

# Global Biogeochemical Cycles®



## RESEARCH ARTICLE

10.1029/2025GB008804

## Global Natural Soil N<sub>2</sub>O Emissions: An Analysis With a Global Biogeochemistry Model From 1990 to 2023

Ye Yuan<sup>1</sup>  and Qianlai Zhuang<sup>1,2</sup> 

<sup>1</sup>Department of Earth, Atmospheric, and Planetary Science, Purdue University, West Lafayette, IN, USA, <sup>2</sup>Department of Agronomy, Purdue University, West Lafayette, IN, USA

### Key Points:

- Global undisturbed natural soil N<sub>2</sub>O emissions rose steadily (1990–2023), with tropics contributing ~70% of the total flux
- Using observed land cover (European Space Agency Climate Change Initiative) leads to 30% lower N<sub>2</sub>O estimates compared with potential vegetation due to forest fragmentation
- Majority of N<sub>2</sub>O emissions come from background processes, then N fixation, N deposition, and rock weathering

### Supporting Information:

Supporting Information may be found in the online version of this article.

### Correspondence to:

Q. Zhuang,  
qzhuang@purdue.edu

### Citation:

Yuan, Y., & Zhuang, Q. (2026). Global natural soil N<sub>2</sub>O emissions: An analysis with a global biogeochemistry model from 1990 to 2023. *Global Biogeochemical Cycles*, 40, e2025GB008804. <https://doi.org/10.1029/2025GB008804>

Received 21 AUG 2025

Accepted 25 MAR 2026

**Abstract** Atmospheric N<sub>2</sub>O, the dominant ozone-depleting substance and a potent greenhouse gas, has risen notably over recent decades. Using a process-based model, we simulated the sensitivity of N<sub>2</sub>O emissions from undisturbed natural soils to the representation of historical land-cover change from 1990 to 2023 by factoring the effects of atmospheric nitrogen deposition, biological nitrogen fixation, rock weathering, and soil uptake. Simulations based on the potential vegetation distribution data show average emissions of  $6.24 \pm 0.72$  Tg N yr<sup>-1</sup> with a significant upward trend ( $+0.021$  Tg N yr<sup>-1</sup>) from 1990 to 2023, while European Space Agency Climate Change Initiative land cover estimates were 30% lower, underscoring the sensitivity of N<sub>2</sub>O estimates to land-cover representation. Most emissions stem from background processes ( $69.8\% \pm 4.5\%$ ), followed by nitrogen fixation ( $16.3\% \pm 2.6\%$ ), atmospheric deposition ( $9.2\% \pm 1.3\%$ ), and rock weathering ( $4.7\% \pm 1.1\%$ ). The accelerating trend of N<sub>2</sub>O emissions under changing climate conditions and key uncertainties are tied to used land-cover data sets, limited observation data, and unresolved hydrological extremes.

**Plain Language Summary** Nitrous oxide (N<sub>2</sub>O) is a powerful greenhouse gas that also depletes the ozone layer. Natural ecosystems, such as forests, grasslands, and wetlands, play an important role in releasing N<sub>2</sub>O into the atmosphere. In this study, we used a process-based ecosystem model and high-resolution land cover data from satellites to estimate how much N<sub>2</sub>O has been emitted globally by natural ecosystems from 1990 to 2023. We found that tropical regions contributed most of the emissions and that human-driven land-cover changes, such as deforestation, have significantly altered the natural N<sub>2</sub>O budget. This work helps improve our understanding of how natural terrestrial ecosystems contribute to climate change and supports future efforts to monitor and reduce greenhouse gas emissions.

## 1. Introduction

Nitrous oxide (N<sub>2</sub>O) is the leading ozone-depleting substance and a potent long-lived greenhouse gas. Its atmospheric concentrations have risen from 270 ppb in 1750 to 336 ppb in 2023, with an accelerated increase since 1980 (Butterbach-Bahl et al., 2013; Tian et al., 2024).

Globally, the largest sources of N<sub>2</sub>O emissions originate from natural soil processes (Tian et al., 2024). To estimate large-scale gaseous nitrogen (N) losses from terrestrial ecosystems, researchers have developed a range of methodologies, broadly categorized into bottom-up and top-down approaches. Bottom-up methods encompass inventory-based assessments, statistical extrapolations of field measurements, mass balance techniques, and process-based modeling (Harris et al., 2022; Kroeze et al., 1999; Tian et al., 2024), while top-down approaches use atmospheric inversion techniques to infer emissions based on observed atmospheric concentrations (Thompson et al., 2019). Among bottom-up approaches, process-based modeling stands out for its ability to explicitly simulate the underlying biogeochemical processes that control N<sub>2</sub>O emissions while integrating diverse environmental and anthropogenic drivers. Their ability to resolve spatial and temporal emission patterns makes them especially useful in regions with high nitrogen inputs (Thompson et al., 2019; Tian et al., 2024).

Many current process-based land models primarily represent internal nitrogen cycling, and typically include only biological nitrogen fixation (BNF) and atmospheric nitrogen deposition as external nitrogen inputs, with deposition prescribed from atmospheric chemistry model products (Stocker et al., 2016; Vitousek et al., 2013). Models such as CLM4.5, CLM5, JSBACH, JULES-ES, LPJ-GUESS, CLASSIC, ELM, ORCHIDEE, and LPX-Bern typically rely on simplified, empirical representations of BNF and deposition (Asaadi & Arora, 2021; Davies-Barnard et al., 2020; Ghimire et al., 2016; Goll et al., 2017; Lawrence et al., 2019; Ma et al., 2022; Mathison

© 2026. The Author(s).

This is an open access article under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

et al., 2023; Tian et al., 2024; Vuichard et al., 2019; Zhu et al., 2019), while neglecting other potentially important sources such as nitrogen released through rock weathering. Recent studies have identified rock weathering as a significant and widespread source of reactive nitrogen that can contribute to N<sub>2</sub>O emissions (Houlton et al., 2018; Morford et al., 2016; Wan et al., 2021; Wooliver et al., 2019). Moreover, nitrogen losses such as ammonia (NH<sub>3</sub>) volatilization are often omitted, and mechanistic representations of both symbiotic and free-living nitrogen fixation are generally lacking (Yuan, Zhuang, Zhao, & Liu, 2025). These limitations underscore the need for more comprehensive modeling frameworks that integrate multiple nitrogen sources and loss pathways to improve the understanding of terrestrial nitrogen cycling and its contribution to N<sub>2</sub>O emissions. The spatiotemporal variability of nitrogen deposition further complicates accurate quantification of soil N<sub>2</sub>O fluxes, contributing to significant uncertainty in nitrogen–climate interactions within the Earth system. Some bottom-up N<sub>2</sub>O studies have used potential vegetation or pre-industrial land-cover maps as proxies for actual land cover, potentially overlooking the effects of contemporary land use (Tian et al., 2024). Such frameworks treat potential vegetation as a static baseline against which historical land-use and land-cover change (LUC) effects are quantified, introducing uncertainty in the representation of background N<sub>2</sub>O emissions. While large-scale initiatives such as the Global N<sub>2</sub>O Model Intercomparison Project (NMIP) employ dynamic land-cover data to account for LUC, the specific sensitivity of natural soil N<sub>2</sub>O emissions to the static versus dynamic representation of natural vegetation extent has not been systematically isolated.

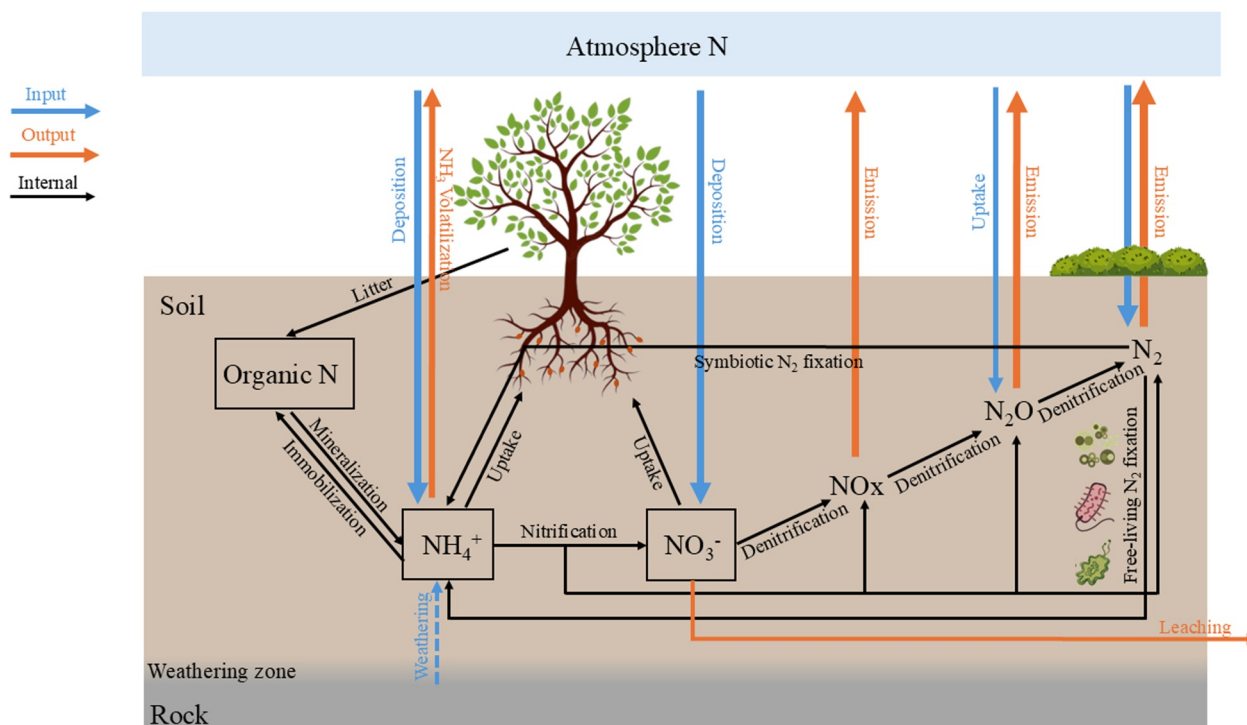
Land-cover change exerts substantial biogeochemical and biophysical impacts on climate by altering greenhouse gas emissions and surface energy balance, through shifts in albedo, evapotranspiration, and surface roughness (Liu et al., 2017; Pielke, 2005). These changes have been shown to significantly affect simulations of energy, water, and carbon fluxes in global land surface models (Harper et al., 2023). In particular, deforestation is responsible for an estimated 53%–58% of the difference between current and potential biomass stocks (Erb et al., 2018), which has substantial implications for N<sub>2</sub>O emissions from natural terrestrial ecosystems. The exclusion of actual land cover dynamics in modeling frameworks may therefore lead to significant biases in the simulation of nitrogen cycling and associated greenhouse gas fluxes.

In this study, we enhanced the Terrestrial Ecosystem Model (TEM) by integrating a more comprehensive nitrogen cycle framework that includes additional nitrogen input and output processes and integrating land cover data derived from the European Space Agency Climate Change Initiative (ESA-CCI; Copernicus Climate Change Service, 2019) to address the gap by providing a targeted, diagnostic analysis of how the assumption of a static potential vegetation baseline affects simulated natural soil N<sub>2</sub>O emissions, independent of managed lands, fertilizer application, or other anthropogenic inputs. The updated TEM was calibrated, validated, and applied to quantify N<sub>2</sub>O emissions from natural terrestrial ecosystems globally over the period 1990–2023.

## 2. Method

### 2.1. Description of TEM

The TEM is a global biogeochemical model that simulates water, carbon (C), and nitrogen (N) cycling in terrestrial ecosystems (McGuire et al., 1997; Melillo et al., 1993; Yuan, Zhuang, Zhao, & Liu, 2025; Yuan, Zhuang, Zhao, & Shurpali, 2025; Zhuang et al., 2002, 2003). The nitrogen dynamics module builds on earlier work (McGuire et al., 1997; Yuan, Zhuang, Zhao, & Shurpali, 2025; Yuan, Zhuang, Zhao, & Shurpali, 2025) and incorporates key processes including nitrogen inputs from plant litter and atmospheric deposition, biological N fixation, plant uptake, net mineralization, and nitrogen losses. The module also represents the influence of soil physical conditions on nitrification, denitrification, and N<sub>2</sub>O fluxes. TEM simulates both N<sub>2</sub>O production within soil and net N<sub>2</sub>O emission to the atmosphere. Net N<sub>2</sub>O emission is calculated as the difference between N<sub>2</sub>O production and soil N<sub>2</sub>O uptake, with gas transport represented using Fick's law (Equations S1–S12, Yuan, Zhuang, Zhao, & Shurpali, 2025). These processes follow the stoichiometric principles of soil C–N interactions. In this study, we revise the N cycling algorithms in TEM by adding nitrogen inputs from bedrock weathering and outputs via NH<sub>3</sub> volatilization (Figure 1). Inorganic N from weathering is derived from Houlton et al. (2018) and Wan et al. (2021), while NH<sub>3</sub> volatilization is simulated using process-based algorithms adopted from Montes et al. (2009) and Zhao and Zhuang (2024), which were developed and evaluated against observational data sets in their respective studies.



