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Direct evidence for phosphorus limitation on Amazon forest productivity

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The productivity of rainforests growing on highly-weathered tropical soils is expected to be limited by phosphorus (P) availability[1]. Yet, controlled fertilisation experiments have failed to demonstrate a dominant role for P in controlling tropical forest net primary productivity (NPP). Recent syntheses have demonstrated that responses to N addition are as large as to P [2], and adaptations to low P availability appear to allow NPP to be maintained across major soil P gradients [3]. Thus, the extent to which P availability limits tropical forest productivity is highly uncertain. The majority of the Amazonia, however, is characterised by soils even more depleted in P than where most tropical fertilisation experiments have previously taken place[2]. Thus, we established the first P, nitrogen (N), and base cation addition experiment in an old growth Amazon rainforest, with the site's low soil P content representative of ~60% of the basin. Here we show that NPP increased exclusively with P addition. After 2 years, strong responses were observed in fine root (+29%) and canopy productivity (+19%), but not stem growth. The direct evidence of P limitation of NPP suggests that P availability may restrict Amazon forest responses to CO_2 fertilisation[4], with major implications for future carbon sequestration and forest resilience to climate change.

The inclusion of nutrient cycling in Earth systems models has substantially reduced predictions of future C uptake by vegetation under elevated atmospheric CO_2 ([4,5,6,7]). Furthermore, fundamental differences between the cycles of nitrogen (N) and rock-derived elements such as P, mean that P limitation may place a greater constraint on plant responses to CO_2 fertilisation than N limitation[8,9]. During soil development[10], the weathering of rocks or parent material provides the major source of P for initial vegetation development. Over millions of years, however, the parent material is gradually depleted, and available P, as well as rock-derived base cations such as calcium (Ca), magnesium (Mg) and potassium (K), may be lost via leaching or made unavailable through occlusion by iron and aluminium-oxides, with organic forms of P becoming key pools in depleted and highly weathered systems[10,11]. Meanwhile, N tends to accumulate over time, with inputs from biological fixation and atmospheric deposition exceeding N losses[12]. For these reasons, a long-standing paradigm in tropical ecology (the so-called P paradigm) has been that forest productivity on

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highly-weathered soils, such as in those in central Amazonia, is primarily limited by plant available P[13], with a potential secondary role of other rock-derived elements. Supporting this paradigm, seminal forest ecology studies demonstrated very low levels of P and base cations in plant tissues in Amazonia[14], and high C:P ratios in litterfall of tropical forest more generally[1]. In Amazonia, greater wood productivity has also been observed in forests growing on fertile soils in western Amazonia when compared to less fertile sites in central and eastern portions of the basin, with relationships with total soil phosphorus being strongest[15,16]. However, across the Amazon basin, climatic and edaphic factors covary[17] influencing species distributions, standing forest biomass and turnover rates[16]. Thus, directly determining the extent to which soil fertility controls tropical forest growth, and which elements are most important, remains a key knowledge gap[18], and addressing this is critical for understanding forest growth dynamics and predicting responses to CO_2 fertilisation[19].

By minimising confounding factors, manipulation experiments can identify directly which specific elements limit forest productivity[20]. Although no large-scale N, P and base cation experiment has been carried out in Amazonia until now, a recent synthesis study argued that there is as much evidence for N limitation of tropical forest productivity as there is for P (ref 2). For example, in Costa Rica, P additions did not elicit any changes in litterfall and fine root productivity in two years after fertilisation[21], and in Panama, an increase in litter production with P addition was evident only 8 years after fertilisation[22], with initial responses stronger for N additions, at least in the rainy season[23]. Critically, previous nutrient manipulation studies in primary tropical rain forests have mainly taken place where total soil P contents are much greater than in central and eastern Amazonia (~443-1600 mg kg^{-1} *versus* 70-120 mg kg^{-1} in typical Amazon Ferralsols). In Amazonia, fertilisation experiments have been carried out in secondary forests, but little evidence for strong P limitation has been observed[24,25], with N availability found to be important during initial forest recovery[26,27]. There have been fertilisation experiments in forests growing on soils with P as low as in Amazonia in Cameroon[28] and Borneo[29]. These studies have also generally failed to provide clear support for the P paradigm, with no positive effects of P addition being observed[28], or with responses to N being at least as large as those to P[29]. However, the tree communities were very different to those found across Amazonia, with fundamental differences in nutrient uptake strategies including contrasting mycorrhizal associations. Therefore, while previous fertilisation studies strongly question the ubiquity of P limitation in tropical forests, their results cannot be extrapolated to Amazonian forests, especially those growing on low fertility soils in central and eastern regions of the basin.

To address this major knowledge gap, in 2017 in lowland tropical evergreen rainforest near Manaus, Brazil, we set up a large-scale fully factorial N, P and base cation-addition experiment (the Amazon Fertilisation Experiment-AFEX), manipulating 8 hectares of forest across 32 plots in four blocks[30]. The Ferralsols of the study site have low concentrations of total P and base cations that are characteristic of up to 60% of Amazon forest soils[31] (Fig. 1). To determine directly which nutrient(s) control Amazon forest productivity, we measured the responses of fine root, stem wood, and litterfall production between 2017 and 2019 (see Methods), making nearly 1500 measurements of canopy production, quantifying root productivity every three months across 160 locations and measuring the growth of 4849 trees. Importantly, our base cation treatment added the same amount of calcium as in the super-triple phosphate that was used in the P addition treatment. Thus, comparisons between these treatments ensure that the effects of P can be isolated.

