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Variations in Microbial Residue and Its Contribution to SOC between Organic and Mineral Soil Layers along an Altitude Gradient in the Wuyi Mountains

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Abstract: Microbes are crucial components of soil, and their residue carbon plays a significant role in the formation and stabilization of soil carbon pools. However, current research on microbial residue carbon has predominantly focused on surface soils, with limited studies on deep soils. The patterns of variation along soil profiles and their controlling factors remain unclear. Therefore, this study aimed to investigate the soils from different elevations in the Wuyi Mountains, specifically focusing on the organic layers (0–10 cm) and mineral layers (30–40 cm). Amino sugars were utilized as biomarkers for the microbial residue, and the RDA (redundancy analysis) method was employed to analyze the patterns of microbial residue carbon in different soil layers and to identify the factors that control them. The results indicate that there are significant differences in the microbial residue carbon content and its contribution to soil organic carbon (SOC) between the different soil layers. Specifically, between the organic layer and the mineral layer, the microbial residue carbon content exhibited an increasing trend, whereas its contribution to SOC decreased. This finding suggests that soil layer type has a notable impact on microbial residue carbon content and its contribution to SOC. Moreover, fungal residue carbon content was found to be higher than bacterial residue carbon content in both soil layers. However, the ratio of fungal residue carbon to bacterial residue carbon gradually decreased between the organic layer and the mineral layer. This implies that although fungal residue carbon remains dominant, the contribution of bacterial residue carbon to the soil carbon pool increases as the soil transitions to the mineral layer. The total soil carbon content, elevation, and C/N ratio exhibited positive correlations with fungal and bacterial residue carbon, indicating their significant roles in the accumulation of microbial residue carbon in soils. Notably, elevation emerged as a key regulating factor in the accumulation of microbial residue carbon, explaining 85.8% and 67.9% of the variations observed in the organic layer and the mineral layer respectively. These research findings contribute to a better understanding of the soil carbon cycling process and its mechanisms, providing a scientific basis for developing strategies to enhance soil carbon sequestration by manipulating micro-organisms.

Keywords: microbial residue carbon; deep soils; soil carbon stabilization; soil organic carbon; soil properties

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1. Introduction

In recent years, global warming has become an increasingly serious threat to human survival and development. Soil, as the largest carbon sink in terrestrial ecosystems, has

a carbon storage capacity that is two–three times greater than that of vegetation and the atmosphere [1]. Even small changes in soil carbon can lead to amplified positive feedback to climate warming [2]. Therefore, conducting in-depth research on the mechanisms of carbon formation, accumulation, and stability regulation in terrestrial ecosystems is very important in the formulation of the corresponding measures to mitigate global warming.

Microbes are crucial components of soil and play a vital role in the carbon cycling process [3–5]. They act as decomposers, regulating the turnover of nonmicrobial-sourced carbon, and they contribute to the formation of microbial-sourced carbon [6]. Recent studies have shown that microbial residues are the primary contributors to the stable soil carbon pool [7]. Therefore, Liang et al. recently proposed the hypothesis of the microbe-mediated "Microbial Carbon Pump" mechanism [6], which posited that microbes could convert plant-derived carbon into their own biomass and quickly convert it into stable microbial secondary metabolites and residue carbon. While active microbes make up less than 5% of the soil organic carbon pool, their residues can remain stable in the soil after microbial death [8]. Through the iteration process of microbial reproduction, growth, and death [9,10], the soil "entombing effect" occurs, leading to the continuous production and accumulation of stable organic carbon from microbial sources, which contributes to the formation of a soil carbon pool [11,12]. In fact, existing data indicate that microbial residue carbon is often 40 times that of microbial biomass carbon and can provide up to 80% of soil organic matter content (SOM) [13]. Furthermore, microbial residues have a longer turnover time and a longer residence time in the soil than microbial live carbon due to the stability of the microbial cell walls, making them even more critical in long-term soil carbon sequestration [11]. As a result, soil microbial residue carbon plays an irreplaceable role in the formation and accumulation of the stable soil carbon pool.

Due to the high sensitivity of soil microbes to changes in the surrounding environment [14], their metabolism and turnover are easily influenced by external conditions. As a result, the activity and metabolic processes of soil micro-organisms undergo corresponding changes, which, in turn, affect the formation and accumulation of soil microbial residues [15,16]. Altitude variations bring about simultaneous changes in factors such as light intensity, water availability, temperature, soil nutrients, litter quality, and plant root systems [16]. These changes contribute to variations in vertical zonation, soil physicochemical properties, and vegetation types [17]. When considering the inherent spatial heterogeneity of soil, the vertical zonation differences resulting from altitude gradients can potentially exacerbate the spatial heterogeneity of soil, thereby impacting the formation and accumulation of soil microbial residues.

Deep soils (>20 cm) are estimated to contain approximately 50% of the global organic carbon reservoir [18–20]. When compared to topsoil (<20 cm), deep soils exhibit longer carbon storage times and play a vital role in the carbon cycle and climate regulation of terrestrial ecosystems. However, current research studies have primarily focused on microbial residues in surface soils, neglecting the potential contribution of microbial-derived carbon in deep soils, which may be equally or even more significant. Deep soils exhibit distinct physicochemical characteristics, including SOC, total nitrogen, pH, and moisture levels, meaning it is very different to topsoil [20]. These differences affect microbial activity, metabolic processes, and community structure, potentially leading to divergent responses to environmental changes between microbial-derived carbon and deep soils. Climate factors indirectly influence the accumulation of microbial residues in deep soils by regulating plant inputs and microbial production [21]. This indicates that deep soils are also subject to climatic conditions, and even subtle climate fluctuations can result in substantial changes in soil carbon stocks. Studies have yielded conflicting findings regarding the contribution of microbial residue carbon to organic carbon at increasing soil depths, suggesting that the role of soil microbial residues in the stable SOC pool in deep soils is unclear [22,23]. Therefore, investigating the distribution of microbial residues in different soil layers and their contribution to organic carbon can help optimize soil

management and carbon sequestration strategies, providing essential insights for global carbon cycling and climate change research.

