THE COMPOSITION AND DIVERSITY OF SOIL FUNGAL COMMUNITY UNDER *TILIA AMURENSIS* TREES ALONG AN ALTITUDE GRADIENT ON CHANGBAI MOUNTAINS, CHINA

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Abstract. Soil fungi are important for nutrient cycling and soil carbon storage. Although many factors affect fungal community structure, there are few studies that determine the effect of altitude on mountain slopes with invariable vegetation. In this study, we investigated the diversity and composition of soil fungal communities using Illumina MiSeq sequencing along an altitudinal gradient (700 to 1000 m) under *Tilia amurensis* trees, a tree species that is typical for northern slopes of Changbai Mountains, Jilin Province, China. The results showed that soil physicochemical factors were significantly affected by altitude. Basidiomycota and Mortierellomycota and Ascomycota were the dominant fungal phyla in the investigated soils, but their fractions varied with altitude. Alpha diversity increased significantly with altitude. Redundancy analysis revealed that soil factors explained 19.58% of the total variation in fungal community structure, whereas soil nutrients (in particular microbial biomass carbon and nitrogen, total phosphorus, and total nitrogen) and pH were the most important factors affecting the fungal communities. Overall, the changes in soil physicochemical properties with elevation are important in shaping the fungal diversity and composition of soil under *T. amurensis* trees in the investigated locations.
Keywords: *altitudinal gradients, soil fungal community, soil nutrients, Illumina sequencing, fungal diversity*

Introduction

Soil is an important habitat for fungal communities, whose members can be either pathogens or symbionts of plants and animals (Wang et al., 2015a; Sui et al., 2022). Soil can perform important ecological functions such as decomposition (Frey et al., 2016). Soil temperature generally decreases with increasing altitude, which affects the local soil microbial community structure and diversity (Liu et al., 2013). By analysis of soil communities at various altitudes, a better understanding of the driving factors behind fungal community structure, diversity and richness can be obtained, providing insights in their ecological significance and of the spatial distribution pattern of microorganisms and their influencing factors (Shen et al., 2013; Ping et al., 2017).

At present, general conclusions about the differences of soil microbial communities with altitude cannot be drawn due to conflicting results obtained from different studies.

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For example, Ren et al. (2021) reported a decrease of soil fungal community diversity with elevation (1308–2600 m) in the Qinling Mountains, China, but a study in Argentina (400–3000 m) found no difference in the fungal richness related to elevation (Geml et al., 2014). Along an altitude gradient from 3106 to 4479 m Wang et al. (2015b) described that the fungal richness produced a U-shaped trend, whereas Liu et al. (2018) found that the fungal community diversity index did not vary with altitude. These results are highly variable, and suggest that further exploring the differences of the microbial communities at various altitudes is needed to better understand the underlying mechanisms. Altitude affects the local vegetation type (Wu et al., 2013), and that is an important factor affecting soil microbial community, as, for instance, litter and root exudates of different tree species have direct effects on microbial community composition (Sui et al., 2021). In addition, vegetation can indirectly affect the physicochemical properties of (forest) soils, including the soil pH, organic matter content, soil structure, and even the microclimate, which in turn have important impacts on soil microbial communities (Frey et al., 2016; Wu et al., 2019; Weng et al., 2021). Wang et al. (2014) showed that in an area of the Hanshan Mountains (China), different vegetation types at different altitudes significantly affected the fractions of bacterial, fungal biomass and the soil microbial community composition. Most of the published studies towards soil microbial diversity at different altitudes dealt with different vegetation types, which may explain a lack of consistency in the results. It is important to control for vegetation type variables in order to explore differences in microbial community structure along an altitudinal gradient, which may then better reflect the response of soil microorganisms to future climate change.

Changbai Mountain National Nature Reserve (China) is an important gene pool of biodiversity in Northeast Asia. Its rich species diversity makes it a research hotspot (Yang et al., 2003; Zhang et al., 2013; Liu et al., 2019). Different dominant tree species are distributed at different altitudes, and the diverse and complex vegetation types and biological communities make it a key area of ecological protection in China. The unique environment harbors relatively unique fungal communities, providing it an excellent place to study the effect of altitudinal distribution of microorganisms. The deciduous tree *Tilia amurensis* Rupr. is dominant at a wide altitude distribution on the northern slopes of Changbai Mountains (Kang et al., 2021), and such areas were selected to analyze the soil characteristics and fungal communities at four altitudes, from 700 to 1000 m. These sites with abundant *Tilia amurensis* trees were used to 1) compare their fungal diversity and community composition, and (2) evaluate the relationships between the soil fungal community and soil physicochemical properties. The obtained results improve our understanding of the fungal diversity in soils from Changbai Mountains, and give insights into the ecological roles of those fungal communities and the driving factors on their evolution related to elevation in the environment of *Tilia amurensis* environment.

