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

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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.

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 field experiments (including above and belowground information) 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, mean temperature and precipitation, with Nup increasing in warmer and wetter areas. In contrast, NUE is driven by soil biotic and abiotic 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 at a global scale.

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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.

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 predicting 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.

The soil community (i.e. microbes and fungi) plays a crucial role in global biogeochemical cycles governing processes such as N fixation, nitrification, denitrification and general organic matter and nutrient turnover (Aber et al., 2001; Sinsabaugh et al., 2002; Sinsabaugh et al., 2008; Crowther et al., 2019; Delgado-Baquerizo et al., 2020). In turn, the soil community can also act as a buffer in case of nutrient excess (Wall et al., 2015) or contribute to nutrient foraging in case of nutrient deficiencies (Chen et al., 2018), shaping ecosystem functioning (Bardgett and van der Putten, 2014). Therefore, the soil community is expected to substantially interfere with in the plants Nup and NUE. N deposition is another agent relevant for global N cycles, which has increased from ~30 to ~80 Tg N/year worldwide since 1850 (Kanakidou et al., 2016) with an associated increase in 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 ensemble 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). Consequently, 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. 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.

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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, wet, and with higher levels of N deposition, exhibit the highest rates of Nup. Our results show that N deposition is strongly contributing to fulfilling the N demand in productive environments, alleviating potential N limitations and allowing high plant Nup levels. On the other hand, our empirical results did not show important relationships between plant Nup and soil microbial interactions nor soil physico-chemical variables (Fig. 1a). Those results include no significant relationship between soil N stocks and Nup at a global scale (Fig. S1a), which has been further tested following a univariate approach. This result discourages the use of soil N to infer N availability.

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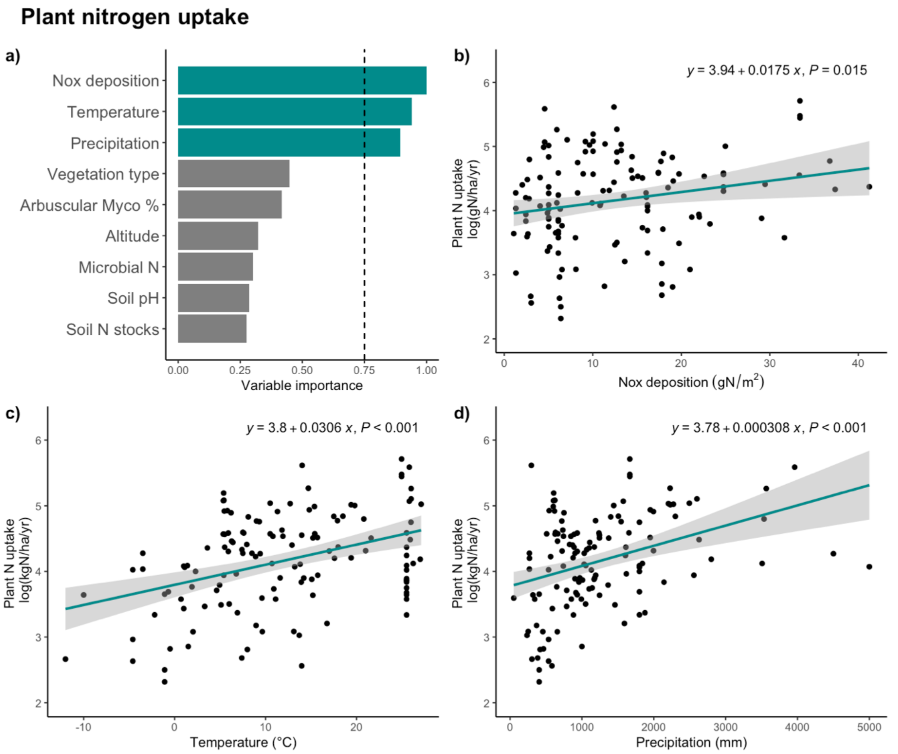
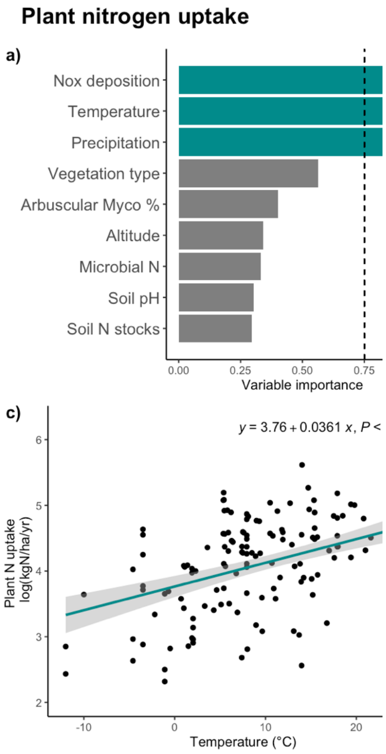


