

REVIEW SUMMARY

ECOSYSTEM ECOLOGY

Evidence, causes, and consequences of declining nitrogen availability in terrestrial ecosystems

Rachel E. Mason*, Joseph M. Craine, Nina K. Lany, Mathieu Jonard, Scott V. Ollinger, Peter M. Groffman, Robinson W. Fulweiler, Jay Angerer, Quentin D. Read, Peter B. Reich, Pamela H. Templer, Andrew J. Elmore*

BACKGROUND: The availability of nitrogen (N) to plants and microbes has a major influence on the structure and function of ecosystems. Because N is an essential component of plant proteins, low N availability constrains the growth of plants and herbivores. To increase N availability, humans apply large amounts of fertilizer to agricultural systems. Losses from these systems, combined with atmospheric deposition of fossil fuel combustion products, introduce copious quantities of reactive N into ecosystems. The negative consequences of these anthropogenic N inputs—such as ecosystem eutrophication and reductions in terrestrial and aquatic biodiversity—are well documented. Yet although N availability is increasing in many locations, reactive N inputs are not evenly distributed globally. Furthermore, experiments and theory also suggest that global change factors such as elevated atmospheric CO₂, rising temperatures, and altered precipitation and disturbance regimes can reduce the availability of N to plants and microbes in many terrestrial ecosystems. This can occur through increases in biotic demand for N or

reductions in its supply to organisms. Reductions in N availability can be observed via several metrics, including lowered nitrogen concentrations ([N]) and isotope ratios ($\delta^{15}\text{N}$) in plant tissue, reduced rates of N mineralization, and reduced terrestrial N export to aquatic systems. However, a comprehensive synthesis of N availability metrics, outside of experimental settings and capable of revealing large-scale trends, has not yet been carried out.

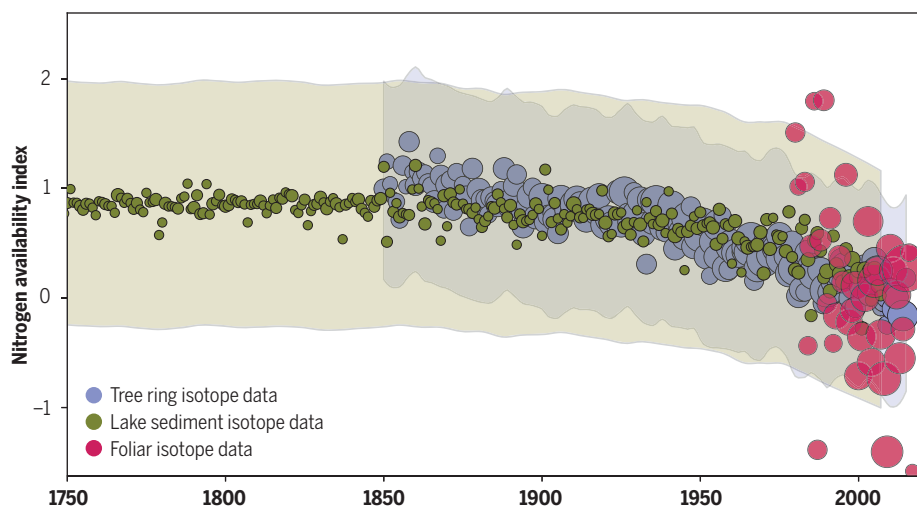
ADVANCES: A growing body of observations confirms that N availability is declining in many nonagricultural ecosystems worldwide. Studies have demonstrated declining wood $\delta^{15}\text{N}$ in forests across the continental US, declining foliar [N] in European forests, declining foliar [N] and $\delta^{15}\text{N}$ in North American grasslands, and declining [N] in pollen from the US and southern Canada. This evidence is consistent with observed global-scale declines in foliar $\delta^{15}\text{N}$ and [N] since 1980. Long-term monitoring of soil-based N availability indicators in unmanipulated systems is rare. However, forest studies in the northeast US have demonstrated

decades-long decreases in soil N cycling and N exports to air and water, even in the face of elevated atmospheric N deposition. Collectively, these studies suggest a sustained decline in N availability across a range of terrestrial ecosystems, dating at least as far back as the early 20th century.

Elevated atmospheric CO₂ levels are likely a main driver of declines in N availability. Terrestrial plants are now uniformly exposed to ~50% more of this essential resource than they were just 150 years ago, and experimentally exposing plants to elevated CO₂ often reduces foliar [N] as well as plant-available soil N. In addition, globally-rising temperatures may raise soil N supply in some systems but may also increase N losses and lead to lower foliar [N]. Changes in other ecosystem drivers—such as local climate patterns, N deposition rates, and disturbance regimes—individually affect smaller areas but may have important cumulative effects on global N availability.

OUTLOOK: Given the importance of N to ecosystem functioning, a decline in available N is likely to have far-reaching consequences. Reduced N availability likely constrains the response of plants to elevated CO₂ and the ability of ecosystems to sequester carbon. Because herbivore growth and reproduction scale with protein intake, declining foliar [N] may be contributing to widely reported declines in insect populations and may be negatively affecting the growth of grazing livestock and herbivorous wild mammals.

Spatial and temporal patterns in N availability are not yet fully understood, particularly outside of Europe and North America. Developments in remote sensing, accompanied by additional historical reconstructions of N availability from tree rings, herbarium specimens, and sediments, will show how N availability trajectories vary among ecosystems. Such assessment and monitoring efforts need to be complemented by further experimental and theoretical investigations into the causes of declining N availability, its implications for global carbon sequestration, and how its effects propagate through food webs. Responses will need to involve reducing N demand via lowering atmospheric CO₂ concentrations, and/or increasing N supply. Successfully mitigating and adapting to declining N availability will require a broader understanding that this phenomenon is occurring alongside the more widely recognized issue of anthropogenic eutrophication. ■



Intercalibration of isotopic records from leaves, tree rings, and lake sediments suggests that N availability in many terrestrial ecosystems has steadily declined since the beginning of the industrial era. Reductions in N availability may affect many aspects of ecosystem functioning, including carbon sequestration and herbivore nutrition. Shaded areas indicate 80% prediction intervals; marker size is proportional to the number of measurements in each annual mean.

The list of author affiliations is available in the full article online.

*Corresponding author. Email: rachel.e.mason1@gmail.com

(R.E.M.); aelmore@umces.edu (A.J.E.)

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Evidence, causes, and consequences of declining nitrogen availability in terrestrial ecosystems

Rachel E. Mason^{1*†}, Joseph M. Craine², Nina K. Lany³, Mathieu Jonard⁴, Scott V. Ollinger⁵, Peter M. Groffman^{6,7}, Robinson W. Fulweiler^{8,9}, Jay Angerer¹⁰, Quentin D. Read^{1†‡}, Peter B. Reich^{11,12,13}, Pamela H. Templer⁹, Andrew J. Elmore^{1,14*}

The productivity of ecosystems and their capacity to support life depends on access to reactive nitrogen (N). Over the past century, humans have more than doubled the global supply of reactive N through industrial and agricultural activities. However, long-term records demonstrate that N availability is declining in many regions of the world. Reactive N inputs are not evenly distributed, and global changes—including elevated atmospheric carbon dioxide (CO₂) levels and rising temperatures—are affecting ecosystem N supply relative to demand. Declining N availability is constraining primary productivity, contributing to lower leaf N concentrations, and reducing the quality of herbivore diets in many ecosystems. We outline the current state of knowledge about declining N availability and propose actions aimed at characterizing and responding to this emerging challenge.

