https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

How does nitrogen control soil organic matter turnover and composition? – Theory and model

Chun Chung Yeung[1], Harald Bugmann[1], Frank Hagedorn[2], Margaux Moreno Duborgel[2], Olalla Díaz-Yáñez[1]

[1]Forest Ecology, Institute of Terrestrial Ecosystems, Department of Environmental Systems Science, ETH Zurich, 8092 Zurich, Switzerland

[2]Forest Soils and Biogeochemistry, Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf, Switzerland

Correspondence to: Chung C. Yeung (cyeung@ethz.ch)

Abstract. Nitrogen (N) enrichment triggers diverse responses of different soil organic carbon (SOC) pools, but a coherent mechanism to explain them is still lacking. To address this, we formulated dynamic soil CN models integrating several hypothesized N-induced decomposer responses (irrespective of plant responses), i.e., decomposition retardation under increasing N excess and stimulation under decreasing N-limitation, N-responsive microbial turnover and carbon use efficiency (CUE), and a priming effect induced by changing microbial biomass. To evaluate the relevance of each response on SOC turnover, they were incrementally combined into multiple model variants, and systematically tested against diverse observations from meta-analyses of N addition experiments and SOC fraction data from forests spanning wide environmental gradients.

Our results support the idea that N directly controls the response of multiple C pools via changing decomposition and microbial physiology. Under N addition, only the model variants that incorporated both the responses of 1) decomposition retardation with increasing N-excess and 2) decomposition stimulation with decreasing N limitation were able to reproduce the common observation of a greater increase of surface organic horizon (LFH) relative to topsoil SOC, and of particulate organic carbon (POC) relative to mineral-associated carbon (MAOC). In addition, cold and warm forests respectively experienced more decomposition retardation and stimulation under N addition. Furthermore, incorporating N-responsive microbial turnover and CUE helped reproduce microbial biomass reduction, and the latter was also critical for microbial biomass C:N homeostasis, which in turn constrained the estimation of N-limitation and excess.

Synthesizing the model findings and literature, we propose that N addition accelerates the decomposition of N-limited detritus, which supplies C to intermediate processed pools (i.e., light fraction C), and retards the decomposition of processed organic matter with lower C:N ratios (both light fraction C and MAOC). This explains the large light fraction C accumulation under N addition or contemporary N deposition in temperate forests. Collectively, our model experiment provided robust mechanistic insights on soil N-C interaction, and challenged the common model assumption of plant being the primary respondent to N. We recommend our simple model for further testing and ecological applications.

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

Keywords: *nitrogen addition; nitrogen deposition, soil organic carbon; process-based model; labile carbon and nitrogen; threshold elemental ratio; carbon use efficiency*

1 Introduction

Forest soils are large reservoirs of soil organic carbon (SOC) and nitrogen (N) globally. However, the storage of C and N in forest soils varies greatly at the regional and local scale (van der Voort et al., 2016), reflected by varying organic matter (OM) composition across environmental gradients (i.e., the amount and proportion of deadwood, litter at varying decay stages, particulate organic matter, mineral-associated organic matter, etc.). Capturing this variation is a challenge as many factors drive OM composition, and soil models were typically only used to predict bulk SOC data (Le Noë et al., 2023; Zhang et al., 2020). As a result, state-of-the-art models have repeatedly produced diverged, uncertain SOC projections under global change drivers (Bruni et al., 2022; Palosuo et al., 2012; Sulman et al., 2018; Todd-Brown et al., 2013; Wieder et al., 2018), likely because individual C pools (and their decomposers) respond differently to global change factors (Lugato et al., 2021; Rocci et al., 2021; Xiao et al., 2018). Constraining simulated OM composition is therefore essential to increase confidence in projections of future soil C balances.

Enhanced N deposition is a major global change factor, with up to 10-fold increase over the last century (Galloway et al., 2008). Recent meta-analyses have documented an average increase of bulk mineral SOC stocks and surface organic horizon (LFH) under N deposition, where the accumulation generally increased with increasing dose and duration of N addition (Janssens et al., 2010; Liu & Greaver, 2010; Ramirez et al., 2012; Tang et al., 2023; Xu et al., 2021). However, this "average increase" is complicated by considerable variation among studies differing in location, form of N input, and initial OM composition whereby individual C pools respond variably (Jian et al., 2016; Tan et al., 2020; Tang et al., 2023; Waldrop et al., 2004; Zuccarini et al., 2023). Efforts to synthesize the diverse responses into a coherent theory and model are lacking, with soil N-C interaction being considered as a largely unresolved challenge to date (Chen et al., 2020; Cheng et al., 2018; Eastman et al., 2024; Hagedorn et al., 2012; Marshall et al., 2023; Sutton et al., 2008; Tang et al., 2023).

Experimental studies have begun to unravel key processes underlying the effects of N on OM turnover. These include changes in exo-enzyme investment (Chen et al., 2018a, b; Jian et al., 2016), microbial biomass and community composition (Treseder, 2008; Yang et al., 2022; Zhang et al., 2018), as well as plant litter production and allocation (Chen et al., 2015; Magnani et al., 2007). However, except for the fertilizing effect on plant production, these mechanistic insights have largely been overlooked in the development of state-of-the-art soil models (Bonan & Levis, 2010; Bouskill et al., 2014; Chen et al., 2019; Parton et al., 1987; Sun et al., 2016; Ťupek et al., 2016; Zaehle & Friend, 2010). Eastman et al. (2024) recently investigated the CASA and MIMICS models under N addition. The models reproduced most plant but only limited soil responses, despite post-hoc parameter adjustment, which the authors attributed as a lack of relevant microbial processes in the models. Contrary to the primacy of plant responses assumed in models, many experimental studies have concluded that

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

N addition has a larger effect on microbial decomposition. This is evidenced by N addition studies documenting decreased heterotrophic CO_2 fluxes despite increased litter C inputs, and the predominant preservation of "old" C instead of a gain of "new" C in isotopic studies (Bowden et al., 2019; Franklin et al., 2003; Frey et al., 2014; Griepentrog et al., 2015; Hagedorn et al., 2003; Liu et al., 2024).

Furthermore, nitrogen affects individual C pools in opposite directions, thereby shaping OM composition. Excess N typically suppresses the decomposition of lignin-containing recalcitrant substrates (e.g., litter and processed particulate organic matter – POC; Cotrufo & Lavallee, 2022), as well as protein-rich, low C:N compounds typical for mineral-associated organic matter (MAOC; Kopittke et al., 2018). This is due to the suppression of both oxidative lignin enzyme and hydrolytic peptidase activities under excess N (Allison et al., 2008; Carreiro et al., 2000; Chen et al., 2018b; Frey et al., 2014; Gallo et al., 2004; Geisseler et al., 2010; Jian et al., 2016; Liu et al., 2023a; Rappe-George et al., 2017). In contrast, N stimulates the decomposition of labile C substrates (e.g., cellulose) and substrates with a high C:N ratio (e.g., deadwood). This is due to the stimulation of cellulolytic enzyme activities (e.g., β-1,4-glucosidase) and the alleviation of N-limitation to microbial growth (Allison et al., 2009; Bebber et al., 2011; Carreiro et al., 2000; Hobbie et al., 2012; Jian et al., 2016; Jing et al., 2021; Micks et al., 2004). These diverse N effects comprise a range of microbial adaptive responses at multiple scales, from immediate physiological reactions to changes in community composition. Integrating these individual threads of mechanism is only possible via constructing and testing a process-based model.

1.1 Conceptual model and hypotheses

In spite of the diversity of soil C responses to N, they are governed by discernible stoichiometric patterns. In this contribution, we synthesized a stoichiometric model that links soil N availability with the decomposition of various C pools (Fig. 1). The cornerstone of our modelling is the choice of relevant variables. We first considered the labile C:N ratio, defined as the ratio of readily available C and N resource supply to decomposers (Kuzyakov, 2002). We then considered the Threshold Elemental Ratio (TER; Mooshammer et al., 2014a; Sinsabaugh et al., 2013), defined as the optimal ratio of C and N resources for decomposers at which no nutrient limitation occurs. Conceptually, whenever labile C:N (supply) equals TER (demand), microbial decomposition is at its fastest (Fig. 1; Chen et al., 2014). However, when labile C:N and TER differ, this constitutes either N-excess (process 1) or N-limitation (process 2), where both conditions reduce decomposition rates, but have opposite response under N addition (Fig. 1).

Labile C:N supply and demand further control microbial turnover since excess N lowers microbial biomass C:N, corresponding to fast-turnover copiotrophs and vice versa for oligotrophs (process 3; Fierer et al., 2012; Zhou et al., 2017). Both excess and limitation of N constitute a stoichiometric imbalance and reduce carbon use efficiency (process 4; Manzoni et al., 2010; Sinsabaugh et al., 2016). Processes 3 and 4 influence microbial biomass (also necromass) production and may jointly explain the commonly observed reduction of microbial biomass under N addition, which may further impact

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

decomposition (Bradford et al., 2017; Lladó et al., 2017; Treseder, 2008; Wu et al., 2023; Xu et al., 2021; process 5, Table 1).

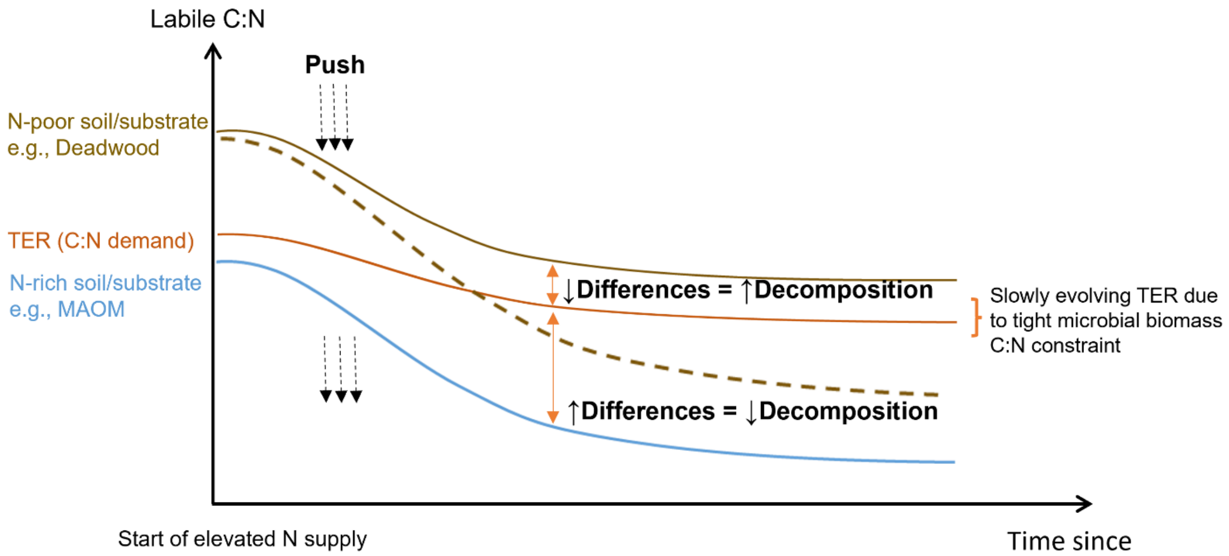


Figure 1. Conceptual model of the hypothesized relationship of resource labile C:N, TER and decomposition rate . Exogenous N addition "pushes" the labile C:N supply curve down. Two general cases emerge: (1) the gap between C:N supply and demand diminishes in soils or substrates that are originally N-poor, e.g., deadwood (brown curve), resulting in decomposition stimulation; or (2) the gap between C:N supply and demand enlarges in soils or substrates that are originally N-rich, e.g., mineral-associated organic matter (blue curve), resulting in decomposition retardation. It is possible for the downward push (N addition) to be large enough to cross from decomposition stimulation to retardation (dashed line).

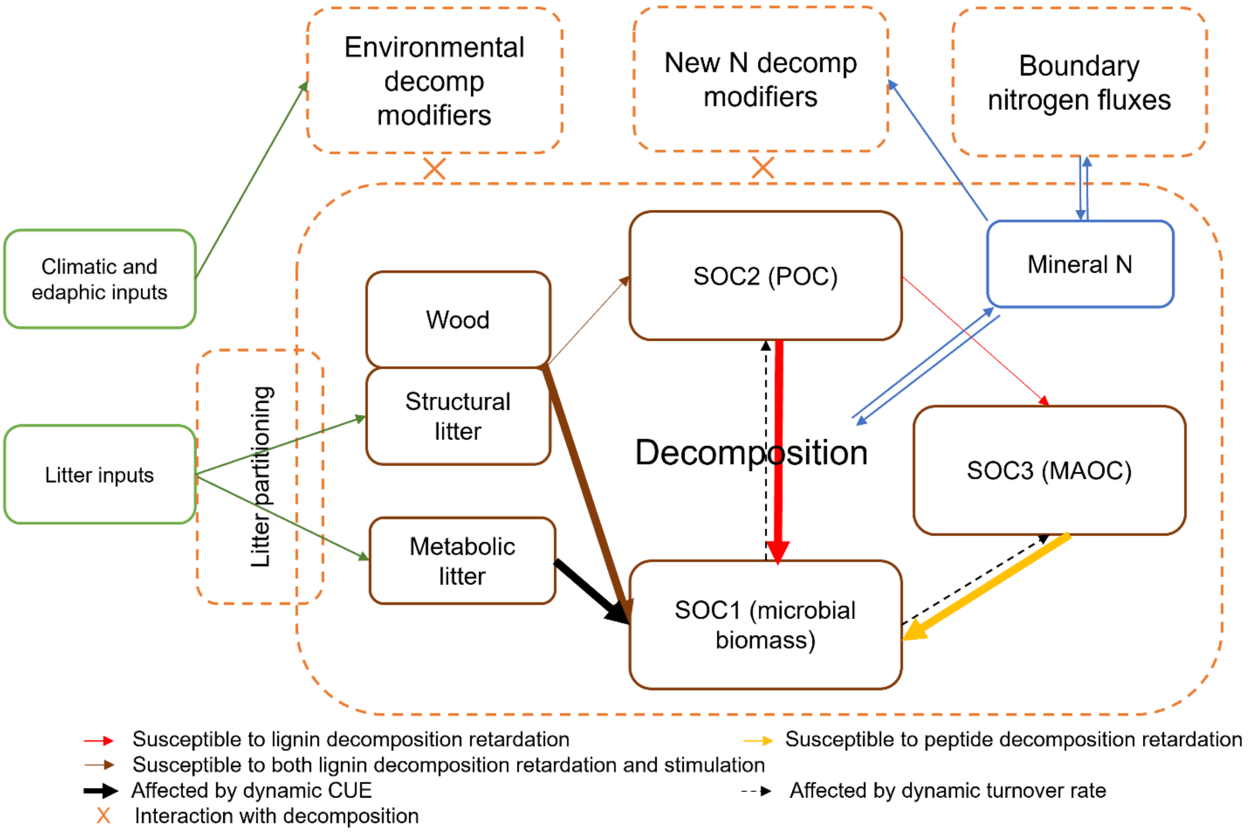
Base on this conceptual model, we developed mathematical equations capturing these five new N-induced decomposer responses, which were then implemented in a base model derived from CENTURY (Parton et al., 2010; Stergiadi et al., 2016). To test the validity of the five hypothesized responses, we combined them to create multiple model variants (along with a benchmark base model without any N response), and tested them against diverse data including experimental N addition responses of multiple C variables and individual SOC fractions across wide environmental gradients of Swiss forests. This allowed us to evaluate the ecological relevance of each new process and propose a coherent mechanism of N effects on the soil C cycle, overcoming the limits of experimental studies investigating one process at a time. Our guiding hypothesis is as follows: higher soil N availability (e.g., from exogenous N addition) increases the low C:N pools (e.g., POC, MAOC) via decomposition retardation, but decreases the high C:N detritus (e.g., fresh litter and deadwood) by stimulating its decomposition. This drives changes in the composition of SOC (Fig. 1). We expect this to be captured by some of our N effect model variants but not by the base model.

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

115 ## 2 Materials and Methods

2.1 General model description

Our base model is derived from CENTURY v4.6 (Parton et al., 1987; Stergiadi et al., 2016), and its parameterization follows ForCent, the forest version of CENTURY (Parton et al., 2010). It explicitly simulates C and N pools and fluxes dynamically with a monthly timestep. Litter C input and environmental conditions are model inputs in this study (Fig. 2), with the
120 exception that soil water content is dynamically simulated by a coupled ForClim v4.0.1, a forest model that has been tested extensively across climatic gradients in central Europe (Bugmann, 1996; Huber et al., 2021; Eq. (S12)). The equilibrium soil C pools of this base model were largely unresponsive to N addition as long as litter input was held constant (similar findings for the original ForCent model, cf. Savage et al., 2013).



125 **Figure 2. The overall model of this study, its inputs, state variables and processes. Brown solid boxes indicate the monthly updated state variables. All state variables (pools) exist in both the surface and mineral soil layers (0-20 cm), except for SOC3, which only exists in the mineral soil. Green boxes represent inputs to drive the model. Dashed boxes contain soil processes that run at a monthly time step. SOC1, SOC2 and SOC3 denote the carbon of fast-turnover, intermediate-turnover and slow-turnover SOM, respectively.**

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

We briefly describe our base model below, which consists of three basic parts inherited from CENTURY: **litter partitioning, decomposition, and boundary mineral N fluxes** (Fig. 2). The full model and parameter documentation is available as supplementary materials.

Litter partitioning transforms the raw litter inputs (leaf, fine root, and twig) into two C pools: recalcitrant "structural" and labile "metabolic" litter based on their lignin:N ratios (Parton et al., 1987; Eq. (S8)). These two litter pools then undergo decomposition. Coarse woody debris has its own state variable pool distinct from structural and metabolic litter (Fig. 2).

Decomposition follows first-order kinetics with respect to C substrate quantity (Eq. (1 & 2)). Decomposition breaks down structural and metabolic litter, deadwood, and the SOC pools (SOC1, SOC2 and SOC3, approximating microbial biomass C, POC and MAOC, respectively, see Berardi et al. (2024)), leading to CO_2 release and a transfer of C between pools. In addition to decomposition, a first-order bioturbation further transfers C from surface SOC2 to mineral soil SOC2, following the equation in ForCent (Parton et al., 2010; Eq. (S25)).

$$\frac{dC_x(t)}{dt} = I(t) - gTcflow_x(t) \qquad (1)$$

$$gTcflow_x = C_x \times kDec_x \times \prod_{i=1}^{n} f(\varepsilon_i)_x \qquad (2)$$

where C_x is a state variable carbon pool x at the current timestep t, I is the C input to C_x at time t, $gTcflow_x$ is the total amount of C flowing out of C_x at time t, $kDec_x$ is the monthly turnover rate parameter of C_x, and $f(\varepsilon_i)_x$ is the ith environmental decomposition modifier (among n modifiers) associated with C_x at time t. Details can be found in Eq. (S21-25).

