

## Article

# Soil Phosphorus Availability Controls Deterministic and Stochastic Processes of Soil Microbial Community along an Elevational Gradient in Subtropical Forests

Rongzhi Chen <sup>1,†</sup> , Jing Zhu <sup>1,†</sup>, Lan Jiang <sup>1</sup>, Lan Liu <sup>2</sup>, Cheng Gao <sup>3</sup> , Bo Chen <sup>1</sup>, Daowei Xu <sup>1</sup>, Jinfu Liu <sup>1</sup> and Zhongsheng He <sup>1,\*</sup> 

- <sup>1</sup> College of Forestry, Key Laboratory of Fujian Universities for Ecology and Resource Statistics, Cross-Strait Nature Reserve Research Center, Fujian Agriculture and Forestry University, Fuzhou 350002, China; chenrozen0412@gmail.com (R.C.); hdly0718@126.com (J.Z.); jln0629@163.com (L.J.); cb137751120@163.com (B.C.); xudaowei2004446@126.com (D.X.); fjlf@fafu.edu.cn (J.L.)
- <sup>2</sup> College of Forestry, Hainan University, Haikou 570288, China; lanliu@hainanu.edu.cn
- <sup>3</sup> State Key Laboratory of Mycology, Institute of Microbiology, Chinese Academy of Sciences, Beijing 100101, China; gaoc@im.ac.cn
- \* Correspondence: jxhzs85@fafu.edu.cn; Tel.: +86-130-6726-8912
- † These authors contributed equally to this study.

**Abstract:** Revealing the assembly mechanisms of the soil microbial community, which is crucial to comprehend microbial biodiversity, is a central focus in ecology. The distribution patterns of microbial elevational diversity have been extensively studied, but their assembly processes and drivers remain unclear. Therefore, it is essential to unravel the relationship between the deterministic and stochastic processes of the microbial community assembly and elevational gradients. Here, our study built upon previous physicochemical analyses of soil samples collected along an elevational gradient (900–1500 m) in Daiyun mountain, a subtropical forest located in southeastern China. Using the phylogenetic-bin-based null model analysis (icamp) and multiple regression on matrices approach, we explored the major drivers that influence the assembly processes of soil bacterial and fungal community across elevations. The results showed that: (1) bacterial rare taxa exhibited a broad habitat niche breadth along the elevational gradient; (2) homogeneous selection and homogenizing dispersal proved to be the most important assembly processes for the bacterial and fungal community; (3) soil phosphorus availability mediated the relative importance of deterministic and stochastic processes in the soil microbial community. Notably, the relative abundance of dominant microbial taxa controlled by homogeneous selection and homogenizing dispersal increased with increasing soil phosphorus availability. Collectively, the assembly processes of microbial elevational communities of the subtropical mountains in China can be explained to some extent by variations in the soil phosphorus availability. This conclusion provides valuable insights into the prediction of soil microbial diversity and phosphorus nutrient cycling in subtropical montane forests.

**Keywords:** elevational gradients; community assembly processes;  $\beta$  diversity; phylogenetic-bin-based null model analysis; dominant microbial taxa; soil phosphorus availability



**Citation:** Chen, R.; Zhu, J.; Jiang, L.; Liu, L.; Gao, C.; Chen, B.; Xu, D.; Liu, J.; He, Z. Soil Phosphorus Availability Controls Deterministic and Stochastic Processes of Soil Microbial Community along an Elevational Gradient in Subtropical Forests. *Forests* **2023**, *14*, 1475. <https://doi.org/10.3390/f14071475>

Academic Editor: Choonsig Kim

Received: 23 May 2023

Revised: 5 July 2023

Accepted: 15 July 2023

Published: 18 July 2023



**Copyright:** © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

## 1. Introduction

Soil microbial communities play a crucial role in nutrient cycling and energy flow within terrestrial ecosystems [1,2]. Notably, in this regard, variations in microbial community species' composition across space, known as microbial  $\beta$  diversity, is a central focus of ecology [3], and is typically determined by deterministic and stochastic processes [3,4]. Thus, uncovering the assembly processes of soil microbial communities can offer vital insights into the generation and maintenance of biodiversity [5].

Understanding the deterministic and stochastic processes that control soil microbial assembly is crucial for predicting the response of microbial  $\beta$  diversity to environmental changes [6]. Deterministic processes highlight the relationship between microbial  $\beta$  diversity with the biotic and abiotic factor, and are classified into homogeneous and heterogeneous selection at different local scales [3]. The homogeneous selection usually leads to a reduction in  $\beta$  diversity, while heterogeneous selection implies that community assembly may differ greatly with variations in environmental conditions over time and space [7]. In contrast, stochastic processes emphasize that microbial  $\beta$  diversity is primarily mediated by dispersal events, ecological drift, genetic mutations, and historical contingencies [8]. Homogenizing dispersal and dispersal limitation are regarded as the primary factors influencing regional species pools and community assembly [7,9]. Early views suggested that deterministic or stochastic processes independently determine microbial community structure [10,11]. Recent studies on microbial  $\beta$  diversity patterns generally indicate that deterministic and stochastic processes act on community assembly together, although their relative importance may vary [12]. However, it is widely acknowledged that assembly processes tend to operate at the finer biological organizations rather than at the whole communities [12,13]. It is likely that the diversification rate, dispersal ability, and susceptibility to drift variation vary substantially among different microbial individual lineages/taxa [14]. Hence, revealing environmental filtering and other assembly processes in microbial individual lineages [3] will help ascertain the underlying mechanisms of soil microbial  $\beta$  diversity.

The influence of abiotic factors on soil microbial community assembly varies with different regional scales [15]. Generally, large spatial scales exhibit greater environmental heterogeneity, resulting in enhanced environmental filtering and reduced ecological drift. Meanwhile, dispersal is a key contributor to the variability of a regional species pool [3,16]. However, the local scales have not been thoroughly explored due to the limited number of individuals and relatively complex microenvironment. Additionally, the microenvironment of small spatial scales may make the microbial communities more homogeneous [17], which enhances ecological drift [16]. Elevation strongly mediates environmental attributes (e.g., temperature and light), resulting in soil characteristics and vegetation alterations [18]. Consequently, elevational gradients provide a natural experimental platform for investigating the assembly of soil microbial communities [19,20]. Previous studies have mainly focused on the distribution patterns of soil microorganisms (bacteria, archaea, and fungi) and the ecological drivers that control microbial diversities across elevations [19,21,22]. However, our understanding of the assembly mechanisms of soil microorganisms along elevational gradients remains incomplete, which impedes our ability to fully comprehend how drivers control soil microbial community assembly.

The forest ecosystem is the most intricate terrestrial ecosystem [23]. The climatic conditions of montane forests depend on various factors, including topography, elevation, and the interplay between the forest nutrient cycle and global climate [24]. Similarly, the diversity and rarity of montane forests, community assembly, migration, and niche evolution collectively contribute to montane forest biodiversity patterns [24]. In particular, the habitat niche is a pivotal trait that impacts species sorting and dispersal in shaping ecological communities [25]. Taken together, these forest factors create an ideal experimental region for studying the assembly of soil microbial communities [26]. The studies revealed that the interplay of forest environmental factors dominates the community structure in phylogenetic and functional traits [27]. In subtropical forests, soil phosphorus limitation is a commonly observed phenomenon [28]. In nutrient-impoverished soils, soil microbial communities (bacteria or fungi) may be primarily driven by phosphorus or nitrogen availability [29], which can further restrict microbial community assembly [28]. In a long-term fertilization experiment, Ma et al. [30] found that alterations in soil stoichiometry (N/P) and phosphorus availability shape fungal communities by influencing fungal enzyme activity and functional gene abundance. Similarly, Peng et al. [31] identified that soil phosphorus plays a critical role not only in shaping the diversity and community structure of both

abundant and rare bacteria but also in mediating the balance between the deterministic and stochastic processes. Thus, we hypothesize that phosphorus availability plays an essential role in the soil microbial community assembly of subtropical forest ecosystems. However, the drivers that determine the assembly processes of the dominant microbial community in the forest ecosystem are poorly resolved. Therefore, elucidating the correlations between dominant microbial taxa controlled by major assembly processes and environmental factors can provide vital insights into the complex mechanisms of the forest ecosystem.

Daiyun mountain belongs to a typical montane forest ecosystem on the southeastern coast of China [32]. The pronounced distinctions in climatic attributes between different elevational gradients create typical vegetation cover types. This distinctive feature offers an ideal setting for studying the soil microbial community along an elevational gradient [33]. In previous studies, we examined the stoichiometric characteristics of soil carbon, nitrogen, and phosphorus along the elevational gradient and found that soil phosphorus, as a major limiting factor, fluctuates with changes in elevation [34]. Thus, it is crucial to determine the extent to which these fluctuations in soil phosphorus levels impact the microbial community in Daiyun mountain. Although recent investigations have explored the structure and functional diversity of soil microbial communities in Daiyun mountain [33,35], there is still a significant knowledge gap regarding the assembly of these communities across elevations. To fill this knowledge gap, we used high-throughput metagenomic technologies to evaluate the effects of deterministic and stochastic processes on soil bacterial and fungal community assembly along the elevational gradients. Here, our main hypothesis is as follows: (1) homogeneous assembly processes are enhanced in soil microbial community along an elevational gradient, and homogeneous selection likely serves as the major assembly process of the microbial community. Furthermore, we propose that (2) soil phosphorus availability mediates the abundance and assembly of dominant microbial taxa as the microbial community structure is strongly associated with the soil and vegetation phosphorus content [36], and whether the mechanism exists in Daiyun mountain. To address the two hypotheses, we applied phylogenetic-bin-based null model analysis (icamp) [14] to quantitatively speculate the assembly mechanisms of soil microbial community in Daiyun mountain, while also further analyzing microbial individual lineages.