Materials and methods

Research site

The Changbai Mountains (126°55’–129°00’E; 41°23’–42°36’N) are located in Jilin Province, in the northeastern part of China with a continental temperate monsoon climate. Along the increasing altitude from 530 to 2200 m, the mean annual temperature decreases from 4.8 to 2.9 °C, and the mean annual precipitation increases from 632 to 1154 mm.

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Four areas of different elevations were selected where pure *T. amurensis* populations with same understory vegetation were present, at 700, 800, 900 and to 1000 m above sea level on a north-facing slope. The GPS positions of each elevation were shown in *Table A1*. At each elevation, soil samples were collected from under five *T. amurensis* trees in October 2017. For each tree, soil samples (0–20 cm depth) were collected from 10 randomly selected sites around the tree at a distance of approximately 1 m from the stem. After removal of the surface litter and humus layer, the soil was sampled with a soil sampler (50 mm diameter) and the 10 locations around one tree were combined. Roots and plant residues were removed and the fresh soil samples were sieved through 2 mm meshes and subdivided into two aliquots. One part was stored at 4 °C for analysis of soil physicochemical properties and enzyme actives, and the other part was stored at -80 °C for DNA extraction.

Measurements of soil chemical properties

The soil pH was determined with a pH meter after mixing with 0.01 M $CaCl_2$ (1:2.5, wt:vol) and shaking for 30 min. Soil moisture content (SMC) was determined by comparison of fresh wet weight and dry weight following 24 h drying at 120 °C. The soil organic carbon (SOC) and total nitrogen (TN) contents were measured with an elemental analyzer (VarioEL III, Germany). Nitrogen in the form of ammonium (NH_4^+-N) and nitrate (NO_3^--N) was extracted from 10 g soil with 2 M KCl as previously described (Miranda et al., 2001). The total phosphorus (TP) content was determined following a $HClO_4$-H_2SO_4 incubation (Adeloju et al., 1984) and the available phosphorus (AP) fraction following a $NaHCO_3$ extraction (Olsen et al., 1954). The NH_4^+-N, NO_3^--N and AP concentrations were then measured with a continuous flow analytical system (SKALAR San++, Skalar, The Netherlands). Total potassium (TK) was measured following digestion with concentrated HF (Jackson, 1958) and the available potassium (AK) was extracted with acetic acid and ammonium (Mehlich, 1984), after which quantification was done using inductively coupled plasma atomic emission spectrometry (ICP-AES-7500, Shimadzu, Japan). Microbial biomass of C (MBC) and N (MBN) was determined by chloroform fumigation using 0.5 M K_2SO_4.

Microbial DNA extraction

Microbial DNA was extracted from 1 g of thawed soil (stored at −80 °C until use) per sample (5 samples per altitude), using a MOBIO Power Soil Extraction Kit (Mo Bio Laboratories, Carlsbad, CA, USA). Following elution, the DNA quantity was measured with a NanoDrop 2000 spectrophotometer (Thermo Scientific, USA).

Illumina MiSeq sequencing

The isolated DNA was used as a template for amplification of the ITS hypervariable region of the fungal ITS rRNA gene using primers ITS1 (5'-CTTGGTCATTTAGAGGAAGTAA-3') and ITS2 (5′- GCTGCGTTCATCGATGC -3′) (Fouts et al., 2012). A 6-bp barcode sequence unique to each sample was added to the primers. The PCR reaction was performed in triplicate in a 25 μL mixture containing 2.5 μL of TransStart Buffer, 2 μL of dNTPs, 1 μL of each primer, and 20 ng of template DNA. The PCR conditions were as follows: 94 °C denaturation for 3 min followed by 30 cycles of 94 °C for 30 s, 56 °C for 30 s, 72 °C for 60 s, and a final extension at 72 °C for 8 min.

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DNA libraries concentration was validated by Qubit 3.0 Fluorometry. The DNA was diluted to 10 nM and DNA libraries were multiplexed and loaded on an Illumina MiSeq platform (Illumina, San Diego, CA, USA). Sequencing was performed using PE300 paired-ends following standard protocols.

Analysis of the sequences

The QIIME data analysis package was used for ITS rRNA data analysis as described elsewhere (Huang et al., 2019). Briefly, forward and reverse reads were joined and assigned to samples by means of the barcodes, after which the barcode and primer sequences were removed. Quality filtering of joined sequences removed sequences not fulfilling the following criteria: sequence length > 200 bp, no ambiguous bases, mean quality score ≥ 20. Chimeric sequences were removed using UCHIME. The remaining sequences were compared to a reference database (RDP Gold database).

