Soil fungal β-diversity rather than α-diversity increases with increasing oceanic island area

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Abstract

Fungi have huge biodiversity and play important roles in soil biogeochemical cycling and ecosystem services in island ecosystems. Although island biogeography has been widely studied in macroorganisms, the relationship between soil fungal diversity and area in islands is less documented. Here, we examine soil fungal communities of 18 oceanic islands belonged to two types of islands (8 general islands in Wanshan and 10 coral islands in Xisha) in South China Sea through Illumina Miseq sequencing techniques. Our results showed that soil fungal α-diversity (species richness) was significantly different among the oceanic islands, with a higher value in Wanshan than in Xisha islands. Soil fungal α-diversity was significantly affected by soil potassium and magnesium (Mg) and plant community in Wanshan islands but by soil Mg in Xisha islands. Soil fungal community composition was significantly different in Wanshan and Xisha islands and influenced by soil, plant community and spatial distance. Ecological stochasticity model showed that the fungal community assembly was mainly structured by deterministic process regardless of island types. The fungal β-diversity (community turnover), but not α-diversity was significantly increased with increasing island area. Our findings may have implications for better predicting soil fungal community dynamics in island systems and for enhancing insight into microbial biodiversity conservation.

Keywords

α-diversity; β-diversity; community composition; island; species-area relationship

1. Introduction

Islands are characterized by their geographical isolation and simple biotas and have been served as a model system for developing and testing basic evolutionary and ecological theory or hypothesis (Warren et al., 2015; Whittaker et al., 2017). Island-related researches primarily emerged since the pioneering work of the theory of island biogeography (MacArthur & Wilson, 1967), which was considered as the dominant symbol of a transition from descriptive to analytical approaches in ecology and biogeography (Losos & Ricklefs, 2010). Subsequently, there were a large body of observational and empirical works on the biogeography of island-dwelling macroorganisms (Stuart et al., 2012; Cabral et al., 2019; Rojas-Sandoval et al., 2020). Soil fungi, as an important component of belowground microorganisms, have remarkable biodiversity and are major ecological players in biogeochemical (organic matter and nutrients) cycling and other ecosystem functioning on Earth (Philippot et al., 2013; Nilsson et al., 2019). Compared with island studies of animals and plants, however, we know much less regarding the diversity and biogeography of soil microorganisms in island ecosystems (Li et al., 2020).

In general, a positive species–area relationship (SAR) leads to higher species richness on large islands according to the classic theory of island biogeography (MacArthur & Wilson, 1967). The SAR has been well tested with insular animals and plants (Macarthur & Wilson, 1963; Lomolino, 1984; Kohn & Walsh, 1994; Losos & Ricklefs, 2010; Rojas-Sandoval et al., 2020). The usefulness of SAR in explaining species richness patterns of microorganisms has also been investigated in some 'virtual island' systems. For example, the SAR was observed for bacterial α-diversity in water-filled treeholes of large European beech trees (Bell et al., 2005) and smaller sump tanks (analogous to islands) contained lower diversity (van der Gast et al., 2005), indicated that island biogeography theory held for the bacterial communities. Similarly, ectomycorrhizal fungal species richness was found to increase with the sizes of tree islands (Peay et al., 2007; Glassman et al., 2017). In a recent study, Li et al. (2020) did not observed significant SAR for soil fungi in inland islands. However, to our knowledge, there is no study regarding soil fungal SAR from the oceanic islands.

Besides α-diversity, microbial β-diversity (community turnover) has also been attracting great attentions. Exploring the microbial β-diversity can lead to insight into the mechanisms generating and maintaining microbial biodiversity in ecosystems (Ettema & Wardle, 2002; Beck et al., 2015; Mori et al., 2018). The positive relationship of microbial β-diversity and area, as a universal biogeographic pattern

was observed in mainland ecosystems by using the distance-decay approach (Horner-Devine et al., 2004; Beck et al., 2015; David et al., 2016; Zheng et al., 2020). However, there is less available knowledge on the relationships between the microbial β-diversity and area in island systems (Li et al., 2020). For example, a significantly positive relationship was observed between soil fungal β-diversity and area, and the habitat heterogeneity and/or dispersal limitation were considered as potential mechanisms influencing soil fungal communities in inland islands (Li et al., 2020).

To explore the microbial community assembly patterns and the processes resulting in these patterns is pivotal to gaining a more mechanistic understanding of biodiversity maintenance and community stability (Chase, 2010; Nemergut et al., 2013). The relative importance of deterministic and stochastic processes in structuring soil fungi community assembly is depended on scales (Caruso et al., 2012; Kivlin et al., 2014; Schroter et al., 2019) and habitats (Powell et al., 2015; Zhao et al., 2019). For instance, soil fungal communities were more strongly affected by deterministic processes in systems with less disturbance (bogs, moors, etc.) than in more intensive land use systems such as managed grasslands and arable systems (Powell et al., 2015). In general, stochasticity plays a dominant role at relatively smaller geographic scales, whereas determinism dominates at larger scales (*e.g.*, Zhao et al., 2019). Although community assembly of soil fungi on mainland ecosystems were well studied, we have known less regarding assembly mechanisms of fungal communities in the oceanic islands.

In order to understand the biogeography of soil fungi in different island systems, we examined the soil fungal communities in 18 oceanic islands belonged to two types of islands (including 8 general islands and 10 coral islands) in South China Sea using Illumina Miseq sequencing techniques. There are great differences observing between two types of islands, such as plant community structure and soil properties. We analysed the relationships between fungal α- and β-diversities and island area. Meanwhile, we tried to quantify the strength of stochasticity of fungal community assembly and further to detect whether any differentially potential drivers influencing the fungal community diversities between two island types. We propose two hypotheses: (H_1) fungal β-diversity rather than α-diversity increases with island area and (H_2) fungal α- and β-diversities are structured by different factors in general and coral islands.

2. Materials and methods

2.1. Sites and sampling

This study was conducted at 18 oceanic islands located in South China Sea **(Fig. S1)**, which were classified into two types of islands, *i.e.* 8 general islands in Wanshan islands (1.51-42.8 km among the islands; from the mainland 30.5–64.5 km) and 10 coral islands in Xisha islands (0.5-95 km among the islands; from the mainland 372–590 km) **(Table S1)**. The distance between Wanshan and Xisha islands is *ca.* 685 km **(Fig. S1)**. In each of 18 islands, we established 3-20 plots (20 m × 20 m, > 50 m apart from each other) in each island according to the island size **(Table S1)**. Within each plot, 10 soil cores (3.5 cm in diameter, 10 cm in depth) were randomly collected and combined into one composite sample, which resulted in a total of 203 soil samples. The samples were transported in an ice box to the laboratory and sieved through a 2-mm sieve to remove roots and debris. One portion of the samples was stored at –80 ^{o}C until DNA extraction; another portion was air-dried for analyses of the soil properties.

2.2. Plant and soil properties

Plant species richness was investigated in each established plot **(Table S1)**. Soil pH was determined with a soil-to-water ratio of 2:5 (w/v) using a glass electrode (FE20, Mettler Toledo). The metal ions of potassium (K) and magnesium (Mg), and total phosphorus (P) were measured by an inductively coupled plasma-atomic emission spectrometer (ICP-AES, iCAP 6300, Thermo Jarrell Ash Co. USA). Soil total carbon (C) and total nitrogen (N) were determined with an Elementar Vario EL III (Elementar Analysensysteme GmbH, Germany). Information about soil properties among 18 islands is given in **Table S2**.

