Global Change Biology

WILEY

SPECIAL ISSUE Reviewing the State of Global Change Biology: A Dedication to Steve Long

Global Change Biology

INVITED REVIEW OPEN ACCESS

Three Decades of Soil N_2O Research—Insights and Gaps

Klaus Butterbach-Bahl[1,2] | Laurent Philippot[3] | João Serra[1] | Whendee L. Silver[4] | Stephen Ogle[5,6] | Diego Abalos[1]

[1]Land-CRAFT, Department of Agroecology, Aarhus University, Aarhus, Denmark | [2]Institute for Meteorology and Climate Research (IMK-IFU), Karlsruhe Institute of Technology, Garmisch-Partenkirchen, Germany | [3]Univ Bourgogne Europe, INRAE, Institut Agro Dijon, Agroecologie, Dijon, France | [4]Department of Environmental Science, Policy and Management, University of California Berkeley, Berkeley, California, USA | [5]Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado, USA | [6]Department of Ecosystem Science and Sustainability, Colorado State University, Fort Collins, Colorado, USA

Correspondence: Klaus Butterbach-Bahl (klaus.butterbach-bahl@agro.au.dk)

Received: 11 May 2026 | **Revised:** 27 June 2026 | **Accepted:** 29 July 2026

Keywords: denitrification | microbial ecology | modeling | N_2O | nitrification | process

ABSTRACT

Nitrous oxide (N_2O) is a potent greenhouse gas (GHG) whose atmospheric concentration continues to rise, largely driven by nitrogen (N) inputs to agricultural soils. Over the past three decades, research on soil N_2O emissions has advanced substantially, yet key uncertainties still constrain mitigation efforts. Here, we synthesize developments in measurement techniques, process understanding, microbial ecology, and modelling from the 1990s to the present, and identify critical gaps for future research. Advances in high-frequency measurements, laser spectroscopy, and isotopic approaches have revealed the importance of temporal "hot moments" and spatial "hotspots," challenging earlier assumptions based on sparse sampling. Concurrently, molecular and multi-omic tools have transformed our understanding of the microbial drivers of N_2O production and consumption, highlighting the role of community composition, truncated pathways, and previously overlooked N_2O-producing and reducing organisms. Process-based models have evolved from research tools into policy-relevant frameworks underpinning GHG inventories, with emerging integration of data assimilation, ensemble modelling, and artificial intelligence. However, despite these advances, persistent challenges remain in linking scales, reducing uncertainties, and translating mechanistic insights into scalable mitigation strategies. Closing these gaps offers a unique opportunity to translate decades of scientific progress into next-generation mitigation strategies that align agricultural productivity with climate stabilization goals.

1 | Introduction

Nitrous oxide (N_2O) is an important GHG in the atmosphere, contributing about 6% to observed global warming (IPCC 2019). The atmospheric concentration of N_2O has increased from approximately 280 parts per billion by volume (ppbv) in preindustrial times to approximately 440 ppbv in 2025, with an increasing growth rate since 1985, reaching > 1 ppbv per year in recent years (WMO 2025) (Figure 1). With a global warming potential nearly 300 times higher than CO_2 and an atmospheric lifetime of 114 years, the undamped increase in atmospheric N_2O concentrations is alarming, as it makes achieving climate goals difficult (Clark et al. 2020). The main driver of this increase is the use of organic and synthetic N fertilizers. Agricultural sources, specifically fertilized agricultural soils, accounted for over 60% of total global anthropogenic emissions in 2020, which is an increase of about 65% since 1980 (Tian et al. 2024). There is an urgent need to reduce agricultural N_2O emissions without jeopardizing food production. However, progress in identifying mitigation options is hindered by limitations and uncertainties related to measurements, understanding of the involved processes, and modeling. In this mini-review, we summarize developments in agricultural soil N_2O emission research since the 1990s and

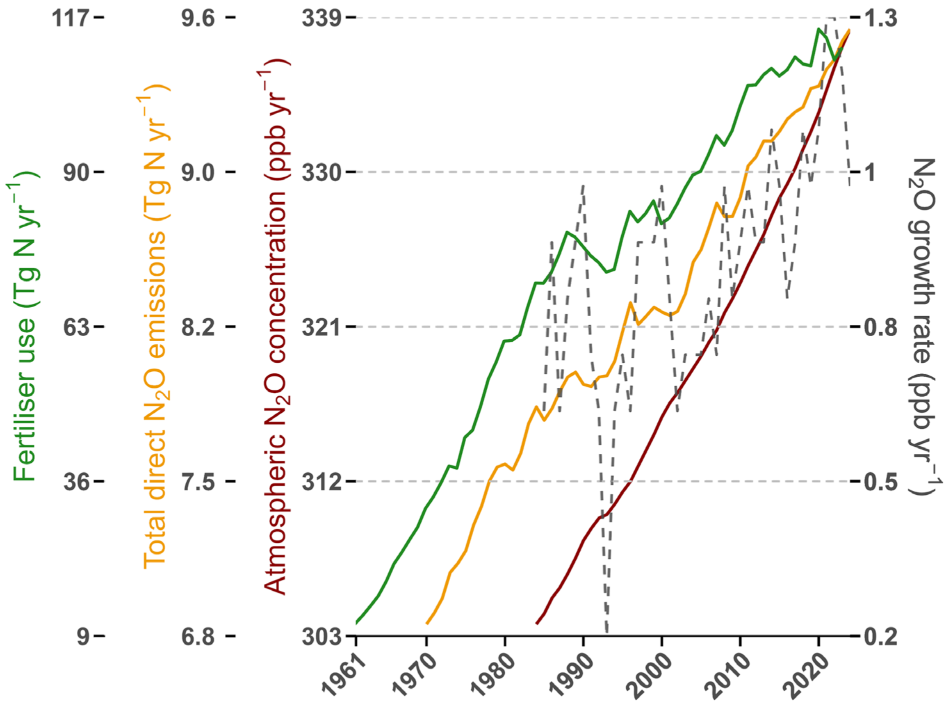

FIGURE 1 | Changes in atmospheric nitrous oxide (N_2O; ppb year^{-1}) concentrations (WMO 2025), total direct N_2O emissions from fertilized land (Tg N-N_2O year^{-1}; EDGAR 2025), fertilizer use (Tg N year^{-1}; Ludemann et al. 2024), and the growth rate of atmospheric N_2O (WMO 2025; ppb year^{-1}) over the last few decades from 1961 to 2024, although this study focuses on 1991–2025.

identify ways to move forward, resolving research gaps and identifying tangible mitigation options that allow for reducing the N_2O footprint of agricultural production under environmental change conditions.

2 | Advances in Soil Nitrous Oxide Measurements

Publications from the 1990s on agricultural soil N_2O emissions primarily relied on manual, infrequent sampling campaigns that usually only covered the crop-growing period (Stehfest and Bouwman 2006) (Figure 2a,b). The standard procedure was to collect gas samples with syringes and often store them for weeks before analyzing them in laboratories. Gas chromatography was the usual analytical method (Mosier and Mack 1980; Mosier et al. 1996) (Figure 2c). Due to the technique's relatively low sensitivity (around 1–2 ppbv), the required chamber closure time was 30–60 min. This resulted in flux detection limits of 3–5 µg N_2O-N m^{-2} h^{-1} at best. Additionally, changes in chamber headspace concentrations had to be thoroughly checked for linearity, which affected flux calculations (Hutchinson and Mosier 1981). For example, one had to decide whether to use linear or non-linear functions for calculating fluxes (Venterea et al. 2009). Flux sampling frequency was mostly biweekly or monthly (Figure 2d) and often excluded non-seasonal fluxes because the non-vegetation period was generally assumed to contribute little to annual fluxes. Consequently, due to the low sampling frequency and sparse or missing off-season measurements, studies often failed to capture important peak emissions or missed high emission events altogether. This led to significant underestimates of annual emissions and high uncertainty, which were unknown at the time (Shang et al. 2020, 2024; Buma 2024).

Around the end and beginning of the 20th century, an increasing number of studies of managed and natural ecosystems (Figure 2e) demonstrated that freeze–thaw (Christensen and Tiedje 1990; Papen and Butterbach-Bahl 1999; Wagner-Riddle et al. 2007) and soil rewetting periods (Ruser et al. 2006) trigger significant pulses of N_2O emissions. These emissions can contribute disproportionately to annual emissions (Matzner and Borken 2008; Wagner-Riddle et al. 2017) (Figure 2f). In addition to temporal hot moments of emissions, spatial hotspots such as clumps of residues incorporated into the soil were found to be important factors in improving understanding of the magnitude of soil N_2O fluxes (Groffman et al. 2009; Kravchenko et al. 2017). These findings have led to an increased use of automated measurement systems, as well as recommendations for more frequent sampling (Barton et al. 2015; Grace et al. 2020) and a focus on spatial flux variability (e.g., Breuer et al. 2000; Savage et al. 2014). However, due to their high cost, limited number of providers, and difficulty of operating them in field settings, automated chamber flux measurements are still relatively uncommon for N_2O measurements.

Progress in developing laser spectroscopy technologies, particularly quantum cascade lasers (QCLs) and cavity ring-down spectroscopy (CRDS), has enabled high-precision, continuous, and rapid measurements with detection limits below one part per billion (ppb) since the 2000s. Following these advancements, several groups began measuring soil N_2O fluxes using micrometeorological methods such as eddy covariance and flux gradient (Christensen et al. 1996; Laville et al. 1999; Fowler et al. 2009). Today, laser spectroscopes can operate at near-room temperature with thermoelectric cooling, eliminating the need for liquid N. However, the high cost of instrumentation for QCL- or CRDS based eddy covariance

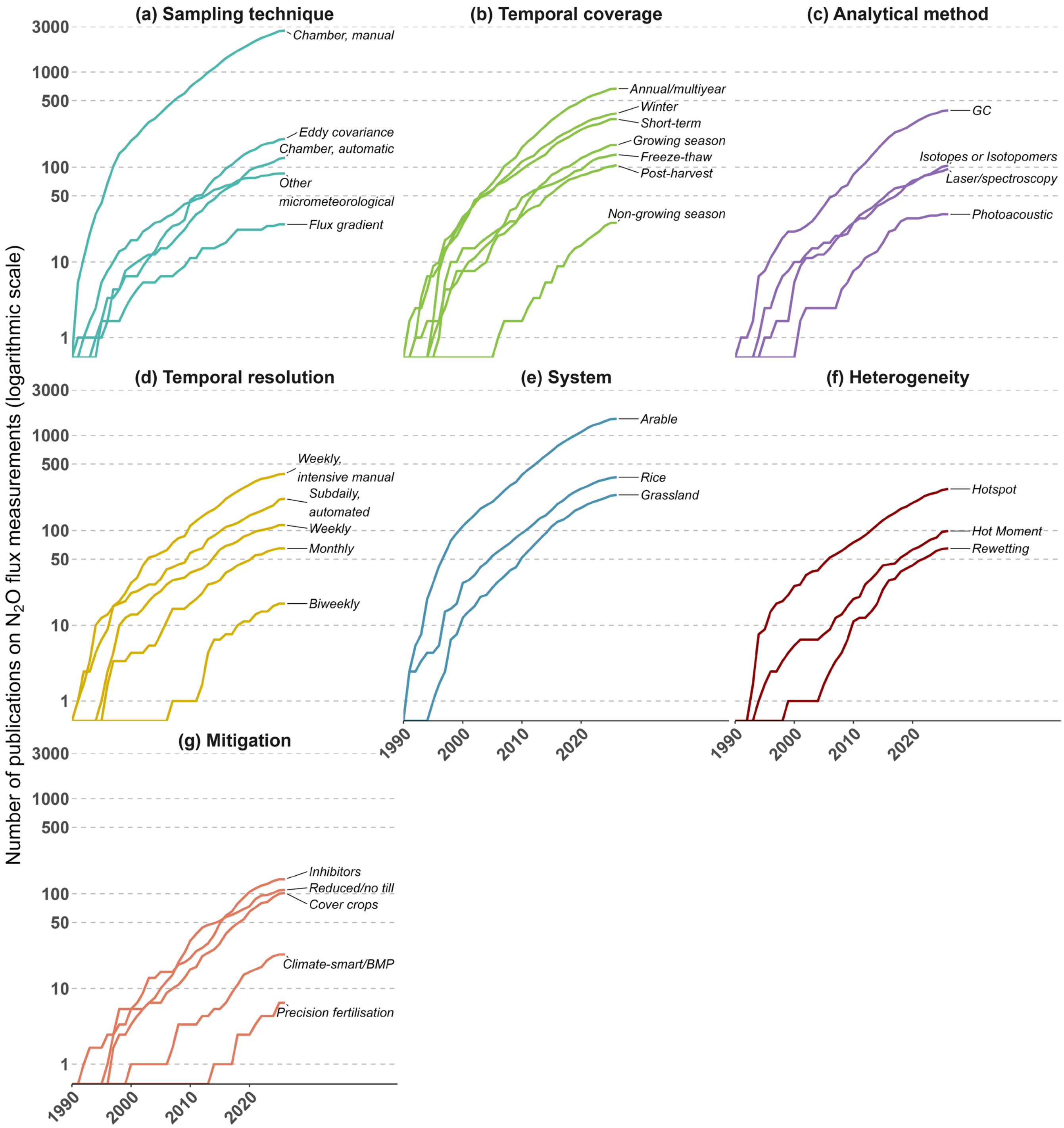

FIGURE 2 | Temporal development of N_2O flux measurement techniques and research focus. (a) Underlying flux measurement technique; (b) Temporal coverage of measurements; (c) Analytical method for measuring sample air N_2O concentration; (d) Temporal resolution of flux measurements; (e) Ecosystem types studied; (f) Spatial heterogeneity; (g) N_2O mitigation options. The number of publications (y axis) are log scaled. Within temporal resolution, intensive manual measurements reflect discontinuous daily-to-weekly manual chamber campaigns. The analysis is based on the number of published manuscripts during the period from January 1990 to December 2025 ($n = 3406$ publications) from Web of Science. For details about the query and data used, the reader is referred to Serra (2026).

measurements of N_2O fluxes has prevented this method from becoming widespread. These costs can be reduced slightly by using the flux gradient method or by positioning the EC flux tower between two fields with different land management practices and fluxes, which are then partitioned according to a footprint analysis of wind directions. This is because one high-precision N_2O instrument can be used to measure fluxes in two (EC; e.g., Fuchs et al. 2018) to four (flux gradient, e.g., Wagner-Riddle et al. 1997) fields. Furthermore, micrometeorological measurements of N_2O fluxes require predominantly flat and homogeneous terrain and management of hundreds of meters in lateral extent (Denmead 2008). This makes it difficult to study landscape hotspots caused by topography or other biogeochemical drivers, so static chamber approaches

TABLE 1 | Status and summary of the most advanced technical and measurement developments.

