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# 1 Direct evidence for phosphorus limitation on Amazon forest productivity

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11 **The productivity of rainforests growing on highly-weathered tropical soils is expected to be limited**  
12 **by phosphorus (P) availability<sup>1</sup>. Yet, controlled fertilisation experiments have failed to demonstrate**  
13 **a dominant role for P in controlling tropical forest net primary productivity (NPP). Recent syntheses**  
14 **have demonstrated that responses to N addition are as large as to P<sup>2</sup>, and adaptations to low P**  
15 **availability appear to allow NPP to be maintained across major soil P gradients<sup>3</sup>. Thus, the extent to**  
16 **which P availability limits tropical forest productivity is highly uncertain. The majority of the**  
17 **Amazonia, however, is characterised by soils even more depleted in P than where most tropical**  
18 **fertilisation experiments have previously taken place<sup>2</sup>. Thus, we established the first P, nitrogen (N),**  
19 **and base cation addition experiment in an old growth Amazon rainforest, with the site's low soil P**  
20 **content representative of ~60% of the basin. Here we show that NPP increased exclusively with P**  
21 **addition. After 2 years, strong responses were observed in fine root (+29%) and canopy productivity**  
22 **(+19%), but not stem growth. The direct evidence of P limitation of NPP suggests that P availability**  
23 **may restrict Amazon forest responses to CO<sub>2</sub> fertilisation<sup>4</sup>, with major implications for future carbon**  
24 **sequestration and forest resilience to climate change.**

25 The inclusion of nutrient cycling in Earth systems models has substantially reduced predictions of future C  
26 uptake by vegetation under elevated atmospheric CO<sub>2</sub> (<sup>4,5,6,7</sup>). Furthermore, fundamental differences  
27 between the cycles of nitrogen (N) and rock-derived elements such as P, mean that P limitation may place  
28 a greater constraint on plant responses to CO<sub>2</sub> fertilisation than N limitation<sup>8,9</sup>. During soil development<sup>10</sup>,  
29 the weathering of rocks or parent material provides the major source of P for initial vegetation development.  
30 Over millions of years, however, the parent material is gradually depleted, and available P, as well as rock-  
31 derived base cations such as calcium (Ca), magnesium (Mg) and potassium (K), may be lost via leaching  
32 or made unavailable through occlusion by iron and aluminium-oxides, with organic forms of P becoming  
33 key pools in depleted and highly weathered systems<sup>10,11</sup>. Meanwhile, N tends to accumulate over time, with  
34 inputs from biological fixation and atmospheric deposition exceeding N losses<sup>12</sup>. For these reasons, a long-  
35 standing paradigm in tropical ecology (the so-called P paradigm) has been that forest productivity on

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36 highly-weathered soils, such as in those in central Amazonia, is primarily limited by plant available P<sup>13</sup>,  
37 with a potential secondary role of other rock-derived elements. Supporting this paradigm, seminal forest  
38 ecology studies demonstrated very low levels of P and base cations in plant tissues in Amazonia<sup>14</sup>, and high  
39 C:P ratios in litterfall of tropical forest more generally<sup>1</sup>. In Amazonia, greater wood productivity has also  
40 been observed in forests growing on fertile soils in western Amazonia when compared to less fertile sites  
41 in central and eastern portions of the basin, with relationships with total soil phosphorus being strongest<sup>15,16</sup>.  
42 However, across the Amazon basin, climatic and edaphic factors covary<sup>17</sup> influencing species distributions,  
43 standing forest biomass and turnover rates<sup>16</sup>. Thus, directly determining the extent to which soil fertility  
44 controls tropical forest growth, and which elements are most important, remains a key knowledge gap<sup>18</sup>,  
45 and addressing this is critical for understanding forest growth dynamics and predicting responses to CO<sub>2</sub>  
46 fertilisation<sup>19</sup>.

