

1 **Title:**

2 **Future CO₂ 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 **(CO₂) 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 5th Climate Model**
41 **Intercomparison Project (CMIP5). Here, we simulate a planned free-air CO₂ enrichment**
42 **experiment in the Amazon with an ensemble of 14 terrestrial ecosystem models. The**
43 **model ensemble represents diverse plant functional strategies and generates a series of**
44 **testable hypotheses. We show that phosphorus availability reduces the projected CO₂-**
45 **induced biomass carbon growth by about 50% to 79 ± 63 g C m⁻² yr⁻¹ over 15 years**
46 **compared to estimates from carbon and carbon-nitrogen models. Our results suggest that**
47 **the region's resilience to climate change may be much less than previously assumed.**
48 **Variation in the biomass carbon response among the phosphorus-enabled models is**
49 **considerable, ranging from 5 to 140 g C m⁻² yr⁻¹, due to contrasting assumptions relating**
50 **to the flexibility in plant phosphorus use and acquisition strategies. Experimental design**
51 **needs to be targeted to reduce the uncertainties around the phosphorus feedback on the**
52 **CO₂ fertilization effect.**

53 The intact Amazon rainforest acts as a substantial carbon (C) sink, completely offsetting carbon
54 dioxide (CO₂) emissions from fossil fuel combustion and land use change in the Amazon
55 region^{1,2}. Increasing atmospheric CO₂ concentrations from anthropogenic activity may be the
56 primary factor for the current Amazon net C sink^{1,3}, via so-called CO₂ fertilization (an increase
57 in photosynthetic C uptake by plants under higher CO₂), which is projected to continue into the
58 future by global models⁴⁻⁶. The CO₂ fertilization effect has been observed experimentally in
59 field experiments that were conducted predominantly in the temperate zone. In these
60 experiments, the eCO₂ induced increase in C uptake was generally low when other factors, such
61 as soil nitrogen (N), were limiting⁷⁻⁹. To date, whole-ecosystem-scale experiments, i.e., free-
62 air CO₂ enrichment (FACE) have never been conducted in the tropics^{10,11}.

63 Over large parts of the Amazon and the tropics worldwide, phosphorus (P), not N, is assumed
64 to be the key limiting nutrient, as most P has been lost or occluded from plant uptake during
65 millions of years of soil pedogenesis^{12,13}. Forests growing on these highly weathered old soils
66 may nonetheless be highly productive due to the evolution of multiple strategies for P
67 acquisition and use, enabling tight cycling of P between plants and soils^{14,15}. Despite this

68 knowledge, quantifying the control of P on plant physiology, growth, and plant-soil interactions
69 in global models, and hence its role in the forests' response to eCO₂, remains challenging^{16,17}.
70 This challenge is exacerbated by the scarcity of observations and distinctive species responses
71 in hyperdiverse tropical forests¹⁸.

72 Here, we study the potential interactions between eCO₂ and nutrient (N and P) feedbacks in a
73 mature Amazonian rainforest by simulating the planned AmazonFACE experiment (+200 ppm;
74 <http://amazon-face.org/>) with an ensemble of ecosystem models (n = 14, Extended Data Table
75 3), including three C, five carbon-nitrogen (CN), and six carbon-nitrogen-phosphorus (CNP)
76 models^{19–24}. The AmazonFACE experiment is located in a well-studied, highly productive
77 tropical forest in Central Amazonia^{25,26}, growing on a strongly weathered *terra firme* Ferralsol.
78 This ecosystem represents the low end of the plant-available P spectrum in the Amazon,
79 consistent with ~32% of the Amazon rainforest's cover fraction²⁷. *In situ* measurements were
80 used to parameterise the models and to evaluate simulated ambient conditions (Extended Data
81 Table 1, 2). Our aim was to generate *a priori* model-based hypotheses to highlight the state-of-
82 the-knowledge and guide measurement strategies for AmazonFACE and other ecosystem
83 manipulation experiments to gain crucial process understanding of P control on the CO₂
84 fertilization effect.

85 Simulated eCO₂ (+200 ppm) had a positive effect on plant biomass C across all models but was
86 weakest in the CNP models (Fig. 1a). The eCO₂ conditions induced average biomass C gains
87 of 163 ± 65 , 145 ± 83 , and 79 ± 63 g C m⁻² yr⁻¹ (mean \pm SD) over 15 years in the C, CN and
88 CNP models, respectively (Fig. 1a). Limitations by P thus reduced the predicted biomass C sink
89 by 52% and 46% compared to that in the C and CN models, respectively, with considerable
90 variation across and within model groups (Extended Data Fig. 1). Plot inventories at the
91 AmazonFACE site during the 2000s indicate an aboveground biomass increment of 23 g C m²
92 yr⁻¹, substantially below the Amazon-wide¹ estimate of 64 g C m² yr⁻¹. The model ensemble
93 represents ambient conditions, such as productivity and leaf area index, reasonably well, but
94 ensemble members show divergence in other ecosystem characteristics, such as the biomass C
95 increment, which range from 5 to 114 g C m² yr⁻¹. There is, however, no clear pattern in
96 performance between the model groups, so that we judge that these differences do not have
97 bearing on the conclusions of our study (see more discussion in Extended Data Fig. 2).

98 Gross and net primary productivity (GPP and NPP, respectively) are both stimulated by eCO₂
99 in all models, both initially (after 1 year of eCO₂) and until the end of the simulation. The CNP
100 models show the strongest decline from the initial response due to P limitation (Fig. 1b, c). The

101 final response of NPP to eCO₂ was a 35%, 29%, and 9% stimulation for the C, CN and CNP
102 models, respectively. In general, in the CN and CNP models, nutrient limitation is defined as
103 nutrient demand being greater than nutrient supply. However, models differ in their
104 assumptions on how nutrient limitation controls productivity and C allocation in response to
105 eCO₂, so that divergent responses on plant carbon use efficiency (CUE = NPP / GPP) are
106 simulated (Extended Data Table 3). In some CN models, CUE increases because N limitation
107 is hypothesized to reduce autotrophic respiration (Ra) via lower tissue N content. Some CNP
108 models, however, assume a direct downregulation of growth and hence the plant CUE decreases
109 (Extended Data Fig. 3). Elevated CO₂ induced higher fine root investments of NPP in some CN
110 and CNP models to aid nutrient acquisition (Fig. 1c; Extended Data Fig. 4). Predicted changes
111 in allocation with eCO₂ cause a general increase in biomass turnover across all but one of the
112 models, partially offsetting the positive biomass response (Extended Data Table 4). Changes in
113 turnover play a minor role in our 15 years simulation period but rather control the long-term
114 future CO₂ effect on the biomass C sink^{28,29}.

115 Plant growth under eCO₂ is lowest in CNP models as the low availability of soil labile P restricts
116 P uptake either immediately or over time (Extended Data Fig. 5). We considered the modelled
117 P limitation on plant growth to be realistic, as the models and observations agree on soil labile
118 P being very low (Extended Data Fig. 2). Other site observations support the fact that P is
119 extremely critical for plant productivity, such as high leaf N:P ratios of 37 and high plant P
120 resorption (before litter fall) of 78% (Extended Data Table 1). While P limitation consistently
121 reduces the eCO₂-induced biomass C sink, there is significant variation among CNP models
122 due to contrasting process representations (Fig. 2; Extended Data Table 3). P shortages
123 downregulate growth (i.e., NPP) in all CNP models, directly or via photosynthesis. The major
124 differences in the model assumptions relate to how they modify P supply and demand to
125 alleviate plant P shortages, including either (i) enhancing plant P use efficiency (PUE = NPP /
126 P uptake) or (ii) upregulating P acquisition mechanisms. The models assume that PUE may
127 change if tissue nutrient ratios are flexible, if C allocation changes among tissues with different
128 stoichiometry, and/or if P resorption is variable (Fig. 2). Flexible stoichiometry is considered
129 in all CNP models except ELM-CTC, although with varying degrees of flexibility. Greater fine
130 root C allocation with plant P stress is considered in some, and P resorption is a fixed fraction
131 of leaf tissue P in all models (Fig. 2).

132 Models differ in their representation of soil P acquisition mechanisms; three of the six models
133 (ELM-ECA, ELM-CTC, GDAY) consider desorption of P from mineral surfaces (i.e., the

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

141 Diverging representations of plant P use and acquisition among the CNP models cause
142 predictions of the eCO₂-induced biomass C sink to range from 5 g C m⁻² yr⁻¹ to 140 g C m⁻² yr⁻¹
143 (Fig. 3a; Extended Data Fig. 1). Greater plant PUE occurred in four of the models, for which
144 shifts in tissue C:N and N:P due to eCO₂ led to increases in biomass C:P ranging from ~200 to
145 1600 g C g P⁻¹ (Fig. 3c). Higher fine root investment with eCO₂, at the expense of less “P-
146 costly” wood, offset some increases in PUE in some models. Flexible biomass stoichiometry
147 altered decomposition dynamics and induced progressive P limitation in response to eCO₂, i.e.,
148 litter stoichiometry shifted towards lower quality (less N and P in relation to C), reducing net P
149 mineralization rates from microbial decomposition, causing P to become increasingly
150 unavailable to plants and accumulating in soil organic matter (Fig. 3d, e). This plant-soil-
151 microbial feedback slowed the cycling of P in the ecosystem and exacerbated the initial P
152 limitation (see Ref. ³⁰ for a similar feedback during pedogenesis).

153 Enhanced plant P acquisition under eCO₂ effectively alleviated P limitation in two CNP models
154 (ELM-CTC and ELM-ECA) (Fig. 3e). In both, eCO₂ increased the liberation of P from the
155 secondary pool, as higher plant P demand and uptake diminished the labile P pool, in turn
156 causing higher desorption rates. P desorption is thus only indirectly, and not mechanistically,
157 enhanced by plants in these models. Biochemical mineralization of P under eCO₂ responded
158 positively in both of the models, but added only notably to additional P acquisition in ELM-
159 CTC (Fig. 3e). Although three CNP models simulated higher fine root investments, the actual
160 P uptake return per fine root increment was marginal or came only into effect in the long-term
161 (Extended Data Fig. 6).

162 Observations document ample N cycling in the system, e.g., high leaf N contents, indicative
163 δ¹⁵N values, high rates of N oxide emissions, and low leaf N resorption^{31,32}, and thereby suggest
164 that plant growth is not directly affected by N availability. The CN models, however, simulate
165 increased nitrogen use efficiency (NUE) and biomass C:N ratios, in response to insufficient N
166 uptake under eCO₂ (Extended Data Fig. 5). Plant N availability may be underestimated in the

167 models, since the plant-available mineral N supply was $<7 \text{ g N m}^{-2}$ across all models, as opposed
168 to 17.5 g N m^{-2} observed in the top 10 cm only (Extended Data Fig. 2). These results highlight
169 an important gap in our knowledge also related to the dynamics of N availability, and its
170 potential interaction with P dynamics (Table 1).

171 In summary, the model ensemble encapsulates a range of plausible hypotheses and represents
172 a potential range of biomass C responses to eCO_2 under low soil P availability. The assumption
173 of a lacking ability of plants to acquire more soil P and a limited capacity for plants to use P
174 more efficiently resulted in effectively zero biomass C gain with eCO_2 . Conversely, flexible
175 stoichiometry, in combination with enhanced plant P acquisition, were the key mechanistic
176 responses leading to biomass gain with eCO_2 . Divergences in the simulated eCO_2 response lead
177 us to the following testable hypotheses, and call for directed field measurements (Table 1):

178 H1. Low soil P availability will strongly constrain future plant biomass growth response to
179 eCO_2 either by downregulating photosynthesis or limiting plant growth directly, or a
180 combination thereof.

181 H2. Despite the limited soil P supply, plasticity in vegetation stoichiometry and allocation
182 patterns will allow for some biomass growth under eCO_2 .

183 H3. Plants will increase investments in P acquisition to increase P supply and allow biomass
184 growth under eCO_2 either via greater P interception through fine root production or via greater
185 P liberation from P desorption or biochemical mineralization of P.

