Evaluation of simulated N cycling using observations from a ^{15}N tracer experiment in a mixed deciduous forest

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Abstract. Nitrogen availability constrains ~~the~~ terrestrial carbon uptake and storage, yet large uncertainties remain in the magnitude of the effect, because the interactions of the carbon and nitrogen (N) dynamics are challenging to observe in undisturbed ecosystems at relevant timescales. Long-term experiments with ^{15}N tracer applications allow the study of the nitrogen cycle in a fairly undisturbed manner, and they are therefore a valuable data source to test the biogeochemical dynamics simulated by terrestrial biosphere models. In this study we applied the model QUINCY (QUantifying Interactions between Terrestrial Nutrient CYcles and the climate system), which includes an explicit representation of terrestrial ^{15}N fluxes and pools. We used observations from a long-term (10-year) ^{15}N tracer experiment in a temperate deciduous forest to evaluate the nitrogen dynamics simulated by QUINCY. Recovery in soil N dominated overall ecosystem ^{15}N recovery in both observations and simulations over the long-term. The observed gradual movement of the ^{15}N tracer to lower soil layers was also captured by the model. However, in the short-term the modeled uptake and losses of ^{15}N for leaves and fine roots were too fast, and recovery in litter and surface soil was too slow, indicating that the model likely overestimated plant competitiveness for newly added N relative to soil microbes. Downward vertical transport of ^{15}N tracer in the soil was slower in the model compared to measurements, which may be indicative either of too little bioturbation or vertical transport via leaching. Overall, the QUINCY model results showed good agreement with the observations, making it a valuable tool ~~to study long term~~ for studying long-term nitrogen dynamics. Running the model ~~for~~ over an extended period indicated that the ecosystem retained a very large share of the added ^{15}N tracer (>90%), and that this retention persisted over multi-decadal timescales. This study shows that explicit inclusion of isotopic tracers allows for a more ~~profound~~ thorough evaluation of carbon-nitrogen turnover and dynamics and thereby can contribute to reduce uncertainties in modelling nitrogen ~~flow and constrains~~ cycling and constraints in terrestrial ecosystems.

1 Introduction

Climate change influences plant-atmosphere interactions as ecosystems ~~face~~ experience new conditions (Canadell et al., 2022). It is crucial to have a better understanding of the capacity of vegetation to take up atmospheric CO_2 and the fate of terrestrial carbon (C) storage, as potential feedbacks may attenuate or further accelerate climate change. The ~~bio-availability~~ bioavailability of nitrogen (N) ~~has~~ plays a pivotal role in the carbon sink potential of vegetation and soils, as bioavailable N is scarce in many ecosystems ~~given~~ owing to limited inputs from atmospheric deposition and biological nitrogen fixation (LeBauer and Treseder, 2008), but plants require N ~~in~~ for the the photosynthetic machinery and ~~to construct~~ for constructing new biomass (Bonan, 2016). Understanding the role of the N cycle ~~on~~ in the terrestrial C cycle is especially important as terrestrial N limitation is expected to intensify in response to the ~~increasing~~ rising atmospheric CO_2 (Cambron et al., 2025; Rogers et al., 2017).

At the same time, ~~humans~~ human activities have not only perturbed the C cycle, but also the natural N cycle ~~by~~ through industrial combustion processes ~~as well as~~ and agricultural fertilization (Gruber and Galloway, 2008). ~~The~~ As a result, the amount of reactive N has increased ~~and led~~ leading to increased N deposition across many ~~parts~~ regions of the world (Galloway et al., 2008). These anthropogenic influences on the nitrogen cycle have diverse effects on natural ecosystems, such as eutrophication, air pollution and biodiversity loss (Gong et al., 2024; Schlesinger, 2009). Increased N deposition also influences C sequestration, ~~such as stimulation of~~ by stimulating tree growth and ~~altered~~ altering soil decomposition processes (Zaehle and Dalmonech, 2011). The magnitude of the effect of N deposition in forests has been debated (Gurmesa et al., 2022; Magnani et al., 2007; Sutton et al., 2008; Reay et al., 2008). The global N-induced increases in forest net carbon uptake have been estimated to ~~be in the range of~~ range from 130 ~~–~~to 345 $\mathrm{Tg\,C\,yr^{-1}}$ by several studies using different approaches (de Vries et al., 2014; Du and de Vries, 2018; Fleischer et al., 2019; Jain et al., 2009; Thomas et al., 2010; Schulte-Uebbing and de Vries, 2018; Wang et al., 2017; Zaehle and Dalmonech, 2011), with a smaller recent estimate of 41 $\mathrm{Tg\,C\,yr^{-1}}$ from a data-based approach (Schulte-Uebbing et al., 2022).

There has been a trend in declining N availability in unfertilized ecosystems globally, which has lasted for decades (Craine et al., 2018; Mason et al., 2022; Bassett et al., 2026). Declining N deposition ~~due to~~ resulting from air pollution legislation has contributed to reduced N inputs ~~for~~ to forests in Europe and north-eastern North America (Lloret and Valiela, 2016; Schmitz et al., 2019). Declining N deposition, taking place simultaneously with decreases in sulphur deposition, has been shown to have positive effects on some ~~forests~~ forest ecosystems (Dalton et al., 2024).

An important uncertainty in the response of the carbon cycle to ~~additions of N~~ N additions is the fate of the ~~extra~~ added N in the ecosystem (Nadelhoffer et al., 1999b). The response depends on the fraction of N that is retained in the ecosystem rather than lost to leaching or gaseous ~~losses~~emissions, and the partitioning of the retained nitrogen ~~into~~ among pools with a narrow C:N ratio, such as soil organic matter, or a wider C:N ratio, such as woody biomass (Gurmesa et al., 2022; Nadelhoffer et al., 1999b). ~~Knowing~~ Quantifying the fate of the incoming N to the ecosystem is therefore crucial.

Terrestrial biosphere models (TBMs) are useful tools ~~in~~ for predicting the trajectories of terrestrial C stocks in soil and vegetation (Friedlingstein et al., 2025; Seiler et al., 2022), ~~as they in principle can~~ because they can, in principle, account for

the numerous interactions between the N and C cycles. However, modelling of the N cycle is challenging ~~, as~~ because many processes are involved but comprehensive data sets to evaluate the models are scarce (Meyerholt et al., 2020), ~~since measuring~~ partly because many aspects of the N cycle ~~is difficult~~ are difficult to measure (Vicca et al., 2018). Results from manipulation experiments, including both N fertilization and tracer addition studies, are important resources for the further evaluation and development of the N cycle description in ~~the~~ TBMs (Thomas et al., 2015).

N fertilization experiments in forests have a long history, the earliest ~~originating from~~ dating back to the early 20th century (Högberg et al., 2017). These experiments have been valuable ~~in~~ for estimating optimal N fertilization for forest ~~management~~ growth as well as ~~in increasing the~~ for increasing our understanding of the N cycle in these ecosystems (Högberg et al., 2017). These data have also been used ~~in~~ for model development (Meyerholt and Zaehle, 2015; Caldararu et al., 2020). However, these experiments have limitations, as fertilized ecosystems are no longer in their natural state, and fertilization may lead to N saturation or species replacement (LeBauer and Treseder, 2008; Van Houtven et al., 2019). In model development it is often preferable to have observations of ~~the~~ ecosystems at their natural state. Additionally, it is difficult to trace the effects of individual N cycle processes beyond their influence on tree biomass, although such insights are needed to further improve our understanding ~~and model representation~~ these processes and their representation in models.

Isotopic tracer experiments can overcome these issues, as very small additions of nitrogen ~~as~~ in the form of highly enriched ^{15}N are ~~enough~~ sufficient to allow the tracer to be tracked across different soil and vegetation pools (Buchmann et al., 1995; Lin et al., 2024; Nadelhoffer et al., 1999a; Schleppi and Wessel, 2021). Traditionally, these observations are challenging and expensive to ~~make~~obtain. However, improved measurement techniques have made ~~these observations more frequent, offering~~ such observations more common, providing more data (Schleppi and Wessel, 2021) that can also be used for model development. These observations have revealed many important aspects of the nitrogen cycle that would otherwise have been ~~challenging to address (Craine et al., 2015; Robinson, 2001), for~~ difficult to study (Craine et al., 2015; Robinson, 2001). For example the uptake of N by the forest canopy has been quantified (Ferraretto et al., 2022; Li et al., 2025).

These isotopic tracer experiments have been used ~~in testing~~ to test models without an explicit ^{15}N cycle (Cheng et al., 2019; Thomas et al., 2013) and have provided insights into nitrogen turnover rates and competition for N between plants and soil microbes. A more direct use of these ^{15}N observations is to compare them with the simulated ^{15}N cycle ~~if explicitly described in a model~~in models that explicitly represent it, as in the TBM QUINCY (QUantifying Interactions between terrestrial Nutrient CYcles and the climate system) (Thum et al., 2019). While ~~site-level models used to study~~ site-level models used for studying tracer experiments have been developed (e.g., Inselsbacher et al., 2013; Müller et al., 2014; Liu et al., 2026) and some simple ~~model~~ models do describe the ^{15}N cycle (Vitousek et al., 2024), QUINCY, as a TBM has the advantage of having fully coupled energy, water, carbon, and nutrient cycles, allowing the study of several aspects of biogeochemical cycling.

