Representation of phosphorus cycle in Joint UK Land Environment Simulator (vn5.5_JULES-CNP)

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Abstract

Most Land Surface Models (LSMs), the land components of Earth system models (ESMs), include representation of N limitation on ecosystem productivity. However only few of these models have incorporated phosphorus (P) cycling. In tropical ecosystems, this is likely to be particularly important as N tends to be abundant but the availability of rock-derived elements, such as P, can be very low. Thus, without a representation of P cycling, tropical forest response in areas such as Amazonia to rising atmospheric CO_2 conditions remains highly uncertain. In this study, we introduced P dynamics and its interactions with the N and carbon (C) cycles into the Joint UK Land Environment Simulator (JULES). The new model (JULES-CNP) includes the representation of P stocks in vegetation and soil pools, as well as key processes controlling fluxes between these pools. We evaluate JULES-CNP at the Amazon nutrient fertilization experiment (AFEX), a low fertility site, representative of about 60% of Amazon soils. We apply the model under ambient CO_2 and elevated CO_2. The model is able to reproduce the observed plant and soil P pools and fluxes under ambient CO_2. We estimate P to limit net primary productivity (NPP) by 24% under current CO_2 and by 46% under elevated CO_2. Under elevated CO_2, biomass in simulations accounting for CNP increase by 10% relative to at contemporary CO_2, although it is 5% lower compared with CN and C-only simulations. Our results highlight the potential for high P limitation and therefore lower CO_2 fertilization capacity in the Amazon forest with low fertility soils.

1. Introduction

Land ecosystems currently take up about 30% of anthropogenic CO_2 emissions (Friedlingstein *et al.*, 2020), thus buffering the anthropogenic increase in atmospheric CO_2. Tropical forests play a major role in the land carbon (C) cycle, account for about half of global Net Primary Production (NPP)(Schimel *et al.*, 2015), and store the highest above ground carbon among all biomes (Pan *et al.*, 2011; Mitchard, 2018).

The C sink capacity of tropical forests may be constrained by nutrient availability for plant photosynthesis and growth (Vitousek and Howarth, 1991; Elser *et al.*, 2007; LeBauer and Treseder, 2008) via either P (Nordin, Högberg and Näsholm, 2001; Shen *et al.*, 2011) and/or N related processes (DeLuca, Keeney and McCarty, 1992; Perakis and Hedin, 2002). Global process-based models of vegetation dynamics and function suggest a continued land C sink in the tropical forests, largely attributed to the CO_2 fertilization effect (Sitch *et al.*, 2008; Schimel, Stephens and Fisher, 2015; Koch, Hubau and Lewis, 2021). However, many of these models typically do not consider P constraints on plant growth (Fleischer *et al.*, 2019), which is likely to be an important limiting nutrient in tropical ecosystems, characterised by old and heavily weathered soils. The importance of nutrient cycling representation in Earth System Models (ESMs), and the lack thereof, was highlighted by Hungate *et al.* (2003) and Zaehle and Dalmonech (2011), showing the significance of nutrient inclusion in ESMs for generating more realistic estimations of the future evolution of the terrestrial C sink. However, in the Coupled Climate C Cycle Model Inter-comparison Project (C4MIP), none of the participating ESMs included N dynamics (Friedlingstein *et al.*, 2006). Seven years later, for the update in CMIP5 (Anav *et al.*, 2013), three models out of eighteen with N dynamics were included. Although much progress has been made in the inclusion of an N cycle in ESMs so far, none of the CMIP5 models included P cycling and in the most recent CMIP6, only one model includes P (ACCESSESM1.5 model) (Arora *et al.*, 2020).

The long history of soil development in tropical regions which involves the loss of rock-derived nutrients through weathering and leaching on geologic timescales (Vitousek et al., 1997, 2010) results in highly weathered soils. Soil P is hypothesized to be among the key limiting nutrients to plant growth in tropical forests, unlike temperate forest where N is hypothesised to be the main constraint. Low P availability in tropical soils is related to the limited un-weathered parent material or organic compounds as source of P (Walker and Syers, 1976), active sorption (Sanchez, 1977) and high occlusion (Yang and Post, 2011) which further reduce plant available P. While N can impact the terrestrial C sink response to increasing atmospheric CO_2 by changing plant C fixation capacity (Luo et al., 2004) via the continuous inputs of N into ecosystems from atmospheric deposition and biological N fixation (Vitousek et al., 2010), the lack of large P inputs into ecosystems and slow rates of P input and output to and from ecosystems, especially those growing on highly weathered soil, makes P limitation a stronger constraint on ecosystems response to elevated CO_2 (eCO_2) than N (Gentile et al., 2012; Sardans, Rivas-Ubach and Peñuelas, 2012). Hence, a separate knowledge is needed to understand how nutrient availability controls tropical compared to the temperate forest productivity. This causes considerable uncertainty in predicting the future of the Amazon forest C sink (Yang *et al.*, 2014).

There is evidence to suggest P limitation on plant productivity in the Amazon forest (Malhi, 2012) where it has been shown that the younger, more fertile west and south-west Amazon soils have higher tree turnover (Phillips et al., 2004; Stephenson and Van Mantgem, 2005) and stem growth rates (Malhi *et al.*, 2004) and lower above ground biomass (Baker *et al.*, 2004; Malhi *et al.*, 2006) compared to their central and eastern counterparts. Total soil P has been found as the best predictor of stem growth (Quesada *et al.*, 2010) and of total NPP (Aragão *et al.*, 2009) across this fertility gradient, and foliar P is positively related to plant photosynthetic capacity (V_{cmax} and J_{cmax}) in these forests (Mercado *et al.*, 2011).

However, modelling studies are unable to reproduce observed spatial patterns of NPP and biomass in the Amazon due to missing processes such as flexible C allocation, spatial variation of biomass turnover (Cleveland *et al.*, 2015) and due to the lack of inclusion of soil P constraints on plant productivity and function. Recent modelling work has focused on improving process and parameter representation using the observational data of spatial variation in woody biomass residence time (Johnson *et al.*, 2016), soil texture and soil P to parameterise the maximum RuBiCo carboxylation capacity (V_{cmax}) (Castanho *et al.*, 2013). Results from these studies successfully represent observed patterns of Amazon forest biomass growth increases with increasing soil fertility. However, the full representation of these interactions and the impact of the soil nutrient availability on biomass productivity is still missing in most of ESMs.

