

1 **Title:**

2 **Future CO<sub>2</sub> fertilization of the Amazon forest hinges on plant phosphorus use and**  
3 **acquisition**

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35 **Global terrestrial models currently predict that the Amazon rainforest will continue to**  
36 **act as a carbon sink in the future primarily due to the rising atmospheric carbon dioxide**  
37 **(CO<sub>2</sub>) concentration, effectively enhancing its resilience and slowing the pace of climate**  
38 **change. Soil phosphorus impoverishment in parts of the Amazon basin limits biomass**  
39 **growth, but the role of phosphorus availability in limiting its future carbon uptake has**  
40 **not been considered in global model ensembles, e.g., during the Coupled Model**  
41 **Intercomparison Project for the 5<sup>th</sup> Assessment Report of the United Nations**  
42 **Intergovernmental Panel on Climate Change. Here, we simulate a planned free-air CO<sub>2</sub>**  
43 **enrichment experiment in the Amazon with an ensemble of 14 terrestrial ecosystem**  
44 **models. We show that phosphorus feedbacks reduce the CO<sub>2</sub>-induced biomass carbon**  
45 **sink to  $79 \pm 63 \text{ g C m}^{-2} \text{ yr}^{-1}$  over 15 years, a reduction of ~50% compared to estimates from**  
46 **carbon and carbon-nitrogen models. Our results suggest that the region's resilience to**  
47 **climate change may be much smaller than previously assumed. Variation in the biomass**  
48 **C response among the phosphorus-enabled models is considerable, ranging from 5 to 140**  
49 **g C m<sup>-2</sup> yr<sup>-1</sup>, due to contrasting assumptions relating to the flexibility in plant phosphorus**  
50 **use and acquisition strategies. The model ensemble involuntarily represents diverse plant**  
51 **functional strategies and generates a series of testable hypotheses. Experimental design**  
52 **need to be targeted to reduce the uncertainties around the phosphorus feedback on the**  
53 **CO<sub>2</sub> fertilization effect.**

54 The intact Amazon rainforest acts as a substantial carbon (C) sink, completely offsetting carbon  
55 dioxide (CO<sub>2</sub>) emissions from fossil fuel combustion and land use change in the Amazon  
56 region<sup>1,2</sup>. Increasing atmospheric CO<sub>2</sub> concentrations from anthropogenic activity may be the  
57 primary driving force for the current Amazon net carbon sink<sup>1,3</sup>, and global models assume that  
58 this CO<sub>2</sub> fertilization effect will continue to provide this globally significant ecosystem service  
59 into the future<sup>4-6</sup>. The stimulatory effect of elevated carbon dioxide (eCO<sub>2</sub>) on photosynthesis

60 and tree growth has been observed experimentally in greenhouses and in the field in open top  
61 chamber and free-air CO<sub>2</sub> enrichment (FACE) experiments. To date, whole-ecosystem-scale  
62 experiments (i.e., FACE) have mainly been conducted in the temperate zone and never in the  
63 tropics<sup>7,8</sup>. In these experiments, the eCO<sub>2</sub>-induced increase in C uptake is generally low when  
64 other factors, such as soil nitrogen (N), are limiting<sup>9,10</sup>.

65 Over large parts of the Amazon and the tropics worldwide, phosphorus (P), not N, is assumed  
66 to be the key limiting nutrient, as most P has been lost or occluded from plant uptake during  
67 millions of years of soil pedogenesis<sup>11,12</sup>. Forests growing on these highly weathered old soils  
68 may nonetheless be highly productive due to the evolution of multiple strategies for P  
69 acquisition and use, enabling tight cycling of P between plants and soils<sup>13,14</sup>. Despite this  
70 knowledge, quantifying the control of P on plant physiology, growth, and plant-soil interactions  
71 in global models, and hence its role in the forests' response to eCO<sub>2</sub>, remains challenging<sup>15</sup>.  
72 This challenge is exacerbated by the scarcity of observations and distinctive species responses  
73 in hyperdiverse tropical forests<sup>16</sup>.

74 Here, we study the potential interactions between eCO<sub>2</sub> and nutrient (N and P) feedbacks in a  
75 mature Amazonian rainforest by simulating the planned AmazonFACE experiment (+200 ppm;  
76 <http://amazon-face.org/>) with an ensemble of ecosystem models (n = 14, Extended Data Table  
77 3), including three C, five carbon-nitrogen (CN), and six carbon-nitrogen-phosphorus (CNP)  
78 models<sup>17-22</sup>. The AmazonFACE experiment is located in a well-studied, highly productive  
79 tropical forest in Central Amazonia<sup>23,24</sup>, growing on a strongly weathered *terra firme* Ferralsol.  
80 This ecosystem represents the low end of the plant-available P spectrum in the Amazon,  
81 consistent with ~32% of the Amazon rainforest's cover fraction<sup>25</sup>. *In situ* measurements were  
82 used to parameterise the models and to evaluate simulated ambient conditions (Extended Data  
83 Table 1, 2). Our aim was to generate *a priori* model-based hypotheses to highlight the state-of-  
84 the-knowledge and guide measurement strategies for AmazonFACE and other ecosystem

85 manipulation experiments to gain crucial process understanding of P control on the CO<sub>2</sub>  
86 fertilization effect.

87 Simulated eCO<sub>2</sub> (+200 ppm) had a positive effect on plant biomass C across all models but was  
88 weakest in the CNP models (Fig. 1a). The eCO<sub>2</sub> conditions induced average biomass C gains  
89 of  $163 \pm 65$ ,  $145 \pm 83$ , and  $79 \pm 63$  g C m<sup>-2</sup> yr<sup>-1</sup> after 15 years in the C, CN and CNP models,  
90 respectively (Fig. 1a). Limitations by P thus reduced the predicted biomass C sink by 52% and  
91 46% compared to that in the C and CN models, respectively, with considerable variation across  
92 and within model groups (Extended Data Fig. 1). Plot inventories at the AmazonFACE site  
93 during the 2000s indicate an ambient aboveground biomass sink of 23 g C m<sup>2</sup> yr<sup>-1</sup>, with an  
94 Amazon-wide<sup>1</sup> estimate of 64 g C m<sup>2</sup> yr<sup>-1</sup>. The model ensemble represents ambient conditions,  
95 such as productivity and LAI, reasonably well but the set of models does diverge on some  
96 ecosystem characteristics, such as ambient biomass C increases, which range from 5 to 114 g  
97 C m<sup>2</sup> yr<sup>-1</sup> (see more discussion on ambient model performance in Extended Data Fig. 2).

98 Gross and net primary productivity (GPP and NPP, respectively) are both stimulated by eCO<sub>2</sub>  
99 in all models, both initially (after 1 year of eCO<sub>2</sub>) and at the end of the simulation. The CNP  
100 models show the strongest decline over the 15-year period from the initial response due to P  
101 limitation (Fig. 1b, c). The final response of NPP to eCO<sub>2</sub> was a 35%, 29%, and 9% stimulation  
102 for the C, CN and CNP models, respectively. In general, in the CN and CNP models, nutrient  
103 limitation is defined as nutrient demand being greater than nutrient supply. But models differ  
104 in their assumptions on how nutrient limitation controls productivity and C allocation in  
105 response to eCO<sub>2</sub>, so that divergent responses on plant carbon use efficiency (CUE = NPP /  
106 GPP) are simulated (Extended Data Table 3). In some CN models, CUE increases because N  
107 limitation is hypothesized to reduce autotrophic respiration (Ra) via lower tissue N content. In  
108 contrast, some CNP models (e.g., CABLE and ELM-ECA) assume a direct downregulation of  
109 growth or growth efficiency (i.e., NPP) but only a small reduction in GPP, and hence the plant

110 CUE decreases under nutrient limitation (Extended Data Fig. 3). Elevated CO<sub>2</sub> induced higher  
111 fine root investments of NPP in some CN and CNP models to aid nutrient acquisition (Fig. 1c;  
112 Extended Data Fig. 4). Predicted changes in allocation with eCO<sub>2</sub> cause a general increase in  
113 biomass C turnover across all but one of models, partially offsetting the positive biomass C  
114 response (Extended Data Table 4). Changes in turnover largely control the long-term future  
115 CO<sub>2</sub> effect on the biomass C sink<sup>26,27</sup>.