Annual NPP rapidly increased with the addition of P in a Central Amazon Forest. After two years of P addition, annual NPP significantly increased by 1.16 Mg C ha^{-1} yr^{-1}, or 15.6% (+P (with P addition): 8.60 ± 0.33 *versus* -P (without P addition): 7.44 ± 0.21 Mg C ha^{-1} yr^{-1}; $F_{1,27} = 9.56$, $p = 0.005$; Fig. 2a), due to greater canopy and fine root productivity. No significant effects of N and base cation addition were observed on total NPP or any of its components measured. The increase in NPP may have been driven by the increase in P availability stimulating GPP[32], and/or through reductions in autotrophic respiration[33]. It has been shown that forests growing on high fertility soils may produce biomass more efficiently and thus show greater carbon use efficiency (CUE, the ratio of net carbon gain to gross carbon assimilated,

NPP/GPP)[34]. Although the direct causes of changes are not yet clear, our results clearly demonstrate that NPP in this forest is limited by P alone. The observed increase in NPP with +P, and the lack of any N response, strongly contrasts with a meta-analysis based on previous tropical forest fertilisation studies[2], with the lower levels of soil P in Amazonia likely explaining this contrast (Fig. 1). We have previously observed that base cation addition affects root morphology and mycorrhizal colonisation[30]. Thus, while base cation availability did not appear to limit NPP, they do appear to influence key belowground processes.

We observed a substantial 0.83 Mg C ha^{-1} yr^{-1}, or 19% (+P: 5.19 ± 0.15 *versus* -P: 4.36 ± 0.12 Mg C ha^{-1} yr^{-1}; $F_{1,30} = 18.3$, $p < 0.001$; Fig. 2b), increase in canopy productivity. Investment in leaf production provides a return revenue stream of photosynthate that can promote NPP of other tissues and can be used to acquire other limiting resources[35], such as light and nutrients. We observed weak evidence towards higher leaf area index (LAI) with P addition over the first 1.5 years of the experiment (3.6% increase: +P: 5.75 ± 0.10 *versus* -P: 5.55 ± 0.15 m^2 m^{-2}; $F_{1,27} = 1.76$, $p = 0.20$; Extended Data Figure 1), which may have had minor contributions to enhanced rates of C gain. The increase in litterfall productivity in our site appears to result from a decrease in leaf life span, which was estimated to have decreased by 10 to 20% following phosphorus addition (+P: 1.03 ± 0.04 *versus* -P: 1.15 ± 0.05 yr; $F_{1,30} = 4.08$, $p = 0.05$ and +P: 1.15 ± 0.05 *versus* -P: 1.56 ± 0.07; $F_{1,27} = 28.4$, $p = 0.0000127$, analysis based on fresh and litter leaves, respectively – see methods; Extended Data Figure 2). Therefore, the increases in leaf turnover appear important in driving the greater canopy productivity in response to P addition, and so far no substantial LAI increment was observed.

Fine root productivity responded strongly to P addition, increasing by 0.35 Mg C ha^{-1} yr^{-1}, and had the strongest relative increase of 29.4% in the top 30 cm of soil (+P: 1.54 ± 0.09 *versus* -P: 1.19 ± 0.06 Mg C ha^{-1} yr^{-1}; $F_{1,30} = 9.24$, $p = 0.005$; Fig. 2b). The overall increase in fine root productivity over two years of fertilisation, was greater compared to observations during the first 12 months (23.4% ref 30). Fine root productivity increased significantly in the top 10 cm of soil depth (+P: 0.96 ± 0.05 *versus* -P: 0.71 ± 0.04 Mg C ha^{-1} yr^{-1}; $F_{1,30} = 12.9$, $p = 0.001$; Table S25-27), but below 10 cm, although fine root productivity was ~20% greater following P addition, this difference was not statistically significant (+P: 0.58 ± 0.04 *versus* -P: 0.48 ± 0.03 Mg C ha^{-1} yr^{-1}; $F_{1,30} = 3.56$, $p = 0.069$; Table S29-30). The greater fine root productivity in the upper soil layer may be due to the low mobility of P in the soil[36], with most of the added P likely to remain in the top 10 cm, where it can be rapidly taken up by roots[30,37,38], or soil microbes. In a nearby site, at least 40% of fine root productivity was shown to occur below 30 cm[39]. Thus, while it is unlikely that reductions in productivity below 30 cm could have compensated for the increased root growth near the surface, across the full rooting depth the overall stimulation of fine root production will probably have been lower than 29%.

There is very limited information on fine root productivity responses to nutrient addition in old growth tropical rainforests. In a fertilisation experiment in Panama, while fine root productivity was not measured directly, K addition induced significant changes, decreasing fine root standing biomass, increasing fine root turnover, and reducing root tissue density, leading to shifts toward the construction of fine roots with a more acquisitive strategy[40,41]. In one of the few studies that measured root productivity responses to large-scale nutrient additions in the tropics, in a secondary tropical forest (~30 years) in Costa Rica, the addition of P did stimulate root productivity one year after fertilisation, but this appeared to be at the expense of aboveground tissue production, with no overall effect of nutrient addition on total productivity[42]. The clear increase in fine root productivity in our experiment also contrasts strongly with results observed in temperate forests, where reductions in root productivity and soil respiration (less heterotrophic and autotrophic respiration) have generally been observed following experimental fertilisation and alleviation of N limitation[43].

