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Research article

Shifts of understory vegetation induced by thinning drive the expansion of soil rare fungi

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ABSTRACT

The gap formation due to forest thinning regulates the understorey microclimate, ground vegetation, and soil biodiversity. However, little is known about abundant and rare taxa's various patterns and assemblage mechanisms under thinning gaps. Thinning gaps with increasing sizes (0, 74, 109, and 196 m2) were established 12 years ago in a 36-year-old spruce plantation in a temperate mountain climate. Soil fungal and bacterial communities were analyzed by MiSeq sequencing and related to soil physicochemical properties and aboveground vegetation. The functional microbial taxa were sorted by FAPROTAX and Fungi Functional Guild database. The bacterial community stabilized under varied thinning intensities and was not different from the control plots, whereas the richness of the rare fungal taxa was at least 1.5-fold higher in the large gaps than in the small ones. Total phosphorus and dissolved organic carbon were the main factors influencing microbial communities in soil under various thinning gaps. The diversity and richness of the entire fungal community and rare fungal taxa increased with the understorey vegetation coverage and shrub biomass after thinning. Gap formation by thinning stimulated the understorey vegetation, the rare saprotroph (Undefined Saprotroph), and mycorrhizal fungi (Ectomycorrhizal-Endophyte-Ericoid Mycorrhizal-Litter Saprotroph-Orchid Mycorrhizal and Bryophyte Parasite-Lichen Parasite-Ectomycorrhizal-Ericoid Mycorrhizal-Undefined Saprotroph), which may accelerate nutrient cycling in forest ecosystems. However, the abundance of Endophyte-Plant Pathogens increased by eight times, which showed the potential risk for the artificial spruce forests. Thus, fungi may be the driving force of forest restoration and nutrient cycling under the increasing intensity of thinning and may induce plant diseases. Therefore, vegetation coverage and microbial functional diversity should be considered to evaluate the sustainability of the artificial forest ecosystem and forest restoration.

1. Introduction

Forest thinning stimulates gap formation, which accelerates the growth rate and health of the remaining trees and changes the species and functional diversity of undergrowth due to increased availability of solar radiation, soil temperature, moisture, and nutrients (Ares et al., 2010; Scharenbroch and Bockheim, 2007; Verschuyl et al., 2011). Natural regeneration of the gaps shifts pure plantations into heterogeneous forests with complex structures (Albrecht and McCarthy, 2006; Iverson et al., 2008). It was shown that thinning altered forest ecology and critical ecosystem components, including microbial communities and especially fungi (Lin et al., 2016). Thinning at the initial stage provided

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saprophytic soil microorganisms with vegetative substrates such as green leaves, shoots, and dead roots. This increased soil respiration (Ohashi et al., 1999) and the biomass/activity of microorganisms (Hagerman et al., 1999) and changed the structure of the soil microbial community (Lin et al., 2016). Soil microbial biomass (the sum of PLFA biomarkers) decreased 1.93 times in forest gaps because actinomycetes and nonspecific bacteria are sensitive to high soil temperatures and evaporation, especially in medium-size gaps (Paul et al., 2002; Yang et al., 2017). Forest thinning also negatively affected the underground total fungal and ectomycorrhizal fungal biomass (Collado et al., 2020). However, the conclusions about soil microbial community variations after forest thinning are inconsistent (Chen et al., 2015; Lewandowski et al., 2015). Thus, profiling abundant and rare soil microbial subcommunities in thinning gaps is essential for understanding the ecological influences of thinning method on inefficient artificial forests.

The abundant species in the composition of soil microbial communities contribute to the functioning of forest ecosystems and sustain carbon (C), nitrogen (N), and phosphorus (P) cycling (Falkowski et al., 2008; Singh et al., 2010). Moreover, these allow us to predict shifts in environmental conditions by the abundant microbial members, especially under anthropogenic changes (Ge et al., 2010; Zhang et al., 2011). Compared with the abundant taxa of soil microorganisms, rare species are also essential players in nutrient cycling, greenhouse gas emissions, and organic pollutant degradation (Jousset et al., 2017). Since rare species are at risk of extinction (Lawton, 1994), they represent a reservoir of genetic diversity with redundant functions (Boraks et al., 2020; Pascoal et al., 2021) that is capable of responding rapidly to environmental changes and disturbances (Epstein, 2009; Lennon and Jones, 2011). Rare bacterial communities not only contribute to C processing functions, including degradation and fermentation of aromatic compounds, including pollutants (Dell'Anno et al., 2012), but also have nitrification, nitrate reduction, and ammo oxidation functions (Zhou et al., 2020). Zhang et al. (2019) suggested that microorganisms' rare biosphere is vital in regulating available soil N in ecosystems under climate change. However, few studies on rare species have focused on both the bacterial and fungal communities in the forest management process.

The minority of the microbial communities are rare species (Kaminsky and Morales, 2018) that showed a characteristic distribution and abundance (some rare OTUs in *Alphaproteobacteria, Bacteroidetes*) and were strongly affected by environmental filtering (Jiao et al., 2017, 2019; Jiao and Lu, 2020). The formation of an assembly of abundant and rare fungi was mediated by divergent environmental factors (Jiao and Lu, 2020; Wan et al., 2021) like a high content of soil organic C (SOC) provided more ecological niches for rare fungi than the abundant components (Lin et al., 2022). Since environmental change and microbial abundance are very dynamic, the abundant part of the population may become rarer as the ecological variables worsen, and vice versa. It was shown that more than half of the taxa cycle between abundance and rarity, while 6% always remain rare (Pedrós-Alió, 2012). Thus, they influence the formation of an assembly of communities by preventing the invasion of new species and may stabilize community functions under fluctuating environmental conditions through insurance effects (Yachi and Loreau, 1999; Jousset et al., 2017). However, the relative abundance of "rare biospheres" of soil bacteria and fungi did not change under climatic shifts such as simulated temperature and precipitation increases (Zhang et al., 2019). In addition, rare microorganisms are essential players in the host-associated microbiome of plants and animals, where they prevent the establishment of pathogens and stimulate host immunity (Jousset et al., 2017). Thus, rare species provide a reservoir of genetic resources that may be activated under suitable conditions, as at least one species will perform a given process under given environmental conditions (Lynch and Neufeld, 2015). However, the distribution pattern of rare fungal species in restored and managed forest plantations remains unclear.