98   So far, several dynamic global vegetation models have been developed to represent P cycling within the soil
99   (Yang *et al.*, 2013; Hou *et al.*, 2019) and between plant and soils for tropical forests particularly (Yang *et al.*,
100 2014; Zhu *et al.*, 2016; Goll *et al.*, 2017). Furthermore, a comprehensive study included several models with C-
101 N-P cycling and their feedbacks on the atmospheric C fixation and biomass growth in Amazon forests under
102 ambient and eCO$_2$ conditions (Fleischer *et al.*, 2019). Despite these developments, data to underpin them and
103 their projections, particularly for the tropics, is sparse and remains challenging particularly for the Amazon
104 forest (Reed *et al.*, 2015; Jiang *et al.*, 2019). Moreover, due to the lack of detailed measurements, the P-related
105 processes such as ad/desorption and uptake represented in these models are under-constrained and likely
106 oversimplified, thus the future predictions of Amazon forest responses to eCO$_2$ and climate change are
107 uncertain. To fill this gap, in this study, we will use data collected as part of the Amazon Fertilization
108 Experiment (AFEX), the first project that focuses on experimental soil nutrient manipulation in the Amazon,
109 with a comprehensive data collection program covering plant ecophysiology, C stocks and fluxes, soil processes
110 including P stocks.
111
112 Here, we describe the implementation of the terrestrial P cycle in the Joint UK Land Environment Simulator
113 (JULES) (Clark *et al.*, 2011), the land component of the UK Earth System Model (UKESM), following the prior
114 N cycle development (Wiltshire *et al.*, 2021). The model (JULES-CNP) is parameterized and then evaluated
115 using AFEX data and from other sites in central Amazonia. AFEX provides the required input data on key plant
116 and soil P pools. To test the model, we followed the protocol of Fleischer *et al.*, (2019), to predict nutrient
117 limitations on land biogeochemistry under ambient and eCO$_2$. Predictions of the CO$_2$ fertilization effect in
118 JULES-CNP are compared to those in current versions of the model with coupled C and N cycles (JULES-CN)
119 and with C cycle only (JULES-C).
120
121
122 **2.   Material and methods**
123
124 **2.1 JULES**
125
126 JULES is a process-based model that integrates water, energy, C cycling (JULES-C) (Clark *et al.*, 2011) and N
127 cycling (JULES-CN) (Wiltshire *et al.*, 2021) between the atmosphere, vegetation and soil (Best *et al.*, 2011;
128 Clark *et al.*, 2011). Vegetation dynamics are represented in JULES using the TRIFFID model, using nine
129 distinct plant functional types (PFTs) (tropical and temperate broadleaf evergreen trees, broadleaf deciduous
130 trees, needle-leaf evergreen and deciduous trees, C3 and C4 grasses, and evergreen and deciduous shrubs), as
131 well as height competition (Harper *et al.*, 2016). JULES simulates Gross Primary Productivity (GPP) based on a
132 coupled photosynthesis and water balance scheme, from which autotrophic respiration for each living tissue
133 (leaf, wood, root) is subtracted to estimate NPP. NPP is then allocated to increase tissue C stocks and to spread,
134 i.e., expand the fractional coverage of the PFT. The resultant PFT fractional coverages depend in addition on
135 competition across PFTs for resources, e.g., light. Tissue turnover and vegetation mortality add C into the litter
136 pools. Representation of soil organic C (SOC) follows the RothC equations (Jenkinson *et al.*, 1990; Jenkinson
137 and Coleman, 2008) defining four C pools: decomposable plant material (DPM) and resistant plant material
138 (RPM), which receive direct input from litterfall, and microbial biomass (BIO) and humified material (HUM)
139 which receive a fraction of decomposed C from DPM and RPM which is not released to the atmosphere. The
140 limitation of N on SOC is applied to the vegetation and soil components using a dynamic C:N ratio to modify
141 the mineralization and immobilization processes as described in Wiltshire *et al.*, (2021). Note that the soil
142 component of JULES-CN can be run either as a single box model or vertically resolved over soil depth (JULES-
143 CNlayered), and in this paper we build upon the vertically resolved version described in Wiltshire et al. (2021).
144
145 **2.2 JULES-CNP**
146
147 JULES-CNP includes the representation of the P cycle in JULES version (vn5.5). It includes P fluxes within the
148 vegetation and soil components, and the specification of P pools and processes related to P cycling within the
149 soil column (Figure.1). A parent material pool is introduced to consider the input of weathered P. The adsorbed,
150 desorbed and occluded fractions of P for both organic and inorganic P are also represented. However, except for
151 parent material and occluded P pools, all other pools are estimated at each soil layer. The description of changes
152 in pools and associated relative fluxes are explained in detail in the next sections.
153
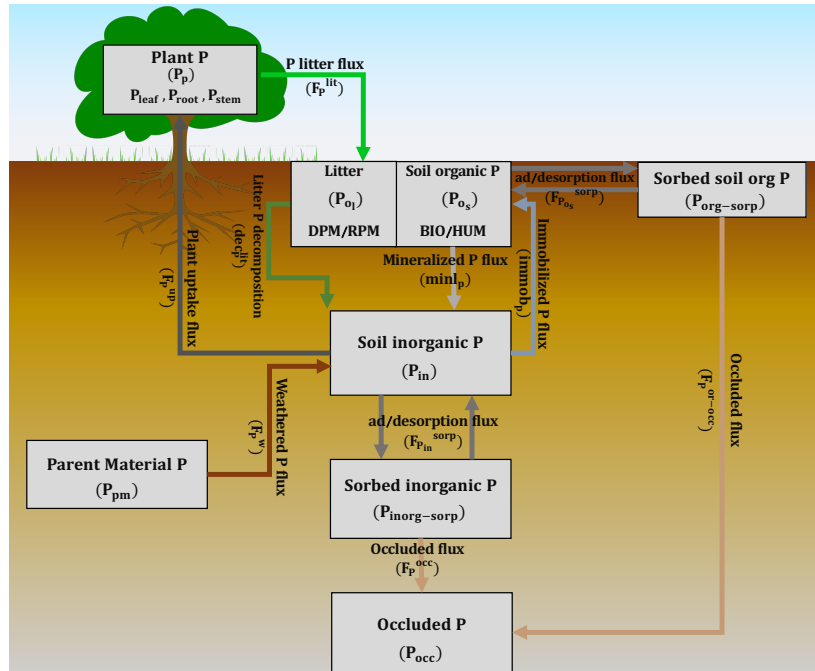
154
155 **Figure. 1-** JULES CNP model scheme
156
157 **2.2.1   P pools**
158
159 JULES represents eight P pools comprising organic and inorganic P: in plant P (P_P) and soil pools (in each soil
160 layer (n)): litter P (P_{O_l}), soil organic P (P_{O_s}), soil inorganic P (P_{in}), organic sorbed ($P_{org-sorp}$), inorganic sorbed
161 ($P_{inorg-sorp}$) and occluded (P_{occ}) P comprised of both organic and inorganic P. All pools are in units of kg P m^{-2}
162 (Fig 1, Tables 1 and 2).
163
164 Plant P pool is composed of leaf (P_{leaf}), fine root (P_{root}) and stem together with coarse root (P_{stem}), which are
165 related to their associated C pools ($C_{leaf}, C_{root}, C_{stem}$) in (kg C m^{-2}) and C to P ratios ($C{:}P_{leaf}, C{:}P_{root} C{:}P_{stem}$)
166 as follows:
167
168 $P_{leaf} = \frac{C_{leaf}}{C{:}P_{leaf}}$ (eq.1)
169
170 $P_{root} = \frac{C_{root}}{C{:}P_{root}}$ (eq.2)
171
172 $P_{stem} = \frac{C_{stem}}{C{:}P_{stem}}$ (eq.3)
173
174 Therefore, the plant P pool (P_P) is the sum of all vegetation P pools as follows:
175
176 $P_p = P_{leaf} + P_{root} + P_{stem}$ (eq.4)
177 The plant P pool (P_P) is estimated as the difference between the input, plant uptake $F_P{}^{Up}$ (eq.21) and output of
178 this pool, plant litter flux $F_P{}^{lit}$ (eq.23), with both fluxes expressed in kg P m^{-2} yr^{-1} as follows:
179
180 $\frac{dP_p}{dt} = F_P{}^{up} - F_P{}^{lit}$ (eq.5)
181
182 The litter P pool (P_{O_l}) is estimated as a sum of P_{DPM} and P_{RPM} pools. Each pool (i) is formed by the fluxes of
183 plant litter input ($F_P{}^{lit}$) and the outgoing decomposed P ($dec_P{}^{lit}$) both expressed in kg P m^{-2} yr^{-1} (eq.23).

4

184 Furthermore, the plant litter input is modified based on the plant type material ratio α (in order to distribute the
185 litter input based on the DPM/RPM fraction) as follows:

187 $$\frac{dP_{DPM}}{dt} = F_{P_n}{}^{lit} \times \alpha - dec_{P_{i,n}} \qquad (eq.6)$$

189 $$\frac{dP_{RPM}}{dt} = F_{P_n}{}^{lit} \times (1-\alpha) - dec_{P_{i,n}} \qquad (eq.7)$$

191 $$dP_{O_l} = \sum_{n=1}^{N} P_{DPM_n} + \sum_{n=1}^{N} P_{RPM_n} \qquad (eq.8)$$

193 The soil organic pool (P_{O_S}) is represented as the sum of P_{BIO} and P_{HUM}. These pools are estimated from the
194 difference between P inputs from immobilized ($immob_P$) and desorbed P $F_{P_{O_S}}{}^{desorp}$ and P outputs from
195 mineralized ($minl_P$), and adsorbed P fluxes ($F_{P_{O_S}}{}^{sorp}$) (adsorption: eq. 34 and desorption: eq.35) with all
196 fluxes expressed in kg P m^{-2} yr^{-1} as follows:

198 $$\frac{dP_{BIO}}{dt} = 0.46 \times immob_{P_i} + F_{P_{O_S}{}_{i,n}}{}^{desorp} - minl_{P_i} - F_{P_{O_S}{}_{i,n}}{}^{sorp} \qquad (eq.9)$$

200 $$\frac{dP_{HUM}}{dt} = 0.54 \times immob_{P_i} + F_{P_{O_S}{}_{i,n}}{}^{desorp} - minl_{P_i} - F_{P_{O_S}{}_{i,n}}{}^{sorp} \qquad (eq.10)$$

202 $$dP_{O_S} = \sum_{n=1}^{N} P_{BIO_n} + \sum_{n=1}^{N} P_{HUM_n} \qquad (eq.11)$$

205 The inorganic sorbed P pool ($P_{inorg-sorp}$) is represented as the difference between the input flux of inorganic
206 sorption ($F_{P_{in}}{}^{sorp}$) and output fluxes of inorganic desorption ($F_{P_{in}}{}^{de-sorp}$) and occluded P($F_P{}^{occ}$), with all
207 fluxes expressed in kg P m^{-2} yr^{-1} as follows:

209 $$\frac{dP_{inorg-sorp}}{dt} = \sum_{n=1}^{N} F_{P_{in_n}}{}^{sorp} - \sum_{n=1}^{N} F_{P_{in_n}}{}^{de-sorp} - \sum_{n=1}^{N} F_{P_n}{}^{occ} \qquad (eq.12)$$

211 The occluded (P_{occ}) P pool is represented as the sum of input fluxes of occluded P from both organic ($F_P{}^{or-occ}$)
212 and inorganic P pools ($F_P{}^{occ}$) expressed in kg P m^{-2} yr^{-1}, as follows:

214 $$\frac{dP_{occ}}{dt} = \sum_{n=1}^{N} F_{P_n}{}^{occ} + \sum_{n=1}^{N} F_{P_n}{}^{or-occ} \qquad (eq.13)$$

216 The organic sorbed P pool ($P_{org-sorp}$) is represented as the difference between the input flux of organic sorption
217 ($F_{P_{O_{S_n}}}{}^{sorp}$) and output fluxes of organic desorption ($F_{P_{O_{S_n}}}{}^{de-sorp}$) and occluded P($F_{P_n}{}^{occ}$), with all fluxes
218 expressed in kg P m^{-2} yr^{-1} as follows:

220 $$\frac{dP_{org-sorp}}{dt} = \sum_{n=1}^{N} F_{P_{O_{S_n}}}{}^{sorp} - \sum_{n=1}^{N} F_{P_{O_{S_n}}}{}^{de-sorp} - \sum_{n=1}^{N} F_{P_n}{}^{or-occ} \qquad (eq.14)$$

222 P from parent material (P_{pm}) pool depends on the weathering flux ($F_P{}^{w}$) in kg P m^{-2} yr^{-1} (eq.37) as follows:

224 $$\frac{dP_{pm}}{dt} = -\sum_{n=1}^{N} F_{P_n}{}^{w} \qquad (eq.15)$$

226 ### 2.2.2. P fluxes

228 NPP in JULES is calculated as the difference between GPP and autotrophic respiration. In JULES-CNP, GPP,
229 autotrophic respiration, and NPP represent the potential amount of C, available for tissue growth and spread
230 assuming no nutrient limitation. The reported NPP in the literature often includes other C fluxes related to the
231 exudates, volatiles production and non-structural carbohydrates (Chapin *et al.*, 2011; Walker *et al.*, 2021) which
232 are challenging to measure (Malhi, Doughty and Galbraith, 2011). Therefore, actual Biomass Production (BP),
233 as defined by Walker *et al.*, (2021), is calculated based on NPP and the availability and costs associated with
234 procurement of sufficient inorganic N and P for uptake. Hence, if the system is limited by the availability of N
235 and/or P, BP will be adjusted to match the growth that can be supported with the limited N or P supply, with any