The environmental decomposition modifiers reduce the rate of decomposition and bioturbation under suboptimal climatic and edaphic conditions including temperature, relative soil water content, ratio of precipitation to potential evapotranspiration (proxy of anaerobic conditions), pH and sand content (Parton et al., 2010, Eq. (S9-20)). The calculation of realized decomposition (Eq. (2)) also leads to net N mineralization or immobilization, determined by the C:N ratio of the decomposing substrate and the computed C:N ratios of new organic matter entering the receiving pool (Eq. (S26-28)).

Boundary mineral N fluxes include N deposition, N fixation and soil mineral N loss. Nitrogen deposition is divided into two time periods: 1) *Historical* N deposition calculated by the default equation of CENTURY (Eq. (S38)), and 2) *Contemporary* N deposition based on measured and interpolated data as model input (cf. *"Study sites and model inputs"*). Nitrogen fixation is determined by the central estimate equation in Cleveland et al. (1999) (see also Wieder et al., 2015 and Eq. (S39)). Soil mineral N loss includes leaching and plant uptake, which depend on soil water balances and clay content (Eq. (S40-46)).

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

2.2 Base model selection

We refined certain processes and parameter to ensure that our base model reasonably matches observed C stocks, and to reduce biases unrelated to nitrogen. This was necessary as ForCent was originally parameterized and applied on only one site (Parton et al., 2010) and may not capture all the environmental (e.g., pH) gradients of SOC turnover, where pH in particular was shown to be an influential factor in Swiss forests (González-Domínguez et al.,2019). To select the base model, we evaluated several model versions: 1. Model with and without a pH retardation effect on decomposition (Eq. (S15)) since it is used in some versions of CENTURY only (v4.5 or above, cf. Berardi et al., 2024; Stergiadi et al., 2016); 2. Model with and without a pH retardation effect on bioturbation, since acidity also strongly suppresses faunal bioturbation (Desie et al., 2020; Persson et al., 2007; Taylor et al., 2019), which ForCent did not consider; 3. Alternative turnover rate parameter for the SOC3 (MAOC) pool (i.e., *kDec5*, see Supplement 2), since this parameter value was highly uncertain in ForCent (Parton et al., 2010). We tested the ForCent parameter value against the same parameter in the original CENTURY (roughly three times higher, Parton et al., 1987) as preliminary testing showed that ForCent's MAOC turnovers very slowly and is insensitive to environmental perturbations.

To select the best base model, we compared the simulated outputs averaged over 55-85 years after the onset of contemporary N deposition (roughly corresponding to the timeframe of elevated anthropogenic N emission (cf. "*Simulation setup*")) with observed LFH stocks, SOC stocks (0-20 cm), LFH:SOC and SOC:N (0-20cm), measured in the 1990s and 2000s (van der Voort et al., 2016). We evaluated the deviation between simulated and observed data and computed RMSE. The best-performing model was selected as the basis to implement our new N effect models.

2.3 Nitrogen-induced decomposer responses

To implement the N effects, we separated the mineral N pools into the surface organic horizon and the mineral soil instead of just one homogeneous pool as in the original CENTURY. This allows for calculating separate labile C:N in the surface and mineral soil, and to reconcile simulated mineral N distribution with tracer N studies that tracked the spatiotemporal fate of added N (Li et al., 2019; Templer et al., 2012). Following these modifications, we formulated five equations embodying decomposer adaptive responses to changing N availability. We used all equations without calibrating the parameters, which were derived from independent meta-analyses or reviews to maintain model generality (see Supplement 2).

1. **Decomposition retardation of lignin-containing OM and MAOC under N-excess**: We implemented decomposition retardation for lignin-containing pools (structural litter, wood, SOC2) and the protein-rich pool (SOC3) (J. Chen et al., 2018; Chen et al., 2014; Frey et al., 2014; Jian et al., 2016). The retardation effect increases linearly with N excess (labile C:N < TER, Eq.(3)) until it reaches maximum retardation. The maximum effect is based on enzyme reduction data reported in meta-analyses. This retardation effect is multiplied with $gTcflow_x$ the same way as the other decomposition modifiers in Eq. (2).

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

$$gNDRF_x = \begin{cases} 1 & \text{if } ((gLabileCN_x - gTER_i) > 0) \\ 1 + \left((1 - kNDRFmin_s) \times \dfrac{(gLabileCN_x - gTER_i)}{gTER_i} \right) & \text{if } ((gLabileCN_x) < gTER_i \text{ and } gLabileCN_x > 0) \\ kNDRFmin_s & \text{if } (gLabileCN_x = 0) \end{cases} \quad (3)$$

where $gNDRF_x$ is the N-induced decomposition retardation effect for C_x pool. $kNDRFmin_s$ is the maximum reduction (lowest value) for each OM type s (either lignin-containing materials i.e., structural litter, wood, SOC2, or proteinaceous material i.e., SOC3). The extent of retardation is controlled by two variables calculated monthly: 1) labile C:N supply ($gLabileCN_x$), and 2) microbial C:N demand ($gTER_i$). The lower $gLabileCN_x$ is relative to $gTER_i$, the stronger the effect.

$$gLabileCN_x = \frac{(MetabC_i + gTcflow_x)}{(MetabN_i + MinerlN_i + gTnflow_x)} \quad (4)$$

where the numerator is the sum of all labile C consisting of $MetabC_i$ – the most labile C pool in layer i (same layer as C_x) and $gTcflow_x$ – the potential decomposable amount of C_x before N-related decomposition retardation applies. The denominator is the same but with N, plus an additional mineral N pool in layer i. $Metab$ and $MinerlN$ are assumed to be evenly diffused within the modeled soil layer. $gLabileCN_x$ is calculated for every instance of C_x decomposition and hence implicitly accounts for C and N resource heterogeneity in proximity to each substrate.

The optimal C:N demand of microbes ($gTER_i$) follows the equation in Sinsabaugh et al. (2013) and Doi et al. (2010):

$$gTER_i = \frac{(SOC1_i/SON1_i)}{kCUEmax} \quad (5)$$

where $SOC1_i/SON1_i$ is the microbial biomass C:N in soil layer i , and $kCUEmax$ is the theoretical thermodynamic maximum CUE (Sinsabaugh et al., 2016). We assumed that the maximum N use efficiency equals to 1 and is thus omitted from the equation (Cui et al., 2023). This optimal TER formulation is necessary as TER is directly compared to labile C:N, instead of to the bulk C:N of composite OM. $gTER_i$ is calculated per layer because there is only one microbial pool per layer, and microbial biomass C:N (hence TER) is inherently less variable than labile C:N due to homeostasis.

2. **Decomposition stimulation of high C:N substrates by alleviating N limitation**: We implemented an explicit mass balance constraint that restricts C decomposition under N limitation (cf. Manzoni & Porporato, 2009). This simultaneously captures N addition stimulating the decomposition of N-limited (high C:N) substrates (Allison et al., 2009; Bebber et al., 2011; Micks et al., 2004). Essentially, mineral N shortage restricts the decomposition of high C:N OM into low C:N OM (Eq. (6, 7)):

$$gTcflow\_red_x = \frac{gNdiff \times CN_{donor}}{(CN_{donor}/CNtransfer_{receiver}) - 1} \quad (6)$$

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

where $gTcflow\_red_x$ is the amount of C decomposition to be subtracted from $gTcflow_x$ (Eq. (2)) based on the shortage of microbially-available N ($gNdiff, Eq. (7)$), i.e., more available N alleviates the shortage and lowers $gTcflow\_red_x$. CN_{donor} is the C:N ratio of the decomposing pool, $CNtransfer_{receiver}$ is the calculated C:N ratio of new materials entering the receiver pool (Eq. (S26 & S27)). The equation was derived algebraically and conforms to mass balance. $gNdiff$ is calculated as:

$$gNdiff = \left((gTcflow_x/CN_{donor}) + MinerlN_i\right) - (gTcflow_x/CNtransfer_{receiver}) \qquad (7)$$

3. **Dynamic microbial turnover rate**: We introduced a dynamic turnover rate of the microbial pool to replace the original turnover parameter, based on the evidence that a lower microbial C:N (under higher N availability) correlates with an increased abundance of fast-turnover copiotrophs, and vice versa for slow-turnover oligotrophs (Fierer et al., 2012; Leff et al., 2015; Rousk and Bååth, 2011). Essentially, the microbial turnover rate $gDec3_i$ varies linearly between the maximum and minimum microbial C:N (Eq. (8)):

$$gDec3_i = kDec3min_i + \left(kVarat1_1 - (SOC1_i/SON1_i)\right) \times \frac{(kDec3max_i - kDec3min_i)}{(kVarat1_1 - kVarat1_2)} \qquad (8)$$

where $kDec3min_i$ and $kDec3max_i$ are the minimum and maximum turnover rates representing oligotrophic and copiotrophic microbial communities respectively, calculated using the ratio of copiotroph and oligotroph turnover rates (Rousk and Bååth, 2011). $kVarat1_1$ and $kVarat1_2$ are CENTURY's parameters representing the maximum and minimum microbial C:N, respectively.

4. **Dynamic microbial carbon use efficiency**: We introduced dynamic CUE (replacing constant CUE) responsive to the stoichiometric imbalance between labile C:N and TER, approximating the stoichiometric theory by Sinsabaugh et al. (2016). Essentially, CUE decreases in response to an increasing deviation of labile C:N from TER as in $gNDRF_x$ (Eq. (3)) until a minimum CUE is reached (Eq. (9)).

$$gCUE_x = \begin{cases} kCUEmax & \text{if } ((gLabileCN_x - gTER_i) = 0) \\ kCUEmax - \dfrac{(kCUEmax - kCUEmin)}{gTER_i} \times (|gLabileCN_x - gTER_i|) & \text{if } (0 < (|gLabileCN_x - gTER_i|) < gTER_i) \\ kCUEmin & \text{if } ((|gLabileCN_x - gTER_i|) > gTER_i) \end{cases} \qquad (9)$$

where $gCUE_x$ is the CUE of the decomposing C_x (x can be MetabC, StrucC, WoodC, SOC2, SOC3 that decompose to form SOC1), $kCUEmax$ and $kCUEmin$ are parameters constraining the maximum and minimum attainable CUE respectively.

5. **Microbial biomass effect on decomposition (MB_eff)**: We implemented a microbial biomass control on decomposition (Eq. (10)) due to the common co-occurrence of microbial biomass decrease and SOC stock increase under N addition (Lladó et al., 2017; Treseder, 2008; Xu et al., 2021). We assumed that decomposition rate is related to "relative microbial biomass" via a logistic relationship. Relative microbial biomass is calculated as the ratio of actual microbial biomass (SOC1) to the

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

total labile C resources that are potentially convertible to microbial biomass (Eq. (11)), inspired by Guenet et al. (2016), Sulman et al. (2014), and Wutzler & Reichstein (2008). This microbial biomass effect Eq. (10) is multiplied with C_x like the other decomposition modifiers:

$$gMB\_eff_i = \left(kPrimemax - e^{\left(-\ln\left(\frac{kPrimemax}{kPrimemax-1}\right)\right)\times gRelMBC_i + \ln(kPrimemax)}\right) \qquad (10)$$

wheregMB_eff_i is a logistic function controlled by $kPrimemax$ which represents the maximum monthly priming effect, and the explanatory variable $gRelMBC_i$ which represents relative microbial biomass in layer i. This function passes through 1 at $gRelMBC_i = 1$ and theoretically captures both positive and negative priming when $gRelMBC_i$ is above or below 1, respectively. $gRelMBC_i$ is calculated monthly as:

$$gRelMBC_i = \frac{SOC1_{i,m}}{\sum_{x,i} C_{x,,m-1} \times kDec\_rel_{x,i} \times gCUE_{x,m-1}} \qquad (11)$$

where the denominator is the sum of all C pools (except SOC1) in the last month (*m-1*) in soil layer i multiplied with their respective relative turnover rate $kDec\_rel_{x,i}$ and the most recent carbon use efficiency $gCUE_{x,m}$. $kDec\_rel_{x,i}$ is defined as the ratio of the decomposition rate parameter of each C pool x relative to the same parameter for metabolic litter (the most labile C) i.e., it extracts the labile portion of each C substrate.

We combined these five processes (Table 1) into two groups of model variants: those considering decomposition retardation under excess N only (hereafter referred as "$\mathrm{Nex_{retard}}$ model"), and those considering both retarding (under excess N) and stimulating (under limiting N) effects on decomposition (hereafter referred as "$\mathrm{Nex_{retard}} + \mathrm{Nlim_{stim}}$ model"). We then incrementally increased model complexity by including more microbial feedbacks: dynamic turnover, dynamic CUE, and microbial biomass feedback, which resulted in eight model variants to explore the response space (Table 1). The model variants are organized in this way to reflect our prior assumption of their causal relevance (e.g., the concurrent decrease in microbial biomass and decomposition is possibly a mere correlation, whereas widespread experiments showed that lignin-degrading enzymes are clearly reduced by N addition). This "Lego" incremental modelling approach is similar to the approach by Zhang et al. (2020) and Wutzler & Reichstein (2008).

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

Table 1. Overview of the five newly implemented N-driven decomposer responses. Different responses are combined to form eight model variants of increasing complexity.

Nitrogen adaptive responses				
1. Nex$_{retard}$ Decomposition retardation with increasing N excess	**2. Nlim$_{stim}$** Decomposition stimulation with decreasing N-limitation	**3. Dynamic microbial turnover** Microbial turnover rate in response to microbial biomass C:N	**4. Dynamic CUE** Microbial carbon use efficiency in response to N excess or limitation	**5. MB_eff** Secondary microbial biomass control on decomposition
Model variants combining the adaptive responses in incremental complexity				
Model group: Nex$_{retard}$	1	1+3	1+3+4	1+3+4+5
Model group: Nex$_{retard}$ + Nlim$_{stim}$	1+2	1+2+3	1+2+3+4	1+2+3+4+5

2.4 Study sites and model inputs

We first tested the base model with data from the Swiss ICP Level II long-term forest plots (n = 16, Thimonier et al., 2005). These plots have comprehensive ancillary measured data including N deposition and aboveground litterfall, which allowed us to ensure the reliability of our input data during model development. Secondly, to evaluate our N effect models, we used a larger dataset from 54 Swiss forest sites covering wide environmental gradients (e.g., MAT: 1-12 ºC; MAP: 587-1847 mm; pH: 3.1-7.6), selected based on maximizing the orthogonality of temperature, moisture, soil, and landform-related variables (González-Domínguez et al., 2019). There are some overlaps between the ICP Level-II plots and the 54 sites in terms of site names, but they belong to separate soil sampling campaigns differing in time and location.

For every site, we compiled model input data related to climate, soil, litter, and N deposition to drive the simulations: Monthly temperature and precipitation data were obtained from the 1979-2013 high-resolution monthly climatic data of CHELSA v1.2 (Karger et al., 2017), and extended to long-term climate by stochastic sampling of the monthly climatic data based on their statistical distributions (Huber et al., 2021).

Contemporary N deposition data are available as measured throughfall N fluxes for most ICP Level II sites (taking the averages from the first sampling year to 2015), and missing data were replaced by estimates in Thimonier et al. (2005, 2010). For the 54 forest sites without dedicated deposition monitoring, we used interpolated raster data compiled from air pollution inventories of the years 1990, 2000, 2005, and 2010, conducted by the Swiss Federal Office for the Environment (Rihm and Achermann, 2016; Rihm and Künzle, 2023). The reliability of these map data was validated with the measured data from the aforementioned ICP Level II sites (Pearson r = 0.91). We acknowledge that these N deposition data are representative of the

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

1990s and 2000s when N deposition was on decline and hence were likely underestimated (cf. Gharun et al., 2021, N deposition peaked around 1980).

Soil water holding capacity (*kBS*) down to 1m depth was extracted from the 250 m-resolution map in Baltensweiler et al. (2021). For locations that have no value on the map, we calculated average *kBS* from the eight adjacent cells. Measured soil texture (sand, silt, clay, fine earth density) and pH were obtained from WSL soil inventory data (Walthert et al., 2013).

Litter input (foliage, twig, fine root, exudate, coarse deadwood debris) was generated by the species-explicit ForClim model forced under these climatic and edaphic inputs (Eq. (S3-7)). We took the average litter production of 200 forest patches in the last 100 years of no-management, equilibrium simulations (Bugmann, 1996). Several warm, low-elevation spruce forests resulted from past management practices (Gosheva et al., 2017) were not captured by these natural equilibrium simulations. We therefore re-simulated these sites as pure spruce stands. However, these stands had abnormally low simulated litter production and SOC stocks (likely because reality is not at equilibrium), and hence we increased all litter in these low-elevation spruce stands by a scaling factor of 1.5, according to the measured aboveground litterfall in one of the stands (Table S1). We checked the validity of the simulated aboveground litter against plot-level measurements from the ICP Level II sites (Pearson r = 0.79), as well as the litter estimates in Gosheva (2017), which showed that our litter inputs were within reasonable ranges (Fig. S1).

2.5 Simulation setup

We used two sets of simulations to evaluate our N effect model variants. First, we performed “N-addition simulations”, where N was added artificially to mimic manipulation experiments. Second, “Contemporary simulations” were run with contemporary N deposition data only to reflect real-world conditions (also used in “*Base model selection*”). In all simulations, we first ran the models for 3000 years until all C pools were at steady-state. In the Contemporary simulations, we extended the simulation under contemporary N deposition by 85 years, as we took the simulation outputs averaged over 55-85 years after the onset of contemporary N deposition. In the N-addition simulations, we extended the simulation using contemporary N deposition for 50 years only, and from then on, we added 100 kg N ha^{-1} y^{-1} on top of the contemporary N deposition as an N treatment. Higher N addition levels were not tested because they are mostly relevant for croplands, not forests (Gundersen et al., 1998).

2.6 Model validation and analysis of results

We prepared two types of validation data for the two sets of simulations.

