

Article

Higher Soil Aggregate Stability in Subtropical Coniferous Plantations Than Natural Forests Due to Microbial and Aggregate Factors

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Abstract: Forest restoration and soil structure stabilization are the focus of forestry and ecology. However, the combined mechanisms of soil microorganisms and organic and inorganic aggregate binding agents on soil aggregation is unclear. In order to explore the effects of subtropical forest restoration types on soil aggregates and the underlying mechanisms, we collected soil samples from subtropical natural forests and coniferous and broad-leaved plantations that are commonly used for forest restoration. The mean weight diameter (MWD) of the soil aggregate was used to indicate the aggregates' stability. The soil microbial diversity and structure, the organic and inorganic aggregate binding agents including the mycorrhizal density, the glomalin-related soil protein and the Fe and Al oxides were investigated. Results showed that the Shannon and Simpson indices of soil microbial communities in the coniferous plantations were both significantly higher than those in the natural forests. At the annual level, compared with the natural forests, the plantations decreased the proportion of 0.25–1 mm aggregates while the MWD significantly increased. The forest type also significantly affected the mycorrhizal density, the easily extractable glomalin-related soil proteins (EEG) and the Fe oxide. A variance decomposition analysis showed that soil microbial communities, organic and inorganic binding agents, and their interactions together contributed to the aggregates' composition and stability by 75.07%. The MWD was positively correlated with the microbial diversity, mycorrhizal density and Fe oxide. We therefore suggest that the combined effects of the soil microbial communities and the organic (mycorrhizal density) and inorganic binding agents (Fe oxide) can be the main mechanisms of soil aggregation in the study area, resulting in a higher soil aggregate stability in the subtropical coniferous plantation than in the natural forest.

Keywords: soil aggregate stability; soil microbial community function; metal oxides; glomalin-related soil protein; forest restoration type; subtropical forests



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1. Introduction

Many forests have been degraded in recent years, and forest restoration is a widespread global concern in forestry and ecological research [1]. According to the Food and Agriculture Organization of the United Nations (FAO), natural disasters and human activities have reduced the area of old-growth forests by 81 million hectares worldwide since 1990 [2]. Different approaches including a variety of coniferous and/or broad-leaved pure and/or mixed plantations have been used to restore degraded forests [3,4]. Many scholars have reported on the impacts of forest restorations on the plant community's composition, diversity, structure and succession [5–7].

A forest's soil is the basis for maintaining the health of the forest's ecosystem and the growth and development of the trees [8]. Its fertility and quality can reflect the ability of soil to provide nutrients and water for plant growth [9,10]. As the most basic structural

unit of soil, soil aggregates are the reservoirs of nutrients and the habitats of various microorganisms, and thus the quantity and quality of the aggregates determine the soil properties and fertility [11,12]. Some scholars have studied the impacts of different forest restorations and soil conservation techniques on soil and water conservation capacity [13–16]. Exploring the effects of forest restorations on the composition and stability of aggregates can provide new insights to develop effective forest restoration measures.

The soil aggregate's stability is usually expressed by the mean weight diameter (MWD) of the aggregate that is calculated based on the proportion of aggregates with different sizes in the soil [9]. Therefore, the formation of the aggregates directly affects the aggregate's composition and stability. Among the factors that contribute to the formation of aggregates, soil microorganisms are the most important biological factors [12,17]. Previous studies show that soil microorganisms participate in the formation of the aggregates [17,18], and that the aggregate's stability is closely related to the diversity of the microbial communities [9,19,20]. Soil microorganisms can decompose the soil's organic carbon [21] to promote the formation of large aggregates [22]. In addition, plant roots and their symbiotic fungal hyphae mechanically entangle with the soil particles to form large aggregates [23,24]. Thus, mycorrhizal density can also affect the aggregate's composition and stability [25]. In addition, the glomalin-related soil protein (GRSP) secreted by the arbuscular mycorrhizal fungus [26] is also an important organic aggregate binding agent. The type of GRSP affects the MWD [27,28], while some other studies claim that the MWD is not affected by the mycorrhizal or the GRSP [29,30]. The mechanisms on the aggregate's stability maintenance and the specific aggregate binding agents are uncertain.

There are also some inorganic aggregate binding agents, mainly consisting of Fe and Al oxides [31]. They bond clay minerals with soil particles to form stable soil aggregates [32]. Although there have been many studies on the mechanisms of microbial [17], organic and inorganic aggregate binding agents on the formation of aggregates [25,33], their combined effects are rarely studied. In particular, it is still unclear whether the forest restorations affect the aggregates' compositions and stability through these factors.

Subtropical forests in China have unique vegetation types and structures among global forest ecosystems. Evergreen broad-leaved forests are the zonal vegetation [34]. The degradation of forests has profoundly impacted the ecosystem's structure and function [7,35]. The degradation of forest ecosystems caused by commercial logging, climate change, forest fires and engineering destruction has reduced the ecosystem's stability [36], biodiversity [36] and vegetation productivity [37], and also greatly weakened the material cycle and energy flow in the ecosystem [1]. However, the impacts of different forest types (especially the different plantations used in forest restoration) on soil aggregates and the underlying mechanisms are still unclear. Therefore, we selected subtropical zonal natural forests and coniferous and broad-leaved plantations that are used in regional forest restorations. Our objectives were to explore the effects of the type of forest restoration on the soil aggregates and the underlying mechanisms. Our hypotheses were: (1) the stability of the soil aggregates in the plantations was higher than that in the natural forests, and (2) the soil microbial communities and the organic and inorganic aggregate binding agents would be combined to affect the composition and stability of the aggregates.

2. Materials and Methods

2.1. Study Site

The research site was located in the Jinzi State-owned Forest Farm (30°17' E–30°24' E, 109°04' N–109°23' N) at Lichuan City, Hubei Province, China (Figure 1). The area is representative of a typical subtropical monsoon climate. The annual average temperature is 15.5–16.2 °C, the absolute high temperature is 39 °C, the absolute low temperature is −17.1 °C, the annual average precipitation is 1475–1700 mm, the annual average relative humidity is 80%–82%, and the frost-free period is 270–279d. The soil in the study sites is Ferric Luvisols according to the Soil Taxonomy classification (USDA, 2012).