Quality-filtered reads were binned for taxonomic classification using the UNITE8.0 database (Nilsson et al., 2018). Sequences were grouped into operational taxonomic units (OTUs) using the clustering program VSEARCH (version 1.9.6) against the UNITE8.0 database (https://unite.ut.ee/) and pre-clustered at 97% sequence identity. The Ribosomal Database Program (RDP) classifier was used to assign taxonomic categories to all OTUs at a confidence threshold of 0.8.

Sequences were rarefied prior to calculation of alpha diversity. Alpha diversity indices (Ace, Chao1, Shannon and Simpson index) were calculated in QIIME. Beta diversity was calculated using Bray-Curtis dissimilarity. Principal coordinate analysis was performed and visualized using non-metric multidimensional scaling (NMDS). Correlations between all data were assessed in a redundancy analysis (RDA).

Statistical analysis

Soil properties were assessed for differences among different altitudes by one-way analysis of variance (ANOVA) and Tukey's HSD post-hoc testing, and Pearson correlation analysis was used to investigate possible correlations among fungal communities and soil properties. These analyses were performed with SPSS version 22.0 software. Anosim was performed using the vegan package (Dixon, 2003) of R software (v.3.2.5, R Development Core Team, 2016) based on OTU level.

Results

Soil physicochemical properties

The physicochemical properties of the four soil samples taken at different altitudes are summarized in *Table 1*. No significant differences were found between the different altitude samples for pH, TK, TP and AP ($P > 0.05$). The other physical and chemical properties were significantly different ($P < 0.05$). The soil pH ranged from 5.48 to 6.15, which is typical for boreal forest soils. The ammonium nitrogen content was lower at 900 m altitude than at the other altitudes. Nitrate nitrogen content at 900 m was significant lower altitude than at 100 altitude but was not significant different with 700 m and 800 m. The obtained values for water content (SMC), microbial biomass for C (MBC) and N (MBN) were also lower at 900 m compared to the other samples.

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Fungal alpha diversity

Following amplification and sequencing of fungal ribosomal ITS sequences of all samples (four altitudes, 5 replicates) alpha diversity indices of the reads were calculated (*Table 2*). The ACE index was higher for the 800 m compared to 700 m or 900 m ($P < 0.05$). There were no significant differences in Chao index values, but the Shannon index was lower at 700 m than at 1000 m ($P < 0.05$). This suggests that the fungal communities in these samples display different diversity patterns at different altitudes.

The fungal beta diversity (calculated at an OTU level of 97%) of 700 m, 800 m, 900 m and 1000 m were significantly different (Anosim result: $R = 0.25$, $P < 0.01$). When the fungal community structure was analyzed by principal coordinate analysis, this showed that the fungal communities were clearly separated by altitude (*Fig. 1*).

Composition of the soil fungal community

The obtained sequence reads were attributed to OTUs, that belonged to 35 fungal phyla in total. Sequences that could not be classified to a known phylum level were uniformly classified as “others”. Based on the relative abundance, the dominant phyla in all samples were Basidiomycota, followed byAscomycota and Mortierellomycota (*Fig. 2a*). The percentages of the main phyla are listed in *Table A2*.

The soil collected at 700 m altitude contained Basidiomycota at a relative abundance (r.a.) of 79.5%, followed by Mortierella (r.a. 11.5%), and Ascomycota (6.4%) (*Table A2*). Compared to this, at an altitude of 800 m the r.a. of Basidiomycota had decreased, but that of and Mortierellomycota and Ascomycota had increased (*Fig. 2a*). At an altitude of 900 m, the most noted change was an increase of Basidiomycota, while this decreased again at 1000 m. That latter sample contained the largest number of unclassified reads.

At the genus level, *Mortierella*, *Sebacina*, *Inocybe*, and *Russula* were the genera with the highest r.a. (*Fig. 2b*; *Table A2*), exceeding 10% in at least one sample, although their fractions varied between the sampled attitudes. Notably, *Mortierella* and *Sebacina* members were less abundant at 700 m compared to the other three altitudes, while *Inocybe* was less abundant at 800 m. The fraction of *Russula* was less variable, but *Piloderma* was hardly detected at 1000 m and was present at low abunacne at 700 m, while it was quite abundant at 800 and 900 m (*Fig. 2b*; *Table A2*). Members of *Descolea* and *Lactifluus* were found highly abundant at 700 m but were hardly detected in the other samples. *Tomentella* was quite abundant at 800 m and *Hygrocybe* members were only found at 900 m. The other genera did not reach > 5% r.a. in any of the samples (*Table A2*).

Relationship between fungal community structure and environmental characteristics

The fungal OTUs were combined with the determined soil characteristics and altitudes in a redundancy analysis (RDA). Soil characteristics and altitude together explained 19.58% of the total fungal community variation: the first axis (RDA1) explained 11.99% and the second axis (RDA2) 7.59% of species abundance differences (*Fig. 3*). Moreover, values for MBC, MBN, TN, and AK showed positive correlations with the soil fungal community structure at 700 m altitude. At 800 m, TN, TK, MBC, MBN, MC, and TP showed a positive correlation with the soil fungal community structure. There was a positive correlation between pH and soil fungal community structure at an altitude of 900 m. Lastly, at 1000 m SOC, TP, AP, MC, NH_4^+, NO_3^-, and pH were positively correlated with the soil fungal community structure at an altitude of 1000 m.

