

Dear Editor of Geoscientific Model Development,

We thank the reviewers for their support and their comments. We have modified the manuscript according to your comments and queries and believe that these changes have greatly improved our manuscript. The main changes are:

- Clarification of the spinup protocol
- Improvement of the discussion about the model limitations

We are grateful for all these very relevant comments and suggestions that have clarified key points of the manuscript. Please find a detailed response to each question/comment point by point below in [blue](#) (text fragments are *in blue italics*).

Response to reviewer 1

This paper describes the addition of a nitrogen cycle to ISBA land surface model. The authors show that the CN model improves agreement with observations from the FACE experiments at Oak Ridge and Duke.

The paper is clear and concise, and could benefit from only a few minor clarifications:

[The referee's comments and suggestions have improved the manuscript.](#)

- Fig 3: why does spinup protocol change CN results at Oak Ridge but not Duke?

[At Duke, the spinup protocol does not affect the results because the system is in any case not N limited whereas it is at Oak Ridge. Due to the difference of vegetation type between the two sites, the NC ratio of leaves is higher at Oak Ridge leading to a higher N demand.](#)

- Line 118: where does the 90 % limit come from?

[We have followed the same formulation as Zaehle and Friend \(2010\), since it seems relevant to not completely deplete the labile pool when the system is N limited.](#)

- Line 142: is the model sensitive to these parameters?

[We thank the referee for this question that brought light on a typo mistake in eq. 7, which was corrected in the revised manuscript. We performed a sensitivity analysis in which the parameter \$\lambda\$ was increased and decreased by 62.5 % and the parameter \$k\$ was increased and decreased by 33.3 %. The effect denoted by \$r\$ on the NPP is quantified using this equation:](#)

$$r = \frac{(NPP_{\text{new}} - NPP_{\text{ref}})}{NPP_{\text{ref}}} \quad (1)$$

[where \$NPP_{\text{new}}\$ is the NPP computed using a new value for \$k\$ or \$\lambda\$. Results for both sites under ambient and elevated \$CO_2\$ are summarized in the following Table. Both parameters have contrasting effects: increasing \$k\$ results in higher NPP while a decrease in \$k\$ leads to a decrease of NPP. It is the other way round for \$\lambda\$ changes. Decreasing \$\lambda\$ raises the dampening effect : it takes longer to reach the maximum value of \$NC_{\text{leaf}}\$ \(see Figures 1 et 2 on the bottom left and right\). Therefore, N demand is lower and there is less N limitation, this yields a higher NPP. Decreasing \$k\$ results in the opposite behavior because it decreases the dampening effect \(see Figures 1 et 2 on the top left and right\).](#)

Typos / wording suggestions:

- Line 8: “confronting” → “comparing” [Done and acknowledged.](#)

		Ambient CO ₂		Elevated CO ₂	
		Duke	Oak Ridge	Duke	Oak Ridge
Change in λ	+ 62.5 %	- 2 %	- 7 %	- 3 %	- 7 %
	-62.5 %	+ 1 %	+ 4 %	+4 %	+3 %
Change in k	+33 %	+1 %	+3 %	+2 %	+2 %
	-33 %	-3 %	-7 %	-4 %	-7 %

Table 1. Change in NPP in % when varying k or λ

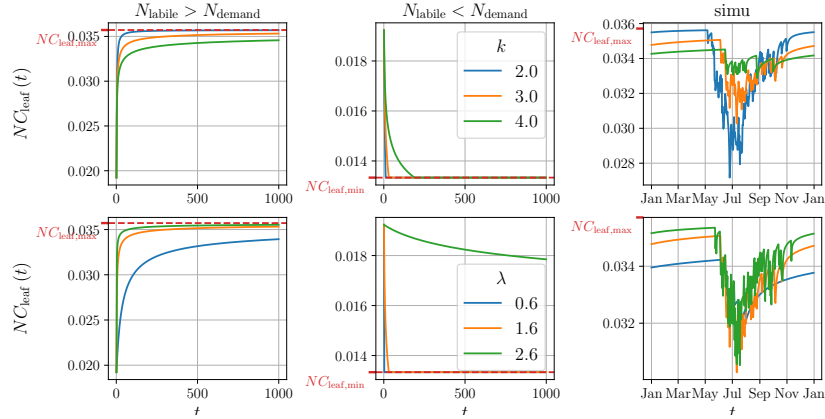


Figure 1. Duke : 1000 iterations of NC_{leaf} computation using eq. 7 for $N_{labile} > N_{demand}$ (left), $N_{labile} < N_{demand}$ (middle) and results from simulation (right). On top : $\lambda = 1.6$ and k varies, bottom : $k = 3.0$ and λ varies.

