

Land-use change alters patterns of soil biodiversity in arid lands of northwestern China

Feng-Rui Li · Ji-Liang Liu · Wei Ren · Lu-Lu Liu

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Abstract

Background and aims Irrigation-maintained artificial oases (AO) in arid regions of northwestern China provide vital human settlement sites. Recent human population increases has caused rapid AO expansion, mainly through transforming natural grassland to arable and afforested land. Here, we assessed how soil biodiversity is affected by various AO expansion strategies, each representing historical land-use regimes.

Methods We sampled six dominant functional groups of soil biota, covering multiple trophic levels: macrofauna consumers (predators and insect herbivores), mesofauna decomposers (Oribatida and Collembola), and microbial decomposers (bacteria and fungi). Sampling was carried out in three AO sites of northwestern China, each containing distinct land uses: natural grasslands (NG; non-

irrigated), shrub (*Haloxylon ammodendron*) plantations (SP; non-irrigated), tree (*Populus gansuensis*) plantations (TP; irrigated), and arable lands (AL; irrigated).

Results The conversion of NG to SP, TP, and AL eliminated or reduced the abundance of some NG-adapted taxa. Their replacements were exotic species better suited for anthropogenic habitats. As a result, community composition shifted in all six functional groups, with greater differences between NG and TP and AL than between NG and SP. Based on taxonomic gains and losses within each group, we determined that NG to SP conversion positively affected diversity among predators, Collembola, and fungi, but negatively affected diversity of insect herbivores and Oribatida. Bacterial diversity remained unaffected. However, converting NG to TP and AL significantly promoted diversity in all six functional groups, although effect sizes differed.

Conclusions Our results suggest that different AO expansion strategies differentially affected the diversity and structure of belowground communities, which in turn, cascaded down to ecosystem functioning differently. These findings not only contribute to a better understanding of how the diversity and community composition within soil food-webs respond to land-use change but also provide key insights into the development of management strategies for AO ecosystems in drylands to mitigate the negative impact of land-use change on soil biodiversity and ecosystem functioning.

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Introduction

Anthropogenic changes in land use and management intensity are a major driver of soil biodiversity in terrestrial ecosystems (Filser et al. 1995; Foley et al. 2005; Jetz et al. 2007; Jangid et al. 2008; Newbold et al. 2015). Land-use change can lead to habitat loss, fragmentation, and simplification (Fahrig 2003, 2017; Van Nouhuys 2005; Ewers and Didham 2006; Mortelliti et al. 2011; Mantyka-pringle et al. 2012; Buchmann et al. 2013; Jantz et al. 2015). As a result, non-native species may invade and completely replace native species, leading to landscape-level shifts in soil biodiversity pattern (Fahrig 2003; Krauss et al. 2012; De Vries et al. 2013; Barnes et al. 2014). Despite being widely documented in a variety of terrestrial ecosystems (Falcucci et al. 2007; Koellner and Geyer 2013; Zhang et al. 2014; Newbold et al. 2015; Krashevskaya et al. 2016; Paz-Kagan et al. 2017; Szoboszlay et al. 2017), the effects of land-use change on soil biodiversity are not well understood in economically important artificial oasis (AO) ecosystems that occur widely in arid regions of northwestern China (Fu et al. 2009).

Irrigation-maintained AO ecosystems in the northwestern China's arid regions provide vital human settlement sites for millennia (Cheng et al. 2014; Zhao et al. 2016). Rapid growth of human populations in the AO areas over the last five decades has resulted in rapid AO expansion, mainly through transforming natural grasslands to arable fields, along with afforested trees and shrubs that act as shelterbelts of agricultural landscapes (Li et al. 2003, 2016). Typically, arable fields receive both irrigation and fertilization, tree plantations receive only irrigation, while shrub plantations receiving neither.

Converting natural grasslands to other land-use types dramatically alters habitat characteristics, including vegetation type, plant community composition, diversity, productivity, and soil properties (Mortelliti et al. 2011; Fahrig 2017). These changes may affect demographic processes relevant for population growth, reproduction, and survival of belowground communities (Ewers and Didham 2006; Guisan and Rahbek 2011), with potentially negative impact on soil biodiversity and ecosystem functioning (Bardgett and van der Putten 2014; Byrnes et al. 2014; Delgado-Baquerizo et al. 2016). Soil contains an extremely wide range of functional groups, including microbial decomposers at basal trophic levels, micro/mesofauna decomposers and consumers at intermediate trophic levels, as well as macrofauna

decomposers and consumers (e.g., detritivores, herbivores, predators, and omnivores) at high trophic levels (Holt 1997; McCann et al. 2005; De Vries et al. 2013). Previous studies investigating the effects of changing land use on AO soil biodiversity have focused on only one or a few taxa, such as ground-dwelling spiders, beetles (Li et al. 2014; Feng et al. 2015), mites, collembolans (Li et al. 2013), or soil bacteria (Li et al. 2015). It is known that soil functional groups contribute to key ecosystem functions and services through complex non-trophic and trophic interactions with each other (Goudard and Loreau 2008; Megias et al. 2011; Griffin et al. 2013; Wagg et al. 2014; Filazzola et al. 2017). To date, no studies have been conducted to comprehensively assess how different AO expansion strategies, representing different anthropogenic land-use regimes, influence patterns of soil biodiversity at multiple trophic levels.

To address this knowledge gap, a study was performed in an arid region in northwestern China. In this study, we measured the abundance and richness of six dominant soil functional groups and the variables of key environmental factors that influence the distribution of functional groups in natural grasslands (non-irrigated), shrub plantations (non-irrigated), tree plantations (irrigated), and arable lands (irrigated) at three AOs in northwestern China. Sampled organisms spanned multiple trophic levels and body sizes, including macrofauna consumers (predators and insect herbivores), mesofauna decomposers (Oribatida and Collembola), and microbial decomposers (bacteria and fungi). With these data, we aimed to: (1) evaluate changes in the abundance, composition, and richness of soil faunal and microbial communities across different AO expansion strategies, and (2) determine the relative importance of environmental factors in shaping the variation in community composition between habitats across sites. We predicted that the studied six functional groups would differ in responses to AO expansion strategies, because of differences in their life history, body size, dispersal ability, trophic position, and resource requirements.

Materials and methods

Study area and site description

The study was carried out in a century-old AO zone of Linze County, Gansu Province, northwestern China

(39°21' N, 100°07' E; 1384 m a.s.l.; Fig. 1a). The region's climate is temperate, arid, and continental, with cold winters and hot, dry summers. Mean annual precipitation (based on 30-year records) is 116.8 mm, 80% of which occurs during the growing season (May to September). Mean annual pan-potential evaporation is 2390 mm. Mean annual air temperature is 7.6 °C, with the lowest temperature (−27.3 °C) occurring in January, and the highest temperature (39.1 °C) occurring in July.

The Linze oasis zone covers an area of approximately 4460 km² and comprises several small, isolated AOs, three of which (separated by at least 1 km) were selected for this study. In the Linze oasis, surface water from rainfall and glacier/snow-melt runoff in nearby mountains is available for irrigation (Wang et al. 2010). On the fringes of each AO, four land-use types (Fig. 1b) were chosen: natural grassland (NG), a mature native shrub (*Haloxylon ammodendron*) plantation (SP; 32 years old), a mature native poplar tree (*Populus gansuensis* C. Wang et H. L. Yang) plantation (TP; 36 years old), and arable land (AL; average 34 years old). Between-habitat distances ranged from 500 to 1000 m.

