Soil Biology and Biochemistry 189 (2024) 109272

Contents lists available at ScienceDirect

Soil Biology and Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Aligning theoretical and empirical representations of soil carbon-to-nitrogen stoichiometry with process-based terrestrial biogeochemistry models

Katherine S. Rocci[a,b,*], Cory C. Cleveland[c], Brooke A. Eastman[d], Katerina Georgiou[e], A. Stuart Grandy[f,g], Melannie D. Hartman[h], Emma Hauser[c], Hannah Holland-Moritz[f,g], Emily Kyker-Snowman[i], Derek Pierson[j], Peter B. Reich[b,k], Else P. Schlerman[f,g], William R. Wieder[a,l]

[a] *Institute of Arctic and Alpine Research, University of Colorado, Boulder, CO, USA*
[b] *Institute for Global Change Biology, University of Michigan, Ann Arbor, MI, USA*
[c] *Department of Ecosystem and Conservation Sciences, W.A. Franke College of Forestry and Conservation, University of Montana, Missoula, MT, USA*
[d] *Department of Biology, West Virginia University, Morgantown, WV, USA*
[e] *Physical and Life Sciences Directorate, Lawrence Livermore National Laboratory, Livermore, CA, USA*
[f] *Department of Natural Resources and the Environment, University of New Hampshire, Durham, NH, USA*
[g] *Center of Soil Biogeochemistry and Microbial Ecology (Soil BioME), University of New Hampshire, Durham, NH, USA*
[h] *Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO, USA*
[i] *Carbon Direct, New York, NY, USA*
[j] *Rocky Mountain Research Station, United States Forest Service, Boise, ID, USA*
[k] *Department of Forest Resources, University of Minnesota, St. Paul, MN, USA*
[l] *Climate and Global Dynamics Laboratory, National Center for Atmospheric Research, Boulder, CO, USA*

ABSTRACT

Soil carbon-nitrogen (C:N) stoichiometry acts as a control over decomposition and soil organic matter formation and loss, making it a key soil property for understanding ecosystem dynamics and projected ecosystems responses to global environmental change. However, the controls of soil C:N and how they respond to increasing pressures from global change agents are not fully understood. The "foundational" controls on soil C:N, namely plant and microbial C:N, have been used to predict soil C:N, but fail to accurately simulate all ecosystems and may be insufficient for predictions under global environmental change. We present an "emerging" representation of controls of soil C:N that includes plant-microbe-mineral feedbacks that have been shown to regulate soil C:N. We argue that including representation of these emerging drivers in process-based terrestrial biogeochemistry models, which include biological N fixation, mycorrhizae, priming, root exudation of organic acids, and mineralogy (including soil texture, mineral composition, and aggregation), will improve mechanistic representation of soil C:N and associated processes. Such improvements will produce models that will better simulate a variety of ecological states and predict soil C:N when global changes modify plant-microbe-mineral interactions. Here, we align our empirical understanding of controls of soil C:N with those controls represented in models, identifying contexts where emerging drivers might be particularly important to represent (e.g., priming and root exudation in nutrient-limited conditions) and areas of future work. Additionally, we show that implementing emerging drivers of soil C:N results in different simulated outcomes at steady state and in response to elevated atmospheric CO_2. Our review and preliminary simulations support the need to incorporate emerging drivers of soil C:N into process-based terrestrial biogeochemistry models, allowing for both theoretical exploration of mechanisms and potentially more accurate predictions of land biogeochemical responses to global change.

1. Introduction

Ecological stoichiometry, the study of the interactions of elements in ecological systems, is an organizing principle in ecology that provides a theoretical framework to explore how elements regulate plant growth, decomposition rates, and nutrient cycling at multiple scales (Elser et al., 2000). In soil, carbon-to-nitrogen (C:N) stoichiometry could be seen as a master variable that governs the flows of C and N between plants, microbes, and soils. Changes in soil C:N also reflect changes in soil C and N storage, which modify carbon cycle-climate feedbacks and nutrient limitation of plant growth, respectively. Further, soil C:N can be indicative of mechanistic changes in the system and represents the N

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* Corresponding author. Institute of Arctic and Alpine Research, University of Colorado, Boulder, CO, USA.
E-mail address: Katie.Rocci@colorado.edu (K.S. Rocci).

https://doi.org/10.1016/j.soilbio.2023.109272
Received 28 July 2023; Received in revised form 29 November 2023; Accepted 3 December 2023

requirement of C storage, important for land management aiming to increase soil C storage (Buchkowski et al., 2019; Cotrufo et al., 2019). Indeed, as our understanding of soil organic matter (SOM) dynamics advances, the role of soil stoichiometry remains an important aspect of ecosystem biogeochemistry (Buchkowski et al., 2019). Despite this central role and advancing knowledge, the controls of SOM C:N stoichiometry in process-based models of terrestrial biogeochemistry ("models'' hereafter; Supplementary Table 1)—which both emerge from and are informed by measurements and theory (Blankinship et al., 2018)—have remained largely stagnant and mostly consist of the C:N ratios of plant and microbial inputs. However, numerous recent studies have identified additional plant, microbial, and physico-chemical controls of SOM C:N stoichiometry that are largely missing from model formulations (e.g., Cotrufo et al., 2019; Possinger et al., 2020; Song et al., 2022; Amorim et al., 2022). These missing controls likely underlie global patterns in soil C:N and may be particularly important under global change scenarios where climate change, elevated CO_2, and N enrichment (from fertilization or atmospheric deposition) may alter the availability of and demand for N (Terrer et al., 2016, Souza and Billings, 2021). The goal of this perspective is to evaluate controls of soil C:N with a focus on gaps in both our theoretical understanding and model formulations. We first describe the foundational representation of soil C:N controls currently present in most models. Then, we describe an emerging representation of soil C:N controls, derived from empirical work that is informing a more complete and nuanced theoretical understanding, with the ultimate goal of aligning this representation with formulations in models. Finally, we explore how implementing the emerging representation of soil C:N controls could influence predictions of soil C and N cycling under global change.

2. Foundational representation of soil C:N

2.1. *Conceptual understanding of soil carbon-to-nitrogen stoichiometry*

The influence of plant C:N on soil processes has been recognized for at least forty years, when lower C:N plant material was found to decompose more quickly than higher C:N plant material (Melillo et al., 1982, Enríquez et al., 1993). Faster decomposition of lower C:N plant material occurs, in part, because it is better aligned with the relatively lower and more strongly constrained C:N ratio of the microbes that decompose it (plant C:N = 9–1160; microbial biomass C:N = 1–86; Fig. 1; Cleveland and Liptzin, 2007). The relative stoichiometric homeostasis of the soil microbial biomass C:N thus drives soil C and N recycling, where microbes mineralize excess C or N not used to build their biomass to CO_2 and ammonium, respectively. This process, termed consumer-driven nutrient recycling (Elser and Urabe, 1999), converts relatively high and variable plant C:N to relatively low and less variable C:N during microbial decomposition (Tipping et al., 2016). Indeed across multiple ecosystems and data sources we see a consistent decrease in the C:N stoichiometry of different ecosystem components as highly variable plant inputs pass through a more stoichiometrically constrained microbial filter to generate SOM (Fig. 1). Previously, SOM was thought to largely consist of variably decomposed plant material, but it is now largely accepted that SOM also includes microbial materials that persist due to their physical or chemical inaccessibility to further decomposition (Cotrufo et al., 2013; Lehmann and Kleber, 2015; Kallenbach et al., 2016). Thus, the stoichiometry of bulk SOM reflects contributions of both higher C:N plant material and lower C:N microbial biomass and by-products. The stoichiometry of bulk SOM also depends on the relative contribution of different SOM fractions (Buchkowski et al., 2019). The relatively low C:N of stable SOM pools (e.g., mineral-associated organic matter or MAOM) results from the greater contribution of microbial material (von Lützow et al., 2007), whereas the higher C:N of particulate organic matter (POM) is due to greater contributions of structural plant material (von Lützow et al., 2007; Haddix et al., 2016, Fig. 1a). This theoretical understanding informed a "foundational representation" of soil stoichiometry that guides conceptual models, where plant C:N drives SOM C:N variability and nutrient recycling, while microbial C:N constrains it. (Fig. 2a). Additionally, environmental variables like temperature, moisture, and nutrient

