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

Mahdi (André) Nakhavali¹, Lina M. Mercado¹,², Iain P. Hartley¹, Stephen Sitch¹, Fernanda V Cunha³, Raffaello di Ponzio³, Laynara F. Lugli³, Carlos A. Quesada³, Kelly M. Andersen¹,⁴,⁵, Sarah E. Chadburn⁶, Andy J. Wiltshire¹,⁷, Douglas B. Clark², Gyovanni Ribeiro³, Lara Siebert³, Anna C. M. Moraes³, Jéssica Schmeisk Rosa³, Rafael Assis³ and José L. Camargo³

¹University of Exeter, College of Life and Environmental Sciences, Exeter, EX4 4QE, United Kingdom
²UK Centre for Ecology and Hydrology, Wallingford, OX10 8BB, United Kingdom
³Coordination of Environmental Dynamics, National Institute of Amazonian Research, Manaus, AM 69060-062, Brazil
⁴University of Edinburgh, School of Geosciences, Edinburgh, EH8 9AB, UK
⁵Nanyang Technological University, Asian School of the Environment, Singapore, 639798, Singapore
⁶College of Engineering, Mathematics, and Physical Sciences, University of Exeter, Exeter, EX4 4QE, United Kingdom
⁷Correspondence Office Hadley Centre, Exeter, Devon, EX1 3PB, United Kingdom

Correspondence to: Mahdi (André) Nakhavali (m.nakhavali@exeter.ac.uk)

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 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, accounting for about half of global net primary production (NPP) (Schimel et al., 2015), and store the highest aboveground carbon among all biomes (Pan et al., 2011; Mitochondrion, 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, Högborg 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 hypothesized to be the main constraint (Aerts and Chapin, 1999; Luo et al., 2004). Low P availability in tropical soils is related to the limited unweathered 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; Sardinas, 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 aboveground 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 (Vcmax and Jcmax) 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 (Vcmax) (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 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).

2. Material and methods

2.1 JULES

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

![Diagram of JULES-CNP model scheme]

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

### 2.2.1 P pools

JULES represents eight P pools comprising organic and inorganic P: plant P (P<sub>p</sub>) and soil P pools (in each soil layer (n)), litter P (P<sub>litter</sub>), soil organic P (P<sub>org</sub>), soil inorganic P (P<sub>inorg</sub>), organic sorbed (P<sub>org-sorp</sub>), inorganic sorbed (P<sub>inorg-sorp</sub>), parent material (P<sub>pm</sub>) and occluded (P<sub>acc</sub>) P comprised of both organic and inorganic P. All pools are in units of kg P m<sup>-2</sup> (Fig 1, Tables 1 and 2).

Plant P pool is composed of leaf (P<sub>leaf</sub>), fine root (P<sub>root</sub>) and stem together with coarse root (P<sub>stem</sub>), which are related to their associated C pools (C<sub>leaf</sub>, C<sub>root</sub>, C<sub>stem</sub>) in (kg C m<sup>-2</sup>) and fixed C to P ratios (C: P<sub>leaf</sub>, C: P<sub>root</sub>, C: P<sub>stem</sub>) as follows:

\[
P_{leaf} = \frac{c_{leaf}}{c_{Pleaf}}
\]  
(eq.1)
\[ P_{\text{root}} = \frac{C_{\text{root}}}{C_{\text{P root}}} \]

(eq. 2)

\[ P_{\text{stem}} = \frac{C_{\text{stem}}}{C_{\text{P stem}}} \]

(eq. 3)

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

\[ P_p = P_{\text{leaf}} + P_{\text{root}} + P_{\text{stem}} \]

(eq. 4)

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

\[ \frac{dP_p}{dt} = F_p^{\text{up}} - F_p^{\text{lit}} \]

(eq. 5)

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

\[ \frac{dP_{\text{DPM}}}{dt} = F_p^{\text{lit}} \times \alpha - \text{dec}_p^{\text{DPM},n} \]

(eq. 6)

\[ \frac{dP_{\text{RPM}}}{dt} = F_p^{\text{lit}} \times (1 - \alpha) - \text{dec}_p^{\text{RPM},n} \]

(eq. 7)

\[ P_{\text{lit}} = \sum_{n=1}^{N} P_{\text{DPM},n} + \sum_{n=1}^{N} P_{\text{RPM},n} \]

(eq. 8)

The soil organic pool \( (P_{\text{org}}) \) is represented as the sum of \( P_{\text{BIO}} \) and \( P_{\text{HUM}} \). These pools are estimated from the difference between P inputs from total immobilized \( (F_{\text{immob},p}) \) distributed between BIO and HUM based on fixed fraction (0.46 for BIO, 0.54 for HUM) (Jenkinson et al., 1990; Jenkinson and Coleman, 2008) and desorbed \( P_{\text{bio}}, F_{\text{bio}} \) adsorption \( P_{\text{soil}} \) and P outputs from mineralized \( (F_{\text{min},p}) \), and adsorbed P fluxes \( (F_{\text{soil}}) \) (adsorption: eq. 40 and desorption: eq. 41) with all fluxes expressed in kg P m\(^{-2}\) yr\(^{-1}\) as follows:

\[ \frac{dP_{\text{BIO}}}{dt} = 0.46 \times F_{\text{immob},p} + F_{\text{soil}}^{\text{desorption}} - F_{\text{min},p}^{\text{BIO},n} - F_{\text{soil}}^{\text{adsorption}} \]

(eq. 9)

\[ \frac{dP_{\text{HUM}}}{dt} = 0.54 \times F_{\text{immob},p} + F_{\text{soil}}^{\text{desorption}} - F_{\text{min},p}^{\text{HUM},n} - F_{\text{soil}}^{\text{adsorption}} \]

(eq. 10)

\[ P_{\text{org}} = \sum_{n=1}^{N} P_{\text{BIO},n} + \sum_{n=1}^{N} P_{\text{HUM},n} \]

(eq. 11)

