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Community Structure and Maintenance Mechanisms of Ectomycorrhizal Fungi of Four Coniferous Species in Eastern Inner Mongolia

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Abstract

In this study, we focused on four major coniferous species in the eastern part of Inner Mongolia, namely *Larix gmelinii* var. *principis-rupprechtii* (Mayr) Pilg., *Larix gmelinii* (Rupr.) Kuzen., *Pinus tabuliformis* Carrière and *Pinus sylvestris* var. *mongolica* Litv. and carried out a systematic study on their ectomycorrhiae (EM) fungi. The present study was based on high-throughput sequencing. Based on the high-throughput sequencing data, analyzed by bioinformatics and statistical methods, the results showed that (1) a total of 150 operational taxonomic units (OTUs) were obtained, which belonged to 26 evolutionary branches of Basidiomycota and Ascomycota, respectively. Among them, *Tricholoma*, *Tomentella-thelephora*, *Suillus-rhizopogon*, *Wilcoxina*, *Piloderma*, *Pustularia*, *Hygrophorus*, *Sebacina* and *Amphinematylospora* are the EM fungi shared by four conifer species. (2) The species diversity and community composition of EM fungi differed significantly among tree species and sample plots, while soil total nitrogen (N) content and nitrogen/phosphorus (N/P) ratio were the main factors affecting community structure. (3) The Neutral Community Model (NCM) and β-Nearest Taxon Index (β-NTI) showed that stochastic processes dominated the construction of EM fungal communities. The results of this study revealed the geographical distribution pattern and maintenance mechanisms of EM fungal communities of four coniferous species in the eastern part of Inner Mongolia, which provides a scientific basis for the restoration practice of disturbed ecosystems and the sustainable development of the regional economy.

Keywords: coniferous species; ectomycorrhizal fungi; community structure; stochastic processes

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1. Introduction

Ectomycorrhizal (EM) fungi play a crucial role in forest ecosystems, particularly in the growth and nutrient uptake of coniferous tree species. They form symbiotic relationships with plant root systems, helping host plants obtain nutrients and water from the soil while receiving carbon sources from the plants [1]. Additionally, EM fungi significantly enhance host plants' resistance to environmental stresses through multiple physiological and biochemical mechanisms. Regarding drought tolerance, EM fungi mitigate oxidative damage and maintain cellular turgor pressure by regulating stomatal conductance,

promoting photosynthesis, activating antioxidant enzyme systems, and accumulating osmoprotectants [2]. Under salt stress, EM fungi mitigate damage by regulating ion uptake, reducing Na^+ accumulation, and enhancing osmotic regulation capacity [3]. Salt stress is a major abiotic stress factor affecting plant growth and productivity, and EM fungi can help plants adapt to this stress [4]. In heavy metal-contaminated environments, mycelium reduces the biotoxicity of heavy metals and their uptake by plants through adsorption, immobilization, formation of mycelium sheaths, and enhanced nutrient absorption. EM fungi enhance plant tolerance to heavy metal stress, with extracellular chelation serving as the primary mechanism for heavy metal tolerance. Studies have also revealed that EM fungi reduce heavy metal accumulation in plant aboveground parts [5]. EM fungi can also induce plant systemic immunity, competing with pathogens for resources and space, altering the rhizosphere microbial community, and producing antimicrobial substances to enhance resistance against pathogens. This induced systemic immunity resembles the immune response triggered by beneficial microorganisms, helping plants resist attacks from multiple pathogens [6,7]. The interaction between plants and EM fungi is a complex process involving the synergistic action of multiple physiological and biochemical mechanisms, enabling plants to better adapt to various environmental stresses [8]. The structure and maintenance mechanisms of EM fungal communities are influenced by various factors, including climate, soil type, ecological drift, and dispersal limitations [9–12]. Therefore, studying the EM fungal community structure of specific regions and tree species is of great significance for understanding the functions and succession of forest ecosystems.

Understanding the mechanisms underlying microbial community assembly is crucial for comprehending the maintenance of biodiversity and predicting its response to global change. The maintenance of EM fungal communities involves various ecological processes, including deterministic and stochastic processes [13]. The primary factors influencing deterministic processes include abiotic factors (such as climatic conditions and soil physical and chemical properties) and biotic factors (such as host plant specificity) [9], while stochastic processes include ecological drift, dispersal limitations, and EM fungal interspecific interactions (such as competitive exclusion) [10–12]. Ecological drift refers to changes in species abundance caused by random birth, death, and migration events. In EM fungal communities, ecological drift may lead to certain species becoming more common or rare without explicit environmental selection [14]. For example, in *sorghum* systems under drought stress, studies have shown that fungal community assembly is influenced by random forces, particularly during early developmental stages and periods of drought stress [14]. Dispersal limitation refers to the inability of species to reach all potential habitats due to limitations in their dispersal capacity. For EM fungi, spore dispersal may be constrained by factors such as distance, wind, and animal activity, thereby influencing community composition [15]. Studies have shown that at the regional scale, EM fungal community composition is influenced by dispersal limitations, meaning that communities farther apart geographically exhibit lower similarity [16]. However, the specific mechanisms and their interactions in shaping the relative importance of EM fungal communities in different ecosystems require further research to clarify.

