Tomomichi Kato
University of Tsukuba, Tsukuba, Ibaraki, Japan
Handling Topical Editor, Geoscientific Model Development (GMD)

Re: GMD-2018-41

Dear Dr. Kato,

Thanks so much for sending us two referees' comments and suggestions on our manuscript "Carbon-nitrogen coupling under three schemes of model representation: Traceability analysis" (GMD-2018-41). We greatly appreciate the two reviewers for their valuable comments and suggested amendments. Their inputs have helped improve the paper tremendously. We have carefully studied the comments from the reviews and made revisions based on them in this version of manuscript.

In the revised manuscript, we have addressed all the comments from the two referees. Specifically, we added the Figure 5 for annual averaged size and C:N ratio of each C pool and the Figure 6b for the CUE in the C-only version and the three C-N schemes of TECO model. We also have added a new figure (Figure S2) in the supplemental information to show the annual averaged N content for each C pool among the three C-N schemes. In the Materials and Methods and Results sections, we also have shown the different effects of C-N coupling hypotheses among three simulations as suggested by both referees. We clarified our discussions based on more referenced results as suggested by the referee #1 and discussed the differences with the original models (CLM4.5bgc and O-CN) as suggested by referee #2. We greatly appreciate the suggestions from the reviewers, as addressing them has strengthened the manuscript.

We confirm that all authors have met the authorship criteria.

We also declare that the submitted work is our own and that copyright has not been breached in seeking its publication.

Here are our detailed responses to the reviews. Please note that the comments from the referees are in ***italics*** followed by our responses in **regular** text.

We hope you will find our revision satisfactory for publication in ***Geoscientific Model Development***.

Yours Sincerely,

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Response letter to comments (gmd-2018-41)

Will Wieder's comment (Referee #1)

General comments

Du and co-authors present a very interesting study using a matrix approach to compare the implementation of three distinct representations of C-N biogeochemistry in the TECO land model. The mathematical approach seems very powerful and the results are compelling.

[**Response**] Thanks so much for your positive comment.

I'd encourage the authors to unpack their results more to make findings more accessible to readers not familiar with any of the N schemes presented here. Refocusing the text around big differences in assumptions being made between each modeling approach and how that translates to the different C stocks and fluxes would be very helpful.

[**Response**] Thanks very much for your suggestions. In this revised version, we added more results (e.g., C pool sizes and C:N ratio in Figure 5, CUE in Figure 6b, the sensitivity of N processes to ecosystem C storage capacity in Figure 10c, and N pool sizes in Figure S2) to support our findings. Based on our results, we displayed the different N and C fluxes under different C-N schemes (Figures 3 and 4) and the different C and N status among plant tissues, litter and soil pools (Figures 5 and 6) as well as the ecosystem C storage capacity (Figure 7). To evaluate the alternative representations of C-N processes dominating the ecosystem C storage capacity, we applied the traceability analysis framework to trace the key factors in different schemes. We found that different process assumptions caused divergent C residence time and plant production among different C-N schemes in this study (Figures 8-10). We added the detailed information and discussion in both Result and Discussion sections in Lines 372-381, 386-389, 425-428 and 498-501.

The discussion only sparing refers to the display items presented in the results, making me wonder if the ideas being discussed are just the authors' opinions or if they can clearly be demonstrated by results presented here. On revision, please reference display items to support claims being made in the discussion.

[**Response**] Sorry for the confusion. We carefully revised the whole manuscript and also referenced more necessary results in the Discussion section accordingly. As a consequence, our manuscript has been considerably improved. We hope you will find our revision satisfactory.

Finally, there are enough grammatical errors to be distracting in the text. Some of these a highlighted in technical corrections, below, but revisions to the manuscript should be made for language fluency.

[**Response**] We carefully revised the manuscript according to the comments, paid attention to the grammar, and made necessary changes. We also asked a native English speaker (Mrs. Megan C. Foster) to revise the whole manuscript. Please see below for the detailed responses point by point. As a consequence, our manuscript has been considerably improved. We hope you will find our revision satisfactory.

Specific comments

Line 60: For a paper that's more generally about the implementation and assumptions of C-N coupling in land models it strikes me as odd to lead off the introduction with an immediate nod to nitrogen fixation. Fixation is important, but leading off with a brief discussion sets up unrealistic expectations for the reader for what's ultimately being discussed in the paper.

[**Response**] Thanks for your comments and suggestions. We deleted the description of nitrogen fixation and have rephrased this paragraph carefully, especially emphasizing the processes of carbon-nitrogen coupling in affecting the terrestrial ecosystem C storage.

Line 84: References are needed to support these claims, as it seems to conflate C cycle uncertainty (e.g. Arora et al. 2013) with C-N representation in models, which is not accurate.

Line 86: Similarly, references are needed as the 'contradictory results' from implementation of C-N models have not been clearly established in the literature.

[**Response**] We revised the descriptions of the related references (Arora et al., 2013; Zaehle et al., 2015; Sokolov et al., 2008; Wania et al., 2012; Walker et al., 2015) and added them in our revised manuscript in Lines 85 and 89.

Line 97: I may be forgetting something, but don't recall the Xia et al (2013) paper accomplishing all that it's being credited for here. Maybe other references are needed where the authors demonstrate how the matrix approach has been used for 'benchmark analyses, model intercomparisons, and data model fusion, and improved model predictive power'? Otherwise revise this sentence to avoid implying a single paper did all this work.

[**Response**] Thanks for your comments and suggestions. We added some references and modified the sentence as "The traceability analysis has been developed to diagnose the simulation results within (Xia et al. 2013; Ahlström et al., 2015) and among (Rafique et al., 2016; Zhou et al., 20) models.".

Figs 1 & 2. How is mineral N retranslocated from the litter pool? After a leaf has fallen do plants still have access to this N? Doesn't retranslocation occur before senescence?

[**Response**] Sorry for the mistake. The mineral N was retranslocated to other tissues before the live tissues (i.e., leaves, fine roots and live stems) senescence in TECO model. We simply added an arrow to plant growth module to represent the retranslocation of the mineral N to other tissues in the Figs. 1 and 2. We described it in Lines 158.

Fig 2. I really appreciate the effort to clearly spell out different assumptions between different C-N coupling schemes and map onto the structure of TECO's C and N pools. I fear this figure is too jumbled with small, tilted text to be useful, and would encourage authors to spend some time cleaning up this display item so it's more clear & useful.

[Response] Thanks so much for your suggestions. We deleted all the numbers and rearranged the text in the figure to clarify the display.

From the description in the methods, it seems like the entire coupling of C-N biogeochemistry occurs through the different implementation of the N scalar from each scheme (Eq. 30). Is this true? If so, documenting how the aspects summarized in Table 1 are actually being implemented seems important (either in the main text, SI, or an appendix). If this is where the magic happens it should be clearly spelled out using language from the N related (red) text in Fig 1.

[**Response**] Sorry for the confusion. The N scalar is set as the respiration and decomposition rate modifier, which considers the changes of N content to compare with the initial condition (Eq. 33). Depending on both the N supply and loss for each C pool, the N scalar mainly affects the C residence time directly (Fig 7). The different aspects among three C-N coupling schemes introduce different effects on N supply and losses directly and/or indirectly, and thus affect the C residence time via N scalar. Beside the N scalar, the different representations summarized in Table 1 also introduce other aspects to affect the C storage. For example, the different implementations of the N down regulation have differently constrained power on GPP (although those powers were not significant in this study); the different assumptions on tissue C:N ratio led to different C allocation ratio (eq.1-6) and further affect the baseline residence time (eq.30); the different representations of plant N uptake and biological N fixation result in different C investment, and thus the different autotrophic respiration. In this revised version, we added those description and discussion in both Method and Discussion sections in Lines 319, 406-409, and 529-536.

In previous work this author group has demonstrated that the matrix approach gives identical results to the conventional system of differential equations. Can a similar plot be made with a CN version of TECO? That is, can lumping a coupled C:N model into a "N scalar" (eq. 33) account for everything that's going on in the model? I'm assuming it can, but this is never clearly demonstrated in the results.

[**Response**] That version of TECO-CN had incorporated the "N scalar" into the respiration and decomposition rate modifier (Du et al. 2017), which had been used in the previous work (e.g., Zaehle et al., 2014). In this study, N scalar is a key factor, and we separated it from the environmental scalar (ξ_E) and baseline carbon residence time ($\tau_E^{'}$) in the traceability analysis framework to trace the different effects that were introduced by the three C-N schemes. We also compared our TECO-CN version with the version used in Zaehle et al., 2014. We found that the results matched well (See Figure R1 below).

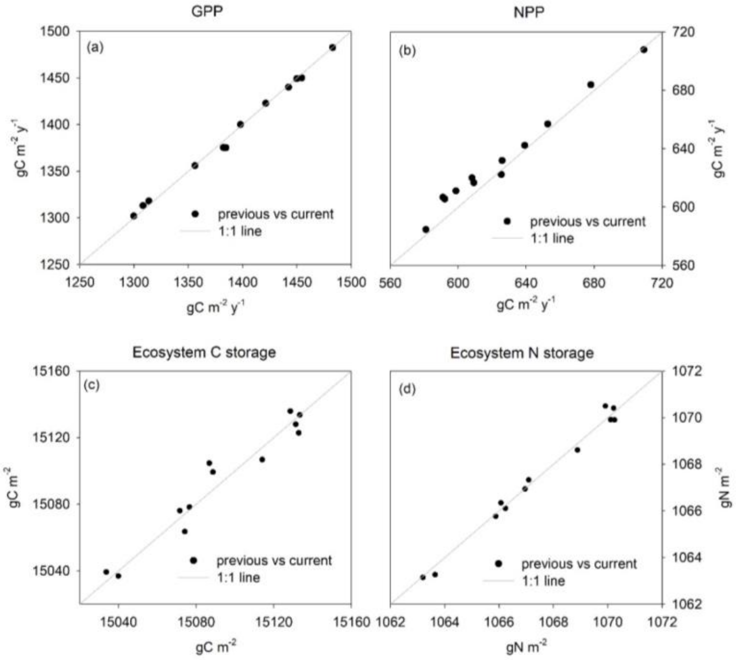

Figure R1. Comparisons of GPP, NPP, ecosystem C storage and ecosystem N storage at the steady state from this study vs. the TECO-CN version used previous work.

Besides difference in NUE (Fig. 5) I'm struck by the differences in carbon use efficiency (CUE, the ratio of NPP:GPP) among N models that's attributable to large difference in autotrophic respiration among models. Is this worth displaying or discussing further?

[**Response**] Thanks for your suggestions. Yes, we found that carbon use efficiency (CUE) varied among three N schemes. The SM2 has the highest CUE while SM3 has the lowest CUE among three C-N schemes. We added this result in Fig 5b. The direct factors of those differences mainly attribute to difference in autotrophic respiration and N limitation on production (i.e., down-regulation effect). For the SM2, plant uptake N does not need to cost C, which lead to the highest CUE. In the SM3, however, the lowest CUE is due to both the C cost of plant actively uptake N and the assumption that increases respiration to remove the excess C. In this revised version, we added those Results and Discussion sections in Lines 386-389 and 498-501.

Why did SM1 increase the mean residence time of C relative to the control model (Figs 6 inset & 7). I'm assuming it's because of N 'limitation' of passive C turnover? Does this seem realistic? It must be caused by relatively quick turnover of this pool and an low C:N ratio of SOM in SM1, or low respiration coefficient in fluxes between slow and passive pools that are driving a high immobilization flux in SM1 (Fig. 3)? Alternatively, does the stoichiometry of litter quality drive these results? More details on these mechanisms seem worth discussing?

