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

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Abstract

Most Land Surface Models (LSMs), the land components of Earth system models (ESMs), include representation of nitrogen (N) limitation on ecosystem productivity. However only few of these models have incorporated phosphorus (P) cycling. In tropical ecosystems, this is likely to be important as N tends to be abundant but the availability of rock-derived elements, such as P, can be very low. Thus, without a representation of P cycling, tropical forest response in areas such as Amazonia to rising atmospheric CO_2 conditions remains highly uncertain. In this study, we introduced P dynamics and its interactions with the N and carbon (C) cycles into the Joint UK Land Environment Simulator (JULES). The new model (JULES-CNP) includes the representation of P stocks in vegetation and soil pools, as well as key processes controlling fluxes between these pools. We evaluate JULES-CNP 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 apply the model under elevated CO_2 (600 ppm) at our study site to quantify the impact of P limitation on CO_2 fertilization. We compare our results against the 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 CO_2. We estimate P to limit net primary productivity (NPP) by 24% under current CO_2 and by 46% under elevated CO_2. Under elevated CO_2, biomass in simulations accounting for CNP increase by 10% relative to at contemporary CO_2, although it is 5% lower compared with CN and C-only simulations. Our results highlight the potential for high P limitation and therefore lower CO_2 fertilization capacity in the Amazon forest with low fertility soils.

1. Introduction

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

The C sink capacity of tropical forests may be constrained by nutrient availability for plant photosynthesis and growth (Vitousek and Howarth, 1991; Elser *et al.*, 2007; LeBauer and Treseder, 2008) via either P (Nordin, Högberg and Näsholm, 2001; Shen *et al.*, 2011) and N related processes (DeLuca, Keeney and McCarty, 1992; Perakis and Hedin, 2002). Global process-based models of vegetation dynamics and function suggest a continued land C sink in the tropical forests, largely attributed to the CO_2 fertilization effect (Sitch *et al.*, 2008; Schimel, Stephens and Fisher, 2015; Koch, Hubau and Lewis, 2021). However, many of these models typically do not consider P constraints on plant growth (Fleischer *et al.*, 2019), which is likely to be an important limiting nutrient in tropical ecosystems, characterised by old and heavily weathered soils. The importance of nutrient cycling representation in Earth System Models (ESMs), and the lack thereof, was highlighted by Hungate *et al.* (2003) and Zaehle and Dalmonech (2011), showing the significance of 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 (ACCESSESM1.5 model) (Arora *et al.*, 2020).

The long history of soil development in tropical regions which involves the loss of rock-derived nutrients through weathering and leaching on geologic timescales (Vitousek et al., 1997, 2010) results in highly weathered soils. Soil P is hypothesized to be among the key limiting nutrients to plant growth in tropical forests (Vitousek *et al.*, 1997, 2010; Hou *et al.*, 2020), unlike temperate forest where N is hypothesised to be the main constraint(Aerts and Chapin, 1999; Luo *et al.*, 2004). Low P availability in tropical soils is related to the limited un-weathered parent material or organic compounds as source of P (Walker and Syers, 1976), active sorption (Sanchez, 1977) and high occlusion (Yang and Post, 2011) which further reduce plant available P. Although N limitation can impact the terrestrial C sink response to increasing atmospheric CO_2 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 CO_2 (eCO_2) than N (Gentile et al., 2012; Sardans, Rivas-Ubach and Peñuelas, 2012). This causes considerable uncertainty in predicting the future of the Amazon forest C sink (Yang *et al.*, 2014).

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

However, modelling studies are unable to reproduce observed spatial patterns of NPP and biomass in the Amazon due to missing information on nutrient availability and soil fertility impact on productivity (Wang, Law and Pak, 2010; Vicca *et al.*, 2012; Yang *et al.*, 2014) and due to the lack of inclusion of soil P constraints on plant productivity and function. Nevertheless, some modelling works 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 RuBiCo carboxylation capacity (V_{cmax}) (Castanho *et al.*, 2013). Results from these studies successfully represent observed patterns of Amazon forest biomass growth increases with increasing soil fertility. However, the full representation of these interactions and the impact of the soil nutrient availability on biomass productivity is still missing in most of ESMs.

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.*, 2014; Zhu *et al.*, 2016; Goll *et al.*, 2017). Furthermore, a comprehensive study included several models with C-N-P cycling and their feedbacks on the atmospheric C fixation and biomass growth in Amazon forests under ambient and eCO_2 conditions (Fleischer *et al.*, 2019). Despite these developments, data to underpin them and their projections, particularly for the tropics, is sparse and remains challenging particularly for the Amazon forest (Reed *et al.*, 2015; Jiang *et al.*, 2019). Moreover, due to the lack of detailed measurements, the P-related processes such as ad/desorption and uptake represented in these models are under-constrained and likely oversimplified, thus the future predictions of Amazon forest responses to eCO_2 and climate change are uncertain. To fill this gap, in this study, we will use data collected as part of the Amazon Fertilization Experiment (AFEX), the first project that focuses on experimental soil nutrient manipulation in the Amazon, with a comprehensive data collection program covering plant ecophysiology, C stocks and fluxes, soil processes including P stocks. Thus, our model parameterization compared to prior P modelling studies includes detailed P processes representation using the site measurements.

Here, we describe the development and implementation of the terrestrial P cycle in the Joint UK Land Environment Simulator (JULES) (Clark *et al.*, 2011), the land component of the UK Earth System Model (UKESM), following the structure of the prior N cycle development (Wiltshire *et al.*, 2021). The model (JULES-CNP) is parameterized and calibrated using novel in situ P soil and plant data from a well-studied forest site in Central Amazon near to Manaus, Brazil with soil P content representative of 60% of soils across the Amazon basin. We then evaluate the model against carbon stocks and fluxes from data sets from our study site and the nearby K34 field site. To test the model, we followed the protocol of Fleischer *et al.*, (2019), to predict nutrient limitations on land biogeochemistry under ambient and eCO_2. Predictions of the CO_2 fertilization effect in JULES-CNP are compared to those in current versions of the model with coupled C and N cycles (JULES-CN) and with 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 cycling (JULES-CN) (Wiltshire *et al.*, 2021) between the atmosphere, vegetation and soil (Best *et al.*, 2011; Clark *et al.*, 2011). Vegetation dynamics are represented in JULES using the TRIFFID model, using nine distinct plant functional types (PFTs) (tropical and temperate broadleaf evergreen trees, broadleaf deciduous trees, needle-leaf evergreen and deciduous trees, C3 and C4 grasses, and evergreen and deciduous shrubs), as well as height competition (Harper *et al.*, 2016). JULES simulates Gross Primary Productivity (GPP) based on a coupled photosynthesis and water balance scheme, from which autotrophic respiration for each living tissue (leaf, wood, root) is subtracted to estimate NPP. In JULES we assume a process-based leaf-level photosynthesis scaled up to the canopy. Therefore, in JULES CNP in order to keep consistency with JULES C-CN, we also assume a multi-level canopy, and leaf N and P in exponentially decreases through the canopy (CanRadMod 6) (Clark *et al.*, 2011). NPP is then allocated to increase tissue C stocks and to spread, i.e., expand the fractional coverage of the PFT. The resultant PFT fractional coverages depend in addition on competition across PFTs for resources, e.g., light. Tissue turnover and vegetation mortality add C into the litter pools. Representation of soil organic C (SOC) follows the RothC equations (Jenkinson *et al.*, 1990; Jenkinson and Coleman, 2008) defining four C pools: decomposable plant material (DPM) and resistant plant material (RPM), which receive direct input from litterfall, and microbial biomass (BIO) and humified material (HUM) which receive a fraction of decomposed C from DPM and RPM which is not released to the atmosphere. The limitation of N on SOC is applied to the vegetation and soil components using a dynamic C:N ratio to modify the mineralization and immobilization processes as described in Wiltshire *et al.*, (2021). Note that the soil component of JULES-CN can be run either as a single box model or vertically resolved over soil depth (JULES-CN layered), and in this paper we build 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). 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 (Figure.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. However, despite JULES-CN that includes N leaching and deposition, P leaching and deposition are omitted in the current version of JULES-CNP.