The eastern region of Inner Mongolia possesses unique climatic conditions and soil types, providing a special environmental backdrop for studying the diversity and community structure of EM fungi. Studies targeting *Pinus sylvestris* var. *mongolica* in Horqin Sandy Land of Inner Mongolia [17], *Picea mongolica* in the Baiyin'ao Bao Nature Reserve [18], *Pinus sylvestris* var. *mongolica* in Honghuaerji [19], *Larix principis-rupprechtii* in Heili River and Helan Mountain Nature Reserve [20] and *Larix gemelinii Rupr.* in the Great Khingan Mountains [21] have also yielded some results, but these studies were conducted only at the local scale. For the EM fungal communities of key coniferous tree species in this

region (such as *Larix gmelinii* var. *principis-rupprechtii* (Mayr) Pilg., *Larix gmelinii* (Rupr.) Kuzen., *Pinus tabuliformis* Carrière and *Pinus sylvestris* var. *mongolica* Litv.), there is a lack of in-depth research on the systematic structure, geographical distribution patterns, ecological construction processes, and the comprehensive influence of environmental factors at the regional scale.

Given this, this study focuses on the four coniferous tree species mentioned above in the eastern region of Inner Mongolia, utilizing high-throughput sequencing technology combined with bioinformatics and statistical methods, with the aim of: (1) investigating the diversity and community composition of EM fungi in the four coniferous tree species; (2) analyzing the correlation between soil physical and chemical properties, climatic conditions, and EM fungal community structure; identify key influencing factors and their interrelationships; (3) reveal the geographical distribution patterns and maintenance mechanisms of EM fungal communities (i.e., the relative contributions of deterministic and random processes in community assembly). The research findings can provide a scientific basis for ecosystem restoration and regional economic development practices and serve as a reference for studies on the assembly mechanisms and functions of EM fungal communities in different host plants.

2. Materials and Methods

2.1. Study Sites and Sample Collection

The study was conducted in Chifeng City, Inner Mongolia Autonomous Region, with four study sites established: Huanggangliang (E 117°31′, N 43°34′), Heilihé (E 118°27′, N 41°21′), Saihanwula (E 118°14, N 44°17′), and Wangyedian (E 118°10′, N 41°45′). The study area is primarily characterized by hilly and highland terraces, with a northwest-high, southeast-low topography and an average elevation of 1300–2000 m. In these areas, four conifer species serve as the primary woody EM host plants, alongside other EM hosts such as Betulaceae, Fagaceae, and Salicaceae species. Climate information for the sampling sites was extracted from the World Clim dataset [22], revealing that the selected sites are located in semi-arid and cold-temperate climate zones, with mean annual temperatures (MAT) ranging from −0.3 to 5.5 °C and mean annual precipitation (MAP) ranging from 374 to 483 mm in Table S1.

This study selected four secondary forests with an average age of 20–50 years, characterized by dense canopy closure and a thick understory layer of shrubs and saplings, all in a vigorous growth phase. Sampling was completed in July 2021. Due to climatic gradient constraints, *Larix gmelinii* var. *principis-rupprechtii* samples were collected from four sites, while samples for the other three conifer species originated from only two sites (Table S1). At each site, 3–7 individual trees were selected from each conifer species (with spacing between trees > 10 m). Fine roots were collected using the drag-and-pull method along three directions of the main trunk, with 1–3 fine roots collected per tree. A total of 12 root samples were collected from *Larix gmelinii* var. *principis-rupprechtii,* 11 from *Larix gmelinii*, 14 from *Pinus tabulaeformis*, and 14 from *Pinus sylvestris* var. *mongolica*. Subsequently, samples were stored in ice packs and immediately transported to the laboratory for cryopreservation at −80 °C. Concurrently with fine root sampling, soil samples (approximately 200 g) were collected from the rhizosphere of each individual, air-dried, and sieved (through a 2 mm mesh) for physicochemical analysis.

2.2. Soil Properties Analysis

The soil physical and chemical properties measured include total nitrogen (N), total phosphorus (P), total calcium (Ca), total magnesium (Mg), and the nitrogen/phosphorus ratio (N/P). The specific operations involved are outlined as follows: N content was de-

termined by the semi-micro Kjeldahl method, P content was determined using a Thermo Fisher Scientific iCAP 6300 (Cambridge, UK) inductively coupled plasma emission spectrometer, the N/P ratio was calculated, and Ca and Mg content were determined using an Optima 8000 PerkinElmer (Shelton, CT, USA) inductively coupled plasma emission spectrometer in Table S1.

