https://doi.org/10.5194/egusphere-2024-3661
Preprint. Discussion started: 13 January 2025

Nitrogen deposition and climate drive plant nitrogen uptake while soil factors drive nitrogen use efficiency in terrestrial ecosystems

Helena Vallicrosa[1,2,3], Katrin Fleischer[4,5], Manuel Delgado-Baquerizo[6], Marcos Fernández-Martínez[7], Jakub Černý[8], Di Tian[9], Angeliki Kourmouli[10,11], Carolina Mayoral[11,12], Diego Grados[13], Mingzhen Lu[14,15], César Terrer[1]

1 Department of Civil and Environmental Engineering, Massachusetts Institute of Technology, Cambridge, Massachusetts, USA.

2 Community Ecology Unit, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, CH-8903 Birmensdorf, Switzerland

3 Plant Ecology Research Laboratory PERL, School of Architecture, Civil and Environmental Engineering ENAC, EPFL, CH-1015 Lausanne, Switzerland

4 Department of Biogeochemical Signals, Max-Planck-Institute for Biogeochemistry, Jena, Germany.

5 Section Systems Ecology, Amsterdam Institute for Life and Environment, Vrije Universiteit Amsterdam, The Netherlands

6 Laboratorio de Biodiversidad y Funcionamiento Ecosistémico, Instituto de Recursos Naturales y Agrobiología de Sevilla (IRNAS), CSIC, Sevilla, Spain

7 CREAF, E08193 Bellaterra (Cerdanyola del Vallès), Catalonia, Spain.

8 Forestry and Game Management Research Institute, Strnady 136, Jíloviště 252 02, Czech Republic.

9 State Key Laboratory of Efficient Production of Forest Resources, Beijing Forestry University, Beijing 100083, China

10 Lancaster Environment Centre, Lancaster University, Lancaster, UK

11 Birmingham Institute of Forest Research, University of Birmingham, United Kingdom

12 School of Biosciences, Edgbaston Campus, University of Birmingham, United Kingdom

13 Department of Agroecology, Climate and Water, Aarhus University, 8830 Tjele, Denmark

14 Department of Environmental Studies, New York University, New York, NY 10012, USA.

15 Santa Fe Institute, New Mexico, NM 87501, USA

Correspondence to: Helena Vallicrosa (helena.vallicrosa@gmail.com)

ABSTRACT

The role of plants in sequestering carbon is a critical component in mitigating climate change. A key aspect of this role involves plant nitrogen (N) uptake (Nup) and N use efficiency (NUE), as these factors directly influence the capacity of plants to store carbon.

https://doi.org/10.5194/egusphere-2024-3661
Preprint. Discussion started: 13 January 2025

However, the contribution of N deposition and soil factors (biotic and abiotic) in addition to climate to plant N cycle, remains inadequately understood, introducing significant uncertainties into climate change projections. Here, we used ground-based observations across 159 locations to calculate Nup and NUE and identify their main drivers in natural ecosystems. We found that global plant Nup is primarily driven by N deposition, air temperature and precipitation, with Nup increasing in warmer and wetter areas. In contrast, NUE is driven by soil biotic and abiotic factors, with little direct control by climatic factors. Specifically, NUE decreased with the intensity of the colonization by arbuscular mycorrhizal fungi and increased with soil pH and soil microbial stocks. Nup and NUE presented opposite latitudinal distributions, with Nup higher on tropical latitudes and NUE higher towards the poles. Total soil N stocks were not found to be a driver of Nup or NUE. We also compared our results with TRENDY models and found that models may overestimate Nup by ~ 100 Tg N yr^{-1} in the tropics and triple the standard deviation on boreal latitudes. Our findings emphasize the effect of N deposition and soil microbes that, in addition to climate and soil pH, are crucial for accurately predicting ecosystems' capacity to sequester carbon and mitigate climate change.

Plain language summary
We used field empirical data worldwide to calculate plant nitrogen uptake (Nup) and nitrogen use efficiency (NUE) in woodlands and grasslands and determine its drivers, which can be used as empirical validation for models. Even though some regions of the world have decreased their N deposition, N deposition is still the most important driver explaining plant nitrogen uptake, aside from climatic variables.

https://doi.org/10.5194/egusphere-2024-3661
Preprint. Discussion started: 13 January 2025

1.Introduction

Climate and nutrient availability play significant roles in the capacity of plants to sequester carbon (C). Nitrogen uptake (Nup) and nitrogen use efficiency (NUE) are fundamental processes in plant-soil N cycling, which in turn impact biodiversity, ecosystem productivity, C sequestration, food security and human health (Peñuelas et al., 2020). Hence, realistic quantifications of Nup and (NUE) and the understanding of their drivers are crucial to predict the fate of terrestrial ecosystems under a changing environment. Climate, biomass production, and Nup are strongly intertwined, where hotter and wetter ecosystems have the capacity to grow more, increase their N demand and therefore absorb more N if available (Berntson et al., 1998; Wu et al., 2011). Nonetheless, several factors can affect N availability. Traditionally, total soil N stocks were used to proxy N availability or plant Nup. Although this correlation is weak, it is still used in a modeling perspective (Stevens et al., 2015; Vicca et al., 2018) assuming that total soil N, positively correlates with N availability. Recent advances in plant-soil science revealed the remarkable importance of the soil biotic community in N availability related processes and plant growth (Aber et al., 2001; Sinsabaugh et al., 2002; Sinsabaugh et al., 2008; Crowther et al., 2019; Delgado-Baquerizo et al., 2020; Etzold et al., 2020). Thus, by extension, soil microorganisms (e.g., soil microbes stocks and mycorrhizal associations) could potentially affect Nup and NUE. In addition, N deposition has increased from ~30 to ~80 Tg N/year worldwide since 1850 (Kanakidou et al., 2016), with substantial effects on global biogeochemical fluxes and N availability (Elser et al., 2010; Battye et al., 2017; Peñuelas et al., 2020). Consequently, reliable quantifications of plant Nup and NUE need to include climatic factors as well as soil biotic factors and N deposition.

N regulates the capacity of ecosystems to store C (Hungate et al., 2003; Fernández-Martínez et al., 2014; 2019; Wang et al., 2017) and respond to climate change drivers (Fleischer et al., 2019; Terrer et al., 2019; Walker et al., 2021; Zhou et al., 2022) being the C-N assembly relevant for land surface models (LSM). Eight of the LSM of the TRENDY ensemble (Sitch et al., 2015), a model ensamble designed to disentangle the effects of climate, CO2, land-use and land cover change, include representations of the N cycle and plant N uptake. Nonetheless, its parameterization of N cycling is poorly constrained by observations (Zaehle et al., 2014; Fowler et al., 2015; Braghiere et al., 2022). As a consequence, when models are assembled, the result leads to accumulated uncertainty (Prentice et al., 2015; Franklin et al., 2020) and therefore divergent predictions of the land sink (Zaehle et al., 2014; Stocker et al., 2016; Arora et al., 2020). Furthermore, when accounting for N interactions, LSM do generally not consider the direct effects of microorganisms' missing out on the role of soil bacteria or mycorrhizae on plant nutrient uptake. Thus, including global calculations of plant Nup and NUE based on empirical data as well as accounting for climate, N deposition, and soil biomass interactions would potentially refine the N accountability in LSM.

https://doi.org/10.5194/egusphere-2024-3661
Preprint. Discussion started: 13 January 2025

Here, we gathered information from 159 plots worldwide that describe woodlands and grasslands across different biomes to calculate plot-based plant Nup and plant NUE using exclusively empirical field data. Our analyses combine N concentration and net primary productivity (NPP) data in different aboveground and belowground plant tissues (i.e., leaves, roots, stem). We used linear models to identify the drivers of Nup and NUE, including N deposition, soil microbes, woodiness and climatic factors. We then upscaled those results using the machine-learning models to quantify yearly plant Nup and plant NUE at a global scale in natural terrestrial ecosystems (woodlands and grasslands) and compared these results with simulations from LSM. We hypothesize that factors such as N deposition and soil microorganisms have significant impacts on Nup and NUE respectively, playing a role as important as climatic drivers. We expect the ground-based data, and incorporation of these N-relevant drivers to increase the accuracy of global Nup quantifications. Thus, a mismatch between our estimation and current TRENDY simulation outputs is expected.