Figure 1. a) Variable importance plot for the general linear model (GLM) describing plant nitrogen uptake (Nup). The dashed line is set at 0.75, separating the threshold for important variables. The GLM model pseudoR^2 was 0.349. Linear regressions were displayed describing plants' nitrogen and important 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 the main NUE drivers (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, plant species prone to be colonized by arbuscular mycorrhizae, are less efficient in N use to build biomass. In contrast, 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). Despite climatic variables such as MAT and MAP not appearing as important variables explaining NUE, they are to some extent represented in the soil variables. As shown in Table S2, soil variables are not independent of climatic variables since they have some degree of correlation.



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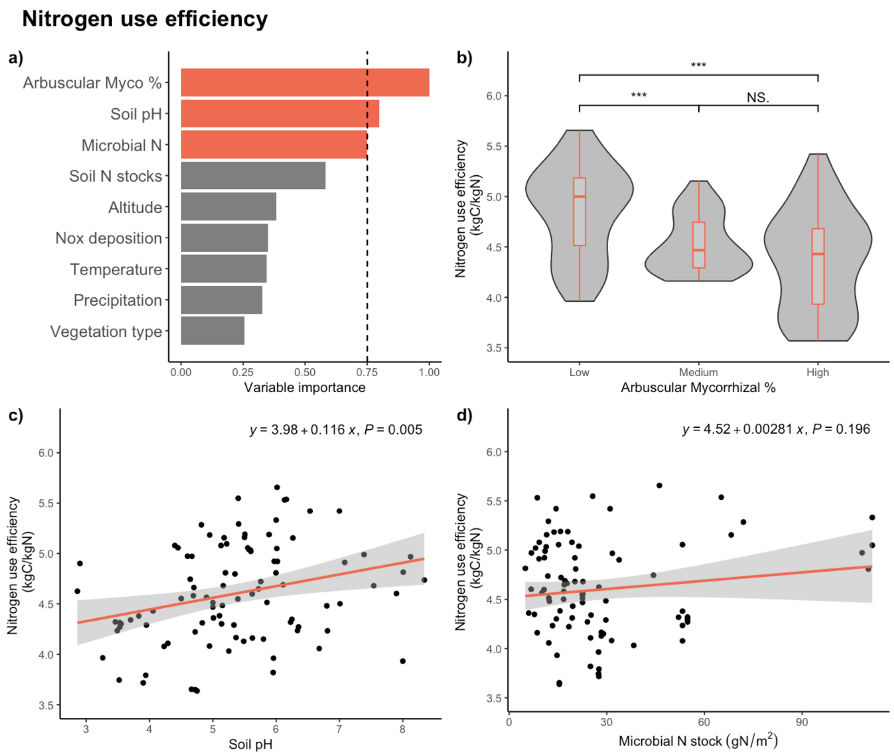

*Figure 2. a) Variable importance plot for the generalized linear model describing nitrogen use efficiency (NUE). The model preudoR2 was 0.355. The dashed line is set at 0.75, separating the threshold for important variables. In b) arbuscular mycorrhizae percentage is divided into low, medium, and high, 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

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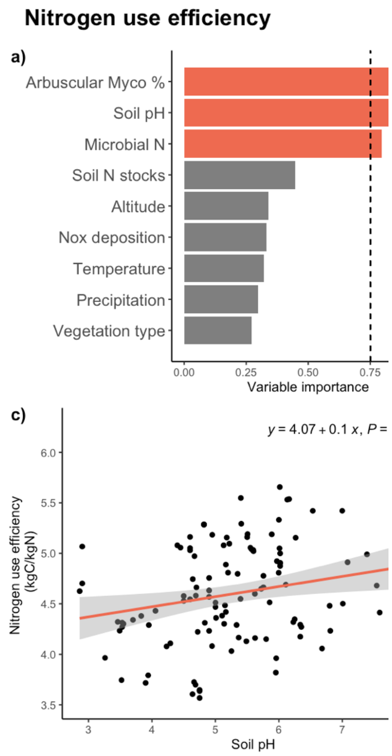

