Response to reviewers for Cheng et al., submitted to *Biogeosciences*
https://www.biogeosciences-discuss.net/bg-2018-505/#discussion

To the reviewers and editor: Thank you for taking the time to provide your thoughtful feedback on our manuscript. We appreciate your support of the peer-review publication process and open-access science. Below are our responses to your comments, with the original reviewer comment in black and our response in blue—including changes we will make to our manuscript.

Editor's Comments

many thanks for your detailed responses to the reviewer comments. The manuscript may be acceptable for Biogeosciences after some major revisions. When revising, please make sure that your responses are adquately reflected in the revised manuscript. Please also explicity consider how much this modified version of CLM needed to interpret the 15N data is representative of the model behaviour of the CLM5 version used for climate assessments.

Please find attached our most recent manuscript with previously proposed changes to our text incorporated. In response to the Editor's comments, we have also added new text and modified existing text throughout the manuscript to emphasize how results from our modified version of CLM (which we now describe as CLM5 with a closed N cycle) inform knowledge about how the modeling and empirical communities can work in tandem to improve N cycling in the default version of CLM (which we now describe as the model configured with an open N cycle). Overall, the comparison between the open and closed versions of the N cycles in CLM5 allowed us to confirm that the difference in N cycle tightness between the model and field data was not the reason for the mismatch in N fate between CLM5 and ^{15}N experimental measurements. From this comparison, we identify that to improve the match between field and model-measured N fates in the version of CLM5 that will be used for climate assessments, future research could explore improvements to: a) the estimates of C:N ratios of plant and soil pools and their importance in better retaining N inputs in ecosystems, b) reduced fluxes of N deposition, N fixation, and denitrification, and c) competition between immobilizers and plants for soil inorganic N. In our abstract, results section, and discussion section, we indicate which patterns between both versions of the model are similar and explicitly define when there is a divergent response between the models. We also more clearly state that our suggested changes to CLM5 are based on our understanding of similarities between the modified and default configurations of the model's N cycle. Finally, we revised the conclusions to make these points clearer to the reader.

Reviewer 1 Comments

1. Cheng et al. present a model-data comparison of ecosystem N recovery at several temperate forest sites, using two versions of the CLM5 -land model and a number of 15N tracer field experiments. They also use the results to give estimates of ecosystem C storage responses to changes in N availability. The paper is very well written and thoroughly describes the conducted work in good detail. I particularly like the design of Figure 2 to visualize the model-data aspect. The study design is relevant, as C-N models are best informed by field experiments that include measurement estimates of both C and N processes. It is also an advance over other model studies such as Meyerholt & Zaehle (2015), where only one site was used for a model-data comparison of ecosystem N recovery. However, I am not convinced that this study is a good fit for BG, as it suffers from model limitations that make the results not meaningful to a general biogeoscientific audience, whereas the study has

interesting insights for the land modelling community that are laid out in the discussion (e.g. section 4.1). Therefore, I see the paper as a fit for e.g. GMD, but cannot recommend publication in BG.

We appreciate the reviewer's recognition of our manuscript's contribution to the modeling community. Although the model we evaluated is limited in the ways it depicts C and N cycling, we believe our results are still useful to both modelers and empiricists. Below we identify some ways we, and the other reviewers, identify our manuscript as relevant to the broader biogeochemistry community.

- First, our study is the first to synthesize ^{15}N tracer recovery data from across multiple measurement sites over a time period of up to almost 20 years. This synthesis is useful both for empiricists and modelers interested in using field data to evaluate N cycle processes in both field and modeled ecosystems.
- Second, our study is the first to evaluate the movement of N additions, its long-term fates, and the response of temperate forest C stocks to added N in a land model (CLM5) that is part of a state-of-the-art climate model (Community Earth System Model) on a timescale longer than a few years. This model is widely used by biogeochemists, climate scientists, and policy makers—making it a particularly important model to evaluate for its carbon cycle sensitivity to N. CLM5 is also one of the few U.S. terrestrial models involved in the global Coupled Model Intercomparison Project (CMIP) and until recently, was the only one part of this project with a N cycle. Modeling experiments that more closely simulate field experiments, such as the one we present in our paper, have also been recently discussed as important additions to understanding the biogeochemistry of ecosystems, including in Wieder et al. (submitted) and Prentice et al. (2015).
- Third, *Biogeosciences*' scope states that "Experimental, conceptual, and modelling approaches are welcome." Our study directly brings together experimentalists and modelers—as well as data from both field experiments and modeling experiments—to demonstrate how measurements and models can be used in concert to identify limitations in an Earth system model used to project future climate and biogeochemistry.

To emphasize these points, we will modify the last paragraph of the introduction in the following ways:

- Include sentences that say "…to date, there have only been a handful of individual site-level field studies published that have examined the long-term fates of N….This study addresses this gap by compiling a summary of ^{15}N recovery data from long-term ^{15}N tracer experiments" (Page 4, Lines 18-20).
- Replace the last two sentences of the introduction with the following language that better describes our contributions to both the field and modeling community: "Through this novel data-model comparison project, we provide a synthesis of long-term, ecosystem ^{15}N addition experiments—and identify how differences in temporal dynamics of N cycling between field measurements and CLM5 lead to divergences in measured and modeled N fate and ecosystem C responses to N additions" (Page 4, Lines 24-26).

2. The main issue I see is that neither the standard or the adjusted version of CLM5 used here appear capable of simulating plausible C and N cycle representations, the conclusion being that they cannot presently be used to give e.g. meaningful estimates of C sink responses to N change. The authors are

> aware of this for the standard version and fully describe the changes they made to come up with the adjusted version that is supposed to be a better fit for the site selection. To my understanding, however, they fix a hole (unrealistic equilibrium C and N stocks) by creating another one (e.g. eliminating "denitrification"). This fixes some site specific measures, but it also creates a C-N model without a plausible N cycle.

We share the reviewer's interest in the process of denitrification, and how to improve its field quantification and model representation; both characterizations remain highly challenging and active areas of research. This flux is extremely difficult to constrain with field measurements due to both its high degree of spatiotemporal heterogeneity and the challenge of measuring N_2 fluxes (Groffman et al., 2006; Butterbach-Bahl et al., 2013). There is a growing body of N_2O measurements, but these fluxes from temperate forests are usually extremely small (e.g., summarized by Butterbach-Bahl et al. (2013) and Liu and Greaver (2010); averaging 0.0087+0.0025 kg N_2O–N ha^{-1} yr^{-1} per 1 kg N ha^{-1} yr^{-1}). These values fail to capture the larger losses of N as N_2, for which there are few stand-scale annual estimates. New techniques for measuring N_2 flux concurrent with continuous soil environmental data have allowed estimates of whole catchment denitrification for a just a few sites, yielding estimates of 0.16 - 0.26 g N m^{-2} yr^{-1} (Duncan et al., 2013) and ~0.39 g N m^{-2} yr^{-1} (Morse et al., 2015) at deciduous hardwood sites receiving 0.8-1.0 g N m^{-2} yr^{-1} in N deposition.

We turned the process of denitrification off in one of our model configurations for two reasons. First, these handful of field-based measurements of denitrification in temperate forests (mentioned above) reported that rates of denitrification were relatively small. Second, ecosystem N stocks are well-measured compared to gaseous N input or output fluxes, and the constraint of the observed soil N stocks could be reached only by greatly reducing or even halting denitrification coincident with reducing N fixation to better match site-level conditions (which lack symbiotic N fixers and near negligible heterotrophic N fixation; e.g., Tjepkema (1979), Roskoski (1980), Grant and Binkley (1987), Hendrickson (1990), Barkmann and Schwintzer (1998)). Similar soil N stocks could have been achieved with small rates of both types of N gas flux, but addressing the model's overestimates of N fixation and denitrification are topics of active research and development. In the current version of the model, denitrification accounts for 99% of modeled N losses (Figure 1), which is inconsistent with relatively well-measured hydrologic N losses and ^{15}N tracer results such as those summarized here: Catchment data from hundreds of sites across the Northeast U.S. show that NO_3^- leaching amounts to <10% and up to ~50% of N deposition of 6-11 kg N ha^{-1} yr^{-1}; loss of DON amounts to another 1 or more kg N ha^{-1} yr^{-1} (Aber et al., 2003). In addition, past studies that we have cited report that previous versions of CLM grossly overestimate (> 90%) denitrification both spatially and temporally (Houlton et al., 2015; Nevison et al., 2016). Rather than include this process in our adjusted model and its implausibly high estimates for these temperate forests, we turned off denitrification to test model performance with inputs and loss fluxes closer to reported measurements for these types of forests (e.g., Yanai et al. (2013) and Bernal et al. (2012)). Our two model configurations serve as sensitivity tests so that we can understand the fate of N additions in a system with a relatively closed N cycle, and another with a highly open N cycle.

We do acknowledge both versions of the model imperfectly represent N cycle processes. However, given the popular and continued use of CLM5, CESM, their model outputs, and their use in international climate simulation comparisons, identifying the limitations to these models is important for developing appropriate interpretations and uses of these models and their projections in the biogeosciences community. Comparing the default version of CLM5 against a version with denitrification eliminated allowed us to specifically identify if, and how, excessively high N inputs and losses contributed to the drastic underestimation of N recovery in simulated forests. Considering this comment and other reviewer suggestions, we will reframe our two models as representative of two alternative scenarios—one with a highly open N cycle (model with high N inputs with denitrification on) and one with a relatively closed N cycle (more realistic N inputs with denitrification off). In addition to shifting language of "default" and "modified" models to "open" and "closed" models, we will add the following sentences in the Methods (Section 2.3.1) to clarify why the adjusted (now "closed") version of the model was included. These sentences will read:

"Prior versions of CLM also greatly underestimate measured rates of N losses to leaching and runoff in these ecosystems (e.g., MacDonald et al. (2002), Aber et al. (2003), Nevison et al. (2016), Thomas et al. (2013a)). Because CLM5 continues to underestimate leaching and overestimate N inputs and denitrification losses (see below; Fig. 1), we simulated how each of the field sites in Table 1 would respond to N additions under a) CLM's default N cycle with high N inputs and losses (i.e., open N cycle), and b) under an alternative "closed" version of the model where N inputs were reduced to better match observations and N losses to denitrification were correspondingly halted to allow the model to build realistic soil N pools, along with N leaching losses (see Section 3.1)…Our alternative model included in this study is thus an oversimplification included to examine model C-N responses in ecosystems with a much more closed N cycle than the widely used version, details of which can be found in Lawrence et al. (2018). Our results below highlight how sensitive CLM5 is to the openness of its N cycle, an emergent property that should be the focus of future model development" (Page 7, Lines 7-11 and Page 8, Lines 6-9)

Similarly, our dC/dN calculations provide an estimate of what the model simulates to be the C response of ecosystems to N addition and how sensitive CLM5 is to changes in N cycle openness. To make this clear to the reader, we will add additional text within our results and discussion section saying that our dC/dN estimate provides a sensitivity test for how dC/dN changes with the openness of a system's N cycle through our comparison of open and closed model depictions of N cycling against our best estimate of dC/dN from field measurements. The first sentence of the section will read, "To scale and compare the effect of plant and soil N recoveries on forest C sinks between CLM5 with a closed N cycle and field measurements, we estimated changes in plant, soil, and total C stocks (i.e., sum of plant and soil stocks) in response to N tracer or fertilizer additions—referred to as $(dC/dN)_{plant,}$ $(dC/dN)_{soil,}$ $(dC/dN)_{total}$, respectively (Fig. 4)" (Page 13, Lines 2-4). We will also end this section with the following caveat: "Because of existing model limitations in N cycle representation, model-estimated values of dC/dN are intended to provide a sensitivity test of how the modeling of N fates can affect model estimates of ecosystem C response to N additions relative to what is expected from field measurements" (Page 14, Lines 10-11).

3. Apparently on average, live wood C:N ratios are at the level of foliage (Table 2)?

Yes, the model prognostically predicts that live wood C:N ratios are similar to leaf C:N as indicated in Table 2. We also find these C:N ratios for live wood to be too low, and discuss the importance of assembling field measurements to constrain modeled C:N ratios of plant pools in Section 4.2.

4. The adjusted ecosystem N residence time appears rather arbitrary with a huge range (p9l18).

It is interesting to note the large range in ecosystem N residence times (note: in response to Comment 17, we will be changing this terminology to "turnover time"). However, the mean ecosystem turnover time for the default model (880 years) is similar to the field-based estimate of turnover time at Arnot Forest (Goodale, 2017) or Hubbard Brook (Yanai et al., 2013) (i.e., [7-8 tons of N ha^{-1} in soils and plants] / 8-9 kg ha^{-1} of N deposition = ~800-1000 years), for example. The wide range in model-estimated turnover time across sites results from ecosystem-specific differences, including variations in factors governing organic N storage in soils (e.g., texture, past disturbance). We will add this sentence into the revised manuscript: "The wide range in ecosystem N turnover time results from site-specific differences, including factors governing N storage in soils (e.g., texture, past disturbance)" (Page 11, Lines 1-2).

5. Also, although the presentation is commendably thorough, the model formulations of key N processes are not clearly given. Since this is central to what we can expect the model to do as far as N, they deserve explicit description beyond reference to other studies (in particular, Lawrence et al. 2018 is not listed in the references). At this state it is not clear how N fixation is calculated - the model uses FUN, but Shi et al. describe that FUN is only used to determine the partioning between uptake and symb BNF, whereas total N input uses CLM4 standard? So is BNF still NPP-based? Similarly, it is not clear how loss fluxes are determined in this study - but ecosystem N inputs and outputs a central to how N recovery is calculated.

We will include the following additional text about how N fixation is calculated in CLM5: "Free-living biological N fixation is calculated as a function of annual evapotranspiration and added to the soil mineral N pool. Symbiotic N fixation is passed directly to the plant and depends on plant N demand, the cost of N fixation for the plant, and soil temperature (Lawrence et al., 2018; Lawrence et al., in review); details on the model's representation of N fixation is available at https://escomp.github.io/ctsm-docs/doc/build/html/tech_note/FUN/CLM50_Tech_Note_FUN.html)" (Page 6, Lines 11-14).

6. In my opinion, these model-related problems push the study more towards a well-presented model-tuning exercise - which is not bad at all and definitely needed for model evaluation, but not relevant to the broader BG readership. To this end, I disagree with the authors on some of the early discussion points: "Our study provides insight into which model assumptions are consistent, or inconsistent, with experimental results." (p13l13) - So if fixed ecosystem N inputs, unrealistic C:N ratios and the elimination of gaseous N losses lead to a number that is consistent with experiments, does that make the assumptions correct?

In our earlier response to Comment 2 (and in responses to Comments 16 and 39), switching our descriptions of the models from “default” and “adjusted” to “open” and closed” should shift emphasis to comparing two versions of the model that represent ecosystem extremes in N cycling openness, of which the closed model better matches known N input and leaching loss fluxes in these forests. These two model versions serve as a sensitivity test of how forest biogeochemistry changes when the system is more closed versus more open. We believe that pointing out the difference in N recovery between these two versions of CLM5 is of interest to a broad biogeochemistry readership to identify the contrast between observations and model simulations (Houlton et al., 2015), and because this kind of comparison encourages field data on key ecosystem processes and traits to be synthesized so that further work can be done to improve model representations of ecology.

7. Other things: - I think the title should state that the study is about N recovery rather than C sinks. Also, I understand "decadal" to mean decade-by-decade, rather than "some experiments last over 10 years".

We changed our title to shift focus to N recovery (fate) as suggested by the reviewer, while retaining our intended scope of analysis examining C cycle responses at decadal timescales (using the Oxford English Dictionary definition of “belonging to a decade or period of ten years.”) We do think it is important to indicate that our analysis includes comparisons of N recovery at timescales relevant to meaningful C storage and to capture more than transient short-term effects. We have modified our title to read, “Decadal fates and impacts of nitrogen additions on temperate forest carbon storage: A data-model comparison.”

8. - Abstract p2l11 ff: It appears that for longer timescales, model plants did not acquire more than twice the experimental N recovered (23% vs 13%).

We will adjust the wording to read, “In particular, the model configuration with a closed N cycle simulated that plants acquired more than twice the amount of added N recovered in 15N tracer studies on short timescales (CLM5: 46 ± 12%; observations: 18 ± 12%; mean across sites ± 1 standard deviation), and almost twice as much on longer timescales (CLM5: 23 ± 6%; observations: 13 ± 5%)” (Page 2, Lines 7-10).

9. - very minor point, I was a bit confused by the order of in-text citations for multiple references in the same bracket. Since the order is not by year or by name, it is by relevance? But this can’t be the case for the citations in p3l12f.?

We will adjust the order of citations in our manuscript to be listed by year and then alphabetically by author last name.

10. - p6l25: There is a double "g N" in the middle.

We will correct this typo.

Reviewer 2 Comments

11. This paper tested a terrestrial ecosystem model with coupled C and N cycles against 13 long-term 15N tracer addition experiments at 8 temperate forest sites. It thus targets a central quantity that has received great attention and has served to synthesize the complex nature of C-N cycle interactions: Where and how much N is retained in the ecosystem? How much C is additionally stored in plants and soil per added N? Model evaluation in this respect is thus a highly welcome exercise. The model in its original version is a widely used global vegetation model and is used as a compoenent within a coupled Earth System Model. A careful examination is thus important also for understanding the power and limits of respective ESM simulations (which will be part of CMIP6, I guess). Because this model (CLM5) overestimates N inputs and losses (too open N cycling), a re-configured version is used here, where N cycle openness is drastically reduced by reduced prescribed N deposition, artificially supressed N fixation, and artificially supressed denitrification. Tracer studies suggest important contribution of recovery by immobilisation. Both model configurations overestimated N recovery in plants. The adjusted model version simulated N recovery in soils ok, while the original version underestimated soil N recovery. Regarding implications for C: the model has too low C:N ratios in wood and thereby underestimates the amount of C sequestered per N added, thus balancing the overestimation in simulated plant N recovery. The relevance of the two quantities (% recovery in different pools, and dC/dN) is high and the model evaluation has promise to yield useful insights into a key mechanism. Confronting models with data is in general a very important way forward to addressing known unresolved deficiencies in models. The present paper takes a step in that direction. Therefore, I am looking forward to some (major) revisions of the present manuscript and consider that the paper (after revision) may be a valuable contribution to this field and suitable for publication in Biogeosciences. However, I have a few concerns regarding the comparability of observed and modelled quantities which need careful additional explanation and justification. In addition, I consider that the discussion of the insights gained and the recommendations given for further research are too generic and am not convinced that proposed steps will advance the field, or even the performance of the model used here. Looking at the fate of N additions also provides insights into the complex interactions between microbes and different soil compartments (surface, depth, mineral N). However, the complex behaviour of the system also points to difficulties related to the model setup for mimicking the experiments. These limitations should be addressed better and possibly alternatives explored before the paper is re-considered for publication. Having said that, I appreciated the well-written text and clear presentation.

We thank the reviewer for describing how our paper adds value to the biogeochemistry community, particularly in how we identify model deficiencies in CLM5's estimates of C:N ratios and soil recovery of ecosystem N additions. To minimize reader confusion that our adjusted model is supposed to be an alternative version of CLM5, we have changed the descriptions of our two model versions from “default” and “adjusted” to “closed” and “open.” In this way, our two models represent extremes in how much N recovery could occur in open and closed ecosystems (i.e., our simulations represent the sensitivity of the response to open and closed systems). We discuss the reviewer's concerns about a) the comparability of field data to model output and b) recommendations for further research and improved model performance in more detail in the reviewer's more specific comments below (Comments 12 and 13).

12. I'm asking myself about the comparability of simulated N recovery (Eq. 1) and 15Nbased results and what underlying assumptions have to be met. One is perfect mixing in the respective pool. It could be that the N added in the field enters the system in such a way as to favour accumulation in the litter by being taken up by microbes (immobilisation), and is never fully mixed within the entire mineral N pool available to the plant. In contrast, in the model it is added directly to the mineral N pool and is well mixed (by design). Once N is immobilised (in nature), this doesn't preclude that additional N (that would otherwise have fuelled immobilisation) is now available to the plant and leads to an increase in overall plant N uptake. However, this N then doesn't carry the signature. If this is indeed a possibility, then one would have to either compare total N stocks in observations analously to Eq. 1. This problem of the field-model comparison is discussed on l.16, p. 15 and it is pointed out that the tracer is added (in the field) to litter layer where immobilisation occurs, whereas in the model it's added to the mineral N pool. The suggested solution to this conceptual mismatch is making the model more complex and I'm not convinced this is a path worth taking. Wouldn't it just do the trick to add the N (in the model) to the litter pool and thus decrease its C:N ratio?

To clarify, when N deposition is vertically distributed into the soil column, it is not distributed *evenly* through the soil column. N deposition is distributed according to an *exponential* function to represent rooting depth distributions. Approximately 40% of added N deposition (including our simulated tracer and fertilizer) is distributed through the top 2 cm, and approximately 95% is distributed in the top 20 cm.

To make this clear to the reader, we will add this sentence in the methods section explaining how N deposition is distributed: "When N deposition is added to the inorganic soil N pool, it is distributed vertically through the soil column according to an exponential profile; approximately 40% of N deposition is added to the top 2 cm and approximately 95% is added to the top 20 cm." We will also modify the following sentence in the discussion section to read: "Furthermore, N additions (e.g., N deposition) are directly added to the dissolved inorganic N pool, which the model immediately distributes throughout the soil column according to an exponential profile; approximately 40% of N deposition is added to the top 2 cm and approximately 95% is added to the top 20 cm" (Page 6, Lines 8-10). We will also delete this paragraph in the discussion, "In addition, N additions (e.g., N deposition) are directly added to the dissolved inorganic N pool, which the model immediately distributes throughout the soil column. However, in ^{15}N tracer experiments, the tracer is applied directly on top of leaf litter to mimic N deposition and a vertical gradient of N use in soils forms because microbial activity and demand for N is greatest at the soil surface (Iversen et al., 2011; Li and Fahey, 2013) where fresh C inputs are greatest, C:N ratios are high, and microbes have the opportunity to rapidly capture this tracer. To capture this vertical gradient of immobilization found in field experiments, the model could add inorganic N to the surface soil layers, only, and allow it to mix more deeply through advective or diffusive fluxes." We will now indicate the difference in how the tracer is applied in the model and in the field with the following sentence located two paragraphs above: "Although the model and field experiments differ in how they apply the N tracer to soil (directly into the inorganic soil N pool versus on top of the litter, respectively), the large magnitude of the observed soil N sink and the model's poor ability to reproduce it suggests that modeling a stronger soil immobilization sink should be a priority" (Page 17, Lines 14-16).

