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Environmental Filtering Drives Local Soil Fungal Beta Diversity More Than Dispersal Limitation in Six Forest Types along a Latitudinal Gradient in Eastern China

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Abstract: Biogeographic patterns of soil fungal diversity have been well documented in forest ecosystems, but the underlying mechanisms and processes that shape these patterns remain relatively unknown. This study took soil samples from 300 forest plots spanning six forest types along a latitudinal gradient in eastern China, which ranges from tropical rainforest to boreal forest ecosystems. A null-model analysis was used to compare the observed soil fungal beta diversity (β-diversity) with the β-diversity expected from random sampling of each local species pool. We also compared the relative importance of environmental and spatial variables on soil fungal β-diversity among forest types along the latitudinal gradient. Our results found that observed β-diversity was greater than expected β-diversity in all six forest types, which means that species tend to be more aggregated than expected. We determined that this species aggregation resulted from both environmental filtering and species dispersal limitations. Further, environmental variables had stronger influences on β-diversity than spatial dispersions. Additionally, the co-occurrence network showed that more species interactions occurred in the mid-latitude forests which lead to decreased soil fungal β-diversity and low interpretations of environmental and spatial variables. Study of these processes in different forest types along latitudinal gradients will provide important insights that local differences in the relative importance of different community assembly processes creates different gradients in global biodiversity.

Keywords: forest ecosystem; soil fungal beta diversity; community assembly; environmental filtering; dispersal limitation; microbial communities

1. Introduction

Over the past several decades, researchers have found that soil microbes exhibit some biogeographic patterns in species diversity and distribution [1]. The mechanisms underlying these biogeographic patterns are difficult to distinguish in forest ecosystems because multiple community assembly processes may govern biogeographic variation in soil microbe diversity [2,3]. For example, soil fungal community composition could result from niche processes (such as environmental filtering) [4,5]. Alternatively, neutral processes associated with dispersal limitations also contribute to the patterns of a soil fungal community [6,7]. These processes are difficult to separate, and therefore

a more comprehensive perspective should integrate both processes to understand how and why their relative influences vary across forest types [8].

One way to disentangle multiple community assembly processes is to examine patterns of diversity across forest types, with a particular focus on beta-diversity (β-diversity). Patterns of site-to-site variation in species community assemblage, known as β-diversity, can provide fundamental insights into the importance of community assembly processes in generating community structure along biogeographical gradients [3,9]. The concept of β-diversity links not only the relationship between local diversity and regional diversity, but also captures the fundamental point of environmental gradients on species assemblages [10,11]. Soil microbial β-diversity is often associated with three main community assembly mechanisms. First, niche-based processes, for example, environmental filtering, could increase β-diversity [12]. This is because species are selected from a regional species pool based on their niche, but subsequent filtering of species composition could vary with environmental factors [13,14]. Many environmental factors, such as temperature and soil parameters play important roles in structuring microbial communities [15–18]. Second, species dispersal limitation, a key component of the neutral theory [19], also could increase β-diversity [20,21]. Increasing evidence shows that dispersal limitation has an important role in determining the composition of soil microbial communities, since individual species tend to disperse to nearby areas, and closer sites will always contain more similar species than those further apart [22]. Thus, dispersal limitation could lead to aggregated distributions of soil microbial species [23] and increase β-diversity. Third, variations in β-diversity patterns can also result from species interactions [14,24], with greater interspecific competition decreasing β-diversity [25]. These mechanisms are widely recognized as key factors for shaping soil microbial distribution but understanding how these processes affect soil microbial β-diversity patterns in forests with different environments have until recently received limited attention [26].

Mechanisms shaping soil microbial communities are ultimately governed by the underlying structure of the environment gradients [21,27]. A strong role of environmental heterogeneity or homogeneity on the microbial community has been observed among different regions [21,28]. The difference in soil microbial diversity among locations may be due to the variety of environmental gradients [29,30]. It is also likely that the striking gradients in species composition may attribute to changes of species dispersal limitation across geographic scales [31]. Dispersal limitation varies with different geographic gradients, and such gradient-dependent patterns have also been observed in soil microorganisms [32]. In addition, biotic interactions within fungal communities may vary along latitudinal gradients, resulting in different strengths of assembly of different mechanisms across forest ecosystems [33]. Yet, few studies to date have focused on how these complex assembly processes shape observed patterns together in soil fungal diversity in different forest types across latitudinal gradients.

