ORIGINAL ARTICLE

Litter inputs and phosphatase activity affect the temporal variability of organic phosphorus in a tropical forest soil in the Central Amazon

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Abstract

Purpose The tropical phosphorus cycle and its relation to soil phosphorus (P) availability are a major uncertainty in projections of forest productivity. In highly weathered soils with low P concentrations, plant and microbial communities depend on abiotic and biotic processes to acquire P. We explored the seasonality and relative importance of drivers controlling the fluctuation of common P pools via processes such as litter production and decomposition, and soil phosphatase activity.

Methods We analyzed intra-annual variation of tropical soil phosphorus pools using a modified Hedley sequential fractionation scheme. In addition, we measured litterfall, the mobilization of P from litter and soil extracellular phosphatase enzyme activity and tested their relation to fluctuations in P- fractions.

Results Our results showed clear patterns of seasonal variability of soil P fractions during the year. We found that modeled P released during litter decomposition was positively related to change in organic P fractions, while net change in organic P fractions was negatively related to phosphatase activities in the top 5 cm.

Conclusion We conclude that input of P by litter decomposition and potential soil extracellular phosphatase activity are the two main factors related to seasonal soil P fluctuations, and therefore the P economy in P impoverished soils. Organic soil P followed a clear seasonal pattern, indicating tight cycling of the nutrient, while reinforcing the importance of studying soil P as an integrated dynamic system in a tropical forest context.

Keywords Amazon · Hedley fractionation · Lowland tropical forest · Phosphatase activity · Phosphorus cycle · Leaf litter

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Introduction

The Amazon Basin contains about one third of the world's remaining tropical forests (Mayaux et al. 2005), playing an important role in the global carbon (C) cycle. Currently, the Amazon rainforest absorbs ~ 0.5 GT C yr^{-1} (Pan et al. 2011), but recent evidence suggests that it is losing its C-sink capacity, potentially induced by rising temperatures and greater drought frequency or by reaching a new state of equilibria adapting to changing climate conditions (Brienen et al. 2015; Hubau et al. 2020; Gatti et al. 2021). One factor that could change the response of the forest to climate change is the CO_2-fertilization effect. This effect occurs when higher atmospheric CO_2 levels would allow an increase in photosynthesis rates, and could augment forest productivity (Zhu et al. 2016). However, the magnitude of this effect may depend on several factors, such as availability of light, water, and nutrients (Du et al. 2020). While in natural forest ecosystems in temperate regions nitrogen (N) is the most limiting nutrient for plant productivity (Oren et al. 2001; Vitousek 1982), tropical forest ecosystems are generally considered to be constrained by phosphorus (P) availability (Hofhansl et al. 2020; Turner et al. 2018; Townsend et al. 2011; Vitousek 1984) with feedbacks to the nitrogen cycle (Nasto et al. 2014; Quesada et al. 2010). Across the Amazonian basin, soil P has been shown to be positively related to forest productivity (Aragão et al. 2009; Quesada et al. 2012). The inclusion of P cycles in regional dynamic vegetation models suggest P limitation will be important in controlling forest productivity and the responses of tropical biomes to global change (Fleischer et al. 2019; Terrer et al. 2019). However, many key processes controlling P availability in tropical forests remain poorly understood.

Approximately 60% of Amazonian forests grow on geologically old and highly weathered soils, typically Ferralsols or Acrisols, with low nutrient concentrations (Quesada et al. 2011). This is in line with assumptions of the P pedogenetic model conceptualized by Walker and Syers (1976), where rock derived (mineral) P ends up in organic, occluded, and non-occluded (i.e., more available) pools at the start of pedogenesis, but after the parent material as a P source is depleted, P availability declines sharply. Total P declines during this soil aging process, due to losses - like leaching - from the system. Eventually most soil P will be either occluded or in organic pools - a phenomenon described as a "terminal steady state" (Walker and Syers 1976). In older, more weathered soils, a larger proportion of P can be found in organic forms and highlights the increased importance of biological activity.

While P is an essential element for plants and microbes, the directly plant-available fraction is usually a relatively small pool compared to the total P concentration (Tiessen 2008), and chemical availability of P is determined by the solubility of ortho-P in a soil, which is mainly defined by sorption-desorption kinetics (Hinsinger 2001). A common method to characterize P accessibility in soils was developed by Hedley et al. (1982), to identify a series of P fractions based on their solubility that represent different levels of bioavailability for inorganic (P_i) and organic P fractions (P_o) (Tiessen and Moir 1993). The P_i fractions include water-soluble P, which should be directly available to plants, but also P bound to aluminum (Al) and iron (Fe), up to P bound to calcium (Ca) and primary P minerals and is therefore usually poorly accessible to plants (Cross and Schlesinger 1995). In soils with low or no Ca, this last fraction is likely to consist of recalcitrant organic matter or otherwise occluded P. In comparison to other anions, P_i has a relatively low mobility in soil (Johnson and Cole 1980). High kaolinite clay contents and high amounts of Al and Fe oxides amplified by low soil pH, common for tropical soils, facilitate sorption of P_i, further reducing its mobility (McGechan and Lewis 2002). The P_o fractions are more difficult to interpret than P_i fractions. They are on the same solubility continuum from water to Ca-bound, being directly derived from plant or microbial sources or from soil organic matter (SOM). Organic P forms are more complex (e.g. phospholipids, DNA, phosphate monoesters, glucophosphates, phytic acids) and have the potential to be an important contributor to P-bioavailability through chemical and biochemical plant acquisition strategies (Darch et al. 2016).

Plants have evolved various mechanisms to maintain a bioavailable pool of P; these mechanisms include an increased presence of root mats dominating the forest floor, fine roots, association with mycorrhizae for P uptake, root exudation of enzymes for mineralization of organic compounds, or exudation to change sorption or microbial activity through the "priming" effect (Buendía et al. 2014; Herrera et al.

1978; Hinsinger 2001; Lugli et al. 2020; Stark and Jordan 1978; Steidinger et al. 2015). With declining plant available P and a relatively larger organic P pool (Turner et al. 2007), plant strategies for efficient recycling and uptake are increasingly relevant (Roberts et al. 2015). Plants might apply different strategies to compete for P (Nasto et al. 2017; Raven et al. 2018; Steidinger et al. 2015). From a plant perspective, those strategies can be categorized as either foraging or mining strategies (Richardson et al. 2011). Foraging strategies serve to explore more soil, while mining strategies are used to access forms of P by chemical alteration in the soil, for example through the excretion of enzymes (Hinsinger 2001; Lloyd et al. 2001). Although it is tough to distinguish the origins of soil phosphatase, root phosphatase appears to only account for a small part of total soil phosphatase activity, underlining the relative importance of microbial processes in the rhizosphere for P dynamics (Cabugao et al. 2021). While organic bound P is not directly available, phosphatases catalyzing the degradation of organic molecules might rapidly change the available pool of P in the tropics (Turner et al. 2018; Wood et al. 2016) and thus can be used as a general proxy for demand of P (Vance et al. 2003).