116 Plant growth under eCO<sub>2</sub> is lowest in CNP models as the low availability of soil labile P restricts  
117 P uptake either immediately (CABLE, ELM-ECA, GDAY) or over time (CABLE-POP, ELM-  
118 CTC, ORCHIDEE) (Extended Data Fig. 5). We considered the modelled P limitation on plant  
119 growth to be realistic, as the models and observations agree on soil labile P being very low  
120 (Extended Data Fig. 2). Other observations support the fact that P is extremely critical for plant  
121 productivity, such as high leaf N:P ratios of 37 and high plant P resorption (before litter fall) of  
122 78% (Extended Data Table 1). P limitation consistently reduces the eCO<sub>2</sub>-induced biomass C  
123 sink, but there is significant variation among CNP models due to contrasting process  
124 representations (Fig. 2; Extended Data Table 3).

125 P shortages downregulate growth (i.e., NPP) in all models, either directly, via photosynthesis,  
126 or via a combination of both processes. No model considers P effects on Ra. The major  
127 differences among the models relate to how they modify P supply and demand to alleviate plant  
128 P shortages, including either (i) enhancing plant P use efficiency ( $PUE = NPP / P \text{ uptake}$ ) or (ii)  
129 upregulating P acquisition mechanisms. PUE may change if tissue nutrient ratios are flexible,  
130 if C allocation changes among tissues with different stoichiometry, and/or if P resorption is  
131 variable. Flexible stoichiometry is considered in all CNP models except ELM-CTC, although  
132 with varying degrees of flexibility, such that the stoichiometry in CABLE and ORCHIDEE is  
133 effectively fixed (Fig. 2). Greater fine root C allocation in response to plant P stress is

134 considered in ELM-ECA, GDAY and ORCHIDEE, and P resorption is a fixed fraction of leaf  
135 tissue P in all models (Fig. 2).

136 In regards to modelled soil P acquisition mechanisms; three of the six models (ELM-ECA,  
137 ELM-CTC, GDAY) consider desorption of P from mineral surfaces (i.e., the secondary or  
138 strongly sorbed P pool), whereas the others assume P in those pools to be unavailable to plants.  
139 All the models include biochemical mineralization of organic P via phosphatase, but only three  
140 (ELM-ECA, ELM-CTC and ORCHIDEE) include the functionality to increase P acquisition  
141 via this mechanism under plant P stress (Fig. 2; Extended Data Table 3). Litter and soil  
142 stoichiometry are considered with varying degrees of flexibility. Soil labile P limits microbial  
143 decomposition rates of litter and soil, so that decomposition is reduced when immobilization  
144 demands for P exceed soil labile P availability (Fig. 2; Extended Data Table 3).

145 Diverging depictions of plant P use and acquisition among the CNP models cause predictions  
146 of the eCO<sub>2</sub>-induced biomass C sink to range from 5 g C m<sup>-2</sup> yr<sup>-1</sup> in CABLE to 140 g C m<sup>-2</sup> yr<sup>-1</sup>  
147 in ORCHIDEE (Fig. 3a; Extended Data Fig. 1). Greater plant PUE occurred in four of the  
148 models, GDAY, ELM-ECA, CABLE-POP, and ORCHIDEE, for which shifts in tissue C:N and  
149 N:P due to eCO<sub>2</sub> led to increases in biomass C:P ranging from ~200 to 1600 g C g P<sup>-1</sup> (Fig. 3c).  
150 Higher fine root investment with eCO<sub>2</sub>, at the expense of less “P-costly” wood, offset some  
151 increases in PUE in ELM-ECA and GDAY. Although higher fine root allocation was simulated  
152 temporarily in ORCHIDEE (Extended Data Fig. 4), investment in wood increased over the full  
153 simulation period, as was also the case in CABLE-POP (Fig. 3b).

154 Flexible biomass stoichiometry altered decomposition dynamics and induced progressive P  
155 limitation in response to eCO<sub>2</sub>, i.e., litter stoichiometry shifted towards lower quality (less N  
156 and P in relation to C), reducing net P mineralization rates from microbial decomposition,  
157 causing P to become increasingly unavailable to plants and accumulating in soil organic matter  
158 (Fig. 3d, e). Consequently, ecosystem P retention increased marginally in some models as P

159 leaching rates decreased. This plant-soil-microbial feedback slowed the cycling of P in the  
160 ecosystem and exacerbated the initial P limitation (see Ref. <sup>28</sup> for a similar feedback during  
161 pedogenesis).

162 Enhanced plant P acquisition under eCO<sub>2</sub> effectively alleviated P limitation in two CNP models  
163 (ELM-CTC and ELM-ECA). In both, eCO<sub>2</sub> increased the liberation of P from the secondary  
164 pool, as higher plant P demand and uptake diminished the labile P pool, in turn causing higher  
165 desorption rates. P desorption is thus only indirectly, and not mechanistically, enhanced by  
166 plants in these models. Biochemical mineralization of P under eCO<sub>2</sub> responded positively in  
167 both of the models, but added only notably to additional P acquisition in ELM-CTC (Fig. 3e).  
168 Although three CNP models simulated higher fine root investments (ELM-ECA, GDAY, and  
169 ORCHIDEE), the actual P uptake return per fine root increment was marginal or came only into  
170 effect in the long-term (Extended Data Fig. 6).

171 In summary, the model ensemble encapsulates a range of plausible hypotheses and represents  
172 a potential range of biomass C responses to eCO<sub>2</sub> under low soil P availability. At the one end,  
173 CABLE assumes no plant-enabled mechanisms to acquire more P and a limited capacity for  
174 plants to use P more efficiently, resulting in effectively zero biomass C gain with eCO<sub>2</sub>. The  
175 remaining models predicted some biomass C gain with eCO<sub>2</sub>. Flexible stoichiometry was the  
176 key mechanistic response to eCO<sub>2</sub> in four of these models. ELM-CTC had no change in  
177 stoichiometry, but nonetheless predicted an increase in biomass C gain under eCO<sub>2</sub> based on an  
178 increase in plant P acquisition because of enhanced P mineralization and desorption.

179 Our results also indicate the control of N availability on modelled plant growth. The CN models  
180 simulate increased nitrogen use efficiency (NUE) and biomass C:N ratios, as N uptake was not  
181 sufficient under eCO<sub>2</sub> (Extended Data Fig. 5). Direct N limitation of plant growth is, however,  
182 not expected, as observations document ample N cycling in the system, e.g., high leaf N  
183 contents, indicative  $\delta^{15}\text{N}$  values, high rates of N oxide emissions, and low N retention<sup>29,30</sup>. Plant

184 N availability may be underestimated in the models, since the plant-available mineral N supply  
185 was  $<7 \text{ g N m}^{-2}$  across all models, as opposed to  $17.5 \text{ g N m}^{-2}$  observed in the top 10 cm only  
186 (Extended Data Fig. 2). These results highlight an important gap in our knowledge related to  
187 the dynamics of N availability, and its potential interaction with P dynamics. Future  
188 experiments should help reduce the uncertainty surrounding N effects on P limitation, in  
189 particular for regions predominantly or co-limited by N.

190 Divergences in the simulated eCO<sub>2</sub> response lead us to the following testable hypotheses:

191 H1. Low soil P availability will strongly constrain future plant biomass growth response to  
192 eCO<sub>2</sub> either by downregulating photosynthesis or limiting plant growth directly, or a  
193 combination thereof.

194 H2. Despite the limited soil P supply, plasticity in vegetation stoichiometry and allocation  
195 patterns will allow for some biomass growth under eCO<sub>2</sub>.

196 H3. Plants will increase investments in P acquisition to increase P supply and allow biomass  
197 growth under eCO<sub>2</sub> either via greater P interception through fine root production or via greater  
198 P liberation from P desorption or biochemical mineralization of P.

199 These process- and model-based hypotheses deepen a previously carried out accounting  
200 analysis of potential N and P limitation<sup>31</sup>. Furthermore, we add to a model intercomparison  
201 carried out in advance of the EucFACE experiment<sup>32</sup> by extending the range of plant P  
202 feedbacks considered across CNP models. This work highlighted H1: two stoichiometrically  
203 constrained CNP models predicted that strong P limitation will curtail the growth response to  
204 eCO<sub>2</sub> in subtropical Australia. Consistent with this hypothesis, aboveground growth has not  
205 increased with eCO<sub>2</sub> in that experiment over the initial years<sup>33</sup>. This finding underlines that  
206 monitoring efforts need to place a strong(er) focus on belowground carbon allocation and soil  
207 nutrient dynamics. Additionally, the model ensemble does not yet consider the P effect on Ra



208 and respiration under different degrees of nutrient limitation need further monitoring during  
209 experiments to further elucidate P effects on the plant C budget and address H1.