## 2. Materials and Methods

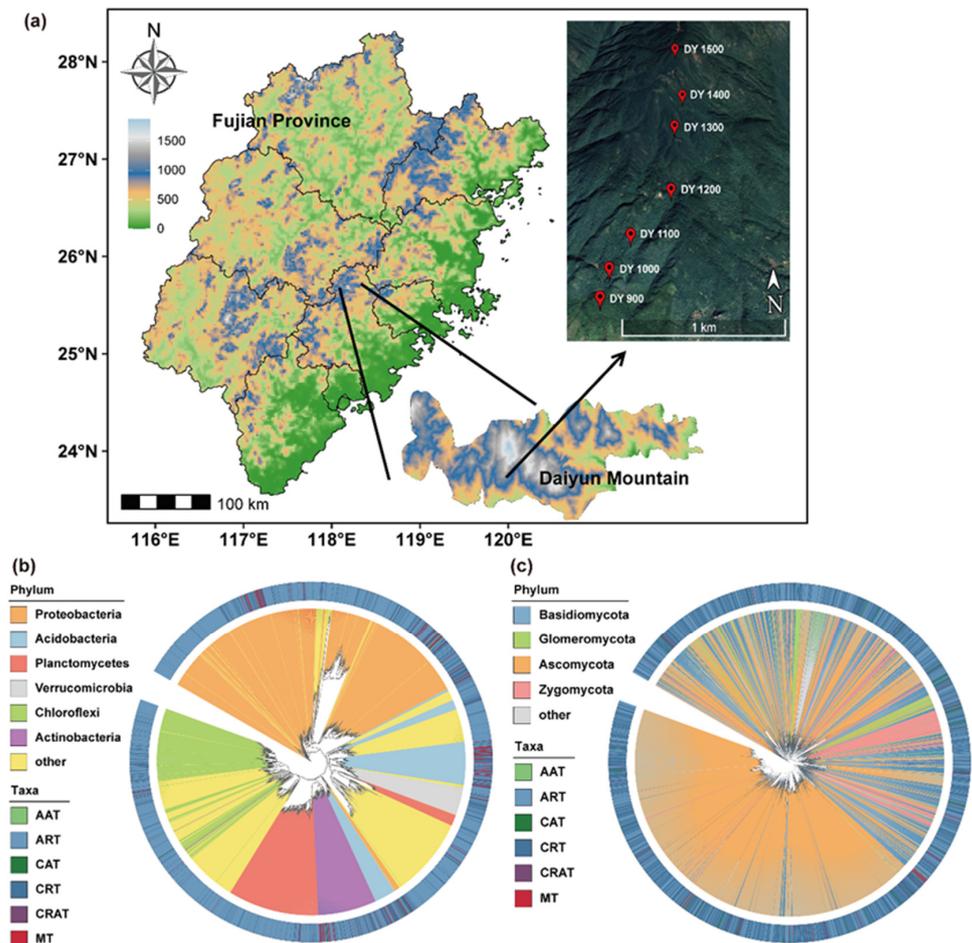
### 2.1. Study Location

This study was conducted in Daiyun Mountain National Nature Reserve (118°05′~118°20′ E, 25°38′~25°43′ N) located in the southeastern region of China, which lies within the transitional zone between subtropical and south subtropical forests [34] (Figure 1a). The reserve spans a total area of 134.72 km<sup>2</sup>, with the highest peak of Daiyun mountain reaching an elevation of 1856 m. The major soil type in the area is mountain Ferric Acrisols soil (900–1600 m a.s.l.), according to the World Reference Base for Soil Resources (WRB) [34]. In addition, this region belongs to a mid-subtropical montane climate with a mean annual temperature approximately ranging from 12.1 to 16.9 °C, and the mean annual relative humidity exceeding 80% [34]. The natural forest in this site is mainly composed of coniferous forest (e.g., *Pinus massoniana* Lamb, *P. taiwanensis* Hayata, *Cunninghamia lanceolata* (Lamb.) Hook) and evergreen broad-leaved forest (e.g., *Castanopsis fabri* Hance, *C. eyrei* (Champ.) Tutch) [33].

### 2.2. Soil Samples and Data Collection

In July 2018, seven standard elevational plots (20 m × 30 m) were set up along an elevation of 900–1500 m (DY9, DY10, DY11, DY12, DY13, DY14, and DY15) on the southern slope of Daiyun mountain [37]. The slopes were measured using a GPS device (Magellan eXplorist 510, Santa Clara, CA, USA). Each elevational plot was divided into three sample plots (10 m × 20 m), and within each sample plot, soils collected by five-point method were mixed to create a soil sample. In total, 21 soil samples were collected. Then, we packed the soil samples to ice boxes and brought them to the laboratory. All soil samples were sieved

through 2 mm to remove plants roots, and animal residues, then divided them into two separate parts for soil DNA extraction and physicochemical analyses, respectively.



**Figure 1.** The elevation map of the sampling sites in southeast China (a). Phylogenetic distributions for the bacterial (b) and fungal (c) phylum, the annulus shows each OTU classified by AAT, ART, CAT, CRT, CRAT and MT. AAT: absolutely abundant taxa; ART: absolutely rare taxa; CAT: conditionally abundant taxa; CRAT: conditionally rare or abundant taxa; CRT: conditionally rare taxa; MT: moderate taxa. AAT and CAT were collectively considered as AT (abundant taxa), ART and CRT as RT (rare taxa). DY 900 indicates the elevational sample site at the elevation of 900 m in Daiyun mountain, and so on.

### 2.3. Soil Physicochemical Analyses

Soil pH was measured using pH potentiometry (water-soil ratio 2.5:1). Soil water content (SWC) was determined by the drying method. Soil temperature (ST) was measured every four hours using temperature recorders (DS1922L-F50 iButton, Maxim Integrated, San Jose, CA, USA). Soil available nitrogen (AN) content was determined by the alkaline solution diffusion method. Soil available phosphorus (AP) content was determined by the molybdenum antimony anti-colourimetric method. An elemental analyzer (Vario MAX cube CN, Elementar Analysensysteme GmbH, Langenselbold, Germany) was used to determine the total carbon (TC) and total nitrogen (TN) content in natural air-dried soil samples. Total phosphorus (TP) content and total potassium (TK) content were measured by the acid nitrification digestion of soil samples, and the resulting supernatant was analyzed using an inductively coupled plasma optical emission spectrometer (PE OPTIMA 8000, PerkinElmer, Waltham, MA, USA). The results of soil physicochemical contents related to the He et al. [33].

#### 2.4. DNA Extraction and High-Throughput Amplicon Sequencing

Total soil DNA was extracted using the BioFast Soil Genomic DNA Extraction Kit (BioFlux Company, Hangzhou, China) following the manufacturer's instructions. The extracted DNA was detected by 1% agarose gel electrophoresis, and the concentration of DNA was assessed by the NanoDrop 2000C spectrophotometer (Thermo Scientific, Waltham, MA, USA). Next, the purified DNA was collected by gel recovery kit (TianGen Biotech Co., Ltd., Beijing, China) and stored at  $-20\text{ }^{\circ}\text{C}$  in the refrigerator. The V3-V4 region (338F/806R) of the 16S rRNA gene for the bacteria and the ITS1 region (ITS5-1737F/ITS2-2043R) of the fungal 18S rRNA gene were amplified by high-throughput amplicon sequencing technology, respectively. Polymerase chain reaction (PCR) was carried out according to the following thermal program: pre-denaturation at  $95\text{ }^{\circ}\text{C}$  for 5 min, denaturation at  $95\text{ }^{\circ}\text{C}$  for 30 s, annealing at  $50\text{ }^{\circ}\text{C}$  for 30 s, extension at  $72\text{ }^{\circ}\text{C}$  for 40 s for 25 cycles, and final extension at  $72\text{ }^{\circ}\text{C}$  for 7 min. PCR products were electrophoresed on a 2% agarose gel, and then collected using a gel recovery kit (AxyPrepDNA, Axygen, Hangzhou, China). The samples were sequenced using the IonS5TmXL sequencing platform by the single-end sequencing technology.

#### 2.5. Statistical Analyses

All packages for statistical analyses were performed in R v4.2.1.

##### 2.5.1. Soil Microbial Community Structure Analysis

Quality filtering on the raw reads were performed under specific filtering conditions to obtain the high-quality clean reads according to the Cutadapt (V1.9.1) quality controlled process [38]. Next, the reads were compared with the reference database (Silva database) using the UCHIME algorithm (UCHIME Algorithm) to detect chimera sequences [39,40], and then the chimera sequences were removed [41]. Then, the clean reads were finally obtained. Sequences with  $\geq 97\%$  similarity were assigned to the same OTUs in Uparse software (Uparse v7.0.1001) [42]. For each OTU representative sequence, the Silva Database was used based on the Mothur algorithm to annotate taxonomic information [40]. OTUs' abundance information was normalized using a standard of sequence numbers corresponding to the sample with the least sequences. In the study, the OTUs were classified into six different taxa (AAT, ART, MT, CRT, CAT, and CRAT) based on their relative abundance [43]. AAT and CAT were collectively identified as abundant taxa, while ART and CRT were recognized as rare taxa [44]. The *dplyr* package was used to calculate all OTUs across elevations, those with higher relative abundance and greater contributions to the major assembly processes were deemed as dominant microbial taxa. According to the annotation information, the relative abundance of the microbial phylum was selected for heatmap analysis using the *heatmap* package. Additionally, the phylogenetic trees were constructed using FastTree in Qiime2 [45], before being annotated and visualized in the *ggtree* and *treeio* packages.

##### 2.5.2. Habitat Niche Breadth Analysis

The habitat niche breadth of the microbial taxa is a crucial factor to consider when studying deterministic and stochastic processes, particularly in relation to the dispersal of microbial communities [46]. Microbial taxa with a wider niche breadth can exhibit greater metabolic flexibility and dispersal ability at the community level [46]. The *spaa* package was used to calculate the niche breadth (Levins' niche breadth) and niche overlap in different microbial taxa [47]. Normality tests were performed in the *base* package, and the niche breadth of the three taxa was evaluated by the 'LSD-test' function ( $p < 0.05$ ) in the *agricolae* package.