With the current model structure, we cannot add the tracer or fertilizer to the model's litter pool because it does not contain an inorganic N pool. In addition, if we added the tracer or fertilizer only to the top 2 cm of the soil, this change could have consequences on how N moves through the soil over the course of years—affecting the movement of mineralized N and leaching. Currently, the model has a diffusivity coefficient of 1 cm^2 yr^{-1}, which means it would take approximately 100 years for N to move down 10 cm. The exponential profile in the model helps to counter the model's minimal representation of vertical movement of N through the soil. While adding an explicit inorganic N pool to the litter, or explicitly capturing the vertical movement of N through soils, could be important, including them in the model with rigorous evaluation is beyond the scope of this study.

13. My other concern/question is that 15N data is compared to simulated N pool size changes. The most direct comparison would be to track a 15N tracer also in the model, but I understand that this is beyond the scope here. But can the two be compared in an experimental setup, where no additional N is added as fertiliser (see entries with 0 g N yr-1 m-2 in Table 1). How is this handled in the model? The denominator in Eq. 1 is zero in this case. In that sense, I'm asking myself about what is the advantage of using tracer studies as opposed to just looking at biomass changes in response to fertilisation. Adding a clearer motivation for the approach chosen here in the intro and/or discussion may address this question.

In Table 1, the "amount of N fertilizer" refers only to the added amount of fertilizer applied in the field—which we used in our simulations of fertilized sites. To simulate sites with no additional fertilizer, we used the approach in Thomas et al. (2013b) where a small amount of N (0.5 g N m^{-2} yr^{-1}) was added into the soil inorganic N pool, as described in our Methods section. Because Thomas et al. (2013b) used an older version of CLM, we also conducted a sensitivity analysis (Figure S1-S2) to confirm this amount as the smallest amount of N we could apply in our simulations while recovering a reasonable amount of that added N (which we refer to as the model tracer). In this way, our denominator in Equation 1 is not 0 g m^{-2} $year^{-1}$, but 0.5 g N m^{-2} yr^{-1} (or 0.5 g N m^{-2} yr^{-1} + differences in N fixation between the tracer and control simulation in the open version of the model).

We focused on simulating field-based tracer studies in order to leverage ^{15}N datasets to evaluate CLM's performance in simulating not only C sinks, but also the fate of added N. We find that the model actually simulates plausible C storage, but because of compensating errors in its simulation of N retention and C:N stoichiometry—errors that would not be identified if we solely examined the C storage term. Field-based tracer studies provide an advantage over the method of measuring biomass changes in response to N deposition in situations where N deposition or fertilization rates are small, partly because the tracer fate can be measured much more precisely than changes in either C or N stocks. That is, soil C, and especially N stocks, are large and heterogenous relative to small changes in these stocks. Tracer studies, however, can identify the accumulation of N in soils even with large background N stocks.

We will add additional language about this motivation at the beginning of the discussion section, which will read: "This study compares estimates of ecosystem recovery of N additions between CLM5—a land model with coupled C and N cycles—and long-term ^{15}N tracer experiments in temperate deciduous and evergreen forests" (Page 15, Lines 11-12)."

14. Data availability: In the introduction (p. 4, l.26), it is stated that "we first compiled a summary of 15N recovery data from long- term 15N tracer experiments that can be used to evaluate N cycling in other

land models. " However, the data is not made accessible (only upon request). This aspect seriously hinders progress and I was disappointed to see it here.

The data we compiled and used in this manuscript are listed in the supplement, Table S1. There were a few sites where the data are listed as "available on request" because the most recent data are currently in the process of being published. We will add these numbers into our manuscript if those papers are published before our revised manuscript is available online. Otherwise, we will update this manuscript with an addendum when those numbers are published. We will also update the sentence in the Data Availability section to read, "^{15}N tracer data, along with key citations, are available in Table S1."

15. I was a bit disappointed by the discussion where it is suggested that the inclusion of more processes (p.14, l.26) would lead to a better model-data agreement. This is a common "reflex" seen in many publications but often doesn't resolve model deficiencies that are implied by its "core", and it doesn't take into consideration possible shortcomings of the nature of model-data comparison itself. Increasing model complexity often leads to more problems and yet more calls for adding processes. Here, this suggestion is rather disconnected from the findings presented here, and I was disappointed to see it here.

Our suggestions sought to identify and explain a few specific processes that we considered most likely to improve model performance in simulating the plant-soil dynamics that the model failed to capture here, such as a) improving mycorrhizal associations (which in part have been added to CLM5), b) adding mechanisms for priming, and c) adding an organic N pool that plants can access. These three sets of processes have all been previously identified as potentially key to N cycling (as indicated by the citations we included in our discussion section), either through modeling or empirical experiments. In Comment 41, Reviewer 3 also discusses that our suggestions have been shown to be feasible to incorporate into ecosystem and global models. As such, we would like to keep this paragraph (and the one that follows, which details more specifically why we think these three components could address model limitations) in our discussion section. We will also add additional citations, including Tang and Riley (2014) and (Zhu et al., 2016).

However, we do recognize the important balance between adding model complexity at the expense of model certainty in large-scale terrestrial land models, particularly if an added process or parameter is not well-measured. We will include additional discussion of this tradeoff at the end of this discussion section. In particular we plan to include the following: "It is important to note that additions of parameters or process-based representation of ecological processes can add uncertainty to model projections. To limit this added uncertainty, new model representations should be designed and evaluated using robust and representative, process-based datasets—as discussed in modeling papers, including Prentice et al. (2015), Lovenduski and Bonan (2017), Lombardozzi et al. (2018), and Sulman et al. (2018)" (Page 18, Lines 6-9).

16. I am intrigued by the issues of N cycle openness in the CLM5 model and would be interested to learn more about how the results for N fate presented here yield new insights into this problem and how it can be resolved. The model was re-configured here with much reduced N inputs (deposition and fixation) and an unrealistic suppression of denitrification. While this allowed authors to achieve

plausible results for N recovery, it gives the impression that a wrong model behaviour was "fixed" by an unrealistic assumption. Does this study yield insights into how this could be resolved better?

We share this interest, and now present our results as two extremes of N cycle openness. In response to this comment and Comment 2 above, we have provided additional explanation on the rationale for vastly reducing the default model's denitrification rates, and we recognize that the reality about these assumptions lies somewhere between the two model scenarios we present. The default model largely fails to capture the plant-soil N competition indicated by the ^{15}N tracer studies, and this failure is why we propose a few potential steps for their improvement in our Discussion section (also discussed in response to Comment 15). The two model configurations should be viewed as a sensitivity test of the response of open and closed systems.

Our study, like prior analysis of earlier versions of CLM (Koven et al., 2013; Thomas et al., 2013a; Thomas et al., 2013b; Houlton et al., 2015) demonstrates that denitrification, N deposition, and N fixation all need to be addressed. Although our comparison of two model versions do not explicitly identify a way to fix the prognostic representation of denitrification and N fixation, our study does indicate that adjustments to losses are best done in concert with tests that adjust inputs. We emphasize the effect of N cycle openness on N fates in the discussion section, as discussed in our response to Comment 40.

17. p.9, l.17: The calculation of N residence time: Is this calculated from the transient response or after model spinup? It has to be in steady state in order to calculate residence time = stock / loss flux. The enormous difference in residence time may just be the result of reduced N losses in a transient response.

The calculations of N residence time that we report in the results section are calculated from the end of our transient simulations. However, we also include calculations of N residence time done at steady state in Table S2. After spin up, ecosystem N residence times are similar in magnitude to those calculated at the end of the transient simulations. To avoid confusion about whether our calculations are done in steady state, we will change terminology of residence time to turnover time. The variation in turnover time across sites was addressed in our response to Comment 4.

18. Sec. 3.1, p.): Quantification of how often N cycles through the system before it's lost, as the ratio of whole-ecosystem N residence time to plant N residence time. I am suspicious of this calculation. Once it's in the soil (and stays there for a long time), it's not actually cycling. As a more insightful charecterization of the N cycle in the two alternative model configurations, I would recommend to calculate an N cycle openness similar to Cleveland et al. 2013 PNAS as the fraction of new N to total N in new production, or Nin / (rN:C * NPP - Nresorb), which is in steady state equal to Nout / (rN:C * NPP - Nresorb).

We thank the reviewer for suggesting this alternative metric. The reviewer is correct of course, that once N is in the soil, it can stay there a long time, but not forever (see comment above). The metric we use in our paper (i.e., the turnover time of the N in the ecosystem divided by that in the vegetation) helps meet the goals of our paper by distinguishing very clearly the differences in N cycling between the closed and opened systems (formerly adjusted and default models). Thus, we would like to continue using this metric so that we can quantitatively demonstrate how open or closed these two model configurations are relative to each other. The Cleveland et al. metric does not seem to clearly distinguish between the open and closed systems in the model because Nin is the same in the open and closed systems, and both systems have similar rates of NPP. A simple interpretation of our metric is how many times on average N cycles through plants before it is lost from the ecosystem.

19. I did not learn much from the analysis by PFT. Is there a hypothesis for why PFTs would differ in their response? This part needs a motivation, otherwise it appears here a “just because we can”. It also remains unclear why CLM results differ between these PFTs. What mechanisms are responsible for differences?

We hypothesized that PFTs would differ in their N fates because of differences in growing season length and the C:N ratios of foliage, which would influence the C:N ratio of litter as well as rates of decomposition and transfer of N to litter and soil pools with longer turnover times. The hypothesis that PFT traits influence N recovery through immobilization rates is supported by the larger portion of N immediately recovered in soils compared to plants (Fig. 5b v. 5a).

We will add these two sentences to the beginning of the PFT section to motivate this analysis. The sentences will read: “In the field, forest types might respond to N deposition differently because of differences in their plant and ecosystem traits (Cornelissen 1996). In CLM5, the evergreen and deciduous PFTs differ especially in foliage C:N (see Table 2) and timing of plant N demand, which should alter decomposition and N mineralization” (Page 14, Lines 13-15).

20. Model and observational results are reported as a mean (?) and a relative standard deviation (?). The SD is calculated from year-to-year variability, but is then treated as a standard error and a p-value is calculated to test for the significance of the difference between observed and modelled values. In my understanding, this is not permissible. The model is not stochastic, thus the variability in model results is not uncertainty. I would recommend to present numbers for the mean relative bias as mean((modobs)/mean(obs)).

In Figure 3, the bars represent the distance between the 1st and 3rd interquartile range of the data (which include the measured or modeled recoveries across sites). Similarly, in Figure 4, error bars represent 1 standard deviation across the ^{15}N data measured across the field sites. Although each site measured recoveries at different timepoints after the tracer was added, the standard deviation in Figure 4 predominately represents variation across sites rather than temporal variation. In these figures and with our ANOVAs, we are identifying whether differences exist between groups of data. We agree that calculating relative bias is a nice approach to describing how far away the model is from the measurements. However, part of the goal of our paper was to synthesize and illustrate the temporal patterns in N recovery across the decadal timescale for the field sites. Switching to mean relative bias would remove the presentation of the absolute values of the field data, and reduce the accessibility of the field results to readers—particularly those interested in the empirical data.

In our figure captions, we will more clearly define that the standard deviations or interquartile range represent cross-site variation and that we are comparing differences between groups, as opposed to comparing the means of two groups.

21. I liked the intuitive characterisation of the mode used here: Maybe this could be complemented to provide additional (intuitive) model understanding on the following points: How does foliage C:N and Vcmax (which is predicted separately, I guess) interact? What drives what? How is allocation (shoot:root ratio) simulated? How are N losses simulated (scaling with a mineral N pool, or with the mineralisation flux, or. . .)? What happens to C paid as C cost for N uptake (respired as CO2)? Can the litter-soil transfer be N limited (slowing decomposition rates)? A word more on stoichiometry optimisation applied here? Is there a feedback between plant belowground C investments and SOM decomposition rates?

We will add additional information about the model structure to the methods section, including the following sentences (Note: We felt that discussing the specifics of allocation would distract the reader from the main points of our study, and have added a reference to the CLM5 documentation with information about allocation. Much of our cited literature in the methods also go into more details about these model representations):

- "Denitrification occurs in the anoxic portion of the soil and is constrained by decomposition and the availability of nitrate" (Page 6, Lines 15-16).
- Environmental conditions influence a leaf's photosynthetic capacity. "Specifically, the maximum rate of carboxylation ($V_{c,max}$) is influenced by the amount of leaf N allocated for carboxylation, as well as day length and season" (Page 5, Lines 23-24).
- "The amount of N that is allocated to individual sub-plant pools is determined based on a fixed set of allometric ratios and the amount of N the plant has for new growth. Additional details on how stoichiometry is optimized can be found in the CLM5 documentation referenced below" (Page 6, Lines 1-3).
- "Rates of decomposition are limited by soil moisture, soil temperature, and N availability. As litter decomposes into soil organic matter, a portion of C is respired and N is transferred from litter pools through to soil pools" (Page 6, Lines 17-18).

We will also clarify in our methods section that the C costs are respired by editing the sentence to read, "plants pay C costs (which are respired) for acquiring N from symbiotic N fixation, uptake of soil N, and retranslocation (Page 6, Lines 3-4).

22. In the introduction, it may be worth citing Magnani et al., 2007 and the debate on realistic dC/dN values that ensued in response.

Magnani et al., 2007 did spur an interesting debate about what realistic dC/dN values are. However, subsequent papers, including Sutton et al. (2008) addressed most of the problems that were part of the Magnani et al. 2007 analysis that spurred so much debate.

We will modify the end of the first paragraph to introduce the importance of calculating dC/dN. The last sentence of the first paragraph will read, "Thus, evaluating model representations of N cycling is critical to increasing our understanding of the magnitude of ecosystem C response to changes in N inputs (dC/dN; Sutton et al. (2008)) and how dC/dN influences the size of the terrestrial C sink over the 21st century" (Page 3, Lines 13-15).

23. Fig. 2: Unclear what bars represent. Are these the observations? If not, I highly recommend adding observations here as well. Missing info in caption. What is meant by "scenario"?

The stacked bars do represent observations. We will change the figure caption description from "field measurements" to "observations." "Scenario" refers to each simulation for a site and specific N input. We will remove "For each scenario" to avoid confusion.

24. It is argued that results for only Harvard forest are shown because it provides the longest record length. I would find it highly revealing if Fig. 2 could include results for other sites too.

Our previous attempts to incorporate all sites into one figure made the plots difficult to interpret, but results for all of the sites are included in Figures S3-S5. We modified the figure caption to make this information clearer to the reader. The sentence now reads, "Plots of recoveries at all other sites and for the default version of CLM5 at Harvard Forest are in Figs. S3-S5."

25. p.3, l.6: Add exchanged between the land surface and the atmosphere under future scenarios of increasing CO2 and climate change.

We will add "under future scenarios of increasing CO_2 and climate change" to this sentence as suggested by the reviewer.

26. p.3, l.31: A soil C:N of 5 seems very low. Where did you get this number from?

C:N ratios of 5 have been measured in deep, low C soils at Arnot Forest (Goodale, 2017), while the 25 is lower than the value from Nadelhoffer et al. (1999) which was reported as an upper bound for the forest floor. We will add the Arnot Forest citation to this sentence.

27. p.6, l.7: GSWP3 data: Didn't find any data under the URL given.

We will revise the link to the data http://search.diasjp.net/en/dataset/GSWP3_EXP1_Forcing and add its citation to this dataset: Hyungjun Kim. (2017). *Global Soil Wetness Project Phase 3 Atmospheric Boundary Conditions (Experiment 1)* [Data set]. Data Integration and Analysis System (DIAS).

28. p.6, l.12: Using locally measured meteorology, elevation, soil parameters, at the experimental sites? This could be quite important.

For each forest, we used local meteorology prescribed from the GSWP3 dataset (see Comment 27), and elevation soil characteristics derived from high-resolution input datasets as listed in the CLM5 documentation. Because not all of our forest sites had meteorological tower data, we used the model's input variables for these grid cells in order to maintain consistency.

29. p.7, l.16: Equally spread across days?

Yes. We will add this information into the methods section. The sentence will read, "...we applied the N "tracer" equally across days during April through September to capture the most active portion of the growing season."

30. p.7, l.18: Site names appear here before being introduced. Would be worth having a short paragraph at the beginning of Methods about the locations and characteristics of sites.

The beginning of our Methods (Section 2.1) described the Table we included with locations and characteristics of these sites. To help link that section to this portion of the Methods section, we will reference the Table in section 2.2. The sentence will read: "In CLM5, we ran sensitivity tests for two of our eight model sites (see Table 1 for a full list, including site names), an old growth forest (Alptal) and a younger forest (Harvard NET), which confirmed that the smallest amount of N we could apply while maintaining realistic ecosystem N recovery responses at both sites was 0.5 g N m^{-2} y^{-1} (Fig. S1), consistent with Thomas et al. 2013b" (page 8, Lines 16-18).

31. p.9, l.16: Change "equivalent" to "similar in magnitude".

We will make this change in the text.

32. p.9, l.17: Add *N* residence time.

We will make this change in the text.

33. p.11, l.14: Better write "per unit N tracer added" (if that's correct).

We will revise the sentence to better describe Eqn. 2. Upon editing, the sentence will read, "For the model, annual dC/dN values were computed directly (i.e., "direct approach") as the difference between the total plant or total soil C stocks between the baseline and "tracer" (or fertilizer) simulation divided by the difference in the amount of cumulatively added N between the two simulations (Eqn. 2)" (Page 13, Lines 4-6).

34. p.11, l.18: Why not use values measured in the field? Not available? What literature?

The literature-based estimate we mentioned in this sentence refers to published field literature from the sites we analyzed in our paper. We adjusted the sentence to better reflect that information. The mean of the published values are listed in Table 2, with individual site values listed in Table S3. The sentence now reads, "...using the measured ^{15}N recovery in each pool and published field-measured values of C:N for that site's particular pool (Table 2, Eqn. 3)."

Reviewer 3

35. This is a well written manuscript that presents an important model-data comparison exercise to identify model failures and successes in CLM5. The author's assembled an impressive data set and

use this to test CLM5's ability to capture 15N tracer recoveries and dC/dN ratios across a suite of forested ecosystems. Both reviewers have provided extensive key insights and areas for improvement for this manuscript. As such, I will keep my comments brief to not duplicate their efforts. Both Reviewer 2 and the authors in the discussion (Page 15 Line 19) suggest that adding the "tracer" N to the mineral soil pool may make it too accessible to plants. Why not perform this experiment at one of the sites at least? This would allow you to identify whether the mode of N delivery is driving the high recovery seen in plants.

We addressed in depth the difficulty of developing a model version where we could add the "tracer" only to the litter pool or top surface layers of the soil in our response to Comment 12. Overall, approximately 50% of added N deposition (including a tracer and fertilizer) is distributed into the top 2 centimeters (and approximately 95% is in the top 20 centimeters), and so most of the added tracer or fertilizer is available in the top layers of the soil. Attempts to only add the tracer into the top layer of the soil would require significant modeling changes and evaluation that are beyond the scope of this study

36. Both Reviewer's highlighted that turning denitrification off may make the adjusted model simulation unrealistic. I am not an expert in gaseous losses from forested ecosystems but from my understanding I believe they dwarf those of leaching losses particularly for aerobic well drained soils that are N limited. Maybe an empirical reference to support low rates of denitrification would help here.

We addressed questions about turning off denitrification in our response to Comment 2. Briefly, although simulated losses of N to denitrification dwarf leaching losses in various versions of CLM (Koven et al., 2013; Thomas et al., 2013a; Houlton et al., 2015; Nevison et al., 2016), this particular imbalance has been identified as a problem by these and related studies. While few field measurements exist to quantitatively constrain full denitrification losses, leaching losses are relatively well-measured and vastly exceed current model predictions (see response above for Comment #2 for more details and further citations).

37. Similarly, most readers are not actively aware of reasonable values in N residence times. Can you put the differences between the default and adjusted CLM into context with literature values?

It's true that residence times of N (note: We are changing this terminology to "turnover times" as discussed in our response to Comment 17) in ecosystems are rarely computed or reported for field studies. Nonetheless, they can be calculated (as described in our response to Comment 4) for each site using the soil N stocks and rate of major input or output fluxes (for these systems, N deposition). Because we are changing our descriptions of the two model versions from "default" and "adjusted" to "open" and "closed," the comparisons of the turnover times will serve to show how differently N cycles through the two model versions—as opposed to representing a comparison to what we might expect to find in the field. Adding a range of values calculated from sites may detract from the main message of this section that the two models represent extremes of N cycling (open N cycle and closed N cycle).

38. On aside here: The use of default and adjusted combined with direct and indirect make the results difficult to digest. Why not call them open and closed N cycles or observed C:N vs. modeled C:N or some similar variant that makes sense.

We agree with the reviewer that calling our two models “open” and “closed” could be easier for some readers to digest. It also allows us to describe how our two models are representative of either extreme of N cycling in ecosystems and to reduce confusion about whether the “adjusted” model is supposed to be “better” with denitrification turned off. We will correspondingly change references to “default” and “adjusted” to “open” and “closed” in revisions.

39. What is driving the variability in wood C:N in both CLM5 versions? Is this due to LUNA? How robust is the overall observed dataset in C:N ratios. Is there only a few observations per site or are there more?

The FlexCN module in CLM5 prognostically calculates the C:N of each plant tissue (Ghimire et al., 2016); thus with the FUN module (Shi et al., 2015), when foliar C:N increases, the plant spends more C on acquiring N (Lawrence et al., in review). CLM5 applies a tissue C allocation to specific plant pools that is parameterized for each plant functional type (see Lawrence et al. (in review); CN Allocation section in Lawrence et al. (2018)).

The number of observations for wood C:N ratios varies by site and depends on how many tree cores were taken. For example, at Arnot Forest, 40-50+ wood samples were collected during each sampling date (Goodale, 2017). Table S3 includes citations for the tracer experiments, which include methods for sampling trees. We will modify the last sentence of the caption for Table 2 to read: “Site-reported or estimated values for C:N ratios for each site and their references (which describe the sampling methods for each pool), are in Table S3.”

40. The discussion highlights reasons why the default and adjusted CLM5 can capture 15N recovery rates and dC/dN ratios but fails to address whether CLM5 needs to remain as is or have a more closed N cycle. This is almost a bigger issue than where the tracer is going given that the model is somewhat able to get the right answer for the wrong reason there.

