Biogeographic Changes in Forest Soil Microbial Communities of Offshore Islands—A Case Study of Remote Islands in Taiwan

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Abstract: Biogeographic separation has been an important cause of faunal and floral distribution; however, little is known about the differences in soil microbial communities across islands. In this study, we determined the structure of soil microbial communities by analyzing phospholipid fatty acid (PLFA) profiles and comparing enzymatic activities as well as soil physio-chemical properties across five subtropical granite-derived and two tropical volcanic (andesite-derived) islands in Taiwan. Among these islands, soil organic matter, pH, urease, and PLFA biomass were higher in the tropical andesite-derived than subtropical granite-derived islands. Principal component analysis of PLFAs separated these islands into three groups. The activities of soil enzymes such as phosphatase, β-glucosidase, and β-glucosaminidase were positively correlated with soil organic matter and total nitrogen. Redundancy analysis of microbial communities and environmental factors showed that soil parent materials and the climatic difference are critical factors affecting soil organic matter and pH, and consequently the microbial community structure.

1. Introduction

Soil microbial communities contribute to soil ecology by playing critical roles in mineralizing soil organic matter and nutrient cycling [1]. The distribution of soil microbes is non-random and displays spatial aggregation [2]. In the forest soil, microbial distribution can be linked to soil types [3], tree species [4], and climatic conditions such as temperature and precipitation [5]. These variables controlling microbial communities can be altered by the distribution of islands—the geographical effect—resulting in various spatial patterns of microbial associations and nutrient cycling [6]. Only a few studies have so far addressed the diversity of soil microbial community structures in different islands [7,8].

Many studies have indicated that the effects of temperature and moisture of regional climates along a biogeographic distribution could influence soil community structures and soil enzymatic activities [9,10]. In addition, soil pH was found to be another primary factor affecting microbial composition and function along a biogeographical distribution [6]. The influence of soil type on microbial properties is even more important than the season or management system, as established in a long-term field farming system trial [3]. The cycling of nutrients in the soil involves chemical and biochemical reactions that are driven/catalyzed by soil enzymes [11]. Microbial communities contain unique phospholipid ester-linked fatty acids (PLFAs) [12], and thus quantifying the PLFAs can estimate the abundance of the major microbial communities in the soil.

The objective of this study was to investigate the biogeographical separation of microbial community structures in forest soils by measuring PLFAs and soil enzyme activities in

the archipelagoes of Matsu Islets (MIs), Orchid Island (OI), and Green Island (GI). Matsu Islets (MIs) are offshore islands of mainland China with soil derived from granite parent materials. Orchid Island (OI) and Green Island (GI), two tropical volcanic islands, are located offshore of Taiwan and have soils derived from parent materials of andesite. We hypothesized that the climate and soil parent materials regulate soil chemical properties and soil microbial activities, consequently changing the microbial community structure. The larger goal of this study was to elucidate whether soil properties play critical roles in the biogeographic distribution of soil microbial communities in offshore islands.