##### 2.5.3. Null Model Analysis

Compared to other null model analyses, the phylogenetic-bin-based null model analysis (icamp) demonstrates a higher quantitative expression in the assessment of community

assembly [14]. Based on the *icamp* model analysis, the assembly processes of the soil microbial community comprised homogeneous selection (HoS), heterogeneous selection (HeS), homogenizing dispersal (HD), dispersal limitation (DL), and drift (DR). The observed microbial taxa were initially classified into ‘bins’ according to their phylogenetic relationship. The  $\beta$ -net relatedness index ( $\beta$ NRI) and Raup Crick metric (RC) of each bin were used to assess the relative importance of different assembly processes within individual lineages [14]. Pairwise comparisons with  $\beta$ NRI  $< -1.96$  were deemed to be controlled by homogeneous selection within each bin, whereas those with  $\beta$ NRI  $> 1.96$  were considered to be influenced by heterogeneous selection. The remaining pairwise comparisons, where  $|\beta$ NRI|  $\leq 1.96$ , were subdivided using the taxonomic diversity metric RC. Comparisons with RC  $< -0.95$  were controlled by homogenizing dispersal, while those with RC  $> 0.95$  were controlled by dispersal limitation. Values with  $|\beta$ NRI|  $\leq 1.96$  and  $|RC| \leq 0.95$  represented the impacts of drift and other assembly processes. Meanwhile, we assigned weights to each process within bins based on the relative abundance of each bin [14], enabling us to estimate the relative importance of each process at different elevations. To ensure the accuracy of the *icamp* model analysis, we used the confidence metric and 1000 permutations [14]. In addition, we employed bootstrapping in the *icamp* package to estimate the variation in the relative importance of each process at different elevations. To select the dominant microbial taxa controlled by major assembly processes [48], we used the *dplyr* package and visualized by the iTOL v5 [49].

#### 2.5.4. Correlation Analysis

To identify the effects of environmental factors on major assembly processes, we firstly used the ‘*varclus*’ function in the *Hmisc* package to assess the redundancy (Spearman  $\rho^2 = 0.7$ ) among environmental variables [50]. Secondly, the Mantel test in the *vegan* package was used to determine the correlation between environmental factors and major assembly processes [51], with the Mantel *r* (spearman coefficient) being calculated. To further investigate the correlation between dominant microbial taxa and environmental factors, we conducted multiple regression on matrices (MRM) analysis using the *vegan* package and the *ecodist* package [52]. Furthermore, the linear regression model was established using the ‘*lm*’ function in the *stats* package.

### 3. Results

#### 3.1. Soil Microbial Community Composition and Structure

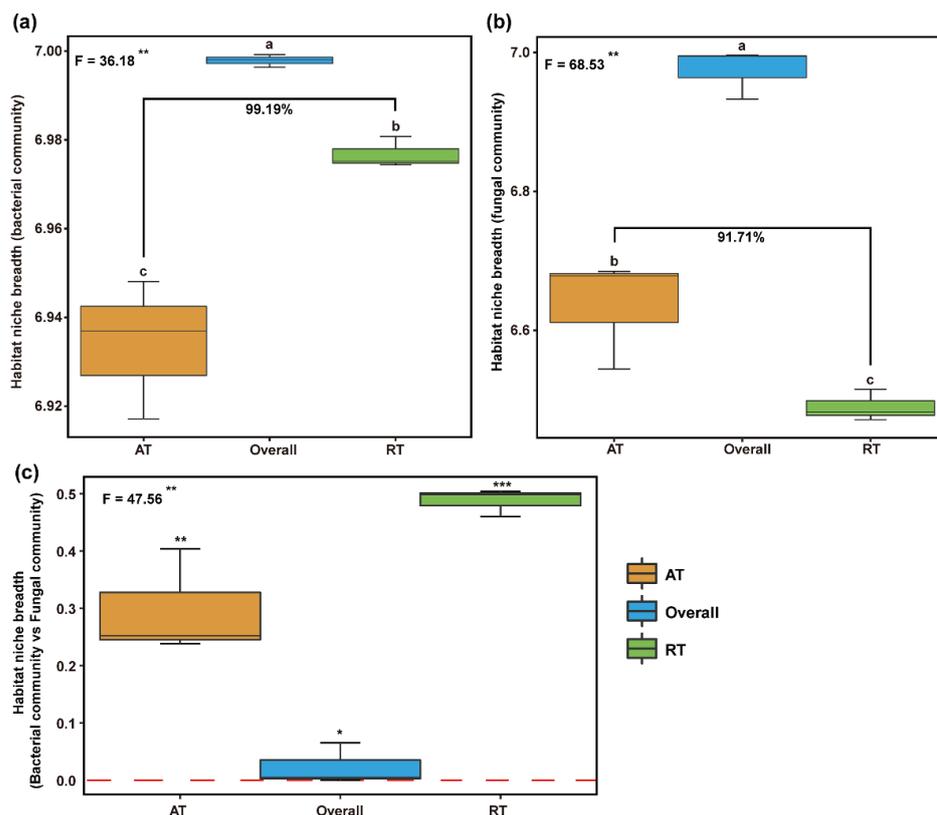
The soil bacterial community consisted primarily of *Proteobacteria*, *Acidobacteria*, *Actinobacteria*, *Chloroflexi*, *Planctomycetes*, and *Verrucomicrobia* along the elevational gradient. *Proteobacteria* (33.4% of all OTUs), *Acidobacteria* (8.1%), and *Actinomycetes* (6.3%) were the dominant bacterial phylum (Figure 1b). On the other hand, the fungal community was mainly composed of *Basidiomycota*, *Ascomycota*, *Zygomycota*, *Glomeromycota* and *Chytridiomycota*. *Ascomycota* (61.5% of all OTUs) and *Basidiomycota* (26.2%) were the dominant fungal phylum (Figure 1c). Among the total bacterial OTUs, 0.2% (16) were classified as abundant taxa, 7.1% (434) as moderate taxa, and 92.6% (5675) as rare taxa (Figure S1a). For the total fungal OTUs, abundant taxa accounted for 0.8% (32), moderate taxa for 0.3% (13), and rare taxa for 96.8% (3714) (Figure S1b).

The heatmap analysis revealed the distribution pattern of soil microbes across different elevations. The bacterial community at the elevation of 900 m (DY9B), 1000 m (DY10B) and 1100 m (DY11B) were clustered, indicating that their community structure was more similar to each other, and differed from those at the elevation of 1200 m (DY12B), 1300 m (DY13B), 1400 m (DY14B), and 1500 m (DY15B) (Figure S2a). Meanwhile, the fungal community structure of the seven elevations was classified into three groups (Figure S2b).

#### 3.2. Habitat Niche Breadth

Differences in habitat niche breadth were observed among the overall, abundant, and rare taxa in the soil microbial community. In the bacterial community, the overall taxa

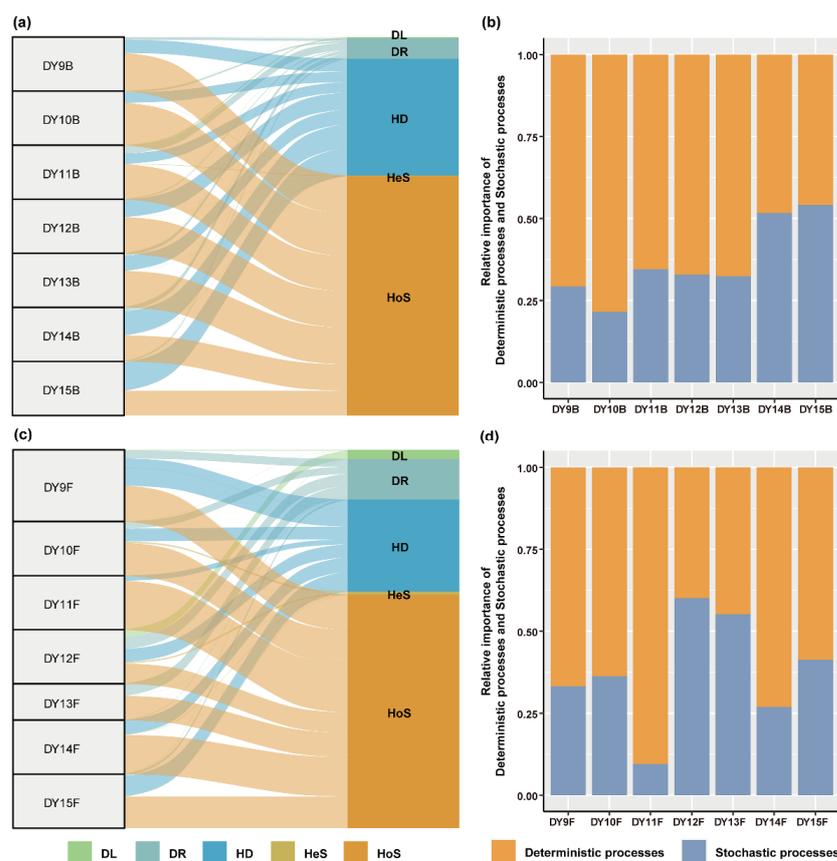
exhibited the widest niche breadth, followed by the rare taxa and abundant taxa (Figure 2a). This suggests that the abundant taxa use limited resources within the bacterial community. For the soil fungal community, the rare taxa had the narrowest niche breadth (Figure 2b), which implied that the rare taxa are at a disadvantage in resource competition. Additionally, the niche breadths in the bacterial community were significantly broader ( $p < 0.05$ ) than those in the fungal community for the three taxa (Figure 2c). The niche overlap between both the abundant and rare microbes exceeded 90%.