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

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

76 Annual NPP rapidly increased with the addition of P in a Central Amazon Forest. After two years of P  
77 addition, annual NPP significantly increased by 1.16 Mg C ha<sup>-1</sup> yr<sup>-1</sup>, or 15.6% (+P (with P addition): 8.60  
78 ± 0.33 versus -P (without P addition): 7.44 ± 0.21 Mg C ha<sup>-1</sup> yr<sup>-1</sup>; F<sub>1,27</sub> = 9.56, p = 0.005; Fig. 2a), due to  
79 greater canopy and fine root productivity. No significant effects of N and base cation addition were  
80 observed on total NPP or any of its components measured. The increase in NPP may have been driven by  
81 the increase in P availability stimulating GPP<sup>32</sup>, and/or through reductions in autotrophic respiration<sup>33</sup>. It  
82 has been shown that forests growing on high fertility soils may produce biomass more efficiently and thus  
83 show greater carbon use efficiency (CUE, the ratio of net carbon gain to gross carbon assimilated,

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

90 We observed a substantial 0.83 Mg C ha<sup>-1</sup> yr<sup>-1</sup>, or 19% (+P: 5.19 ± 0.15 *versus* -P: 4.36 ± 0.12 Mg C ha<sup>-1</sup>  
91 yr<sup>-1</sup>; F<sub>1,30</sub> = 18.3, *p* < 0.001; Fig. 2b), increase in canopy productivity. Investment in leaf production provides  
92 a return revenue stream of photosynthate that can promote NPP of other tissues and can be used to acquire  
93 other limiting resources<sup>35</sup>, such as light and nutrients. We observed weak evidence towards higher leaf area  
94 index (LAI) with P addition over the first 1.5 years of the experiment (3.6% increase: +P: 5.75 ± 0.10 *versus*  
95 -P: 5.55 ± 0.15 m<sup>2</sup> m<sup>-2</sup>; F<sub>1,27</sub> = 1.76, *p* = 0.20; Extended Data Figure 1), which may have had minor  
96 contributions to enhanced rates of C gain. The increase in litterfall productivity in our site appears to result  
97 from a decrease in leaf life span, which was estimated to have decreased by 10 to 20% following phosphorus  
98 addition (+P: 1.03 ± 0.04 *versus* -P: 1.15 ± 0.05 yr; F<sub>1,30</sub> = 4.08, *p* = 0.05 and +P: 1.15 ± 0.05 *versus* -P:  
99 1.56 ± 0.07; F<sub>1,27</sub> = 28.4, *p* = 0.0000127, analysis based on fresh and litter leaves, respectively – see methods;  
100 Extended Data Figure 2). Therefore, the increases in leaf turnover appear important in driving the greater  
101 canopy productivity in response to P addition, and so far no substantial LAI increment was observed.

102 Fine root productivity responded strongly to P addition, increasing by 0.35 Mg C ha<sup>-1</sup> yr<sup>-1</sup>, and had the  
103 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  
104 ha<sup>-1</sup> yr<sup>-1</sup>; F<sub>1,30</sub> = 9.24, *p* = 0.005; Fig. 2b). The overall increase in fine root productivity over two years of  
105 fertilisation, was greater compared to observations during the first 12 months (23.4% ref 30). Fine root  
106 productivity increased significantly in the top 10 cm of soil depth (+P: 0.96 ± 0.05 *versus* -P: 0.71 ± 0.04  
107 Mg C ha<sup>-1</sup> yr<sup>-1</sup>; F<sub>1,30</sub> = 12.9, *p* = 0.001; Table S25-27), but below 10 cm, although fine root productivity was  
108 ~20% greater following P addition, this difference was not statistically significant (+P: 0.58 ± 0.04 *versus*  
109 -P: 0.48 ± 0.03 Mg C ha<sup>-1</sup> yr<sup>-1</sup>; F<sub>1,30</sub> = 3.56, *p* = 0.069; Table S29-30). The greater fine root productivity in  
110 the upper soil layer may be due to the low mobility of P in the soil<sup>36</sup>, with most of the added P likely to  
111 remain in the top 10 cm, where it can be rapidly taken up by roots<sup>30,37,38</sup>, or soil microbes. In a nearby site,  
112 at least 40% of fine root productivity was shown to occur below 30 cm<sup>39</sup>. Thus, while it is unlikely that  
113 reductions in productivity below 30 cm could have compensated for the increased root growth near the  
114 surface, across the full rooting depth the overall stimulation of fine root production will probably have been  
115 lower than 29%.