- Line 86: “Gazeous” → “Gaseous”
Done and acknowledged.
- Line 148: “loss” → “lost”
Done and acknowledged.
- Line 189: “do” → “does”
Done and acknowledged.
- Line 404: “forest forest” → “forest floor”?
Done and acknowledged.
- Line 460: “tight” → “tied”?
Done and acknowledged.

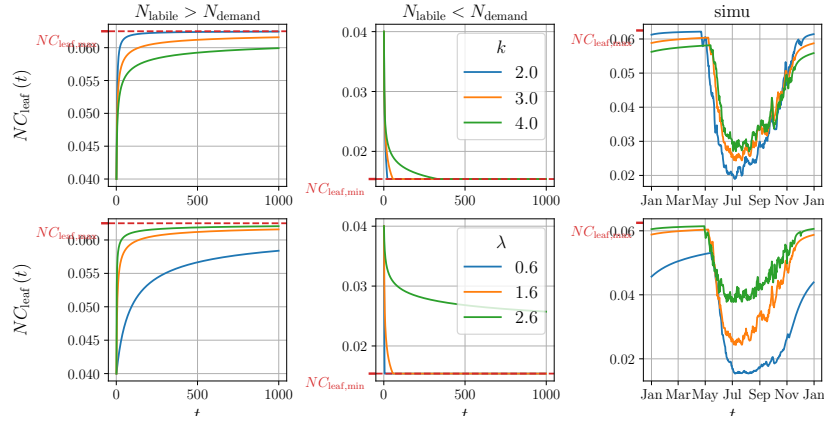


Figure 2. Oak Ridge : 1000 iterations of NC_{leaf} computation using eq. 7 for $N_{\text{labile}} > N_{\text{demand}}$ (left), $N_{\text{labile}} < N_{\text{demand}}$ (middle) and results from simulation (right). On top : $\lambda = 1.6$ and k varies, bottom : $k = 3.0$ and λ varies.

Reviewer 2

This manuscript presents a well-documented model; however, several aspects related to nitrogen cycling formulation and spin-up strategy require clarification to ensure reproducibility and consistency of model behavior. We thank the referee for his/her support. The referee's comments and suggestions have helped to improve the revised manuscript.

Major comments:

Spin up

The equilibrium spin-up produces soil carbon stocks approximately five times larger than observations after more than 1000–2000 years of simulation. While the use of an observation-constrained initialization is reasonable, the large discrepancy between equilibrium and observed soil carbon raises concerns regarding model structure and/or parameterization, particularly in soil carbon turnover processes.

This is a good point. There are good reasons for this large discrepancy. 1) we ran the spin up with a present day climate forcing (except for atmospheric CO_2 concentration forced at pre-industrial during spinup), much more favorable for vegetation growth. 2) Disturbances such as fires or diseases are not represented. 3) We did not represent the past land use changes. Both sites were likely forested until the 1700s. Duke was a mowed grassland for at least 200 years before tree plantation in 1983, and Oak Ridge was a cropland. Agricultural practices, lead to drastic reduction of soil C content as documented in Chapter 4 of special report on Climate Change and Land (Intergovernmental Panel On Climate Change, 2022). It is then very likely that the observed soil C content in the 1990ies at Duke and Oak Ridge is still very much representative of agricultural land instead of forest. Poeplau et al. (2011) indicates that a forest needs to be in place for at least 150 years after agriculture to get a doubling of soil carbon content. Here the FACE experiment only started about 15 years after tree plantation. The first two points are already addressed at line 339 of the revised manuscript with corrections. We have amended the text as follows to highlight why the equilibrium SOC content is far from the observations:

In addition, the land use changes are not taken into account. Both sites have an agricultural past: mowed grass at Duke and crops at Oak Ridge (Hamilton et al., 2002; Iversen et al., 2012). Chapter 4 of special report on Climate Change and Land (Intergovernmental Panel On Climate Change, 2022) documents a strong reduction of soil C content in cropland and grasslands compared to forest. This may explain a large part of the discrepancies between the model and the observations.

