1	Carbon-nitrogen coupling under three schemes of model		
2	representation: a traceability analysis		
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23 Abstract The interaction between terrestrial carbon (C) and nitrogen (N) cycles has been incorporated into more and more land surface models. However, the scheme of C-N coupling 24 differs greatly among models, and how these diverse representations of C-N interactions will 25 affect C-cycle modeling remains unclear. In this study, we explored how the simulated 26 27 ecosystem C storage capacity in the terrestrial ecosystem (TECO) model varied with three different commonly-used schemes of C-N coupling. The three schemes (SM1, SM2, and 28 29 SM3) have been used in three different coupled C-N models (i.e., TECO-CN, CLM 4.5, and O-CN, respectively). They differ mainly in the stoichiometry of C and N in vegetation and 30 31 soils, plant N uptake strategies, down-regulation of photosynthesis, and the pathways of N import. We incorporated the three C-N coupling schemes into the C-only version of TECO 32 model, and evaluated their impacts on the C cycle with a traceability framework. Our results 33 showed that all of the three C-N schemes caused significant reductions in steady-state C 34 storage capacity compared with the C-only version with the magnitudes of -23%, -30% and -35 54% for SM1, SM2, SM3, respectively. These reduced C storage capacity was mainly 36 derived from the combined effects of decreases in net primary productivity (NPP, -29%, -15% 37 and -45%) and changes in mean C residence time (MRT, 9%, -17% and -17%) for SM1, SM2, 38 39 and SM3, respectively. The differences in NPP are mainly attributed to the different 40 assumptions on plant N uptake, plant tissue C:N ratio, down-regulation of photosynthesis, and biological N fixation. In comparison, the alternative representations of the plant vs. 41 42 microbe competition strategy and the plant N uptake, combining with the flexible C:N ratio in vegetation and soils, led to a notable spread MRT. These results highlight that the diverse 43 44 assumptions on N processes represented among different C-N coupled models could cause additional uncertainty to land surface models. Understanding their difference can help us 45 46 improve the capability of models to predict future biogeochemical cycles of terrestrial 47 ecosystems.

Keywords: carbon-nitrogen coupling, traceability analysis, carbon storage capacity, nitrogen
limitation, carbon residence time

50

51 **1. Introduction**

The terrestrial ecosystem carbon (C) storage is jointly determined by ecosystem C input (i.e., 52 net primary productivity, NPP) and mean residence time (MRT), which are strongly affected 53 by the terrestrial nitrogen (N) availability (Vitousek et al., 1991; Hungate et al., 2003; Luo et 54 al., 2017). Nitrogen is an essential component of enzymes, proteins, and secondary 55 metabolites (van Oijen and Levy, 2004). Plant and microbial production require N to meet 56 their stoichiometric demands, affecting the C balance and nutrient turnover of ecosystems 57 (Cleveland et al., 2013; Wieder et al., 2015b). Since N limitation is widespread for plant 58 59 growth in terrestrial ecosystems (LeBauer et al., 2008), N availability is often highly correlated with key ecological processes, such as C assimilation (Field and Mooney, 1986; 60 61 Du et al., 2017), allocation (Kuzyakov et al., 2013), plant respiration (Sprugel et al., 1996), 62 and litter and soil organic matter (SOM) decomposition (Terrer et al., 2016). Nitrogen 63 dynamics thus plays an important role in governing the terrestrial ecosystem C storage (García-Palacios et al., 2013; Shi et al., 2015). 64

65 Given the importance of N availability on C sink projections (Hungate et al., 2003; Wang and Houlton 2009, Zaehle et al., 2015, Wieder et al., 2015b), N processes are increasingly 66 incorporated into biogeochemical models. The representation of N cycling and their feedback 67 to C cycling in models reflects what has been established in the ecosystem research 68 community. Early C-N coupled models demonstrated that the N availability limited C storage 69 capacity with associated effects on plant photosynthesis and growth in many terrestrial 70 ecosystems (Melillo et al., 1993; Luo et al., 2004). Recent studies have largely confirmed 71 72 these results by improving C-N coupling models with multiple hypotheses (Zhou et al., 2013; Zaehle et al., 2014; Thomas et al., 2015). These hypotheses include the plant down-regulation 73 74 productivity based on N required for cell construction or N availability for plant absorption (Thornton et al., 2009; Gerber et al., 2010), constant or flexible stoichiometry for allocation 75 76 and tissue (Wang et al., 2001; Shevliakova et al., 2009; Zaehle et al., 2010), competition between plants and microbes for soil nutrients (Zhu et al., 2017), Evapotranspiration (ET)- or 77 NPP-driven empirical functions to generate spatial estimates of biological N fixation (BNF) 78 (Cleveland et al., 1999; Wieder et al., 2015a; Meyerholt et al., 2016), and respiration of 79 excess C to obtain N from environment and/or to prevent the accumulation of C beyond the 80 81 storage capacity (Zaehle et al., 2010). The knowledge has significantly helped improve our understanding of the terrestrial C-N coupling and is an important basis to develop 82 comprehensive terrestrial process-based models (Thornton et al., 2007; Thomas et al., 2013). 83

84 However, simulated results of the terrestrial C cycle illustrated considerable spread among models, and much of uncertainty arose from predictions of N effects on C dynamic (Arora et 85 al., 2013; Zaehle et al., 2015). The contradictory results were largely from different 86 representations of fundamental N processes (e.g., the degree of flexibility of C:N ratio in 87 vegetation and soils, plant N uptake strategies, pathways of N import, decomposition, and the 88 representations of the competition between plants and microbes for mineral N) (Sokolov et al., 89 2008; Wania et al., 2012; Walker et al., 2015). Furthermore, the methodology used to derive 90 the C-N coupling schemes among models varied largely, which might be invalid for the 91 92 model intercomparisons to provide insight into the underlying mechanism of N status for terrestrial C cycle projection. 93

In the past decades, terrestrial models integrated more and more processes to improve 94 model performance (Koven et al., 2013; Todd-Brown et al., 2013; Wieder et al., 2014). The 95 more processes incorporated, the more difficult it becomes to understand or evaluate model 96 97 behavior (Luo et al., 2015). The traceability analysis has been developed to diagnose the 98 simulation results within (Xia et al. 2013; Ahlström et al., 2015) and among (Rafique et al., 99 2016; Zhou et al., 2018) models. Based on the traceability analysis framework, key traceable 100 elements, including fundamental properties of the terrestrial C cycle and their representations in shared structures among existing models, can be identified and characterized under 101 102 different sources of variation (e.g., external forcing and uncertainty in processes) compared to the achieved predictive ability. The traceability analysis enables diagnosis of where models 103 are clearly lacking predictive ability and evaluation of the relative benefit when more or 104 alternative components are added to the models (Luo et al., 2015). 105

This study is designed to examine the effects of C-N coupling under different schemes of 106 107 model representation on ecosystem C storage in the Terrestrial Ecosystem (TECO) model with the traceability analysis framework. Three schemes of model representation were 108 conducted mainly based on TECO-CN (SM1), CLM 4.5 (SM2), and O-CN (SM3, Table 1). 109 The three C-N schemes differ in degrees of flexibility of C:N ratio in vegetation and soils, 110 plant N uptake strategies, pathways of N import, and the representations of the competition 111 112 between plants and microbes for soil available N. Based on the forcing data of ambient CO₂ concentration, N deposition, and meteorological data (i.e., air temperature, soil temperature, 113 114 relative humidity, vapour pressure deficit, precipitation, wind speed, photosynthetically 115 active radiation) obtained from Duke Forest during the period of 1996-2007, we conduct 116 three alternative C-N coupling schemes (i.e., SM1, SM2 and SM3) as well as C-only in

