Relationships Between Soil Microbial Communities and Plant Communities on Different Slope Aspects in a Subalpine Coniferous Forest

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Abstract

Purpose The local microclimate of different slope aspects in the same area can not only impact soil environment and plant community but also affect soil microbial community. However, the relationship between aboveground plant communities and belowground soil microbial communities on various slope aspects has not been well understood.

Methods We investigated the above- and belowground relationship on different slope aspects and explored how soil properties influence this relationship. Plant community attributes were evaluated by plant species richness and plant total basal area. Soil microbial community was assessed based on both 16S rRNA and ITS rRNA, using High-throughput Illumina sequencing.

Results There was no significant correlation between plant richness and soil bacterial community composition on the north slope, but there was a positive correlation on the south slope and a significantly negative correlation on the flat site. There was a significantly negative correlation between soil fungal community composition and plant total basal area, which did not change with the slope aspect. In addition, there was no significant correlation between plant community species richness and soil microbial species richness.

Conclusions In subalpine coniferous forests, the relationship between plant-soil bacteria varies with slope aspect, but the plant-soil fungi relationship is relatively consistent across different slope aspects. These results can improve our understanding of the relationship between plant and soil microorganisms in forest ecosystems under microtopographic changes and have important implications for the conservation of biodiversity and forest management in subalpine coniferous forests.

1. Introduction

The relationship between plant community and soil microbial community in terms of composition, structure, and diversity lies at the heart of exploring above- and belowground linkages (Bakker et al. 2013a; Vos et al. 2013). Plants can directly regulate the composition of soil microbes by changing the imported quantity and quality of litter or root exudates to the soil (Ushio et al. 2008; Bainard et al. 2016) and indirectly affect the diversity and distribution patterns of soil microbial communities by changing the physical and chemical properties of soil (Krashevskaya et al. 2015; Deng et al. 2016). In return, soil microorganisms can directly promote plant growth by forming interspecific relationships with plants (Hagedorn et al. 2019; Tedersoo et al. 2020) and indirectly affect plant community structure dynamics by regulating soil nutrient cycling (Van Der Putten et al. 2001; Bezemer et al. 2005; Latz et al. 2012). However, although the interactions between plants and soil microbes have been ubiquitously studied, there is still have a limitation to the comprehensive plant-soil community relationship knowledge in the field.

The mechanisms and influence factors of the linkage of plant community and soil microbial community have been widely studied (Broughton and Gross 2000; Van Der Heijden et al. 2008). An increase in

aboveground plant species richness could lead to the diversification of belowground resources (Vos et al. 2013). Therefore, there is a generally positive correlation between the plant and soil microbial richness (Santonja et al. 2017; Otsing et al. 2018). For instance, in grassland ecosystems, increased plant richness promotes soil microbial species richness (Eisenhauer et al. 2010; Sauheitl et al. 2010), and also significantly affects microbial community structure (Schlatter et al. 2015). In addition, considering the possible significant effects of plant productivity on soil community composition (Zak et al. 2003), aboveground plant biomass is equally important for the soil microbial community (Li et al. 2015). Li et al. (2018) found that plant aboveground biomass was pivotal to soil microbial functional community in semiarid grassland (Li et al. 2018). Due to the different metabolic pathways, rates, and competitive abilities of soil bacteria and fungi under varied soil carbon sources (Uroz et al. 2016), they differ in responses to aboveground plant communities. Soil fungi have a closer relationship with plant growth because of their higher efficiency in decomposing soil organic matter and forming symbiotic mycorrhiza with plants more easily (Grover et al. 2015). An increase in pathogenic fungi in plant roots would drive a negative density dependence among the same species, so the accumulation of ectomycorrhiza is beneficial to plants (Chen et al. 2019a; van der Putten et al. 2016). Instead, as soil bacteria have a closer relationship with plant species diversity because of their rapid decomposing efficiency, they could promote niche differentiation of plant communities (Lyons and Lindo 2020). Additionally, a plant-soil relationship may be covered by abiotic factors, due to the covariation between biotic and abiotic factors (Qiu et al. 2018). For instance, soil environmental factors, such as soil pH and soil nutrient content, affected the relationship between plant and soil microbial communities negatively (Liu et al. 2020c). However, there is a lack of comprehensive analysis on the relationship between aboveground plant biomass, plant richness, and soil microbial community (bacteria and fungi), which holds the key to exploring the above- and belowground relationship (Chen et al. 2019b; Qiang et al. 2021).