2.3. DNA extraction, PCR and sequencing

Genomic DNA was extracted from 0.25 g frozen soil using a PowerSoil DNA isolation kit (MoBio Laboratories, Inc. USA) according to the manufacturer's instruction. The concentration of DNA was measured using a TBS 380 fluorescence spectrophotometer (Promega, USA). Fungal ITS2 region was amplified using the primers fITS7 (5'-GTGARTCATCGAATCTTTG-3') and ITS4 (5'-TCCTCCGCTT-ATTGATATGC-3') linked with a 12-base barcode to distinguish the sample origin. The thermocycling conditions were as follows: 94ºC for 5 min,

followed by 32 cycles of 1 min at 94ºC, 50 s at 56ºC, and 1 min at 68ºC. Each DNA sample was amplified for three times. The PCR products were purified using a PCR product gel purification kit (Axygen, Union City, CA, USA), and 50 ng purified DNA from each sample was pooled and adjusted to 10 ng μL^{-1}. The pooled DNA was subjected to sequencing on an Illumina MiSeq PE250 platform for sequencing using the paired end (2 × 250 base pair (bp)) option at the Environmental Genome facilities of Chengdu Institute of Biology, Chinese Academy of Sciences, China.

2.4. Sequence processing

The raw sequences were filtered using 'Quantitative Insights into Microbial Ecology' (QIIME v. 1.7.0) to remove low-quality reads with an average quality score < 20, without valid primer sequence or barcode sequence, containing ambiguous bases or length < 250 bp. Chimeric sequences were detected using the 'chimera.uchime' command in Mothur 1.32.2 (Schloss et al., 2009) by comparison with entries in the unified system for the DNA-based fungal species linked to the classification (UNITE) database (Kõljalg et al., 2013). Nonchimeric ITS2 sequences were clustered into different operational taxonomic units (OTUs) at a 97% sequence similarity level based on the UPARSE pipeline using the USEARCH v8.0 after discarding replicated sequences and singletons (Edgar, 2013). The representative sequence (the most abundant) from each OTU was selected through the 'get.oturep' command and classified using the SINTAX algorithm (Edgar, 2016) against the UNITE database with a confidence threshold of 65%. To eliminate potential effects of uneven sequence depths across samples on fungal community analysis, the number of sequences per sample was rarefied to the smallest sample size using the 'sub.sample' command in Mothur for further analysis. The raw sequences have been submitted to the Environmental Genomic Cloud (http://egcloud.cib.cn) with the sample nos XXX. The fungal identification information in the current study is shown in **Table S3**.

2.5. Statistical analysis

All statistical analyses were conducted in R-4.0.2 (R Core Team, 2020). Fungal α-diversity was defined as the observed OTU richness (*i.e.*, OTU number) of each soil sample. Multiple comparisons of group mean of OTU richness among the 18 oceanic islands were carried out with pairwise comparisons after the nonparametric Kruskal-Wallis test where data did not satisfy homogeneity of variance, at $P < 0.05$. The difference in α-diversity and the relative abundance of dominant OTUs between

two island groups (Wanshan vs Xisha islands) was analyzed using the independent two-sample T-test. Plant community composition data were conducted the principal component (PC) analysis using the 'rda' command in the 'vegan' package (Oksanen et al., 2013). Subsequently, to quantify the effects of soil variables, plant species richness and composition (PC), and their interactions on soil fungal α-diversity, we employed linear mixed-effects models to control for the random effect of site, using the 'lme4' package (De Boeck et al., 2011).

Fungal β-diversity was defined as community turnover (dissimilarity) amongst samples using the Sørensen index (presence/absence data) (Legendre & Legendre, 1998). The fungal community composition was ordinated using nonmetric multidimensional scaling (NMDS) with dissimilarity matrices using the 'metaMDS' function in the 'vegan' package. To evaluate the effect of the sites on fungal β-diversity at scales of two types of islands and 18 islands, the permutational multivariate analysis of variance (PerMANOVA) was conducted based on distance matrices using 'adonis' function in the 'vegan' package with 999 permutations. Principal coordinate of neighbor matrices (PCNM) vectors with positive eigenvalues were calculated based on geographical coordinates (latitude and longitude) using the 'PCNM' command in the 'PCNM' package (Dray et al., 2006). The 'varpart' function in the 'vegan' package was used to partition the variation of soil fungal β-diversity by the individual and interactive effects of spatial distance (PCNM), soil and plant (richness and community composition) parameters. To test the homogeneity of the fungal community among different islands (Anderson & Walsh, 2013), beta dispersions of Simpson dissimilarity (free from richness variance) was explored by the 'betadisper' function in the 'vegan' package.

The normalized stochasticity ratio (NST) was tested with simulated communities by considering abiotic filtering, competition, environmental noise, and spatial scales (Ning et al., 2019). The modified stochasticity ratio (MST) index was calculated using the 'tNST' function in the 'NST' package to represent the contribution of stochasticity to community assembly (Ning et al., 2019). The MST index, a special transformation/case of NST, ranges from 0% to 100%, a 0% indicates no contribution of stochasticity, whereas 100% indicates the community assembly being completely stochasticity-driven. Particularly, this index was developed with 50% as the boundary point between more deterministic (< 50%) and more stochastic (> 50%) assemblies. Moreover, a neutral community model was used to determine the contribution of stochastic process to fungal community assembly by predicting the relationship between the occurrence frequency of OTUs (the proportion of local communities in

which each OTU is detected) and their abundance (the mean relative abundance across all local communities) (Sloan et al., 2006). This model emphasizes the effect of stochastic dispersal and drift but ignores the ecological difference between species and their response to the surrounding environment. In this model, the estimated migration rate (*m*) was a parameter for evaluating the probability that a random loss of an individual in a local community would be replaced by dispersal from the metacommunity. The parameter R^2 represented the overall fit to the neutral model. An R^2 value closer to 1 implied that the community was consistent with neutral process of dispersal and ecological drift, whereas $R^2 < 0$ was no fit. These parameters were determined using non-linear least squares fitting in the 'minpack.lm' package (Elzhov et al., 2016). Calculation of 95% confidence intervals around the model prediction were conducted by bootstrapping with 1,000 bootstrap replicates in the 'HMisc' package (Harrell, 2020). The relationships between fungal α-diversity or β-diversity and the island sizes were analyzed using the type II linear regression (ordinary least squares) in the 'lmodel2' package (Legendre, 2011). Akaike information criterion (AIC) values were employed to judge whether the quadratic model was better than the linear model (Burnham & Anderson, 2002).

3. Results

3.1. Identification fungi

After quality control, we obtained 5,154,835 quality filtered ITS2 sequences from 6,790,156 raw sequences, in which 3,968,623 sequences were identified into 9,852 fungal OTUs. We did normalization using 3373 sequences (3373–60467 sequences among soil samples) and obtained 7,629 fungal OTUs (684,719 reads), which were distributed in 10 phyla (relative abundance 92.26%) and 644 unidentified fungal OTUs (7.74%). The fungal community was dominated by Ascomycota (3,980 OTUs, 46.9%) and Basidiomycota (2,427 OTUs, 26.4%) **(Fig. S2)**. The rarefaction curves of 18 islands roughly tended to reach an asymptote, reflecting that the majority of distinct fungal OTUs could be recovered **(Fig. S3)**.

