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EDITORIAL

In-N-Out: A hierarchical framework to understand and predict soil carbon storage and nitrogen recycling

Soils play a crucial role in the fight against climate change. Through proper management, they can contribute significantly to atmospheric carbon (C) drawdown. On the other hand, greenhouse gas emissions from soils may trigger strong positive feedbacks to global warming. One key challenge is that soil C accrual requires nitrogen (N), but the addition of N fertilizers has cascading impacts on nitrous oxide (N_2O) emissions and atmospheric and water pollution. Robust understanding and models are needed to predict outcomes of climate and land-use changes on soil C-N biogeochemistry to guide solutions, policies, and investments. The world is looking to ecosystem ecologists to advise large-scale efforts to co-manage soil C and N stocks. Are we ready for the challenge? Globally, plant C inputs to soils need to increase and soil C outputs via microbial C mineralization need to decrease, while N mineralization and internal N recycling need to be maintained to support plant productivity and avoid detrimental environmental impacts. Do we know where and how to achieve these outcomes?

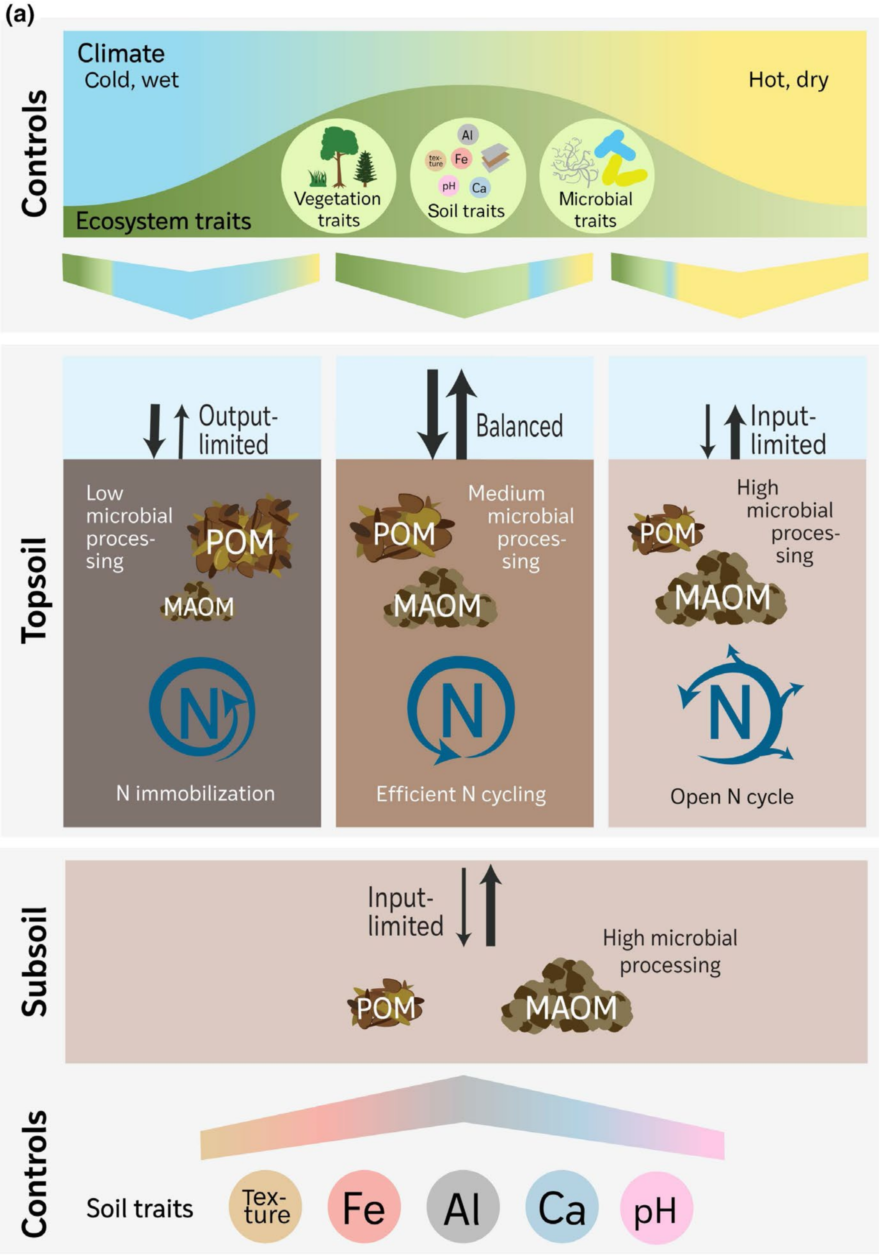
As the field of ecosystem ecology has matured, we have gained a deep understanding of the interconnected C, N, and water cycles in terrestrial ecosystems. We can articulate and model many of the underlying mechanisms that drive the coupling and decoupling of these cycles. Yet, the complexity of the ecosystems and the diverse conditions in which they operate impede us from predicting how these mechanisms interact to drive emergent processes and patterns. Unraveling how soil C storage and N recycling will respond to climate change in specific locations and under specific land uses is a major challenge. We need an overarching theoretical framework to address this challenge and, to be truly transformative, this new framework must be quantitatively translated into mathematical models of C, N, and water dynamics that are verifiable and able to accurately reproduce biogeochemical dynamics from the poles to the tropics.