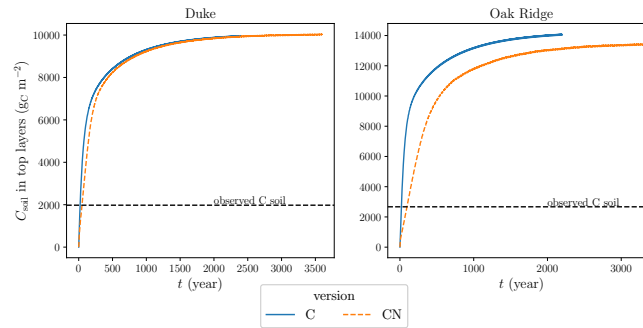


Figure 3. Soil carbon evolution in top layers during spinup at Duke (left) and Oak Ridge (right) for the C version of the model in blue and for the CN version in orange. The black dashed line is the observed C soil content.

The modeled NPP is broadly consistent with observations in both spin-up approaches; therefore, the substantial overestimation of equilibrium soil carbon likely does not arise from carbon inputs. Instead, it suggests potential biases in decomposition rates, soil carbon residence times, or stabilization mechanisms. The current explanation based on similar NPP between the C and CN simulations mainly addresses nitrogen limitation but does not fully explain the unrealistic equilibrium soil carbon state.

In addition to the above comment, C losses are underestimated since the leaching of dissolved organic carbon is not represented. Moreover, native temperate forest can hold up to 20 300 g of soil organic matter per square meter, which corresponds to 13 340 gC m^{-2} (Crews and Rumsey, 2017). This is the order of magnitude we obtain.

Since the manuscript adopts an observation-constrained initialization instead of the equilibrium state, the authors should further clarify why the equilibrium solution is unrealistic and provide justification for the selected initialization strategy. In addition, showing the temporal evolution of soil carbon during the “real” spin-up period would help demonstrate whether the system exhibits any drift toward the higher equilibrium state over longer timescales.

The evolution of SOC content in the first soil layers during the spinup is depicted in Figure 3. Simulations from ‘spinup real’ start when crossing the dashed black line. Figure 4 shows the evolution of SOC content in all soil layers during all simulation phases (spinup, industrial period, plantation and FACE experiment on ambient plot). Soil C is not at equilibrium in the simulation, which is expected as the forest has been replanted recently. This is probably the same in the real world: a study points out that no SOC equilibrium was reached within 120 years of reforestation on a former cropland (Poeplau et al., 2011). On top of the land use change issue, there is also no guarantee that the real system is reaching an equilibrium state because the atmospheric CO_2 concentration has been rising. We add a sentence at the end of Section 3.3 to clarify this aspect:

In this configuration, the system is not at equilibrium. This is closer to the real soil status due to the recent reforestation.

BNF

It may be oversimplified to link biological nitrogen fixation (BNF) directly to NPP in a C–N model, given that BNF is the largest natural nitrogen source and can vary substantially across ecosystems. The model may produce overly positive feedback between CO_2 fertilization and nitrogen input. Recent models often use more mechanistic representations of BNF rather than simple NPP-based relationships (Kou-Giesbrecht et al., 2022; Yuan et al., 2025). The authors are encouraged to expand the discussion on potential model improvements and the implications and limitations of using this simplified parameterization.

References:

- Kou-Giesbrecht, S., & Arora, V. K. (2022). Representing the Dynamic Response of Vegetation to Nitrogen Limitation via Biological Nitrogen Fixation in the CLASSIC Land Model. *Global Biogeochemical Cycles*, 36(6), e2022GB007341. <https://doi.org/10.1029/2022GB007341>
- Yuan, Y., Zhuang, Q., Zhao, B., & Liu, L. (2025). Improving the quantification of global free-living and symbiotic nitrogen