186 These model-based hypotheses deepen a previous analysis of potential N and P limitation on C
187 accumulation based on mass balance principle³³. Furthermore, we add to a model
188 intercomparison carried out in advance of the EucFACE experiment³⁴ by extending the range
189 of plant P feedbacks considered across CNP models. This work highlighted H1: two
190 stoichiometrically constrained CNP models predicted that strong P limitation will curtail the
191 growth response to eCO_2 in Australia. Consistent with this hypothesis, aboveground growth has
192 not increased with eCO_2 in that experiment over the initial years³⁵. This finding underlines that
193 monitoring efforts need to place a strong(er) focus on belowground carbon and nutrient
194 dynamics, in addition to canopy-scale photosynthesis and aboveground growth dynamics.
195 Additionally, Ra dependence on P content and plant stress from drought or nutrient limitation
196 need further monitoring during experiments to fully elucidate the plant C budget and address
197 H1 (Table 1).

198 Nutrient fertilization experiments support H2, as plasticity in leaf stoichiometry at the
199 individual level, along with plasticity in P resorption efficiency, was observed³⁶. Across the
200 Amazon, community-weighted leaf N:P in the field varied from 13 to 42 g N g P⁻¹ (n = 64)
201 (Ref. ³²), which place our site, with a mean of 37, closer to the high end. GDAY predicted the
202 most plausible increase in the leaf N:P ratio from 34 to 38 (Extended Data Fig. 7). Two models
203 predicted strong increases in the leaf N:P ratio with eCO₂ but started off with much lower initial
204 values. The degree to which plasticity in stoichiometry and resorption can aid plant PUE under
205 eCO₂ in highly P-limited sites that are already at the end of the observed spectrum remains to
206 be seen (H2). Monitoring plant tissue stoichiometry, including wood with much higher N:P
207 ratios, combined with assessments of P resorption in CO₂ and nutrient fertilization experiments
208 will reduce uncertainties (Table 1).

209 Based on previous observations⁸, a number of models assume increased fine root investment,
210 as well as higher biochemical P mineralization and P desorption from mineral surfaces, under
211 eCO₂-induced nutrient limitation (H3). The effect of increased fine root biomass on nutrient
212 uptake was limited in our simulations and ambient fine root allocation fractions were highly
213 variable among the models, ranging from 5-30% of NPP (Extended Data Fig. 4, 6). Both these
214 modelled results highlight model deficiencies in belowground processes³⁷ that need addressing
215 (Table 1). There is evidence that phosphatase activity in litter and soil and the presence of low-
216 molecular-weight acids used to liberate P from organic matter or from mineral surfaces increase
217 with plant P demand³⁸. This was predicted by ELM-CTC in our simulations, which also showed
218 Amazon-wide that “[with] enhanced phosphatase production, productivity in the highly P-
219 limited areas can be sustained under elevated CO₂ conditions”³⁹. Plants invest in P liberation
220 and acquisition, but if these mechanisms can be upregulated under eCO₂ and over what time
221 frame this may occur remain open questions. Quantification of such a response is lacking, as
222 are estimates of the associated plant C costs to acquire P via these and other mechanisms, such
223 as mycorrhizal symbiosis^{15,40} (Table 1). The P gain and C cost for P acquisition mechanisms,
224 as well as the associated plant-soil-microbial interactions, need to be assessed by analyses of
225 soil, microbial and root nutrition, and via novel techniques investigating enzyme and labile C
226 dynamics⁴¹. Monitoring of belowground fine root dynamics needs to include the surface litter
227 layer, commonly explored by fine roots in P-impooverished ecosystems in the Amazon, not yet
228 quantified nor considered in models (Table 1).

229 Previous model projections suggest a sustained fertilization effect of CO₂ on the Amazon C
230 sink but have not considered feedbacks from low soil P availability^{5,6}. Our study demonstrates

231 that, based on the current generation of CNP models, the omission of P feedbacks is highly
232 likely to cause an overestimation of the Amazon rainforest's capacity to sequester atmospheric
233 CO₂. Considering P limitation on the CO₂ fertilization effect in future predictions may indicate
234 that the forest is less resilient to higher temperatures and changing rainfall patterns than
235 previously thought^{6,42}. Periods of water deficit may contribute to the eCO₂ fertilization effect
236 on productivity due to its water saving effect³⁴, or due to alterations of decomposition processes.
237 Our study site experienced years with significantly less than average precipitation, e.g. in 2000
238 and 2009, however, in our simulations this increased the positive response of GPP and NPP to
239 eCO₂ only marginally (Extended Data Figure 8 and 9). Models lack the appropriate sensitivity
240 of plant responses to changes in water availability, and even more so when precipitation sums
241 are that high⁴³. Interactions of water and P availability and their consequences on the CO₂
242 fertilization effect remain uncertain⁴⁴ and is an area where field measurements will allow us to
243 better constrain model responses (Table 1).

244 Although P is likely to reduce the biomass C sink response to CO₂ in regions with low plant-
245 available P supply, our results suggest that plasticity in plant P use and plant P acquisition
246 mechanisms, may at least partially alleviate P limitation under eCO₂ and enable CO₂
247 fertilization of biomass growth. The model ensemble may be interpreted as representing a range
248 of possible tropical plant functional strategies and growth responses to low P availability under
249 eCO₂. Responses are expected to be species-specific, as were plant growth responses to low P
250 supplies in another tropical region¹⁸. The ecosystem-scale response to P limitation under eCO₂
251 will thus depend on the relative contributions of the various P acquisition and P use strategies
252 across individuals, their interactions and to what extent these processes can be upregulated
253 under eCO₂. All of which ultimately need to be described and represented in a single model
254 framework in order to accurately predict the Amazon rainforest's response to future climate
255 change.

256 AmazonFACE has the unique opportunity to experimentally address these key areas of
257 uncertainty, not only by integrating the proposed measurements across seasons and at the
258 ecosystem scale (summary in Table 1) but also by assessing species-specific responses to eCO₂
259 in relation to trait expression. Amazon-wide expression of plant functional strategies may then
260 be inferred by applying the mechanistic interplay between trait expression and edaphic
261 conditions. The key to predicting the future of the world's largest tropical forest under eCO₂
262 thus lies in obtaining experimental data on, and subsequently modelling, different plant P
263 acquisition and use strategies, as well as their interactions in a competing plant community.

264 **END NOTES**

265 **Author contributions**

266 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
267 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.,
268 C.v.R., Y.-P.W., X.Y., S.Z., and Q.Z. performed model simulations. K.F. wrote the
269 manuscript with contributions from all co-authors.

270 **Acknowledgements**

271 We thank the many scientists involved in the development of the models used in our study;
272 the many scientists, field and laboratory technicians and other staff involved in collecting and
273 analysing the field data; and everyone involved in the planning and conductance of the
274 AmazonFACE project. Oak Ridge National Laboratory is operated by UT-Battelle, LLC,
275 under contract DE-AC05-00OR22725 with the US Department of Energy. We thank the DFG
276 for financing the workshop that made this study possible (grant No. RA 2060/4-1) and for
277 providing funds to K.F. (grant No. RA 2060/5-1.)

278 **REFERENCES**

- 279 1. Brien, R. J. W. *et al.* Long-term decline of the Amazon carbon sink. *Nature* **519**,
280 344–348 (2015).
- 281 2. Phillips, O. L. & Brien, R. J. W. Carbon uptake by mature Amazon forests has
282 mitigated Amazon nations' carbon emissions. *Carbon Balance Manag.* **12**, 1 (2017).
- 283 3. Cernusak, L. A. *et al.* Tropical forest responses to increasing atmospheric CO₂: Current
284 knowledge and opportunities for future research. *Funct. Plant Biol.* **40**, 531–551
285 (2013).
- 286 4. Ciais, P. *et al.* The physical science basis. Contribution of working group I to the fifth
287 assessment report of the intergovernmental panel on climate change. *Chang. IPCC*
288 *Clim.* 465–570 (2013).
- 289 5. Cox, P. M. *et al.* Sensitivity of tropical carbon to climate change constrained by carbon
290 dioxide variability. *Nature* **494**, 341–344 (2013).
- 291 6. Huntingford, C. *et al.* Simulated resilience of tropical rainforests to CO₂-induced
292 climate change. *Nat. Geosci.* **6**, 268–273 (2013).
- 293 7. Talhelm, A. F. *et al.* Elevated carbon dioxide and ozone alter productivity and

- 294 ecosystem carbon content in northern temperate forests. *Glob. Chang. Biol.* **20**, 2492–
295 2504 (2014).
- 296 8. Norby, R. J., Warren, J. M., Iversen, C. M., Medlyn, B. E. & McMurtrie, R. E. CO₂
297 enhancement of forest productivity constrained by limited nitrogen availability. *Proc.*
298 *Natl. Acad. Sci.* **107**, 19368–19373 (2010).
- 299 9. Zaehle, S. *et al.* Evaluation of 11 terrestrial carbon-nitrogen cycle models against
300 observations from two temperate Free-Air CO₂Enrichment studies. *New Phytol.* **202**,
301 803–822 (2014).
- 302 10. Hofhansl, F. *et al.* Amazon forest ecosystem responses to elevated atmospheric CO₂
303 and alterations in nutrient availability: filling the gaps with model-experiment
304 integration. *Front. Earth Sci.* **4**, (2016).
- 305 11. Norby, R. J. *et al.* Model-data synthesis for the next generation of forest free-air CO₂
306 enrichment (FACE) experiments. *New Phytol.* **209**, 17–28 (2016).
- 307 12. Lloyd, J., Bird, M. I., Veenendaal, E. M. & Kruijt, B. Should Phosphorus Availability
308 Be Constraining Moist Tropical Forest Responses to Increasing CO₂ Concentrations?
309 *Glob. Biogeochem. Cycles Clim. Syst.* 95–114 (2001).
- 310 13. Vitousek, P. M. Litterfall, nutrient cycling, and nutrient limitation in tropical forests.
311 *Ecology* **65**, 285–298 (1984).
- 312 14. Quesada, C. A. *et al.* Basin-wide variations in Amazon forest structure and function are
313 mediated by both soils and climate. *Biogeosciences* **9**, 2203–2246 (2012).
- 314 15. Lambers, H., Raven, J. A., Shaver, G. R. & Smith, S. E. Plant nutrient-acquisition
315 strategies change with soil age. *Trends Ecol. Evol.* **23**, 95–103 (2008).
- 316 16. Reed, S. C., Yang, X. & Thornton, P. E. Incorporating phosphorus cycling into global
317 modeling efforts: A worthwhile, tractable endeavor. *New Phytol.* **208**, 324–329 (2015).
- 318 17. Jiang, M., Caldararu, S., Zaehle, S., Ellsworth, D. S. & Medlyn, B. E. Towards a more
319 physiological representation of vegetation phosphorus processes in land surface
320 models. *New Phytol.* 1–7 (2019).
- 321 18. Turner, B. L., Brenes-Arguedas, T. & Condit, R. Pervasive phosphorus limitation of
322 tree species but not communities in tropical forests. *Nature* **555**, 367–370 (2018).
- 323 19. Goll, D. S. *et al.* A representation of the phosphorus cycle for ORCHIDEE (revision

