

Effects of close-to-nature management of Plantation on the structure and ecological functions of different habitat specificity taxa of soil microorganisms

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Research Article

Keywords: Habitat specificity, Soil Microorganisms, Near-Naturalization, Nitrogen Mineralization, Plantation Forests

Posted Date: April 25th, 2022

DOI: <https://doi.org/10.21203/rs.3.rs-1537724/v1>

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Abstract

Aims: To investigate the changes in community structure with different habitat specificity of soil microbial and the differences of effects on soil nitrogen mineralization during the near-naturalization process, as well as to evaluate the effects of planted forest on close-to-nature operations.

Methods: Forest with 65-years succession sequence of near-naturalization was used as research plots in the Baxianshan National Nature Reserve at the eastern foot of Yanshan Mountain in the warm temperate zone in northern China. Three typical stages of near-naturalization, namely, pure *Pinus tabulaeformis* forest, mixed forest and near-natural forest, were set up with natural secondary forest without naturalization as a control. We also classified soil microorganisms into three groups according to the degree of habitat specificity: generalized, neutral and specialized. Soil physicochemical properties, enzyme activities, and rates of nitrogen mineralization processes were measured, and soil fungal and bacterial community structures were analyzed using high-throughput sequencing.

Results: (1) total carbon, organic carbon, total nitrogen, nitrate nitrogen and ammonia nitrogen contents were higher in natural secondary forests than those in near-naturalized stands, while pH, effective phosphorus, total phosphorus and dry matter contents were the highest in the near-natural forest stage. Acid phosphatase and cellulase activities of natural secondary forest soils were significantly higher than that of near-naturalized stands, but dehydrogenase and β -glucosidase activities and the rate of nitrogen mineralization-related processes were the lowest in natural secondary forests, (2) Under the same habitat specificity, the fungal niche width was larger than the bacterial niche width, and increased with the increase of the degree of approaching naturalization, but was significantly smaller than that of natural secondary forests. (3) The effect of near-naturalization on the spatial richness of microbial communities decreased with degree of habitat specificity and showed a temporal decay (the difference in community structure was greater in the early stages than in the later stages). (4) The explanation of community structure by soil physicochemical and enzymatic activities decreased with habitat specificity, pH was the dominant factor affecting the structure of fungal generalized and neutral taxa, urease activity mainly affects fungal specialized taxa, and the distribution of bacterial communities was mainly influenced by the chemical characteristics of soil carbon, nitrogen and phosphorus, (5) The structure of the dominant genera of each habitat-specific group in the natural secondary forest was significantly different from that of the near-naturalized forest, and the abundance distribution of the dominant genera well explained the differences in soil nitrogen mineralization processes.

Conclusion: Generalist taxa of soil microbial were more pronounced to close-to nature development of planted forest. Close-to-nature operations have resulted in positive improvements in both soil nutrients and microbial community structure, but still differed significantly from those in natural forests.

Introduction

Forest ecosystems play key roles in producing primary productivity, regulating nutrient biogeochemical cycling and providing various important ecosystem services (Bolscher et al. 2016, Sasmito et al. 2020). Changes in dominant populations during forest succession can bring about changes in soil microbes and their mediated soil nutrient dynamics (Brock et al. 2020, Luo et al. 2019, Vanderhoof et al. 2021). Some progress has been made on the characteristics and mechanisms of interactions between above-ground communities and below-ground microbes during forest vegetation changes (Morriën et al. 2017, Liu et al. 2008, Liu et al. 2019). However, the variability in the responses of different habitat-specific taxa in the soil microbial communities to changes in forest soil characteristics and the heterogeneity of their contributions to soil ecological functions, as well as the mechanisms, still need to be further explored.

The current rapid increase in the area of plantation forests is in response to the ecological crisis of massive destruction of natural forests and continued decline in ecosystem services (Liu et al. 2018). The cultivation of monoculture plantations has rapidly restored above-ground biomass (Moghaddam. 2014), diversity (Li et al. 2014, Chaudhary et al. 2016, Van et al. 2013) and carbon sequestration capacity of damaged ecosystems. However, the low diversity and stability of forest ecosystems caused by the monoculture of planted forest species, and the disadvantages of excessive density leading to competitive mortality has been gradually coming to light (Zhou et al. 2019). The interruption of nutrient cycling resulted in increasing nutrient deficiencies in the soil (Yu et al. 2019), which was detrimental to the healthy development of forest ecosystems. Therefore, scientific nurturing and management of planted forests will play a positive role in improving the instability of the community structure and the fragility of ecosystem functions. Close-to-nature management is a method of forest management that actively or passively develops planted forest communities into more diverse vegetation communities dominated by native species to improve the diversity and stability of forest ecosystems and promote healthy forest ecosystem recovery (Hou et al. 2021). This approach allows forest stands to produce close to their natural state (Lin et al. 2007, Guo et al. 2006, Mao et al. 2008), thus maximizing the dynamic balance of forest biomes, restoring natural species with artificial assistance, maximizing forest species diversity, improving ecosystem stability and restoring ecosystem functions (Sujii et al. 2017).

The degradation of ecosystems resulting from deforestation and monoculture plantations inevitably lead to soil degradation (Ferraz et al. 2014, Herrmann et al. 2005, Salvati et al. 2015), including both degradation of soil physicochemical properties due to differences in tree species characteristics and management practices, and degradation of soil quality and ecological services due to soil. This includes both degradation of soil physical and chemical properties due to differences in tree species characteristics and management practices, and degradation of soil quality and ecological services due to ecological and biological characteristics (Lal 2015). The former is mainly due to soil nutrient deficiencies caused by slow decomposition rates of apoplast litter and low nutrient return rates in monoculture plantations (Epron et al. 2015), while the latter is induced by changes in the structure and functional groups of soil microorganisms (Mitchell et al. 2016, Raiesi et al. 2015, Lian et al. 2015), especially changes in plant-soil microbial coexistence relationships which have caused imbalances in microflora relationships and even the loss of key functional groups in planted forests (Zechmeister et al.

2015, Liang et al. 2011). It was generally accepted that there were important interactions between below-ground microbial community structure and above-ground plant community composition (Cline et al. 2015). It has been shown that different microbial community structures were distributed under different tree species (Huang et al. 2017, Weand et al. 2010, Templer et al. 2003), and that significant changes in soil microbial communities occurred during the conversion of planted pure forest mixed forest (Huang et al. 2017, Ming et al. 2018). Studies have shown that different ecological factors could also influence or even determine soil microbial community structure, such as soil physicochemical properties (Schweitzer et al. 2008, Zhalina et al. 2015, Rousk et al. 2010a, Wan et al. 2015, You et al. 2014, Fierer et al. 2009), elevation (Zhang et al. 2014) and vegetation type (Geml et al. 2017). The quantity and quality of apoplastic and root secretions were altered during the near-naturalistic succession of planted forests (wang et al. 2018, Malchair et al. 2009), which would shape the soil microbial community by affecting soil physicochemical properties (Huang et al. 2017, Ming et al. 2018). Conversely, changes in microbial community structure influenced basic soil ecological functions and nutrient cycling (Pardo L.H. et al. 2011) such as nutrients that sustained plant productivity through mineralization and competition, which in turn acted as important regulators of plant productivity through vegetation growth and reproduction (van der Heijden et al. 2008), maintaining ecosystem sustainability (Singh et al. 2018).

Habitat-specific differences among species in biomes result from heterogeneity in their adaptability to the environment. Communities often include less diverse and widely distributed rich taxa and more diverse and rare species with specialized distributions (Pedrós et al. 2006, Logares et al. 2015). This heterogeneity of microbial communities in soil ecosystems shapes the diversity and variability of interactions between habitat-specific taxa and soils. At present, most studies on soil microbial communities were only based on the traditional taxonomy of bacteria, fungi, actinomycetes and archaea, or even only one of these taxa, but few studies have been conducted to further differentiate soil microbial according to the degree of their habitat specificity (Zhang et al. 2018). During 65-years of close-to-nature management and restoration of the *P. tabulaeformis* plantation in Baxianshan National Nature Reserve, a successional sequence from *P. tabulaeformis* forest to mixed coniferous forest to near-natural forest was formed, which provided a valuable natural laboratory for studying the interactions between soil microbial communities and soil properties during vegetation restoration through the spatial instead of temporal method. In this study, we classified soil bacteria and fungi into generalized, neutral and specialized taxa according to their distribution of niche width, and investigated their structure and distribution along the near-naturalization gradient in response to soil properties and the differences in the role of different taxa in soil nitrogen mineralization. The findings of the study will help to reveal the interaction mechanisms between the environmental adaptation heterogeneity of soil microorganisms and soil changes during the successional gradient of plantation forests, and will also provide a reliable reference and scientific theoretical guidance for the geotechnical control and sustainable management of plantation forests.