**Figure 2.** The habitat niche breadth of the bacterial (a) and fungal (b) community along the elevational gradient, and comparison between them (c). AT: abundant taxa; RT: rare taxa; Overall: all taxa. The letters above bars indicate the significance ( $* p < 0.05$ ) among AT, Overall, RT for bacterial (a) and fungal (b) community, while the asterisks above bars (c) indicate the differences ( $* p < 0.05$ ,  $** p < 0.01$ ,  $*** p < 0.001$ ) in the habitat niche breadth between bacterial and fungal community. The line between AT and RT indicate the niche overlap.

### 3.3. Soil Microbial Community Assembly Processes and Their Influencing Factors

The relative importance of assembly processes varied along the elevational gradient, with homogeneous selection (HoS) and homogenizing dispersal (HD) serving as the two most pivotal assembly processes for the soil microbial community at all elevations (Figure 3a,c). In the bacterial community, the relative importance of HoS (45.9%–78.5%) and HD (18.7%–52%) varied significantly across elevations. The relative importance of HoS (78.5%) was highest at an elevation of 1000 m. The relative importance of HD (52%) peaked at 1500 m, where the relative importance of HoS (45.9%) was the lowest. For the fungal community, the relative importance of HoS (37.5%–90.5%) was much higher than that of HD (9.4%–37.3%). The relative importance of HoS was 90.5% and 72.6% at the elevation of 1100 m and 1400 m, respectively. Meanwhile, the relative importance of fungal HD remained less than 40% at all elevations (Figure S3). Furthermore, we found that the deterministic and stochastic processes of the bacterial community tended to balance out with higher elevations (Figure 3b). For the fungal community, deterministic processes were found to be more important than stochastic processes (Figure 3d).



**Figure 3.** Variations between microbial assembly processes (a,c) and elevations, and the relative importance of deterministic and stochastic processes in bacterial (b) and fungal (d) community assembly along the elevational gradient. HoS: homogeneous selection; HeS: heterogeneous selection; HD: homogenizing dispersal; DL: dispersal limitation; DR: drift. DY9B indicates that the bacterial community at the elevation of 900 m in Daiyun mountain, and so on.

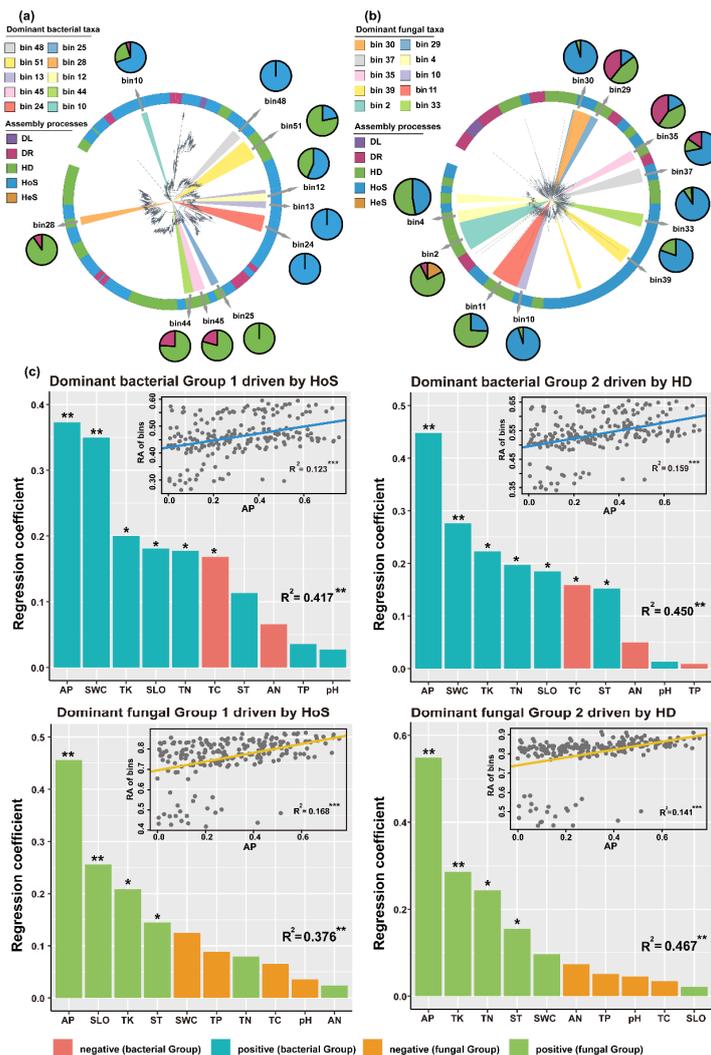
Using the Mantel test, we determined the contribution of the environmental factors mediating the two major assembly processes (Table S1). Soil available phosphorus (AP) was significantly and positively correlated with HoS (bacteria:  $r = 0.382$ ,  $p < 0.05$ ; fungi:  $r = 0.471$ ,  $p < 0.05$ ) and HD (bacteria:  $r = 0.497$ ,  $p < 0.05$ ; fungi:  $r = 0.499$ ,  $p < 0.05$ ); thus, AP served as the best predictor for HoS and HD along the elevational gradient. We observed a significant correlation between the soil total phosphorus (TP) content and HD (bacteria:  $r = 0.642$ ,  $p < 0.05$ ; fungi:  $r = 0.535$ ,  $p < 0.05$ ). Subsequently, the strong effect of soil temperature (ST) in the bacterial community was observed, as the relative importance of HoS ( $r = 0.400$ ,  $p < 0.05$ ) and HD ( $r = 0.602$ ,  $p < 0.01$ ) significantly varied with ST.

### 3.4. Soil Microbial Community Assembly Processes Based on Individual Lineages

Based on the icamp model, the bacterial 6126 OTUs were divided into 52 phylogenetic bins (Figure S4a) and the fungal 3836 OTUs were divided into 42 phylogenetic bins (Figure S4b). Of the bacterial bins, HoS dominated 31 bins (59.6% of bin numbers and 59.3% of relative abundance) and HD dominated 14 bins (26.9% of bin numbers and 31.6% of relative abundance, Table S2a). For the fungal bins, HoS dominated 19 bins (45.2% of bin numbers and 47.5% of relative abundance) and HD dominated 15 bins (35.7% of bin numbers and 35.0% of relative abundance, Table S2b). Thus, we found that the dominance of HoS was stronger than HD for both bacterial and fungal bins.

Of the bacterial and fungal bins, ten bins controlled by two major assembly processes were selected, respectively. The 10 bacterial bins constituted 19.3% of the total bacterial abundance, with 49.4% and 58.6% contributions for HoS and HD (Table S2a), respectively. Of these, five bins were mainly controlled by HoS (Group 1B), and five mainly by HD

(Group 2B, Figure 4a). Comparatively, the 10 fungal bins accounted for 30.0% of the total fungal abundance, with 60.7% and 55.6% contributions for HoS and HD (Table S2b), respectively. Of these, five bins were mainly controlled by HoS (Group 1F), and five mainly by HD (Group 2F, Figure 4b). The selected bins (Group 1B, Group 2B, Group 1F, and Group 2F) were deemed the dominant microbial taxa. The dominant bacterial taxa controlled by HoS and HD included *Proteobacteria*, *Acidobacteria*, *Actinobacteria*, *Verrucomicrobia*, and *Firmicutes* (Table S3a). Additionally, the dominant fungal taxa controlled by HoS and HD included *Basidiomycota*, *Ascomycota*, and *Zygomycota* (Table S3b). More importantly, the dominant microbial taxa controlled by HoS and HD primarily belonged to rare taxa (Table S3).



**Figure 4.** Variations in assembly processes across dominant bacterial taxa (a) and dominant fungal taxa (b) based on the icamp model. The phylogenetic trees for the microbial taxa are displayed at the center, the colors represent dominant microbial taxa (‘bin’) controlled by HoS and HD. The annuluses show that major assembly processes control different microbial taxa. Pie charts show the contribution of each dominant taxa (‘bin’) to assembly processes. HoS: homogeneous selection; HeS: heterogeneous selection; HD: homogenizing dispersal; DL: dispersal limitation; DR: drift. The effect of environmental factors on the relative abundance of dominant bacterial taxa and dominant fungal taxa by multiple regression on matrices (MRM) (c). The insets show the linear regressions between AP and the relative abundance of dominant microbial taxa. The significance level is \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ . SWC: soil water content; ST: soil temperature; TC: total carbon; TN: total nitrogen; TP: total phosphorus; TK: total potassium; AP: available phosphorus; SLO: slope; AN: available nitrogen; RA: relative abundance.

### 3.5. Correlation between Environmental Factors and Dominant Microbial Taxa

Considering the interaction of environmental factors along elevational gradients, we further used the MRM model to establish the correlation between environmental factors and the dominant microbial taxa (Figure 4c). Our results revealed that AP was the most important variable for predicting the abundance of dominant microbial taxa ( $p < 0.01$ ). Interestingly, the most important predictor of the dominant microbial taxa was consistent with the best factor predicting the major community assembly processes (Table S1, Figure 4c) and the most significant and positive linear regressions was found between AP and the relative abundance of dominant microbial taxa ( $p < 0.001$ ). Soil water content (SWC), total potassium content (TK), total nitrogen content (TN), and slope (SLO) were observed to have a strong effect on the dominant bacterial taxa ( $p < 0.05$ ). The total carbon content (TC) had a significantly negative correlation with the relative abundance of dominant bacterial taxa ( $p < 0.05$ ). In addition, the TK and ST were the dominant drivers for the dominant fungal taxa ( $p < 0.05$ ).

## 4. Discussion

### 4.1. Structure of Soil Microbial Community along the Elevational Gradient

In our study, the dominant bacterial phylum consisted mainly of *Proteobacteria*, *Acidobacteria*, and *Actinobacteria* (Figure 1b), and the dominant fungal phylum was *Ascomycota* and *Basidiomycota* (Figure 1c). These findings are consistent with the previous conclusions on the spatial distribution of soil microorganisms in subtropical montane forests [53,54]. *Proteobacteria*, as a major bacterial phylum, play an essential role in responding to soil nutrients [55]. In addition, *Basidiomycota* explains the spatial properties of the plant root community in environmental heterogeneity [56].