2. Materials and Methods

The study was conducted on several remote islands: the archipelagoes of Matsu Islets (MIs), Orchid Island (OI), and Green Island (GI) (Figure 1). MIs are located 10–50 km offshore of mainland China and face the Taiwan Strait. Five MI islands, Beigan (MI-BG) (26°22′ N, 119°99′ E), Nangan (MI-NG) (26°15′ N, 119°93′ E), Dongju (MI-DJ) (25°95′ N, 119°97′ E), Hsiju (SJ) (25°97′ N, 119°94′ E), and Dongyin (MI-DY) (26°36′ N, 120°49′ E) Islands, were used in the sampling. These subtropical islands have a mean precipitation of about 1000 mm and annual average temperature of 18.6 °C. In the 1950s, the military started a large-scale afforestation effort on the islands. The forests on the islands are broadleaf and dominated by the tree species *Acacia confuse*, *Casuarina equisetifolia*, and *Ficus microcarpa*. The soil on these islands comes from granite parent material, and we classified it is as Haplustults based on the United States Department of Agriculture (USDA) Soil Taxonomy key [13].
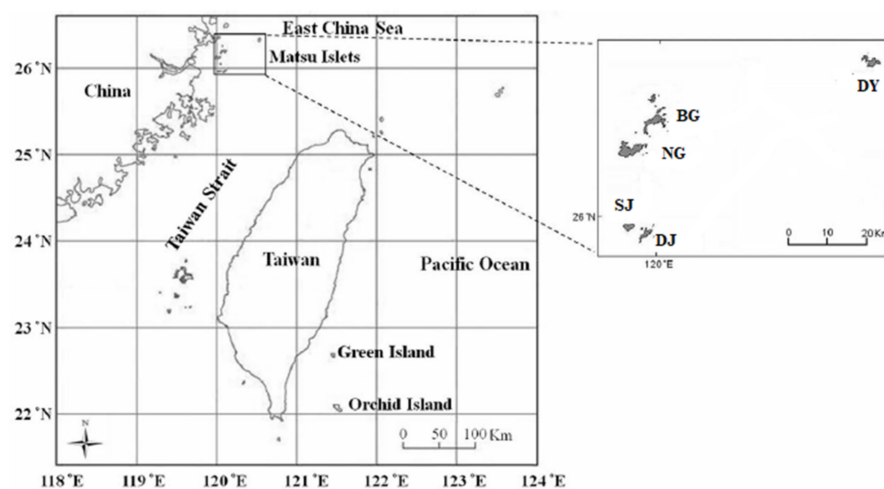

Figure 1. Sampling sites on offshore islands (Adapted from Lin et al. [5]). Site abbreviations are in Table 1.

Table 1. Soil microbial biomass and activity characteristics of different islands.

Island	Abbreviation	pH [§]	Org C [§] (g kg^{-1})	C_{mic} [§] (μg g^{-1})	C_{mic}/C_{org} (%)	Respiration (μg g^{-1} h^{-1})	Metabolic Quotient (qCO_2)
Matsu (Nangan)	MI-NG	4.86 b	24.0 c	448.5 de	1.90 a	2.89 c	5.75 c
Matsu (Beigan)	MI-BG	4.24 b	57.1 a	641.7 c	1.17 b	3.66 bc	5.67 c
Matsu (Donju)	MI-DJ	4.81 b	21.0 c	412.7 e	1.99 a	2.32 c	5.44 c
Matsu (Shiju)	MI-SJ	4.47 b	22.9 c	503.9 d	2.25 a	2.73 c	5.41 c
Matsu (Dongyin)	MI-DY	4.85 b	29.7 c	565.8 c	1.91 a	5.4 b	9.64 a
Orchid	OI	6.10 a	64.0 a	1241.6 b	1.95 a	8.84 a	7.17 b
Green	GI	6.43 a	44.9 b	1963.5 a	2.34 a	10.3 a	9.86 a

[§] Data from Lin et al. [5]; C_{mic}: microbial biomass C; Values in each column followed by the same letter are not significantly different at $p = 0.05$ based on Duncan's multiple range test.

Orchid Island (OI) and Green Island (GI) are tropical volcanic islands. OI (22°01′ N, 121°34′ E) is located about 60 km from the southeastern part of Taiwan and faces the Pacific Ocean, with a mean precipitation of >3000 mm and annual average temperature of 22.6 °C. The vegetation is natural and little disturbed secondary tropical broadleaved forest. GI (22°39 N, 121°29) is located about 30 km east from Taiwan and faces the Pacific Ocean; it has a mean temperature of 23.5 °C and mean precipitation of about 2500 mm. Compared to OI, vegetation in GI is heavily disturbed by wildfire and human activities. A large-scale afforestation effort was conducted in the 1960s, and consequently most of the area is now covered with secondary broadleaved forest. The dominant tree species in these broadleaf forests are *Ardisia sieboldii*, *Schefflera octophylla*, and *Ficus nervosa.* The soils on these two islands come from andesite parent material, and we classified them as Paleudults based on the USDA Soil Taxonomy key [13].