As an important topographic factor, the slope aspect can control the spatial redistribution patterns of energy and water and create a local microenvironment (Cantón et al. 2004). Changes in slope aspect often led to huge differences in the soil environment (Lexer and Bugmann 2017; Wu et al. 2017), which may be suitable for the growth of various plants and soil microbes. In the Northern Hemisphere, for example, the southern slopes, which have more solar radiation, are relatively drier, hotter, and have higher soil nutrient content. Thus, there are more diverse plant and soil microbial species on the SS (Chai et al. 2018; Liu et al. 2020b). On the contrary, the northern slope is featured by less solar radiation, lower soil evaporation, a wetter environment, and more insufficient soil aeration. Therefore, the soil microbial diversity is relatively low (Chu et al., 2016), but vegetation coverage and vegetation density are usually higher on the NS (Måren et al. 2015). Based on the discrepancy of plant community and soil microbial community caused by slope changes, the relationship between aboveground and belowground communities may also change (Mitchell et al. 2012). Gilliam et al. (2014) simply assessed the plant-soil relationship in temperate forests showed that different slope aspects' soil microbes were linked with different forest layers (Gilliam et al. 2014). However, most previous studies only focused on plant communities (Bennie et al. 2006; Åström et al. 2007; Nadal-Romero et al. 2014) and soil microbial

communities (Chu et al. 2016; Liu et al. 2017; Chai et al. 2018) on various slope aspects, but less concerned about the rule of above- and belowground relationship changing with it.

In this study, we investigated the plant community characteristics, soil physical and chemical properties, and soil bacterial and fungal communities and analyzed the relationships between plant communities and soil bacterial and fungal communities on different slope aspects in subalpine forests in southwest China. Subalpine coniferous forests are characterized by shallow soil layers, fragile habitats, complex topography, and variable microclimate conditions (Zhao et al. 2019). Wanglang Nature Reserve's subalpine coniferous forest, located in Southwest Sichuan, is one of the biodiversity conservation hotspots in China (Myers et al. 2000). Its diverse vegetation and soil biological assemblage provide an ideal place for studying ecosystem processes. We proposed the following hypotheses: (1) plant community diversity was positively correlated with soil microbial diversity; (2) owing to different living strategies of soil microorganisms, soil fungi would have a stronger relationship with plant biomass, while soil bacteria were relative to plant abundance more; (3) slope changes lead to different microenvironmental conditions on the slope, and the relationship between plant and soil microbial communities follows.

2. Materials And Methods

2.1 Site description

The study area is located in the Wanglang National Nature Reserve of Sichuan Province (104.02°E, 33.00°N), which is a typical subalpine coniferous forest with an altitude of 2850–2930 m. The area has a Daba-Songpan subhumid climate and is affected by monsoons with obvious dry and wet seasons. The rainy season lasts from May to October. The annual average temperature is 2.9°C, the average temperature in January is -6.1°C, the average temperature in July is 12.7°C, and the annual precipitation is 859.9 mm. The soil types are mainly subalpine meadow soil and mountain dark brown loam. Well-preserved subalpine dark coniferous forests are distributed in this area. The sampling area was located in a dynamic forest plot of 25.2 ha consisting of 18 lines and 35 rows with a total of 630 quadrats, with a projection area of 20 m×20 m per quadrat (Condit, 1998) (Fig. 1). With the oldest trees aged over 600 years, the dominant species are spruce and fir in our study area. The main tree layer species are *Abies faxoniana* and *Picea purpurea*, the main shrub layer species are *Philadelphus purpurascens* and *Sorbus koehneana*, and the main herb layer species are *Cystopteris pellucida*, *Cardamine tangutorum*, *Eutrema yunnanense*, etc.