- 117 TECO model framework to compare their effects on the ecosystem C storage capacity. The
- 118 N-processes sensitivity analysis was carried out to evaluate the variability in estimated
- ecosystem C storage caused by the process-related parameters at the steady state.
- 120

121 **2.** Materials and methods

122 **2.1 Data sources**

- 123 The datasets used in this study were taken from the Duke free-air CO₂ enrichment (FACE)
- 124 experiment, located in the Blackwood Division, North Carolina, USA (35.97° N, 79.08° W).
- 125 The flux tower lies on a 15-year-old loblolly pine (*Pinus taeda L.*) plantation. The
- 126 meteorological forcing data were downloaded from the AmeriFlux database at
- 127 <u>http://ameriflux.lbl.gov</u>, including ambient CO₂ concentration ([CO₂]), air temperature at the
- top canopy (Ta), soil temperature (Ts), photosynthetically active radiation (PAR), relative
- humidity (*RH*), vapor pressure deficit (*VPD*), precipitation, wind speed [*Ws*], and N
- deposition. All forcing data sets are available from 1996 to 2007. To set the initial condition
- 131 for the models, we collected the related datasets from the previous studies. Standing biomass
- and biomass production data at each plot for plant compartments (i.e., foliage, fine root and
- 133 woody biomass, including branches and coarse roots) were taken from McCarthy et al.
- 134 (2010). The C and N concentration data for each plant compartment based on Finzi et al.
- 135 (2007) were used to estimate C and N stocks and fluxes. Plant N demand and uptake were
- 136 calculated from these data measured by Finzi et al. (2007). The C and N concentrations of
- 137 litter and SOM were obtained from Lichter et al. (2008).
- 138

139 2.2 Model description and C-N schemes

140 **2.2.1 TECO-CN**

The terrestrial ecosystem C-N coupling model (TECO-CN) used in the present study is a
variant of the TECO-Carbon-only version (TECO-C) by incorporating additional key N
processes (Fig. 1). TECO-C model is a process-based ecosystem model designed to examine

- 144 critical processes regulating interactive responses of plants and ecosystems to climate change.
- 145 It has four major components: canopy photosynthesis module, plant growth module, soil
- 146 water dynamic module, and soil C dynamic module. The canopy photosynthesis and soil
- 147 water dynamic modules run at hourly time step while the plant growth and soil C dynamic
- 148 modules run at the daily time step. The detailed description of the TECO-C model can be
- 149 found in Weng and Luo (2008).

150 The N cycle added to the TECO model for this study is simplified following the structure of Luo & Reynolds (1999), Gerber et al. (2010), and Wang et al. (2010). It has a similar 151 structure to the TECO-C model (Fig. 1). There are nine organic N pools and one inorganic 152 soil N pool, including plant, litter and soil N pools. The plant N pools include leaves, wood, 153 roots, and mineral N in plant tissues. The litter and soil N pools include metabolic and 154 structural litter N, fast, slow, and passive soil organic N (SON), and soil mineral N pools. The 155 total plant N demand on each time step is calculated following the NPP allocation to new 156 tissue growth based on their C:N ratios. To meet the demand, the plant N supply is calculated 157 158 from three parts, including the retranslocated N from senescing tissues, plant uptake from soil mineral N pool, and external N sources from atmospheric deposition and biological N 159 fixation. The N absorbed by roots enters into the mineral N pool in plant tissues, and then is 160 allocated to the remaining plant pools with plant growth. The N in leaves and fine roots is 161 reabsorbed before senescence. Plant litters will enter metabolic or structural pools depending 162 on their C:N ratios. 163

The allocation coefficients act as the key factor to determine the baseline C residence time in this study. Plant assimilated C allocating to the leaves, stems and roots depends on their growth rates, which vary with phenology (Luo et al., 1995; Denison and Loomis, 1989; Shevliakova et al., 2009; Weng and Luo, 2008):

168
$$b_l = \frac{1}{1+c_1+c_2}$$
 (1)

169
$$b_s = \frac{c_2}{1 + c_1 + c_2}$$
 (2)

170 $b_r = \frac{c_1}{1+c_1+c_2}$ (3)

where b_l , b_s and b_r are the partitioning coefficient of newly assimilated C to leaves, stems and roots, respectively. Parameters c_1 and c_2 are calculated as:

173
$$c_1 = \frac{bm_l}{bm_r} * \frac{CN_l^i}{CN_l^0}$$
(4)

174

175

where
$$bm_l$$
 and bm_r are the leaf and root biomass; CN_l^i and CN_l^0 represent the C:N ratios of

 $c_{1} = 0.5 + 250e^{3} + 51.4 + 0.00021 + h^{2}$

(5)

the leaf pool at 0 and current time step, respectively; SLA is specific leaf area; h is plant

177 height, which is calculated as:

178
$$h = h_{max}(1 - \exp(-h_1 * bmP))$$
 (6)

where h_{max} is the maximum canopy height; h_1 is an empirical parameter and *bmP* is plant biomass.

182 2.2.2 C-N coupling schemes

- 183 We conducted four experiments including three simulations with their representations of C-N
- 184 coupling schemes (SM1, SM2 and SM3) and an additional C-only simulation in TECO model
- 185 framework. The three C-N interaction simulations include one original scheme in TECO-CN
- 186 model and the other two schemes representing CLM4.5-BGC and O-CN. The three C-N
- 187 coupling schemes differ in the representation of down-regulation of photosynthesis, the
- degree of flexibility of C:N ratio in vegetation and soils (i.e., fixed C:N ratio in SM2, flexible
- 189 C:N ratio in SM1 and SM3), plant N uptake strategies, pathways of N import to the plant
- 190 reserves, and the competition between plants, and microbes for soil mineral N (Table1, Fig.
- 191
- 192

193 **SM1 (TECO-CN)**

2).

The N down-regulation of photosynthesis in SM1 is determined by the comparison betweenplant N demand and actual supply of N:

196

$$f_{dreg} = \min(\frac{N_{sup}}{N_{demand}}, 1)$$
(7)

197 where N_{sup} (g N m⁻² s⁻¹) is actual supply of N obtained from re-translocated N, plant N 198 uptake, and biological N fixation. N_{demand} (g N m⁻² s⁻¹) is plant N demand, which is 199 calculated as:

200

204

$$N_{demand} = \sum_{i=leaf,wood,root} \frac{C_i}{CN_i^0}$$
(8)

where C_i is the C pool size of plant tissue at the current time step, and CN_i^0 is the C:N ratio of plant tissue at the last time step.

203 The re-translocated N is calculated as:

$$N_{retrans} = \sum_{i=leaf,wood,root} r_i \times outC_i/CN_i \tag{9}$$

where r_i is the N resorption coefficient, CN_i is the C:N ratio and $outC_i$ (g C m⁻² s⁻¹) is the value of C leaving plant pool *i* at each time step.