First, to evaluate the outputs of the *N-addition simulations*, we compiled N addition meta-analysis data of the transient responses of various C pools and fluxes (i.e., the percentage difference between N treatment and unmanipulated control). Validation with meta-analysis responses was recommended by Wieder, Allison, et al. (2015) and is crucial for making

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

reliable C projections under global change (Le Noë et al., 2023). The surface organic layer (LFH) responses were extracted from the dataset in Liu & Greaver (2010); SOC, POC and MAOC responses were taken from the combined datasets of Tang et al. (2023) and Wu et al. (2023) (overlapping studies not duplicated); soil heterotrophic respiration (Rh) responses were extracted from Liu, Men et al. (2023); microbial biomass (MBC) and microbial biomass C:N (MBC:MBN) responses were from Jia et al. (2020) and Zhang et al. (2018). No precise depth information of the microbial samples was available, thus we assumed they were derived from the surface and mineral soil equally, for comparison with the simulation results. We further filtered all meta-analysis responses to forest and woodland ecosystems, ≥4 years experimental duration, and a fertilization rate between 40 and 150 kg N ha^{-1} yr^{-1}. After the filtering, the durations of most N addition experiments were within the range of 5-15 years and hence we also averaged simulated responses over this time span. A summary of the filtered meta-analyses data is provided in Table S2.

We evaluated the models against the relative changes of different C pools and microbial attributes. We expected that the large environmental gradients in our simulated forest sites (54 Swiss forests) and the meta-analysis global forest samples are comparable qualitatively, given that most experiments were conducted in temperate forests, and that broad patterns of N addition response are generally consistent across ecosystems and biomes (Ramirez et al., 2012; Wu et al., 2023; Xu et al., 2021). Lastly, we used multiple linear regression to disentangle the contribution of various environmental factors to the variance of the simulated responses. Predictors with a generalised variance inflation factor (VIF) >10 were removed.

Second, for the *Contemporary simulations*, we compiled fraction data consisting of the organic FH horizons, 0-20cm POC (free + occluded light fraction) and MAOC (clay-associated fine heavy fraction) (González-Domínguez et al., 2019; Griepentrog et al., 2014). FH and POC are further combined into "light fraction C" to handle sites with no recorded FH layer, and to reduce uncertainties associated with bioturbation and vertical distribution of root. We tested the models' ability to match 1) the proportion of MAOC to total SOC (= sum of MAOC and light fraction C, without coarse detritus since it was not measured), as well as 2) the proportion of MAOC and light fraction C to total litter input (including coarse detrital inputs). We expected that these proportions are controlled by N availability according to our guiding hypothesis. However, unlike N addition experiments isolating added N as the explanatory factor, these OM proportions arose from a combination of long-term climatic, mineralogic, biotic and management influences. We therefore conducted multiple regression accounting for many site factors to avoid a misattribution of confounding factors (see Table S3). The influence of N availability was handled by using either MAOC:N or light fraction C:N as an explanatory variable in our regression models, as they integrate information about the N availability conditions surrounding the respective OM pools over long term (instead of an unspecific bulk SOC:N ratio).

We first evaluated the models against observed MAOC:N and light fraction C:N, which can reveal mechanistic shortcomings but are rarely validated in modelling studies (e.g., differences in observed and simulated MAOC:N may imply a mis-calculation of MAOC derived from plant matter vs. microbial products). Second, we regressed the OM proportions against

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

the these fraction C:N ratios, along with other site factors. We evaluated the null hypothesis that all model variants and observation are the same concerning the relationship between OM proportions and OM C:N ratios ($\alpha = 0.05$), handled by a "*C:N ratio* × *Variant*" interaction, where "*Variant*" is a categorical variable that includes both the model ID and observation, and the latter is set as the reference level.

In these analyses, we were mainly concerned with the relationships between variables (e.g., ratios of C pools, slopes of regressions; Mahnken et al., 2022; Manzoni & Cotrufo, 2024), instead of matching exact C stock sizes using our no-management, constant litter simulations that must have caused C stocks to deviate from reality. That is, a close quantitative match of C stocks may not actually be desirable under the uncertainty of simulated site history, an uncertainty ignored by most soil modelling studies.

3 Results

3.1 Base model selection

Organic layer (LFH) stocks (Fig. 3a) were largely underestimated by the base model with no pH decomposition retardation effect. Conversely, the models that incorporated it generally overestimated LFH stocks slightly. The pH effect on bioturbation had a similar effect of increasing LFH stocks but at a smaller magnitude. Overall, models having pH effects tended to have a much lower RMSE and slope closer to 1.

All models generally overestimated mineral topsoil SOC stocks (Fig. 3b), and the inclusion of the pH retardation effect on decomposition increased this overestimation. Models considering the high SOC3 turnover parameter value reduced the RMSE substantially.

All models generally underestimated the LFH:SOC ratios (Fig. 3c), especially those with the low SOC3 turnover parameter. Including the pH effect on bioturbation consistently improved the RMSE. For SOC:N ratios, they were largely underestimated by models with no pH effect on decomposition, and their performance was consistently improved when using the high SOC3 turnover parameter value (Fig. 3d).

In sum, the best base model with low RMSE in general included the pH effects on decomposition and bioturbation, and the high SOC3 turnover parameter. Hence, this combination of processes and parameters was included in the base model for the subsequent simulations of the N effects.

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

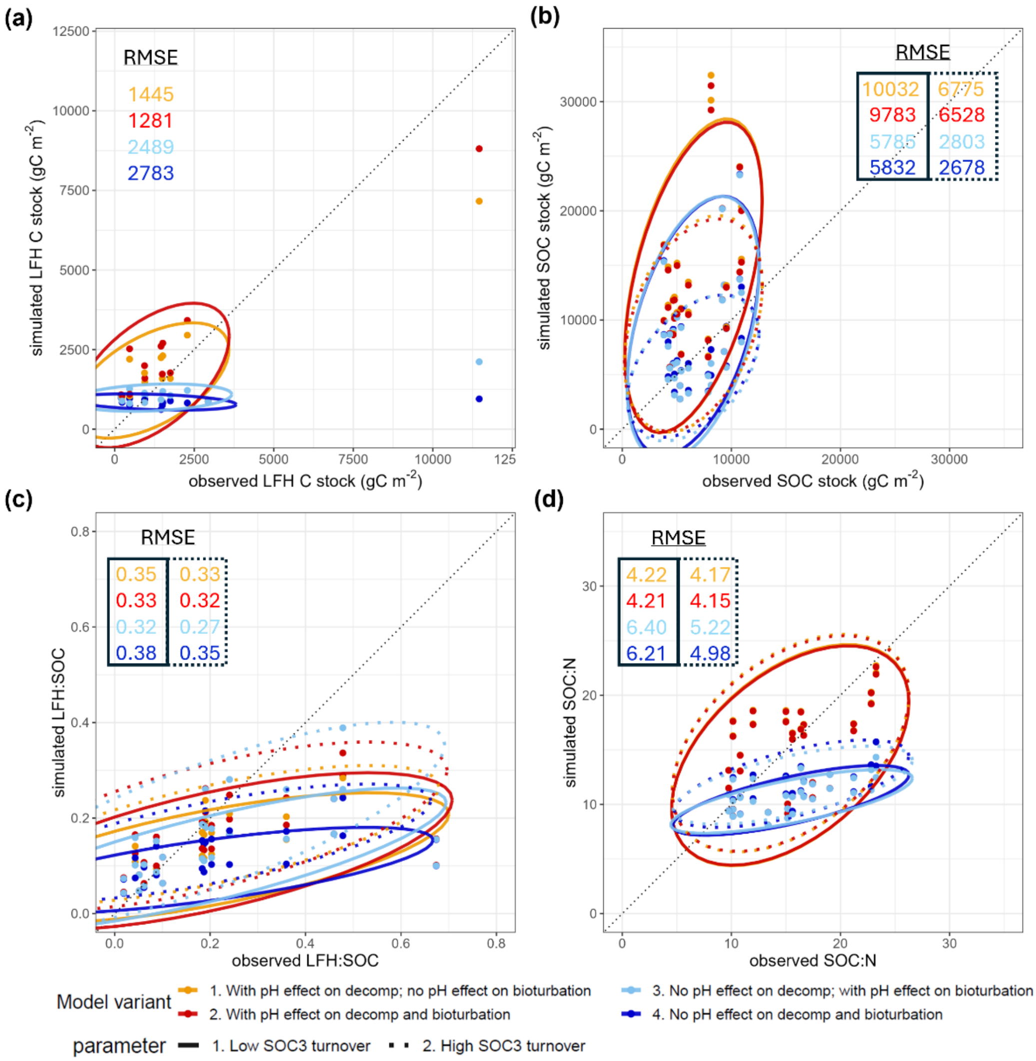


Figure 3. Simulated vs. observed (a) LFH C stock, (b) SOC stock (0-20 cm), (c) LFH:SOC ratio, (d) SOC:N ratio (0-20 cm) at the Swiss ICP Level II sites (n = 16) among base model variants: with or without a pH effect on decomposition, with or without a pH effect on bioturbation, and with the ForCent low SOC3 turnover or the CENTURY high SOC3 turnover parameter. Ellipses represent the range of 95% confidence ellipses (Fox and Weisberg, 2011).

3.2 Nitrogen addition simulation: soil C-cycle responses

The meta-analysis data showed that on average, LFH increased (+27.6%) more than mineral soil SOC (+10.4%), and POC increased (+18.7%) more than MAOC (+8.9%) under N addition (Fig. 4abcd). These patterns were best reproduced by the Nex_{retard} + $Nlim_{stim}$ model variants (i.e., considering decomposer adaptive response to both N-excess and N-limitation), but neither by the base model (0% response) nor the simple Nex_{retard} models without dynamic CUE and microbial biomass

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

feedback (MB_eff). The simple Nex_{retard} models produced negative LFH responses that were well below the meta-analysis lower quartiles (Fig. 4a). Conversely, the Nex_{retard} + $Nlim_{stim}$ variants yielded responses that were generally between the meta-analysis means and lower quartiles (Fig. 4abcd). In all model variants, MAOC was largely unresponsive to N addition (Fig. 4d). However, the MAOC response of the Nex_{retard} + $Nlim_{stim}$ variants continued to increase on a longer time scale beyond the 5-15 year period (Fig. S3), nearing the meta-analysis response. The time course of the other responses is presented in Fig. S4 for reference.

For the microbial attributes (Fig. 4ef), the base model had no microbial biomass response but a strongly negative microbial biomass C:N response, which the simple Nex_{retard} models also predicted. All the other more complex models had milder microbial C:N responses which were generally close to the meta-analysis mean and lower quartile. Nex_{retard} models that incorporated dynamic microbial turnover featured negative responses of microbial biomass around the lower quartile, but the Nex_{retard} + $Nlim_{stim}$ counterparts had microbial biomass responses around the upper quartile (Fig. 4e). However, it must be noted that the simulated positive microbial biomass responses were mainly from the surface, whereas experimental measurements likely included more mineral soil samples.

For the deadwood and litter responses which we had insufficient observation data (Fig. 4gh), the Nex_{retard} + $Nlim_{stim}$ models featured large negative responses. Including more microbial feedbacks (dynamic CUE and MB_eff) reduced these negative response and drove the response to positive ranges for the simple Nex_{retard} models. Lastly, total dead organic C stock responded in a similar direction as the deadwood response but opposite direction as the Rh responses (Fig. 4j). All models reproduced Rh within the meta-analysis interquartile range but the Nex_{retard} + $Nlim_{stim}$ models with microbial feedbacks were the closest to the mean (Fig. 4i).

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

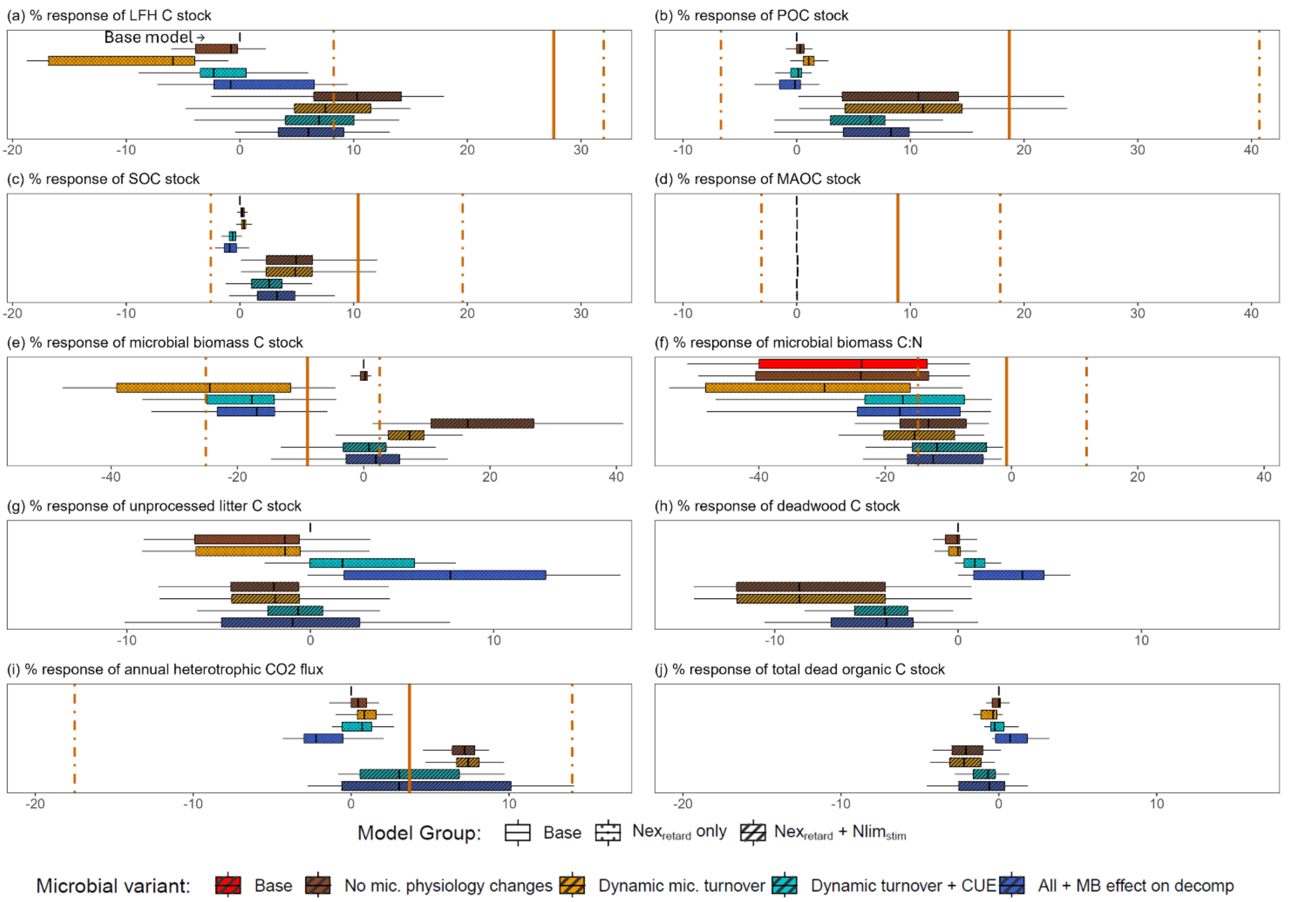


Figure 4. Simulated responses of 54 Swiss forest sites under N addition: % difference in treatment (+100 kg N/ha/y) vs. control of (a) LFH C stock, (b) mineral soil POC stock, (c) mineral soil SOC stock, (d) mineral soil MAOC stock, (e) MBC (surface + mineral soil), (f) MBC:MBN (surface + mineral soil), (g) surface fresh litter C stock, (h) deadwood C stock, (i) annual heterotrophic respiration (surface + mineral soil), and (j) total dead organic C stocks in the base model and eight model variants averaged over the year 5-15 after the start of N addition. The solid orange vertical lines are the meta-analysis means, and the dot-dash lines are the lower and upper quartile values.

We further analyzed the site factors influencing the size of the N response in Fig. 4. We found that the Nex$_{retard}$ only and the Nex$_{retard}$ + Nlim$_{stim}$ model variants formed two distinct groups, each influenced differently by the site factors (Table 2).

In the Nex$_{retard}$ models, most environmental factors were not significant, reflecting the small inter-site variance in their predictions. An exception is ambient N deposition, which had significant positive effects on various C pools but a negative effect on deadwood. In contrast, in the Nex$_{retard}$ + Nlim$_{stim}$ models, ambient N deposition had significantly negative effects on the N response of SOC, POC and R$_h$, while positively affecting deadwood responses. Moreover, climatic effects were notable as MAT (warmer) and MAP (wetter) showed significant positive effects on the response of LFH, SOC, POC, MBC and Rh, but a negative effect on deadwood. There was a clear opposite direction of the environmental effects when comparing deadwood with the other C pools in the Nex$_{retard}$ + Nlim$_{stim}$ models.

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

Table 2. Multiple-regression of the site factors that control simulated % response of selected C-cycle variables under N addition. Standardized coefficients are scaled by their standard deviation.

LFH response	Nex_{retard} models		Nex_{retard} + $Nlim_{stim}$ models	
Predictors	Std. Coefficient	P-value	Std. Coefficient	P-value
Intercept	NA	0.04*	NA	0.5
MAT	-0.12	0.19	0.17	0.03*
MAP	-0.28	<0.0001***	0.18	<0.0001***
sand	-0.02	0.76	0	0.98
Ambient Ndep†	0.14	0.12	0.14	0.06.
Broadleaf: conifer litterfall	0.08	0.15	-0.13	0.01**
Initial LFH	-0.18	0.53	-1.18	<0.0001***
Initial deadwood	0.24	0.38	1.22	<0.0001***

SOC response	Nex_{retard} models		Nex_{retard} + $Nlim_{stim}$ models	
Predictors	Std. Coefficient	P-value	Std. Coefficient	P-value
Intercept	NA	0.39	NA	0.67
MAT	-0.04	0.62	0.49	<0.0001***
MAP	0.05	0.41	0.45	<0.0001***
sand	0.05	0.58	-0.01	0.88
Ambient Ndep†	0.17	0.03*	-0.27	0**
Broadleaf: conifer litterfall	-0.14	0.01**	-0.11	0.05*
Initial SOC	-0.01	0.93	-0.61	<0.0001***
Initial deadwood	0.01	0.96	0.26	0.05.

