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# Global distribution and drivers of forest biome foliar N:P ratios

## Abstract

**Aim**

To create global maps of foliar N:P ratios across ecosystems, based on modeled climate, soil, and N and P deposition data. Identify global drivers of woody vegetation N:P ratios and explore the role of genetic legacy (phylogenetics) in foliar N:P ratios of woody plants.

**Location**

Woody cover for all over the world

**Time period**

Now. Data collected from 1990 to 2016

**Major taxa studies**

Woody plants

**Methods**

We compiled a database of 20851 foliar N:P records and we assigned them into Boreal, Temperate coniferous, Temperate broadleaved and Tropical. We applied neural networks to predict N:P global distribution maps, generalized linear models to asses environmental drivers and generalized linear mixed models to disentangle the effect of genetic legacy.

**Results and Main conclusions**

Foliar N:P ratios are negatively associated with latitude, with higher N:P ratios occurring in tropical forests and lower N:P ratios occurring in boreal forests. Globally, N:P ratios indicate greater levels of P limitation than N limitation. The influence of environmental factors varied among the four forest biomes, likely due to contrasting combined environmental conditions; this finding would have been obscured had we conducted a single "forest biome" analysis. Genetic legacy explained significant variation in woody plant foliar N:P ratios and we suggest its inclusion in future studies to improve N:P ratio predictions.

**Keywords**

Neural network; elemental composition; global map; genetic drivers; N:P ratio; C-cycle; forest ecology; biogeochemistry; N limitation; P limitation

## 1. Introduction

In terrestrial systems, the ratio of nitrogen (N) to phosphorus (P) (N:P) content of plant foliar tissue is an indicator of spatio-temporal variations in plant physiological and ecosystem biogeochemical function, including N and/or P limitation or co-limitation (Schreeg et al., 2014), species niche occupation (Peñuelas et al., 2019), and vegetation carbon (C) retention capacity (Güsewell 2004; Ågren 2008; Tian et al., 2018). For example, in natural and agricultural ecosystems, biomass growth is constrained by N:P leaf ratios (Vitousek & Howarth, 1991; Van Duren & Pegtel 2000; Das et al. 2006).

The relationship between foliar N:P content and terrestrial ecosystem biogeochemical function may be described by the growth rate hypothesis (GRH) that states that fast growing species require rapid protein synthesis, which in turn, requires large amounts of P-rich RNA. When essential resources, such as N or light, are at high levels of availability, increased growth rate is dependent on increases in P-rich RNA, as indicated by research that shows N:P ratios, particularly of leaf tissue, is negatively correlated with plant growth rate (Peng et al., 2011a; Rivas-Ubach et al., 2012; Yu et al., 2012; Yan et al., 2015; Jing et al., 2017). Under non-limiting conditions, balanced foliar N:P ratios of mature plants may be 14-16 on a mass basis (Elser et al., 2000; Knecht & Göransson, 2004; Zhang & Elser, 2017), although further research is needed for confirmation (Sardans et al., 2021), because Güsewell (2004) and Greenwood et al. (2008) reported ratios of N:P on a mass basis of <10 indicate limited N and ratios >20 indicate limited P, in contrast to Koerselman & Meuleman (1996), who reported ratios of <14 indicate limited N and ratios >16 indicate limited P. In terrestrial plants N:P increases relatively at low growth rates and decreases relatively at high growth rate. This relation is explained through the slow or rapid use of P respectively in the process of amino acid and protein synthesis. At low growth rates and low cell concentration of N and P, protein synthesis is mostly limited by N concentrations (amino acids) concentrations whereas at high N and P cell concentrations and high concentrations of amino acids and RNA the concentration of P limits the amino acid assemblage and thus protein synthesis and the possibilities to grow (Ågren, 2004; Yu et al., 2012). In this relationships, though, N concentrations scales slower than P concentrations in leaves and its correlation is not linear (Ågren, 2004, 2008; Reich and Oleksyn, 2004; Kerkhoff and Enquist, 2005; Niklas et al., 2005; Niklas and Cobb, 2005; Sardans et al., 2012; Sardans et al., 2016, b; Tian et al., 2018).

These links between plant growth rate and overall N:P ratios also vary with ontogeny and climate conditions. At initial stages of development, N:P ratios are negatively correlated with plant growth, due to the allocation of the nutrients to biomass production (Zhang et al., 2019), whereas at the mature growth stage, when plants invest greater proportions of N and P to non-growth functions, this relation becomes weaker (Kerkhoff and Enquist, 2005; Peñuelas and Sardans, 2009; Rivas-Ubach et al., 2012; Zhang et al., 2019). Temperature and water availability have been shown to increase community level N:P ratios (Fan et al., 2016), due to more favorable growth conditions (Sardans et al., 2011; Sun et al., 2017), while under drought conditions, N:P ratios may shift to improve water use efficiency (Rivas-Ubach et al., 2012; Qiao et al., 2018; Sun et al., 2019; Peñuelas et al., 2020; Sardans et al., 2021).

