Biogeosciences Discuss., https://doi.org/10.5194/bg-2018-505
Manuscript under review for journal Biogeosciences
Discussion started: 19 December 2018

Decadal impacts of nitrogen additions on temperate forest carbon sinks: 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). 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 of CLM5 overestimated plant N recovery following N additions. In particular, the adjusted configuration simulated that plants acquired more than twice the amount of added N recovered in ^{15}N tracer studies, on both short (CLM5: 46% ± 12%; observations: 18% ± 12%; mean across sites ± 1 standard deviation) and longer timescales (CLM5: 23% ± 6%; observations: 13% ± 5%). The default version of CLM5 underestimated long-term ^{15}N recovery in soils, while soil N recoveries in the adjusted configuration 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, soil N recoveries in CLM5 occurred from the cycling of N through plants rather than through direct immobilization in the soil, as 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 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 (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 et al., 2015; Wieder et al., 2015b; Medlyn et al., 2015; Zaehle and Dalmonech, 2011; Meyerholt and Zaehle, 2018), but not all global land models 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; Zaehle and Friend, 2010; Smith et al., 2014; Goll et al., 2017; Sokolov et al., 2008), 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 (Medlyn et al., 2015; Thomas et al., 2013b; Thomas et al., 2015; Zhu et al., 2016). Thus, evaluating model representations of N cycling is critical to increasing confidence in projections of the terrestrial C sink over the 21st century, particularly in ecosystems experiencing changes in anthropogenic N inputs.

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 (Galloway et al., 2003; Vitousek et al., 1997). 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 (Frey et al., 2014; Janssens et al., 2010), 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 (Nadelhoffer et al., 1999a; Currie et al., 2004; Emmett et al., 1998a; Templer et al., 2012; Lovett et al., 2013; Lu et al., 2010; Wang et al., 2018). Woody plant tissues have higher C:N ratios (100-500) than foliage and roots (20-40), which allows 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 (5-25) (Nadelhoffer et al., 1999c; Zechmeister-Boltenstern et al., 2015; Yang and Luo, 2010), 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., 1999c).

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 (Templer et al., 2012; Nadelhoffer et al., 1999c; Curtis et al., 2011; Tietema et al., 1998), as well as from warm and humid sites in China (Wang et al., 2018; Gurmesa et al., 2016), 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; Lewis and Kaye, 2012; Providoli et al., 2006; Perakis and Hedin, 2001; 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 comparisons between model simulations and field experiments ultimately provide more relevant constraints on decadal or centennial-scale forest C uptake and N cycling dynamics than short-term studies that often reflect transient dynamics (Perakis and Hedin, 2001; Providoli et al., 2006; Templer et al., 2012; Jefts et al., 2004). 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 retained N could accumulate in soil pools or be lost from the ecosystem entirely (Nadelhoffer et al., 2004; Wessel et al., 2013; Goodale, 2017; Krause et al., 2012). However, the long-term fates of N deposition in land models have not yet been evaluated against a synthesis of field measurements. In this study, we evaluated 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 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. 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 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, we evaluate both the short-term and longer-term responses of the model's C sinks to N additions. 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 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., $V_{c,max}$) based on environmental conditions (Ali et al., 2016). Second, plants can alter and optimize their stoichiometry (FlexCN), which removed the down-regulation of gross primary productivity (GPP) that was used in CLM4 and CLM4.5 (Ghimire et al., 2016). Third, in the Fixation and Uptake of Nitrogen (FUN) module, plants pay C costs 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 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 (Thomas et al., 2013a; Koven et al., 2013; Thornton et al., 2007; Oleson et al., 2013). New N enters an ecosystem through N deposition, and free-living and symbiotic N fixation. 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. Subsequent losses of N occur through production of N gases during nitrification and denitrification, 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. 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 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 (Global Soil Wetness Project Phase 3 (GSWP3; http://hydro.iis.u-tokyo.ac.jp/GSWP3/). 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 Default and adjusted 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). Thus, we ran default and adjusted model configurations of CLM5 for each ^{15}N field experiment. In the default 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), exceeding the estimated rate of about 0.1 g N m^{-2} y^{-1} for pre-industrial times (Fakhraei et al., 2016; Holland et al., 1999). The temperate forests we simulated rarely contain plants with N-fixing symbionts, and have rates of free-living N fixation around 0.1 g N m^{-2} y^{-1} (Tedersoo et al., 2018; Vitousek et al., 2013). 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 (Houlton et al., 2015; Thomas et al., 2013a), accounting for 99% of all N losses (Fig. 1b).