QUINCY has already been used ~~in~~ by Caldararu et al. (2022) to explain the drivers of long-term trends in ~~natural abundance~~ natural-abundance measurements of ^{15}N in plant tissues. In the present study, we compared QUINCY with observations from a ^{15}N tracer experiment conducted in a temperate mixed deciduous forest, where the fate of the applied ^{15}N tracer has been ~~studied~~ tracked for a decade~~following the experiment~~. We specifically aimed to evaluate the temporal dynamics of the tracer signal in different pools over an 11-yr period, the partitioning of the ^{15}N signal among different ecosystem compart-

ments, how well the model reproduced these patterns, and what ~~potential developmental needs this assessment offers for~~ this assessment reveals about potential improvements to nitrogen cycle modelling. We also conducted a simulation experiment to ~~study~~ investigate the fate of the ^{15}N over decadal timescales and to consider the impact of N ~~input~~ inputs on the carbon pools of the ecosystem. In particular, we address the following research questions:

- How realistic are the simulated ~~plant N pool turnover rates~~ turnover rates of plant N pools?
- How well ~~can we~~ does the model simulate retention of the ^{15}N tracer in the ecosystem?
- How long does the ^{15}N tracer ~~stay~~ remain in the ecosystem and where ~~will it~~ does it ultimately end up?

2 Materials and methods

2.1 ^{15}N experiment and the experiment site

2.1.1 Site description

The Arnot Forest (42 ° 17' N, 76 ° 38~~W' '~~ W, 503 m elevation) is located in ~~central~~ Central New York State, ~~the U.S. The annual mean~~ USA. The mean annual temperature is 7.8 °C and the annual mean precipitation is 930 mm (Goodale, 2017). The forest consists mostly of second-growth mixed hardwoods established naturally after harvest in ~~1873-1887~~ between 1873 and 1887 and fires in 1900-1911 (Fain et al., 1994). The dominant species include white ash (*Fraxinus americana*), red maple (*Acer rubrum*), quaking aspen (*Populus tremuloides*), basswood (*Tilia americana*) and ~~some~~ with smaller amounts of eastern hemlock (*Tsuga canadensis*) (Goodale, 2017). ~~The stand is evenly composed of tree biomass with~~ Tree biomass is approximately evenly divided between ectomycorrhizal and arbuscular mycorrhizal ~~associations~~species. The soil ~~structure~~ consists of 18 % clay, 41 % silt and 40 % sand and the pH is 4.4, measured at the 0-10 cm depth (Fahey et al., 2013). Leaves usually emerge in early to ~~mid May~~ mid-May and most leaf fall occurs by the end of October.

2.1.2 Tracer addition experiment

In 2007, 0.21 $kg\,ha^{-1}$ of ^{15}N tracer was applied as 99 atom % $^{15}N{-}KNO_3$, split into three equal applications of 0.07 $kg\,ha^{-1}$ applied on 30 April, 31 July and 30 October (Goodale et al., 2015). The total amount of the three applications ~~equals <~~was less than 3% of one year of nitrogen deposition at the site. The tracer was sprayed ~~on~~ onto the forest floor. Measurements of ^{15}N in fine and coarse roots ~~located in the upmost soil layer (0-10 cm depth)~~ from the uppermost soil layer 10 cm of soil were conducted in late November 2007. Tree N and ^{15}N pools (foliage, wood, bark, coarse and fine roots) and soil pools down to 50 cm were measured in summers 2006 and 2008, one year before and after the tracer additions~~, in summers 2006 and 2008. Later measurement occurred in 2012-2013~~ . Additional measurements were made in 2012–2013 (5-6 years after tracer addition), when soil and root samples were taken in October 2012 and the aboveground pools were sampled in June 2013. The ~~last~~ final measurements of the plant and soil ^{15}N pools were collected in 2017, 10 years after the tracer addition. The wood pools were

not measured at this ~~point~~time. In the observations, up to 26 samples were taken for the foliage pool, and around 20 for other aboveground plant pools and soil pools (Goodale et al., 2015; Goodale, 2017). Fine and coarse roots were represented by up to 10 samples, with somewhat smaller sample sizes in deeper layers. The standard error for the stock estimates were around 5-10 %, with highest uncertainties for the fine roots. The ^{15}N observations were on the order of 10-20 %, again with the highest standard error for the fine roots.

The fraction (~~as~~ %) of the added ^{15}N tracer recovered in each of the pools $^{15}N_{Rec}$ was computed ~~using~~ from each pool's N storage (M_{poolN}) and the change in mean atom ^{15}N ~~after the~~ following tracer addition ($^{15}N_{post}$) relative to the mean pre-addition value ($^{15}N_{pre}$) and the total mass of added tracer ($M_{^{15}Nadded}$):

$$^{15}N_{Rec}(\%) = \frac{(atom\%^{15}N_{post} - atom\%^{15}N_{pre}) * M_{poolN}}{M_{^{15}Nadded}} * 100 \quad (1)$$

2.2 Model description of QUINCY

QUINCY is a terrestrial biosphere model that simulates the energy, water, carbon, and nutrient (nitrogen and phosphorus) cycles (Thum et al., 2019). For simplicity, in this study we ~~applied~~ ran the model with soil phosphorus availability set to non-limiting levels, such that plant and soil biogeochemical processes operated at average observed P contents. ~~Parallel to~~ Alongside the nitrogen cycle, ~~a~~ an explicit representation of the ^{15}N cycle has been implemented, largely following the description of isotopic discrimination processes by Robinson (2001). Different ecosystems are represented by different plant functional types (PFTs) and in the ~~site level~~ site-level version each site is represented by ~~one~~ a single PFT.

We outline ~~here~~ some of the basic characteristics of the model here, and a full description of the model ~~can be found in~~ is provided by Thum et al. (2019). Plants ~~contain three fast-lived~~ comprise three short-lived pools (leaves, fine roots and fruits), a non-structural storage pool (reserve) and a seasonal, non-respiring pool (labile), along with three structural tissue types (sapwood, heartwood and coarse roots). All vegetation and soil pools in ~~the QUINCY model~~ QUINCY contain carbon, nitrogen and ^{15}N. Photosynthesis in the ~~multi-layered~~ multilayered canopy is calculated following the formulation ~~by~~ of Kull and Kruijt (1998). Photosynthetic parameters depend on the leaf N concentration (Friend et al., 1997). Leaf ~~mass and N concentrations~~ biomass and N concentration respond to soil N availability (Hyvönen et al., 2008). Plant nutrient uptake depends on ~~fine root~~ fine-root biomass, soil mineral nutrient concentration and plant nutrient demand.

~~The newly~~ Newly acquired carbon, nitrogen and ^{15}N are first ~~placed in~~ allocated to the labile pool, from which they can be used for ~~new growthof tissues~~tissue growth, respiration or storage in the reserve pool. The potential growth rate is influenced by the PFT-specific allometric relationships ~~between~~ among leaves, sapwood and fine and coarse roots. Belowground carbon allocation increases under nutrient or water stress. Actual growth is further controlled by the nutrient demand of each plant pool ~~,~~ and the nutrients available for growth~~and it can~~ , and may also be limited by air temperature and soil moisture. Flexible stoichiometry is ~~allowed~~ permitted for leaves and fine roots.

Symbiotic biological nitrogen fixation (BNF) by ~~microbial-tree partnership~~ microbial–tree partnerships is described as a dynamic trade-off ~~of~~ between carbon and nitrogen opportunity costs, following Rastetter et al. (2001) and Meyerholt et al. (2016). Asymbiotic BNF in the litter layer depends on soil temperature, soil moisture~~as well as on~~ , and the N deficit in litter

decomposition. Nitrogen fixed through this mechanism is added to the fast soil organic ~~material~~ matter pool. The parameters governing BNF ~~have been~~ were adjusted to align with the findings of Davies-Barnard and Friedlingstein (2020).

The simulated soil has a vertically layered structure, with 15 layers of exponentially increasing soil ~~depth~~ thickness down to 9.5 m. The soil biogeochemical processes largely follow the CENTURY model approach (Parton et al., 1993). Each soil layer ~~has organic pools ,~~ contains organic pools consisting of metabolic (soluble), structural (polymeric), and woody litter pools, ~~fast and slow overturning~~ fast- and slow-overturning organic matter (SOM), ~~and~~ as well as inorganic ammonium (NH_4) and nitrate (NO_3) pools. The litter and SOM pool turnover rates ~~are dependent~~ depend on soil temperature and moisture, described by first-order kinetics~~functions~~. The stoichiometry of the litter pools is determined by the respective plant pool stoichiometries along with the plant resorption capacity for each nutrient. The fraction of resorption to the labile pool for leaves before shedding is 50 % and for wood 20 % during conversion of sapwood to ~~dead heartwood. Fine root death~~ heartwood. Fine-root mortality is assumed to be dominated by predation and therefore no nutrient resorption occurs from ~~them. The fast SOM pool stoichiometry for~~ fine roots. The C:N stoichiometry of the fast SOM pool is affected by available inorganic N while the slow SOM pool stoichiometry is assumed to be fixed. Plants and ~~microbes compete over~~ soil microorganisms compete for the inorganic nutrients ~~, determined by~~ according to their nutrient demand. Nitrification and denitrification processes depend on the aerobic status, temperature~~and moisture in~~ , and moisture of each soil layer (Zaehle and Dalmonech, 2011). As a further development ~~to~~ of the baseline version of the model (Thum et al., 2019), nitrate assimilation ~~of~~ by soil microorganisms (i.e. immobilisation of nitrate from the solute pool to the fast ~~soil~~ SOM pool) was implemented. ~~While~~ Although this allows more rapid uptake of ^{15}N from nitrate in the soil, this change has limited overall impact on the model results, as N immobilisation by microbial growth is primarily determined by the stoichiometric imbalance between litter and SOM, as well as by the potential litter decomposition rate in the model.

