

Dear Editor, Dear Reviewers,

we are grateful for the constructive and inspirational comments to the first version of the manuscript. We thank you for the opportunity to send a revised version of the manuscript.

Below you will find point to point replies to the comments including the changes made to the manuscript.

Most significant changes made to the manuscript include:

- We added to the introduction, methods and discussion text about the role of nitrogen deposition at the site.
- We improved representation of Fig. 1
- We included inorganic nitrogen to the simulated N values profile in Fig. 3c and Fig. 2 and in tables 1 and S2. The value was small (8 grams of N per m² compared to 1652 g N per m² for organic N), but as it had been part of the observed value, reporting it also for simulations is logical
- For several observed vegetation related variables the sigma 15N values were slightly off, as the pre-labeling value had not been subtracted, as should have been. The figures 2 and 3 were correct. The values were corrected in the text.
- Bark had been measured and it was a substantial location for the signal, and its value had been added to the observed values, but this was unfortunately not brought up clearly in the earlier version of the manuscript. We apologize for not being clear about this and have now added this point to the manuscript.
- A section on N status of the forest was added to the Discussion.
- The conclusions were re-written.

Additionally small grammar corrections were made on the text.

We hope that you will take the revised version into the review process.

Kind regards,

Tea Thum

(On behalf of all the authors)

Reply to Reviewer 1

The reviewer comments are in magenta, the replies from the authors in black and text in manuscript in italics.

General Comments:

This is a thorough and well-conceived paper describing efforts to use experimental observations to validate a terrestrial biosphere model, with the goal of evaluating how effectively this model describes ecosystem retention of excess nitrogen. The authors use results from a ^{15}N tracer experiment, where plant and soil N retention was measured three times over ten years, to evaluate the QUINCY model's ability to describe the movement of N through a temperate deciduous forest ecosystem.

The authors are quite thorough in their discussion of the model and how it relates to field observations over time, and do an effective job at explaining where mismatches between simulated and observed N pools occur. The science presented here is sound, and I do not see any critical issues in the methods or interpretation of results in this paper. The work described here is a solid contribution to the literature and should be of interest to BG readers.

My primary critiques are with the contextualization of the study and the results. While the bulk of the paper is spent discussing the model behavior in relation to field observations, there needs to be more attention given to the implications of this work, particularly in the Discussion.

We thank the reviewer for their positive and insightful feedback on the paper. We have tried to improve the manuscript in line with the provided suggestions and pay closer attention to the implications of this work.

Specific Comments by section:

Introduction

- Lines 29-43: Authors should acknowledge long-term decreasing trend in N deposition in certain temperate regions due to air pollution legislation, particularly in Europe and North America. This is particularly relevant given the location of the study in the Northeast U.S. See Mason et al. (2022; <https://doi.org/10.1126/science.abh3767>) and related literature, including Craine et al. (2018; <https://doi.org/10.1038/s41559-018-0694-0>) and Groffman et al. (2018; <https://doi.org/1007/s10533-018-0445-y>).

This is indeed a very relevant point and we have added to the revised version the following text (L40-44):

“There has been a trend in declining N availability in unfertilized ecosystems globally, which has lasted for decades (Craine et al., 2018; Mason et al., 2022; Bassett et al. 2026). Declining N deposition due to air pollution legislation has contributed to reduced N inputs for forests in Europe and north-eastern North America (Lloret and Valiela, 2016; Schmitz et al.

2019). *Declining N deposition, taking place simultaneously with decreases in sulphur deposition, has been shown to have positive effects on some forests (Dalton et al., 2024).*”

The trend that the reviewer is here mentioning was also noticed at the long-term monitoring site close to our study site and we’re now bringing up this information in the Methods section and also added discussion in the Discussion section, which influence this might have for our study.

- A little more background on the QUINCY model is needed in the introduction. We need to understand more about why this model is chosen. Is it the only model that includes an explicit ^{15}N cycle? If not, is there anything of note that makes this model most suited to simulating results from this experiment?