Human activities have caused extensive changes in climate, land use, ecosystem function, and biogeochemical cycles, including that of nitrogen (N) (1). N is a fundamental component of plant proteins, which are necessary to support the growth of plants and the herbivores that feed upon them. Thus, N availability has a strong influence on the structure and function of many ecosystems. The dominant form of N in the biosphere is highly stable N₂ gas, which humans convert into reactive forms of N through fertilizer production and planting of N₂-fixing crops, and as a by-product of fossil fuel combustion. Application of this reactive N to ecosystems, intentionally or via the deposition of airborne NO₃⁻ and NH₃,

increases N availability, defined here as the supply of N to plants and microbes relative to their demand for N (Box 1). As N availability rises, a cascade of effects occurs, including increased plant N concentrations, shifts in above- and belowground species abundance and diversity, and increased N losses to the atmosphere and aquatic ecosystems. The negative consequences of these changes, which present serious threats to environmental quality and the well-being of human communities, have been the subject of extensive research and discussion (1).

At the same time, a growing body of evidence suggests that the problem of excess N coexists with a much less widely recognized issue: declining N availability in terrestrial systems that are not subject to high levels of anthropogenic N inputs. Although humans have more than doubled the total global supply of reactive N (1), the largest inputs occur in agricultural and urban areas and downstream locations, and levels of atmospheric N deposition vary widely by region and over time. Large areas of Earth's terrestrial surface, including much of Australia, sub-Saharan Africa, parts of Asia and South America, and vast swaths of boreal forest, have not yet been subject to high levels of N deposition. In addition, elevated N deposition in parts of

North America, much of Europe, and some regions of Southeast Asia has decreased in recent decades (2, 3). Therefore, many terrestrial ecosystems are potentially susceptible to changes in ecosystem drivers that may reduce the availability of N. These changes include elevated atmospheric CO₂, rising global temperatures, and altered precipitation and disturbance regimes (4–7).

Declines in terrestrial N availability can be driven by increases in primary productivity that result in N demand outstripping N supply, decreases in external N inputs, decreases in soil N cycling rates, and/or increases in N losses. Experiments and theory predict declines in N availability in many ecosystems under the influence of a number of global change factors (4, 5, 7–9), but a comprehensive synthesis of N availability metrics, capable of revealing large-scale trends, has yet to be carried out. Acknowledging the substantial evidence of excess reactive N in areas of high anthropogenic inputs, our goal for this paper is to present evidence of declines in N availability in forests, grasslands, and other terrestrial ecosystems outside of agricultural and urban locations.

We show how changes in the N cycle can be evaluated, and we review the likely causes of N availability declines. We then assess their potential consequences for ecosystems and society. Finally, we identify the research that is needed in response to this emerging issue. Akin to trends in atmospheric CO₂ or global temperatures, large-scale declines in N availability are likely to present long-term challenges that will require informed management and policy actions in the coming decades.

Tracking the N cycle

Determining large-scale trajectories of N availability requires monitoring of the N cycle. Yet of all global changes caused by human activity, changes in N availability and cycling are among the most challenging to study. Whereas changes in atmospheric CO₂, precipitation, and atmospheric temperature are routinely monitored and reported globally, tracking the N cycle requires drawing inferences from a suite of indicators collected over a range of scales in space and time (Fig. 1). These indicators include metrics of soil microbial activity, plant N assimilation, and ecosystem N inputs and outputs, which must then be assembled to determine trends in N availability at regional or global scales.

Changes in ecosystem N availability can be inferred from measures of N inputs, internal soil N cycling processes, plant N status, and N losses (Fig. 1). In unfertilized ecosystems, reactive forms of N are added via lightning, biological N₂ fixation, rock weathering, and atmospheric N deposition. These reactive forms of N (NO₃⁻, NH₄⁺, and small organic molecules) are cycled by plants and soil

¹National Socio-Environmental Synthesis Center, Annapolis, MD, USA. ²Jonah Ventures, Boulder, CO, USA. ³Northern Research Station, USDA Forest Service, Durham, NH, USA.

⁴Earth and Life Institute, Université catholique de Louvain, Louvain-la-Neuve, Belgium. ⁵Earth Systems Research Center, University of New Hampshire, Durham, NH, USA.

⁶Advanced Science Research Center, The Graduate Center, City University of New York, New York, NY, USA. ⁷Cary Institute of Ecosystem Studies, Millbrook, NY, USA.

⁸Department of Earth and Environment, Boston University, Boston, MA, USA. ⁹Department of Biology, Boston University, Boston, MA, USA. ¹⁰Fort Keogh Livestock and Range Research Laboratory, USDA Agricultural Research Service, Miles City, MT, USA. ¹¹Department of Forest Resources, University of Minnesota, St. Paul, MN, USA.

¹²Institute for Global Change Biology and School for Environment and Sustainability, University of Michigan, Ann Arbor, MI, USA. ¹³Hawkesbury Institute for the Environment, Western Sydney University, Penrith, New South Wales, Australia. ¹⁴Appalachian Laboratory, University of Maryland Center for Environmental Science, Frostburg, MD, USA.

*Corresponding author. Email: rachel.e.mason1@gmail.com (R.E.M.); aelmore@umces.edu (A.J.E.)

†Present address: Center for Global Discovery and Conservation Science, Arizona State University, Tempe, AZ, USA.

‡Present address: USDA Agricultural Research Service, Southeast Area, Raleigh, NC, USA.

Box 1. Nitrogen availability is defined as the supply of N relative to demand by plants and microbes. By accounting for demand, this definition differs from one based solely on N supply. Although an increase in N supply can cause N availability to rise, N availability may decline if demand for N increases by more than any increase in N supply.