3.2. Fungal α-diversity

Fungal α-diversity (OTU richness) was significantly different among the 18 islands ($P < 0.001$**, Fig. 1A**). The average fungal α-diversity was significantly higher in Wanshan islands than in Xisha islands **(Fig. 1B)**. We did not observe any significantly

correlational relationship between fungal α-diversity and island area in Wanshan, Xisha and total islands **(Fig. 2A)**. The results of linear mixed-effects models showed that the fungal α-diversity was significantly affected by soil K, Mg and N in total islands, soil K and Mg and plant community composition (PC1 and PC2) in Wanshan islands and soil Mg in Xisha islands **(Table 1)**.

3.3. Fungal β-diversity

We observed higher relative abundance of Mortierellomycota but lower relative abundance of Ascomycota in Wanshan islands than in Xisha islands **(Fig. S2)**. The OTU5749, OTU1295, OTU5468, OTU358 and OTU6298 were abundant in Wanshan islands, but OTU5355, OTU5897, OTU18 and OTU4867 were rich in Xisha islands **(Fig. S4)**. Moreover, PerMANOVA analysis showed that the fungal community composition was significantly distinct in 8 islands in Wanshan ($R^2 = 0.187$; $P < 0.001$), 10 islands in Xisha ($R^2 = 0.261$; $P < 0.001$) and two types of islands (Wanshan vs Xisha, $R^2 = 0.094$; $P < 0.001$). Meanwhile, the NMDS analysis also showed similar results (**Fig. 3**). Interestingly, we found significantly exponential relationships between fungal β-diversity and island area in Wanshan, Xisha and total islands (all $P < 0.05$, **Fig. 2B**). These results were further supported by beta dispersions of Simpson dissimilarity, which indicated significantly strong fungal β-diversity among larger islands than among smaller islands both in Wanshan islands ($P = 0.005$, **Fig. 4A**) and Xisha islands ($P < 0.0001$, **Fig. 4B**). Moreover, the results of variation partitioning analysis showed that fungal community was explained by plant community composition (17.92%), space (8.96%) and soil properties (6.11%) in Wanshan islands, by spatial distance (11.63%), soil properties (10.96%), and plant community composition (8.87%) in Xisha islands, and by plant community composition (18.06%), soil properties (12.82%), and spatial distance (7.11%) in total islands **(Fig. 5)**.

The MST model showed that the MST value of each island ranged from 24.4 to 43.3% in Wanshan, 11.7 to 46.9% in Xisha, and 11.7 to 46.9% in total islands, indicating that fungal community assembly was mainly shaped by deterministic process **(Fig. 6A)**. Furthermore, an apparently lower MST value was observed in Wanshan islands (23.9%) than in Xisha islands (31.7%), suggesting a stronger deterministic effect in Wanshan islands as compared to Xisha islands **(Fig. 6B)**. In addition, the neutral community model showed that the goodness of fit was similar among Wanshan (39.7% of the variations explained), Xisha (38.9% of the variations explained), and total (41.2% of the variations explained) islands **(Fig. 7)**. The

migration rate (*m*) was consistently low (0.016 to 0.024, compared with 1), reflecting strong deterministic process driving the fungal community assemblies of three datasets **(Fig. 7A-C)**. Moreover, this parameter was lower in Wanshan (m = 0.018) than in Xisha (m = 0.024), indicating that the deterministic process even be more important in shaping the fungal community assembly in Wanshan islands as compared with Xisha islands.

4. Discussion

4.1. α-diversity

We found that fungal α-diversity was relatively higher in Wanshan than in Xisha islands. This may be because plant species richness is higher in Wanshan than in Xisha islands **(Table S1)**, as the well-known tight interaction of plants contributing C to fungi (*e.g.*, Mueller et al., 2014; Chen et al., 2017; Hiiesalu et al., 2017). In addition, according to the theory of island biogeography, smaller isolation degree (distance) from Wanshan islands to the mainland (potential source communities), compared with Xisha islands, could be interpreted as another evidence for higher α-diversity in Wanshan islands. Furthermore, we found that no correlation was observed between fungal α-diversity (species number) and island area, regardless of island types **(Fig. 2A)**. Similarly, soil fungal α-diversity was also unaffected by island area in a land-bridge island system (Li et al., 2020).

4.2. β-diversity

The fungal community composition was significantly different in Wanshan and Xisha islands in this study. This might be caused by substantial differences in relative abundances of some fungi, such as phyla Ascomycota and Mortierellomycota and some fungal OTUs between Wanshan islands and Xisha islands. In addition, the significant difference in plant species richness between two island types as mentioned above may also attributed to the observed differentiation of fungal community compositions. Furthermore, we found that soil fungal β-diversity significantly and positively correlated to island area, irrespective of total, Wanshan, and Xisha islands. Likewise, fungal β-diversities increased with island area (Li et al., 2020). Given that fungal β-diversity rather than α-diversity increased with island area, it was interpreted that this positive relationship of β-diversity and island area would be arisen from greater habitat heterogeneity on larger islands as compared with smaller islands,

according to a conceptual diagram proposed by Li et al. (2020).

We found that fungal community assembly was mainly driven by deterministic process rather than stochastic process. Similarly, soil fungal community assembly was strongly shaped by the deterministic process, which was mainly filtered from great environmental heterogeneity including host plants and soil organic matter from dry sclerophyll forest to coastal heathlands (Beck et al., 2015) and soil fertility in tea plantation ecosystems (Guo et al., 2020). Indeed, we found that fungal community was strongly affected by plant and soil (selection effect) compare to geographic distance (concerning dispersal limitation) **(Fig. 5)**. In addition, before the stable fungal community was formed, species could be further added through speciation, long-distance dispersal and migration over past land-bridges and global trade (Tedersoo et al., 2014). Once the community composition developed relatively stable, niche-based (selection) process certainly dominated soil fungal community assembly, because of the neutral-related processes became much less important (Zhou et al., 2014).

Furthermore, we found that fungal community assembly in Wanshan islands seemed to be more deterministic driven compared with Xisha islands **(Fig. 6B)**. Indeed, we found that plant and soil exerted much stronger impacts on fungal community composition in Wanshan islands than in Xisha islands, according to the variation partitioning results **(Fig. 5)**. In addition, we found that geographic distance also affected fungal community composition. The distance effect is often considered to represent the influence of dispersal, and dispersal could be stochastic to a large extent (Lowe et al., 2014; Zhou & Ning, 2017). The effect of spatial distance on the fungal community suggests that the fungal community assembly is also impacted by stochastic process, while it is not the major force, as reported in former findings (Beck et al., 2015; Guo et al., 2020). Therefore, we could not completely exclude potential effect of stochastic process on fungal community assembly.

5. Conclusions

We investigated soil fungal diversity amongst 18 oceanic islands belonging to general (Wanshan) and coral (Xisha) islands in South China Sea. Fungal α-diversity was higher in Wanshan than in Xisha islands. In addition to soil Mg, plant and soil K significantly impacted fungal α-diversity in Wanshan islands. Soil fungal community composition was different in Wanshan and Xisha islands. The deterministic process mainly structured the fungal community assembly, with a higher force in Wanshan

than in Xisha islands. Fungal β-diversity, but not α-diversity was significantly and positively related to island area. Our findings have implications for enhancing the predictability of soil fungal community dynamics and for biodiversity conservation in discrete habitats and fragmented landscapes.

