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14 **Abstract**

15 Subtropical forests play a crucial role in global cycle, yet their carbon sink capacity is
16 significantly constrained by phosphorus availability. Models that omit phosphorus
17 dynamics risk overestimating carbon sinks, potentially undermining the scientific basis for
18 carbon neutrality strategies. In this study, we developed TECO-CNP Sv1.0, a coupled
19 carbon-nitrogen-phosphorus model based on the Terrestrial ECOSystem (TECO) model,
20 explicitly capturing key biogeochemical interactions and nutrient-regulated carbon cycling.
21 The model simulates how plant growth and carbon partitioning respond to both external
22 soil nutrient availability and internal physiological constraints, enabling plant acclimation
23 to varying nutrient conditions. Using observations from a phosphorus-limited subtropical
24 forest in East China, we first evaluated model performance on estimating state variables
25 with empirically calibrated parameters. Compared to the C-only and coupled C-N
26 configurations, the CNP model better reproduced observed plant and soil C, N, and P pools.
27 To systematically optimize model parameters and reduce uncertainties in predictions, we
28 further incorporated a built-in data assimilation framework for parameter optimization. The
29 CNP model with optimized parameters significantly improved carbon flux estimates,
30 reducing root mean square errors and enhancing concordance correlation coefficients for
31 gross primary productivity, ecosystem respiration, and net ecosystem exchange. By
32 explicitly incorporating phosphorus dynamics and data assimilation, this study provides a
33 more accurate and robust framework for predicting carbon sequestration in phosphorus-
34 limited subtropical forests.



35 **1 Introduction**

36 Accurately representing phosphorus (P) cycling in land surface models (LSMs) is crucial
37 for projecting terrestrial carbon sink dynamics under climate change (Wieder et al., 2015).
38 As an essential element, P availability regulates plant growth and ecosystem productivity
39 (Walton et al., 2023; Vitousek et al., 2010). For instance, nutrient addition experiments in
40 an old-growth Amazon rainforest demonstrated that net primary productivity increased
41 exclusively with P addition (Cunha et al., 2022). Likewise, in subtropical mature forests,
42 soil P availability was found to exert dominant control over plant functional traits at both
43 species and community levels (Cui et al., 2022). Recent global syntheses have revealed a
44 more widespread distribution of terrestrial P limitation than previously recognized (Hou et
45 al., 2020; Du et al., 2020, Xia & Wan, 2008; Elser et al., 2007). More concerning is that P
46 limitation is expected to intensify (Wang et al., 2023; Luo et al., 2022) due to factors such
47 as N deposition-induced N:P stoichiometric imbalance (Peng et al., 2019; Lu and Tian,
48 2017; Du et al., 2016; Peñuelas, 2013) and reduced P availability under elevated CO₂
49 concentration (Wang et al., 2023). Consequently, incorporating P limitation into LSMs has
50 become a pressing challenge for improving carbon cycle projections (Fisher & Koven,
51 2020; Achat et al., 2016; Reed et al., 2015).

52 To address this challenge, several modeling groups have incorporated a prognostic P
53 cycle into their existing frameworks over the past decade, including CASACNP (Carnegie-
54 Ames-Stanford Approach; Wang et al., 2010), JSBACH (Jena Scheme for Biosphere-
55 Atmosphere Coupling in Hamburg; Goll et al., 2012), CLM-CNP (Community Land
56 Model; Yang et al., 2014), among others. These pioneering efforts in coupled carbon-
57 nitrogen-phosphorus (C-N-P) modeling have laid a solid foundation for increasing
58 incorporation of P cycling in LSMs (e.g., Goll et al., 2017; Nakhavali et al., 2022) and
59 demographic vegetation models (Knox et al., 2024), shedding light on how P limitation
60 constrains ecosystem productivity under elevated atmospheric CO₂ (Wang et al., 2024;
61 Fleischer et al., 2019; Medley et al., 2016). However, current C-N-P models often yield
62 "right answers for wrong reasons" (Jiang et al., 2024a), largely due to two key limitations:
63 (1) calibration and validation data are predominantly derived from a narrow range of
64 ecosystems, with most coupled C-N-P models relying on *in-situ* data from tropical regions,



65 particularly Hawaii and the Amazon (e.g., Nakhavali et al., 2023; Yang et al., 2014; Goll
66 et al., 2012, 2017; Zhu et al., 2016), and (2) oversimplified representations of P cycling
67 processes (Achat et al., 2016; Reed et al., 2015), such as the absence of physiological
68 mechanisms governing vegetation P uptake (Jiang et al., 2019). Addressing these gaps
69 require advancing coupled C-N-P model with improved mechanistic process-based
70 representations and broader ecosystem applicability (Jiang et al., 2024a).

71 Subtropical forest ecosystems are recognized as important carbon sinks in the global
72 carbon cycle (Pan et al., 2024; Keenan et al., 2018; Yu et al., 2014). In particular, East
73 Asian monsoon subtropical forests exhibit high carbon sink capacity, with an average net
74 ecosystem productivity of about $400 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Yu et al., 2014). These ecosystems are
75 likely subject to substantial phosphorus limitation, as evidenced by a meta-analysis of
76 nutrient addition experiments showing that forest productivity exhibits the strongest
77 standardized response to P addition in the subtropical regions (25–40 latitude; Hou et al.,
78 2021). Moreover, intensive nitrogen deposition may further exacerbate P limitation (Zhu
79 et al., 2016; Yu et al., 2014). Accurately projecting of the future carbon sink capacity of
80 subtropical forests is essential for assessing their role in climate change mitigation
81 (Friedlingstein et al., 2023; Requena Suarez et al., 2019; Grassi et al., 2017). However,
82 substantial uncertainties remain in current model projections of subtropical carbon
83 dynamics (Wei et al., 2024), highlighting the urgent need for improved carbon cycle
84 predictions through better representation of coupled C-N-P interactions in these regions.

85 In this study, we develop TECO-CNP Sv1.0, an advanced version of the Terrestrial
86 ECOSystem (TECO) model (Weng & Luo, 2008, 2011), incorporating detailed mechanistic
87 representations of coupled C-N-P cycling processes, such as dynamic plant growth
88 response to soil available nutrient through modified growth rates and allocation patterns,
89 and the combined physical and physiological controls on phosphorus uptake. Additionally,
90 we integrated a data assimilation module based on a Bayesian probabilistic inversion
91 approach (Xu et al., 2006; Ma et al., 2017; Shi et al., 2016, 2018; Zhou et al., 2020),
92 providing an efficient framework for model reparameterization and broader applications.
93 Based on comprehensive observations from a P-limited subtropical evergreen broadleaf
94 forest in eastern China, we further test two key hypotheses: (1) the CNP model can



95 reproduce ecosystem state variables through traditional spin-up and manual parameter
96 tuning, and (2) the built-in data assimilation system can substantially improve carbon flux
97 predictions.

98 **2 Materials and Methods**

99 **2.1 TECO developments**

100 The TECO-CNP model has evolved from its precursor model, the Terrestrial ECOsystem
101 model (TECO, Weng & Luo, 2008). The TECO model is a process-based ecosystem model
102 encompassing eight organic carbon pools and a plant non-structural carbohydrate (NSC)
103 pool (Weng & Luo, 2008). The representation of the NSC pool in TECO is advantageous
104 for capturing the seasonal decoupling of growth and nutrient acquisition within plants
105 (Zavistic & Polle, 2018; Jones et al., 2020) and for managing C that is not utilized for plant
106 growth under nutrient-limited conditions (Nakhavali et al., 2022; Haverd et al., 2018). The
107 TECO model has been part of model intercomparison ensembles (Zaehle et al., 2014; De
108 Kauwe et al., 2014) and has been applied across diverse ecosystem types, such as grassland
109 (Weng & Luo, 2008; Zhou et al., 2021), temperate coniferous forests (Luo et al., 2003;
110 Weng & Luo, 2011; Jiang et al., 2017) and deciduous broadleaf forests (Jiang et al., 2017)
111 and northern peatland (Ma et al., 2017, 2022; Huang et al., 2017).

112 Simplified N and P cycling were incorporated in the TECO successively (Shi et al.,
113 2016; Du et al., 2018; Du et al., 2021), where the structure of the carbon processes was
114 expressed as a matrix form (Luo et al., 2003; Xu et al., 2006; Weng & Luo, 2011). Thus,
115 the photosynthesis was simulated aided by an external model, for instance, Shi et al. (2016)
116 utilized MAESTRA to generate the gross primary productivity. The processes related to
117 the N and P cycle were only represented in a parsimonious way in the matrix versions. For
118 example, the nutrient uptake process was simplified at a constant rate, and the interactions
119 of carbon, nitrogen and phosphorus were treated implicitly (Shi et al., 2016; Du et al., 2021).

120 In this study, we developed TECO-CNP, a coupled C-N-P model based on the full
121 version of TECO, which fundamentally differs from previous matrix-based approaches.
122 This new model explicitly represents the mechanistic processes of nutrient cycling (Sect.
123 2.2), with a focus on nutrient regulation of carbon cycling. Specifically, the model



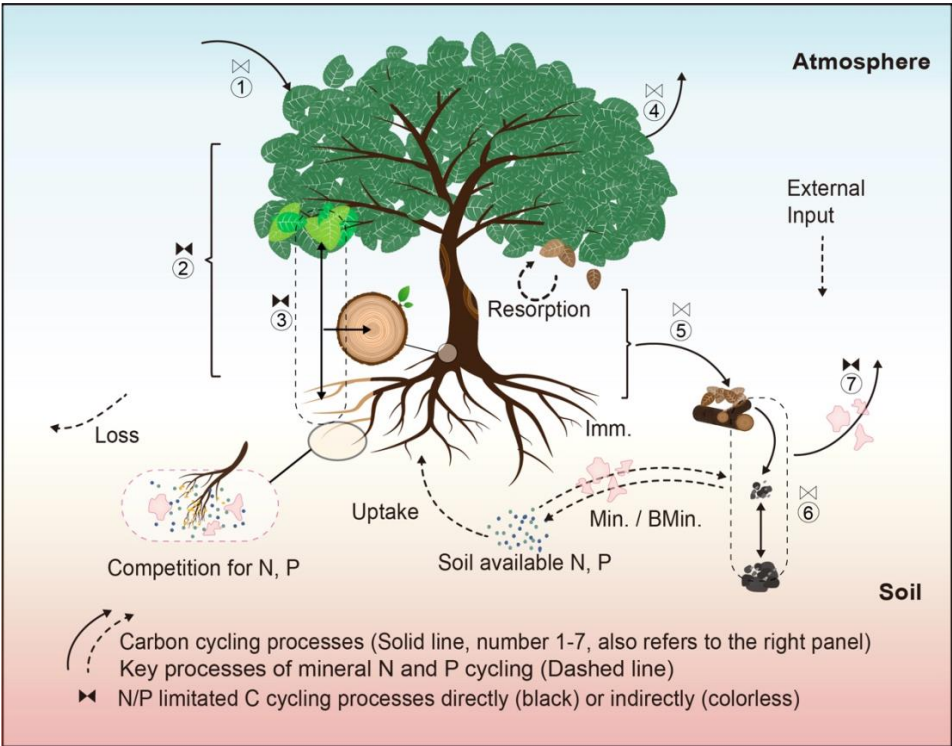
124 incorporates four key nutrient-carbon interactions: (1) growth rate limitations controlled
125 by internal plant nutrient concentrations and nutrient supply-demand relationships; (2)
126 allocation patterns dependent on nitrogen and phosphorus availability; (3) decomposition
127 processes constrained by microbially-mediated nutrient availability; and (4) carbon costs
128 associated with nutrient uptake and fixation. These process-based implementations, which
129 aim to provide a more realistic representation of terrestrial biogeochemical cycles, are
130 described in detail in the following sections.

131 **2.2 Model description**

132 We introduce a comprehensive biogeochemical N and P cycle into the full TECO, named
133 TECO-CNP Sv1.0. Key processes of N and P cycling and their interactions with the carbon
134 cycle have been represented using reliable mechanistic assumptions based on our
135 experimental measurements or validated by state-of-the-art LSMs. In the following
136 sections, we first document an overview of the carbon cycle and highlight the effects of
137 nutrient limitation on the carbon cycle in Sect. 2.2.1. We then describe the shared and
138 specific N and P cycling processes in Sects. 2.2.2 and 2.2.3, respectively.