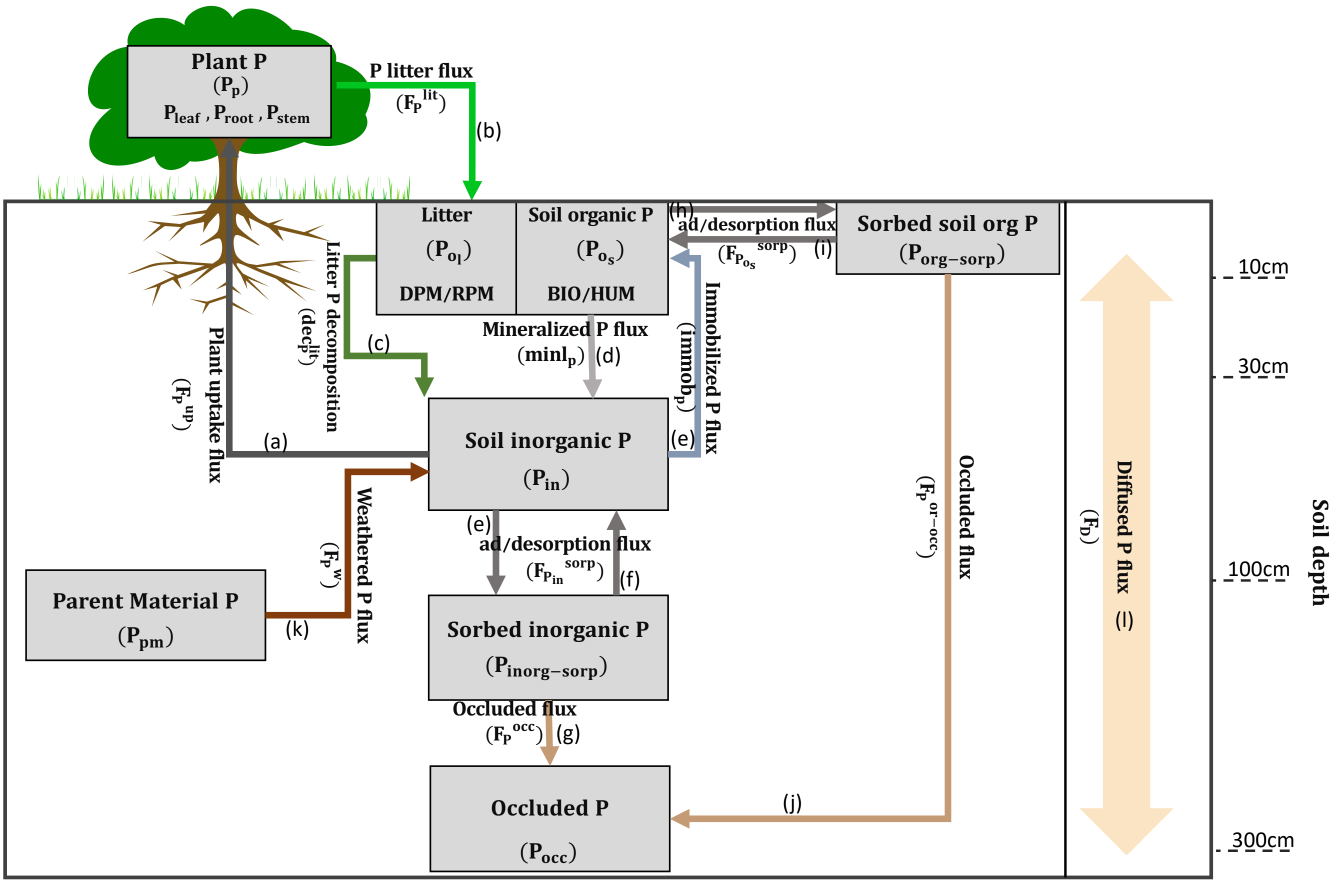

Figure.1 – JULES CNP model scheme

2.2.1 P pools

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

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

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

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

$$P_{stem} = \frac{C_{stem}}{C\!:\!P_{stem}} \qquad \text{(eq.3)}$$

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

$$P_p = P_{leaf} + P_{root} + P_{stem} \qquad \text{(eq.4)}$$

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

$$\frac{dP_P}{dt} = {F_P}^{up} - {F_P}^{lit} \qquad \text{(eq.5)}$$

The litter P pool (P_{O_l}) is estimated as a sum of P_{DPM} and P_{RPM} pools. Each pool is formed by the fluxes of plant litter input (${F_P}^{lit}$) and the outgoing decomposed P (${dec_P}^{lit}$) both expressed in kg P m^{-2} yr^{-1} (eq.28-29). Furthermore, the plant litter input is modified based on the plant type material ratio α (in order to distribute the litter input based on the DPM/RPM fraction) as follows:

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

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

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

The soil organic pool (P_{O_S}) is represented as the sum of P_{BIO} and P_{HUM}. These pools are estimated from the difference between P inputs from total immobilized (F_{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 ${F_{P_{O_S}}}^{desorp}$and P outputs from mineralized (F_{minl_P}), and adsorbed P fluxes (${F_{P_{O_S}}}^{sorp}$) (adsorption: eq. 40 and desorption: eq.41) with all fluxes expressed in kg P m^{-2} yr^{-1} as follows:

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

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

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

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

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

Descripting of the occluded (P_{occ}) P pool follows Wang *et al.*, (2007) and Hou *et a*l., (2019) and is represented as the sum of input fluxes of occluded P from both organic (${F_P}^{or-occ}$) (eq. 42) and inorganic P pools (${F_P}^{occ}$) expressed in kg P m^{-2} yr^{-1}, as follows:

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

Descripting 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 (${F_{P_{O_{S_n}}}}^{sorp}$) and output fluxes of organic desorption (${F_{P_{O_{S_n}}}}^{desorp}$) and occluded P($F_{P_n}^{occ}$), with all fluxes expressed in kg P m^{-2} yr^{-1} as follows:

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

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

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

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 represent 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), ie 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, volatiles production 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 growth 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 (ψ_t) (kg C m^{-2} yr^{-1}) is calculated as:

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

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

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

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

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

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

where λ is the leaf, root and stem re-translocation (at daily timestep) coefficient (Clark *et. al.,* 2011) and γ 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 ($\emptyset_t$) to sustain growth (P-related: ($\emptyset_{gP}$), N-related: ($\emptyset_{gN}$)) and to sustain vegetation spreading (to increment PFT fractional coverage) (P-related: ($\emptyset_{SP}$), N-related: ($\emptyset_{SN}$)) 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 ($\emptyset_g$) and spreading ($\emptyset_s$) is controlled by the dominant demand between P ($\emptyset_{gP}$) and N ($\emptyset_{gN}$) as follows:

$$\emptyset_t = \emptyset_g + \emptyset_s \quad \text{(eq.19)}$$
$$\emptyset_{gP} = \frac{P_p}{C_V}\left(\Pi_c - \frac{dC_v}{dt} - \psi_g\right) \quad \text{(eq.20)}$$
$$\emptyset_{sP} = \frac{P_p}{C_V}\left(\Pi_c - \frac{dC_v}{dt} - \psi_s\right) \quad \text{(eq.21)}$$
$$\emptyset_{gN} = \frac{N_v}{C_V}\left(\Pi_c - \frac{dC_v}{dt} - \psi_g\right) \quad \text{(eq.22)}$$
$$\emptyset_{sN} = \frac{N_v}{C_V}\left(\Pi_c - \frac{dC_v}{dt} - \psi_s\right) \quad \text{(eq.23)}$$
$$\emptyset_g = \begin{cases} \emptyset_{gP} & \emptyset_{gP} \times \frac{C_V}{P_p} > \emptyset_{gN} \times \frac{C_V}{N_v} \\ \emptyset_{gN} & \emptyset_{gN} \times \frac{C_V}{N_v} > \emptyset_{gP} \times \frac{C_V}{P_p} \end{cases} \quad \text{(eq.24)}$$

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

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), Π_c is nutrient-unlimited, or potential, NPP (kg C m^{-2} yr^{-1}), ψ_g is excess C due to either P or N limitation for plant growth (kg C m^{-2} yr^{-1}) and ψ_s is excess C due to either P or N limitation for vegetation spreading (kg C m^{-2} yr^{-1}).