With declining delivery rate of P_i from mineral sources, recycling of P and the dynamics in the organic P pools become increasingly important. One of the largest fluxes of organic matter in tropical forests is leaf litterfall (Hofhansl et al. 2012), with fluctuations and annual phenological cycles driven by changes in water availability and solar irradiation (Wu et al. 2016). Seasonality of rainfall is an important determinant of litterfall, though fluctuations may vary per region (Chave et al. 2010). Litterfall and its decomposition constitutes an important flux of organic material (and thus nutrients like P) to the soil (Luizão 1989), to maintain nutrient stocks and mineralize P bound in organic molecules and ultimately to plant uptake facilitating biomass production. However, there is an offset between litterfall peak production in the drier season and the mineralization of nutrients in Central Amazonia (Luizão and Schubart 1987). Typically, microorganisms decompose litter, showing a quick initial release of soluble nutrients at the onset of decomposition, which gradually reduces over time (Prescott and Vesterdal 2021). A large part of P released from litter is inorganic (Noack et al. 2012; Schreeg et al. 2017). Moreover, seasonal fluctuations in precipitation also affect decomposition dynamics, not only through the release of soluble compounds, but also by affecting soil moisture and the activity of the microbial community (Krishna and Mohan 2017). If nutrient pulses aboveground are synchronized with nutrient availabilities and plant strategies belowground, this might have implications for our understanding of the dynamic nutritional system that underlies the functioning of the forest (Janssen et al. 2021).

In this study, we aimed to evaluate the temporal dynamics of soil Hedley P fractions in a Central Amazonian forest with low soil P concentration. We suspected that different soil P fractions are not static but vary over time. We expected fluctuations to be most pronounced in the top 5 cm where the biological activity is highest, while in the soil below (5-15 cm) we would expect the same pattern but with a smaller amplitude. Moreover, we hypothesized that seasonal variation is driven by fluctuating inputs (litterfall), subsequential decomposition derived organic and inorganic P inputs to the soil, exchange between soil P fractions (catalyzed by phosphatase activities, among others), and outputs (i.e. plant uptake). We aimed to identify the relative importance of drivers controlling the fluctuation of different P pools, such as litterfall inputs, litter decomposition and phosphatase activity from either plant roots or microbes to degrade P_o compounds. We found that fluctuations in P_o are driven by (1) litterfall inputs, and on the other hand (2) degradation by phosphatase activity, such that (3) both litterfall and enzyme activities follow a seasonal pattern, which reflects differences in biological activity and soil P-release, reflected in soil P_i fractions if not taken up by plants and microbes.

Methods

Site description

The study was carried out at the AmazonFACE experimental site (2°35'40"S, 60°12'29"W) in Central Amazonia (more info on https://amazonface.inpa.gov.br/), approximately 70 km north of Manaus, Brazil, in the "Cuieiras" experimental reserve (Estação Experimental de Silvicultura Tropical - EEST, see also Lapola and Norby 2014; Pereira et al. 2019). Characteristic for the area are old-growth tropical forests locally known as "Terra Firme" forests, situated on plateaus

with nutrient poor and clay-rich soils classified as Geric Ferralsols, with a pH of 3.94, in soils with 68% clay, 20% sand and 12% silt (Quesada et al. 2010). Average annual rainfall is about 2,400 mm, with a drier period from June to October, while the average temperature fluctuates from 25.8°C in April to 27.9°C in September (Araújo et al. 2002).

Soil sample collection

Soils were sampled from 18 sampling points. On 6 locations along a 400 m north-south transect (every 80m), we sampled 3 points in the east-west direction, with a distance of 10m between the 3 sampling points. The sampling scheme was adopted to consistently sample soils close to the AmazonFACE plots (for details, see Lapola and Norby 2014), without disturbing soil within the plots. Soils were sampled in February, May, August, and November 2016, using a custom-made steel soil corer (ø 10 cm). Soils were sampled at 0-5 cm and 5-15 cm depth and transported to the lab for sieving (2 mm), root and detritus removal and further processing. Soil aliquots were stored after weighing and oven drying (48 h at 65°C) until further analysis, while enzyme activity measurements were performed in fresh soil within 3 days of sampling. Moisture contents of fresh soil were calculated from the weight differences before and after drying (Fig. 1) to express all soil properties throughout this study on a dry soil basis. Soils were analyzed individually and not bulked. All analyses were performed at the LTSP (Laboratório Temático de Solos e Plantas) laboratory at INPA (Instituto Nacional de Pesquisas da Amazônia) in Manaus, Brazil, nationally certified by Embrapa Soils (2016 Fertility Laboratory Quality Analysis Program, PAQLF, https://www.embrapa.br/en/solos/paqlf) and by the PIATV (Esalq/USP) inter-laboratorial program of vegetation tissue analysis (Grade A, http://piatv.com.br/).

Soil P-fractionation

Phosphorus fractions were determined in oven dried soils, with an adaptation of the sequential extraction method developed by Hedley et al. (1982; described by Tiessen and Moir 1993; adapted by Quesada et al. 2010, Fig. 2). The extractant sequence was an
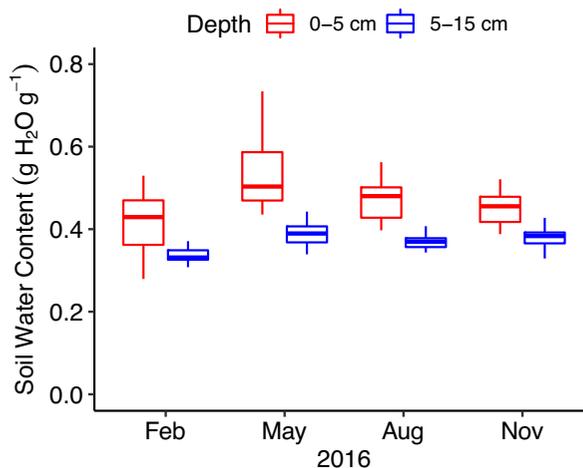

