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Altitudinal patterns of soil and microbial C:N:P stoichiometry in subtropical forests in Daming Mountain, South China

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Introduction: Altitude-induced variations in hydrothermal conditions and vegetation affect the carbon (C), nitrogen (N), and phosphorus (P) contents in both soil and microbial biomass. However, the specific patterns of changes in these nutrients and their stoichiometry in response to altitudinal changes remain unclear.

Methods: In this study, we analyzed the altitudinal patterns of soil and microbial biomass C:N:P stoichiometry across three soil layers (0−20, 20−40, and 40−60 cm) in the subtropical mountain ecosystems on Daming Mountain, South China.

Results: Our results revealed that soil C content and C:N ratio in the 0−20 cm layer initially increased and then decreased with increasing altitude. Meanwhile, soil P content in the 40−60 cm layer decreased. Soil microbial biomass P content initially decreased and then increased with altitude across all soil layers, whereas soil microbial biomass C:P and N:P ratios exhibited opposite trends. For soil and microbial biomass C:P and N:P ratios along the altitudinal gradient, soil microbial growth was mainly restricted by P, with this limitation being more pronounced at mid-to-low altitudes. Soil microbial biomass C, N, and P contents were positively correlated with soil C, N, and P contents and their ratios, available N (AN), available P (AP), and soil water content (SWC), but negatively correlated with soil bulk density, soil pH and soil temperature. In contrast, microbial biomass C, N, and P stoichiometric ratios exhibited the opposite or non-significant relationships with these factors. Notably, AN, AP, and SWC were the dominant factors affecting soil microbial biomass C:N:P stoichiometry.

Discussion: These findings contribute to the understanding of soil nutrient stoichiometry and their responses to environmental changes in subtropical mountain ecosystems.

KEYWORDS

altitude, nutrient limitation, soil microbial biomass, ecological stoichiometry, Daming Mountain

1 Introduction

Ecological stoichiometry focuses on the dynamic balance of energy and multiple chemical elements within ecosystems (Elser et al., 2000a; Elser et al., 2000b). It reveals how organisms respond to external resources and the mechanisms underlying nutrient supply and balance in ecological processes. This is primarily achieved by scaling up carbon (C), nitrogen (N), and phosphorus (P) (Koerselman and Meuleman, 1996; Wang et al., 2018), which are the most essential elements in living organisms. The ecological stoichiometry of these elements can reflect nutrient cycling and coupling relationships across different components (Hobbie et al., 2002; Schindler, 2003). Soil and microorganisms play crucial roles in biogeochemical cycles (Li et al., 2021). Soil C, N, and P contents are the nutrient bases for plant growth. Their stoichiometric ratios are key indicators affecting soil organic matter mineralization and the effectiveness of soil microbial biomass (Paul, 2007; Qiao et al., 2020; Wang et al., 2021). Moreover, soil microorganisms act as decomposers of plant and soil nutrients. Their biomass C, N, and P contents typically refer to the total C, N, and P contents in microorganisms smaller than 5,000 μm^3 (Brookes, 2001). Soil microbial biomass can reflect soil quality changes, influencing the cycles of soil materials and the energy flows driven by microorganisms (Falkowski et al., 2008; Gao et al., 2022). Therefore, the stoichiometric relationships between soil nutrients and microbial biomass can effectively reflect the structure and function of biogeochemical cycles in soil ecosystems (Li et al., 2012).

Mountain ecosystems have integral ecological processes due to their highly heterogeneous environments determined by climate and topography (Christmann and Menor, 2021; Zhang et al., 2021; Nandy et al., 2022; Zhao et al., 2025). In particular, altitude is a key topographic factor that has received considerable attention in research on responses to environmental changes (Beniston, 2003; Jiang et al., 2019; Hou et al., 2021). Environmental shifts, including temperature, precipitation, and light at different altitudes, exert direct or indirect impacts on the distribution of soil nutrients and microbial biomass by regulating soil physicochemical properties (Körner, 2007; Rahbek et al., 2019; He et al., 2020). Soil and microbial biomass ecological stoichiometry have been widely studied across large-scale latitude and longitude patterns, revealing general biogeographic patterns (Pan et al., 2021; Gao et al., 2022; Wan et al., 2023; Feng et al., 2024). However, variations in soil and microbial biomass stoichiometry along altitudinal gradients remain unclear, likely due to differences in geographical location, altitude range, and vegetation types (Chang et al., 2016; He et al., 2016; Liu et al., 2021; Xiong et al., 2022; Jia et al., 2023; Tong et al., 2023; Zhang et al., 2023; Zhu et al., 2024). Some studies have demonstrated that soil and microbial biomass C, N, and P contents increase with rising altitude (Chang et al., 2016; Liu et al., 2021; Xiong et al., 2022; Jia et al., 2023). However, in other studies, the opposite trend was observed in soil C, N, and P stoichiometric ratios (Tong et al., 2023), as well as in microbial biomass C and P contents (Zhang et al., 2023). In addition, non-linear relationships have been detected in the altitudinal patterns of soil and microbial biomass stoichiometry (He et al., 2016; Zhu et al., 2024). For example, soil and microbial biomass P content initially decreased and then increased, while the N:P ratio exhibited the opposite trend with increasing altitude on

Dinghu Mountain (He et al., 2016) and Wuyi Mountain (Zhu et al., 2024). Therefore, further studies are needed to better understand the general patterns of soil and microbial biomass stoichiometry along altitudinal gradients and identify the important factors influencing these patterns.

To date, most studies on the altitudinal patterns of soil and microbial biomass C, N, and P stoichiometry have primarily focused on the topsoil (He et al., 2016; Chen et al., 2024; Zhu et al., 2024), with relatively few studies on the subsoil (Zuo et al., 2021; Huang et al., 2023; Wu et al., 2024). Soil less than 20 cm in depth is usually regarded as topsoil. The subsoil, which lies below 20 cm in depth, stores more than 50% of the total global soil C storage (Rumpel and Kögel-Knabner, 2011). The significantly different soil environment conditions—such as temperature, moisture, porosity, and pH—in the topsoil and subsoil lead to variations in soil nutrients and microbial biomass (Jobbágy and Jackson, 2000; Chen et al., 2022). Soil nutrients and microbial biomass in different soil layers may respond differently to altitude. In the topsoil, soil P content increases with increasing altitude, while soil N content increases in the subsoil (Wu et al., 2024). In contrast, microorganisms remain relatively stable at different altitudes owing to low subsoil nutrient availability (Zuo et al., 2021). However, some studies have indicated consistent responses of soil and microbial biomass nutrients to altitude across different soil layers (Zhao et al., 2019; Huang et al., 2023). Although previous studies have elucidated the responses of soil nutrients and microbial biomass to altitude in different soil layers, research focusing on subtropical mountain ecosystems remains limited. Therefore, using an altitudinal gradient to examine soil nutrients and microbial biomass responses to environmental changes while considering soil layer variations can provide a more comprehensive understanding of nutrient dynamics and ecosystem functioning in subtropical mountain ecosystems.

Daming Mountain has the typical monsoon evergreen broad-leaved forests found in southern China. These forests are relatively well-preserved, with high plant diversity and characteristic vertical zonation (Li J. L. et al., 2023; Li Y. F. et al., 2023). Previous studies have explored soil properties along the altitudinal gradient on this mountain. For example, Zhao et al. (2013) found that soil organic matter increased with altitude across different soil layers (0–20, 20–40, and 40–60 cm). In contrast, total N and P contents exhibited a pattern of initial decrease followed by an increase in the middle and lower soil layers. This pattern was mainly attributed to variations in vegetation types, temperature, and precipitation at different altitudes. However, research on the stoichiometry of C, N, and P in microbial biomass across soil layers, as well as their relationships to soil properties, remains limited.

