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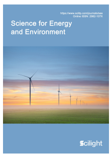

Review

Sustainable Nitrogen Cycle: Mechanisms, Anthropogenic Perturbations, and Pathways to Global Resilience

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Abstract: Nitrogen (N) is an essential constituent of all living organisms and a primary nutrient limiting life on Earth, mediating critical biogeochemical processes across the atmosphere, hydrosphere, biosphere, and pedosphere. The natural nitrogen cycle is a finely tuned network of microbial, physical, and chemical transformations that regulate the availability of reactive nitrogen (Nr) while maintaining environmental equilibrium. However, anthropogenic activities—particularly industrial nitrogen fixation via the Haber–Bosch process, intensive agriculture, and fossil fuel combustion—have drastically perturbed this cycle, leading to a tripling of global Nr inputs since the pre-industrial era. This perturbation has triggered cascading environmental crises, including eutrophication of aquatic ecosystems, atmospheric pollution, greenhouse gas emissions, and biodiversity loss, while simultaneously threatening food security and human health. Achieving a sustainable nitrogen cycle is therefore central to addressing global sustainability challenges, including the United Nations Sustainable Development Goals (SDGs). In this Review, we synthesize the latest advances in our understanding of the natural nitrogen cycle and its anthropogenic perturbations, highlight the complex interactions between nitrogen cycling and climate change, food-energy-water (FEW) nexus, and ecosystem resilience, and outline actionable pathways to restore and sustain nitrogen balance at local, regional, and global scales. We emphasize the need for integrated, transdisciplinary approaches that combine microbial ecology, biogeochemistry, agronomy, policy, and technology to mitigate Nr losses, enhance nitrogen use efficiency (NUE), and reconcile food production with environmental protection. Finally, we identify key knowledge gaps and future research priorities that will be critical for advancing toward a sustainable nitrogen cycle and safeguarding planetary health.

Keywords: sustainable nitrogen cycle; reactive nitrogen; nitrogen use efficiency; food-energy-water nexus; climate-nitrogen feedbacks

1. Introduction

Nitrogen is a fundamental building block of life, underpinning the structure and function of all organisms through its role in proteins, nucleic acids, and chlorophyll. The global nitrogen cycle is a complex biogeochemical network that governs the transformation of nitrogen between inert atmospheric dinitrogen (N_2, accounting for 78% of Earth's atmosphere) and bioavailable reactive nitrogen (Nr) forms, including ammonium (NH_4^+), nitrate

(NO$_3^-$), nitrite (NO$_2^-$), and gaseous nitrogen oxides (NO$_x$) and nitrous oxide (N$_2$O) [1]. For millennia, this cycle operated in relative equilibrium, driven by microbial processes such as nitrogen fixation, nitrification, denitrification, and ammonification, which regulated Nr availability and prevented excessive accumulation in the environment [2].

The 20th century marked a paradigm shift in the global nitrogen cycle with the invention of the Haber–Bosch process, which enabled the industrial fixation of atmospheric N$_2$ into ammonia (NH$_3$)—the basis of synthetic nitrogen fertilizers [3]. This technological breakthrough, combined with the intensification of agriculture and the burning of fossil fuels, has dramatically increased global Nr inputs from ~15 Tg N yr^{-1} in the pre-industrial era to ~150 Tg N yr^{-1} today, with projections of further increases under business-as-usual scenarios [4,5]. While this increase has been critical for sustaining global food production (supporting ~50% of the global population), it has also disrupted the natural balance of the nitrogen cycle, leading to widespread environmental degradation and human health risks [6].

The concept of a "sustainable nitrogen cycle" emerged in response to these challenges, aiming to reconcile the dual needs of ensuring sufficient Nr for food security and limiting Nr losses to the environment to protect ecosystems and climate [7]. Achieving this balance requires a comprehensive understanding of the natural nitrogen cycle, the mechanisms and impacts of anthropogenic perturbations, and the development of integrated strategies to enhance NUE, mitigate Nr pollution, and restore ecosystem function. In this Review, we provide an up-to-date synthesis of the current state of knowledge on the sustainable nitrogen cycle, identify key challenges and knowledge gaps, and outline pathways to advance global nitrogen sustainability [8].

2. The Natural Nitrogen Cycle: Microbial Mechanisms and Ecosystem Interactions

The natural nitrogen cycle is driven by a diverse array of microbial communities that mediate distinct nitrogen transformation processes, forming a complex network rather than a linear sequence of events [9]. These processes are tightly linked to other biogeochemical cycles (e.g., carbon, phosphorus, and sulfur) and are regulated by environmental factors such as temperature, pH, moisture, and substrate availability. Below, we summarize the key microbial processes of the natural nitrogen cycle and their ecological significance. The core innovations and key scientific questions have been shown in Figure 1.

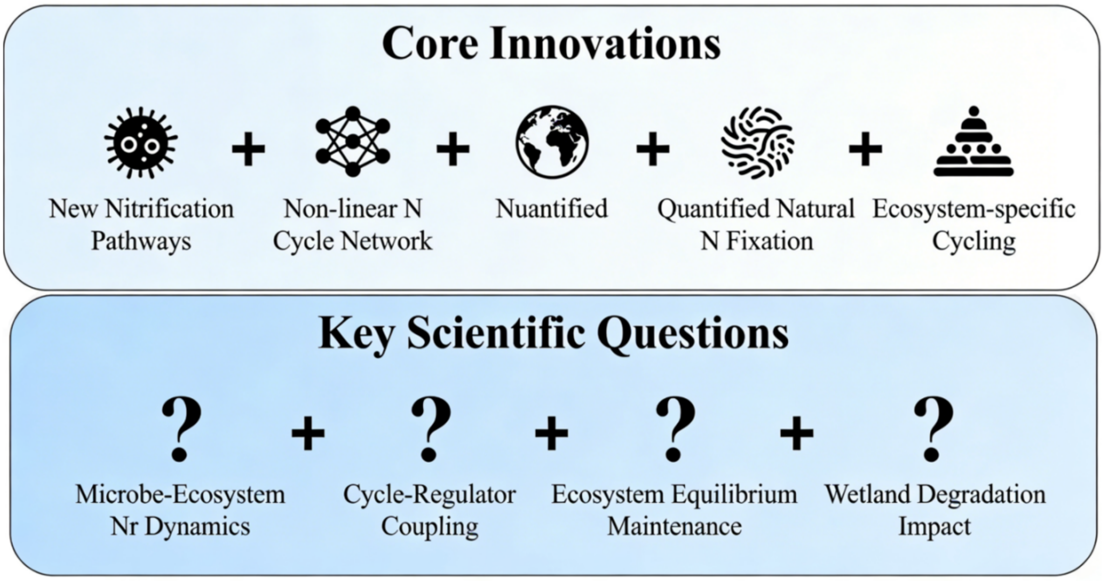

Figure 1. The core innovations and key scientific questions.