Most species in all ecosystems are rare species, especially in the microbial community [57]. Our results supported this view, as the majority of soil microbes along the elevational gradient belonged to rare taxa (Figure 1b,c). More importantly, bacterial rare taxa displayed a broader habitat niche breadth and made a greater contribution to the major assembly processes (Figure 2a, Table S3). A possible explanation for this is that bacterial rare taxa are more susceptible to environmental filtering than abundant taxa [58]. And, the  $\beta$  diversity of bacterial rare taxa is more strongly controlled by stochastic processes (i.e., dispersal) and weak environmental filtering [59], we suspect that more rare species may be involved in dispersal events. The habitat niche breadth of abundant taxa was broader than that of rare taxa in the fungal community (Figure 2b), which suggests that fungal abundant taxa have greater versatility in metabolism than rare taxa. The result is supported by the fact that the fungal abundant taxa expressed substantially broader response thresholds as well as stronger phylogenetic signals for the ecological preferences along environmental gradients compared to rare taxa [60]. Yet, as bacteria exhibit superior functionality in resource utilization and metabolism [61], they tend to be more resilient to environmental stressors and less susceptible to species sorting processes than fungi [62]. Our result may provide evidence for this view, where the niche breadth of all bacterial taxa was wider than that of fungal taxa along the elevational gradient (Figure 2c).

### 4.2. Mechanisms for the Soil Microbial Community Assembly

Homogeneous selection and homogenizing dispersal were the two most important assembly processes along the elevational gradient in Daiyun mountain (Figure 3a,c), corresponding to our first hypothesis. The habitat at small spatial scales can only sustain a limited number of individuals [17], and since homogeneous selection and homogenizing dispersal can reduce  $\beta$  diversity [63,64], we speculate that microbial community along the elevational gradient of Daiyun mountain may exhibit lower  $\beta$  diversity. Biotic factors play an important role in microbial community assembly [3]. For instance, soil fungal richness was found to mediate the assembly processes of bacterial communities, with stochastic processes showing a negative correlation with increased fungal richness [65]. Meanwhile, Bahram et al. [66] observed a decrease in the species richness of forest fungal commu-

nities with higher elevation. Remarkably, the fungal richness decreased with increasing elevation at the elevation from 1000 to 1500 m (Table S4), while the relative importance of stochastic processes in bacterial community increased (Figure 3b), which was consistent with the above views. Deterministic processes, stochastic processes, or a trade-off between the two may control the microbial community assembly across different spatiotemporal scales [67–69]. In our study, the results show that the trade-off between deterministic and stochastic processes controlled the bacterial community assembly (Figure 3b), whereas deterministic processes were the major assembly processes driving the fungal community (Figure 3d). In general, the assembly mechanisms of soil microbial communities are a combination of scale-dependent and species-dependent characteristics.

Homogeneous selection and homogenizing dispersal were mediated mainly by soil available phosphorus, the effect of phosphorus availability on major assembly processes was stronger in fungal community than in bacterial community (Table S1). Available phosphorus content was significantly and positively correlated with the relative importance of homogeneous selection and homogenizing dispersal (Table S1), which is a possible explanation for the fact that decreased soil phosphorus availability can limit microbial growth and community structure [28]. In general, soil phosphorus is mainly the limiting factor of forest ecosystem primary productivity in tropical and subtropical regions [70]. Additionally, the biogeochemical cycle of phosphorus in vegetation is an essential component of the geochemical cycle of phosphorus in montane systems. Plant leaf phosphorus can remarkably affect the spatial distribution of soil available phosphorus [36], which indirectly influences the assembly of soil microbial communities. This may be responsible for the fact that soil phosphorus availability mediated the assembly of soil microbial community in subtropical forests. Moreover, soil phosphorus remains the major limiting element in Daiyun mountain [34]. The extremely low utilization of soil phosphorus in this area is primarily due to the vertical and horizontal migration of phosphorus across the soil profile and surface runoff [71]. In the future, supplementing soil phosphorus content could be used to investigate the impact of phosphorus nutrient cycling on microbial community assembly at finer levels on a local scale.

Various environmental factors played a pivotal role in driving changes in the microbial community. Notably, a significant effect of soil temperature on the bacterial community assembly was observed (Table S1). This can be attributed to the fact that temperature influences the metabolic rate of microorganisms and their competitive interactions [72], thereby resulting in changes in the community assembly of microorganisms. In previous studies, soil pH has been a crucial factor affecting the structure of microbial communities [73,74]. However, our study investigated an elevational gradient on a local scale, and soil pH levels were relatively stable in the Daiyun mountain [34]. Therefore, we found that the soil pH had a low impact on the microbial community assembly along the elevational gradient (Table S1).

#### 4.3. Assembly Processes of the Dominant Microbial Taxa

While most previous studies have focused on assembly processes at the community level, our study delves deeper by examining the mechanisms of microbial assembly at the individual level (Figure 4a,b). Of the all microbial bins, we selected five bins dominated by homogeneous selection and five bins dominated by homogenizing dispersal. These specific bins were identified as the dominant microbial taxa controlled by the major assembly processes (Table S3). We found that rare taxa played a greater role in the relative abundance of Group 2B and Group 2F, whereas abundant taxa had a stronger impact on the relative abundance of Group 1B and Group 1F (Table S3). This indicates that dominant rare taxa may have more individuals involved in dispersal events, while dominant abundant taxa may be more susceptible to environmental filtering along the elevational gradient. However, our findings are inconsistent with the conclusions of Liu et al. [58] and Jousset et al. [75]. One reasonable explanation is that our survey had a relatively restricted scope, as forest climate and topography have a notable impact on the spatiotemporal distribution of both abundant

and rare taxa [76,77]. Furthermore, it is important to recognize that the construction of abundant and rare taxa is governed by different stochastic processes [77]. In short, microbial communities can be controlled by different ecological processes depending on the spatiotemporal scales of the study [78].

Most importantly, our results demonstrate that soil available phosphorus also drove changes in the dominant microbial taxa, through homogeneous selection and homogenizing dispersal (Table S1, Figure 4c). Additionally, the relative abundance of dominant microbial taxa increased significantly with increasing soil phosphorus availability (Figure 4c), supporting our second hypothesis. Water availability and land-use intensification can affect the biomass and function of soil microorganisms [79]. This rationale may provide support for our result, as the soil water content is an important driver of dominant bacterial community composition across elevations (Figure 4c). Based on the findings of Baldock et al. [80] and Carletti et al. [81], it has been suggested that soil mineral assemblages contribute to the stability and recalcitrance of soil carbon, rendering it inaccessible to soil bacteria and thereby selecting for specific bacterial taxa. This may explain the negative correlation observed between TC and dominant bacterial taxa (Figure 4c). The unique montane climate creates a habitat for the majority of species and plays a key role in regional biodiversity [24]. Typically, the generation and maintenance of montane biodiversity are mainly influenced by the regional area, productivity, and topography [24]. Our findings show that the slope and soil temperature had strong effects on microbial abundance and community structure (Table S1, Figure 4c).

#### 4.4. Limitations and Prospects of the Study

While our study is grounded in elevational gradients within a relatively restricted local scale, it is an indicative investigation of subtropical forests. Future work should focus on proving a causal relationship between soil phosphorus availability and microbial assembly at a regional scale. Furthermore, several potential limitations should be considered in the context of the present study. Firstly, forest bacterial communities are primarily affected by soil abiotic variables, whereas fungal communities are mainly mediated by plant biomass [82]. It is necessary to consider that tree species richness has a vital impact on soil microbial diversity in subtropical forests [26]. In addition, understory vegetation not only fosters a positive interaction with microbial communities but also plays an important role in maintaining ecosystem stability [83]. Climate-vulnerable cryptogamic plants in montane cloud forests may also alter the structure and function of fungal community [84]. For example, the sampling site at the elevation of 1100 m lies in a *C. lanceolata* forest, which likely leads to enhanced deterministic processes in the soil fungal community (Figure 3d). Secondly, the diversity of animals in the forest ecosystem is known to be much higher than that in other terrestrial ecosystems [85]. The soil fauna and wildlife's habits can change the microbial community assembly, and the microenvironment in soil fauna could also affect the surrounding soil microorganisms [86]. In a forthcoming study, investigating microbial community assembly will require considering biotic factors, physical factors, and biological correlation networks to more fully elucidate the ecological functions of the community.

## 5. Conclusions

Our study sheds light on the assembly mechanisms of soil microbial community along an elevational gradient in subtropical forests. At a local scale, homogeneous ecological processes play a major role in microbial community assembly. Soil phosphorus availability mediated the relative importance of homogeneous selection and homogenizing dispersal in bacterial and fungal community assembly. Specifically, the trade-off of deterministic and stochastic processes alters microbial  $\beta$  diversity by adjusting the relative abundance of dominant microbial taxa depending on soil phosphorus availability. Our findings represent an important advancement in revealing the underlying principles of microbial community assembly in subtropical forests by the assessment of environmental factors affecting the major assembly processes, which provides essential insights into the microbial distribution

patterns. In the future, we need to investigate the nutrient cycling of phosphorus and the responses of plant and animal factors to soil microbial community assembly, which is crucial for understanding the generation and maintenance of forest biodiversity.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f14071475/s1>, Table S1: Mantel test of environmental factors against the relative importance of homogeneous selection and homogenizing dispersal in shaping soil bacterial and fungal community; Table S2: The relative abundance of each bin and contribution for all assembly processes in soil bacterial (a) and fungal (b) community; Table S3: The number and relative abundance of dominant bacterial (a) and fungal (b) taxa among phylum; Table S4: The richness of bacterial and fungal taxa in all elevation sample plots; Figure S1: The abundance of OTUs in the bacterial (a) and fungal (b) community; Figure S2: The heatmap of the dominant bacterial (a) and fungal (b) community along the elevational gradient; Figure S3: The relative importance of homogeneous selection and homogenizing dispersal on microbial community in different elevations; Figure S4: The abundance of bacterial (a) and fungal (b) bins.