Therefore, in the present study, we established forest plots along altitudinal gradients on Daming Mountain and analyzed the C, N, and P stoichiometric characteristics of soil and microbial biomass across altitudinal gradients in different soil layers. We aimed to (1) examine the altitudinal patterns of C, N, and P contents and their ratios in soil and microbial biomass across different soil layers and (2) identify the dominant factors influencing the C, N, and P stoichiometric characteristics of microbial biomass. The findings will enhance our understanding of the mechanisms and ecological implications of soil and microbial biomass C, N, and P stoichiometric characteristics responses to changes in altitude. This study also offers a theoretical basis for determining the soil C, N, and

FIGURE 1
The location of the sampling sites on Daming Mountain, Guangxi, South China.
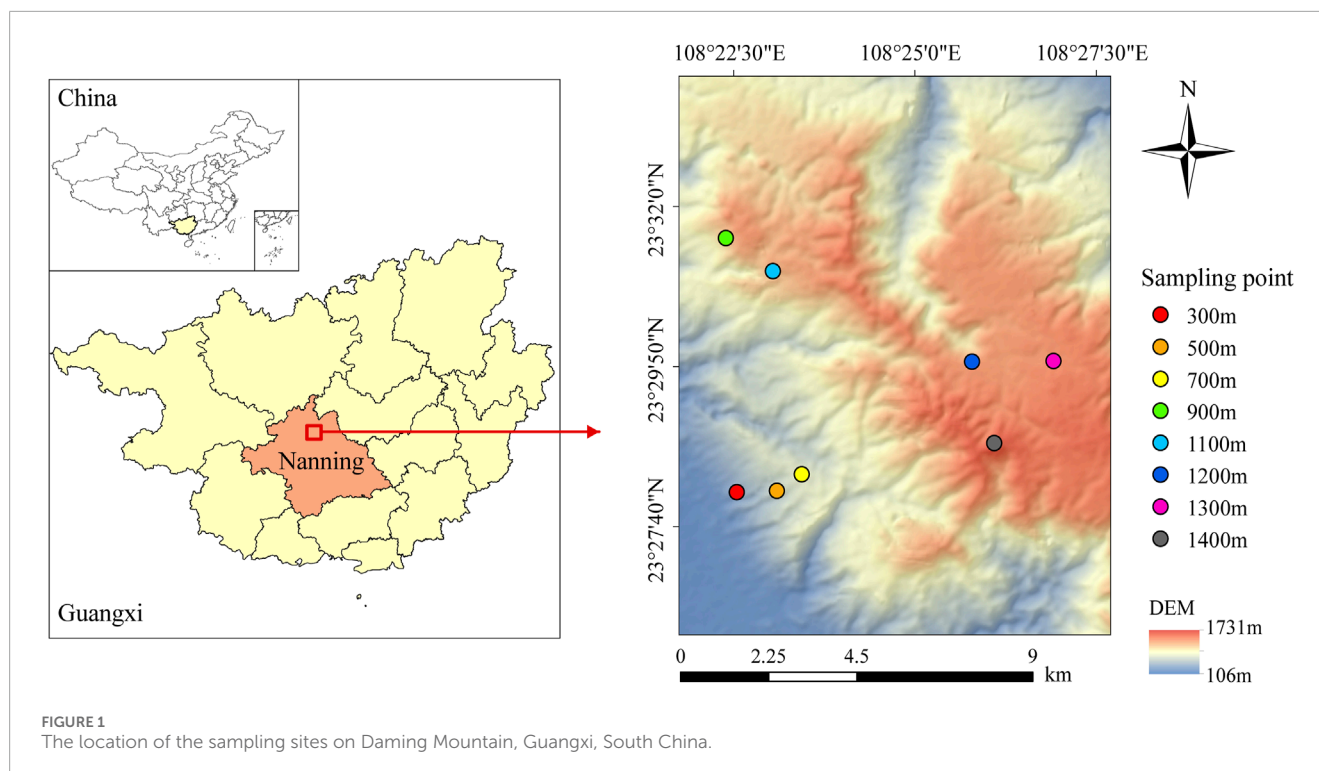
P cycling processes in subtropical mountain ecosystems and their regulatory mechanisms.

2 Materials and methods

2.1 Study area

The study area was located in Daming Mountain, Nanning City, Guangxi, South China (23°27′–23°32′N, 108°22′–108°27′E) (Figure 1). The Tropic of Cancer crosses the mountain, indicating that the area is located in a subtropical monsoon climate zone. The region has an annual average temperature of 15.1°C, with a maximum temperature of 21.9°C and a minimum temperature of 5.8°C. The annual average precipitation is 2,630.3 mm, with approximately 50% of the total occurring from June to August (Hu et al., 2025). The average annual sunshine duration ranges from 1,295.4 to 1,665.1 h, and the annual average relative humidity is 90%. The altitude ranges from 115 to 1,760 m. The zonal vegetation is characterized by south subtropical monsoon evergreen broad-leaved forests, with dominant species including *Clethra bodinieri*, *Engelhardia roxburghiana*, *Rhodoleia championii*, *Symplocos lancifolia*, and *Machilus thunbergii*. The soil types are predominantly red and yellow soil, with the soil pH between 3.9 and 4.7 (Li J. L. et al., 2023; Li Y. F. et al., 2023; Hu et al., 2025).

2.2 Sample collection and analysis

In July 2023, eight altitudinal gradients were selected from 300 to 1,400 m (Figure 1), with the location, slope aspect, slope degree,

forest types, soil types, and dominant tree taxa from each altitude summarized in Table 1. At each altitude, three 20 × 20 m plots were established, with a minimum distance of 100 m between plots, totaling 24 plots. Soil samples were collected from each plot using the five-point method from three layers: 0–20 cm (topsoil), 20–40 cm (sub-topsoil), and 40–60 cm (subsoil) in depth. Soil samples from the same layer were mixed uniformly to form a single composite sample, comprising a total of 72 samples (24 plots × 3 soil layers). The collected soil samples were transported back to the laboratory in a 4°C cooler. Plant roots and stones were removed, and the samples were sieved through a 2 mm mesh. Each soil layer sample was divided into two portions. One portion (fresh soil) was used for measuring the microbial biomass C, N, and P contents, while the other portion was air-dried for determining soil C, N, and P contents and physicochemical properties. Intact soil samples were collected from each plot using a ring cutter to measure soil water content (SWC) and bulk density (SBD). In addition, soil moisture and temperature data loggers were installed in each plot to monitor soil temperature (ST).

ST was measured at a soil depth of 8 cm using TMS-3 data loggers (TOMST s.r.o., Prague, Czech Republic) (Wild et al., 2019). SWC was determined using the oven-drying method, while SBD was measured using the ring knife method. Soil pH was measured with a pH meter (soil:water ratio of 1:2.5) (Bao, 2000). Soil organic carbon (SOC) content was measured using the acidified dichromate ($K_2Cr_2O_7$-H_2SO_4) oxidation-external heating method (Nelson and Sommers, 1982). Soil total nitrogen (STN) content was determined using the micro-Kjeldahl digestion method (Bremner, 1996). Available nitrogen (AN) content was extracted with 2 M KCl solution and then measured using a continuous flow analyzer (San++System, Skalar, Holland) (Keeney and Nelson,

TABLE 1 Basic information of each altitude.