POC response	Nex_{retard} models		Nex_{retard} + $Nlim_{stim}$ models	
Predictors	Std. Coefficient	P-value	Std. Coefficient	P-value
Intercept	NA	0**	NA	0.71
MAT	-0.03	0.72	0.46	<0.0001***
MAP	0.05	0.38	0.43	<0.0001***
sand	0.24	0.01**	-0.02	0.72
Ambient Ndep†	0.24	0.01**	-0.27	0**
Broadleaf: conifer litterfall	-0.16	0.01*	-0.16	0.01**
Initial POC	0.02	0.96	-0.64	<0.0001***
Initial deadwood	0.09	0.81	0.22	0.11

MBC response	Nex_{retard} models		Nex_{retard} + $Nlim_{stim}$ models	
Predictors	Std. Coefficient	P-value	Std. Coefficient	P-value
Intercept	NA	0.03*	NA	0.04*
MAT	-0.03	0.7	0.32	<0.0001***
MAP	-0.1	0.03*	0.3	<0.0001***
sand	0.08	0.12	-0.02	0.74
Ambient Ndep†	0.19	0.01**	-0.13	0.07.
Broadleaf: conifer litterfall	0.03	0.46	-0.09	0.07.
Initial MBC	0.25	0.04*	-0.62	<0.0001***
Initial deadwood	0.09	0.44	0.65	<0.0001***

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

Deadwood response	Nex_{retard} models		Nex_{retard} + $Nlim_{stim}$ models	
Predictors	Std. Coefficient	P-value	Std. Coefficient	P-value
Intercept	NA	<0.0001***	NA	0.78
MAT	0.05	0.46	-0.61	<0.0001***
MAP	-0.06	0.2	-0.34	<0.0001***
sand	-0.13	0**	0.06	0.27
Ambient Ndep†	-0.14	0.04*	0.37	<0.0001***
Broadleaf: conifer litterfall	0.03	0.51	0.09	0.14
Initial deadwoodC	-0.22	<0.0001***	0.27	<0.0001***
Rh response	Nex_{retard} models		Nex_{retard} + $Nlim_{stim}$ models	
Predictors	Std. Coefficient	P-value	Std. Coefficient	P-value
Intercept	NA	0.99	NA	0.87
MAT	-0.07	0.35	0.17	0.05.
MAP	0.07	0.19	0.19	0**
sand	-0.02	0.69	0.11	0.05*
Ambient Ndep†	-0.04	0.57	-0.21	0.01*
Broadleaf: conifer litterfall	0.05	0.32	0.03	0.61
Initial deadwoodC	0.32	<0.0001***	0.53	<0.0001***

* For P-values, one asterisk indicates p < 0.05, two asterisks indicate p < 0.01, three asterisks indicate p < 0.001.

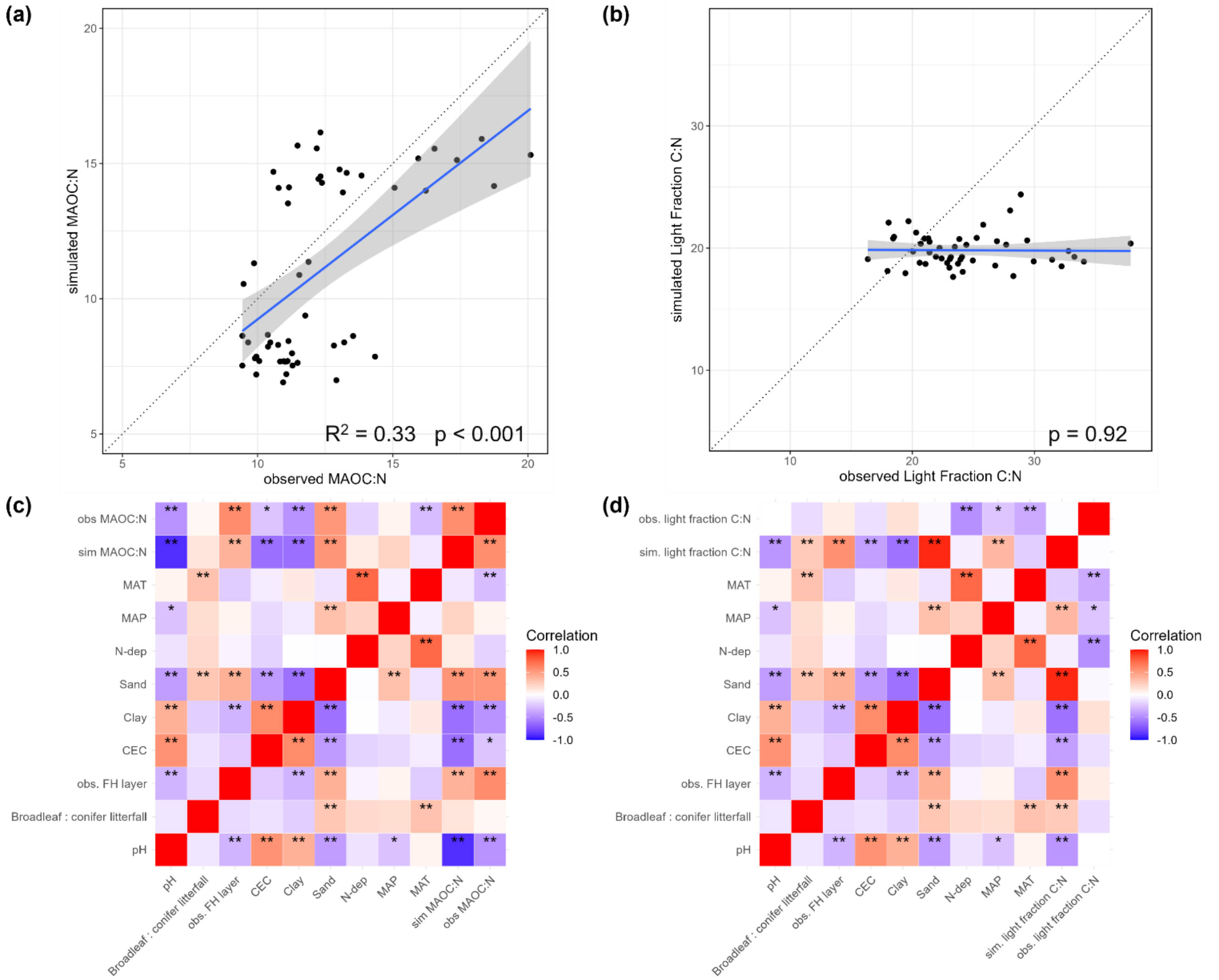
† Ambient Ndep is the contemporary N deposition level without artificial N addition.

3.3 Contemporary simulation: Organic matter proportions across Swiss forests

First, we evaluated MAOC:N and light fraction C:N as we used them as proxies that reflect the N-status of soils. Despite the models capturing MAOC:N reasonably including the correlations with environmental factors (R^2 = 0.33, P < 0.001, Fig. 5ac), this was not the case for light fraction C:N where models underestimated it substantially (Fig. 5b). Lower MAOC:N (N-rich) was mainly associated with warmer, high pH, high CEC and clayey sites (Fig. 5c). The observed light fraction C:N had a negative correlation with MAT, MAP and N deposition, which could not be captured by the simulation (Fig. 5bd).

Second, we evaluated the partial regression relationships between OM proportions and these C:N ratios (holding other predictors at their means). The observed proportion of MAOC to total SOC (coarse detritus not included) showed a significant negative relationship with MAOC:N (i.e., lower MAOC:N associating with more MAOC; Fig. 6a). The slope of this observed relationship was matched by the Nex_{retard} + $Nlim_{stim}$ models with dynamic CUE and microbial biomass feedback enabled (Table S3, p > 0.05). The observed ratios of MAOC: annual litter showed a positive but non-significant relationship with MAOC:N (Fig. 6b). This was again echoed only by the microbial model variants considering dynamic CUE and microbial biomass feedback (Table S3, p > 0.05), and the other models varied substantially from the observed trend. Lastly, the light fraction C: annual litter ratios had non-significant relationships with light fraction C:N in both observations and models.

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025



445 **Figure 5. A comparison of simulated and observed (a) MAOC:N, (b) Light Fraction C:N ratios, and (c & d) their respective correlations to environmental factors (** are correlations with P-value < 0.05, and * is P < 0.1). We averaged all model variants here since they produced very similar outputs.**

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

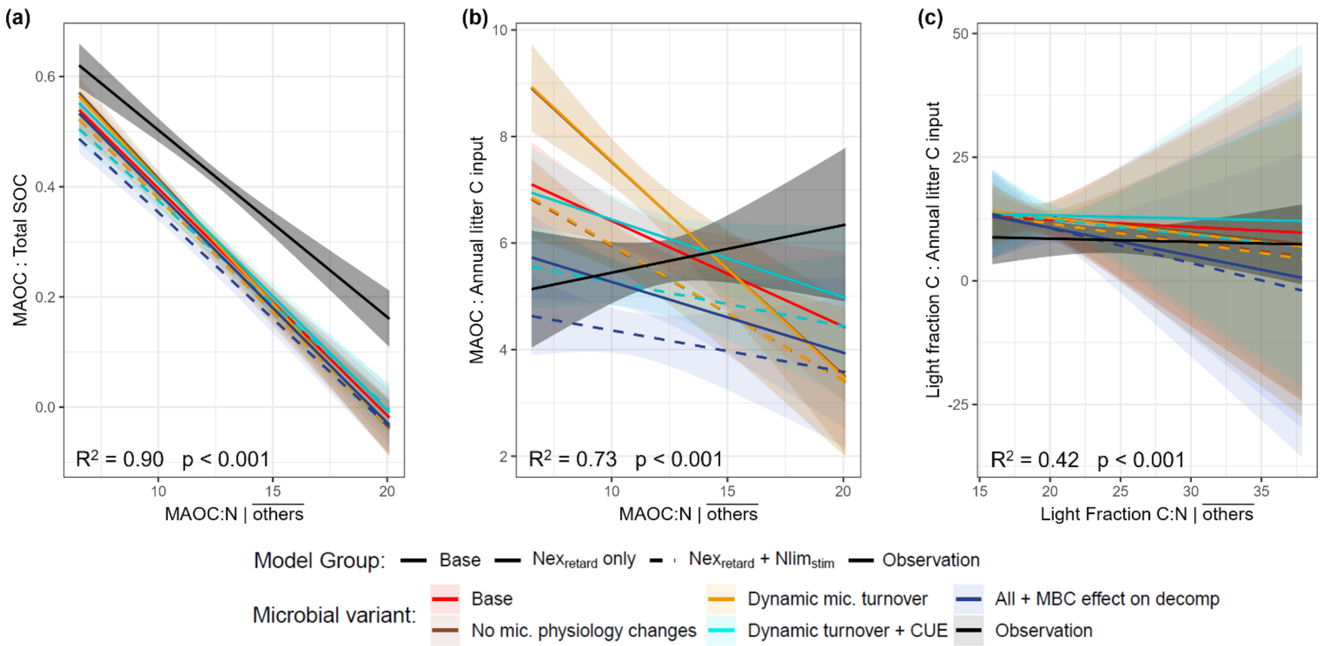


Figure 6. Partial regression plots of organic matter proportions against various C:N ratios (holding other predictors at mean levels): (a) MAOC: total SOC vs. MAOC:N, (b) MAOC: annual litter input vs. MAOC:N (c) Light Fraction C: annual litter input vs. light fraction C:N, of the 54 Swiss forest sites. Total SOC is defined as MAOC plus light fraction C (excluding coarse woody detritus, which was not measured), and annual litter inputs include all litter both woody and non-woody. In the regressions, the model variants together with observations constitute a categorical variable that interacts with the C:N ratios to detect differences between models and observations. The full multiple regression equations are documented in Table S3 and the adjusted R^2 and P-values in the plots correspond to these full regressions.

4. Discussion

To our knowledge, this is the first ever study that elucidates the diverse effects of N on multiple soil C pools (and Rh) across a large number of sites, with a hypothesis-driven model experiment. Previous studies typically adopted parameter adjustment to represent a one-off, static response to N in a process-deficient model (Chen et al., 2019; Eastman et al., 2024; Tonitto et al., 2014; Whittinghill et al., 2012), or derived detailed theoretical enzymatic models containing many uncertain parameters and hence difficult to verify the relevance of each process (Moorhead & Sinsabaugh, 2006; Schimel & Weintraub, 2003; Sinsabaugh & Shah, 2012; Wutzler et al., 2017). Below, we discussed the model performance of each model variant and then synthesized a coherent mechanistic picture of soil N-C interaction based on our findings.

4.1 Base model performance

The base model over-estimated topsoil SOC stocks, which have various potential causes. First, simulated C turnover rates may be too low, as the overestimation was greatly alleviated by an increase in SOC3 (MAOC) turnover. Second, the overestimation may arise due to the assumption of no-management, whereas in reality most Swiss forests have undergone past management that likely reduced C stocks (e.g., logging, deadwood removal, litter raking; Gimmi et al., 2013; Gosheva et al., 2017; Risch et al., 2008; Wäldchen et al., 2013). Furthermore, SOC stocks generally have longer turnover (hence recovery) times than LFH upon the cessation of management or disturbance (Hiltbrunner et al., 2013; Schulze et al., 2009), which may simultaneously explain why observed LFH:SOC tended to be higher than simulated LFH:SOC.

Modelling the effects of pH on soil C cycling is important but remains under-studied (Leifeld et al., 2008; Sinsabaugh et al., 2008; Wieder et al., 2013, 2015b). The contradictory results of the retarding effect of pH on decomposition (improving LFH but worsening SOC stocks) imply that the pH effect in CENTURY is not formulated properly. CENTURY assumes that all C pools experience the same pH in the soil profile (including coarse wood logs). In reality, the F and H horizons are usually the most acidic (Takahashi, 1997), more acidic than fresh litter, deadwood (Burgess-Conforti et al., 2019; Khanina et al., 2023) and mineral soils with increasing depth (Iwashima et al., 2012; Solly et al., 2020). Hence, the pH retardation effect may be weaker outside the FH horizons. A more realistic, non-uniform pH effect may be necessary. Moreover, pH has complex interactions with soil minerals and polyvalent ions to stabilize OM (Rowley et al., 2018; Solly et al., 2020; Ye et al., 2018), which is not considered in most models (Sokol et al., 2022).

In summary, the selected base model improved several variables when incorporating the pH effect on decomposition and bioturbation, and enhanced SOC3 turnover, but it overestimated topsoil SOC particularly under acidic conditions (irrespective of nitrogen effects). Nonetheless, we emphasize that matching exact C stock sizes is not the aim here, as we are mainly concerned with the response of various C pools under changing N availability.

4.2 Exogenous nitrogen effects on soil organic matter

Under N addition, model variants considering both decomposition retardation and stimulation (i.e., response to both N-excess and N-limitation, i.e., Nex_{retard} + $Nlim_{stim}$) reproduced the common pattern of a larger LFH increase compared to SOC, and of POC compared to MAOC under N addition qualitatively (cf. Liu & Greaver, 2010; Tang et al., 2023; Wu et al., 2023; Xu et al., 2021). These patterns aligned with our guiding hypothesis partially (Fig. 1). Mechanistically, they can be further explained as follows: POC and FH (i.e. light Fraction), not MAOC, receive C directly from detrital (e.g. deadwood) decomposition, which is stimulated by N addition (Allison et al., 2009; Bebber et al., 2011; Błońska et al., 2019; Kuyper et al., 2024; Lagomarsino et al., 2021). As a corollary, the MAOC response mainly depended on decomposition retardation because MAOC comprises less plant detritus-derived C (Whalen et al., 2022). In addition, the surface receives direct N addition and contain more detritus than the mineral soil (He et al., 2018; Kurz et al., 1996). Consequently, the surface tends to experience stronger N effects than the mineral soil.

In summary, N addition (range ≈ 40-150 kg N ha^{-1} y^{-1}) accelerates the decomposition of N-limited detritus, where the processed C becomes plant-derived organic matter (FH and POC, i.e., light fraction C). Furthermore, N retards the decomposition of all processed organic matter with lower C:N ratios i.e., both light fraction and MAOC (Fig. 7). Although

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

we did not have sufficient data to evaluate the response of detritus decomposition, this mechanism has been corroborated by many studies. Berg & Matzner (1997) and Knorr et al. (2005) found that the decomposition of fresh, N-limited litter was stimulated by N addition, contrary to the retardation in older, processed litter humus more enriched in lignin and nitrogen. Chen et al. (2015) found that N addition retarded litter decomposition in N-rich forests but not in N-limited forests in China. Bonanomi et al. (2017) found that high C:N substrates decomposed faster when inoculated to N-rich soils, but not for initially low C:N litter. Aside from leaf litter (the most commonly assessed litter), Allison et al. (2009) clearly demonstrated that wood decomposition was also stimulated by N addition at low dose (< 100 kg N ha^{-1} y^{-1}).

Many past studies attributed SOC accumulation under N addition to simplistic decomposition retardation through reduced microbial biomass (Lladó et al., 2017; Treseder, 2008; Wu et al., 2023; Xu et al., 2021). However, if the large increase of light fraction C is driven solely by decomposition retardation, it would be even harder to explain the short-term MAOC increase as MAOC receives roughly half of its C from the decomposition of light fraction (Angst et al., 2021; Whalen et al., 2022). Moreover, Rh was not reduced significantly in either simulations or meta-analysis, further implying that retardation may not be the sole mechanism. Considering the N-induced decomposition stimulation of N-limited detritus can resolve the inconsistency, a process absent in most soil models (Manzoni and Porporato, 2009).

Another advantage of including decomposer N-limitation responses (i.e., $Nlim_{stim}$ or N-responsive CUE, cf. Manzoni & Porporato, 2009) is the homeostasis of microbial biomass C:N. In the absence of either $Nlim_{stim}$ or N-responsive CUE, the simple Nex_{retard} models produced erroneous response under N addition (e.g., strongly negative LFH and microbial C:N response). The latter indicates a failure of microbial biomass C:N (hence TER) homeostasis, which paradoxically led to a larger decrease of TER than labile C:N under N addition (decreasing N excess, data not shown). That is, microbial C:N homeostasis is needed for constraining microbial N-limitation and excess. This suggests the need to incorporate N-limitation microbial response in models, but it remains unclear whether current models have improved in this regard since the seminal review conducted by Manzoni & Porporato (2009).