2.2 Vegetation and soil sampling

The vegetation survey and soil sampling times for this study were from May to September 2019 and July to August 2020, respectively. We selected 170 samples (NS: 42, FS: 81, SS: 47) from the total 630 plots in the field randomly (Fig. 1b), which to investigate the basic information of trees, shrubs, and grasses in each plot and to collect the soil samples. For the tree layer, we surveyed all tree individuals with a DBH ≥ 3 cm in the sample square, recorded the species name, measured DBH tree height, total basal area, plant

species richness, etc. For the shrub layer, two 5 m × 5 m plots on the diagonal of each 20 m × 20 m plot were selected to investigate. The herb layer was sampled at every 10 m in the 20 m × 20 m plot for nine 1 m × 1 m squares were selected for investigation.

The soil samples were collected by a soil auger (inner diameter: 3.8 cm, depth: 0–10 cm). After clearing litter and gravel, a five-point sampling method was used, with one auger at each of the four corners and the center of the sample square being used to take samples that were combined into a single composite sample. After removed plant residues, rocks, and other impurities, the soil sample was passed through a 2 mm sieve and then divided into two parts. One part was stored at 4°C for the analysis of basic soil physical and chemical properties; the other part was stored in the refrigerator at –80°C to measure the soil microbial community composition.

2.3 Soil physiochemical properties

The soil pH was determined using a pH meter (PHS-3C, Lei-Ci, Shanghai, China). The soil moisture content (SWC) was measured by the air blast drying method (drying at 105°C for 8 h). The content of soil organic matter (SOM) was determined by the potassium dichromate volumetric method. Determination of total nitrogen (TN) was performed by the Kjeldahl method. Determination of available nitrogen (AN) was determined by the alkali hydrolysis diffusion method. Total phosphorus (TP) and available phosphorus (AP) were determined by antimony and molybdenum resistance colorimetry (Lu, 2000).

2.4 DNA extraction, amplification, high-throughput sequencing, and bioinformatics analysis

Total genomic DNA samples were extracted using the OMEGA Soil DNA Kit (M5635-02) (OmegaBio-Tek, Norcross, GA, USA), following the manufacturer's instructions, and stored at -20°C before further analysis. The quantity and quality of extracted DNAs were measured using a NanoDrop NC2000 spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA) and agarose gel electrophoresis, respectively.

The V3–V4 region of 16S rRNA was sequenced for bacterial community analysis using the primer pair 338F (5'-ACT CCT ACG GGA GGC AGC A-3') and 806R (5'-GGA CTA CHV GGG TWT CTA AT-3'). The internal transcribed spacer 1 (ITS1) region of the nuclear rRNA operon was sequenced for fungal community analysis using the primer pair ITS5 (5'-GGA AGT AAA AGT CGT AAC AAG G-3') and ITS2 (5'-GCT GCGTTC TTC ATC GAT GC-3'). PCR amplicons were purified with Vazyme VAHTSTM DNA Clean Beads (Vazyme, Nanjing, China) and quantified using the Quant-iT PicoGreen dsDNA Assay Kit (Invitrogen, Carlsbad, CA, USA). After the individual quantification step, amplicons were pooled in equal amounts, and pair-end 2-250 bp sequencing was performed using the Illumina NovaSeq platform with NovaSeq 6000 SP Reagent Kit (500 cycles) at Shanghai Personal Biotechnology Co., Ltd (Shanghai, China).

Microbiome bioinformatics was performed with QIIME2 2019.4 (Bolyen et al. 2018) with slight modifications according to the official tutorials (<https://docs.qiime2.org/2019.4/tutorials/>). Briefly, raw

sequence data were demultiplexed using the demux plugin followed by primer cutting with the cutadapt plugin. Sequences were then quality filtered, denoised, and merged, and chimeras were removed using the DADA2 plugin (Callahan et al. 2016). Nonsingleton amplicon sequence variants (ASVs) were aligned with mafft (Kato et al. 2002) and used to construct a phylogeny with fasttree2 (Price et al. 2009). A total of 15,070,916 sequences were identified as bacterial domains, and 25,628 ASVs were annotated, while a total of 14,638,423 sequences were defined as fungal domains, and 39,774 ASVs were annotated.