Altitudes (m asl.)	Plot	Latitude	Longitude	Slope aspect	Slope degree (°)	Forest types	Soil types	Dominant species
300	DMS01	23°28′03.35″	108°22′38.13″	South	19	Monsoon evergreen broadleaf forest	Mountain latosolic red soil	*Lindera metcalfiana, Microdesmis caseariifolia* and *Sloanea leptocarpa*
	DMS02	23°28′08.03″	108°22′32.70″	South	27			
	DMS03	23°28′02.10″	108°22′26.35″	Southeast	28			
500	DMS04	23°28′09.13″	108°23′05.95″	West	45	Monsoon evergreen broadleaf forest	Mountain latosolic red soil	*Clethra bodinieri, Engelhardia roxburghiana* and *Symplocos lancifolia*
	DMS05	23°28′10.14″	108°23′04.74″	South	25			
	DMS06	23°28′09.57″	108°23′01.75″	West	15			
700	DMS07	23°28′24.04″	108°23′27.16″	North	12	Montane evergreen broadleaf forest	Mountain red soil	*Rhodoleia championii, Rhododendron moulmainense* and *Clethra bodinieri*
	DMS08	23°28′22.50″	108°23′26.50″	Northwest	20			
	DMS09	23°28′23.28″	108°23′28.94″	North	18			
900	DMS10	23°31′35.70″	108°22′19.01″	West	40	Montane evergreen broadleaf forest	Mountain yellow soil	*Rhodoleia championii, Machilus thunbergii* and *Erythroxylum sinense*
	DMS11	23°31′34.18″	108°22′23.66″	Southwest	30			
	DMS12	23°31′29.54″	108°22′29.12″	Southwest	35			
1,100	DMS13	23°31′07.96″	108°23′01.20″	Southeast	14	Montane evergreen broadleaf forest	Mountain yellow soil	*Castanopsis fargesii, Rhododendron cavaleriei* and *Morella rubra*
	DMS14	23°31′07.22″	108°23′02.64″	Southwest	19			
	DMS15	23°31′08.02″	108°23′07.01″	Southeast	20			
1,200	DMS16	23°29′55.56″	108°25′46.66″	North	10	Montane evergreen deciduous mixed forest	Mountain yellow soil	*Castanopsis eyrei, Litsea elongata,* and *Engelhardia roxburghiana*
	DMS17	23°29′53.80″	108°25′47.38″	Northwest	9			
	DMS18	23°29′58.75″	108°25′48.05″	North	16			
1,300	DMS19	23°29′57.90″	108°26′53.92″	Northwest	3	Montane elfin forest	Mountain meadow soil	*Machilus thunbergii, Schima argentea,* and *Engelhardia roxburghiana*
	DMS20	23°29′54.32″	108°26′54.89″	North	2			
	DMS21	23°29′53.69″	108°26′55.92″	North	2			
1,400	DMS22	23°28′47.75″	108°26′05.63″	Southwest	8	Montane elfin forest	Mountain meadow soil	*Camellia fraterna, Michelia maudiae* and *Symplocos sumuntia*
	DMS23	23°28′47.47″	108°26′06.36″	Southwest	6			
	DMS24	23°28′48.06″	108°26′08.99″	Southwest	4			

1982). Soil total phosphorus (STP) content was determined using the molybdenum-antimony anti-colorimetric method (Olsen and Sommers, 1982). Available phosphorus (AP) content was determined using ultraviolet spectrophotometry after extraction with NaHCO₃ solution (Olsen et al., 1954). Soil microbial biomass carbon (MBC), nitrogen (MBN), and phosphorus (MBP) were measured using the chloroform fumigation-extraction method (Brookes et al., 1982; Vance et al., 1987).

2.3 Data analysis

Before analysis, data normality and homogeneity of variance were tested using the Kolmogorov–Smirnov and Levene's tests, respectively. A one-way analysis of variance (ANOVA) and *post hoc* Duncan's test were performed to examine the differences in C, N, and P stoichiometric characteristics of soil and microbial biomass and physicochemical properties across different soil layers. Regression

analysis was conducted to evaluate the altitudinal patterns of soil and microbial biomass C, N, and P stoichiometric characteristics and physicochemical properties. Specifically, quadratic regression models were applied to assess the relationships between altitude and each variable, with altitude serving as the independent variable and the stoichiometric characteristics or physicochemical properties as dependent variables. Pearson's correlation analysis was used to determine the relationships between soil and microbial biomass C, N, and P stoichiometric characteristics and physicochemical properties. The correlation coefficients (r) were calculated to quantify the strength and direction of these relationships. Redundancy analysis (RDA) was used to identify the primary factors influencing the C, N, and P stoichiometric characteristics of soil microbial biomass. Statistical analyses were conducted with SPSS 26.0 (IBM, Chicago, IL, USA). Regression, correlation, and redundancy analyses were performed using the "stats," "psych," and "vegan" packages in R (R Core Team, version 4.3.1), respectively.

3 Results

3.1 Responses of soil physicochemical properties to altitude and soil depth

With increasing altitude, AN did not change significantly across all layers, whereas AP decreased first and then increased significantly in all layers. In the 0–20 cm layer, SWC and SBD increased and decreased significantly, respectively. Soil pH increased significantly with increasing altitude in the 20–40 and 40–60 cm layers (Figure 2). Additionally, ST decreased significantly with increasing altitude (Supplementary Figure S1).

With increasing soil layer, AN, AP, and SWC decreased significantly, whereas SBD and pH increased significantly (Table 2). The highest AN, AP, and SWC were noted in the 0–20 cm layer, with mean values of 279.95 ± 20.56, 2.9 ± 0.42 mg kg^{-1}, and 53.49 ± 3.63%, respectively. The highest SBD and pH were observed in the 40–60 cm layer, with mean values of 1.28 ± 0.04 g cm^{-3} and 3.9 ± 0.05, respectively.

3.2 Responses of soil C, N, and P stoichiometric characteristics to altitude and soil depth

STN, the SOC:STP ratio, and the STN:STP ratio did not change significantly with increasing altitude across all soil layers. In the 0–20 cm layer, SOC and the SOC:STN ratio initially increased and then decreased significantly with altitude. With increasing altitude, STP in the 40–60 cm layer decreased, while the SOC:STN ratio in the 20–40 cm layer increased significantly (Figure 3).

With the increase in soil layer, soil C, N, and P contents and their ratios all decreased significantly. The highest value was recorded in the 0–20 cm layer (Table 2). The mean values of SOC, STN, and STP were 46.77 ± 2.71, 2.58 ± 0.13, and 0.35 ± 0.02 g kg^{-1}, respectively. The SOC:STN, SOC:STP, and STN:STP ratios were 19.25 ± 1.65, 137.26 ± 7.75, and 7.89 ± 0.58, respectively.

3.3 Responses of soil microbial biomass C, N, and P stoichiometric characteristics to altitude and soil depth

MBC and MBN exhibited no significant differences with increasing altitude across all soil layers. MBP in all layers and the MBC:MBN ratio in the 40–60 cm layer initially decreased and then increased significantly with altitude, whereas the MBC:MBP and MBN:MBP ratios exhibited an opposite trend across all layers (Figure 4).

As soil depth increased, soil microbial biomass C, N, and P contents decreased significantly while their ratios increased (Table 2). The highest MBC, MBN, and MBP values were observed in the 0–20 cm layer, with mean values of 637.3 ± 53.01, 107.31 ± 8.43, and 24.82 ± 4.15 mg kg^{-1}, respectively. The highest MBC:MBN and MBC:MBP ratios were detected in the 40–60 cm layer, with mean values of 8.19 ± 0.84 and 59.39 ± 6.61, respectively. The highest mean value of MBN:MBP was 9.78 ± 1.12 observed in the 20–40 cm layer.

3.4 Relationships between soil properties and microbial biomass stoichiometry

Soil microbial C, N, and P contents were positively correlated with soil C, N, and P contents and their ratios, AN, AP, and SWC. However, they were negatively correlated with SBD and soil pH. MBP was significantly negatively correlated with ST. The MBC:MBP and MBN:MBP ratios were strongly positively correlated. These ratios were significantly negatively correlated with MBP, the SOC:STN ratio, the SOC:STP ratio, AP, and SWC and highly positively correlated with ST. The MBC:MBN ratio was significantly negatively correlated with MBC, MBN, the MBN:MBP ratio, AN, SWC, and soil C, N, and P contents, and significantly positively correlated with SBD and pH (Figure 5).