[**Response**] Thanks so much for your comments and suggestions. Yes, the slower turnover rate of passive SOM pool dominated a longer mean ecosystem residence time in SM1 compared with those in C-only version. Our results showed that lower heterotrophic respiration rate (Figure 4) and C:N ratio of passive SOM (Figure 5b) as well as higher immobilization flux (Figure 3) jointly 'limited' the turnover rate of passive SOM pool. For the SM1, the microbe immobilization dominates a low C:N ratio and then affects the decomposition cascade for passive SOM (Fig 8). The reason is that the representation of N immobilization in TECO-CN has the potential to accumulate N:

$$Imm_N = \begin{cases} \sum_{i=4}^{8} min\left(\left(\frac{C_i}{CN0_i} - \frac{C_i}{CN_i}\right), 0.1 * SN_{min}\right) \; for\ CN_i \geq CN0_i \\ \sum_{i=4}^{8} min\left(\left(\frac{C_i}{CN_i} - \frac{C_i}{CN0_i}\right), 0.1 * SN_{min}\right) \; for\ CN_i < CN0_i \end{cases}$$

We added this equation and more information in Method and Discussion sections.

Figures 7 and 9 seem like really interesting, powerful strengths of the tractability analysis presented here. In my estimation there's not nearly enough text in the results or discussion to walk readers through what's being shown here. Unpacking the information communicated in these figures would help readers access what's being shown and how the tractability analysis helps us understand differences among model formulations. (Note, some of this could even fall into the introduction and methods by foreshadowing key differences among model formulations that are important to the results presented here from the start).

[**Response**] Thanks for your comments and suggestions. In the revised version, we reorganized the information communicated in these figures carefully, mainly tracing how the different hypotheses among C-N coupling schemes modulate the ecosystem C storage based on traceability analysis. We hope that you satisfy our revision.

Line 508: If this is the most striking difference, is there a take home figure that clearly communicated this message? As presented, I'm not sure this conclusion is well supported by the results or discussion.

[**Response**] Sorry for the confusion. Originally, we used the sensitivity of N processes to NPP and ecosystem residence time (τ_E) among three C-N coupling schemes to display this difference, which was shown in the previous Fig. 9. In the revised version, we extended this sensitivity to ecosystem C storage (NPP × τ_E) in Fig. 10 based on the different representations among three C-N schemes. We emphasized the difference and added more discussion in Lines 425-428 and 501-505.

Technical corrections

Line 37: For clarity, replace 'them' with 'the three C-N coupling schemes'

Line 43: Consider replacing 'divergent' with 'differences in'?

Line 58 & 64: Avoid starting a sentence with an abbreviation, that is write out 'Nitrogen'.

Line 59: 'Requires' should be plural

Line 66, I'd add Hungate et al. (2003) to this list of references

[**Response**] Done as suggested.

Line 71: It seems odd to talk about progressive N limitation as occurring with "growth enhancement when N mineralization increases". Is Dr. Luo comfortable with this definition?

[**Response**] Sorry for the confusion. We revised the sentence as "Early C-N coupled models demonstrated that the N availability limits ecosystem C storage capacity with associated effects on plant photosynthesis and growth in many terrestrial ecosystems…"

Line 72: Awkward. Please revise for fluency & clarity.

[**Response**] Sorry for the confusion. We revised this sentence as "Recent studies have largely confirmed these results by improving C-N coupling models with multiple hypotheses."

Line 80: These are from Cleveland et al (1999), not my work, and their implementation in models is summarized nicely by Meyerholt et al. (2016).

[**Response**] Thanks for pointing out our mistake. We added these two references and replaced the "Wieder et al., 2015" to "Wieder et al., 2015a".

Line 129: Should this be 'data', not 'date'?

[**Response**] Sorry for the mistake. We replaced "date" by "data".

Also from what plots, the meteorological *paragraph starts off discussing the AmeriFlux tower, but are the biomass data from the control FACE plots?*

[**Response**] Sorry for the confusion. The forcing data used in this study were taken from the AmeriFlux database, while the biomass data were taken from the reference study. To clarify this point, we revised the first sentence of this paragraph as “The forcing data used in this study were taken from the Duke free-air CO_2 enrichment (FACE) experiment….”.

Line 138, 180: I’m a little confused. Is this the first publication of TECO-CN2.0, if so they should be referenced? If not, are there other versions of TECO-CN and how does the implementation of C-N biogeochemistry differ in the present model?

[**Response**] Sorry for the confusion. There are two versions of TECO-CN model. The first version was used in Zaehel et al., 2014 and this study, and the second version is a simplified version used for data assimilation (e.g., models in Shi et al., 2015 and Du et al., 2017). Both versions are the variant of the TECO-C version published in Weng and Luo, 2008. To make it clear in this study, we replaced “TECO-CN” with “TECO-CN2.0” accordingly.

Table 1: References to Thorton et al are actually for CLM4cn (not CLM4.5bgc, as implied in the table). The implementation of C-N biogeochemistry is similar in each model, but the structure and stoichiometry of SOM pools are different in each? Please clarify in the text and references which version of the model is used for SM2.

[**Response**] The version of CLM4.5bgc is used for SM2 in this study. We changed the references as “Koven et al., 2013” and “Oleson et al., 2013”.

Fig. 1. It seems odd to have N fixation going directly to soil mineral N pools. I realize that CLM (and likely other models) do this, but the simplification should at least be noted in the text?

[**Response**] Thanks for your comments. We added a new dotted arrows from N fixation to plant part in Figure1 and the description “*set N fixation as an option when the plant N uptake is enough for growth in terms of C investment” in the legend of Figure1.

Fig.1 Why doesn’t the soil C-N module need to take up mineral N? This seems to contradict Fig. 2, and could be corrected with two-sided arrows?

[**Response**] Thanks for pointing out our mistake. As suggested, we replaced those one-sided arrows with two-sided arrows in Figure 1.

Throughout section 2.2.2 should units for fluxes be communicated?

[**Response**] Thanks for pointing out what we have neglected. The units were added in the revised version.

Eq. 19. This would give a fixation flux in gN/m2/s, but TECO doesn’t work on that time step?

[**Response**] Yes, the unit of biological N fixation flux is g N m^{-2} s^{-1}. We added it in the revised version.

Line 321. What are all these abbreviations? Regardless, there's too many here to be coherent, and I'd encourage these to be written out fully throughout the text.

[**Response**] Thanks for your comments and suggestions. We deleted "i.e., DRP, PS, PUN, PMC, BNF, RtrN and SS" in this section.

Line 349. These differences are relative to the C only control? If so restating this here may help clarify?

[**Response**] Yes, these differences are relative to the results of TECO-C. In the revised version, we added "by comparison with the TECO-C version" in this sentence.

Line 351 this sentence is awkward and needs to be revised?

[**Response**] Sorry for the confusion. In the revised version, we deleted this sentence "The NPP and plant N uptake (PNU) jointly determine the N use efficiency (NUE)."

Line 396: this list of abbreviations is neither intuitive, commonly used, nor helpful. I find the later use of the abbreviations confusing and recommend just writing out the processes being discussed in full.

[**Response**] Sorry for the confusion. As suggested, we wrote out these processes in full and deleted these abbreviations in this section.

Line 420: doesn't SM2 use NPP to calculate BNF rates?

[**Response**] Thanks for pointing out our mistake. Yes, SM2 used NPP not ET to calculate BNF rate in this study. We revised the sentence as "… SM2 and SM3 simulated BNF explicitly, which used the modified empirical relationships of BNF with NPP and evapotranspiration (ET), respectively.".

Lines 445-450: Where are these results shown in the work presented here?

[**Response**] Thanks for pointing out what we have neglected. After we added a new figure (Figure 5) about C pools and their C:N ration for different treatments, these results are mainly shown in Figure 3 and Figure 5. We revised those sentences as "N stress increased tissue C:N ratio (Figure 5b), leading to a high microbial N immobilization (Figure 3) and then a lower net N mineralization (Fig 3a, g and m), which allowed plant cell construction with a lower N requirement. The inclusion of flexible C:N stoichiometry appeared to be an important feature allowing models to capture the ecosystem response to climate variability through adjusting the C:N ratio of nonphotosynthetic tissues or the whole-plant allocation among tissues (Figure 9) with different C:N ratios…".

Line 463: where are these oscillations shown in the work presented?

[**Response**] We added the related results in this sentence as "Therefore, the different impacts of ecosystem N status induce oscillating N limitation on MRT (Figure 8) due to the inherently different assumptions of C-N interactions among three C-N coupling schemes".

Line 473: This line really makes me wonder if the approach outlined here is 'right'? Regardless, it makes me think that differences among models are 100% attributable to differences in stoichiometric assumptions among models. If so, should a list of pools and their C:N ratio SM1, 2, and 3 be communicated?

[**Response**] Thanks for your comments. We added a new figure in the revised version (Figure 5). Please see below for details.

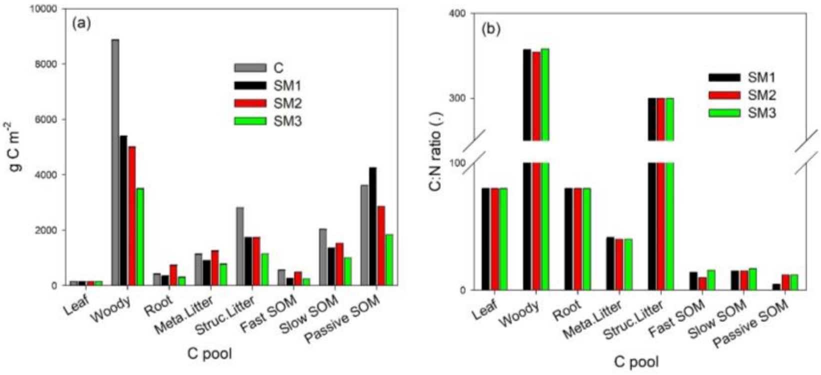

Figure 5. The annual average sizes of carbon pools (panel a) at the steady-state among 1996-2007 for C-only version and the three C-N schemes (SM1, SM2 and SM3) and the C:N ratio (panel b) of each carbon pools for the three C-N schemes (SM1, SM2 and SM3) in TECO-CN model.

Line 483: Ah, so win SM1, is there a progressive decline in litter quality that ends driving high soil N demand as the decomposition cascade tries to meet stoichiometric demand, whereas SM3 allow this extra C to be blown off through heterotrophic respiration? Alternatively, is it higher autotrophic respiration in SM3 (through increased fine root C allocation) that allows the extra C to be blown off (line 501) Sorry, I'm not familiar enough with all of these approaches to understand what each model is doing.

[**Response**] Sorry for the confusion. Yes. For the SM1, our results showed that plant nonphotosynthetic tissues (mainly wood) and litter quality impact the C:N ratio (Figure 5) and further affect their decomposition cascade for fast and slow SOM pools (Figure 6 and

Figure 8). However, this was not the case for the passive SOM pool, where microbe immobilization dominates a low C:N ratio and then affects the decomposition cascade (please see response above).

For the SM3, both the hypothesis of increasing respiration to remove the excess C accumulated under N stress and the higher C investment for the BNF led to decrease in C input and then limit the microbe immobilization for the passive SOM pool.

Line 488 what's being absorbed?

[**Response**] Sorry for the confusion. We removed the "absorption" and revised the sentence as "This mechanism promotes the respiration of the faster turnover pools (fast and slow SOM pools), leading to decrease in MRT in these two pools (Figure 8)"

Line 490: I'm still confused about what's causing differences between SM1 and SM3. For readers less familiar with these schemes can the difference between the approached be unpacked a bit more, as this seems like a powerful strength of the traceability analysis?

