



RESEARCH ARTICLE

Intra-annual dynamics of soil and microbial C, N, and P pools in a Central Amazon Terra Firme forest

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Abstract

Background: Tropical ecosystem functioning is influenced by seasonal fluctuations in precipitation, but the impact on soil nutrient cycling and microbial stoichiometry is not fully understood.

Aim: This study investigates the magnitude of intra-annual fluctuations in nutrient availability and microbial biomass in a tropical forest soil by examining carbon (C), nitrogen (N), and phosphorus (P) pools.

Methods: We analyzed the total, extractable, and microbial C, N, and P contents and their stoichiometry in Terra Firme Ferralsols, representative for the central Amazon basin.

Results: We observed intra-annual variations in resource availability, particularly between wet and dry seasons. Despite relatively stable total C, N, and P stocks throughout the year, we observed a decrease in extractable organic C and available (Olsen) P and an increase in extractable N in the dry season compared to the wet season. Microbial biomass pools and stoichiometry also varied across sampling dates and soil depths: relative to microbial-C and -N, microbial-P decreased in both wet and dry season and increased in the transition from wet to dry season.

Conclusions: Our research highlights intra-annual variation in nutrient pools, particularly dynamic microbial carbon and nutrient fractions, in weathered tropical forest soils.

KEYWORDS

intra-annual variability, microbial biomass, nutrient ratios, tropical forest soil

1 | INTRODUCTION

Soils are crucial for sustaining forest productivity and ecosystem functioning by facilitating the cycling of carbon (C), nutrients, and water (Crowther et al., 2019; Quesada et al., 2020). In weathered tropical

soils, nitrogen (N) is usually relatively abundant, since it can be assimilated from the atmosphere by N₂ fixation and increases with soil age (e.g., see Hedin et al., 2009). On the other hand since P is lost from soils over geological time (Walker & Syers, 1976), low soil phosphorus (P) concentrations in these soils are considered to limit tropical forest

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productivity (Cunha et al., 2022). Consequently, P availability in most tropical soils depends largely on the mineralization of organic forms of P, following a seasonal pattern mediated by microbial activity (Schaap et al., 2021).

In tropical forests, seasonality has also been observed in tree growth (Hofhansl et al., 2014) and leaf production (Wagner et al., 2016), which subsequently affects C assimilation and litter return to the soil (Chave et al., 2010; Wu et al., 2016). The dynamics of fine roots have also been shown to be seasonal (Cordeiro et al., 2020; Green et al., 2005; Yavitt & Wright, 2001). Hence, both plant leaf and root turnover are driven by fluctuations in precipitation resulting in variation in organic matter inputs and turnover in tropical forest soils. In tropical forests like the Amazon, where temperature is less of a constraining factor, moisture is the main driver of soil microbial activity (Meir et al., 2008). Accordingly, (heterotrophic) soil respiration (Chambers et al., 2004) and decomposition have been reported to show seasonal variation (Dossa et al., 2020; Sanches et al., 2008; Wieder & Wright, 1995). Since microbial activity catalyzes the decomposition of soil organic matter (SOM), soil nutrient availability for both microbes and plants may be limited by mineralization of leaf litter.

The mineralization rate of SOM and plant litter is affected by their quality, commonly expressed as C:N:P ratios. Substrates with higher C:N or C:P ratios and complex carbon compounds decompose slower than substrates with more favorable quality, suggesting a potential N- or P-limitation on decomposition processes or decomposer communities (Wieder et al., 2009; Zechmeister-Boltenstern et al., 2015). Generally, C:N and C:P ratios of SOM decrease with microbial turnover as C is respired in the process (Chen et al., 2022). In soils, microbial N is often correlated with microbial C content, whereas the relationship between microbial C and P is less predictable (Hartman & Richardson, 2013). One possible explanation might be the intracellular storage of excess C and P, decoupling metabolic activity from resource supply for some microbial groups (Kulakovskaya, 2015; Mason-Jones et al., 2023). Microbes can maintain relatively homeostatic stoichiometric ratios of C:N (Spohn, 2016); in general, bacteria have a tighter, lower C:N range compared to fungi (Xu et al., 2013; Zechmeister-Boltenstern et al., 2015). Therefore, changes in soil microbial biomass C:N:P ratios have been attributed to shifts in microbial community composition, for instance, changes in fungal relative to bacterial abundance in soil (Fanin et al., 2013; Soong et al., 2020). In this way, exploring stoichiometric ratios of resources and consumers can indicate intra-annual metabolic constraints on ecological processes (Mooshammer, Wanek, Hämmerle et al., 2014).

Understanding the processes and interactions that drive soil C and nutrient dynamics improves our ability to make climate-related predictions about this major C sink. The interplay between climate and soil processes is particularly relevant as changes in precipitation patterns are predicted for the Amazon Forest (Douville et al., 2021). Although intra-annual fluctuations of litter-microbe-soil interactions are well-documented for temperate biomes (e.g., Prevost-Boure et al., 2011; Han et al., 2022; Jevon et al., 2022; Schneckner et al., 2023), knowledge about these dynamics in tropical forests is still emerging. This study therefore examines the connection between precipitation, litter

input, soil, and microbial nutrient pools and their stoichiometry over the course of a year. Since most short-term SOM cycling takes place in the topsoil (Balesdent et al., 2018), we focused our campaign on shallow soil depths (0–5 and 5–15 cm) in a highly weathered Ferralsol. In these soils, we investigated variation in total, extractable, and microbial C, N, and P and their relative stoichiometry. We hypothesized that:

1. intra-annual fluctuations in total nutrient concentrations are more pronounced in the surface soil (0–5 cm), due to exposure to seasonal organic matter inputs. Additionally, we expect the surface soil to have relatively higher stoichiometric ratios since this material is of more recent origin;
2. soil extractable C, N, and P concentrations dynamically respond to intra-annual climate variations and increase during the wet season resulting from the decomposition of freshly deposited litter from the preceding dry season;
3. increased resource availability in the wet season results in higher microbial C, N, and P contents. However, due to stoichiometric homeostasis, we expect a relatively constrained response of microbial stoichiometry.

