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ORIGINAL PAPER

Forest thinning alleviates the negative effects of precipitation reduction on soil microbial diversity and multifunctionality

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Abstract

Thinning is an important forest management practice to mitigate the adverse effects of increased drought on tree growth and productivity. However, the responses of the soil microbial community and its functions to thinning and drought have received little attention in planted forests. In this study, we assessed the combined effects of thinning (30% and 45% of trees removed) and precipitation reduction (− 30%) on soil fungal and bacterial communities and the multifunctionality associated with carbon, nitrogen, and phosphorus cycling during one growing season (from April to September) in a 16-year-old larch plantation. We found that 45% thinning, but not 30%, significantly increased soil multifunctionality during the growing season (except for April and May) and fungal diversity in June. In contrast, precipitation reduction significantly decreased soil multifunctionality during the growing season and fungal diversity in June. Thinning also considerably suppressed the relative abundance of ectomycorrhizal (ECM) fungi during the growing season, whereas precipitation reduction significantly increased the relative abundance of ECM fungi in June and July. Furthermore, soil multifunctionality was more related to ECM and saprotrophic fungal communities than to bacterial communities. Our results suggest that a high thinning level can mitigate the negative effect of precipitation reduction on soil multifunctionality and fungal diversity, and this effect depends on the sampling month. Therefore, thinning is recommended as a tool to mitigate the impact of precipitation reduction on soil multifunctionality and the microbial community in larch plantations.

Keywords Soil multifunctionality · Precipitation reduction · Forest thinning · Fungal diversity · Bacterial diversity · Microbial community composition

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Introduction

Thinning is a core silvicultural practice that has been traditionally and widely implemented to promote tree growth and plantation productivity by reducing competition for soil resources between trees (Gavinet et al. 2019, 2020; Sohn et al. 2016). Global climate change is predicted to alter precipitation regimes, and drought is expected to become more frequent (Dai 2013; McDowell et al. 2016). Climate change will negatively affect forest productivity, soil microbial community composition, and ecosystem functions, such as nutrient cycling and soil organic matter decomposition (Brödlin et al. 2019; Chen et al. 2017; Hedo de Santiago et al. 2016; Peng et al. 2011). In this context, thinning has gained renewed interest as an adaptive approach to improving forest resistance and resilience to drought (Mausolf et al. 2018). Previous studies on drought mitigation by thinning have mainly focused on the response of aboveground communities, such as plant productivity, and community composition (Gavinet et al. 2019; Sohn

et al. 2013). However, belowground responses, particularly those of soil microbial communities and their relationship to functions, have received much less attention (Bastida et al. 2019; Beier et al. 2012). Soil microorganisms, such as bacteria and fungi, are the primary regulators of C and nutrient cycling in forest ecosystems (Delgado-Baquerizo et al. 2020; Maaroufi et al. 2019; Treseder and Holden 2013). Therefore, understanding the responses of soil microorganisms and their functions to thinning and drought is undoubtedly necessary for forest management practices to adapt forested plantations to future climate change.

Soil microbial communities are sensitive to changes in environmental factors such as drought and tree thinning (Brockett et al. 2012; Manzoni et al. 2016; Singh et al. 2010). Previous studies have shown that precipitation reduction changes soil microbial communities by directly altering soil water availability and indirectly regulating plant productivity and litter inputs (Manzoni et al. 2014). Soil microbial biomass decreased significantly by 12.9% in forests soil under precipitation reduction experiments (Ren et al. 2018). A recent meta-analysis showed that precipitation reduction negatively impacts soil microbial diversity (Yang et al. 2021a). On the other hand, thinning has been found to increase soil water availability resulting from reducing the loss of soil water through transpiration (Lagergren et al. 2008), interception of precipitation and competition for water among trees (Gebhardt et al. 2014). In turn, this silvicultural practice may lead to a positive effect on soil microbial activity, because soil moisture affects the kinetics of microbial enzymes and change the microbial community composition by altering diffusion of soluble substrates and extracellular enzymes (Hassett and Zak 2005; Zhou et al. 2020) However, only a few studies have investigated the combined impacts of drought and thinning on the soil microbial community in semiarid natural forests, and they found that the resistance of the soil microbial community to drought was fostered by thinning, but without considering the relationship between soil microbial community (e.g., functional groups) with multiple function, necessitating further investigation to improve our mechanistic understanding of such relationships (Bastida et al. 2017, 2019).

Forest soils provide multiple ecosystem functions (i.e., multifunctionality), and these functions occur simultaneously rather than individually. Traditionally, researchers have investigated the response of a single function or several individual functions (e.g., soil organic C decomposition and N mineralization) to environmental changes (Xu et al. 2021b; Zhou et al. 2019). For instance, precipitation reduction decreases the soil respiration rate, phosphorus bioavailability, and organic C stability (Hu et al. 2019; Yang et al. 2021b; Zhang et al. 2020). However, a single process cannot well represent the complexity of terrestrial ecosystems (Byrnes et al. 2014; Delgado-Baquerizo et al. 2020). Multifunctionality has recently been widely used as a composite indicator of soil quality (Manning et al. 2018; Megyes et al. 2021), to increase our ability to understand and predict the functions provided by soil microorganisms (Singh et al. 2018; Wagg et al. 2019). Recent ecosystem multifunctionality studies have primarily focused on exploring the relationship between biodiversity and ecosystem multifunctionality (Delgado-Baquerizo et al. 2016; Li et al. 2022; Wagg et al. 2019). It is generally believed that soil microbial diversity is positively related to multifunctionality in terrestrial ecosystems (Delgado-Baquerizo et al. 2016, 2020; Jing et al. 2015). In addition, some scholars believe that community composition provides more information than diversity in predicting multifunctionality because community composition can reveal whether a specific species is present or plays key roles, but diversity cannot (Maestre et al. 2012; Xu et al. 2021a). Furthermore, the importance of fungi and bacteria in ecosystem functioning may depend on the ecosystem itself. For example, soil bacteria are more important for regulating soil multifunctionality in croplands and grasslands (Jing et al. 2015; Li et al. 2021), whereas they are predominantly regulated by fungi in boreal and subtropical forests (Li et al. 2019; Xu et al. 2021a). Wagg et al. (2019) also suggested that simultaneously considering both bacterial and fungal community characteristics is generally a better predictor of multifunctionality related to soil C and nutrient cycling. Despite numerous studies on the relationship between soil microbes and multifunctionality, we are still far from fully understanding the changes in soil microbial communities and their relationship with multifunctionality, especially under the predicted changes in precipitation with disturbances such as thinning in forest plantations (Beier et al. 2012; Giguère-Tremblay et al. 2020; Peco et al. 2017).

Larch (*Larix* spp.) is a dominant timber species for afforestation and reforestation in northeast China. Larch plantations, as ectomycorrhizal (ECM)-dominated forests, are influenced by the effects of both forest management and climate change, such as precipitation reduction. In this study, we established a combined thinning (three levels) and precipitation reduction (two levels) experiment to quantify the changes in soil multifunctionality and the microbial community in a 16-year-old larch plantation for one growing season (from April to September). We hypothesize that 1) soil bacterial and fungal diversities and multifunctionality are increased by thinning and decreased by precipitation reduction; and 2) the change in soil multifunctionality under thinning and precipitation reduction is mainly regulated by the fungal community.

Materials and methods

Study area

The study was conducted at the Qingyuan Long-term Experimental Station, Chinese Academy of Forestry, located in the mountainous region of Liaoning Province,

northeast China (42°20′ N, 124°49′ E, and 300–1000 m above sea level). This region is characterized by a continental monsoon climate with a mean annual temperature of 4.7 °C and a mean annual frost-free period of 130 days (Zhu et al. 2007). The growing season is from early May to late September (Yang et al. 2013). The soil in the study area is a typical brown forest soil classified as Udalfs with silt loam textures according to the USDA soil taxonomy (Soil Survey Staff 2006). Soil pH ranged from 5.5 to 6.5 (Wang et al. 2021). According to meteorological station data from the study area, the annual average precipitation was approximately 752.1 mm with a maximum of 1165.1 mm and a minimum of 514.7 mm over the last 50 years. During the drought years of 1976, 1977, 2001, and 2011, precipitation amounts decreased by approximately 200 mm, which is ~ 30% less than the long-term mean annual precipitation of 752.1 mm at the Qingyuan Weather Station in the last 50 years.