The Wuyi Mountains, located in China's central subtropical zone, have the world's largest intact subtropical, evergreen, and broad-leaved forest ecosystem at the same latitude. It covers the largest global belt and reaches a maximum altitude of 2158 m [24–26]. The region features different soil types, including red soil, yellow–red soil, yellow soil, and meadow soil, as well as various vegetation types, such as broad-leaved forests, coniferous forests, sub-alpine shrub forests, and meadows [24–26]. These different types of soil and vegetation exhibit distinct vertical distribution characteristics, which are based on the climate, soil type, and vegetation type, making the area an ideal site for studying the relationship among soil microbial residue carbon, altitude, and soil layers. This article focuses on the organic and mineral layers of soil at different elevations in the Wuyi Mountains, China, using amino sugars as microbial residue markers and employing redundancy analysis (RDA) and other methods to investigate the changes in microbial residue content and their contribution to SOC accumulation. The aim of this study was to clarify the following questions: (1) Are there differences in the contribution of microbial residue carbon to the SOC pool at different soil depths? (2) What are the main driving factors for microbial residue carbon in different soil layers in the Wuyi Mountains?

2. Materials and Methods

2.1. Study Location

The study area was situated at Wuyi Mountain National Nature Reserve (117°27′~117°51′ E, 27°33′~27°54′ N), which is located in the northwest of Fujian Province, China. The climate type is a mid-subtropical monsoon climate, with the average annual temperature ranging from 12 °C to 18 °C, the average relative humidity approximately 82%~85%, the average annual fog more than 100 d, and the average annual precipitation approximately 2000 mm. The area is characterized by high terrain and undulations, and its main peak is Huanggang Mountain, with a height of 2158 m. There are obvious differences among soil characteristics and vegetation communities in this area. From low to high soil types, there are mountain red soil, mountain yellow–red soil, mountain yellow soil, and alpine meadow soil. The vertical height continues to rise, and the distribution of the vertical band spectrum is also quite complete. From the foothills to the top of the mountain, the forest types are evergreen, broad-leaved forests; coniferous and broad-leaved forests; coniferous forests; sub-alpine dwarf forests; and alpine meadow forests [24–26]. The main types of vegetation in this area are *Phyllostachy edulis*; *Pinus massoniana* Lamb.; *Cunninghamia lanceolata* (Lamb.) Hook.; *Castanopisi carlesii* (Hemsl.) Hay.; *Cyclobalanopsi glauca* Thunb.; *and Calamagrostis brachytricha* (L.) Roth.

2.2. Sample Setting and Soil Sampling

Based on the literature and field surveys of Wuyi Mountain Nature Reserve, this study set up four altitude gradients ranging from 760 m to 2130 m (Figure 1). At each gradient, three plots of forest (projected area: 10 m × 10 m) were selected (Table 1, cited from [26]). Soil samples were collected in two parts, one for determining soil bulk density using a ring knife (5 cm in diameter and 5 cm in height) and the other for the determination of soil chemical properties using a soil corer (5 cm in diameter and 10 cm in depth). Three soil cores were collected and mixed as representative samples for each plot. A total of 15 non-ring knife and 15 ring knife soil samples were collected, with the non-ring knife soil samples air-dried and passed through a 2 mm sieve in the laboratory. The altitude, longitude and latitude of each plot were recorded using GPS (Magellan Explorist 610) (Magellan Corporation, City of Santa Clara, CA, USA).

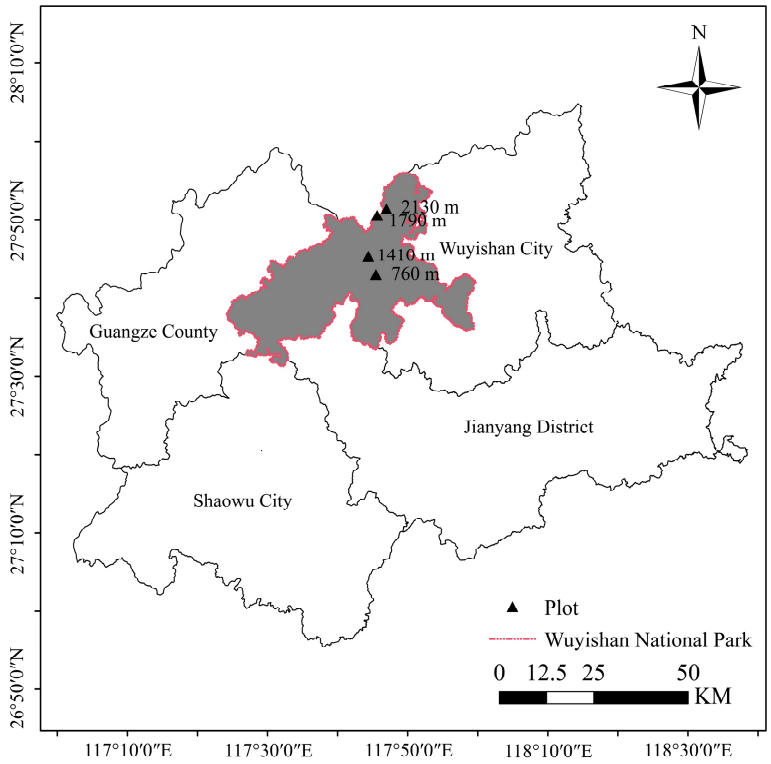

Figure 1. Locations of four plots along an elevational gradient in the Wuyishan National Park. The number next to the triangle represents the elevation (m).