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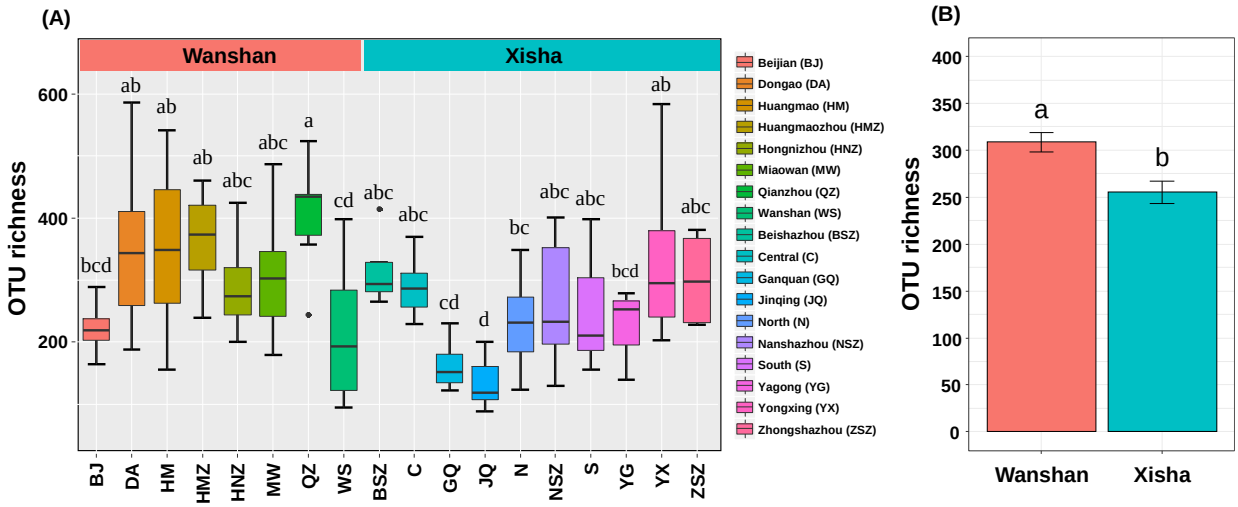


Figure 1.

Fungal α-diversity (mean OTU richness) in 18 oceanic islands **(A)** and in Wanshan islands and Xisha islands **(B)**.

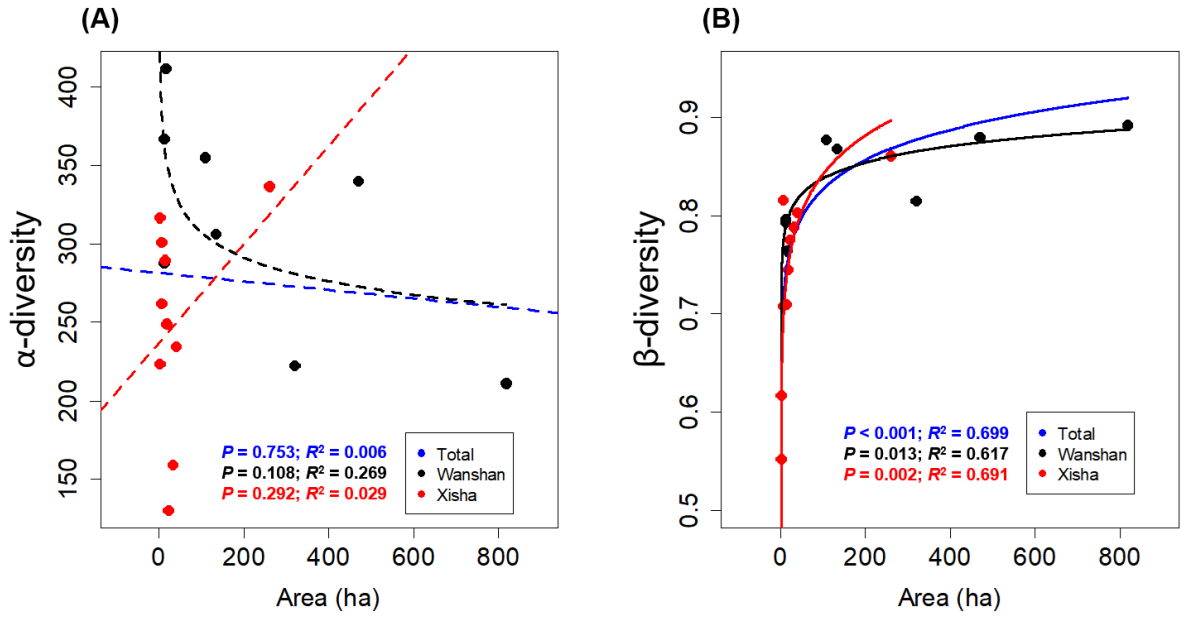


Figure 2.

The relationships between the observed fungal α-diversity **(A)** and β-diversity **(B)** and island area at Wanshan, Xisha and total islands.

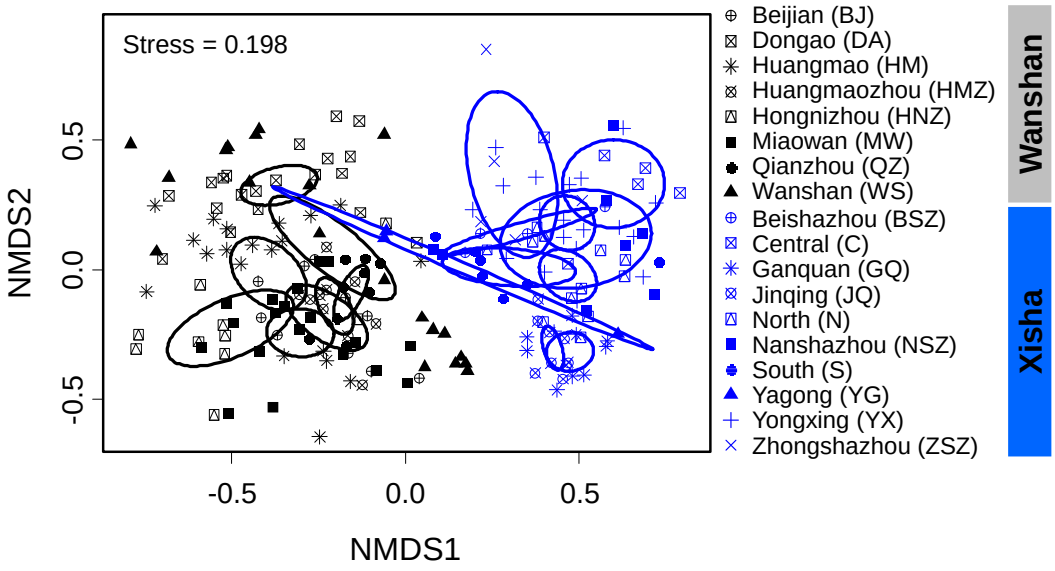


Figure 3.

Non-metric multidimensional scaling (NMDS) of the fungal community compositions in 18 islands. Ellipses indicate 95% confidence intervals around centroids of different islands.

