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Commentary

A microbial framework for nitrogen cycling solutions in agroecosystems

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Nitrogen use in agriculture often prioritizes immediate yield gains at the expense of the environment and agroecosystem health. This problem persists because current solutions for crop nitrogen use inefficiency focus too narrowly on inputs and overlook the internal processes that govern nitrogen's fate, from crop uptake and environmental losses to storage and transfer between various organic pools. We synthesize recent research developments in soil nitrogen biogeochemistry into an aspirational and accessible microbe-centered framework that clarifies understanding of nitrogen accumulation, recycling, and plant uptake processes in soil. This framework can guide scientific exploration and practical applications to boost crop yields, enrich soil organic matter, and reduce environmental nitrogen losses.

The nitrogen problem

Over-enrichment of nitrogen (N) can greatly harm ecosystems, yet this nutrient is essential for living things as a key component of proteins and other biomolecules. All the N we ingest ultimately comes from plant growth, which is often N-limited. To overcome this limitation and increase crop yields, global N use has skyrocketed to 110 Tg globally: today, it is estimated that synthetic N fertilizers are directly responsible for the agricultural products that feed 3.5 billion people.[1] However, N losses from the plant-soil system are large, at a global total of 8.15 Tg N yr^{-1} from just maize and wheat in 2020 alone.[2]

N losses from agroecosystems create myriad unintended consequences.[3] N leaching into drinking water poses serious health risks and requires costly remediation. Agriculture is the source of about three-quarters of global anthropogenic emissions of nitrous oxide, a gas 273 times more potent than carbon dioxide as an atmospheric warming agent.[4] In aquatic ecosystems, N pollution reduces biodiversity in surface waterways and contributes to harmful marine algal blooms. Soil N losses limit potential crop growth and subsequent soil organic carbon (C) accumulation, hampering efforts to mitigate climate change.

To address these issues, researchers and producers have sought to increase fertilizer N use efficiency (NUE; agronomic NUE = crop N yield/N input). Most improvements have come from crop genetics or from fertilization practices and technologies to manage the 4Rs of inorganic nutrient stewardship: the "right" source, rate, time, and place. However, limited adoption and inconsistent, site-specific benefits, ranging from no effect to <50% reduction in N loss, have constrained the overall impacts of these approaches.[5] Moreover, ample inorganic fertilizer use during crop breeding has selected for varieties that have less capacity to forage for soil organic N, hindering efforts to increase system-wide NUE.[6] Thus, to synchronize plant N requirements with soil supply, we will need interventions that incorporate new insights about how the plant-microbe-soil system governs N availability.[7]

Changing concepts in plant N nutrition

In recent decades, a proliferation of biogeochemical research on mechanisms driving the soil N cycle has begun to reshape our understanding of plant N nutrition. For nearly two centuries prior, agronomists had based management decisions almost exclusively on the amount of inorganic N circulating in the soil, with less consideration given to N in soil organic matter (SOM). However, most agricultural soils have 15–20 times more N in SOM than is applied annually as fertilizer, and often more than half of N removed by maize in industrial systems derives from SOM.[3] It is increasingly clear that SOM, which can incorporate, store, and release massive amounts of N, and the microbial communities that underpin this cycling, are underused levers in N fertility management worldwide.

SOM N is not only abundant but also dynamic. Soil organic N is in constant flux due to microbial assimilation and turnover that rapidly cycles N between inorganic and organic forms. For instance, up to 40% of inorganic N fertilizer can be incorporated into soil microbial biomass or stabilize on soil particles within days to weeks of application.[8] Microbes can remobilize N from SOM, but the rate and mechanisms of remobilization differ between SOM fractions that range in chemical complexity and extent of physical stabilization (i.e., dissolved, particulate, or mineral-associated).[9]

Plants further modify the stabilization and mobilization dynamics of SOM N in critical ways. By shaping microbial community structure and function and establishing physical and chemical gradients in the soil, plants exert a significant capacity to regulate N transformations and control their own N supply.[10] For example, N mineralization can more than double in the zone under plant root influence to exceed crop N requirements.[11] To optimize nutrient acquisition during periods of environmental stress and changing nutrient availability, plants can alter their resource allocation into root growth and symbioses with mycorrhizal fungi. Plant traits enabling interactions with microbes and soil differ among plant communities, species, and lines and are constrained by soil characteristics. Such observations have invigorated interest in developing management approaches that shape plant-soil-microbe interactions and SOM dynamics to improve NUE.

