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Inconsistent diversity patterns of soil fungi and woody plants among habitat types in a karst broadleaf forest

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ABSTRACT

The diversity patterns of macroorganisms (i.e., plants) among different habitats have been well documented, however, those of microorganisms (i.e., fungi) as well as the relationships between them are still unclear. Here, we tested whether and to what degree fungal diversity was related to habitat types and compared diversity patterns of woody plants and soil fungi. We carried out field investigations on soil fungi in different habitat types (i.e., valleys, foothills, hillsides, and hilltops) in a 25-ha karst broadleaf forest in Southwest China. The tree richness, Shannon index, and Simpson index significantly increased from valleys to hilltops. While the soil fungal N_1 diversity (the exponential Shannon index) marginally increased toward valleys, fungal N_0 (richness) and N_2 (the inverse Simpson index) diversity exhibited significantly reduced and increased patterns, respectively, from valleys to hilltops. The major fungal functional groups (i.e., EcM, AM, saprotrophic, and pathogenic fungi) showed similar increasing richness patterns in valleys. Moreover, woody plant alpha diversity was an important indicator of fungal functional groups except for EcM and AM fungi. In addition, woody plants increased in species turnover rate (β_{SIM}) from valleys to hilltops, while fungal species had a concave distribution. The patterns of nestedness (β_{SNE}) for tree species decreased from valleys to hilltops, while the opposite was true for soil fungal species. Our findings indicated that the diversity patterns of woody plants and fungi were inconsistent among habitat types, and the relationships between fungal and woody plant communities depended on habitat types in the karst forest.

1. Introduction

Soil fungi plays a key role in nutrient cycling and ecosystem function in terrestrial ecosystems, i.e., the decomposition of plant litter, conditioning of plant pathogens (Zeilinger et al., 2016), and mutualistic interactions with plants (Smith and Read, 2008). On one hand, soil fungi influence plant communities *via* soil nutrient availability and mediate plant coexistence (van der Putten et al., 2013; Bever et al., 2015; Bennett and Cahill, 2016). On the other hand, plants affect fungal communities *via* specificity for hosts (Verbruggen et al., 2012) and generating diverse organic substrates and microhabitats (Wardle, 2006; Dickie, 2007). Moreover, individual fungal taxa also differ in their capacities to acquire energy from plant resources, which is influenced by litter nutrient content *via* abundance and activity of extracellular enzymes (Schneider et al., 2012). Strong interactions exist between plant and soil microbial communities in terrestrial ecosystems. Although many studies on plant communities among habitat types or at different scales have been widely conducted, a clear understanding of their interactions with soil microbial communities remains elusive.

Fungal diversity could increase plant diversity (van der Heijden et al., 1998) *via* direct and indirect effects on soil organisms and the food web (Wardle et al. 2004). Specifically, soil symbiotic and pathogenic microbes can affect plant diversity by altering plant dominance (van der Heijden et al., 2008). Mutualistic symbionts such as mycorrhizal fungi facilitate plant nutrient uptake and improve plant resistance to disease (van der Heijden et al., 2006). Meanwhile, plant diversity is suspected to facilitate soil microbial diversity by providing diverse plant hosts for symbiotic and pathogenic biomes (Eisenhauer

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et al., 2010; Millard and Singh, 2010), and also provide diverse food resources and microhabitats. However, the relationship between soil microbial diversity and plant diversity varies and depends on different ecosystems, climate zones, and habitats. For example, plant diversity could predict patterns in soil microbial community composition (i.e., beta diversity) across grasslands worldwide (Prober et al., 2015). Furthermore, the community dissimilarities of total fungi and dominant guilds significantly increased with increasing plant phylogenetic distance (Yang et al., 2019). While diversity patterns between soil fungi and plants were contrasting along a latitude gradient over five climate zones in China, which indicated that plant and microbial diversity lack similarity among habitat types (Hu et al., 2019). Moreover, mechanisms influencing soil fungal diversity and community composition differed between ridge and valley habitats, and the relationships between fungal and woody plant assemblages depended on habitat types in subtropical forest ecosystems (Gao et al., 2017). Therefore, the relationships between plant diversity and fungal diversity as well as the drivers in the different habitats are not yet clearly understood. As karst ecosystems have a specific geography and are fragile (Peng et al., 2008), research on the diversity patterns of fungi and plants is scant.

Karst forests are distributed centrally in Southwest China. The Mulun National Nature Reserve, a karst forest in Guangxi Province, has high plant species diversity and strong habitat heterogeneity (i.e., a wide variation in topographic and soil conditions), which potentially afford niches capable of hosting diverse fungal communities (Legendre et al., 2009; Du et al., 2017). Mountainous karst forests are a common landscape in karst regions (Peng et al., 2008), and have four main habitat types, valleys, foothills, hillsides, and hilltops, each having distinct plant characteristics and soil environments (Song et al., 2015). These habitat types differ in soil, convexity, outcrop rock coverage, soil depth, and microclimatic variables, which would affect fungal community assembly and dispersal ability (Prober et al., 2015; Matsuoka et al., 2016), and likely drive the relationships between fungal and plant assembly. Therefore, disentangling the relationship between plants and their associated fungi would greatly improve our understanding about forest health, nutrient cycling, and ecosystem stability in karst forest ecosystems.

Here, we collected 82 soil samples in four habitat types (valleys, foothills, hillsides, and hilltops) from a 25-ha karst broadleaf forest in Southwest China. We determined woody plant species richness and community structure before soil sampling, which offered us an opportunity to compare diversity and community structure patterns between plants and soil fungi. Accordingly, we hypothesized that (1) the diversity pattern of soil fungi differs from that of woody plants among habitat types; (2) fungal diversity is highly related to woody plant diversity in the karst forest. To test these hypotheses, we examined soil fungal communities in quadrats n different habitat types in a 25-ha karst broadleaf forest plot in Mulun National Nature Reserve using Illumina Hiseq sequencing of ITS rRNA genes. Then, we analyzed fungal community composition, diversity, and the relationships among fungal, plant, and abiotic variables in these forest habitats.