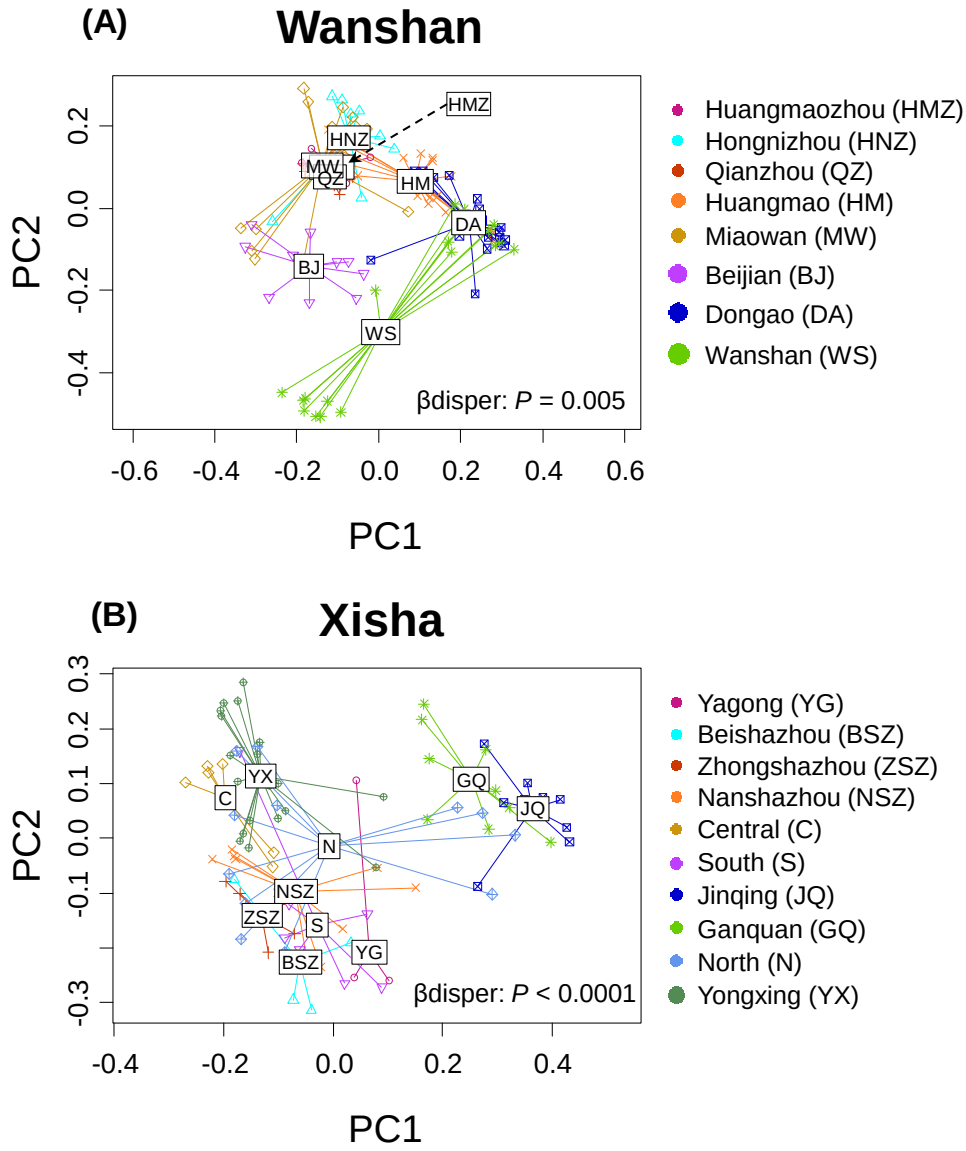


Figure 4.

The fungal community turnover analyses for Wanshan islands **(A)** and Xisha islands **(B)** based on the dispersion index (Simpson dissimilarity).

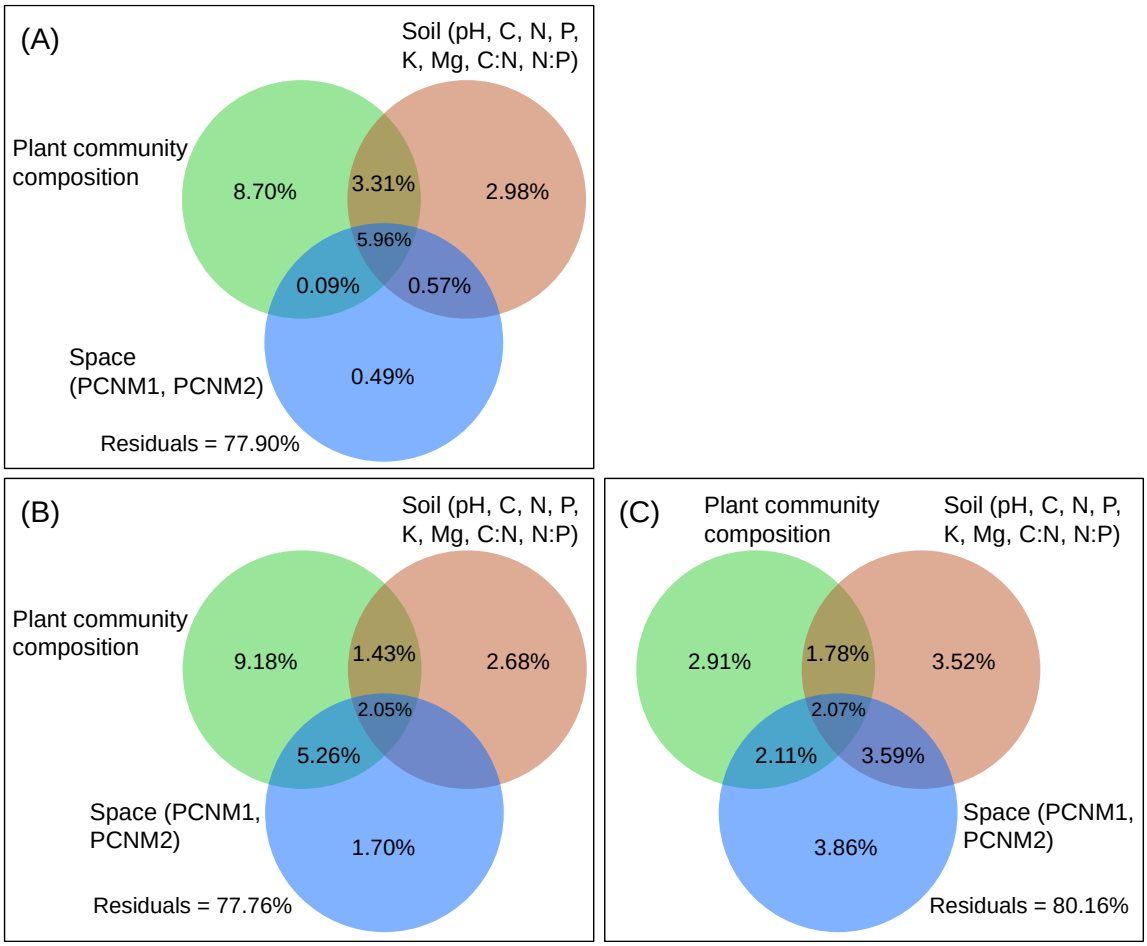


Figure 5.

Variation partitioning analyses showing the pure and shared effects of plant, soil and space on fungal community composition. Numbers indicate the proportion of explained variation.