- 324 4520). *Geosci. Model Dev.* **10**, 3745–3770 (2017).
- 325 20. Wang, Y.-P., Law, R. M. & Pak, B. A global model of carbon, nitrogen and
326 phosphorus cycles for the terrestrial biosphere. *Biogeosciences* **7**, 2261–2282 (2010).
- 327 21. Haverd, V. *et al.* A new version of the CABLE land surface model (Subversion
328 revision r4601) incorporating land use and land cover change, woody vegetation
329 demography, and a novel optimisation-based approach to plant coordination of
330 photosynthesis. *Geosci. Model Dev.* **11**, 2995–3026 (2018).
- 331 22. Comins, H. N. & McMurtrie, R. E. Long-Term Response of Nutrient-Limited Forests
332 to CO₂ Enrichment; Equilibrium Behavior of Plant-Soil Models. *Ecol. Appl.* **3**, 666–
333 681 (1993).
- 334 23. Zhu, Q., Riley, W. J., Tang, J. & Koven, C. D. Multiple soil nutrient competition
335 between plants, microbes, and mineral surfaces: model development, parameterization,
336 and example applications in several tropical forests. *Biogeosciences* **13**, 341–363
337 (2016).
- 338 24. Yang, X., Thornton, P. E., Ricciuto, D. M. & Post, W. M. The role of phosphorus
339 dynamics in tropical forests – a modeling study using CLM-CNP. *Biogeosciences* **11**,
340 1667–1681 (2014).
- 341 25. Malhi, Y. *et al.* Comprehensive assessment of carbon productivity, allocation and
342 storage in three Amazonian forests. *Glob. Chang. Biol.* **15**, 1255–1274 (2009).
- 343 26. Araújo, A. C. *et al.* Comparative measurements of carbon dioxide fluxes from two
344 nearby towers in a central Amazonian rainforest: The Manaus LBA site. *J. Geophys.*
345 *Res.* **107**, 8090 (2002).
- 346 27. Quesada, C. A. *et al.* Soils of Amazonia with particular reference to the RAINFOR
347 sites. *Biogeosciences* **8**, 1415–1440 (2011).
- 348 28. Friend, A. D. *et al.* Carbon residence time dominates uncertainty in terrestrial
349 vegetation responses to future climate and atmospheric CO₂. *Proc. Natl. Acad. Sci.*
350 **111**, 3280–3285 (2014).
- 351 29. Walker, A. P. *et al.* Predicting long-term carbon sequestration in response to CO₂
352 enrichment: How and why do current ecosystem models differ? *Global Biogeochem.*
353 *Cycles* **29**, 476–495 (2015).
- 354 30. Vitousek, P. M. *Nutrient cycling and limitation: Hawai'i as a model system.* Princeton

- 355 *University Press* (2004).
- 356 31. Nardoto, G. B. *et al.* Basin-wide variations in Amazon forest nitrogen-cycling
357 characteristics as inferred from plant and soil 15N:14N measurements. *Plant Ecol.*
358 *Divers.* **7**, 173–187 (2014).
- 359 32. Fyllas, N. M. *et al.* Basin-wide variations in foliar properties of Amazonian forest:
360 phylogeny, soils and climate. *Biogeosciences* **6**, 2677–2708 (2009).
- 361 33. Wieder, W. R., Cleveland, C. C., Smith, W. K. & Todd-Brown, K. Future productivity
362 and carbon storage limited by terrestrial nutrient availability. *Nat. Geosci.* **8**, 441–444
363 (2015).
- 364 34. Medlyn, B. E. *et al.* Using models to guide field experiments: a priori predictions for
365 the CO₂ response of a nutrient- and water-limited native Eucalypt woodland. *Glob.*
366 *Chang. Biol.* **22**, 2834–2851 (2016).
- 367 35. Ellsworth, D. S. *et al.* Elevated CO₂ does not increase eucalypt forest productivity on a
368 low-phosphorus soil. *Nat. Clim. Chang.* **7**, 279–282 (2017).
- 369 36. Wright, S. J. *et al.* Plant responses to fertilization experiments in lowland, species-rich,
370 tropical forests. *Ecology* **99**, 1129–1138 (2018).
- 371 37. Warren, J. M. *et al.* Root structural and functional dynamics in terrestrial biosphere
372 models--evaluation and recommendations. *New Phytol.* **205**, 59–78 (2015).
- 373 38. Hoosbeek, M. R. Elevated CO₂ increased phosphorous loss from decomposing litter
374 and soil organic matter at two FACE experiments with trees. *Biogeochemistry* **127**, 89–
375 97 (2016).
- 376 39. Yang, X., Thornton, P. E., Ricciuto, D. M. & Hoffman, F. M. Phosphorus feedbacks
377 constraining tropical ecosystem responses to changes in atmospheric CO₂ and climate.
378 *Geophys. Res. Lett. Res.* 7205–7214 (2016).
- 379 40. Vicca, S. *et al.* Fertile forests produce biomass more efficiently. *Ecol. Lett.* **15**, 520–
380 526 (2012).
- 381 41. Wang, Y. & Lambers, H. Root-released organic anions in response to low phosphorus
382 availability: recent progress, challenges and future perspectives. *Plant Soil* (2019).
- 383 42. Gatti, L. V. *et al.* Drought sensitivity of Amazonian carbon balance revealed by
384 atmospheric measurements. *Nature* **506**, (2014).

- 385 43. Powell, T. L. *et al.* Confronting model predictions of carbon fluxes with measurements
386 of Amazon forests subjected to experimental drought. *New Phytol.* **200**, 350–365
387 (2013).
- 388 44. He, M. & Dijkstra, F. A. Drought effect on plant nitrogen and phosphorus: A meta-
389 analysis. *New Phytol.* **204**, 924–931 (2014).
- 390
- 391

392 Table 1. List of key processes and variables that need to be constrained by observational
 393 estimates in order reduce uncertainty in P cycle control on the eCO₂ effect ecosystem models.

(H1) Plant C budget	Measurements needed
Canopy scale C assimilation	<ul style="list-style-type: none"> • Seasonal dynamics of leaf area and photosynthetic capacity • Photosynthetic acclimation
Plant tissue respiration	<ul style="list-style-type: none"> • Control of drought stress, nutrient limitation and P content • Wood and root respiration
Biomass growth	<ul style="list-style-type: none"> • Belowground biomass compartments • Long term growth rates
(H2) Plant P use	
Plant tissue C:P and N:P stoichiometry	<ul style="list-style-type: none"> • Plasticity versus adaptability to (experimental) change in eCO₂ or nutrient availability • Functionality of tissue P • Wood P content /stoichiometry
Plant tissue P resorption	<ul style="list-style-type: none"> • P content in live tissue and fresh litter • Plasticity versus adaptability to (experimental) change in eCO₂ or nutrient availability
(H3) Plant P acquisition	
P desorption due to plant exudation	<ul style="list-style-type: none"> • Interactions with microorganisms (directly or via microorganisms) • Cost of exudation vs. plant P uptake
P acquisition due to fine root production	<ul style="list-style-type: none"> • Surface litter activity • Fine root allocation fractions • Fine root productivity vs. plant P uptake
Biochemical P mineralization (via phosphatase)	<ul style="list-style-type: none"> • Phosphatase activity and relation to P mineralization • Plant production of phosphatase vs. plant-induced production by microorganisms • Cost of phosphatase production vs. plant P acquisition
Other interactions	
Plant N availability	<ul style="list-style-type: none"> • Ecosystem N budget • Symbiotic and free-living N fixation • Control of N availability on P acquisition
Plant water availability	<ul style="list-style-type: none"> • Control on P mineralization and transport dynamics • Control on of water and P limitation on eCO₂ effect

Title:

Future CO₂ fertilization of the Amazon forest hinges on plant phosphorus use and acquisition

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Abstract

Global terrestrial models currently predict that the Amazon rainforest will continue to act as a carbon sink in the future primarily due to the rising atmospheric carbon dioxide (CO₂) concentration, effectively enhancing its resilience and slowing the pace of climate change¹⁻³. Soil phosphorus impoverishment in parts of the Amazon basin limits biomass growth, but the role of phosphorus availability in limiting its future carbon uptake has not been considered in global model ensembles, e.g., during the Coupled Model Intercomparison Project (CMIP5) While it is widely accepted that soil phosphorus impoverishment in most of the Amazon basin limits biomass growth⁴, the role of phosphorus availability in limiting future Amazon forest carbon uptake has not been considered in global ecosystem model ensembles, e.g., during the Coupled Model Intercomparison Project for the 5th Assessment Report of the United Nations Intergovernmental Panel on Climate Change³. Here, we simulate a planned free-air CO₂ enrichment experiment in the Amazon with an ensemble of 14 terrestrial ecosystem models, including models that account for nitrogen and phosphorus feedbacks. The model ensemble represents diverse tropical plant functional strategies and generate a series of testable hypotheses. We show that phosphorus availability reduces the projected CO₂-induced biomass carbon growth to $79 \pm 63 \text{ g C m}^{-2} \text{ yr}^{-1}$ over 15 years, a reduction of ~50% compared to estimates from carbon and carbon-nitrogen models. We show that incorporating phosphorus feedbacks reduces the CO₂-induced biomass carbon sequestration to $79 \pm 63 \text{ g C m}^{-2} \text{ yr}^{-1}$ over 15 years, a reduction of 46-52% compared to carbon and carbon-nitrogen models. Our results The model ensemble suggests that the anticipated future Amazon carbon sink, and hence the region's resilience to climate change, may be much **less** smaller than previously assumed.

Modelled phosphorus feedbacks restrict the size of the biomass carbon (C) sink under elevated CO₂ concentrations, but the v Variation in the biomass carbon response among the phosphorus-enabled models is considerable, ranging from 5 to 140 g C m⁻² yr⁻¹. Predictions vary, due to contrasting assumptions relating to the flexibility in plant phosphorus use and acquisition strategies that allow CO₂ fertilization of biomass growth despite low phosphorus availability to plants. Our results generate a series of testable hypotheses, aiding e Experimental design, needs to be targeted to directly reduce the uncertainties around the phosphorus feedback on the CO₂ fertilization effect. The model ensemble involuntarily represents diverse tropical plant functional strategies and growth responses to phosphorus availability⁵, which ultimately need to be described and represented in a single framework in order to accurately predict the Amazon rainforest's response to future climate change.

Introduction

The intact Amazon rainforest acts as a substantial carbon (C) sink, completely offsetting carbon dioxide (CO₂) emissions from fossil fuel combustion and land use change in the Amazon region^{1,2,6,7}. Increasing atmospheric CO₂ concentrations from anthropogenic activity may be the primary ~~driving foreefactor~~ for the current Amazon ~~net Cearbon~~ sink^{1,3,4,6}, via so-called CO₂ fertilization (an increase in photosynthetic C uptake by plants under higher CO₂), which is projected to continue into the future by global models⁴⁻⁶.and global models assume that this CO₂-fertilization effect will continue to provide this globally significant ecosystem service into the future³. The CO₂ fertilization effect has been observed experimentally in field experiments that were conducted predominantly in the temperate zone.The stimulatory effect of elevated carbon dioxide (eCO₂) on photosynthesis and tree growth has been observed experimentally in greenhouses and in the field in open top chamber and free-air CO₂ enrichment (FACE) experiments. ~~To date, whole-ecosystem-scale experiments (i.e., FACE) have mainly been conducted in the temperate zone and never in the tropics⁷⁻⁸.~~ In these experiments, the eCO₂-induced increase in C uptake was generally low when other factors, such as soil nitrogen (N), were limiting^{7-9,10}. To date, whole-ecosystem-scale experiments, i.e., free-air CO₂ enrichment (FACE) have never been conducted in the tropics^{10,11}.

Over large parts of the Amazon and the tropics worldwide, phosphorus (P), not N, is assumed to be the key limiting nutrient, as most P has been lost or occluded from plant uptake during millions of years of soil pedogenesis^{12,13}. Forests growing on these highly weathered old soils may nonetheless be highly productive due to the evolution of multiple strategies for P acquisition and use, enabling tight cycling of P between plants and soils^{14,15}. Despite this knowledge, quantifying the control of P on plant physiology, growth, and plant-soil interactions in global models, and hence its role in the forests' response to eCO₂, remains challenging^{16,17,16}. This challenge is exacerbated by the scarcity of observations and ~~idiosynceratic-distinctive~~ species responses in hyperdiverse tropical forests¹⁸.

Here, we study the potential interactions between eCO₂ and nutrient (N and P) feedbacks in a mature Amazonian rainforest by simulating the planned AmazonFACE experiment (+200 ppm; <http://amazon-face.org/>) with an ensemble of ecosystem models (n = 14, Extended Data Table 3), including three C, five carbon-nitrogen (CN), and six carbon-nitrogen-phosphorus (CNP) models¹⁹⁻²⁴. The AmazonFACE experiment is located in a well-studied, highly productive tropical forest in Central Amazonia^{25,26}, growing on a strongly weathered *terra firme* Ferralsol. This ecosystem represents the low end of the plant-available P spectrum in the Amazon,

consistent with ~32% of the Amazon rainforest's cover fraction²⁷. *In situ* measurements were used to parameterise the models and to evaluate simulated ambient conditions (Extended Data Table 1, 2). Our aim was to generate *a priori* model-based hypotheses to highlight the state-of-the-knowledge and guide measurement strategies for AmazonFACE and other ecosystem manipulation experiments to gain crucial process understanding of P control on the CO₂ fertilization effect.