Table 1. Basic information of sample plots.

ID	Altitude (m)	Number of Plots	Vegetation Type	Soil Type	Bulk Density ($g \cdot cm^{-3}$)	pH Value
1	760	3	Evergreen, broad-leaved forest	Mountain red soil	0.98 ± 0.11	3.83 ± 0.04
2	1410	3	Coniferous forest	Mountain yellow–red soil	0.65 ± 0.14	3.83 ± 0.04
3	1790	3	Sub-alpine dwarf forest	Mountain yellow soil	0.56 ± 0.03	3.71 ± 0.08
4	2130	3	Alpine meadow	Alpine meadow soil	0.44 ± 0.05	4.05 ± 0.08

Note: The soil bulk density and pH value in the table were all measured in the organic layer of soil.

2.3. Measurement of Soil Properties

The physical and chemical properties of soils determined in this study included the soil bulk density, pH, soil organic carbon and total nitrogen (TN). The soil bulk density was measured using the ring knife method [26], while the soil pH was determined using a pH meter in a 1:2.5 (soil and deionized water) suspension [27]. Soil organic carbon was determined using the potassium dichromate oxidation–external heating method [27], and TN was quantified using a CN element analyzer (Elementar Corporation, Hanau, Germany) [26].

2.4. Amino Sugar Analysis

The specific operation process of amino sugar extraction and determination was according to the literature [28]. Soil samples containing 0.4 mg of nitrogen were weighed and mixed with 10 mL of 6 M HCl in a hydrolysis flask, placed at 105 °C for 8 h, cooled to room temperature, and then filtered [12]. The residue was thoroughly dried using a rotary evaporator under vacuum at 52 °C, dissolved in water, and stored in glass vials at −18 °C. The extracted aminosaccharides were derivatized with o-phenylene terephthalaldehyde (OPA) and, finally, the aminosaccharides were detected by gas chromatography on an

HP-5 gas chromatography capillary column (30 m × 0.25 mm × 0.25 μm) (Agilent Technologies, Santa Clara, CA, USA) and quantified using a flame ionization detector (Agilent Technologies, Agilent 6890A, USA).

Due to the complex structure and diverse components of microbial residues, accurate quantification of their value remains challenging. However, microbial residue can be characterized by quantifying the amino sugar biomarker present in them. Currently, the most reliable method for measuring microbial residues in soil is through the quantification of amino sugars. The amino sugars that can be accurately measured in soil are mainly glucosamine (GluN), which is mainly derived from fungal cell wall, muramic acid (MurA), which is derived solely from bacterial cell walls, and aminogalactose, the source of which remains unclear.

The use of glucosamine and muramic acid enables the estimation of the carbon content of fungal residues and bacterial residues, respectively. This allows for the exploration of the respective roles of fungi and bacteria in soil organic carbon formation. The formula used to calculate the carbon content of microbial residues is as follows: microbial residue carbon content = fungal residue carbon content (Fungal-C) + bacterial residue carbon content (Bacterial-C), as follows:

$$\text{Fungal-C} = [(\text{GluN} - 2 \times \text{MurA}) \times 179.2 \times 9] \quad (1)$$

$$\text{Bacterial-C} = \text{MurA} \times 45 \quad (2)$$

2.5. Statistical Analysis

To analyze the variation in soil properties at different altitudes, a single-factor analysis of variance (ANOVA) was conducted in R, using the AVO function. Multiple comparisons were performed using Duncan's method to determine the significant level of difference based on the "agricolae" package. Redundancy analysis (RDA) was performed using CANOCO 5.0.

3. Results

3.1. Variations in the Amino Sugar Content of the Soil Organic Matter Layer and the Mineral Layer across the Altitude Gradients

A comparative analysis of the amino sugars in the organic matter layer (0–10 cm) and the mineral layer (30–40 cm) at different altitudes in the study area (Figure 2) revealed that both the altitude and the soil layer significantly influenced the contents of four kinds of amino sugars: galactose amino (GalN), glucosamine (GluN), mannose-amine (ManN), and cytosolic acid (MurN). The content of all four types of amino sugars showed an increasing trend with altitude. Additionally, the contents of the amino sugars were significantly higher than that in the soil mineral layer. GluN accounted for the largest proportion of amino sugars in the soil, while MurN accounted for the least.

We observed that the amino sugar content was significantly different among the soil layers at a low altitude (760 m) ($p > 0.05$: Figure 2). The amino sugar content also showed significant differences between the organic and mineral layers at altitudes between 1410 and 1790 m ($p < 0.05$: Figure 2). At a high altitude (2130 m), the contents of GluN and ManN were significantly different ($p < 0.05$: Figure 2b,d); however, there was no significant difference in the MurN and GalN content. In the organic layer, the contents of MurN, GalN, and GluN exhibited a significant increase at altitudes between 1790 m and 2130 m ($p < 0.05$: Figure 2a,c,d). In contrast, the contents of Mann, GalN, and GluN significantly increased at altitudes between 760 m and 1410 m ($p < 0.05$: Figure 2b–d). In the mineral layer, the amino sugar content remained relatively stable at altitudes between 760 m and 1410 m ($p > 0.05$: Figure 2), after which it increased significantly ($p < 0.05$: Figure 2).