Shrubs *Calligonum mongolicum* and *Nitraria sphaerocarpa* dominated sampled NG, with the shrub layer covering 26.9 ± 3.9% (mean ± SE) and the herbaceous layer covering 9.6 ± 3.5%, respectively. Sampled SP had been planted with seedlings from a commercial nursery, followed by irrigation for 3 years only. Further irrigation was unnecessary as natural precipitation and groundwater were sufficient for established *H. ammodendron* seedlings (Tian et al. 2014). Shrub- and herb-layer covers were 77.3 ± 2.6% and 7.8 ± 3.6%, respectively. Sampled TP were planted with saplings and irrigated annually. Average trunk diameter at breast height was 24.9 ± 3.1 cm, average tree height was 19.2 ± 1.9 m, average existing stand density was 2340 ± 350 stems ha⁻¹, and average herb-layer cover was 2.3 ± 2.9%. Sampled AL were monocropped spring maize (*Zea mays* L.) fields (for commercial production of hybrid seed) that began cultivation 10 years ago. Maize plants were sown with 50-cm row spacing and mulched with plastic film. Aboveground biomass (seeds plus stalks) was 25.4 ± 3.3 t ha⁻¹. Maize fields were annually irrigated (9000–10,000 m³ ha⁻¹) and fertilized with complex NPK fertilizers (250–350 kg N ha⁻¹, 150–200 kg P₂O₅ ha⁻¹, and 100–150 kg K₂O ha⁻¹). For the past 30 years, farmyard manure had also been applied in 2–3-year intervals at rates of 12,000–15,000 kg ha⁻¹.

Sampling of soil fauna communities

At each AO site, three sampling plots (20 m × 20 m) per land-use type were randomly established at least 50 m apart (Gao et al. 2014). Five subplots (2 m × 2 m), at least 8 m apart, were randomly set up within each sampling plot. The total number of samples was 180 (five subplots per plot × three plots per land-use type × four land-use types per AO × three AOs). Five soil samples (50 cm × 50 cm, 20 cm depth) were taken from the five subplots in late August 2014, at peak abundance and richness in flora and fauna communities (Liu et al. 2017). Soil macrofauna were hand-sorted in the field. Simultaneously, five smaller soil samples (10 cm × 10 cm, 10 cm depth) were taken from each subplot and transported to the laboratory. Oribatid mites and collembolans were extracted from these samples using a modified Berlese-Tullgren apparatus for 48 h (Li et al. 2013). All macro- and meso-fauna specimens were preserved in 75% ethanol and identified to the family level based on published keys (Song et al. 1999; Yin 2000; Zheng and Gui 2004; Cai et al. 2011).

Measurements of soil and vegetation variables

After macro- and meso-fauna communities were sampled, aboveground biomass and species richness of plant communities were measured using five 1 m² quadrats in each of the five subplots. Aboveground herbaceous biomass in each quadrat was clipped at ~1 cm height, dried for 72 h at 60 °C, and weighed. After plant surveys, five 10-cm-deep soil cores (7 cm diameter) were taken from the five subplots and mixed to form a composite soil sample. After removing visible plant roots and stones, composite samples were passed through a 2-mm sieve and divided into two halves. The first half was air-dried and subsequently stored at 4 °C for analyses of soil physicochemical properties. Soil pH and electrical conductivity (as a proxy for soil salinity) were measured in a 1:5 soil: water solution using an electronic pH meter (Mettler Toledo 320-S; Mettler-Toledo Instruments Co. Ltd., Shanghai, China) and an electronic conductivity meter (DDSJ-308A; INESA Scientific Instrument Co. Ltd., Shanghai, China). To calculate the C: N ratio, soil organic carbon and total nitrogen were determined using a C/N analyzer (Elementaranalysatoren, Multi EA 2000, Analytik Jena, AG, Germany). Soil

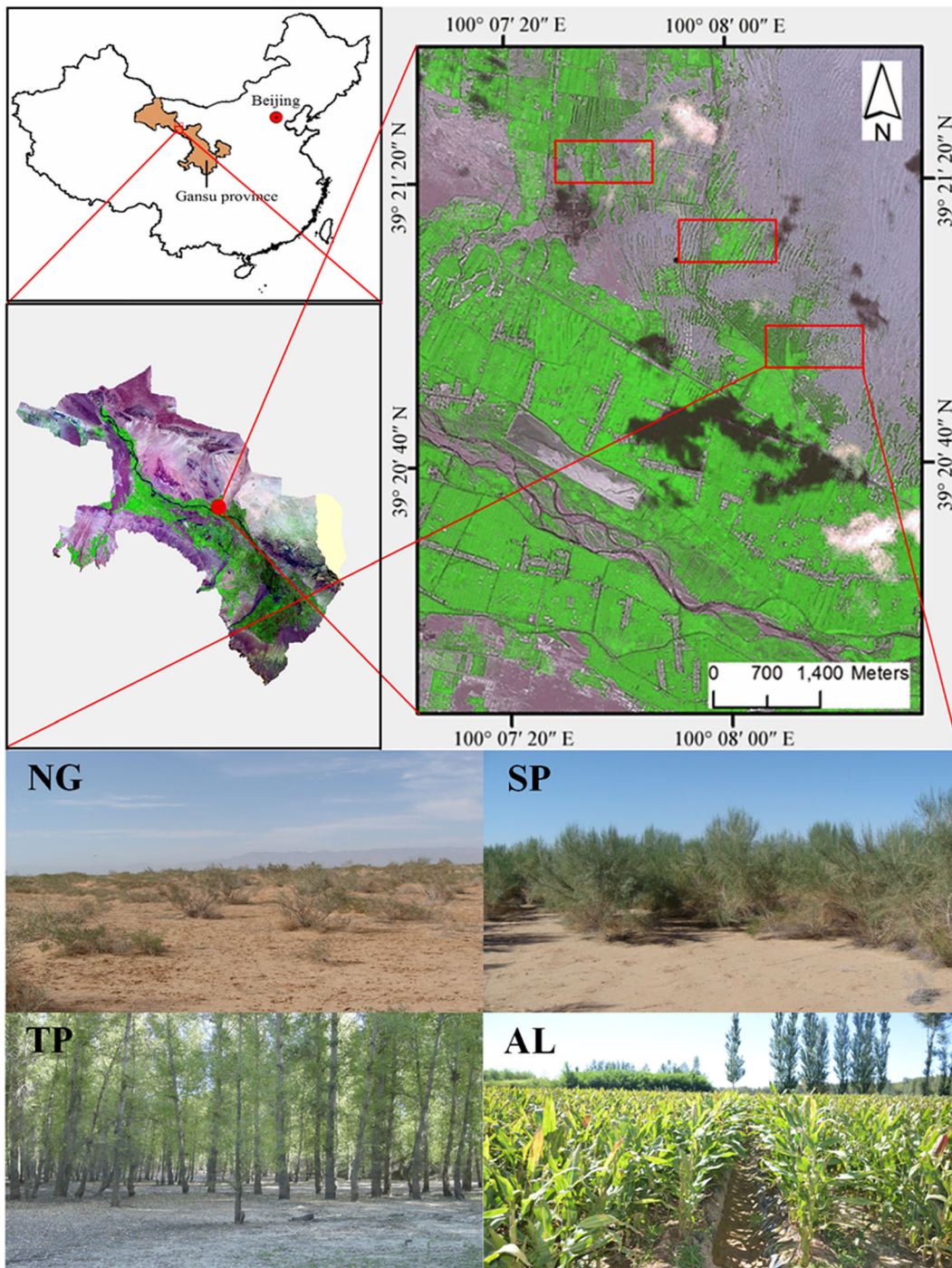


Fig. 1 The study site is located in the middle reaches of the Heihe River Basin in Gansu Province, northwestern China. NG, natural grassland; SP, planted shrub (*Haloxylon ammodendron*) plantation; TP, planted tree (*Populus gansuensis*) plantation; and AL, arable land

moisture content was determined using undisturbed soil cores (100 cm^3 , 10 cm depth) taken from the

same five subplots, oven-dried for 72 h at $105\text{ }^\circ\text{C}$, and weighed. The second half of the soil samples

was packed in polyethylene bags and immediately stored at $-20\text{ }^{\circ}\text{C}$ until DNA extraction. Next-generation high-throughput sequencing was applied to determine composition and diversity of soil bacterial and fungal communities.