2.3. DNA Extraction, PCR, and MiSeq Sequencing

In the laboratory setting, root samples were meticulously washed with tap water to ensure their cleanliness and integrity. Subsequently, intact root samples were meticulously divided into segments measuring approximately 2 cm in length. The selection of intact mycorrhizae for analysis was conducted at random, with 200 slices from each plant selected for examination. Morphological characteristics such as shape, color, dendrites, fungal hyphae, surface texture, transparency, and the presence or absence of vesicles were documented. The 10,200 mycorrhizae samples were then preserved in a refrigerator set at −80 °C. The extraction of DNA was performed using a modified cetyltrimethylammonium bromide (CTAB) method [23]. and the ITS2 region was amplified by polymerase chain reaction (PCR) using a two-step method [24–26]. First, the first round of PCR was performed with the fungus-specific primers ITS1f (5′-CTTGGTCATTTAGAGGAAGTAA-3′) and ITS4 (5′-TCCTCCCCTCCTTAGAGGAAGTAA-3′) utilized as primers to amplify the entire ITS region, and subsequently, fITS7 (5′-GTGARTCATCGAATCTTTG-3′) and ITS4 with base tag sequences were employed as primers to amplify the fungal ITS2 region. The purified samples were then subjected to sequencing on the Illumina Miseq double-end sequencing platform at the Chengdu Institute of Biology, Chinese Academy of Sciences.

2.4. Bioinformatic Analysis

Initially, low-quality sequences were filtered using the QIIME platform (v.v.1.9.0) [27]. Subsequently, sequences in the ITS2 region of the quality control data were extracted using ITSx software (v. 1.0.3) [28], and sequences in the Unified Fungal Species Database [29] were referenced. Chimeric sequences in the ITS2 region were examined and removed using Usearch v11. The UPARSE pipeline was then used to classify the non-chimeric ITS2 region sequences into OTUs according to 97% sequence similarity [30]. Then, the representative sequences (with the highest number of sequences) of each OTU were classified into OTUs using the National Center for Biotechnology Information (NCBI) and UNITE (v. 8.3) reference databases for the basic local alignment search tool (BLAST) (v. 2.2.31+) [31]. Each OTU was identified to the best taxonomic position by referring to the taxonomic criteria of Tedersoo et al. [32], and the EM fungi were identified according to the method of Kõljalg et al. [29]. The raw sequence data reported in this paper have been deposited in the Genome Sequence Archive in the National Genomics Data Center, China National Center for Bioinformation/Beijing Institute of Genomics, Chinese Academy of Sciences (GSA: CRA028857) which are publicly accessible at CRA028857.

2.5. Statistical Analysis

The classification of EM fungi was performed using R-3.6.1 [33], and alpha diversity metrics, including Chao1 and Shannon indices, were computed with the vegan package [34]. The Chao1 index serves as an estimator for the total number of operational taxonomic units (OTUs) based on the observed OTU count. In contrast, the Shannon index reflects the diversity of OTUs across various samples. This study employed two approaches—cmdscale and metaMDS—to integrate Principal Coordinate Analysis (PCoA) and Non-Metric Multi-Dimensional Scaling (NMDS), avoiding metric-based measurements. By utilizing the ordiellipse function, the 95% confidence intervals for EM fungal communities associated with different coniferous tree species were determined. Furthermore, the envfit command

was applied to analyze the influence of geographical locations, climate, and soil factors, thereby identifying the primary drivers shaping the structure of the EM fungal community. The adonis command was used to validate these findings through Permutational Multivariate Analysis of Variance (PERMANOVA) analysis. To investigate the assembly mechanisms of the EM fungal community, the β-Nearest Taxon Index (βNTI) was adopted. Specifically, the comdistnt function in the picante package [35] was utilized to quantify pairwise phylogenetic turnover among communities based on the β-Mean Nearest Taxon Distance (βMNTD). The mntd and ses.mntd functions were employed to calculate the Mean Nearest Taxon Distance (MNTD) and the Beta Taxonomic Index (BTI). A value of $|\beta NTI| > 2$ indicates that the phylogenetic turnover rate significantly exceeds (or falls below) the spatial distribution expectation, implying a deterministic process dominates. Conversely, when $|\beta NTI| < 2$, no significant difference exists between the phylogenetic turnover rate and the expected spatial distribution, suggesting stochastic processes play a more significant role in community assembly. Additionally, Sloan's Neutral Community Model (NCM) [36] was applied to assess the assembly process by correlating the migration rate "m" of individual fungal OTUs with their occurrence frequency and abundance (after logarithmic transformation). All results were visualized using ggplot2.

3. Results

3.1. Fungal Database Summary

A total of 626 OTUs were identified from 596,723 sequences. Among them, 200 OTUs were identified as EM fungi. After sample standardization, 150 OTUs were finally obtained for subsequent analysis. These 150 OTUs belonged to 2 phyla, 4 classes, 4 orders, 10 families and 29 genera. Among them, the dominant genera were *Tricholoma*, *Tomentella* and *Suillus*, accounting for 18%, 17% and 14% of the total sequences, respectively (Figure 1).