The impact of secondary successional areas on microbial communities under thinning also includes vegetation-related factors such as diversity, coverage, and biomass that may be altered (Xu et al., 2022). Communities of soil bacteria and fungi change following plant traits, such as productivity (Sayer et al., 2017), due to close interactions between microorganisms and plants in the rhizosphere (Huang et al., 2014; Grime and Pierce, 2012). Previously it was shown that the establishment of secondary succession promoted soil microbial diversity by increasing the diversity of microhabitats and providing diverse plant hosts for symbiotic and pathogenic microorganisms (Yang et al., 2020). The growth of secondary vegetation accelerates the accumulation of litter and root biomass, which provides sufficient C resources and nutrients for microbial growth, thus, could affect the diversity of soil microbial communities. However, there is no information regarding the potential association between understorey vegetation properties and soil microbial communities.

The objective of this study was i) to explore the response of the microbial communities in spruce plantations to thinning of various intensities and ii) to deepen the understanding of the response of rare taxa of fungal communities to that process. We aimed i) to uncover the fungal and bacterial communities strongly responsive to different forest thinning intensities, ii) to assess the rare taxa under thinning-induced forest gaps, and iii) to evaluate the biotic and abiotic factors affecting the soil microbial communities and rare taxa. Given that fungi have a more significant response to aboveground vegetation communities (Qiang et al., 2021) and are sensitive to temperature, moisture, and nutrients in large gaps (Scharenbroch and Bockheim, 2007; Verschuyl et al., 2011), we hypothesized that (1) diversity of microbial community would be higher in large gaps than in control and smaller gap sizes; and (2) fungal and bacterial communities, especially rare fungal taxa, would be modulated by the aboveground vegetation community and probably soil conditions, including soil N, C, and moisture.

2. Materials and methods

2.1. Study area

The Maoxian Mountain Ecosystem Research Station of the Chinese Academy of Sciences in Sichuan (31°37′N and 103°54′E), situated in a temperate mountain climate, served as the site for the experiment. The area experiences an average annual precipitation of 900 mm and the mean monthly temperature fluctuates between −1.1 °C and 18.8 °C (Pang et al., 2016). The vegetation is dominated by Minjiang fir (*Abies faxoniana*) and spruce (*Picea asperata*), and the soil type is Haplic Luvisol (pH in water is 5.27) (Chen et al., 2010; Pang et al., 2016). The primary subalpine forests in this region were cut down at a large scale from the 1940s to the 2000s (Pang et al., 2016). Reforestation was performed in the cutting areas for the initial purpose of timber requirements, and such plantations comprised approximately 60% of forest areas in western Sichuan Province (Pang et al., 2016). Most monoculture plantations were therefore designed to satisfied the timber requirement (Pang and Bao, 2011). Spruce represents one of the characteristic tree species commonly cultivated in the subalpine region of the eastern Tibetan Plateau, the experimental site was a 36-year-old spruce monoculture plantation planted in 1985 (Jiang et al., 2010). The forest is disturbed by the collection of litter (equivalent to 17–20 g C m^{-2} yr^{-1} in the fall), wild mushrooms, and traditional Chinese medicinal plants in the spring every year (Pang et al., 2016).

In 2008, the canopy leaf area index and the tree canopy coverage were approximately 3.5 and 92%, respectively, and the mean diameter of trees at breast height was 15.4 cm with 11.2 m mean height (Pang et al., 2016). The presence of monoculture and high-density spruce plantations have been linked to reduced soil fertility, forest productivity, and ecological function (Bao et al., 2007). To address these issues, thinning was implemented in a 5-ha spruce plantation to enhance soil fertility and forest productivity, which simulates natural gap formation (Jiang et al., 2010; Pang et al., 2016). There were four thinning gap

sizes, including control (no thinning), small (74 m^2), intermediate (109 m^2), and large (196 m^2) gaps. Calculation of gap size was based on the polygon area that was enclosed by trees bordering the gap. A randomized complete block design with three replicates was established. 20 × 15 m plots of four thinning intensities with 100 m spacing between the plots were randomly assigned in each block. The thinning was conducted on 27.11.2008 by an electric saw. The cut trees' stems, branches, and leaves were removed from thinning plots, but understorey shrubs, herbaceous species, and stumps above the ground up to 50 cm were retained (Yang et al., 2017). All the experimental plots were fenced with wire netting.

2.2. Soil property analyses

The soil was collected at 0–10 cm depth in August 2020, 13 years after the thinning. One quadrate of 4 × 4 m in the central points for all gaps was chosen and assigned as the sampling point for each plot to avoid edge effects. In each designated plot, a total of five 2.5 cm diameter soil cores were randomly collected and subsequently pooled together to create a composite sample. The composite sample was then divided into two equal portions for further analysis: one part was used for determining physicochemical characteristics, and the other was used for microbial analysis (Illumina MiSeq sequencing). Each soil sample was passed through a 2 mm sieve. The soil pH value was measured in a 1:2.5 (w/v) soil/water suspension. Bulk density was determined using the cutting-ring method. Dried soil samples were subsequently ground to pass through a 0.25-mm sieve for the analysis of total nitrogen (TN) and soil organic carbon (SOC), which were determined through dry combustion using the Multi N/C®2100(S) (Analytik Jena AG, Germany). For the analysis of dissolved organic carbon (DOC) and nitrogen (DON), 5 g of fresh soil were shaken with 50 mL of 2 M KCl for an hour in 250 mL flasks on a reciprocating shaker at a speed of 200 r min^{-1}. The soil extracts were then filtered and subjected to analysis using a TOC/TN analyzer (Vario TOC, DKSH, China). Finally, the contents of NH_4^+ and NO_3^- were analyzed using a flow analyzer from SEAL Analytical (Germany). The chlorostannous reduced molybdophosphoric blue colour method was used to determine Olsen P (OP) (Olsen et al., 1954). The total P (TP) was determined using H_2SO_4–$HClO_4$ digestion and HCl–H_2SO_4 extraction and analyzed by the molybdenum blue method (Lu, 2000).

2.3. Survey of vegetation in forest gaps

A site of 1 m^2 in the specified quadrates was randomly selected to cut off all the aboveground parts of vegetation to determine the aboveground biomass. Within each plot, survey quadrates 1 × 1 meters for herbaceous vegetation and 2 × 2 meters for shrubs were randomly established. Identification and statistical analyses of aboveground trees, shrubs, and herbs were conducted based on authoritative references such as the National Plant Specimen Resource Center (http://www.cvh.ac.cn) and "Flora Reipublicae Popularis Sinicae". The ratio of vegetation projection area to land area within each quadrat was then calculated to determine vegetation coverage. In addition, all roots in each soil sample were meticulously collected with tweezers to minimize damage to the fine roots. The roots were then placed in Petri dishes, washed with distilled water to remove soil particles, and dried for 7 day at 60 °C before being weighed.