Isotopic discrimination of ^{15}N occurs during biological nitrogen fixation, ammonification, plant and microbial N uptake, and processes associated with nitrification and denitrification. Fractionation parameters were taken from Robinson (2001) (Table A1). However, the model does not represent fractionation ~~from~~ associated with mycorrhizal-mediated N uptake. Biomass growth and ~~retranslocation of N are assumed to not~~ N retranslocation are assumed not to fractionate N.

2.3 Model set-up

In this study, the model was run at ~~a site scaleand the site was described with~~ the site scale, with the site represented by a summergreen broadleaf deciduous forest PFT. QUINCY ~~runs at~~ uses a half-hourly ~~timestep and requires as forcing variables~~ time step and requires air temperature, humidity, precipitation, air pressure, short- and longwave radiation, wind ~~velocity~~speed, atmospheric CO_2, $^{13}CO_2$, $^{14}CO_2$ mole fractions and NH_x, NO_y and PO_4 deposition rates ~~. Further information needed for sites are~~ as forcing variables. Additional site information includes geographical coordinates and soil physical and chemical ~~parameters~~ properties (texture, bulk density, rooting depth and soil depth, inorganic P content). The turnover rates of vegetation and soil pools for this PFT ~~can be found~~ are listed in Table S1.

We ~~made a model simulation for the Arnot forest~~ simulated the Arnot Forest using meteorological data from the CRU JRA v2.1 dataset (University of East Anglia Climatic Research Unit, 2020), which ~~was~~ were disaggregated to half-hourly ~~data~~

resolution using a statistical weather generator (Zaehle and Friend, 2010). ~~The annual~~ Annual atmospheric CO_2 ~~concentration was~~ concentrations were taken from Le Quéré et al. (2018) and N deposition data from Lamarque et al. (2010, 2011). The prescribed N deposition (0.87 $gN\,m^{-2}\,yr^{-1}$~~) (~~; Fig. S1) was similar to the observations at the site (0.7~~ 0.9 –~~ 0.9 $gN\,m^{-2}\,yr^{-1}$). The level of ~~nitrogen deposition has~~ N deposition decreased by about ~~one third~~ one-third between 2000 and 2020, from 1.3 $gN\,m^{-2}\,yr^{-1}$ to 0.9 $gN\,m^{-2}\,yr^{-1}$ at a long-term monitoring site operated by the US Environmental Protection Agency, which is located close to the site (Butler et al., 2015; U.S. Environmental Protection Agency Clean Air Markets Division, 2024). This level of ~~deposition can be considered as changing from high load to moderate (Xie et al., 2024). The soil~~ N deposition is considered to represent a transition from high to moderate deposition (Xie et al., 2024). Soil texture and pH were taken from the observations (Fahey et al., 2013). We did not include woody litter in the analysis, ~~since it is not largely taking part~~ because it plays only a minor role in the $\delta^{15}N$ cycle ~~at the studied timescale~~ over the timescale considered here. We combined observations of new wood, old wood and bark and compared ~~these to~~ them with simulated sapwood and heartwood, ~~together with labile~~labile, and reserve pools. Although bark can be considered an active pool in the ^{15}N cycle (Goodale, 2017), it ~~was not explicitly described~~ is not explicitly represented in the model.

First, a ~~1000-year-long~~ 1000-year spinup was performed by cycling driving data between the years 1901 and 1930. After this a model simulation was ~~done for the years 1901 to 2018~~performed for 1901–2018, using transient climate, CO_2 ~~concentration~~ concentrations and N deposition for the site. In the simulations the ^{15}N tracer was ~~placed~~ applied as NO_3 solute in the uppermost soil layer ~~at the same days~~ on the same dates as the tracer application was performed in the ~~tracer addition~~ experiment. For the scenario run extending further 30 years ~~from the final year~~ beoynd 2018, the climatic forcing was ~~prepared using the current day~~ generated using the present-day climate and the CO_2 from the ~~RCP 8.5~~ RCP8.5 scenario (Riahi et al., 2011).

Additional sensitivity tests were performed to assess the extent to which the simulation results depend on the assumed fraction of N retention during leaf senescence, as well as on the turnover rate of soil organic matter pools. In these tests, we varied the coefficient determining the amount of nutrients ~~being taken back~~ returned to the reserve pool before leaf senescence, or increased the turnover rates of the soil pools, ~~that would cause them to be smaller~~thereby reducing their size. As these changes affected the overall model performance without improving ~~correspondence~~ agreement with the observed characteristics of the carbon and nitrogen cycle or ~~stronly~~ strongly affecting the temporal evolution of the tracer distribution, we ~~simply applied the model using~~ used the default parameters for this PFT ~~instead of~~ rather than performing rigorous parameter tuning.

3 Results

3.1 Comparison between magnitudes of observed and simulated pools and fluxes

First, we investigated the overall model performance in reproducing the observed characteristics of the Arnot site ~~,~~ vegetation and soil pools as well as C and N fluxes ~~,~~ because differences in pools between the observations and simulations influence the $\delta^{15}N$ values from the tracer experiment (Table 1)~~:~~. If a pool was overestimated in the simulations, the magnitude of the ^{15}N signal would be ~~low-biased given the~~ biased low given observation-based flux partitioning. It is important to note that the model was not calibrated to this particular site and the default parameter values were used.

The simulated annual gaseous N fluxes were of the same order of magnitude as the observations, ~~in particular considering that the uncertainty range of the observationsis large~~particularly considering the large uncertainty range in the observations. Although key indicators of productivity were comparable to the observations (wood production and leaf C, which is related to leaf area index), the model showed notable deviations from the observed partitioning of carbon and nitrogen in vegetation. The model underestimated the amount of belowground carbon, ~~specifically fine root~~ especially fine-root biomass, while generally exhibiting a tighter C:N stoichiometry in leaves, ~~root~~roots, and woody biomass. Discrepancies in leaf ~~litter fall~~ litterfall were possibly the result of ~~a combination of~~ under-reporting in the observations ~~in combination~~ combined with the omission of the coniferous hemlock species in the model. Comparison of leaf mass and leaf ~~litter fall~~ litterfall stoichiometry suggests that leaf N resorption during leaf senescence was ~~less~~ lower than the assumed 50% in the model. In the observations, the mortality exceeded the wood production, which was not reproduced by the model~~, which~~ . Instead, the model estimated that wood production and mortality were roughly balanced. The N flux ~~of~~ associated with mortality was larger than the observed, probably because the observation-based estimate of mortality only accounted for the mortality of woody biomass, whereas the mortality term in the model also accounted for leaf, root, and fruit biomass.

The litter (also denoted as Oi) C pool was overestimated in the simulations compared ~~to~~ with the observations. Given the discrepancy between observed litter C:N ~~and litter fall~~ ratio and litterfall C:N ratio, it appeared likely that processes during litter decomposition already affected observed litter C:N, whereas the ~~litter pool reported by the model was~~ model's litter pool represents fresh, undecomposed litter. The simulations strongly overestimated soil C, as it was almost twice the observed value (Table 1), where the ~~fast overturning~~ fast-turnover pool contributed to 17 % of the total soil C pool and 18 % of the total soil N pool. The soil C:N ratio of the combined simulated fast and slow soil pools was similar to the observations. The observed soil C:N ratios declined strongly with soil depth, whereas~~- as per modelassumption -~~, as assumed by the model, the simulated soil C:N ~~ratios~~ ratio remained nearly constant ~~throughout the different~~ across soil layers (Table S2).

In the observations (Table S3), the natural abundance δ^{15}N values of leaves (-2.1 ‰) and coarse roots (-2.4 ‰) were most depleted and the wood (-1.2 ‰) was the most enriched vegetation ~~pools~~pool. The simulated leaf δ^{15}N ~~in leaves~~ values (-2.3 vs. -2.1 ‰) and wood (-1.2 vs. -1.1 ‰) were similar to the observations. The simulated δ^{15}N in coarse roots (-1.4 ‰) was ~~not as depleted as~~ less depleted than in the observations (-2.4 ‰). The natural abundance δ^{15}N levels in the litter layer and soil were more enriched than in the simulations, with the difference being largest in the deepest soil layers (Table S3).

3.2 δ^{15}N signal: Temporal evolution in vegetation

In the experiment the tracer was sprayed on top of the litter layer. In the simulations, we added the incoming tracer to the N deposition ~~, from where~~ flux, from which it directly entered the ~~soil solution~~ soil-solution NO_3 pool of the uppermost soil layer. This slight difference may cause some discrepancies in the comparison, as in the model, the soil-solution NO_3 ~~solute~~ pool of the first soil layer is directly accessible to ~~the vegetation~~ plants and soil microbes. Given the ~~timscale~~ timescale of this analysis, however, we assumed that delays in tracer transfer from the litter layer into the soil would not ~~strongly~~ substantially affect tracer accessibility to plants and soil microbial biomass, and would therefore have little effect on our results.

