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ORIGINAL PAPER

Prescribed burning alters soil microbial community structure by changing soil physicochemical properties in temperate forests of northern China

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Abstract Prescribed burning is commonly used to maintain forest ecosystem functions and reduce the risk of future wildfires. Although many studies have investigated the response of microbial community to wildfires in forest ecosystems, the effects of prescribed burnings on soil microbial community structure are less studied. It is also unclear that how post-fire soil physiochemical properties changes affected soil microbial communities. Here, we studied the impacts of prescribed burning on soil microbiome in three typical temperate forests of northern China by collecting soil physicochemical and high-throughput sequencing for 16S rRNA and 18S rRNA was applied to analyze the diversity and community composition of soil microbes (bacteria and fungi). Compared with pre-fire condition, prescribed burning significantly decreased Chao1 index and altered soil bacterial communities ($P < 0.05$), whereas it had no significant effect on fungal diversity and community structure of the ($P > 0.05$). *Planctomycetes* and *Actinobacteria* made the greatest contributions to the bacterial community dissimilarity between the pre-fire and post-fire conditions. The main variables influencing the post-fire soil microbial community structure are soil pH, available phosphorus, total nitrogen, and the ratio of soil total carbon to soil total nitrogen, which could account for 73.5% of the variation in the microbial community structure in these stands. Our findings demonstrated a great discrepancy in the responses of bacteria and fungi to prescribed burning. Prescribed burning altered the soil microbial structure by modifying the physicochemical properties. Our results pointed that it is essential to evaluate the impact of prescribed burnings on forest ecosystem functions. These findings provide an important baseline for assessing post-fire microbial recovery in the region and offer critical guidance for restoration efforts.

Keywords Prescribed burning · High-throughput sequencing · Temperate forest · Bacteria · Fungi

Introduction

Soil microbes is a key driver in the processes of organic matter decomposition, soil humus formation, and the regulation of soil energy, further act a great attribution to forest structure and function (Allison and Treseder 2008; Trivedi et al. 2016). In areas that are prone to wildfires, prescribed burnings are frequently employed to change the fuel load and continuity as well as to lessen the likelihood and size

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of these flames (Alcañiz et al. 2018; Burrows and McCaw 2013; Fernandes et al. 2013). However, there is still a great debate on the effect of conducting prescribed burnings in forest ecosystems, as there is no consensus on its effects on the function of forest ecosystems (e.g., soil microclimate and nutrient dynamics) (Bradstock and Williams 2009; Franklin et al. 2003; Heikkala et al. 2016). Fires can impact forest soil properties and microorganisms through direct and indirect ways (Köster et al. 2021), further caused changes in ecosystem nutrients cycling (Alcañiz et al. 2018). Currently, studies mainly focus on how prescribed burnings affect soil physiochemical properties (Akburak et al. 2018; Hubbert et al. 2006; Wang et al. 2012, 2019b), but the research on its influence on soil microbes is still lacking. Several studies have found that the response of soil microbial community structure to fire varies among different ecosystems (Brown et al. 2019; Qin and Liu 2021; Díaz Raviña et al. 2018), which were mainly caused by the difference in the effect of fire on soil physiochemical properties (Certini 2005). As the effects of prescribed burnings on forest ecosystem sustainability and functions are not yet clear, it is critical to systematically study the effect of prescribed burnings on the soil microbial communities. This allows us to demonstrate the links between the soil microbes and the soil physiochemical variables in the post-fire forest ecosystem. (Barreiro and Díaz-Raviña 2021; Francos et al. 2019).

In general, compared with wildfires, the influence of prescribed burnings on soil properties is still limited (Lucas-Borja et al. 2019b; Neary and Leonard 2021). However, there has been so many studies showing that soil properties significantly changed also after prescribed burnings (Francos et al. 2019; Hamman et al. 2008; McKee 1982). For soil physical properties, soil structure compactness, bulk density and water repellence all show an increasing trend after prescribed burning, and soil moisture content and soil porosity have an opposite trend (Granged et al. 2011; Hubbert et al. 2006; Kennard and Gholz 2001). The impact of prescribed burning on soil chemical properties is relatively complex. One study found that the post-fire soil pH were still significantly higher than pre-fire levels at 35 years after prescribed burning (Muqaddas et al. 2015), which may due to the complete oxidation of organic matter and cation release (Certini 2005; Scharenbroch et al. 2012). However, some other studies found that soil pH remained after prescribed burning, and it could be attributed to low fire intensity (Neill et al. 2007; Switzer et al. 2012; Valkó et al. 2016). Soil carbon is an important substrate supplier associated with soil microorganisms across global biomes (Bastida et al. 2021). Post-fire soil total carbon content always increased due to the incomplete combustion of organic matter and charcoal formation under low fire intensity (González-Pérez et al. 2004; Switzer et al. 2012; Wang et al. 2019b). While some studies reported that soil total carbon content remained (Bennett et al. 2014; Girona-García et al. 2018; Roaldson et al. 2014) or decreased after a single prescribed burning (Brockway et al. 2002; Guo et al. 2006; Lavoie et al. 2010; Roaldson et al. 2014), which mainly caused by the influence of post-fire climate-topography interaction on erosional losses (Bennett et al. 2014) and the impact of post-fire plant recovery and microbial activity on C immobilization and mineralization (Alcañiz et al. 2016; Banerjee et al. 2016; García-Fraile et al. 2016). Soil nitrogen content is also an important factor determining the microbial community and limiting forest primary productivity (Dai et al. 2018; Tang et al. 2018), and always positively affected by prescribed burnings. In case of repetitive prescribed burnings, some studies have indicated the loss of total nitrogen from post-fire soils (Muqaddas et al. 2015; Scharenbroch et al. 2012). However, higher nitrogen content was found after a single prescribed burning but decreased after repetitive burning (Blankenship and Arthur 1999). Phosphorous content is usually detected following prescribed burnings (McKee 1982; Merino et al. 2019; Wang et al. 2019a). Normally, nutrient availability changed ephemerally, as the amount of available phosphorous and inorganic N returns to pre-fire levels within one year after fire (Úbeda et al. 2005). While several studies have also indicated that prescribed burnings might affect soil nutrients in a long-term period (Lavoie et al. 2010; Roaldson et al. 2014; Shakesby et al. 2015).

Fire affects soil organisms depending on its intensity and duration, fuel load and soil nutrient availability (Bellido 1987; Girona-García et al. 2018; Múgica et al. 2018; Wang et al. 2016). In wet soils, fire temperatures decrease with depth because of soil thermal conductivity, but surface fire temperatures can rise up to 300 °C in dry soils (Marcelli et al. 2004). The temperature are already over the thresholds mortality of 100 °C for some fungus and 110 °C for some bacteria (Badía et al. 2017; Certini 2005; Neary et al. 2005). Recently, numerous researches have sought to investigate how fire disturbance altered the soil microbial community, and they have found that fire could have an impact on it both directly by heating or killing organisms and indirectly by altering their living conditions. (e.g. the increase in soil nutrient availability and quantity, the heterogeneity and pH) (Pressler et al. 2019; Wang et al. 2019b; Zhang et al. 2021; Zhou et al. 2020). Studies have indicated that post-fire microbial community changed complicatedly, especially in the short-term perspective (Moya et al. 2021; Pereg et al. 2018; Zhang et al. 2019). Sáenz de Miera et al. (2020) studied that fire decreased soil bacterial diversity within two months post-fire in Mediterranean ecosystem. Qin and Liu (2021) found that richness and diversity of bacteria and fungi decreased and fungi became more sensitive to fire than bacteria at six months after fire. However, Oliver et al. (2015) reported that prescribed burning has no impact on fungal communities in southeastern US forest ecosystem, and Brown et al. (2019) found that bacterial communities have a more pronounced response to fire than fungi at one year after fire.