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Table 1. *Physicochemical characteristics of the soil obtained in the vicinity of T. amurensis trees at four altitudes in the Changbai Mountains, China*

Alt. (m)	pH	NH_4^+-N ($mg \cdot kg^{-1}$)	NO_3^--N ($mg \cdot kg^{-1}$)	SMC (%)	TN ($g \cdot kg^{-1}$)	TK ($g \cdot kg^{-1}$)	TP ($g \cdot kg^{-1}$)	AK ($mg \cdot kg^{-1}$)	AP ($mg \cdot kg^{-1}$)	MBC ($mg \cdot kg^{-1}$)	MBN ($mg \cdot kg^{-1}$)	SOC ($g \cdot kg^{-1}$)
700	5.48±0.28a	53.06±7.05a	5.99±1.48ab	48.19±1.49a	26.64±7.07ab	4.21±0.47a	0.06±0.01a	21.09±3.29a	10.28±1.93a	510.54±76.55a	54.87±10.44a	13.99±0.97a
800	6.05±0.23a	59.96±5.69a	6.61±2.09ab	38.52±2.25b	33.27±4.63a	3.44±0.71a	0.08±0.02a	21.70±2.60a	16.12±1.95a	420.52±25.92a	49.12±3.11b	17.31±1.74a
900	5.88±0.17a	18.48±1.55b	2.37±0.28b	19.17±1.09c	11.69±2.26b	2.74±0.33a	0.05±0.00a	12.28±0.96b	9.74±2.98a	55.52±11.85c	7.30±0.90c	10.77±1.39a
1000	6.15±0.11a	54.97±9.80a	11.32±3.18a	44.59±3.71ab	18.02±8.12ab	2.74±0.84a	0.07±0.01a	18.21±2.87ab	14.48±2.20a	249.32±25.54b	26.41±3.81b	15.85±1.22a

Values represent means ± standard deviations (n = 5). Different letters indicate significant ($P < 0.05$) differences between individual means assessed by one-way ANOVA followed by Tukey's HSD post-hoc testing. Abbreviations: NH_4^+, ammonium nitrogen; NO_3^-, nitrate nitrogen; SMC, soil moisture content; TN, total nitrogen; TK, total potassium; TP, total phosphorus; AK, available potassium; AP, available phosphorus; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; SOC, soil organic carbon

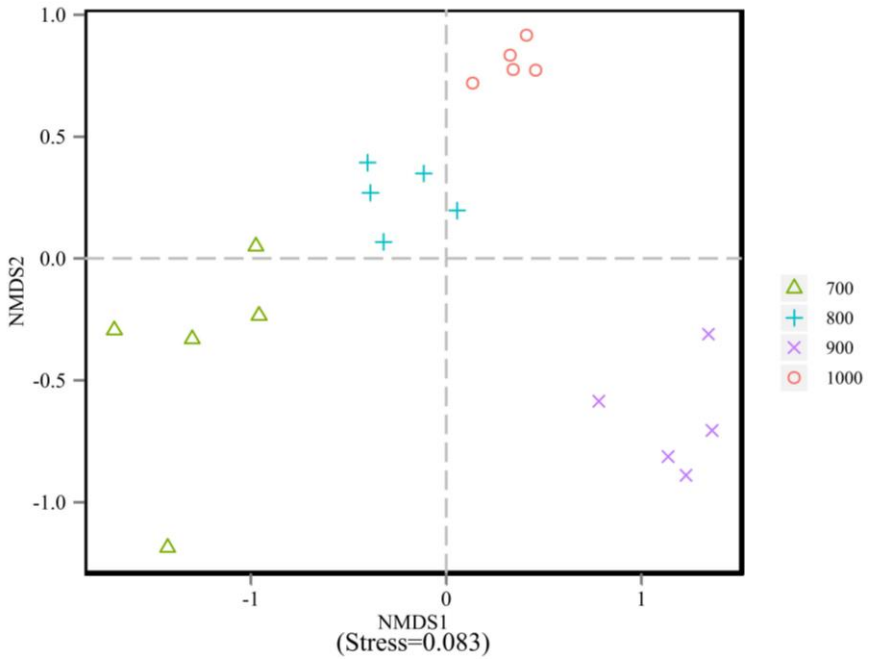

Figure 1. *Principal coordinate analysis of soil fungal communities, as characterized by ITS amplicon sequencing, at the four altitudes*

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Table 2. *Fungal alpha diversity of the soil samples at four altitudes*