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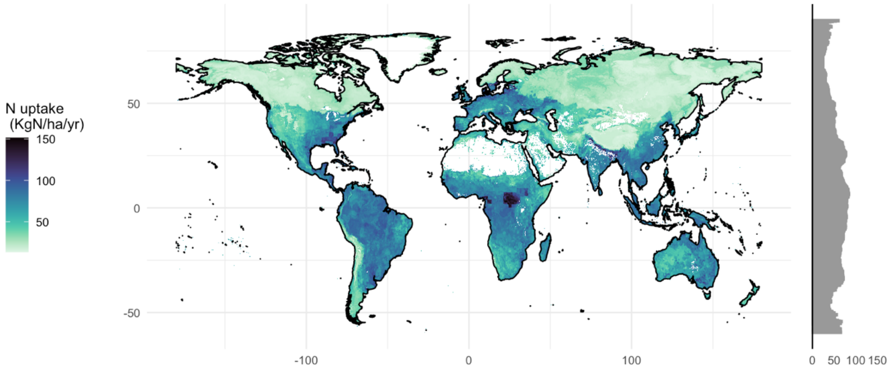
temperate latitudes in Europe, the eastern United States, Southeast Asia, East Australia, most of South America, and central Africa, with the most intense spot around Congo, where there is the most N deposition, temperature and precipitation combined (Fig. 3a). Therefore, Nup map shows an NPP influence,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

a) Global nitrogen uptake: 842.215 ± 236.110 Tg N/yr



b) Average nitrogen use efficiency: 110.262 ± 19.40 kg C/Kg N

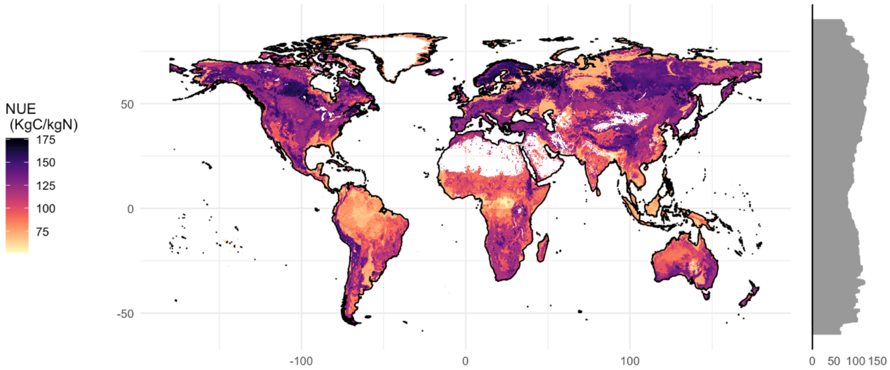


Figure 3. Upscaled global maps describing a) Plant nitrogen uptake and b) Nitrogen use efficiency. The total amount of nitrogen uptake calculated per year is 842.215 Tg of N with a standard deviation of ± 236.11. The mean value of global nitrogen use efficiency is 110.26 kg of C per kg of N, and its 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

(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 exceeding our range of confidence, assuming a significantly larger Nup (Fig. S7).

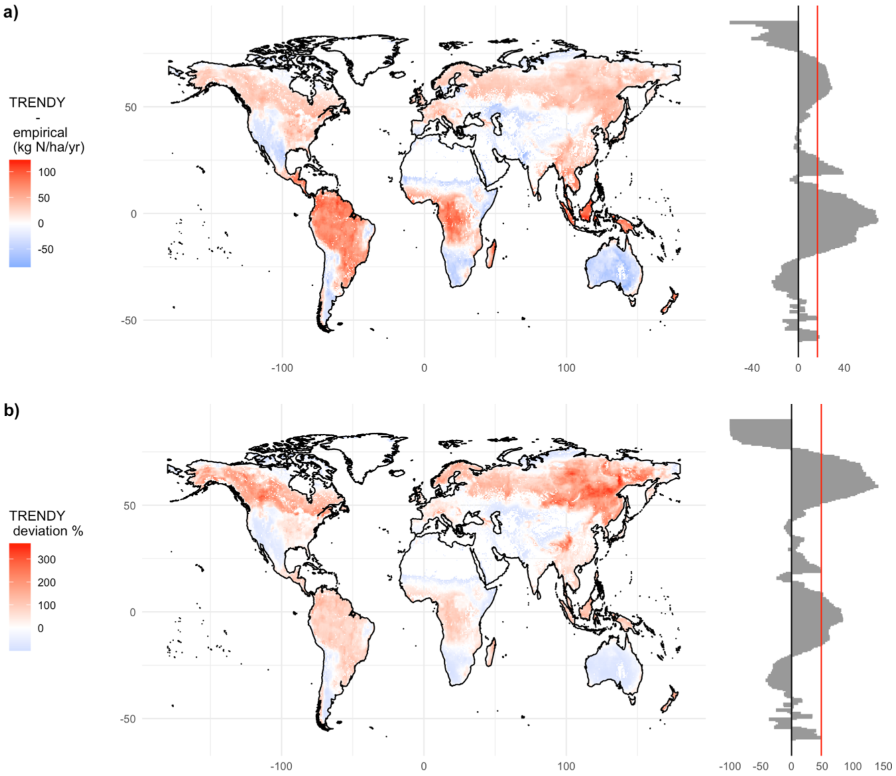


Figure 4. Comparison between the mean of the nitrogen uptake provided by TRENDY v8 models minus the upscaled nitrogen uptake. The red color stands for higher values on the TRENDY model, and the blue color stands for higher nitrogen uptake values on the upscaled approach. In a) units in kg N ha^{-1} yr^{-1} 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 ± 236 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

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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 levels during the last four decades (Ackerman et al., 2019). Nonetheless, these reductions do not translate yet into how N deposition effects natural woodlands and grasslands, showing to still be the main driver for plant Nup. 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 extra input of N coming from N deposition is not being captured by biomass and enhances 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.