Larch plantations have been developed within secondary forests to meet the demand for timber and other forest products since the 1960s, and they represent 65% of conifer plantations in northeast China, and are subjected to second or later rotations (Yang and Zhu 2015). The usual management of larch plantations in the study area involves thinning with ~ 30% of trees removed at ~ 16 years. In this context, a 16-year-old larch [*Larix kaempferi* (Lamb.) Carr.] plantation was selected on a northwest-facing slope of 10°, with an elevation ranging from 352 to 395 m above sea level. The plantation was established in 2004 by planting 2-year-old seedlings at a density of 2500 trees ha^{-1} (2 m × 2 m planting grid) after clear-cutting ~ 45-year-old larch plantations. When investigated in 2018, the stocking density was 2000 stems ha^{-1} with a mean diameter at breast height of 12.1 cm, and an average height of 15.1 m. Understory vegetation, consisting mainly of herbs, was poorly and inadequately developed, with an average coverage of 5%-10%, owing to the high coverage of larch trees (90%).

Experimental design and sampling

The experiment was conducted a factorial experiment using a split-plot design for thinning and precipitation reduction treatments in a larch plantation in 2019. The three thinning levels consisted of no thinning (CK), 30% of trees removed (T30), and 45% removed (T45), and two levels of precipitation treatment included natural precipitation (N) and 30% precipitation reduction (R) applied to subplots with each thinning treatment. Briefly, five replicate blocks were established, each consisting of three 28.3 m × 28.3 m plots with the CK, T30, and T45 treatments having 10 m buffer zone. Two subplots (10 m × 12 m), with a 2–3 m wide buffer zone, were established in each plot. One subplot was randomly assigned to natural precipitation, whereas the other received the precipitation reduction treatment. Thinning was performed from March to April 2019 using the traditional thinning-from-below approach and manual felling with a chainsaw, rather than heavy machinery, to lessen the disturbance at the soil surface. Thinning involves cutting deformed and poorly growing trees and evening up the distribution of the remaining trees. After thinning, for the precipitation reduction treatment, four 3 m × 10 m interception roofs were covered with ten 3 × 0.33–0.37 m (0.33, 0.35, and 0.37 m in the T45, T30, and CK plots, respectively) plastic sheets mounted to icon wireframes in each precipitation reduction subplot to cover 37%, 35%, and 33% of the ground area under the tree canopy in the CK, T30, and T45 plots, respectively. Based on the measurement of throughfall (80.1% for CK, 84.9% for T30, and 90.3% for T45 plots), the net input of precipitation was reduced by ~ 30% compared to natural precipitation. The roof was kept at an approximately 15° slope by setting the two sides at different heights (2.5 m for one side and 1.5 m for the other) to ensure quick drainage of ambient rainfall by gravity. To eliminate surface water flow and lateral movement of soil water into the subplots, we excavated a 0.5 m deep trench. The precipitation reduction treatment was conducted from May 2019 to October 2020. Finally, in May 2019, 30 subplots (10 m × 12 m) were set up (three levels of thinning treatment × two levels of precipitation treatment × five replicates). The abbreviations utilized in this study are as follows: CKN (no thinning with natural precipitation), CKR (no thinning with precipitation reduction), T30N (30% thinning with natural precipitation), T30R (30% thinning with precipitation reduction), T45N (45% thinning with natural precipitation), and T45R (45% thinning with precipitation reduction).

Soil samples were collected during the larch growing season (23rd April, 30th May, 28th June, 28th July, 29th August, and 29th September, 2020). After removing the litter layer, six soil cores (10 cm in diameter and 10 cm in depth) were randomly collected and mixed into a composite sample per subplot. Soil samples were sieved through a 2-mm sieve to remove roots, stones and visible soil animals, and then divided into three subsamples. One part was air-dried for the measurement of soil organic C (SOC), total N (TN), total P (TP) and available P (AP). The other part was stored at 4 °C for the measurement of exchangeable ammonium N (NH_4^+-N), nitrate N (NO_3^--N), dissolved organic C (DOC), enzymes, and microbial biomass within a week. The third part was stored at − 80 °C for high-throughput sequencing. Finally, 180 soil samples (6 sampling months × 30 subplots) were obtained.

Soil chemical parameter and enzyme activity analyses

The soil water content (SWC) was measured by oven drying to a constant mass at 105 °C. The soil temperature (ST) was measured at a depth of 10 cm using a portable temperature probe. SOC was measured using potassium dichromate oxidation (Nelson and Sommers 1996), and TN was determined using the Kjeldahl method (Bremner 1996). TP was determined using a Mo-Sh anti-colorimetric method, and AP was measured colorimetrically using sodium bicarbonate extracts (Lu 1999). DOC was extracted with distilled water at a soil: solution ratio of 1:5 by shaking for 2 h, followed by centrifugation at 1503 × g for 10 min and filtration, and was measured using a TOC analyzer (Shimadzu, Kyoto, Japan) (Jones and Willett 2006). Exchangeable NH_4^+-N and NO_3^--N were determined using a continuous flow analyzer (Scalar SANplus Segmented Flow Analyzer, The Netherlands) following extractions of fresh soil with 2 M KCl (Wang et al. 2020). Soil microbial biomass C (MBC) and N (MBN) were determined using the chloroform fumigation extraction method (Joergensen and Mueller 1996).

Soil hydrolase activities, β-glucosidase (BG), N-acetyl-glucosamine (NAG), cellobiohydrolase (CBH), and acid phosphatase (ACP) were measured using conventional *p*-nitrophenyl (*p*NP)-ester based assays (Caldwell et al. 1999; Chaer et al. 2009). Briefly, soil suspensions were prepared by adding fresh soil (2 g dry weight equivalent) to 125 mL of 50 mM sodium acetate buffer (pH 5.5) and continuously stirring the homogenate. One milliliter of soil slurry was combined with 1 mL of substrate (BG: 10 mM *p*NP-β-glucoside; NAG: 5 mM *p*NP-N-acetyl-glucosamide; CBH: 5 mM *p*NP-β-D-cellobioside; and ACP: 25 mM *p*NP-phosphate) and incubated for 2–4 h at 28 °C. At the end of the incubation, 0.1 mL of 1 M NaOH was added to terminate the reactions, and the soil solution was filtered and analyzed colorimetrically at 410 nm. The soil hydrolase activity was expressed as μmol *p*NP g^{-1} dry soil h^{-1}. Soil oxidase activities, including polyphenol oxidase (PPO) and peroxidase (POD), were determined using L-3,4-dihydroxyphenylalanine (L-DOPA) as the substrate (DeForest 2009; Saiya-Cork et al. 2002). A 1 mL aliquot of soil slurry was mixed with 1 mL of 10 mM L-DOPA in 50 mM acetate buffer for PPO and 1 mL of L-DOPA and 0.2 mL of hydrogen peroxide for POD and then incubated in the dark at 20 °C for 2 h. The suspensions were centrifuged at 1503 × g for 2 min and activity was quantified by measuring the absorbance at 450 nm. Oxidase activities were expressed as μmol g^{-1} dry soil h^{-1} (DeForest 2009). The surface (10 cm depth) volumetric soil moisture content was measured once every hour from April to October 2020 using a soil moisture sensor attached to a FieldScout SMEC 300 (Spectrum Technology, Plainfield, IL, USA). Precipitation was measured using rain gauges on an open site near the study site. The information is shown in Fig. S1.

Quantifying soil multifunctionality

We measured 15 soil functional variables related to C (SOC, DOC, MBC, BG, and CBH, PPO and POD), N (TN, exchangeable NH_4^+-N, NO_3^--N, MBN and NAG), and P (TP, AP and ACP) storage and cycling. These variables represent a range of soil processes including biogeochemical cycling (C, N, and P), and available nutrient supply (Cui et al. 2020; Liu et al. 2017). Soil multifunctionality was calculated using an averaging approach, which has been widely used in multifunctionality analyses (Qiu et al. 2021). To obtain the average multifunctionality index, we tested all variables for normal distribution using the Shapiro–Wilk test prior to analysis, and logarithm or square root transformation was performed when necessary (Xu et al. 2021a). Subsequently, all variables were standardized by a maximum observed value on a 0–1 scale, and the average of these transformed values was calculated as the final result (Byrnes et al. 2014).