2. Results and discussion

2.1 Nitrogen uptake and nitrogen use efficiency

Our findings indicate that N deposition and climate are fundamental factors explaining plant Nup on a global scale (Fig. 1). Further analysis revealed a positive relationship between Nup and accumulated N deposition, mean annual temperature (MAT), and mean annual precipitation (MAP). Thus, regions that are warm and wet, and also experience higher levels of N deposition, exhibit the highest rates of Nup. Our empirical results did not show important relationships between plant Nup and soil microbial interactions nor soil physico-chemical variables including soil N stocks at a global scale (Fig. 1a). We further tested the univariate relation between Nup and total soil N stocks with no significant relation among them (Fig. S1a).

https://doi.org/10.5194/egusphere-2024-3661
Preprint. Discussion started: 13 January 2025

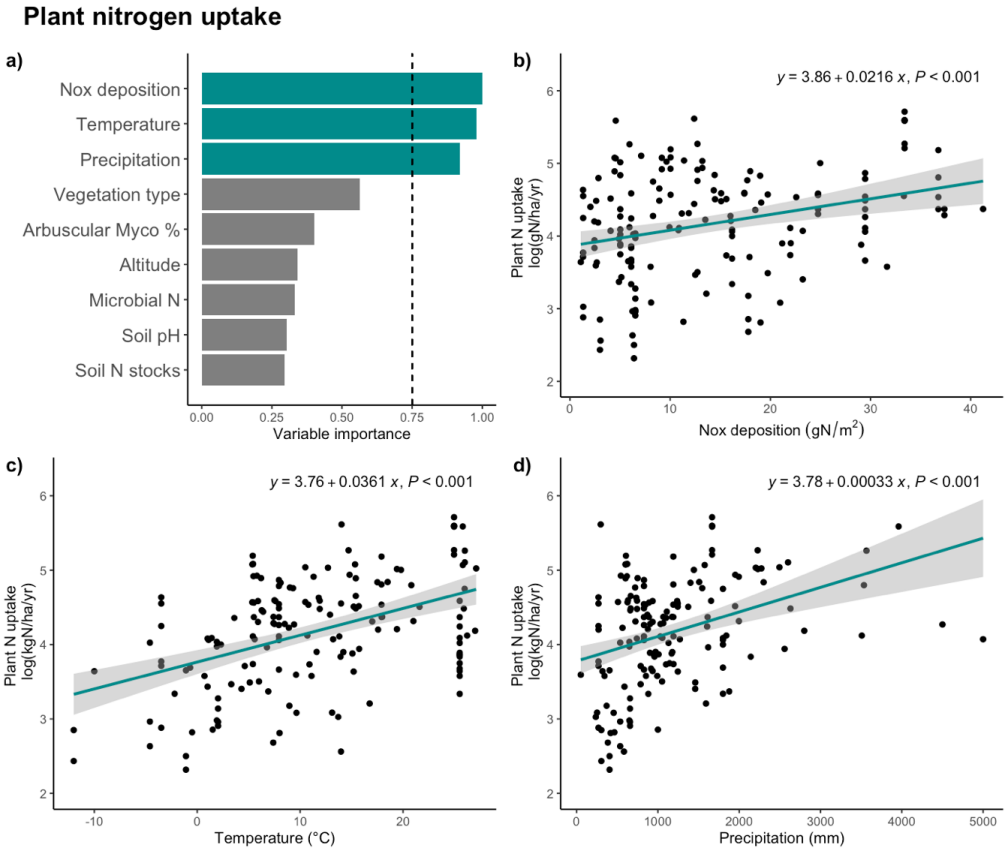

Figure 1. a) Variable importance plot for the general linear model describing plant nitrogen uptake (Nup). The dashed line is set at 0.8, separating the threshold for important variables. The model preudoR2 was 0.349. Linear regressions were displayed describing plants' nitrogen and important variables b) accumulated Nox deposition from 1901 to 2021, c) mean annual temperature, and d) mean annual precipitation. Equation and p-value per regression displayed. Acronyms: Nox: oxidized nitrogen, N: nitrogen, Myco %: Mycorryzal percentage.

In contrast, when describing NUE our model selection analysis identified soil biotic and abiotic factors as NUE drivers with little direct control by climatic factors (Fig. 2). Specifically, our results described NUE decreased with AM % but a positive relation between soil pH, soil microbial N stocks and NUE was found. Thus, when plant species are more colonized by arbuscular mycorrhizae, are less efficient in N use to build biomass. In contraposition, basic pH and abundant soil microbial stocks facilitate higher NUE rates. Even though soil variables appear to be important for NUE, soil N stocks remain unrelated to NUE in the model and when tested individually (Fig. S1b).

https://doi.org/10.5194/egusphere-2024-3661
Preprint. Discussion started: 13 January 2025

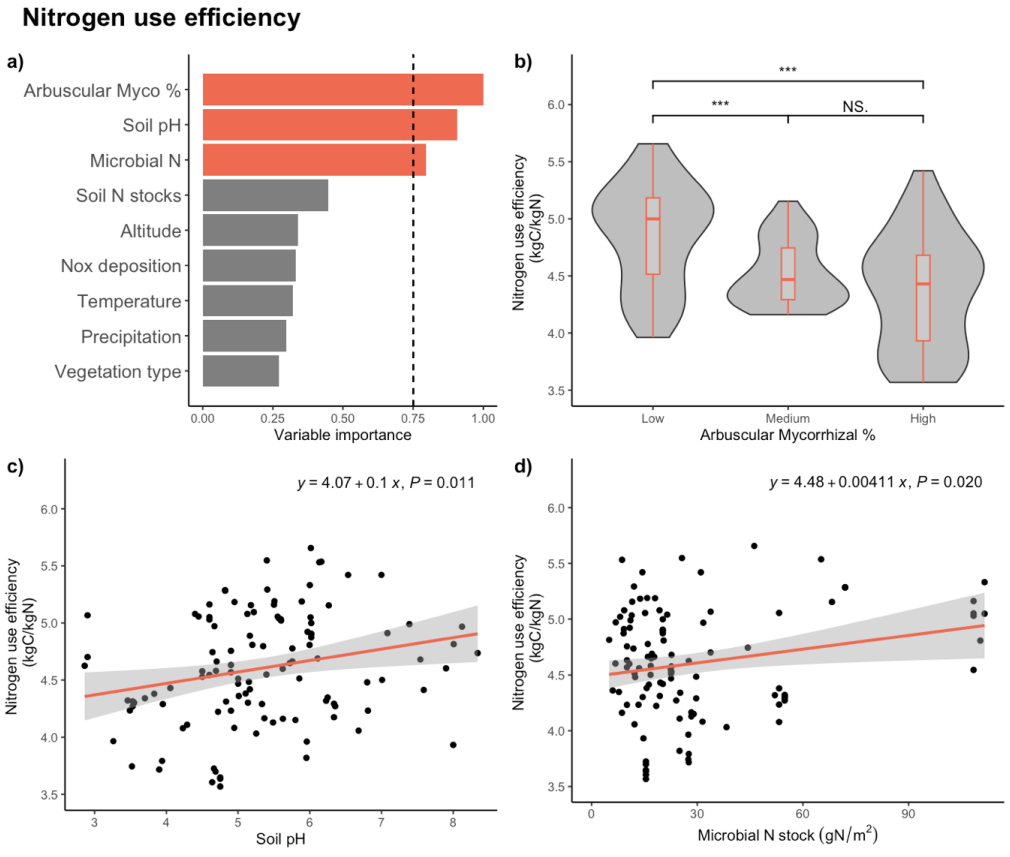

*Figure 2. a) Variable importance plot for the generalized linear model describing nitrogen use efficiency (NUE). The model preudoR2 was 0.355. The dashed line is set at 0.75, separating the threshold for important variables. In b) arbuscular mycorrhizae percentage is divided into low, medium, and high, and NUE is displayed. * = P-value < 0.05, ** = P-value < 0.01, *** = P-value < 0.001. Linear regressions were displayed describing plants' nitrogen use efficiency c) soil pH and d) microbial N stocks. Equation and p-value per regression displayed.*

2.2 Global maps of Nup and NUE

Next, we used a machine-learning model to understand the global magnitude and distribution of Nup and NUE when the relationships found at the site-level are extrapolated at a global scale. For methodological consistency, the XGBoost model was trained using the same nine variables as the linear model. We identified temperature, precipitation, and N deposition as the most critical factors for describing Nup (Fig. S2), which aligned with those in the linear model, albeit in a slightly different order. Partial dependence plots further corroborated these relationships, showing consistent correlation signs with those observed in the linear models (Fig. S3). The upscaled Nup map showed a total yearly Nup of 842.215 ± 236.11 Tg of N, with a mean coefficient of variation of 26.77 % (Fig. S4) and an r^2 of 0.54 (Fig. S2). The lowest Nup values were on boreal latitudes and mountain ranges such as the Rocky Mountains in the USA, the Andes in South America, the different mountain ridges in Europe, and the Himalayan plateau in Asia. The higher rates of Nup are predicted in

https://doi.org/10.5194/egusphere-2024-3661
Preprint. Discussion started: 13 January 2025

temperate latitudes in Europe, the eastern United States, Southeast Asia, East Australia, most of South America and central Africa, with the most intense spot around Congo, where there is the most N deposition, temperature and precipitation combined (Fig. 3a). Therefore, Nup map shows an NPP influence, driven by temperature and precipitation, but added to an N deposition distribution that shades the strictly latitudinal distribution of Nup.

