

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 nitrogen (N) limitation on ecosystem productivity. However only few of these models have incorporated phosphorus (P) cycling. In tropical ecosystems, this is likely to be 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 CO₂ 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 develop and evaluate JULES-CNP using in situ data collected at a low fertility site in the Central Amazon, with a soil P content representative of 60% of soils across the Amazon basin, to parameterise, calibrate and evaluate JULES-CNP. Novel soil and plant P pool observations are used for parameterisation and calibration and the model is evaluated against C fluxes and stocks, and for those soil P pools not used for parameterisation/calibration. We then evaluate the model at additional P limited test sites across the Amazon, in Panama and Hawaii showing a significant improvement over the C and CN only versions of the model. The model is then applied under elevated CO₂ (600 ppm) at our study site Central Amazon to quantify the impact of P limitation on CO₂ fertilization. We compare our results against current state of the art CNP models using the same methodology that was used in the AmazonFACE model intercomparison study. The model is able to reproduce the observed plant and soil P pools and fluxes used for evaluation under ambient CO₂. We estimate P to limit net primary productivity (NPP) by 24% under current CO₂ and by 46% under elevated CO₂. Under elevated CO₂, biomass in simulations accounting for CNP increase by 10% relative to contemporary CO₂ conditions, although it is 5% lower compared with CN and C-only simulations. Our results highlight the potential for high P limitation and therefore lower CO₂ fertilization capacity in the Amazon forest with low fertility soils.

1. Introduction

Land ecosystems currently take up about 30% of anthropogenic CO₂ emissions (Friedlingstein *et al.*, 2020), thus buffering the anthropogenic increase in atmospheric CO₂. Tropical forests play a major role in the land 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 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 CO₂ 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 nitrogen 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 (Bentsen *et al.*, 2013; Long *et al.*, 2013; Ji *et al.*, 2014). 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 (ACCESS-ESM1.5 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 (Vitousek *et al.*, 1997, 2010; Hou *et al.*, 2020), unlike temperate forest where N is hypothesised to be the main constraint (Aerts and Chapin, 1999; Luo *et al.*, 2004). 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. Although N limitation can impact the terrestrial C sink response to increasing atmospheric CO₂ by changing plant C fixation capacity (Luo *et al.*, 2004), this can be partially ameliorated over time by input of N into the biosphere via the continuous inputs of N into ecosystems from atmospheric deposition and biological N fixation (Vitousek *et al.*, 2010). P-limitation is pervasive in natural ecosystems (Hou *et al.*, 2020) and the lack of large P inputs into ecosystems, especially those growing on highly weathered soil, may make P limitation a stronger constraint on ecosystem response to elevated CO₂ (eCO₂) than N (Gentile *et al.*, 2012; Sardans, Rivas-Ubach and Peñuelas, 2012). 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, one possible reason being the lack of inclusion of soil P constraints on plant productivity and function (Wang, Law and Pak, 2010; Vicca *et al.*, 2012a; Yang *et al.*, 2014). Nevertheless, some modelling studies have 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 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.

So far, several dynamic global vegetation models have been developed to represent P cycling within the soil (Yang *et al.*, 2013; Haverd *et al.*, 2018) and between plant and soils for tropical forests particularly (Yang *et al.*,

106 2014; Zhu *et al.*, 2016; Goll *et al.*, 2017). Furthermore, a comprehensive study included several models with C-
107 N-P cycling and their feedbacks on the atmospheric C fixation and biomass growth in Amazon forests under
108 ambient and elevated CO₂ conditions (eCO₂) (Fleischer *et al.*, 2019). Despite these developments, data to
109 underpin them and their projections, particularly for the tropics, is sparse and remains challenging particularly
110 for the Amazon forest (Reed *et al.*, 2015; Jiang *et al.*, 2019). Moreover, due to the lack of detailed
111 measurements, the P-related processes such as ad/desorption and uptake represented in these models are under-
112 constrained and likely oversimplified, thus the future predictions of Amazon forest responses to eCO₂ and
113 climate change are uncertain. To fill this gap, in this study, we use data collected as part of the Amazon
114 Fertilization Experiment (AFEX), the first project that focuses on experimental soil nutrient manipulation in the
115 Amazon, with a comprehensive data collection program covering plant ecophysiology, C stocks and fluxes, soil
116 processes including P stocks. Thus, our model parameterization compared to prior P modelling studies includes
117 detailed P processes representation using the site measurements.

118
119 Here, we describe the development and implementation of the terrestrial P cycle in the Joint UK Land
120 Environment Simulator (JULES) (Clark *et al.*, 2011), the land component of the UK Earth System Model
121 (UKESM), following the structure of the prior N cycle development (Wiltshire *et al.*, 2021) and utilising state of
122 the art already tested and implemented descriptions of P cycling in other land surface models (Wang, Houlton
123 and Field, 2007; Zhu *et al.*, 2016; Goll *et al.*, 2017).

124 The model (JULES-CNP) is parameterized and calibrated using novel in situ P soil and plant data from a well-
125 studied forest site in Central Amazon near to Manaus, Brazil with soil P content representative of 60% of soils
126 across the Amazon basin. The new developed P component estimates the sorption of the soil organic and
127 inorganic P based on the saturation status of the adsorbed P pools, which is unique compared to the other
128 existing P models and enable more realistic estimation of P ad/desorption processes. We first evaluate the model
129 at our study site but also at additional five test sites across the Amazon, in Panama and Hawaii. We then apply
130 the model under ambient and eCO₂ following the protocol of Fleischer *et al.*, (2019) to predict nutrient
131 limitations on land biogeochemistry under these conditions. Predictions of the CO₂ fertilization effect in JULES-
132 CNP are compared to those in current versions of the model with coupled C and N cycles (JULES-CN) and with
133 C cycle only (JULES-C).

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136 2. Material and methods

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139 2.1 JULES

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142 JULES is a process-based model that integrates water, energy, C cycling (JULES-C) (Clark *et al.*, 2011) and N
143 cycling (JULES-CN) (Wiltshire *et al.*, 2021) between the atmosphere, vegetation and soil (Best *et al.*, 2011;
144 Clark *et al.*, 2011). Vegetation dynamics are represented in JULES using the TRIFFID model, using nine
145 distinct plant functional types (PFTs) (tropical and temperate broadleaf evergreen trees, broadleaf deciduous
146 trees, needle-leaf evergreen and deciduous trees, C3 and C4 grasses, and evergreen and deciduous shrubs), as
147 well as height competition (Harper *et al.*, 2016). Leaf-level photosynthesis (Collatz *et al.*, 1991; Collatz, Ribas-
148 Carbo and Berry, 1992) is scaled to estimate canopy level Gross Primary Productivity (GPP) using a multilayer
149 approach that accounts for vertical variation of radiation interception and partition of sunlit and shaded leaves
150 and associated vertical variation of leaf N and P -exponential decrease through the canopy (Clark *et al.*,
151 2011; Mercado *et al.* 2007, Mercado *et al.* 2009) - while the C:P and N:P ratios remain the same. NPP is estimated
152 as the difference between GPP and autotrophic respiration for each living tissue (leaf, wood, root). NPP is then
153 allocated to increase tissue C stocks and to spread, i.e., expand the fractional coverage of the PFT. The resultant
154 PFT fractional coverages also depend on competition across PFTs for resources, e.g., light. Tissue turnover and
155 vegetation mortality add C into the litter pools. Representation of soil organic C (SOC) follows the Rothamsted
156 Carbon model RothC equations (Jenkinson *et al.*, 1990; Jenkinson and Coleman, 2008) defining four C pools:
157 decomposable plant material (DPM) and resistant plant material (RPM), which receive direct input from
158 litterfall, and microbial biomass (BIO) and humified material (HUM) which receive a fraction of decomposed C
159 from DPM and RPM which is not released to the atmosphere. The limitation of N on SOC is applied to the
160 vegetation and soil components using a dynamic C:N ratio to modify the mineralization and immobilization
161 processes as described in Wiltshire *et al.*, (2021). Note that the soil component of JULES-CN can be run either
162 as a single box model or vertically resolved over soil depth (JULES-CN layered), and in this paper we build
163 upon the vertically resolved version described in Wiltshire *et al.* (2021).

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2.2 JULES-CNP

JULES-CNP includes the representation of the P cycle in JULES version (vn5.5) and it is built on existing and well tested representations of P cycling in other global land surface models (Wang, Houlton and Field, 2007; Yang *et al.*, 2014; Goll *et al.*, 2017; Sun *et al.*, 2021). It includes P fluxes within the vegetation and soil components, and the specification of P pools and processes related to P cycling within the soil column (Fig. 1). A parent material pool is introduced to consider the input of weathered P. The adsorbed, desorbed and occluded fractions of P for both organic and inorganic P are also represented. However, except for parent material and occluded P pools, all other pools are estimated at each soil layer. The description of changes in pools and associated relative fluxes are explained in detail in the next sections. Although JULES-CN includes N leaching and deposition, P leaching and deposition are not included in the current version of JULES-CNP.

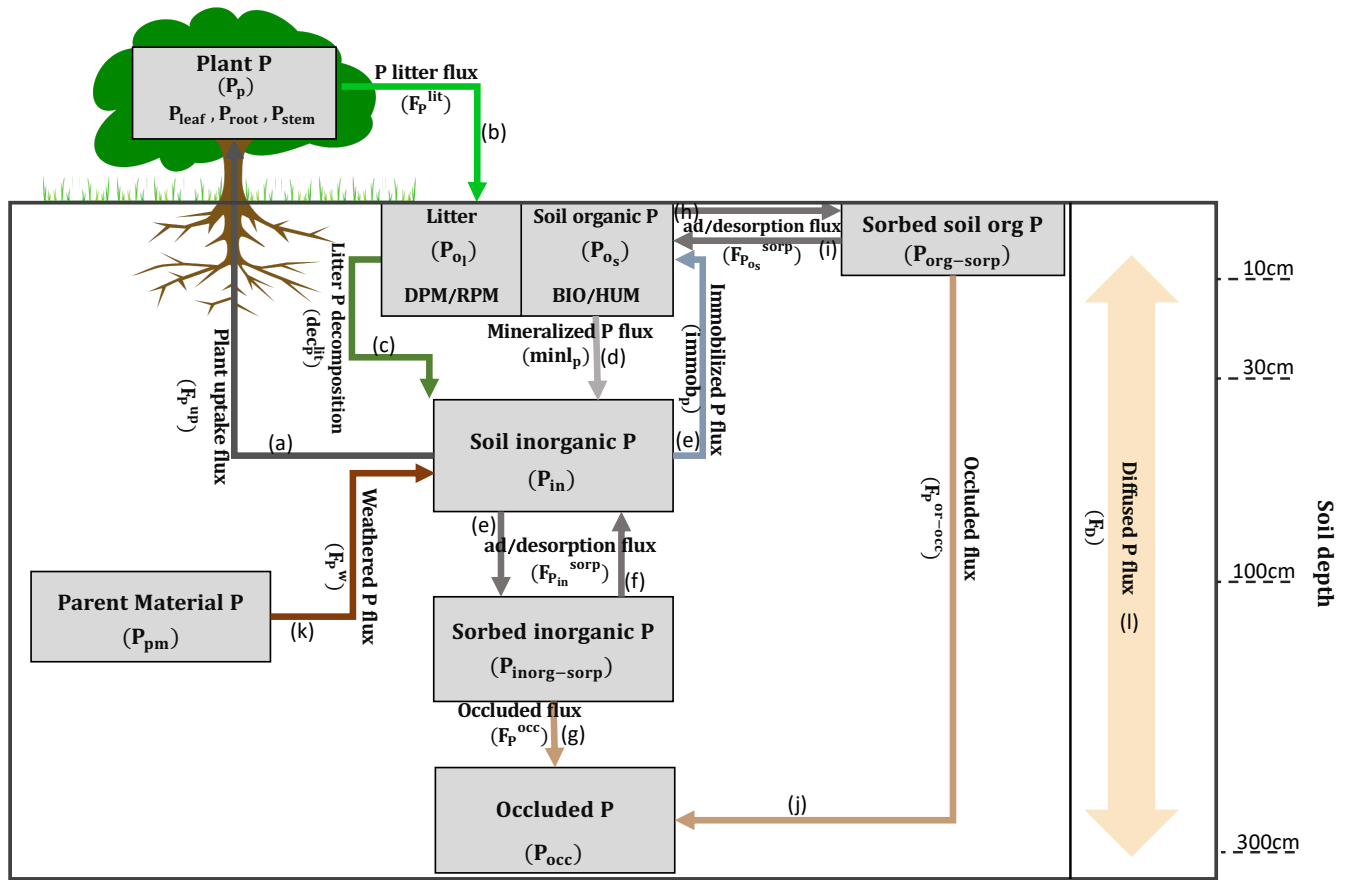


Figure.1 – JULES-CNP model scheme including P pools (grey boxes) and fluxes (arrows)

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2.2.1 P pools

JULES represents eight P pools comprising organic and inorganic P: plant P (P_p) and soil P pools (in each soil layer (n)), litter P (P_{0l}), soil organic P (P_{0s}), soil inorganic P (P_{in}), organic sorbed ($P_{org-sorp}$), inorganic sorbed ($P_{inorg-sorp}$), parent material (P_{pm}) and occluded (P_{occ}) P comprised of both organic and inorganic P. All pools are in units of kg P m^{-2} (Fig 1, Tables 1 and 2).

