



Article Phosphorus Limitation of Trees Influences Forest Soil Fungal Diversity in China

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Abstract: Fungal-biogeography studies have shown global patterns of biotic interactions on microbial biogeography. However, the mechanisms underlying these patterns remain relatively unexplored. To determine the dominant factors affecting forest soil fungal diversity in China, soil and leaves from 33 mountain forest reserves were sampled, and their properties were measured. We tested three hypotheses and established the most realistic one for China. The results showed that the soil fungal diversity (Shannon index) varied unimodally with latitude. The relative abundance of ectomycorrhizae was significantly positively correlated with the leaf nitrogen/phosphorus. The effects of soil available phosphorus and pH on fungal diversity depended on the ectomycorrhizal fungi, and the fungal diversity shifted by 93% due to available phosphorus, potassium, and pH. Therefore, we concluded that latitudinal changes in temperature and the variations in interactions between different fungal guilds (ectomycorrhizal, saprotrophic, and plant pathogenic fungi) did not have a major influence. Forest soil fungal diversity was affected by soil pH, available phosphorus, and potassium, which are driven by the phosphorus limitation of trees.



1. Introduction

Forest soil fungi are an important type of microorganism involved in the decomposition of organic matter in the forest soil, which can provide nutrients to plants through symbiosis with plants, and forest soil fungi diversity plays a pivotal role in maintaining the balance of the forest ecosystem [1]. The latitudinal gradient in forest soil fungal biodiversity has recently attracted considerable interest from ecologists [2,3]. Previously, little was known about how the fungal biodiversity of forest soils varies across latitudinal gradients [4,5]. Although fungal-biogeography studies have shown global patterns of biotic interactions in microbial biogeography, the mechanisms underlying these patterns remain relatively unexplored because it is difficult to distinguish the relevant factors that possibly modulate the soil fungi diversity [5,6]. At present, no key factors have been identified that can explain the global biogeographic pattern of microorganisms [7,8]. In addition, studies have focused mainly on single predictors rather than the mechanisms underlying these biogeographical patterns, making some of the findings of the studies questionable [9]. However, to date, knowledge of the mechanisms underlying soil fungi distribution has lagged behind in comparison with that of microorganisms. Additionally, there are few studies on the geographic mechanism of soil fungal diversity in different forest types [2]. Soil fungi play pivotal roles in the maintenance of the functions of forest ecosystems, and it is of great significance to investigate the major factors that can explain soil fungal diversity [10,11].

In general, as the latitude increases (from the warm tropics to the cold polarities), biodiversity gradually decreases [12]. Some studies suggest that soil fungi in forest ecosystems follow a similarly universal latitudinal trend caused by temperature change, even though



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Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). bacteria tend to not follow this pattern [13,14]. The possible underlying mechanism is that the latitude changes in temperature are often associated with variations in plant productivity and biodiversity, and the soil fungi diversity in warm, tropical soils is higher than that in cold poles [15-17]. The strongest evidence supporting this theory is that soil fungal richness is negatively correlated across the latitudinal gradients globally [5,18]. Another theory suggests that forest soil fungal biodiversity is mainly determined by plant–fungal interactions or interactions between different fungal guilds [16,19]. Soil symbiotic fungi (e.g., ectomycorrhizal fungi [EMF]) and plants belong to a mutually beneficial symbiosis relationship, and there is a close material exchange and energy circulation between soil fungi and plants, especially in high-latitude environments with limited nutrients [20,21]. The high abundance of EMF possibly promotes nutrient exchange between plants and fungi, thereby meeting the nutrient requirements of plants, and subsequently improves fungal diversity via positive plant–EMF feedback [22]. Furthermore, it is reported that plant pathogenic fungi in soils play essential roles in promoting the coexistence of plant species [23]. Thus, the forest soil fungal biodiversity may be affected by plant-soil-fungal interactions [24-26].