Materials And Methods

Study area description

The study site is located in the Baxianshan National Nature Reserve (117°30'35"-117°36'24"E, 40°7'24"-40°13'53"N, 270-1052 m a.s.l.) at the eastern foot of the Yanshan Mountains in northern China. The reserve has a total area of 1049 hm² and a warm-temperate humid continental monsoon climate. The main vegetation types in the reserve are warm temperate deciduous broad-leaved secondary forests, as well as evergreen coniferous forests and mixed coniferous and broad-leaved forests. The deciduous broad-leaved forest is the regional vegetation type of the reserve, i.e. the natural secondary forest used as a control in this study, while the evergreen coniferous forest and the mixed forest are the successional sequence formed by the near-naturalization of the planted *P. tabulaeformis* forest. The tree layer is dominated by light-loving broad-leaved species, including *Quercus mogolica*, *Q. variabilis*, *Q. dentata*, *Q. aliena* and *Juglans mandshurica*, as well as the artificial coniferous species *P. tabulaeformis*, the shrub layer is dominated by the genera *Lespedeza*, *Magnolia* and *Spiraea*, while the herbaceous layer is dominated by the families of Gramineae and Cyperaceae.

Sample plot setting and soil sampling

Based on the proportion of *P. tabulaeformis* in the tree layer of the community, the near-naturalization sequence of the planted *P. tabulaeformis* forest was divided into three clearly distinguishable development stages: pure *P. tabulaeformis* forest, mixed of deciduous and broad-leaved forest and near-natural forest, where pure *P. tabulaeformis* was a community with more than 90% *P. tabulaeformis* in the tree layer, representing the early stage of the close-to-nature operation, mixed forest with 40%-60% *P. tabulaeformis*, representing the middle stage, and near-natural forest with less than 20% *P. tabulaeformis*, representing the late stage operation. The deciduous broad-leaved zonal vegetation communities, which had not been developed by naturalization, were selected as controls to evaluate the effects of close-to-nature operation, i.e. natural secondary forests. Basic geographical information (Table 1), as well as the names and numbers of tree species in the tree layer, were recorded in a number of 20 m×30 m sample plots in each of the four types of forest, and 0-10 cm topsoil was collected in each sample plot according to the five-point sampling method. The soil samples were mixed thoroughly and divided into two parts, one part was stored in liquid nitrogen for molecular biology extraction assay and the other part was stored at room temperature and brought back to the laboratory for physical and chemical analysis as soon as possible.

Table 1 Basic information of the community quadrats

Quadratats	Stand type	Elevation(m)	Longitu(°)	Latitude(°)	Slope(°)	Aspect	Coverag of arbor layer	proportion of <i>P.tabuliformis</i>	Dominant species of arbor layer
1	Pure forest of <i>P. tabuliformis</i> (P)	701	117.562	40.203	18.4	SW207	0.85	95%	<i>Pinus tabuliformis</i>
2		686	117.562	40.201	3.1	E78	0.85	90%	<i>P. tabuliformis</i>
3		598	117.563	40.196	18.1	SE110	0.90	90%	<i>P. tabuliformis</i>
4	Medium coniferous broadleaved mixed forest (M) (M)	599	117.564	40.196	7.7	S172	0.8	60%	<i>P. tabuliformis</i> , <i>Q. dentata</i> Thumb, <i>Q</i>
5		701	117.562	40.202	23.6	SW208	0.9	55%	<i>P. tabuliformis</i> , <i>Quercus aliena</i> Bl.
6		720	117.551	40.201	12.2	SW220	0.8	60%	<i>P. tabuliformis</i> , <i>Q. aliena</i>
7		608	117.564	40.196	1.9	SW250	0.6	40%	<i>P. tabuliformis</i> , <i>Q. dentata</i> . <i>Variabilis</i> Blume
8	Near natural forest (NNF)	825	117.557	40.204	18	SE154	0.7	15%	<i>Q. aliena</i> , <i>Q. variabilis</i> , <i>P. tabuliformis</i>
9		817	117.556	40.204	32.3	SW214	0.7	15%	<i>Q. aliena</i> , <i>P. tabuliformis</i> , <i>Q. variabilis</i> ,
10		806	117.558	40.212	21.9	SW206	0.6	20%	<i>Q. variabilis</i> , <i>Evodia dahiellii</i> (Benn) Hemsl. <i>P. tabuliformis</i>
11		585	117.563	40.196	6.5	SE144	0.6	20%	<i>Q. dentata</i> , <i>Q. aliena</i> , <i>P. tabuliformis</i>
12		510	117.556	40.190	20.8	SE115	0.8	15%	<i>Q. aliena</i> , <i>Q. variabilis</i> , <i>P. tabuliformis</i>
13		504	117.556	40.189	17.2	S197	0.6	20%	<i>Q. aliena</i> , <i>Juglans mandshurica</i> , Maxim. <i>P. tabuliformis</i>
14	Natural secondary forest (NF)	1018	117.554	40.212	23	S180	0.5	0	<i>Q. mogolica</i> Fisch. Ex ledeb
15		1030	117.224	40.313	25	SW195	0.4	0	<i>Q. mogolica</i>
16		1002	117.510	40.078	20	SW215	0.6	0	<i>Q. mogolica</i>
17		894	117.554	40.204	30	SE151	0.3	0	<i>Q. mogolica</i>
18		886	117.554	40.202	25	SE134	0.5	0	<i>Q. mogolica</i>
19		876	117.554	40.204	30	SE137	0.6	0	<i>Q. aliena</i> , <i>J. mandshurica</i>
20		822	117.556	40.205	26.7	SE157	0.8	0	<i>Q. mogolica</i> , <i>E. dahiellii</i>
21		506	117.555	40.189	26.7	S193	0.7	0	<i>Q. aliena</i> , <i>E. dahiellii</i>
22		402	117.550	40.187	17.8	SE120	0.6	0	<i>Q. aliena</i>
23		396	117.549	40.185	42.2	SW207	0.5	0	<i>E. dahiellii</i>
24		395	117.550	40.185	29	S175	0.85	0	<i>Koelreuteria paniculate</i> Laxm., <i>Q. aliena</i> ,
25		296	117.539	40.184	18.8	S195	0.5	0	<i>Q. variabilis</i>
26		288	117.538	40.185	17.3	W253	0.6	0	<i>Q. aliena</i> , <i>Q. variabilis</i>
27	299	117.540	40.184	18.6	S256	0.6	0	<i>Q. variabilis</i>	

Determination of soil physicochemical, enzyme activity and nitrogen mineralization characteristics

Soil water content and dry matter were determined using the Chinese standard HJ613-211 (Ministry of Environmental Protection PRC, 2011a), pH was determined using the KCl dissolution electrode method, total nitrogen and total carbon were determined using the CN analyzer, organic carbon content was determined using the potassium dichromate oxidation method (Ministry of Environmental Protection PRC, 2011b), various ionic forms of nitrogen were determined by KCl leaching spectrophotometric method (Ministry of Environmental Protection PRC, 2012, Standardization Administration of China, 2016), total phosphorus was determined by microwave digestion spectrophotometry, and available phosphorus by $\text{NH}_4\text{F-HCl}$ leaching spectrophotometry (Ministry of Environmental Protection PRC, 2012). Soil enzymatic activity was measured using the method in the book of Lin (2010), and ecological processes associated with nitrogen mineralization include net nitrogen mineralization (Eq. 1), ammonification (Eq. 2) and nitrification (Eq. 3) (Lin 2010), with the amount of change in ammoniacal, nitrate- and nitroso-nitrogen used to characterize the relative contribution of different processes to net nitrogen mineralization.