In the adjusted configuration, 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 (Reay et al., 2008; Galloway et al., 2003). Then we set N deposition from 1975 to present to the site-reported (Table 1) N deposition rate (Engardt et al., 2017) 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 (Galloway et al., 2013;

Driscoll et al., 2003). 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 (Tedersoo et al., 2018; Cleveland et al., 1999). With these dramatically lower rates for N inputs (Fig. 1a, left panel), 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 (Groffman et al., 2018; Aber et al., 2003; Gundersen et al., 2006).

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" during April through September to capture the most active portion of the growing season. In CLM5, we ran sensitivity tests for two model sites, 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 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 recovery in the default configuration of CLM5 (reported in Table S1) includes a small effect of N fixation rates changing in response to added "tracer" or fertilizer. Calculated recoveries in the adjusted configuration (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 (Sutton et al., 2008; De Schrijver et al., 2008; Frey et al., 2014; Thomas et al., 2013a). Model dC/dN (g C g 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. (1999c):

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

where $N\ recovery$ is the N recovery of the ith component of a measured plant or soil stock (e.g., foliage, wood, litter), $C{:}N_{pool(i)}$ is the C:N ratio of the ith 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 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.

Biogeosciences Discuss., https://doi.org/10.5194/bg-2018-505
Manuscript under review for journal Biogeosciences
Discussion started: 19 December 2018

3 Results

Below, we first report the effects of two N cycle configurations (default and adjusted) 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 of default and adjusted configurations of CLM5

Ecosystem traits describing the C and N cycles at the end of the historical simulations for the default and adjusted configurations of CLM5 are reported in Table 3, along with available site measurements. The two model configurations differed greatly in their rates of N inputs and losses in 1850 as well as throughout the historical simulation (Fig. 1). Observed soil C stocks were typically higher than modeled in CLM5 ($p < 0.01$, Table 3). However, both model configurations 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, the two model configurations differed by an order of magnitude in ecosystem residence time (i.e., pool size divided by total N loss fluxes). The adjusted configuration had a whole-ecosystem mean N residence time of 6550 ± 5250 (mean ± 1 SD) years compared to 880 ± 370 years in the default configuration ($p < 0.01$; Table S2). By comparing the ratio between the mean residence time of N in the whole-ecosystem to the residence 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 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 the default configuration ($p < 0.01$). Consequently, the same unit of N in the adjusted configuration has a longer retention time in plants than the default configuration, which could lead the 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 default configuration (see Section 2.3.1), we focus the remainder of the study on results from the adjusted configuration. For completeness, results of N recovery for the default configuration of 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 and experimental N treatment 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. At both Harvard Forest PFTs, plants in CLM5 simulations 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 the two model configurations. However, total ecosystem recovery was generally lower in the default configuration of the model relative to 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 estimated more than twice the mean plant N recovery of tracer (46 ± 12%; mean ± 1 SD) than was measured in the field (18 ± 12%; $p < 0.001$; 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 modeled plant N recoveries (23 ± 6%) 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 adjusted configuration, the default configuration of CLM5 overestimated short-term (38 ± 7%; $p < 0.001$) and long-term (20 ± 6%; $p < 0.05$) plant recovery and estimated short-term soil N recovery (39 ± 14%) similar to observations. Distinct from the adjusted version, the default configuration underestimated (45 ± 15%) long-term soil N recovery ($p < 0.001$).

On average, 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 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%. The default configuration of CLM5 also estimated that short-term ecosystem recovery (77 ± 14%) was similar to observations. However, unlike the adjusted configuration of CLM5, the default configuration estimated that longer-term ecosystem recovery was lower than observations (65 ± 16%, $p < 0.05$).