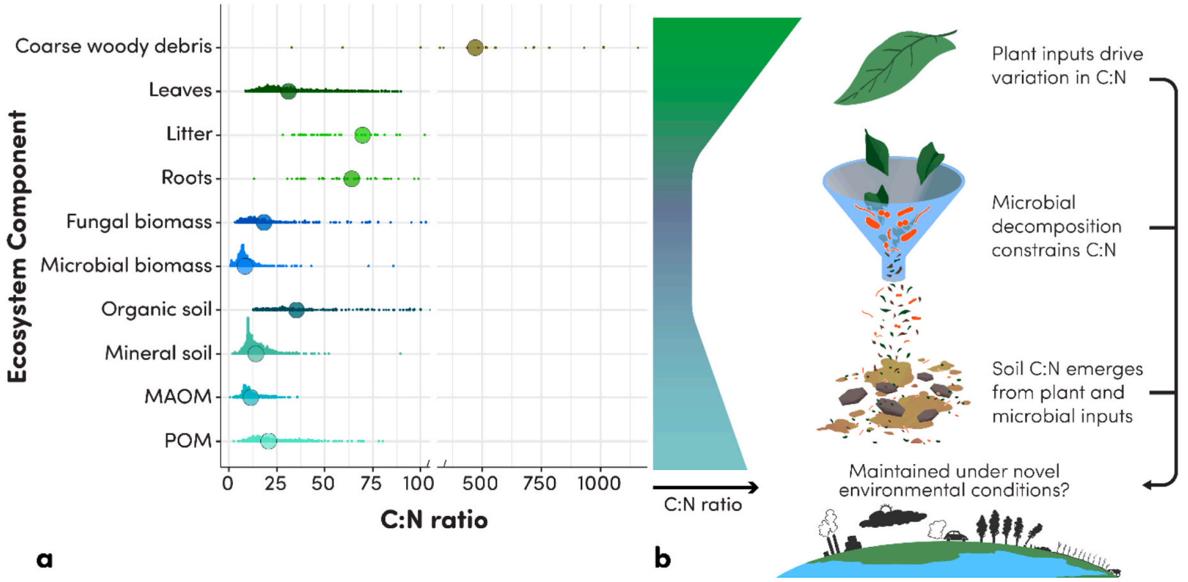

Fig. 1. (a) Empirically derived C:N ratios of different ecosystem components showing a narrowing of C:N ratios along the plant-microbe-soil continuum. Filled circles depict arithmetic means and small points arrayed as histograms depict individual observations. Data sources: coarse woody debris (Weedon et al., 2009); leaves (Dynarski et al., 2023); fresh litter and standing roots (NEON, 2023a; NEON, 2023b); fungal biomass (Zhang and Elser, 2017); microbial biomass (Xu et al., 2013); organic and mineral soil (Tipping et al., 2016); MAOM and POM (MAOM = mineral-associated organic matter; POM = particulate organic matter; Georgiou et al., 2022a). B) Conceptual depiction of the foundational representation of the decomposition process (funnel) that transforms relatively high plant C:N to relatively lower soil C:N, due to contribution of both plant and microbial materials to bulk SOM, with expected changes in the C:N ratio during this process. Earth with global change processes at bottom depicts uncertainty in the ability of the drivers above to simulate soil C:N under novel environmental conditions and thus the need to incorporate additional drivers of soil C:N beyond plant and microbe C:N.

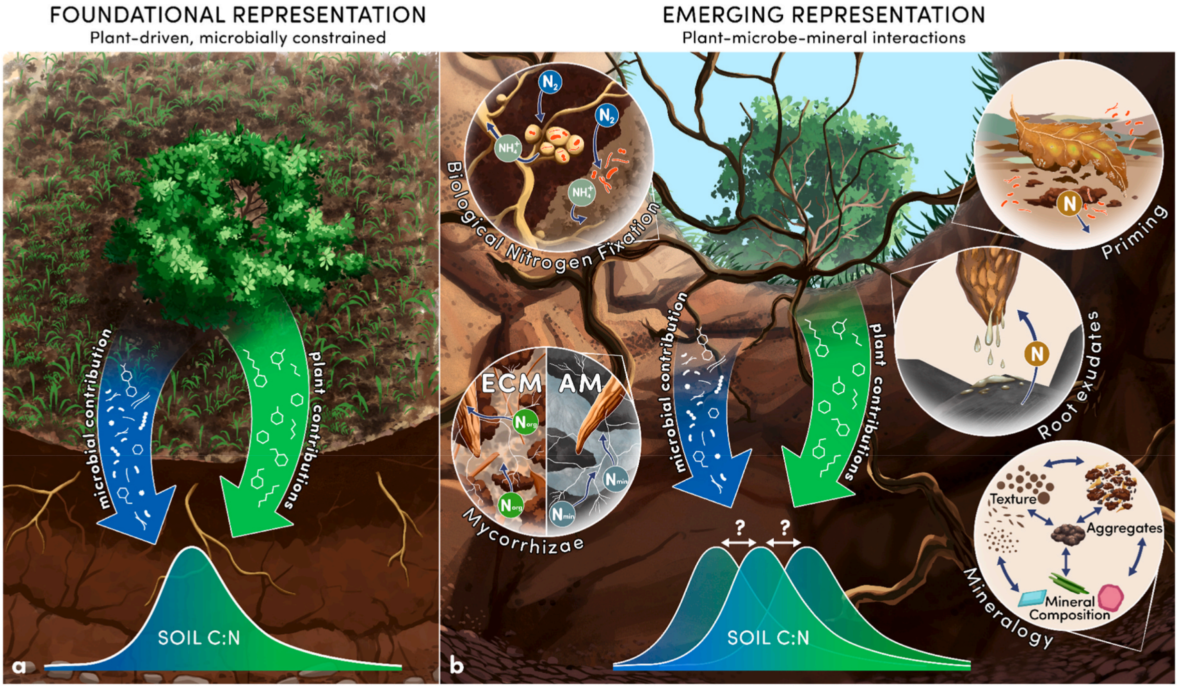

Fig. 2. Conceptual illustration showing foundational and emerging representations of the controls on C:N stoichiometry. (a) In the foundational representation, relatively high C:N plant material (green) combines with relatively low C:N microbial inputs (blue) to create the distribution of soil C:N values. Because plants have a wider range of C:N than microbes, plant C:N drives wider variation in soil C:N while microbial contributions constrain soil C:N, hence the right-skew of the histogram depicting soil C:N variation. In the foundational representation, this plant-centric focus is depicted as a "top-down" view of the soil C:N. (b) In the emerging representation, additional drivers of soil C:N that are typically absent from foundational representation of soil C:N are depicted (circular vignettes). Additional factors that may influence soil C:N can be broadly grouped into plant and microbe feedbacks and soil physico-chemical effects, and include the specific drivers of biological nitrogen fixation, mycorrhizae, priming, root exudates, and mineralogy (including soil texture, mineral composition, and aggregation). These drivers act through a diversity of mechanisms and thus can differentially influence C:N in ways that may be unrelated to initial plant C:N. This potential for variation in soil C:N due to the emerging drivers is depicted as shifts in the soil C:N histogram. In the emerging representation, this focus on processes occurring in the soil is depicted with a "bottom-up" view that emphasizes plant-microbe-mineral interactions.

availability that control rates of microbial decomposition impact the balance between plant and microbial contributions to SOM C:N (Wieder et al., 2009), suggesting that changes to climate, nutrient pollution (e.g., N deposition), and environmental conditions may change the controls of soil C:N in the future.

2.2. Implementation of foundational representation in models

Most current ecosystem biogeochemistry models (e.g. DayCent, PnET, or TEM) and land models that are used for global-scale projections (e.g. CLM, JSBACH, or LPJ-Guess; Davies-Barnard et al., 2020; Kou-Giesbrecht et al., 2023) are structured and parameterized with the foundational representation of soil C:N (Supplementary Table 1). Under these assumptions, simulated rates of soil C and N cycling reflect formulations of pool-specific turnover times, donor and receiver pool stoichiometry, and C use efficiency (CUE, which determines the fraction of heterotrophic respiration; Parton et al., 1993; Parton et al., 1994; Thornton and Rosenbloom, 2005). Nitrogen mineralization versus immobilization occurs to balance donor pool transfers of C and N with receiver pool stoichiometry. Generally, these models implicitly represent microbial activity (Schimel 2001), using environmentally sensitive first-order kinetics to define the turnover of litter and soil organic matter pools. The microbially-implicit modeling approach typically simulates down-regulation of decomposition rates when inorganic N availability is limiting, which generally occurs during transfers of material from high C:N litter to low C:N soil organic matter pools (Metherell, 1992; Parton et al., 1993; Bonan et al., 2013; Thomas et al., 2015). By contrast, models that explicitly represent microbial activity do not by default exhibit down-regulation of decomposition rates because of N limitation. For example, Kyker-Snowman et al. (2020) included overflow respiration of donor-pool C when N availability fails to meet the stoichiometric demands of decomposer biomass. This approach also eliminates the need to directly parameterize soil stoichiometry. Instead, soil C:N emerges from the relative contribution of microbial by-products (with a lower C:N ratio and narrower range) and plant detritus that bypasses the microbial filter and enters different SOM pools (Sulman et al., 2017; Zhang et al., 2021; Eastman et al., 2023). This is exemplified in the microbially-explicit model MIMICS-CN, where soil C:N is strongly influenced by plant input chemistry and which we use in case studies throughout this paper (Fig. 3). Despite differences in how soil C:N is determined in microbially-implicit vs -explicit approaches, both approaches rely on the foundational representation of soil C:N.

Model formulations that implement the foundational representation do represent dynamic flows of C and N during field decomposition, but falter in certain ecosystems (i.e. tundra and arid grasslands) and generally underestimate variation in soil C:N (Parton et al., 2007; Bonan et al., 2013; Kyker-Snowman et al., 2020, Juice et al. in review). The accuracy and reliability of these models are insufficient for simulating the full spectrum of ecosystems and may falter under novel environmental conditions (e.g., global environmental change; Fig. 1b, bottom; Wieder et al., 2019b). For example, recent research shows that interactions between plants, microbes, and the soil matrix strongly regulate soil C and N cycling, and consequently SOM C:N stoichiometry (e.g., Keiluweit et al., 2015; Jilling et al., 2018; Possinger et al., 2020; Daly et al., 2021; Terrer et al., 2021). Representing these mechanisms is paramount for improving mechanistic representation of soil C:N and predicting changes in soil C:N under global change.