Main text

Simulated eCO₂ (+200 ppm) ~~over a period of 15 years~~ had a positive effect on plant biomass C across all models but was weakest in the CNP models (Fig. 1a). The eCO₂ conditions induced average biomass C gains of 163 ± 65 , 145 ± 83 , and 79 ± 63 g C m⁻² yr⁻¹ (mean \pm SD over 15 years) in the C, CN and CNP models, respectively (Fig. 1a). Limitations by P thus reduced the predicted biomass C sink ~~strength~~ by 52% and 46% compared to that in the C and CN models, respectively, with considerable variation across and within model groups (Extended Data Fig. 1). Plot inventories at the AmazonFACE site during the 2000s indicate an ~~ambient~~ aboveground biomass ~~sink~~ increment of 23 g C m⁻² yr⁻¹, substantially below the with an Amazon-wide¹ estimate of 64 g C m⁻² yr⁻¹. The model ensemble represents ambient conditions, such as productivity and leaf area index, reasonably well, but ensemble members show divergence on other ecosystem characteristics, such as the biomass C increment, which range from 5 to 114 g C m⁻² yr⁻¹. There is, however, no clear pattern in performance between the model groups, so that we judge that these differences do not have bearing on the conclusions of our study (see more discussion in Extended Data Fig. 2). ~~The model ensemble represents these and other ambient conditions, such as productivity and standing biomass C stock, reasonably well, with biomass C increases ranging from 5 to 114 g C m⁻² yr⁻¹ in the ambient model runs (Extended Data Fig. 2).~~

Gross and net primary productivity (GPP and NPP, respectively) are both stimulated by eCO₂ in all models, both initially (after 1 year of eCO₂) and until at the end of the simulation ~~after 15 years~~. The CNP models show the strongest decline from the initial response due to P limitation (Fig. 1b, c). The final response of NPP to eCO₂ was a 35%, 29%, and 9% stimulation for the C, CN and CNP models, respectively. In general, in the CN and CNP models, nutrient limitation is defined as nutrient demand being greater than nutrient supply. However, models differ in their assumptions on how nutrient limitation controls productivity and C allocation in response to eCO₂, so that divergent responses on plant carbon use efficiency (CUE = NPP / GPP) are simulated (Extended Data Table 3). ~~Although both N and P limitations reduce the effect of~~

~~eCO₂ on GPP, NPP and biomass increase, they have different effects on plant carbon use efficiency (CUE = NPP / GPP). Differing model assumptions relating to how nutrient feedbacks control productivity and C allocation in response to eCO₂ cause these divergent responses (Extended Data Table 3). In some CN models, CUE increases because N limitation is hypothesized to reduce autotrophic respiration (Ra) via lower tissue N content. In contrast, some CNP models, however, (e.g., CABLE and ELM-ECA) assume a direct downregulation of growth or growth efficiency (i.e., NPP) but only a small reduction in GPP, and hence the plant CUE decreases under nutrient limitation (Extended Data Fig. 3). Elevated CO₂ induced higher fine root investments of NPP in some CN and CNP models to aid nutrient acquisition (Fig. 1c; Extended Data Fig. 4). Furthermore, eCO₂ induced higher fine root investments of NPP in some CN and CNP models to aid nutrient acquisition (Fig. 1c; Extended Data Fig. 4).~~

Predicted changes in allocation with eCO₂ cause a general increase in biomass C turnover across all but one of the models, ~~as C allocation moved from longer lived tissues (wood) towards leaves and roots (with shorter lifespans). Tissue specific turnover rates are assumed to be constant in all models. Higher biomass C turnover partially offsetting the positive biomass C response (Extended Data Table 4). Changes in turnover play a minor role in our 15 year simulation period but rather control the long-term future CO₂ effect on the biomass C sink^{28,29} and introduce additional uncertainty into the future CO₂ effect on biomass C²⁶. Nevertheless, the modelled NPP response dominates the biomass C response to eCO₂ over the 15 year simulation period.~~

Plant growth under eCO₂ is lowest in CNP models as the low availability of soil labile P restricts P uptake either immediately (~~CABLE, ELM-ECA, GDAY~~) or over time (~~CABLE-POP, ELM-CTC, ORCHIDEE~~) (Extended Data Fig. 5). We considered the modelled P limitation on plant growth to be realistic, as the models and observations agree on soil labile P being very low (Extended Data Fig. 2). The models simulated <1.1 g labile P m⁻² to 4 m depth in the ambient run (with the exception of ELM-CTC) (Extended Data Fig. 2). Observations indicate 1.6 g resin P m⁻² to 30 cm depth, which is thus slightly higher than the model predictions. However, both modelled and observed soil labile P are very low. Other site observations support at the site indicate the fact that P is extremely critical for plant productivity, such as high leaf N:P ratios of 37 and high plant P resorption (in plant tissue before litter fall) of 78% (Extended Data Table 1). While ~~Consequently, we considered the modelled P limitation on plant growth to be realistic. Although the~~ P limitation consistently reduces the eCO₂-induced biomass C sink, there is significant variation among CNP models due to contrasting process representations (Fig. 2;

Extended Data Table 3). P shortages downregulate growth (i.e., NPP) in all CNP models, ~~either directly or, via photosynthesis, or via a combination of both processes. No model considers P effects on Ra.~~ The major differences ~~in the among the~~ model assumptions relate to how they modify P supply and demand to alleviate plant P shortages, including either (i) enhancing plant P use efficiency (PUE = NPP / P uptake) or (ii) upregulating P acquisition mechanisms. The models assume that PUE may change if tissue nutrient ratios are flexible, if C allocation changes among tissues with different stoichiometry, and/or if P resorption is variable (Fig. 2)~~can be adjusted~~. Flexible stoichiometry is considered in all CNP models except ELM-CTC, although with varying degrees of flexibility,~~such that the stoichiometry in CABLE and ORCHIDEE is considered effectively fixed (Fig. 2).~~ Greater fine root C allocation with in response to plant P stress is considered in some, ELM-ECA, GDAY and ORCHIDEE, and P resorption is a fixed fraction of leaf tissue P in all models (Fig. 2).

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

Diverging ~~depictions representations~~ of plant P use and acquisition among the CNP models cause predictions of the eCO₂-induced biomass C sink to range from 5 g C m⁻² yr⁻¹ ~~in CABLE~~ to 140 g C m⁻² yr⁻¹ ~~in ORCHIDEE~~ (Fig. 3a; Extended Data Fig. 1). Greater plant PUE occurred in four of the models, ~~GDAY, ELM-ECA, CABLE POP, and ORCHIDEE,~~ for which shifts in tissue C:N and N:P due to eCO₂ led to increases in biomass C:P ranging from ~200 to 1600 g C g P⁻¹ (Fig. 3c). Higher fine root investment with eCO₂, at the expense of less “P-costly” wood, offset some increases in PUE in ~~ELM-ECA and GDAY~~ some models. ~~Although higher fine root allocation was simulated temporarily in ORCHIDEE (Extended Data Fig. 4), investment in wood increased over the full simulation period, as was also the case in CABLE POP (Fig. 3b).~~ Flexible biomass stoichiometry altered decomposition dynamics and induced progressive P limitation in response to eCO₂, i.e., litter stoichiometry shifted towards lower quality (less N

and P in relation to C), reducing net P mineralization rates from microbial decomposition, causing P to become increasingly unavailable to plants and accumulating in soil organic matter (Fig. 3d, e). ~~As a consequence, ecosystem P retention increased marginally in some models as P-leaching rates decreased.~~ This plant-soil-microbial feedback slowed the cycling of P in the ecosystem and exacerbated the initial P limitation (see Ref. ³⁰ for a similar feedback during pedogenesis).

Enhanced plant P acquisition under eCO₂ effectively alleviated P limitation in two CNP models (ELM-CTC and ELM-ECA) (Fig. 3e). In both, eCO₂ increased the liberation of P from the secondary pool, as higher plant P demand and uptake diminished the labile P pool, in turn causing higher desorption rates. P desorption is thus only indirectly, and not mechanistically, enhanced by plants in these models. Biochemical mineralization of P under eCO₂ responded positively in both of the models, but added only notably to additional P acquisition in ELM-CTC ~~over the course of the simulation~~ (Fig. 3e). Although three CNP models simulated higher fine root investments (~~ELM-ECA, GDAY, and ORCHIDEE~~), the actual P uptake return per fine root increment was marginal ~~and/or~~ came only into effect in the long-term ~~, thus contributing little over our simulation period~~ (Extended Data Fig. 6).

Observations document ample N cycling in the system, e.g., high leaf N contents, indicative $\delta^{15}\text{N}$ values, high rates of N oxide emissions, and low N retention^{31,32}, and thereby suggest that plant growth is not directly affected by N availability. ~~In summary, the model ensemble encapsulates a range of plausible hypotheses and represents a potential range of biomass C responses to eCO₂ under low soil P availability. At the one end, CABLE assumes no plant-enabled mechanisms to acquire more P and a limited capacity for plants to use P more efficiently, resulting in effectively zero biomass C gain with eCO₂. The remaining models predicted some biomass C gain with eCO₂. Flexible stoichiometry was the key mechanistic response to eCO₂ in four of these models. ELM-CTC had no change in stoichiometry, but nonetheless predicted an increase in biomass C gain under eCO₂ based on an increase in plant P acquisition as a result of enhanced P mineralization and desorption.~~

~~Our model simulations also highlight the complementary role of N availability at our site.~~ The CN models, however, simulate increased nitrogen use efficiency (NUE) and biomass C:N ratios, in response to insufficient N uptake ~~was not sufficient~~ under eCO₂ (Extended Data Fig. 5). Plant N availability may be underestimated in the models, since the plant-available mineral N supply was <7 g N m⁻² across all models, as opposed to 17.5 g N m⁻² observed in the top 10 cm only (Extended Data Fig. 2). ~~Both CN and CNP versions of GDAY and CABLE POP were~~

~~included in the model ensemble, allowing the N effect alone to be inferred. These models indicated that N limitation occurred, as leaf and biomass C:N were predicted. In terms of N availability, the simulated N availability may thus be underestimated in the models. These results highlight an important gap in our knowledge related to the dynamics of N availability, and moreover its potential interaction with P dynamics. Future experiments should help reduce the uncertainty surrounding N effects on P limitation (Table 1), with potential implications for regions predominantly or co-limited by N.~~

In summary, the model ensemble encapsulates a range of plausible hypotheses and represents a potential range of biomass C responses to eCO₂ under low soil P availability. The assumption of a lacking ability of plants to acquire more soil P and a limited capacity for plants to use P more efficiently. At the one end, CABLE assumes no plant-enabled mechanisms to acquire more P and a limited capacity for plants to use P more efficiently, resulting in effectively zero biomass C gain with eCO₂. Conversely, The remaining models predicted some biomass C gain with eCO₂. Flexible stoichiometry, in combination with enhanced plant P acquisition, were the was the key mechanistic responses leading to biomass gain with eCO₂ in four of these models. ELM-CTC had no change in stoichiometry, but nonetheless predicted an increase in biomass C gain under eCO₂ based on an increase in plant P acquisition as a result of enhanced P mineralization and desorption.

Divergences in the simulated eCO₂ response lead us to the following testable hypotheses, and call for directed field measurements (Table 1):

÷

H1. Low soil P availability will strongly constrain future plant biomass growth response to eCO₂ either by downregulating photosynthesis or limiting plant growth directly, or a combination thereof.

H2. Despite the limited soil P supply, plasticity in vegetation stoichiometry and allocation patterns will allow for some biomass growth under eCO₂.

H3. Plants will increase investments in P acquisition to increase P supply and allow biomass growth under eCO₂ either via greater P interception through fine root production or via greater P liberation from P desorption or biochemical mineralization of P.