[**Response**] Sorry for the confusion. Based on the different hypotheses (list in Table 1) between SM1 and SM3, we found that SM1 mainly adjusted plant tissue and soil C:N ratio to reach equilibrium under N stress, while SM3 mainly cost the excess C via increasing respiration to get equilibrium under N stress. The two different strategies lead to different C allocation (Figure 9) and stoichiometric status (Figure 5), and then affect plant production (Figures 4 and 5), baseline residence time and ecosystem residence time (Figure 8) as well as ecosystem C storage (Figure 7). We added these results in the revised manuscript according to your suggestions.

Anonymous Referee #2

[General comments] In this paper, the authors evaluate three different schemes of Carbon-Nitrogen coupling in a terrestrial model, which can largely change both C and N dynamics reproduced by models. For this, they used an existent framework for analyzing the difference between the models. This paper is clearly written, and the results are informative for readers. I recognize the importance of this study because CN coupling is one of the emergent processes to be evaluated / constrained in such land ecosystem modeling.

[**Response**] Thank so much for your positive comment. No responses needed.

However, I think there are places to be improved: the figures are informative, but the explanation is not enough for readers. My comments will not require a lot of effort to improve.

[**Response**] Thanks so much for your comments and suggestions. We carefully revised the whole manuscript according to your comments and suggestions. We went through the text several times and made necessary changes. Please see below for the detailed responses.

[Detailed comments] P6, L129: "biomass production date" should be "biomass production rate"?

[**Response**] Thanks so much for pointing out our mistake. Here it is not "rate", either. It should be "data". We replaced "date" by "data" as suggested by referee #1.

P6, L129: What purpose the data "standing biomass and biomass production date" used for your study? Do you mean the datasets are used to determine the parameters associated with the processes? In addition, CN concentration for plant and soil (Finzi et al., and Lichter et al.) are also used for your analysis (I suppose the SM2 simulation need such data because of the fixed CN ratio, but it is not clear in the text). Please clarify them.

[**Response**] Sorry for the confusion. In this study, the data of both biomass and CN concentration are used to set initial values of C, N pool sizes and CN ratio for TECO-C and TECO-CN model. To make it clear, we added "To set the initial condition for the models, we collected the related datasets from previous studies." in the Lines 130-131.

P6, L138: It might be better to clearly mention first that the model is newly developed and used in this study for the first time.

[**Response**] Sorry for the confusion. There are two versions of TECO-CN model. The first version is used in Zaehel et al., 2014 and this study, and the second version is a simplified version used for data assimilation (e.g., Shi et al., 2015 and Du et al., 2017). Both versions are the variant of the TECO-C version published in Weng and Luo (2008). To make it clear in this study, we replaced "TECO-CN" with "TECO-CN 2.0" accordingly.

P7, eq(1)-(6): The detail description of C allocation scheme of TECO-CN v2 is shown here, but it seems the equations are not referred in other places. In my simple thinking, the detail descriptions with the equations are not necessary for your analysis, and it looks no problem if your put them into supplement. If you want to keep the eqs in the main body, it should be qualitative explanations how the C allocation scheme act on CN dynamics in simulations.

[**Response**] Thanks for your suggestions. Under the traceability analysis framework, the C allocation coefficients are used to calculate the baseline C residence time (Eq. 29). In this study, since both the matrix *A* and *C* are the same among different treatments (i.e., C-only, SM1, SM2 and SM3), the allocation coefficients (vector *B*) act as the key factor to determine the baseline C residence time. To clarify it, we added "The allocation coefficients act as the key factor to determine the baseline C residence time in this study" in the Lines 164-165.

P8, L177- : Although it is shown in the Table 1, it will be helpful for readers to mention here again the fact that CN ratio in SM2 scheme is fixed, while other two are flexible.

[**Response**] Thanks for your comments. We added “(i.e., fixed C:N ratio in SM2, flexible C:N ratio in SM1 and SM3)” in the Lines 188-189.

P12, L309: Which level of CO_2 concentration do you give to the model in the spin-up? Are the CO_2 concentration and climate forcing in simulations given as a cyclic manner? Please clarify them

[**Response**] We used the CO_2 concentration of 1996-2007 from 361.3 to 382.0 ppmv. Yes, we recycled the CO_2 concentration and climate forcing in simulations to the steady state (more than 1000 cycles for each simulation). To clarify it, we added “In this study, the meteorological forcings of 1996-2007 with the time step of half an hour were used to run the models to the steady state” in the Lines 328-329.

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- P13, L319: “SˆCRT” should be “SˆMRT”?

[**Response**] Thanks for pointing out our mistake. We corrected to “S_i^{MRT}” in this revised version.

- P15, L390: It looks less references to your figures and tables in the discussion section: It was a bit difficult for me to figure out which claims in the discussion section are supported by your own results.

[**Response**] Thanks for pointing out this issue. We added more references in the Discussion section. In addition, we added more figures (Figs 5b and 6) to show our results to support the Discussion section. Please also see the responses to the first comment above.

- P15, L405: You mention here that SM1 has a feedback from leaf N concentration to photosynthetic capacity, but eq.(7) seems not. I have overlooked something, but if the SM1 actually has leaf-N concentration feedback, you should touch it in the section 2.1.1.

[**Response**] Thanks for your comments. The plant N demand in the Eq.7 is calculated as:

$$N_{demand} = \frac{C_{leaf}}{CN_{leaf}} + \frac{C_{wood}}{CN_{wood}} + \frac{C_{root}}{CN_{root}}$$

C_{leaf}, C_{wood} and C_{root} are the current time step C pool sizes of plant tissues, CN_{leaf}, CN_{wood} and CN_{root} are the last time step C:N ratio of leaf, wood and root, respectively. To make it clear, we added this equation to Line 200.

P16, L426 “C cost of fixing”: Is the effect of C cost actually considered in your simulation of SM3? Which equation in the section 2.2.2 represents the effect? In addition, if you consider the C cost in the SM3 simulation, does the lowest NPP of SM3 attribute to the increase of autotrophic respiration in SM3? It would be nice if you can discuss on this.

[**Response**] Thanks for your comments and suggestions. Yes, we used the same C cost coefficient for N fixation (BNF) in SM1 and SM3. The different values of C investment for N fixation are due to the different strategies between SM1 and SM3, resulting in the different autotrophic respiration and NPP (Figure 3). For SM3, the calculation of BNF used the empirical relationship of BNF with evapotranspiration explicitly, while SM1 represents BNF as an option combining with the plant N uptake as the N source in terms of C investment (Table 1). In other word, plant actively selects the N source on the basis of investment. Our results showed that the strategy in SM1 lead to higher plant NUE than that in SM3 (Figure 5). We added those information in the Discussion section in Lines 472-474 and 494-496.

- P16, L427: I will appreciate if you can add more explanation why BNF of SM1 lead to the highest NUE. In my understanding, if BNF in SM1 works as the complement to nitrogen uptake, the process works to increase the uptake, and then the NUE(=NPP/PNU) should be decreased. I wonder the SM1 has a mechanism to have BNF that satisfy a minimum N requirement by plants, but it was not clear.

[**Response**] Sorry for the confusion. As our response above, SM1 represents BNF as an option combining with the plant N uptake as the N source in terms of C investment. Our results showed that this strategy lead to the highest NUE among three C-N schemes. In order to eliminate confusion, we revised the sentence as "On the other hand, SM1 applied a different strategy, which set BNF as an option when the plant N uptake is not enough in terms of C investment, leading to the highest plant NUE but the lowest response of BNF to NPP".

- P16, L428: Although same N loss process are shared between the schemes, I suppose the original models (TECO-CN/CLM/OCN) actually differ in that point. Readers can get benefit if you can discuss it briefly.

[**Response**] Thanks for your comments and suggestions. We added "In the original CLM4.5 and O-CN (Oleson et al., 2013; Zaehle et al., 2010), soil mineral N pool is divided into two pools (ammonium and nitrate). The leaching is only active on the nitrate pool, while the ammonium pool is assumed to be unaffected by leaching. This hypothesis may reduce the correlation between leaching and total soil mineral N." in the Lines 478-482.

- P17, L443: You discuss here how CN ratio in SM1 scheme affects the N regulation on plant production processes. As you discuss in the section 4.2, SM3 also has the mechanism of flexible CN ratio. How did the flexibility of SM3 act on plant production processes?

[**Response**] Thanks for pointing out what we have neglected. In this revised version, we added "However, this was not the case for the SM3 since both hypotheses of increasing respiration to remove the excess C under N stress and the higher C investment for the BNF lead to the decrease in C input and then limits the microbial immobilization for the passive SOM pool." in the Lines 498-501.

- P17, L445 "leading to a high microbial N immobilization": I cannot understand why high CN ratio in plant tissues bring models to have a high microbial N immobilization. Need further detail.

[**Response**] Most previous studies showed that litter quality (ie., C:N ratio) could affect the rate of microbial N immobilization (i.e., Zaehle et al., 2014; Thomas et al., 2015). When the fresh litter inputs soil part with higher C:N ratio than SOM, the microbial demand for mineral N increases to maintain the stoichiometry balance itself, which enhances the N immobilization potential. We revised the sentence as "N stress increased litter C:N ratio, leading to a high microbial N immobilization to keep their stoichiometry balance and then a lower net N mineralization…."

-P18, L475 "Fig. 6c" is likely to be "Fig. 7c"?

- P18, L498: Maybe "Fig. 7" is likely to be "Fig. 8".

[**Response**] Thanks for pointing out our mistakes. In this revised version, we added a new figure (i.e., Figure 5) and changed those figure numbers accordingly.

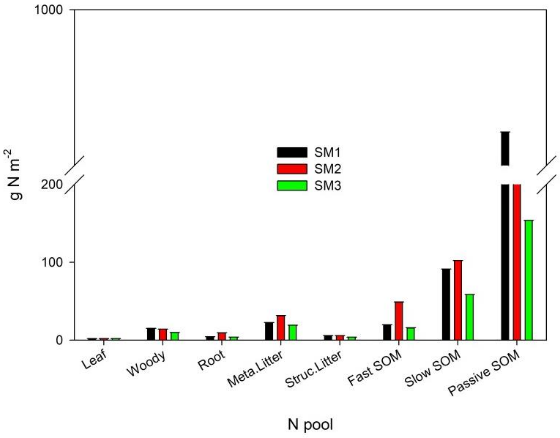
- P18, L484: What does "structural litter quality" mean?

[**Response**] Sorry for the confusion. In the TECO-CN model, based on different decomposability, the plant litter is divided into two parts: metabolic litter and structural litter. Based on our results, we deleted the "structural" in this sentence.

In the analysis, plant production and C/N status are evaluated in steady state. Although I recognize the usefulness of the analysis using steady states, I believe many readers get interested how your conclusions can be extended to non-steady state simulations, because N limitation on C cycle can be intensified in the condition where CO2 concentration increasing. I will be happy if I can see the discussion on this. In addition, displaying N status in the three simulations will be helpful for readers to get the whole picture of the CN dynamics: mineral N is displayed (in Fig.3), but others (plant, litter, and SOM) are not. Since your analysis is based on steady-state, such information can be a support to understand the relationship between N-fluxes and N-pools. My suggestion is to include it in supplement.

[**Response**] Thanks so much for your comments and suggestions. We agree that analysis of N limitation on C cycle on the non-steady state is really interesting and critical. However, it is difficult to simulate ecosystem C processes on the non-steady state. In this study, the traceability analysis method is only for the steady-state simulations. Our next step is to develop a transient traceability analysis for the non-steady state. In this revised version, we added some discussion to show this caveat for the non-steady state in the Lines 452-454 and 469-471.