Soil fungi are crucial components of microbial communities in forest ecosystems, where they play fundamental ecological roles in soil formation, conservation and regulating nutrient cycling [34]. To investigate the mechanisms underlying soil fungal β-diversity in different forest types along a latitudinal gradient, we took soil samples from 300 forest plots spanning six forest types in eastern China that ranged from tropical (18°43′ N) to cold temperate climates (53°27′ N). We compared soil fungal β-diversity in six forest types and analyzed whether it was different from a null model based on random sampling from the regional species pool [11]. Deviations of β-diversity from the null expectation (β-deviation) would suggest an overriding role for biogeographical processes that determine the distributions of soil fungi. Positive β-deviations would indicate that species are more spatially aggregated (or discrete clustering) due to dispersal limitation or environmental filtering; negative β-deviations indicate that species are over-dispersed as a result of species interactions; finally, β-deviations of zero would indicate that species are determined by stochastic processes [3,11]. We aimed to address the following main questions: (1) How does soil fungal β-diversity vary among forest types along a latitudinal gradient? Do soil fungi show aggregation or over-dispersed distribution? (2) What are the changes of community assembly processes that shape soil fungal β-diversity in different forest

types across latitudinal gradients? Does the relative importance of underlying community assembly processes vary across different forest types?

2. Materials and Methods

2.1. Experimental Design and Field Sampling

Six forest types from south to north of eastern China across the latitudinal gradient were selected in our study. Those forests span a latitudinal range from 18°43′ N to 53°27′ N (Figure 1). The mean annual temperature ranges from 24.5 to –5.5 °C. The mean annual precipitation ranges from 460 to 2449 mm. The selected forest types were named according to the classification given by Zhang [35]. These forest types are the major forest types of eastern China: tropical rain forest (TRF), subtropical evergreen broad-leaved forest (SEB), subtropical evergreen-deciduous broad-leaved mixed forest (SED), warm-temperate deciduous broad-leaved forest (WDB), temperate needle-leaf and deciduous broad-leaved mixed forest (TDB) and cold-temperate deciduous needle-leaf forest (CDN). Information about site locations and vegetation are given in Table 1.

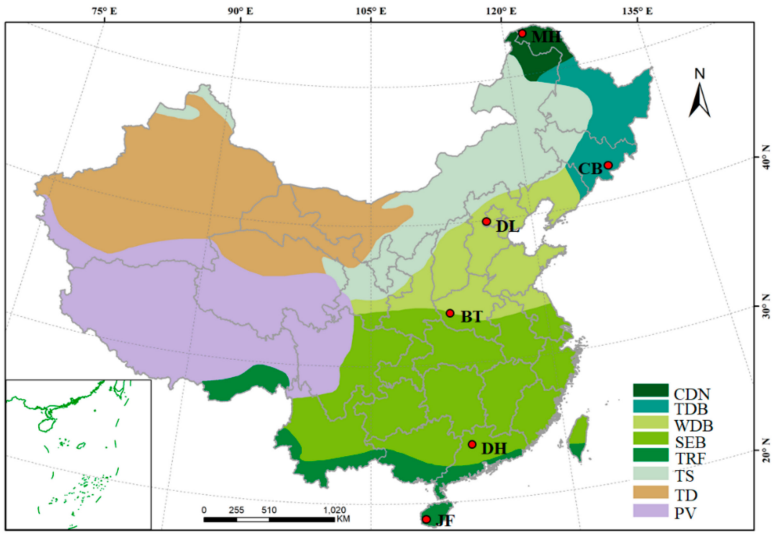


Figure 1. Locations of the sampling sites in six forest types of eastern China. TRF, tropical rain forest; SEB, subtropical evergreen broad-leaved forest; WDB, warm-temperate deciduous broad-leaved forest; TDB, temperate needle-leaf and deciduous broad-leaved mixed forest; CDN, cold-temperate deciduous needle-leaf forest; TS, temperate steppe; TD, temperate desert; PV, Qinghai–Tibet Plateau alpine vegetation; JF, Jianfeng Mountain; DH, Dinghu Mountain; BT, Baotian Mountain (forest type: subtropical evergreen-deciduous broad-leaved mixed forest (SED)); DL, Dongling Mountain; CB, Changbai Mountain; MH, Mohe.

Table 1. Site information for the six forest types in eastern China.

