

Global patterns of terrestrial nitrogen and phosphorus limitation

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Nitrogen (N) and phosphorus (P) limitation constrains the magnitude of terrestrial carbon uptake in response to elevated carbon dioxide and climate change. However, global maps of nutrient limitation are still lacking. Here we examined global N and P limitation using the ratio of site-averaged leaf N and P resorption efficiencies of the dominant species across 171 sites. We evaluated our predictions using a global database of N- and P-limitation experiments based on nutrient additions at 106 and 53 sites, respectively. Globally, we found a shift from relative P to N limitation for both higher latitudes and precipitation seasonality and lower mean annual temperature, temperature seasonality, mean annual precipitation and soil clay fraction. Excluding cropland, urban and glacial areas, we estimate that 18% of the natural terrestrial land area is significantly limited by N, whereas 43% is relatively P limited. The remaining 39% of the natural terrestrial land area could be co-limited by N and P or weakly limited by either nutrient alone. This work provides both a new framework for testing nutrient limitation and a benchmark of N and P limitation for models to constrain predictions of the terrestrial carbon sink.

The primary productivity of terrestrial plants is widely limited by essential nutrients, especially nitrogen (N) and phosphorus (P)^{1–4}. The substrate-age hypothesis⁵ predicts an increasing P limitation from geologically young Arctic and boreal ecosystems towards tropical forest, which have relatively little ‘weatherable’ rock P (refs^{6,7}). In contrast, biological N fixation and N mineralization both show the opposite latitudinal trend, which contributes to a general poleward increase of N limitation^{8–10}. Moreover, fire disturbances generally volatilize more N than P and may contribute to N limitation in fire-prone biomes^{11,12}. Anthropogenic N deposition may increase P limitation in hotspot regions^{13–17}, and elevated atmospheric carbon dioxide (CO₂) and warming-induced longer growing seasons are likely to result in greater nutrient limitation in terrestrial ecosystems^{18,19}. On a global scale, N and P limitation probably constrains current and future ecosystem responses to elevated CO₂ concentrations and climate change^{20,21}. Therefore, understanding the spatial heterogeneity in nutrient limitation remains a high priority.

Several approaches have been used to infer nutrient limitation, including fertilization experiments and thresholds of leaf N:P ratios^{1–3,22–26}. Fertilization experiments can directly test nutrient limitation²⁵, but global meta-analyses of field fertilization experiments had difficulties in finding robust large-scale spatial patterns in nutrient limitation, potentially attributable to combining different growth indicators or using effect-size metrics not standardized by the level of nutrient addition^{1–3}. Alternatively, thresholds of leaf N:P ratio (for example, 14:1 versus 16:1 or 10:1 versus 20:1) have been used to indicate N or P limitation indirectly^{22–24}, but a recent assessment of these thresholds indicates relatively large uncertainties²⁶.

Leaf N resorption efficiency (NRE) and P resorption efficiency (PRE) have been shown to increase with lower N and P availability, respectively^{27,28}, illustrating a trade-off between nutrient recycling within a plant and uptake from the environment. Han et al.²⁹ proposed an indicator for N and P limitation based on the difference of NRE and PRE for woody plants and found significant latitudinal and climatic trends. In addition, Reed et al.³⁰ found that NRE/PRE ratios increased with latitude and decreased with mean annual temperature (MAT) and mean annual precipitation (MAP). However, both analyses were conducted for individual species and were not necessarily representative of ecosystem nutrient limitation.

Based on the stoichiometric homeostasis theory³¹ and Liebig’s law of the minimum³², we defined an indicator using plant leaf NRE and PRE to estimate N and P limitation at the ecosystem scale. We further applied this approach to a newly constructed database of paired resorption efficiency of N and P for terrestrial plants (PRENP, version 1.0) (Fig. 1, Supplementary Fig. 1 and Supplementary Table 1). Unlike previous studies that focused on single-nutrient resorption separately^{27,28,33–35}, our PRENP database only included studies that simultaneously measured leaf NRE and PRE. We also compiled a global database of field-diagnosed nutrient (N or P) limitation (NuLi, version 1.0) (Supplementary Table 2) to validate our predictions of N and P limitation.

A framework to estimate nutrient limitation

Leaf nutrient demand is met by both internally resorbed nutrients and externally derived nutrients from the environment¹⁰. Based on the stoichiometric homeostasis theory³¹, the demand ratio of N versus P for a mature leaf ($N : P_{\text{mature leaf}}$) should be relatively constant to maintain leaf functioning, as described by equation (1):