Plant P pool is composed of leaf (P_{leaf}), fine root (P_{root}) and stem together with coarse root (P_{stem}), which are related to their associated C pools (C_{leaf} , C_{root} , C_{stem}) in (kg C m^{-2}) and fixed C to P ratios ($C:P_{leaf}$, $C:P_{root}$, $C:P_{stem}$) as follows:

$$P_{leaf} = \frac{C_{leaf}}{C:P_{leaf}} \quad (\text{eq.1})$$

195 $P_{root} = \frac{C_{root}}{C:P_{root}}$ (eq.2)

196
197 $P_{stem} = \frac{C_{stem}}{C:P_{stem}}$ (eq.3)

198
199 Therefore, the plant P pool (P_p) is the sum of all vegetation P pools as follows:

201 $P_p = P_{leaf} + P_{root} + P_{stem}$ (eq.4)

202
203 Description of the plant P pool (P_p) follows Zhu *et al.*, (2016) and is estimated as the difference between the
204 input, plant uptake F_p^{up} (eq.26) and output of this pool, plant litter flux F_p^{lit} (eq.28), with both fluxes
205 expressed in kg P m⁻² yr⁻¹ as follows:

206
207 $\frac{dP_p}{dt} = F_p^{up} - F_p^{lit}$ (eq.5)

208
209 The litter P pool (P_{ol}) is estimated as a sum of P_{DPM} and P_{RPM} pools over soil layers (n). Each pool is formed by
210 the fluxes of plant litter input (F_p^{lit}) and the outgoing decomposed P (dec_p^{lit}) both expressed in kg P m⁻² yr⁻¹
211 (eq.28-29). Furthermore, the plant litter input is modified based on the plant type material ratio α (in order to
212 distribute the litter input based on the DPM/RPM fraction) as follows:

214 $\frac{dP_{DPM}}{dt} = F_{P_n}^{lit} \times \alpha - dec_{P_{DPM},n}$ (eq.6)

215
216 $\frac{dP_{RPM}}{dt} = F_{P_n}^{lit} \times (1 - \alpha) - dec_{P_{RPM},n}$ (eq.7)

217
218 $P_{ol} = \sum_{n=1}^N P_{DPM,n} + \sum_{n=1}^N P_{RPM,n}$ (eq.8)

219
220 The soil organic pool (P_{os}) is represented as the sum of P_{BIO} and P_{HUM} . These pools are estimated from the
221 difference between P inputs from total immobilized (F_{immob_p}) distributed between BIO and HUM based on
222 fixed fraction (0.46 for BIO, 0.54 for HUM) (Jenkinson *et al.*, 1990; Jenkinson and Coleman, 2008) and
223 desorbed P, $F_{P_{os}}^{desorp}$ and P outputs from mineralized (F_{minl_p}), and adsorbed P fluxes ($F_{P_{os}}^{sorp}$) (adsorption:
224 eq. 40 and desorption: eq.41) with all fluxes expressed in kg P m⁻² yr⁻¹ as follows:

225
226 $\frac{dP_{BIO}}{dt} = 0.46 \times F_{immob_{P_n}} + F_{P_{os_{BIO},n}}^{desorp} - F_{minl_{P_{BIO},n}} - F_{P_{os_{BIO},n}}^{sorp}$ (eq.9)

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228 $\frac{dP_{HUM}}{dt} = 0.54 \times F_{immob_{P_n}} + F_{P_{os_{HUM},n}}^{desorp} - F_{minl_{P_{BIO},n}} - F_{P_{os_{HUM},n}}^{sorp}$ (eq.10)

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230 $P_{os} = \sum_{n=1}^N P_{BIO,n} + \sum_{n=1}^N P_{HUM,n}$ (eq.11)

231
232
233 Description of the inorganic sorbed P pool ($P_{inorg-sorp}$) follows Wang *et al.*, (2007) and is represented as the
234 difference between the input flux of inorganic sorption ($F_{P_{in}}^{sorp}$) (eq. 37) and output fluxes of inorganic
235 desorption ($F_{P_{in}}^{desorp}$) (eq. 38) and occluded P (F_p^{occ}) (eq. 39), with all fluxes expressed in kg P m⁻² yr⁻¹ as
236 follows:

237
238 $\frac{dP_{inorg-sorp}}{dt} = \sum_{n=1}^N F_{P_{in},n}^{sorp} - \sum_{n=1}^N F_{P_{in},n}^{desorp} - \sum_{n=1}^N F_{P_n}^{occ}$ (eq.12)

239
240 The description of the occluded (P_{occ}) P pool follows Wang *et al.*, (2007) and Hou *et al.*, (2019) and is
241 represented as the sum of input fluxes of occluded P from both organic (F_p^{or-occ}) (eq. 42) and inorganic P
242 pools (F_p^{occ}) expressed in kg P m⁻² yr⁻¹, as follows:

243
244 $\frac{dP_{occ}}{dt} = \sum_{n=1}^N F_{P_n}^{occ} + \sum_{n=1}^N F_{P_n}^{or-occ}$ (eq.13)

245

246 The description of the organic sorbed P pool ($P_{org-sorp}$) follows Wang *et al.*, (2007) and is represented as the
 247 difference between the input flux of organic sorption ($F_{P_{OS_n}^{sorp}}$) and output fluxes of organic desorption
 248 ($F_{P_{OS_n}^{desorp}}$) and occluded P ($F_{P_n^{occ}}$), with all fluxes expressed in kg P m⁻² yr⁻¹ as follows:

$$249 \frac{dP_{org-sorp}}{dt} = \sum_{n=1}^N F_{P_{OS_n}^{sorp}} - \sum_{n=1}^N F_{P_{OS_n}^{desorp}} - \sum_{n=1}^N F_{P_n^{or-occ}} \quad (\text{eq.14})$$

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 254 P from parent material (P_{pm}) pool follows Wang *et al.*, (2007) and depends on the weathering flux (F_p^w) (eq.
 255 43) in kg P m⁻² yr⁻¹ as follows:

$$257 \frac{dP_{pm}}{dt} = - \sum_{n=1}^N F_{P_n^w} \quad (\text{eq.15})$$

258 259 260 **2.2.2. C and P fluxes**

261
 262 NPP in JULES is calculated as the difference between GPP and autotrophic respiration. In JULES-CNP,
 263 potential NPP represents the amount of C, available for tissue growth (C density increase) on a unit area, and
 264 spreading (vegetation cover increase as a result of reproduction and recruitment), i.e., to increase the area
 265 covered by the vegetation type, assuming no nutrient limitation. The reported NPP in the literature often
 266 includes other C fluxes related to the exudates, production of volatiles and non-structural carbohydrates (Malhi
 267 *et al.*, 2009; Chapin *et al.*, 2011; Walker *et al.*, 2021) which are challenging to measure (Malhi, Doughty and
 268 Galbraith, 2011). Therefore, actual NPP is for our purposes equal to Biomass Production (BP), and is calculated
 269 as potential NPP minus excess C (lost to the plant through autotrophic respiration), with the latter the C that
 270 cannot be used to grow new plant tissue due to insufficient plant nutrient supply. Hence, if the system is limited
 271 by the availability of N and/or P, NPP will be adjusted to match the growth that can be supported with the
 272 limited N or P supply, with any excess carbohydrate lost through excess C.
 273 The total excess C term (ψ_t) (kg C m⁻² yr⁻¹) is calculated as:

$$275 \psi_t = \psi_g + \psi_s \quad (\text{eq.16})$$

276
 277 where ψ_g and ψ_s are the excess C fluxes due to growth (g) and spread (s) and are assumed to be rapidly respired
 278 by plants.

279
 280 Therefore, BP is calculated as the difference between potential NPP (Π_c) and total excess C:

$$282 BP = \Pi_c - \psi_t \quad (\text{eq.17})$$

283
 284 The litter production in JULES before limitation is estimated as follows:

$$286 F_{C_n}^{lit} = \gamma_{leaf} C_{leaf} + \gamma_{root} C_{root} + \gamma_{wood} C_{wood} \quad (\text{eq.18})$$

287
 288 where γ is a temperature dependent turnover rate representing the phenological state (Clark *et al.*, 2011). P
 289 limitation is applied on the C litter production similar to the N scheme of JULES (JULES-CN) (Wiltshire *et al.*,
 290 2021). In JULES-CN the N limitation effect on the litter production is captured by estimating the available C for
 291 litter production as a difference between the NPP and excess C (Wiltshire *et al.*, 2021).

292
 293 Similar to other P-enabled models (Yang *et al.*, 2014; Goll *et al.*, 2017), JULES-CNP follows the same structure
 294 as its N model component. Description of the plant P and N demand follow Wang *et al.*, (2007) and are
 295 represented by the sum of demand (ϕ_t) to sustain growth (P-related: (ϕ_{gP}), N-related: (ϕ_{gN})) and to sustain
 296 vegetation spreading (to increment PFT fractional coverage) (P-related: (ϕ_{sP}), N-related: (ϕ_{sN})) and is
 297 expressed in (P-related in kg P m⁻² yr⁻¹; N-related in kg N m⁻² yr⁻¹). The total demand for growth (ϕ_g) and
 298 spreading (ϕ_s) is controlled by the dominant demand between P (ϕ_{gP}) and N (ϕ_{gN}) as follows:

$$299 \phi_t = \phi_g + \phi_s \quad (\text{eq.19})$$

$$301 \quad \phi_{gP} = \frac{P_p}{C_V} \left(\Pi_c - \frac{dC_V}{dt} - \psi_g \right) \quad (\text{eq.20})$$

$$302 \quad \phi_{sP} = \frac{P_p}{C_V} \left(\Pi_c - \frac{dC_V}{dt} - \psi_s \right) \quad (\text{eq.21})$$

$$303 \quad \phi_{gN} = \frac{N_v}{C_V} \left(\Pi_c - \frac{dC_V}{dt} - \psi_g \right) \quad (\text{eq.22})$$

$$304 \quad \phi_{sN} = \frac{N_v}{C_V} \left(\Pi_c - \frac{dC_V}{dt} - \psi_s \right) \quad (\text{eq.23})$$

$$305 \quad \phi_g = \begin{cases} \phi_{gP} & \phi_{gP} \times \frac{C_V}{P_p} > \phi_{gN} \times \frac{C_V}{N_v} \\ \phi_{gN} & \phi_{gN} \times \frac{C_V}{N_v} > \phi_{gP} \times \frac{C_V}{P_p} \end{cases} \quad (\text{eq.24})$$

$$306 \quad \phi_s = \begin{cases} \phi_{sP} & \phi_{sP} \times \frac{C_V}{P_p} > \phi_{sN} \times \frac{C_V}{N_v} \\ \phi_{sN} & \phi_{sN} \times \frac{C_V}{N_v} > \phi_{sP} \times \frac{C_V}{P_p} \end{cases} \quad (\text{eq.25})$$

307

308

309 where $\frac{P_p}{C_V}$ is the inverse of whole plant C:P ratio, $\frac{N_v}{C_V}$ is inverse plant C:N ratio, $\frac{dC_V}{dt}$ is rate of change in plant C
 310 (see Clark *et al.*, (2011) for more detail), Π_c is nutrient-unlimited, or potential, NPP ($\text{kg C m}^{-2} \text{ yr}^{-1}$), ψ_g is excess
 311 C due to either P or N limitation for plant growth ($\text{kg C m}^{-2} \text{ yr}^{-1}$) and ψ_s is excess C due to either P or N
 312 limitation for vegetation spreading ($\text{kg C m}^{-2} \text{ yr}^{-1}$).

313

314 Equations 20 and 22 are solved by first setting $\psi_g = 0.0$ to find the total plant P (eq. 20) and N demand (eq.22).

315 If the P and N demand for growth are less than the available P and N and fractional coverage (λ) (NPP fraction

316 used for fractional cover increment; for detail see Wiltshire *et al.*, (2021)) at the considered timestep Δt then

317 there is no limitation to growth (*i. e.* $\phi_{gP} < \frac{(1-\lambda)P_{avail}}{\Delta t}$; $\phi_{gN} < \frac{(1-\lambda)N_{avail}}{\Delta t}$). Where there is limited P and/or N

318 availability, the uptake equals the available P and N ($\phi_{gP} = \frac{(1-\lambda)P_{avail}}{\Delta t}$; $\phi_{gN} = \frac{(1-\lambda)N_{avail}}{\Delta t}$), and the plant

319 growth which cannot be achieved due to nutrient constraints will be deducted from potential NPP, here termed

320 excess C term (ψ_g), to give an actual NPP. Following Wiltshire *et al.*, 2021, we assume excess C is respired by

321 the plant.

322

323 Similarly, in order to estimate the P and N demand for spreading (eq. 21 and 23), initially the excess C from
 324 spreading is set to 0.0 ($\psi_s = 0.0$), *i.e.* under the assumption that there is no nutrient limitation. If the P and N

325 demand for spreading are lower than the available P and N and fractional coverage (λ) ($\phi_{sP} <$

326 $\frac{(1-\lambda)P_{avail}}{\Delta t}$; $\phi_{sN} < \frac{(1-\lambda)N_{avail}}{\Delta t}$), then there is no limitation on spreading and in case of limited P and N

327 availability, the uptake equals the available P and N ($\phi_{sP} = \frac{(1-\lambda)P_{avail}}{\Delta t}$; $\phi_{sN} = \frac{(1-\lambda)N_{avail}}{\Delta t}$), and the excess C

328 for spread (ψ_s) is subtracted from potential NPP.

329

330 Plant P uptake (F_p^{up}) (arrow a in Fig 1) is estimated based on the P demand for growth and spreading (ϕ_t) and

331 the root uptake capacity (u^{max}) ($\text{kg P kg}^{-1} \text{ C yr}^{-1}$), as follows:

332

$$333 \quad F_p^{up} = \begin{cases} \phi_t & \phi_t \leq u^{max} \\ u^{max} & \phi_t > u^{max} \end{cases} \quad (\text{eq.26})$$

334

335 Plant P uptake (F_p^{up}) varies spatially depending on the root uptake capacity (u^{max}) followed by Goll *et al.*,
 336 (2017). Therefore, in regions with limited P supply, the plant P uptake is limited to the u^{max} and consequently
 337 impacts the excess C and BP.