Site	Forest Type	Dominant Tree Species	Location
JF	Tropical rain forest	*Gironniera subaequalis* Planch. *Cryptocarya chinensis* Hemsl.(Lauraceae)	18°44′22″ N 108°51′59″ E
DH	Subtropical evergreen broad-leaved forest	*Schima superba* (Theaceae) *Castanea henryi* (Skan) Rehd. et Wils	23°10′03″ N 112°10′01″ E

Table 1. *Cont.*

Site	Forest Type	Dominant Tree Species	Location
BT	Subtropical evergreen-deciduous broad-leaved mixed forest	*Quercus aliena .var. acuteserrata* Maxim. ex Wenz.	33°29′32″ N 111°55′32″ E
DL	Warm-temperate deciduous broad-leaved forest	*Quercus variabilis* Blume *Quercus wutaishanica* Mayr	39°57′27″ N 115°25′29″ E
CB	Temperate needle-leaf and deciduous broad-leaved mixed forest	*Pinus koraiensis* Sieb. et Zucc. *Betula platyphylla* Suk	42°20′51″ N 128°8′55″ E
MH	Cold-temperate deciduous needle-leaf forest	*Larix gmelinii* (Ruprecht) Kuzeneva *Betula platyphylla* Suk	53°27′46″ N 122°20′20″ E

JF, Jianfeng Mountain; DH, Dinghu Mountain; BT, Baotian Mountain; DL, Dongling Mountain; CB, Changbai Mountain; MH, Mohe.

A total of 300 plots (fifty 20 × 20 m plots in each forest type) were sampled. In each forest type, the ranges of elevations and slopes were similar. The farthest distance between the two plots was about 9 km in each forest type and plots were far from any areas with recent anthropogenic disturbance. Our spatial sampling approach was appropriate to capture the potential responses of soil fungal species composition to fine-grained environmental heterogeneity and the effects of distance among locations at similar scales. Five soil cores taken at depths ranging from 0 to 10 cm were combined into a single sample for each 20 × 20 m plot. Roots and rocks were removed before homogenizing each soil sample. Each soil sample was taken to the laboratory in an ice box and then kept at −80 °C for subsequent DNA extraction and molecular test.

2.2. Climate Data and Geographic Distance

We obtained the mean annual temperature and the mean annual precipitation of each plot from the WorldClim database (www.worldclim.org) [36]. Geographic coordinates and the elevation of each plot were recorded with a handheld GPS. The pairwise geographic distance between plots was calculated using the Imap package in R using the coordinates.

2.3. Soil Physicochemical Analysis

Soil pH was measured with a digital pH meter (Mettler-Toledo GmbH, Greifensee, Switzerland) using a 1:2.5 (volume) soil/water mixture. Soil water content (SWC) was weighed after drying in an oven at 105 °C for 48 h. Soil organic carbon (SOC), soil total nitrogen (STN) and soil available nitrogen (SAN) were measured in the laboratory according to standard methods [37]. Soil C/N ratio was determined from the soil organic carbon and total nitrogen concentrations.

2.4. Amplification, Illumina Sequencing and Bioinformatics

We extracted microbial genomic DNA using the MoBio PowerSoil DNA isolation kit (MoBio Laboratories, Carlsbad, CA, USA) [38]. We assessed the quality and concentrations of the extracted DNA using a NanoDrop Spectrophotometer (NanoDrop Technologies Inc., Wilmington, DE, USA), and each sample was stored at −20 °C until further use. The universal primers ITS4 (5′-TCCTCCGCTTATTGATATGC-3′) and gITS7F (5′-GTGA RTCATCGARTCTTTG-3′) were used for PCR amplification. PCR products for each sample were pooled and purified using SanPrep DNA Gel Extraction Kit (Sangon Biotech, Shanghai, China). All the PCR products were mixed in equal molar amounts for library construction, and then sequenced with the Illumina MiSeq platform. The details of the PCR procedure and Miseq sequencing were described previously [39].

Raw sequence data were processed using the QIIME software platform (1.7.0). The sequence libraries were split and denoised to avoid diversity overestimation. A total of 7000 sequences per sample were performed. Operational taxonomic units (OTUs) were clustered with a 97% similarity cutoff using the UPARSE pipeline, and chimeric sequences were identified and removed using UCHIME [40] Singleton OTUs and OTUs that were assigned to non-fungal organisms or that had unreliable BLAST matches were removed. These OTUs were then used as a foundation for calculating β-diversity metrics using QIIME software platform (1.7.0) [41].