No significant effects of the nutrient addition were detectable on stem wood productivity (P: $F_{1,24} = 0.001$, $p = 0.97$; cations: $F_{1,27} = 0.01$, $p = 0.92$; N: $F_{1,26} = 0.003$, $p = 0.96$). Mean stem wood productivity was 1.85 ± 0.39 Mg C ha^{-1} $year^{-1}$ (DBH > 10 cm). While plants that grow in high-fertility soils can increase the

concentration of nutrients in tissues, with the potential to promote growth[44], species in low-fertility sites may be adapted to allocate nutrients to tissues with higher P demand (more active), prioritising roots and leaves, increasing photosynthetic and metabolic capacities, promoting ion uptake, tissue growth and maintenance[45]. In addition, the advantage of higher woody biomass production occurs only if it provides a competitive advantage over neighbouring trees (competition for light) or decreases the risk of mortality[46]. The rapid responses to P addition observed for the canopy and fine roots are important and enhance our understanding of nutrient limitation in Amazon forests, but longer-term monitoring of the experiment is required to determine whether the responses of different NPP components, and resource allocation, change over time, and whether a stem wood productivity response becomes apparent.

While attributing variation in forest productivity to P availability across fertility gradients in Amazonian has proven challenging due to confounding variation in tree species composition and both climatic and soil physical factors, our results suggest that P availability may be critical in controlling geographical variation in canopy and fine root productivity across the basin. Along a natural soil fertility gradient spanning the Amazon Basin, fine root productivity, measured in the top 30 cm and extended to 1 m depth, increased on average by ~28% and canopy productivity also increased by ~28% from East (less fertile soils) to West (high-fertility soils)[47]. Thus, after two years of P addition, the 29.4% stimulation in fine root productivity in our experiment is comparable to the difference in fine root productivity between Amazon regions with contrasting soil fertility (Extended Data Table 1). The observed 19% increase in canopy productivity with P addition (Fig. 2b) is lower than the 28% greater litterfall production in fertile Western forests of the basin (Peru, Colombia), compared with low-fertility sites in Central and Eastern Amazonia (Brazil)[47] (Extended Data Table 1). This may be explained by spatial variability representing the combination of direct P effects as well as changes in the species present, with a greater dominance of fast-growing species with lower wood density in the western Amazon[16]. However, overall, the similar magnitudes of the responses observed in our experiment, in which confounding variation in climatological variables, other edaphic factors, and species present has been minimised, to the patterns observed across major soil fertility gradients, strongly suggest that P availability is a critical in controlling geographical variation in fine root and canopy productivity across the basin.

Direct demonstration of limitation by P, rather than N, of NPP in a Central Amazon forest has major implications for predicting forest responses to climate change and rising atmospheric CO_2. In contrast to the N cycle, the P cycle has no major gaseous phase, and aqueous losses are low[9]. Therefore, while ecosystem N stocks can increase under elevated CO_2 if rates of biological fixation increase, or aqueous or gaseous losses are reduced[8], in ecosystems with highly weathered soils there is little opportunity for total P stocks to change due the lack of inputs and outputs[9]. For this reason, P limitation may place a stronger constraint on forest responses to rising atmospheric CO_2 than N limitation, questioning the potential for current high rates of C uptake in Amazonia to be maintained. Recent model projections demonstrated that the inclusion of P in dynamic global vegetation models reduced predictions of C uptake and biomass production in Amazon forests[4], decreasing forest C sink, and contributing to more rapid global climate change[7]. Furthermore, because the resistance of tropical forests to climate change depends on their ability to respond positively to rising CO_2 levels, if the responses to elevated CO_2 are limited by P availability, Amazon forests growing in low fertility soils may be more vulnerable than currently recognised[48]. Testing this suggestion directly with experimental manipulations of atmospheric CO_2 in tropical rainforests remains an urgent research priority, with the AmazonFACE (https://amazonface.inpa.gov.br/en/index.php) experiment aiming to do just that. Overall, in contrast to recent meta-analyses and the results from experiments in different tropical regions, our results provide direct evidence for P availability controlling forest productivity in the low fertility soils that characterise central and eastern Amazonia, with no evidence for a role of N. This new understanding of the role of nutrient limitation in Amazon forests has critical implications for current and future mitigation policies required to avoid the most dangerous consequences of climate change.

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Figure 1| Total soil phosphorus measured in primary forest plots across the Amazon Basin, showing the low P concentration at our site and across central and eastern Amazonia. A fertility gradient across the basin is shown, with red circles showing the lowest concentration of total phosphorus and blue circles showing the highest concentration of total phosphorus. The two large scale fertilisation experiments in Central American *terra firme* tropical forest are also shown, highlighting the five to eighteen-fold greater total phosphorus concentrations than in central Amazon. Total phosphorus concentrations are derived from Quesada and Lloyd 2016 (ref 49), except the values of Costa Rica[21] and Panama[40]. *In Costa Rica, values are available only for the 0-10 cm soil depth. For the other sites, values are for 0-30 cm soil depth.