Altitude	Ace index	Chao1 index	Shannon index
700 m	380 ± 24.01b	383 ± 26.58a	2.5 ± 0.37b
800 m	440 ± 5.07a	438 ± 6.17a	3.4 ± 0.29ab
900 m	393 ± 14.24b	407 ± 19.86a	3.5 ± 0.18ab
1000 m	413 ± 10.37ab	418 ± 9.86a	3.8 ± 0.16a

Values represent means ± standard deviations (n = 5). Different letters indicate significant ($P < 0.05$) differences between individual means assessed by one-way ANOVA followed by Tukey's HSD post-hoc testing

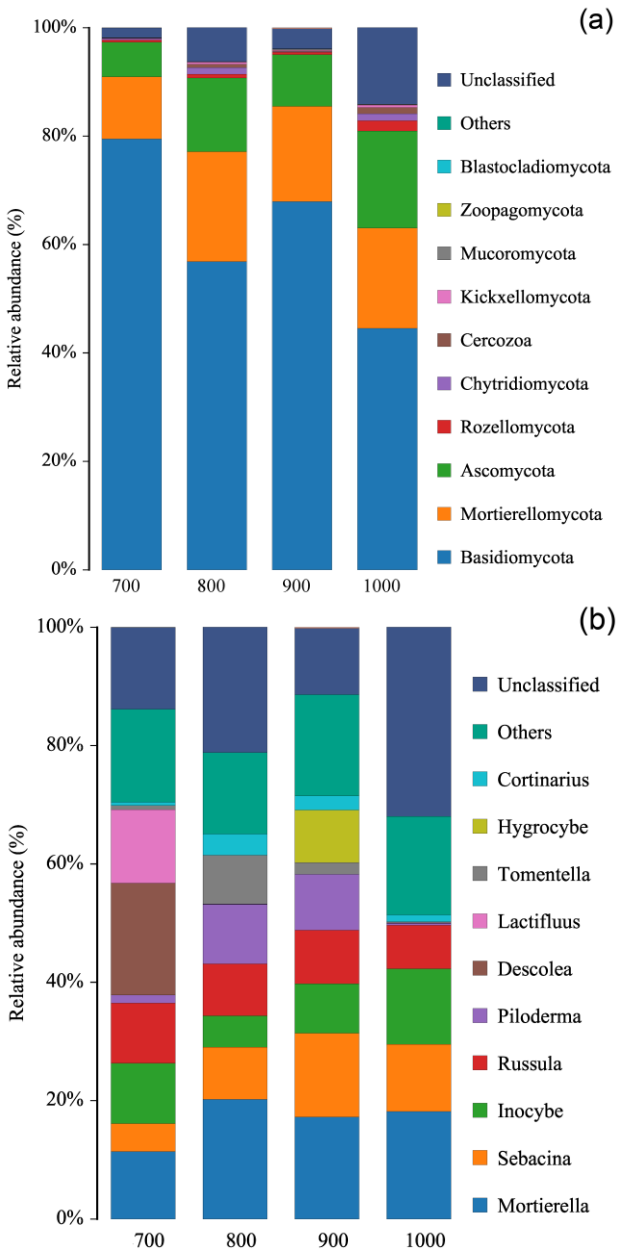

Figure 2. *Relative abundance of the dominant fungal phyla (a) and genera (b) in the soils obtained from soil under T. amurensis trees at the indicated altitudes (700 to 1000 m). The combined results of 5 soil samples per altitude are shown*