We agree with the reviewer that one of the most important issues our data-model comparison points out is unrealistic fluxes of N inputs and denitrification. From our analysis, we provide additional support for needing to create more accurate input datasets for N deposition as well as improving prognostic calculations of N fixation and denitrification. We have modified the beginning of the discussion to add a section that highlights this. This section will read as:

4.1 Modeling Ecosystem Inputs and Losses

Our analysis of CLM5 configured with an open N cycle (i.e, the default configuration of N cycling in CLM5) identified that the model continues to have large biases in N losses (Fig. 1)—similar to assessments of previous versions of the model (Koven et al., 2013; Thomas et al., 2013b; Houlton et al., 2015; Nevison et al., 2016). Specifically, CLM5 has unrealistically high rates of denitrification and low rates of N leaching and runoff compared to field measurements. We also identified that pre-industrial N deposition in CLM5 was higher than expected from reconstructions (Fakhraei et al., 2016; Holland et al., 1999) for the Northeast United States and parts of Europe (Fig. 1). Although simulations with an open N cycle shared some similar responses to N additions as simulations with a closed N cycle, having higher N deposition and denitrification fluxes (i.e., the default version of CLM5) typically led to a) less total ecosystem recovery of N inputs than simulations using a closed N cycle and b) an underestimation of long-term soil N recovery compared to observations. In adjusting N inputs and losses in CLM5 to better match field expectations, many of the simulated ecosystem stocks and fluxes (i.e., plant N, soil N, plant C, leaf area, and ANPP) remained similar to observations and simulations using an open N cycle (Table 3). Given that the openness of an ecosystem's N cycle changes the ecosystem's recovery of N inputs within a decadal timescale, we suggest that future model development not only test new mechanistic representations of N fixation and denitrification, but do so in concert with modified N input datasets to ensure that both inputs and losses capture field expectations.

41. I disagree slightly with Reviewer 2 in regards to the idea that identifying model failures that could be addressed by adding in new processes is not fruitful. Many of the efforts the authors have raised to increase plant-microbial competition by adding in explicit microbial representations and interactions between plants and microbes have proven feasible in models at the ecosystem and global scale.

We appreciate the reviewer's perspective about new processes in models. We discuss the balance between adding model complexity and minimizing model uncertainty in our response to Comment 15.

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Decadal fates and impacts of nitrogen additions on temperate forest carbon ~~sinks~~storage: A data-model comparison

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Abstract. To accurately capture the ~~measured~~ impacts of nitrogen (N) on the land carbon (C) sink in Earth system models, model responses to both N limitation and ecosystem N additions (e.g., from atmospheric N deposition and fertilizer) need to be evaluated. The response of the land C sink to N additions depends on the fate of these additions—that is, how much of the added N is lost from the ecosystem through N loss pathways, or recovered and used to increase C storage in plants and soils. Here, we evaluate the C-N dynamics of the latest version of a global land model, the Community Land Model 5 (CLM5), and compare how the model varies when ecosystems have large N inputs and losses (i.e., an open N cycle) or small N inputs and loses (i.e., a closed N cycle)~~. Because the default version of CLM5 overestimated the magnitude of N inputs and losses compared to observations, we configured an adjusted version of CLM5 with more conservative assumptions about these fluxes~~. We then compared the short- (< 3 years) and longer-term (5-17 years) simulations of N fate in CLM5 against observations from 13 long-term ^{15}N tracer addition experiments at eight temperate forest sites. ~~Both the default and adjusted configurations~~Simulations using both open and closed N cycles ~~of CLM5~~ overestimated plant N recovery following N additions. In particular, ~~the adjusted~~ the model configuration with a closed N cycle ~~configuration~~ simulated that plants acquired more than twice the amount of added N recovered in ^{15}N tracer studies~~,~~ on ~~both~~ short timescales (CLM5: 46~~%~~ ± 12%; observations: 18~~%~~ ± 12%; mean across sites ± 1 standard deviation), and almost twice as much on longer timescales (CLM5: 23~~%~~ ± 6%; observations: 13~~%~~ ± 5%). ~~The default version of CL~~The model configuration~~M5~~ with an open N cycle underestimated long-term ^{15}N recovery in soils, while soil N recoveries in ~~the adjusted configuration~~simulations with closed N cycles were closer to observations on both the short (CLM5: 40~~%~~ ± 10%; observations: 54~~%~~ ± 22%) and longer-term (CLM5: 59~~%~~ ± 15%; observations: 69~~%~~ ± 18). However, in both ~~configurations~~open and closed sets of simulations, soil N recoveries in CLM5 occurred from the cycling of N through plants rather than through direct immobilization in the soil, as is often indicated by ~~the~~ tracer studies. Although CLM5 overestimated plant N recovery, the simulated increase in C stocks to recovered N was not larger than estimated by observations, largely because the model's assumed C:N ratio for wood was nearly half that suggested by ~~field~~ measurements at ~~our~~ the field sites. Overall, results suggest that simulating accurate ecosystem responses to changes in N additions requires increasing soil competition for N relative to plants, and examining model assumptions of C:N stoichiometry—which should also improve model estimates of other terrestrial C-N processes and interactions.

1 Introduction

Biogeochemical processes in plants and soils influence Earth's climate by controlling how much carbon dioxide (CO_2) can be removed from the atmosphere and placed into long-term storage in terrestrial ecosystems (Bonan, 2008). Currently, Earth system model ensembles that compare multiple models against each other persistently show a large uncertainty around estimates of CO_2 fluxes exchanged between the land surface and the atmosphere under future scenarios of increasing CO_2 and climate change (Friedlingstein et al., 2006; Anav et al., 2013; Friedlingstein et al., 2014). This uncertainty is mainly driven by differences in how models represent biological processes on land and their responses to increasing atmospheric CO_2 concentrations (Lovenduski and Bonan, 2017; Bonan and Doney, 2018). Nutrient limitation is one factor that is likely to constrain CO_2 fertilization of the biosphere (Zaehle and Dalmonech, 2011; Medlyn et al., 2015; Wieder et al., 2015b; Zaehle et al., 2015; Meyerholt and Zaehle, 2018), but not all global land models used in coupled climate-land simulations include explicit representations of the nitrogen (N) cycle~~ in coupled climate-land simulations~~. As more global land models add and examine the impacts of coupled carbon (C) and N cycles (Thornton et al., 2007; Sokolov et al., 2008; Zaehle and Friend, 2010; Smith et al., 2014; Goll et al., 2017), additional sources of uncertainty will be added into these models (Wieder et al., 2015a; Lovenduski and Bonan, 2017). Some of the principal uncertainties in simulating terrestrial C-N interactions lie in how models represent plant acquisition of N from soil and the relative competitiveness among plants, decomposers, and denitrifying microbes for soil N (Thomas et al., 2013b; Medlyn et al., 2015; Thomas et al., 2015; Zhu et al., 2016b). Thus, evaluating model representations of N cycling is critical to increasing ~~confidence ~~our~~in~~ understanding of ~~projections of ~~the magnitude of ecosystem C response to changes in N inputs (dC/dN; ~~(Sutton et al., 2008)the terrestrial C sink over the 21st century~~Sutton et al. (2008))~~, particularly in ecosystems experiencing changes in anthropogenic N inputs.~~ and how dC/dN influences the size of the terrestrial C sink over the 21st century.

Human uses of fossil fuels, N-fixing plants, and fertilizers have more than doubled rates of N inputs to terrestrial ecosystems compared to preindustrial conditions (Vitousek et al., 1997; Galloway et al., 2003). Increased emissions of reactive N from combustion processes and agricultural sources have led to increases in atmospheric N deposition (Galloway et al., 2003; Vet et al., 2014), which can have multiple effects on forests and other terrestrial ecosystems (e.g., Aber et al. 1998). These effects include shifts in rates of tree growth (Solberg et al., 2009; Thomas et al., 2010) and soil decomposition (Janssens et al., 2010; Frey et al., 2014), as well as increased soil emissions of nitrous oxide (Butterbach-Bahl et al., 2002). The fate of N deposition in plants, soils, or N loss pathways from forests is central to quantifying the effect of N deposition on terrestrial C storage (Emmett et al., 1998a; Nadelhoffer et al., 1999a; Currie et al., 2004; Lu et al., 2010; Templer et al., 2012; Lovett et al., 2013; Wang et al., 2018). Woody plant tissues have higher C:N ratios (e.g., 100-500) than foliage and roots (e.g., 20-40), which allow~~s~~ trees to build more organic C per unit N taken up by plants compared to other plant types. Similarly, woody tissues have C:N ratios that are one to two orders of magnitude higher than soil organic matter (e.g., 5-25) (Nadelhoffer et al., 1999b; Yang and Luo, 2010; Zechmeister-Boltenstern et al., 2015;

Goodale, 2017), allowing trees to store much more additional C if they successfully compete for N deposition than if N is retained in soil; no additional C is stored in forests when N is lost from the system by denitrification or N leaching (Nadelhoffer et al., 1999b).

The fate of N deposition in terrestrial ecosystems has been quantified through field tracer experiments that apply a small amount of highly enriched N with its stable isotope (^{15}N) to the forest and subsequently measure the recoveries of that ^{15}N tracer in plant and soil pools. Reviews of these ^{15}N experiments, which are located predominately in North America and Europe (Tietema et al., 1998; Nadelhoffer et al., 1999b; Curtis et al., 2011; Templer et al., 2012), as well as ~~from~~ in warm and humid sites in China (Gurmesa et al., 2016; Wang et al., 2018), indicate that the total amount and partitioning of recovered ^{15}N varies across sites, but that litter and soil pools typically dominate as sinks for N inputs during the first few years after tracer application. These litter and soil ^{15}N sinks often occur directly through microbial or chemical processes within days or weeks after tracer application, without first passing through plants (Berntson and Aber, 2000; Perakis and Hedin, 2001; Providoli et al., 2006; Lewis and Kaye, 2012; Goodale et al., 2015). These ^{15}N tracer studies are also useful for quantitatively evaluating coupled C-N cycle processes in land models. For example, Thomas et al. (2013b) used mean results from short-term tracer experiments (< 3.5 years) to test the responses of two coupled C-N models that treat plant and soil responses to N additions differently: O-CN (Zaehle and Friend, 2010) and the Community Land Model 4 (CLM4) (Thornton et al., 2007). That analysis showed that CLM4 lost a large fraction of incoming N inputs to N gases, while the N retained in the ecosystem was distributed relatively evenly between plants and soils. In contrast, OCN better estimated total ecosystem retention of N inputs, and projected that soils dominated the short-term fate of added N.

~~Long-term C~~Comparisons ~~between~~ of model simulations ~~and~~ with long-term field experiments ultimately provide more relevant constraints on decadal or centennial-scale forest C uptake and N cycling dynamics than ~~than~~ comparisons using short-term field studies that often reflect transient dynamics (Perakis and Hedin, 2001; Jefts et al., 2004; Providoli et al., 2006; Templer et al., 2012). For example, field studies indicate that N initially retained in litter and soil could redistribute to plants and enable additional C uptake over the long-term; ~~or~~ alternatively, retained N could accumulate in soil pools or be lost from the ecosystem entirely (Nadelhoffer et al., 2004; Krause et al., 2012; Wessel et al., 2013; Goodale, 2017). However, the long-term fates of N deposition in land models have not yet been evaluated against a synthesis of field measurements. This is in part because, to date,~~,~~ there have only been a handful of individual site-level field studies published that have examined the long-term fates of N additions (e.g., Nadelhoffer et al. (2004) and Krause et al. (2012))~~ In this study~~. This study addresses this gap by compiling a summary of ^{15}N recovery data from long-term ^{15}N tracer experiments. We then use these data to ~~, we~~ evaluate~~d~~ the capability of an updated version of the Community Land Model (i.e., CLM5)—~~, which is~~ the land component of the Community Earth System Model that will be part of the next phase of the Coupled Model Intercomparison Project (CMIP6)—~~,~~in its ability to accurately simulate the impacts of ecosystem N inputs on annual to decadal timescales. ~~The model~~CLM5 includes new, more mechanistic representations of plant N processes, following earlier changes to soil C-N dynamics in CLM4.5 (see Section 2.2), which could affect the fate and impact of N in ecosystems. Through this novel data-model comparison project, we provide a synthesis of long-term, ecosystem ^{15}N addition experiments—and identify how differences in temporal dynamics of N cycling between field measurements and CLM5 lead to divergences in measured and modeled N fate and ecosystem C responses to N additions.

~~To evaluate this version of the model, we first compiled a summary of ^{15}N recovery data from long-term ^{15}N tracer experiments that can be used to evaluate N cycling in other land models. We then used these data to evaluate how CLM5 simulates the fate of N in plant and soil pools and compared these results to measurements from a set of forests with long-term tracer studies.~~

2 Methods

To assess CLM5's ability to accurately simulate C-N dynamics on both short and longer timescales, we first compiled existing and newly available field data from eight sites that applied a ^{15}N tracer at least a decade ago. We ran model simulations for each site to examine how ~~simulated~~ N fates and C sink responses to N additions might differ in simulated ecosystems with high N inputs and losses (characteristic of an open N cycle) and simulated ecosystems with low N inputs and losses (characteristics of a closed N cycle). Comparing these two kinds of N cycles, described in more detail in Section 2.3.1, allows us to examine how sensitive CLM5 is to the "openness" of an ecosystem's N cycle. ~~between two configurations of the model's N cycle (Section 2.3.1): one is CLM5's "default" configuration of the N cycle; the second is an "adjusted" configuration where we decreased denitrification and lowered N deposition and N fixation rates to be more consistent with an assessment of published values. In our study,~~ W~~w~~e also evaluate ~~both the short-term and longer-term responses of the~~how the model's C sinks responds~~s~~ to N additions on both the short-term and longer-term. We define short-term recovery as time points within 3 years after the tracer was applied because the majority of rapid changes in modeled N recovery occur during this time (see Results) and many ^{15}N experiments report results within 1-3 years after tracer application (Templer et al., 2012). Longer-term recovery includes time points after 3 (i.e., 5 –17) years.

2.1 ^{15}N tracer field experimental sites

At each of the eight field sites used to evaluate CLM5 (Table 1), a ^{15}N tracer was added at least 10 years ago, often under both ambient and fertilized conditions. These sites span a range of environmental conditions in North America and Europe, and include two plant functional types (PFTs) in CLM5: broadleaf deciduous temperate (BDT) and needleleaf evergreen temperate (NET) trees. Present-day ambient N deposition at these sites ranges from approximately 0.8 to 2.0 g N m^{-2} y^{-1}. Across sites, a ^{15}N tracer was added—as either ammonium, nitrate, or in some cases, in both forms—to five ^{15}N experiments under ambient conditions and to eight experiments under fertilized conditions, with additions ranging from 2.5 to 7.5 g N m^{-2} y^{-1}. Available field measurements of ^{15}N recovery from these sites are in SI Table 1.

2.2 Model description

We evaluated CLM5 (development version 16_r253) in both ~~its default and adjusted configurations (see Section 2.3.1) as to~~ its ability to estimate the site-level fate of ecosystem N inputs against the eight experimental sites listed in Table 1. CLM5 is the terrestrial component of the Community Earth System Model (CESM 2.0) and has undergone several changes to its C and N biogeochemistry since CLM4. Briefly, in CLM4.5, the model's original soil biogeochemistry was replaced with a vertically-resolved CENTURY-based approach and is described in detail by Koven et al. (2013) and Oleson et al. (2013). In CLM5, three important changes were made to plant C and N dynamics. First, the Leaf Utilization of Nitrogen for Assimilation (LUNA) module allows plants to adjust their photosynthetic capacity (i.e., the maximum rate of carboxylation; $V_{c,max}$) based on environmental conditions (Ali et al., 2016). Specifically, $V_{c,max}$ is influenced by the amount of leaf N allocated for carboxylation, as well as day length and season. Second, plants can alter and optimize their stoichiometry (FlexCN module), which removed the down-regulation of gross primary productivity (GPP) that was used in CLM4 and CLM4.5 (Ghimire et al., 2016). The amount of N that is allocated to individual sub-plant pools is determined based on a fixed set of allometric ratios and the amount of N the plant has for new growth. Additional details on how stoichiometry is optimized can be found in the CLM5 documentation referenced below. Third, in the Fixation and Uptake of Nitrogen (FUN) module, plants pay C costs (which are respired) for acquiring N from symbiotic N fixation, uptake of soil N, and retranslocation (Shi et al., 2015). Additional information about these modifications, as well as other changes to model processes and parameterizations can be found in the model documentation ~~-~~(Lawrence et al., 2018).

As in prior versions of the model, C and N cycles in CLM5 are coupled at 30-minute time steps through plant and soil competition for soil N and internal recycling of plant and soil material through litterfall (Thornton et al., 2007; Koven et al., 2013; Oleson et al., 2013; Thomas et al., 2013a). New N enters an ecosystem through N deposition, and free-living and symbiotic N fixation. When N deposition is added to the inorganic soil N pool, it is distributed vertically through the soil column according to an exponential profile; approximately 40% of N deposition is added to the top 2 cm and approximately 95% is added to the top 20 cm. When the amount of soil N is smaller than the total N demand, soil N is divided between plants and an implicit representation of microbial immobilization into soil and litter based on each N sink's proportionate demand to the total N demand. Free-living biological N fixation is calculated as a function of annual evapotranspiration and added to the soil mineral N pool. Symbiotic N fixation is passed directly to the plant and depends on plant N demand, the cost of N fixation for the plant, and soil temperature (Lawrence et al., 2018; Lawrence et al., in review); details on the model's representation of N fixation is available at https://escomp.github.io/ctsm-docs/doc/build/html/tech_note/FUN/CLM50_Tech_Note_FUN.html. Subsequent losses of N occur through production of N gases during nitrification and denitrification. Denitrification occurs in the anoxic portion of the soil and is constrained by decomposition and the availability of nitrate. After gaseous losses, N is lost~~, and then~~ through water—specifically through surface runoff of dissolved inorganic N over land to stream flow and sub-surface leaching through the soil column; the model does not simulate losses of organic N. Rates of decomposition are limited by soil moisture, soil temperature, and N availability. As litter decomposes into soil organic matter, a portion of C is respired and N is transferred from litter pools through to soil pools. In all our simulations (described below), we turned off transient losses of biomass N from fire and harvest because these disturbances infrequently occur at the sites we simulated.

2.3 Model simulations

For each site and ~~model~~ N cycle configuration (see 2.3.1 below), initial ecosystem C and N stocks for 1850 were generated using a spin-up approach where the model was run using 1850 concentrations of CO_2 (285 ppm) and the model's standard climate forcing dataset from the ~~(~~Global Soil Wetness Project Phase 3 (GSWP3; http://search.diasjp.net/en/dataset/GSWP3_EXP1_Forcing~~http://hydro.iis.u-tokyo. ac.jp/GSWP3/~~) developed by Kim (2017). Specifically, we ran the model for 500 years in accelerated decomposition mode by cycling through the 1901-1920 climate forcing dataset, and then for a minimum of 1500 years in regular mode until soil and plant C and N stocks achieved steady state. Subsequently, we ran a historical simulation from 1850 to 2010 (~~,~~ or until 2015 for Arnot Forest, where ^{15}N recovery was measured after 2010)~~,~~ using transient GSWP3 climate, N deposition, and atmospheric CO_2. We ran CLM5 in single-point mode for each site, and modified each site's grid cell area to contain a single PFT and land surface unit (e.g., no lakes). Finally, following Thomas et al. (2013a), we implemented a harvest in the year that established the observed, present-day stand age for each site. For Arnot Forest, simulations cycled through the 2006-2010 forcing data for the model years 2011-2015.

2.3.1 Modeling ~~Default~~ open and ~~adjusted~~ closed N cycles in CLM5 ~~model configurations~~

Similar to prior versions of the model, ~~the default version of~~ CLM5 has unrealistically high N inputs and losses for temperate forests (Thomas et al., 2013a; Thomas et al., 2013b). Prior versions of CLM also greatly underestimate measured rates of N losses to leaching and runoff in these ecosystems (e.g., MacDonald et al. (2002), Aber et al. (2003), Nevison et al. (2016), Thomas et al. (2013a)). Because CLM5 continues to underestimate leaching and overestimate N inputs and denitrification losses (see below; Fig. 1), we simulated how each of the field sites in Table 1 would respond to N additions under a) CLM's default N cycle with high N inputs and losses (i.e., open N cycle), and b) under an alternative "closed" version of the model where N inputs were reduced to better match observations and N losses to denitrification were correspondingly halted to allow the model to build realistic soil N pools, along with N leaching losses (see Section 3.1).~~Thus, we ran default and adjusted model configurations of CLM5 for each ^{15}N field experiment.~~ In ~~the~~ CLM5's ~~default~~ configuration with an open N cycle~~configuration of CLM5~~, N deposition rates are from atmospheric modeling simulations described in Lamarque et al. (2010). In the year 1850 (Fig. 1a), the N deposition rate in CLM5 averaged across our sites was 0.4 ± 0.3 g N m^{-2} y^{-1} (mean ± 1 standard deviation; SD across modeled sites), exceeding the estimated rate of about 0.1 g N m^{-2} y^{-1} for pre-industrial times (Holland et al., 1999; Fakhraei et al., 2016). The temperate forests we simulated also rarely contain plants with N-fixing symbionts, and have rates of free-living N fixation closer to around 0.1 g N m^{-2} y^{-1} (Vitousek et al., 2013; Tedersoo et al., 2018). However, CLM5 has symbiotic N fixation rates in 1850 of 0.5 ± 0.3 g N ~~g N~~ m^{-2} y^{-1} and mean free-living N fixation of 0.3 ± 0.03 g N m^{-2} y^{-1}. In addition, losses of N to denitrification were as high as previously found in CLM4 and CLM4.5 (Thomas et al., 2013a; Houlton et al., 2015), accounting for 99% of all N losses (Fig. 1b).

In the ~~adjusted~~ configuration of CLM5 with a closed N cycle, we changed the model's ecosystem N inputs to be more consistent with historical reconstructions and measurements that suggest 19th century NO_x emissions were smaller (Hoesly et al., 2018) than those estimated by Lamarque et al. (2010). To achieve this, we first lowered pre-industrial N deposition to 0.1 g N m^{-2} y^{-1} for the year 1850 (Fakhraei et al., 2016) and to 0.2 g N m^{-2} y^{-1} in 1950 to account for the doubling in N deposition and NOx emissions from widespread use of fertilizers produced by the Haber-Bosch process (Galloway et al., 2003; Reay et al., 2008). Then we set N deposition from 1975 to present to the site-reported ~~(Table 1)~~ N deposition rate (Engardt et al., 2017) in Table 1, and used linear interpolation to calculate N deposition between 1850-1950 and 1950-1975. After 1975, N deposition was held constant to roughly match regional trends (Driscoll et al., 2003; Galloway et al., 2013). To adjust N fixation rates, we turned off symbiotic N fixation and set free-living N fixation at all sites to 0.1 g N m^{-2} y^{-1} to match field expectations (Cleveland et al., 1999; Tedersoo et al., 2018). With these dramatically lower rates for N inputs (Fig. 1a, left panel), simulated C and N stocks ~~in the adjusted configuration of the model~~ were too small, which required us to turn off N losses from denitrification to achieve realistic baseline plant and soil C stocks (Table 3; Section 3.1). With denitrification turned off, hydrologic losses of N increased so that the model's present-day sub-surface leaching and runoff fluxes each increased to around 0.1 g N m^{-2} y^{-1} (Fig. 1b, right panel), which is within the range measured in temperate forest stream water (Aber et al., 2003; Gundersen et al., 2006; Groffman et al., 2018). A model that simulates small fluxes of both heterotrophic N fixation inputs and denitrification losses might best match observations of these processes in these temperate forests (Tjepkema, 1979; Roskoski, 1980; Hendrickson, 1990; Barkmann and Schwintzer, 1998; Bernal et al., 2012; Duncan et al., 2013; Morse et al., 2015), but requires substantial model development to achieve (Thomas et al., 2013a; Houlton et al., 2015). Our alternative model included in this study is thus an oversimplification included to examine model C-N responses in ecosystems with a much more closed N cycle than the widely used version, details of which can be found in Lawrence et al. (2018). Our results below highlight how sensitive CLM5 is to the openness of its N cycle, an emergent property that should be the focus of future model development.