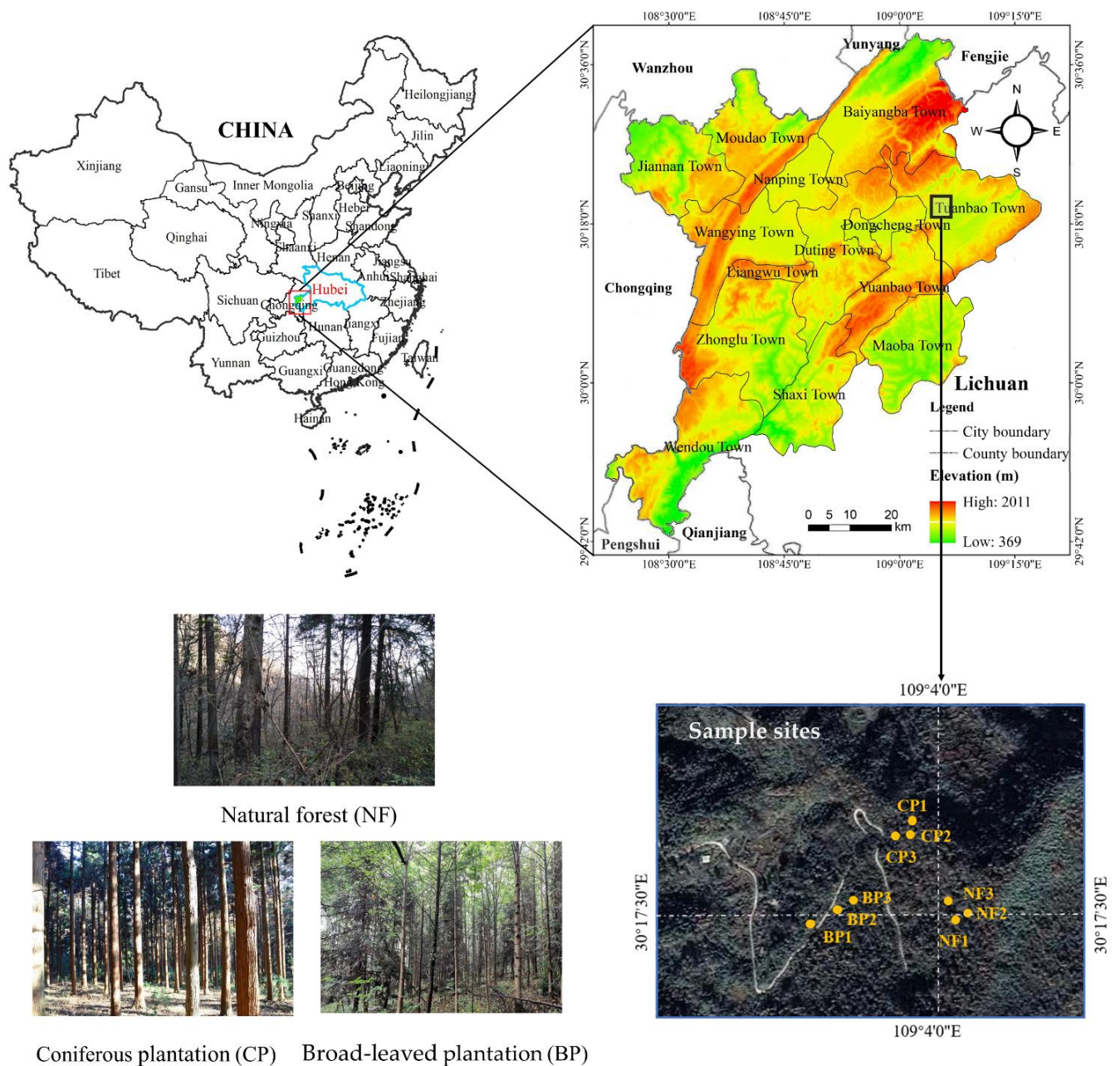


Figure 1. Location of the study site and forests. (Source: Google® Maps®).

The study area has a forest coverage rate of over 95%, which is mainly covered by well-preserved natural forests and secondary forests. There are many types of plantations and all of the plantations originate from secondary forests. Coniferous plantations mainly include *Cunninghamia lanceolata* and *Pseudolarix amabilis*, and the main broad-leaved tree species are *Liriodendron chinense* and *Castanea henryi*. The plantations are protected from anthropogenic disturbances by the prohibition of harvesting, fuel wood collection, and domestic grazing, but were subjected to regular plantation management.

2.2. Experimental Design and Sampling

Natural forests (NF), *C. lanceolata* plantations (coniferous plantations, CP) and *L. chinense* (broad-leaved plantations, BP) were selected in this study. There were three replicated stands set for each forest type (Figure 1). There were three fixed plots of 20 × 20 m (more than 50 m away from each other and the stand edges, surrounding roads and vari-

ously aged or other forests) set in each stand. A total of five complete soil profiles were dug around each plot to determine the soil development and soil thickness. The average density of the NF, CP and BP was 1673, 1658 and 1439 trees/hm², respectively, the average tree height was 18.67, 22.78 and 21.52 m, respectively, and the average diameter at breast height (DBH) was 13.97, 16.60 and 18.56 cm, respectively. All the plantations were subjected to silvicultural treatments only once in their first 3–4 years, including the tending and thinning of the understory vegetation. The overview of each stand is shown in Table 1.

Table 1. Overview of each stand.

Forest	Forest Type	Longitude (E)	Latitude (N)	Elevation (m)	Slope Aspect	Stand Age
NF1	Natural forest	109°4′3.41″	30°17′30.31″	1485	19° E	Mature forest
NF2	Natural forest	109°4′4.03″	30°17′31.44″	1482	18° NE	Mature forest
NF3	Natural forest	109°4′2.33″	30°17′32.29″	1468	23° NE	Mature forest
CP1	Coniferous plantation	109°3′53.48″	30°17′44.08″	1382	17° N	Near-mature forest
CP2	Coniferous plantation	109°3′54.15″	30°17′43.75″	1394	16° N	Near-mature forest
CP3	Coniferous plantation	109°3′54.78″	30°17′43.35″	1393	20° NE	Near-mature forest
BP1	Broad-leaved plantation	109°3′42.83″	30°17′27.07″	1560	10° NE	Near-mature forest
BP2	Broad-leaved plantation	109°3′51.12″	30°17′29.82″	1534	17° NW	Near-mature forest
BP3	Broad-leaved plantation	109°3′52.56″	30°17′30.55″	1541	10° N	Near-mature forest

The soil samples (0–10 cm) were taken in March 2021 (when the precipitation was low) and October 2021 (when the precipitation was high), respectively (Figure 2). During each sampling, 4 undisturbed soil samples were randomly collected from each plot to determine the soil's bulk density. An HH2 moisture meter (Delta-T Devices Ltd., Cambridge, UK) was used to determine the soil's moisture and temperature while soil sampling. In each plot, six 10-cm-deep soil cores were collected randomly using a stainless steel soil auger (diameter = 8.7 cm) and combined into one composite soil sample. Each soil sample was split into three parts: (1) was passed through a 2-mm sieve to measure the soil microbial community's properties immediately after sampling, (2) was air-dried and passed through a 2-mm sieve to determine the soil's physicochemical properties, and (3) was separated from the remaining undisturbed air-dried samples along the natural grain and was passed through an 8-mm sieve for the aggregate's classification and determination.