Fig. 1 Soil water contents in $g\,H_2O\,g^{-1}$ for each sampling date, at both sampling depths ($n = 18$)

anion exchange membrane (resin strip) in water, 0.5 M $NaHCO_3$ (bicarbonate fraction, pH 8.5), 0.1 M NaOH (hydroxide fraction) and 1 M HCl (hydrogen chloride fraction, Fig. 2), each of them shaking for 16 hours. All extracts were analyzed for inorganic P_i. In addition, the $NaHCO_3$ and NaOH extracts were digested with a sulfuric acid solution (H_2SO_4, 0.9 M) and analyzed for total P, which allowed the calculation of their respective organic (P_o) fraction. As an adaption to the Hedley et al./Tiessen and Moir (1993) method, the concentrated HCl-extraction step and digestion of the soil residue were not followed. Instead, another soil subsample was analyzed for total P by digestion with a concentrated sulfuric acid solution (H_2SO_4, 18 M), followed by H_2O_2 (Quesada et al. 2010). All seven extracts were analyzed for PO_4 concentrations photometrically (712 nm) using the Murphy-Riley method and are given in $\mu g\,g^{-1}$ dry soil (Murphy and Riley 1962). Resulting fractions include four inorganic (P_i) fractions (in order of decreasing availability); the resin fraction, the bicarbonate fraction, the hydroxide fraction, and the hydrogen chloride fraction, along with the organic bicarbonate and hydroxide extractable fractions (P_o). The residual P fraction was obtained from subtracting the sum of the extractable inorganic and organic P fractions from the total P (Fig. 2). All analyses were accompanied by two method blanks (no soil) to account for contamination or background signal, and possible lab variation was accounted for by
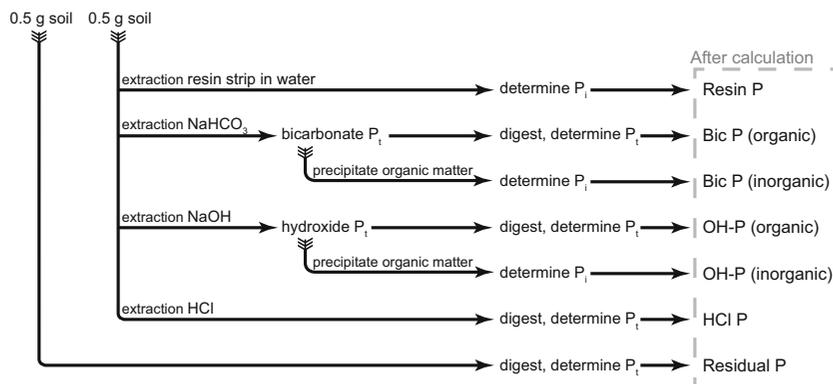
Fig. 2 Schematic view of the Hedley fractionation method for sequential extraction of P, modified from Tiessen and Moir (1993). The organic P (P_o) is the difference between the inorganic P (P_i) and the total P (P_t). The residual fraction is the difference between the total P from the entire sample and the sum of the extractable fractions. Details in Methods section 'Soil P-fractionation'

analyzing standards during each batch of photometric extract reading. The blanks from the standard curves (calibration blanks) were used to calculate the detection limit for each batch (defined as $3 \times SD$ of the blanks) during analysis. Readings were discarded if they were under the detection limit, except for the method blanks that were subtracted from each sample value to account for background noise or contamination. Tests of the fractionation method resulted in an average coefficient of variation for individual soils analyzed in different batches of 0.11 for the resin fraction, 0.17 for the inorganic $NaHCO_3$ fraction, 0.14 for the organic $NaHCO_3$ fraction, 0.09 for the inorganic $NaOH$ fraction, 0.13 for the organic $NaOH$ fraction, and 0.20 for the HCl fraction.

Litterfall and P-input

Litterfall was collected biweekly at two of the AmazonFACE plots located along the transect (used in this study) starting in August 2015. Litter traps (0.5×0.5 m, n=24) were installed 1 m above the ground, 12 traps per plot in a circular pattern. The total litter was dried, separated into leaf litter and other litter fractions, weighed, and analyzed for total P (for total P subsamples were digested with nitric-perchloric acid and concentrations determined with the Murphy-Riley method as described above). Total litter P was scaled up to g m^{-2}, with the standard error showing the dif-

ferences between individual litter traps. We aimed to estimate P release from litter over time accounting for a potential delay (time lag) between leaf litterfall, its decomposition, and subsequent P release into soil. To estimate P release from leaf litter over time, we used data from a litter decomposition experiment conducted at the same study site. The decomposition experiment measured remaining nutrients in litter, including P, which we used to fit a simple model following an exponential decline as Eq. (1) (adapted from Olson 1963), with f as the mass fraction of remaining P in leaf litter:

$$f(x) = e^{-bx} \qquad (1)$$

with $b = 0.00178$ as decomposition constant ($R^2 = 0.82$, data from Martins et al. 2021) for the available 188 days of the decomposition data. We did not take into account further data on litter stoichiometry or litter biomass, only the values for remaining P were used. To estimate P loss from litter from a certain litter subsample on a given day, the differential of Eq. 1, presented here as Eq. 2:

$$f'(x) = -b \times e^{-bx} \qquad (2)$$

was used. We combined this formula with litterfall data (i.e. leaf litter per day for each sampling interval) to account for seasonal variation in inputs, and

summed the litter P-loss from litterfall (up to an arbitrarily chosen thousand days prior) to get an estimation of the litter P-input to soil (litter P-loss) on a given day from the following Eq. 3:

$$-\sum_{t=0}^{1000} r \times c_{t=0}(-b \times e^{-bt}) \tag{3}$$

where t are the days prior to the day of interest (1000 days), $c_{t=0}$ is the amount of litter at the start of each t and r is the initial concentration of litter P. Note that we use this formula with the same decomposition constant for the whole year, in both the wetter and the drier season. It is worth noting that the decomposition experiment took place across rainfall regimes as well, and that precipitation might have a limited impact on decomposition (Sanches et al. 2008).

Potential extracellular soil acid phosphatase activity

We used a fluorescence method for analyzing potential extracellular acid phosphatase enzyme activities based on Marx et al. (2001) and calculations from G erman et al. (2011). Acid phosphatase was assayed in soil slurries of 0.5 g of fresh soil in 50 ml sodium acetate buffer (pH 5.5) and vortexed for 1 minute before pipetting (200μl) in a black 96-well microplate. As a substrate, we used 4-methylumbelliferyl phosphate (M8168 Sigma), using Methylumbellliferyl as a standard (M1381 Sigma). In addition we measured substrate controls, sample controls and blanks to account for potential quenching effects. Microplates were incubated in the dark for 60 minutes (at 20°C) and fluorescence was measured using an Infinite F200 Pro plate reader (Tecan Austria GMBH, Grödig, Austria), with fluorescence intensity measured from the top ($\lambda_{excitation}$ = 360 and $\lambda_{emission}$ = 440 nm). Potential extracellular acid phosphatase activities were calculated following German et al. (2011) and are given in μmol g^{-1} day^{-1}, indicating potential activity of the enzyme at substrate saturation on a dry weight basis.