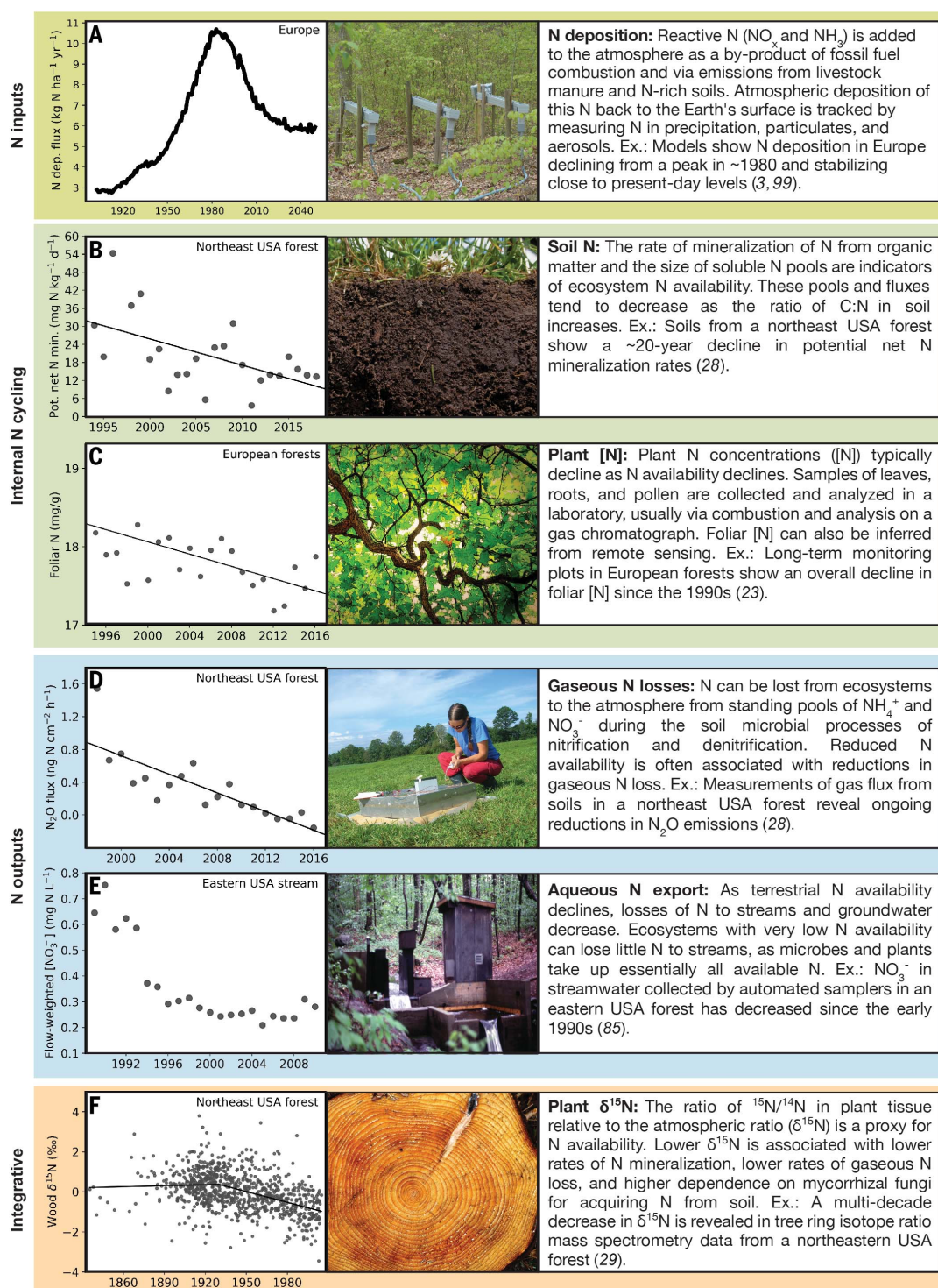


Fig. 1. Changes in the N cycle can be detected by monitoring ecosystem N inputs, internal soil N cycling and plant N status, and N losses. In contrast to the well-established monitoring of global atmospheric CO_2 , for example, tracking N availability requires observing a comprehensive set of metrics that are often highly variable in space and time and the measurement of which involves considerable effort. Lower N input rates (A), smaller pools and fluxes of plant-available soil N (B), decreased plant N status (C), and lower N losses (D and E) over time may indicate

reductions in N availability, whereas N stable isotope ratios (F) provide a measure that integrates over several determinants of N availability. For (A) to (F), respectively, example time series of N availability indicators, here primarily taken from forest ecosystems, are adapted from (3, 99), (28), (23), (28), (85), and (29). [Photo credits: (A) M. Jonard; (B) Natural Resources Conservation Service/CC BY 2.0; (C) milomingo/CC BY-NC-ND 2.0; (D) A. Contosta; (E) US Forest Service, Northern Research Station; and (F) B. Kasman]

microbes, so measurements of plant N and microbial activity are important tools for tracking N availability. Soil microbes can release N from organic matter into soluble organic N (solubilization), transform organic N to inorganic forms (mineralization), and oxidize NH_4^+ into NO_3^- (nitrification). Soil microbes can also acquire organic and inorganic N from soil solution so that it becomes unavailable to plants in the short term (immobilization). Net mineralization, the balance between mineralization and immobilization, is often estimated from the change in inorganic N in soil solution over a period of time in the absence of plants.

The balance between net mineralization or solubilization and immobilization is highly dependent on factors such as the C:N ratio of organic matter, which is thus an additional indicator of N availability. This ratio is driven by the N concentration ([N]) of plant biomass, which tends to decrease when N availability decreases (10). Carbon and N concentrations in samples of plant tissues are measured in the laboratory through combustion and elemental analysis. Transfers of N to water bodies and the atmosphere can also be proxies for N

availability, as ecosystem losses of N occur to a greater extent when N availability is high. Quantifying N transfers requires simultaneous measurement of N concentration in water or air and the flux of water or air across the boundary of interest. All of these measurements are important for understanding N cycle changes but are rarely implemented on large spatial or temporal scales, owing to their complexity and cost.

Given the spatial and temporal variability of the N cycle and the number of processes involved, metrics that can integrate N cycling processes into a single value are particularly useful for tracking changes over time. Natural abundance N isotope ratios ($\delta^{15}\text{N}$), measured in plant, wood, and sediment samples through mass spectrometry, have emerged as a useful tool for this purpose (10). Biological processes that lead to increased N loss via gaseous or leaching pathways tend to discriminate against ^{15}N and favor ^{14}N . Over time, N loss from systems with high N availability—i.e., high N supply relative to demand—therefore increases the $\delta^{15}\text{N}$ value of the inorganic N pool that remains available to plants. In addition, as N availability increases, plants rely less on

mycorrhizal fungi, which transfer ^{15}N -depleted N to plants (11). Consequently, plants growing under conditions of high N availability are enriched in ^{15}N relative to plants growing under low N availability.

Evidence of declining N availability in terrestrial ecosystems

Measurements of $\delta^{15}\text{N}$ in leaves, wood, and sediments indicate that declines in N availability extend over a wide geographic area and date back to at least the early 1900s. A global dataset of $\delta^{15}\text{N}$ in leaves, composed of ~40,000 measurements from unfertilized locations since 1980, reveals a decrease in N availability throughout the period of record (Fig. 2A) (12). Isotopic signatures of recently acquired N are stored in wood, so the $\delta^{15}\text{N}$ of wood can also be used to reconstruct extended time series of N availability. Aggregating multiple site-level trajectories in wood $\delta^{15}\text{N}$ from forests across the continental US demonstrates a pronounced decrease in N availability since the mid-19th century, particularly in cool, wet regions (Fig. 2B) (13). Despite integrating more processes than plant $\delta^{15}\text{N}$ over a larger spatial scale, the $\delta^{15}\text{N}$ of organic matter in lake