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2.5 NUE global drivers and implications

Our results predict a mean NUE of 110 ± 19 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 a global scale.

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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 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 on 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.

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2.6 Latitudinal discrepancies between Nup map and TRENDY

LPX-Bern and CLM5.0, models included in the TRENDY ensemble, projected Nup values significantly above our estimations, being 1471 and 1454 Tg N/yr respectively (Fig. S7). Even though the average of all TRENDY models falls within our Nup confidence range differences become relevant through space. In tropical and northern latitudes, TRENDY models projected higher values than our estimations. On the other hand, TRENDY models projected lower Nup values in southern latitudes, western Asia and at the Rocky Mountains. 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 more accurate Nup and NUE values.

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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 systematic geographical sampling biases are underrepresenting the global south. In this study, 28 % of the data comes from areas below 15º latitude, outside the US, Europe, or China (Fig. S8). When accounting for ecosystem representativity, the Whittaker diagram shows we have a representation of all the biomes (Fig. S9), showing the lowest representativity on subtropical deserts, tundra, and temperate rainforest. Nonetheless, we acknowledge that calculations based on empirical data, especially when a portion of the data has undergone a gap-filling process, can still have

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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.

Global scale approaches such as this one, are intended to provide broad quantifications of planetary processes assuming a scale-precision compromise. Because of that, we do not advise using our approach to seek fine-scale precision, since our results may overlook local particularities and differences between forest type, species distribution, or management practices.

This study is focused on a quantitative approach at a 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. We also encourage empirical studies sampling underrepresented biomes, specially from the global south. Approaches such as those 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 enhancing our understanding of the N cycle and its interactions with ecosystems.

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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 Data extraction

We gathered 159 field plot data representing 129 different sites in natural conditions coming from published data or repositories (Table S1). The data included information on the 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 at the same location and time. In situ measurements for foliage

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and fine roots are the most relevant for Nup calculation (Dybzinski et al., 2024), so all our data points include biomass production (NPP) and N content (N%) of leaves and roots. We gathered 45 data points, representing 28% of the data, coming from latitudes under the 15º latitude, despite 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 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.

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 (% of colonization) based on Soudzilovskaia et al. 2020, and categorized it into 0, 50, or 100 arbuscular mycorrhizal (AM) percentages, since AM is the most abundant and common throughout the globe. When dominant species were not provided, we extracted the AM% of colonization 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.

4.2 Nitrogen uptake and Nitrogen use efficiency 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:

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4.2 Environmental data

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

$$Nup = (NPPleaves * Nleaves + NPPstem * Nstem + NPProots * Nroots) - (NPPleaves * Nleaves - NPPlitter * Nlitter)$$

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

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.

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

NUE = Nitrogen use efficiency (kg C / kg N)
NPP = Net primary production (kg of biomass/ha/yr)
Nup = Plant nitrogen uptake (kg N/ha/yr)

4.3 Linear statistical analysis

Nup and NUE values correlate 34% (Fig. S10). 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). With the less correlated variables, we created generalized linear models using Nup and NUE as dependent variables. The family was set up as Gamma with an inverse link to fulfill the residual normality requirements. We also calculated the Variance Inflation Factor (VIF) with the *vif* function of the car R package (Fox and Weisberg, 2019) of the aggregated model to validate VIF's lower than 4. 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), which is a standard method based on Akaike weights (Giam and Olden, 2016). 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).

4.4 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 standard ratio of 70:20:10, respectively (Lever et al., 2016). 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). XGBoost is a non-parametric model particularly indicated for high performance in sample sizes above 100 data points, overcoming potential problems of autocorrelation and optimizing predictive power. We trained an XGBoost model using the

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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 (prediction R^{2}) at a maximum depth of 6, minimum child weight of 1, and eta of 0.3, which are generally standard values. 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.

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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 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.

4.5 Nitrogen uptake comparison with TRENDY models ensemble

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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, and the average of all of them combined, to obtain a final yearly value. Then, we calculated the difference between each model included in the TRENDY ensemble and our Nup estimations. After, we averaged all the fNup values in a unique spatial explicit representation and compared it with our estimations. We also calculated the latitudinal mean of the difference to achieve a latitudinal profile and calculated the overall mean.

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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

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