Soil DNA extraction, PCR amplification, and Illumina MiSeq sequencing

Total DNA was extracted from each soil sample (0.5 g) using a DNA Kit (Omega Bio-Tek, Inc., Doraville, GA, USA) according to the manufacturer's instructions. The concentration and purification of DNA were checked using a NanoDrop2000 spectrophotometer (Thermo Scientific, Wilmington, DE, USA), and DNA quality was detected by 1% agarose gel electrophoresis. The V3–V4 region of the bacterial 16S rRNA gene was amplified using primer pairs 338F (5′-ACTCCTACGGGAGGCAGCAG-3′) and 806R (5′-GGACTACHVGGGTWTCTAAT-3′) (Caporaso et al. 2012), and the fungal ITS1 region was amplified using primer pairs ITS1F (5′-CTTGGTCATTTAGAG GAAGTAA-3′) and ITS2R (5′-GCTGCGTTCTTCATC GATGC-3′) (Gardes and Bruns 1993). PCR reactions were performed in a reverse cycler PCR system (GeneAmp 9700, ABI, USA) with the following program: 3 min of denaturation at 95 °C, 35 cycles (fungi) or 27 cycles (bacteria) of 95 °C for 30 s, 55 °C for 30 s, 72 °C for 45 s, and a final extraction at 72 °C for 10 min. PCR products were extracted from 2% agarose gels and purified using an AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, USA). Purified amplicons were combined at equimolar concentrations and paired-end sequenced on the Illumina MiSeq PE 250 platform (Illumina, USA) at Majorbio Bio-Pharm Technology Co. Ltd. (Shanghai, China).

Bioinformatics analysis

Raw FASTQ files were demultiplexed, quality filtered by Trimmomatic, and merged using FLASH (0.19.6) under

the following standards: (a) read segments with an average quality score < 20 in a 50 bp sliding window were truncated; (b) primers were precisely matched, allowing mismatches between 2 nucleotides, and read segments containing ambiguous bases were deleted; and (c) sequences with overlaps longer than 10 bp were combined according to their overlapping portion (Han et al. 2021). The ITS1 region was extracted from the remaining fungal sequences using the fungal ITSx software package (Bengtsson-Palme et al. 2013). Dereplication and singletons were performed by USEARCH version 8.0 using the command *fastx_uniques* and *sortbysize*, respectively. The nonchimeric sequences of ITS1 and 16S were clustered into operational taxonomic units (OTUs) at a 97% sequence similarity level using USEARCH, and then chimeric sequences were identified and removed using MOTHUR (version v.1.30.2 https://www.mothur.org/wiki/Download_mothur). After that, the taxonomic assignment of the ITS1 sequences was selected for searching against the UNITE database version 18.11.2018 using the sintax function in USEARCH (Edgar 2016), and the taxonomic assignment of the 16S rRNA was performed using the Ribosomal Database Project classifier with a confidence cutoff (*P*) value of 0.65 (Yao et al. 2019). A total of 8,779,391 fungal and 8,407,255 bacterial sequences were obtained using the ITS1F/ITS2R and 338F/806R primer sets for 180 soil samples. The number of fungal sequences varied from 34,843 to 74,651, with an average length of 242, and the number of bacterial sequences varied from 30,505 to 74,864, with an average length of 417. Based on the method of Yao et al. (2019), OTUs with < 10 reads from all samples were removed, as their sequences could contain PCR or sequencing errors. In addition, the number of considered sequences in each sample was normalized to the lowest sample size to ensure an equal sampling depth (20535 for bacteria and 33951 for fungi). Fungal functional guilds have been identified based on FUNGuild (Nguyen et al. 2016), and this functional prediction method has been widely used to understand soil fungal communities (Averill et al. 2021; Lekberg et al. 2021). Some fungi do not fall exclusively into a single guild because their presence depends on the life stage and environmental conditions (Nguyen et al. 2016). Therefore, the three major functional groups of ECM fungi, SAP fungi (sum of wood, dung, soil, and undefined saprotrophs), and pathogens that completely belonged to a single guild were selected for the following analysis (Zhou et al. 2020). After removal of nonfungal and < 10 read OTUs, a total of 4967 fungal OTUs were found across 180 soil samples, and 1943 OTUs were assigned by FUNGuild. A total of 243 ECM fungal OTUs and 853 SAP fungal OTUs were obtained. For bacteria, a total of 8408 OTUs remained after the removal of nonbacterial and < 10 read OTUs. Finally, raw sequence reads were deposited in the SRA (BioProject PRJNA789094 for fungi and PRJNA849713 for bacteria).

Statistical analysis

All statistical analyses were carried out in R (4.0.2). We conducted a three-way analysis of variance (ANOVA) to test the effects of thinning, precipitation reduction, sampling month and their interactions on soil multifunctionality, microbial diversity indices, the relative abundance of fungi and bacteria at the phylum and class levels (relative abundance > 1%), and fungal functional groups. Square root of the relative abundance of fungi and bacteria was necessary to meet the normality and homogeneity of variances for ANOVA. Significant differences among treatments within the same sampling month were compared using Tukey's HSD test at $P < 0.05$. Nonmetric multidimensional scaling (NMDS) plots (using the Bray–Curtis distance matrix with the "metaMDS" function in *vegan*) were used to visualize the separation of soil microbial communities between treatments and sampling months. Permutational multivariate analysis of variance (PERMANOVA) was performed to test the effects of thinning, precipitation reduction, sampling month, and their interactions on the soil microbial community composition using the "adonis2" function in the *vegan* package. Furthermore, a pairwise multilevel comparison was performed using the "pairwiseadonis" function to test for significant differences between the natural precipitation and precipitation reduction treatments in each thinning treatment and growth month. We used Pearson's correlation analysis to determine the relationships between soil properties and microbial diversity. Subsequently, based on prior knowledge, we applied piecewise structural equation modeling (pSEM) to further explore the direct effects of thinning and precipitation reduction, and the indirect effects via changes in microbial diversity (OTU richness) and community composition (represented by NMDS1) on soil multifunctionality by using the *piecewiseSEM* package. The thinning and precipitation treatment as two categorical exogenous variables with "1 (CK), 2 (T30), 3 (T45)" and "0 (N), 1 (R)", respectively, were specified fixed effects, while sampling month were termed as random intercept effects (Wu et al. 2022). The model fit of pSEM was assessed using Fisher's C statistic, and the model was considered to have an adequate fit to the data when it had a Fisher's C statistic with $P > 0.05$ (Shipley 2009). A random forest model was used to identify the main credible predictors of soil multifunctionality including microbial taxa (abundant ECM and SAP genera based on relative abundance > 0.1%) (Banerjee et al. 2019). The percent increment of the mean squared error (%IncMSE) and the increase in node purity were used to determine the significance of the predictors. The significance of the models and cross-validated R^2 values were assessed with 1000 permutations of the response variables using the *A3* package. Similarly, the significance of each predictor for the response variables was assessed using the *rfPermute* package.

Results

Soil variables and multifunctionality

Three-way ANOVA showed that thinning, precipitation reduction, and sampling month significantly affected SWC, DOC, exchangeable NH_4^+-N, NO_3^--N, and AP concentrations, MBC, and MBN, and the activities of BG, NAG, CBH, ACP, and POD, as well as the interaction between thinning and precipitation reduction on exchangeable NH_4^+-N and MBN and NAG, CBH, and ACP activities (Table S1). Compared to the CK treatment, the T45 treatment, but not the T30 treatment, significantly increased SWC, DOC, NO_3^--N, and AP concentrations, MBC, and MBN, and the activities of BG, NAG, CBH, ACP, and POD, whereas the precipitation reduction treatment significantly decreased these variables (Table S2). In more detail, SWC increased by an average of 3.7% under the T30 treatment and an average of 20.5% under the T45 treatment (Table S2). Notably, SWC decreased under the precipitation reduction treatment by an average of 17.1% (Table S2). Furthermore, SWC was significantly lower in June (16.0 ± 2.0%) and July (15.9 ± 2.1%) than in other sampling months (ranging from 25.4 ± 1.6% to 34.7 ± 1.3%) (Table S2).

Three-way ANOVA showed that soil multifunctionality was significantly influenced by thinning, precipitation reduction, sampling month and their interactions (Table S1). Compared to the CK treatment, the T45 treatment significantly increased soil multifunctionality in all growing months under both precipitation conditions, except in April and May under the precipitation reduction treatment (Fig. 1). In addition, compared to the CK treatment, the T30 treatment significantly decreased soil multifunctionality in April and June under the natural precipitation treatment (Fig. 1). Furthermore, compared to the natural precipitation treatment, the precipitation reduction treatment significantly decreased soil multifunctionality under the thinning treatments in all growing months, except for the T30 treatment in April, May, June, August, and September. These results suggest that a high thinning level positively affects soil multifunctionality and that this effect depends on the sampling month under the precipitation reduction treatment.