2. Materials and methods

2.1. Study sites description

Our study was conducted in the Mulun National Nature Reserve (107°54′01″- 108°05′51″E, 25°07′01-25°12′22″N) in northwestern Guangxi Province, China. The reserve owns mixed evergreen and deciduous broadleaf forest with a typical landscape of karst mountains and heterogeneity habitats (Song et al., 2015). It has a subtropical monsoon climate, with 19.38 °C average annual temperature and 1529 mm average annual precipitation.

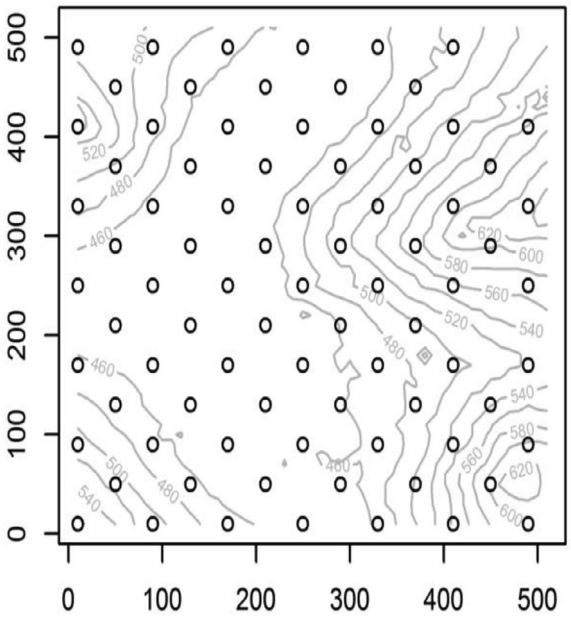

Fig. 1. The sampling location in the 25 ha Mulun forest plot. The number in the map represent elevation (m). The circles represent location of sampled soil cores.

2.2. Experiment design and data collection

In the reserve, we built a karst broadleaf forest plot with an area of 25 ha (500 × 500 m) in 2014. Details about plot construction and investigation following standard field protocol (http://www.ctfs.si.edu) and the topography measuring described by Du et al. (2017). A multivariate regression tree technique was used to divided the habitats into four types (valleys, foothills, hillsides, and hilltops) based on the topographic variables of each plot (elevation, slope, aspect, and convexity) (Du et al., 2017). During the investigation of the forest plot, we chose 20, 22, 21, and 19 plots with 20 × 20 m in valleys, foothills, hillsides, and hilltops, respectively (Fig. 1). The diversity indices of woody plant (richness, Shannon index, and Simpson index) were gained according to Green et al. (2005). Tree density, soil depth, and outcrop rock coverage were calculated according to the method mentioned by Du et al. (2017). Details about the sample plots were shown in Table 1.

2.3. Soil sample collection

We conducted soil microbial sampling in October 2016. Eight random samples (0–10 cm) were collected around the center of the chosen plot with a soil auger (5 cm inner diameter) after removing litters and mixed evenly into on composite sample. We gained a total of 82 samples (Fig. 1). The samples were divided into two parts after sieving through a 2-mm mesh: one part of each sample was kept in a liquid nitrogen tank from the forest to the laboratory and then stored at −80 °C for DNA extraction; the second part was air-dried for physical and chemical analysis. Soil pH, organic carbon (SOC), total nitrogen (TN), total phosphorus (TP), total potassium (TK), available nitrogen (AN), available phosphorus (AP), and available potassium (AK) were determined according to Bao (2000).

2.4. DNA extraction, PCR, and high-throughput sequencing

Soil microbial DNA was extracted in triplicate from each soil sample with ®SPIN soil DNA kit (Fast, MP), according to the manufacturer's instructions. The concentration and quality of the extracted DNA were checked by electrophoresis on 1.0% agarose. The extracted soil DNA was kept at −80 °C for PCR amplification and analysis.

Table 1
Details of vegetation, soil, topography in the sampled plots.

Variables	Habitats	No. of samples	Mean	Standard error	Min.	Max.	CV (%)
Sthick	Valley	20	37.97a	3.36	11.67	66.56	39.57
	foothill	22	16.81b	1.85	4.57	36.33	51.75
	hillside	21	13.48b	1.74	1.72	31.54	59.01
	hilltop	19	17.49b	2.25	2.38	38.21	56.05
Rock coverage	Valley	20	23.03b	5.10	0.00	75.00	***98.99***
	foothill	22	62.53a	5.72	5.00	95.00	42.87
	hillside	21	66.02a	4.08	20.00	95.00	28.31
	hilltop	19	61.22a	5.84	0.00	95.00	41.60
Slope	Valley	20	7.81d	1.07	0.96	19.22	61.14
	foothill	22	27.06c	2.34	5.52	45.14	40.49
	hillside	21	38.85b	2.50	11.06	54.18	29.52
	hilltop	19	49.46a	2.27	19.95	62.21	**20.00**
Convexity	Valley	20	-.78b	0.19	−2.15	0.84	***−106.68***
	foothill	22	-.99b	0.29	−4.79	1.91	***−139.02***
	hillside	21	-.34b	0.46	−4.52	4.30	***−623.26***
	hilltop	19	1.61a	0.80	−2.30	9.42	***217.50***
Richness	Valley	20	11.30d	1.14	3.00	22.00	45.04
	foothill	22	24.32c	2.18	12.00	52.00	42.00
	hillside	21	40.14b	3.05	12.00	65.00	34.77
	hilltop	19	47.21a	2.57	26.00	65.00	**23.77**
Shannon	Valley	20	.91c	0.10	0.10	1.89	51.28
	foothill	22	2.14b	0.15	0.75	3.29	32.99
	hillside	21	3.04a	0.12	0.95	3.60	**18.68**
	hilltop	19	3.13a	0.09	2.21	3.60	**12.84**
Density	Valley	20	202.85bc	14.03	87.00	326.00	30.93
	foothill	22	172.91c	13.78	53.00	317.00	37.38
	hillside	21	242.24b	33.73	74.00	735.00	63.81
	hilltop	19	363.68a	31.09	182.00	718.00	37.26
pH	Valley	20	7.23c	0.11	6.35	8.08	**6.73**
	foothill	22	7.39abc	0.10	6.67	8.25	**6.21**
	hillside	21	7.63a	0.09	6.58	8.15	**5.14**
	hilltop	19	7.55ab	0.11	6.44	8.00	**6.28**
SOC	Valley	20	51.73b	4.29	28.96	121.45	37.11
	foothill	22	61.15ab	4.16	43.66	115.03	31.91
	hillside	21	71.84a	4.46	40.81	129.39	28.46
	hilltop	19	63.62ab	5.45	31.17	121.12	37.33
TN	Valley	20	6.03c	0.29	4.37	9.17	**21.54**
	foothill	22	8.35a	0.61	4.54	14.41	34.31
	hillside	21	8.24ab	0.69	3.00	13.86	38.63
	hilltop	19	6.72bc	0.44	3.25	11.49	28.71
TP	Valley	20	1.81a	0.16	0.47	2.75	39.52
	foothill	22	1.65a	0.14	0.54	2.81	40.76
	hillside	21	1.57a	0.17	0.25	3.39	50.74
	hilltop	19	1.09b	0.15	0.32	2.12	58.10
TK	Valley	20	5.18ab	0.63	1.32	11.16	54.11
	foothill	22	5.68a	0.54	2.07	11.00	44.39
	hillside	21	6.42a	0.74	1.52	13.96	52.90
	hilltop	19	3.88b	0.57	1.05	9.37	64.39
AN	Valley	20	370.07bc	34.15	200.71	860.20	41.27
	foothill	22	449.73ab	31.36	203.76	757.21	32.71
	hillside	21	524.56a	33.42	286.44	768.51	29.19
	hilltop	19	339.13c	25.51	166.71	545.46	32.79
AP	Valley	20	6.94a	0.97	1.83	18.54	62.43
	foothill	22	4.55bc	0.66	1.80	13.51	67.83
	hillside	21	6.05ab	0.62	2.29	10.87	46.74
	hilltop	19	4.18bc	0.80	0.95	13.43	**83.67**
AK	Valley	20	4.17b	0.58	1.46	9.75	61.72
	foothill	22	6.16a	0.59	1.80	12.91	44.75
	hillside	21	4.93ab	0.49	1.68	8.88	45.94
	hilltop	19	3.83b	0.39	1.23	7.07	44.43