A co-benefit of managing soils for organic N is the potential to increase global soil C stocks, since N is one of the critical nutrients controlling soil C accumulation.[12] However, even as we enlarge SOM-N pools, N must continue to be released from organic to inorganic forms for plant uptake, necessitating decomposition of some SOM. To achieve a balance between building and using SOM, we could increase N inputs and/or reduce N losses—especially by diverting losses into SOM-N accumulation—to offset the amount of N exported during crop harvest. We illustrate this principle as a new term: NUE_agroecosystem.

Nitrogen in crops and SOM: NUE_agroecosystem

To center agricultural N management around N uptake in not only crops but also SOM, we can update a classical agroecosystem N mass balance equation by including an SOM term:

$$\text{N inputs} - \text{Environmental N losses} = \text{Crop N yield} + \text{SOM N accumulation}$$

where N inputs include synthetic N fertilizers, atmospheric N fixation (free and symbiotic), and organic amendments such as animal manure and crop residues, and N outputs include N leaching, denitrification, and volatilization.

This mass balance takes a system-level view of the fate of N, balancing the benefits of crop yield and SOM accumulation against the environmental impacts of N loss.[13] We can use this mass balance equation to produce a variation of the NUE equation that emphasizes N accumulation in the crop and SOM:

$$\text{NUE\_agroecosystem} = (\text{Crop N} + \text{SOM N accumulation}) / \text{N inputs}$$

This is an update to previous agronomic NUE indices, which, at their most basic, are calculated as crop yield per unit N input. The minor modification of adding an SOM-N accumulation term highlights a major insight: management interventions can shift N out of the environmental loss term into the SOM-N accrual term without necessarily lowering crop yields. If management can decrease environmental N losses, fewer N inputs are needed to achieve crop yield and SOM goals. Thus, a key aspect of an optimized agroecosystem N cycle is that it diverts N away from losses by redirecting it into SOM and plants. To achieve this, we must understand how to incorporate inorganic N into the organic cycle, retain it as SOM until it is needed, and transfer it efficiently into plants.

ACCUMULATION, RECYCLING, AND UPTAKE OF NITROGEN (ARUN) FRAMEWORK

We propose the "ARUN" framework (Figure 1) to synthesize recent advances into a clear and accessible schema of the agroecosystem N cycle. By helping to organize and translate newer biogeochemical concepts into actionable ideas, ARUN helps researchers, practitioners, and decision-makers shape the biogeochemistry of agroecosystems to meet our goals for N management, yield, long-term soil fertility, and environmental health. The framework describes SOM's interdependent, three-part nature as (1) a reservoir for N that can accumulate and persist in the soil (*accumulation*), (2) a subject of continuous and often rapid transformations between different pools of plant material and soil organic and inorganic N (*recycling*), and (3) an ongoing source of bioavailable N, the supply of which is controlled by continuous microbial processes and plants actively driving SOM turnover (*uptake*). ARUN integrates the broad principles of ecological[14] and integrated nutrient management[15] with emerging insights into plant-microbe-SOM feedback mechanisms[7,9–11,16] to inspire practical strategies that enhance NUE_agroecosystem.

ARUN is grounded in the core purpose of any soil fertility program: to closely align N inputs with N exported through crop harvest. To accomplish this, judicious use of inorganic N can supplement organic inputs during accumulation,[14,15] with less of the disruption to biological processes that may result from larger inorganic N applications.[17] For efficient N accumulation, an agroecosystem needs an abundance of plant roots and their symbionts like mycorrhizal fungi poised to take up N inputs; this emphasizes the importance of permanent soil cover with living plants.[18] Such plants and their belowground inputs will support microbial activity and conversion of loss-prone inorganic to stable organic N, which are highest when there is abundant C.