Description of the inorganic sorbed P pool \( (P_{\text{inorg-sorption}}) \) follows Wang et al., (2007) and is represented as the difference between the input flux of inorganic sorption \( (F_{\text{in},p}^{\text{adsorption}}) \) (eq. 37) and output fluxes of inorganic desorption \( (F_{\text{in},p}^{\text{desorption}}) \) (eq. 38) and occluded P \( (F_{\text{P,oc}},) \) (eq. 39), with all fluxes expressed in kg P m\(^{-2}\) yr\(^{-1}\) as follows:

\[ \frac{dP_{\text{inorg-sorption}}}{dt} = \sum_{n=1}^{N} F_{\text{in},p}^{\text{adsorption}} - \sum_{n=1}^{N} F_{\text{in},p}^{\text{desorption}} - \sum_{n=1}^{N} F_{\text{P,oc}} \]

(eq. 12)

The description of the occluded \( (P_{\text{oc}}) \) P pool follows Wang et al., (2007) and Hou et al., (2019) and is represented as the sum of input fluxes of occluded P from both organic \( (F_{\text{P,oc}},) \) (eq. 42) and inorganic P pools \( (F_{\text{P,oc}}) \) expressed in kg P m\(^{-2}\) yr\(^{-1}\), as follows:

\[ \frac{dP_{\text{oc}}}{dt} = \sum_{n=1}^{N} F_{\text{P,oc}} + \sum_{n=1}^{N} F_{\text{P,oc}}^{\text{adsorption}} \]

(eq. 13)
The description of the organic sorbed P pool ($P_{org-sorp}$) follows Wang et al., (2007) and is represented as the difference between the input flux of organic sorption ($F_{P_{org-sorp}}$) and output fluxes of organic desorption ($F_{P_{org-sorp}}^{desorp}$) and occluded P ($P_{n,acc}^{desorp}$), with all fluxes expressed in kg P m$^{-2}$ yr$^{-1}$ as follows:

$$\frac{dP_{org-sorp}}{dt} = \sum_{n=1}^{N} F_{P_{org-sorp}}^{sorp} - \sum_{n=1}^{N} F_{P_{org-sorp}}^{desorp} - \sum_{n=1}^{N} F_{P_{n,acc}}^{desorp}$$  

(eq.14)

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

$$\frac{dP_{pm}}{dt} = -\sum_{n=1}^{N} F_{p,w}^{pm}$$  

(eq.15)

2.2.2. C and P fluxes

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

The total excess C term ($\psi_t$) (kg C m$^{-2}$ yr$^{-1}$) is calculated as:

$$\psi_t = \psi_g + \psi_s$$  

(eq.16)

where $\psi_g$ and $\psi_s$ are the excess C fluxes due to growth (g) and spread (s) and are assumed to be rapidly respired by plants.

Therefore, BP is calculated as the difference between potential NPP ($\Pi_c$) and total excess C:

$$BP = \Pi_c - \psi_t$$  

(eq.17)

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

$$F_{cn}^{lit} = \gamma_{leaf}C_{leaf} + \gamma_{root}C_{root} + \gamma_{wood}C_{wood}$$  

(eq.18)

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

Similar to other P-enabled models (Yang et al., 2014; Goll et al., 2017), JULES-CNP follows the same structure as its N model component. Description of the plant P and N demand follow Wang et al., (2007) and are represented by the sum of demand ($\phi$) to sustain growth (P-related: $\phi_{g_P}$, N-related: $\phi_{n_P}$) and to sustain vegetation spreading (to increment PFT fractional coverage) (P-related: $\phi_{sp_P}$, N-related: $\phi_{sp_n}$) and is 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 ($\phi_g$) and spreading ($\phi_s$) is controlled by the dominant demand between P ($\phi_{g_P}$) and N ($\phi_{n_P}$) as follows:

$$\phi_t = \phi_g + \phi_s$$  

(eq.19)
\[ \phi_{SP} = \frac{P_{p}}{C_v} \left( \Pi_s - \frac{dC_v}{dt} - \psi_s \right) \quad (eq.21) \]

\[ \phi_{SN} = \frac{P_{p}}{C_v} \left( \Pi_s - \frac{dC_v}{dt} - \psi_s \right) \quad (eq.23) \]

\[ \phi_g = \begin{cases} 
\phi_{GP} \times \frac{C_v}{P_{p}} > \phi_{GN} \times \frac{C_v}{N_v} \\
\phi_{GN} \times \frac{N_v}{P_{p}} > \phi_{GP} \times \frac{C_v}{P_{p}} \\
\phi_{GP} \times \frac{C_v}{N_v} > \phi_{SN} \times \frac{C_v}{P_{p}} \\
\phi_{SN} \times \frac{N_v}{P_{p}} > \phi_{SP} \times \frac{C_v}{P_{p}} 
\end{cases} \quad (eq.24) \]

\[ \phi_s = \begin{cases} 
\phi_{SP} \times \frac{C_v}{P_{p}} > \phi_{SN} \times \frac{C_v}{P_{p}} \\
\phi_{SN} \times \frac{N_v}{P_{p}} > \phi_{SP} \times \frac{C_v}{P_{p}} 
\end{cases} \quad (eq.25) \]

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

(see Clark et al., (2011) for more detail), \( \Pi_s \) is nutrient-unlimited, or potential, NPP (kg C m\(^{-2}\) yr\(^{-1}\)), \( \psi_s \) is excess C due to either P or N limitation for plant growth (kg C m\(^{-2}\) yr\(^{-1}\)) and \( \psi_g \) is excess C due to either P or N

limitation for vegetation spreading (kg C m\(^{-2}\) yr\(^{-1}\)).

If the P and N demand for growth are less than the available P and N and fractional coverage (\( \lambda \)) (NPP fraction used for fractional cover increment; for detail see Wiltshire et al., (2021)) at the considered timestep \( \Delta t \) then 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 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 growth which cannot be achieved due to nutrient constraints will be deducted from potential NPP, here termed excess C term (\( \psi_g \)), to give an actual NPP. Following Wiltshire et al., 2021, we assume excess C is respired by the plant.