In addition, we added a new figure (Figure 5, please see above) for the sizes of C pools and C:N ratios according to your and the fist referee's comments. We also added a single figure (please see below) for N pools in supplement. We hope you will find our revision satisfactory.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Struc.Litter
Fast SOM
Slow SOM
Passive SOM
N pool

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Carbon-nitrogen coupling under three schemes of model representation: a ~~Traceability~~ traceability analysis

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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 differs greatly among models, and how these diverse representations of C-N interactions will affect C-cycle modeling remains unclear. In this study, we explored how the simulated ecosystem C storage capacity in the terrestrial ecosystem (TECO) model varie~~s~~d with three different commonly-used schemes of C-N coupling. The three schemes (SM1, SM2, and SM3) have been used in three different coupled C-N models (i.e., TECO-CN~~ 2.0~~, CLM 4.5, and O-CN, respectively). They differ mainly in the stoichiometry of C and N in vegetation and soils, plant N uptake strategies, down-regulation of photosynthesis, and the pathways of N import~~, and the competition between plants and microbes for soil mineral N~~. We incorporated ~~them~~ the three C-N coupling schemes into the C-only version of TECO model, and evaluated their impacts on the C cycle with a traceability framework. Our results showed that all of the three C-N schemes ~~resulted in~~caused significant reductions in steady-state C storage capacity compared with the C-only version with ~~, but~~ the magnitudes of ~~varied with~~ -23%, -30% and -54% for SM1, SM2, SM3, respectively. These reduced C storage capacity ~~is~~ was ~~largely~~mainly derived from~~ due to~~ the combined effects~~ation~~ of decreases in net primary productivity (NPP~~) by~~, -29%, -15% and -45%) and~~ with~~ changes in~~of~~ mean C residence time (MRT~~) by~~, 9%, -17% and -17%) for SM1, SM2, and SM3, respectively. The ~~divergent~~ differences in NPP are mainly attributed to the different 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 ~~and~~vs. 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 assumptions on N processes represented~~ation~~ among different C-N coupled models could cause additional uncertainty to land surface models. Understanding their difference can help us ~~to~~ improve the capability of models to predict future biogeochemical cycles ~~on~~of terrestrial ecosystems~~ land~~.

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

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1. Introduction

The terrestrial ecosystem carbon (C) storage is jointly determined by ecosystem C input (i.e., net primary productivity, NPP) and mean residence time (MRT), which are strongly affected ~~modulated~~ by the terrestrial nitrogen (N) availability ~~of nitrogen (N) for plant and microbial growth~~ (Vitousek et al., 1991; Hungate et al., 2003; ~~Wieder et al., 2015;~~ Luo et al., 2017). Nitrogen is an essential component of enzymes, proteins, and secondary metabolites (van Oijen and Levy, 2004). Plant and microbial production require N to meet their stoichiometric demands, ~~influenc~~affecting the C balance and nutrient turnover of ecosystems ~~-~~(Cleveland et al., 2013; Wieder et al., 2015b). Since N limitation is widespread for plant growth in terrestrial ecosystems (LeBauer et al., 2008). ~~On one hand, increasing ecosystem C assimilation with atmospheric CO_2 increases the C:N ratios both in plant and soil, thus reduces the amount of additional N required (Rastetter et al., 1992). On the other hand, increasing soil C:N ratio leads to decomposing micoorganisms costing more nitrogen, further affecting nitrogen mineralization and reducing efficiency of C assimilation (Gill et al., 2002). Although there is abundant N in the atmosphere, it is difficultcost a lot of energy to make it available for biological systems (Houlton et al., 2008). As a consequence, the biological~~ N availability ~~, which strongly affects C storage in ecosystems,~~ is often highly correlated with key ~~metabolic~~ ecological ~~rate~~processes, ~~s~~ such as ~~photosynthesis~~ C assimilation (Field and Mooney, 1986; Du et al., 2017), ~~plant~~ allocation (Kuzyakov et al., 2013) ~~and~~, plant ~~and~~ respiration (Sprugel et al., 1996), and litter and soil organic matter (SOM) decomposition (Terrer et al., 2016). Nitrogen dynamics thus plays~~s~~ an important role in governing the ~~C balance and turnover of~~ terrestrial ecosystem C storage (García-Palacios et al., 2013; Shi et al., 2015).

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 incorporated into biogeochemical models. The representation of N cycling and their feedback to C cycling in models reflects what has been established in the ecosystem research community. Early C-N coupled models demonstrated that the N availability ~~limits~~ limited C storage capacity with associated ~~influences~~ effects on plant photosynthesis and growth ~~and can lead to growth enhancement when N mineralization increases~~ in many terrestrial ecosystems ~~(i.e., progressively increasing N limitation)~~ (Melillo et al., 1993; Luo et al., 2004). Recent studies have largely confirmed these results by improving C-N coupling models with multiple hypotheses ~~Evidences from more recently studies have largely confirmed these~~

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~~results and have generated multiple hypotheses for improving C-N coupling models~~ (Zhou et al., 2013; Zaehle et al., 2014; Thomas et al., 2015). These hypotheses~~ey~~ include the plant down-regulation 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 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 NPP-driven empirical functions to generate spatial estimates of biological N fixation (BNF) (Cleveland et al., 1999; Wieder et al., 2015a; Meyerholt et al., 2016), and respiration of excess C to obtain N from environment and/or to prevent the accumulation of C beyond the storage capacity (Zaehle et al., 2010). The~~se~~ knowledge ha~~ve~~s significantly helped improve our understanding of the terrestrial C-N coupling and ~~are~~is an important basis to develop comprehensive terrestrial process-based models (Thornton et al., 2007; Thomas et al., 2013). 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 al., 2013; Zaehle et al., 2015). The contradictory results were largely from different representations of fundamental N processes (e.g., the degree of flexibility of C:N ratio in vegetation and soils, plant N uptake strategies, pathways of N ~~export~~import, decomposition, and the representations of the competition between plants and microbes for mineral N) (Sokolov et al., 2008; Wania et al., 2012; Walker et al., 2015). Furthermore, the methodology used to derive the C-N coupling schemes among models varie~~s~~d largely, which might~~ay~~ be invalid for the model intercomparisons~~s~~ to provide insight into the underlying mechanism of N status for terrestrial C cycle projection.

In the past decades, terrestrial models integrated more and more processes to improve model performance (Koven et al., 2013; Todd-Brown et al., 2013; Wieder et al., 2014). ~~While~~ T~~t~~he more processes incorporated, the more difficult it becomes to understand or evaluate model behavior~~s~~ (Luo et al., 2015). The traceability analysis has been developed to diagnose the simulation results within (Xia et al. ~~(~~2013; Ahlström et al., 2015) and among (Rafique et al., 2016; Zhou et al., 2018) models~~developed a traceability analysis framework that helped improve the comparability of models and data, evaluated impacts of additional model components (Ahlström et al., 2015) (references??), facilitated benchmark analyses (Luo et al., 2012), model intercomparisons (Zhou et al., 2018), and data-model fusion (Hararuk et al., 2014), and improved model predictive power (Huang et al., 2018)~~. Based on the traceability analysis framework, key traceable elements, including fundamental properties of the terrestrial C cycle and their representations in shared structures among existing models, can be identified and characterized under different sources of variation (e.g., external forcing and uncertainty in processes) compared to the achieved predictive ability. The traceability analysis ~~framework~~ enables diagnosis of where models are clearly lacking predictive ability and evaluation of the relative benefit when more or alternative components are added to the models (Luo et al., 2015).

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Th~~e present~~is study is designed to examine the effects of C-N coupling under different schemes of model representation on ecosystem C storage in the Terrestrial Ecosystem (TECO) model with the traceability analysis framework. Three schemes of model representation were conducted mainly based on TECO-CN~~ 2.0~~ (SM1), CLM 4.5 (SM2), and O-CN (SM3, Table 1). The three C-N schemes differ in degrees of flexibility of C:N ratio in vegetation and soils, plant N uptake strategies, pathways of N import, and the representations of the competition between plants and microbes for soil available N. Based on the forcing data of ambient CO_2 concentration, N deposition, and meteorological data (i.e., air temperature, soil temperature, relative humidity, vapour pressure deficit, precipitation, wind speed, photosynthetically active radiation) obtained from Duke Forest during the period of 1996-2007, we conduct three alternative C-N coupling schemes (i.e., SM1, SM2 and SM3) as well as C-only in TECO model framework to compare their effects on the ecosystem C storage capacity~~ using traceability analysis framework~~. The 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.

2. Materials and methods

2.1 Data sources

The~~ forcing~~ datasets used in this study were taken from the ~~AmeriFlux site at~~ Duke free-air CO_2 enrichment (FACE)~~Forest~~ experiment, located in the Blackwood Division, North Carolina, USA (35.97° N, 79.08° W). The flux tower lies on a 15-year-old loblolly pine (*Pinus taeda L.*) plantation. The meteorological forcing data were downloaded from the AmeriFlux database at http://ameriflux.lbl.gov, including ambient CO_2 concentration ($[CO_2]$), 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 for the models, we collected the related datasets from the previous studies. Standing biomass and biomass production data~~date~~ at each plot for plant compartments (i.e., foliage, fine root and woody biomass, including branches and coarse roots) were taken from McCarthy et al. (2010). The C and N concentration data for each plant compartment based on Finzi et al. (2007) were used to estimate C and N stocks and fluxes. Plant N demand and uptake were calculated from these data ~~following~~ measured by Finzi et al. (2007). The C and N concentrations of litter and SOM were obtained from Lichter et al. (2008).

2.2 Model description and C-N schemes

2.2.1 TECO-CN ~~2.0~~

The terrestrial ecosystem C-N coupling model (TECO-CN~~, version 2.0~~) used in the present study is a variant of the TECO-Carbon-only version (TECO-C) by incorporating additional key N processes (~~Figure~~Fig. 1). TECO-C model is a process-based ecosystem model designed to examine critical processes regulating interactive responses of plants and ecosystems to climate change. It has four major components: canopy photosynthesis module, plant growth module, soil water dynamic module, and soil C dynamic module. The canopy photosynthesis and soil water dynamic modules run at hourly time step while the plant growth and soil C dynamic modules run at the daily time step. The detailed description of the TECO-C model can be found in Weng and Luo (2008).

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 structure to the TECO-C model (~~Figure~~Fig. 1). There are nine organic N pools and one inorganic soil N pool, including plant, litter and soil N pools. The plant N pools include leaves, wood, roots, and mineral N in plant tissues. The litter and soil N pools include metabolic and structural litter N, fast, slow, and passive soil organic N (SON), and soil mineral N pools. The total plant N demand on each time step is calculated following the NPP allocation to new tissue growth based on their C:N ratios. To meet the demand, the plant N supply is calculated 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 fixation. The N absorbed by roots enters into the mineral N pool in plant tissues, and then is allocated to the remaining plant pools with plant growth. The N in leaves and fine roots is reabsorbed before senescence. Plant litters will enter metabolic or structural pools depending on their C:N ratios.

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

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

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

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

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:

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

$$c_2 = 0.5 * 250e^3 * SLA * 0.00021 * h^2 \qquad (5)$$

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 the leaf pool at 0 and current time step, respectively; SLA is specific leaf area; h is plant height, which is calculated as:

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

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

2.2.2 C-N coupling schemes

We conducted four experiments including three simulations with their representations of C-N coupling schemes (SM1, SM2 and SM3) and an additional C-only simulation in TECO model framework. The three C-N interaction simulations include one original scheme in TECO-CN~~2.0~~ model and the other two schemes representing CLM4.5-BGC and O-CN. The three C-N 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 C:N ratio in SM1 and SM3), plant N uptake strategies, pathways of N import to the plant reserves, and the competition between plants, and microbes for soil mineral N (Table1, ~~Figure~~Fig. 2).