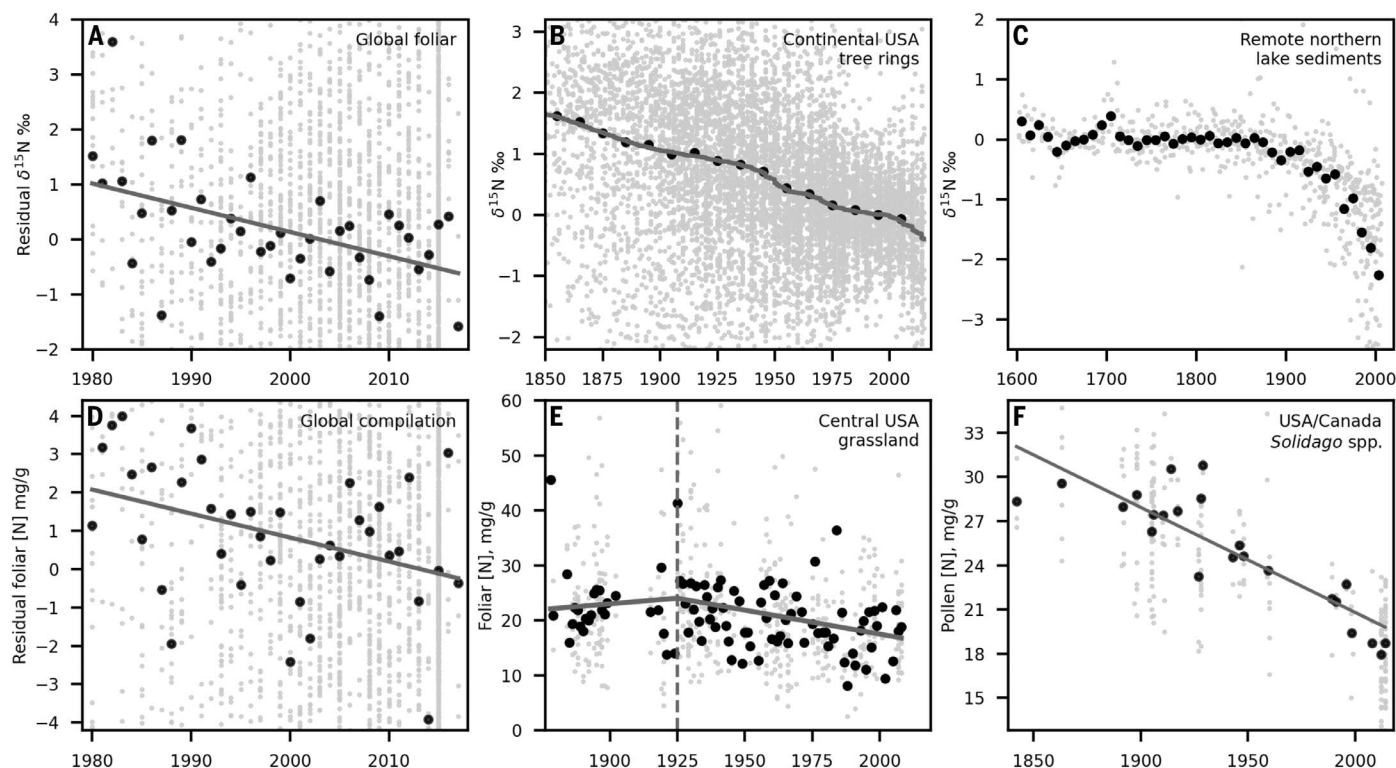


Fig. 2. Evidence of declining N availability comes from long-term global and regional studies. A global foliar $\delta^{15}\text{N}$ compilation (A) demonstrates a decrease in ecosystem N availability since 1980, whereas tree ring and lake sediment $\delta^{15}\text{N}$ datasets (B and C) from the continental US to the Arctic reveal large-scale declines dating back to at least the early 20th century. Few plant [N] time series cover large temporal and geographic extents. However, statistically significant declines are observed in a global foliar [N] compilation

dating back to 1980 (D), as well as in long-term records of foliar [N] from a central US grassland (E) and pollen [N] from the US and southern Canada (F). Data and fits adapted from original publications (12, 13, 15, 16, 22); (C) shows the 25 datasets in (15) offset to a common mean. Fits (if any) are as presented in the original papers; all declining trends are significant at the $P < 0.05$ level. Gray points denote individual measurements; black points indicate annual or decadal mean values.

sediments can be used to further extend N availability reconstructions (14). Likely owing to the strong influence of local urban and agricultural land use on N availability, no coherent changes in N availability over the past 500 years are apparent at the global scale in lake sediment data (14). However, downturns in $\delta^{15}\text{N}$ in sediments from remote lakes from the Rocky Mountains to the Arctic (15) suggest a decline in N availability over a large area starting around 1895 (Fig. 2C).

The foliar $\delta^{15}\text{N}$ record from herbarium samples provides further evidence of long-term declines in N availability. In central and northern US grasslands, the foliar $\delta^{15}\text{N}$ of leaves stored in herbaria suggests that N availability has been declining there since roughly 1940 (16, 17). Herbarium studies from Europe and Asia also largely find consistent, declining trends, with data from various species in the western Mediterranean region showing a decrease in foliar $\delta^{15}\text{N}$ since the 1920s (18) or 1940s (19). Foliar $\delta^{15}\text{N}$ data from herbarium specimens of *Arabidopsis thaliana* spanning Eurasia and North Africa document a decline in N availability over the period beginning in 1842, although the onset of the decline is not specified (20). A set of more recent foliar $\delta^{15}\text{N}$ measurements, from the 2000s and 2010s over a ~3000-km transect across the Tibetan Plateau, also exhibit a decline (21).

Within individual species, foliar [N] tends to increase with increasing N availability and decrease with decreasing N availability. In parallel to $\delta^{15}\text{N}$, a global compilation of foliar [N] measurements since 1980 demonstrates an overall decline (Fig. 2D) (12). Herbarium studies show that foliar [N] in grassland species in the central and northern US has decreased by approximately 3 to 8 mg g⁻¹ (18 to 30%) since around 1930 (16, 17) (Fig. 2E), and a trend of increasing C:N has been found in *Arabidopsis thaliana* specimens from across this species' broad native range (20). Long-term reductions in [N] are not limited to leaves; other herbarium records indicate that [N] in goldenrod (*Solidago* spp.) pollen from multiple locations across the US and southern Canada has decreased by ~10 mg g⁻¹ (33%) since the early 1900s (Fig. 2F) (22).

Over shorter time scales, ongoing monitoring of European forests demonstrates a general pattern of decreasing foliar [N] (23, 24). Averaged over all species and locations, foliar [N] has been decreasing by 0.04 ± 0.004 mg g⁻¹ year⁻¹ since at least 1995 (a reduction of 4.4% in 20 years; Fig. 1C) (23). Few large-scale foliar [N] time series exist outside of Europe and North America. On the scale of individual sites, comparisons of recent collections and herbarium samples from Panama and the Democratic Republic of the Congo have shown increasing and stable foliar [N], respectively (25, 26). In samples from across

China, foliar [N] has increased since the 1980s in tandem with a rise in atmospheric N deposition (27).

There are few long-term records that track multiple components of the N cycle, but those that do exist provide valuable insights into the changes occurring as N availability declines. At the Hubbard Brook Experimental Forest (HBEF) in New Hampshire, US, a >50-year monitoring effort covering multiple ecological variables has provided the most detailed published record of declining N availability (28). Dendroisotopic and sediment $\delta^{15}\text{N}$ records from HBEF imply that the decline in N availability began in approximately 1930, after a period of intense logging (Fig. 1F) (29). Export of NO_3^- in streams at HBEF has decreased since the early 1970s, although N deposition at this site began to decrease only in the early 2000s. Gaseous losses of N_2O , a symptom of high N availability in forests, have also declined since measurements began in 1998 (Fig. 1D). Potential net N mineralization and nitrification rates have steadily fallen since the 1970s (Fig. 1B), whereas the C:N ratio of the forest floor has increased (30). At other forest sites in the eastern US, long-term monitoring plots reveal trends consistent with declining N availability (31), including declines in soil $\text{NH}_4\text{-N}$ (32), forest floor [N] (33), and net N mineralization and nitrification (33, 34).

In summary, long-term datasets tracking the N cycle indicate decreasing N availability in multiple locations across Europe and North America, contributing to a pattern of declining N availability in unfertilized terrestrial ecosystems worldwide (12). The trend toward lower N availability likely does not extend to locations that receive high levels of anthropogenic N, such as urban and agricultural areas and regions experiencing very high levels of atmospheric N deposition [e.g., China (27)], where N availability is characterized by elevated supply. Long-term N availability datasets are scarce in many regions of the world, including most of Asia, the tropics, and the Southern Hemisphere in general. Nonetheless, the forest and grassland ecosystems that exhibit declining N availability represent diverse environments across North America and Eurasia. As well as suggesting that this phenomenon may be affecting large portions of Earth's terrestrial surface, the diverse and widespread nature of the affected ecosystems suggest a shared set of mechanisms underlying the decline in N availability.

Drivers of declining N availability

Multiple environmental changes on both global and local scales may be driving declines in ecosystem N availability (Fig. 3). Elevated atmospheric CO_2 levels (e CO_2) in particular have long been suspected of reducing N availability (35). Atmospheric CO_2 has now reached

its highest level in millions of years, and terrestrial plants are now uniformly exposed to ~50% more of this essential resource than just 150 years ago. In experiments that expose plants to e CO_2 , reduced foliar [N] and increased foliar C:N are consistent outcomes (4, 36). Experiments have also commonly, although not universally, documented N limitation of CO_2 -fertilized ecosystems and a reduction in plant-available soil N (8, 37, 38). Indeed, observational studies find patterns of declining foliar [N] and N availability that are consistent with the expected effects of e CO_2 . These patterns include a strong inverse correlation over time between atmospheric CO_2 and plant [N] (22, 23); a spatially uniform decline in foliar [N] and $\delta^{15}\text{N}$, suggesting a common driver (17); and changes in multiple soil N variables, consistent with the expected consequences of increased C inputs (28). Mirroring these outcomes, CO_2 reduction experiments (8) and evidence from periods of low atmospheric CO_2 in the planet's history (39, 40) show the reverse effects: increases in plant [N] and N mineralization.