Table 1. Observed (in bold) and simulated carbon and nitrogen pools and fluxes. The simulated values are 20 year averages. Soil value refers to the top 50 cm of soil.

Storage	C ($gC\,m^{-2}$)	N ($gN\,m^{-2}$)	C:N
Leaf	**140** 120	**4.0** 5.3	**35** 23
Fine roots	**270** 62	**5.3** 2.3	**51** 27
Coarse roots	**810** 580	**6.8** 3.7	**119** 155
Wood and bark	**9920** 12 009	**23** 75	**431** 160
Litter	**260** 366	**7.3** 3.6	**36** 101
Soil	**7600** 14 709	**737.4** 1660	**12** 8.9
Flux	C ($gC\,m^{-2}\,yr^{-1}$)	N ($gN\,m^{-2}\,yr^{-1}$)	C:N
Leaf litterfall	**96** 147	**1.5** 3.1	**63** 47
Mortality	**250** 129	**0.5** 0.9	**500** 143
Wood production	**154** 182	**0.5** 1.2	**334** 152
N_2O flux	-	**0.006** 0.01	-
N_2 flux	-	**0.04-0.8** 0.31	-

Similar to observations, simulations showed a rapid $\delta^{15}N$ enrichment of both leaves and fine roots in the year after the tracer ~~was applied~~addition, but the simulated ~~declines~~ decline of $\delta^{15}N$ enrichment over the next decade ~~were~~ was faster and larger than observed for these pools (Fig. 1). Simulated leaf $\delta^{15}N$ enrichment (Fig. 1a) showed ~~some small increases~~ a small increase already in 2007, but reached its highest level of 51.4 ‰ in 2008 (~~hitherto~~hereafter, all values reported are relative to the initial natural abundance $\delta^{15}N$), ~~51.4 ‰,~~ the year after ~~the~~ tracer addition. One year later, the simulated $\delta^{15}N$ enrichment decreased by more than 50 % and reached a ~~steady low-level~~ low, steady enrichment (5.9 ‰) by 2012. The observations showed a smaller enrichment peak than the simulations (27.1 ‰), but the ~~following decline was smaller and slower~~ subsequent decline was slower and less pronounced than the simulated decline.

The fine ~~roots~~ root (Fig. 1b) observations showed a similar behavior ~~compared to the~~ to that of leaves, with a large increase in $\delta^{15}N$ enrichment (46.6 ‰) ~~in~~ during the year of ~~the~~ labeling and some decrease in the first year after labeling (27.1 ‰)~~then~~, followed by a smooth decline by approximately 50 % over the following decade. The first observed $\delta^{15}N$ value in 2007 includes only the ~~upmost~~ uppermost layer (0-10 cm), whereas the other observations include fine roots in all the soil layers. The value in the upmost layer is larger than averaged ~~over all the~~ across all soil layers, as it is where the largest amount of fine root biomass is located and the $\delta^{15}N$ enrichment decreases with depth. The simulations approximately matched the ~~similar~~ observed $\delta^{15}N$ enrichment peak (~~value~~ with a value of 25.5 ‰) observed in 2008, then showed a faster and larger decline than in the observations, dropping by two-thirds within five years and stabilizing at a lower level of $\delta^{15}N$ enrichment compared to the observations.

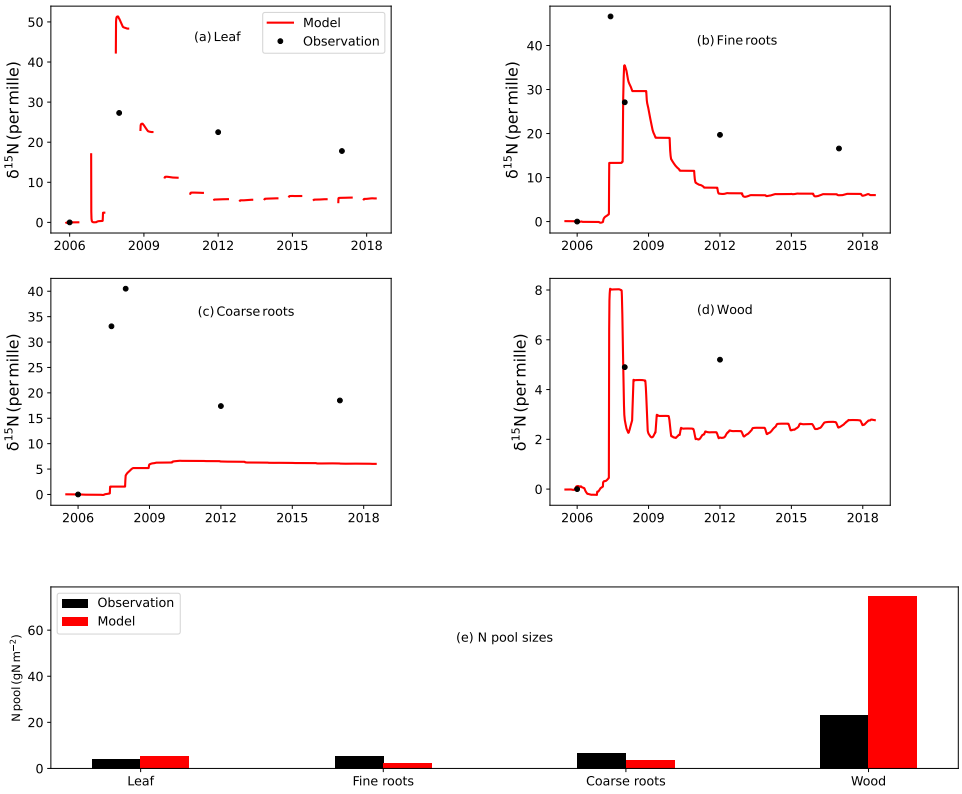

Figure 1. The temporal change of the observed (in black) and simulated (in red) δ^{15}N from the reference value in the different vegetation pools (a - leaf, b - fine roots, c - coarse roots, d - wood, including ~~both~~ sapwood, heartwood and bark) and the sizes of the corresponding nitrogen pools (e). Note: The line representing leaf δ^{15}N is not continuous due to the absence of leaves during the dormant season.

The observed ~~coarse roots~~ coarse-root δ^{15}N values (Fig. 1c) showed a smaller peak in 2007 (33.1 ‰) than fine roots, but had a larger δ^{15}N enrichment peak in 2008 than ~~the leaf and~~ either the leaf or fine root pools. This ~~is suggesting~~ suggests that the tracer was first captured by fine roots and then ~~moved into~~ was subsequently transferred to the coarse roots in the following year in the observations. After ~~the peak value of~~ peaking in 2008, the observed values declined, levelling off ~~to~~ at approximately half of the δ^{15}N peak by 2012. The simulations did not show such a distinct peak, only a small, gradual increase in the first four years (up to 6.6 ‰) ~~and then the~~ after which the simulated δ^{15}N ~~sustained at a steady level, with some slow decrease to level~~ remained nearly constant, decreasing only slightly to 6.1 ‰, ~~lower than the observations~~ well below the observed value (16.1 ‰).

The observed wood δ^{15}N ~~in the wood compartment~~ (including bark) increased by 4.9 ‰ in 2008 compared to the ~~pre-labelled situation~~ pre-labeling value and increased slightly further by 2012 (Fig. 1d). The simulations showed a larger δ^{15}N enrichment peak (8.1 ‰), ~~but the peak declined within four years to a level of~~ which declined to 2.7 ‰ within four years.

3.3 δ^{15}N signal: Temporal evolution in soil

The observed soil δ^{15}N ~~signal~~ enrichment after 2006 was much larger than the simulated one in all soil pools (Fig. 2), which may ~~partially be the result of~~ partly result from the overestimation of the ~~simulated~~ soil N pools in the simulation in both shallow (3.4-fold overestimated in ~~simulations~~simulation) and deep soil (2.2-fold overestimated in the simulation) (Fig. 3, Table S2). The observations showed a δ^{15}N enrichment peak of 106.4 ‰ in the litter layer compared ~~to~~ with the pre-experiment ~~situation~~ value and a decrease to about 10.4 ‰ ~~in a decade. In the simulations, the increase in~~ over the following decade. The simulated ^{15}N ~~tracer occurred~~ enrichment peaked later and only reached a ~~enrichment peak~~ value of 28.9 ‰ and a ~~decline~~ declined to a level of 4.6 ‰ ~~in a~~ over the following decade. In the observed shallow soil layer (0-10 cm), the tracer caused a δ^{15}N enrichment ~~peak~~ of 9.2 ‰ in 2008 and a slow increase to a level of 12.4 ‰ in a decade. ~~Only an increase~~ By contrast, the simulations showed an increase only of 3.2 ‰ ~~was seen in the simulations~~ and the δ^{15}N enrichment started to slowly decrease, ~~being at the level of~~ reaching 2.7 ‰ after a decade. The deeper soil layers experienced an increase in δ^{15}N by 1.7 ‰ in 2008 and this value slowly increased up to 2.1 ‰ in a decade. The ~~simulations only~~ simulation, however, showed an increase ~~by up to~~ of only 0.43 ‰ in a decade.