2.4. Sequencing

The E.Z.N.A.® soil DNA Kit (Omega Bio-Tek, Norcross, GA, U.S.) was utilized to extract DNA from frozen soil samples weighing 0.5 g. The obtained DNA concentration and purity were evaluated with the aid of a NanoDrop 2000 UV–Vis spectrophotometer (Thermo Scientific, Wilmington, USA). DNA quality was ascertained via 1% agarose gel electrophoresis. Amplification of the V4 hypervariable regions of the 16S rRNA gene was performed for bacteria using primers 515F and 806R (Peiffer et al., 2013), while ITS (internal transcribed spacers) were amplified using ITS1F and ITS2 (White et al., 1990; Gardes and Bruns, 1993) for fungi. The thermocycler PCR system (GeneAmp 9700, ABI, USA) was utilized to carry out the PCR process, with a programme comprising a 1 min duration at 94 °C, 27 cycles of 45 s at 94 °C, 30 s at 56 °C, 90 s at 72 °C, and a final extension at 72 °C for 10 min.

The PCR system utilized in this study consisted of 4 μL of 5 × FastPfu Buffer, 2 μL of 2.5 mM dNTPs, 0.8 μL of each primer (5 μM), 0.4 μL of FastPfu Polymerase, and 10 ng of template. The PCR products were subsequently extracted from a 2% agarose gel, and purified through the application of the AxyPrep DNA Gel Extraction Kit, which was manufactured by Axygen Biosciences, located in Union City, CA, USA. To ensure precision in quantification, the purified samples were subjected to analysis using the QuantiFluor™-ST, developed by Promega in the USA, as per the guidelines provided by the manufacturer.

The purified amplicons were then pooled in equimolar concentrations and subjected to paired-end sequencing, utilizing an Illumina MiSeq platform, following standard protocols. The sequencing procedure was conducted by Majorbio Bio-Pharm Technology Co. Ltd., located in Shanghai, China. The raw sequencing data generated were deposited into the NCBI Sequence Read Archive (SRA) database for further analysis. (Accession Number: SAMN20702137-SAMN20702148 (bacteria); SAMN20703352-20703363 (fungi)).

The raw fastq files were subjected to quality filtering using Trimmomatic, and then merged by FLASH. We then generated rarefaction curves for each sample using the database and approach that was utilized for the fungal taxonomy assignment. The rarefaction curves of each sample were flattened out (Fig. S1). OTUs were clustered using UPARSE (version 7.1 http://drive5.com/uparse/) and a 97% similarity cut-off was employed. The taxonomy of each 16S rRNA gene sequence and ITS sequence was analyzed using the Silva (SSU123) 16S rRNA database (Release 138 http://www.arb-silva.de) and Unite database (Release 8.0 http://unite.ut.ee/index.php), respectively.

For functional classification of bacteria and fungi, we used the FAPROTAX and Fungi Functional Guild databases, respectively (Sansupa et al., 2021; Nguyen et al., 2016). OTUs with a relative abundance >1% were designated as "abundant taxa", while those with a relative abundance <0.01% were classified as "rare taxa" (Liang et al., 2020).

2.5. Statistical analyses

To investigate the effects of thinning intensity on soil properties and microorganisms, a one-way ANOVA was employed. The model's residuals were subjected to normality and homogeneity tests using the Shapiro–Wilk and Levene's tests, respectively. Soil available P was transformed by the Box-Cox method with the best lambda (2.00) to meet the ANOVA assumptions. If the richness data of rare taxa guilds did not satisfy the homogeneity of residual distribution after conversion, Kruskal-Wallis analysis was performed. Tukey's test compared the other indices that met the assumptions ($p < 0.05$). The analyses were performed with SPSS software (Version 21.0). The richness (Chaos) and Shannon–Wiener indices (H′) of the microbial community were calculated (Shannon and Weaver, 1949; Chao, 1984).

To assess the correlation between fungal and vegetation communities, unitary linear recursive analysis was carried out using Origin 2019 software. Redundancy analysis (RDA) of environmental characteristics and microbial communities was conducted in the package ''Vegan'' (R-3.6.2). Package "Venn" was used for the Venn diagrams. Additionally, two-way network analysis was performed to identify the relationships between rare fungi and plants. The resulting data were exported from the cloud platform of Majorbio and visualized using Cystoscope 3.8.0.

Table 1
Physico-chemical soil properties.

	SM(%)	BD (g cm^{-3})	pH	C (%)	N (%)	TP (g kg^{-1})	Box-Cox (OP) (Box-Cox (mg kg^{-1}))	DOC (mg kg^{-1})	DON(mg kg^{-1})	NH_4^+(μg g^{-1})	NO_3^-(μg g^{-1})
Control	58.6 ± 5.42 a	0.79 ± 0.08 a	5.12 ± 0.08 a	5.21 ± 0.41 a	0.39 ± 0.01 a	0.48 ± 0.00 a	111 ± 13.4 a	556 ± 42.9 a	255 ± 12.2 a	35.7 ± 4.16 a	4.07 ± 2.00 a
SG	52.1 ± 2.69 a	0.86 ± 0.08 a	5.34 ± 0.19 a	4.87 ± 0.34 a	0.39 ± 0.02 a	0.50 ± 0.03 a	85.1 ± 18.9 a	534 ± 40.8 a	249 ± 6.2 a	38.1 ± 9.19 a	3.53 ± 1.71 a
MG	55.4 ± 1.78 a	0.88 ± 0.03 a	5.15 ± 0.06 a	5.38 ± 0.38 a	0.41 ± 0.01 a	0.48 ± 0.02 a	138 ± 88.9 a	621 ± 70.9 a	254 ± 10.1 a	33.8 ± 4.27 a	3.87 ± 0.77 a
LG	52.6 ± 2.97 a	0.85 ± 0.03 a	5.15 ± 0.07 a	4.73 ± 0.42 a	0.37 ± 0.03 a	0.47 ± 0.05 a	89.4 ± 41.2 a	582 ± 36.1 a	252 ± 3.13 a	31.2 ± 3.54 a	6.20 ± 1.46 a
SEM	0.04	0.06	0.11	0.34	0.02	0.03	49.4	49.6	8.66	5.76	1.55

Note: Lowercase letters show significant ($p < 0.05$) differences between gaps as assessed by ANOVA. SM: soil moisture; BD: soil bulk density; TP: soil total phosphorus; OP: Olsen phosphorus; DOC: dissolved organic carbon; DON: dissolved organic nitrogen; SEM: standard errors for of mean; SG: small gap; MG; intermediate gap; LG: large gap. Data presents mean ± SD, n = 3.