Formula

$$\text{Net mineralization rate (mg/(kg} \cdot \text{d))} = (\text{NH}_4^+\text{-N} + \text{NO}_2^-\text{-N} + \text{NO}_3^-\text{-N})_t - (\text{NH}_4^+\text{-N} + \text{NO}_2^-\text{-N} + \text{NO}_3^-\text{-N})_0 \quad (1)$$

$$\text{Ammonification rate (mg/(kg} \cdot \text{d))} = \frac{\text{NH}_4^+\text{ }_t - \text{NH}_4^+\text{ }_0}{\text{Soil dry weight (g)} \times 7 \text{ d}} \quad (2)$$

$$\text{Nitrification rate (mg/(kg} \cdot \text{d))} = \frac{\text{NO}_3^-\text{ }_t \text{ } (\mu\text{g)} - \text{NO}_3^-\text{ }_0 \text{ } (\mu\text{g)}}{\text{Soil dry weight (g)} \times 15 \text{ d}} \quad (3)$$

Where t indicates the moment of the end of the incubation and 0 means the moment of the beginning of the incubation.

Soil microbial sequencing and community structure analysis

DNA extraction, amplification and purification Soil microbial genomic DNA was extracted using a reagent Kits, followed by bacterial 16s rDNA (primer 27F: AGAGTTTGTACCTGGCTCAG, 1492R: TACGGYTACCTGTTAYGACTT) and fungal ITS sequences (primer ITS1F: 5'-CTTGGTCATTAGAGGAAGTAA-3, ITS2: 5'-GCTGCGTTCCTCATCGATGC-3') were amplified. The resulting PCR products were purified by the VAHTS-TM DNA Clean Beads method and tested for purity and quantification.

Sequencing and analysis Libraries were quality-checked by the Qsep-400 method and constructed libraries were sequenced on machine using illumina novaseq6000. The quality of the original sequences was controlled by the sliding window command of Fastp. Paired Clean-Reads were obtained by removing the terminal primer sequences using cutadpt software, Raw tags were obtained by merging them according to the overlap of paired-end sequences using the fastq-mergepairs command, Raw data quality was controlled by the sliding windows function of Fastp to obtain Paired-end Clean tags.

OUTs clustering and species annotation Cluster analysis was performed using UPARSE at the 97% similarity level, and the usearch command was used to remove affine sequences and singleton OTUs in the process. Each clustered OUTs was annotated into seven taxonomic classes of boundary, phylum, order, family, genus and species by the sine method through the 16s in silva or the ITS database in Unite. and the community abundance tables for each rank were obtained. The present study was carried out mainly on the generic taxonomic rank.

Data processing

Significance of differences at the $P=0.05$ level for each indicator of soil physicochemical properties was calculated using the anova analysis scheffe method of spss 19.0 software. Levins niche widths were calculated using the 'spaa' package of R 4.0.0 software, and the frequency of occurrence at the genus level was randomized and rearranged 1000 times using the replacement method of the 'EcolUtilis' package, respectively, and the zero distribution of the niche width index was calculated for these genera. Based on the generalized taxa having a wider niche width than the specialized taxa (Wilson et al. 2015), genera with actual niche width indices above the upper 95% confidence interval of the zero distribution were defined as generalized taxa, genera below the lower 95% confidence interval of the zero distribution were defined as specialized taxa, and genera within the 95% confidence interval of the zero distribution were defined as neutral taxa (Wu et al. 2017a). The 'vegan' package non-metric multidimensional scaling (NMDS) method was used to analyze differences in community structure between stand types, and redundancy analysis RDA function of the same 'vegan' package was used to analyze the effects of soil physicochemical and enzyme activity on microbial community structure as well as the interpretation of differences in soil nitrogen mineralization processes by dominant genera (with abundance >1%) in each habitat-specific group. Mapping was done using the R 4.0.0 basic program package and 'ggplot2' package.

Results

Effects of close-to-nature management of planted forests on soil properties

Among the soil nutrients indices, total carbon, total nitrogen, total phosphorus, available phosphorus, nitrate-nitrogen content and pH all first decreased and then increased with the progress of near-naturalization, while organic carbon, ammoniacal nitrogen, nitrite-nitrogen, dry matter content and C/N ratio presented the opposite trend of first climbing up and then following down. Total carbon, organic carbon, total nitrogen, nitrate-nitrogen and ammoniacal nitrogen were all higher in natural secondary forest soils than in near-naturalized stands, while total phosphorus, available phosphorus, pH and dry matter content were highest in near-natural forest. Among the soil enzyme activities, cellulase and urease activities tended to increase during the near-

naturalization process, while acid phosphatase activity tended to decrease and β -glucosidase and dehydrogenase activities first increased and then decreased. The acid phosphatase and urease activities in natural secondary forests were significantly higher than those in the plantation development sequence, while β -glucosidase and dehydrogenase activities were significantly lower than those in the plantation successional sequence. The rate of soil N mineralization ecological processes was significantly faster in near-naturalization sequence stands than in natural secondary forest (Table 2).

Table 2

Comparison of soil properties between near-naturalized stands and natural secondary forest (P: *Pinus tabulaeformis* forest; M: Mixed forest; NNF: Near-natural forest; NF: Natural secondary forest)

	SOC (mg/kg)	AP (mg/kg)	TP (mg/kg)	NO ₃ -N (mg/kg)	NH ₄ ⁺ -N (mg/kg)	pH
P	79.40 ± 14.02b	38.58 ± 32.35a	545.80 ± 159.60a	13.32 ± 2.26b	8.10 ± 0.72ab	4.79 ± 0.19b
M	95.88 ± 13.18ab	33.89 ± 43.06a	472.02 ± 88.10a	9.97 ± 3.55c	8.72 ± 7.46ab	4.64 ± 0.34b
NNF	79.94 ± 17.85b	45.40 ± 10.99a	563.10 ± 193.30a	15.42 ± 3.73b	4.84 ± 3.05b	5.85 ± 0.38a
NF	105.41 ± 21.03a	40.28 ± 33.67a	532.09 ± 159.40a	21.17 ± 8.00a	10.50 ± 3.98a	5.74 ± 0.88a
	Moisture content (%)	Dry matter (%)	TC (%)	TN (%)	C/N	NO ₂ ⁻ -N
P	38.87 ± 4.93a	95.71 ± 1.19a	7.18 ± 3.55a	0.52 ± 0.26a	13.87 ± 1.26ab	1.22 ± 0.63b
M	32.64 ± 5.66b	97.11 ± 0.97a	5.16 ± 0.37b	0.36 ± 0.04b	14.55 ± 0.71a	2.84 ± 1.39a
NNF	32.11 ± 9.31b	96.73 ± 3.27a	7.15 ± 1.16a	0.56 ± 0.12a	12.97 ± 0.77b	2.26 ± 2.72ab
NF	38.23 ± 5.85a	95.89 ± 1.90a	7.55 ± 2.78a	0.61 ± 0.06a	12.35 ± 0.86b	1.70 ± 2.23ab
	Cellulase (μg/(g·min))	Urease (μg/(g·h))	β -Glucosidase (μg/(g·h))	Dehydrogenase (μg/(g·h))	Acid phosphatase (μg/(g·min))	Nitrification rate (μg/(g·d))
P	0.097 ± 0.086b	5.23 ± 1.63b	0.83 ± 0.78ab	0.39 ± 0.35a	5.83 ± 1.10ab	0.26 ± 0.02a
M	0.178 ± 0.054ab	5.24 ± 1.81b	1.24 ± 0.98a	0.61 ± 0.54a	5.29 ± 1.29ab	0.15 ± 0.14b
NNF	0.199 ± 0.093ab	9.61 ± 1.34a	1.01 ± 0.51ab	0.46 ± 0.37a	4.36 ± 1.52b	0.27 ± 0.08a
NF	0.213 ± 0.062a	8.98 ± 2.78a	0.59 ± 0.54b	0.33 ± 0.38a	6.85 ± 3.73a	0.14 ± 0.79b
	Change in ammonia N (mg/kg)	Change in nitrite N (mg/kg)	Change in nitrate N (mg/kg)	Total net mineralization (mg/kg)	Ammoniation rate (mg/(kg·m))	
P	-1.05 ± 2.99ab	0.53 ± 1.48a	24.54 ± 6.85b	24.02 ± 9.06a	37.04 ± 1.42ab	
M	-3.34 ± 8.03ab	-1.67 ± 1.31a	30.30 ± 8.00a	25.39 ± 15.39a	54.74 ± 27.24a	
NNF	1.33 ± 3.19a	-0.92 ± 2.85a	26.38 ± 8.91a	26.79 ± 7.90a	34.38 ± 12.82ab	
NF	-5.01 ± 3.49b	-0.52 ± 2.20a	10.38 ± 15.64c	14.00 ± 9.59b	23.42 ± 12.38b	