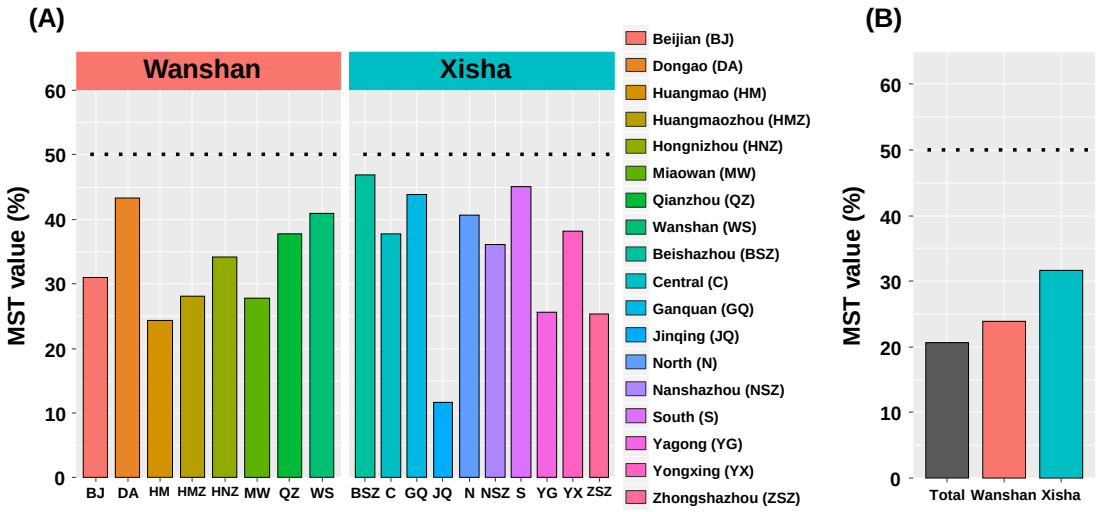


Figure 6.

Modified stochasticity ratio (MST) analysis showing the fungal community assembly pattern. The MST values amongst 18 islands **(A)** and the average MST values in Wanshan, Xisha and total islands **(B)**.

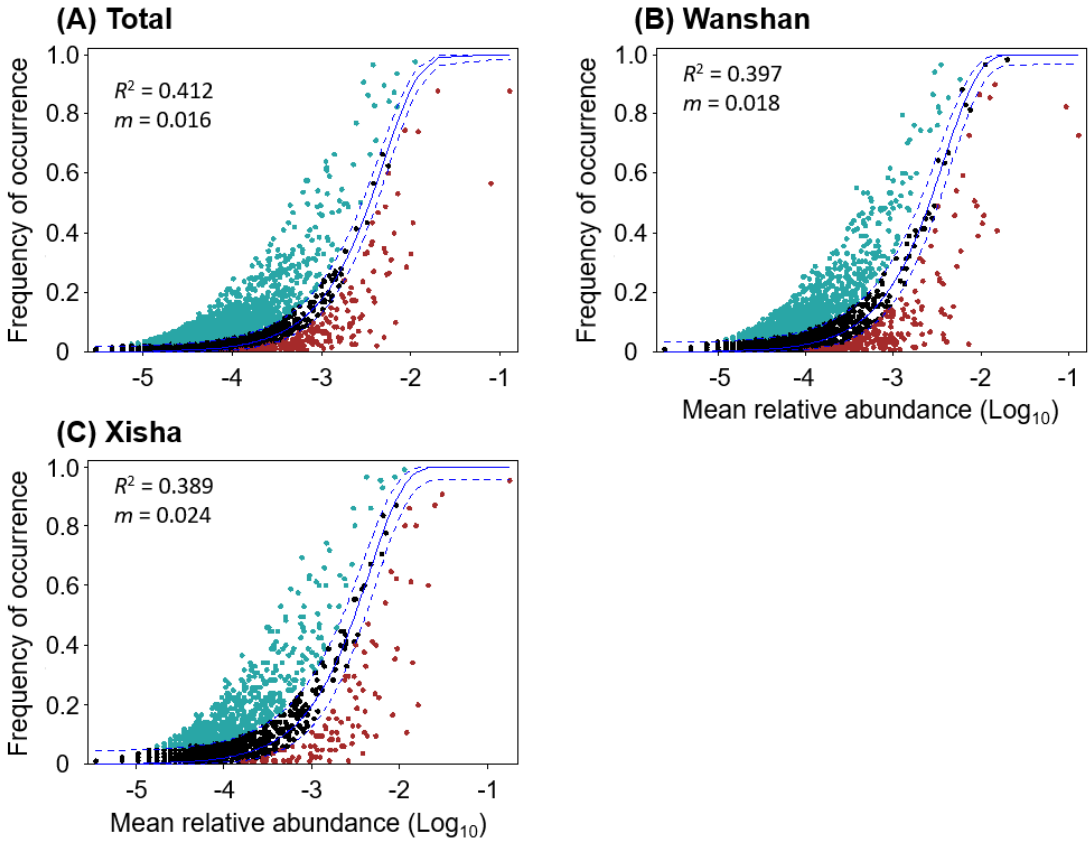


Figure 7.

The neutral community model showed that the neutral interpretation gave a good fit to fungal community distribution the total **(A)**, Wanshan **(B)**, and Xisha **(C)** datasets. The predicated occurrence frequency was shown as a solid blue line, and dashed blue lines represent 95% confidence intervals around the model prediction; red and light blue dots indicate the fungal operational taxonomic units that occur less and more frequently than given by the model; R^2 and m indicated the degree of fitting to the neutral community model and the immigration rate, respectively.

Table 1.

Soil fungal α-diversity predicted by plant and abiotic variables as explored by linear mixed-effects models controlling random effect of site

Fungal richness	**Independent variable**	**Slope**	***SE***	***df***	***t***	P_{adj}
Total data	K	3.279	0.880	176	3.727	< **0.001**
	Mg	12.07	4.189	176	2.882	**0.004**
	N	11.68	5.312	176	2.198	**0.029**
Wanshan	K	4.634	1.003	105	4.621	< **0.001**
	Plant PC1	37.06	9.176	105	4.038	< **0.001**
	Plant PC2	-26.53	7.378	105	-3.596	< **0.001**
	Mg	53.01	20.16	105	2.630	**0.010**
Xisha	Mg	8.084	3.688	70	2.192	**0.032**