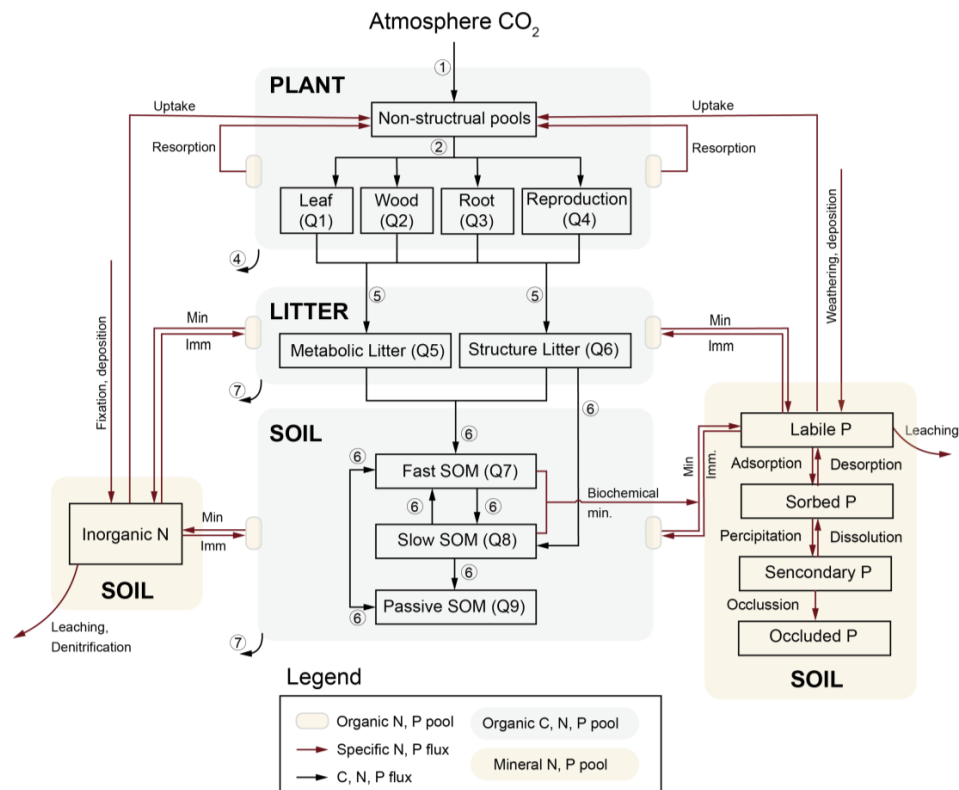
139 **2.2.1 Nutrient-limited carbon cycle**

140 The carbon cycle in the new model builds upon the TECO model, incorporating processes
141 such as photosynthesis, plant growth controlled by allocation and phenology, autotrophic
142 and heterotrophic respiration, litter production, and carbon transfer (Fig. 1). See Luo et al.,
143 (2003) and Weng & Luo (2008) for detailed descriptions. These processes regulate the
144 dynamics of plant, litter, and soil pools (Fig. 2). Nutrients directly or indirectly constrain
145 them. For instance, plant growth rates and carbon allocation strategies are directly
146 influenced by internal nutrient availability within pools and soil-accessible nitrogen and
147 phosphorus. Additionally, resource limitations adhere to Liebig's law of the minimum,
148 where the nutrient-constrained process is hindered only by the most limiting resources
149 (Rastetter, 2011).



150

151 **Figure 1. The schematic diagram of the biogeochemical processes of the carbon,**
152 **nitrogen and phosphorus cycles and associated interactions in TECO-CNP.**
153 Representation of carbon cycling processes controlled by nitrogen and phosphorus in
154 TECO-CNP. Solid lines indicate carbon cycling processes (labelled 1-7) comprise (1)
155 photosynthesis, (2) carbon allocation, (3) plant growth, (4) autotrophic respiration, (5) litter
156 production, (6) carbon transfer, and (7) heterotrophic respiration. These processes are
157 controlled directly by nitrogen and phosphorus (black control characters) or indirectly
158 (colorless control characters). Dashed lines indicate the common processes controlling the
159 dynamics of soil available nitrogen and phosphorus, simplified as plant uptake,
160 mineralization, immobilization, biogeochemical mineralization, external input and loss.
161 Irregular pink shapes represent competition for soil available nitrogen and phosphorus
162 between plants and microorganisms. Min., mineralization; BMin., biochemical
163 mineralization; Imm., Immobilization.



164
165 **Figure 2. Model structure of TECO-CNP.** The model represents the nine organic carbon,
166 nitrogen, and phosphorus stocks within the plant (denoted as Q1-4), litter (Q5-7), and soil
167 (Q7-9). Fluxes among these organic pools are depicted by black arrows. Specific N and P
168 fluxes are indicated by dark red arrows, with associated processes labeled accordingly. Min
169 denotes mineralization, and Imm denotes immobilization. The circled numbers (1-7)
170 correspond to the carbon cycling processes in Fig 1.



173 The canopy-level photosynthesis is simulated by a two-leaf model, which consists of
174 a radiation sub-model and a coupled sub-model of stomata-photosynthesis-transpiration
175 for sunlight and shaded leaves (Wang & Leuning, 1998). Leaf photosynthesis is estimated
176 by the equations derived from the Farquhar model (Farquhar et al., 1980) and a stomatal
177 conductance model (Ball et al., 1987; Leuning et al., 1995). The photosynthesis of a single
178 leaf is then upscale to the canopy level (Wang & Leuning, 1998). We hypothesize that
179 plant photosynthesis is downregulated as photosynthetic surface area decreases when
180 nutrient limits the plant growth. Plant growth is adjusted based on the nutrient limitation
181 factor calculated at each time step, meaning that plants tend to reduce growth under low
182 nutrient conditions to avoid nutrient deficiency within the organism (Veneklaas et al.,
183 2012). Accordingly, the nutrient-constrained growth rate (GP_a) is dependent on the
184 potential growth rate (GP_p) and nutrient limitation scalar for plant growth (L_{GP}) as the
185 following equation:

$$GP_{a,i} = GP_{p,i} * L_{GP} , \quad (1)$$

186 where subscript i indicates leaf ($i = 1$), wood ($i = 2$), root ($i = 3$) or reproduction ($i = 4$)
187 (Table 1). The difference between actual and potential plant growth is referred to as excess
188 carbon, which implicitly represents the carbon lost from NSC pool through various
189 pathways to cope with nutrient limitations.

190 The nutrient limitation scalar for plant growth incorporates both the nutrient status of
191 plant tissues and soil nutrient supply (Fig. 1b). which can be expressed as:

$$L_{GP} = L_{in,leaf} L_{sp} , \quad (2)$$

192 where $L_{in,leaf}$ and L_{sp} represent the nutrient limitation factors derived from leaf nutrient
193 concentration (Eq. 3-5) and the nutrient demand-supply process (Eq. 6-8), respectively.
194 Shifts in leaf nutrient concentrations act as a potential limiting factor for plant growth,
195 implying the mechanism by which changes in leaf nutrient concentration can impact
196 photosynthesis (Ellsworth et al., 2022; Sterner & Elser, 2002). Description of limitation
197 factors that account for plant tissue's nutrient concentration can be given by:

$$L_{in,i} = \min(L_{in,N,i}, L_{in,P,i}) , \quad (3)$$



$$L_{in,N,i} = \frac{R_{N,i}}{R_{N,i} + k_{CN}}, \quad (4)$$

$$L_{in,P,i} = \frac{R_{P,i}}{R_{P,i} + k_{CP}}, \quad (5)$$

198 where R_N and R_P represent the C:N ratios and C:P ratios, respectively. k_{CN} and k_{CP} are
199 empirical parameters. A study by Cui et al. (2020) reveals that the Tiantong site is identified
200 as a P-limited ecosystem, as indicated by the leaf N:P thresholds from Koerselman and
201 Meuleman (1996). Thus, we adopted the values of k_{CP} (0.0006 gC gP⁻¹) in Wang et al.,
202 2010) to achieve a N limitation when N:P < 16 (gN gP⁻¹) and otherwise plant growth is
203 limited by P. k_{CN} (0.01 gN gC⁻¹) is given based on the results of Linder & Rook (1984).

204

205 **Table 1** Variables for carbon cycling processes in TECO-CNP.

Variables	Description	Unit
GP _p	Potential plant growth rate without nutrient limitation	gC m ⁻² h ⁻¹
GP _a	Nutrient-limited plant growth rate	gC m ⁻² h ⁻¹
D _{a,x}	Actual decomposition rate of litter pool m or soil pool j , accounting for nutrient limitation, $x = m, j$	gC m ⁻² h ⁻¹
D _x	Potential decomposition rate of litter pool m or soil pool j , controlled by soil temperature and moisture, $x = m, j$	gC m ⁻² h ⁻¹
NPP _i	Net primary productivity allocated to plant pool i	gC m ⁻² h ⁻¹
F _{new,C,i}	Newly input carbon from NSC pool for plant growth	gC m ⁻² h ⁻¹
b _{C,i}	Allocation fraction of carbon to plant pool i	unitless
r _{i,j}	Fraction of carbon from plant pool i to litter pools j	unitless
BM _{root}	Plant root biomass	gC m ⁻²
BM _{root*}	Root biomass density	g biomass m ⁻³
f _{nsc}	Plant labile carbon limiting factor	unitless
f _w	Soil moisture limiting factor	unitless
f _T	Soil temperature limiting factor	unitless
W	Soil water availability index	unitless
κ	Light availability factor	unitless

206 * i indicates leaf ($i = 1$), wood ($i = 2$), root ($i = 3$) or reproduction ($i = 4$), j indicates metabolic litter (j
207 = 5) or structure litter ($j = 6$), and m indicates fast SOM ($m = 7$), slow SOM ($m = 8$) and passive SOM
208 ($m = 9$).



209 The nutrient demand-supply limitation factor is calculated as a function of plant
210 nutrient uptake and demand. When nutrient demand is not satisfied, the value of the
211 limitation factor falls below one, thereby impacting plant growth. This assumption is in
212 line with the field findings that reveal an increase in plant productivity under nutrient
213 addition (Cunha et al., 2022; Liang et al., 2021). Description of nutrient demand-supply
214 limitation factor (L_{sp}) can be given by:

$$L_{sp} = \min(L_{sp,N}, L_{sp,P}), \quad (6)$$

$$L_{sp,N} = \frac{1}{1 + \exp(-12 * \frac{F_{up,N}}{F_{dm,N}} + 6)}, \quad (7)$$

$$L_{sp,P} = \frac{1}{1 + \exp(-12 * \frac{F_{up,P}}{F_{dm,P}} + 6)}, \quad (8)$$

215 where $F_{up,N}$ and $F_{up,P}$ represent plant nutrient uptake for N and P, respectively, which is
216 determined by both supply and demand (Eq. 23). $F_{dm,N}$ and $F_{dm,P}$ represent the plant
217 required N and P to sustain a given NPP (Eq. 24). We implemented a logistic function to
218 represent the phosphorus limitation factor, which provides a more mechanistically sound
219 representation of nutrient limitation compared to the simple linear ratio. This formulation
220 ensures a smooth transition between phosphorus-limited and phosphorus-sufficient
221 conditions, with values bounded between zero and one. The coefficients were carefully
222 selected to maintain appropriate sensitivity in the transition zone while avoiding unrealistic
223 sharp thresholds. This sigmoidal response better reflects the gradual physiological
224 adjustments of plants to varying nutrient availability and is consistent with a theoretical
225 understanding of nutrient limitation effects on plant growth. The method of determining
226 whether plants are nutrient-limited based on the supply-demand method is widely
227 employed in many models, for example, CASACNP (Wang et al., 2010), CLM-CNP (Yang
228 et al., 2014) and ORCHIDEE (revision 4520; Goll et al., 2017).

229 The carbohydrates available for plant growth will be redistributed among the plant
230 pools based on their actual growth rates. A prescribed proportion of those allocated to
231 reproductive processes (Sitch et al., 2003; Smith et al., 2001), such as flower formation,
232 fruit development, and seed production, are stored in the reproductive pool. Vegetation



233 growth is assumed to take priority over reproduction (Zust et al., 2015; Tang et al., 2021).
234 Thus, the plant's reproductive allocation is zero when the leaf area index (LAI) is below
235 the minimum threshold. After allocating 12% of the available and growth carbon to the
236 reproduction pool if the LAI is below the minimum threshold), the remaining carbon is
237 distributed among leaf, wood, and root based on a resource limitation allocation scheme as
238 follows.

239 The dynamic allocation for leaf, wood, and root is regulated by light availability, soil
240 water supply, canopy phenological status (Luo et al., 1995; Denison & Loomis, 1989;
241 Arora and Boer, 2005), and plant's internal nutrient status (Fig. 1b). This allocation strategy
242 permits a reduction in photosynthetic surface area and enhanced root growth under nutrient
243 limitation, exemplifying a structural adjustment in line with the observations (Keith et al.,
244 1997; Thomas et al., 2015; Yan et al., 2016). The allocation fractions for leaf, wood, and
245 root are given by:

$$b_{C,leaf} = \frac{\varepsilon_L * L_{in,leaf}}{1 + \omega(2 - \kappa - W)}, \quad (9)$$

$$b_{C,wood} = \frac{\varepsilon_W * L_{in,wood} + \omega(1 - \kappa)}{1 + \omega(2 - \kappa - W)}, \quad (10)$$

$$b_{C,root} = \frac{(1 - \varepsilon_L * L_{in,leaf} - \varepsilon_W * L_{in,wood}) + \omega(1 - \kappa)}{1 + \omega(2 - \kappa - W)} = 1 - b_{C,leaf} - b_{C,wood}, \quad (11)$$

246 where $b_{C,leaf}$, $b_{C,wood}$ and $b_{C,root}$ represent the carbon fractions available for growth
247 allocated to leaf, wood, and root, respectively. W is the root zone soil water availability
248 stress factor (Arora & Boer, 2005). The soil water availability is weighted by the existing
249 fraction of roots in each soil layer (Weng & Luo et al., 2008; Arora & Boer, 2005). κ
250 represents the availability of light (Arora & Boer, 2005). Parameters ε_W , ε_L , and ω are
251 calibrated based on the broadleaf evergreen PFT parameters given in Arora and Boer
252 (2005). $L_{in,wood}$ and $L_{in,leaf}$ represent the limitation factor determined by the nutrient
253 status of tissues (Eq. 3-5), designed to capture the reduction of C allocated to leaf and wood
254 as an adaptation to nutrient limitation (Binkley et al., 1995; Yan et al., 2016) and the
255 negative correlation between fine root biomass and soil fertility (Fortier et al., 2019).