The ARUN framework especially departs from input-centric perspectives in its emphasis on the management goals of recycling and retaining N that might otherwise be lost and improving organic N remobilization and uptake by plants. This entails converting N inputs into SOM to reduce the size of the standing pool while stimulating just enough N mineralization for immediate plant use,[14] with any excess inorganic N immobilized by microbes. Management can support active microbial communities to both mineralize and immobilize N, for example by introducing both organic N (via N-fixing microbes and animal wastes) and C-rich organic matter (e.g., plant residues) that increases microbial growth and demand for N. Fewer N losses can originate from the small inorganic N pools that result from equally

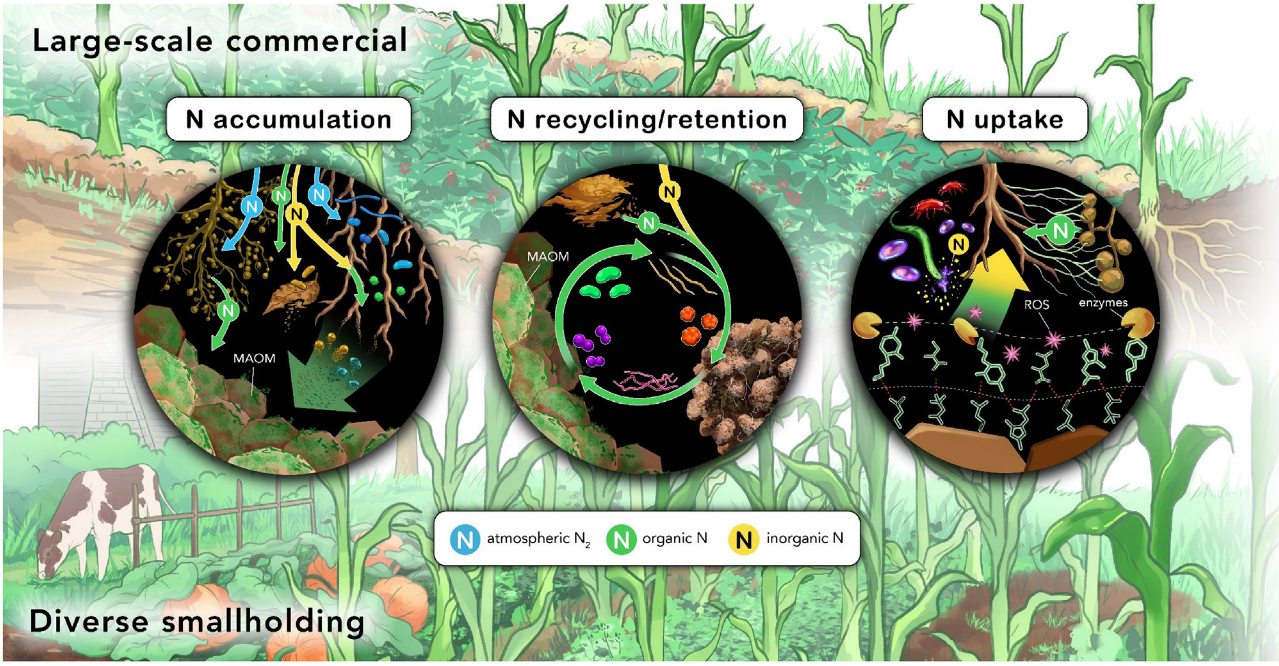

Figure 1. The accumulation, recycling, and uptake of N (ARUN) framework
This framework integrates organic and inorganic N inputs to improve NUE_agroecosystem. ARUN applies to different farming systems, represented here by large/commercial (top) and smallholder operations (bottom), providing producers flexibility to optimize nutrient inputs based on availability and NUE_agroecosystem goals. ARUN recognizes three interrelated biogeochemical compartments with unique controlling mechanisms and management impacts: N accumulation, recycling and retention, and uptake. Accumulation (left bubble): new N inputs should support NUE_agroecosystem, aligning with crop yields and SOM goals. Microbial N fixation (blue arrows) and other organic inputs (green arrows) are augmented by inorganic fertilizer (yellow arrows) and N is quickly removed from the soluble pool via roots, active microbial decomposers, and stabilization on minerals. Recycling (center bubble): N shuttling between soluble, microbial, particulate, and mineral-stabilized pools is crucial for NUE_agroecosystem. This microbe-driven process facilitates a stable N supply over the short and long term, reduces N losses, and supports crop yields and SOM accumulation. Uptake (right bubble): plant N uptake is supported in the root zone by root-microbe interactions and food web dynamics that mobilize mineral-associated and other organic N pools, accelerate mineralization-immobilization processes, promote root extension to enable uptake of previously inaccessible inorganic N, and favor direct transfer of N from legumes to cash crops via mycorrhizal fungal hyphae. Management interventions to improve NUE_agroecosystem can include an array of agroecological practices that target one or more compartments in a wide range of management systems, from soils with high SOM concentrations to degraded or coarse-textured soils that are co-limited by multiple nutrients. Abbreviations: N_2, dinitrogen gas; MAOM, mineral-associated organic matter; ROS, reactive oxygen species. Illustration by Elena Hartley.

