abundances of EcM and AM fungi among symbiotic fungi were detected in the *S. psammophila* and *A. ordosica* shrublands, respectively (Fig. 6d and e).

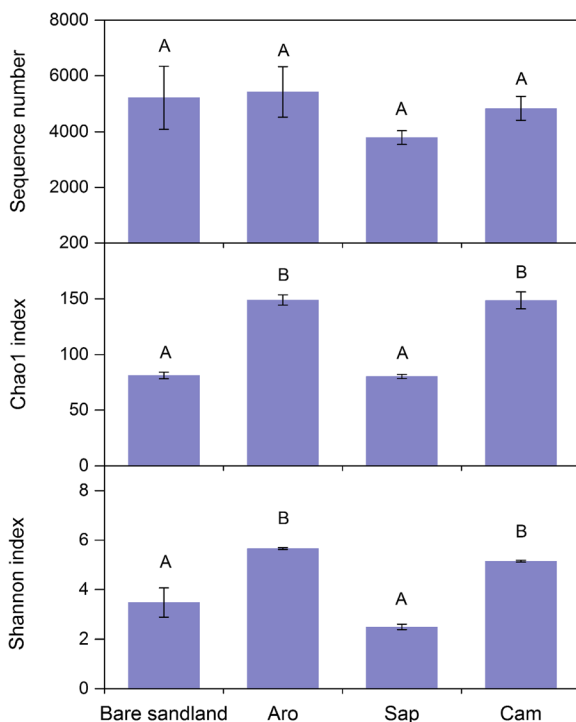


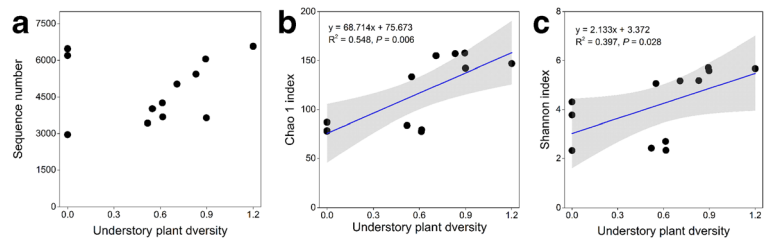
Fig. 1 Fungal α -diversity, including sequence number, Chao1 index, and Shannon index, in the bare sandland and different shrublands. Different capital letters indicate significant differences ($P < 0.05$). Data are shown as mean values \pm SE, $n = 3$. Aro, *Artemisia ordosica*; Sap, *Salix psammophila*; Cam, *Caragana microphylla*

Discussion

Variation in fungal diversity after revegetation

Inconsistent with our prediction, soil fungal diversity was not higher in shrublands than that in bare sandland (Fig. 1). Generally, the diversity of soil fungi increase with habitat development and soil complexity (Van Der Heijden et al. 2008; Liu et al. 2015). In the present study, while higher soil nutrient contents were detected in the *S. psammophila* shrubland than in the bare sandland, there was no significant difference in fungal diversity (Table 2; Fig. 1). The three shrub species, which belong to three different families, can change soil characteristics through their different fine-root distribution, production, and decomposition rates (Lai et al. 2016). However, compared to global-scale differences (Tedersoo et al. 2014; Wardle and Lindahl 2014), the minor differences in soil properties between the bare sandland and the shrublands were unlikely to significantly affect the diversity of soil fungi. In addition to the soil

Fig. 2 Relationships between understory plant diversity and fungal diversity. Grey regions indicate 95% confidence intervals around the regressions ($n = 3$)



characteristics, aboveground plant species are also a key factor that affects fungal diversity (Tedersoo et al. 2016; Zuo et al. 2016). Plants differ in provision of photosynthetic C for soil fungal growth, which allows plant communities to shape the specificity of fungal groups, thus affecting the diversity of soil fungi (Dickie 2007). The C from *S. psammophila* detritus might enable the growth of specific fungi that belong to a single taxon, such as Basidiomycota (Fig. 3), and hence result in low fungal diversity. Moreover, greater plant detritus production increases the amount of organic substrates that enter the soil, thereby elevating fungal diversity (Waldrop et al. 2006; Cline et al. 2018). Although *S. psammophila* provided the greatest amount of detritus to soil microbes (Lai et al. 2014, 2016), the availability of C in the *S. psammophila* shrubland might be lower than in the other two shrublands.

In shrub-dominated desert ecosystems, shrub species affect understory plant communities by providing shade and beneficial nutrient conditions (Pugnaire et al. 2004).