2.5 Statistical analysis

In this study, slopes with $0^{\circ}\text{N} \leq \text{slope direction} < 90^{\circ}\text{E}$ or $270^{\circ}\text{W} < \text{slope direction} < 360^{\circ}\text{N}$ and $\text{slope} \geq 5^{\circ}$ were defined as NS, plots with $\text{slope} < 5^{\circ}$ were defined as FS, and slopes with $0^{\circ}\text{S} \leq \text{slope direction} < 90^{\circ}\text{W}$ or $270^{\circ}\text{E} < \text{slope direction} < 360^{\circ}\text{S}$ and $\text{slope} \geq 5^{\circ}$ were defined as SS (Fig. 1b). Calculation of related indexes of plant community characteristics: total plant richness was considered the total number of trees, shrubs, and herbs in each quadrat; the aboveground plant biomass was represented by the total basal area (TBA) of trees and shrubs.

ASV-level alpha diversity indices, such as the Chao1 richness estimator, species richness, and Shannon diversity index were calculated using the ASV table in QIIME2, and the UniFrac distance difference between pairs of groups was determined using t-test and Monte Carlo tests with 1000 permutations and visualized by a boxplot. Beta diversity analysis using Bray-Curtis metrics was used to investigate structural changes in microbial communities between samples, visualized by principal coordinate analysis (PCoA). The R package "Vegan" was used to assess the significance of structural differentiation of microbiota between groups, and PERMANOVA analysis of similarities (ANOSIM) (McArdle and Anderson 2001) were used for the difference test. ANOVAs and LSD tests were used to study the differences in soil physicochemical properties and plant community characteristics on different slope aspects. General linear regression was used to analyze the relationship between plant community characteristics and the soil microbial community (the PCo1 axis score was used to describe the soil bacterial and fungal community composition). The correlation between the soil physical and chemical properties of the plant community and the soil microbial community was explored by Pearson correlation analysis (R package "corplot"). The above statistical analysis was conducted in R Version 4.0.3. (R Core Team, 2020). Partial correlation analysis (SPSS 23.0) was used to explore the relationship between the plant community and soil microbial community after controlling for other environmental factors.

3. Results

3.1 Soil physicochemical properties on different aspects

The ANOVA tests showed that there were certain differences in the physical and chemical properties of the soil in various aspects (Table 1; $P < 0.05$). Specifically, compared with those in the NS and SS, most soil nutrient contents were significantly lower on the FS, as follows: soil total phosphorus (TP) ($0.69 \pm 0.18 \text{ g kg}^{-1}$), soil available phosphorus (AP) ($18.17 \pm 1.17 \text{ mg g}^{-1}$), soil total nitrogen (TN) ($5.62 \pm 0.28 \text{ g}$

kg⁻¹), soil organic matter (SOM) (155.16 ± 5.80 g kg⁻¹), and soil available N (AN) (0.79 ± 0.06 g kg⁻¹). There were no differences between the NS (58.69 ± 0.01%) and SS (58.91 ± 0.01%) in the soil water content, but both aspects had significantly higher values than the FS (54.60 ± 0.01%) (*P* < 0.05). The soil pH was 6.67 ± 0.67 on the NS, 7.36 ± 0.5 on the FS, 7.00 ± 0.49 on the SS, and there was a significant difference between the three aspects. The distribution of soil physicochemical properties under different aspects was visualized by principal component analysis (PCA), combined with the PERANOVA test, and there were significant differences in the physical and chemical properties of the soil between the different aspects (*P* < 0.05) (Fig. S1).

Table 1

Basic information of soil physical and chemical properties in the study site. Data were mean ± SE (n=42,81,47) statistical analysis and LSD multiple comparisons were performed by ANOVA, different letters indicated significant differences (p<0.05)

Variable	North slope	Flat	South slope	Total
Soil pH	6.67±0.67a	7.36±0.5b	7±0.49c	6.99±0.05
Soil moisture (%)	62.51±0.07b	54.63±0.11a	57.45±0.04c	56.81±0.01
Soil Total P (g kg ⁻¹)	1.07±0.24b	0.69±0.18a	1±0.19b	0.87±0.02
Soil available P (mg g ⁻¹)	28.57±10.12b	18.17±10.5a	28.24±9.19b	23.52±0.86
Soil Total N (g kg ⁻¹)	8.54±2.37b	5.62±2.48a	8.71±2.04b	7.20±0.21
Soil available N (g kg ⁻¹)	1.04±0.26b	0.79±0.35a	1.34±0.39c	1.00±0.03
Soil Organic Matter (g kg ⁻¹)	222.14±63.73b	155.16±52.16a	238.09±62.66b	194.64±5.31