210 Nutrient fertilization experiments support H2, as plasticity in leaf stoichiometry at the  
211 individual level, along with plasticity in P resorption efficiency, was observed<sup>34</sup>. Across the  
212 Amazon, leaf nutrient assessments indicate a leaf N:P range of 13 to 42 (n = 64) (Ref. <sup>30</sup>), which  
213 place our site, with a community mean ratio of 37, at the high end. GDAY thus predicted the  
214 most plausible increase in the leaf N:P ratio from 34 to 38 (Extended Data Fig. 7). CABLE-  
215 POP and ELM-ECA predicted strong increases in the leaf N:P ratio with eCO<sub>2</sub> but started off  
216 with much lower initial values. The degree to which plasticity in stoichiometry and resorption  
217 can aid plant PUE in highly P-limited sites that are already at the end of the observed spectrum  
218 remains to be seen (H2). Monitoring plant tissue and fresh litter nutrient content in CO<sub>2</sub> and  
219 nutrient fertilization experiments will give an indication of the plasticity of these plant use  
220 mechanisms in response to eCO<sub>2</sub>.

221 Based on previous observations<sup>10</sup>, a number of models assume increased fine root investment,  
222 as well as higher biochemical P mineralization and P desorption from mineral surfaces, under  
223 eCO<sub>2</sub>-induced nutrient limitation (H3). The effect of increased fine root biomass on nutrient  
224 uptake was limited in our simulations and ambient fine root allocation fractions were highly  
225 variable among the models, ranging from 5-30% of NPP (Extended Data Fig. 4, 6). Both these  
226 modelled results highlight model deficiencies in belowground processes<sup>35</sup>. There is evidence  
227 that phosphatase activity in litter and soil and the presence of low-molecular-weight acids used  
228 to liberate P from organic matter or from mineral surfaces increase with plant P demand<sup>36</sup>. This  
229 was predicted by ELM-CTC in our simulations, which also showed Amazon-wide that “[with]  
230 enhanced phosphatase production, productivity in the highly P-limited areas can be sustained  
231 under elevated CO<sub>2</sub> conditions”<sup>37</sup>. Plants invest in P liberation and acquisition, but if these  
232 mechanisms can be upregulated under eCO<sub>2</sub> and over what time frame this may occur remain

233 open questions. Quantification of such fluxes is lacking, as are estimates of the associated plant  
234 C costs to acquire P via these and other mechanisms, such as mycorrhizal symbiosis<sup>14,38</sup>. The P  
235 gain and C cost for P acquisition mechanisms, as well as the associated plant-soil-microbial  
236 interactions, need to be assessed by analyses of soil, microbial and root nutrition, and via novel  
237 techniques investigating enzyme and labile C dynamics. Monitoring of belowground fine root  
238 dynamics needs to include fine root activity in surface litter, a common phenomenon in P-  
239 impoverished ecosystems in the Amazon, not yet quantified nor considered in models.

240 Previous model projections suggest a sustained fertilization effect of CO<sub>2</sub> on the Amazon C  
241 sink but have not considered feedbacks from low soil P availability<sup>4,5</sup>. Our study demonstrates  
242 that, based on the current generation of CNP models, the omission of P feedbacks is highly  
243 likely to cause an overestimation of the Amazon rainforest's capacity to sequester atmospheric  
244 CO<sub>2</sub>. Considering P limitation on the CO<sub>2</sub> fertilization effect in future predictions may indicate  
245 that the forest is less resilient to higher temperatures and changing rainfall patterns than  
246 previously thought<sup>4,39</sup>. Periods of water deficit may contribute to the eCO<sub>2</sub> fertilization effect  
247 on productivity due to its water saving effect<sup>32</sup>. Our study site experienced years with  
248 significantly less than average precipitation, e.g. in 2000 and 2009, however, in our simulations  
249 this added marginally to the modelled CO<sub>2</sub> effect (Extended Data Figure 8 and 9). Models are  
250 not yet very apt to simulate water deficits and their consequences on plant growth and mortality  
251 in general, and even more so when precipitation totals are that high<sup>40</sup>. Interactions of water and  
252 P availability and their consequences on the CO<sub>2</sub> fertilization effect remain uncertain and need  
253 urgent clarification<sup>41</sup>.

254 Although P is likely to reduce the biomass C sink response to CO<sub>2</sub> in regions with low plant-  
255 available P supply, our results suggest that plasticity in plant P use and plant P acquisition  
256 mechanisms, may enable CO<sub>2</sub> fertilization of biomass growth. The model ensemble may be  
257 interpreted as involuntarily representing a range of possible tropical plant functional strategies

258 and growth responses to low phosphorus availability. Responses to eCO<sub>2</sub> are expected to be  
259 species-specific, as were plant growth responses to low P supplies in another tropical region<sup>16</sup>.  
260 The ecosystem-scale response to P limitation under eCO<sub>2</sub> will thus depend on the relative  
261 contributions of the various P acquisition and P use strategies across individuals, their  
262 interactions and to what extent these processes can be upregulated under eCO<sub>2</sub>. All of which  
263 ultimately need to be described and represented in a single model framework in order to  
264 accurately predict the Amazon rainforest's response to future climate change.

265 AmazonFACE has the unique opportunity to experimentally address these key areas of  
266 uncertainty, not only by integrating the proposed measurements across seasons and at the  
267 ecosystem scale but also by assessing species-specific responses to eCO<sub>2</sub> in relation to trait  
268 expression. Amazon-wide expression of plant functional strategies may then be inferred by  
269 applying the mechanistic interplay between trait expression and edaphic conditions. The key to  
270 predicting the future of the world's largest tropical forest under eCO<sub>2</sub> thus lies in obtaining  
271 experimental data on, and subsequently modelling, different plant P acquisition and use  
272 strategies, as well as their interactions in a competing plant community.

273 **END NOTES**

274 **Author contributions**

275 D.M.L., A.R., and K.F. conceived the study. L.F., S.G., A.G., F.H., R.N., C.A.Q., K.J.S., and  
276 O.J.V.-B. collected field data. K.F., D.G., M. de K., M.J., V.H., J.H., F.L., L.M.M., B.P.,  
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278 manuscript with contributions from all co-authors.