2.1. Key Microbial Nitrogen Transformation Processes

Nitrogen fixation is the conversion of inert atmospheric N$_2$ to bioavailable NH$_4^+$, carried out by diazotrophic microorganisms (e.g., cyanobacteria, rhizobia, and archaea) that possess the nitrogenase enzyme complex. This process is the primary natural source of Nr, contributing ~50–70 Tg N yr^{-1} globally, with contributions from terrestrial (e.g., leguminous plants, free-living soil diazotrophs) and marine (e.g., cyanobacterial blooms) ecosystems. Nitrogen fixation is energetically costly, requiring large amounts of

ATP and reducing power, and is therefore sensitive to environmental conditions such as oxygen availability (which inhibits nitrogenase activity) and nutrient limitation (e.g., phosphorus and iron).

Nitrification is the aerobic oxidation of NH_4^+ to NO_3^-, a two-step process mediated by distinct microbial groups. Traditionally, this process was thought to be carried out by ammonia-oxidizing bacteria (AOB) and archaea (AOA), which convert NH_4^+ to NO_2^-, followed by nitrite-oxidizing bacteria (NOB), which convert NO_2^- to NO_3^-. However, recent discoveries have identified complete ammonia-oxidizing archaea and bacteria (comammox), which can carry out both steps of nitrification independently, reshaping our understanding of nitrification dynamics in diverse ecosystems [10]. Additionally, direct ammonia oxidation (dirammox) has been discovered as an alternative nitrification pathway, further expanding the diversity of microbial mechanisms involved in Nr production [11]. Nitrification plays a critical role in regulating Nr availability in soils and aquatic systems, as NO_3^- is highly mobile and can be readily taken up by plants or lost via leaching and denitrification.

Denitrification is the anaerobic reduction of NO_3^- or NO_2^- to gaseous nitrogen forms (NO, N_2O, or N_2), carried out by a diverse group of heterotrophic bacteria, archaea, and fungi [12]. This process is the primary pathway for Nr removal from the environment, returning Nr to the atmosphere as inert N_2 and thus closing the nitrogen cycle. However, incomplete denitrification can lead to the production of N_2O—a powerful greenhouse gas with a global warming potential 298 times that of CO_2 over a 100-year period—and NO, which contributes to air pollution and ozone depletion. Denitrification rates are regulated by oxygen availability, organic carbon availability (as an energy source), and the ratio of NO_3^- to other electron acceptors.

Ammonification (or mineralization) is the decomposition of organic nitrogen (e.g., proteins, nucleic acids) to NH_4^+, carried out by heterotrophic microorganisms during the breakdown of organic matter. This process releases NH_4^+ that can be taken up by plants or oxidized via nitrification, linking the organic and inorganic components of the nitrogen cycle. Ammonification rates are influenced by temperature, moisture, and the quality of organic matter (e.g., carbon-to-nitrogen ratio, C:N).

Other nitrogen transformation processes, including anaerobic ammonium oxidation (anammox) [13], dissimilatory nitrate reduction to ammonium (DNRA), and nitrifier denitrification, also play important roles in regulating Nr cycling in specific environments (e.g., anoxic soils, wetlands, and marine sediments) [14,15]. These processes contribute to Nr retention or loss and are increasingly recognized as critical components of the microbial nitrogen-cycling network.

2.2. Ecosystem-Specific nitrogen Cycling

The structure and function of the nitrogen cycle vary across different ecosystems, reflecting differences in microbial community composition, environmental conditions, and ecological interactions. Terrestrial ecosystems (e.g., forests, grasslands, and agricultural soils) are major sites of nitrogen fixation, nitrification, and denitrification, with soil properties (e.g., pH, texture, organic matter content) and land use strongly influencing Nr dynamics. For example, grasslands—covering more than 40% of Earth's land surface—play a crucial role in nitrogen cycling, with precipitation regimes significantly affecting Nr input, harvest, and surplus at the global scale. Forest ecosystems are typically N-limited, with tight coupling between nitrogen and carbon cycling, as Nr availability regulates primary productivity and carbon sequestration.

Aquatic ecosystems (e.g., lakes, rivers, and oceans) are critical for Nr transport and transformation, with rivers and streams acting as conduits for Nr from terrestrial to marine environments. Marine ecosystems are dominated by microbial nitrogen cycling, with cyanobacterial nitrogen fixation and anammox being major processes regulating Nr availability in the open ocean. Coastal ecosystems (e.g., estuaries, mangroves, and salt marshes) are hotspots of denitrification and anammox, removing significant amounts of Nr from the environment and mitigating eutrophication in coastal waters [16].

Wetlands are particularly important for nitrogen cycling, as their anoxic conditions promote denitrification and DNRA, leading to high Nr retention. Wetland loss and degradation—due to agricultural expansion and urbanization—have therefore reduced Nr removal capacity, contributing to increased Nr losses to aquatic ecosystems and atmospheric N_2O emissions.

3. Anthropogenic Perturbations of the Nitrogen Cycle: Mechanisms and Impacts

Anthropogenic activities have emerged as the dominant driver of the global nitrogen cycle, perturbing Nr inputs, transformations, and losses across all ecosystems [17]. The primary anthropogenic sources of Nr include industrial nitrogen fixation (Haber–Bosch process), agricultural activities (synthetic fertilizer application, livestock production, and crop residue management), fossil fuel combustion, and wastewater discharge. These activities have disrupted the natural balance of the nitrogen cycle, leading to a range of environmental, ecological, and human health impacts. The anthropogenic nitrogen cycle perturbation has been shown in Figure 2.