Similarly, in order to estimate the P and N demand for spreading (eq. 21 and 23), initially the excess C from 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 demand for spreading are lower than the available P and N and fractional coverage (\( \lambda \)) (\( \phi_{SP} < \frac{(1-\lambda)P_{avail}}{\Delta t} \); \( \phi_{SN} < \frac{(1-\lambda)N_{avail}}{\Delta t} \)), then there is no limitation on spreading and in case of limited P and N 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 for spread (\( \psi_s \)) is subtracted from potential NPP.

Plant P uptake (\( P_{p}^{up} \)) (arrow a in Fig 1) is estimated based on the P demand for growth and spreading (\( \psi_s \)) and the root uptake capacity (\( u_{max} \)) (kg P kg\(^{-1}\) C yr\(^{-1}\)), as follows:

\[ P_{p}^{up} = \begin{cases} 
\phi_t \leq u_{max} \\
\phi_t > u_{max} 
\end{cases} \quad (eq.26) \]

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

The root uptake capacity depends on the maximum root uptake capacity (\( v_{max} \)) (kg P kg\(^{-1}\) C yr\(^{-1}\)), root depth (\( d_{root} \)), the concentration of inorganic P at different soil depths (\( P_{in} \)), and a half saturation term at which half of the maximum uptake capacity is reached using inorganic P at different soil depths (\( P_{n} \)), a scaling uptake ratio (\( K_p \)) (pmol P l\(^{-1}\)), unit conversion (\( C_f \)) (1 kg P\(^{-1}\)), and soil moisture (\( \theta \)) (1 m\(^{-3}\)), as follows:

\[ u_{max} = v_{max} \times d_{root} \times \sum_{n=1}^{N} P_{in} \times \left( \frac{1}{\sum_{n=1}^{N} P_{in} + C_f \times K_p \times \theta} \right) \quad (eq.27) \]
Description of the litter production of P ($F_{\text{litt}}$) (arrow b in Fig 1) follows JULES-CN as in Wiltshire et al., (2021) and is calculated based on the litter flux of C (kg C m$^{-2}$ yr$^{-1}$) using leaf, root and wood turnovers (yr$^{-1}$), and through the vegetation dynamics due to large-scale disturbance and litter production density, as follows:

$$F_{\text{litt}} = \left( \frac{1-k_{\text{leaf}}}{C_{P_{\text{leaf}}}} \right) R_{\text{leaf}} + \left( \frac{1-k_{\text{root}}}{C_{P_{\text{root}}}} \right) R_{\text{root}} + \left( \frac{1-k_{\text{stem}}}{C_{P_{\text{stem}}}} \right) R_{\text{stem}} \quad (\text{eq. 28})$$

where $\lambda$ is the leaf, root and stem re-translocation (at daily timestep) coefficient (Zaehle and Friend, 2010; Clark et al., 2011) and the related C:P ratios for P fraction and $\gamma$ is a temperature dependent turnover rate representing the phenological state (Clark et al., 2011).

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

$$\text{dec}_P = \frac{\sum_{n=1}^{N} R_n}{C:P_{\text{litt}}} \quad (\text{eq. 29})$$

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

$$C:P_{\text{litt}} = \frac{\sum_{n=1}^{N} \text{litt}_n}{P_{\text{litt}}} \quad (\text{eq. 30})$$

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

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

$$F_{\text{imm}} = \frac{\sum_{n=1}^{N} R_n \times \text{resp_frac}}{C:P_{\text{soil}}} \quad (\text{eq. 32})$$

The soil respiration from each soil layer ($R_{\text{ln}}$) is estimated from potential soil respiration ($R_{\text{pot,n}}$) for the DPM, RPM pools and the litter decomposition rate modifier ($F_{\text{P}}$) as follows:

$$R_{\text{ln}} = R_{\text{pot,n}} \times F_{\text{P}} \quad (\text{eq. 33})$$

where the description of $F_{\text{P}}$ for P pools ($F_{\text{P,n}}$) follows Wang et al.,(2007) and is estimated based on the soil pool (BIO/HUM) mineralization ($\text{minl}_{\text{p-BIO,n}}$, $\text{minl}_{\text{p-HUM,n}}$) and immobilization ($\text{immob}_{\text{p-BIO,n}}$, $\text{immob}_{\text{p-HUM,n}}$) (in kg P m$^{-2}$ yr$^{-1}$), soil inorganic P ($P_{\text{inorg,n}}$) (in kg P m$^{-2}$), and litter pools (DPM/RPM) demand (in kg P m$^{-2}$ yr$^{-1}$) as follows:

$$F_{\text{P,n}} = \frac{(\text{minl}_{\text{p-BIO,n}} + \text{minl}_{\text{p-HUM,n}} - \text{immob}_{\text{p-BIO,n}} - \text{immob}_{\text{p-HUM,n}}) + P_{\text{inorg,n}}}{\text{DEM}_{\text{PDM,n}} + \text{DEM}_{\text{RPM,n}}} \quad (\text{eq. 34})$$

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

$$\text{DEM}_{\text{k,n}} = \text{immob}_{\text{p-pot,k}} - \text{minl}_{\text{p-pot,k}} \quad (\text{eq. 35})$$

The $F_{\text{P,n}}$ estimated for N pools ($F_{\text{P,N,n}}$) follows the same formulation as P (see Wiltshire et al., 2021 for further details) and the $F_{\text{P,n}}$ is estimated based on a higher rate modifier between N and P as follows:
\[ F_{in} = \begin{cases} F_{P_{in}} & F_{P_{in}} > F_{P_{in} \text{max}} \\ F_{P_{in} \text{max}} & F_{P_{in}} \leq F_{P_{in} \text{max}} \end{cases} \] (eq.36)