Four replicate plots of 50 × 50 m were sampled for each island—except for GI, where only three replicates were sampled. Matsu Islets were sampled in October 2016, and Orchid Island and Green Island were sampled in November 2016 and February 2017, respectively. After removing the surface litter, samples at each plot were collected at three points with a soil auger (8 cm in diameter and 10 cm deep) to make a composite sample. Soil samples were stored at 4 °C in the dark until microbial biomass and enzymatic activity analyses, which were completed within one month of field collection. Portions of soil samples were freeze-dried at −20 °C immediately after sampling to analyze PLFAs. Other subsamples were dried and ground for chemical analyses. Aliquots of fresh soil samples were weighed and oven-dried at 105 °C to determine moisture content.

Soil organic C (C_{org}) and total N (N_{tot}) concentrations were determined using an NSC analyzer (NA1500 Series 2, Fisons, Italy). Soil pH values in air-dried samples were measured using a combination of glass electrodes (soil: water ratio 1:2.5) [14].

Soil basal respiration was estimated using an alkali method [15] from the average CO_2 flux rate over a three-day incubation after seven days of pre-incubation. The soil was adjusted to 60% water-holding capacity. After pre-incubation, the plastic tube (with soil inside) was removed and carefully placed into another 250-mL serum bottle with a beaker at the bottom containing 20 mL of 0.05 M NaOH. The serum bottle was capped and incubated at 25 °C for 3 days. After incubation, $BaCl_2$ was added and the 20 mL NaOH solution in the beaker was titrated using 0.05 M HCl with phenolphthalein. Basal respiration was calculated based on the CO_2 produced during the incubation. The microbial quotient (qCO_2) was calculated as the ratio of respiration to microbial biomass C (C_{mic}), while the data on C_{mic} came from Lin et al. [5].

Phosphatase activity was determined followed the method of Tabatabai and Bremner [16]. Cellulase and xylanase activities were determined using the method of Schinner and von Mersi [17]. Arylsulfatase activity was determined based on Tabatabai and Brem-

ner [18]. Urease, protease, and β-glucosaminidase activities were determined as described in Kandeler and Gerber [19], Ladd and Butler [20], and Parham and Deng [21].

PLFA extraction and analysis followed the method of Frostegård et al. [22]. Lipids were extracted using a single-phase mixture of chloroform-methanol-citrate (1:2:0.8). FAME content was analyzed by capillary gas chromatography and flame ionization detection using a Thermo Finnigan Trace chromatographer as described in Chang et al. [23]. The fatty acid nomenclature used is described in Frostegård et al. [22]. The total amounts of PLFAs were used to indicate the total microbial biomass. The sum of PLFAs (i15:0, a15:0, 15:0, i16:0, 16:1ω7c, 17:0, i17:0, cy17:0, 18:1ω7c, and cy19:0) was considered to be the bacterial origin. PLFAs 16:1ω7c, cy17:0, 18:1ω7c, and cy19:0 represent gram-negative (G−) bacteria, while PLFAs i15:0, a15:0, i16:0, and i17:0 represent gram-positive (G+) bacteria. PLFAs 18:2ω6,9c are considered to be common fungi-16:1ω5c is arbuscular mycorrhizal fungi and 10Me18:0 is actinomycetes, as described in Zogg et al. [24] and Zelles [25].

Data obtained from fresh samples were converted to the oven-dried basis using soil moisture content. A one way analysis of variance and Duncan's multiple range test were performed to compare each measurement among the different islands. Principal component analysis was used to compare the relative concentrations (mol%) of individual fatty acids across different community structures. Redundancy analysis was conducted using Canoco for Windows (Version 5.0) to determine whether the microbial communities and soil enzymatic activities could be correlated to environmental factors that we evaluated in parallel studies, such as microbial biomass C (C_{mic}), microbial biomass N (N_{mic}), C_{org}, and N_{tot} [5]. Statistical analyses, unless specified, were conducted using SPSS v18.0 (SPSS, Chicago, IL, USA). $p < 0.05$ was considered statistically significant.

