

Calibrating soil nitrogen turnover in biogeochemical models with ^{15}N tracing data

Kathrin Fuchs^{*} , Clemens Scheer, David Kraus^{}, Andrew Smerald, Fawad Khan, Benjamin Wolf^{}

Institute of Meteorology and Climate Research, Atmospheric Environmental Research (IMKIFU), Karlsruhe Institute of Technology (KIT), Garmisch-Partenkirchen, 82467, Germany

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ABSTRACT

Process-based biogeochemical models dynamically simulate the coupled Carbon (C), nitrogen (N), and water cycles in plant-soil-atmosphere systems, making them useful for understanding and upscaling the effects of management and climate change on N flows in agricultural systems. These models use conceptual pools such as plant tissue, microbial biomass and organic matter with different decomposability, which exchange material according to the selected model structure. The evaluation of model design and the validation of internal turnover fluxes is challenging as datasets typically include only yields and measurements of trace gases leaving the system, with limited information on how specific C and N pools contribute to distinct flows. Regarding the N cycle in particular, microbial immobilization and mineralization have remained largely unconstrained in biogeochemical models. Isotopically enriched, ^{15}N -labelled, mineral fertilizer or slurry can be used as a tracer to quantify N processes and transformations, including plant uptake, soil retention, and losses of fertilizer N. Here, we combine data from a ^{15}N -labelling experiment with the isotope model SIMONE to better constrain N turnover in the biogeochemical model LandscapeDNDC. The results show that LandscapeDNDC overestimated the allocation of applied fertilizer N into the plants while underestimating the retention in the soil pool and contribution to N loss pathways. At the same time, the model underestimated uptake of N from mineralized soil organic matter (SOM). Assuming that the internal mineralization-immobilization-humification cycle was underestimated, the corresponding turnover rates were calibrated based on fertilizer ^{15}N recovery in plants and soil. This calibration not only improved the simulation of plant uptake of ^{15}N for all seasons – the original main objective – but also led to better agreement with mineralization and immobilization rates inferred from ^{15}N measurements in soil and plants. Our results demonstrate how the combination of isotope modeling with ^{15}N recovery data can be used to effectively constrain biogeochemical process parameters.

1. Introduction

In many terrestrial ecosystems, productivity is limited by the availability of biologically available nitrogen (N), also referred to as reactive N (N_r) in contrast to atmospheric N_2 which is inaccessible to most organisms. An increased supply of N_r typically increases biomass production, tightly coupling the N cycle with the carbon (C) cycle (Vitousek et al., 1997). For this reason, a profound understanding of processes in the soil that regulate the availability of N to plants and consequently their ability to take up carbon dioxide (CO_2) is paramount for projecting – among others – agricultural yields and the rate of atmospheric CO_2 increase as well as ecosystems feedback to climate change (Esser et al., 2011; Gruber and Galloway, 2008).

Two key N transformation processes, mineralization - i.e. the decomposition of soil organic matter (SOM) into plant-available, inorganic N forms, primarily ammonium (NH_4^+) - and microbial N uptake (immobilization) regulate plant N availability, since plants and soil microbes compete for N produced through mineralization or provided as fertilizer. However, these processes cannot be studied directly in a non-invasive way as the available methods rely on soil sampling that decouples the sample from the living plant, or additionally require the addition of substrate, which may stimulate processes (Hart et al., 1993; Khan et al., 2025b; Kirkham and Bartholomew, 1954). Beyond that, measurements of these process rates are snapshots that need to be repeated frequently within a growing season in order to characterize their dependence on influencing factors such as soil moisture and soil

^{*} Corresponding author.

E-mail address: kathrin.fuchs@kit.edu (K. Fuchs).

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temperature, an endeavor that has been undertaken rarely (Booth et al., 2005; Elrys et al., 2021). Even with relatively frequent sampling, these measurements produce time series that are sparse relative to the rapid and episodic nature of N transformation processes, making it difficult to derive reliable estimates of cumulative seasonal gross mineralization. Moreover, the balance between mineralization and immobilization alone does not necessarily represent plant-available N, as additional microbial pathways, such as denitrification, can substantially modify N availability.

As an alternative to direct measurement of mineralization and immobilization, the contribution of N that originates from mineralization of SOM to plant N can be quantified in agricultural systems by adding fertilizers that were labelled with ^{15}N , the heavy rare stable isotope of the prevalent ^{14}N atom (Scheer and Rütting, 2023). In such experiments, the share of ^{15}N taken up by plants, reflects the amount of N available for plants and the degree to which microbes and plants compete for mineral N. A series of such ^{15}N labelling experiments in temperate grasslands and temperate cropping systems (Buchen-Tschiskale et al., 2023; Khan et al., 2025a) as well as in irrigated sub-tropical cropping systems (Scheer et al., 2025), showed that on average across the studies, only 17–35% of fertilizer N is recovered (taken up) by plants, indicating that microbes effectively immobilize fertilizer N. Meanwhile, 35–50% of the added N is recovered in soil pools, with the remainder lost via leaching or gaseous emissions in the form of nitrate, ammonia, nitric oxide (NO), nitrous oxide (N_2O) and dinitrogen (N_2). Globally, only 47% of the fertilizer is converted into agricultural products (Lassaletta et al., 2014), with the rest contributing to N losses which are associated with substantial environmental impacts ranging from climate warming and health impacts to biodiversity loss (Erisman et al., 2013; Fowler et al., 2013; Liu et al., 2010).

Reducing N losses and improving N use efficiency in agroecosystems requires the development of mitigation strategies and the assessment of their impact on regional to global scales (Butterbach-Bahl et al., 2013). Process-based biogeochemical models provide a key tool for this task: they dynamically simulate the coupled C and N cycles in the plant-soil system, serving as a crucial tool for calculating agricultural yields and environmental N losses. Following successful model application at validation sites, utilization of these model allows upscaling to regional or global scales and projecting yield development under climate change conditions (Haas et al., 2013; Holzworth et al., 2014; Jägermeyr et al., 2021; Parton et al., 2001). Additionally, they can help assess the impact of management practices on yields, investigate the effect of mitigation practices on N losses, and assess the effects of mitigation practices on national or regional scales (Fuchs et al., 2020; Kraus et al., 2016; Smerald et al., 2022). Biogeochemical models represent C and N turnover using process equations, typically based on a pool concept in which a limited number of soil organic matter (SOM) pools with distinct, parameter-controlled turnover rates determine the accessibility of C and N. In croplands, for instance, after fertilization, plants and microbes compete for mineral N. Microbially assimilated N enters SOM cycling and is partitioned into faster- and slower-turnover pools, whereas N taken up directly by plants bypasses SOM turnover and is removed via harvest.

However, there are some indications that biogeochemical models may underestimate the internal turnover of C and N. (1) They show a very limited capacity in simulating background N_2O emissions and a clearly higher capacity in simulating directly fertilizer-driven emissions (Fuchs et al., 2020). (2) There are significant challenges associated with the process of simulating the isotopic composition of N in topsoil (Houlton et al., 2015). (3) High measured gross mineralization rates which represent snapshots of the mineralization rate at a given time, have not been reflected in the outputs of biogeochemical models (Grosz et al., 2021; Melzer, 2021). Despite the great potential of isotope studies for improving biogeochemical models, most biogeochemical models cannot directly make use of the results of ^{15}N tracing studies as they are incapable of simulating isotope processes. This significantly complicates model validation regarding competition of microbes and plants for N and the rapid soil-internal interplay between mineralization and

immobilization. This shortcoming can be remedied by the SIMONE (Stable Isotope Model for Nutrient cycles) framework (Denk et al., 2019) which uses process rates (e.g., mineralization, nitrification, denitrification) and pool sizes (e.g., ammonium and nitrate) provided by a biogeochemical nutrient cycle model to simulate the isotopic composition of N in various soil N pools. Consequently, it provides a framework to simulate ^{15}N tracing experiments that provide information on the fate of ^{15}N -labelled fertilizer, offering a new way to refine parameterizations in models that describe plant-soil N transformations, a largely unexplored territory until now.

In this study, we use the biogeochemical model LandscapeDNDC in conjunction with the SIMONE model to improve the parameterization of the mineralization-immobilization-humification (MIH) cycle based on an in-situ ^{15}N tracing experiment at an arable cropping system. We calibrate the model against the tracer data and evaluate how the improved parameterization affects simulated N fluxes, in particular gaseous N losses.

We hypothesize that (1) internal cycling (mineralization & immobilization rates) of N in the LandscapeDNDC model are underestimated, (2) adjustment of the internal mineralization-immobilization-humification cycle improves the simulation of ^{15}N recovery in plants and soil and (3) that the increase in internal N cycling increases N losses due to leaching, nitrification and denitrification.

2. Material and methods

2.1. Site description

The field experiment was conducted at a cropland site located near the Research Farm Gladbacherhof of the Justus-Liebig University Giessen in Selters, Germany (50°21'28.8"N, 8°15'47.4"E, elevation 310 m a.s.l.), as described in detail by (Khan et al., 2025a, 2025b). The temperate climate of the site is characterized by an average annual temperature of 9.3 °C and an average precipitation of 655 mm (Khan et al., 2025b). The soil is classified according to the World Reference Base as Haplic Luvisol, a fertile soil that is well-suited for agricultural production. Over the past decade, the field has received synthetic N fertilizer and sewage sludge supplies, reflecting a conventionally managed approach with "high external input" (HEI, Table 1). During the pre-experimental years 2012–2020, the field received annual inputs of 410 kg C ha⁻¹ yr⁻¹ and 184 kg N ha⁻¹ yr⁻¹ on average.