Quantification of plant N:P ratios may be used as a tool to understand plant community structure and function (Zhao et al., 2019), including across successional stages within biomes, where they are expected to be lower in rapidly growing pioneer plant species, such as grasses, than in slow growing, late-successional species, such as tree species (Peñuelas et al., 2013; Sardans and Peñuelas, 2013; Busch et al., 2018). For example, N:P ratios increase with successional stage in African savanna vegetation (grasses: 8.6; broad-leaf trees: 13.7; and, fine-leaf trees: 18) (Ratnam et al., 2008) and in eastern China (grassland: 7.38; early successional mixed forest: 14-16; late successional mixed forest: 18-20) (Yan et al., 2008). These associations are related to plant life history strategies that tend to vary across several stages of succession, as indicated by the associations between high N:P ratios and stress-tolerators, low N:P ratios and fast-growing, ruderal species, and intermediate N:P ratios and competitor species (Yan et al., 2008; Busch et al., 2018; Peñuelas et al., 2019). Changes in N:P ratios are known to affect the structure of terrestrial food webs (Fanin et al., 2013; et al., 2014; Zechmeister-Boltenstern et al., 2015; Paseka and Grunberg, 2019), while imbalances between N and P decrease ecosystem C retention capacity (Carnicer et al., 2015; Peñuelas et al., 2013) and affect ecosystem species composition, structure, diversity, and function (Sterner and Elser, 2002; Peñuelas et al., 2019;2020; Sardans et al., 2021).

In addition to local and regional scale variations in terrestrial foliar N and P concentrations and ratios, global-scale studies of their patterns and drivers have revealed monotonic decreases in N:P ratios from tropical to polar latitudes (McGroddy et al., 2004, Reich and Oleksyn, 2004; Kerkhoff et al., 2005; Yuan and Chen, 2009; Zhang et al. 2018, 2019b) that are consistent with latitudinal increases in N:P ratios with mean annual precipitation and temperature and the soil-age hypothesis (Walker and Sayers, 1976) that states older tropical soils may be more N-abundant and P-limited than relatively younger soils. However, these patterns and drivers of N:P ratios are inconsistent with findings of regional scale studies that have reported latitudinal increases in N:P (De Frenne et al., 2013; Sardans et al., 2016a,b; Zhang et al., 2019b). Our objectives were to a) use three approaches to create global maps of foliar N:P ratios across ecosystems, based on modeled climate, soil, and N and P deposition data; b) identify global drivers of woody vegetation N:P ratios; and, c) explore the role of genetic legacy (phylogenetics) in foliar N:P ratios of woody plants.

## 2. Materials and Methods

### 2.1 Database compilation

We compiled 25761 and 23815 globally distributed georeferenced records of woody plant N and P foliar concentrations, respectively, from the TRY (http://www.try-db.org) and ICP Forests (http://icp-forests.net) databases, the Catalan Forest Inventory (Gracia et al., 2004) and 230 published articles (Table S1). Data comprised comparable analytical methodologies, based on elemental analyses for N and sample acid digestion coupled to optical detection methods for P, for foliar samples collected between 1990 and 2016. Data with 2× standard deviation (SD) were considered outliers and removed to avoid mistakes in data collation or transcription; N:P ratios were then calculated from the remaining values, before data with 2× SD were again removed. Following outlier removal, our database comprised 20851 records.

Soil, climate, and N and P deposition data for locations of the georeferenced foliar N:P ratio data were input to the database using *raster* (Hijmans, 2020) and *sf* (Pebesma, 2018) R packages. Initially, we considered 34 soil variables from the Land-Atmosphere Interaction Research Group at Sun Yat-sen University (Shangguan et al., 2014), 26 climate variables, comprising the standard bioclimate variables from the WorldClim version 2 database (Fick and Hijmans, 2017), and evapotranspiration and aridity index data from the CGIAR-CSI v2 database (Trabucco & Zomer, 2019) at 1-km resolution at the equator. The climate data comprise estimations interpolated from a globally distributed, meteorological time series (1970-2000) and adjusted for topography. Twelve N deposition variables, based on reduced, oxidized, inorganic, and organic forms of N deposition, at 25-km resolution at the equator from 1984 to 2016 were extracted from Ackerman et al. (2018); data were downscaled to 1-km using the *res* function in the R *raster* package (Hijmans, 2020). Mean P deposition data for the period 1997−2013 were derived from Wang et al. (2017) at a resolution of 1 km. Following exclusion of some variables, due to redundancy, the final database comprised 73 soil, climate, and N and P deposition variables as drivers of woody plant foliar N:P concentrations (Table S2).

The database was divided into four types of forest biome, comprising tropical, temperate coniferous, temperate broadleaved and boreal, based on the WWF ecoregion map (Olson et al., 2001) that classifies "tundra" and "boreal forest/taiga" as boreal forests, "temperate broadleaf and mixed forests", "temperate grasslands, savannas and scrublands", "montane grasslands and scrublands", "Mediterranean forests, woodlands and scrub", "temperate conifer forests" and "deserts and xeric scrublands" from >30° latitude as temperate forests, and "tropical and subtropical moist broadleaved forest", "tropical and subtropical dry broadleaved forest", "tropical and subtropical grasslands, savannas and scrublands", "tropical and subtropical coniferous forests", "mangroves", "flooded grasslands and savannas", and "deserts and xeric scrublands" <30° latitude as tropical forests (Table S3 ab). The distinction between temperate coniferous and broadleaf forests was based on species taxonomy.