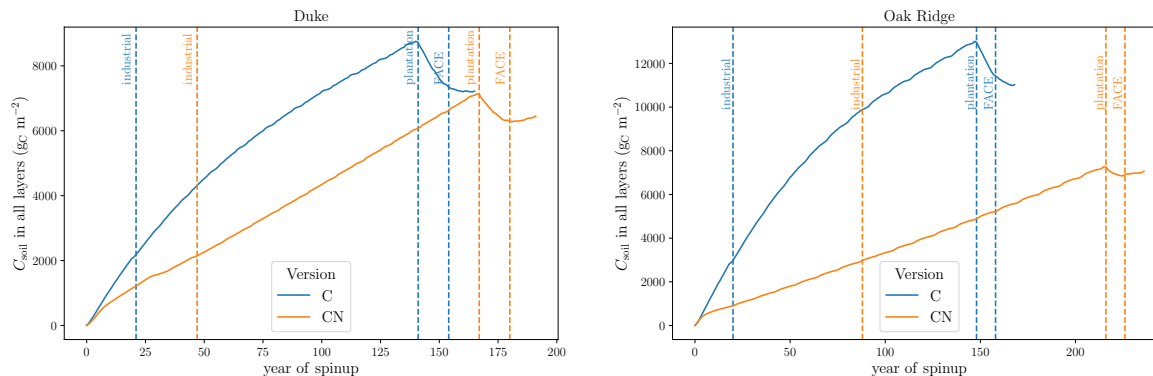


Figure 4. Soil carbon evolution in all soil layers during all simulation phases (spinup, industrial period, plantation and FACE experiment on ambient plot) at Duke (left) and Oak Ridge (right) for the C version of the model in blue and for the CN version in orange. The vertical dashed lines represent the beginning of each phase.

fixation in natural terrestrial ecosystems: present-day estimates and 21st century projections. Environmental Research Letters. <https://doi.org/10.1088/1748-9326/ae198ce>:

Noted. We amended the text as follows at the end of section 4.3.

We have implemented a straightforward BNF parametrization as it has been done in other land surface models. However, some works are critical about the pertinence of using NPP to model BNF and its validity is questioned (Wieder et al., 2015; Hupperts et al., 2021; Davies-Barnard et al., 2020). In particular, for future predictions, the NPP dependent parametrization is sensitive to CO₂ increase and is probably not realistic (Thomas et al., 2015; Reis Ely et al., 2025). Following the work of Kou-Giesbrecht and Arora (2022), next steps will be dedicated to implement a more process-based parametrization of BNF. First, it is important to differentiate symbiotic from asymbiotic BNF as it does not involve the same processes (Meyerholt et al., 2016; Hupperts et al., 2021; Kou-Giesbrecht et al., 2025). On one hand, symbiotic BNF is directly linked to plant needs and is another direct N source in addition to the root N uptake. A resource optimization framework such as proposed by Rastetter et al. (2001) integrates the C cost of each process and improves the model response to elevated CO₂ and increase in N deposition (Meyerholt et al., 2016; Fisher et al., 2010; Kou-Giesbrecht and Arora, 2022). On the other hand, free living BNF plays a crucial role in providing mineral N needed for specific environmental functionalities such as litter decomposition. This pathway dominates some ecosystems where N fixer species are scarce (Reed et al., 2011). Moreover, both symbiotic and asymbiotic processes are temperature dependent but with contrasting optimums. Due to the predicted rising temperature, this is an important aspect to consider (Kou-Giesbrecht and Arora, 2022; Yuan et al., 2025).

N deposition

What are the fractions of NH_4^+ and NO_3^- in the N deposition? Please specify. The simulation period is 20 years, and the N deposition in Table 1 appears to use a fixed ratio. If time-series N deposition data were not used, consider adding a sensitivity analysis or discussion, as global time-series N deposition datasets are available.