A confluence of recent developments is leading us toward a breakthrough in our ability to model and predict soil C and N processes at the ecosystem scale. First, our mechanistic understanding of soil organic matter (SOM) dynamics has been greatly advanced (Basile-Doelsch et al., 2020) enabling a new generation of SOM models based on measurable pools and fluxes (Zhang et al., 2021 and references therein). However, these advances have been largely C-centric with less attention focused on understanding the shifts in soil N dynamics across ecosystems in response to climate and interactions with C availability. Second, there is an emerging emphasis on SOM dynamics in subsoils (i.e., soils below the top c. 20–30 cm; or below the A horizon), which hold more than half of the total SOM but have not yet been explicitely incoporated into most ecosystem models. Finally, the establishment of large-scale research and observatory networks provide data and samples to parameterize and test empirical and conceptual models across ecosystems and soil depths, creating exciting new opportunities.

Based on current understanding, we propose advancing our MEMS framework, which links plant input to microbial processing and mineral-associated SOM formation (Cotrufo et al., 2013), into a new broader conceptual and quantitative framework. Our In-N-Out framework identifies a hierarchical and interactive structure of controls on soil C and N cycling (Figure 1a). We expect resource limitation to be the major constraint on biogeochemical processes. Plant versus microbial activity limitation is a key determinant of soil C storage and N recycling, driving the dynamic coupling/decoupling of C and N cycles, within ranges imposed by the relatively constrained C:N stoichiometry of microbial and faunal biomass, and organic matter pools in soil (Cleveland & Liptzin, 2007). Our framework represents multiple hypotheses that can be empirically tested using quantifiable proxies (Figure 1b) and represented in ecosystem models (e.g., Zhang et al., 2021).

Our understanding of bulk soil C storage has significantly advanced (Basile-Doelsch et al., 2020; Wiesmeier et al., 2019). However, while we can now identify the drivers of soil organic C at different spatial scales, we lack a hierarchical structure of controls operating across different ecosystems. We posit that these specific controls are the result of interactions between climate, vegetation, and soil traits. In particular, we expect climate to be the first overarching control under extreme climates, but vegetation, microbial and soil traits to become direct drivers under mesic climates (Figure 1a).

In soils, organic C and N are highly intertwined. Organic C is stored in a myriad of different chemical compounds, many of which contain N and/or are formed through microbial activity that demands N. Furthermore, SOM contains more N per unit C than plant biomass. Thus, soil organic C storage is linked to N availability and can result in N immobilization in SOM with feedbacks to plant productivity. Conversely, when N is available in excess of plant and microbial demand, the C and N cycles decouple, and N is lost from the system. Soil organic matter stocks, their formation, persistence, and response to N availability and disturbances can be better described if SOM is broadly divided into a particulate organic matter (POM)



(b)

Proxy	Biogeochemical process
SOC/NPP	C input vs. C output limitation
Δ^{15}N (SOM vs. inputs)	C–N coupling; openness of N cycle
POM storage	Microbial inhibition
MAOM storage	Microbial transformation + mineral protection
SOC/NPP	C input vs. C output limitation
C:N of soil, MAOM, and POM	N demand of soil C storage