2.4 Model N recovery calculations

To calculate N recoveries in ecosystems under ambient N deposition in CLM5, we followed the approach of Thomas et al. (2013b) of adding a small amount of additional N into the N deposition input stream, which enters the model's inorganic soil pool as NH_4^+. Across the field studies, ^{15}N tracers were applied differently, with variation in N ~~-~~addition rates, forms ($^{15}NH_4^+$ or $^{15}NO_3^-$), and timing (Table 1), although most tracer applications were distributed across the growing season. For our simulations under ambient N deposition, we implemented a consistent approach across all simulations by adding a 0.5 g N m^{-2} y^{-1} "tracer" in the model during the first year the tracer was applied in the field. In the first year, we applied the N "tracer" in the model equally across days during

April through September to capture the most active portion of the growing season. In CLM5, we ran sensitivity tests for two of our eight model sites (see Table 1 for a full list, including site names), an old growth forest (Alptal) and a younger forest (Harvard NET), which confirmed that the smallest amount of N we could apply while maintaining realistic ecosystem N recovery responses at both sites was 0.5 g N m^{-2} y^{-1} (Fig. S1), consistent with Thomas et al. (2013b). A sensitivity test for Harvard NET also indicated that the mean N recovery across the last 20 years of the historical simulation was relatively insensitive to which months within the growing season the N “tracer” was applied (Fig. S2). For simulations with fertilization, we applied the site-reported fertilization rate (Table 1) in the model during all years the fertilizer was applied in the field—but only during April through September of each of those years, as we did for simulations under ambient N deposition.

Annual N recovery was then calculated for each ~~model~~ N cycle configuration, site, and year by taking the difference in N stocks between a baseline simulation without a “tracer” or fertilization treatment and its corresponding simulation with “tracer” or fertilizer added, according to:

$$N\ recovery\ (t) = \frac{N\ stock(t)_{N\ addition} - N\ stock(t)_{baseline}}{\sum_0^t N\ inputs_{N\ addition} - \sum_0^t N\ inputs_{baseline}} \qquad (1)$$

where $N\ stock(t)_{N\ addition}$ is the N addition simulation’s N stock at year t since the application of the “tracer” or fertilizer, $N\ stock(t)_{baseline}$ is the N stock from the simulation without a “tracer” or fertilizer added, and ~~where~~ $N\ inputs_{N\ addition}$ and $N\ inputs_{baseline}$ are the total amounts of N entering the ecosystem in the N addition and baseline simulations at each time, respectively. N inputs are the sum of N deposition, the added “tracer” or fertilizer, and biological and free-living N fixation. Total vegetation stocks in the model include N in all aboveground and belowground plant pools, including plant stem, foliage, fine roots, and coarse roots. Soil N stocks include N in litter, organic matter, and soil inorganic N pools. We did not include coarse woody debris in the soil stock because coarse woody debris is rarely measured in ^{15}N tracer experiments. Simulated N recovery in coarse woody debris is possible in CLM5, although this pool accounted for less than 3% of recovered N. Thus, we applied the field definition of total ecosystem recovery to the model results as well—defining total ecosystem recovery in the model as the sum of the plant and soil pools. We note that N recoveries~~y~~ in ecosystems simulated with open N cycles~~the default configuration of CLM5~~ (reported in Table S1) include~~s~~ a small effect of N fixation rates changing in response to added “tracer” or fertilizer. Calculated recoveries in ~~in the adjusted configuration~~simulated ecosystems with closed N cycles (shown in the Results) are a response to the added “tracer” or fertilizer alone, because the control and N addition simulations have the same, fixed N-fixation rates.

2.5 Calculating ecosystem C response to N additions

To examine the impact of model-estimated N fates on the land C sink, we calculated the modeled change in plant or soil C storage per unit change in N input (g C g^{-1} N; i.e., dC/dN), which is frequently done to quantify the impacts of N additions on ecosystem C pools (De Schrijver et al., 2008; Sutton et al., 2008; Thomas et al., 2013a; Frey et al., 2014). Model dC/dN (g C g^{-1} N~~$^{-1}$~~) for each C pool of interest (e.g. total soil or total plant pool) was calculated for each year according to:

$$\frac{dC}{dN}(t)_{model} = \frac{C\ stock(t)_{N\ addition} - C\ stock(t)_{baseline}}{\sum_0^t N\ inputs_{N\ addition} - \sum_0^t N\ inputs_{baseline}} \qquad (2)$$

where *C stock(t)*$_{N\ addition}$ is the mean C plant or soil stock at time *t* in the N addition simulation since the application of the "tracer" or fertilizer, and *C stock(t)*$_{baseline}$ is the mean C plant or soil stock at time *t* in the baseline simulation since the application of the tracer in the N addition simulation. Alternatively, we can estimate both the field and model dC/dN using the method from Nadelhoffer et al. (1999b):

$$\frac{dC}{dN}(t) = \sum_{i=1}^{n} N\ recovery_i \times C:N_{pool(i)} \qquad (3)$$

where *N recovery* is the N recovery of the *i*th component of a measured plant or soil stock (e.g., foliage, wood, litter), $C{:}N_{pool(i)}$ is the C:N ratio of the *i*th component that makes up a particular stock, and the summation is over *i* pools that make up the total plant or soil stock. We based our C:N ratios for stocks on site-reported values from the literature (see Table 2). Ecosystem dC/dN is the sum of plant and soil dC/dN.

2.6 Statistical analyses

To determine whether differences existed among the variation between observations and model outputs, we used paired student t-tests with Bonferroni correction for multiple comparisons or ANOVA analyses. For all statistical analyses, we used the Shapiro test to check for normally distributed residuals and the Levene test for homoscedasticity across sites and their field-sampled timepoints. When statistical assumptions were not met, we tested for differences using the Kruskal-Wallis test and a post-hoc Dunn test with a Bonferroni correction.

3 Results

Below, we first report the effects of ~~two N cycle configurations (default and adjusted)~~N cycle openness (i.e., high or low N inputs and losses) on modeled ecosystem C and N stocks (Section 3.1). Next, we compare model output to available observations for a) the change in N recovery over time at individual sites (Section 3.2), b) the mean change in N recovery in plant and soil pools on short- (< 3 years) and longer (> 3 years; 5 to 17 years) timescales for all tracer experiments in this study (Section 3.3.1), c) the estimated impacts of these N fates on C stocks (i.e., dC/dN; Section 3.3.2), and finally, d) the patterns in N recovery that emerge by PFT and fertilizer treatment (Section 3.4).

3.1 ~~Comparison~~ N cycle openness: Comparison of CLM5 with open and closed N cycles ~~of default and adjusted configurations of CLM5~~

E~~E~~cosystem traits ~~describing the C and N cycles at~~from the end of the historical simulations ~~for the default and adjusted configurations of CLM5~~ are reported in Table 3, along with available site measurements. Simulations using a relatively open N cycle had ~~The two model configurations~~ differen~~t~~d ~~greatly in their~~ rates of N inputs and losses in 1850 ~~as well~~and ~~as~~ throughout the historical simulation than simulations using a relatively closed N cycle (Fig. 1). Observed soil C stocks were typically higher than modeled under both open and closed N cycles in CLM5 ($p < 0.01$, Table 3). However, ~~both model configurations produced~~simulations with both an open and closed N cycle produced present-day aboveground net primary productivity rates (ANPP), leaf area index, plant C stocks, and plant and soil N stocks that were statistically similar to observations ($p > 0.05$, Table 3).

~~Despite producing present-day ecosystem N stocks that were roughly equivalent~~However, these two model configurations ~~the two model configurations~~ differed by an order of magnitude in their estimated ecosystem N turnover time (i.e., pool size divided by total N loss fluxes). ~~The adjusted configuration~~Simulations using a closed N cycle had a mean ~~had a whole-~~ecosystem ~~mean~~ N turnover time ~~of~~ of 650~~5~~0 ± 53~~2~~0~~5~~0 years (mean ± 1 SD across simulated sites) ~~years~~ compared to 880 ± 370 years in simulations using an open N cycle ~~the default configuration~~ ($p < 0.01$; Table S2). The wide range in ecosystem N turnover time results from site-specific differences, including variations in factors governing organic N storage in soils (e.g., texture, past disturbance). By comparing the ratio between the mean ~~residence~~ turnover time of N in the ~~whole-~~ecosystem to the mean ~~residence~~ turnover time of N in plants, we quantified how frequently N cycles through the plant pool. This metric describes the potential for a unit of N to be used by plants to produce C before it is lost from the system. ~~In~~ In simulations with a closed N cycle~~the adjusted configuration~~, N cycled through plants an average of 210 ± 190 times before it was lost, while it only cycled through plants 26 ± 15 times in simulations with ~~in the default configuration~~ an open N cycle ($p < 0.01$). Consequently, the same unit of N in ~~the adjusted configuration~~a closed N cycle has a longer retention time in plants than ~~the default configuration~~when the N cycle is open—~~,~~which could lead ~~the~~ the model configuration with a closed N cycle ~~adjusted configuration~~ to produce more plant and soil C per unit of N. Given high biases in the N input and loss rates in the model with an~~the default configuration~~ open N cycle (see Section 2.3.1), we focus the remainder of the study on results from the ~~adjusted~~ model configuration with a closed N cycle~~configuration~~. For completeness, results of N recovery for CLM5 using a closed N cycle, which is the default ~~the default~~ configuration of N cycling in CLM5, are ~~listed next to the results from the adjusted configuration~~ in Table S1.

3.2. Site-level decadal changes in N recovery

The model-measurement comparisons of N recovery for each site, experimental N treatment, and N cycle configuration are given in Table S1 and shown in Fig. 2 and Figs. S3-S6. In this section, we highlight the recovery at Harvard Forest BDT (deciduous) and Harvard Forest NET (evergreen) under ambient N deposition because Harvard Forest provides the longest record for a model-measurement inter-comparison with ^{15}N tracer results. Under a closed N cycle, both Harvard Forest PFTs simulated that plants were the dominant, immediate fate of added N, accounting for 63% of added N in the BDT stand and 49% in the NET stand in the first year after N addition. In contrast, field measurements demonstrate that plants acquired < 10% of added tracer, and that soils were the dominant sink for ^{15}N (Fig. 2; Nadelhoffer et al. (2004)). After the first year, the model estimated that the N initially taken up by plants moved to soils within 3 years in the deciduous stand and within 5 years in the evergreen stand, after which the recovered N subsequently stayed in the soil pool—accounting for approximately 70% of the added N at the end of two decades. This pattern was typical across the sites we simulated and across ecosystems under open and closed N cycles. However, total ecosystem recovery was generally lower in ecosystems with an open N cycle ~~the default configuration of the model~~ relative to ecosystems with a closed N cycle ~~the adjusted configuration~~ (Fig. S3-S6).

In our data-model comparison, CLM5 was typically unable to capture inter-site variations in N recovery across PFT and fertilization levels, likely due to both model errors and measurement uncertainty (Fig. 2, Figs. S3-S6). For example, the measured total recovery of tracer at Harvard Forest evergreen forest appeared to increase with time (Nadelhoffer et al., 2004), which may be a result of changes in the sampling locations of soil cores between sampling events (i.e., soil sampling was done further inside plot boundaries in later years than in early sampling years). Thus, in Section 3.3, we discuss changes in the temporal patterns in simulated and observed N recovery averaged across sites, aggregated to the short-term (< 3 years) and longer-term (> 3 years) to capture the temporal break in slow and fast changes in simulated N recovery. The small number of sites for each forest type (deciduous or evergreen) and fertilizer treatment (ambient or fertilized) also limited statistical comparisons by these factors. Thus, to reach more statistically-robust conclusions, we combined both PFTs and fertilizer treatments in Section 3.3, and examine qualitative differences by these factors in Section 3.4.

3.3. Mean response in CLM5

3.3.1 Change in N recovery in CLM5

Across all sites and treatments, there were 14 field measurements from 13 experiments reporting ^{15}N tracer recovery within 3 years of the start of N additions (i.e., short-term) and 14 field measurements from nine experiments reporting ^{15}N recovery after 3 years (i.e., longer-term; Table 1). On the short-term, ~~the adjusted configuration~~CLM5 with a closed N cycle estimated more than twice the mean plant N recovery of tracer (46 ± 12%; mean ± 1 SD across simulated sites) than was measured in the field (18 ± 12%; mean ± 1 SD across field measurements; $p < 0.001$; Fig. 3a). Short-term tracer recovery in soil was modeled to be 40 ± 10%, compared to the observational mean of 54 ± 22% (Fig. 3c), and was not statistically different from observations. Tracer recovery in plants decreased over time in both CLM5 and the field studies. On the longer-term, the ~~adjusted configuration~~closed N cycle led to modeled plant N recoveries (23 ± 6%) that were closer to observations (13 ± 5%) than they were on the short-term (Fig. 3b), but were still roughly twice the observed values ($p < 0.001$; Fig. 3b). The modeled decrease in mean plant N recovery over time corresponded with an increase in mean soil N recovery (to 59 ± 15%) that was statistically similar to observations on the longer-term (69 ± 18%; Fig. 3d). The model's initially high plant N recovery and its later increase in soil N recovery indicate that CLM5 estimates soils to become a dominant sink for N on the long-term, but this response is a result of an over-competitive plant pool that transfers recovered N to soils through turnover of plant litter. Similar to ~~the~~ the model configuration with a closed N cycle~~adjusted configuration~~, ~~the default configuration of CLM5~~CLM5 with an open N cycle overestimated short-term (38 ± 7%; $p < 0.001$) and long-term (20 ± 6%; $p < 0.05$) plant N recovery and estimated short-term soil N recovery (39 ± 14%) similar to observations. ~~Distinct from the adjusted~~ However, CLM5 with~~version, the default configuration~~an open N cycle underestimated~~ed~~ (45 ± 15%) ~~-~~long-term soil N recovery ($p < 0.001$).

On average, CLM5 with a closed N cycle ~~the adjusted version of CLM5~~ simulated that most added N remained in the ecosystem over both short and longer timescales (Figs. 3e and 3f). Within 3 years of simulated tracer or fertilizer addition, the mean whole-ecosystem recovery of N under a closed N cycle ~~in the adjusted configuration~~ was 87 ± 14%, which was similar to the observational mean of 72 ± 23%. On the longer term, simulations indicate that these forests retained added N with minimal loss (83 ± 17%), which was similar to the observational mean of 82 ± 16%. CLM5 with an open N cycle ~~The default configuration of CLM5 also estimated~~simulated ~~that~~ short-term ecosystem recovery (77 ± 14%) that was similar to observations. However,~~ unlike the adjusted configuration of CLM5, the default configuration~~ an open N cycle in CLM5 led to a~~ estimated that~~ longer-term ecosystem recovery that was lower than observations (65 ± 16%, $p < 0.05$).

3.3.2 Change in C response to N additions in CLM5

To scale and compare the effect of plant and soil N recoveries on forest C sinks between CLM5 with a closed N cycle and field measurements, we estimated changes in plant, soil, and total C stocks (i.e., sum of plant and soil stocks) in response to N tracer or fertilizer additions—referred to as $(dC/dN)_{plant}$, $(dC/dN)_{soil}$, $(dC/dN)_{total}$, respectively~~—in the adjusted configuration of CLM5 and in field measurements~~ (Fig. 4). For the model, annual dC/dN values were computed directly (i.e., "direct approach") as the difference between the ~~in~~ total plant or total soil C stocks between the baseline and "tracer" (or fertilizer) simulation divided by the difference in the amount of cumulatively added N between the two simulations ~~simulated by CLM5 after the modeled N "tracer" or fertilizer was applied~~ (Eqn. 2). To estimate the effect of field-measured ^{15}N recoveries on forest C pools, we used the scaling exercise presented by Nadelhoffer et al. (1999b) that we described in Eqn. 3, where for each experimental timepoint, dC/dN is estimated for foliage, wood, bark, fine roots, and coarse roots (when available), the O horizon, and the mineral soil using the measured ^{15}N recovery in each pool and the ~~literature~~published field-measured ~~-based estimate~~values of C:N for that site's particular pool (Table 2, Eqn. 3). Because differences in model and field-estimates of dC/dN can occur from differences in total N recovery, distribution of recovered N across sub-pools, or C:N ratios of sub-pools, we also used Eqn. 3 to compute a second model-based dC/dN using the same estimates of field-based C:N ratios, except that bark is not modeled in CLM5 ~~(Eqn. 3)~~. This second, indirect approach allows us to remove sub-pool C:N ratios as a confounding factor in estimates of dC/dN. We used these two methods to calculate model dC/dN in order to a) directly show the model's overall C response to N additions and b) account for substantial differences in modeled and field-based approximations of C:N ratios in plant and soil pools (Table 2). It should be noted that this scaling exercise depends on the accuracy of the C:N ratios measured in the field, and operates under the assumption that C:N ratios of plant tissue and soil horizons stay constant over time. Despite these limitations, this budgeting method allows us to roughly compare differences in ecosystem C response to N additions between CLM5 and field measurements.

Averaged across experiments, the short-term direct estimate of $(dC/dN)_{plant}$ in CLM5 under a closed N cycle (right-most white bar in Fig~~s~~. 4a) was similar to the field-based estimate (left-most white bar in Fig~~s~~. 4a), despite the greater than two-fold difference in plant N recovery between modeled and observed values (Fig~~s~~. 3a). Within three years of N additions, the direct $(dC/dN)_{plant}$ in CLM5 was 26 ± 8 g C g^{-1} N, compared to the field estimate of 19 ± 14 g C g^{-1} N (Fig. 4a). On the decadal timescale, direct $(dC/dN)_{plant}$ in CLM5 became higher than the observational estimate (28 ± 7 and 18 ± 7 g C g^{-1} N, respectively, $p < 0.05$, Fig. 4b). Differences between the directly-modeled $(dC/dN)_{plant}$ and field $(dC/dN)_{plant}$ may also be due to differences in C:N ratios of plant sub-pools. In particular, the C:N of wood in CLM5 is substantially lower (~266-293) than field-based estimates (411 ± 110, Table 2), compensating for the model's over-estimate in N recovery. When the same C:N ratios are used for both field- and model-based estimates of $(dC/dN)_{plant}$, the over-estimation of N recovery in CLM5 is carried more dramatically into $(dC/dN)_{plant}$: the simulated $(dC/dN)_{plant}$ (Fig 4a and 4b, center white bars) becomes substantially higher than observations on both the short (52 ± 15 g C g^{-1} N, $p < 0.001$) and the longer-term (45 g ± 15 g C g^{-1} N, $p < 0.001$).

In soils, the direct approach to calculating $(dC/dN)_{soil}$ (right-most gray bars in Figs. 4a and 4b) in ~~ecosystems~~ CLM5 with a closed N cycle estimated that soil C stocks would decrease within three years of N additions (-2 ± 4 C g^{-1} N), and increase slightly in the long term (5 ± 3 g C g^{-1} N). This short-term decline in soil C in response to N additions is a result of decreasing litter C stocks. In contrast, observations indicate that soils retain ^{15}N, which can be associated with C accumulation (12 ± 5 g C g^{-1} N; Fig. 4a, $p < 0.001$). On the long-term, measured soil C stocks (15 ± 5 g C g^{-1} N; Fig. 4b, $p < 0.001$) increased more than direct estimates from CLM5. When using the same soil C:N ratios to calculate $(dC/dN)_{soil}$ in CLM5 as estimated from observations, short- and longer-term soil $(dC/dN)_{soil}$ become similar between the model and field estimates (Fig 4a and 4b, center bars; 10 ± 3 g C g^{-1} N and 15 ± 6 g C g^{-1} N, respectively). Overall, CLM5 directly estimates a short-term $(dC/dN)_{total}$ of 24 ± 7 g C g^{-1} N and a longer-term $(dC/dN)_{total}$ of 33 ± 9 g C g^{-1} N, while the longer-term estimate ranges from 30 to 106 g C g^{-1} N when using field-estimated C:N ratios. Generally, ~~the~~ CLM5 with an open N cycle ~~default configuration~~ followed similar patterns as ~~th~~the model configuration with the closed N cycle ~~e adjusted configuration~~ for ~~both~~ short and long-term plant and soil dC/dN, except that long-term plant dC/dN was not statistically different between the CLM5 and observations. Because of existing model limitations in N cycle representation, model-estimated values of dC/dN are intended to provide a sensitivity test of how the modeling of N fates can affect model estimates of ecosystem C response to N additions relative to what is expected from field measurements.

3.4 Impacts of forest type and fertilization

In the field, forest types might respond to N deposition differently because of differences in their plant and ecosystem traits (Cornelissen, 1996). In CLM5, the evergreen and deciduous PFTs differ especially in their foliage C:N (see Table 2) and timing of plant N demand, which should alter decomposition and N mineralization. However, s~~S~~tatistical comparisons between modeled and measured recoveries of N additions by forest type and fertilizer treatment are difficult to construct because of the small number of sites available for each category. Despite these limitations, we identified a few recurring differences between a) deciduous and evergreen forests, as well as b) between ambient N deposition and fertilizer conditions.

Under ambient conditions, ~~the adjusted configuration of CLM5~~simulations using a closed N cycle ~~simulated~~ had~~that~~ plants ~~had~~ with notably more mean recovery of added N in two BDT (64%) forests than in four NET forests (44%) on the short term (Table 4, Fig. 5). On the long term, the amount of N recovered in modeled plants decreased in both forest types with no difference between the two PFTs (20-23%; Table 4, Figure 5). Conversely, simulated recovery of added N in soil was higher in NET (52%, n=4) than in BDT (32%, n=2) forests on the short term. However, CLM5 estimated similar long-term recoveries of N additions in soil (72 to 73%) in both PFTs, similar to long-term patterns of simulated plant N recovery. In contrast, measured recoveries of ^{15}N did not differ by forest type for plants or soils at either time point, except for short-term soil N recovery (Table 4, Figs. 5a and 5c). ~~The default configuration~~Simulations of CLM5 with an open N cycle followed similar patterns, except there was an underestimation of long-term soil recovery in both PFTs (Table 4).