3.3.2 Change in C response to N additions in CLM5

To scale the effect of plant and soil N recoveries on forest C sinks, 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, dC/dN values were computed directly (i.e., “direct approach”) as the difference in total plant or total soil C stocks 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. (1999c) 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-based estimate 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 (right-most white bar in Figs. 4a) was similar to the field-based estimate (left-most white bar in Figs. 4a), despite the greater than two-fold difference in plant N recovery between modeled and observed values (Figs. 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 becomes 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 estimating $(dC/dN)_{soil}$ (right-most gray bars in Figs. 4a and 4b) 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}; 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 default configuration followed similar patterns as the adjusted configuration for both short and long-term plant and soil dC/dN.

3.4 Impacts of forest type and fertilization

Statistical 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 simulated that plants had 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 followed similar patterns, except there was an underestimation of long-term soil recovery in both PFTs (Table 4).

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 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 the 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 default configuration of CLM5 generally followed similar trends as 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 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 (Thomas et al., 2013b; Nevison et al., 2016; Koven et al., 2013; Houlton et al., 2015). 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). 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, we examined CLM5 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 response 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 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. 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 Plant-Soil N Competition, Plant N Uptake, and Soil N Immobilization

In CLM5, plants are the dominant short-term sink for N additions, with soils becoming the dominant sink for N thereafter, as leaf and fine root litter is incorporated into soils. However, field experiments demonstrate the opposite pattern—large amounts of N are directly recovered in soils from the start of tracer application, without passing through plants (Nadelhoffer et al., 2004; Goodale, 2017; Tietema et al., 1998; Emmett et al., 1998a; Gundersen et al., 1998). Two decades ago, Nadelhoffer et al. (1999c) 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 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 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, 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; Sulman et al., 2017; Terrer et al., 2016). 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 v. adjusted configuration, and fertilized v. ambient simulations). The large magnitude of the observed soil N sink and the model's poor ability to reproduce it 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. 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).

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., 1999c; Templer et al., 2012). However, CLM5 estimated a different plant N response depending on forest type, 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 did produce similar trends in a decline in long-term soil N recovery in response to fertilizer treatment (Table 4), 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.

4.2 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 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, 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 $(dC/dN)_{total}$ 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 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 2a, 2b). When the difference in C:N ratios between the model and field measurements were accounted for by using the means from available data at our sites, the model's estimated $(dC/dN)_{total}$ increased to a range from 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. 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 simulated that, on average, adding N to temperate forests yielded 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 (Frey et al., 2014; Janssens et al., 2010). 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.

4.3 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 carbon storage relies on how well land models can project the long-term response of plant and soil C stocks to environmental change, including shifts in N deposition. 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. Incorporating 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 can be found in the citations listed 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).

6 Acknowledgements

We would like to acknowledge high-performance computing support from Cheyenne (doi:10.5065/D6RX99HX) and Yellowstone (ark:/85065/d7wd3xhc) provided by NCAR's Computational and Information Systems Laboratory, sponsored by the National Science Foundation and other agencies. SJC, WRW, DLL, CLG and RQT were supported in part by the US Department of Agriculture NIFA Award 2015-67003-23485. SJC, PGH, and CLG also received support from NSF-ETBC 10-21613. KJN acknowledges sabbatical support from the University of Copenhagen. We thank Erik Kluzek, Keith Oleson, Richard Valent, Silverio Vasquez, Davide Del Vento, and other staff at NCAR’s Computational and Information Systems Laboratory for their support with running simulations.

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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.

Biogeosciences Discuss., https://doi.org/10.5194/bg-2018-505
Manuscript under review for journal Biogeosciences
Discussion started: 19 December 2018