338 The root uptake capacity depends on the maximum root uptake capacity (v_{max}) ($\text{kg P kg}^{-1} \text{ C yr}^{-1}$), root depth
 339 (d_{root}), the concentration of inorganic P at different soil depths (P_{in}), and a half saturation term at which half of
 340 the maximum uptake capacity is reached using inorganic P at different soil depths (P_{in}), a scaling uptake ratio
 341 (K_p) ($\mu\text{mol P l}^{-1}$), unit conversion (C_f) (1 kg P^{-1}), and soil moisture (θ) (1 m^{-2}), as follows:

342

$$343 \quad u^{max} = v_{max} \times d_{root} \times \sum_{n=1}^N P_{in_n} \times \left(\frac{1}{\sum_{n=1}^N P_{in_n} + c_f \times K_p \times \theta_n} \right) \quad (\text{eq.27})$$

344

345 Description of the litter production of P ($F_{P_n}^{lit}$) (arrow b in Fig 1) follows JULES-CN as in Wiltshire *et al.*,
 346 (2021) and is calculated based on the litter flux of C ($\text{kg C m}^{-2} \text{ yr}^{-1}$) using leaf, root and wood turnovers (yr^{-1}),
 347 and through the vegetation dynamics due to large-scale disturbance and litter production density, as follows:
 348

$$349 \quad F_{P_n}^{lit} = \left(\frac{(1-k_{leaf})\gamma_{leaf}C_{leaf}}{C:P_{leaf}} \right) + \left(\frac{(1-k_{root})\gamma_{root}C_{root}}{C:P_{root}} \right) + \left(\frac{\gamma_{wood}C_{wood}}{C:P_{stem}} \right) \quad (\text{eq.28})$$

350
 351 where λ is the leaf, root and stem re-translocation (at daily timestep) coefficient (Zaehle and Friend, 2010; Clark
 352 *et al.*, 2011) and the related $C:P$ ratios for P fraction and γ is a temperature dependent turnover rate representing
 353 the phenological state (Clark *et al.*, 2011).
 354
 355

356 The decomposition of litter (dec^{lit}) (arrow c in Fig 1) depends on soil respiration (R) ($\text{kg C m}^{-2} \text{ yr}^{-1}$), the litter
 357 $C:P$ ratio ($C:P_{lit}$) at each soil layer (n) as follows:
 358

$$359 \quad dec_p^{lit} = \frac{\sum_{n=1}^N R_n}{C:P_{lit}} \quad (\text{eq.29})$$

360
 361 where the $C:P_{lit}$ is calculated based on litter C pool (DPM and RPM) (lit^C) ($\text{kg C m}^{-2} \text{ yr}^{-1}$) and litter P pool
 362 (P_{O_l}) as follows:
 363

$$364 \quad C:P_{lit} = \frac{\sum_{n=1}^N lit_n^C}{P_{O_{ln}}} \quad (\text{eq.30})$$

365
 366 The mineralized (F_{minl_p}) (arrow d in Fig 1) and immobilized (F_{immob_p}) (arrow e in Fig 1) P fluxes are
 367 calculated based on C mineralization and immobilization, $C:P$ ratios of plant (i) (DPM/RPM) ($C:P_{plant}$) and
 368 soil (HUM/BIO) ($C:P_{soil}$), soil pool potential respiration (R_{POT_i}) ($\text{kg C m}^{-2} \text{ yr}^{-1}$) and the respiration partitioning
 369 fraction ($resp_frac$) as follows:
 370

$$371 \quad F_{minl_p} = \frac{\sum_{n=1}^N R_{POT_{i,n}}}{C:P_{plant}} \quad (\text{eq.31})$$

$$372 \quad F_{immob_p} = \frac{\sum_{n=1}^N R_{i,n} \times resp_frac}{C:P_{soil}} \quad (\text{eq.32})$$

373
 374 The soil respiration from each soil layer ($R_{i,n}$) is estimated from potential soil respiration ($R_{POT_{i,n}}$) for the
 375 DPM, RPM pools and the litter decomposition rate modifier (F_{P_n}) as follows:
 376
 377

$$378 \quad R_{i,n} = R_{POT_{i,n}} \times F_{P_n} \quad (\text{eq.33})$$

379
 380 where the description of F_{P_n} for P pools (F_{P_n}) follows Wang *et al.*, (2007) and is estimated based on the soil
 381 pool (BIO/HUM) mineralization ($minl_{p-BIO_n}$, $minl_{p-HUM_n}$) and immobilization ($immob_{p-BIO_n}$,
 382 $immob_{p-HUM_n}$) (in $\text{kg P m}^{-2} \text{ yr}^{-1}$), soil inorganic P (P_{inorg_n}) (in kg P m^{-2}), and litter pools (DPM/RPM) demand
 383 (in $\text{kg P m}^{-2} \text{ yr}^{-1}$) as follows:
 384

$$385 \quad F_{P_n} = \frac{(minl_{p-BIO_n} + minl_{p-HUM_n} - immob_{p-BIO_n} - immob_{p-HUM_n}) + P_{inorg_n}}{DEM_{DPM_n} + DEM_{RPM_n}} \quad (\text{eq.34})$$

386
 387 The net demand associated with decomposition of litter pools ($DEM_{k,n}$) represents the P required by microbes
 388 which convert DPM and RPM into BIO and HUM. The limitation due to insufficient P availability is estimated
 389 based on the potential mineralization ($minl_{p-pot}$) and immobilization ($immob_{p-pot}$) (in $\text{kg P m}^{-2} \text{ yr}^{-1}$) of pools
 390 (k) as follows:
 391

$$392 \quad DEM_{k,n} = immob_{p-pot,k} - minl_{p-pot,k} \quad (\text{eq.35})$$

393
 394 The F_{P_n} estimated for N pools (F_{P_n}) follows the same formulation as P (see Wiltshire *et al.*, 2021 for further
 395 details) and the F_{P_n} is estimated based on a higher rate modifier between N and P as follows:
 396

$$F_{P_n} = \begin{cases} F_{PP_n} & F_{PP_n} > F_{PN_n} \\ F_{PN_n} & F_{PN_n} > F_{PP_n} \end{cases} \quad (\text{eq.36})$$

398

399 Description of the fluxes of adsorption ($F_{P_{in_n}}^{sorp}$) (arrow e in Fig 1) and desorption ($F_{P_{in_n}}^{desorp}$) (arrow f in Fig
400 1) of inorganic P in kg P m⁻² yr⁻¹ follow Wang *et al.*, (2010) and are calculated based on soil inorganic (P_{in_n}) and
401 sorbed inorganic ($P_{inorg-sorbed_n}$) P pools and inorganic adsorption ($K_{sorp-in}$), desorption ($K_{desorp-in}$)
402 coefficients (kg P m⁻² yr⁻¹) and maximum sorbed inorganic (P_{in-max}) (kg P m⁻²) as follows:
403

$$F_{P_{in_n}}^{sorp} = P_{in_n} \times K_{sorp-in} \times \frac{(P_{in-max_n} - P_{inorg-sorbed_n})}{P_{in-max_n}} \quad (\text{eq.37})$$

405

$$F_{P_{in_n}}^{desorp} = P_{inorg-sorbed_n} \times K_{desorp-in} \quad (\text{eq.38})$$

407

408 Description of the occluded inorganic P flux ($F_{P_n}^{occ}$) (arrow g in Fig 1) follows Wang *et al.*, (2007) and Hou *et al.*,
409 (2019) and is calculated based on sorbed inorganic P pool and P occlusion rate (K_{occ}) (kg P m⁻² yr⁻¹) as
410 follows:

411

$$F_{P_n}^{occ} = P_{inorg-sorbed_n} \times K_{occ} \quad (\text{eq.39})$$

413

414 Description of the fluxes of adsorption ($F_{P_{OS_n}}^{sorp}$) (arrow h in Fig 1) and desorption ($F_{P_{OS_n}}^{desorp}$) (arrow i in Fig
415 1) of organic P follow Wang *et al.*, (2010) are calculated based on soil organic and sorbed organic P pools and
416 organic adsorption ($K_{sorp-or}$) (kg P m⁻² yr⁻¹), desorption ($K_{desorp-or}$) coefficients (kg P m⁻² yr⁻¹) and maximum
417 sorbed organic ($P_{org-max}$) (which corresponds to the sorbed soil P saturation, thus modifying the sorption rate
418 respectively) (kg P m⁻²) as follows:
419

$$F_{P_{OS_n}}^{sorp} = P_{OS_n} \times K_{sorp-or} \times \frac{(P_{or-max_n} - P_{org-sorbed_n})}{P_{or-max_n}} \quad (\text{eq.40})$$

421

$$F_{P_{OS_n}}^{desorp} = P_{org-sorbed_n} \times K_{desorp-or} \quad (\text{eq.41})$$

423

424 Description of the occluded organic P flux ($F_{P_n}^{or-occ}$) (kg P m⁻² yr⁻¹) (arrow j in Fig 1) follows Wang *et al.*,
425 (2007) and Hou *et al.*, (2019) is calculated based on sorbed organic P pool ($P_{org-sorbed_n}$) and P occlude rate
426 (K_{occ}) (kg P m⁻² yr⁻¹) as follows:
427

428

$$F_{P_n}^{or-occ} = P_{org-sorbed_n} \times K_{occ} \quad (\text{eq.42})$$

429

430 Description of the P flux from weathered parent material ($F_{P_n}^w$) (arrow k in Fig 1) follows Wang *et al.*, (2007)
431 and is calculated based on amount of P in the parent material (P_{pm}) and P weathering rate (K_w) (kg P m⁻² yr⁻¹) as
432 follows:
433

434

$$F_{P_n}^w = P_{pm_n} \times K_w \quad (\text{eq.43})$$

435

436 Description of P diffusion between soil layers (F_{D_n}) expressed in (kg P m⁻² yr⁻¹) (arrow l in Fig 1) follows Goll
437 *et al.*, (2017) and is calculated following Fick's second law and it is a function of the diffusion coefficient (Dz)
438 in m² s⁻¹, the concentration of inorganic P at different soil depths (P_{in}) in kg P m⁻², the distance (z) between the
439 midpoints of soil layers in metres and seconds to year unit conversion (Yr):
440

$$F_{D_n} = \frac{\partial}{\partial z} (D_{zn} \frac{\partial P_{zn}}{\partial z}) \times Yr \quad (\text{eq.44})$$

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Table 1. Model variables

Variable	Unit	Definition
ψ	kg C m ⁻² yr ⁻¹	Excess C flux
\emptyset	kg P m ⁻² yr ⁻¹	Plant demand for uptake
Π_c	kg C m ⁻² yr ⁻¹	Potential NPP
u^{max}	kg P kg ⁻¹ C yr ⁻¹	Root uptake capacity
DEM	kg P m ⁻² yr ⁻¹	Plant pool P associated decomposition 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
$F_{PO_S}^{sorp}$	kg P m ⁻² yr ⁻¹	Sorbed organic P flux
$F_{P_{in}}^{sorp}$	kg P m ⁻² yr ⁻¹	Sorbed inorganic P flux
$F_{PO_S}^{desorp}$	kg P m ⁻² yr ⁻¹	Desorbed organic P flux
$F_{P_{in}}^{desorp}$	kg P m ⁻² yr ⁻¹	Desorbed 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
F_{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
F_{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
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_{POT}	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

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Table 2. P Model parameters

Parameter	Value	Unit	Eq.	Description	Source
C and N related					
α	0.25	-	6	Plant type material ratio	(Clark <i>et al.</i> , 2011)
a_{wl}	1.204	kg C m ⁻²	50	Allometric coefficient	calibrated
σ_l	0.0375	kg C m ⁻² per unit LAI	48	Specific leaf density	Clark <i>et al.</i> , 2011
b_{wl}	1.667	-	50	Allometric exponent.	Clark <i>et al.</i> , 2011
f_{dr}	0.005	-	47	Respiration scale factor	Calibrated
$resp_frac$	0.25	-	32	Respiration fraction	(Clark <i>et al.</i> , 2011)
k_{leaf}	0.5	-	28	Leaf N re-translocation coefficient	(Zachle and Friend, 2010)
k_{root}	0.2	-	28	Root N re-translocation coefficient	(Zachle and Friend, 2010)
d_{root}	3.0	-	27	Root fraction in each soil layer	(Clark <i>et al.</i> , 2011)
v_{int}	7.21	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	45	Intercept in the linear regression between V_{cmax} and N_{area}	Calibrated (Clark <i>et al.</i> , 2011)
v_{sl}	19.22	$\mu\text{mol CO}_2 \text{ gN}^{-1} \text{ s}^{-1}$	45	Slope in the linear regression between V_{cmax} and N_{area}	Calibrated (Clark <i>et al.</i> , 2011)
LMA	131.571852	g m ⁻²	45	Observed Leaf Mass per Area	Study site
$Leaf\ N$	1.79007596	g g ⁻¹	45, 46	Foliar N concentrations	Study site
P related					
$C:P_{soil}$	1299.6	-	32	Soil C:P ratio	(Fleischer <i>et al.</i> , 2019)
v_{max}	0.0007	kg P kg ⁻¹ C yr ⁻¹	27	Maximum root uptake capacity	Calibrated (Goll <i>et al.</i> , 2017)
P	0.7083062	g kg ⁻¹	46	Foliar P concentrations	Study site
c_f	3.1×10^{-5}	l kg P ⁻¹	27	Conversion factor	(Goll <i>et al.</i> , 2017)
D_z	0.001	m ² s ⁻¹	44	Diffusion coefficient	(Burke <i>et al.</i> , 2017)
K_{occ}	1.2×10^{-5}	yr ⁻¹	39, 42	P occlusion rate	(Yang <i>et al.</i> , 2014)
K_p	3.0	kg P l ⁻¹	27	Scaling uptake ratio	Calibrated
$K_{sorp-in}$	0.0054	kg P m ⁻² yr ⁻¹	37	Inorganic P adsorption coefficient	Calibrated (Hou <i>et al.</i> , 2019)
$K_{sorp-or}$	0.00054	kg P m ⁻² yr ⁻¹	40	Organic P adsorption coefficient	Calibrated
K_{in-max}	0.0075	kg P m ⁻² yr ⁻¹	37	Maximum sorbed inorganic P	Study site
K_{or-max}	0.0042	kg P m ⁻² yr ⁻¹	40	Maximum sorbed organic P	Study site
K_w	3×10^{-6}	kg P m ⁻² yr ⁻¹	43	P weathering rate	(Wang <i>et al.</i> , 2010)

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2.3 Study sites

This study primarily uses data from two nearby sites in Central Amazon in Manaus, Brazil. The main site from here on termed *study site* (2°35′21.08″ S, 60°06′53.63″ W) (Lugli *et al.*, 2020) is for model development and evaluation. The second site is the Manaus K34 flux site (2°36′32.67″ S, 60°12′33.48″ W) which provides meteorological station data for running the model but also provides data for model evaluation. Our *study site* is the main lowland tropical forest site maintained by the National Institute for Amazon Research (INPA). Research at this site focuses on projects, combining experimental approaches (Keller *et al.*, 2004; Malhi *et al.*, 2009) with modelling (Lapola and Norby, 2014). We use detailed novel soil and plant P pool data from the *study site* (Lugli *et al.*, 2020, 2021) for model parameterisation and calibration and carbon stock data for model validation. The *study site* has a very similar forest, geomorphology, soil chemistry and species composition to the well-known and studied K34 flux site (Araújo *et al.*, 2002). The average reported annual precipitation is 2431 (mm yr⁻¹), with a monthly range of 95 to 304 (mm month⁻¹), and averaged temperature is 26°C (Araújo *et al.*, 2002). Soil type at this site is Geric Ferrosol with a high clay content and weathering activities (Malhi *et al.*, 2004).