Figure 2 | The effect of N, P and base cation availability on total net primary productivity and its components. a, The responses of total net primary productivity (NPP), representing the sum of NPP components. Only the statistically significant P effects are shown for total NPP, as N, base cation and all interactions had no effect (Table S2-4). **b-d,** The individual components of NPP where litterfall, stem wood and fine root productivity are shown in green, brown and orange bars, respectively. **b,** Litterfall productivity showed an increase with P addition only, and base cation (**c**) and N (**d**) are shown for comparison (Table S6-8). **b,** In stem wood productivity there was no effect of any nutrient addition (Table S32-33). **b,** Fine root productivity (0-30 cm) showed an increase with P addition only, and base cation (**c**) and N (**d**) are shown for comparison (Table S21-23). Both 0-10 and 10-30 cm had higher fine root productivity with P addition, but only the 0-10 cm layer had significantly different means. Means ± 1SE are presented, n=16 plots. The dotted lines represent the mean values for the control plots (no nutrients added; n=4 plots) for comparison purposes. Linear mixed models were performed to evaluate responses in total NPP and its components to added nutrients, where nutrient additions and their interactions were fixed effects and block was a random effect with the general full model formula *lmer*(response ~ N * P * Cations + (1|Block) . Only P addition remained in significant models after model simplification. All differences in mean values between plots with and without added nutrients with $p < 0.01$ are indicated. Cation (**c**) and nitrogen (**d**) panels for NPP components are added for comparison only.

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Author contribution H.F.V.C., C.A.Q., I.P.H. and K.M.A. planned the study. H.F.V.C., R.P., A.M., M.P., J.S.R., B.B., A.L., S.D.C., S.T., F.A., L.S.S., G.R., R.L.A., A.C.S., B.T., C.M., L.F.L., E.O. and J.L.C collected the data and/or helped with project logistics. I.P.H., L.M., L.A., T.D., L.N., P.M. and C.A.Q wrote the grants that funded this research. H.F.V.C., K.M.A. and I.A organised the datasets. H.F.V.C., K.M.A., I.A. and A.M. conducted the statistical analyses. H.F.V.C., L.F.L., I.P.H., C.A.Q., L.M., S.G., I.A., K.M.A., F.D.S., T.D., A.L., P.M., R.P., R.L.A., L.A. and L.N discussed the results and the structure of the paper and improved the manuscript.

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METHODS

Site. This research was part of the Amazon Fertilisation Experiment (AFEX), a large-scale fertilisation experiment installed in a lowland tropical forest, 80 km north of Manaus, Brazil, in Central Amazonia (lat 2° 30`S, long 60° W) at one of the continuous old growth evergreen forests of the Biological Dynamics of Forest Fragments Project (BDFFP)[51]. The experimental site is located in *terra firme* forest and has a high-species diversity, with about 280 plant species (≥10 cm DBH) per hectare[52]. The dominant tree families in our site are Lecythidaceae, Sapotaceae, Fabaceae and Burseraceae, and the most abundant species are *Micrandropsis scleroxylon*, *Protium hebetatum*, *Eschweilera wachenheimii*, *Scleronema micranthum* and *Eschweilera truncata*.

The mean annual air temperature is *c.* 26 °C[53], and the mean annual precipitation is 2400 mm with a dry season from June to October, when monthly precipitation can reach less than than 100 mm[54]. Above ground biomass (AGB) was estimated to be 322 ± 54 Mg ha^{-1} (tree individuals ≥ 10 diameter at breast height - DBH) with mean wood density of 0.67 g cm^{-3} [55]. Local soils are geric Ferrasols (WRB Soil Classification) also known as Oxisols (USDA Soil Taxonomy) [56,57]. The soils are deep (≥ 400 cm) with good particle aggregation, friable and with low subsoil bulk density (0.8 – 1.2 g cm^{-3}) [58], typically acidic (pH ~ 4.1), with low concentrations of nutrients such as P (total P = 87.5 mg kg^{-1}), calcium (Ca) (0.034 cmolc kg^{-1}), and K (0.066 cmolc kg^{-1}). The soil texture of the site is 7.69% sand, 14.75% silt, and 77.55% clay.

Experimental design. AFEX is composed of thirty-two 50 m x 50 m plots distributed across four blocks separated by at least 200 m[30]. Each of the four blocks comprises eight plots, which are separated by at least 50 m, representing eight treatments applied in a fully factorial design: control (with no addition of nutrients), N, P, CATIONS (Ca, Mg, K), N+P, N+CATIONS, P+CATIONS and N+P+CATIONS.

Fertilisation consists of 125 kg ha^{-1} $year^{-1}$ of N as urea ($CO(NH_2)_2$), 50 kg ha^{-1} $year^{-1}$ of P as triple superphosphate ($Ca(H_2PO_4)_2$) and base cations with 160 kg ha^{-1} $year^{-1}$ as dolomitic limestone ($CaMg(CO_3)_2$ for Ca and Mg plus 50 kg ha^{-1} $year^{-1}$ as potassium chloride (KCl) for K. Annual doses of N, P and K are similar to the Panama fertilisation experiment, in order to facilitate comparisons[59], while the addition rates of Ca within the base cation treatment equals the addition rate of Ca in the triple superphosphate, allowing us to directly determine the effect of the added P. Nutrient additions are split into three equal applications over the course of each wet season, with nutrients added every year since May 2017. The results presented here correspond to forest growth after 2 years of field measurements.