The plant N uptake (g N m⁻² s⁻¹) from soil mineral N pool is a function of root biomass density (Root_{total}, g C m⁻²) and N demand of plants, following McMurtrie *et al.* (2012)

209
$$N_{uptake} = min(max(0, N_{demand} - N_{retrans}), f_{U,max} \times SN_{mine} \times \frac{Root_{total}}{Root_{total} + Root_0})$$
 (10)

- where N_{demand} is the N demand of plants; SN_{mine} (g N m⁻²) is the soil mineral N; $f_{\text{U,max}}$ is the
- 211 maximum rate of N absorption per step when *Root*_{total} approaches infinity; and *Root*₀ (g C m⁻²)
- is a constant of root biomass at which the N-uptake rate is half of the parameter $f_{U,max}$.
- 213 The biological N fixation (g N $m^{-2} s^{-1}$) is calculated as:

214
$$N_{BNF} = \min(\max(0, N_{demand} - N_{retrans} - N_{uptake}), n_{fix} \times f_{nsc} \times NSC) \quad (11)$$

where $n_{fix} = 0.0167$ is the maximum N fixation ratio and f_{nsc} is the nutrient limiting factor. f_{nsc} is calculated as

217
$$f_{nsc} = \begin{cases} 0, & NSC < NSC_{min} \\ \frac{NSC - NSC_{min}}{NSC_{max} - NSC_{min}}, & NSC_{min} < NSC < NSC_{max} \\ 1, & NSC > NSC_{max} \end{cases}$$
(12)

where NSC_{min} (g C m⁻²) and NSC_{max} (g C m⁻²) are the minimal and maximal sizes of nonstructural C pool, respectively.

220 The soil microbial immobilization (g N $m^{-2} s^{-1}$) is calculated as:

221
$$Imm_{N} = \begin{cases} \sum_{i=4}^{8} min\left(\left(\frac{C_{i}}{CN_{i}} - \frac{C_{i}}{CN_{i}}\right), 0.1 * SN_{min}\right) for CN_{i} \ge CN0_{i} \\ \sum_{i=4}^{8} min\left(\left(\frac{C_{i}}{CN_{i}} - \frac{C_{i}}{CN0_{i}}\right), 0.1 * SN_{min}\right) for CN_{i} < CN0_{i} \end{cases}$$
(13)

Two pathways of N loss are modeled. One is gaseous loss (N_{gas_loss} , g N m⁻² s⁻¹) and another is leaching (N_{leach} , g N m⁻² s⁻¹). Both are proportional to the availability of soil mineral N (SN_{min} , g N m⁻²). The equations are:

225
$$N_{gas_loss} = f_{ngas} \times e^{\frac{T_{soil} - 25}{10}} \times SN_{min}$$
(14)

226
$$N_{leach} = f_{nleach} \times \frac{V_{runoff}}{h_{depth}} \times SN_{min}$$
(15)

where $f_{ngas} = 0.001$ and $f_{nleach} = 0.5$, $T_{soil}(^{\circ}C)$ is the soil temperature, V_{runoff} (mm s⁻¹) is the value of runoff, and h_{depth} (mm) is the soil depth.

229

230 SM2 (CLM4.5bgc)

231 The N down-regulation of photosynthesis in SM2 is calculated as:

232
$$f_{dreg} = \frac{CF_{allo} - CF_{avail_alloc}}{CF_{GPP_{pot}}}$$
(16)

- where CF_{allo} (g C m⁻² s⁻¹) is the total flux of allocated C, which is determined by available
- mineral N. CF_{avail_alloc} (g C m⁻² s⁻¹) is the potential C flux from photosynthesis, which can

be allocated to new growth. $CF_{GPP_{pot}}$ (g C m⁻² s⁻¹) is the potential gross primary productivity

- 236 (GPP) when there is no N limitation.
- 237 The re-translocated N (g N $m^{-2} s^{-1}$) is calculated as:

$$N_{retrans} = \min(N_{demand} \times \frac{N_{retrans_{ann}}}{N_{demand_{ann}}}, N_{retrans_{avail}})$$
(17)

where $N_{retrans_{ann}}$ (gN m⁻² y⁻¹) is the previous year's annual sum of re-translocated N obtained from senescing tissues, $N_{demand_{ann}}$ (g N m⁻² y⁻¹) is the previous year's annual sum of plant N demand. $N_{retrans_avail}$ (g N m⁻² s⁻¹) is the available re-translocated N in senescing tissues, which is calculated by the proportional of senescing tissues.

243 The plant N uptake (g N $m^{-2} s^{-1}$) is described as:

$$N_{uptake} = (N_{demand} - N_{retrans}) \times f_{plant_demand}$$
(18)

where f_{plant_demand} is the fraction (from 0 to 1) of the plant N demand, which can be met given the current soil mineral N supply and competition with heterotrophs. f_{plant_demand} is set to be equal to the fraction of potential immobilization demand (f_{immob_demand}) that is calculated as:

249

244

238

$$f_{plant_demand} = f_{immob_demand} = \frac{SN_{min}}{N_{plant_demand} + N_{immob_demand}}$$
(19)

where N_{immob_demand} (g N m⁻² s⁻¹) is the total potential N immobilization demand (i.e., total potential microbial N demand).

252 The biological N fixation (g N $m^{-2} s^{-1}$) is calculated as:

$$N_{BNF} = \frac{1.8(1 - e^{-0.03 \times NPP_{py}})}{(86400 \times 365)}$$
(20)

where NPP_{py} (g C m⁻² y⁻¹) is the previous-year NPP.

255

261

253

256 SM3 (O-CN)

257 The N down-regulation of photosynthesis in SM3 is calculated as:

 $f_{dreg} = a + b \times N_{leaf/LAI} \tag{21}$

where *a* and *b* are empirical constants, and $N_{leaf/LAI}$ (g N m⁻²) is foliage N per unit leaf area.

- 260 The re-translocated N (g N $m^{-2} s^{-1}$) is calculated as:
 - $N_{retrans} = \sum_{i=leaf,root} \tau_i \times f_{trans,i}$ (22)

262 where τ (g N m⁻² s⁻¹) is the foliage or roots shed each step. $f_{trans,leaf} = 0.5$ and $f_{trans,root} =$

- 263 0.2 are the fractions of N re-translocated when the tissue dies off.
- 264 The plant N uptake (g N $m^{-2} s^{-1}$) is calculated as:

265
$$N_{uptake} = v_{max} \times SN_{min} \times (k_{Nmin} + \frac{1}{N_{min} \times K_{Nmin}}) \times f(T_{soil}) \times f(NC_{plant}) \times C_{root}$$
 (23)

where v_{max} is maximum N uptake capacity per unit fine root mass, k_{Nmin} is the rate of N

uptake not associated with Michaelis-Menten Kinetics, K_{Nmin} is the half saturation

268 concentration of fine root N uptake. $f(T_{soil})$ is calculated as:

269
$$f(T_{soil}) = \exp\left(308.56 * \left(\frac{1}{56.02} - \frac{1}{T_{soil} + 46.02}\right)\right)$$
(24)

270 where T_{soil} (°C) is soil temperature.