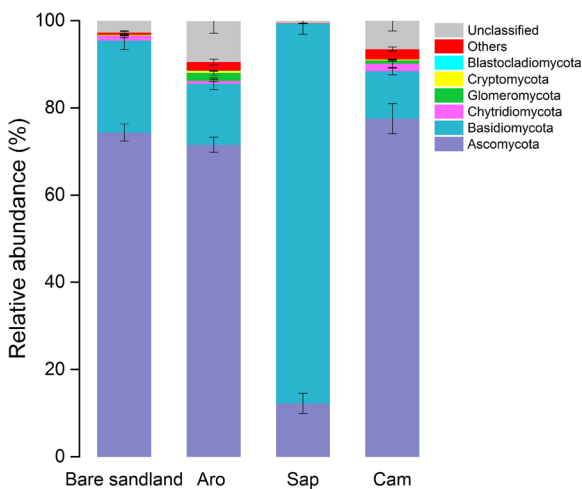


Fig. 3 Mean relative abundances of the major phyla of soil fungi in the bare sandland and different shrublands. Data are shown as mean values \pm SE, $n = 3$. Aro, *Artemisia ordosica*; Sap, *Salix psammophila*; Cam, *Caragana microphylla*

In this study, understory plant diversity had a significantly positive correlation with both the fungal Chao1 and Shannon indices ($R^2 = 0.548$, $P = 0.006$, and $R^2 = 0.397$, $P = 0.028$, respectively; Fig. 2b and c). Dominant woody plants may indirectly affect soil fungi by regulating understory plant diversity (Gömöryová et al. 2013). However, some studies have suggested that dominant plant species usually have a stronger effect on the diversity of soil fungi than the diversity of aboveground plants and that the dominance of one tree species can maintain increased fungal diversity (Mölder et al. 2014; Tedersoo et al. 2016). A study of a semi-arid area indicated that, after introducing a shrub species (*C. microphylla*) to a degraded steppe, the light fraction of SOC, which is the major driver of soil microbial diversity, increased at the 0–20 cm depth level (Lai et al. 2017). Therefore, further research concerning

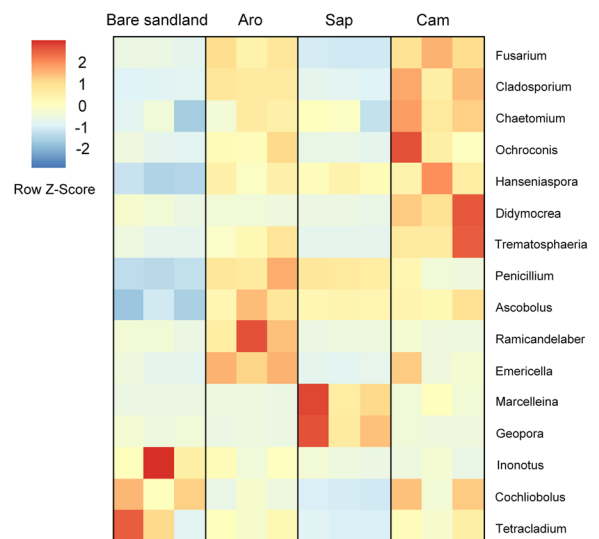


Fig. 4 Heat map comparison of the dominant soil fungal genera detected in the bare sandland and different shrublands. Only genera with a relative abundance of $>1\%$ are shown. Relative abundances of genera are expressed as median centred Z-scores between all samples. Each sample column contains the result of single replicates ($n = 3$). Aro, *Artemisia ordosica*; Sap, *Salix psammophila*; Cam, *Caragana microphylla*

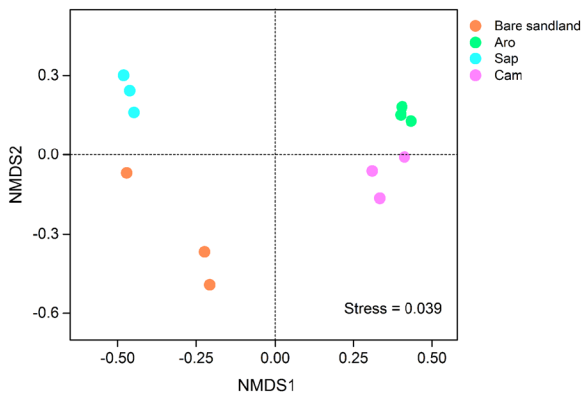


Fig. 5 Ordination of soil fungal community structure based on operational taxonomic units (OTUs), as determined by non-metric multidimensional scaling (NMDS) using the Bray–Curtis similarity index. Stress = 0.039, $n = 3$. Aro, *Artemisia ordosica*; Sap, *Salix psammophila*; Cam, *Caragana microphylla*

differences in the effects of dominant shrub species and their associated herbaceous plants on fungi in drylands should be conducted.