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Fertilization altered the simulated partitioning of N between plants and soils over short and long timescales, and generally reduced overall recovery of N in the ecosystem (Table 4, Figure 5). ~~Simulations~~ Simulations with a closed N cycle ~~using the adjusted configuration of CLM5~~ yielded lower recovery of N in deciduous plants (32%) than the two unfertilized stands (64%) on the short term. For the evergreen stands, modeled plant recovery of N did not differ between the four unfertilized and six fertilized stands, although there was considerable variation among the latter. Simulations for both forest types contradict observations showing that fertilization increases short-term plant recovery of tracer N regardless of forest type (Table 4). However, both measurements and ~~the~~ simulations using a closed N cycle ~~adjusted model and measurements~~ demonstrated that fertilization led to a decline in the amount of tracer retained in soil in the long-term (Table 4). ~~The~~ The model configuration with an open N cycle ~~default configuration of CLM5~~ generally followed similar trends as CLM5 with a~~-~~ closed N cycle~~the adjusted configuration~~.

Overall, we find evidence suggesting that a) under ambient treatments, CLM5 simulates differences in short-term plant N recovery between deciduous and evergreen forests, while measurements show no discernable difference (Table 4); b) the movement of N from plant to soil pools over the decadal timescale occurs in a distinctly different manner between CLM5 and measurements (Fig. 5); and c) the model and measurements respond differently to fertilizer in the short term, but both estimate declines in soil N recovery after at least 3 years of fertilizer additions (Table 4).

4 Discussion

This study compares estimates of ecosystem recovery of N additions between CLM5—~~,~~a ~~-~~land model with coupled C and N cycles—~~,~~and ~~-~~long-term ^{15}N tracer experiments ~~that track how N moves through~~in temperate deciduous and evergreen forests. ~~Our study provides insight into which model assumptions are consistent, or inconsistent, with experimental results. First, we identified that the default configuration of CLM5 continues to have biases in N losses (Fig. 1)—similar to previous versions of CLM~~ (Koven et al., 2013; Thomas et al., 2013b; Houlton et al., 2015; Nevison et al., 2016)~~. Specifically, CLM5 has unrealistically high rates of denitrification and low rates of N leaching and runoff compared to field measurements. We also identified that pre-industrial N deposition in CLM5 was higher than expected from reconstructions~~ (Holland et al., 1999; Fakhraei et al., 2016)~~ for the Northeast United States and parts of Europe (Fig. 1). After adjusting N inputs and losses to better match field expectations, many of the simulated ecosystem stocks and fluxes (i.e., plant N, soil N, plant C, leaf area, and ANPP) in the adjusted configuration of CLM5 were similar to those estimated by the default configuration of the model—and estimates of these traits from both configurations were statistically indistinguishable from observations (Table 3). Both model configurations typically shared the same responses in N recovery, except that the default configuration a) had less total ecosystem recovery of N inputs than the adjusted configuration and b) underestimated long-term soil N recovery compared to observations.~~

~~Using the adjusted configuration of the N cycle, which applies more accurate N fluxes to spin up ecosystem C and N pools, w~~We examined CLM5, with a focus on simulations with a more closed N cycle, along three important axes of terrestrial C-N modeling: its ability to simulate a) the decadal patterns of N recovery in plant and soil pools, b) the plant and soil C responses to the model's estimates of N recovery, and c) the potential impacts of forest type and fertilizer treatment on the partitioning of recovered N in ecosystems. Below, we discuss the role of N inputs and losses in ecosystem N recovery. Based on the N recovery patterns in simulations run with an open and closed N cycle, we identify some potential causes for the discrepancy between modeled and observed N fates in plants and soils—~~,~~focusing on plant uptake and soil immobilization processes and recommending changes for modeling plant-soil-microbial competition in the version of CLM5 that will be used in future CMIP experiments. We then compare our model estimates of the effects of N additions on forest C sinks with other measurements in the literature, and discuss potential mechanisms behind differences in these responses. Last, we discuss the ^{15}N tracer dataset as a tool for evaluating CLM5 and other land models.

4.1 Modeling Ecosystem Inputs and Losses

Our analysis of CLM5 configured with an open N cycle (i.e, the default configuration of N cycling in CLM5) identified that the model continues to have large biases in N losses (Fig. 1)—similar to assessments of previous versions of the model (Koven et al., 2013; Thomas et al., 2013b; Houlton et al., 2015; Nevison et al., 2016). Specifically, CLM5 has unrealistically high rates of denitrification and low rates of N leaching and runoff compared to field measurements. We also identified that pre-industrial N deposition in CLM5 was higher than expected from reconstructions (Fakhraei et al., 2016; Holland et al., 1999) for the Northeast United States and parts of Europe (Fig. 1). Although simulations with an open N cycle shared some similar responses to N additions as simulations with a closed N cycle, having higher N deposition and denitrification fluxes (i.e., the default version of CLM5) typically led to a) less total ecosystem recovery of N inputs than simulations using a closed N cycle and b) an underestimation of long-term soil N recovery compared to observations. In adjusting N inputs and losses in CLM5 to better match field expectations, many of the simulated ecosystem stocks and fluxes (i.e., plant N, soil N, plant C, leaf area, and ANPP) remained similar to observations and simulations using an open N cycle (Table 3). Given that the openness of an ecosystem's N cycle changes the ecosystem's recovery of N inputs within a decadal timescale, we suggest that future model development not only test new mechanistic representations of N fixation and denitrification, but do so in concert with modified N input datasets to ensure that both inputs and losses capture field expectations.

4.2~~1~~ Plant-Soil N Competition, Plant N Uptake, and Soil N Immobilization

Compared to observations, ~~In CLM5, ~~plants in CLM5 are a larger than expected ~~the dominant~~ short-term sink for N additions in simulations using open and closed N cycles, with soils becoming the dominant sink for N thereafter, as leaf and fine root litter is incorporated into soils. ~~However, ~~F~~f~~ield experiments demonstrate the opposite pattern—large amounts of N are directly recovered in soils from the start of tracer application, without passing through plants (Emmett et al., 1998a; Gundersen et al., 1998; Tietema et al., 1998; Nadelhoffer et al., 2004; Goodale, 2017). Two decades ago, Nadelhoffer et al. (1999b) used earlier ^{15}N tracer studies to illustrate similar problems in an earlier generation of models, but issues continue to persist in how these C-N competition processes are represented. The overly strong plant sink for N additions in CLM5—both when the N cycle is open and closed—~~-~~likely results in part from how the model handles N competition between plants and soil immobilization, as well as the model's representation of the plant uptake and soil immobilization processes themselves. Our results suggest the need for additional improvements to CLM5~~the default model~~'s partitioning of N among plants, soils, and N loss pathways—similar to results shown in earlier studies with CLM4 (Thomas et al., 2013b)—even after substantial changes to the model's soil (Koven et al., 2013) and plant (Lawrence et al., 2018) C-N biogeochemistry have been made since earlier versions.

In CLM5, the amount of N that plants can acquire depends on how much inorganic soil N is available as well as the total demand for N from all modeled ecosystem processes, including soil immobilization, denitrification, and nitrification (Lawrence et al., 2018). When there is not enough N to meet the total demand from both plants and immobilization, inorganic soil N is divided between plants and soils by proportionately scaling their individual demands to the total demand. Plants can then take up their allocated portion of soil inorganic N if they have enough available C to pay for the cost of taking up that N. Given that plants recover too much added N on the short-term, regardless if the N cycle is open or closed, an option for reducing plant access to N without reducing the availability of inorganic N for immobilization is to increase the costs for plants to acquire N. To date, CLM has also used the long-standing assumption that plants acquire N only from inorganic N pools rather than organic N, and that plant demand does not affect N mineralization rates. However, evolving views of plant-soil interactions suggest more complex representations of both processes may be needed, in which plant mycorrhizal associations and priming can enable plants to acquire N from litter and soil organic matter, rather than relying solely on inorganic N (Schimel and Bennett, 2004; Phillips et al., 2013; Tang and Riley, 2014; Terrer et al., 2016; Zhu et al., 2016a; Sulman et al., 2017). Allowing plants to access N from organic as well as inorganic N pools in the model might seem a counterintuitive suggestion, given that plants already show excessive acquisition of newly added inorganic N. But the inclusion of these microbial-driven processes of N acquisition would both better match current understanding of plant-soil-microbial interactions, and could allow plants to meet their overall N demand even if competition for inorganic N by immobilization were increased (see below), and allow for added inorganic N to be retained in the soils longer, similar to observations.

Contrary to our model results, field experiments summarized here and elsewhere (e.g., Tietema et al. 1998, Curtis et al. 2011, Templer et al. 2012) demonstrate that soils dominate the fate of added ^{15}N, and that this soil N sink is both rapid and direct, without passing through plants. For example, ^{15}N tracer studies at two sites simulated here, Alptal (Providoli et al., 2006) and Arnot Forest (Goodale et al., 2015), as well as at other temperate forests (Seely et al., 1998; Perakis and Hedin, 2001; Hagedorn et al., 2005; Lewis and Kaye, 2012), show that large quantities of ^{15}N can be recovered in association with soil organic matter pools within days to weeks of its addition, including in the soil clay or "heavy" fractions, which are generally the most stable components of soil. CLM5 currently immobilizes little N directly into soil, particularly when N input fluxes are high (~~default~~ open v. ~~adjusted~~ closed ~~configuration~~N cycle, and fertilized v.

ambient simulations). Furthermore, N additions (e.g., N deposition) are directly added to the dissolved inorganic N pool, which the model immediately distributes throughout the soil column according to an exponential profile. Although the model and field experiments differ in how they apply the N tracer to soil (directly into the inorganic soil N pool versus to the top of litter, respectively), t~~T~~he large magnitude of the observed soil N sink and the model's poor ability to reproduce it suggests ~~indicate~~ that modeling a stronger soil immobilization sink should be a priority.

Several soil processes and ecosystem traits that are involved in immobilization are not currently represented in CLM5, and could help increase the N demand for soil immobilization. The model's current soil C-N dynamics (Koven et al., 2013) were adapted largely from the CENTURY model, which has implicit microbial processes rather than explicit representation of microbial N uptake and turnover—processes that form a dominant pathway for N incorporation into soil organic matter (Bingham and Cotrufo, 2016). Incorporating an explicit representation of microbial biomass, and providing microbes with access to inorganic soil N before plants can access it should increase rates of soil immobilization of added inorganic N—particularly because microbial activity and demand for N is greatest at the soil surface (Iversen et al., 2011; Li and Fahey, 2013) where fresh C inputs are greatest, C:N ratios are high, and microbes have the opportunity to rapidly capture N deposition. Previous modeling work has shown that explicitly representing microbes improves soil C stock projections (Wieder et al., 2013), and that more precisely representing plant and microbial biomass and their enzyme affinity for inorganic N better captures the fates of N in grasslands (Zhu et al., 2017).

Field Code Changed

Field Code Changed

~~In addition, N additions (e.g., N deposition) are directly added to the dissolved inorganic N pool, which the model immediately distributes throughout the soil column. However, in ^{15}N tracer experiments, the tracer is applied directly on top of leaf litter to mimic N deposition and a vertical gradient of N use in soils forms because microbial activity and demand for N is greatest at the soil surface (Iversen et al., 2011; Li and Fahey, 2013) where fresh C inputs are greatest, C:N ratios are high, and microbes have the opportunity to rapidly capture this tracer. To capture this vertical gradient of immobilization found in field experiments, the model could add inorganic N to the surface soil layers, only, and allow it to mix more deeply through advective or diffusive fluxes.~~

Field experiments also demonstrate that when ecosystem N inputs increase (e.g., with fertilizer), the recovery of ^{15}N subsequently increases in plants and decreases in soils on the short and longer-term (Nadelhoffer et al., 1999b; Templer et al., 2012). ~~However~~But~~,~~ under both open and closed N cycles, CLM5 estimated a different short-term plant N response depending on forest type, generally estimating a decrease in plant N recovery in deciduous forests and a slight increase in evergreen forests (Table 4). This response is likely due in part to excess plant uptake of N in forests after the tracer is applied in the model. However, the model generally ~~did~~ produced ~~similar trends in~~ a decline in long-term soil N recovery in response to fertilizer treatment (Table 4), except for the mean soil N recovery in evergreen forests with open N cycles~~, although it was smaller in magnitude~~. Model development that incorporates plant-soil-microbial dynamics, as described above, would likely yield larger decreases in soil recovery of increased N additions because soils would recover more N additions under ambient conditions before fertilizer is added. It is important to note that additions of parameters or process-based representation of ecological processes can add uncertainty to model projections. To limit this added uncertainty, new model representations should be designed and evaluated using robust and representative, process-based datasets—as discussed in modeling papers, including Prentice et al. (2015), Lovenduski and Bonan (2017), Lombardozzi et al. (2018), and Sulman et al. (2018).

4.3~~2~~ Forest Carbon Sequestration from N Deposition

Despite plants in CLM5 being overly competitive for ecosystem N additions, the model did not dramatically overestimate the response of ecosystem C pools to N additions in simulations with closed N cycles when compared to observations (Fig. 4a and 4b). Instead, CLM5 directly estimated a longer-term $(dC/dN)_{total}$, ranging from 19 to 45 g C g^{-1} N in simulations with closed N cycles, close to the lower bound of the 50 to 75 g C g^{-1} N range of dC/dN estimated from measurements of forest growth across a N deposition gradient (Sutton et al., 2008), and similar to the range measured in temperate forests (-2 to 48 kg C kg^{-1} N) summarized by Frey et al. (2014). Similarly, CLM5's estimates of $(dC/dN)_{total}$ for simulations with closed N cycles also fall within the range modeled by O-CN (2 to 79 g C g^{-1} N) and CLM4 (24 to 30 g C g^{-1} N) for temperate forest ecosystems (Zaehle and Friend, 2010; Thomas et al., 2013a). However, modeled estimates of dC/dN can be difficult to interpret against field estimates of dC/dN or those reported by other models because estimates of dC/dN depend not only on N recovery in plant and soil pools, but also on the C:N ratios of these pools.

For example, our directly-measured model results for $(dC/dN)_{total}$ initially appeared counterintuitive because CLM5 estimated approximately twice as much recovery of N in plants than measured in field experiments. In CLM5, the C:N ratio of dead wood is approximately half the value of what is measured at field sites (Table 2). In addition, plant C:N ratios in the model appear to have an important role in immobilization—as a higher C:N ratio of plant litter in NET forests led to higher rates immobilization compared to BDT forests (~~Figure~~ Figs. 2a and~~,~~ 2b). When the difference in C:N ratios between the model and field measurements were accounted for by using the mean C:N ratios~~s~~ from available data at our sites, the model's estimated $(dC/dN)_{total}$ increased to a range ~~from~~ of 30 to 106 g C g^{-1} N, a range much larger than observed estimates. While this range overlaps with the observed ranges, the high end of the range exceeds the observations. This discrepancy between observed and modeled C:N ratios would also apply to the default version of CLM5, where ecosystems generally have an open N cycle. Thus, we recommend that options for improving the calculation of C:N ratios of plant pools in CLM5 be explored in order for CLM5 to more accurately and mechanistically model the correct ecosystem C responses to N additions. To accomplish this, additional field measurements would be needed to evaluate changes to model estimates of C:N ratios and to constrain them to reasonable values.

CLM5 ~~also~~ simulations~~ed~~ with both open and closed N cycles indicated that~~, on average,~~ adding N to temperate forests yielded on average a small loss of soil C on the short term (due to declines in the litter pool), and a small increase on the long-term (Fig. 4). These dynamics are consistent with modeled relief of N limitation to litter decomposition in the short-term (Bonan et al., 2012), and with increased plant NPP on the long-term. Yet reviews of long-term N addition studies in mature forests show increases in soil C stocks that are associated with reduced rates of decomposition rather than an increase in plant litter production

Field Code Changed

(Janssens et al., 2010; Frey et al., 2014). The increase in soil C stocks might be explained by the changes to the plant-soil-microbial feedbacks described above, in which plant acquisition of N under ambient N availability is mediated by microbial symbionts that drive decomposition, and these processes slow when external N supplies increase. Explicit representation of plant-soil-microbial feedbacks, such as in Sulman et al. (2017), could improve model representation of both soil C responses to N addition as well as the plant and soil N fates discussed above.

4.4~~3~~ Evaluating N Fate in Modeled Forests

Model evaluation can often be a challenge because of the availability and consistency of how field measurements are taken and analyzed. To build a useful dataset that can be leveraged for model evaluation and for potential benchmarking (Luo et al., 2012; Collier et al., 2018), differences between N recovery estimates from different field experiments need to be reconciled. Even when focusing on temperate deciduous and evergreen forests, we found a wide variation in the measurements of N recovery within each forest type. This range in measurements made it difficult to identify how much of the mismatch between measurements and CLM5 was a consequence of model weaknesses alone. For example, calculations of tracer recovery in soils can depend on uncertainties associated with soil organic N pool measurements—usually the largest and most difficult pool to quantify in terrestrial ecosystem (Nadelhoffer et al., 2004). Accuracy at some sites in part depends on how well-constrained measurements of bulk density are, the number of soil cores taken, and the depth of the soil cores—which ranged across sites from as shallow as 5 cm in Bear Brook Forest to as deep as 50 cm at Arnot Forest. In long-term field studies, changes to field sampling procedures over time add uncertainty to comparisons between observed and modeled temporal trends, as well as uncertainty in evaluating the model's N recovery response to fertilizer and forest type. Increasing the number of long-term ^{15}N tracer experiments at evergreen and deciduous forests could help constrain estimates of N recovery in plant and soil pools at these two forest types—leading to a more robust dataset for future model evaluations.

In addition, measurement data from other biomes are needed to evaluate the global impact of CLM5's estimates of N recovery in plant and soil pools. Currently, most tracer experiments are in North America and Europe, which represent a subset of ecosystem types and climates that exist globally. One of the few ^{15}N experiments in tropical forests indicates that soil retention of ^{15}N is similar to that found in temperate forests (Gurmesa et al., 2016), even though tropical forests are typically limited by phosphorus availability and N (Hedin et al., 2009). Additional tracer experiments in the tropics would allow us to evaluate whether this pattern is anomalous for forests in this biome and whether the response of CLM5's tropical PFTs to N additions is similar to that modeled for temperate PFTs. Finally, increasing the number of sampling events at current and future field sites will expand our capacity to test more nuanced hypotheses about temporal patterns in dC/dN over time, both during the first few years after tracer application when more dramatic changes in ^{15}N recovery in plant and soil pools occur, and for timescales longer than two decades.

5 Conclusions

The accuracy of Earth system model projections of ~~future~~ land ~~carbon~~ C storage relies on how well land models can ~~project~~ simulate the long-term responses of plant and soil C stocks to environmental change, including to shifts in N deposition. To evaluate a land model commonly used in global model intercomparison projects, we simulated temperate and evergreen forests in CLM5 with open and closed N cycles, and subsequently compared the modeled fate and effect of N additions on C stocks against measurements from long-term ^{15}N tracer experiments. Overall, we found that a sizable portion of N additions in CLM5 is taken up first by plants and then moved into long-term soil pools through the recycling of plant litter—contrary to field experiments that indicate N additions are predominately immobilized and retained in soils. Even though CLM5 overestimated plant N recovery on the short and longer-term, the modelled plant dC/dN responses were similar to those based on observations—although the model slightly over-estimated long-term plant dC/dN when a closed N cycle was used. An overestimation of plant dC/dN did not typically occur because the model's C:N ratios for wood were smaller than those generally found in the field, which compensated for the model's plant pool that was overly competitive for N additions. For similar reasons, CLM5 underestimated soil dC/dN, even though the modeled mean N recoveries in soil were similar to observations (except for when the model under-estimated long-term soil N recovery when using an open N cycle). Overall, our data-model comparison suggests further exploration into a) more accurate representations of N inputs, N losses, and C:N ratios in CLM5, and b) ~~Our data-model comparison of plant and soil N recovery in temperate forests indicates that CLM5 overestimates recovery of N additions in plants. Although temporal patterns in N fate and partitioning differ between CLM5 and observations, CLM5 estimates ecosystem C responses to N additions that are similar to observations—because of compensating differences in plant C:N ratios between observations and the model. of CLM5 that will be used in~~ i~~I~~ncorporating additional plant-soil-microbial processes in land models to increase soil immobilization and reduce initial plant N uptake of N additions.~~ should improve the mechanistic interactions in forests that occur between C and N cycles, which may help avoid future challenges in projecting climate under changing environmental conditions.~~

Data availability

Model output and scripts used to analyze data presented in this manuscript are available upon request. ^{15}N tracer data, along with key citations, ~~can be found in the citations listed~~ are available in Table S1~~ or through communication with site PIs~~. The most recent version of CLM5 is publicly available through the Community Terrestrial System Model (CTSM) git repository (https://github.com/ESCOMP/ctsm).

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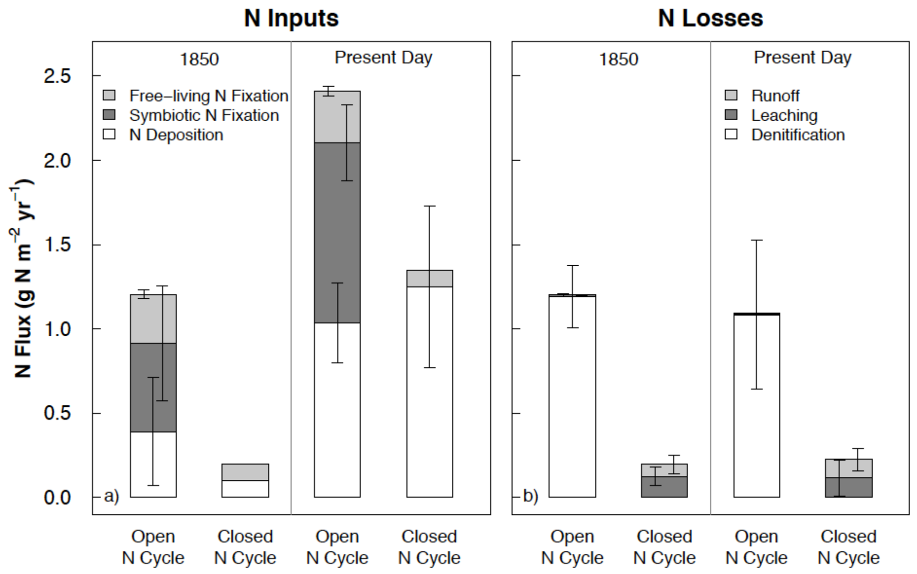
Table 1: Site information for long-term ^{15}N experiments in Europe and North America, including corresponding plant functional type (PFT) in CLM5, which is either broadleaf deciduous temperate (BDT) or needleleaf evergreen temperate (NET) tree. The year of stand establishment is the year in which we implemented a harvest in the model to simulate the forest's reported stand age. N deposition is reported as throughfall or the sum of wet and dry N deposition as compiled from available literature. Tracer experiments at plots receiving ambient N deposition and fertilizer treatments are described on separate lines for each site.