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236 excess carbohydrate lost through exudates. The total excess C term (exudates, ψ_t) (kg C m^{-2} yr^{-1}) is calculated
237 as:
238
239 $$\psi_t = \psi_g + \psi_s \qquad\qquad\qquad\text{(eq.16)}$$
240
241 where ψ_g and ψ_s are the exudates due to growth (g) and spread (s) and are assumed to be rapidly respired by
242 plants.
243
244 P limitation is applied on the C litter production similar to the N scheme of JULES (JULES-CN) (Wiltshire *et*
245 *al.*, 2021). In JULES-CN the N limitation effect on the litter production is captured by estimating the available C
246 for litter production as a difference between the NPP and exudates (Wiltshire *et al.*, 2021).
247
248 BP is calculated as the difference between NPP and total exudates:
249
250 $$BP = NPP - \psi_t \qquad\qquad\qquad\text{(eq.17)}$$
251
252 The plant P demand is represented by the sum of demand to sustain growth ($\emptyset_g$) and to sustain vegetation
253 spreading (to sustain PFT fractional coverage increment) ($\emptyset_s$) and is expressed in (kg P m^{-2} yr^{-1}), as follows:
254
255
256 $$\emptyset_t = \emptyset_g + \emptyset_s \qquad\qquad\qquad\text{(eq.18)}$$
257 $$\emptyset_g = \varepsilon_{pc}\left(\Pi_c - \frac{dC}{dt} - \psi_g\right) \qquad\qquad\qquad\text{(eq.19)}$$
258 $$\emptyset_s = \varepsilon_{pc}\left(\Pi_c - \frac{dC}{dt} - \psi_s\right) \qquad\qquad\qquad\text{(eq.20)}$$
259
260 where ε_{pc} is plant P:C ratio, Π_c is the NPP (kg C m^{-2} yr^{-1}), ψ_g are exudates due to the P limitation for plant
261 growth (kg C m^{-2} yr^{-1}) and ψ_s are exudates due to the P limitation for vegetation spreading (kg C m^{-2} yr^{-1}).
262
263 Plant P uptake ($F_p{}^{up}$) is estimated based on the P demand for growth and spreading ($\emptyset_t$) and the root uptake
264 capacity (u^{max}) (kg P kg^{-1} C yr^{-1}), as follows:
265
266 $$F_p{}^{up}{}_n = \begin{cases} \emptyset_t & \emptyset_t \leq u^{max} \\ u^{max} & \emptyset_t > u^{max} \end{cases} \qquad\qquad\qquad\text{(eq.21)}$$
267
268 The plant P uptake ($F_p{}^{up}$) varies spatially depending on the root uptake capacity (u^{max}). Therefore, in regions
269 with limited P supply, the plant P uptake is limited to the u^{max} and consequently impacts the exudates and BP.
270 The root uptake capacity depends on the maximum root uptake capacity (v_{max}) (kg P kg^{-1} C yr^{-1}), root depth
271 (d_{root}), the concentration of inorganic p at different soil depths (P_{in}), and a half saturation term at which half of
272 the maximum uptake capacity is reached using inorganic p at different soil depths (P_{in}), a scaling uptake ratio
273 (K_p) (μmol P l^{-1}), unit conversion (C_f) (1 kg P^{-1}), and soil moisture (θ) (l m^{-2}), as follows:
274
275 $$u^{max} = v_{max} \times d_{root} \times \sum_{n=1}^{N} P_{in_n} \times \left(\frac{1}{\sum_{n=1}^{N} P_{in_n} + c_f \times K_p \times \theta_n}\right) \qquad\qquad\text{(eq.22)}$$
276
277 The litter production of P ($F_{P_n}{}^{lit}$) is calculated based on the litter flux of C (kg C m^{-2} yr^{-1}) using leaf, root and
278 wood turnovers (yr^{-1}), and through the vegetation dynamics due to large-scale disturbance and litter production
279 density, as follows:
280
281 $$F_{P_n}{}^{lit} = (1 - \lambda_{leaf})\gamma_{leaf}C_{leaf} \times \varepsilon_{pc-leaf} + (1 - \lambda_{root})\gamma_{root}C_{root} \times \varepsilon_{pc-root} + \gamma_{wood}C_{wood} \times \varepsilon_{pc-root}$$
282 $$\text{(eq.23)}$$
283
284 where λ is the leaf and root P re-translocation coefficient (Zaehle and Friend, 2010) and γ is a temperature
285 dependent turnover rate representing the phenological state (Clark *et al.*, 2011) and respective C:P ratios.
286
287
288
289

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290 The decomposition of litter (dec^{lit}) depends on soil respiration (R) (kg C m^{-2} yr^{-1}), the litter C:P ratio (ε_{cp}) at
291 each soil layer (n) as follows:
292

293 $dec_P{}^{lit} = \frac{\sum_{n=1}^{N} R_n}{\varepsilon_{cp}}$ (eq.24)

294
295 where the C:P ratio is calculated based on litter C pool (DPM and RPM) (lit^C) (kg C m^{-2} yr^{-1}) and litter P pool
296 (P_{O_l}) as follows:
297

298 $\varepsilon_{cp} = \frac{\sum_{n=1}^{N} lit_n{}^C}{P_{O_{l_n}}}$ (eq.25)

299
300 The mineralized ($minl_P$) and immobilized ($immob_P$) P fluxes are calculated based on C mineralization and
301 immobilization, C:P ratios (ε_{cp}) of plant (i) (DPM/RPM) and soil (HUM/BIO), soil pool potential respiration
302 (R_{P_i}) (kg C m^{-2} yr^{-1}) and the respiration partitioning fraction (resp_frac) as follows:
303

304 $minl_P = \frac{\sum_{n=1}^{N} R_{P_{i,n}}}{\varepsilon_{cp_i}}$ (eq.26)

305
306 $immob_P = \frac{\sum_{n=1}^{N} R_{i,n} \times resp\_frac}{\varepsilon_{cp_{soil}}}$ (eq.27)

307
308 However, the soil pool potential respiration for the plant pools (DPM/RPM) is further modified based on the
309 litter decomposition rate modifier (F_{P_n}) as follows:
310

311 $R_{i,n} = R_{P_{i,n}} \times F_{P_n}$ (eq.28)

312
313 where the F_{P_n} is estimated based on the soil pool (BIO/HUM) mineralization and immobilization, soil inorganic
314 P and plant pools (DPM/RPM) demand as follows:
315

316 $F_{P_n} = \frac{(minl_{P-BIO_n} + minl_{P-HUM_n} - immob_{P-BIO_n} - immob_{P-HUM_n}) + P_{inorg_n}}{DEM_{DPM_n} + DEM_{RPM_n}}$ (eq.29)

317
318 The plant pool demand ($DEM_{k,n}$) is estimated based on the potential mineralization ($minl_{p-pot}$) and
319 immobilization ($immob_{p-pot}$) of plant pools (k) as follows:
320

321 $DEM_{k,n} = immob_{p-pot,k} - minl_{p-pot,k}$ (eq.30)

322
323 The fluxes of adsorption ($F_{P_{in_n}}{}^{sorp}$) and desorption ($F_{P_{in_n}}{}^{desorp}$) of inorganic P in kg P m^{-2} yr^1 are calculated
324 based on soil inorganic (P_{in_n}) and sorbed inorganic ($P_{inorg-sorbed_n}$) P pools and inorganic adsorption
325 ($K_{sorp-in}$), desorption ($K_{desorp-in}$) coefficients (kg P m^{-2} yr^{-1}) and maximum sorbed inorganic (P_{in-max}) (kg P
326 m^{-2}) as follows:
327

328 $F_{P_{in_n}}{}^{sorp} = P_{in_n} \times K_{sorp-in} \times \frac{\left(P_{in-max_n} - P_{inorg-sorbed_n}\right)}{P_{in-max_n}}$ (eq.31)

329
330 $F_{P_{in_n}}{}^{desorp} = P_{inorg-sorbed_n} \times K_{desorp-in}$ (eq.32)

331
332
333
334 The occluded inorganic p flux is calculated based on sorbed inorganic P pool and P occlusion rate (K_{occ}) (kg P
335 m^{-2} yr^{-1}) as follows:
336
337 $F_{P_n}{}^{occ} = P_{inorg-sorbed_n} \times K_{occ}$ (eq.33)

338
339 The fluxes of adsorption and desorption of organic P are calculated based on soil organic and sorbed organic P
340 pools and organic adsorption ($K_{sorp-or}$) (kg P m^{-2} yr^{-1}), desorption ($K_{desorp-or}$) coefficients (kg P m^{-2} yr^{-1}) and

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341 maximum sorbed organic ($P_{org-max}$) (which corresponds to the sorbed soil P saturation, thus modifying the
342 sorption rate respectively) (kg P m^{-2}) as follows:
343

344 $$F_{P_{O_{S_n}}}^{sorp} = P_{O_{S_n}} \times K_{sorp-or} \times \frac{\left(P_{or-max_n} - P_{org-sorbed_n}\right)}{P_{or-max_n}} \qquad \text{(eq.34)}$$
345

346 $$F_{P_{O_{S_n}}}^{desorp} = P_{org-sorbed_n} \times K_{desorp-or} \qquad \text{(eq.35)}$$
347

348 The occluded organic p flux ($F_{P_n}^{or-occ}$) (kg P m^{-2} yr^{-1}) is calculated based on sorbed organic P pool
349 ($P_{org-sorbed_n}$) and P occlude rate (K_{occ}) (kg P m^{-2} yr^{-1}) as follows:
350

351 $$F_{P_n}^{or-occ} = P_{org-sorbed_n} \times K_{occ} \qquad \text{(eq.36)}$$
352

353 The p flux from weathered parent material is calculated based on amount of P in the parent material (P_{pm}) and P
354 weathering rate (K_w) (kg P m^{-2} yr^{-1}) as follows:
355

356 $$F_{P_n}^{w} = P_{pm_n} \times K_w \qquad \text{(eq.37)}$$
357

358 P diffusion between soil layers (F_{D_n}) expressed in (kg P m^{-2} yr^{-1}) is calculated following Fick's second law and
359 it is a function of the diffusion coefficient (Dz) in m^2 s^{-1}, the concentration of inorganic P at different soil depths
360 (P_{in}) in kg P m^{-2}, the distance (z) between the midpoints of soil layers in metres and seconds to year unit
361 conversion (Yr):
362

363 $$F_{D_n} = \frac{\partial}{\partial z}\left(D_{z_n}\frac{\partial P_{S_n}}{\partial z}\right) \times Yr \qquad \text{(eq.38)}$$
364