256 Canopy phenology is represented by annual variation in LAI. The beginning of a
257 growing season is determined by growing degree days. Leaf senescence results from low
258 air temperature and soil moisture (Arora & Boer, 2005), reducing LAI. The litter
259 production rates of wood and root are prescribed. The phenological parameters are adjusted
260 according to the vegetation characteristics in the studied evergreen forest (Table S1).

261 Carbon transfer between litter pools and soil organic pools through microbial
262 decomposition (Luo & Reynold, 1999; Weng & Luo, 2008). The decomposition of litter
263 and soil organic matter (SOM) is diminished when the amount of available inorganic N
264 and P restricts nutrient immobilization during decomposition:

$$D_{a,j} = D_j * L_{de} , \quad (12)$$

$$D_{a,m} = D_m * L_{de} , \quad (13)$$

265 where j indicates metabolic litter ($j = 5$) or structure litter ($j = 6$), and m indicates fast SOM
266 ($m = 7$), slow SOM ($m = 8$) and passive SOM ($m = 9$). D_a is the nutrient-constrained
267 decomposition rate, and D is the default decomposition rate controlled by the soil
268 temperature and moisture (Weng & Luo, 2008). L_{de} is the limiting factor of
269 decomposition, and the calculation involves dividing the un-limited net mineralization rate
270 by the size of the inorganic nutrient pool, which can be addressed in the following
271 equations:

$$L_{de,N} = \max\left(0, 1 + \frac{F'_{N,net}}{N_{min}}\right) , \quad (14)$$

$$L_{de,P} = \max\left(0, 1 + \frac{F'_{P,net}}{P_{lab}}\right) , \quad (15)$$

$$L_{de} = \min(L_{de,N}, L_{de,P}) , \quad (16)$$

272 where $F'_{N,net}$ and $F'_{P,net}$ represent the net mineralization rate for nitrogen and phosphorus,
273 respectively, assuming no nutrient limitation on mineralization (Wang et al., 2010).



2.2.2 Shared processes in the N and P cycle

The shared processes of N and P cycling include plant uptake, resorption, allocation, transfer from plant to the soil through litterfall, and transfer between organic litter and soil pools via biological mineralization and N, P biological immobilization (Fig. 2). To avoid duplication, these shared processes were described collectively. The organic N (Q_N) and P pools (Q_P) are coupled with C pools through flexible stoichiometry within plant, litter, and soil pools. Inorganic nutrient components consist of one inorganic soil N pool (N_{min}) and four inorganic soil P pools, including labile P, P_{lab} ; sorbed P, P_S ; secondary P, P_{SS} ; and occluded P, P_O . The key variables of N and P cycling are listed in Tables 2 and 3, respectively, and the key parameters are presented in Table 4.

The initial size of the organic nutrient pool is determined by the carbon pool sizes and the carbon to nutrient ratios. The dynamics of organic nitrogen and phosphorus transfer from donor to recipient pools within plants, litter, and soil are coupled with carbon cycling through flexible stoichiometry. The dynamic of plant nutrient pools can be expressed as:

$$\frac{d}{dt}Q_{\chi,i}(t) = F_{new,\chi,i} - Q_{C,i} * \tau_i * R_{\chi,i}^{-1}, \quad (17)$$

$$F_{new,\chi,i} = F_{new,C,i} * R_{\chi,i}^{-1} + (Q_{C,i} * R_{\chi,i,0}^{-1} - Q_{C,i} * R_{\chi,i}^{-1}) \quad (18)$$

where subscript χ = N, P, $F_{new,\chi,i}$ represents the newly input nutrients from non-structural nutrient pool to sustain plant growth (Table 2), $F_{new,C,i}$ is determined by the newly input carbon from NSC pool to plant pool i and stoichiometric ratios (Eq. 25). $R_{\chi,i,0}$ and $R_{\chi,i}$ denote the initial and updated C:N (or C:P) ratios of plant pool i . $Q_{C,i}$ and τ_i represent the carbon pool size and turnover rate of plant pool i . The dynamically constrained nutrient redistribution process in plants (Eq. 18) follows the principles of stoichiometric homeostasis theory (Sterner & Elser, 2002) and helps avoid excessive flexibility in stoichiometry during model simulations (Meyerholt & Zaehle, 2015; Goll et al., 2017).



297 **Table 2** Common variables for N and P cycle modeling.

Variable	Description	Unit
$F_{up,\chi}$	Amount of nutrient uptake by plant roots	$\text{g m}^{-2} \text{h}^{-1}$
$F_{res,\chi}$	Amount of nutrient resorption before tissue litterfall	$\text{g m}^{-2} \text{h}^{-1}$
$F_{dm,\chi}$	Nutrient demand for plant growth	$\text{g m}^{-2} \text{h}^{-1}$
$F_{sp,\chi}$	Soil nutrient supply	$\text{g m}^{-2} \text{h}^{-1}$
$u_{Croot,\chi}$	Root uptake capacity	$\text{g m}^{-2} \text{h}^{-1}$
$F_{new,\chi,i}$	Nutrient input for plant pool i	$\text{g m}^{-2} \text{h}^{-1}$
$F_{\chi,min,x}$	Mineralization fluxes of litter or soil pools, $x = m, j$	$\text{g m}^{-2} \text{h}^{-1}$
$F_{\chi,imm,x}$	Immobilization fluxes of litter or soil pools, $x = m, j$	$\text{g m}^{-2} \text{h}^{-1}$
$F_{\chi,min,total}$	Total mineralization flux	$\text{g m}^{-2} \text{h}^{-1}$
$F_{\chi,imm,total}$	Total immobilization flux	$\text{g m}^{-2} \text{h}^{-1}$
$F_{\chi,net}$	Net mineralization flux	$\text{g m}^{-2} \text{h}^{-1}$
$F_{\chi,in}$	Nutrient input to ecosystem	$\text{g m}^{-2} \text{h}^{-1}$
$F_{\chi,loss}$	Nutrient loss from ecosystem	$\text{g m}^{-2} \text{h}^{-1}$
$F_{\chi,leach}$	Nutrient loss through leaching	$\text{g m}^{-2} \text{h}^{-1}$
$F_{\chi,fert}$	Nutrient fertilization rate	$\text{g m}^{-2} \text{h}^{-1}$
$F_{\chi,dep}$	Nutrient atmospheric deposition rate	$\text{g m}^{-2} \text{h}^{-1}$
$F_{P2L,ij}$	Nutrient flux from plant pool i to litter pool j	
$R_{\chi,i}$	Carbon: nutrient ratio of plant pool i	g gC^{-1}
c_k	Unit conversion factor for root uptake capacity	unitless
V_{runoff}	Volume of drainage water	mm s^{-1}
D_{soil}	Soil depth	cm
T_{soil}	Soil temperature	$^{\circ}\text{C}$
$f_{\chi,leach}$	Scalar for nutrient leaching	unitless
Θ	Volumetric soil water content	$\text{m}^3 \text{m}^{-3}$
$L_{in,i}$	Tissue nutrient concentration stress factor of plant pool i	unitless
L_{sp}	Nutrient uptake stress factor	unitless
L_{de}	Nutrient limitation factor for decomposition	unitless
L_{GP}	Nutrient limitation scalar for plant growth	unitless
$f_{\chi,ratio}$	Nutrient concentration stress scalar affecting nutrient uptake	unitless

298 * χ indicates N or P. Subscripts i, m, j refer to Table 1.

299



300 **Table 3** Specific variables in N and P cycle modeling.

Variables	Description	Unit
N cycling specific		
$F_{N,fix}$	N fixation rate	$gN\ m^{-2}\ h^{-1}$
C_{fix}	Carbon cost for biological N fixation	$gN\ gC\ m^{-2}\ h^{-1}$
$F_{N,gas}$	N loss in gaseous form	$gN\ m^{-2}\ h^{-1}$
P cycling specific		
K	Permeability of the soil to P	$m^2\ h^{-1}$
α_{root}	Represents the fraction of the reduction in P concentration surrounding the roots relative to the initial concentration	unitless
P_{lab}	Soil labile P	$gP\ m^{-2}$
P_{lab}'	Root surface soil labile P	$gP\ m^{-2}$
ΔP_{lab}	P concentrations in the soil solution at the root surface compared to the labile P in the surrounding soil outside the root's diffusive zone	$gP\ m^{-2}$
P_s	Sorbed P	$gP\ m^{-2}$
P_{ss}	Secondary P	$gP\ m^{-2}$
P_o	Occluded P	$gP\ m^{-2}$
FP_{biomin}	P biochemical mineralization rate	$gP\ m^{-2}\ h^{-1}$
FP_{diff}	Diffusion of P from the surroundings to the root surface	$gP\ m^{-2}\ h^{-1}$
F_{wea}	P weathering rate	$gP\ m^{-2}\ h^{-1}$

301

302



303 **Table 4.** Parameters for nitrogen and phosphorus cycling in TECO-CNP.

Short name	Value	Description	Reference
N cycling			
k_{cn}	0.01	Empirical parameter for nitrogen concentration limitation (gN gC^{-1})	Ref 1
α_N	0.20	Fraction of N relocated before littering (Unitless)	Ref 2
$F_{N,dep}$	3.60	N deposition ($\text{gN m}^{-2} \text{yr}^{-1}$)	Ref 4
v_{fix}	1.67×10^{-3}	Maximum N fixation ratio ($\text{gN gC}^{-1} \text{m}^{-2} \text{h}^{-1}$)	Ref 5
$v_{max,N}$	5.40	Maximal root uptake capacity for N ($\mu\text{mol gC}^{-1} \text{h}^{-1}$)	Ref 6
$k_{N,1}$	2.00×10^{-3}	Parameter to match the observed rate of increase in overall N uptake at high mineral N concentration ($\mu\text{mol l}^{-1}$)	Ref 6
$k_{N,2}$	98.00	For Michaelis-Menten constants, mineral N concentration at which uptake equals $v_{max}/2$ ($\mu\text{mol l}^{-1}$)	Ref 6
P cycling			
$v_{max,P}$	1.39	Maximal root uptake capacity for P ($\mu\text{mol gC}^{-1} \text{h}^{-1}$)	Ref 6
$k_{P,1}$	0.01	Parameter to match the observed rate of increase in overall P uptake at high labile P concentration ($\mu\text{mol l}^{-1}$)	Ref 6
$k_{P,2}$	3.00	For Michaelis-Menten constants, labile P concentration at which uptake equals $v_{max}/2$ ($\mu\text{mol l}^{-1}$)	Ref 7
S_{max}	133.00	Maximum amount of sorbed P (gP m^{-2})	Ref 8
K_s	64.00	An empirical parameter for describing the equilibrium between labile P and sorbed P (gP m^{-2})	Ref 8
v_m	2.05×10^{-5}	Rate constant of conversion from sorbed P to secondary P ($\text{gP m}^{-2} \text{h}^{-1}$)	Ref 1
v_{dis}	2.40×10^{-6}	Rate constant of conversion from secondary P to sorbed P ($\text{gP m}^{-2} \text{h}^{-1}$)	Calibrated
λ_{up}	25.00	N cost of plant root P uptake (gN gP^{-1})	Ref 1
λ_{ptase}	15.00	N cost of phosphatase production (gN gP^{-1})	Ref 1
κ_m	150.00	Michaelis-Menten constant for biochemical P mineralization (gN gP^{-1})	Ref 1
v_{max}	0.02	Maximal specific rate of biochemical P mineralization ($\text{gP m}^{-2} \text{h}^{-1}$)	Ref 1
k_{cp}	0.00	Empirical parameter for phosphorus concentration limitation (gN gC^{-1})	Ref 1
α_P	0.40	Fraction of P relocated before littering (Unitless)	Ref 2
F_{wea}	0.05	P weathering rate ($\text{gP m}^{-2} \text{yr}^{-1}$)	Ref 1
$F_{P,dep}$	0.06	Atmospheric P deposition rate ($\text{gP m}^{-2} \text{yr}^{-1}$)	Ref 4
r_d	3.10×10^5	Root specific density (g biomass m^{-3})	Ref 9
r_r	2.90×10^{-4}	Fine root radius (mm)	Ref 6
f_1	1.58	Empirical parameters for calculation of the tortuosity factor (Unitless)	Ref 10
f_2	-0.17	Empirical parameters for calculation of the tortuosity factor (Unitless)	Ref 10
K_0	3.20×10^{-6}	Diffusion coefficient of phosphate in free water at 25 °C ($\text{m}^2 \text{h}^{-1}$)	Ref 11
Θ_1	0.12	relative water content ($\text{m}^3 \text{m}^{-3}$)	Ref 6
α_p	0.40	Fraction of P relocated before littering (Unitless)	Ref 2

304 * For reference codes, see Table S4



305 Nutrients newly acquired from root uptake ($F_{up,\chi}$) and tissue resorption ($F_{res,\chi}$) enter
306 the labile nutrient pool, which buffers the nutrient dynamics and mitigates imbalances
307 between supply and demand (Weng et al., 2017). Thus, the dynamics of plant labile nutrient
308 pools are modeled as:

$$\frac{d}{dt}NS_{\chi}(t) = F_{up,\chi} + F_{res,\chi} - \sum_i F_{new,\chi,i} . \quad (19)$$

309 Since the reproduction pool is designed as a long-term pool supporting a series of
310 reproductive events, from flower bud formation to fruiting, no resorption is prescribed in
311 this pool. The relocation of nutrients from senesced plant tissues ($F_{res,\chi}$) is modeled as:

$$F_{res,\chi} = \sum_i \alpha_{\chi} \times Q_{C,i} * \tau_i * R_{\chi,i}^{-1} \text{ (i } \neq \text{ reproduction) ,} \quad (20)$$

312 where α_{χ} is the resorption rate and the second term represents the loss of carbon from plant
313 pool i (Table 4). We assume that the different plant organs have the same and fixed
314 resorption rate to simplify this process. Additionally, we prescribe a higher resorption rate
315 for P at 0.4 compared to N at 0.2, considering the higher phosphorus use efficiency in the
316 P-limit habitat (Xu et al., 2020).