Topic	1990s	2020–2025	References
Sampling	Manual	Automated	Grace et al. 2020
Flux method	Predominantly closed chamber	Auto-chamber, EC/Flux gradient	Hensen et al. 2013
Frequency	Weekly/Monthly	Subdaily/Daily	See Figure 2
Study length	Predominantly cropping season	Predominantly year round	See Figure 2
Scale	Small plots	Small plots to landscapes	Daly et al. 2025
N_2O analytics (precision)	GC-ECD (±1 ppbv)	QCL/CRDS (0.05–0.5 ppbv)	Kostinek et al. 2019
N_2O-isotopes (precision)	Laboratory-based IRMS (1‰–2‰)	IRMS/In-situ laser spectroscopy (< 1‰)	Havsteen et al. 2026

are usually used for landscape and topography effect studies (Corre et al. 1996; Wangari et al. 2023). The expense and land areas required for micro-meteorological flux measurement approaches also makes it very difficult, nearly impossible, to replicate and thoroughly test different agricultural practices aimed at reducing N_2O emissions. This means that mitigation practices continue to be mostly tested by smaller-scale (e.g., 8 × 3 m) field trials and automated chambers (Figure 2g) (Butterbach-Bahl et al. 2025). Micrometeorological techniques and instrumentation continue to be developed. Laser spectroscopes are becoming smaller, more robust, lighter, and more affordable, and micrometeorological flux measurements such as EC and flux gradient approaches and software solutions are becoming easier to apply by a wider research community.

Advances in the development of laser instrumentation have enabled portable measurements in the field. For example, the fast-box method (Hensen et al. 2013) can be used to explore spatial flux variability at a landscape scale (Wangari et al. 2023). Specifically, the instruments' high sensitivity reduces chamber closure times to a few minutes. In addition to being used for fast-box flux measurements, the instruments can be connected to automated chambers (Savage et al. 2014). Thus, the increases in sensor sensitivity allows to increase the number of chambers that can be sampled while reducing the bias that long periods of chamber closure may have on crop growth and soil environmental conditions.

Additionally, QCL- or CDRS measured atmospheric N_2O concentrations are the standard for tall tower measurements. Such measurements enable top-down estimates of N_2O fluxes at regional to national scales and deliver critical information for validating and improving bottom-up estimates for inventory purposes (Del Grosso et al. 2022).

As QCL and IRMS isotope ratio mass spectrometry become more robust and sensitive, one of the most fascinating areas of research is the ability to measure high-precision, in situ, site-specific N_2O isotopomer signals. Nitrous oxide isotopomers differ in their isotopic compositions of N (^{14}N and ^{15}N) and oxygen (^{16}O and ^{18}O) within their asymmetric, linear molecular structures. The positioning of the isotopes provides a unique "fingerprint" that can be used to judge underlying N_2O production and consumption processes, such as bacterial and fungal denitrification and nitrification, as well as quantify the extent of N_2O reduction to N_2 (dinitrogen) during denitrification (Brenninkmeijer and Rockmann 1999; Ostrom et al. 2007; Denk et al. 2017). Currently, N_2O isotopomer measurements may require cryo-focusing and preconcentration of air samples. However, as measurement sensitivity improves rapidly, this may soon change, allowing for real-time, in situ measurements of N_2O isotope fingerprints of emitted N_2O (Havsteen et al. 2026). One of the remaining obstacles is the limited availability of calibration gases for N_2O isotopomers, which are currently primarily provided by research institutions rather than commercial suppliers. Therefore, interlaboratory comparison studies are needed and underway to refine calibration standards and to further develop methodological approaches (Yu et al. 2020) (Table 1).

3 | Process Studies and Underlying Process Understanding

3.1 | Drivers of N_2O Emissions via Nitrification and Denitrification

In the 1990's, researchers were making use of advances in IRMS to explore pathways of N_2O production and consumption in soils (Poth and Focht 1985; Stevens et al. 1997). The dominant biological processes resulting in N_2O production are nitrification and denitrification. Efforts focused on differentiating nitrifier denitrification (i.e., where the same organism completes both processes, often under fluctuating redox conditions) from simultaneous nitrification–denitrification, where nitrate (NO_3^-) is rapidly reduced to N_2O or N_2 in adjacent anoxic microsites in soils where redox gradients occur, from canonical denitrification (Stein 2011). An enriched ammonium ($^{15}NH_4^+$) tracer was used to determine the proportion of $^{15}N_2O$ produced via nitrification, while labeled $^{15}NO_3^-$ was added to quantify rates of canonical denitrification (Stevens et al. 1997). To further differentiate nitrification-derived N_2O production from canonical denitrification, researchers started to use low concentrations of acetylene to block ammonia monooxygenase (Myrold 1990). Studies from the 1990's showed that a variety of factors, including fertilizer use, soil moisture content, and the deposition of animal waste, could impact the relative importance of nitrification versus denitrification as a source of N_2O (Mulvaney et al. 1997; Stevens et al. 1997; Clough et al. 1998).

While isotope tracers remain a valuable tool for exploring the dynamics of N_2O production, the technique can produce some artifacts. Ammonium tracer addition can stimulate nitrification, and NO_3^- addition can increase denitrification by enhancing microbial substrate availability. Nitrification can proceed rapidly, within minutes to hours of substrate addition in some soils, making it difficult to distinguish between nitrifier denitrification and canonical denitrification (Silver et al. 2001). The acetylene inhibition technique can also produce artifacts; it does not act uniformly on all nitrifiers, may not diffuse well into moist or wet soils, and can be metabolized in soils with the byproducts providing a potential energy source for denitrifiers (Knowles 1990; Bollmann and Conrad 1997). Thus, partitioning N_2O emissions between nitrification and denitrification remains a challenge.

3.2 | Gross N_2O Production and N_2:N_2O Ratio Measurements

A gas-flow soil core method was developed in the mid 1980s for measuring denitrification in a laboratory setting (Parkin et al. 1984; Tiedje et al. 1989). An advantage of the gas flow soil core method is the ability to strictly control headspace gas composition, moisture, temperature, and redox conditions. It also allows replacing the N_2 gas of the soil atmosphere with an inert gas such as helium, allowing for the measurement of N_2O and N_2 fluxes to approximate complete, or gross denitrification rates (Groffman et al. 2006; Wen et al. 2016; Yankelzon et al. 2025). While this method advanced the mechanistic understanding of denitrification and N_2O dynamics, it necessitated changing soil gas composition and thus did not necessarily represent field conditions.

In the early 2010s, a new method was developed to estimate gross gas fluxes from soils, built on the ^{15}N pool dilution approach (Kirkham and Bartholomew 1954). Called the N_2O pool dilution method, this approach uses isotopically labeled $^{15}N_2O$ coupled with a conservative tracer (e.g., sulfur hexafluoride (SF_6)) to simultaneously account for production of $^{14}N_2O$ via isotope dilution, N_2O consumption via loss of the original labeled N_2O, and leakage via SF_6 accounting (Yang et al. 2011). The addition of the $^{15}N_2O$ tracer, primarily as an end product, results in less stimulation of N_2O production compared with the addition of substrates like NH_4^+ and NO_3^-. However, limited diffusion of the $^{15}N_2O$ label could lead to underestimates of N_2O consumption and an overestimate of N_2O production, with reported errors on the scale of 10% (Yang et al. 2011). Estimating gross production of N_2O allows for the approximation of the N_2O yield, defined as the relative N_2O versus N_2 produced via denitrification (Yang et al. 2011). This method has been applied in both a laboratory and field setting using manual chambers, providing new insights into N_2O consumption and gross production (Yang and Silver 2016; Stuchiner and von Fischer 2022). Importantly, the $^{15}N_2O$ pool dilution characterizes N_2O consumption in soils but does not allow capturing the direct intracellular denitrification of NO_3^- to N_2, a process that has yet to be quantified.

Quantifying the N_2O yield from soils and the associated drivers could facilitate management to lower N_2O emissions from agriculture. Ideally, both N_2O and N_2 could be used to quantify denitrification rates, but measurements of N_2 are complicated by the high background atmospheric concentrations (about 78.1%) relative to fluxes from soils. Isotope tracing of N_2 fluxes requires large inputs of both NO3- and a strong ^{15}N label for detection and thus may be used only for heavily fertilized agricultural systems (Takeda et al. 2024), conditions that are unrealistic for some agricultural ecosystems such as grazing land and some N-fixing crops. High concentrations of acetylene can inhibit N_2O reductase enzyme activity and have been used to estimate total denitrification, but the method suffers from the same shortcomings as mentioned above for nitrification inhibition (Knowles 1990; Bollmann and Conrad 1997). The ratio of N_2 to argon (Ar) is widely used in marine systems to estimate N_2 emissions. It is based on the use of Ar as an inert, conservative tracer and thus changes in the ratio of N_2 to Ar result from changes in the concentrations of N_2 (Yang and Silver 2012). There are several challenges to accurately quantifying the N2:Ar ratio from soil fluxes, including fractioning effects from temperature, moisture, and transport. These fractionating factors lead to a high detection limit, reducing the utility of this approach for most field conditions (Yang and Silver 2012). However, advances in IRMS and controlled chamber environments may facilitate the use of this method in the future.

A promising way forward could as well be the use of enhanced Raman gas spectroscopy (Blohm et al. 2024), which allows the sensitive and selective detection and isotopic differentiation of N2 and N_2O. Though it has only been tested in laboratory settings thus far due to its high instrumental demands, the technique is suitable for experiments involving natural or artificial (He/O_2 or Ar/O_2) atmospheres, with or without isotopic labels. The latest tests show that with reduced background N2 levels and using artificial He/O_2 or Ar/O_2 atmospheres, changes in headspace N2 concentrations at the ppb level can be measured (Merian et al. 2024).

4 | Microbial Ecology of N_2O

4.1 | Early Culture-Based Insights Into the N_2O Producing Microorganisms

By the early 1990s, it was already recognized that denitrifiers, ammonia oxidizers (nitrifiers), and nitrate-ammonifiers (DNRA) were capable of producing N_2O under certain conditions, although the understanding of the underlying mechanisms was strongly uneven across these guilds.

At that time, only ammonia-oxidizing bacteria (AOB) had been identified and most studies were almost exclusively centered on *Nitrosomonas europaea* serving as the dominant model organism, with N_2O production by other AOB lineages remaining largely unexplored until the late 1990s (Jiang and Bakken 1999). The key enzymes involved in nitrification—including ammonia monooxygenase (AMO), hydroxylamine oxidoreductase (HAO), and nitrite oxidoreductase (NXR)—were later characterized throughout the 1990s (McTavish et al. 1993; Igarashi et al. 1997; Spieck et al. 1998).

DNRAs were still described primarily among enteric and fermentative bacteria but the actual ecological role of DNRA was still unclear (Tiedje 1988; Cole 1996). The nitrate reductase

(NAR) and multiheme cytochrome c nitrite reductase (NRF) have been purified since the early 80s, while the corresponding genes were progressively identified and characterized during the 1990s (Berks et al. 1995; Simon 2002).

In contrast, the phylogenetic diversity of denitrifiers was already known to be important. Thus, denitrification had been documented across a wide range of bacterial taxa, as well as in archaea (e.g., Tomlinson et al. 1986) and fungi (e.g., Shoun et al. 2012). Characterization of denitrifying isolates had revealed large physiological differences among denitrifiers, particularly in their capacity to reduce N_2O to N_2, already pointing at a possible role of the composition of microbial communities for understanding N_2O fluxes (Conrad 1996; Cavigelli and Robertson 2001). All the main reductases catalyzing the four denitrification steps—NAR, copper and cd1 nitrite reductases, nitric oxide reductase (NIR) and nitrous oxide reductase (NOS)—had already been purified for over a decade (Hochstein and Tomlinson 1988) and denitrification genes were sequenced from a handful of bacterial strains, predominantly Proteobacterial (Zumft 1997).

4.2 | The Emergence of Molecular Microbial Ecology

In the late 1990s, research on the ecology of microorganisms involved in N_2O emissions underwent a decisive shift from culture-based approaches to molecular, culture-independent methods. The shift was largely driven by the recognition that about 1% of the microorganisms could be cultivated (Hofer 2018), raising concerns about the ecological validity of process interpretations only based on a limited number of cultured strains, which were not necessarily representative of natural populations in the environment. DNA extraction from the environment combined with the development of functional gene markers targeting key steps of the nitrification, DNRA, and denitrification processes allowed assessing the diversity of the microorganisms involved in N_2O production and consumption across environments, bypassing the cultivation bias (Rotthauwe et al. 1997; Hallin and Lindgren 1999; Philippot et al. 2002). These tools were rapidly complemented by real-time approaches to quantify the abundances of these guilds (Grüntzig et al. 2001; Henry et al. 2004, 2006).