473 In addition to the *study site* we use data from other P limited locations from the Amazon, Panama and Hawaii
 474 (Table 3) for model evaluation. Old-growth forest sites in the Amazon are located across a fertility gradient
 475 from west to east (AGP-01, SA3, CAX,) with detailed C cycle measurements available (Aragão *et al.*, (2009)).
 476 The site in Panama is located in the Gigante Peninsula in the Barro Colorado Nature Reserve and is a 200 year
 477 old semi-deciduous rainforest (Wright *et al.*, 2011) growing on Oxisols developed on Miocene basalt (Dieter,
 478 Elsenbeer and Turner, 2010) with the topsoil a dominant clay texture (Turner and Condon, 2013). It is the
 479 location of a long term running nutrient fertilization experiment since 1998 (Mirabello *et al.*, 2013). The site in
 480 Hawaii (Hawaii Kokee) is a P limited chronosequence that developed on the 4 million year old oxisols soil
 481 (Vitousek, 2004) and has a long term fertilization experiment. Site information is provided in Table 3.
 482
 483

Table 3. Test sites name, location and climate characterises.

Site	Name	Location		Climate	
		Lat.	Lon.	Rainfall (mm yr ⁻¹)	Temperature(°C)
Study site	AFEX project	-2.58	-60.11	2431	26
AGP-01	Agua pudre plot E	-3.72	-70.3	2723	25.5
CAX	Caxiuanã flux tower site	-1.72	-51.5	2314	26.9
SA3	Tapajós flux tower site	-2.5	-55	1968	26.1
Gig. Pen.	Gigante peninsula (control data)	-9.1	-79.84	2600	26
Hawaii K.	Hawaii Kokee (control data)	22.13	-159.62	2500	16

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485

2.4 Model parameterisation, calibration and evaluation at study site

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487

488 We use observations from the four control plots of the study site to parameterise, calibrate and evaluate different
 489 processes in JULES (Table 4). The observations were collected at 4 soil depths and processed using the Hedley
 490 sequential fractionation (Hedley, Stewart and Chauhan, 1982; Quesada *et al.*, 2010). Observed Leaf Mass per
 491 Area (LMA), leaf N and leaf P estimated from fresh leaves were used as input parameters to JULES to estimate
 492 photosynthetic capacity and respiration parameters. JULES vn5.5 (JULES CN in this study) estimates V_{cmax}
 493 ($\mu\text{mol m}^{-2} \text{s}^{-2}$) based on Kattge *et al.* (2009) using foliar N concentrations in area basis (*nleaf*), as follows:
 494

495

$$V_{cmax} = v_{int} + v_{sl} * nleaf \quad (\text{eq.45})$$

496

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

500

$$\ln(V_{cmax}) = 3.946 + 0.921 \ln(N) + 0.121 \ln(P) + 0.282 \ln(N) \ln(P) \quad (\text{eq.46})$$

501

502

503 Where N and P are foliar concentrations in area basis.

504

505 Implementation of eq. 46 resulted in higher V_{cmax} than in the original version of JULES. A higher V_{cmax} predicted
 506 higher leaf and plant respiration (eq.47). Constrained by observations of NPP and plant respiration at the study
 507 site, we modified one of the most uncertain parameters in the description of plant respiration (f_{dr}) (eq.47) which
 508 is the scale factor for leaf dark respiration (R_d) as follows:
 509

510

$$R_d = f_{dr} V_{cmax} \quad (\text{eq.47})$$

511

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

514

515 Observations of aboveground biomass were used to calibrate the non PFT dependent allometric relationships in
 516 JULES (Clark *et al.* 2011) (eq 48-50) for leaf, root and wood C. Specifically, the a_{wl} parameter (eq 50) was
 517 modified from 0.65 to 1.204 to match better tropical forest allometry:

518

$$C_{leaf} = \sigma_l L_b \quad (\text{eq.48})$$

519

$$C_{root} = C_{leaf} \quad (\text{eq.49})$$

$$C_{stem} = a_{wl} L_b^{b_{wl}} \quad (\text{eq.50})$$

Where σ_l is specific leaf density (kg C m⁻² per unit LAI), L_b is balanced (or seasonal maximum) leaf area index (m² m⁻²), a_{wl} is allometric coefficient (kg C m⁻²) and b_{wl} is the allometric exponent.

Note that JULES-CNP uses the C3 and C4 photosynthesis model from Collatz et al., 1991; Collatz, Ribas-Carbo and Berry, 1992, which does not include estimation of J_{max} .

JULES-CNP has fixed stoichiometry and C:P ratios of leaf and root (measured), and wood (estimated from fresh coarse wood (Lugli, 2013)) which were taken from the *study site* 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: P_{in}), organic bicarbonate P (organic P: P_{O_S}), NaOH organic P (sorbed organic P: $P_{org-sorp}$), NaOH inorganic P (sorbed inorganic P: $P_{inorg-sorp}$), residual P (occluded P: P_{occ}) and HCL P (parent material P: P_{pm}) (Table 4). The measurements were collected between 2017 and 2018 in control plots. All measurements were conducted in 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.

Vegetation C stocks were derived based on tree diameter measurements at breast height, that are linked to allometric equations and wood density databases to estimate the C stored in each individual tree, and then scaled to the plot (Chave *et al.*, 2014).

The organic and inorganic soil P was assumed to be always at equilibrium with the relative sorbed pools (Wang, Law and Pak, 2010). Thus, in order to cap P sorption and uptake capacity, the maximum sorption capacities (P_{in-max_n} , P_{or-max_n} , eq.37 and 39) (adopted from (Wang, Houlton and Field, 2007)) were prescribed using maximum observed sorbed inorganic and organic P. Hence, the maximum sorption capacity defines the equilibrium state of sorbed and free-soil P. Moreover, despite the initial representation of the parent material pool in JULES and its depletion through weathering (eq. 43), 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. Remaining parameters used to describe soil P fluxes (eqn.s 27-44) were prescribed using values from the literature (Table 4).

We used a combination of data from the *study site* and the nearby K34 site for model evaluation of C fluxes (GPP, NPP) and C pools (soil and vegetation C, leaf, root and wood C) with no calibration of plant and soil organic and soil inorganic P pools included (Table 4).

Table 4. Observations from study site (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	Evaluation	Fleischer et al., 2019, K34
	Soil C	Evaluation	Malhi et al., 2009, K34
	CUE	Evaluation	Malhi et al., 2009, K34
	Veg C	Evaluation	Study site
	Leaf C	Evaluation	Study site
	Wood C	Evaluation	Study site
	Root C	Evaluation	Study site
	LAI	Initialisation	Study site
LMA	Parameterisation	Study site	
P associated	Resin	Evaluation	Study site
	Pi Bic	Evaluation	Study site
	Po Bic	Evaluation	Study site
	Po NaOH	Calibration	Study site
	Pi NaOH	Calibration	Study site
	P residual	Parameterisation	Study site
	P HCL	Parameterisation	Study site
	Leaf N	Parameterisation	Study site
	Leaf P	Parameterisation	Study site
	Root P	Parameterisation	Study site
Plant C:P ratio	Parameterisation	Study site	

557 **2.4.1 Model parameterisation and evaluation at test sites**

558
559 JULES-CNP was parameterised using reported C:P ratios and maximum sorbed organic and inorganic P for
560 each test site (Table 5) as follows:

561
562 **Table 5.** Additional test sites data used for model parameterisation
563

	AGP-01 ^{a,b}	CAX ^{a,b}	SA3 ^{a,b}	Gig. Pen. ^c	Hawaii K. ^{b,d}
<i>LeafC:P</i>	600	600	600	700	691.5
<i>RootC:P</i>	1000	1000	1000	1750	1100
<i>WoodC:P</i>	3000	3000	3000	5500	5937.5
<i>SoilC:P</i>	2000	2000	2000	800	2000
<i>K_{or-max}</i>	0.001	0.001	0.001	0.0033	0.001
<i>K_{in-max}</i>	0.001	0.001	0.001	0.0185	0.001

564 ^aC:P ratios from Wang, Law and Pak, 2010 and ^bmaximum sorbed P capacities from Yang *et al.*, 2014.

565 ^cMirabello *et al.*, 2013 ^dC:P ratios from Vitousek, 2004

566
567 Model evaluation at test sites, was performed using observed NPP, litterfall, autotrophic respiration, biomass and
568 soil C pools taken from different sources. We used NPP and litterfall for the Amazon sites from Aragão *et al.*,
569 (2009) and for Gigante Peninsula from Chave *et al.*, (2003), Hawaii Kokee NPP as reported in Goll *et al.*,
570 (2017) and litterfall as reported in (Yang *et al.*, 2014). Plant respiration was only available at two of Amazon
571 sites (AGP and CAX) (Malhi *et al.*, 2009). The biomass and soil C pools for Amazon sites (CAX and SA3) are
572 taken from Malhi *et al.*, (2009) and biomass from AGP is taken from Jiménez *et al.*, (2009). The Gigante
573 Peninsula biomass is taken from Chave *et al.*, (2003), soil C from Turner *et al.*, (2015), and the Hawaii Kokee C
574 pools are taking as reported in Yang *et al.*, (2014).
575

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578 **2.5 JULES simulations**

579
580 JULES was first applied at the K34 flux tower site using observed meteorological forcing data from 1999-2019
581 (Fleisher *et al.* 2019) at half hourly resolution. The following meteorological variables are needed to drive JULES
582 (model inputs) (Best *et al.*, 2011): atmospheric specific humidity (kg kg^{-1}), atmospheric temperature (K), air
583 pressure at the surface (Pa), short and longwave radiation at the surface (W m^{-2}), wind speed (m s^{-1}) and total
584 precipitation ($\text{kg m}^{-2} \text{s}^{-1}$). Furthermore, the averaged measured LAI from study site was used to initialise the
585 vegetation phenology module, but was allowed to vary in subsequent prognostic calculations. Soil organic and
586 inorganic sorbed P pools were initialised with study site observations. The JULES-CNP simulations were
587 initialized following the same methodology as in Fleischer *et al.*, (2019), by the spin-up from 1850 resulted in
588 equilibrium state (Figure S1). The spin up was performed separately for three versions of JULES (C/CN/CNP)
589 following the same procedure. Furthermore, the transient run was performed for the period 1851-1998 using
590 time-varying CO_2 and N deposition fields. Finally, for the extended simulation period (1999-2019) two runs
591 were performed, the first with ambient the second elevated CO_2 concentrations.
592

593 We evaluate the impact of including a P cycle in JULES using three model configurations (JULES C, CN and
594 CNP). We apply JULES in all three configurations using present day climate under both ambient CO_2 and $e\text{CO}_2$.
595 Ambient and $e\text{CO}_2$ were prescribed following Fleischer *et al.*, (2019), with present-day CO_2 based on global
596 monitoring stations, and an abrupt (step) increase in atmospheric CO_2 of +200 ppm on the onset of the transient
597 period (i.e., 1999). However, the comparison period is limited to 2017-18 for which the P measurements are
598 available.

599 We compare simulated C fluxes (GPP, NPP, litterfall C), C stocks (total vegetation, fine root, leaf, wood, soil)
600 and the CO_2 fertilization effect across model configurations. The CO_2 fertilization effect ($\text{CO}_{2\text{fert-eff}}$) (eq.51)
601 is calculated based on simulated vegetation C under ambient ($\text{VegC}(a\text{CO}_2)$) and $e\text{CO}_2$ ($\text{VegC}(e\text{CO}_2)$) as
602 follows:
603

$$604 \text{CO}_{2\text{fert-eff}} = \frac{(\text{VegC}(e\text{CO}_2) - \text{VegC}(a\text{CO}_2)) \times 100}{\text{VegC}(a\text{CO}_2)} \quad (\text{eq.51})$$

605
606

607 Furthermore, the net biomass increases due to CO₂ fertilization effect (ΔC_{veg}) is estimated as follows:

$$608 \Delta C_{veg} = \Delta BP - \Delta litterfall C \quad (eq.52)$$

610 We studied the Water Use Efficiency (WUE) (eq. 53) at half-hourly timestep, then aggregated per month as one
611 of the main indicators of GPP changes (Xiao *et al.*, 2013), and soil moisture content (SMCL), as one of the
612 main controllers of maximum uptake capacity (eq. 27), in order to better understanding the changes in GPP, P
613 demand and uptake as well as excess C fluxes.

$$614 WUE = GPP/Transpiration \quad (eq.53)$$

617 Moreover, we also estimated the Carbon Use Efficiency (CUE) as an indicator of the required C for the growth
618 (Bradford and Crowther, 2013) as follows:

$$619 CUE = BP/GPP \quad (eq.54)$$

622 We use JULES-CNP to evaluate the extent of P limitation under ambient and eCO₂ at this rainforest site in
623 Central Amazon. P limitation is represented by the amount of C that is not used to grow new plant tissue due to
624 insufficient P in the system (excess C) (eq. 27). The excess C flux is highly dependent on the plant P and the
625 overall P availability to satisfy demand. We also explore the distribution of the inorganic and organic soil P and
626 their sorbed fraction within the soil layers and under ambient and eCO₂.