~~If only~~ When only the soluble litter was considered (Fig. 2a) the ~~fit~~ agreement between simulation (~~increase in enrichment peakafter labelling now~~ simulated peak: 40.9 ‰) and observation was slightly better. The reason for this discrepancy lies in the immediate "adsorption" of the tracer signals when sprayed ~~to~~ onto the litter surface, which cannot be represented by the model, since uptake of inorganic N ~~into litter pools~~ by the litter pool is not a flux represented in the model. Instead, the δ^{15}N tracer ~~addition was directly put~~ was added directly to the soluble NO_3 pool, from ~~where it is subject to~~ which it was available for plant and microbial uptake, the latter of which generates fast SOM, as well as leaching and gaseous emissions. In the ~~simulations~~simulation, the δ^{15}N signal in the litter ~~was derived only from litter fall~~ originated solely from litterfall of enriched plant material, and thus most of the added δ^{15}N tracer ~~addition ended up being~~ was immobilised by plants or soil microbes. In fact, while Figures 2b,c show that the model did not capture the magnitude of the bulk SOM δ^{15}N signal, when only ~~considering the fast pool~~the fast SOM pool was considered, the observed change in SOM was well captured in the ~~top soil layer (increase in enrichment peak up to~~ topsoil layer (peak enrichment of 12.2 ‰) (Fig. 3b). The observed δ^{15}N values in the deeper layers ~~did not vary a lot~~showed little variation, similar to ~~those changesmodelled~~the simulated changes, although a slight propagation of the surface signal to lower layers can be seen in later years.

The ~~development of~~ vertical distribution of the ^{15}N tracer ~~at different depths shows~~ showed that the observed soil was more enriched in 2006 than the simulated soil throughout the depth profile (Fig. 3). ~~Also~~Furthermore, the observed δ^{15}N signal in the soil was most depleted ~~on~~ in the top layer, and most enriched at around 0.25 m depth. In the simulations the soil became steadily more enriched towards deeper layers in 2006.

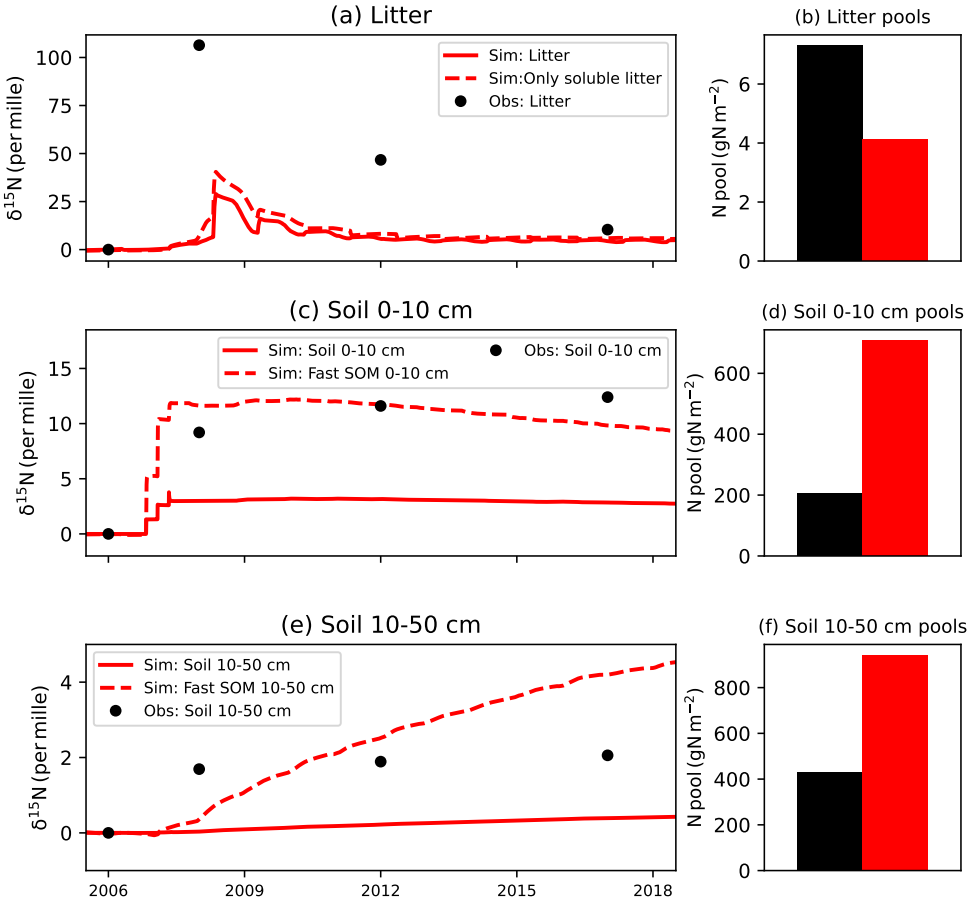

Figure 2. The temporal evolution of the observed (in black) and simulated (in red) δ^{15}N signal from the reference value before labeling in the different soil pools (a - litter, c - soil between 0-10 cm depth, e - soil between 10-50 cm) and the sizes of the corresponding measured and simulated nitrogen pools (b, d, f). The dashed line shows in a) the soluble litter only, in b) the fast soil organic matter pool between 0-10 cm depth and c) the fast soil organic matter pool between 10-50 cm.

The temporal changes in soil δ^{15}N were much larger in the observations than in the ~~simulations, as was seen already~~ simulation, as already shown in Fig. 2. In 2008 the increase in observed soil δ^{15}N ~~was notable already to the~~ extended to a depth of 30 cm~~and then during the coming years ,~~ , and during the following years the enrichment continued to increase slowly in the ~~top~~ upper soil layers. In the ~~simulations~~ simulation, the temporal dynamics were ~~instead~~ different. The top layer was most enriched in 2008 and ~~started depleting afterwards~~subsequently became depleted. In 2008, the signal had not yet reached the layers below 20 cm in the ~~simulations and in~~ simulation. During the following years~~the enrichment due to~~ , the enrichment resulting from the δ^{15}N tracer addition ~~moved to the lower layersgradually. Comparison between~~ gradually propagated to

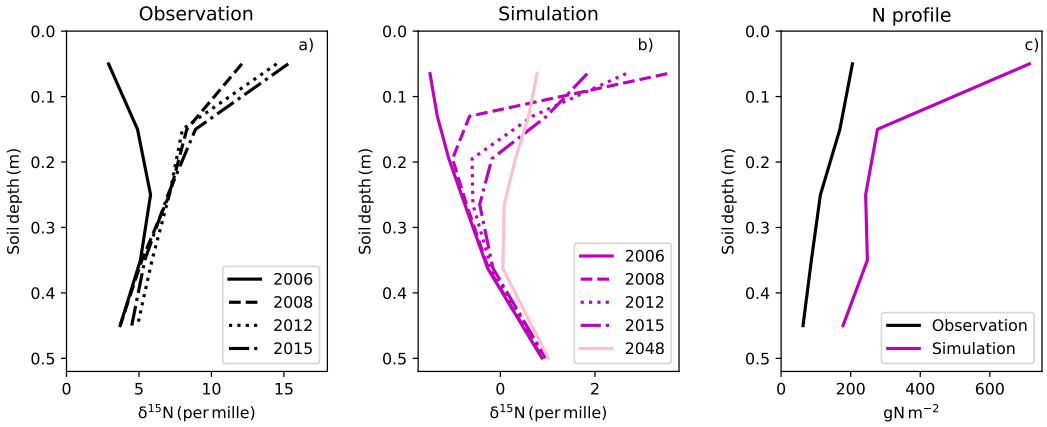

Figure 3. The temporal evolution of the observed δ^{15}N at different depths (a) and simulated (b) and the soil profiles of nitrogen (organic and inorganic) in observations and simulations (c).

deeper soil layers. Comparison of the observed and simulated soil N ~~profile~~ profiles showed that the ~~simulations had a large nitrogen~~ simulation overestimated the soil N pool in the top layer, ~~below which~~ whereas below this layer the vertical gradient was more stable and ~~comparable to the observations~~ similar to that observed (Fig. 3).

3.4 Recovery of tracer in present day climate and future

The total ~~amount of recovery~~ recovery of the tracer was close to 100 % in the ~~simulations~~ simulation (Fig. 4)~~. In the observations~~ , whereas it was around 70 % ~~. Both observations and simulations~~ in the observations. Both the observations and the simulation showed a large fraction of the δ^{15}N signal remaining in the shallow soil layer, and the relative contribution ~~from the~~ of deeper soil layers ~~was only slowly increasing with~~ increased only slowly over time. The observations showed a noticeable fraction of the δ^{15}N signal ~~staying~~ remaining in the litter layer, which was almost depleted by 2017, whereas in the ~~simulations~~ simulation the litter pool ~~did not have a prominent role~~was of minor importance.