Statistical analysis

Data organization and calculations were performed with the "tidyverse" package (version 1.3.0, Wickham et al. 2019), graphs were made with the package "ggplot2" (version 3.3.2, Wickham et al. 2016). We calculated daily litter P loss based on field collections

of litter and Eq. 3. Each soil P fraction was evaluated for differences between months and soil depths with linear models or linear mixed models using the lme function from the "nlme" package (version 3.1-148, Pinheiro et al. 2020) with the month and soil depth as fixed factors. We used sample location as a random effect and evaluated the best model fit according to the Akaike information criterion (AIC). For all fractions, models were allowed different variances per group combination (month and depth) using the VarIdent variance structure. Because the model fit was better with only depth included in VarIdent for the inorganic bicarbonate fraction, and month only for the HCl fraction, those models were fitted with only the mentioned grouping term in the variance structure. The models' residuals were checked for homogeneity and normality and variables were log-transformed if needed.

Since we hypothesized that P fractions changed over time, we calculated ΔP_o (the change in P_o fractions between two consecutive sampling dates for each sampling point). The same procedure as above was followed, with the ΔP_o as response variable, either phosphatase or litter P loss as the first fixed variable in separate models (since litter P-loss was not location-specific, while phosphatase was), the sample location was added as a random effect if this improved the model fit. We tested the influence of litter P inputs and phosphatase activity for each organic P fraction separated by soil depth. Again, resulting models were validated with visual checks of residuals on homogeneity and normality. All analyses were performed with R version 3.6.3 (R Core Team 2020).

Results

Soil P-fractions and their dynamics

Total soil P was 143.6 μg g^{-1} for the top 5 cm ($\pm$ SE 0.55), and 117.7 μg g^{-1} for 5-15 cm depth ($\pm$ SE 0.73, Table 1). The P concentrations of all, except the HCl and residual fractions, were higher in the top 5 cm compared to 5-15 cm soil depth. The extractable inorganic fractions accounted for 29.1 μg g^{-1} ($\pm$ SE 0.12, 20 % of total P) at 0-5 cm, and for 17.4 μg g^{-1} ($\pm$ SE 0.07, 15% of total P) at 5-15 cm, the organic fractions accounted for 42.5 μg g^{-1} ($\pm$ SE 0.34, 28% of P) and 23.3 μg g^{-1} ($\pm$ SE 0.16, 19%) respectively.

Table 1 Average total P and soil P fractions ($\pm$ SE) from the Hedley fractionation, in $\mu g\ g^{-1}$, with $n = 69$

Fraction		0-5 cm	5-15 cm
Total P		143.59 ($\pm$ 0.61)	112.50 ($\pm$ 0.43)
P_i	Resin	7.94 ($\pm$ 0.05)	3.75 ($\pm$ 0.03)
	NaHCO$_3$	4.85 ($\pm$ 0.04)	1.61 ($\pm$ 0.02)
	NaOH	14.31 ($\pm$ 0.06)	9.89 ($\pm$ 0.03)
	HCl	2.05 ($\pm$ 0.02)	2.12 ($\pm$ 0.02)
P_o	NaHCO$_3$	8.38 ($\pm$ 0.08)	5.82 ($\pm$ 0.04)
	NaOH	32.03 ($\pm$ 0.28)	17.55 ($\pm$ 0.13)
Residual P		78.43 ($\pm$ 0.56)	72.61 ($\pm$ 0.37)

Details on the extraction procedure in the Methods section 'Soil P-fractionation'

The residual P accounted for most of the total P, on average 78.4 ($\pm$ SE 0.56, 51%) at 0-5 cm and 72.6 $\mu g\ g^{-1}$ ($\pm$ SE 0.37, 65%) at 5-15 cm.

Our results show that soil P fluctuated over the course of the year (Fig. 3) and differed between soil depths (0-5 cm and 5-15 cm) for most fractions (Table 2). Generally, the top 5 cm had higher P concentrations, reflected mainly in the extractable P fractions; the residual fraction did not show a significant effect of soil depth. The most labile fraction, resin P, was higher in the 0-5 cm (7.9, $\pm$ SE 0.05) as compared to the 5-15 cm layer (3.8, $\pm$ SE 0.03) and increased 38% from February to May, but decreased again until November (-15% between May and August, and -48% between August and November). The 5-15 cm resin fraction was significantly larger in February compared to the other months (60% higher than the average), while November had a significantly smaller resin fraction (51% below average). The inorganic bicarbonate P fraction showed some significant differences between months in the topsoil, but those differences were not found at 5-15 cm. For the inorganic hydroxide fraction the November sampling proved significantly lower than the May and August samplings at both depths. The hydrogen chloride fraction had a more diverse pattern, with significantly higher values in February at both soil depths (Table 2).

In contrast to inorganic P fractions, the organic P fractions showed a stronger temporal fluctuation.

Table 2 Analysis of variance F statistics, with p values in parentheses, for each fractions' responses to sampling time (Month), sampling depth (Layer) and their interaction as fixed factors

	Model terms	df	F (p)
Resin	Intercept	1, 113	819.4 (<0.0001)
	Month	3, 113	45.0 (<0.0001)
	Layer	1, 113	112.7 (<0.0001)
	Month x Layer	3, 113	7.44 (0.0001)
NaHCO$_3$ inorganic	Intercept	1, 113	146.7 (<0.0001)
	Month	3, 113	8.17 (0.0001)
	Layer	1, 113	156.5 (<0.0001)
	Month x Layer	3, 113	12.9 (<0.0001)
NaHCO$_3$ organic	Intercept	1, 113	1747 (<0.0001)
	Month	3, 113	39.4 (<0.0001)
	Layer	1, 113	19.7 (<0.0001)
	Month x Layer	3, 113	ns
NaOH Inorganic	Intercept	1, 112	1332 (<0.0001)
	Month	3, 112	3.03 (0.0322)
	Layer	1, 112	131.5 (<0.0001)
	Month x Layer	3, 112	6.50 (0.0004)
NaOH organic	Intercept	1, 113	1196 (<0.0001)
	Month	3, 113	45.7 (<0.0001)
	Layer	1, 113	106.6 (<0.0001)
	Month x Layer	3, 113	ns
HCl	Intercept	1, 113	1851 (<0.0001)
	Month	3, 113	6.92 (0.0001)
	Layer	1, 113	ns
	Month x Layer	3, 113	ns
Residual	Intercept	1, 109	1602 (<0.0001)
	Month	3, 109	5.77 (0.0010)
	Layer	1, 109	ns
	Month x Layer	3, 109	ns

Includes sampling location as a random effect where this led to an improved model fit. Only significant values ($p < 0.05$) are shown

While the F values for the inorganic fractions generally indicate a larger effect size for sampling depth, the organic fractions generally show a relatively stronger effect of the sampling month, and therefore show a stronger influence of seasonality. We found no direct trade-off between fractions, e.g., relatively smaller

organic fractions did not lead to an increase in the inorganic fractions, but rather varied in roughly the same way across inorganic and organic forms.