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

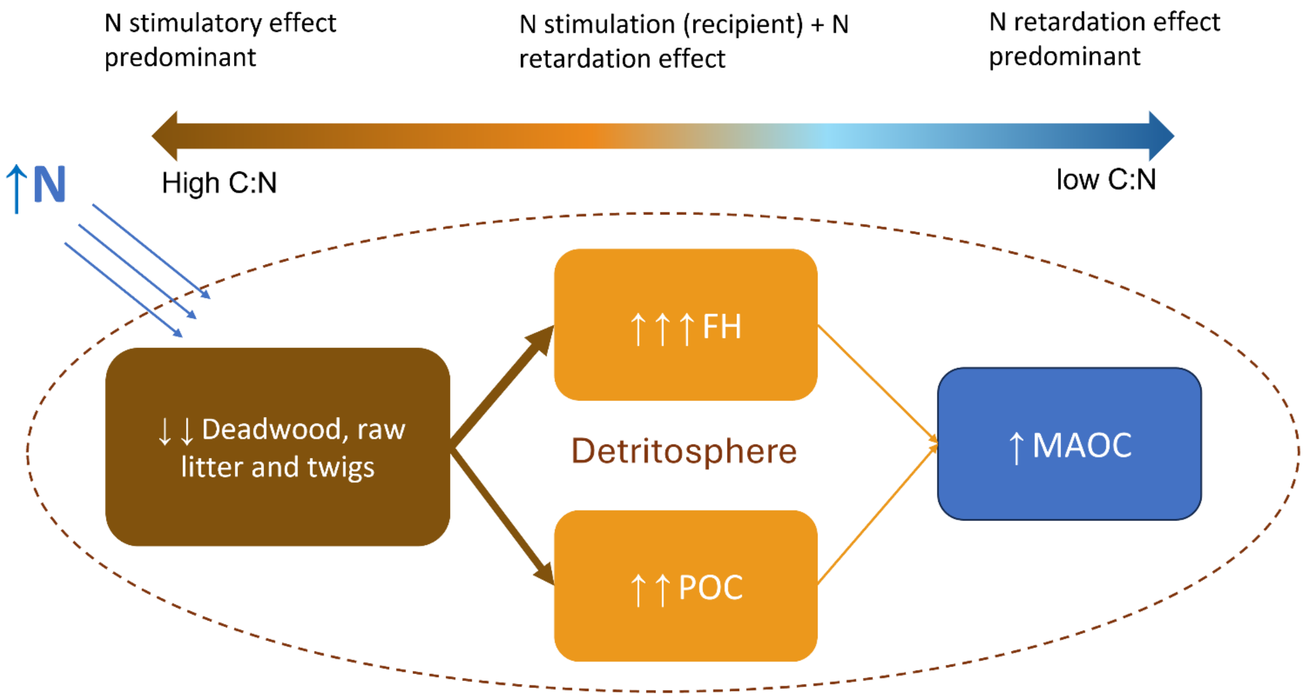


Figure 7. A synoptic overview of the main decomposition effects of boundary N inputs on various organic matter pools.

Faster microbial turnover drove the microbial biomass reduction under N addition, with minimal impacts on other C pools. A shift towards copiotrophic communities is indeed commonly observed under N addition (Fierer et al., 2012; Gravuer and Eskelinen, 2017; Leff et al., 2015; Zechmeister-Boltenstern et al., 2011; Zhou et al., 2017). Enabling dynamic CUE (mainly CUE reduction) also reduced microbial biomass, but this reduced the size of other C pools (light fraction and MAOC) that receive necromass (cf. Wang et al., 2021). In turn, enabling microbial biomass control (MB_eff) somewhat counteracted this reduction: as CUE decreases, biomass and necromass decrease, and a lower microbial biomass retards decomposition. This pathway of feedback to C cycle corresponds to the balance of "microbial priming vs. necromass entombment effect" in Liang et al. (2017). Altogether, enabling these microbial feedbacks mainly improved the responses of microbial attributes and Rh, but did not alter the main patterns driven by $Nlim_{stim}$.

Lastly, the retardation and stimulation effects are modulated by environmental factors (cf. Table 2). We found that cold soils are generally more prone to decomposition retardation. Indeed, a number of studies showed that colder, particularly boreal sites experienced more Rh reduction than warm sites (Chen et al., 2023; Guo et al., 2023; Marshall et al., 2021; Zhong et al., 2016). The likely explanation is that colder sites have smaller basal N fluxes, which translate to a larger N excess (hence retardation) when a fixed amount of N was added in experiments. In parallel, N addition favors copiotrophs and suppresses oligotrophic, ectomycorrhizal communities more common in cold forests, resulting in a stronger decomposition retardation

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

of recalcitrant substrates (Kuyper et al., 2024; Lilleskov et al., 2019; Zhou et al., 2017). In contrast, in warm sites, the N-induced responses of soil C are driven primarily by the decomposition stimulation of detritus. Decomposers have high potential activities in warm favorable conditions but are limited by N in detritus (Allison et al., 2009; Cai et al., 2024; Maslov and Maslova, 2021). As a result, N addition releases this limitation and promotes decomposition (Fig. 7).

4.3 Contemporary nitrogen effect on soil organic matter

Despite the poorly simulated light fraction C:N, we found strong negative relationships between MAOC:N and MAOC:total SOC in both observations and models (here, total SOC = MAOC + light fraction C). We interpret this as N-rich (low MAOC:N) soils favoring the formation and/or protection of MAOC in the long term. First, N-rich, labile litter contains more water-soluble compounds (instead of structural compounds) that may readily form MAOC (instead of the light fraction C) (Cotrufo et al., 2013, 2015; Sokol et al., 2022). This is accounted for in the base model, and hence all models inherited this negative relationship. Second, the remaining difference between models is explained by how N influenced MAOC and light fraction C accumulation, where 1) the Nex_{retard} + $Nlim_{stim}$ models favored light fraction, but 2) the Nex_{retard} models favored MAOC at low MAOC:N. Our validation showed that light fraction C may accumulate more readily than MAOC under the N conditions in Swiss forest soils, similar to our findings regarding N addition.

However, this negative trend disappears when considering the relationship between MAOC:N and MAOC:total litter C input, which reveals the overall conversion efficiency of detrital C to MAOC and its persistence after conversion. In high MAOC:N soils (coinciding with cold, coniferous, acidic, thick organic layer), the ratio of MAOC:total litter C is maintained (hence, no negative trend), due to 1) the slower MAOC turnover in these soils (Kleber et al., 2015; Shi et al., 2020), and 2) the abundant dissolved C released in coniferous forest floors throughout the year (instead of just in autumn), which is conducive to the formation of MAOC (Andivia et al., 2016; Bramble et al., 2024; Córdova et al., 2018). Our models do not contain dissolved C dynamics and hence underestimated the conversion to MAOC in these high MAOC:N soils. Moreover, there was an overestimated conversion to MAOC at low MAOC:N, but including more microbial feedbacks alleviated this, possibly due to reduced microbial processing and necromass entombment.

Nonetheless, the differences between model variants were small unlike in N-addition simulations. A possible explanation is that the contemporary N gradient in these regional forests is small, or at least insufficiently accounted for by the model inputs we used (e.g., our contemporary N deposition input data are likely underestimated, cf. Gharun et al. (2021)). Moreover, undisturbed temperate forests internally recycle at least 70% of the N from the breakdown of OM (Cleveland et al., 2013; Spohn et al., 2021), which negates any retardation effect N might have (i.e., internally recycled N has a different effect than exogenous N). Nonetheless, without accurate and complete boundary N input data (N deposition, N fixation, and even pedogenic N sources, cf. Houlton et al., 2018), it remains difficult to evaluate the true impact of in-situ N gradients on soil organic matter.

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

4.4 Limitations

We acknowledge that the simulated N addition responses are only qualitatively comparable to the meta-analysis responses, as their environmental gradient coverage differs slightly (cf. Table S2). For SOC, POC, MAOC responses, the meta-analyses encompass warmer and wetter sites than the 54 Swiss forests. Hence, these sites in the meta-analyses might experience stronger N-induced detrital decomposition stimulation, according to our analysis of environmental correlates (cf. Table 2). This possibly drove the clearer patterns of LFH > SOC increase and POC > MAOC increase in the meta-analysis. In contrast, the meta-analysis of Rh featured colder and drier sites than our 54 forests. Colder and drier sites have smaller base N fluxes and hence are prone to decomposition retardation under N excess. This may explain why the meta-analysis Rh responses were in more negative ranges than the simulated outputs. Furthermore, the deadwood response influenced the responses of FH and POC pools and the overall belowground C balance strongly. However, deadwood data remains scarce, and many studies concluded net soil C sequestration without considering deadwood, which should be cautioned. Lastly, due to the limited number of observations, we did not further split the dataset to validate possible duration- and dose-dependent responses, which may be valuable to further improve the reliability of SOC projections (Le Noë et al., 2023).

Causal attribution is another challenge. Feedback to plant litter production and soil acidification are two other possibilities that have been implicated to explain N addition effects on soil C. First, nitrogen addition generally increases aboveground litterfall, which would increase and potentially improve the LFH response (Chen et al., 2015; Janssens et al., 2010). Root litter tends to decrease or stay relatively constant, which may have uncertain influence on SOC stocks (Chen et al., 2015; Feng et al., 2023; Frey et al., 2014; Peng et al., 2017; Yue et al., 2021). However, our study, as well as many others (cf. Bowden et al., 2019; Frey et al., 2014; Hagedorn et al., 2003; Liu et al., 2024) challenged the assumption that plant litter is the dominant response to N, given our Nex_{retard} + $Nlim_{stim}$ models captured multiple observational patterns without considering plant response. Nevertheless, the $Nlim_{stim}$ effect by definition interacts synergistically with plant litter inputs, further model tests with litter response enabled are still valuable (Xia et al., 2018).

Second, acidification suppresses decomposition (Averill and Waring, 2018; Tian and Niu, 2015; Wu et al., 2023; Ye et al., 2018). Our minimum Nex_{retard} parameter (i.e., maximum retardation effect) does not distinguish the cause of decomposition decline since N addition rate, N-surplus and pH decrease are generally collinear (Tian and Niu, 2015; Zhou et al., 2017), and hence our Nex_{retard} effect may implicitly include an acidification effect already. Nonetheless, studies showed that N addition and acid addition (or acidic soils) drove different microbial community patterns, as N addition predominantly increased copiotrophic taxa that overshadow the selection of oligotrophs (e.g., Acidobacteria) under acidic conditions (Bardhan et al., 2012; Choma et al., 2020; Fierer et al., 2012; Lauber et al., 2009; Zhou et al., 2017). Furthermore, Ramirez et al. (2010) found that even alkaline N compounds retarded decomposition, and acidification also cannot explain potential decomposition stimulation highlighted by our study. Therefore, N likely has a stronger, direct selection effect on microbes and enzymes, and N-induced acidification effects are secondary unless when there is extreme acidification (e.g., in agricultural lands), a conclusion also supported by the meta-analysis of Zhou et al. (2017).

Another uncertainty is the lack of MAOC response in our N addition simulations (Fig. 4D). However, MAOC did respond on a longer time scale in the Nex_{retard} + $Nlim_{stim}$ models (cf. Fig. S3), close to the response in temperate forests reported by Wu et al. (2023). This implies that the simulated MAOC turnover is too low to have a detectable short-term response, which echoes the findings of our base model. The likely reason is that experimentally fractionated MAOC contains sub-fractions of labile, fast-turnover compounds, which are not represented by the modelled "homogeneously-stable" MAOC (Brunmayr et al., 2024; Guo et al., 2022; Schrumpf & Kaiser, 2015; Sokol et al., 2022). The turnover times of MAOC vary from decades to millennia (Guo et al., 2022; Kleber et al., 2015; Lavallee et al., 2020), but the current MAOC maximum turnover parameter cannot reproduce decadal turnover times even under optimal soil conditions. Increasing the MAOC turnover parameter value, or further separating MAOC into sub-fractions may hence be necessary.

4.5 Outlooks

The recent review by Kuyper et al. (2024) and the study by Eastman et al. (2024) found a lack of soil models capable of explaining the diversity of C responses to N. To our knowledge, we presented the first process-based model capable of reproducing multiple C responses to exogenous N addition. Despite the limitations, we gained significant ecological knowledge with our hypothesis-driven, incremental model variants. Our approach (similar to Zhang et al. (2020)) is different than common approaches such as whole-model comparisons and parameter tuning that encompass many confounding changes at once and are difficult to test ecological hypotheses, and to extrapolate model findings (Wieder et al., 2015b). We thus highly encourage future model studies to adopt a similar hypothesis-driven approach.

Our simplified implicit representation of enzymatic processes may be an additional advantage. We based our models on only two endogenously-calculated variables: labile C:N and TER, as enzymes are largely a function of labile resources supply and demand (Sinsabaugh and Shah, 2012). This greatly reduces the parameter requirement to explicitly describe various kinetics, growth, allocation, and nutrient use efficiency responses in enzymatic models, which are often hard to estimate and hence relegated to assumptions (Chandel et al., 2023; Moorhead et al., 2012; Moorhead & Sinsabaugh, 2006; Schimel & Weintraub, 2003; Wang et al., 2013). Our simple formulations permit easy implementation in any dynamic soil CN model that calculates labile (readily-available) C:N and microbial biomass C:N.

Lastly, our model may be useful in other global change contexts (e.g., elevated CO_2 and warming) that entails changes in labile C and N availability. For instance, elevated CO_2 may increase labile C:N and intensify N-limitation, resulting in responses such as detrital decomposition retardation and microbial N mining (decomposition stimulation) from native SOM (Chen et al., 2014). Altogether, we encourage the use of our model (particularly the Nex_{retard} + $Nlim_{stim}$ model containing microbial feedbacks up to dynamic CUE) for further testing and ecological applications.

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

5. Conclusion

Through our hypothesis-driven model experiment, we demonstrated that incorporating direct N effects on decomposer alone can reconcile model outputs with multiple observed patterns in soils, challenging the common assumption that plant is the primary respondent to N. Under N addition, models that included the decomposition stimulation response under decreasing N limitation could reproduce a larger increase of LFH compared to topsoil SOC, as well as POC compared to MAOC commonly observed in experiments. Implementing dynamic microbial turnover drove microbial biomass reduction, while dynamic CUE was critical for maintaining microbial C:N homeostasis to prevent erroneous estimation of N-limitation and excess. Based on these results, we propose that N addition influences soil C dynamics primarily by speeding up high C:N detritus decomposition, while retarding the decomposition of processed OM with lower C:N ratios, as hypothesized. However, the intermediate pools POC and FH (the light fraction) showed the largest positive responses because they receive C directly from detritus decomposition, despite not having the lowest C:N ratio. Consequently, at contemporary levels of N deposition, we expect that most temperate forests will accumulate (or have accumulated) light fraction C predominantly, likely at the expense of high C:N detritus. Altogether, our model experiment provided robust mechanistic insights to soil N-C interaction, and we recommend our simple model for further testing and ecological applications.

References

Allison, S. D., Czimczik, C. I., and Treseder, K. K.: Microbial activity and soil respiration under nitrogen addition in Alaskan boreal forest, Global Change Biology, 14, 1156–1168, https://doi.org/10.1111/j.1365-2486.2008.01549.x, 2008.

Allison, S. D., LeBauer, D. S., Ofrecio, M. R., Reyes, R., Ta, A.-M., and Tran, T. M.: Low levels of nitrogen addition stimulate decomposition by boreal forest fungi, Soil Biology and Biochemistry, 41, 293–302, https://doi.org/10.1016/j.soilbio.2008.10.032, 2009.

Andivia, E., Rolo, V., Jonard, M., Formánek, P., and Ponette, Q.: Tree species identity mediates mechanisms of top soil carbon sequestration in a Norway spruce and European beech mixed forest, Annals of Forest Science, 73, 437–447, https://doi.org/10.1007/s13595-015-0536-z, 2016.

Angst, G., Mueller, K. E., Nierop, K. G., and Simpson, M. J.: Plant-or microbial-derived? A review on the molecular composition of stabilized soil organic matter, Soil Biology and Biochemistry, 156, 108189, 2021.

Averill, C. and Waring, B.: Nitrogen limitation of decomposition and decay: How can it occur?, Global Change Biology, 24, 1417–1427, https://doi.org/10.1111/gcb.13980, 2018.

Baltensweiler, A., Walthert, L., Hanewinkel, M., Zimmermann, S., and Nussbaum, M.: Machine learning based soil maps for a wide range of soil properties for the forested area of Switzerland, Geoderma Regional, 27, e00437, https://doi.org/10.1016/j.geodrs.2021.e00437, 2021.

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

Bardhan, S., Jose, S., Jenkins, M. A., Webster, C. R., Udawatta, R. P., and Stehn, S. E.: Microbial community diversity and composition across a gradient of soil acidity in spruce–fir forests of the southern Appalachian Mountains, Applied Soil Ecology, 61, 60–68, https://doi.org/10.1016/j.apsoil.2012.04.010, 2012.

Bebber, D. P., Watkinson, S. C., Boddy, L., and Darrah, P. R.: Simulated nitrogen deposition affects wood decomposition by cord-forming fungi, Oecologia, 167, 1177–1184, https://doi.org/10.1007/s00442-011-2057-2, 2011.

Berardi, D. M., Hartman, M. D., Brzostek, E. R., Bernacchi, C. J., DeLucia, E. H., von Haden, A. C., Kantola, I., Moore, C. E., Yang, W. H., Hudiburg, T. W., and others: Microbial-explicit processes and refined perennial plant traits improve modeled ecosystem carbon dynamics, Geoderma, 443, 116851, https://doi.org/10.1016/j.geoderma.2024.116851, 2024.

Berg, B. and Matzner, E.: Effect of N deposition on decomposition of plant litter and soil organic matter in forest systems, Environ. Rev., 5, 1–25, https://doi.org/10.1139/a96-017, 1997.

Błońska, E., Lasota, J., Tullus, A., Lutter, R., and Ostonen, I.: Impact of deadwood decomposition on soil organic carbon sequestration in Estonian and Polish forests, Annals of Forest Science, 76, 102, https://doi.org/10.1007/s13595-019-0889-9, 2019.

Bonan, G. B. and Levis, S.: Quantifying carbon-nitrogen feedbacks in the Community Land Model (CLM4), Geophysical Research Letters, 37, https://doi.org/10.1029/2010GL042430, 2010.

Bonanomi, G., Cesarano, G., Gaglione, S. A., Ippolito, F., Sarker, T., and Rao, M. A.: Soil fertility promotes decomposition rate of nutrient poor, but not nutrient rich litter through nitrogen transfer, Plant Soil, 412, 397–411, https://doi.org/10.1007/s11104-016-3072-1, 2017.

Bouskill, N. J., Riley, W. J., and Tang, J. Y.: Meta-analysis of high-latitude nitrogen-addition and warming studies implies ecological mechanisms overlooked by land models, Biogeosciences, 11, 6969–6983, https://doi.org/10.5194/bg-11-6969-2014, 2014.

Bowden, R. D., Wurzbacher, S. J., Washko, S. E., Wind, L., Rice, A. M., Coble, A. E., Baldauf, N., Johnson, B., Wang, J.-J., Simpson, M., and Lajtha, K.: Long-term Nitrogen Addition Decreases Organic Matter Decomposition and Increases Forest Soil Carbon, Soil Science Society of America Journal, 83, S82–S95, https://doi.org/10.2136/sssaj2018.08.0293, 2019.