The decrease in foliar [N] under e CO_2 is typically attributed to a set of interlinked processes: increased C assimilation that leads to dilution of foliar N (36, 41), plant responses that reduce investment and incorporation of N into leaves (41, 42), and mechanisms that limit soil N supply (4). Support for the dilution hypothesis includes concurrent declines among a suite of foliar nutrients in addition to N (23, 24). Beyond dilution, e CO_2 can lead to changes in N allocation among plant organs, including reductions in RuBisCO (ribulose-1,5-bisphosphate carboxylase-oxygenase) levels in leaves, which in turn increase C assimilation per unit leaf N (41, 42). Reductions in foliar [N] therefore partly imply a decrease in leaf-level N demand. However, this does not necessarily translate to lower N demand at the whole-plant or stand level, as net primary productivity increases with e CO_2 . Total plant N uptake may increase along with this growth stimulation (43), but not always to the extent necessary to satisfy increased N demand and avoid declines in N availability and foliar [N] (38). In addition, when e CO_2 does not lead to an increase in productivity, plant N acquisition appears to be diminished (4).

Reductions in plant [N] lead to changes in plant litter chemistry that may influence soil N supplies over time. Elevated C:N in leaf litter, along with an increased flow of C to soil in litter, roots, and root exudates, can promote N immobilization by microbes, reducing the supply of N to plants and potentially further decreasing plant [N] (35, 44, 45). A decrease in plant-available soil N, both in absolute terms and relative to demand, has been observed in numerous e CO_2 studies (8, 37, 38, 46), although other factors such as warming-induced increases

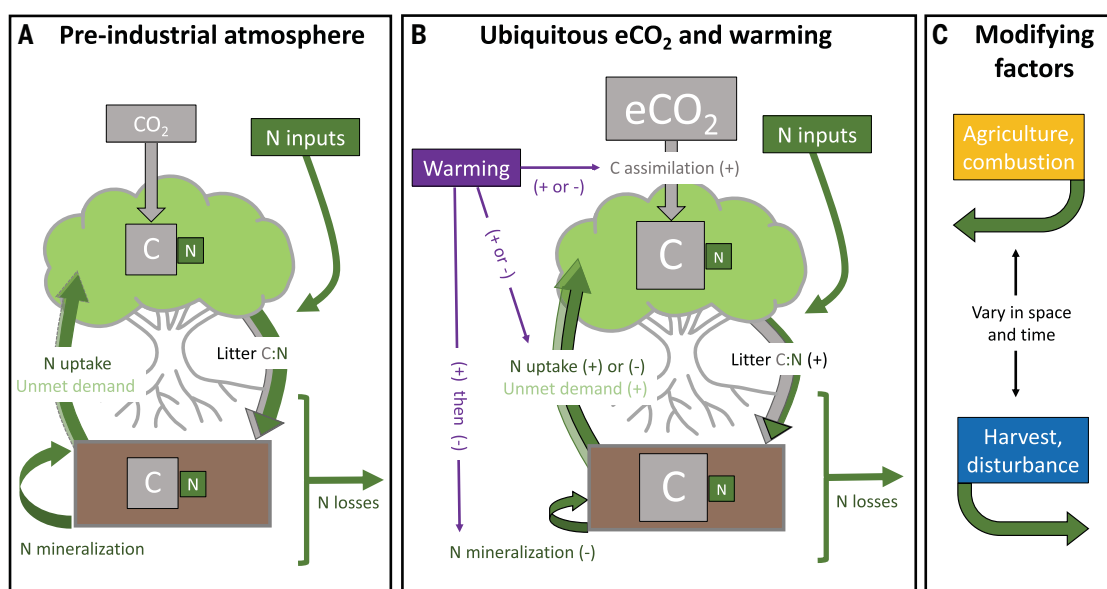


Fig. 3. Multiple global change factors may lead to declines in N availability.

In contrast to the atmospheric conditions of pre-industrial times (**A**), present-day eCO₂ (**B**) directly increases assimilation of C by plants, thus increasing foliar C:N and lowering foliar [N]. Plants may invest more in acquiring N from soil but may not be able to obtain sufficient N to meet increased N demand. At the same time, higher C:N in litter may reduce net mineralization of N, lowering soil N supply and plant N uptake and further reducing foliar [N]. Rising temperatures tend to increase N mineralization and plant growth in the

short term but may lead to increased N losses and depletion of labile N pools in the longer term. (**C**) Ecosystem N inputs from lightning and biological N fixation are frequently supplemented by inputs from agriculture and combustion, and N outputs can be augmented by harvest of livestock (among other products) and disturbances such as fire. In comparison to eCO₂ and rising global temperatures, these factors vary spatially and can be affected on fairly short time scales by land management and use, air quality regulations, and so forth.

in net mineralization may be able to counteract this reduction (46, 47).

In addition to the direct effects of eCO₂, rising global temperatures affect both plant and microbial processes associated with N supply and demand. Observations across climate gradients demonstrate that plants in warmer environments have lower foliar [N] than those in colder environments (48, 49), suggesting that sustained warming will reduce foliar [N]. Reductions in foliar [N] can result from both long-term (genetic adaptation) and short-term (phenotypic plasticity) processes. Common garden experiments confirm a genetic basis for metabolic adaptation favoring elevated foliar [N] in colder environments (49). Ecophysiological studies support the role of warmer temperatures in reducing foliar [N] in conifers grown from seed, showing that short-term metabolic adjustments to warming also reduce foliar [N] (50). At the whole-plant scale, warming often improves conditions for growth—one such example is longer growing seasons, which can cause plant N demand to outstrip supply (51) and may be associated with reduced plant [N].

Countering plant metabolic adjustments and increases in demand, rising temperatures generally stimulate microbial processes, reducing the residence time of labile organic matter and increasing N supply to plants (52). However, with sustained warming, rates of N

cycling do not increase for all ecosystems (53). Warming can also lead to increases in ecosystem N loss pathways (6). Meta-analyses of field warming experiments show mixed results as to whether warming generally increases foliar [N] (54, 55), likely a result of integrating multiple processes related to N supply and demand across diverse ecosystems. Overall, the effects of long-term warming on ecosystem N availability depend on the balance between increases in demand and any increases in supply relative to losses, which will largely be determined by soil organic matter dynamics and any concurrent changes in soil moisture. Especially in dry regions, temperature- and eCO₂-induced changes to soil water deficits could influence both net N mineralization rates and plant N demand.

Elevated atmospheric CO₂ is ubiquitous, and mean annual temperatures are also rising worldwide. Other changes—e.g., in local climate patterns, N deposition rates, and ecosystem disturbance regimes—individually affect smaller areas. Nonetheless, they may have important cumulative effects on global N availability. For example, reduced winter snow cover has been shown to induce soil freezing, fine root damage, reduced net N mineralization, and subsequently reduced N availability (28). Similarly, warmer springs can increase vernal asynchrony, lengthening spring conditions conducive to soil microbial mineralization, N leaching, and

denitrification, ultimately leading to reductions in N availability during the growing season (28, 51). Projected increases in the frequency and intensity of precipitation may exacerbate N losses through leaching and denitrification (7, 56).

In some areas where N deposition was recently high, air quality regulation has successfully reduced deposition rates. Reductions in N deposition rates tend to result in lower foliar [N] and soil solution NO₃⁻ (3, 34). Nevertheless, decreases in N deposition cannot fully explain declining terrestrial N availability. In many cases, the decline began before N deposition started to decrease (28), dates back to before N deposition became widespread in the 1950s (13, 17, 22), and/or is taking place in locations in which N deposition has never reached high levels (17).