Taxonomic composition of fungi and bacteria

The fungal community was dominated by the phyla Ascomycota (39.5%), Basidiomycota (36.7%) and Mortierellomycota (13.2%), which accounted for > 89.4% of the total fungal sequences (Fig. 2a). The bacterial community was dominated by the phyla Actinobacteria (28.3%), Proteobacteria (25.7%), and Acidobacteria (21.2%), which accounted for > 75.3% of the total bacterial sequences (Fig. 2b). Furthermore, thinning, precipitation reduction and sampling month significantly affected the relative abundance of the dominant fungal phyla, but not the dominant bacterial phyla (Table S3). The relative abundance of Ascomycota and Basidiomycota significantly decreased by the thinning treatments and increased by the precipitation reduction treatment. In contrast, the relative abundance of Mortierellomycota and Rozellomycota significantly increased by the thinning treatments and decreased by the precipitation reduction treatment (Table S4).

Three-way ANOVA showed that the relative abundances of ECM and SAP fungi were significantly influenced by thinning, precipitation reduction, sampling month and their interactions. However, the relative abundance of SAP fungi was unaffected by thinning, whereas the relative abundance of pathogens was significantly affected by sampling month (Fig. 2c; Table S3). Compared to the CK treatment, the T45 treatment but not the T30 treatment significantly decreased the relative abundance of ECM fungi in all sampling months under the natural precipitation condition and in June under the precipitation reduction condition (Fig. S2a). In addition, the precipitation reduction treatment significantly increased the relative abundance of ECM fungi in June and July under the CK, T30, and T45 treatments, and in August under the T30 treatment (Fig. S2a). In contrast, the precipitation

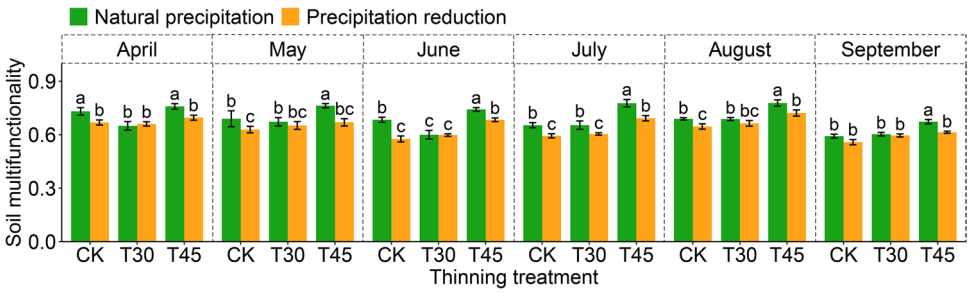

Fig. 1 Soil multifunctionality in thinning and precipitation reduction treatments during the growing season. Data are means ± SE ($n = 5$). Different letters indicate significant differences among treatments within the same sampling month based on Tukey's HSD test at $P < 0.05$ level. CK: no thinning; T30: 30% of trees removed; T45: 45% trees removed

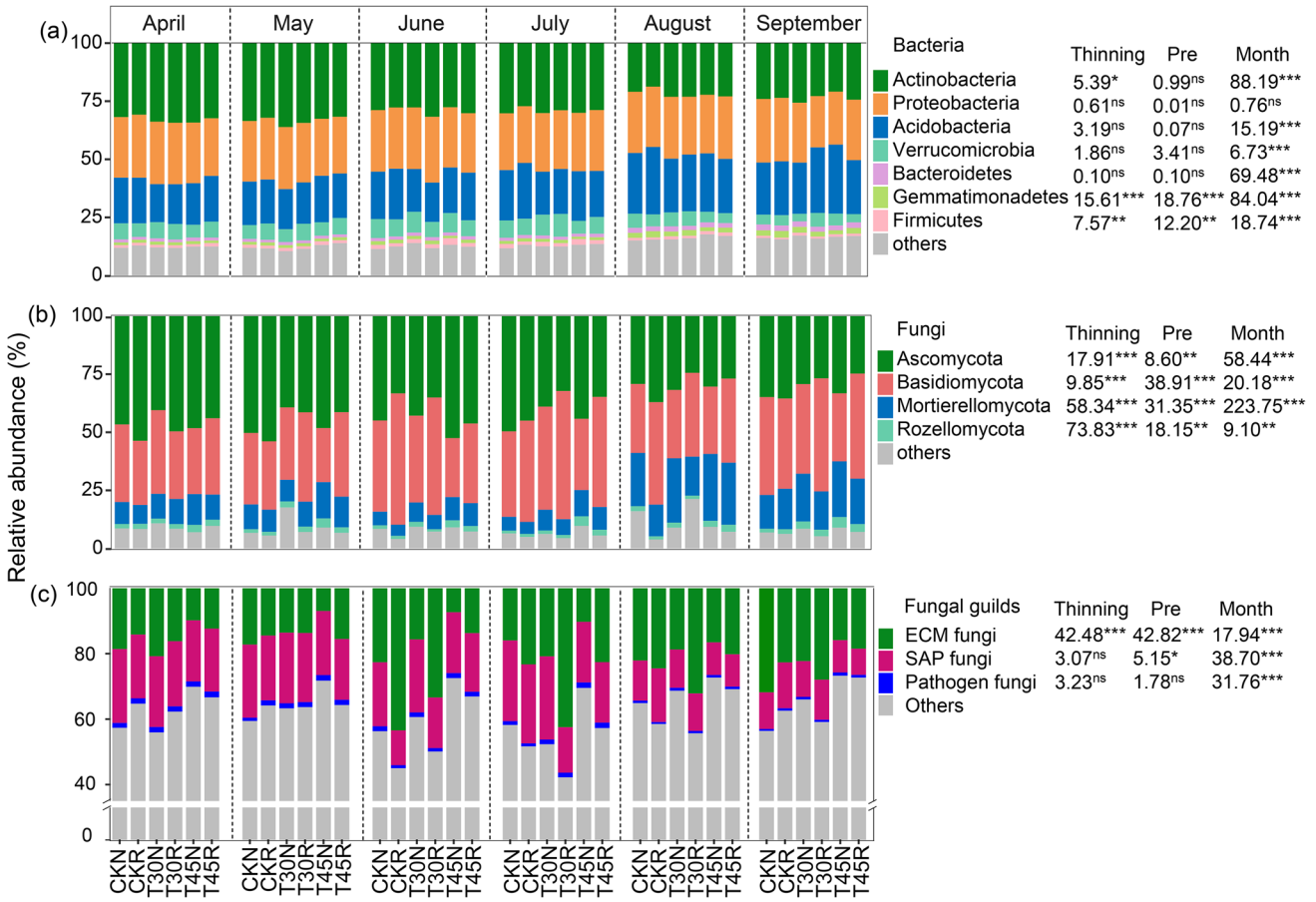

Fig. 2 Relative abundance of bacteria and fungi in thinning and precipitation reduction treatments during the growing season. (**a**) Bacteria at the phylum level, (**b**) Fungi at the phylum level, (**c**) Three of the major fungal guilds, including ectomycorrhizal (ECM) fungi, saprotrophic (SAP) fungi, and pathogen. Three-way ANOVA showing the effects of thinning, precipitation reduction, sampling month and their interactions on bacteria and fungi. Asterisks indicate the statistical significance (^{ns} $P>0.05$, * $P<0.05$, ** $P<0.01$, ***$P<0.001$). Others include the rare taxa (relative abundance < 1%) and the unclassified groups. CKN: no thinning with natural precipitation; CKR: no thinning with precipitation reduction; T30N: 30% thinning with natural precipitation; T30R: 30% thinning with precipitation reduction; T45N: 45% thinning with natural precipitation; T45R: 45% thinning with precipitation reduction

reduction significantly decreased the relative abundance of SAP fungi in June under the CK treatment and July under the T30 treatment (Fig. S2b). These results suggest that the relative abundance of ECM fungi was negatively affected by thinning and positively affected by precipitation reduction, but this effect was dependent on the sampling month.