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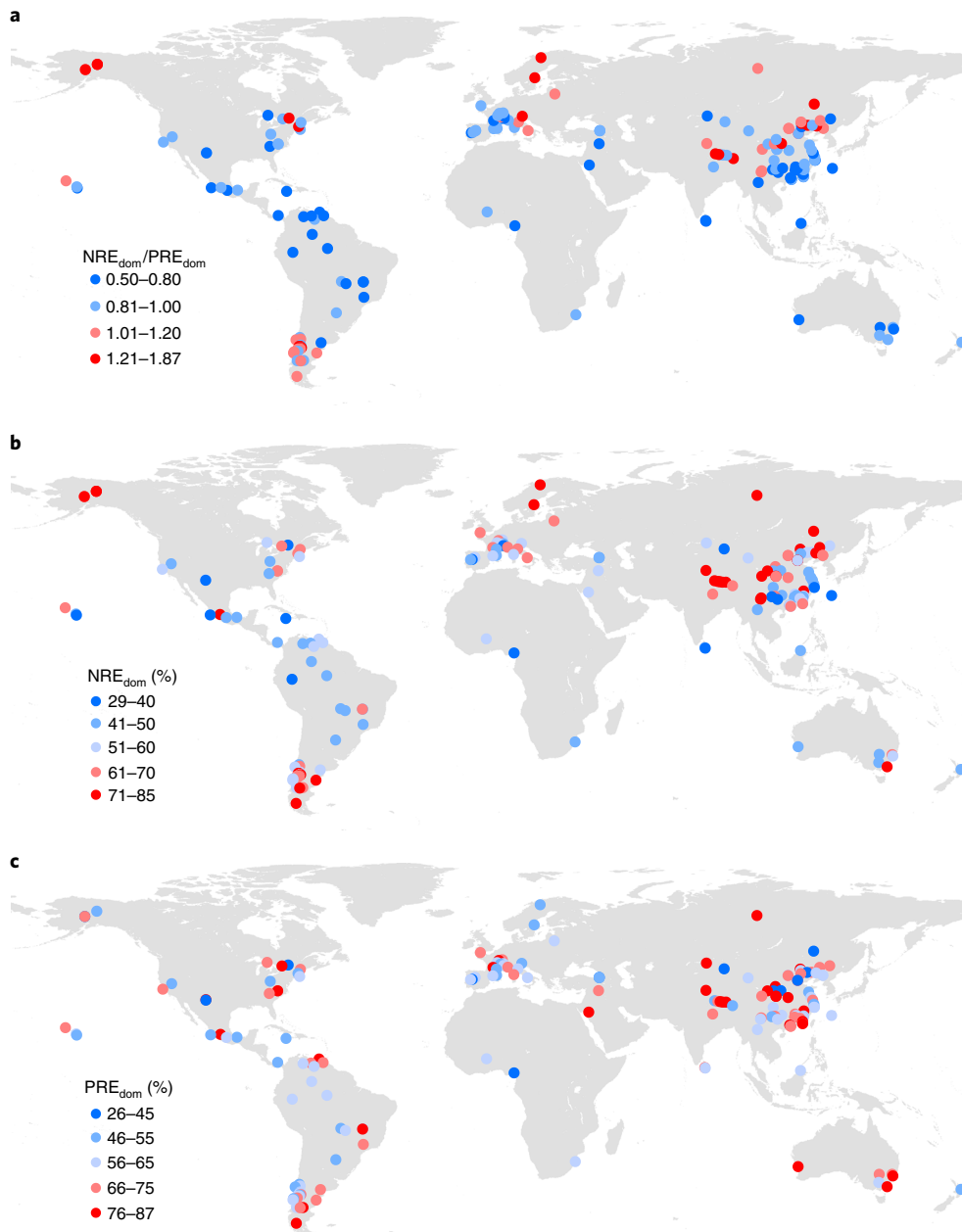


Fig. 1 | Spatial distributions in the PRENP database. a–c, NRE_{dom}/PRE_{dom} (**a**), NRE_{dom} (**b**) and PRE_{dom} (**c**). The figure was created using Arcgis 10.1 (ESRI).

$$\frac{N_{LR} + N_{LE}}{P_{LR} + P_{LE}} = N : P_{mature\ leaf} \quad (1)$$

where N_{LR} and P_{LR} indicate the amounts of leaf-resorbed N and P, respectively, and N_{LE} and P_{LE} indicate the amounts of leaf N and P that are externally derived. Based on Liebig's law of the minimum³², we define N to be more limiting than P when the amounts of externally derived N and P are unable to match the N:P demand ratio for mature leaves (equation (2)):

$$\frac{N_{LE}}{P_{LE}} < N : P_{mature\ leaf} \quad (2)$$

That is, N should generally be more limiting than P when the ratio of leaf-resorbed N versus P exceeds the N:P demand ratio for mature leaves (equation (3)):

$$\frac{N_{LR}}{P_{LR}} > N : P_{mature\ leaf} \quad (3)$$

Equation (3) can then be transformed into equation (4):

$$\frac{NRE}{PRE} > 1 \quad (4)$$

$NRE/PRE > 1$ (or \ln -transformed $NRE/PRE > 0$) thus indicates stronger N limitation than P limitation. Alternatively, P is more limiting when the NRE/PRE ratio is < 1 (or \ln -transformed $NRE/PRE < 0$). One initial test of this ratio was applied to N-fixing plants, which are thought to be limited by P and should show a NRE/PRE ratio below 1. Accordingly, 37 N-fixing plants in our database showed an average of \ln -transformed NRE/PRE ratio (-0.30 ± 0.05) significantly lower than 0 ($P < 0.001$), which supports the use of NRE/PRE to indicate N and P limitation.