Recently, more attention has been paid to nutrient limitations, especially phosphorus (P) limitations, which affect soil fungal biodiversity [27]. Globally, as the latitude increases, forest ecosystems vary from P limitation to nitrogen (N) limitation, but most of the forest areas in China are P limited [28]. A meta-analysis of 65 field studies across the Earth's major forest ecosystems revealed that P limitations may shift with changes in biodiversity [29]. Research and model simulation based on resource optimization theory revealed that the biodiversity of forests was P limited [30,31]. Similarly, soil fungal diversity may also be affected by P limitations following the resource optimization theory. The changes of soil P bioavailability in different plant ecosystems possibly affect the material exchange and energy flow between plants and between plant–soil fungi, which affect the soil fungi biodiversity [32–34]. Forest soil fungal diversity alleviates the P limitation of plants by regulating the form of soil bioavailable P [8,35]. Plant symbiotic fungi (such as EMF) play pivotal roles in plant–microbe–soil interactions because they can exchange P and other nutrients [8,35,36]. P limitation may thus be considered a key factor affecting fungal diversity in forest ecosystems with diverse microbial species [33].

Which theory can best reflect the actual mechanism of forest soil fungal diversity construction? To address this question, we explored the following three hypotheses: (1) fungal diversity is mainly correlated with latitudinal change in temperature; (2) the latitudinal change of forest soil fungal diversity is mainly determined by the various interactions between different fungal guilds (such as EMF, saprotrophic, and plant pathogenic fungi); (3) the latitudinal change of forest soil fungal diversity is mainly dominated by the shift in the P limitation of trees. If the first hypothesis is the most realistic, the forest soil fungal diversity should be positively correlated with latitude [13]. If the second hypothesis is the most realistic, fungal guilds (such as ectomycorrhizal, saprotrophic, and plant pathogenic fungi) should be correlated with soil fungal diversity [37]. Finally, if the third hypothesis is the most realistic, the forest soil fungal diversity should be correlated with leaf N/P, which could reflect the P limitation of plants, along with soil available nutrition (such as P and potassium (K)) or pH [38]. To test these three hypotheses and establish which is the most realistic one for China, leaf and soil samples were collected from 33 forest reserves across China.

2. Materials and Methods

2.1. Soil and Leaf Sampling

The leaves and soil samples needed for the experiment were collected from 33 mountain forest reserves in China (Figure 1). These forest reserves are located within the range of latitude (21.40°–53.56° N) and longitude (101.03°–128.52° E). These areas are characterized by rich vegetation types (tropical forest, subtropical forest, temperate deciduous broadleaf forest, temperate mixed coniferous–broadleaf forest, boreal forest), mean annual precipitation (from 299 mm to 2209 mm), mean annual temperature (from -5.5 °C to 22.7 °C), mean annual humidity (from 46.4% to 80%), mean annual evapotranspiration (from 604 mm to 1278 mm) (Table 1). In each forest reserve, 9–15 sampling plots were randomly selected along the same aspect of the mountain, and 5 topsoil samples (5 cm depth) were randomly collected and immediately stored in a precooled polyethylene bag in each plot. At the same time, leaves of the dominant trees' species in each plot were sampled; specifically, 10 leaves were sampled from 2–5 healthy adult trees, and leaves were merged into a mixed sample for subsequent analysis. More details regarding the methods are available in Song and Zhou [39]. All meteorological data in the present study were downloaded from the National Meteorological Science Data Center of China (http://data.cma.cn (accessed on 14 April 2019)).



Figure 1. Map of forest station that was used for sampling.

2.2. Soil and Leaf Analysis

The MoBio PowerSoil DNA extraction kit (Carlsbad, CA, USA) was used to extract the DNA of soil samples. The primer sets ITS3 (5'–GCATCGATGAAGAACGCAGC–3') and ITS4 (5'–TCCTCCGCTTATTGATATGC–3') were used to determine the fungal community composition by polymerase chain reaction (PCR). The PCR reactions were performed as follows: 98 °C for 30 s, followed by 35 cycles of 98 °C for 10 s, 52 °C for 25 s, and 72 °C for 30 s, final extension 72 °C for 8 min. The EZNA Gel Extraction Kit (Omega BioTek, Doraville, GA, USA) and MiSeq NextGen platform (Illumina, San Diego, CA, USA) were used to purify and sequence the PCR products, respectively. After removing low-quality bases, FLASH (version 1.2) was used to merge paired-end reads [40]. MOTHUR (version 1.36) was used to demultiplex merged sequences to samples based on their unique barcodes [41]. Operational taxonomic units (OTUs) were clustered at the 97% similarity threshold by using USEARCH. OTUs were classified into different functional taxa by using FUNGuild [42]. After the samples were dried and ground, a Finnigan MAT 253 Isotope Ratio Mass Spectrometer and Flash 2000 EA-HT Elemental Analyzer (Thermo