Fine root productivity. The productivity of fine roots was measured every three months using the ingrowth core method as described in detail in Lugli et al. (2021). In each plot, the five ingrowth cores were bulked into a composite sample per plot, divided into depths of 0-10 cm and 10-30 cm, and roots were removed from the soil core by hand in the field over a period of 60 minutes, which was split into 15 minutes time intervals. Subsequently, fine roots (<2 mm diameter) were cleaned, dried at 60 °C until constant mass and weighed.

Different curve types were fitted to the first 60 minutes of manual root extraction and used to predict the pattern of extraction up to 180 minutes[30,60].

We used the census from November 2017 to September 2019, comprising two years of data collection (Year 1: November 2017 to Sept 2018 and Year 2: Dec 2018 to Sep 2019 in a total of 8 ingrowth core collections). Total fine root productivity (0-30 cm) was summed for both years and the annual mean root productivity was obtained dividing the root productivity by two. To convert root productivity from biomass to C, we used C data from the root tissues carried out in the study area[30], in which the average C concentration was 43.94%. Fine root productivity was expressed in Mg C ha^{-1} $year^{-1}$.

Stem wood productivity. To calculate stem wood productivity, the stem diameter of all identified trees with a diameter at breast height (DBH) ≥ 10 cm were recorded annually at the end of the wet season (May) from 2017 - 2019. An allometric equation specific for tropical moist forest[61] was applied to convert tree DBH (cm), species wood density (g cm^{-3}) and a bioclimatic parameter (*E*) in woody biomass. The equation has the following expression:

$$AGB = \exp(-2.024 - 0.896E + 0.920 \ln(WD) + 2.795 \ln(D) - 0.0461 [\ln(D)^2])$$

This is the slightly modified Eq 7 of Chave et al. 2014 given by the biomass package, where woody biomass can be inferred in the absence of height measurements. The bioclimatic parameter (E) is a measure of environmental stress[61] related to climatic water deficit, temperature seasonality and precipitation seasonality, inferred when the site coordinates were given (lat 2° 40`S; long 60° W).

Wood density was estimated for each species from the *getWoodDensity* function from R *biomass* package using the global wood density database as a reference[62,63], ideally assigned to species, but to genus level where species-level wood density data were not available. Of the total number of individuals, 55.1% of the wood densities were obtained at the species level, 37.1% at the genus level and for the remaining 7.9% of the individuals, we assumed the average wood density of the plot, because species was not identified or was absent in the database.

Stem wood productivity was calculated as the change in stem biomass of surviving trees added to the biomass of the recruited individuals divided by the census length. For 4600 tree individuals, we selected a census length of two years (2017-2019) and for 249 trees where one census was missing (*e.g.*: tree not measured in 2017, recruited in 2018 census, measurement error), annual productivity was calculated using one year interval (2017-2018 or 2018-2019). Recruitment was the inclusion of new individuals who reached 10 cm of DBH in the 2019 inventory (42 trees). 22 trees with DBH > 15 cm in 2019 that were not measured in at least two censuses were not considered in the analyses. For 38 trees that died in 2019, productivity was calculated by the difference in biomass between 2018 and 2017.

The change in biomass was then summed over all trees ≥ 10 cm DBH in each plot (2500 m^2) and extrapolated to estimate the change in biomass per hectare. To convert biomass values into C, we assumed that dry stem biomass corresponds to 50% C[64] and stem wood productivity was expressed in Mg C ha^{-1} $year^{-1}$. To avoid or minimise potential errors, we used some parameters to check for quality control of the data. We used data that fell inside both of the following criteria: diametric growth smaller than 4 cm yr^{-1} and a negative growth limit of -0.5 cm across the census intervals. Small negative DBH increments were included to accommodate measurement error and also because trees may shrink by a small amount due to hydrostatic effects in times of drought[65].

Litterfall Productivity. Litterfall production was estimated by sampling litterfall every fifteen days in five litter traps (0.25 m^2) placed 1 m above the ground within the central area of each plot (30 x 30 m). Litterfall includes leaves, twigs and thin branches with diameter < 2 cm, reproductive material (flowers, fruits and seeds), residues (other fractions not identified) and insect frass that were oven-dried at 65 °C to constant mass and weighed.

We used data from the census of July 2017 to June 2019, where this period comprises two years. Litterfall productivity in g m^{-2} day^{-1} was extrapolated to Mg ha^{-1} $year^{-1}$ and the average was obtained considering two years of collection (Moraes et al, in prep; Supplementary material). Litter material was estimated to be 50% C, based on mean values in our site, to convert biomass productivity into C productivity and it was also expressed in Mg C ha^{-1} $year^{-1}$.