SM1 (TECO-CN~~2.0~~)

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

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

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

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

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

The re-translocated N is calculated as:

$$N_{retrans} = \sum_{i=leaf,wood,root} r_i \times outC_i / CN_i$$ (~~8~~9)

where r_i is the N resorption coefficient, CN_i is the C:N ratio~~n~~ and $outC_i$ (g C m^{-2} s^{-1}) is the value of C leaving plant pool i ~~in~~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)

$$N_{uptake} = min(\max(0, N_{demand} - N_{retrans}), f_{U,\max} \times SN_{\mathrm{mine}} \times \frac{Root_{\mathrm{total}}}{Root_{\mathrm{total}} + Root_0})$$ (~~9~~10)

where N_{demand} is the N demand of plants; SN_{mine} (g N m^{-2}) is the soil mineral N ~~(gN m^{-2})~~; $f_{U,\max}$ is the 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 ~~(g C m^{-2})~~ at which the N-uptake rate is half of the parameter $f_{U,\max}$.

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

$$N_{BNF} = \min(\max(0, N_{demand} - N_{retrans} - N_{uptake}), n_{fix} \times f_{nsc} \times NSC)$$ (~~10~~11)

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

$$f_{nsc} = \begin{cases} 0, & NSC < NSC_{min} \\ \frac{NSC - NSC_{min}}{NSC_{max} - NSC_{min}}, & NSC_{min} < NSC < NSC_{max} \\ 1, & NSC > NSC_{max} \end{cases}$$ (~~11~~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.

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

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$$Imm_N = \begin{cases} \sum_{i=4}^{8} min\left(\left(\frac{C_i}{CN0_i} - \frac{C_i}{CN_i}\right), 0.1 * SN_{min}\right) \; for\ CN_i \geq CN0_i \\ \sum_{i=4}^{8} min\left(\left(\frac{C_i}{CN_i} - \frac{C_i}{CN0_i}\right), 0.1 * SN_{min}\right) \; for\ CN_i < CN0_i \end{cases} \qquad (13)$$

~~Two pathways of~~

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}). ~~They b~~Both are proportional to the availability of soil mineral N (SN_{min}, g N m^{-2}). The equations are:

$$N_{gas\_loss} = f_{ngas} \times e^{\frac{T_{soil}-25}{10}} \times SN_{min} \qquad (\cancel{12}14)$$

$$N_{leach} = f_{nleach} \times \frac{V_{runoff}}{h_{depth}} \times SN_{min} \qquad (\cancel{13}15)$$

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

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SM2 (CLM4.5bgc)

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

$$f_{dreg} = \frac{CF_{allo} - CF_{avail\_alloc}}{CF_{GPP_{pot}}} \qquad (\cancel{14}16)$$

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 (GPP) when there is no N limitation.

The re-translocated N (g N m^{-2} s^{-1}) is calculated as:

$$N_{retrans} = \min(N_{demand} \times \frac{N_{retrans_{ann}}}{N_{demand_{ann}}}, N_{retrans\_avail}) \qquad (\cancel{15}17)$$

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.

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

$$N_{uptake} = (N_{demand} - N_{retrans}) \times f_{plant\_demand} \qquad (\cancel{16}18)$$

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:

$$f_{plant\_demand} = f_{immob\_demand} = \frac{SN_{min}}{N_{plant\_demand}+N_{immob\_demand}}$$ (~~17~~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).

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

$$N_{BNF} = 1.8(1 - e^{-0.03 \times NPP_{py}}) \Big/ (86400 \times 365)$$ (~~19~~20)

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

SM3 (O-CN)

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

$$f_{dreg} = a + b \times N_{leaf/LAI}$$ (~~20~~21)

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

The re-translocated N (g N m^{-2} s^{-1}) is calculated as:

$$N_{retrans} = \sum_{i=leaf,root} \tau_i \times f_{trans,i}$$ (~~21~~22)

where τ (g N m^{-2} s^{-1}) is the foliage or roots shed each step. $f_{trans,leaf} = 0.5$ and $f_{trans,root} = 0.2$ are the fractions of N re-translocated when the tissue d~~ying~~ies off.

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

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

(~~22~~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 concentration of fine root N uptake. $f(T_{soil})$ is calculated as:

$$f(T_{soil}) = \exp\left(308.56 * \left(\frac{1}{56.02} - \frac{1}{T_{soil}+46.02}\right)\right)$$ (~~23~~24)

where T_{soil} (^{o}C) is soil temperature.

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

$$f(NC_{plant}) = \max\left(\frac{NC_{plant} - nc_{leaf,max}}{nc_{leaf,min} - nc_{leaf,max}}, 0\right)$$ (~~24~~25)

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

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$$NC_{plant} = \frac{N_{leaf}+N_{root}+N_{labile}}{C_{leaf}+C_{root}+C_{labile}}$$ (~~25~~26)

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

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$$N_{BNF} = 0.1 \times \max(0.0234 \times 30 \times AET + 0.172, 0) / (86400 \times 365)$$ (~~26~~27)

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where AET (mm y^{-1}) is the mean annual evapotranspiration.

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2.3 Traceability analysis framework

The traceability analysis framework was used to evaluate the variation of the modeled ecosystem C storage capacity under different C-N schemes (~~Figure~~Fig. S1). According to the traceability analysis framework (Xia et al., 2013), the modeled C storage capacity can be traced to (i) a product of NPP and ecosystem residence time (τ_E). The latter τ_E can be further traced to (ii) baseline C residence time (τ_E'), which is usually preset in a model according to vegetation characteristics and soil types, (iii) N scalar (ξ_N), (iv) environmental scalars (ξ) including temperature (ξ_T) and water (ξ_W) scalars, and (v) the external climate forcing. The framework for decomposing modeled C storage capacity into a few traceable components is 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, 2011):

$$\frac{dX(t)}{dt} = BU(t) - A\xi CX(t)$$ (~~27~~28)

where $X(t) = (X_1(t), X_2(t), \ldots, X_8(t))^T$ 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, respectively, in the TECO model (Weng and Luo, 2008). $B = (b_1, b_2, b_3, 0, \ldots, 0)^T$ represents the ~~partitioning coefficients~~partitioning coefficients of the photosynthetically fixed C into different plant pools. *U(t)* is the input of fixed C via plant photosynthesis. *A* is an 8 × 8 matrix representing the C 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 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 can be obtained by making Eqn.(~~27~~28) equal to zero as described in Xia et al. (2013):

$$X_{ss} = (A\xi C)^{-1}BU_{ss}$$ (~~28~~29)

The vector U_{ss} is the ecosystem C influx at the steady state. The partitioning (B vector), transfer coefficients (A matrix), and exit rates (C matrix) in Eqn. (~~27~~28) together determine the baseline C residence time (τ'_E):

$$\tau'_E = (AC)^{-1}B$$ (~~29~~30)

The baseline C residence time (τ'_E) in Eqn. (~~29~~30), N scalars (ξ_N) and environmental scalars (ξ_E) values together determine the C residence time (τ_E):

$$\tau_E = \xi^{-1}\tau'_E = (\xi_N \times \xi_E)^{-1}\tau'_E$$ (~~30~~31)

Thus, the C storage capacity is jointly determined by the ecosystem residence time (τ_E) and ~~steady~~ steady-state C influx (U_{ss}):

$$X_{ss} = \tau_E U_{ss}$$ (~~31~~32)

The environmental scalar is further separated into the temperature (ξ_T) and water (ξ_W) scalar ~~components~~s, which can be represented as:

$$\xi_E = \xi_T \times \xi_W$$ (~~32~~33)

As the respiration and decomposition rate modifier, ~~T~~the N scalar is given by vector $\xi_N = (\xi_{N1}(t),\ \xi_{N2}(t), \ldots, \xi_{N8}(t))^T$. The component $\xi_{Ni}(t)$ quantifies the changes of N content at each time step compared with initial condition in the C ~~plant~~ pool i. It is calculated as:

$$\xi_{Ni} = \exp\left(-\frac{CN_i^0 - CN_i^n}{CN_i^0}\right)$$ (~~33~~34)

where CN_i^0 and CN_i^n are the C:N ratios of the pool i at 0 and n time step, respectively.

2.4 Model simulations and sensitivity analysis

To obtain the modeled C storage capacity, we spun up the TECO model with the C-only and three C-N coupling schemes to the steady state using the semi-analytical solution method developed by Xia et al. (2012). In this study, the meteorological forcings of 1996-2007 with the 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.(~~28~~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) ~~and~~as well as ecosystem C storage capacity to each main N process in three schemes were calculated as:

$$S_i^{NPP}(P) = \frac{NPP_i^+(P) - NPP_i^-(P)}{NPP_i^0}$$ (~~34~~35)

$$S_i^{MRT}(P) = \frac{MRT_i^+(P) - MRT_i^-(P)}{MRT_i^0}$$ (~~35~~36)

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

where $S_i^{NPP}(P)$, ~~and~~ $S_i^{M\cancel{C}RT}(P)$, and $S_i^{ECSC}(P)$ ($i = 1, 2, 3$) represent the sensitivities of ~~the~~ NPP, ~~and~~ 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) ~~(ie., DRP, PS, PUN, PMC, BNF, RtrN and SS)~~ 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~~in~~ the same way as NPP and calculated using Eqn.(~~29~~30) and Eqn.(~~30~~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*.

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3. Results

3.1 Simulations of C and N dynamics at steady state

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 (~~Figure~~Fig. 3). The simulated soil N mineralization and plant N uptake fluxes in SM2 displayed the largest daily variation~~s~~ (0.0015 and 0.00086 g N m^{-2}d^{-1}, respectively) and annual mean values (1.26 and 0.23 g N m^{-2}yr^{-1}, respectively) among three C-N schemes. For the N leaching flux, SM1 showed the largest daily variation (0.04 g N m^{-2}d^{-1}) and annual mean value (0.36 g N m^{-2}yr^{-1}). However, the biological N fixation (BNF) flux in SM1 showed the largest daily variation (0.028 g N m^{-2}d^{-1}) ~~but~~ but with the smallest annual value (0.04 g N m^{-2}yr^{-1}) among three C-N schemes. ~~For t~~The N immobilization fluxes in ~~,~~ SM3 ~~simulated~~ 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 SM3 displayed the similar patterns on the daily and annual dynamics.

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 ~~strength~~ magnitude (~~Figure~~Fig. 4). Specifically, the three N schemes ~~resulted in~~caused significant reductions in GPP (10%, 10% and 12% for SM1, SM2 and SM3, respectively) compared to the C-only TECO model. Similar response patterns were also found on NPP, ecosystem respiration, and heterotrophic respiration. Among the three schemes, SM3 had the strongest effect (45%, 12% and 45% reduction for NPP, ecosystem respiration, and heterotrophic respiration, respectively), while SM2 had the weakest effect (15%, 8% and 13%, respectively) and ~~there was~~ the effect of SM1 was relatively moderate ~~the effect in SM1~~ ~~was moderate~~ (29%, 10% and 29%, respectively). However, by comparison with the TECO-C version, both the SM1 and SM2 schemes increased the autotrophic respiration ~~(R-auto)~~ by 12% and 27%, respectively, and SM2 scheme increased the NEE 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).