Effect of close-to-nature management on the niche width and abundance of various habitat specificity taxa of soil microorganisms

A total of 46,873 OUTs attributed to 537 genera were yielded by sequencing and cluster analysis of bacteria, which were divided into 17 generalized genera, 203 neutral genera and 317 specialized genera taxa. 1619 OUTs in sum attributed to 355 genera were yielded through by sequencing and cluster analysis of fungi, with 58 genera of generic, 153 genera of neutral and 144 genera of specialized taxa. The top genera in terms of abundance in each of the fungal groups were *Ilyonectria*, *Archaeorhizomyces*(*), *Gliocladiopsis* for the generalist group, *Fusarium*, *Cladosporium*, *Botryotrichum* for the neutral group, *Aspergillus*, *Erysiphe*, *Paecilium* for the specialist group. In the bacterial community they were the generalized taxa: *Bauldia*, *Hyphomicrobium*, *Chthonomonas*; the neutral taxa: *Sphingomonas*, *Halliangium*, *Rhodoplanes*; the specialized taxa: *Candidatus-udaeobacter*, *KB41*, *Candidatus-solibacter* (*), *Bradyrhizobium* (the addition of * to the genus name indicates significantly difference of abundance between at least two forest stands). Analyzing by genera with the abundance greater than 1%, the abundance and numbers of fungi were significantly higher than those of bacteria, and both showed significantly lower abundance of the generalized taxa than the neutral and specialized taxa (Figs. 1,2).

The niche width of soil fungi is greater than that of bacteria for taxa of the same habitat specificity in each forest stage (Fig. 3 FG-BG, FN-BN, FS-BS), but there is no difference between different taxa of the same forest stage (Fig. 3 FG-FN-FS, BG-BN-BS). The niche width of all taxa increased with near-naturalization and was significantly lower than that of natural secondary forests. The increase showed a pattern of generalized taxa > neutral taxa > specialized taxa, i.e. slowing down with increasing habitat specificity (Fig. 3). In terms of abundance, specialized taxa of bacterial and fungal both decreased with near-naturalization. The abundance of generalized and neutral taxa showed an increase in fungi with near-naturalization and was lower than in natural secondary forests, but a decrease in bacteria and was higher than in natural secondary forests (Fig. 4).

Effect of close-to-nature management on the community structure of soil microbial

The impact of near-naturalization on the β -diversity of soil fungal and bacterial communities showed the trend of generalized taxa > neutral taxa > specialized taxa (Fig. 5 FG-FN-FS, BG-BN-BS). For the generalized taxa of fungi, the coordinate points of *P. tabulaeformis* forest, mixed forest and near-natural forest could be divided into different areas (Fig. 5 FG). For the neutral taxa, the coordinate points of *P. tabulaeformis* forest were clearly differentiated from other near-naturalized forest stands. This indicated a significant impact on the structure and distribution of the neutral taxa in the first and middle stages, but the effect was weaker in the later stages (Fig. 5 FN). For the specialized taxa, coordinates of *P. tabulaeformis* stands could still be separated from the others, but the coordinate of other forest stands were indistinguishable from each other, especially the near-natural forest and natural secondary forest, indicating a very similar community structure between them (Fig. 5 FS). For the soil bacterial community, the structure of the generalized taxa was relatively clearly differentiated with near-naturalization (Fig. 5 BG), while the neutral and specialized taxa only showed a clear distinction between *P. tabulaeformis* forest and other stands, the heterogeneity of the community structure between mixed, near-natural and natural secondary stands was already minimal (Fig. 5 BN BS).

Influence of soil physicochemical properties and enzyme activity on the community structure of soil microbial taxa

Soil physicochemical properties and enzyme activity explained more of the bacterial community structure than the fungal community, and both decreased with habitat specificity (Figs. 6, 7). Physicochemical content better explained microbial community structure than soil enzyme activity. The structure of fungal generalized and neutral taxa responded most significantly to pH (Fig. 6G N), suggesting that changes in soil pH were the main factor driving variation in the structure of such soil microorganisms during near-naturalization, while the distribution and structure of fungal specialized taxa were mainly influenced by urease activity (Fig. 6 S). The distribution of all soil bacterial taxa was dominated by soil carbon- and nitrogen-related characteristics (Fig. 7).

For the generalized taxa of fungi, the RDA axis 1 explained 20.81% of the variation and the axis 2 explained 12.16%, with soil pH being the most significant influence on the RDA axis 1 and the most influenced by dry matter content on the RDA axis 2 (Fig. 6G). The structure of neutral taxa was most influenced by pH on the RDA axis 1 and by dehydrogenase activity on axis 2 (Fig. 6N). In combination with the characteristics presented on the distribution of each community coordinate, the increase in pH may be the main factor driving the difference in the structure of soil fungal generalized and neutral taxa between pre-near-naturalized and later stands. The structure of specialized taxa was mainly influenced by urease activity on the RDA axis 1 and total nitrogen on the RDA axis 2 (Fig. 6S).

The RDA axis 1 explained 32.36% of the structural variation in bacterial generalized taxa and axis 2 explained 16.51%, with C/N ratio being the most strongly correlated with the axis 1 and water content with the axis 2 (Fig. 7G). For neutral taxa, total phosphorus and C/N ratio were the most explained indicators on axis 1 and total carbon and total nitrogen on axis 2 (Fig. 7N). For specialized taxa, C/N ratio and total nitrogen interpreted the most highly on axis 1 and total phosphorus and acid phosphatase on axis 2. Combined with the characteristics of the community's coordinate distribution, the decrease in C/N ratio drove the difference in bacterial structure between early to mid and late period of near-naturalization to the greatest extent, while the decrease in total phosphorus content also drove the difference between generalized and neutral taxa. (Fig. 7S).

Explanation of soil ecological processes by dominant genera abundance with different degrees of habitat specificity

The community structure of the top 1% of genera in terms of abundance of each taxon well explained the soil nitrogen mineralization. The community structure of each taxon manifested significant difference between near-naturalized sequence and natural secondary forests, which can be clearly shown in the RDA diagram (Fig. 8,9). The values of natural secondary forest sample sites were significantly lower than those of near-naturalized stands on axis 1 of RDA plot, consistent with the conclusion that nitrogen mineralization rates were lower in natural secondary forests. This revealed that heterogeneity in community structure drives the differences in nitrogen mineralization processes between near-naturalized and natural forest stands.

The community structure of fungal specialized taxa explained the most of the nitrogen mineralization process with 58.6% of the variation explained by the RDA axis 1 and 22.71% by the RDA axis 2. This was followed by the generalized taxa with 50.4% explained by the RDA axis 1 and 20.14% by the RDA axis 2. The structure of neutral taxa explained 49.78% of the variance by the RDA axis 1 and 17.73% by the RDA axis 2. The amount of net nitrogen mineralization was the most highly interpreted indicator of generalized and neutral taxa on the RDA axis 1. Among the generalized taxa, *Staphylotrichum* was the genus with the highest strength and positive correlation with soil nitrogen mineralization, *Gliocladiopsis* also showed a strong positive correlation with the amount of ammonia nitrogen change and nitrification rate, but the high abundant *Archaeorhizomyces* and *Ilyonectria* showed a negative correlation with soil nitrogen mineralization (Fig. 8G). Of the neutral taxa, *Purpureocillium* was the most strongly positively correlated with net mineralization and *Condenascus* with nitrification rates as well as *Botryotrichum* with ammonification rates, but the high abundant *Cladosporium* also showed a negative correlation with nitrogen mineralization (Fig. 8N). Soil nitrification rate was the most highly interpreted indicator of the structure of specialized taxa, and the strongest correlation was with *Paecilomyces*. *Erysiphe* showed the strongest positive correlation with the amount of ammoniacal nitrogen change while *Russula* showed a clear negative relationship with the nitrogen mineralization. However, the highest abundance of *Aspergillus* was not strongly correlated with nitrogen mineralization (Fig. 8S).