**Author Contributions:** Conceptualization, formal analysis, methodology, writing—original draft, and writing—review and editing: R.C.; conceptualization, formal analysis, investigation, methodology, writing—review and editing original draft manuscript: J.Z.; investigation, formal analysis: L.J.; writing—review and editing original draft manuscript: L.L.; writing—review and editing original draft manuscript: C.G.; investigation: B.C.; formal analysis, writing—review and editing original draft manuscript: D.X.; conceptualization, supervision, writing—review and editing, and funding acquisition: J.L.; conceptualization, supervision, writing—review and editing, and funding acquisition: Z.H. All authors have read and agreed to the published version of the manuscript.

**Funding:** This work was supported by the National Natural Science Foundation of China (grant numbers 31700550, 31770678); Fujian Province Forestry Science and Technology Project of China (grant number 2022FKJ11); and Forestry Peak Discipline Construction Project of Fujian Agriculture and Forestry University (grant number 72202200205).

**Data Availability Statement:** Not applicable.

**Acknowledgments:** We wish to express our thanks for the support received from the Administration Bureau of Daiyun Mountain National Nature Reserve in Dehua city, Fujian province, allowing us to provide experimental materials and sites. The authors wish to thank Xinguang Gu, Cong Xing, Xuelin Wang for the experimental work. The author also sincerely appreciates the helpful and constructive comments provided by the reviewers of the draft manuscript.

**Conflicts of Interest:** The authors declare that they have no known competing financial interest or personal relationships that could have appeared to influence the work reported in this paper.

## References

1. Young, I.M.; Crawford, J.W. Interactions and self-organization in the soil-microbe complex. *Science* **2004**, *304*, 1634–1637. [[CrossRef](#)]
2. Falkowski, P.G.; Fenchel, T.; Delong, E.F. The microbial engines that drive Earth's biogeochemical cycles. *Science* **2008**, *320*, 1034–1039. [[CrossRef](#)]
3. Zhou, J.Z.; Ning, D.L. Stochastic community assembly: Does it matter in microbial ecology? *Microbiol. Mol. Biol. Rev.* **2017**, *81*, e00002–e00017. [[CrossRef](#)] [[PubMed](#)]
4. Hanson, C.A.; Fuhrman, J.A.; Horner-Devine, M.C.; Martiny, J.B.H. Beyond biogeographic patterns: Processes shaping the microbial landscape. *Nat. Rev. Microbiol.* **2012**, *10*, 497–506. [[CrossRef](#)]
5. Gao, C.; Guo, L.D. Progress on microbial species diversity, community assembly and functional traits. *Biodivers. Sci.* **2022**, *30*, 22429. (In Chinese) [[CrossRef](#)]
6. Chalmandrier, L.; Pansu, J.; Zinger, L.; Boyer, F.; Coissac, E.; Génin, A.; Gielly, L.; Lavergne, S.; Legay, N.; Schilling, V.; et al. Environmental and biotic drivers of soil microbial  $\beta$ -diversity across spatial and phylogenetic scales. *Ecography* **2019**, *42*, 2144–2156. [[CrossRef](#)]
7. Stegen, J.C.; Lin, X.J.; Fredrickson, J.K.; Konopka, A.E. Estimating and mapping ecological processes influencing microbial community assembly. *Front. Microbiol.* **2015**, *6*, 370. [[CrossRef](#)] [[PubMed](#)]
8. Martiny, J.B.H.; Eisen, J.A.; Penn, K.; Allison, S.D.; Horner-Devine, M.C. Drivers of bacterial  $\beta$ -diversity depend on spatial scale. *Proc. Natl. Acad. Sci. USA* **2011**, *108*, 7850–7854. [[CrossRef](#)] [[PubMed](#)]

9. Stegen, J.C.; Lin, X.J.; Fredrickson, J.K.; Chen, X.Y.; Kennedy, D.W.; Murray, C.J.; Rockhold, M.L.; Konopka, A. Quantifying community assembly processes and identifying features that impose them. *ISME J.* **2013**, *7*, 2069–2079. [[CrossRef](#)]
10. Fargione, J.; Brown, C.S.; Tilman, D. Community assembly and invasion: An experimental test of neutral versus niche processes. *Proc. Natl. Acad. Sci. USA* **2003**, *100*, 8916–8920. [[CrossRef](#)] [[PubMed](#)]
11. Chave, J. Neutral theory and community ecology. *Ecol. Lett.* **2004**, *7*, 241–253. [[CrossRef](#)]
12. Nemergut, D.R.; Schmidt, S.K.; Fukami, T.; O'Neill, S.P.; Bilinski, T.M.; Stanish, L.F.; Knelman, J.E.; Darcy, J.L.; Lynch, R.C.; Wickey, P.; et al. Patterns and processes of microbial community assembly. *Microbiol. Mol. Biol. Rev.* **2013**, *77*, 342–356. [[CrossRef](#)]
13. Graham, E.B.; Crump, A.R.; Resch, C.T.; Fansler, S.; Arntzen, E.; Kennedy, D.W.; Fredrickson, J.K.; Stegen, J.C. Coupling spatiotemporal community assembly processes to changes in microbial metabolism. *Front. Microbiol.* **2016**, *7*, 1949. [[CrossRef](#)]
14. Ning, D.L.; Yuan, M.T.; Wu, L.W.; Zhang, Y.; Guo, X.; Zhou, X.S.; Yang, Y.F.; Arkin, A.P.; Firestone, M.K.; Zhou, J.Z. A quantitative framework reveals ecological drivers of grassland microbial community assembly in response to warming. *Nat. Commun.* **2020**, *11*, 4717. [[CrossRef](#)] [[PubMed](#)]
15. Gao, Q.; Yang, Y.F.; Feng, J.J.; Tian, R.M.; Guo, X.; Ning, D.L.; Hale, L.; Wang, M.M.; Cheng, J.M.; Wu, L.W.; et al. The spatial scale dependence of diazotrophic and bacterial community assembly in paddy soil. *Glob. Ecol. Biogeogr.* **2019**, *28*, 1093–1105. [[CrossRef](#)]
16. Chase, J.M.; Myers, J.A. Disentangling the importance of ecological niches from stochastic processes across scales. *Philos. Trans. R. Soc. B Biol. Sci.* **2011**, *366*, 2351–2363. [[CrossRef](#)]
17. Wang, P.D.; Li, S.P.; Yang, X.; Zhou, J.Z.; Shu, W.S.; Jiang, L. Mechanisms of soil bacterial and fungal community assembly differ among and within islands. *Environ. Microbiol.* **2020**, *22*, 1559–1571. [[CrossRef](#)]
18. Zhang, B.; Xue, K.; Zhou, S.T.; Che, R.X.; Du, J.Q.; Tang, L.; Pang, Z.; Wang, F.; Wang, D.; Cui, X.Y.; et al. Phosphorus mediates soil prokaryote distribution pattern along a small-scale elevation gradient in Noijin Kangsang Peak, Tibetan Plateau. *FEMS Microbiol. Ecol.* **2019**, *95*, fiz076. [[CrossRef](#)] [[PubMed](#)]
19. Li, J.B.; Shen, Z.H.; Li, C.N.; Kou, Y.P.; Wang, Y.S.; Tu, B.; Zhang, S.H.; Li, X.Z. Stair-step pattern of soil bacterial diversity mainly driven by pH and vegetation types along the elevational gradients of Gongga mountain, China. *Front. Microbiol.* **2018**, *9*, 569. [[CrossRef](#)]
20. Shigyo, N.; Umeki, K.; Hirao, T. Plant functional diversity and soil properties control elevational diversity gradients of soil bacteria. *FEMS Microbiol. Ecol.* **2019**, *95*, fiz025. [[CrossRef](#)]
21. Yeh, C.F.; Soininen, J.; Teittinen, A.; Wang, J.J. Elevational patterns and hierarchical determinants of biodiversity across microbial taxonomic scales. *Mol. Ecol.* **2019**, *28*, 86–99. [[CrossRef](#)]
22. Shen, C.C.; Gunina, A.; Luo, Y.; Wang, J.J.; He, J.Z.; Kuzyakov, Y.; Hemp, A.; Classen, A.T.; Ge, Y. Contrasting patterns and drivers of soil bacterial and fungal diversity across a mountain gradient. *Environ. Microbiol.* **2020**, *22*, 3287–3301. [[CrossRef](#)] [[PubMed](#)]
23. Lladó, S.; López-Mondéjar, R.; Baldrian, P. Forest soil bacteria: Diversity, involvement in ecosystem processes, and response to global change. *Microbiol. Mol. Biol. Rev.* **2017**, *81*, e00063-16. [[CrossRef](#)] [[PubMed](#)]
24. Rahbek, C.; Borregaard, M.K.; Colwell, R.K.; Dalsgaard, B.; Holt, B.G.; Morueta-Holme, N.; Nogues-Bravo, D.; Whittaker, R.J.; Fjeldsø, J. Humboldt's enigma: What causes global patterns of mountain biodiversity? *Science* **2019**, *365*, 1108–1113. [[CrossRef](#)] [[PubMed](#)]
25. Pandit, S.N.; Kolasa, J.; Cottenie, K. Contrasts between habitat generalists and specialists: An empirical extension to the basic metacommunity framework. *Ecology* **2009**, *90*, 2253–2262. [[CrossRef](#)]
26. Wu, H.L.; Xiang, W.H.; Ouyang, S.; Forrester, D.I.; Zhou, B.; Chen, L.X.; Ge, T.D.; Lei, P.F.; Chen, L.; Zeng, Y.L.; et al. Linkage between tree species richness and soil microbial diversity improves phosphorus bioavailability. *Funct. Ecol.* **2019**, *33*, 1549–1560. [[CrossRef](#)]
27. Zhou, W.S.; Zhang, Y.X.; Zhang, S.; Yakimov, B.N.; Ma, K.M. Phylogenetic and Functional Traits Verify the Combined Effect of Deterministic and Stochastic Processes in the Community Assembly of Temperate Forests along an Elevational Gradient. *Forests* **2021**, *12*, 591. [[CrossRef](#)]
28. Teste, F.P.; Lambers, H.; Enowashu, E.E.; Laliberté, E.; Marhan, S.; Kandeler, E. Soil microbial communities are driven by the declining availability of cations and phosphorus during ecosystem retrogression. *Soil Biol. Biochem.* **2021**, *163*, 108430. [[CrossRef](#)]
29. Siles, J.A.; Margesin, R. Abundance and diversity of bacterial, archaeal, and fungal communities along an altitudinal gradient in Alpine forest soils: What are the driving factors? *Microb. Ecol.* **2016**, *72*, 207–220. [[CrossRef](#)] [[PubMed](#)]
30. Ma, X.M.; Zhou, Z.; Chen, J.; Xu, H.; Ma, S.H.; Dippold, M.A.; Kuzyakov, Y. Long-term nitrogen and phosphorus fertilization reveals that phosphorus limitation shapes the microbial community composition and functions in tropical montane forest soil. *Sci. Total Environ.* **2023**, *854*, 158709. [[CrossRef](#)] [[PubMed](#)]
31. Peng, Z.H.; Wang, Z.F.; Liu, Y.; Yang, T.Y.; Chen, W.M.; Wei, G.H.; Jiao, S. Soil phosphorus determines the distinct assembly strategies for abundant and rare bacterial communities during successional reforestation. *Soil Ecol. Lett.* **2021**, *3*, 342–355. [[CrossRef](#)]
32. Xu, D.W.; Liu, J.F.; Marshall, P.; He, Z.S.; Zheng, S.Q. Leaf litter decomposition dynamics in unmanaged *Phyllostachys pubescens* stands at high elevations in the Daiyun Mountain National Nature Reserve. *J. Mt. Sci.* **2017**, *14*, 2246–2256. [[CrossRef](#)]
33. He, Z.S.; Gu, X.G.; Jiang, L.; Xu, D.W.; Liu, J.F.; Li, W.Z.; Chen, W.W. Characteristics and its influencing factors of forest soil dominant bacterial community in different elevations on the southern slope of Daiyun Mountain, Fujian Province of eastern China. *J. Beijing For. Univ.* **2022**, *44*, 107–116. (In Chinese)