365 **Table 1.** Model variables

Variable	Unit	Definition
ψ	kg C m^{-2} yr^{-1}	Excess C exudates
$\emptyset$	kg P m^{-2} yr^{-1}	Plant demand for uptake
Π_c	kg C m^{-2} yr^{-1}	Plant C uptake
u^{max}	kg P kg^{-1} C yr^{-1}	Root uptake capacity
DEM	kg P m^{-2} yr^{-1}	Plant pool P demand
dec_P^{lit}	kg P m^{-2} yr^{-1}	Litter decomposition
F_D	kg P m^{-2} yr^{-1}	Plant diffusion flux
F_P	-	Plant litter decomposition rate modifier
F_p^{lit}	kg P m^{-2} yr^{-1}	Plant litter flux
F_p^{up}	kg P m^{-2} yr^{-1}	Plant uptake
$F_{P_{O_S}}^{sorp}$	kg P m^{-2} yr^{-1}	Sorbed organic P flux
$F_{P_{in}}^{sorp}$	kg P m^{-2} yr^{-1}	Sorbed inorganic P flux
F_p^{occ}	kg P m^{-2} yr^{-1}	Occluded inorganic P flux
F_p^{or-occ}	kg P m^{-2} yr^{-1}	Occluded organic P flux
F_p^{w}	kg P m^{-2} yr^{-1}	Weathered P flux
$immob_P$	kg P m^{-2} yr^{-1}	Immobilized P flux
lit_C	kg C m^{-2} yr^{-1}	C litter flux
lit_{frac}	-	Litter fraction
lit_{leaf}	kg C m^{-2} yr^{-1}	Leaf litter flux
lit_{root}	kg C m^{-2} yr^{-1}	Root litter flux
lit_{wood}	kg C m^{-2} yr^{-1}	Woody litter flux
$minl_P$	kg P m^{-2} yr^{-1}	Mineralized P flux
P_p	kg P m^{-2}	Plant P pool
P_{O_l}	kg P m^{-2}	Litter organic pool

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P_{O_s}	kg P m^{-2}	Soil organic pool
P_{in}	kg P m^{-2}	Soil inorganic pool
$P_{inorg-sorp}$	kg P m^{-2}	Soil inorganic sorbed pool
$P_{org-sorp}$	kg P m^{-2}	Soil organic sorbed pool
P_{occ}	kg P m^{-2}	Soil occluded pool
P_{pm}	kg P m^{-2}	Parent material pool
R	kg C m^{-2} yr^{-1}	Total respiration
R_p	kg C m^{-2} yr^{-1}	Total potential respiration
R^s	kg C m^{-2} yr^{-1}	Soil respiration
R_d	kg C m^{-2} yr^{-1}	Leaf dark respiration
T_{ref}	K	Soil reference temperature
T_s	K	Soil temperature
Veg_c	kg C m^{-2}	Sum of biomass
z	m	Soil depth

366
367

Table 2. P Model parameters

Parameter	Value	Unit	Eq.	Description	Source
α	PFT dependent	-	6	Plant type material ratio	(Clark *et al.*, 2011)
f_{dr}	0.005	-	41	Respiration scale factor	Calibrated
ε_{cp}	1299.6	-	27	C:P ratio	(Fleischer *et al.*, 2019)
v_{max}	PFT dependent	kg P kg^{-1} C yr^{-1}	22	Maximum root uptake capacity	(Goll *et al.*, 2017)
d_{root}	PFT dependent	-	22	Root fraction in each soil layer per PFT	(Clark *et al.*, 2011)
c_f	-	1 kg P^{-1}	22	Conversion factor	(Goll *et al.*, 2017)
D_z	Depth dependent	m^2 s^{-1}	38	Diffusion coefficient	(Burke *et al*, 2017)
K_{occ}	1.2×10^{-5}	yr^{-1}	33,36	P occlusion rate	(Yang *et al.*, 2014)
K_p	PFT dependent	kg P l^{-1}	22	Scaling uptake ratio	Calibrated
$K_{sorp-in}$	0.0054	kg P m^{-2} yr^{-1}	31	Inorganic P adsorption coefficient	Calibrated (Hou *et al.*, 2019)
$K_{sorp-or}$	0.00054	kg P m^{-2} yr^{-1}	34	Organic P adsorption coefficient	Calibrated
K_{in-max}	0.0075	kg P m^{-2} yr^{-1}	31	Maximum sorbed inorganic P	AFEX
K_{or-max}	0.0042	kg P m^{-2} yr^{-1}	34	Maximum sorbed organic P	AFEX
K_w	3×10^{-6}	kg P m^{-2} yr^{-1}	37	P weathering rate	(Wang *et al.*, 2010)
$resp\_frac$	Pool dependent	kg C m^{-2} yr^{-1}	27	Respiration fraction	(Clark *et al.*, 2011)

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369

2.3 Study sites

370
371 We apply JULES C, CN and CNP to a well-studied site in central Amazonia, where the K34 eddy covariance
372 tower is located (Araújo *et al.*, 2002). This is the main lowland tropical forest site maintained by the National
373 Institute for Amazon Research (INPA). Research at this site focuses on pre-experimental, plot, and full-scale
374 long-term projects, combining experimental approaches (Keller *et al.*, 2004; Malhi *et al.*, 2009) with modelling
375 (Lapola and Norby, 2014). Moreover, a recent manipulation experiment at this site provides an opportunity for
376 future model testing under P fertilization. The K34 site has very similar forest, geomorphology, soil chemistry
377 and species composition to the AFEX site, where the nutrient manipulation experiment takes place and we used
378 the control measurements for model evaluation (Lugli *et al.*, 2021). The average reported annual precipitation is
379 2431 (mm yr^{-1}), with a monthly range of 95 to 304 (mm month^{-1}), and averaged temperature is 26°C (Araújo *et*
380 *al.*, 2002). Moreover, the soil class at this site is Geric Ferrosol with a high clay content and weathering
381 activities (Malhi *et al.*, 2004). The AFEX site has a similar condition to K34 site with a dominant old growth
382 vegetation and a very low P content (Lugli *et al.*, 2021).
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2.4 Model parameterisation, calibration and evaluation

We use observations from the four control plots of the Amazon Fertilization Experiment to parameterise, calibrate and evaluate different processes in JULES (Table 3). The observations were collected at 4 soil depths and processed using the Hedley sequential fractionation (Hedley, Stewart and Chauhan, 1982; Quesada *et al.*, 2010). Observed Leaf Mass per Area (LMA) leaf N and leaf P estimated from fresh leaves were used as input parameters to JULES to estimate photosynthetic capacity and respiration parameters. JULES vn5.5 estimates V_{cmax} (μmol m^{-2} s^{-2}) based on Kattge et al. (2009) using foliar N concentrations in area basis, as follows:

$$V_{cmax} = v_{int} + v_{sl} * nleaf \tag{eq.39}$$

where v_{int} is the estimated intercept and v_{sl} is the slope of the linear regression derived for the V_{cmax} estimation. We incorporated an additional P dependency on the estimation of V_{cmax} following Walker et al. (2014) as follows:

$$\ln(V_{cmax}) = 3.946 + 0.921\ln(N) + 0.121\ln(P) + 0.282\ln(N)\ln(P) \tag{eq.40}$$

Where N and P are foliar concentrations in area basis.

Implementation of eq. 40 resulted in higher V_{cmax} than in the original version of JULES. A higher V_{cmax} predicted higher leaf and plant respiration (eq.41). Constrained by observations of NPP and plant respiration at the study site, we modified one of the most uncertain parameters in the description of plant respiration (f_{dr}) (eq.41) which is the scale factor (f_{dr}) for leaf dark respiration (R_d) as follows:

$$R_d = f_{dr} V_{cmax} \tag{eq.41}$$

The default value for this scale factor is 0.01 (Clark *et al.*, 2011), and for JULES-CNP simulations at our study site it was modified to 0.005.

Observations of aboveground biomass were used to calibrate the non PFT dependent allometric relationships in JULES (Clark et al 2011) (eq 42-44) for leaf ($\mathcal{L}$), root ($\mathcal{R}$) and stem ($\mathcal{W}$) C. Specifically, the a_{wl} parameter (eq 44) was modified from 0.65 to 1.204 to match better tropical forest allometry:

$$\mathcal{L} = \sigma_l L_b \tag{eq.42}$$
$$\mathcal{R} = \mathcal{L} \tag{eq.43}$$
$$\mathcal{W} = a_{wl} L_b{}^{b_{wl}} \tag{eq.44}$$

Where σ_l is specific leaf density (kg C m^{-2} per unit LAI), L_b is balanced (or seasonal maximum) leaf area index (m^2 m^{-2}), a_{wl} is allometric coefficient (kg C m^{-2}) and b_{wl} is allometric exponent.

C:P ratios of leaf and root (measured), and stem (estimated: (Lugli, 2013)) were taken from AFEX and prescribed in JULES to simulate P dynamics in the plant. The following belowground data were used to represent various soil P pools: Resin and bicarbonate inorganic P (inorganic P), organic bicarbonate P (organic P), NaOH organic P (sorbed organic P), NaOH inorganic P (sorbed inorganic P), residual P (occluded P) and HCL P (parent material P) (Table 3). The measurements were collected between 2017 and 2018 under a control treatment. All measurements were conducted at four soil layers (0-5 ,5-10, 10-20, 20-30 cm). However, to be consistent with the JULES model soil layer discretization scheme, we defined 4 soil layers (0-10 cm, 10-30 cm, 30-100 cm and 100-300 cm) and we used the average between 0 and 30 cm to compare against the measurement from the same depth for model evaluation.

In order to cap P sorption and uptake capacity, the maximum sorption capacities (P_{in-max_n}, P_{or-max_n}, eq.31 and 34) were prescribed using observed sorbed inorganic and organic P. Hence, the maximum sorption capacity defines the equilibrium state of sorbed and free-soil P. Moreover, as the magnitude of changes in the occluded and parent material pools are insignificant over a short-term (20 years) simulation period (Vitousek *et al.*, 1997), these two pools were prescribed using observations for these two pools. Remaining parameters used to describe soil P fluxes (eq.s 22 -38) were prescribed using values from the literature (Table 3).

We used a combination of data from AFEX and the nearby site K34 for model evaluation of C fluxes (GPP, NPP) and C pools (soil and vegetation C, leaf, root and stem C) (Table 3).