Fisher Scientific Inc., Waltham, MA, USA) were used to measure the values of δ^{13} C, N, and P contents of the leaf samples. More details and the representative fungal OTU sequences can be found in Song and Zhou [39].

Table 1. Location, climate, and ve	egetation	information	of sample	ing sites.
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ID	Latitud (°N)	e Longitude (°E)	MAP (Mean e Annual Precipita- tion, mm)	MAT (Mean Annual Tempera- ture, °C)	MAH (Mean Annual Humid- ity, %)	MAE (Mean Annual Evapo- transpira- tion, mm)	Vegetation type
XSBN	21.4	101.56	1507	22.7	79	649	Tropical forest
SWD	21.89	107.91	1821	22.7	78.4	959	Tropical forest
DH	23.17	112.54	2073	21.5	79.2	976	Subtropical forest
AL	24.53	101.03	985	17.7	66.6	1278	Subtropical forest
NL	24.9	113.05	2082	19.5	77	750	Subtropical forest
DY	25.65	118.22	2011	20.3	76.9	978	Subtropical forest
LG	26.37	108.18	1558	16.3	80	674	Subtropical forest
JG	26.55	114.12	2084	18.7	78	689	Subtropical forest
ŴG	27.46	114.17	2068	18.2	78.1	690	Subtropical forest
LI	27.58	102.39	1119	16.3	61.1	1230	Subtropical forest
LQ	27.89	119.19	2209	18.5	75.2	792	Subtropical forest
FĨ	27.9	108.71	1501	15.2	79	604	Subtropical forest
GG	29.54	101.96	1049	11.2	62	1088	Subtropical forest
TM	30.36	119.43	1696	16.9	71.2	864	Subtropical forest
DBS	31.09	115.78	1420	16.1	74.3	707	Subtropical forest
SNJ	31.49	110.31	1052	15.9	73.1	661	Subtropical forest
JF	33.69	105.68	728	13.2	64.7	920	Temperate deciduous broard leaf forest
QL a	33.86	107.47	733	13.9	67.2	882	Temperate deciduous broard leaf forest
OL b	34	107.44	704	13.6	66.7	892	Temperate deciduous broard leaf forest
QL c	34.04	107.79	692	13.7	66.3	908	Temperate deciduous broard leaf forest
XLD	35.02	112.47	642	13.4	64.3	1039	Temperate deciduous broard leaf forest
GD	37.89	111.44	469	9.7	53.3	1171	Temperate deciduous broard leaf forest
WYZ	38.72	113.84	525	11.1	52.1	1048	Temperate deciduous broard leaf forest
SYK	38.74	105.91	299	8.9	46.4	1275	Temperate deciduous broard leaf forest
BMY	40.83	117.61	655	8.6	54.4	1058	Temperate deciduous broard leaf forest
CB a	42.08	128.07	948	5.1	69.5	725	Temperate mixed coniferous-broard leaf forest
CBb	42.21	127.85	929	5	69.1	722	Temperate mixed coniferous-broard leaf forest
SHB	42.44	117.51	537	4.4	54.9	1072	Temperate mixed coniferous-broard leaf forest
SHWL	44.21	118.72	503	3.4	55	1084	Temperate mixed coniferous-broard leaf forest
XX	46.63	128.52	692	2.8	70.3	700	Temperate mixed coniferous-broard leaf forest
DX a	50.32	123.05	495	-2.9	66.9	723	Boreal forest
DX b	51.63	123.52	371	-3.5	65.9	677	Boreal forest
MH	53.56	122.34	486	-5.5	64.4	697	Boreal forest

2.3. Statistical Analysis

The R packages "lavaan" and "piecewiseSEM" for structural equation modeling (SEM) were used to determine the pathways related to the observed effects of environmental predictors [43,44]. Fisher's C test was used to confirm the goodness of the modeling results. The illustration of the forest distribution map and the statistical analyses were performed by ArcGIS 10.2 (ESRI Inc., Redlands, CA, USA) and IBM SPSS Statistics 23.0 (IBM Inc., Endicott, NY, USA), respectively.