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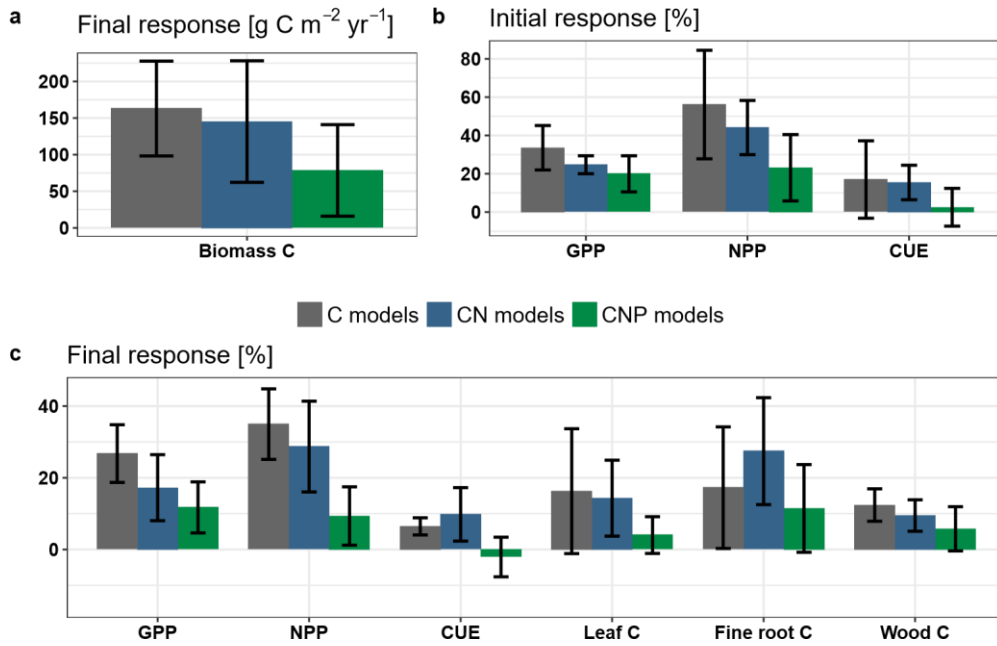
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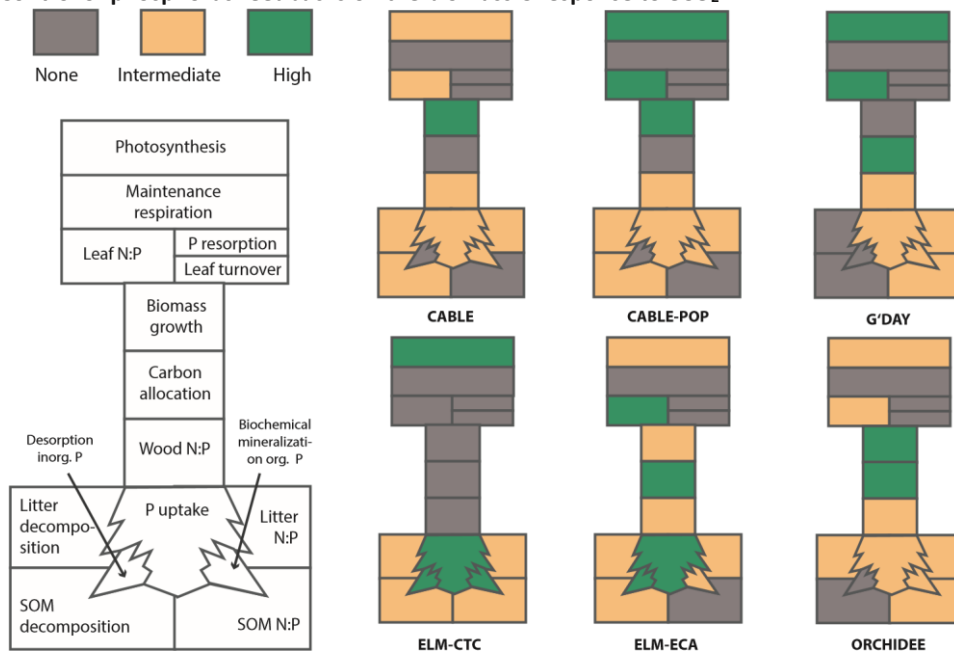


390

391 **Figure 1: The predicted effect of eCO<sub>2</sub> on biomass C, productivity and biomass**  
 392 **compartments**, averaged over C (grey), CN (blue) and CNP (green) model groups. **a**, The  
 393 final absolute response of biomass growth, calculated as the mean annual response over the 15  
 394 years of eCO<sub>2</sub> per model group in  $\text{g C m}^{-2} \text{yr}^{-1}$ . **b**, Initial relative responses of productivity  
 395 (GPP and NPP), and CUE (=NPP/GPP) in %, calculated as the mean response in the first year.  
 396 **c**, Final relative responses of productivity and CUE, as well as total leaf, fine root and wood  
 397 C, calculated as the mean response after 15 years (mean of 13th to 17th year), all in %.  
 398 Responses to eCO<sub>2</sub> are the differences between the elevated and ambient model run, shown as  
 399 mean and standard deviation per model group, individual model outputs are shown in  
 400 Extended Data Figure 1 and 3.

401

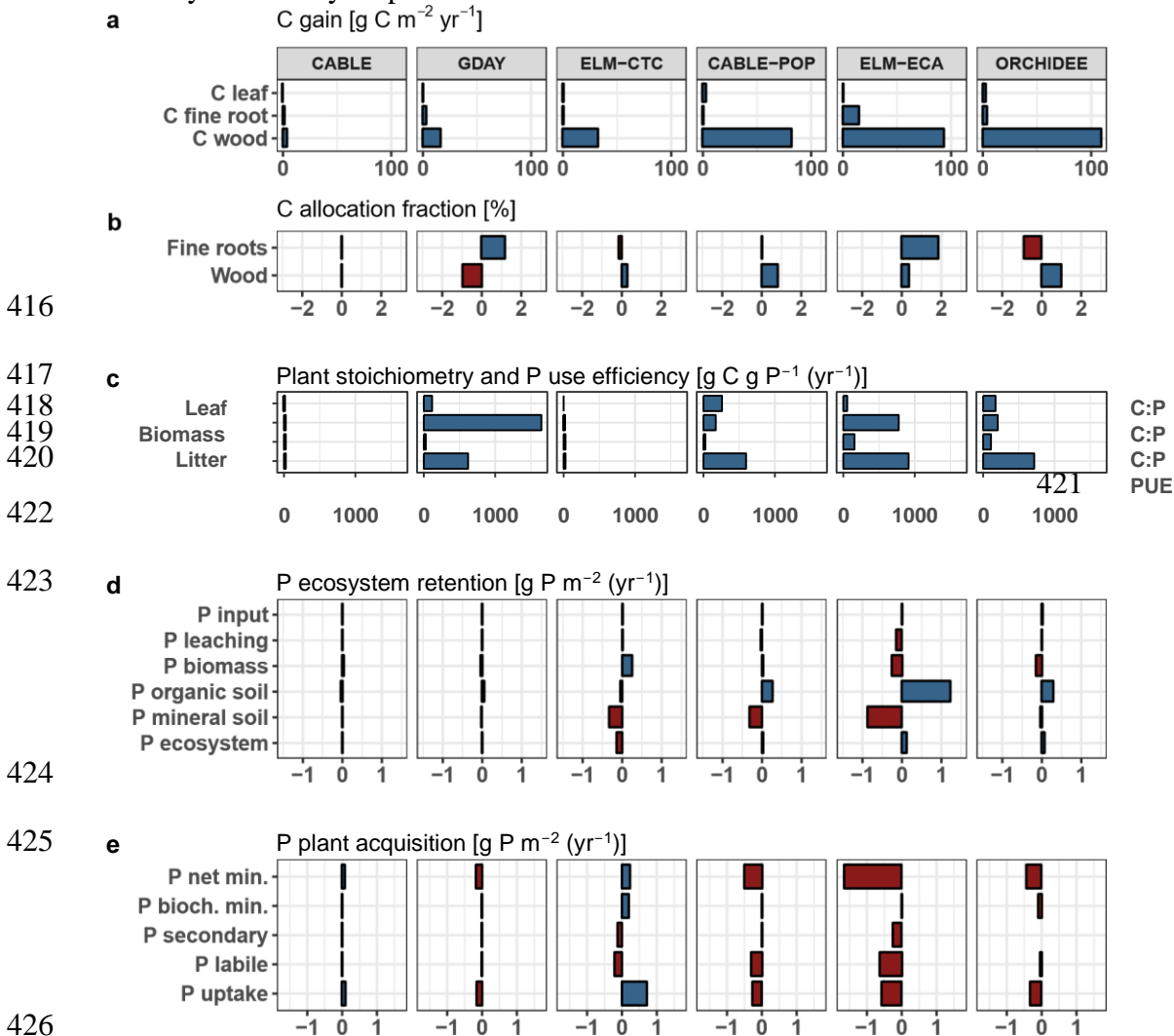
**Control of phosphorus feedbacks on the biomass C response to eCO<sub>2</sub>**



402



403 **Figure 2: Strength of phosphorus feedbacks in controlling the biomass C response**  
 404 **to eCO<sub>2</sub> for the six CNP models.** Ecosystem processes are highlighted that depend (or not  
 405 depend) on the P cycle, for which classes (none, intermediate, high) indicate the degree to  
 406 which the considered P feedback causes a response of biomass C to eCO<sub>2</sub> in our simulations. P  
 407 limitation causes strong or intermediate downregulation of photosynthesis with eCO<sub>2</sub> across  
 408 all models. Maintenance respiration, leaf turnover and P resorption are not responsive to P  
 409 feedbacks in any of the models. Leaf N:P responds to eCO<sub>2</sub> in most models, but is fixed in  
 410 ELM-CTC, narrowly bound in CABLE, and at its maximum in ORCHIDEE. P limitation  
 411 causes direct downregulation of biomass growth in CABLE, CABLE-POP, ELM-ECA and  
 412 ORCHIDEE. Allocation shifts towards roots to alleviate P limitation is considered in GDAY,  
 413 ELM-ECA and ORCHIDEE. Desorption of P from mineral surfaces is only considered in  
 414 ELM-ECA and ELM-CTC, and biochemical P mineralization is considered in many models,  
 415 but only effectively responsive in ELM-CTC.