Some studies have developed a ^{15}N model to e.g. study tracer experiments (e.g. Müller et al, 2004; Liu et al., 2026). These are used at site scale. QUINCY is a relatively new model that has been developed with a particular focus on the nutrient cycles, and it can be run at multiple different spatial scales. QUINCY has fully coupled water, energy, carbon and nitrogen fluxes, therefore allowing studies of many aspects of biogeochemical cycles and interactions between vegetation and atmosphere.

We have now added to the text (L75-79):

“While site level models used to study tracer experiments have been developed (e.g. Inselbacher et al, 2013, Mueller et al., 2014, Liu et al., 2026) and some simple models do describe the ^{15}N cycle (Vitousek et al., 2024), QUINCY as a TBM has the advantage of having fully coupled energy, water, carbon and nutrient cycles, allowing to study several aspects of biogeochemical cycling.”

Methods

- Line 93-94: What is the background N deposition at the site? Generally, what are the trends in that deposition? Is it increasing or decreasing, and how does it compare to places with high N deposition?

The background deposition at the site was previously included in Table 1, but we have now moved this information to the Methods section, as suggested also by the other reviewer. In addition, we made a plot of the N deposition input used in the model in the supplementary material (Fig. S1).

There is a US Environmental Protection Agency long-term monitoring site located approximately 14 km north of the study site. N deposition has indeed decreased by about one third between 2000 and 2020, from 13.4 to 8.9 kg N ha⁻¹ yr⁻¹. Compared to areas experiencing high levels of N deposition (e.g. the critical load for temperate forests has been estimated to be 10–15 kg N ha⁻¹ yr⁻¹; Xie et al., 2024), this level of deposition can be considered as changing from high load to moderate.

We have added these points to the Methods section (L68-73):

“The prescribed N deposition (0.87 gN m⁻² yr⁻¹) (Fig. S1) was similar to the observations at the site (0.7-0.9 gN m⁻² yr⁻¹). The level of nitrogen deposition has decreased by about one

third between 2000 and 2020, from $1.3 \text{ gN m}^{-2} \text{ yr}^{-1}$ to $0.9 \text{ gN m}^{-2} \text{ yr}^{-1}$, at a long-term monitoring site operated by the US Environmental Protection Agency, which is located close to the site (Butler et al., 2015; U.S. Environmental Protection Agency Clean Air Markets Division, 2024). This level of deposition can be considered as changing from high load to moderate (Xie et al. 2024)."

Results

- Table 1: Color coding to quickly show under or over estimation would be helpful

This is indeed a good idea. However, the guidelines to the authors in the Biogeosciences (<https://www.biogeosciences.net/submission.html#figurestable>) state that: "*Coloured table cells should be avoided.*" This is why we decided not to follow this suggestion. We considered adding in some other way to have the bias visibly, but the table was already quite busy, so we didn't have a good solution.

- Figure 1: would benefit from larger panels. The figure is hard to read as it is.

We apologize for the unclear figure. To remedy this, we increased the size of the panels, tick marks and extended the lowest panel to fill the two columns.

- Table 2: Same as Table 1, use color coding for under and over estimation

As mentioned above, we interpreted the journal guidelines so that this would not be recommended.

Discussion

- Section 4.1 is very dense, I recommend splitting with subheadings to make it more digestible.

We completely agree with the reviewer and are grateful for this suggestion. Section 4.1 was indeed lengthy and dense. For now, we have split it into two sections: temporal dynamics of the tracer signal in vegetation and soil. We also split the first section of the results to mirror the same.

- Line 297-298: Do you have a sense for why the model underestimated these C and N pools? If so, that should be stated.

The sentence in lines 297-298 was:

"It is important to note that the model underestimated the C and N pool size of fine roots and C pool size of the leaves, and this might have some influence on the occurring dynamics."

The simulated size of leaf C pool was not largely underestimated (14 %) and the underestimation of C pool was much more severe for the fine roots. The leaf C:N ratio is 23, which is closer to the lower end of the allowed C:N ratio for this plant functional type in QUINCY. The allowed range for the C:N ratio in QUINCY for this plant functional type has been estimated from the TRY database (Kattge et al., 2011) and is between 13.7 and 38.7 (Miinalainen et al., 2025). In N limited conditions the plants could allocate more biomass to

fine roots in order to increase N uptake from the soil. Because the simulated leaf C:N ratio was lower than the observed and was not close to the upper threshold, its influence in the allocation is likely not pronounced.