**Figure 1.** Structure of the nitrogen (N) cycle in Terrestrial Ecosystem Model (TEM), including three main components: external N inputs, internal cycling, and N outputs. Blue arrows indicate N input pathways, including atmospheric deposition, nitrogen release from rock weathering, biological nitrogen fixation, and atmospheric gas uptake. Orange arrows represent N output pathways, including leaching and gaseous losses (e.g.,  $\text{NH}_3$ ,  $\text{NO}_x$ ,  $\text{N}_2\text{O}$ , and  $\text{N}_2$ ). Black arrows illustrate internal nitrogen cycling within TEM, including litterfall, mineralization, immobilization, plant uptake, nitrification, and denitrification. Nitrogen leaching is represented primarily as nitrate loss because  $\text{NO}_3^-$  is highly mobile in soil water. Immobilization is represented mainly as microbial uptake of  $\text{NH}_4^+$ , reflecting the lower energetic cost of ammonium assimilation compared with nitrate reduction.

## 2.2. Model Calibration, Validation, and Uncertainties

Observational data for model calibration and evaluation were compiled from peer-reviewed literature using the keywords “ $\text{N}_2\text{O}$ ” or “nitrous oxide.” Data were obtained either directly from the authors or digitized from published figures. Only observations spanning  $\geq 4$  months were included, and screened for outliers using Q–Q plots and Z-score filtering. The final data set comprised 1,062 observations from 65 sites across diverse ecosystems, including 4 Xeric Shrubland/Woodland, 3 Mediterranean Shrubland, 7 Wet Tundra, 5 Alpine/Dry Tundra, 8 Grassland, 7 Boreal Forest, 3 Temperate Evergreen Forest, 8 Temperate Coniferous Forest, 9 Temperate Deciduous Forest, and 11 Tropical Forest sites (Figure S1 and Table S1 in Supporting Information S1).

Model calibration and validation were performed for each plant functional type (PFT) using Bayesian optimization with 5-fold stratified cross-validation to ensure balanced site representation. Calibrations were aligned exactly with the measurement periods of each site to ensure temporal consistency.  $\text{N}_2\text{O}$  emissions were aggregated to monthly rates for comparison because the model was run at a monthly time step, which corresponds to the monthly resolution of the primary input data. In addition, our study focuses on long-term trends and mean annual balances, for which a monthly time step provides an appropriate balance between computational efficiency and capturing the essential system dynamics. This temporal aggregation also helps reduce noise that may arise from daily or hourly variability.

Bayesian optimization was implemented via the Python package *scikit*, and the parameter set with the lowest RMSE across folds was selected as the best-performing set to drive TEM simulations (Table S4 in Supporting Information S1). Simulated cumulative  $\text{N}_2\text{O}$  emissions using the best performing parameter set closely matched observations, capturing site-level annual cumulative  $\text{N}_2\text{O}$  emissions across a range of biomes (Figure S2 in Supporting Information S1). This validation confirms the model's utility for estimating large-scale, long-term fluxes. However, the comparison at the annual timescale indicates that the model's ability to simulate high-frequency (e.g., daily or monthly) temporal variability is limited, consistent with the model's design and resolution.

To assess uncertainty, we conducted ensemble simulations using all five parameter sets, providing a robust estimate of parameter-driven variability.

### 2.3. Regional Extrapolation

To generate spatially and temporally explicit global  $\text{N}_2\text{O}$  emission estimates, we ran TEM at a  $0.5^\circ \times 0.5^\circ$  resolution using land cover, soil, and climate data sets from various sources (Table S5 in Supporting Information S1). Monthly climate forcing (1990–2023) was obtained from ERA5 (Hersbach et al., 2023), and atmospheric  $\text{CO}_2$  concentrations from the NOAA Global Monitoring Laboratory (NOAA Global Monitoring Laboratory, 2025). Soil bulk density and pH data were sourced from the Global Soil Bulk Density Map and Global Database of Soil Properties (Carter & Scholes, 2000; Global Soil Data Task, 2000). Nitrogen deposition ( $\text{NH}_x$  and  $\text{NO}_y$ ) was derived from ACCMIP multi-model data sets (Lamarque et al., 2013) for 1980, 2000, and 2030, with linear interpolation applied between years. The sensitivity of our results to this interpolation was tested against time-series nitrogen deposition data from Tian et al. (2022), as discussed in Section 3.6. Bedrock weathering fluxes were based on Houlton et al. (2018), assuming that all nitrogen enters the soil as  $\text{NH}_4^+$  (Houlton et al., 2018; Wan et al., 2021). These data were resampled and formatted for TEM, including model modifications to accommodate  $\text{NH}_x$ ,  $\text{NO}_y$ , and rock weathering N inputs. We spun up TEM using fixed climate forcing to reduce sensitivity to initial conditions and allow ecosystem pools to approach equilibrium for subsequent transient simulations. The model was initialized using a cyclic forcing of the first 30-year climate sequence, repeated for 5 cycles to reach a total of 150 years. This length is consistent with our previous studies (Qu et al., 2018). During spin-up, the equilibrium of the water, carbon, and nitrogen cycles was evaluated using predefined absolute tolerance thresholds.

### 2.4. Land Use and Land Cover Change

In addition to using the potential vegetation map (PVM) from Melillo et al. (1993), we incorporated land cover information from the ESA-CCI data set at 300 m resolution, spanning 1992 to 2022, to assess the impact of historical land use and land cover change on natural ecosystem  $\text{N}_2\text{O}$  emissions. Annual ESA land cover maps at 300 m resolution were aggregated by applying  $0.5^\circ \times 0.5^\circ$  resolution mask and summarizing land cover types and pixel numbers within each grid cell. Referring to the cross-walking table provided by Harper et al. (2023), ESA land cover classes were converted into fractional PFTs and subsequently mapped to the TEM-specific PFT categories (Table S2 and S3 in Supporting Information S1), allowing up to six TEM-PFTs per  $0.5^\circ \times 0.5^\circ$  grid cell. Each land cover configuration was simulated individually. Total  $\text{N}_2\text{O}$  emissions were computed by summing the emissions from each PFT multiplied by their area in each grid. This approach allowed for high-resolution representation of land cover dynamics while maintaining computational efficiency.

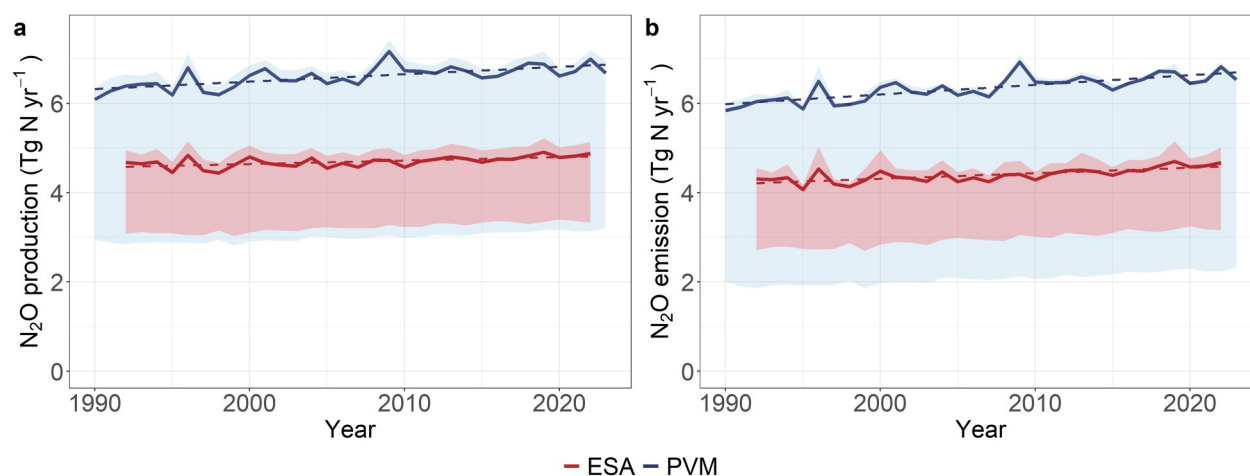
### 2.5. Statistic Analysis

Statistical analyses were conducted in R 4.3.3 (R Core Team, 2024). Trends in global  $\text{N}_2\text{O}$  fluxes were evaluated using the Mann-Kendall test and Sen's slope via the “trend” package. Differences across PFTs were assessed with one-way ANOVA and post hoc Tukey's HSD tests using the “stats” package.

## 3. Results

### 3.1. Global Estimation of Terrestrial Natural Ecosystem $\text{N}_2\text{O}$ Emissions

Global net  $\text{N}_2\text{O}$  emissions averaged  $6.24 \pm 0.72 \text{ Tg N yr}^{-1}$  from 1990 to 2023, with annual values ranging from  $5.84 \text{ Tg N yr}^{-1}$  in 1990 to a peak of  $6.92 \text{ Tg N yr}^{-1}$  in 2009. Emissions exhibited pronounced interannual variability, with peaks in 2009 and 2022 ( $6.92$  and  $6.82 \text{ Tg N yr}^{-1}$ , respectively) and a trough in 1995 ( $5.88 \text{ Tg N yr}^{-1}$ ).  $\text{N}_2\text{O}$  production followed a similar trajectory but remained consistently higher, averaging  $6.57 \pm 0.45 \text{ Tg N yr}^{-1}$ , reflecting a persistent production-emission gap (Figure 2). Model uncertainty was substantial. For the potential vegetation simulations, the lower bounds ranged from  $1.85$  to  $2.33 \text{ Tg N yr}^{-1}$ , while for the ESA-CCI based simulations they ranged from  $2.70$  to  $3.25 \text{ Tg N yr}^{-1}$ , likely reflecting limitations in parameterization and observational constraints. The upper bounds were  $5.92$ – $7.08 \text{ Tg N yr}^{-1}$  for the potential vegetation case and  $4.17$ – $5.15 \text{ Tg N yr}^{-1}$  for the ESA-based case, both closely aligned with the estimates from the best-performing parameter set. Emission estimates based on the ESA-CCI land-cover data set were systematically lower than those derived from the PVM, averaging  $4.14$ – $4.70 \text{ Tg N yr}^{-1}$ . On average, using time-series land



**Figure 2.** Global  $\text{N}_2\text{O}$  production (a) and  $\text{N}_2\text{O}$  emissions (b) under different land cover representations. “ESA” denotes estimates derived from the European Space Agency Climate Change Initiative land cover data set, while “PVM” represents estimates based on the potential vegetation map. The shaded blue and red areas indicate the range of model uncertainties resulting from parameter variability, derived from an ensemble of five parameter sets obtained through stratified cross-validation.