The structure of the generalized taxa of bacteria mostly explained soil nitrogen mineralization at 62.95% on the RDA axis 1 and 16.22% on the axis 2. Net nitrogen mineralization was the highest explained by the generalized and specialized taxa on the RDA axis 1. Among the generalized taxa, *Nocardia* was highly negatively and strongly correlated with the nitrogen mineralization, the highest correlation with net nitrogen mineralization was *Hyphomicrobium*, and *Bauldia* positively but not strongly correlated with nitrification rates (Fig. 9G). Among the specialized taxa, *Bradyrhizobium* was

most strongly negatively correlated with each process of mineralization, while *Candidatus-solibacter* and *Nitrospira* were significantly positively correlated with nitrification rate (Fig. 9S). Soil nitrification rate was the most highly interpreted indicator for neutral taxa on the RDA axis 1 and strongest positive correlations were with *Hirschia* and *Chtoniobater*. *Rhodoplanes* was strongly negatively correlated with the mineralization process (Fig. 9N).

Discussion

Effect of close-to-nature management on niche width and abundance of soil microbial taxa with different habitat-specificity

In terms of genera with abundance > 1%, the abundant and numerous of fungi were both obviously more than that of bacteria. This could be explained by the fact that fungi tend to be better adapted to the low nutrient status of soils than bacteria (Joergensen et al. 2008) and tended to be able to use organic matter with difficult decomposition and high C/N ratio (Blagodatskaya et al. 1998). Pedrós-Alió (2006) and Logares et al (2015) noted that abundant taxa in the community were few and widely distributed, and the rare taxa were many and limited in distribution, which was consistent with the characters of taxa number in this study, but contradicted the finding that the abundance of generalized taxa was obviously lower than that of neutral and specialized taxa. The reason was that the generalized taxa may have been derived from the retention of soil or root microorganisms prior to plantation cultivation, and their abundance has declined significantly with changes in soil properties and root decomposition. The study also showed that the niche widths of all soil microbial taxa increased with near naturalized succession and were lower than in natural secondary forest, demonstrating that close-to-nature management has played a positive role in improving the suitability of soil habitats for microbial. However, there were still a significant gap between them and natural secondary forests. The rapid uptake of soil nutrients by vegetation during the early stages of reforestation after vegetation destruction caused a reduction in soil available carbon and nitrogen, providing relatively oligotrophic conditions for soil microorganisms (Sun et al. 2017), which was consistent with the finding of low organic carbon content in the soils of *P. tabulaeformis* forests in this study. The increase in soil nutrient quality and quantity during near-naturalization provided conditions for the transition from oligotrophic to co-nutrient and for ecological niche differentiation and coexistence of soil microorganisms. Wu (2017a) showed that abundant taxa tended to show stronger temporal variability than rare taxa, which was consistent with the greater variability between near-naturalization stages of generalized taxa in our study. Thus, the close-to-nature management has already achieved the effect of improving the nutrient-poor soil conditions in the early stages of afforestation and promoting healthy development of microbial communities, but the operation needs to be adapted and sustained over time.

Near-naturalization affected the structure of soil microbial taxa by changing the physicochemical properties of the soil

Studies have shown that soil nutrient content is mostly characterized by single-peaked changes during near-naturalization, i.e. the maximum or minimum values occurred in the mixed forest stage. Changes in soil nutrients among successional stages was usually due to changes in the quality of the litter substrate in response to vegetation development, which caused changes in the decomposition, synthesis and distribution of subsurface organic matter with succession (Bai et al. 2019; Bläsko et al. 2015). It is possible that soil microorganisms in mixed forests have higher carbon and nitrogen utilization, and more nitrogen is used by their growth, thus reducing the content in the soil (Wen et al. 2014). The high organic carbon content and β -glucosidase activity is in line with Huang (2013), who manifested that soil hydrolase activity and organic carbon stability were increased in mixed forests. Similarly, it has been shown that mixing tree species significantly increases soil urease activity, which was consistent with the findings in this paper that urease activity increases with near naturalization (Lucas et al. 2012; Yu et al. 2015). It has also been noted that deciduous broadleaf forests have a higher efficiency of nitrogen cycling and a faster uptake of nutrient nitrogen in the soil compared to coniferous forests (Forstner et al. 2019; Guénon et al. 2017), which is inconsistent with the higher ammonia, nitrate and total nitrogen as well as lower nitrogen mineralization in natural secondary forests compared to near-naturalized successional stands. The significantly lower carbon and nitrogen-related nutrient contents in the near-naturalized stands than in natural secondary forest, coupled with the faster nitrogen mineralization rate, suggested that the nitrogen loss of the former stands was more severe than that of the latter forest, implying that the close-to-nature operation have not yet fully recovered their soil nutrient levels at this stage.

Community structural variability decreased with the degree of habitat specificity during the near-naturalization of planted forests, i.e. the differences between generalized taxa at different stages were greater than those of neutral and specialized taxa. Specialized taxa were more sensitive to environmental change and so was mainly influenced by environmental filtering, whereas generalized taxa had a wider range of adaptation to the heterogeneity generated by environmental change, so dispersal may be the main factor contributing to their differences in community structure (Wu et al. 2017b; Liu et al. 2015). Thus, the small heterogeneity of community structure of the specialized taxa in this study was consistent with the characteristic of insignificant differences in soil physicochemical properties. In contrast, generalist taxa may be retained in natural secondary forests and near-naturalized stands by residual root systems or root secretions, and changes in their dependent root microenvironments over the decades have resulted in a large variation in generalist taxa structure. Tang et al. (2017) have found significant differences in soil microbial community structure by inoculating different soil types with same original microorganisms, interpreting this as Variability of substrate properties shaping differences in microbial community structure. This could also explain the significant differences in generalized taxa among forest stands. However, dominant species in different habitat-specific taxa tend to respond to environmental changes, so we suggest that differences in resource competition between taxa may also be an important factor in the variation in community structure in response to near-naturalization.

Our study also showed that soil bacterial community structure pronounced more positively to near-naturalization than fungi. Distribution of bacterial community was mainly influenced by soil carbon and nitrogen content and C/N ratio, while the structure fungi were more influenced by pH and urease activity. Soil fungal and bacterial diverse assemblage processes may differ (Yang et al. 2017), with strategy-dependent feedbacks in fungal communities highly correlated with vegetation type and litter quality (e.g. leaf C/N) (Roy et al. 2015; Wu et al. 2013), while bacterial community assemblages may be

more dependent on soil properties (Jiang et al. 2018). Previous reports have suggested soil pH or C/N ratio the main factor controlling soil microbial community structure (Zhalnina et al. 2015; Wan et al. 2015; Wu et al. 2017b; Rousk et al. 2010b; Aciego et al. 2009). Underground fungal communities have been shown to be closely related to plant species diversity and identity (Bahram et al. 2015; Peay et al. 2013), but changes in abiotic soil parameters could also interact with the effects of vegetation on soil fungi (Sundqvist et al. 2013). For example, fungal diversity in alpine grasslands on the Tibetan Plateau was negatively correlated with soil SOC and total nitrogen, but this trend was reversed in alpine meadows, suggesting that the interaction between vegetation type and soil nutrients affects fungal community structure (Zhang et al. 2017). Fungi were not very environment-dependent and tended to be able to adapt to diverse and heterogeneous environments, but were more sensitive to pH responses. The findings of this study echo all of the above literature. It has also been shown that soil enzyme activity was closely related to microbial communities (Midgley et al. 2016), but in this paper only soil urease activity has a high degree of explanation for the structure of fungal specialized taxa, which may suggest that fungal specialized taxa may be closely related to the chemical transformation of ammonia, as the molecular ammonia from decomposition of urea may serve as a substrate of the taxa. This was consistent with the conclusion that fungal specialized taxa were the most explanatory of soil nitrogen mineralization processes.