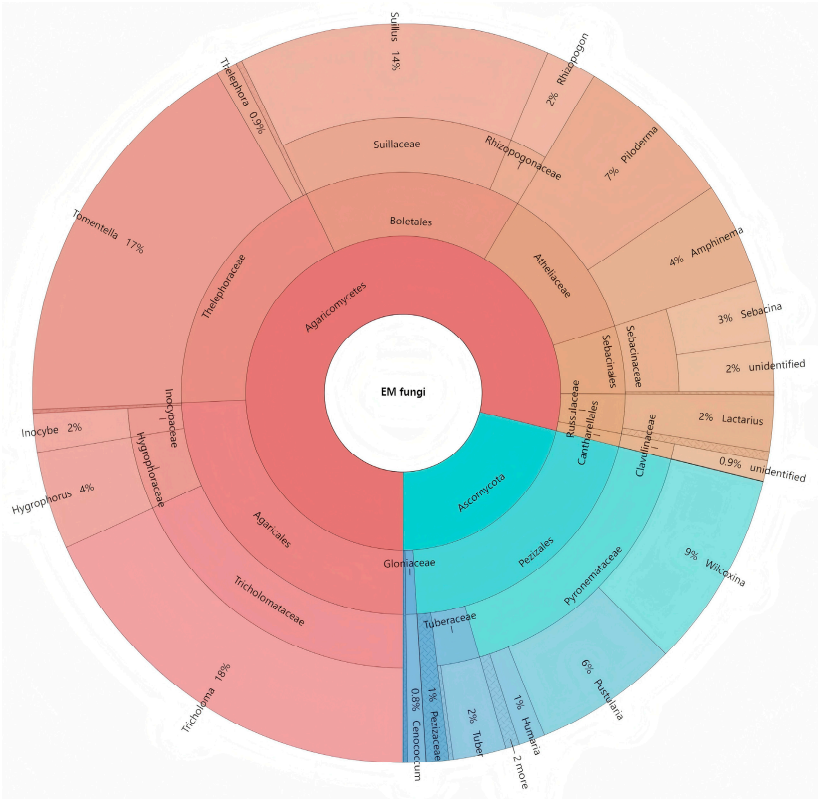

Figure 1. Krona chart of taxonomic affiliation of ectomycorrhizal fungi and their relative abundances. Inner circles represent higher taxonomic ranks and more detailed taxonomic ranks are presented in outer circles.

The analysis revealed that 72% of phylogenetic lineages belonged to Basidiomycota, while the remaining 28% were affiliated with Ascomycota. Nine dominant ectomycorrhizal (EM) fungal genera were shared among the four coniferous species: *Tricholoma*, *Tomentella/thelephora*, *Suillus/rhizopogon*, *Wilcoxina*, *Piloderma*, *Pustularia*, *Hygrophorus*, *Sebacina*, and *Amphinema/tylospora* (Figure 2). Notably, host-specific distribution patterns emerged: *Tricholoma* exhibited its highest relative abundance in *Larix gmelinii* but the lowest in *Pinus tabuliformis*. *Tomentella/thelephora* demonstrated peak abundance in *Larix principis-rupprechtii* while showing minimal presence in *L. gmelinii*. *Suillus/rhizopogon* predominated in *P. tabuliformis* but was least represented in *L. principis-rupprechtii*. *Wilcoxina* reached maximum levels in *Pinus sylvestris* var. *mongolica* but minimum levels in *L. gmelinii*. *Piloderma* displayed contrasting abundance patterns between *L. gmelinii* (highest) and *P. tabuliformis* (lowest). *Pustularia* showed preferential colonization of *P. sylvestris* var. *mongolica* over *P. tabuliformis*. *Hygrophorus* exhibited host affinity toward *L. principis-rupprechtii* rather than *P. tabuliformis*. *Sebacina* and *Amphinema/tylospora* both demonstrated significant preference for *P. tabuliformis*, while registering minimal abundance in *L. gmelinii*. These findings collectively indicate substantial interspecific variation in EM fungal community composition across host tree species.