Reference:

Ackerman, D., Millet, D.B. and Chen, X., 2019. Global estimates of inorganic nitrogen deposition across four decades. Global Biogeochemical Cycles, 33(1), pp.100-107.
Tian, H., Bian, Z., Shi, H., Qin, X., Pan, N., Lu, C., Pan, S., Tubiello, F. N., Chang, J., Conchedda, G., Liu, J., Mueller, N., Nishina, K., Xu, R., Yang, J., You, L., and Zhang, B.: History of anthropogenic Nitrogen inputs (HaNi) to the terrestrial biosphere: a 5 arcmin resolution annual dataset from 1860 to 2019, Earth Syst. Sci. Data, 14, 4551-4568, <https://doi.org/10.5194/essd->

We suppose that all the deposition enters the mineral pool, where we consider that 40 % of the nitrogen is NH_4^+ and 60 % is NO_3^- . We took a constant value for simplicity as literature suggests little changes in deposition during the 10 years of experiment at both sites. The dataset of Tian et al. (2022), indicate during the experiment period, that the total N deposition is $1.23 \pm 0.05 \text{ g}_\text{N} \text{ m}^{-2} \text{ y}^{-1}$ at Duke and $1.23 \pm 0.04 \text{ g}_\text{N} \text{ m}^{-2} \text{ y}^{-1}$ at Oak Ridge, with a tendency of $0.01 \text{ g}_\text{N} \text{ m}^{-2} \text{ y}^{-2}$ increase at both sites. Further technical developments will include the possibility to have a dynamic N deposition forcing.

Comparison:

The evaluation of the newly implemented nitrogen cycle is limited, as the comparison with observations is restricted to N_2O emissions and nitrate leaching at a single site and have difference in magnitude. While the scarcity of site-level nitrogen observations is well known and represents a general limitation in evaluating land surface models, key fluxes such as N_2O emissions and biological nitrogen fixation have been synthesized in previous literature and modeling studies, and could be used as potential benchmarks for comparison.

We thank the referee for their suggestions. We included in Section 4.3 comparison with literature estimates for N_2O and BNF fluxes. The modified paragraphs read as follows :

A new global BNF estimate suggests that the BNF rate used in this study overestimates this flux (Reis Ely et al., 2025). They evaluate a BNF flux of $0.35 \text{ g}_\text{N} \text{ m}^{-2} \text{ y}^{-1}$ for evergreen needleleaf forests such as Duke and of $0.61 \text{ g}_\text{N} \text{ m}^{-2} \text{ y}^{-1}$ for deciduous broadleaf forests such as Oak Ridge.

.. Calibration of the gaseous outputs is difficult due to the limited number of observations available at these sites. A multi-site analysis carried out by Ma et al. (2022) provides estimates of the N_2O fluxes. In temperate evergreen coniferous forests, the average flux is of $0.0568 \text{ g}_\text{N} \text{ m}^{-2} \text{ y}^{-1}$. As a comparison, the model yields on average at Duke on ambient plots $0.0142 \text{ g}_\text{N} \text{ m}^{-2} \text{ y}^{-1}$. For temperate deciduous forests, the observed value is $0.0470 \text{ g}_\text{N} \text{ m}^{-2} \text{ y}^{-1}$ and at Oak Ridge the average flux on the ambient plots is $0.0267 \text{ g}_\text{N} \text{ m}^{-2} \text{ y}^{-1}$. Gas losses will be studied in the future on agricultural surfaces where more N_2O data are available.

Minor comments:

Line 78-80: Please list the names of those land models.

Done and acknowledged.

Line 184: I think it is inappropriate to state that denitrification occurs only under anaerobic conditions, as aerobic denitrification has also been reported. Please revise the description.

We agree with the referee. The sentence has been revised as follows:

We model autotrophic nitrification that occurs under aerobic conditions and denitrification carried out by denitrifiers under anaerobic conditions.

Line 210: The $\text{N}_2\text{O}/\text{N}_2$ product ratio of denitrification is variable and strongly regulated by environmental conditions such as oxygen availability, soil moisture, pH, carbon availability, and microbial community composition. It is acceptable if the study not focus on gas emission, but would be worth to discuss.

That's a good point, we amended the text as follows:

This is a simplified representation. The amount of N_2O produced is linked to the microbial community in the soil. More complex models explicitly describe the nitrifiers and denitrifiers population dynamics (Li et al., 2000; Ma et al., 2022). The ratio can also be temperature and humidity dependent such as proposed by Xu-Ri and Prentice (2008).

Figure 3: Miss the C real line.

Many thanks for highlighting this. The C real line is not missing, it coincides with the C eq line. There is indeed no reason for the two cases to be different in the C only version. The biomass reservoirs are set to 0 after the industrialization period and the

plantation and FACE experiments are of the same duration. Without N constraints, this leads to similar biomass pools and thus NPP. We made an error at Duke, the biomass pools were not reset to 0. The Figure has been corrected.