DNA extraction and sequencing

Soil genomic DNA was extracted from 0.5 g of dried soil per sample with the QIAGEN DNA Stool Mini Kit (QIAGEN, Hilden, Germany), following manufacturer protocol. Extracted DNA was diluted to 10 ng/ μL , checked using 1% agarose gel electrophoresis, and stored at $-20\text{ }^{\circ}\text{C}$ until PCR analysis. Soil bacterial communities were evaluated through amplifying the V4 region of 16S rRNA gene using primers 515F and 806R (forward primer: 5'-GTGC CAGCMGCCGCGGTAA-3', reverse primer: 5'-GGACTACHVGGGTWTCTAAT-3'). Soil fungal communities were evaluated through amplifying Internal Transcribed Spacer (ITS) rRNA gene using primers 1737F and 2043R (forward primer: 5'-GGAA GTAAAAGTCGTAACAAGG-3', reverse primer: 5'-GCTGCGTTCTTCATCGATGC-3'). Reverse primers contained a 6-bp error-correcting barcode unique to each DNA sample.

All PCR amplifications were performed in 30- μL reaction volumes, containing 15 μL Phusion High-Fidelity PCR Master Mix (New England Biolabs, Ipswich, MA, USA), 0.2 μM forward/reverse primers, and 10 ng template DNA. Thermocycling conditions were as follows: 98 $^{\circ}\text{C}$ for 1 min; followed by 30 cycles of denaturation at 98 $^{\circ}\text{C}$ for 10 s, annealing at 50 $^{\circ}\text{C}$ for 30 s, extension at 72 $^{\circ}\text{C}$ for 30 s; and ending with 72 $^{\circ}\text{C}$ for 5 min. Amplicons (200–400 bp) were confirmed on 2% EtBr agarose gels and purified using a GeneJET Gel Extraction Kit (Thermo Fisher Scientific, Carlsbad, CA, USA). Following quantitation, equal concentrations of purified amplicons were combined into a single tube. Sequencing libraries were generated with a NEB Next Ultra DNA Library Prep Kit for Illumina (New England Biolabs, Ipswich, MA, USA) following manufacturer protocol, and index codes were added. Library quality was assessed on a Qubit 2.0 Fluorimeter (Thermo Fisher Scientific, Carlsbad, CA, USA) and Agilent Bioanalyzer 2100. Pooled amplicons were paired-end sequenced (2×300 bp) on the Illumina MiSeq platform (Illumina Inc., San Diego, CA, USA).

Paired-end reads were merged with FLASH (Jia et al. 2016), a fast and accurate tool designed specifically for overlapping reads. Sequence reads were assigned according to sample-specific barcodes. Sequences were analyzed in QIIME (Quantitative Insights into Microbial Ecology), with in-house Perl scripts for calculating alpha- (within sample) and beta- (between sample) diversity. Reads went through QIIME quality filters before pick_de_novo_otus.py was used to select operational taxonomic units (OTUs) with the OTU table. Sequences at 97% nucleotide similarity were assigned to the same OTUs with UPARSE v7.0.1001 (<http://drive5.com/uparse/>). A representative sequence per OTU was screened and used to assign taxonomic composition in the Greengenes (bacterial 16S rRNA) and Unite (fungal ITS rRNA) databases. Taxonomic abundance per sample was generated at phylum, class, order, family, genus, and species levels. We further calculated relative abundance of each taxonomic classification in bacterial and fungal communities.

Statistical analyses

Subplot data per sampling plot were pooled (for taxonomic richness) and averaged (for abundance). We focused only on bacteria, fungi, Collembola, Oribatida, predators, and insect herbivores. Predator, insect herbivore, Collembola, and Oribatida diversity was assessed by measuring abundance (number of individuals m^{-2}) and family richness (number of families m^{-2}). Soil bacterial and fungal diversity was assessed by measuring OTU richness (number of bacterial and fungal OTUs) (Terrat et al. 2017). Pearson's correlations were used to detect multicollinearity among environmental variables: soil moisture content (SMC), soil pH, soil electrical conductivity (EC), soil organic carbon (SOC), soil total nitrogen (TN), C:N ratio, aboveground herbaceous biomass (AHB), and herbaceous species richness (HSR). High correlations between TN and SMC (Pearson's $r = 0.88$), SOC and SMC (Pearson's $r = 0.91$), as well as TN and SOC (Pearson's $r = 0.89$) led to the exclusion of TN and SOC from subsequent analyses.

Assumptions of normality and homogeneity of variance in response variables were tested with Kolmogorov–Smirnov and Levene's tests. When necessary, data were transformed with $\log_{10}(x)$, or $\log_{10}(x + 1)$ if zeros

were present. One-way ANOVAs and Tukey's HSD post hoc tests were used to test for differences in functional group diversity between NG and the three anthropogenic habitats (maize fields, tree plantations, and shrub plantations). Pearson's correlations were also used to examine the relationship between environmental variables and functional group diversity. These analyses were performed in SPSS 21.0 (IBM, Armonk, NY, USA).

Additionally, a permutational multivariate analysis of variance (PERMANOVA) on Bray-Curtis dissimilarities was performed in PRIMER 6 (Clarke and Gorley 2006) to determine variation in functional-group community composition among land-use types. Community compositional differences across NG and anthropogenic habitats were graphically illustrated with non-metric multi-dimensional scaling (NMDS) ordination on Bray-Curtis dissimilarities. Kruskal's formula was used to calculate stress values for each NMDS; values <0.2 indicated that a particular configuration was a good reproduction of the observed distance matrix (Clarke 1993). Percentage contribution per taxon to community dissimilarity between NG and anthropogenic habitats was determined using a SIMPER analysis (similarity percentages-species contributions) in PRIMER v6. Finally, variance partitioning analysis in CANOCO 5.0 (Ter Braak and Šmilauer 2012) was used to determine the shared and independent contributions of environmental variables to compositional changes in functional-group communities.

Results

Shifts in diversity and community composition of soil macrofauna consumers

We collected 3141 soil macrofaunal individuals from the four land-use types; insect and non-insect predators accounted for 44.6% of the total abundance, while insect herbivores accounted for 28.7% (Table S1). Soil predator community composition differed significantly among land-use types (PERMANOVA: $F_{3, 35} = 21.91$, $P < 0.001$). Accordingly, NMDS revealed strong separation of predator communities between NG and SP ($t = 3.76$, $P < 0.001$), NG and TP ($t = 5.56$, $P < 0.001$), as well as NG and AL ($t = 5.38$, $P < 0.001$). Community differentiation was greater between NG and irrigated habitats (TP, AL) than between NG and non-irrigated

SP (Fig. 2a). Further, SIMPER analyses revealed that average Bray-Curtis dissimilarities were 0.80 between NG and AL, 0.76 between NG and TP, and 0.50 between NG and SP, respectively. On average, converting NG to SP increased predator abundance by 50% and predator richness by 29% (Fig. 3) through the arrival of Salticidae, Asilidae, and Dolichopodidae. Converting NG to TP increased predator abundance by 224% and predator richness by 27% through the arrival of Lycosidae, Nesticidae, Asilidae, Carabidae, Staphylinidae, and Lithobiidae. Similarly, converting NG to AL increased predator abundance by 254% and predator richness by 85% through the arrival of Lycosidae, Asilidae, Carabidae, Cicindelidae, Coccinellidae, Staphylinidae, Geophilidae, and Scolopendrellidae (Fig. 3; Table S1).