317 Litter nutrient dynamics is given by:

$$\frac{d}{dt}Q_{\chi,j}(t) = F_{P2L,ij} - Q_{C,j} * \tau_j * R_{\chi,j}^{-1} , \quad (21)$$

318 where $F_{P2L,ij}$ represent the nutrient flux from plant pool i to metabolic litter ($j = 5$) and
319 structure litter ($j = 6$):

$$F_{P2L,ij} = \begin{cases} (1 - \alpha_{\chi})Q_{C,i} * R_{\chi,i}^{-1} * \tau_i * r_{i,j} , i = 1, 2, 3 \\ Q_{C,i} * R_{\chi,i}^{-1} * \tau_i * r_{i,j} , i = 4 \end{cases} , \quad (22)$$

320 where $r_{i,j}$ represents the fraction of plant carbon to different litter pools.

321 The TECO-CNP model exclusively considers the active uptake of inorganic P through
322 specialized transporters on the root surface (Schachtman et al., 1998), as inorganic P is the
323 form most readily absorbed by plants (Bielecki, 1973). Plants possess specific transporters
324 and mechanisms dedicated to transmembrane transport, ensuring they can acquire P even
325 from soil solutions with low P concentrations, where the P concentration can be as low as



one-thousandth of the intracellular concentration (Schachtman et al., 1998). Therefore, we assume that plants absorb only inorganic P from the soil. Similarly, we also only consider the plant uptake of inorganic N. Soil labile nutrients taken up by plants is generally contingent upon both nutrient demand for growth (Wang et al., 2010) and root uptake capacity (Grant et al., 1999, 2001; Goll et al., 2017) that related to root morphology and soil nutrient concentrations. The nutrient demand-supply scheme has been widely employed in most coupled C-nutrient models (Achat et al., 2016). We assume plants will not consume nutrients beyond their luxury consumption demand for assimilating nutrients (Van Wijk et al., 2003; Chapin, 1980). Therefore, the $F_{up,\chi}$ is determined by either the nutrient demand ($F_{dm,\chi}$) or the nutrients supplied by soil ($F_{sp,\chi}$), whichever is lower:

$$F_{up,\chi} = \begin{cases} F_{dm,\chi} & (F_{dm,\chi} < UC_{root,\chi}) \\ F_{sp,\chi} & (F_{dm,\chi} > UC_{root,\chi}) \end{cases} \quad (23)$$

The $F_{dm,\chi}$ is determined by the invested C for newly formatted tissues (NPP_i) and C:nutrient ratios. The actual demand is considered as the difference between the demand for growth and resorption capacity:

$$F_{dm,\chi} = \sum_i \frac{F_{new,C,i}}{R_{\chi,i}} - F_{res,\chi}, \quad (24)$$

$$F_{new,C,i} = NPP_a * b'_{C,i}, \quad (25)$$

where NPP_a represents the net primary productivity derived from actual plant growth (Eq. 1), $b'_{C,i}$ denotes the $b_{C,i}$ (Eq. 9-11) specifically influenced by the leaf phenology (Weng & Luo, 2008).

The nutrients supplied from soil to plants depend not only on the amount of P in the soil but also on soil conditions and the root uptake capacity. We implemented the function of $F_{sp,\chi}$ as described by Goll et al. (2017), and it is calculated by the function of root biomass (BM_{root}), and root uptake capacity ($uc_{root,\chi}$), soil temperature scalar (f_T) and the nutrient balance scalar ($f_{\chi,ratio}$) as follows:

$$F_{sp,\chi} = BM_{root} * uc_{root,\chi} * f_T * f_{\chi,ratio}. \quad (26)$$



347 The linear index scalar $f_{\chi, ratio}$ regulates the balance between C, N, and P by constraining
348 nutrient uptake rates based on prescribed maximum ratios (Eq. 27-28), thereby preventing
349 resource overconsumption (Goll et al., 2017). Experiments have shown that N addition
350 enhances the uptake of both N and P, suggesting a benefit for P uptake when more N is
351 available (Zhu et al., 2021). Thus, we assume the dependence of P uptake on the plant P:N
352 ratio is modeled as a function of the P:N ratio of the plant and leaves. This regulatory
353 mechanism helps prevent excessive P uptake, which would constitute luxury consumption
354 for the plant (Schachtman et al., 1998). Similarly, if nitrogen uptake exceeds the plant's
355 requirements, it also constitutes luxury consumption. Therefore, to avoid luxury absorption
356 and nutrient accumulation, the uptake of N (or P) by roots needs to be regulated based on
357 the N:C (or P:N) ratios within plant tissues (Goll et al., 2017). The maximum uptake occurs
358 when the leaf N:C (or P:N) ratio is equal to the minimum leaf N:C (or P:N) ratio, which is
359 calculated using a minimum function:

$$f_{P, ratio} = \min \left(\max \left(\frac{pn_{plant} - pn_{leaf, max}}{pn_{leaf, min} - pn_{leaf, max}}, 0.0 \right), 1.0 \right), \quad (27)$$

$$f_{N, ratio} = \min \left(\max \left(\frac{nc_{plant} - nc_{leaf, max}}{nc_{leaf, min} - nc_{leaf, max}}, 0.0 \right), 1.0 \right), \quad (28)$$

360 where $pn_{leaf, max}$ and $pn_{leaf, min}$ are prescribed maximum and minimum values of leaf
361 P:N ratios, $nc_{leaf, max}$ and $nc_{leaf, min}$ are prescribed maximum and minimum values of leaf
362 N:C ratios.

363 Root uptake capacity function for nutrients ($uc_{root, \chi}$) incorporates both linear and
364 Michaelis-Menten components to accurately represent the uptake process, considering the
365 low-affinity and high-affinity transporter systems operating in parallel for a given solute
366 concentration (Goll et al., 2017). Notably, the root uptake capacity for soil labile P ($u_{root, P}$)
367 considers the replenishment of P from soil around the roots to root surfaces (Goll et al.,
368 2017) rather than the total labile P in soil volume (Schachtman et al., 1998; Johnson et al.,
369 2003). Hence, the calculation of root uptake capacity for N and P can be expressed as
370 follows:



$$u_{root,P} = v_{max,P} * P'_{lab} \left(\frac{k_{P_{m1}}}{c_k} + \frac{1}{P_{lab} + c_k k_{P_{m2}}} \right), \quad (29)$$

$$u_{root,N} = v_{max,N} * N_{min} \left(\frac{k_{N_{m1}}}{c_k} + \frac{1}{N_{min} + c_k k_{N_{m2}}} \right), \quad (30)$$

371 where $v_{max,\chi}$ is the maximum uptake capacity (Table 4). N_{min} and P_{lab} is the soil mineral
372 N pool and labile P pool. P'_{lab} represents the dissolved labile P concentration at the root
373 surface and depends on the diffusion of soil labile P from the soil surrounding the roots to
374 the root surface (Table 3; Eq. 53). c_k is a unit conversion factor using the soil-type specific
375 parameter for soil moisture content at saturation as an approximation of pore space
376 following Smith et al. (2014). $k_{\chi_{m1}}$ was chosen to match the observed rate of increase in
377 overall P uptake at high dissolved labile P concentration (low-affinity transporter), and
378 $k_{\chi_{m2}}$ is a parameter for Michaelis-Menten constants, dissolved phosphorus concentration
379 at which uptake equals $\frac{v_{max}}{2}$.

380

381 Mineralization and immobilization occur simultaneously. The nutrient mineralization
382 fluxes are estimated based on the litter and soil organic matter decomposition, assuming
383 similar rates for C, N, and P mineralization (Wang et al., 2010; Yang et al., 2014). The
384 mineralization rate is determined by multiplying the litter and soil C pool turnover fluxes
385 with the nutrient-to-carbon ratio. This can be mathematically represented by the following
386 equations:

$$F_{\chi,min,j} = Q_C(t) \tau_j \xi(t) R_{\chi,j}^{-1}, \quad (31)$$

$$F_{\chi,min,m} = Q_C(t) \tau_m \xi(t) R_{\chi,m}^{-1}, \quad (32)$$

387 where $Q_C(t) \tau \xi(t)$ estimates the C decomposition rate under environmental stress for litter
388 or soil pool. The total mineralization ($F_{\chi,min,total}$) is estimated as the sum of mineralization
389 rate for each pool, which can be expressed as follows:

$$F_{\chi,min,total} = \sum_j F_{\chi,min,j} + \sum_m F_{\chi,min,m}. \quad (33)$$



390 Nutrients are immobilized during the decomposition process of litter and SOM,
391 ultimately entering the SOM pools. Consequently, only three SOM pools can be the
392 receiving pools. The dependency of immobilization rates on the ratios of the receiving
393 pools, under the assumption of approximately constant stoichiometry ratios of SOM pools
394 (Tian et al., 2010; McGroddy et al., 2004), is described as:

$$F_{\chi,imm,m} = \sum_{jm} f_{L2S,jm} \xi(t) \tau_j X_j(t) R_{\chi,m}^{-1} + \sum_{mm} f_{S2S,mm} \xi(t) \tau_m X_m(t) R_{\chi,m}^{-1}, \quad (34)$$

395 where $R_{\chi,m}^{-1}$ represent the N:C ratio ($\chi = N$) or the P:C ratio ($\chi = P$) of the existing SOM.

396 The total amount of immobilization is then calculated as follows:

$$F_{\chi,imm,total} = \sum_m F_{\chi,imm,m}. \quad (35)$$

397 Therefore, the net nutrient mineralization is calculated by the difference of total
398 mineralization and total immobilization:

$$F_{\chi,net} = F_{\chi,min,total} - F_{\chi,imm,total}. \quad (36)$$

399 When net mineralization is negative, the decomposition rate is limited by nutrient
400 availability, L_{NP} . Since the N:C ratio of the soil pool is higher than that of the litter pool,
401 microbes extract inorganic nitrogen from the soil mineral N pool, leading to negative net
402 mineralization and a L_{NP} value less than one. A similar approach has been applied in the
403 CASA-CNP model (Wang et al., 2007).

404 Plants and microorganisms utilize dissolved inorganic N and P from soil to fulfill their
405 growth requirements (Vitousek et al., 2010). We assume microbial processes modulate
406 nutrient availability for plants (Jiang et al., 2024b; Pellitier et al., 2023; Jonasson et al.,
407 1999), i.e., the nutrient limitation on plant growth will be alleviated if the net mineralization
408 is positive. Furthermore, the competition between plants and microorganisms for nutrients
409 can be simplified by emphasizing the sequence of immobilization and plant uptake (Achat
410 et al., 2016). In the TECO-CNP model, immobilization takes precedence in nutrient access
411 through decomposing litter and soil organic matter. A similar method was used in many
412 models, e.g., models of the CENTURY family (e.g., Parton et al., 1988); O-CN (Zaehle
413 and Friend 2010); ORCHIDEE (revision 4520; Goll et al., 2017). This also aligns with
414 recent findings regarding the competition between plants and microbes under elevated



415 CO₂. (Keane et al., 2023). Specifically, in the acidic grassland, aboveground productivity
416 and P uptake declined by 11% and 20%, respectively, while P immobilization into
417 microbial biomass increased by 36%.

418 2.2.3 Distinct processes in N and P cycle

419 The dynamic of soil inorganic N (N_{min}) is described as:

$$\frac{dt}{d} N_{min} = F_{fix} + F_{N,fert} + F_{N,dep} - F_{N,leach} - F_{N,gas}, \quad (37)$$

420 where F_{fix} , $F_{N,fert}$ and $F_{N,dep}$ represent the biological N₂-fixation, atmospheric N
421 deposition, and biological N fixation (Tables 2, 3). $F_{N,leach}$ and $F_{N,gas}$ represent the N
422 leaching and gaseous N loss.