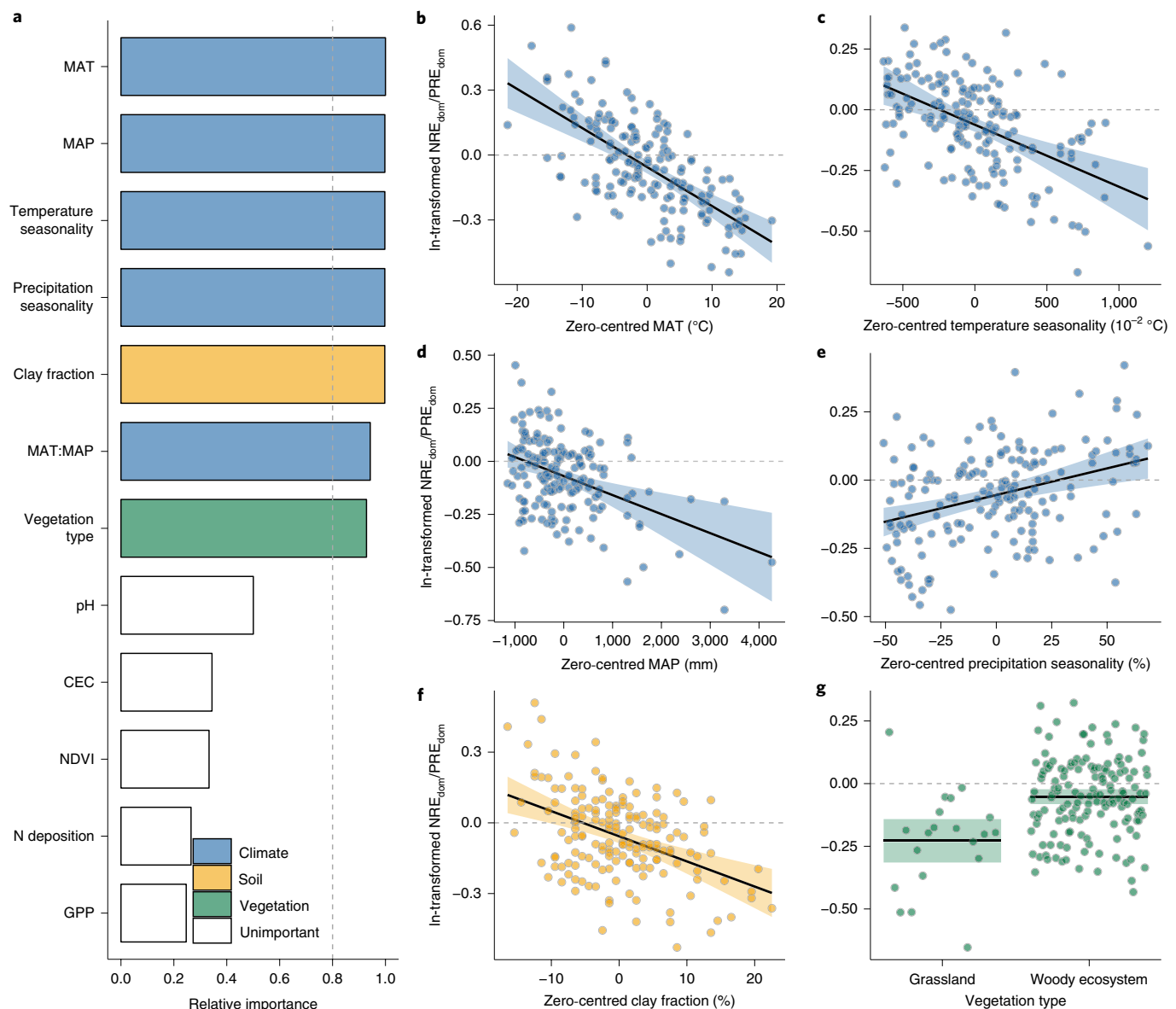


Fig. 2 | Potential predictors. a–g. The relative importance of potential predictors (**a**) and partial regression plots with the predictors MAT (**b**), temperature seasonality (**c**), MAP (**d**), precipitation seasonality (**e**), soil clay fraction (**f**) and vegetation type (**g**). The importance is based on the sum of the Akaike weights derived from model selection using corrected Akaike information criterion. The cutoff is set at 0.8 (dashed line in **a**) to differentiate among the most important predictors. Note that the values of MAT, MAP, temperature seasonality, precipitation seasonality and soil clay fraction were zero-centred.