Bradford, M. A., Veen, G. F. (Ciska), Bonis, A., Bradford, E. M., Classen, A. T., Cornelissen, J. H. C., Crowther, T. W., De Long, J. R., Freschet, G. T., Kardol, P., Manrubia-Freixa, M., Maynard, D. S., Newman, G. S., Logtestijn, R. S. P., Viketoft, M., Wardle, D. A., Wieder, W. R., Wood, S. A., and van der Putten, W. H.: A test of the hierarchical model of litter decomposition, Nat Ecol Evol, 1, 1836–1845, https://doi.org/10.1038/s41559-017-0367-4, 2017.

Bramble, D. S. E., Ulrich, S., Schöning, I., Mikutta, R., Brandt, L., Poll, C., Kandeler, E., Mikutta, C., Konrad, A., Siemens, J., Yang, Y., Polle, A., Schall, P., Ammer, C., Kaiser, K., and Schrumpf, M.: Formation of mineral-associated organic matter in temperate soils is primarily controlled by mineral type and modified by land use and management intensity, Global Change Biology, 30, e17024, https://doi.org/10.1111/gcb.17024, 2024.

Bruni, E., Chenu, C., Abramoff, R. Z., Baldoni, G., Barkusky, D., Clivot, H., Huang, Y., Kätterer, T., Pikuła, D., Spiegel, H., Virto, I., and Guenet, B.: Multi-modelling predictions show high uncertainty of required carbon input changes to reach a 4‰ target, European Journal of Soil Science, 73, e13330, https://doi.org/10.1111/ejss.13330, 2022.

Brunmayr, A. S., Hagedorn, F., Moreno Duborgel, M., Minich, L. I., and Graven, H. D.: Radiocarbon analysis reveals underestimation of soil organic carbon persistence in new-generation soil models, Geoscientific Model Development, 17, 5961–5985, https://doi.org/10.5194/gmd-17-5961-2024, 2024.

Bugmann, H. K. M.: A Simplified Forest Model to Study Species Composition Along Climate Gradients, Ecology, 77, 2055–2074, https://doi.org/10.2307/2265700, 1996.

Burgess-Conforti, J. R., Moore, P. A., Owens, P. R., Miller, D. M., Ashworth, A. J., Hays, P. D., Evans-White, M. A., and Anderson, K. R.: Are soils beneath coniferous tree stands more acidic than soils beneath deciduous tree stands?, Environ Sci Pollut Res, 26, 14920–14929, https://doi.org/10.1007/s11356-019-04883-y, 2019.

Cai, M., Zhang, Y., Zhao, G., Zhao, B., Cong, N., Zhu, J., Zheng, Z., Wu, W., and Duan, X.: Excessive climate warming exacerbates nitrogen limitation on microbial metabolism in an alpine meadow of the Tibetan Plateau: Evidence from soil ecoenzymatic stoichiometry, Science of The Total Environment, 930, 172731, https://doi.org/10.1016/j.scitotenv.2024.172731, 2024.

Carreiro, M. M., Sinsabaugh, R. L., Repert, D. A., and Parkhurst, D. F.: Microbial Enzyme Shifts Explain Litter Decay Responses to Simulated Nitrogen Deposition, Ecology, 81, 2359–2365, https://doi.org/10.1890/0012-9658(2000)081[2359:MESELD]2.0.CO;2, 2000.

Chandel, A. K., Jiang, L., and Luo, Y.: Microbial Models for Simulating Soil Carbon Dynamics: A Review, Journal of Geophysical Research: Biogeosciences, 128, e2023JG007436, https://doi.org/10.1029/2023JG007436, 2023.

Chen, H., Li, D., Gurmesa, G. A., Yu, G., Li, L., Zhang, W., Fang, H., and Mo, J.: Effects of nitrogen deposition on carbon cycle in terrestrial ecosystems of China: A meta-analysis, Environmental Pollution, 206, 352–360, https://doi.org/10.1016/j.envpol.2015.07.033, 2015.

Chen, H., Li, D., Zhao, J., Xiao, K., and Wang, K.: Effects of nitrogen addition on activities of soil nitrogen acquisition enzymes： A meta-analysis, Agriculture, Ecosystems & Environment, 252, 126–131, https://doi.org/10.1016/j.agee.2017.09.032, 2018a.

Chen, J., Luo, Y., van Groenigen, K. J., Hungate, B. A., Cao, J., Zhou, X., and Wang, R.: A keystone microbial enzyme for nitrogen control of soil carbon storage, Science Advances, 4, eaaq1689, https://doi.org/10.1126/sciadv.aaq1689, 2018b.

Chen, J., Xiao, W., Zheng, C., and Zhu, B.: Nitrogen addition has contrasting effects on particulate and mineral-associated soil organic carbon in a subtropical forest, Soil Biology and Biochemistry, 142, 107708, https://doi.org/10.1016/j.soilbio.2020.107708, 2020.

Chen, R., Senbayram, M., Blagodatsky, S., Myachina, O., Dittert, K., Lin, X., Blagodatskaya, E., and Kuzyakov, Y.: Soil C and N availability determine the priming effect: microbial N mining and stoichiometric decomposition theories, Global Change Biology, 20, 2356–2367, https://doi.org/10.1111/gcb.12475, 2014.

Chen, Y., Chen, J., and Luo, Y.: Data-driven ENZYme (DENZY) model represents soil organic carbon dynamics in forests impacted by nitrogen deposition, Soil Biology and Biochemistry, 138, 107575, https://doi.org/10.1016/j.soilbio.2019.107575, 2019.

Chen, Y., Xia, A., Zhang, Z., Wang, F., Chen, J., Hao, Y., and Cui, X.: Extracellular enzyme activities response to nitrogen addition in the rhizosphere and bulk soil: A global meta-analysis, Agriculture, Ecosystems & Environment, 356, 108630, https://doi.org/10.1016/j.agee.2023.108630, 2023.

Cheng, S., Fang, H., and Yu, G.: Threshold responses of soil organic carbon concentration and composition to multi-level nitrogen addition in a temperate needle-broadleaved forest, Biogeochemistry, 137, 219–233, https://doi.org/10.1007/s10533-017-0412-z, 2018.

Choma, M., Tahovská, K., Kaštovská, E., Bárta, J., Růžek, M., and Oulehle, F.: Bacteria but not fungi respond to soil acidification rapidly and consistently in both a spruce and beech forest, FEMS Microbiology Ecology, 96, fiaa174, https://doi.org/10.1093/femsec/fiaa174, 2020.

Cleveland, C. C., Townsend, A. R., Schimel, D. S., Fisher, H., Howarth, R. W., Hedin, L. O., Perakis, S. S., Latty, E. F., Von Fischer, J. C., Elseroad, A., and Wasson, M. F.: Global patterns of terrestrial biological nitrogen (N2) fixation in natural ecosystems, Global Biogeochemical Cycles, 13, 623–645, https://doi.org/10.1029/1999GB900014, 1999.

Cleveland, C. C., Houlton, B. Z., Smith, W. K., Marklein, A. R., Reed, S. C., Parton, W., Del Grosso, S. J., and Running, S. W.: Patterns of new versus recycled primary production in the terrestrial biosphere, Proceedings of the National Academy of Sciences, 110, 12733–12737, https://doi.org/10.1073/pnas.1302768110, 2013.

Córdova, S. C., Olk, D. C., Dietzel, R. N., Mueller, K. E., Archontouilis, S. V., and Castellano, M. J.: Plant litter quality affects the accumulation rate, composition, and stability of mineral-associated soil organic matter, Soil Biology and Biochemistry, 125, 115–124, https://doi.org/10.1016/j.soilbio.2018.07.010, 2018.

Cotrufo, M. F. and Lavallee, J. M.: Chapter One - Soil organic matter formation, persistence, and functioning: A synthesis of current understanding to inform its conservation and regeneration, in: Advances in Agronomy, vol. 172, edited by: Sparks, D. L., Academic Press, 1–66, https://doi.org/10.1016/bs.agron.2021.11.002, 2022.

Cotrufo, M. F., Wallenstein, M. D., Boot, C. M., Denef, K., and Paul, E.: The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter?, Global Change Biology, 19, 988–995, https://doi.org/10.1111/gcb.12113, 2013.

Cotrufo, M. F., Soong, J. L., Horton, A. J., Campbell, E. E., Haddix, M. L., Wall, D. H., and Parton, W. J.: Formation of soil organic matter via biochemical and physical pathways of litter mass loss, Nature Geosci, 8, 776–779, https://doi.org/10.1038/ngeo2520, 2015.

Cui, Y., Moorhead, D. L., Peng, S., and Sinsabaugh, R. L.: New insights into the patterns of ecoenzymatic stoichiometry in soil and sediment, Soil Biology and Biochemistry, 177, 108910, https://doi.org/10.1016/j.soilbio.2022.108910, 2023.

Desie, E., Van Meerbeek, K., De Wandeler, H., Bruelheide, H., Domisch, T., Jaroszewicz, B., Joly, F.-X., Vancampenhout, K., Vesterdal, L., and Muys, B.: Positive feedback loop between earthworms, humus form and soil pH reinforces earthworm abundance in European forests, Functional Ecology, 34, 2598–2610, https://doi.org/10.1111/1365-2435.13668, 2020.

Eastman, B. A., Wieder, W. R., Hartman, M. D., Brzostek, E. R., and Peterjohn, W. T.: Can models adequately reflect how long-term nitrogen enrichment alters the forest soil carbon cycle?, Biogeosciences, 21, 201–221, https://doi.org/10.5194/bg-21-201-2024, 2024.

Feng, H., Guo, J., Peng, C., Kneeshaw, D., Roberge, G., Pan, C., Ma, X., Zhou, D., and Wang, W.: Nitrogen addition promotes terrestrial plants to allocate more biomass to aboveground organs: A global meta-analysis, Global Change Biology, 29, 3970–3989, https://doi.org/10.1111/gcb.16731, 2023.

Fierer, N., Lauber, C. L., Ramirez, K. S., Zaneveld, J., Bradford, M. A., and Knight, R.: Comparative metagenomic, phylogenetic and physiological analyses of soil microbial communities across nitrogen gradients, ISME J, 6, 1007–1017, https://doi.org/10.1038/ismej.2011.159, 2012.

Franklin, O., Högberg, P., Ekblad, A., and Ågren, G. I.: Pine Forest Floor Carbon Accumulation in Response to N and PK Additions: Bomb 14C Modelling and Respiration Studies, Ecosystems, 6, 644–658, https://doi.org/10.1007/s10021-002-0149-x, 2003.

Frey, S. D., Ollinger, S., Nadelhoffer, K., Bowden, R., Brzostek, E., Burton, A., Caldwell, B. A., Crow, S., Goodale, C. L., Grandy, A. S., Finzi, A., Kramer, M. G., Lajtha, K., LeMoine, J., Martin, M., McDowell, W. H., Minocha, R., Sadowsky, J. J., Templer, P. H., and Wickings, K.: Chronic nitrogen additions suppress decomposition and sequester soil carbon in temperate forests, Biogeochemistry, 121, 305–316, https://doi.org/10.1007/s10533-014-0004-0, 2014.

Gallo, M., Amonette, R., Lauber, C., Sinsabaugh, R. L., and Zak, D. R.: Microbial Community Structure and Oxidative Enzyme Activity in Nitrogen-amended North Temperate Forest Soils, Microb Ecol, 48, 218–229, https://doi.org/10.1007/s00248-003-9001-x, 2004.

Galloway, J. N., Townsend, A. R., Erisman, J. W., Bekunda, M., Cai, Z., Freney, J. R., Martinelli, L. A., Seitzinger, S. P., and Sutton, M. A.: Transformation of the Nitrogen Cycle: Recent Trends, Questions, and Potential Solutions, Science, 320, 889–892, https://doi.org/10.1126/science.1136674, 2008.

Geisseler, D., Horwath, W. R., Joergensen, R. G., and Ludwig, B.: Pathways of nitrogen utilization by soil microorganisms–a review, Soil Biology and Biochemistry, 42, 2058–2067, https://doi.org/10.1016/j.soilbio.2010.08.021, 2010.

Gharun, M., Klesse, S., Tomlinson, G., Waldner, P., Stocker, B., Rihm, B., Siegwolf, R., and Buchmann, N.: Effect of nitrogen deposition on centennial forest water-use efficiency, Environ. Res. Lett., 16, 114036, https://doi.org/10.1088/1748-9326/ac30f9, 2021.

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

Gimmi, U., Poulter, B., Wolf, A., Portner, H., Weber, P., and Bürgi, M.: Soil carbon pools in Swiss forests show legacy effects from historic forest litter raking, Landscape Ecol, 28, 835–846, https://doi.org/10.1007/s10980-012-9778-4, 2013.

González-Domínguez, B., Niklaus, P. A., Studer, M. S., Hagedorn, F., Wacker, L., Haghipour, N., Zimmermann, S., Walthert, L., McIntyre, C., and Abiven, S.: Temperature and moisture are minor drivers of regional-scale soil organic carbon dynamics, Sci Rep, 9, 6422, https://doi.org/10.1038/s41598-019-42629-5, 2019.

Gosheva, S.: The drivers of SOC storage: the effect of climate, forest age, and physicochemical soil properties in Swiss forest soils, Doctoral Dissertation, University of Zurich, 2017.

Gosheva, S., Walthert, L., Niklaus, P. A., Zimmermann, S., Gimmi, U., and Hagedorn, F.: Reconstruction of Historic Forest Cover Changes Indicates Minor Effects on Carbon Stocks in Swiss Forest Soils, Ecosystems, 20, 1512–1528, https://doi.org/10.1007/s10021-017-0129-9, 2017.

Gravuer, K. and Eskelinen, A.: Nutrient and Rainfall Additions Shift Phylogenetically Estimated Traits of Soil Microbial Communities, Frontiers in Microbiology, 8, 2017.

Griepentrog, M., Bodé, S., Boeckx, P., Hagedorn, F., Heim, A., and Schmidt, M. W. I.: Nitrogen deposition promotes the production of new fungal residues but retards the decomposition of old residues in forest soil fractions, Global Change Biology, 20, 327–340, https://doi.org/10.1111/gcb.12374, 2014.

Griepentrog, M., Eglinton, T. I., Hagedorn, F., Schmidt, M. W. I., and Wiesenberg, G. L. B.: Interactive effects of elevated CO2 and nitrogen deposition on fatty acid molecular and isotope composition of above- and belowground tree biomass and forest soil fractions, Global Change Biology, 21, 473–486, https://doi.org/10.1111/gcb.12666, 2015.

Guenet, B., Moyano, F. E., Peylin, P., Ciais, P., and Janssens, I. A.: Towards a representation of priming on soil carbon decomposition in the global land biosphere model ORCHIDEE (version 1.9.5.2), Geoscientific Model Development, 9, 841–855, https://doi.org/10.5194/gmd-9-841-2016, 2016.

Gundersen, P., Emmett, B., Kjønaas, O., Koopmans, C., and Tietema, A.: Impact of nitrogen deposition on nitrogen cycling in forests: a synthesis of NITREX data, Forest Ecology and management, 101, 37–55, https://doi.org/10.1016/S0378-1127(97)00124-2, 1998.

Guo, P., Kong, D., Yang, L., and Sun, X.: Differences in Characteristics of Sample Sites Explain Variable Responses of Soil Microbial Biomass to Nitrogen Addition: A Meta-Analysis, Ecosystems, 26, 1703–1715, https://doi.org/10.1007/s10021-023-00859-9, 2023.

Guo, X., Viscarra Rossel, R. A., Wang, G., Xiao, L., Wang, M., Zhang, S., and Luo, Z.: Particulate and mineral-associated organic carbon turnover revealed by modelling their long-term dynamics, Soil Biology and Biochemistry, 173, 108780, https://doi.org/10.1016/j.soilbio.2022.108780, 2022.

Hagedorn, F., Spinnler, D., and Siegwolf, R.: Increased N deposition retards mineralization of old soil organic matter, Soil Biology and Biochemistry, 35, 1683–1692, https://doi.org/10.1016/j.soilbio.2003.08.015, 2003.

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

Hagedorn, F., Kammer, A., Schmidt, M. W. I., and Goodale, C. L.: Nitrogen addition alters mineralization dynamics of 13C-depleted leaf and twig litter and reduces leaching of older DOC from mineral soil, Global Change Biology, 18, 1412–1427, https://doi.org/10.1111/j.1365-2486.2011.02603.x, 2012.

He, H., Zhang, C., Zhao, X., Fousseni, F., Wang, J., Dai, H., Yang, S., and Zuo, Q.: Allometric biomass equations for 12 tree species in coniferous and broadleaved mixed forests, Northeastern China, PLOS ONE, 13, e0186226, https://doi.org/10.1371/journal.pone.0186226, 2018.

Hiltbrunner, D., Zimmermann, S., and Hagedorn, F.: Afforestation with Norway spruce on a subalpine pasture alters carbon dynamics but only moderately affects soil carbon storage, Biogeochemistry, 115, 251–266, https://doi.org/10.1007/s10533-013-9832-6, 2013.

Hobbie, S. E., Eddy, W. C., Buyarski, C. R., Adair, E. C., Ogdahl, M. L., and Weisenhorn, P.: Response of decomposing litter and its microbial community to multiple forms of nitrogen enrichment, Ecological Monographs, 82, 389–405, https://doi.org/10.1890/11-1600.1, 2012.

Houlton, B. Z., Morford, S. L., and Dahlgren, R. A.: Convergent evidence for widespread rock nitrogen sources in Earth's surface environment, Science, 360, 58–62, https://doi.org/10.1126/science.aan4399, 2018.

Huber, N., Bugmann, H., Cailleret, M., Bircher, N., and Lafond, V.: Stand-scale climate change impacts on forests over large areas: transient responses and projection uncertainties, Ecological Applications, 31, e02313, https://doi.org/10.1002/eap.2313, 2021.

Iwashima, N., Masunaga, T., Fujimaki, R., Toyota, A., Tayasu, I., Hiura, T., and Kaneko, N.: Effect of vegetation switch on soil chemical properties, Soil Science and Plant Nutrition, 58, 783–792, https://doi.org/10.1080/00380768.2012.738183, 2012.

Janssens, I. A., Dieleman, W., Luyssaert, S., Subke, J.-A., Reichstein, M., Ceulemans, R., Ciais, P., Dolman, A. J., Grace, J., Matteucci, G., Papale, D., Piao, S. L., Schulze, E.-D., Tang, J., and Law, B. E.: Reduction of forest soil respiration in response to nitrogen deposition, Nature Geosci, 3, 315–322, https://doi.org/10.1038/ngeo844, 2010.

Jia, X., Zhong, Y., Liu, J., Zhu, G., Shangguan, Z., and Yan, W.: Effects of nitrogen enrichment on soil microbial characteristics: From biomass to enzyme activities, Geoderma, 366, 114256, https://doi.org/10.1016/j.geoderma.2020.114256, 2020.