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

128 No significant effects of the nutrient addition were detectable on stem wood productivity (P: F<sub>1,24</sub> = 0.001,  
129 *p* = 0.97; cations: F<sub>1,27</sub> = 0.01, *p* = 0.92; N: F<sub>1,26</sub> = 0.003, *p* = 0.96). Mean stem wood productivity was 1.85  
130 ± 0.39 Mg C ha<sup>-1</sup> year<sup>-1</sup> (DBH > 10 cm). While plants that grow in high-fertility soils can increase the

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

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

158 Direct demonstration of limitation by P, rather than N, of NPP in a Central Amazon forest has major  
159 implications for predicting forest responses to climate change and rising atmospheric CO<sub>2</sub>. In contrast to  
160 the N cycle, the P cycle has no major gaseous phase, and aqueous losses are low<sup>9</sup>. Therefore, while  
161 ecosystem N stocks can increase under elevated CO<sub>2</sub> if rates of biological fixation increase, or aqueous or  
162 gaseous losses are reduced<sup>8</sup>, in ecosystems with highly weathered soils there is little opportunity for total P  
163 stocks to change due the lack of inputs and outputs<sup>9</sup>. For this reason, P limitation may place a stronger  
164 constraint on forest responses to rising atmospheric CO<sub>2</sub> than N limitation, questioning the potential for  
165 current high rates of C uptake in Amazonia to be maintained. Recent model projections demonstrated that  
166 the inclusion of P in dynamic global vegetation models reduced predictions of C uptake and biomass  
167 production in Amazon forests<sup>4</sup>, decreasing forest C sink, and contributing to more rapid global climate  
168 change<sup>7</sup>. Furthermore, because the resistance of tropical forests to climate change depends on their ability  
169 to respond positively to rising CO<sub>2</sub> levels, if the responses to elevated CO<sub>2</sub> are limited by P availability,  
170 Amazon forests growing in low fertility soils may be more vulnerable than currently recognised<sup>48</sup>. Testing  
171 this suggestion directly with experimental manipulations of atmospheric CO<sub>2</sub> in tropical rainforests remains  
172 an urgent research priority, with the AmazonFACE (<https://amazonface.inpa.gov.br/en/index.php>)  
173 experiment aiming to do just that. Overall, in contrast to recent meta-analyses and the results from  
174 experiments in different tropical regions, our results provide direct evidence for P availability controlling  
175 forest productivity in the low fertility soils that characterise central and eastern Amazonia, with no evidence  
176 for a role of N. This new understanding of the role of nutrient limitation in Amazon forests has critical  
177 implications for current and future mitigation policies required to avoid the most dangerous consequences  
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280 **Figure 1 | Total soil phosphorus measured in primary forest plots across the Amazon Basin, showing**  
 281 **the low P concentration at our site and across central and eastern Amazonia.** A fertility gradient across  
 282 the basin is shown, with red circles showing the lowest concentration of total phosphorus and blue circles  
 283 showing the highest concentration of total phosphorus. The two large scale fertilisation experiments in  
 284 Central American *terra firme* tropical forest are also shown, highlighting the five to eighteen-fold greater  
 285 total phosphorus concentrations than in central Amazon. Total phosphorus concentrations are derived from  
 286 Quesada and Lloyd 2016 (ref 49), except the values of Costa Rica<sup>21</sup> and Panama<sup>40</sup>. \*In Costa Rica, values  
 287 are available only for the 0-10 cm soil depth. For the other sites, values are for 0-30 cm soil depth.

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

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## 329 **METHODS**

330 **Site.** This research was part of the Amazon Fertilisation Experiment (AFEX), a large-scale fertilisation  
331 experiment installed in a lowland tropical forest, 80 km north of Manaus, Brazil, in Central Amazonia (lat  
332  $2^{\circ} 30' S$ , long  $60^{\circ} W$ ) at one of the continuous old growth evergreen forests of the Biological Dynamics of  
333 Forest Fragments Project (BDFFP)<sup>51</sup>. The experimental site is located in *terra firme* forest and has a high-  
334 species diversity, with about 280 plant species ( $\geq 10$  cm DBH) per hectare<sup>52</sup>. The dominant tree families in  
335 our site are Lecythidaceae, Sapotaceae, Fabaceae and Burseraceae, and the most abundant species are  
336 *Micrandropsis scleroxylon*, *Protium hebetatum*, *Eschweilera wachenheimii*, *Scleronema micranthum* and  
337 *Eschweilera truncata*.