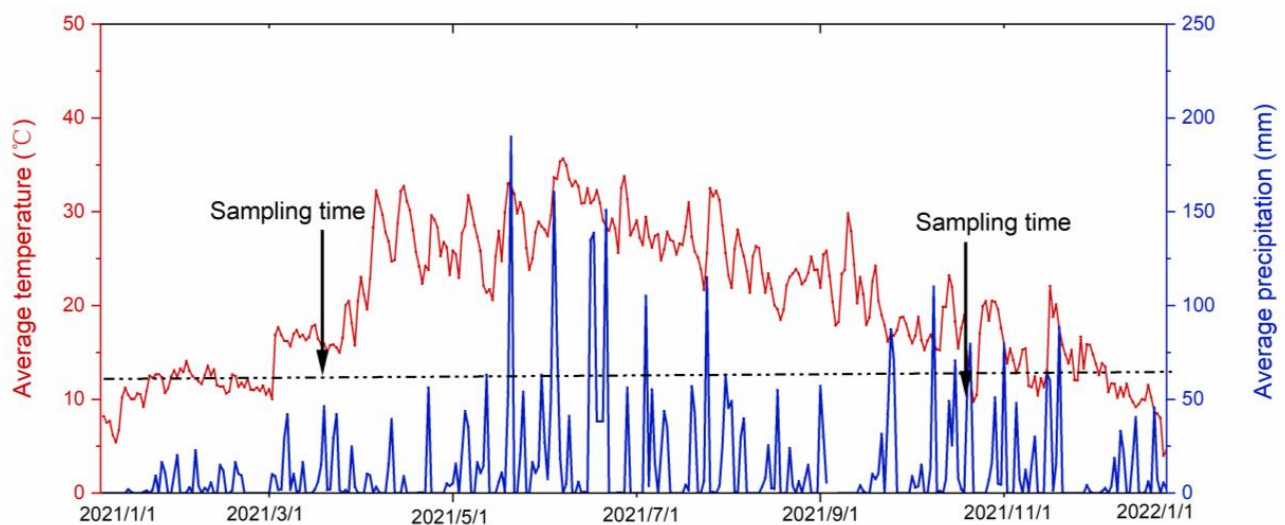


Figure 2. Precipitation and air temperature characteristics at the study site. The arrows indicate the sampling dates, and the dotted line shows the average monthly precipitation.

2.3. Measurements

2.3.1. Soil Physicochemical Properties

The soil's pH was determined by a digital pH meter from a 1:2.5 (weight to volume) suspension of soil and distilled water. The soil's organic carbon (SOC) and total nitrogen (TN) contents were determined by an elemental analyzer (Vario Macro Cube, Elementar Analysensysteme GmbH, Hanau, Germany). The total phosphorus (TP) was measured using the molybdenum antimony blue colorimetric method. The available phosphorus (AP) was measured using the ammonium acetate extraction method [38].

2.3.2. Soil Microbial Analysis

The soil's microbial DNA was extracted using a PowerSoil DNA Isolation Kit (MO BIO Laboratories, Carlsbad, CA, United States) within one week of its collection and was then used for metagenomic sequencing. The methods for the metagenomic library construction, sequencing, quality control, non-redundant gene sets construction and annotation processes were carried out as described in a previous study [39]. Briefly, the metagenomic libraries were sequenced on NovaSeq. The sequence assembly was performed using IDBA-UD and Newbler (<https://ngs.csr.uky.edu/Newbler>) (accessed on 18 January 2022), and contigs (≥ 300 bp) were predicted with MetaGene. A non-redundant gene catalog was constructed using CD-HIT with 95% identity and 90% coverage. All high-quality reads were then aligned (95% identity) against the gene catalog via SOAPaligner. To obtain the taxonomic information, BLASTP (Version 2.3.0) was employed to compare representative sequences with the NCBI NR database. The taxonomic alpha diversity was calculated by Shannon and Simpson diversity indices using QIIME software. We used percentages to express the relative microbial abundance.

2.3.3. Classification of Soil Aggregate and Possible Influencing Factors

The water-stable aggregates were fractionated using the wet sieving method with an aggregate analyzer (DIK-2001, Daiki Co., Saitama, Japan) [40]. A total of four aggregate size fractions (including >2 mm, 1–2 mm, 0.25–1 mm and <0.25 mm) were obtained. The fractions collected from each sieve were dried at 70 °C and weighed to calculate the aggregate's stability, as expressed by the mean weight diameter (MWD):

$$\text{MWD} = \sum_i^n \bar{d} \times m_i \quad (1)$$

where m_i is the percentage mass fraction of aggregates remaining on the i th sieve, $\bar{d}$ is the average aperture of the i th and $(i + 1)$ th mesh (mm) and n is the total number of aggregates ($n = 4$).

The Fe and Al oxides in each soil sample were extracted using dithionite–citrate–bicarbonate (DCB) under normal conditions that included a heating process (at 75–80 °C in a water bath) and a physical disturbance (15 min of stirring). The solution after the reaction was collected by centrifugation to determine the contents of the soil's Fe and Al oxides by an ICP–OES (ThermoFisher, Waltham, MA, USA) [40].

Mycorrhizal density was determined using the Trillium blue staining-squared cross method [41]. The GRSP, including the total glomalin-related soil protein (TG) and the easily extractable glomalin-related soil protein (EEG), was extracted and measured based on previous studies [42,43].

2.4. Statistical Analysis

To compare the samples and examine the effects of forest and sampling time on the soil's microbial alpha diversity and other properties of the soil, repeated-measures analysis of variance (ANOVA) with Tukey HSD were performed. The normality (Shapiro-Wilks) and homogeneity of variances tests (Hartley's F test) were performed before the ANOVA. Nonmetric multidimensional scaling (NMDS) and principal coordinate analysis (PCoA) were employed for graphically exploring differences in the microbial communities' structures

between forests according to the Bray–Curtis dissimilarity using the microbial operational taxonomic unit (OTU) dataset.