At the ecosystem scale, the ratio of average leaf NRE to PRE weighted by the leaf mass of all species is in theory capable of indicating N or P limitation. However, species-specific leaf mass is rarely reported together with NRE and PRE. As a result, we used the ratio of site-averaged NRE (NRE_{dom}) to site-averaged PRE (PRE_{dom}) of the dominant species as an approximate indicator ($\text{NRE}_{\text{dom}}/\text{PRE}_{\text{dom}}$). We modelled global $\text{NRE}_{\text{dom}}/\text{PRE}_{\text{dom}}$ and found that the diagnosed limiting nutrients based on $\text{NRE}_{\text{dom}}/\text{PRE}_{\text{dom}}$ agree well with the results of field fertilization experiments in our NuLi database (see below and Supplementary Table 2). Overall, $\text{NRE}_{\text{dom}}/\text{PRE}_{\text{dom}}$ appears to be a useful indicator of ecosystem N and P limitation.

Global mapping of N and P limitation

$\text{NRE}_{\text{dom}}/\text{PRE}_{\text{dom}}$ in our dataset is log-normally distributed (Shapiro–Wilk test, $W=0.99$, $P=0.11$) and shows a global geometric mean of 0.90 (median=0.90), as determined by NRE_{dom} (geometric

mean=55%, median=57%) and PRE_{dom} (geometric mean=61%, median=63%) (Fig. 1 and Supplementary Fig. 2). The maxima (95th–100th percentile) of NRE_{dom} (81–86%) and PRE_{dom} (80–87%) are comparable, which implies that N and P have similar maximum resorption efficiencies.

To predict global patterns of N and P limitation, we considered 11 potential predictors as suggested in the literature^{4,5,8,9,13,36}, including variables that define climate (MAT, MAP, temperature seasonality and precipitation seasonality), soil fertility (N deposition, soil clay fraction, soil pH and cation exchange capacity (CEC)) and vegetation characteristics (vegetation type, gross primary production (GPP) and normalized difference vegetation index (NDVI) (Supplementary Table 3 gives more details). Model selection analysis, based on corrected Akaike information criterion, showed that the best model describing $\ln\text{-transformed } \text{NRE}_{\text{dom}}/\text{PRE}_{\text{dom}}$ included MAT, MAP, temperature seasonality, precipitation seasonality, soil