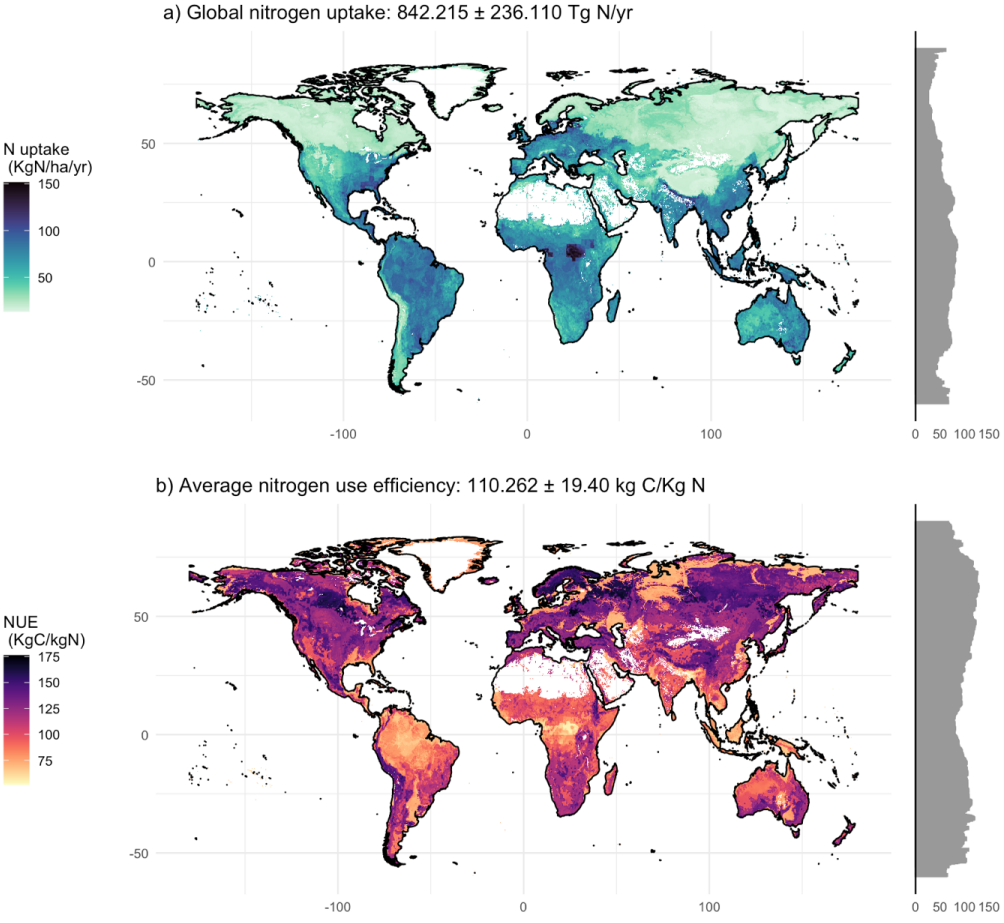

Figure 3. Upscaled global maps describing a) Plant nitrogen uptake and b) Nitrogen use efficiency. The total amount of nitrogen uptake calculated per year is 842.215 Tg of N with a standard deviation of ± 236.11. The mean value of global nitrogen use efficiency is 110.26 kg of C per kg of N, and its standard deviation is 19.40. White color describes no data due to a lack of grasslands or woody vegetation.

The machine-learning models describing NUE showed the importance of microbial N stocks, altitude, precipitation, soil pH, and AM% as NUE drivers (Fig. S5). These results generally align with the variable importance shown in the linear models, with the addition of precipitation and altitude. The variables´ relation showed similar general trends as in the linear model (Fig. S6). The average predictions for NUE at a global scale were 110.262 units of C per unit of N with a mean coefficient of variation of 17.89 % (Fig. S4) and an r^2 of 0.44

https://doi.org/10.5194/egusphere-2024-3661
Preprint. Discussion started: 13 January 2025

(Fig. S5). The map distribution showed general lower NUE around the Equator, and progressively increasing towards the poles. Nonetheless, some heterogeneous parches alternating high and low NUE can be found between 50 and 60 degrees latitude north (Fig. 3b).

2.3 Global-scale Nup comparison with TRENDY models

We further seek to compare our estimates for the total yearly Nup upscaled from field observations with the mean of the Nup provided by the eight models included in TRENDY. When comparing TRENDY Nup with our Nup upscaled projections, we found clear geospatial pattern differences. TRENDY models produce higher Nup in the tropical regions, reaching differences of around 100 kg N ha^{-1} yr^{-1} in those areas (Fig. 4a) representing more than 100% of the Nup estimated by field observations (Fig. 4b). Other areas like the north and northeast of North America, Southeast Asia, and north of Eurasia also appear to have higher Nup values in TRENDY models than in field observations. In boreal latitudes, the TRENDY models deviation for Nup could even reach 300% of overestimation. On the other hand, areas where the upscaled approach projects higher values than the TRENDY models, are the austral latitudes, the Middle Eastern regions, the Somali peninsula, and the Rocky Mountains (Fig. 4). Overall, TRENDY models estimate higher values of Nup, by 16.61 kg N ha^{-1} yr^{-1}, meaning the 48.54 % of the variability. When aggregating the total year Nup, LPX-Bern and CLM5.0 were the models that predicted overall values exceding our range of confidence, assuming a significantly larger Nup (Fig. S7).

https://doi.org/10.5194/egusphere-2024-3661
Preprint. Discussion started: 13 January 2025