Variance decomposition analysis (VPA) was performed to examine the relative contributions of the soil's microbial communities and the organic and inorganic binding agents to the soil's aggregates. The Pearson correlation coefficient was used to evaluate the relationships among the soil's microbial alpha diversity, the organic and inorganic binding agents, and the soil aggregate's composition and stability.

R (v.4.1.3) was used for statistical testing. The NMDS, PCoA and VPA were performed using the “vegan” package (v.2.6–4). All tests were performed with the significance at $p < 0.05$, unless otherwise stated.

3. Results

3.1. Soil Physicochemical Properties

The soil temperature, pH, bulk density, SOC, TN, TP and AP were significantly different among the forests ($p < 0.05$, Table 2), and the significance varied with time. On the whole, compared with the natural forests, the coniferous and broad-leaved plantations significantly decreased the bulk density ($p < 0.05$), but significantly increased the TP and AP ($p < 0.05$). The SOC showed a trend of BP > NF > CP.

3.2. Composition and Diversity of Soil Microbial Communities

Proteobacteria, Actinobacteria and Firmicutes were the top three taxa in the soil's microbial communities in the study area, accounting for more than 95% in total (Table 3). However, the forest type had no significant effect on their relative abundances ($p > 0.05$). Among the top 10 phylum, only the relative abundances of Verrucomicrobia and Nitrospirae were significantly affected by the forest type. They showed a trend of CP > BP > NF, and the difference between the CPs and the NFs was significant ($p < 0.05$).

The forest type significantly affected the Shannon and Simpson indices of the microbial communities ($p < 0.05$, Figure 3). The Shannon and Simpson index of the CPs was significantly increased by 7.7% and 1.3% compared with those of the NFs ($p < 0.05$), while those of the BPs were not significantly different from those of the NFs or the CPs ($p > 0.05$). In addition, the NMDS and PCoA showed consistent results (Figure 4), that is, there were certain differences in the soil's microbial communities' structure between the forests, especially between the natural forests and the plantations. The contribution rate of the first and second component of the PCoA to the difference was 38.87% and 23.25%, respectively.

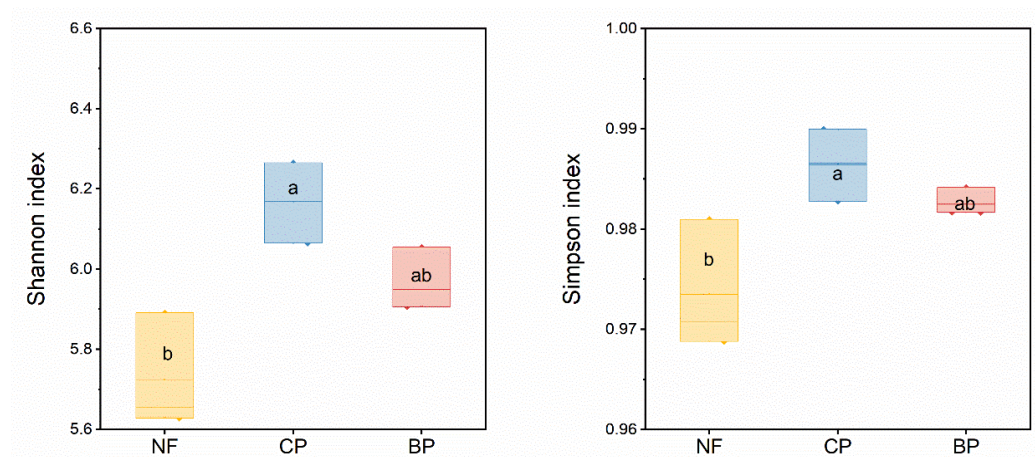


Figure 3. Effect of forest type on alpha diversity of soil microbial communities. NF, natural forest; CP, coniferous plantation; BP, broad-leaved plantation. Different letters indicate significant differences between forests ($p < 0.05$).

Table 2. Effect of forest type on soil physicochemical properties. NF, natural forest; CP, coniferous plantation; BP, broad-leaved plantation. Different superscripted letters indicate significant differences between forests ($p < 0.05$).

Property		SM (%)	ST (°C)	pH	BD (g/cm ³)	SOC (g/kg)	TN (g/kg)	C/N	TP (g/kg)	AP (mg/kg)
March	NF	41.96 ± 3.24 ^a	10.00 ± 0.30 ^a	5.21 ± 0.22 ^b	1.12 ± 0.13 ^a	17.64 ± 0.97 ^{ab}	2.60 ± 0.24 ^b	6.87 ± 0.64 ^a	0.28 ± 0.04 ^b	1.23 ± 0.26 ^b
	CP	60.10 ± 2.68 ^a	9.61 ± 0.07 ^a	6.39 ± 0.31 ^a	0.73 ± 0.02 ^a	14.78 ± 0.49 ^b	2.49 ± 0.03 ^b	5.95 ± 0.25 ^a	0.89 ± 0.09 ^a	1.25 ± 0.21 ^b
	BP	36.06 ± 5.49 ^a	9.22 ± 0.17 ^a	5.67 ± 0.11 ^{ab}	1.12 ± 0.12 ^a	18.32 ± 0.89 ^a	3.63 ± 0.15 ^a	5.05 ± 0.14 ^a	0.86 ± 0.10 ^a	3.01 ± 0.38 ^a
October	NF	63.95 ± 6.42 ^a	20.23 ± 0.30 ^a	4.12 ± 0.01 ^a	1.20 ± 0.24 ^a	14.88 ± 0.33 ^a	4.23 ± 0.22 ^a	3.52 ± 0.10 ^a	0.43 ± 0.04 ^b	1.41 ± 0.14 ^b
	CP	60.52 ± 8.08 ^a	19.37 ± 0.25 ^a	4.19 ± 0.04 ^a	0.83 ± 0.06 ^a	12.70 ± 0.41 ^a	3.43 ± 0.22 ^a	3.72 ± 0.16 ^a	0.64 ± 0.08 ^{ab}	1.66 ± 0.12 ^b
	BP	71.24 ± 5.70 ^a	18.13 ± 0.17 ^b	4.15 ± 0.02 ^a	0.96 ± 0.04 ^a	16.43 ± 1.73 ^a	4.16 ± 0.38 ^a	3.94 ± 0.16 ^a	0.90 ± 0.11 ^a	3.22 ± 0.36 ^a
Whole	NF	52.96 ± 5.88 ^a	15.12 ± 2.30 ^a	4.67 ± 0.26 ^a	1.16 ± 0.12 ^a	16.26 ± 0.77 ^{ab}	3.42 ± 0.39 ^a	5.20 ± 0.80 ^a	0.36 ± 0.04 ^b	1.32 ± 0.14 ^b
	CP	60.31 ± 3.81 ^a	14.49 ± 2.19 ^a	5.29 ± 0.51 ^a	0.78 ± 0.04 ^b	13.74 ± 0.54 ^b	2.96 ± 0.23 ^a	4.83 ± 0.51 ^a	0.76 ± 0.08 ^a	1.45 ± 0.14 ^a
	BP	53.65 ± 8.63 ^a	13.68 ± 2.00 ^a	4.91 ± 0.34 ^a	1.04 ± 0.07 ^b	17.37 ± 0.97 ^a	3.90 ± 0.22 ^a	4.49 ± 0.27 ^a	0.88 ± 0.07 ^a	3.12 ± 0.24 ^a
<i>p</i> values in ANOVA	Forest	0.213	0.004	0.027	0.012	0.020	0.039	0.190	0.008	0.003
	Time	0.013	<0.001	<0.001	0.952	0.027	<0.001	<0.001	0.176	0.117
	F × T	0.106	0.034	0.033	0.639	0.890	0.056	0.018	<0.001	0.799