Post-fire soil physicochemical properties changes will alter the structure of soil microbial communities (Barreiro and Díaz-Raviña 2021). For example, a study in the temperate region of Australia found that post-fire short-term increase in soil nitrogen pools can effectively increase the relative abundance of *Actinobacteria*, *Proteobacteria* and *Firmicutes* (Prendergast-Miller et al. 2017). Additionally, pyrogenic carbon, which is a by-product of fire, also alters the bacterial community (Wang et al. 2019b). Studies have shown positive/neutral effects on fungal diversity due to nutrient redistribution after prescribed burning (Giuditta et al. 2019; Kranz and Whitman 2019; Pereira et al. 2021), but recent meta-analysis also have shown that prescribed burnings may effect fungal diversity negatively, and it vary among different ecosystems (Dove and Hart 2017; Pressler et al. 2019). However, prescribed burning management in northern China is restricted by huge fuel load, so studies about prescribed burning is still lacking, especially for its effects on soil microbes.

To fill the research gap, we evaluated short-term soil microbial community changes and explored how post-fire soil physiochemical properties changes affect soil microbial community in a prescribed burning area located in three temperate forests (dominated by *Pinus koraiensis*, *Quercus mongolica*, and *Larix gmelinii*, respectively) of northern China. Soil properties and soil microbial communities were analysed before and one year after the prescribed burning event. From previous studies, we raised two hypotheses: (1) prescribed burning has a significant effect on the soil microbial community, but soil fungi and bacteria differently responded to the prescribed burning; (2) changes in soil physiochemical properties alter soil microbial community structure.

Materials and methods

Site description

Our research area is situated in the northeast Heilongjiang Province in China. It is a low hilly area, with an average elevation of 220 m. The study area falls under the northern temperate continental monsoon climate, low precipitation (mean annual precipitation of 640 mm). Local mean average temperature is 2.9 °C. According to USDA soil taxonomy, soils of the area is Alfisols (Soil Survey Staff 2022).

Experimental design

We selected three areas with specific dominant planation tree species, including *Larix gmelinii*, *Pinus koraiensis*, and *Quercus mongolica,* as the research object in Hegang City, Heilongjiang Province, China (129°39′00″ E – 132°31′00″ E, 47°03′30″ N – 48°21′00″ N). Local fire risk season can be divided into spring and autumn period. According to air humidity and soil moisture content, local prescribed burnings are always conducted at late autumn fire prevention period to reduce forest fuel load and avoid coming spring wildfire. Within each forest type, three stands measuring 20 m × 20 m (400 m^2) were selected for prescribed burning. The prescribed burning was carried out on November 3rd, 2018, and the basic stand information for three forest types is presented in Table 1 and Fig. 1.

Pre- and post-fire aboveground fuel load collection, heat of combustion and fire intensity are measured as described by Dou et al. (2023), and the details are listed in Table 2.

Soil sampling and physicochemical properties analysis

Soil samples were collected 24 h before (November 2nd, 2018) and one year after the burning (November 4th, 2019). Five soil samples (0 – 5 cm) were randomly

Table 1 Basic topographic and stand information

Forest type	DBH (cm)	MTH (m)	AS (a)	Slope (°)	Pre-fire OML (cm)	Post-fire OML (cm)	Shrub and herb species
Quercus mongolica	12.49 ± 1.13	8.53 ± 0.31	34	16.83 ± 1.23	5.29 ± 1.10	0.90 ± 0.22	*Carex cinerascens*, *Vicia sepium*, *Lespedeza bicolor*, *Gymnocarpium dryopteris*
Pinus koraiensis	26.34 ± 1.85	11.27 ± 0.15	59	20.70 ± 2.38	2.61 ± 0.44	0.26 ± 0.03	*Carex cinerascens*, *Lespedeza bicolor*, *Athyrium brevifrons*, *Dasiphora fruticosa*
Larix gmelinii	19.31 ± 1.72	13.58 ± 0.35	34	7.89 ± 0.49	3.37 ± 0.41	1.75 ± 0.32	*Carex cinerascens*, *Athyrium brevifrons*, *Lactuca sibirica*, *Lespedeza bicolor*

DBH Diameter at breast height, *MTH* Mean tree height, *AS* Age of stand, *OML* The depth of the organic layer

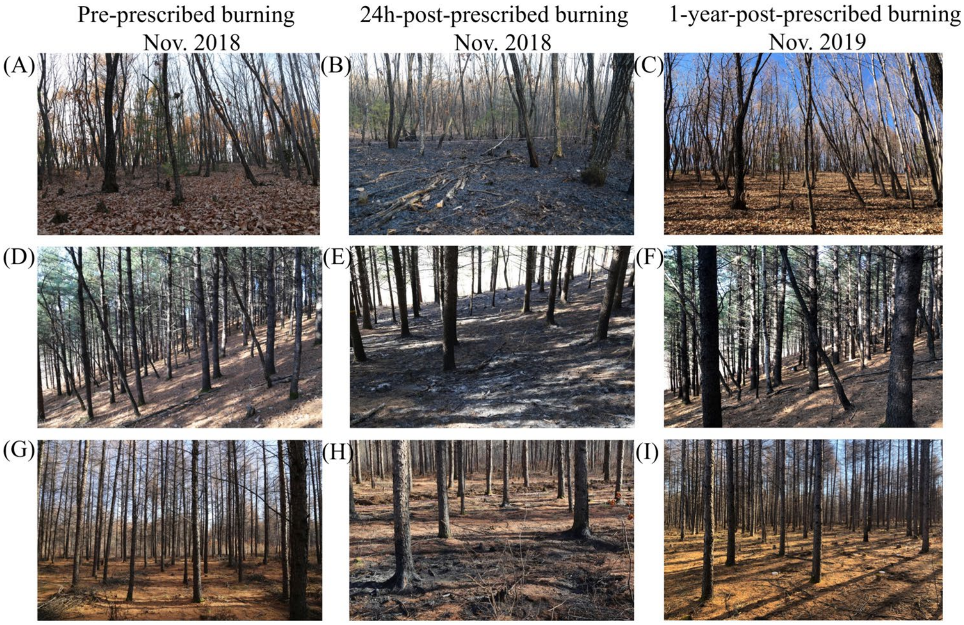


Fig. 1 Pre- and post-fire stands conditions of of *Quercus mongolica* (**A**, **B**, **C**), *Pinus koraiensis* (**D**, **E**, **F**), and *Larix gmelinii* (**G**, **H**, **I**) forests in Northeast China

Table 2 Weather conditions and fire behaviour variables at the time of the prescribed burning of *Pinus koraiensis*, *Quercus mongolica*, *Larix gmelinii* forests

Forest type	Maximum temperature (°C)	Minimum relative humidity (%)	Wind speed (km h^{-1})	Pre-fire fuel load (t ha^{-1})	Post-fire fuel load (t ha^{-1})	Head-fire spread rate (m h^{-1})	Intensity (kW m^{-1})	Tree mortality (%)
Pinus koraiensis	12.1 ± 0.47	54.20 ± 0.66	0.70 ± 0.55	9.56 ± 2.00	0.87 ± 0.20	150.60 ± 2.94	653.90 ± 158.96	3.17 ± 0.29
Quercus mongolica	15.9 ± 2.05	50.17 ± 1.28	1.15 ± 0.64	6.40 ± 2.20	0.93 ± 0.39	100.50 ± 12.36	273.56 ± 100.68	5.33 ± 0.58
Larix gmelinii	14.23 ± 1.39	50.08 ± 1.11	0.80 ± 0.40	4.70 ± 1.11	1.61 ± 0.57	70.36 ± 4.51	110.17 ± 49.68	2.00 ± 1.00

obtained in each stand by using a stainless soil corer, and then composite them as one, and separated it into three samples (in total 27 soil samples in all forest types). All the soil samples were sieved through a 2-mm sieve, and each of them has been divided into two parts, one was stored at − 80 °C for nucleic acid extraction, and another was stored at + 4 °C for further soil characteristics analysis.