Site	Latitude, Longitude	PFT	Year of Stand Establishment	N Deposition (g N m^{-2} y^{-1})	Years N Fertilizer Applied	Amount of N Fertilizer (g N m^{-2} y^{-1})	First Year Tracer Applied	Number of Years After Tracer Application that Recovery was Measured
Harvard (USA)	42°30' N, 72°10' W	BDT	1945[a]	0.8[a]	None	0.0[b]	1991[b]	1, 8, 17
					1988-Present[b]	5.0[b]	1991[b]	1, 8, 17
Arnot (USA)	42°17'N, 76°38'W	BDT	1911[c]	0.9[c]	None	0.0[f]	2007[c]	1, 6
Bear Brook (USA)	44°52'N, 68°06W	BDT	1945[d]	0.8[d]	1989-2016[e,f]	2.5	1991*	1
Harvard (USA)	42°30' N, 72°10' W	NET	1926[a]	0.8[a]	None	0.0	1991[b]	1, 8, 17
					1988-Present[b]	5.0[b]	1991[b]	1, 8, 17
Klosterhede (Denmark)	56°29'N, 8°24'E	NET	~1920[h]	2.0[h]	None	0.0	1992[g]	1, 17
					1992-1996 and 1999-Present[h]	3.5[h]	1992[g]	1, 17
Gårdsjön (Sweden)	58°04'N, 12°03'E	NET	1910[i]	1.5[j]	1991-Present[i]	4.0[i]	1992[k]	2
Aber (Wales)	53°13'N, 4°00'W	NET	1960[g]	1.5[g]	1990-Present	3.5[g]	1992[g]	3
					1990-Present	7.5[g]	1992[g]	3
Alptal (Switzerland)	47°02, 8°43'E	NET	~ 1750[l]	1.7[l]	None	0.0	2000	1, 3, 9
					1995-Present[l]	2.5[l]	2000	2, 7, 14

[a]Magill et al. (2004), [b]Nadelhoffer et al. (2004), [c]Goodale (2017), [d]Elvir et al. (2006), [e]I. Fernandez, pers. comm., [f]Nadelhoffer et al. (1999a), [g]Tietema et al. (1998), [h]Gundersen (1998), [i]Seftigen et al. (2013), [j]Moldan et al. (2006), [k]Kjønaas and Wright (2007), [l]Krause et al. (2012), *we did not simulate the second tracer application that took place in 2012 at the fertilized plots in Bear Brook.



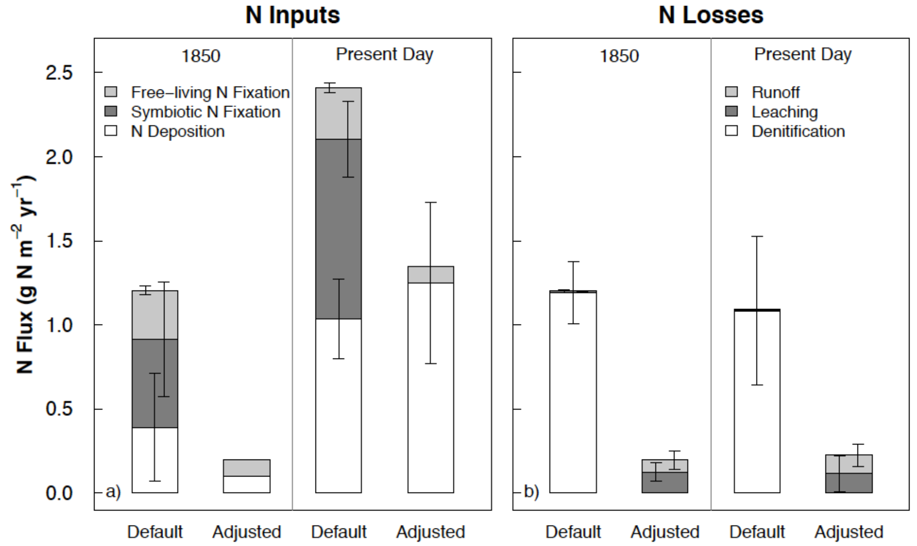


Figure 1: Rates of a) nitrogen (N) inputs and b) N losses averaged across sites for 1850 (using the last 20 years of the spin-

sources that were > 0.1% of total fluxes. ~~In the adjusted model~~For ecosystems using a closed N cycle, N deposition, free-living N fixation, and N deposition were set to observation-based estimates; denitrification was turned off because of the uncertainty around the portion of N losses ~~that is~~ due to this loss term (See Section 2.3.1). Error bars represent 1 standard deviation simulated across sites.

Table 2: Mean C:N values for ~~C:N of~~ plant and soil pools reported in site-specific literature and simulated by CLM5 (averaged across sites). Model means (± 1 standard deviation across simulated sites~~; SD~~) are the average of C:N ratios from the last 20 years of the baseline simulation from ~~the~~ simulations with a closed N cycle~~adjusted configuration of CLM5~~. Observational means (± 1 standard deviation across measured site data) are based off s~~S~~ite-reported or field-estimated values for C:N ratios, which are listed for each site, along ~~and~~ with their references (which describe the sampling methods for each pool), ~~are~~ in Table S3.

C:N	Observational Estimate	Model BDT Mean[a]	Model NET Mean[a]
Leaf	37 ± 12	24 ± 0.4	63 ± 0.9
Fine Roots	45 ± 10	43 ± 0.7	46 ± 0.7
Coarse Roots	90 ± 20	26 ± 0.5 (live)[a] 266 ± 7 (dead)[a]	28 ± 0.3 (live)[a] 266 ± 7 (dead)[a]
Wood	411 ± 110	26 ± 0.5 (live)[a] 266 ± 7 (dead)[a]	26 ± 0.5 (live)[a] 293 ± 8 (dead)[a]
Bark	182 ± 55	Not modeled	Not modeled
Organic Layer	26 ± 6	59 ± 6	99 ± 10
Mineral Layer	21 ± 6	11 ± 0.004	11 ± 0.006

[a] In CLM5, wood and coarse roots have the same C:N ratios and are split into live and dead pools. In this table, we have listed modelled live biomass as coarse roots and modelled dead biomass as wood.

Table 3: Comparison of mean nitrogen (N) and carbon (C) stocks and annual fluxes in modelled ecosystems with an open and closed N cycle ~~the default and adjusted versions of CLM5~~ at the end of baseline historical simulations. Sites fall into one of two plant functional types (PFT) in CLM5, broadleaf deciduous temperate (BDT) or needleleaf evergreen temperate (NET) tree. Model values are the mean of the last 20 years of the historical simulation and include total plant (above and belowground plant pools) and soil (excluding coarse woody debris and to the depth of field measurements) stocks. The total depth of the soil column in CLM5 is approximately 7.5 m at our simulated sites. ANPP and C stocks reported in the literature as organic matter or biomass were converted to units of C by assuming that 50% of organic matter is C.

Site (PFT)	~~Model Version~~Data	Aboveground Net Primary Productivity (ANPP) (g C m^{-2} y^{-1})	Maximum Annual Leaf Area Index (LAI) (m^2 m^{-2})	Plant C (g C m^{-2})	Soil C (g C m^{-2})	Plant N (g N m^{-2})	Soil N (g N m^{-2})
Harvard (BDT)	~~default~~Open N cycle	271	2.9	6820	3060 (20 cm) 5930 (total)	40	269 (20 cm) 527 (total)
	~~adjusted~~Closed N cycle	260	2.7	7010	3310 (20 cm) 6470 (total)	39	292 (20 cm) 576 (total)
	O~~o~~bservation	373[a]	5.3[b]	10,110[c]	9~~,~~710[c]	24[d]	415 (20 cm)[d]
Bear Brook (BDT)	Open N cycle~~default~~	260	2.7	7720	1540 (10 cm) 7330 (total)	42	133 (10 cm) 650 (total)
	Closed N cycle~~adjusted~~	281	3.0	8750	1800 (10 cm) 8720 (total)	48	155 (10 cm) 775 (total)
	~~o~~Observation	446[e]	7.6[f]	5830[g]	5910[g]	20[g]	285 (10 cm)[g]
Arnot (BDT)	Open N cycle~~default~~	279	3.0	10680	8510 (50 cm) 10720 (total)	56	755 (50 cm) 954 (total)
	Closed N cycle~~adjusted~~	270	2.9	10930	9130 (50 cm) 11540 (total)	56	810 (50 cm) 1028 (total)
	O~~o~~bservation	270[h]	NR	10380	7270[h]	37 [h]	645 (50 cm)[h]
Harvard (NET)	Open N cycle~~default~~	339	4.0	10690	3610 (20 cm) 7010 (total)	53	305 (20 cm) 610 (total)
	Closed N cycle~~adjusted~~	287	3.3	9880	3610 (20 cm) 7120 (total)	47	305 (20 cm) 621 (total)
	O~~o~~bservation	294[a]	4.4[b]	12370[c]	11050[c]	21[d]	460 (20 cm)[d]
Gårdsjön (NET)	Open N cycle~~default~~	398	4.9	14580	4980 (30 cm) 9750 (total)	69	539 (38 cm) 850 (total)
	Closed N cycle~~adjusted~~	422	5.3	15830	5520 (30 cm) 10920 (total)	75	606 (38 cm) 958 (total)
	O~~o~~bservation	275[i]	NR	NR	18880[j]	82[i]	584 (38 cm)[j]
Aber (NET)	Open N cycle~~default~~	388	4.8	9130	4760 (30 cm) 8940 (total)	49	417 (30 cm) 793 (total)
	Closed N cycle~~adjusted~~	348	4.2	8320	3760 (30 cm) 6920 (total)	43	329 (30 cm) 613 (total)
	O~~o~~bservation	NR	NR	NR	17700 (30 cm)[k]	NR	955 (30 cm)[l]
Klosterhede (NET)	Open N cycle~~default~~	366	4.4	13130	4030 (30 cm) 7740 (total)	61	339 (30 cm) 670 (total)
	Closed N cycle~~adjusted~~	413	5.2	14520	4170 (30 cm) 7990 (total)	68	359 (30 cm) 700 (total)
	O~~o~~bservation	352[k]	6.0[m]	12450 [k]	13270 (30 cm) [k]	91[k]	441 (30 cm [k]
Alptal (NET)	Open N cycle~~default~~	421	5.2	17450	7740 (25 cm) 14160 (total)	80	657 (25 cm) 1234 (total)
	Closed N cycle~~adjusted~~	382	4.6[a]	14420	6310 (25 cm) 11570 (total)	66	542 (25 cm) 1014 (total)
	O~~o~~bservation	355[n]	3.8[n]	13140[o]	9810[o]	60[n]	435 (25 cm)[n]

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NR: not reported in literature
[a] Magill et al. (2004)

[b] Zhao et al. (2011)
[c] Frey et al. (2014)
[d] Nadelhoffer et al. (2004)
[e] Magill et al. (1996)
[f] Elvir et al. (2006)
[g] Nadelhoffer et al. (1999a)
[h] Goodale (2017)
[i] Kjønaas and Stuanes (2008)
[j] Emmett et al. (1998b)
[k] personal communication with P. Gundersen
[l] Emmett et al. (1998b)
[m] Beier (1998)
[n] Krause et al. (2012)
[o] personal communication with P. Schleppi

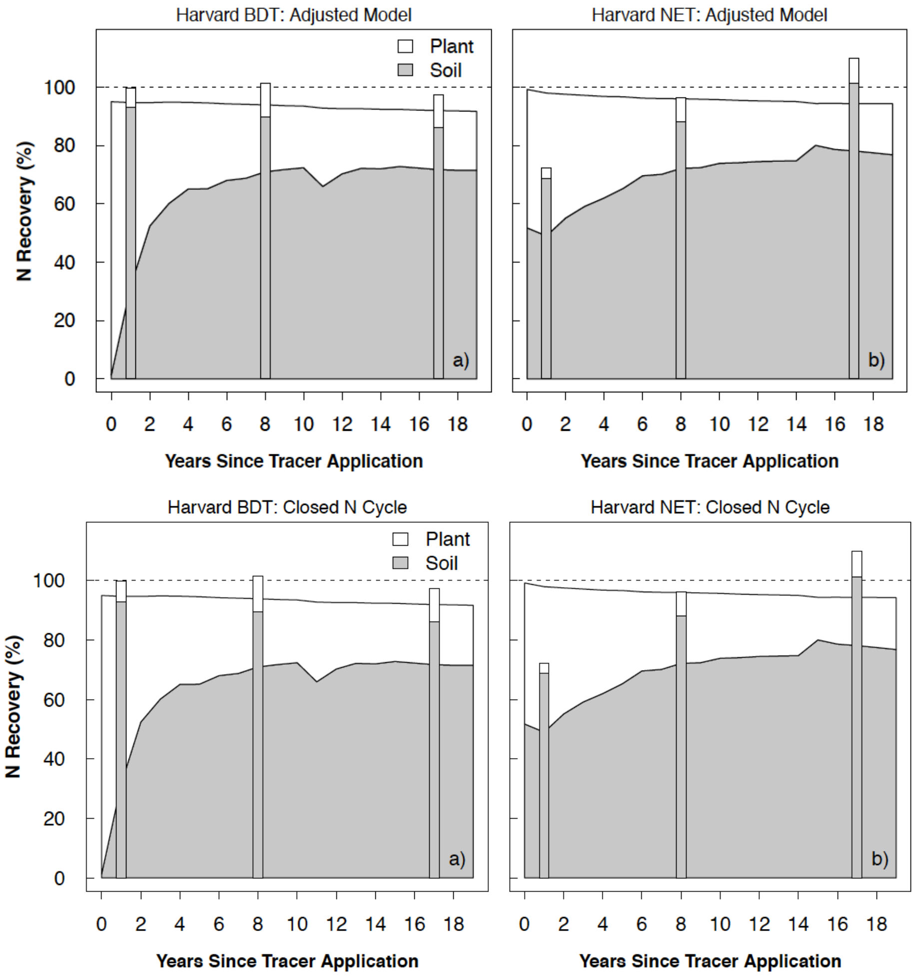
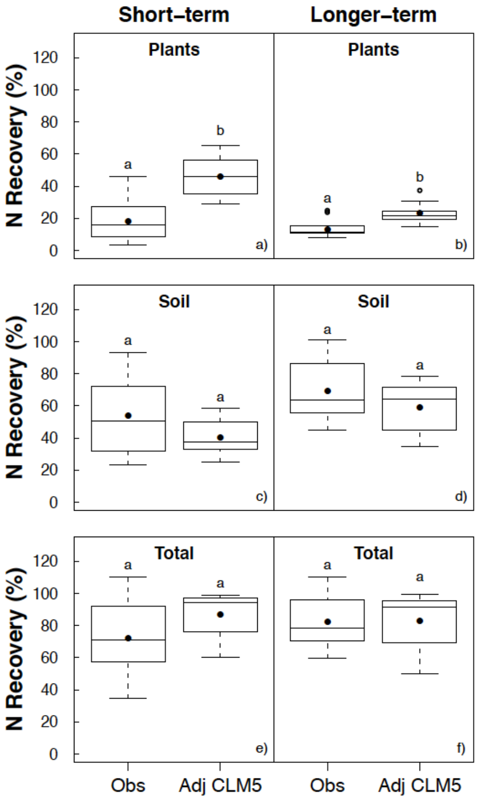


Figure 2: Modeled recovery of N additions for Harvard Forest broadleaf deciduous temperate tree~~s~~ (BDT; left panel) and needleleaf evergreen temperate tree~~s~~ (NET; right panel). Simulations were done using ~~the adjusted version of CLM5~~ a closed N cycle and are compared to ~~field measurements~~observations (stacked bars). The modeled soil stock includes the organic soil, inorganic soil, and litter pools (excluding coarse woody debris). ~~For each scenario,~~ Rrecovery is calculated as the difference in stock size between a control simulation and a simulation with a "tracer" added as 0.5 g m^{-2} between April-September in year 0. Plots of recoveries ~~from~~ at ~~other~~ all other sites and for the ~~default~~ version of CLM5 with an open N cycle at Harvard Forest are shown in Figs. S3-S5.


Short–term
Longer–term
Plants
Plants
Soil
Soil
Total
Total
N Recovery (%)
0
20
40
60
80
100
120
a
b
a
b
a
a
a
a
a
a
a
a
a)
b)
c)
d)
e)
f)
Obs
Adj CLM5
Obs
Adj CLM5

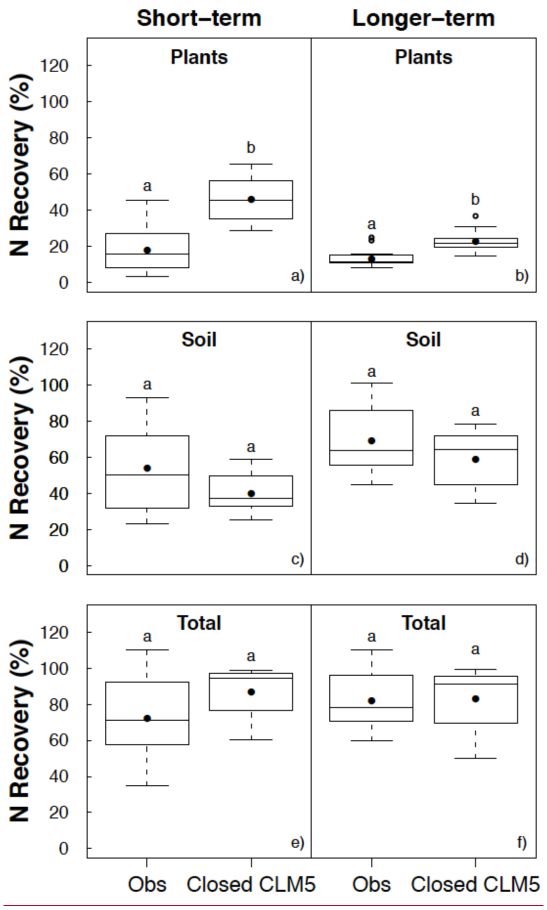
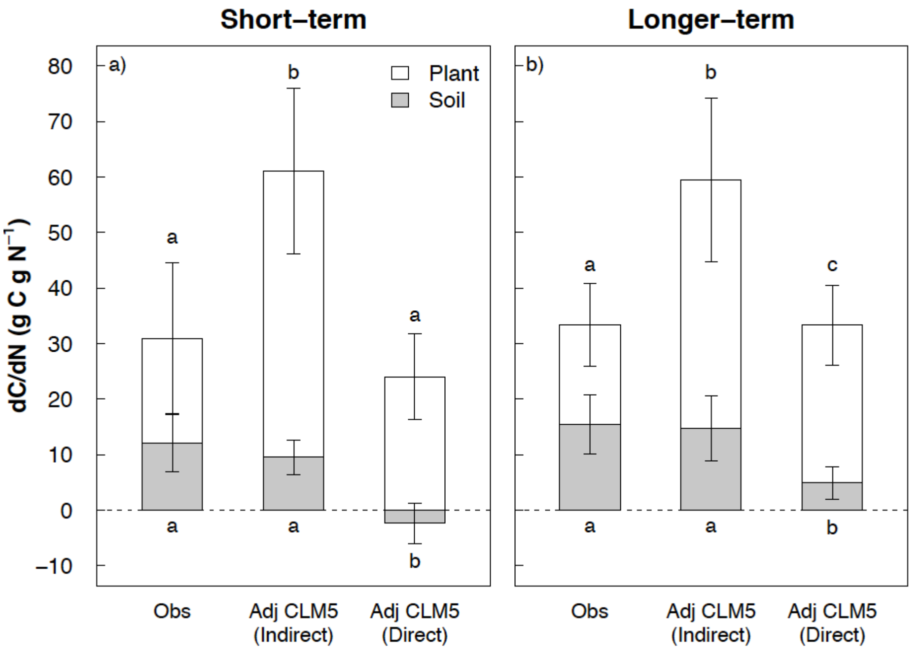
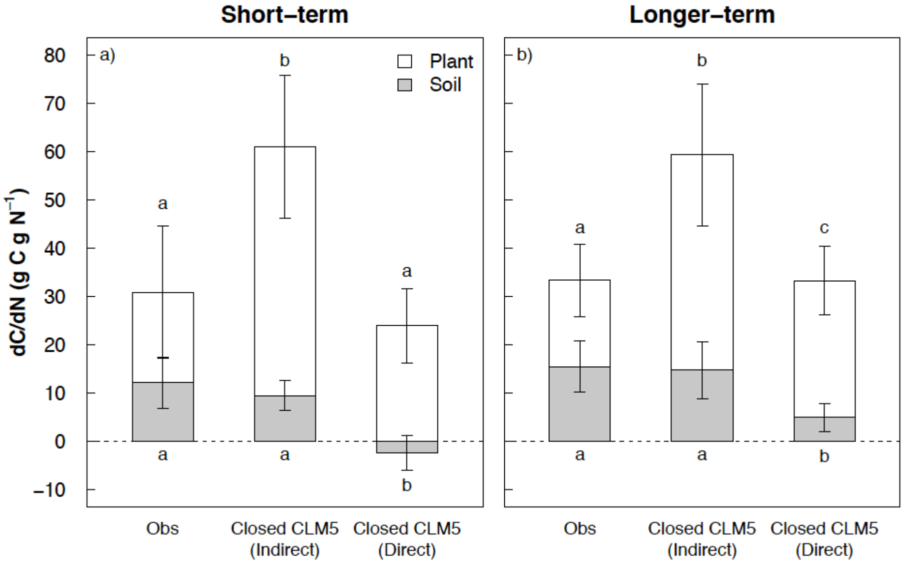


Figure 3: Boxplot showing the mean (filled dot), median (horizontal line), 1st quartile, and 3rd quartile of N recovery (%) on the short-term (< 3 years) and longer-term (> 3 years) from ^{15}N experiments with available data (Obs) and ~~adjusted~~ model simulations using a closed N cycle (~~Adj~~ Closed CLM5). Field and modelled data are an aggregate of values from both plant functional types (PFTs) and all N fertilization or ambient conditions. Whiskers extend to the minimum and maximum N recoveries that are not outliers, which are represented by open circles. Variation in observations occurs from differences measured across sites; variation in the model data occurs from differences estimated by CLM5 across modelled sites. Different letters indicate groups that are statistically different ($p < 0.05$).