Equations 20 and 22 are solved by first setting $\psi_g = 0.0$ to find the total plant P (eq. 20) and N demand (eq.22). If the P and N demand for growth are less than the available P and N and fractional coverage (λ) (NPP fraction used for fractional cover increment; for detail see Wiltshire *et al.,* (2021)) at the considered timestep Δt then there is no limitation to growth ($i.e. \emptyset_{gP} < \frac{(1-\lambda)P_{avail}}{\Delta t}$; $\emptyset_{gN} < \frac{(1-\lambda)N_{avail}}{\Delta t}$). Where there is limited P and/or N availability, the uptake equals the available P and N ($\emptyset_{gP} = \frac{(1-\lambda)P_{avail}}{\Delta t}$; $\emptyset_{gN} = \frac{(1-\lambda)N_{avail}}{\Delta t}$), and the plant growth which cannot be achieved due to nutrient constraints will be deducted from potential NPP, here termed excess C term (ψ_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 (λ) ($\emptyset_{sP} < \frac{(1-\lambda)P_{avail}}{\Delta t}$; $\emptyset_{sN} < \frac{(1-\lambda)N_{avail}}{\Delta t}$), then there is no limitation on spreading and in case of limited P and N availability, the uptake equals the available P and N ($\emptyset_{sP} = \frac{(1-\lambda)P_{avail}}{\Delta t}$; $\emptyset_{sN} = \frac{(1-\lambda)N_{avail}}{\Delta t}$), and the excess C for spread (ψ_s) is subtracted from potential NPP.

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

$${F_p}^{up}{}_n = \begin{cases} \emptyset_t & \emptyset_t \le u^{max} \\ u^{max} & \emptyset_t > u^{max} \end{cases} \quad \text{(eq.26)}$$

Description of the plant P uptake (${F_p}^{up}$) 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_{in}), a scaling uptake ratio (K_p) (µmol P l^{-1}), unit conversion (C_f) (1 kg P^{-1}), and soil moisture (θ) (l m^{-2}), as follows:

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

Description of the litter production of P (${F_P}_n^{lit}$) (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:

$${F_P}_n^{lit} = (1 - k_{leaf})\gamma_{leaf}C_{leaf} \times C{:}P_{leaf} + (1 - k_{root})\gamma_{root}C_{root} \times C{:}P_{root} + \gamma_{wood}C_{wood} \times C{:}P_{stem} \quad \text{(eq.28)}$$

where λ 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 γ is a temperature dependent turnover rate representing the phenological state (Clark *et al.*, 2011).

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

$$dec_P{}^{lit} = \frac{\sum_{n=1}^{N} R_n}{C\!:\!P_{lit}} \qquad \text{(eq.29)}$$

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

$$C\!:\!P_{lit} = \frac{\sum_{n=1}^{N} lit_n{}^C}{P_{O_{l_n}}} \qquad \text{(eq.30)}$$

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

$$F_{minl_{P_n}} = \frac{\sum_{n=1}^{N} R_{POT_{i,n}}}{\varepsilon_{cp_i}} \qquad \text{(eq.31)}$$

$$F_{immob_{P_n}} = \frac{\sum_{n=1}^{N} R_{i,n} \times resp\_frac}{C\!:\!P_{soil}} \qquad \text{(eq.32)}$$

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

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

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

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

The net demand associated with decomposition of litter pools ($DEM_{k,n}$) 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 ($minl_{p-pot}$) and immobilization ($immob_{p-pot}$) (in kg P m^{-2} yr^{-1}) of pools (k) as follows:

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

The F_{P_n} estimated for N pools ($F_{P_{N_n}}$) follows the same formulation as P (see Wiltshire *et al.*, 2021 for detail) and the F_{P_n} is estimated based on a higher rate modifier between N and P as follows:

$$F_{P_n} = \begin{cases} F_{P_{P_n}} & F_{P_{P_n}} > F_{P_{N_n}} \\ F_{P_{N_n}} & F_{P_{N_n}} > F_{P_{P_n}} \end{cases} \qquad \text{(eq.36)}$$

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

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

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

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

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

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

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

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

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

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

Description of the P flux from weathered parent material ($F_{P_n}^{w}$) (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:

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

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 (*Dz*) 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 midpoints of soil layers in metres and seconds to year unit conversion (Yr):

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

Table 1. Model variables

Variable	Unit	Definition
ψ	kg C m^{-2} yr^{-1}	Excess C flux
$\emptyset$	kg P m^{-2} yr^{-1}	Plant demand for uptake
Π_c	kg C m^{-2} yr^{-1}	Potential NPP
u^{max}	kg P kg^{-1} C yr^{-1}	Root uptake capacity
DEM	kg P m^{-2} yr^{-1}	Plant pool P associated decomposition demand
${dec_P}^{lit}$	kg P m^{-2} yr^{-1}	Litter decomposition
F_D	kg P m^{-2} yr^{-1}	Plant diffusion flux
F_P	-	Plant litter decomposition rate modifier
F_p^{lit}	kg P m^{-2} yr^{-1}	Plant litter flux
F_p^{up}	kg P m^{-2} yr^{-1}	Plant uptake
${F_{P_{O_S}}}^{sorp}$	kg P m^{-2} yr^{-1}	Sorbed organic P flux
${F_{P_{in}}}^{sorp}$	kg P m^{-2} yr^{-1}	Sorbed inorganic P flux
${F_{P_{O_S}}}^{desorp}$	kg P m^{-2} yr^{-1}	Desorbed organic P flux
${F_{P_{in}}}^{desorp}$	kg P m^{-2} yr^{-1}	Desorbed inorganic P flux
F_p^{occ}	kg P m^{-2} yr^{-1}	Occluded inorganic P flux
$F_p^{or\text{-}occ}$	kg P m^{-2} yr^{-1}	Occluded organic P flux
F_p^{w}	kg P m^{-2} yr^{-1}	Weathered P flux
$F_{immob\,P}$	kg P m^{-2} yr^{-1}	Immobilized P flux
lit_C	kg C m^{-2} yr^{-1}	C litter flux
lit_{frac}	-	Litter fraction
lit_{leaf}	kg C m^{-2} yr^{-1}	Leaf litter flux
lit_{root}	kg C m^{-2} yr^{-1}	Root litter flux
lit_{wood}	kg C m^{-2} yr^{-1}	Woody litter flux
$F_{minl\,P}$	kg P m^{-2} yr^{-1}	Mineralized P flux
P_p	kg P m^{-2}	Plant P pool
P_{O_l}	kg P m^{-2}	Litter organic pool
P_{O_s}	kg P m^{-2}	Soil organic pool
P_{in}	kg P m^{-2}	Soil inorganic pool
$P_{inorg-sorp}$	kg P m^{-2}	Soil inorganic sorbed pool
$P_{org-sorp}$	kg P m^{-2}	Soil organic sorbed pool
P_{occ}	kg P m^{-2}	Soil occluded pool
P_{pm}	kg P m^{-2}	Parent material pool
R	kg C m^{-2} yr^{-1}	Total respiration
R_{POT}	kg C m^{-2} yr^{-1}	Total potential respiration
R^s	kg C m^{-2} yr^{-1}	Soil respiration
R_d	kg C m^{-2} yr^{-1}	Leaf dark respiration
T_{ref}	K	Soil reference temperature
T_s	K	Soil temperature
Veg_c	kg C m^{-2}	Sum of biomass
z	m	Soil depth