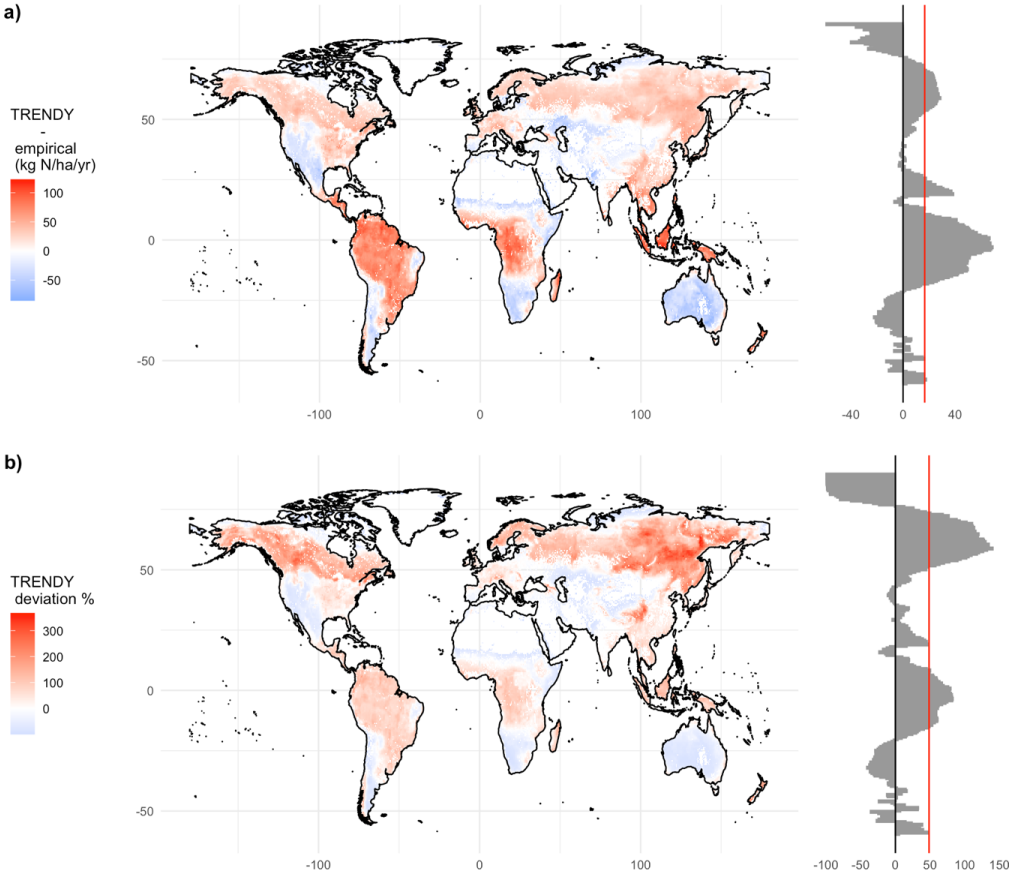

Figure 4. Comparison between the mean of the nitrogen uptake provided by TRENDY v8 models minus the upscaled nitrogen uptake. The red color stands for higher values on the TRENDY model, and the blue color stands for higher nitrogen uptake values on the upscaled approach. In a) units in kg N ha^{-1} yr^{-1} and in b) units in percentage of deviation from field upscaling. Latitudinal aggregation on the right, with a red vertical line showing a) the mean of the total comparison at 16.61 kg N ha^{-1} yr-1 and b) the mean percentage of deviation at 48.54%.

2.4 Nup global drivers and implications

Our models estimated the annual global plant Nup at 842.215 ± 236.110 Tg of N. This figure is consistent with the findings of Peng et al., 2023, which estimated 950 ± 260 Tg of N, and Braghiere et al., 2022, with an estimated uptake of 841.8 Tg N. The slight variations can be attributed to differences in methodologies and data sources (simultaneous plot-averaged records vs individual-level records) used in these studies. In our study, linear models and machine learning models are consistent when determining N deposition, temperature, and precipitation as global drivers of Nup. Hotter and wetter environments increase biological activity, leading to more biomass production and therefore more N demand. An increase in N demand with enough N availability is associated with an increase in Nup. The accumulation of N deposition throughout time originating from anthropogenic sources has been increasing the N availability in some areas, generally close to industrial or agroforestry pools. Hence, in a global change context where CO_2 fertilization and temperature increase

https://doi.org/10.5194/egusphere-2024-3661
Preprint. Discussion started: 13 January 2025

have generated a greening effect (Ruehr et al., 2023), areas with higher N deposition were able to better supply the increasing N demand. Thus, according to our results, anthropogenic N supply may have become a Nup driver as important as climate.

These results are concerning since our data emphasize the far-reaching influence of human-induced nitrogen deposition in shaping global Nup patterns. Some regions such as Europe, the Eastern USA, and the tropics have decreased their N deposition during the last four decades (Ackerman et al., 2019). Nonetheless, these efforts do not translate yet on low N deposition effects in natural woodlands and grasslands. This sustained entrance of anthropogenic N has been associated with a fertilization effect, enhancing the land C sink by 0.72 Pg C yr^{-1} during the 2010s (Gurmesa et al., 2022). Nonetheless, this N fertilization effect showed evidence of saturation in forests and grasslands (Tian et al., 2016; Peng et al., 2020), where the biomass production and therefore the C sink increase slowed down. Consequently, this input of N not being captured by biomass will enhance the N leaching associated with eutrophication, acidification, loss of biodiversity, and N_2O emissions (Aber et al., 1989; Gundersen et al., 1998; Bobbink et al., 2010) exacerbating environmental problems.

2.5 NUE global drivers and implications

Our results predict a mean NUE of 110.262 ± 19.40 kg C per kg N. Our results indicate soil biotic and abiotic factors drive NUE in natural ecosystems. The main divergence between linear models and machine learning models is the importance of altitude and precipitation, which showed explicit relevancy only in machine learning models. We attribute these differences to the nature of the models, where machine-learning models accommodate correlations without modifying their variable importance. Thus, the important variables in the linear model could also have embedded important latitudinal gradients and therefore altitudinal or precipitation gradients. Our NUE predictions contrasted with Peng et al., 2023, which predicts a mean NUE of 76 ± 26 kg C per kg of N. The main difference between studies is that our approach included biotic factors, such as mycorrhizal associations and microbial interactions, that described NUE better than abiotic factors. In contrast, Peng et al., 2023 focused their predictions only on abiotic factors. In that regard, we do not consider environmental variables such as precipitation to be totally detached from NUE relations, since they are somewhat drivers of important biotic variables such as AM %, soil pH, and microbial N stocks. Nonetheless, the results showed that including biotic variables may result in more efficient use of N by plants at global scale.

The response of NUE has been postulated as a method to assess N saturation in plant communities (Shcherbak et al., 2014). A negative relation between N addition and NUE and lower NUE levels would indicate N saturation (Iversen et al., 2010). In our study, tropical areas are shown to have the lowest NUE, being the less N limited and matching with previous global upscaling studies using different approaches (Du et al., 2020; Vallicrosa et al., 2022). According to the soil age hypothesis (Walker and Syers, 1976), N accumulates in ecosystems through time due to biological processes. Thus, newer formation areas, such as high elevation or lower pH areas are those showing higher values of NUE and where N is

https://doi.org/10.5194/egusphere-2024-3661
Preprint. Discussion started: 13 January 2025

expected to be more limiting. Our results only show a modest effect of N saturation due to N deposition, so further studies are needed to better assess where and under what circumstances areas are N saturated due to N deposition.

Biological activity, such as the type of mycorrhizal associations and soil microbes N stocks, was found to have a strong impact in the terrestrial N cycle. Arbuscular mycorrhizal associations are the most abundant in the tropics (Soudzilovskaia et al., 2019) and are theorized to be more efficient in nutrient capture and more abundant in areas with fast N cycling (Averill et al., 2019). Our models show that AM associations have lower NUE, possibly driven by the abundance of N and the high efficiency of AM associations in N acquisition. Conversely, N obtention was more efficient in areas with high soil microbes stocks. As described by Kuzyakov and Xu 2013, we hypothesize a potential competition effect between soil microbes and plants for N, but further studies are needed to corroborate this relation. Thus, given the importance of biological activity in fixing and transforming N, it is reasonable that total soil N stocks, that include N in all forms and aggregations, would not be a good indicator of N availability and plant N uptake.

2.6 Discrepancies between Nup map and TRENDY

TRENDY model ensemble projects substantially higher Nup values than the empirical upscaling. These differences were especially relevant in the tropics in absolute terms and in boreal latitudes in % of deviation. This mismatch could be associated with an overestimation of terrestrial C sink capacity and a misinterpretation of the role of vegetation in N cycling. A possible explanation of this phenomenon would be the overestimation of biomass production by LSM when not accounting for growth-limiting factors such as phosphorus availability, drought, or overall biotic competition. Alternatively, overestimation when accounting for N concentration in tissues could also lead to Nup overestimation, which would necessarily reflect in overall lower NUE values. In our calculations, we embraced the variability of N concentration and net primary productivity among tissues and leaf resorption to generate a truthfully Nup and NUE values.

2.7 Representativity and future research

An inherent challenge in ecological studies of this scale is to ensure the global representativeness of the dataset, since there are systematic geographical sampling biases underrepresenting the global south. In this study, the 28 % of the data comes from areas below 15º latitude, outside the US, Europe, or China (Fig. S8). When accounting for ecosystems representativity, the Whittaker diagram shows we have a representation of all the biomes (Fig. S9), showing the lowest representativity on subtropical desert, tundra, and temperate rainforest. Nonetheless, we acknowledge that calculations based on empirical data, especially when a portion of the data have undergone a gap-filling process, can still have biases associated with sampling and the upscaling process, which are mainly defined by the more represented biomes of the observations. Still, we believe that calibrating and cross-checking models built over mathematical assumptions with field measurements is necessary to better root models to reality.

https://doi.org/10.5194/egusphere-2024-3661
Preprint. Discussion started: 13 January 2025

This study is focused on a quantitative approach at global scale, attempting to target variables' relative importance on Nup and NUE along with its correlations to environmental and biotic variables. In future research, specific data detailing the different N fractions obtained at a global scale (e.g. organic-inorganic, ammonium-nitrate) and a more mechanistic frame are strongly encouraged. Approaches such as in Niu et al., 2016 quantifying the fraction of Nup taken by plants, leached and retained in the soil at a global scale are crucial to enhance our understanding of the N cycle and its interactions with ecosystems.