3.2 Vegetation characteristics and soil microbial communities on different aspects

ANOVA analysis in the characteristics of aboveground vegetation on various slope aspects showed that the plant species richness (71.28 ± 2.31) on the SS was the highest, and they were significantly different from those on the NS (47.14 ± 1.20) and the FS (51.84 ± 1.90) (*P* < 0.05; Fig. 2A). The TBA was the highest on the FS (174.30 ± 6.42 m² ha⁻¹) and significantly different from that on the NS (144.22 ± 8.33 m² ha⁻¹) (*P* < 0.05; Fig. 2B).

In our study, the soil bacterial ASV richness (2607.57 ± 68.07) and fungal ASV richness (447.04 ± 14.96) were the lowest on the FS, being significantly lower than that of the NS (Bacteria: 2607 ± 43.15; Fungi: 589.02 ± 34.82) or SS (Bacteria: 2816 ± 36.86; Fungi: 578.30 ± 14.23), while the difference between the NS and the SS was not significant. The bacterial Chao1 index of the SS (5530.74 ± 239.38) was significantly higher than that of the FS (4735.68 ± 114.35) or the NS (4792.72 ± 195.26), while the fungal

Chao1 index of the FS (452.84 ± 15.13) was significantly lower than that of the NS (596.55 ± 34.94) or of the SS (586.76 ± 26.64). The bacterial Shannon index of the FS (10.48 ± 0.03) was the lowest significantly lower than the NS (10.57 ± 0.05) or the SS (10.69 ± 0.03) ($P < 0.05$). The fungal Shannon index was not significantly different among the three slope aspects ($P > 0.05$; Fig. 3).

The PCoA results showed that soil bacteria were significantly isolated on the first axis by each slope aspect (Fig. 4A), while soil fungi were not (Fig. 4B). Further ANOSIM test showed that the composition of the soil bacterial community (PERMANOVA, $P = 0.001$, $r^2 = 0.0807$) and soil fungal community (PERMANOVA, $P = 0.003$, $r^2 = 0.0234$) were significantly different on different aspects.

The soil bacteria in this study area were mainly Proteobacteria, Acidobacteria, and Actinobacteria; the soil fungi were mainly Basidiomycota, Ascomycota, and Mortierellomycota (Fig. 5). At the phylum level, for bacteria, the relative abundance of Actinobacteria and Bacteroidetes on the FS was significantly lower than that on the SS ($P < 0.05$), while the relative abundance of Rokubacteria and Nitrospirae on the FS were the highest ($P < 0.05$), and had no significant difference between the NS and SS ($P > 0.05$; Fig. S2). For soil fungi, only the relative abundance of Ascomycota at the phylum level was significantly higher on the NS than on the FS ($P > 0.05$), and there was no significant difference in the other phyla among the three slope aspects (Fig. S3).

3.3 Relationships between the plant community and soil microbial community

Our results showed that the soil bacterial community composition was significantly positively correlated with the plant species richness on the SS ($r^2 = 0.14$, $P < 0.05$) and had a negative relationship on total and FS ($r^2 = 0.21$, $P < 0.001$), but we did not find a significant correlation on the NS (Fig. 6g). In further analysis, dominant bacterial phyla were also correlated with plant communities. Bacteroidetes and Firmicutes on the NS soils were significantly positively correlated with plant species richness, while Nitrospirae were significantly negatively correlated with TBA. There was no significant correlation between the dominant bacteria and plant richness on the FS, but there was a positive correlation between Nitrospirae and Rokubacteria and TBA. On the SS, Nitrospirae and Actinobacteria were negatively correlated with TBA. There was no significant correlation between the ASVs species richness of bacteria or fungi and aboveground vegetation characteristics on each slope aspect (Fig. 6).