Table 2. P Model parameters

Parameter	Value	Unit	Eq.	Description	Source
				C and N related	
α	0.25	-	6	Plant type material ratio	(Clark *et al.*, 2011)
a_{wl}	1.204	kg C m^{-2}	50	Allometric coefficient	calibrated
σ_l	0.0375	kg C m^{-2} per unit LAI	48	Specific leaf density	Clark *et al.*, 2011
b_{wl}	1.667	-	50	Allometric exponent.	Clark *et al.*, 2011
f_{dr}	0.005	-	47	Respiration scale factor	Calibrated
$resp\_frac$	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	μmol CO_2 m^{-2} s^{-1}	45	Intercept in the linear regression between V_{cmax} and N_{area}	Calibrated (Clark *et al.*, 2011)
v_{sl}	19.22	μmol CO_2 gN^{-1} s-1	45	Slope in the linear regression between V_{cmax} and N_{area}	Calibrated (Clark *et al.*, 2011)
LMA	131.571852	g m-2	45	Observed Leaf Mass per Area	Study site
$Leaf\ N$	1.79007596	g g-1	45, 46	Foliar N concentrations in area basis	Study site
				P related	
$C\!:\!P_{soil}$	1299.6	-	32	Soil C:P ratio	(Fleischer *et al.*, 2019)
v_{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_z	0.001	m^2 s^{-1}	44	Diffusion coefficient	(Burke *et al*, 2017)
K_{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
$K_{sorp-in}$	0.0054	kg P m^{-2} yr^{-1}	37	Inorganic P adsorption coefficient	Calibrated (Hou *et al.*, 2019)
$K_{sorp-or}$	0.00054	kg P m^{-2} yr^{-1}	40	Organic P adsorption coefficient	Calibrated
K_{in-max}	0.0075	kg P m^{-2} yr^{-1}	37	Maximum sorbed inorganic P	Study site
K_{or-max}	0.0042	kg P m^{-2} yr^{-1}	40	Maximum sorbed organic P	Study site
K_w	3×10^{-6}	kg P m^{-2} yr^{-1}	43	P weathering rate	(Wang *et al.*, 2010)

2.3 Study sites

This study 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 pre-experimental, plot, and full-scale long-term projects, combining experimental approaches (Keller *et al.*, 2004; Malhi *et al.*, 2009) with modelling (Lapola and Norby, 2014). Moreover, a recent manipulation experiment at this site provides an opportunity for future model testing under P fertilization. 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 eddy covariance 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). Moreover, the soil class at this site is Geric Ferrosol with a high clay content and weathering activities (Malhi *et al.*, 2004).

2.4 Model parameterisation, calibration and evaluation

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

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

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:

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

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 (f_{dr}) for leaf dark respiration (R_d) as follows:

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

The default value for this scale factor is 0.01 (Clark *et al.*, 2011), and for JULES-CNP simulations at our study site it was modified to 0.005.
Observations of aboveground biomass were used to calibrate the non PFT dependent allometric relationships in JULES (Clark et al 2011) (eq 48-50) for leaf, root and stem C. Specifically, the a_{wl} parameter (eq 50) was modified from 0.65 to 1.204 to match better tropical forest allometry:

$$C_{leaf} = \sigma_l\, L_b \quad \text{(eq.48)}$$
$$C_{root} = C_{leaf} \quad \text{(eq.49)}$$
$$C_{stem} = a_{wl}\, {L_b}^{b_{wl}} \quad \text{(eq.50)}$$

Where σ_l is specific leaf density (kg C m^{-2} per unit LAI), L_b is balanced (or seasonal maximum) leaf area index (m^2 m^{-2}), a_{wl} is allometric coefficient (kg C m^{-2}) and b_{wl} is allometric exponent.
Note that JULES CNP uses C3 and C4 photosynthesis model from Collatz et al., 1991; Collatz, Ribas-Carbo and Berry, 1992, which does not include estimation of J_{max}.
JULES-CNP has fixed stoichiometry and C:P ratios of leaf and root (measured), and wood (estimated from fresh coarse wood (Lugli, 2013)) which were taken from the *study site* and prescribed in JULES to simulate P dynamics in the plant. The following belowground data were used to represent various soil P pools: Resin and bicarbonate inorganic P (inorganic P:P_{in}), organic bicarbonate P (organic P: P_{OS}), NaOH organic P (sorbed organic P: $P_{org-sorp}$), NaOH inorganic P (sorbed inorganic P : $P_{inorg-sorp}$), residual P (occluded P: P_{occ}) and HCL P (parent material P: P_{pm}) (Table 3). The measurements were collected between 2017 and 2018 in control plots. All measurements were conducted at four soil layers (0-5 ,5-10, 10-20, 20-30 cm). However, to be consistent with the JULES model soil layer discretization scheme, we defined 4 soil layers (0-10 cm, 10-30 cm, 30-100 cm and 100-300 cm) and we used the average between 0 and 30 cm to compare against the measurement from the same depth for model evaluation.
Vegetation C stocks were derived based on tree diameter measurements at breast height, that are linked to allometric equations and wood density databases to estimate the C stored in each individual tree, and then scaled to the plot (Chave *et al.*, 2014).

The organic and inorganic soil P assumed to be always at equilibrium with the relative sorbed pools (Wang, Law and Pak, 2010). Thus, in order to cap P sorption and uptake capacity, the maximum sorption capacities (P_{in-max_n}, P_{or-max_n}, eq.37 and 39) (adopted from (Wang, Houlton and Field, 2007)) were prescribed using maximum observed sorbed inorganic and organic P. Hence, the maximum sorption capacity defines the equilibrium state of sorbed and free-soil P. Moreover, 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 (eq.s 27-44) were prescribed using values from the literature (Table 3).

We used a combination of data from *Study site* and the nearby site K34 for model evaluation of C fluxes (GPP, NPP) and C pools (soil and vegetation C, leaf, root and stem C) with no calibration on plant and soil organic and soil inorganic P polls included (Table 3).

Table 3. 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
	Stem 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

2.5 JULES simulations

JULES was applied at the K34 flux tower site using observed meteorological forcing data from 1999-2019 (Fleisher et a 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 Fleischer et al., (2019), by the spin-up from1850 recycling climatology to reach equilibrium state (Figure S1) and 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 CO_2 and N deposition fields. Finally, for the extended simulation period (1999-2019) two runs were performed, the first with ambient the second elevated CO_2 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 CO_2 and elevated CO_2 (eCO_2). Ambient and eCO_2 were prescribed following Fleischer *et al.*, (2019), with present-day CO_2 based on global monitoring stations, and an abrupt (step) increase in atmospheric CO_2 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 CO_2 fertilization effect across model configurations. The CO_2 fertilization effect $\left(CO2_{fert-eff}\right)$ (eq.51) is calculated based on simulated vegetation C under ambient ($VegC\ (aCO_2)$) and eCO_2 ($VegC\ (eCO_2)$) as follows:

$$CO2_{fert-eff} = \frac{(VegC\ (eCO_2) - VegC\ (aCO_2)) \times 100}{VegC\ (aCO_2)} \quad \text{(eq.51)}$$

Furthermore, the net biomass increases due to CO_2 fertilization effect ($\Delta Cveg$) is estimated as follows:

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

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.