These molecular studies initially focused in the early 2000s on describing the diversity and abundance of N-cycling microbial guilds, revealing a greater diversity than previously recognized as well as strong environmental and anthropogenic controls on their distribution (Wallenstein et al. 2006; Enwall et al. 2005; Shen et al. 2008; Zhou et al. 2011). Patterns of niche partitioning among functional groups became evident, reflecting differences in ecological strategies and in their responses to environmental conditions (Philippot et al. 2009; Di et al. 2009). Research then increasingly moved beyond purely trait-based molecular approaches by incorporating microbial activity measurements for linking the abundance and/or the diversity of these microbial guilds to process rates and N_2O emissions. These efforts were framed either within an ecological perspective, drawing on biodiversity–ecosystem functioning relationships, or within a biogeochemical framework seeking to improve predictive models of N cycling by explicitly incorporating microbial communities (Hallin et al. 2009; Rich and Myrold 2004; Patra et al. 2006; Salles et al. 2009). While some studies reported significant correlations between functional community abundance or diversity and process rates, others highlighted large variability and weak predictive power, underscoring the complexity of linking microbial community ecology to ecosystem functions.

4.3 | Expanding the Diversity of Micro-Organisms Involved in N_2O Fluxes and Importance of Truncated Pathways

After the major breakthrough that ammonia-oxidation was not restricted to ammonia-Oxidizing Bacteria (AOB), but is also carried out by ammonia-Oxidizing archaea (AOA) (Francis et al. 2005; Könneke et al. 2005; Leininger et al. 2006), several studies demonstrated that AOA are also capable to produce N_2O (Santoro et al. 2011; Löscher et al. 2012), thereby contributing to N_2O emissions across terrestrial and aquatic ecosystems, although generally with lower yields than AOB. A further expansion of nitrifier diversity came with the discovery of *Comammox Nitrospira*, which can perform the complete nitrification pathway (Daims et al. 2015; van Kessel et al. 2015). Comammox (COMplete AMMonia Oxidation) can produce N_2O, likely from abiotic reaction, and at lower rates to both AOB and AOA, suggesting a minor contribution to N_2O emissions from most environments (Han et al. 2021).

Characterization of the denitrification system in fungi showed that it is based on a copper nitrite reductase (NirK) and a cytochrome P450 nitric oxide (NO) reductase, while lacking the N_2O reductase, thereby making N_2O a terminal product, a trait that is widespread among fungi (Shoun et al. 2012; Maeda et al. 2015). Various approaches have been used to quantify the contribution of fungi to N_2O production, including substrate-induced respiration inhibition, and stable isotope analyses, each with distinct strengths and limitations. A significant contribution of fungi was reported in some soil environments, sometimes exceeding that of bacteria (e.g., Laughlin and Stevens 2002; Wankel et al. 2017).

This truncated denitrification pathway in fungi, with the lack of N_2O reductase, as well as in a subset of bacteria, challenged the traditional view of denitrification as a canonical, complete pathway and instead supports a modular organization of the process, in which some organisms lack one or several steps such as the genetic capacity to reduce N_2O to N_2. This has important implications for N_2O emissions, as it indicates that N_2O reduction is not only controlled by environmental or physiological factors affecting the expression or activity of N_2O reductase (e.g., pH, substrate availability) (Bakken et al. 2012) but is also intrinsically constrained by the composition of microbial communities, in particular by the relative abundance of organisms genetically capable of N_2O reduction. As organisms lacking this gene are acting as net N_2O sources regardless of favorable environmental conditions for N_2O reduction, N_2O production can be due to the combined effects of physiological processes and the genetic potential of the resident microbial community, thereby linking N_2O emissions to microbial community composition (Philippot et al. 2011).

4.4 | Microbial N_2O Sinks—from Discovery to Mitigation Strategies

Several years after the landmark synthesis by Chapuis-Lardy et al. (2007), which highlighted the potential of soils to act as sink for N_2O, a major breakthrough came with the discovery of a previously unrecognized clade of N_2O, indicating that the diversity of N_2O consumers had been underestimated (Jones et al. 2013; Sanford et al. 2012). This new clade termed nosZII is widespread and most often at least as abundant as the typical canonical nosZI (Jones et al. 2013, 2014; Orellana et al. 2014). This discovery not only expanded the known diversity of bacteria capable to reduce N_2O, but had ecological implications for a better understanding of N_2O emissions, as many members of this newly identified nosZ clade II lack the other denitrification genes, thereby being purely a potential N_2O sink without contributing to N_2O production (Graf et al. 2014; Hallin et al. 2018). Subsequent studies demonstrated that the soil N_2O sink capacity was mostly explained by the abundance and diversity of this new nosZII clade (Jones et al. 2014), with the nosZII clade rather than nosZI being negatively related to in situ N_2O emissions (Domeignoz-Horta et al. 2018; Xu et al. 2020; Xiang et al. 2023). Te ecological importance of this new clade was further confirmed experimentally by showing that inoculation of a non-denitrifier nosZII bacteria in soil could significantly decrease N_2O emissions, thereby providing proof of concept that nosZ enrichment can help mitigating N_2O emissions (Domeignoz-Horta et al. 2016). Building on this work, Hiis et al. (2024) showed the potential of nosZII- enriched organic amendment for reducing agricultural N_2O emissions. These findings reinforced the view that microbial community composition, and particularly the balance between N_2O producers and reducers, is an important determinant of N_2O emissions.

Microbial mitigation strategies are not restricted to nosZII-bacteria as members of the canonical nosZI clade can also contribute to lowering N_2O emissions. The most compelling example is provided by the N fixing rhizobia establishing symbiosis with legume plants such as soybean. Across the world, more than 120 million hectares of soybean are cultivated, the vast majority being inoculated with rhizobial strains to ensure efficient N fixation. These rhizobial strains can vary in their denitrification capacity and in particular to carry nosZI and reduce N_2O. Afterthe initial findings that *Bradyrhizobium japonicum* can reduce N_2O in the soybean rhizoshere, subsequent studies showed that inoculation with single or mixed rhizobial strains carrying *nosZ*, as well as with genetically modified strains with enhanced N_2O reductase activity, increased N_2O reduction both in the rhizosphere and within nodules, thereby shifting the system toward a net N_2O sink (Sameshima-Saito et al. 2006; Hénault and Revellin 2011; Akiyama et al. 2016; Itakura et al. 2013). Moreover, several studies showed that plant–microbe interactions can not only enhance N_2O reduction but also suppress N_2O production. Thus, in a pioneering work, Subbarao et al. (2009) demonstrated that plant root exudates can contain biological nitrification inhibitors (BNI) affecting the ammonia monooxygenase. Cultivation of a grass releasing such BNI for 3 years resulted in decreased soil ammonia-oxidizers along with nitrification activity and N_2O emissions. This discovery initiated more than a decade of research on biological nitrification inhibition, recently leading to the transfer of a chromosome region controlling BNI production to elite wheat cultivars, resulting in reduced soil nitrification and lower N_2O emissions (Subbarao et al. 2021). Collectively, these findings highlight the potential of leveraging plant–microbe interactions as a scalable strategy to reduce agricultural N_2O emissions.

More recently, the discovery of a previously unknown protein family involved in N_2O reduction (clade III lactonase-nosZ) further expanded the diversity of N_2O-reducing microorganisms (He et al. 2025). This identification of another N_2O reductase in previously unrecognized taxa suggests that microbial N_2O sinks remain incompletely characterized, opening new avenues for both understanding and mitigating N_2O emissions.

4.5 | The Multi-Omic Area and the Overlooked Role of Biotic Interactions

Since 2020, a multi-omic era has emerged in microbial ecology, integrating genomes, metagenomes, metatranscriptomes, and proteomes. Comparative analyses of more than 60,000 genomes along with metagenome and metatranscriptome datasets showed that partial denitrifiers generally outnumber complete denitrifiers, and that the potential to initiate denitrification is more common than the potential to reduce N_2O to N_2, supporting the view that completion of the pathway is a community-level effort (Pold et al. 2025). Likewise, screening of more than 1,000,000 genomes for DNRA reductases revealed that about 40% of ammonifiers carry at least one denitrification gene and thus a higher potential for N_2O production than consumption (Saghaï et al. 2023). A combination of metagenomics and metatranscriptomics to understand the production of denitrification intermediates revealed early *nosZ* transcription yet delayed N_2O reduction in an acidic soil (Frostegård et al. 2022), underscoring the persistent difficulty in linking community-level DNA or RNA data to process rates due to regulatory mechanisms at multiple levels (Philippot and Hallin 2005; Rocca et al. 2015). Another reason is that such approaches often overlook biotic interactions between community members. This is well illustrated by the work of He et al. (2024), who characterized a metabolic cooperation between a fermentative *Serratia* sp. and a N_2O-reducing *Desulfosporosinus* sp. isolated from an acidic soil that sustained N_2O reduction at low pH.

Similarly, biotic interactions such as viral infection may represent an additional layer of control on microbial N_2O fluxes. Viruses can infect soil nitrifiers and carry auxiliary metabolic genes associated with denitrification and nitrification (Gazitúa et al. 2021; Kim et al. 2019; Lee et al. 2024). Experimental work further demonstrated that introducing different viral loads into agricultural soils altered prokaryotic community structure and significantly affected greenhouse gas emissions, including N_2O (Huang et al. 2024). These findings identify viral regulation as a new and potentially important frontier in the microbial ecology of N_2O and more broadly in N-cycling, with phage therapy offering another potential approach to mitigate soil N_2O emissions (Song et al. 2025).

5 | Modeling of Soil N_2O Emissions

5.1 | First Generation of Process-Based Biogeochemical Models

Early experimental work on N_2O emissions focused on understanding microbial N transformations, especially nitrification and denitrification, and their sensitivity to soil moisture, temperature, oxygen (O_2) status, and substrate availability. These insights motivated the first process-based biogeochemical models (PBMs) in the 1980s–1990s, which explicitly represented soil C and N pools and fluxes rather than relying on empirical emission factors. Pioneering frameworks such as CENTURY (Parton et al. 1987; Parton 1996) and its daily version DayCent (Parton et al. 1998), as well as DNDC (Li et al. 1992; Li et al. 1994), linked N_2O production to soil mineral N, water-filled pore space, temperature, and labile C availability. These models were initially research tools, used to explore process controls and explain observed variability and episodic "hot moments" of N_2O emissions. In subsequent years, these models were refined to better differentiate between N_2O production by nitrification and denitrification based on O_2 and substrate availability. These models use either a functional relationship between soil moisture, soil respiration, and a texture-dependent index of gas diffusivity (Del Grosso et al. 2000) or explicitly calculate the partial O_2 pressure in soil layers. The latter method considers gas diffusion as it is affected by soil water content, texture, soil organic carbon (SOC), plant oxygen transport via aerenchyma (e.g., rice), and microbial and root oxygen consumption (Li et al. 2000; Kraus et al. 2015) and is referred to as the "anaerobic balloon concept," in which denitrification is restricted to the calculated anaerobic part of the soil.

As PBMs demonstrated their ability to reproduce field-level variability, the next challenge became their application in different systems, management conditions, and spatial scales. To meet this challenge, the 2000s saw the expansion of several PBMs originally focused on crop and soil dynamics, toward greater scope and complexity with the integration of biogeochemical components for simulating N_2O emissions. Models such as DSSAT (Basso et al. 2011) and APSIM (Vogeler et al. 2013) incorporated algorithms from DayCent, evolving into more comprehensive modeling frameworks with modular structures that represent soil processes, plant growth, and biosphere–atmosphere exchanges. These frameworks also enable seamless simulation of land-use and land-management changes (Haas et al. 2013; Hénault et al. 2005; Izaurralde et al. 2017). Despite these advances, models differ substantially in their representation of key processes, including the explicit versus implicit treatment of microbial dynamics, the coupling of C and N cycles, and the simulation of gas diffusion and redox conditions. Such developments, particularly the integration of algorithms from different modeling systems, necessitate rigorous calibration and re-evaluation of PBMs. At present, however, the extent of evaluation among PBMs capable of simulating N_2O emissions remains highly variable and also limited by the availability of N_2O emissions data, particularly datasets with continuous measurements.

At the same time, PBMs were increasingly used for scenario analysis of mitigation assessments at field level under varying management and climate conditions (Abalos et al. 2016; Rafique et al. 2011), and for up-scaling from field to regional or national levels (Butterbach-Bahl et al. 2004; Del Grosso et al. 2009). Model intercomparison studies highlighted both their strengths (process realism, ability to capture management effects) and weaknesses (parameter uncertainty, data requirements, structural differences) (Butterbach-Bahl et al. 2004, 2013). These structural differences represent irreducible uncertainty across models, which cannot be resolved within a single modelling framework, motivating the development of ensemble approaches.

5.2 | Use of Models for N_2O Inventories

A major conceptual shift occurred with the integration of PBMs into GHG inventories, redefining their role from pure research tools to policy-relevant accounting frameworks. In the 2000s, there was a formal recognition of PBMs for use in national GHG inventories under the IPCC inventory framework. In the 2006 IPCC Guidelines, Tier 3 methods are defined as approaches that rely on models and/or measurement systems driven by high resolution, country-specific data and that explicitly represent spatial and temporal variability beyond simple emission factors (IPCC 2006).

Within this framework, PBMs are explicitly considered eligible Tier 3 methodologies when they are well documented, rigorously evaluated, and shown to be more accurate than Tier 1 methods, and subject to appropriate quality assurance and quality control procedures. This institutionalization imposed new requirements on models, including building modelling protocols to enhance transparency, reproducibility, and consistency, fundamentally changing the priorities in modelling design. Building on these guidelines, the United States has applied a Tier 3 approach based on process-based modelling to estimate direct soil N_2O emissions in its national greenhouse gas inventory since the late 2000s (Ogle et al. 2013; US-EPA 2009, 2015).

