Structural and Functional Characteristics of Generalist and Specialist Soil and Root-Inhabiting Fungi in Pinus sylvestris var. mongolica Forests of Hulunbuir Sandy Land: Postprint

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Abstract

This study investigated the community structure and functional differences of generalist and specialist fungi in soil and roots of Mongolian pine forests and their relationships with soil physicochemical properties, aiming to reveal the key microbiological mechanisms influencing ecosystem functions of Mongolian pine forests. Using natural and planted Mongolian pine forests (24, 35, and 44 years old) in the Hulunbuir Sandy Land as research objects, high-throughput sequencing technology was employed to analyze the community structure and functional group differences of generalist and specialist fungi in soil and roots. The results showed that: (1) Generalist fungi in soil and roots shared 169 OTUs, soil fungal specialists retained 603 OTUs, and root-inhabiting fungal specialists retained 216 OTUs; the dominant genera of soil fungal generalists were Tricholoma and Suillus, those of root-inhabiting fungal generalists were Tricholoma, Suillus, and Cadophora, the dominant genus of soil fungal specialists was Penicillium, and that of root-inhabiting fungal specialists was Acephala. (2) Symbiotic trophic fungi accounted for 28.49%-47.21% of soil fungal generalists, with ectomycorrhizal fungi as the dominant ecological functional group, showing a trend of first increasing then decreasing with stand age; saprotrophic fungi accounted for 17.01%-40.01% of soil fungal specialists, with the relative abundance in plantations being lower than that in natural forests, and showing a trend of first decreasing then recovering with increasing stand age; symbiotic trophic fungi accounted for 43.25%-54.45% of root-inhabiting fungal specialists, with ectomycorrhizal fungi as the dominant ecological functional group, showing an increasing trend with stand age, and the relative abundance in natural forests being higher than that in plantations. (3) Soil organic matter and available phosphorus contents in natural Mongolian pine forests were significantly higher than those in plantations ($P<0.05$); with increasing stand age, soil organic matter, total phosphorus, available nitrogen, and available phosphorus in plantations increased significantly ($P<0.05$); soil pH decreased but not significantly ($P>0.05$); generalists were significantly correlated with soil organic matter, ammonium nitrogen, and total potassium ($P<0.05$); root-inhabiting specialists were significantly correlated with the aforementioned factors ($P<0.05$) and also with soil total nitrogen ($P<0.05$); soil specialists were significantly correlated with total potassium, readily available nitrogen, and nitrate nitrogen ($P<0.05$). The driving factors of fungal community structure in Mongolian pine forests exhibited significant niche differentiation characteristics, and the research results contribute to a deeper understanding of the ecological functions of soil and root-inhabiting fungi in Mongolian pine forests of the Hulunbuir Sandy Land, providing a scientific basis for the sustainable management and conservation of Mongolian pine forests.

Full Text

Structure and Functional Characteristics of Generalist and Specialist Fungi in Soil and Roots of Pinus sylvestris var. mongolica Forests in the Hulunbuir Desert