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

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:

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

We use JULES-CNP to evaluate the extent of P limitation under ambient and eCO_2 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 layer and under ambient and eCO_2.

To test the sensitivity of the P and C related processes to the model P parameters, six sets of simulations were conducted with modified plant C:P stoichiometry (Plant C:P: *SENS1*), P uptake scaling factor (K_P) (Kp: *SENS2*), inorganic (KP_sorb_in: *SENS3*) and organic (KP_sorb_or: *SENS4*) P adsorption coefficients ($K_{sorp-or}, K_{sorp-in}$), and maximum inorganic (KP_sorb_in_max: *SENS5*) and organic (KP_sorb_or_max: *SENS6*) sorbed P (K_{or-max}, K_{in-max}). These values were prescribed to vary between ±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 haver their own level of uncertainty, we took the 50% of the 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 perform inter-models comparison with 15 models studied by Fleischer *et al.*, (2019) we also studied the response of GPP, NPP and BP to eCO_2 for both initial (1999) and 15 years periods (between 1999-2013).

3. Results

3.1 Model application under ambient CO_2

3.1.1 Calibration of simulated soil P pools

The maximum sorption capacities ($P_{in-max_n}, P_{or-max_n}$, eq.37 and 40) were calibrated to the observed P pools. As a result, JULES-CNP could reproduce the measured soil p pools (Figure. 2 and Table 4). Simulated inorganic soil P and sorbed organic and inorganic soil P closely matched the observations (Table 5 and Figure. 2). However, simulated organic soil P overestimates the observations by 60 %.

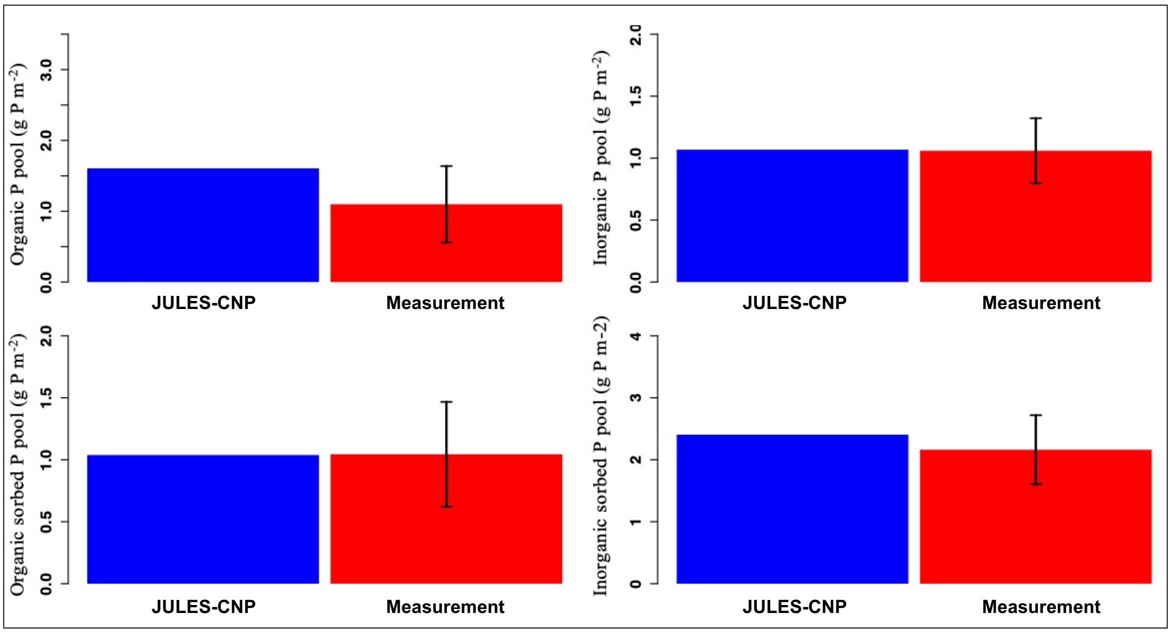

Figure. 2- Modelled vs measured soil phosphorus pools under ambient CO_2 (for the soil depth of 0-30cm). Black line represents standard deviation

Table 4. 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 CO_2**	**Modelled Elevated CO_2**
Organic P (g P m^{-2})	1.09±0.53	1.6	1.57
Inorganic P (g P m^{-2})	1.05±0.33	1.07	0.96
Sorbed organic P (g P m^{-2})	1.04±0.42	1.04	1.03
Sorbed inorganic P (g P m^{-2})	2.1±0.55	2.4	2.4
Occluded P (g P m^{-2})	7.98±2.38	prescribed	prescribed
Weathered P (g P m^{-2})	0.59±12	prescribed	prescribed
Total vegetation P (g P m^{-2})	4.15	4.66	5.11
Soil P – 30cm (g P m^{-2})	13.85	14.7	14.56
Total ecosystem P (g P m^{-2})	-	35.97	35.97
P litter flux (g P $m^{-2} yr^{-1}$)	0.3	0.28	0.29

3.1.2 Model evaluation

JULES CNP-CNP could reproduce the plant and soil C (Figure.2 and Table 5) and N pools and fluxes (Figure S6 and Table 6) pools and fluxes under ambient CO_2. Our results show that simulated GPP, is within the range of measurement (3.02 kg C m^{-2} yr^{-1} model vs 3-3.5 kg C m^{-2} yr^{-1} observed, respectively, Table 5).

Simulated NPP, is close to the measured values (NPP: 1.14 - 1.31 observed vs 1.26 modelled kg C m^{-2} yr^{-1}) with autotropic respiration (RESP) also closely following the observations (1.98 observed vs 1.81 modelled kg C m^{-2} yr^{-1}). Biomass production is estimated as a difference between NPP and the amount of C which is not fixed by plants due to the insufficient P in the system (excess C) (eq. 27). The excess C flux is highly dependent on the plant P and the overall P availability to satisfy demand (Table 5). Simulated flux of excess C is 0.3 kg C m^{-2} yr^{-1} under ambient CO_2. In JULES-CNP this flux is subtracted from NPP in order to give the BP (eq. 17) (Table 5). Our simulated litterfall overestimates the observations by 32%, however simulated vegetation and its components (fine root, leaf and wood) and soil C stocks match well the observations (Table 5).

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

Carbon pools and fluxes	Measured	Modelled Ambient CO_2	Modelled Elevated CO_2
GPP (kg C m^{-2} yr^{-1})	3.0 – 3.5	3.06	3.9
NPP_{pot} (kg C m^{-2} yr^{-1})	-	1.27	1.77
Plant respiration (kg C m^{-2} yr^{-1})	1.98	1.78	2.12
Excess C flux (kg C m^{-2} yr^{-1})	-	0.30	0.81
Biomass Production (kg C m^{-2} yr^{-1})	1.14±0.12	0.96	0.94
Litter C flux (kg C m-^{2} yr^{-1})	0.69±0.15	0.91	0.83
Leaf C (kg C m^{-2})	0.37±0.2	0.38	0.40
Wood C (kg C m^{-2})	22.01	22.4	24.71
Root C (kg C m^{-2})	0.37±0.2	0.38	0.40
Vegetation C (kg C m^{-2})	22.75±0.3	23.16	25.52
Soil C stock (kg C m^{-2})	12.7	13.2	12.71
LAI (m^2 m^{-2})	5.6±0.36	5.77	6.12

3.1.3 Comparison of JULES C, CN and CNP under ambient CO_2

We compare simulated C pools and fluxes from JULES-C, JULES-CN and JULES-CNP (Figure. 3). There is no difference between C stocks and fluxes in simulations from JULES C and CN indicating that there is no N limitation at this tropical site in the CN simulations. However, simulated BP and litter flux of C by JULES C/CN are higher than in JULES-CNP but also overestimate the observations (litter flux of JULES C/CN: 1.18, JULES CNP: 0.91 and obs 0.69 (kg C m^{-2} yr^{1}) and BP of JULES C/CN: 1.24, JULES CNP: 0.96 and obs1.14-1.31 (kg C m^{-2} yr^{-1}), respectively). By including the P cycling in JULES an 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 version (JULES C/CN: 0.38 vs. JULES CNP: 0.31, obs: 0.34 ±0.1(dimensionless).