2.5. Statistical Analyses

Soil fungal β-diversity was calculated for each forest type. We defined β-diversity as the community dissimilarity among plots using Bray–Curtis dissimilarity matrices [42]. Principle coordinates analysis (PCoA) was used to explore overall patterns of soil fungal community composition based on Bray–Curtis dissimilarity distances (QIIME software platform 1.7.0.). Soil heterogeneity of each sampling region was tested using the coefficient of variation (CV) for each soil variable. A higher coefficient of variation indicated higher soil heterogeneity [43]. We then used polynomial curve fitting to estimate the relationship between CV and forest types (Origin software 8.5).

A null-model analysis was applied to compare the observed β-diversity with the β-diversity expected from random sampling of each local species pool. After 999 randomization iterations of the null model, a standardized effect size (β-deviation) was calculated as the difference between the observed and expected dissimilarity [3,11]. One-way analysis of variance was used to determine the significant differences of soil fungal β-diversity and β-deviation in all forest types (SPSS 19.0, IBM, New York, NY, USA).

To analyze the influences of environmental and spatial variables on β-diversity, distance-based redundancy analysis (dbRDA) was used to detect the partitioning of variation in β-deviation among environmental and spatial factors (R vegan package) [11]. Environmental variables for each forest type included: six soil variables (soil pH, soil water content, soil organic carbon, soil total nitrogen, soil available nitrogen and soil C/N ratio); two climate variables (the mean annual precipitation and the mean annual temperature); and two topographic variables (elevation and slope). Spatial variables included: coordinates (latitude and longitude of each plot) and spatial eigenfunctions calculated from principal components of neighbor matrices [44,45]. Collinearity among environmental factors was checked before dbRDA was performed [46]. Then, we used forward selection ('ordiR2step' in the R vegan package) to partition variation in β-deviations into individual fractions explained by environmental and spatial variables [11,47]. We also analyzed the relationships between matrices for β-diversity and environmental variables using Mantel tests with Spearman correlations ('vegan' package in R) [48]. Soil fungal species–species (OTU–OTU) interaction networks were calculated using SparCC, a tool that can estimate correlation values from compositional data. The quality of reads was grouped at 97% sequence identity, and the 500 most abundant OTUs in each forest were selected for calculation. SparCC correlations above 0.6 or below −0.6 and reaching statistical significance ($p < 0.01$) were used in network analyses [49]. The co-occurrence of networks in each forest was calculated and visualized using the platform Gephi [50]. The nodes in the networks represent the OTUs at 97% identity, and the significant correlations between nodes were represented by edges (connections) [51].

3. Results

The dominant soil fungal phyla across the sampling sites were listed in Table S1. Soil fungal β-diversity showed significant changes along latitudes with the lowest β-diversity in mid-latitude forests (WDB and TDB, $p < 0.01$; Figure 2). This result was confirmed by the PCoA analysis of community composition, which showed that soil fungal species tend to be more clustered in mid-latitude forests than in high and low latitude forests (TRF, SEB, SED and CDN; Figure 3).

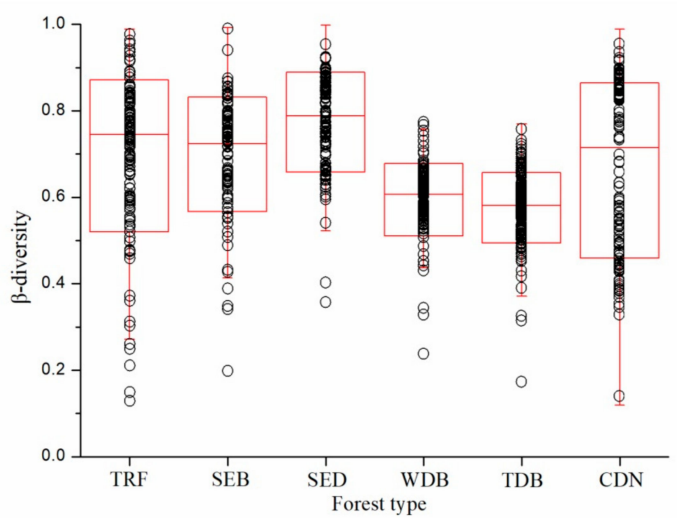


Figure 2. Soil fungal beta-diversity (β-diversity) in six forest types along a latitudinal gradient. TRF, tropical rain forest; SEB, subtropical evergreen broad-leaved forest; SED, subtropical evergreen-deciduous broad-leaved mixed forest; WDB, warm-temperate deciduous broad-leaved forest; TDB, temperate needle-leaf and deciduous broad-leaved mixed forest; CDN, cold-temperate deciduous needle-leaf forest. The same for below.