The two organic soil P fractions showed their highest average values in May for both depths (Fig. 3). While other months had lower averages for the organic fractions, not all contrasts were significant. The changes in the organic fractions followed a pattern of a substantial increase in May, and a decline thereafter.

Since the organic fractions showed the clearest variation, we calculated the differences between consecutive sampling dates (Table 3). Between February and May, the organic P in the top 5 cm increased by a little over 27 μg g^{-1}, increasing the size of the organic fractions in 3 months with +69% for both P_o fractions. Between May and August, the organic fractions declined (-47% for bicarbonate P_o, -44% for hycdroxide P_o), with no increase in the inorganic pools (Fig. 3). The same pattern can be observed for the 5-15 cm depth, albeit in lower concentrations. November showed the lowest concentrations of P_o, indicating a continued depletion in the dry season.

Litterfall and litter decomposition

The total leaf litterfall amounted to 5377 kg ha^{-1} y^{-1} ($\pm$ SE 49, or an average of 1.47 $\pm$ SE 0.01 g m^2 day^{-1}) (Fig. 4a), the annual amount of P in that litter was 0.71 kg ha^{-1} y^{-1} ($\pm$ SE 0.01, or an average of 194.8 $\pm$ SE 1.8 μg m^2 day^{-1}). Litterfall showed a clear seasonal pattern, with a peak at the end of the drier part of the year (August). According to the applied decomposition model, the estimated litter P-loss in 2016 averaged 190.9 ($\pm$ SE 0.03) μg m^2 day^{-1} (including decomposition of leaf litter produced from previous years), accounting for the time between litterfall and P mobilization from litter to soil (Fig. 4b). The cumulative modeled P input over the whole year amounted to 0.69 kg ha^{-1};

giving a modeled average daily input of P to the soil of 196 μg m^2 day^{-1} ($\pm$ SE 0.06) between February and May, 174 μg m^2 day^{-1} ($\pm$ SE 0.04) between May and August and 193 μg m^2 day^{-1} ($\pm$ SE 0.06) between August and November. Overall, the half time for litter P was 379 days according to the model, and because decomposition follows an exponential pattern most of this loss took place at the start of decomposition (i.e., with each daily litter input).

Extracellular acid phosphatase activities

Potential phosphatase activity at 0-5 cm soil depth amounted to 119.0 μmol g^{-1} day^{-1} ($\pm$ SE 0.6) on average, at 5-15 cm the average was 69.9 μmol g^{-1} day^{-1} ($\pm$ SE 0.5). Phosphatase activity ranged from 91.5 μmol g^{-1} day^{-1} ($\pm$ SE 1.6) in May, to 148.8 μmol g^{-1} day^{-1} ($\pm$ SE 1.8) in August (in the topsoil), while the 5-15 cm depth showed a similar pattern with a lower average of 48.2 μmol g^{-1} day^{-1} ($\pm$ SE 0.9) in February, to a high 97.9 μmol g^{-1} day^{-1} ($\pm$ SE 1.4) in August (Fig. 5).

Combining litter, enzyme, and organic P dynamics

Phosphatase activity was related to the changes in organic P (ΔP_o) (Fig. 6 a, b). In the 0-5 cm depth a negative relationship was observed between the phosphatase and the change in organic bicarbonate P ($F_{(1, 49)} = 11.86$, $p < 0.01$), and a significant negative relationship between phosphatase and the changes in the organic hydroxide fractions ($F_{(1,46)} = 16.76$, $p < 0.001$), while at the 5-15 cm depth the regression results were not significant, despite following similar pattern as in the top 5 cm.

We evaluated the average P loss from litter, i.e. P input to soil, between sampling dates, and its effect on the organic fraction changes (ΔP_o) (Fig. 6 c, d) as was done with potential phosphatase activity above. The effect of P loss from litter on the change in the organic

Table 3 Average change in the organic fractions of P (ΔP_o) in μg g^{-1}, between sampling dates. Standard error between brackets

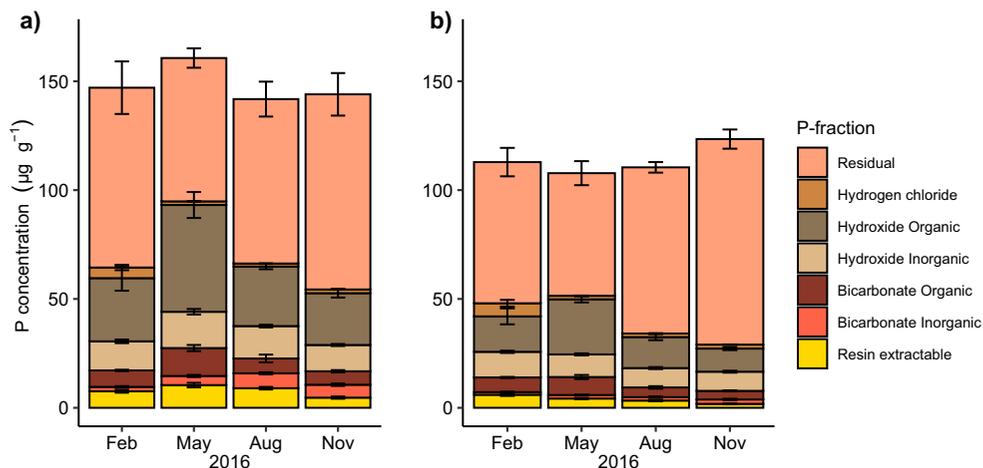|	Change between	Feb - May (n = 15)	May - Aug (n = 18)	Aug - Nov (n = 18)
0-5 cm	NaHCO$_3$ Organic	+ 5.44 ($\pm$ 1.52)	− 6.02 ($\pm$ 2.63)	− 0.64 ($\pm$ 1.38)
	NaOH Organic	+ 21.78 ($\pm$ 7.55)	− 21.69 ($\pm$ 6.21)	− 3.56 ($\pm$ 2.32)
5-15 cm	NaHCO$_3$ Organic	+ 2.13 ($\pm$ 1.15)	− 3.83 ($\pm$ 1.20)	− 0.51 ($\pm$ 0.74)
	NaOH Organic	+ 8.71 ($\pm$ 4.27)	− 11.05 ($\pm$ 2.09)	− 3.63 ($\pm$ 1.29)