### 2.2 Global models of woody plant foliar N:P ratios

#### *Neural Networks*

One model per forest biome was built based on neural networks (NN) using the *keras* package in R (Allaire & Chollet, 2019). The Kaiser-Meyer-Olkin method was applied to each of the four subsets of data for the 53 climate, soil, and deposition variables to exclude those that were most strongly autocorrelated and to avoid overparameterization; the correlation threshold was settled according to result in 19 remaining variables (Table S4). Then, the datasets with remaining variables were randomly divided into training (60%), test (20%), and validation (20%) subsets (Lever et al., 2016), and data were standardized using *scale* function in R (R core team, 2020). Due to the greater number of data records derived from Europe, data collected from outside the region were weighted to avoid any potential European bias. We built independent NNs for the four forest biomes, where they were constructed with one input layer, two hidden layers of 128 densely connected neurons and one output layer comprising one neuron. The validation data were used to cross-validate the accuracy of the model following the K-fold methodology and the root mean squared error (RMSE), mean, SD, coefficient of variation, and $R^2$ were calculated for each model; the mean of values (±SE) from each repetition was calculated to obtain a final stable value.

The model predictions were extrapolated to the ESA-CCI land cover map v2.0.7b (ESA, 2017), at 300-m resolution, for the four forest biomes by element in three global raster maps; the resolution was modified to 1000-m using the aggregate function of the *raster* package in R (Hijmans, 2020), with mode as a gathering parameter. Then, the land-cover map was reclassified (Table S5.4) to the four forest biomes to match it with our predictions and use it to mask vegetation to determine the distribution of each forest type. The NN predictions were plotted at 1-km resolution in three raster longitude/latitude WGS 84 (World Geodesic System, 1984) projections, with the predicted woody plant foliar N:P ratios for mature leaves. Uncertainty maps were also provided for each element using the mean SE.

*Generalized linear models*

To test for associations between the soil, climate, and N and P deposition variables and N:P ratios, we selected the 10 most important variables, based on their NN variable importance, among which, a subset of the six least correlated variables was created and used to build generalized linear models (GLMs), with first-degree interactions following the gamma family distribution with inverse link. We then applied the dredge function in the *MuMIn* R package (Barton, 2019) to select the final models, based on the lowest Akaike information criterion, that comprised a maximum of six variables and interactions per model. The determined proportion of deviance explained by the GLM, or a pseudo-$R^2$ value, was calculated using the Dsquared function in the *modEvA* (Barbosa et al., 2015) R package.

*Generalized linear mixed models*

We used Bayesian generalized linear mixed models (GLMMs) in the *MCMCglmm* R package to understand the combined role of phylogeny and species compared with the roles of the soil, climate, and deposition predictors used for the NN. For the NN predictors, we again selected the 10 most important variables for each forest type and element, based on their importance in the NN, and created a subset of the six least strongly correlated fixed variables. For phylogeny, we used the phylogenetic tree provided by Qian and Jin (2015) that contained 744 of the species in our database; the species and their phylogenetic relations conformed to the random part of the models. The four models followed the form: element ~ var1+var2+var3+var4+var5+var6, random=phylogeny+species. The random variables, comprising species and phylogeny, describe the long-term evolutionary effects on genotypes, where phylogeny targets the response magnitude, due to phylogenetic distance, and species targets interspecific variability not directly related to phylogenetic distance.

### 2.3 Soil age

We used the USDA classification (Soil survey staff, 2014) of soil taxonomy at the order level to determine the influence of substrate age on woody plant foliar N:P ratios in the four forest types. We grouped the predicted N:P ratios from the NNs by their corresponding soil order and then compared the orders using ANOVA and Tukey's post hoc test with the HSD.test function in the *agricolae* (Mendiburu, 2020) R package; the results were visualized as violin plots by soil order, using ggplot2 (Wickham, 2016) by mean descending order.

## 3. Results

### 3.1 Global distribution of woody plant foliar N:P ratios

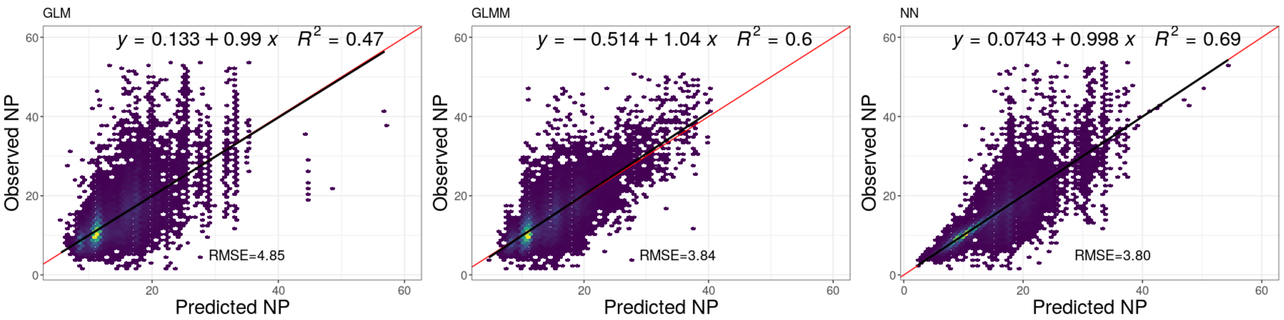

**Figure 1** Predicted versus observed foliar N:P values across the four forest biomes estimated by generalized linear modelling (GLM), generalized linear mixed modelling (GLMM), and neural networks (NN). Black line is the fitted linear model between predicted and expected values; red line is line of unity.