423 Biological nitrogen fixation, a dominant source of new nitrogen in terrestrial
424 ecosystems (Chapin et al., 2011; Vitousek et al., 2013), is performed by N₂-fixing
425 symbionts in plant roots (i.e., symbiotic N₂-fixation; Vitousek et al., 2002; Augusto et al.,
426 2013). This process enhances nitrogen availability when carbon is sufficient for additional
427 nutrient acquisition (Fisher et al., 2010), which is given by:

$$F_{fix} = v_{fix} * f_{nsc} * NSC * f_N, \quad (38)$$

428 where $v_{fix} = 0.00167$ (gN gC⁻¹ m⁻² h⁻¹) is the maximum N fixation rate. v_{fix} is chosen
429 based on estimates ranging from 58 Tg N yr⁻¹ (Vitousek et al., 2013) to 100 Tg N yr⁻¹
430 (Wiltshire et al., 2021) for a global NPP of 60 Pg C yr⁻¹. The term $f_{nsc} * NSC$ represents
431 the limitation of NSC on nitrogen fixation, implicitly capturing the carbon constraint on
432 this process (Chou et al., 2018; Taylor et al., 2021). To prevent unrealistic nitrogen fixation,
433 a scaling function (f_N) is applied, as nitrogen fixation is an energy-intensive process
434 (Gutschick, 1981; Goll et al., 2017). The f_N is calculated as:

$$f_N = \begin{cases} \frac{N_{max} - N_{min}}{N_{max}} & N_{max} < N_{min} \\ 0 & otherwise \end{cases}. \quad (39)$$

435 The carbon cost for biological N fixation is calculated by a function of soil temperature
436 (T_{soil}) with the observed C cost range (Fisher et al., 2010):



$$C_{fix} = -6.25 * \left(\exp \left(-3.62 + 0.27 * T_{soil} * \left(1 - 0.5 \left(\frac{T_{soil}}{25.15} \right) \right) \right) - 2 \right). \quad (40)$$

437 Nitrogen loss occurs in two pathways: gaseous loss (FN_{gas}), and leaching ($F_{N,leach}$).
438 Losses from denitrification and volatilization are not distinguished separately. Both are
439 proportional to the availability of soil mineral N (N_{min}). The expression of N leaching is:

$$F_{N,leach} = f_{N,leach} \frac{V_{runoff}}{D_{soil}} N_{min}, \quad (41)$$

440 where $f_{N,loss} = 0.001$ and $f_{N,leach} = 0.5$, V_{runoff} is the soil surface runoff and D_{soil} is the
441 soil depth. Moreover, the gaseous loss is dependent on the soil temperature and soil mineral
442 N. The equation is:

$$F_{gas} = f_{N,loss} e^{\frac{(T_{soil}-25)}{10}} N_{min}. \quad (42)$$

443 The specific processes of the P cycle include biochemical mineralization, weathering,
444 the dynamics of different inorganic soil P components, and the diffusion pathways of soil
445 labile P. In addition to biological mineralization, organic P can be mineralized through
446 direct cleavage by extracellular enzymes produced by plant roots and other organisms
447 (McGill and Cole, 1981). This process decouples the P cycle from the C and N cycles,
448 serving as an adaptive mechanism that can be enhanced under P-limited conditions
449 (Lambers et al., 2006). This decoupling allows for phosphorus acquisition from organic
450 matter without releasing carbon dioxide. We consider this process an N-consuming one,
451 aiming to represent the chemical characteristic that phosphatases are N-rich enzymes and
452 their production in plants can be N-limited (Treseder and Vitousek, 2001; Wassen et al.,
453 2013). The biochemical mineralization of P can be expressed by:

$$FP_{biomin} = \frac{v_{max}(\lambda_{up} - \lambda_{ptase})}{\lambda_{up} - \lambda_{ptase} + \kappa_m} \sum_m K_m Q_{P,m}, \quad (43)$$

454 where v_{max} is maximal specific rate of biochemical P mineralization. λ_{up} is N cost of plant
455 root P uptake. λ_{ptase} is N cost of phosphatase production, κ_m is Michaelis-Menten
456 constant for biochemical P mineralization. K_m and $Q_{P,m}$ represent turnover rate and
457 phosphorus pool size of slow ($m = 8$) and passive pools ($m = 9$).



458 The external phosphorus input ($F_{P,in}$) is modeled as:

$$F_{P,in} = F_{wea} + F_{P,fert} + F_{P,dep} , \quad (44)$$

459 where F_{wea} , $F_{P,fert}$, and $F_{P,dep}$ represent phosphorus input rates from weathering,
460 fertilization, and deposition. Based on the soil texture at the Tiantong site (Song & Wang,
461 1995), the weathering rate is set to $0.005 \text{ (gP m}^{-2} \text{ year}^{-1})$ (Wang et al., 2010). The deposition
462 rate of phosphorus has been set to $0.06 \text{ (gP m}^{-2} \text{ year}^{-1})$ (Zhu et al., 2016).

463 Labile phosphorus (P_{lab}) can be directly utilized by plants or microorganisms and
464 adsorbed onto soil particles, organic matter, and other minerals as adsorbed phosphorus
465 (P_S) (Vitousek et al., 2010). The assumption is made that the rapid equilibration of P_{lab}
466 with P_S occurs within a timestep of less than one hour (Olander and Vitousek, 2005). For
467 the 1-hour time step used in our study, we therefore assume that P_{lab} and P_S are in a state
468 of equilibrium. The equilibrium assumption is applied extensively (e.g., Wang et al., 2007,
469 Yang et al., 2014). The relationship between them is described by a Langmuir isotherm
470 (Barrow, 2008):

$$P_S = \frac{S_{max} P_{lab}}{K_S + P_{lab}} , \quad (45)$$

471 where S_{max} is the maximum amount of sorbed P in the soil, and K_S is the empirical
472 constant representing the tendency of soil labile P to be sorbed. S_{max} and K_S is set as 133
473 and 64 (Wang et al., 2010), respectively, according to the soil sorption capacity and
474 substrate age (Olander and Vitousek, 2005) at Tiantong site. The differential form of Eq.
475 45 is:

$$\frac{dP_S}{dt} = \frac{S_{max} P_{lab}}{(K_S + P_{lab})^2} \frac{dP_{lab}}{dt} . \quad (46)$$

476 Assuming equilibrium between P_{lab} and P_S , we can model the simultaneous changes in
477 P_{lab} and P_S as follows:

$$\frac{d(P_S + P_{lab})}{dt} = F_{P,net} + F_{P,in} + F_{P,biomin} - F_{up,P} - F_{P,leach} - v_m P_S , \quad (47)$$

$$F_{P,net} = F_{P,min,total} - F_{P,imm,total} , \quad (48)$$



where $F_{P,net}$ is the net mineralization of litter and soil phosphorus pool, $F_{P,biomin}$ is the P flux from biochemical mineralization, U_P represents the plant uptake of P, $F_{P,leach}$ represents the loss of labile P from leaching (Eq. 52), and v_m is the rate constant for the transformation of sorbed P to secondary P. Based on Eq. 47 and Eq. 48, the dynamics of labile phosphorus can be expressed as follows:

$$\frac{dP_{lab}}{dt} = (F_{P,net} + F_{P,in} + F_{P,biomin} - F_{up,P} - F_{P,loss} - v_m P_S) \frac{1}{1 + \frac{S_{max} P_{lab}}{(K_S + P_{lab})^2}}, \quad (49)$$

Secondary mineral phosphorus (P_{SS}) can be dissolved and enter the labile P pool or encapsulated by iron oxides to form closed-P (P_o ; Walker & Syers, 1976; Vitousek et al., 2010). The dynamics of P_{SS} and P_o can be modeled as:

$$\frac{dP_{SS}}{dt} = v_m P_S - v_{dis} P_{SS} - v_o P_{SS}, \quad (50)$$

$$\frac{dP_o}{dt} = v_o P_{SS} - v_{re} P_o, \quad (51)$$

where v_{dis} and v_o is the rate constant for the conversion of secondary P to labile and sorbed P, and occluded P, respectively. v_{re} is the rate constant for occluded P re-entering the cycle as bioavailable phosphorus, indicating that occluded phosphorus can transition back into available forms (Huang et al., 2014; Schubert et al., 2020). In this study, we assume that the formation of occluded P pool and loss of occluded P can be considered negligible within the short timescale of simulations (Weihrauch & Opp, 2018). The P losses from organic matter only occur in two SOM pools with a slow turnover rate: slow and passive SOM pools (Wang et al. 2010). P leaching from soil inorganic labile pool and is proportional to the availability of soil labile P. Description of P leaching below:

$$F_{P,leach} = f_{p,leach} \frac{V_{runoff}}{D_{soil}} P_{lab}, \quad (52)$$

where V_{runoff} is the value of runoff, D_{soil} is the soil depth. $f_{p,leach}$ is an empirical parameter for P leaching, representing the fraction of soil mineral P for leaching.

Notably, due to the low mobility of phosphorus in the soil (Vitousek et al., 2010), the actual P concentration that roots can absorb depends on the diffusion of P from the surrounding soil to the root surface (P'_{lab}). This is consistent with the experimental finding



500 that roots acquire most inorganic phosphorus primarily through diffusion along
501 concentration gradients (Laliberté et al., 2015). Thus, the root uptake capacity for soil labile
502 P ($u_{root,P}$) considers the replenishment of P from soil around the roots to root surfaces
503 (Schachtman et al., 1998) rather than the total labile P in soil volume (Johnson et al., 2003).
504 Thus, the root surface P concentration is calculated by the following equation:

$$P'_{lab} = a_{root} * \frac{P_{lab}}{\theta}, \quad (53)$$

505 where θ is the volumetric soil water content and a_{root} representing the fraction of the
506 reduction in P concentration surrounding the roots relative to the initial concentration.
507 a_{root} is updated after plant uptake as:

$$\frac{da_{root}}{dt} = \frac{FP_{diff} - F_{up,P}}{P_l}, \quad (54)$$

508 where FP_{diff} is the diffusion of P from the surroundings to the root surface, which is the
509 function of the permeability of the soil to P (K) and the difference in the P concentrations
510 between the soil solution at the root surface and the labile P in the surrounding soil volume
511 outside the diffusive zone around the root (ΔP_{lab})

$$FP_{diff} = -K * \Delta P_{lab}. \quad (55)$$

512 ΔP_{lab} can be described as:

$$\Delta P_{lab} = (a_{root} - 1) \frac{P_{lab}}{\theta}. \quad (56)$$

513 The K has been calculated analogously to the diffusion coefficient of phosphorus in soils
514 following Barraclough and Tinker (1981), which accounts for the increased path length in
515 soil using a tortuosity factor (f_t), and it is a broken-line function of the volumetric soil
516 water content (θ). The K and f_t can be calculated based on the following equations:

$$K = K_0 c_\theta \theta t f \frac{1}{r_{diff}}, \quad (57)$$

$$f_t = \begin{cases} f_1 \theta + f_2 & \text{for } \theta \geq \theta_1 \\ \frac{\theta(f_1 \theta + f_2)}{\theta_1} & \text{otherwise} \end{cases}, \quad (58)$$



517 where θ_1 is soil water content at which the two functions intersect according to Barraclough
518 and Tinker (1981), f_1 and f_2 are empirical parameters (Barraclough and Tinker, 1981), D_0
519 is diffusion coefficient in free water, c_θ is a unit conversion factor, r_{diff} is diffusion path,
520 which can be calculated from the function of root length density (RLD , Bonan et al., 2014):

$$r_{diff} = \min(0.1, (\pi RLD)^{0.5}) . \quad (59)$$

521 We assume that the diffusion path can be approximated as half the average distance
522 between roots. We limit the diffusion path length to 0.1 m because the influence of active
523 P uptake by roots on soil P concentrations is negligible beyond a distance of 10 cm (Li et
524 al., 1991). RLD is given by:

$$RLD = \frac{B_{root}^*}{r_d \pi r_r^2} , \quad (60)$$

525 where r_d is the root-specific density and πr_r^2 is the cross-sectional area calculated from the
526 fine root radius, r_r , and B_{root}^* is the root biomass density per unit soil volume.