Near-naturalization affected soil nitrogen mineralization by altering soil microbial community structure

Linking soil microbial structure and function to the soil nitrogen cycle is a good way to study various ecosystem issues (You et al. 2014, Bahram et al. 2015, Stefanowicz 2016). Soil nitrogen mineralization is an important link in the biogeochemical cycling of nitrogen, closely related to the rate of nitrogen turnover and availability in forest ecosystems. Studying the community composition of abundant taxa is crucial to understanding ecosystem function as they often play a key role in nutrient cycling (Wu et al. 2017a), but recently there has been an increasing emphasis on the importance of specialized taxa (Lynch et al. 2015). It was shown that the structure of dominant genus with abundance >1% differed significantly between natural secondary forest and near-naturalized stands, and that nitrification rate and net nitrogen mineralization were the most highly interpreted indicators on the RDA axis 1, which could be explained by the fact that differences in soil microbial community structure between natural secondary stands and near-naturalized stands drove differences in nitrogen mineralization-related processes, especially nitrification rate and net mineralization. From the analysis, fungal genera with high abundance tended to be negatively associated with nitrogen mineralization processes, such as *Ilyonectria* and *Archaeorhizomyces*, while *Staphylotrichum* has been proved to be the most positively associated with nitrogen mineralization, especially the ammonification, but the abundance was not high. Some studies have shown that the abundance of *Ilyonectria* is negatively correlated with soil N stoichiometry, suggesting its possible involvement in nitrogen-related metabolic processes (Carrona et al. 2020), while *Archaeorhizomyces* has been shown to be positively correlated with N and to increase carbon use efficiency and growth under high N availability (Jørgensen et al. 2022). *Paecilomyces* in the specialized taxa was positively correlated with nitrification rate to a high degree and with the greatest intensity, which is in full agreement with Liu (2016) who concluded that *Paecilomyces* has a strong nitrification and deamination activity. *Erysiphe* was positively correlated with the change in ammonia nitrogen. *Russula* was indicated to be significantly negatively correlated with nitrogen mineralization, which was shown to grow best in the highest applied nitrogen. This was consistent with its significant negative correlation with nitrogen mineralization (Avis et al. 2005), the process by which organic nitrogen decomposes and caused its content to decline. The highest abundance of *Aspergillus*, however, was not highly correlated with nitrogen mineralization. Mention of the generalized taxa of bacteria, the highest correlation with total net mineralization was found in *Hyphomicrobium*, a genus with strong nitrogen fixation activity and from which nitrogen fixation genes were isolated (Mergel et al. 2001), leading us to speculate that it provides more substrate for nitrogen mineralization through nitrogen fixation. The high negative correlation between *Nocardia* and nitrogen mineralization may be related to its predominant involvement in denitrification under relevant conditions, and the genus has been shown to play an important role in denitrification treatments with simultaneous nitrification and denitrification (Güclü et al. 2014). Among the specialized taxa, *Candidatus* is an anaerobic ammonia-oxidizing bacterium, a process that contributes little to nitrogen production in forest soils (Xi et al. 2016), suggesting mainly nitrification. *Candidatus* tends to be less diverse in natural forests than in planted forest restoration succession sequences (Meng et al. 2016), which was consistent with the lower rate of nitrogen mineralization in natural secondary forests than the near-naturalization sequence derived from this study, since ammonia oxidation was an important process for nitrogen mineralization. *Bradyrhizobium*, a typical nitrogen-fixing rhizobacterium, was shown to be significantly positively correlated with plant leaf nitrogen content (Morvan et al. 2020), which corresponds to the negative correlation between this genus and soil nitrogen mineralization, as the ammonia produced by nitrogen fixation is absorbed by the plant and assimilated into the various plant nitrogen forms, reducing the substrate for soil ammonification and nitrification.

Conclusions

The effect of plantation management on the ecological niche width, abundance and community structure of various groups of soil microorganisms and the contribution of each group to soil nitrogen mineralization was investigated from the perspective of the differences in the responses of different habitat-specific taxa of soil microorganisms to plantation naturalization. The effect of plantation naturalization management was evaluated with reference to natural secondary forests. The results showed that the soil nutrient content of the near-naturalized forest was mostly lower than that of the natural secondary forest, but the rate of soil nitrogen mineralization was just the opposite. The community structure of soil microbial generalist taxa responded more positively to naturalization than neutral and specialized taxa, and correlated better with variation in soil physicochemical properties. This suggests that near-naturalization acts primarily on generalized taxa to alter soil properties and thus soil ecological processes. In conclusion, close-to-nature operation has improved the soil nutrient conditions and microbial community structure to a certain extent, but there were still significant differences with the soil conditions of natural secondary stands, especially the dominant genus community structure and nitrogen mineralization processes. Therefore, it is necessary to add anthropogenic measures in the process of close-to-nature management to promote the development of soil conditions in plantation forests to natural secondary forest conditions, so as to better promote the renewal and diversification of above-ground

vegetation and improve the stability of the entire community in the near-naturalized forest stands. The study may also shed new light on the effects of stand change on soil microorganisms from a habitat specificity perspective.

Declarations

Funding: The authors declare that no funds, grants, or other support were received during the preparation of this manuscript.

Acknowledgements: We would like to express our sincere gratitude for the help from the staff of The Baxianshan Nature Reserve during the field survey and sampling.

Author Contributions: All authors contributed to the study conception and design. Field survey, material collection, indoor experiments were performed by [Zhenlu Qiu] and [Mei Zhang]. Data collection and analysis were performed by [Zhenlu Qiu] and [Cong Shi]. The first draft of the manuscript was written by [Zhenlu Qiu] and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript."

Competing Interests: The authors have no relevant financial or non-financial interests to disclose

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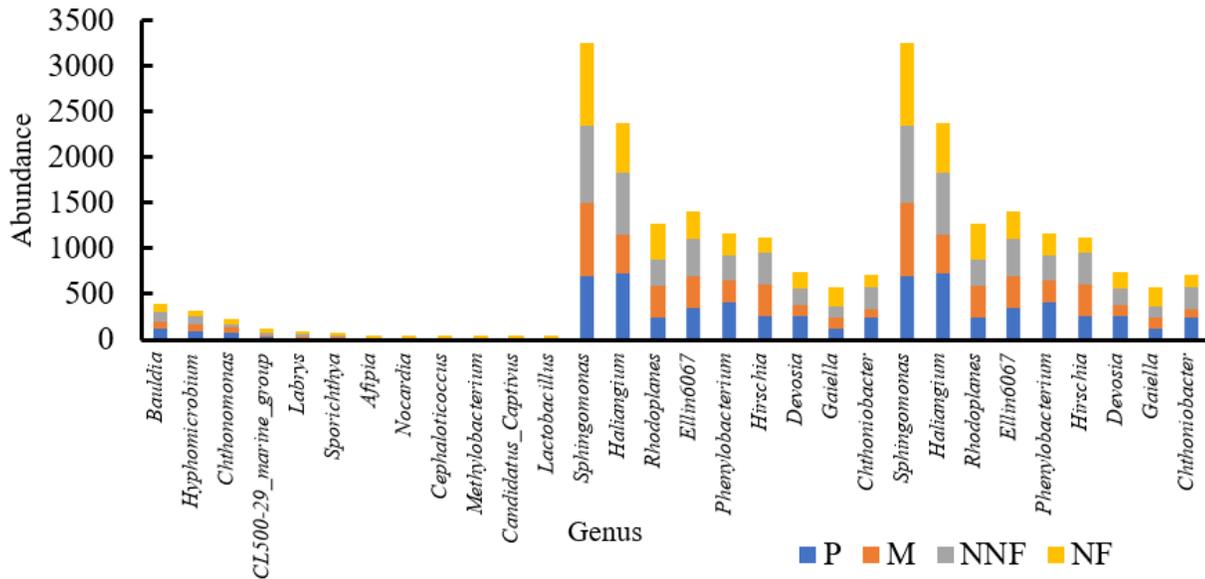


Figure 1
 Variation in abundance of major genera of bacterial taxa by ecological niche with near-naturalisation (P: *Pinus tabulaeformis* forest, M: Mixed forest, NNF: Near-natural forest, NF: Natural secondary forest)