628 2.5.1 Model sensitivity

630 To test the sensitivity of the P and C related processes to individual model P parameters, six sets of simulations
631 were conducted independently with modified plant C:P stoichiometry (Plant C:P: *SENS1*), P uptake scaling
632 factor (K_p) (K_p : *SENS2*), inorganic ($K_{p_sorb_in}$: *SENS3*) and organic ($K_{p_sorb_or}$: *SENS4*) P adsorption
633 coefficients ($K_{sorp-or}$, $K_{sorp-in}$), and maximum inorganic ($K_{p_sorb_in_max}$: *SENS5*) and organic
634 ($K_{p_sorb_or_max}$: *SENS6*) sorbed P (K_{or-max} , K_{in-max}). These values were prescribed to vary between $\pm 50\%$
635 of the observed values and their effect on C pools (plant and soil C) and fluxes (NPP and excess C), and P pools
636 (plant, soil, and soil sorbed P) was assessed. As the derived model parameters from measurements have their
637 own level of uncertainty, we took 50% change to test these parameters at reasonable degree. However, the
638 occluded and weathered P pools are prescribed for this model application, the occluded and weather P
639 coefficients (other two P-related model parameters) were not part of sensitivity tests.

640 Our model evaluation period is limited to years 2017-18 due to the P measurement availability. However, in
641 order to compare with 15 models studied by Fleischer *et al.*, (2019) we also studied the response of GPP, NPP
642 and BP to eCO₂ for both initial (1999) and 15 years periods (between 1999-2013).

643 2.5.1 Simulations at test sites

649 To perform JULES (C, CN, CNP) simulations at test sites we extracted the meteorological input data to drive
650 the model from a global dataset (CRU-NCEP)(Harris *et al.*, 2014) by selecting the closest grid cell to each site
651 when data were not available for a given site (Table 3). Soil texture ancillaries for each site were extracted from
652 a global soil data (HWSD) (Nachtergaele *et al.*, 2010). All simulations were initialised from a global JULES-CN
653 run (Wiltshire *et al.*, 2020) extracted for each site and further spun-up for 2000 years over the 1980-2000 period
654 for the three versions of JULES (C/CN/CNP). Finally, the transient (2000-2013) run was performed using the
655 output of the spin-up for each site.

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664 3. Results

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666 3.1 Model application under ambient CO₂

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668 3.1.1 Calibration of simulated soil P pools at study site

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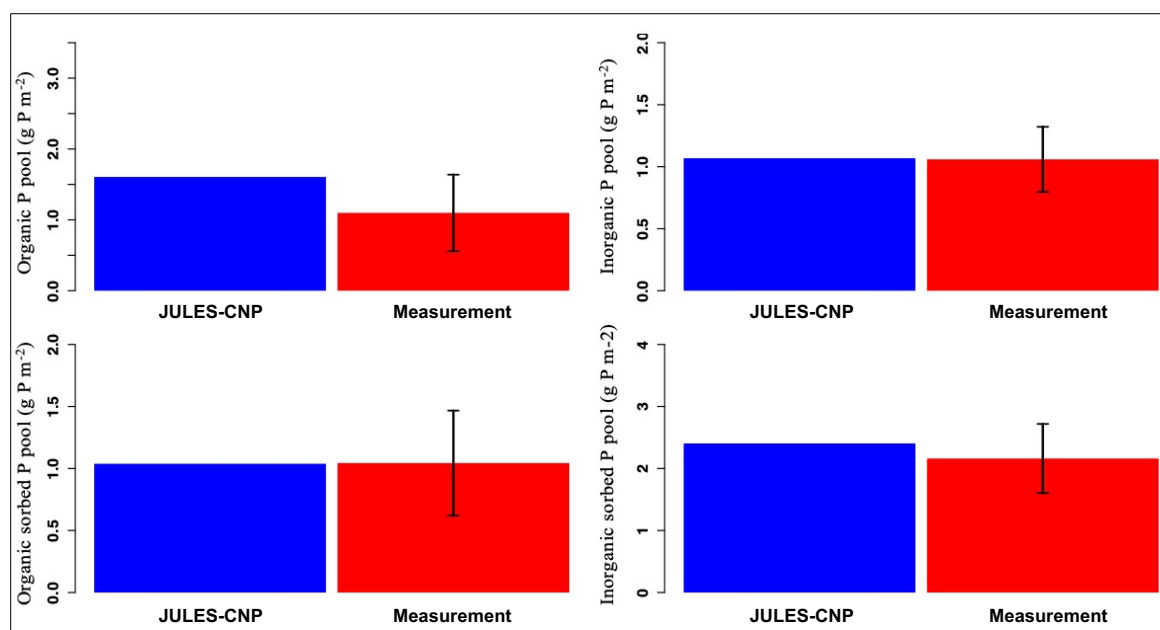
670 The maximum sorption capacities (P_{in-max_n} , P_{or-max_n} , eq.37 and 40) were calibrated to the observed P pools.

671 As a result, JULES-CNP could reproduce the measured soil P pools (Fig. 2 and Table 6). Simulated inorganic

672 soil P and sorbed organic and inorganic soil P closely matched the observations (Table 7 and Fig. 2). However,

673 simulated organic soil P overestimates the observations by 60 %.

674



675

676 **Figure. 2-** Modelled vs measured soil phosphorus pools under ambient CO₂ (for the soil depth of 0-30cm). Black line
677 represents standard deviation

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679

680 **Table 6.** Observed and simulated phosphorus pools and fluxes. Occluded and weathered P pools were prescribed using the
681 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

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687 **3.1.2 Model evaluation**

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689 JULES-CNP could reproduce the plant and soil C (Figure 2 and Table 7) and N pools and fluxes (Figure S6 and
690 Table 8) under ambient CO₂. Our results show that simulated GPP, is within the range of measurement (3.02 kg
691 C m⁻² yr⁻¹ model vs 3-3.5 kg C m⁻² yr⁻¹ observed, respectively, Table 7).

692
693 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
694 autotrophic respiration (RESP) also closely following the observations (1.98 observed vs 1.81 modelled kg C m⁻²
695 yr⁻¹). Biomass production is estimated as a difference between NPP and the amount of C which is not fixed by
696 plants due to the insufficient P in the system (excess C) (eq. 27). The excess C flux depends on the plant P and
697 the overall P availability to satisfy demand (Table 7). The simulated flux of excess C is 0.3 kg C m⁻² yr⁻¹ under
698 ambient CO₂. In JULES-CNP this flux is subtracted from NPP in order to give the BP (eq. 17) (Table 7). Our
699 simulated litterfall overestimates the observations by 32%, however simulated vegetation and its components
700 (fine root, leaf and wood) and soil C stocks match well the observations (Table 7).

701
702 **Table 7.** Observed and simulated carbon pools and fluxes with JULES-CNP (between period 2017-18)

	Carbon pools and fluxes		
	Measured	Modelled Ambient CO₂	Modelled Elevated CO₂
GPP (kg C m ⁻² yr ⁻¹)	3.0 – 3.5	3.06	3.9
NPP_{pot} (kg C m ⁻² yr ⁻¹)	-	1.27	1.77
Plant respiration (kg C m ⁻² yr ⁻¹)	1.98	1.78	2.12
Excess C flux (kg C m ⁻² yr ⁻¹)	-	0.30	0.81
Biomass Production (kg C m ⁻² yr ⁻¹)	1.14±0.12	0.96	0.94
Litter C flux (kg C m ⁻² yr ⁻¹)	0.69±0.15	0.91	0.83
Leaf C (kg C m ⁻²)	0.37±0.2	0.38	0.40
Wood C (kg C m ⁻²)	22.01	22.4	24.71
Root C (kg C m ⁻²)	0.37±0.2	0.38	0.40
Vegetation C (kg C m ⁻²)	22.75±0.3	23.16	25.52
Soil C stock (kg C m ⁻²)	12.7	13.2	12.71
LAI (m ² m ⁻²)	5.6±0.36	5.77	6.12

703
704 **3.1.3 Comparison of JULES C, CN and CNP under ambient CO₂ at study site**

705
706 We compare simulated C pools and fluxes from JULES-C, JULES-CN and JULES-CNP (Figure 3). There is no
707 difference between C stocks and fluxes in simulations from JULES C and CN indicating that there is no N
708 limitation at this tropical site in the CN simulations. However, simulated BP and litter flux of C by JULES
709 C/CN are higher than in JULES-CNP but also overestimate the observations (litter flux of JULES C/CN: 1.18,
710 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 obs 1.14-
711 1.31 (kg C m⁻² yr⁻¹), respectively). By including P cycling in JULES an excess C flux of 0.3 (kg C m⁻² yr⁻¹) is
712 simulated, indicating a 24% P limitation to BP at this site according to JULES-CNP, which represents a 29%
713 decrease in BP compared to JULES-C/CN. Consequently, the total vegetation C stock for models without P
714 inclusion is higher than the CNP version (+3% difference) due to the lack of representation of P limitation. The
715 simulated soil C stock in JULES C and JULES CN is also higher than in the CNP version (JULES C/CN: 13.93
716 vs. JULES-CNP: 13.18 (kg C m⁻² yr⁻¹)) and higher than the observations. Moreover, CUE in JULES C/CN
717 (eq.54) is higher than observations and JULES-CNP (JULES C/CN: 0.38 vs. JULES-CNP: 0.31, obs: 0.34
718 ±0.1(dimensionless)).

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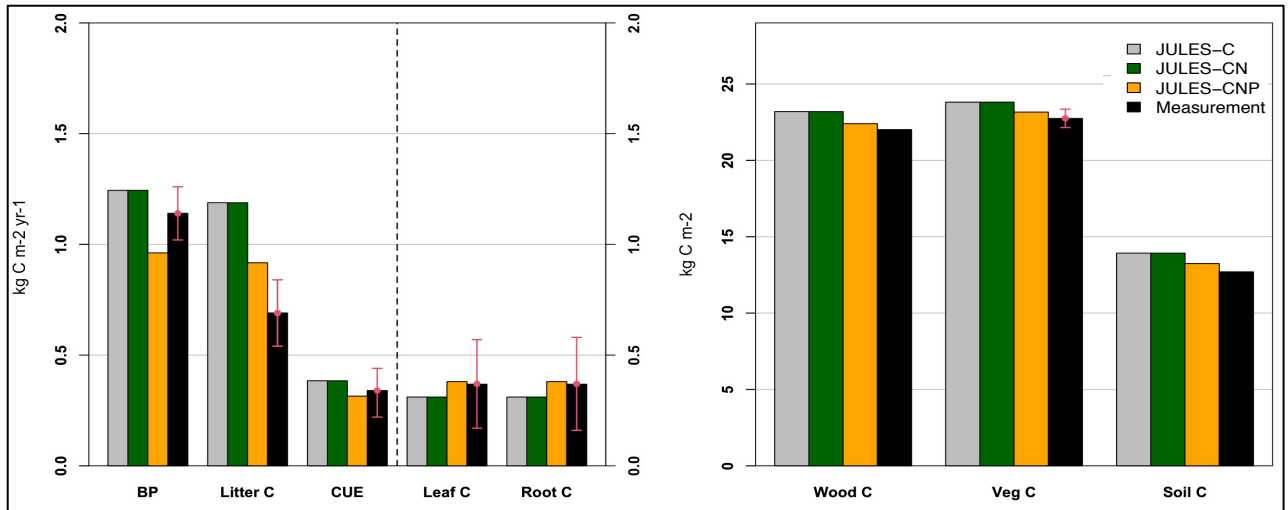


Figure 3- JULES C, CN, CNP modelled vs measured C pools (Leaf, root, wood, Veg and Soil C) (in kg C m⁻²) and fluxes (BP and Litter C) (in kg C m⁻² yr⁻¹) and CUE under ambient CO₂. Note that CUE is unitless.