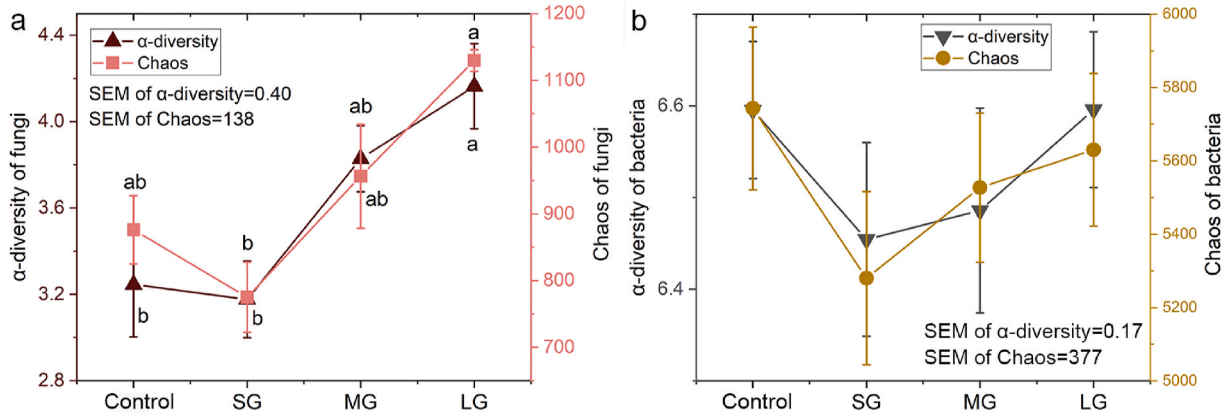

Fig. 1. Shannon-Wiener and Chaos index of soil fungal (a) and bacterial (b) communities in thinning gaps of spruce plantations on OTU level. Control: no thinning; SG: small gaps; MG: intermediate gaps; LG: large gaps. SEM: Standard errors for differences of means. Data are the mean ± SE, n = 3. Letters indicate significant differences ($p < 0.05$).

3. Results

3.1. Response of understorey vegetation and soil properties to thinning gap intensity

Soil properties (e.g., pH, TN, and SOC) were not affected by gap size due to forest thinning (Table 1). The diversity and richness of the understorey were comparable between the gap sizes (Fig. S2); however, the plant biomass was six times, and the cover of the understorey shrubs was four times higher in the large gaps than in the control (Fig. S2).

3.2. Response of soil bacterial communities to thinning gap intensity

In total, 797,315 sequences of bacteria were obtained from all soil samples, with 9011 OTUs based on a 97% similarity level. A total of 518 families were detected from 43 phyla, 135 classes, and 325 orders of bacteria. The sequences of Xanthobacteraceae were the most abundant at the family level, followed by those of Chthoniobacteraceae (Fig. S3). The bacterial Shannon–Wiener index and richness were the same between the gap sizes on the OUT level ($p > 0.05$) (Fig. 1).

The OTUs of chemoheterotrophy were the most abundant functional group, followed by those of aerobic_chemoheterotrophy, nitrogen_fixation, and animal_parasites_or_symbiots (Fig. 2). Richness of rare bacterial functional groups in small gaps showed the lowest value than under other thinning intensities (Fig. 3).

3.3. Response of soil fungal communities to thinning gap intensity

There were 757,636 sequences of fungi obtained from all soil samples. A total of 3095 OTUs based on a 97% similarity level were detected from 128 orders, 284 families, and 561 genera. *Tricholoma* dominated at the genus level, followed by *Sebacina*, *Mortierella,* and *Saitozyma* (Fig. S3). Both the diversity and richness of fungi were at least 1.5-fold higher in large gaps than in small gaps on the OUT level ($p > 0.05$) (Fig. 1).

The functional guilds of ectomycorrhizal dominated in the whole fungal communities, the ectomycorrhizal-fungal parasite in the rare fungal taxa, and fungal parasite-undefined saprotroph dominated in abundant fungal taxa (Fig. 2). The variation of rare and abundant taxa under changing thinning intensity was quantitatively estimated by calculating the functional α-diversity (Shannon index) and richness (Fig. 3). Our results showed that rare taxa of fungal communities had a significantly high richness in large gaps than without thinning and in the small gaps (Fig. 3). In addition, we found from the Venn diagrams that fungi had more taxa than bacteria, both at the OUT level and at the functional level, that cannot be shared at different thinning intensities, both in whole and rare taxa (Fig. S4; Fig. S5).

3.4. Relationship between environment induced by thinning and soil microbial communities

The stability of the total and rare soil bacterial community was maintained by the soil properties, which were not affected by thinning (Fig. 4c and d; Table 1). Aboveground vegetation coverage and biomass