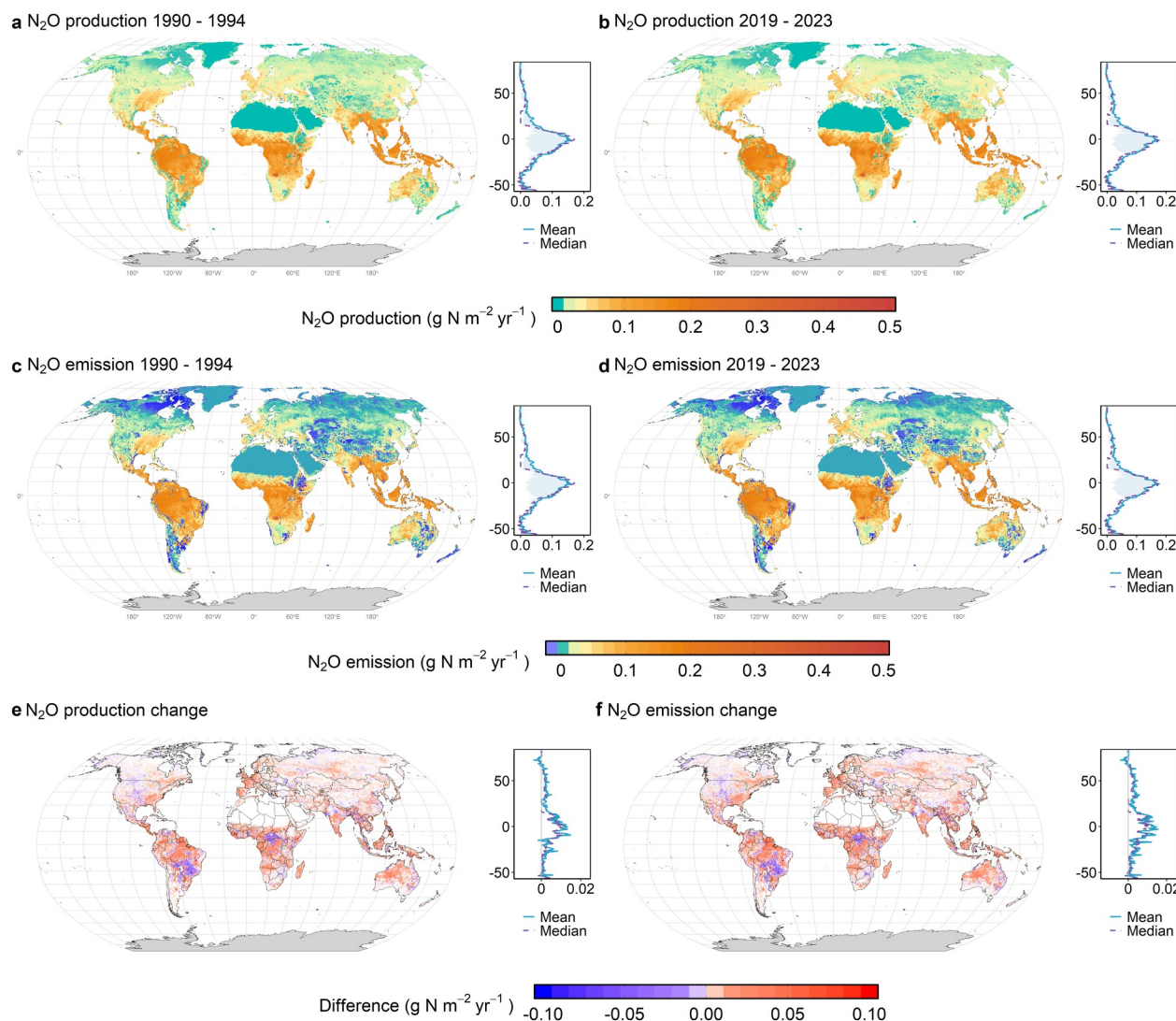
cover, the ESA-based estimates accounted for  $69.15\% \pm 1.54\%$  of net emissions and  $70.95\% \pm 1.47\%$  of  $\text{N}_2\text{O}$  production relative to PVM-based estimates, reflects historical conversion yields estimates of  $\text{N}_2\text{O}$  emissions from remaining natural soils that are 30% lower than estimates based on potential vegetation, underscoring the strong sensitivity of modeled global  $\text{N}_2\text{O}$  fluxes to land-cover representation. Mann-Kendall test revealed significant upward trends in  $\text{N}_2\text{O}$  emissions and production across all data sets. On average,  $\text{N}_2\text{O}$  emissions during 2019–2023 were  $0.6 \text{ Tg N yr}^{-1}$  (approximately 10%) higher than those during 1990–1994. Modeled  $\text{N}_2\text{O}$  production showed a strong increasing trend ( $p < 0.001$ ; Sen’s slope =  $0.016 \text{ Tg N yr}^{-1}$ , 95% CI: 0.008–0.022), while net emissions exhibited an even steeper trend ( $p < 0.001$ ; slope =  $0.021 \text{ Tg N yr}^{-1}$ , 95% CI: 0.014–0.027). Although trends from the ESA-CCI based estimates were less pronounced due to a shorter time series ( $n = 31$ ), they remained statistically significant for both production ( $p < 0.05$ ; slope =  $0.008 \text{ Tg N yr}^{-1}$ , 95% CI: 0.004–0.01) and net emissions ( $p < 0.001$ ; slope =  $0.014 \text{ Tg N yr}^{-1}$ , 95% CI: 0.009–0.018). These consistently positive and statistically robust trends across data sets confirm that global  $\text{N}_2\text{O}$  emissions have accelerated significantly from 1990 to 2023, with variation in magnitude driven primarily by land-cover inputs.

### 3.2. Spatial Distribution

Spatially, tropical regions exhibited the highest  $\text{N}_2\text{O}$  production and emissions (orange areas in panels a–d, Figure 3), whereas the northern high latitudes and global drylands showed low emissions and functioned as net  $\text{N}_2\text{O}$  sinks (blue areas in panels c–d, Figure 3). The latitudinal distribution clearly identified the tropics ( $0^\circ$ – $23.5^\circ$ ) as dominant hotspots, accounting for approximately 70% of global  $\text{N}_2\text{O}$  emissions. Between 1990–1994 and 2019–2023, both  $\text{N}_2\text{O}$  production and emissions increased globally, with the most significant growth observed in tropical and subtropical zones. However, regional variability is evident: while much of the tropics experienced rising emissions, certain areas, such as central South America and central Africa, exhibited localized declines, potentially linked to climate variability or shifts in nitrogen inputs. In contrast, emissions in temperate regions showed moderate increases, while boreal emissions remained relatively stable (Figure 3).

### 3.3. Production and Emission Variations Across Different Plant Functional Types

$\text{N}_2\text{O}$  emissions varied significantly among PFTs ( $p < 0.001$ ), with tropical forests exhibiting the highest mean emissions ( $0.114 \pm 0.006 \text{ g N m}^{-2} \text{ yr}^{-1}$ ), followed by temperate deciduous forests ( $0.038 \pm 0.003 \text{ g N m}^{-2} \text{ yr}^{-1}$ ) and grasslands ( $0.035 \pm 0.006 \text{ g N m}^{-2} \text{ yr}^{-1}$ ) (Figure S3 in Supporting Information S1). No significant differences were found between Mediterranean shrublands and alpine tundra ( $p = 0.64$ ), or between temperate evergreen forests and shrublands ( $p = 0.89$ ), suggesting similar underlying emission drivers in these ecosystems. The lowest emissions occurred in wet tundra and temperate evergreen forests, both below  $0.01 \text{ g N m}^{-2} \text{ yr}^{-1}$ .



**Figure 3.** Spatial patterns and latitudinal distributions of  $\text{N}_2\text{O}$  production and emissions based on the potential vegetation map. Panels (a) and (b) show the spatial distribution and latitudinal profile of  $\text{N}_2\text{O}$  production, averaged over two 5-year periods: 1990–1994 and 2019–2023, respectively. Panels (c) and (d) present  $\text{N}_2\text{O}$  emissions for the same time periods. Panels (e) and (f) show the changes in average  $\text{N}_2\text{O}$  production and emissions between 1990–1994 and 2019–2023, respectively (2019–2023 minus 1990–1994).

$\text{N}_2\text{O}$  production also differed significantly among PFTs ( $p < 0.001$ ). Tropical forest again showed the highest production rates ( $0.115 \pm 0.005 \text{ g N m}^{-2} \text{ yr}^{-1}$ ), approximately 9.5 times greater than in alpine tundra ( $0.011 \pm 0.0003 \text{ g N m}^{-2} \text{ yr}^{-1}$ ). Temperate deciduous forests ( $0.042 \pm 0.002 \text{ g N m}^{-2} \text{ yr}^{-1}$ ) and grassland ( $0.037 \pm 0.002 \text{ g N m}^{-2} \text{ yr}^{-1}$ ) followed. Boreal forests and temperate conifer forests had comparable production rates ( $\sim 0.018 \text{ g N m}^{-2} \text{ yr}^{-1}$ ;  $p > 0.05$ ), while Mediterranean shrublands and temperate evergreen forest were slightly lower ( $0.017\text{--}0.018 \text{ g N m}^{-2} \text{ yr}^{-1}$ ). Wet tundra and alpine tundra had the lowest  $\text{N}_2\text{O}$  production, though wet tundra emissions were marginally higher than alpine tundra ( $p < 0.05$ ). Interquartile range (IQR) values (e.g., tropical forest: 0.006; alpine tundra: 0.0003) indicate a greater variability in high-emission PFTs, suggesting stronger environmental sensitivity in tropical regions.

### 3.4. Seasonal Variability in $\text{N}_2\text{O}$ Productions and Emissions

Figure S4 in Supporting Information S1 highlights strong seasonal contrasts in  $\text{N}_2\text{O}$  fluxes between tropical and temperate regions. Tropical ecosystems emitted more  $\text{N}_2\text{O}$  annually ( $0.008 \pm 0.0006 \text{ g N m}^{-2} \text{ yr}^{-1}$ ) than temperate ecosystems ( $0.002 \pm 0.001 \text{ g N m}^{-2} \text{ yr}^{-1}$ ), with emissions peaking in October and showing low

seasonal variation ( $CV = 7\%$ ). In contrast, temperate regions displayed pronounced seasonality, with summer peaks (July:  $0.004 \text{ g N m}^{-2} \text{ yr}^{-1}$  in the Northern Hemisphere; January:  $0.005 \text{ g N m}^{-2} \text{ yr}^{-1}$  in the Southern Hemisphere) and winter lows (December:  $0.0004 \text{ g N m}^{-2} \text{ yr}^{-1}$  in the Northern Hemisphere; July:  $0.001 \text{ g N m}^{-2} \text{ yr}^{-1}$  in the Southern Hemisphere). This resulted in seasonal amplitudes of nearly 9.7-fold in the Northern Hemisphere and 4.7-fold in the Southern Hemisphere, with high variability ( $CV = 83\%$  and  $37\%$ , respectively). The tropical-to-temperate emission ratio ranged from 1.92 during summer to 19.37 in winter, underscoring the disproportionate contribution of tropical systems to the global  $\text{N}_2\text{O}$  budget, particularly outside the growing season.

### 3.5. The Effects of Actual Land Use and Land Cover Change

The natural area represented in the ESA-CCI land cover data set covers  $79.33 \pm 0.14\%$  of that in the potential vegetation map (PVM;  $133,561,319 \text{ km}^2$ ). This discrepancy likely accounts for the lower  $\text{N}_2\text{O}$  estimates in ESA-based simulations, yielding only  $69.15 \pm 1.54\%$  of net emissions and  $70.95 \pm 1.47\%$  of production compared to PVM-based results. Among PFTs, only grassland and alpine tundra show greater spatial extent in ESA-CCI relative to the TEM PVM; all other PFTs exhibit reduced coverage. The most significant decline is observed in tropical forests, the PFT with the highest  $\text{N}_2\text{O}$  emission rates that occupies just  $44.5 \pm 0.54\%$  of their potential extent in the ESA-CCI data set. This substantial reduction largely explains the lower  $\text{N}_2\text{O}$  fluxes in ESA-based simulations. This finding aligns with Harper et al. (2023), who demonstrated that incorporating ESA-CCI-based PFT maps into the ORCHIDEE model significantly altered energy, water, and carbon fluxes, particularly in areas where woody vegetation was replaced by grasslands or bare soil, patterns that mirror our findings for nitrogen fluxes. Notably,  $\text{N}_2\text{O}$  emission hotspots in tropical regions frequently coincide with zones of rapid land-use change and agricultural expansion. Their persistence and spatial expansion over recent decades underscore the growing influence of tropical ecosystems on the global  $\text{N}_2\text{O}$  budget and highlight their vulnerability to anthropogenic pressures.

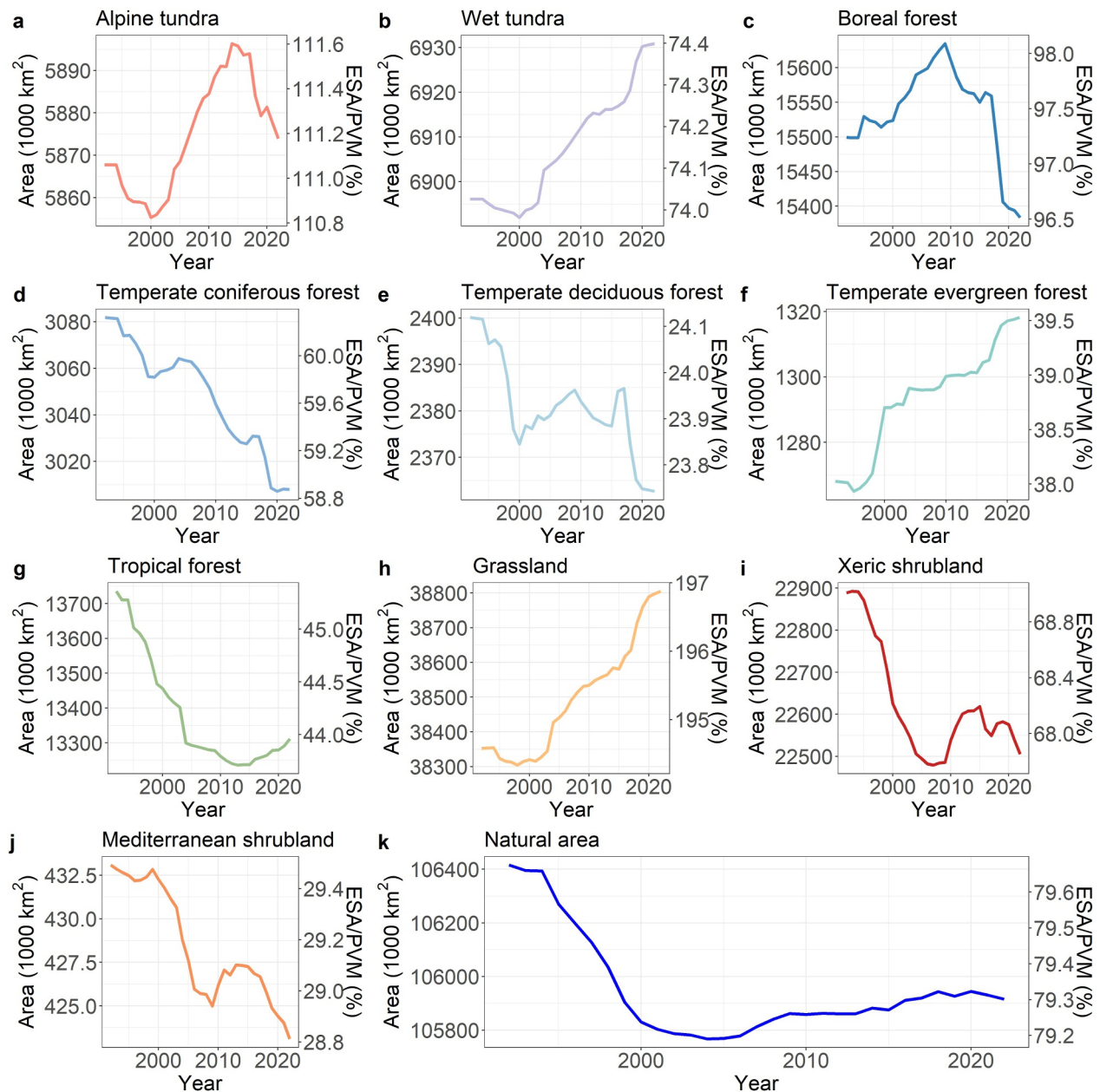
In addition to tropical forests, temperate deciduous forest ( $23.93\% \pm 0.10\%$ ), temperate conifer forest ( $59.66\% \pm 0.45\%$ ), and temperate evergreen forest ( $38.78 \pm 0.49\%$ ) also show substantial area reductions relative to PVM estimates (Figure 4). These likely reflect widespread deforestation and land conversion, resulting in fragmented landscapes interspersed with grasslands, croplands, pastures, and urban areas (Ma et al., 2023). The use of finer-scale land cover products such as ESA-CCI improves the representation of sub-grid heterogeneity at  $0.5^\circ \times 0.5^\circ$  resolution, offering a more realistic alternative to the PVM's assumption of homogeneous vegetation.