449
450 **Table 3.** Observations from AFEX (taken during 2017-2018) and from Manaus site K34 used for model parameterisation and evaluation

Process	Variables	Purpose of use	Reference and site
C associated	GPP	Evaluation	Fleischer et al., 2019, K34
	NPP	-//-	Fleischer et al., 2019, K34
	Soil C	-//-	Malhi et al., 2009, K34
	CUE	-//-	Malhi et al., 2009, K34
	Veg C	-//-	AFEX project measurements
	Leaf C	-//-	AFEX project measurements
	Stem C	-//-	AFEX project measurements
	Root C	-//-	AFEX project measurements
	LAI	Initialisation	AFEX project measurements
	LMA	Parameterisation	AFEX project measurements
P associated	Resin	Evaluation	AFEX project measurements
	Pi Bic	Evaluation	-//-
	Po Bic	-//-	-//-
	Po NaOH	-//-	-//-
	Pi NaOH	-//-	-//-
	P residual	Parameterisation	-//-
	P HCL	-//-	-//-
	Leaf N	-//-	-//-
	Leaf P	-//-	-//-
	Root P	-//-	-//-
	Plant C:P ratio	-//-	-//-

451
452 **2.5 JULES simulations**
453
454 JULES was applied at the K34 flux tower site using observed meteorological forcing data from 1999-2019
455 (Fleisher et a 2019) at half hourly resolution. The following meteorological variables are needed to drive JULES
456 (Best *et al.*, 2011): atmospheric specific humidity (kg kg^{-1}), atmospheric temperature (K), air pressure at the
457 surface (Pa), short and longwave radiation at the surface (W m^{-2}), wind speed (m s^{-1}) and total precipitation (kg
458 m^{-2} s^{-1}). Furthermore, the LAI measurements from AFEX were used to initialise the vegetation phenology
459 module. All soil P pools were initialised with AFEX observations. To reach equilibrium between pools and
460 fluxes, JULES-CNP was run 1000 times recycling a 20-year climate (1999-2019) and constant present-day CO_2
461 until reaching steady state (Figure. S1). Finally, the transient run for the period 1999-2019 was then performed
462 using time-varying observed CO_2 and N deposition. Furthermore, the eCO_2 experiment runs for the period 1999-
463 2019 was performed using the transient run forcing data. Note that the spin up was performed separately for
464 three versions of JULES (C/CN/CNP) following the same procedure.
465
466 We evaluate the impact of including a P cycle in JULES using three model configurations (JULES C, CN and
467 CNP). We apply JULES in all three configurations using present day climate under both ambient CO_2 and
468 elevated CO_2 (eCO_2). Ambient and eCO_2 were prescribed following Fleischer *et al.*, (2019), with present-day
469 CO_2 based on global monitoring stations, and a step increase in CO_2 of +200 ppm on the onset of the transient
470 period (i.e., 1999). However, the comparison period is limited to 2017-18 for which the P measurements are
471 available.
472
473 We compare simulated C fluxes (GPP, NPP, litterfall C), C stocks (total vegetation, fine root, leaf, wood, soil)
474 and the CO_2 fertilization effect across model configurations. The CO_2 fertilization effect $\left(CO2_{fert-eff}\right)$ (eq.45)
475 is calculated based on simulated vegetation C under ambient ($VegC\ (aCO_2)$) and eCO_2 ($VegC\ (eCO_2)$) as
476 follows:
477
478 $$CO2_{fert-eff} = \frac{(VegC\ (eCO_2) - VegC\ (aCO_2)) \times 100}{VegC\ (aCO_2)}$$ (eq.45)
479
480 Furthermore, the net biomass increases due to CO_2 fertilization effect ($\Delta Cveg$) is estimated as follows:
481 $$\Delta C_{veg} = \Delta BP - \Delta litterfall\ C$$ (eq.46)
482

483 We studied the Water Use Efficiency (WUE) (eq. 47), as one of the main indicators of GPP changes (Xiao *et*
484 *al.*, 2013), and soil moisture (SMCL), as one of the main controllers of maximum uptake capacity (eq. 22), in
485 order to better understanding the changes in GPP, P demand and uptake as well as exudates fluxes.
486
487 $WUE = GPP/Transpiration$ (eq.47)
488
489 Moreover, we also estimated the Carbon Use Efficiency (CUE) as an indicator of the required C for the growth
490 (Bradford and Crowther, 2013) as follows:
491
492 $CUE = BP/GPP$ (eq.48)
493
494 We use JULES-CNP to evaluate the extent of P limitation under ambient and eCO_2 at this rainforest site in
495 Central Amazon. P limitation is represented by the amount of C that is not fixed by plants due to the insufficient
496 P in the system (exudates) (eq. 22). The exudate flux is highly dependent on the plant P and the overall P
497 availability to satisfy demand. We also explore the distribution of the inorganic and organic soil P and their
498 sorbed fraction within the soil layer and under ambient and eCO_2.
499
500 To test the sensitivity of the P and C related processes to the model P parameters, two sets of simulations were
501 conducted with modified C:P ratio of the leaf, stem, and root pools. These values were prescribed to vary
502 between ±50% of the observed values and their effect on C pools (plant and soil C) and fluxes (NPP and
503 exudates), and P pools (plant, soil, and soil sorbed P) was assessed.
504
505 Our model evaluation period is limited to years 2017-18 due to the P measurement availability. However, in
506 order to perform inter-models comparison with 15 models studied by Fleischer *et al.*, (2019) we also studied the
507 response of GPP, NPP and BP to eCO_2 for both initial (1999) and 15 years periods (between 1999-2013).
508
509 **3.   Results**
510
511 **3.1   Model application under ambient CO_2**
512
513 **3.1.1   Calibration of simulated soil P pools**
514
515 The maximum sorption capacities (P_{in-max_n}, P_{or-max_n}, eq.31 and 34) were calibrated to the observed P pools.
516 As a result, JULES-CNP could reproduce the measured soil p pools (Figure. 2 and Table 4). Simulated
517 inorganic soil P and sorbed organic and inorganic soil P closely matched the observations (Table 5 and Figure.
518 2). However, simulated organic soil P overestimates the observations by 60 %.
519
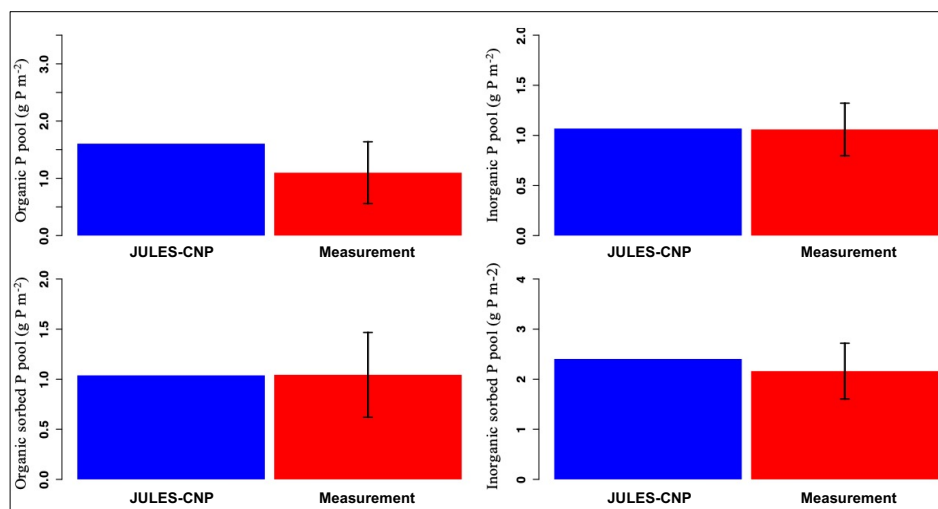
520
521 **Figure. 2-** Modelled vs measured soil phosphorus pools under ambient CO_2 (for the soil depth of 0-30cm). Black line
522 represents standard deviation
523

524 **Table 4.** Observed and simulated phosphorus pools and fluxes. Occluded and weathered P pools were prescribed using the
525 observed values (between period 2017-18).

	Phosphorus pools and fluxes		
	Measured	Modelled Ambient CO_2	Modelled Elevated CO_2
Organic P (g P m^{-2})	1.09±0.53	1.6	1.57
Inorganic P (g P m^{-2})	1.05±0.33	1.07	0.96
Sorbed organic P (g P m^{-2})	1.04±0.42	1.04	1.03
Sorbed inorganic P (g P m^{-2})	2.1±0.55	2.4	2.4
Occluded P (g P m^{-2})	7.98±2.38	prescribed	prescribed
Weathered P (g P m^{-2})	0.59±12	prescribed	prescribed
Total vegetation P (g P m^{-2})	4.15	4.66	5.11
Soil P – 30cm (g P m^{-2})	13.85	14.7	14.56
Total ecosystem P (g P m^{-2})	-	35.97	35.97
P litter flux (g P m^{-2}yr^{-1})	0.3	0.28	0.29

3.1.2 Model evaluation

JULES-CNP could reproduce the plant and soil C pools and fluxes under ambient CO_2 (Figure. 2 and Table 5). Our results show that simulated GPP, is within the range of measurement (3.02 kg C m^{-2} yr^{-1} model vs 3-3.5 kg C m^{-2} yr^{-1} observed, respectively, Table 5).

Simulated NPP, is close to the measured values (NPP: 1.14 - 1.31 observed vs 1.26 modelled kg C m^{-2} yr^{-1}) with autotropic respiration (RESP) also closely following the observations (1.98 observed vs 1.81 modelled kg C m^{-2} yr^{-1}). Biomass production is estimated as a difference between NPP and the amount of C which is not fixed by plants due to the insufficient P in the system (exudates) (eq. 22). The exudate flux is highly dependent on the plant P and the overall P availability to satisfy demand (Table 5). Simulated flux of exudates is 0.3 kg C m^{-2} yr^{-1} under ambient CO_2. In JULES-CNP this flux is subtracted from NPP in order to give the BP (eq. 17) (Table 5). Our simulated litterfall overestimates the observations by 32%, however simulated vegetation and its components (fine root, leaf and wood) and soil C stocks match well the observations (Table 5).