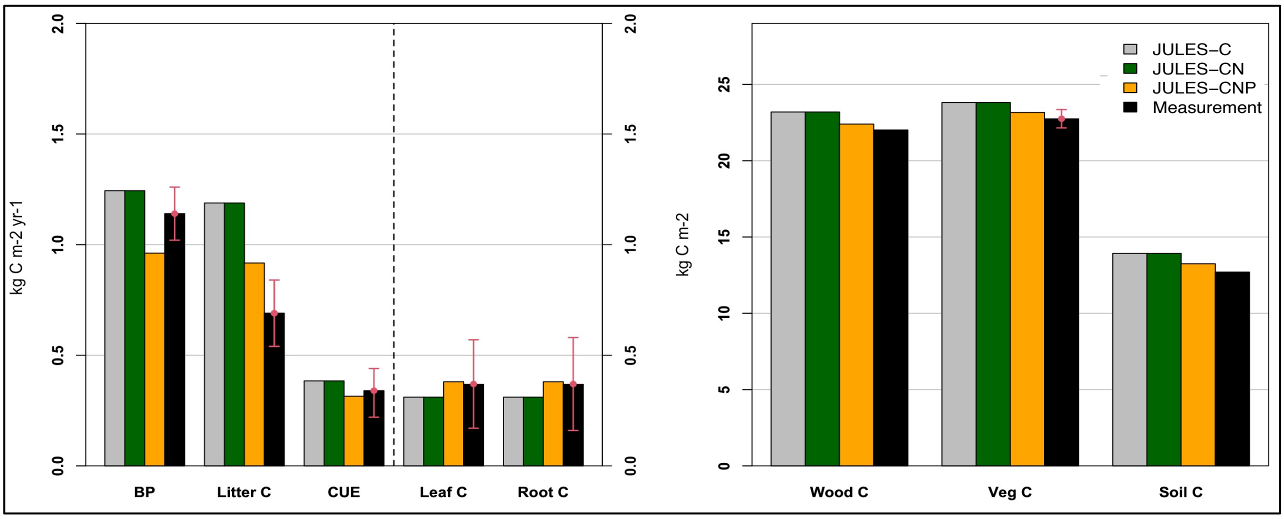

Figure. 3- JULES C, CN, CNP modelled vs measured C pools (Leaf, root, wood, Veg and Soil C) (in kg C m^{-2}) and fluxes (BP and Litter C) (in kg C m^{-2} yr^{-1}) and CUE under ambient CO_2. Note that CUE is unitless.

3.1.4 Model sensitivity

The results indicate that among all the corresponding C and P pools and fluxes, the excess C flux – which demonstrates P limitation to growth – shows the highest sensitivity to changes in C:P ratios, K_P and K_{or-max}, K_{in-max}. A decrease in plant C:P results in a large increase in excess C. This is due to the higher plant P demand as a result of lower plant C:P ratios. An increase in the uptake factor and maximum sorbed organic and inorganic P also results in an increase in excess C. This is due to the higher uptake demand through higher uptake capacity (due to higher K_P) and lower available P for uptake due to higher organic and inorganic sorbed P (due to higher K_{or-max}, K_{in-max}). Since the total P in the system is lower than the plant demand, the uptake capacity and sorbed P, higher P limitation is placed on growth (decreasing BP) which results in an increase in excess C and decrease in plant C, but also soil C which is a result of lower litter input (Figure 4). Total soil P shows low sensitivity to changes in plant C:P and uptake factor but high sensitivity to maximum inorganic sorbed P. Moreover, sorbed P shows middle to high sensitivity to maximum organic and inorganic sorbed P respectively (Figure. S5). Nevertheless, organic and inorganic P adsorption coefficients ($K_{sorp-or}$, $K_{sorp-in}$) show no sensitivity to C and P pools and fluxes. This is due to limiting the organic and inorganic P sorption terms controlled only by maximum sorption, hence no effect applied by organic and inorganic adsorption coefficients.

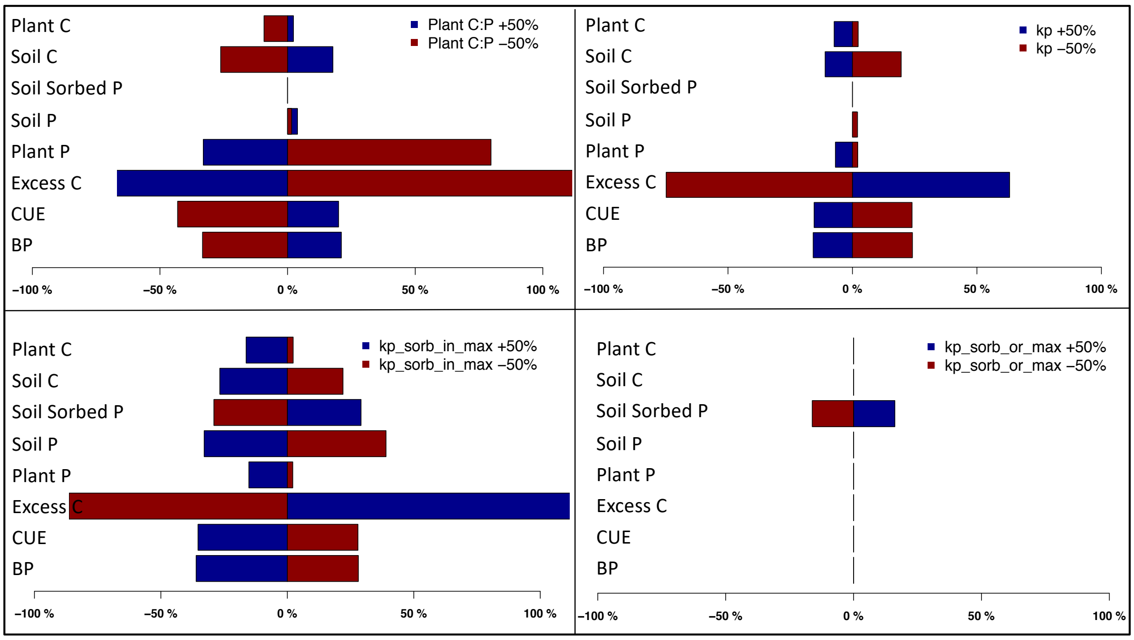

Figure. 4- Model sensitivity test results and corresponding C and P pools and fluxes under ambient CO_2.

3.2 Model application under elevated CO_2

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

The eCO_2 simulation using JULES CNP yields a higher GPP compared to the ambient CO_2 (0.83 (kg C m^{-2} yr^{-1}) increase), as a result of CO_2 fertilization. Moreover, due to the GPP increase, NPP and RESP follows the same trend and increased compared to ambient CO_2 (NPP: 0.49 and RESP:0.3 (kg C m^{-2} yr^{-1}) increase) (Table 5). The total simulated vegetation C pool increases under eCO_2 compared to ambient CO_2 (0.41 kg C m^{-2}), hence the estimated plant P (estimated as a fraction of C:P ratios) increases as well (+0.45 (g P m^{-2})) (Fig 6, Table 4). Thus, the simulated plant P demand is higher, and as the total available soil P for uptake is limited, the simulated 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 yields close to the ambient CO_2 (1.6 g P m^{-2}) (Table 5). This is due to the same parameterization of the output fluxes from this pool for eCO_2 and ambient CO_2. The simulated pool of inorganic P under eCO_2 decreases compared to the ambient CO_2 by 0.11 (g P $m-^{2}$) due to the increased plant P pools and slight increase in uptake (+0.13 %).
However, the simulated sorbed organic and inorganic soil P from eCO_2 are similar to those simulated under the ambient CO_2 which is due to the same parameterizing of sorption function (maximum sorption capacity) from the ambient CO_2 run as explained in calibration section. Moreover, the modelled occluded and weathered soil P yield similar to those in the ambient CO_2 simulation (Table 5) which is due to the same prescribed observational data that was used for this simulation.