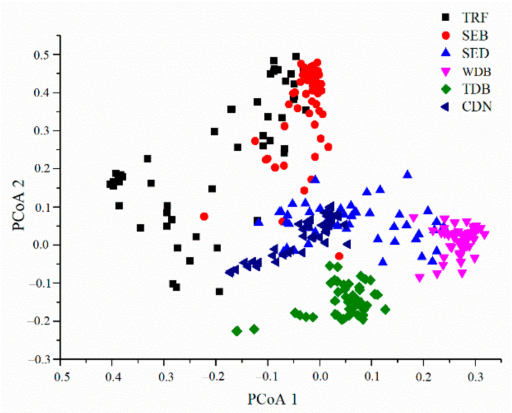


Figure 3. Principle coordinates analysis (PCoA) illustrating patterns of soil fungal communities grouped by different forest types.

Our null model analysis revealed that observed soil fungal β-diversity was greater than expected in all forest types, regardless of latitude. Consequently, all β-deviations were positive, which suggests that soil fungal species composition is in general aggregated (or clumped) in all six forest types. However, β-deviations were lower in the mid-latitude forests (WDB and TDB, $p < 0.01$) with less species aggregation (Figure 4).

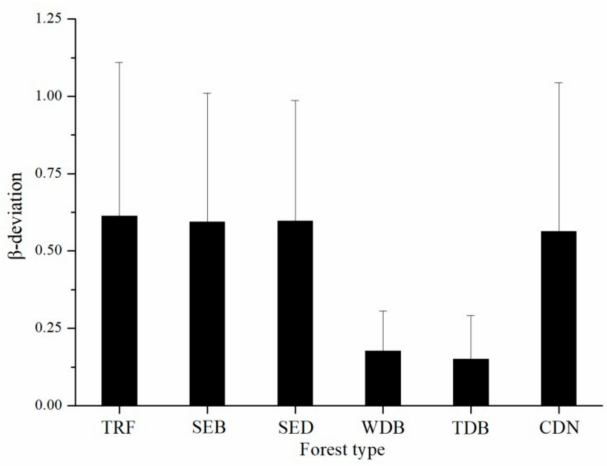
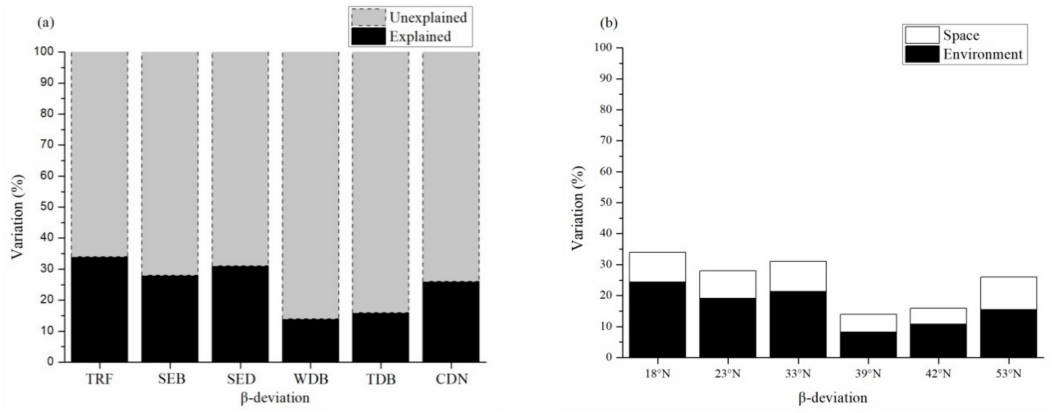


Figure 4. Variation in soil fungal β-deviation in six forest types along a latitudinal gradient.

Whether intraspecific aggregation resulted from environmental filtering or species dispersal limitation was identified, results indicated that both environmental variables and spatial gradients explained a large fraction of the soil fungal β-deviations in each forest type (Figure 5). Environmental and spatial variables explained 26%–34% of the β-deviations in low and high latitude forests (TRF, SEB, SED and CDN), and only explained 14% and 16% in mid-latitude forests (WDB and TDB) (Figure 5a). In addition, environmental variables explained a larger fraction of the β-deviations than spatial variables in all six forest types (Figure 5b). Among these environmental variables, soil pH, soil organic carbon, soil total nitrogen, soil available nitrogen and soil C/N ratio significantly affected β-diversity (Table 2). The CV of soil variables that were significant predictors was higher than those that were not significant, which showed the relative importance of soil heterogeneity in determining β-diversity patterns in low- and high-latitude locations (TRF, SEB, SED and CDN; Figure 6).