These model-based hypotheses deepen a previous analysis of potential N and P limitation on C accumulation based on mass balance principle³³~~deepen a previously carried out accounting analysis of potential N and P limitation by considering process-based nutrient cycles in dynamic~~

~~ecosystem models~~²⁹. Furthermore, ~~the set of model-based hypotheses we~~ add to a model intercomparison carried out in advance of the EucFACE ~~experiment~~³⁴ ~~experiment~~³²—by extending the range of plant P feedbacks considered across CNP models. This work highlighted H1: two stoichiometrically constrained CNP models predicted that strong P limitation will curtail the growth response to eCO₂ in Australia. Consistent with this hypothesis, aboveground growth has not increased with eCO₂ in that experiment over the initial years³⁵. This finding underlines ~~the fact that ongoing and future~~ monitoring efforts need to place a strong(er) focus on belowground carbon ~~allocation~~ and ~~soil~~-nutrient dynamics in addition to ~~photosynthetic rates~~ canopy-scale photosynthesis and aboveground growth dynamics. Additionally, Ra dependence on P content and plant stress from drought or nutrient limitation ~~the model ensemble does not yet consider the P effect on Ra, while strong links between N and Ra are included. Respiration responses under nutrient limitation~~ need further monitoring during experiments to further elucidate ~~P effects on~~ the plant C budget and address H1 (Table 1).

Nutrient fertilization experiments support H2, as plasticity in leaf stoichiometry at the individual level, along with plasticity in P resorption efficiency, was observed³⁶. Across the Amazon, community-weighted leaf N:P in the field varied from leaf nutrient assessments indicate a leaf N:P range of 13 to 42 g N g P⁻¹ (n = 64) (Ref. ³²), which place our site, with a community-mean ratio of 37, closer to the high end at the extreme high end. GDAY ~~thus~~ predicted the most plausible increase in the leaf N:P ratio from 34 to 38 (Extended Data Fig. 87). ~~CABLE POP and ELM ECA~~ Two models predicted strong increases in the leaf N:P ratio with eCO₂ but started off with much lower initial values. The degree to which plasticity in stoichiometry and resorption can aid plant PUE under eCO₂ in highly P-limited sites that are already at the end of the observed spectrum remains to be seen (H2). Monitoring plant tissue stoichiometry, including wood with much higher N:P ratios, combined with assessments of P resorption and fresh litter nutrient content in CO₂ and nutrient fertilization experiments will give an indication of the plasticity of these plant use mechanisms in response to eCO₂ reduce uncertainties (Table 1).

Based on previous observations⁸, a number of models assume increased fine root investment, as well as higher biochemical P mineralization and P desorption from mineral surfaces, under eCO₂-induced nutrient limitation (H3). ~~Although simulated, t~~ The effect of increased fine root biomass on nutrient uptake was limited in our simulations and . Likewise, ambient fine root allocation fractions were highly variable among the models, ranging from 5-30% of NPP (Extended Data Fig. 4, 6). Both these observations highlight model deficiencies in belowground

processes³⁷ ~~that need addressing (Table 1). In regards to the P liberation pathways,~~ There is evidence that phosphatase activity in litter and soil and the presence of low-molecular-weight acids used to liberate P from organic matter or from mineral surfaces increase with plant P demand³⁸. This ~~process~~ was predicted by ELM-CTC in our simulations, which also ~~indicated showed~~ Amazon-wide that “[with] enhanced phosphatase production, productivity in the highly P-limited areas can be sustained under elevated CO₂ conditions”³⁹. ~~In situ observations at the AmazonFACE site and elsewhere indicate that p~~Plants invest in P liberation and acquisition, but if these mechanisms ~~can be upregulated enhance P gain~~ under eCO₂ and over what time frame this ~~process may~~ occurs remain open questions. Quantification of such ~~a fluxes response~~ is lacking, as are estimates of the associated plant C costs to acquire P via these and other mechanisms, such as mycorrhizal symbiosis^{15,40}. ~~(Table 1). Monitoring of belowground fine root dynamics during manipulation experiments needs to include fine root activity in surface litter, which is a common plant mechanism in P-impooverished ecosystems in the Amazon but is not yet quantified nor considered in models.~~ The P gain and C cost for ~~P acquisition different~~ mechanisms, ~~as well as the associated plant-soil-microbial interactions, need~~ to be assessed by analyses of soil, microbial and root nutrition, ~~and~~ -via novel techniques investigating enzyme ~~activity and~~ -labile C ~~dynamics~~⁴¹ ~~(low molecular weight acids), or other approaches allowing the associated plant-soil-microbial interactions to be inferred. Monitoring of belowground fine root dynamics during manipulation experiments needs to include the fine root activity in surface litter layer, which is a commonly explored by fine roots in plant mechanism in P-impooverished ecosystems in the Amazon, but is not yet quantified nor considered in models (Table 1).~~

Conclusion

Previous model projections suggest a sustained fertilization effect of CO₂ on the Amazon C sink but have not considered feedbacks from low soil P availability^{5,6}. Our study demonstrates that, based on the current generation of CNP models, the omission of P feedbacks is highly likely to cause an overestimation of the Amazon rainforest’s capacity to sequester atmospheric CO₂. Considering P limitation on the CO₂ fertilization effect in future predictions may indicate that the forest is less resilient to higher temperatures and changing rainfall patterns than previously thought^{6,42}. ~~Periods of water deficit may contribute to the eCO₂ fertilization effect on productivity due to its water saving effect~~³⁴, ~~or due to alterations of decomposition processes. Our study site experienced years with significantly less than average precipitation, e.g. in 2000 and 2009, however, in our simulations this increased the positive response of GPP and NPP to~~

eCO₂ only marginally (Extended Data Figure 8 and 9). Models lack the appropriate sensitivity of plant responses to changes in water availability, and even more so when precipitation sums are that high⁴³. Interactions of water and P availability and their consequences on the CO₂ fertilization effect remain uncertain⁴⁴ and is an area where field measurements will allow us to better constrain model responses (Table 1).

Although P is likely to reduce the biomass C sink response to CO₂ in regions with low plant-available P supply, our results suggest that plasticity in plant P use and plant P acquisition mechanisms, may at least partially alleviate P limitation under eCO₂ and enable CO₂ fertilization of biomass growth.~~may enable CO₂ fertilization of biomass growth, even in regions with a very low plant available P supply.~~ The ~~spread of responses across our CNP model ensemble~~model ensemble may be interpreted as representing a range of possible tropical plant functional strategies and growth in responses to low P availability under eCO₂. Responses ~~to eCO₂~~ are likely expected to be species-specific, as ~~were was found for~~ plant growth responses to low P supplies in another tropical region¹⁸. The ecosystem-scale response to P limitation under eCO₂ will thus depend on the relative contributions of the various P acquisition and P use strategies across individuals, their interactions and to what extent these processes can be upregulated under eCO₂. All of which ultimately need to be described and represented in a single model framework in order to accurately predict the Amazon rainforest's response to future climate change.

AmazonFACE has the unique opportunity to experimentally address these key areas of uncertainty ~~with suitable measurements~~, not only by integrating the proposed measurements across seasons and at the ecosystem scale (summary in Table 1) but also by assessing species-specific responses to eCO₂ in relation to trait expression. Amazon-wide expression of plant functional strategies may then be inferred by applying the mechanistic interplay between trait expression and edaphic conditions. The key to predicting the future of the world's largest tropical forest under eCO₂ thus lies in obtaining experimental data on, and subsequently modelling, different plant P acquisition and use strategies, as well as their interactions in a competing plant community.

END NOTES

Author contributions

D.M.L., ~~and~~ 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 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., C.v.R., Y.-P.W., X.Y., S.Z., and Q.Z. performed model simulations. K.F. wrote the manuscript with input from all co-authors.

Acknowledgements

We thank the many scientists involved in the development of the models used in our study; the many scientists, field and laboratory technicians and other staff involved in collecting and analysing the field data; and everyone involved in the planning and conductance of the AmazonFACE project. Oak Ridge National Laboratory is operated by UT-Battelle, LLC, under contract DE-AC05-00OR22725 with the US Department of Energy. K.F. is funded by the DFG grant No. RA 2060/5-1.

REFERENCES ^[KF1]

1. Brien, R. J. W. *et al.* Long-term decline of the Amazon carbon sink. *Nature* **519**, 344–348 (2015).
2. Phillips, O. L. & Brien, R. J. W. Carbon uptake by mature Amazon forests has mitigated Amazon nations' carbon emissions. *Carbon Balance Manag.* **12**, 1 (2017).
3. Cernusak, L. A. *et al.* Tropical forest responses to increasing atmospheric CO₂: Current knowledge and opportunities for future research. *Funct. Plant Biol.* **40**, 531–551 (2013).
4. Ciais, P. *et al.* The physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change. *Chang. IPCC Clim.* 465–570 (2013). doi:10.1017/CBO9781107415324.015
5. Cox, P. M. *et al.* Sensitivity of tropical carbon to climate change constrained by carbon dioxide variability. *Nature* **494**, 341–344 (2013).
6. Huntingford, C. *et al.* Simulated resilience of tropical rainforests to CO₂-induced climate change. *Nat. Geosci.* **6**, 268–273 (2013).
7. Talhelm, A. F. *et al.* Elevated carbon dioxide and ozone alter productivity and ecosystem carbon content in northern temperate forests. *Glob. Chang. Biol.* **20**, 2492–

2504 (2014).

8. Norby, R. J., Warren, J. M., Iversen, C. M., Medlyn, B. E. & McMurtrie, R. E. CO₂ enhancement of forest productivity constrained by limited nitrogen availability. *Proc. Natl. Acad. Sci.* **107**, 19368–19373 (2010).
9. Zaehle, S. *et al.* Evaluation of 11 terrestrial carbon-nitrogen cycle models against observations from two temperate Free-Air CO₂ Enrichment studies. *New Phytol.* **202**, 803–822 (2014).
10. Hofhansl, F. *et al.* Amazon forest ecosystem responses to elevated atmospheric CO₂ and alterations in nutrient availability: filling the gaps with model-experiment integration. *Front. Earth Sci.* **4**, (2016).
11. Norby, R. J. *et al.* Model-data synthesis for the next generation of forest free-air CO₂ enrichment (FACE) experiments. *New Phytol.* **209**, 17–28 (2016).
12. Lloyd, J., Bird, M. I., Veenendaal, E. M. & Kruijt, B. Should Phosphorus Availability Be Constraining Moist Tropical Forest Responses to Increasing CO₂ Concentrations? *Glob. Biogeochem. Cycles Clim. Syst.* 95–114 (2001).
13. Vitousek, P. M. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* **65**, 285–298 (1984).
14. Quesada, C. A. *et al.* Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. *Biogeosciences* **9**, 2203–2246 (2012).
15. Lambers, H., Raven, J. A., Shaver, G. R. & Smith, S. E. Plant nutrient-acquisition strategies change with soil age. *Trends Ecol. Evol.* **23**, 95–103 (2008).
16. Reed, S. C., Yang, X. & Thornton, P. E. Incorporating phosphorus cycling into global modeling efforts: A worthwhile, tractable endeavor. *New Phytol.* **208**, 324–329 (2015).
17. Jiang, M., Caldararu, S., Zaehle, S., Ellsworth, D. S. & Medlyn, B. E. Towards a more physiological representation of vegetation phosphorus processes in land surface models. *New Phytol.* 1–7 (2019).
18. Turner, B. L., Brenes-Arguedas, T. & Condit, R. Pervasive phosphorus limitation of tree species but not communities in tropical forests. *Nature* **555**, 367–370 (2018).
19. Goll, D. S. *et al.* A representation of the phosphorus cycle for ORCHIDEE (revision 4520). *Geosci. Model Dev.* **10**, 3745–3770 (2017).