Fig. 3 Cumulative Hedley soil P fractions determined in 4 campaigns at a) 0-5 cm depth, and b) at 5-15 cm soil depth. In their sequential extraction order (i.e. first extraction on the bottom, last extraction on top, stacked so the top of the bar represents total P). Concentration per dry soil, error bar represents standard error ($n = 18$)

P fractions was significant, this time for all organic fractions. In the topsoil, bicarbonate ΔP_o showed a slightly weaker relation to the litter input ($F(1, 49) = 13$, $p < 0.01$) than in the 5-15 cm depth ($F(1, 49) = 14.27$, $p < 0.01$) while for hydroxide ΔP_o this relation was slightly stronger at 0-5 cm ($F(1, 49) = 16.16$, $p < 0.01$) compared to the lower depth ($F(1,49) = 16.57$, $p < 0.01$). The phosphatase showed a negative relationship with the change in organic fractions, whereas litter inputs showed a positive relation with the change in organic fractions; despite some variation in strength of the response, phosphatase decreased the size of the organic fractions, while litter P inputs increased the size of the organic fractions.

Discussion

Overview

In this study we aimed to disentangle the controls over seasonal dynamics of soil P cycling in a tropical forest, by studying P inputs by leaf litter, changes of several fractions of soil P through time, as well as

Fig. 4 a) Leaf litter collected at the AmazonFACE study site in 2016, and b) the modeled P-loss from that litter according to Eq. (3), used in this study as soil P-input from litter. Note that the litter data used to calculate this litter P loss is not entirely shown in a) (i.e. pre-2016 data was also used to get soil P-input). Details in Methods section 'Litterfall and P-input'
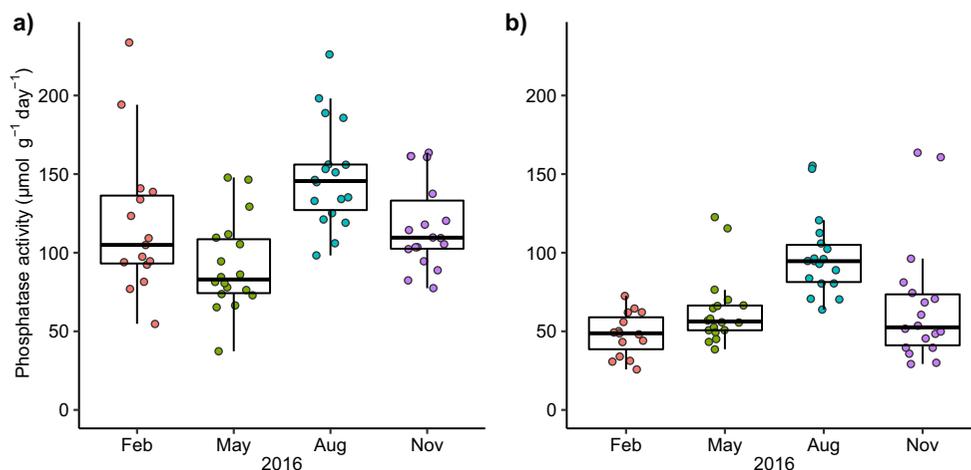
Fig. 5 Potential activities of soil extracellular acid phosphatase (n=18 per timepoint) at a) 0-5 cm depth, and b) at 5-15 cm depth

phosphatase activity catalyzing the turnover of organic P. Given that the soils at our study site are very old, we would expect that P inputs drive soil P cycling. In line with our hypothesis that P availability varies seasonally we found a clear seasonality of soil P fractions. Furthermore, we found that soil phosphatase activities were significantly negatively related to net changes in organic P fractions at the 0-5 cm depth (with higher phosphatase activity causing a decline in P_o pools, or a lower phosphatase activity causing an increase in P_o pools, in particular in the top 5 cm of soil.), but not significant at 5-15 cm. The decomposition model, relating the observed fluctuations in litterfall to changes in the soil organic P fractions, confirmed our hypothesis that input of P from litter decomposition and associated activities of microbial and plant derived phosphatases were controlling soil (organic) P fluctuation in central Amazonian terra-firme forests.

Soil P pools and turnover

Our results suggest that the organic P fraction was the most variable component of the local soil P pool intra-annually, arguably driving soil P_i availability though mineralization into plant accessible pools. However, we could not detect a clear seasonal pattern for P_i pools. Our site showed typical P concentrations reported for Ferralsols. Quesada et al. (2010) reported that two thirds of the studied soils across the Amazon contain below 100 mg kg^{-1} total extractable P. When comparing our results with other natural ecosystems, the total P concentration and total extractable P at

our study site were low (Cross and Schlesinger 1995; Johnson et al. 2003; Turner and Engelbrecht 2011; Yang and Post 2011), especially considering the 5-15 cm soil depth, which could arguably be more suitable for comparison since this depth is more representative of mineral soil P stocks. The top layer played a more active role in biological (re)cycling and showed larger seasonal fluctuations, and P decreased rapidly from the top 5 cm down to 5-15 cm. As Johnson et al. (2003) and others have argued, the controls over labile P might be less dependent on soil weathering status (and thus total P) than often assumed; other mechanisms, including sorption-desorption dynamics, redox state, and mineralization, are likely to play a large role.