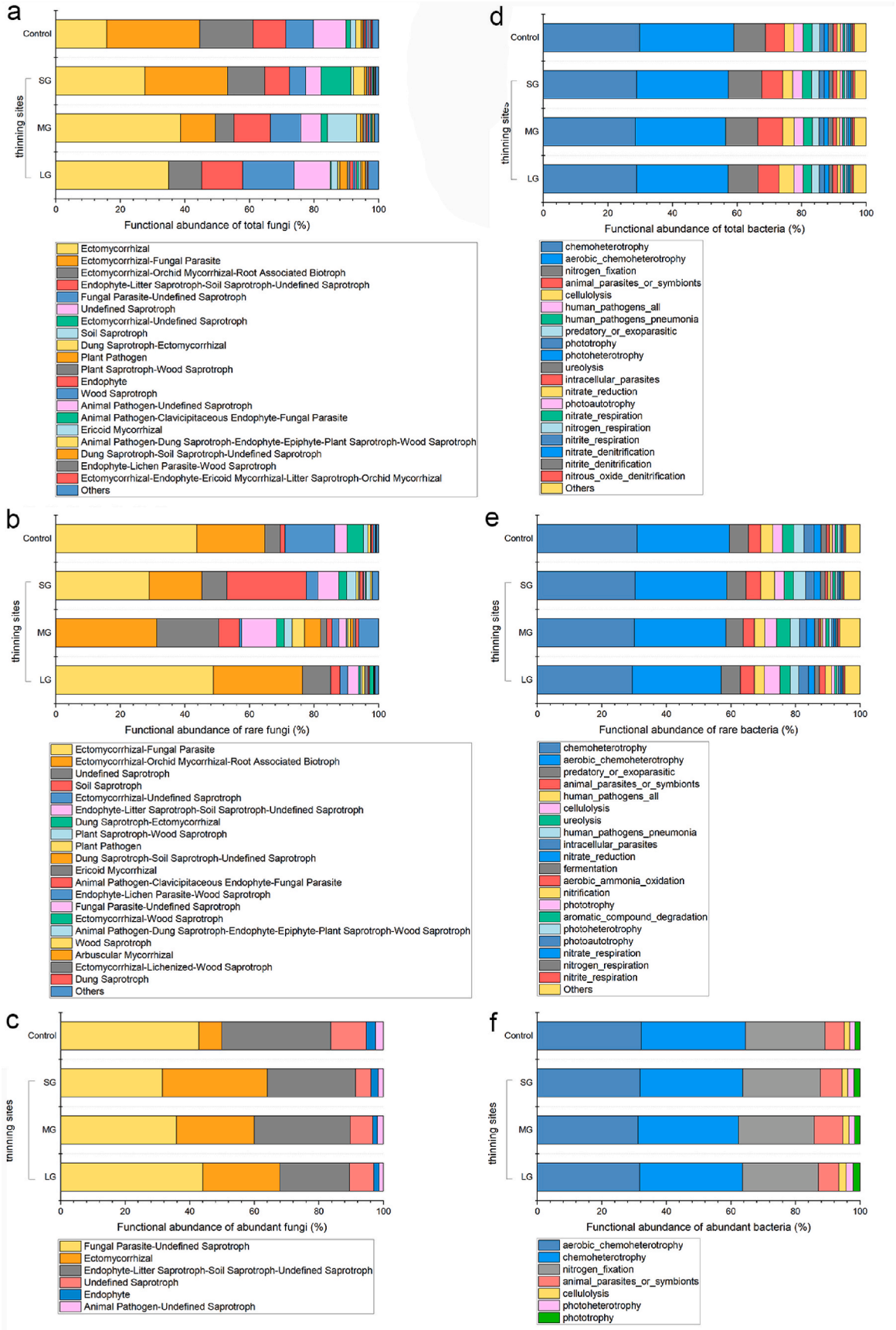

Fig. 2. The abundance of soil fungi at the functional level (a, b, c) and bacteria at the family level (d, e, f) in thinning gaps of spruce plantations. Control: no thinning; S: small gaps; M: intermediate gaps; L: large gaps.

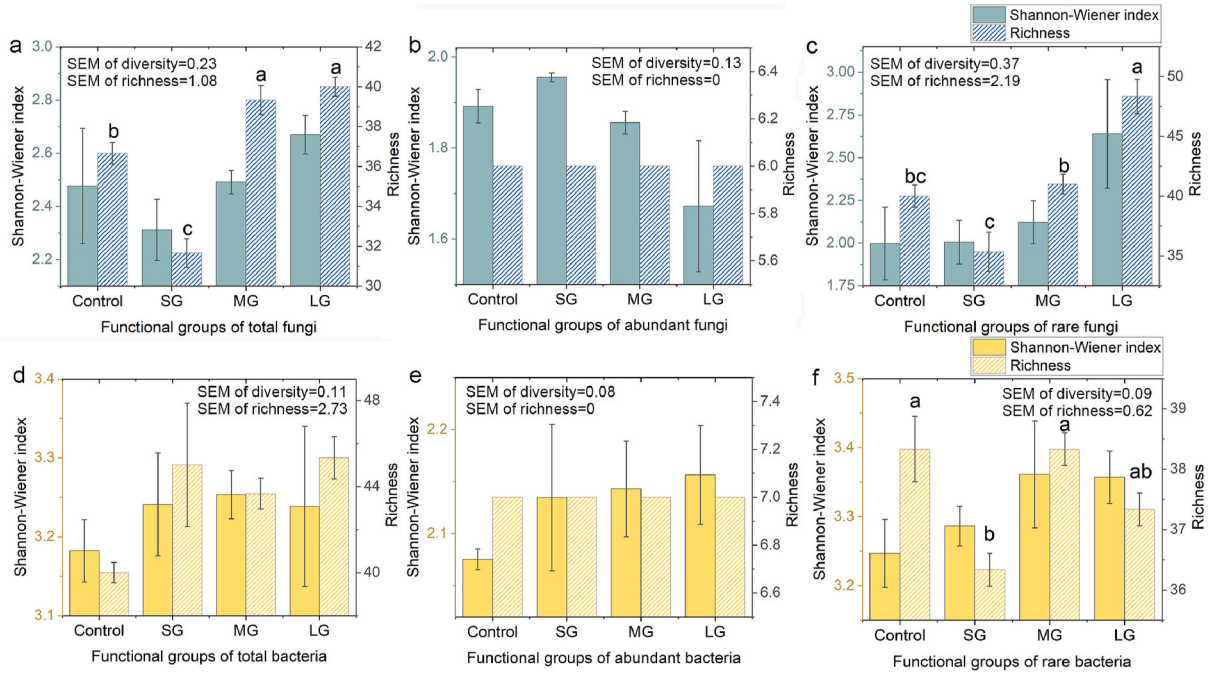

Fig. 3. Diversity and richness of soil fungal (a) and bacterial (b) communities in thinning gaps of spruce plantations at the functional level. Control: no thinning; SG: small gaps; MG: intermediate gaps; LG: large gaps. Data are the mean ± SE, n = 3. Letters indicate significant differences ($p < 0.05$). SEM: standard errors for differences of means.

had no significant effect on the diversity and richness of rare bacterial taxa (Fig. S6). The diversity of the understorey plants, soil TP and DOC affected the distribution pattern of the entire fungal community (Fig. 4). Fungal diversity and richness increased with aboveground biomass ($p < 0.05$), and fungal richness increased with shrub coverage ($p < 0.05$) (Fig. S6). The richness of rare fungi increased to 1.37 times with the development of shrub coverage and aboveground biomass due to thinning intensity (Fig. 3; Fig. S6).

By the comparison under varied thinning intensity, undefined Saprotroph (Saprotroph), Endophyte-Plant Pathogen (Pathotroph), Ectomycorrhizal-Endophyte-Ericoid Mycorrhizal-Litter Saprotroph-Orchid Mycorrhizal (Symbiotroph), Animal Pathogen-Endophyte-Lichen Parasite-Plant Pathogen-Wood Saprotroph (Pathotroph-saprotroph), Dung Saprotroph-Endophyte-Wood Saprotroph (Saprotroph), Animal Pathogen-Undefined Saprotroph (Pathotroph-saprotroph) and Bryophyte Parasite-Lichen Parasite-Ectomycorrhizal-Ericoid Mycorrhizal-Undefined Saprotroph (Pathotroph-saprotroph-symbiotroph) showed significant variations in rare taxa (Fig. 5a; Table S1). The highest OTUs number of Dung Saprotroph-Endophyte-Wood Saprotroph existed in control (no thinning); however, the other functional guilds all reached the highest value in large gaps (Fig. 5a).

As shown in the two-way network (Fig. 5b), critical understorey vegetation regulated the abundance of soil rare fungal taxa, including *Viburnum betulifolium* (BZ), *Deutzia longifolia* (CF) and *Polygonum* spp. (C). *Polygonum* spp. had a very high richness in different gaps (Table S2) and had positive relationships with rare taxa. Moreover, Endophyte-Soil-Saprotroph (ak) was the critical node in rare fungal functional taxa (Table S3). Besides, this kind of saprotroph was positively related to the understorey plants, such as *Polygonatum sibiricum* (AF), *Spiraea salicifolia* (BC), *Toxicodendron vernicifluum* (CG), etc. (Fig. 5b). Thus, aboveground vegetation and soil properties together affected the maintenance and fluctuation of the fungal community under different thinning gap sizes (Fig. 4; Fig. S6; Fig. 5).