Line 389: Did you perform any statistical significance tests, or is the conclusion based solely on visual comparison that the nitrogen cycle does not affect the results?

Thank you for highlighting this unclear explanation. The analysis of carbon partitioning for the CN version is also done using Table 6. We have only one value per year, so for the tendency statistical tests can not be done. The average carbon allocation is computed over these three years. The sentence has been revised as follows:

Inclusion of the nitrogen cycle does not affect the partitioning of carbon in the biomass, neither its evolution during the three years.

Table 7: Why is the simulated SOC approximately double the observed value if the spin-up was stopped once the model matched the observations?

Between the spinup and the FACE experiments, we simulate 133 years at Duke and 138 years at Oak Ridge during which the atmospheric CO₂ concentration is the historical one. This is almost three times for Duke and one and a half times for Oak Ridge the spinup duration.

Figure 8 and 9: Please specify what each line represents in description, as the abbreviations are difficult to read and interpret. Thank you for the suggestion, the description of Figure 8 and 9 have been modified accordingly.

Table 8: Why the response of Duke is generally larger than Oak Ridge?

The response of the nitrogen cycle is driven by the carbon cycle. NPP is more enhanced at Duke, this is inherited from the PFT. BNF response is thus higher at Duke. The strength of the response on output fluxes at Duke is to sustain the greater increase of NPP at Duke. Also, $N_{\min}$ is lower at Oak Ridge and more limiting in ambient CO₂. It remains so in elevated CO₂ since the N inputs are similar.

Line 444: The statement that leaf N/C ratio is “the only one flexible” is model-specific and should be clarified as a model assumption. Now it is implied as a general ecological characteristic.

Done and acknowledged.

Line 462: Why is mineralization at Oak Ridge relatively high during winter but not Duke?

Mineralization is high in winter due to biomass turnover and decomposition. N/C ratios are lower in the biomass at Duke than Oak Ridge. Thus there is less N released.

Line 475: There are other environmental factors that influence BNF, not only N status; see the reference provided previously. We acknowledge this comment and have addressed it, see above.

4.3 Modeled N dynamics: The nitrogen dynamics are shown in averaged seasonal variations. Could you also present the interannual variability over the simulation period (1996–2006)?

Figure 5 shows the interannual variability over the simulation period (1996–2006) of the nitrogen dynamics. Interannual variability was not investigated in this work. It could be the object of another study.

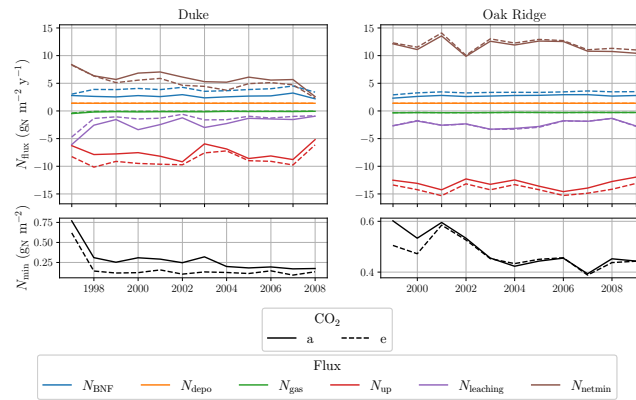


Figure 5. Interannual variability of the bulk mineral N pool (bottom) and its input and output fluxes (top), at Duke (left) and Oak Ridge (right), at ambient (plain line) and elevated CO_2 (dashed line). Input fluxes are positive and are the following : biological fixation N_{BNF} , deposition N_{depo} , and net mineralization N_{netmin} . Output fluxes are negative and are the following : gas losses N_{gas} , plant uptake N_{up} and leaching N_{leaching} . Pool content is shown in $\text{g}_\text{N} \text{ m}^{-2}$ and fluxes are in $\text{g}_\text{N} \text{ m}^{-2} \text{ y}^{-1}$.