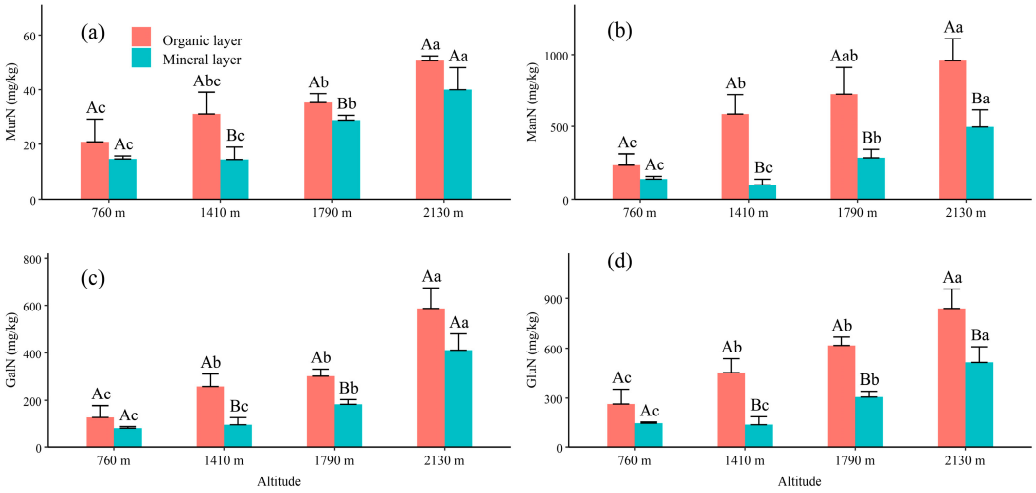

Figure 2. Variation in amino sugar (cytosolic acid (MurN, (**a**)); mannose-amine (ManN, (**b**); galactose amino (GalN, (**c**), and glucosamine (GluN, (**d**))) contents in soil organic matter layer and mineral layer at different altitudes. Different uppercase letters indicate significant differences ($p < 0.05$) between the organic matter layer (0–10 cm) and the mineral layer (30–40 cm). Different lowercase letters indicate significant differences ($p < 0.05$) between altitudes. Bars represent mean ± SD. $p < 0.05$.

3.2. Variations in Microbial Residue Carbon in the Organic and Mineral Layers across the Altitude Gradients

For the same soil layer, the trends in the contents of fungal, bacterial, and overall microbial carbon residues (Figure 3) according to altitude were similar to those of the amino sugar content (Figure 2), which increased with altitude. In the soil organic matter layer, significant differences were observed in the contents of the fungal residues at different altitudes ($p < 0.05$: Figure 3a), whereas significant differences in the contents of microbial and bacterial residues were only observed between the altitudes of 1790 m and 2130 m ($p < 0.05$: Figure 3b,c). In the soil mineral layer, significant variations in the contents of fungal, bacterial, and microbial residues were observed between the altitudes of 1410 m and 2130 m ($p < 0.05$: Figure 3a–c).

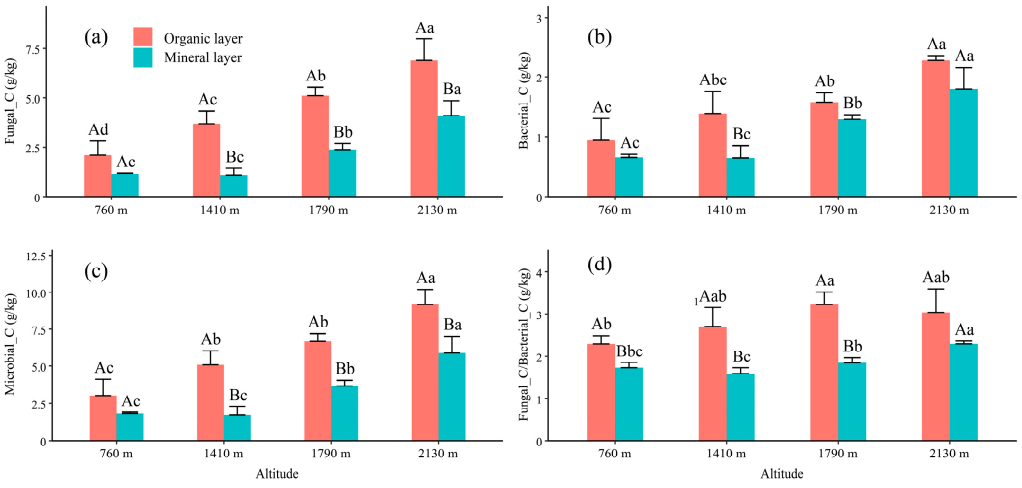

Figure 3. Variation in microbial residue carbon content (Fungal-C, (**a**); Bacterial-C, (**b**); Microbial-C, (**c**), and Fungal-C/Bacterial-C, (**d**)) in the soil organic matter layer and the mineral layer at different altitudes. Different uppercase letters indicate significant differences ($p < 0.05$) between the organic matter layer (0–10 cm) and the mineral layer (30–40 cm). Different lowercase letters indicate significant differences ($p < 0.05$) between altitudes. Bars represent mean ± SD. $p < 0.05$.