The ~~amount of~~ δ^{15}N signal in coarse roots was pronounced in the observations, but not in the simulation. Both ~~observations and~~ the observations and the simulation showed a contribution from the fine roots. The simulation showed a substantial contribution from the wood pool already in 2008~~by a considerable amount~~, which remained substantial ~~throughout the years~~thereafter. In the observations the ~~recovery~~ transfer of δ^{15}N to the wood pool occurred in 2008 and increased in 2012 (~~the wood pool has not been~~ wood was not measured in 2017~~and we have just kept its value the same to~~ ; values for 2012 ~~in this plot~~were retained for visualization). This difference occurred ~~, partially because we had attributed all of the~~ partly because we attributed all labile and reserve ^{15}N to the woody pool, whereas in reality the signal may be ~~mixed between coarse root~~ partitioned between coarse roots and woody reserve storage. The simulation showed a large ~~recovery of the~~ fraction of the recovered δ^{15}N ~~signal~~ in leaves in 2008 (9.5 %), while the observations showed a recovery of only 1.9 % ~~recovery rate~~ for that year. When ~~considering the separation of~~ soil and plant pools were considered separately, the observations showed a prominent signal in the soil already in

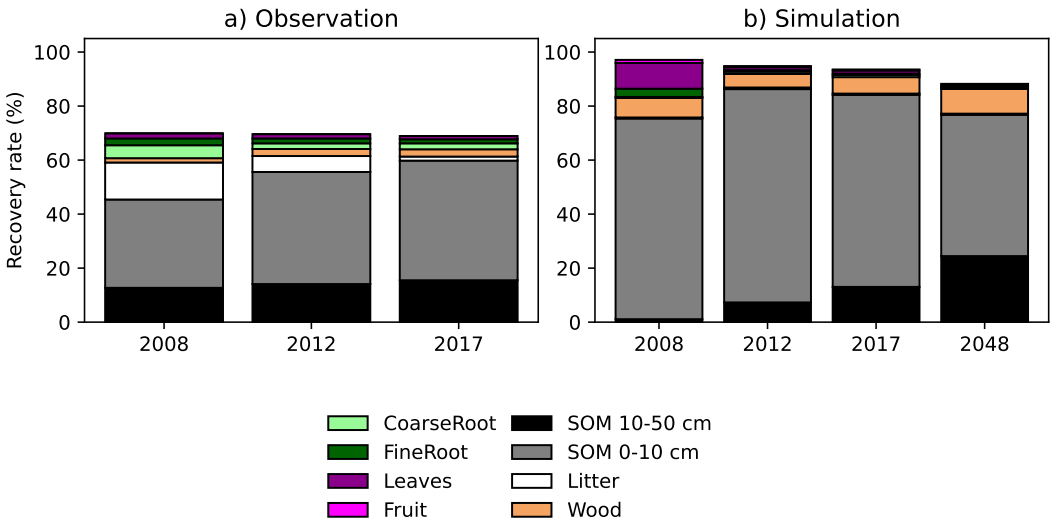

Figure 4. The temporal evolution of the observed (a) and simulated (b) recovery rates of different plant and soil pools in different years.

Table 2. The recovery rates in the soil and vegetation pools in different years. The observed values are in bold and the simulation results in a regular font. Also the percentual amount of the whole recovered signal in the plants is shown.

Year	2008	2012	2017	2048
Soil	**59.1** 75.8	**61.5** 86.9	**61.3** 84.6	77.2
Plants	**10.8** 21.3	**8.1** 7.9	**7.6** 8.9	11.0
% in plants	**15.5** 28.1	**11.6** 9.1	**11.0** 10.5	14.3

2008, and its relative contribution ~~was decreasing in~~ decreased over the following years (Table 2). ~~The recovery~~ Recovery of the label in the ~~plants~~ plant pools peaked at 11 % the year after the tracer addition, then stabilized at 8 % ~~at the year~~ in years 5 and 10. In the simulations, the relative contribution to plants was larger than in the observations in 2008, but ~~close~~ was similar to the observations in 2012 and 2017 (Table 2).

In order to track how much of the δ^{15}N signal remained in the ecosystem over longer timescales, we made a scenario simulation for an additional 30 years. The simulated total recovery rate of the system remained high until the end of the simulation, suggesting a ~~fairly~~ relatively closed simulated nitrogen cycle at the site (Fig. 4b). Most of the signal remained in the soil, with the deeper ~~parts~~ soil layers gaining δ^{15}N signal from the top soil layers. ~~The~~ Over time, the woody pool became

Table 3. Simulated δ^{15}N recovery in different plant and soil pools in 2017 and 2048.

Pool	2017	2048
Leaf	1.15	0.68
Fine roots	0.53	0.34
Coarse roots	0.79	0.60
Wood	6.09	9.13
Litter	0.46	0.43
Fast SOM (depth 0-50 cm)	71.1	52.3
Slow SOM (depth 0-50 cm)	13.0	24.4

~~more prominent vegetation storage for the signal with time~~an increasingly important vegetation pool for storing the δ^{15}N signal.

The vertical profile of simulated δ^{15}N in soil (Fig. 3b) ~~showed that with time it became flatter throughout the soil profile and at the same time~~the upmost layers ~~got depleted. Comparison between~~ became more uniform over time, while the uppermost soil layers became depleted. A comparison of the simulated δ^{15}N values ~~of different~~ in different ecosystem pools in 2017 and 2048 (Table 3) indicates that all ~~other vegetation pools~~vegetation pools, except the wood pool~~showed a slow decrease in the values during this time~~ , showed a gradual decrease in δ^{15}N during this period. The δ^{15}N in the litter was slowly decreasing. ~~The~~ In the soil, δ^{15}N decreased in the fast SOM pool ~~decreased,~~ but increased in the slow SOM pool.

4 Discussion

4.1 Temporal dynamics of the ^{15}N tracer signal in vegetation

Our ~~simulations~~ simulation showed how the ^{15}N tracer signal ~~sprayed on~~ applied to the forest floor ~~moved to different ecosystem pools during decennial time scales~~was transferred among ecosystem pools over decadal timescales. Despite some conceptual differences in the description of the manipulation experiment, the QUINCY model successfully simulated many features ~~seen~~ observed in the observations. The comparison ~~to~~ with the observations was especially interesting when ~~considering~~ evaluating the N turnover rates of the vegetation pools. These suggest that the model's turnover rates of N were too fast for the leaves and fine roots. This occurred despite the seemingly higher N retention of leaves during senescence in the model. It is important to note that the model underestimated the C and N pool size of fine roots and C pool size of the leaves, and this might have some influence on the ~~occurring~~ simulated dynamics. Although the simulated total plant C pool (12 771 $\mathrm{gC\,m^{-2}}$) was close to the observed value (11 140 $\mathrm{gC\,m^{-2}}$), the other vegetation C pools, except for wood, were underestimated. This suggests that QUINCY has some difficulties ~~with~~ in representing C allocation. The simulated total N in vegetation (86.3 $\mathrm{gN\,m^{-2}}$) was over double the observed amount (39.2 $\mathrm{gN\,m^{-2}}$), reflecting the overestimation of ~~N in the soil~~ soil N.

Since this is a deciduous forest and the turnover ~~rate~~ time of fine roots is set to 0.7 years in the model, it is likely that the ^{15}N ~~got~~ tracer was transferred too quickly away from the compartments that are used to build leaves and fine roots. In the observations, the coarse roots showed a large ^{15}N peak, ~~that was not at all seen in the simulation which showed~~ whereas the simulation showed only a gradual increase~~instead. The model structure did~~. The current model structure does not accommodate a quick response from the coarse roots, that currently have a turnover ~~rate~~ time of eight years. The observations ~~had~~ showed a larger signal in the coarse roots, because the movement of the signal to the upper tree parts required transport, e.g., via diffusion or xylem transport, and additionally the ~~observations of coarse roots include xylem within them~~ coarse-root observations included xylem tissue (Tegeder and Masclaux-Daubresse, 2018; Van Der Heijden et al., 2015). In QUINCY, we could account for the larger xylem concentration in coarse roots by partitioning the labile and reserve ~~pool between~~ pools among coarse roots, leaves and woody biomass, whereas in this study for simplicity we have assumed they ~~would be allocated in~~ were allocated to sapwood. Given the simulated peak ^{15}N signal in labile+reserve pool, partitioning 11 % of ~~the labile+reserve~~ this pool to coarse roots would reduce this mismatch. This suggests that the timescale of the transfer of the ^{15}N signal within the plant (from ~~coarse-roots~~ coarse roots to woody and leaf compartments), is potentially significantly larger (~~in~~ on the order of months to few years), than the ~~near~~ nearly instantaneous redistribution of nitrogen in the plant as assumed by the model.

Finally, it ~~needs to~~ should be mentioned that the definition of coarse and fine roots differed slightly between ~~model and observations, as in~~ the model and the observations. In the observations, roots thicker than 1 mm were considered coarse roots (Goodale, 2017), whereas the threshold was 2 mm in the model. The ~~cut-off point of~~ 1 mm cut-off point for the fine roots in these observations was chosen to align with earlier studies conducted at this site (Goodale et al., 2015; Goodale, 2017). It has also been ~~demonstrated~~ shown that fine roots ~~measuring~~ with diameters less than 1 mm ~~in diameter~~ constitute the majority of ~~fine root~~ fine-root biomass and exhibit the greatest sensitivity to nutrient availability in this and similar forest types (Fisk et al., 2004; Frey et al., 2025). We therefore do not expect this discrepancy between the ~~simulations~~ simulation and observations to have a significant impact on the comparison.