Insect-herbivore community composition also differed significantly among land-use types (PERMANOVA: $F_{3, 35} = 15.53$, $P < 0.001$). Average dissimilarity was 0.44 between NG and SP (NMDS: $t = 2.96$, $P = 0.003$), 0.34 between NG and TP ($t = 3.25$, $P < 0.001$), and 0.49 between NG and AL ($t = 3.97$, $P < 0.001$) (Fig. 2b). Converting NG to SP decreased herbivore abundance by 160% and richness by 117% (Fig. 3), as some NG-adapted taxa (Curculionidae, Noctuidae, and Scarabaeidae) disappeared and others (Tenebrionidae) decreased in abundance. Converting NG to TP, in contrast, increased herbivore abundance by 111% and richness by 28%, as Melolonthidae appeared and existing taxa (Curculionidae and Elateridae) increased. Converting NG to AL did not affect insect herbivore abundance, but increased richness by 33%, due to the arrival of Elateridae and Melolonthidae (Fig. 3; Table S1).

Shifts in diversity and community composition of soil mesofauna decomposers

We collected 2644 soil mesofaunal individuals from the four land-use types, with Oribatida and Collembola accounting for 48.8 and 28.5% of the total abundance, respectively (Table S2). Soil collembolan communities differed markedly among land-use types (PERMANOVA: $F_{3, 35} = 31.27$; $P < 0.001$). Average dissimilarity was 0.22 between NG and SP ($t = 5.33$, $P < 0.001$), 0.46 between NG and TP ($t = 5.09$, $P < 0.001$), and 0.32 between NG and AL ($t = 6.73$, $P < 0.001$) (Fig. 2c). Overall collembolan richness did not change under NG-to-SP conversion, but collembolan

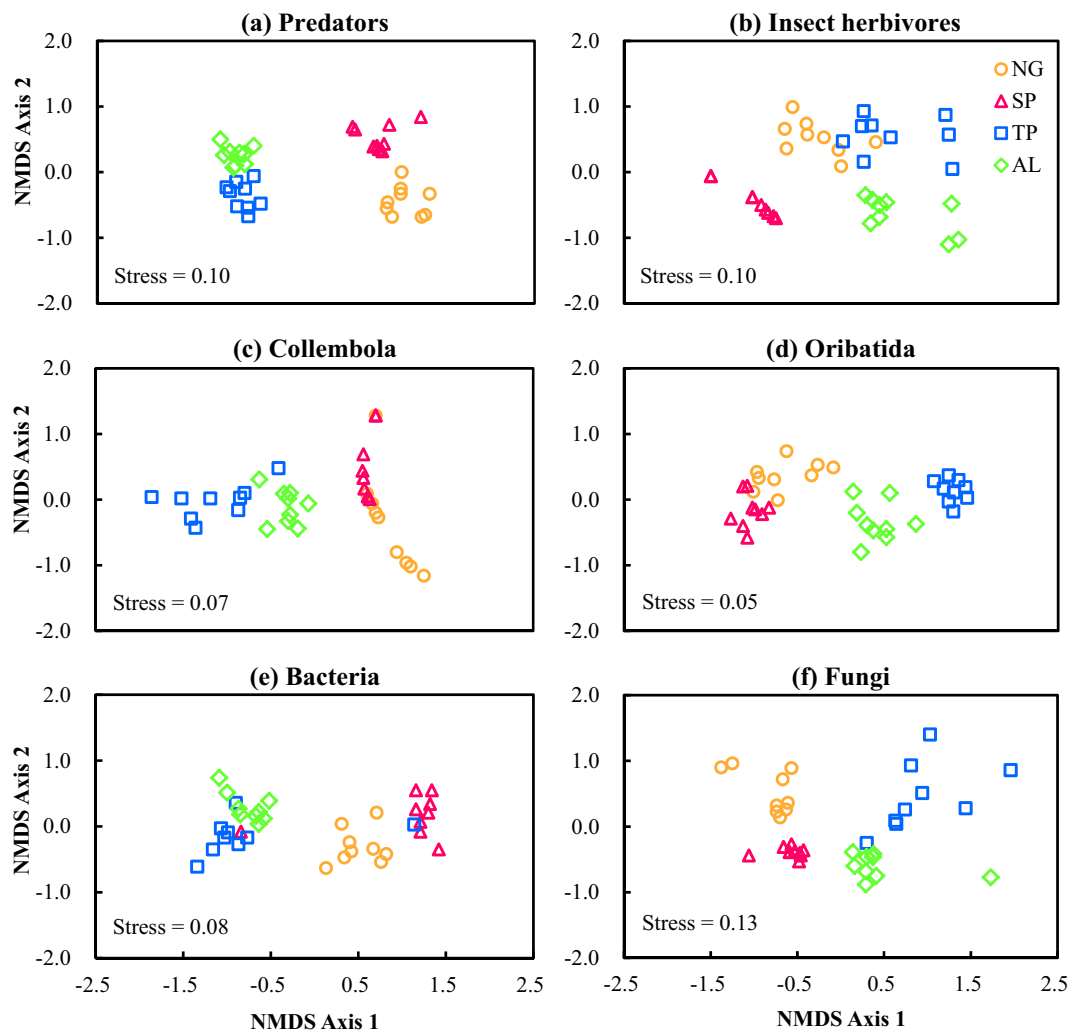


Fig. 2 Results of the non-metric multidimensional scaling (NMDS) ordination of community dissimilarity (Bray-Curtis) for **a** soil macrofauna predators, **b** soil macrofauna insect herbivores, **c** soil mesofauna Collembola, **d** soil mesofauna Oribatida, **e** soil bacteria, and **f** soil fungi. Dissimilarities were calculated using family abundance data for predators, insect herbivores, Collembola, and Oribatida, and using OTU (operational

taxonomic unit) abundance data for bacteria and fungi. Open circles represent natural grassland; open triangles represent shrub plantation; open squares represent tree plantation; and open rhombuses represent arable land. The stress value was calculated for each NMDS ordination to evaluate how well a particular configuration reproduces the observed distance matrix. Stress values <0.2 were considered good

abundance increased drastically (by 509%) with increased Isotomidae abundance. Converting NG to TP drastically increased collembolan abundance (+2800%) and richness (+140%). Likewise, converting NG to AL dramatically increased collembolan abundance (+3450%) and richness (+110%). Changes in collembolan communities under the latter two conversions were due to increased Entomobryidae and Isotomidae abundance, coupled with gains of new taxa (Hypogastruridae and Sminthuridae in both, plus Neelidae in TP only) (Fig. 3; Table S2).