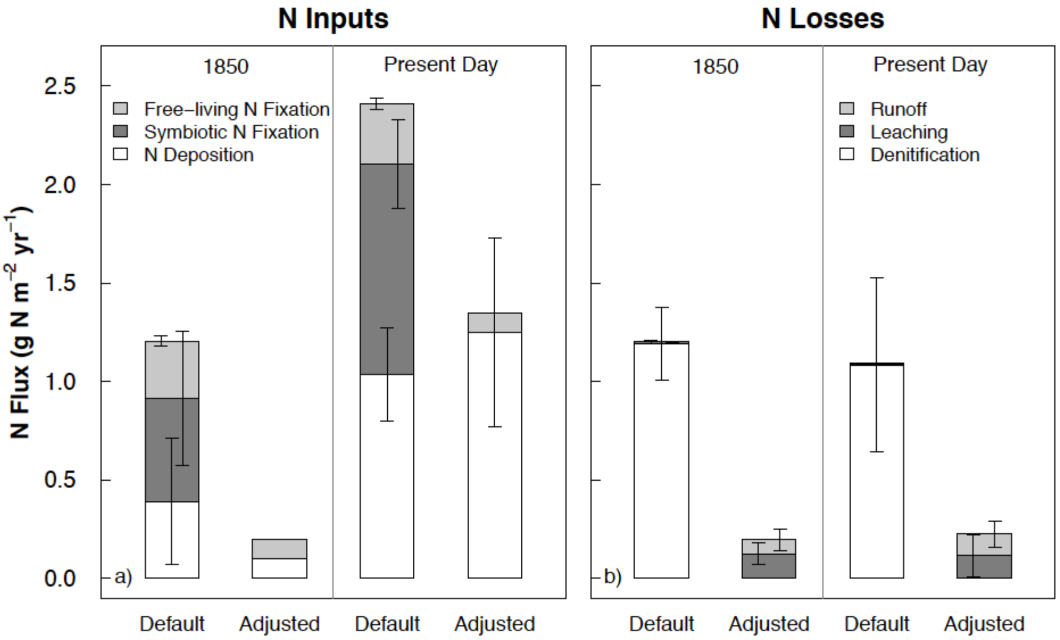

Figure 1: Rates of a) nitrogen (N) inputs and b) N losses averaged across sites for 1850 (using the last 20 years of the spin up simulation) and the present day (using the last 20 years of the historical baseline simulation; see Section 2.3) for both versions of CLM5 (default, adjusted). Mean inputs and losses include sources that were > 0.1% of total fluxes. In the adjusted model, 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 across sites. 5

Table 2: Mean values for C:N of plant and soil pools reported in site-specific literature and by CLM5 (averaged across sites). Model means (± 1 standard deviation; SD) are the average of C:N ratios from the last 20 years of the baseline simulation from the adjusted configuration of CLM5. Site-reported or estimated values for C:N ratios for each site and their references 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 the default and adjusted versions of CLM5 at the end of baseline historical simulations. 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	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	271	2.9	6820	3060 (20 cm) 5930 (total)	40	269 (20 cm) 527 (total)
	adjusted	260	2.7	7010	3310 (20 cm) 6470 (total)	39	292 (20 cm) 576 (total)
	obs	373[a]	5.3[b]	10,110[c]	9,710[c]	24[d]	415 (20 cm)[d]
Bear Brook (BDT)	default	260	2.7	7720	1540 (10 cm) 7330 (total)	42	133 (10 cm) 650 (total)
	adjusted	281	3.0	8750	1800 (10 cm) 8720 (total)	48	155 (10 cm) 775 (total)
	obs	446[e]	7.6[f]	5830[g]	5910[g]	20[g]	285 (10 cm)[g]
Arnot (BDT)	default	279	3.0	10680	8510 (50 cm) 10720 (total)	56	755 (50 cm) 954 (total)
	adjusted	270	2.9	10930	9130 (50 cm) 11540 (total)	56	810 (50 cm) 1028 (total)
	obs	270[h]	NR	10380	7270[h]	37[h]	645 (50 cm)[h]
Harvard (NET)	default	339	4.0	10690	3610 (20 cm) 7010 (total)	53	305 (20 cm) 610 (total)
	adjusted	287	3.3	9880	3610 (20 cm) 7120 (total)	47	305 (20 cm) 621 (total)
	obs	294[a]	4.4[b]	12370[c]	11050[c]	21[d]	460 (20 cm)[d]
Gårdsjön (NET)	default	398	4.9	14580	4980 (30 cm) 9750 (total)	69	539 (38 cm) 850 (total)
	adjusted	422	5.3	15830	5520 (30 cm) 10920 (total)	75	606 (38 cm) 958 (total)
	obs	275[i]	NR	NR	18880[j]	82[i]	584 (38 cm)[j]
Aber (NET)	default	388	4.8	9130	4760 (30 cm) 8940 (total)	49	417 (30 cm) 793 (total)
	adjusted	348	4.2	8320	3760 (30 cm) 6920 (total)	43	329 (30 cm) 613 (total)
	obs	NR	NR	NR	17700 (30 cm)[k]	NR	955 (30 cm)[l]
Klosterhede (NET)	default	366	4.4	13130	4030 (30 cm) 7740 (total)	61	339 (30 cm) 670 (total)
	adjusted	413	5.2	14520	4170 (30 cm) 7990 (total)	68	359 (30 cm) 700 (total)
	obs	352[k]	6.0[m]	12450[k]	13270 (30 cm)[k]	91[k]	441 (30 cm[k]
Alptal (NET)	default	421	5.2	17450	7740 (25 cm) 14160 (total)	80	657 (25 cm) 1234 (total)
	adjusted	382	4.6[a]	14420	6310 (25 cm) 11570 (total)	66	542 (25 cm) 1014 (total)
	obs	355[n]	3.8[n]	13140[o]	9810[o]	60[n]	435 (25 cm)[n]