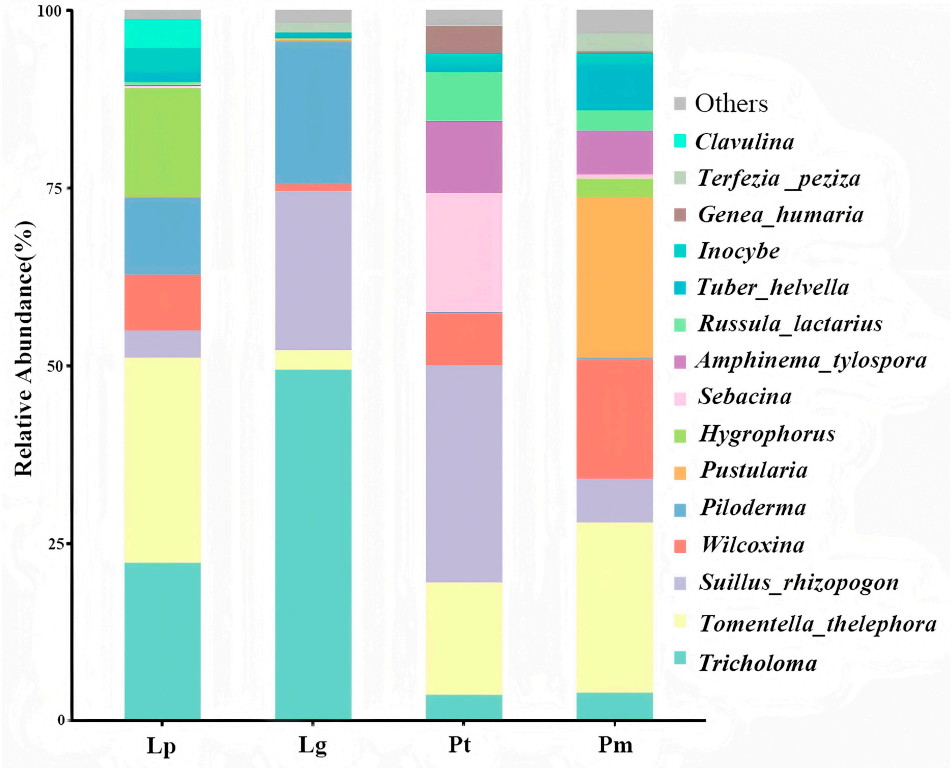

Figure 2. Species composition of root EM fungi of four conifer species. Note: Lp, *Larix gmelinii* var. *principis-rupprechtii* (Mayr) Pilg. Lg, *Larix gmelinii* (Rupr.) Kuzen. Pt, *Pinus tabuliformis* Carrière Pm, *Pinus sylvestris* var. *mongolica* Litv.

3.2. Diversity of EM Fungi in Four Coniferous Species

The species accumulation curves demonstrated that ectomycorrhizal (EM) fungal diversity associated with roots of four coniferous species failed to reach plateau, indicating that additional sampling would yield new EM fungal taxa. Both Shannon and Chao1 indices revealed distinct EM fungal community compositions among the four coniferous species (Figure 3). Significant interspecific differences in EM fungal diversity were observed, with particularly pronounced disparities between *Pinus tabuliformis* and *Larix gmelinii* ($p < 0.001$), and statistically significant differences between *P. tabuliformis* and *Larix principis-*

rupprechtii ($p < 0.05$). Spatial heterogeneity analysis showed significant differences in EM fungal diversity between three sampling sites of *L. principis-rupprechtii* (Saihanwula vs. Huangganglang, and Saihanwula vs. Wangyezheng; $p < 0.05$). Similarly, notable differences emerged between two sampling locations of *L. gmelinii* (Huangganglang vs. Saihanwula; $p < 0.05$).