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Abstract

This study investigated the community structure and functional differences between generalist and specialist fungal species in the soil and roots of *Pinus sylvestris* var. *mongolica* forests and their relationships with soil physicochemical properties, aiming to reveal key microbial mechanisms influencing ecosystem functioning. Using natural forests and plantations (24-, 35-, and 44-year-old) of *P. sylvestris* var. *mongolica* in the Hulunbuir Desert as study objects, high-throughput sequencing technology was employed to analyze differences in community structure and functional groups of generalist and specialist fungi in soil and roots. The results showed: (1) Soil and root-associated generalist fungi shared 169 operational taxonomic units (OTUs), soil specialist fungi retained 603 OTUs, and root-associated specialist fungi retained 216 OTUs. The dominant genera in soil generalist fungi were *Tricholoma* and *Suillus*, while root-associated generalist fungi were dominated by *Tricholoma*, *Suillus*, and *Cadophora*. *Penicillium* was the dominant genus in soil specialist fungi, and *Acephala* dominated root-associated specialist fungi. (2) Symbiotic trophic fungi accounted for 28.49%–47.21% of soil generalist fungi, with ectomycorrhizal fungi as the dominant ecological functional group, showing a trend of first increasing then decreasing with stand age. Saprophytic trophic fungi comprised 17.01%–40.01% of soil specialist fungi. Compared with natural forests, plantations had lower relative abundance of saprophytic trophic fungi, which showed a trend of decreasing first and then increasing with stand age. Symbiotic trophic fungi accounted for 43.25%–54.45% of root-associated specialist fungi, with ectomycorrhizal fungi as the dominant functional group, increasing with stand age and showing higher relative abundance in natural forests than in plantations. (3) Soil organic matter and available phosphorus content in natural *P. sylvestris* var. *mongolica* forests were significantly higher than in plantations ($P<0.05$). With increasing stand age, soil organic matter, total phosphorus, available nitrogen, and available phosphorus in plantations increased significantly ($P<0.05$), while soil pH decreased but not significantly ($P>0.05$). Generalist fungi were significantly correlated with soil organic matter, ammonium nitrogen, and total potassium ($P<0.05$). Root-associated specialist fungi were significantly correlated with these factors ($P<0.05$) and also with total nitrogen ($P<0.05$). Soil specialist fungi were significantly correlated with total potassium, available nitrogen, and nitrate nitrogen ($P<0.05$). The drivers of fungal community structure showed significant ecological niche differentiation. These findings contribute to a deeper understanding of the ecological functions of soil and root-associated fungi in *P. sylvestris* var. *mongolica* forests and provide a scientific basis for sustainable management and protection of these forests in the Hulunbuir Desert.

Keywords: soil fungi; root-associated fungi; habitat generalist; habitat specialist; community structure; ecological function; soil physicochemical properties

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Soil fungi are critical drivers of material and energy flow in soil ecosystems, participating in organic matter decomposition, nutrient cycling, and biodiversity maintenance. Their community structure and functional characteristics directly influence plant growth, development, and reproduction. Root-associated fungi are soil fungal groups that colonize or diffuse into host root systems, enhancing plant nutrient and water absorption capacity while obtaining photosynthetic products from the host as an energy source. To cope with competition from invasive species and environmental changes, some fungi adapt by becoming generalists or specialists to improve their survival capabilities. Generalist species exhibit broad ecological adaptability, can survive in diverse soil and habitat conditions, and play important roles in new species formation, ecosystem function maintenance, and stability. Specialist species have strict requirements for specific resources, can utilize resources that other species cannot or rarely use, or use them more efficiently, and typically survive only in one or a few specific habitats. This characteristic gives them strong specificity and limitations in ecosystems, exerting important influences on plant growth and stress resistance. The coexistence of these two functional groups is significant for soil ecosystem health and plant growth and development.

From the perspective of ecological driving mechanisms, the distribution patterns of fungal generalists and specialists are primarily controlled by host plant characteristics and environmental factors. Fungal-plant symbiosis is one of the main driving forces of plant evolution, and the two have formed close interactions during long-term evolutionary processes. Host plant preference determines fungal community composition and is a key factor influencing the community structure of generalist and specialist fungi. At broad spatial scales, differences in climate conditions such as temperature, precipitation, humidity, and light intensity caused by geographical location are key factors affecting the community structure and function of generalists and specialists. At fine spatial scales, soil physicochemical properties such as water content, porosity, and nutrient content influence the community composition and functional characteristics of generalists and specialists. Additionally, studies on forest ecosystems have shown that stand age is an important factor affecting changes in soil and root-associated fungal community functions. Increasing stand age means plant root expansion, death, and renewal, which affect soil structure and soil organic matter accumulation, thereby influencing soil microbial community structure and function. Young stands typically allocate more energy to growth and development, whereas mature stands may allocate more resources to maintaining ecosystem stability and resilience. These differences in resource allocation affect the quality and quantity of root exudates, which in turn influence the composition and functional characteristics of generalist and specialist fungi in soil and roots.