338 The mean annual air temperature is *c.*  $26^{\circ} C$ <sup>53</sup>, and the mean annual precipitation is 2400 mm with a dry  
339 season from June to October, when monthly precipitation can reach less than 100 mm<sup>54</sup>. Above ground  
340 biomass (AGB) was estimated to be  $322 \pm 54$  Mg ha<sup>-1</sup> (tree individuals  $\geq 10$  diameter at breast height -  
341 DBH) with mean wood density of  $0.67$  g cm<sup>-3</sup><sup>55</sup>. Local soils are geric Ferrasols (WRB Soil Classification)  
342 also known as Oxisols (USDA Soil Taxonomy)<sup>56,57</sup>. The soils are deep ( $\geq 400$  cm) with good particle  
343 aggregation, friable and with low subsoil bulk density ( $0.8 - 1.2$  g cm<sup>-3</sup>)<sup>58</sup>, typically acidic (pH  $\sim 4.1$ ), with  
344 low concentrations of nutrients such as P (total P =  $87.5$  mg kg<sup>-1</sup>), calcium (Ca) ( $0.034$  cmolc kg<sup>-1</sup>), and K  
345 ( $0.066$  cmolc kg<sup>-1</sup>). The soil texture of the site is 7.69% sand, 14.75% silt, and 77.55% clay.

346 **Experimental design.** AFEX is composed of thirty-two 50 m x 50 m plots distributed across four blocks  
347 separated by at least 200 m<sup>30</sup>. Each of the four blocks comprises eight plots, which are separated by at least  
348 50 m, representing eight treatments applied in a fully factorial design: control (with no addition of  
349 nutrients), N, P, CATIONS (Ca, Mg, K), N+P, N+CATIONS, P+CATIONS and N+P+CATIONS.

350 Fertilisation consists of 125 kg ha<sup>-1</sup> year<sup>-1</sup> of N as urea (CO(NH<sub>2</sub>)<sub>2</sub>), 50 kg ha<sup>-1</sup> year<sup>-1</sup> of P as triple  
351 superphosphate (Ca(H<sub>2</sub>PO<sub>4</sub>)<sub>2</sub>) and base cations with 160 kg ha<sup>-1</sup> year<sup>-1</sup> as dolomitic limestone (CaMg(CO<sub>3</sub>)<sub>2</sub>)  
352 for Ca and Mg plus 50 kg ha<sup>-1</sup> year<sup>-1</sup> as potassium chloride (KCl) for K. Annual doses of N, P and K are  
353 similar to the Panama fertilisation experiment, in order to facilitate comparisons<sup>59</sup>, while the addition rates  
354 of Ca within the base cation treatment equals the addition rate of Ca in the triple superphosphate, allowing  
355 us to directly determine the effect of the added P. Nutrient additions are split into three equal applications  
356 over the course of each wet season, with nutrients added every year since May 2017. The results presented  
357 here correspond to forest growth after 2 years of field measurements.

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

364 Different curve types were fitted to the first 60 minutes of manual root extraction and used to predict the  
365 pattern of extraction up to 180 minutes<sup>30,60</sup>.

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

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

$$377 \text{ AGB} = \exp(-2.024 - 0.896E + 0.920 \ln(\text{WD}) + 2.795 \ln(D) - 0.0461 [\ln(D)^2])$$

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

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

388 Stem wood productivity was calculated as the change in stem biomass of surviving trees added to the  
389 biomass of the recruited individuals divided by the census length. For 4600 tree individuals, we selected a  
390 census length of two years (2017-2019) and for 249 trees where one census was missing (*e.g.*: tree not  
391 measured in 2017, recruited in 2018 census, measurement error), annual productivity was calculated using  
392 one year interval (2017-2018 or 2018-2019). Recruitment was the inclusion of new individuals who reached  
393 10 cm of DBH in the 2019 inventory (42 trees). 22 trees with DBH > 15 cm in 2019 that were not measured  
394 in at least two censuses were not considered in the analyses. For 38 trees that died in 2019, productivity  
395 was calculated by the difference in biomass between 2018 and 2017.