Leaf area index (LAI). A LAI-2200C (LI-COR Biotechnology, Lincoln, Nebraska USA) was used to measure LAI inside the central 30 m x 30 m of each plot. Sixteen measurement points were made in each plot, on a grid with an even spacing of 10 m. Measurements made on these 16 points per plot were averaged to represent plot means. The data were collected from 6 am to 5 pm, avoiding recording data between 12:00 and 2:00 pm, to avoid direct sun. The LAI-2200C requires an above canopy reading for reference, and in our case the optical sensor was placed in a clearing to log automatically while the operator collected manually below the canopy. The sensors were always placed in the same compass direction (both in the west in the morning and east in the afternoon) and we used a view cap of 45° in the sensors to remove the operator from the sensor's view. The sensors were matched before the data collection. The raw data were analysed using the FV2200 software, where LAI was obtained (m^2 one sided foliage area/ m^2 ground area) and computed with 4 rings. These four rings read radiation in 4 angles, which are 7°, 23°, 38° and 53°. The data were collected during 10 to 13 October 2017, 22 to 25 March 2018, 07 to 10 August 2018 and between 29 October and 02 November 2018. LAI was based on these 4 collections, and was transformed to a single value representing the mean LAI over one year.

Total Productivity. We calculated total productivity, using the following equation:

$$NPP_{total} = NPP_{fineroots} + NPP_{stem} + NPP_{litterfall}$$

All terms are expressed in Mg C ha^{-1} $year^{-1}$.

Leaf residence time. This parameter was calculated by dividing the leaf biomass by annual leaf fall productivity (from July 2017 to July 2018) in Mg dry biomass ha^{-1} yr^{1} ([66]). Leaf biomass was calculated by dividing the mean LAI of four campaigns (10 to 13 October 2017, 22 to 25 March 2018, 07 to 10 August 2018 and between 29 October and 02 November 2018) by specific leaf area (SLA). The SLA was included in two approaches: 1) Obtained from a census in October 2018, from about 8 individuals per plot from canopy dominant trees (-P: 83.36 ± 1.83 cm^2 g^{-1} and +P: 88.02 ± 2.49 cm^2 g^{-1}, -CATIONS: 85.61 ± 2.25 cm^2 g^{-1} and +CATIONS: 85.77 ± 2.28 cm^2 g^{-1}, -N: 85.54 ± 2.67 cm^2 g^{-1} and +N: 85.85 ± 1.76 cm^2 g^{-1}, based on mean values in our site; Andersen et al, unpublished) 2) Obtained from sampling in litter traps (-P: 162.50 ± 26 g m^{-2} and +P: 128.75 ± 11 g m^{-2}). Transformations from LMA to SLA were made when necessary. The numerator, leaf biomass in g m^2 was extrapolated to Mg ha^{-1}. The denominator, leaf fall productivity was based on 24 collections, and was transformed to a single value representing the mean leaf fall productivity over one year.

Data analyses. Linear mixed models were used to test the effect of added nutrients and their interaction in the factorial design N*P*base cations. The model simplification method used to find the best model was the step function in *lmerTest* package, based on the drop1 function which systematically drops fixed factors in order of the model hierarchy[67]. We started with the full model including all nutrients and their interaction, and followed a stepwise backward elimination on non-significant effects based on chi square test comparing two consecutive models. When dropping interaction effects significantly changed the model fit, they were retained in the model and the elimination process was completed. When all fixed effects were dropped from the model, the intercept was accepted as the final model. A probability <0.05 was adopted to determine significance. Results are reported for the best fit model in the text and figures. The denominator *degrees of freedom* were estimated using the Satterthwaite approximation. The four blocks were used as random factors and the response variables were fine root, stem wood, litterfall productivity, total productivity, leaf area index and leaf residence time. All models were run using *lme4* and *lmerTest* R packages[68]. We tested

the assumptions for normality and homogeneity of variance to meet assumptions for linear models, using the Shapiro-Wilk and Levene tests. Since no interactions between nutrients were found, all plots where a specific nutrient was not added (i.e – P, n = 16) are compared to all plots where that nutrient was added (i.e., +P, n = 16) [22,30]. Original datasets from this study are publically available (Moraes et al. 2020[69], Cunha et al. 2021a[70], Cunha et al. 2021b[71], Cunha et al. 2021c[72]). Compiled datasets and R scripts used for statistical analyses, figures and tables are available at https://github.com/kmander7/Paper-AFEX-NPP.

Data availability. Data that support the findings of this study have been deposited in NERC Environmental Information Data Centre at (https://doi.org/10.5285/b3a55011-bf46-40f5-8850-86dc8bc4c85d) for root biomass, at (https://doi.org/10.5285/c2587e20-ba4a-4444-8ce9-ccdec15b0aa3) for tree census, at (https://doi.org/10.5285/c0294ec9-45d6-464c-b543-ce9ece9fd968) for litterfall production and at (https://doi.org/10.5285/6e70665f-b558-4949-b42a-49fbaec7e7cc) for leaf area index. Global Wood Density Database can be requested from http://datadrayad.org/handle/10255/dryad.235. Plot mean datasets for all response variables and AFEX plot treatment identifications are available at https://github.com/kmander7/Paper-AFEX-NPP.