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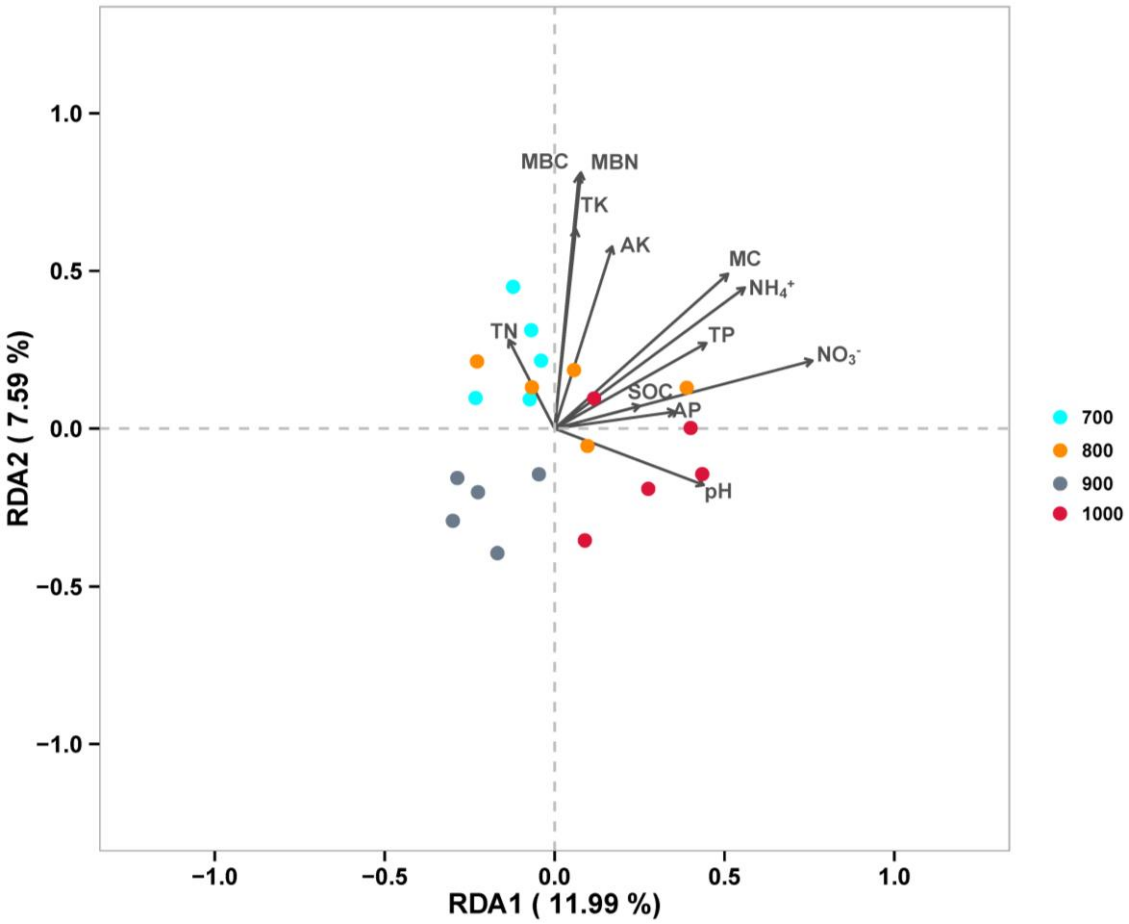

Figure 3. *Redundancy analysis (RDA) of soil fungal OTUs, soil characteristics and altitude. Arrows identify correlations of the fungal community with shown parameters. Abbreviations: NH_4^+, ammonium nitrogen; NO_3^-, nitrate nitrogen; SMC, soil moisture content; TN, total nitrogen; TK, total potassium; TP, total phosphorus; AK, available potassium; AP, available phosphorus; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; SOC, soil organic carbon*

Pearson correlation analyses were used to further explore the relationships between soil physicochemical properties and the relative abundances of the 9 most abundant fungal phyla and the 9 most abundant genera. Only significant correlations ($P < 0.05$) are mentioned here. At the phylum level (*Table 3*), the relative abundance of Basidiomycota was negatively correlated with soil nitrate, while the abundances of Chytridiomycota, Cercozoa, Kickxellomycota and Zoopagomycota correlated positively with this parameter. A positive correlation as also observed between Chytridiomycota and ammonium as well as TP, and a negative correlation was found between Mucoromycota and AK and TK. At the genus level only the abundance of *Lactifluus* significantly correlated, with both MBC and MBN (*Table 3*).

Discussion

As described in the literature, specific soil microbial communities and their diversity varies with altitudes (Zhang et al., 2018). This was confirmed here, where vegetation

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was dominated by *Tilia amurensis* trees, but significant differences in the Shannon index and Ace index of soil fungi was observed at different altitudes (*Table 2*). The soil Shannon index at 1000 m was significant higher than at 700 m, but was not significant different with 800 m and 900 m (*Table 2*). Since the aboveground vegetation was the same for all investigated sites, it can be inferred that soil physico-chemical properties are mostly responsible for the difference of soil fungal diversity at different altitudes. At an altitude of 700 m to 1000 m, the habitat is suitable for the survival of a wide variety of soil microorganisms, but selection by local soil characteristics may be the reason why soil fungal diversity gradually increases along the altitude. Yang et al. (2017) observed a monotonic decrease in soil fungal diversity (investigated by culture-dependent methods) along elevation from 700 to 2600 m at Changbai Mountain. Ping et al. (2017) described a U-shaped pattern for soil fungal diversity over elevation of 700 m to 1044 m in Korean pine forests in the same area. Most likely, different processes drive the elevational distribution of fungal communities (Zhou et al., 2021). In our study, the variation trend of soil ACE abundance index along the altitude was not consistent with that of Shannon, indicating there is no uniform fungal diversity pattern on the altitude gradient.