3. Results

3.1. Latitudinal Variations

As the latitude increased, the soil fungi Shannon index increased first and then decreased, and reached a peak at around 40° N (Figure 2A). The leaf N/P and the relative

abundance of EMF were significantly positively correlated with latitude (Figure 2B,C). Soil available P increased with latitude and then decreased significantly with latitude (Figure 2D). Soil available K and pH increased with latitude significantly (Figure 2E,F). The relative abundances of saprophytic fungi and plant pathogenic fungi were not correlated with latitude.



Figure 2. Relationship between latitude and (**A**) Shannon diversity index of soil fungi, (**B**) leaf N/P, soil (**C**) EMF relative abundance, (**D**) available P, (**E**) available K, and (**F**) pH.

3.2. Associations with Leaf N/P and Soil Fungal Communities

The soil fungi Shannon index was related to leaf N/P significantly in a unimodal trend and peaked at a value of approximately 10 (Figure 3A). The fungi Shannon index was significantly positively correlated with soil available P, K, and pH (Figure 3B–D). The EMF was significantly positively correlated with leaf N/P as well (Figure 4A). Soil pH, available P, and K were associated with leaf N/P in unimodal trends and peaked at a value of approximately 15 (Figure 4B–D). As the plant pathogens increased, the EMF continued to decrease; there was a significant negative correlation between the plant pathogens and EMF (Figure S1A). The leaf δ^{13} C varied with the plant pathogens in a bathtub-curve pattern (Figure S1B). Soil available P significantly decreased with the EMF relative abundance (Figure S1C).



Figure 3. Relationship between Shannon diversity index of soil fungi and (**A**) the N/P of leaves and soil (**B**) available P, (**C**) available K, and (**D**) pH.



Figure 4. Relationship between the N/P of leaves and soil and (**A**) EMF relative abundance, (**B**) pH, (**C**) available P, and (**D**) available K.

The SEM explained 66% of the variation in the fungal Shannon index and provided evidence that leaf N/P played essential roles in regulating the influence of latitudinal fungal diversity (Figure 5). In addition, the effects of soil available P and pH on fungal diversity depended on EMF, with the fungal Shannon index appearing to be shifted by 93% due to soil available P, K, and pH, respectively (Figure 5). These findings suggest that the P limitation of trees is the major predictor of soil fungal diversity.



Figure 5. Structural equation model describing the influence of driving factors on the forest soil fungal OTU Shannon index in China. The numbers next to the arrows indicate the effect size of the relationship. Red represents positive correlation, and grey represents negative correlation. * p < 0.05, ** p < 0.01, *** p < 0.001. Fisher's C = 25.823, P = 0.172, DF = 20, AIC = 71.823, BIC = 106.243.

4. Discussion

4.1. Biogeographical Variations in Soil Fungal Communities

The temperature in China gradually decreases from south to north, thus causing the plant and animal diversity to gradually decrease. If the forest soil fungal diversity was al-so following this pattern, it should be positively correlated with latitude [13,45,46]. However, the soil fungal diversity (Shannon index) showed a parabolic variation across latitudes; this shows that the first hypothesis was not the most realistic.