3. Conclusion

We showed that accumulated N deposition and climatic variables are the main global-scale factor describing Nup, where regions that are warm and wet and also experience higher levels of N deposition, exhibit the highest rates of Nup. This result highlights the far-reaching influence of nitrogen deposition in shaping the global Nup pattern. Interestingly, NUE was shown to be driven by soil biotic and abiotic factors, emphasizing the importance of soil microorganisms and pH as regulators of the N cycle. We further revealed that total soil N stocks are not a Nup nor NUE driver. Our upscaling showed large spatial-explicit differences with TRENDY Nup values, where TRENDY projects higher absolute values around the tropics and higher deviation values in boreal latitudes. This mismatch in the spatial correlation between empirical data and land system models could substantially affect model accuracy and future predictions of the C sink, where the tropical capacity to store C might have been overestimated. Our results provide insights to understand better the C – N interactions, N cycling, and absorption in terrestrial ecosystems and highlight that N deposition largely impacts plant Nup worldwide.

4. Methods

4.1 Plant data gathering

We gathered 159 (Table S1) field plot data in natural conditions, including dominant species and vegetation type (grassland, coniferous or broadleaved), foliar and root N concentration, foliar and root biomass production, and stem biomass production in the case of woody plants on the same location and time. In situ measurements for foliage and fine roots are the most relevant for Nup calculation (Dybzinski et al., 2024), so all our datapoints include biomass production (NPP) and N content (N%) of leaves and roots. We gathered 45 datapoints, representing a 28% of the data, coming from latitudes under the 15º latitude, despite of the systematic lack of field sampling on some regions of the earth such as the global south. We also complemented the dataset with field values of litter biomass production, litter N concentration, stem N concentration, soil pH, soil C %, soil N %, soil texture, soil moisture, mean annual precipitation, mean annual air temperature, and altitude. We included woody and grassland natural environments (Fig. S8), including representation from most biomes according to Whitakker's diagram (Fig. S9). Each data point covered by the analysis has been collected from 1984 to 2022. If stem N was missing, happening in 25% of the data entries, we gap-filled it with the mean value of its vegetation type (coniferous=0.33 or broadleaved=0.52%). With leaves, stem and roots we calculated the gross Nup (see in the next section). By subtracting the amount of N recovered during

https://doi.org/10.5194/egusphere-2024-3661
Preprint. Discussion started: 13 January 2025

leaf senescence we obtain the net Nup. If litter biomass was missing, 52% of the time, we assumed it to be the same amount of green leaf biomass production. If litter N concentration was missing, we calculated the net Nup using the predicted value from a linear model created with net Nup in the base of gross Nup, in 33% of the entries. This model had an r2 of 0.88, a p-value < 2.2e-16, and a correlation of 0.72 between gross and net Nup.

4.2 Environmental data

We extracted mean annual precipitation from WorldClim2 (Fick and Hijmans, 2017), as well as soil pH, soil C, and soil N, soil moisture, soil bulk density, and soil texture from soilGrids (Poggio et al., 2021). All soil data for the topsoil layer (0-15 cm). We also identified the potential mycorrhizal association from the dominant species based on Soudzilovskaia et al. 2020, and categorized it into 0, 50, or 100 arbuscular mycorrhizal (AM) percentages. When dominant species were not provided, we extracted the AM% based on the AM map of Soudzilovskaia et al. 2019 and the coordinates of our samples. Moreover, we extracted the microbial N stock from Xu et al. 2013. We calculated and obtained the accumulated oxidized N deposition from Yang and Tian, 2022 from 1901 to 2022 by georeferencing each field plot. Oxidized and reduced N deposition are correlated and are thought to have similar ecological effects (Sutton and Fowler, 1993; Yang and Tian, 2022). Oxidized forms generally come from combustion reactions while reduced forms generally come from agricultural practices. We decided to use the oxidized form because it is the most equally distributed at a global scale.

4.3 Nitrogen uptake calculation

We calculated the increase in annual N stock for each tissue (leaves, stem, roots, and litter) by multiplying the biomass increase by its N concentration. We obtained the gross annual Nup by aggregating tissue's Nup (roots, leaves, and stem if woody). To account for the N that has been reabsorbed before senescence, we subtracted the litter N stock from the green leaves N stock. We subtracted the reabsorbed N from the gross Nup to obtain the final net Nup value as follows:

$$GrossNup = (NPPleaves * Nleaves + NPPstem * Nstem + NPProots * Nroots)$$

$$NetNup = GrossNup - (NPPleaves * Nleaves - NPPlitter * Nlitter)$$

Nup = Plant nitrogen uptake (kg N/ha/yr)
NPP = Net primary production (kg N/ha/yr)
N = Nitrogen (% of dry weight)

4.4 Nitrogen use efficiency calculation

We calculated the nitrogen use efficiency (NUE) by calculating the total amount of biomass produced in leaves, stems, and root tissue divided by the amount of nitrogen in each tissue. It will give the amount of biomass produced by a unit of nitrogen.

$$NUE = (NPP_{leaves}/Nup_{leaves}) + (NPP_{stem}/Nup_{stem}) + (NPP_{roots}/Nup_{roots})$$

https://doi.org/10.5194/egusphere-2024-3661
Preprint. Discussion started: 13 January 2025

NUE = Nitrogen use efficiency (kg C / kg N)
NPP = Net primary production or biomass increase (kg N/ha/yr)
Nup = Nitrogen uptake by tissue calculates as NPP * N %

4.5 Linear statistical analysis

From the available variables collected, we selected the less correlated ones using the *cor* function in R to deal with multicollinearity. The less correlated variables selected were mean annual air temperature, mean annual precipitation, altitude, arbuscular mycorrhizae percentage, microbial N stock, soil N stock, soil pH, accumulated oxidized N deposition from 1901 to 2022, and woodiness. The biggest collinearity among variables was 0.52 between mean annual temperature and AM presence (Table S2). Generalized linear models were created using Nup and NUE as dependent variables and the family was set up as Gamma with an inverse link to fulfill the residuals normality requirements. We performed a model selection using the *dredge* function in the MuMIn R package (Barton, 2023) and chose the best linear model based on its lowest AIC. We calculated the variable importance using the function *sw* on the MuMIN R package (Barton, 2023). We calculated the pseudo R square of the models using the function pR2 from the package pscl (Jackman, 2020). Figures were created using the R package *ggplot2 (*Wickham, 2016*)*.

4.6 Nitrogen uptake and nitrogen use efficiency upscaling

To upscale Nup and NUE to global grasslands and woody vegetation, we used extreme gradient boosting (XGBoost) models splitting the database into train, test, and validation using a ratio of 70:20:10, respectively. Extreme gradient boosting is a machine learning algorithm that builds ensemble decision trees, applying regularization and pruning techniques to improve performance and prevent overfitting (Chen et al., 2016). We trained an XGBoost model using the R package *xgboost* (Chen et al., 2023), forcing an early stop based on minimum root mean squared error to avoid overfitting and setting up the objective as a gamma regression. We optimized the parameters based on performance at a maximum depth of 6, minimum child weight of 1, and eta of 0.3. We considered the same independent variables included in the linear model without interactions. We repeated this process 20 times with random database separation to stabilize the variability due to randomness in subset splitting. We extracted the variable importance of each model using the function *xgb.plot.importance* on the *xgboost* R package (Chen et al., 2023), calculated the mean of the values among the 20 different training sets, and displayed it using ggplot. We calculated partial dependence plots using the function *partial* in *purrr* R package (Wickham and Henry, 2023) to explore the non-linear relations on the models. To calculate the model performance, we calculated the mean squared error of the test set and the r squared of the predicted vs observed in the validation subset, considering the validation set as completely independent.