At the same altitude, the trend of fungal residue carbon, bacterial residue carbon, and microbial residue carbon (Figure 3) varied in a similar way to the amino sugar (Figure 2) content, indicating that the residual carbon content in the soil organic layer was higher than that in the soil mineral layer. Furthermore, significant differences in the carbon content of the fungi and microbial residues were observed between the two soil layers at altitudes between 1410 m and 2130 m ($p < 0.05$: Figure 3a,c); however, the carbon content of the bacterial residues was only significantly different between the two soil layers at altitudes between 1410 m and 1790 m ($p < 0.05$: Figure 3b).

When comparing the contents of fungal (Figure 3a) and bacterial (Figure 3b) residue carbon, it was found that the content of the fungal residue carbon in the different soil layers and at different altitudes was higher than that of the bacterial residue carbon. However, the proportion of fungal and bacterial residue carbon in the microbial residue carbon changed between the organic layer and the mineral layer: the proportion of fungal residue carbon (Figure 3a) decreased (from 74.17% to 66.34% on average), whereas the proportion of bacterial residue carbon (Figure 3) increased (25.83% to 33.66%). In addition, it was observed that the ratio of fungal-to-bacterial residues fluctuated according to altitude in the soil organic layer, whereas it remained relatively stable in the mineral layer (Figure 3d). There was a significant difference between the altitudes of 1410 m and 2130 m ($p < 0.05$: Figure 3d). Furthermore, there was a decreasing trend in the ratio of fungal-to-bacterial residue carbon between the organic layer and the mineral layer, with a significant difference in the fungal and bacterial residue carbon ratio between the organic and mineral layers at altitudes between 760 m and 1790 m ($p < 0.05$: Figure 3d).

3.3. Variations in Microbial Residue Carbon and SOC Inorganic and Mineral Layers across Altitude Gradients

The contribution of fungal, bacterial, and microbial residue carbon to SOC (Figure 4) across different altitudes and soil layers showed significant differences in terms of the contribution of the amino sugars (Figure 2) and the microbial residue carbon (Figure 3). For the same soil layer, the contribution of fungal, bacterial, and microbial residue carbon to SOC did not exhibit an obvious trend in relation to altitude (Figure 4). At the same altitude, the contribution of soil microbial, fungal, and bacterial residue carbon to SOC in the organic layer (microbial 8.24%; fungal 6.03%; bacterial 2.21%) was lower than that in the mineral layer (microbial 12.45%; fungal 8.07%; bacterial 4.38%) (Figure 4). Except for the low-altitude area (760 m), the contribution of the fungal, bacterial, and microbial residue carbon to SOC in the organic and mineral layers was significantly different at other altitudes (1410–2130 m) ($p < 0.05$) (Figure 4).

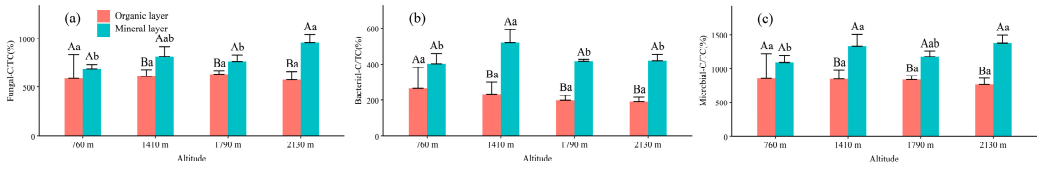

Figure 4. Contribution rate of microbial residue carbon to SOC (Fungal-C/TC, (**a**); Bacterial-C/TC, (**b**) and Microbial-C/TC, (**c**)) in the soil organic matter layer and the mineral layer at different altitudes. Different uppercase letters indicate significant differences ($p < 0.05$) between the organic matter layer (0–10 cm) and the mineral layer (30–40 cm). Different lowercase letters indicate significant differences ($p < 0.05$) between altitudes. Bars represent mean ± SD. $p < 0.05$.

3.4. Relationships among Fungal Residue Carbon, Bacterial Residue Carbon, Microbial Residue Carbon, and Soil Physicochemical Properties

In this study, we used a generalized linear model to assess the correlation between microbial residue carbon (including fungal and bacterial residues) and the soils' physicochemical properties. Our aim was to investigate the relative contributions of various environmental factors to the variations in the microbial residue carbon at different soil depths.

It showed that the fungal residue carbon, bacterial residue carbon, and microbial residue carbon at different soil depths had a significant positive correlation with the elevation or TC ($p < 0.01$; Figure 5, Table 2). They were also significantly correlated with C/N ($p < 0.05$; Table 2) at each soil layer. However, fungal residue carbon, bacterial residue carbon, and microbial residue carbon exhibited a significant negative correlation with BD) ($p < 0.05$; Figure 5, Table 2) at each soil layer.