Of the three approaches used to predict woody plant foliar N:P ratios, greatest predictive power, based on predicted vs observed $R^2$, was provided by NNs ($R^2 = 0.69$; RMSE = 3.80) (Figure 1). The NNs predicted mean N:P ratios for the forest types were greatest in tropical forests (20.7±2.0), followed by temperate broadleaved forests (18.8±1.7), temperature coniferous forests (14.4±1.5), and boreal forests (12.4±1.7) (Table 1).

**Table 1** Neural network performance for all morphoclimatic groups. RMSE = Root mean squared error. MAE = Mean absolute error. SD = Standard deviation. CV = Coefficient of variation

| | **Tropical** | **Temperate coniferous** | **Temperate broadleaves** | **Boreal** |
|---|---|---|---|---|
| **RMSE (%)** | 7.077 | 3.622 | 5.619 | 1.918 |
| **MAE (%)** | 5.504 | 2.614 | 4.181 | 1.370 |
| **Mean (%)** | 20.698 | 14.442 | 18.827 | 12.346 |
| **SD (%)** | 1.972 | 1.453 | 1.677 | 1.730 |
| **CV (%)** | 0.095 | 0.101 | 0.089 | 0.140 |

The global distribution of woody plant foliar N:P ratios, based on NN predictions (Figure 2), confirmed lowest ratios are largely concentrated in boreal regions, particularly in northern Europe, as well as other regions, including India, northern Sub-Saharan Africa, and Patagonia. In contrast, regions with higher N:P ratios are generally located in the tropics and subtropics, including Amazonia, southeast Asia, southern Sub-Saharan Africa but also including southern Africa, Siberia, and north, south west Australia. Particularly, this high N:P levels in Siberia also match with a high SE (Standard error) zone in the predictions (Figure S1).

**Table 2** Summary of the generalized linear model per morphoclimatic group.

| | | Estimate | Pr(>\|t\|) |
|---|---|---|---|
| **Tropical** | **(Intercept)** | 0.050 | 0.000 |
| | **Soil base saturation** | 0.000 | 0.002 |
| | **Soil cation exchange capacity** | 0.001 | 0.000 |
| | **Potential evapotranspiration seasonality** | -0.001 | 0.000 |
| | **Maximum December, January, February precipitation** | -0.000 | 0.000 |
| | **Soil base saturation:soil cation exchange capacity** | -0.000 | 0.000 |
| | **Soil base saturation:Potential evapotranspiration seasonality** | 0.000 | 0.000 |
| | **AIC / pR$^2$** | 25536.497 | 0.230 |
| **Temperate coniferous** | **(Intercept)** | 0.045 | 0.000 |
| | **Aridity index** | -0.000 | 0.000 |
| | **Potential evapotranspiration seasonality** | 0.001 | 0.000 |
| | **Maximum June, July, August precipitation** | 0.001 | 0.000 |
| | **Mean temperature of the driest quarter** | -0.002 | 0.000 |
| | **Aridity index:Mean temperature of the driest quarter** | 0.000 | 0.000 |
| | **Potential evapotranspiration seasonality:Maximum June, July, August precipitation** | -0.000 | 0.000 |
| | **AIC / pR$^2$** | 61842.197 | 0.115 |
| **Temperate broadleaved** | **(Intercept)** | 0.087 | 0.000 |
| | **Minimum June, July, August precipitation** | 0.001 | 0.000 |
| | **Daily mean solar radiation** | -0.000 | 0.000 |
| | **Precipitation of the driest month** | -0.001 | 0.000 |
| | **Precipitation of the driest quarter** | -0.000 | 0.000 |
| | **Minimum June, July, August precipitation:Daily mean solar radiation** | 0.000 | 0.000 |
| | **Daily mean solar radiation:Precipitation of the driest quarter** | 0.000 | 0.000 |
| | **AIC / pR$^2$** | 35556.667 | 0.098 |
| **Boreal** | **(Intercept)** | 0.186 | 0.000 |
| | **Maximum June, July, August precipitation** | -0.006 | 0.000 |
| | **Mean temperature of warmest quarter** | -0.008 | 0.012 |
| | **Precipitation of wettest quarter** | 0.002 | 0.000 |
| | **Maximum June, July, August precipitation:Mean temperature of warmest quarter** | 0.000 | 0.000 |
| | **Maximum June, July, August precipitation:Precipitation of wettest quarter** | -0.000 | 0.000 |
| | **Mean temperature of warmest quarter:Precipitation of wettest quarter** | -0.000 | 0.000 |
| | **AIC / pR$^2$** | 8655.749 | 0.103 |