Description of the fluxes of adsorption (\(F_{in}^{\text{sorp}}\)) (arrow e in Fig 1) and desorption (\(F_{in}^{\text{desorp}}\)) (arrow f in Fig 1) of inorganic P in kg P m\(^{-2}\) yr\(^{-1}\) follow Wang et al., (2010) and are calculated based on soil inorganic (\(P_{in}\)) and sorbed inorganic (\(P_{\text{org-sorbed}}\)) P pools and inorganic adsorption (\(K_{\text{sorp-in}}\)), desorption (\(K_{\text{desorp-in}}\)) coefficients (kg P m\(^{-2}\) yr\(^{-1}\)) and maximum sorbed inorganic (\(P_{\text{in-max}}\)) (kg P m\(^{-3}\)) as follows:

\[ F_{in}^{\text{sorp}} = P_{in} \times K_{\text{sorp-in}} \times \left(\frac{P_{\text{in-max}} - P_{\text{inorg-sorbed}}}{P_{\text{in-max}}}\right) \] (eq.37)

\[ F_{in}^{\text{desorp}} = P_{\text{inorg-sorbed}} \times K_{\text{desorp-in}} \] (eq.38)

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

\[ F_{in}^{\text{occ}} = P_{\text{inorg-sorbed}} \times K_{\text{occ}} \] (eq.39)

Description of the fluxes of adsorption (\(F_{os}^{\text{sorp}}\)) (arrow h in Fig 1) and desorption (\(F_{os}^{\text{desorp}}\)) (arrow i in Fig 1) of organic P follow Wang et al., (2010) are calculated based on soil organic and sorbed organic P pools and organic adsorption (\(K_{\text{sorp-or}}\)) (kg P m\(^{-2}\) yr\(^{-1}\)), desorption (\(K_{\text{desorp-or}}\)) coefficients (kg P m\(^{-2}\) yr\(^{-1}\)) and maximum sorbed organic (\(P_{\text{org-max}}\)) (which corresponds to the sorbed soil P saturation, thus modifying the sorption rate respectively) (kg P m\(^{-3}\)) as follows:

\[ F_{os}^{\text{sorp}} = P_{os} \times K_{\text{sorp-or}} \times \left(\frac{P_{\text{or-max}} - P_{\text{org-sorbed}}}{P_{\text{or-max}}}\right) \] (eq.40)

\[ F_{os}^{\text{desorp}} = P_{\text{org-sorbed}} \times K_{\text{desorp-or}} \] (eq.41)

Description of the occluded organic P flux (\(F_{os}^{\text{occ}}\)) (kg P m\(^{-2}\) yr\(^{-1}\)) (arrow j in Fig 1) follows Wang et al., (2007) and Hou et al., (2019) is calculated based on sorbed organic P pool (\(P_{\text{org-sorbed}}\)) and P occlude rate (\(K_{\text{occ}}\)) (kg P m\(^{-2}\) yr\(^{-1}\)) as follows:

\[ F_{os}^{\text{occ}} = P_{\text{org-sorbed}} \times K_{\text{occ}} \] (eq.42)

Description of the P flux from weathered parent material (\(F_{P}^{w}\)) (arrow k in Fig 1) follows Wang et al., (2007) 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 follows:

\[ F_{P}^{w} = P_{pm} \times K_{w} \] (eq.43)

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 et al., (2017) and is calculated following Fick’s second law and it is a function of the diffusion coefficient (\(D_{x}\)) in m\(^2\) s\(^{-1}\), the concentration of inorganic P at different soil depths (\(P_{in}\)) in kg P m\(^{-2}\), the distance (\(z\)) between the midpoint of soil layers in metres and seconds to year unit conversion (\(Yr\)):

\[ F_{D_n} = \frac{\partial}{\partial z} (D_{x} \frac{\partial P_{in}}{\partial z}) \times Yr \] (eq.44)
## Table 1. Model variables

| Variable | Unit | Definition |
|----------|------|------------|
| $y$      | kg C m$^{-2}$ yr$^{-1}$ | Excess C flux |
| $\phi$   | kg P m$^{-2}$ yr$^{-1}$ | Plant demand for uptake |
| $n_c$    | kg C m$^{-2}$ yr$^{-1}$ | Potential NPP |
| $u_{\text{max}}$ | kg P kg$^{-1}$ C yr$^{-1}$ | Root uptake capacity |
| $DEM$    | kg P m$^{-2}$ yr$^{-1}$ | Plant pool P associated decomposition demand |
| $\text{dec}_{\text{litter}}$ | 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 |
| $F_p^{\text{litter}}$ | kg P m$^{-2}$ yr$^{-1}$ | Plant litter flux |
| $F_p^{\text{up}}$ | kg P m$^{-2}$ yr$^{-1}$ | Plant uptake |
| $F_{\text{org}_{\text{sorped}}}$ | kg P m$^{-2}$ yr$^{-1}$ | Sorbed organic P flux |
| $F_{\text{inorg}_{\text{sorped}}}$ | kg P m$^{-2}$ yr$^{-1}$ | Sorbed inorganic P flux |
| $F_{\text{desorped}}$ | kg P m$^{-2}$ yr$^{-1}$ | Desorbed organic P flux |
| $F_{\text{inorg}_{\text{desorped}}}$ | kg P m$^{-2}$ yr$^{-1}$ | Desorbed inorganic P flux |
| $F_{\text{occluded}}$ | kg P m$^{-2}$ yr$^{-1}$ | Occluded inorganic P flux |
| $F_p^{\text{occluded}}$ | kg P m$^{-2}$ yr$^{-1}$ | Occluded organic P flux |
| $F_{\text{weathered}}$ | kg P m$^{-2}$ yr$^{-1}$ | Weathered P flux |
| $F_{\text{immobilized}}$ | kg P m$^{-2}$ yr$^{-1}$ | Immobilized P flux |
| $l_{\text{litter}}$ | kg C m$^{-2}$ yr$^{-1}$ | C litter flux |
| $l_{\text{litter fraction}}$ | - | Litter fraction |
| $l_{\text{litter leaf}}$ | kg C m$^{-2}$ yr$^{-1}$ | Leaf litter flux |
| $l_{\text{litter root}}$ | kg C m$^{-2}$ yr$^{-1}$ | Root litter flux |
| $l_{\text{litter wood}}$ | kg C m$^{-2}$ yr$^{-1}$ | Woody litter flux |
| $F_{\text{mineralized P}}$ | kg P m$^{-2}$ yr$^{-1}$ | Mineralized P flux |
| $P_p$    | kg P m$^{-2}$ | Plant P pool |
| $P_{O1}$ | kg P m$^{-2}$ | Litter organic pool |
| $P_{O2}$ | kg P m$^{-2}$ | Soil organic pool |
| $P_{in}$ | kg P m$^{-2}$ | Soil inorganic pool |
| $P_{\text{inorganic sorbed}}$ | kg P m$^{-2}$ | Soil inorganic sorbed pool |
| $P_{\text{organic sorbed}}$ | kg P m$^{-2}$ | Soil organic sorbed pool |
| $P_{\text{occluded}}$ | kg P m$^{-2}$ | Soil occluded pool |
| $P_{\text{parent material}}$ | kg P m$^{-2}$ | Parent material pool |
| $R$      | kg C m$^{-2}$ yr$^{-1}$ | Total respiration |
| $R_{\text{potential}}$ | 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 |
| $T_{\text{ref}}$ | K | Soil reference temperature |
| $T_s$    | K | Soil temperature |
| Veg $c$  | kg C m$^{-2}$ | Sum of biomass |
| $z$      | m | Soil depth |
### Table 2. P Model parameters