At present, the United States remains the only country to implement a nationally operational IPCC Tier 3 approach based on PBMs for estimating direct soil N_2O emissions. Most other countries continue to rely on Tier 1 or Tier 2 emission factor–based methods, despite the widespread use of PBMs in research, scenario analysis, and mitigation assessments (Del Grosso et al. 2022; US EPA, O 2024). Nevertheless, several countries are actively developing or evaluating PBM-based approaches to support future Tier 3 methods for soil N_2O emissions in their national inventories, particularly where agricultural soils represent a key emission source. Notable examples include the application of DNDCv.CAN in Canada (Daly et al. 2025) and LandscapeDNDC in Europe (Haas et al. 2022) and Denmark (Butterbach-Bahl et al. 2025). The 2019 Refinement to the 2006 IPCC Guidelines further clarified expectations regarding transparency, evaluation and uncertainty characterization, and time series consistency for higher tier methodologies, thereby strengthening the methodological basis for PBM adoption (Ogle et al. 2020). Despite their conceptual advantages, Tier 3 PBM applications remain resource intensive and are therefore typically limited to key source categories, with resulting estimates carefully benchmarked against observations as well as lower tier inventory methods.

5.3 | Next-Generation Approaches in Process-Based N_2O Modelling

Process-based N_2O models have evolved from mechanistic research tools into operational methods for reporting N_2O emissions and are likely to become the backbone of IPCC Tier 3 inventory methodologies. Process-based models are now entering a new phase where ensemble approaches, data assimilation, and AI are used to improve accuracy and uncertainty characterization while preserving process understanding.

The use of model ensemble approaches is emerging as a robust strategy for Tier 3 estimation of N_2O emissions with PBMs (Basso et al. 2025). By integrating outputs from multiple models with differing structures, parameterizations, and representations of N cycling, ensembles may help capture structural uncertainty based on the variability in the heuristic understanding of the processes as encoded in PBMs. This approach may improve the reliability of national GHG inventories by providing more credible estimates and uncertainty bounds, while also reducing biases associated with individual models. Ensemble methods can be implemented through simple multi-model averaging (Ehrhardt et al. 2018), but other approaches may also be possible, such as Bayesian model averaging or other statistical approaches using weighting schemes based on model performance against observations (van Oijen et al. 2011; Dormann et al. 2018; Hinne et al. 2020). As computational capacity and data availability increase, ensemble approaches are expected to play a central role in advancing Tier 3 methodologies and supporting transparent, policy-relevant N_2O reporting.

As parameter uncertainty and equifinality became a major limitation in PBMs, model-data fusion (MDF) approaches emerged in the 2010s to become a key framework for improving N_2O simulations integrating observations with mechanistic representations of N cycling. Model data fusion employs approaches such as Bayesian inference and data assimilation to constrain model parameters and reduce uncertainties in microbial processes like nitrification and denitrification. By assimilating diverse datasets, including satellite remote sensing and isotopic information, MDF improves representation of spatiotemporal variability in N_2O emissions. In particular, N_2O isotopomers (e.g., site preference and $\delta^{15}N/\delta^{18}O$) provide strong constraints on simulated process partitioning and reduction efficiency, helping disentangle contributions from different production pathways and reducing equifinality (Yoshida and Toyoda 2000; Lewicka-Szczebak et al. 2020; Ibraim et al. 2020). Model data fusion also enables quantification of parameter and predictive uncertainty, supporting more robust scenario analyses. Remaining challenges include scale mismatches, uncertainties in isotopic fractionation, and balancing process detail with model complexity.

More recently, AI and machine-learning (ML) methods have been combined with PBMs to exploit the strengths of both while addressing some of their individual limitations. Pure ML approaches can reproduce complex patterns but lack extrapolative power and interpretability, whereas PBMs embed process knowledge but remain imperfect. The key challenge now is to leverage and combine the predictive power of ML while preserving process-based interpretability and extrapolation capacity of PBMs, which are necessary requirements for scenario analyses and policy applications.

Hybrid approaches with potential to improve N_2O simulations include: (i) Knowledge-Guided ML, where PBMs generate synthetic data to train ML architectures (Liu et al. 2024); (ii) Coupled PBM–ML ensembles, which can outperform either method alone in predicting N_2O fluxes at regional scales (Sharma et al. 2026); and (iii) Digital twin concepts, especially in managed systems, where AI is layered on top of mechanistic models for real-time prediction and mitigation design. These developments are increasingly relevant for future Tier 3 inventories, as they offer pathways to improved accuracy and scalability—provided transparency and reproducibility standards are maintained, and uncertainty can be quantified in a statistically robust manner (Figure 3).

6 | Gaps and Outlook

Despite three decades of substantial progress in measuring, understanding, and modelling soil N_2O emissions, key gaps continue to limit our ability to predict and mitigate emissions with confidence. These gaps increasingly lie not in isolated domains, but at the interfaces between scales, disciplines, and applications.

A central challenge remains the linking of processes across scales, from microbial pathways to field fluxes and ultimately to regional and national inventories. While molecular and isotopic approaches have revealed unprecedented detail at the biochemistry and organismic level and provided new insights on pathways involved in N_2O production and consumption, their integration into predictive frameworks remains limited. Bridging this gap requires moving beyond correlations between microbial traits and fluxes toward mechanistic representations that capture how community composition, physiological regulation, and biotic interactions regulate N_2O yields under dynamic field conditions.

A second major gap concerns the quantification of complete denitrification, particularly the partitioning between N_2O and N_2. While advances such as ^{15}N tracing and N_2O pool dilution have improved estimates of gross production and consumption, robust field-scale quantification of N_2 fluxes remains elusive. This limits our ability to constrain N_2O yields—a key variable for both process understanding and mitigation. Overcoming this challenge will require methodological innovation, including improved isotopic techniques, sensor development, and integration of multiple lines of evidence.

Third, measurement limitations continue to constrain our understanding of spatiotemporal variability. Although high-frequency and micrometeorological approaches have demonstrated the importance of emission "hot moments" and "hotspots," their widespread application remains restricted by cost, logistical complexity, and scale requirements. As a result, observational datasets are still sparse and unevenly distributed, particularly across climates, soil types, and management systems. Expanding measurement networks and leveraging

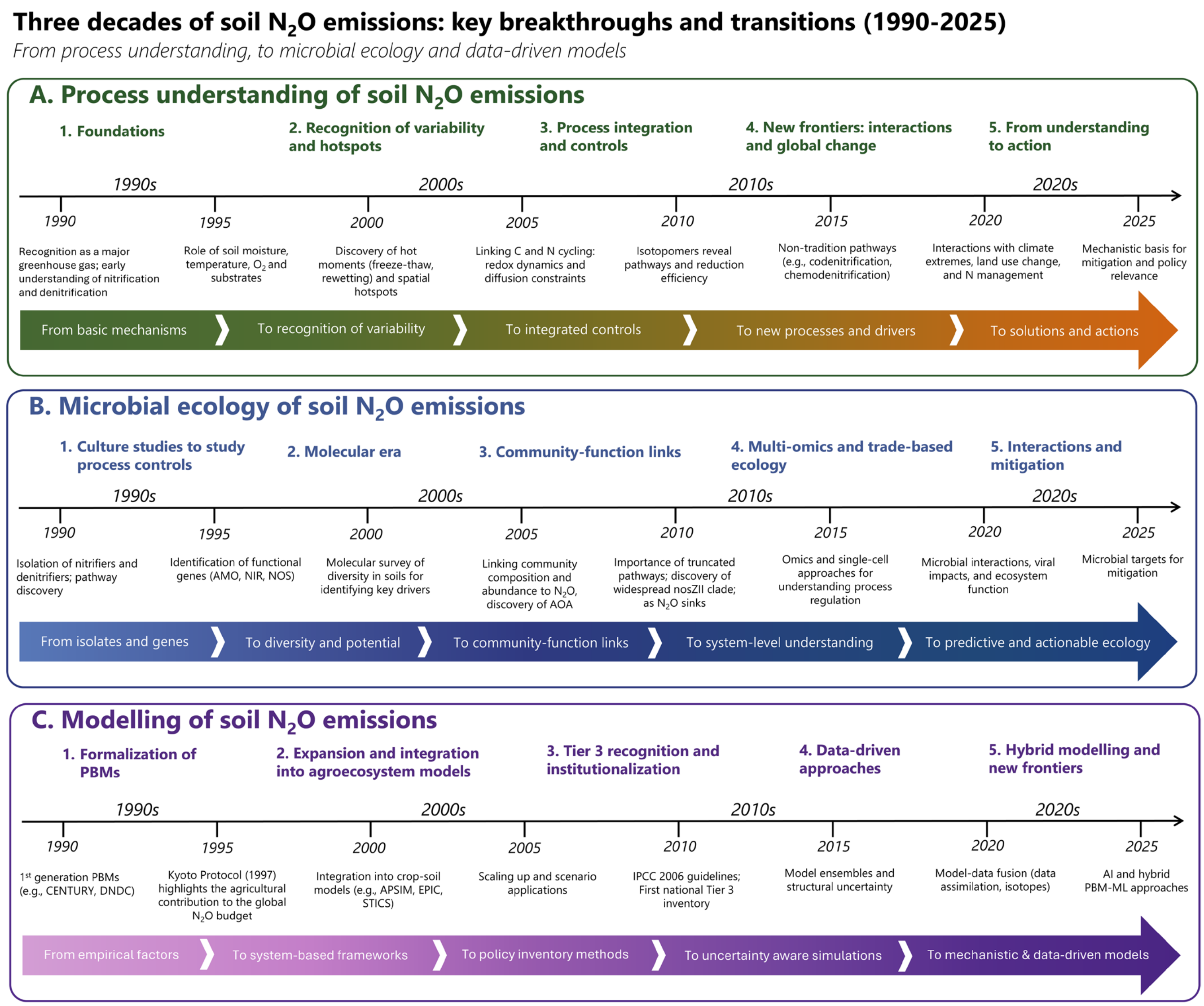

FIGURE 3 | Progress in N_2O Research and Key Breakthroughs and Transitions from 1990 to 2025 across three domains: (A) process understanding, (B) microbial ecology, and (C) modelling of soil N_2O emissions. (A) summarizes the transition from the early understanding of nitrification and denitrification as dominant N_2O-producing processes to the recognition of environmental covariates, climate extremes, land use changes, and nitrogen management as interacting controls. (B) highlights advances in microbial ecology, from culture-based identification of nitrifiers and denitrifiers to functional genes and enzymes, omics and single-cell approaches, and more recently, targeted microbial interactions for mitigation. (C) shows the evolution of how soil N_2O emissions were modelled, from early process-based biogeochemical models to their expansion into crop-soil models, use in greenhouse gas inventories, and the recent hybridization with machine learning approaches.

emerging low-cost and portable technologies will be essential to better characterize variability and reduce uncertainty.

A fourth gap lies in model uncertainty and integration. Process-based models have become central tools for both scientific understanding and GHG accounting, yet they remain affected by parameter uncertainty, structural differences, and equifinality. While model–data fusion, ensemble approaches, and hybrid process–ML frameworks offer promising pathways forward, challenges persist in reconciling model complexity with data availability, and in ensuring transparency and reproducibility for policy applications. In particular, the integration of isotopic constraints and microbial information into models remains in its infancy.

Fifth, research on N_2O is far too focused on N_2O alone. N_2O fluxes must be understood as part of the ecosystem N cycle, which is closely linked to the C cycle. Therefore, measuring only N_2O fluxes without considering the full N budget, which includes all inputs (mainly biological N fixation and N deposition in natural systems and N fertilization in managed systems) and outputs (by gaseous or hydrological pathways or harvest), carries the risk of overlooking N pollution swapping. This hinders the development and testing of mechanistic models and the identification of N_2O (and environmental N loss) mitigation options. Regarding the latter, one might consider targeting not the magnitude of N_2O emissions itself, but rather reducing yield-scaled emissions per product, specifically for N_2O and, in general, with regard to environmental N losses. One example of such a comprehensive measuring-modeling approach is the AgNUE and SmartField initiatives. These pioneering projects establish a transatlantic N (and C) monitoring platform to test N_2O mitigation efforts within the context of total N/C balance measurements for

Denmark (SmartField; Butterbach-Bahl et al. 2025) and across Europe and the United States (AgNUE 2026).

Finally, there is a critical implementation gap between scientific knowledge and scalable mitigation. Although numerous mitigation options have been identified, their effectiveness is often context-dependent and difficult to generalize across systems as technologies and approaches for temperate, rainfed agricultural systems may not apply to agricultural systems in tropical climates or in semi-arid regions. Moreover, the translation of mechanistic insights into decision-support tools, incentives, and monitoring frameworks for farmers and policymakers remains limited. Bridging this gap will require closer integration of experimental research, modelling, and socio-economic considerations, as well as the development of robust monitoring, reporting, and verification (MRV) systems.

Looking ahead, emerging approaches, including real-time isotopomer measurements, new approaches for quantifying gross N_2O production and N_2 fluxes, microbiome-informed management, and AI-enabled digital twins of agroecosystems, offer new opportunities to address these challenges. Realizing their potential depends on coordinated efforts to integrate data across scales, harmonize methodologies, and develop open, interoperable modeling frameworks that can be tested using publicly available, high-quality datasets on ecosystem N (and C) cycling and N_2O losses. In this context, the next phase of N_2O research will be defined less by incremental advances within disciplines than by our ability to synthesize across them. Achieving meaningful reductions in agricultural N_2O emissions will require not only improved process understanding but also the development of predictive, scalable, and actionable solutions.

Author Contributions

Laurent Philippot: conceptualization, investigation, writing – original draft, methodology, visualization, writing – review and editing, formal analysis, supervision. **Klaus Butterbach-Bahl:** conceptualization, writing – original draft, writing – review and editing, visualization, supervision, investigation, methodology, formal analysis. **João Serra:** conceptualization, investigation, writing – original draft, methodology, visualization, writing – review and editing, formal analysis, supervision. **Stephen Ogle:** supervision, formal analysis, methodology, visualization, writing – review and editing, writing – original draft, investigation, conceptualization. **Diego Abalos:** conceptualization, investigation, writing – original draft, methodology, visualization, writing – review and editing, formal analysis, supervision. **Whendee L. Silver:** conceptualization, investigation, writing – original draft, methodology, visualization, writing – review and editing, formal analysis, supervision.