Short–term
Longer–term
dC/dN (g C g N^{-1})
80
70
60
50
40
30
20
10
0
−10
a)
b)
☐ Plant
▨ Soil
a
b
a
a
a
b
a
b
c
a
a
b
Obs
Adj CLM5 (Indirect)
Adj CLM5 (Direct)
Obs
Adj CLM5 (Indirect)
Adj CLM5 (Direct)


Short–term
Longer–term
dC/dN (g C g N^{-1})
80
70
60
50
40
30
20
10
0
−10
a)
b)
☐ Plant
▨ Soil
a
b
a
a
a
b
a
b
c
a
a
b
Obs
Closed CLM5 (Indirect)
Closed CLM5 (Direct)
Obs
Closed CLM5 (Indirect)
Closed CLM5 (Direct)

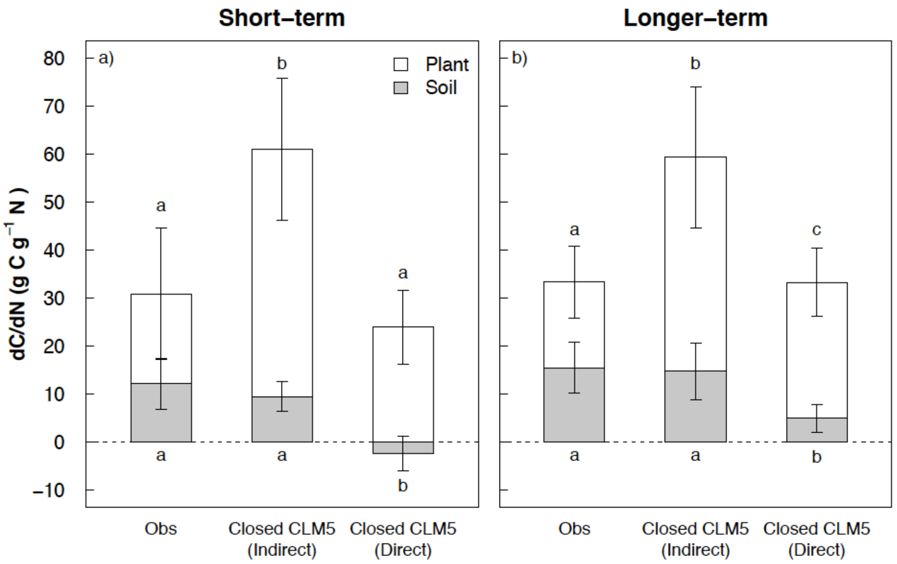


Figure 4: Mean short-term (< 3 years) and long-term (> 3 years) response of C stocks to added N (dC/dN) estimated from ^{15}N experiments (Obs) and ~~adjusted~~ model simulations using a closed N cycle (Closed~~Adj~~ CLM5). The dC/dN for field experiments (left-most bars in Fig. 4a and 4b) is calculated by multiplying the site-level ^{15}N recovery for foliage, wood, bark, fine roots, coarse roots, O horizon, and mineral soil horizon by the C:N ratio for each pool (Eqn. 3, see Table S3 for C:N ratios) and then averaging the total plant or total soil dC/dN across sites. For equivalent comparison to observations, model dC/dN (center bars in Figs. 4a and 4b) is calculated indirectly using observational C:N ratios (Indirect) and Eqn 3 as well as directly from the model using the model's C:N ratios (Direct) according to Eqn 2 (right-most bars in Figs. 4a and 4b). For plant dC/dN, data from Gårdsjön, Aber low, and Aber high experiments were not included because sub-pools from plants were not reported. For soil dC/dN, data from Gårdsjön and Bear Brook Fertilized were not included because sub-pools from soils were not reported. Error bars represent 1 standard deviation. Variation in the observations occurs from differences in N recoveries and C:N ratios measured across plant and soil sub-pools and sites; variation in the indirect model estimates occurs from differences in N recoveries estimated by CLM5 across modelled sites and from variation in measured C:N ratios; variation in the direct model estimates occurs from differences in CLM5's stocks and C:N ratios across modelled sites. Different letters indicate groups that are statistically different ($p < 0.05$) for plants (above the white bars) and for soils (below the gray bars).

Table 4: N recovery ~~from~~ in CLM5 simulations using an open N cycle (i.e., the default ~~(Def CLM)~~version of CLM5) and a closed N cycle ~~and adjusted configuration of CLM (Adj CLM)~~ compared to observations ~~(Obs)~~ for plant and soil stocks on the short (< 3 years) and longer-term (> 3 years). Data are separated according to PFT (broadleaf deciduous temperate; BDT and needleleaf evergreen temperate; NET trees) and fertilization treatment, as well as aggregated across all sites (combined across PFTs and fertilization treatment). The number of data points for each N recovery is listed in parentheses.

		BDT		NET		Combined
Timescale and Stock	Data	Ambient (%)	Fertilized (%)	Ambient (%)	Fertilized (%)	Combined (%)
Short-term Plant	~~Def CLM~~Open N cycle	49 (2)	36 (2)	35 (4)	37 (6)	38 (14)
	Closed N cycle~~Ddj CLM~~	64 (2)	32 (2)	44 (4)	47 (6)	46 (14)
	Observations	9 (2)	18 (2)	13 (4)	26 (6)	18 (14)
Short-term Soil	Open N cycle~~Def CLM~~	25 (2)	26 (2)	54 (4)	37 (6)	39 (14)
	Closed N cycle ~~Adj CLM~~	32 (2)	34 (2)	52 (4)	37 (6)	40 (14)
	Observations	76 (2)	48 (2)	49 (4)	52 (6)	54 (14)
Long-term Plant	Open N cycle~~Def CLM~~	15 (3)	18 (2)	20 (4)	23 (5)	20 (14)
	Closed N cycle ~~Adj CLM~~	23 (3)	17 (2)	20 (4)	28 (5)	23 (14)
	Observations	10 (3)	11 (2)	13 (4)	16 (5)	13 (14)
Long-term Soil	Open N cycle~~Def CLM~~	55 (3)	34 (2)	43 (4)	44 (5)	45 (14)
	Closed N cycle ~~Adj CLM~~	72 (3)	35 (2)	73 (4)	50 (5)	59 (14)
	Observations	79 (3)	60 (2)	78 (4)	58 (5)	69 (14)

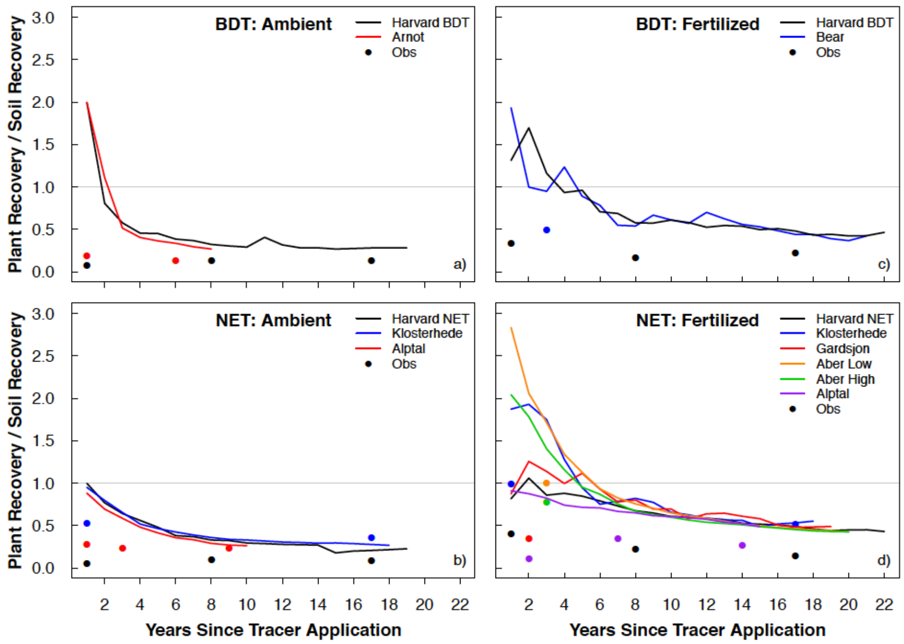


Figure 5: Ratio of plant recovery and soil recovery of added N into a,c) broadleaf deciduous temperate (BDT) and b,d) needleleaf evergreen temperate (NET) forests ~~predicted by the adjusted configuration CLM5~~ for sites with a closed N cycle under ambient deposition (a,b) and fertilized (c,d) conditions. Circles represent the ratio of plant to soil recovery of ^{15}N as measured in field experiments. A ratio of 1.0 represents equal recovery of N in plant and soil pools.

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Supplementary Information

Table S1: Published ^{15}N recovery measurements and CLM5~~-model~~ simulated~~ion~~ N recoveries for each site and experiment, including for both open (Open CLM) and closed (Closed CLM) N cycle configurations~~default (def CLM) and adjusted (adj CLM) configurations of CLM5~~.

Site	Years Since Tracer Application	Foliage	Wood	Bark	Fine Roots	Coarse Roots	Ground Plants	Organic Soil	Mineral Soil	Total Plant*	Total Soil	~~Def~~ Open CLM Plant	~~Adj~~ Closed CLM Plant	Open ~~Def~~ CLM Soil	~~Adj~~ Close CLM Soil
Arnot[a,b]	1	1.9	0.6	1.0	2.5	4.9	NA	13.7	45.3	10.9	59.0	50	65	26	33
	6	1.6	1.5	1.2	1.8	2.1	NA	5.9	56.5	8.2	62.4	16	24	63	73
Harvard BDT[c,d,e]	1	1.2	0.6	0.5	4.6	NA	NA	81.9	11.1	6.8	92.9	47	63	25	32
	8	3.8	2.1	1.7	4.2	NA	NA	73.9	15.7	11.8	89.6	14	23	56	71
	17	available upon request to site PI										14	20	48	72
Harvard BDT Fertilized[c,d,e]	1	5.9	2.9	1.6	13.7	NA	NA	44.6	27.4	24.0	72.0	31	29	26	31
	8	3.1	3.1	2.2	3.1	NA	NA	55.4	16.0	11.5	71.4	21	20	34	35
	17	available upon request to site PI										14	15	33	34
Harvard NET[c,d,e]	1	1.0	0.1	0.2	2.3	NA	NA	60.0	8.8	3.6	68.7	38	49	51	49
	8	2.9	1.3	0.6	3.4	NA	NA	56.2	31.9	8.1	88.1	24	24	58	72
	17	available upon request to site PI										18	16	60	78
Harvard NET Fertilized[c,d,e]	1	9.6	0.4	0.9	8.7	NA	NA	33.9	15.2	19.7	49.1	29	36	26	40
	8	6.1	1.1	0.9	5.1	NA	NA	34.9	24.3	13.2	59.2	20	26	31	43
	17	available upon request to site PI										16	20	32	45
Alptal[f,g,h]	1	2.3	3.0	with wood	6.6	0.4	19.0	25.6	19.6	12.3	45.2	39	44	52	50
	3	0.9	1.0	with wood	3.3	1.8	20.5	22.5	7.3	6.9	29.8	30	34	58	59
	9	3.7	2.6	2.3	3.1	1.1	3.8	42.6	13.3	12.8	55.9	29	19	9	70
Alptal Fertilized[f,g,h]	2	4.6	3.0	0.8	with organic soil	NA	5.0	55.0	21.0	8.4	76.0	36	45	54	51
	7	6.9	3.9	0.8	2.6	1.4	1.5	29.3	15.4	15.6	44.7	30	37	55	55
	14	5.0	4.4	2.0	2.7	1.2	0.9	39.6	18.9	15.3	58.5	24	31	53	59
Klosterhede[i]	1	9.9	3.3	0.4	6.9	7.0	20.1	41.5	10.4	27.4	51.8	32	47	52	50

	17	12.0	4.6	1.2	3.4	2.3	0.2	61.6	3.8	23.5	65.4	11	19	45	70
Klosterhede Fertilized[i]	1	16.8	6.3	0.7	11.2	10.7	3.2	23.9	22.5	45.8	46.4	38	63	52	34
	17	12.7	3.8	1.1	2.7	4.4	0.0	36.7	11.5	24.7	48.2	24	25	47	46
Bear Brook Fertilized[j]	3	2.4	9.1	NA	NA	NA	NA	NA	NA	11.4	23.3	40	35	27	37
Gårdsjön Fertilized[k]	2	NA	NA	NA	NA	NA	NA	NA	NA	28.0	82.0	39	47	43	37
Aber Low Fertilization[l]	3	NA	NA	NA	NA	NA	NA	17.0	15.0	32.0	32.0	49	56	29	33
Aber High Fertilization[l]	3	NA	NA	NA	NA	NA	NA	11.0	15.0	20.0	26.0	32	35	21	25

*plant recovery from field recoveries excludes ground vegetation.

NA: not available

[a] Goodale (2017)

[b] personal communication with C. Goodale

[c] Nadelhoffer et al. (1999b)

[d] Nadelhoffer et al. (2004)

[e] personal communication with K. Nadelhoffer

[f] Krause et al. (2012)

[g] personal communication with P. Schleppi

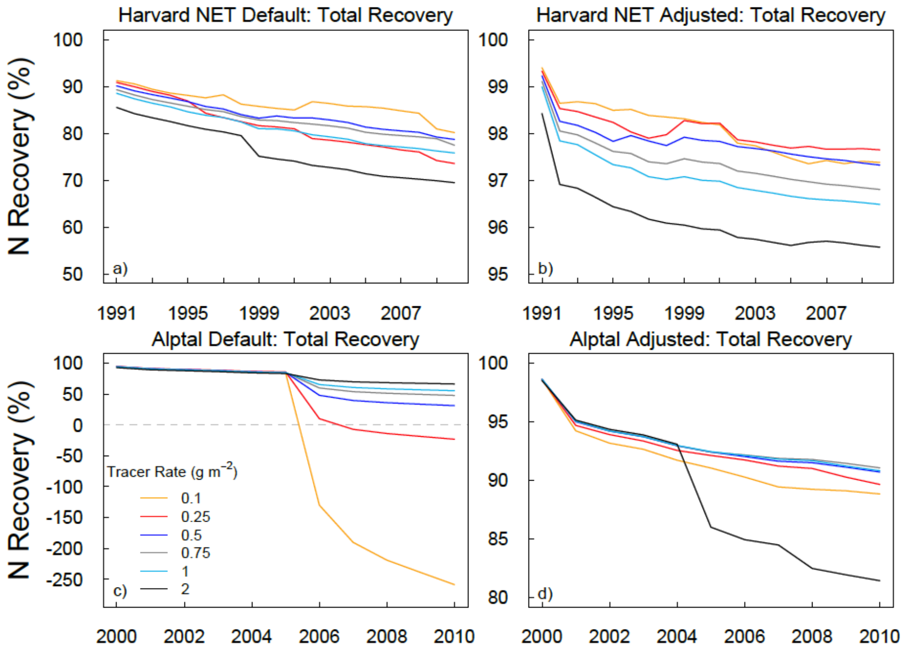
[h] Providoli et al. (2005) and paper with data from fertilized 1997

[i] Gundersen (1998)

[j] Nadelhoffer et al. (1999a)

[k] Nadelhoffer et al. (1999c)

[l] Tietema et al. (1998)


Harvard NET Default: Total Recovery
Harvard NET Adjusted: Total Recovery
Alptal Default: Total Recovery
Alptal Adjusted: Total Recovery
N Recovery (%)
N Recovery (%)
100
90
80
70
60
50
a)
100
99
98
97
96
95
b)
1991
1995
1999
2003
2007
1991
1995
1999
2003
2007
100
50
0
-50
-100
-150
-200
-250
c)
Tracer Rate (g m^{-2})
0.1
0.25
0.5
0.75
1
2
100
95
90
85
80
d)
2000
2002
2004
2006
2008
2010
2000
2002
2004
2006
2008
2010

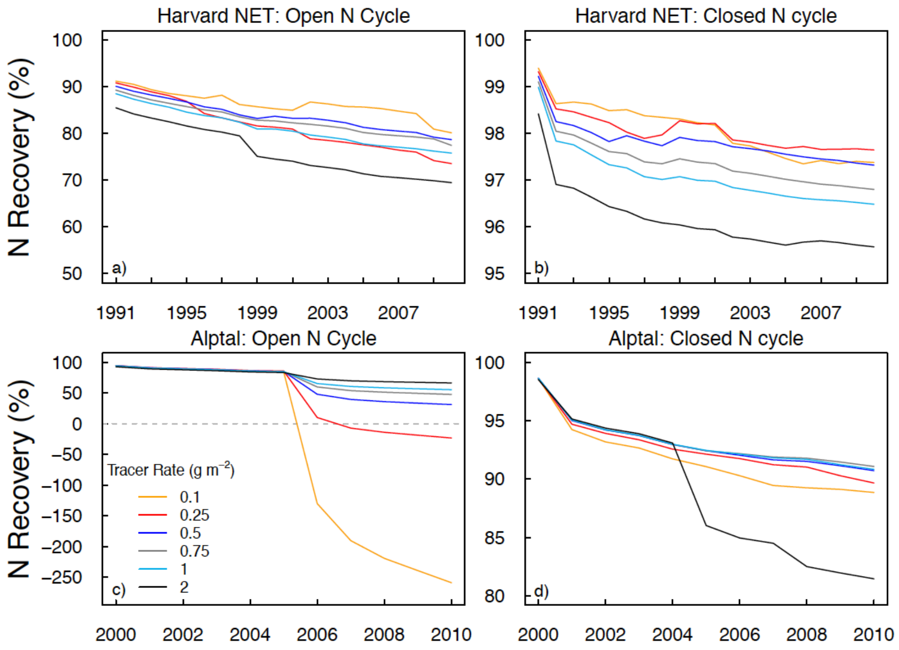


Figure S1: Results from a sensitivity study done at Harvard (a, b) needleleaf temperate tree (NET) plant functional type (PFT) and Alptal (c, d) on the amount of tracer that should be applied during the growing season (April-September) for ~~the~~ both open and closed ~~default and adjusted~~ N cycles ~~configurations of~~in CLM5.

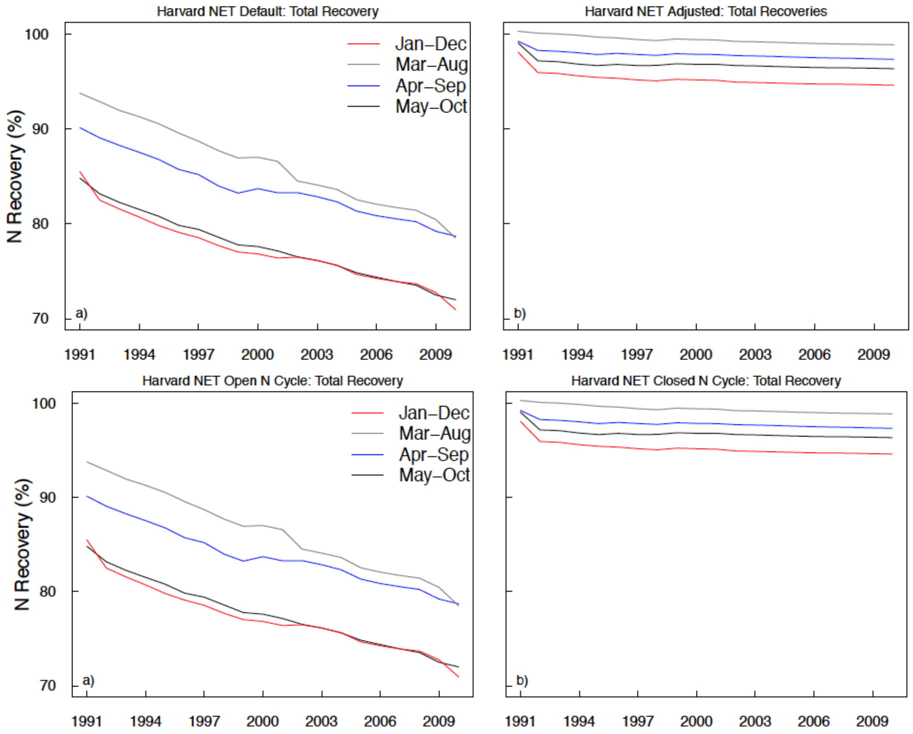


Figure S2: Results from the sensitivity study at Harvard needleleaf evergreen tree (NET) plant functional type (PFT) on the timing of applying 0.5 g N m^{-2} into the ecosystem under a) ~~default~~ an open N cycle and b) ~~adjusted~~ a closed N cycle in~~configurations of~~ CLM5.

Table S2: ~~Residence~~ Turnover time of N in plant, soil, and total ecosystem ~~N~~ pools in CLM5 for ecosystems with open and closed N cycles~~the default and adjusted configurations of CLM5~~. Values shown are averaged across the last 20 years of the 1850 spinup simulation and for the last 20 years of the historical simulation. ~~Residence~~ Turnover time is calculated a) for plants as the plant stock divided by losses from litterfall, b) for soils as the soil stock divided by losses from plant uptake, denitrification, leaching, and runoff, and c) for the ecosystem as the ecosystem stock divided by losses from denitrification, leaching, and runoff.