271 C_{root} (g C m⁻²) is fine root mass. $f(NC_{plant})$ is the dependency of N uptake on plant N 272 status, and is calculated as:

273
$$f(NC_{plant}) = \max(\frac{NC_{plant} - nc_{leaf,max}}{nc_{leaf,min} - nc_{leaf,max}}, 0)$$
(25)

where $nc_{leaf,min}$ and $nc_{leaf,max}$ are the minimum and maximum foliage N concentration, respectively. NC_{plant} (g N g⁻¹C) is taken as the mean N concentration of foliage, fine root, and labile N pools, representing the active and easily translocatable portion of plant N:

277
$$NC_{plant} = \frac{N_{leaf} + N_{root} + N_{labile}}{C_{leaf} + C_{root} + C_{labile}}$$
(26)

The biological N fixation (g N $m^{-2} s^{-1}$) is calculated as:

279
$$N_{BNF} = 0.1 \times \max(0.0234 \times 30 \times AET + 0.172, 0) / (86400 \times 365)$$
 (27)

where AET (mm y⁻¹) is the mean annual evapotranspiration.

281

282 **2.3 Traceability analysis framework**

The traceability analysis framework was used to evaluate the variation of the modeled 283 284 ecosystem C storage capacity under different C-N schemes (Fig. S1). According to the traceability analysis framework (Xia et al., 2013), the modeled C storage capacity can be 285 traced to (i) a product of NPP and ecosystem residence time (τ_E). The latter τ_E can be further 286 traced to (ii) baseline C residence time (τ'_E), which is usually preset in a model according to 287 vegetation characteristics and soil types, (iii) N scalar (ξ_N), (iv) environmental scalars (ξ) 288 including temperature (ξ_T) and water (ξ_W) scalars, and (v) the external climate forcing. The 289 290 framework for decomposing modeled C storage capacity into a few traceable components is 291 built upon a pool- and flux- structure, which is adopted in all of the terrestrial C models. The structure can well be represented by a matrix equation (Luo et al., 2003; Luo and Weng, 292 293 2011):

294
$$\frac{dX(t)}{dt} = BU(t) - A\xi CX(t)$$
(28)

where $X(t) = (X_1(t), X_2(t), ..., X_8(t))^T$ is an 8×1 vector describing eight C pool sizes in leaf, root, wood, metabolic litter, structural litter, fast, slow, and passive soil organic C, 296 respectively, in the TECO model (Weng and Luo, 2008). $B = (b_1, b_2, b_3, 0, ..., 0)^T$ represents 297 the partitioning coefficients of the photosynthetically fixed C into different plant pools. U(t)298 is the input of fixed C via plant photosynthesis. A is an 8×8 matrix representing the C 299 300 transfer between pools. ξ is an 8 × 8 diagonal matrix of control of plant N status and environmental scalars on C decay rate at each time step. C is an 8×8 diagonal matrix 301 302 representing the C exit rates from a pool at each time step. The C storage capacity equals to the sum of C in all pools at the steady state (X_{ss}) , which 303 can be obtained by making Eqn.(28) equal to zero as described in Xia et al. (2013): 304 $X_{ss} = (A\xi C)^{-1} B U_{ss}$ 305 (29)The vector U_{ss} is the ecosystem C influx at the steady state. The partitioning (B vector), 306 transfer coefficients (A matrix), and exit rates (C matrix) in Eqn. (28) together determine the 307 baseline C residence time (τ'_E) : 308 $\tau'_E = (AC)^{-1}B$ (30)309 The baseline C residence time (τ'_E) in Eqn. (30), N scalars (ξ_N) and environmental scalars (ξ_E) 310 values together determine the C residence time (τ_E) : 311 $\tau_E = \xi^{-1} \tau'_E = (\xi_N \times \xi_E)^{-1} \tau'_E$ (31)312 Thus, the C storage capacity is jointly determined by the ecosystem residence time (τ_E) and 313 steady-state C influx (U_{ss}) : 314 $X_{ss} = \tau_F U_{ss}$ (32)315 The environmental scalar is further separated into the temperature (ξ_T) and water (ξ_W) scalars, 316 which can be represented as: 317 $\xi_E = \xi_T \times \xi_W$ 318 (33)As the respiration and decomposition rate modifier, the N scalar is given by vector $\xi_N =$ 319 $(\xi_{N1}(t), \xi_{N2}(t), \dots, \xi_{N8}(t))^T$. The component $\xi_{Ni}(t)$ quantifies the changes of N content at 320 each time step compared with initial condition in the C pool *i*. It is calculated as: 321 $\xi_{Ni} = \exp(-\frac{CN_i^0 - CN_i^n}{CN_i^0})$ (34)322 where CN_i^0 and CN_i^n are the C:N ratio of the pool *i* at 0 and *n* time step, respectively. 323 324 2.4 Model simulations and sensitivity analysis 325 To obtain the modeled C storage capacity, we spun up the TECO model with the C-only and 326

295

three C-N coupling schemes to the steady state using the semi-analytical solution method 327

developed by Xia et al. (2012). In this study, the meteorological forcings of 1996-2007 withthe time step of half an hour were used to run the models to the steady state. Once the

simulations are spun up to the steady state, C and N fluxes and state variables as well as the

matrix elements A, C, B, and ξ in Eqn.(29) from all time steps in the last recycle of the

climate forcing were saved for the traceability analysis.

The sensitivities of both NPP and mean C residence time (MRT) as well as ecosystem C
storage capacity to each main N process in three schemes were calculated as:

335
$$S_i^{NPP}(P) = \frac{NPP_i^+(P) - NPP_i^-(P)}{NPP_i^0}$$
(35)

336
$$S_i^{MRT}(P) = \frac{MRT_i^+(P) - MRT_i^-(P)}{MRT_i^0}$$
(36)

$$S_i^{ECSC}(P) = S_i^{NPP}(P) \times S_i^{MRT}(P)$$
(37)

where $S_i^{NPP}(P)$, $S_i^{MRT}(P)$, and $S_i^{ECSC}(P)$ (i = 1, 2, 3) represent the sensitivities of NPP, MRT and ecosystem C storage capacity to the N-process *P* in the scheme *i*, respectively. $NPP_i^+(P)$ and $NPP_i^-(P)$ are the annual mean values of NPP that were simulated in scheme *i* based on the value of the N-process *P* (i.e., list in Table 1) by increasing 50% and decreasing 50%, respectively. $MRT_i^+(P)$ and $MRT_i^-(P)$ are the annual mean values of MRTs that were simulated at the same way as NPP and calculated using Eqn.(30) and Eqn.(31). NPP_i^0 and MRT_i^0 are the annual mean values of NPP and MRT at the steady state in the scheme *i*.

345

346 **3. Results**

347 **3.1 Simulations of C and N dynamics at steady state**

348 At the steady state, the dynamics of N fluxes and soil mineral N showed different patterns

among three C-N schemes in the TECO model (Fig. 3). The simulated soil N mineralization

- and plant N uptake fluxes in SM2 displayed the largest daily variation (0.0015 and 0.00086 g
- $N \text{ m}^{-2}\text{d}^{-1}$, respectively) and annual mean values (1.26 and 0.23 g N m⁻²yr⁻¹, respectively)
- among three C-N schemes. For the N leaching flux, SM1 showed the largest daily variation
- 353 $(0.04 \text{ g N m}^{-2}\text{d}^{-1})$ and annual mean value $(0.36 \text{ g N m}^{-2}\text{yr}^{-1})$. However, the biological N
- fixation (BNF) flux in SM1 showed the largest daily variation (0.028 g N m⁻²d⁻¹) but with the
- smallest annual value (0.04 g N m⁻²yr⁻¹) among three C-N schemes. The N immobilization
- fluxes in SM3 displayed the largest daily variation (0.0013 g N $m^{-2}d^{-1}$) and SM1 showed the
- largest annual mean value (1.15 g N $m^{-2}yr^{-1}$). The dynamics of soil mineral N in SM2 and
- 358 SM3 displayed the similar patterns on the daily and annual dynamics.