CV, coefficient variation; Sthick, soil thickness; Rock coverage, outcrop rock coverage; SOC, soil organic carbon; TN, soil total nitrogen; TP, soil total phosphorus; TK, soil total potassium; AN, soil available nitrogen; AP, soil available phosphorus; AK, soil available potassium. Different small letters in the same row indicated significant differences at $p < 0.05$ level.

The fungal ITS-1 region was amplified with the primers ITS1F (GGAAGTAAAAGTCG TAACAAGG) and IST2 (GCTGCGTTCTTCATCG ATGC) (Mukherjee et al., 2014). The PCR reaction was performed in a 15 μl mixture of Phusion Master Mix 2x (Thermo Fisher Scientific Inc., Waltham, MA, USA), including 3 μl of each primer (6 μM), 10 μl of DNA template (5–10 ng), and 2 μl H_2O. These samples were denatured at 98 ˚C for 60 s and then amplified by 30 cycles of 98 ˚C for 10 s, 50 ˚C for 30 s, and 72 ˚C for 30 s, and an extension at 72 ˚C for 5 min. Each sample was amplified in three replicates and then the relative amplicons were mixed to provide one final PCR product, the amplified ITS rRNA fragment was subjected to electrophoresis in 2% agarose gels. Finally, a total of 82 PCR products were achieved and an equal amount of PCR product from each sample was put in a single tube and sent to Illumina's HiSeq platform at the Novogene Biotechnology Co., Ltd. (Beijing, China).

2.5. Bioinformatics

Reads of fungal ITS genes were demultiplexed, quality-filtered, and processed *via* QIIME based on three criteria (Caporaso et al., 2012). First, the reads with 300 bp at any position were truncated with an average quality score < 20 over a 50-bp sliding window, and then the truncated reads with < 50 bp were discarded. Second, reads were cutoff that contained matching barcodes, mismatches between two nucleotides in primer matching, and ambiguous bases. Subsequently, sequences that only overlapped > 10 bp were assembled according to their overlapped sequence and the reads that could not be assembled were removed. Sequence analysis was conducted using the USEARCH v5.2.32 to filter and denoise from the data by clustering similar sequences using a 97% threshold. The UPARSE pipeline was applied to select ITS rRNA operation taxonomic unites (OTU) at the 97% similarity threshold (Edgar, 2013). Final OTUs were generated on the clustering results and taxonomic assignment was performed based on the UNITE reference database (Köljalg et al., 2013). Fungal functional groups (i.e., pathogens, saprotrophs, ectomycorrhizal (EcM) fungi, and AM fungi) were assigned using FUNGuild (https://github.com/UMNFuN/FUNGuild) according to Tedersoo et al. (2014) and Nguyen et al. (2016). A random resampling procedure was conducted to build subsets to a depth of 5000 sequences per soil sample for further analysis to correct sampling error. At last, the complete dataset was sent to the Sequence Read Archive (SRA) database of the National Center for Biotechnology Information (NCBI) under the accession number of PRJNA 639703.

2.6. Statistical analyses

The generalized diversity, Hill number (N_a) was proposed to control the variability associated with rare taxa by differentially weighting them (Hill 1973). Due to the generality and flexibility in controlling the effects of rare taxa in microbial communities, Hill number became an excellent framework for microbial diversity studies (Kang et al., 2016) and was used to described fungal diversity in the study. It was calculated by the formula (Kang et al., 2016),