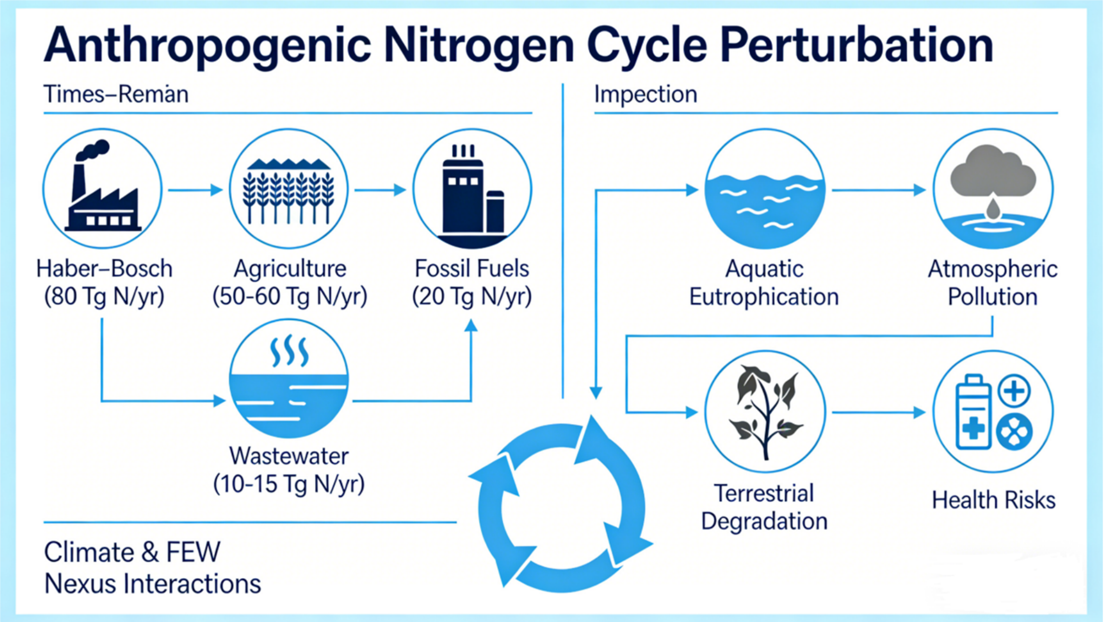

Figure 2. The anthropogenic nitrogen cycle perturbation.

3.1. Major Anthropogenic Nr Sources

Industrial nitrogen fixation via the Haber–Bosch process is the largest anthropogenic source of Nr, contributing ~80 Tg N yr^{-1} globally [18]. This process is used to produce synthetic nitrogen fertilizers, which have been critical for increasing agricultural productivity and addressing food security challenges. However, the Haber–Bosch process is energy-intensive, accounting for ~1–2% of global energy consumption and ~1.5% of global CO_2 emissions, contributing to climate change.

Agricultural activities are the second-largest source of anthropogenic Nr, with synthetic fertilizer application, livestock production, and crop residue management contributing ~50–60 Tg N yr^{-1} [19]. Livestock production is a major contributor to Nr emissions, responsible for ~one-third of total anthropogenic Nr emissions, primarily through NH_3 volatilization from manure and urine, and N_2O emissions from denitrification in animal waste storage and agricultural soils. Crop residue management—particularly the burning of residues—also contributes to NO_x emissions, further increasing Nr inputs to the atmosphere.

Fossil fuel combustion (e.g., coal, oil, and gas) contributes ~20 Tg N yr^{-1} to global Nr inputs, primarily through the emission of NO_x during combustion [20]. These emissions are a major source of air pollution, contributing to the formation of smog, acid rain, and tropospheric ozone, and also contribute to N_2O emissions, a potent greenhouse gas.

Wastewater discharge (domestic, industrial, and agricultural) contributes ~10–15 Tg N yr^{-1} to aquatic ecosystems, primarily in the form of NH_4^+ and NO_3^- [21]. Inadequate wastewater treatment leads to increased Nr loads in rivers, lakes, and coastal waters, contributing to eutrophication and harmful algal blooms.

3.2. Environmental and Ecological Impacts of Anthropogenic Nr Perturbations

The excessive input and mismanagement of anthropogenic Nr have triggered cascading environmental and ecological impacts across terrestrial, aquatic, and atmospheric ecosystems, with far-reaching consequences for planetary health [22]. These impacts are interconnected, often amplifying one another through complex biogeochemical feedbacks, and pose significant challenges to global sustainability.

3.2.1. Aquatic Ecosystem Eutrophication and Degradation

Eutrophication—caused by excessive Nr (and phosphorus) inputs—is the most widespread impact of anthropogenic nitrogen perturbation on aquatic ecosystems [23]. Nr transported from terrestrial ecosystems via surface runoff, groundwater leaching, and wastewater discharge accumulates in lakes, rivers, estuaries, and coastal oceans, stimulating the overgrowth of phytoplankton (harmful algal blooms, HABs) and aquatic plants. This overgrowth depletes dissolved oxygen in the water column (hypoxia or anoxia) through microbial decomposition of organic matter, forming “dead zones” where most aquatic organisms cannot survive [24]. Currently, more than 400 dead zones have been identified globally, covering over 245,000 km^2, with the largest in the Baltic Sea, Gulf of Mexico, and East China Sea [24].

HABs, fueled by Nr enrichment, produce toxins (e.g., microcystins, saxitoxins) that are harmful to aquatic organisms, wildlife, and humans—posing risks to drinking water safety and recreational use of water bodies. Additionally, eutrophication alters aquatic food webs, reduces biodiversity, and impairs ecosystem services such as fisheries production, water purification, and carbon sequestration [25]. Coastal ecosystems are particularly vulnerable, as Nr inputs from rivers and wastewater discharge often coincide with other stressors (e.g., ocean acidification, warming), exacerbating degradation of coral reefs, seagrass beds, and mangroves.

3.2.2. Atmospheric Pollution and Climate Change

Anthropogenic Nr emissions (NO_x, NH_3, N_2O) contribute significantly to atmospheric pollution and climate change, with direct and indirect impacts on air quality and planetary energy balance [20]. NO_x emissions from fossil fuel combustion and agricultural activities react with volatile organic compounds (VOCs) in the presence of sunlight to form tropospheric ozone (O_3), a harmful air pollutant that causes respiratory diseases (e.g., asthma, chronic obstructive pulmonary disease) in humans and damages crops and vegetation [26]. Tropospheric ozone also acts as a greenhouse gas, contributing to global warming with a global warming potential (GWP) ~12 times that of CO_2 over a 100-year period.

NH_3 volatilization from agricultural soils and livestock production reacts with sulfur oxides (SO_x) and NO_x in the atmosphere to form ammonium nitrate (NH_4NO_3) and ammonium sulfate ($(NH_4)_2SO_4$) aerosols—major components of fine particulate matter ($PM_{2.5}$) [27]. $PM_{2.5}$ can penetrate deep into the respiratory and cardiovascular systems, increasing mortality and morbidity from heart disease, stroke, and lung cancer; globally, Nr-related $PM_{2.5}$ is estimated to cause over 3 million premature deaths annually [28]. These aerosols also affect the Earth’s radiation balance, contributing to regional cooling (offsetting some warming from greenhouse gases) but also reducing visibility and altering precipitation patterns.

N_2O is the third most important greenhouse gas (after CO_2 and methane, CH_4), with a GWP 298 times that of CO_2 over a 100-year period and an atmospheric lifetime of ~120 years. Anthropogenic N_2O emissions—primarily from agricultural soils (denitrification and nitrification), livestock production, and industrial processes—account for ~60% of global N_2O emissions [29]. These emissions contribute to global warming and stratospheric ozone depletion, as N_2O is a major source of reactive nitrogen in the stratosphere, where it catalyzes the destruction of ozone molecules.