## 3.2 Environmental drivers of N:P ratios

The GLM used to test impacts of potential environmental drivers on woody plant foliar N:P ratios (Table 2) (global $R^2 = 0.47$ and RMSE = 4.85; Figure 1) showed positive relations with soil base saturation and soil cation exchange capacity in tropical forests and negative relations with potential evapotranspiration seasonality and maximum December, January and February precipitation (forest type $R^2 = 0.23$). In temperate coniferous forests (forest type $R^2 = 0.11$), there are positive relations with potential evapotranspiration seasonality and maximum June, July and August precipitation and negative relations with aridity index and mean temperature of the driest quarter, while in temperate broadleaf forests (forest type $R^2 = 0.10$), minimum June, July and August precipitation is positively related to foliar N:P ratios and daily mean solar radiation, precipitation of the driest month and precipitation of the driest quarter are negatively related to foliar N:P ratios; in boreal forests (forest type $R^2 = 0.10$), there is a positive relation with precipitation of the wettest quarter and negative relations with maximum June, July and August precipitation and mean temperature of the warmest quarter (Table 2).

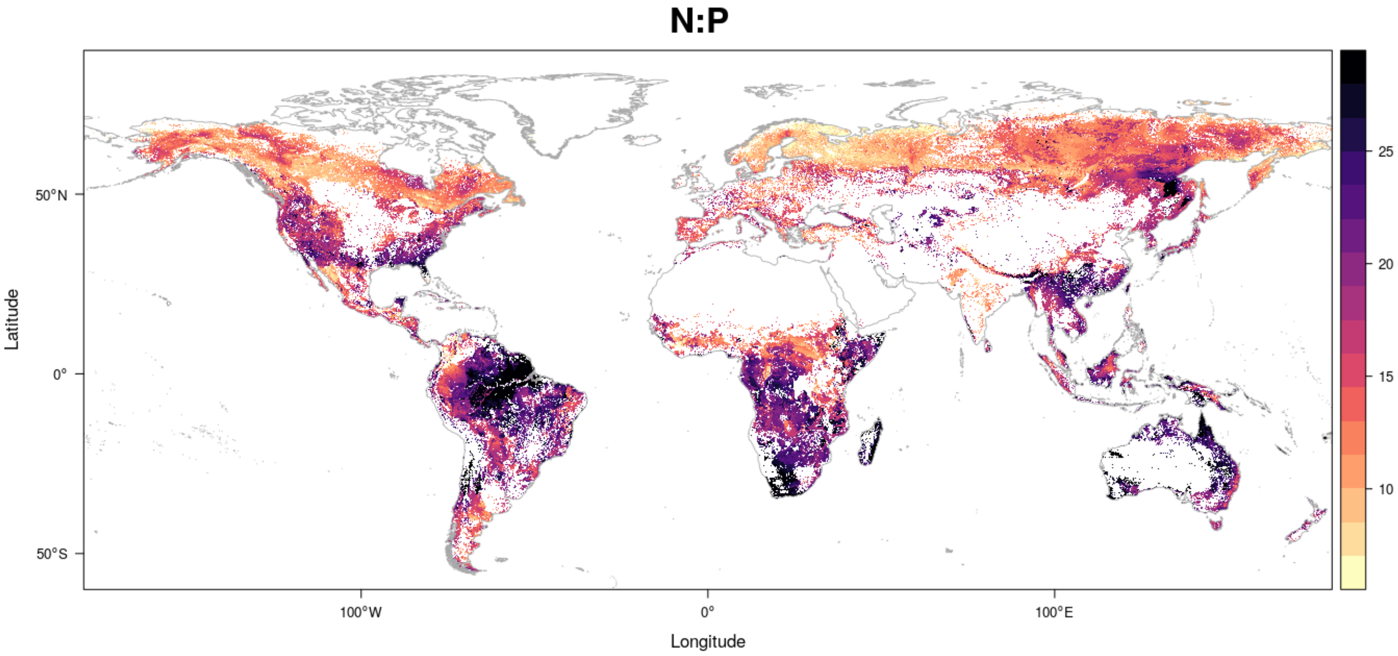

**Figure 2** Predicted woody plant foliar N:P ratios across global forest biomes; unshaded areas indicate lack of data.

### 3.3 Phylogeny and N:P ratios

The GLMM used to test the association of phylogeny to woody plant foliar N:P ratios (global R2 = 0.6 and RMSE = 3.84; Figure 1) showed that the variability explained by the random factors phylogeny and species in N:P ratios is greater than of the variability explained by the fixed environmental factors. The variability in N:P ratios explained by phylogeny + species ranges from 40.2% for tropical forests to 82.7% for boreal forests, while variability explained by phylogeny ranges from 6.8% for tropical forests to 50.0% for temperate coniferous and variability explained by species ranged from 29.9% for temperate broadleaf forests to 64.1% for boreal forests (Table 3).