Soil oribatid mite communities also differed markedly among land-use types (PERMANOVA: $F_{3, 35} = 15.55$; $P < 0.001$). Average dissimilarity was 0.24 between NG and SP ($t = 3.10$, $P < 0.001$), 0.58 between NG and TP ($t = 4.09$, $P < 0.001$), and 0.40 between NG and AL ($t = 4.12$, $P < 0.001$) (Fig. 2d). Converting NG to SP decreased oribatid abundance by 29% and richness by 31%. Conversely, converting NG to TP drastically increased oribatid abundance by 509% and richness by 295%, as Ceratozetidae, Damaeidae, Euphthiracaridae, and Oppiidae rose in abundance, while Camisiidae,

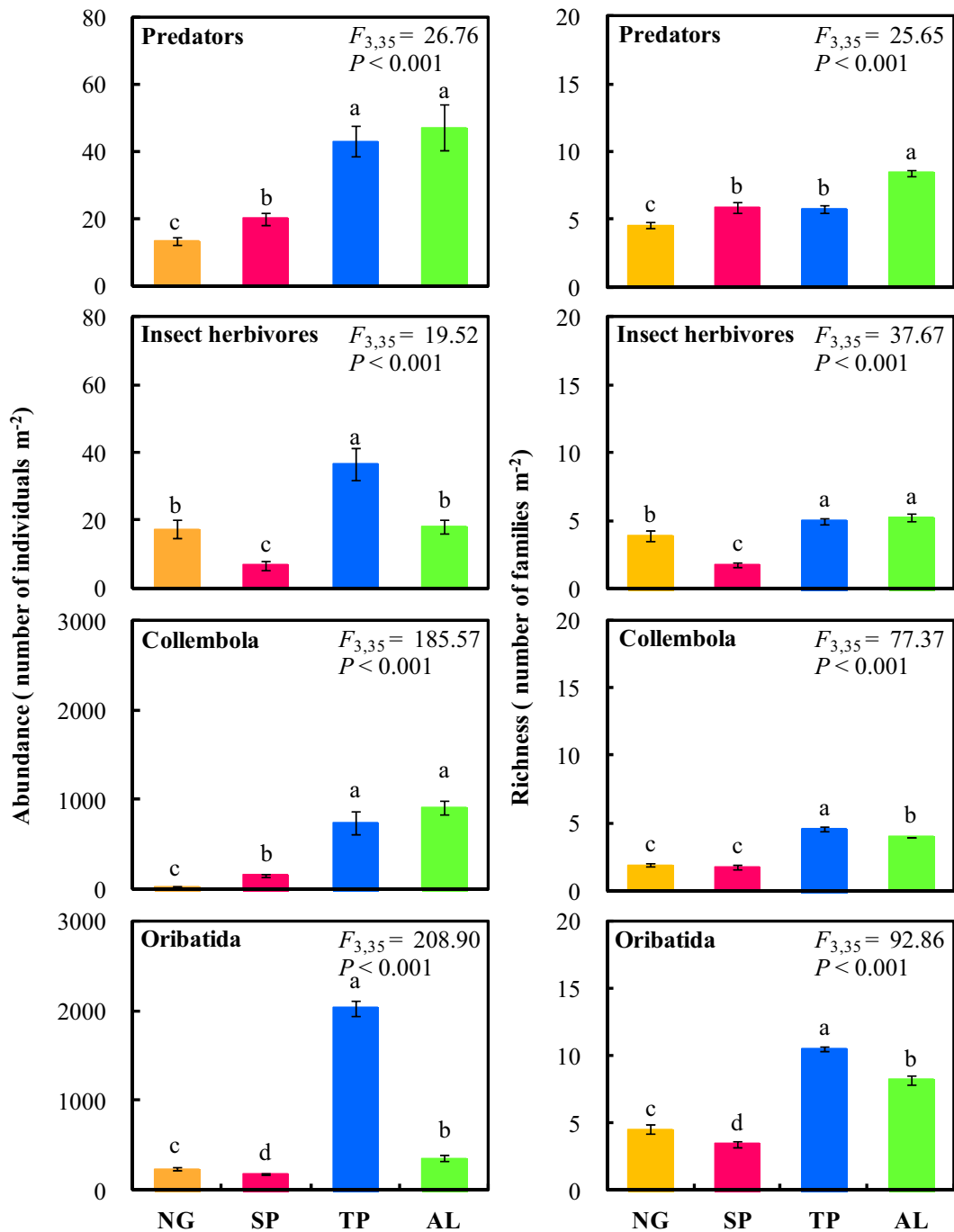


Fig. 3 Changes in the abundance and family richness of four dominant functional groups of soil macro- and meso-fauna (predators, insect herbivores, collembolans, and oribatid mites) in response to the conversion of natural grassland (NG) to shrub

plantation (SP), tree plantation (TP), and arable land (AL). Means (\pm standard error) with different letters indicate significant differences among land-use types (Tukey HSD test, $P < 0.05$)

Nothridae, Scheloribatidae, Tectocephidae, and Xylobatidae appeared in the soil. Converting NG to AL increased oribatid abundance by 49% and richness by

78%, resulting from elevated Ceratozetidae and Damaeidae abundance, coupled with gains of Nothridae, Scheloribatidae, and Tectocephidae (Fig. 3; Table S2).

Shifts in soil bacterial diversity and community composition

We obtained 1,688,253 high-quality sequences from the four land-use types. These 16S rRNA gene sequences were classified into 149,554 OTUs, representing 7 phyla, 15 classes, 27 orders, 45 families, and 72 genera/species. The two most abundant phyla were Actinobacteria and Crenarchaeota, accounting for 50.9 and 28.5% of total sequence abundance, respectively (Table S3).

Soil bacterial community composition differed significantly among land-use types (PERMANOVA: $F_{3,35} = 25.81$; $P < 0.001$). Average dissimilarity was 0.27 between NG and SP (NMDS, $t = 3.05$, $P = 0.003$), 0.35 between NG and TP ($t = 5.57$, $P < 0.001$), and 0.34 between NG and AL ($t = 6.36$, $P < 0.001$) (Fig. 2e). Although NG-to-SP-conversion did not substantially change overall bacterial OTU richness (Fig. 4), relative sequence abundance decreased in one Actinobacteria species and one Firmicutes species, but increased in two Actinobacteria, one Bacteroidetes, one Crenarchaeota, and two Proteobacteria. Moreover, four NG-adapted species (one Bacteroidetes, two Firmicutes, and one Proteobacteria) were lost (Table S3). In contrast, converting NG to TP and AL increased overall bacterial OTU richness, despite the loss of four NG-adapted species (two Ascomycota and two Proteobacteria).

Shifts in soil fungal diversity and community composition

We obtained 1,467,811 high-quality sequences from the four land-use types. These ITS rRNA gene sequences were classified into 21,493 OTUs, representing 34 phyla, 108 classes, 181 orders, 362 families, and 783 genera/species. Of the 34 phyla, Ascomycota accounted for 74.7% of total sequence abundance (Table S4). Fungal communities differed significantly among land-use types (PERMANOVA: $F_{3,35} = 4.91$; $P < 0.001$). Average dissimilarity was 0.64 between NG and SP ($t = 1.55$, $P = 0.007$), 0.82 between NG and TP ($t = 2.05$, $P < 0.001$), and 0.75 between NG and AL ($t = 2.48$, $P < 0.001$) (Fig. 2f).

Converting NG to SP increased overall fungal OTU richness by 80.4% (Fig. 4). This increase was the result of decreased relative sequence abundance of 22 NG-adapted species (18 Ascomycota, two Zygomycota, and two other fungal species), increased abundance of 33 additional species (25 Ascomycota, six Basidiomycota, and two Zygomycota), and gains of 17 new species