2 | MATERIALS AND METHODS

2.1 | Site description

This study was carried out at the AmazonFACE experimental site (2°35'40"S 60°12'29"W) in Central Amazonia (more information available at amazonface.inpa.gov.br/), approximately 70 km north of Manaus, Brazil, in the experimental reserve Cuieiras (Estação Experimental de Silvicultura Tropical; see also Pereira et al., 2019), which is also the base for the LBA-K34 tower and several experimental observation stations. The meteorology of the area is well described and reported (Araújo et al., 2002; Fuentes et al., 2016; Saleska et al., 2013), and additional data can be obtained from nearby meteorological stations or the Amazon Tall Tower Observatory (e.g., inmet.gov.br or Andreae et al., 2015). Average annual rainfall is about 2400 mm, with a relatively drier period from June to November (hereafter: dry season), whereas average temperature fluctuates from 25.8°C in April to 27.9°C in September (Araújo et al., 2002). The average daily precipitation during this study at the AmazonFACE site is compared with the 2001–2022 average daily precipitation in Manaus (Figure 1). The precipitation pattern at the study site followed the long-year average but with slightly wetter summer months. These differences might be due to increased interception by tower-based rain gauges above the canopy, whereas Manaus data were collected at ground level at a standardized meteorological station.

The area is characterized by old-growth tropical forests, locally known as “Terra Firme” forests. These forests are located on plateaus with nutrient poor and clay rich soils (>70% clay) classified as Geric Ferralsols (Quesada et al., 2010). Across the Amazon basin, approximately 60% of the soils are described as Ferralsols or Acrisols. They are dominated by Iron-(hydr)oxides, highly weathered, and depleted in

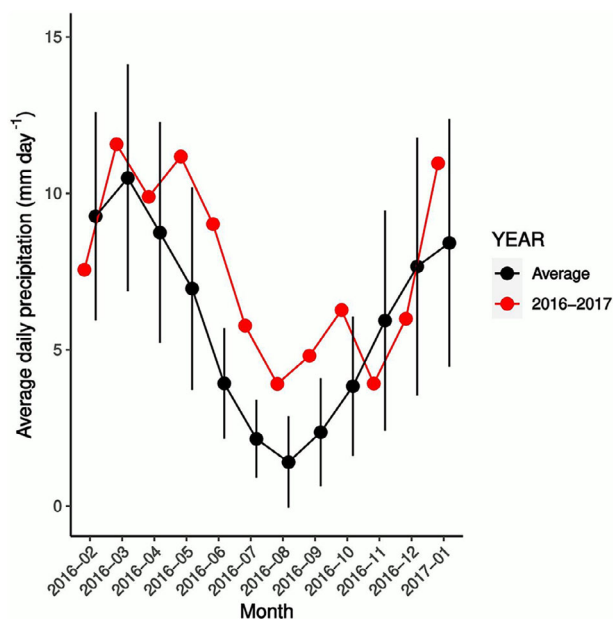


FIGURE 1 Precipitation at the AmazonFACE plots, daily average (red line and dots \pm SE) per month. For reference, the black line is the average precipitation in Manaus for 2001–2022, calculated from publicly available data from INMET (<https://portal.inmet.gov.br/>).

P and other mineral nutrients (Quesada et al., 2011). These soils usually have a thin (approx. 3–5 cm thick) A horizon with a higher organic matter content, followed by an AC horizon with decreasing organic matter contents with depth. The primary productivity of forests growing on such soils is assumed to be limited by the availability of P (Cunha et al., 2022; Hou et al., 2020), and microbial processes are considered to be limited by P in tropical soils as well (Camenzind et al., 2018).

2.2 | Sample collection and processing

Soils were sampled from 18 sampling points. On 6 locations along a 400 m north–south transect (every 80 m), we sampled 3 points in the east–west direction, with a distance of 10 m between the 3 sampling points. The sampling scheme was adopted to consistently sample soils close to the AmazonFACE plots (for details, see Lapola & Norby, 2014) without disturbing soil within the plots. Soils were sampled in February (wet season), May (wet season), August (dry season), and November (dry season) 2016 using a custom-made steel soil corer (\varnothing 10 cm). The soils were sampled at depths of 0–5 and 5–15 cm and transported to the lab for sieving (2 mm), removal of roots and debris, and further processing. Analyses of fresh soils (microbial and extractable fractions) were conducted within 3 days after collection, whereas soil aliquots for further analysis (total C, N, and P for this study) were stored after oven drying (48 h at 65°C). Drying at 65°C avoided the oxidation of labile organic matter. Except for total C and N content, all analyses were performed at the LTSP laboratory (Laboratório Temático de Solos e Plantas) at INPA (Instituto Nacional de Pesquisas da Amazônia) in Manaus, Brazil. Some data have previously been used in Schaap et al. (2023; total and extractable C, N, and P) and Schaap et al. (2021; total P).

2.3 | Total, extractable, and microbial C, N, and P

Total soil C (C_t) and N (N_t) content were determined in dry milled composited samples (three replicate samples pooled by sampling location, separated by layer) using an EA (IRMS). Inorganic C was assumed to be negligible at an average soil pH of 3.94 (Quesada et al., 2010). Total P (P_t) was determined in dry 0.5 g aliquots with the molybdate blue method (Murphy & Riley, 1962) after acid digestion using a concentrated sulfuric acid solution (H_2SO_4 , 18 M), followed by H_2O_2 (Quesada et al., 2010; see also Schaap et al., 2021).

Extractable organic carbon (C_e) and extractable nitrogen (N_e) were determined in KCl extracts (2 g of fresh soil in 20 mL of 1 M KCl) and analyzed on a TOC/TN analyzer (TOC-V CPH E200V TNM-1 220 V; Shimadzu). For extractable inorganic P (P_e), we used the Olsen-P method (Olsen et al., 1954), where extracts were obtained from 2 g of fresh soil shaken for 1 h in 20 mL of 0.5 M $NaHCO_3$ before filtering. The filtered extract was then analyzed colorimetrically with the molybdate blue method (Murphy & Riley, 1962).