3.1.4 Model evaluation at test sites under ambient CO₂

Evaluation of JULES C, CN and CNP at five test sites against the observed C pools and fluxes demonstrate that the inclusion of P processes improved the simulation of C pools and fluxes across all test sites (Figure 4). At all Amazon sites JULES C and CN overestimated BP compared to JULES-CNP which estimated lower BP values which were closer to the measurements for AGP (JULES-C: +35%, JULES-CN: +33%; JULES-CNP: +21%), CAX (JULES-C: +45%, JULES-CN: +44%; JULES-CNP: +7%) and SA3 (JULES-C: +27%, JULES-CN: +26%; JULES-CNP: -23%). Moreover, at Gigante Peninsula the C and CN versions overestimated BP (+42% and +40%, respectively), and CNP slightly underestimated BP (-15%). Furthermore, at the Hawaii Kokee site, all three versions of JULES underestimated the BP (C:-8%, CN:-8%, CNP: -32%). The litterfall and respiration fluxes in JULES-CNP have decreased compared to the JULES C and CN versions which overestimated both fluxes at all the test sites compared to the measurements. The litterfall flux comparisons show a significant overestimation using JULES C and CN versions across all the tested sites. Along the Amazon sites inclusion of P limitation reduced the litterfall flux but still overestimated (AGP: +50%, CAX: +24% and SA3: +16%) and at Gigante Peninsula and Hawaii Kokee slightly underestimated (Gigante Peninsula: -9% and Hawaii Kokee -19%). The respiration measurements were only available at two Amazon sites (CAX and SA3) at which inclusion of P limitation resulted in a well estimated flux at both sites compared to the JULES C/CN versions (CAX site: C-only: +38%, CN: +38%, CNP: -1%; SA3 site: C-only: +38%, CN: +38%, CNP: -2%). The total vegetation biomass also reduced using JULES-CNP compared to the other versions and yield closer values to the measurements across all the sites. However, except at the AGP site in which all three versions of JULES slightly underestimated the biomass (C: -1%, CN: -1%, CNP: -6%), at the other test sites JULES-CNP estimated lower biomass pools compared to the other versions which overestimated total vegetation biomass. Similarly, the soil C pool was overestimated prior to P limitation inclusion in JULES at the test sites, and the JULES-CNP estimated a closer value compared to the measurements (slight underestimation at CAX and SA3 sites: -5% and -18% respectively, and close values at Gigante Peninsula and Hawaii Kokee: +3% and +4%, respectively).

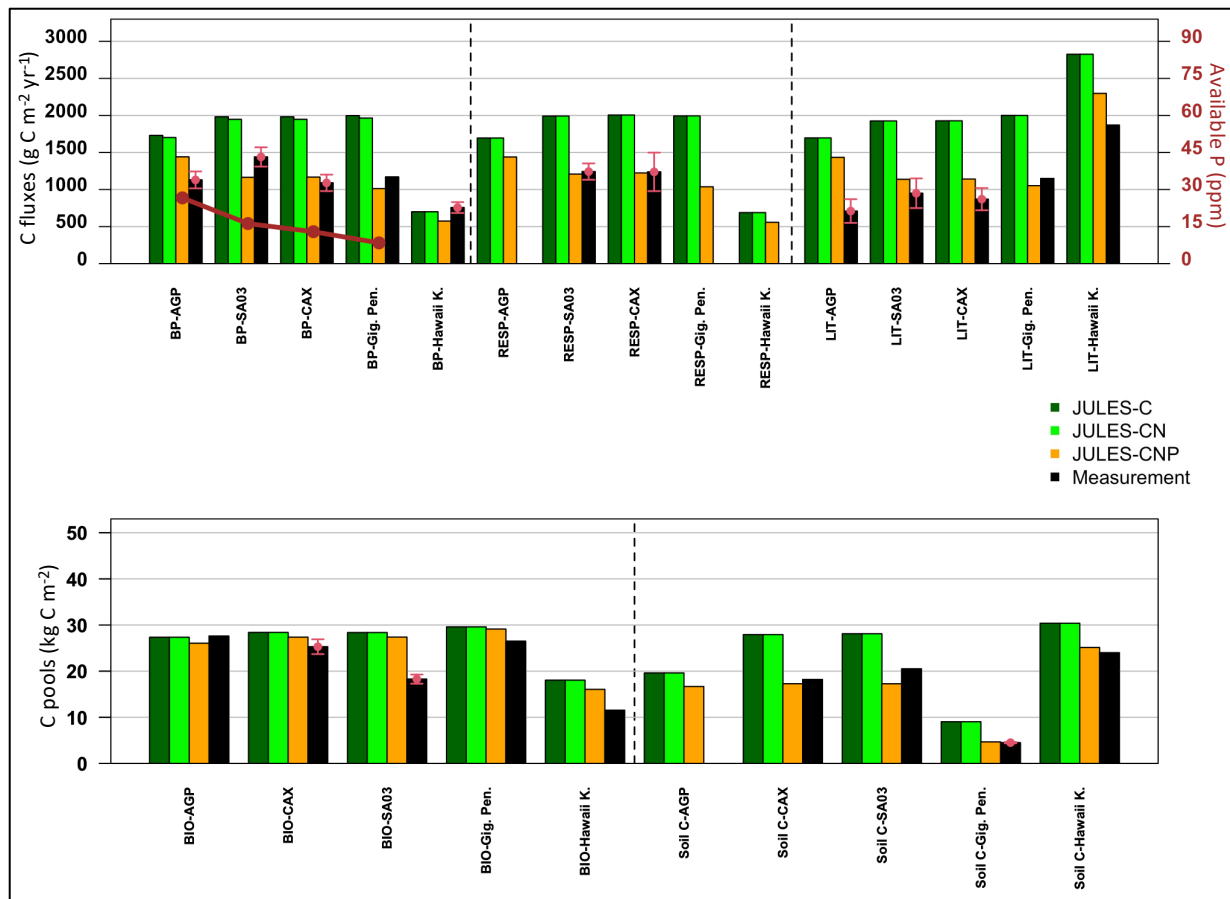


Figure 4- Observed and simulated (JULES C, CN, CNP) C fluxes and pools (averaged measurements: red points, sd: red arrows) and available observed P (dark red points and lines (reported in ppm)) at test sites across the Amazon (AGP, SA03, CAX), Gigante Peninsula (Gig. Pen.) and Hawaii Kokee (Hawaii K.).

3.1.5 Model sensitivity

The results indicate that among all the corresponding C and P pools and fluxes, the excess C flux – which demonstrates P limitation to growth – shows the highest sensitivity to changes in C:P ratios (Figure 5-a), K_P (Figure 5-b), and K_{or-max} (Figure 5-c) and K_{in-max} (Figure 5-d). A decrease in plant C:P results in a large increase in excess C. This is due to the higher plant P demand as a result of lower plant C:P ratios. An increase in the uptake factor and maximum sorbed organic and inorganic P also results in an increase in excess C. This is due to the higher uptake demand through higher uptake capacity (due to higher K_P) and lower available P for uptake due to higher organic and inorganic sorbed P (due to higher K_{or-max} , K_{in-max}). Since the total P in the system is lower than the plant demand, the uptake capacity and sorbed P, higher P limitation is placed on growth (decreasing BP) which results in an increase in excess C and decrease in plant C, but also soil C which is a result of lower litter input (Figure 5). Total soil P shows low sensitivity to changes in plant C:P and uptake factor but high sensitivity to maximum inorganic sorbed P. Moreover, sorbed P shows middle to high sensitivity to maximum organic and inorganic sorbed P respectively (Figure. S5). Nevertheless, organic and inorganic P adsorption coefficients ($K_{sorp-or}$, $K_{sorp-in}$) show no sensitivity to C and P pools and fluxes. This is due to limiting the organic and inorganic P sorption terms to be controlled only by maximum sorption capacity, hence no effect applied by organic and inorganic adsorption coefficients.

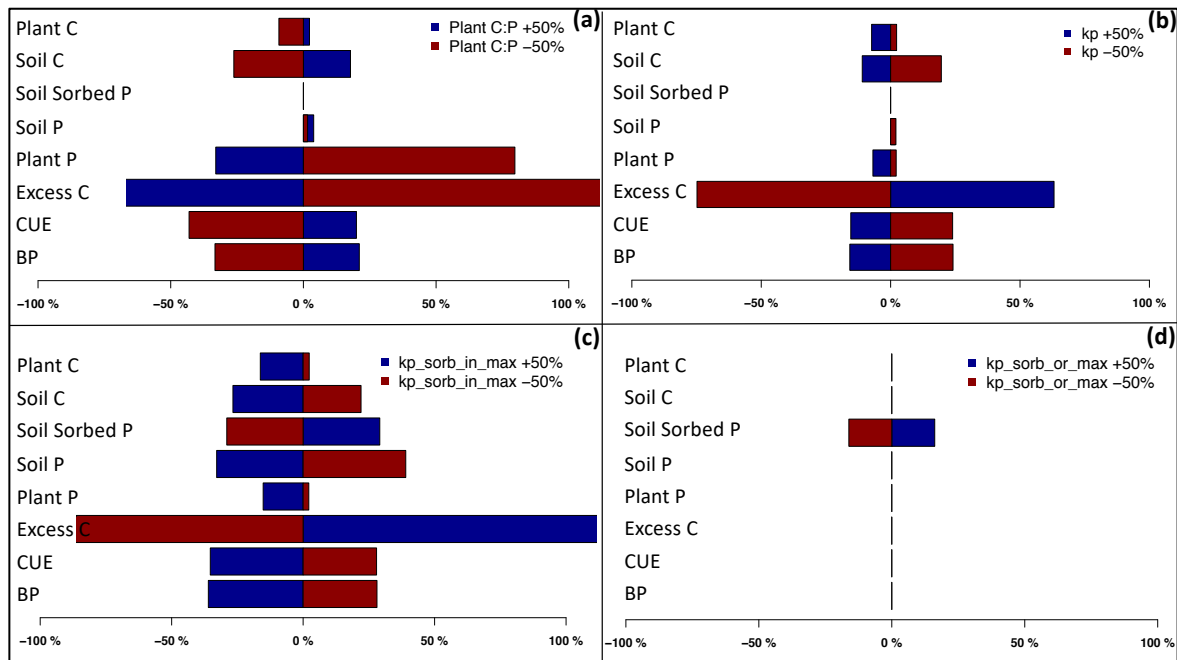


Figure 5- Sensitivity of C and P pools to variation in key model parameters: prescribed tissue C:P (a), Kp(b), Kp_sorb_in(c), Kp_sorb_or(d) under ambient CO₂.

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3.2 Model application under elevated CO₂

3.2.1 Simulated plant and soil C and P pools and fluxes -JULES-CNP: eCO₂ vs ambient CO₂

The eCO₂ simulation using JULES-CNP yields a higher GPP compared to the ambient CO₂ (0.83 (kg C m⁻² yr⁻¹) increase), as a result of CO₂ fertilization. Moreover, due to the GPP increase, NPP and RESP also increased compared to ambient CO₂ (NPP: 0.49 and RESP:0.3 (kg C m⁻² yr⁻¹) increase) (Table 7). The total simulated vegetation C pool increases under eCO₂ compared to ambient CO₂ (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 6). Thus, the simulated plant P demand is higher, and as the total available soil P for uptake is limited, the simulated excess C flux increases to 0.51(kg C m⁻² yr⁻¹). Moreover, despite the higher NPP under eCO₂ compared to simulated NPP under ambient CO₂, due to the substantial increase in simulated excess C, the BP is similar to the ambient CO₂ (2% difference).

The simulated organic soil P under eCO₂ were close to those under ambient CO₂ (1.6 g P m⁻²) (Table 7). This is due to the same parameterization of the output fluxes from this pool for eCO₂ and ambient CO₂. The simulated pool of inorganic P under eCO₂ decreases compared to the ambient CO₂ 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 eCO₂ are similar to those simulated under the ambient CO₂ which is due to the same parameterization of sorption function (maximum sorption capacity) from the ambient CO₂ run as explained in calibration section. Moreover, the modelled occluded and weathered soil P were similar to those in the ambient CO₂ simulation (Table 7) 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 CO₂

JULES C/CN show higher vegetation and soil C pools, BP and litter flux compared to JULES-CNP: (Table 8, Figure. S2). Under eCO₂, 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 excess C flux of 0.81 (kg C m⁻² yr⁻¹) equivalent to 46% P limitation under eCO₂. As a result of P limitation and eCO₂, the simulated CO₂ fertilization effect estimated based on changes in biomass under ambient and eCO₂ 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.

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Table 8. Simulated C pools and fluxes with JULES C/CN and difference in percentage with JULES-CNP model under eCO₂. 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%

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3.2.2.1 Inter-models under elevated CO₂

Following Fleischer *et al.*, (2019), we report the simulated response to eCO₂ 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 eCO₂, simulated GPP and NPP during the 1st year increase by 30% and 61% respectively and by 28% and 52% after 15 years (Figure. 6). However, using JULES-CNP, eCO₂ 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 eCO₂ using JULES C/CN, respectively. However, using JULES-CNP, simulated CUE for the 1st and after 15 years is reduced by 7% and 17% in response to eCO₂.

Simulated total biomass (leaf, fine root and wood C) (ΔC_{veg}) using JULES- C/CN for the 1st and 15 years of eCO₂ increased by 9% and 13% respectively. However, using JULES-CNP ΔC_{veg} only increases by 0.5% and 9% for 1st and 15 years of eCO₂, respectively.