Pre- and post-fire soil volumetric water content at the 5-cm depth ($VWC_{5,}$ m^3/m^3) was measured using a soil moisture probe (EC-5, Decagon Devices, Inc., USA). Soil pH was analyzed by using the glass electrode method (water: soil = 2.5: 1) (Sartorius PB-10, Gottingen, Germany). Soil total nitrogen (TN, kg m^{-2}) and total carbon (TC, kg m^{-2}) from the collected samples were analyzed by a Multi N/C 3100 Analyser (Analytic Jena, Thuringia, Germany). NH_4^+–N (mg kg^{-1}) and NO_3^--N (mg kg^{-1}) were determined as described by Dou et al. (2023). Available phosphorus (AP, mg kg^{-1}) was measured as described by Hu et al. (2019). Soil samples were measured as soon as possible after being brought back to the laboratory.

DNA extraction, PCR amplification and sequence analyses

Total microbial genomic DNA samples were extracted by using the DNeasy PowerSoil Kit (QIAGEN, Inc., Netherlands) and stored at − 20 °C prior to further analysis. DNA extraction and PCR amplification are as described by Zhang et al. (2022), Sun et al. (2022) and He et al. (2022). Sequence analyses are as described by Wang and Xie (2020).

Statistical analyses

To determine the effects of prescribed burning, forest types and their interactions to the soil physicochemical properties and soil OTU-level α-diversity index (Chao1 index), the analysis of variance (ANOVA) and Tukey's honestly significant difference (HSD) test were performed with 'agricolae' package in R (Mendiburu 2010).

Diversity analysis were performed by using UniFrac distance metrics (Lozupone et al. 2011) to investigate the structural variation of microbial communities across samples. Nonmetric multidimensional scaling (NMDS) analysis based on Bray–Curtis dissimilarity, and Permutational multivariate analysis of variance (PERMANOVA, permutations = 999) and nonparametric multivariate analysis of variance (Adonis) were used to identify the difference between pre- (24 h before prescribed burning) and post-fire (after prescribed burning) the microbial (bacterial and fungal) community compositions. To find out the bacterial phylum that made the greatest contribution to the community dissimilarity in both pre- and post-fire plots, 100 random forests constituted of 10,000 trees were computed using the default settings of the "randomForest" function implemented in the randomForest package (Liaw and Wiener 2002). The characterization of different forest stands before and after the prescribed burning was described by using the linear discriminant analysis (LDA) effect size (LEfSe) method (https://huttenhower.sph.harvard.edu/lefse/) for biomarker discovery (Segata et al. 2011), and the effect size threshold for the logarithmic LDA score was 2 for all the biomarkers evaluated in this study.

A disturbance-based redundancy analysis (dbRDA) was used to examine the variation in soil microbial community (bacteria and fungi) composition explained by soil physicochemical characteristics. The model construction, variables and axes significant permutation test (post hoc permutation tests with 999 permutations) and variance inflation factor analysis was conducted. We further performed Variance Partitioning Analysis (VPA) to quantify the effects of soil physicochemical characteristics (VWC$_5$, pH, AP, NH$_4^+$–N, NO$_3^-$–N, TC, TN, C:N) on the pre- and post-fire microbial community composition (Borcard et al. 1992). The above analysis was carried out by the Vegan package in R v. 4.1.3 (R 2022).

Results

Effect of prescribed burning on soil physicochemical properties

Soil physicochemical properties were significantly altered by the prescribed burning (Fig. 2. When compared to the pre-fire level, post-fire soil pH, NH$_4^+$–N, NO$_3^-$–N, AP, TC and TN are all significantly increased), but VWC$_5$ significantly decreased ($P < 0.05$, Fig. 2). Although the C:N ratio decreased approximately 32% in post-fire stands, it was not statistically significant ($P > 0.05$, Fig. 2).

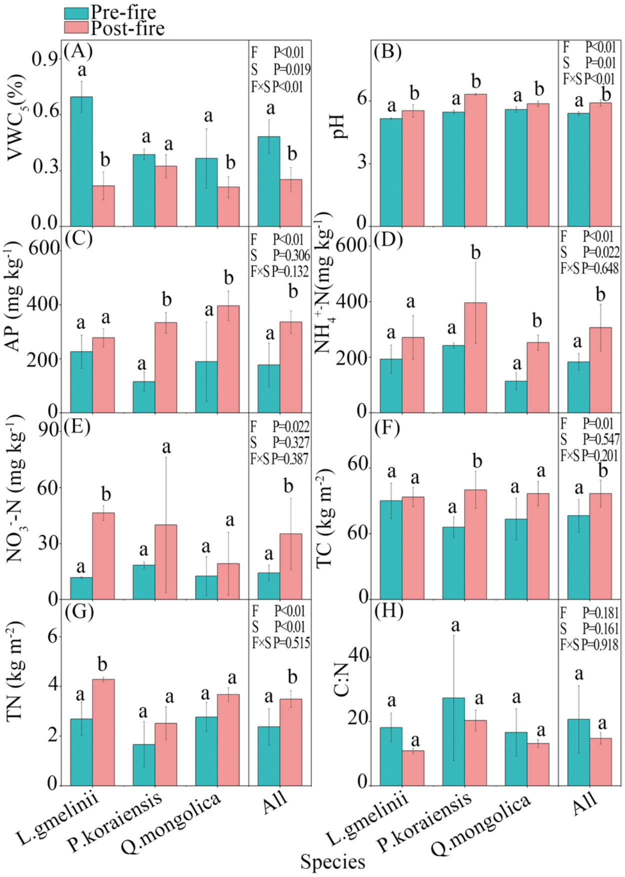


Fig. 2 Effect of prescribed burning on soil physicochemical characteristics. F represents the prescribed burning effect, S represents the species (forest type) difference, and F × S represents the interaction between the prescribed burning effect and the species difference. VMC5 represents the soil volume water content at 5 cm soil depth; AP represents available phosphorus; TC represents soil total carbon; TN represents soil total nitrogen; and C:N represents the ratio of soil total carbon to soil total nitrogen. Mean values are shown, and the error bars represent the standard deviation (N = 3). Lowercase letters for a given variable indicate significant differences ($P < 0.05$) before and after prescribed burning based on one-way ANOVA, followed by Tukey's HSD test

Our research found that soil VWC$_5$, pH, NH$_4^+$–N and TN were significantly different among three forest types (areas with different dominant tree species) (Fig. 2). The soil AP, NO$_3^-$–N, TC and C:N ratio were not significantly different among three forest types ($P > 0.05$, Fig. 2). In addition, we found prescribed burning-forest type interaction significant impact soil VWC$_5$ and pH ($P < 0.05$, Fig. 2).

Effect of prescribed burning on soil bacterial and fungal α-diversity

Prescribed burning significantly decreased bacterial Chao1 index ($P < 0.05$), but slightly increased the fungal richness in post-fire stands, even this increasing trend was not statistically significant ($P > 0.05$, Fig. 3). The richness soil fungi, but not bacteria, was significantly different among various forest types ($P < 0.05$, Fig. 3). No significant interaction effect of prescribed burning and forest type was observed on bacterial and fungal richness in the pre- and post-fire stands ($P > 0.05$, Fig. 3).

Effect of prescribed burning on soil bacterial and fungal community composition

For bacteria, *Proteobacteria*, *Acidobacteria*, *Verrucomicrobia*, *Actinobacteria*, *Chloroflexi*, *Nitrospirae*, *Gemmatimonadetes*, and *Planctomycetes* were the dominant taxa in all stands both before and after prescribed burning (Fig. 4). One year after the fire, the relative abundance of *Acidobacteria* was significantly increased in all stands, while *Actinobacteria* was significantly decreased in all post-fire stands ($P < 0.05$, Figs. 4, 5). Meanwhile, the post-fire response of *Acidobacteria* among different forest types was different, as fire disturbance led to a significant decrease of abundance of *Acidobacteria* in *Pinus koraiensis* and *Quercus mongolica* forests, but had no significant effect *Larix gmelinii* forests (Fig. 1). For fungi, *Basidiomycota*, *Ascomycota*, other fungi, and *Zygomycota* were the dominant taxa in all pre- and post-fire stands. Compared to pre-fire conditions, the relative abundance of *Basidiomycota* and *Ascomycota* showed no significant change in all post-fire stands ($P > 0.05$, Fig. 6).