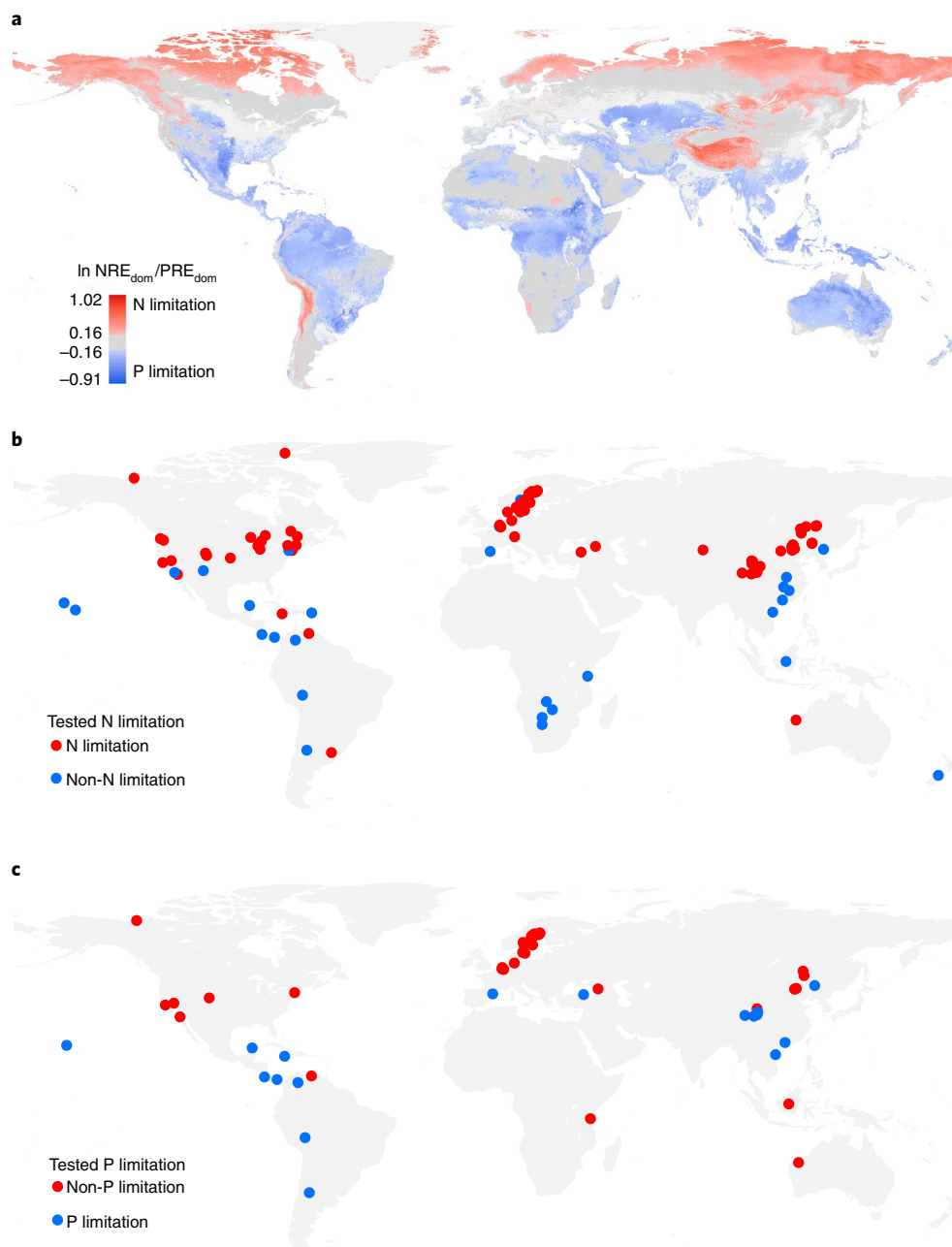


Fig. 3 | Global mapping of N and P limitation. a–c, Global mapping of predicted N and P limitation (**a**) as compared to field-diagnosed N (**b**) and P (**c**) limitation. All the sites from the NuLi database are shown in **b** ($n=106$) and **c** ($n=53$), but only sites ($n=46$ and 30 , respectively) located in areas with absolute values of $\ln\text{-transformed } \text{NRE}_{\text{dom}}/\text{PRE}_{\text{dom}} > 0.16$ were used to validate the model predictions. The dark grey shading in **a** indicates areas with $\ln\text{-transformed } \text{NRE}_{\text{dom}}/\text{PRE}_{\text{dom}}$ that range from -0.16 to 0.16 . The light grey shading in **a** indicates cropland, urban and glacial areas. The figure was created using Arcgis 10.1 (ESRI).

clay fraction, the interaction of MAT and MAP, and vegetation type (that is, woody ecosystems and grasslands) as important predictors (Fig. 2a and Supplementary Table 4; deviance explained 54%). The relative importance of the predictors (Fig. 2a) supported removing soil pH, CEC, NDVI, GPP and N deposition from the final model. In addition, diagnostic analyses showed that statistical assumptions (homoscedasticity, multivariate normality, independence of residuals and low multicollinearity) were met for the linear model (Supplementary Tables 4–8 and Supplementary Figs. 3 and 4).

Climate is the most important factor to affect nutrient limitation in our analysis (Fig. 2a). Partial regression analysis indicates that $\ln\text{-transformed } \text{NRE}_{\text{dom}}/\text{PRE}_{\text{dom}}$ decreased significantly with higher

MAT ($P < 0.001$; Fig. 2b), greater temperature seasonality ($P < 0.001$; Fig. 2c) and higher MAP ($P < 0.001$; Fig. 2d), but increased with greater precipitation seasonality ($P < 0.001$; Fig. 2e). The trends of $\text{NRE}_{\text{dom}}/\text{PRE}_{\text{dom}}$ with MAT and MAP were predominantly attributable to a significant decrease of NRE_{dom} with both MAT ($P < 0.001$; Supplementary Fig. 5a) and MAP ($P < 0.001$; Supplementary Fig. 5b). The different trends of NRE_{dom} and PRE_{dom} might be attributable to the fact that P availability is strongly determined by soil parent materials^{4,36}, whereas N availability is mainly determined by biological N fixation and mineralization, which depend strongly on climate^{8,10}. Moreover, MAT and MAP showed a significant interaction ($P < 0.01$; Fig. 2a and Supplementary Table 4), probably attributable,

Table 1 | Limiting nutrients diagnosed in major terrestrial biomes

Biome	N limited		P limited		Undiagnosed	
	Area (%)	Mean (5th–95th)	Area (%)	Mean (5th–95th)	Area (%)	Mean (5th–95th)
TSF	0	–	91	–0.30(–0.43––0.19)	9	–0.09(–0.16–0.05)
TBMF	2	0.19(0.16–0.26)	30	–0.26(–0.40––0.17)	68	–0.01(–0.14–0.13)
TCF	35	0.24(0.16–0.39)	11	–0.24(–0.35––0.17)	54	0.03(–0.13–0.15)
BF	48	0.26(0.17–0.39)	0	–	52	0.06(–0.05–0.15)
TSSS	0	–	56	–0.28(–0.50––0.17)	44	–0.06(–0.15–0.07)
TGS	3	0.22(0.16–0.34)	52	–0.31(–0.51––0.18)	45	–0.01(–0.14–0.13)
MGS	59	0.37(0.18–0.60)	11	–0.25(–0.38––0.17)	30	0.00(–0.14–0.14)
Tundra	96	0.36(0.21–0.53)	0	–	4	0.08(–0.04–0.16)
Desert	3	0.26(0.16–0.47)	46	–0.26(–0.41––0.17)	51	–0.05(–0.15–0.11)
MFWS	2	0.23(0.16–0.35)	39	–0.23(–0.36––0.16)	59	–0.08(–0.15–0.06)