$$N_a = \left(\sum_{i=1}^{S} P_i^a \right)^{1/(1-a)}$$

where $a = 0$, N_0 means the number of taxa; $a = 1$, N_1 means the exponential Shannon index; $a = 2$, N_2 represent the inverse Simpson index. Then, regression analysis was conducted to assess the relationships among habitat types and the three fungal alpha diversity indices, which performed using R version 3.4.0. Then, random forest analysis was used to identify the important predictors of soil fungal and functional fungal richness in the karst forest soils by using the 'randomForest' package in R (Breiman, 2001). The corresponding significance for the effects of the predictors on the soil fungal and functional fungal richness was assessed using the 'rfPermute' package in R (Archer, 2013). Next, distance-based redundancy analysis (db-RDA) was used to identify the relationship between the soil specific fungal taxa and environmental variables, and the relationship between dominant woody plant species (a total of 227 species in the forest plot) and the functional fungal groups. To increase the explanatory of the db-RDA model, the most high-abundance OTUs profiles (> 1000 sequences per OTU) were selected as the response variables (a total of 231 OTUs). The manual forward selection procedure and a Monte Carlo test with 999 permutations were performed to verify significance of predictors ($P < 0.05$) by the CANOCO 5.0 software package. Finally, the multiple-site beta diversity (i.e., Sørensen's multiple-site dissimilarity index) was used to compare differences between woody plants and soil fungi based on the presence or absence of data. And the dissimilarity index includes two components, i.e., the turnover component of Sørensen dissimilarity (β_{SIM},) and the nestedness component of Sørensen dissimilarity (β_{SNE}) (Baselga, 2010; Shen et al., 2014). The analysis of beta diversity and the dissimilarity index was conducted using the 'betapart' package in R and the variance analyses (ANOVAs) among habitat types were conducted in SPSS 19.0.

3. Results

3.1. Details of sampled habitats and fungal database

The topography in the karst forest had strong habitat heterogeneity (variable slope and convexity) with shallow soil (ranging from 13.48 to 37.97 cm), high outcrop rock coverage (> 60% except in the valley), especially in the hilltops (Table 1). The richness, Shannon index, and density of woody plants in the hilltops were significantly larger than those in the other three habitats ($p < 0.05$) (Table 1). Basically, the fertility in the foothills and hillsides with moderate variability (25% < CV ≤ 75%, except soil pH) was better than that in the valley and hilltops (Table 1).

We assigned 7,522,479 high-quality sequences to 11,413 OTUs after filtering out chimeras and sequences of non-fungal origin and removing singletons. In order to ensure the comparability of fungal alpha and beta diversity between samples, we rarified soil samples to 5000 sequences and obtained sequence data for 82 soil samples. This reduced the number of fungal OTUs to 116. The number of OTUs, across the forest plot, ranged from 73 to 110. The dominant fungal phyla were *Ascomycota* (50.1%), *Zygomycota* (42.1%), and *Basidiomycota* (6.9%), which accounted for 99.1% of the total fungal sequences. Other phyla comprised only 0.9% of the sequences (Fig. 1S and Fig. 2S). The most OTU-rich phyla were *Ascomycota* (87 OTUs), *Basidiomycota* (16 OTUs), and *Zygomycota* (11 OTUs).

3.2. Diversity patterns of soil fungal and tree community

The tree richness, Shannon index, and Simpson index significantly increased from the valleys to the hilltops (Fig. 2). The overall fungal N_1 diversity only marginally increased toward valleys and showed larger variation on hills than in valleys, while the soil fungal richness (N_0) and N_2 diversity exhibited significantly reduced and increased patterns, respectively, from valleys to hilltops (Fig. 2). The fungal taxonomic groups at the phylum level displayed no clear patterns of dominant fungi among the habitat types (Fig. 2S). The major fungal functional groups had similar richness patterns: the richness of EcM, AM, saprotrophic, and pathogenic fungi was higher in the valleys (Fig. 3).

According to the random forest analysis, the most important environmental predictors for total fungal richness and pathogen fungal richness were alpha diversity of woody plant (i.e., species richness, Shannon-Wiener index, and Simpson index). Location (Y) and slope aspect significantly affected EcM fungal richness. In addition, the Shannon-Wiener index and the Simpson index for woody plants were variables significantly affecting the richness of saprotrophic fungi. However, no significant environmental variables were found to predict AM fungal richness (Fig. 4).

3.3. Fungal and plant community composition

The RDA model selection procedure showed that woody plants were the most important predictors of soil fungal community structure across the forest plot (Fig. 5A) and twelve woody plant species were selected as the significant predictors to affect functional fungal groups (Fig. 5B). According to our multiple-site beta diversity analysis, tree species increased in species turnover rate (β_{SIM}) from valleys to hilltops (Fig. 6A), while fungal species showed a concave distribution (Fig. 6C). Meanwhile, the patterns of nestedness (β_{SNE}) for trees and soil fungal species were also opposing. The β_{SNE} of tree species decreased from valleys to hilltops, while that of soil fungal species had an increasing pattern (Fig. 6B and D).