To predict the values at a global scale, we used the spatial explicit mean annual precipitation, mean annual temperature, and altitude variables provided by WorldClim2 (Fick and Hijmans, 2017); the microbial N stocks by Xu et al. 2013; the oxidized accumulated N deposition from 1909 to 2022 calculated from Yang and Tian 2022 and soil N stocks and

https://doi.org/10.5194/egusphere-2024-3661
Preprint. Discussion started: 13 January 2025

soil pH provided by soilGrids 2.0 (Poggio et al., 2021) at 15 cm depth. We reclassified the European Space Agency Land Cover (ESA-LC) map (Defourny, 2019) (Table S3) and we downscaled its resolution to 2 km using the raster R package (Hijmans, 2023). We upscaled each of the 20 Nup and NUE models using the trained XGBoost models and their prediction per pixel at 2 km resolution and calculated the mean to obtain the final maps. We parallelized the process using the *parallel* function and *spaDES.tools* R package (McIntire and Chubaty 2023) to accelerate the upscaling. We masked areas not considered woodlands or grasslands in natural conditions according to the European Space Agency cover map (Defourny, 2019) (Table S3), and then, we obtained a map of the yearly Nup, Nup standard deviation, and annual NUE. We obtained the final number of yearly Nup by summing all the pixels available.

4.7 Nitrogen uptake comparison with TRENDY models ensemble

We obtained the available Nitrogen uptake of Vegetation (fNup) variable associated with all the available models in TRENDY v8 S3 (Sitch et al., 2015; Le Quéré et al., 2018). The models containing fNup are ORCHIDEE, LPX-Bern, LPJ-GUESS, JULES, JSBACH, DLEM, CLM5.0, and Cable-POP, and the S3 experiment in the simulation considering the adaptation of CO_2, land use, N deposition, and climate from 1850 representing current environmental conditions. We calculated the yearly mean Nup from 1984 to 2022 for each model. Then, we calculated the difference between each TRENDY model and our Nup estimations. We also calculated the latitudinal mean of the difference to achieve a latitudinal profile and calculated the overall mean.

Contributions

H.V. and C.T. conceived the project; C.T. got the funding and supervised the work; H.V., C.M., A.K., J.C., and D.T. collected and compiled the data; H.V. curated and analyzed the data, created the visuals and wrote the first draft; H.V., C.T., M.D.B., M.F.M., M.L., D.G., contributed with substantial ideas and feedback on the manuscript; all authors revised, edited, and agreed on the final manuscript.

Data availability statement

The data gathered for this study, code and produced models are available at Zenodo (Vallicrosa Pou, 2024).

Competing interests

The authors declare no competing interests

Acknowledgments

We acknowledge the members of the Terrer Lab for providing scientific consulting as well as mental and emotional support during the investigation. We acknowledge the Pioneer Center Land-CRAFT, Department of Agroecology, Aarhus University for making possible this collaboration with D.G. J.C. was supported by the National Agency of Agricultural Research of the Czech Republic (Project No. QK22020008) and the Ministry of Agriculture (CR), institutional support MZE-RO0123, and he thanks FGMRI technician staff for help with field

https://doi.org/10.5194/egusphere-2024-3661
Preprint. Discussion started: 13 January 2025

and lab works. M.F.M was supported by the European Research Council project ERC-StG-2022-101076740 STOIKOS and a Ramón y Cajal fellowship (RYC2021-031511-I) funded by the Spanish Ministry of Science and Innovation, the NextGenerationEU program of the European Union, the Spanish plan of recovery, transformation and resilience, and the Spanish Research Agency.

References

Aber, J.D., Nadelhoffer, K.J., Steudler, P. & Melillo, J.M. (1989) Nitrogen saturation in northern forest ecosystems. BioScience, 39, 378– 386.

Aber, J., and J. Melillo. 2001. Terrestrial ecosystems. Second edition. Harcourt Academic Press, San Diego, California, USA.

Ackerman, D., Millet, D. B., & Chen, X. (2019). Global estimates of inorganic nitrogen deposition across four decades. *Global Biogeochemical Cycles*, 33, 100– 107. https://doi.org/10.1029/2018GB005990

Arora, V. K., Katavouta, A., Williams, R. G., Jones, C. D., Brovkin, V., Friedlingstein, P., et al. (2020). Carbon-concentration and carbon-climate feedbacks in CMIP6 models and their comparison to CMIP5 models. Biogeosciences, 17(16), 4173–4222. https://doi.org/10.5194/ bg-17-4173-2020

Averill, C., Bhatnagar, J. M., Dietze, M. C., Pearse, W. D. & Kivlin, S. N. Global imprint of mycorrhizal fungi on whole-plant nutrient economics. *Proc. Natl Acad. Sci. USA* 116, 23163–23168 (2019).

Bartoń K (2023). _MuMIn: Multi-Model Inference_. R package version 1.47.5, <https://CRAN.R-project.org/package=MuMIn>.

Bauters, M., Verbeeck, H., Rütting, T., Barthel, M., Bazirake Mujinya, B., Bamba, F., Bodé, S., Boyemba, F., Bulonza, E., Carlsson, E., Eriksson, L., Makelele, I., Six, J., Cizungu Ntaboba, L., & Boeckx, P. (2019). Contrasting nitrogen fluxes in African tropical forests of the Congo Basin. *Ecological Monographs*, *89*(1), 1–17. https://doi.org/10.1002/ecm.1342

Bauters, M., Janssens, I.A., Wasner, D. *et al.* Increasing calcium scarcity along Afrotropical forest succession. *Nat Ecol Evol* 6, 1122–1131 (2022). https://doi.org/10.1038/s41559-022-01810-2

BERNTSON, G.M., RAJAKARUNA, N. and BAZZAZ, F.A. (1998), Growth and nitrogen uptake in an experimental community of annuals exposed to elevated atmospheric CO2. Global Change Biology, 4: 607-626. https://doi.org/10.1046/j.1365-2486.1998.00171.x

Bobbink*, R. et al. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. Ecol. Appl. 20, 30–59 (2010).*

Braghiere, R. K., Fisher, J. B., Allen, K., Brzostek, E., Shi, M., Yang, X., et al. (2022). Modeling global carbon costs of plant nitrogen and phosphorus acquisition. *Journal of Advances in Modeling Earth Systems*, 14, e2022MS003204. https://doi.org/10.1029/2022MS003204

Chen, T., and Guestrin, C. XGBoost: A scalable Tree Boosting System. arXiv:1603.02754v3

https://doi.org/10.5194/egusphere-2024-3661
Preprint. Discussion started: 13 January 2025

Chen T, He T, Benesty M, Khotilovich V, Tang Y, Cho H, Chen K, Mitchell R, Cano I, Zhou T, Li M, Xie J, Lin M, Geng Y, Li Y, Yuan J (2023). _xgboost: Extreme Gradient Boosting_. R package version 1.7.5.1, <https://CRAN.R-project.org/package=xgboost>.

Crowther TW, van den Hoogen J, Wan J, Mayes MA, Keiser AD, Mo L, et al. The global soil community and its influence on biogeochemistry. Science. 2019;365:eaav0550.

Defourny, P. (2019): ESA Land Cover CCI project team; ESA Land Cover Climate Change Initiative (Land_Cover_cci): Global Land Cover Maps, Version 2.0.7. Centre for Environmental Data Analysis, date of citation. https://catalogue.ceda.ac.uk/uuid/b382ebe6679d44b8b0e68ea4ef4b701c

Delgado-Baquerizo M, Reich PB, Trivedi C, Eldridge DJ, Abades S, Alfaro FD, et al. Multiple elements of soil biodiversity drive ecosystem functions across biomes. Nat Ecol Evol. 2020;4:210–20.

Du, E., Terrer, C., Pellegrini, A.F.A. et al. Global patterns of terrestrial nitrogen and phosphorus limitation. Nat. Geosci. 13, 221–226 (2020). https://doi.org/10.1038/s41561-019-0530-4

Dybzinski, R., Segal, E., McCormack, M.L. et al. Calculating Nitrogen Uptake Rates in Forests: Which Components Can Be Omitted, Simplified, or Taken from Trait Databases and Which Must Be Measured In Situ?. Ecosystems 27, 739–763 (2024). https://doi.org/10.1007/s10021-024-00919-8

Elser JJ, Fagan WF, Kerkhoff AJ, Swensson NG, Enquist BJ. 2010. Biological stoichiometry of plant production: metabolism, scaling and ecological response to global change. New Phytologist 186: 593–608.