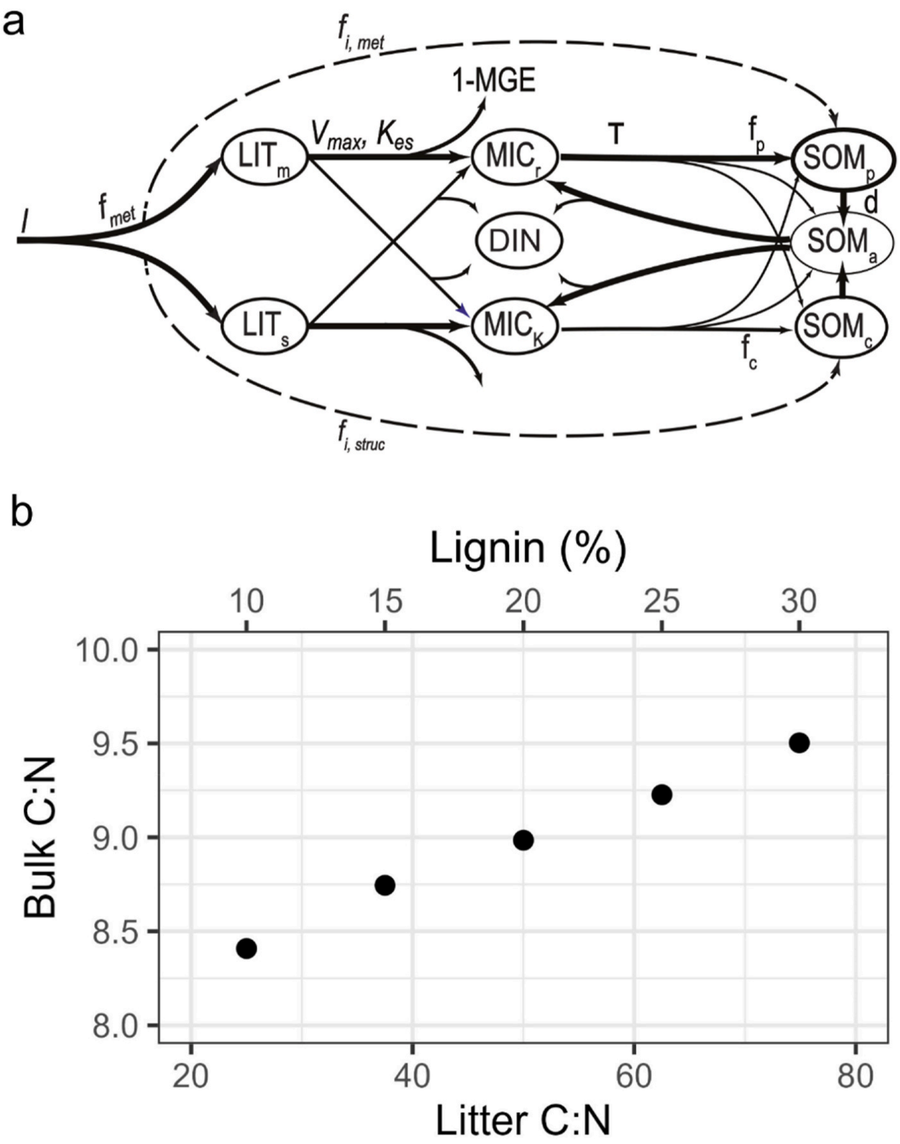

Fig. 3. (a) Wiring diagram for MIMICS-CN model, which we use in case studies throughout this paper. Briefly, litter inputs (I) are split into metabolic and structural pools (LIT_m and LIT_s) which are decomposed by microbial communities having copiotrophic and oligotrophic growth strategies (MIC_r and MIC_K, respectively), where both litter (f_i) and microbial turnover (T) can contribute to the physicochemically stabilized and chemically stabilized soil organic matter pools (SOM_p and SOM_c, respectively), and SOM_p and SOM_c contribute to an available SOM pool (SOM_a) that can be accessed by microbes. Detailed description of the model can be found in Kyker-Snowman et al. (2020) building upon Wieder et al. (2014). (b) MIMICS-CN simulations of bulk soil C:N in a hypothetical temperate deciduous forest where only the chemical quality (defined as the C:N ratio and lignin content) of litterfall inputs to surface soils are modified.

3. Emerging representation of soil C:N

The empirical evidence of important drivers beyond plant and microbe C:N that shape soil C:N ratios informs an “emerging representation” of the controls of soil C:N variation (Fig. 2b). We use the word “emerging” to explicitly acknowledge that many of the processes we describe below are already recognized as important for soil C:N in some subfields of soil science and represented in some models. However, we aim to clarify the importance of and collate these “emerging drivers” so that they can be aligned with model assumptions. We group these emerging drivers into plant and microbe feedbacks and soil physico-chemical effects that are absent from the foundational representation of soil C:N. The foundational representation considers plants and microbes as drivers of variability in soil C:N, and does not consider how soil C:N might feed back on the quantity and quality of plant inputs and subsequent microbial activity nor how minerals could act as a filter on soil C:N stoichiometry. Plant, microbial, and soil physico-chemical drivers have the potential, at least in certain circumstances, to improve the mechanistic representations of modeled soil C:N, even if they do not alter predictions of spatial variation in soil C:N. We review the empirical evidence for the importance of these emerging drivers and whether they align with assumptions in models. We focus on drivers that are evidenced as empirically important because adding additional processes to models can require additional input data, parameter optimization, and computational costs. Thus, there must be careful consideration of the balance between model complexity and realism when adding additional processes to models. We note that no one model is likely able to represent all of the processes we discuss below, but that representing the emerging drivers in some models will allow for research questions better tailored to systems where a given driver is particularly important.

3.1. Plant and microbe feedbacks

3.1.1. Biological nitrogen fixation

Biological N fixation represents a process that could influence soil C:N in ways not captured in the foundational representation of soil C:N controls. N fixation occurs through two general pathways: as plant symbiotic N fixation, where N is fixed for direct plant use via a symbiotic relationship with root-nodulating bacteria, and as "free-living" N fixation, where N is fixed by both autotrophic and heterotrophic bacteria that occupy a diversity of non-vascular plant niches (e.g., soil, leaf litter, wood, etc.; Vitousek et al., 2013; Cleveland et al., 2022). Both forms contribute new N inputs that enhance relative plant and soil N content, and thus may be hypothesized to reduce soil C:N (Vitousek et al., 1987; Vitousek and Walker, 1989; Adams et al., 2016; Gou et al., 2023). However, experimental and empirical studies have shown that invasion and/or introduction of N-fixing plants can have positive, negative, or neutral effects on soil C:N (Johnson and Curtis, 2001; Liao et al., 2008).

Although N fixation has been implemented in many models, it is commonly simulated using phenomenological relationships between empirically derived N fixation rates and net primary production or evapotranspiration (Wieder et al., 2015; Meyerholt et al., 2016). Symbiotic N fixation (alone) is most often included in models as an addition of N to the plant pool. By contrast, when free-living N fixation is included in models, it is often represented as an addition of N to the mineral N pool (Metherell et al., 1993; Reed et al., 2011; Hartman et al., 2018; Lawrence et al., 2019). These formulations of N fixation could promote increased microbial activity and subsequent input to SOM pools when microbial growth is associated with increased labile plant material and reduced microbial N limitation, such as in CORPSE-FUN, thereby reducing SOM C:N (Sulman et al., 2017).

More mechanistic implementations of N fixation could more accurately simulate how N fixation shapes SOM C:N stoichiometry. Potential model improvements include representations of non-symbiotic, rather than solely symbiotic, N inputs, N fixation inputs based on both C supply and N demand (rather than one or the other), and benchmarking against new and emerging empirical estimates of global N fixation (Vitousek et al., 2013; Davies-Barnard and Friedlingstein, 2020). Improved model representations of N fixation would further advance models that simulate N fixation using a resource optimization strategy, which are currently the most advanced representations of N fixation (e.g., GFDL-LM3-BNF, CLM5, and CABLE; Fisher et al., 2010; Shi et al., 2016, Lawrence et al., 2019; Peng et al., 2020, Kou-Giesbrecht et al., 2021). Given that increasing atmospheric CO_2 concentrations are hypothesized to favor N fixation over much of the world (Novotny et al., 2007; Hungate et al., 2009; Nasto et al., 2019), improved representations of N fixation in models may be critical for accurately simulating soil C:N under global change.