* SM, soil moisture; ST, soil temperature; BD, bulk density; SOC, soil organic carbon; TN, total nitrogen; C/N, ratio of SOC to TN; TP, total phosphorus; AP, available phosphorus. F × T, Forest × Time.

Table 3. Effect of forest type on soil microbial relative abundance (%) at phylum level (top 10). Different superscripted letters indicate significant differences between forests ($p < 0.05$).

Kingdom	Phylum	Natural Forest	Coniferous Plantation	Broad-Leaved Plantation
Bacteria	Proteobacteria	80.75 ± 1.00 ^a	82.06 ± 0.73 ^a	82.25 ± 0.59 ^a
Bacteria	Actinobacteria	14.32 ± 0.58 ^a	12.70 ± 0.83 ^a	12.88 ± 0.84 ^a
Bacteria	Firmicutes	1.90 ± 0.55 ^a	1.68 ± 0.51 ^a	2.14 ± 0.64 ^a
Bacteria	Bacteroidetes	0.17 ± 0.05 ^a	1.21 ± 0.80 ^a	0.20 ± 0.02 ^a
Bacteria	Acidobacteria	1.68 ± 0.28 ^a	1.23 ± 0.11 ^a	1.42 ± 0.24 ^a
Fungi	Ascomycota	0.48 ± 0.32 ^a	0.11 ± 0.02 ^a	0.11 ± 0.05 ^a
Bacteria	Verrucomicrobia	0.24 ± 0.02 ^b	0.35 ± 0.03 ^a	0.32 ± 0.03 ^{ab}
Bacteria	Nitrospirae	0.02 ± 0.01 ^b	0.13 ± 0.03 ^a	0.07 ± 0.01 ^{ab}
Bacteria	Chloroflexi	0.11 ± 0.01 ^a	0.14 ± 0.04 ^a	0.21 ± 0.03 ^a
Bacteria	Planctomycetes	0.15 ± 0.02 ^a	0.17 ± 0.01 ^a	0.19 ± 0.03 ^a

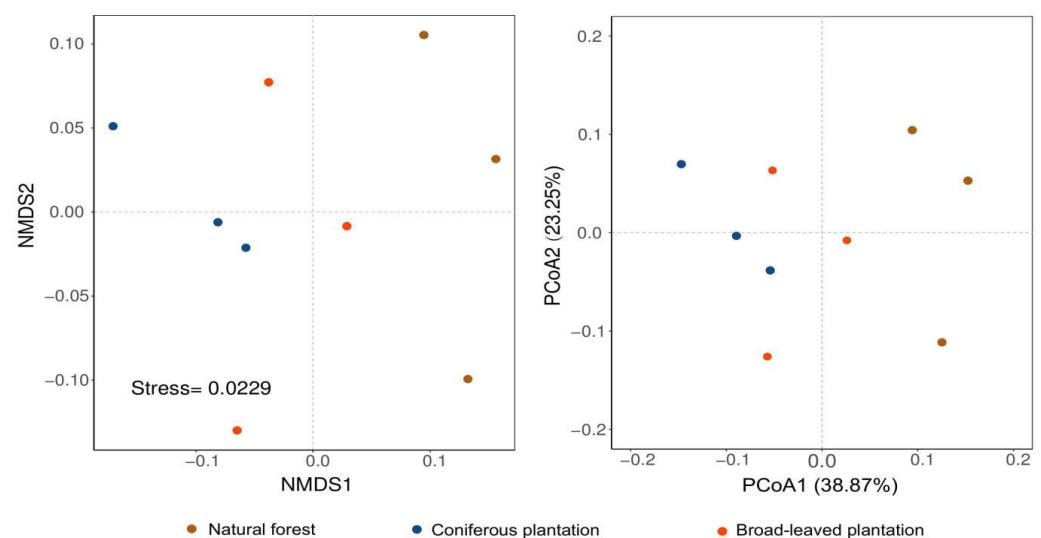


Figure 4. Nonmetric multidimensional scaling (NMDS) and principal coordinate analysis (PCoA) of soil microbial communities based on Bray–Curtis dissimilarity.

3.3. Soil Aggregate Properties and Influencing Factors

The soil in the study area mainly consisted of >2 mm aggregates (more than 90%, Figure 5). In March, only the proportion of 1–2 mm aggregates was significantly different among the forests ($p < 0.05$). It was not significantly different in the NFs from the CPs ($p > 0.05$), while both were significantly higher than in the BPs ($p < 0.05$). In October, the proportion of >2 mm aggregates in the CPs was significantly higher than those in the NFs and the BPs, while that of the 1–2 mm aggregates was the opposite ($p < 0.05$). On the whole, the proportion of 0.25–1 mm aggregates in the two plantations was significantly lower than that in the NFs ($p < 0.05$). However, no matter in which time period, the forest type had no significant effect on the proportion of <0.25 mm aggregates ($p > 0.05$).

The forest type significantly affected the MWD ($p < 0.05$, Figure 6). The MWD of the CPs and of the BPs in March and October were both significantly higher than that of the NFs ($p < 0.05$). On the whole, the CPs significantly increased the MWD by 4.5% as compared with the NFs ($p < 0.05$), while there was no significant difference between the BPs and the NFs ($p > 0.05$).