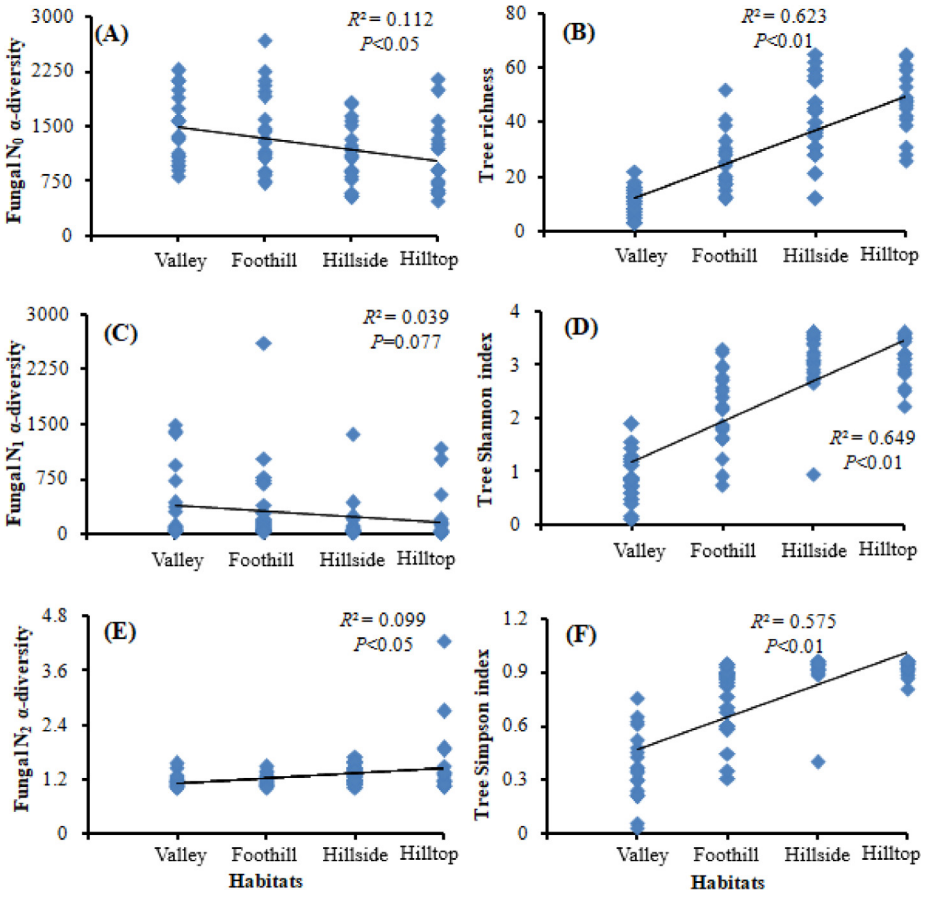

Fig. 2. Plant and soil fungal alpha diversity among habitat types in the karst broadleaf forest. (A) Fungal N_0 α-diversity; (B) Tree richness; (C) Fungal N_1 α-diversity; (D) Tree Shannon index; (E) Fungal N_2 α-diversity; (F) Tree Simpson index. Valley, the habitat of valleys; Foothill, the habitat of foothills; Hillside, the habitat of hillsides; Hilltop, the habitat of hilltops.

3.4. Relationships between fungal and woody plant diversity

Soil fungal richness (N_0) had significant negative relationships with tree species richness (Spearman rho = -0.434, $P < 0.001$), tree Shannon-Wiener index (Spearman rho = -0.381, $P < 0.001$), and tree Simpson index (Spearman rho = -0.365, $P = 0.001$). The soil fungal N_1 diversity index also had a strong negative correlation with woody plant species richness, Shannon-Wiener index, and Simpson index (Spearman rho = -0.394, P < 0.001; Spearman rho = -0.335, $P = 0.002$; and Spearman rho = -0.315, $P = 0.004$, respectively). Conversely, the soil fungal N_2 diversity index had a strong positive correlation with woody plant species richness, Shannon-Wiener index, and Simpson index (Spearman rho = 0.358, $P = 0.358$; Spearman rho = 0.315, $P = 0.004$; and Spearman rho = 0.300, $P = 0.006$, respectively).

4. Discussion

4.1. Linkages between plant and fungal diversity

The landscape-based fungal habitats investigated in our study were in a karst mixed evergreen and deciduous broadleaf forest plot and were the same plant habitats previously delineated by Du et al. (2017) and Song et al. (2018). Consistent with our first hypothesis, the soil fungal diversity pattern differed from woody plant diversity pattern among habitat types. Our results indicated that both fungal and woody plant communities are strongly influenced by habitat types, but fungal communities are less sensitive than the plant communities to the variations in the elevation of the quadrats (445.7–639.4 m asl) in the karst forest (Fig. 1S and Fig. 2S), which was inconsistent with a study in ridge and valley habitats in a subtropical mountain forest (Gao et al., 2017). Interestingly, similar patterns were found for fungal function groups, i.e., the richness of EcM, AM, saprotrophic, and pathogenic fungi was higher in the valleys (Fig. 3). Although the vascular species richness and Shannon diversity was lower in the valleys (Fig. 2B and D), the soil nutrient was richer and soil particles was finer in the valleys (Song et al., 2015) where is favor to fungal growth. However, several studies have found significant differences in soil fungal communities across altitudinal gradients in natural ecosystems, such as in Argentina (400–3000 m asl, Geml et al., 2014), Switzerland (400–3200 m asl, Pellissier et al., 2014), and China (530–200 m asl, Shen et al., 2014), and across latitudinal gradients in forest ecosystems across the five climate zones of China (18.7–53 °E, Hu et al., 2019). These results could be driven by the strong altitudinal or latitudinal gradients of the habitat types, which are closely correlated with climate, soil, and vegetation dynamics, which affect soil fungal communities (Procter et al., 2014; Tedersoo et al., 2014).

Prober et al. (2015) and Hu et al. (2019) found that plant community composition correlated with soil fungal community composition in grasslands and forests, respectively, which indicated plant community had key roles in shaping the fungal community in the two ecosystems. Our results in karst forest ecosystems agreed with these previous reports. Woody plants were thought to have greater effects on soil fungal communities than herbs, since fungi are the primary decomposer of woody debris with high lignin content and EcM fungi tend to form symbiotic relationships with trees (Rineau et al., 2013). In our study, *Itoa orientalis* and *Cryptocarya microcarpa* significantly influenced the distribution of AM, pathogenic, and saprotrophic fungal communities, while *Tirpitzia sinensis* and *Clausena dunniana* significantly and negatively affected EcM fungi (Fig. 5B). This phenomenon suggested that the richness of functional fungal groups was highly related to the abundance of host plants, which could be due to significant effect of host phylogeny in community assembly of total fungi, EM fungi, plant pathogenic fungi and saprotrophic fungi (Wehner et al., 2014; Erlandson et al., 2018; Wang et al., 2019; Yang et al., 2019). Given that many