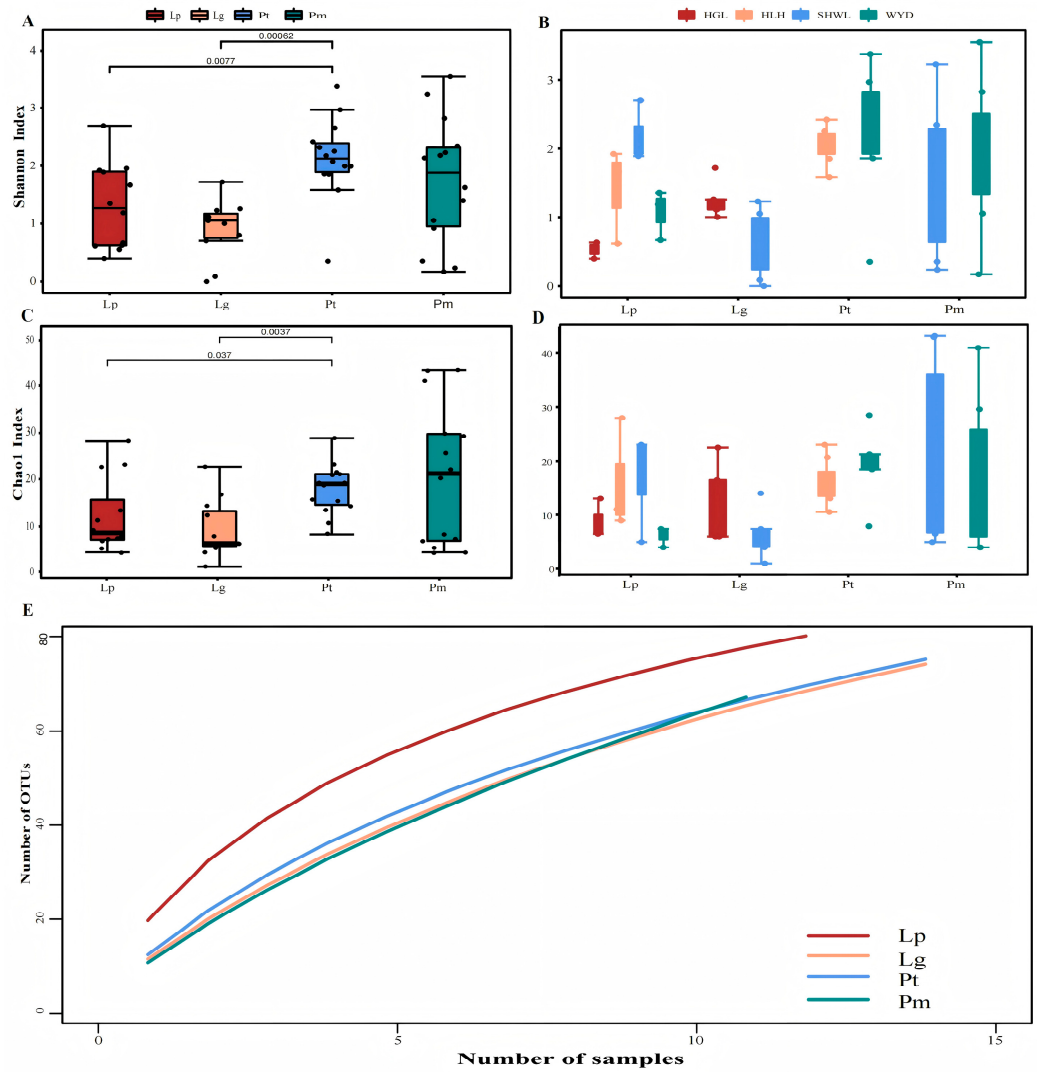

Figure 3. Differences between two species were tested according to wilcox.test. Cumulative curves (**E**) of EM fungi Shannon indexes (**A**,**B**), Chao1 indexes (**C**,**D**) and operational taxonomic units (OTUs) of four conifer species. Note: HGL, Huangganglang. HLH, Heilihe. SHWL, Saihanwula. WYD, Wangyedian. Lp, *Larix gmelinii* var. *principis-rupprechtii* (Mayr) Pilg. Lg, *Larix gmelinii* (Rupr.) Kuzen. Pt, *Pinus tabuliformis* Carrière Pm, *Pinus sylvestris* var. *mongolica* Litv.

In this study, we conducted PCoA and NMDS ordination analyses to investigate the beta diversity of EM fungi associated with root systems of four coniferous species (Figure 4). The PCoA results revealed that the first principal coordinate explained 29.97% of variance, while the second accounted for 16.76%. Significant differentiation was detected both among tree species (Adonis test: R2 = 0.112, $p < 0.001$) and across sampling sites (Adonis test: R2 = 0.115, $p < 0.001$). NMDS ordination combined with envfit analysis further identified soil nitrogen (N) content and N/P ratio as key determinants governing the compositional variation in EM fungal communities in coniferous root systems.

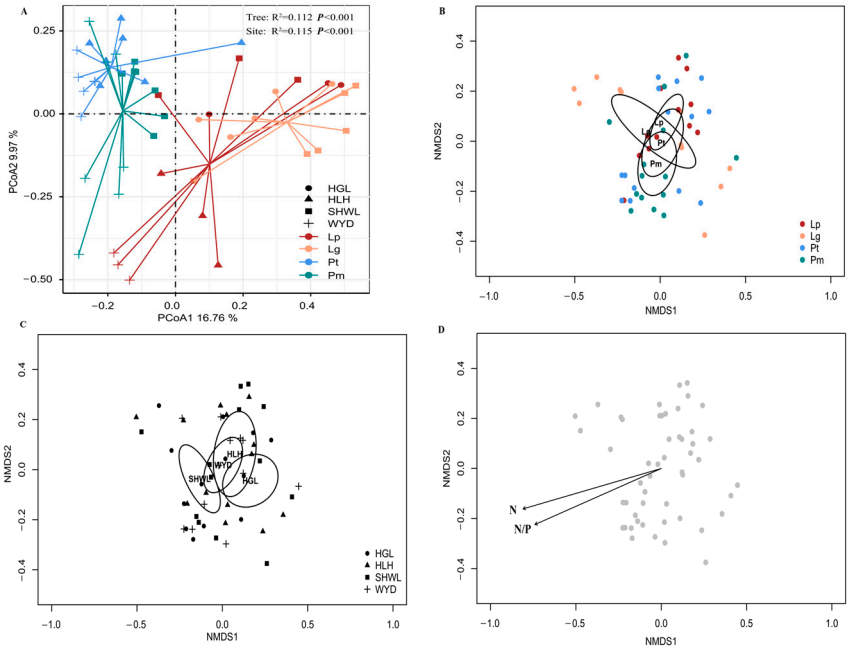

Figure 4. PCoA (**A**) and NMDS (**B**,**C**) ordination analyses of differences between four conifer EM fungal species and sample sites. Ellipses represent 95% confidence intervals around each site centroid. Soil variables conform to the NMDS ranking (**D**). N, total nitrogen content, N/P, nitrogen to phosphorus ratio. Note: HGL, Huanggangliang. HLH, Heilihe. SHWL, Saihanwula. WYD, Wangyedian. Lp, *Larix gmelinii* var. *principis-rupprechtii* (Mayr) Pilg. Lg, *Larix gmelinii* (Rupr.) Kuzen. Pt, *Pinus tabuliformis* Carrière Pm, *Pinus sylvestris* var. *mongolica* Litv.