FIGURE 1 (a) Graphical representation of our conceptual In-N-Out framework. Arrows in the control panels (top and bottom) are color-coded according to potential controls. In the top control panel, the blue-to-yellow gradient represents dominance of climatic controls while the green gradient represents dominance of ecosystem traits controls. In the bottom control panel, the colors represent contributions of different potential controls on subsoil processes (texture, mineralogy, and pH). We hypothesize that in systems where plant photosynthesis is more constrained than microbial activity (right panel), soil biogeochemical cycling becomes limited by C inputs. In these systems, microbes process the limited plant C inputs, resulting in topsoils with minimal particulate organic matter (POM) accumulation, and low soil C stocks with relatively high mineral-associated organic matter (MAOM) accumulation controlled by the availability of soil minerals for stabilization of microbial products. We further hypothesize that C input-limited systems have N in excess of demand, resulting in decoupling of the N and C cycles, and the opening of N cycle to losses from the soil. By contrast, in systems characterized by conditions where microbes are more inhibited than plants (left panel), topsoil biogeochemistry becomes limited by C outputs. We expect these systems to be characterized by higher POM relative to MAOM accumulation. Most of the soil N remains immobilized in POM, imposing significant N limitation. Systems with balanced plant C inputs vs. microbial C outputs (center) are expected to have an equal share of POM and MAOM and efficient, closed internal N recycling. Furthermore, we expect systems where either C input or output is limiting to have relatively simple structures of controls, with climate being the first and main driver. By contrast, in systems where C input and output limitations are not climatically driven, ecosystem traits emerging from the interaction of plant, microbial, and soil traits are significant drivers of soil C and N dynamics, with more complex structures of controls. Finally, we expect that subsoils are input-limited and have less complex control structures than topsoils, largely dominated by soil traits, including mineral properties. O_2 availability is also a major driver of microbial inhibition, depending on the interaction between climate and soil properties, not explicitly addressed in the figure. (b) Proxies we propose to use to test the In-N-Out framework and hypotheses. Others may also apply. The rationale for these proxies is explained here. SOC/NPP: soils that store more C per unit of C input from plants indicate that microbial decomposition, responsible for C output, proceeds at a slower rate and therefore is more limited than plant productivity, the dominant C input. $\Delta^{15}N$ (SOM vs. inputs): Soils that maintain larger mineral N pools susceptible to loss pathways have a relatively high SOM $\delta^{15}N$ while systems with tighter internal N recycling and coupling of C and N cycles have SOM that is less ^{15}N-enriched than the inputs. POM storage: POM is made primarily of plant residue, and it dominates in soils where microbial decomposition is inhibited or slow, as in peat soils. POM can also be high in undisturbed soils, where microbial decomposition is not accelerated by disturbance, such as tillage. MAOM storage: MAOM is predominantly made of low molecular weight compounds and microbial products, and it requires minerals for stabilization. It accumulates in soils with highly soluble and easily decomposable plant inputs, and high soil matrix capacity. Since mineral protection renders it less vulnerable to disturbance, it is a higher proportion of total SOM in highly disturbed soils. C:N of soil, MAOM, and POM: The C:N stoichiometry of bulk soil and SOM pools reflects the amount of C that can be stored per unit of N in soils. POM, having a higher and more plastic C:N ratio, has a lower N demand of C storage [Colour figure can be viewed at wileyonlinelibrary.com]

and a mineral-associated organic matter (MAOM) pool (Lavallee et al., 2020). Light POM is predominantly of plant origin and thus contains many structural C-compounds with low N content. It persists (<50 years) in soil because of microbial inhibition to decomposition through various mechanisms including inherent POM biochemical recalcitrance, physical protection in aggregates, and other climatic and environmental constraints (e.g., limiting temperatures, water, O_2, or nutrients). MAOM has a higher share of microbial products richer in N. It persists (10–1000 years) in soil because of chemical bonding to minerals and physical protection in fine aggregates. We hypothesize that at ecosystem scales the relative accumulation of POM reflects microbial limitation and leads to limitations of N availability (e.g., peat soils), while the relative dominance of MAOM reflects plant productivity limitation, and opening of the N cycle (e.g., dryland soils; Figure 1a). Ecosystems where plant inputs are balanced by microbial outputs have an equal share of POM and MAOM, maintaining soil C stocks and recycling N to sustain productivity. Additionally, bulk soil, POM, and MAOM C:N stoichiometry can be used as a proxy for the N demand of C storage (Figure 1b).