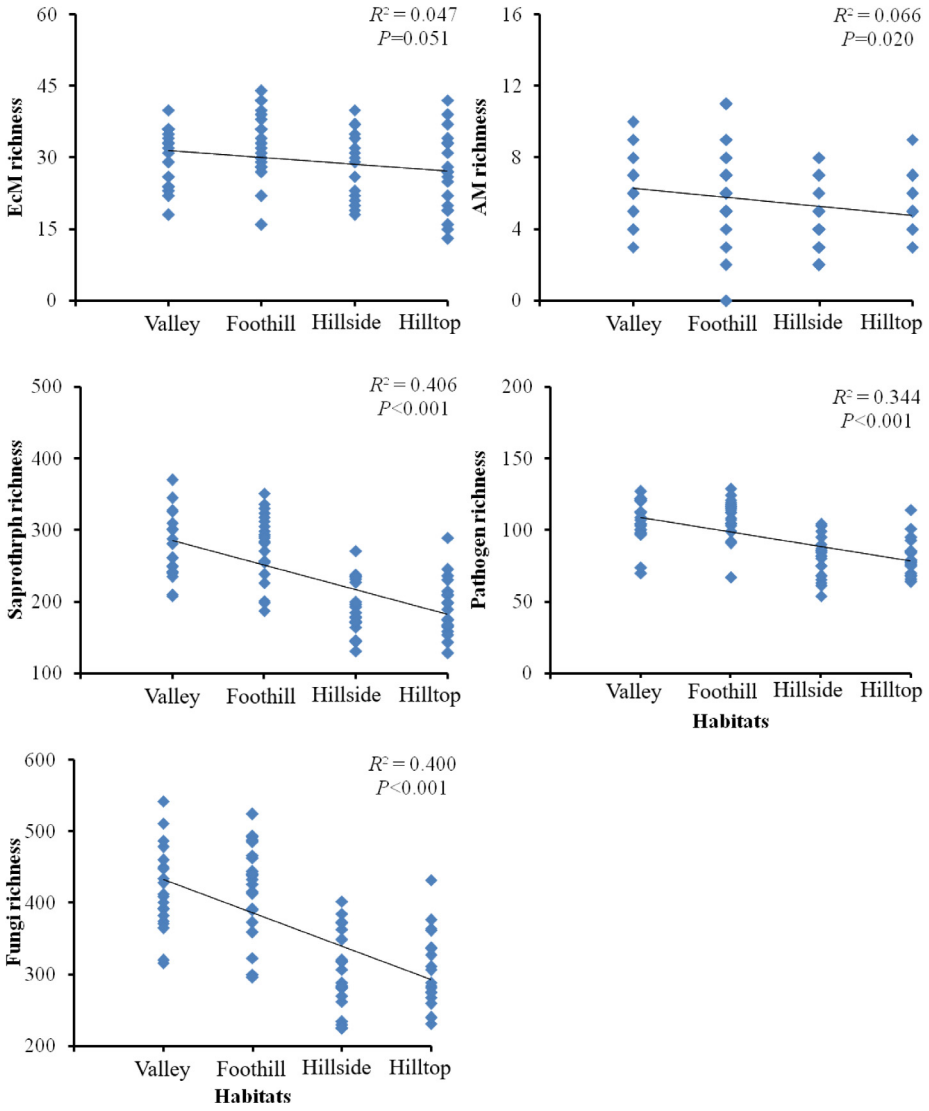

Fig. 3. Relationships between the richness of fungal functional groups and habitats in the karst forest. The values of fungal functional group richness for each site were presented. Valley, the habitat of valleys; Foothill, the habitat of foothills; Hillside, the habitat of hillsides; Hilltop, the habitat of hilltops.

studies demonstrated the strong influences of edaphic variables on fungal richness (i.e., soil pH, nutrients) (Glassman et al. 2017), the effects of plant functional traits, such as phylogeny, the contents of rhizospheric exudates and litter chemistry (Rineau et al., 2013; Schneider et al., 2012; Wang et al., 2019; Yang et al., 2019), need to be addressed in future studies in order to disentangle the plant-related effects.

We also compared the species turnover rate (β_{SIM}) and nestedness (β_{SNE}) between woody plants and soil fungi as influenced by habitat types. Species turnover is often related to spatial distance and environmental classification (Qian et al., 2005). We found that tree species β_{SIM} increased in valleys (Fig. 6A), while fungi had a concave species turnover pattern (Fig. 6C), which indicated that diverse environmental filtering processes shape plant and fungal species assemblages. The higher plant and fungal species turnover at hilltops may be due to greater habitat specialization with the appearance of more primary species (Song et al., 2015; Du et al., 2017) and poorer soil (Song et al., 2015). Nestedness refers to a nonrandom process of species loss due to a result of any factor that promotes disentangling community assembly (Orrock and Watling, 2010). While the nestedness (β_{SNE}) pattern of trees completely differed from that of fungi (Fig. 6B and D), this difference likely reflected that stochastic events, such as wood deposition, had different effects on the plant and fungal communities. For example, Ager et al. (2010) found that disturbance would cause higher abundance of the locally most dominant microbial taxon.

4.2. Factors that affecting fungal and woody plant diversity in the karst forest

Different associations of abiotic variables were clearly correlated with these fungal compositions among habitat types (Fig. 4). For example, total, saprotrophic, and pathogenic fungal richness in the karst forest were mainly related to various associations of soil and plant-related variables (Fig. 4), as documented in previous studies (Tedersoo et al., 2014; Prober et al., 2015; Matsuoka et al., 2016; Gao et al. 2017). Meanwhile, the results also verified that soil fungal richness (OTUs) was substantially influenced by Shannon-wiener index and density of wood plants in the karst forest (Peng et al., 2019). In addition, changes in EcM fungal composition were significantly correlated to geographic distance (i.e., location and slope aspect) (Fig. 4), in accordance with previous studies (Gao et al., 2017; Peay et al., 2010; Peay and Bruns 2014). The findings indicated that dispersal limitation, an indicator of neutral process (McGill et al., 2006), strongly structured EcM fungal community in the karst forest. This maybe ascribe to geographic barriers reducing or limiting migration of EcM fungi, for example, spores