Battye, W., Aneja, V.P. and Schlesinger, W.H. (2017), Is nitrogen the next carbon? Earth's Future, 5: 894-904. https://doi.org/10.1002/2017EF000592

Etzold S, Ferretti M, Reinds GJ, Solberg S, Gessler A, Waldner P, Schaub M, Simpson D, Benham S, Hansen K, Ingerslev M, Jonard M, Karlsson PE, Lindroos A-J, Marchetto A, Manninger M, Meesenburg H, Merilä P, Nöjd P, Rautio P, Sanders TGM, Seidling W, Skudnik M, Thimonier A, Verstraeten A, Vesterdal L, Vejpustková M, de Vries W (2020) Nitrogen deposition is the most important environmental driver of growth of pure, even-aged and managed European forests. Forest Ecology and Management 458: 117762. DOI: 10.1016/j.foreco.2019.117762

Fernández-Martínez, M., Vicca, S., Janssens, I. *et al.* Nutrient availability as the key regulator of global forest carbon balance. *Nature Clim Change* 4, 471–476 (2014). https://doi.org/10.1038/nclimate2177

Fernández-Martínez, M., Sardans, J., Chevallier, F. *et al.* Global trends in carbon sinks and their relationships with CO2 and temperature. *Nature Clim Change* 9, 73–79 (2019). https://doi.org/10.1038/s41558-018-0367-7

Fick, S.E. and R.J. Hijmans, 2017. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37 (12): 4302-4315.

Finzi AC, Norby RJ, Calfapietra C, Gallet-Budynek A, Gielen B, Holmes WE, Hoosbeek MR, Iversen CM, Jackson RB, Kubiske ME, Ledford J, Liberloo M, Oren R, Polle A, Pritchard S, Zak DR, Schlesinger WH, Ceulemans R. 2007.Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO2. Proceedings of the National Academy of Sciences 104: 14014-14019.

https://doi.org/10.5194/egusphere-2024-3661
Preprint. Discussion started: 13 January 2025

Fleischer, K., Rammig, A., De Kauwe, M. G., Walker, A. P., Domingues, T. F., Fuchslueger, L., et al. (2019). Amazon forest response to CO2 fertilization dependent on plant phosphorus acquisition. Nature Geoscience, 12(9), 736–741. https://doi.org/10.1038/s41561-019-0404-9

Fowler D, Steadman CE, Stevenson D, Coyle M, Rees RM, Skiba UM, Sutton MA, Cape JN, Dore AJ, Vieno M, Simpson D, et al. Effects of global change during the 21st century on the nitrogen cycle. Atmospheric Chemistry and Physics. 2015; 15(24): 13849-13893. https://doi.org/10.5194/acp-15-13849-2015

Franklin, O., Harrison, S.P., Dewar, R. *et al.* Organizing principles for vegetation dynamics. *Nat. Plants* 6, 444–453 (2020). https://doi.org/10.1038/s41477-020-0655-x

Gundersen, P., Emmett, B.A., Kjonaas, O.J., Koopmans, C.J. & Tietema, A. (1998) Impact of nitrogen deposition on nitrogen cycling in forests: a synthesis of NITREX data. Forest Ecology and Management, 101, 37– 55.

Gurmesa, G.A., Wang, A., Li, S. *et al.* Retention of deposited ammonium and nitrate and its impact on the global forest carbon sink. *Nat Commun* 13, 880 (2022). https://doi.org/10.1038/s41467-022-28345-1

Hijmans R (2023). _raster: Geographic Data Analysis and Modeling_. R package version 3.6-20, https://CRAN.R-project.org/package=raster

Hungate, B.A., *et al.*, Nitrogen and Climate Change. *Science*302,1512-1513(2003). DOI:10.1126/science.1091390

Iversen C M, Bridgham S D and Kellogg L E 2010 Scaling plant nitrogen use and uptake efficiencies in response to nutrient addition in peatlands *Ecology* 91 693–707

Jackman, S (2020). pscl: Classes and Methods for R Developed in the Political Science Computational Laboratory. United States Studies Centre, University of Sydney. Sydney, New South Wales, Australia. R package version 1.5.5.1. URL https://github.com/atahk/pscl/

Kanakidou, M., Myriokefalitakis, S., Daskalakis, N., Fanourgakis, G., Nenes, A., Baker, A. R., Tsigaridis, K., & Mihalopoulos, N. (2016). Past, present, and future atmospheric nitrogen deposition. Journal of the Atmospheric Sciences, 73(5), 2039–2047. https://doi.org/10.1175/JAS-D-15-0278.1

Kuzyakov, Y. and Xu, X. (2013), Competition between roots and microorganisms for nitrogen: mechanisms and ecological relevance. New Phytol, 198: 656-669. https://doi.org/10.1111/nph.12235

Le Quéré, C. et al., Global Carbon Budget 2018, Earth Syst. Sci. Data, 10, 2141-2194, DOI: 10.5194/essd-10-2141-2018, 2018.

McIntire E, Chubaty A (2023). _SpaDES.tools: Additional Tools for Developing Spatially Explicit Discrete Event Simulation (SpaDES) Models_. R package version 2.0.0, <https://CRAN.R-project.org/package=SpaDES.tools>.

Niu, S., Classen, A.T., Dukes, J.S., Kardol, P., Liu, L., Luo, Y., Rustad, L., Sun, J., Tang, J., Templer, P.H., Thomas, R.Q., Tian, D., Vicca, S., Wang, Y.-P., Xia, J. and Zaehle, S. (2016), Global patterns and substrate-based mechanisms of the terrestrial nitrogen cycle. Ecol Lett, 19: 697-709. https://doi.org/10.1111/ele.12591

Peng, Y, Chen, HYH, Yang, Y. Global pattern and drivers of nitrogen saturation threshold of grassland productivity. Funct Ecol. 2020; 34: 1979–1990. https://doi.org/10.1111/1365-2435.13622

https://doi.org/10.5194/egusphere-2024-3661
Preprint. Discussion started: 13 January 2025