3.1.2. Mycorrhizae

Mycorrhizal type and associated plant traits influence soil C:N stoichiometry and nutrient cycling through differences in their nutrient acquisition strategies. Ericoid- and ectomycorrhizal- (ECM) dominated ecosystems typically have higher litter and soil C:N ratios and slower rates of nutrient cycling compared to arbuscular mycorrhizal- (AM) dominated ecosystems (Phillips et al., 2013; Averill et al., 2014). The direct connections between plant litter quality and soil stoichiometry are captured by the plant-to-soil pathway in the foundational representation of soil C:N. However, mycorrhizae allow for a two-way relationship between plants and soil. As mycorrhizae receive C from plant roots, they can either produce enzymes to mine nutrients from SOM (ECM) or expand their hyphal network to more efficiently exploit soil inorganic N (AM; Brzostek et al., 2013; Midgley et al., 2016; Tedersoo and Bahram, 2019). Strategies related to these different nutrient economies may be particularly important for biogeochemistry in forest ecosystems, which can vary in the relative abundance of mycorrhizal types, and in ecosystems experiencing shifts in plant species composition, such as shrub encroachment in the Arctic (Wookey et al., 2009). Yet, explicit representations of these plant-mycorrhizal relationships are largely missing from models.

Some attempts have been made to represent plant-mycorrhizal relationships in models with variations in belowground plant C inputs across mycorrhizal type and soil N availability (Baskaran et al., 2017; Sulman et al., 2017; He et al., 2018; Shi et al., 2016; Huang et al., 2022). Overall, these modeling experiments show that incorporating mycorrhizae increases model-observation agreement of soil C stocks and C:N ratios. Meanwhile, they suggest that simulating plant-mycorrhizal relationships may constrain the impacts of climate change on soil biogeochemistry and plant productivity. For example, as nutrient demand increases with elevated CO_2, ECM associations allow plants to mine SOM for N, enhancing plant productivity to a greater extent than AM systems that are less likely to mine N from SOM (Terrer et al., 2021). At the same time, this process typical of ECM-dominated ecosystems can increase competition between ECM and free-living saprotrophs, reducing the overall decomposition of SOM by saprotrophs and increasing soil C stocks and C:N ratios (Averill et al., 2014). Thus, incorporating these plant-mycorrhizal associations into models may also capture the divergent responses of forest ecosystems with different mycorrhizal associations to global changes like elevated CO_2 (Sulman et al., 2019), as has been observed at Free-Air Carbon Enrichment (FACE) sites (Terrer et al., 2016).

3.1.3. Plant priming of soil microbial activity

Soil priming, the accelerated decomposition of SOM via inputs of plant C, is a process with complex mechanistic underpinnings and highly variable responses to global changes (reviewed in Bernard et al., 2022). In some cases, plant priming may align with the foundational understanding of the plant-soil-stoichiometric continuum, where greater decomposition of fresh plant input increases microbial contributions to SOM and lowers soil C:N (Chen et al., 2014). However, at least three mechanisms may drive soil responses that likely differ from what is captured using foundational representations of soil C:N. First, higher soil microbial activity under priming may simultaneously accelerate decomposition rates of C-rich POM (in addition to decomposition of fresh plant input), reducing bulk C stocks and decreasing soil C:N (Bernard et al., 2022). Second, in nutrient-limited conditions, selective mining of N from SOM can occur when soil microbes use labile plant exudates as an energy source and preferentially immobilize N or N-rich material from SOM, thereby increasing SOM C:N (Chen et al., 2014; Hicks et al., 2020; Na et al., 2022). Third, priming could alter microbial community composition, favoring microbial functional groups that preferentially degrade substrates with high or low C:N ratios (Geyer et al., 2020). Therefore, representation of priming may be particularly important in scenarios where we expect changes to plant input quantity and quality (e.g., changes in plant community composition or allocation) and nutrient limitation (e.g., elevated CO_2, Mason et al., 2022).

Priming effects are not typically included in first order models because SOM turnover times are only modified by environmental scalars (e.g., temperature and moisture). A notable exception is the ORCHIDEE-PRIM model, which represents priming by modifying turnover times with changes in plant productivity, but only represents C (Guenet et al., 2016). Explicit representation of microbial activity, however, may provide more sophisticated, testable representations of priming mechanisms, including higher turnover rates, microbial N-mining, or preferential degradation of different SOM pools by different microbial functional types (Schimel, 2023). Indeed, microbially explicit models may include an emergent representation of priming due to relationships between substrate availability and microbial growth (Schimel, 2023). Current models that specifically simulate priming operate on relatively short or small temporal or spatial scales, with the goal of better understanding the complex interactions of microbes, OM, and minerals and dynamics of priming (Bernard et al., 2022). For example, the SYMPHONY model (Perveen et al., 2014) simulates N-mining in priming, but only at landscape to ecosystem scales. However, the importance of incorporating priming at larger scales is increasingly recognized (Terrer et al., 2021).

3.1.4. Root exudation of organic acids

In addition to root exudates that accelerate microbial activity and N mineralization via priming, plants also produce exudates that can directly increase SOM availability. Root exudation of organic acids (e.g., oxalic acid) can directly destabilize MAOM by locally lowering the pH in the rhizosphere, thereby chelating or competing with previously mineral-bound organic matter (Keiluweit et al., 2015; Jilling et al., 2018). This effectively promotes faster turnover of organic matter, as MAOM typically has long turnover times and low C:N ratios (Lavallee et al., 2020). Thus, organic acids may increase the availability of decomposable substrates and accelerate rates of N mineralization and plant N uptake (Jilling et al., 2018; Daly et al., 2021). Given the relatively low C:N of MAOM, its decomposition would tend to drive a loss of N-rich OM and subsequently increase the bulk soil C:N ratio.

Currently, depolymerization of SOM by enzymes and decomposers is considered the rate limiting step for N mineralization (Schimel and Bennett, 2004; Mooshammer et al., 2014), which ultimately constrains plant N availability and primary production in models. MAOM is often considered inaccessible to plants and microbes, though recent advances suggest that it may be an important plant N source (Jilling et al., 2018; Lavallee et al., 2020; Daly et al., 2021). As such, the direct effects of plant root inputs on the turnover of MAOM is virtually absent in models. Instead, in most models MAOM-like pools are represented with long turnover times that are modified by environmental scalars (temperature or moisture) and potentially modified by soil properties like soil texture or clay content. Very few models actually represent root exudation, and those that do only partially represent complex priming effects. For example, FUN-CORPSE only considers mycorrhizal response to exudates (Sulman et al., 2017). The closest approximation may be from the model ecosys, which simulates root exudation and exchange of organic C for organic N and P (Grant et al., 2016, Mekonnen et al., 2019; Chang et al., 2020; Bouskill et al., 2022). However, none of these models represent direct destabilization of MAOM caused by root exudation of organic acids. Indeed, consideration of mycorrhizae, priming, and organic acids introduces additional complexities to the emerging representation of soil C:N that are worth exploring further in models. As a preliminary step towards this exploration, we investigate the influence of priming, which could both increase or decrease soil C:N, and that of root exudation of organic acids, which we expect to increase soil C:N, below.

3.1.5. Biotic case study: simulating priming and desorption in the MIMICS-CN model

As a case study, we explored the potential effects of root exudation that causes priming and desorption (via exudation of organic acids) on steady state pools simulated by the MIMICS-CN model (Kyker-Snowman et al., 2020; Eastman et al., 2023). We use this case study and those in following sections (sections 3.2.2 and 4.1) to illustrate the potential importance of the emerging drivers of soil C:N but acknowledge that studies at larger scales and with different models will be needed to fully evaluate the importance of the emerging drivers for soil C:N. All experiments were performed in a hypothetical temperate deciduous forest with identical climate, litterfall inputs, litter quality and soil conditions. In all simulations, we calculated bulk soil C:N ratios as well as steady state C pools to explore the mechanisms driving changes in bulk soil C:N. The baseline simulation received root exudates as inputs to the metabolic litter pool (LIT_m) with a defined C:N ratio of 15 (Kyker-Snowman et al., 2020). This baseline experiment was designed to illustrate an implicit representation of root exudation fluxes, which are handled with the same stoichiometry as relatively labile plant litter. At steady state, the baseline experiment simulated a bulk soil C:N ratio of 9.6, total steady state C of 6.4 kgC m^{-2}, microbial biomass was 1.5% of soil C pools, and 43% of SOM was in the SOM_P pool (physico-chemically protected SOM, which we equate with MAOM; Fig. 4). The bulk soil C:N stoichiometry and fraction of the SOM_P pool were lower than median observational estimates (Fig. 5, discussed below), which is consistent with previous work with MIMICS-CN (Kyker-Snowman et al., 2020).

In a second "priming" experiment we more explicitly considered the effects of priming via root exudation by transferring 10% of metabolic litter inputs to the microbially-available SOM pool (SOM_a) at initialization. This simulation was designed to represent potential plant priming of soil microbes without changing the quantity or chemical quality of plant inputs to soils. This representation of priming increased total microbial biomass and the relative abundance of oligotrophic microbes (MIC_K), which resulted in a slightly higher microbial biomass C:N compared to the baseline experiment (7.0 vs. 6.9, respectively). In response to priming, microbial community shifts accelerated decomposition of litter and SOM_C pools, relative to the baseline simulation, which slightly decreased total C stocks and bulk soil C:N ratio (6.2 kgC m^{-2} and 9.5, respectively; Fig. 4). Broadly, these results are consistent with stimulation of oligotrophic microbial communities that have a competitive advantage over copiotrophic communities when utilizing more chemically complex substrates (Fontaine et al., 2003). In our simulations, oligotrophs increased in relative abundance and produced more enzymes that decompose litter and SOMc (comparable to POM). Yet, the magnitude of the effects on steady state pools and bulk soil stoichiometry were relatively small. The subtle changes in soil C stocks and C:N ratio may indicate that either the priming effect does not exert a strong control of steady-state behavior in the model, or that our simple priming experiment does not capture more complex priming mechanisms (Hicks et al., 2020; Karhu et al., 2022; Na et al., 2022). However, this simple priming experiment captures priming-induced directional changes in microbial community composition and soil C:N that are consistent with theoretical expectations, suggesting that more work is needed to evaluate whether the magnitude of these changes are appropriate.