The RDA revealed that the first two axes explained approximately 65.91% of the total variation (Figure 6). Environmental factors had a significant impact on microbial biomass C, N, and P stoichiometric characteristics. Moreover, SWC, AP, and AN were identified as the factors that explained the greatest amount of variance, accounting for 72.0%, 65.1%, and 64.3% of the variance, respectively (Supplementary Table S1).

4 Discussion

4.1 Altitudinal patterns of soil C:N:P stoichiometry

Topography, climate, and biological factors interact along the altitudinal gradient to create high spatial variability in soil nutrients (Yu et al., 2018). In the present study, SOC in the 0–20 cm layer initially increased and then decreased significantly with increasing altitude. At lower altitudes (300–500 m), SOC increased with altitude, consistent with the findings of Zhao et al. (2013) in a similar altitude range on Daming Mountain. This pattern can be attributed to vegetation dynamics and climatic

FIGURE 2
Variations in soil physicochemical properties at different altitudes. **(A)** AN, available nitrogen; **(B)** AP, available phosphorous; **(C)** SWC, soil water content; **(D)** SBD, soil bulk density; **(E)** Soil pH. $^{ns}p > 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.
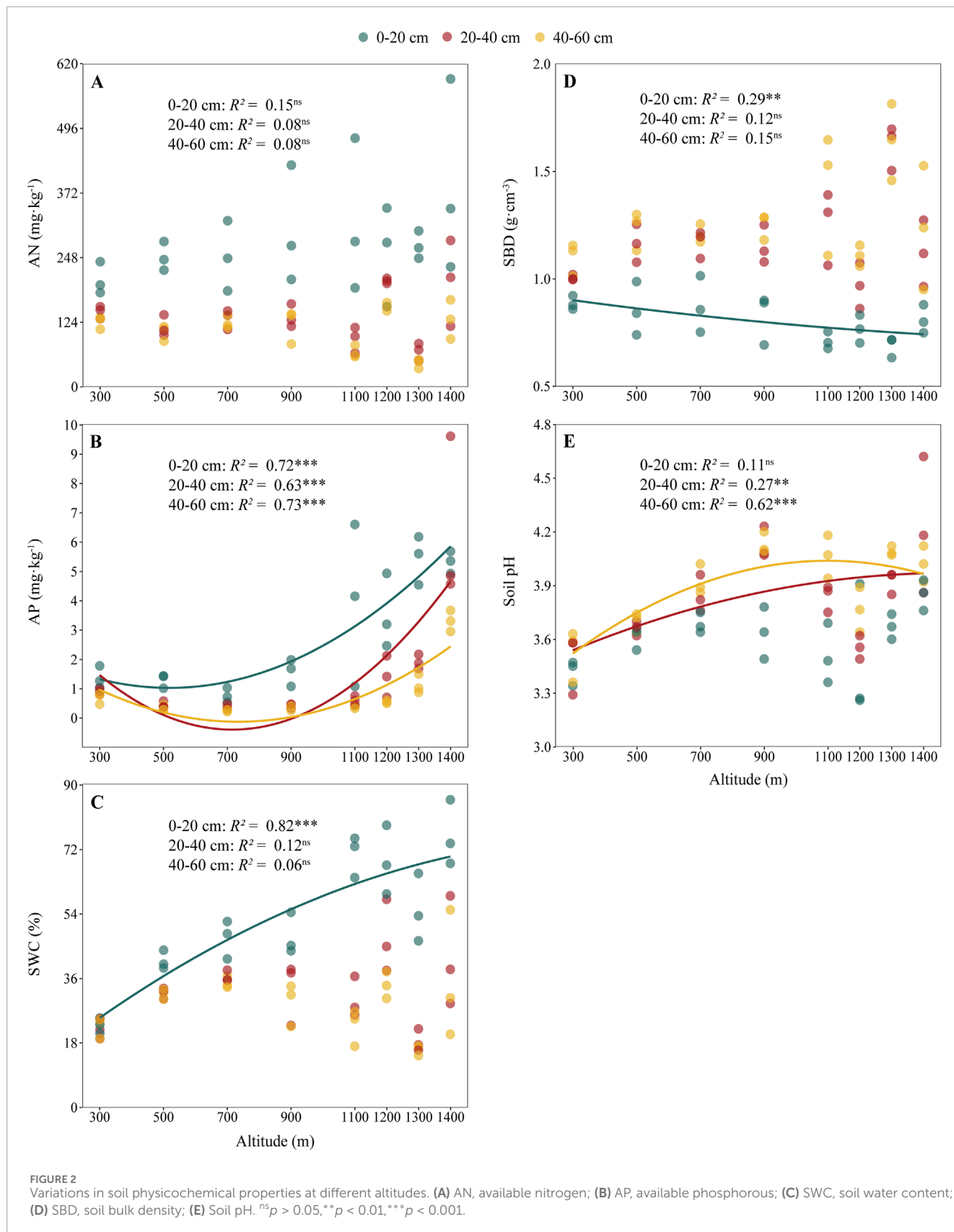
TABLE 2 Differences in soil and microbial biomass C, N, and P stoichiometric characteristics and physicochemical properties across different soil layers.