2.2. Management practices

The experiment was conducted over the course of three cropping seasons from autumn 2020 to autumn 2022. Green rye was sown in October 2020 at a density of 300 kernels m⁻². Cattle slurry (volume of 25 m³ ha⁻¹; 88 kg N ha⁻¹; 750 kg C ha⁻¹) was applied on April 8th 2021 using a dragging hose. Following the green rye harvest on the May 10th, cattle slurry (20 m³ ha⁻¹; 74.8 kg N ha⁻¹; 600 kg C ha⁻¹) was applied on May 31st 2021 as a pre-sowing application for silage maize and incorporated using a disc harrow followed by a rotary tiller. Silage maize was subsequently sown at a plant density of 9 plants m⁻². Silage maize harvest took place on September 30th, followed by the sowing of rye grass on October 2nd 2021. Rye grass obtained slurry applications on March 29th 2022 (25 m³ ha⁻¹; 85.3 kg N ha⁻¹; 750 kg C ha⁻¹) and on May 25th 2022 (20 m³ ha⁻¹; 65.6 kg N ha⁻¹; 600 kg C ha⁻¹). Rye grass was cut on May 20th, July 5th and September 22nd 2022. Management in the experimental tracing plot followed the field management of the surrounding parcel, with minor variations in slurry volume and N amount due to the ad hoc addition of a label to a slurry of unknown composition.

2.3. ^{15}N tracing experiment and additional measurements

The experiment was conducted by Khan et al. (2025a) and was described in detail in the publication. Recovery of ^{15}N in soil and plants was measured on four 0.30 m by 0.75 m plots that had received ^{15}N

Table 1

Soil process parameters used to calibrate the model to observed ^{15}N soil recoveries. Default parameters (p_{def}) and calibrated parameters (p_{cal}) were used in the N-calibrated model setup and in the ^{15}N calibrated model setup, respectively.

Name	Default p_{def}	^{15}N Calibrated $p_{\text{cal}} = k_{\text{opt}} \times$ p_{def} ($k_{\text{opt}} = 3.5$)	Description
METRX_KR_DC_HUM1	0.0063	0.021	Decomposition constant of labile humus
METRX_KR_DC_HUM2	0.0012	0.0042	Decomposition constant of recalcitrant young humus
METRX_KR_DC_HUM3	0.000025	0.0000875	Decomposition constant of recalcitrant old humus
METRX_KR_HU_AORG_HUM1	0.01	0.035	Rate constant for humification of active organic material to labile humus
METRX_KR_HU_AORG_HUM2	0.01	0.035	Rate constant for humification of active organic material to recalcitrant humus

labelled manure with an enrichment of 10 at%. Flux rates of N_2 were measured in soil-plant mesocosms (diameter 0.16 m, 85 at% enrichment, 4 replicates) using the ^{15}N gas flux method, NH_3 emissions were determined using semi-open chambers (0.16 m diameter, 4 replicates), and NO_3^- leaching was measured using self-integrating accumulators (SIA, TerAquat, Nürtingen, Germany) at 1 m depth (0.1 m diameter, 4 replicates).

Additionally, soil samples were collected in 7–17 cm depth for determining mineral N, as well as gross nitrification and gross mineralization via the ^{15}N isotope pool dilution technique (Dannenmann et al., 2006; Kirkham and Bartholomew, 1954), as described in detail by Khan et al. (2025a). These results were used as independent dataset to validate nitrification and mineralization rates simulated by LandscapeDNDC after calibration with ^{15}N tracing data.

2.4. LandscapeDNDC and the MeTr^x soil model

The LandscapeDNDC model framework includes several sub-models to simulate C, N and water cycling in the plant soil system of arable, grassland and forest ecosystems (Haas et al., 2013; Kraus et al., 2016). All sub-models represent the respective ecosystem domain in a vertical 1-D column, thereby assuming laterally homogeneous conditions. In this study we used the PlaMo^x plant model (Kraus et al., 2016; Liebermann et al., 2020) for simulating the crop growth in hourly timesteps together with the sub-models MeTr^x for C and N soil biogeochemistry (Kraus et al., 2015), CanopyECM for microclimate (Grote et al., 2009), and WatercycleDNDC for the water cycle (Kiese et al., 2011; Li et al., 1992). For this study LandscapeDNDC version 1.35 (revision 12066) was used (<https://ldndc.imk-ifu.kit.edu/>). LandscapeDNDC has been evaluated in several studies for predicting yields, soil C and N dynamics and associated greenhouse gas emissions and nitrate leaching (Denk et al., 2019; Houska et al., 2017; Kraus et al., 2016; Liebermann et al., 2018, 2020; Rahimi et al., 2021).

The MeTr^x bio-geochemistry sub-model represents the processes mineralization, humification, nitrification, denitrification and ammonia (NH_3) volatilization (Kraus et al., 2015). Organic matter from above- and belowground plant residues or root exudates is allocated to soil litter pools, which decompose providing dissolved organic matter and NH_4^+ .

Both can be assimilated by microbes or further transformed by them to NO_2^- , NO_3^- , NO , N_2O or N_2 via nitrification and denitrification. Dissolved substances can be leached and immobilized by plants while gaseous substances can be lost to the atmosphere. Microbial turnover plays a central role in coupling C and N dynamics: upon microbial death, necromass is either rapidly recycled to DOM and NH_4^+ or humified into more stable SOM pools, thereby determining the incorporation of newly added C and N into the SOM continuum. Microbial C and N transformations follow Michaelis–Menten kinetics and respond to soil temperature, moisture, pH, and texture.

Soil organic C and N turnover is described by decomposition and humification processes as well as microbial growth kinetics. The overall mineralization–immobilization–humification (MIH) scheme is illustrated in Fig. 1 and can be organized into four parts.

1. Decomposition of humus, with one fraction entering DON (1a) and the remaining fraction being released as mineral N (1b).
2. Immobilization of NO_3^- , NH_4^+ (2a), and DON (2b) into microbial biomass.
3. Decay of microbial biomass to DON (3a) and mineralization to mineral N (3b).
4. Humification of DON.

Two different types of rate formulations are relevant for the MIH cycle. Decomposition and humification of conceptual soil organic matter pools, representing particulate or mineral-associated fractions, are represented as first-order turnover processes controlled by rate coefficients and environmental response functions (temperature, moisture, pH, texture). The balance between decomposition and humification regulates the redistribution of nitrogen (N) between humus pools, where carbon (C) and nitrogen (N) are not directly available to microbes and plants, and dissolved organic and mineral N pools, where microbes and plants compete for N. In contrast, microbial immobilization and plant N uptake depend on substrate availability and are described using Michaelis–Menten-type kinetics, including maximum uptake rates and substrate affinity coefficients.

To test our hypothesis that fertilizer-derived ^{15}N is more rapidly incorporated into humus pools and taken up by plants at a lower rate, we modified the first-order turnover coefficients for decomposition and humification during calibration. Increasing humus decomposition (process 1a in Fig. 1) releases inaccessible N from humus pools into mineral N pools available to plants and microbes, thereby diluting fertilizer-derived ^{15}N and potentially reducing plant recovery of ^{15}N . In contrast, increasing humification promotes the transfer of DON into stable SOM pools. All other parameters, including the Michaelis–Menten coefficients for microbial growth and plant N uptake, were kept unchanged. This allowed us to isolate the effect of accelerated internal N cycling on ^{15}N recovery in plants and soil, leaching, nitrification, and denitrification.

2.5. SIMONE model

SIMONE is an off-line model that mimics the process structure and numeric calculation sequences of a given model, in this case LandscapeDNDC, to simulate the isotopic composition of N pools, as well as the intramolecular isotopic composition in case of N_2O (Denk et al., 2019). The isotopic composition of the various pools changes due to isotope mixing and isotope fractionation. While isotope fractionation is calculated for the substrate and product of each process that transforms one N-containing chemical species into another, isotope mixing is calculated for the transport of the transformation reaction product into the target pool, as well as for the transport of gases and solutes from one layer to another.

Isotope mixing is calculated using a mass balance equation for atom fractions (Coplen, 2011) and isotope fractionation is calculated in terms of isotope ratios based on the closed-system Rayleigh equation. Rayleigh

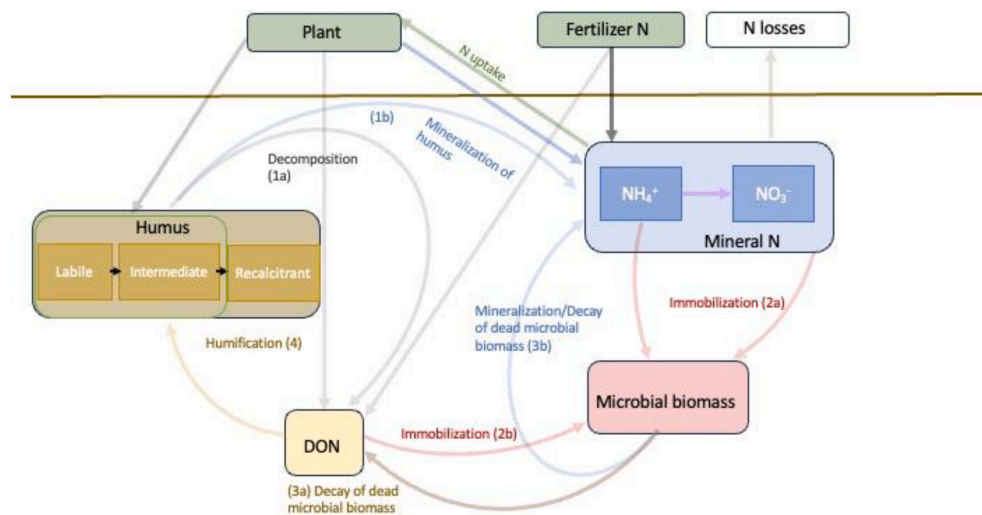


Fig. 1. N cycling as represented in LandscapeDNDC. In organic fertilization, part of the applied nitrogen is also directly attributed to DON or urea, which then gradually converts to NH_4^+ .

distillation calculates the isotopic composition of the substrate based on the initial isotope ratios of the substrate, the fraction of remaining substrate, and the isotope effect (a measure of the isotope fractionation (Denk et al., 2019)). To this end, SIMONE utilizes the simulated N transformation rates, soil N pool sizes, and transport rates of gaseous and dissolved N compounds between soil layers that are provided by the biogeochemical model, but it does not modify these inputs. The standard deviation of fractionation factors used by SIMONE ranges between 1 and 10 per mille (Denk et al., 2017). Sensitivity studies of the effect of isotopic fractionation on pool isotopic composition carried out during the development of the SIMONE model showed that a shift of isotope fractionation factor by 10 per mille leads to a shift of pool isotopic composition of 1 to 6 per mille. For natural abundance studies, this shift is large compared to the pool isotopic composition. However, in the tracing experiment used in this work, ^{15}N enrichment in soil or plant amounted to approx. 379 per mille. Thus, a shift of 1 to 6 per mille in model result translates into a shift of 0.3 to 1.6% recovery. Thus, isotope fractionation is negligible for simulating ^{15}N tracing experiments, but relevant for natural abundance simulations.