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

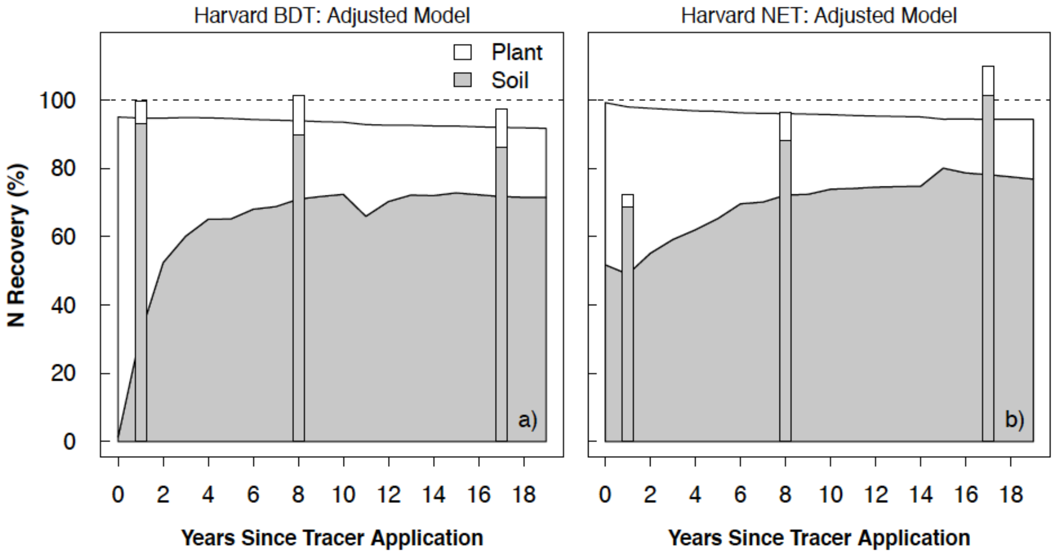

Figure 2: Modeled recovery of N additions for Harvard Forest broadleaf deciduous temperate trees (BDT; left panel) and needleleaf evergreen temperate trees (NET; right panel). Simulations were done using the adjusted version of CLM5 and 5 are compared to field measurements (stacked bars). The modeled soil stock includes the organic soil, inorganic soil, and litter pools (excluding coarse woody debris). For each scenario, recovery 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 other sites and for the default version of CLM5 are in Figs. S3-S5.