4. Discussion

4.1. Changes in microbial community structure under thinning

Forest gaps due to thinning increased the diversity of the soil fungi, while diversity and species abundance of the bacterial community was not sensitive (Table 1; Fig. 2). Fungi had faster succession rates than bacteria under the development of secondary plant community (Wang et al., 2019), and under the plant community shift, the fungal community became heterogeneous (Dong et al., 2016; Qiang et al., 2021), while the bacteria remained more homogeneous (Montagna et al., 2018). Similar vegetation diversity and richness formed litter with the same composition (Fig. S2). Thus, bacteria, the main groups degrading litter-derived organics, did not show different community compositions under these thinning intensities.

The differences in the fungal community caused by thinning correlated with the changes in aboveground biomass and coverage (Fig. S6) rather than soil properties (Table 1). This might be attributed to the life strategies of plant species, the chemical composition and amount of litter, and root exudates (Grime and Pierce, 2012; Huang et al., 2014), and shows that the plant community is a crucial predictor of the composition of the fungal community (Odriozola et al., 2021). Different aboveground biomass of the understory plant community with similar richness and diversity (Fig. S3) is essential for regulating solar radiation, wind speed, and humidity in the forests (De Frenne et al., 2019, 2021). These alterations adjust microbial photochemical mineralization and photo-faciliation which can affect the litter decomposition rate and alter the nutrient utilization by microorganisms indirectly (Wu et al., 2022). However, the stability of bacterial communities in the thinning gaps, which was seen from the constant abundance of *Bacteroidetes*, *Nitrospirae*, and *Gemmatimonadetes* (Cai et al., 2020). In this study, it is reflected in the stability of *Xanthobacteraceae*, *Chthoniobacteraceae* and *Gemmataceae*, which are related to i) unchanged stoichiometry of available nutrients in the soil (Fig. S2), and ii) diverse strategies of substrates utilization, which are characteristic of the bacterial community.

Both biotic and abiotic factors facilitated the diversity of soil

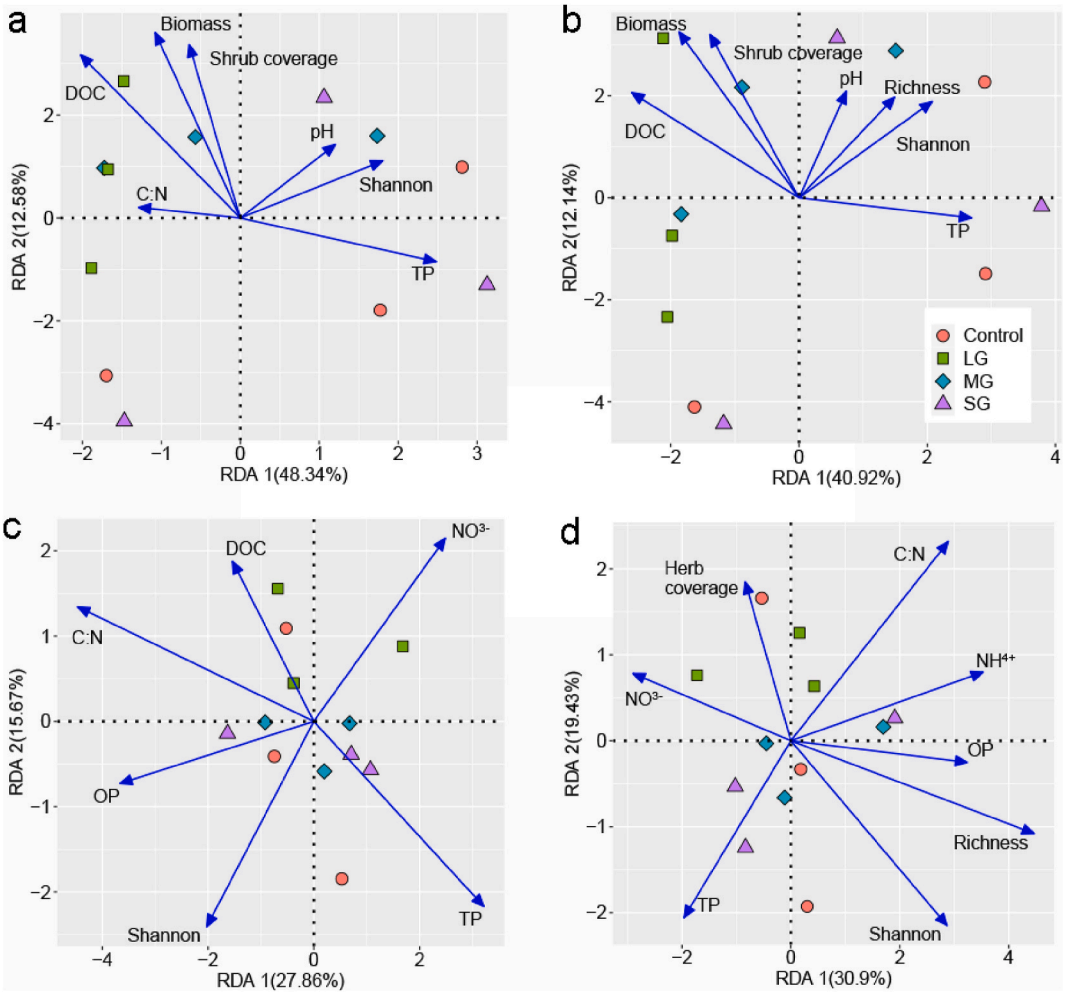

Fig. 4. RDA of the relationships between total and rare fungal (a, b)/bacterial (c, d) communities and environmental properties in various gap thinning treatments of spruce plantations. Control: No thinning; SG: Small gap; MG: Intermediate gap; LG: large gap; Shannon: Shannon–Wiener index of understorey plants; Richness: Richness of understorey plants; Biomass: aboveground biomass of understorey plants; OP: Olsen phosphorus; TP: Total phosphorus; BD: Bulk density; C:N: Ratio of soil organic carbon to total nitrogen; DOC: Dissolved organic carbon.