3. Results

3.1. Soil Properties and Microbial Biomass

Among the MI islets, most soil samples had similar chemical properties such as pH, C_{org}, N_{tot} contents, and the ratios of C_{mic}/C_{org} (except for high C_{org}) in the MI-BG soil (Table 1). Soil respiration and qCO_2 were the highest in the MI-DY soil, but no significant differences were found between other islets. By comparison, soil pH was significantly lower in MI soils than in OI or GI ones (Table 1). C_{org} and N_{tot} were also significantly higher in OI and GI than MI soils, except for MI-BG soil. Soil respiration was significantly higher in GI and OI than MI soils. qCO_2 was higher in GI and OI soils than MI soils (except for the MI-DY soil).

3.2. Soil Enzyme Activities

Among MI islets, soil cellulase, xylanase, phosphatase, β-glucosaminidase, and proteinase activities were significantly higher in MI-BG soil than others (Table 2). However, urease and β-glucosidase showed no significant difference among MI islet soils.

By comparison, urease, acid phosphatase, β−glucosamidase, and arylsulfatase activities were highest in the OI soil; however, glucosidase was not significantly different among these soils. Proteinase was significantly higher in GI soil than other soils.

Table 2. Soil enzymatic activities of different islands.

Island	Abbreviation	Cellulase (µg glucose $g^{-1}d^{-1}$)	Xylanase (µg glucose $g^{-1}d^{-1}$)	Urease (mmole NH_4^+-N $g^{-1}h^{-1}$)	Phosphatase (µg nitrophenol $g^{-1}h^{-1}$)	β–Glucosaminidase (µg nitrophenol $g^{-1}h^{-1}$)	Glucosidase (µg nitrophenol $g^{-1}h^{-1}$)	Arylsulfatase (µg nitrophenol $g^{-1}h^{-1}$)	Proteinase µg tyrosine $g^{-1}2h^{-1}$
Matsu (Nangan)	MI-NG	762 b	2955 b	1.08 b	1574 b	260 bc	101 a	97.0 cd	92.5 b
Matsu (Beigan)	MI-BG	3070 a	6608 a	1.79 b	1987 b	403 a	135 a	97.3 cd	199 ab
Matsu (Donju)	MI-DJ	1149 b	3190 b	1.34 b	870 c	211 c	93.0 a	42.7 d	153 b
Matsu (Shiju)	MI-SJ	704 b	2331 b	0.85 b	755 c	253 bc	120 a	128 c	141 b
Matsu (Dongyin)	MI-DY	677 b	2722 b	2.18 b	565 c	87.0 d	106 a	119 cd	162 b
Orchid	OI	960 b	2530 b	10.5 a	2762 a	340 ab	127 a	788 a	180 ab
Green	GI	973 b	3347 b	2.37 b	842 c	95.3 d	91 a	308 b	340 a

Values in each column followed by the same letter are not significantly different at p = 0.05 based on Duncan's multiple range test.

3.3. PLFA Biomarkers

Among MI islets, soil total PLFAs, and the abundance of G+, G− bacteria and actinobacteria were significantly higher in MI-DY soil than in others (Table 3). The levels of both fungal and arbuscular mycorrhizal fungal PLFA biomarkers were also highest in MI-DY soils. The ratio of fungi/bacteria was higher in MI-NG and MI-DY soils than in others. The ratio of G+/G− in MI-NG and MI-DY was lower than in other soils.

Table 3. Soil biomass content based on phospholipid acid biomarkers (nmol g^{-1} soil) and the ratios of the biomarkers of different islands.