The mycorrhizal density in the soil in the CPs and the BPs was significantly higher than that in the NFs ($p < 0.05$), while the TG was not significantly affected by the forest type ($p > 0.05$, Figure 7). Although the EEG in the NFs and the BPs were significantly higher than the CPs in October ($p < 0.05$), there was no significant difference between them at the

annual level ($p > 0.05$). For the inorganic aggregate binding agents, the contents of the soil's Fe oxide in the plantations were higher than those of the natural forests in March and the whole year, while no significant difference was detected in the Al oxide content among the forests ($p > 0.05$).

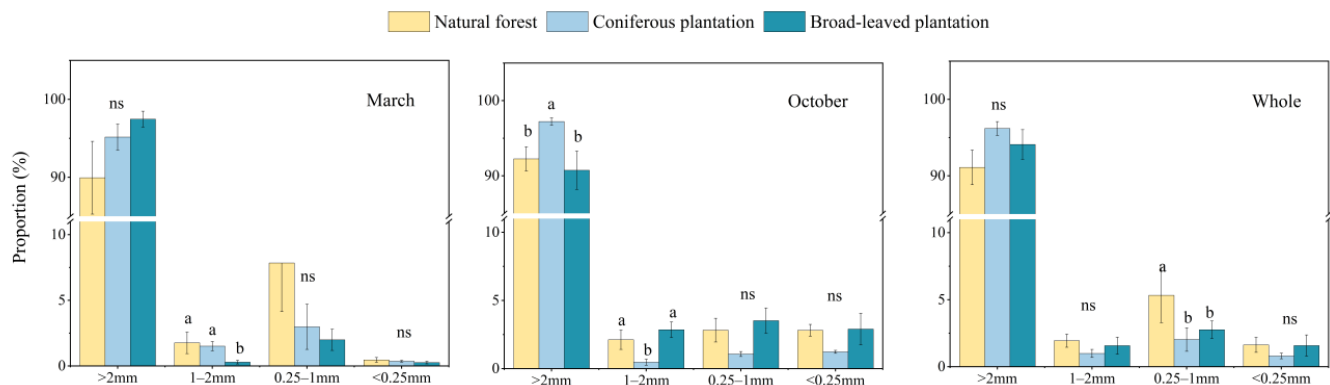


Figure 5. Effect of forest type on the proportion of different soil aggregates. Different letters indicate significant differences between forests ($p < 0.05$). ns, $p > 0.05$.

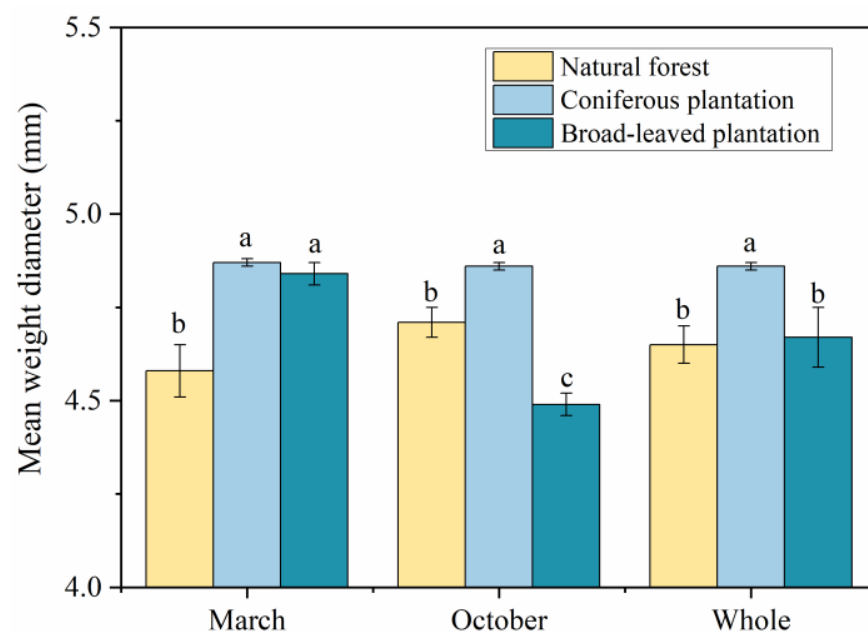


Figure 6. Effect of forest type on the stability of soil aggregates shown as mean weight diameter. Different letters indicate significant differences between forests ($p < 0.05$).

The soil's microbial communities and the organic and inorganic aggregate binding agents explained 75.07% of the variation of the aggregates' composition and stability (Figure 8). They contributed 12.56%, 11.34% and 21.45%, respectively. The interactions between the microbial communities and the organic and inorganic binding agents accounted for 9.76% and 8.67%, respectively, and the interaction between the organic and inorganic binding agents accounted for 6.73%.

A Pearson correlation analysis (Figure 9) showed that there was a significant positive correlation between the soil's microbial diversity indices ($p < 0.001$), and they both significantly and positively correlated with the Fe oxide ($p > 0.05$). Meanwhile, the MWD was positively correlated with the microbial diversity indices, the mycorrhizal density and the Fe oxide ($p < 0.05$). However, there were significant negative correlations between the proportion of >2 mm aggregates and that of aggregates with other sizes ($p < 0.01$).