Acknowledgements

We would like to thank Heidi McGhee and Favour Modupe Ayedun for their support with the literature and formatting of the manuscript. Klaus Butterbach-Bahl, Diego Abalos, and Stephen Ogle acknowledge the funding provided by the Novo Nordisk Foundation through the SmartField initiative (Grant NNF24SA0091172) and the Agricultural nitrogen use efficiency platform (AgNUE) (Grant NNF25SA0112735).

Funding

Klaus Butterbach-Bahl, Diego Abalos, and Stephen Ogle acknowledge the funding provided by the Novo Nordisk Foundation through the SmartField initiative (Grant NNF24SA0091172) and the Agricultural nitrogen use efficiency platform (AgNUE) (Grant NNF25SA0112735).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The authors have nothing to report.

References

Abalos, D., W. N. Smith, B. B. Grant, C. F. Drury, S. MacKell, and C. Wagner-Riddle. 2016. “Scenario Analysis of Fertilizer Management Practices for N_2O Mitigation From Corn Systems in Canada.” *Science of the Total Environment* 573: 356–365. https://doi.org/10.1016/j.scitotenv.2016.08.153.

AgNUE. 2026. “Agricultural Nitrogen Use Efficiency Platform.” https://agnue.com/.

Akiyama, H., Y. T. Hoshino, M. Itakura, et al. 2016. “Mitigation of Soil N_2O Emission by Inoculation With a Mixed Culture of Indigenous Bradyrhizobium Diazoefficiens.” *Scientific Reports* 6, no. 1: 32869. https://doi.org/10.1038/srep32869.

Bakken, L. R., L. Bergaust, B. Liu, and Å. Frostegård. 2012. “Regulation of Denitrification at the Cellular Level: A Clue to the Understanding of NO Emissions From Soils.” *Philosophical Transactions of the Royal Society, B: Biological Sciences* 367, no. 1593: 1226–1234. https://doi.org/10.1098/rstb.2011.0321.

Barton, L., B. Wolf, D. Rowlings, et al. 2015. “Sampling Frequency Affects Estimates of Annual Nitrous Oxide Fluxes.” *Scientific Reports* 5: 15912. https://doi.org/10.1038/srep15912.

Basso, B., J. T. Ritchie, F. J. Pierce, R. P. Braga, and J. W. Jones. 2011. “Simulation of Maize Yield and Nitrous Oxide Emission Under Different Nitrogen Management.” *Agricultural Systems* 104: 548–561.

Basso, B., T. Tadiello, N. Millar, et al. 2025. “A Multi Model Ensemble Reveals Net Climate Benefits From Regenerative Practices in US Midwest Croplands.” *Scientific Reports* 15, no. 1: 24881. https://doi.org/10.1038/s41598-025-08419-y.

Berks, B. C., S. J. Ferguson, J. W. B. Moir, and D. J. Richardson. 1995. “Enzymes and Associated Electron Transport Systems That Catalyse the Respiratory Reduction of Nitrogen Oxides and Oxyanions.” *Biochimica et Biophysica Acta, Bioenergetics* 1232, no. 3: 97–173. https://doi.org/10.1016/0005-2728(95)00092-5.

Blohm, A., C. Domes, and T. Frosch. 2024. “Isotopomeric Peak Assignment for N_2O in Cross-Labeling Experiments by Fiber-Enhanced Raman Multigas Spectroscopy.” *Analytical Chemistry* 96, no. 7: 2883–2892. https://doi.org/10.1021/acs.analchem.3c04236.

Bollmann, A., and R. Conrad. 1997. “Acetylene Blockage Technique Leads to Underestimation of Denitrification Rates in Oxic Soils due to Scavenging of Intermediate Nitric Oxide.” *Soil Biology & Biochemistry* 29, no. 7: 1067–1077. https://doi.org/10.1016/S0038-0717(97)00007-2.

Brenninkmeijer, C. A., and T. Rockmann. 1999. “Mass Spectrometry of the Intramolecular Nitrogen Isotope Distribution of Environmental Nitrous Oxide Using Fragment-Ion Analysis.” *Rapid Communications in Mass Spectrometry: RCM* 13, no. 20: 2028–2033. https://doi.org/10.1002/(SICI)1097-0231(19991030)13:20%3C2028::AID-RCM751%3E3.0.CO;2-J.

Brenninkmeijer, C. A., and T. Rockmann. 1999. “Mass Spectrometry of the Intramolecular Nitrogen Isotope Distribution of Environmental Nitrous Oxide Using Fragment-Ion Analysis.” *Rapid Communications in Mass Spectrometry: RCM* 13, no. 20: 2028–2033.

Breuer, L., H. Papen, and K. Butterbach-Bahl. 2000. "N_2O Emission From Tropical Forest Soils of Australia." *Journal of Geophysical Research* 105: 353–367.

Buma, B. 2024. "Including Non-Growing Season Emissions of N_2O in US Maize Could Raise Net CO_2e Emissions by 31% Annually." *Agricultural & Environmental Letters* 9: e20146. https://doi.org/10.1002/ael2.20146.

Butterbach-Bahl, K., E. M. Baggs, M. Dannenmann, R. Kiese, and S. Zechmeister-Boltenstern. 2013. "Nitrous Oxide Emissions From Soils: How Well Do We Understand the Processes and Their Controls?" *Philosophical Transactions of the Royal Society B* 368, no. 1621: 20130122. https://doi.org/10.1098/rstb.2013.0122.

Butterbach-Bahl, K., M. Kesik, P. Miehle, H. Papen, and C. Li. 2004. "Quantifying the Regional Sourcestrength of N-Trace Gases Across Agricultural and Forest Ecosystems With Process Based Models." *Plant and Soil* 260: 311–329. https://doi.org/10.1023/B:PLSO.0000030186.81212.fb.

Butterbach-Bahl, K., A. B. Værge, C. Dold, et al. 2025. "From Field Measurements to National Inventories and Smart Incentives—The SmartField Approach for Agricultural Soil N_2O Fluxes." *Environmental Research Letters* 20, no. 11: 114078. https://doi.org/10.1088/1748-9326/ae1625.

Cavigelli, M. A., and G. P. Robertson. 2001. "Role of Denitrifier Diversity in Rates of Nitrous Oxide Consumption in a Terrestrial Ecosystem." *Soil Biology & Biochemistry* 33, no. 3: 297–310. https://doi.org/10.1016/S0038-0717(00)00141-3.

Chapuis-Lardy, L., N. Wrage-Mönnig, A. Metay, J.-L. Chotte, and M. Bernoux. 2007. "Soils, a Sink for N_2O? A Review." *Global Change Biology* 13: 1–17. https://doi.org/10.1111/j.1365-2486.2006.01280.x.

Christensen, S., P. Ambus, J. R. M. Arah, et al. 1996. "Nitrous Oxide Emission From an Agricultural Field: Comparison Between Measurements by Flux Chamber and Micrometerological Techniques." *Atmospheric Environment* 30, no. 24: 4183–4190. https://doi.org/10.1016/1352-2310(96)00145-8.

Christensen, S., and J. M. Tiedje. 1990. "Brief and Vigorous N_2O Production by Soil at Spring Thaw." *Journal of Soil Science* 41, no. 1: 1–4. https://doi.org/10.1111/j.1365-2389.1990.tb00039.

Clark, M. A., N. G. G. Domingo, K. Colgan, et al. 2020. "Global Food System Emissions Could Preclude Achieving the 1.5° and 2°C Climate Change Targets." *Science* 370, no. 6517: 705–708. https://doi.org/10.1126/science.aba7357.

Clough, T. J., S. F. Ledgard, M. S. Sprosen, and M. J. Kear. 1998. "Fate of 15N Labelled Urine on Four Soil Types." *Plant and Soil* 199, no. 2: 195–203. https://doi.org/10.1023/A:1004361009708.

Cole, J. 1996. "Nitrate Reduction to Ammonia by Enteric Bacteria: Redundancy, or a Strategy for Survival During Oxygen Starvation?" *FEMS Microbiology Letters* 136, no. 1: 1–11. https://doi.org/10.1111/j.1574-6968.1996.tb08017.x.

Conrad, R. 1996. "Soil Microorganisms as Controllers of Atmospheric Trace Gases (H_2, CO, CH_4, OCS, N_2O, and NO)." *Microbiological Reviews* 60, no. 4: 609–640. https://doi.org/10.1128/mr.60.4.609-640.1996.

Corre, M. D., C. Van Kessel, and D. J. Pennock. 1996. "Landscape and Seasonal Patterns of Nitrous Oxide Emissions in a Semiarid Region." *Soil Science Society of America Journal* 60, no. 6: 1806–1815. https://doi.org/10.2136/sssaj1996.03615995006000060028x.

Daims, H., E. V. Lebedeva, P. Pjevac, et al. 2015. "Complete Nitrification by Nitrospira Bacteria." *Nature* 528, no. 7583: 504–509. https://doi.org/10.1038/nature16461.

Daly, E. J., D. Burton, G. K. MacDonald, et al. 2025. "canN2Onet—A Canadian Nitrous Oxide Collaboration Network to Meet Greenhouse Gas Emission Reduction Targets." *Environmental Research Letters* 20, no. 8: 084028. https://doi.org/10.1088/1748-9326/ade818.

Del Grosso, S. J., S. M. Ogle, C. Nevison, et al. 2022. "A Gap in Nitrous Oxide Emission Reporting Complicates Long-Term Climate Mitigation." *Proceedings of the National Academy of Sciences of the United States of America* 119, no. 31: e2200354119. https://doi.org/10.1073/pnas.2200354119.

Del Grosso, S. J., D. S. Ojima, W. J. Parton, et al. 2009. "Global Scale DAYCENT Model Analysis of Greenhouse Gas Emissions and Mitigation Strategies for Cropped Soils." *Global and Planetary Change* 67, no. 1: 44–50. https://doi.org/10.1016/j.gloplacha.2008.12.006.

Del Grosso, S. J., W. J. Parton, A. R. Mosier, D. S. Ojima, A. E. Kulmala, and S. Phongpan. 2000. "General Model for N_2O and N_2 Gas Emissions From Soils due to Dentrification." *Global Biogeochemical Cycles* 14: 1045–1060. https://doi.org/10.1029/1999GB001225.

Denk, T. R. A., J. Mohn, C. Decock, et al. 2017. "The Nitrogen Cycle: A Review of Isotope Effects and Isotope Modeling Approaches." *Soil Biology & Biochemistry* 105: 121–137. https://doi.org/10.1016/j.soilbio.2016.11.015.

Denmead, O. T. 2008. "Approaches to Measuring Fluxes of Methane and Nitrous Oxide Between Landscapes and the Atmosphere." *Plant and Soil* 309, no. 1: 5–24. https://doi.org/10.1007/s11104-008-9599-z.

Di, H. J., K. C. Cameron, J. P. Shen, et al. 2009. "Nitrification Driven by Bacteria and Not Archaea in Nitrogen-Rich Grassland Soils." *Nature Geoscience* 2, no. 9: 621–624. https://doi.org/10.1038/ngeo613.

Domeignoz-Horta, L. A., L. Philippot, C. Peyrard, et al. 2018. "Peaks of In Situ N_2O Emissions Are Influenced by N_2O-Producing and Reducing Microbial Communities Across Arable Soils." *Global Change Biology* 24: 360–370. https://doi.org/10.1111/gcb.13853.

Domeignoz-Horta, L. A., M. Putz, A. Spor, et al. 2016. "Non-Denitrifying Nitrous Oxide-Reducing Bacteria—An Effective N_2O Sink in Soil." *Soil Biology & Biochemistry* 103: 376–379. https://doi.org/10.1016/j.soilbio.2016.09.010.

Dormann, C. F., J. M. Calabrese, G. Guillera-Arroita, et al. 2018. "Model Averaging in Ecology: A Review of Bayesian, Information-Theoretic, and Tactical Approaches for Predictive Inference." *Ecological Monographs* 88, no. 4: 485–504. https://doi.org/10.1002/ecm.1309.

EDGAR. 2025. "Emissions Database for Global Atmospheric Research Community GHG Database, a Collaboration Between the European Commission, Joint Research Centre (JRC), the International Energy Agency (IEA), and Comprising IEA-EDGAR CO_2, EDGAR CH_4, EDGAR N_2O, EDGAR F-GASES Version EDGAR_2025_GHG (2025)." European Commission, JRC (Datasets). https://edgar.jrc.ec.europa.eu/report_2025#intro.

Ehrhardt, F., J.-F. Soussana, G. Bellocchi, et al. 2018. "Assessing Uncertainties in Crop and Pasture Ensemble Model Simulations of Productivity and N_2O Emissions." *Global Change Biology* 24, no. 2: e603–e616. https://doi.org/10.1111/gcb.13965.

Enwall, K., L. Philippot, and S. Hallin. 2005. "Activity and Composition of the Denitrifying Bacterial Community Respond Differently to Long-Term Fertilization." *Applied and Environmental Microbiology* 71, no. 12: 8335–8343. https://doi.org/10.1128/AEM.71.12.8335-8343.2005.

Fowler, D., K. Pilegaard, M. A. Sutton, et al. 2009. "Atmospheric Composition Change: Ecosystems–Atmosphere Interactions." *Atmospheric Environment, ACCENT Synthesis* 43, no. 33: 5193–5267. https://doi.org/10.1016/j.atmosenv.2009.07.068.

Francis, C. A., K. J. Roberts, J. M. Beman, A. E. Santoro, and B. B. Oakley. 2005. "Ubiquity and Diversity of Ammonia-Oxidizing Archaea in Water Columns and Sediments of the Ocean." *Proceedings of the National Academy of Sciences of the United States of America* 102, no. 41: 14683–14688. https://doi.org/10.1073/pnas.0506625102.