Table 5. Observed and simulated carbon pools and fluxes with JULES_CNP (between period 2017-18)

	Carbon pools and fluxes		
	Measured	Modelled Ambient CO_2	Modelled Elevated CO_2
GPP (kg C m^{-2} yr^{-1})	3.0 – 3.5	3.06	3.9
NPP (kg C m^{-2} yr^{-1})	1.14-1.31	1.27	1.77
Plant respiration (kg C m^{-2} yr^{-1})	1.98	1.78	2.12
Exudates (kg C m^{-2} yr^{-1})	-	0.30	0.81
Biomass Production (kg C m^{-2} yr^{-1})	-	0.96	0.94
Litter C flux (kg C m^{-2} yr^{-1})	0.69	0.91	0.83
Leaf C (kg C m^{-2})	0.37	0.38	0.40
Wood C (kg C m^{-2})	22.01	22.4	24.71
Root C (kg C m^{-2})	0.37	0.38	0.40
Vegetation C (kg C m^{-2})	22.75	23.16	25.52
Soil C stock (kg C m^{-2})	12.7	13.2	12.71
LAI (m^2 m^{-2})	5.6	5.77	6.12

3.1.3 Comparison of JULES C, CN and CNP under ambient CO₂

We compare simulated C pools and fluxes from JULES-C, JULES-CN and JULES-CNP (Figure. 3). There is no difference between C stocks and fluxes in simulations from JULES C and CN indicating that there is no N limitation at this tropical site in the CN simulations. However, simulated BP and litter flux of C by JULES C/CN are higher than in JULES-CNP but also overestimate the observations (litter flux of JULES C/CN: 1.18, JULES CNP: 0.91 and obs 0.69 (kg C m^{-2} yr^{1}) and BP of JULES C/CN: 1.24, JULES CNP: 0.96 and obs1.14-1.31 (kg C m^{-2} yr^{-1}), respectively). By including the P cycling in JULES an exudate flux of 0.3 (kg C m^{-2} yr^{-1}) is simulated, indicating a 24% P limitation to BP at this site according to JULES CNP, which represents a 29% decrease in BP compared to JULES-C/CN. Consequently, the total vegetation C stock for models without P inclusion is higher than the CNP version (+3% difference) due to the lack of representation of P limitation. The simulated soil C stock in JULES C and JULES CN is also higher than in the CNP version (JULES C/CN: 13.93 vs. JULES CNP: 13.18 (kg C m^{-2} yr^{-1})) and higher than the observations. Moreover, CUE in JULES C/CN (eq.42) is higher than observations and JULES CNP version (JULES C/CN: 0.38 vs. JULES CNP: 0.31, obs: 0.34 ±0.1(dimensionless).
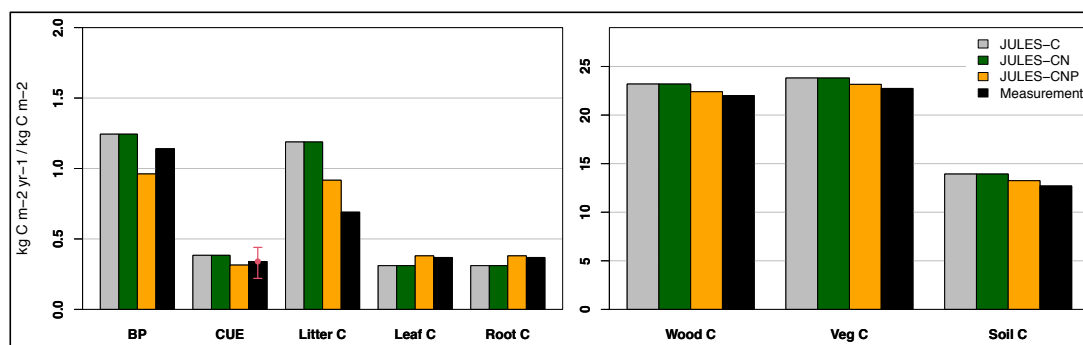
Figure. 3- JULES C, CN, CNP modelled vs measured C pools (in kg C m^{-2}) and fluxes (in kg C m^{-2} yr^{-1}) under ambient CO₂. Note that CUE is unitless.

3.1.4 Model sensitivity to C:P stoichiometry

Model sensitivity to plant C:P stoichiometry was tested at ±50% change from default values. The results indicate that among all the corresponding C and P pools and fluxes, the exudate flux -which determines P limitation to NPP - shows the highest sensitivity to changes in C:P ratios. The decrease of the plant C:P results in a large increase in exudates. This is due to the higher plant P demand as a result of lower plant C:P ratios. Since the total P in the system is lower than the plant demand, higher P limitation is placed on C fixation (decreasing BP) which results in an increase in exudates (Figure. 4) but also causes a decrease in soil C which is a result of the lower fixed C by the plants. Moreover, total soil P shows low sensitivity to changes in plant C:P, and total plant C and soil sorbed P pools show no sensitivity to plant C:P ratios.
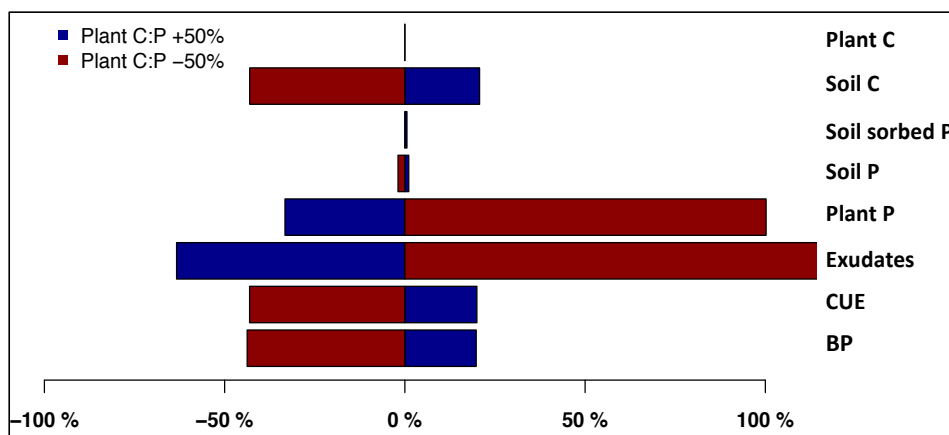
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Figure. 4- Model sensitivity test results and corresponding C and P pools and fluxes under ambient CO_2.

3.2 Model application under elevated CO_2

3.2.1 Simulated plant and soil C and P pools and fluxes -JULES CNP: eCO_2 vs ambient CO_2

The eCO_2 simulation using JULES CNP yields a higher GPP compared to the ambient CO_2 (0.83 (kg C m^{-2} yr^{-1}) increase), as a result of CO_2 fertilization. Moreover, due to the GPP increase, NPP and RESP follows the same trend and increased compared to ambient CO_2 (NPP: 0.49 and RESP:0.3 (kg C m^{-2} yr^{-1}) increase) (Table 5). The total simulated vegetation C pool increases under eCO_2 compared to ambient CO_2 (0.41 kg C m^{-2}), hence the estimated plant P (estimated as a fraction of C:P ratios) increases as well (+0.45 (g P m^{-2})) (Fig 6, Table 4). Thus, the simulated plant P demand is higher, and as the total available soil P for uptake is limited, the simulated exudate flux increases to 0.51(kg C m^{-2} yr^{-1}). Moreover, despite the higher NPP under eCO_2 compared to simulated NPP under ambient CO_2, due to the substantial increase in simulated exudates, the BP is similar to the ambient CO_2 (2% difference).

The simulated organic soil P under eCO_2 yields close to the ambient CO_2 (1.6 g P m^{-2}) (Table 5). This is due to the same parameterization of the output fluxes from this pool for eCO_2 and ambient CO_2. The simulated pool of inorganic P under eCO_2 decreases compared to the ambient CO_2 by 0.11 (g P m^{-2}) due to the increased plant P pools and slight increase in uptake (+0.13 %).

However, the simulated sorbed organic and inorganic soil P from eCO_2 are similar to those simulated under the ambient CO_2 which is due to the same parameterizing of sorption function (maximum sorption capacity) from the ambient CO_2 run as explained in calibration section. Moreover, the modelled occluded and weathered soil P yield similar to those in the ambient CO_2 simulation (Table 5) which is due to the same prescribed observational data that was used for this simulation.

3.2.2 Comparison of JULES C, CN and CNP under elevated CO_2

JULES C/CN show higher vegetation and soil C pools, BP and litter flux compared to JULES-CNP: (Table 6, Figure. S2). Under eCO_2, simulated NPP using JULES C-CN is 4.5% higher than JULES CNP and the BP with JULES- C/CN is 96.8% higher than in JULES-CNP which simulates an exudates flux of 0.81 (kg C m^{-2} yr^{-1}) equivalent to 46% P limitation under eCO_2. As a result of P limitation and eCO_2, the simulated CO_2 fertilization effect estimated based on changes in biomass under ambient and eCO_2 was reduced from 13% with JULES-C/CN to 10% JULES-CNP. Moreover, the CUE from JULES C/CN is 87.5% higher than the JULES CNP as a result of high P limitation over biomass production.

15

Table 6. C pools and fluxes using JULES C/CN and difference in percentage with JULES CNP model under eCO_2. A positive % means larger respective values simulated with JULES C and JULES CN than with JULES CNP (between period 2017-18).

	GPP	NPP	BP	CUE	Litter C	Leaf C	Root C	Wood C	Soil C
JULES C/CN	4.1	1.85	1.85	45%	1.77	0.42	0.42	26.1	19.2
JULES CNP	3.9	1.77	0.94	24%	0.83	0.4	0.4	24.71	12.71
ΔC/CN: CNP	5.1%	4.5%	96.8%	87.5%	113.3%	5%	5%	5%	51.1%

3.2.2.1 Inter-models under elevated CO_2

Following Fleischer *et al.*, (2019), we report the simulated response to eCO_2 for year 1999 (initial: CO2 effect) and 1999-2013 (15 years: final effect) which are different than our evaluation period (2017-18). Using JULES C and JULES CN under eCO_2, simulated GPP and NPP during the 1st year increase by 30% and 61% respectively and by 28% and 52% after 15 years (Figure. 5). However, using JULES CNP, eCO_2 increases simulated GPP, NPP and BP responses during the 1st year by 29%,51% and 20% and by 28%, 43% and 7%, after 15 years respectively.