For each time step, N species, and soil layer, SIMONE computes the ^{15}N mass in each pool, converts isotope ratios to the δ -notation by using the isotope ratio of the international reference material AIRN₂ ($\delta^{15}\text{N}$), and the site preference for N₂O.

2.6. Simulation setup

To evaluate the benefit of additional ^{15}N data, we compared two model setups: On the one hand the N-calibrated setup, in which plant parameters were adjusted to reflect plant N uptake in the best-possible way, but the MeTr^x soil model was used with its default mineralization-immobilization-humification (MIH) parameterization, and on the other hand a ^{15}N -calibrated setup, in which plant parameters were adjusted to reflect plant N uptake in the best-possible way and MIH MeTr^x parameters were adjusted based on the isotopic information provided by the SIMONE simulations.

2.6.1. N-calibrated setup

Site-specific soil data from Khan et al. (2025a, b) were used to initialize soil properties including bulk density, pH, soil texture (clay, silt, sand), organic C and N content, and soil hydrological parameters (field capacity, wilting point, saturated hydraulic conductivity). The soil profile was discretized into 46 layers with thicknesses of 0.005, 0.008, 0.01, and 0.05 m down to depths of 0.02, 0.1, 0.3 and 0.9 m, respectively.

Daily climate input comprised maximum and minimum air temperature ($^{\circ}\text{C}$), precipitation (mm), relative humidity (%), global radiation (W m^{-2}), and wind speed (m s^{-1}), measured at Gladbacherhof; gaps were filled using data from the nearby DWD station Runkel-Ennerich (8.143 N, 50.3942 E). Nitrogen deposition was set to $14 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ based on German Environmental Agency data (UBA Hintergrundbelastungsdaten Stickstoff, 2013–2015), and atmospheric CO_2 concentration was fixed at 420 ppm (global average 2022).

Agricultural management (sowing, slurry application, harvesting, and cutting) was implemented according to site records for 2012–2020 and according to the experimental management in 2021 and 2022. Before the experiment, 20% of crop residues were assumed to remain on the field, whereas in the ^{15}N tracing plots the above-ground biomass was completely removed in 2021 and 2022.

A stepwise calibration approach was used for calibrating species parameters, whereby parameters were calibrated sequentially for first targeting plant biomass and second N in plant biomass. Only the species parameters necessary were adjusted; all other species parameters were kept at their default values.

Step 1: The first objective was to obtain the correct total dry matter production, i.e. to correctly represent carbon in biomass and biomass allocation. The Michaelis–Menten half-saturation constant controlling root nitrogen uptake (Ω_{KMNU}) and the maximum nitrate and ammonium uptake rates ($\Omega_{\text{UNO}_3/\text{NH}_4}$) were calibrated to achieve the correct overall biomass production. To reproduce the observed biomass yield and carbon partitioning, the fraction of biomass allocated to roots (Ω_{FROOT}) was also calibrated (Table S1).

Step 2: The second objective was to reproduce the nitrogen content of both the total biomass and the harvested yield. This was achieved by calibrating the target nitrogen concentrations of the different plant compartments, i.e. fruit ($\Omega_{\text{NCFRUMIN}/\text{MAX}}$), foliage ($\Omega_{\text{NCFOLMIN}/\text{MAX}}$) and living structural tissue ($\Omega_{\text{NCLSTMIN}/\text{MAX}}$) (Table S1).

For the SIMONE simulations, default isotopic δ values from Denk et al. (2019) were used to initialize plant and soil pools and to parameterize unlabeled slurry. For each crop (green rye, silage maize, ryegrass), a separate SIMONE simulation was conducted with the crop-specific ^{15}N labeling amount. Unlabeled slurry applications were represented using the default parameters of Denk et al. (2019), while labelled slurry applications were assigned the experimentally determined ^{15}N signatures for the respective cropping seasons (Khan et al., 2025a). In addition, the model system was run under natural

abundance (NA) conditions using default parameters, providing NA simulation outcomes required to calculate ^{15}N excess for each pool.

2.6.2. ^{15}N -calibration setup

To adjust internal N cycling in LandscapeDNDC, an acceleration of the internal MIH cycle was implemented by multiplying the decomposition constants of the three humus pools and the two humification constants by a common factor k (0.5 to 3.5 in steps of 0.5). Using a single factor preserves the relative dynamics and weighting of decomposition and humification processes and reduces five free parameters to one, improving identifiability and limiting overfitting. For each value of k , the set of locally adjusted species-specific plant parameters was modified so that simulated plant N uptake remained consistent with observations (Table S1), providing a robust basis for comparing modeled and observed ^{15}N plant uptake. The optimal factor k (k_{opt}) was identified by minimizing the root-mean-square error (RMSE) between observed and SIMONE modeled ^{15}N soil recoveries, with n denoting the number of observations:

$$\text{RMSE}(k) = \sqrt{\frac{1}{n} \sum_{j=1}^n [^{15}\text{N}_{\text{obs},j} - ^{15}\text{N}_{\text{mod},j}(k)]^2} \quad \text{Equation 1}$$

Apart from the factor k and the refined species-specific parameters, all other initial conditions and boundary conditions were identical to those in the N-calibrated setup.

2.7. Post-processing

The excess ^{15}N in each pool was calculated from subtracting the results of the natural abundance simulation run from results of the respective enriched simulation run. Recoveries in the soil were calculated as the amount of excess ^{15}N in all soil pools divided by the total amount of applied ^{15}N for each cropping season (green rye, silage corn, ryegrass).

The ^{15}N recovery refers to the fraction of stable N isotope ^{15}N that can be detected after a certain period in plants, soil, leachates or as gas emissions after it has been added as a tracer. Thus, the recovery of ^{15}N in plant biomass was determined by dividing the excess ^{15}N in the plant (aboveground + belowground) by the total amount of applied ^{15}N for each cropping season. In the case of ryegrass, which was cut three times, the aboveground biomass was considered for the first two cuts, while the total biomass, including the root biomass, was included in the third cut. The yields of all three harvests were added up in accordance with the experimental publication.

The recovery in soil pools was calculated by dividing the ^{15}N excess in the soil pool at harvest by the total amount of applied ^{15}N for each crop. For the gaseous N losses and NO_3 leaching, the ^{15}N recovery was calculated as the respective cumulative ^{15}N loss from labelling to harvest divided by the amount of applied ^{15}N .

3. Results

3.1. Soil meteorological conditions

The model accurately reproduced the temporal dynamics of soil temperature (T_s) and water-filled pore space (WFPS) for both model setups, as demonstrated by the correlation coefficients of 0.93 and 0.71 for T_s and WFPS, respectively (see Fig. S1). The model captured seasonal patterns as well as short-term fluctuations following changes in air temperature and rain events, while minor discrepancies in WFPS occurred during individual events, leading to an overall accuracy of 1.9 °C for T_s and 11% for WFPS in terms of RMSE. Systematic biases were small, as indicated by mean differences in T_s and WFPS of -0.68 °C and -4.25%, respectively.

3.2. Plant biomass dry weight and nitrogen

With a bias below 10%, simulated above-ground biomass for both the N and the ^{15}N calibration showed good agreement with observations

for green rye and silage maize, as well as for the first ryegrass cut (Fig. 2A). However, the second and third ryegrass cuts could not be reproduced: the ^{15}N calibration underestimated the second cut, whereas the N-calibrated model setup underestimated both the second and the third.

For below-ground biomass, the ^{15}N calibration reproduced measured root biomass well for green rye and silage maize (Fig. 2B). Under the N-calibrated setup, ryegrass root biomass was overestimated.

Total N uptake (above- and below-ground) was accurately reproduced for green rye and silage maize, again with a bias below 10% (Fig. 2C and D). In contrast, ryegrass N uptake in the second and third cuts could not be captured satisfactorily, even after adjustment of species-specific parameters.

3.3. Recoveries of ^{15}N in plants and soil

3.3.1. Recoveries under the N-calibrated model setup

The N-calibrated model setup overestimated plant ^{15}N uptake across all crop seasons by 10–21% (Fig. 3A). Simulated plant recoveries were 63% for green rye (observed: 42 ± 7%), 44% for maize (observed: 34 ± 7%), and 58% for ryegrass at final harvest (observed: 39 ± 3%).

Soil ^{15}N recovery was underestimated in two of the three seasons under the N-calibrated model setup by 6 and 13 percentage points (Fig. 3B). However, simulated soil ^{15}N recovery was accurate for the silage maize season, with a deviation of less than 5 percent points. Soil ^{15}N recoveries were 29% for green rye (observed 35% ± 4% SE), 66% for maize (observed 61% (±3 SE) and 21% for ryegrass (observed: 44% ± 2% SE; see Fig. 3b).