359 Compared with the TECO-C model, the three C-N coupling schemes introduced significant signs of N limitation on forest growth at the steady state but with varying 360 magnitude (Fig. 4). Specifically, the three N schemes caused significant reductions in GPP 361 (10%, 10% and 12% for SM1, SM2 and SM3, respectively) compared to the C-only TECO 362 model. Similar response patterns were also found on NPP, ecosystem respiration, and 363 heterotrophic respiration. Among the three schemes, SM3 had the strongest effect (45%, 12% 364 and 45% reduction for NPP, ecosystem respiration, and heterotrophic respiration, 365 respectively), while SM2 had the weakest effect (15%, 8% and 13%, respectively) and the 366 effect of SM1 was relatively moderate (29%, 10% and 29%, respectively). However, by 367 comparison with the TECO-C version, both the SM1 and SM2 schemes increased the 368 autotrophic respiration by 12% and 27%, respectively, and SM2 scheme increased the NEE 369 370 by 32%. Due to the NSC pool of TECO model, NEE were positive in all the experiments at the steady state (Weng and Luo, 2008). 371

Three C-N coupling schemes induced different effects on C and N stoichiometric status 372 for different pools (Figs. 5 and S2). All three schemes had significant limitation signs on 373 woody, structural litter, fast and slow SOM pools but with different magnitudes (Fig. 5a). 374 SM2 had the highest C sizes for the roots (731.8 g C m⁻²) and metabolic litter (1252.1 g C m⁻ 375 ²), while SM1 had the highest C size for passive SOM pool (4249.5 g C m⁻²). SM2 had the 376 constant C:N ratios for all the displaying pools (Fig. 5b), while the C:N ratios for three 377 378 displaying pools (leaf, root and structural litter) had no significant change in both SM1 and SM3. As for both woody and metabolic litter pools, SM1 and SM3 had higher C:N ratios 379 380 (357.2 and 357.9, respectively) compared with SM2 (354). SM1 had the lowest C:N ratio (4.6) 381 for soil passive SOM pool among the three schemes. 382 The divergent effects of three C-N schemes on plant N uptake (Fig. 3), autotrophic

respiration, and NPP (Fig. 4) lead to different N use efficiency (NUE) and carbon use

efficiency (CUE) (Fig. 6). SM1 had the highest NUE (159.1 g C g^{-1} N), mainly resulting from

its lowest plant N uptake. In contrast, SM3 had the lowest NUE (67.3 g C g^{-1} N) as a result of

its smallest NPP. Because of the hypothesis of N uptake for free, SM2 had the highest CUE

(0.54) among three C-N schemes, which was close to that in the C-only version (0.57).

However, SM3 had the lowest CUE (0.35) due to both C cost for plant actively uptake N and

the assumption that increase respiration to remove the excess C.

390

391 3.2 Simulation of C storage capacity

- 392 The ecosystem C storage capacity also differed greatly among the three C-N coupling schemes and the C-only version of TECO model (Fig. 7). The C-only version had the largest 393 C storage capacity (19.5 Kg C m⁻²) among the four simulations due to its highest NPP (879.9 394 g C m⁻² yr⁻¹). The C storage capacity in SM1 (15.1 Kg C m⁻²) was close to that in SM2 (13.7 395 Kg C m⁻²). The SM3 had the lowest C storage capacity (8.9 Kg C m⁻²) among the four 396 simulations as a result of its smallest NPP (483.9 g C m⁻² yr⁻¹) and relative short MRT (18.6 397 years). By comparison with the C-only version, the three C-N schemes all induced different 398 reductions on NPP (-29%, -15% and -45% for SM1, SM2, SM3, respectively) and further 399 400 reduced their ecosystem C storage capacity. For the MRT, SM1 exhibited positive effects
- 401 (+9%) relative to that in the C-only version, while another two schemes induced negative
- 402 ones (i.e., -16.9% in SM2 and -16.7% in SM3).
- 403

404 **3.3. Ecosystem C residence time**

- Ecosystem C residence time (τ_E) is collectively determined by baseline residence time, N 405 scalar, and environmental scalars as shown in Eqn. (31). Specifically, differences in τ_E among 406 three C-N coupling schemes and C-only TECO model are determined by baseline residence 407 408 time and the effects of N scalar on eight plant C pools (Fig. 8). For example, SM1 had the 409 longest τ_E because the N scalar had very strong control on passive SOM. The baseline residence time was further determined by the C allocation (Fig. 9). Overall, compared with 410 411 C-only version, the additional N processes enhanced the partitioning coefficient of NPP to roots (33%, 82% and 53% for SM1, SM2 and SM3, respectively) but decreased the 412 413 partitioning coefficient to wood (-25%, -45% and -34%, respectively). Furthermore, the decreased partitioning coefficient to wood (b2) regulated the variations of the baseline 414 415 residence time of wood, structural litter, slow and passive SOM. However, the increased partitioning coefficient to roots (b3) determined the variations of the baseline residence time 416 417 of roots and metabolic litter.
- 418

419 **3.4. Sensitivity of N processes to NPP and MRT**

- 420 For either NPP or MRT, the N processes had different sensitivities among the three C-N
- 421 schemes of TECO model (Fig. 10). For NPP, plant C:N ratio had the highest sensitivities in
- 422 both SM1 (0.32) and SM2 (0.53). However, plant N uptake in SM3 had the highest
- 423 sensitivity (0.87) for NPP. For MRT, competition between plants and microbes, down-
- regulation of photosynthesis and plant C:N had the highest sensitivities in SM1 (0.27), SM2
- 425 (0.19) and SM3 (0.56), respectively. As the NPP and MRT jointly determined the ecosystem

426 C storage capacity, the plant tissue C:N ratio, down-regulation of photosynthesis, and plant N
427 uptake had the highest sensitivities for the ecosystem C storage capacity in SM1 (0.06), SM2
428 (0.09) and SM3 (0.26), respectively.