**Table 3** Summary of generalized linear mixed model. Variability explained by for the whole model and by random and fixed part. Phylogeny, species and units belongs to random variability explained. R2c = R2m + R2

| | $R^2$c | $R^2$m (fixed) | $R^2$ (random) | Phylogeny | Species | Units |
|---|---|---|---|---|---|---|
| **Tropical** | 0.527 | 0.125 | 0.402 | 0.068 | 0.392 | 0.540 |
| **Temperate coniferous** | 0.832 | 0.005 | 0.827 | 0.500 | 0.331 | 0.169 |
| **Temperate broadleaved** | 0.692 | 0.019 | 0.672 | 0.387 | 0.299 | 0.315 |
| **Boreal** | 0.851 | 0.022 | 0.829 | 0.206 | 0.641 | 0.153 |

### 3.4 Soil age as a driver of N:P ratios

Woody plant foliar N:P ratios vary among soil orders (Figure 3) and tend to be higher from Oxisols (mean = 19.1) that occur in tropical wet forests of south America and central Africa, followed by Ultisols (mean = 16.3) that occur in South-eastern Asia and in sparse spots in the tropical fringe. In contrast, lowest N:P ratios are found from Spodosols (mean = 11.4) that typically occur in cold and humid regions, such as Atlantic Europe, Scandinavia, and Canada, followed by Vertisols (mean = 11.6), known to be conformed by expansive clay with high nutrient retention that occur in isolated zones with exchanging floods and drought periods such as east Australia, south India, Sudan between others.

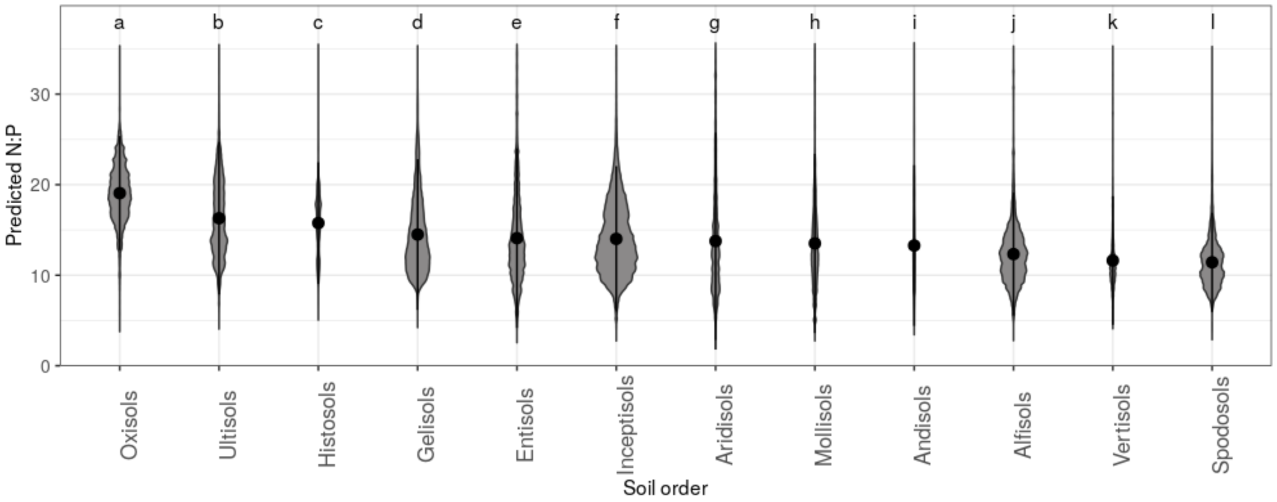

**Figure 3** Variation in predicted global woody plant foliar N:P ratios among USDA soil taxonomy orders. Predicted values differ significantly among soil types ($P < 0.05$).

## 4. Discussion

### 4.1 Global distribution maps of foliar N:P ratios

We constructed a high resolution global map of N:P ratios using NNs trained with environmental variables that identifies forest regions with N and P limitation, that play a role in the biogeochemical function of ecosystems. Although global foliar N and P maps are available (Butler et al., 2017; Moreno-Martínez et al., 2018; Vallicrosa et al., 2021), this is the first gridded N:P ratio map at the global scale constructed from an extensive N:P database using machine learning tools. We chose not to calculate global distribution of wood plant foliar N:P based on currently available N and P maps, because this approach would aggregate errors for each element and assume drivers of foliar N and P are the same as drivers of N:P ratios. Thus, we trained specific N:P ratio models to test for their drivers.

We found that our model predictions follow the substrate age hypothesis (Walker and Syers 1976), where foliar N:P ratios are high in the tropics and low at boreal latitudes (Chadwick et al., 1999; Vitousek et al., 2010) (Table 1). In the same direction, our results could perfectly match with the retrogression process, where older soils with absence of rejuvenating processes suffer specially of P depletion, which could be responsible for a decrease in ecological functions (Peltzer et al., 2010). Our results showed that woody plant foliar N:P ratios range from 12.34 in boreal forests to 20.70 in tropical forests. Given limitations of N and P limitation occur when N:P ratios are <10 and >20 respectively, (Güsewell, 2004; Greenwood et al. 2008), our results indicate that woody vegetation tends to be more P limited than N limited. Our predictions are supported and match with the results reported by Du et al. (2020) that showed 18% of the global terrestrial surface, excluding agricultural, urban, and glacial areas, was under N limitation while 43% was P limited, predominantly in the tropics (Table S5, Figure S2).