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

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

| Site       | Name                                | Location     | Climate   |
|------------|-------------------------------------|--------------|-----------|
| Study site | AFEX project                        | -2.58        | 2431      | 26        |
| AGP-01     | Agua pudre plot E                   | -3.72        | 2723      | 25.5      |
| CAX        | Caxiuanã flux tower site            | -1.72        | 2314      | 26.9      |
| SA3        | Tapajós flux tower site             | -2.5         | 1968      | 26.1      |
| Gig. Pen.  | Gigante peninsula (control data)    | -9.1         | 2600      | 26        |
| Hawaii K.  | Hawaii Kokee (control data)         | 22.13        | 2500      | 16        |

2.4 Model parameterisation, calibration and evaluation at study site

We use observations from the four control plots of the study site to parameterise, calibrate and evaluate different processes in JULES (Table 4). The observations were collected at 4 soil depths and processed using the Hedley sequential fractionation (Hedley, Stewart and Chauhan, 1982; Quesada et al., 2010). Observed Leaf Mass per Area (LMA), leaf N and leaf P estimated from fresh leaves were used as input parameters to JULES to estimate photosynthetic capacity and respiration parameters. JULES vn5.5 (JULES CN in this study) estimates \( V_{cmax} \) \((\mu\text{mol m}^{-2} \text{s}^{-1})\) based on Kattge et al. (2009) using foliar N concentrations in area basis (\( n_{leaf} \)), as follows:

\[
V_{cmax} = v_{int} + v_{sl} \times n_{leaf}
\]  
(eq.45)

where \( v_{int} \) is the estimated intercept and \( v_{sl} \) is the slope of the linear regression derived for the \( V_{cmax} \) estimation.

We incorporated an additional P dependency on the estimation of \( V_{cmax} \) following Walker et al. (2014) as follows:

\[
\ln(V_{cmax}) = 3.946 + 0.921 \ln(N) + 0.121 \ln(P) + 0.282 \ln(N) \ln(P)
\]  
(eq.46)

Where N and P are foliar concentrations in area basis.

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

\[
R_d = f_{dr} V_{cmax}
\]  
(eq.47)

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

Observations of aboveground biomass were used to calibrate the non PFT dependent allometric relationships in JULES (Clark et al. 2011) (eq 48-50) for leaf, root and wood C. Specifically, the \( a_{w1} \) parameter (eq 50) was modified from 0.65 to 1.204 to match better tropical forest allometry:

\[
C_{leaf} = \sigma_{1} L_{b}
\]  
(eq.48)

\[
C_{root} = C_{leaf}
\]  
(eq.49)
520 \[ C_{\text{stem}} = a_{wL} \cdot L_{b} \cdot b_{wL} \quad \text{(eq. 50)} \]

521 Where \( \sigma_{L} \) is specific leaf density (kg C m\(^{-2}\) per unit LAI), \( L_{b} \) is balanced (or seasonal maximum) leaf area index (m\(^{2}\) m\(^{-2}\)), \( a_{wL} \) is allometric coefficient (kg C m\(^{-3}\)) and \( b_{wL} \) is the allometric exponent.

522 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 \( J_{\text{max}} \). 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: \( P_{\text{in}} \)), organic bicarbonate P (organic P: \( P_{\text{o}} \)), NaOH organic P (sorbed organic P: \( P_{\text{org-sorp}} \)), NaOH inorganic P (sorbed inorganic P: \( P_{\text{inorg-sorp}} \)), residual P (occluded P: \( P_{\text{occ}} \)) and HCL P (parent material P: \( P_{\text{pm}} \)) (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.

527 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).

528 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 \( (P_{\text{in-max}} \cdot P_{\text{org-max}} \text{ eq.37 and 39}) \) (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 (eqns 27-44) were prescribed using values from the literature (Table 4).

531 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).

534 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 |
2.4.1 Model parameterisation and evaluation at test sites

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

| Leaf C:P | CAX | SA3 | Gig. Pen. | Hawaii K |
|----------|-----|-----|-----------|----------|
| AGP-01   | 600 | 600 | 700       | 691.5    |
| Root C:P | 1000| 1000| 1750      | 1100     |
| Wood C:P | 3000| 3000| 5500      | 5937.5   |
| Soil C:P | 2000| 2000| 800       | 2000     |
| K_{or-max} | 0.001 | 0.001 | 0.0033 | 0.001 |
| K_{in-max} | 0.001 | 0.001 | 0.0185 | 0.001 |

Table 5. Additional test sites data used for model parameterisation

- C:P ratios from Wang, Law and Pak, 2010 and maximum sorbed P capacities from Yang et al., 2014.
- Mirabello et al., 2013: C:P ratios from Vitousek, 2004

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

2.5 JULES simulations

JULES was first applied at the K34 flux tower site using observed meteorological forcing data from 1999-2019 (Fleisher et al, 2019) at half hourly resolution. The following meteorological variables are needed to drive JULES (model inputs) (Best et al., 2011): atmospheric specific humidity (kg kg⁻¹), atmospheric temperature (K), air pressure at the surface (Pa), short and longwave radiation at the surface (W m⁻²), wind speed (m s⁻¹) and total precipitation (kg m⁻² s⁻¹). Furthermore, the averaged measured LAI from study site was used to initialise the vegetation phenology module, but was allowed to vary in subsequent prognostic calculations. Soil organic and inorganic sorbed P pools were initialised with study site observations. The JULES-CNP simulations were initialized following the same methodology as in Fleisher et al., (2019), by the spin-up from1850 resulted in equilibrium state (Figure S1). The spin up was performed separately for three versions of JULES (C/CN/CNP) following the same procedure. Furthermore, the transient run was performed for the period 1851-1998 using time-varying CO₂ and N deposition fields. Finally, for the extended simulation period (1999-2019) two runs were performed, the first with ambient the second elevated CO₂ concentrations.