The proportion of area and mean values (5th and 95th percentiles) of \ln -transformed $\text{NRE}_{\text{dom}}/\text{PRE}_{\text{dom}}$ are shown. Predicted values of \ln -transformed $\text{NRE}_{\text{dom}}/\text{PRE}_{\text{dom}} < -0.16$, > 0.16 and ranging from -0.16 to 0.16 indicate P-limited, N-limited and undiagnosed areas (co-limited by N and P or weakly limited by either nutrient alone), respectively. Cropland, urban and glacial areas were excluded from the analysis. TSF, tropical and subtropical forest; TBMF, temperate broadleaf and mixed forest; TCF, temperate coniferous forest; BF, boreal forest; TSSS, tropical and subtropical savannas and shrublands; TGS, temperate grasslands and shrublands; MGS, montane grasslands and shrublands; MFWS, Mediterranean forests, woodlands and scrubs.

in part, to the fact that temperature can partially counteract the role of additional precipitation by promoting evapotranspiration.

Partial regression analysis also shows a significant decrease in \ln -transformed $\text{NRE}_{\text{dom}}/\text{PRE}_{\text{dom}}$ with higher soil clay fraction ($P < 0.001$; Fig. 2f). This relationship probably arises because soils with a high clay fraction are strongly weathered and relatively poor in P availability^{4,5}. Moreover, we found that grasslands have a significantly lower $\text{NRE}_{\text{dom}}/\text{PRE}_{\text{dom}}$ than that of woody ecosystems ($P < 0.001$; Fig. 2g and Supplementary Table 4), which implies that plant conservation of P is more important in grasslands. As driven by shifts in climate, soil and vegetation variables, $\text{NRE}_{\text{dom}}/\text{PRE}_{\text{dom}}$ shows a significant increase towards higher latitudes ($P < 0.001$; Supplementary Fig. 6a) with a stronger latitudinal trend for NRE_{dom} (Supplementary Fig. 6b) than for PRE_{dom} (Supplementary Fig. 6c).

We also employed a random forest approach using all 11 predictors in parallel to the linear model, but cross-validated R^2 values indicated that the linear model is statistically superior using fewer predictors (Supplementary Fig. 7). Therefore, we used the linear model to predict global N and P limitation (Fig. 3a). Given a model residual standard error of 0.16 (Supplementary Table 4), predicted values of \ln -transformed $\text{NRE}_{\text{dom}}/\text{PRE}_{\text{dom}}$ that ranged from -0.16 to 0.16 were identified as insufficient statistically to identify nutrient limitation based on a theoretical threshold of 0 for \ln -transformed $\text{NRE}_{\text{dom}}/\text{PRE}_{\text{dom}}$ (equation (4)). Within the statistically meaningful ranges (\ln -transformed $\text{NRE}_{\text{dom}}/\text{PRE}_{\text{dom}} < -0.16$ or > 0.16), our approach successfully identified 83% (38/46) of the cases of N limitation and 83% (25/30) of those of P limitation compared with results of field experiments (Supplementary Table 2).

Global patterns of N and P limitation

Our predictions showed a strong latitudinal pattern of N and P limitation (Fig. 3a) and relatively close agreement with the results of field experiments that tested both N (Fig. 3b) and P limitation (Fig. 3c) (Supplementary Table 2). Moreover, there is a transition to N limitation at higher elevations in some lower-latitude regions (for example, the Tibetan Plateau, the Andes and the South African Plateau) (Fig. 3a), probably attributable to an elevational decrease in temperature and consequent changes in soil and vegetation.

Excluding cropland, urban and glacial areas, our model estimated that 18% of the natural terrestrial land area was significantly limited by N (\ln -transformed $\text{NRE}_{\text{dom}}/\text{PRE}_{\text{dom}} > 0.16$), whereas 43% of the land area was P limited (\ln -transformed $\text{NRE}_{\text{dom}}/\text{PRE}_{\text{dom}} < -0.16$) (Supplementary Table 9). However, our model was unable to

diagnose limiting nutrients in 39% of natural terrestrial land area (\ln -transformed $\text{NRE}_{\text{dom}}/\text{PRE}_{\text{dom}}$ that ranged from -0.16 to 0.16) (Supplementary Table 9), which could indicate a co-limitation by N and P or a weak limitation by either nutrient alone. By overlapping our predictions with a global map of major terrestrial biomes³⁷, we showed that N limitation prevails relatively more in boreal forest, tundra, temperate coniferous forest and montane grasslands and shrublands, whereas P is more limiting in tropical and subtropical forest, temperate broadleaf and mixed forest, deserts, Mediterranean biomes, and grasslands, savannas and shrublands in tropical, subtropical and temperate regions (Table 1). Overall, our global mapping of N and P limitation provides additional details and information on spatial heterogeneity to those of existing assessments based on nutrient fertilization experiments alone^{1–3}.