Altered ecosystem disturbance regimes and associated losses of N may also have contributed to historic and ongoing declines in N availability. Through harvesting of biomass, N has been continuously—and is increasingly (57, 58)—exported from ecosystems (in the form of livestock, timber, and other products) and transported to the most-populated watersheds. The frequency of fires is also rising in many locations and is associated with higher N losses over decadal time scales (5, 59): In savanna grasslands and broadleaf forests, frequent burning has been found to reduce

soil N by almost 40% over six decades (5). Where frequent N losses occur without substantial inputs, such as in most rangelands that are grazed without use of fertilizers and in situations where supplemental feeding is not feasible (e.g., most pastoral livestock systems), a long-term decline in N availability will be difficult to avoid.

Consequences of declining N availability

Nitrogen availability affects multiple ecosystem processes and services. Researchers have begun to investigate the effects of declining N availability on ecosystem function and have found evidence of impacts on the global C cycle, herbivore nutrition, and water quality. For example, although terrestrial primary productivity has increased globally in response to eCO₂ (60) and longer growing seasons (61), helping to buffer anthropogenic CO₂ emissions, declining N availability likely constrains this response (51, 62, 63). In global change experiments, eCO₂ treatment alone tends to increase net primary productivity and C storage less than CO₂ enrichment combined with N addition (64), indicating a reduction in N availability under eCO₂ that limits primary productivity. Satellite observations of primary productivity have confirmed the dependence of CO₂ fertilization on N and also suggest that a recent weakening of the CO₂ fertilization effect is due in part to declining N availability (65). Without the widening gap between N supply and demand, the terrestrial C sink would likely be greater.

The reductions in foliar [N] that accompany declining N availability may reduce the growth and reproduction of herbivorous insects. Insect herbivore growth rates and abundance are strongly dependent on the availability of protein as a food source (66), and as protein and N concentrations are positively correlated in leaves, plant N concentrations are a good index of host plant quality for insect herbivores (67). Experiments show that insect herbivores may initially respond to reduced plant [N] by increasing consumption (68, 69), but declines in plant [N] ultimately reduce insect growth, survival, reproduction, and population size (70–72). At the community level, decreases in plant [N] are expected to change the relative abundance of insect species present (73) and reduce biomass transfer to higher trophic levels (74).

In a central US grassland ecosystem, a 36% decline in grasshopper abundance has been linked to a 42% decline in foliar [N] that has taken place over the past 30 years (75). In eCO₂ experiments, a 16% reduction in foliar [N] (with concomitant changes in other plant characteristics) resulted in a 22% decrease in insect herbivore abundance (69). Given the magnitude of foliar [N] decline seen in long-term datasets, declining foliar [N] may be contributing substantially to global declines

in terrestrial insect abundance that have averaged ~9% per decade since 1925 (76). Although reductions in insect abundance have been attributed to factors as varied as rising temperatures and agricultural practices, reduced N availability could exacerbate the effects of factors such as pesticides (77) and provide a unifying explanation of patterns observed across ecosystems.

Because N concentrations are tightly linked among plant organs, decreases in foliar [N] are likely accompanied by decreases in root, stem, and pollen [N] and would thus also affect insects that consume these other parts of the plant. For example, reductions in pollen N concentration (Fig. 2F) (22), which can reduce the ability of bees to resist pests and overwinter, could contribute to declines in pollinator abundance. Whereas declining N availability may have negative effects on insects, so too may N enrichment (78). This emphasizes the need to better understand the mechanisms linking N availability and insect performance and identify management and policy actions that avoid both excess and insufficient N.

As in insects, growth rates in vertebrate herbivores are often limited by feed protein supply (79). Although there are few long-term records of dietary quality for herbivores, regular collection of fecal samples from cattle grazing on rangelands across the US allows the reconstruction of dietary protein concentrations. Independent of any changes in precipitation, crude protein concentrations have been declining since measurements began in 1995 (80). Because of changes in genetics, cattle weights in the US have increased over the past 50 years despite the decline in dietary quality (81). However, for other large herbivores that do not receive protein supplementation or undergo strong genetic selection by humans, the decline in foliar [N] may be reducing body size and reproduction. For example, bison from regions with lower plant protein concentrations gain weight more slowly, and low protein concentrations are associated with lower reproduction rates (82) (Fig. 4).

Terrestrial N availability strongly influences the N loading of headwater streams and, ultimately, coastal receiving waters. In principle, decreasing streamwater inorganic N concentration influences the amount and biochemical composition of primary producers (83), initiating bottom-up effects that can propagate to higher trophic levels (84). Long-term records from many stream ecosystems lacking substantial anthropogenic N inputs have exhibited declining inorganic N concentrations in recent decades (28, 85, 86). Under these conditions, primary and secondary production are expected to decline, and recently reported declines in aquatic insect populations (87) are consistent with these expectations. In coastal systems, large reductions in N inputs have caused declines in

fish productivity (88, 89) and fish landings (90). Therefore, changes in inputs from terrestrial ecosystems experiencing declining N availability have the potential to affect watershed N budgets and coastal ecosystem processes.

However, most aquatic systems continue to receive N inputs from local agriculture, wastewater, and other anthropogenic sources. Declining terrestrial N availability in the parts of these watersheds that are not subject to heavy anthropogenic N loading would initially be expected to improve downstream aquatic conditions overall. This may include increases in some stream taxa (76) and in coastal ecosystems, greater water clarity, increased abundance of submerged macrophytes, and increases in oxygen concentrations (91). Given the continued high level of anthropogenic N inputs to coastal systems, any effects of declining terrestrial N availability will most likely be difficult to detect. Long-term watershed monitoring will be required to correctly associate water quality improvements with improvements in N management and response to external factors such as rising CO₂.

Responses to declining N availability

Since the mid-20th century, increasingly high-profile research and discussion has focused on the negative effects of excess N on terrestrial and aquatic ecosystems. As a result, reduction of anthropogenic N inputs to the Earth system is widely recognized as a high priority. The emerging evidence of a large-scale decline in N availability in unmanaged ecosystems does not contradict previous work that has documented the effects of excess N. Nitrogen is certainly being applied in excess to many agricultural ecosystems, high levels of atmospheric deposition can occur, and the consequences of excess N addition for coastal receiving waters are substantial. Instead, the evidence presented here is a strong indication that the world is now experiencing a dual trajectory in N availability (12), in which many areas are exposed to excessive levels of reactive N while others are experiencing declining N availability.

Fundamentally, declining N availability adds to the already overwhelming case for reducing anthropogenic CO₂ emissions. Emissions reductions are needed to stabilize the climate system and moderate ecosystem changes that are a direct consequence of eCO₂. In tandem with much-needed curbs on emissions, research, management, and policy attention to declining N availability should also become a priority (Fig. 5).