527 **2.3 Model validation**

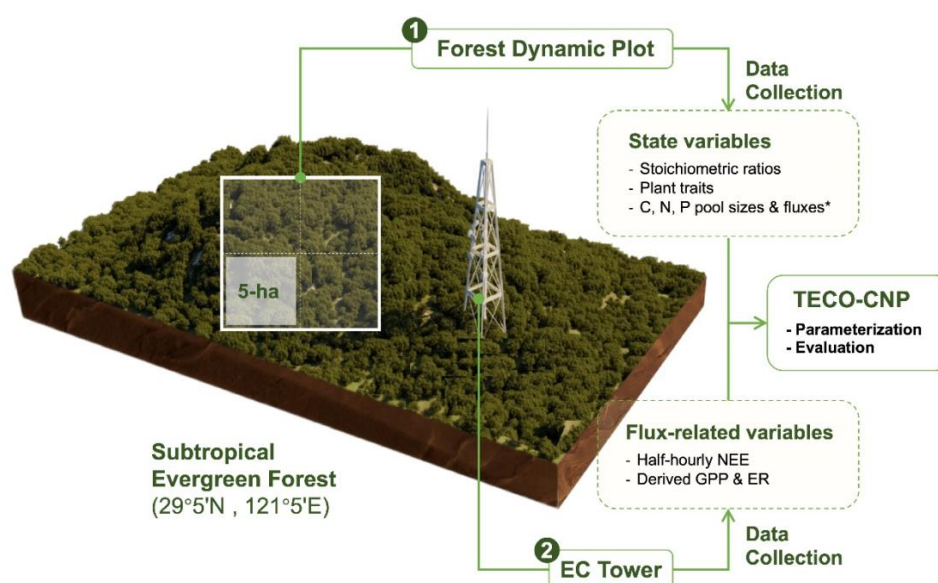
528 **2.3.1 Study site**

529 The tension between high carbon sink capacity and nutrient limitations in subtropical
530 forests warrants detailed investigation to understand the role of nutrients in carbon cycling
531 processes in these regions. To this end, we selected a mature subtropical evergreen
532 broadleaf forest in eastern China, located at the Zhejiang Tiantong Forest Ecosystem
533 National Observation and Research Station (Tiantong, 29°48' N, 121°47' E, Fig. 3) for the
534 newly model development. The Tiantong forest has been preserved free from human
535 disturbance since the mid-twentieth century. The average reported annual temperature of
536 Tiantong is 17°C, and annual precipitation is 1600 mm (Cui et al., 2022). The soil type is
537 mainly mountainous yellow-red soil, with the parent material primarily composed of
538 Mesozoic sedimentary rocks, acidic igneous rocks, and residual weathering products of
539 granite (Song & Wang, 1995).

540 Research at this site identified the dominant role of soil phosphorus in driving
541 variations in plant functional traits (Cui et al., 2022), suggesting phosphorus deficiency in
542 this mature forest. Consequently, this phosphorus-limited mature subtropical forest with



543 abundant field observations can contribute to the development of carbon-nutrient coupling
544 models and further explore phosphorus-limited carbon cycling processes within the
545 ecosystem through the integration of modeling and experiments.



546 **Figure 3. Schematic diagram of the observation system at Tiantong subtropical**
547 **evergreen forest (29°5' N, 121°5' E).** The system comprises: (1) a forest dynamic plot for
548 monitoring ecosystem state variables, including stoichiometric ratios, plant traits, and C,
549 N, P pools and fluxes. These measurements were conducted in a 5-ha subplot of the whole
550 plot. The asterisk (*) indicates manual periodic measured fluxes. And (2) an eddy
551 covariance (EC) flux tower providing half-hourly NEE measurements, from which GPP
552 and ER were derived. These observations were used for TECO-CNP model
553 parameterization and evaluation. Detailed measurement protocols are described in
554 Methods, and specific variable applications are listed in Tables S1-S3. The site topography
555 and elevation data were obtained from © Google Maps and rendered using Blender.

557

558 2.3.2 Data for model evaluation

559 The data used for model calibration and validation were primarily derived from our field
560 measurements and literature focusing on the same site (Fig. 3, Tables S1-S3). Forcing data,



561 collected at 1-hour intervals from site-level meteorological observations, include
562 precipitation (mm), relative humidity (%), air and soil temperatures ($^{\circ}\text{C}$), vapor pressure
563 deficit (Pa), wind speed (m s^{-1}), and photosynthetically active radiation ($\mu\text{mol m}^{-2} \text{s}^{-1}$).
564 Forcing data from 2001 were used for model spin-up.

565 Model parameters were primarily derived from site observations, supplemented with
566 literature values when site-specific data were unavailable (Tables 4, S1-S3). Plant traits,
567 including specific leaf area (SLA, $\text{cm}^2 \text{g}^{-1}$), leaf area index (LAI, $\text{m}^2 \text{m}^{-2}$), plant height (H,
568 m), maximum rate of carboxylation (V_{cmax} , $\mu\text{mol m}^{-2} \text{s}^{-1}$), and maximum rate of electron
569 transport (J_{max} , $\mu\text{mol m}^{-2} \text{s}^{-1}$), were measured at the species level and scale up to
570 community-level traits using the community-weight mean method. N and P resorption
571 efficiencies were determined for dominant species (i.e., *Schima superba*, *Lithocarpus*
572 *glaber*) at the Tiantong site. External inputs of N and P, including deposition and
573 weathering, were assumed to occur at constant rates. Deposition rates for N and P were
574 prescribed based on the observed range (Zhu et al., 2016), while the P weathering rate
575 followed the specific weathering rate for *Ustisol* soils (Wang et al., 2010).

576 Second, for model validation, we primarily used measured values of plant and soil C:
577 N: P pools, along with carbon flux data from the site's eddy covariance tower (Fig. 3).
578 Organic plant and soil pool (kg m^{-2}) measured at the site encompass C, N and P content
579 across leaf, wood, root, reproductive organs (fruit and flower), and soil. Soil C, N, and P
580 pools were measured to a depth of 60 cm, which aligned with the soil profile depth
581 specified in the model configuration. Soil inorganic pool (g m^{-2}) includes measurements
582 of soil mineral N and labile P. Litterfall rates ($\text{kg m}^{-2} \text{yr}^{-1}$) for C, N, and P from leaf, wood,
583 and fruit and flower pools are also available. Soil respiration ($\text{kg m}^{-2} \text{yr}^{-1}$) and
584 mineralization rates for N and P ($\text{g m}^{-2} \text{d}^{-1}$), secondary P (g m^{-2}), and occluded P (g m^{-2})
585 sourced from the literature. We obtained quality-controlled hourly eddy covariance
586 measurements of gross primary productivity (GPP, $\text{g C m}^{-2} \text{h}^{-1}$), ecosystem respiration (ER,
587 $\text{g C m}^{-2} \text{h}^{-1}$), and net ecosystem exchange (NEE, $\text{g C m}^{-2} \text{h}^{-1}$) for 2021.

588 2.3.3 Data assimilation

589 We optimized the carbon-related parameters for CNP configurations by utilizing GPP, ER,
590 and NEE data in 2021 at the study site. Based on the initial carbon pool sizes from the spin-



up process, we focus on the parameters that determine the carbon input and retention (Table 6), including SLA, $V_{\max}$, temperature sensitivity (Q_{10}), and turnover rate (T_1 - T_9). The prior range of parameters was prescribed according to the situ measurement or assumed as the range of the distribution to be $[\theta_0/3, 3\theta_0]$, where θ_0 is the default value. Using the Bayesian probabilistic inversion approach, we estimated the posterior distribution of model parameters based on prior knowledge of parameters.

Bayesian probabilistic inversion approach is based on Bayes' theorem:

$$p(\theta|Z) \propto \frac{p(Z|\theta) \times p(\theta)}{p(Z)}, \quad (61)$$

where $p(\theta|Z)$ is the posterior distribution of the parameters θ given the observations Z . Here, we assume that the prior knowledge of parameter distribution $p(\theta)$ is uniformly distributed. $p(Z|\theta)$ is the likelihood function for a parameter set calculated with the assumption that each parameter is independent from all other parameters and has a normal distribution with a zero mean:

$$p(Z|\theta) \propto \exp \left\{ - \sum_{t \in Z_i} \frac{[Z_i(t) - X(t)]^2}{2\sigma^2(t)} \right\}, \quad (62)$$

where $Z_i(t)$ is the observations of carbon fluxes at time t , $X(t)$ is the simulated corresponding variable, and $\sigma(t)$ is the standard deviation of the observation set.

Posterior probability distributions of parameters were obtained using a Metropolis-Hastings (M-H) algorithm (MCMC). The detailed description of M-H algorithm can be found in Xu et al. In brief, the M-H algorithm consists of iterations of a proposing step and a moving step. In the proposing step, a new parameter set θ^{new} is proposed based on the previously accepted parameter set θ^{old} and a proposal distribution ($r \times (\theta_{\max} - \theta_{\min})/D$):

$$\theta^{new} = \theta^{old} + r \times (\theta_{\max} - \theta_{\min})/D, \quad (63)$$

where $\theta_{\max}$ and $\theta_{\min}$ corresponding to the upon and low values of prescribed ranges, r is a random variable between -0.5 and 0.5, and D is used to control the proposed step size and was set to 5 (Xu et al., 2006). The new set of parameter values would be accepted when $\frac{p(\theta^{new}|Z)}{p(\theta^{old}|Z)}$ is equal or greater than a uniform random number from 0 to 1 (Xu et al., 2006).



615 We get 10,000 accepted samples from the MCMC chain. The first 5000 accepted
616 samples were discarded considering the burn-in period. We randomly selected 1,000
617 parameter sets from the accepted space to run the simulations in 2021. The mean and
618 maximum likelihood estimations are calculated to compare the parameters.

619 **2.3.4 Model performance evaluation**

620 The state variables estimations from three nutrient coupling configurations of TECO-CNP:
621 (1) carbon-only (C-only), (2) carbon-nitrogen coupled (CN), and (3) carbon-nitrogen-
622 phosphorus coupled (CNP) are evaluated against observations. Model initialization
623 involved a spin-up process using 2001 meteorological forcing data until reaching a quasi-
624 equilibrium state, which is defined as inter-annual variations less than $0.05 \text{ gC m}^{-2} \text{ yr}^{-1}$ in
625 the slowest pools. Following initialization, we conducted transient simulations from 2002
626 to 2021 using the tuned parameter set. To evaluate model performance, we compared pool
627 sizes from different nutrient coupling configurations (C, CN, and CNP) in 2021 with
628 observed data (Tables S1-S3), assuming our mature forest study site was at a quasi-steady
629 state where inter-annual changes in major pool sizes were negligible. The configuration
630 that produced pool sizes closest to observations was selected to determine the initial state
631 for subsequent simulations. Model performance was further evaluated by comparing
632 simulated carbon fluxes in 2021 against observational data using both manually tuned and
633 optimized parameters. The model evaluation metrics for carbon fluxes included the Root
634 Mean Square Error (RMSE) and concordance correlation coefficient (CC), which quantify
635 the absolute errors and the agreement between simulated and observed values. All
636 statistical analyses and data visualizations were implemented in R (version 4.3.1).

637 **3 Results & Discussion**

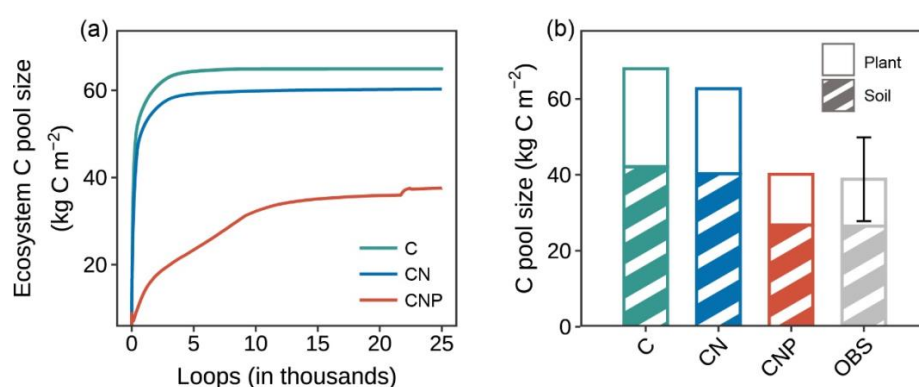
638 **3.1 Evaluate the carbon-nutrient configurations**

639 **3.1.1 Carbon cycle**

640 The CNP configuration accurately reproduced carbon pool sizes across ecosystem
641 components, while the C and CN configurations tended to overestimate these pools (Fig.
642 4, Fig. 5a). In this P-limited site, the introduction of phosphorus limitations in CNP



643 configurations progressively reduced carbon pool sizes compared to the C-only and CN
644 configuration (Fig. 4a). This reduction reflects a fundamental assumption in carbon-
645 nutrient coupled models that nutrient availability constrains carbon sequestration (Wieder
646 et al., 2015; Sun et al., 2017) through various physiological processes (Jiang et al., 2019).
647 At the ecosystem level (Fig. 4b), the C-only and CN configurations substantially
648 overestimated total carbon stocks by 73.7% and 57.5%, respectively, while the CNP
649 configuration produced estimates much closer to observed values with only a slight
650 overestimate of 1.9%. The partitioning between plant and soil pools (Fig. 4b) showed that
651 this overestimation occurred in both compartments, with the CNP configuration providing
652 the closest match to observations.