The same procedure as for C_e , N_e , and P_e was followed for microbial biomass, but with a 24 h chloroform fumigation prior to extraction with KCl or $NaHCO_3$ (Vance et al., 1987). Filtered extracts (2 g of $CHCl_3$ fumigated fresh soil in 20 mL of 1 M KCl) were analyzed using a TOC/TN analyzer (TOC-V CPH E200V/TNM-1 220 V; Shimadzu), and the difference between these extracts and C_e/N_e extracts was calculated as microbial C (C_m) and N (N_m) on a dry soil basis. Similarly, microbial P (P_m) concentrations were calculated from the difference between P_e and the fumigated soil extractable P concentrations determined in $NaHCO_3$ extracts (2 g of $CHCl_3$ fumigated fresh soil shaken for 1 h in 20 mL of 0.5 M $NaHCO_3$). The resulting C_m , N_m , and P_m values were not adjusted by any extraction efficiency factor.

2.4 | Statistical analyses

All calculations were performed in R (version 4.2.1; R Core Team, 2022). Soil stoichiometric ratios were calculated as molar ratios. Whenever their mean is expressed, we use the mean of the natural log of the individual ratios (as recommended by Isles, 2020). To facilitate comparison with other studies, the mean of the log-transformed ratios was transformed back to their natural exponent.

To assess if parameters varied over time (i.e., between collection dates), we applied linear mixed-effect models using sampling location as a random effect (*lme* function from the *nlme* package version 3.1-160; Pinheiro et al., 2022). Subsequently, model residuals were evaluated for assumptions of normality, homoskedasticity, and independence. Some variables needed the removal of outliers or the application of the varIdent variance structure, as is indicated in the respective results. The most parsimonious model structure was selected by comparing the AIC of the respective models. When significant differences between sampling campaigns were established, we calculated the least squares model means and performed Tukey's HSD test for significant differences between groups (*lsmeans* from the *emmeans* package, version 1.8.2; Lenth, 2022).

2.5 | Microbial fractions

Previous studies have reported the “microbial quotient” of soils, which is commonly calculated from the microbial biomass carbon divided by the total organic carbon contents (e.g., Anderson, 2003; Sparling, 1992); in other words, microbial carbon as a fraction of total carbon. Here, we extended that line of thought by calculating this quotient not only for microbial carbon, but also for N and P. This resulted in three distinct (but related) microbial fractions: C_m/C_t , N_m/N_t , and P_m/P_t .

As the C, N, and P are important indicators of soil nutrient status and are usually related, we visualized microbial fractions (or quotients) of the respective C, N, or P pool in relation to each other. More specific, we plotted monthly average ratios of C_m/C_t to N_m/N_t and fractions of C_m/C_t to P_m/P_t and N_m/N_t to P_m/P_t fractions (Figure 5). This allows to interpret (1) the distance from the origin as an indication of the size of the microbial biomass relative to total C and nutrient contents; and (2) divergence from the 1:1 stoichiometric equilibrium of bulk soil and microbial biomass nutrient ratios. Points below (i.e., to the right of) the 1:1 equilibrium line would indicate higher stoichiometric ratios in the microbial biomass as compared to the bulk soil; equally, lower microbial ratios relative to the soil would result in points above (or to the left of) this 1:1 line.

3 | RESULTS

3.1 | Limited intra-annual variation of total soil C, N, and P concentrations

The average concentration of total soil C (C_t) at 0–5 cm soil depth was $64.33 \pm 3.25 \text{ mg g}^{-1}$. It was at its lowest in November (dry season) yet was significantly elevated in May and August (Figure 2a, Table S1). At 5–15 cm depth, the C_t concentration was significantly lower, averaging $28.52 \pm 1.53 \text{ mg g}^{-1}$, and followed the same temporal pattern as in the top 5 cm.

Total soil N (N_t) averaged $3.25 \pm 0.14 \text{ mg g}^{-1}$ at 0–5 cm depth, remained constant for the first three sampling dates, but dropped significantly in November (Figure 2d). At 5–15 cm soil depth, N_t was lower ($2.13 \pm 0.08 \text{ mg g}^{-1}$). The concentrations were significantly higher in February ($2.57 \pm 0.30 \text{ mg g}^{-1}$) compared to lowest values in November ($1.88 \pm 0.06 \text{ mg g}^{-1}$).

Total soil P (P_t) in the top 5 cm averaged $0.14 \pm 0.00 \text{ mg g}^{-1}$, peaking in May with $0.15 \pm 0.01 \text{ mg g}^{-1}$, and was at its lowest in November with $0.13 \pm 0.01 \text{ mg g}^{-1}$ (Figure 2g). At 5–15 cm depth, P_t was $0.12 \pm 0.00 \text{ mg g}^{-1}$ on average, with no significant differences between months.

3.2 | Intra-annual dynamics of extractable C, N, and P

In the top 5 cm, the average concentration of extractable organic C (C_e) was $1047.56 \pm 71.79 \text{ } \mu\text{g g}^{-1}$, peaking during the wet months

(February and May) and significantly lower concentrations in August and November (Figure 2b, Table S1). At 5–15 cm, C_e averaged $927.31 \pm 74.60 \text{ } \mu\text{g g}^{-1}$, with the highest concentration in May (1727.64 ± 126.43) and lowest in August ($455.73 \pm 11.53 \text{ } \mu\text{g g}^{-1}$). However, those differences could not be assessed with our model due to heteroskedasticity even after outlier removal and the addition of a variance structure.

In contrast, the extractable N (N_e) in the upper 5 cm was $105.58 \pm 3.57 \text{ } \mu\text{g g}^{-1}$, with a maximum in August ($135.3 \pm 5.05 \text{ } \mu\text{g g}^{-1}$), and the lowest value in February ($92.52 \pm 5.82 \text{ } \mu\text{g g}^{-1}$; Figure 2e). At 5–15 cm soil depth, the average total N_e was lower ($79.18 \pm 2.51 \text{ } \mu\text{g g}^{-1}$) compared to the top 5 cm but followed the same pattern with peaks in August ($95.92 \pm 2.39 \text{ } \mu\text{g g}^{-1}$) and lowest values in February ($62.02 \pm 2.66 \text{ } \mu\text{g g}^{-1}$).