Pinus sylvestris var. *mongolica* has strong adaptability, cold resistance, tolerance to poor soil conditions, and a well-developed root system. It is the preferred species for windbreak and sand fixation as well as soil and water conservation in wind-sand areas of northern China, and is also an important economic and ornamental tree. Existing research has primarily focused on the ecological adaptation strategies, evolutionary dynamics, and community assembly of single-niche generalist and specialist fungi in forest ecosystems. Studies have shown that generalist species have wider niches and stronger environmental adaptability, with their distribution mainly driven by stochastic processes, whereas specialist species depend on specific environmental conditions and are dominated by deterministic processes. However, key scientific questions regarding the structural composition, dynamic response patterns, and functional synergy of generalists and specialists across different niches require further investigation. Therefore, this study used natural and plantation forests of *P. sylvestris* var. *mongolica* in the Hulunbuir Desert as research objects to compare and analyze the structural and functional characteristics of generalist and specialist fungi in soil and roots, and to explore the influence of soil physicochemical properties, thereby providing a scientific basis for sustainable management and protection of *P. sylvestris* var. *mongolica* forests to ensure both ecological health and economic benefits.

1.1 Study Area Overview

Natural forest sample plots and plantation plots were established in the Inner Mongolia Honghuaerji National Nature Reserve for *Pinus sylvestris* var. *mongolica* (48°44 N, 120°01 E) and the Inner Mongolia Hailar National Forest Park (49°12 N, 119°33 E) in the southeastern Hulunbuir Desert. The region has a mid-temperate semi-humid continental monsoon climate, with an average annual evaporation of 1100–1200 mm, average annual temperature of -0.78°C, average annual rainfall of 348.4 mm, and average annual sunshine duration of 2500 h. The main soil type is aeolian sandy soil, and the dominant tree species is *P. sylvestris* var. *mongolica*. Natural vegetation includes *Salix gordejevii*, *Artemisia desertorum*, and *Potentilla bifurca*.

1.2 Sample Plot Setup and Sample Collection

In August, during the peak growth period of *P. sylvestris* var. *mongolica*, sample plots were established in middle-aged (24 years), near-mature (35 years), and mature (44 years) plantations and natural forests with identical site conditions and management measures, based on forest inventory data and field surveys. Within each forest type, 20 m × 20 m quadrats were set up as replicates. Within each quadrat, tree height, diameter at breast height, and canopy density were measured. Three standard *P. sylvestris* var. *mongolica* trees were selected in each quadrat, with spacing greater than 20 m between trees. Surface cover within a 50 cm radius of the base of each standard tree was first removed, then soil profiles were excavated. Soil samples (0–20 cm depth) were collected using soil cores, and fine roots were carefully extracted. Three soil samples from the same quadrat were mixed, placed in sealed plastic bags, and labeled, then stored in a portable incubator at 4°C. A total of 36 soil samples and 36 fine root samples were collected for molecular biological identification. Simultaneously, three mixed dry soil samples were collected in the same manner, placed in sealed plastic bags, numbered, and used for determining soil physicochemical properties.

1.3 Soil Physicochemical Property Determination

Soil water content (SWC) was determined using the aluminum box drying-weighing method; soil porosity was measured using the ring knife drying-weighing method; soil pH was measured using a pH analyzer (Shanghai Leici, China) with a 1:2.5 soil-water ratio. Total potassium (TK) content was determined by flame photometry after sodium hydroxide fusion. Soil organic carbon content (SOC) was measured using the potassium dichromate dilution-heat method, and soil organic matter (SOM) content was calculated. Total phosphorus (TP) content was determined using the molybdenum-antimony anti-colorimetric method. Total nitrogen (TN) content was measured using the indophenol blue colorimetric method. Available nitrogen (AN) content was determined using the alkali diffusion method. Available phosphorus (AP) content was measured using sodium bicarbonate extraction and molybdenum-antimony anti-colorimetric method. Ammonium nitrogen (NH_4^+-N) and nitrate nitrogen (NO_3^--N) were extracted with 2 mol/L KCl and measured using a continuous flow analyzer.