Frostegård, Å., S. H. W. Vick, N. Y. N. Lim, L. R. Bakken, and J. P. Shapleigh. 2022. "Linking Meta-Omics to the Kinetics of Denitrification Intermediates Reveals pH-Dependent Causes of N_2O Emissions and

Nitrite Accumulation in Soil." *ISME Journal* 16, no. 1: 26–37. https://doi.org/10.1038/s41396-021-01045-2.

Fuchs, K., L. Hörtnagl, N. Buchmann, W. Eugster, V. Snow, and L. Merbold. 2018. "Management Matters: Testing a Mitigation Strategy for Nitrous Oxide Emissions Using Legumes on Intensively Managed Grassland." *Biogeosciences* 15, no. 18: 5519–5543. https://doi.org/10.5194/bg-15-5519-2018.

Gazitúa, M. C., D. R. Vik, S. Roux, et al. 2021. "Potential Virus-Mediated Nitrogen Cycling in Oxygen-Depleted Oceanic Waters." *ISME Journal* 15, no. 4: 981–998. https://doi.org/10.1038/s41396-020-00825-6.

Grace, P. R., T. van der Weerden, D. W. Rowlings, et al. 2020. "Global Research Alliance N_2O Chamber Methodology Guidelines: Considerations for Automated Flux Measurement." *Journal of Environmental Quality* 49: 1126–1140. https://doi.org/10.1002/jeq2.20124.

Graf, D. R. H., C. M. Jones, and S. Hallin. 2014. "Intergenomic Comparisons Highlight Modularity of the Denitrification Pathway and Underpin the Importance of Community Structure for N_2O Emissions." *PLoS One* 9, no. 12: e114118. https://doi.org/10.1371/journal.pone.0114118.

Groffman, P. M., M. A. Altabet, J. K. Böhlke, et al. 2006. "Methods for Measuring Denitrification: Diverse Approaches to a Difficult Problem." *Ecological Applications* 16, no. 6: 2091–2122. https://doi.org/10.1890/1051-0761(2006)016[2091:mfmdda]2.0.co;2.

Groffman, P. M., K. Butterbach-Bahl, R. W. Fulweiler, et al. 2009. "Challenges to Incorporating Spatially and Temporally Explicit Phenomena (Hotspots and Hot Moments) in Denitrification Models." *Biogeochemistry* 93, no. 1: 49–77. https://doi.org/10.1007/s10533-008-9277-5.

Grüntzig, V., S. C. Nold, J. Zhou, and J. M. Tiedje. 2001. "*Pseudomonas stutzeri* Nitrite Reductase Gene Abundance in Environmental Samples Measured by Real-Time PCR." *Applied and Environmental Microbiology* 67, no. 2: 760–768. https://doi.org/10.1128/AEM.67.2.760-768.2001.

Haas, E., M. Carozzi, R. S. Massad, K. Butterbach-Bahl, and C. Scheer. 2022. "Long Term Impact of Residue Management on Soil Organic Carbon Stocks and Oxide Emissions From European Croplands." *Science of the Total Environment* 836: 154932. https://doi.org/10.1016/j.scitotenv.2022.154932.

Haas, E., S. Klatt, A. Fröhlich, et al. 2013. "LandscapeDNDC: A Process Model for Simulation of Biosphere-Atmosphere-Hydrosphere Exchange Processes at Site and Landscape Scale." *Landscape Ecology* 28: 615–636. https://doi.org/10.1007/s10980-012-9772-x.

Hallin, S., C. M. Jones, M. Schloter, and L. Philippot. 2009. "Relationship Between N-Cycling Communities and Ecosystem Functioning in a 50-Year-Old Fertilization Experiment." *ISME Journal* 3, no. 5: 597–605. https://doi.org/10.1038/ismej.2008.128.

Hallin, S., and P.-E. Lindgren. 1999. "PCR Detection of Genes Encoding Nitrite Reductase in Denitrifying Bacteria." *Applied and Environmental Microbiology* 65, no. 4: 1652–1657. https://doi.org/10.1128/AEM.65.4.1652-1657.1999.

Hallin, S., L. Philippot, F. E. Löffler, R. A. Sanford, and C. M. Jones. 2018. "Genomics and Ecology of Novel N_2O-Reducing Microorganisms." *Trends in Microbiology* 26, no. 1: 43–55. https://doi.org/10.1016/j.tim.2017.07.003.

Han, P., D. Wu, D. Sun, et al. 2021. "N_2O and NOy Production by the Comammox Bacterium *Nitrospira inopinata* in Comparison With Canonical Ammonia Oxidizers." *Water Research* 190: 116728. https://doi.org/10.1016/j.watres.2020.116728.

Havsteen, J. C., M. Fatima, S. Brunamonti, et al. 2026. "Correction and Calibration Protocol for Isotope Data via CRDS: A Study Case for N_2O and Other Isotope Systems." *Atmospheric Measurement Techniques* 19: 3557–3580. https://doi.org/10.5194/egusphere-2025-4954.

He, G., G. Chen, Y. Xie, et al. 2024. "Sustained Bacterial N_2O Reduction at Acidic pH." *Nature Communications* 15, no. 1: 4092. https://doi.org/10.1038/s41467-024-48236-x.

He, G., W. Wang, G. Chen, et al. 2025. "A Novel Bacterial Protein Family That Catalyses Nitrous Oxide Reduction." *Nature* 646, no. 8083: 152–160. https://doi.org/10.1038/s41586-025-09401-4.

Hénault, C., F. Bizouard, P. Laville, et al. 2005. "Predicting In Situ Soil N_2O Emission Using NOE Algorithm and Soil Database." *Global Change Biology* 11, no. 1: 115–127. https://doi.org/10.1111/j.1365-2486.2004.00879.x.

Hénault, C., and C. Revellin. 2011. "Inoculants of Leguminous Crops for Mitigating Soil Emissions of the Greenhouse Gas Nitrous Oxide." *Plant and Soil* 346, no. 1: 289–296. https://doi.org/10.1007/s11104-011-0820-0.

Henry, S., E. Baudoin, J. C. López-Gutiérrez, F. Martin-Laurent, A. Brauman, and L. Philippot. 2004. "Quantification of Denitrifying Bacteria in Soils by *nirK* Gene Targeted Real-Time PCR." *Journal of Microbiological Methods* 59, no. 3: 327–335. https://doi.org/10.1016/j.mimet.2004.07.002.

Henry, S., D. Bru, B. Stres, S. Hallet, and L. Philippot. 2006. "Quantitative Detection of the nosZ Gene, Encoding Nitrous Oxide Reductase, and Comparison of the Abundances of 16S rRNA, narG, nirK, and nosZ Genes in Soils." *Applied and Environmental Microbiology* 72, no. 8: 5181–5189. https://doi.org/10.1128/AEM.00231-06.

Hensen, A., U. Skiba, and D. Famulari. 2013. "Low Cost and State of the Art Methods to Measure Nitrous Oxide Emissions." *Environmental Research Letters* 8, no. 2: 025022. https://doi.org/10.1088/1748-9326/8/2/025022.

Hiis, E. G., S. H. W. Vick, L. Molstad, et al. 2024. "Unlocking Bacterial Potential to Reduce Farmland N_2O Emissions." *Nature* 630, no. 8016: 421–428. https://doi.org/10.1038/s41586-024-07464-3.

Hinne, M., Q. F. Gronau, D. van den Bergh, and E.-J. Wagenmakers. 2020. "A Conceptual Introduction to Bayesian Model Averaging." *Advances in Methods and Practices in Psychological Science* 3: 200–215. https://doi.org/10.1177/2515245919898657.

Hochstein, L. I., and G. A. Tomlinson. 1988. "The Enzymes Associated With Denitrification." *Annual Review of Microbiology* 42: 231–261. https://doi.org/10.1146/annurev.mi.42.100188.001311.

Hofer, U. 2018. "The Majority Is Uncultured." *Nature Reviews Microbiology* 16, no. 12: 716–717. https://doi.org/10.1038/s41579-018-0097-x.

Huang, X., L. P. P. Braga, C. Ding, et al. 2024. "Impact of Viruses on Prokaryotic Communities and Greenhouse Gas Emissions in Agricultural Soils." *Advanced Science* 11, no. 48: 2407223. https://doi.org/10.1002/advs.202407223.

Hutchinson, G. L., and A. R. Mosier. 1981. "Improved Soil Cover Method for Field Measurement of Nitrous Oxide Fluxes." *Soil Science Society of America Journal* 45, no. 2: 311–316. https://doi.org/10.2136/sssaj1981.03615995004500020017x.

Ibraim, E., T. Denk, B. Wolf, et al. 2020. "Denitrification Is the Main Nitrous Oxide Source Process in Grassland Soils According to Quasi-Continuous Isotopocule Analysis and Biogeochemical Modeling." *Global Biogeochemical Cycles* 34, no. 6: e2019GB006505. https://doi.org/10.1029/2019GB006505.

Igarashi, N., H. Moriyama, T. Fujiwara, Y. Fukumori, and N. Tanaka. 1997. "The 2.8 Å Structure of Hydroxylamine Oxidoreductase From a Nitrifying Chemoautotrophic Bacterium, *Nitrosomonas europaea*." *Nature Structural Biology* 4, no. 4: 276–284. https://doi.org/10.1038/nsb0497-276.

IPCC. 2006. "Institute for Global Environmental Strategies (IGES) on Behalf of the IPCC." In *IPCC Guidelines for National Greenhouse Gas Inventories*, edited by S. Eggelston, L. Buendia, K. Miwa, T. Ngara, and K. Tanabe. IPCC.

IPCC. 2019. *Refinement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories*, edited by E. Calvo Buendia, K. Tanabe, A. Kranjc, et al. IPCC.

Itakura, M., Y. Uchida, H. Akiyama, et al. 2013. "Mitigation of Nitrous Oxide Emissions From Soils by *Bradyrhizobium japonicum* Inoculation." *Nature Climate Change* 3, no. 3: 208–212. https://doi.org/10.1038/nclimate1734.

Izaurralde, R. C., W. B. McGill, J. R. Williams, et al. 2017. "Simulating Microbial Denitrification With EPIC: Model Description and Evaluation." *Ecological Modelling* 359: 349–362. https://doi.org/10.1016/j.ecolmodel.2017.06.007.

Jiang, Q. Q., and L. R. Bakken. 1999. "Nitrous Oxide Production and Methane Oxidation by Different Ammonia-Oxidizing Bacteria." *Applied and Environmental Microbiology* 65, no. 6: 2679–2684.

Jones, C. M., D. R. Graf, D. Bru, L. Philippot, and S. Hallin. 2013. "The Unaccounted Yet Abundant Nitrous Oxide-Reducing Microbial Community: A Potential Nitrous Oxide Sink." *ISME Journal* 7, no. 2: 417–426. https://doi.org/10.1038/ismej.2012.125.

Jones, C. M., A. Spor, F. P. Brennan, et al. 2014. "Recently Identified Microbial Guild Mediates Soil N_2O Sink Capacity." *Nature Climate Change* 4, no. 9: 801–805. https://doi.org/10.1038/nclimate2301.

Kim, J. G., S. J. Kim, V. Cvirkaite-Krupovic, et al. 2019. "Spindle-Shaped Viruses Infect Marine Ammonia-Oxidizing Thaumarchaea." *PNAS* 116, no. 31: 15645–15650. https://doi.org/10.1073/pnas.1905682116.

Kirkham, D., and W. V. Bartholomew. 1954. "Equations for Following Nutrient Transformations in Soil, Utilizing Tracer Data." *Soil Science Society of America Journal* 18, no. 1: 33–34. https://doi.org/10.2136/sssaj1954.03615995001800010009x.

Knowles, R. 1990. "Acetylene Inhibition Technique: Development, Advantages, and Potential Problems." In *Denitrification in Soil and Sediment*, edited by N. P. Revsbech and J. Sørensen, 151–166. Springer US. https://doi.org/10.1007/978-1-4757-9969-9_9.

Könneke, M., A. E. Bernhard, J. R. de la Torre, C. B. Walker, J. B. Waterbury, and D. A. Stahl. 2005. "Isolation of an Autotrophic Ammonia-Oxidizing Marine Archaeon." *Nature* 437, no. 7058: 543–546. https://doi.org/10.1038/nature03911.

Kostinek, J., A. Roiger, K. J. Davis, et al. 2019. "Adaptation and Performance Assessment of a Quantum and Interband Cascade Laser Spectrometer for Simultaneous Airborne In Situ Observation of CH_4, C_2H_6, CO_2, CO and N_2O." *Atmospheric Measurement Techniques* 12, no. 3: 1767–1783. https://doi.org/10.5194/amt-12-1767-2019.

Kraus, D., S. Weller, S. Klatt, et al. 2015. "A New LandscapeDNDC Biogeochemical Module to Predict CH_4 and N_2O Emissions From Lowland Rice and Upland Cropping Systems." *Plant and Soil* 386: 125–149. https://doi.org/10.1007/s11104-014-2255-x.

Kravchenko, A. N., E. R. Toosi, A. K. Guber, et al. 2017. "Hotspots of Soil N_2O Emission Enhanced Through Water Absorption by Plant Residue." *Nature Geoscience* 10, no. 7: 496–500. https://doi.org/10.1038/ngeo296.

Laughlin, R. J., and R. J. Stevens. 2002. "Evidence for Fungal Dominance of Denitrification and Codenitrification in a Grassland Soil." *Soil Science Society of America Journal* 66, no. 5: 1540–1548. https://doi.org/10.2136/sssaj2002.1540.

Laville, P., C. Jambert, P. Cellier, and R. Delmas. 1999. "Nitrous Oxide Fluxes From a Fertilised Maize Crop Using Micrometeorological and Chamber Methods." *Agricultural and Forest Meteorology* 96, no. 1: 19–38. https://doi.org/10.1016/S0168-1923(99)00054-4.