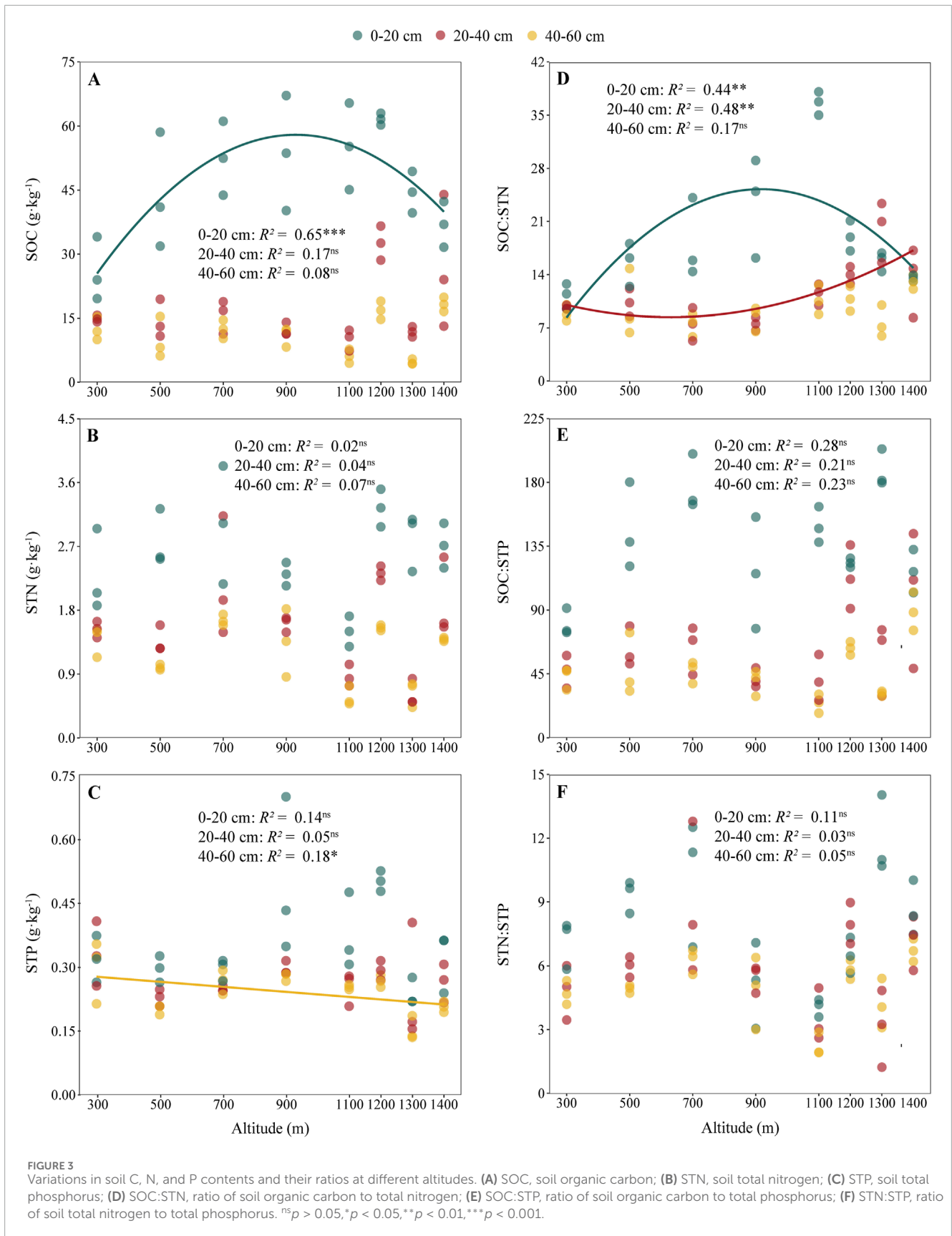| Parameters	0–20 cm	20–40 cm	40–60 cm
AN (mg·kg^{-1})	279.95 ± 20.56[a]	136.52 ± 10.97[b]	108.65 ± 7.76[c]
AP (mg·kg^{-1})	2.9 ± 0.42[a]	1.55 ± 0.43[b]	0.87 ± 0.2[b]
SBD (g·cm^{-3})	0.8 ± 0.02[b]	1.18 ± 0.04[a]	1.28 ± 0.04[a]
SWC (%)	53.49 ± 3.63[a]	32.57 ± 2.26[b]	28.26 ± 1.84[b]
Soil pH	3.61 ± 0.04[b]	3.83 ± 0.06[a]	3.9 ± 0.05[a]
SOC (g·kg^{-1})	46.77 ± 2.71[a]	17.33 ± 1.89[b]	11.43 ± 1.01[c]
STN (g·kg^{-1})	2.58 ± 0.13[a]	1.55 ± 0.13[b]	1.19 ± 0.09[c]
STP (g·kg^{-1})	0.35 ± 0.02[a]	0.27 ± 0.01[b]	0.24 ± 0.01[b]
SOC:STN	19.25 ± 1.65[a]	11.8 ± 0.9[b]	9.67 ± 0.52[b]
SOC:STP	137.26 ± 7.75[a]	66.03 ± 6.6[b]	48.12 ± 4.35[b]
STN:STP	7.89 ± 0.58[a]	5.88 ± 0.49[b]	4.98 ± 0.31[b]
MBC (mg·kg^{-1})	637.3 ± 53.01[a]	364.31 ± 38.11[b]	252.98 ± 27.18[b]
MBN (mg·kg^{-1})	107.31 ± 8.43[a]	60.51 ± 6.5[b]	38.92 ± 5.2[c]
MBP (mg·kg^{-1})	24.82 ± 4.15[a]	10.13 ± 2.32[b]	5.22 ± 0.76[b]
MBC:MBN	5.97 ± 0.16[b]	6.13 ± 0.21[b]	8.19 ± 0.84[a]
MBC:MBP	38.97 ± 4.95[b]	57.31 ± 6.21[a]	59.39 ± 6.61[a]
MBN:MBP	6.72 ± 0.88[a]	9.78 ± 1.12[a]	8.77 ± 1.08[a]

Values indicated means ± standard error. Different lowercase letters indicate significant differences among different soil layers ($p < 0.05$). AN, available nitrogen; AP, available phosphorous; SBD, soil bulk density; SWC, soil water content; SOC, soil organic carbon; STN, soil total nitrogen; STP, soil total phosphorus; SOC:STN, ratio of soil organic carbon to total nitrogen; SOC:STP, ratio of soil organic carbon to total phosphorus; STN:STP, ratio of soil total nitrogen to total phosphorus; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; MBP, microbial biomass phosphorus; MBC:MBN, ratio of microbial biomass carbon to nitrogen; MBC:MBP, ratio of microbial biomass carbon to phosphorus; MBN:MBP, ratio of microbial biomass nitrogen to phosphorus.
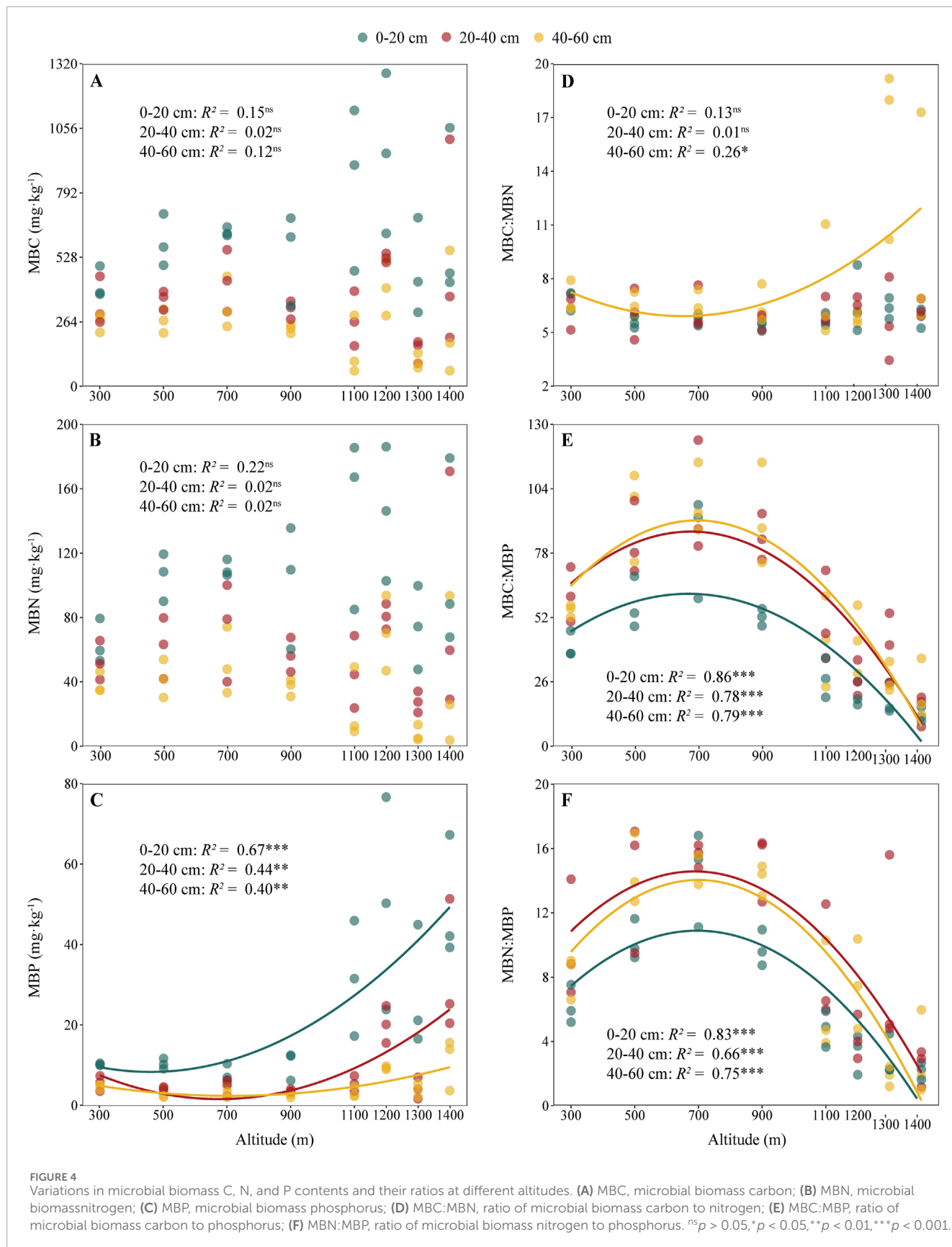
conditions across different altitude zones. In low-altitude areas, monsoon evergreen broadleaf forests dominate, characterized by high biomass production and substantial litter. However, the high temperatures in this zone accelerate microbial decomposition of organic matter, partially offsetting SOC accumulation. As altitude increases, the vegetation transitions to montane evergreen broadleaf forests, which maintain sufficient litter input. Cooler temperatures slow decomposition, resulting in peak SOC accumulation. In high-altitude areas, montane elfin forests prevail and are characterized by decreased plant biomass and litter (Feng et al., 2022; Li J. L. et al., 2023). The cooler temperatures at high-altitude areas further constrain microbial activity (Li S. et al., 2024), contributing to a net decrease in SOC. The role of litter input in SOC dynamics is further highlighted by a previous study on litter hydrological properties (Hu et al., 2025). Hu et al. (2025) demonstrated that litter mass and thickness initially increased with altitude, reaching