Monitoring and assessment

Despite strong indications of declining N availability in many places and contexts, spatial and temporal patterns are not yet well enough understood to efficiently direct global management efforts. A comprehensive assessment

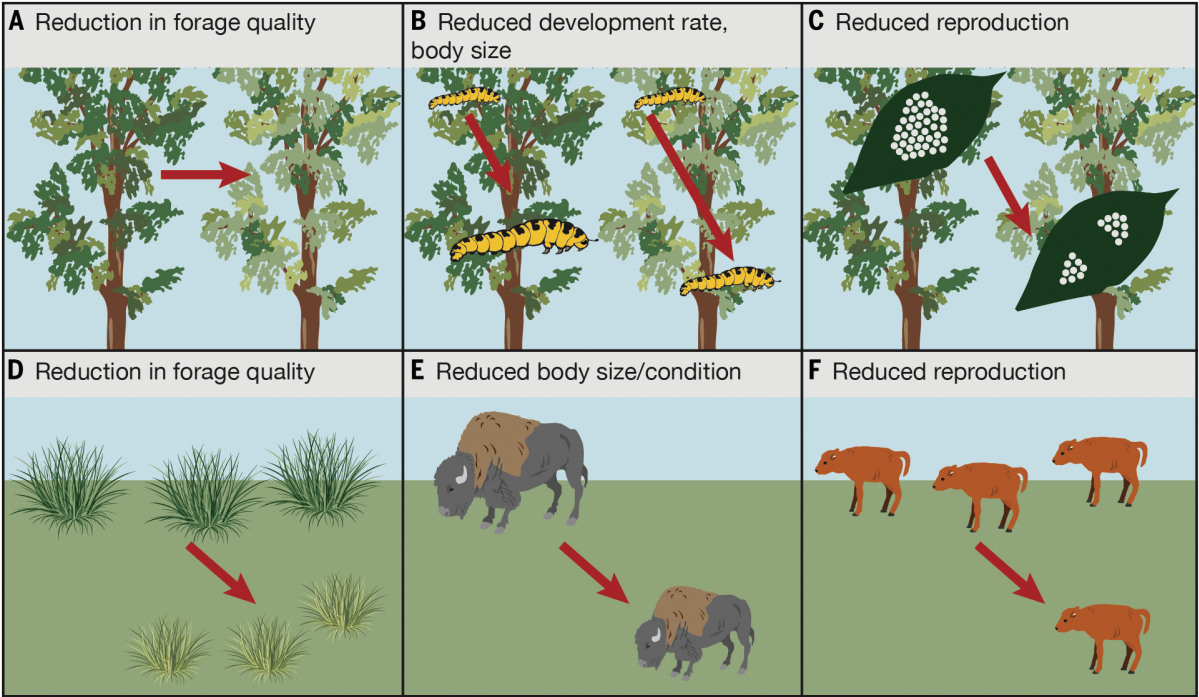


Fig. 4. Impacts of declines in foliar N concentrations on herbivore performance. Reduction in forage quality (**A** and **D**) may result in reduced herbivore body size and/or development rate (**B** and **E**) and reproduction (**C** and **F**) because herbivore growth rates and populations are often limited by protein availability.

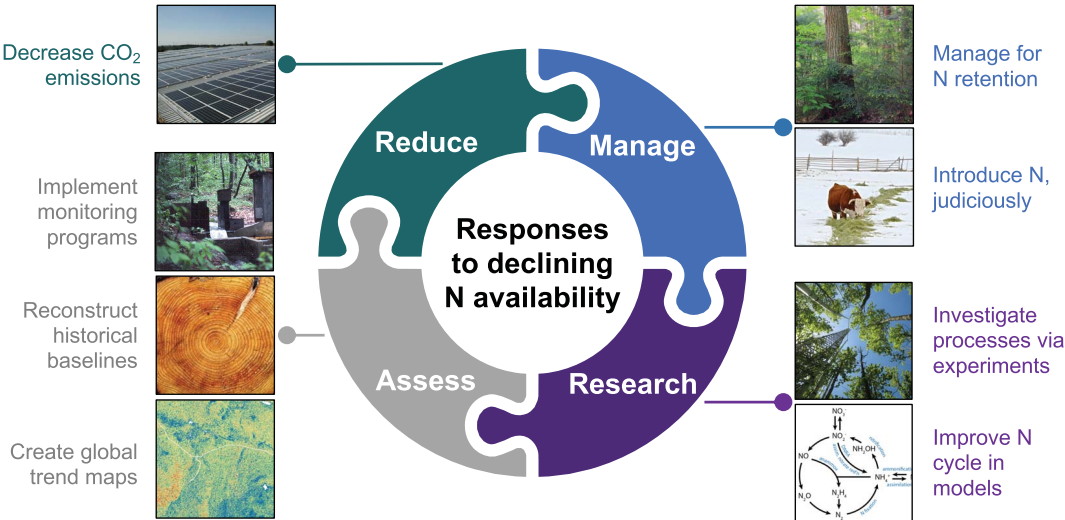


Fig. 5. Addressing the root cause of declining N implies reducing CO₂ emissions, whereas ecosystem assessments and continued research are needed to inform management actions. Variation in N availability trends over space and time can be elucidated through field monitoring campaigns, reconstruction of historical records, and creation of maps via hyperspectral remote sensing techniques. Continued experimentation is required to better understand

the processes driving, and resulting from, reductions in N availability. Incorporating this knowledge in ESMs will clarify how declining N may affect the ability of ecosystems to buffer CO₂ emissions. [Image credits (counterclockwise from top left): h080/CC BY-SA 2.0; US Forest Service, Northern Research Station; B. Kasman; S. Ollinger; M. Kirk/CC BY-SA 4.0; US Department of Energy, Oak Ridge National Laboratory/CC BY 2.0; L. Lamsa/CC BY 2.0; and N. Tonelli/CC BY 2.0]

program would involve monitoring of N availability metrics such as N concentrations in plant tissues, net N mineralization in soils, N concentrations in aquatic ecosystems, and herbivore dietary quality. Systematic collec-

tion of satellite hyperspectral remote sensing data will soon help facilitate assessment of foliar [N] across broader spatial scales than those possible with current airborne instrumentation or field sampling. Continental-

scale monitoring of N deposition has provided important information about N supply, but complex spatial patterns of rising, falling, and stabilizing trends (2, 3) justify expanded instrumentation.

Collectively, these data could be assembled into an annual state-of-the-N-cycle report that would represent a comprehensive resource for scientists, managers, and policy-makers. Data products could include global maps of changing N availability. For example, net primary productivity trends and levels of (or trends in) atmospheric N deposition can be used to estimate N demand and supply and to generate maps of N availability (Fig. 6). Although this captures only a subset of N availability drivers, the resulting visualization is consistent with the evidence of declining N availability in North America and Europe and of rising N availability in China. It also suggests that large areas outside these relatively well-studied regions may be experiencing decreasing N availability (12). Additional N availability datasets would allow such maps to be calibrated and refined.

In addition to contemporaneous monitoring, reconstructions of N availability from herbaria, tree rings, and sediments are necessary to understand historical trajectories and set baselines that can be used to guide management efforts. Combining such datasets, similar to how multiple proxies have been intercalibrated to reveal past climates and atmospheric chemistry, would provide additional long-term context for interpreting recent trends. To demonstrate the potential of long-term, multi-proxy N availability reconstructions, we adapted the standard paleoecological approach of intercalibrating different records [$\delta^{15}\text{N}$ of lake sediments, tree rings, and foliar samples (12, 13, 15)] to produce a ~250-year record of $\delta^{15}\text{N}$ spanning continental-to-global scales (Fig. 6). The combined record shows that N availability was fairly constant until a

decline began in the early 20th century. Expanding the geographic and temporal coverage of the data used to construct similar diagrams will provide new perspectives on recent trends and help to explain regionally specific causal mechanisms.

Research challenges

Beyond monitoring and reconstructions, research into the ecosystem processes involved in declining N availability is needed (3, 34). In ecosystems that have been subject to high levels of anthropogenic N inputs, such as central and western Europe, declining N availability may present welcome opportunities for restoration. However, hysteresis, differential responses of different ecosystem components, and concurrent changes in other environmental conditions complicate predictions of the speed and direction of ecosystem trajectories under declining N inputs (3, 34, 88).

Declining N availability is also likely to affect plant N:P stoichiometry, which in turn influences plant, herbivore, and microbial community composition (92). At the same time, alterations in the availability of other nutrients mean that changes in ecosystem stoichiometry are not entirely predictable. For example, despite declining N deposition, foliar [P] has decreased more rapidly than foliar [N] in European forests, leading to an increase in foliar N:P (23, 24). Although we focus on declines in N availability here, research into the effects of declining N availability will need to consider changes in the availability of other nutrients as well.