(**a**) (**b**)

Figure 5. Soil fungal β-deviation explained by environmental and spatial variables in six forest types along a latitudinal gradient. (**a**) Total variation in β-deviation based on distance-based redundancy analysis. (**b**) Variation in β-deviations explained by environmental and spatial variables after forward model selection.

Table 2. Correlations of soil fungal β-diversity with environmental distance (averaged at the plot level) from Mantel tests in six forest types.

Environmental Variable	TRF		SEB		SED		WDB		TDB		CDN	
	ρ	*p*	ρ	*p*	ρ	*p*	ρ	*p*	ρ	*p*	ρ	*p*
MAP	0.05	n.s.	0.04	n.s.	0.07	n.s.	0.06	n.s.	0.02	n.s.	0.06	n.s.
MAT	0.03	n.s.	0.07	n.s.	0.08	n.s.	0.04	n.s.	0.01	n.s.	0.04	n.s.
Elevation	0.09	n.s.	0.02	n.s.	0.05	n.s.	0.04	n.s.	0.06	n.s.	0.02	n.s.
Slope	0.1	n.s.	0.03	n.s.	0.02	n.s.	0.05	n.s.	0.04	n.s.	0.01	n.s.
Soil pH	0.22	0.02	0.08	n.s.	0.04	n.s.	0.1	n.s.	0.16	0.04	0.03	n.s.
SWC	0.09	n.s.	0.07	n.s.	0.12	n.s.	0.04	n.s.	0.06	n.s.	0.08	n.s.
SOC	0.28	0.001	0.23	0.02	0.08	n.s.	0.01	n.s.	0.02	n.s.	0.22	0.02
STN	0.25	0.01	0.08	n.s.	0.24	0.01	0.1	n.s.	0.15	0.04	0.09	n.s.
SAN	0.05	n.s.	0.25	0.01	0.23	0.01	0.21	0.02	0.04	n.s.	0.05	n.s.
Soil C/N	0.09	n.s.	0.14	0.04	0.2	0.02	0.09	n.s.	0.01	n.s.	0.19	0.02

MAP, mean annual precipitation; MAT, mean annual temperature; SWC, soil water content; SOC, soil organic carbon; STN, soil total nitrogen; SAN, soil available nitrogen; soil C/N, soil C/N ratio; ρ, rho correlation; n.s., not significant.

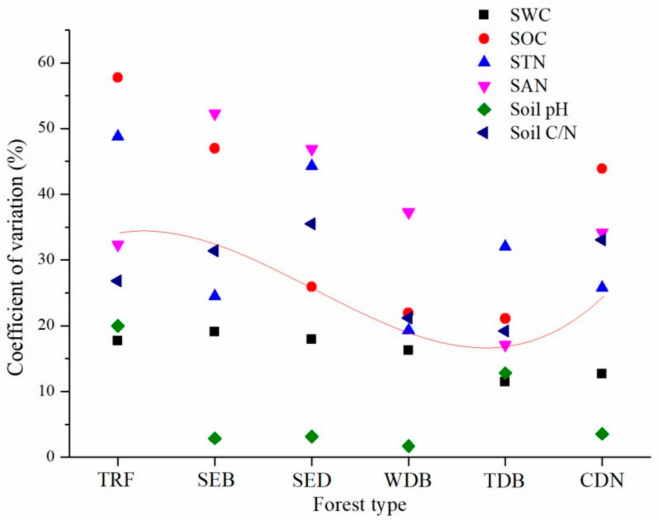


Figure 6. Coefficient of variation (CV) for soil variables in six forest types along a latitudinal gradient. The higher variation means higher soil heterogeneity. The other CVs for climatic and topographic variables have no significant relationship to soil fungal β-diversity and are not shown in the figure.

The topological features of co-occurrence networks showed that the number of edges was higher in mid-latitude forests (WDB and TDB) than in other forests (Figure 7). Overall, the frequency of soil fungal species co-occurrences showed a hump-shaped pattern with highest competition in the mid-latitude forests.