3.3. Ecological Process Analysis of EM Fungi in Four Conifer Species

This study used βNTI to assess the ecological processes driving EM fungal community assembly. Most βNTI values ranged between −2 and 2 (Figure 5A), with only 3.5% of cases exhibiting βNTI values exceeding 2, indicating that stochastic processes dominated. Consistent with these findings, NCM analysis further confirmed that community structure was primarily shaped by stochastic mechanisms (Figure 5B).

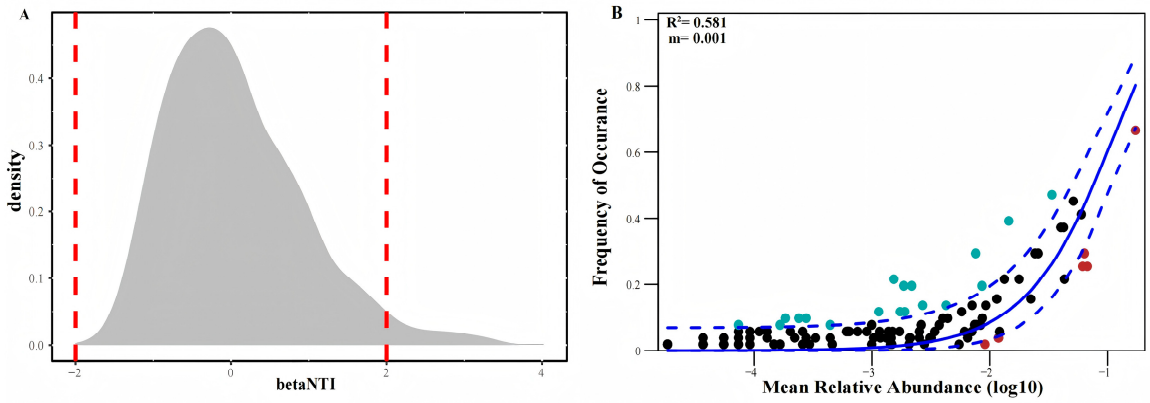

Figure 5. βNTI of fungal OTUs (**A**) and NCM Index (**B**). Dashed red lines indicate the critical values for βNTI, specifically βNTI = −2 and βNTI = 2. Solid blue line represents the predicted occurrence frequency, and dashed blue lines represent 95% confidence intervals around the model prediction. Black dots represent the relationship between the frequency of occurrence and the mean relative abundance (log10 transformed) of microbial communities in different samples. Light blue and red dots indicate the OTUs that occur more and less frequently than given by the model; R2 indicates the fit to the neutral model; m indicates immigration rate.

4. Conclusions

This study indicates that total nitrogen content and the N/P ratio are key soil factors influencing the structure of EM fungal communities. First, nitrogen content directly participates in metabolic synthesis and energy cycling within fungi [37]. High-nitrogen environments typically favor the survival and competitive advantage of fungal groups with efficient nitrogen uptake capabilities (e.g., certain Basidiomycota species) [38]. Second, the N/P ratio reflects soil nutrient balance. Imbalanced N/P ratios may induce host trees to alter carbon allocation strategies, thereby indirectly influencing the types of fungi with which they form symbiosis [39]. This study aligns with findings by Dong Peng et al. [40] in Hulunbuir sandy larch forests, both emphasizing the dominant role of total nitrogen and N/P ratios. However, other research indicates that available nitrogen (rather than total nitrogen) is the primary driver of EM fungal community dynamics [41]. We hypothesize that these discrepancies may stem from differences in nitrogen availability and forms due to varying parent materials, soil formation processes, and organic matter content. For instance, faster leaching of available nitrogen in sandy soils may amplify its influence on community assembly [42,43]. Furthermore, although previous studies have identified mean annual temperature (MAT) as a significant climatic factor influencing EM fungal communities [44–46], this study did not detect a significant effect of MAT. This is likely because all four sampling sites are located within a temperate semi-arid zone with relatively small climatic gradient variations, where temperature variability is insufficient to elicit significant community responses. In summary, soil properties collectively shape EM fungal community structure through multiple pathways, including direct nutrient supply, modification of the soil microenvironment, and interactions with hosts.

Clustering of OTUs from four conifer species and EM fungal species composition maps reveal shared dominant EM fungal groups (e.g., *Tricholoma*, *Tomentella-thelephora*) performing key ecological functions. *Tricholoma* promotes nitrogen and phosphorus uptake while enhancing host stress resistance through symbiosis with plant roots [47–51]; *Tomentella-thelephora* decomposes organic matter, participates in carbon and nitrogen cycling, and maintains ecosystem material flow and stability [49,52,53]. The conservation of host plant phylogenetic niches and variations in root exudates significantly influence EM fungal colonization and community composition [41,44,54,55]. The dominant group composition identified in this study differs from previous research [56–58], potentially due to host specificity or regional climate-shaped fungal species pools. Further functional genomics and field control experiments are needed to elucidate their ecological roles.