In the model, the tracer was added to the top layer of solute NO_3 which enabled direct access ~~to the plant~~ by plants and bypassed the litter layer. The trees ~~were taking~~ took up this nitrogen into labile and reserve plant N pools in the model. This caused the simulated plants to have more of the ^{15}N than the soil ~~in the simulations than observed in~~ than observed at the end of ~~2007, but already in~~ 2007. However, by 2008~~the plants had relatively more of the signal in the observations than in~~, the observations showed a relatively larger fraction of the tracer in the plants than the simulations. This difference suggests that the simulated plant pools had too high turnover rates for nitrogen, as was also seen separately for the leaves and ~~fine roots~~ fine-root compartments. In addition, the strong uptake of the tracer by the litter layer and ~~an ensuing~~ followed by the gradual release of ^{15}N could also have influenced the plant signal in the observations. In the observations~~the recovery rate in the coarse roots was noticeable still~~, the recovery of the ^{15}N in coarse roots remained substantial during the last years of the experiment and this supports the ~~fact that the signal was still slowly degrading~~ hypothesis that the tracer was still being slowly released from the litter and being transported to the plants. Generally the relative recovery of ^{15}N between plants and ~~soils were~~ soil was comparable between the ~~simulations~~ simulation and the observations in later years. However, during the few first years the model estimated nearly ~~double~~ twice the recovery of ^{15}N in plants ($\sim$ 21 %) ~~than in~~ as the observations ($\sim$ 11 %), in line with

what has been found out in the earlier modeling studies that modeled general N dynamics rather than explicit ^{15}N cycling (e.g. Cheng et al., 2019).

4.2 Temporal dynamics of the ^{15}N tracer signal in soil

Implementation of nitrate assimilation ~~of~~ by soil microorganisms was a key process ~~in order to successfully simulate~~ for successfully simulating the tracer experiment at the Arnot ~~forest~~Forest. The observed and measured ecosystem ~~pools differed in their magnitude of N~~ N pool magnitudes differed, which also influences the interpretation of ^{15}N temporal dynamics. These differences were pronounced in the soil, with the modeled total soil N pool (1656 $\mathrm{gN\,m^{-2}}$) ~~being~~ was more than twice ~~the size that observed~~ as large as the observed pool (744 $\mathrm{gN\,m^{-2}}$). Since in the model the slow soil pool was large, but it was not taking up a lot of the ^{15}N signal due to its lower turnover rate, its large size caused low values of the ^{15}N tracer signal. This ~~influence was shown~~ effect was demonstrated by isolating the fast pools (Fig. 2), that better captured the observed ~~magnitude~~ changes in the magnitude of the ^{15}N signal in the uppermost soil organic matter layer.

In the observations, the ^{15}N signal ~~occurred in~~ reached deeper soil layers, down to 0.35 meters (observed layer depth 0.3-0.4 m), ~~already after~~ after only one year and at 0.45 m (observed layer depth 0.4-0.5 m) within five years. In the simulation, the downward movement of the ^{15}N signal was slower. ~~Various factors may contribute~~ Several factors may have contributed to this finding, including a too large uptake of the signal by vegetation and soil ~~biota~~microbes, a too small movement of NO_3, or an underestimation of the transport ~~via~~ by bioturbation. Bioturbation in the model is ~~described as~~ represented as a simple diffusive flux as in Koven et al. (2013), but with the rate declining with soil depth driven by a decline on the fine root biomass density. This decline might be too strong in QUINCY, but also the amount of C allocation to roots was ~~low-biased~~ underestimated in the model, which might have contributed to a too weak bioturbation flux. A further contribution may be that a fraction of the leaching flux was simulated to occur via lateral flow and not deep drainage, effectively partitioning the leaching loss into a lateral component that prevented a fast and deep penetration of the ^{15}N signal in the soil.

In the observations, the top soil layers became enriched ~~because~~ as the ^{15}N from the overlying litter layer was incorporated into the soil organic matter. The top layers showed some depletion by 2018. The ~~simulations~~ simulation showed larger changes in the top layers ~~across the years~~ over time and also the ^{15}N tracer ~~started to be~~ was also transported to deeper soil layers, which ~~caused~~ resulted in a flattening of the vertical ~~soil profile of~~ ^{15}N soil profile (Fig. 3). These differences between the model results and observations stem from conceptual differences. It is likely that in the observations the ^{15}N tracer got attached to the litter layer and was being released slowly still after several years, ~~causing continued enrichment to~~ resulting in a continued enrichment of the top soil layer. This is possible in the real world ~~,~~because the observed litter pool includes early stages of decomposition, typically associated with an increase in N concentration due to immobilisation of mineral N by ~~the~~ decomposers, which facilitates the rapid incorporation of ^{15}N. In the model, the litter pool only contains fresh litter and any derivates, including immobilized mineral N, that are ~~partitioned~~ transferred to the fast SOM pool. Disentangling these conceptual differences from any model ~~failure~~ structural deficiencies is challenging. It is of note that the considerable overestimation of the soil N pool ~~, that occurred at all depths, was partly influencing the outcome that the~~ that occurred across all soil depths

partly contributed to the simulated soil ^{15}N signal ~~was more depleted in the model than in the observations~~being more depleted than observed.

The ^{15}N tracer ~~sprayed~~ was applied as NO_3 remained for a very long time in the soil according to ~~our results for observations and~~ both the observations and the model analysis. This is in line with other natural forest ecosystem ^{15}N studies (Lin et al., 2024; Templer et al., 2012), where the largest compartment ~~for the recovery~~ of recovered ^{15}N was also the soil organic matter. It has been suggested that the NO_3 ~~would be incorporated to organic matter by abiotic factors~~ can be incorporated into soil organic matter through abiotic processes (Fitzhugh et al., 2003). These ~~kind~~ kinds of processes are not yet ~~modelled in our~~ implemented in the current model set-up.

4.3 N status of the forest

The ~~natural abundance~~ natural-abundance soil $\delta^{15}N$ differed between the observations and the simulation in 2006, prior to the start of the experiment, with observed soil $\delta^{15}N$ values being more enriched than those in the simulation. Greater soil $\delta^{15}N$ enrichment is often associated with increased N losses via gaseous pathways which ~~fractionate strongly~~ strongly discriminate against $\delta^{15}N$ (Craine et al., 2018; Feng et al., 2023). This could indicate a less closed N cycle and weaker N limitation in the observations than in the ~~simulations~~simulation. However, following the initial tracer loss, the observed $\delta^{15}N$ recovery remained relatively stable over time, suggesting ~~fairly~~ relatively efficient long-term N retention and a relatively closed N cycle. The mycorrhizal fungi present at the site are known to strongly fractionate N isotopes (Hobbie and Ouimette, 2009; Hobbie and Högberg, 2012), which may ~~also contribute~~ have also contributed to the enriched soil $\delta^{15}N$ values in the observations. Leaf stoichiometry can be considered ~~to be~~ a proxy for leaf N status (Sheng et al., 2021). The simulation showed a lower leaf C:N ratio than the observations, suggesting weaker N limitation in the ~~simulations~~simulation.

N deposition ~~has been declining~~ declined during the study period. In ~~N limited~~ N-limited ecosystems such a decline might lead to a more closed N cycle. ~~Yet~~However, in boreal forests, the role of increasing atmospheric CO_2 has been shown to be ~~an even more important cause~~ a more important driver for a reduction in N availability than changes in N deposition (Bassett et al., 2026) and ~~this might be similar in temperate forest~~a similar response may occur in temperate forests. Overall, changes in ~~the~~ N limitation during the ~~11 year study do not likely influence~~ 11-year study period are unlikely to have influenced our conclusions.

4.4 Recovery rates and future

The ~~measurement of recovery rate~~ ecosystem-scale recovery of the ^{15}N tracer ~~at the ecosystem scale~~ is very challenging (Craine et al., 2015). Recovery of the tracer ~~signal~~ remained close to 100 % in the model throughout the decade ~~after~~ following tracer addition. In the observations, recovery was also close to 100 % in the days following each tracer addition, but declined to 77 % by the end of the ~~addition~~ year, largely due to losses during ~~mid-summer~~ midsummer (Goodale et al., 2015). This N was most likely lost via gaseous pathways (denitrification), as measured leaching losses of ^{15}N during the first seven months were very low (<1 %). This recovery ~~was quite~~ is very similar to the average recovery rate of 77.9% for deciduous forests (Templer et al., 2012).

The large difference in total recovery rates between ~~observations and~~ the observations and the simulation originates from ~~how~~ the way the ^{15}N tracer input to the ecosystem is represented in the model. In our simulation the ^{15}N tracer entered directly ~~to~~ into the soluble NO_3 pool of the uppermost soil layer from where it can be taken up by plants or soil microbes, before any ~~gas losses occur~~gaseous losses occurred. Some gas losses are likely to occur, but ~~since~~ because their magnitude cannot be prescribed with ~~certainty~~confidence, it was not possible to ~~describe this~~ explicitly represent them in the model with this approach. Despite the discrepancy in the total recovery rates, we can use our results to investigate how the ^{15}N ~~is propagating~~ propagates through the different ecosystem compartments.