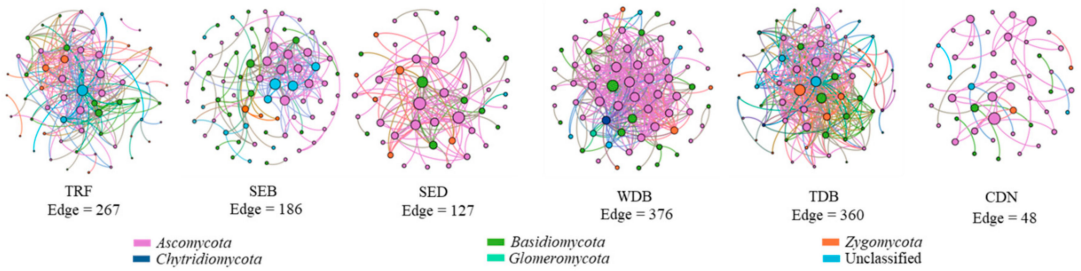


Figure 7. Network co-occurrence analysis of soil fungal communities in six forest types along a latitudinal gradient. Nodes are labeled at the phylum level. The correlations between operational taxonomic units (OTUs) are represented by edges that connect these nodes.

4. Discussion

Despite these recent efforts to describe different soil fungal β-diversity at different habitats [4,33,52], few studies have focused on whether soil fungi communities present aggregation or diffusion distribution in different forest types along a latitudinal gradient. Although soil fungal β-diversity was found to be remarkably lowest in mid-latitude forests (WDB and TDB) (Figure 2), our null model analysis revealed that soil fungal species tend to be more aggregated in all forest types (Figure 4). Species aggregation can emerge through different community assembly processes, including environmental filtering and dispersal limitation [3]. After applying a model for predicting soil fungal β-diversity that combines spatial and environmental properties, our study further found that environmental filtering by SOC, STN, SAN, soil C/N and soil pH and dispersal limitation appear to work together to determine soil fungal β-diversity (Figure 5a). However, it does not mean that environmental filtering and dispersal limitation processes operate in a similar role in different forest types. The explanation of environmental properties was greater than spatial variables, which means the environmental filter had a stronger influence than dispersal limitation in shaping soil fungal β-diversity patterns in all forest types (Figure 5b). This result is partially consistent with the niche theory which indicates that species can spread anywhere the environment is suitable [53,54]. In addition, the lowest β-deviations in mid-latitude forests suggest that some other community assembly processes (e.g., biotic interactions) decrease species aggregation in those forests [55].

Different soil fungal β-diversity patterns among forest types could be the result of different levels of environmental heterogeneity within forests (Table 2, Figure 6) [33]. Soil fungal community composition has been proven to result from different environmental conditions [4,56]. For example, soil heterogeneity has proved to be an important factor that contributes to soil microbial β-diversity in soils [43]. Habitat specialization resulting from species adaptive strategies has an important role in determining species' distributions [57]. This crucial process is strongly driven by environmental heterogeneity [58]. Thus, in comparison with relatively homogeneous environments in mid-latitude forests (Figure 6), heterogeneous soil environment in low- and high-latitude forests (TRF, SEB, SED and CDN) may increase β-diversity by enhancing environmental filtering. The effects of different heterogeneous soil factors on soil fungal β-diversity can be explained from the following existing studies. For example, soil nutrients always tend to accumulate heterogeneously in forest ecosystems [59], and the variation of soil nutrients can be extraordinarily high even at fine spatial scales [4]. Due to variation in utilization of edaphic nutrients by fungal species, which vary in their ability to produce enzymes [60,61], soil nutrient heterogeneity can substantially influence soil fungal anabolism and foraging strategies [62,63]. Thus, the heterogeneity of soil C/N and soil pH among forest types along a latitudinal gradient were key factors constraining soil fungal β-diversity patterns in our study. Overall, this result together with other results showing soil nutrients (such as soil C and N) and soil pH are important determinants of soil fungal β-diversity [64,65]. Our results also show that soil fungal β-diversity in different forest types is affected by different soil C/N and soil pH, and there is no one soil parameters that is responsible for β-diversity in all forest types. This result reflects the variability and unpredictability of soil factors that affect β-diversity in different forest types.

Some studies considered that soil pH has little effect on soil fungal communities [66,67], others identified soil pH as an important predictor of soil fungal communities at both global [68] and fine [4] spatial scales. Those uncertainties of the effect of soil pH on soil fungal communities may be due to the lack of comparative study. Our results suggest that soil pH could be a driver that explains β-diversity in TRF and TDB with relatively higher soil pH CVs, however, the lack of a significant relation with other forests shows that it is still weak to confirm soil pH as a determinant of soil fungal β-diversity in a forest ecosystem. This may be because although soil pH can directly affect fungal community composition by imposing a physiological constraint on soil fungal survival and growth [69], little effect will exist if soil pH is in a stable range [70]. Furthermore, soil pH may also affect fungal communities indirectly; only when there is significant interaction can soil pH impact soil

fungal β-diversity significantly, for example, through soil nutrient availability and altered interactions between soil fungi and bacteria [71].