The average extractable inorganic P (P_e) in the top 5 cm was $2.29 \pm 0.17 \text{ } \mu\text{g g}^{-1}$, peaking in May with $2.94 \pm 0.26 \text{ } \mu\text{g g}^{-1}$, and a minimum in November with $1.37 \pm 0.14 \text{ } \mu\text{g g}^{-1}$ (Figure 2h). At 5–15 cm depth, the average P_e was $1.10 \pm 0.08 \text{ } \mu\text{g g}^{-1}$, with the highest values in the wet season and the lowest in the dry season.

3.3 | Highly dynamic microbial C, N, and P pools

We observed a highly dynamic microbial C, N, and P pools. On average, the microbial C (C_m) concentration in the top 5 cm was $826.85 \pm 48.99 \text{ } \mu\text{g g}^{-1}$, with no significant differences in average concentrations between sampling months (Figure 2c). At 5–15 cm depth, the average C_m was $674.98 \pm 56.17 \text{ } \mu\text{g g}^{-1}$ (5–15 cm), peaking in May (1026.12 ± 167.96) and significantly lower in the dry season (August and November).

The average microbial N (N_m) in the top 5 cm was $81.33 \pm 7.22 \text{ } \mu\text{g g}^{-1}$, showing no significant differences between the first 3 months but reaching a low in November ($42.43 \pm 3.81 \text{ } \mu\text{g g}^{-1}$, Figure 2f). At 5–15 cm, the average N_m was lower ($47.10 \pm 4.13 \text{ } \mu\text{g g}^{-1}$) but followed the same temporal pattern as in the top 5 cm.

Microbial P (P_m) averaged $2.49 \pm 0.27 \text{ } \mu\text{g g}^{-1}$ at 0–5 cm and ranged from the highest values in February ($4.49 \pm 0.65 \text{ } \mu\text{g g}^{-1}$) to lowest values in November ($1.50 \pm 0.33 \text{ } \mu\text{g g}^{-1}$). At 5–15 cm depth, P_m was even lower (average $1.04 \pm 0.15 \text{ } \mu\text{g g}^{-1}$), peaking in February ($1.95 \pm 0.35 \text{ } \mu\text{g g}^{-1}$) and reaching its lowest concentration in November ($0.36 \pm 0.05 \text{ } \mu\text{g g}^{-1}$; Figure 2i).

3.4 | Higher C:N:P ratios in the topsoil, some exceptions

In the top 5 cm, the average ratio for extractable $C_e:N_e$ was 10.3 and increased to 11.6 in the soil below (Figure 3b,e,h). The $C_e:P_e$ ratio averaged 1202 at 0–5 cm depth, whereas at 5–15 cm, this ratio was 2290. The $N_e:P_e$ ratio was 116.3 on average in the top 5 cm, whereas in the 10 cm below, this ratio rose to 189.8.

For microbial $C_m:N_m$ at the upper 5 cm the average ratio was 11.87, whereas in the soil below this ratio was 18.2 (Figure 3c,f,i). The average