Because of the way ~~we described~~ the tracer experiment was represented in the model, the litter layer also did not show the pronounced recovery of the ~~signal, as was~~ ^{15}N signal observed in the measurements (Fig. 4). ~~We captured some important~~ Nevertheless, the model captured several key characteristics of the observations: a large recovery of the signal in the top soil layers and an increasing recovery of the signal with time in the lower soil layers. The simulation supported a ~~long~~ long-term retention of N ~~in~~ within the ecosystem. This was ~~especially visible~~ particularly evident in the scenario results ~~from year~~ for 2048, as the total recovery rate ~~was still staying~~ remained high (88 %). The movement of the ^{15}N ~~continued to the lower~~ tracer continued into deeper soil layers and the wood became ~~a more prominent storage~~ an increasingly important storage pool of the ^{15}N tracer over time, with only very low losses of the ^{15}N tracer from the ecosystem. Approximately 11 % of the recovered tracer resided in the plant organs, of which more than 80 % was stored in wood (corresponding to 9 % of total recovery). Due to the high C:N ratio of wood, wood can potentially sequester more carbon per unit of nitrogen than other plant compartments. For NO_3 tracer experiments in temperate forests, Lin et al. (2024) found that almost half of the tracer in plants would reside in stem and branches, that would correspond to wood in our simulations, and more than half in roots and leaves. Our ~~results would therefore suggest a larger impact on carbon sequestration, but our results span over decadal timescale, that has not been captured by the observations .~~ model simulations suggested a larger fraction of the plant compartment's tracer residing in wood than that reported by Lin et al. (2024), implying a greater potential for carbon sequestration. In addition, our simulations cover a longer time span than is currently available from observations

4.5 Uncertainties in the study

This study has a number of uncertainties. In the measurements the heterogeneity and large mass of the soil ~~poses a~~ pose a considerable challenge (Templer et al., 2012). In the simulation we can capture the overall behaviour based on process understanding. To ~~corroborate,~~ determine whether the issues ~~discovered at Arnot forest~~ identified at Arnot Forest are generic model ~~deficits~~deficiencies, it would be valuable to extend the analysis to ~~more~~ additional experiments.

Since our aim was to assess the N retention ~~rates in the ecosystem and the recovery rates~~ at the ecosystem scale and ^{15}N recovery in the different ecosystem compartments, we consider ~~our~~ the model results to be ~~robust enough for the kind of analysisthat we performed. Caldararu et al. (2022) have~~ sufficiently robust for this type of analysis. Caldararu et al. (2022) used Latin hypercube sampling to assess the influence of uncertain fractionation rates for different processes (e.g. Robinson, 2001) in the QUINCY model. They found that uncertainties of ~~the~~ these fractionation rates did not ~~influence~~ affect the overall conclusions of their study.

While the QUINCY model covers most fluxes of the terrestrial N cycle, a few processes are missing: it has ~~been long~~ long been known that some plants are able to ~~use also~~ also ac quire organic nitrogen directly from ~~organic material~~ soil organic matter (Näsholm et al., 1998, 2009), and that symbioses with ectomycorrhizae can also ~~support this process~~ facilitate this uptake (Averill et al., 2014; Chalot and Brun, 1998; Tunlid et al., 2022), but the QUINCY model currently does not include these processes. ~~This missing process~~ Their omission might be relevant because half of the trees at the site had ectomycorrhizal associations.

The ~~simulations of~~ simulation in this study used the basic soil model (Thum et al., 2019) included in ~~the QUINCY model~~QUINCY. To include abovementioned processes it would be ~~better~~ preferable to use as a starting point the more detailed soil model of QUINCY, Jena Soil Model (JSM) (Yu et al., 2020a), which explicitly represents microbial processes and organic matter stabilisation. This new model has been shown to improve the ~~results of soil profile~~ simulation of soil profiles at different sites (Yu et al., 2020a, b) ~~due to microbial process representation as well as~~ owing to its representation of microbial process and its inclusion of organo-mineral association. Including ~~of more processes instead of~~ more explicit process representations instead of relying on first-order kinetics ~~descriptions~~ brings the simulation results closer to reality and ~~also~~ simulating this tracer study would likely also benefit from using JSM. Using JSM might also help in more realistic representation of immobilization, that has often been ~~found~~ identified as a limitation in N cycle modelling studies (Cheng et al., 2019). To ~~be able to~~ fully benefit from the increased process representation of the JSM in future studies, observations ~~on~~ of microbial biomass, mineral-associated organic carbon and their ^{15}N values as well as dissolved organic carbon would be ~~relevant, so that~~ valuable for improving our understanding of the underlying processes~~can be understood~~.

~~In the~~ ^{15}N tracer studies ~~it has also been noticed~~ have also shown that the ^{15}N signal ~~also enters the~~ is incorporated into old wood (Tomlinson et al., 2014). This ~~kind of~~ process is not described in the model and would not be captured. In reality~~also the canopy is directly taking up~~ , the canopy can also directly take up atmospheric N deposition in some cases (Ferraretto et al., 2022) (but see Da Ros et al. (2023)) and thereby influencing the carbon uptake of vegetation (Li et al., 2025), even though the soil is the most important pathway for the N entering the plants (Craine et al., 2015). In the Arnot ~~forest~~ Forest experiment we simulated the ^{15}N tracer experiment, ~~where~~ in which the tracer was sprayed ~~on~~ onto the forest floor. The application of the tracer on the forest floor ~~allows a lower recovery rate~~ results in lower recovery rates of the tracer than would happen if it was applied on the canopy (Li et al., 2025; Templer et al., 2012). At ~~the moment~~ present we do not have a mechanism in the QUINCY model that would ~~describe~~ include a mechanism for the uptake of N deposition via leaves.

5 Conclusions

Improving the representation of the N cycle in models in terrestrial ecosystem models is of high importance, ~~since~~ as the N cycle ~~has~~ plays a central role in determining ~~the~~ future terrestrial C cycle projections. In this study, we simulated a ^{15}N tracer experiment conducted ~~at~~ in a temperate deciduous forest ~~with~~ using the QUINCY model, which explicitly ~~includes~~ represents the ^{15}N cycle. This ~~allowed~~ enabled us to assess the pathways, turnover rates~~and storages of N in~~ , and storage of N within the ecosystem. ~~Comparison between the observations and simulation results helped to reveal needs~~ Comparing the simulation

Table A1. Parameters for the calculation of isotopic fractionation from Robinson (2001).

Symbol	Description	Value	Unit
$R_{ref,C13}$	Reference isotopic mixing ratio of $^{15}N/^{14}N$	0.0036765	$\frac{mol}{mol}$
$\epsilon^{mic}_{uptake,NH_4}$	Discrimination due to microbial NH_4 uptake	17.0	‰
$\epsilon^{mic}_{uptake,NO_3}$	Discrimination due to microbial NO_3 uptake	13.0	‰
$\epsilon^{plant}_{uptake,NH_4}$	Discrimination due to plant NH_4 uptake	13.5	‰
$\epsilon^{plant}_{uptake,NO_3}$	Discrimination due to plant NO_3 uptake	9.5	‰
ϵ_{nit}	Discrimination due to N_2O and NO production during NH_4 oxidation (nitrification)	47.5	‰
$\epsilon_{nitrate,production}$	Discrimination due to NO_3 production during nitrification	25.0	‰
ϵ_{denit}	Discrimination due to denitrification	31.0	‰
$\epsilon_{ammonification}$	Discrimination due to NH_4 production	2.5	‰

with the observations helped to identify priorities for model improvement, ~~such as further examining turnover rates~~ including a more detailed evaluation of leaf and ~~fine root~~ fine-root N pools and the vertical transport of N in the soil. ~~The~~ Most of the N stored in plant organs ~~mostly resided in wood, implying~~ was allocated to wood, suggesting a greater C sequestration ~~capacity~~ potential of the trees than if ~~N would have been placed in another plant organ~~the N had been allocated to other plant organs.

Overall, the model was successful in simulating the main characteristics of the ^{15}N tracer experiment, taking into consideration some conceptual differences between the model setup and the real-world ~~. This gives reliance on~~ system. This increases confidence in the model's ~~N cycle description~~ representation of the N cycle and the ability to simulate the ^{15}N cycle. QUINCY can therefore be used in studies related to N dynamics and climate change, such as ~~helping~~ to examine the role of changing N deposition and increasing atmospheric CO_2 ~~in~~ over decadal timescales, as studied for example by Bassett et al. (2026). Recent ~~spaceborn~~ spaceborne observations of $\delta^{15}N$ (Yang et al., 2025) together with QUINCY's ability to simulate the ^{15}N cycle and leaf chlorophyll, which is also observable from space and simulated by QUINCY (Miinalainen et al., 2025), ~~will help to move towards better~~ provide new opportunities to improve our understanding of the global N cycle.

Code and data availability. The scientific part of the QUINCY code is available under a GPL v3 license. The source code is available online https://doi.org/10.17871/quincy-model-2019), but its access is restricted to registered users. Readers interested in running the model should request a username and password via the Git repository.

The data used in this study, the meteorological forcing to run the model and the model results are available in METIS open data repository (https://fmi.b2share.csc.fi/records/16d17c16f1d54f60bb52591a03f1a5be).

Appendix A

A1

Author contributions. SZ designed the study. TT performed the simulations, analysis and wrote the first draft. CG provided the measured data. Interpretation of results was developed through discussion between all authors. All the authors took part in re-visioning and commenting of the manuscript.

Competing interests. The authors declare no competing interests.

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