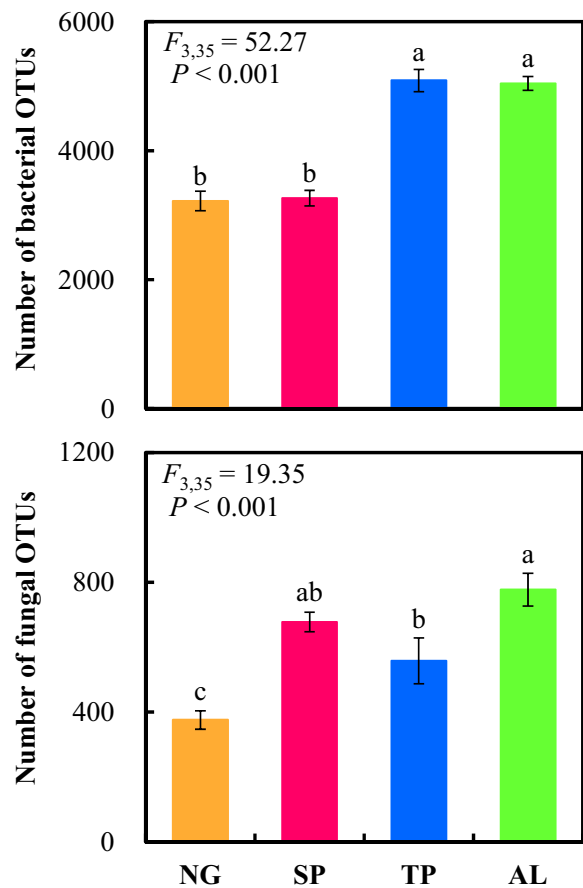


Fig. 4 Changes in bacterial OTU richness (the number of bacterial OTUs) and fungal OTU richness (the number of fungal OTUs) in response to the conversion of natural grassland (NG) to shrub plantation (SP), tree plantation (TP), and arable land (AL). Means (\pm standard error) with different letters indicate significant differences among land-use types (Tukey HSD test, $P < 0.05$)

(nine Ascomycota, six Basidiomycota, and two Chytridiomycota). Similarly, converting NG to TP increased fungal OTU richness by 49% (Fig. 4), as a result of increased abundance in 25 existing species (16 Ascomycota, four Basidiomycota, four Zygomycota, and one other fungal species) and gains of 23 new species (16 Ascomycota, six Basidiomycota, and one Zygomycota). However, abundance decreased among 35 NG-adapted species (29 Ascomycota, one Basidiomycota, one Chytridiomycota, two Zygomycota, and two other fungal species), while five NG-adapted species (three Ascomycota, one Basidiomycota, and one Zygomycota) were lost as well. Converting NG to AL increased fungal OTU richness by 107% (Fig. 4), due to increased abundance of 49 existing species (36 Ascomycota, four Basidiomycota, one Chytridiomycota, five

Zygomycota, and three other fungal species) and gains of 24 new species (17 Ascomycota, six Basidiomycota, and one Zygomycota). Simultaneously, the abundance of 27 NG-adapted species decreased (23 Ascomycota, one Chytridiomycota, one Zygomycota, and two other fungal species) and four NG-adapted species disappeared (two Ascomycota, one Basidiomycota, and one Zygomycota) (Table S4).

Relative contribution of environmental variables to variation in functional-group community composition

The conversion of NG to anthropogenic habitats significantly altered environmental conditions, but responses of individual environmental variables differed (Table 1). Variance partitioning analyses showed that the six environmental variables collectively explained more variation in community compositions of collembolans (82.2%) and oribatid mites (81.6%) than of predators (70.5%), insect herbivores (62.6%), bacteria (67.2%), and fungi (47.3%) (Table 2). The two strongest environmental predictors for community differentiation in insect herbivores were SMC and EC, whereas the strongest predictors for oribatids were EC and AHB. Additionally, SMC, EC, and AHB were the best predictors for community differentiation in predators, collembolans, bacteria, and fungi (Table 2).

Across all land-use types, predator abundance was positively correlated with SMC and C:N, but negatively correlated with pH, EC, and AHB. Additionally, predator richness was positively correlated with SMC and

negatively correlated with AHB (Fig. 5). Insect herbivore abundance was positively correlated with SMC and C: N, but negatively correlated with pH, EC, and AHB. Insect herbivore richness was positively correlated with SMC, C: N, and HSR, but negatively correlated with pH, EC, and AHB. Collembolan abundance was positively correlated with SMC and C: N and negatively correlated with pH, EC, and AHB. Collembolan richness was positively correlated with SMC, C:N, and HSR, but negatively correlated with pH, EC, and AHB. Oribatid abundance and richness were positively correlated with SMC, C: N, and HSR, whereas they were negatively correlated with pH, EC, and AHB. Bacterial OTU richness was positively correlated with SMC, C: N, and HSR and negatively correlated with pH, EC, and AHB. Fungal OTU richness was positively correlated with SMC and negatively correlated with AHB (Fig. 5). Furthermore, multiple regressions showed that environmental factors exerted a stronger influence on variability in abundances of collembolans, oribatids, and bacteria than of predators, herbivores, and fungi (Fig. 5).

Discussion

To our knowledge, this is the first study to document how AO expansion strategies may affect ecosystem functioning in northwestern China's arid regions through altering the diversity and structure of belowground communities (macro-, meso-, and micro-organisms). Below, we discuss our findings and their implications for conservation management of important AO ecosystems in drylands worldwide.

Table 1 Environmental variables (mean \pm standard error) measured in natural grasslands (NG), shrub (*Haloxylon ammodendron*) plantations (SP), tree (*Populus gansuensis*) plantations (TP), and arable lands (AL) in an arid region in northwestern China

	NG	SP	TP	AL	F _{3,35}	P
Soil moisture (%)	2.2 \pm 0.1 ^d	2.9 \pm 0.1 ^c	5.6 \pm 0.2 ^b	11.8 \pm 0.4 ^a	609.58	< 0.001
pH	9.5 \pm 0.1 ^a	9.4 \pm 0.1 ^a	8.8 \pm 0.1 ^b	9.0 \pm 0.1 ^b	14.68	< 0.001
Electrical conductivity ($\mu\text{s cm}^{-1}$)	165.5 \pm 19.8 ^b	282.5 \pm 38.4 ^a	55.1 \pm 1.5 ^d	88.2 \pm 4.3 ^c	51.75	< 0.001
Soil organic carbon (g kg ⁻¹)	1.0 \pm 0.1 ^d	1.7 \pm 0.3 ^c	5.1 \pm 0.6 ^b	7.5 \pm 0.4 ^a	89.71	< 0.001
Soil total nitrogen (g kg ⁻¹)	0.2 \pm 0.1 ^c	0.3 \pm 0.1 ^{bc}	0.5 \pm 0.1 ^b	1.1 \pm 0.1 ^a	50.45	< 0.001
C:N ratio	5.0 \pm 0.6 ^{bc}	5.1 \pm 0.3 ^c	11.3 \pm 0.9 ^a	6.7 \pm 0.6 ^b	20.17	< 0.001
Aboveground herbaceous biomass (g m ⁻²)	67.3 \pm 16.8 ^a	31.4 \pm 7.0 ^b	12.8 \pm 0.7 ^d	18.7 \pm 1.3 ^c	94.29	< 0.001
Herbaceous species richness (no. of species m ⁻²)	2.2 \pm 0.3 ^a	1.9 \pm 0.4 ^b	2.8 \pm 0.3 ^a	2.1 \pm 0.1 ^a	6.32	0.002

Means with different superscript letters within each variable indicate statistically significant differences among land-use types (Tukey HSD test, $P < 0.05$)

Table 2 Variation partitioning analysis for quantifying the relative contribution of the environmental variables to the variation (measured as inertia) in community composition of six dominant functional groups of soil biota. Environmental variables included soil moisture content (SMC), soil pH (pH), soil electrical conductivity (EC), soil C: N ratio (C: N), aboveground herbaceous biomass (AHB), and herbaceous species richness (HSR)