With regard to ^{15}N allocation within the soil profile, the simulations agree well with observations, showing a steep decrease in ^{15}N recovery with depth (Fig. 4). Most of the applied ^{15}N was recovered in the top 30 cm of soil in the model, as observed. Measurements revealed small amounts of ^{15}N below 30 cm, with <4% in the green rye, <8% in the silage maize and <2% in the ryegrass seasons. The simulations show that only <2% of applied ^{15}N were found below 30 cm at harvest during each season, indicating that the model slightly underestimated downward transport of fertilizer N to deeper soil layers.

3.3.2. Recoveries under the ^{15}N calibration

The acceleration of the MIH cycle (section 2.4.) improved the agreement between simulations and measurements (Fig. 3c), as ^{15}N plant recovery remained at 64% for green rye, and decreased to 35, and 39% for silage maize and ryegrass. While the ^{15}N plant recoveries for the maize and ryegrass seasons were within the measurement uncertainty, the plant recovery for the green rye season was overestimated to a similar extent as in the N-calibrated model setup. Soil ^{15}N recovery under the ^{15}N calibrated model setup increased to an accurate representation of observed recoveries, i.e. 34% for green rye (observed 35% ± 4% SE), 64% for maize (observed 61% (±3 SE) and 41% for ryegrass (observed: 44% ± 2% SE; see Fig. 3d). Across the soil profile, simulations with the ^{15}N calibrated model setup represented the observed pattern of ^{15}N recovery well, with improved agreement in the top soil horizons and a steep decrease in ^{15}N recovery with depth (Fig. 4).

3.4. Effects of the ^{15}N calibration on N turnover internal mineralization immobilization cycle

Best agreement of measured and modeled ^{15}N recovery in soil was found for a k -factor of 3.5 (k_{opt}), i.e., a 3.5-fold increase (+250%) of decomposition and humification parameters (Table 1).

Consequently, the ^{15}N calibration increased the dominant fluxes in the MIH cycle by approximately a factor of two (Table 2, Fig. 5). The decomposition of humus to DON (1a) as well as the mineralization of humus to soil mineral N (1b) increased by 113% due to the ^{15}N calibration. The microbial assimilation of mineral N (2a) increased by 83%,

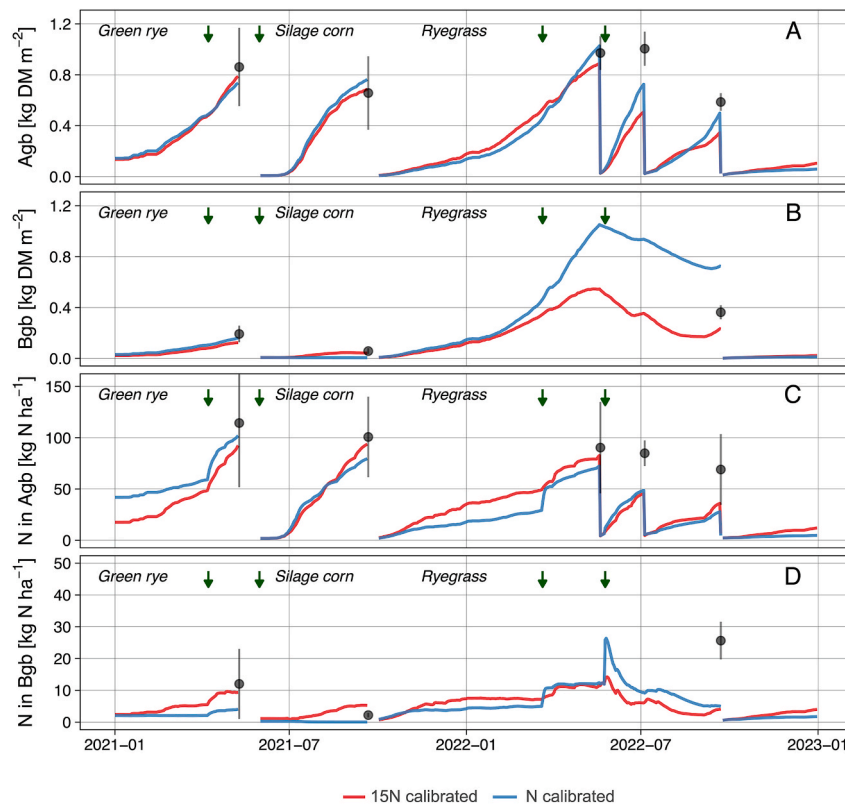


Fig. 2. Time series of dry aboveground biomass (agb expressed as dry matter (DM), A) and belowground biomass (bgb, B) dynamics and net nitrogen uptake in agb (C) and bgb (D) under the N-calibrated and ^{15}N -calibrated parameter sets. Observations are shown as black symbols; error bars indicate the 95% confidence interval, calculated as $\text{mean} \pm t \times \text{SE}$, with $t = 3.182$ for $n = 4$ replicates.

mainly due to increased assimilation of NO_3^- . The microbial assimilation of dissolved N (2b) increased by 133%. Simultaneously, mineralization from the microbial pools (3a) increased by 91%. Accordingly, the decay of microbial biomass N transferred to the DON pool increased (3b; +83%), leading to an increase in the humification of dissolved organic N (4, +84%).

3.5. Dynamics of mineralization rates, nitrification rates and mineral N concentrations and development of soil C and N pools

Measured mineralization rates showed a pattern of low values during the green rye season and elevated values in the maize season, which was well represented by the model (Fig. 6A, Table S2). Nevertheless, gross mineralization rates were underestimated by the model under the N-calibrated setup, ranging from 0.2 to 2.9 $\text{kgN}^{-1} \text{ha}^{-1} \text{d}^{-1}$ during 2021 (Measured: 0.19–3.35 $\text{kgN}^{-1} \text{ha}^{-1} \text{d}^{-1}$; 0.07–0.17 m; Fig. 6A), with the largest underestimation from July to October. Under the ^{15}N calibrated setup, gross mineralization increased to 0.6–4.0 $\text{kgN}^{-1} \text{ha}^{-1} \text{d}^{-1}$, with a similar pattern and a slightly less pronounced underestimation in July to October. Median gross mineralization rates increased from 0.3 $\text{kgN}^{-1} \text{ha}^{-1} \text{d}^{-1}$ (Obs: 1.4 $\text{kgN}^{-1} \text{ha}^{-1} \text{d}^{-1}$) to 0.6 $\text{kgN}^{-1} \text{ha}^{-1} \text{d}^{-1}$ by the ^{15}N calibration.

The dynamics of gross nitrification were well captured by both the N-calibrated and the ^{15}N calibrated model setup, closely matching the observed temporal patterns, except for a very high measurement in July (Fig. 6B). Calibration led to an increase in mean simulated soil gross nitrification from 0.3 to 0.7 $\text{kgN}^{-1} \text{ha}^{-1} \text{d}^{-1}$, remaining lower than mean measured values (2.6 $\text{kgN}^{-1} \text{ha}^{-1} \text{d}^{-1}$; Fig. 6B), but plausible regarding the large spatial variability across samples indicated by the error bars.

Nitrate concentrations were slightly underestimated by the model under the default setup, ranging from 0 to 1.86 $\text{kgN}^{-1} \text{ha}^{-1}$ during 2021 (Observed: 0.40–4.52 $\text{kgN}^{-1} \text{ha}^{-1}$; 0.07–0.17 m; Fig. 6C–Table S3). Under

the ^{15}N calibrated setup, simulated nitrate concentrations increased to 4.24 $\text{kgN}^{-1} \text{ha}^{-1}$, consistent with the range of measured concentrations. Median NO_3^- concentrations increased from 0.002 to 0.29 $\text{kgN}^{-1} \text{ha}^{-1}$, remaining lower than observations (Obs: 0.80 $\text{kgN}^{-1} \text{ha}^{-1}$).

Similarly, simulated NH_4^+ concentrations under the N-calibrated model setup were below 2.1 $\text{kgN}^{-1} \text{ha}^{-1}$, regarding very low measured NH_4^+ concentrations of 0.21 to 1.9 $\text{kgN}^{-1} \text{ha}^{-1}$ (Fig. 6D). Nevertheless, similar to NO_3^- concentrations, median NH_4^+ concentrations increased under the ^{15}N -calibrated setup from 0.006 to 0.075 $\text{kgN}^{-1} \text{ha}^{-1}$ (Obs: 0.49 $\text{kgN}^{-1} \text{ha}^{-1}$).

Cumulative mineralization rates were 408 and 244 $\text{kgN}^{-1} \text{ha}^{-1} \text{yr}^{-1}$ for the years 2021 and 2022, respectively, under the N-calibrated setup. They increased to 675 and 528 $\text{kgN}^{-1} \text{ha}^{-1} \text{yr}^{-1}$ for the years 2021 and 2022 in the ^{15}N calibrated setup (Fig. 7A). Similarly, cumulative immobilization rates increased from 399 to 209 $\text{kgN}^{-1} \text{ha}^{-1} \text{yr}^{-1}$ for the N-calibrated setup for 2021 and 2022 to 660 and 470 $\text{kgN}^{-1} \text{ha}^{-1} \text{yr}^{-1}$ for the ^{15}N calibrated setup (Fig. 7B).

As a consequence of the ^{15}N calibration, the positive soil N stock changes in the N-calibrated model setup (gain of 32 $\text{kg N ha}^{-1} \text{yr}^{-1}$ over the full simulation period) turned into soil N stock losses of 12 $\text{kgN}^{-1} \text{ha}^{-1} \text{yr}^{-1}$ (Fig. 7C). Consistently, soil C stocks shifted from a small increase of 0.36 $\text{t C ha}^{-1} \text{yr}^{-1}$ to a small loss of 0.45 $\text{t C ha}^{-1} \text{yr}^{-1}$ over the same period.