Three C-N coupling schemes ~~introduced~~induced ~~in~~ different effects on C and N stoichiometric status for different pools (Figs.~~ure~~ 5 and ~~Figure~~ S2). All three schemes had significant limitation signs on woody, structural litter, fast and slow SOM pools but with different ~~strength~~magnitudes (~~Figure~~Fig. 5a). SM2 had the highest C sizes for the roots (731.8 g C m^{-2}) and metabolic litter (1252.1 g C m^{-2}) ~~pools. However~~, while~~,~~ SM1 had the highest C size for passive SOM pool (4249.5 g C m^{-2}). ~~For the C:N ratio,~~ SM2 had the constant C:N ratios for all the displaying pools (~~Figure~~Fig. 5b)~~. Compared with the SM2~~, while the C:N ratios for three displaying pools (leaf, root and structural litter) had no significant change in both SM1 and SM3. ~~But in~~As for both woody and metabolic litter pools, SM1 and SM3 had higher C:N ratios (357.2 and 357.9, respectively) compared with SM2 (354). SM1 had the lowest C:N ratio (4.6) for soil passive SOM pool among the three schemes.

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~~The NPP and plant N uptake (PNU) joint determine the N use efficiency (NUE).~~ The divergent effects of three C-N schemes on plant N uptake (~~Figure~~Fig. 3), autotrophic respiration, ~~NPP~~ and ~~PNU~~ NPP (~~Figure~~Fig. 4) lead to different N use efficiency (NUE) and carbon use efficiency (CUE) (~~Figure~~Fig. ~~5~~6). SM1 had the highest NUE (159.1 g C g^{-1} N), mainly resulting from its lowest plant N uptake~~PNU~~. 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~~of~~ plant actively uptake N~~ cost C~~ and the assumption that increase respiration to remove the excess C~~accumulated C~~.

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3.2 Simulation of C storage capacity

The ecosystem C storage capacity also differed greatly among the three C-N coupling schemes ~~as well as with~~ and the C-only version of TECO model (Fig. ~~6~~7). The C-only version had the largest C storage capacity (19.5 Kg C m^{-2}) among the four simulations~~,~~ ~~resulting from~~ due to its highest NPP (879.9 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 Kg C m^{-2}). The SM3 had the lowest C storage capacity (8.9 Kg C m^{-2}) among the four simulations as a result of its smallest NPP (483.9 g C m^{-2} yr^{-1}) and relative short MRT (18.6 years). By comparison with the C-only version, the three C-N schemes all induced different reductions on NPP (-29%, -15% and -45% for SM1, SM2, SM3, respectively) and further reduced their ecosystem C storage capacity. For the MRT, SM1 ~~the three C-N schemes~~ exhibited positive ~~contrasting~~ effects ~~between SM1~~ (+9%) relative to that in the C-only version, while ~~and~~ another two schemes induced negative ones (i.e., -16.9% in SM2 and -16.7% in SM3) ~~compared with the C-only TECO model~~.

3.3. Ecosystem C residence time

Ecosystem C residence time (τ_E) is collectively determined by baseline residence time, N scalar, and environmental scalars as shown in Eqn. (~~30~~31). Specifically, differences in τ_E among three C-N coupling schemes and C-only TECO model are determined by baseline residence time and the effects of N scalar on eight plant C pools (Fig. ~~7~~8). For example, SM1 had the longest τ_E because the N scalar had very strong control on passive SOM. The baseline residence time ~~were~~ was further determined by the C allocation ~~pattern~~ (Fig. ~~8~~9). Overall, compared with C-only version, the additional N processes enhanced the partitioning coefficient of NPP to roots (33%, 82% and 53%~~, respectively~~ for SM1, SM2 and SM3, respectively) but~~, while it~~ decreased the partitioning coefficient to wood (~~-~~-25%, -45% and -34%, respectively). Furthermore, the decreased partitioning coefficient to wood (b2) regulated the variations of the baseline 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 of roots and metabolic litter.

3.4. Sensitivity of N processes to NPP and MRT

For either NPP or MRT, the N processes had different sensitivities among the three C-N schemes of TECO model (Fig. ~~9~~10). For NPP, plant C:N ratio had the highest sensitivities in both SM1 (0.32) and SM2 (0.53). However, plant N uptake in SM3 had the highest 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 (0.19) and SM3 (0.56), respectively. As the NPP and MRT jointly determined the ecosystem C storage capacity, the plant tissue C:N ratio, down-regulation of photosynthesis, and plant N uptake had the highest sensitivities for the ecosystem C storage capacity in SM1 (0.06), SM2 (0.09) and SM3 (0.26), respectively.

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4. Discussions

4.1 Underlying N processes and plant production

Gross or net primary production (i.e., GPP or NPP~~ or GPP~~) is regulated by the amount of N availability~~le~~ for plant growth through the N demand, which is set by the relative proportion of 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 effects from multiple processes of the C-N interaction, mainly including down-regulation of photosynthetic capacity ~~(DRP)~~ by N availability, the ecosystem's balance of N inputs and losses (i.e., net ecosystem N exchange~~, NNE~~), plant N uptake~~ (PNU)~~, soil N mineralization ~~(SNM)~~, and the C:N stoichiometry of vegetation and soils. However, due to a lack of consensus on the nature of the mechanisms, the representation of these processes varies greatly among diverse models (Zaehle et al., 2014).

There are two common alternative assumptions ~~of~~ for the down-regulation of photosynthesis~~DRP~~ 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 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 effects on GPP (Fig~~ure~~s. ~~.~~3a and 3g). The probable reason is that the TECO model calculates photosynthesis by light availability ~~vs.~~and carboxylation rate based on the Farquhar model (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 limiting factors of photosynthetic biochemistry (the maximum rate of carboxylation, V_{cmax}, and the maximum rate of electron transport at saturating irradiance, V_{jmax}). Th~~ Note that th~~e two assumptions of ~~N ~~down-regulation of photosynthesis may have different time-dependent effects on GPP in nonsteady-state systems (Xu et al., 2012; Walker et al., 2017)~~-~~.

At or near the steady state, ~~NNE ~~net ecosystem N exchange is driven by the processes of N input via deposition and fixation and N loss via leaching and volatilization~~ stoichiometry~~ (Zaehle et al., 2014; Thomas et al., 2015). Previous studies have stated that analyzing the steady-state 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 schemes might partly result from their different representations of BNF (Fig~~ure~~s. 3 and

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10). ~~For example~~Specifically, SM2 and SM3 simulated BNF explicitly, which used modified empirical relationships of~~to calculate~~ BNF ~~based on~~ with NPP ~~evapotranspiration (ET)~~ and evapotranspiration (ET)~~NPP~~, respectively. These phenomenological relationships generally captured biogeographical observations of higher rates of BNF in humid environments with high solar radiation (Wieder et al., 2015a). However, the highest response of NPP in only ET-driven BNF (i.e., SM3) may illustrate that not only energetic but also C costs of ‘fixing’ atmospheric di-N (N_2) into a biologically usable form (NH_3) 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 nonsteady state, the NPP-driven BNF creates a positive feedback between BNF and NPP, possibly causing large impact on C dynamic and terrestrial C storage (Wieder et al., 2015a). On the other hand, SM1 applied a different strategy, which ~~represents~~ set BNF as an ~~complement~~ option when ~~to the~~~~combining with~~ the plant N uptake is enough for growth ~~as the sources~~ in terms of C investment, leading to the highest plant NUE (~~Figure~~Fig. 6a) but ~~the~~ a ~~lowest~~ lower response of BNF to NPP (~~Figure~~Fig. 10a). Another driving factor of ~~NNE~~ the net ecosystem N exchange is the N loss, which depends on the rate of leaching and volatilization. In this study, ~~U~~using the same formulation as proportion~~al~~ to the size of soil mineral N pool among the three schemes, the ~~divergent~~ 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; Zaehle et al., 2010), the soil mineral N pool is divided into two pools (ammonium and nitrate).~~,~~ T~~t~~he N leaching is only valid~~acts only~~ on the nitrate pool, while the ammonium pool is assumed to be unaffected by leaching. This hypothesis may reduce the correlation between leaching and total soil mineral N.

The processes of ~~PNU~~ 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 capacity (~~Figure~~Fig. 10). However, to our knowledge, exploring those processes exactly in models is limited by inadequate representation of above- and below-ground interactions that control the patterns of N allocation and whole-plant stoichiometry (Zaehle et al., 2014; Thomas et al., 2015). Plant tissue, litter, and SOM are the primary sinks of N in terrestrial ecosystems, while N in these forms is not directly available for ~~PNU~~plant uptake, leading to an increase in N demand ~~due to~~for plant growth.~~ On the other hand, t~~ These N must turn over to become available for plant uptake~~growth~~. Therefore, the time for N to stay in these unavailable pools controls the transactional delay between the 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 growth ~~(see next section)~~. In

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th~~e present~~is study, SM1 had the highest NUE ~~from~~ due to the combined effects of ~~PNU~~ plant N uptake based on C investment strategy (as described above) and flexible tissue C:N ratio. Nitrogen stress increased tissue C:N ratio (~~Figure~~Fig. 5b), leading to a high microbial N immobilization and then a lower net N mineralization (~~Figure~~Fig. 3), which allowed plant cell construction with a lower N requirement. However, this was not the case for the SM3 since both ~~the~~ hypothes~~e~~is of increasing respiration to remove the excess C ~~accumulated~~ under N stress and the 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 ~~(i.e., PS&SS)~~ appeared to be an important feature allowing models to capture responses of the ecosystem C storage capacity ~~response~~ to climate variability through adjusting the C:N ratio of nonphotosynthetic tissues or the whole-plant allocation among tissues (Fig~~ures~~s. 9 and 1~~Figure 1~~0) with different C:N ratios (Zaehle & Friend, 2010). ~~However, it is unclear whether those regulatory mechanisms exist in reality. Further modelling approaches need more reliable framework to predict stoichiometric flexibility.~~

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 inputs from N fixation and N deposition, N losses from leaching and denitrification, and N gain from the turnover of litter and SOM through tissue senescence and decomposition. As 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 (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 limitation on productivity of plants and soil organisms, ~~largely~~ because these effects involve various impacts on C transfer among pools and C release from each pool via decomposition and respiration (Thompson & Randerson, 1999; Xia et al., 2013). Therefore, the different impacts of ecosystem N status induce oscillating N limitation on MRT (Fig~~ures~~s. 8 and ~~Figure~~ 10) due to the inherently different assumptions of C-N interactions among three C-N coupling schemes (Zhou et al., 2012; Shi et al., 2018)~~(references??)~~.

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

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(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 assumed the same effects for this component in all four experiments~~, which is thus not discussed further in this section~~.

In our study, the N scalar was based on the dynamics of C:N ratios (Eqn. ~~33~~34). Therefore, N scalar had no effect on MRT in SM2, resulting from the assumption of fixed C:N ratio in all C pools (Fig~~ure~~s.~~.~~ ~~6c~~5b and 8c). In both SM1 and SM3, however, the N scalar had large effects on the SOM pool, which is probably related to different mechanisms. Specifically, N scalar in the SM1 had the contrasting effects on MRT of fast and passive SOM pools (i.e., negative vs. positive, respectively), which may largely be attributed to the plant and microbe competition strategy combining with a much larger passive SOM pool in TECO-CN~~2.0~~ model (Du et al., 2017; Zhu et al., 2017). Under N stress, the competition between plants and microbes is expected to be intensified, resulting in increasing C:N ratio of nonphotosynthetic tissues (e.g., wood and root) and the total C:N ratio. This effectively prevents N limitation of cell construction and corresponds to an increase in whole-plant NUE (Thomas et al., 2015). In this case, higher C:N ratio in those tissues lowers structural litter quality, leading to soil 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 remove the excess ~~accumulated~~ C, which is a stoichiometry-based implementation to prevent the accumulation of labile C under N stress (Zaehle & Friend, 2010; Thomas et al., 2015). This mechanism promotes ~~absorption and~~ respiration of the faster turnover pools (fast and slow SOM pools, ~~Figure~~Fig. 5a), leading to increased C:N ratio and ~~further~~ decreased~~ in~~ the MRT in these two pools (~~Figure~~Fig. 8).