427 **Figure 3: Key responses of biomass C gain, stoichiometry, allocation, and P**  
 428 **dynamics to eCO<sub>2</sub> for the CNP models,** contrasted are positive (blue) from negative (red)  
 429 responses. **a,** Mean annual change in standing leaf, fine root and wood C over 15 years,  
 430 increasing across models from left to right in g C m<sup>-2</sup> yr<sup>-1</sup>. **b,** The mean change in C allocation  
 431 for fine roots and wood in %. **c,** Mean change in tissue stoichiometry in absolute terms in g C  
 432 g P<sup>-1</sup> and change in P use efficiency over 15 years in g C g P<sup>-1</sup> yr<sup>-1</sup>. **d,** Mean change in

433 ecosystem P input and output (leaching) fluxes in  $\text{g P m}^{-2} \text{ yr}^{-1}$  and mean change in final P  
434 stock in biomass, organic soil, mineral soil and total ecosystem in  $\text{g P m}^{-2}$ . **e**, Mean change in  
435 plant P acquisition processes, including change in net P mineralization, biochemical P  
436 mineralization and P uptake in  $\text{g P m}^{-2} \text{ yr}^{-1}$  and secondary and labile P pools in  $\text{g P m}^{-2}$ . For  
437 both, **d** and **e**, P flux changes are differences of cumulative fluxes after 15 years and P pool  
438 changes are differences in pools after 15 years.

#### 439 **CO<sub>2</sub> fertilization of the Amazon forest hinges on plant phosphorus use and** 440 **acquisition**

441 We present here supplementary information to the main text of the study "CO<sub>2</sub> fertilization  
442 of the Amazon forest hinges on plant phosphorus use and acquisition" by Fleischer et al.,  
443 submitted to Nature Geoscience.

444 The individual models' biomass C responses to eCO<sub>2</sub> are shown in **Extended Data**  
445 **Figure 1**, where the absolute and relative effect of eCO<sub>2</sub> on cumulative biomass C is included.  
446 The variation in their predictions among and within the model groups becomes apparent.  
447 While CNP models (in green) generally predict lower biomass C gain with eCO<sub>2</sub> compared to  
448 Only (grey) and CN models (blue), some CNP models exceed predictions by the other model  
449 groups. Assumptions on how plant P use and P acquisition is dealt with in the models cause  
450 these diverging responses.

451 The individual models' performance in representing ambient conditions of key ecosystem  
452 variables are shown in **Extended Data Figure 2**. Models' generally represented ambient  
453 conditions well at the study site, such as GPP, NPP and LAI. GPP was lower than observed in  
454 some models, while LAI was either over- or underestimated by some models. Considering the  
455 uncertainties surrounding field observations, we judged these deviations as acceptable. For  
456 biomass C, models diverged noticeably, which is controlled by productivity and turnover  
457 dynamics simultaneously. While we have relatively reliable measurements of aboveground  
458 biomass C, belowground components remain more uncertain and are not considered in the  
459 observational-based estimate here. Models on the other hand consider total biomass C, which  
460 adds to the differences among models and observations. Ambient annual biomass C increment  
461 varied strongly across the models, for which we included the Amazon-wide estimate from  
462 Brienen et al. 2015 as an observation (see main text for complete reference). The estimate  
463 from our site is lower (see main text), but associated to higher uncertainties due to few  
464 censuses. For both, biomass C and biomass C increment, there was no clear pattern between  
465 the model groups, so that we judge that these differences did not control the overall  
466 conclusions of our study.

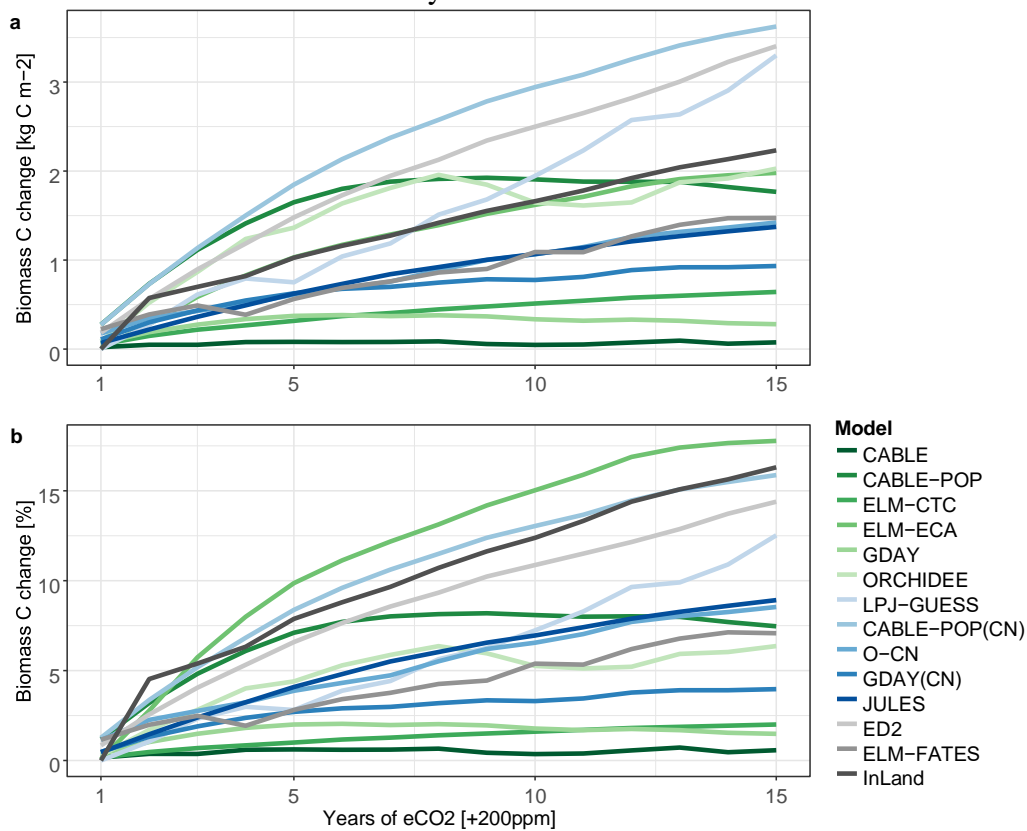
467 The models simulated less than  $1.1 \text{ g labile P m}^{-2}$  to 4 m depth in the ambient run (with the  
468 exception of ELM-CTC), which is the plant available soil P. Observations indicate  $1.6 \text{ g resin}$   
469  $\text{P m}^{-2}$  to 30 cm depth. Resin P is considered to be directly plant-available, representing the  
470 modelled soil labile P pool, although direct comparisons are hampered as P fractionations are  
471 operationally defined. Observations are thus slightly higher but both modelled and observed  
472 values on soil labile P are considered to be very low and the resulting modelled P limitation to  
473 be realistic.

474 The individuals models' simulation results on the relative eCO<sub>2</sub> effect on primary  
475 productivity (GPP, NPP), plant tissue C stocks and plant CUE are shown in **Extended Data**  
476 **Figure 3**. The models' plant C allocation fractions and the respective relative effect of eCO<sub>2</sub>  
477 thereon is shown in **Extended Data Figure 4**. The individuals models' simulation results on

478 the relative eCO<sub>2</sub> effect on N and P uptake, NUE and PUE, as well as plant tissue  
479 stoichiometry is shown in **Extended Data Figure 5**.

480 The relationship between eCO<sub>2</sub> induced P uptake, fine root allocation, and the respective  
481 return of P uptake per unit fine root allocation for three CNP models are shown in **Extended**  
482 **Data Figure 6**. The three models (ELM-ECA, GDAY, and ORCHIDEE) simulated a higher  
483 fine root investment with eCO<sub>2</sub>, but a heightened relative return of P was only achieved  
484 temporarily, after some time, or not at all. The absolute effect of eCO<sub>2</sub> on NUE, PUE and  
485 stoichiometry for the individual models is shown in **Extended Data Figure 7**. Both CN and  
486 CNP versions of GDAY and CABLE-POP were included in the model ensemble, allowing the  
487 N and P effect alone to be inferred. Their respective CN versions, and some other CN models,  
488 indicated that N limitation occurred, as leaf and biomass C:N were predicted to increase under  
489 eCO<sub>2</sub> (Extended Data Fig. 7). The inclusion of both CN and CNP versions for GDAY and  
490 CABLE-POP supported the fact that P cycle limitations reduced the eCO<sub>2</sub> induced biomass C  
491 sink, as the main comparison across the C, CN and CNP model group indicated.