microorganisms (Fig. 4; Lange et al., 2014). Low soil bulk density favoured bacterial populations (Li et al., 2002; Sun et al., 2020); NH_4^+ contents affected the relative abundances of *Acidimicrobiia*, *Nitrospira*, and *Solibacteres* (Zeng et al., 2019); DOC explained the differences in abundance and richness of fungal functional communities between the thinning intensities (Fig. 4) because this pool is an essential and readily available C source. Mycorrhizal and saprotrophic fungi have overlapping fundamental niches concerning the colonization of substrates with different qualities (lignin and N content) (Bödeker et al., 2016). Mycorrhizal fungi restrained the activities of more efficient litter saprotrophs (Bödeker et al., 2016). In the large gaps, the proportion of saprotrophs increased compared with other thinning intensities. The decline in the proportion of ECM also indicated the competition between their ecological niches and resources (Fig. 2), for example for P (Attiwill and Leeper, 1987). Ectomycorrhizal association is one of the strategies for plants to resist the P limitation and controls the content of P available forms (Beever and Burns, 1981), which can explain the relationships between total P and the shifts of fungal communities under thinning (Fig. 4). Saprotrophic fungi can also store P in mineral forms inside of their mycelium and assimilate P in organic forms that could be released after fungal death (Ceci et al., 2018). However, the content of SOC and N showed consistency under different thinning intensities (Table 1), which can explain the stable composition of dominant bacterial and fungal groups in our study area (Fig. 3). Thus, bulk density and NH_4^+, DOC, and TP contents were the most critical factors affecting and maintaining the bacterial and fungal functional communities in the spruce forest after thinning.

4.2. *Effects of forest thinning intensity on rare fungi*

The diversity of rare fungal species declined in the small gaps compared to the control (Fig. 3) because of the sensitivity to disturbance (Xue et al., 2021). The small forest gap lacks the original vegetation (spruce), sunlight, and space for the development of secondary shrubs and herbs. In contrast, with thinning intensity, the diversity and richness of total and rare fungi increased highly due to more diverse microenvironmental niches and high small-scale heterogeneity of soil properties created by the increased biomass of plant species, especially by shrubs and herbaceous (Fig. 3). Increased biomass and coverage of herbs and shrubs indirectly created the following conditions: accelerated nutrient input and cycling (Gao et al., 2019) within the gaps, and supported the survival of some rare taxa which classified into saprotrophs (Undefined Saprotroph), pathogens (Endophyte-Plant Pathogen), symbionts (Ectomycorrhizal-Endophyte-Ericoid Mycorrhizal-Litter Saprotroph-Orchid Mycorrhizal, Hebeloma), Pathotroph-saprotrophs (Animal Pathogen-Endophyte-Lichen Parasite-Plant Pathogen-Wood Saprotroph,

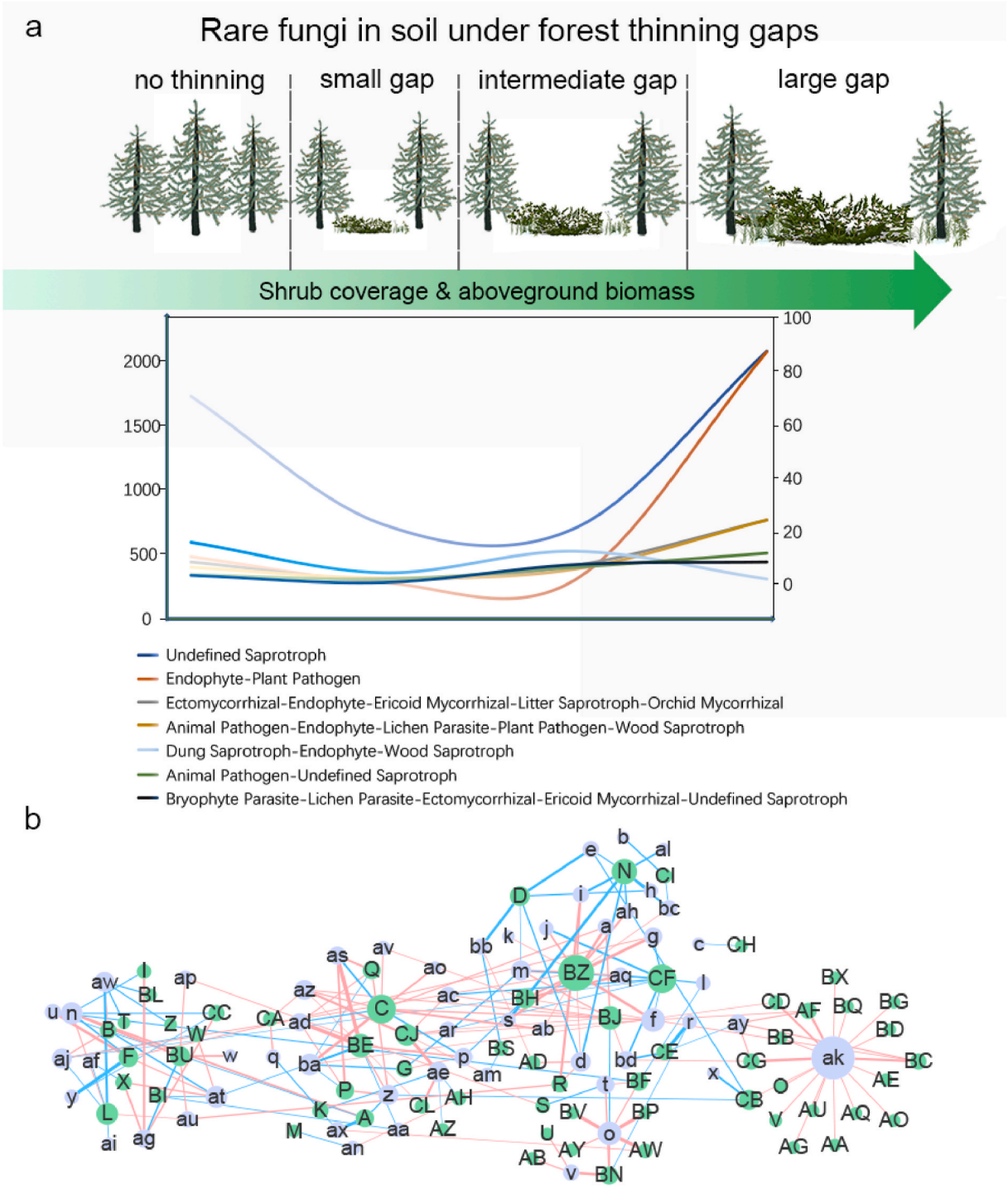

Fig. 5. Development (a) and network (b) of rare fungal OTUs according to their functions and depending on the thinning gap size in the forest. Blue and red lines represent negative and positive relationships between plant species (green nodes) and rare fungal guilds (purple nodes), respectively. The nodes' information was shown in Table S2; S3. Lines between nodes: The red lines represent positive correlations ($r > 0.04$, $p < 0.05$), and the blue lines represent negative correlations ($r > 0.04$, $p < 0.05$). The thickness of the line segment represents the difference in the correlation coefficient. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Animal Pathogen-Undefined Saprotroph) and Pathotroph-saprotroph -symbiotrophs (Bryophyte Parasite-Lichen Parasite-Ectomycorrhizal -Ericoid Mycorrhizal-Undefined Saprotroph) (Table S1). Thus, the rare fungal taxa increased with thinning intensity because they can raise functional redundancy of the whole fungal community (Liang et al., 2020) without the depression of dominant groups.