In a third "priming + desorption" experiment, we considered the potential role of organic root acids liberating MAOM. Here, we repeated the priming experiment, but also increased the desorption rate of SOM_P (comparable to MAOM) by 10% relative to the baseline simulation. Increasing the desorption rate decreased the size of the SOM_P pool relative to both the baseline and priming experiments. As the SOM_P pool in MIMICS has a relatively low C:N ratio, reducing the size of this soil fraction increases bulk soil C:N ratios slightly above baseline values (9.7; Fig. 4). Again, the changes in total soil C stocks and C:N stoichiometry associated with this simplistic consideration of organic acids liberating MAOM are relatively small, but the direction of these changes are in line with theoretical expectations (Keiluweit et al., 2015; Jilling et al., 2018). This experiment also underscores the data and knowledge gaps associated with the extent to which organic acids from root exudates may accelerate desorption of MAOM (Jilling et al., 2021). It is technically challenging to quantify these fluxes even in lab incubations with artificial roots at sub-millimeter scales (Keiluweit et al., 2015) and scaling these insights to larger, more field-relevant scales remains speculative. Progress likely requires a more advanced empirical understanding and representation of soil physico-chemical properties and their influences of SOM dynamics.

3.2. Soil physico-chemical effects

3.2.1. Mineralogy

Three interrelated factors provide a robust 'bottom-up', soil-driven regulation of soil C:N ratio: soil texture, mineral composition, and aggregation. Texture, which describes the relative proportions of sand, silt, and clay particles, is known to impact the C:N stoichiometry of SOM because charged clay surface particles can form stable associations with charged moieties like amino groups (Jilling et al., 2018), leading to N enrichment in clay fractions compared to sand fractions (Haddix et al., 2016; Amorim et al., 2022). Increased clay content increases total

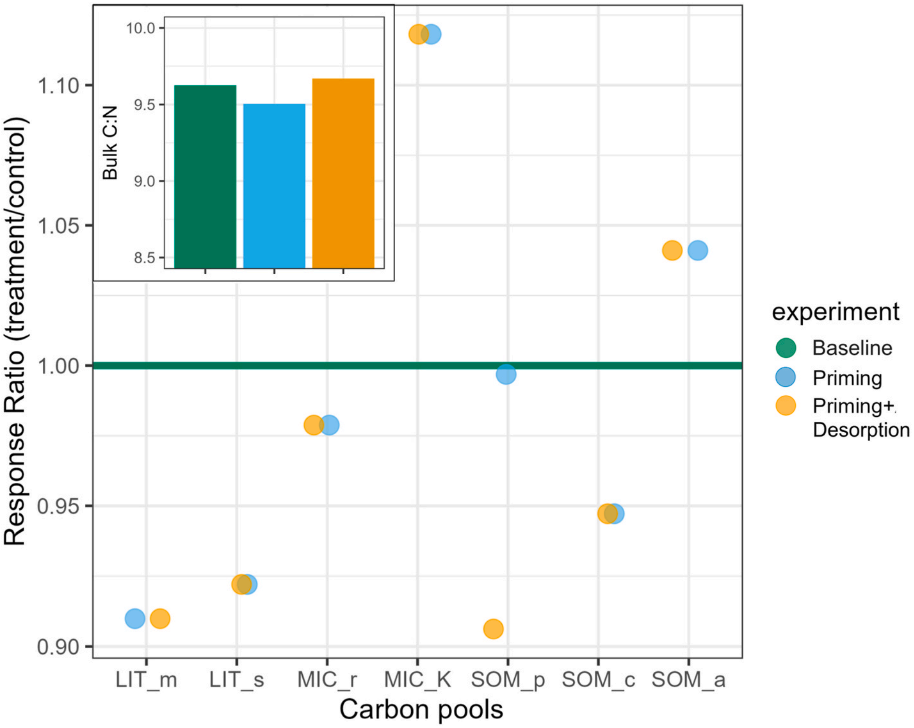

Fig. 4. Response ratio of C stocks in various pools of MIMICS-CN under priming (blue) and priming + desorption (yellow) experiments as compared to the baseline (green). Bulk soil C:N ratios for each experiment are shown in the inset plot. LIT_m = metabolic litter; LIT_s = structural liter; MIC_r = copiotroph microbial biomass; MIC_K = oligotroph microbial biomass; SOM_p = physically protected SOM; SOM_c = chemically protected SOM; SOM_a = active SOM.

surface charge and surface area available for organo-mineral interactions that form MAOM. MAOM is often defined as the size fraction associated with silt and clay (Leuthold et al., 2022). Thus, as this fraction increases, we expect more organic matter to accumulate in MAOM with comparatively low C:N ratio. However, silt may contain primary particles, have substantially less surface charge, and be a microsite for accumulating fungal residues with relatively high C:N ratios (Six et al., 2006, von Lützow et al., 2007). These factors can lead to variation in the relationship between MAOM fractions and soil C:N ratios that depend upon the relative proportions of silt and clay and at the same time their geochemical properties.

Some studies indicate that N-rich organic compounds may be preferentially adsorbed by certain types of soil colloids (Kaiser and Zech, 2000; Kleber et al., 2005; Mikutta et al., 2010; Yu et al., 2013; Jilling et al., 2018; Zhao et al., 2020), potentially accounting for variable C:N ratios depending on mineral composition. Recent studies show sorption of both N-rich microbial products and N-free aromatic compounds to soil mineral surfaces (Kramer et al., 2017; Kopittke et al., 2018; Gao et al., 2021). This variation in sorption may arise from variation in surface charge or nano-scale topographic characteristics of minerals (Vogel et al., 2014). Iron (Fe) and aluminum (Al) may be uniquely strong binding agents in soils rich in these minerals (e.g., Andisols). These soils exhibit preferential binding of low C:N SOM in organo-metal nanocomposites (<2 μm) and associations between N-rich compounds and ferrihydrite (an Fe mineral) concentrations (Asano et al., 2018; Zhao et al., 2020). Importantly, Fe content has been shown to be negatively associated or uncorrelated with clay content in certain environments, indicating the unique influence of Fe minerals (Rasmussen et al., 2018; Zhao et al., 2020). Soil pH can also interact with mineral composition, through controlling the relative importance of select SOM stabilization mechanisms (e.g., organo-metal complexation in acidic soils to exchangeable calcium in basic soils; Rasmussen et al., 2018). For example, the amount of pedogenic oxide-hydroxides affects the density of hydroxyl-groups and the formation of mineral associations via ligand exchange; pH can affect the protonation of these hydroxyl-groups and thereby the propensity for ligand exchange (Kleber et al., 2005). Thus, pH interacts with mineral type to drive relative sorption of C or N, potentially driving N-enrichment in Fe and Al minerals in humid and acidic environments and in phyllosilicates in dry and basic environments.

The texture and mineral composition of soil also regulate soil aggregation, which is another control over soil C:N ratios (Schweizer et al., 2023). Aggregates are clusters of soil particles (sand, silt, clay) held together by various organic and inorganic binding agents. Aggregation processes influence the types of organic matter stabilized and the corresponding C:N ratios vary based on the aggregate size, formation, and binding mechanisms, all of which depend on numerous factors, including mineral and organic C content, faunal activity, and land cover (Elliott 1986; Fonte et al., 2007; An et al., 2010; Maaβ et al., 2015; Haddix et al., 2020). For instance, it is known that microaggregates (<250 μm) accumulate N-rich compounds, primarily derived from microbial sources, and efficiently form MAOM (Fulton-Smith and Cotrufo, 2019). In contrast, larger macroaggregates (>250 μm) typically form around POM with high C:N ratios (Six et al., 2000). Roots and certain fungal hyphae also stabilize macroaggregates, and in the process their biomass becomes somewhat protected from decomposition within the aggregate (Graf and Frei, 2013; Lehmann et al., 2020). Tillage and other destabilizing forces that break apart larger aggregates speed up the decomposition of POM. This favors the accumulation of smaller, more resistant, and stable aggregates filled with lower C:N ratio SOM, ultimately resulting in lower bulk soil C:N (Grandy and Robertson, 2007).