### 3.6. Effects of N Fixation, Deposition, Weathering, and $\text{N}_2\text{O}$ Uptake

To isolate the contributions of different nitrogen inputs to  $\text{N}_2\text{O}$  emissions, we conducted a sequential exclusion experiment, removing BNF, atmospheric deposition, and nitrogen weathering from the model. The decomposition analysis revealed that background emissions accounted for the largest portion ( $4.63 \pm 0.15 \text{ Tg N yr}^{-1}$ ;  $69.8 \pm 4.5\%$ ), followed by nitrogen fixation ( $1.05 \pm 0.15 \text{ Tg N yr}^{-1}$ ;  $16.3\% \pm 2.6\%$ ), deposition ( $0.60 \pm 0.04 \text{ Tg N yr}^{-1}$ ;  $9.2\% \pm 1.3\%$ ), and weathering ( $0.30 \pm 0.04 \text{ Tg N yr}^{-1}$ ;  $4.7\% \pm 1.1\%$ ) (Figures 5a and 5b). These findings align with previous estimates, such as Cen et al. (2024), who reported that nitrogen deposition accounted for approximately 9.0% of global forest soil  $\text{N}_2\text{O}$  emissions. A similar pattern was observed for  $\text{N}_2\text{O}$  production, with background processes dominating ( $80.4\% \pm 2.9\%$ ) and smaller but non-negligible contributions from nitrogen fixation ( $9.3\% \pm 1.9\%$ ) and deposition ( $7.7 \pm 1.6\%$ ).

While deposition and weathering remained stable, the contribution from nitrogen fixation rose significantly, from 13.7% (1990–1994) to 16.4% (2020–2023;  $p < 0.001$ , Sen's slope =  $+0.08\% \text{ yr}^{-1}$ ). Conversely,  $\text{N}_2\text{O}$  uptake declined from 6.4% to 3.4% over the same period ( $p < 0.001$ , Sen's slope =  $-0.006\% \text{ yr}^{-1}$ ), likely due to reduced atmospheric-soil concentration gradients as soil  $\text{N}_2\text{O}$  levels increased.

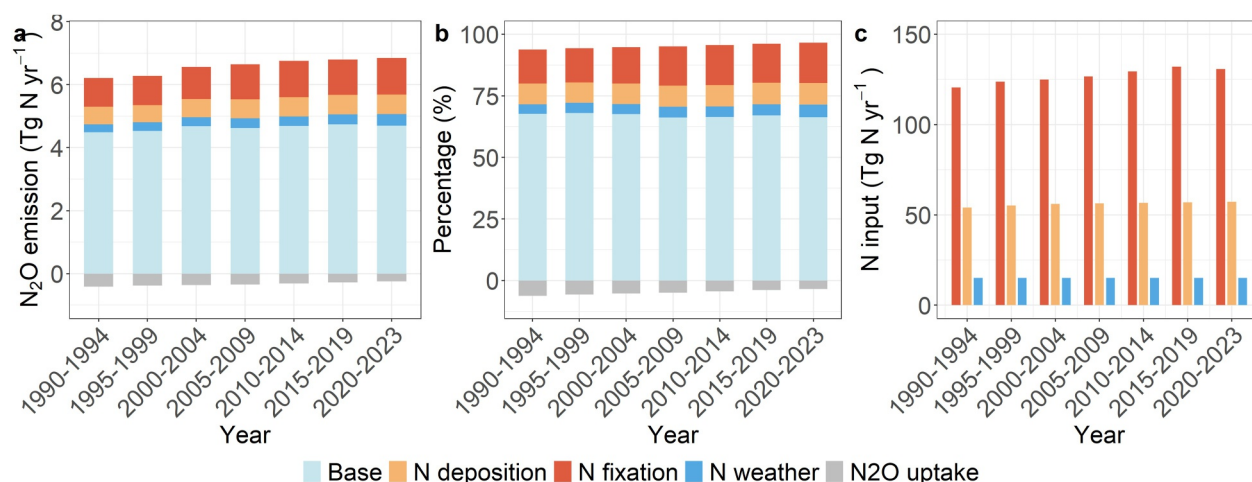
To evaluate the influence of land-cover representation on the attribution results, we conducted additional simulations using ESA-CCI based land-cover data and repeated the factor-contribution analysis. The decomposition analysis shows that background emissions account for the largest share ( $2.8 \pm 0.06 \text{ Tg N yr}^{-1}$ ;  $63.8 \pm 0.9\%$ ), followed by BNF ( $1.03 \pm 0.07 \text{ Tg N yr}^{-1}$ ;  $23.3\% \pm 1.01\%$ ), atmospheric deposition ( $0.42 \pm 0.01 \text{ Tg N yr}^{-1}$ ;  $9.5\% \pm 0.35\%$ ), and rock weathering ( $0.15 \pm 0.02 \text{ Tg N yr}^{-1}$ ;  $3.38\% \pm 0.44\%$ ) (Figure S7 in Supporting Information S1). In comparison, the ESA-based simulations yielded lower contributions for background emissions but a higher relative contribution from BNF, although their rank order remained unchanged. Overall, while



**Figure 4.** Temporal changes in ESA-derived plant functional type (PFT) areas from 1992 to 2022, based on European Space Agency Climate Change Initiative land cover data were converted to TEM-specific PFT classifications. Panels (a–j) show changes in the area and percentage of individual PFTs, while panel (k) displays the total natural area and the ratio of ESA-derived area to that from the potential vegetation map.

absolute magnitudes differ substantially between the two land-cover representations, primarily due to differences in the extent of natural land area, the relative ranking of drivers is consistent. This indicates that land-cover representation strongly affects total emission magnitude but exerts limited influence on the hierarchical importance of individual nitrogen inputs at the global scale. Consequently, the attribution of dominant controls on natural soil  $N_2O$  emissions remain robust across land-cover assumptions.

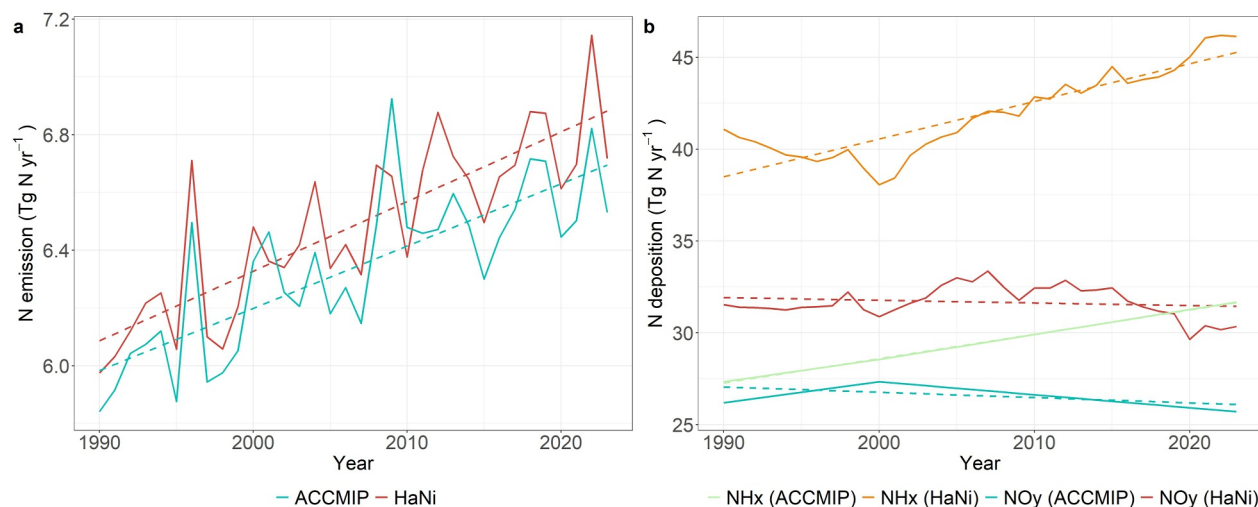
Several annual time-series nitrogen deposition data sets are available, including those from Ackerman et al. (2019) and Tian et al. (2022). To evaluate the potential impact of using linearly interpolated ACCMIP deposition data, we compared simulated  $N_2O$  emissions with an alternative simulation driven by the time-series HaNi deposition data set from Tian et al. (2022). The comparison shows that global natural soil  $N_2O$  emissions simulated with the HaNi data set are  $0.15 \pm 0.12 \text{ Tg N yr}^{-1}$  ( $2.3 \pm 1.8\%$ ) higher than those using the interpolated



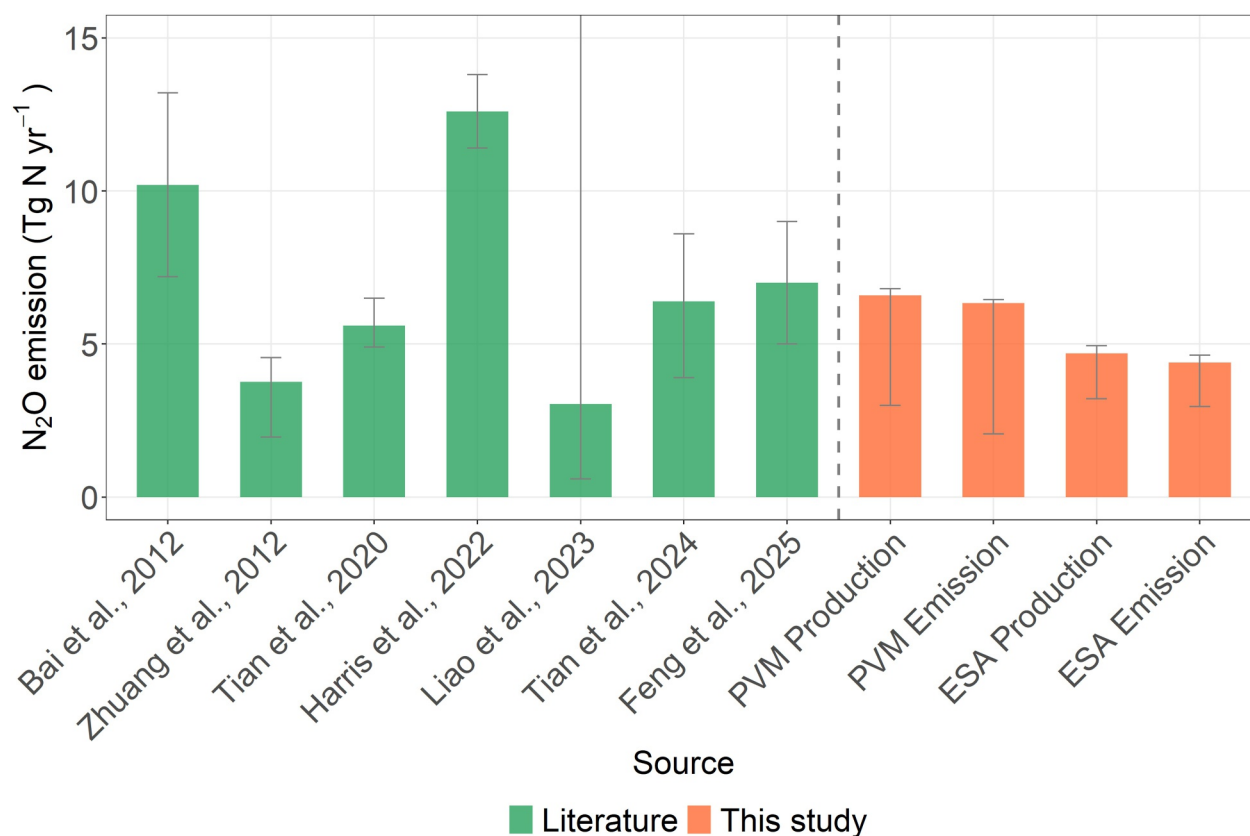
**Figure 5.** Panel (a) shows 5-year average simulated background  $N_2O$  emissions and contributions from biological nitrogen fixation, atmospheric nitrogen deposition, nitrogen weathering, and  $N_2O$  uptake based on the potential vegetation map. Panel (b) presents the corresponding percentage contributions of each component to total emissions. Panel (c) represents annual N inputs of nitrogen fixation, deposition and rock weathering ( $Tg\ N\ yr^{-1}$ ).