34. Jiang, L.; He, Z.S.; Liu, J.F.; Xing, C.; Gu, X.G.; Wei, C.S.; Zhu, J.; Wang, X.L. Elevation gradient altered soil C, N, and P stoichiometry of *Pinus taiwanensis* forest on Daiyun mountain. *Forests* **2019**, *10*, 1089. [[CrossRef](#)]
35. He, Z.S.; Wang, Z.W.; Zhu, J.; Chen, J.J.; Gu, X.G.; Jiang, L.; Chen, B.; Wu, Z.Y.; Liu, J.F.; Chen, W.W. Forest soil microbial community structure characteristics and its influencing factors at different elevations on the southern slope of Daiyun mountain. *Environ. Sci.* **2022**, *43*, 2802–2811. (In Chinese)
36. Wang, W.T.; Sun, Z.H.; Mishra, S.; Xia, S.W.; Lin, L.X.; Yang, X.D. Body size determines multitrophic soil microbiota community assembly associated with soil and plant attributes in a tropical seasonal rainforest. *Mol. Ecol.* **2022**. *early view*. [[CrossRef](#)] [[PubMed](#)]
37. Li, M.J.; He, Z.S.; Jiang, L.; Gu, X.G.; Jin, M.G.; Chen, B.; Liu, J.F. Distribution pattern and driving factors of species diversity and phylogenetic diversity along altitudinal gradient on the south slope of Daiyun Mountain. *Acta Ecol. Sin.* **2021**, *41*, 1148–1157. (In Chinese)
38. Martin, M. Cutadapt removes adapter sequences from high-throughput sequencing reads. *EMBnet J.* **2011**, *17*, 10–12. [[CrossRef](#)]
39. Edgar, R.C.; Haas, B.J.; Clemente, J.C.; Quince, C.; Knight, R. UCHIME improves sensitivity and speed of chimera detection. *Bioinformatics* **2011**, *27*, 2194–2200. [[CrossRef](#)] [[PubMed](#)]
40. Quast, C.; Pruesse, E.; Yilmaz, P.; Gerken, J.; Schweer, T.; Yarza, P.; Peplies, J.; Glöckner, F.O. The SILVA ribosomal RNA gene database project: Improved data processing and web-based tools. *Nucleic Acids Res.* **2012**, *41*, D590–D596. [[CrossRef](#)]
41. Haas, B.J.; Gevers, D.; Earl, A.M.; Feldgarden, M.; Ward, D.V.; Giannoukos, G.; Ciulla, D.; Tabbaa, D.; Highlander, S.K.; Sodergren, E.; et al. Chimeric 16S rRNA sequence formation and detection in Sanger and 454-pyrosequenced PCR amplicons. *Genome Res.* **2011**, *21*, 494–504. [[CrossRef](#)]
42. Edgar, R.C. UPARSE: Highly accurate OTU sequences from microbial amplicon reads. *Nat. Methods* **2013**, *10*, 996–998. [[CrossRef](#)]
43. Dai, T.J.; Zhang, Y.; Tang, Y.S.; Bai, Y.H.; Tao, Y.L.; Huang, B.; Wen, D.H. Identifying the key taxonomic categories that characterize microbial community diversity using full-scale classification: A case study of microbial communities in the sediments of Hangzhou Bay. *FEMS Microbiol. Ecol.* **2016**, *92*, fiw 150. [[CrossRef](#)]
44. Liang, Y.T.; Xiao, X.; Nuccio, E.E.; Yuan, M.T.; Zhang, N.; Xue, K.; Cohan, F.M.; Zhou, J.Z.; Sun, B. Differentiation strategies of soil rare and abundant microbial taxa in response to changing climatic regimes. *Environ. Microbiol.* **2020**, *22*, 1327–1340. [[CrossRef](#)]
45. Subramanian, B.; Gao, S.H.; Lercher, M.J.; Hu, S.N.; Chen, W.H. Evolview v3: A webserver for visualization, annotation, and management of phylogenetic trees. *Nucleic Acids Res.* **2019**, *47*, W270–W275. [[CrossRef](#)] [[PubMed](#)]
46. Wu, W.X.; Lu, H.P.; Sastri, A.; Yeh, Y.C.; Gong, G.C.; Chou, W.C.; Hsieh, C.H. Contrasting the relative importance of species sorting and dispersal limitation in shaping marine bacterial versus protist communities. *ISME J.* **2018**, *12*, 485–494. [[CrossRef](#)]
47. Zhang, J.L. *Spaa 0.2.2—Species Association Analysis, R Package Version 0.2.2*; The R Project for Statistical Computing: Vienna, Austria, 2016.
48. Yang, L.Y.; Ning, D.L.; Yang, Y.F.; He, N.P.; Li, X.Z.; Cornell, C.R.; Bates, C.T.; Filimonenko, E.; Kuzyakov, Y.; Zhou, J.Z.; et al. Precipitation balances deterministic and stochastic processes of bacterial community assembly in grassland soils. *Soil Biol. Biochem.* **2022**, *168*, 108635. [[CrossRef](#)]
49. Letunic, I.; Bork, P. Interactive Tree Of Life (iTOL) v5: An online tool for phylogenetic tree display and annotation. *Nucleic Acids Res.* **2021**, *49*, W293–W296. [[CrossRef](#)] [[PubMed](#)]
50. Wang, X.B.; Lü, X.T.; Yao, J.; Wang, Z.W.; Deng, Y.; Cheng, W.X.; Zhou, J.Z.; Han, X.G. Habitat-specific patterns and drivers of bacterial  $\beta$ -diversity in China's drylands. *ISME J.* **2017**, *11*, 1345–1358. [[CrossRef](#)]
51. Oksanen, J.; Blanchet, F.G.; Friendly, M.; Kindt, R.; Legendre, P.; McGlinn, D.; Minchin, P.R.; O'Hara, R.B.; Simpson, G.L.; Solymos, P. *Vegan: Community Ecology Package, R package version 2.4-3*; The R Project for Statistical Computing: Vienna, Austria, 2016.
52. Lichstein, J.W. Multiple regression on distance matrices: A multivariate spatial analysis tool. *Plant Ecol.* **2007**, *188*, 117–131. [[CrossRef](#)]
53. Chen, L.; Xiang, W.H.; Wu, H.L.; Ouyang, S.; Lei, P.F.; Hu, Y.J.; Ge, T.D.; Ye, J.; Kuzyakov, Y. Contrasting patterns and drivers of soil fungal communities in subtropical deciduous and evergreen broadleaved forests. *Appl. Microbiol. Biotechnol.* **2019**, *103*, 5421–5433. [[CrossRef](#)]
54. Wang, X.L.; Liu, J.F.; He, Z.S.; Xing, C.; Zhu, J.; Gu, X.G.; Lan, Y.Q.; Wu, Z.Y.; Liao, P.C.; Zhu, D.H. Forest gaps mediate the structure and function of the soil microbial community in a *Castanopsis kawakamii* forest. *Ecol. Indic.* **2021**, *122*, 107288. [[CrossRef](#)]
55. Lv, X.F.; Yu, J.B.; Fu, Y.Q.; Ma, B.; Qu, F.Z.; Ning, K.; Wu, H.F. A meta-analysis of the bacterial and archaeal diversity observed in wetland soils. *Sci. World J.* **2014**, *2014*, 437684. [[CrossRef](#)] [[PubMed](#)]
56. López-Angulo, J.; de la Cruz, M.; Chacón-Labela, J.; Illuminati, A.; Matesanz, S.; Pescador, D.S.; Pías, B.; Sánchez, A.M.; Escudero, A. The role of root community attributes in predicting soil fungal and bacterial community patterns. *New Phytol.* **2020**, *228*, 1070–1082. [[CrossRef](#)] [[PubMed](#)]
57. Dee, L.E.; Cowles, J.; Isbell, F.; Pau, S.; Gaines, S.D.; Reich, P.B. When do ecosystem services depend on rare species? *Trends Ecol. Evol.* **2019**, *34*, 746–758. [[CrossRef](#)]
58. Liu, L.M.; Yang, J.; Yu, Z.; Wilkinson, D.M. The biogeography of abundant and rare bacterioplankton in the lakes and reservoirs of China. *ISME J.* **2015**, *9*, 2068–2077. [[CrossRef](#)] [[PubMed](#)]