Code availability. The R code used to find the best model for each variable is available in the Supplementary material. R scripts used to generate the Supplementary material are available at https://github.com/kmander7/Paper-AFEX-NPP

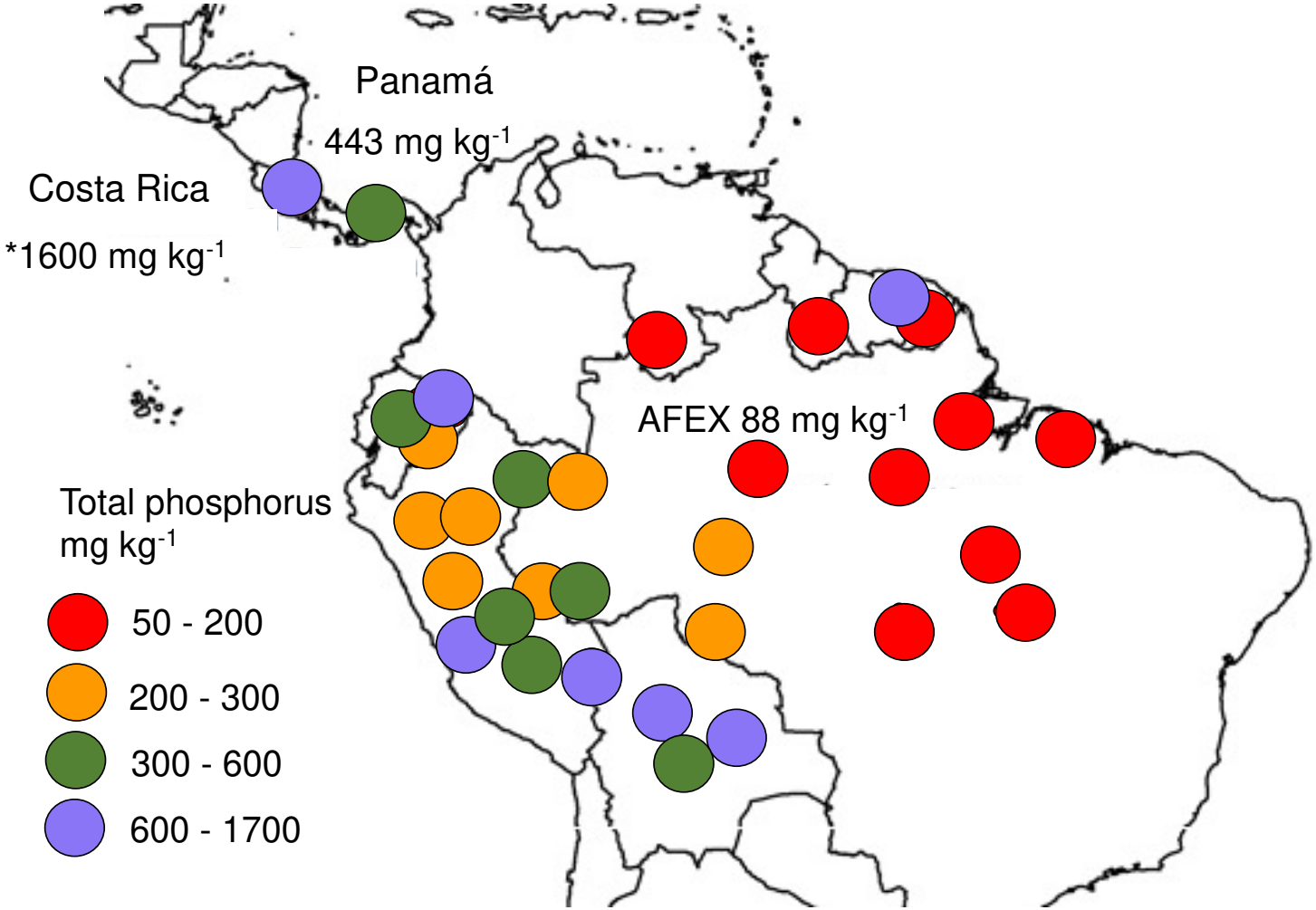
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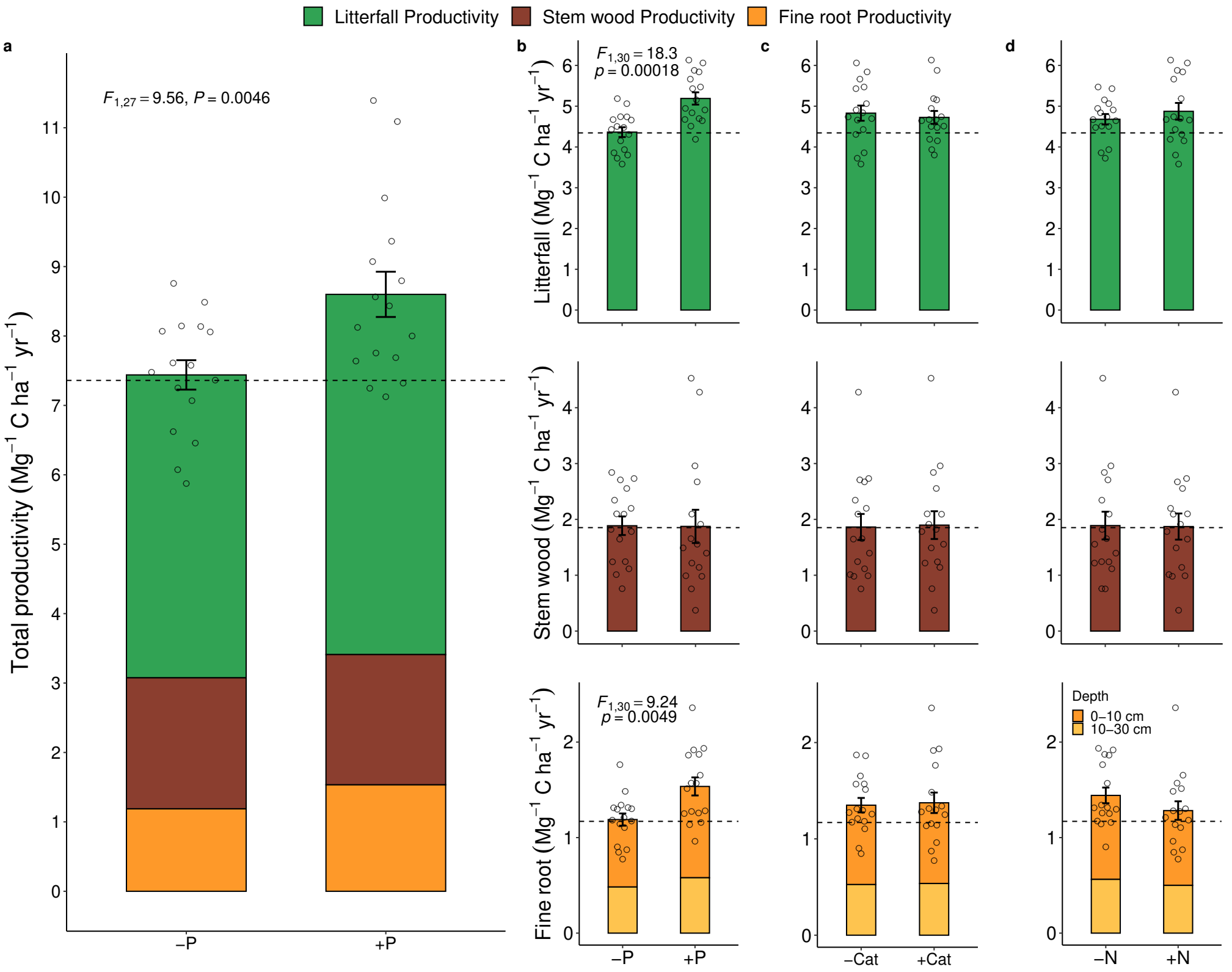
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Extended Data Figure 1| Nutrient addition effects on Leaf area index. LAI was measured over four field campaigns across treatments in a lowland forest in Central Amazon. Each panel represents mean ± 1SE LAI with (+) or without (-) the addition of specific nutrients (phosphorus addition (a); base cation addition (b); nitrogen addition (c)), based on the average LAI across the four field campaigns, n= 16 plots. No significant differences among the means were detected in linear mixed models for any of the nutrients. The dotted lines represent the mean values for the control plots (no nutrients added; n = 4 plots) for comparison purposes.