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

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

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

414 **Leaf area index (LAI).** A LAI-2200C (LI-COR Biotechnology, Lincoln, Nebraska USA) was used to  
415 measure LAI inside the central 30 m x 30 m of each plot. Sixteen measurement points were made in each  
416 plot, on a grid with an even spacing of 10 m. Measurements made on these 16 points per plot were averaged  
417 to represent plot means. The data were collected from 6 am to 5 pm, avoiding recording data between 12:00  
418 and 2:00 pm, to avoid direct sun. The LAI-2200C requires an above canopy reading for reference, and in  
419 our case the optical sensor was placed in a clearing to log automatically while the operator collected  
420 manually below the canopy. The sensors were always placed in the same compass direction (both in the  
421 west in the morning and east in the afternoon) and we used a view cap of  $45^\circ$  in the sensors to remove the  
422 operator from the sensor's view. The sensors were matched before the data collection. The raw data were  
423 analysed using the FV2200 software, where LAI was obtained ( $\text{m}^2$  one sided foliage area/  $\text{m}^2$  ground area)  
424 and computed with 4 rings. These four rings read radiation in 4 angles, which are  $7^\circ$ ,  $23^\circ$ ,  $38^\circ$  and  $53^\circ$ . The  
425 data were collected during 10 to 13 October 2017, 22 to 25 March 2018, 07 to 10 August 2018 and between  
426 29 October and 02 November 2018. LAI was based on these 4 collections, and was transformed to a single  
427 value representing the mean LAI over one year.

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

$$429 \text{NPP}_{\text{total}} = \text{NPP}_{\text{fineroots}} + \text{NPP}_{\text{stem}} + \text{NPP}_{\text{litterfall}}$$

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

431 **Leaf residence time.** This parameter was calculated by dividing the leaf biomass by annual leaf fall  
432 productivity (from July 2017 to July 2018) in  $\text{Mg dry biomass ha}^{-1} \text{yr}^{-1}$  (<sup>66</sup>). Leaf biomass was calculated by  
433 dividing the mean LAI of four campaigns (10 to 13 October 2017, 22 to 25 March 2018, 07 to 10 August  
434 2018 and between 29 October and 02 November 2018) by specific leaf area (SLA). The SLA was included  
435 in two approaches: 1) Obtained from a census in October 2018, from about 8 individuals per plot from  
436 canopy dominant trees (-P:  $83.36 \pm 1.83 \text{ cm}^2 \text{ g}^{-1}$  and +P:  $88.02 \pm 2.49 \text{ cm}^2 \text{ g}^{-1}$ , -CATIONS:  $85.61 \pm 2.25$   
437  $\text{cm}^2 \text{ g}^{-1}$  and +CATIONS:  $85.77 \pm 2.28 \text{ cm}^2 \text{ g}^{-1}$ , -N:  $85.54 \pm 2.67 \text{ cm}^2 \text{ g}^{-1}$  and +N:  $85.85 \pm 1.76 \text{ cm}^2 \text{ g}^{-1}$ , based  
438 on mean values in our site; Andersen et al, unpublished) 2) Obtained from sampling in litter traps (-P:  
439  $162.50 \pm 26 \text{ g m}^{-2}$  and +P:  $128.75 \pm 11 \text{ g m}^{-2}$ ). Transformations from LMA to SLA were made when  
440 necessary. The numerator, leaf biomass in  $\text{g m}^2$  was extrapolated to  $\text{Mg ha}^{-1}$ . The denominator, leaf fall  
441 productivity was based on 24 collections, and was transformed to a single value representing the mean leaf  
442 fall productivity over one year.