In most soil biogeochemical models, minerals can indirectly control bulk soil stoichiometry by modulating the proportion and persistence of organic matter in mineral-associated pools. Given the ubiquity of measurements, most models use soil texture as a proxy for mineral sorptive capacity (Rasmussen et al., 2018; Sulman et al., 2018; Georgiou et al., 2021). In particular, some models use clay content (e.g., MIMICS and CORPSE; Wieder et al., 2019a), while many others use the sum of clay and silt content (e.g., Millennial, COMISSION, MEMS; Abramoff et al., 2018; Ahrens et al., 2020; Zhang et al., 2021). Mineral-associated OM pools in most models are primarily composed of microbial byproducts and necromass with relatively low C:N ratios, and to a lesser degree from direct sorption of dissolved or particulate organic matter; thus, texture ultimately acts as a control of bulk soil C:N stoichiometry. Only a subset of models currently represent mineral composition effects via equations relating pH and MAOM – namely, the Millennial, ecosys, and MEMS models (Grant et al., 2012, Zhang et al., 2021; Abramoff et al., 2022, this issue). The Millennial and COMISSION models also include broad classes of mineralogy by separating soils into low- and high-activity minerals, based on whether soils are dominated by 1:1 or 2:1 clays, respectively (Ahrens et al., 2020; Abramoff et al., 2022, this issue). Aggregation is a possible pathway for mineral control over soil C:N that only two C-only models have incorporated. Both AggModel and Millennial allow for both POM and MAOM to be captured in aggregates, whereas AggModel represents the hierarchy of micro- and macro-aggregates and Millennial has a single aggregate pool (Segoli et al., 2013; Abramoff et al., 2018). While neither AggModel nor Millennial currently considers N, protection of POM in aggregates might allow for higher C:N POM pools to persist, effectively increasing soil C:N. The frameworks developed in these models could someday help to understand the relationship between soil C:N and aggregate formation. To gain a preliminary understanding of the role of mineralogy in shaping soil C:N ratios we evaluate the relationships between SOM fractions, mineral variables, and soil C:N in both empirical data and models.

3.2.2. *Physico-chemical case study: Evidence for proxy variable inclusion in models*

For almost 30 years, soil scientists have called for correspondence between measured and modeled pools of SOM (Christensen, 1996; Elliott, 1986; Blankinship et al., 2018) and, increasingly, models are formulated to model measurable pools of SOM from physical fractionations (Luo et al., 2014; Abramoff et al., 2018; Robertson et al., 2019). MAOM, operationally defined as the pool associated with silt and clay, is expected to preferentially contain microbial residues and consequently have a relatively low C:N ratio (Grandy at el. 2007, Lavallee et al., 2020), presumably leading to positive associations between silt + clay content and MAOM content, and negative associations of each of these with soil C:N. However, the strength of silt and clay control of stabilization of organic matter and, consequently, soil C:N, especially as compared to other mineralogical factors, remains contentious in theoretical and empirical work and variable in model formulations (Bailey et al., 2018; Rasmussen et al., 2018; Sulman et al., 2018; Wieder et al., 2018).

We explored the potential strength of silt and clay control, as well as several proxy variables as emerging indicators of mineral effects on C:N stoichiometry in models and in observational synthesis data, namely Georgiou et al. (2022a, b) and the Soils Data Harmonization database (SoDaH; Wieder et al., 2021). Using Georgiou et al. (2022a), we found soil C:N was lower in soils with higher proportions of silt + clay (Fig. 5a). These silt + clay-rich soils were also associated with a greater proportion of C in MAOM (Fig. 5a), consistent with theoretical understanding of MAOM (Lavallee et al., 2020). This observation is already captured in MIMICS-CN (Fig. 5b) and could likely be demonstrated with other models that use SOM pool structures that represent MAOM and POM (e.g., MEMS, Millennial, and CORPSE; Sulman et al., 2017, Zhang et al., 2021; Abramoff et al., 2022, this issue). These findings support calls for further work benchmarking modeled SOM pools to measured ones (Berardi et al., 2020). Currently, this benchmarking has only been carried out for a few models with and without these measurable pools explicitly represented (Zimmermann et al., 2007; Zhang et al., 2021). Given strong relationships between SOM pools and soil C:N, greater benchmarking efforts are likely to improve confidence in simulations of soil C:N as well as soil biogeochemistry more broadly.

While our data suggest that bulk soil C:N is partly controlled by soil texture, the utility of other proxies for mineralogy is underexplored. To investigate the relevance of other mineralogical factors, we compared drivers of soil C:N in the SoDaH database to those in model simulations. For the observational data, we filtered the SoDaH database to isolate topsoil (<20 cm) data from studies that measured soil C:N and litter C:N. We generated model data by running global simulations of a microbially-explicit (MIMICS-CN; Kyker-Snowman et al., 2020) and a microbially-implicit (CASA-CNP; Wang et al., 2010) model forced with the same globally-gridded forcing data in a biogeochemical testbed (Wieder et al., 2018; detailed in Supplementary Material A). We then used multiple linear regressions (MLRs) to determine which variables emerged as important relative drivers of measured (SoDaH) and modeled (MIMICS-CN and CASA-CNP) soil C:N (detailed in Supplementary Material A). We analyze these below as qualitative comparisons, given the different geographic extents and data coverage between the observational data and models. For both measured and modeled data, we considered a three-factor MLR with mean annual temperature (MAT), clay content, and litter C:N as predictors for measured or modeled soil C:N. We also considered a seven-factor MLR with additional mineralogical factors as predictors for measured soil C:N, to evaluate which of these may be missing from model formulations (Table 1). For the three-factor MLRs, MIMICS-CN reasonably captured the relative importance of drivers in the SoDaH database whereas CASA-CNP depicted lower relative importance of clay, likely because it uses clay + silt to compute passive C formation, and higher relative importance of litter C:N, aligning with the more foundational

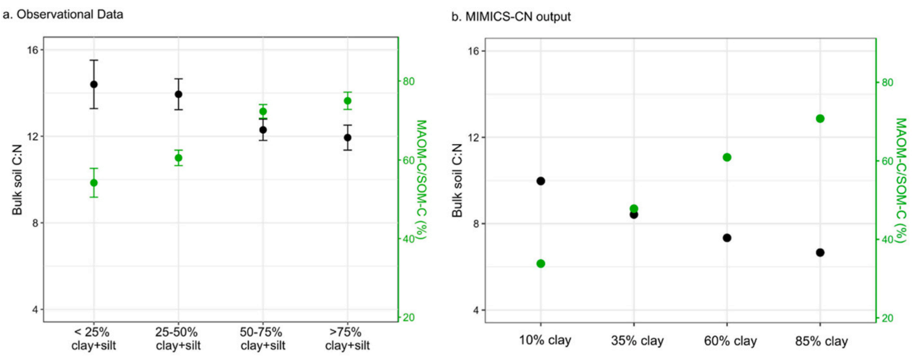

Fig. 5. Bulk soil stoichiometry (C:N ratio; left y-axis, black points) and percentage of bulk soil organic carbon that is mineral-associated (right y-axis; green points) across different soil texture regimes. (a) Soil texture regimes are summarized by ranges in clay plus silt percentages. Points and error bars represent means ± 95% confidence intervals on the mean from an observational synthesis of soil fractions consisting of >1200 measurements (n = 166, 388, 411, and 261 in the <25%, 25–50%, 50–75%, >75% clay + silt content regimes, respectively; Georgiou et al., 2022a). (b) MIMICS-CN output for a hypothetical temperate deciduous forest for soils with different amounts of clay, which is the controlling variable for sorption in MIMICS-CN, rather than silt + clay. MAOM-C/SOM-C is calculated from MIMICS output as SOMp/(SOMa + SOMc + SOMp)*100%.

Table 1
Results from multiple linear regression (MLR) analyses of a subset of the SoDaH database and model outputs (Supplementary Material A). The dependent variable in each model is observed or modeled soil C:N. Relative importance percentages show the percentage of the total variance explained by each statistical model that a given individual variable explains. "NA" indicates a variable that was not included in a given model. Greener cells have higher relative importance percentages. MAT is mean annual temperature; MAP is mean annual precipitation; Fe_ox, Al_ox, and Si_ox, and Fe_dith, Al_dith, and Si_dith, are oxalate-extractable and dithionite-extractable iron, aluminum and silica, respectively.

				Relative importance percentage											
MLR type	n	R^2	AIC	MAT	Clay	Litter C:N	MAP	Depth	pH	Fe_ox	Al_ox	Si_ox	Fe_dith	Al_dith	Si_dith
SoDaH observations	239	0.28	607	20.9%	46.5%	32.6%	NA	NA	NA	NA	NA	NA	NA	NA	NA
SoDaH observations	239	0.52	386	9.7%	15.5%	9.4%	8.7%	1.9%	10.5%	4.5%	9.3%	4.9%	11.1%	12.5%	1.8%
MIMICS-CN model	2697	0.80	3318	31.1%	31.4%	37.5%	NA	NA	NA	NA	NA	NA	NA	NA	NA
CASA-CNP model	2697	0.06	7500	32.7%	2.8%	64.6%	NA	NA	NA	NA	NA	NA	NA	NA	NA

representation of soil C:N (Table 1). Notably, the CASA-CNP MLR likely had a very low R^2 value because it has prescribed ranges for the C:N of various pools and bulk C:N stems from the balance across those pools, exemplifying how fixed pool C:N fails to capture important drivers of soil C:N. In contrast with the three-factor MLRs, the seven-factor MLR with all possible proxies identifies clay, Fe, Al, and pH as the strongest relative drivers of measured soil C:N (Table 1). This suggests mineral composition, with Fe, Al, and pH as proxies, in addition to soil texture (e.g., clay), are important drivers of soil C:N relative to the variables considered here. However, mineral composition control of organic matter stabilization, and consequently soil C:N, is represented in few models (Ahrens et al., 2020; Abramoff et al., 2022, this issue).