Jian, S., Li, J., Chen, J., Wang, G., Mayes, M. A., Dzantor, K. E., Hui, D., and Luo, Y.: Soil extracellular enzyme activities, soil carbon and nitrogen storage under nitrogen fertilization: A meta-analysis, Soil Biology and Biochemistry, 101, 32–43, https://doi.org/10.1016/j.soilbio.2016.07.003, 2016.

Jing, H., Li, J., Yan, B., Wei, F., Wang, G., and Liu, G.: The effects of nitrogen addition on soil organic carbon decomposition and microbial C-degradation functional genes abundance in a *Pinus tabulaeformis* forest, Forest Ecology and Management, 489, 119098, https://doi.org/10.1016/j.foreco.2021.119098, 2021.

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., and Kessler, M.: Climatologies at high resolution for the earth's land surface areas, Sci Data, 4, 170122, https://doi.org/10.1038/sdata.2017.122, 2017.

Khanina, L., Bobrovsky, M., Smirnov, V., and Romanov, M.: Wood decomposition, carbon, nitrogen, and pH values in logs of 8 tree species 14 and 15 years after a catastrophic windthrow in a mesic broad-leaved forest in the East European plain, Forest Ecology and Management, 545, 121275, https://doi.org/10.1016/j.foreco.2023.121275, 2023.

Kleber, M., Eusterhues, K., Keiluweit, M., Mikutta, C., Mikutta, R., and Nico, P. S.: Chapter One - Mineral–Organic Associations: Formation, Properties, and Relevance in Soil Environments, in: Advances in Agronomy, vol. 130, edited by: Sparks, D. L., Academic Press, 1–140, https://doi.org/10.1016/bs.agron.2014.10.005, 2015.

Knorr, M., Frey, S. D., and Curtis, P. S.: Nitrogen Additions and Litter Decomposition: A Meta-Analysis, Ecology, 86, 3252–3257, https://doi.org/10.1890/05-0150, 2005.

Kopittke, P. M., Hernandez-Soriano, M. C., Dalal, R. C., Finn, D., Menzies, N. W., Hoeschen, C., and Mueller, C. W.: Nitrogen-rich microbial products provide new organo-mineral associations for the stabilization of soil organic matter, Global Change Biology, 24, 1762–1770, https://doi.org/10.1111/gcb.14009, 2018.

Kurz, W. A., Beukema, S. J., and Apps, M. J.: Estimation of root biomass and dynamics for the carbon budget model of the Canadian forest sector, Can. J. For. Res., 26, 1973–1979, https://doi.org/10.1139/x26-223, 1996.

Kuyper, T. W., Janssens, I. A., and Vicca, S.: Chapter 8 - Impacts of nitrogen deposition on litter and soil carbon dynamics in forests, in: Atmospheric Nitrogen Deposition to Global Forests, edited by: Du, E. and Vries, W. de, Academic Press, 133–155, https://doi.org/10.1016/B978-0-323-91140-5.00012-9, 2024.

Kuzyakov, Y.: Review: Factors affecting rhizosphere priming effects, Journal of Plant Nutrition and Soil Science, 165, 382–396, https://doi.org/10.1002/1522-2624(200208)165:4<382::AID-JPLN382>3.0.CO;2-#, 2002.

Lagomarsino, A., De Meo, I., Agnelli, A. E., Paletto, A., Mazza, G., Bianchetto, E., and Pastorelli, R.: Decomposition of black pine (Pinus nigra JF Arnold) deadwood and its impact on forest soil components, Science of the Total Environment, 754, 142039, 2021.

Lauber, C. L., Hamady, M., Knight, R., and Fierer, N.: Pyrosequencing-Based Assessment of Soil pH as a Predictor of Soil Bacterial Community Structure at the Continental Scale, Applied and Environmental Microbiology, 75, 5111–5120, https://doi.org/10.1128/AEM.00335-09, 2009.

Lavallee, J. M., Soong, J. L., and Cotrufo, M. F.: Conceptualizing soil organic matter into particulate and mineral-associated forms to address global change in the 21st century, Global Change Biology, 26, 261–273, https://doi.org/10.1111/gcb.14859, 2020.

Le Noë, J., Manzoni, S., Abramoff, R., Bölscher, T., Bruni, E., Cardinael, R., Ciais, P., Chenu, C., Clivot, H., Derrien, D., Ferchaud, F., Garnier, P., Goll, D., Lashermes, G., Martin, M., Rasse, D., Rees, F., Sainte-Marie, J., Salmon, E., Schiedung, M., Schimel, J., Wieder, W., Abiven, S., Barré, P., Cécillon, L., and Guenet, B.: Soil organic carbon models need independent time-series validation for reliable prediction, Commun Earth Environ, 4, 1–8, https://doi.org/10.1038/s43247-023-00830-5, 2023.

Leff, J. W., Jones, S. E., Prober, S. M., Barberán, A., Borer, E. T., Firn, J. L., Harpole, W. S., Hobbie, S. E., Hofmockel, K. S., Knops, J. M. H., McCulley, R. L., La Pierre, K., Risch, A. C., Seabloom, E. W., Schütz, M., Steenbock, C., Stevens, C. J., and Fierer, N.: Consistent responses of soil microbial communities to elevated nutrient inputs in grasslands across the globe, Proceedings of the National Academy of Sciences, 112, 10967–10972, https://doi.org/10.1073/pnas.1508382112, 2015.

Leifeld, J., Zimmermann, M., and Fuhrer, J.: Simulating decomposition of labile soil organic carbon: effects of pH, Soil Biology and Biochemistry, 40, 2948–2951, https://doi.org/10.1016/j.soilbio.2008.08.019, 2008.

Li, S., Gurmesa, G. A., Zhu, W., Gundersen, P., Zhang, S., Xi, D., Huang, S., Wang, A., Zhu, F., Jiang, Y., Zhu, J., and Fang, Y.: Fate of atmospherically deposited NH4+ and NO3− in two temperate forests in China: temporal pattern and redistribution, Ecological Applications, 29, e01920, https://doi.org/10.1002/eap.1920, 2019.

Liang, C., Schimel, J. P., and Jastrow, J. D.: The importance of anabolism in microbial control over soil carbon storage, Nat Microbiol, 2, 1–6, https://doi.org/10.1038/nmicrobiol.2017.105, 2017.

Lilleskov, E. A., Kuyper, T. W., Bidartondo, M. I., and Hobbie, E. A.: Atmospheric nitrogen deposition impacts on the structure and function of forest mycorrhizal communities: a review, Environmental Pollution, 246, 148–162, https://doi.org/10.1016/j.envpol.2018.11.074, 2019.

Liu, J., Dai, L., Chen, Q., and Guo, X.: Nitrogen addition favors terrestrial ecosystem carbon sink: A global meta-analysis, Science of The Total Environment, 174826, 2024.

Liu, L. and Greaver, T. L.: A global perspective on belowground carbon dynamics under nitrogen enrichment, Ecology Letters, 13, 819–828, https://doi.org/10.1111/j.1461-0248.2010.01482.x, 2010.

Liu, Y., Dong, L., Zhang, H., Deng, Y., Hu, B., and Wang, W.: Distinct roles of bacteria and fungi in mediating soil extracellular enzymes under long-term nitrogen deposition in temperate plantations, Forest Ecology and Management, 529, 120658, https://doi.org/10.1016/j.foreco.2022.120658, 2023a.

Liu, Y., Men, M., Peng, Z., Chen, H. Y. H., Yang, Y., and Peng, Y.: Spatially explicit estimate of nitrogen effects on soil respiration across the globe, Global Change Biology, 29, 3591–3600, https://doi.org/10.1111/gcb.16716, 2023b.

Lladó, S., López-Mondéjar, R., and Baldrian, P.: Forest Soil Bacteria: Diversity, Involvement in Ecosystem Processes, and Response to Global Change, Microbiology and Molecular Biology Reviews, 81, 10.1128/mmbr.00063-16, https://doi.org/10.1128/mmbr.00063-16, 2017.

Lugato, E., Lavallee, J. M., Haddix, M. L., Panagos, P., and Cotrufo, M. F.: Different climate sensitivity of particulate and mineral-associated soil organic matter, Nat. Geosci., 14, 295–300, https://doi.org/10.1038/s41561-021-00744-x, 2021.

Magnani, F., Mencuccini, M., Borghetti, M., Berbigier, P., Berninger, F., Delzon, S., Grelle, A., Hari, P., Jarvis, P. G., Kolari, P., Kowalski, A. S., Lankreijer, H., Law, B. E., Lindroth, A., Loustau, D., Manca, G., Moncrieff, J. B., Rayment, M., Tedeschi, V., Valentini, R., and Grace, J.: The human footprint in the carbon cycle of temperate and boreal forests, Nature, 447, 849–851, https://doi.org/10.1038/nature05847, 2007.

Mahnken, M., Cailleret, M., Collalti, A., Trotta, C., Biondo, C., D'Andrea, E., Dalmonech, D., Marano, G., Mäkelä, A., Minunno, F., Peltoniemi, M., Trotsiuk, V., Nadal-Sala, D., Sabaté, S., Vallet, P., Aussenac, R., Cameron, D. R., Bohn, F. J., Grote, R., Augustynczik, A. L. D., Yousefpour, R., Huber, N., Bugmann, H., Merganičová, K., Merganic, J., Valent, P., Lasch-Born, P., Hartig, F., Vega del Valle, I. D., Volkholz, J., Gutsch, M., Matteucci, G., Krejza, J., Ibrom, A., Meesenburg, H., Rötzer, T., van der Maaten-Theunissen, M., van der Maaten, E., and Reyer, C. P. O.: Accuracy, realism and general applicability of European forest models, Global Change Biology, 28, 6921–6943, https://doi.org/10.1111/gcb.16384, 2022.

Manzoni, S. and Cotrufo, M. F.: Mechanisms of soil organic carbon and nitrogen stabilization in mineral-associated organic matter – insights from modeling in phase space, Biogeosciences, 21, 4077–4098, https://doi.org/10.5194/bg-21-4077-2024, 2024.

Manzoni, S. and Porporato, A.: Soil carbon and nitrogen mineralization: Theory and models across scales, Soil Biology and Biochemistry, 41, 1355–1379, 2009.

Manzoni, S., Trofymow, J. A., Jackson, R. B., and Porporato, A.: Stoichiometric controls on carbon, nitrogen, and phosphorus dynamics in decomposing litter, Ecological Monographs, 80, 89–106, https://doi.org/10.1890/09-0179.1, 2010.

Marshall, J. D., Peichl, M., Tarvainen, L., Lim, H., Lundmark, T., Näsholm, T., Öquist, M., and Linder, S.: A carbon-budget approach shows that reduced decomposition causes the nitrogen-induced increase in soil carbon in a boreal forest, Forest Ecology and Management, 502, 119750, https://doi.org/10.1016/j.foreco.2021.119750, 2021.

Marshall, J. D., Tarvainen, L., Zhao, P., Lim, H., Wallin, G., Näsholm, T., Lundmark, T., Linder, S., and Peichl, M.: Components explain, but do eddy fluxes constrain? Carbon budget of a nitrogen-fertilized boreal Scots pine forest, New Phytologist, 239, 2166–2179, https://doi.org/10.1111/nph.18939, 2023.

Maslov, M. N. and Maslova, O. A.: Nitrogen limitation of microbial activity in alpine tundra soils along an environmental gradient: Intra-seasonal variations and effect of rising temperature, Soil Biology and Biochemistry, 156, 108234, https://doi.org/10.1016/j.soilbio.2021.108234, 2021.

Micks, P., Downs, M. R., Magill, A. H., Nadelhoffer, K. J., and Aber, J. D.: Decomposing litter as a sink for 15N-enriched additions to an oak forest and a red pine plantation, Forest Ecology and Management, 196, 71–87, https://doi.org/10.1016/j.foreco.2004.03.013, 2004.

Moorhead, D. L. and Sinsabaugh, R. L.: A Theoretical Model of Litter Decay and Microbial Interaction, Ecological Monographs, 76, 151–174, https://doi.org/10.1890/0012-9615(2006)076[0151:ATMOLD]2.0.CO;2, 2006.

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

Moorhead, D. L., Lashermes, G., and Sinsabaugh, R. L.: A theoretical model of C- and N-acquiring exoenzyme activities, which balances microbial demands during decomposition, Soil Biology and Biochemistry, 53, 133–141, https://doi.org/10.1016/j.soilbio.2012.05.011, 2012.

Mooshammer, M., Wanek, W., Hämmerle, I., Fuchslueger, L., Hofhansl, F., Knoltsch, A., Schnecker, J., Takriti, M., Watzka, M., Wild, B., Keiblinger, K. M., Zechmeister-Boltenstern, S., and Richter, A.: Adjustment of microbial nitrogen use efficiency to carbon:nitrogen imbalances regulates soil nitrogen cycling, Nat Commun, 5, 3694, https://doi.org/10.1038/ncomms4694, 2014.

Palosuo, T., Foereid, B., Svensson, M., Shurpali, N., Lehtonen, A., Herbst, M., Linkosalo, T., Ortiz, C., Rampazzo Todorovic, G., Marcinkonis, S., Li, C., and Jandl, R.: A multi-model comparison of soil carbon assessment of a coniferous forest stand, Environmental Modelling & Software, 35, 38–49, https://doi.org/10.1016/j.envsoft.2012.02.004, 2012.

Parton, W. J., Schimel, D. S., Cole, C. V., and Ojima, D. S.: Analysis of Factors Controlling Soil Organic Matter Levels in Great Plains Grasslands, Soil Science Society of America Journal, 51, 1173–1179, https://doi.org/10.2136/sssaj1987.03615995005100050015x, 1987.

Parton, W. J., Hanson, P. J., Swanston, C., Torn, M., Trumbore, S. E., Riley, W., and Kelly, R.: ForCent model development and testing using the Enriched Background Isotope Study experiment, Journal of Geophysical Research: Biogeosciences, 115, https://doi.org/10.1029/2009JG001193, 2010.

Peng, Y., Guo, D., and Yang, Y.: Global patterns of root dynamics under nitrogen enrichment, Global Ecology and Biogeography, 26, 102–114, https://doi.org/10.1111/geb.12508, 2017.

Persson, T., Lenoir, L., and Taylor, A.: Bioturbation in different ecosystems at Forsmark and Oskarshamn, 2007.

Ramirez, K. S., Craine, J. M., and Fierer, N.: Nitrogen fertilization inhibits soil microbial respiration regardless of the form of nitrogen applied, Soil Biology and Biochemistry, 42, 2336–2338, https://doi.org/10.1016/j.soilbio.2010.08.032, 2010.

Ramirez, K. S., Craine, J. M., and Fierer, N.: Consistent effects of nitrogen amendments on soil microbial communities and processes across biomes, Global Change Biology, 18, 1918–1927, https://doi.org/10.1111/j.1365-2486.2012.02639.x, 2012.

Rappe-George, M. O., Choma, M., Čapek, P., Börjesson, G., Kaštovská, E., Šantrůčková, H., and Gärdenäs, A. I.: Indications that long-term nitrogen loading limits carbon resources for soil microbes, Soil Biology and Biochemistry, 115, 310–321, https://doi.org/10.1016/j.soilbio.2017.07.015, 2017.

Rihm, B. and Achermann, B.: Critical Loads of Nitrogen and their Exceedances. Swiss contribution to the effects-oriented work under the Convention on Long-range Transboundary Air Pollution (UNECE)., Federal Office for the Environment, Bern, Environmental studies, 78, 2016.

Rihm, B. and Künzle, T.: Nitrogen deposition and exceedances of critical loads for nitrogen in Switzerland 1990–2020, Meteotest commissioned by the Federal Office for the Environment, 2023.

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

Risch, A. C., Jurgensen, M. F., Page-Dumroese, D. S., Wildi, O., and Schütz, M.: Long-term development of above- and below-ground carbon stocks following land-use change in subalpine ecosystems of the Swiss National Park, Can. J. For. Res., 38, 1590–1602, https://doi.org/10.1139/X08-014, 2008.

Rocci, K. S., Lavallee, J. M., Stewart, C. E., and Cotrufo, M. F.: Soil organic carbon response to global environmental change depends on its distribution between mineral-associated and particulate organic matter: A meta-analysis, Science of The Total Environment, 793, 148569, https://doi.org/10.1016/j.scitotenv.2021.148569, 2021.

Rousk, J. and Bååth, E.: Growth of saprotrophic fungi and bacteria in soil, FEMS Microbiology Ecology, 78, 17–30, https://doi.org/10.1111/j.1574-6941.2011.01106.x, 2011.

Rowley, M. C., Grand, S., and Verrecchia, É. P.: Calcium-mediated stabilisation of soil organic carbon, Biogeochemistry, 137, 27–49, https://doi.org/10.1007/s10533-017-0410-1, 2018.

Savage, K. E., Parton, W. J., Davidson, E. A., Trumbore, S. E., and Frey, S. D.: Long-term changes in forest carbon under temperature and nitrogen amendments in a temperate northern hardwood forest, Global Change Biology, 19, 2389–2400, https://doi.org/10.1111/gcb.12224, 2013.

Schimel, J. P. and Weintraub, M. N.: The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model, Soil Biology and Biochemistry, 35, 549–563, https://doi.org/10.1016/S0038-0717(03)00015-4, 2003a.

Schimel, J. P. and Weintraub, M. N.: The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model, Soil Biology and Biochemistry, 35, 549–563, https://doi.org/10.1016/S0038-0717(03)00015-4, 2003b.

Schrumpf, M. and Kaiser, K.: Large differences in estimates of soil organic carbon turnover in density fractions by using single and repeated radiocarbon inventories, Geoderma, 239–240, 168–178, https://doi.org/10.1016/j.geoderma.2014.09.025, 2015.

Schulze, K., Borken, W., Muhr, J., and Matzner, E.: Stock, turnover time and accumulation of organic matter in bulk and density fractions of a Podzol soil, European Journal of Soil Science, 60, 567–577, https://doi.org/10.1111/j.1365-2389.2009.01134.x, 2009.

Shi, Z., Allison, S. D., He, Y., Levine, P. A., Hoyt, A. M., Beem-Miller, J., Zhu, Q., Wieder, W. R., Trumbore, S., and Randerson, J. T.: The age distribution of global soil carbon inferred from radiocarbon measurements, Nat. Geosci., 13, 555–559, https://doi.org/10.1038/s41561-020-0596-z, 2020.