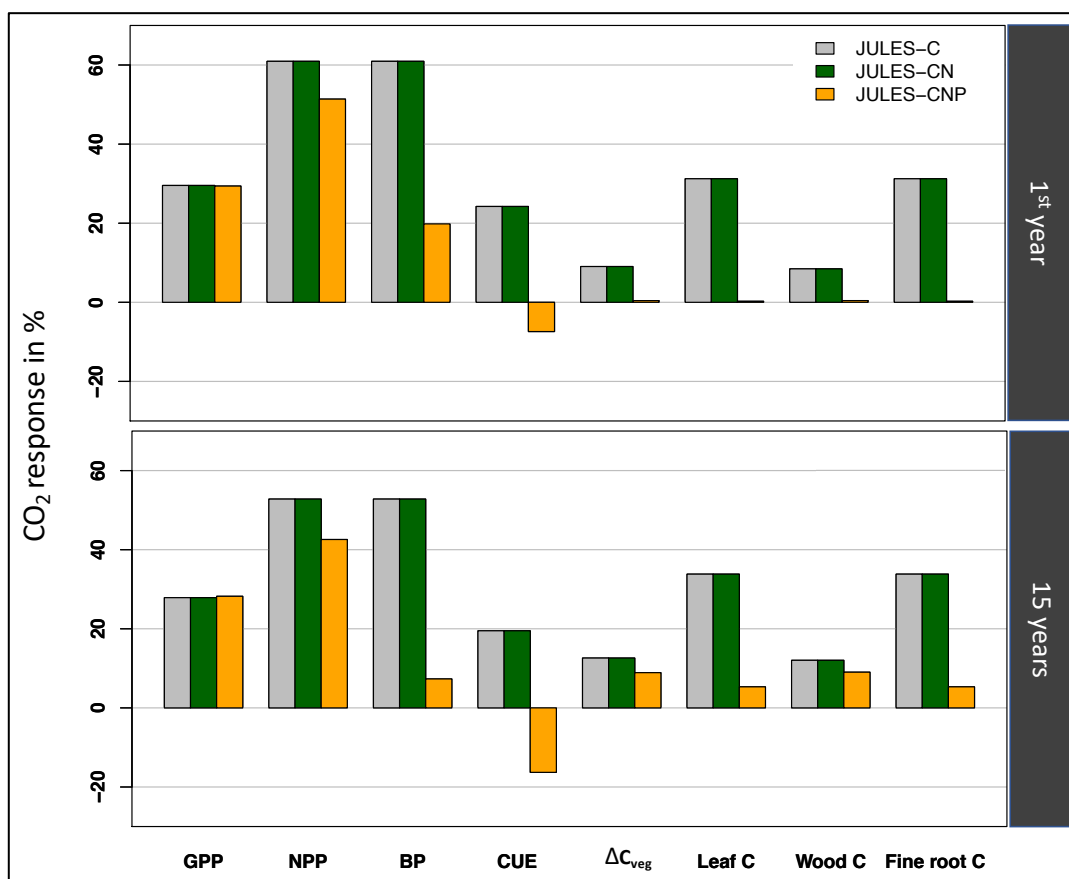


Figure. 6- Relative effect of eCO₂ on simulated GPP, NPP, BP, CUE, ΔC_{veg} , leaf C, wood C and fine root C, using three versions of JULES model in 1st (initial response) and 15 years periods (final response).

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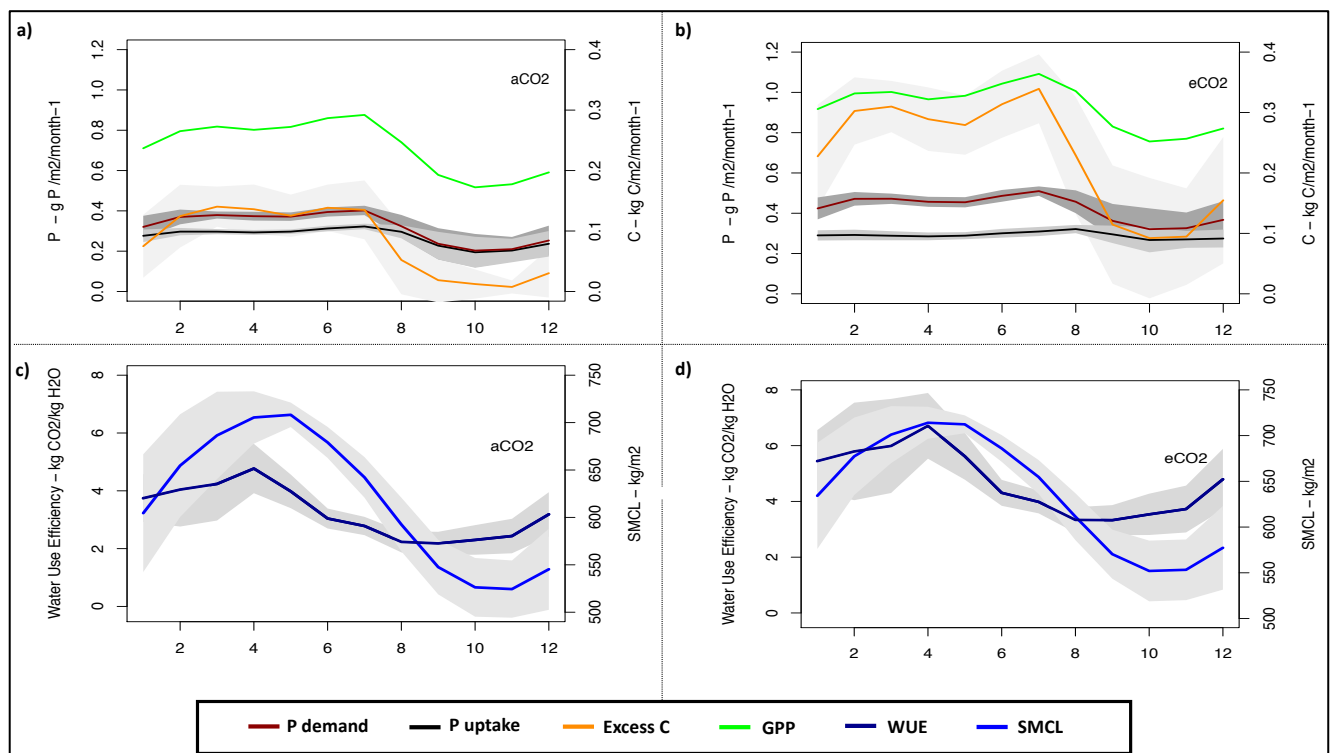
843 **3.3 Plant P Demand, uptake and excess C under ambient and elevated CO₂**
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845 To understand further the CP-cycle dynamics, we studied the monthly averaged plant P demand and the relative
 846 (limited) P uptake (eq. 26) under both ambient and elevated CO₂ conditions (Figure. 7).
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848 Under ambient CO₂ condition the highest GPP is estimated at $0.29 \pm 0.016 \text{ kg C m}^{-2} \text{ month}^{-1}$ in July and the
 849 lowest at $0.17 \pm 0.051 \text{ kg C m}^{-2} \text{ month}^{-1}$ in October (Figure. 7-a). The estimated WUE and SMCL in October is
 850 among the lowest estimated monthly values at $2.3 \pm 0.51 \text{ kg CO}_2/\text{kg H}_2\text{O}$ and $526.2 \pm 31 \text{ kg m}^{-2}$ respectively
 851 (Figure. 7-c). The highest P demand is estimated at $0.4 \pm 0.02 \text{ g P m}^{-2} \text{ month}^{-1}$ in July and the lowest demand at
 852 $0.2 \pm 0.08 \text{ g P m}^{-2} \text{ month}^{-1}$ in October. Consequently, the highest and lowest uptake (0.32 ± 0.01 and $0.19 \pm 0.07 \text{ g P}$
 853 $\text{m}^{-2} \text{ month}^{-1}$, respectively). The excess C for the highest and lowest GPP and demand periods are estimated at
 854 0.4 ± 15 and $0.04 \pm 0.07 \text{ kg C m}^{-2} \text{ month}^{-1}$, respectively.
 855

856 However, similar to ambient CO₂, under eCO₂ condition the highest estimated GPP is in July at $0.36 \pm 0.017 \text{ kg}$
 857 $\text{C m}^{-2} \text{ month}^{-1}$ and lowest for October $0.25 \pm 0.062 \text{ kg C m}^{-2} \text{ month}^{-1}$ (Figure. 7-b). The estimated WUE and soil
 858 moisture content (SMCL) for the lowest GPP period is among the lowest monthly estimated values at 3.5 ± 0.74
 859 $\text{kg CO}_2/\text{kg H}_2\text{O}$ and $552 \pm 33 \text{ kg m}^{-2}$ for October respectively (Figure. 7-d). The highest P demand is estimated
 860 for July at $0.51 \pm 0.02 \text{ g P m}^{-2} \text{ month}^{-1}$ with the uptake flux of $0.31 \pm 0.02 \text{ g P m}^{-2} \text{ month}^{-1}$ and the lowest demand
 861 is estimated for October at $0.32 \pm 0.1 \text{ g P m}^{-2} \text{ month}^{-1}$ with the estimated uptake flux of $0.26 \pm 0.06 \text{ g P m}^{-2} \text{ month}^{-1}$
 862 ¹. The highest excess C flux is also for July at $1.01 \pm 0.17 \text{ kg C m}^{-2} \text{ month}^{-1}$ and lowest for October $0.27 \pm 0.29 \text{ kg}$
 863 $\text{C m}^{-2} \text{ month}^{-1}$, respectively.
 864

865 However, despite the P limitation in both eCO₂ and ambient CO₂ conditions, the P uptake flux under eCO₂ is
 866 higher than the ambient CO₂ condition. This is due to the higher WUE and increased SMCL (controlling uptake
 867 capacity (eq. 27)) under eCO₂ condition, hence more water availability during the dry season to maintain
 868 productivity and critically transport P to the plant (see eq. 27), compared to ambient CO₂ condition (Figure. 7-c
 869 and d). Additionally, in JULES both the vertical discretisation (Burke, Chadburn and Ekici, 2017) and
 870 mineralisation terms (Wiltshire *et al.*, 2021) depend on the soil moisture and temperature. Thus, higher P
 871 concentration and uptake under eCO₂ condition.
 872



873 **Figure. 7-** Simulated monthly plant P demand and uptake ($\text{g P m}^{-2} \text{ month}^{-1}$), excess C and GPP ($\text{kg C m}^{-2} \text{ month}^{-1}$) under a)
 874 aCO₂ and b) eCO₂, water use efficiency ($\text{g m}^{-2} \text{ month}^{-1}$) under c) ambient CO₂ (aCO₂) and d) eCO₂ conditions. The grey area
 875 represents the standard deviation.
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3.4 Soil P pools profile under ambient CO₂ and elevated CO₂

We explored the distribution of the inorganic and organic soil P and their sorbed fraction within the soil layers and under different CO₂ conditions (Figure. S3). Both the ambient and eCO₂ simulations have a close inorganic soil P distribution at the topsoil layer (0-30cm) (0.85 vs. 0.9 (g P m⁻²) respectively) as well as similar organic soil P distribution (0.85 vs 0.9 (g P m⁻²) respectively).

However, the organic soil P and sorbed forms of inorganic and organic soil P profiles are not changing significantly between different sets due to the similar parameterization of the processes that control these pools (processes which are related to the physical aspects of soils, hence not changing under eCO₂ condition) and the same parameter values used for both ambient and eCO₂ runs.

Moreover, the soil P within 30cm soil depth for ambient and eCO₂ conditions is at 14.7 (g P m⁻²) and 14.56 (g P m⁻²) respectively, and the total ecosystem P for both ambient and eCO₂ conditions is at 35.97 (g P m⁻²).

However, the slightly lower soil P in the eCO₂ condition is due to the higher plant P demand compared to the ambient condition, hence the higher allocated P vegetation (10%) under eCO₂ condition.

4. Discussion

Studies show the significant role of the tropical forests, and Amazonia in particular, in C uptake and regulating atmospheric CO₂ (Brienen *et al.*, 2015; Phillips *et al.*, 2017). As soil P availability is low in the majority of Amazonia (Quesada *et al.*, 2012), the competition for nutrients by both plant and soil communities is high (Lloyd *et al.*, 2001). The responses of these communities to eCO₂ under P limited conditions remains uncertain (Fleischer *et al.*, 2019). These responses in P enabled models are represented in different ways regarding the excess C which is not used for plant growth due to P limitation. Either growth is directly downregulated taking the minimum labile plant C, N and P (Goll *et al.*, 2017), or photosynthesis is downregulated via V_{cmax} and J_{max} (Comins and McMurtrie, 1993; Yang *et al.*, 2014; Zhu *et al.*, 2016) and models like JULES-CNP downregulate NPP via respiration of excess carbon that cannot be used for growth due to plant nutrient constraints (Haverd *et al.*, 2018). The estimated CUE depends on the modelling approach. Models that down regulate the photosynthetic capacity and GPP consequently (Comins and McMurtrie, 1993; Yang *et al.*, 2014; Zhu *et al.*, 2016) simulate a positive CUE response to CO₂ fertilization while models that down regulate the NPP and respire the excess C (Haverd *et al.*, 2018) simulate a negative CUE response (Fleischer *et al.*, 2019) which is in line with field studies showing lower CUE when nutrient availability declines (Vicca *et al.*, 2012b). However, this remains a major uncertainty in understanding the implication of P limitation on terrestrial biogeochemical cycles.

The JULES-CNP structure represent key P processes in both plant and soil pools and can be applied to the Amazon region using existing soil (Quesada *et al.*, 2011) and foliar structural and nutrient (Fyllas *et al.*, 2009) data for parameterisation. The model can be applied globally and under future climate projections using global soil P data (Sun *et al.*, 2021) for model initialization and PFT-specific plant (Zechmeister-Boltenstern *et al.*, 2015) and soil stoichiometries (Zechmeister-Boltenstern *et al.*, 2015; Tipping *et al.*, 2016), sorption and weathering ratios (based on lithological class specific from the GLiM lithological map (Hartmann and Moosdorf, 2012) and soil shielding from Hartmann *et al.*, (2014)).

4.1. Evaluation of model performance

At the study site, JULES-CNP could reproduce the magnitude of soil organic and inorganic P pools and fluxes. The relative distribution of total organic P, total inorganic P and residue P fractions of total P in soils under Brazilian Eucalyptus plantations (Costa *et al.*, 2016) shows inorganic P fraction of 28% from total soil P which is close to our estimation of 24% and organic P fraction of 30% from total soil P which is higher than our estimated fraction of 18%. Thus, we may need to improve the process representation or parameters that control the organic P concentration, such as litter flux and decomposition, soil organic P mineralization, and immobilization in the future.

Our estimated maximum P uptake, which represents the actual available P for plant uptake (Goll *et al.*, 2017), for both ambient and eCO₂, is highly correlated with the plant P demand ($R^2 = 0.96$ and 0.52 respectively). The plant P demand depends on the GPP changes which are reflected by the WUE (Hatfield and Dold, 2019). Hence, under ambient CO₂, JULES-CNP simulates lower GPP and plant P demand during the dry season than during the wet season. Sufficient P uptake during these periods results in the lowest P limitation, thus the lowest simulated excess C. Nevertheless, under eCO₂ the same pattern is simulated but a higher availability of soil P due to the stomatal closure in the dry season. Hence, due to the plant's more efficient water usage, the soil

939 moisture in the dry season is higher (Xu *et al.*, 2016) which impacts our capped P uptake flux (eq. 27) and
940 increases the uptake capacity respectively.