429

430 **4. Discussions**

431 **4.1 Underlying N processes and plant production**

Gross or net primary production (i.e., GPP or NPP) is regulated by the amount of N 432 availability for plant growth through the N demand, which is set by the relative proportion of 433 434 biomass growth in the different plant components and their C:N stoichiometry (Zaehle et al., 2014; Thomas et al., 2015). The limitation of equilibrium N on plant production reflects the 435 effects from multiple processes of the C-N interaction, mainly including down-regulation of 436 photosynthetic capacity by N availability, the ecosystem's balance of N inputs and losses (i.e., 437 net ecosystem N exchange), plant N uptake, soil N mineralization, and the C:N stoichiometry 438 of vegetation and soils. However, due to a lack of consensus on the nature of the mechanisms, 439 the representation of these processes varies greatly among diverse models (Zaehle et al., 440 2014). 441

There are two common alternative assumptions for the down-regulation of photosynthesis 442 443 that have been implemented in models: (1) the change in photosynthetic capacity is directly associated with the magnitude of plant available N (e.g., SM2), and (2) N limitation is 444 445 associated with foliage N, which feeds back to limit photosynthetic capacity (e.g., SM1 and SM3). Our results showed that both assumptions had significant limitations with similar 446 447 effects on GPP (Figs. 3a and 3g). The probable reason is that the TECO model calculates 448 photosynthesis by light availability and carboxylation rate based on the Farquhar model 449 (Farquhar et al., 1980). The effects of N stress under the TECO framework, either associated with plant available N or associated with foliage N concentration, are estimated according to 450 limiting factors of photosynthetic biochemistry (the maximum rate of carboxylation, V_{cmax} , 451 and the maximum rate of electron transport at saturating irradiance, V_{imax}). The two 452 assumptions of down-regulation of photosynthesis may have different time-dependent effects 453 on GPP in nonsteady-state systems (Xu et al., 2012; Walker et al., 2017). 454 At or near the steady state, net ecosystem N exchange is driven by the processes of N 455 input via deposition and fixation and N loss via leaching and volatilization (Zaehle et al., 456

457 2014; Thomas et al., 2015). Previous studies have stated that analyzing the steady-state

458 condition is useful to understand N effects because the balance between external N sources

and N losses determine whether an ecosystem is N limited (Rastetter et al., 1997; Menge et

al., 2009; Thomas et al., 2015). In this study, divergent NPP responses among the three 460 schemes might partly result from their different representations of BNF (Figs. 3 and 10). 461 Specifically, SM2 and SM3 simulated BNF explicitly, which used modified empirical 462 relationships of BNF with NPP and evapotranspiration (ET), respectively. These 463 phenomenological relationships generally captured biogeographical observations of higher 464 rates of BNF in humid environments with high solar radiation (Wieder et al., 2015a). 465 However, the highest response of NPP in only ET-driven BNF (i.e., SM3) may illustrate that 466 not only energetic but also C costs of 'fixing' atmospheric di-N (N₂) into a biologically 467 468 usable form (NH₃) broadly affect NPP (Gutschick 1981, Rastetter et al., 2001). This was because SM3 considered C investments in BNF while SM2 did not. By contrast, for the 469 nonsteady state, the NPP-driven BNF creates a positive feedback between BNF and NPP, 470 possibly causing large impact on C dynamic and terrestrial C storage (Wieder et al., 2015a). 471 On the other hand, SM1 applied a different strategy, which set BNF as an option when the 472 plant N uptake is enough for growth in terms of C investment, leading to the highest plant 473 NUE (Fig. 6a) but a lower response of BNF to NPP (Fig. 10a). Another driving factor of the 474 net ecosystem N exchange is the N loss, which depends on the rate of leaching and 475 476 volatilization. In this study, using the same formulation as proportion to the size of soil 477 mineral N pool among the three schemes, the different annual mean magnitude of N leaching was more correlated to soil mineral N. In the original CLM4.5 and O-CN (Oleson et al., 2013; 478 479 Zaehle et al., 2010), the soil mineral N pool is divided into two pools (ammonium and nitrate). The N leaching is only valid on the nitrate pool, while the ammonium pool is assumed to be 480 481 unaffected by leaching. This hypothesis may reduce the correlation between leaching and 482 total soil mineral N.

483 The processes of plant N uptake and net N mineralization determine how N moves through the plant-soil system, thereby triggering N limitation on plant growth and C storage 484 capacity (Fig. 10). However, to our knowledge, exploring those processes exactly in models 485 is limited by inadequate representation of above- and below-ground interactions that control 486 the patterns of N allocation and whole-plant stoichiometry (Zaehle et al., 2014; Thomas et al., 487 2015). Plant tissue, litter, and SOM are the primary sinks of N in terrestrial ecosystems, while 488 N in these forms is not directly available for plant uptake, leading to an increase in N demand 489 490 for plant growth. These N must turn over to become available for plant uptake. Therefore, the 491 time for N to stay in these unavailable pools controls the transactional delay between the 492 incorporation of N into plant unavailable pool and becomes available for plant uptake. In this way, the residence time of N in SOM appears to be an important factor for governing plant 493

494 growth. In this study, SM1 had the highest NUE due to the combined effects of plant N uptake based on C investment strategy (as described above) and flexible tissue C:N ratio. 495 Nitrogen stress increased tissue C:N ratio (Fig. 5b), leading to a high microbial N 496 immobilization and then a lower net N mineralization (Fig. 3), which allowed plant cell 497 construction with a lower N requirement. However, this was not the case for the SM3 since 498 both hypotheses of increasing respiration to remove the excess C under N stress and the 499 500 higher C investment for the BNF lead to the decrease in C input and then limits the microbial immobilization for the passive SOM pool. The inclusion of flexible C:N stoichiometry 501 502 appeared to be an important feature allowing models to capture responses of the ecosystem C storage capacity to climate variability through adjusting the C:N ratio of nonphotosynthetic 503 504 tissues or the whole-plant allocation among tissues (Figs. 9 and 10) with different C:N ratios 505 (Zaehle & Friend, 2010).

506

507 4.2 Ecosystem N status and C residence time

Ecosystem N status in models, including plant-available and unavailable N forms, is set by N 508 inputs from N fixation and N deposition, N losses from leaching and denitrification, and N 509 gain from the turnover of litter and SOM through tissue senescence and decomposition. As 510 511 noted above, external N cycle (i.e., N inputs and N losses) couples the N processes within the plant-litter-SOM system, being mainly associated with the limitation of plant production 512 513 (Vitousek et al., 2004; Vicca et al., 2012; Craine et al., 2015). The effects of ecosystem N status on C mean residence time (MRT), however, has been much less studied than N 514 515 limitation on productivity of plants and soil organisms, because these effects involve various impacts on C transfer among pools and C release from each pool via decomposition and 516 517 respiration (Thompson & Randerson, 1999; Xia et al., 2013). Therefore, the different impacts of ecosystem N status induce oscillating N limitation on MRT (Figs. 8 and 10) due to the 518 519 inherently different assumptions of C-N interactions among three C-N coupling schemes (Zhou et al., 2012; Shi et al., 2018). 520

At the steady state, the different effects of N status on changes in modelled MRT can be attributed to: the different rate of soil N mineralization dependent on the total amount of N in SOM and its turnover time, immobilization based on the competition strategy between plants and microbes and their stoichiometry, and different deployment of reabsorbed N. The traceability framework in this study can trace those different effects into three components (i.e., climate forcing, N scalar, and baseline MRT) based on three alternative C-N coupling

schemes under the TECO model framework. Since the forcing data are identical, we assumedthe same effects for this component in all four experiments.