Island	Abbreviation	Total PLFAs	Bacteria	Fungi	AMF Fungi	Actinobacteria	G+	G−	G+/G−	Fungi/ Bacteria
Matsu (Nan-gan)	MI-NG	23.0 e	9.43 d	0.973 cd	0.724 c	0.374 c	5.26 d	3.84 c	1.37 c	0.10 a
Matsu (Beigan)	MI-BG	37.2 cd	15.9 cd	0.948 cd	1.14 bc	0.572 c	9.95 bc	5.32 c	1.91 a	0.057 bc
Matsu (Donju)	MI-DJ	22.7 e	9.92 d	0.448 c	0.617 c	0.449 c	6.18 d	3.37 c	1.84 ab	0.047 bc
Matsu (Shiju)	MI-SJ	30.2 de	13.7 d	0.681 c	1.01 bc	0.504 c	8.23 cd	5.0 c	1.64 b	0.050 bc
Matsu (Dongyin)	MI-DY	48.7 bc	21.6 bc	1.66 b	1.44 b	0.772 c	11.4 bc	9.56 b	1.19 c	0.080 ab
Orchid	OI	50.6 b	23.7 b	0.753 c	1.09 bc	1.77 b	12.8 b	10.4 b	1.27 c	0.035 c
Green	GI	95.2 a	43.6 a	2.66 a	3.71 a	2.73 a	21.3 a	20.7 a	1.02 d	0.067 abc

Please refer to the footnotes in Table 2.

By comparison, soil total PLFAs, and the abundance of G+, G− bacteria and actinobacteria were significantly higher in GI than MI or OI soils. The levels of both fungal and arbuscular mycorrhizal fungal PLFA biomarkers were also highest in GI soil. The ratios of G+/G− were significantly lower in GI than OI or MI soils, while the ratio of fungi/bacteria was lowest in OI soil.

3.4. Soil Microbial Community Structure

Soil microbial communities, as analyzed by the principal component analysis of PLFA levels, could be divided into three major clusters: OI, GI, and MI. The first and second principal components (PC1, PC2) accounted for 68.7% of the PLFAs (Figure 2a). PC1 differentiated the GI soil from the other soils, and PC2 differentiated between MI and OI soils according to their geographic locations. The principal component analysis loadings identified the PLFA markers that were most important to geographic variations were as follow: high positive loadings for G+ bacteria (i15:0, a15:0, i17:0,), high positive loadings for G− bacteria (cy17:0 and cy19:0), and positive loading for actinobacteria (10Me16:0 and 10Me18:0) contributed to the PC1 axis (Figure 2b).
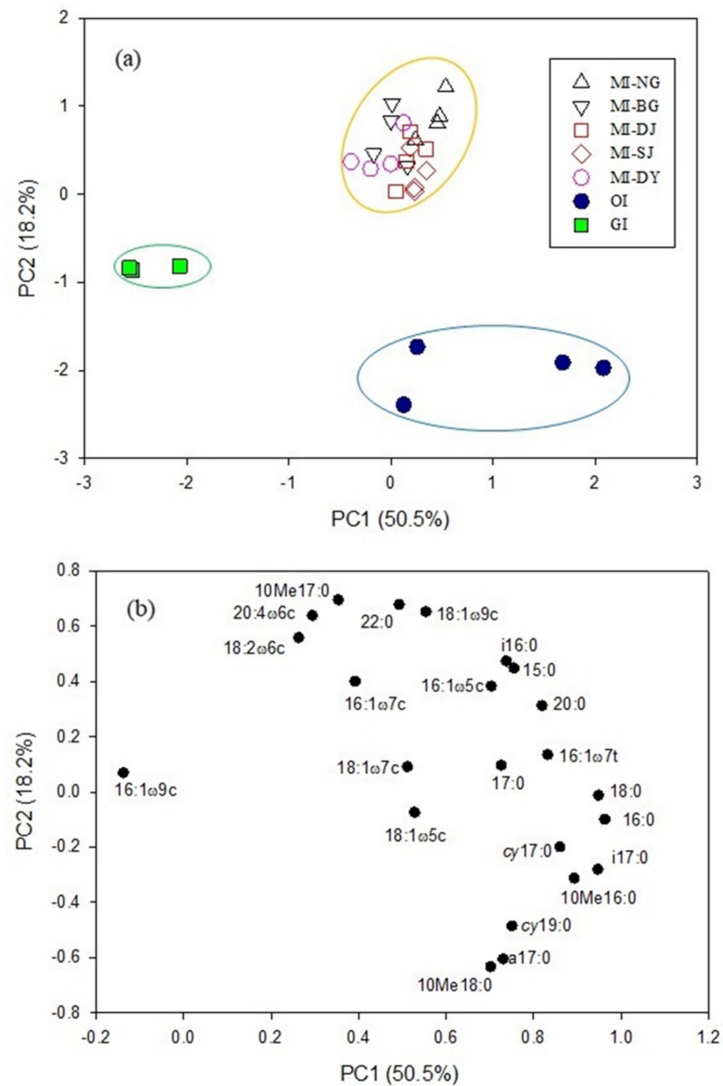
Figure 2. Plots of the first two principle components (PCs) from the principal component analysis of the mole % of microbial phospholipid fatty acid content of soil samples of different island. (**a**) Sample distribution of the first two PCs. (**b**) Corresponding loading values of fatty acid distribution of two PCs.