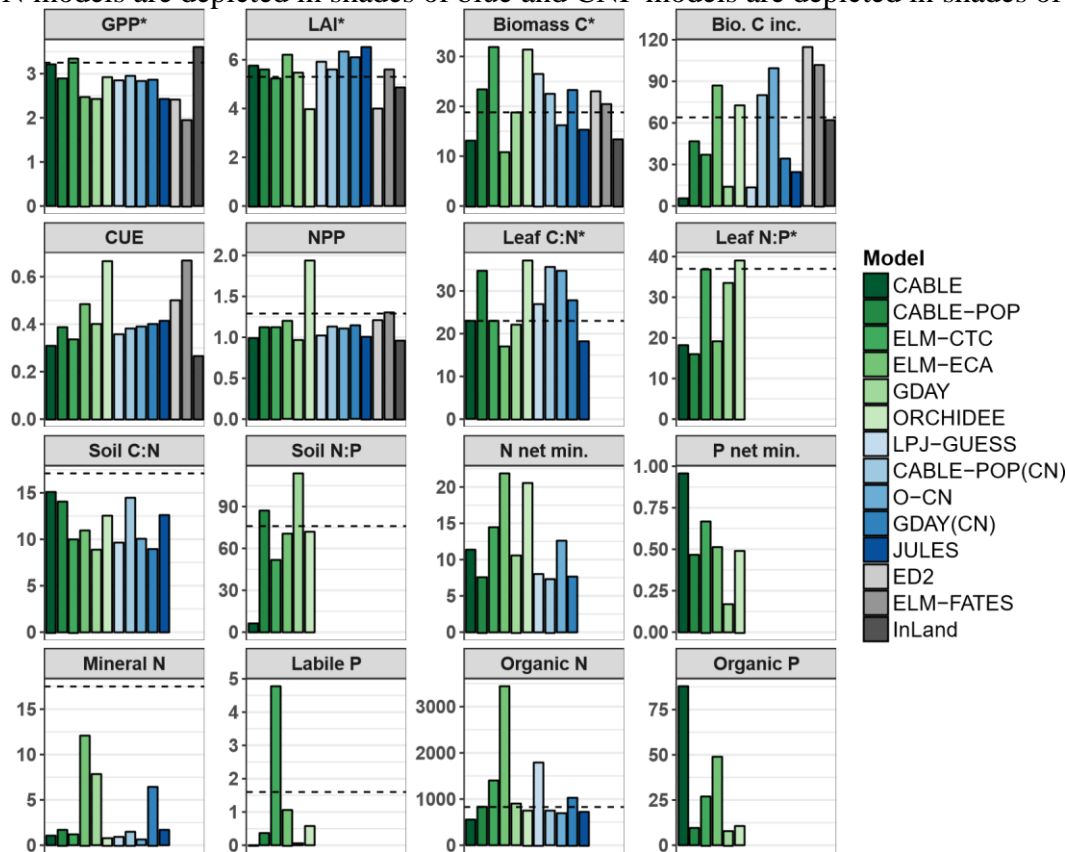
492 Model driving data of precipitation are plotted as annual precipitation over the course of  
493 the 15 year study period in **Extended Data Figure 8**. Precipitation (and other climate) data  
494 was derived from the K34 fluxtower, which experienced two years of strong precipitation  
495 deficit during the study period, 2000 and 2009. The relative eCO<sub>2</sub> response of GPP and NPP is  
496 plotted against annual precipitation in the **Extended Data Figure 9** to test for potential  
497 interactions of eCO<sub>2</sub> and droughts in the study region. While some models show a significant  
498 effect of precipitation on the strength of the eCO<sub>2</sub> effect on GPP, the slope of the line is very  
499 shallow, so that we can conclude that variations in water availability contributed little to the  
500 simulated eCO<sub>2</sub> effect in our study.



501

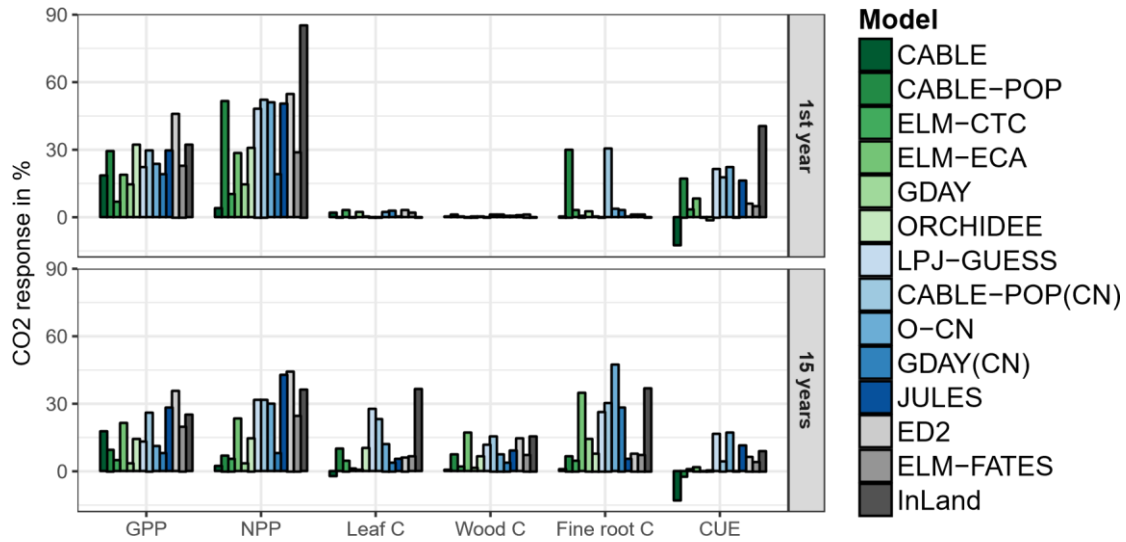
502 **Extended Data Figure 1: Cumulative effect of eCO<sub>2</sub> on biomass C per model. a,**  
503 **Absolute cumulative effect on biomass C in kg C m<sup>-2</sup>, and b, relative cumulative effect on**

504 biomass C in %. See legend for individual model names. C-only models are in shades of grey,  
 505 CN models are depicted in shades of blue and CNP models are depicted in shades of green.



506

507 **Extended Data Figure 2: Ambient model conditions compared to *in situ***  
 508 **observations.** Individual models' values are mean conditions over the ambient simulation.  
 509 Horizontal dotted lines indicate observations when available (see sources in Extended Data  
 510 Table 1). Measurements marked with a ? were provided to modelers beforehand. C fluxes  
 511 (GPP, NPP) are in  $\text{kg C m}^{-2} \text{yr}^{-1}$ , biomass C is aboveground only in  $\text{kg C m}^{-2}$ , and biomass C  
 512 increment in  $\text{g C m}^{-2} \text{yr}^{-1}$ . The observational estimate for biomass C increment is based on the  
 513 Amazon-wide estimate from Brienen et al. 2015 ( $64 \text{ g C m}^{-2} \text{yr}^{-1}$  for the 2000s, C.I.  $45\text{-}78 \text{ g C}$   
 514  $\text{m}^{-2} \text{yr}^{-1}$ ). CUE is calculated as the ratio of NPP per GPP. LAI is in  $\text{m}^2/\text{m}^2$ . Leaf and soil  
 515 stoichiometry are ratios of C, N and P content in dry matter, respectively. Leaf stoichiometry  
 516 was parameterised only in some models (see Extended Data Table 2). Fluxes of net N and P  
 517 mineralisation are in  $\text{g N/P m}^{-2} \text{yr}^{-1}$ . Soil mineral N pool and labile P pool (both considered  
 518 plant-available), as well as soil organic N and P pool, are in  $\text{g N/P m}^{-2}$ . Observations for soil  
 519 nitrogen content are based on top 10 cm, and for labile P on top 30cm. Modeled values are  
 520 based on a soil depth of 4m. See legend for individual model names. C-only models are  
 521 in shades of grey, CN models are depicted in shades of blue and CNP models are depicted in  
 522 shades of green.