ACCMIP data (Figure 6). Under the HaNi forcing, the simulated contributions from  $NO_y$  and  $NH_x$  deposition are  $5.1 \pm 0.76\ Tg\ N\ yr^{-1}$  ( $19.2\% \pm 2.9\%$ ) and  $12.43 \pm 1.26\ Tg\ N\ yr^{-1}$  ( $42.17\% \pm 3.6\%$ ) higher than those from ACCMIP, respectively.

This limited sensitivity arises because, at the global scale and in natural ecosystems, the interannual variability in nitrogen deposition is relatively small compared with its strong spatial gradients during the simulation period. As a result, the interpolation approach captures the dominant signal controlling long-term integrated  $N_2O$  emissions. This robustness also reflects the integrated long-term nature of soil nitrogen cycling, in which deposition represents second fraction of total nitrogen inputs, less than 10% compared with background emission and BNF. Consequently, differences in the temporal resolution of the deposition data sets have only a minor influence on the simulated global  $N_2O$  budget.



**Figure 6.** Temporal trends of global  $N_2O$  emissions simulated using the HaNi and ACCMIP nitrogen deposition data sets for the period 1990–2023 (a), and corresponding trends in  $NO_y$  and  $NH_x$  deposition from the two data sets (b).



**Figure 7.** Comparison of annual N<sub>2</sub>O emission estimates (Tg N yr<sup>-1</sup>) from literature studies and model simulations. Error bars indicate reported uncertainty ranges.

## 4. Discussion

### 4.1. Comparison With Other Studies

Our model estimates are broadly consistent with recent literature when compared under comparable land-cover assumptions (Figure 7), although some discrepancies remain. Simulations using the ESA-CCI land cover yielded global N<sub>2</sub>O production and emissions of 4.69 [3.21–4.95] and 4.40 [2.96–4.64] Tg N yr<sup>-1</sup>, respectively. These values fall toward the lower end of previously reported ranges but remain within the overall uncertainty bounds of recent estimates based on contemporary land-use and land-cover conditions, including Tian et al. (2020, 2024; 5.6 [4.9–6.5] Tg N yr<sup>-1</sup> and 6.4 [3.9–8.6] Tg N yr<sup>-1</sup>), but lower than estimates from Feng et al. (2025; 7.0 ± 2.0 Tg N yr<sup>-1</sup>), Bai et al. (2012; 10.2 ± 3.0 Tg N yr<sup>-1</sup>), and Harris et al. (2022; 12.6 ± 1.2 Tg N yr<sup>-1</sup>), and higher than the machine learning studies from Zhuang et al. (2012; 3.77 [1.96–4.56] Tg N yr<sup>-1</sup>) and Liao et al. (2023; 3 [0.6–18.3] Tg N yr<sup>-1</sup>). We calculated a global natural soil N<sub>2</sub>O estimate by multiplying their reported mean emission rates by the global areas of forests and grasslands using a mean emission rate of 0.039 g N m<sup>-2</sup> yr<sup>-1</sup> for forests (range: 0.009–0.184 g N m<sup>-2</sup> yr<sup>-1</sup>) and 0.045 g N m<sup>-2</sup> yr<sup>-1</sup> for grasslands (range: 0.006–0.336 g N m<sup>-2</sup> yr<sup>-1</sup>). Using a global forest area of 4.14 billion hectares (FAO, 2025a) and a grassland area of 3.2 billion hectares (FAO, 2025b), this yields approximately 3 Tg N yr<sup>-1</sup> (range: 0.6–18.3 Tg N yr<sup>-1</sup>). The PVM-based simulations produced higher values (6.59 and 6.34 Tg N yr<sup>-1</sup>), representing potential emissions under idealized natural vegetation. The difference between the ESA-CCI and PVM-based estimates highlights the strong sensitivity of modeled N<sub>2</sub>O fluxes to land-cover representation. Recent studies generally report global natural soil N<sub>2</sub>O emissions in the range of 4–9 Tg N yr<sup>-1</sup> (e.g., Feng et al., 2025; Tian et al., 2020, 2024). Our ESA-CCI-based estimates fall toward the lower end of this range, while the PVM-based results are closer to the mid-to-upper portion. These differences largely reflect contrasting land-cover representations: the ESA-CCI based simulations account for historical land-use changes and exclude managed lands, whereas the PVM-based simulations represent potential natural vegetation under idealized conditions.

In addition, these discrepancies likely stem from differences in model parameterization, input data, and representation of key biogeochemical processes. Higher estimates from Bai et al. (2012) and Harris et al. (2022), which are based on isotope modeling, highlight methodological differences across approaches. The lower estimates reported by Zhuang et al. (2012) and Liao et al. (2023) may be attributed to differences in temporal coverage or that process-based models capture additional climate sensitivities not fully represented in the observationally trained machine learning models.

In our simulation, tropical regions contributed 70% of global N<sub>2</sub>O emissions, consistent with the latitudinal gradient reported by Tian et al. (2019), which identified a single tropical peak accounting for 69% of global emissions. This pattern is also supported by the artificial neural network study by Zhuang et al. (2012). Our estimated tropical emission rate ( $0.114 \pm 0.006 \text{ g N m}^{-2} \text{ yr}^{-1}$ ) closely matches Tian et al.'s value ( $0.11 \pm 0.02 \text{ g N m}^{-2} \text{ yr}^{-1}$ ) but is approximately half the estimate reported by Feng et al. (2025;  $0.21\text{--}0.28 \text{ g N m}^{-2} \text{ yr}^{-1}$ ). For grasslands, our simulation yielded much lower N<sub>2</sub>O emissions ( $0.035 \pm 0.006 \text{ g N m}^{-2} \text{ yr}^{-1}$ ) compared to Feng et al.'s range of  $0.08\text{--}0.17 \text{ g N m}^{-2} \text{ yr}^{-1}$  across C<sub>3</sub> and C<sub>4</sub> grasses, about half the lower bound of their estimate. However, our estimate is closer to the value reported by Liao et al. (2023), which is  $0.045 (0.006\text{--}0.336) \text{ g N m}^{-2} \text{ yr}^{-1}$  for grasslands.

#### 4.2. Limitations and Future Directions

This study is subject to several limitations. First, model calibration and validation are restricted by the limited spatiotemporal coverage of observational data sets, particularly in dryland regions such as Africa and the Middle East (Figure S1 in Supporting Information S1). Expanding monitoring networks in these areas would improve the representation of key drivers, such as soil moisture, temperature, and nitrogen availability that regulate N<sub>2</sub>O emissions. Increased use of isotopic techniques (e.g.,  $\delta^{15}\text{N}$ ) could also help distinguish microbial sources of N<sub>2</sub>O, thereby enhancing our mechanistic understanding of the underlying processes. Strengthening the observational infrastructure would reduce model uncertainties and improve nitrogen cycle representation.

Second, the model's  $0.5^\circ \times 0.5^\circ$  spatial resolution may not sufficiently capture the substantial heterogeneity in landscape features and soil properties such as soil organic carbon and total nitrogen stocks. While we used 300-m ESA-CCI land cover data for improved spatial detail, other inputs such as meteorology, soil, and topography remained uniform within each grid. Higher-resolution modeling could enhance N<sub>2</sub>O estimates but at high computational cost. Therefore, developing innovative approaches to balance spatial resolution and computational efficiency is essential for future studies. Promising directions include knowledge-guided machine learning methods (Liu et al., 2022) and machine learning-based meta-models (Aderole et al., 2025), which can approximate complex biogeochemical processes at lower computational expense.

Third, using a monthly time step constrains the model's ability to capture short-term, high-impact events such as extreme precipitation, which are increasingly recognized as important drivers of elevated N<sub>2</sub>O emissions due to their strong influence on soil moisture dynamics and microbial processes (Chen et al., 2025). Such events can disrupt hydrological regimes and biogeochemical cycles and boost greenhouse gas emissions (Hutchins et al., 2019; Vereecken et al., 2022). Moreover, reanalysis data sets such as ERA5 have demonstrated considerable errors in representing extreme precipitation, especially in tropical regions and China (Jiang et al., 2021; Lavers et al., 2022). These inaccuracies in meteorological inputs may further compound uncertainties in N<sub>2</sub>O emission estimates, underscoring the need for bias-corrected climate forcing data sets in earth system modeling.

Fourth, our model does not account for perturbed fluxes resulting from land-cover change, which can cause significant time-varying shifts in N<sub>2</sub>O emissions. The reduction in the calculated natural source is, however, accompanied by a large and well-documented increase in anthropogenic emissions from agricultural soils following land conversion. For instance, converting tropical forests to agriculture typically triggers a short-term emission pulse lasting up to 5 years, followed by a decline below those of the original forest, especially if pastures degrade or croplands are unfertilized (Davidson & Artaxo, 2004; Meurer et al., 2016). When abandoned farmland transitions to secondary forest, emissions rise slowly but usually stay below those of mature forests or fertilized fields (Davidson et al., 2007; Sullivan et al., 2019). Tian et al. (2024) modeled both the short-term increase in emissions from the post-deforestation pulse effect and the long-term decrease associated with the reduction of mature forest area. The combined effect of these transitions leads to a net reduction of approximately  $0.5 \text{ Tg N}_2\text{O yr}^{-1}$ , equivalent to 7.7% of total natural soil N<sub>2</sub>O emissions. These dynamic effects remain unaccounted for in our framework and should be integrated into future modeling to better capture land-use impacts on N<sub>2</sub>O fluxes.

## 5. Conclusion

This study identifies a persistent rise in global N<sub>2</sub>O emissions from 1990 to 2023 (+0.021 Tg N yr<sup>-1</sup>,  $p < 0.001$ ), with tropical ecosystems accounting for 70% of the total flux. Emissions based on remote sensing land cover (ESA-CCI) were 30% lower than those using potential vegetation, highlighting how land use change, especially the reduction of tropical forests to 44.5% of their potential extent, leads to significant underestimation in global natural soil N<sub>2</sub>O emissions. This quantification underscores that the contribution of natural ecosystems to the contemporary N<sub>2</sub>O budget is declining not only due to changes in climate and N deposition but also due to their reduced physical extent. Accurately tracking this declining natural baseline is essential for attributing changes in the global budget to specific anthropogenic drivers (e.g., fertilizer use vs. land cover change).

Despite robust trends, uncertainties remain, stemming from limited observational data, simplifications in model structure, and biases in meteorological and land cover inputs. The coarse spatial and temporal resolution used in this study likely mask short-term pulse emissions linked to extreme weather events. Future modeling efforts would benefit higher-resolution simulations to better capture fine-scale variability and extreme event impacts. Addressing these limitations requires (a) higher-resolution modeling to capture fine-scale and event-driven variability and finer-resolution models to resolve short-term pulse emissions, (b) expanded use of isotopic techniques to attribute microbial pathways, and (c) integration of dynamic, time-varying land-use and land-cover changes into Earth system models.

## Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

## Availability Statement

The TEM codes, outputs, and samples of the running directory can be accessed via the Purdue University Research Repository (Yuan & Zhuang, 2025).

## Acknowledgments

This research has been supported by the National Science Foundation (Grant 1802832).