3.6. Total N losses in different loss pathways

Measured N_2 emissions for green rye, silage maize, and ryegrass were low to moderate, with cumulative losses of 0.37, 1.7, and 3.37 kg N ha^{-1} for green rye, silage maize, and ryegrass, respectively. For the N-calibrated model setup, N_2 losses were generally underestimated in all seasons (Table 3). The simulations reflected the pattern of higher emissions in the silage maize season compared to the green rye season

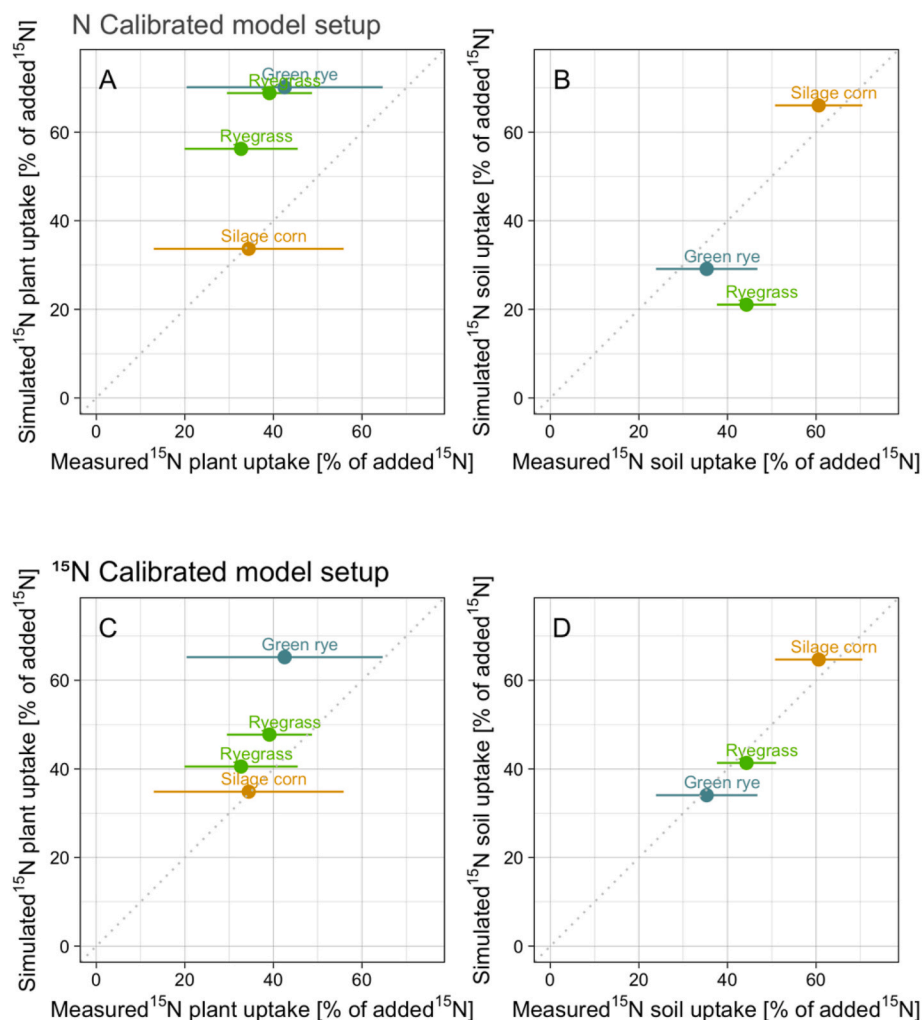


Fig. 3. Comparison of measured (x-axis) with simulated (y-axis) ^{15}N recoveries in plants (left panels) and soil (right panels). Green rye, silage corn and ryegrass are shown in blue, light green and brown, respectively. Ryegrass was fertilized twice, and plant recoveries were given as cumulative values for both events, whilst soil was only excavated once after final harvest. 95% confidence intervals are given, calculated as $\text{mean} \pm t \times \text{SE}$, with $t = 3.182$ for $n = 4$ replicates. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

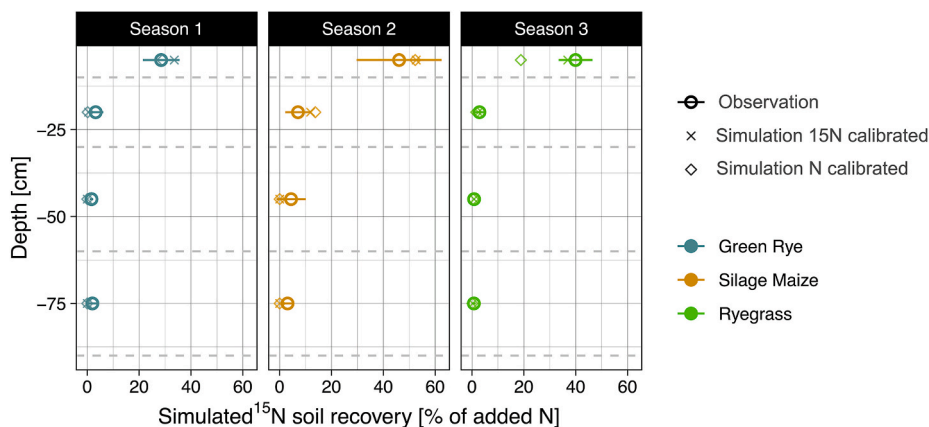


Fig. 4. Measured and simulated soil ^{15}N after harvest in the different soil depths. Error bars represent the 95% confidence intervals of the observations ($\text{mean} \pm t \times \text{SE}$, with $t = 3.182$ since $n = 4$).

but did not reproduce the even higher N_2 losses during the ryegrass season. The ^{15}N calibration increased denitrification by 350–850% per season, thereby reducing the underestimation of N_2 losses, but remaining below the measurements (by factor 5–10).

Measured N_2O emissions were low for green rye and ryegrass and moderate for corn with cumulative emissions amounting to 0.09, 1.36 and 0.11 kg N ha^{-1} , for green rye, corn and ryegrass, respectively. For the N-calibrated model setup, simulated N_2O emissions were 0.08, 0.18

Table 2

Cumulative annual N fluxes of the internal mineralization-immobilization (MI) cycle for N and ^{15}N calibrations, respectively. Process ID refers to the arrows in Figs. 1 and 5.

Process ID	Flux	Process	N calibrated setup [kg N ha ⁻¹ yr ⁻¹]	^{15}N calibrated setup [kg N ha ⁻¹ yr ⁻¹]
1a	Humus → DON	Decomposition	73	155
1b	Humus → Mineral N	Mineralization	73	155
2a	Mineral N → Active microbes	Microbial N assimilation	275	504
2b	DON → Active microbes	Microbial N assimilation	28	61
3a	Dead microbes → DON	Decay of microbial biomass	81	155
3b	Dead and active microbes → Mineral N	Mineralization	226	413
4	DON → Labile Humus	Humification	154	283

and 0.04 kg N ha⁻¹ for green rye, corn and rye grass, respectively. Thus, the model accurately represented the pattern of highest losses during the maize season, showing good agreement for green rye and rye grass, but underestimating losses for silage maize. The N₂O losses increased by 100–350% after the ^{15}N calibration, resulting in an overestimation (at a low level) during the green rye and rye grass season and persisting underestimation in the maize season (Table 3).

Ammonia volatilization was low (2.2 kg N ha⁻¹) in the green rye season, negligible after the maize fertilization and large for the ryegrass season (12.4 kg N ha⁻¹), when the slurry was surface applied. The model was able to accurately simulate NH₃ emissions during all seasons (Table 3), with a slight underestimation during the green rye season. Ammonia volatilization was essentially unaffected by the ^{15}N calibration.

Leaching losses amounted to 2.3, 0, and 7.1 kg N ha⁻¹ for the green rye, silage maize, and ryegrass seasons, respectively. Under the N-calibrated model setup, leaching was simulated close to zero for all three seasons, reproducing the absence of leaching in the maize season but underestimating losses in green rye and especially ryegrass. Under the ^{15}N -calibrated setup, simulated leaching increased to 4.4 kg N ha⁻¹ in the green rye season, thereby overestimating observations, while remaining low (<0.5 kg N ha⁻¹) in the maize and ryegrass seasons.

3.7. Fertilizer-derived ^{15}N losses and ^{15}N fertilizer budgets

The analysis of the fate of the labelled slurry, hereafter referred to as the ^{15}N fertilizer budget, quantifies the relative contributions of the individual N fluxes to the total ^{15}N recovery. While the simulated ^{15}N fertilizer budget is always closed, the observed budgets are typically not closed, exhibiting an unrecovered fraction of ^{15}N .

NH₃ emissions occurred immediately after slurry application, as a direct physicochemical loss of fertilizer N without involvement of intermediate assimilative biotic soil processes. Accordingly, the simulated fraction of fertilizer N lost as NH₃ was very similar across all model setups. The observed fraction of fertilizer ^{15}N emitted as NH₃ was well reproduced in the maize and ryegrass seasons, and similarly underestimated in the green rye season, consistent with the absolute fluxes (Fig. 8, Table 3).

N₂ emissions derived from the ^{15}N -labelled fertilizer were consistently underestimated across all three seasons. While the observations indicate that 0.3–2.1% of the applied ^{15}N was emitted as N₂, the model simulated less than 0.1% in all seasons. This demonstrates a strong underestimation of directly fertilizer-derived N₂ emissions, suggesting that denitrification to N₂ from recently applied fertilizer N is insufficiently represented in the model.