The total plant C in observations was $11\,140\text{ gC m}^{-2}$ and in the simulation $12\,771\text{ gC m}^{-2}$, so they were relatively close to each other, with the simulations showing 15% overestimation, and the observation-based estimate includes an unknown error. All the other plant C pools than the wood pool were underestimated by the model. This is likely the result of the simulated allometric relationships that are not aligned with the observations or the time-scale of hard wood formation. Either parameter is not well constrained from the available site-level observations.

We have added discussion about this issue to the manuscript (L319-322):

“Although the simulated total plant C pool ($12\,771\text{ gC m}^{-2}$) was close to the observed value ($11\,140\text{ gC m}^{-2}$), the other vegetation C pools, except for wood, were underestimated. This suggests that QUINCY has some difficulties with C allocation. The simulated total N in vegetation (86.3 gN m^{-2}) was over double the observed amount (39.2 gC m^{-2}), reflecting the overestimation of N in the soil.”

Lines 316-318: There should be some further explanation for this, as 2mm is typically the standard cutoff for fine roots. Do the authors believe that this impacted results at all? Either way, the effect of this discrepancy, or lack thereof, should be specified.

The reviewer is referring to the fact that the measurements had a cutoff of 1 mm and the simulation had a cutoff of 2 mm for the fine roots.

Generally, both 1 mm and 2 mm are used as cutoff thresholds in the observations. The cutoff of 1 mm was chosen so that these observations would be consistent with earlier studies of the site (Goodale et al., 2015 and Goodale, 2017). Furthermore, it has been demonstrated (e.g. Fisk et al. 2004; Frey et al., 2025) that $<1\text{ mm}$ fine roots constitute the majority of fine root biomass and exhibit the greatest sensitivity to nutrient availability in this and similar forest types.

The discrepancy in the cutoff threshold between the model and observations could lead to the model overestimating the amount of fine roots and underestimating the amount of coarse roots. However, the model was underestimating the fine roots more considerably than the coarse roots. (The ratio between coarse and fine root C was 3.0 in the observations and 9.3 in the simulations.)

The observations showed more modest turnover than the model simulations for the ^{15}N signal in the fine roots (Fig. 1b). In the observations the long-term behaviour between fine and coarse roots did not differ much, whereas in the simulations the dynamics in the fine and coarse roots were very different because of the model structure (Fig 1b,c). Because of this, we would not expect that the different cutoff threshold impacted strongly our results.

We have added these points to the revised manuscript (lines 338-342):

“The cut-off point of 1 mm for the fine roots in these observations was chosen to align with earlier studies conducted at this site (Goodale et al., 2015; Goodale, 2017). It has also been demonstrated that fine roots measuring less than 1 mm in diameter constitute the majority of fine root biomass and exhibit the greatest sensitivity to nutrient availability in this and similar forest types (Fisk et al., 2004; Frey et al., 2025). We do not expect this discrepancy between the simulations and observations to have a significant impact on the comparison.”

- Lines 401-408: This presents the question of why you did not use the JSM rather than the basic soil model in QUINCY. The authors should provide a justification for not choosing JSM (benefits of simpler parameters, computational power, etc.)

JSM has been developed for studying detailed soil processes and while it can be a very valuable tool for understanding processes such as soil exudation (Schufft et al., 2025), but to make its application worthwhile, more site-specific information on specifically the microbial stoichiometry and mineral sorption characteristics of the soil would be important. We therefore followed the principle of Occam's razor and applied the simpler model with less free parameters in this study.

We added the following text to lines 450-453 to address this point:

“To be able to benefit from the increased process representation of the JSM in future studies, observations on microbial biomass, mineral-associated organic carbon and their ^{15}N values as well as dissolved organic carbon would be relevant, so that the underlying processes can be understood.”