References

- Crews, T. and Rumsey, B.: What Agriculture Can Learn from Native Ecosystems in Building Soil Organic Matter: A Review, *Sustainability*, 9, 578, <https://doi.org/10.3390/su9040578>, 2017.
- Davies-Barnard, T., Meyerholt, J., Zaehle, S., Friedlingstein, P., Brovkin, V., Fan, Y., Fisher, R. A., Jones, C. D., Lee, H., Peano, D., Smith, B., Wärlind, D., and Wiltshire, A. J.: Nitrogen Cycling in CMIP6 Land Surface Models: Progress and Limitations, *Biogeosciences*, 17, 5129–5148, <https://doi.org/10.5194/bg-17-5129-2020>, 2020.
- Fisher, J. B., Sitch, S., Malhi, Y., Fisher, R. A., Huntingford, C., and Tan, S.-Y.: Carbon Cost of Plant Nitrogen Acquisition: A Mechanistic, Globally Applicable Model of Plant Nitrogen Uptake, Retranslocation, and Fixation, *Global Biogeochemical Cycles*, 24, 2009GB003 621, <https://doi.org/10.1029/2009GB003621>, 2010.
- Hamiton, J. G., DeLucia, E. H., George, K., Naidu, S. L., Finzi, A. C., and Schlesinger, W. H.: Forest Carbon Balance under Elevated CO_2 , *Ecosystems ecology*, 2002.
- Hupperts, S. F., Gerber, S., Nilsson, M.-C., and Gundale, M. J.: Empirical and Earth System Model Estimates of Boreal Nitrogen Fixation Often Differ: A Pathway toward Reconciliation, *Global Change Biology*, 27, 5711–5725, <https://doi.org/10.1111/gcb.15836>, 2021.
- Intergovernmental Panel On Climate Change: Climate Change and Land: IPCC Special Report on Climate Change, Desertification, Land Degradation, Sustainable Land Management, Food Security, and Greenhouse Gas Fluxes in Terrestrial Ecosystems, Cambridge University Press, 1 edn., ISBN 978-1-009-15798-8 978-1-009-15801-5, <https://doi.org/10.1017/9781009157988>, 2022.
- Iversen, C. M., Keller, J. K., Garten, C. T., and Norby, R. J.: Soil Carbon and Nitrogen Cycling and Storage throughout the Soil Profile in a Sweetgum Plantation after 11 Years of CO_2 -enrichment, *Global Change Biology*, 18, 1684–1697, <https://doi.org/10.1111/j.1365-2486.2012.02643.x>, 2012.
- Kou-Giesbrecht, S. and Arora, V. K.: Representing the Dynamic Response of Vegetation to Nitrogen Limitation via Biological Nitrogen Fixation in the CLASSIC Land Model, *Global Biogeochemical Cycles*, 36, e2022GB007 341, <https://doi.org/10.1029/2022GB007341>, 2022.
- Kou-Giesbrecht, S., Reis Ely, C. R., Perakis, S. S., Cleveland, C. C., Menge, D. N. L., Reed, S. C., Taylor, B. N., Batterman, S. A., Crews, T. E., Dynarski, K. A., Gei, M., Gundale, M. J., Herridge, D. F., Jovan, S. E., Peoples, M. B., Piipponen, J., Rodríguez-Caballero, E., Salmon, V. G., Soper, F. M., Staccone, A. P., Weber, B., Williams, C. A., and Wurzbarger, N.: Overestimated Natural Biological Nitrogen Fixation Translates to an Exaggerated CO_2 Fertilization Effect in Earth System Models, *Proceedings of the National Academy of Sciences*, 122, e2514628 122, <https://doi.org/10.1073/pnas.2514628122>, 2025.
- Li, C., Aber, J., Stange, F., Butterbach-Bahl, K., and Papen, H.: A Process-Oriented Model of N_2O and NO Emissions from Forest Soils: 1. Model Development, *Journal of Geophysical Research: Atmospheres*, 105, 4369–4384, <https://doi.org/10.1029/1999JD900949>, 2000.