	1850		**Last 20 Years**	
	~~Default~~ Open N cycle (years)	**~~Adjusted~~Closed N cycle (years)**	**~~Default~~Open N cycle (years)**	**~~Adjusted~~Closed N cycle (years)**
Plants				
Harvard BDT	29	30	17.6	18.0
Harvard NET	72	72	53.6	56.8
Arnot	29	30	23.7	24.5
Aber	72	71	42.6	42.0
Alptal	73	71	64.1	58.5
Bear Brook	29	30	19.4	20.5
Klosterhede	72	73	58.0	55.1
Gårdsjön	73	73	58.9	59.0
Soil				
Harvard BDT	93	114	70	95
Harvard NET	115	137	100	132
Arnot	143	170	122	158
Aber	131	161	95	101
Alptal	184	217	146	152
Bear Brook	117	136	93	114
Klosterhede	111	130	92	98
Gårdsjön	137	151	111	128
Ecosystem				
Harvard BDT	501	7142	578	6914
Harvard NET	679	5238	1597	16236
Arnot	57	10606	1065	12319
Aber	658	3557	441	1430
Alptal	2023	47976	1067	3127
Bear Brook	836	7019	888	6727
Klosterhede	596	6902	542	2775
Gårdsjön	1084	7787	873	2903

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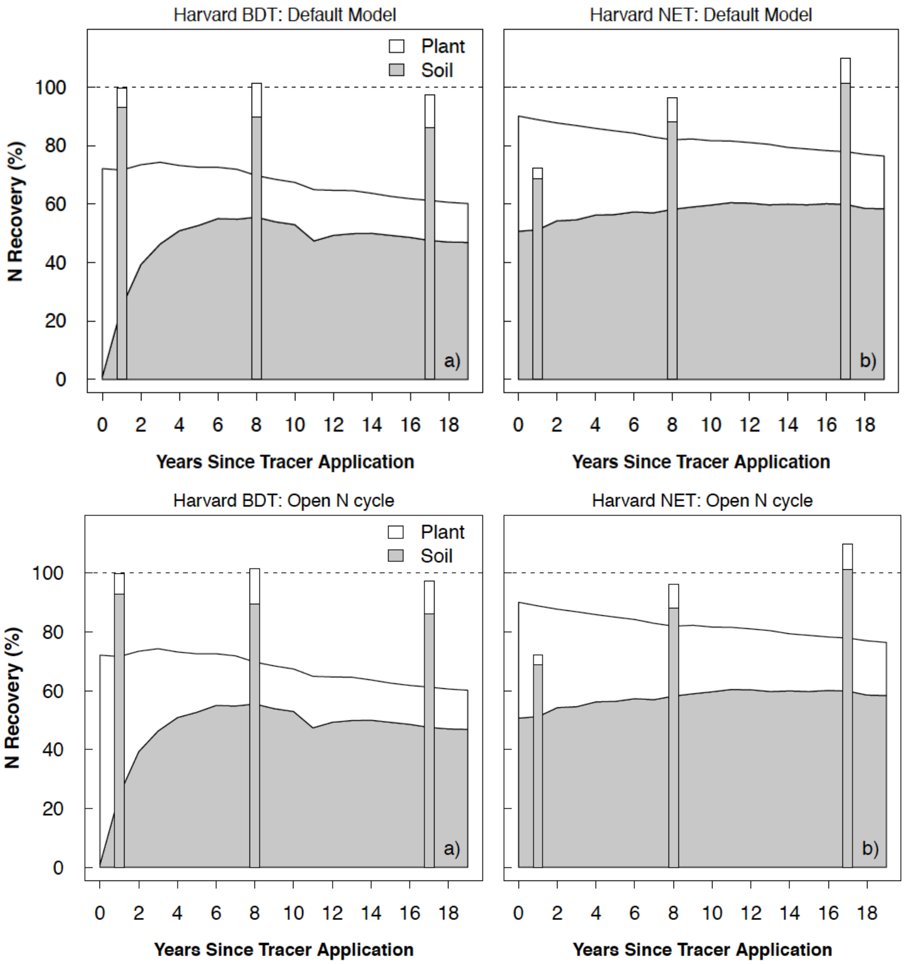
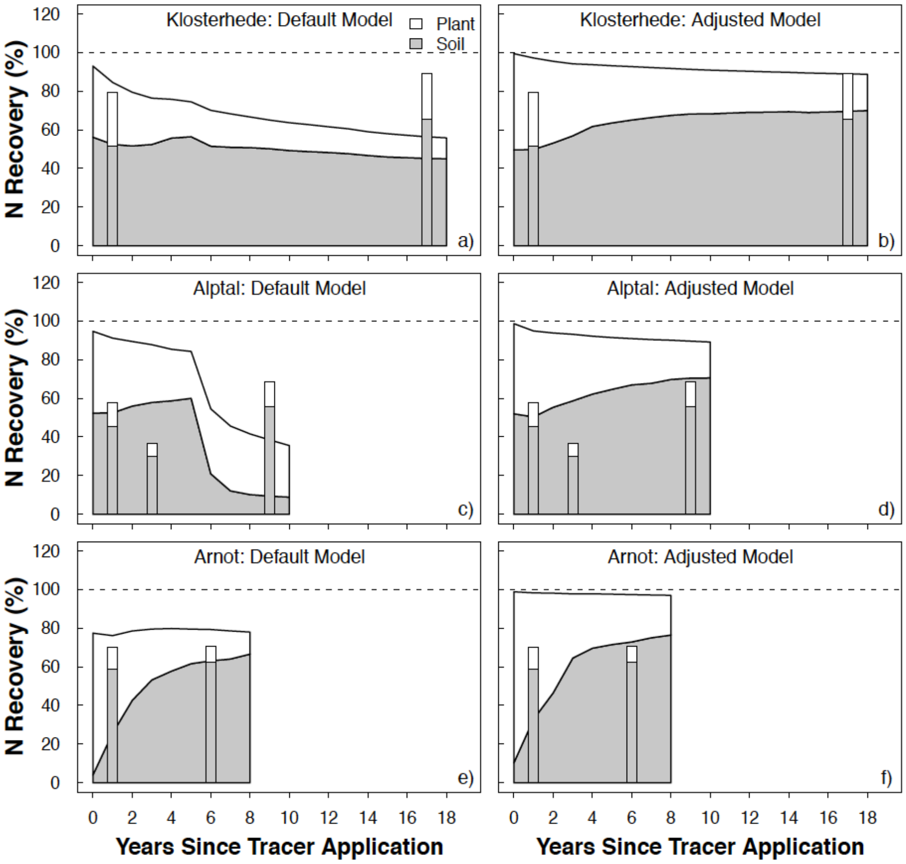


Figure S3: Modeled recovery of N additions in plant and soil pools at ~~in default configurations of CLM5 for ambient N deposition conditions at~~ Harvard Forest under open N cycling and ambient N deposition for a) broadleaf deciduous tree and b) needleleaf evergreen tree plant functional types (PFT). Thin, stacked bars represent observations. Recovery is calculated as the difference in stock size between a baseline simulation and a simulation with a "tracer" added as 0.5 g m^{-2} between April-September in the first year a ^{15}N tracer was applied in the field (see Methods).


Klosterhede: Default Model
Plant
Soil
a)
Klosterhede: Adjusted Model
b)
Alptal: Default Model
c)
Alptal: Adjusted Model
d)
Arnot: Default Model
e)
Arnot: Adjusted Model
f)
N Recovery (%)
0
20
40
60
80
100
120
0
2
4
6
8
10
12
14
16
18
Years Since Tracer Application

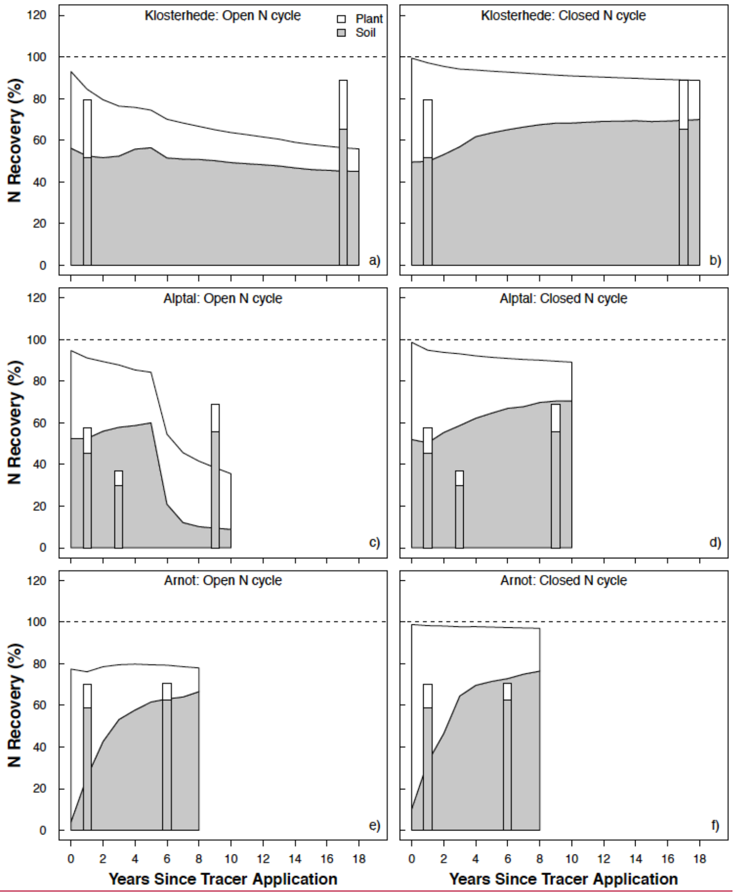
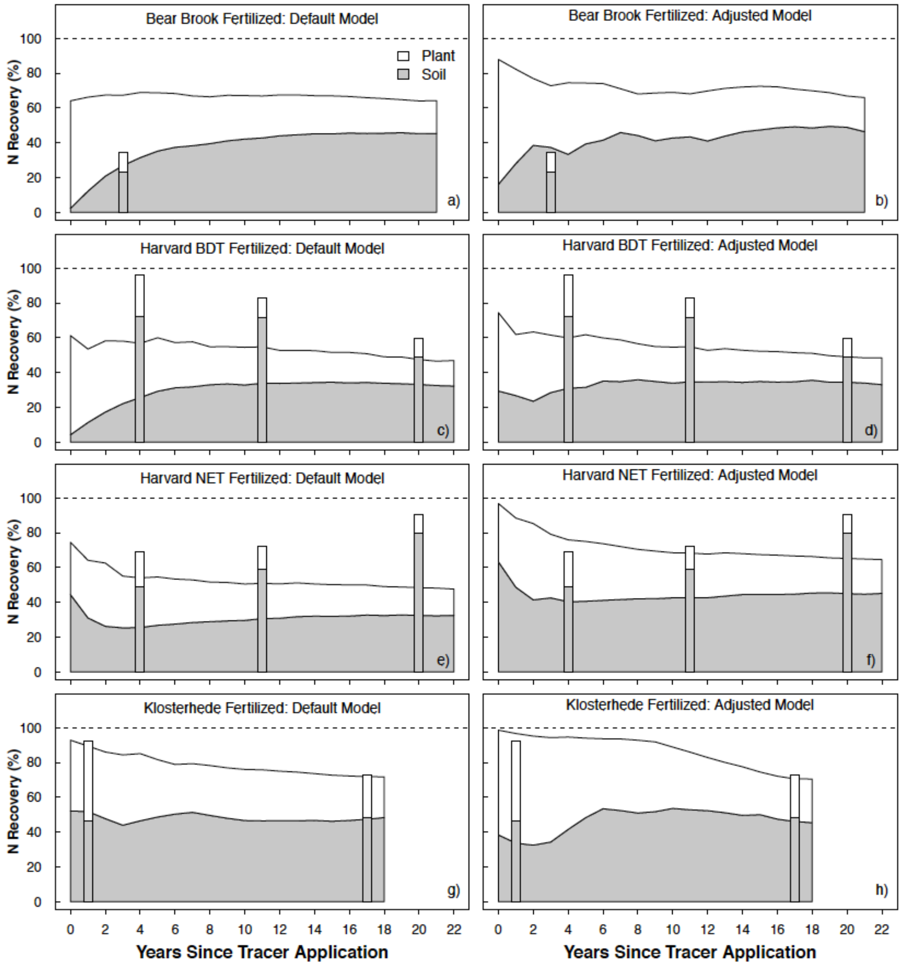


Figure S4: Modeled recovery of N additions in plant and soil pools in ecosystems with open and closed N cycles ~~default and adjusted configurations of CLM5 for~~under ambient N deposition conditions. Thin, stacked bars represent observations. Recovery is calculated as the difference in stock size between a baseline simulation and a simulation with a "tracer" added as 0.5 g m^{-2} between April-September in the first year a ^{15}N tracer was applied in the field (see Methods).


Bear Brook Fertilized: Default Model
Bear Brook Fertilized: Adjusted Model
Harvard BDT Fertilized: Default Model
Harvard BDT Fertilized: Adjusted Model
Harvard NET Fertilized: Default Model
Harvard NET Fertilized: Adjusted Model
Klosterhede Fertilized: Default Model
Klosterhede Fertilized: Adjusted Model
Plant
Soil
N Recovery (%)
0
20
40
60
80
100
Years Since Tracer Application
0
2
4
6
8
10
12
14
16
18
20
22
a)
b)
c)
d)
e)
f)
g)
h)

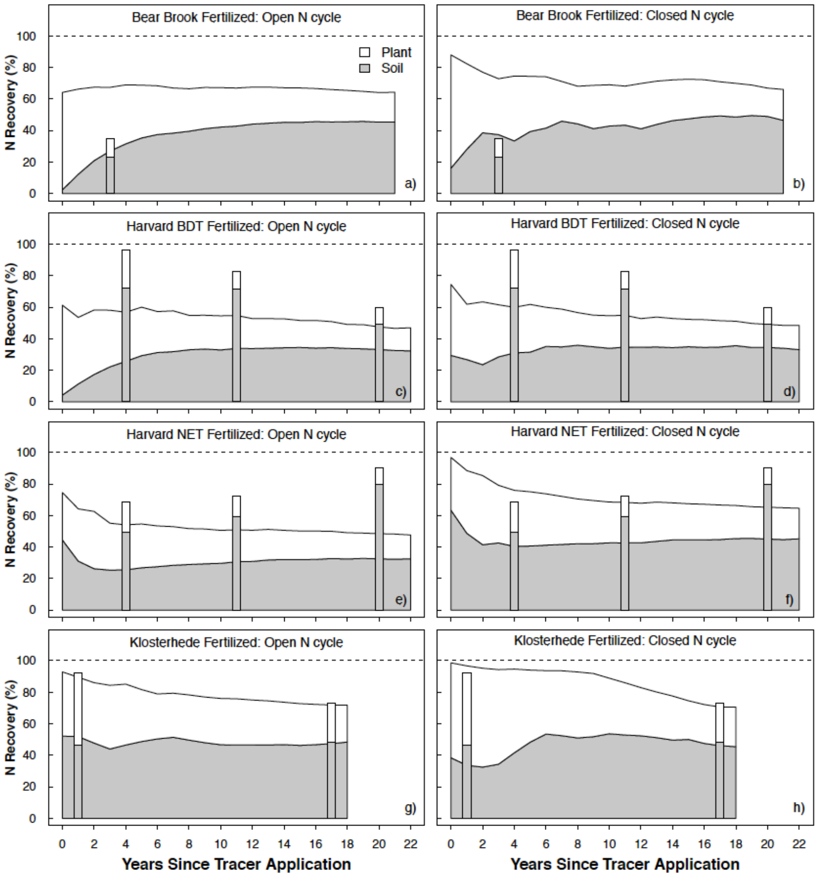
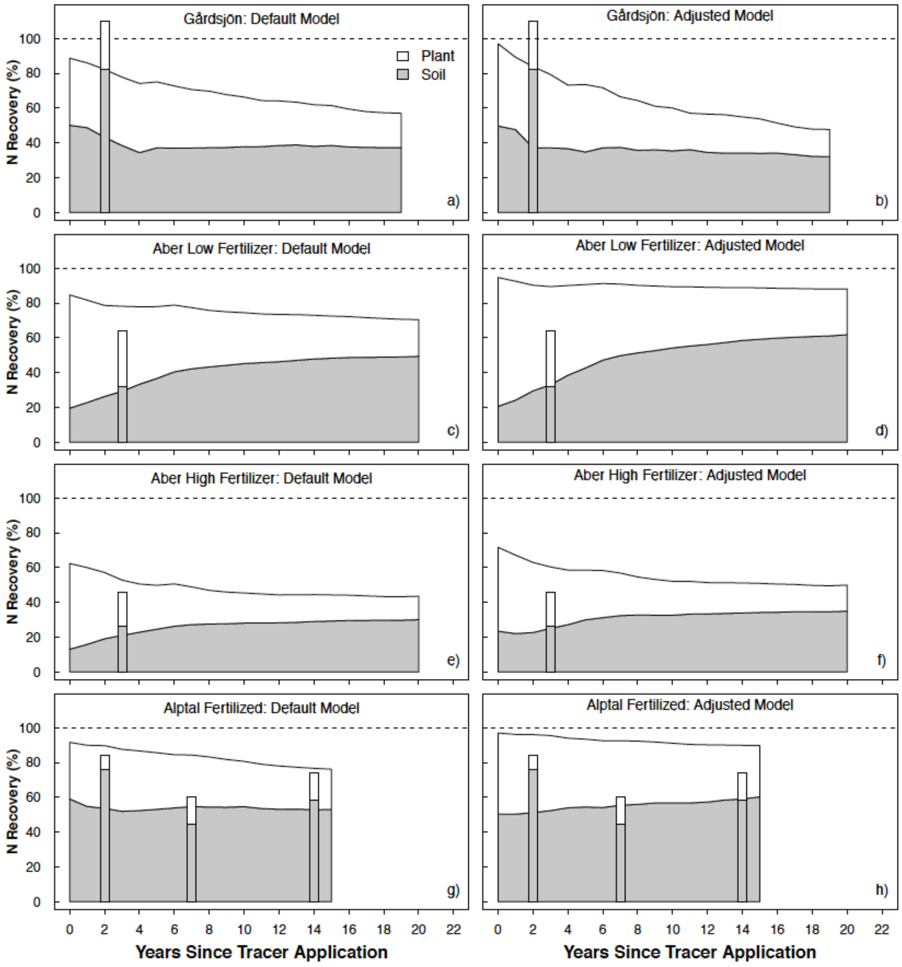


Figure S5: Modeled recovery of N additions in plant and soil pools of sites in ~~default and adjusted configurations of CLM5~~ecosystems with open and closed N cycles compared to field measurements (thin, stacked bars) for sites under multi-year N fertilization. ~~For each scenario,~~ R~~r~~ecovery is calculated as the difference in stock size between a baseline simulation and a simulation with N fertilizer added into the soil mineral N pool between April-September (see Methods).


Gårdsjön: Default Model
Gårdsjön: Adjusted Model
Aber Low Fertilizer: Default Model
Aber Low Fertilizer: Adjusted Model
Aber High Fertilizer: Default Model
Aber High Fertilizer: Adjusted Model
Alptal Fertilized: Default Model
Alptal Fertilized: Adjusted Model
☐ Plant
▨ Soil
N Recovery (%)
0
20
40
60
80
100
0
2
4
6
8
10
12
14
16
18
20
22
Years Since Tracer Application
a)
b)
c)
d)
e)
f)
g)
h)

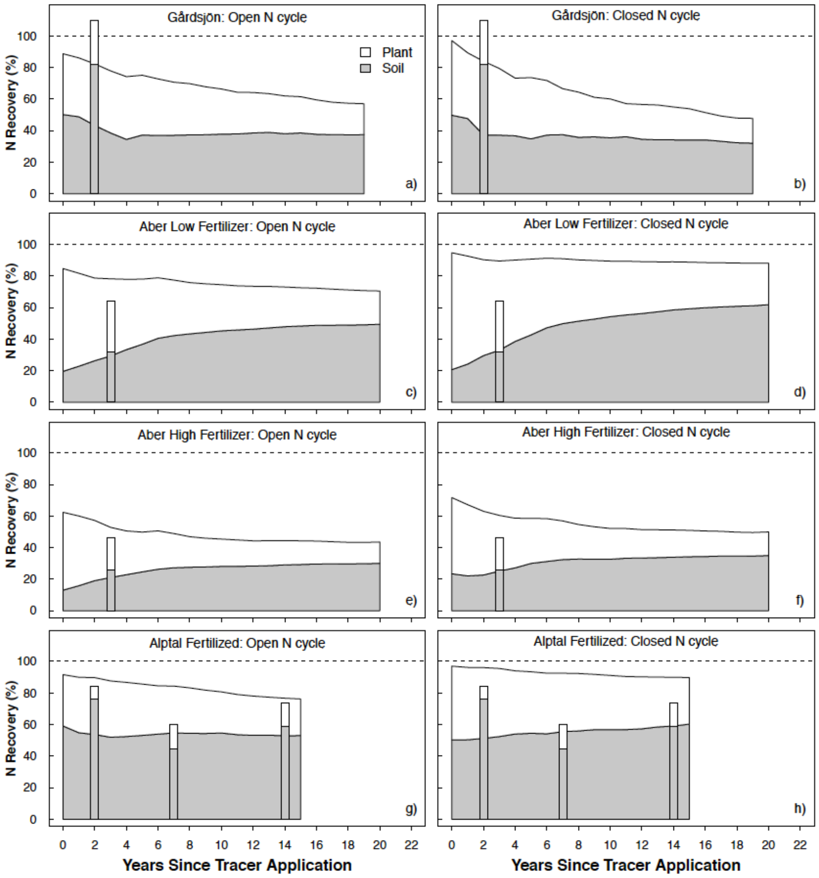


Figure S6: Modeled recovery of N additions in plant and soil pools of sites ~~in default and adjusted configurations of CLM5~~for ecosystems under closed and open N cycles compared to field measurements (thin, stacked bars) for sites under multi-year N fertilization. ~~For each scenario,~~ Rrecovery is calculated as the difference in stock size between a control simulation and a simulation with N fertilizer added into the soil mineral N pool between April-September (see Methods).

Table S3: C:N ratios of sub-pools for plants and soils as reported in literature.

Site	Foliage	Wood	Bark	Fine Roots	Coarse Roots	Organic Soil	Mineral Soil	Citations
Harvard BDT	25	338	126	50	NA	24	20	Nadelhoffer et al., 2004; Nadelhoffer et al. 1999
Harvard NET	42	337	253	41	NA	25	19	Nadelhoffer et al., 2004; Nadelhoffer et al. 1999
Arnot	35	638	154	47	109	39	9	Goodale 2017
Alptal[a]	42	500	167	56	91	19	17	Provioldi et al. 2005
Klosterhede[b]	63	333	200	52	70	33	29	Emmett 1998 (FEM), Gundersen and Rasmussen 1995, Tietema et al. 1998 (FEM), personal communication with P. Gundersen
Harvard BDT Fertilized	23	321	120	48	NA	21	23	Nadelhoffer et al., 2004; Nadelhoffer et al. 1999
Harvard NET Fertilized	35	409	253	24	NA	23	26	Nadelhoffer et al., 2004; Nadelhoffer et al. 1999
Bear Brook Fertilized	37	413	NA	NA	NA	23	19	Nadelhoffer et al. 1999
Gårdsjön	NA	NA	NA	NA	NA	32	31	Emmett 1998, FEM
Aber[b]	28	NA	NA	NA	NA	22	18	Emmett 1998, FEM
Mean ± 1 SD	37 ± 12	411 ± 110	182 ± 55	45 ± 10	90 ± 20	26 ± 6	21 ± 6	

NA: not available from literature

[a] C:N ratios of all plant subpools at Alptal were estimated by assuming 50% of biomass is carbon, and then dividing by the N concentration reported in the literature.

[b] C:N ratios for foliage at Aber were estimated by assuming 50% of biomass is carbon, and then dividing by the N concentration reported in the literature.