## References

- Ackerman, D., Millet, D. B., & Chen, X. (2019). Global estimates of inorganic nitrogen deposition across four decades. *Global Biogeochemical Cycles*, 33(1), 100–107. <https://doi.org/10.1029/2018gb005990>
- Aderere, M. O., Srivastava, A. K., Butterbach-Bahl, K., & Rahimi, J. (2025). Integrating machine learning with agroecosystem modelling: Current state and future challenges. *European Journal of Agronomy*, 168, 127610. <https://doi.org/10.1016/j.eja.2025.127610>
- Asaadi, A., & Arora, V. K. (2021). Implementation of nitrogen cycle in the CLASSIC land model. *Biogeosciences*, 18(2), 669–706. <https://doi.org/10.5194/bg-18-669-2021>
- Bai, E., Houlton, B. Z., & Wang, Y. P. (2012). Isotopic identification of nitrogen hotspots across natural terrestrial ecosystems. *Biogeosciences*, 9(8), 3287–3304. <https://doi.org/10.5194/bg-9-3287-2012>
- Butterbach-Bahl, K., Baggs, E. M., Dannenmann, M., Kiese, R., & Zechmeister-Boltenstern, S. (2013). Nitrous oxide emissions from soils: How well do we understand the processes and their controls? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1621), 20130122. <https://doi.org/10.1098/rstb.2013.0122>
- Carter, A. J., & Scholes, R. J. (2000). SoilData v2.0: Generating a global database of soil properties [Dataset]. *CSIR Environmentek, Pretoria, South Africa*. <https://www.fao.org/soils-portal/data-hub/soil-maps-and-databases/harmonized-world-soil-database-v20/en/>
- Cen, X., Müller, C., Kang, X., Zhou, X., Zhang, J., Yu, G., & He, N. (2024). Nitrogen deposition contributed to a global increase in nitrous oxide emissions from forest soils. *Communications Earth & Environment*, 5(1), 532. <https://doi.org/10.1038/s43247-024-01647-6>
- Chen, Z., Zhang, N., Li, Y., Xu, S., Liu, Y., Miao, S., & Ding, W. (2025). Extreme rainfall amplified the stimulatory effects of soil carbon availability on N<sub>2</sub>O emissions. *Global Change Biology*, 31(4), e70164. <https://doi.org/10.1111/gcb.70164>
- Copernicus Climate Change Service, Climate Data Store. (2019). Land cover classification gridded maps from 1992 to present derived from satellite observation [Dataset]. *Copernicus Climate Change Service (C3S) Climate Data Store (CDS)*. <https://doi.org/10.24381/cds.006f2c9a>
- Davidson, E. A., & Artaxo, P. (2004). Globally significant changes in biological processes of the Amazon Basin: Results of the large-scale Biosphere–Atmosphere experiment. *Global Change Biology*, 10(5), 519–529. <https://doi.org/10.1111/j.1529-8817.2003.00779.x>
- Davidson, E. A., De Carvalho, C. J. R., Figueira, A. M., Ishida, F. Y., Ometto, J. P. H. B., Nardoto, G. B., et al. (2007). Recuperation of nitrogen cycling in Amazonian forests following agricultural abandonment. *Nature*, 447(7147), 995–998. <https://doi.org/10.1038/nature05900>
- Davies-Barnard, T., Meyerholt, J., Zaehle, S., Friedlingstein, P., Brovkin, V., Fan, Y., et al. (2020). Nitrogen cycling in CMIP6 land surface models: Progress and limitations. *Biogeosciences*, 17(20), 5129–5148. <https://doi.org/10.5194/bg-17-5129-2020>
- Erb, K.-H., Kastner, T., Plutzer, C., Bais, A. L. S., Carvalhais, N., Fetzel, T., et al. (2018). Unexpectedly large impact of forest management and grazing on global vegetation biomass. *Nature*, 553(7686), 73–76. <https://doi.org/10.1038/nature25138>
- FAO. (2025a). Global forest resources assessment 2025: Main report. *Food and Agriculture Organization of the United Nations*. <https://doi.org/10.4060/cd6709en>
- FAO. (2025b). Land statistics 2001–2023: Global, regional and country trends (FAOSTAT Analytical Briefs, No. 107). *Food and Agriculture Organization of the United Nations*. <https://doi.org/10.4060/cd5765en>
- Feng, M., Liu, G., Wang, Y., Chang, J., & Peng, S. (2025). Isotopic partitioning of gaseous nitrogen emissions of natural terrestrial ecosystems. *Environmental Research Letters*, 20(3), 034053. <https://doi.org/10.1088/1748-9326/adbb06>

- Ghimire, B., Riley, W. J., Koven, C. D., Mu, M., & Randerson, J. T. (2016). Representing leaf and root physiological traits in CLM improves global carbon and nitrogen cycling predictions. *Journal of Advances in Modeling Earth Systems*, 8(2), 598–613. <https://doi.org/10.1002/2015MS000538>
- GLOBAL SOIL DATA TASK. (2000). Global gridded surfaces of selected soil characteristics (IGBP-DIS) [Dataset]. *ORNL Distributed Active Archive Center*. <https://doi.org/10.3334/ORNLDAAAC/569>
- Goll, D. S., Winkler, A. J., Raddatz, T., Dong, N., Prentice, I. C., Ciais, P., & Brovkin, V. (2017). Carbon–nitrogen interactions in idealized simulations with JSBACH (version 3.10). *Geoscientific Model Development*, 10(5), 2009–2030. <https://doi.org/10.5194/gmd-10-2009-2017>
- Harper, K. L., Lamarche, C., Hartley, A., Peylin, P., Ottlé, C., Bastrikov, V., et al. (2023). A 29-year time series of annual 300 m resolution plant-functional-type maps for climate models. *Earth System Science Data*, 15(3), 1465–1499. <https://doi.org/10.5194/essd-15-1465-2023>
- Harris, E., Yu, L., Wang, Y.-P., Mohn, J., Henne, S., Bai, E., et al. (2022). Warming and redistribution of nitrogen inputs drive an increase in terrestrial nitrous oxide emission factor. *Nature Communications*, 13(1), 4310. <https://doi.org/10.1038/s41467-022-32001-z>
- Hersbach, H., Bell, B., Berrisford, P., Biavati, G., Horányi, A., Muñoz Sabater, J., et al. (2023). ERA5 monthly averaged data on single levels from 1940 to present [Dataset]. *Copernicus Climate Change Service (C3S) Climate Data Store (CDS)*. <https://doi.org/10.24381/cds.fl7050d7>
- Houlton, B. Z., Morford, S. L., & Dahlgren, R. A. (2018). Convergent evidence for widespread rock nitrogen sources in Earth's surface environment. *Science*, 360(6384), 58–62. <https://doi.org/10.1126/science.aan4399>
- Hutchins, D. A., Jansson, J. K., Remais, J. V., Rich, V. I., Singh, B. K., & Trivedi, P. (2019). Climate change microbiology—Problems and perspectives. *Nature Reviews Microbiology*, 17(6), 391–396. <https://doi.org/10.1038/s41579-019-0178-5>
- Jiang, Q., Li, W., Fan, Z., He, X., Sun, W., Chen, S., et al. (2021). Evaluation of the ERA5 reanalysis precipitation dataset over Chinese Mainland. *Journal of Hydrology*, 595, 125660. <https://doi.org/10.1016/j.jhydrol.2020.125660>
- Kroeze, C., Mosier, A., & Bouwman, L. (1999). Closing the global N<sub>2</sub>O budget: A retrospective analysis 1500–1994. *Global Biogeochemical Cycles*, 13(1), 1–8. <https://doi.org/10.1029/1998GB900020>
- Lamarque, J.-F., Dentener, F., McConnell, J., Ro, C.-U., Shaw, M., Vet, R., et al. (2013). Multi-model mean nitrogen and sulfur deposition from the Atmospheric Chemistry and Climate Model Intercomparison Project (ACCMIP): Evaluation of historical and projected future changes. *Atmospheric Chemistry and Physics*, 13(16), 7997–8018. <https://doi.org/10.5194/acp-13-7997-2013>
- Lavers, D. A., Simmons, A., Vamborg, F., & Rodwell, M. J. (2022). An evaluation of ERA5 precipitation for climate monitoring. *Quarterly Journal of the Royal Meteorological Society*, 148(748), 3152–3165. <https://doi.org/10.1002/qj.4351>
- Lawrence, D. M., Fisher, R. A., Koven, C. D., Oleson, K. W., Swenson, S. C., Bonan, G., et al. (2019). The community land model version 5: Description of new features, benchmarking, and impact of forcing uncertainty. *Journal of Advances in Modeling Earth Systems*, 11(12), 4245–4287. <https://doi.org/10.1029/2018MS001583>
- Liao, J., Huang, Y., Li, Z., & Niu, S. (2023). Data-driven modeling on the global annual soil nitrous oxide emissions: Spatial pattern and attributes. *Science of the Total Environment*, 903, 166472. <https://doi.org/10.1016/j.scitotenv.2023.166472>
- Liu, L., Xu, S., Tang, J., Guan, K., Griffith, T. J., Erickson, M. D., et al. (2022). KGML-ag: A modeling framework of knowledge-guided machine learning to simulate agroecosystems: A case study of estimating N<sub>2</sub>O emission using data from mesocosm experiments. *Geoscientific Model Development*, 15(7), 2839–2858. <https://doi.org/10.5194/gmd-15-2839-2022>
- Liu, S., Bond-Lamberty, B., Boysen, L. R., Ford, J. D., Fox, A., Gallo, K., et al. (2017). Grand challenges in understanding the interplay of climate and land changes. *Earth Interactions*, 21(2), 1–43. <https://doi.org/10.1175/EI-D-16-0012.1>
- Ma, J., Olin, S., Anthoni, P., Rabin, S. S., Bayer, A. D., Nyawira, S. S., & Arneeth, A. (2022). Modeling symbiotic biological nitrogen fixation in grain legumes globally with LPJ-GUESS (v4.0, r10285). *Geoscientific Model Development*, 15(2), 815–839. <https://doi.org/10.5194/gmd-15-815-2022>
- Ma, L., Hurr, G., Tang, H., Lamb, R., Lister, A., Chini, L., et al. (2023). Spatial heterogeneity of global forest aboveground carbon stocks and fluxes constrained by spaceborne LiDAR data and mechanistic modeling. *Global Change Biology*, 29(12), 3378–3394. <https://doi.org/10.1111/gcb.16682>
- Mathison, C., Burke, E., Hartley, A. J., Kelley, D. I., Burton, C., Robertson, E., et al. (2023). Description and evaluation of the JULES-ES set-up for ISMIP2b. *Geoscientific Model Development*, 16(14), 4249–4264. <https://doi.org/10.5194/gmd-16-4249-2023>
- McGuire, A. D., Melillo, J. M., Kicklighter, D. W., Pan, Y., Xiao, X., Helfrich, J., et al. (1997). Equilibrium responses of global net primary production and carbon storage to doubled atmospheric carbon dioxide: Sensitivity to changes in vegetation nitrogen concentration. *Global Biogeochemical Cycles*, 11(2), 173–189. <https://doi.org/10.1029/97GB00059>
- Melillo, J. M., McGuire, A. D., Kicklighter, D. W., Moore, B., Vorosmarty, C. J., & Schloss, A. L. (1993). Global climate change and terrestrial net primary production. *Nature*, 363(6426), 234–240. <https://doi.org/10.1038/363234a0>
- Meurer, K. H. E., Franko, U., Stange, C. F., Rosa, J. D., Madari, B. E., & Jungkunst, H. F. (2016). Direct nitrous oxide (N<sub>2</sub>O) fluxes from soils under different land use in Brazil—A critical review. *Environmental Research Letters*, 11(2), 023001. <https://doi.org/10.1088/1748-9326/11/2/023001>
- Montes, F., Rotz, C. A., & Chaoui, H. (2009). Process modeling of ammonia volatilization from ammonium solution and manure surfaces: A review with recommended models. *Transactions of the ASABE*, 52(5), 1707–1720. <https://doi.org/10.13031/2013.29133>
- Morford, S. L., Houlton, B. Z., & Dahlgren, R. A. (2016). Direct quantification of long-term rock nitrogen inputs to temperate forest ecosystems. *Ecology*, 97(1), 54–64. <https://doi.org/10.1890/15-0501.1>
- NOAA Global Monitoring Laboratory. (2025). *Trends in atmospheric carbon dioxide*. National Oceanic and Atmospheric Administration. Retrieved from <https://gml.noaa.gov/ccgg/trends/>
- Pielke, R. A. (2005). Land use and climate change. *Science*, 310(5754), 1625–1626. <https://doi.org/10.1126/science.1120529>
- Qu, Y., Maksyutov, S., & Zhuang, Q. (2018). Technical Note: An efficient method for accelerating the spin-up process for process-based biogeochemistry models. *Biogeosciences*, 15(13), 3967–3973. <https://doi.org/10.5194/bg-15-3967-2018>
- R Core Team. (2024). *R: A language and environment for statistical computing*. Version 4.3.3. R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Stocker, B. D., Prentice, I. C., Cornell, S. E., Davies-Barnard, T., Finzi, A. C., Franklin, O., et al. (2016). Terrestrial nitrogen cycling in Earth system models revisited. *New Phytologist*, 210(4), 1165–1168. <https://doi.org/10.1111/nph.13997>
- Sullivan, B. W., Nifong, R. L., Nasto, M. K., Alvarez-Clare, S., Dencker, C. M., Soper, F. M., et al. (2019). Biogeochemical recuperation of lowland tropical forest during succession. *Ecology*, 100(4), e02641. <https://doi.org/10.1002/ecy.2641>
- Thompson, R. L., Lassaletta, L., Patra, P. K., Wilson, C., Wells, K. C., Gressent, A., et al. (2019). Acceleration of global N<sub>2</sub>O emissions seen from two decades of atmospheric inversion. *Nature Climate Change*, 9(12), 993–998. <https://doi.org/10.1038/s41558-019-0613-7>
- Tian, H., Bian, Z., Shi, H., Qin, X., Pan, N., Lu, C., et al. (2022). History of anthropogenic Nitrogen inputs (HaNi) to the terrestrial biosphere: A 5 arcmin resolution annual dataset from 1860 to 2019. *Earth System Science Data*, 14(10), 4551–4568. <https://doi.org/10.5194/essd-14-4551-2022>