Uncertainties and implications

Previous studies conducted for individual species^{27,28,33–35} provide important, but incomplete, insights into the prevailing nutrient limitation at the ecosystem scale. Our approach based on $\text{NRE}_{\text{dom}}/\text{PRE}_{\text{dom}}$ partially overcomes this challenge and may be better suited for diagnosing the prevailing limiting nutrients. Owing to the uncertainty of our approach, nutrient limitation was undetermined in a proportion of the natural terrestrial ecosystems. Future studies would benefit from additional data to support the analyses using the ecosystem mean NRE/PRE weighted by species-specific leaf mass or abundance. We recommend that researchers in field studies measure such variables whenever possible and compare the results to those of nutrient fertilization experiments. Moreover, nutrients other than N and P that are not considered here, such as sulfur, potassium, calcium, magnesium, and other micronutrients, can also limit terrestrial productivity^{38,39}, but they are not likely to be limiting nutrients globally. Nevertheless, our map appears fairly robust because it is based on drivers determined by model selection and identified from empirical data, which strengthens the current understanding for patterns of N and P limitation, and is consistent with the results of field experiments.

Our analysis presents a static estimate of global N and P limitation, but many factors can restructure such patterns. For instance, anthropogenic N emissions have altered global N deposition, which can shift N limitation towards P limitation in some regions^{13,14,17}. CO_2 enrichment may increase nutrient limitation attributable to an enhanced nutrient accumulation in plant biomass and litters^{18,21,40}. Climate warming may favour biological

N fixation and N mineralization and thereby improve ecosystem N availability at mid-to-high latitudes^{8,41,42}. By providing data on global terrestrial N and P limitation, our work could potentially help vegetation models and Earth system models to constrain predictions of terrestrial carbon cycling in response to N deposition, elevated CO₂ concentrations and climate change.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41561-019-0530-4>.

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Methods

Dataset. We compiled a global database of PRENP version 1.0 in leaves of terrestrial plants based on literature surveyed via the Web of Science (<http://isiknowledge.com>), Google Scholar (<https://scholar.google.com>) and the China National Knowledge Infrastructure (<http://www.cnki.net>). The key words 'nitrogen resorption' and 'phosphorus resorption' were used to search published studies of leaf NRE and PRE. Data were included only when NRE and PRE were measured simultaneously. To avoid misattributing natural nutrient limitation due to anthropogenic disturbances, we excluded data for intensively managed ecosystems (for example, agroforest, fertilized plantations, sown pastures, croplands and urban forests). Overall, our database includes 925 observations of leaf NRE and PRE for 585 species from 135 publications, with 627 observations for 377 dominant species across 171 sites (Fig. 1, Supplementary Fig. 1 and Supplementary Table 1). We also recorded corresponding information on all reported species, dominant species, site location (longitude and latitude), MAT (°C) and MAP (mm) from the literature. Information on the dominant species was derived primarily based on statements by the authors in the original literature.

To validate our predictions of nutrient limitation, we compiled a global database of nutrient (N or P) limitation (NuLi, version 1.0) based on the growth response to experimental nutrient additions in relatively unmanaged ecosystems. An ecosystem was diagnosed to be limited by a certain nutrient if additions of the nutrient significantly stimulated plant growth. By synthesizing experimental results from 84 publications, the NuLi database includes information on N limitation at 106 sites and P limitation at 53 sites, and information on site location (longitude and latitude), MAT and MAP (Supplementary Table 2).

In addition to MAT and MAP, we further retrieved a variety of climate (temperature seasonality, standard deviation $\times 100$; precipitation seasonality, coefficient of variation), soil fertility (N deposition, soil clay fraction, soil pH and CEC) and vegetation variables (for example, vegetation type, GPP and NDVI) from multiple data products at relatively fine spatial resolution (more details given in Supplementary Table 3). These variables were used as potential predictors for global N and P limitation.

Calculation of nutrient resorption efficiency. Nutrient resorption efficiency (NuR (%)) for N (NRE) or P (PRE) is defined as the mass-based proportional withdrawal of a nutrient during senescence:

$$\text{NuR} = \left(1 - \frac{\text{mass of nutrient in senesced leaves}}{\text{mass of nutrient in mature leaves}} \right) \times 100\% \quad (5)$$

Concentration-based nutrient resorption efficiency (NuR_c (%)), also frequently used in the literature, is calculated as:

$$\text{NuR}_c = \left(1 - \frac{\text{concentration of nutrient in senesced leaves}}{\text{concentration of nutrient in mature leaves}} \right) \times 100\% \quad (6)$$

However, it substantially underestimates the actual nutrient resorption efficiency due to leaf mass loss during senescence³³. If nutrient resorption was originally estimated on a concentration basis, we then used a mass loss correction factor (MLCF) to calculate the mass-based NuR for N and P:

$$\text{NuR} = (1 - (1 - \text{NuR}_c) \times \text{MLCF}) \times 100\% \quad (7)$$

where MLCF was 0.780, 0.784, 0.745, 0.640 and 0.713 for evergreen broadleaves, deciduous broadleaves, conifers, forbs and graminoids, respectively³³.