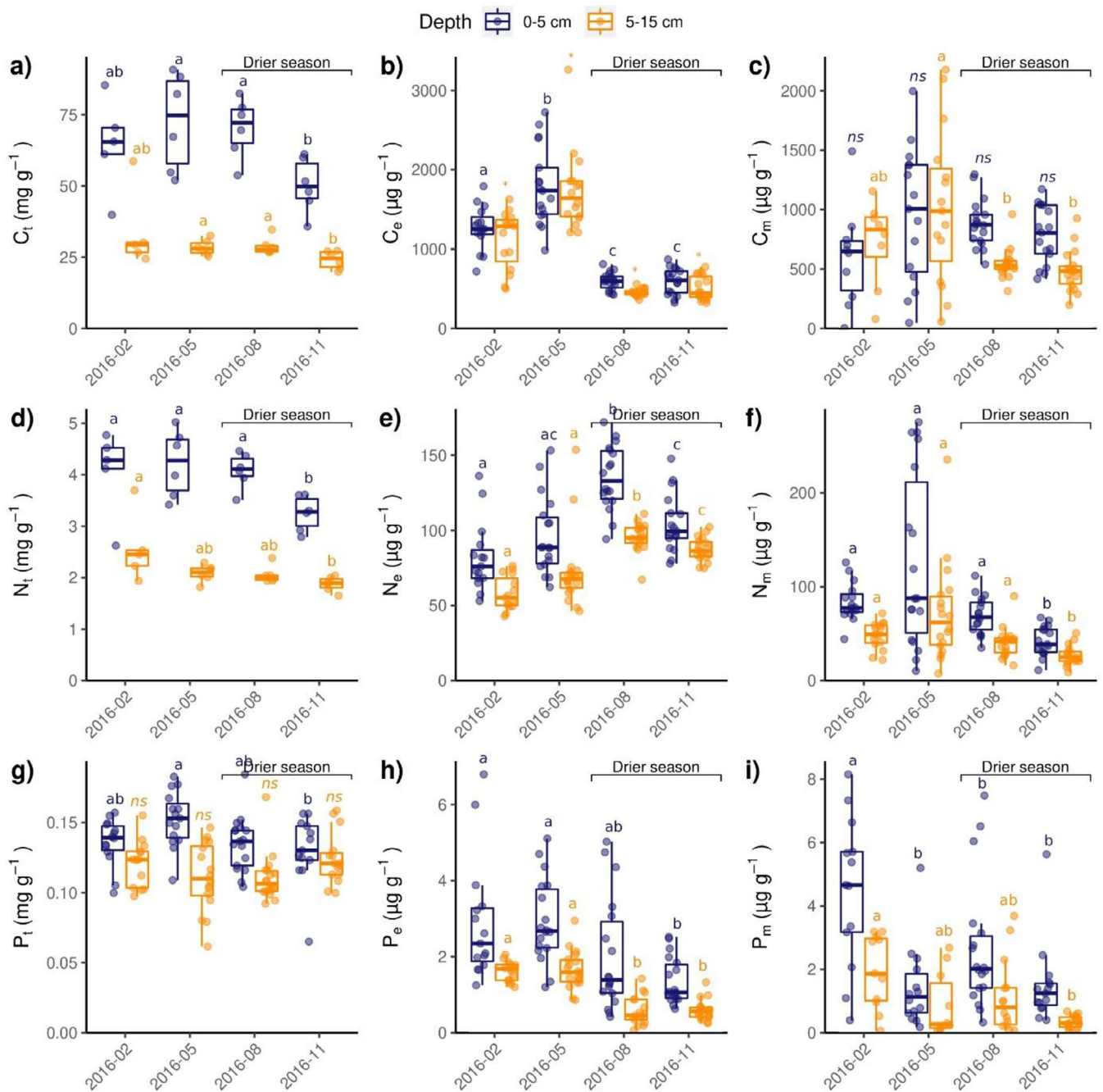


FIGURE 2 Concentrations of soil (a) total carbon (C_t , $n = 6$, per timepoint), (b) KCl extractable C (C_e , $n = 18$), (c) microbial C (C_m , $n = 18$), (d) total nitrogen (N_t , $n = 6$), (e) KCl extractable N (N_e , $n = 18$), (f) microbial N (N_m , $n = 18$), (g) total phosphorus (P_t , $n = 18$), (h) inorganic bicarbonate-extractable P (P_e , $n = 18$), and (i) microbial P contents (P_m , $n = 18$) at 0–5 cm and 5–15 cm soil depth over the course of a year. Boxplots show the minimum, first quartile, median, third quartile, maximum, and all observations on a dry soil basis. Different letters indicate significant differences ($p < 0.05$) between months, at the same soil depth. * Indicates a persistent violation of assumptions, ns indicates a lack of significance. For further details see Table S1.

$C_m:P_m$ ratio was 1094, whereas at 5–15 cm, this ratio rose to 2333. The average $N_m:P_m$ ratio was 86.3 in the top 5 cm, whereas in the 5–15 cm below, this ratio dropped to 147.4.

The $C_t:N_t$ ratio averaged 19.0 in the top 5 cm, and 15.5 at 5–15 cm depth (Figure 3). The average $C_t:P_t$ ratio in the upper 5 cm was 1186,

and at 5–15 cm it was 635. An average $N_t:P_t$ ratio of 61.9 was found in the top 5 cm, whereas at 5–15 cm depth, this ratio decreased to 41.0. For C_t , N_t , and P_t contents at 5–15 cm, the first and last sampling campaigns, respectively, showed higher and lower ratios of $C_t:N_t$ and $C_t:P_t$, indicating fluctuating SOM quality during the year.