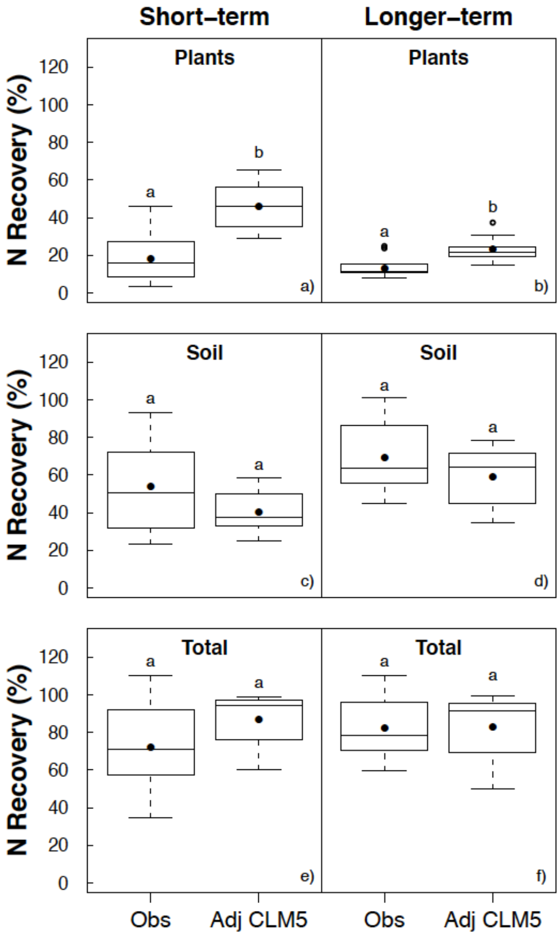

Figure 3: Boxplot showing the mean (filled dot), median (horizontal line), 1st quartile, and 3rd quartile of N recovery (%) on the short-term (< 3 years) and longer-term (> 3 years) from ^{15}N experiments with available data (Obs) and adjusted model simulations (Adj CLM5). Data are an aggregate of values 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. Different letters indicate groups that are statistically different ($p < 0.05$).