941
942 Overall, JULES-CNP reproduced the observed C pools and fluxes which are in the acceptable ranges compared
943 to the measurements. However, using the JULES default V_{cmax} estimation method (eq. 40), the model slightly
944 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,
945 we used the improved V_{cmax} estimation method based on N and P (eq. 46) which resulted in a final estimated
946 GPP closer to the measurements (3.06 kg C m⁻² yr⁻¹).

947
948 Our results show an increase in GPP (21%) in response to eCO₂ which is higher than the average increase of
949 GPP reported in mature eucalyptus forests (11%), also growing under low P soils at the free air CO₂ enrichment
950 experiment (EucFACE) facility in Australia (Jiang *et al.*, 2020). This can be related to the lower decrease of
951 biomass growth response estimated by JULES-CNP (-3%) compared to the measurements from mature
952 eucalyptus forests (-8%) (Ellsworth *et al.*, 2017), due to the P limitation which was shown to impact the above-
953 ground biomass growth response in mature forests (Körner *et al.*, 2005; Ryan, 2013; Klein *et al.*, 2016).

954
955 In order to estimate the biomass production (BP), we deducted the excess C fluxes from NPP. Using JULES
956 C/CN models, the simulated biomass productivity enhancement due to eCO₂ (49%) is in the middle range of the
957 reported for different biomes by Walker *et al.*, (2021). Moreover, our estimated difference of BP between
958 ambient and eCO₂ conditions (2%) is close to the estimated difference for mature forests (3%) (Jiang *et al.*,
959 2020).

960
961 A global estimation for tropical forests using the CASA-CNP model which includes N and P limitations on
962 terrestrial C cycling, shows that NPP is reduced by 20% on average due to the insufficient P availability (Wang,
963 Law and Pak, 2010) which is close to our estimated P limitation of 24%. This finding is in line with a field study
964 that shows a strong correlation between the total NPP and the soil available P (Aragão *et al.*, 2009).
965 The estimated decrease of NPP in response to eCO₂ as a result of P limitation is in line with the findings from
966 CLM-CNP model at five tropical forests (Yang *et al.*, 2014) which indicates the CO₂ fertilization dependency
967 on the processes that affect P availability or uptake.

968
969 Our estimated CUE (0.31) is close to that by Jiang *et al.* (2020) for mature eucalyptus forests (0.31±0.03), as
970 well as to the measurement for our study site (0.34 ±0.1). There is currently a lack of representation of stand age
971 in JULES-CNP which can significantly affect CUE (e.g. mature trees are less responsive to the nutrient
972 limitations) (De Lucia *et al.*, 2007; Norby *et al.*, 2016). However, a recent development of Robust Ecosystem
973 Demography (RED) model in JULES (Argles *et al.*, 2020) and its integration into JULES-CNP in the future can
974 address this issue.

975
976 Under low P availability, all available P is considered to be adsorbed or taken by plant and microbes for further
977 consumption, with leaching considered to be minor within the time scales of our study period (Went and Stark,
978 1968; Bruijnzeel, 1991; Neff, Hobbie and Vitousek, 2000). Despite studies that show the possibility of P
979 fixation as a source of available P for plants (Van Langenhove *et al.*, 2020; Gross *et al.*, 2021), due to the strong
980 fixation of P in the soil (Aerts & Chapin, 2000; Goodale, Lajtha, Nadelhoffer, Boyer, & Jaworski, 2002), the P
981 deposited is unlikely to be available to plants in the short term (de Vries *et al.*, 2014), for this reason this
982 version of JULES-CNP did not include P deposition. However both P deposition and leaching are likely to have
983 a very important role on sustaining the productivity of tropical forests in the Amazon over longer time scales
984 (Van Langenhove *et al.*, 2020) and needs to be considered in future studies. Moreover, biochemical
985 mineralisation is also not included in the current version of JULES-CNP which only accounts for total
986 mineralization. However, models that include this process show no significant difference between total and
987 biochemical mineralized P which can be due to complexity of identifying the inclination of mineralization
988 versus uptake (Martins *et al.*, 2021). Lastly, in order to capture plant internal nutrient impact on the C storage,
989 future work should focus on implementing recent developments including Non-Structural Carbohydrate pools
990 (NSC) (Jones *et al.*, 2020) in JULES-CNP.

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4.1.1. Evaluation of model performance at test sites

Overall, inclusion of P processes in JULES-CNP improved the previously overestimated C fluxes and pools using JULES-C and -CN versions. Generally, the biomass productivity tends to follow the observed P availability (Figure 4), where the sites with higher available P for uptake simulated higher productivity which is in line with observations across P availability in the Amazon (Aragão *et al.*, 2009). Nevertheless, this tendency could be altered if the natural conditions in these forests are perturbed. For instance, in case of the high mortality events in these P limited sites (Malhi *et al.*, 2009; Pyle *et al.*, 2009), regrowing forests developing over the highly weathered oxisols with limited available P (Davidson *et al.*, 2004), results in the shifting limitation from P to N (Herbert, Williams and Rastetter, 2003). Hence, the controlling processes under N limitation will be N-related and processes such as N leaching or outgassing (Yang *et al.*, 2014) will define the productivity. This shifting in limitation condition is not represented by JULES-CNP, therefore at few tested sites the model overestimated the P limitation, thus underestimated the productivity below the measured values. Moreover, the higher (than other sites) BP in JULES C/CN at the the Gigante Peninsula is related to the higher solar radiation in the forcing data at this site (Figure S8).

The estimated litterfall and respiration fluxes were considerably lower with JULES-CNP than JULES-C and -CN due to the lower simulated NPP with the former in closer agreement with the observations at all sites. Consequently, the total vegetation and soil C pools have lower values under the P limitation (Malhi *et al.*, 2009), which could not be captured by JULES-C and -CN and successfully represented by JULES-CNP.

As shown in Figure 5, JULES-CNP is highly sensitive to the five parameters needed to run JULES-CNP in addition to JULES-C and JULES-CN which were prescribed for simulations at test sites. The successful model performance at these sites demonstrates the importance of these parameters in JULES-CNP with implications for global scale simulations.

4.2. Inter-models Comparison of JULES C, CN and CNP

The comparison of simulated GPP enhancement across JULES versions for the 1st year is within the middle range of the 1st year CO₂ responses of the C/CN models studied by Fleischer *et al.*, (2019) evaluating simulated eCO₂ effects at a site in Manaus using the same meteorological forcing and methodology used in this study for a range of DGVM's. However, comparison for 15 years of eCO₂, shows that the simulated response with JULES-CNP is on the higher end of Fleischer *et al.*, (2019) study which is due to the higher estimated biomass growth by JULES-CNP (Table S1). Similarly, using JULES-CNP our estimated GPP enhancement is on the higher end of model estimations in Fleischer *et al.*, (2019). Moreover, comparing the GPP responses between different versions of (JULES C/CN and CNP), the JULES-CNP shows a slightly higher response to CO₂ fertilization associated with the higher WUE changes (Xiao *et al.*, 2013) (Figure. S4). This is due to the higher sensitivity of the plant to water availability than P availability in the P limited system (He and Dijkstra, 2014). Hence, under eCO₂ due to water-saving strategy of plants and stomatal closure (Medlyn *et al.*, 2016), simulated transpiration is decreased (Sampaio *et al.*, 2021) and photosynthesis is enhanced compared ambient CO₂.

To that end, the monthly changes of WUE in JULES-CNP are highly correlated to the GPP, hence the lowest and highest WUE follow the same periods as GPP similar to responses captured with models studied by Fleischer *et al.*, (2019) (Table. S1).

Our estimated NPP enhancement using JULES C/CN models for both 1st and 15 years period is within the middle range of the models in Fleischer *et al.*, (2019). Nevertheless, JULES-CNP response of BP is in the lower band of the CNP models in Fleischer *et al.*, (2019) and close to the estimations from CABLE (Haverd *et al.*, 2018) and ORCHIDEE (Goll *et al.*, 2017) models, which may be due to the similar representation of P processes and limitation between these models. However, our results show a 29% decrease in NPP using JULES-CNP compared to JULES-C/CN which is smaller than the differences between the CLM-CNP and CLM-CN versions (51% decrease) (Yang *et al.*, 2014). The lower estimated decrease in JULES highlights the need to further study the fully corresponding plant C pools and fluxes to the changes in soil and plant P. Therefore, future work should be focused on the improvement of the total P availability and the plant C feedbacks. Moreover, there are other environmental factors such as temperature which shows a possible impact on the CO₂ elevation and the changes of NPP (Baig *et al.*, 2015) which needs further improvement in our model.

The CUE estimations of 1st year and 15 years response to CO₂ elevation from JULES C/CN are in the middle range of C/CN models in Fleischer *et al.*, (2019). However, the estimated CUE using JULES-CNP for 1st and 15 years are in the low range of CNP models reported by Fleischer *et al.*, (2019) which is due to the same reason discussed for NPP comparison.

1059 Finally, our estimated total biomass enhancement (ΔC_{veg}) using JULES C/CN for the 1st and 15 years are in the
1060 middle range of C/CN models from Fleischer *et al.*, (2019) and in lower range of CNP models from Fleischer *et al.*
1061 *et al.*, (2019) using JULES-CNP. Nevertheless, while JULES-CNP includes the trait-based parameters (Harper *et al.*
1062 *et al.*, 2016), other functions such as flexible C allocation and spatial variation of biomass turnover are still
1063 missing and future model improvement should be focused on their inclusion.

1064 1065 **5. Conclusion**

1066 Land ecosystems are a significant sink of atmospheric CO₂, ergo buffering the anthropogenic increase of this
1067 flux. While tropical forests contribute substantially to the global land C sink, observational studies show that a
1068 stalled increase in carbon gains over the recent decade (Brienen *et al.*, 2015; Hubau *et al.*, 2020). However
1069 modelling studies that lack representation of P cycling processes predict an increasing sink (Fernández-Martínez
1070 *et al.*, 2019; Fleischer *et al.*, 2019). This is particularly relevant for efforts to mitigate dangerous climate change
1071 and assumptions on the future efficacy of the land C sink. Therefore, in this study, we presented the full
1072 terrestrial P cycling and its feedback on the C cycle within the JULES framework. Our results show that the
1073 model is capable of representing plant and soil P pools and fluxes at a site in Central Amazon and across the
1074 extended P limited test sites in Amazon, Gigante Peninsula and Hawaii chronosequence provided with site level
1075 data for model parameterisation. Moreover, the model estimated a significant NPP limitation under ambient
1076 CO₂, due to the high P deficiency at these sites which is representative of Central Amazon and tropical P limited
1077 sites, and elevated CO₂ resulted in a further subsequent decrease in the land C sink capacity relative to the
1078 model without P limitation. While our study is a step toward the full nutrient cycling representation in ESMs, it
1079 can also help the empirical community to test different hypotheses (i.e., dynamic allocation and stoichiometry)
1080 and generate targeted experimental measurements (Medlyn *et al.*, 2015).

1081 1082 *Code availability*

1084 The modified version of JULES vn5_5 and the P extension developed for this paper are freely available on Met
1085 Office Science Repository Service:
1086 https://code.metoffice.gov.uk/svn/jules/main/branches/dev/mahdinakhavali/vn5.5_JULES_PM_NAKHAVALI/
1087 after registration (http://jules-lsm.github.io/access_req/JULES_access.html) and completion of software license
1088 form. Codes for compiling model available at: (<https://doi.org/10.5281/zenodo.5711160>). Simulations were
1089 conducted using two sets of model configurations (namelists): ambient CO₂ condition
1090 (<https://doi.org/10.5281/zenodo.5711144>) and elevated CO₂ condition
1091 (<https://doi.org/10.5281/zenodo.5711150>).

1092 *Data availability*

1093 The model outputs related to the results in this paper are provided on Zenodo repository
1094 (<https://doi.org/10.5281/zenodo.5710898>). All the R scripts used for processing the model outputs and
1095 producing results in form of table or figures are provided on Zenodo repository
1096 (<https://doi.org/10.5281/zenodo.5710896>).

1097 *Author contributions.* MAN, LMM, SS, SEC, CAQ, AJW, IAP, KMA and DBC developed the model, per-
1098 formed simulations and analysis. CAQ, FVC, RP, LFL, KMA, GR, LS, ACMM, JSR, RA and JLC provided the
1099 measurements for the model parasitisation and evaluation. MAN, LMM, SS, IAP, SEC, FVC, RP, LFL, KMA
1100 and DBC contributed in writing the manuscript.

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1102 *Competing interests.* The authors declare no competing interests

1103
1104 *Acknowledgments.* This work and its contributors (MAN, LMM, KMA and IPH) were supported by the UK
1105 Natural Environment Research Council (NERC) grant no. NE/LE007223/1. MAN, LMM, SS, IPH were also
1106 supported by the Newton Fund through the Met Office Climate Science for Service Partnership Brazil (CSSP
1107 Brazil). LMM acknowledges support from the Natural Environment Research Council, grant NEC05816 LTS-
1108 M-UKESM. LFL was also supported by AmazonFACE programme (CAPES) and the National Institute of
1109 Amazonian Research, grant no: 88887.154643/2017-00. The authors acknowledge contributions from Celso
1110 Von Randow towards data curation of the meteorological forcing used in this study and Daniel Goll for
1111 modelling insight. We would like to thank Alessandro C. de Araújo and the Large-Scale Biosphere-Atmosphere
1112 Program (LBA), coordinated by the National Institute for Amazon Researches (INPA), for the use and
1113 availability of data.

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