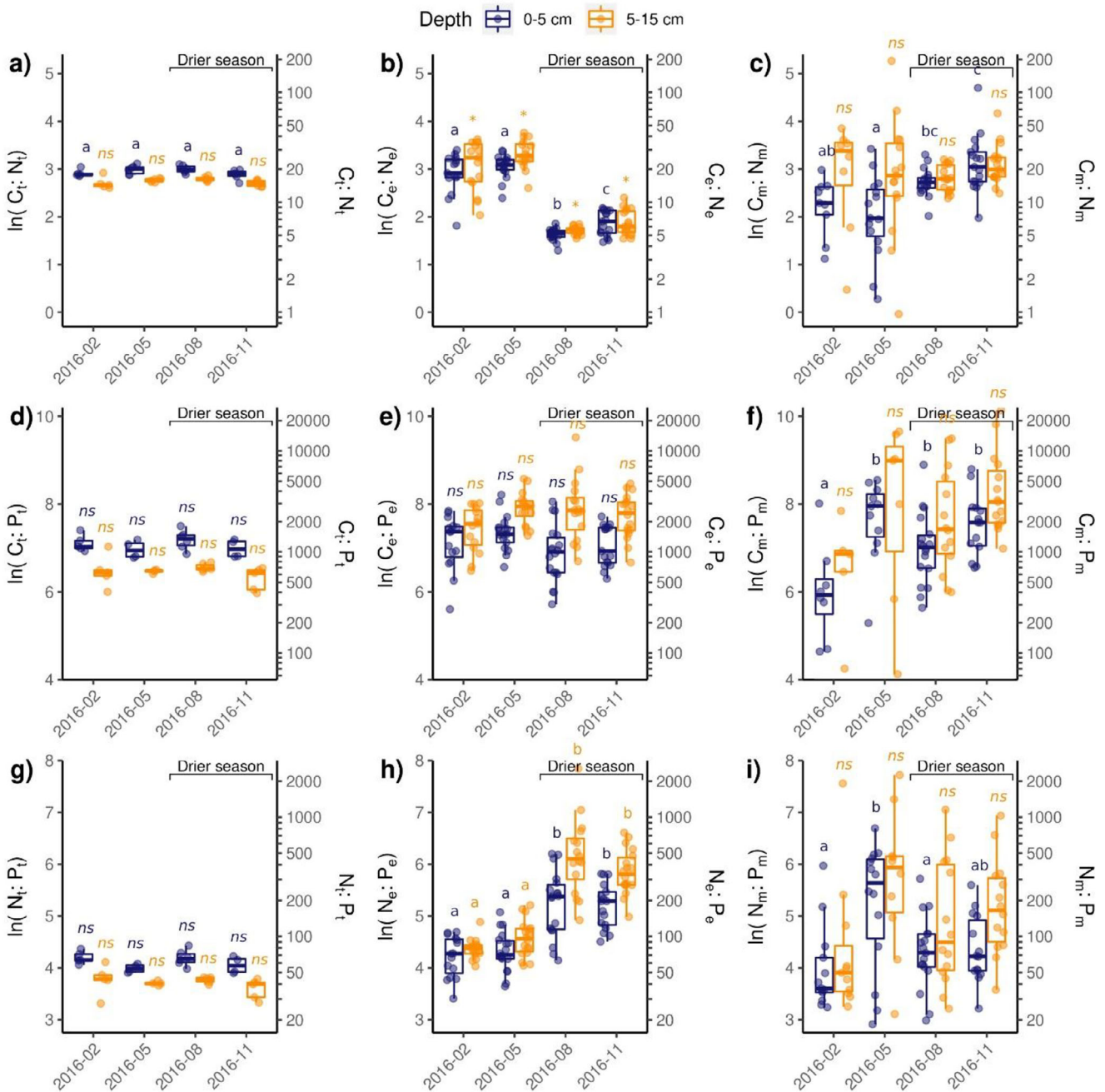


FIGURE 3 Soil (a) total C:N ($n = 6$), (b) extractable C:N ($n = 18$), and (c) microbial C:N ($n = 18$), (d) total C:P ($n = 6$), (e) extractable C:P ($n = 18$), (f) microbial C:P ($n = 18$), (g) total N:P ($n = 6$), (h) extractable N:P ($n = 18$), and (i) microbial N:P ratios ($n = 18$). The secondary axis shows the natural exponent of the \ln transformed values. Boxplots show the minimum, first quartile, median, third quartile, and maximum of natural log-transformed values. For both the $C_m:N_m$ and $C_m:P_m$, one observation in February is omitted (outside of plot range). Different letters indicate significant differences ($p < 0.05$) between months, at the same soil depth. * Indicates a persistent violation of assumptions, *ns* indicates a lack of significance. For further details see Table S1.

3.5 | Intra-annual dynamics of microbial C, N, and P fractions

To gain insight into the dynamics of the microbial pools, we related microbial C, N, and P to soil total C, N, and P during a year (Figure 4). Throughout the year, the microbial C fraction was smaller at 0–5 cm depth than at 5–15 cm, whereas the opposite was true for the microbial

P fraction. The microbial nitrogen N fractions were more consistent between depths. In the top 5 cm, the average C_m/C_t fraction remained stable throughout the year (Figure 4a), whereas N_m/N_t increased during the wet period and sharply declined with the onset of the drier period (Figure 4b), and P_m/P_t declined during the wet period and remained stable during the drier period (Figure 4c). At 10–15 cm soil depth, N_m/N_t followed a similar pattern as compared to 0–5 cm depth,

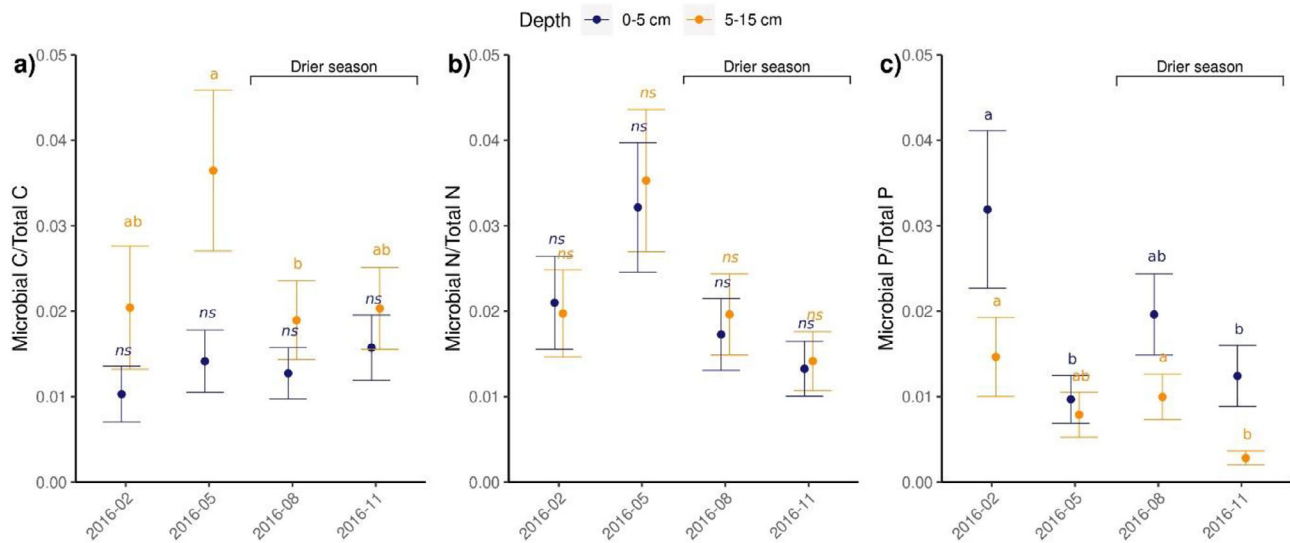


FIGURE 4 Microbial C, N, and P as a fraction of the bulk soil C, N, and P contents at 0–5 cm and 5–15 cm depth; a) shows the microbial C as a fraction of total C over time, b) shows microbial N as a fraction of total N over time, and c) shows microbial P as a fraction of total P over time. Error bar indicates standard error. Different letters indicate significant differences ($p < 0.05$) between months, at the same soil depth. * Indicates a persistent violation of assumptions, ns indicates a lack of significance. For further details see Table S2.

whereas C_m/C_t increased during the wet period and decreased toward the drier period. This is in contrast with P_m/P_t , decreasing during the wet period.

During the wet season (February–May) we observed a more pronounced increase in the ratio of microbial N_m/N_t compared to the ratio of C_m/C_t (Figure 4a,b). However, as we move towards and into the drier period (May–August–November), the N_m/N_t ratio decreased more than the C_m/C_t ratio (Figure 4a,b). Although the C_m/C_t ratio at 0–5 cm remained constant during the year, the P_m/P_t ratio decreased during the wet season, increased towards the drier season, and tended to decrease during the drier season (Figure 4a,c). At 5–15 cm soil depth, the P_m/P_t ratio followed a similar but less pronounced pattern as observed for the top soil (Figure 4c).

While comparing N and P pools over time at 0–5 cm depth, we can observe how during the wet season the N_m/N_t ratio increased, whereas P_m/P_t decreased. However, during the drier season, these nutrients showed a similar pattern. At 5–15 cm depth, these nutrients followed a similar pattern, albeit less pronounced. P_m increased toward the drier season at both depths. We observed relative decreases of P_m during the wet season, increases toward the drier season, and decreases during the dry season at both depths. However, during the wet period and the following transition toward the drier period, N_m and P_m showed opposing trends.