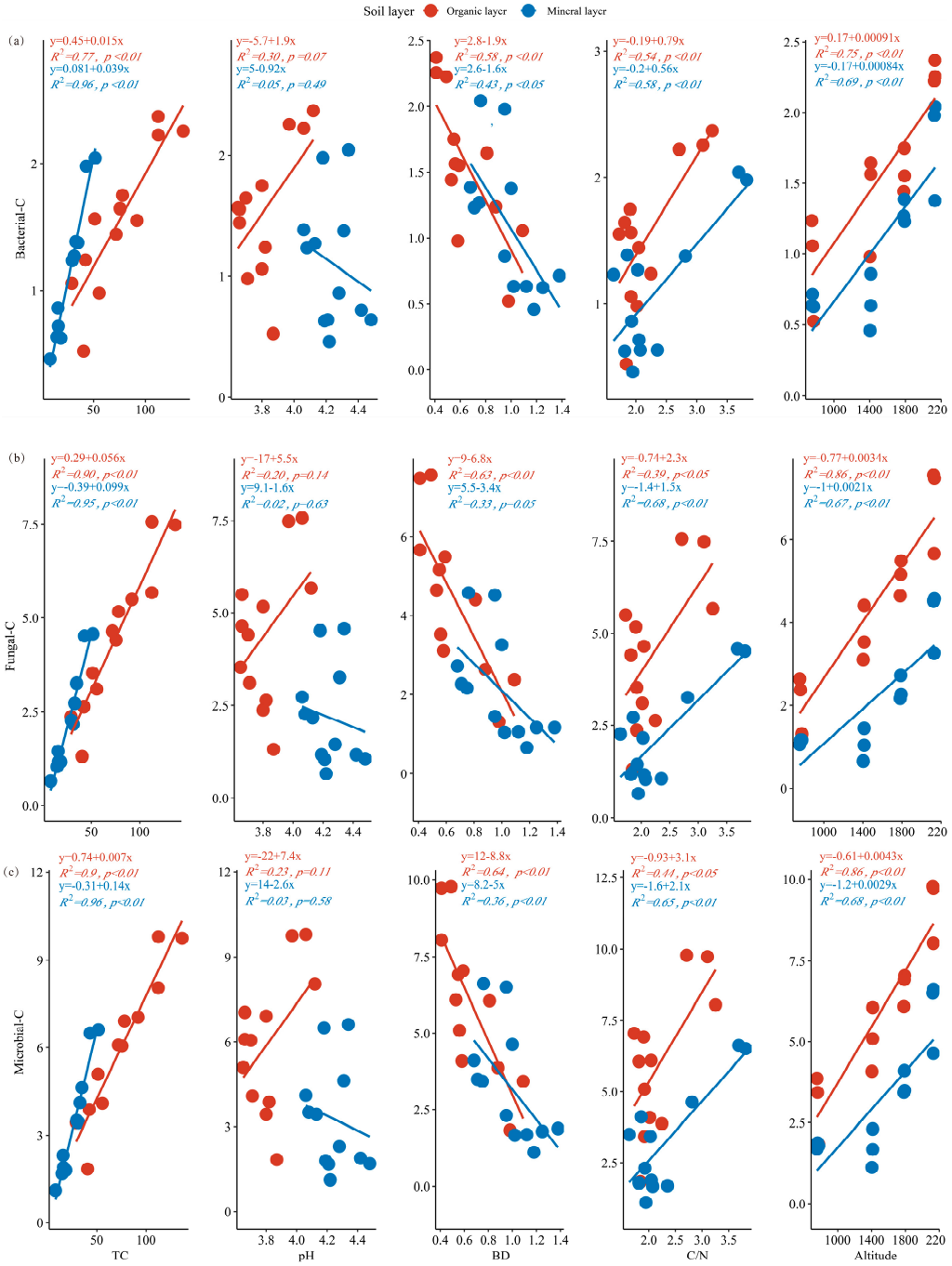

Figure 5. Relationship among bacterial (**a**), fungal (**b**), and microbial (**c**) dead residue carbon and the soils' physical and chemical properties.

Table 2. Ranking of the explanatory power of environmental factors and significance test results.

Soil Layer	Environmental Variables	Rank Ordering of Explanatory Power	Explanation % of Environmental Variables	F	*p*
Organic layer	Altitude	1	85.8%	60.2	0.002
	TC	2	5.7%	6.0	0.038
	BD	3	0.7%	0.7	0.448
	C/N	4	0.2%	0.2	0.724
	pH	5	0.2%	0.2	0.748
Mineral layer	Altitude	1	67.9%	21.2	0.004
	TC	2	28.0%	61.3	0.002
	C/N	3	2.3%	9.9	0.008
	BD	4	0.1%	0.2	0.776

The results of the RDA analysis indicated that the first ordination axis explained the variation in the soil microbial residue carbon in both soil layers, with a total explanatory rate of 92.59% and 98.2% (Figure 6) in the soil organic matter and mineral layers, respectively. The Monte Carlo permutation tests confirmed the significance of the first two ordination axes in both soil layers ($p < 0.05$: Table 2), indicating the high reliability of the results and the ability of environmental factors to explain the variation in soil microbial residue carbon. Forward selection was used to rank the environmental factors that influence changes in the fungal residue carbon, bacterial residue carbon, and microbial residue carbon contents. Monte Carlo permutation tests were performed for significance testing. In the soil organic layer, elevation was found to be the most influential environmental factor on the changes in all three types of residue carbon contents, with an explanatory power of 85.8%. This was followed by TC, BD, C/N, and pH. The effect of elevation ($p < 0.01$: Table 2) on the changes in all three types of residue carbon contents was significant. The TC also had a significant effect ($p < 0.05$: Table 2). In the soil mineral layer, elevation was, again, found to be the most influential environmental factor on the changes in all three types of residue carbon content, with an explanatory power of 67.9%. This was followed by the TC, C/N, and BD. The elevation, TC, and C/N had significant effects ($p < 0.01$: Table 2) on the changes in all three types of residue carbon contents, while the BD did not reach significance ($p > 0.05$: Table 2). In summary, the results suggest that elevation is the most important environmental factor affecting changes in the soil microbial residue carbon content, with the TC also playing a significant role.