According to Helfenstein et al. (2020), turnover times for the extractable inorganic fractions of the Hedley fractionation procedure are minutes to hours for the resin and bicarbonate fractions, while hydroxide fractions have a turnover of days to months, and only hydrochloric acid fractions have longer residence times. The P_i pools may vary in their bioavailability and since the turnover times of the more available fractions may be fast (Helfenstein et al. 2020), it is likely that we may have missed some of the variation between sampling intervals. In our study, labile P_i fractions showed little variation and were not related to either litter inputs or phosphatase activity. This could be due to an adverse effect on P_i fractions caused by sample pre-treatment (oven drying at 65°C), which could have affected solubility and inflating the fraction sizes of especially the most labile fractions (see also Ajiboye et al. 2004). However, across
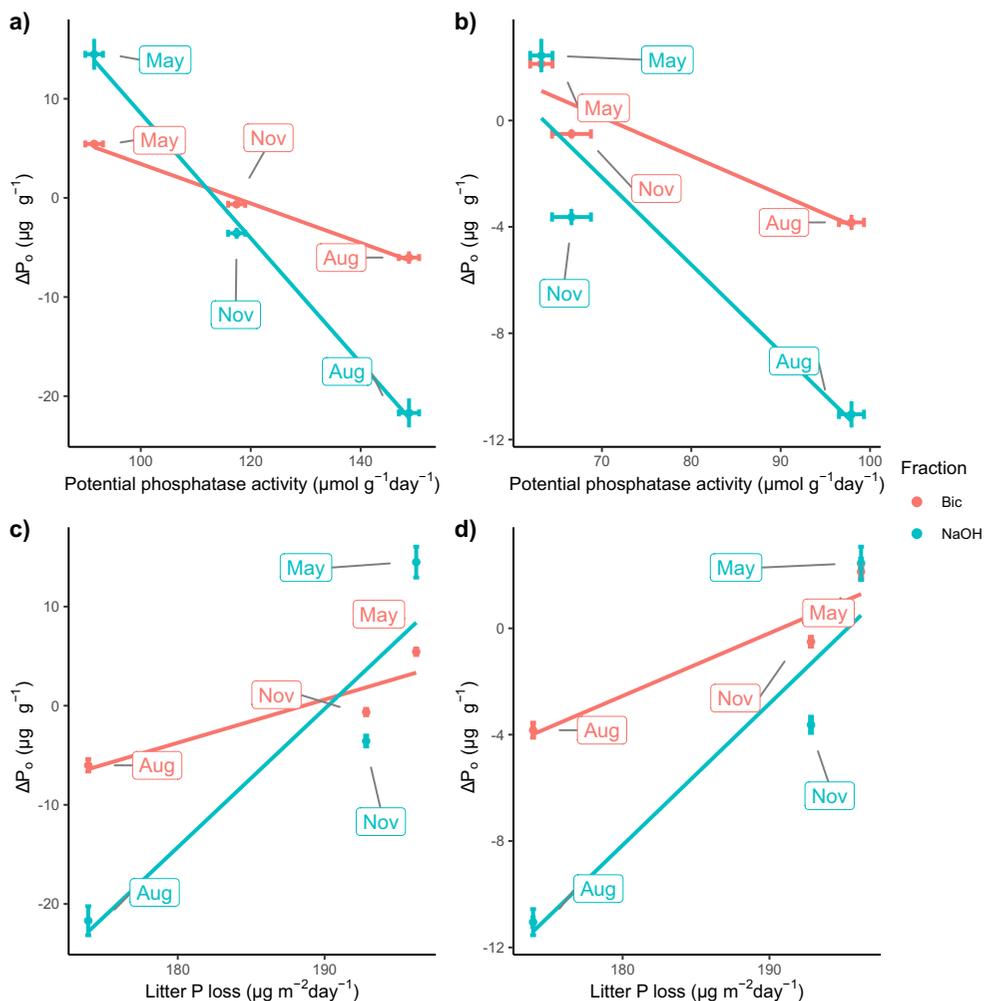
Fig. 6 Relation between average changes in the organic fractions of soil P (ΔP_o) and assumed drivers of those changes. a) relation between average phosphatase and ΔP_o at 0-5 cm depth, b) at 5-15 cm depth, c) the relation of modeled litter inputs (average between sampling dates, Fig. 4) with average ΔP_o at 0-5 cm, and d) at the 5-15 cm depth. This graphical representation of the found effects does not depict the applied (mixed) models referred to in the text, since here only the averages of the tested relations are shown. Error bars show the standard error

sampling dates soil water content was not highly variable (Fig. 1) and did not significantly affect labile P_i fractions. The less available (slow turnover) fractions are probably better represented considering the products of mineralization of P_o do not stay in the soil solution long enough for a net increase of available P_i pools to be detectable at our sampling frequency.

In a tropical ecosystem, organic P fractions are crucial as buffer for the shorter-term P-availability, while the actual variability of the (inorganic) ortho-P fractions might be hard to measure in an observational study, especially when P-demand and thus turnover is high. In tropical soils, organic forms of tropical soil P

can constitute about a quarter of total P according to Turner and Engelbrecht (2011) although there is substantial variation across the Amazon (Quesada et al. 2010). Approximately two thirds of the organic P fraction can be bound in the microbial biomass (Turner et al. 2015). While in our study the proportion of organic P compared to total P is similar overall, we show substantial variation over the year. The relative peak of the organic P in May, together with the low concentration of organic P in November (about a factor 2 difference) have large implications suggesting that the organic fractions are the prime regulator of more available forms; if the regulator "stock" of P_o

varies, the cycled P_i is likely to be impacted by the same magnitude at shorter time spans. Although the importance of organic P has been well described and is of central importance to the Walker and Syers model (1976), its annual variation is known to a lesser extent.

The effect of soil phosphatase and litter decomposition

High phosphatase activity indicates a high P demand (Allison et al. 2011) but absolute values of soil phosphatase activities at our study site were low compared to global averages (Margalef et al. 2017) which suggests that P limitation is not as high as in other (tropical) forests. However, this meta-analysis was done with colorimetric assays, and fluorescent assays generally show lower values (Nannipieri et al. 2011). Our results are slightly higher than other fluorescent enzyme assays performed in tropical forest soils (e.g. Turner and Wright 2014; Nottingham et al. 2016). Even so, absolute activities might not be the best indicator of nutrient limitation (Moorhead et al. 2016), and should be used with caution. Interestingly, phosphatase activity was not related to the size of the inorganic P fractions but rather to the organic fractions. As mentioned before, the soil drying process might have affected the solubility of the more labile fractions, limiting their accuracy. Even so, this result might indicate that the (labile) inorganic P fractions are rapidly taken up by plants and microbes. Moreover it suggests that plant roots and the microbial community are able to access organic P-pools by releasing enzymes, but also that the organic P pool, including P stored in microbial biomass, can act a buffer stabilizing the P-supply throughout the year.

The production of phosphatase is demand driven, rather than supply driven (Kitayama 2013), but there are alternative hypotheses including a supply-driven philosophy (Turner 2008), as well as indications that P cycling in tropical forests may be affected by climate, and especially precipitation (Huang et al. 2011; Wood et al. 2016). In our study, it might very well be that the in-situ mineralization rates were generally not limited by climate at any time during the year (as is suggested by our relatively constant soil moisture throughout the year, Fig. 1), but by enzyme or substrate availability. If phosphatase activity peaks when the soil organic P fractions are relatively small, P

demand might be driving investments in phosphatase since the substrate has largely been transformed. On the other hand, the higher investment in phosphatases could be synchronized with higher inputs of substrate from litter, and therefore variation in enzyme production could be supply- rather than demand-driven. It is also worth emphasizing that the potential enzyme activities were rather high throughout, which suggests that the in situ mineralization rates were more dependent on P_o supply than on P_i demand. However, due to the nature of nutrient re-cycling between vegetation and soil it is challenging to distinguish cause and effect. What we can conclude, however, is that the phosphatase, whether demand-driven or supply-driven in its activity, is correlated with changes in the organic P fractions and thus affects P-availability.