During the green rye and ryegrass seasons, the simulated ^{15}N -N₂O losses under both model setups were in good agreement with observations (Fig. 8), as it was the case for total N₂O losses (Table 3). However, ^{15}N -N₂O losses, were overestimated during the maize season under both model setups (Fig. 8), even though the total N₂O flux in the maize season was underestimated (Table 3). Thus, the modeled amount of N₂O derived (directly) from fertilizer, was too high, while the contribution of non-fertilizer N sources to N₂O production was too low during this period.

^{15}N -NO₃ was not measured during the experiment. The model predicted no NO₃ leaching from labelled fertilizer N.

4. Discussion

Competition between plants and soil microbes for N exerts a significant influence on the partitioning of newly available N between plant uptake and soil retention (Hodge et al., 2000). In the field experiment that formed the basis of this study (Khan et al. 2025a, 2025b), plant N recovery across cropping seasons ranged from 34 to 42%, while soil N recovery accounted for 35–61% of the total fertilizer applied. These

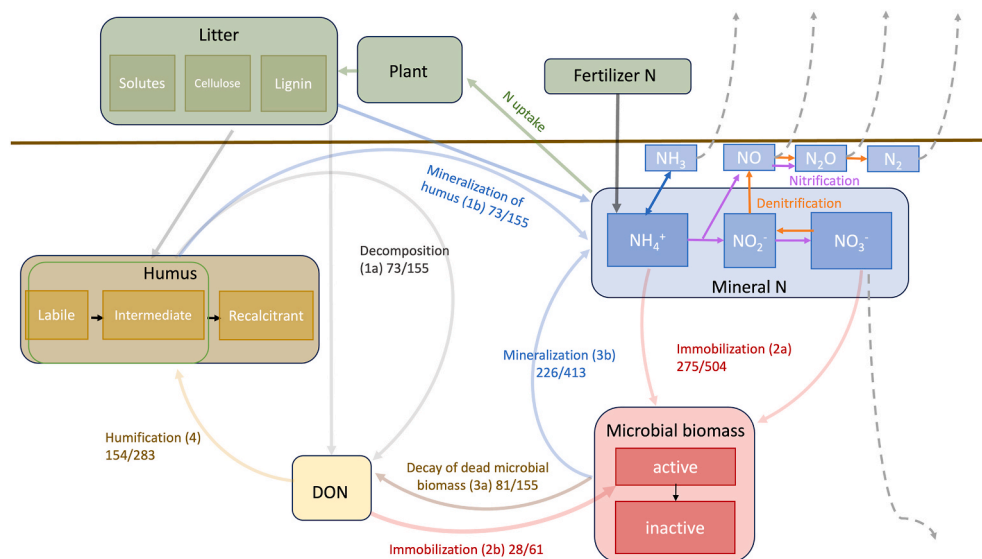


Fig. 5. Comparison of N fluxes before and after ^{15}N calibration. The numbers next to each arrow indicate the annual amount of N [kg N ha⁻¹ yr⁻¹] transferred from one pool to another averaged across both experimental years under the N-calibrated and ^{15}N calibrated model setup, respectively.

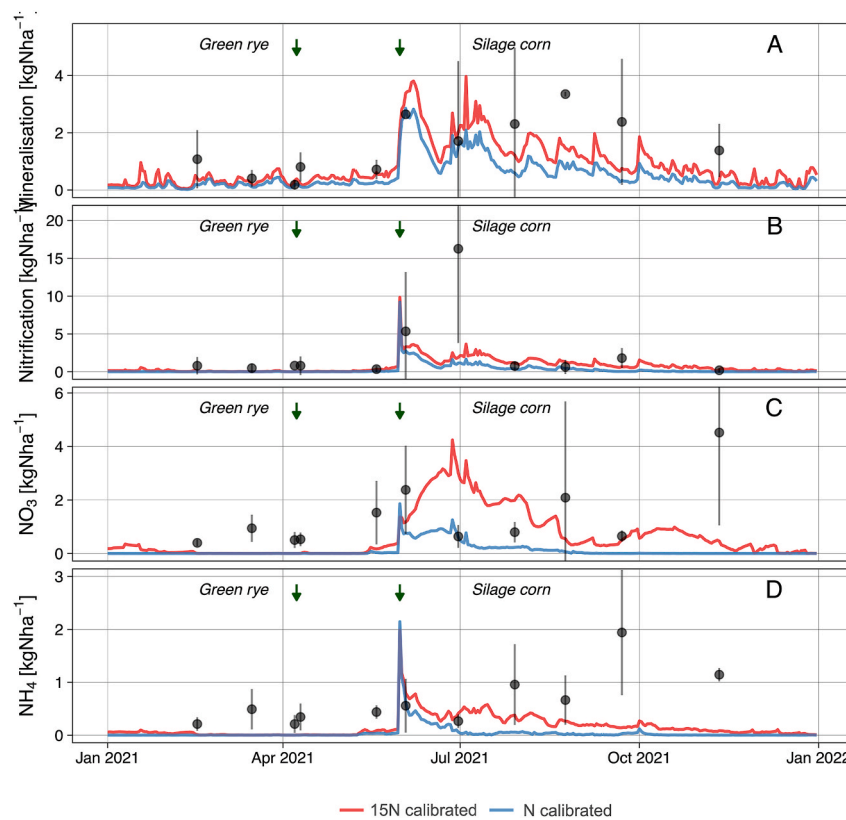


Fig. 6. Time series of daily mineralization (A) and nitrification (B) rates, and amount of nitrate (NO₃⁻; C) and ammonium (NH₄⁺; D) measured at 0.07–0.17 m soil depth (black symbols) and simulated (coloured lines) under the N-calibrated and ¹⁵N-calibrated model setups. Error bars indicate the 95% confidence interval, calculated as mean ± t × SE, with t = 3.182 for n = 4 replicates.

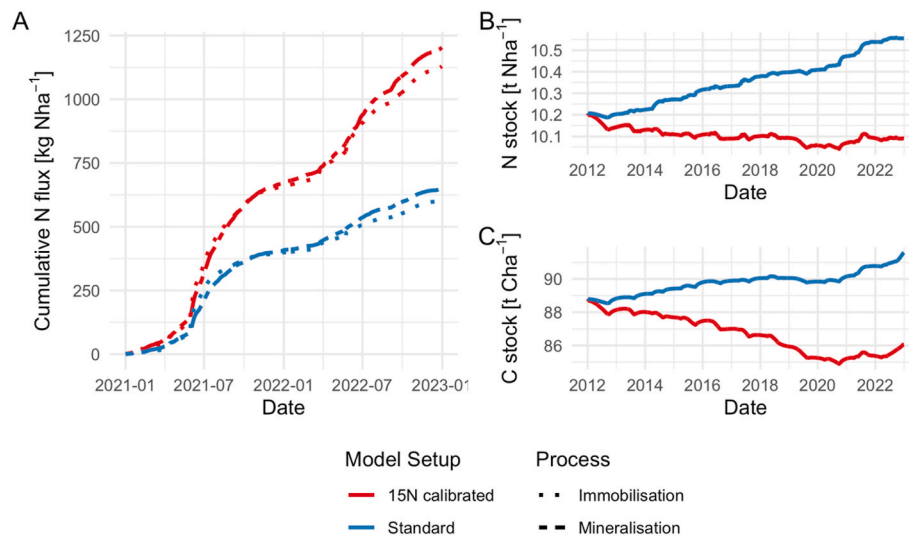


Fig. 7. Simulated cumulative mineralization and immobilization rates integrated over the entire soil profile (0–0.9 m) during the experiment (A), and the development of carbon (C) and nitrogen (N) stocks for both model setups over the full simulation period (B, C).

findings indicate a central role of microbial immobilization for the transfer of fertilizer N to SOM and for regulating plant N availability. A dominance of N originating from SOM mineralization in plant uptake has been widely observed across temperate and tropical systems. Studies report that only 18–42% of plant N is fertilizer-derived, with the remainder originating from soil N pools, even under high fertilizer inputs (Belyaeva et al., 2024; Dourado-Neto et al., 2010; Takeda et al., 2022). Simultaneously, the majority is initially retained in the soil

(Gardner and Drinkwater, 2009; Khan et al., 2025a). Therefore, it is important that biogeochemical models reflect this consistent, empirical pattern. However, total plant N uptake alone cannot distinguish between correct and incorrect N acquisition pathways. While models can match bulk plant N, they can severely misrepresent the partitioning of fertilizer versus soil-derived N. This is where ¹⁵N data becomes essential, as it reveals and corrects the underlying mechanisms of N partitioning, even when bulk plant N appears to be well simulated.

Table 3

Total N losses in form of N_2 , N_2O , NH_3 and NO_3 in $[kg\ N\ ha^{-1}]$ from measurements, the N-calibrated and the ^{15}N calibration setup. Simulation results were aggregated over the measurement period, which was four weeks after each fertilization event for N_2 , the main growing season for N_2O , one week after fertilization for NH_3 , and from planting date to harvest for NO_3 .