In our study, the N scalar was based on the dynamics of C:N ratios (Eqn. 34). Therefore, N 529 scalar had no effect on MRT in SM2, resulting from the assumption of fixed C:N ratio in all 530 C pools (Figs. 5b and 8c). In both SM1 and SM3, however, the N scalar had large effects on 531 the SOM pool, which is probably related to different mechanisms. Specifically, N scalar in 532 the SM1 had the contrasting effects on MRT of fast and passive SOM pools (i.e., negative vs. 533 positive, respectively), which may largely be attributed to the plant and microbe competition 534 535 strategy combining with a much larger passive SOM pool in TECO-CN model (Du et al., 2017; Zhu et al., 2017). Under N stress, the competition between plants and microbes is 536 expected to be intensified, resulting in increasing C:N ratio of nonphotosynthetic tissues (e.g., 537 wood and root) and the total C:N ratio. This effectively prevents N limitation of cell 538 construction and corresponds to an increase in whole-plant NUE (Thomas et al., 2015). In 539 this case, higher C:N ratio in those tissues lowers structural litter quality, leading to soil 540 541 microbes to immobilize more N to maintain their stoichiometric balance (Hu et al., 2001; Manzoni et al., 2010). However, in the SM3, increased respiration acted as a mechanism to 542 remove the excess C, which is a stoichiometry-based implementation to prevent the 543 544 accumulation of labile C under N stress (Zaehle & Friend, 2010; Thomas et al., 2015). This mechanism promotes respiration of the faster turnover pools (fast and slow SOM pools, Fig. 545 546 5a), leading to increased C:N ratio and decreased MRT in these two pools (Fig. 8). In the traceability framework, the baseline MRT is determined by the potential 547 548 decomposition rates of C pools (C matrix), coefficients of C partitioning of NPP (B vector), 549 and transfer coefficients between C pools (A matrix, Eqn. [30]. Xia et al., 2013). The matrices 550 A and C are preset in the TECO model according to vegetation characteristics and soil texture (Weng and Luo., 2008). Therefore, the notable spread in baseline MRT across the C-N 551 schemes was induced by the *B* vector, which was modified by different N-limitation 552 assumptions (Eqns. 1-6). Conceptually, in order to meet the N demand, plants adjust NPP 553 allocation to N absorption tissues (e.g., roots). In this study, three schemes all had similar 554 trends of adjusting allocation C from wood to roots (Fig. 9), but with different mechanisms. 555 For both SM1 and SM3, increased root C allocation was mainly driven by N uptake capacity, 556 which is associated with plant competitiveness in SM1 and the respiration of excess labile C 557 558 in SM3, respectively. However, for SM2, increasing root C allocation may occur in spin-up stage from plant adjustment to whole-plant allocation among tissues to fit fixed C:N ratio. 559 560

561 **5.** Conclusions

The C-N coupling has been represented in ecosystem and land surface models with different 562 schemes, generating great uncertainties in model predictions. The most difference among 563 terrestrial C-N coupling models occurs with the degree of flexibility of C:N ratio in 564 vegetation and soils, plant N uptake strategies, down-regulation of photosynthesis, and the 565 representations of the pathways of N import. In this study, we evaluated alternative 566 representations of C-N interactions and their impacts on C cycle using the TECO model 567 framework. Our traceability analysis showed that different representations of C-N coupling 568 569 processes lead to divergent effects on both plant production and C residence time, and thus the ecosystem C storage capacity. The plant production are mainly affected by the different 570 assumptions on net ecosystem N exchange, plant N uptake, net N mineralization, and the C:N 571 ratio of vegetation and soil. In comparison, the alternative representations of the plant and 572 microbe competition strategy, combining with the flexible C:N ratio in vegetation and soils, 573 led to a notable spread effects on C residence time. Identifying the representations of main C-574 N processes under different schemes can help us improve the N-limitation assumptions 575 employed in terrestrial ecosystem models and forecast future C sink in response to climate 576 change. 577

578

579 *Code availability*. The code for TECO-CN and the three C-N coupling schemes is available
at https://github.com/zgdu/TECO-CN-2.0-new.

581 *Data availability*. The data for this paper are available upon request to the corresponding582 authors.

583 *Competing interests.* The authors declare that they have no conflict of interest.

584

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592 Figure legends

- **Figure 1.** Schematic diagram of the terrestrial ecosystem carbon (C) and nitrogen (N)
- 594 coupling model (TECO-CN). (A) Canopy module, (B) Plant growth module, (C) Soil water
- dynamics module, (D) Soil carbon-nitrogen coupling module. Rectangles represent the
- $carbon and nitrogen pools. R_a$, autotrophic respiration. R_h , heterotrophic respiration. Retr., re-
- translocation. NSC, nonstructural carbohydrate. MNP, mineral N in plant tissues. SOM, soil
- 598 organic matter. * set N fixation as an option when the plant N uptake is enough for growth in 599 terms of C investment.**Figure 2.** Schematic diagram illustrating the major carbon (C) and
- terms of C investment.Figure 2. Schematic diagram illustrating the major carbon (C)
 nitrogen (N) flows and stores in a terrestrial ecosystem, enclosing with alternative
- assumptions of N processes represent in SM1, SM2 and SM3, respectively. Light-blue arrows
- 602 indicate C-cycle processes and red arrows show N-cycle processes. Met./Str. Litter,
- 603 metabolic and/or structural litters; SOM, soil organic matter. * set N fixation as an option
- 604 when the plant N uptake is enough for growth in terms of C investment in SM1, but go 605 directly to soil minoral N pool in SM2 and SM2
- directly to soil mineral N pool in SM2 and SM3.
- Figure 3. Simulated nitrogen fluxes and soil mineral nitrogen from three carbon-nitrogen
 coupling schemes (SM1, SM2 and SM3) in TECO-CN model for 1996 to 2007 at Duke
 Forest.
- Figure 4. Simulated annual (a-f) and mean (g-l) carbon fluxes from carbon-only version and
 carbon-nitrogen coupled with three schemes (SM1, SM2 and SM3) of TECO model for 1996
 to 2007 at Duke Forest. GPP, gross primary productivity; NPP, net primary productivity;
 NEE, net ecosystem exchange of CO₂; R-eco, ecosystem respiration; R-heter, heterotrophic
 respiration; R-auto, autotrophic respiration.
- **Figure 5.** The annual average sizes of carbon pools (panel a) at the steady-state among 1996-
- 615 2007 for C-only version and the three C-N schemes (SM1, SM2 and SM3) and the C:N ratio
- 616 (panel b) of each carbon pools for the three C-N schemes (SM1, SM2 and SM3) in TECO-617 CN model
- 617 CN model.
- Figure 6. The nitrogen use efficiency (NUE, panel a) in three C-N schemes of TECO model
 (SM1, SM2 and SM3) and the carbon use efficiency (CUE, panel b) at the steady-state
- among C-only version and the three C-N schemes of TECO model (SM1, SM2 and SM3).
- **Figure 7.** Simulation of annual ecosystem carbon storage capacity for 1996 to 2006 at Duke
- Forest by carbon in flux (NPP, x axis) and ecosystem residence time (τ_E , y axis) in TECO
- model framework with three carbon-nitrogen coupling schemes (SM1, SM2 and SM3) and in
- $\label{eq:technological} \text{TECO C-only model (C). Inset (a), ecosystem carbon residence time (τ_E) in SM1, SM2, SM3}$
- and C-only model; inset (b), mean ecosystem carbon storage simulated among SM1, SM2,
- 626 SM3 and C-only model; inset (c), relative change of NPP and ecosystem residence time
- 627 simulated among three schemes compared with in C-only model.
- **Figure 8.** Determination of carbon-pool residence times based on traceability framework in
- TECO C-N model with three C-N coupling schemes (SM1, SM2 and SM3) and TECO C-
- only model (C). Panel (a), baseline residence time; panel (b), mean residence time, and panel
- 631 (c), nitrogen scalar.
- **Figure 9.** Coefficients of partitioning of NPP to nonstructural C (NSC), root, woody and leaf in C-only model (C) and C-N coupling model with three schemes (SM1, SM2 and SM3).