Soil microbial diversity and community composition

Three-way ANOVA indicated that thinning, precipitation reduction and sampling month significantly influenced soil bacterial, total, ECM, and SAP fungal OTU richness, with one exception: SAP fungal OTU richness was not significantly influenced by thinning (Table S3). Compared to the CK treatment, the T45 treatment did not significantly change bacterial OTU richness in all growing months under both precipitation conditions, except that the T30 treatment significantly decreased bacterial OTU richness in April, May, and August under natural or reduced precipitation conditions (Fig. 3a). In contrast, compared to the CK treatment, the T45 treatment (but not the T30 treatment) significantly increased the total fungal OTU richness in June, July, and August under natural or reduced precipitation conditions (Fig. 3b). Furthermore, compared to the CK treatment, ECM fungal OTU richness was significantly decreased by the T45 treatment in April, June, July, and August, and by the T30 treatment in April, July, and September under natural or reduced precipitation conditions (Fig. 3c). In addition, the T45 and T30 treatments did not significantly affect SAP fungal OTU richness (Fig. 3d). These results suggest that a high thinning level positively affects total fungal OTU richness and negatively affects ECM fungal OTU richness. This effect depends on the sampling month under both precipitation conditions. Furthermore, precipitation reduction

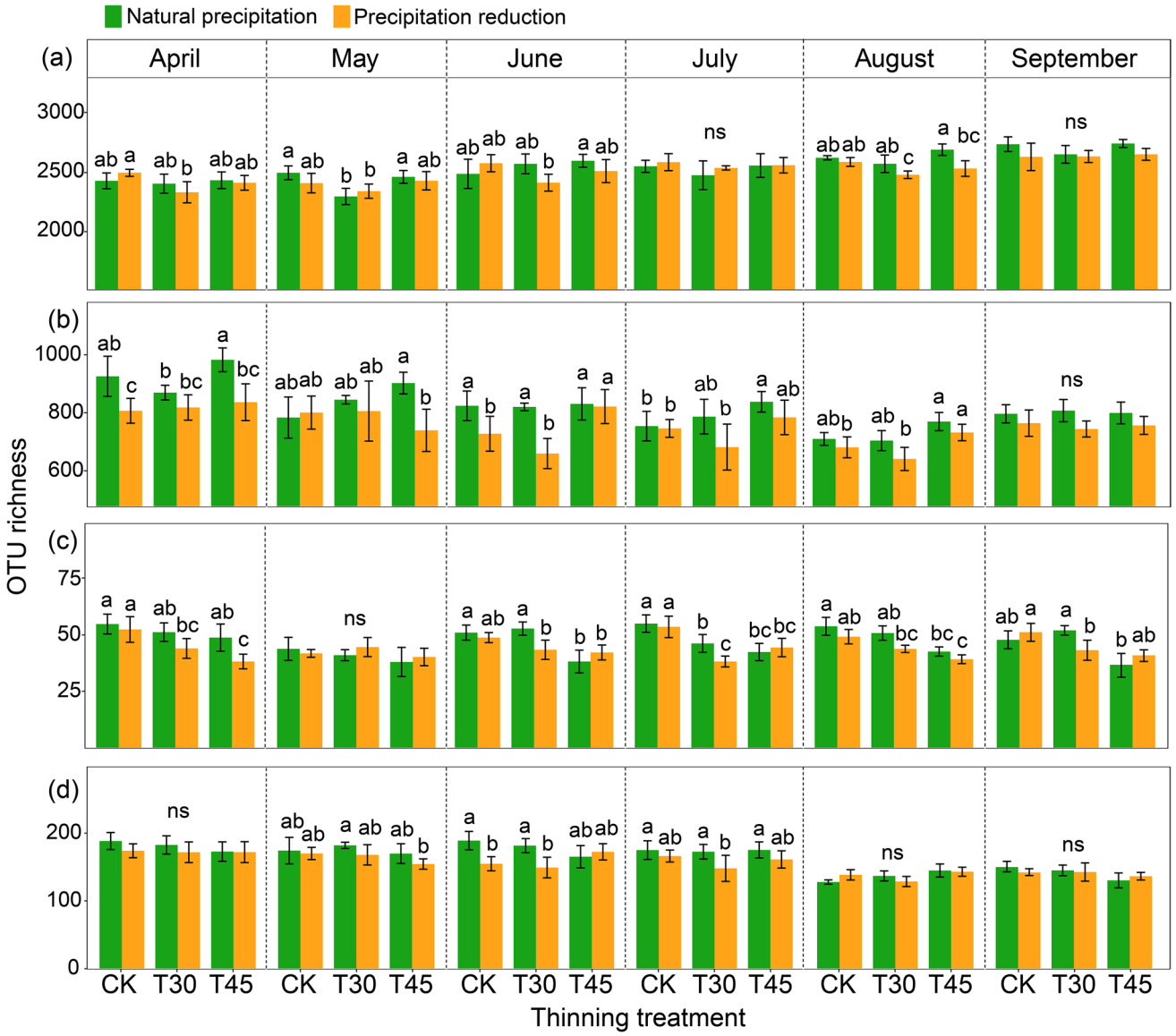

Fig. 3 Operational taxonomic unit (OTU) richness of bacteria and fungi in thinning and precipitation reduction treatments during the growing season. (**a**) Bacteria, (**b**) Total fungi, (**c**) Ectomycorrhizal (ECM) fungi, (**d**) Saprotrophic (SAP) fungi. Data are means ± SE ($n = 5$). Different letters indicate significant differences among treatments within the same sampling month based on Tukey's HSD test at $P < 0.05$ level. CK: no thinning; T30: 30% of trees removed; T45: 45% trees removed

significantly decreased bacterial OTU richness under the T30 and T45 treatments in August, total fungal OTU richness under the CK and T45 treatments in April, and under the CK and T30 treatments in June. These results suggest that the effects of thinning and precipitation reduction on microbial OTU richness were more pronounced in June, and July than in other sampling months.

The PEMANOVA and NMDS showed that the community compositions of bacteria, total, ECM and SAP fungi were significantly affected by sampling month ($R^2 = 0.280$, $P < 0.001$; $R^2 = 0.216$, $P < 0.001$; $R^2 = 0.108$, $P < 0.001$; $R^2 = 0.222$, $P < 0.001$), thinning ($R^2 = 0.051$, $P < 0.001$; $R^2 = 0.145$, $P < 0.001$; $R^2 = 0.201$, $P < 0.001$; $R^2 = 0.137$, $P < 0.001$), precipitation reduction ($R^2 = 0.011$, $P < 0.01$; $R^2 = 0.030$, $P < 0.001$; $R^2 = 0.041$, $P < 0.001$; $R^2 = 0.023$, $P < 0.001$), and the interaction between thinning and precipitation reduction ($R^2 = 0.019$, $P < 0.01$; $R^2 = 0.037$, $P < 0.001$; $R^2 = 0.023$, $P < 0.001$; $R^2 = 0.048$, $P < 0.001$) (Fig. 4a-d). Furthermore, precipitation reduction did not significantly affect the bacterial community composition under each thinning treatment and growth month (except in July and August under the CK and T45 treatments) (Fig. 4e). In contrast, precipitation reduction significantly affected the total, ECM, and SAP community compositions in each thinning

treatment and growth month (except for ECM fungi in May under the CK and T30 treatments and SAP fungi in July under the CK treatment) (Fig. 4f–h). These results suggest that the fungal community composition was more sensitive to thinning and precipitation reduction than the bacterial community composition. Furthermore, the total and ECM fungal community compositions under the CK and T30 treatments responded more strongly to precipitation reduction than those under the T45 treatment in June and July.

Linking soil properties, microbial community and multifunctionality

Pearson correlations revealed that SWC, exchangeable NH_4^+-N, MBN, CBH, ACP, and soil multifunctionality were positively and significantly correlated with fungal diversity (i.e., OTU richness and Shannon index), but negatively correlated with bacterial OTU richness and the relative abundance of ECM fungi (Fig. 5a). The Mantel test showed that soil exchangeable NH_4^+-N was significantly correlated with bacterial, total, ECM, and SAP fungal microbial compositions, and SWC had significant influences on bacterial, total, and ECM fungal compositions. Importantly, total and ECM fungal compositions, rather than bacterial and SAP fungal compositions, showed a significant relationship with soil multifunctionality (Fig. 5b). Piecewise structural equation modeling showed that soil multifunctionality was affected by thinning and precipitation reduction, directly and indirectly through the ECM fungal richness and composition, and SAP fungal composition (Fig. 6). Among ECM and SAP fungi, *Piloderma, Aspergillus*, and *Tomentella* were the three most important predictors of soil multifunctionality (Fig. 7a). Furthermore, soil multifunctionality was significantly and negatively correlated with the relative abundance of *Piloderma* from June to September, and the relative abundance of *Tomentella* in June, July and September, whereas it was significantly and positively correlated with the relative abundance of *Aspergillus* from June to August (Fig. 7b).