Strong coupling of shrub species and fungal community composition

In support of our second hypothesis, soil fungal community structure differed markedly after rehabilitation with different shrub species (Fig. 5). Meanwhile, among the soil properties, SOC content was the only variable significantly related to the composition of the fungal community ($R = 0.235$, $P = 0.038$; Table 3). Similarly, previous studies showed that the variation in SOC storage depends on shifts in the composition of soil fungal communities, not the other way around (Clemmensen et al. 2015). In addition, unlike bacterial communities, which are heavily shaped by soil parameters, fungal composition is more closely associated with plants (Schmidt et al. 2014). After revegetation with different shrub species, the substantial amelioration of

Table 3 Correlations between fungal community composition and understory plant traits/soil properties as determined by Mantel test ($n = 3$)

| | SWC | pH | SOC | TN | TP | Diversity |
|-----|--------|-------|--------------|-------|-------|--------------|
| R | -0.065 | 0.067 | 0.235 | 0.172 | 0.095 | 0.285 |
| P | 0.607 | 0.276 | 0.038 | 0.101 | 0.233 | 0.031 |

Bold type indicates a significant correlation ($P < 0.05$). SWC soil water content, SOC soil organic carbon, TN total nitrogen, TP total phosphorus; Diversity, understory plant diversity

microclimate and soil nutrient conditions under shrubs promoted the growth of different herbaceous species, which thereby influenced the fungal composition (Gömöryová et al. 2013). It has been indicated that a substantial shift in the composition of the soil fungal community is followed by plant host introduction and depends on plant identity (Bell et al. 2014). In this study, the SOC content was found to significantly differ among the three shrublands (Table 2), which might be attributed to the disparate soil fungal assemblages.

As anticipated, the three shrublands were associated with disparate fungal communities (Fig. 3). Across all samples, the phylum with the greatest relative abundance was the Ascomycota. This result was in accordance with the findings that the Ascomycota are often predominant in environments with scarce soil nutrients that suffer drought stress (Vargas-Gastélum et al. 2015; Wang et al. 2016a). On the other hand, in the *S. psammophila* shrubland, the Basidiomycota was the dominant phylum. It has been shown that most Ascomycota and Basidiomycota species are regarded as being predominantly decomposers (Baldrian et al. 2012). Thus, the different constituents of plant detritus in the three shrublands would affect the fungal composition, especially the species of the Ascomycota and Basidiomycota phyla. Compared to the *A. ordosica* and *C. microphylla* shrublands, plant residue in the *S. psammophila* shrubland might contain a relatively higher proportion of recalcitrant C (e.g., lignin and cellulose) than of other C forms, resulting in an increased number of Basidiomycota species, which are able to degrade lignin and cellulose (Blackwood et al. 2007; Wang et al. 2016b).

Among the functional groups, saprotrophic fungi were the dominant group in our study (Fig. 6). Many saprotrophic fungi belong to Ascomycota and Basidiomycota (Sterkenburg et al. 2015; Wang et al. 2016b), and they are the main decomposers of plant detritus (Baldrian et al. 2011). Our results show that the relative abundance of saprotrophic fungi was similar among the three shrublands (Fig. 6a), although the three shrub species provide the soil with significantly different fine-root necromass (Lai et al. 2014, 2016). Additionally, many dominant genera, with relative abundances greater than 1% and belonging to saprotrophic fungi, showed no significant difference in the relative abundance among the three shrublands (Table S2). One possible explanation may be that the relative abundance of saprotrophs was similar, while their total biomass was