a maximum at mid-altitudes (around 700 m), and then decreased at higher altitudes (up to 1,400 m). The similar altitudinal trends in litter, as reported by Hu et al. (2025), and in SOC, as observed in our study, suggest that litter input plays a critical role in regulating SOC accumulation along the altitudinal gradient.

In the present study, SOC, STN, and STP significantly decreased with increasing soil layers, consistent with previous findings (Qiao et al., 2020; Wang et al., 2021; Chen et al., 2022). The primary sources of soil C and N are litter inputs. After microbial decomposition, these nutrients tend to accumulate in the topsoil layer (Luo et al., 2020). Therefore, the response of topsoil SOC to altitude is stronger than that of deeper soil layers. The difference in the altitudinal trends of the SOC:STN ratio between the 0–20 and 20–40 cm layers further highlights distinct soil processes at different depths. In the 0–20 cm layer, the SOC:STN ratio is primarily influenced by variations in SOC, driven by higher organic matter inputs from litter and root exudates (Jobbágy and Jackson, 2000; Rumpel and Kögel-Knabner, 2011). Consequently, the altitudinal trends of SOC and the SOC:STN ratio in the 0–20 cm layer are similar, exhibiting an initial increase followed by a decrease with altitude. In contrast, the 20–40 cm layer exhibited a different SOC:STN dynamic, with a consistent increase along the altitudinal gradient. This pattern is likely attributed to slow organic matter decomposition, leaching of nitrogen from the surface, and reduced root activity in the deeper layer (Fontaine et al., 2007; Yamashita et al., 2010; Iversen et al., 2017). We found that although STP decreased with increasing soil layer, its variation range was small (0.24–0.35 g kg^{-1}), similar to a previous study (0.28–0.38 g kg^{-1}) (Qiao et al., 2020). This is because soil P is a sedimentary element primarily derived from rock weathering with a low migration rate (Smeck, 1985). As SWC increased with altitude, STP was leached to deeper soil layers, causing a significant reduction in STP in the 40–60 cm layer with increasing altitude.

The soil C, N, and P stoichiometric ratio is a key index to estimate soil quality (Jiang et al., 2024). A soil C:N ratio of less than 25:1 likely indicates sufficient soil N and a high degree of organic matter mineralization (Paul, 2007). In our study, the decreased SOC:STN (19.25) ratio in the topsoil suggests sufficient C and N contents, which may promote microbial activity and organic matter decomposition. High microbial use efficiency of organic matter can enhance nutrient availability and support plant growth, particularly in ecosystems with sufficient soil nutrients (Prommer et al., 2020; Duan et al., 2023). However, the relationship between microbial efficiency and plant growth can vary depending on soil types, plant species, and local environmental conditions, potentially influencing nutrient cycling and microbial activity (Muhammad et al., 2025). The soil C:P ratio is commonly used to assess the potential of microorganisms for P release or uptake during the mineralization of organic matter. A low soil C:P ratio generally promotes microorganisms to release P during the decomposing of organic matter and increases soil P availability. The soil N:P ratio serves as a diagnostic indicator of N saturation and is often used to determine the threshold for nutrient limitation. (Jiang et al., 2019). In our study, the SOC:STP (137.26) and STN:STP (7.89) ratios in the topsoil were both higher than the global terrestrial (72.0, 5.9) (Cleveland and Liptzin, 2007), Chinese tropical and subtropical (78.0, 6.4) (Tian et al., 2010), and the Guangxi forest averages (69.60, 5.53)

FIGURE 3
Variations in soil C, N, and P contents and their ratios at different altitudes. **(A)** SOC, soil organic carbon; **(B)** STN, soil total nitrogen; **(C)** STP, soil total phosphorus; **(D)** SOC:STN, ratio of soil organic carbon to total nitrogen; **(E)** SOC:STP, ratio of soil organic carbon to total phosphorus; **(F)** STN:STP, ratio of soil total nitrogen to total phosphorus. $^{ns}p > 0.05, ^*p < 0.05, ^{**}p < 0.01, ^{***}p < 0.001$.