- Ma, M., Song, C., Fang, H., Zhang, J., Wei, J., Liu, S., Chen, X., Zhang, K., Yuan, W., and Lu, H.: Development of a Process-Based N₂ O Emission Model for Natural Forest and Grassland Ecosystems, *Journal of Advances in Modeling Earth Systems*, 14, e2021MS002460, <https://doi.org/10.1029/2021MS002460>, 2022.
- Meyerholt, J., Zaehle, S., and Smith, M. J.: Variability of Projected Terrestrial Biosphere Responses to Elevated Levels of Atmospheric CO₂ Due to Uncertainty in Biological Nitrogen Fixation, *Biogeosciences*, 13, 1491–1518, <https://doi.org/10.5194/bg-13-1491-2016>, 2016.
- Poeplau, C., Don, A., Vesterdal, L., Leifeld, J., Van Wesemael, B., Schumacher, J., and Gensior, A.: Temporal Dynamics of Soil Organic Carbon after Land-Use Change in the Temperate Zone - Carbon Response Functions as a Model Approach: SOIL ORGANIC CARBON AND LAND-USE CHANGE, *Global Change Biology*, 17, 2415–2427, <https://doi.org/10.1111/j.1365-2486.2011.02408.x>, 2011.
- Rastetter, E. B., Vitousek, P. M., Field, C., Shaver, G. R., Herbert, D., and gren, G. I.: Resource Optimization and Symbiotic Nitrogen Fixation, *Ecosystems*, 4, 369–388, <https://doi.org/10.1007/s10021-001-0018-z>, 2001.
- Reed, S. C., Cleveland, C. C., and Townsend, A. R.: Functional Ecology of Free-Living Nitrogen Fixation: A Contemporary Perspective, *Annual Review of Ecology, Evolution, and Systematics*, 42, 489–512, <https://doi.org/10.1146/annurev-ecolsys-102710-145034>, 2011.
- Reis Ely, C. R., Perakis, S. S., Cleveland, C. C., Menge, D. N. L., Reed, S. C., Taylor, B. N., Batterman, S. A., Clark, C. M., Crews, T. E., Dynarski, K. A., Gei, M., Gundale, M. J., Herridge, D. F., Jovan, S. E., Kou-Giesbrecht, S., Peoples, M. B., Piipponen, J., Rodríguez-Caballero, E., Salmon, V. G., Soper, F. M., Staccone, A. P., Weber, B., Williams, C. A., and Wurzbarger, N.: Global Terrestrial Nitrogen Fixation and Its Modification by Agriculture, *Nature*, 643, 705–711, <https://doi.org/10.1038/s41586-025-09201-w>, 2025.
- Thomas, R. Q., Brookshire, E. N. J., and Gerber, S.: Nitrogen Limitation on Land: How Can It Occur in Earth System Models?, *Global Change Biology*, 21, 1777–1793, <https://doi.org/10.1111/gcb.12813>, 2015.
- Tian, H., Bian, Z., Shi, H., Qin, X., Pan, N., Lu, C., Pan, S., Tubiello, F. N., Chang, J., Conchedda, G., Liu, J., Mueller, N., Nishina, K., Xu, R., Yang, J., You, L., and Zhang, B.: History of Anthropogenic Nitrogen Inputs (HaNi) to the Terrestrial Biosphere: A 5 Arcmin Resolution Annual Dataset from 1860 to 2019, *Earth System Science Data*, 14, 4551–4568, <https://doi.org/10.5194/essd-14-4551-2022>, 2022.
- Wieder, W. R., Cleveland, C. C., Smith, W. K., and Todd-Brown, K.: Future Productivity and Carbon Storage Limited by Terrestrial Nutrient Availability, *Nature Geoscience*, 8, 441–444, <https://doi.org/10.1038/ngeo2413>, 2015.
- Xu-Ri and Prentice, I. C.: Terrestrial Nitrogen Cycle Simulation with a Dynamic Global Vegetation Model, *Global Change Biology*, 14, 1745–1764, <https://doi.org/10.1111/j.1365-2486.2008.01625.x>, 2008.
- Yuan, Y., Zhuang, Q., Zhao, B., and Liu, L.: Quantifying Global Biological Nitrogen Fixation with In-Situ Data and a Process-Based Biogeochemistry Model, <https://doi.org/10.22541/essoar.174060605.54073858/v1>, 2025.
- Zaehle, S. and Friend, A. D.: Carbon and Nitrogen Cycle Dynamics in the O-CN Land Surface Model: 1. Model Description, Site-Scale Evaluation, and Sensitivity to Parameter Estimates, *Global Biogeochemical Cycles*, 24, n/a–n/a, <https://doi.org/10.1029/2009GB003521>, 2010.