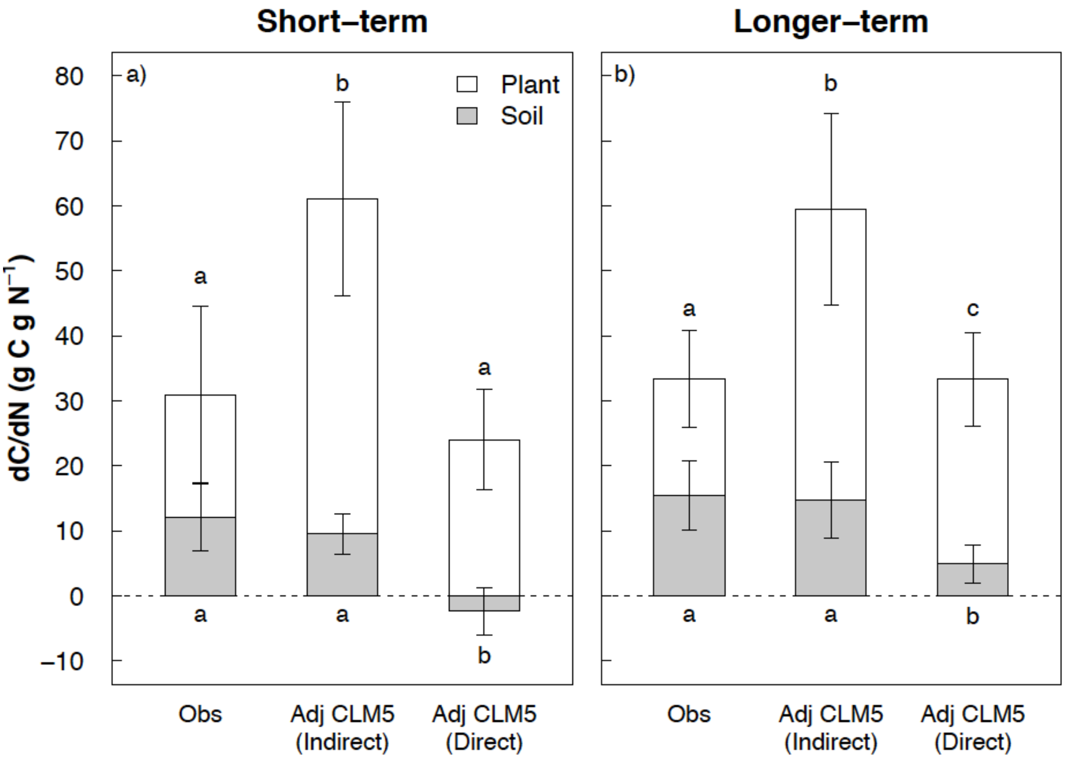

Figure 4: Mean short-term (< 3 years) and long-term (> 3 years) response of C stocks to added N (dC/dN) estimated from ^{15}N experiments (Obs) and adjusted model simulations (Adj CLM5). The dC/dN for field experiments (left-most bars in Fig. 4a and 4b) is calculated by multiplying the site-level ^{15}N recovery for foliage, wood, bark, fine roots, coarse roots, O horizon, and mineral soil horizon and 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 (obs C:N) and Eqn 3 as well as directly from the model using the model's C:N ratios (model C:N) 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. 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 the default (Def CLM) 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	49 (2)	36 (2)	35 (4)	37 (6)	38 (14)
	Ddj CLM	64 (2)	32 (2)	44 (4)	47 (6)	46 (14)
	Obs	9 (2)	18 (2)	13 (4)	26 (6)	18 (14)
Short-term Soil	Def CLM	25 (2)	26 (2)	54 (4)	37 (6)	39 (14)
	Adj CLM	32 (2)	34 (2)	52 (4)	37 (6)	40 (14)
	Obs	76 (2)	48 (2)	49 (4)	52 (6)	54 (14)
Long-term Plant	Def CLM	15 (3)	18 (2)	20 (4)	23 (5)	20 (14)
	Adj CLM	23 (3)	17 (2)	20 (4)	28 (5)	23 (14)
	Obs	10 (3)	11 (2)	13 (4)	16 (5)	13 (14)
Long-term Soil	Def CLM	55 (3)	34 (2)	43 (4)	44 (5)	45 (14)
	Adj CLM	72 (3)	35 (2)	73 (4)	50 (5)	59 (14)
	Obs	79 (3)	60 (2)	78 (4)	58 (5)	69 (14)

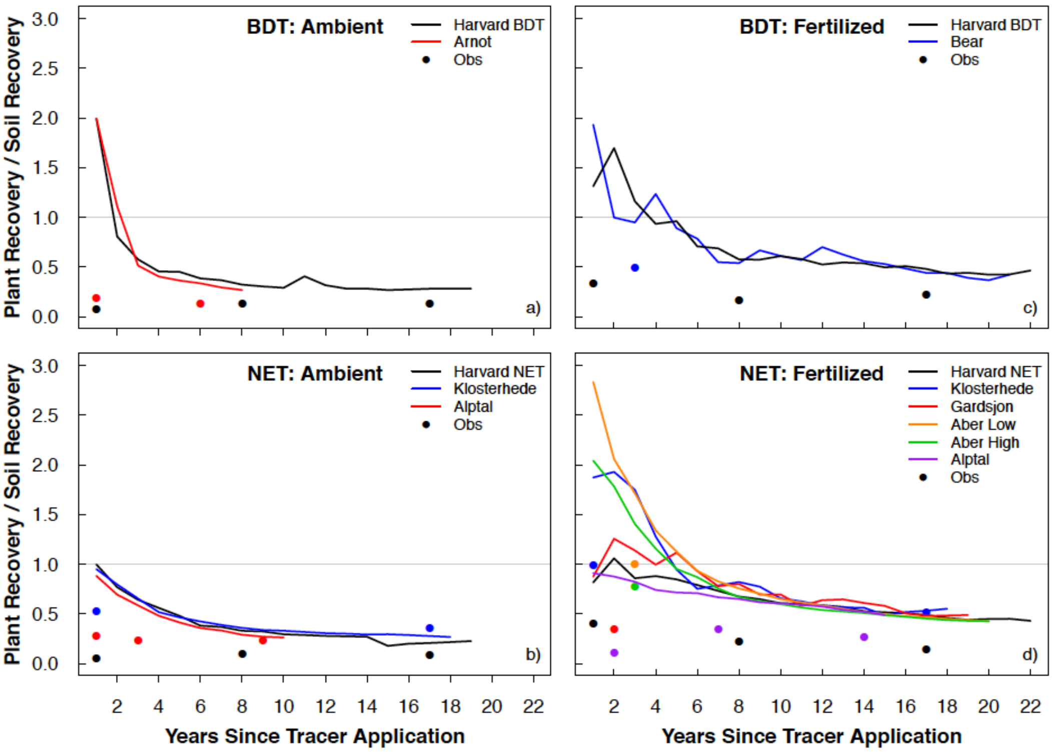

Figure 5: Ratio of plant recovery and soil recovery of added N into a,c) broadleaf deciduous temperate (BDT) and b,d) needleleaf evergreen temperate (NET) forests predicted by the adjusted configuration CLM5 for sites under ambient deposition (a,b) and fertilized (c,d) conditions. Circles represent the 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.