3.5. Correlation among Soil Properties and Microbial Communities

To evaluate the relationships among soil enzyme activities and environmental factors, a redundancy analysis was conducted using soil enzyme activities and environmental variables (Figure 3). Soil samples from the OI and GI were well separated from the MI samples based on RDA analysis. Soil enzyme activities were positively correlated with soil C_{mic}, N_{mic}, C_{org}, and N_{tot}, suggesting that C_{org} and N_{tot} had strong effects on the enzyme activities in these soils.
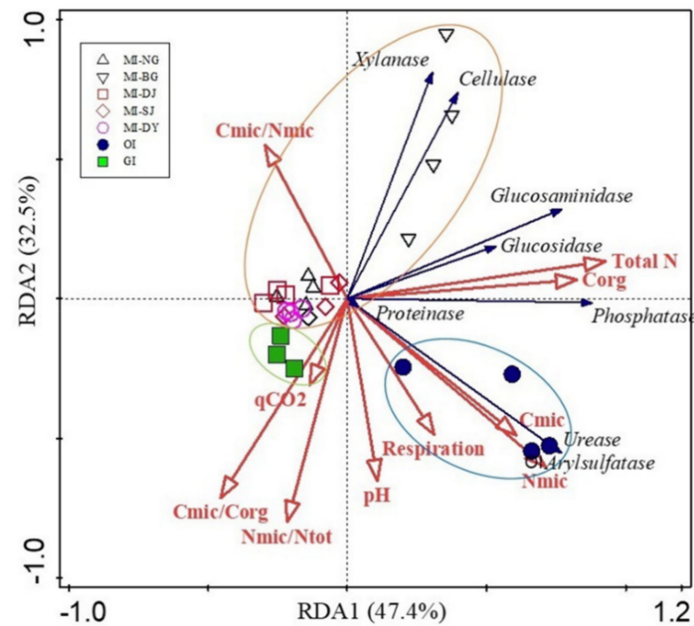
Figure 3. Redundancy analysis (RDA) results of the relationship between soil variables and enzymatic properties of the different islands.