In the traceability framework, the baseline MRT is determined by the potential decomposition rates of C pools (*C* matrix), coefficients of C partitioning of NPP (*B* vector), and transfer coefficients between C pools (*A* matrix, Eqn. [~~29~~30]. Xia et al., 2013). The matrices *A* and *C* are preset in the TECO model according to vegetation characteristics and soil texture~~s~~ (Weng and Luo., 2008). Therefore, the notable spread in baseline MRT across the C-N schemes was induced by the *B* vector, which was modified by different N-limitation assumptions (Eqns. 1-6). Conceptually, in order to meet the N demand, plants adjust NPP allocation to N absorption tissues (e.g., roots). In this study, three schemes all had similar trends of adjusting allocation C from wood to roots (~~Figure~~Fig.~~.~~ ~~7~~9), but with different mechanisms. For both SM1 and SM3, increased root C allocation was mainly driven by N uptake capacity, which is associated with plant competitiveness in SM1 and the respiration of excess labile C 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.

5. Conclusions

The C-N coupling has been represented in ecosystem and land surface models with different schemes, generating great uncertainties in model predictions. The most ~~striking~~ difference among terrestrial C-N coupling models occurs with the degree of flexibility of C:N ratio in vegetation and soils, plant N uptake strategies, ~~pathways of N import,~~down-regulation of photosynthesis,~~-~~ and the representations of the pathways of N import.~~competition between plants and microbes for soil mineral N.~~ In this study, we evaluated alternative representations of C-N interactions and their impacts on C cycle using the TECO model framework. Our traceability analysis showed that different representations of C-N coupling 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 assumptions on net ecosystem N exchange, plant N uptake, net N mineralization, and the C:N ratio of vegetation and soil. In comparison, the alternative representations of the plant and microbe competition strategy, combining with the flexible C:N ratio in vegetation and soils, led to a notable spread effects on C residence time. Identifying the representations of main C-N processes under different schemes can help us ~~to~~ improve the N-limitation assumptions employed in terrestrial ecosystem models and forecast~~ing~~ future C sink ~~dynamic~~ in response to climate change.

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

Data availability. The data for this paper are available upon request to the corresponding authors.

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

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Figure legends

Figure 1. Schematic diagram of the terrestrial ecosystem carbon (C) and nitrogen (N) coupling model (TECO-CN~~2.0~~). (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 organic matter. * set N fixation as an option when the plant N uptake is enough for growth in 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.~~[1,2,3] alternative assumptions of N processes represent in scheme 1, 2 and 3, respectively~~. 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 CO_2; 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 1996-2007 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 ~~5~~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).

~~The nitrogen use efficiency (NUE) in three C-N schemes of TECO model (SM1, SM2 and SM3).~~

Figure ~~6~~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 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, SM3 and C-only model; inset (c), relative change of NPP and ecosystem residence time simulated among three schemes compared with in C-only model.

Figure ~~7~~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 (c), nitrogen scalar.

Figure ~~8~~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 ~~9~~10. The sensitivity of nitrogen processes to NPP (panel a),~~ and~~ ecosystem residence time (τ_E, panel b), and ecosystem C storage capacity (panel c) among three carbon-nitrogen 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 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 of key processes in the carbon-nitrogen cycle.

	SM1 (TECO-CN~~2.0~~)[a]	**SM2 (CLM4.5)**[b,c]	**SM3 (O-CN)**[d,e]
~~Photosynthesis~~ ~~d~~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

[a]See this study; [b]~~Thornton~~Koven et al. (2013~~2007~~), [c]~~Thornton~~Oleson et al. (2013~~2009~~); [d] Zaehle &Friend (2010), [e]Zaehle et al. (2011).

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

Figure 1. TECO-CN ~~2.0~~

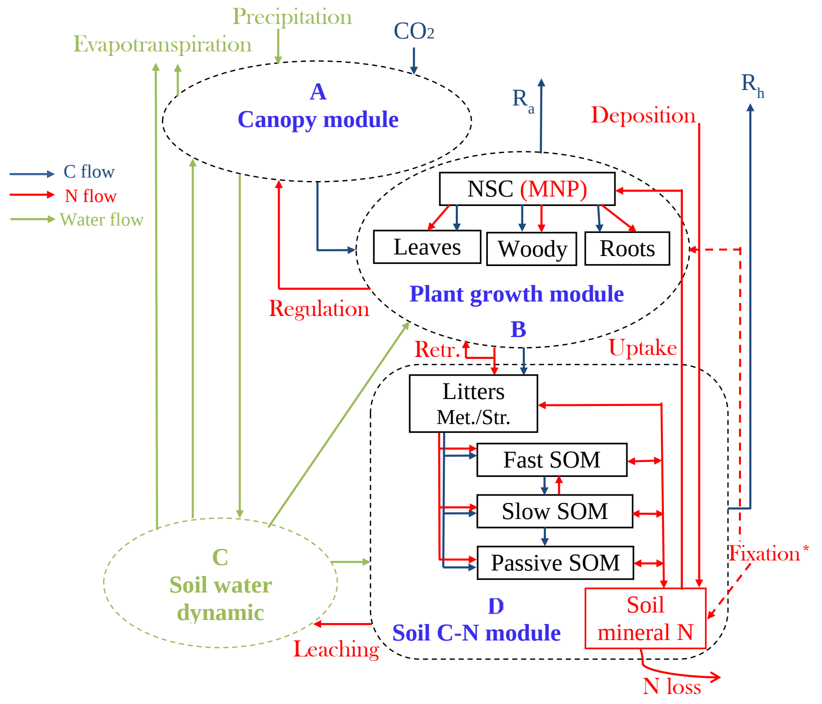


Figure 1. Schematic diagram of the terrestrial ecosystem carbon (C) and nitrogen (N) coupling model (TECO-CN~~2.0~~). (A) Canopy module, (B) Plant growth module, (C) Soil water dynamics module, (D) Soil carbon-nitrogen coupling module. Rectangles represent the carbon and nitrogen pools. R_a, autotrophic respiration. R_h, heterotrophic respiration. Retr., re-translocation. NSC, nonstructural carbohydrate. MNP, mineral N in plant tissues. SOM, soil organic matter. * set N fixation as an option when the plant N uptake is enough for growth in terms of C investment.

Figure 2

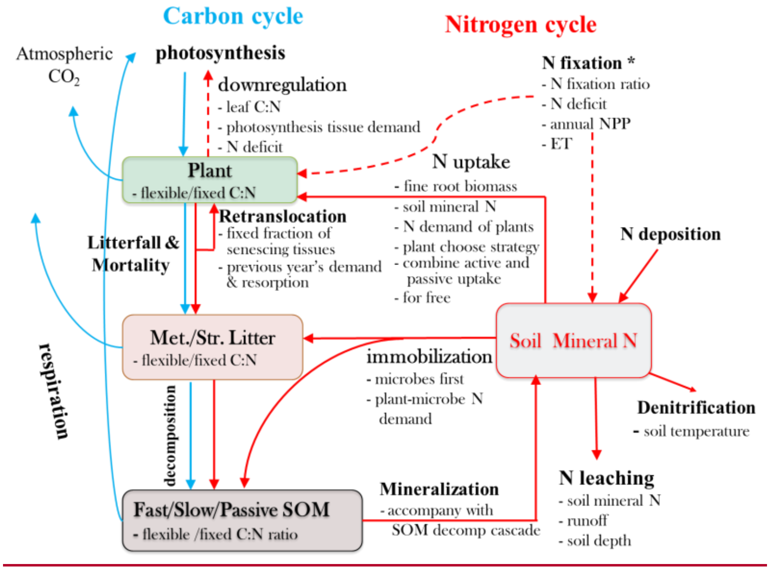


Figure 2. Schematic diagram illustrating the major carbon (C) and nitrogen (N) flows and stores in a terrestrial ecosystem, enclosing with alternative assumptions of N processes represent in SM1, SM2 and SM3, respectively.~~.~~ Light-blue arrows indicate C-cycle processes and red arrows show N-cycle processes.~~[1,2,3] alternative assumptions of N processes represent in scheme 1, 2 and 3, respectively.~~ 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

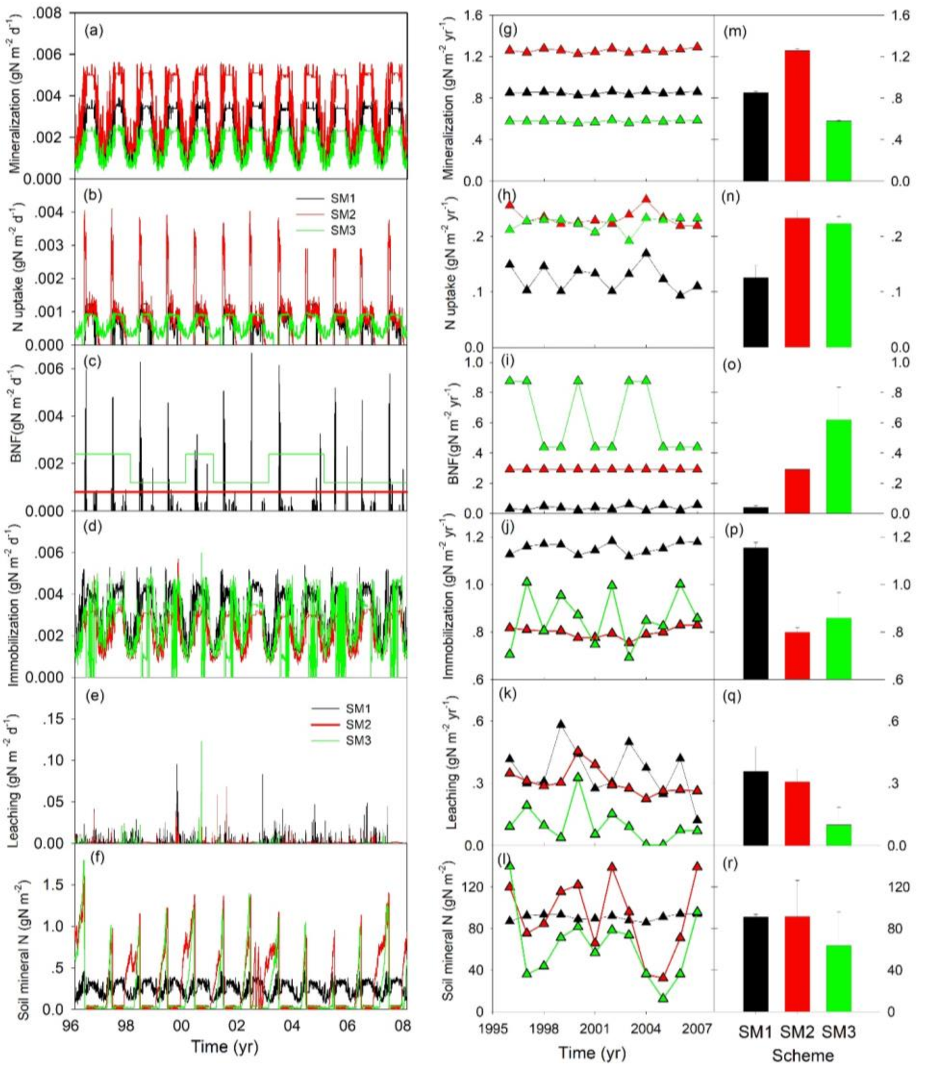


Figure 3. Simulated nitrogen fluxes and soil mineral nitrogen from three carbon-nitrogen coupling schemes (SM1, SM2 and SM3) in TECO-CN model for 1996 to 2007 at Duke Forest.