20. Wang, Y.-P., Law, R. M. & Pak, B. A global model of carbon, nitrogen and phosphorus cycles for the terrestrial biosphere. *Biogeosciences* **7**, 2261–2282 (2010).
21. Haverd, V. *et al.* A new version of the CABLE land surface model (Subversion revision r4601) incorporating land use and land cover change, woody vegetation demography, and a novel optimisation-based approach to plant coordination of photosynthesis. *Geosci. Model Dev.* **11**, 2995–3026 (2018).
22. Comins, H. N. & McMurtrie, R. E. Long-Term Response of Nutrient-Limited Forests to CO² Enrichment; Equilibrium Behavior of Plant-Soil Models. *Ecol. Appl.* **3**, 666–681 (1993).
23. Zhu, Q., Riley, W. J., Tang, J. & Koven, C. D. Multiple soil nutrient competition between plants, microbes, and mineral surfaces: model development, parameterization, and example applications in several tropical forests. *Biogeosciences* **13**, 341–363 (2016).
24. Yang, X., Thornton, P. E., Ricciuto, D. M. & Post, W. M. The role of phosphorus dynamics in tropical forests – a modeling study using CLM-CNP. *Biogeosciences* **11**, 1667–1681 (2014).
25. Malhi, Y. *et al.* Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests. *Glob. Chang. Biol.* **15**, 1255–1274 (2009).
26. Araújo, A. C. *et al.* Comparative measurements of carbon dioxide fluxes from two nearby towers in a central Amazonian rainforest: The Manaus LBA site. *J. Geophys. Res.* **107**, 8090 (2002).
27. Quesada, C. A. *et al.* Soils of Amazonia with particular reference to the RAINFOR sites. *Biogeosciences* **8**, 1415–1440 (2011).
28. Friend, A. D. *et al.* Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO₂. *Proc. Natl. Acad. Sci.* **111**, 3280–3285 (2014).
29. Walker, A. P. *et al.* Predicting long-term carbon sequestration in response to CO₂ enrichment: How and why do current ecosystem models differ? *Global Biogeochem. Cycles* **29**, 476–495 (2015).
30. Vitousek, P. M. *Nutrient cycling and limitation: Hawai'i as a model system.* Princeton University Press (2004).

31. Nardoto, G. B. *et al.* Basin-wide variations in Amazon forest nitrogen-cycling characteristics as inferred from plant and soil 15N:14N measurements. *Plant Ecol. Divers.* **7**, 173–187 (2014).
32. Fyllas, N. M. *et al.* Basin-wide variations in foliar properties of Amazonian forest: phylogeny, soils and climate. *Biogeosciences* **6**, 2677–2708 (2009).
33. Wieder, W. R., Cleveland, C. C., Smith, W. K. & Todd-Brown, K. Future productivity and carbon storage limited by terrestrial nutrient availability. *Nat. Geosci.* **8**, 441–444 (2015).
34. De Kauwe, M. G. *et al.* Using models to guide field experiments: a priori predictions for the CO₂ response of a nutrient- and water-limited native Eucalypt woodland. *Glob. Chang. Biol.* **22**, 2834–2851 (2016).
35. Ellsworth, D. S. *et al.* Elevated CO₂ does not increase eucalypt forest productivity on a low-phosphorus soil. *Nat. Clim. Chang.* **7**, 279–282 (2017).
36. Wright, S. J. *et al.* Plant responses to fertilization experiments in lowland, species-rich, tropical forests. *Ecology* **99**, 1129–1138 (2018).
37. Warren, J. M. *et al.* Root structural and functional dynamics in terrestrial biosphere models—evaluation and recommendations. *New Phytol.* **205**, 59–78 (2015).
38. Hoosbeek, M. R. Elevated CO₂ increased phosphorous loss from decomposing litter and soil organic matter at two FACE experiments with trees. *Biogeochemistry* **127**, 89–97 (2016).
39. Yang, X., Thornton, P. E., Ricciuto, D. M. & Hoffman, F. M. Phosphorus feedbacks constraining tropical ecosystem responses to changes in atmospheric CO₂ and climate. *Geophys. Res. Lett. Res.* 7205–7214 (2016).
40. Vicca, S. *et al.* Fertile forests produce biomass more efficiently. *Ecol. Lett.* **15**, 520–526 (2012).
41. Wang, Y. & Lambers, H. Root-released organic anions in response to low phosphorus availability: recent progress, challenges and future perspectives. *Plant Soil* (2019). doi:10.1007/s11104-019-03972-8
42. Gatti, L. V. *et al.* Drought sensitivity of Amazonian carbon balance revealed by atmospheric measurements. *Nature* **506**, (2014).

43. Powell, T. L. *et al.* Confronting model predictions of carbon fluxes with measurements of Amazon forests subjected to experimental drought. *New Phytol.* **200**, 350–365 (2013).
44. He, M. & Dijkstra, F. A. Drought effect on plant nitrogen and phosphorus: A meta-analysis. *New Phytol.* **204**, 924–931 (2014).

Table 1. List of key processes and variables that need to be constrained by observational estimates in order reduce uncertainty in P cycle control on the eCO₂ effect ecosystem models.

<u>(H1) Plant C budget</u>	<u>Measurements needed</u>
<u>Canopy scale C assimilation</u>	<ul style="list-style-type: none"> • <u>Seasonal dynamics of leaf area and photosynthetic capacity</u> • <u>Photosynthetic acclimation</u>
<u>Plant tissue respiration</u>	<ul style="list-style-type: none"> • <u>Control of drought stress, nutrient limitation and P content</u> • <u>Wood and root respiration</u>
<u>Biomass growth</u>	<ul style="list-style-type: none"> • <u>Belowground biomass compartments</u> • <u>Long term growth rates</u>
<u>(H2) Plant P use</u>	
<u>Plant tissue C:P and N:P stoichiometry</u>	<ul style="list-style-type: none"> • <u>Plasticity versus adaptability to (experimental) change in eCO₂ or nutrient availability</u> • <u>Functionality of tissue P</u> • <u>Wood P content /stoichiometry</u>
<u>Plant tissue P resorption</u>	<ul style="list-style-type: none"> • <u>P content in live tissue and fresh litter</u> • <u>Plasticity versus adaptability to (experimental) change in eCO₂ or nutrient availability</u>
<u>(H3) Plant P acquisition</u>	
<u>P desorption due to plant exudation</u>	<ul style="list-style-type: none"> • <u>Interactions with microorganisms (directly or via microorganisms)</u> • <u>Cost of exudation vs. plant P uptake</u>
<u>P acquisition due to fine root production</u>	<ul style="list-style-type: none"> • <u>Surface litter activity</u> • <u>Fine root allocation fractions</u> • <u>Fine root productivity vs. plant P uptake</u>
<u>Biochemical P mineralization (via phosphatase)</u>	<ul style="list-style-type: none"> • <u>Phosphatase activity and relation to P mineralization</u> • <u>Plant production of phosphatase vs. plant-induced production by microorganisms</u> • <u>Cost of phosphatase production vs. plant P acquisition</u>
<u>Other interactions</u>	
<u>Plant N availability</u>	<ul style="list-style-type: none"> • <u>Ecosystem N budget</u> • <u>Symbiotic and free-living N fixation</u> • <u>Control of N availability on P acquisition</u>
<u>Plant water availability</u>	<ul style="list-style-type: none"> • <u>Control on P mineralization and transport dynamics</u> • <u>Control on of water and P limitation on eCO₂ effect</u>

395 **METHODS**

396 **Site description**

397 Model simulations were conducted at the AmazonFACE experimental site in Central Amazonia
398 (2°35'39" S, 60°12'29" W). AmazonFACE is an integrated model-experiment project that aims
399 to assess the effects of high CO₂ concentrations on the ecology and resilience of the Amazon
400 rainforest (<http://amazon-face.org/>). The experiment is currently being established and is situated
401 in a *terra firme* forest on a plateau characterized by highly weathered, deep, clay sediment soil
402 (with a clay fraction of 76%), classified as a Geric Ferrasol¹. The site and the surrounding area
403 have been subjected to various long-term measurement activities²⁻⁶, coordinated by the Large-
404 Scale Biosphere-Atmosphere Program (LBA; <http://lba2.inpa.gov.br/>) in Amazonia, including the
405 “K34” eddy covariance flux tower⁷, located approximately 2 km away from AmazonFACE site.
406 Mean annual precipitation at K34 from January 2000 to December 2015 was 2600 mm yr⁻¹, and
407 the mean temperature was 26°C.

408 **Model descriptions**

409 Fourteen ecosystem models with contrasting representations of ecosystem functioning and nutrient
410 cycling were applied to the experiment (Extended Data Table 3). C cycle dynamics without
411 nutrient cycle feedbacks are represented in the “C-only” models (InLand, ED2 and ELM-
412 FATES)⁸⁻¹⁰; C and N dynamics are represented in the “CN” models (LPJ-GUESS, O-CN, JULES,
413 CABLE-POP(CN) and GDAY(CN))¹¹⁻¹³; and C, N, and P dynamics are represented in the “CNP”
414 models (ELM-ECA, ELM-CTC, CABLE, CABLE-POP, ORCHIDEE, and GDAY)¹⁴⁻¹⁹. Four of
415 the models are dynamic vegetation models: CABLE-POP considers dynamic establishment and
416 mortality with fixed plant functional type (PFT) composition, while LPJ-GUESS, ED2 and ELM-
417 FATES also consider dynamic PFT composition. Photosynthesis is based on formulations by
418 Farquhar²⁰ or derivations thereof in all of the models^{21,22} (Extended Data Table 3).

419 Prognostic C allocation fractions are based on functional relationships among tissues, e.g., fixed
420 ratios between sapwood and leaf area in CABLE-POP, LPJ-GUESS, ED2, GDAY, ORCHIDEE,
421 O-CN, JULES, and ELM-FATES, and on resource dependence, e.g., higher root allocation under
422 water or nutrient stress in LPJ-GUESS, ELM-ECA, GDAY, O-CN, ORCHIDEE, ED2 and ELM-
423 FATES. C allocation fractions are fixed in InLand and CABLE.

424 Nutrient limitation is determined by the difference between demand and supply (via root uptake
425 and resorption) of N or P, with the most limiting nutrient determining the degree of limitation. The
426 photosynthetic parameters V_{cmax} and/or J_{max} are controlled by leaf N in all CN and CNP models
427 except JULES, while leaf P additionally downregulates gross primary productivity (GPP) in all
428 CNP models except ORCHIDEE. N controls net primary productivity (NPP) in some of the
429 models, i.e., O-CN, JULES, ORCHIDEE, CABLE and CABLE-POP, and additionally
430 downregulates growth efficiency (GPP/LAI) in CABLE and CABLE-POP.

431 Maintenance respiration is dependent on temperature in all models and is additionally controlled
432 by tissue N content in all of the models that consider the N cycle with the exception of GDAY,
433 where R_a is a fixed fraction of GPP. Plant tissue stoichiometry in the CN and CNP models is either
434 fixed (ELM-CTC and JULES) or varies within or without bounds (all other models). The nutrient
435 resorption rates in the CN and CNP models are always fixed fractions of the nutrient content in
436 leaves and roots. Competition for nutrients between plant uptake and decomposition processes is
437 handled differently. Nutritional demands for the decomposition process (representing microbial
438 demands) are met entirely first in some models (CABLE, O-CN, ORCHIDEE, and GDAY), are
439 based on relative demands between decomposition and plant uptake (ELM-CTC), or are
440 determined via a multiple consumer approach including adsorption to mineral surfaces (ELM-
441 ECA). Nutrient uptake is a function of plant demand and nutrient availability in all models and is
442 further controlled by a measure of root mass in LPJ-GUESS, GDAY, ORCHIDEE, and O-CN.

443 Soil organic matter (SOM) decomposition is limited by soil mineral N availability in most CN and
444 CNP models (except O-CN and ORCHIDEE) and additionally by labile P availability in most CNP
445 models (except GDAY and ORCHIDEE). P in SOM can also be mineralized via phosphatase,
446 decoupling the P cycle from the C and N cycle, termed biochemical P mineralization in the P
447 models. Biochemical P mineralization is a function of the slow SOM pool turnover in CABLE,
448 CABLE-POP and GDAY, as well as substrate availability in ORCHIDEE, ELM-ECA and ELM-
449 CTC. Biochemical P mineralization is upregulated with higher plant P stress, representing higher
450 phosphate production (not specified if by plants or microbes), in ELM-ECA, ELM-CTC and
451 ORCHIDEE.

452 N inputs originate from N deposition (prescribed by model protocol) and N fixation (prescribed
453 individually). N fixation is either fixed, calculated empirically as a fraction of NPP or

454 evapotranspiration (GDAY, JULES, ORCHIDEE, ALM-CTC, LPJ-GUESS, CABLE, and
455 CABLE-POP), or based on an optimization scheme (ELM-ECA and O-CN). P inputs originate
456 from weathering (prescribed individually) and deposition (prescribed by model protocol). Release
457 of P from rock weathering is a fixed, soil type-specific rate in CABLE and CABLE-POP, a
458 function of the parent P pool in ELM-ECA, ELM-CTC, and GDAY or described as a function of
459 lithology, runoff and air temperature in ORCHIDEE. N and P losses occur from leaching, modelled
460 as a function of the size of the labile P and mineral N pool, respectively, and additionally controlled
461 by runoff in ELM-ECA and ORCHIDEE.