At the regional scale, our model predictions support the old, climatically buffered and infertile landscapes theory (Hopper, 2009), which states these types of landscape, such as the Cape floristic region in South Africa and the Southwest Floristic Region of Australia, are characterized by high levels of P limitation (Lambers et al., 2008, 2010; Oliveira et al., 2015), as indicated by the high N:P ratios for southern Africa and southwest Australia. We also found differences in N:P ratios between temperate coniferous (mean = 14.4) and broadleaf forests (mean = 18.8) (Table 1) that may indicate successional differences, as many coniferous trees are typically fast-growing and early successional species, which require higher proportions of P than broadleaf species that tend to be slower-growing, late successional species, with lower requirements for P (Peñuelas et al., 2013; Sardans and Peñuelas, 2013; Busch et al., 2018). On the other hand, we would like to be cautious with the high N:P levels in Siberia, which coincide with high SE levels (Figure S1). Siberia has the lowest density sampling in the hole globe and it is also an environment with high seasonality (Zimov et al., 1996). The period of the data collection may have conditioned the final prediction levels not entirely representing the reality for the hole year.

### 4.2 Environmental drivers

Our decision to model environmental drivers of woody plant foliar N:P ratio by forest biome at the global scale was justified, because impacts of the drivers varied among biomes and with latitude, with apparently contrasting effects. For example, potential evapotranspiration seasonality was negatively related to foliar N:P ratios in tropical forests and positively related to those in temperate coniferous forests, while in temperate coniferous and broadleaf forests, low water availability, expressed in aridity index or precipitation levels, was negatively related with foliar N:P ratios; these results may indicate that foliar N decreases in temperate latitudes under low levels of water availability (Sardans et al., 2008). In contrast to what occurs at temperate latitudes, greater levels of precipitation at boreal forests lead to lower N:P ratios, indicating that mineral leaching, which tends to affect N more than P (N is more mobile than P), may be more of a constraint than water availability, particularly at these high latitudes where N is frequently more limiting than P (Åström et al., 2005; Lepistö et al., 2008). Foliar N:P ratios were related to soil properties only in tropical forests, supporting previous studies that have shown key links between soil properties and tropical foliar elemental composition (Both et al., 2018, Hernández-Vargas et al., 2019).

### 4.3 Genetic factors

Phylogeny and species are related with more variability in foliar N:P ratios than environmental factors for each of the forest biomes (Table 3), supporting previous studies in which genetic legacy effects were found to explain most of the variability in woody plant foliar N, P, and potassium concentrations at the global scale (Sardans et al., 2021; Vallicrosa et al., 2021). Genetic legacy effects are a product of long- and short-term evolutionary processes (represented by phylogeny and species, respectively), during which species adapt to shifts in abiotic and biotic stressors, caused by climate, soil, and interactions with other species. While phylogeny includes ancient adaptation and differentiation from other clades, species include more genetic and epigenetic factors which, through evolutionary convergence or divergence can generate similar or different N:P ratios. High concentrations of N and P coincide with lower N:P ratio and high growth rates in pioneer/opportunistic species while there is a significant trend to less N and P concentrations and high N:P ratio in more stress tolerant species (Sardans and Peñuelas 2013; Sardans et al., 2021). However, the way how species/genotype separation is associated to differences in foliar N:P ratio is difficult to establish. The statistical analyses show this association, but further research is warranted to discern the causes of this association.

Most of the variance explained by the environmental factors in glm, was explained by genetic legacy effects in glmm. Genotypes are associated with particular soil and climatic traits, so phylogeny incorporates climatic and soil conditions to some extent. Indeed, strong genetic legacy signals for foliar elemental composition have recently been reported at local, regional, and global scales (Castellanos et al., 2018; de la Riva et al., 2017; Hu et al., 2018; Reimann et al., 2018; Sardans and Peñuelas, 2015, Sardans et al, 2015, 2016a), supporting studies of the biogeochemical niche hypothesis in plants (Peñuelas et al., 2008, 2010, 2019; Sardans et al., 2021) that have reported phylogeny and species, as proxies of overall genetic legacy, explain >75% of the variability in foliar elemental composition.

Disentangling single genetic legacy effects is problematic and highlights the large proportion of variability in boreal forest woody species N:P ratios that is explained by species (Table 3). Globally, boreal ecosystems contain lower levels of vascular plant diversity (Brummitt et al., 2020) and forests in these climate zones tend to be dominated by low numbers of coniferous species (Freedman, 1999), even some exception may occur. Thus, this higher level of woody species homogeneity and associated lower levels of species coexistence and interspecific competition are likely to lead to lower levels of phenotypic plasticity and greater stability of foliar N:P ratios. In the other forest biomes, where levels of species diversity and heterogeneity are greater, it is likely that species foliar N:P ratios reflect levels of species coexistence (Peñuelas et al. 2019; Sardans et al., 2021), thus limiting the predictive power of phylogeny and species, as supported by our results that showed tropical forest foliar N:P ratios were least explained by these random factors. Northern tree species are adapted to resist hard conditions and can be considered stress-tolerant species, and consequently they tend to have more conservative strategies and lower levels of plasticity resulting from their strict adaptation to a concrete hard stress (Grime, 1977; Güsewell 2004). The more stress tolerant species commonly present higher N:P ratios and narrower variability in N:P ratios (Güsewell, 2005, Yu et al., 2011; Peñuelas et al., 2019).