523

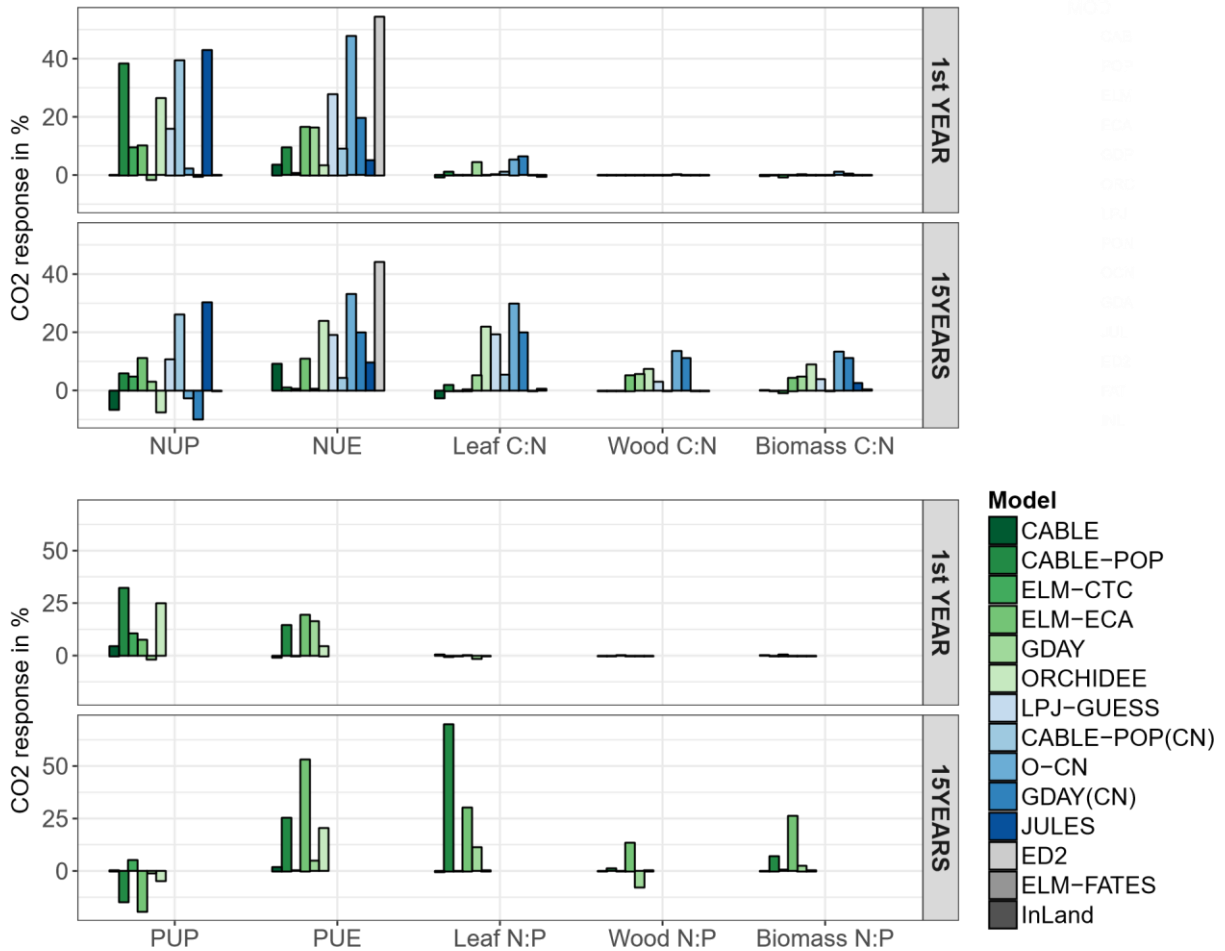
524 **Extended Data Figure 3: Relative effect of eCO<sub>2</sub> on GPP, NPP, leaf C, wood C, fine**  
 525 **root C and plant CUE.** Shown are initial effects (1st year) on top and final effect after 15  
 526 years of eCO<sub>2</sub> (mean of 13th to 17th year), both in %. See legend for individual model names.  
 527 C-only models are in shades of grey, CN models are depicted in shades of blue and CNP  
 528 models are depicted in shades of green.



529

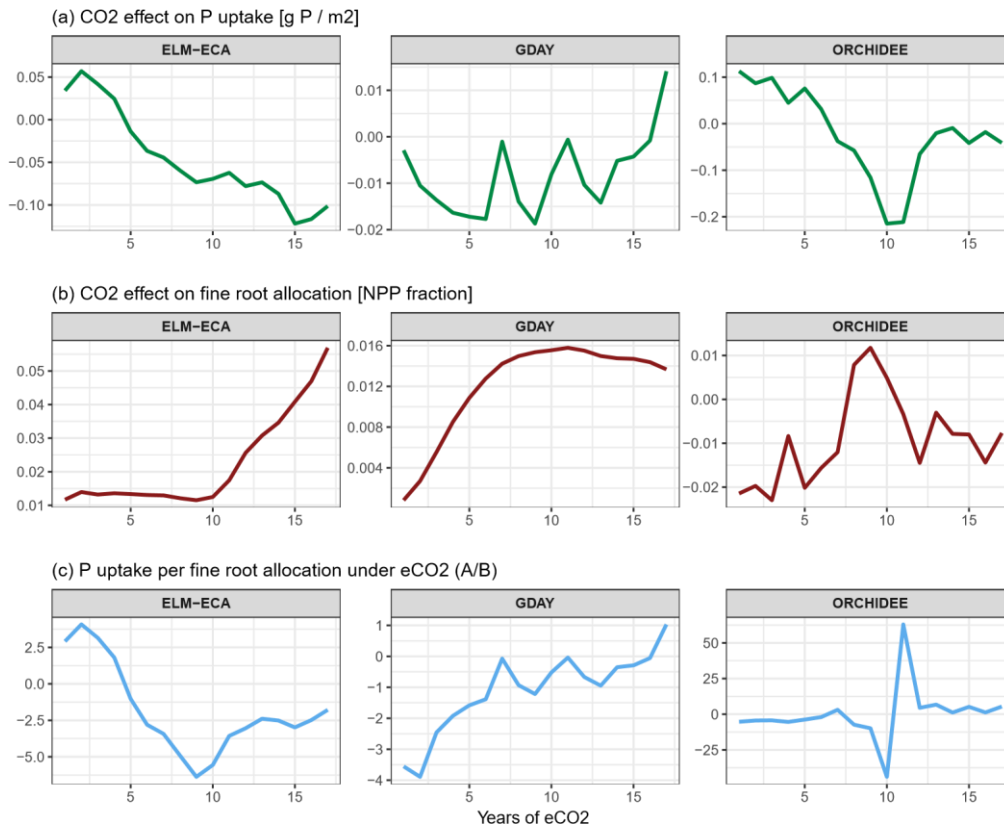
530 **Extended Data Figure 4: Ambient C allocation to plant tissues and the effect of eCO<sub>2</sub>**  
 531 **thereon.** Mean and standard deviation of ambient C allocation to leaf, wood, coarse and fine

532 root per model in % (top), and annual effect of eCO<sub>2</sub> on C allocation fractions over 15 years  
 533 per model in % (bottom). See legend for tissue compartments; leaf is displayed in green, wood  
 534 in red, coarse root in dark blue and fine root in light blue. Note individual y-axis scaling in  
 535 bottom graph.