Supporting Materials

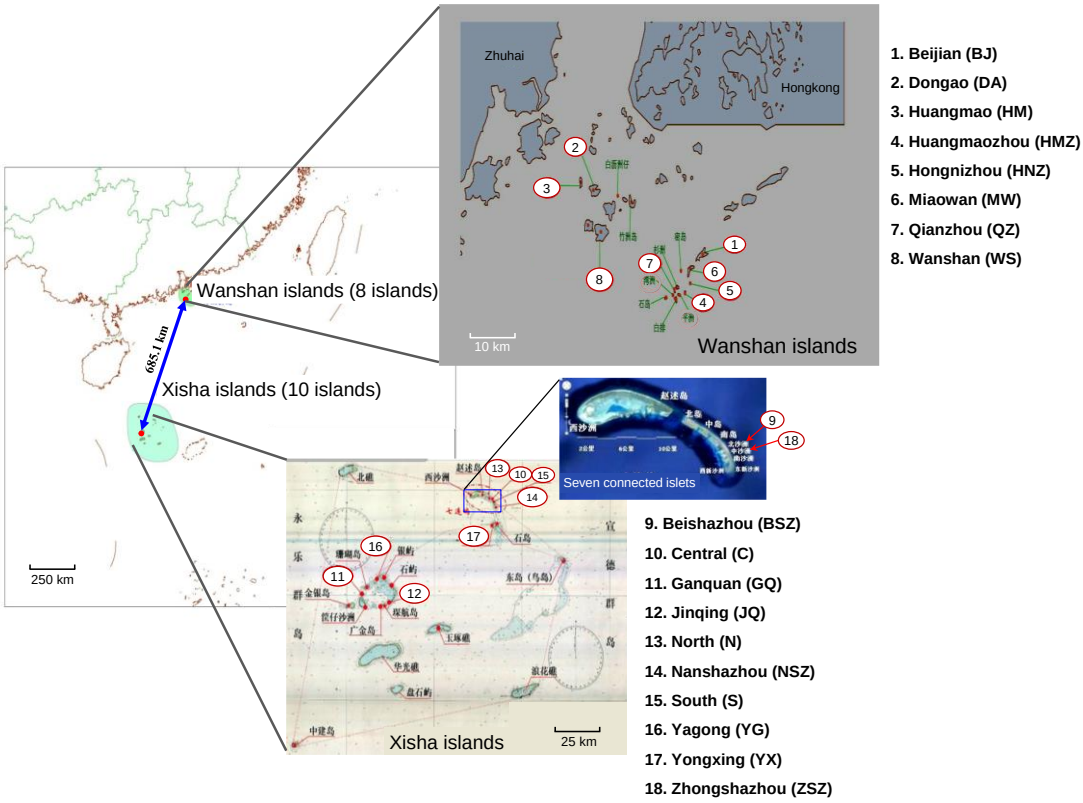


Figure S1.

Geographic locations of sampling islands. Two clustered groups of Wanshan islands and Xisha islands are showed by green regions. The geographic distance between Wanshan islands and Xisha islands is 685.1 km. The geographic distance from Wanshan islands to mainland is 30.5–64.5 km, and the geographic distance from Xisha islands to mainland is 372–590 km.

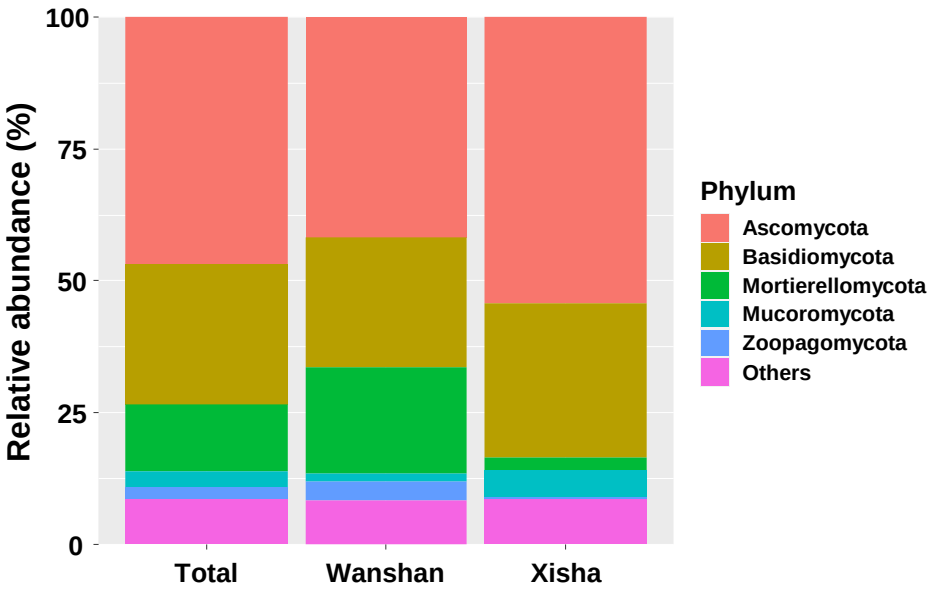


Figure S2.

Relative abundance of fungal community at phylum level.

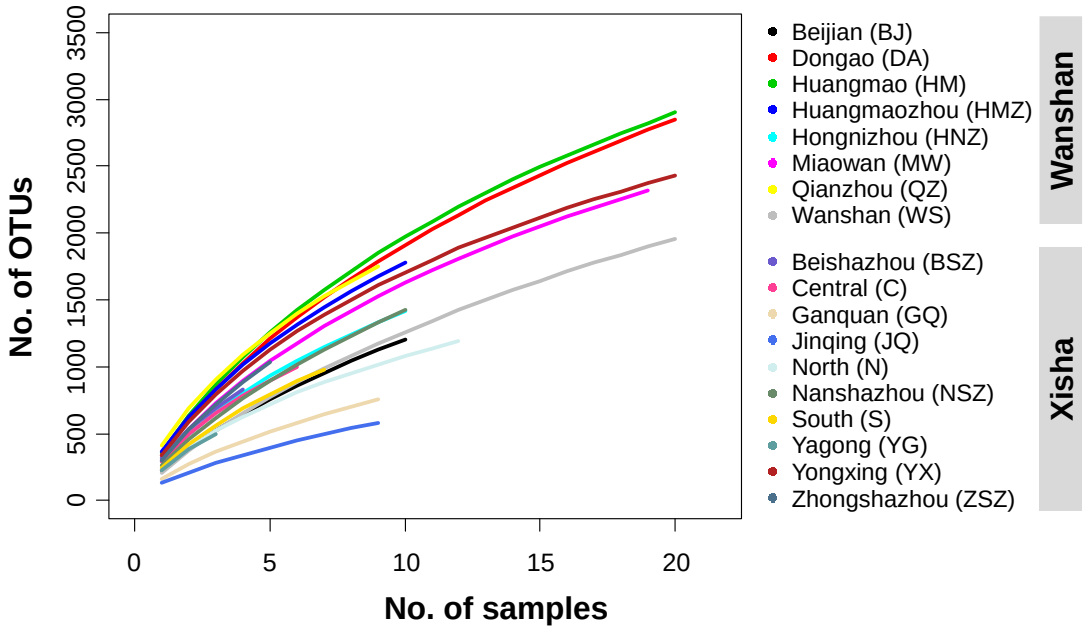
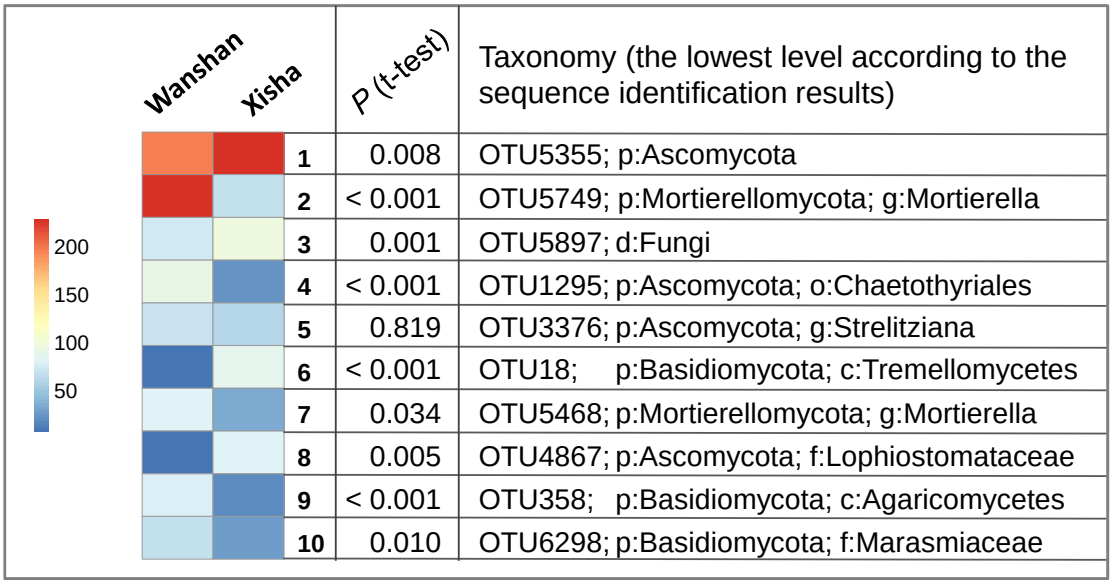


Figure S3.