Certain studies suggest that such a peak (40° N) in fungal diversity might be caused by the variation in plant–soil interactions, in which EMF was the most important factor [24–26,47]. They found that the latitude variation of soil EMF diversity was similar to the variation in

the entire fungal diversity, which indicates that soil fungal diversity was mainly dominated by EMF [25,48]. Furthermore, the plant pathogenic fungi could also strongly affect the soil fungal diversity through the negative density-dependent hypothesis in forests [23]. However, we found that the EMF increased with latitude, indicating that the survival of trees in cold regions was more dependent on EMF than that in warm regions [47,49]. There was no significant relationship between saprotrophic and plant pathogenic fungal diversity and latitude. These results showed that fungal guilds were not correlated with latitude. Instead, EMF can inhibit pathogens, which is beneficial to plants [50]. Furthermore, leaf δ^{13} C can reflect plant long-term water-use efficiency, and it was reported that plant pathogenic fungi could affect leaf δ^{13} C [51,52]. These findings showed that EMF improved the host performance, ecosystem services, and plant diversity through positive density dependence or protection of plants [23,53,54], but soil fungal diversity does not rely on them. Therefore, the second hypothesis is also not the most realistic [37].

4.2. Associations between P Limitation and Soil Fungal Diversity

The soil fungi Shannon index first increased and then decreased with leaf N/P, and it reached a peak at a value of approximately 10 at around 40° N. Generally, leaf N/P reached a value of approximately 10, indicating that the nutritional limitation of plants shifted from P to N limitation. Therefore, the correlation between leaf N/P and fungal Shannon index suggests that the soil fungal diversity was strongly affected by nutritional limitation [55,56]. Leaf N/P was positively significantly correlated with latitude, in contrast with the global pattern [38]. Although we collected leaves of only dominant trees, the variation in whole plant leaf N/P with latitude is moderate in China [57]. As the latitude increased, the relative abundance of EMF also increased significantly, which is possibly due to the competitive dominance of EMF symbiotic with the most common tree species [53,58]. EMF can inhibit the mycorrhizal root colonization of neighboring arbuscular mycorrhizal herbs by promoting litter accumulation and limiting nutrient access, which enhances the competitive advantage of EMF trees [59,60]. During such processes, the dominant trees have been shown to absorb more nutrients, especially N, thus making the leaf N/P of the most common trees higher than other plants in high latitude areas, while the leaf N/P of whole plants was not significantly different from that of lower latitudes [61–64]. Meanwhile, tree roots deposit their exudates into the soil to promote mineral transformation and improve stress resistance [65,66], thus leading to soil available K being positively correlated with latitude.

Soil available P significantly increased with latitude and then decreased significantly with latitude, which was similar to the latitude variation of the fungal Shannon index. This indicates that fungal diversity was strongly affected by the plant utilization of P. Trees in colder areas or areas with P limitation rely more on EMF; therefore, the EMF was significantly positively correlated with latitude and leaf N/P [33,49]. More EMF, together with more root exudates, could release more available P and K under P limitation but would also acidify the soil [67–69]. Compared with arbuscular mycorrhizal fungi (AMF), the acidification effect of EMF is not strong. Moreover, EMF can absorb acidic exudates from roots; therefore, EMF can reduce soil acidification [70,71]. However, when trees were under extreme P limitation (leaf N/P > 15), the root–microbial systems absorbed more P and K. They also deposit more exudates into the soil so that the acidification is enhanced, resulting in lower soil pH and decreasing available P and K. Therefore, soil pH and available P and K concentrations are beneficial to soil fungi diversity [31,33,51]; therefore, there was a very significant positive correlation between soil fungi Shannon index and soil available P, K, and pH.

5. Conclusions

Compared with temperature and the various interactions between different fungal guilds, the P limitation of the trees was more similar to the dominant factor which influenced the latitudinal variations of forest soil fungal diversity in China. The SEM constructed

from the observed effects of environmental predictors explained 66% of the variation in the fungal Shannon index, and the fungal Shannon index changed by 93% due to soil available P, K, and pH variation driven by P limitation. Our study indicated that P limitation was the major factor that influenced the diversity and stability of the underground fungal community. Therefore, more attention should be paid to nutrient limitation in future research on the mechanisms of fungal diversity.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/ 10.3390/f13020223/s1, Figure S1: Relationships between soil–plant pathogen and (A) EMF relative abundance and (B) leaf δ^{13} C. Relationship between (C) soil available P and EMF relative abundance.

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