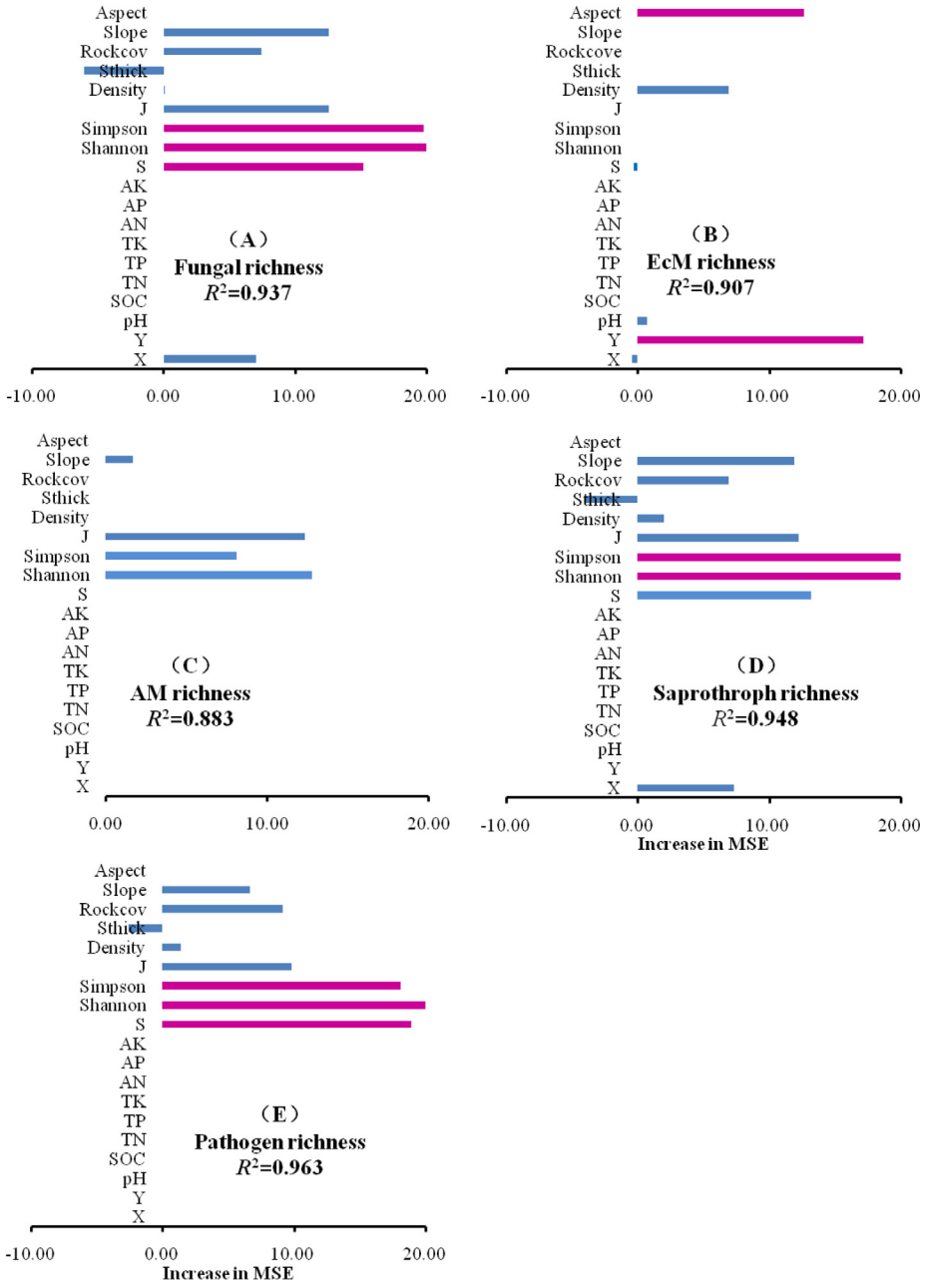

Fig. 4. Random forest estimates of relative importance (% of increase of mean square error, MSE) of environmental variables for predicting alpha diversity of soil fungal and fungal functional groups. (A) Fungal richness; (B) EcM richness; (C) AM richness; (D) Saprotroph richness; (E) Pathogen richness. The accuracy was calculated separately for each tree and averaged from values of all tree (10,000 trees). Significant factors are shown in purple ($P < 0.05$). X and Y represent the spatial location of plot i (i.e., i(X, Y)), with the bottom left (southwestern) corner as the point of origin (0, 0), the Y axis running north and south, and the X axis running east and west; pH, soil pH value; SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus; TK, total potassium; AN, available nitrogen; AP, available phosphorus; AK, available potassium; S, the woody plant species richness in the plot; Shannon, Shannon-Wiener index of woody plants in the plot; Simpson, the Simpson index of woody plants; J, the evenness of woody species in the plot; Density, woody plant density in the plot; Sthick, soil thickness; Rockcov, outcrop rock coverage; Slope, slope degree; Aspect, slope aspect. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and mycelia (Peay et al., 2010). However, no selected environmental factors were found to predict AM fungi pattern, which partly indicated that AM fungi and plants were interdependent (Horn et al., 2017).

Given the symbiotic and parasitic relationships between soil fungi and plants (Peay et al., 2010), a positive relationship between soil fungi and plant diversity was expected. However, we found negative correlations (N_0, $p < 0.01$; N_1, $p > 0.05$) and a weak positive correlation (N_2, $p > 0.05$) between plant and fungal alpha diversity (Table 1S). Our finding was not consistent with the resource diversity hypothesis that plant communities with high diversity produced diverse and complex organic substrates that favored specialization in fungal communities and resulted in highly diverse local communities (Yang et al., 2017). This inconsistency may be explained by the potential influence of stochastic spore dispersal and priority effects in fungal community assembly may override the influence of resource supply in fungal communities (Fukami et al., 2010; Peay and Bruns, 2014). It may also be because community-assembly processes and species interactions were important controls on fungal communities overwhelming substantial differences in abiotic conditions (Maynard et al., 2018). The weak positive correlation between plant and fungal alpha diversity (N_2) was also presented in forest plots covering five climate zones in China (Hu et al., 2019). Importantly, the random forest model showed that woody plant alpha diversity was an important indicator of total fungi, saprotroph fungi, and pathogen fungi richness (Fig. 4), which indicated that plant host phylogeny affected pathogenic and saprotrophic fungi (Wang et al., 2019; Yang et al., 2019) and then on the total fungal richness. In our study, tree alpha diversity significantly affected fungal communities among the habitat types (Fig. 5A), which indicated that high woody plant diversification would permit larger fungal diversity by increasing the richness of substrates entering soils and thus the niches available for soil fungi (Waldrop et al., 2006). These results supported our second hypothesis and suggested that fungal diversity was highly related to tree diversity in the karst forest. Some researchers have documented that the resource diversity hypothesis about plant and fungal diversity has occurred at regional scales (Yan et al., 2016; Hiiesalu et al., 2017), but not at the global scale (Tedersoo et al., 2014)