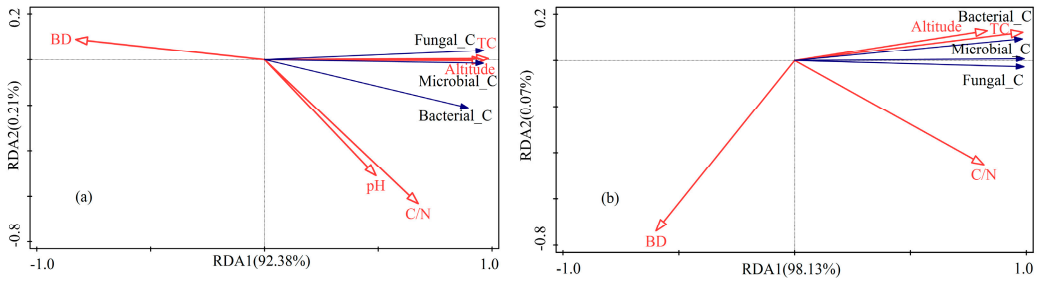

Figure 6. The relationship among microbial residue-derived carbon (bacterial and fungal) and environmental variables in organic (**a**) and mineral (**b**) soil layers, according to redundancy analysis (RDA). TC—total carbon; BD—bulk density; C/N—ratio of carbon to nitrogen; Microbial-C—microbial residue-derived carbon; Bacterial-C—bacterial residue-derived carbon; and Fungal-C—fungal residue-derived carbon.

4. Discussion

4.1. Relationship between Microbial Residue Distribution and Environmental Factors

Our study demonstrated that elevation significantly influences the accumulation of microbial residue carbon. As the elevation increased, the carbon content of microbial

residue increased in both soil layers, which was consistent with previous research findings [29]. The accumulation of microbial residue carbon in soil primarily depends on the balance between microbial formation and decomposition [30]. Altitude changes can influence climatic conditions, such as temperature and precipitation, which, in turn, affect the accumulation of microbial residues in the soil. In the Wuyishan National Park, there is a significant variation in altitude. In the lower areas (760 m), the higher temperature leads to a faster turnover rate of microbial biomass, which hinders the accumulation of microbial residues [31]. Conversely, in the higher areas (2130 m), the lower temperature favors the accumulation of carbon content in microbial residues [32]. Furthermore, the predominant vegetation type in the higher areas is alpine meadow, characterized by well-developed root systems capable of producing more root exudates for microbial utilization [33]. This promotes the growth of soil micro-organisms, resulting in higher microbial biomass, which, in turn, facilitates the accumulation of microbial residues. The above research highlights that variations in climatic conditions (temperature and humidity) and vegetation types due to the altitude gradient in the Wuyishan National Park are significant factors influencing the formation and accumulation of microbial residues.

Our study illustrated that the carbon content of microbial residues in the organic layers of soil at different altitudes is higher than that in the mineral layers. There are several potential reasons for this phenomenon. First, it may be attributed to the input and quality of litter, which has a significant impact on microbial processes. The input of fresh litter provides abundantly available carbon sources and nutrients for micro-organisms in the topsoil, promoting their growth and development [12] and enhancing their activity. As a result, soil micro-organisms in the topsoil exhibit a much higher nutrient and available carbon absorption rate than those in the subsoil, making the topsoil a hotspot for microbial activity [34]. This dynamic indicates that the organic matter layer experiences a higher microbial growth and turnover rate [35], which is favorable for the formation of microbial residues and the sequestration of organic carbon. Furthermore, the low C/N ratio of fresh litter, similar to the C/N ratio of micro-organisms, makes it a high-quality substrate that stimulates microbial turnover and accelerates the accumulation of microbial residues [36]. These findings underscore the crucial role of litter input in the accumulation of microbial residues in the organic layer of our study area. However, vegetation types and distribution vary with altitude, impacting litter input in terms of quantity and quality, thereby directly or indirectly influencing the accumulation of microbial residues. Therefore, future research should take into consideration the impact of litter variations on the accumulation of microbial residues. Second, although the mineral layer of the soil also receives carbon from root systems and rhizosphere deposits, as well as soluble carbon from litter and the organic layer, the anaerobic conditions and reduced input of plant-derived carbon in the mineral layer hinder microbial activity and metabolism [2], resulting in limited microbial growth efficiency and reproduction. Under the conditions of nutrient deficiency and substrate limitation in the mineral layer of the soil, microbial residues are preferentially utilized as carbon or nitrogen sources to support microbial reproduction and growth [29], impeding the formation of microbial residues in the soil. Consequently, the accumulation of microbial residue carbon decreases as the soil depth increases. However, studies have indicated that in subtropical regions, abundant rainfall can cause the leaching of dissolved organic matter (DOM), thereby providing a substantial amount of carbon sources and nutrients to deep soil micro-organisms, promoting their growth and development. Simultaneously, inadequate drainage in deep soil leads to waterlogging [35,37], which inhibits soil respiration and fosters the accumulation of deep microbial residues [38]. This finding diverges from our research results. Therefore, when considering that precipitation may be a critical regulating factor in the accumulation of deep soil microbial residues, further investigations should be undertaken to examine the influence of rainfall on the trend of microbial residue carbon content's variation in line with soil depth.