Conclusion

- This should be tightened up, as it reads too much like a restating of the discussion.

Thanks for this remark. We agree with the reviewer and have re-written the conclusion section by keeping this in mind.

- The paper ends abruptly and would benefit from a sentence or two summing up the primary findings, stating the implications of those findings, and suggesting future directions for this work (similar to what was stated in the abstract).

This is a very good point. We have added a couple sentences to end the manuscript that pave the way for future directions, e.g. making use of remote sensing products together with QUINCY (lines 471-475):

“QUINCY can therefore be used in studies related to N dynamics and climate change, such as helping to examine the role of changing N deposition and increasing CO_2 in decadal timescales, as studied for example by Bassett et al. (2026). Recent spaceborn observations of ^{15}N (Yang et al., 2025) together with QUINCY's ability to simulate the ^{15}N cycle and leaf chlorophyll, which is also observable from space and simulated by QUINCY (Miinalainen et al., 2025), will help to move towards better understanding of the global N cycle.”

Technical Corrections:

- Line 213: Typo, “The observations showed a smaller enrichment peak as the simulations”, replace “as” with “than”

Thanks, we corrected this.

- Line 345 & 353: Typo, should be ^{15}N

Thanks for the remark. We have now corrected this.

- Line 346-348: Sentence is a bit confusing and contains a typo on line 347

The sentence that the reviewer is referring to is:

“In the observations the top soil layers became more enriched from the incorporation of ^{15}N from the overlying litter layer, whereas in the simulated top soil was most enriched one year after the tracer application, and then became more depleted as the signal moved deeper to the soil and the vertical soil profile of the ^{15}N tracer started to get flatter (Fig. 3).”

We apologize for the unclear formulation and typo. We have now modified the text to make clearer what was relevant for the observations and for the simulations.

“In the observations the top soil layers became enriched because the ^{15}N from the overlying litter layer was incorporated into the soil organic matter. The top layers showed some depletion by 2018. The simulations showed larger changes in the top layers across the years and also the ^{15}N tracer started to be transported to deeper soil layers, which caused a flattening of the vertical soil profile of ^{15}N (Fig. 3).”

References

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Reply to Reviewer 2

The reviewer comments are in magenta, the replies from the authors in black and text in manuscript in italics.

This manuscript tracks nitrogen dynamics within a temperate deciduous broadleaf forest by running a ¹⁵N tracer addition experiment both at a site in New York and a paired experiment in the QUINCY land model. The observational data are used to evaluate the nitrogen cycling processes in QUINCY and include ¹⁵N measurements across soil and plant pools. The observations span approximately 10 years and the model simulations match this time frame while also including a simulation at 30 years following the end of the observational data.

Overall the model does a good job at tracking the observations and where there are deviations the authors do a good job at explaining the why model and observations may deviate and how this information can be used to improve the QUINCY model. The study is well conducted, and the manuscript is well written. The topic is also to be of high interest to readers and is a good fit for Biogeosciences. In general, my comments are minor.

We would like to thank the reviewer for their positive feedback and the insightful comments, which helped us to improve the manuscript.

1. L1-2: First sentence seems a little circular (i.e., climate change influences... new conditions due to changing climate). Rewrite.

Thanks, that's a good point. We shortened the first sentence to:

"Climate change influences plant-atmosphere interactions as ecosystems face new conditions (Canadell et al., 2022)."

2. L51: Can you provide a citation or more detailed explanation of optimal N fertilization for forest management?

The citation for this sentence was the same as in the previous sentence. We have now repeated that here.

3. L79: Change "will" to "does" in the question, as the question includes the present.

Thanks, we changed that.

4. L110: Although this paper used deciduous temperate broadleaf as a PFT, from this sentence it is unclear if a site (or for simulations at larger spatial scales, a grid cell) can be represented by more than one PFT (i.e., a mix of PFTs).

That's right, apologies for the confusion. We modified the sentence to make clear that the site level version uses one PFT per site (lines 120-121):

"Different ecosystems are represented by different plant functional types (PFTs) and in the site level version each site is represented by one PFT."