The concept of a "mineral filter" (Mikutta et al., 2019) acting as a bottom-up control of SOM composition is supported overall by our analyses (i.e. the high relative importance of silt and clay, pH and specific extractable metals; Fig. 5; Table 1). Although the patterns observed here do not definitively justify incorporating new mineral-related variables or processes into models, they could be explored further in models or in field or lab experiments. Field experiments could be used to explore possible mechanistic relationships between pH and mineral composition. Using such a relationship, pH is an easily measured variable that could be used to improve models, for example by making the model coefficient of clay stabilization dependent on pH, as in the MEMS (Zhang et al., 2021) and Millennial (Abramoff et al., 2022, this issue) models. The relative importance of dithionite-extractable Fe and Al in driving soil C:N in our results also supports the importance of mineral composition. Increased use of chemical extractions, which are more expensive and less widely measured, may be useful in identifying the specific minerals (e.g. Fe and Al oxides) that stabilize low C:N microbial residues (Rasmussen et al., 2018). More widespread measurements of specific soil mineralogy coupled to detailed mechanistic studies exploring the affinities of different minerals for N-enriched organic moieties (e.g. amino acids) may provide clarity about the role of edaphic factors in filtering SOM and soil C:N. These measurements would allow proxies like pH and soil Fe and Al oxides to be included in models as external parameters, used during model initialization, or even dynamic state variables, as has been done for redox reactions (Maggi et al., 2008; Rizzo et al., 2014; Calabrese and Porporato, 2019). Representing dynamic pH or mineralogy could be particularly important under variable soil moisture, N or heavy metal pollution, or when considering how pedogenic processes influence organic matter stabilization at millennial timescales. Better representation of mineralogy, as well as the plant and microbial drivers above, will be key for models' ability to predict soil C:N under global change.

4. Implications for studying global change

Global changes, such as rising atmospheric CO_2, N deposition, and changing climate influence the entire plant-soil system. For example, elevated CO_2 generally increases and N deposition generally decreases the C:N of vegetative tissues and litter entering the soil system (Yang et al., 2011; Sardans and Penuelas, 2012; Yue et al., 2017; Sun et al., 2020). While these changes to vegetation C:N stoichiometry will likely introduce numerous feedbacks in the plant-soil system, the net effects of these opposing influences are not well characterized. Models are valuable tools for exploring the trajectories of these global changes and understanding the possible large-scale implications of variable controls of soil stoichiometry for C and N dynamics (Wieder et al., 2019b). Examining elevated CO_2 and N deposition in coupled C–N models therefore presents a good opportunity to evaluate our foundational versus emerging representations of the controls of soil C:N stoichiometry. Importantly, other global changes, such as changes in temperature and moisture, land use change, and increases in wildfire occurrence and severity, will likely influence soil C:N differently under the foundational versus emerging representations but we focus on elevated CO_2 and N deposition here for brevity (Sistla et al., 2014; Pellegrini et al., 2018; Sun et al., 2021a,b).

4.1. Elevated CO_2

As atmospheric CO_2 rises, plant tissue C:N ratios typically increase (Cotrufo et al., 1998; Wang et al., 2021; Gojon et al., 2022), altering the chemistry of litter inputs to the soil system. Higher litterfall C:N ratios appear to reduce decomposition rates and soil N availability, possibly inducing progressive N limitation of vegetation growth (Luo et al., 2004; Liang et al., 2016; Craine et al., 2018; Mason et al., 2022). Simultaneously, under elevated CO_2 plants can shift allocation patterns to potentially mitigate N limitation (Phillips et al., 2009). To increase N uptake, plants increase C allocation to roots and root exudates that both directly enhance plant nutrient access, while also stimulating soil microbial activity that mineralizes nutrients (Phillips et al., 2011; Cheng et al., 2012; Terrer et al., 2016). Both litter chemistry and plant C allocation changes under elevated CO_2 could increase soil C:N through greater incorporation of high C:N plant material and N mining from N-rich SOM, respectively (De Graaff et al., 2006; Phillips et al., 2011). However, N could also be mined from higher C:N SOM pools, like POM, that are more accessible to microbes, thereby reducing bulk soil C:N (Sulman et al., 2014). Thus, the relative influence of litter chemistry and root exudation effects on soil C:N are uncertain but likely important for a better mechanistic understanding of ecosystem responses to elevated CO_2.

However, accurately capturing ecosystem biogeochemical responses to elevated CO_2 remains challenging for land models (Zaehle et al., 2014, Davies-Barnard et al., 2020; Eastman et al., 2023; Hauser et al., 2023). Part of this challenge lies in simulating appropriate plant and soil responses to elevated CO_2 and their interactions. To explore potential soil biogeochemical responses to elevated CO_2 we conducted a series of idealized model experiments with MIMICS-CN. Building on the steady-state results presented in the biotic case study (section 3.1.5; Fig. 4), we ran a series of 50-year transient simulations for the priming treatment under a pair of elevated CO_2 scenarios. In the first experiment we represented elevated CO_2 as a 20% step increase in net primary production (NPP) and a 10% increase in litterfall C:N, relative to the "ambient" conditions under which the models were initialized (Norby et al., 2005; Wang et al., 2021). For the second experiment we repeated these step increases in productivity and litterfall C:N, but also increased allocation of C to root exudates from 10% to 20% of metabolic litterfall inputs, without increasing the total amount of inputs, to evaluate the influence of this emerging driver. For brevity we calculated the response ratio of different soil pools and fluxes simulated by MIMICS-CN after 50 years under elevated CO_2 divided by their initial "ambient" state.

Increased NPP and litterfall C:N were most influential on soil biogeochemistry when allocation to root exudates also increased, indicating the importance of representing this emerging driver (Fig. 6a). Increased C allocation to exudates increased microbial biomass, and particularly that of oligotrophs (reduced MICr:MICK). Oligotrophs preferentially decomposed the high C:N SOMc pool (comparable to POM), thereby slightly reducing bulk soil C:N. Field manipulations also report increased microbial biomass and negligible changes in bulk soil C:N responses under elevated CO_2 that are consistent with our model results (Yue et al., 2017; Zou et al., 2023). However, empirical studies also suggest that under elevated CO_2, both the ratio of copiotrophs:oligotrophs and the POM pool increase (Rocci et al., 2021; Sun et al., 2021b). Additionally, N mineralization increased in our experiments under elevated CO_2 (Fig. 6a). This reflects higher rates of litter N inputs (from increased NPP) that occurred with our elevated CO_2 experiment but runs contrary to what may be expected under progressive N limitation (Luo et al., 2004). Indeed, when we isolated the potential effects of lower litter quality under elevated CO_2, MIMICS-CN showed reduced N mineralization rates, as expected from progressive N limitation (Supplementary Fig. 1). We also compare our simulations to the observations from the Duke free-air CO_2 enrichment (FACE) experiment because this site exhibits the priming responses we evaluate here. We note that this is intended to be a more qualitative comparison than a rigorous validation, and note that field measurements were derived from distinct studies under different periods of elevated CO_2 treatment. We find remarkably similar increases in microbial biomass and similar minimal responses of bulk C:N and SOMc (comparable to the free light fraction of SOM) as observed values for our 10% allocation simulations (Fig. 6b; Lichter et al., 2005; Drake et al., 2011). However, as noted above, increased N mineralization and reduced copiotroph to oligotroph ratio are opposite to observed decreases in N mineralization from a 100-day incubation and increases in the bacterial to fungal ratio (somewhat comparable to the copiotroph to oligotroph ratio, Fig. 6b, Billings and Ziegler, 2005; Feng et al., 2010). Our experiments highlight that plant-microbe-mineral interactions, represented by priming via root exudates (an emerging driver), provide a more nuanced assessment of soil C:N responses to elevated CO_2 but that further investigation is needed to revise structural assumptions or parameterization of MIMICS-CN, or other models trying to represent the emerging representation of soil C:N under global change.