Pathway	Crop	Measured ($\pm$ SE)	N calibrated	^{15}N calibrated
N_2 [$kg\ N\ ha^{-1}$]	Green rye	0.37 ($\pm$ 0.07)	0.02	0.09
	Maize	1.70 ($\pm$ 0.11)	0.06	0.57
	Ryegrass	3.37 ($\pm$ 1.80)	0.01	0.05
N_2O	Green rye	0.09 ($\pm$ 0.01)	0.08	0.16
	Maize	1.36 ($\pm$ 0.01)	0.18	0.55
	Ryegrass	0.11 ($\pm$ 0.01)	0.04	0.18
NH_3	Green rye	2.20 ($\pm$ 0.13)	0.49	0.44
	Maize	0.16 ($\pm$ 0.03)	0.00	0.00
	Ryegrass	12.74 ($\pm$ 1.31)	11.88	12.69
NO_3	Green rye	2.30 ($\pm$ 0.01)	0.05	4.39
	Maize	0.00 ($\pm$ 0.01)	0.00	0.44
	Ryegrass	7.10 ($\pm$ 1.53)	0.00	0.11

LandscapeDNDC demonstrates this problem: despite simulating total plant N reasonably well under its N calibrated setup, the model substantially overestimated direct fertilizer N uptake by crops (Fig. 3). A similar result was reported in a temperate deciduous forest by Thum (Thum et al., 2025) who applied the terrestrial ecosystem model QUINCY (QUantifying Interactions between Terrestrial Nutrient CYcles and the climate system (Thum et al., 2019); with its explicit representation of terrestrial ^{15}N fluxes and pools to evaluate N dynamics using data from a long-term (10-year) ^{15}N tracer experiment. Like in our study, discrepancies emerged over shorter timescales: the model simulated uptake and losses of ^{15}N into leaves and fine roots more rapidly than observed, while recovery in litter and surface soils lagged the observations. These findings suggest that also QUINCY overestimates plant competitiveness for newly available N relative to soil microbial processes. In comparison to QUINCY, LandscapeDNDC places a stronger emphasis on the explicit and mechanistic representation of soil N transformations. While both models include key processes such as mineralization, immobilization, nitrification and denitrification these are represented in a more aggregated form in QUINCY, whereas LandscapeDNDC resolves microbial-mediated pathways, intermediate pools, and environmental controls in greater detail. Thus, the consistency of findings between QUINCY and LandscapeDNDC, despite fundamental differences in process representation and model complexity, indicates that the underlying biases in N fate, particularly the overestimation of plant uptake relative to soil retention-are robust across models. Additionally, overestimation of

fertilizer recovery in plants and underestimation of fertilizer recovery in soils is consistent with findings from a study using the biogeochemical model APSIM, which underestimated immobilization, legacy N contributions, and fertilizer N losses under its N-calibrated parameterization when apparent fertilizer recovery was calculated (Takeda et al., 2025). Thus, this body of literature indicates that underestimation of soil mineralization-immobilization-humification (MIH) cycling is a systematic issue across biogeochemical models and agroecosystems.

4.1. Using ^{15}N recovery in plants and soil for improving soil mineralization-immobilization N cycling

Assuming that the internal MIH-cycling has been underestimated, it is logical to calibrate the mineralization and immobilization rates directly. The most frequently used method for the determination of mineralization and immobilization rates is the isotope pool dilution method and its further developments (IPD; (Hart et al., 1994; Kirkham and Bartholomew, 1954). In this method, labelled mineral N ($^{15}N-NH_4^+$ or $^{15}N-NO_3^-$) is added to soil samples, and mineralization and nitrification are determined from the dilution of labelled mineral N with unlabeled NH_4^+ or NO_3^- originating from mineralization of SOM or nitrification of unlabeled NH_4^+ , respectively. The addition of labelled mineral N significantly complicates the IPD method, as mineralization and nitrification rates are usually determined in disturbed soil samples and in absence of living plants. Since the availability of substrate for mineralization and nitrification may increase due to mechanical destruction of aggregates and roots, and the lack of plants taking up NH_4^+ , the IPD method may give only limited information on actual in-situ N transformation rates (Rütting et al., 2011). In addition, the determination of microbial immobilization of NH_4^+ and NO_3^- suffers from substrate stimulation, as immobilization rates are determined using label consumption. These aspects suggest that direct comparison of measured mineralization and immobilization rates with model outputs and their direct use for calibration may be misleading. Furthermore, the large spatial heterogeneity in soils leads to high variability across samples, which is reflected in the large error bars (Fig. 6). Together with the low number of feasible samples (here $n = 4$) and the relatively limited measurement frequency due to workload constraints, these factors highlight the limitations in drawing precise conclusions from the dataset and in making direct model-data comparisons. In this context, ^{15}N recoveries provide a more robust alternative for constraining mineralization-immobilization turnover, as they integrate N partitioning over time for both plant uptake and soil retention. Consequently, ^{15}N recovery in plants and soil was used as calibration target in this study, while measured gross N transformation rates from IPD were used for model validation only.

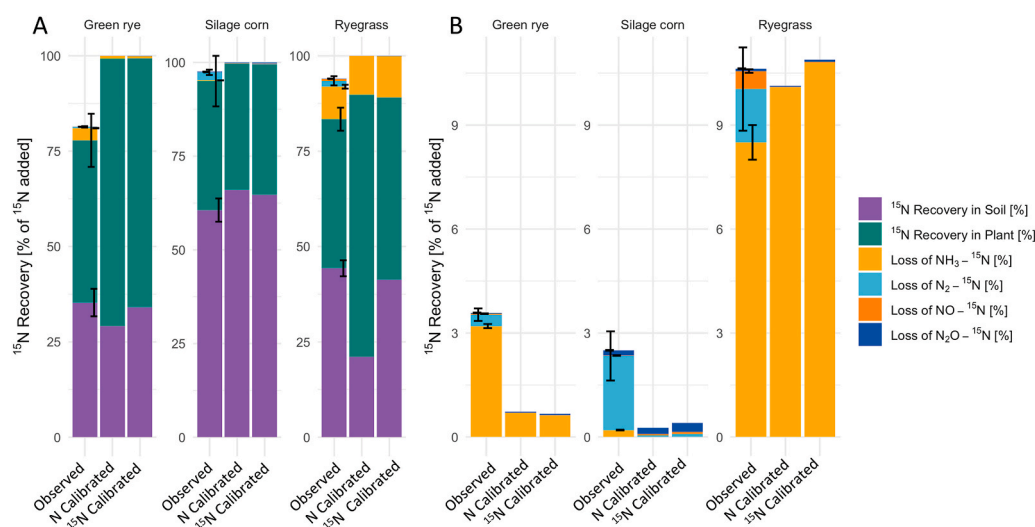


Fig. 8. Observed ^{15}N fertilizer budget based on ^{15}N recovery compared with simulations from the N calibrated and ^{15}N -calibrated setups. (A) Percentage of applied fertilizer N recovered in different pools at harvest. (B) Zoomed view of gaseous N losses. Bars represent means and error bars indicate standard errors.

Though the measured rates of mineralization and nitrification may not directly reflect actual N turnover rates in the soil, seasonal dynamics and order of magnitude of measured rates provide orientation for modeled N turnover. LandscapeDNDC generally captured the observed seasonal pattern of N mineralization, with low rates during the green rye season and higher rates during the maize season (Fig. 6A), measured mineralization rates being consistent with values reported for agricultural soils (Booth et al., 2005; Cookson et al., 2005; Elrys et al., 2021; Khan et al., 2025b). However, the N-calibrated setup consistently underestimated mineralization, particularly between July and October. Calibration using ^{15}N data increased simulated gross mineralization, but systematic underestimation remained during August to September. As indicated above, the discrepancy between measured and modeled nitrification may be due to systematic underestimation by the model or systematic overestimation by the measurement method. One fundamental assumption in the derivation of the IPD method (Kirkham and Bartholomew, 1954) is that immobilized ^{15}N is not remobilized during the incubation (referred to as reflux). Violation of this assumption however results in underestimation of gross N mineralization and a preceding study confirmed that tracer reflux is negligible for incubation times up to 48 h (Braun et al., 2018). Also, overestimation due to substrate stimulation is unlikely, as in the isotope pool dilution technique, the process product (NH_4^+ for mineralization and NO_3^- for nitrification) instead of the substrate is added in labelled form in case of mineralization and nitrification. Nevertheless, increased mineralization under the calibrated setup led to higher simulated NH_4^+ and NO_3^- concentrations which agreed better with observations (Fig. 6C and D), reflecting the coupling between mineralization and soil inorganic N pools. Overall, the results suggest that accurate representation of mineralization dynamics is critical for reproducing soil inorganic N pools, and that ^{15}N calibration can substantially improve model performance, even if deviations between measurement and model results persist during periods of high N turnover. However, it is noteworthy that measured and simulated nitrification generally agreed across all seasons (Fig. 6B), while measurements showed substantial NO_3^- immobilization without a corresponding increase in autotrophic nitrification (Khan et al., 2025b). This suggests an important contribution from heterotrophic nitrification stimulated by organic N inputs from slurry. Heterotrophic nitrification is not explicitly represented in the model, which may contribute to the underestimation of internal soil N cycling and the rapid transfer of ^{15}N into SOM. Additionally, overall underestimation of nitrification may entail underestimation of total denitrification, particularly N_2 production. Consistent with this interpretation, the underestimated recovery of ^{15}N in N_2 losses indicates that fertilizer-derived N_2 emissions are insufficiently represented by the model.

Beyond N cycling, we evaluated whether ^{15}N calibration affected carbon cycling. The calibration procedure shifted the simulated site from slight net soil carbon sequestration to slight soil carbon loss. To assess whether this change reflected realistic CO_2 respiration dynamics, we evaluated ecosystem respiration predictions during the maize season, the only period with available measurements (supplementary material, Fig. S2). The dark chambers were placed between the maize rows and, thus, may underestimate ecosystem respiration as the chamber frame restrains growth of plant roots into the chamber area to some extent. Simulated seasonal soil CO_2 was underestimated by 16% and 7%, respectively, but remained within observational uncertainty both before and after ^{15}N calibration (N calibrated: $18.9 \text{ kg C ha}^{-1} \text{ d}^{-1}$; ^{15}N calibrated: $20.8 \text{ kg C ha}^{-1} \text{ d}^{-1}$; observations: $22.5 \pm 3.5 \text{ kg C ha}^{-1} \text{ d}^{-1}$ SD). Thus, ^{15}N Calibration improved agreement with observed mean values. Despite limited CO_2 data availability, this consistency between measured respiration and modeled C cycling demonstrates that ^{15}N -based calibration does not introduce unrealistic changes to carbon cycle representation.