Some ericoid mycorrhizal fungi (Ectomycorrhizal-Endophyte-Ericoid Mycorrhizal-Litter Saprotroph-Orchid Mycorrhizal and Ectomycorrhizal-Orchid Mycorrhizal-Root Associated Biotroph) belonging to rare taxa that are associated with understorey plants were found in the large gaps (Fig. 5). The increase of Orchid and Ericoid mycorrhizal fungi may point to the expansion of host vegetation with the recovery of the understory vegetation. However, only some negative correlations between herbaceous plants (*Houttuynia Cordata*) and ericoid mycorrhizal guilds were found in the network (Fig. 5). Therefore, we suggested that the biomass and coverage of secondary shrubs,

rather than herbs, under the large forest gap expand, occupying the existing space. The space and number of herbs were reduced by the crowding of some shrubs, which explained a negative correlation between herbs and rare microbial taxa. The number of shrubs did not change drastically but was sufficient to provide niches for some rare mycorrhizal groups. Therefore, secondary shrubs can support the development of rare mycorrhizal groups in spruce forests.

Thinning intensity profoundly influenced some rare species of saprotrophic fungi through forest-related factors (Awad et al., 2019, Fig. 5; Fig. S7). Rare saprotrophic fungi (undefined Saprotroph) that showed the increase of the abundance in large gaps could contribute significantly to the litter decomposition (Rayner and Boddy, 1988). Increasing aboveground biomass (Fig. S3) reports the high contribution of aboveground input which can be manipulated by saprophytic fungi in litter decomposition processes and then regulate the nutrient cycle. *Striatibotrys* are mainly isolated from soil and responsible for decomposing plant materials, possibly related to saprotrophs (Lombard et al., 2016). The genus *Cylindrodendrum* is regarded as a semiaquatic saprotroph (Lombard et al., 2014). Zopfiella spp. is a saprotroph isolated from plant debris that is decomposed under anaerobic conditions (Shearer and Crane, 1978). These saprophytic fungi live in water remnants; however, they were found in large gaps, although soil moisture was similar between the gaps of various intensities (Table 1). We suggested the higher aboveground vegetation biomass could protect these rare fungi from direct sunlight and provide an appropriate environment for their development. Thus, some rare saprophytic fungi were also involved in the decomposition of decaying plant litter, and their abundance increased with the size of forest thinning gaps.

The diversity and richness of understory vegetation remained unchanged with the thinning intensity (Fig. S3), indicating that thinning did not promote the development of exotic plant species, which the "Janzen-Connell effect" can explain. This effect defines the species' coexistence and regulation of plant populations by the presence of specific natural enemies. In the case of the present study, rare pathogens (*Endophyte-Plant Pathogen*, *Animal Pathogen-Endophyte-Lichen Parasite-Plant Pathogen-Wood Saprotroph*, *Animal Pathogen-Undefined Saprotroph*, and *Bryophyte Parasite-Lichen Parasite-Ectomycorrhizal-Ericoid Mycorrhizal-Undefined Saprotroph*) were detected (Fig. 5); still, the number of them was lower ($p < 0.05$) under small and medium thinning gaps compare to the large (Table S1). Following the "Janzen-Connell effect," pathogenic fungi and host-specific natural enemies (herbivorous animals) restricted the aggregation of original species and the entry of new plant species into the gaps and explained constant values of diversity and richness of understory community. Although the infection of plants by pathogens inhibits the infection of mycorrhizal fungi and vice versa (Liu and Chen, 2007), both fungal groups increased in the large forest gaps because of higher undergrowth biomass and coverage compared to other thinning intensities (Fig. S6). The increase in *Endophyte-Plant Pathogen* under the large forest gaps is almost eight times greater compared to the control. An increase in the size of secondary succession within planted forests is not only an opportunity for effective restoration. Still, it may also present unknown challenges and risks to vegetation growth and development. Therefore, proper planning of stand window size is essential for forest restoration to protect forest health and sustainability.

5. Conclusions

The gaps formed by the thinning of secondary forests led to the natural restoration of understorey communities. Soil bacterial communities were not affected by gap size, while the diversity and richness of fungi in large gaps increased by 30% relative to that of the control. The increase in the rare taxa reflected the transformation of the fungal community in the gaps. The functional guilds of rare fungal taxa, including *undefined Saprotroph* (Saprotroph), *Endophyte-Plant Pathogen* (Pathotroph), *Ectomycorrhizal-Endophyte-Ericoid Mycorrhizal-Litter Saprotroph-Orchid Mycorrhizal* (Symbiotroph), *Animal Pathogen-Endophyte-Lichen Parasite-Plant Pathogen-Wood Saprotroph* (Pathotroph-saprotroph), *Animal Pathogen-Undefined Saprotroph* (Pathotroph-saprotroph) and *Bryophyte Parasite-Lichen Parasite-Ectomycorrhizal-Ericoid Mycorrhizal-Undefined Saprotroph* (Pathotroph-saprotroph-symbiotroph) increased with the thinning intensity. Bacterial and fungal communities were affected by soil bulk density and NH_4^+, DOC, and TP contents. Fungal diversity and richness, especially of the rare species, increased with the growth of understorey vegetation (coverage and biomass). Therefore, mutual stimulation or restriction between vegetation and soil fungal communities exists during the natural restoration of forests on such a small scale. Not only the increased plant biomass created beneficial conditions for the whole microbial communities, but also the risks of rare pathogenic fungi development increased. High intensity of thinning did not promote the restoration of environmental conditions, which should be considered for forest plantation management. Although our study revealed that rare taxa dramatically increased in large thinning gaps in spruce artificial forests, the ecological effects of these functional groups under thinning gaps still need future investigation. It also needs to be verified whether plant pathogenic fungi, developing under a particular range of thinning intensity, can contribute to ecosystem services.

Author contributions statement

Xueyong Pang: Investigation, Conceptualization, Methodology, Supervision. Wei Qiang: Investigation, Conceptualization, Methodology, Data curation, Visualization, Writing – original draft, Writing – review & editing. Anna Gunina and Yakov Kuzyakov: Writing – review & editing, Supervision. Ruyi Luo, Yan Zhang and Bing Liu: Investigation, Data curation, Formal analysis.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2023.118119.

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