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

JULES C/CN show higher vegetation and soil C pools, BP and litter flux compared to JULES-CNP: (Table 6, Figure. S2). Under eCO_2, simulated NPP using JULES C-CN is 4.5% higher than JULES CNP and the BP with JULES- C/CN is 96.8% higher than in JULES-CNP which simulates an 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 6. C pools and fluxes using JULES C/CN and difference in percentage with JULES CNP model under eCO_2. A positive % means larger respective values simulated with JULES C and JULES CN than with JULES CNP (between period 2017-18).

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

3.2.2.1 Inter-models under elevated CO_2

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

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

Simulated total biomass (leaf, fine root and wood C) (ΔC*veg*) using JULES C/CN for the 1st and 15 years of eCO_2 increases by 9% and 13% respectively. However, using JULES CNP ΔC*veg* only increases by 0.5% and 9% for 1st and 15 years of eCO_2, respectively.

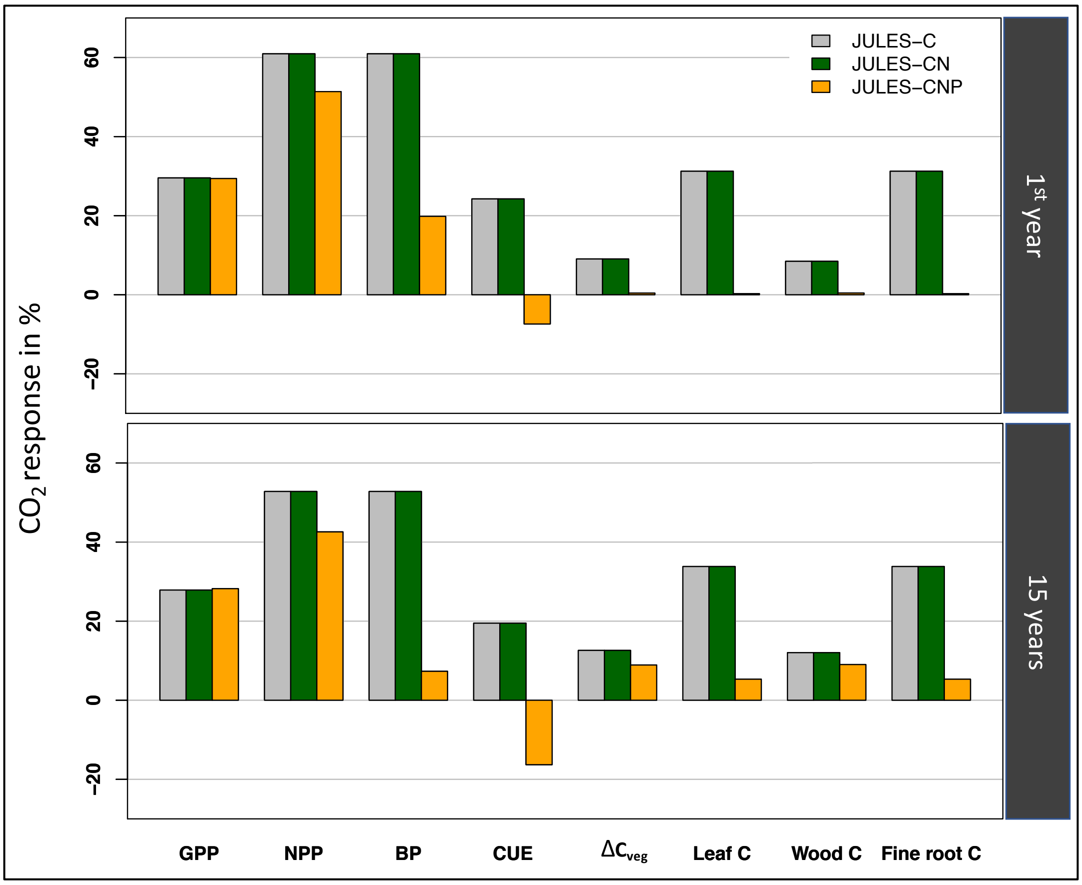

Figure. 5- Relative effect of eCO_2 on simulated GPP, NPP, BP, CUE, Δ*Cveg*, leaf C, wood C and fine root C, using three versions of JULES model in 1st (initial response) and 15 years periods (final response).

3.3 Plant P Demand, uptake and excess C under ambient and elevated CO_2

To understand further the CP-cycle dynamics, we studied the monthly averaged plant P demand and the relative (limited) P uptake (eq. 26) under both ambient and elevated CO_2 conditions (Figure. 6).

Under ambient CO_2 condition the highest GPP is estimated at 3.5±0.19 kg C m^{-2} $month^{-1}$ in July and the lowest at 2.06±0.61kg C m^{-2} $month^{-1}$ in October (Figure. 6-a). The estimated WUE and SMCL in October is among the lowest estimated monthly values at 2.3±0.51 kg CO_2/kg H_2O and 526.2±31 kg m^{-2} respectively (Figure. 6-c). The highest P demand is estimated at 0.4±0.02 g P m^{-2} $month^{-1}$ 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 CO_2, under eCO_2 condition the highest estimated GPP is in July at 4.36±0.21 kg C m^{-2} $month^{-1}$ and lowest for October 3.02±0.75 kg C m^{-2} $month^{-1}$ (Figure. 6-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 CO_2/kg H_2O and 552±33 kg m^{-2} for October respectively (Figure. 6-d). The highest P demand is estimated for July at 0.51±0.02 g P m^{-2} $month^{-1}$ 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 eCO_2 and ambient CO_2 conditions, the P uptake flux under eCO_2 is higher than the ambient CO_2 condition. This is due to the higher WUE and increased SMCL (controlling uptake capacity (eq. 27)) under eCO_2 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 CO_2 condition (Figure. 6-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 eCO_2 condition.