1.4 Fungal Molecular Biology Identification

Fine root tips were cut and ground with liquid nitrogen in a mortar. DNA was extracted from 0.25 g of fine root and fresh soil samples using the MoBio PowerSoil DNA Isolation Kit. The fungal universal primers ITS1F (5 -CTTGGTCATTTAGAGGAAGTAA-3) and ITS2 (5 -GCTGCGTTCTTCATCGATGC-3) were used to amplify the ITS1 region. PCR products were purified using the Beckman Coulter Agencourt AMPure XP nucleic acid purification kit. Amplified products were detected by gel electrophoresis and sequenced on the Illumina MiSeq PE300 high-throughput sequencing platform. After amplicon sequencing, raw data were processed using the QIIME platform, which normalized samples based on minimum total abundance and filtered low-abundance operational taxonomic units (OTUs). Representative sequences were compared using BLAST. If the similarity reached or exceeded 97%, identification to species level was possible; if similarity was 90%-97%, identification to genus level was possible. Dominant genera were defined as those with relative abundance $ $10%, and common genera as those with 1%-10% abundance.

1.5 Data Processing and Analysis

The Dispersal Niche Continuum Index (DNCI) was used to analyze community assembly processes. After 999 permutations of the community matrix, the assembly of soil and root-associated fungal communities in different stands was simultaneously determined by stochastic and deterministic processes. The interaction between soil and root-associated fungi was mainly affected by diffusion processes. The classification of generalists and specialists was based on the distribution of fungal taxa across the entire community. The Specialist-Generalist-Clamtest module was used to classify fungi in both systems, and the Indicator function was used to remove differential indicator species. To improve classification accuracy, the Specialist-Generalist-Too rare module was used to screen soil and root-associated fungal communities, and fungal communities were further filtered for inter-group differences using the Indicspecies function to obtain the generalist and specialist fungal communities for this study. DNCI values were calculated to quantify community assembly processes. A negative DNCI index indicates that dispersal processes contribute more to community assembly, while a positive value indicates that niche differentiation processes contribute more.

The relative abundance stacked bar charts and cluster heatmaps of generalists and specialists were plotted. Based on FUNGuild analysis results, the ecological functional categories of generalist and specialist fungi were classified, retaining categories with "highly probable" and "probable" confidence levels. Trophic types were divided into three categories: symbiotrophic, saprotrophic, and pathotrophic, with other fungi having compound trophic types classified as other trophic types. The Ggcor module was used for Mantel test analysis of the correlation between generalist/specialist fungal communities and soil properties, and the Vegan package was used for redundancy analysis (RDA) of the top five dominant genera of generalists and specialists with soil properties.

2.1 Community Structure Composition of Generalists and Specialists

Generalist and specialist fungi in natural and plantation *P. sylvestris* var. *mongolica* forests retained a total of 169 OTUs in soil and roots, 603 OTUs in soil specialists, and 216 OTUs in root-associated specialists. At the phylum level, the dominant phyla in soil generalist fungi were Ascomycota (16.71%-41.74%) and Basidiomycota (56.47%-82.37%). With increasing stand age, Ascomycota showed a trend of first decreasing then increasing, while Basidiomycota showed the opposite pattern. Root-associated generalist fungi were dominated by Ascomycota (51.84%-89.92%) and Basidiomycota (9.95%-47.89%). Ascomycota increased with stand age, while Basidiomycota decreased. In generalist fungi, the difference between natural forests and plantations was that natural forests had much higher relative abundance of Basidiomycota than Ascomycota.

Soil specialist fungi were dominated by Ascomycota (46.43%-80.39%), Basidiomycota (9.96%-42.81%), and Mortierellomycota (1.68%-8.42%). Natural forests had a unique dominant fungal group, Mucoromycota (3.23%). With increasing stand age, Basidiomycota showed a trend of first increasing then decreasing, while Mortierellomycota showed the opposite pattern. Root-associated specialist fungi were dominated by Ascomycota (52.71%-76.58%) and Basidiomycota (23.27%-46.20%). Ascomycota showed a trend of first increasing then decreasing with stand age, while Basidiomycota showed the opposite pattern. Overall, generalist fungi had greater abundance of Basidiomycota than Ascomycota, while the opposite was true for specialist fungi.