Table 3. *Person's rank correlations between the relative abundances of dominant fungal taxa (top: phylum, bottom: genus) and soil physicochemical variables*

Phylum	**pH**	**NH_4^+-N**	**NO_3^--N**	**MC**	**TN**	**TK**	**TP**	**AK**	**AP**	**MBC**	**MBN**
Basidiomycota	-0.299	-0.148	-0.488*	0.009	0.277	-0.111	-0.403	0.082	-0.088	0.196	0.127
Mortierellomycota	0.208	0.036	0.233	-0.152	-0.18	0.121	0.242	-0.197	-0.117	-0.091	-0.027
Ascomycota	0.219	0.194	0.307	0.061	-0.14	-0.003	0.351	0.133	0.308	-0.195	-0.219
Rozellomycota	0.145	0.099	0.418	0.221	-0.072	-0.265	0.121	-0.008	0.192	-0.12	-0.155
Chytridiomycota	0.118	0.559*	0.683**	0.335	-0.125	0.167	0.571**	0.321	0.11	0.11	0.146
Cercozoa	0.217	0.415	0.674**	0.261	-0.277	0.044	0.436	0.089	0.076	-0.092	-0.049
Kickxellomycota	0.299	0.319	0.572**	0.154	-0.254	0.027	0.428	-0.09	0.159	-0.116	-0.028
Mucoromycota	0.158	-0.241	-0.307	-0.358	-0.105	-0.453*	0.105	-0.577**	0.329	-0.441	-0.394
Zoopagomycota	0.275	0.158	0.749**	0.239	-0.4	-0.081	-0.011	0.072	0.117	-0.176	-0.19
Genus											
Mortierella	0.207	0.049	0.221	-0.139	-0.16	0.125	0.249	-0.19	-0.106	-0.077	-0.014
Sebacina	0.135	-0.061	-0.21	-0.305	-0.22	-0.078	0.221	0.048	0.284	-0.351	-0.407
Inocybe	0.196	0.15	0.18	0.164	-0.121	-0.099	-0.228	0.287	-0.306	-0.05	-0.227
Russula	-0.132	0.171	-0.185	0.087	-0.016	0	-0.102	0.257	-0.137	-0.084	-0.23
Piloderma	-0.043	-0.208	-0.022	-0.3	0.028	-0.416	-0.182	0.039	-0.02	-0.063	-0.025
Descolea	-0.143	-0.057	0.009	0.278	0.2	0.244	0.279	0.221	0.122	0.093	0.182
Lactifluus	-0.321	0.18	-0.052	0.232	0.244	0.039	-0.193	-0.001	0.024	0.554*	0.556*
Tomentella	0.445*	0.127	-0.201	0.035	0.228	-0.207	-0.318	-0.108	0.349	0.086	0.031
Hygrocybe	0.299	-0.381	-0.198	-0.429	-0.136	0.063	-0.13	-0.314	-0.078	-0.378	-0.353

*Correlation is significant at the 0.05 level (one-tailed). ** Correlation is significant at the 0.01 level (two-tailed)

Abbreviations: NH_4^+, ammonium nitrogen; NO_3^-, nitrate nitrogen; SMC, soil moisture content; TN, total nitrogen; TK, total potassium; TP, total phosphorus; AK, available potassium; AP, available phosphorus; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; SOC, soil organic carbon

The dominant phyla we detected was Basidiomycota, consistent with the findings of others (Ping et al., 2017). The same mountains were studied in 2000, and although that study investigated higher altitudes (700–1200 m) and the sites were covered with a

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different vegetation (Korean pine forest) they also reported dominance of Basidiomycota (Ping et al., 2017). However, when Ni et al. (2018) studied soil fungi above 2000 m in Changbai Mountains (above the tree line), the highest abundant phylum was Zygomycota, a phylum we did not find abundant. Altitude will affect a series of factors such as vegetation composition, soil structure, temperature and moisture, availability of nutrients and decomposed organic matter, and microbial activity (Klose et al., 2006). All these factors may affect the structure and composition of soil microbial communities. Members of Basidiomycota can decompose lignin, and usually live in environments with rich resources and high plant abundance (Ni et al., 2018). Our study sites were covered with deciduous trees whose litter is rich in lignin, which may explain the high abundance of Basidiomycota. We further detected relatively large fractions of Mortierellomycota and Ascomycota. Members of the latter phylum are typically resistant to environmental pressures that enable their survival in soil (Ping et al., 2017). Notably, their fraction was higher at the highest investigated altitude, where environmental variation may be more severe. Mortierellomycota are saprophytic fungi, mainly living in soils rich in organic matter, and these are key microbial members of soil carbon and nutrient transformation (Zhou et al., 2021). The organic matter content of the soil studied here is high, providing sufficient nutrients for these fungi. This is also consistent with the findings of Ping et al. (2017). This shows that with unaltered aboveground vegetation, the findings at different altitudes are consistent with previous research results, in that soil type and altitude determine the composition of soil fungi.