The degree to which N is recycled versus lost within soils can be quantified with stable isotopes. The natural abundance of the ^{15}N:^{14}N isotopes in soil relative to atmospheric N_2 has been used as an indicator of terrestrial N cycling dynamics because N loss pathways (nitrification, denitrification, and ammonia volatilization) fractionate against the heavier ^{15}N isotope while biological N fixation does not (Hogberg, 1997). Thus, the ^{15}N enrichment of SOM can be used as a proxy for the degree of openness of the N cycle (Figure 1b), or the degree of C and N cycle decoupling. Hotter, drier climates tend to have more open N cycling than cooler, wetter environments (Amundson et al., 2003). Within climate regions, vegetation can influence soil $\delta^{15}N$ because different plant N acquisition strategies. Vegetation is more likely to influence total $\delta^{15}N$ in soils with larger proportions of N in POM, which reflects more recent and less processed litter inputs, than systems with larger proportions of N in MAOM, which has undergone microbial transformations and is more consistently enriched in ^{15}N. We expect microbial-limited, POM-dominated soil to have a lower ^{15}N enrichment than plant input-limited, MAOM-dominated soil (Figure 1a). There have been limited analyses of the relative structure of these multiple drivers on N cycling in terrestrial systems at different soil depths and their interaction with soil C dynamics, leading to an important knowledge gap.

We also hypothesize (Figure 1a) that subsurface SOM dynamics are inherently C input-limited and more strongly affected by soil traits (e.g., texture and mineralogy) than climate (Mathieu et al., 2015). Physicochemical and biological properties differ markedly between subsoils and topsoils and, while the exact delineation between topsoil and subsoil can vary across soil types, there is an increasing evidence that models of soil C and N storage and cycling should consider topsoils and subsoils separately (Zhang et al., 2021). Subsoils typically have a lower organic matter content and are characterized by ^{14}C ages thousands of years greater than the surface, lower C/N ratio, and a higher natural abundance of the heavy C and N isotopes than topsoils (Rumpel & Kogel-Knabner, 2011). Microbial biomass and activity are lower in subsoil than in topsoil and subsoil microbes rely more on SOM as a C source than on fresh plant inputs. Deep SOM is thought to be made mostly of microbial products. Plant inputs are limited and lignin, and POM generally does not accumulate in subsoil, despite lower litter mass loss rates having been reported at depth. These findings point to a higher degree of SOM recycling at depth. Additionally, when subsoils are treated with de-mineralizing agents (i.e., hydrofluoric acid), they lose a much higher proportion of their C than topsoils, suggesting a higher degree of mineral association at depth (Rumpel & Kogel-Knabner, 2011).

We encourage the use of large datasets from ecosystems around the world to test this hierarchical framework of C and N cycling controls, using the proposed proxies (Figure 1b) and others. We hope the In-N-Out framework can help advance understanding of the feedbacks between climate, land cover, and soil C and N cycling, enabling us to more accurately predict outcomes of climate and land-use changes on soil biogeochemistry to guide solutions, policies, and investments.

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DATA AVAILABILITY STATEMENT

No data are presented.

M. Francesca Cotrufo[1,2]
Jocelyn M. Lavallee[1,2]
Yao Zhang[2]
Paige M. Hansen[1]
Keith H. Paustian[1,2]
Meagan Schipanski[1]
Matthew D. Wallenstein[1]

[1]*Department of Soil and Crop Science, Colorado State University, Fort Collins, CO, USA*
[2]*Natural Resources Ecology Laboratory, Colorado State University, Fort Collins, CO, USA*
Email: francesca.cotrufo@colostate.edu

ORCID

M. Francesca Cotrufo https://orcid.org/0000-0002-6191-8953

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