high rates of N immobilization and mineralization in soils with these plant-microbe-SOM dynamics.[16]

Microbial functions are central to the ARUN framework, accumulating and cycling N through different SOM pools to make it available to plants (Figure 2).[19] Microbes control ubiquitous N reactions such as nitrification and denitrification and also perform key functions in introducing and stabilizing N into soil, transferring N between solid and dissolved pools, and shaping plant physiological responses. This diverse spectrum of microbial functions underlies all stages of the bioavailable N life cycle. To enhance N accumulation, retention, and timely release during critical plant growth stages, we will require additional research into the controls on, and responsiveness to management, of these microbe-SOM interactions.

ARUN describes an approach to N management that balances three interrelated goals: optimizing crop yields, increasing SOM, and minimizing N pollution. It acknowledges that SOM accumulation, essential for soil C storage, requires proportional N retention. By reducing N losses to the environment, more N inputs can be allocated to both crop uptake and SOM formation. As new SOM forms and mineralizes, particularly through plant-microbe interactions, it synchronizes plant needs with N availability in a self-reinforcing loop that reduces N losses.

Future directions for the ARUN framework

With ARUN, we organize scientific concepts into a parsimonious framework to guide hypothesis generation and update society's perspective on soil N cycling and management. ARUN shifts us away from a focus on plant uptake of inorganic N fertilizer inputs, which has underpinned decades of research and interventions with unsatisfactory results. Instead, ARUN showcases how all agricultural N integrates into a microbe-driven biogeochemical system where SOM plays a crucial intermediary role between inputs and plants.

Despite considerable scientific progress in the agroecosystem N cycling research ARUN synthesizes, much uncertainty remains. We know little about how organic and inorganic N inputs interact with microbial traits and soil properties to contribute to N accumulation in various SOM pools, including particulate organic matter and mineral-associated organic matter.[16] We lack an understanding of how N recycling dynamics differ among microbial communities with varying traits like C and N use efficiency. We can explore how soil food webs help recycle organic N, for example through microbial predation and viral lysis, and whether agricultural management can manipulate crop roots to capture loss-prone N better. Building on recent research into how plant-microbe interactions influence N uptake, we can potentially customize plant functional traits for local soil conditions through species selection, crop diversification, and breeding.[6,10,11] This includes exploring topics such as nutrient resource economics, plant-microbe signaling mechanisms, plant genetics, and associations with mycorrhizal fungi and other microorganisms, as well as examining how these interact with inorganic inputs, specific SOM pools, and environmental conditions.

Cover crops illustrate how ARUN can help us address remaining knowledge gaps. Past research has explored how legumes accumulate N through biological fixation and how grass cover crops capture and recycle N that might be lost between seasons, but major questions remain in each ARUN biogeochemical compartment. During accrual, how much cover crop N persists as recent and decomposed litter vs. as microbial N or more stable mineral-associated organic matter? During recycling, do interactions with inorganic N fertilizer inputs enhance or suppress retention of cover crop and fertilizer N? During uptake, how are root-microbe interactions including mycorrhizal associations impacted by cover crop use and what are the implications