The results from the redundancy analysis of microbial communities and environmental factors also showed similar patterns to those observed from the principal component analysis (Figure 4). Soil C_{org} and N_{tot} were both positively related to microbial communities, while the ratio of G+/G− was negatively correlated with soil environmental factors. In summary, distinct soil physiochemical chemical properties and soil organic C and N were responsible for the development of soil bacterial, fungal, and actinobacterial communities across the islands.
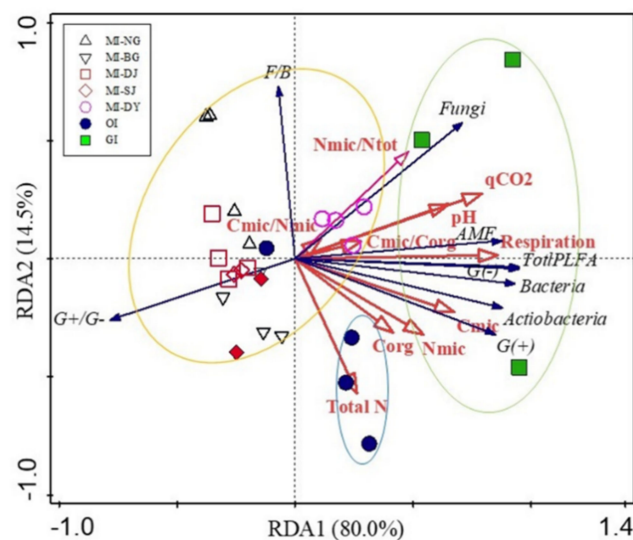

Figure 4. Redundancy analysis (RDA) of the correlations between soil parameters (chemical properties and microbial biomass) and microbial communities of the different islands.

4. Discussion

4.1. Soil Chemistry and Biological Properties of the Different Islands

We observed that the soil microbial communities and enzyme activities varied across offshore islands. Soil parent material and chemical properties may play significant roles in discriminating soil microbial communities and biochemical activities among the islands.

Forests in MI are dominated by relatively young-growth trees, whereas those in OI and GI comprise more mature trees and less evidence of disturbance. As a result, OI and GI forests accumulated higher soil C_{org} content and had more C_{mic} and soil respiration than did those in MI. Tonon et al. [26] reported that microbial biomass was higher in older forests, and that C_{org} and N_{tot} were the important factors affecting variations in microbial biomass. In addition, high C_{org} content in tropical island soils could provide sufficient nutrient availability for microbial growth [27]. Tufekcioglu et al. [28] showed that soil respiration rates were highly correlated with soil C_{org}. Romanowicz et al. [29] indicated that high temperature and precipitation in tropical soils could change the bacterial composition and increase microbial activities at elevated temperature, which would lead to high microbial biomass production in environments with high available C [30]. Some studies showed soil respiration responses to precipitation and temperature and found that increases in precipitation and temperature increase soil respiration [31,32]. The high qCO_2 means that microorganisms must produce high CO_2 to meet energy demands under low available decomposable substrates [33]. Wardle and Ghani [34] indicated that qCO_2 has some limitations because it can be insensitive to disturbance and stress. These studies suggest that qCO_2 might respond to not only biological factors, but also environmental factors, such as substrate quality, soil parent material, and temperature [35–37]. The ecophysiological state of soil microbes were shown to respond to soil acidity due to soil parent material and lower pH, resulting in lower qCO_2 [38]. On the other hand, values of qCO_2 increased as the result of metabolic activation, which means higher maintenance energy requirement at high temperatures [39]; this supports our results of high qCO_2 in the OI and GI soils.

4.2. The Differences in Soil Enzyme Activity among the Islands

In this study, soil enzyme activities were strongly correlated with soil C_{org} and soil pH (Figure 3). Soil enzyme activity is generally positively correlated with soil organic matter [11]. Our examination of the relationships between the soil enzyme activities and environmental variables by redundancy analysis showed that OI soil was separate from MI and GI soils (Figure 3). Urease and arylsulfatase in OI soil were significantly highest (Table 2), and were also highly correlated with soil pH and soil microbial biomass. OI and GI soil have the same soil parent material and pH; however, OI soil contained higher C_{org} and N_{tot} than did GI soil, and thus the OI soil had greater enzyme activities than did the GI soil. Meanwhile, the low urease activity in MI soils is probably due to the low soil pH. Pommerening-Roser and Koops [40] indicated that low soil pH was not conducive to urease.