The RDA applied here found that soil physicochemical properties significantly correlated with soil fungal community structure (*Fig. 3*), although the relationships between soil fungal community structure and soil physicochemical properties varied at different altitudes (*Table 3*). At 700 m and 800 m the fungal communities were mostly affected by nutrient content (e.g. MBC, MBN, TN, AK), but this was less noticeable at 900 and 1000 m, where pH had more of an effect. On a small scale, the community structure of soil microorganisms is mainly affected by nutrient content, and when the scale is large, pH is an important factor (Shen et al., 2013). The presence of particular fungi can be closely related to plants, and since all our samples were taken under *Tilia* trees, any impact from above-ground vegetation, such as the composition and content of litter, can be ignored.

The Pearson correlation analyses indicated that the 9 most abundant fungal phyla and genera were mainly affected by NH_4^+-N, NO_3^--N, TK, AK and pH. Fungi play important roles as plant decomposers, pathogens, and symbionts in terrestrial ecosystems (Yang et al., 2017). Plant species also affect microbial community structure due to differences in root depth, root exudates, canopy coverage, and litter quality and quantity (Zak et al., 2003). However, there is no consensus on the correlation between plant diversity and soil fungal community structure. The vegetation type, species composition and vertical structure of different altitudes can strongly vary along a mountain slope, to a variable extent influencing soil organic matter, nutrient availability, and microbial community composition. Added to this are differences in habitat surface reflectance, temperature, light penetration, etc., that also affect soil microbial community composition, structure, and diversity (Yarwood et al., 2010; Jodi et al., 2013). Feedback mechanisms exist, as a given soil microbial community can have positive or negative effects on plant growth by maintaining and transforming soil nutrients, thereby affecting the composition of the plant community

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that then again affects the soil microbial community (Philippot et al., 2013). These effects could be ruled out here, giving insights into the real effect of altitude (between 700 and 1000 m) in the Changbai Mountain for soil on which *Tilia amurensis* trees grow.

Conclusions

The distribution patterns and driving factors of soil fungal community composition and diversity were determined for soil at different altitudes under *Tilia amurensis* trees in Changbai Mountains. Significant differences in the composition and diversity of soil fungal communities were found at different altitudes, with an upward trend in diversity along the elevation. In absence of vegetation variation, the composition of the soil fungal community is closely related to the physical and chemical properties of the soil. At the lower altitudes soil nutrients were the main factors affecting the fungal composition, while at the higher altitudes soil nutrients and pH jointly drove fungal community composition. The results of this study not only increase our understanding of the composition and diversity patterns of fungal communities at a local elevation scale, but also provide a theoretical basis for predicting the response, adaptation and feedback of microbial communities to changes in environmental conditions.

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APPENDIX

Table A1. *The position of each elevation in Changbai Mountains, China*

Altitudes (m)	Latitude	Longitude
700	42°34’30”	127°56’20”
800	42°20’48”	128°05’30”
900	42°18’20”	128°07’40”
1000	42°15’50”	128°09’25”

Table A2. *Relative abundance of the dominant fungal phyla (top) and genera (bottom) in soil below T. amurensis trees at four altitudes of Changbai Mountains, China*

Phylum	700 m	800 m	900 m	1000 m
Basidiomycota	79.49%	56.85%	67.93%	44.54%
Mortierellomycota	11.45%	20.29%	17.56%	18.49%
Ascomycota	6.40%	13.59%	9.55%	17.91%
Others	0.82%	3.00%	1.08%	4.96%
Unclassified	1.81%	5.73%	3.71%	12.90%

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Genus				
Mortierella	11.40%	20.20%	17.22%	18.14%
Sebacina	4.70%	8.82%	14.17%	11.35%
Inocybe	10.19%	5.31%	8.37%	12.80%
Russula	10.19%	8.78%	9.04%	7.35%
Piloderma	1.36%	10.06%	9.44%	0.31%
Descolea	18.92%	0.04%	0.00%	0.03%
Lactifluus	12.43%	0.00%	0.00%	0.06%
Tomentella	0.68%	8.26%	1.96%	0.20%
Hygrocybe	0.00%	0.00%	8.92%	0.00%
Cortinarius	0.56%	3.57%	2.38%	1.15%
Clavulina	2.78%	2.12%	0.08%	0.07%
Peziza	0.27%	0.04%	0.39%	3.77%
Entoloma	3.79%	0.03%	0.18%	0.00%
Membranomyces	0.24%	0.94%	0.91%	1.24%
Clavulinopsis	0.07%	2.55%	0.52%	0.00%
Elaphomyces	2.25%	0.00%	0.10%	0.03%
Amphinema	0.14%	0.80%	0.01%	1.08%
Leotia	0.54%	0.02%	1.09%	0.11%
Laccaria	0.02%	0.63%	0.15%	0.86%
Others	5.64%	6.65%	13.70%	9.50%
Unclassified	13.80%	20.64%	11.20%	30.77%

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