We reported significant intra-annual variation in most soil C, N, and P pools. The interaction between inputs, nutrient availability, and microbes resulted in higher nutrient concentrations in the top 5 cm of soil as compared to the layer below. In the wet season, we observed an increase in extractable C and P, whereas extractable N showed a decrease. There was a distinct difference between the dynamics of N and P in the microbial pools. This led to a variable microbial stoichiometry, with changes across different sampling dates and soil

depths, hinting at a highly dynamic microbial community. Overall, our results highlight surprisingly high intra-annual variation in nutrient pools in highly weathered tropical forest soils, which seems to be an effect of wet-dry seasonal dynamics.

4 | DISCUSSION

4.1 | High turnover in the surface soil layer

Consistent with our first hypothesis, we observed more pronounced fluctuations of nutrients and their stoichiometric ratios in the top 5 cm. C_t and N_t concentrations in the top 5 cm were roughly double those in the 10 cm below. In more mineral soil, C is bound to the mineral soil matrix and Fe/Al-oxides (Souza et al., 2017) and undergoes fewer temporal fluctuations (Cotrufo & Lavelle, 2022; Lavelle et al., 2020). In contrast to the sharp decline with depth in the C_t and N_t content, P_t was more similar between depths. Soil P is comprised of several fractions, including an occluded (adsorbed) fraction and organic fractions related to the inputs of litter (Schaap et al., 2021); it is plausible that the large recalcitrant pool would mask intra-annual patterns when observing total P.

The C:N ratio for fresh litter was 35.6 (Martins et al., 2021), and this study reports a soil $C_t:N_t$ ratio of 19.0 and 15.5 in the top 5 cm and 5–15 cm depth, respectively. At our site, the average soil C:N ratio of 15.5 at 5–15 cm is similar to that reported for tropical forest soils by Xu et al. (2013), whereas others reported markedly higher values for tropical forests (Silver et al., 2000). Total C:N ratios remained largely similar throughout the year. The observed N_t dynamics dominate the observed stoichiometric changes for the C:N and N:P ratios. The depth differentiation between the total C:N, C:P, and N:P ratios followed the

same pattern for all those ratios; they were slightly lower at 5–15 cm depth. This is in line with earlier reports that found a relative decrease in nutrient ratios with depth (Chen et al., 2022), suggesting that C is increasingly lost with depth since at deeper depths the organic material is older (Balesdent et al., 2018). The average reported soil C:P was 1078.4, higher than average C:P ratios of tropical soils in general (169.4; Xu et al., 2013), suggesting a pronounced P limitation of the NPP in the studied forest (Cunha et al., 2022; Menge et al., 2012). The higher C:P and N:P found in the topsoil further signals a higher turnover of new inputs compared to the deeper soil.

4.2 | Dynamics of extractable C and nutrient pools within a year

In our second hypothesis, we postulated extractable C and nutrient concentrations would increase during the wet season due to decomposition of litter deposited in the preceding dry season. We confirmed this hypothesis for soil extractable C_e and P_e , which increased in the wet season but N_e peaked in the dry season.

In the wet season, higher substrate leaching from accumulated plant litter and easier substrate diffusion likely increased microbial activity, increasing C and P availability. Soil moisture is an important control over soil C-cycling and nutrient availability (Cusack et al., 2019), and despite stable soil moisture during our campaign (Figure S1), increased leaching of dissolved material in the wet season could be a mechanism through which C reaches deeper layers. Precipitation events can result in pulses of soil CO_2 emission (Meir et al., 2008), litter C leachate losses (Schwendenmann & Veldkamp, 2005), and river C discharge (Waterloo et al., 2006). Leaf litter leachate can also desorb P in tropical soils (Schreeg et al., 2013), possibly explaining the increase in P_e during the wet season.

During the dry season, microbial access to and turnover of C_e and nutrients could have been reduced. Moreover, in months with less precipitation, decreased root presence was found (Cordeiro et al., 2020), which could result in lower plant P_e uptake. This suggests that even small intra-annual shifts and a change in the frequency of climate anomalies could lead to substantial changes in plant nutrient uptake and thus critically affect the synchrony of resource availability and plant acquisition capacity (Nord & Lynch, 2009).

The leaching of dry deposited N from the canopy (Umana & Wanek, 2010) could partly explain the contrasting pattern of N_e . Organic N is depolymerized to amino acids and other N forms, then further mineralized into ammonium (NH_4^+) (Geisseler et al., 2010). After NH_4^+ nitrification, nitrate (NO_3^-) may be lost in wet conditions due to leaching, whereas soluble N compounds may accumulate in the dry season. Dry conditions can lead to increased adsorbed ammonium concentrations (Homyak et al., 2017). Despite the importance of N for plants and microbes, it is not considered a limiting nutrient in tropical forests; highly weathered tropical soils are sometimes considered N-saturated (Hedin et al., 2009). This saturation of N could also explain the contrasting pattern of N_e if the N cycle is an open cycle, as opposed to the “closed” P cycle that forces organisms to (re)cycle P_e efficiently.

The lack of accumulation of the extractable fractions of C and P in the dry season suggests high microbial and plant demand for C_e and P_e . The simultaneous decrease in C_e and P_e , but not N_e , from the wet to dry season could also indicate a change in the nutrient mineralization dynamics by the microbial community.

4.3 | Non-homeostatic stoichiometry suggests dynamic microbial community

Our hypothesis was that there would be minimal variation in microbial stoichiometry between sampling dates. This is based on the understanding that microbes can adjust their functioning and nutrient use efficiency to substrate quality, thereby regulating homeostasis (Mooshammer, Wanek, Zechmeister-Boltenstern et al., 2014; Spohn, 2016). However, since we were unable to establish such homeostatic behavior of the microbial biomass, we anticipated the substrate to have a strong influence over microbial functioning. Consequently, we expected variation in total C:N:P stoichiometry to be mirrored in microbial C:N:P stoichiometry. Contrary to these expectations, the C_m , N_m , and P_m content as fractions of total nutrient contents (C_m/C_t , N_m/N_t , and P_m/P_t ratios) also demonstrated significant variation over the course of a year (Figure 4).