The soil fungal community composition and TBA were significantly negatively correlated both on three aspects ($r^2 = 0.1$, $P < 0.05$, Fig. 6a). At the fungal species level, the relative abundance of Basidiomycota was positively correlated with plant TBA. On each slope aspect, the relationship between other dominant phyla of fungi and plant richness was not significantly different (Fig. 7B).

3.4 Possible influencing factors of the plant-soil relationship

In total, after SWC and AP were controlled, the relationship between plant richness and soil bacterial ASVs species richness changed from significant to non-significant. After controlling the soil nutrient contents (SOM, AP, TN, TP), the relationship between plant richness and the soil bacterial community composition changed from significant to non-significant. On the NS, after controlling for AP, the relationship between soil bacterial ASVs richness and plant richness or between the soil bacterial richness and TBA changed from non-significant to significant, while controlling for other soil abiotic factors did not change those relationships; however, regardless of the control of any soil environmental factor, the relationship between the soil fungal community and plant community was not significantly different. On the FS, after controlling for soil AP, TP, and TN, the relationship between soil fungal ASVs richness and plant richness changed from non-significantly to significantly, while soil bacterial community composition and plant richness changed from significant to non-significant after soil pH was controlled; however, no matter what soil abiotic factors were controlled, the other relationships were not affected. On the SS, after controlling for soil pH, the relationship between soil microbial community composition and plant community characteristics changed from significant to non-significant, and there was no significant change in other relationships (Fig. 8).

4. Discussion

4.1 Relationship between plant community and soil microbial species richness

The results showed that neither plant species richness nor TBA had a significant relationship with soil bacterial or fungal ASVs richness on either slope aspect in the subalpine coniferous forest of Wanglang, which was in contrast to our hypothesis. Most of the strong positive correlations between plant community diversity and soil microbial diversity observed in previous studies were found in grassland ecosystems (Schlatter et al. 2015). Forest ecosystems are more complex and have a larger natural plant diversity gradient that contains more covariant factors of soil microbial diversity. Many other factors, such as climate and soil topography, may also affect soil microbial diversity (Carney et al. 2004). Therefore, in our study, changes in soil physical and chemical properties among slope aspects may affect the relationship between plant diversity and soil microbial diversity. We found that under the influence of soil TP content, the relationship between plants and soil microorganisms on the FS showed a significant correlation, which shows that soil P covers the potential relationship between plants and soil microbial diversity. Due to the relatively lower soil P content on the FS, under the condition of limited mineral nutrition resources in the environment may weaken the relationship between plant-soil microbial diversity by limiting factors (Gyaneshwar et al. 2002; Garcia et al. 2015).

Despite the high plant species richness in the subalpine coniferous forest, trees with high biomass, such as *Abies faxoniana* Rehd., provide large amounts of coniferous litter to the ground. Due to differences in productivity and nutrient content between plant species, which means that diverse plant species do not represent more resource availability (van der Heijden et al. 1998; Ladygina and Hedlund 2010). Therefore,

this top-down effect is more likely to indirectly affect soil microbial species richness by influencing the resource competition phenotype of soil microorganisms, regulating the interaction between competing species of soil microbial communities (Bakker et al. 2013b), or affecting the diversity of some specific soil microbial functional groups rather than only species diversity (Li et al. 2017). As a result, the relatively weak plant-soil microbial diversity relationship in our study may be the account of the stronger influence of the soil environment on soil microbes or the mismatch of the environmental resource supply relationship. Consequently, the relationship between plant-soil microbial species diversity is not simple and linear.

4.2 Relationship between plant community and soil microbial community composition

In this study, we found that the plant community characteristics significantly affected the composition of the soil microbial community, the response of bacteria and fungi to the plant community was inconsistent, and their relationship was also followed by slope aspect change, and soil fungal community composition is connected with aboveground plant biomass and that soil bacterial community composition is associated with plant species richness, which was consistent with our second and third hypotheses.

Fungi are known to form close symbioses (such as mycorrhizal fungi) or pathogenic relationships with plants, and their growth is directly dependent on plant litter and biological interactions with plant roots (Wardle 2006; Gao et al. 2013). Compared with fungi, soil bacteria inhabit smaller soil ecological niches, usually indirectly related to plant roots (Vos et al. 2013), so the relationship between plants and soil bacteria is more indirect (Chen et al. 2019b). Therefore, in the subalpine coniferous forest of Wanglang, soil fungi form a close symbiotic relationship with plants that affect plant growth and development. The soil bacterial community is associated with plants that have abundant aboveground resources to provide more ecological niches in which to live.