We evaluate the impact of including a P cycle in JULES using three model configurations (JULES C, CN and CNP). We apply JULES in all three configurations using present day climate under both ambient CO₂ and eCO₂. Ambient and eCO₂ were prescribed following Fleisher et al., (2019), with present-day CO₂ based on global monitoring stations, and an abrupt (step) increase in atmospheric CO₂ of +200 ppm on the onset of the transient period (i.e., 1999). However, the comparison period is limited to 2017-18 for which the P measurements are available.

We compare simulated C fluxes (GPP, NPP, litterfall C), C stocks (total vegetation, fine root, leaf, wood, soil) and the CO₂ fertilization effect across model configurations. The CO₂ fertilization effect (\( CO_{2}\text{fert-eff} \)) (eq.51) is calculated based on simulated vegetation C under ambient (\( VegC (aCO_2) \)) and eCO₂ (\( VegC (eCO_2) \)) as follows:

\[
CO_{2}\text{fert-eff} = \frac{(VegC (eCO_2) - VegC (aCO_2)) \times 100}{VegC (aCO_2)}
\]  

(eq.51)

Furthermore, the net biomass increases due to CO₂ fertilization effect (\( \Delta Veg \)) is estimated as follows:
\[ \Delta C_{\text{aveg}} = \Delta BP - \Delta \text{litter fall C} \quad (\text{eq.} 52) \]

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

\[ \text{WUE} = \text{GPP/Transpiration} \quad (\text{eq.} 53) \]

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

\[ \text{CUE} = \text{BP/GPP} \quad (\text{eq.} 54) \]

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

### 2.5.1 Model sensitivity

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

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

#### 2.5.1 Simulations at test sites

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

3.1 Model application under ambient CO₂

3.1.1 Calibration of simulated soil P pools at study site

The maximum sorption capacities ($P_{\text{in-max}}$, $P_{\text{or-max}}$, eq. 37 and 40) were calibrated to the observed P pools. As a result, JULES-CNP could reproduce the measured soil P pools (Fig. 2 and Table 6). Simulated inorganic soil P and sorbed organic and inorganic soil P closely matched the observations (Table 7 and Fig. 2). However, simulated organic soil P overestimates the observations by 60%.

![Figure 2: Modelled vs measured soil phosphorus pools under ambient CO₂ (for the soil depth of 0-30 cm). Black line represents standard deviation](image)

Table 6. Observed and simulated phosphorus pools and fluxes. Occluded and weathered P pools were prescribed using the observed values (between period 2017-18).

| Phosphorus pools and fluxes | Measured          | Modelled Ambient CO₂ | Modelled Elevated CO₂ |
|-----------------------------|-------------------|-----------------------|------------------------|
| 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±0.12         | prescribed            | prescribed             |
| Total vegetation P (g P m⁻²)| 4.15              | 4.66                  | 5.11                   |
| Soil P – 30 cm (g P m⁻²)    | 13.85             | 14.7                  | 14.56                  |
| Total ecosystem P (g P m⁻²) | -                 | 35.97                 | 35.97                  |
| P litter flux (g P m⁻² yr⁻¹)| 0.3               | 0.28                  | 0.29                   |
3.1.2 Model evaluation

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

Simulated NPP, is close to the measured values (NPP: 1.14 - 1.31 observed vs 1.26 modelled kg C m⁻² yr⁻¹) with autotropic respiration (RESP) also closely following the observations (1.98 observed vs 1.81 modelled kg C m⁻² yr⁻¹). Biomass production is estimated as a difference between NPP and the amount of C which is not fixed by plants due to the insufficient P in the system (excess C) (eq. 27). The excess C flux depends on the plant P and 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 ambient CO₂. In JULES-CNP this flux is subtracted from NPP in order to give the BP (eq. 17) (Table 7). Our simulated litterfall overestimates the observations by 32%, however simulated vegetation and its components (fine root, leaf and wood) and soil C stocks match well the observations (Table 7).

Table 2. 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 (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 (m² m⁻²)            | 5.6±0.36 | 5.77                  | 6.12                  |

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

We compare simulated C pools and fluxes from JULES-C, JULES-CN and JULES-CNP (Figure 3). There is no difference between C stocks and fluxes in simulations from JULES C and CN indicating that there is no N limitation at this tropical site in the CN simulations. However, simulated BP and litter flux of C by JULES C/CN are higher than in JULES-CNP but also overestimate the observations (litter flux of JULES C/CN: 1.18, JULES-CNP: 0.91 and obs 0.69 (kg C m⁻² yr⁻¹) and BP of JULES C/CN: 1.24, JULES-CNP: 0.96 and obs 1.14-1.31 (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 simulated, indicating a 24% P limitation to BP at this site according to JULES-CNP, which represents a 29% decrease in BP compared to JULES-C/CN. Consequently, the total vegetation C stock for models without P inclusion is higher than the CNP version (+3% difference) due to the lack of representation of P limitation. The simulated soil C stock in JULES C and JULES CN is also higher than in the CNP version (JULES C/CN: 13.93 vs. JULES-CNP: 13.18 (kg C m⁻² yr⁻¹)) and higher than the observations. Moreover, CUE in JULES C/CN (eq.54) is higher than observations and JULES-CNP (JULES C/CN: 0.38 vs. JULES-CNP: 0.31, obs: 0.34 ±0.1(dimensionless).
Figure 3- JULES C, CN, CNP modelled vs measured C pools (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 CO\(_2\). Note that CUE is unitless.