5. L134-135: BNF is mentioned but my understanding is that it was not simulated for this study. Does the model allow BNF to be switched on and off for a PFT or is it always happening or does it occur in some PFTs but not others? Also, is there asymbiotic, free-living BNF?

Apologies for the lack of clarity on this topic. Asymbiotic BNF in the litter layer is dependent on soil temperature, soil moisture, the N deficit in litter decomposition, and a parameter that describes the maximum potential fixation rate. Additionally, asymbiotic BNF is suppressed if the amounts of ammonium and nitrate in the litter layer exceed a critical threshold. Nitrogen fixed through this mechanism is added to the fast soil organic matter pool. These parameters have been adjusted to align with the findings of Davies-Barnard and Friedlingstein (2020).

Symbiotic BNF by trees is based on Rastetter et al. (2001) and Meyerholt et al. (2016). It is described as a dynamic trade-off of carbon and nitrogen opportunity costs.

We have added the following text to the manuscript (lines 134-138):

“Symbiotic biological nitrogen fixation (BNF) by microbial-tree partnership is described as a dynamic trade-off of carbon and nitrogen opportunity costs, following Rastetter et al. (2001) and Meyerholt et al. (2016). Asymbiotic BNF in the litter layer depends on soil temperature, soil moisture as well as on the N deficit in litter decomposition. Nitrogen fixed through this mechanism is added to the fast soil organic material pool. The parameters governing BNF have been adjusted to align with the findings of Davies-Barnard and Friedlingstein (2020).”

We removed the earlier sentence (*“Biological nitrogen fixation (BNF) calculation is based on plant demand and the relative costs of root uptake of mineral nutrients and biological fixation (Meyerholt et al., 2016).”*)

6. L174-175: Given that N deposition is prescribed and not affected by the processes in the ecosystem, perhaps this sentence should be moved to the Methods.

We initially placed this sentence in the Results section because the prescribed value is based on a global product. However, we agree with the reviewer and have now moved it to the Methods section, removing the line from the table:

“The prescribed N deposition ($0.87 \text{ gN m}^{-2} \text{ yr}^{-1}$) was similar to the observations at the site ($0.7\text{-}0.9 \text{ gN m}^{-2} \text{ yr}^{-1}$).”

7. L218-220: This sentence is unclear. It states that fine root d15N is higher in the top layer for (0-10 cm), in part because there is a lot of fine root biomass at 10-20 cm. That does not make sense to me as it suggests the high root biomass at 10-20 cm should decrease d15N in the top layer.

The reviewer is referring to points in these two sentences:

“The first observed $\delta^{15}\text{N}$ value in 2007 includes only the upmost layer (0-10 cm), whereas the other observations include fine roots in all the soil layers. The value in the upmost layer is larger than averaged over all the layers, since a lot of fine root biomass is located also at depth 10-20 cm and the $\delta^{15}\text{N}$ enrichment decreases with depth.”

We apologize for the unclear expression in this original version. There are less roots in the 10-20 cm layer than in the utmost 0-10 cm. We modified the latter sentence into (L238-239):

“The value in the upmost layer is larger than averaged over all the layers, as it is where the largest amount of fine root biomass is located and the $\delta^{15}\text{N}$ enrichment decreases with depth.”

8. L254: Add “soil” after “simulated”.

Thanks, we made this addition.

9. L282-283: In addition to the simulations, the observations also point to a fairly closed nitrogen cycle (excluding the initial loss in recovery following immediate application but looking at the differences in Figure 4a between 2008, 2012, 2017).

The reviewer has a good point. We have added this point to the discussion (Section 4.3), along with discussing what we can infer about the N limitation of the model and simulations (more on this in the reply to comment #14).

10. L334-336: I think it would be clearer to say “This influence was shown by isolating the fast pools...”.

Certainly, we modified the sentence according to the suggestion.

11. L381-382: This sentence is unclear.

The sentence that the reviewer is referring to is:

“Because of the high C:N ratio in wood, this would imply larger carbon sink compared to N residing in other compartments”.