462 The number of inorganic P pools and their precise definition varies among the models. We consider
463 two inorganic P pools relevant for our analysis: the labile P pool and the secondary P pool. The
464 labile P pool encompasses plant-available inorganic P, represented in most CNP models by two
465 separate pools connected by sorption dynamics and effectively in equilibrium (described by
466 Langmuir dynamics in most models and a linear approach in ORCHIDEE). The labile P pools
467 follow different nomenclature in the models but are comparable in functionality: the P in soil
468 solution (called labile or solution P) is readily available to plants in the model time step, while the
469 non-dissolved P (referred to as sorbed or sorbed labile P pool) can become available to plants on
470 yearly to decadal time scales due to desorption. The secondary P pool represents P strongly sorbed
471 by minerals, which is largely unavailable but may enter the labile P pool on centennial time scales
472 and, depending on model assumptions, may be driven by plant P stress.

473 **Model simulations**

474 Models were forced with 16 years of observed local meteorology (2000 to 2015) from the K34
475 flux tower⁷. Meteorological data from July 1999 to December 2015 of near-surface air
476 temperature, rainfall, downward shortwave radiation, downward longwave radiation, vapour
477 pressure deficit, surface pressure, relative humidity, and wind speed were available for model
478 input. Specific humidity was calculated based on observed relative humidity and surface pressure.
479 All data time series were subject to quality control (i.e., removal of outliers) and gap filling using
480 the variables' climatological mean. Precipitation data gaps were filled from a nearby weather
481 station of the Tropical Rainfall Measuring Mission network.

482 Simulations are initialized with a spin-up routine resulting in equilibrium conditions of C stocks
483 (and N, and P, if applicable) representing the year 1850. The 16-year meteorological time series

484 are continuously repeated throughout the whole spin-up, during the transient phase (1851 to 1998),
485 and during our model-experiment phase (1999 to 2013), representative of a 15-year long
486 AmazonFACE experiment. Global datasets are used as inputs for atmospheric CO₂^{23,24}, N
487 deposition^{25,26}, and P deposition²⁷. Atmospheric CO₂, N and P deposition levels were set to 284.7
488 ppm, 1.43 kg N ha⁻¹ yr⁻¹, and 0.144 kg P ha⁻¹ yr⁻¹ in 1850, respectively, and follow historical
489 changes during the transient and model experiment phase.

490 Other site parameters used for parameterization of the models are derived from *in situ*
491 measurements and include rooting and soil depth (set to rooting depth), soil hydraulic parameters,
492 specific leaf area (SLA), and soil texture (Extended Data Table 2). Soil hydraulic parameters are
493 derived from pedotransfer functions²⁸ and site-specific measurements of soil properties²⁹. Soil
494 hydraulic parameters were included in models that accounted for this functionality to allow for a
495 better representation of soil water dynamics in tropical soils (Extended Data Table 2).

496 Two model experiments are performed over the 15-year long experiment phase by each model to
497 assess the effect of elevated CO₂: 1) the ambient run (AMB) and 2) the elevated CO₂ run (ELE).
498 In the AMB run, the atmospheric CO₂ is set to ambient levels and is employed for model evaluation
499 against *in situ* measurements, including C fluxes from the K34 flux tower. The ELE run represents
500 the planned AmazonFACE experiment with a step change increase of 200 ppm at the start of the
501 model experiment and continuous tracking of CO₂ levels in AMB plus 200 ppm thereafter. Model
502 outputs are analysed in biological years of seasonality (July to June), and the difference between
503 the elevated CO₂ run and the control run are used to infer the model-based CO₂ effect.

504 **Model output analysis**

505 The analysis of the modelled output includes the evaluation of modelled ambient conditions
506 relative to *in situ* observations and hypotheses-based analyses of the modelled CO₂ responses. We
507 employ a structural analysis of the model simulations^{30–32}, splitting model outcomes into the
508 underlying processes to identify crucial model assumptions determining diverging predictions for
509 the FACE experiment. We focus on the simulated increase in biomass C due to eCO₂ and the
510 underlying nutrient control thereon.

511 Biomass C dynamics are a result of primary productivity, C allocation and turnover. We first
512 analyse the effect of eCO₂ on gross primary productivity (GPP), net primary productivity (NPP),
513 autotrophic respiration (Ra), and the resulting plant carbon use efficiency (CUE), where CUE =

514 NPP/GPP. We then assess changes in NPP allocation fractions to biomass compartments of wood,
515 fine roots and leaves, and the resulting effect on biomass C turnover in response to eCO₂. Specific
516 tissue turnover rates are fixed in all models, but overall biomass C turnover changes as a result of
517 changing C allocation to tissue compartments. Turnover rates of biomass C pools are calculated
518 as the fraction of total litter fall per total biomass pool size (Extended Data Table 4).

519 Plant nutrient cycle feedbacks to eCO₂ are assessed by splitting the responses into plant N uptake
520 (NUP) and plant N use efficiency (NUE), where $NUE = NPP/NUP$, and similarly into P uptake
521 (PUP) and P use efficiency (PUE), where $PUE = NPP/PUP$. The responses of NUE and PUE to
522 eCO₂ are further split into changes in tissue C allocation (differing in C:N and N:P ratios) and
523 changes in tissue stoichiometry (flexible C:N and N:P ratios). Soil nutrient cycle feedbacks to
524 eCO₂ are determined by separating eCO₂ responses in N and P mineralization rates (N and P
525 mineralization from microbial decomposition of SOM and biochemical P mineralization of organic
526 P via phosphatase) and the balance of ecosystem N and P inputs (N fixation, N and P deposition,
527 and P weathering) and losses (N and P leaching).

528

529 **DATA AVAILABILITY STATEMENT**

530 The model driving data and model outputs will be made publicly available on figshare under
531 <https://figshare.com/> once the manuscript is accepted. Site data used for model evaluation and
532 calibration are available in the Supplementary Information. All other data are available from the
533 corresponding author upon reasonable request.

534

535 **REFERENCES METHODS**

- 536 1. Quesada, C. A. *et al.* Variations in chemical and physical properties of Amazon forest
537 soils in relation to their genesis. *Biogeosciences* **7**, 1515–1541 (2010).
- 538 2. Chambers, J. Q. *et al.* Respiration from a Tropical Forest Ecosystem : Partitioning of
539 Sources and Low Carbon Use Efficiency. *Ecol. Appl.* **14**, 72–88 (2004).
- 540 3. Malhi, Y. *et al.* Comprehensive assessment of carbon productivity, allocation and storage
541 in three Amazonian forests. *Glob. Chang. Biol.* **15**, 1255–1274 (2009).

- 542 4. Aragão, L. E. O. C. *et al.* Above- and below-ground net primary productivity across ten
543 Amazonian forests on contrasting soils. *Biogeosciences* **6**, 2759–2778 (2009).
- 544 5. Holm, J. A., Chambers, J. Q., Collins, W. D. & Higuchi, N. Forest response to increased
545 disturbance in the central Amazon and comparison to western Amazonian forests.
546 *Biogeosciences* **11**, 5773–5794 (2014).
- 547 6. Hadlich, H. L. *et al.* Recognizing Amazonian tree species in the field using bark tissues
548 spectra. *For. Ecol. Manage.* **427**, 296–304 (2018).
- 549 7. Araújo, A. C. *et al.* Comparative measurements of carbon dioxide fluxes from two nearby
550 towers in a central Amazonian rainforest: The Manaus LBA site. *J. Geophys. Res.* **107**,
551 8090 (2002).
- 552 8. Kucharik, C. J. *et al.* Testing the performance of a dynamic global ecosystem model:
553 Water balance, carbon balance, and vegetation structure. *Global Biogeochem. Cycles* **14**,
554 795–825 (2000).
- 555 9. Fisher, R. A. *et al.* Taking off the training wheels : the properties of a dynamic vegetation
556 model without climate envelopes, CLM4.5 (ED). 3593–3619 (2015).
- 557 10. Medvigy, D., Wofsy, S. C., Munger, J. W., Hollinger, D. Y. & Moorcroft, P. R.
558 Mechanistic scaling of ecosystem function and dynamics in space and time: Ecosystem
559 Demography model version 2. *J. Geophys. Res. Biogeosciences* **114**, (2009).
- 560 11. Smith, B. *et al.* Implications of incorporating N cycling and N limitations on primary
561 production in an individual-based dynamic vegetation model. *Biogeosciences* **11**, 2027–
562 2054 (2014).
- 563 12. Zaehle, S. & Friend, A. D. Carbon and nitrogen cycle dynamics in the O-CN land surface
564 model: 1. Model description, site-scale evaluation, and sensitivity to parameter estimates.
565 *Global Biogeochem. Cycles* **24**, 1–13 (2010).
- 566 13. Best, M. J. *et al.* The Joint UK Land Environment Simulator (JULES), model description
567 Part 1: Energy and water fluxes. *Geosci. Model Dev.* **4**, 677–699 (2011).

- 568 14. Zhu, Q., Riley, W. J., Tang, J. & Koven, C. D. Multiple soil nutrient competition between
569 plants, microbes, and mineral surfaces: model development, parameterization, and
570 example applications in several tropical forests. *Biogeosciences* **13**, 341–363 (2016).
- 571 15. Yang, X., Thornton, P. E., Ricciuto, D. M. & Post, W. M. The role of phosphorus
572 dynamics in tropical forests - a modeling study using CLM-CNP. *Biogeosciences* **11**,
573 1667–1681 (2014).
- 574 16. Wang, Y. P., Law, R. M. & Pak, B. A global model of carbon, nitrogen and phosphorus
575 cycles for the terrestrial biosphere. *Biogeosciences* **7**, 2261–2282 (2010).
- 576 17. Haverd, V. *et al.* A new version of the CABLE land surface model (Subversion revision
577 r4601) incorporating land use and land cover change, woody vegetation demography, and
578 a novel optimisation-based approach to plant coordination of photosynthesis. *Geosci.*
579 *Model Dev.* **11**, 2995–3026 (2018).
- 580 18. Goll, D. S. *et al.* A representation of the phosphorus cycle for ORCHIDEE (revision
581 4520). *Geosci. Model Dev.* **10**, 3745–3770 (2017).
- 582 19. Comins, H. N. & McMurtrie, R. E. Long-Term Response of Nutrient-Limited Forests to
583 CO₂ Enrichment; Equilibrium Behavior of Plant-Soil Models. *Ecol. Appl.* **3**, 666–681
584 (1993).
- 585 20. Farquhar, G. D., von Caemmerer, S. & Berry, J. A. A biochemical model of
586 photosynthetic CO₂ assimilation in leaves of C₃ species. *Planta* **149**, 78–90 (1980).
- 587 21. Collatz, G. J., Ball, J. T., Grivet, C. & Berry, J. A. Physiological and Environmental-
588 Regulation of Stomatal Conductance, Photosynthesis and Transpiration - a Model That
589 Includes a Laminar Boundary-Layer. *Agric. For. Meteorol.* **54**, 107–136 (1991).
- 590 22. Kull, O. & Kruijt, B. Leaf photosynthetic light response: A mechanistic model for scaling
591 photosynthesis to leaves and canopies. *Funct. Ecol.* **12**, 767–777 (1998).
- 592 23. Etheridge, D. M. *et al.* Natural and anthropogenic changes in atmospheric CO₂ over the
593 last 1000 years from air in Antarctic ice and firn. *J. Geophys. Res. Atmos.* **101**, 4115–4128
594 (1996).