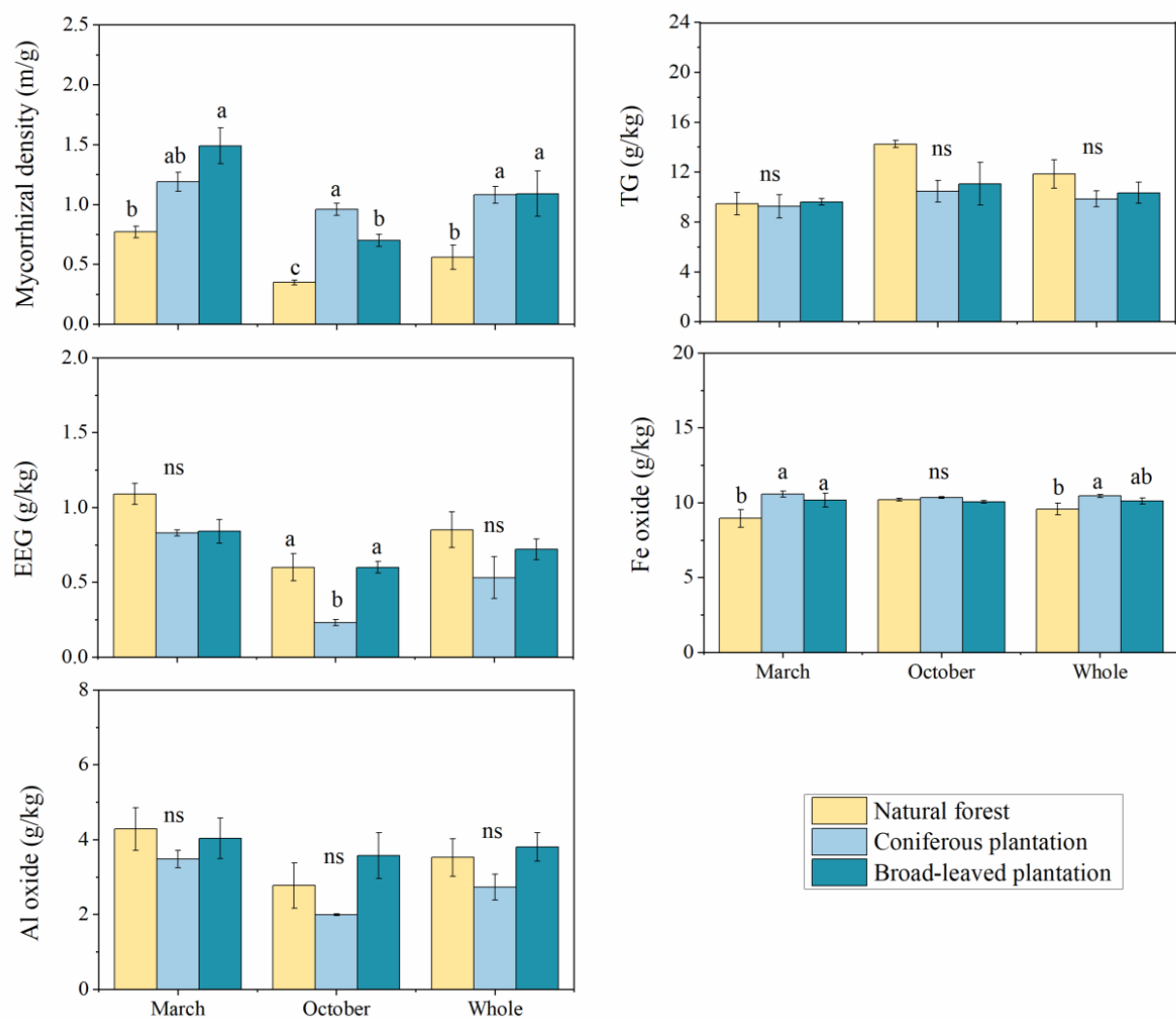


Figure 7. Effect of forest type on mycorrhizal density, total glomalin-related soil protein (TG), easily extractable glomalin-related soil protein (EEG), free Fe oxide and free Al oxide. Different letters indicate significant differences between forests ($p < 0.05$). ns, $p > 0.05$.

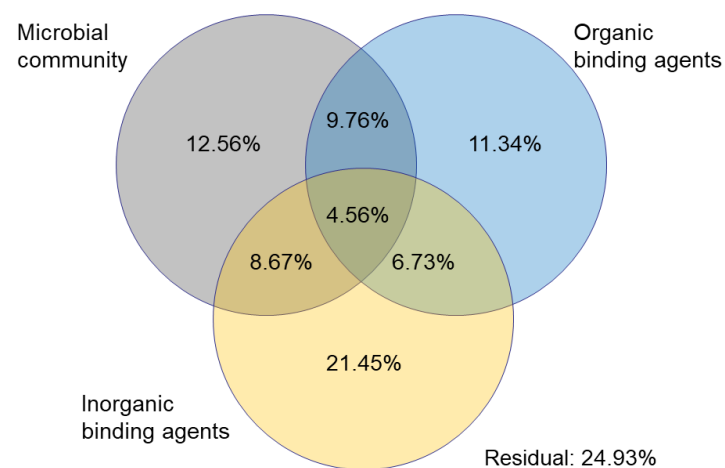


Figure 8. Variance variation analysis (VPA) showing the variance in the aggregates' composition and stability explained by soil's microbial community diversity and organic and inorganic binding agents.

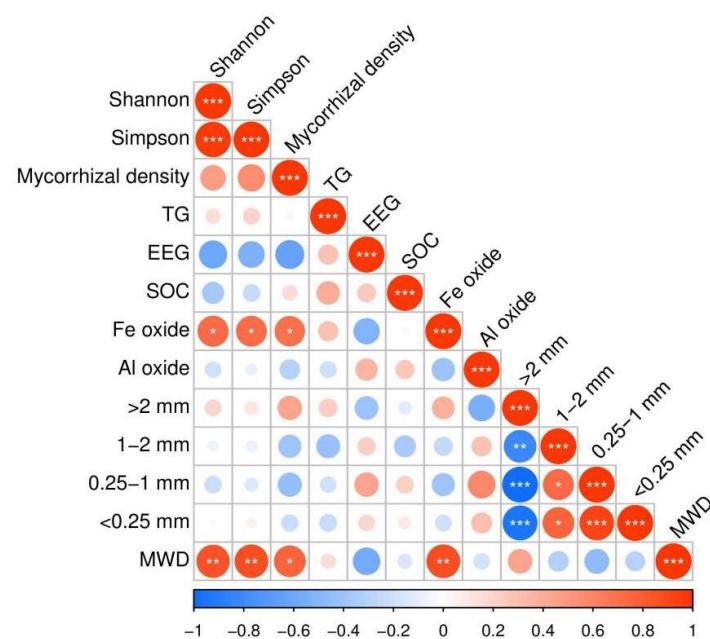


Figure 9. Correlation between soil microbial community diversity, organic and inorganic binding agents, and aggregate composition and stability. TG, total glomalin-related soil protein; EEG, easily extractable glomalin-related soil protein; SOC, soil organic carbon; >2 mm, 1–2 mm, 0.25–1 mm, <0.25 mm, the proportion of different soil aggregates. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