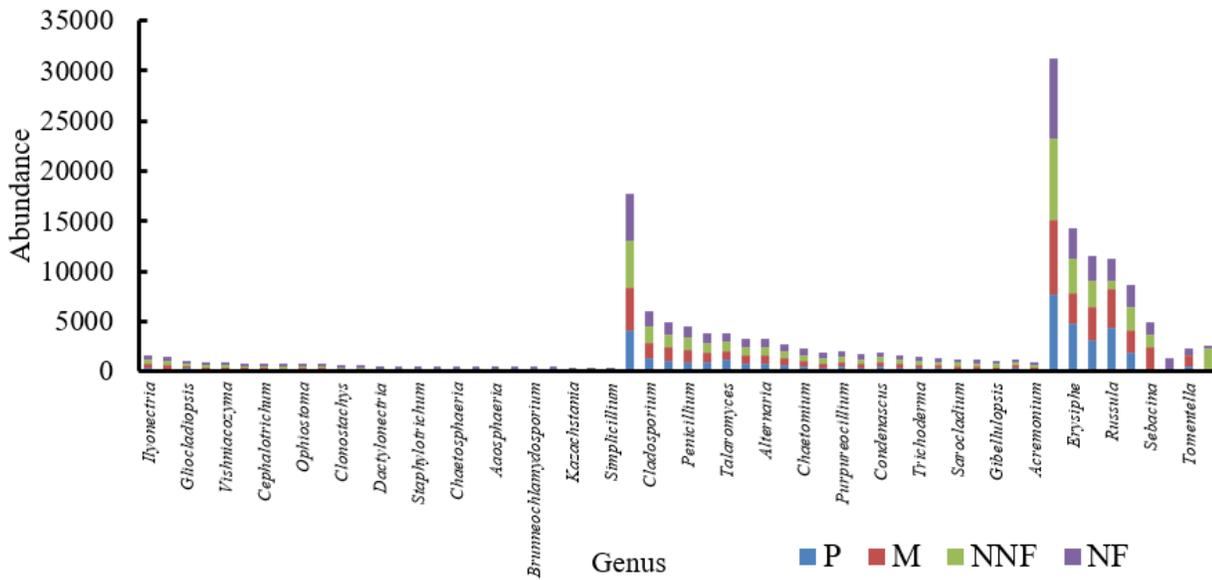


Figure 2
 Variation in abundance of major genera of fungal taxa by ecological niche with near naturalization (P: *Pinus tabulaeformis* forest, M: mixed forest, NNF: near natural forest, NF: natural secondary forest)

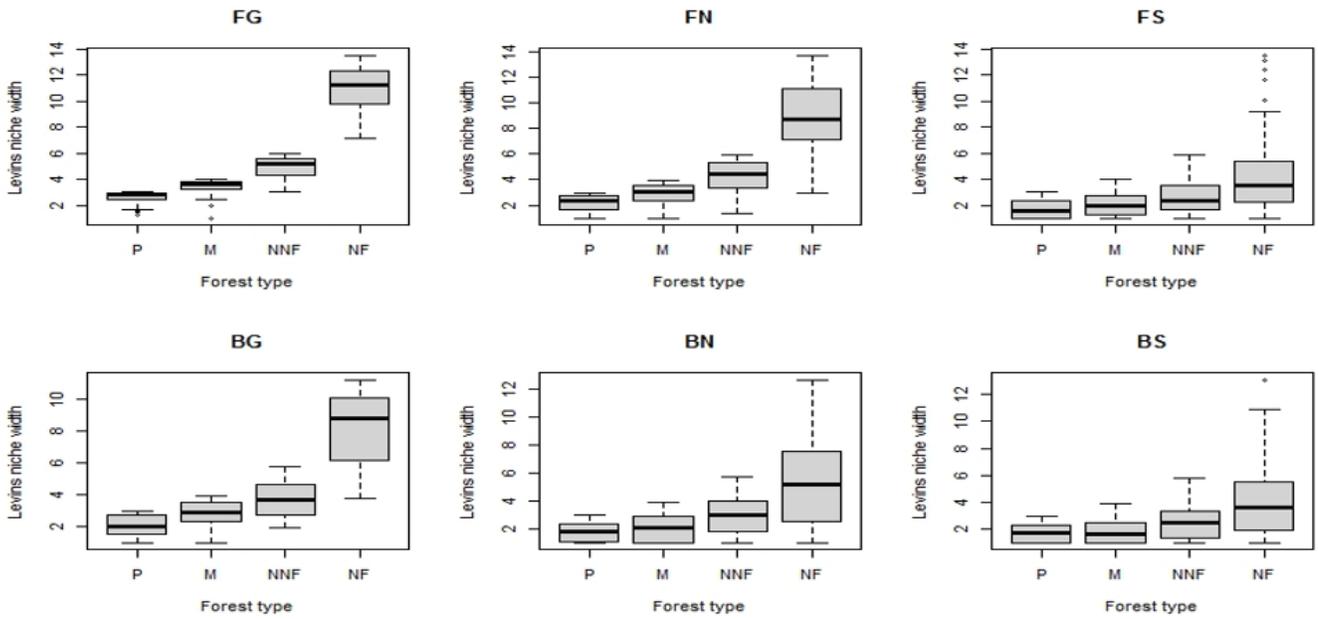


Figure 3
 Variation in the niche width of each habitat specific taxa of soil bacteria and fungi with near-naturalization (P: *Pinus tabulaeformis* forest, M: mixed forest, NNF: near-natural forest, NF: natural secondary forest, F: fungi, B: bacteria, G: generalized taxa, N: neutral taxa, S: specialized taxa)

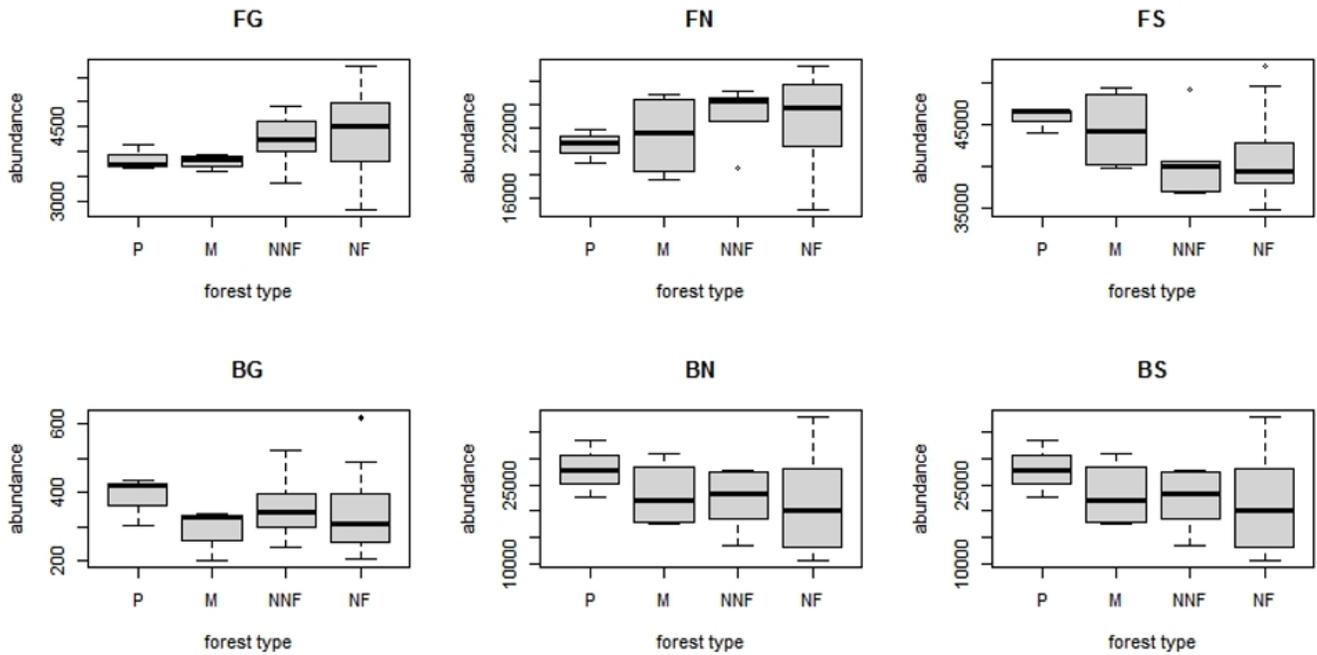


Figure 4
 Changes in the abundance of soil bacteria and fungi by habitat specificity with near-naturalization (P: *Pinus tabulaeformis* forest, M: mixed forest, NNF: near-natural forest, NF: natural secondary forest, F: fungi, B: bacteria, G: generalized taxa, N: neutral taxa, S: specialized taxa)