- **Figure 10.** The sensitivity of nitrogen processes to NPP (panel a), ecosystem residence time
- $(\tau_E, \text{ panel b})$, and ecosystem C storage capacity (panel c) among three carbon-nitrogen
- 636 coupling schemes (SM1, SM2 and SM3). DRP, down-regulation of photosynthesis; PS, plant
- tissue C:N ratio; PNU, plant N uptake; PMC: plant and microbe competition; BNF, biological
- 638 N fixation; RtrN, re-tranlocation N; SS, soil pool C:N ratio.

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Table1. Summary of the nitrogen-carbon coupling schemes used and the representation ofkey processes in the carbon-nitrogen cycle.

	SM1 (TECO-CN) ^a	SM2 (CLM4.5) ^{b,c}	SM3 (O-CN) ^{d,e}
Down-regulation of photosynthesis by N availability (DRP)	Based on the comparison between plant N demand and actual supply	Based on the available soil mineral N relative to the N demanded to allocate photosynthate to tissue	Based on foliage N concentration, which varies with N deficiency
Plant tissue stoichiometry (PS)	Flexible plant C:N ratio	Fixed plant C:N ratio	Flexible plant C:N ratio
Plant N uptake (PNU)	Based on fine root biomass, soil mineral N and N demand of plant. Plants itself choose the strategy between uptake from soil mineral N and fix N ₂ by comparing C investment	Based on N required to allocate NPP to tissue. Plants uptake N for free	Combining active and passive uptake of mineral N based on fine root C, soil mineral N, plant transpiration flux, increases with increased plant N demand
N competition between plants and microbes (PMC)	Microbes have first access to soil mineral N	Based on demand by both microbial immobilization and plant N uptake	Microbes have first access to soil mineral N, the competitive strength of plants increases under nutrient stress
Biological N fixation (BNF)	Based on the nitrogen demand of plants and maximum N fixing ratio considering nutrient concentration	f(NPP)	f(ET)
Deployment of re- translocated N (RtrN)	Fixed fraction of litter	Based on available N in the tissue and the previous year's annual sum of plant N demand	Fixed fraction of dying leaf and root tissue
Soil organic matter stoichiometry (SS)	Flexible soil C:N ratio	Fixed soil C:N ratio	Flexible soil C:N ratio
N leaching	Function of soil mineral N pool and runoff	Function of soil mineral N pool and runoff	Function of soil mineral N and runoff

^aSee this study; ^bKoven et al. (2013), ^cOleson et al. (2013); ^d Zaehle &Friend (2010), ^eZaehle
et al. (2011).

850 C, carbon; N, nitrogen; NPP, net primary productivity; ET, evapotranspiration.



Figure 1. Schematic diagram of the terrestrial ecosystem carbon (C) and nitrogen (N)

coupling model (TECO-CN). (A) Canopy module, (B) Plant growth module, (C) Soil water

dynamics module, (D) Soil carbon-nitrogen coupling module. Rectangles represent the

 R_a , autotrophic respiration. R_h , heterotrophic respiration. Retr., re-

translocation. NSC, nonstructural carbohydrate. MNP, mineral N in plant tissues. SOM, soil
organic matter. * set N fixation as an option when the plant N uptake is enough for growth in

860 terms of C investment.



Figure 2. Schematic diagram illustrating the major carbon (C) and nitrogen (N) flows and
stores in a terrestrial ecosystem, enclosing with alternative assumptions of N processes
represent in SM1, SM2 and SM3, respectively. Light-blue arrows indicate C-cycle processes
and red arrows show N-cycle processes. Met./Str. Litter, metabolic and/or structural litters;
SOM, soil organic matter. * set N fixation as an option when the plant N uptake is enough for
growth in terms of C investment in SM1, but go directly to soil mineral N pool in SM2 and
SM3.



Figure 3. Simulated nitrogen fluxes and soil mineral nitrogen from three carbon-nitrogen
coupling schemes (SM1, SM2 and SM3) in TECO-CN model for 1996 to 2007 at Duke
Forest.



Figure 4. Simulated annual (a-f) and mean (g-l) carbon fluxes from carbon-only version and
carbon-nitrogen coupled with three schemes (SM1, SM2 and SM3) of TECO model for 1996
to 2007 at Duke Forest. GPP, gross primary productivity; NPP, net primary productivity;
NEE, net ecosystem exchange of CO₂; R-eco, ecosystem respiration; R-heter, heterotrophic
respiration; R-auto, autotrophic respiration.



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Figure 5. The annual average sizes of carbon pools (panel a) at the steady state among 1996-

- 889 2007 for C-only version and the three C-N schemes (SM1, SM2 and SM3) and the C:N ratio
- (panel b) of each carbon pools for the three C-N schemes (SM1, SM2 and SM3) in TECO-CN model.



Figure 6. The nitrogen use efficiency (NUE, the ratio of NPP:PNU, panel a) in three C-N
schemes of TECO model (SM1, SM2 and SM3) and the carbon use efficiency (CUE, the
ratio of NPP:GPP, panel b) at the steady-state among C-only version and the three C-N
schemes of TECO model (SM1, SM2 and SM3).

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Figure 7. Simulation of annual ecosystem carbon storage capacity for 1996 to 2006 at Duke 902 Forest by carbon in flux (NPP, x axis) and ecosystem residence time (τ_E , y axis) in TECO 903 model framework with three carbon-nitrogen coupling schemes (SM1, SM2 and SM3) and in 904 TECO C-only model (C). The hyperbolic curves represent constant values (shown across the 905 906 curves) of ecosystem carbon storage capacity. Inset (a), ecosystem carbon residence time (τ_E) in SM1, SM2, SM3 and C-only model; inset (b), mean ecosystem carbon storage simulated 907 among SM1, SM2, SM3 and C-only model; inset (c), relative change of NPP and ecosystem 908 residence time simulated among three schemes compared with in C-only model. 909





Figure 8. Determination of carbon-pool residence times based on traceability analysis 913

framework in TECO C-N model with three C-N coupling schemes (SM1, SM2 and SM3) and 914 TECO C-only model (C). Panel (a), baseline residence time; panel (b), mean residence time,

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and panel (c), nitrogen scalar. 916



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920 Figure 9. Coefficients of partitioning of NPP to nonstructural C (NSC), root, woody and leaf

921 in C-only model (C) and C-N coupling model with three schemes (SM1, SM2 and SM3).

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926 Figure 10. The sensitivity of nitrogen processes to NPP (panel a), ecosystem residence time

927 (τ_E , panel b), and ecosystem C storage capacity (panel c) among three carbon-nitrogen

928 coupling schemes (SM1, SM2 and SM3). DRP, down-regulation of photosynthesis; PS, plant

929 tissue C:N ratio; PNU, plant N uptake; PMC: plant and microbe competition; BNF, biological

930 N fixation; RtrN, re-tranlocation N; SS, soil pool C:N ratio.

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