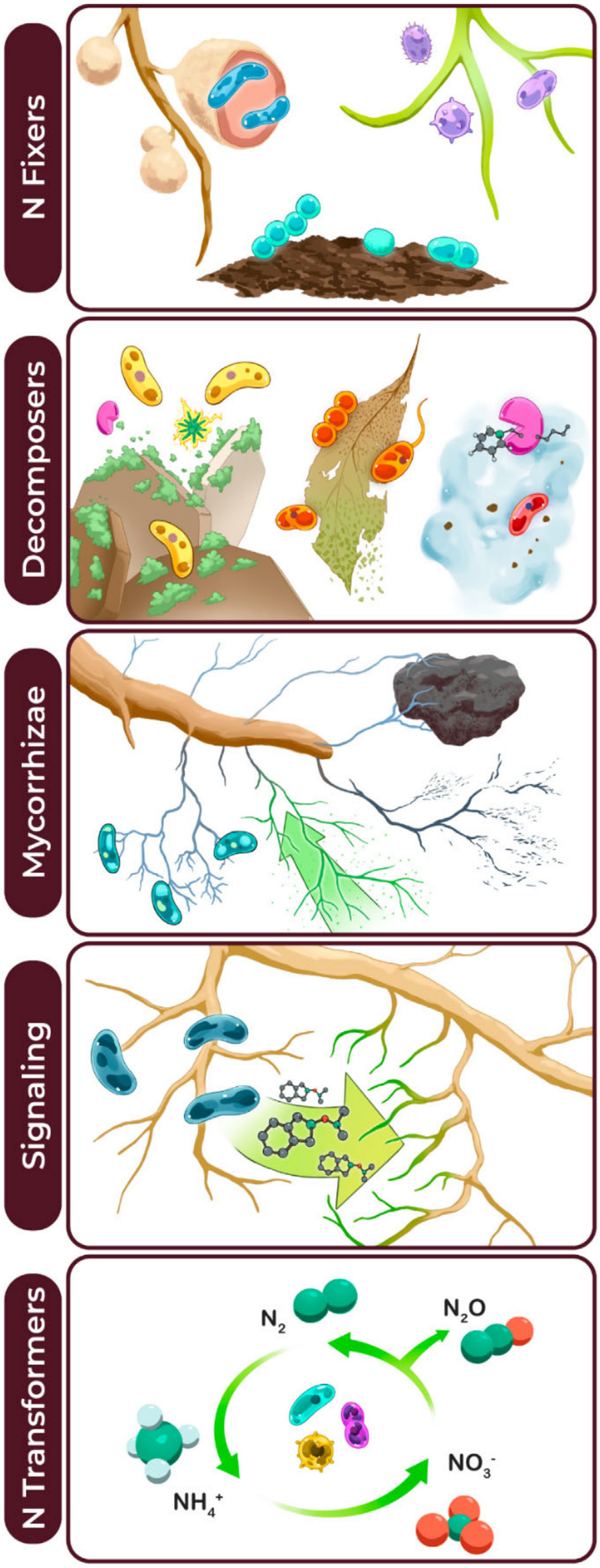

Figure 2. Microbial functional groups are pivotal in soil bioavailable N cycling and plant N uptake

N-fixers: atmospheric N-fixers, categorized as symbiotic (e.g., rhizobia in legume nodules, left), free-living (in bulk soil, middle), or associative (root zone dwelling, right), provide new N inputs to soils that help offset exported N. Decomposers: a functionally diverse class, decomposers can produce organic acids and oxidants to mobilize mineral-associated organic matter (left), break down particulate organic matter (middle), and assimilate dissolved inorganic and organic N (right). Mycorrhizae: mycorrhizal fungal hyphae extend plant nutrient capture capabilities (clockwise from top right) by accessing organic matter occluded within aggregates, recycling hyphal necromass, translocating N from soil to roots, and stimulating decomposition by other microbes. Signaling: some microbes in the root zone directly communicate with plants via chemical signals to alter root growth and other factors that influence nutrient acquisition. Mineral N transformers: Some microbes use reduction-oxidation chemical transformations to regulate transitions between mineral N states with different bioavailability and vulnerability to environmental loss. Abbreviations: N_2, dinitrogen gas; N_2O, nitrous oxide; NO_3^-, nitrate; NH_4^+, ammonium. Illustration by Elena Hartley.

for enabling plants to access nutrients from different sources?

By unifying current biogeochemical information into a streamlined framework, we hope that ARUN can guide the research and innovation agenda to explore the life cycle of agricultural soil N using an integrated systems approach that centers organic matter and biological transformations. This should not only advance ongoing inquiry into the interactions between plants, microbes, and soil that govern N cycling but also organize emerging insights so growers, industry, and decision-makers can develop novel management interventions and policies that enhance efficient N use in agroecosystems.

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DECLARATION OF INTERESTS

The authors declare no competing interests.

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