3.1.4 Model evaluation at test sites under ambient CO\(_2\):

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 (Gigane 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).
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 \( K_{or}^{\text{max}} \) (Figure 5-c) and \( K_{in}^{\text{max}} \) (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 \( K_{or}^{\text{max}}, K_{in}^{\text{max}} \)). 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 \( (K_{sorp-orr}, K_{sorp-in}) \) 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.
3.2 Model application under elevated CO$_2$

### 3.2.1 Simulated plant and soil C and P pools and fluxes - JULES-CNP: eCO$_2$ vs ambient CO$_2$

The eCO$_2$ simulation using JULES-CNP yields a higher GPP compared to the ambient CO$_2$ (0.83 kg C m$^{-2}$ yr$^{-1}$) increase, as a result of CO$_2$ fertilization. Moreover, due to the GPP increase, NPP and RESP also increased compared to ambient CO$_2$ (NPP: 0.49 and RESP:0.3 kg C m$^{-2}$ yr$^{-1}$) increase (Table 7). The total simulated vegetation C pool increases under eCO$_2$ compared to ambient CO$_2$ (0.41 kg C m$^{-2}$), hence the estimated plant P (estimated as a fraction of C:P ratios) increases as well (+0.45 g P m$^{-2}$) (Fig. 6, Table 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 eCO$_2$ compared to simulated NPP under ambient CO$_2$, due to the substantial increase in simulated excess C, the BP is similar to the ambient CO$_2$ (2% difference).

The simulated organic soil P under eCO$_2$ were close to those under ambient CO$_2$ (1.6 g P m$^2$) (Table 7). This is due to the same parameterization of the output fluxes from this pool for eCO$_2$ and ambient CO$_2$. The simulated pool of inorganic P under eCO$_2$ decreases compared to the ambient CO$_2$ by 0.11 g P m$^{-2}$ due to the increased plant P pools and slight increase in uptake (+0.13 %).

However, the simulated sorbed organic and inorganic soil P from eCO$_2$ are similar to those simulated under the ambient CO$_2$ which is due to the same parameterization of sorption function (maximum sorption capacity) from the ambient CO$_2$ run as explained in calibration section. Moreover, the modelled occluded and weathered soil P were similar to those in the ambient CO$_2$ 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 CO$_2$

JULES C/CN show higher vegetation and soil C pools, BP and litter flux compared to JULES-CNP: (Table 8, Figure. S2). Under eCO$_2$, simulated NPP using JULES C-CN is 4.5% higher than JULES-CNP and the BP with JULES C-CN is 96.8% higher than in JULES-CNP which simulates an excess C flux of 0.81 kg C m$^{-2}$ yr$^{-1}$ equivalent to 46% P limitation under eCO$_2$. As a result of P limitation and eCO$_2$, the simulated CO$_2$ fertilization effect estimated based on changes in biomass under ambient and eCO$_2$ was reduced from 13% with JULES C-CN to 10% JULES-CNP. Moreover, the CUE from JULES C-CN is 87.5% higher than the JULES-CNP as a result of high P limitation over biomass production.
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).

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

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).
3.3 Plant P Demand, uptake and excess C under ambient and elevated CO₂

To understand further the CP-cycle dynamics, we studied the monthly averaged plant P demand and the relative (limited) P uptake (eq. 26) under both ambient and elevated CO₂ conditions (Figure. 7).

Under ambient CO₂ condition the highest GPP is estimated at 0.29±0.016 kg C m⁻² month⁻¹ in July and the lowest at 0.17±0.051 kg C m⁻² month⁻¹ in October (Figure. 7-a). The estimated WUE and SMCL in October is among the lowest estimated monthly values at 2.3±0.51 kg CO₂/kg H₂O and 526.2±31 kg m⁻² respectively (Figure. 7-c). The highest P demand is estimated at 0.4±0.02 g P m⁻² month⁻¹ in July and the lowest demand at 0.2±0.08 g P m⁻² month⁻¹ in October. Consequently, the highest and lowest uptake (0.32±0.01 and 0.19±0.07 g P m⁻² month⁻¹, respectively). The excess C for the highest and lowest GPP and demand periods are estimated at 0.4±15 and 0.04±0.07 kg C m⁻² month⁻¹, respectively.

However, similar to ambient CO₂, under eCO₂ condition the highest estimated GPP is in July at 0.36± 0.017 kg C m⁻² month⁻¹ and lowest for October 0.25±0.062 kg C m⁻² month⁻¹ (Figure. 7-b). The estimated WUE and soil moisture content (SMCL) for the lowest GPP period is among the lowest monthly estimated values at 3.5±0.74 kg CO₂/kg H₂O and 552±33 kg m⁻² for October respectively (Figure. 7-d). The highest P demand is estimated for July at 0.51±0.02 g P m⁻² month⁻¹ with the uptake flux of 0.31±0.02 g P m⁻² month⁻¹ and the lowest demand is estimated for October at 0.32±0.1 g P m⁻² month⁻¹ with the estimated uptake flux of 0.26±0.06 g P m⁻² month⁻¹. The highest excess C flux is also for July at 1.01±0.17 kg C m⁻² month⁻¹ and lowest for October 0.27±0.29 kg C m⁻² month⁻¹, respectively.

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

**Figure. 7** - Simulated monthly plant P demand and uptake (g P m⁻² month⁻¹), excess C and GPP (kg C m⁻² month⁻¹) under a) aCO₂ and b) eCO₂, water use efficiency (g m⁻² month⁻¹) under c) ambient CO₂ (aCO₂) and d) eCO₂ conditions. The grey area represents the standard deviation.
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 3.3). 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 $Y_{max}$ 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 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...
...future work should focus on implementing recent developments including Non-Structural Carbohydrate pools (NSC) (Jones et al., 2020) in JULES-CNP.