At the genus level, soil generalist fungi had 7 dominant and common genera, accounting for 75.94%-85.19% of total sequences. Natural forests were dominated by *Tricholoma* and *Suillus*, with *Tricholoma* relative abundance showing a significant increasing trend with stand age ($P<0.05$). Root-associated generalist fungi had 6 dominant and common genera, accounting for 54.25%-73.66% of total sequences. Natural forests were dominated by *Tricholoma*, middle-aged plantations by *Tricholoma* and *Cadophora*, near-mature plantations by *Suillus*, and mature plantations by *Tricholoma*. Compared with natural forests, the relative abundance of *Mycena* in plantations decreased significantly ($P<0.05$), while *Inocybe* and *Cadophora* increased significantly ($P<0.05$). With increasing stand age, *Tricholoma* relative abundance showed a significant increasing trend ($P<0.05$), while *Inocybe* and *Cadophora* decreased significantly ($P<0.05$).

Soil specialist fungi had 8 dominant and common genera, accounting for 43.71%-75.14% of total sequences. Natural forests were dominated by *Penicillium* and *Geminibasidium*, middle-aged plantations had no dominant genus with *Penicillium* having the highest relative abundance, and both near-mature and mature plantations were dominated by *Penicillium*. The relative abundance of *Geminibasidium* in plantations was significantly lower than in natural forests ($P<0.05$). With increasing stand age, *Penicillium* relative abundance in plantations first increased then decreased. Root-associated specialist fungi had 6 dominant and common genera, accounting for 54.25%-84.91% of total sequences. Natural forests were dominated by *Acephala* and *Tricholoma*, middle-aged plantations by *Inocybe*, near-mature plantations by *Acephala*, and mature plantations by *Acephala* and *Chloridium*. The relative abundance of *Acephala* in middle-aged plantations was extremely significantly lower than in natural forests and other plantation age classes ($P<0.01$). The relative abundance of *Tricholoma* in natural forests was significantly higher than in plantations ($P<0.05$).

2.2 Ecological Functions of Generalists and Specialists

Symbiotic trophic fungi accounted for 28.49%-47.21% of soil generalist fungi, with ectomycorrhizal fungi as the dominant ecological functional group, showing a trend of first increasing then decreasing with stand age. Saprotrophic fungi accounted for 17.01%-40.01% of soil specialist fungi. Compared with natural forests, plantations had significantly lower relative abundance of saprotrophic fungi ($P<0.05$), which showed a trend of decreasing first then increasing with stand age. Symbiotic and pathotrophic fungi showed the opposite trend. Symbiotic trophic fungi accounted for 43.25%-54.45% of root-associated specialist fungi, saprotrophic fungi accounted for 1.62%-4.28%, and other trophic fungi accounted for 0.04%-0.93%. The dominant ecological functional group was ectomycorrhizal fungi, which increased with stand age and had higher relative abundance in natural forests than in plantations.

The main difference between generalists and specialists was that specialist fungi had significantly higher relative abundance of saprotrophic fungi than generalists ($P<0.05$), and pathotrophic fungi had the highest relative abundance in soil specialist fungi. Natural forests and mature plantations had similar functional structures, with relative abundance of other trophic fungi exceeding 28.14%-63.63%, and the dominant ecological functional groups were pathotrophic fungi. With increasing stand age, the relative abundance of other trophic fungi increased significantly ($P<0.05$), while the relative abundance of symbiotic trophic fungi decreased significantly ($P<0.05$).

2.3 Correlation Between Generalists/Specialists and Soil Properties

The distribution of soil physicochemical properties in *P. sylvestris* var. *mongolica* forests is shown in Table 2. Soil organic matter and available phosphorus content in natural forests were significantly higher than in plantations ($P<0.05$), while soil water content, pH, total potassium, and available nitrogen were significantly lower than in plantations ($P<0.05$). With increasing stand age, soil organic matter, total phosphorus, available nitrogen, and available phosphorus in plantations increased significantly ($P<0.05$), while pH decreased but not significantly ($P>0.05$).

Mantel test results (Figure 4) showed that the distribution of soil generalist fungi was significantly correlated with soil organic matter ($P<0.01$); soil specialist fungi were significantly correlated with pH ($P<0.05$). Root-associated generalist fungi were significantly correlated with soil organic matter ($P<0.05$) and total potassium ($P<0.01$). Root-associated specialist fungi were extremely significantly correlated with soil organic matter and total potassium ($P<0.01$), significantly correlated with available nitrogen and ammonium nitrogen ($P<0.05$), and also significantly correlated with total nitrogen ($P<0.05$). Soil specialist fungi were significantly correlated with total potassium, available nitrogen, and nitrate nitrogen ($P<0.05$).