We apologize for the unclarity and have modified this sentence to (L423-424):

“Due to the high C:N ratio of wood, wood can sequester more carbon per unit of nitrogen than other plant compartments.”

12. L397-400: It would be helpful to comment on whether trees at the site form ectomycorrhizal or arbuscular mycorrhizal symbioses.

Sure. The site consists evenly of trees having ectomycorrhizal and arbuscular mycorrhizal associations. We have added this information to both the site description and to this discussion point.

13. L409 and 534-537: The authors names should be written for this reference (instead of just the abbreviation).

Apologies for this oversight. We have fixed this.

14. Can it be inferred that N limitation is stronger in the simulations than the observations? Figure 3c shows higher soil N in the simulation and figure 1e shows higher aboveground

pools and lower belowground pools in the model (i.e., greater relative investment in aboveground tissues in the model).

Perhaps the strength of the N limitation could be inferred from the leaf stoichiometry and the difference in $\delta^{15}\text{N}$ between the soil and plant compartments. The simulations show a leaf C:N ratio of 23, whereas the observations show a ratio of 35. This would suggest that the simulations have lower nitrogen limitation than the observations.

Another metric for the nitrogen deficiency can be considered to be the $\delta^{15}\text{N}$ difference between the plants and the soil. In the observations this difference (in 2006, before the start of the experiment) was 4.6 per mille (average of all the plant pools -1.83 per mille ; average of all the soil pools: 2.74 per mille). In the simulations, this value was 0.5 per mille (averaged plant pool: -1.67 per mille; averaged soil pool: -1.15). The $\delta^{15}\text{N}$ in plants is usually closer to the soil value in N limited systems. However, the observational values also demonstrate the influence of mycorrhizae, which fractionate strongly, and can result in enriched soil values.

Although the N limitation has some influence on the allometric relationship between leaves and fine roots in QUINCY (Thum et al., 2019), it would not itself determine the differences in the above- and belowground nitrogen pools.

We have added discussion about the N status of the observed ecosystem and simulations in the discussion in Section 4.3.

15. I think the manuscript would benefit from a greater discussion of the implications of the study, particularly in the Conclusions section.

We thank the reviewer for this comment and agree with it. We have rewritten the Conclusions to include more of the work's work's implications. These points include:

- as the simulations show, a large proportion of the tracer remained in the wood compared to the other plant compartments. This would indicate a larger sink potential of vegetation due to the larger C:N ratio in wood compared to the other plant compartments

- this study further highlights the functionality of the ^{15}N cycle implemented in QUINCY, paving the way for the use of novel ^{15}N satellite products (such as by Yang et al., 2025) in the study of global level biogeochemical cycles

- shows that such tracer experiments can be used to evaluate the turnover rates of the nitrogen pools in these models

16. Sentences in the main text that introduce the figures or tables are unnecessary (e.g., L206, L253, L264, L287-288). However, upon deleting them, some sentences will need to explicitly mention figures (e.g., in parentheses).

Sure, we changed this according to the suggestion.

17. Sometimes the 15 in ^{15}N is not superscript.

We have now gone through the manuscript carefully and fixed this.

18. Figure 1c shows some ^{15}N in coarse roots in the model simulations. This seems inconsistent with Figure 4b which shows no recovery in coarse roots in model simulations.

Thank you for this insightful remark. In the model simulations, the recovery of the coarse roots happens some years after the tracer is added, reaching a maximum level of 6.6 per mille. However, this is not visible in Fig. 4, which shows the recovery rates for the different pools. When calculating the recovery rates, the size of the pool is taken into account, and the value for the recovery rate for the coarse roots in 2012, for example, is 0.84%, which is not visible in the bar.

19 Figure 1 caption: There is no panel f. As for the description of panel d, should that be a combination of sapwood and heartwood?

Thanks for noticing this mistake, which stems from an earlier version of the figure. Indeed, in the current figure we do not have panel f and sapwood and heartwood are combined. We have now corrected this in the caption.

20 Figure 3c: Is this total soil N (inorganic plus organic)?

This is a very good remark. In the original figure only organic was shown, but we added in the inorganic and also mention this now in the caption.

References

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