- Tian, H., Pan, N., Thompson, R. L., Canadell, J. G., Suntharalingam, P., Regnier, P., et al. (2024). Global nitrous oxide budget (1980–2020). *Earth System Science Data*, 16(6), 2543–2604. <https://doi.org/10.5194/essd-16-2543-2024>
- Tian, H., Xu, R., Canadell, J. G., Thompson, R. L., Winiwarer, W., Suntharalingam, P., et al. (2020). A comprehensive quantification of global nitrous oxide sources and sinks. *Nature*, 586(7828), 248–256. <https://doi.org/10.1038/s41586-020-2780-0>
- Tian, H., Yang, J., Xu, R., Lu, C., Canadell, J. G., Davidson, E. A., et al. (2019). Global soil nitrous oxide emissions since the preindustrial era estimated by an ensemble of terrestrial biosphere models: Magnitude, attribution, and uncertainty. *Global Change Biology*, 25(2), 640–659. <https://doi.org/10.1111/gcb.14514>
- Vereecken, H., Amelung, W., Bauke, S. L., Bogen, H., Brüggemann, N., Montzka, C., et al. (2022). Soil hydrology in the Earth system. *Nature Reviews Earth & Environment*, 3(9), 573–587. <https://doi.org/10.1038/s43017-022-00324-6>
- Vitousek, P. M., Menge, D. N. L., Reed, S. C., & Cleveland, C. C. (2013). Biological nitrogen fixation: Rates, patterns and ecological controls in terrestrial ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1621), 20130119. <https://doi.org/10.1098/rstb.2013.0119>
- Vuichard, N., Messina, P., Luyssaert, S., Guenet, B., Zaehle, S., Ghattas, J., et al. (2019). Accounting for carbon and nitrogen interactions in the global terrestrial ecosystem model ORCHIDEE (trunk version, rev 4999): Multi-scale evaluation of gross primary production. *Geoscientific Model Development*, 12(11), 4751–4779. <https://doi.org/10.5194/gmd-12-4751-2019>
- Wan, J., Tokunaga, T. K., Brown, W., Newman, A. W., Dong, W., Bill, M., et al. (2021). Bedrock weathering contributes to subsurface reactive nitrogen and nitrous oxide emissions. *Nature Geoscience*, 14(4), 217–224. <https://doi.org/10.1038/s41561-021-00717-0>
- Wooliver, R., Pellegrini, A. F. A., Waring, B., Houlton, B. Z., Averill, C., Schimel, J., et al. (2019). Changing perspectives on terrestrial nitrogen cycling: The importance of weathering and evolved resource-use traits for understanding ecosystem responses to global change. *Functional Ecology*, 33(10), 1818–1829. <https://doi.org/10.1111/1365-2435.13377>
- Yuan, Y., & Zhuang, Q. (2025). Quantification of global terrestrial natural ecosystem nitrous oxide emissions from 1990 to 2023 with an improved nitrogen cycle modeling framework [Dataset]. <https://doi.org/10.4231/G9QM-9V96>
- Yuan, Y., Zhuang, Q., Zhao, B., & Liu, L. (2025). Improving the quantification of global free-living and symbiotic nitrogen fixation in natural terrestrial ecosystems: Present-day estimates and 21st century projections. *Environmental Research Letters*, 20(12), 124005. <https://doi.org/10.1088/1748-9326/ae198c>
- Yuan, Y., Zhuang, Q., Zhao, B., & Shurpali, N. (2025). Impacts of permafrost degradation on N<sub>2</sub>O emissions from natural terrestrial ecosystems in northern high latitudes: A process-based biogeochemistry model analysis. *Global Biogeochemical Cycles*, 39(4), e2024GB008439. <https://doi.org/10.1029/2024GB008439>
- Zhao, B., & Zhuang, Q. (2024). Nitrogen cycling feedback on carbon dynamics leads to greater CH<sub>4</sub> emissions and weaker cooling effect of Northern peatlands. *Global Biogeochemical Cycles*, 38(4), e2023GB007978. <https://doi.org/10.1029/2023GB007978>
- Zhu, Q., Riley, W. J., Tang, J., Collier, N., Hoffman, F. M., Yang, X., & Bisht, G. (2019). Representing nitrogen, phosphorus, and carbon interactions in the E3SM land model: Development and global benchmarking. *Journal of Advances in Modeling Earth Systems*, 11(7), 2238–2258. <https://doi.org/10.1029/2018MS001571>
- Zhuang, Q., Lu, Y., & Chen, M. (2012). An inventory of global N<sub>2</sub>O emissions from the soils of natural terrestrial ecosystems. *Atmospheric Environment*, 47, 66–75. <https://doi.org/10.1016/j.atmosenv.2011.11.036>
- Zhuang, Q., McGuire, A. D., Melillo, J. M., Clein, J. S., Dargaville, R. J., Kicklighter, D. W., et al. (2003). Carbon cycling in extratropical terrestrial ecosystems of the Northern Hemisphere during the 20th century: A modeling analysis of the influences of soil thermal dynamics. *Tellus B: Chemical and Physical Meteorology*, 55(3), 751–776. <https://doi.org/10.1034/j.1600-0889.2003.00060.x>
- Zhuang, Q., McGuire, A. D., O'Neill, K. P., Harden, J. W., Romanovsky, V. E., & Yarie, J. (2002). Modeling soil thermal and carbon dynamics of a fire chronosequence in interior Alaska. *Journal of Geophysical Research*, 107(D1). <https://doi.org/10.1029/2001JD001244>

## References From the Supporting Information

- Aini, F. K., Hergoualc'h, K., Smith, J. U., & Verchot, L. (2015). Nitrous oxide emissions along a gradient of tropical forest disturbance on mineral soils in Sumatra. *Agriculture, Ecosystems & Environment*, 214, 107–117. <https://doi.org/10.1016/j.agee.2015.08.022>
- Alvarez, C. R., Rimski-Korsakov, H., Lupi, A. M., Romaniuk, R. I., Cosentino, V. R. N., Ciarlo, E. A., & Steinbach, H. S. (2020). Soil nitrous oxide emissions from Eucalyptus plantation in Argentina. *Forest Ecology and Management*, 473, 118301. <https://doi.org/10.1016/j.foreco.2020.118301>
- Bell, M. J., Cloy, J. M., Topp, C. F. E., Ball, B. C., Bagnall, A., Rees, R. M., & Chadwick, D. R. (2016). Quantifying N<sub>2</sub>O emissions from intensive grassland production: The role of synthetic fertilizer type, application rate, timing and nitrification inhibitors. *The Journal of Agricultural Science*, 154(5), 812–827. <https://doi.org/10.1017/S0021859615000945>
- Bowden, R. D., Rullo, G., Stevens, G. R., & Steudler, P. A. (2000). Soil fluxes of carbon dioxide, nitrous oxide, and methane at a productive temperate deciduous Forest. *Journal of Environmental Quality*, 29(1), 268–276. <https://doi.org/10.2134/jeq2000.00472425002900010034x>
- Butterbach-Bahl, K., Gasche, R., Huber, C., Kreutzer, K., & Papen, H. (1998). Impact of N-input by wet deposition on N-trace gas fluxes and CH<sub>4</sub>-oxidation in spruce forest ecosystems of the temperate zone in Europe. *Atmospheric Environment*, 32(3), 559–564. [https://doi.org/10.1016/S1352-2310\(97\)00234-3](https://doi.org/10.1016/S1352-2310(97)00234-3)
- Cantarel, A. A. M., Bloor, J. M. G., Deltroy, N., & Soussana, J.-F. (2011). Effects of climate change drivers on nitrous oxide fluxes in an upland temperate grassland. *Ecosystems*, 14(2), 223–233. <https://doi.org/10.1007/s10021-010-9405-7>
- Chen, H., Gurmessa, G. A., Zhang, W., Zhu, X., Zheng, M., Mao, Q., et al. (2016). Nitrogen saturation in humid tropical forests after 6 years of nitrogen and phosphorus addition: Hypothesis testing. *Functional Ecology*, 30(2), 305–313. <https://doi.org/10.1111/1365-2435.12475>
- Christiansen, J. R., Gundersen, P., Frederiksen, P., & Vesterdal, L. (2012). Influence of hydromorphic soil conditions on greenhouse gas emissions and soil carbon stocks in a Danish temperate forest. *Forest Ecology and Management*, 284, 185–195. <https://doi.org/10.1016/j.foreco.2012.07.048>
- Cui, Q., Song, C., Wang, X., Shi, F., Yu, X., & Tan, W. (2018). Effects of warming on N<sub>2</sub>O fluxes in a boreal peatland of Permafrost region, Northeast China. *Science of the Total Environment*, 616–617, 427–434. <https://doi.org/10.1016/j.scitotenv.2017.10.246>
- Dannenmann, M., Díaz-Pinés, E., Kitzler, B., Karhu, K., Tejedor, J., Ambus, P., et al. (2018). Postfire nitrogen balance of Mediterranean shrublands: Direct combustion losses versus gaseous and leaching losses from the postfire soil mineral nitrogen flush. *Global Change Biology*, 24(10), 4505–4520. <https://doi.org/10.1111/gcb.14388>
- Davidson, E. A., Nepstad, D. C., Ishida, F. Y., & Brando, P. M. (2008). Effects of an experimental drought and recovery on soil emissions of carbon dioxide, methane, nitrous oxide, and nitric oxide in a moist tropical forest. *Global Change Biology*, 14(11), 2582–2590. <https://doi.org/10.1111/j.1365-2486.2008.01694.x>