Extended Data Figure 2| Nutrient addition effects on Leaf residence time (LRT). Leaf residence time (yr) across treatments in a lowland forest in Central Amazon. Two separate measures of specific leaf area were used in the leaf residence time calculations based on: 1) fresh canopy leaves of common families represented across all plots sampled for a photosynthesis campaign (**a**-**c**); 2) composite leaf litter collected in the plots (**d**-**f**). Leaf residence time showed a decrease with P addition only (**a**, **d**) for both LRT estimates, with cations (**b**, **e**) and N (**c**, **f**) being shown for comparison. Means ± 1SE are presented, n= 16 plots. Linear mixed models were performed to evaluate responses in leaf residence time to added nutrients. The dotted lines represent the mean values for the control plots (no nutrients added; n = 4 plots) for comparison purposes.

Extended Data Table 1| NPP comparisons along the Basin. Total P (mg kg^{-1}), N (%) and sum of base cations (SB in $cmol_c$ kg^{-1} refer to the sum of Ca+Mg+K+Na), canopy, fine roots and stem wood net primary productivity (Mg C ha^{-1} yr^{-1}), from low fertility soils in eastern Amazonian sites (CAX 03, MAN 05, CAX 06) and more fertile soils in western sites (TAM 05, AGP 02, TAM 06) according to their total soil P concentrations. Components of net primary productivity are derived from Aragão et al. 2009. Aragão et al. 2009 presents fine root productivity to 1 m, so we have extended our data to 1 m by dividing by 0.6, based on the study of Cordeiro et al. 2020 that demonstrated that 40% of fine root productivity was located below 30 cm at a nearby site on the same soil type. The percentage indicates the magnitude of differences between more fertile and least fertile sites.


Panamá
443 mg kg-1
Costa Rica
*1600 mg kg-1
AFEX 88 mg kg-1
Total phosphorus
mg kg-1
50 - 200
200 - 300
300 - 600
600 - 1700


Litterfall Productivity
Stem wood Productivity
Fine root Productivity
a
b
c
d
$F_{1,27} = 9.56$, $P = 0.0046$
Total productivity (Mg^{-1} C ha^{-1} yr^{-1})
$F_{1,30} = 18.3$
$p = 0.00018$
Litterfall (Mg^{-1} C ha^{-1} yr^{-1})
Stem wood (Mg^{-1} C ha^{-1} yr^{-1})
$F_{1,30} = 9.24$
$p = 0.0049$
Fine root (Mg^{-1} C ha^{-1} yr^{-1})
Depth
0–10 cm
10–30 cm
–P
+P
–Cat
+Cat
–N
+N