Overall, JULES-CNP reproduced the observed C pools and fluxes which are in the acceptable ranges compared to the measurements. However, using the JULES default $V_{\text{max}}$ estimation method (eq. 40), the model slightly underestimates the total GPP (2.9 kg C m$^{-2}$ yr$^{-1}$ vs. 3.3-3.5 kg C m$^{-2}$ yr$^{-1}$). Therefore, in this version of the model, we used the improved $V_{\text{max}}$ estimation method based on N and P (eq. 46) which resulted in a final estimated GPP closer to the measurements (3.06 kg C m$^{-2}$ yr$^{-1}$).

Our results show an increase in GPP (21%) in response to eCO$_2$ which is higher than the average increase of GPP reported in mature eucalyptus forests (11%), also growing under low P soils at the free air CO$_2$ enrichment experiment (EucFACE) facility in Australia (Jiang et al., 2020). This can be related to the lower decrease of biomass growth response estimated by JULES-CNP (-3%) compared to the measurements from mature eucalyptus forests (-8%) (Ellsworth et al., 2017), due to the P limitation which was shown to impact the above-ground biomass growth response in mature forests (Körner et al., 2005; Ryan, 2013; Klein et al., 2016).

In order to estimate the biomass production (BP), we deducted the excess C fluxes from NPP. Using JULES C/CN models, the simulated biomass productivity enhancement due to eCO$_2$ (49%) is in the middle range of the reported for different biomes by Walker et al., (2021). Moreover, our estimated difference of BP between ambient and eCO$_2$ conditions (2%) is close to the estimated difference for mature forests (3%) (Jiang et al., 2020).

A global estimation for tropical forests using the CASA-CNP model which includes N and P limitations on terrestrial C cycling, shows that NPP is reduced by 20% on average due to the insufficient P availability (Wang, Law and Pak, 2010) which is close to our estimated P limitation of 24%. This finding is in line with a field study that shows a strong correlation between the total NPP and the soil available P (Aragão et al., 2009).

The estimated decrease of NPP in response to eCO$_2$ as a result of P limitation is in line with the findings from CLM-CNP model at five tropical forests (Yang et al., 2014) which indicates the CO$_2$ fertilization dependency on the processes that affect P availability or uptake.

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

Under low P availability, all available P is considered to be adsorbed or taken by plant and microbes for further consumption, with leaching considered to be minor within the time scales of our study period (Went and Stark, 1968; Bruijnzee, 1991; Neff, Hobbie and Vitousek, 2000). Despite studies that show the possibility of P fixation as a source of available P for plants (Van Langenhove et al., 2020; Gross et al., 2021), due to the strong fixation of P in the soil (Aerts & Chapin, 2000; Goodale, Lattha,Nadelhoffer, Boyer, & Jaworski, 2002), the P deposited is unlikely to be available to plants in the short term (de Vries et al., 2014), for this reason this version of JULES-CNP did not include P deposition. However both P deposition and leaching are likely to have a very important role on sustaining the productivity of tropical forests in the Amazon over longer time scales (Van Langenhove et al., 2020) and needs to be considered in future studies. Moreover, biochemical mineralisation is also not included in the current version of JULES-CNP which only accounts for total mineralization. However, models that include this process show no significant difference between total and biochemical mineralized P which can be due to complexity of identifying the inclination of mineralization versus uptake (Martins et al., 2021). Lastly, in order to capture plant internal nutrient impact on the C storage, future work should focus on implementing recent developments including Non-Structural Carbohydrate pools (NSC) (Jones et al., 2020) in JULES-CNP.
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., 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.
Finally, our estimated total biomass enhancement ($\Delta$C_{veg}) using JULES C/ CN for the 1st and 15 years are in the middle range of C/CN models from Fleischer et al., (2019) and in lower range of CNP models from Fleischer et al., (2019) using JULES-CNP. Nevertheless, while JULES-CNP includes the trait-based parameters (Harper et al., 2016), other functions such as flexible C allocation and spatial variation of biomass turnover are still missing and future model improvement should be focused on their inclusion.

5. Conclusion

Land ecosystems are a significant sink of atmospheric CO$_2$, ergo buffering the anthropogenic increase of this flux. While tropical forests contribute substantially to the global land C sink, observational studies show that a stalled increase in carbon gains over the recent decade (Brienen et al., 2015; Hubau et al., 2020). However, modelling studies that lack representation of P cycling processes predict an increasing sink (Fernández-Martínez et al., 2019; Fleischer et al., 2019). This is particularly relevant for efforts to mitigate dangerous climate change and assumptions on the future efficacy of the land C sink. Therefore, in this study, we presented the full terrestrial P cycling and its feedback on the C cycle within the JULES framework. Our results show that the model is capable of representing plant and soil P pools and fluxes at a site in Central Amazon and across the extended P limited test sites in Amazon, Gigante Peninsula and Hawaii chronosequence provided with site level data for model parameterisation. Moreover, the model estimated a significant NPP limitation under ambient CO$_2$, due to the high P deficiency at these sites which is representative of Central Amazon and tropical P limited sites, and elevated CO$_2$ resulted in a further subsequent decrease in the land C sink capacity relative to the model without P limitation. While our study is a step toward the full nutrient cycling representation in ESMs, it can also help the empirical community to test different hypotheses (i.e., dynamic allocation and stoichiometry) and generate targeted experimental measurements (Medlyn et al., 2015).

Code availability

The modified version of JULES vn5.5 and the P extension developed for this paper are freely available on Met Office Science Repository Service: https://code.metoffice.gov.uk/svn/jules/main/branches/dev/mahdinakhavali/vn5.5_JULES_PM_NAKHAVALI/ after registration (http://jules-lsm.github.io/access_req/JULES_access.html) and completion of software license form. Codes for compiling model available at: (https://doi.org/10.5281/zenodo.5711150). Simulations were conducted using two sets of model configurations (namelists): ambient CO$_2$ condition (https://doi.org/10.5281/zenodo.5711144) and elevated CO$_2$ condition (https://doi.org/10.5281/zenodo.5711150).

Data availability

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

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