4.3. Soil Microbial Community Structure of Different Islands

Studies have shown that total PLFAs and bacteria are positively related to soil C_{org} and N_{tot} [23,41]. High total PLFAs, bacteria, and G+ bacteria in the soils of MI-BG and MI-DY among the MI islets should be due to high C_{org} and N_{tot} in the soils of these islands. Bacteria are generally neutrophils, preferring to grow in environments of pH 6–8 [42,43], whereas fungi are better suited at pH 4–5 [44]. The mean pH of the MI soils was significantly lower than those of the OI and GI soils; thus, relatively low pH of MI soils resulted in significantly lower abundances of bacterial PLFAs and higher ratios of fungi/bacteria. This is consistent with previous studies showing that the ratio of fungi/bacteria increased with decreasing soil pH [45]. In addition, Frestegard et al. [22] pointed out that the ratio of ergosterol/bacteria decreases with increasing soil pH. Other studies have also shown the importance of soil pH on bacterial growth [46].

Some studies have shown that G− bacteria grow better under substrate-rich conditions, and slow-growing specialists, such as G+ bacteria, are more competitive than G− bacteria in resource-limited areas [12,47]. The ratio of G+/G− bacteria was lower in GI and OI than most MI soils, suggesting that OI and GI soils provided a substrate-rich environment for G− bacteria. In similar study sites, Lin et al. [5] indicated that OI and GI soils had higher Verrucomicrobia (a phylum of heterotrophic G− bacteria) abundances than did MI

soils. In addition, Shen et al. [48] found that Verrucomicrobia was significantly correlated with soil pH and the C/N ratio. OI soils contain higher C_{org}, N_{tot}, and pH than do MI soils, resulting in a high abundance of G$-$ bacteria such as Verrucomicrobia. Therefore, in addition to the relatively low disturbance and high accumulation of organic matter content in the OI and GI forest soils, the soil chemistry developed from parent materials might play an essential role in developing microbial communities in these soils. Wagai et al. [49] suggested that the soils derived from different parent materials actively affect the microbial community in forest soils. Thus, both the andesite-derived and granite-derived soils shape soil microbial community structure, and the mechanism distinguishing these structures appears to be soil pH changes [50].

The principal component analysis of PLFAs showed that microbial communities are clustered closely in MI soils and scattered in OI and GI soils (Figure 2). In a previous study, Lin et al. [5] showed that the differences in C_{org} and pH between subtropical granite and tropical andesite islands deeply affected microbial community structure. Xiong et al. [51] noted that both geographic distance—e.g., annual precipitation difference—and chemical factors—e.g., pH—govern bacterial biogeography in lake sediments across the Tibetan Plateau. These results indicate that geographic distribution and soil parent material resulting in variations in soil nutrients and pH are significant drivers of microbial communities and their activities.

5. Conclusions

The geographic distributions of soil enzyme activities and microbial communities were identified on islands across different climate conditions and soil parent materials. The total PLFAs and bacterial abundances were lower in subtropical granite soils than in tropical andesite ones. Soil microbial communities were closely clustered in subtropical granite soils, but were separate in tropical andesite soils. This difference was highly correlated with soil properties due to soil parent material. This study showed that microbial activities and community structures are determined by soil chemical properties caused by different soil parent material and climate conditions. Tropical warm and humid conditions induce the weathering of parent material and help andesite soils secure more nutrients than subtropical granite soils, which might be the critical reason why the former supports higher microbial abundance and activity. Further pedological study is needed to ascertain the mechanism behind the relationship between nutrient supply and microbial communities in these soils. In addition, due to the limited scale and numbers of islands, further study is still needed to clarify the relationship between climate and parent materials affecting changes in soil microbial communities.

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