- 595 24. MacFarling Meure, C. *et al.* Law Dome CO₂, CH₄ and N₂O ice core records extended
596 to 2000 years BP. *Geophys. Res. Lett.* **33**, L14810 (2006).
- 597 25. Lamarque, J. F. *et al.* Historical (1850-2000) gridded anthropogenic and biomass burning
598 emissions of reactive gases and aerosols: Methodology and application. *Atmos. Chem.*
599 *Phys.* **10**, 7017–7039 (2010).
- 600 26. Lamarque, J. F. *et al.* Global and regional evolution of short-lived radiatively-active gases
601 and aerosols in the Representative Concentration Pathways. *Clim. Change* **109**, 191–212
602 (2011).
- 603 27. Wang, R. *et al.* Global forest carbon uptake due to nitrogen and phosphorus deposition
604 from 1850 to 2100. *Glob. Chang. Biol.* **23**, 4854–4872 (2017).
- 605 28. Tomasella, J. & Hodnett, M. Pedotransfer functions for tropical soils. in *Developments in*
606 *Soil Science* **30**, 415–429 (Elsevier, 2004).
- 607 29. Marthews, T. R. *et al.* High-resolution hydraulic parameter maps for surface soils in
608 tropical South America. *Geosci. Model Dev.* **7**, 711–723 (2014).
- 609 30. De Kauwe, M. G. *et al.* Where does the carbon go? A model-data intercomparison of
610 vegetation carbon allocation and turnover processes at two temperate forest free-air
611 CO₂ enrichment sites. *New Phytol.* **203**, 883–899 (2014).
- 612 31. Walker, A. P. *et al.* Comprehensive ecosystem model-data synthesis using multiple data
613 sets at two temperate forest free-air CO₂ enrichment experiments: Model performance at
614 ambient CO₂ concentration. *J. Geophys. Res. Biogeosciences* **119**, 937–964 (2014).
- 615 32. Zaehle, S. *et al.* Evaluation of 11 terrestrial carbon-nitrogen cycle models against
616 observations from two temperate Free-Air CO₂ Enrichment studies. *New Phytol.* **202**,
617 803–822 (2014).

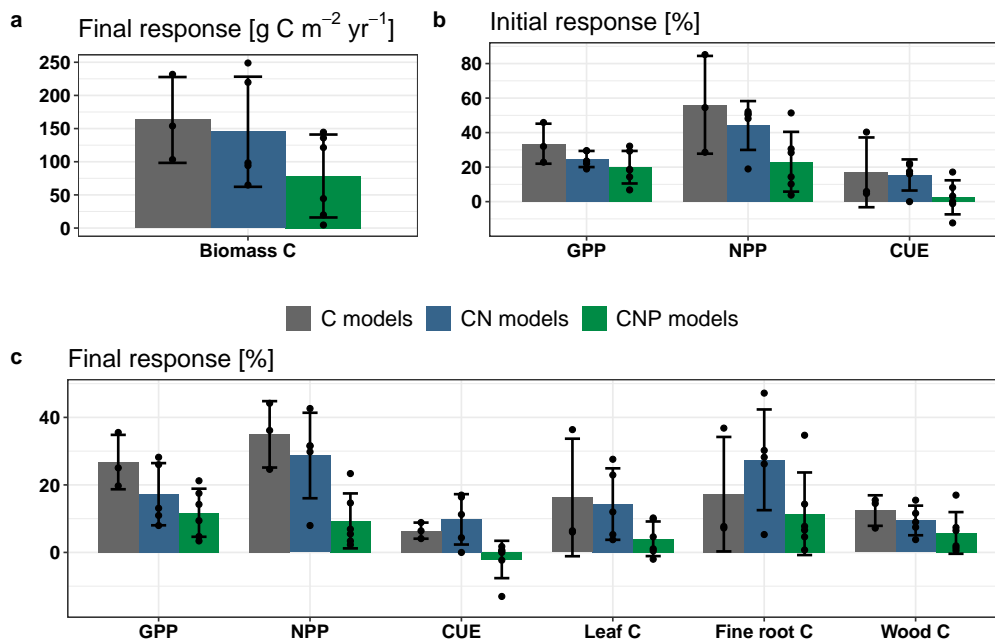


Figure 1: **The predicted effect of eCO₂ on biomass C, productivity and biomass compartments**, averaged over C (grey), CN (blue) and CNP (green) model groups. **a**, The final absolute response of biomass growth, calculated as the mean annual response over the 15 years of eCO₂ per model group in $\text{g C m}^{-2} \text{ yr}^{-1}$. **b**, Initial relative responses of productivity (GPP and NPP), and CUE (=NPP/GPP) in %, calculated as the mean response in the first year. **c**, Final relative responses of productivity and CUE, as well as total leaf, fine root and wood C, calculated as the mean response after 15 years (mean of 13th to 17th year), all in %. Responses to eCO₂ are the differences between the elevated and ambient model run, shown as mean and standard deviation per model group, and individual model results as dots. See also corresponding Extended Data Figure 1 and 3.

Control of phosphorus feedbacks on the biomass C response to eCO₂

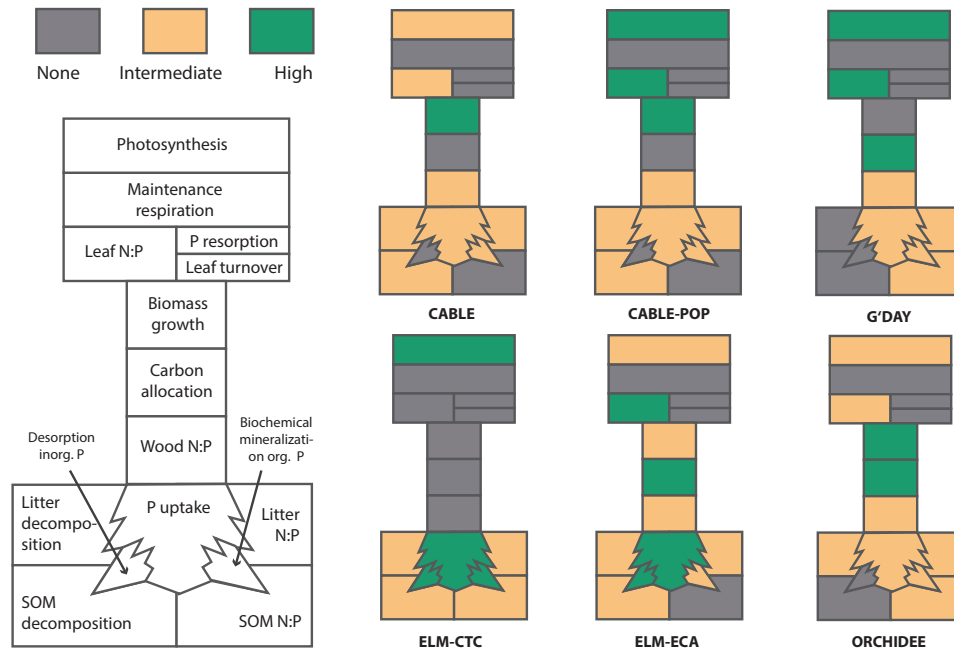


Figure 2: **Strength of phosphorus feedbacks in controlling the biomass C response to eCO₂ for the six CNP models.** Ecosystem processes are highlighted that depend (or not depend) on the P cycle, for which classes (none, intermediate, high) indicate the degree to which the considered P feedback causes a response of biomass C to eCO₂ in our simulations. P limitation causes strong or intermediate downregulation of photosynthesis with eCO₂ across all models. Maintenance respiration, leaf turnover and P resorption are not responsive to P feedbacks in any of the models. Leaf N:P responds to eCO₂ in most models, but is fixed in ELM-CTC, narrowly bound in CABLE, and at its maximum in ORCHIDEE. P limitation causes direct downregulation of biomass growth in CABLE, CABLE-POP, ELM-ECA and ORCHIDEE. Allocation shifts towards roots to alleviate P limitation is considered in G'DAY, ELM-ECA and ORCHIDEE. Desorption of P from mineral surfaces is only considered in ELM-ECA and ELM-CTC, and biochemical P mineralization is considered in many models, but only effectively responsive in ELM-CTC.

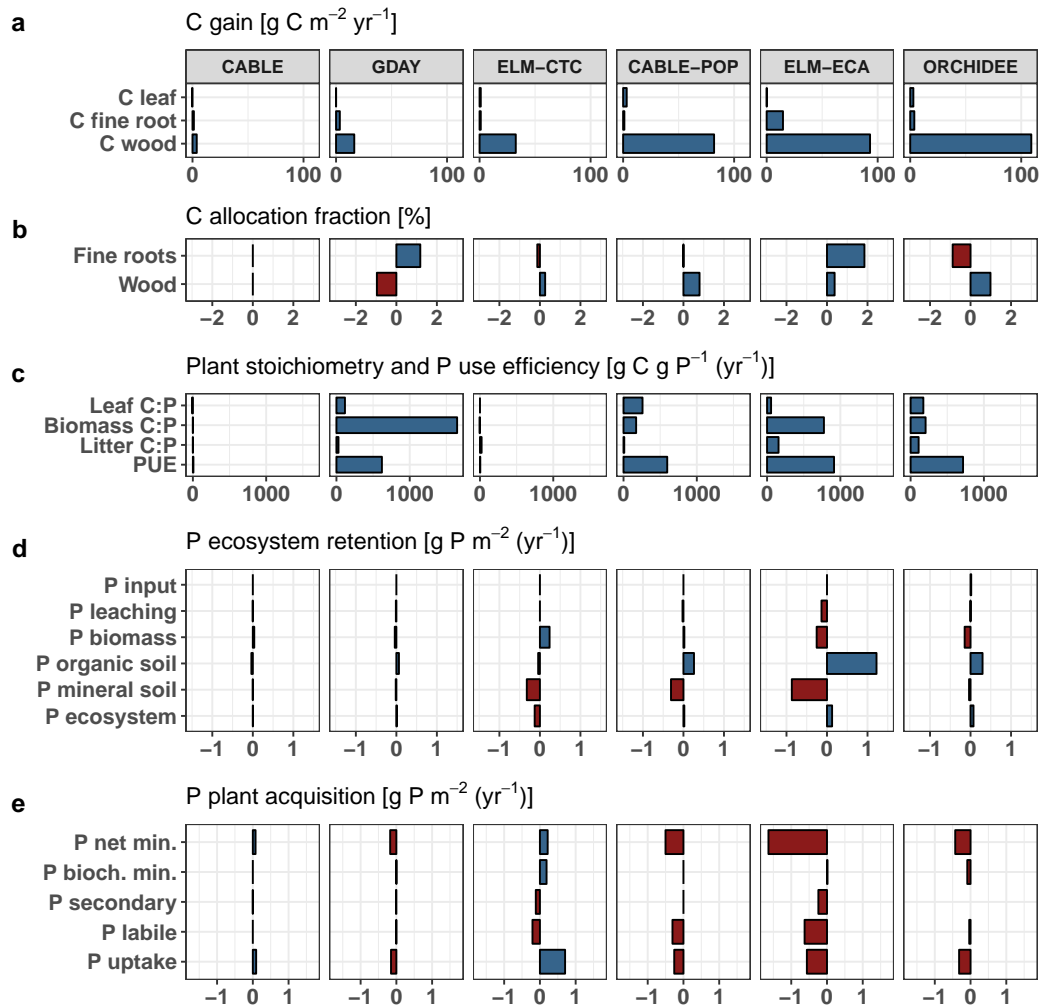


Figure 3: **Key responses of biomass C gain, stoichiometry, allocation, and P dynamics to eCO₂ for the CNP models**, contrasted are positive (blue) from negative (red) responses. **a**, Mean annual change in standing leaf, fine root and wood C over 15 years, increasing across models from left to right in $\text{g C m}^{-2} \text{yr}^{-1}$. **b**, The mean change in C allocation for fine roots and wood in %. **c**, Mean change in tissue stoichiometry in absolute terms in g C g P^{-1} and change in P use efficiency over 15 years in $\text{g C g P}^{-1} \text{yr}^{-1}$. **d**, Mean change in ecosystem P input and output (leaching) fluxes in $\text{g P m}^{-2} \text{yr}^{-1}$ and mean change in final P stock in biomass, organic soil, mineral soil and total ecosystem in g P m^{-2} . **e**, Mean change in plant P acquisition processes, including change in net P mineralization, biochemical P mineralization and P uptake in $\text{g P m}^{-2} \text{yr}^{-1}$ and secondary and labile P pools in g P m^{-2} . For both, **d** and **e**, P flux changes are differences of cumulative fluxes after 15 years and P pool changes are differences in pools after 15 years.