3.2.3. Terrestrial Ecosystem Degradation and Biodiversity Loss

Anthropogenic Nr inputs have profound impacts on terrestrial ecosystems, altering plant community composition, microbial diversity, and biogeochemical cycling [30]. Many terrestrial ecosystems (e.g., temperate forests, grasslands, and tundra) are naturally N-limited, and excessive Nr deposition can shift these ecosystems to N-saturation—a state where Nr inputs exceed biological demand, leading to increased Nr losses via leaching, denitrification, and runoff [31].

N-saturation reduces soil pH (acidification) by increasing NO_3^- leaching and the release of protons (H^+), which mobilize toxic metals (e.g., aluminum, Al^{3+}) and reduce the availability of essential nutrients (e.g., calcium, magnesium, potassium) [31]. This acidification damages plant roots, impairs microbial activity, and reduces plant productivity, particularly in sensitive ecosystems such as coniferous forests and heathlands. Excessive Nr deposition also favors the growth of fast-growing, nitrophilic plant species (e.g., grasses, invasive weeds) over slow-growing, N-sensitive species (e.g., lichens, mosses, and some tree species), leading to shifts in plant community composition and reduced biodiversity [30].

In addition, Nr-induced changes in terrestrial ecosystems affect aboveground and belowground food webs. For example, reduced plant diversity alters the availability of food and habitat for insects, birds, and mammals, leading to declines in herbivore and predator populations. Belowground, excessive Nr inputs can alter microbial community composition—favoring nitrifying and denitrifying microorganisms over other functional groups—disrupting microbial interactions and reducing microbial diversity, which in turn impairs soil health and ecosystem resilience [32].

3.2.4. Impacts on Food Security and Human Health

While anthropogenic Nr inputs have been critical for increasing agricultural productivity and supporting global food security [33], excessive and inefficient use of Nr threatens both food security and human health [34]. In agricultural systems, low NUE (typically <50% globally) leads to significant Nr losses to the environment, reducing the availability of Nr for crop uptake and increasing production costs for farmers [35]. Additionally, Nr-induced environmental degradation (e.g., eutrophication, soil acidification, and ozone pollution) impairs agricultural productivity: tropospheric ozone alone reduces global crop yields by 5–15% for major staples (e.g., wheat, rice, maize), threatening food security in vulnerable regions [36].

Human health risks associated with anthropogenic Nr perturbations are multifaceted and widespread. As noted earlier, Nr-related air pollutants ($PM_{2.5}$, tropospheric ozone) cause respiratory and cardiovascular diseases, leading to premature mortality [36]. Contamination of drinking water with NO_3^- (from agricultural runoff and wastewater discharge) poses risks of methemoglobinemia (blue baby syndrome) in infants and is linked to increased risks of certain cancers (e.g., gastric, colorectal) in adults. Additionally, Nr enrichment in food chains can lead to the accumulation of toxins (e.g., from HABs) in seafood, posing risks to human health through dietary exposure [21]. Finally, climate change driven by N_2O emissions exacerbates existing health risks (e.g., heat-related illnesses, the spread of vector-borne diseases), creating indirect but significant threats to global public health [37].

3.3. Interactions between Nitrogen Perturbations, Climate Change, and the Food-Energy-Water (FEW) Nexus

Anthropogenic perturbations of the nitrogen cycle are tightly intertwined with climate change and the FEW nexus, forming complex, bidirectional feedback loops that amplify global sustainability challenges [6]. Climate change affects the nitrogen cycle by altering environmental conditions (temperature, precipitation, CO_2 concentrations) that regulate microbial nitrogen transformations and Nr transport [1]. For example, rising temperatures increase nitrification and denitrification rates in soils and aquatic ecosystems, leading to increased N_2O emissions and Nr losses. Changes in precipitation patterns (e.g., more frequent extreme rainfall events) enhance Nr runoff from terrestrial to aquatic ecosystems, exacerbating eutrophication, while droughts reduce Nr leaching but may increase NH_3 volatilization and NO_x emissions from agricultural soils.

Conversely, nitrogen perturbations contribute to climate change through N_2O emissions and indirect effects (e.g., altered carbon sequestration) [38]. Excessive Nr inputs can enhance carbon sequestration in N-limited terrestrial ecosystems by increasing plant productivity, but this effect is often transient and reversed once ecosystems become N-saturated [39]. In aquatic ecosystems, eutrophication leads to increased carbon burial in sediments but also enhances microbial decomposition of organic matter, releasing CO_2 and CH_4 to the atmosphere—offsetting any carbon sequestration benefits [30].

The FEW nexus—interactions between food, energy, and water systems—is deeply connected to nitrogen cycling [40]. Food production (agriculture) is the largest consumer of Nr and freshwater, and requires significant energy inputs (e.g., for Haber–Bosch fertilizer production, irrigation, and machinery) [3]. Energy production (fossil fuel combustion) contributes to Nr emissions (NO_x) and consumes water, while water resources are critical for Nr transport and transformation, and water quality is degraded by Nr pollution [16]. Inefficiencies in one system (e.g., low NUE in agriculture) propagate to other systems: excessive Nr use in agriculture degrades water quality, increasing the energy required for water treatment; fossil fuel combustion releases NO_x, which degrades air quality and reduces crop yields; and water scarcity limits agricultural productivity, driving increased Nr use to maintain yields [41]. Achieving a sustainable nitrogen cycle therefore requires integrated management of the FEW nexus, recognizing these interdependencies and optimizing trade-offs between food security, energy production, and water protection [42].

4. Pathways to a Sustainable Nitrogen Cycle: Integrated Strategies for Global Resilience

Restoring and sustaining the global nitrogen cycle requires transdisciplinary, integrated strategies that address the root causes of anthropogenic perturbations, mitigate Nr losses, enhance NUE, and reconcile food production with environmental protection [6]. These strategies must be tailored to local, regional, and global scales, taking into account differences in ecosystem characteristics, socioeconomic conditions, and policy frameworks. Below, we outline key actionable pathways to advance nitrogen sustainability, organized around four core pillars: agricultural optimization, technological innovation, policy and governance, and transdisciplinary research and capacity building. The agricultural optimization, technological innovation and policy governance have been shown in Figure 3.