Rarefaction curves for observed fungal operational taxonomic units (OTUs) in 18 islands.



	P (t-test)	Taxonomy (the lowest level according to the sequence identification results)
1	0.008	OTU5355; p:Ascomycota
2	< 0.001	OTU5749; p:Mortierellomycota; g:Mortierella
3	0.001	OTU5897; d:Fungi
4	< 0.001	OTU1295; p:Ascomycota; o:Chaetothyriales
5	0.819	OTU3376; p:Ascomycota; g:Strelitziana
6	< 0.001	OTU18; p:Basidiomycota; c:Tremellomycetes
7	0.034	OTU5468; p:Mortierellomycota; g:Mortierella
8	0.005	OTU4867; p:Ascomycota; f:Lophiostomataceae
9	< 0.001	OTU358; p:Basidiomycota; c:Agaricomycetes
10	0.010	OTU6298; p:Basidiomycota; f:Marasmiaceae

Figure S4.

Heatmap showing the distribution of top 10 operational taxonomic units (OTUs) in relative abundance between Wanshan islands and Xisha islands.

Table S1.

The basic information of the 18 oceanic islands

No.	Island name	Island type	Latitude (N), Longitude (E)	Area (ha)	Vegetation	Plant richness	Plot number
	Wanshan islands					125±19	
1	Beijian island (BJ)	General	21.8981; 114.0511	319	Wood	123	10
2	Dongao island (DA)	General	22.0244; 113.7100	470	Wood	170	20
3	Huangmao island (HM)	General	22.0383; 113.6654	108	Wood and shrub	145	20
4	Huangmaozhou island (HMZ)	General	21.8206; 113.9590	11.2	Wood and shrub	76	10
5	Hongnizhou island (HNZ)	General	21.8215; 113.9736	11.7	Wood and shrub	63	10
6	Miaowan island (MW)	General	21.8662; 114.0164	133	Wood and shrub	130	19
7	Qianzhou island (QZ)	General	21.8465; 114.0142	15.0	Wood and shrub	75	9
8	Wanshan island (WS)	General	21.9445; 113.7280	818	Wood	217	20
	Xisha islands					16.2±5.1	
9	Beishazhou island (BSZ)	Coral	16.9333; 112.3333	2.00	Shrub and herb	5	4
10	Central island (C)	Coral	16.9588; 112.3347	13.0	Shrub and herb	6	6
11	Ganquan island (GQ)	Coral	16.5000; 111.5833	31.0	Shrub and herb	32	9
12	Jinqing island (JQ)	Coral	16.4666; 111.7333	21.0	Shrub and herb	30	9
13	North island (N)	Coral	16.9666; 112.3166	40.0	Wood	16	12
14	Nanshazhou island (NSZ)	Coral	16.9333; 112.3500	6.00	Shrub and herb	12	10
15	South island (S)	Coral	16.9500; 112.3333	17.0	Shrub and herb	11	7
16	Yagong island (YG)	Coral	16.5666; 111.6833	1.00	Shrub and herb	15	3
17	Yongxing island (YX)	Coral	16.8333; 112.3333	260	Wood and herb	58	20
18	Zhongshazhou island (ZSZ)	Coral	16.9288; 112.3500	5.00	Shrub and herb	12	5

Table S2.

Soil properties of the 18 oceanic islands

Sites	pH	TC (g/kg)	TN (g/kg)	TP (g/kg)	K (g/kg)	Mg (g/kg)	C:N	N:P
	Wanshan islands							
BJ	4.639±0.217f	18.42±2.317d	1.444±0.161c	0.097±0.025c	31.80±1.356b	0.353±0.114c	12.72±0.595d	19.11±2.880ab
DA	4.632±0.256f	14.09±0.798d	1.038±0.075c	0.099±0.018c	21.84±2.725c	0.273±0.042c	14.53±1.108d	13.25±1.259bcd
HM	4.677±0.208f	25.22±2.926cd	1.889±0.185bc	0.161±0.029c	41.57±1.795a	0.574±0.153c	13.34±0.478d	15.16±1.292bc
HMZ	4.706±0.095f	26.87±3.479cd	2.189±0.240bc	0.239±0.039c	29.44±0.857bc	1.138±0.148c	12.14±0.439d	9.993±0.839bcde
HNZ	4.880±0.236ef	50.96±14.61c	3.126±0.737abc	0.149±0.041c	30.01±1.966bc	0.091±0.019c	15.25±0.646d	32.88±11.44a
MW	4.811±0.229f	21.94±2.384d	1.770±0.193c	0.128±0.019c	36.32±1.208ab	0.243±0.043c	12.46±0.223d	16.70±1.538b
QZ	4.957±0.117ef	37.88±11.68cd	2.517±0.197abc	0.301±0.028c	35.60±1.663ab	1.648±0.142c	15.03±4.494d	8.649±0.584bcde
WS	4.241±0.053f	20.92±1.051d	1.599±0.107c	0.098±0.012c	21.79±2.035c	0.367±0.059c	13.53±0.656d	18.69±1.550b
	Xisha islands							
BSZ	9.563±0.072a	117.5±0.330ab	0.275±0.030c	0.251±0.038c	0.233±0.033d	11.93±1.803a	441.0±42.86a	1.157±0.189de
C	8.293±0.164abcd	120.5±5.839ab	1.810±0.541bc	13.77±9.979bc	0.184±0.02d	10.45±1.358a	115.9±38.17cd	1.048±0.450de
GQ	7.820±0.191cd	103.0±14.59b	5.071±1.144a	49.92±16.32a	0.248±0.024d	4.672±0.989b	32.96±10.51d	0.560±0.369e
JQ	8.097±0.081bcd	129.0±5.998ab	4.243±1.168ab	27.44±7.630b	0.209±0.034d	4.966±0.619b	45.39±10.037d	0.196±0.034e
N	8.587±0.096abc	121.8±1.625ab	1.335±0.277c	6.317±2.767c	0.215±0.016d	11.71±0.751a	157.9±33.40bc	1.470±0.318de
NSZ	9.155±0.085ab	118.5±1.057ab	0.561±0.092c	0.539±0.184c	0.177±0.022d	11.08±0.881a	243.9±30.48b	1.569±0.256cde
S	9.489±0.107a	117.4±0.390ab	0.296±0.048c	0.221±0.026c	0.126±0.008d	12.05±0.648a	439.9±46.25a	1.325±0.097de
YG	6.615±1.195de	2.150±0.250d	0.155±0.015c	0.124±0.021c	2.645±0.290d	0.268±0.042c	14.16±2.983d	1.307±0.337de
YX	8.342±0.108abcd	132.1±5.374a	3.932±0.735ab	10.36±2.339bc	1.127±0.414d	10.50±0.472a	99.53±28.80cd	0.959±0.296e
ZSZ	9.558±0.037a	117.9±0.098ab	0.236±0.031c	0.193±0.009c	0.123±0.009d	12.37±0.805a	526.9±51.94a	1.259±0.234de

Table S3.

The identification information of fungal operational taxonomic units (attached as an Excel file).