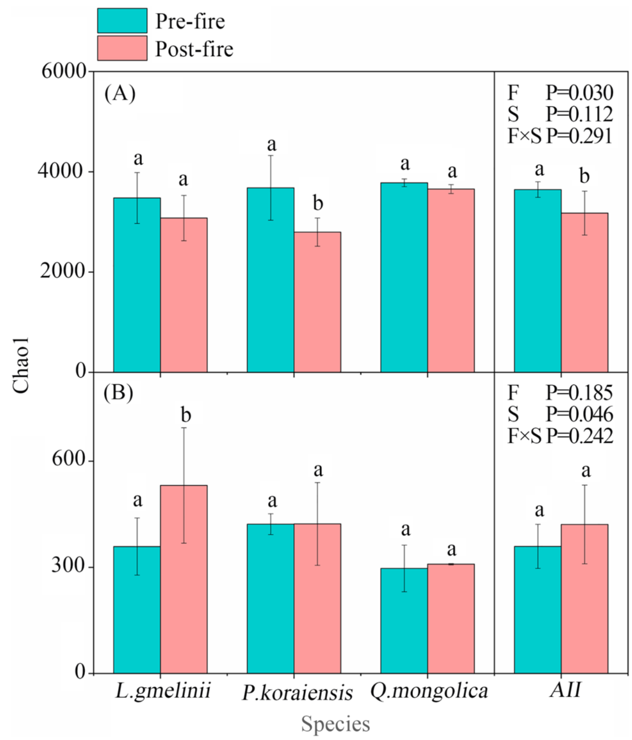


Fig. 3 Effect of prescribed burning on soil bacterial (**A**) and fungal (**B**) α-diversity. F represents the prescribed burning effect, S represents the species (forest type) difference, and F×S represents the interaction between the prescribed burning effect and the species difference. Mean values are shown, and the error bars represent the standard deviation ($N = 3$). Lowercase letters for a given variable indicate significant differences ($P < 0.05$) before and after prescribed burning based on one-way ANOVA, followed by Tukey's HSD test

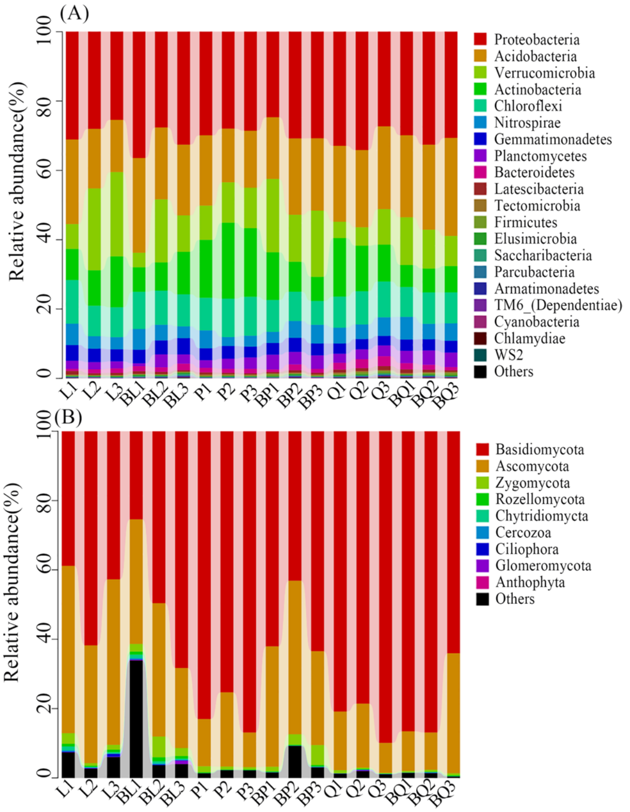


Fig. 4 Relative abundance (%) of bacterial taxa (**A**) and fungal taxa (**B**) at the phylum level. L1, L2, and L3 represent *Larix gmelinii* pre-fire stands; P1, P2 and P3 represent *Pinus koraiensis* pre-stands; Q1, Q2 and Q3 represent *Quercus mongolica* pre-fire stands; BL1, BL2 and BL3 represent *Larix gmelinii* post-fire stands; BP1, BP2 and BP3 represent *Pinus koraiensis* post-fire stands; BQ1, BQ2 and BQ3 represent *Quercus mongolica* post-fire stands

According to NMDS analysis, bacterial community structures in pre- and post-fire stands could be clearly divided for *Pinus koraiensis* and *Quercus mongolica* forests (Fig. 7). However, the fungal community structures could not make a distinction among various forest types (Fig. 7). Two non-parametric statistical analysis (PERMANOVA and Adonis) results also confirmed that bacterial taxonomic composition through pre- and post-fire stands was significantly different compared to the pre-fire stands ($P < 0.05$ for two methods, Table 3), but not fungal community ($P > 0.05$ for the two methods, Table 3). Random forest analysis results indicated that *Planctomycetes* and *Actinobacteria* made the strongest contribution to the difference between pre- and post-fire bacterial community (Fig. 8).

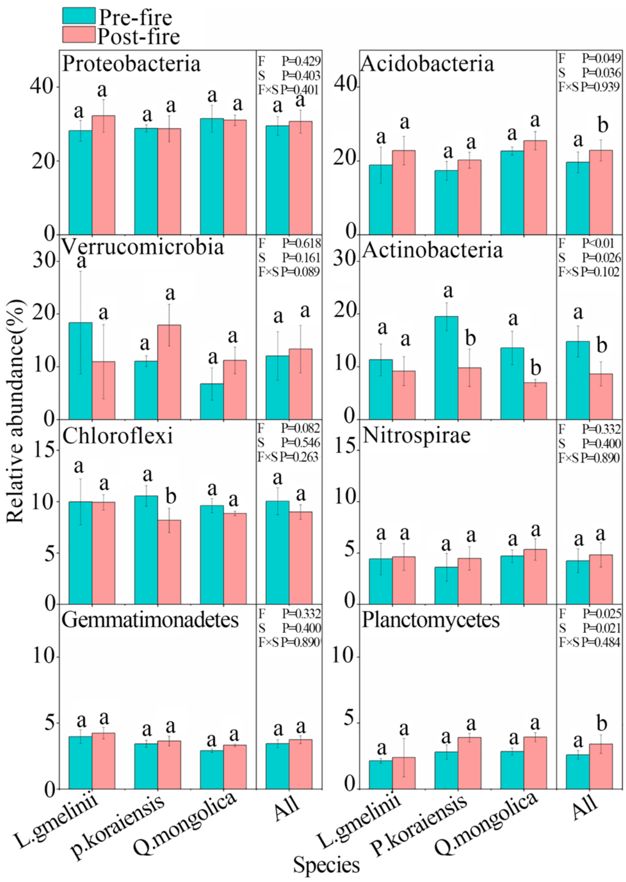


Fig. 5 Effect of prescribed burning on the relative abundance of the dominant bacterial phyla. F represents the prescribed burning effect, S represents the species (forest type) difference, and F×S represents the interaction between the prescribed burning effect and the species difference. Mean values are shown, and the error bars represent the standard deviation ($N=3$). Lowercase letters for a given variable indicate significant differences ($P<0.05$) before and after prescribed burning based on one-way ANOVA, followed by Tukey's HSD test

There are 83 bacterial and 11 fungal clades presented significant differences with an LDA threshold of 2 in the pre- and post-fire stands (Fig. 9). These bacterial and fungal taxa could be considered biomarkers in the corresponding stands.