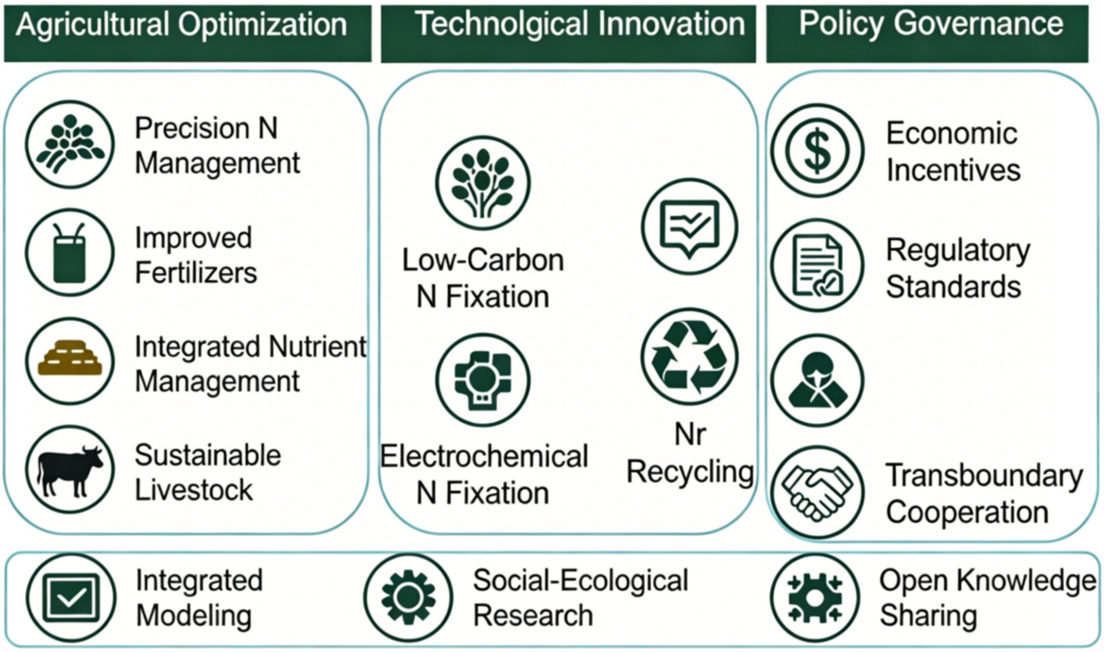

Figure 3. The agricultural optimization, technological innovation and policy governance.

4.1. Agricultural Optimization: Enhancing NUE and Reducing Nr Losses

Agriculture is the largest source of anthropogenic Nr emissions and losses, making it a critical focus for nitrogen sustainability efforts [43]. Optimizing agricultural practices to enhance NUE—defined as the proportion of applied Nr taken up by crops—is a cost-effective strategy to reduce Nr losses while maintaining or increasing crop yields [44]. Key practices include precision nitrogen management, improved fertilizer formulations, integrated nutrient management, and sustainable livestock production.

Precision nitrogen management leverages digital technologies (e.g., remote sensing, soil sensors, drones, and machine learning) to tailor Nr application to crop needs, matching the timing, rate, and placement of fertilizers to spatial and temporal variations in soil Nr availability and crop demand. This approach reduces over-fertilization—a major cause of Nr losses—by ensuring that crops receive only the Nr required for optimal growth. For example, variable rate fertilization (VRF) systems use soil and crop data to adjust fertilizer rates across fields, reducing Nr inputs by 10–30% while maintaining or increasing yields, and decreasing NO_3^- leaching and N_2O emissions by 15–40% in field studies [45].

Improved fertilizer formulations are designed to slow the release of Nr, reduce NH_3 volatilization and NO_3^- leaching, and enhance crop uptake [46]. Controlled-release fertilizers (CRFs)—coated with polymers or other materials that regulate nutrient release—match Nr availability to crop demand over the growing season, increasing NUE by 10–20% and reducing N_2O emissions by 20–50% compared to conventional fertilizers. Stabilized fertilizers, which contain nitrification inhibitors (e.g., dicyandiamide, DCD) or urease inhibitors (e.g., N-(n-butyl) thiophosphoric triamide, NBPT), reduce nitrification and NH_3 volatilization, respectively [47]. For example, urease inhibitors can reduce NH_3 volatilization from urea fertilizers by 30–70%, while nitrification inhibitors can reduce N_2O emissions by 20–60% in agricultural soils [47].

Integrated nutrient management (INM) combines synthetic fertilizers with organic amendments (e.g., manure, compost, crop residues) and biological nitrogen fixation (e.g., leguminous cover crops, intercropping with legumes) to optimize Nr supply and improve soil health [42]. Organic amendments enhance soil organic matter content, improve soil structure, and increase microbial activity, which promotes Nr retention and cycling. Biological nitrogen fixation provides a natural source of Nr, reducing reliance on synthetic fertilizers; for example, intercropping maize with legumes (e.g., beans, peas) can reduce synthetic fertilizer demand by 20–40% while maintaining yields. INM also improves soil fertility over time, enhancing long-term agricultural sustainability and resilience to climate change [48].

Sustainable livestock production practices reduce Nr emissions from livestock systems, which are a major source of NH_3 and N_2O [43]. Key strategies include improving animal diets (e.g., adding feed additives that reduce nitrogen excretion), optimizing manure management (e.g., composting, anaerobic digestion, and covered storage to reduce NH_3 volatilization), and integrating livestock with crop production (e.g., using manure as fertilizer in croplands, closing the nutrient loop). For example, feed additives such as 3-

nitrooxypropanol (3-NOP) can reduce CH_4 emissions by 30–40% and N_2O emissions by 15–25% by altering rumen fermentation, while anaerobic digestion of manure produces biogas (a renewable energy source) and reduces NH_3 volatilization by 40–60%. Integrating livestock and crop production recycles Nr in manure back to croplands, reducing synthetic fertilizer demand and enhancing NUE across the agricultural system [48].

4.2. Technological Innovation: Advancing Nr Mitigation and Recycling

Technological innovation plays a pivotal role in accelerating the transition to a sustainable nitrogen cycle, complementing agricultural practices by enabling more efficient Nr production, reducing Nr losses, and recycling Nr from waste streams. Advances in microbial biotechnology, materials science, and engineering are driving the development of novel technologies that address key bottlenecks in nitrogen management, from industrial fertilizer production to wastewater treatment and atmospheric Nr removal [49].

Low-carbon Nr fixation technologies aim to replace or supplement the energy-intensive Haber–Bosch process, reducing CO_2 emissions associated with synthetic fertilizer production [50]. One promising approach is biological Nr fixation enhancement, which involves engineering diazotrophic microorganisms (e.g., rhizobia, cyanobacteria) to increase nitrogenase activity, improve oxygen tolerance, or enhance symbiotic relationships with crops [49]. For example, genetic modification of rhizobia to express higher levels of nitrogenase has been shown to increase nitrogen fixation in leguminous crops by 15–30% in field trials. Additionally, synthetic microbial consortia—combining diazotrophs with other functional microorganisms (e.g., phosphate-solubilizing bacteria)—can enhance Nr supply while improving soil health, reducing reliance on synthetic fertilizers.