Corresponding simulated CUE during the 1st year and 15 years shows an increase of 24% and 20% in response to eCO_2 using JULES C/CN respectively. However, using JULES CNP, simulated CUE for the 1st and after 15 years is reduced by 7% and17% in response to eCO_2.

Simulated total biomass (leaf, fine root and wood C) ($\Delta Cveg$) using JULES C/CN for the 1st and 15 years of eCO_2 increases by 9% and 13% respectively. However, using JULES CNP $\Delta Cveg$ only increases by 0.5% and 9% for 1st and 15 years of eCO_2, respectively.
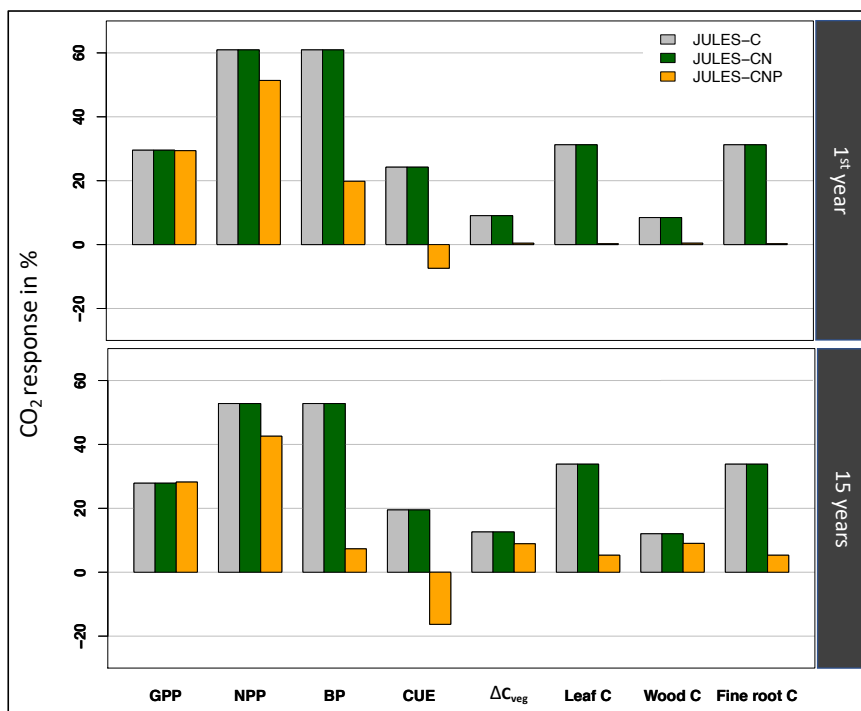
Figure. 5- Relative effect of eCO_2 on simulated GPP, NPP, BP, CUE, $\Delta Cveg$, leaf C, wood C and fine root C, using three versions of JULES model in 1st (initial response) and 15 years periods (final response).

16

3.3 Plant P Demand, uptake and exudates under ambient and elevated CO_2

To understand further the CP-cycle dynamics, we studied the monthly averaged plant P demand and the relative (limited) P uptake (eq. 21) under both ambient and elevated CO_2 conditions (Figure. 6).

Under ambient CO_2 condition the highest GPP is estimated at 3.5±0.19 kg C m^{-2} yr^{-1} in July and the lowest at 2.06±0.61kg C m^{-2} yr^{-1} in October (Figure. 6-a). The estimated WUE and SMCL in October is among the lowest estimated monthly values at 2.3±0.51 kg CO_2/kg H_2O and 526.2±31 kg m^{-2} respectively (Figure. 6-c). The highest P demand is estimated at 0.4±0.02 g P m^{-2} yr^{-1} in July and the lowest demand at 0.2±0.08 g P m^{-2} yr^{-1} in October. Consequently, the highest and lowest uptake (0.32±0.01 and 0.19±0.07 g P m^{-2} yr^{-1}, respectively). The exudates for the highest and lowest GPP and demand periods are estimated at 0.4±15 and 0.04±0.07 kg C m^{-2} yr^{-1}, respectively.

However, similar to ambient CO_2, under eCO_2 condition the highest estimated GPP is in July at 4.36±0.21 kg C m^{-2} yr^{-1} and lowest for October 3.02±0.75 kg C m^{-2} yr^{-1} (Figure. 6-b). The estimated WUE and SMCL for the lowest GPP period is among the lowest monthly estimated values at 3.5±0.74 kg CO_2/kg H_2O and 552±33 kg m^{-2} for October respectively (Figure. 6-d). The highest P demand is estimated for July at 0.51±0.02 g P m^{-2} yr^{-1} with the uptake flux of 0.31±0.02 g P m^{-2} yr^{-1} and the lowest demand is estimated for October at 0.32±0.1 g P m^{-2} yr^{-1} with the estimated uptake flux of 0.26±0.06 g P m^{-2} yr^{-1}. The highest exudate flux is also for July at 1.01±0.17 kg C m^{-2} yr^{-1} and lowest for October 0.27±0.29 kg C m^{-2} yr^{-1}, respectively.

However, despite the P limitation in both eCO_2 and ambient CO_2 conditions, the P uptake flux under eCO_2 is higher than the ambient CO_2 condition. This is due to the higher WUE and increased soil moisture (SMCL) (controlling uptake capacity (eq. 22)) under eCO_2 condition, hence more water availability during the dry season to maintain productivity and critically transport P to the plant (see eq. 22), compared to ambient CO_2 condition (Figure. 6-c and d).
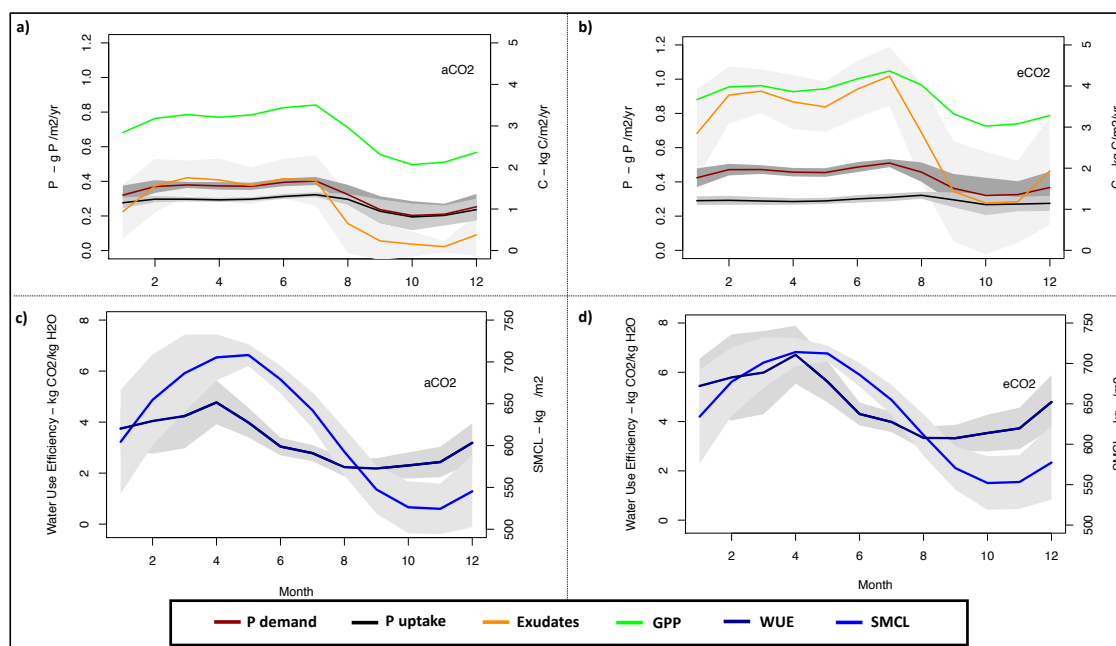
Figure. 6- Simulated monthly plant P demand and uptake (g P m^{-2} yr^{-1}), exudates and GPP (kg C m^{-2} yr^{-1}) under a) aCO_2 and b) eCO_2, water use efficiency (g m^{-2} yr^{-1}) under c) ambient CO_2 (aCO_2) and d) eCO_2 conditions. The grey area represents the standard deviation.

685 ### 3.4 Soil P pools profile under ambient CO_2 and elevated CO_2
686
687 We explored the distribution of the inorganic and organic soil P and their sorbed fraction within the soil layers
688 and under different CO_2 conditions (Figure. S3). Both the ambient and eCO_2 simulations have a close inorganic
689 soil P distribution at the topsoil layer (0-30cm) (0.85 vs. 0.9 (g P m^{-2}) respectively) as well as similar organic
690 soil P distribution (0.85 vs 0.9 (g P m^{-2}) respectively) which is in line with the observational study by Tian *et al.*,
691 (2017).
692
693 However, the organic soil P and sorbed forms of inorganic and organic soil P profiles are not changing
694 significantly between different sets due to the similar parameterization of the processes that control these pools
695 (processes which are related to the physical aspects of soils, hence not changing under eCO_2 condition) and the
696 same parameter values used for both ambient and eCO_2 runs.
697
698 Moreover, the soil P within 30cm soil depth for ambient and eCO_2 conditions is at 14.7 (g P m^{-2}) and 14.56 (g P
699 m^{-2}) respectively, and the total ecosystem P for both ambient and eCO_2 conditions is at 35.97 (g P m^{-2}).
700 However, the slightly lower soil P in the eCO_2 condition is due to the higher plant P demand compared to the
701 ambient condition, hence the higher allocated P vegetation (10%) under eCO_2 condition.
702
703
704 ### 4. Discussion
705
706 Studies show the significant role of the tropical forests, and Amazonia in particular, in C uptake and regulating
707 atmospheric CO_2 (Brienen *et al.*, 2015; Phillips *et al.*, 2017). As soil P availability is low in the majority of
708 Amazonia (Quesada *et al.*, 2012), the competition in both plant and soil communities is high (Lloyd *et al.*,
709 2001). Therefore, the responses of these communities to eCO_2 under P limited conditions are still unclear
710 (Fleischer *et al.*, 2019). Hence, we included the P cycling representation in JULES model to improve the
711 carbon-nutrients feedbacks and study the responses under ambient and eCO_2 conditions in a well-documented
712 low fertility site which is representative of about 60% of Amazon soils (Quesada *et al.*, 2010). Our new
713 developments include in detail all the major P processes in both plant and soil pools and can be applied to the
714 Amazon region using existing soil (Quesada *et al.*, 2011) and foliar structural and nutrient (Fyllas *et al.*, 2009)
715 data for parameterisation.
716
717 ### 4.1. Evaluation of model performance against observations
718
719 JULES-CNP could reproduce the magnitude of plant and different forms of soil P pools and fluxes. The relative
720 distribution of total organic P, total inorganic P and residue P fractions of total P in soils under Brazilian
721 Eucalyptus plantations (Costa *et al.*, 2016) shows inorganic P fraction of 28% from total soil P which is close to
722 our estimation of 24% and organic P fraction of 30% from total soil P which is higher than our estimated
723 fraction of 18%. Thus, we may need to improve the process representation or parameters that control the organic
724 P concentration, such as litter flux and decomposition, soil organic P mineralization, and immobilization in the
725 future.
726
727 Our estimated maximum P uptake, which represents the actual available P for plant uptake (Wang and Goll,
728 2021), for both ambient and eCO_2 conditions, is highly correlated with the plant P demand (R^2 = 0.96 and 0.52
729 respectively). The plant P demand depends on the GPP changes which are reflected by the WUE (Hatfield and
730 Dold, 2019). Hence, under ambient CO_2, JULES CNP simulates lower GPP and plant P demand during the dry
731 season than during the wet season. Sufficient P uptake during these periods results in the lowest P limitation,
732 thus the lowest simulated exudates. Nevertheless, under eCO_2 the same pattern is simulated but a higher
733 availability of soil P due to the stomatal closure in the dry season. Hence, due to the plant's more efficient water
734 usage, the soil moisture in the dry season is higher (Xu *et al.*, 2016) which impacts our capped P uptake flux (eq.
735 22) and increases the uptake capacity respectively.
736
737 Overall, JULES-CNP reproduced the observed C pools and fluxes which are in the acceptable ranges compared
738 to the measurements. However, using the JULES default V_{cmax} estimation method (eq. 39), the model slightly
739 underestimates the total GPP (2.9 kg C m^{-2} yr^{-1} vs. 3-3.5 kg C m^{-2} yr^{-1}). Therefore, in this version of the model,
740 we used the improved V_{cmax} estimation method based on N and P (eq. 40) which resulted a final estimated GPP
741 closer to the measurements (3.06 kg C m^{-2} yr^{-1}).
742
743