59. Liu, N.N.; Hu, H.F.; Ma, W.H.; Deng, Y.; Wang, Q.G.; Luo, A.; Meng, J.H.; Feng, X.J.; Wang, Z.H. Relative importance of deterministic and stochastic processes on soil microbial community assembly in temperate grasslands. *Microorganisms* **2021**, *9*, 1929. [[CrossRef](#)]
60. Jiao, S.; Lu, Y.H. Abundant fungi adapt to broader environmental gradients than rare fungi in agricultural fields. *Glob. Change Biol.* **2020**, *26*, 4506–4520. [[CrossRef](#)]
61. Xu, M.Y.; Zhang, Q.; Xia, C.Y.; Zhong, Y.M.; Sun, G.P.; Guo, J.; Yuan, T.; Zhou, J.Z.; He, Z.L. Elevated nitrate enriches microbial functional genes for potential bioremediation of complexly contaminated sediments. *ISME J.* **2014**, *8*, 1932–1944. [[CrossRef](#)] [[PubMed](#)]
62. Xiao, X.; Liang, Y.T.; Zhou, S.; Zhuang, S.Y.; Sun, B. Fungal community reveals less dispersal limitation and potentially more connected network than that of bacteria in bamboo forest soils. *Mol. Ecol.* **2018**, *27*, 550–563. [[CrossRef](#)]
63. Catano, C.P.; Dickson, T.L.; Myers, J.A. Dispersal and neutral sampling mediate contingent effects of disturbance on plant beta-diversity: A meta-analysis. *Ecol. Lett.* **2017**, *20*, 347–356. [[CrossRef](#)] [[PubMed](#)]
64. Zhang, B.; Xue, K.; Zhou, S.T.; Wang, K.; Liu, W.J.; Xu, C.; Cui, L.Z.; Li, L.F.; Ran, Q.W.; Wang, Z.S.; et al. Environmental selection overturns the decay relationship of soil prokaryotic community over geographic distance across grassland biotas. *eLife* **2022**, *11*, e70164. [[CrossRef](#)]
65. Jiao, S.; Chu, H.Y.; Zhang, B.G.; Wei, X.R.; Chen, W.M.; Wei, G.H. Linking soil fungi to bacterial community assembly in arid ecosystems. *iMeta* **2022**, *1*, e2. [[CrossRef](#)]
66. Bahram, M.; Pöhlme, S.; Kõljalg, U.; Zärre, S.; Tedersoo, L. Regional and local patterns of ectomycorrhizal fungal diversity and community structure along an altitudinal gradient in the Hyrcanian forests of northern Iran. *New Phytol.* **2012**, *193*, 465–473. [[CrossRef](#)]
67. Peay, K.G.; Garbelotto, M.; Bruns, T.D. Evidence of dispersal limitation in soil microorganisms: Isolation reduces species richness on mycorrhizal tree islands. *Ecology* **2010**, *91*, 3631–3640. [[CrossRef](#)]
68. Nemergut, D.R.; Costello, E.K.; Hamady, M.; Lozupone, C.; Jiang, L.; Schmidt, S.K.; Fierer, N.; Townsend, A.R.; Cleveland, C.C.; Stanish, L.; et al. Global patterns in the biogeography of bacterial taxa. *Environ. Microbiol.* **2011**, *13*, 135–144. [[CrossRef](#)] [[PubMed](#)]
69. Wu, B.; Tian, J.Q.; Bai, C.M.; Xiang, M.C.; Sun, J.Z.; Liu, X.Z. The biogeography of fungal communities in wetland sediments along the Changjiang River and other sites in China. *ISME J.* **2013**, *7*, 1299–1309. [[CrossRef](#)] [[PubMed](#)]
70. Liu, Y.; Zhang, G.H.; Luo, X.Z.; Hou, E.Q.; Zheng, M.H.; Zhang, L.L.; He, X.J.; Shen, W.J.; Wen, D.Z. Mycorrhizal fungi and phosphatase involvement in rhizosphere phosphorus transformations improves plant nutrition during subtropical forest succession. *Soil Biol. Biochem.* **2021**, *153*, 108099. [[CrossRef](#)]
71. He, X.L.; Zhou, J.; Wu, Y.H.; Bing, H.J.; Sun, H.Y.; Wang, J.P. Leaching disturbed the altitudinal distribution of soil organic phosphorus in subalpine coniferous forests on Mt. Gongga, SW China. *Geoderma* **2018**, *326*, 144–155. [[CrossRef](#)]
72. Zhou, J.Z.; Deng, Y.; Shen, L.N.; Wen, C.Q.; Yan, Q.Y.; Ning, D.L.; Qin, Y.J.; Xue, K.; Wu, L.Y.; He, Z.L.; et al. Temperature mediates continental-scale diversity of microbes in forest soils. *Nat. Commun.* **2016**, *7*, 12083. [[CrossRef](#)] [[PubMed](#)]
73. Jiao, S.; Lu, Y.H. Soil pH and temperature regulate assembly processes of abundant and rare bacterial communities in agricultural ecosystems. *Environ. Microbiol.* **2020**, *22*, 1052–1065. [[CrossRef](#)]
74. Ni, Y.Y.; Yang, T.; Ma, Y.Y.; Zhang, K.P.; Soltis, P.S.; Soltis, D.E.; Gilbert, J.A.; Zhao, Y.P.; Fu, C.X.; Chu, H.Y. Soil pH determines bacterial distribution and assembly processes in natural mountain forests of eastern China. *Glob. Ecol. Biogeogr.* **2021**, *30*, 2164–2177. [[CrossRef](#)]
75. Jousset, A.; Bienhold, C.; Chatzinotas, A.; Gallien, L.; Gobet, A.; Kurm, V.; Küsel, K.; Rillig, M.C.; Rivett, D.W.; Salles, J.F.; et al. Where less may be more: How the rare biosphere pulls ecosystems strings. *ISME J.* **2017**, *11*, 853–862. [[CrossRef](#)]
76. Liu, S.S.; Wang, F.; Xue, K.; Sun, B.; Zhang, Y.G.; He, Z.L.; Van Nostrand, J.D.; Zhou, J.Z.; Yang, Y.F. The interactive effects of soil transplant into colder regions and cropping on soil microbiology and biogeochemistry. *Environ. Microbiol.* **2015**, *17*, 566–576. [[CrossRef](#)]
77. Yi, M.L.; Fang, Y.; Hu, G.P.; Liu, S.F.; Ni, J.R.; Liu, T. Distinct community assembly processes underlie significant spatiotemporal dynamics of abundant and rare bacterioplankton in the Yangtze River. *Front. Environ. Sci. Eng.* **2021**, *16*, 79. [[CrossRef](#)]
78. Dini-Andreote, F.; Pylro, V.S.; Baldrian, P.; van Elsas, J.D.; Salles, J.F. Ecological succession reveals potential signatures of marine–terrestrial transition in salt marsh fungal communities. *ISME J.* **2016**, *10*, 1984–1997. [[CrossRef](#)] [[PubMed](#)]
79. Wan, X.H.; Chen, X.L.; Huang, Z.Q.; Chen, H.Y.H. Global soil microbial biomass decreases with aridity and land-use intensification. *Glob. Ecol. Biogeogr.* **2021**, *30*, 1056–1069. [[CrossRef](#)]
80. Baldock, J.A.; Skjemstad, J.O. Role of the soil matrix and minerals in protecting natural organic materials against biological attack. *Org. Geochem.* **2000**, *31*, 697–710. [[CrossRef](#)]
81. Carletti, P.; Vendramin, E.; Pizzeghello, D.; Concheri, G.; Zanella, A.; Nardi, S.; Squartini, A. Soil humic compounds and microbial communities in six spruce forests as function of parent material, slope aspect and stand age. *Plant Soil* **2009**, *315*, 47–65. [[CrossRef](#)]
82. Fanin, N.; Kardol, P.; Farrell, M.; Kempel, A.; Ciobanu, M.; Nilsson, M.C.; Gundale, M.J.; Wardle, D.A. Effects of plant functional group removal on structure and function of soil communities across contrasting ecosystems. *Ecol. Lett.* **2019**, *22*, 1095–1103. [[CrossRef](#)] [[PubMed](#)]
83. Chen, W.B.; Su, F.L.; Pang, Z.Q.; Mao, Q.G.; Zhong, B.Q.; Xiong, Y.M.; Mo, J.M.; Lu, X.K. The removal of understory vegetation can rapidly alter the soil microbial community structure without altering the community assembly in a primary tropical forest. *Geoderma* **2023**, *429*, 116180. [[CrossRef](#)]

84. Looby, C.I.; Treseder, K.K. Shifts in soil fungi and extracellular enzyme activity with simulated climate change in a tropical montane cloud forest. *Soil Biol. Biochem.* **2018**, *117*, 87–96. [[CrossRef](#)]
85. Hutchinson, G.E. Homage to Santa Rosalia or why are there so many kinds of animals? *Am. Nat.* **1959**, *93*, 145–159. [[CrossRef](#)]
86. Zhu, D.; Delgado-Baquerizo, M.; Ding, J.; Gillings, M.R.; Zhu, Y.G. Trophic level drives the host microbiome of soil invertebrates at a continental scale. *Microbiome* **2021**, *9*, 189. [[CrossRef](#)] [[PubMed](#)]

**Disclaimer/Publisher’s Note:** The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.