RDA analysis of the top five dominant fungal genera with soil physicochemical properties (Figure 5) showed that soil generalist dominant genera *Tricholoma* and *Suillus* were significantly positively correlated with soil organic matter ($P<0.01$). Root-associated generalist dominant genera *Tricholoma* and *Suillus* were significantly positively correlated with total potassium ($P<0.05$). Soil specialist dominant genera *Penicillium*, *Geminibasidium*, and *Suillus* were significantly positively correlated with pH ($P<0.05$). Root-associated specialist dominant genus *Acephala* was significantly negatively correlated with pH ($P<0.05$) and significantly positively correlated with total potassium ($P<0.05$).

3.1 Community Structure and Environmental Response of Generalists and Specialists

In the fungal communities of *P. sylvestris* var. *mongolica* forests in the Hulunbuir Desert, the dominant phyla for both generalists and specialists were Ascomycota and Basidiomycota. Generalists were dominated by Basidiomycota, while specialists were dominated by Ascomycota. This difference may be related to the ecological functions of the two fungal groups: Ascomycota has diverse nutritional modes, can decompose organic matter saprotrophically, and form symbiotic relationships with *P. sylvestris* var. *mongolica* to promote host nutrient absorption, while Basidiomycota are mainly ectomycorrhizal fungi that build mutualistic symbiotic relationships with *P. sylvestris* var. *mongolica* by expanding root absorption area. Previous studies on *Xanthoceras sorbifolium* soil fungi showed that Ascomycota can produce dormant structures to resist harsh sandy environments, while Basidiomycota have broader adaptation ranges to various soil environmental factors. This study found that compared with plantations, natural forests had higher relative abundance of Basidiomycota and ectomycorrhizal fungi in generalist fungal communities, as well as higher soil organic matter and available phosphorus content. This result is similar to findings from studies on subalpine spruce natural forests and plantations.

At the genus level, *Tricholoma* dominated the fungal generalists in both natural forests and plantations, and its relative abundance increased with stand age. Mantel test analysis showed that *Tricholoma* was widely distributed in habitats with high soil organic matter content but was limited in soils with high pH. This distribution pattern may arise because as stand age increases, the ecosystem gradually matures, soil organic matter continuously accumulates, and soil structure and microenvironment become more stable and diversified, providing more suitable survival conditions for *Tricholoma*. Additionally, *Tricholoma* has efficient enzyme systems that can effectively decompose organic matter such as litter that accumulates with stand age. Finally, the well-developed root systems of mature trees form tighter symbiotic relationships with *Tricholoma*, which obtains more photosynthetic products from trees while helping them absorb nutrients and water, promoting its own proliferation.

Soil and root-associated specialist fungi differed greatly in dominant and common genus composition, mainly due to ecological niche differentiation, selective screening by plant roots, and different microbial interactions. Spatially, the open soil environment provides diverse microenvironments for fungal colonization on soil particles, pores, and organic-inorganic interfaces, allowing them to obtain nutrients by decomposing organic matter. In contrast, the relatively closed root environment requires fungi to adapt to plant root tissue environments and depend on host-provided nutrition. Plant roots strictly screen suitable fungal specialists through physical barriers, chemical signals, and symbiotic compatibility. Additionally, in terms of microbial interactions, soil microbial communities are dominated by resource competition, while root-associated microbes tend to form cooperation relationships centered on plant needs. These factors collectively lead to differences in common genus composition.

3.2 Ecological Functional Characteristics of Generalists and Specialists

During long-term evolution, fungi have evolved diverse ecological adaptation strategies and nutritional modes to cope with environmental changes and survival competition, enabling them to efficiently utilize resources, expand niches, and flexibly adapt to environments, thereby enhancing their survival and reproduction capabilities. This study found that generalist fungi and root-associated specialist fungi were dominated by symbiotrophic fungi, while soil specialist fungi were dominated by saprotrophic and pathotrophic fungi. Symbiotrophic fungi form mutualistic symbioses with plant roots, obtaining photosynthetic products from hosts while enhancing plant mineral nutrient and water absorption efficiency through extensive hyphal networks. Saprotrophic fungi act as key decomposers, playing central roles in soil organic matter transformation and nutrient cycling. Pathotrophic fungi infect host organisms, extracting nutrients from host cells to meet their own growth and reproduction needs.