653
654 **Figure 4. Comparison of carbon pools among different nutrient coupling**
655 **configurations.** (a) Trajectories of ecosystem carbon pools during model spin-up for
656 carbon-only (C), coupled carbon-nitrogen (CN), and coupled carbon-nitrogen-phosphorus
657 (CNP) simulations. The ecosystem carbon pool consists of nine pools within plant, litter,
658 and soil organic matter components. (b) Comparison of simulated and observed (OBS)
659 carbon pools in plant biomass and soil organic matter. Plant carbon pools comprise leaf,
660 wood, and root carbon (excluding reproductive organs due to data unavailability), and soil
661 carbon pools include fast, slow, and passive soil organic carbon components. Error bar for
662 observation represent standard deviation of the sum of plant and soil pools.
663



664 A more detailed examination of individual carbon pools (Fig. 5a) revealed that the
665 overestimation was mainly contributed by wood and soil pools for C and CN configurations,
666 which represent the major carbon stocks in the ecosystem. For plant components, wood
667 carbon stocks were substantially overestimated by approximately 122.2% and 89.6% in C-
668 only and CN configurations, while the CNP configuration showed remarkable agreement
669 with observations with only a 5% deviation. Leaf carbon pools showed similar patterns of
670 overestimation (C: 82.7%, CN: 59.1%, CNP: 3.6%). This improvement in leaf carbon
671 estimation by CNP was further confirmed by its closer mean LAI prediction and leaf
672 litterfall rate with observations compared to C and CN configurations (Table 5). Similarly,
673 the superior performance of CNP in simulating the aboveground carbon pool was also
674 reflected in the total plant C litterfall rate (Table 5), although a moderate overestimation
675 (22.7%) was observed, which could be improved by incorporating reproductive pool
676 measurements in future studies.

677 In contrast, root carbon pools showed overestimation across all configurations, with
678 CNP showing the lowest bias (34.2%) and falling within one standard deviation of
679 observed values (Table S1), while C and CN configurations showed larger deviations (68.8%
680 and 65.1%, respectively). The relatively higher root carbon estimation in CNP may be
681 attributed to its dynamic allocation strategy, which preferentially allocates carbon to roots
682 under nutrient-limited conditions. While our model successfully reproduced the enhanced
683 belowground carbon allocation under nutrient limitation, consistent with experimental
684 evidence (Wu et al., 2025; Gill et al., 2016), the overestimated root carbon suggests
685 additional constraints are needed. Indeed, the nutrient-dependent allocation scheme
686 remains a major source of uncertainty in terrestrial biosphere models (Zaehle et al., 2014;
687 Jiang et al., 2024), highlighting the necessity of improved observational constraints on root
688 turnover and carbon allocation patterns for more accurate process-based simulations.

689

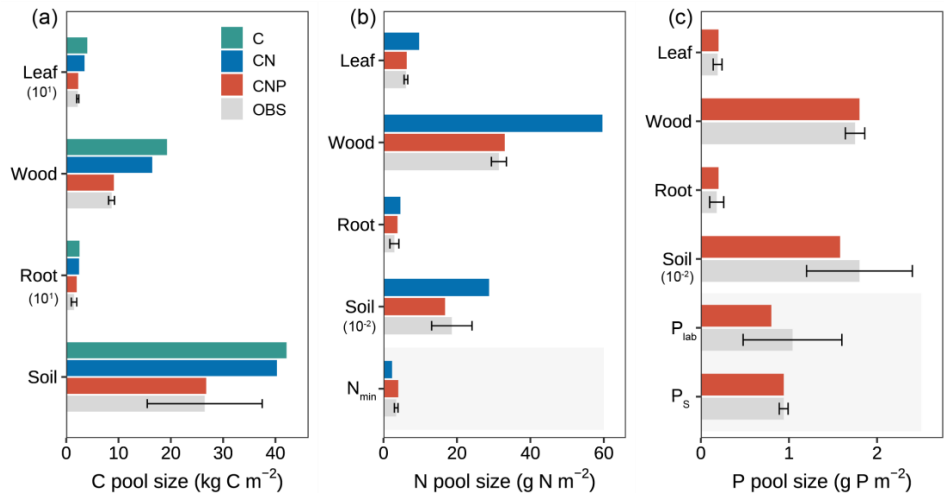


Figure 5. Comparison of simulated and observed ecosystem pools across different nutrient coupling configurations (C-only, CN, and CNP). (a) Carbon pools in vegetation components (leaf, wood, root) and soil, with values for leaf and root scaled by 10¹. (b) Nitrogen pools in vegetation components, soil (scaled by 10⁻²), and mineral nitrogen (N_{min}). (c) Phosphorus pools in vegetation components, soil organic P (scaled by 10⁻²), labile P (P_{lab}), and sorbed P (P_s). Error bars on observed data (OBS) indicate standard deviations. Numbers in parentheses indicate scaling factors applied to improve visualization. Shaded areas indicate inorganic nutrient pools.

Table 5. Observed and simulated carbon, nitrogen and phosphorus fluxes with C, CN and CNP configurations. The plant litterfall rate is the sum of litterfall of leaf, wood and reproductive pool, and the N and P litterfall rate exclude the resorption part.

	C, N and P fluxes				Unit
	C	CN	CNP	OBS	
Leaf C litterfall rate	0.43	0.38	0.25	0.26±0.06	kg C m ⁻² yr ⁻¹
Plant C litterfall rate	0.98	0.86	0.54	0.44±0.04	kg C m ⁻² yr ⁻¹
Plant N litterfall rate	-	11.36	7.44	6.74±0.68	g N m ⁻² yr ⁻¹
Plant P Litterfall rate	-	-	0.24	0.79±0.24	g P m ⁻² yr ⁻¹
Soil respiration	1.72	1.59	1.13	0.99±0.07	kg C m ⁻² yr ⁻¹
N net mineralization	-	18	12.3	13.14±0.73	g N m ⁻² yr ⁻¹



704 For soil carbon pools, while C and CN configurations showed significant
705 overestimations of 59.1% and 52.1%, respectively, the CNP configuration demonstrated
706 the closest agreement with observations with a slight overestimation of 1.06%. Despite the
707 large observational uncertainty in soil carbon stocks (Table S1), the substantial
708 overestimation by C-only and CN configurations was clearly beyond the reasonable range.
709 This distinct improvement in soil carbon estimation by CNP configuration suggests that
710 proper representation of nutrient limitations is crucial for realistic soil carbon predictions
711 (Cui et al., 2024; Wei et al., 2022; Achat et al., 2016). In conclusion, the CNP model
712 consistently shows better alignment with observed carbon pools, particularly in reducing
713 the systematic overestimation seen in the C and CN models.

714 3.1.2 N cycle

715 For nitrogen cycling properties, the CNP configuration exhibited superior performance in
716 simulating nutrient pools compared to CN configurations (Fig. 5b). Regarding plant
717 nitrogen pools, the CN configuration demonstrated substantial overestimations for leaf
718 (59.2%), woody tissue (89.9%), and root N (55.9%). In contrast, the CNP configuration
719 showed markedly improved accuracy, with only slight overestimations of 3.3%, 5.0% for
720 leaf and wood N, and 28.8% for root N. The patterns of plant organic N across model
721 configuration simulations were consistent with the carbon simulation results in both CN
722 and CNP configurations, reflecting the constraints of plant tissue stoichiometry on coupled
723 C-nutrient dynamics (Knox et al., 2024; Wang et al., 2010). For soil N pools, the CNP
724 simulation (16.74 g N m^{-2}) fell within the range of observed values ($18.6 \pm 5.5 \text{ g N m}^{-2}$),
725 whereas the CN configuration substantially overestimated soil N (28.75 g N m^{-2}). The
726 slight underestimation of soil N in CNP relative to observations may be attributed to the
727 flexible soil C:N ratios, as these ratios can vary within certain ranges due to complex
728 microbial processes and organic matter decomposition dynamics (Tian et al., 2010, 2021).
729 The introduction of P cycling into the model resulted in reduced carbon allocation to both
730 plant and soil pools, which consequently led to proportional reductions in organic N pools
731 compared to the CN configuration, ultimately better capturing the observed N pools.

732 For soil mineral N content, the CN configuration underestimated soil mineral N
733 content by 33.3% despite simulating higher net N mineralization rates (Table 5). This



depletion of soil mineral N pool likely resulted from excessive plant N uptake, which was consistent with the substantial overestimation of plant carbon pools in CN configuration (Fig. 5a). In contrast, the CNP configuration showed a moderate overestimation (15.9%) of soil mineral N content, demonstrating better agreement with observations compared to CN. The elevated soil mineral N levels in CNP could be attributed to the higher plant N litterfall rates (10.4% above observations, Table 5), even excluding relocated N fluxes, which compensated for its underestimated net N mineralization rates.

The incorporation of P cycling constraints in the CNP configuration substantially improved the simulation of N pools and fluxes compared to the CN configuration, demonstrating the importance of considering P-N interactions in ecosystem modeling. Notably, some discrepancies in N transformation processes, particularly in soil mineral N dynamics and plant nutrient uptake mechanism, suggest areas for future model refinement.

3.1.3 P cycle

The CNP model showed good overall performance in simulating phosphorus pools across ecosystem compartments (Fig. 5c). For plant components, the model accurately reproduced organic P pools, with slight overestimations of 5.0%, 2.8%, and 10.0% for leaf, wood, and root compartments, respectively. For the soil P, the CNP simulated a lower value (1.58 g P m^{-2}) than observed but within its range (1.8 ± 0.6). Those organic P pools have the same pattern as organic N pools for CNP simulations, as C-N-P is coupled through stoichiometry.

The simulated inorganic P content (0.8 g P m^{-2}) fell within the observed range ($0.48\text{--}1.6 \text{ g P m}^{-2}$). The model successfully reproduced the observed levels of various P pools overall; however, it significantly underestimated plant P litterfall rates by 69% after accounting for resorption (Table 5). This discrepancy suggests potential limitations in the model's representation of nutrient-related processes, for instance, in plant nutrient resorption mechanisms. Nutrient resorption is a crucial physiological process through which plants adapt to varying N and P availability in ecosystems. In our model, we implemented a fixed resorption coefficient (Table 4), which may oversimplify the dynamic nature of nutrient resorption. This simplified representation likely contributes to the contrasting patterns observed in plant nutrient litterfall rates, which overestimate N litterfall while underestimating P litterfall. Plants typically adjust their nutrient resorption



764 efficiency in response to both internal nutrient status and external resource availability
765 (Mao et al., 2015; Sasha et al., 2012; Aerts and Chapin, 2000; Aerts, 1996). The fixed
766 resorption coefficients in the current model structure may not capture these adaptive
767 responses, potentially leading to unrealistic nutrient cycling patterns, especially under
768 varying environmental conditions.

769 The CNP configuration successfully captured the steady-state P distributions across
770 ecosystem pools despite some discrepancies in P cycling processes. Further refinements in
771 P cycling processes, particularly in plant-soil P transfer mechanisms and plant internal P
772 recycling, would be valuable for improving model performance (Jiang et al., 2019; 2024).
773 However, these improvements are currently constrained by limited observational data, as
774 data scarcity remains a major challenge for C-nutrient coupled modeling (Achat et al., 2016;
775 Reed et al., 2015). Future research should prioritize comprehensive field measurements of
776 P cycling processes, including plant P resorption efficiency, soil P transformation rates,
777 and plant-soil P transfer dynamics. Such empirical data would not only help validate and
778 improve model performance but also enhance our understanding of terrestrial P cycling
779 and its interactions with C and N cycles in terrestrial ecosystems.

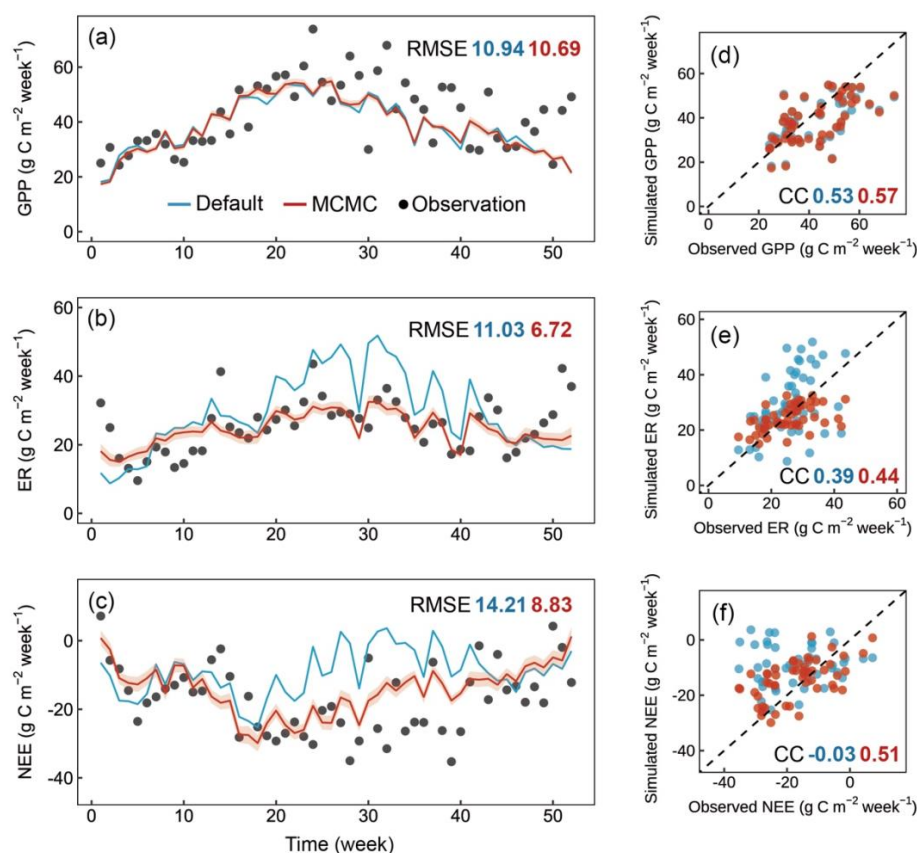
780 **3.2 Evaluate the model-data fusion module**

781 To evaluate the efficiency of the integrated data assimilation module, we compared the
782 carbon fluxes from CNP simulations with default and optimized parameters (Fig. 6, 7). The
783 optimization showed varied improvements across different carbon flux components. For
784 gross primary productivity (GPP), both default and optimized simulations captured the
785 seasonal patterns well, with only minor improvement in RMSE from 10.94 to 10.69 and
786 slightly increased correlation coefficient from 0.53 to 0.57 after optimization (Fig. 6a, e).