Effect of prescribed burning on the relationship between soil microbial community structure and physicochemical characteristics

Our results indicate that soil pH, VWC, and NH_4^+–N significantly impacted the microbial community structure in pre-fire conditions (Fig. 10 and Table 4). For post-fire condition, soil pH, AP, TN and C:N significantly affected the microbial community structure(Fig. 10 and Table 4). Soil physicochemical characteristics could explain 69.43% and 73.54% of the total variability of the microbial community structure in pre- and post-fire stands, respectively.

Discussion

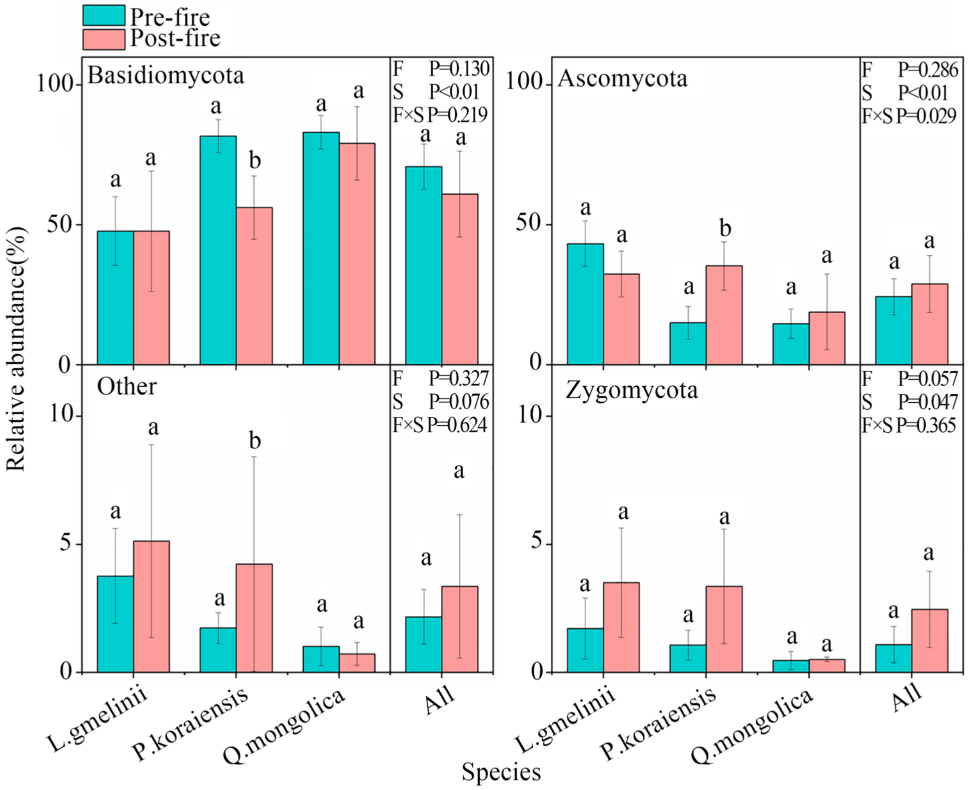
Effects of the prescribed burning on soil physicochemical properties

Prescribed burnings are widely used to reduce forest fuel load, but on the same time they can directly and indirectly affect soil nutrients and microorganisms. Our study showed that prescribed burning had a significant effect on soil physicochemical properties, and soil bacteria and fungi responded inconsistently to prescribed burning in three typical temperate forest in northern China.

Although there were some differences in the plant composition among three forest types (Table 1), the response of soil physicochemical properties to the prescribed burning were relatively consistent among them. This might be due to the fact that prescribed burning on these areas was mainly with low burn intensity. Nonetheless, prescribed burning in all three forest types removed approximately 48% – 90% of the surface organic layer depth, which was sufficient to have a strong effect on soil physicochemical properties. In this study, the prescribed burning significantly decreased soil moisture content. Through the combustion, part of the humus layer is burned, and on the same time black carbon, which remains on soil surface, is produced (Ribeiro-Kumara et al. 2020). All this will effectively increase the solar radiation on the surface and increase the surface transpiration of the burned area, resulting in a decrease in water content (Zimmermann et al. 2012). Burning may also create a water repellency that increases surface runoff and disrupts forest soil moisture retention. Several studies have shown that water repellency will occur when the fire temperatures are between 176 °C and 204 °C (DeBano 1981; Hubbert et al. 2006; Vadilonga et al. 2008). Therefore, the primary cause of the post-fire considerable decrease in water content could have been the surface litter destruction and the generation of the hydrophobic layer.

Our study also found that in all three temperate forest types, soil TC slightly increased after prescribed burning, while the increase was significant only in the *Pinus koraiensis* forest. This might be explained by the relatively high pre-fire surface fuel loads in the *Pinus koraiensis* forest, where large amount of carbon containing ash was produced by the fire and entered to the post-fire soil horizons (González-Pérez et al. 2004). Our results are in line with current research findings, where low intensity surface fires might increase the soil carbon pools due to the increased burned organic matter and biochar (González-Pérez et al. 2004; Merino et al. 2019). Although some researchers have reported neutral effects of prescribed burning on soil carbon pools (Dai et al. 2018; Switzer et al. 2012), condensed aromatic structures was found in post-fire soil carbon, which could resist degradation in soil land contribute to long-term

Fig. 6 Effect of prescribed burning on the relative abundance of the dominant fungal phyla. F represents the prescribed burning effect, S represents the species (forest type) difference, and F × S represents the interaction between the prescribed burning effect and the species difference. Mean values are shown, and the error bars represent the standard deviation ($N = 3$). Lowercase letters for a given variable indicate significant differences ($P < 0.05$) before and after prescribed burning based on one-way ANOVA, followed by Tukey's HSD test



carbon storage (Merino et al. 2019; Santín et al. 2018). Thus, by managing fuel loads and carrying on prescribed burnings, may reduce the risk of wildfires in the future and retain carbon stock in the soil.

Our study indicated that prescribed burning led to a significant increase in total soil nitrogen, which is in accordance with some previous studies that low fire intensity has limited effect on soil nitrogen content, and only fire-induced soil temperatures above 200 ℃ will lead to soil nitrogen loss (DeBano et al. 1979; Francos et al. 2019). In case of prescribed burnings the changes in soil temperatures (within first 2 or 3 cm) are not significant (Alexis et al. 2007). During the burning of fuels, part of the nitrogen is released and it remains with produced ash to soils, where it promotes organic matter decomposition, and the nitrogen fixation (Certini 2005; Hu et al. 2019).

Compared with soil total nitrogen, soil ammonium and nitrate had more positive feedback to prescribed burning. Prescribed burning incurred an increase in soil inorganic nitrogen, and fire rapidly converts organic nitrogen in plants into inorganic nitrogen. However, previous studies have indicated that this increase in inorganic nitrogen will not exceed one year (Covington and Sackett 1992; Liao et al. 2013). Controversially to previous studies, our study found that the level of post-fire soil inorganic nitrogen was still significantly higher than the pre-fire condition, which may be related to the recovery of vegetation after the prescribed burning. The increase in soil ash and soil pH may promote the increase in the number of legumes, which will effectively accelerate the rate of conversion of organic nitrogen to inorganic nitrogen, thereby continuously promoting the increase in inorganic nitrogen content after fire (Hu et al. 2019; Reverchon et al. 2012; Yelenik et al. 2013).

Our findings demonstrated that the amount of soil AP dramatically increased following prescribed burning. A previous study has indicated that prescribed burnings might not intense enough to produce volatilization of soil phosphorus, as which occurs above 700 ℃ (DeBano et al. 1979). However, DeBano et al. (1979) also pointed that the increase in soil AP was caused by heating the organic layer, further changes in soil AP as a consequence of fire could further alter post-fire soil microbial community (Liu et al. 2012; Merino et al. 2019).