In addition, even though mean annual temperature and mean annual precipitation are good predictors of soil fungal community composition at a continental scale [68,72], we showed that these climatic variables cannot predict the pattern of soil fungal β-diversity at local scales along the latitude. This result is inconsistent with those of previous studies which highlighted the weak effects of climate on soil microbial diversity at relatively small spatial scales [73,74]. The weak correlation is likely because climate factors are relatively invariant at local spatial scales.

Soil fungal communities become less similar with increasing geographic distance at both large [75,76] and small spatial scales [31]. Similar dispersal limitation was observed in our study, which showed that there is a limited spatial distribution of soil fungal communities at local scales in six forest types. Dispersal limitation resulted in strong species aggregation of soil fungi, but that effect was second to environmental effects in our study (Figure 5b). This may be because species dispersal itself is affected by environmental factors. Indeed, variation in species dispersal limitation is significantly related to the variability of environmental heterogeneity among different habitats [77]. For example, spatial configuration and environmental variety (e.g., size or isolation of habitats) have important impact on the resistance to movement of many species, and therefore to dispersal abilities in Amazonian forests [78]. Thus, the dispersal limitation of soil fungi in our study may be affected by environmental heterogeneity [79]. In addition, the dispersal limitation of soil fungi may be also due to the property of soil fungal species themselves. Since they are generally larger, soil fungi are more likely to be blocked by geographical barriers than bacteria and archaea [80]. Soil fungi were predominantly hypogenous with relatively short spatial transmission distance, but this may also be due to poor competitions of some fungi that cannot settle in new habitats [5]. For example, fungi in the genus *Glomus* which exist as arbuscular mycorrhizal symbionts undergo dispersal limitation at small scales (<3 km) [81]. This dispersal limitation then reduces the likelihood that soil fungal species reach all suitable habitats, resulting in intraspecific aggregation in all six forest types.

It is noteworthy that the low β-diversity and β-deviation in the mid-latitude forests (WDB and TDB) may be related to community assembly processes that lead to species homogeneity, such as interspecific competition [14,24]. A co-occurrence network-based analysis was used to evaluate the potential contributions of species interactions. This network method has been effectively applied to explore potential microbial interactions beyond those of simple richness and composition in various ecosystems [55,82]. With a series of significant soil fungal species–species correlations, our results suggest that soil fungal species interaction intensity in mid-latitude forests was higher than in low and high latitudes (Figure 7), leading to a decrease in β-diversity and little effect of environmental and spatial variables. The potential explanation for this strong species interaction may be the homogeneous environment in mid-latitude forests, which results in weak niche differentiation between soil fungal species [83,84].

Although the selected environmental parameters and geographic distance explained 14–34% of the variation in soil fungal β-diversity, a large proportion of the variation could not be explained which indicated that soil fungal β-diversity may reflect a series of undiscovered community assembly processes (e.g., ecological drift) [85], plants [86], species pool [25], or some unmeasured environmental factors, such as soil nutrient availability and soil texture [81]. Clearly, the multiple processes and factors which determine soil fungal β-diversity in different forest types, and accurate prediction of changes in soil fungal β-diversity of forest ecosystems at local to global scales require comprehensive data acquisition and targeted sampling along environmental gradients.

5. Conclusions

This study shows a systematic analysis of local soil fungal community assembly processes in six forest types along a latitudinal gradient, which run from the tropics to the cold temperate forests of eastern China. The results show that soil fungal species tend to be more aggregated than expected in

all forest types along a latitudinal gradient. This aggregated distribution of soil fungal β-diversity was explained by a combination of community assembly processes, including environmental filtering and species dispersal limitation. We further found that environmental variables had a stronger influence on soil fungal β-diversity than species dispersal limitation. Additionally, soil fungi showed more species interactions in the mid-latitude forests, which decreased the clustering of soil fungal species. Although it is difficult to disentangle the mechanisms that maintain the compositional patterns of soil fungal communities, our study provides an important attempt to explore fungal β-diversity patterns from forest soil across latitudes, and to consider their complex mechanisms in relation to basic models in theoretical macroecology.

Supplementary Materials: The following are available online at http://www.mdpi.com/1999-4907/10/10/863/s1, Table S1: The dominant soil fungal phyla across the sampling sites.

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