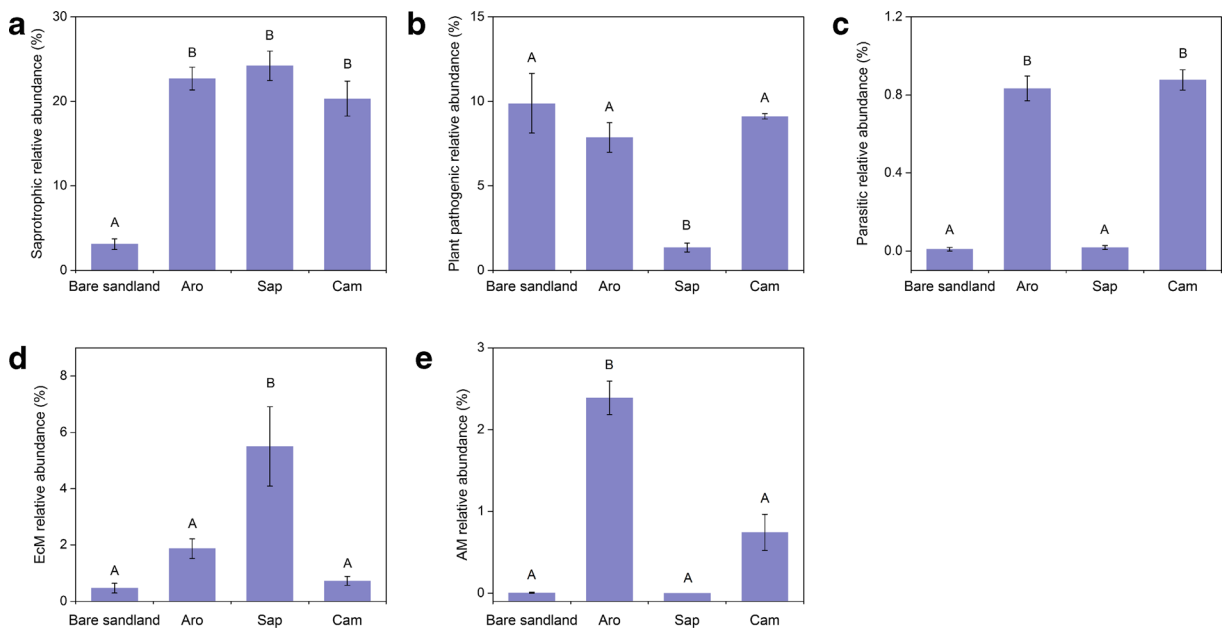


Fig. 6 Mean relative abundances of the major functional groups in the bare sandland and three shrublands. Data are shown as mean values \pm SE, $n = 3$. Aro, *Artemisia ordosica*; Sap, *Salix*

psammophila; Cam, *Caragana microphylla*; EcM, ectomycorrhizal fungi; AM, arbuscular mycorrhizal fungi

at the same time different among the three shrublands. Moreover, it has been shown that EcM fungi can restrict the realized niche of saprotrophs, suppressing their decomposer activity under undisturbed conditions (Bödeker et al. 2016). In our study, the higher relative abundance of EcM fungi in the *S. psammophila* shrubland (Fig. 6d) could be restricting the activity of saprotrophic fungi.

The relative abundances of EcM and AM fungi, the major mycorrhizal fungi, differed significantly among the three shrublands (Fig. 6d and e). Because of their symbiosis with plant roots, the host plant identity is a dominant driver of the composition of mycorrhizal fungal community (Martínez-García et al. 2015; Koorem et al. 2017). In our study, the highest relative abundances of EcM and AM fungi were detected in the *S. psammophila* and *A. ordosica* shrublands, respectively (Fig. 6d and e). A previous study of the same area showed that the dominant shrub species have different fine-root morphology and that *S. psammophila* has the highest fine-root biomass and necromass (Lai et al. 2016). This might contribute to the growth of EcM fungi that potentially have the capacity to decompose soil organic matter (Lindahl and Tunlid 2015). However, AM fungi have no known saprotrophic capabilities; instead, they rely on saprotrophic fungi for

decomposition of complex organic sources (Herman et al. 2012). Thus, the different fine-root necromasses of the three shrublands might have no direct effect on AM fungi. On the other hand, AM fungal communities are strongly related with plant diversity (Hiiesalu et al. 2014). In our study, the relative abundance of AM fungi was positively correlated with understory plant diversity ($P = 0.001$; Table 4). Therefore, *A. ordosica* might affect the diversity and abundance of AM fungi through preserving understory plant diversity.