4.2. Total N losses and recovery of ^{15}N in different loss pathways

Because ^{15}N tracer data are rarely available, most modelling studies do not yet explicitly constrain the allocation of N to plant and soil pools (Scheer and Rütting, 2023; Thum et al., 2025). However, the

partitioning of N between plant uptake and microbial immobilization strongly controls subsequent gaseous and leaching losses. Thus, the lack of constraints on the fate of fertilizer N in biogeochemical affects the simulation of gaseous and leaching losses and reduces the reliability of modeled management effects on these fluxes.

Since N fluxes are intrinsically interrelated and compete with one another, particularly plant N uptake and microbial processes leading to gaseous losses (N_2O , N_2), the calibration of one pathway inevitably affects the others. However, comprehensive measurements of all relevant N fluxes are rarely available, hindering a complete calibration and thus leading to substantial uncertainty in model parameterization and validation models (e.g., Del Grosso et al., 2020; Grosz et al., 2023; Scheer et al., 2025). N_2 emissions in particular are often not quantified. Overall, discrepancies between measured and simulated ^{15}N losses in our study were dominated by uncertainties in denitrification, rather than volatilization or leaching. Across all seasons, the model underestimated measured ^{15}N losses under both the N-calibrated and ^{15}N -calibrated model setup (Table 3, Fig. 8). NH_3 volatilization was simulated accurately and was largely unaffected by calibration. In contrast, N_2 and N_2O losses were consistently underestimated, although they increased under the ^{15}N -calibrated setup due to enhanced SOM mineralization and the resulting increase in substrate supply for nitrification and denitrification. Despite a substantial increase in simulated denitrification rates (by approximately a factor of 15), modeled N_2 and N_2O fluxes remained well below observed values, indicating structural limitations in the representation of denitrification and the need for targeted calibration.

This systematic underestimation of N_2 losses is consistent with previous studies showing that several biogeochemical models, including LandscapeDNDC, underestimate denitrification-derived N_2 emissions (Scheer et al., 2025). Empirical estimates suggest that, on average, $9.7 \pm 1.1\%$ of applied fertilizer N is lost via denitrification in upland soils, with approximately 86% emitted as N_2 (Scheer et al., 2025), and even higher fractions (up to 28% of applied fertilizer N) reported in global assessments (Scheer et al., 2020). A multi-site, multi-objective calibration of LandscapeDNDC explicitly targeting N_2 and N_2O fluxes is currently in progress (Fuchs et al., in prep), which is expected to address these limitations.

Part of the apparent mismatch between modeled and observed ^{15}N losses likely reflects measurement constraints rather than true N mass imbalance. In the experiment, N_2 emissions were measured only during the four weeks following fertilization and only at the soil surface. Such measurements are known to underestimate total denitrification, as substantial N_2 production can occur below the measurement depth, with subsoil denitrification contributing up to $60\text{--}70 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (van Cleemput, 1998; Well et al., 2019). Consequently, a significant fraction of the unrecovered ^{15}N likely represents cumulative denitrification losses beyond the observation period. This suggests that unrecovered ^{15}N , combined with measured N_2 emissions, provides a more appropriate calibration target for denitrification than short-term surface flux measurements alone.

Leaching losses played a minor role in the overall ^{15}N balance. The model predicted negligible leaching under the N-calibrated setup, while the ^{15}N -calibrated setup overestimated NO_3^- leaching in the green rye season and still underestimated it in ryegrass. Simulated leaching predominantly originated from unlabeled soil N pools, including residual N from previous fertilization and mineralized SOM, indicating limited contribution of fertilizer-derived ^{15}N to leaching losses.

In most ^{15}N tracer studies, recoveries are quantified in soil and plant pools, while the remaining fraction is classified as unrecovered, encompassing gaseous losses, leaching, and measurement uncertainty (Gardner and Drinkwater, 2009; Han et al., 2025; Schlingmann et al., 2020; Templer et al., 2012). This unrecovered fraction typically ranges from 30 to 60% in short-to mid-term studies. In contrast, the dataset used in our study (Khan et al., 2025a, 2025b) explicitly includes gaseous ^{15}N losses in addition to soil and plant pools, resulting in unrecovered fractions below 20% across all seasons. During the green rye season, plant ^{15}N uptake was simulated less accurately than in the N-calibrated runs and coincided with a relatively high unrecovered fraction (18.6%). This value exceeds the combined uncertainty of measured recoveries (7.8%; Fig. 8, Khan et al.,

2025a), suggesting either systematic measurement bias or the presence of an unaccounted N sink. In contrast, near-complete recovery was achieved in the maize and ryegrass seasons (2.5% and 5.9%, respectively), both within the joint uncertainty bounds of all measurements, indicating robust ^{15}N fertilizer balances.

4.3. Potentials and limitations of the ^{15}N tracer validation approach

The use of ^{15}N tracer data for model validation provides process-level insight into the allocation of fertilizer N across soil, plant, and loss pathways, thereby complementing conventional approaches based on bulk N fluxes and stocks. By combining measurements of ^{15}N in soil and plants with quantified gaseous losses, our study demonstrates how such datasets can effectively constrain model parameterization and improve the representation of N turnover processes in biogeochemical models.

Extending this approach to multi-site applications could support the development of generalized parameter sets that remain robust across environmental conditions. Multi-objective calibration frameworks that jointly consider yields, N uptake, and loss pathways (e.g. (Fuchs et al., 2024; Houska et al., 2017)), could, in principle, be expanded to include ^{15}N recoveries. However, the integration of isotope-enabled process representations remains computationally demanding, currently limiting routine application. Approaches that reduce this complexity would substantially enhance the applicability of ^{15}N datasets for model development.

Despite these advantages, the approach depends strongly on data quality and completeness. High-quality datasets with low unrecovered fractions remain scarce, as many cropland ^{15}N tracer studies report substantial unrecovered shares and lack measurements of key loss pathways, particularly gaseous emissions and leaching. Our results rely largely on plant ^{15}N at harvest, which represents an integrated, season-long measurement with substantially higher representativeness than direct N turnover measurements (mineralization, immobilization). This characteristic makes it a robust calibration target even with a limited number of observations. Though our data set is one of the few comprising three consecutive tracing experiments for three crop types during two years, this is not comprehensive enough to satisfy both the requirement of considering different climatic conditions and crop types for the calibration and a data set for independent validation of the approach. A practical strategy for improving the validation capability of this approach is the determination of ^{15}N in plant and soil at an additional point in time during the growing season. Moreover, the strongest effect of the ^{15}N calibration occurs during the ryegrass season, which is also associated with the highest level of uncertainty. Please note that this study has a strong explorative character identifying the potential and limitations of the presented approach and that these findings should be considered indicative rather than conclusive, as further validation across multiple sites is necessary.

Nevertheless, ^{15}N tracer experiments provide unique opportunities to evaluate processes that are otherwise difficult to observe. These include the fate and multi-year recovery of organic amendments such as slurry (Frick et al., 2023), short-term microbial immobilization and subsequent stabilization in organic N pools (Jensen et al., 2000; Sørensen, 2004), and the contribution of residual fertilizer N within crop sequences (Dourado-Neto et al., 2010; Smith and Chalk, 2018). In addition, ^{15}N -labelled residues enable the assessment of decomposition dynamics and pre-crop effects across climatic conditions, including their influence on N_2O emissions (Dourado-Neto et al., 2010; Laberge et al., 2006; Williams and Haynes, 1997). Measurements of ^{15}N in leachate and across soil profiles further improve the representation of vertical N transport and retention. Together, these applications demonstrate the value of ^{15}N -based validation for advancing process understanding and reducing structural uncertainty in biogeochemical models.

5. Conclusion

In line with evidence from the literature, this study demonstrates that internal N cycling processes, specifically mineralization and

immobilization, are substantially underestimated biogeochemical and ecosystem models such as the LandscapeDNDC model. Simulations of a ^{15}N tracing experiment revealed a clear overestimation of plant ^{15}N uptake, indicating that soil N turnover rates were too low. By combining the biogeochemical model with the SIMONE isotope module, we applied a novel validation approach that explicitly constrains internal N cycling using ^{15}N recovery data. Recalibration of mineralization and immobilization rates, requiring approximately a twofold increase, substantially improved the agreement between simulated and observed ^{15}N recoveries in both soil and plant pools. This adjustment accelerated internal N cycling and led to markedly improved representation of N fertilizer budgets. However, the revised parameterization also had significant implications for simulated N fluxes: total N losses increased strongly, with nearly doubled emissions of N_2 and N_2O , while NH_3 volatilization remained largely unaffected.

To our knowledge, this is the first study to explicitly use ^{15}N tracer data to constrain internal process rates in a biogeochemical model, moving beyond conventional validation against bulk N fluxes and stocks. By directly linking model parameterization to tracer-based evidence, this approach reveals previously unrecognized biases in simulated N turnover and demonstrates the critical role of internal cycling for accurately predicting plant N uptake, legacy effects, and environmental N losses. These findings highlight the untapped potential of ^{15}N -based validation to improve process representation and reduce structural uncertainty in biogeochemical models, ultimately enhancing predictions of soil-driven and management impacts on N cycling and greenhouse gas emissions.

CRedit authorship contribution statement

Kathrin Fuchs: Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **Clemens Scheer:** Writing – review & editing, Funding acquisition, Conceptualization. **David Kraus:** Writing – review & editing, Investigation. **Andrew Smerald:** Writing – review & editing, Software. **Fawad Khan:** Data curation. **Benjamin Wolf:** Writing – review & editing, Validation, Methodology.

Declaration of competing interest

The authors declare that they have no conflicts of interest, financial or personal, that could have influenced the research, analysis, or interpretation of the results presented in this study.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.soilbio.2026.110320>.

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