Sinsabaugh, R. L. and Shah, J. J. F.: Ecoenzymatic Stoichiometry and Ecological Theory, Annual Review of Ecology, Evolution and Systematics, 43, 313–343, https://doi.org/10.1146/annurev-ecolsys-071112-124414, 2012.

Sinsabaugh, R. L., Lauber, C. L., Weintraub, M. N., Ahmed, B., Allison, S. D., Crenshaw, C., Contosta, A. R., Cusack, D., Frey, S., Gallo, M. E., Gartner, T. B., Hobbie, S. E., Holland, K., Keeler, B. L., Powers, J. S., Stursova, M., Takacs-Vesbach, C., Waldrop, M. P., Wallenstein, M. D., Zak, D. R., and Zeglin, L. H.:

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

Stoichiometry of soil enzyme activity at global scale, Ecology Letters, 11, 1252–1264, https://doi.org/10.1111/j.1461-0248.2008.01245.x, 2008.

Sinsabaugh, R. L., Manzoni, S., Moorhead, D. L., and Richter, A.: Carbon use efficiency of microbial communities: stoichiometry, methodology and modelling, Ecology Letters, 16, 930–939, https://doi.org/10.1111/ele.12113, 2013.

Sinsabaugh, R. L., Turner, B. L., Talbot, J. M., Waring, B. G., Powers, J. S., Kuske, C. R., Moorhead, D. L., and Shah, J. J. F.: Stoichiometry of microbial carbon use efficiency in soils, Ecological Monographs, 86, 172–189, 2016.

Sokol, N. W., Whalen, E. D., Jilling, A., Kallenbach, C., Pett-Ridge, J., and Georgiou, K.: Global distribution, formation and fate of mineral-associated soil organic matter under a changing climate: A trait-based perspective, Functional Ecology, 36, 1411–1429, https://doi.org/10.1111/1365-2435.14040, 2022.

Solly, E. F., Weber, V., Zimmermann, S., Walthert, L., Hagedorn, F., and Schmidt, M. W. I.: A Critical Evaluation of the Relationship Between the Effective Cation Exchange Capacity and Soil Organic Carbon Content in Swiss Forest Soils, Front. For. Glob. Change, 3, https://doi.org/10.3389/ffgc.2020.00098, 2020.

Spohn, M., Aburto, F., Ehlers, T. A., Farwig, N., Frings, P. J., Hartmann, H., Hoffmann, T., Larsen, A., and Oelmann, Y.: Terrestrial ecosystems buffer inputs through storage and recycling of elements, Biogeochemistry, 156, 351–373, https://doi.org/10.1007/s10533-021-00848-x, 2021.

Stergiadi, M., van der Perk, M., de Nijs, T. C. M., and Bierkens, M. F. P.: Effects of climate change and land management on soil organic carbon dynamics and carbon leaching in northwestern Europe, Biogeosciences, 13, 1519–1536, https://doi.org/10.5194/bg-13-1519-2016, 2016.

Sulman, B. N., Phillips, R. P., Oishi, A. C., Shevliakova, E., and Pacala, S. W.: Microbe-driven turnover offsets mineral-mediated storage of soil carbon under elevated CO2, Nature Clim Change, 4, 1099–1102, https://doi.org/10.1038/nclimate2436, 2014.

Sulman, B. N., Moore, J. A. M., Abramoff, R., Averill, C., Kivlin, S., Georgiou, K., Sridhar, B., Hartman, M. D., Wang, G., Wieder, W. R., Bradford, M. A., Luo, Y., Mayes, M. A., Morrison, E., Riley, W. J., Salazar, A., Schimel, J. P., Tang, J., and Classen, A. T.: Multiple models and experiments underscore large uncertainty in soil carbon dynamics, Biogeochemistry, 141, 109–123, https://doi.org/10.1007/s10533-018-0509-z, 2018.

Sun, T., Dong, L., Wang, Z., Lü, X., and Mao, Z.: Effects of long-term nitrogen deposition on fine root decomposition and its extracellular enzyme activities in temperate forests, Soil Biology and Biochemistry, 93, 50–59, https://doi.org/10.1016/j.soilbio.2015.10.023, 2016.

Sutton, M. A., Simpson, D., Levy, P. E., Smith, R. I., Reis, S., Van OIJEN, M., and De VRIES, W.: Uncertainties in the relationship between atmospheric nitrogen deposition and forest carbon sequestration, Global Change Biology, 14, 2057–2063, https://doi.org/10.1111/j.1365-2486.2008.01636.x, 2008.

Takahashi, M.: Comparison of nutrient concentrations in organic layers between broad-leaved and coniferous forests, Soil Science and Plant Nutrition, 43, 541–550, https://doi.org/10.1080/00380768.1997.10414781, 1997.

Tan, X., Machmuller, M. B., Cotrufo, M. F., and Shen, W.: Shifts in fungal biomass and activities of hydrolase and oxidative enzymes explain different responses of litter decomposition to nitrogen addition, Biol Fertil Soils, 56, 423–438, https://doi.org/10.1007/s00374-020-01434-3, 2020.

Tang, B., Rocci, K. S., Lehmann, A., and Rillig, M. C.: Nitrogen increases soil organic carbon accrual and alters its functionality, Global Change Biology, 29, 1971–1983, https://doi.org/10.1111/gcb.16588, 2023.

Taylor, A. R., Lenoir, L., Vegerfors, B., and Persson, T.: Ant and Earthworm Bioturbation in Cold-Temperate Ecosystems, Ecosystems, 22, 981–994, https://doi.org/10.1007/s10021-018-0317-2, 2019.

Templer, P. H., Mack, M. C., Iii, F. S. C., Christenson, L. M., Compton, J. E., Crook, H. D., Currie, W. S., Curtis, C. J., Dail, D. B., D'Antonio, C. M., Emmett, B. A., Epstein, H. E., Goodale, C. L., Gundersen, P., Hobbie, S. E., Holland, K., Hooper, D. U., Hungate, B. A., Lamontagne, S., Nadelhoffer, K. J., Osenberg, C. W., Perakis, S. S., Schleppi, P., Schimel, J., Schmidt, I. K., Sommerkorn, M., Spoelstra, J., Tietema, A., Wessel, W. W., and Zak, D. R.: Sinks for nitrogen inputs in terrestrial ecosystems: a meta-analysis of 15N tracer field studies, Ecology, 93, 1816–1829, https://doi.org/10.1890/11-1146.1, 2012.

Thimonier, A., Schmitt, M., Waldner, P., and Rihm, B.: Atmospheric Deposition on Swiss Long-Term Forest Ecosystem Research (LWF) Plots, Environ Monit Assess, 104, 81–118, https://doi.org/10.1007/s10661-005-1605-9, 2005.

Thimonier, A., Graf Pannatier, E., Schmitt, M., Waldner, P., Walthert, L., Schleppi, P., Dobbertin, M., and Kräuchi, N.: Does exceeding the critical loads for nitrogen alter nitrate leaching, the nutrient status of trees and their crown condition at Swiss Long-term Forest Ecosystem Research (LWF) sites?, Eur J Forest Res, 129, 443–461, https://doi.org/10.1007/s10342-009-0328-9, 2010.

Tian, D. and Niu, S.: A global analysis of soil acidification caused by nitrogen addition, Environ. Res. Lett., 10, 024019, https://doi.org/10.1088/1748-9326/10/2/024019, 2015.

Todd-Brown, K. E. O., Randerson, J. T., Post, W. M., Hoffman, F. M., Tarnocai, C., Schuur, E. a. G., and Allison, S. D.: Causes of variation in soil carbon simulations from CMIP5 Earth system models and comparison with observations, Biogeosciences, 10, 1717–1736, https://doi.org/10.5194/bg-10-1717-2013, 2013.

Tonitto, C., Goodale, C. L., Weiss, M. S., Frey, S. D., and Ollinger, S. V.: The effect of nitrogen addition on soil organic matter dynamics: a model analysis of the Harvard Forest Chronic Nitrogen Amendment Study and soil carbon response to anthropogenic N deposition, Biogeochemistry, 117, 431–454, https://doi.org/10.1007/s10533-013-9887-4, 2014.

Treseder, K. K.: Nitrogen additions and microbial biomass: a meta-analysis of ecosystem studies, Ecology Letters, 11, 1111–1120, https://doi.org/10.1111/j.1461-0248.2008.01230.x, 2008.

Ťupek, B., Ortiz, C. A., Hashimoto, S., Stendahl, J., Dahlgren, J., Karltun, E., and Lehtonen, A.: Underestimation of boreal soil carbon stocks by mathematical soil carbon models linked to soil nutrient status, Biogeosciences, 13, 4439–4459, https://doi.org/10.5194/bg-13-4439-2016, 2016.

van der Voort, T. S., Hagedorn, F., McIntyre, C., Zell, C., Walthert, L., Schleppi, P., Feng, X., and Eglinton, T. I.: Variability in ^{14}C contents of soil organic matter at the plot and regional scale across climatic and geologic gradients, Biogeosciences, 13, 3427–3439, https://doi.org/10.5194/bg-13-3427-2016, 2016.

Wäldchen, J., Schulze, E.-D., Schöning, I., Schrumpf, M., and Sierra, C.: The influence of changes in forest management over the past 200 years on present soil organic carbon stocks, Forest Ecology and Management, 289, 243–254, https://doi.org/10.1016/j.foreco.2012.10.014, 2013.

Waldrop, M. P., Zak, D. R., and Sinsabaugh, R. L.: Microbial community response to nitrogen deposition in northern forest ecosystems, Soil Biology and Biochemistry, 36, 1443–1451, https://doi.org/10.1016/j.soilbio.2004.04.023, 2004.

Walthert, L., Graf Pannatier, E., and Meier, E. S.: Shortage of nutrients and excess of toxic elements in soils limit the distribution of soil-sensitive tree species in temperate forests, Forest Ecology and Management, 297, 94–107, https://doi.org/10.1016/j.foreco.2013.02.008, 2013.

Wang, C., Qu, L., Yang, L., Liu, D., Morrissey, E., Miao, R., Liu, Z., Wang, Q., Fang, Y., and Bai, E.: Large-scale importance of microbial carbon use efficiency and necromass to soil organic carbon, Global Change Biology, 27, 2039–2048, https://doi.org/10.1111/gcb.15550, 2021.

Wang, G., Post, W. M., and Mayes, M. A.: Development of microbial-enzyme-mediated decomposition model parameters through steady-state and dynamic analyses, Ecological Applications, 23, 255–272, https://doi.org/10.1890/12-0681.1, 2013.

Whalen, E. D., Grandy, A. S., Sokol, N. W., Keiluweit, M., Ernakovich, J., Smith, R. G., and Frey, S. D.: Clarifying the evidence for microbial- and plant-derived soil organic matter, and the path toward a more quantitative understanding, Global Change Biology, 28, 7167–7185, https://doi.org/10.1111/gcb.16413, 2022.

Whittinghill, K. A., Currie, W. S., Zak, D. R., Burton, A. J., and Pregitzer, K. S.: Anthropogenic N Deposition Increases Soil C Storage by Decreasing the Extent of Litter Decay: Analysis of Field Observations with an Ecosystem Model, Ecosystems, 15, 450–461, https://doi.org/10.1007/s10021-012-9521-7, 2012.

Wieder, W. R., Bonan, G. B., and Allison, S. D.: Global soil carbon projections are improved by modelling microbial processes, Nature Clim Change, 3, 909–912, https://doi.org/10.1038/nclimate1951, 2013.

Wieder, W. R., Cleveland, C. C., Lawrence, D. M., and Bonan, G. B.: Effects of model structural uncertainty on carbon cycle projections: biological nitrogen fixation as a case study, Environ. Res. Lett., 10, 044016, https://doi.org/10.1088/1748-9326/10/4/044016, 2015a.

Wieder, W. R., Allison, S. D., Davidson, E. A., Georgiou, K., Hararuk, O., He, Y., Hopkins, F., Luo, Y., Smith, M. J., Sulman, B., Todd-Brown, K., Wang, Y.-P., Xia, J., and Xu, X.: Explicitly representing soil microbial processes in Earth system models, Global Biogeochemical Cycles, 29, 1782–1800, https://doi.org/10.1002/2015GB005188, 2015b.

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

Wieder, W. R., Hartman, M. D., Sulman, B. N., Wang, Y.-P., Koven, C. D., and Bonan, G. B.: Carbon cycle confidence and uncertainty: Exploring variation among soil biogeochemical models, Global Change Biology, 24, 1563–1579, https://doi.org/10.1111/gcb.13979, 2018.

Wu, J., Zhang, H., Pan, Y., Cheng, X., Zhang, K., and Liu, G.: Particulate organic carbon is more sensitive to nitrogen addition than mineral-associated organic carbon: A meta-analysis, Soil and Tillage Research, 232, 105770, https://doi.org/10.1016/j.still.2023.105770, 2023.

Wutzler, T. and Reichstein, M.: Colimitation of decomposition by substrate and decomposers – a comparison of model formulations, Biogeosciences, 5, 749–759, https://doi.org/10.5194/bg-5-749-2008, 2008.

Wutzler, T., Zaehle, S., Schrumpf, M., Ahrens, B., and Reichstein, M.: Adaptation of microbial resource allocation affects modelled long term soil organic matter and nutrient cycling, Soil Biology and Biochemistry, 115, 322–336, https://doi.org/10.1016/j.soilbio.2017.08.031, 2017.

Xia, M., Talhelm, A. F., and Pregitzer, K. S.: Long-Term Simulated Atmospheric Nitrogen Deposition Alters Leaf and Fine Root Decomposition, Ecosystems, 21, 1–14, https://doi.org/10.1007/s10021-017-0130-3, 2018.

Xiao, W., Chen, X., Jing, X., and Zhu, B.: A meta-analysis of soil extracellular enzyme activities in response to global change, Soil Biology and Biochemistry, 123, 21–32, https://doi.org/10.1016/j.soilbio.2018.05.001, 2018.

Xu, C., Xu, X., Ju, C., Chen, H. Y. H., Wilsey, B. J., Luo, Y., and Fan, W.: Long-term, amplified responses of soil organic carbon to nitrogen addition worldwide, Global Change Biology, 27, 1170–1180, https://doi.org/10.1111/gcb.15489, 2021.

Yang, Y., Chen, X., Liu, L., Li, T., Dou, Y., Qiao, J., Wang, Y., An, S., and Chang, S. X.: Nitrogen fertilization weakens the linkage between soil carbon and microbial diversity: A global meta-analysis, Global Change Biology, 28, 6446–6461, https://doi.org/10.1111/gcb.16361, 2022.

Ye, C., Chen, D., Hall, S. J., Pan, S., Yan, X., Bai, T., Guo, H., Zhang, Y., Bai, Y., and Hu, S.: Reconciling multiple impacts of nitrogen enrichment on soil carbon: plant, microbial and geochemical controls, Ecology Letters, 21, 1162–1173, https://doi.org/10.1111/ele.13083, 2018.

Yue, K., Fornara, D. A., Li, W., Ni, X., Peng, Y., Liao, S., Tan, S., Wang, D., Wu, F., and Yang, Y.: Nitrogen addition affects plant biomass allocation but not allometric relationships among different organs across the globe, Journal of Plant Ecology, 14, 361–371, https://doi.org/10.1093/jpe/rtaa100, 2021.

Zaehle, S. and Friend, A. D.: Carbon and nitrogen cycle dynamics in the O-CN land surface model: 1. Model description, site-scale evaluation, and sensitivity to parameter estimates, Global Biogeochemical Cycles, 24, https://doi.org/10.1029/2009GB003521, 2010.

Zechmeister-Boltenstern, S., Michel, K., and Pfeffer, M.: Soil microbial community structure in European forests in relation to forest type and atmospheric nitrogen deposition, Plant Soil, 343, 37–50, https://doi.org/10.1007/s11104-010-0528-6, 2011.

https://doi.org/10.5194/egusphere-2025-1022
Preprint. Discussion started: 14 March 2025

Zhang, H., Goll, D. S., Wang, Y.-P., Ciais, P., Wieder, W. R., Abramoff, R., Huang, Y., Guenet, B., Prescher, A.-K., Viscarra Rossel, R. A., Barré, P., Chenu, C., Zhou, G., and Tang, X.: Microbial dynamics and soil physicochemical properties explain large-scale variations in soil organic carbon, Global Change Biology, 26, 2668–2685, https://doi.org/10.1111/gcb.14994, 2020.

Zhang, T., Chen, H. Y. H., and Ruan, H.: Global negative effects of nitrogen deposition on soil microbes, ISME J, 12, 1817–1825, https://doi.org/10.1038/s41396-018-0096-y, 2018.

Zhong, Y., Yan, W., and Shangguan, Z.: The effects of nitrogen enrichment on soil fluxes depending on temperature and soil properties, Global Ecology and Biogeography, 25, 475–488, https://doi.org/10.1111/geb.12430, 2016.

Zhou, Z., Wang, C., Zheng, M., Jiang, L., and Luo, Y.: Patterns and mechanisms of responses by soil microbial communities to nitrogen addition, Soil Biology and Biochemistry, 115, 433–441, https://doi.org/10.1016/j.soilbio.2017.09.015, 2017.

Zuccarini, P., Sardans, J., Asensio, L., and Peñuelas, J.: Altered activities of extracellular soil enzymes by the interacting global environmental changes, Global Change Biology, 29, 2067–2091, https://doi.org/10.1111/gcb.16604, 2023.

Supplements

The following supplementary materials are attached to this article:

Supplement 1: Additional figures and tables

Supplement 2: Full model and parameter documentation

Code and data availability

The model source code (in C# code), model input files, validation data, and results analysis code (in R code) are all made available at Zenodo (https://doi.org/10.5281/zenodo.14879678).

Author contribution

CCY is the first author and is the responsible author for all parts of the work including designing the study and writing the main texts and supplementary materials. HB and ODY are involved in the conception, planning and editing of the entire work. FH and MMD provided the Swiss forest soil validation data, offered scientific advice, and edited the main text.

Acknowledgements

This research cannot be finished without the support from 1) Swiss National Science Foundation whom provides the necessary research funding, 2) The Swiss Federal Institute for Forest, Snow and Landscape Research whom provides the relevant soil data, 3) The Swiss Federal Office for the Environment for providing the nitrogen deposition data, and 4) The Natural Resource Ecology Laboratory at the Colorado State University (especially Dr. Melannie Hartman) for providing the source code of the CENTURY model version 4.6. Additionally, we would like to thank all members of the Forest Ecology Group at ETH Zurich, and the first author would like to specially thank Gina Marano for the crucial support and advice on the use of the ForClim model.

Financial support

This work is funded by the Swiss National Science Foundation (Grant No.: 188882).

Competing interests

One of the authors is a member of the editorial board of Biogeosciences.