Figure 4

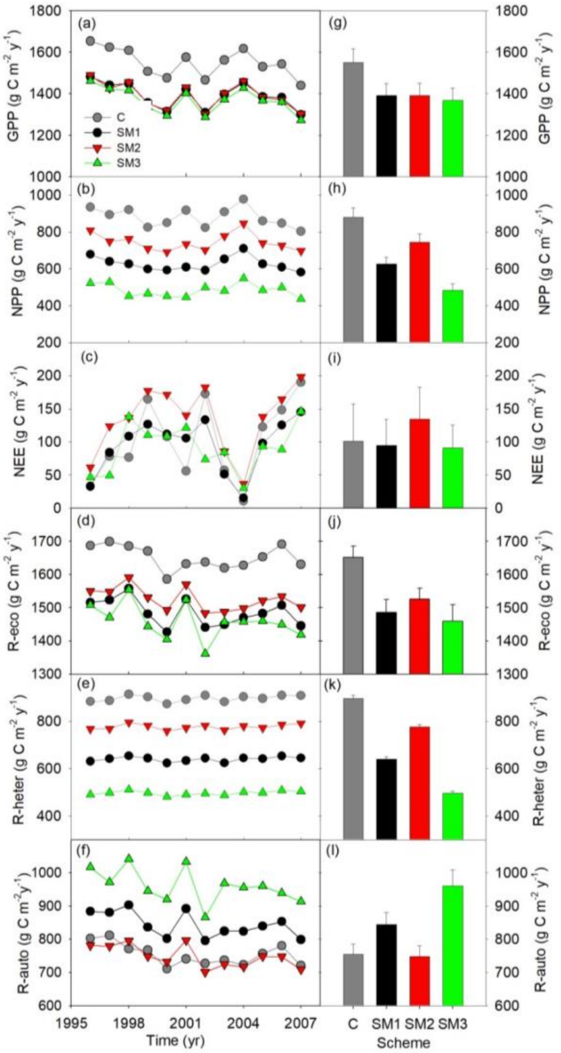


Figure 4. Simulated annual (a-f) and mean (g-l) carbon fluxes from carbon-only version and carbon-nitrogen coupled with three schemes (SM1, SM2 and SM3) of TECO model for 1996 to 2007 at Duke Forest. GPP, gross primary productivity; NPP, net primary productivity; NEE, net ecosystem exchange of CO_2; R-eco, ecosystem respiration; R-heter, heterotrophic respiration; R-auto, autotrophic respiration.

Figure 5

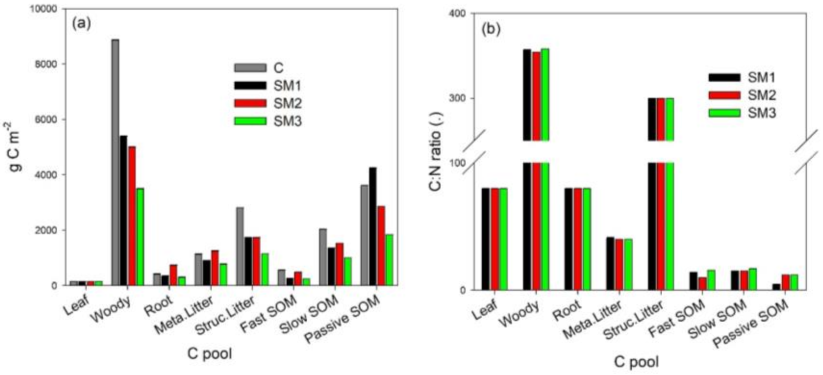


Figure 5. The annual average sizes of carbon pools (panel a) at the steady state among 1996-2007 for C-only version and the three C-N schemes (SM1, SM2 and SM3) and the C:N ratio (panel b) of each carbon pools for the three C-N schemes (SM1, SM2 and SM3) in TECO-CN model.

Figure 6

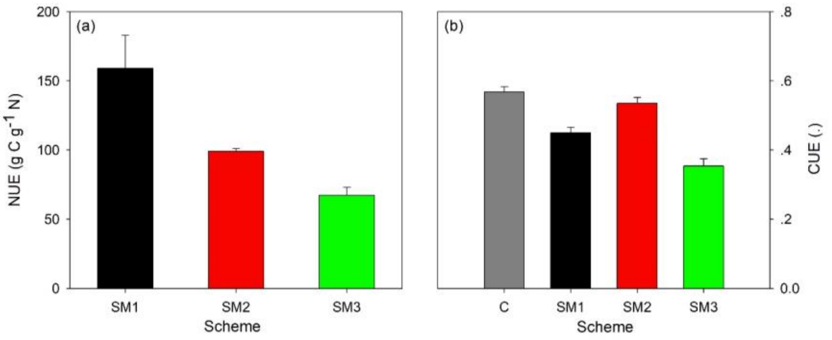


Figure 6. The nitrogen use efficiency (NUE, the ratio of NPP:PNU, panel a) in three C-N schemes of TECO model (SM1, SM2 and SM3) and the carbon use efficiency (CUE, the ratio of NPP:GPP, panel b) at the steady-state among C-only version and the three C-N schemes of TECO model (SM1, SM2 and SM3).

Figure ~~6~~7

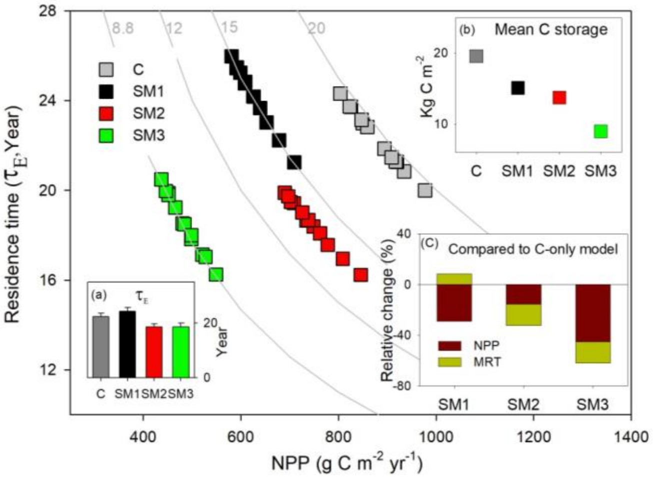


Figure ~~6~~7. Simulation of annual ecosystem carbon storage capacity for 1996 to 2006 at Duke Forest by carbon in flux (NPP, x axis) and ecosystem residence time (τ_E, y axis) in TECO model framework with three carbon-nitrogen coupling schemes (SM1, SM2 and SM3) and in TECO C-only model (C). The hyperbolic curves represent constant values (shown across the 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 among SM1, SM2, SM3 and C-only model; inset (c), relative change of NPP and ecosystem residence time simulated among three schemes compared with in C-only model.

Figure ~~7~~8

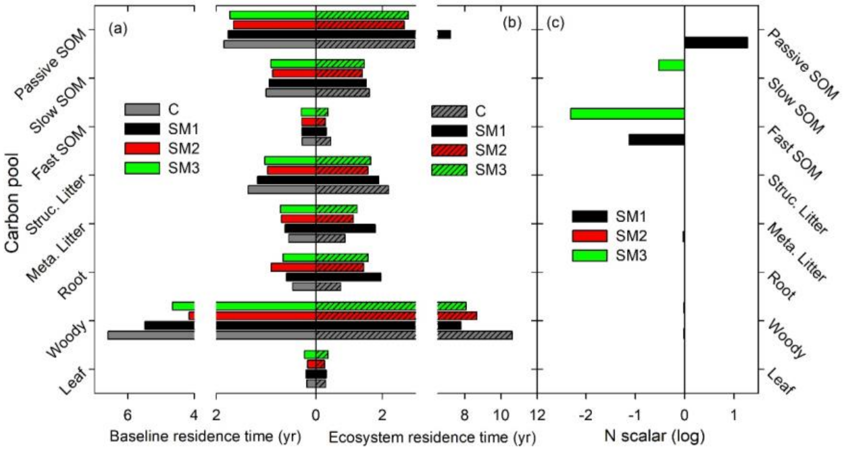


Figure ~~7~~8. Determination of carbon-pool residence times based on traceability analysis framework in TECO C-N model with three C-N coupling schemes (SM1, SM2 and SM3) and TECO C-only model (C). Panel (a), baseline residence time; panel (b), mean residence time, and panel (c), nitrogen scalar.

Figure ~~8~~ 9

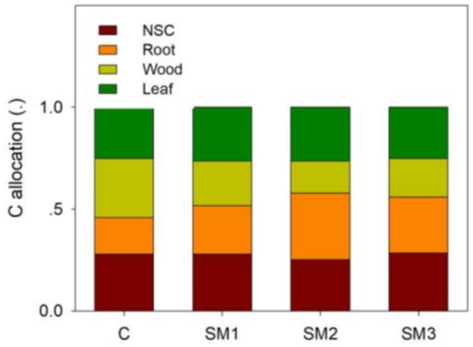
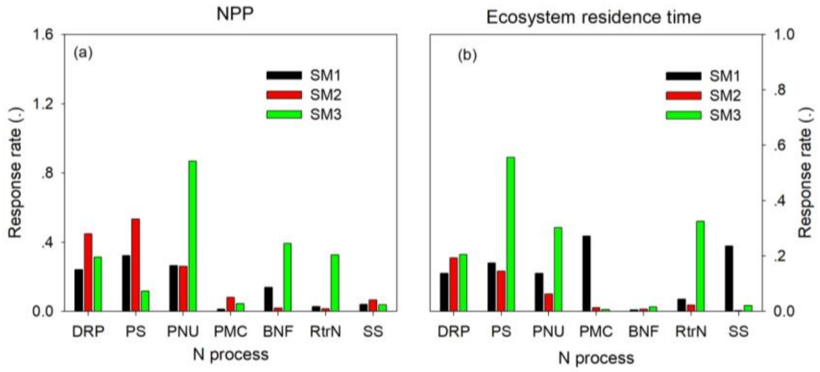


Figure ~~8~~9. Coefficients of partitioning of NPP to nonstructural C (NSC), root, woody and leaf in C-only model (C) and C-N coupling model with three schemes (SM1, SM2 and SM3).

Figure ~~9~~10



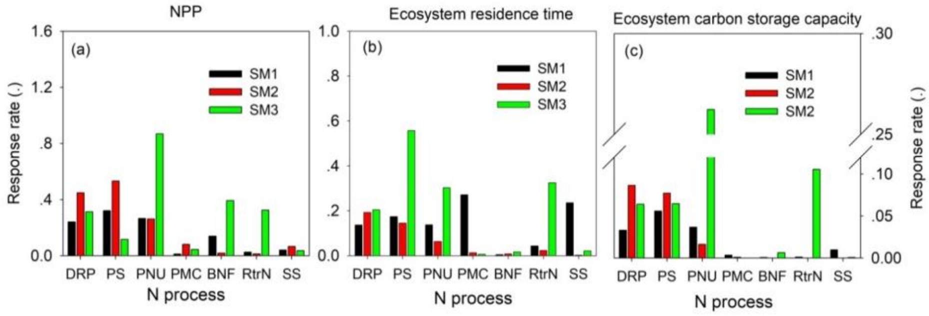


Figure ~~9~~10. The sensitivity of nitrogen processes to NPP (panel a)~~ and~~ , ecosystem residence time (τ_E, panel b), and ecosystem C storage capacity (panel c) among three carbon-nitrogen coupling schemes (SM1, SM2 and SM3). DRP, down-regulation of photosynthesis; PS, plant tissue C:N ratio; PNU, plant N uptake; PMC: plant and microbe competition; BNF, biological N fixation; RtrN, re-tranlocation N; SS, soil pool C:N ratio.