Electrochemical nitrogen fixation (ENF) is another emerging technology that uses renewable electricity to reduce atmospheric N_2 to NH_3 under ambient conditions, avoiding the high temperature and pressure requirements of the Haber–Bosch process [50]. Recent advances in catalyst design (e.g., transition metal nitrides, carbon-based catalysts) have improved the efficiency and selectivity of ENF, with lab-scale systems achieving NH_3 production rates comparable to small-scale Haber–Bosch plants. While challenges remain in scaling up ENF for industrial use (e.g., reducing energy consumption, improving catalyst stability), integration with renewable energy sources (e.g., solar, wind) could enable carbon-neutral Nr production in the future.

Nr loss mitigation technologies focus on capturing and converting Nr losses from agricultural, industrial, and urban systems into usable forms, reducing environmental pollution [43]. For example, ammonia capture technologies—using sorbents (e.g., zeolites, metal-organic frameworks) or scrubbers—can capture NH_3 volatilized from agricultural soils and livestock facilities, converting it into ammonium salts that can be reused as fertilizer. These technologies have been shown to reduce NH_3 emissions by 50–80% in pilot studies, while generating a valuable byproduct that offsets synthetic fertilizer demand.

In aquatic systems, advanced wastewater treatment technologies—such as partial nitritation-anammox (PN/A), membrane bioreactors (MBRs), and electrochemical denitrification—can efficiently remove Nr from wastewater, reducing eutrophication risks [13,51]. PN/A technology, which combines partial nitrification (NH_4^+ to NO_2^-) with anammox ($NH_4^+ + NO_2^- \rightarrow N_2$), requires 60–80% less energy and 90% less organic carbon than conventional nitrification-denitrification processes, making it a cost-effective option for large-scale wastewater treatment. MBRs, which use membranes to separate microbial biomass from treated water, achieve high Nr removal efficiencies (>90%) and produce high-quality effluent that can be reused for irrigation, reducing freshwater demand and Nr discharge to aquatic ecosystems [16].

Nr recycling technologies aim to recover Nr from waste streams (e.g., wastewater, food waste, livestock manure) and convert it into usable products (e.g., fertilizers, biofuels), closing the nitrogen loop [42]. For example, thermal hydrolysis of livestock manure and food waste can break down organic nitrogen into NH_3, which can be captured and converted into ammonium nitrate or urea. This process not only recycles Nr but also produces biogas (a renewable energy source) from organic matter, generating multiple environmental and economic benefits. Additionally, nutrient recovery from urine—using technologies such as vacuum separation, freeze-thaw, or electrochemical processes [52]—can capture up to 80–90% of Nr in urine, converting it into concentrated fertilizers that can be used in agriculture, reducing the need for synthetic fertilizers and wastewater treatment costs [16].

While these innovative technologies offer significant advantages such as high Nr removal efficiency, low carbon footprints, and closed-loop nutrient recycling, they also face notable limitations. For instance, biological nitrogen fixation enhancement is constrained by microbial stability and environmental adaptability; electrochemical nitrogen fixation suffers from high catalyst costs and low large-scale stability; ammonia capture technologies rely on supporting infrastructure and have limited applicability in resource-limited regions; advanced wastewater treatment processes demand high initial investment; and Nr recycling technologies face challenges in cost-effectiveness and standardized operation. These bottlenecks must be addressed to enable large-scale deployment.

4.3. Policy and Governance: Enabling Systemic Change

Effective policy and governance frameworks are essential to drive the widespread adoption of sustainable nitrogen management practices and technologies, addressing market failures and aligning stakeholder incentives [17]. Nitrogen pollution is a classic transboundary environmental problem, requiring coordinated action at local, regional, and global scales, as Nr losses from one region can affect ecosystems and human health in another. Policy interventions must be tailored to different contexts but should prioritize equity, affordability, and co-benefits for climate, biodiversity, and human health [6].

Nitrogen pricing and economic incentives can internalize the environmental and health costs of Nr pollution, encouraging stakeholders to reduce Nr losses and enhance NUE [43]. For example, nitrogen taxes on synthetic fertilizers, livestock manure, or fossil fuel combustion can reduce Nr inputs by increasing the cost of polluting activities; studies have shown that a modest fertilizer tax (e.g., $50–$100 per ton of Nr) can reduce Nr losses by 10–20% while generating revenue for sustainable nitrogen management programs. Conversely, subsidies for sustainable practices (e.g., precision agriculture, organic farming, nutrient recycling) can make these options more affordable for farmers and businesses, particularly in low- and middle-income countries (LMICs) where financial resources are limited [34].

Payment for ecosystem services (PES) schemes can also incentivize Nr reduction by rewarding landowners and communities for adopting practices that enhance Nr retention (e.g., wetland restoration, cover cropping, agroforestry) [40]. For example, PES programs that pay farmers to restore wetlands or plant cover crops can reduce Nr runoff by 20–30% while improving soil health, biodiversity, and carbon sequestration. These schemes can be particularly effective in watersheds where Nr pollution threatens drinking water supplies or aquatic ecosystems, aligning the interests of farmers with those of downstream communities and environmental protection [53].

Regulatory standards and targets are critical to setting clear expectations for Nr reduction and ensuring accountability [17]. National and regional governments can establish mandatory standards for NUE in agriculture, Nr emissions from industrial facilities and livestock operations, and Nr discharge from wastewater treatment plants. For example, the European Union's Nitrates Directive sets limits on nitrogen application rates in agriculture and requires the establishment of nitrate-sensitive areas, reducing eutrophication in European water bodies by 30–40% since its implementation [30]. Similarly, setting global targets for Nr reduction—aligned with the SDGs (e.g., SDG 2: Zero Hunger, SDG 6: Clean Water and Sanitation, SDG 13: Climate Action)—can provide a framework for coordinated action, as seen with the Paris Agreement for climate change [38].

Transboundary cooperation and global governance are essential to address transboundary Nr pollution, such as atmospheric Nr deposition and riverine Nr transport to coastal oceans [4,5]. Regional agreements—such as the Gothenburg Protocol to Abate Acidification, Eutrophication and Ground-Level Ozone in Europe—have successfully reduced transboundary NO_x and NH_3 emissions by setting collective reduction targets for member states [43]. At the global level, establishing a coordinated governance mechanism for nitrogen—similar to the Intergovernmental Panel on Climate Change (IPCC) or the Convention on Biological Diversity (CBD)—can facilitate knowledge sharing, capacity building, and coordinated action, helping to align national policies with global sustainability goals [6]. Additionally, integrating nitrogen into existing global frameworks (e.g., the UN Framework Convention on Climate Change, the UN Water Conference) can raise awareness and mobilize resources for sustainable nitrogen management [17].