Leaf litterfall increased during the drier season, as has been described for other studies conducted in the region (Luizão 1989; Wu et al. 2016). Without a doubt, the phosphorus return via litter inputs was crucial to sustain cycling of nutrients within in the forest. Observations underlining the relation between litter inputs and soil organic P are found for both tropical and temperate forests (Tiessen et al. 1994; Beck and Sanchez 1994; Chen et al. 2003). Litter manipulation and fertilization experiments in Panama found that three years of litter addition induced substantial increases, while litter removal decreased organic P pools (Vincent et al. 2010), whereas after six years this effect decreased (Sheldrake et al. 2017) possibly due to the changes in P_o turnover in the manipulated plots (Sayer et al. 2020). Especially under the litter removal treatment, the decrease in P_o pool size seems to signal its importance, but on such a timespan some additional sources of P from deeper soil or from more recalcitrant fractions could be responsible for maintaining the nutrient cycle (Sayer et al. 2020; Sheldrake et al. 2017). Under P addition, a fertilization experiment in the same area resulted in higher microbial P, as well as significant changes to other microbial nutrients, indicating the links of the P cycle to other nutrients and reenforcing the hypothesis of P-limitation from a microbial point of view (Turner and Wright 2014).

The decomposition model used for our study has a mediating effect on peaks observed in the litterfall and conceptualizes a delay between litterfall and litter soil P input. Even though this model serves well for our time scale, on shorter timescales decomposition

(i.e. litter P loss) can be argued to be more complex and dynamic than our (simple) model; mainly rainfall and soil moisture have controls over the shorter-term dynamics, and there are several transformation pathways that could add an additional layer of complexity to the decomposition process (Prescott and Vesterdal 2021). Moreover, litter P-loss in inorganic forms which constitute the majority of soil P inputs (Noack et al. 2012; Schreeg et al. 2017) might be taken up quickly by plants and microbes alike. The uptake of P_i by plants and the returns of P via root litter are beyond the scope of this study, and our P_o pool includes microbial derived P. The resulting P input to the soil from decomposition might not be as smooth as the model predicts, but it shows that a simple model for decomposition lines up well with soil P if integrated over time, despite the limitation of having only 4 sampling timepoints.

The dynamic nature of the P-cycle

Our study underlines the dynamic nature of the plant-soil system regarding P availability in tropical forest ecosystems. Research in another lowland forest in the Amazon showed the importance of available bicarbonate and hydroxide fractions in P cycling as opposed to more recalcitrant fractions (McGroddy et al. 2008), but the fractions had not been differentiated between inorganic and organic forms. Studies in drier forests or sites with a more pronounced dry season did differentiate between organic and inorganic P. Turner et al. (2015) studied the impact of fertilization on organic soil P fractions in a Panamanian forest (about three times higher total P compared to our site), and found that large parts of the seasonal variation and the fertilization effects were explained by the microbial biomass P, suggesting a relative stable extracellular P_o pool and a more seasonal microbial one. Mirabello and colleagues (2013) found a decline in the organic bicarbonate fraction for the dry season in the same study region, which might indicate increased mineralization during that time and thus would support our findings of increased phosphatase activity in drier months. The hydroxide extractable organic P fraction showed the opposite pattern however. Studies in drier tropical forests also indicate the importance of precipitation in the P-cycle, both in terms of litter dynamics (Valdespino et al. 2009), and sorption of P (Campo

et al. 1998), while Waring et al. (2021) compared different forests and found that soil development stage was the major driver of the soil P balance.

Overall, our results suggest that soil organic P pools in highly weathered tropical soils are more dynamic than previously reported. In low-P soils organic P inputs are the main source of the nutrient and the biological cycling appears to be highly relevant. Future studies should focus on microbial community dynamics to ultimately identify processes driving P-cycles in tropical forests. Turner et al. (2013) highlighted the crucial role of microbial biomass P in the retention and cycling of P during ecosystem development, which indicates that microbial community dynamics might be paramount to understanding organic soil P dynamics in addition to the factors accounted for in this study. Mycorrhizal interactions with different soil fractions and partitioning thereof is adding another layer of complexity to the interaction of P with the ecosystem (Liu et al. 2018). Although ecosystem models are increasingly recognizing the importance of P in tropical systems (Fleischer et al. 2019), and starting to implement P cycle dynamics and processes, mechanistic understanding of P in ecosystem processes is far from complete (Vitousek et al. 2010; Wright et al. 2018). Our results show substantial variability in the soil P pools during the year, contributing a dynamic representation of the P cycle and the seasonal pattern of its different components (i.e., soil P-pools) and its drivers.

This dynamic view of the soil P cycle also indicates a high efficiency of P cycling in tropical forests, of which the deeper implications point toward a sustained limitation by P on forest functioning under global change scenarios (Fleischer et al. 2019). Plants might increase the amount of bioavailable P in the system by accessing relatively occluded forms of P, by mining in deeper soil layers, or by exudation of organic acids to liberate currently unavailable P (Jin et al. 2015). While increased CO_2 might stimulate investments below ground (Hoosbeek 2016)- i.e., increased root growth, root exudation including phosphatases - the current dependence on mineralizing P from organic compounds limits the amount of P that could be easily liberated to sustain an acceleration or intensification of the P-cycle, especially if soils are almost at Walker and Syers' (1976) terminal steady state. If global changes affect the current seasonality,

the tight cycling that is reported here could be affected - leading to a less effective cycling of the nutrient.

Conclusions

Our study considering seasonal variation of soil P and its drivers shows how Central Amazonian soil P fractions may fluctuate inter-annually, in response to litter inputs to the soil and phosphatase through root and microbial demand. Our study indicates that litter P inputs are correlated with the soil organic P pool, while potential biochemical mineralization through soil enzymes showed a negative relation to those organic fractions. Albeit the fact that a tight cycling of P in tropical forest ecosystems indicates that this nutrient is in short supply, the specific limiting steps are still up for debate, and the observed diametric relationship between different factors within the plant-microbe-soil system further highlights the relevance of studying the P-balance as an integrated dynamic system.

Availability of data and material Data used in this manuscript will be made available on a public repository upon publication

Compliance with Ethical Standards

Conflict of Interests The authors declare no conflict of interest.

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