FIGURE 4
Variations in microbial biomass C, N, and P contents and their ratios at different altitudes. **(A)** MBC, microbial biomass carbon; **(B)** MBN, microbial biomassnitrogen; **(C)** MBP, microbial biomass phosphorus; **(D)** MBC:MBN, ratio of microbial biomass carbon to nitrogen; **(E)** MBC:MBP, ratio of microbial biomass carbon to phosphorus; **(F)** MBN:MBP, ratio of microbial biomass nitrogen to phosphorus. $^{ns}p > 0.05, ^{*}p < 0.05, ^{**}p < 0.01, ^{***}p < 0.001$.
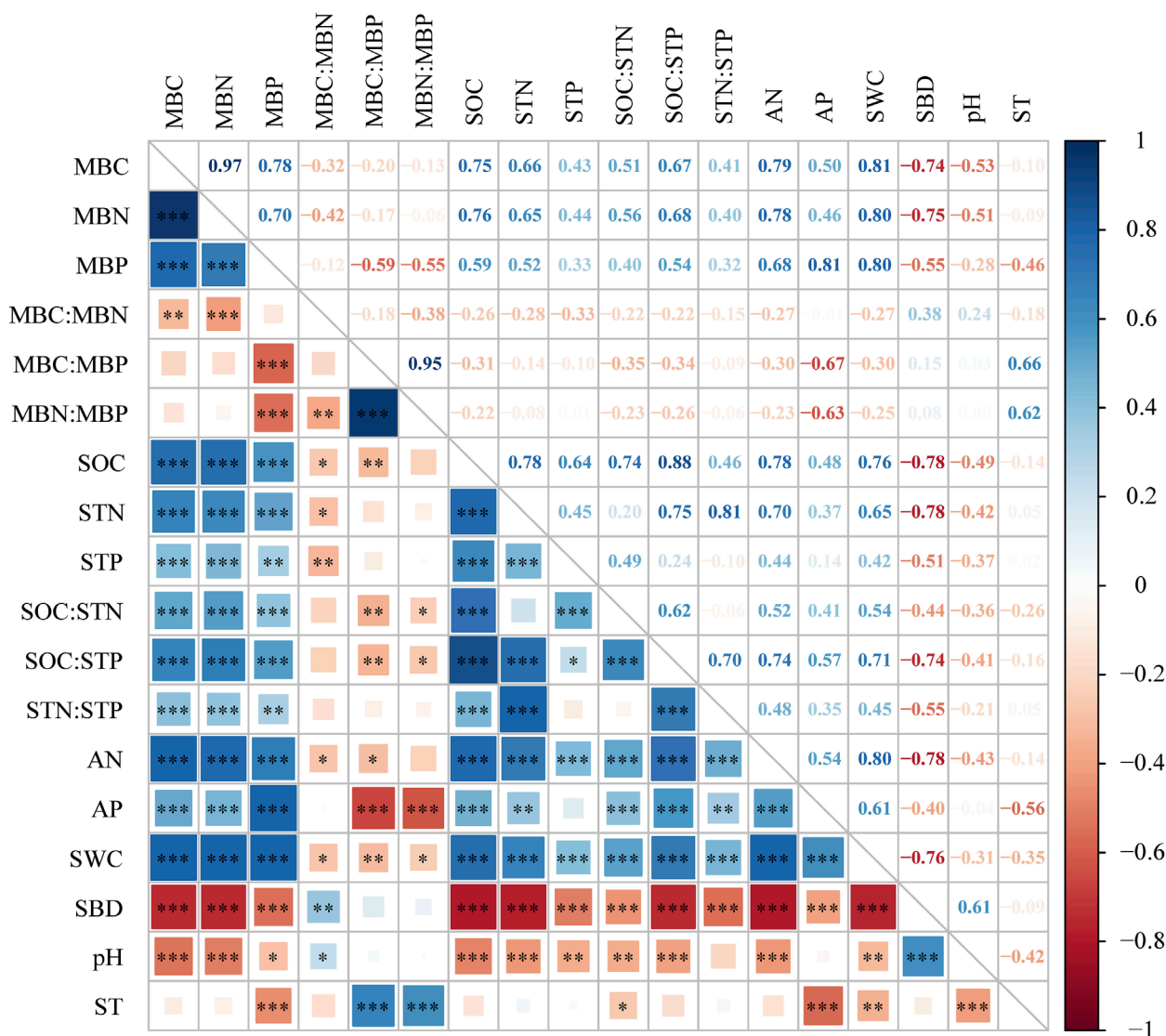
FIGURE 5
Correlation analysis between soil and microbial biomass C, N, and P stoichiometric characteristics and physicochemical properties. SOC, soil organic carbon; STN, soil total nitrogen; STP, soil total phosphorus; SOC:STN, ratio of soil organic carbon to total nitrogen; SOC:STP, ratio of soil organic carbon to total phosphorus; STN:STP, ratio of soil total nitrogen to total phosphorus; MBC: microbial biomass carbon; MBN: microbial biomass nitrogen; MBP, microbial biomass phosphorus; MBC:MBN, ratio of microbial biomass carbon to nitrogen; MBC:MBP, ratio of microbial biomass carbon to phosphorus; MBN:MBP, ratio of microbial biomass nitrogen to phosphorus; AN, available nitrogen; AP, available phosphorous; SWC, soil water content; SBD, soil bulk density; ST, soil temperature.*$p < 0.05$,**$p < 0.01$,***$p < 0.001$.

(Lu et al., 2023). These high C:P and N:P ratios indicate P limitation for soil microorganisms during organic matter decomposition, reflecting low P availability. Moreover, this conclusion is further supported by the low levels of AP (0.87–2.9 mg kg^{-1}) and TP (0.24–0.35 g kg^{-1}), classified as Grade VI (<3 mg kg^{-1}) and Grade V (0.2–0.4 g kg^{-1}), respectively, according to the soil nutrient grading standards of China's second soil census (NSCO, 1992). The results align with previous studies in tropical and subtropical regions, which also indicated P limitation (Mo et al., 2019; van Breugel et al., 2019; Zhu et al., 2024). However, some studies in these regions have indicated N limitation (Hui et al., 2021; Chen et al., 2024). These differences may be influenced by differences in vegetation types and environmental conditions.

4.2 Altitudinal patterns of soil microbial C:N:P stoichiometry

In the present study, MBP generally increased with increasing altitude, primarily due to two reasons. First, as altitude increases, temperature decreases, and soil microorganisms can compensate for reduced activity under low-temperature conditions by increasing microbial biomass P content. This supports the temperature compensation hypothesis (Reich and Oleksyn, 2004; Li et al., 2014). Second, in mid-to-low-altitude areas, the dominant soil type is red soil, characterized by high acidity and abundant iron and aluminum oxides. These properties promote the formation of stable P compounds, reducing P availability. As altitude increases, the soil transitions
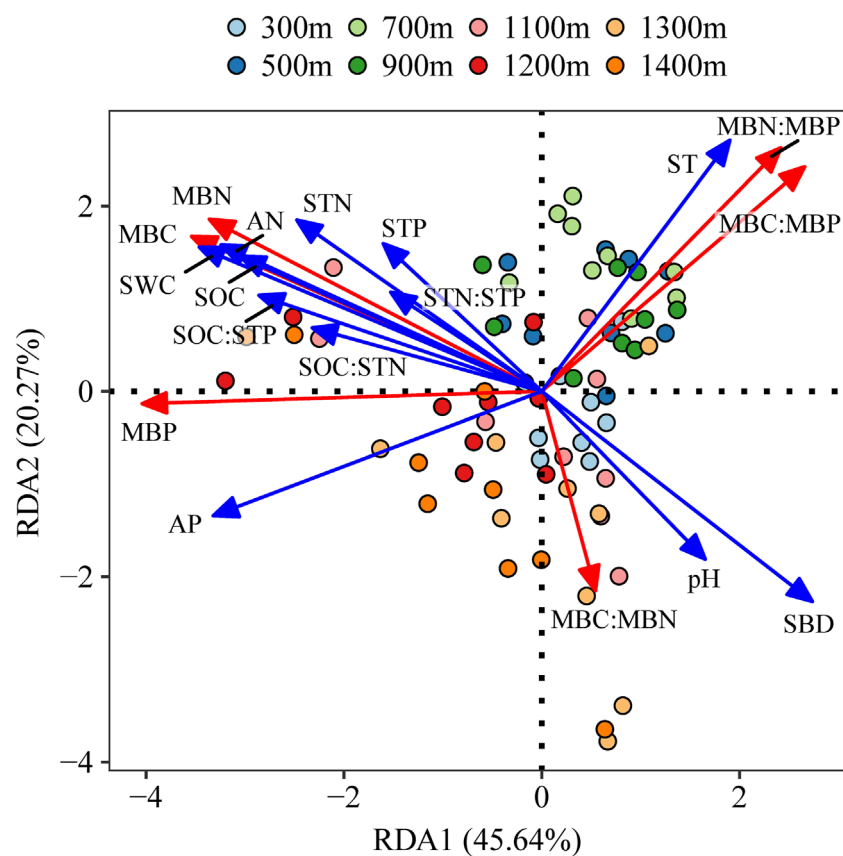
FIGURE 6
Redundancy analysis of soil microbial biomass C, N, and P stoichiometric characteristics with soil C, N, and P stoichiometric characteristics and physicochemical properties. The red and blue lines indicate response variables and explanatory variables, respectively. SOC, soil organic carbon; STN, soil total nitrogen; STP, soil total phosphorus; SOC:STN, ratio of soil organic carbon to total nitrogen; SOC:STP, ratio of soil organic carbon to total phosphorus; STN:STP, ratio of soil total nitrogen to total phosphorus; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; MBP, microbial biomass phosphorus; MBC:MBN, ratio of microbial biomass carbon to nitrogen; MBC:MBP, ratio of microbial biomass carbon to phosphorus; MBN:MBP, ratio of microbial biomass nitrogen to phosphorus; AN, available nitrogen; AP, available phosphorous; SWC, soil water content; SBD, soil bulk density; ST, soil temperature.

to yellow and meadow soils, accompanied by increased pH and decreased iron and aluminum oxide content. This shift reduces P fixation and enhances P availability (Spohn and Widdig, 2017; Fan et al., 2019; Bai et al., 2021; Li J. L. et al., 2023). Consequently, both soil pH and AP increased with altitude. The mineralization of organic P is mainly driven by MBP (McGill and Cole, 1981; Li W. N. et al., 2024), which explains the consistent trends of MBP and AP along the altitudinal gradient. Moreover, SWC changes significantly influence microbial activity and community structure (Cesarz et al., 2022). In this study, SWC increased with altitude and was positively correlated with MBP and AP. This suggests that SWC may play a role in regulating microbial activity and P mineralization. However, both excessive and insufficient SWC can limit microbial biomass and activity (Wei et al., 2017; Gao et al., 2024), indicating that the relationship between SWC and MBP is complex and context-dependent. Therefore, while our results suggest a potential link between SWC and microbial P dynamics, further research is needed to clarify the underlying mechanisms.