Field eCO_2 experiments have provided valuable insights into how declining N availability may arise and progress, but relatively few are operating today, and few have examined multiple global changes (e.g., eCO_2 , warming, precipitation change, biodiversity change) simultaneously. Restoring and expanding such studies would improve our understanding of the processes that are the basis of Earth system models (ESMs). Although it is well recognized that N availability is a fundamental constraint on the ability of the biosphere to absorb CO_2 (62), only around half of current ESMs include interactions between the C and N cycles. In general, when N cycling is included in ESMs, the projected ability of terrestrial ecosystems to absorb CO_2 emissions tends to decrease because of constraints on CO_2 use due to N limitations (93). These models vary in how various components of the N cycle are represented, and they have yet to be parameterized with global N availability datasets.

Further research into the consequences of declining N availability is also needed. The possible role of declining foliar [N] in ongoing declines in insect populations (75, 94) merits particular attention. Declining ecosystem N availability may have relatively direct implications

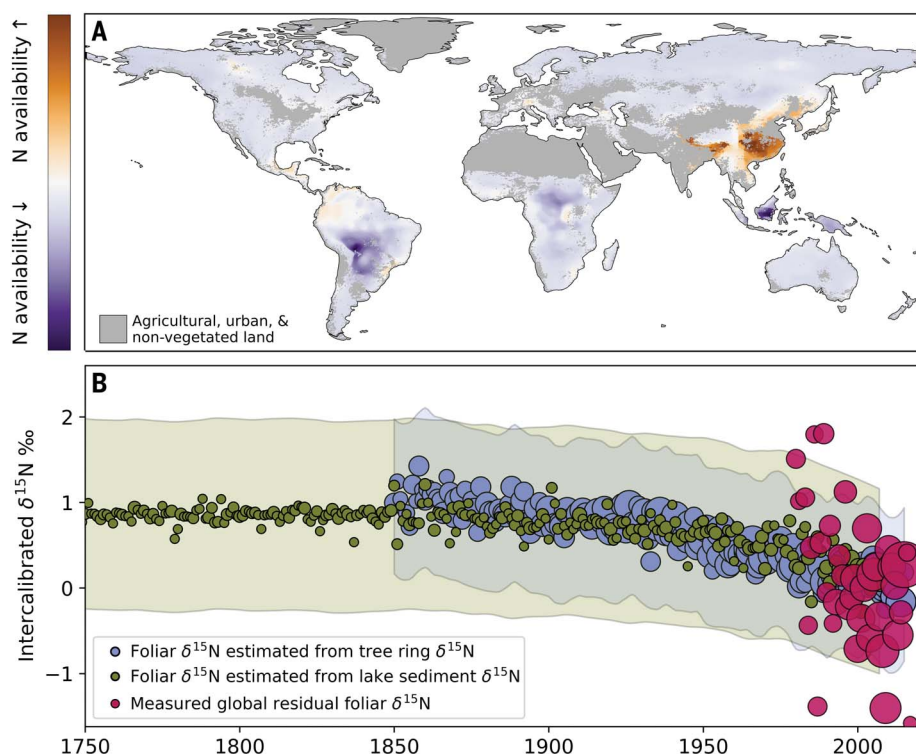


Fig. 6. Mapping the drivers of N supply and demand, and intercalibrating historical N availability records, will provide novel perspectives on trends in global N availability. (A) Comparing trends in net primary productivity (NPP) (approximating N demand) and levels of (or trends in) atmospheric N deposition (approximating N supply) suggests increasing N availability in high-deposition regions such as China and declining N availability in many other regions. This visualization was produced by subtracting global maps of N deposition and N deposition trends (2) from a global map of trends in NPP (100) after normalizing all quantities by dividing by their standard deviation and centering the N deposition map at $10 \text{ kg ha}^{-1} \text{ year}^{-1}$. Future work that incorporates information about other drivers of N supply and demand will provide a more comprehensive picture of changes in N availability. (B) Intercalibrating records from leaves, tree rings, and lake sediments (Fig. 2, A to C) suggests that the declines in N availability began in the early industrial era. Data on tree ring (13) and lake sediment (15) $\delta^{15}\text{N}$ from North America were intercalibrated with a global foliar $\delta^{15}\text{N}$ time series (12) using a Bayesian model that included an ARMA (autoregressive moving average) error structure to account for temporal autocorrelation. Shaded areas indicate 80% prediction intervals; marker size is proportional to the square root of the number of measurements included in each annual mean. One foliar $\delta^{15}\text{N}$ point (at 1982, 3.6) is beyond the scale of the plot.

for human health and well-being that should be investigated. For example, lower protein concentrations in grazing livestock diets may disproportionately affect those who do not have the resources to acquire supplemental feed for their animals. Low-N plants can also increase the abundance of certain locust species, so continued research into feasible and locally appropriate land management practices that promote soil fertility will be valuable (95).

Depending on the context, responses to declining N availability may require meeting increased N demand, compensating for N removed in harvested products, reversing declines in plant [N], and promoting C sequestration. Nutrient additions are commonly used to achieve this kind of ecosystem management goal; for example, salmon carcasses and fertilizers have been added to streams to support salmon populations (96), and N fertilization is routinely used on improved pastures to increase biomass and enhance forage quality for livestock. Such actions could be implemented at larger scales, but this would be contentious given that fertilizer use has historically led to negative impacts such as eutrophication of aquatic systems.

Moreover, the presence of multiple concurrent environmental changes suggests that further research is needed to design N-addition interventions that achieve the intended effects. For example, decreases in foliar [N] under eCO₂ are partly a consequence of fundamental changes to plant metabolic function in a high-CO₂ environment, and foliar [N] tends to remain depressed in experiments that combine moderate N additions and eCO₂ (97). Given that concentrations of P, S, Ca, Mg, and K have decreased in European forests (23, 24), inputs of N alone may not be sufficient to remove nutrient limitations to primary productivity and could induce further nutritional imbalances (24). Overall, any N-addition programs will require careful, evidence-based design, with costs, logistical challenges, and implications for water quality (96) and greenhouse gas emissions (98) taken into account.

Our evolving understanding of the Earth system has led to new concerns about N insufficiency after years of attention to surplus N in the environment. An integrated suite of responses will be needed to simultaneously manage both of these problems. Given the potential implications of declining N availability for food webs, carbon sequestration, and other ecosystem functions and services, it is important that research, management, and policy actions be taken before the consequences of declining N availability become more severe. It can be difficult to create a shared understanding of the N cycle and the many effects of N on ecosystem health and human well-being. The combination of excess N and declining N availability, in which outcomes

vary widely across landscapes, adds to this challenge. Developing dialogues among diverse stakeholders—scientists, ecosystem managers, and others—will be necessary for alleviating and adapting to declining N availability in an N-rich world.

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Evidence, causes, and consequences of declining nitrogen availability in terrestrial ecosystems

Rachel E. Mason Joseph M. Craine Nina K. Lany Mathieu Jonard Scott V. Ollinger Peter M. Groffman Robinson W. Fulweiler Jay Angerer Quentin D. Read Peter B. Reich Pamela H. Templer Andrew J. Elmore

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Declining nitrogen in natural ecosystems

Nitrogen (N) availability is key to the functioning of ecosystems and the cycling of nutrients and energy through the biosphere. However, there is growing evidence that N availability is decreasing in many terrestrial ecosystems. The consequences of declining N availability will be widespread. For example, a decreased concentration of N in leaves reduces the availability of N to insects, contributing to population declines that may then cascade through higher trophic levels. Mason *et al.* reviewed the extent of this phenomenon, and the anthropogenic factors that might be driving it (including climate change and increasing atmospheric carbon dioxide), and discuss how its damaging effects might be mitigated. —AMS

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