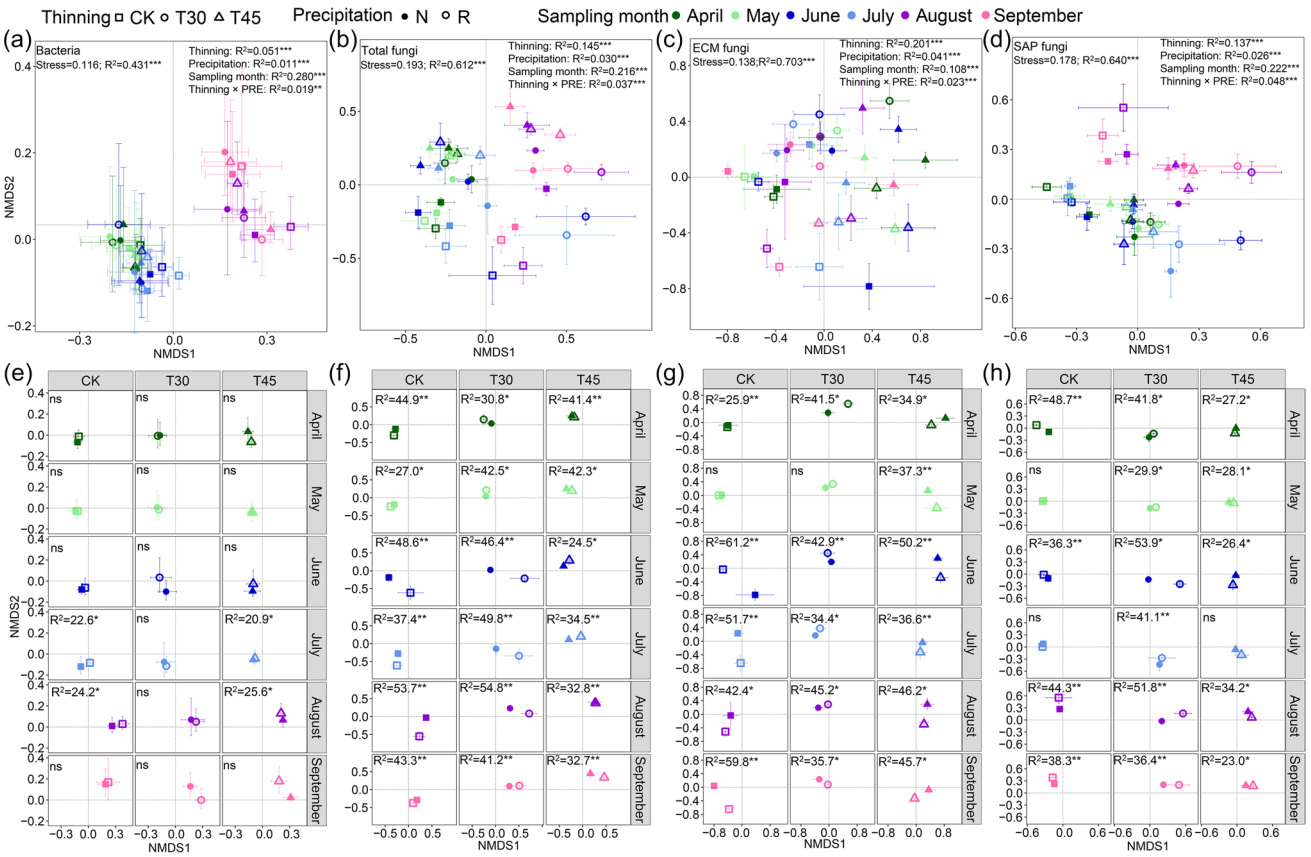

Fig. 4 Non-metric multidimensional scaling (NMDS) analysis based on Bray–Curtis distance matrix of soil bacterial and fungal community compositions. Effects of thinning, precipitation reduction, sampling month and their interactions on the bacterial (**a**), total fungal (**b**), ectomycorrhizal (ECM) fungal (**c**) and saprotrophic (SAP) fungal (**d**) community compositions. Effects of precipitation reduction on the bacterial (**e**), total fungal (**f**), (ECM) fungal (**g**) and SAP fungal (**h**) community compositions in each thinning treatment and growth month. For each point, $n = 5$. Error bars indicate standard deviation. Different colors and shapes represent different treatments and sampling months. CK: no thinning; T30: 30% of trees removed; T45: 45% trees removed. N: natural precipitation; R: precipitation reduction

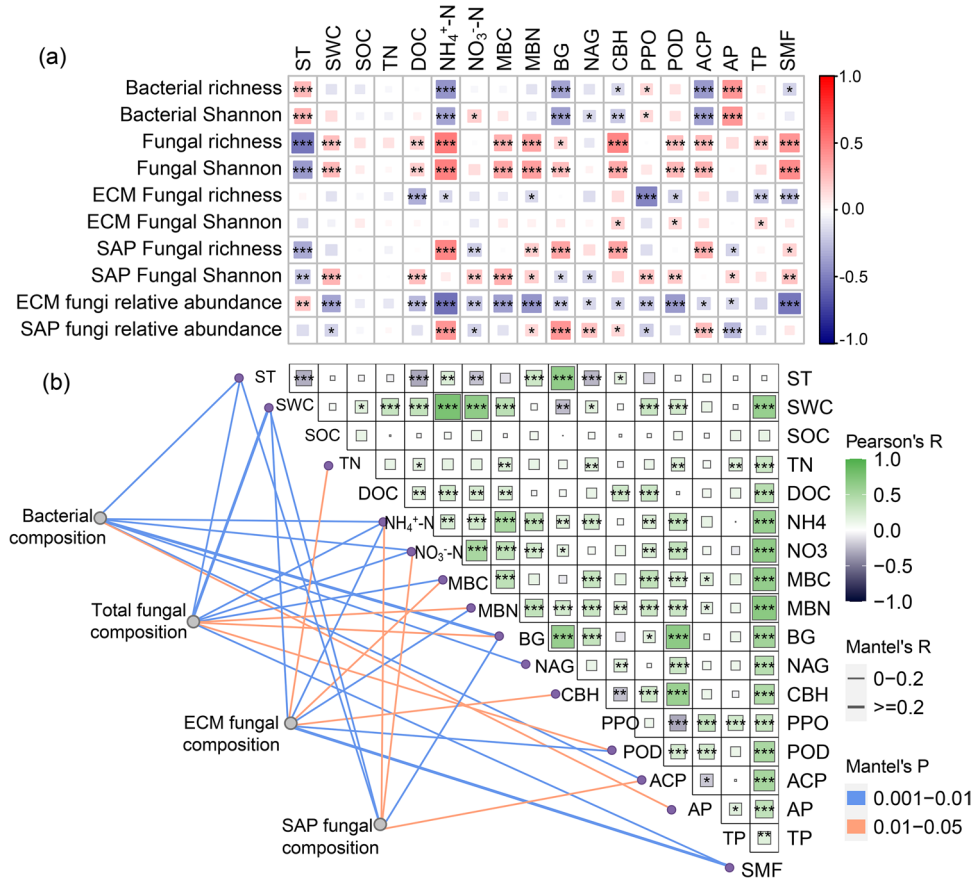

Fig. 5 Correlations between soil properties and microbial diversity (**a**) and microbial community compositions (**b**). soil microbial community composition based on Bray–Curtis distance is related to each soil properties by Mantel test. Line width corresponds to the partial Mantel's *P* statistic, and line color denotes the statistical significance based on 999 permutations. Pairwise comparisons of soil properties are also shown, with a color gradient denoting Pearson's correlation coefficient. Asterisks indicate the statistical significance (* $P<0.05$, ** $P<0.01$, *** $P<0.001$). ST: soil temperature; SWC: soil water content; SOC: soil organic carbon; TN: total nitrogen; TP: total phosphorus; DOC: dissolved organic carbon; Exchangeable NH_4^+-N: ammonium N; NO_3^--N: nitrate N; AP: available phosphorus; MBC: microbial biomass C; MBN: microbial biomass N; βG: β-glucosidase; CBH: cellobiohydrolase; NAG: N-acetyl-glucosaminidase; ACP: acid phosphatase; PPO: polyphenol oxidase; POD: peroxidase; SMF: soil multifunctionality

Discussion

Thinning increased soil multifunctionality and fungal diversity but precipitation reduction had the opposite effects