Variables	Inertia	% variation explained	Contribution (%)	<i>F</i>	<i>P</i>
Predators					
SMC	0.443	44.3	62.8	27.0	0.001
pH	0.019	1.9	2.7	1.9	0.080
EC	0.139	13.9	19.7	11.0	0.001
C:N	0.024	2.4	3.5	2.2	0.029
AHB	0.063	6.3	8.9	5.6	0.001
HSR	0.017	1.7	2.4	1.7	0.110
Total	0.705	70.5			
Residual	0.295				
Total variation	1				
Insect herbivores					
SMC	0.271	27.1	43.3	18.4	0.001
pH	0.039	3.9	6.2	3.0	0.042
EC	0.241	24.1	38.5	10.8	0.001
C:N	0.046	4.6	7.4	3.4	0.018
AHB	0.006	0.6	0.9	0.4	0.782
HSR	0.023	2.3	3.7	1.8	0.151
Total	0.626	62.6			
Residual	0.374				
Total variation	1				
Collembola					
SMC	0.581	58.1	70.6	47.2	0.001
pH	0.023	2.3	2.8	3.6	0.007
EC	0.136	13.6	16.6	15.9	0.001
C:N	0.010	1.0	1.2	1.6	0.184
AHB	0.066	6.6	8.1	9.7	0.002
HSR	0.006	0.6	0.7	1.0	0.399
Total	0.822	82.2			
Residual	0.178				
Total variation	1				
Oribatida					
SMC	0.049	4.9	6.0	6.3	0.002
pH	0.027	2.7	3.3	3.8	0.014
EC	0.619	61.9	75.8	55.3	0.001
C:N	0.021	2.1	2.6	3.2	0.020
AHB	0.085	8.5	10.4	9.5	0.001
HSR	0.015	1.5	1.9	2.4	0.041
Total	0.816	81.6			
Residual	0.184				
Total variation	1				
Bacteria					
SMC	0.097	9.7	14.4	7.2	0.001
pH	0.020	2.0	3.0	1.8	0.045
EC	0.462	46.2	68.7	29.2	0.001
C:N	0.021	2.1	3.1	1.8	0.038

Table 2 (continued)

Variables	Inertia	% variation explained	Contribution (%)	F	P
AHB	0.055	5.5	8.2	4.6	0.001
HSR	0.017	1.7	2.6	1.5	0.072
Total	0.672	67.2			
Residual	0.328				
Total variation	1				
Fungi					
SMC	0.214	21.4	45.3	9.2	0.001
pH	0.024	2.4	5.1	1.3	0.162
EC	0.129	12.9	27.3	6.5	0.001
C:N	0.024	2.4	5.1	1.3	0.161
AHB	0.064	6.4	13.5	3.4	0.001
HSR	0.018	1.8	3.8	1.0	0.445
Total	0.473	47.3			
Residual	0.527				
Total variation	1				

Effects of land-use change on the diversity and structure of belowground communities

In line with our hypothesis, soil functional groups responded differently to AO expansion. When NG was converted to SP, the diversity of predators, collembolans,

and fungi was favored, but insect herbivores and oribatids were at a disadvantage. Moreover, this shift had little impact on bacterial diversity. This considerable variation in response reflects differences in the various functional groups' physiological tolerance to the highly saline surface soil (0–10 cm) of the shrub (*H. ammodendron*)

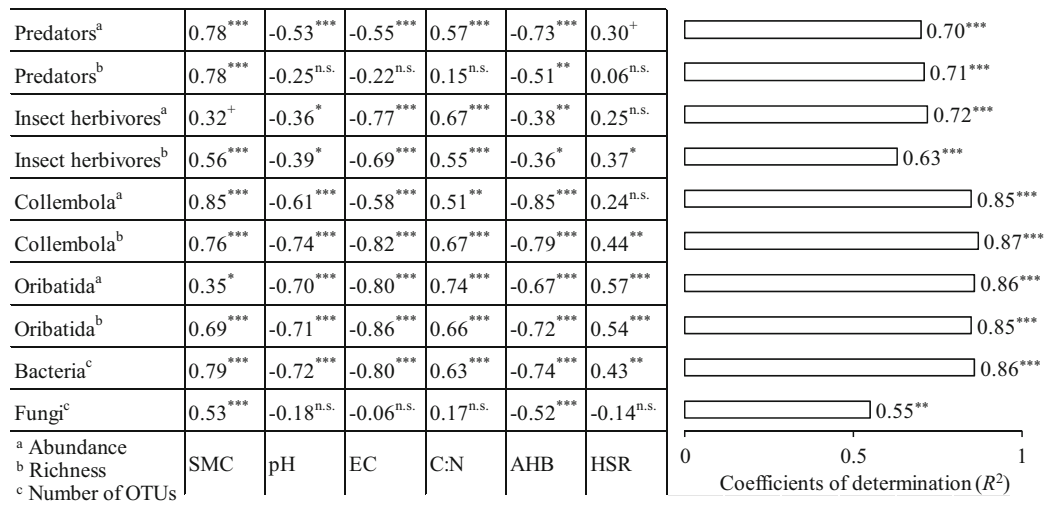


Fig. 5 Pearson's correlations between the diversity of six dominant functional groups of soil biota and environmental variables such as soil moisture content (SMC), soil pH (pH), soil electrical conductivity (EC), soil C: N ratio (C: N), aboveground herbaceous biomass (AHB), and herbaceous species richness (HSR). Correlation coefficients are given (*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$;

⁺ $P < 0.1$; n.s., not significant). The overall effect of the six selected environmental variables on variation in soil functional-group abundance and richness was determined by multiple regression analyses. Model's coefficients of determination (R^2) represent the percentage of variation explained by the environmental variables collectively

plantation. This shrub species possesses special glands for secreting salts that naturally accumulate in surface soil (Zhou 2012). Thus, we observed significantly higher surface soil salinity in SP than in NG. The results indicate that predators, collembolans, and fungi are not simply tolerant but respond positively to increased salinity, due to their higher abundance and diversity in SP relative to NG. Conversely, insect herbivores and oribatids respond negatively to elevated salinity due to their lower abundance and diversity in SP than in NG. A study in agricultural landscapes on the North China Plain reported that different species of ground-dwelling carabid beetles respond differently to salt-induced physiological stress (Liu et al. 2006).

The conversion of NG to TP and AL resulted in strong, consistent positive effects on soil functional-group diversity. Thus, forests and croplands appear to benefit multi-trophic biodiversity, making more diverse and abundant belowground communities compared to NG. Some other studies in northwestern China's arid regions also showed that converting NG to irrigated cropland significantly increased soil mite and collembolan richness and abundance (Li et al. 2013), along with soil bacterial diversity (Li et al. 2015). Notably, functional groups differed in their degree of positive responses. Overall, forest increased abundance and richness of insect herbivores, collembolans, and oribatids, whereas cropland supported greater predator and fungal diversity. Despite this variation between ecosystem types, overall positive effects can be attributed to continuous irrigation, which increased soil moisture but also decreased pH and salinity via the leaching of base cations in strong alkaline soils (Li et al. 2015; Liu et al. 2017). Consequently, the irrigated forest and cropland in our study are more favorable for growth, reproduction, and survival of some existing species as well as new species, thus increasing their diversity and abundance (Nielsen et al. 2010; Koellner and Geyer 2013). Using the data across all land-use types, our correlation analyses support the environmental effects. Specifically, soil moisture was positively correlated with abundance and richness of all six functional groups. Moreover, soil pH and salinity were negatively correlated with the abundance of all six functional groups except fungi (Fig. 5). Some studies in desert biomes also reported that aridity has a major impact on diversity and abundance of soil bacteria and fungi (Andrew et al. 2012; Maestre et al. 2015; McHugh et al. 2017). Nevertheless, the fact that pH and EC negatively related to bacterial

OTU richness but did not relate to fungal OTU richness suggests that soil bacteria are more sensitive to pH and EC than soil fungi. This result is consistent with earlier findings demonstrating that there is a close link between soil characteristics (especially pH) and soil bacterial diversity (Lauber et al. 2009; Rousk et al. 2010; Shen et al. 2013; Griffiths et al. 2016; Terrat et al. 2017).