We found that the slope aspect also altered the relationship between above- and belowground communities by influencing the changes in the soil microenvironment to some extent. For the soil bacterial, the relationships between different slopes and plant communities were not consistent: there were no significant relationships on the NS, but a negative correlation on the FS and a positive correlation on the SS. Except for the NS, soil bacterial community composition was not associated with plant species richness, but we found that the plant species richness and abundance of Bacteroidetes showed a significant correlation. Because of the relatively humid environment, the accumulation of aboveground litter is larger (Table 1), and the decomposition rate is slow on the NS, which can provide abundant food sources for Bacteroides involved in lignin and cellulose degradation (Pankratov et al. 2011). It has been reported that the reason why soil bacterial community composition is not directly related to the plant community is that soil pH may directly affect bacterial community composition under acidic soil conditions (Brodie et al. 2003), the same as our results (Table S2), while plant communities may induce

more changes in the abundance of some soil microbial groups without affecting their community composition (Geisen 2016).

The positive correlation on the SS was consistent with the results of previous studies (Steinauer et al. 2016). The higher light intensity and the average temperature on the SS are conducive to the growth of herbaceous plants (Liu et al. 2020a). According to the trade-off hypothesis when environmental conditions are favorable, plant communities with high species diversity can increase the richness of plant resources and provide more opportunities for soil microorganisms to decompose different resources. Increasing the symbiotic growth pattern of bacteria groups can provide more ecological niches for the survival of underground soil bacteria, which makes the composition of the bacterial community more complex (Schlatter et al. 2015). However, according to the interference of human activities or rivers, the soil layer is thinner, the leaching effect is stronger (He et al. 2018), soil nutrient loss is faster, and the nutrient content is lower on the FS than those with other aspects (Table 1). Under the condition of inferior resource conditions, nutrient supply is limited, and plants and soil bacteria may be in a state of nutrient competition (Kinkel et al. 2011). We observed that with the increase in plant biomass, the relative abundance of Nitrospirae and Rokubacteria which were reported to relate to the soil N species were apparently increased (Ramirez et al. 2012) (Fig. 7). On the FS, there were mostly tall trees with developed roots, which can make better use of nutrient resources and increase the number of bacterial communities involved in soil nutrient conversion, leading to changes in community composition. However, both on the SS and on the FS, the above- and belowground relationship was strongly affected by soil pH. Since soil pH affects both aboveground and belowground communities on both slopes (Tables 2 and 3), it is suggested that covariation factors of the plant community and soil microbial community may be an important reason for the association (Waldrop et al. 2006).

For soil fungi, the relationship between soil fungal community composition and plant biomass tended to be consistent among different aspects, showing a negative correlation, indicating that the interaction between plants and soil fungi in this area was close and the pattern was more uniform. Higher plant biomass can provide more organic carbon to soils, which changes the soil fungal community composition (Huang et al. 2014); therefore, plant biomass is usually positively correlated with soil fungal communities. However, when plants and microorganisms form symbiotic relationships, the relationship between plants and soil fungal community composition is often negative, driven by reciprocal effects, and establishes close connections based on the principle of preferential allocation of resources (Heilmann-Clausen et al. 2016). Plant conspecific negative density-dependent effects (Chen et al. 2019a) indicated that higher conspecific density would limit individual growth, but when plants were symbiotic with ectomycorrhizal fungi, such a restriction effect between ectomycorrhizal plants was weaker, which was more beneficial to plant growth and development (Chai et al. 2018). The study area is dominated by large gymnosperm plants, whose special lignin type and higher content easily symbiosis with Basidiomycota fungi and form ectomycorrhizas (Binder and Hibbett 2006). In addition, we found that Basidiomycota was positively correlated with the aboveground biomass of plants on any slope aspect, indicating that the increase in plant biomass was accompanied by an increase in mycorrhizal fungi, while the decrease in other groups, such as saprophytic pathogenic fungi, suggested that the increase in the

relative abundance of mycorrhizal fungi contributed to the increase in plant biomass in subalpine coniferous forests. In addition, soil TP affected the relationship between aboveground plant biomass and soil fungal community composition on the SS. Because the SS had richer soil nutrient elements, the soil P level was higher (Vogelsang et al. 2006) promoted the fungal community to affect the aboveground productivity of plants through the selection effect, and some plants could directly absorb sufficient nutrients from the soil, thus reducing the dependence of the plant community on soil fungal symbiosis (Lin et al. 2012). Therefore, the influence of the soil phosphorus level on the plant-soil fungi relationship was more significant on the SS.