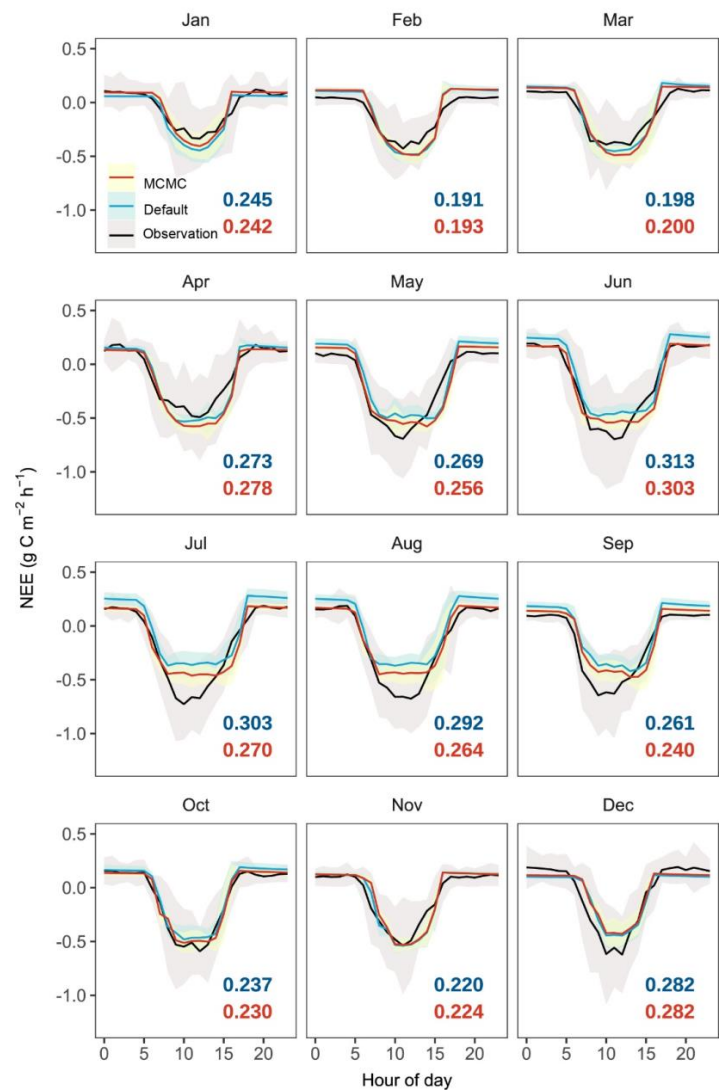
787 The photosynthetic capacity per unit area and photosynthetic surface area, indicated
788 by V_{cmax} and SLA through data assimilation in our case, are key determinants of GPP. Both
789 V_{cmax} and SLA were adjusted within their reference ranges during data assimilation (Fig.
790 8). Although these parameters showed compensatory effects in their adjustments, their
791 combined effect still demonstrated a tendency to enhance GPP (Fig. 6a, e). Notably, the
792 systematic underestimation of GPP particularly during the growing season suggests the
793 need for improving current carbon cycle process representations. These improvements



794 should include (1) the soil moisture control on stomatal conductance specific to evergreen
795 broadleaf forests (Weng & Luo, 2008) and (2) the calculation of sunlit and shaded leaf
796 proportions through more accurate clumping index parameterization in the two-leaf model
797 (Wang et al., 2024; Bi et al., 2022; Yan et al., 2017).



798
799 **Figure 6. Comparison of weekly observed and simulated carbon fluxes using default**
800 **parameters and optimized parameters for Tiantong site in 2021.** (a-c) Time series of
801 observed (black dots) and simulated values with default parameters (blue line) and
802 optimized parameters (red line), where the optimized results are derived from 1000
803 parameter sets randomly selected from 10,000 accepted parameter sets during the data
804 assimilation process (shaded areas represent standard deviation). (d-f) Scatter plots of
805 simulated versus observed values corresponding to the time series above, where the dashed
806 line represents the 1:1 line. CC, correlation coefficient; RMSE, root mean square error.

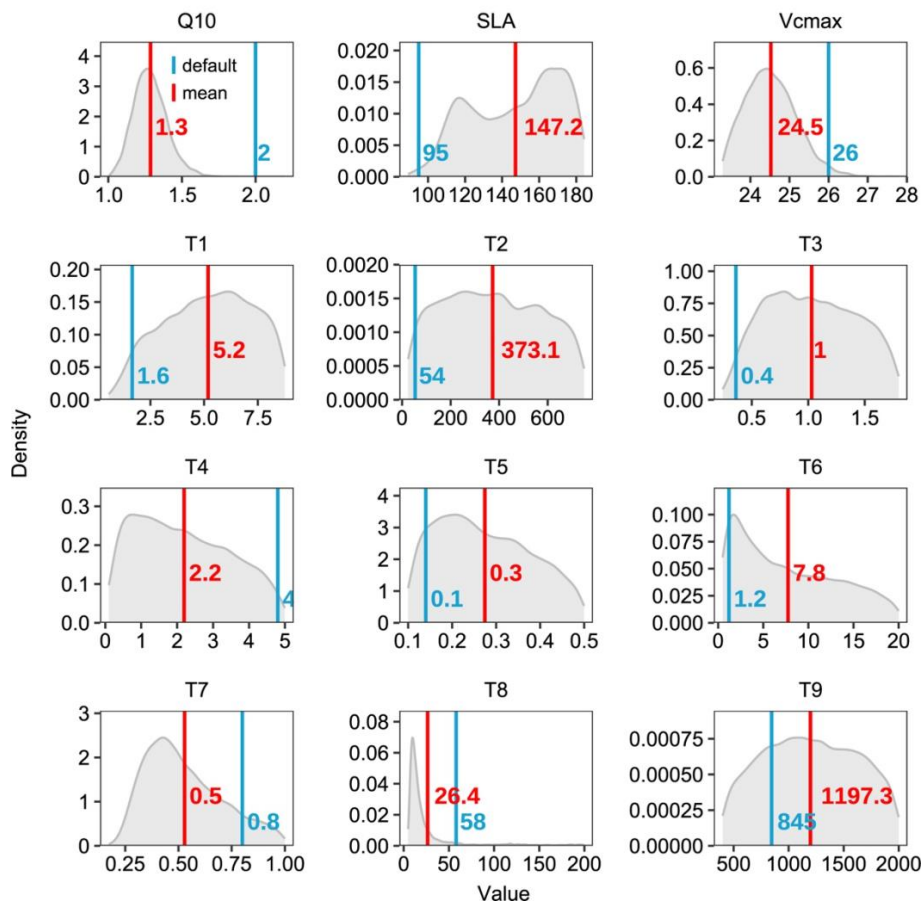


807
808 **Figure 7. Diurnal patterns of hourly net ecosystem exchange (NEE) across different**
809 **months simulated by three model configurations (C, CN, and CNP) compared with**
810 **observations.** Black dots with error bars represent observations (± 1 standard deviation,
811 SD). Colored lines indicate model simulations with shaded areas showing their respective
812 SD ranges. Root mean square errors (RMSE) between model outputs and observations are
813 colored in blue for default parameter simulations and in red for accepted parameter
814 simulations.



815 Ecosystem respiration (ER) showed more substantial improvement with data
816 assimilation, with RMSE decreasing from 11.03 to 6.72 g C per m² per week, particularly
817 in reducing the high-frequency fluctuations present in the default simulation (Fig. 6b). This
818 improvement in ER led to a notable improvement in NEE, where the RMSE decreased
819 from 14.21 to 8.83 g C per m² per week, and the correlation coefficient improved
820 dramatically from -0.03 to 0.51. The significantly improved representation of carbon
821 exchange dynamics with parameter optimization is further confirmed by the diurnal
822 patterns across months (Fig. 7), with reduced RMSE in most months (7 out of 12). However,
823 certain limitations persist, notably the underestimated NEE during midday hours in the
824 growing season, primarily attributed to underestimated GPP, which requires further
825 investigation.

826 The enhancement in ER and NEE primarily resulted from the efficiently constrained
827 key parameters (Table 6, Fig 8) based on the validated state variables (Fig 5). While the
828 default parameters achieved reasonable state variables, the response of state variables to
829 new meteorological forcing conditions required adjustment (Ma et al., 2021). For instance,
830 the Q_{10} and soil carbon residence time (T6-T8) are well-constrained in our case. The
831 temperature sensitivity parameter represents microbial responses to soil temperature, and
832 carbon residence times serve as a proxy for microbial accessibility to carbon substrates
833 rather than just soil carbon properties, both of them related to hetero-respiration. Through
834 the optimization of these parameters, CNP model effectively reduced the high-frequency
835 fluctuations present in the default simulation and better captured the observed temporal
836 dynamics.



837
838 **Figure 8. Posterior distributions of model parameters derived from Bayesian**
839 **calibration.** Grey shaded areas represent parameter posterior distributions, with red and
840 blue vertical lines indicating posterior means and default values, respectively. The
841 parameters (listed in Table 6) include Q₁₀, SLA, V_{cmax}, and carbon residence time
842 parameters (T₁-T₉). The corresponding numerical values are shown in matching colors.
843



844 **Table 6.** Target parameters, their ranges, mean values and maximum likelihood estimation
845 (MLE) of the posterior distribution. Q_{10} represents temperature sensitivity; SLA, specific
846 leaf area; and V_{cmax} , maximum carboxylation rate. T_1 – T_9 indicate turnover times for
847 individual pools.

Parameters	Lower	Upper	Mean	MLE
Q_{10}	1.00	3.00	1.29	1.26
SLA	89.04	184.26	147.23	166.68
V_{cmax}	23.29	29.11	24.52	24.42
Carbon turnover rate				
T_1	0.25	8.76	5.19	6.11
T_2	25.00	750.00	373.13	260.58
T_3	0.24	1.80	1.03	0.79
T_4	0.10	5.00	2.19	0.76
T_5	0.10	0.50	0.27	0.21
T_6	0.50	20.00	7.75	1.69
T_7	0.05	1.00	0.53	0.43
T_8	2.00	200.00	26.41	9.75
T_9	400.00	2000.00	1197.29	1090.48

848

849 4 Conclusions

850 In this study, we developed and evaluated a process-based CNP-coupled model for
851 subtropical evergreen broadleaf forest. The CNP configuration demonstrated superior
852 performance compared to C and CN models across most biogeochemical pools and fluxes,
853 effectively addressing the overestimation issues prevalent in models with simplified
854 biogeochemical processes. The incorporation of phosphorus cycling mechanisms proved
855 crucial for capturing ecosystem dynamics in these phosphorus-limited systems.
856 Furthermore, we implemented and evaluated a model-data fusion framework using the
857 MCMC algorithm, which significantly improved the simulation of carbon fluxes. The
858 optimization of key parameters, such as those controlling photosynthetic capacity,
859 temperature sensitivity, and carbon turnover rate, effectively reduced simulation
860 uncertainties and enhanced model performance. The success of the data assimilation
861 approach not only demonstrates its effectiveness in current model optimization but also



862 provides a promising path for future model improvement and applications across diverse
863 ecosystems. More importantly, integrating data assimilation frameworks with site-level
864 biogeochemical models facilitates a synergistic loop between experimental findings and
865 model development, enhancing our understanding of the nutrient cycle processes and our
866 ability to make reliable predictions. This integrated approach provides a robust framework
867 for improving ecosystem models and advancing our understanding of nutrient cycling
868 under environmental changes.

869

870 **Code availability**

871 The model code is available at <https://doi.org/10.5281/zenodo.15032706>, (Wan, 2025a).

872 **Data availability**

873 The model outputs related to the results in this paper are provided in a Zenodo repository
874 (<https://doi.org/10.5281/zenodo.15033861>, Wan, 2025b). The visualization scripts and
875 associated data for generating all figures are provided in a separate Zenodo repository
876 (<https://doi.org/10.5281/zenodo.15032690>, Wan, 2025c).

877 **Supplement link**

878 The supplement related to this article will be available online at: [Supplement link to be
879 provided by Copernicus].

880 **Author contribution**

881 J.X. and F.W. conceived and designed the study. F.W. developed the model, implemented
882 the code, and performed the analysis. C.B. provided technical support. Y.L. and E.W.
883 provided valuable suggestions for manuscript content and improvement. F.W. wrote the
884 first draft of the manuscript, and all authors reviewed and approved the final version.

885 **Competing interests**

886 The authors declare that they have no conflict of interest.

887



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892 Erqian Cui, and Yang Qiao for maintaining the field measurements and providing the
893 observational data. We also thank Kun Huang and Cuihai You for their assistance in eddy
894 covariance flux data collection and processing.

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