- Drewer, J., Lohila, A., Aurela, M., Laurila, T., Minkinen, K., Penttilä, T., et al. (2010). Comparison of greenhouse gas fluxes and nitrogen budgets from an ombrotrophic bog in Scotland and a minerotrophic sedge fen in Finland. *European Journal of Soil Science*, 61(5), 640–650. <https://doi.org/10.1111/j.1365-2389.2010.01267.x>
- Fan, S., & Yoh, M. (2020). Nitrous oxide emissions in proportion to nitrification in moist temperate forests. *Biogeochemistry*, 148(3), 223–236. <https://doi.org/10.1007/s10533-02000655-w>
- Fierro, A., & Castaldi, S. (2011). Soil N<sub>2</sub>O emissions in a Mediterranean shrubland disturbed by experimental fires. *International Journal of Wildland Fire*, 20(7), 847–855. <https://doi.org/10.1071/WF10120>
- Glatzel, S., & Stahr, K. (2001). Methane and nitrous oxide exchange in differently fertilised grassland in southern Germany. *Plant and Soil*, 231(1), 21–35. <https://doi.org/10.1023/A:1010315416866>
- Goldberg, S. D., & Gebauer, G. (2009). N<sub>2</sub>O and NO fluxes between a Norway spruce forest soil and atmosphere as affected by prolonged summer drought. *Soil Biology and Biochemistry*, 41(9), 1986–1995. <https://doi.org/10.1016/j.soilbio.2009.07.001>
- Gong, Y., Wu, J., Vogt, J., & Le, T. B. (2019). Warming reduces the increase in N<sub>2</sub>O emission under nitrogen fertilization in a boreal peatland. *Science of the Total Environment*, 664, 72–78. <https://doi.org/10.1016/j.scitotenv.2019.02.012>
- Guilbault, M. R., & Matthias, A. D. (1998). Emissions of N<sub>2</sub>O from Sonoran Desert and effluent-irrigated grass ecosystems. *Journal of Arid Environments*, 38(1), 87–98. <https://doi.org/10.1006/jare.1997.0300>
- Guo, Y., Dong, Y., Peng, Q., Li, Z., He, Y., Yan, Z., & Qin, S. (2022). Effects of nitrogen and water addition on N<sub>2</sub>O emissions in temperate grasslands, northern China. *Applied Soil Ecology*, 177, 104548. <https://doi.org/10.1016/j.apsoil.2022.104548>
- Heinzle, J., Kitzler, B., Zechmeister-Boltenstern, S., Tian, Y., Kwatoch Kengdo, S., Wanek, W., et al. (2023). Soil CH<sub>4</sub> and N<sub>2</sub>O response diminishes during decadal soil warming in a temperate mountain forest. *Agricultural and Forest Meteorology*, 329, 109287. <https://doi.org/10.1016/j.agrformet.2022.109287>
- Jiang, C., Yu, G., Fang, H., Cao, G., & Li, Y. (2010). Short-term effect of increasing nitrogen deposition on CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O fluxes in an alpine meadow on the Qinghai-Tibetan Plateau, China. *Atmospheric Environment*, 44(24), 2920–2926. <https://doi.org/10.1016/j.atmosenv.2010.03.030>
- Jones, S. K., Rees, R. M., Skiba, U. M., & Ball, B. C. (2005). Greenhouse gas emissions from a managed grassland. *Global and Planetary Change*, 47(2–4), 201–211. <https://doi.org/10.1016/j.gloplacha.2004.10.011>
- Jørgensen, C. J., & Elberling, B. (2012). Effects of flooding-induced N<sub>2</sub>O production, consumption and emission dynamics on the annual N<sub>2</sub>O emission budget in wetland soil. *Soil Biology and Biochemistry*, 53, 9–17. <https://doi.org/10.1016/j.soilbio.2012.05.005>
- Kiese, R., Hewett, B., Graham, A., & Butterbach-Bahl, K. (2003). Seasonal variability of N<sub>2</sub>O emissions and CH<sub>4</sub> uptake by tropical rainforest soils of Queensland, Australia. *Global Biogeochemical Cycles*, 17(2), 2002GB002014. <https://doi.org/10.1029/2002GB002014>
- Kim, Y. S. (2013). Soil-atmosphere exchange of CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O in northern temperate forests: Effects of elevated CO<sub>2</sub> concentration, N deposition and forest fire. *Eurasian journal of forest research*, 16(1), 1–43.
- Lafuente, A., Recio, J., Ochoa-Hueso, R., Gallardo, A., Pérez-Corona, M. E., Manrique, E., & Durán, J. (2020). Simulated nitrogen deposition influences soil greenhouse gas fluxes in a Mediterranean dryland. *Science of the Total Environment*, 737, 139610. <https://doi.org/10.1016/j.scitotenv.2020.139610>
- Li, K., Gong, Y., Song, W., Lv, J., Chang, Y., Hu, Y., et al. (2012). No significant nitrous oxide emissions during spring thaw under grazing and nitrogen addition in an alpine grassland. *Global Change Biology*, 18(8), 2546–2554. <https://doi.org/10.1111/j.1365-2486.2012.02704.x>
- Liu, X., Zhang, Q., Li, S., Zhang, L., & Ren, J. (2017). Simulated NH<sub>4</sub><sup>+</sup> -N Deposition Inhibits CH<sub>4</sub> Uptake and promotes N<sub>2</sub>O emission in the Meadow Steppe of Inner Mongolia, China. *Pedosphere*, 27(2), 306–317. [https://doi.org/10.1016/S1002-0160\(17\)60318-7](https://doi.org/10.1016/S1002-0160(17)60318-7)
- Lohila, A., Aurela, M., Hatakka, J., Pihlatie, M., Minkinen, K., Penttilä, T., & Laurila, T. (2010). Responses of N<sub>2</sub>O fluxes to temperature, water table and N deposition in a northern boreal fen. *European Journal of Soil Science*, 61(5), 651–661. <https://doi.org/10.1111/j.13652389.2010.01265.x>
- Maljanen, M., Alm, J., Martikainen, P. J., & Repo, T. (2010). Prolongation of soil frost resulting from reduced snow cover increases nitrous oxide emissions from boreal forest soil.
- Maljanen, M., Jokinen, H., Saari, A., Strömmer, R., & Martikainen, P. J. (2006). Methane and nitrous oxide fluxes, and carbon dioxide production in boreal forest soil fertilized with wood ash and nitrogen. *Soil Use & Management*, 22(2), 151–157. <https://doi.org/10.1111/j.14752743.2006.00029.x>
- Matson, A., Pennock, D., & Bedard-Haughn, A. (2009). Methane and nitrous oxide emissions from mature forest stands in the boreal forest, Saskatchewan, Canada. *Forest Ecology and Management*, 258(7), 1073–1083. <https://doi.org/10.1016/j.foreco.2009.05.034>
- McCalley, C. K., Strahm, B. D., Sparks, K. L., Eller, A. S. D., & Sparks, J. P. (2011). The effect of long-term exposure to elevated CO<sub>2</sub> on nitrogen gas emissions from Mojave Desert soils. *Journal of Geophysical Research*, 116(G3), G03022. <https://doi.org/10.1029/2011JG001667>
- Merbold, L., Steinlin, C., & Hagedorn, F. (2013). Winter greenhouse gas fluxes (CO<sub>2</sub>, CH<sub>4</sub>, N<sub>2</sub>O) from a subalpine grassland. *Biogeosciences*, 10(5), 3185–3203. <https://doi.org/10.5194/bg-103185-2013>
- Morishita, T., Aizawa, S., Yoshinaga, S., & Kaneko, S. (2011). Seasonal change in N<sub>2</sub>O flux from forest soils in a forest catchment in Japan. *Journal of Forest Research*, 16(5), 386–393. <https://doi.org/10.1007/s10310-011-0285-2>
- Morishita, T., Matsuura, Y., Kajimoto, T., Osawa, A., Zyryanova, O. A., & Prokushkin, A. S. (2014). CH<sub>4</sub> and N<sub>2</sub>O dynamics of a Larix gmelinii forest in a continuous permafrost region of central Siberia during the growing season. *Polar Science*, 8(2), 156–165. <https://doi.org/10.1016/j.polar.2014.01.004>
- Pang, J., Peng, C., Wang, X., Zhang, H., & Zhang, S. (2023). Soil-atmosphere exchange of carbon dioxide, methane and nitrous oxide in temperate forests along an elevation gradient in the Qinling Mountains, China. *Plant and Soil*, 488(1–2), 325–342. <https://doi.org/10.1007/s1104023-05967-y>
- Peichl, M., Arain, M. A., Ullah, S., & Moore, T. R. (2010). Carbon dioxide, methane, and nitrous oxide exchanges in an age-sequence of temperate pine forests. *Global Change Biology*, 16(8), 2198–2212. <https://doi.org/10.1111/j.1365-2486.2009.02066.x>
- Phillips, R. L., Whalen, S. C., & Schlesinger, W. H. (2001). Influence of atmospheric CO<sub>2</sub> enrichment on nitrous oxide flux in a temperate forest ecosystem. *Global Biogeochemical Cycles*, 15(3), 741–752. <https://doi.org/10.1029/2000GB001372>
- Rowlings, D. W., Grace, P. R., Kiese, R., & Weier, K. L. (2012). Environmental factors controlling temporal and spatial variability in the soil-atmosphere exchange of CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O from an Australian subtropical rainforest. *Global Change Biology*, 18(2), 726–738. <https://doi.org/10.1111/j.1365-2486.2011.02563.x>
- Shvileva, A., Lobo-do-Vale, R., Cruz, C., Castaldi, S., Rosa, A. P., Chaves, M. M., & Pereira, J. S. (2011). Soil-atmosphere greenhouse gases (CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O) exchange in evergreen oak woodland in southern Portugal. *Plant Soil and Environment*, 57(10), 471–477. <https://doi.org/10.17221/223/2011-PSE>
- Soper, F. M., Sullivan, B. W., Nasto, M. K., Osborne, B. B., Bru, D., Balzotti, C. S., et al. (2018). Remotely sensed canopy nitrogen correlates with nitrous oxide emissions in a lowland tropical rainforest. *Ecology*, 99(9), 2080–2089. <https://doi.org/10.1002/ecy.2434>

- Sousa Neto, E., Carmo, J. B., Keller, M., Martins, S. C., Alves, L. F., Vieira, S. A., et al. (2011). Soil-atmosphere exchange of nitrous oxide, methane and carbon dioxide in a gradient of elevation in the coastal Brazilian Atlantic forest. *Biogeosciences*, 8(3), 733–742. <https://doi.org/10.5194/bg-8-733-2011>
- Stuart Grandy, A., & Philip Robertson, G. (2006). Initial cultivation of a temperate-region soil immediately accelerates aggregate turnover and CO<sub>2</sub> and N<sub>2</sub>O fluxes. *Global Change Biology*, 12(8), 1507–1520. <https://doi.org/10.1111/j.1365-2486.2006.01166.x>
- Takakai, F., Desyatkin, A. R., Lopez, C. M. L., Fedorov, A. N., Desyatkin, R. V., & Hatano, R. (2008). CH<sub>4</sub> and N<sub>2</sub>O emissions from a forest-alas ecosystem in the permafrost taiga forest region, eastern Siberia, Russia. *Journal of Geophysical Research*, 113(G2), 2007JG000521. <https://doi.org/10.1029/2007JG000521>
- Ullah, S., & Moore, T. R. (2011). Biogeochemical controls on methane, nitrous oxide, and carbon dioxide fluxes from deciduous forest soils in eastern Canada. *Journal of Geophysical Research*, 116(G3), G03010. <https://doi.org/10.1029/2010JG001525>
- Vanitchung, S., Conrad, R., Harvey, N. W., & Chidthaisong, A. (2011). Fluxes and production pathways of nitrous oxide in different types of tropical forest soils in Thailand. *Soil Science & Plant Nutrition*, 57(5), 650–658. <https://doi.org/10.1080/00380768.2011.608168>
- Voigt, C., Lamprecht, R. E., Maruschak, M. E., Lind, S. E., Novakovskiy, A., Aurela, M., et al. (2017). Warming of subarctic tundra increases emissions of all three important greenhouse gases - Carbon dioxide, methane, and nitrous oxide. *Global Change Biology*, 23(8), 3121–3138. <https://doi.org/10.1111/gcb.13563>
- Wang, F., Li, J., Wang, X., Zhang, W., Zou, B., Neher, D. A., & Li, Z. (2014). Nitrogen and phosphorus addition impact soil N<sub>2</sub>O emission in a secondary tropical forest of South China. *Scientific Reports*, 4(1), 5615. <https://doi.org/10.1038/srep05615>
- Wen, Y., Corre, M. D., Rachow, C., Chen, L., & Veldkamp, E. (2017). Nitrous oxide emissions from stems of alder, beech and spruce in a temperate forest. *Plant and Soil*, 420(1–2), 423–434. <https://doi.org/10.1007/s11104-017-3416-5>
- Wu, X., Brüggemann, N., Gasche, R., Shen, Z., Wolf, B., & Butterbach-Bahl, K. (2010). Environmental controls over soil-atmosphere exchange of N<sub>2</sub>O, NO, and CO<sub>2</sub> in a temperate Norway spruce forest: Spruce forest N<sub>2</sub>O, NO, and CO<sub>2</sub> soil fluxes. *Global Biogeochemical Cycles*, 24(2). <https://doi.org/10.1029/2009GB003616>
- Wu, X., Zang, S., Ma, D., Ren, J., Chen, Q., & Dong, X. (2019). Emissions of CO<sub>2</sub>, CH<sub>4</sub>, and N<sub>2</sub>O fluxes from Forest soil in Permafrost Region of Daxing'an Mountains, Northeast China. *International Journal of Environmental Research and Public Health*, 16(16), 2999. <https://doi.org/10.3390/ijerph16162999>
- Xu, K., Wang, C., & Yang, X. (2018). Five-year study of the effects of simulated nitrogen deposition levels and forms on soil nitrous oxide emissions from a temperate forest in northern China. *PLoS One*, 13(4), e0196622. <https://doi.org/10.1371/journal.pone.0196622>
- Xu, W., Frendrup, L. L., Michelsen, A., Elberling, B., & Ambus, P. L. (2023). Deepened snow in combination with summer warming increases growing season nitrous oxide emissions in dry tundra, but not in wet tundra. *Soil Biology and Biochemistry*, 180, 109013. <https://doi.org/10.1016/j.soilbio.2023.109013>
- Yan, Y., Ganjurjav, H., Hu, G., Liang, Y., Li, Y., He, S., et al. (2018). Nitrogen deposition induced significant increase of N<sub>2</sub>O emissions in an dry alpine meadow on the central Qinghai Tibetan Plateau. *Agriculture, Ecosystems & Environment*, 265, 45–53. <https://doi.org/10.1016/j.agee.2018.05.031>
- Yan, Y., Sha, L., Cao, M., Zheng, Z., Tang, J., Wang, Y., et al. (2008). Fluxes of CH<sub>4</sub> and N<sub>2</sub>O from soil under a tropical seasonal rain forest in Xishuangbanna, Southwest China. *Journal of Environmental Sciences*, 20(2), 207–215. [https://doi.org/10.1016/S1001-0742\(08\)60033-9](https://doi.org/10.1016/S1001-0742(08)60033-9)
- Yue, P., Li, K., Hu, Y., Qiao, J., Wang, S., Ma, X., et al. (2024). The effect of nitrogen input on N<sub>2</sub>O emission depends on precipitation in a temperate desert steppe. *Science of the Total Environment*, 924, 171572. <https://doi.org/10.1016/j.scitotenv.2024.171572>
- Yue, P., Zuo, X., Li, K., Cui, X., Wang, S., Misselbrook, T., & Liu, X. (2021). The driving effect of nitrogen-related functional microorganisms under water and nitrogen addition on N<sub>2</sub>O emission in a temperate desert. *Science of the Total Environment*, 772, 145470. <https://doi.org/10.1016/j.scitotenv.2021.145470>
- Zhang, J., & Han, X. (2008). N<sub>2</sub>O emission from the semi-arid ecosystem under mineral fertilizer (urea and superphosphate) and increased precipitation in northern China. *Atmospheric Environment*, 42(2), 291–302. <https://doi.org/10.1016/j.atmosenv.2007.09.036>
- Zhang, W., Mo, J., Yu, G., Fang, Y., Li, D., Lu, X., & Wang, H. (2008). Emissions of nitrous oxide from three tropical forests in Southern China in response to simulated nitrogen deposition. *Plant and Soil*, 306(1–2), 221–236. <https://doi.org/10.1007/s11104-008-9575-7>