Lee, S., C. Hazard, and G. W. Nicol. 2024. "Activity of Novel Virus Families Infecting Soil Nitrifiers Is Concomitant With Host Niche Differentiation." *ISME Journal* 18, no. 1: wrae205. https://doi.org/10.1093/ismejo/wrae205.

Leininger, S., T. Urich, M. Schloter, et al. 2006. "Archaea Predominate Among Ammonia-Oxidizing Prokaryotes in Soils." *Nature* 442: 806–809. https://doi.org/10.1038/nature04983.

Lewicka-Szczebak, D., M. Piotr Lewicki, and R. Well. 2020. "N_2O Isotope Approaches for Source Partitioning of N_2O Production and Estimation of N_2O Reduction-Validation With the 15N Gas-Flux Method in Laboratory and Field Studies." *Biogeosciences* 17, no. 22: 5513–5537. https://doi.org/10.5194/bg-17-5513-2020.

Li, C., J. Aber, F. Stange, K. Butterbach-Bahl, and H. Papen. 2000. "A Process-Oriented Model of N_2O and NO Emissions From Forest Soils: 1. Model Development." *Journal of Geophysical Research: Atmospheres* 105, no. D4: 4369–4384. https://doi.org/10.1029/1999JD900949.

Li, C., S. Frolking, and T. A. Frolking. 1992. "A Model of Nitrous Oxide Evolution From Soil Driven by Rainfall Events: 1. Model Structure and Sensitivity." *Journal of Geophysical Research: Atmospheres* 97, no. D9: 9759–9776. https://doi.org/10.1029/92JD00509.

Li, C., S. Frolking, and R. Harriss. 1994. "Modeling Carbon Biogeochemistry in Agricultural Soils." *Global Biogeochemical Cycles* 8, no. 3: 237–254. https://doi.org/10.1029/94GB00767.

Liu, L., W. Zhou, K. Guan, et al. 2024. "Knowledge-Guided Machine Learning Can Improve Carbon Cycle Quantification in Agroecosystems." *Nature Communications* 15, no. 1: 357. https://doi.org/10.1038/s41467-023-43860-5.

Löscher, C. R., A. Kock, M. Könneke, J. LaRoche, H. W. Bange, and R. A. Schmitz. 2012. "Production of Oceanic Nitrous Oxide by Ammonia-Oxidizing Archaea." *Biogeosciences* 9, no. 7: 2419–2429. https://doi.org/10.5194/bg-9-2419-2012.

Ludemann, C. I., N. Wanner, P. Chivenge, et al. 2024. "A Global FAOSTAT Reference Database of Cropland Nutrient Budgets and Nutrient Use Efficiency (1961–2020): Nitrogen, Phosphorus and Potassium." *Earth System Science Data* 16: 525–541. https://doi.org/10.5194/essd-16-525-2024.

Maeda, K., A. Spor, V. Edel-Hermann, et al. 2015. "N_2O Production, a Widespread Trait in Fungi." *Scientific Reports* 5, no. 1: 9697. https://doi.org/10.1038/srep09697.

Matzner, E., and W. Borken. 2008. "Do Freeze-Thaw Events Enhance C and N Losses From Soils of Different Ecosystems? A Review." *European Journal of Soil Science* 59, no. 2: 274–284. https://doi.org/10.1111/j.1365-2389.2007.00992.x.

McTavish, H., J. A. Fuchs, and A. B. Hooper. 1993. "Sequence of the Gene Coding for Ammonia Monooxygenase in *Nitrosomonas europaea*." *Journal of Bacteriology* 175, no. 8: 2436–2444. https://doi.org/10.1128/jb.175.8.2436-2444.1993.

Merian, A., A. Silva, S. Wolf, T. Frosch, and T. Forsch. 2024. "Ultrasensitive Raman Gas Spectroscopy for Dinitrogen Sensing at the Parts-Per Billion Level." *Analytical Chemistry* 96, no. 37: 14884–14890. https://doi.org/10.1021/acs.analchem.4c02828.

Mosier, A. R., J. M. Duxbury, J. R. Freney, O. Heinemeyer, and K. Minami. 1996. "Nitrous Oxide Emissions From Agricultural Fields: Assessment, Measurement and Mitigation." *Plant and Soil* 181, no. 1: 95–108. https://doi.org/10.1007/BF00011296.

Mosier, A. R., and L. Mack. 1980. "Gas Chromatographic System for Precise, Rapid Analysis of Nitrous Oxide." *Soil Science Society of America Journal* 44, no. 5: 1121–1123. https://doi.org/10.2136/sssaj1980.03615995004400050048x.

Mulvaney, R. L., S. A. Khan, and C. S. Mulvaney. 1997. "Nitrogen Fertilizers Promote Denitrification." *Biology and Fertility of Soils* 24, no. 2: 211–220. https://doi.org/10.1007/s003740050233.

Myrold, D. D. 1990. "Measuring Denitrification in Soils Using 15N Techniques." In *Denitrification in Soil and Sediment*, edited by N. P. Revsbech and J. Sørensen, 181–198. *Springer US*. https://doi.org/10.1007/978-1-4757-9969-9_11.

Ogle, S. M., L. Buendia, K. Butterbach-Bahl, et al. 2013. "Advancing National Greenhouse Gas Inventories for Agriculture in Developing Countries: Improving Activity Data, Emission Factors and Software Technology." *Environmental Research Letters* 8, no. 1: 015030. https://doi.org/10.1088/1748-9326/8/1/015030.

Ogle, S. M., K. Butterbach-Bahl, L. Cardenas, U. Skiba, and C. Scheer. 2020. "From Research to Policy: Optimizing the Design of a National Monitoring System to Mitigate Soil Nitrous Oxide Emissions." *Current Opinion in Environmental Sustainability* 47: 28–36. https://doi.org/10.1016/j.cosust.2020.06.003.

Orellana, L. H., L. M. Rodriguez-R, S. Higgins, et al. 2014. "Detecting Nitrous Oxide Reductase (nosZ) Genes in Soil Metagenomes: Method Development and Implications for the Nitrogen Cycle." *MBio* 5, no. 3: e01193. https://doi.org/10.1128/mbio.01193-14.

Ostrom, N. E., A. Pitt, R. Sutka, et al. 2007. "Isotopologue Effects During N_2O Reduction in Soils and in Pure Cultures of Denitrifiers." *Journal of Geophysical Research: Biogeosciences* 112, no. G2: 2006JG000287. https://doi.org/10.1029/2006JG000287.

Papen, H., and K. Butterbach-Bahl. 1999. "A 3-Year Continuous Record of Nitrogen Trace Gas Fluxes From Untreated and Limed Soil of a N-Saturated Spruce and Beech Forest Ecosystem in Germany: 1. N_2O Emissions." *Journal of Geophysical Research: Atmospheres* 104, no. D15: 18487–18503. https://doi.org/10.1029/1999JD900293.

Parkin, T. B., H. F. Kaspar, A. J. Sexstone, and J. M. Tiedje. 1984. "A Gas Flow Soil Core Method to Measure Field Denitrification Rates." *Soil Biology and Biochemistry* 16, no. 4: 323–330. https://doi.org/10.1016/0038-0717(84)90026-9.

Parton, W. J. 1996. "The CENTURY Model." In *Evaluation of Soil Organic Matter Models*, edited by D. S. Powlson, P. Smith, and J. U. Smith, 283–291. *Springer*. https://doi.org/10.1007/978-3-642-61094-3_23.

Parton, W. J., M. Hartman, D. Ojima, and D. Schimel. 1998. "DAYCENT and Its Land Surface Submodel: Description and Testing." *Global and Planetary Change* 19, no. 1: 35–48. https://doi.org/10.1016/S0921-8181(98)00040-X.

Parton, W. J., D. S. Schimel, C. V. Cole, and D. S. Ojima. 1987. "Analysis of Factors Controlling Soil Organic Matter Levels in Great Plains Grasslands." *Soil Science Society of America Journal* 51, no. 5: 1173–1179. https://doi.org/10.2136/sssaj1987.03615995005100050015x.

Patra, A. K., L. Abbadie, A. Clays-Josserand, et al. 2006. "Effects of Management Regime and Plant Species on the Enzyme Activity and Genetic Structure of N-Fixing, Denitrifying and Nitrifying Bacterial Communities in Grassland Soils." *Environmental Microbiology* 8, no. 6: 1005–1016. https://doi.org/10.1111/j.1462-2920.2006.00992.x.

Philippot, L., J. Andert, C. M. Jones, D. Bru, and S. Hallin. 2011. "Importance of Denitrifiers Lacking the Genes Encoding the Nitrous Oxide Reductase for N_2O Emissions From Soil." *Global Change Biology* 17, no. 3: 1497–1504. https://doi.org/10.1111/j.1365-2486.2010.02334.x.

Philippot, L., J. Čuhel, N. P. A. Saby, et al. 2009. "Mapping Field-Scale Spatial Patterns of Size and Activity of the Denitrifier Community." *Environmental Microbiology* 11, no. 6: 1518–1526. https://doi.org/10.1111/j.1462-2920.2009.01879.x.

Philippot, L., and S. Hallin. 2005. "Finding the Missing Link Between Diversity and Activity Using Denitrifying Bacteria as a Model Functional Community." *Current Opinion in Microbiology, Ecology and Industrial Microbiology/Edited by Sergio Sánchez and Betty Olson · Techniques/Edited by Peter J Peters and Joel Swanson* 8, no. 3: 234–239. https://doi.org/10.1016/j.mib.2005.04.003.

Philippot, L., S. Piutti, F. Martin-Laurent, S. Hallet, and J. C. Germon. 2002. "Molecular Analysis of the Nitrate-Reducing Community From Unplanted and Maize-Planted Soils." *Applied and Environmental Microbiology* 68, no. 12: 6121–6128. https://doi.org/10.1128/AEM.68.12.6121-6128.2002.

Pold, G., A. Saghaï, C. M. Jones, and S. Hallin. 2025. "Denitrification Is a Community Trait With Partial Pathways Dominating Across Microbial Genomes and Biomes." *Nature Communications* 16, no. 1: 9495. https://doi.org/10.1038/s41467-025-65319-5.

Poth, M., and D. D. Focht. 1985. "15N Kinetic Analysis of N_2O Production by *Nitrosomonas europaea*: An Examination of Nitrifier Denitrification." *Applied and Environmental Microbiology* 49, no. 5: 1134–1141. https://doi.org/10.1128/aem.49.5.1134-1141.1985.

Rafique, R., M. Peichl, D. Hennessy, and G. Kiely. 2011. "Evaluating Management Effects on Nitrous Oxide Emissions From Grasslands Using the Process-Based DeNitrification–DeComposition (DNDC) Model." *Atmospheric Environment* 45, no. 33: 6029–6039. https://doi.org/10.1016/j.atmosenv.2011.07.046.

Rich, J. J., and D. D. Myrold. 2004. "Community Composition and Activities of Denitrifying Bacteria From Adjacent Agricultural Soil, Riparian Soil, and Creek Sediment in Oregon, USA." *Soil Biology & Biochemistry* 36, no. 9: 1431–1441. https://doi.org/10.1016/j.soilbio.2004.03.008Get.

Rocca, J. D., E. K. Hall, J. T. Lennon, et al. 2015. "Relationships Between Protein-Encoding Gene Abundance and Corresponding Process Are Commonly Assumed Yet Rarely Observed." *ISME Journal* 9, no. 8: 1693–1699. https://doi.org/10.1038/ismej.2014.252.

Rotthauwe, J. H., K. P. Witzel, and W. Liesack. 1997. "The Ammonia Monooxygenase Structural Gene amoA as a Functional Marker: Molecular Fine-Scale Analysis of Natural Ammonia-Oxidizing Populations." *Applied and Environmental Microbiology* 63, no. 12: 4704–4712. https://doi.org/10.1128/aem.63.12.4704-4712.1997.

Ruser, R., H. Flessa, R. Russow, G. Schmidt, F. Buegger, and J. C. Munch. 2006. "Emission of N_2O, N_2 and CO_2 From Soil Fertilized With Nitrate: Effect of Compaction, Soil Moisture and Rewetting." *Soil Biology & Biochemistry* 38, no. 2: 263–274. https://doi.org/10.1016/j.soilbio.2005.05.005.

Saghaï, A., G. Pold, C. M. Jones, and S. Hallin. 2023. "Phyloecology of Nitrate Ammonifiers and Their Importance Relative to Denitrifiers in Global Terrestrial Biomes." *Nature Communications* 14, no. 1: 8249. https://doi.org/10.1038/s41467-023-44022-3.

Salles, J. F., F. Poly, B. Schmid, and X. L. Roux. 2009. "Community Niche Predicts the Functioning of Denitrifying Bacterial Assemblages." *Ecology* 90: 3324–3332. https://doi.org/10.1890/09-0188.1.

Sameshima-Saito, R., K. Chiba, J. Hirayama, et al. 2006. "Symbiotic *Bradyrhizobium japonicum* Reduces N_2O Surrounding the Soybean Root System via Nitrous Oxide Reductase." *Applied and Environmental Microbiology* 72, no. 4: 2526–2532. https://doi.org/10.1128/AEM.72.4.2526-2532.2006.

Sanford, R. A., D. D. Wagner, Q. Wu, et al. 2012. "Unexpected Nondenitrifier Nitrous Oxide Reductase Gene Diversity and Abundance in Soils." *Proceedings of the National Academy of Sciences of the United States of America* 109, no. 48: 19709–19714. https://doi.org/10.1073/pnas.1211238109.

Santoro, A. E., C. Buchwald, M. R. McIlvin, and K. L. Casciotti. 2011. "Isotopic Signature of N_2O Produced by Marine Ammonia-Oxidizing Archaea." *Science* 333, no. 6047: 1282–1285. https://doi.org/10.1126/science.1208239.