Stakeholder engagement and capacity building are critical to ensuring the success and acceptability of nitrogen policies and practices [45]. Engaging farmers, industry leaders, indigenous communities, and civil society organizations in policy design and implementation can ensure that interventions are practical, equitable, and responsive to local needs. For example, farmer field schools—where farmers learn about sustainable nitrogen management practices through hands-on demonstrations—have been shown to increase adoption rates of precision agriculture and INM by 40–60% in LMICs [41]. Capacity building programs, focusing on technical training, knowledge transfer, and access to technology, are also essential to empower stakeholders in LMICs, where nitrogen pollution is growing rapidly but resources for sustainable management are limited [40].

4.4. Transdisciplinary Research and Knowledge Integration

Advancing toward a sustainable nitrogen cycle requires transdisciplinary research that integrates insights from microbial ecology, biogeochemistry, agronomy, engineering, economics, policy, and social sciences [49]. Traditional disciplinary approaches have made significant contributions to our understanding of the nitrogen cycle, but addressing the complex, interconnected challenges of nitrogen sustainability requires breaking down disciplinary silos and fostering collaboration across different fields [6].

Integrated nitrogen modeling is a key tool for understanding the impacts of anthropogenic perturbations and evaluating the effectiveness of sustainable nitrogen management strategies [1]. Advanced models—combining process-based biogeochemical models with economic, social, and climate models—can simulate Nr flows across different ecosystems and sectors (agriculture, industry, urban), predict the environmental and socioeconomic impacts of different policy and technology scenarios, and identify optimal pathways to nitrogen sustainability [17]. For example, global nitrogen cycle models (e.g., IMAGE-GNM, MPI-BGC) have been used to project Nr inputs and losses under different climate and land-use scenarios, informing global policy discussions on nitrogen reduction targets [4,5].

However, current models face several limitations, including uncertainties in microbial nitrogen transformation rates, Nr transport processes, and the interactions between nitrogen and other biogeochemical cycles (e.g., carbon, phosphorus) [49]. Addressing these limitations requires increased investment in observational data collection (e.g., long-term monitoring of Nr fluxes, microbial community composition) and model validation, as well as the development of more flexible, adaptive models that can incorporate new scientific discoveries and local context [1].

Social-ecological systems research focuses on understanding the interactions between human societies and nitrogen cycling, recognizing that sustainable nitrogen management depends not only on technical and policy interventions but also on social, cultural, and economic factors [40]. This research includes studying the drivers of farmer behavior (e.g., adoption of sustainable nitrogen practices), the social and economic impacts of nitrogen pollution (e.g., on vulnerable communities), and the equity implications of nitrogen policies (e.g., how fertilizer taxes affect small-scale farmers in LMICs) [45]. By integrating social and ecological insights, this research can help design more equitable, acceptable, and effective sustainable nitrogen management strategies that align with local values and needs [39].

Open data and knowledge sharing are essential to accelerate progress toward a sustainable nitrogen cycle [17]. Making observational data, model outputs, and research findings openly available to researchers, policymakers, and stakeholders can facilitate collaboration, reduce duplication of effort, and enable evidence-based decision-making [4,5]. For example, global databases on Nr inputs, emissions, and losses (e.g., the Global Nitrogen Budget, the EDGAR database) have been instrumental in advancing our understanding of the global nitrogen cycle and informing policy [2]. Additionally, knowledge sharing platforms—such as the International Nitrogen Initiative (INI)—can facilitate collaboration between researchers, policymakers, and practitioners across different regions, helping to transfer best practices and technologies from high-income to low-income countries.

In socio-ecological systems, integrated modeling faces acute challenges including high heterogeneity of human decision-making behaviors, lack of long-term coupled social–ecological observation data, and difficulties in quantifying cultural, economic, and policy drivers across regions. For open data and knowledge sharing, critical limitations remain: inconsistent data standards, incomplete global Nr flux monitoring coverage, insufficient cross-institutional data sharing mechanisms, and unbalanced capacity for data processing and application between developed and developing regions, which hinder the translation of research into practical policies.

5. Knowledge Gaps and Future Research Priorities

Despite significant advances in our understanding of the nitrogen cycle and its anthropogenic perturbations, several key knowledge gaps remain that must be addressed to accelerate progress toward a sustainable nitrogen cycle [1]. These gaps span microbial ecology, biogeochemistry, technology, policy, and social sciences, and require transdisciplinary research efforts to resolve [54]. A brief summary of each aspect is shown in Figure 4.

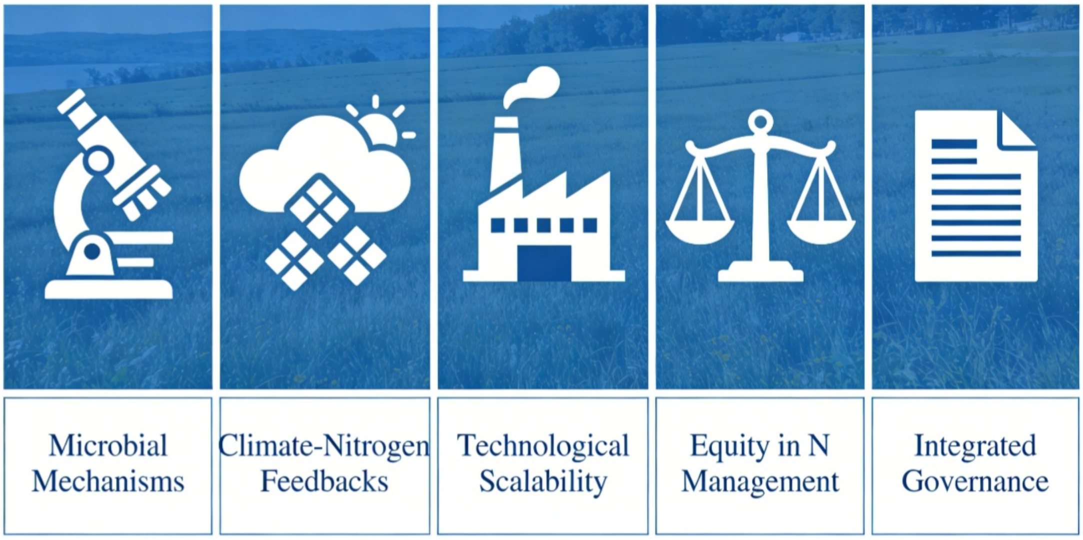

Figure 4. A brief summary of each aspect in understanding of the nitrogen cycle.

5.1. Microbial Mechanisms and Functional Diversity

While recent discoveries (e.g., comammox, dirammox) have expanded our understanding of microbial nitrogen transformations [10], many aspects of microbial nitrogen cycling remain poorly understood [49]. Key knowledge gaps include the ecological roles of understudied nitrogen-transforming microorganisms (e.g., DNRA-performing bacteria, anammox archaea) in different ecosystems, the factors regulating microbial community composition and function in response to Nr inputs and climate change, and the potential for microbial engineering to enhance Nr retention and reduce N_2O emissions [14]. Future research should focus on using advanced molecular techniques (e.g., metagenomics, metatranscriptomics, single-cell genomics) to characterize microbial nitrogen-cycling communities, elucidate their functional roles, and explore their potential for biotechnological applications [49].