Effects of prescribed burning on soil microbial diversity and community composition

In line with our first hypothesis, prescribed burning had a significant effect on the soil microbial community, and soil bacteria and fungi have different responses to prescribed burnings. Our study (results from NMDS and PERMANOVA) showed that prescribed burning significantly changed the soil bacterial community, while it did not change the soil fungal composition. Nelson et al. (2022)

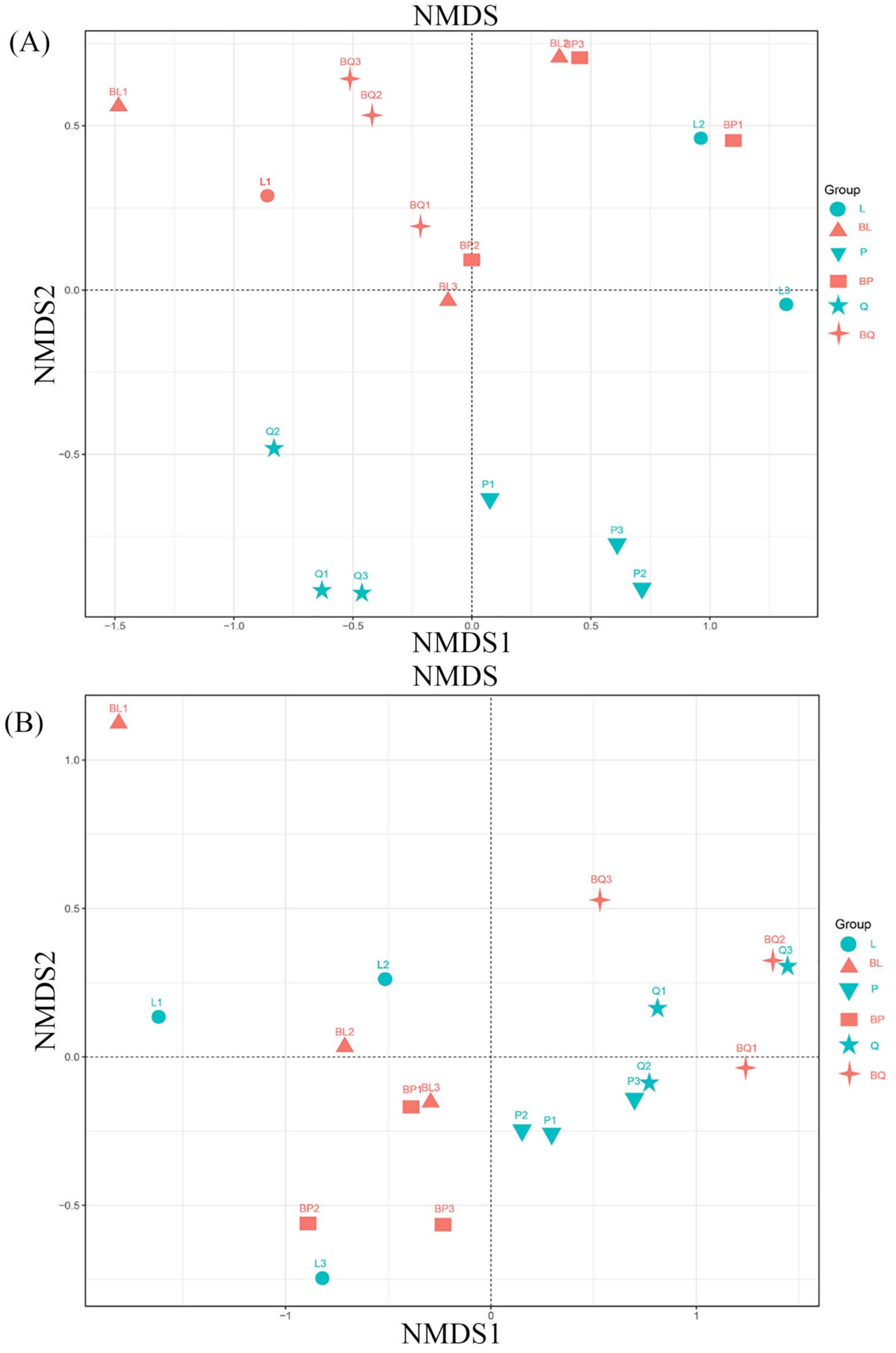


Fig. 7 Nonmetric multidimensional scaling (NMDS) analysis showing differences in bacterial (**A**) and fungal (**B**) community structure before and after prescribed burning according to Bray–Curtis distance. L1, L2, and L3 represent *Larix gmelinii* pre-fire stands; P1, P2 and P3 represent *Pinus koraiensis* pre-stands; Q1, Q2 and Q3 represent *Quercus mongolica* pre-fire stands; BL1, BL2 and BL3 represent *Larix gmelinii* post-fire stands; BP1, BP2 and BP3 represent *Pinus koraiensis* post-fire stands; BQ1, BQ2 and BQ3 represent *Quercus mongolica* post-fire stands

indicated that *Acidobacteria* significantly decreased (by 37.6%) one year after high intensity fire disturbance. This result was inconsistent with our study that showed that *Acidobacteria* significantly increased one year after prescribed burning. This may be due to the inconsistent response of *Acidobacteria* to different burn intensity. Pyrogenic carbon produced under low fire intensity will increase the abundance of *Actinobacteria*, which suggest these microbial groups play an active role in soil pyrogenic carbon metabolism (Khodadad et al. 2011). *Acidobacteria* are considered as a keystone taxa for soil organic matter degradation by playing an important role in soil carbon cycling (Banerjee et al. 2016; García-Fraile et al. 2016). Therefore, the increase in soil TC after prescribed burning in this study may be due to

Table 3 Result of statistical analysis testing for prescribed burning effect on taxonomic of microbial (bacteria and fungi) communities

Statistical approaches		Taxonomic	
		Bacteria	Fungi
PERMANOVA	R	0.24	−0.019
	P	**0.021**	0.522
Adonis	F	2.979	0.875
	P	**0.015**	0.472

Significant effects are indicated in bold. PERMANOVA: Permutational multivariate analysis of variance. Adonis: nonparametric multivariate analysis of variance

the generated pyrogenic carbon and the significant increase in *Acidobacteria*, which in turn accelerated the decomposition rate of soil organic matter.

Previous researches have demonstrated that *Firmicutes*, *Actinobacteria*, and *Proteobacteria* all benefited from wildfire. (Brockway et al. 2002; Smith et al. 2008; Zhou et al. 2020). However, our study indicated that prescribed burning had no significant effect on *Firmicutes* and *Proteobacteria*, but significantly decreased *Actinobacteria*. This may be mainly due to differences in burn intensity and severity (Barreiro and Díaz-Raviña 2021; Lucas-Borja et al. 2019a; Mediavilla et al. 2019), which can significantly affect microbial diversity and community composition. Our findings suggest that wildfires and prescribed burning have quite different effects on soil microbial community structure. Compared to wildfires that can burn with quite high intensity, and lead high severity, prescribed burning usually can't destroy plant roots, which may be the reason why *Firmicutes* and *Proteobacteria* had no significant change after prescribed burning in our study. On the same time *Firmicutes* are able to resist fire disturbance by forming endospores (Ferrenberg et al. 2013), and plant roots and *Proteobacteria* in the rhizosphere soil have a close symbiotic interaction (Wang et al. 2014). In addition, our study found that the abundance of *Planctomycetes* increased significantly after prescribed burning. Mediavilla et al. (2019) found similar results after prescribed burning in the *Cistus ladanifer* forest of Spain. Earlier, there has not been many reports on the effects of prescribed burnings on *Planctomycetes*, but some of the conducted studies have found that *Planctomycetes* could mediate the soil anaerobic NH_4^+ oxidation process, and further affect the soil ammonification processes (Girkin and Cooper 2023). Although, the proportion of *Planctomycetes* in the soil bacterial community was relatively low, our results from random forest analysis showed that prescribed burning mainly changed the soil microbial community structure by affecting *Planctomycetes* and *Actinobacteria*. Therefore, it is necessary to carry out related soil microbial functional gene research in the future, which will help to further quantify the influence of prescribed burning-induced changes in microbial community structure in forest ecosystems.