We also observed significant shifts in functional-group community composition, but the degree of compositional variation differed across land-use conversion regimes. One striking finding was that our data do not support the trophic rank hypothesis, suggesting that habitat loss and fragmentation alter species composition more at higher trophic levels than at lower trophic levels (McCann et al. 2005; Liao et al. 2017). Conversion from NG to SP caused the biggest shift in fungal community composition, followed by predators, insect herbivores, bacteria, oribatid mites, and collembolans. Fungal community composition also experienced the greatest shift in response to conversion of NG to TP, followed by predators, oribatid mites, collembolans, bacteria, and insect herbivores. Additionally, conversion to AL had the largest effect on predator community composition, followed by fungi, insect herbivores, oribatid mites, bacteria, and collembolans. Thus, differentiation among fungal and predator communities was stronger than among insect herbivores, bacteria, oribatid mites, and collembolans. This suggests that changes to fungal and predator communities specifically indicate environmental perturbation associated with land-use change. In other words, soil fungi and predators can be used as two good indicator taxa of anthropogenic habitats in our study.

Another striking finding was that community differentiation in all six groups, except insect herbivores, was markedly greater between NG and irrigated, rather than non-irrigated, habitats. This result highlights that irrigation management was more important than vegetation type in structuring belowground communities in arid ecosystems. Our results are in line with the findings of other studies in drylands demonstrating that water availability was the most important determinant of the distribution and diversity of soil faunal and microbial communities (Mackay et al. 1986; Brockett et al. 2010; Darby et al. 2011; Maestre et al. 2015; McHugh et al. 2017). Increased soil moisture availability in irrigated habitats might drive the replacement of native species by invasive species better suited for the new environments, which in turn, increases species turnover, causing greater community differentiation (Robinson et al. 2018).

Implications for the functioning of AO ecosystems in drylands

The six dominant functional groups under study perform a wide range of fundamental ecosystem functions. Therefore, any changes in their abundance, community composition, and diversity would directly and indirectly (through trophic cascades) alter AO ecosystem functioning and stability (Connolly et al. 2013; Pasari et al. 2013; Wagg et al. 2014; Jing et al. 2015; Soliveres et al. 2016).

Predators and insect herbivores are two dominant components of soil macrofauna communities in the study area (Feng et al. 2015). The three land-use conversion regimes under study differed considerably in their relative influence on predator and insect herbivore diversity. The conversion of NG to SP increased predator abundance and richness, whereas decreased insect herbivore abundance and richness, thus reducing the potential risk of pest outbreaks in agricultural landscapes (Letourneau et al. 2009; Griffin et al. 2013). However, conversion to forests and croplands increased both predator and insect herbivore abundance and richness, suggesting the unpredictable effects on the ecosystem service of biological pest control. This is because biological pest control strongly depends on the ecological balance between populations of predators and insect herbivores (Huffaker et al. 1976; May and Hassell 1988). In general, a diverse and abundant predator community is better able to control insect pests (Riechert and Lawrence 1997; Straub and Snyder 2006; Tschamtko et al. 2007; Straub et al. 2008; Letourneau et al. 2009; Tyljanakis and Romo 2010). In addition, predators and insect herbivores also play a key ecological role as prey for other taxa, especially insectivorous birds, reptiles, and bats. Therefore, altered abundance and richness of both groups will initiate bottom-up cascading effects on predators at higher trophic levels, such as lizards (Filazzola et al. 2017), birds (Mestre et al. 2012), and bats (Böhm et al. 2011).

Collembolans and oribatid mites are dominant components of soil mesofauna communities in the study area (Li et al. 2013). As decomposers, these two functional groups contribute to ecological processes, including soil organic matter decomposition, nutrient cycling, and soil formation (Whitford and Parker 1989; Siepel and Maaskamp 1994; Rusek 1998; Neher et al. 2012; de Groot et al. 2016). The three land-use conversion regimes have been shown to substantially alter abundance, richness, and community composition of collembolans

and oribatid mites, but the magnitude and direction of their effects varied considerably. Converting NG to SP significantly increased collembolan abundance while reducing oribatid abundance and richness, indicating that collembolan-mediated ecosystem services would likely be improved, whereas oribatid-mediated ecosystem services would be harmed. However, converting NG to forest and cropland contributed to the ecosystem services provided by both collembolans and oribatids through drastically increased richness and abundance. These effects would likely trigger a top-down cascade on the potential prey of collembolans and oribatids. Our results corroborate recent work indicating similar effects of land-use conversion on soil mite communities that cascaded down to associated ecosystem services (de Groot et al. 2016). Furthermore, several studies reported that collembolans and oribatids can mobilize inaccessible nutrients through selectively feeding on fungi, bacteria, and other dead organic matter (Kaneko et al. 1998; Maraun et al. 1998; Filser 2002; Jørgensen et al. 2005; Schneider et al. 2005).

As primary decomposers of soil organic matter, soil bacteria and fungi provide fundamental ecosystem services, such as carbon/nitrogen cycling and storage, and plant growth and productivity (de Vries et al. 2013; Bardgett and van der Putten 2014; Delgado-Baquerizo et al. 2016). As specific services differ among functional groups of bacteria and fungi, it stands to reason that heterogeneous effects that various land-use conversions have had on the diversity and community composition of soil bacteria and fungi would differentially affect the ecosystem services. Overall, converting NG to SP substantially altered bacterial community composition but did not change bacterial OTU richness, whereas conversion to forest and cropland significantly altered both. Therefore, the latter two conversion regimes exert a stronger influence on bacteria-mediated ecosystem services than the former. In our study, bacterial communities were dominated by decomposer and nitrogen-cycling taxa Actinobacteria and Crenarchaeota (Xia et al. 2011; Levy-Booth et al. 2014), consistent with other studies in desert biomes (Andrew et al. 2012; Neilson et al. 2012; Maestre et al. 2015; McHugh et al. 2017). Unsurprisingly, shifts in bacterial community composition mainly occurred through changes in the relative abundance of these two taxa, along with Bacteroidetes and Proteobacteria.

Unlike bacteria, all three land-use conversions significantly altered fungal community composition and

enhanced fungal OTU richness, as a result of shifts in relative abundances of dominant taxa, such as Ascomycota, Basidiomycota, Chytridiomycota, and Zygomycota. These fungi are primarily involved in ecological functions, such as litter decomposition, photosynthesis, respiration, nitrogen fixation, and biosynthesis of plant growth hormones (Kuklinsky-Sobral et al. 2004). Therefore, altered soil fungal composition and diversity will strongly influence plant growth and vegetation productivity through effects on soil nutrient availability and nutrient uptake.

Conclusions

This study empirically confirms that focusing on multiple components of soil communities (macro-, meso-, and microorganisms) can accurately predict the impact of land-use change on soil biodiversity and ecosystem functioning. Various AO expansion regimes have led to distinct soil biodiversity patterns that exert differential cascading effects on ecosystem functioning. We show that conversion of grassland to irrigated forest and cropland increases functional-group diversity overall. In contrast, conversion to non-irrigated shrubland has a more complex effect, favoring predator, collembolan, and fungal diversity, but dampening insect herbivore and oribatid diversity. Therefore, the conservation of forests and croplands throughout northwestern China's arid regions is particularly crucial for maintaining AO ecosystem function and stability. Our findings shed light on how land-use change and management intensity interact to drive exotic species invasion and replacement of native species. This study emphasizes the challenge of managing belowground biodiversity in AOs experiencing high anthropogenic disturbance. Therefore, efforts to optimize AO development should fully consider the differential effects of AO expansion strategies on the diversity and community composition of soil macro-, meso-, and microorganisms.

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