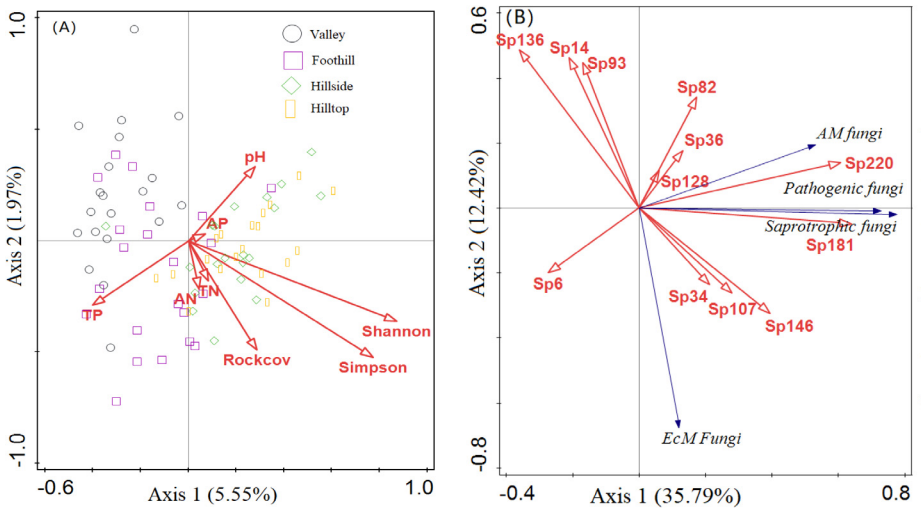

Fig. 5. db-RDA plot showing the relationships between soil fungal community structure and environmental variables (A) and plant community structure (B) in the karst forest. For figure A, the fungal OTUs profiles as the response variables and the red lines represented the environmental variables, and color dots represented soil samples from different forest types. For figure B, the functional fungal groups as the response variables, which were the blue lines, while the red lines represented the plant species; Sp6, *Phoebe neurantha*; Sp14, *Clausena dunniana*; Sp34, *Maese japonica*; Sp36, *Viburnum brachybotryum*; Sp82, *Annamocarya sinensis*; Sp93, *Euonymus subcordatus*; Sp107, *Jatropha curcas*; Sp128, *Eriobotrya japonica*; Sp136, *Tirpitzia sinensis*; Sp146, *Eurycorymbus cavaleriei*; Sp181, *Cryptocarya microcarpa*; Sp220, *Itoa orientalis*. Valley, the habitat of valleys; Foothill, the habitat of foothills; Hillside, the habitat of hillsides; Hilltop, the habitat of hilltops. Each vector points to the direction of increase for a given variable and its length indicated the strength of the correlation between the variable and the ordination scores.

or latitudinal scale (Hu et al., 2019). Our study indicated that the complexity and strength of the relationship between plants and fungi depend on habitat types.

5. Conclusions

Our study represented a systematic and landscape-scale investigation of plant diversity and soil fungal diversity across the valley, foothill, hillside, and hilltop of a karst forest. We provided strong evidence that the diversity patterns of soil fungal communities were inconsistent with those of woody plants across habitats. In addition to our investigation of woody plant community structure and diversity, we also investigated the link between woody plant and soil fungal communities. We found that soil fungal community structure was strongly related to that of woody plants, with strong correlations in both community composition and diversity. In addition, different patterns of species turnover for plants and soil fungi were found among the four habitat types, indicating that diverse environmental filtering processes determined both plant and fungal species assembly. Our results shed light on the soil fungal diversity patterns in a karst forest among habitat types and enriched our knowledge about the relationships between plant diversity and fungal diversity at a landscape scale.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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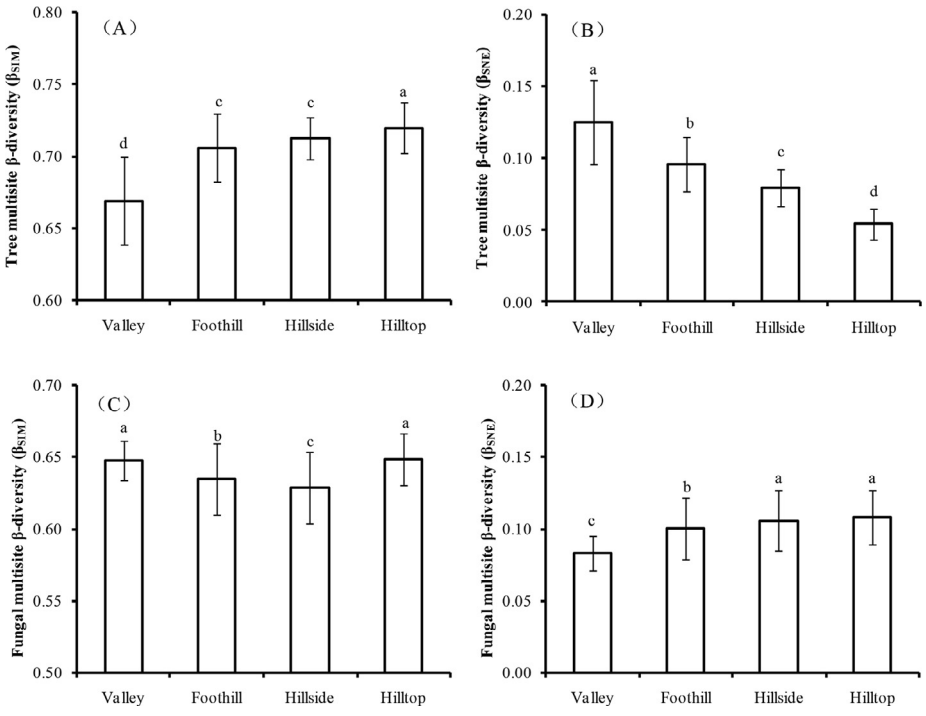

Fig. 6. Multiple-site beta diversities of woody plant and soil fungi (quantified by Sørensen's multiple-site dissimilarity) in different habitats. (A) Tree multiple-site beta diversity (β_{SIM}); (B) tree multiple-site beta diversity (β_{SNE}); (C) fungal multiple-site beta diversity (β_{SIM}); and (D) fungal multiple-site beta diversity (β_{SNE}). Valley, the habitat of valleys; Foothill, the habitat of foothills; Hillside, the habitat of hillsides; Hilltop, the habitat of hilltops.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118367.

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