Basidiomycota, *Ascomycota*, and *Zygomycota* were the dominant fungal taxa in both pre- and post-fire stands. However, the fire did not change the overall fungal community structure in our study areas. There were differences in the response of *Pinus koraiensis* forest fungal species to prescribed burning, where the prescribed burning significantly decreased *Basidiomycota* abundance, and increased *Ascomycota* abundance. Our study is consistent with a previous study, which found that *Basidiomycota*

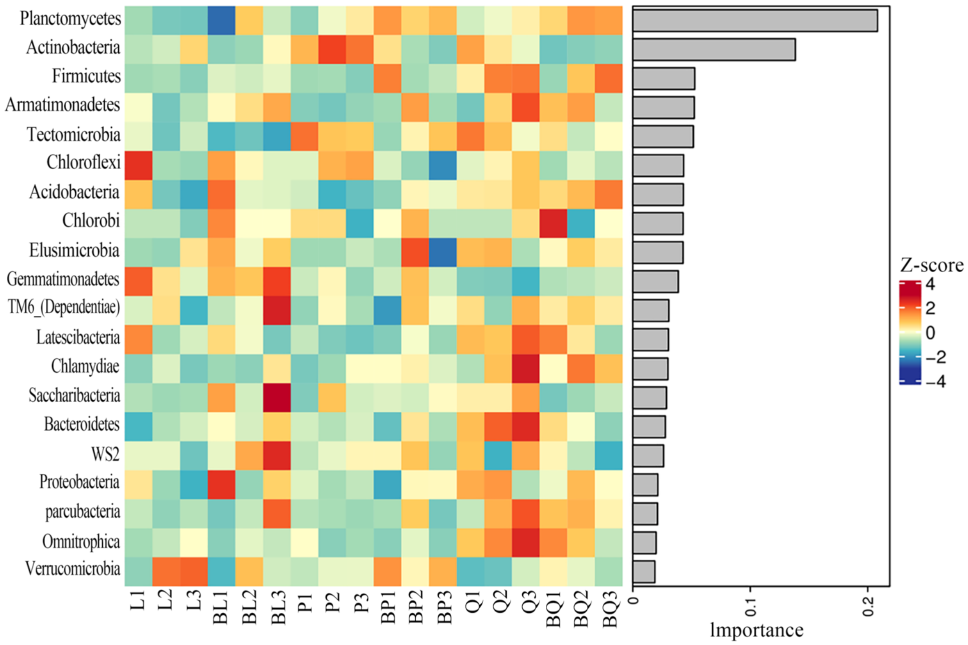


Fig. 8 Random forest analysis showing the contribution of bacterial phyla lead to community dissimilarity between the pre- and post-fire stands. L1, L2, and L3 represent *Larix gmelinii* pre-fire stands; P1, P2 and P3 represent *Pinus koraiensis* pre-stands; Q1, Q2 and Q3 represent *Quercus mongolica* pre-fire stands; BL1, BL2 and BL3 represent *Larix gmelinii* post-fire stands; BP1, BP2 and BP3 represent *Pinus koraiensis* post-fire stands; BQ1, BQ2 and BQ3 represent *Quercus mongolica* post-fire stands

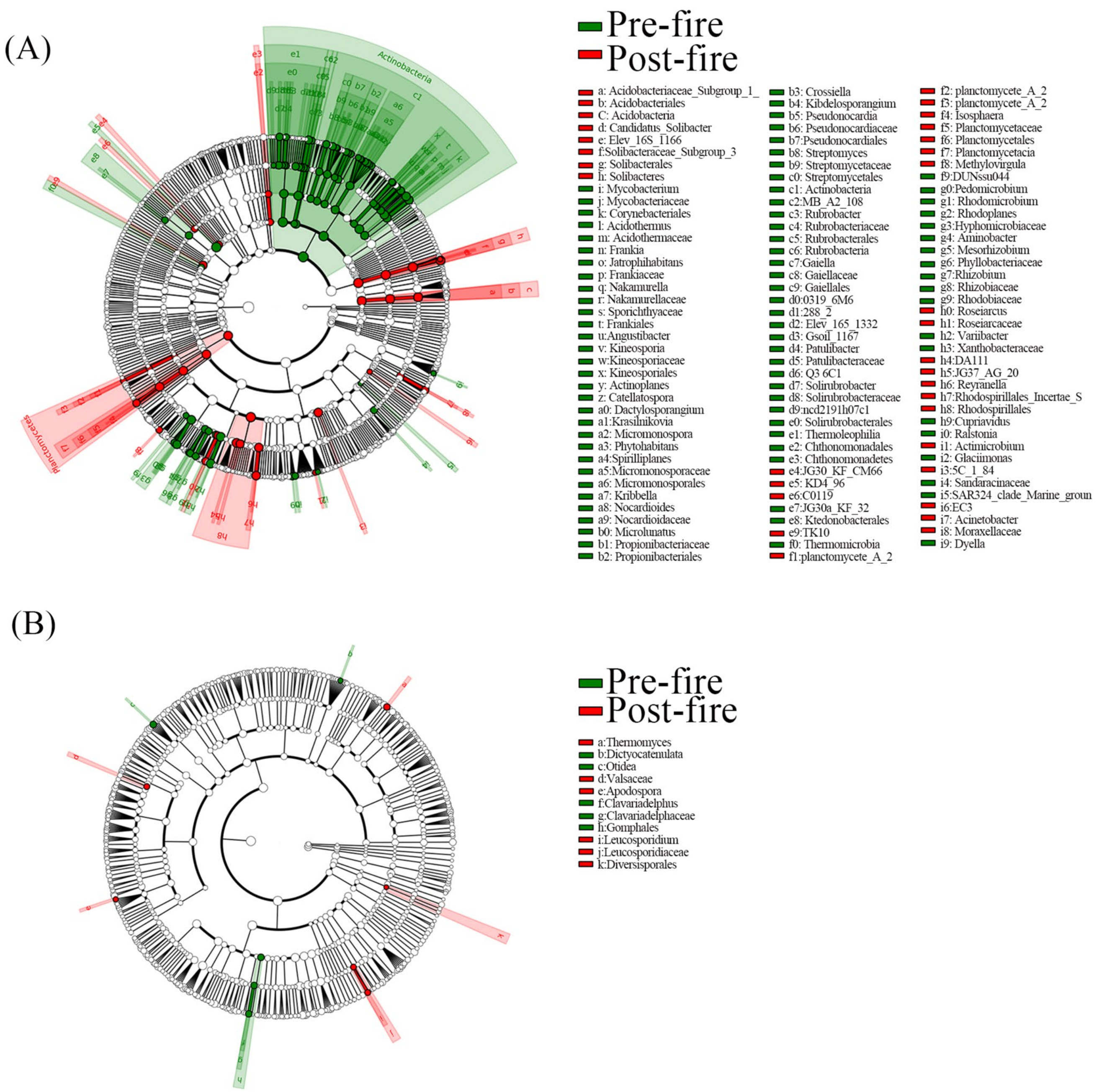


Fig. 9 A linear discriminant analysis effect size method identifies the significantly different abundant taxa of bacteria (**A**) and fungi (**B**) in pre- and post-fire stands. The taxa with significantly different abundance among treatments are represented by coloured dots, and from the centre outward, they represent the kingdom, phylum, class, order, family, and genus levels. The coloured shadows represent trends of the significantly differed taxa. Only taxa meeting a linear discriminant analysis significance threshold of > 2 are shown

were replaced by *Ascomycota* one and two years after a fire disturbance (Hughes et al. 2020). *Ascomycota* are pyrophilous fungi that are fruit prolifically and extensively distributed across burned forests. Pyrophilous fungi act a critical part in the biochar decomposition, carbon sequestration and transient nitrogen pulses capture after fire, and it may be essential for plant early recovery (Filialuna and Cripps 2021).