Overall, specialist fungi had higher relative abundance of saprotrophic fungi than generalists, particularly in soil specialist fungi, mainly because the soil environment provides richer organic matter and pathogenic hosts, with functions focusing on organic matter decomposition and host infection rather than mutualistic relationships with plants. Compared with natural forests, plantations had lower saprotrophic fungal abundance, showing a dynamic pattern of first decreasing then increasing with stand age. This trend may occur because early-stage plantations are dominated by single tree species, providing limited types and quantities of organic substrates that cannot meet the diverse needs of saprotrophic fungi. Additionally, soil disturbance during afforestation, such as tillage and fertilization, destroys original soil ecological structure and microbial community stability. Since saprotrophic fungi are sensitive to soil environment, changes in soil structure and microbial communities make it difficult for them to adapt initially, leading to decreased abundance. With increasing stand age, litter accumulation increases, soil microbial communities stabilize, ecosystem diversity improves, providing richer nutrient sources for saprotrophic fungi and promoting their recovery. However, due to lower overall ecosystem complexity and stability in plantations compared with natural forests, saprotrophic fungal abundance remains lower.

The study also found that the proportion of symbiotrophic fungi in root-associated generalists gradually decreased with stand age. This may be because mature trees have well-developed root systems with enhanced autonomous water and nutrient absorption capacity, reducing their dependence on symbiotrophic fungi. Fungi with different nutritional modes showed clear distribution differences in soil and roots. When the proportion of saprotrophic and pathotrophic fungi increases, tree stress resistance continuously declines and disease risk increases. Pathotrophic fungi that are pathogenic to hosts may transform into saprotrophic fungi, and since endophytes have weaker defense capabilities against saprotrophic fungi than against pathotrophic fungi, host recruitment of endophytes decreases. Based on this, we speculate that *P. sylvestris* var. *mongolica* in plantations is more susceptible to harmful fungal infection. As forest community succession progresses, the complexity and stability of soil and root-associated fungal communities increase, organic matter accumulation provides abundant nutrients for fungi, niche diversification enhances interactions, and improved environmental conditions facilitate fungal growth. Simultaneously, selection pressure adaptation makes community structure more stable and enhances adaptability to environmental changes.

4 Conclusion

Generalist and specialist fungi in *P. sylvestris* var. *mongolica* forests of the Hulunbuir Desert show significant ecological differentiation. In terms of community structure, the two functional groups exhibited significant differences. The dominant phyla were Ascomycota and Basidiomycota for both groups. Generalists were dominated by *Tricholoma*, *Inocybe*, and *Suillus*, while soil specialists were dominated by *Penicillium* and root-associated specialists by *Acephala*. These groups showed varying degrees of significant correlation with soil physicochemical properties, among which soil organic matter, available nitrogen, total nitrogen, and total potassium were key environmental factors driving community structure changes. From an ecological function perspective, during *P. sylvestris* var. *mongolica* growth, generalists primarily promoted nutrient absorption and stress resistance improvement in *P. sylvestris* var. *mongolica* by establishing symbiotic relationships with hosts, while simultaneously improving rhizosphere microenvironments. Specialists participated in organic matter decomposition through saprotrophic nutrition, enhancing system material cycling efficiency. Notably, with increasing stand age, the two functional groups showed a synergistic enrichment pattern: symbiotrophic fungi supported rapid early tree growth, while saprotrophic fungi maintained ecosystem stability in mature stands by promoting organic matter transformation. This functional complementary pattern reflects the adaptive succession characteristics of microbial communities during *P. sylvestris* var. *mongolica* forest development from establishment to maturity. Based on these results, regulating the niche allocation of these two fungal types to fully utilize the complementary functions of generalists in nutrient absorption and specialists in material decomposition can provide a theoretical basis for microbial regulation-based sustainable forest management.

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