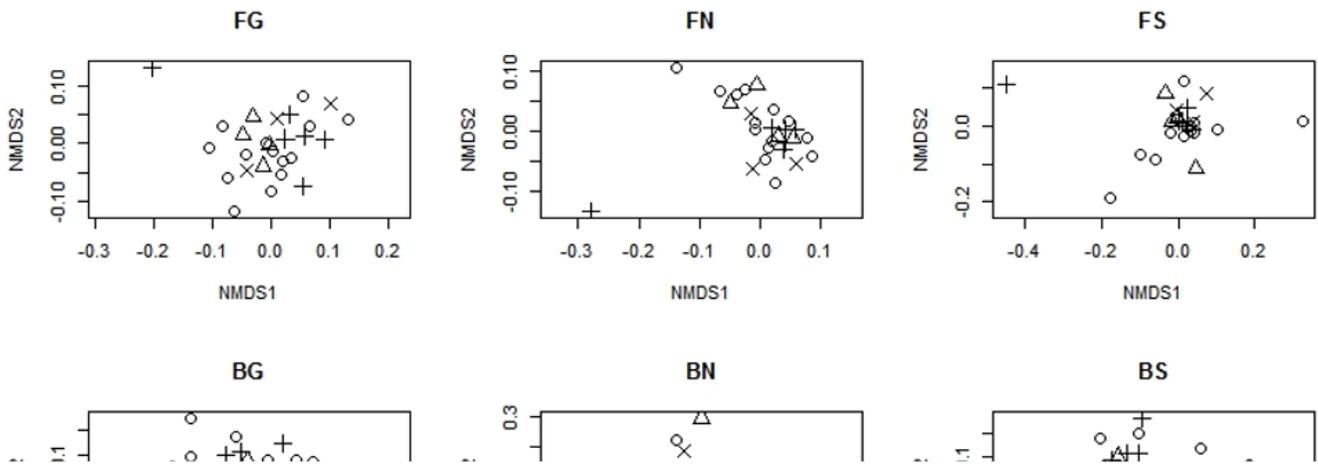


Figure 5
 Variation in β -diversity of different ecological niche groups of soil fungi and bacteria with near-naturalization by NMDS (F: fungi B: bacteria G: generalized taxa N: neutral taxa S: specialized taxa \times : *Pinus. tabulaeformis* forest Δ : mixed forest +: near-natural forest \bullet : natural secondary forest)

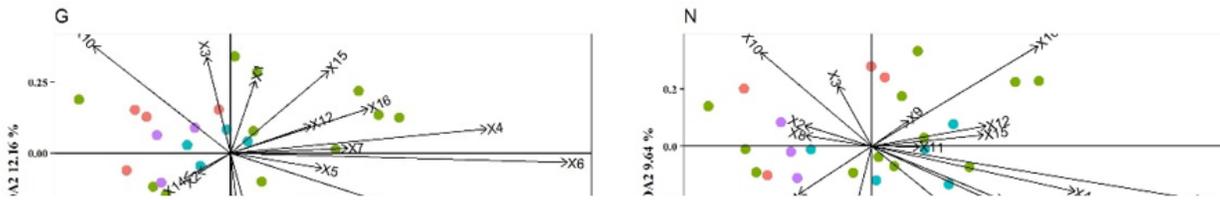


Figure 6
 RDA analysis of soil physicochemical and enzymatic activities on the interpretation of community structure of different ecological niches of fungi (Legend: P: *Pinus tabulaeformis* forest; M: Mixed forest; NNF: Near natural forest; NF: Natural secondary forest; Figure caption: G: Generalized taxa; N: Neutral taxa; S: Specialized taxa; Arrows: X1: Organic carbon; X2: Effective phosphorus; X3: Total phosphorus; X4: Nitrate-nitrogen; X5: Nitrite-nitrogen;

X6: pH; X7: Water content; X8: dry matter content; X9: total carbon; X10: C/N ratio; X11: total nitrogen; X12: cellulase; X13: urease; X14: β -glucosidase; X15: acid phosphatase; X16: dehydrogenase; X17: ammonia nitrogen)

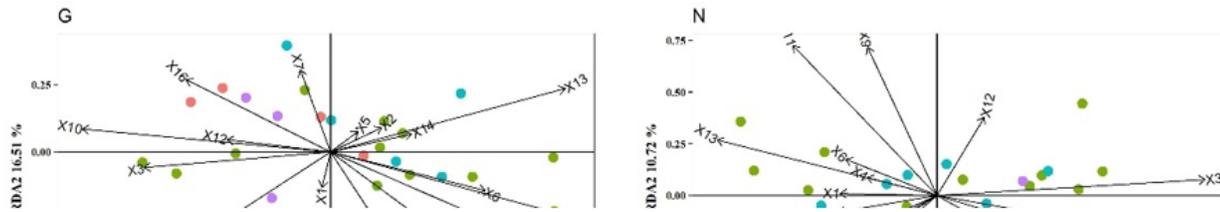


Figure 7

RDA analysis of soil physicochemical and enzymatic activities on the interpretation of community structure of different ecological niches of bacteria (Legend: P: *Pinus tabulaeformis* forest; M: Mixed forest; NNF: Near natural forest NF: Natural secondary forest; Figure caption: G: Generalized taxa, N: Neutral taxa, S: Specialized taxa; Arrows: X1: Organic carbon, X2: Effective phosphorus, X3: Total phosphorus, X4: Nitrate-nitrogen, X5: Nitrite-nitrogen, X6: pH; X7: Water content; X8: dry matter content; X9: total carbon; X10: C/N ratio; X11: total nitrogen; X12: cellulase; X13: urease; X14: β -glucosidase; X15: acid phosphatase; X16: dehydrogenase; X17: ammonia nitrogen)

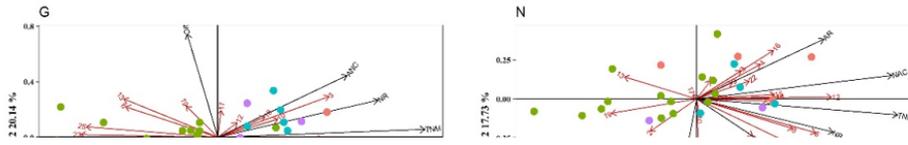


Figure 8

Interpretation of nitrogen mineralization by major genus structure of fungal generalized (G),neutral(N) and specific taxa(S) (legend: P: *Pinus tabulaeformis*; forest M: mixed forest; NNF: near natural forest; NF: natural secondary forest; the black arrows: AR: ammonification rate; NR: nitrification rate; NAC: change in nitrate; ANC: change in ammonia; NIC: change in nitrite TNM: total net mineralization)

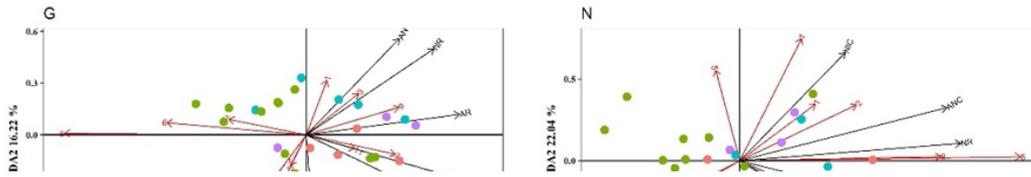


Figure 9

Interpretation of nitrogen mineralization by major genus structure of bacterial generalized (G), neutral (N) and specific taxa (S) (legend: P: *Pinus tabulaeformis* forest; M: mixed forest; NNF: near natural forest; NF: natural secondary forest; AR: ammonification rate; NR: nitrification rate; NAC: change in nitrate; ANC: change in ammonia; NIC: change in nitrite; TNM: total net mineralization)