The first hypothesis was partially supported by our findings that the T45 treatment rather than T30 treatment had a positive effect on soil multifunctionality and fungal OTU richness, and this effect depended on the sampling month. This may partly be explained by thinning intensity, which is one of the main factors controlling the magnitude of thinning effects (Kim et al. 2018; Weng et al. 2007; Zhang et al. 2018). Thinning alters the microclimate and provides favorable conditions for understory vegetation and litter decomposition by opening the forest canopy, stimulating microbial activities, and improving nutrient availability (Dang et al. 2018). A recent meta-analysis concluded that soil moisture content was significantly increased at moderate and heavy intensities, but light thinning did not affect soil moisture content (Zhang et al. 2018). A heavy thinning intensity can leave a larger amount of thinning residue, such as slashes, stumps, and dead roots, than a comparatively light thinning intensity (Adamczyk et al. 2015; Smolander et al. 2015), and it likely provides a more moderate environment for microbial growth by opening the forest canopy. These differences in thinning intensity can result in differential effects on SWC, available nutrients, and enzyme activity (Calev et al. 2016; Chen et al. 2015; Dang et al. 2018; Kim et al. 2019; Ma et al. 2018). In this study, although 30% of the trees were removed in T30 treatment, only ~ 13% of the basal area was removed because of the

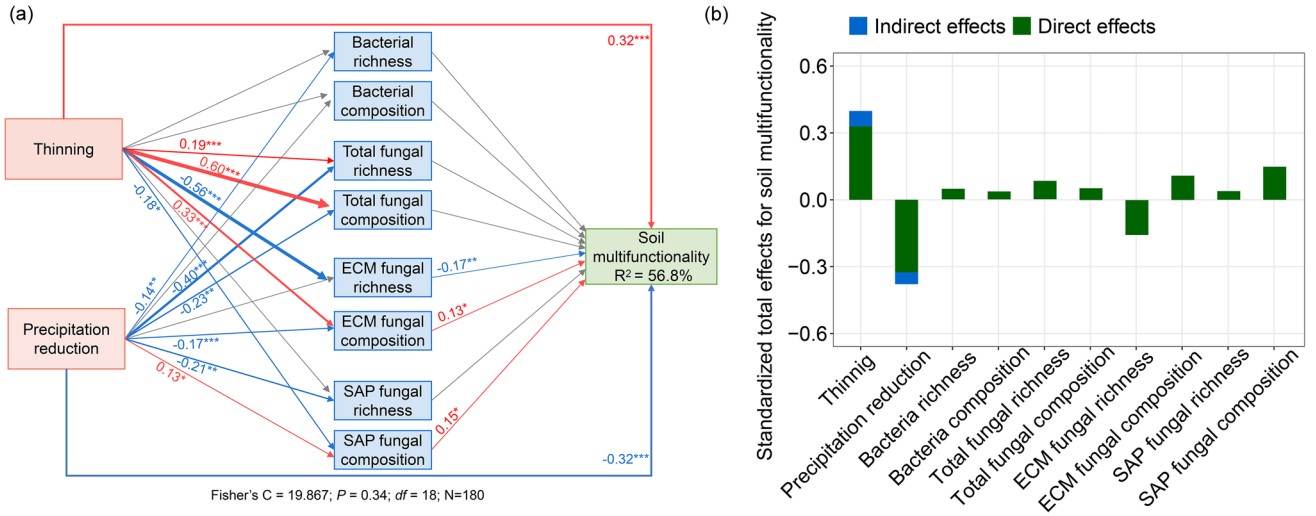

Fig. 6 The piecewise structural equation model (pSEM) showing the direct and indirect effects of the thinning, precipitation reduction, and microbes on soil multifunctionality (**a**) and standardized total effects (direct plus indirect effects) derived from SEM depicted above (**b**). Red lines indicate positive effects, while blue lines indicate negative effects. Grey lines indicate nonsignificant relationships ($P > 0.05$). The width of arrows is proportional to the strength of significant standardized path coefficients. R^2 represents the total variance in the soil multifunctionality index explained by the model

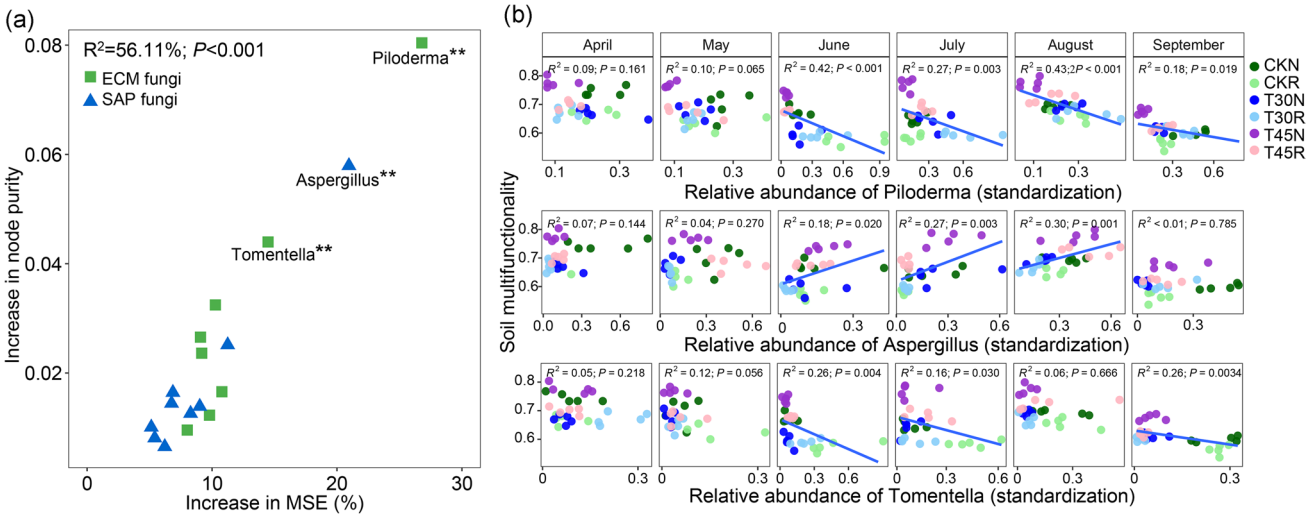

Fig. 7 The main microbial drivers of soil multifunctionality. (**a**) Random forest analysis showing the relative contribution of the ectomycorrhizal (ECM) fungal and saprotrophic (SAP) fungal genus in predicting the soil multifunctionality. The accuracy importance measure was computed for each tree and averaged over the forest (1000 trees). Asterisks indicate the statistical significance (* $P < 0.05$, ** $P < 0.01$). MSE: mean square error. (**b**) Relationships between soil multifunctionality and the top three important drivers of soil multifunctionality

thinning-from-below approach, and the canopy openings created by the T30 treatment were thus all relatively small. Consequently, the T45 treatment produced larger shoots, dying and dead roots as nutritive substrates and fostered a more favorable microclimate for microbial growth and activity than the T30 treatment. Furthermore, available soil nutrients have been observed to increase under thinning treatments by increasing soil moisture content and thus microbial biomass and activities. Tan et al. (2008) found that soil moisture content and net N mineralization rates and available N were higher in the thinned than in the control plots. These results indicate that thinning significantly increased soil multifunctionality, and this effect depended on thinning intensity. On the other hand, high thinning level likely provides a moderate environment for microbial growth by opening the forest canopy as a result of increased soil fungal diversity after thinning (Wang et al. 2019). Previous studies have suggested that thinning

increases soil fungal abundance during the first 21 months postthinning (Lin et al. 2016) and increases the diversity of fungal species (Overby et al. 2015).

Consistent with our first hypothesis, precipitation reduction significantly decreased soil fungal diversity and multifunctionality, and these effects were dependent on the sampling month. Our results showed that the precipitation reduction significantly and directly decreased the soil water content (by an average of 17.1%) and available nutrients, which led to a decline in soil multifunctionality. Many drought experiments have reported decreases in microbial biomass, enzyme activity, and C and N mineralization, which in turn reduce available nutrients by decreasing soil moisture content (Brockett et al. 2012; Yang et al. 2021b; Yu et al. 2012). The impacts of the precipitation reduction on soil microbial biomass and enzyme activities can be explained through direct effects mediated by lower SWC, which may limit microbial growth and substrate diffusion (Brockett et al. 2012; Su et al. 2020). Moreover, drought induced by precipitation exclusion may reduce pore connectivity, thereby decreasing substrate diffusion and restraining the formation of organo-mineral complexes and thus, affecting both microbial biomass and extracellular processes (Bastida et al. 2017; Canarini et al. 2016; Schimel and Schaeffer 2012). In the study area, there was > 1 dryness index in the larch plantation, indicating that the study area was a water-limited region (Yu et al. 2019), and the 16-year-old larch plantation was in the rapid growth stage and was experiencing intense intertree competition due to the high coverage of overstory larch trees (Schaedel et al. 2017). Therefore, we conclude that precipitation reduction can cause strong competition for soil water and nutrients between larch trees and soil microbes during the growing season, especially in June and July (Bastida et al. 2019; Baum et al. 2013). Another important reason for the decrease in soil fungal diversity may be the contribution of the lower DOC, exchangeable NH_4^+-N, and NO_3^--N levels, which provide nutrition substrates for the microorganisms under precipitation reduction. Similarly, a recent meta-analysis showed that reduced precipitation decreases soil water availability and substrate supply to microorganisms and consequently decreases microbial diversity (Yang et al. 2021a).