673 Peng, Y., Prentice, I. C., Bloomfield, K. J., Campioli, M., Guo, Z., Sun, Y., Tian, Di, Wang, X., Vicca, S.,
674 & Stocker, B. D. (2023). Global terrestrial nitrogen uptake and nitrogen use efficiency. *Journal of*
675 *Ecology*, 111, 2676–2693. https://doi.org/10.1111/1365-2745.14208
676
677 Penuelas, J, Janssens, IA, Ciais, P, Obersteiner, M, Sardans, J. Anthropogenic global shifts in biospheric N
678 and P concentrations and ratios and their impacts on biodiversity, ecosystem productivity, food security,
679 and human health. *Glob Change Biol*. 2020; 26: 1962– 1985. https://doi.org/10.1111/gcb.14981
680
681 Poggio, L., de Sousa, L. M., Batjes, N. H., Heuvelink, G. B. M., Kempen, B., Ribeiro, E., and Rossiter, D.:
682 SoilGrids 2.0: producing soil information for the globe with quantified spatial uncertainty, SOIL, 7, 217–
683 240, https://doi.org/10.5194/soil-7-217-2021, 2021.
684
685 Prentice, I. C., Liang, X., Medlyn, B. E., & Wang, Y.-P. (2015). Reliable, robust and realistic: The three R's
686 of next-generation land-surface modelling. Atmospheric Chemistry and Physics, 15(10), 5987–6005.
687 https://doi.org/10.5194/acp-15-5987-2015
688
689 Ruehr, S., Keenan, T.F., Williams, C. et al. Evidence and attribution of the enhanced land carbon sink. Nat
690 Rev Earth Environ 4, 518–534 (2023). https://doi.org/10.1038/s43017-023-00456-3
691
692 Shcherbak I, Millar N and Robertson G P 2014 Global metaanalysis of the nonlinear response of soil nitrous
693 oxide (N_2O) emissions to fertilizer nitrogen *Proc. Natl Acad. Sci. USA* 111 9199–204
694
695 Sinsabaugh, R., Carreiro, M. & Repert, D. Allocation of extracellular enzymatic activity in relation to litter
696 composition, N deposition, and mass loss. *Biogeochemistry* 60, 1–24 (2002).
697 https://doi.org/10.1023/A:1016541114786
698
699 Sinsabaugh, R.L., Lauber, C.L., Weintraub, M.N., Ahmed, B., Allison, S.D., Crenshaw, C., Contosta, A.R.,
700 Cusack, D., Frey, S., Gallo, M.E., Gartner, T.B., Hobbie, S.E., Holland, K., Keeler, B.L., Powers, J.S., Stursova,
701 M., Takacs-Vesbach, C., Waldrop, M.P., Wallenstein, M.D., Zak, D.R. and Zeglin, L.H. (2008), Stoichiometry
702 of soil enzyme activity at global scale. Ecology Letters, 11: 1252-1264. https://doi.org/10.1111/j.1461-
703 0248.2008.01245.x
704
705 Sitch, S., Friedlingstein, P., Gruber, N., Jones, S. D., Murray-Tortarolo, G., Ahlström, A., et al. (2015). Recent
706 trends and drivers of regional sources and sinks of carbon dioxide. Biogeosciences, 12(3), 653–679.
707 https://doi.org/10.5194/BG-12-653-2015
708
709 Soudzilovskaia, N.A., Vaessen, S., Barcelo, M., He, J., Rahimlou, S., Abarenkov, K., Brundrett, M.C., Gomes,
710 S.I.F., Merckx, V. and Tedersoo, L. (2020), FungalRoot: global online database of plant mycorrhizal
711 associations. New Phytol, 227: 955-966. https://doi.org/10.1111/nph.16569
712
713 Stevens C J, Lind E M, Hautier Y and Harpole W S 2015 Anthropogenic nitrogen deposition predicts local
714 grassland primary production worldwide *Ecology* 96 1459–65
715
716 Stocker BD, Prentice IC, Cornell SE, Davies-Barnard T, Finzi AC, Franklin O, Janssens I, Larmola T, Manzoni
717 S, Näsholm T, Raven JA, et al. Terrestrial nitrogen cycling in Earth system models revisited. New
718 Phytologist. 2016; 210(4): 1165-1168. https://doi.org/10.1111/nph.13997
719
720 Sutton, M.A.; Fowler, D. 1993 Estimating the relative contribution of SOx, NOy and NHx inputs to effects
721 of atmospheric deposition Critical loads: concept and applications. Grange-over-Sands Workshop
722
723 Terrer, C., Jackson, R. B., Prentice, I. C., Keenan, T. F., Kaiser, C., Vicca, S., et al. (2019). Nitrogen and
724 phosphorus constrain the CO2 fertilization of global plant biomass. Nature Climate Change, 9(9), 684–
725 689. https://doi.org/10.1038/s41558-019-0545-2

https://doi.org/10.5194/egusphere-2024-3661
Preprint. Discussion started: 13 January 2025

Tian, D., Wang H.,, Sun, J., and Niu, S. Global evidence on nitrogen saturation of terrestrial ecosystem net primary productivity. 2016. Environmental Research Letters, Volume 11, Number 2

Tian, D., Kattge, J., Chen, Y., Han, W., Luo, Y., He, J., Hu, H., Tang, Z., Ma, S., Yan, Z., Lin, Q., Schmid, B., Fang, J. 2019. A global database of paired leaf nitrogen and phosphorus concentrations of terrestrial plants. Ecology 100(9): e02812.

Vallicrosa, H., J. Sardans, J. Maspons, and J. Peñuelas. 2022. "Global distribution and drivers of forest biome foliar nitrogen to phosphorus ratios (N:P)." Global Ecology and Biogeography 31: 861–71.

Vallicrosa Pou, H. (2024). Global plant nitrogen uptake and nitrogen use efficiency. Zenodo. https://doi.org/10.5281/zenodo.13332734

Vicca, S., Stocker, B. D., Reed, S., Wieder, W. R., Bahn, M., Fay, P. A., Janssens, I. A., Lambers, H., Peñuelas, J., Piao, S., Rebel, K. T., Sardans, J., Sigurdsson, B. D., Sundert, K. V., Wang, Y. P., Zaehle, S., and Ciais, P.: Using research networks to create the comprehensive datasets needed to assess nutrient availability as a key determinant of terrestrial carbon cycling, Environ. Res. Lett., 13, 125006,https://doi.org/10.1088/1748-9326/aaeae7, 2018.

Walker, T. W., and J. K. Syers. 1976. "Fate of Phosphorus during Pedogenesis." Geoderma 15: 1–19.
Soudzilovskaia, N.A., van Bodegom, P.M., Terrer, C. *et al.* Global mycorrhizal plant distribution linked to terrestrial carbon stocks. *Nat Commun* 10, 5077 (2019). https://doi.org/10.1038/s41467-019-13019-2

Walker, A.P., De Kauwe, M.G., Bastos, A., Belmecheri, S., Georgiou, K., Keeling, R.F., McMahon, S.M., Medlyn, B.E., Moore, D.J.P., Norby, R.J., Zaehle, S., Anderson-Teixeira, K.J., Battipaglia, G., Brienen, R.J.W., Cabugao, K.G., Cailleret, M., Campbell, E., Canadell, J.G., Ciais, P., Craig, M.E., Ellsworth, D.S., Farquhar, G.D., Fatichi, S., Fisher, J.B., Frank, D.C., Graven, H., Gu, L., Haverd, V., Heilman, K., Heimann, M., Hungate, B.A., Iversen, C.M., Joos, F., Jiang, M., Keenan, T.F., Knauer, J., Körner, C., Leshyk, V.O., Leuzinger, S., Liu, Y., MacBean, N., Malhi, Y., McVicar, T.R., Penuelas, J., Pongratz, J., Powell, A.S., Riutta, T., Sabot, M.E.B., Schleucher, J., Sitch, S., Smith, W.K., Sulman, B., Taylor, B., Terrer, C., Torn, M.S., Treseder, K.K., Trugman, A.T., Trumbore, S.E., van Mantgem, P.J., Voelker, S.L., Whelan, M.E. and Zuidema, P.A. (2021), Integrating the evidence for a terrestrial carbon sink caused by increasing atmospheric CO2. New Phytol, 229: 2413-2445. https://doi.org/10.1111/nph.16866

Wang R, Goll D, Balkanski Y, Hauglustaine D, Boucher O, Ciais P, Janssens I, Pe˜ nuelas J, Guenet B, Sardans J et al. 2017. Global forest carbon uptake due to nitrogen and phosphorus deposition from 1850–2100. Global Change Biology 23: 4854–4872.

Wang, X., Zhao, X. (Eds.), 2022. Protocol for Field Investigation and Literature Data Compilation of Carbon Storage in Terrestrial Ecosystems. Science Press, Beijing.

Wickham, H. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York, 2016.

Wickham H, Henry L (2023). _purrr: Functional Programming Tools_. R package version 1.0.2, <https://CRAN.R-project.org/package=purrr>.

WU, Z., DIJKSTRA, P., KOCH, G.W., PEÑUELAS, J. and HUNGATE, B.A. (2011), Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. Global Change Biology, 17: 927-942. https://doi.org/10.1111/j.1365-2486.2010.02302.x

https://doi.org/10.5194/egusphere-2024-3661
Preprint. Discussion started: 13 January 2025

Xu, X., Thornton, P.E. and Post, W.M. (2013), Global soil microbial biomass C, N and P. Global Ecology and Biogeography, 22: 737-749. https://doi.org/10.1111/geb.12029

Yang, J. and Tian, H. (2022): ISIMIP3a N-deposition input data (v1.2). ISIMIP Repository. https://doi.org/10.48364/ISIMIP.759077.2

Zaehle S, Medlyn BE, De Kauwe MG, Walker AP, Dietze MC, Hickler T, Luo Y, Wang YP, El-Masri B, Thornton P, Jain A, et al. Evaluation of 11 terrestrial carbon-nitrogen cycle models against observations from two temperate Free-Air CO2 Enrichment studies. New Phytologist. 2014; 202(3): 803-822. https://doi.org/10.1111/nph.12697

Zhou G, Terrer C, Huang A, Hungate BA, van Gestel N, Zhou X, van Groenigen KJ. Nitrogen and water availability control plant carbon storage with warming. Sci Total Environ. 2022 Dec 10;851(Pt 1):158243. doi: 10.1016/j.scitotenv.2022.158243. Epub 2022 Aug 23. PMID: 36007637.