744 Our results show an increase in GPP (21%) in response to eCO$_2$ which is higher than the average increase of
745 GPP reported in mature eucalyptus forests (11%), also growing under low P soils at the free air CO$_2$ enrichment
746 experiment (EucFACE) facility in Australia (Jiang *et al.*, 2020). This can be related to the lower decrease of
747 biomass growth response estimated by JULES-CNP (-3%) compared to the measurements from mature forests
748 (-8%) (Ellsworth *et al.*, 2017), due to the P limitation which showed to impact the above-ground biomass
749 growth response in mature forests (Körner *et al.*, 2005; Ryan, 2013; Klein *et al.*, 2016).
750
751 In order to estimate the biomass production (BP), we deducted the exudates fluxes from the NPP. Using JULES
752 C/CN models our estimated biomass productivity enhancement due to eCO$_2$ (49%) is in the middle range of the
753 reported various studies from different biomes by Walker *et al.*, (2021). Moreover, our estimated difference of
754 BP between ambient and eCO$_2$ conditions (2%) is close to the estimated difference for mature forests (3%)
755 (Jiang *et al.*, 2020).
756
757 A global estimation for tropical forests using CASACNP model which includes N and P limitations on
758 terrestrial C cycling, shows that NPP is reduced by 20% on average due to the insufficient P availability (Wang,
759 Law and Pak, 2010) which is close to our estimated P limitation of 24%. This finding is in line with
760 experimental study that shows a strong correlation between the total NPP and the soil available P (Aragão *et al.*,
761 2009). Nevertheless, our model show that the P limitation mimics the same response to the CO$_2$ fertilization
762 similar to sites in pool soils (see ZAR-01 site in Aragão *et al.*, (2009)). The estimated decrease of NPP in
763 response to eCO$_2$ as a result of P limitation is in line with the findings from CLM-CNP model at five tropical
764 forests (Yang *et al.*, 2014) which indicates the CO$_2$ fertilization dependency on the processes that affect P
765 availability or uptake.
766
767 Our estimated CUE (0.31) is close to the estimation by Jing *et al.* (2020) for mature forests (0.31±0.03), as well
768 as to the measurement for our study site (0.34 ±0.1). There is currently a lack of representation of stand age in
769 JULES-CNP which can significantly change this ratio (e.g. mature trees are less responsive to the nutrient
770 limitations) (De Lucia *et al.*, 2007; Norby *et al.*, 2016). However, a recent development of Robust Ecosystem
771 Demography (RED) model into JULES (Argles *et al.*, 2020) and its integration into JULES-CNP in the future
772 can resolve this issue.
773
774 **4.2. Inter-models comparison**
775
776 The comparison of simulated GPP enhancement across JULES versions for the 1st year is within the middle
777 range of the 1st year CO$_2$ responses of the C/CN models studied by Fleischer *et al.*, (2019) evaluating simulated
778 eCO$_2$ effects at a site in Manaus using the same meteorological forcing and methodology used in this study for
779 a range of DGVM's. However, comparison for 15 years of eCO$_2$, shows that the simulated response with
780 JULES CNP is on the higher end of Fleischer *et al.*, (2019) study which is due to the higher estimated biomass
781 growth by JULES CNP (Table S1). Similarly, using JULES CNP our estimated GPP enhancement is on the
782 higher end of model estimations in Fleischer *et al.*, (2019). Moreover, comparing the GPP responses between
783 different versions of (JULES C/CN and CNP), the JULES CNP shows a slightly higher response to CO$_2$
784 fertilization associated with the higher WUE changes (Xiao *et al.*, 2013) (Figure. S4). This is due to the higher
785 sensitivity of the plant to water availability than the P availability in the P limited system (He and Dijkstra,
786 2014). Hence, under eCO$_2$ due to water-saving strategy of plants and stomatal closure (Medlyn *et al.*, 2016),
787 simulated transpiration is decreased (Sampaio *et al.*, 2021) and photosynthesis is enhanced compared ambient
788 CO$_2$.
789
790 To that end, the monthly changes of WUE in JULES CNP are highly correlated to the GPP, hence the lowest
791 and highest WUE follow the same periods as GPP similar to responses captured with models studied by
792 Fleischer *et al.*, (2019) (Table. S1).
793
794 Our estimated NPP enhancement using JULES C/CN models for both 1st and 15 years period is within the
795 middle range of the models in Fleischer *et al.*, (2019). Nevertheless, JULES CNP response of BP is in the lower
796 band of the CNP models by Fleischer *et al.*, (2019) and close to the estimations from CABLE (Haverd *et al.*,
797 2018) and ORCHIDEE (Goll *et al.*, 2017) models, which may be due to the similar representation of P processes
798 and limitation between these models. However, our results show a 29% decrease in NPP using JULES-CNP
799 compared to JULES-C/CN which is smaller than the differences between the CLM-CNP and CLM-CN versions
800 (51% decrease) (Yang *et al.*, 2014). The lower estimated decrease in JULES highlights the need to further study
801 the fully corresponding plant C pools and fluxes to the changes in soil and plant P. Therefore, future work
802 should be focused on the improvement of the total P availability and the plant C feedbacks. Moreover, there are

803   other environmental factors such as temperature which shows a possible impact on the CO_2 elevation and the
804   changes of NPP (Baig *et al.*, 2015) which needs further improvement in our model.
805   The CUE estimations of 1st year and 15 years response to CO_2 elevation from JULES C/CN are in the middle
806   range of C/CN models in Fleischer *et al.*, (2019). However, the estimated CUE using JULES CNP for 1st and 15
807   years are in the low range of CNP models reported by Fleischer *et al.*, (2019) which is due to the same reason
808   discussed for NPP comparison.
809
810   Finally, our estimated total biomass enhancement (ΔC*veg*) using JULES C/CN for the 1st and 15 years are in the
811   middle range of C/CN models from Fleischer *et al.*, (2019) and in lower range of CNP models from Fleischer *et
812   al.*, (2019) using JULES CNP. Nevertheless, while JULES-CNP includes the trait-based parameters (Harper *et
813   al.*, 2016), other functions such as flexible C allocation and spatial variation of biomass turnover are still
814   missing and future model improvement should be focused on their inclusion.
815
816
817   **5.   Conclusion**
818
819   Land ecosystems are a significant sink of atmospheric CO_2, ergo buffering the anthropogenic increase of this
820   flux. While tropical forests contribute substantially to the global land C sink, observational studies show that a
821   stalled increase in carbon gains over the recent decade (Brienen *et al.*, 2015; Hubau *et al.*, 2020). However
822   modelling studies that lack representation of P cycling processes predict an increasing sink (Fernández-Martínez
823   *et al.*, 2019; Fleischer *et al.*, 2019). This is particularly relevant for efforts to mitigate dangerous climate change
824   and assumptions on the future efficacy of the land C sink. Therefore, in this study, we presented the full
825   terrestrial P cycling and its feedback on the C cycle within the JULES framework. Our results show that the
826   model is capable of representing plant and soil P pools and fluxes at a site in Central Amazon. Moreover, the
827   model estimated a significant NPP limitation under ambient CO_2, due to the high P deficiency at this site which
828   is representative of Central Amazon, and elevated CO_2 resulted in a further subsequent decrease in the land C
829   sink capacity relative to the model without P limitation. While our study is a corner stone for full nutrient
830   cycling representation in ESMs, it can also help the empirical community to test different hypotheses (i.e.,
831   dynamic allocation and stoichiometry) and generate targeted experimental measurements (Medlyn *et al.*, 2015).
832
833   *Code and data availability*

844   *Author contributions.* MAN, LMM, SS, SEC, CAQ, AJW, IAP, KMA and DBC developed the model, per-
845   formed simulations and analysis. CAQ, FVC, RP, LFL, KMA, GR, LS, ACMM, JSR, RA and JLC provided the
846   measurements for the model parasitisation and evaluation. MAN, LMM, SS, IAP, SEC, FVC, RP, LFL, KMA
847   and DBC contributed in writing the manuscript.

848
849   *Competing interests.* The authors declare no competing interests
850

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