Fungi as good indicators of soil multifunctionality

Our results showed that fungi rather than bacteria are important soil multifunctionality predictors (Figs. 5 and 6). There are several possible explanations for this finding. The fungal and bacterial communities have different characteristics. Fungi are indispensable for the breakdown of recalcitrant C compounds (e.g., lignin) and ultimately regulate the rates of soil processes, especially in coniferous forests (Treseder and Holden 2013; Treseder et al. 2016; Zhang et al. 2017). However, bacteria are related to the turnover of easily degradable substrates such as dead fungal biomass (Lladó et al. 2017).

Second, fungi can produce various hydrolytic enzymes that can liberate organic C and N and form associations with roots of trees, providing nutrients and water in the forest soil (Baldrian et al. 2013; De Boer et al. 2005; Kyaschenko et al. 2017; Mohan et al. 2014). In incubation experiments, activity of endocellulase, β-galactosidase, β-mannosidase, and β-glucosidase was significantly related to the fungal to bacterial biomass ratio indicating the important role of fungi in their production (Algora Gallardo et al. 2021). In this study, exchangeable NH_4^+-N was the most significant contribution to changes in the fungal community (diversity and composition), providing evidence that there may be a strong N limitation in the studied larch plantation (Fig. 5). Our results are consistent with previous studies that show that soil nutrient content can strongly affect fungal communities, especially when soil nutrient content is limited (Almeida et al. 2019; Odriozola et al. 2021). The availability of N is most commonly the dominant limiting nutrient in northern forested ecosystems (Almeida et al. 2019; Jiang et al. 2021; Teste et al. 2012). Furthermore, when considering single edaphic factors, most soil properties (e.g., SWC, available nutrients, and enzyme activities, but not SOC, TN, and TP) showed a stronger effect on fungal community composition and diversity than on those of bacteria (Fig. 5), indicating that thinning and precipitation reduction regulated soil fungi, rather than bacteria, primarily by changing the availability of soil resources. Thus, soil fungi are more sensitive to thinning and precipitation reduction than bacteria, which are widely found in forest ecosystems (He et al. 2017; Urbanová et al. 2015; Zhou et al. 2020).

Third, the present study found that the relative abundance of ECM fungi and ECM fungal community composition were significantly correlated with soil multifunctionality (Fig. 5). In particular, the relative abundance of ECM fungi responded significantly to precipitation reduction and presented a markedly negative relationship with soil available resources (e.g., SWC, exchangeable NH_4^+-N, DOC, and NO_3^--N), fungal OTU richness, and soil multifunctionality (Fig. 5). Therefore, we inferred that the limitation of available soil resources due to precipitation reduction strongly stimulated ECM fungi, which were mainly responsible for soil water and nutrient uptake for their host. This is consistent with previous studies, which showed that high nutrient availability might inhibit the growth and functions of mycorrhizal microbes (Nilsson et al. 2005; Truong et al. 2019). Meanwhile, the higher relative abundance of ECM fungi may result in the loss of other fungal species, resulting in a shift in fungal composition. For instance, the higher relative abundance of ECM fungi is associated with a lower relative abundance of SAP fungi, which together may slow

soil organic matter decomposition and decrease soil nutrient availability (Männistö et al. 2018; Vasco-Palacios et al. 2018). In addition, thinning suppressed the relative abundance of ECM fungi in a Korean larch planation (Zhou et al. 2020), and timber harvesting negatively affected the relative abundance of ECM fungi in six forest sites in British Columbia (Hartmann et al. 2012). Changes in fine root biomass after thinning may be the main reason for the responses of fungal community composition (Mushinski et al. 2018). Thinning reduces the tree root biomass and consequently decreases the fine root hosts for ECM fungi, which is a potential explanation for the substantial decrease in the relative abundance of ECM fungi after thinning (Castaño et al. 2018; Lin et al. 2016). For instance, *Piloderma* (belonging to ECM fungi) was the most important predictor of soil multifunctionality (Fig. 7), and its relative abundance was significantly reduced by thinning and increased by precipitation reduction (Fig. S3). As discussed above, changes in the relative abundance of ECM fungi may play a critical role in microbial-mediated soil multifunctionality owing to shifts in soil SWC and available nutrients under thinning and precipitation reduction. Recently-developed molecular technology, such as RNA sequencing, metaproteomics, should be used to evaluate active microbial community, which is related more closely to soil functions than the total community (analyzed by DNA) (Bastida et al. 2017; Nannipieri et al. 2020; Yang et al. 2022).

The negative effect of precipitation reduction on soil fungal diversity and multifunctionality is alleviated by thinning

Our results suggest that the negative effect of precipitation reduction on soil fungal diversity and multifunctionality is alleviated by the high thinning level (T45) treatment, and the effect was dependent on the sampling month. First, we observed that the 45% thinning treatment significantly increased soil multifunctionality from June to September, while precipitation reduction produced counteractive effects. Increased thinning intensity led to reduced interception and total stand transpiration due to reducing stand density and thus increased the soil water content (Gebhardt et al. 2014), which led to higher available nutrients, and enzyme activities and thus soil multifunctionality. Meanwhile, fungal OTU richness was significantly decreased by precipitation reduction in June, July, and August. During this period (peak-growing season), more water and nutrients for larch tree growth may induce strong competition for soil water and nutrients between larch trees and soil microbes, especially in June and July, which had lower soil water content (~ 16%). Similarly, the precipitation reduction stimulated the relative abundance of ECM fungi coupled with low soil water content and available nutrients in June and July, but not in other growth months. These results indicate that the counteractive effects of high thinning level treatment and precipitation reduction on soil multifunctionality were found throughout the growing season, but on fungal OTU richness and the relative abundance of ECM fungi in June and July when soil water and nutrients became limited. Previous studies have shown that thinning can effectively mitigate the effects of drought on tree growth by increasing soil water and nutrient availability (Gebhardt et al. 2014; Sohn et al. 2013). Overall, the counteractive effects of the precipitation reduction and high thinning level treatments suggest that the combination of these two treatments may be helpful for the maintenance of soil multifunctionality and fungal OTU richness, particularly when resource availability remains low. The canopy coverage of larch stands should be maintained at ~ 0.7 to maintain soil quality, which allows enough light to maintain many understory species and reduces competition for soil water and nutrients between larch trees and soil microbes. Only the moderate and heavy thinning (> 33% of thinning intensity) treatments, but not the light thinning treatment, significantly increased soil moisture content (Zhang et al. 2018), consistent with our results that the 45% thinning treatment increased significantly soil moisture content and multifunctionality (Table S2).

Conclusions

This study revealed that the responses of soil fungal and bacterial communities and multifunctionality associated with C, N, and P cycling to thinning and precipitation reduction differed in a larch plantation. A high thinning level positively affects soil fungal diversity and multifunctionality, whereas precipitation reduction showed the opposite effect, depending on the sampling month. Furthermore, fungi, rather than bacteria, show a significant relationship with soil multifunctionality, which is indirectly affected by thinning and precipitation reduction through the ECM and SAP fungal composition. Overall, the counteractive effects of the high thinning level and precipitation reduction suggest that the combination of these two treatments may be helpful for the maintenance of soil multifunctionality and fungal OTU richness, especially in June and July. We recommend thinning as a tool to mitigate the impacts of precipitation reduction on soil multifunctionality and the microbial community in larch plantations.

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Author contributions Hongxing Wang, Xiaomei Sun, and Shougong Zhang designed the research; Hongxing Wang, Dongsheng Chen, and Chunyan Wu performed the experiments and collected the data; Hongxing Wang analyzed the data and drafted the manuscript; Liangdong Guo, Xiaomei Sun and Shougong Zhang helped revise the manuscript.

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Data availability The raw sequence data have been deposited in the NCBI Sequence Read Archive (BioProject PRJNA789094 for fungi and PRJNA849713 for bacteria).

Declarations

Competing interests The authors declare no competing interests.

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