This observation of the dynamic microbial biomass as a fraction of total nutrient contents is illustrated by the pattern of the average microbial fractions (Figure 5). This shows how the ratio of microbial nitrogen to total nitrogen (N_m/N_t) increased relative to the microbial carbon to total carbon (C_m/C_t) ratio, indicating a relative enrichment of N_m compared to C_m during the wet season, whereas in the dry season, a decrease in the N_m/N_t versus C_m/C_t ratio can be observed. At 5–15 cm soil depth, the C_m/C_t to N_m/N_t fractions remained near the 1:1 line throughout the year, suggesting uniform temporal changes between total carbon/nitrogen (C_t/N_t) and microbial carbon/nitrogen (C_m/N_m). Once again, we observe high variation of the microbial phosphorus to total phosphorus (P_m/P_t) versus C_m/C_t ratio, indicating a relative decrease of P_m during both the wet and drier season, but an increase during the transition from the wet to the drier season.

These results also point to stoichiometric differentiation in the microbial biomass between depths. Increased abundance of microbial P in the top 5 cm could be the result of new labile inputs being absorbed quickly into the microbial biomass. Phosphorus is less mobile in the soil matrix than dissolved organic C, which could maintain the P-rich microbial biomass in the top layer through fresh inputs but not easily reaching the soil below. Surprisingly, the microbial N fraction did not show differences between sampling depths. We observed a pattern in the microbial N fractions in which May has a relative peak. The large microbial N fraction in the wet season could be due to a shift in microbial composition. A previous report noted non-homeostatic behavior of microbial stoichiometry in (tropical) soils, with especially C:P and N:P ratios showing high variation (Soong et al., 2018). Interestingly, microbial nutrient demand seems to shift toward N acquisition at the end of the wet season and toward P acquisition during the dry season (Schaap et al., 2023).

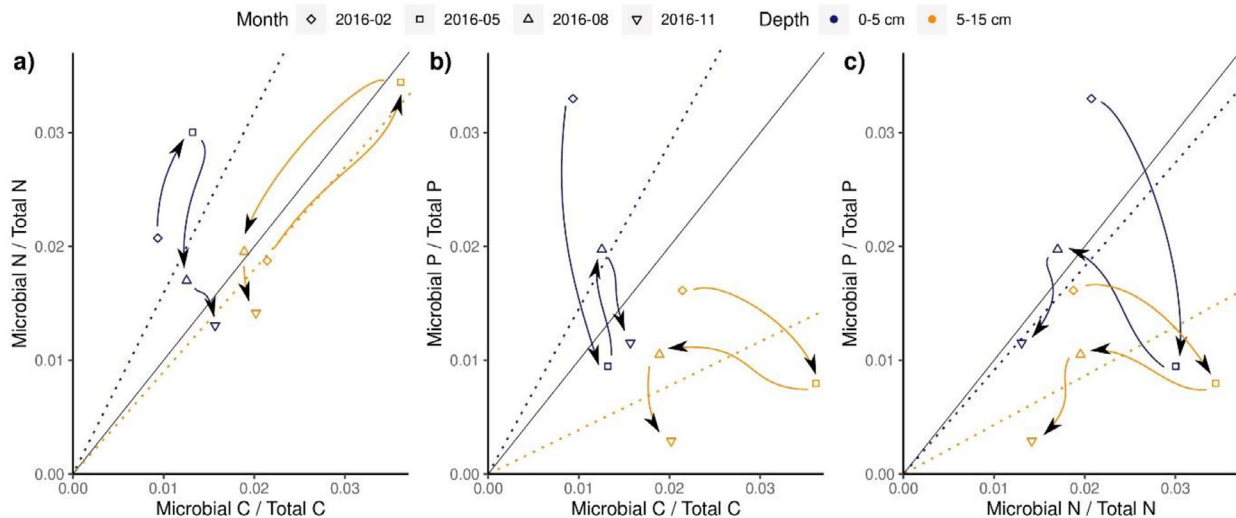


FIGURE 5 Pattern of microbial community C, N, and P as a fraction of bulk soil C_t , N_t , and P_t at 0–5 cm (blue) and 5–15 cm (orange); a) shows C_m/C_t in relation to N_m/N_t , b) shows C_m/C_t in relation to P_m/P_t , and c) shows N_m/N_t in relation to P_m/P_t . Arrows follow the chronological order to emphasize seasonal shifts in microbial stoichiometry. Dotted lines show the averages for the respective depths.

Our results show a relative decrease in N_m compared to C_m during the dry period, potentially due to increased enzyme production in the dry season leading to elevated N demands from microbes (Schaap et al., 2023). During the wet season, we observed relative decreases of P_m compared to N_m . This could be due to shifts in microbial community structure, as shown by Fanin et al. (2013), where the ratio of fungi:bacteria increased with the $N_m:P_m$ ratio. The lower microbial N:P ratios in the top 5 cm (Figure 4c) could thus indicate a higher concentration of bacterial decomposers. We also noted fluctuations in P_m levels throughout the year, with increases in the transition from wet to dry season and decreases during both seasons. These dynamics could be partially attributed to the storage of P in microbial reserves as alternative to shifts in microbial community composition (Kulakovskaya, 2015; Mason-Jones et al., 2023). Such findings underscore the need for further examination of seasonality in the structure and functioning of the microbial community, particularly in relation to the relative abundance of saprotrophic and mycorrhizal fungi and their impact on nutrient demand and turnover in tropical soils.

5 | CONCLUSIONS

In a tropical Terra Firme forest soil, intra-annual climate variability affects total, available, and microbial C, N, and P pools. During the dry season, total and extractable soil C and nutrient pools decrease, whereas extractable N increases. Our study highlights the dynamic microbial stoichiometry as fractions of the total soil resources. Notably, microbial biomass N and P exhibit large fluctuations, which could reflect changes in microbial community structure. By capturing intra-annual shifts in nutrient availability and microbial biomass, we provide a basis for improving insight in how changing climate and seasonality could affect tropical forest functioning by enhancing our understanding of belowground biogeochemical pools and processes.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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