Savage, K., R. Phillips, and E. Davidson. 2014. "High Temporal Frequency Measurements of Greenhouse Gas Emissions From Soils." *Biogeosciences* 11, no. 10: 2709–2720. https://doi.org/10.5194/bg-11-2709-201.

Serra, J. 2026. "Supplementary Data-Three Decades of Soil N_2O Research: Insights and Gaps. Figshare. Dataset." https://doi.org/10.6084/m9.figshare.32135602.v2.

Shang, Z., M. Abdalla, M. Kuhnert, et al. 2020. "Measurement of N_2O Emissions Over the Whole Year Is Necessary for Estimating Reliable

Emission Factors." *Environmental Pollution* 259: 113864. https://doi.org/10.1016/j.envpol.2019.113864.

Shang, Z., X. Cui, K. J. van Groenigen, et al. 2024. "Global Cropland Nitrous Oxide Emissions in Fallow Period Are Comparable to Growing-Season Emissions." *Global Change Biology* 30, no. 2: e17165. https://doi.org/10.1111/gcb.17165.

Sharma, P., B. Basso, A. Manuraj, et al. 2026. "Coupled Machine Learning-Ecosystem Ensemble Models Substantially Improve Predictions of Nitrous Oxide (N_2O) Fluxes From US Croplands." *Proceedings of the National Academy of Sciences of the United States of America* 123, no. 10: e2524808123. https://doi.org/10.1073/pnas.2524808123.

Shen, J., L. Zhang, Y. Zhu, J. Zhang, and J. He. 2008. "Abundance and Composition of Ammonia-Oxidizing Bacteria and Ammonia-Oxidizing Archaea Communities of an Alkaline Sandy Loam." *Environmental Microbiology* 10, no. 6: 1601–1611. https://doi.org/10.1111/j.1462-2920.2008.01578.x.

Shoun, H., S. Fushinobu, L. Jiang, S.-W. Kim, and T. Wakagi. 2012. "Fungal Denitrification and Nitric Oxide Reductase Cytochrome P450nor." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 367, no. 1593: 1186–1194. https://doi.org/10.1098/rstb.2011.0335.

Silver, W. L., D. J. Herman, and M. K. Firestone. 2001. "Dissimilatory Nitrate Reduction to Ammonium in Upland Tropical Forest Soils." *Ecology* 82, no. 9: 2410–2416. https://doi.org/10.1890/0012-9658(2001)082[B2410:DNRTAI]2.0.CO;2.

Simon, J. 2002. "Enzymology and Bioenergetics of Respiratory Nitrite Ammonification." *FEMS Microbiology Reviews* 26, no. 3: 285–309. https://doi.org/10.1111/j.1574-6976.2002.tb00616.x.

Song, W., J. Yao, Y. Fu, et al. 2025. "Viruses Mitigate Soil Nitrogen Loss and N_2O Emissions During Denitrification by Selectively Infecting Denitrifiers." *Nitrogen Cycling* 1: e004. https://doi.org/10.48130/nc-0025-0002.

Spieck, E., S. Ehrich, J. Aamand, and E. Bock. 1998. "Isolation and Immunocytochemical Location of the Nitrite-Oxidizing System in *Nitrospira moscoviensis*." *Archives of Microbiology* 169, no. 3: 225–230. https://doi.org/10.1007/s002030050565.

Stehfest, E., and L. Bouwman. 2006. "N_2O and NO Emission From Agricultural Fields and Soils Under Natural Vegetation: Summarizing Available Measurement Data and Modeling of Global Annual Emissions." *Nutrient Cycling in Agroecosystems* 74, no. 3: 207–228. https://doi.org/10.1007/s10705-006-9000-7.

Stein, L. Y. 2011. "Surveying N_2O-Producing Pathways in Bacteria." *Methods in Enzymology* 486: 131–152. https://doi.org/10.1016/B978-0-12-381294-0.00006-7.

Stevens, R. J., R. J. Laughlin, L. C. Burns, J. R. M. Arah, and R. C. Hood. 1997. "Measuring the Contributions of Nitrification and Denitrification to the Flux of Nitrous Oxide From Soil." *Soil Biology and Biochemistry* 29, no. 2: 139–151. https://doi.org/10.1016/S0038-0717(96)00303-3.

Stuchiner, E. R., and J. C. von Fischer. 2022. "Using Isotope Pool Dilution to Understand How Organic Carbon Additions Affect N_2O Consumption in Diverse Soils." *Global Change Biology* 28, no. 13: 4163–4179. https://doi.org/10.1111/gcb.16190.

Subbarao, G. V., M. Kishii, A. Bozal-Leorri, et al. 2021. "Enlisting Wild Grass Genes to Combat Nitrification in Wheat Farming: A Nature-Based Solution." *Proceedings of the National Academy of Sciences of the United States of America* 118, no. 35: e2106595118. https://doi.org/10.1073/pnas.2106595118.

Subbarao, G. V., K. Nakahara, M. P. Hurtado, et al. 2009. "Evidence for Biological Nitrification Inhibition in Brachiaria Pastures." *Proceedings of the National Academy of Sciences of the United States of America* 106, no. 41: 17302–17307. https://doi.org/10.1073/pnas.0903694106.

Takeda, N., J. Friedl, D. Rowlings, et al. 2024. "In-Situ N_2O and N_2 Data Improved N Budget Simulation With APSIM and LandscapeDNDC in Tropical Sugarcane Systems." *Agriculture, Ecosystems & Environment* 375: 109193. https://doi.org/10.1016/j.agee.2024.109193.

Tian, H., N. Pan, R. L. Thompson, et al. 2024. "Global Nitrous Oxide Budget (1980–2020)." *Earth System Science Data* 16, no. 6: 2543–2604. https://doi.org/10.5194/essd-16-2543-2024.

Tiedje, J. 1988. "Ecology of Denitrification and Dissimilatory Nitrate Reduction to Ammonium." In *Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties*, vol. 717, 179–244. Wiley.

Tiedje, J. M., S. Simkins, and P. M. Groffman. 1989. "Perspectives on Measurement of Denitrification in the Field Including Recommended Protocols for Acetylene Based Methods." *Plant and Soil* 115, no. 2: 261–284. https://doi.org/10.1007/BF02202594.

Tomlinson, G. A., L. L. Jahnke, and L. I. Hochstein. 1986. "*Halobacterium denitrificans* sp. nov., an Extremely Halophilic Denitrifying Bacterium." *International Journal of Systematic and Evolutionary Microbiology* 36, no. 1: 66–70. https://doi.org/10.1099/00207713-36-1-66.

US EPA, O. 2024. "Inventory of U.S. Greenhouse Gas Emissions and Sinks: 1990–2022 [Reports and Assessments]." https://www.epa.gov/ghgemissions/inventory-us-greenhouse-gas-emissions-and-sinks-1990-2022.

US-EPA. 2009. "Inventory of U.S. Greenhouse Gas Emissions and Sinks: 1990–2007." United States Environmental Protection Agency, EPA 430-R-09-004. Washington, D.C.

US-EPA. 2015. "Inventory of U.S. Greenhouse Gas Emissions and Sinks: 1990–2013." EPA 430-R-15-004, US-Environmental Protection Agency. Washington, D.C.

van Kessel, M. A. H. J., D. R. Speth, M. Albertsen, et al. 2015. "Complete Nitrification by a Single Microorganism." *Nature* 528: 555–559. https://doi.org/10.1038/nature16459.

van Oijen, M., D. R. Cameron, K. Butterbach-Bahl, et al. 2011. "A Bayesian Framework for Model Calibration, Comparison and Analysis: Application to Four Models for the Biogeochemistry of a Norway Spruce Forest." *Agricultural and Forest Meteorology* 151, no. 12: 1609–1621. https://doi.org/10.1016/j.agrformet.2011.06.017.

Venterea, R. T., K. A. Spokas, and J. M. Baker. 2009. "Accuracy and Precision Analysis of Chamber-Based Nitrous Oxide Gas Flux Estimates." *Soil Science Society of America Journal* 73, no. 4: 1087–1093. https://doi.org/10.2136/sssaj2008.0307.

Vogeler, I., D. Giltrap, and R. Cichota. 2013. "Comparison of APSIM and DNDC Simulations of Nitrogen Transformations and N_2O Emissions." *Science of the Total Environment, Soil as a Source & Sink for Greenhouse Gases* 465: 147–155. https://doi.org/10.1016/j.scitotenv.2012.09.021.

Wagner-Riddle, C., K. A. Congreves, D. Abalos, et al. 2017. "Globally Important Nitrous Oxide Emissions From Croplands Induced by Freeze–Thaw Cycles." *Nature Geoscience* 10, no. 4: 279–283. https://doi.org/10.1038/ngeo2907.

Wagner-Riddle, C., A. Furon, N. L. Mclaughlin, et al. 2007. "Intensive Measurement of Nitrous Oxide Emissions From a Corn–Soybean–Wheat Rotation Under Two Contrasting Management Systems Over 5 Years." *Global Change Biology* 13, no. 8: 1722–1736. https://doi.org/10.1111/j.1365-2486.2007.01388.x.

Wagner-Riddle, C., G. W. Thurtell, G. K. Kidd, E. G. Beauchamp, and R. Sweetman. 1997. "Estimates of Nitrous Oxide Emissions From Agricultural Fields Over 28 Months." *Canadian Journal of Soil Science* 77, no. 2: 135–144. https://doi.org/10.4141/S96-103.

Wallenstein, M. D., D. D. Myrold, M. Firestone, and M. Voytek. 2006. "Environmental Controls on Denitrifying Communities and Denitrification Rates: Insights From Molecular Methods." *Ecological Applications* 16, no. 6: 2143–2152. https://doi.org/10.1890/1051-0761(2006)016[2143:ecodca]2.0.co;2.

Wangari, G. E., R. M. Mwanake, T. Houska, et al. 2023. "Identifying Landscape Hot and Cold Spots of Soil Greenhouse Gas Fluxes by Combining Field Measurements and Remote Sensing Data." *Biogeosciences* 20: 5029–5067. https://doi.org/10.5194/bg-20-5029-2023.

Wankel, S. D., W. Ziebis, C. Buchwald, et al. 2017. "Evidence for Fungal and Chemodenitrification Based N_2O Flux From Nitrogen Impacted Coastal Sediments." *Nature Communications* 8: 15595. https://doi.org/10.1038/ncomms15595.

Wen, Y., Z. Chen, M. Dannenmann, et al. 2016. "Disentangling Gross N_2O Production and Consumption in Soil." *Scientific Reports* 6, no. 1: 36517. https://doi.org/10.1038/srep36517.

WMO. 2025. "WMO Greenhouse Gas Bulletin—No. 21. World Meteorological Organization." https://wmo.int/files/greenhouse-gas-bulletin-no-21.

Xiang, H., Y. Hong, J. Wu, et al. 2023. "NosZ–II–Type N_2O-Reducing Bacteria Play Dominant Roles in Determining the Release Potential of N_2O From Sediments in the Pearl River Estuary, China." *Environmental Pollution* 329: 121732. https://doi.org/10.1016/j.envpol.2023.121732.

Xu, X., Y. Liu, B. P. Singh, et al. 2020. "*Nos*Z Clade II Rather Than Clade I Determine *in Situ* N_2O Emissions With Different Fertilizer Types Under Simulated Climate Change and Its Legacy." *Soil Biology & Biochemistry* 150: 107974. https://doi.org/10.1016/j.soilbio.2020.107974.

Yang, W. H., and W. L. Silver. 2012. "Application of the N2/Ar Technique to Measuring Soil-Atmosphere N2 Fluxes." *Rapid Communications in Mass Spectrometry* 26, no. 4: 449–459. https://doi.org/10.1002/rcm.6124.

Yang, W. H., and W. L. Silver. 2016. "Gross Nitrous Oxide Production Drives Net Nitrous Oxide Fluxes Across a Salt Marsh Landscape." *Global Change Biology* 22, no. 6: 2228–2237. https://doi.org/10.1111/gcb.13203.

Yang, W. H., Y. A. Teh, and W. L. Silver. 2011. "A Test of a Field-Based 15N–Nitrous Oxide Pool Dilution Technique to Measure Gross N_2O Production in Soil." *Global Change Biology* 17, no. 12: 3577–3588. https://doi.org/10.1111/j.1365-2486.2011.02481.x.

Yankelzon, I., L. Schilling, K. Butterbach-Bahl, et al. 2025. "Lysimeter-Based Full Fertilizer 15N Balances Corroborate Direct Dinitrogen Emission Measurements Using the 15N Gas Flow Method." *Biology and Fertility of Soils* 61, no. 3: 437–454. https://doi.org/10.1007/s00374-024-01801-4.

Yoshida, N., and S. Toyoda. 2000. "Constraining the Atmospheric N_2O Budget From Intramolecular Site Preference in N_2O Isotopomers." *Nature* 405, no. 6784: 330–334. https://doi.org/10.1038/35012558.

Yu, L., E. Harris, D. Lewicka-Szczebak, et al. 2020. "What Can We Learn From N_2O Isotope Data?–Analytics, Processes and Modelling." *Rapid Communications in Mass Spectrometry* 34, no. 20: e8858. https://doi.org/10.1002/rcm.8858.

Zhou, Z. F., Y. M. Zheng, J. P. Shen, L. M. Zhang, and J. Z. He. 2011. "Response of Denitrification Genes *nirS*, *nirK*, and *nosZ* to Irrigation Water Quality in a Chinese Agricultural Soil." *Environmental Science and Pollution Research International* 18: 1644–1652. https://doi.org/10.1007/s11356-011-0482-8.

Zumft, W. G. 1997. "Cell Biology and Molecular Basis of Denitrification." *Microbiology and Molecular Biology Reviews* 61, no. 4: 533–616. https://doi.org/10.1128/mmbr.61.4.533-616.1997.