5.2. Climate-Nitrogen Feedbacks and Ecosystem Resilience

The bidirectional interactions between nitrogen cycling and climate change are complex and not fully understood, particularly under future climate scenarios (e.g., increased temperature, extreme weather events, elevated CO_2 concentrations) [38]. Key knowledge gaps include how climate change will affect microbial nitrogen transformations (e.g., nitrification, denitrification) in different ecosystems, the magnitude and timing of N_2O emissions from different sources under climate change, and how Nr-induced ecosystem degradation will affect the resilience of terrestrial and aquatic ecosystems to climate stressors [1]. Future research should focus on long-term observational studies and manipulative experiments (e.g., warming experiments, CO_2 enrichment studies) to quantify climate-nitrogen feedbacks, as well as integrated modeling to predict their global impacts [17].

5.3. Technological Scalability and Affordability

While several novel technologies (e.g., ENF, PN/A, nutrient recovery) show promise for Nr mitigation and recycling [3], many remain in the lab or pilot scale and face challenges in scaling up to industrial or agricultural use [40]. Key knowledge gaps include the long-term performance and cost-effectiveness of these technologies, their adaptability to different contexts (e.g., LMICs with limited infrastructure), and their environmental co-benefits and trade-offs (e.g., energy use, resource requirements). Future research should focus on scaling up promising technologies, optimizing their design to reduce costs and improve efficiency, and evaluating their environmental and socioeconomic impacts in real-world settings [3].

5.4. Equity and Justice in Nitrogen Management

Nitrogen pollution disproportionately affects vulnerable communities (e.g., low-income populations, indigenous communities) in both high-income and low-income countries, while the benefits of synthetic nitrogen fertilizers (e.g., increased food production) are not equally distributed [39]. Key knowledge gaps include the social and economic impacts of nitrogen pollution on vulnerable communities, the equity implications of nitrogen policies (e.g., fertilizer taxes, PES schemes) [45], and how to design inclusive, equitable sustainable nitrogen management strategies that prioritize the needs of vulnerable populations [55]. Future research should focus on social-ecological systems research, participatory approaches, and case studies of nitrogen justice to address these gaps [31].

5.5. Integrated Governance and Policy Effectiveness

While several policy interventions (e.g., nitrogen taxes, regulatory standards) have been implemented to reduce Nr pollution [43], there is limited understanding of their long-term effectiveness, particularly in complex, transboundary contexts. Key knowledge gaps include how to design policies that integrate nitrogen with climate, biodiversity, and food security goals [38], how to enhance transboundary cooperation for nitrogen management, and how to evaluate the effectiveness of policy interventions across different socioeconomic and ecological contexts. Future research should focus on policy analysis, case studies of successful nitrogen governance, and integrated modeling to identify optimal policy mixes for different regions.

6. Conclusions

The global nitrogen cycle has been drastically perturbed by anthropogenic activities, with far-reaching consequences for ecosystems, climate, food security, and human health. Excessive Nr inputs from industrial nitrogen fixation, agriculture, fossil fuel combustion, and wastewater discharge have triggered cascading environmental crises, including eutrophication, atmospheric pollution, greenhouse gas emissions, and biodiversity loss, while creating complex feedback loops with climate change and the FEW nexus. Achieving a sustainable nitrogen cycle is therefore one of the most pressing global sustainability challenges of the 21st century, requiring urgent, integrated action across all sectors and scales.

This Review has synthesized the latest advances in our understanding of the natural nitrogen cycle and its anthropogenic perturbations, and outlined actionable pathways to restore and sustain nitrogen balance. Nitrogen cycle summary is shown in Figure 5. These pathways are organized around four core pillars: agricultural optimization to enhance NUE and reduce Nr losses; technological innovation to advance Nr mitigation and recycling; policy and governance to enable systemic change; and transdisciplinary research to integrate knowledge and drive innovation. While significant progress has been made in each of these areas, several key knowledge gaps remain, requiring sustained investment in transdisciplinary research and capacity building, particularly in LMICs.

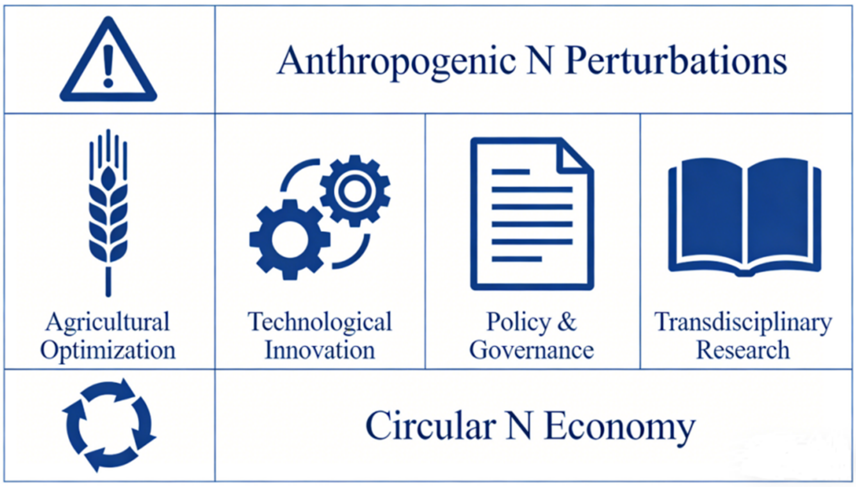

Figure 5. Nitrogen cycle summary.

Achieving a sustainable nitrogen cycle will require a paradigm shift in how we produce, use, and manage nitrogen, moving away from the current linear, polluting model toward a circular, regenerative model that closes the nitrogen loop. This shift will require collaboration across governments, businesses, farmers, researchers, and civil society, as well as a commitment to equity, justice, and co-benefits for climate, biodiversity, and human health. By working together to implement the strategies outlined in this Review, we can restore the natural balance of the nitrogen cycle, safeguard planetary health, and ensure a sustainable future for all.

Future priority research directions should focus on: (1) uncovering the mechanisms and functional diversity of understudied microbial nitrogen transformation processes; (2) quantifying non-linear climate–nitrogen feedbacks and enhancing ecosystem resilience under global change; (3) developing scalable, low-cost, and widely applicable technologies for Nr mitigation and recycling; (4) addressing equity and environmental justice in global nitrogen management to protect vulnerable communities; and (5) establishing coordinated transboundary and global governance frameworks for sustainable nitrogen cycling.

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Conflicts of Interest

The author declares no conflict of interest.

Use of AI and AI-Assisted Technologies

No AI tools were utilized for this paper.

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