Generally, both EcM and AM fungi contribute to C cycling and storage in the ecosystem (Soudzilovskaia et al. 2015). However, only the relative abundance of AM was significantly related to the SOC content ($P = 0.005$; Table 4), and the *A. ordosica* shrubland had the highest SOC content (Table 2). It has been shown that, compared to ecosystems dominated by AM fungi, ECM fungus-dominated ecosystems tend to store more SOC in the soil by reducing soil respiration (Averill et al. 2014; Averill and Hawkes 2016) and that the growth form of EcM fungi is a critical determinant of SOC sequestration (Clemmensen et al. 2015). We speculate that specific groups of EcM fungi (e.g., cord-forming EcM fungi), which are linked to the rapid turnover of soil organic matter (Clemmensen et al. 2015), exhibited a higher relative abundance and limited the SOC

Table 4 Pearson correlation coefficients for the relative abundance of functional fungi and the soil properties/understory plant traits in the shrublands ($n = 3$)

| | Saprotrophic fungi | Pathogenic fungi | Parasitic fungi | EcM fungi | AM fungi |
|-----------------|--------------------|------------------|-----------------|-----------|----------------|
| SWC | 0.314 | 0.303 | 0.352 | −0.200 | 0.785** |
| pH | 0.267 | −0.632 | −0.404 | 0.379 | −0.343 |
| SOC | 0.279 | −0.097 | −0.015 | 0.180 | 0.681* |
| TN | 0.392 | −0.130 | −0.122 | 0.289 | 0.585 |
| TP | 0.296 | −0.271 | −0.307 | 0.392 | 0.525 |
| Plant diversity | 0.069 | 0.683* | 0.600 | −0.416 | 0.897** |

SWC soil water content, SOC soil organic carbon, TN total nitrogen, TP total phosphorus. Plant diversity indicates understory plant diversity. * and ** indicate a significant correlation at the level of 0.05 and 0.01, respectively

accumulation in the *S. psammophila* shrubland. In addition, the microbial use efficiency of plant detritus is important for determining SOC accumulation. Plant litter contains a higher proportion of labile C, which is preferentially decomposed by microbes, and the products of this process contribute to the formation of stable C in the soil (Cotrufo et al. 2013). Though *S. psammophila* produced the most plant litter and recruited the highest relative abundance of EcM fungi, the litter might have had a higher proportion of recalcitrant C, which restricts the microbial use efficiency of plant detritus.

In addition to mycorrhizal fungi, the relative abundance of plant pathogenic fungi was significantly different among the three shrublands (Fig. 6b). *A. ordosica* and *C. microphylla* shrublands had a higher relative abundance of *Fusarium* (Fig. 4; Table S2), which are well known plant pathogens (Li et al. 2014). Pathogens are universal and abundant, leaving no plant species or ecosystem free of their influence, and they play a critical role in structuring plant communities and maintaining plant diversity (Bever et al. 2015). Our results show that the relative abundance of plant pathogenic fungi had a significantly positive correlation with the understory plant diversity in the three shrublands (Table 4). Previous studies have found that density-dependent pathogens can influence the maintenance of aboveground vegetation diversity by mediating competition between plants (Bell et al. 2006; Petermann et al. 2008). Therefore, the higher relative abundance of soil pathogens in the *A. ordosica* and *C. microphylla* shrublands might mediate the relationships between the dominant shrubs and their corresponding understory herbaceous plants to preserve plant diversity in the shrublands. However, greater relative abundance of a specific fungal taxon

does not always result in greater ecosystem functioning. The actual contribution of the specific taxa to the ecological function should be further researched by culture and control experiments.

Importantly, only the fungal community in bulk soil was included in this study. Microbial communities of the rhizosphere significantly contribute to plant health and nutrient cycling (Berg and Smalla 2009) because of their close relationships with plant roots. Therefore, information on the microbial community of the rhizosphere under different shrub species will further help to understand the underlying mechanisms of nutrient cycling. Furthermore, though we delineated fungal OTUs into functional groups using public databases, the detailed roles of fungal species in nutrient cycling and their effect on aboveground community assemblage remain unclear. Thus, functional gene analyses of soil microbial communities should be conducted in future studies.

Conclusions

In summary, revegetation with various shrubs affected the diversity and composition of the soil fungal community. Soil fungal diversity in the *A. ordosica* and *C. microphylla* shrublands, but not the *S. psammophila* shrubland, was greater than that in the bare sandland and exhibited varying relationships with soil properties. The results indicate that the variation in fungal diversity was directly affected by the shrub species on a local scale. In addition, different shrub species had their corresponding specific fungal groups. Differences in specific fungal groups might contribute to differences in SOC sequestration and aboveground plant diversity in the three

shrublands. In conclusion, this study highlights the strong correlation between the soil fungal community and revegetated shrubs in a desert ecosystem, represents the first step toward better comprehension of the plant–fungus relationships in a semi-arid ecosystem, and provides a perspective on the selection of shrub species for restoration of degraded ecosystem in terms of SOC sequestration as well as above- and belowground diversity.

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