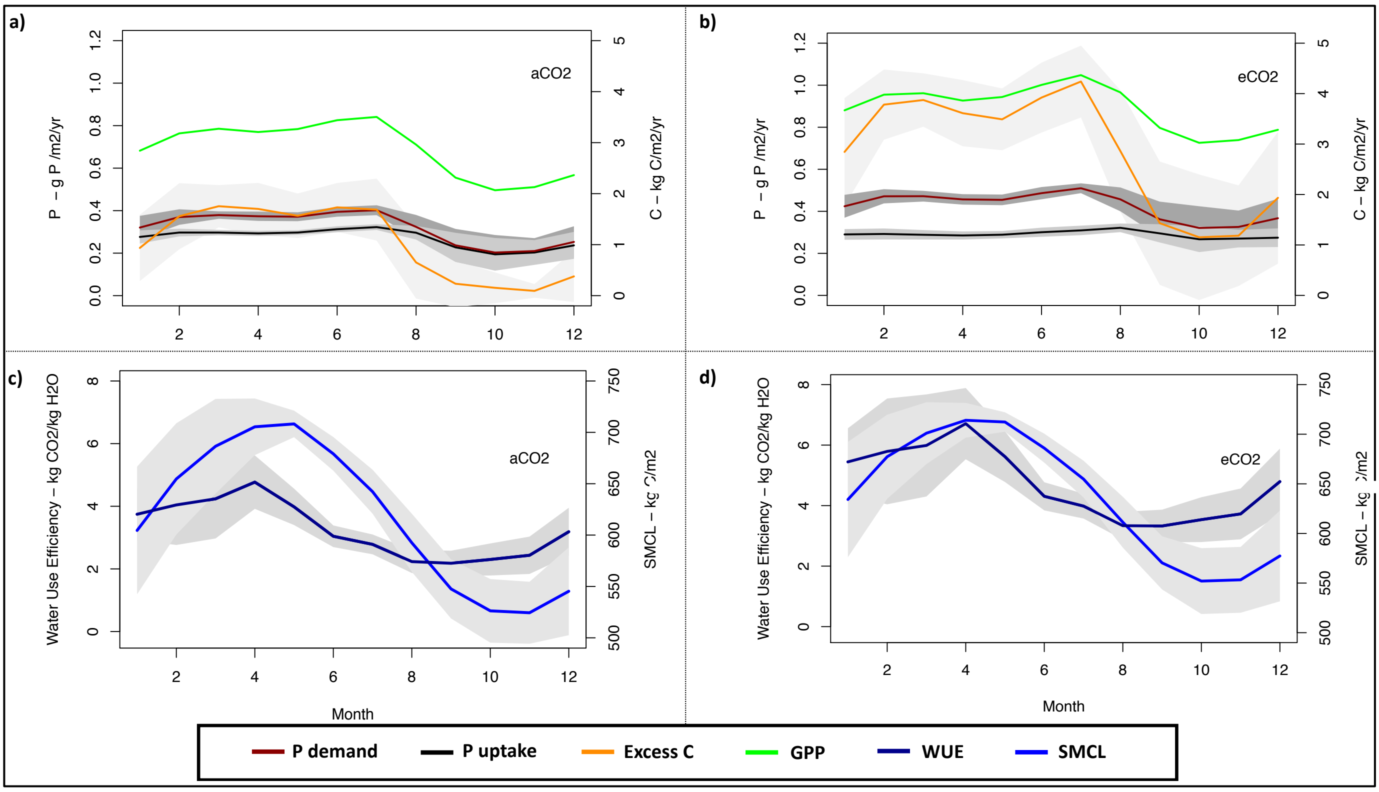

Figure. 6- Simulated monthly plant P demand and uptake (g P m^{-2} yr^{-1}), excess C and GPP (kg C m^{-2} yr^{-1}) under a) aCO_2 and b) eCO_2, water use efficiency (g m^{-2} yr^{-1}) under c) ambient CO_2 (aCO_2) and d) eCO_2 conditions. The grey area represents the standard deviation.

3.4 Soil P pools profile under ambient CO_2 and elevated CO_2

We explored the distribution of the inorganic and organic soil P and their sorbed fraction within the soil layers and under different CO_2 conditions (Figure. S3). Both the ambient and eCO_2 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 eCO_2 condition) and the same parameter values used for both ambient and eCO_2 runs.

Moreover, the soil P within 30cm soil depth for ambient and eCO_2 conditions is at 14.7 (g P m^{-2}) and 14.56 (g P m^{-2}) respectively, and the total ecosystem P for both ambient and eCO_2 conditions is at 35.97 (g P m^{-2}). However, the slightly lower soil P in the eCO_2 condition is due to the higher plant P demand compared to the ambient condition, hence the higher allocated P vegetation (10%) under eCO_2 condition.

4. Discussion

Studies show the significant role of the tropical forests, and Amazonia in particular, in C uptake and regulating atmospheric CO_2 (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 eCO_2 under P limited conditions remains uncertain (Fleischer *et al.*, 2019). These responses in P enabled models are represented in different ways regarding the excess C which is not used for plant growth due to P limitation. Either growth is directly downregulated taking the minimum labile plant C,N and P (Goll *et al.*, 2017), or photosynthesis is downregulated via V_{cmax} and J_{max} (Comins and McMurtrie, 1993; Yang *et al.*, 2014; Zhu *et al.*, 2016) and finally 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 CO_2 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 the studies showing lower CUE when nutrient availability declines (Vicca *et al.*, 2012). However, this remains a major uncertainty in understanding the implication of P limitation on terrestrial biogeochemical cycles.

Our new developments include major 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. Moreover, JULES CNP can be applied at the global scale and for future projections using global soil P data (Sun *et al.*, 2021) for model initialization and PFT-specific plant stoichiometries (Zechmeister-Boltenstern et al. 2015), 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 against observations

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

Our estimated maximum P uptake, which represents the actual available P for plant uptake (Goll *et al.*, 2017), for both ambient and eCO_2 conditions, 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 CO_2, 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 eCO_2 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 moisture in the dry season is higher (Xu *et al.*, 2016) which impacts our capped P uptake flux (eq. 27) and increases the uptake capacity respectively.

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_{cmax} estimation method (eq. 40), the model slightly underestimates the total GPP (2.9 kg C m^{-2} yr^{-1} vs. 3-3.5 kg C m^{-2} yr^{-1}). Therefore, in this version of the model, we used the improved V_{cmax} estimation method based on N and P (eq. 46) which resulted 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 forests (-8%) (Ellsworth *et al.*, 2017), due to the P limitation which showed 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 the NPP. Using JULES C/CN models our estimated biomass productivity enhancement due to eCO_2 (49%) is in the middle range of the reported various studies from 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 CASACNP 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 experimental study that shows a strong correlation between the total NPP and the soil available P (Aragão *et al.*, 2009). Nevertheless, our model show that the P limitation mimics the same response to the CO_2 fertilization similar to sites in pool soils (see ZAR-01 site in 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 the estimation by Jiang *et al.* (2020) for mature 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 change this ratio (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 into JULES (Argles *et al.*, 2020) and its integration into JULES-CNP in the future can resolve this issue. Moreover 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; Bruijnzeel, 1991; Neff, Hobbie and Vitousek, 2000).

Due to the strong fixation of P in the soil (Aerts & Chapin, 2000; Goodale, Lajtha,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 not included in the current version of JULES CNP and it only accounts for total mineralization. However, even the models which includes 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, the future work should focus on implanting a recent developed Non-Structural Carbohydrate (NSC) model (SUGAR) (Jones *et al.*, 2020) in JULES-CNP.

4.2. Inter-models comparison

The comparison of simulated GPP enhancement across JULES versions for the 1st year is within the middle range of the 1st year CO_2 responses of the C/CN models studied by Fleischer *et al.*, (2019) evaluating simulated eCO_2 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 eCO_2, 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 CO_2 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 the P availability in the P limited system (He and Dijkstra, 2014). Hence, under eCO_2 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 CO_2 .

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 by Fleischer *et al.*, (2019) and close to the estimations from CABLE (Haverd *et al.*, 2018) and ORCHIDEE (Goll *et al.*, 2017) models, which may be due to the similar representation of P processes and limitation between these models. However, our results show a 29% decrease in NPP using JULES-CNP compared to JULES-C/CN which is smaller than the differences between the CLM-CNP and CLM-CN versions (51% decrease) (Yang *et al.*, 2014). The lower estimated decrease in JULES highlights the need to further study the fully corresponding plant C pools and fluxes to the changes in soil and plant P. Therefore, future work should be focused on the improvement of the total P availability and the plant C feedbacks. Moreover, there are other environmental factors such as temperature which shows a possible impact on the CO_2 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 CO_2 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 (ΔC_{veg}) using JULES C/CN for the 1^{st} 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. Moreover, the model estimated a significant NPP limitation under ambient CO_2, due to the high P deficiency at this site which is representative of Central Amazon, 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.5711160). 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).

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

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