5. Conclusion

In summary, our study shows that there are significant differences in plant community characteristics and soil microbial community composition and structure in different slope aspects of subalpine coniferous forests. With the change in slope aspect, the correlation between above- and belowground communities varies. Bacteria and fungi respond differently to plant communities. In addition, soil abiotic factors affect some of the connections between these communities. Our results support that there is a certain correlation between the soil microbial community and plants, and it changes with the change in the slope aspect at a local scale. However, this study focused only on plant species richness and plant aboveground biomass and did not consider the role of plant functional traits or microbial functional groups, which may better reflect the relationship among plant-environment microbes. In future research, we will explore these interrelationships in more depth to understand the nature of the mechanisms maintaining terrestrial ecosystem diversity from a more systematic perspective. In short, our research can fill the knowledge gap of above- and belowground relationships between different slope aspects in subalpine coniferous forests and provides a basis for further research on the relationship between above- and belowground biodiversity and ecosystem functions in this area.

Abbreviations

SOM: Soil organic material

SMC: soil moisture content

TP: total phosphorus

TN: total nitrogen

AP: available phosphorus

AN: available nitrogen

BC: bacteria community composition

BR: bacteria ASVs richness

FC: fungal community composition

FR: fungal ASVs richness

TBA: total basal area

PR: plant species richness

NS: the north slope

SS: the south slope

FS: the flat site

Declarations

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Figures

Figure 1

The information of study site and the distribution of sampling sites, n (NS) =42, n (Flat) =81, n (SS) =47.

Figure 2

Characteristics of aboveground plant community on different slope aspects. A) plant species richness, B) total basal area. Different letters indicate that there is a difference between groups, n (NS) =42, n (Flat) =81, n (SS) =47.

Figure 3

Box plot showing soil fungia -diversity: A) Shannon index, B) Chao1 index and C) ASVs Richness; soil bacteria: D) Shannon index, E) Chao1 index and F) ASVs Richness. Middle and lower lines are 75, 50 (median), and 25 quantiles respectively, the longest axis line is not more than 1.5x Box range letters are used to determine whether there is A significant difference between groups, different letters indicate that there is a difference between groups ($P < 0.05$, one-way ANOVA and LSD test), Mean $\pm$ SE, n (NS) = 42, n (Flat) = 81, n (SS) = 47.

Figure 4

PcoA analysis of soil microbial genus levels based on Bray-Cruit distance. A) soil bacteria (PC1:31%, PC2:12%), B) soil fungi (PC1:65%, PC2:18%). Different colors represented different slope aspects.

Figure 5

Species relative abundance of soil microorganisms on different slope aspects. Relative abundance of dominant phyla (A, Top10), genus (B, Top10) of the bacterial community and phyla (C, Top5), genus (D, Top5) of the fungal community.

Figure 6

Coupling between soil microbial community and plant species richness/ total basal area. Points of different colors represent quadrats of different slope aspects, and solid lines indicate that the linear relationship is significant ($P < 0.05$).

Figure 7

Correlation between plant community and soil microbial community at the phylum level. A) soil bacteria (Top 10); B) Soil fungi (Top 5). ***: Correlation is significant at the 0.001 level **: Correlation is significant at the 0.01 level *: Correlation is significant at the 0.05 level.

Figure 8

Partial correlations between plant and soil microbial communities on bulk soil properties. The difference between zero-order (without controlling factors) and partial correlations (factors being controlled) indicate the effects on soil properties influence the relationship between plant and soil microbial communities. ***. Correlation is significant at the 0.001 level **. Correlation is significant at the 0.01 level *. Correlation is significant at the 0.05 level

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