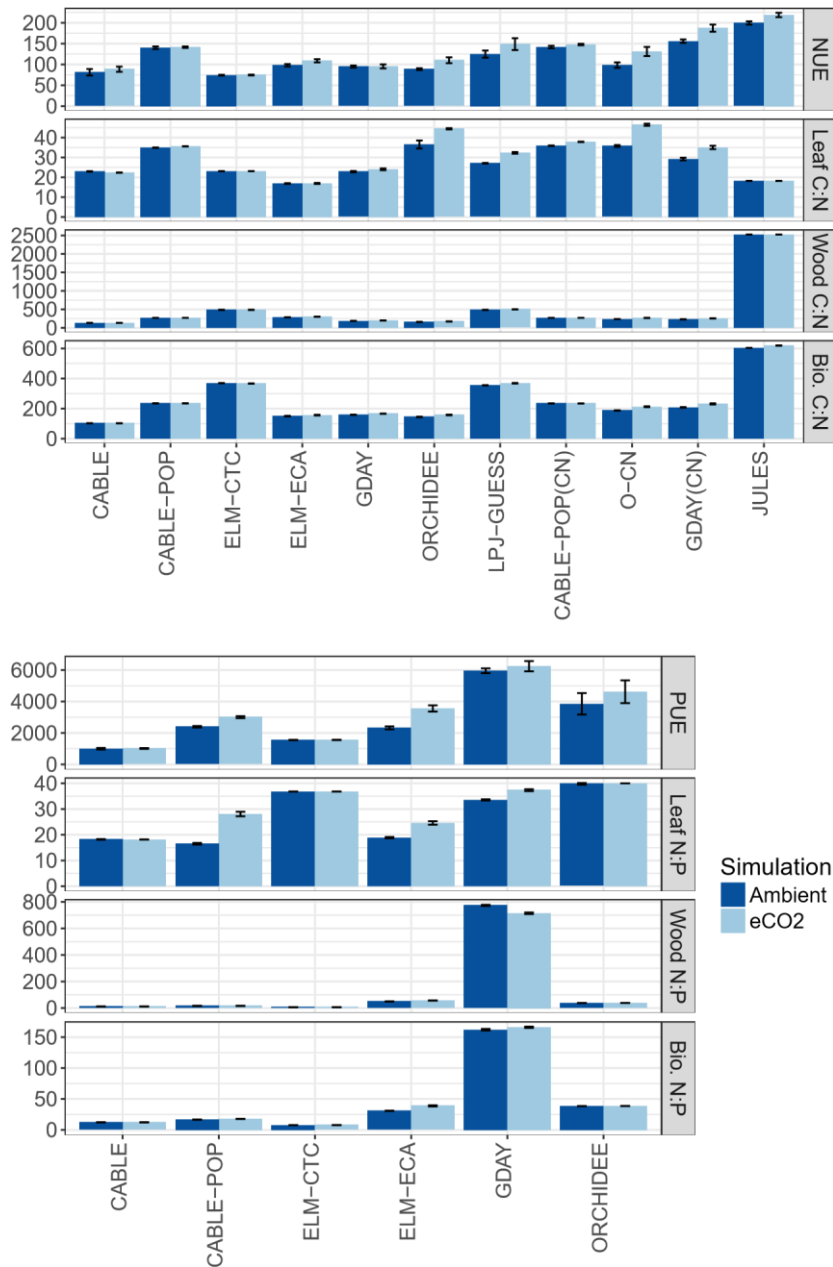
536

537 **Extended Data Figure 5: Relative effect of eCO<sub>2</sub> on N and P uptake, NUE and PUE,**  
 538 **and biomass stoichiometry per model.** Shown are initial effects (1st year), and final  
 539 effects after 15 years of fumigation (mean of 13th to 17th year), for N uptake (NUP), N use  
 540 efficiency (NUE), leaf C:N, Wood C:N, and biomass C:N for all CN and CNP models, in %  
 541 (top). Further displayed are P uptake (PUP), P use efficiency (PUE), leaf N:P, wood N:P, and  
 542 biomass N:P for all CNP models, in % (bottom). See legend for individual model names. C-  
 543 only models are in shades of grey, CN models are depicted in shades of blue and CNP models  
 544 are depicted in shades of green.



545

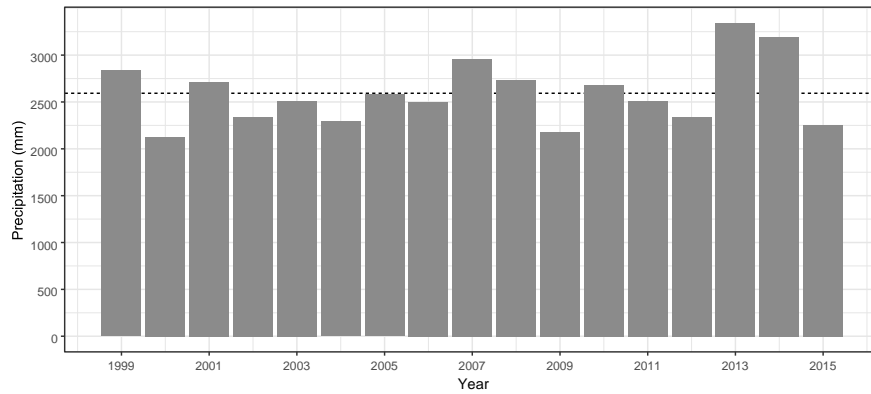
546 **Extended Data Figure 6: Effect of CO<sub>2</sub> on P uptake, fine root investment and the**  
 547 **resulting P uptake per fine root investment. a, CO<sub>2</sub> effect on P uptake, b, CO<sub>2</sub> effect on**  
 548 **fine root allocation, and c, P uptake gain per fine root investment (a/b). Shown for the three**  
 549 **CNP models that predict higher fine root investment with eCO<sub>2</sub>, see plot title for individual**  
 550 **model names.**



551

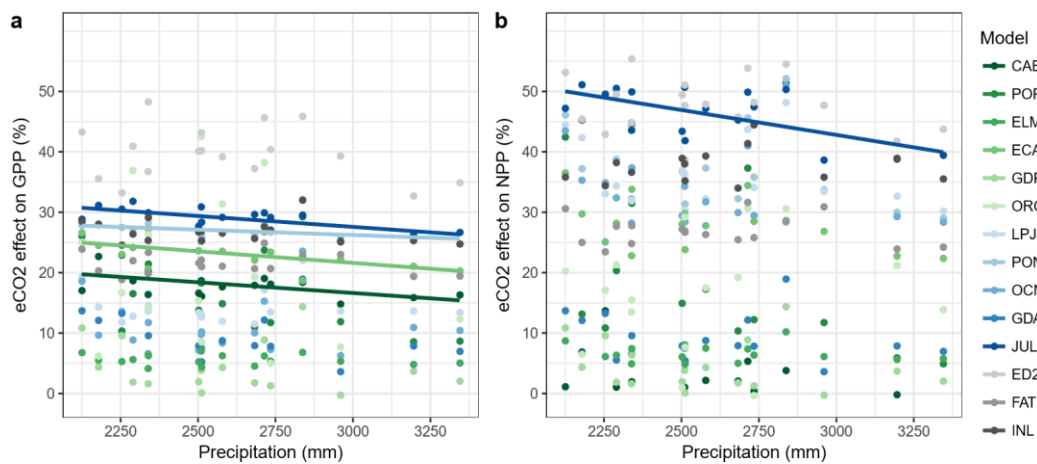
552 **Extended Data Figure 7: Absolute CO<sub>2</sub> effect on nutrient use efficiency and biomass**  
 553 **stoichiometry per model.** Shown are the absolute difference between ambient and eCO<sub>2</sub>  
 554 simulation run at the end of the 15 year simulation experiment (mean and standard deviation  
 555 of 13th to 17th year) for nitrogen use efficiency (NUE), leaf C:N, wood C:N, and plant  
 556 biomass C:N for CN and CNP models (top), and for phosphorus use efficiency (PUE), leaf  
 557 N:P, wood N:P, and plant biomass N:P for CNP models (bottom). See x-axis for individual  
 558 model names.





559

560 **Extended Data Figure 8: Annual precipitation from the fluxtower K34, used as**  
 561 **model driving data.** Shown are sums of annual precipitation in mm, note that years  
 562 represent Southern hemisphere growing season, i.e. 01/07/year to 30/06/year+1.



563

564 **Extended Data Figure 9: Effect of precipitation on the individual models' eCO<sub>2</sub>**  
 565 **effect on GPP and NPP. a,** eCO<sub>2</sub> effect on gross primary production (GPP) (in %) and **b,**  
 566 eCO<sub>2</sub> effect on net primary production (NPP), both against sum of precipitation (in mm)  
 567 throughout the experimental phase (1999-2015). See legend for individual model names. C-  
 568 only models are in shades of grey, CN models are depicted in shades of blue and CNP  
 569 models are depicted in shades of green. Only significant ( $p < 0.05$ ) linear regression lines are drawn in  
 570 the respective colour per model.  
 571