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

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

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

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

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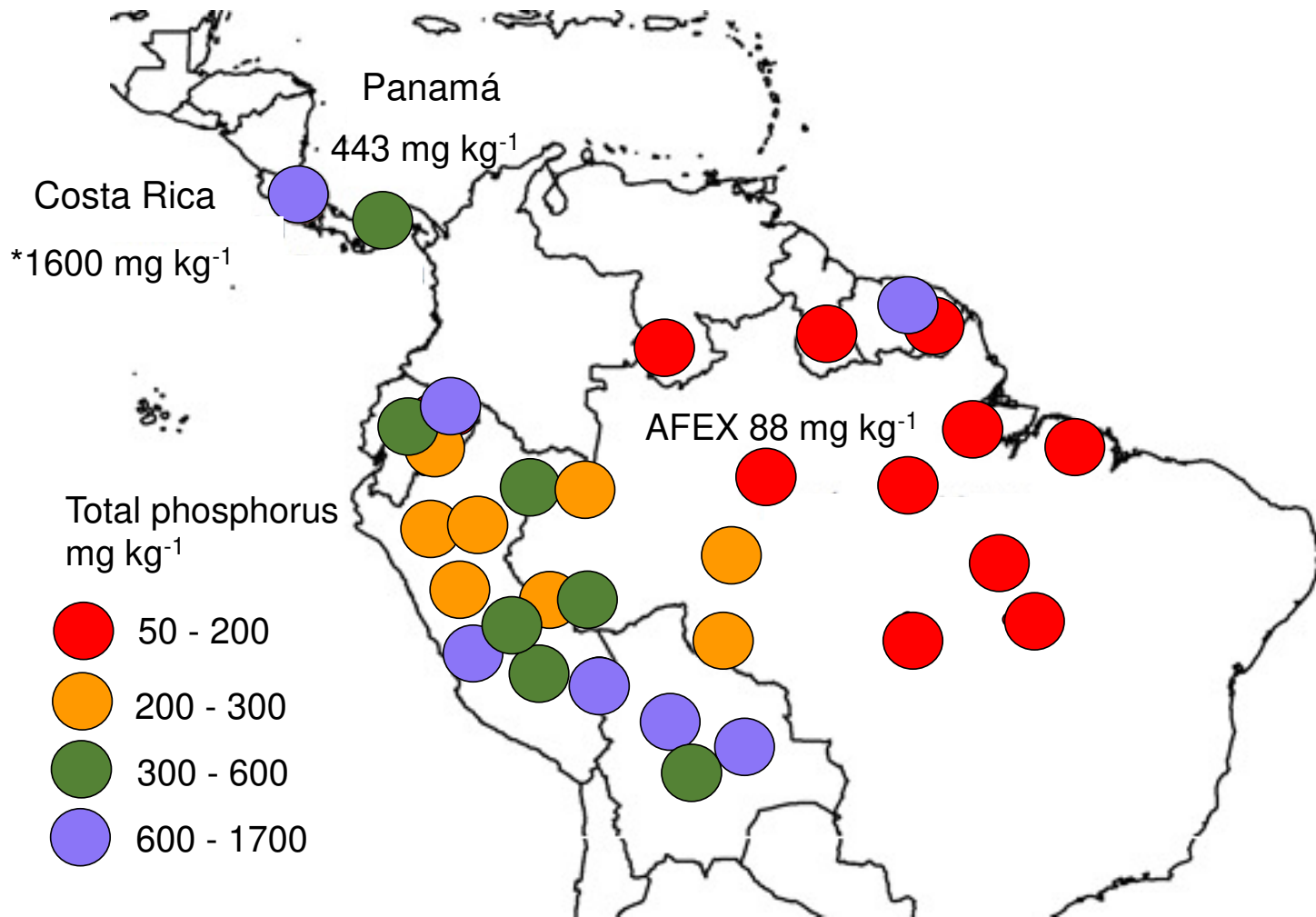
517

518 **Extended Data Figure 1| Nutrient addition effects on Leaf area index.** LAI was measured over four  
519 field campaigns across treatments in a lowland forest in Central Amazon. Each panel represents mean  $\pm$   
520 1SE LAI with (+) or without (-) the addition of specific nutrients (phosphorus addition (a); base cation  
521 addition (b); nitrogen addition (c)), based on the average LAI across the four field campaigns, n= 16 plots.  
522 No significant differences among the means were detected in linear mixed models for any of the nutrients.  
523 The dotted lines represent the mean values for the control plots (no nutrients added; n = 4 plots) for  
524 comparison purposes.

525

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

535 **Extended Data Table 1| NPP comparisons along the Basin.** Total P ( $\text{mg kg}^{-1}$ ), N (%) and sum of base  
536 cations (SB in  $\text{cmol}_c \text{ kg}^{-1}$  refer to the sum of Ca+Mg+K+Na), canopy, fine roots and stem wood net primary  
537 productivity ( $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ ), from low fertility soils in eastern Amazonian sites (CAX 03, MAN 05, CAX  
538 06) and more fertile soils in western sites (TAM 05, AGP 02, TAM 06) according to their total soil P  
539 concentrations. Components of net primary productivity are derived from Aragão *et al.* 2009. Aragão *et al.*  
540 2009 presents fine root productivity to 1 m, so we have extended our data to 1 m by dividing by 0.6, based  
541 on the study of Cordeiro *et al.* 2020 that demonstrated that 40% of fine root productivity was located below  
542 30 cm at a nearby site on the same soil type. The percentage indicates the magnitude of differences between  
543 more fertile and least fertile sites.



■ Litterfall Productivity
 ■ Stem wood Productivity
 ■ Fine root Productivity