4. Discussion

In this study, the soil MWD in the coniferous plantations was significantly higher than that in the NFs, while that of the broad-leaved plantations was only significantly higher than the NFs in March (Figure 6). This suggests that the restoration of degraded forests by coniferous plantations is more helpful than by NFs to improve the aggregate's stability [9,44]. This partially confirms our hypothesis 1. However, our study only lasted one growing season, and thus long-term research is needed to obtain a precise conclusion. The MWD of the broad-leaved plantations was significantly lower than the NFs in October, and this caused the generally insignificant difference of the MWD between the BPs and the NFs. According to the relationship between the MWD and the proportion of aggregates (Figure 9), the MWD is positively correlated with the proportion of >2 mm aggregates and negatively correlated with the proportion of <2 mm aggregates. That is, the increase in the MWD should be limited by an increase in the proportion of >2 mm aggregates and a decrease in the proportion of <2 mm aggregates. However, in October, the mean value of each <2 mm aggregate's proportion in the BPs was higher than that in the NFs (not significant), which also led to the fact that the aggregates' stability of the BPs was not always higher than the NFs. The reason for the change of each aggregate with a different size can be explained by the microbial communities and the various organic and inorganic binding agents, which will be discussed below. Meanwhile, the lower bulk density (Table 1) of the coniferous and broad-leaved plantations resulted in higher porosity [16,45], which makes it easier for plant roots to penetrate the soil [46], and more roots will intertwine with the soil particles to form aggregates [21]. Another result of this study on the fine root biomass (i.e., the fine root biomass of the coniferous forests (10.21 g/m^2) and the broad-leaved forests (9.73 g/m^2) was significantly higher than that of natural forests (4.40 g/m^2)) confirmed our inference from the other side. However, our study differs from some studies showing the significantly higher fine root biomass in natural forests than that in plantations [45,47]. This is most likely due to our different environmental conditions (particularly the tree species) which easily affect soil properties and root characteristics [48].

As so far, the function of the forests' soil microorganisms has become a research hotspot [49,50]. We were surprised to find that the soil microorganisms play an important

role in the formation of aggregates. This is seen from the interaction between the microbial communities and other factors revealed about 36% variation in the aggregates' composition and stability (Figure 8), and the microbial communities' diversity indices were significantly positively correlated with the MWD (Figure 9). This is consistent with previous research [12,17,51]. This is because stable aggregates provide habitats for microbial communities, and the location of the microbial communities in the aggregates affects their function. Therefore, the diversity of the microbial communities was significantly positively correlated with the MWD.

Furthermore, the organic binding agents that are closely related to the microorganisms, usually including mycorrhizal density and the GRSP, directly affect the stability of the aggregates through the hierarchical formation process of the aggregates [17,25,52]. On the one hand, the mycorrhizal density was significantly positively correlated with the MWD, and the correlation with the large aggregates was stronger than with the small aggregates (Figure 9). This indicates that the mycorrhiza preferentially affects the formation of large aggregates [25]. This is because the mycelia in the microbial community play a winding role on the soil particles [53,54]. The mycorrhizal density in the plantations' soil was significantly higher than that in the NFs' (Figure 7), and the plant roots and their mycorrhizal symbionts could intertwine with mycelia to form a huge network, creating forming conditions for the large aggregates [26]. On the other hand, the GRSP secreted by the microbial community (mainly arbuscular mycorrhizal fungi, AMF) during the metabolic process can act as a "glue" to increase the number of aggregates [23,24]. However, the effects of the TG and the EEG on the MWD in this study were not significant (Figure 9). Except for the EEG in the CPs being significantly lower than in the NFs and in the BPs in October, there was no significant difference in the TG or the EEG among the forests (Figure 6). This may be due to the fact that the TG is a stable and difficultly-decomposed component of the GRSP as compared to the EEG [29,30]. Under a high soil temperature and humidity (Table 2, Figure 2), the EEG released by the AMF in a short time is extremely easy to be degraded and transformed [42]. However, although the microbial community's structure and composition were investigated in this study, the abundance and diversity of the AMF were not analyzed in detail. This hinders the further study on the relationship between the GRSP and the aggregates. However, the aggregates' composition and stability were not affected by the GRSP in this study, and so no evidence from the AMF had little impact. Further analysis can be made in the future.

Both the VPA and the Pearson correlation analysis showed that the formation and stability of the aggregates were achieved through the complex interactions of the soil microbial communities and the various binding agents (Figures 8 and 9), which confirms our hypothesis 2. The organic binding agents (mainly mycorrhiza in this study) have been discussed previously, and the inorganic binding agent in this study was Fe oxide, as indicated by the correlation analysis. In oxisol, sesquioxide (such as Fe and Al oxide, etc.) is a key substance for the formation of aggregates [22]. Its charge can be adsorbed on the surface of clay particles to form an oxide film, which promotes the soil particles' cohesion to form aggregates [31]. Some of the literature reported that the stability of the aggregates was influenced by the Fe and Al oxides [55], and by a single metal oxide, [32] or not by them [56]. In this study, the Fe oxide rather than the Al oxide affected the aggregates, which was probably due to the soil type and texture. The state of the Al^{3+} ion in this studied soil was not stable, but the Fe^{3+} ion was stable enough to replace the Al^{3+} and to make the inorganic colloids in the soil closer to each other and coagulate to form the aggregates [55,57]. The higher content of the soil's Fe oxide in the plantations than in the natural forests (Figure 7) further enhanced the aggregates' stability.

At the same time, there was also a significant positive correlation between the microbial communities' diversity and the Fe oxide (Figure 8). The relative abundances of the soil's microorganisms were affected by the soil's acidity, aeration permeability and nutrients. Under acidic environments, the Fe, Al and Mn in the soil could absorb a large amount of P [55]. On the whole, a better nutrient condition in the plantations than in the natural forests (Table 2) might help the plantations to fix more metal ions. Higher nutrient and mineral

contents create favorable conditions for the soil's microorganisms [34] and they integrate to affect the soil's aggregations. Nevertheless, the correlation between the microorganisms and the metal oxides remains unknown and is an interesting direction for future research.

In summary, the soil's microbial community composition, structure and diversity were significantly different among the forests (Table 3, Figures 3 and 4). In particular, the coniferous plantations had higher microbial community diversity than those of the natural forests (Figure 3). This not only enhanced the penetration of the roots into the soil [46], forming higher mycorrhizal density, but also led to greater microbial community activities [58]. The secretions of the microorganisms may also have participated in the soil aggregation by bonding with the soil particles [12,17]. Under the combined effects of the Fe oxide, more and stable aggregates were formed in the subtropical coniferous plantations than in the natural forests.

5. Conclusions

The type of subtropical forest significantly affects the soil microbial community's composition, structure and diversity. The Shannon and Simpson indices of the soil microbial communities in the coniferous plantations are both significantly higher than those in the natural forests. This might further affect the mycorrhizal density. In addition, with the cementation effects from the Fe oxide, the subtropical coniferous plantations have a higher soil aggregate stability than those of the natural forests. We therefore suggest that coniferous plantations can be considered to enhance the aggregate structures in the restoration of subtropical degraded forests. The combined effects of the soil microbial communities, the organic (mycorrhizal density) and inorganic binding agents (Fe oxide) can be the main mechanisms of the soil's aggregation in the study area. Since the microorganisms play important roles in the soil's aggregation, future studies on specific microorganisms (such as AMF) can be strengthened, and long-term research is also necessary.

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