We observed that MBC, MBN, and MBP significantly decreased with increasing soil layer, consistent with the trend of soil nutrients. This is mainly because litter, fine roots, and animal residues are

primarily distributed in the topsoil, providing a substrate for microbial activity. Moreover, the favorable water, temperature, and aeration conditions in the topsoil further promote microbial growth and reproduction, leading to the accumulation of microbial biomass in the surface layer (Bahram et al., 2018; Jiang et al., 2021). As soil depth increases, the availability of nutrients and the oxygen transported by roots decreases, worsening the microbial habitat and limiting microbial biomass distribution. Consequently, the microbial biomass in the subsoil is lower than that in the topsoil (Zhou and Wang, 2015; Wu et al., 2024).

Soil microbial C:N:P stoichiometry is crucial for determining soil nutrient balance and material cycling (Hu et al., 2020). In our study, the MBC:MBP and MBN:MBP ratios initially increased and then decreased with increasing altitude, exhibiting an overall downward trend. This is primarily attributed to the changes in MBP with altitude. The observed trend indicates that P limitation is more pronounced in mid-to-low-altitude regions (300–900 m), which aligns with the findings of He et al. (2016), who reported P limitation at 500–700 m. Our findings also align with those of Zhu et al. (2024), who identified the strongest P limitation at 900 m. The MBC:MBN ratio typically reflects the N supply capacity in the soil. In our

study, the MBC:MBN (5.97) ratio in the topsoil was lower than the global tropical or subtropical average (9.7) (Gao et al., 2022) and the Chinese forests average (8.3) (Xue et al., 2019), indicating higher N availability in the study area. The MBC:MBP ratio is commonly used to evaluate the effectiveness of P use, with a deceased ratio indicating higher P availability. The MBN:MBP ratio can be used to reflect the degree of plant demand for N and P (Hartman and Richardson, 2013). In this study, the MBC:MBP (38.97) ratio in the topsoil was similar to the global tropical or subtropical average (38.0) (Gao et al., 2022) but lower than the average of Chinese forests (54.2) (Xue et al., 2019). The MBN:MBP (6.72) ratio in the topsoil was higher than the global tropical or subtropical average (5.3) (Gao et al., 2022) and the Chinese forests average (6.0) (Xue et al., 2019). These findings indicate that soil microorganisms and plant growth are in a P-limited state in the study area, leading to a tendency for soil microorganisms to assimilate AP and compete with plants for its content.

4.3 Factors controlling soil microbial C:N:P stoichiometry

During the decomposition of plant and animal residues by soil microorganisms, C, N, and P elements are simultaneously released. These elements are also required for the growth and metabolism of soil microorganisms, leading to a coupled relationship between soil nutrient cycling and microbial metabolic processes. This coupling causes the changes in the contents and ratios of C, N, and P to be somewhat synchronous (Khan et al., 2024). This explains our observation of significant correlations between the C, N, and P contents and their ratios in soil and microbial biomass. Specifically, soil microbial biomass C, N, and P contents exhibited a significant positive correlation with soil C, N, and P contents and their ratios. This indicates that soil microbial biomass can be a crucial indicator of soil fertility and effectively characterize the intensity of organic matter metabolism (Hu et al., 2020). However, soil microbial biomass C, N, and P stoichiometric ratios were mostly significantly negatively correlated or not correlated with soil C, N, and P contents and their ratios. This is likely related to microbial metabolic constraints and nutrient competition under P-limited conditions. In the study area, the scarcity of available P in the soil may have driven microorganisms to increase their P assimilation efficiency to sustain growth and metabolic activities, leading to a relative increase in MBP. However, owing to the limited availability of P, microorganisms may reduce their utilization of other nutrients (e.g., C and N), resulting in a relative decrease in MBC and MBN (Wang et al., 2024). This could explain the negative or non-significant correlations between microbial biomass stoichiometric ratios and soil nutrients and stoichiometric ratios (Luo et al., 2024). In addition, P limitation may further regulate microbial demand for C, N, and P by influencing metabolic pathways and enzyme activities. This further contributes to the complexity of the relationship between microbial and soil stoichiometry (Cui et al., 2024).

In the present study, soil microbial biomass C, N, and P contents were significantly positively correlated with soil AN, AP, and SWC. These factors were also the main factors influencing the stoichiometric characteristics of soil microbial biomass C, N, and P. Owing to the significant influence of AN on AP (Zhang et al., 2004), in long-term P-limited subtropical ecosystems, adding N to acidic soils can stimulate soil microorganisms to

secrete more phosphatases to obtain AP (Marklein and Houlton, 2012; Fan et al., 2018). As discussed above, SWC is important for microbial activity and P mineralization, likely by enhancing microbial metabolism and enzyme production (Lei et al., 2023). Therefore, adequate water content and N-enriched soils could facilitate the mineralization of P by soil microorganisms. SBD exhibited a significant negative correlation with soil and microbial biomass C, N, and P stoichiometric characteristics. This is primarily because an increased SBD reduces soil porosity and decreases aeration and water infiltration. It is also detrimental to microbial growth and metabolic activities, inhibiting the decomposition of soil nutrients (Zhu et al., 2012).

5 Conclusion

Based on a field investigation conducted at eight altitudes of Daming Mountain, we demonstrated that soil and microbial biomass C, N, and P stoichiometric characteristics exhibited significant variations across different altitudes and soil layers. With increasing altitude, soil C, N, and P stoichiometric characteristics varied across different soil layers. MBP initially decreased and then increased across all soil layers, whereas the MBC:MBP and MBN:MBP ratios exhibited the opposite trends. We identified AN, AP, and SWC as primary factors affecting soil microbial biomass C, N, and P stoichiometric characteristics. Moreover, P emerged as a limiting factor for soil microbial growth in the study area, with this limitation being more pronounced at mid-to-low altitudes. Therefore, it is necessary to apply P fertilizer strategically, especially in mid-to-low-altitude areas, to improve the soil nutrient supply and ensure P availability in forest management on Daming Mountain. These findings are important for understanding soil nutrient balance and limiting factors in subtropical mountain ecosystems. This study offers insights for informing soil management and the conservation and sustainable development of forest ecosystems in the region.

Data availability statement

The raw data supporting the conclusion of this article will be made available by the authors, without undue reservation.

Author contributions

CH: Conceptualization, Investigation, Data curation, Formal analysis, Methodology, Software, Writing – original draft. ZZ: Conceptualization, Funding acquisition, Supervision, Writing – review & editing. YL: Funding acquisition, Writing – review & editing. GH: Funding acquisition, Writing – review & editing, Conceptualization, Investigation, Supervision.

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Conflict of interest

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/feart.2025.1569387/full#supplementary-material

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