4.2. Nitrogen deposition

While elevated CO_2 drives increases in ecosystem C:N, N deposition, inputs of reactive forms of inorganic and organic N from the atmosphere to ecosystems, might be hypothesized to have the opposite effect. However, ecosystem responses to N deposition are complex and highly variable across broad spatial scales, suggesting N deposition effects might not be so straightforward (Schlesinger, 2009; Kanakidou et al., 2016). With N deposition, plant biomass and shoot:root generally increase and plant shoot, root, and litter C:N generally decrease, which could be expected to favor microbial use of high quality plant material, ultimately favoring MAOM formation and lower SOM C:N (Yang et al., 2011; Averill and Waring, 2018; Sun et al., 2020; Feng et al., 2022). In contrast, N deposition could also increase SOM C:N through reduced lignocellulosic enzyme activity, reduced microbial activity via acidification and C limitation, and reduced strength of mineral-OM bonds (Frey et al. 2004, 2014; Carrara et al., 2018; Pan et al., 2020; Ning et al., 2021; Feng et al., 2022). These effects could specifically increase SOM C:N through reduced decomposition of high C:N SOM (Eastman et al., 2022), reduced N-rich microbial input, and desorption of relatively

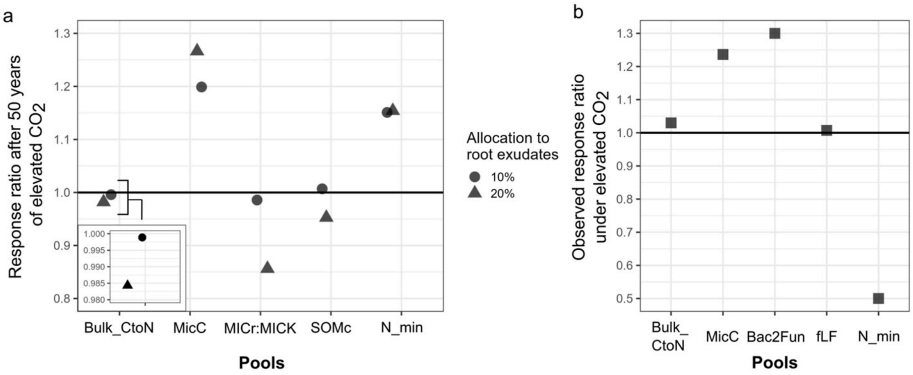

Fig. 6. (a) MIMICS-CN simulation results showing response ratios after 50 years of elevated CO_2 (year 50/year 1) with either 10% (circles) or 20% (triangles) of metabolic litter inputs allocated to root exudates. Elevated CO_2 is implemented as a 20% step increase in net primary production (NPP) and a 10% step increase in litter C:N. Inset shows bulk soil C:N on a finer scale. (b) Observed response ratios to elevated CO_2 from the Duke FACE experiment with data from Billings and Ziegler (2005), Lichter et al. (2005), Feng et al. (2010), and Drake et al. (2011). Note different y-axes. Bulk_CtoN = bulk soil C:N; MicC = microbial C; MICr:MICK = copiotroph-to-oligotroph ratio; SOMc = chemically stabilized soil organic matter; Bac2Fun = bacteria-to-fungi ratio; fLF = free light fraction; N_min = N mineralization.

N-rich OM, respectively. The diversity of effects from N deposition have made it difficult to predict consistent drivers of SOM responses to this global change (Averill and Waring, 2018).

Unless specifically formulated to do so, models struggle to depict the wide array of effects of N deposition. For example, most models add N deposition to the mineral N pool, and simulations generally show increases in plant productivity and consequently microbial activity. However, N deposition generally reduces microbial activity in empirical studies (Zhang et al., 2018). N deposition in models can also modify plant C:N and drive changes in SOM C:N through the foundational representation of soil C:N controls (Fig. 2a; Throop et al., 2004). However, most models lack the mechanistic representation for specific enzyme responses, dynamic and influential soil pH, and N-induced changes in sorption, although the MEND model represents specific enzyme groups (Wang et al., 2022). Eastman et al. (2023) tackled the challenge of representing empirical outcomes from a 30-year N deposition experiment in a mixed hardwood forest in two soil biogeochemistry models (MIMICS-CN and CASA-CN) coupled to the same vegetation model (CASA-CNP). In order to capture empirical responses in these models, the authors had to modify the vegetation allocation scheme and decay rate of the SOMc pool (comparable to POM), and even then only the microbially-explicit model (MIMICS-CN) exhibited increased soil C:N as seen in the empirical comparison (Eastman et al. 2022, 2023). Eastman et al. (2023) demonstrate the difficulty of capturing the multitude of N deposition effects in models and indicate the need to represent plant and microbe feedbacks in models to capture soil C:N responses to N deposition.

Nitrogen is not the only nutrient whose availability will likely be modified by global change. Phosphorus (P), in particular, might also shape soil C:N in ways associated with the emerging representation, largely through interactions with C and N (Townsend et al., 2011). For example, N fixation is limited by P availability, such that changing availability of P could modify N fixation with implications for soil C:N (Houlton et al., 2008). Alternatively, under P limitation, N is allocated to production of phosphatase enzymes that break down SOM, potentially causing a “P-mining” effect that could preferentially breakdown high P MAOM and thus increase soil C:N (Treseder and Vitousek, 2001; Spohn, 2020). These N–P interactions are exemplified in CASA-CNP, CLM-CNP and SCAMPS-CNP and could be used to evaluate effects of P addition on soil C:N (Wang et al., 2010; Yang et al., 2014; Pold et al., 2022). Alternatively, added P could directly exchange with C on mineral surfaces to reduce MAOM C:N, which could be formulated in models similarly to acid root exudation (Spohn and Schleuss, 2019; Rocci et al., 2022). Beyond P, experimentally adding potassium and micronutrients slightly increased soil C:N in globally-distributed grasslands but adding sulfur stoichiometry to a static soil formulation did not reduce C cycle uncertainty (Buchkowski et al., 2019; Seabloom et al., 2021). Thus, there is evidence supporting the influence of nutrient interactions on soil C:N, likely through the emerging drivers. This supports the development of models that represent both the emerging drivers and elements beyond C and N.

5. Conclusions

Foundational representations of soil C:N controls present in most models of soil biogeochemistry are insufficient and could be improved via a more complete, emerging representation of soil C:N controls. These missing emerging controls likely underlie large scale patterns of soil C:N and will likely allow for better predictions of soil C:N responses to global environmental change. The emerging representation of the controls of soil C:N illustrates the tension between simplicity and accurate representation of complex systems in models. Balancing these factors is critical for projecting future biogeochemical and climate outcomes. While the emerging drivers presented have strong empirical support in the literature, there are many other potential additional drivers that can influence soil C:N ratios including photodegradation, microbial physiology, and soil fauna (Moorhead and Callaghan, 1994; de Vries et al., 2013; Mooshammer et al., 2014; Chen et al., 2016). Our review of empirical understanding of the emerging drivers of soil C:N and their representation in models identified research gaps and contexts where drivers might be particularly important. We also showed that implementing the emerging drivers can cause distinct responses of soil C:N to global change. Ultimately, more theoretical, empirical, and modeling studies are needed to establish the relative importance of these emerging drivers for soil C:N stoichiometry and if and how they should be implemented in models. Specifically, current understanding informs the need for future research in the following areas:

- Evaluate the feedbacks of different representations of N fixation in models and how these align with empirically expected feedbacks and change soil C:N
- With improved representations of N fixation in models, determine impact of increased fixation on soil C:N under elevated CO_2
- Use modeling to separately resolve litter quality and N mining/mineralization effects of mycorrhizal fungi on soil C:N
- Determine realistic magnitudes of acid root exudation under steady state and global change conditions and their influence on soil C:N
- Increase collection of mineral composition data to further investigate the importance of pH and metal controls on MAOM, and subsequently bulk soil C:N
- Implement aggregation in a coupled C–N model to evaluate the influence on both biogeochemical cycles
- Investigate relative importance of litter quality versus plant allocation under elevated CO_2 in a coupled plant-soil model and the implications for soil C:N
- Determine the computational cost of adding groups of emerging factors to models to evaluate the feasibility of representing these factors at a global scale

CRediT authorship contribution statement

Katherine S. Rocci: Conceptualization, Data curation, Formal analysis, Writing – original draft, Writing – review & editing, Visualization. **Cory C. Cleveland:** Conceptualization, Data curation, Writing – original draft, Writing – review & editing. **Brooke A. Eastman:** Conceptualization, Writing – original draft, Writing – review & editing. **Katerina Georgiou:** Conceptualization, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **A. Stuart Grandy:** Conceptualization, Writing – original draft, Writing – review & editing. **Melannie D. Hartman:** Conceptualization, Writing – original draft, Writing – review & editing. **Emma Hauser:** Conceptualization, Writing – original draft, Writing – review & editing. **Hannah Holland-Moritz:** Conceptualization, Writing – original draft, Writing – review & editing. **Emily Kyker-Snowman:** Conceptualization, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Derek Pierson:** Conceptualization, Writing – original draft, Writing – review & editing. **Peter B. Reich:** Conceptualization, Writing – original draft, Writing – review & editing. **Else P. Schlerman:** Conceptualization, Writing – original draft, Writing – review & editing. **William R. Wieder:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Modeling in support of emerging soil stoichiometry controls (Original data) (GitHub)

Acknowledgements

We would like to thank artist Elena Hartley/elabarts.com for her illustrations for Figs. 1 and 2. We would also like to thank the editor and reviewers for their helpful comments. The workshop in which this work was developed was funded by USDA-NIFA 2020-67019-31395 awarded to WRW. KSR and WRW were supported by the US National Science Foundation (NSF) award 1926413. PBR and KSR were supported by Biological Integration Institutes award NSF-DBI-2021898 and the Biosciences Initiative at the University of Michigan. PBR was also supported by NSF Long-Term Ecological Research award DEB-1831944. EPS, ASG, HHM, and WRW were supported by NSF Arctic Systems Science Awards 2031253 and 2031238. HHM was also supported by the NSF EMERGE Biology Integration Institute, award # 2022070. CC and EH acknowledge support from an NSF Research Coordination Network grant to investigate nutrient cycling in terrestrial ecosystems (INCyTE; DEB-1754126).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2023.109272.

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