Our results and findings from the LEfSe analysis (at the gene level) showed that *Thermomyces*, *Valsaceae*, and *Apodospora* from the phylum *Ascomycota*, *Leucosporidium* and *Leucosporidiaceae* from the phylum *Basidiomycota*, and *Diversisporales* from the phylum *Glomeromycota* could potentially be used as biomarkers for post-fire stands in temperate forest soil of China. These different fungal species may play important roles as special biomarkers in the

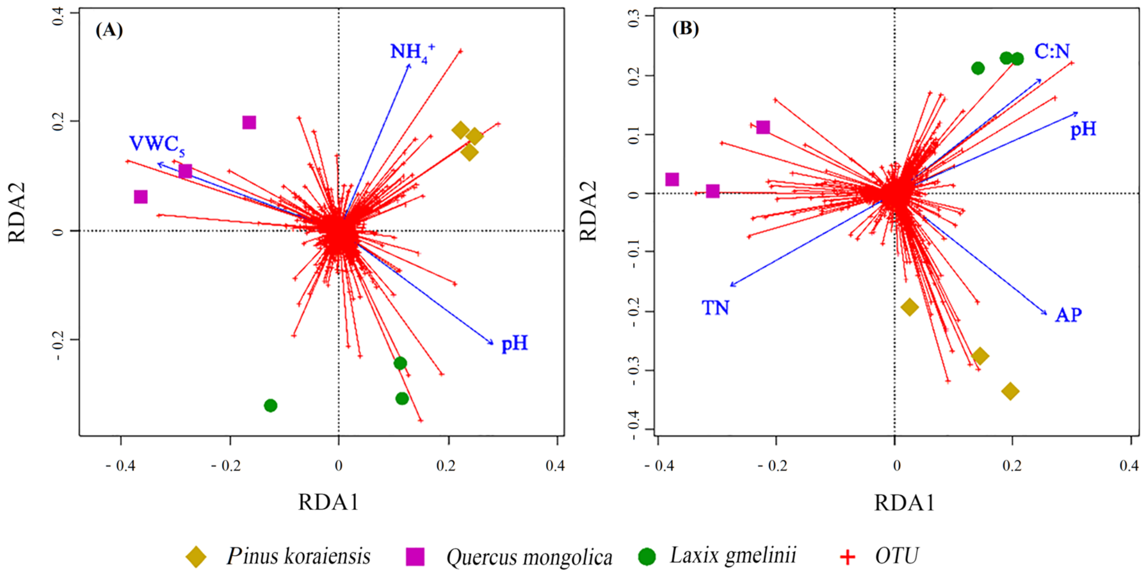


Fig. 10 Ordination plot of a distance-based redundancy analysis (dbRDA) of soil microbial community composition and soil physicochemical characteristics. **A** Pre-fire stands, **B** Post-fire stand

Table 4 Variance partitioning analysis of the contribution (percentage) of soil properties to microbial community structure in pre-fire and post-fire conditions

Variables	Pre-fire				Post-fire			
	%Var	R^2	P	Cum%	%Var	R^2	P	Cum%
VWC$_5$	10.95	0.195	*	10.95	7.92	0.132	0.318	7.92
pH	10.69	0.190	**	21.64	10.97	0.183	**	18.90
AP	8.67	0.154	0.1140	30.31	10.41	0.173	*	29.30
NH_4^+-N	9.97	0.177	*	40.28	8.59	0.143	0.163	37.90
NO_3^--N	7.02	0.125	0.4440	47.30	8.66	0.144	0.192	46.55
TC	8.75	0.156	0.1080	56.05	6.65	0.111	0.717	53.21
TN	7.88	0.140	0.2600	63.93	10.33	0.172	*	63.54
C:N	5.50	0.098	0.9210	69.43	10.00	0.166	*	73.54

VMC$_5$ represents the soil volume water content at 5 cm soil depth; AP represents available phosphorus; TC represents soil total carbon; TN represents soil total nitrogen; C:N represents the ratio of soil total carbon to soil total nitrogen

*, and ** represents non-significant

$P < 0.05$, $P < 0.01$

recovery of forest ecosystems after prescribed burning. For example, *Thermomyces* can withstand high temperatures and receive energy from complex carbon sources, and it also plays a significant role in hemicellulose degradation because by producing hydrolytic enzymes (Maheshwari et al. 2000).

Factors affecting soil microbial communities after prescribed burning

Our results were partially match with our second scientific hypothesis, where we expected that the changes in soil physicochemical properties caused by prescribed burning, might change the soil microbial community structure. We discovered that soil water content, pH and NH_4^+–N were the primary factors influencing the soil microbial community structure in pre-fire stands, while pH, AP, TN, and C:N were the main factors influencing the soil microbial community structure in prescribed burning stands. The soil water content in pre-fire stands was one of the main factors that regulated the microbial community structure, but it was not the case anymore one year after prescribed burning. Previous studies have indicated that maximum of aerobic microbial activity at water content levels is between 50 and 70% (Franzluebbers 1999). In our study, post-fire stands had significantly lower soil water content (< 30%) than pre-fire stands, and this low soil water content lowered microbial activity by lowering intracellular water potential, microbial mobility, and the diffusion of soluble substrates (Butcher et al. 2020; Stres et al. 2008; Zhou et al. 2002). Under unsuitable water conditions, soil microbes need to obtain more soil nutrients to survive (Fuentes-Ramirez et al. 2018; Garcia-Pausas et al. 2022), and this could be the reason why soil water content could not regulate soil microbes after prescribed burning in our study.

We found that soil pH was the main factor regulating soil microbial community structure in both pre- and post-fire conditions. Soil *Acidobacteria*, which represents the acidic soil pH status (Lladó et al. 2016), was one of the main phyla of microorganisms in the pre-fire and post-fire stands. Although soil pH significantly increased after prescribed burning in our study, its status was still acidic, and it continued to regulate microbial community structure after the prescribed burning. Previous studies have suggested that in addition to pH, soil C:N, and extractable organic carbon and nitrogen are important factors dominating forest soil microbial community structure (Blaško et al. 2015; Wan et al. 2015; Liang et al. 2017). Nitrogen is the main limiting factor in boreal and temperate forests (Meunier et al. 2016), and it has been found that the C:N ratio is an indicator of soil nutrient availability (Grosso et al. 2016; Khan et al. 2016; Zhou et al. 2019). Soil NH_4^+–N was the main regulator of soil microbial structure in our pre-fire stands, while prescribed burning significantly increased soil inorganic nitrogen and TN, causing the soil C:N ratio to significantly drop, effectively reduced the nitrogen limitation to soil microorganisms. Additionally, we discovered that soil AP played a significant role in regulating the soil microbial community a year after prescribed burning. Also other studies have indicated that increase in soil AP could stimulate microbial specific life strategy for phosphorus use, especially for bacteria (Gao and DeLuca 2018; Wang et al. 2020). Therefore, it is important to examine the response of specific taxa to different soil phosphorus factions and the underlying mechanism in prescribed burning conditions.

Conclusion

Our study clearly demonstrated that one year after prescribed burning soil VWC_5, pH, NH_4^+-N, NO_3^-–N, AP, TC and TN were significantly changed, and soil bacteria and fungi have different responses to prescribed burning. Prescribed burning significantly decreased the microbial diversity and changed the soil microbial communities of the bacteria. Whereas, prescribed burning had no significant effect on the fungal diversity and communities. *Planctomycetes* and *Actinobacteria* made the greatest contribution to bacterial community dissimilarity between the pre- and post-fire stands. Soil pH, AP, TN and C:N were the dominant factors affecting the soil microbial community structure in the post-fire stands. Prescribed burning reshaped the soil microbial community structure of typical temperate forest ecosystems in northern China via changing soil physiochemical properties. Further research should focus more on the post-fire changes in soil microbial community structure, and how this could affect forest ecosystem functions in prescribed burned areas. This would help to predict changes in forest ecosystem function under the conditions of changing fire regimes.

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