Our study shows that forest species diversity and heterogeneity are key drivers of woody plant foliar N:P proportions, so we recommend their inclusion, along with environmental conditions in future studies of foliar N:P. To facilitate the inclusion of species in global-scale studies of N:P ratios, the Global Biodiversity Information Facility offers free, globally georeferenced species data that may be used in niche modeling of remotely sensed airborne imaging spectroscopy and laser imaging detection and ranging (LiDAR) data added to a clustering algorithm (Yi et al., 2020).

## 5. Conclusions

Our study provides the first global distribution maps of woody plant foliar N:P ratios and confirmation of their negative relation with latitude as a principal driver. Globally, forest biomes are more P limited than N limited, as suggested by previous studies. We found variation in effects of environmental drivers on N:P ratios among forest biomes, due to contrasting associated environmental pressures; these variations would have been masked in a single global “forest biome” analysis. Genetic legacy was a key driver of N:P variability and its inclusion in future studies of N:P ratios will lead to improved prediction of effects of global change on biogeochemical cycles and ecosystem function, including forest primary production, respiration, and C-cycling.

## Data availability statement

The data that support the findings of this study is available at http://glonuteco.creaf.cat/data/ and the resulting N:P map is available in the appendix section.

## Conflict of interest

The authors declare no conflict of interests.

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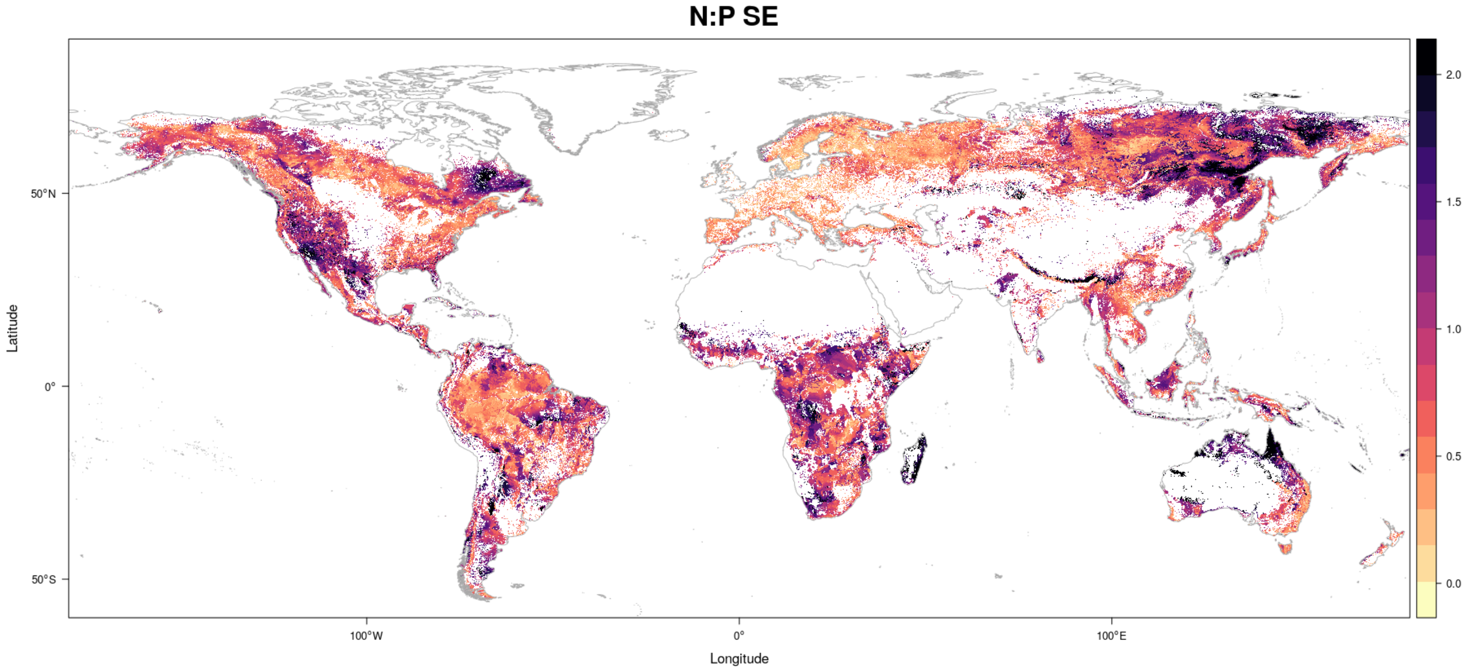

**Figure S1** Predicted woody plant foliar N:P ratios standard error across global forest biomes; unshaded areas indicate lack of data.

**Figure S2** Histogram of predicted N:P foliar values