Shannon index and Chao1 index analyses revealed significant differences in the α diversity of EM fungi among the four conifer species, consistent with previous studies [18–20,44]. These α-diversity differences hold significant ecological implications: EM fungal communities with high α diversity decompose organic matter more efficiently, promote nutrient cycling, and contribute to maintaining ecosystem health and balance [49–51]. β In diversity, PCoA and NMDS sequencing combined with the PERMANOVA test showed that EM fungal communities differed significantly among tree species and locations. This is consistent with the results of previous studies on plants in the Salicaceae, Betulaceae, and Fagaceae [59–61].

The low NCM analysis m value (0.001) and βNTI values falling within the range of −2 to 2 indicate that random processes dominate. One perspective suggests that spatial distance constitutes a barrier to the dispersal of fungal progeny (e.g., fruiting bodies, spores, and mycelium) [32]. Simultaneously, variations in dispersal capacity among fungal species may lead to changes in fungal community composition due to a pioneer effect, demonstrating that pioneer fungi often exhibit a more pronounced advantage in competing for habitat space and resource utilization [62]. Although studies indicate that the mechanisms govern-

ing bacterial and fungal community assembly differ across soil types [12], some research highlights deterministic processes as dominant in fungal community formation [63], while others emphasize the importance of stochastic processes [64,65]. These discrepancies may relate to environmental conditions, plant species, and interactions with other microbial groups within the study areas. In tropical forests, fungal community composition exhibits high spatial and temporal dynamics, with stochastic processes playing a significant role in community assembly [66,67]. In drought-stressed agricultural fields, fungal community assembly is also influenced by stochastic processes [68]. Furthermore, interactions between fungi and other microorganisms affect community assembly. For instance, fungal networks can influence bacterial dispersal and community assembly [69]. Within cheese rind microbial communities, bacteria utilize physical networks formed by fungi for dispersal, and such interactions can shape microbial community structure [69]. Collectively, these findings indicate that stochastic processes significantly influence EM fungal community structure. Future research should further explore the interactions between deterministic and stochastic processes and how they jointly affect EM fungal community assembly.

Combining the results of this study with those of previous studies, it can be seen that both deterministic and stochastic factors play a key role in the construction of EM fungal communities in a specific region of eastern Inner Mongolia, where four coniferous species coexist, but stochastic factors play a dominant role. In this study, soil characteristics were more influential than climatic conditions and geographic distance in terms of abiotic factors influencing the structure of EM fungal communities. This conclusion differs from previous research findings. We speculate that this may be related to ecological drift and random processes that generate diversity, but this needs to be investigated in our future research.

This study acknowledges two potential limitations. First, despite extensive sampling, the species accumulation curves indicated that ectomycorrhizal fungal diversity did not reach an asymptote, suggesting that additional sampling may reveal further taxonomic diversity. Second, the relatively narrow climatic gradient across the four sampling sites may have constrained our ability to fully assess the influence of climate variables on community assembly. Future studies incorporating broader climatic gradients and intensified sampling efforts would enhance the comprehensiveness of these findings.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f16091459/s1, Table S1: Information on geographic coordinate, climatic and soil variables in this study.

Author Contributions: Conceptualization, Y.F., F.L. and J.L. (Jinyan Li); methodology, Y.F. and J.L. (Jinyan Li); software, Y.F. and J.L. (Jinyan Li); validation, J.L. (Jinyan Li) and Z.Y.; formal analysis, Y.F. and J.L. (Jinyan Li); investigation, J.L. (Jinyan Li) Z.Y., X.L., L.W. and J.L. (Jiani Lu); resources, Y.F.; data curation, Y.F. and J.L. (Jinyan Li); writing—original draft preparation, J.L. (Jinyan Li).; writing—review and editing, Y.F. and F.L.; visualization, J.L. (Jinyan Li); supervision, Y.F. and J.L. (Jinyan Li); project administration, Y.F. and J.L. (Jinyan Li); funding acquisition, Y.F. and F.L. All authors have read and agreed to the published version of the manuscript.

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Abbreviations

The following abbreviations are used in this manuscript:

EM	Ectomycorrhiae
OTUs	operational taxonomic units
NCM	Neutral Community Model
β-NTI	β-Nearest Taxon Index
MAT	mean annual temperatures
MAP	mean annual precipitation
CTAB	cetyltrimethylammonium bromide
PCR	polymerase chain reaction
NCBI	National Center for Biotechnology Information
BLAST	basic local alignment search tool
PCoA	Principal Coordinate Analysis
NMDS	Non-Metric Multi-Dimensional Scaling
PERMANOVA	Permutational Multivariate Analysis of Variance
βMNTD	β-Mean Nearest Taxon Distance
MNTD	Mean Nearest Taxon Distance
BTI	Beta Taxonomic Index

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