4.2. The Contribution and Significance of Microbial Residue Carbon to Soil Carbon Pools

Our study illustrated that as the soil depth increases, the contribution of fungal residue carbon, bacterial residue carbon, and microbial residue carbon to soil organic carbon also increases, which aligns with the findings of Wang and Shen et al. [23,39]. This indicates that the contribution of microbial residue carbon to organic carbon is influenced by changes in the soil depth. One perspective suggests that this may be associated with the input of plant litter. A significant amount of plant litter is primarily input into the soil's organic matter layer, contributing to the organic carbon pool [40]. However, as the soil depth increases, the input of carbon from plant sources decreases, resulting in an increased contribution of microbial residue carbon to organic carbon [30,41]. Additionally, another viewpoint proposes that this might be linked to the stability of microbial residues themselves. Despite the organic matter layer of the soil providing abundant nutrients for microbial growth and reproduction, thereby promoting the formation of more microbial residues [34,42,43], microbial residues themselves are not entirely stable and may be utilized as a nutrient source by other micro-organisms [44]. Consequently, when the organic matter layer acts as a hotspot for microbial residues, the utilization of microbial residues is relatively high, resulting in a relatively low contribution to organic carbon. Moreover, this could be attributed to the stabilization mechanism of microbial residues. Recently, Zhu et al. [45] introduced the "Mineral Carbon Pump" (MnCP) model, which highlighted the ability of soil minerals to enhance the stability of organic carbon. Within the soil's mineral layer, the carbon of microbial residues combines with soil minerals to form stable organic–mineral associations [46], exhibiting robust stability. This, in turn, strengthens the long-term sequestration capacity of microbial residues in the mineral layer of the soil, reduces decomposition rates, and enhances their contribution to organic carbon [47].

Our research has revealed a gradual decline in the ratio of fungal residue carbon to bacterial residue carbon from the organic layer to the mineral layer. This trend may be attributed to a relative increase in bacterial-derived carbon content and a corresponding decrease in fungal-derived carbon content. Shao et al. [48] conducted a study suggesting that optimal soil moisture, salinity, and nutrient levels promote fungal growth and lead to the accumulation of fungal residues, whereas bacteria demonstrate greater resilience in harsh environmental conditions. As a result, we postulate that the accumulation of fungal and bacterial residues is likely influenced by the varying soil environment as we transition across different soil layers.

In the organic layer, favorable environmental conditions enhance microbial activity, facilitating the utilization of soil organic carbon, including carbon from microbial sources. In comparison to fungal residues, bacterial residues, being less stable, are more easily decomposed and utilized [2], which inhibits the accumulation of bacterial residues. Additionally, fungi, as aerobic organisms, primarily utilize fresh litter as their preferred carbon source [49], leading to more pronounced competition with bacteria in the organic layer. As the soil depth increases, the limited supply of oxygen restricts fungal growth and metabolic activities, resulting in a reduction in fungal residue accumulation. Conversely, many bacteria can survive and remain active under anaerobic conditions in deeper soil layers, thereby favoring the accumulation of bacterial residues [50]. Moreover, our findings indicate that fungi exhibit a preference for absorbing and utilizing carbon from plant sources, with their carbon utilization relying significantly on the supply of plant-derived substrates [51]. On the other hand, bacteria are better adapted to degrade deceased micro-organisms. As soil depth increases, the decrease in plant litter and root exudates implies a gradual reduction in plant-derived carbon input [52], making microbial-derived carbon the primary source of soil organic carbon. However, in the mineral layer, the decrease in plant-derived carbon input leads to reduced carbon availability for fungi, thereby limiting the growth and development of symbiotic fungi and, consequently, restricting the accumulation of fungal residues in deeper soil layers. Consequently, we propose that when soil layers shift from the organic layer to the mineral layer, the competitive advantage of fungi weakens, whereas bacteria gain dominance. This transition may potentially cause a shift in the soil

microbial community from fungi to bacteria, thereby favoring the accumulation of bacterial residues over fungal residues. Moreover, our findings indicated that fungal residue carbon contributes more significantly to SOC than bacterial residue carbon in both soil layers, suggesting that the carbon derived from fungi predominates in the accumulation of SOC. This observation may be attributed to the distinctive survival strategies employed by fungi and bacteria. Within soil ecosystems, fungi exhibit a greater capacity for assimilating and utilizing recalcitrant substances compared to bacteria [53]. Fungi often display higher rates of carbon source utilization and possess the capability to accumulate greater quantities of residues in terms of C/N and carbon source utilization [54]. On the other hand, it is widely believed that, when compared to fungal residues, bacterial residues are more easily decomposed and have faster turnover [55], which may be attributed to the differences in the nature and composition of their cell walls. Fungal cell walls contain relatively higher levels of recalcitrant substances, such as melanin and chitin, whereas bacterial cell walls mainly consist of peptidoglycan, which is more easily decomposed and utilized [53,56]. Therefore, when compared to fungal residues, bacterial residues are more susceptible to decomposition, and their rapid turnover hinders their long-term sequestration in the soil, thereby reducing their contribution to soil organic carbon.

5. Conclusions

Microbes play a crucial role as important components in soil, and their remnants, referred to as microbial residues, have significant implications for the formation and stability of soil organic carbon pools. This study aimed to quantify the distribution patterns of microbial residues in different soil layers along an altitude gradient and their relative contribution to SOC accumulation. Our findings revealed that the microbial residue carbon content was higher in the organic layer when compared to the mineral layer, and a positive correlation was observed between the soil C/N ratio and microbial residue carbon accumulation. Moreover, as soil depth increased, the contributions of fungal residue carbon, bacterial residue carbon, and total microbial residue carbon to SOC showed a gradual increase, while the ratio of fungal residue carbon to bacterial residue carbon decreased. These results highlight the significance of soil layer variations as the main influencing factor on the accumulation of soil microbial residues. This contributes to a deeper understanding of the role of deep microbial residues in soil carbon stocks, aiding in the comprehension of soil carbon sequestration mechanisms and predicting soil carbon cycling. In future research, when considering potential environmental changes (e.g., seasonal rainfall and climate warming), it is essential to investigate how climate factors impact the stability of deep soil microbial-derived carbon, as this will be crucial in accurately predicting the response of deep SOC to climate change.

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