Statistical analyses. To prepare the datasets for statistical analysis, we averaged values of NRE (NRE_{dom}) and PRE (PRE_{dom}) of the dominant species for each site if more than one dominant species were reported. If measurements for the same site were reported for more than one year, NRE_{dom} and PRE_{dom} were also averaged across the years. Site-level NRE_{dom}/PRE_{dom} was calculated as an indicator of nutrient limitation in the ecosystem. For woody ecosystems (for example, forest and shrublands), only data on the dominant species of the canopy layer were used in our analysis. Using a Shapiro–Wilk test, NRE_{dom}/PRE_{dom} was found to be in line with a log-normal distribution. Therefore, ln-transformed NRE_{dom}/PRE_{dom} was used to follow the statistical analyses. Additionally, values of the corresponding MAT (mean = 12.39°C), MAP (mean = 1,196 mm), temperature seasonality (mean = 665.55 $\times 10^{-2}$ °C), precipitation seasonality (mean = 58.53%), soil clay fraction (mean = 21.46%), soil pH (mean = 62.15 $\times 10^{-1}$), soil CEC (mean = 19.52 mmol kg⁻¹), N deposition (mean = 9.88 kg N ha⁻¹ yr⁻¹), GPP (mean = 11,760 $\times 10^{-4}$ kg C m⁻² yr⁻¹) and NDVI (mean = 5,637 $\times 10^{-4}$) (see more details of the unit for each predictor in Supplementary Table 3) were zero-centred (setting the mean to zero, that is, original value minus mean) to reduce the magnitude of possible correlations of the interaction terms with their constituent terms, and thus reduce the multicollinearity⁴³. The variables used for the global prediction of N and P limitation were also zero-centred using the above-mentioned mean values.

We considered two different approaches to predict global N and P limitation by using 11 potential predictors (Supplementary Table 3). We first conducted a model selection analysis for ln-transformed NRE_{dom}/PRE_{dom} based on corrected Akaike information criterion⁴⁴. The relative importance value, regarded as the overall support for each predictor across all models, was estimated as the sum

of the Akaike weights for the models in which the predictor appeared. A cutoff relative importance value of 0.8 was set to differentiate between the important and unimportant predictors^{44,45}. We then derived a best linear model based on the important predictors.

Diagnostic analyses^{46,47} were conducted to test the assumptions of multiple linear models, which included a linear relationship, homoscedasticity, multivariate normality and independence of residuals⁴⁸. We computed the variance inflation factor, which measures the multicollinearity of predictors in the model. A criterion of variance inflation factor > 3 was used as a cutoff to indicate considerable collinearity⁴⁸. Specifically, we used Moran's Index to test if spatial autocorrelation occurred in the model residuals, which could violate the assumption of normally distributed residuals and cause an increase in type I error rates⁴⁹. The statistical analysis detected no significant spatial autocorrelation for the residuals of our model (observed Moran's Index = 0.034, expected Moran's Index = -0.006, $P = 0.196$). A mixed-effects model was conducted using the lme4 package⁵⁰ and the lmerTest package⁵¹ to test for possible random effects due to measurements in different years or measurements by different researchers across sites. The above-mentioned statistical analyses supported the robustness of the best linear model (more information given in Supplementary Tables 4–8 and Supplementary Figs. 3 and 4). Partial regression plots^{44,52} were created for each important predictor to illustrate its relationship with ln-transformed NRE_{dom}/PRE_{dom} while holding all the other variables constant (by default, median for numeric variables and most common category for factors).

We also trained a random forest model^{53–55} by including all 11 predictors. The performances of both models were compared based on cross-validated R^2 . We then chose the linear model with a better statistical performance for the global mapping of the nutrient limitation at a 1 \times 1 km resolution. Cropland, urban and glacier areas were excluded from the analysis based on the MODIS land-cover map (<https://modis-land.gsfc.nasa.gov/landcover.html>).

Our predictions of limiting nutrients were compared to the results of field nutrient fertilization experiments (NuLi version 1.0). Given a model residual standard error of 0.16 (Supplementary Table 4), the predicted ln-transformed NRE_{dom}/PRE_{dom} with absolute values less than 0.16 were insufficient statistically to identify nutrient limitation based on a theoretical threshold of 0 for ln-transformed NRE_{dom}/PRE_{dom}. We thus only used experimental results from sites with absolute values of ln-transformed NRE_{dom}/PRE_{dom} that exceeded 0.16 to validate the predicted nutrient limitation.

On a basis of Goode homoloxine projection, we estimated the percentages of area being limited by N and P, respectively. By overlapping our predictions with the global biome map³⁷, we summarized the prevailing limiting nutrients across major terrestrial biomes (tropical and subtropical forest; temperate broadleaf and mixed forest; temperate coniferous forest; boreal forest; tropical and subtropical savannas and shrublands; temperate grasslands and shrublands; montane grasslands and shrublands; Mediterranean forests, woodlands and scrubs; tundra; deserts).

Data availability

All data supporting the findings of this study are available in figshare (<https://doi.org/10.6084/m9.figshare.10735652.v1>).

Code availability

The code used in this work can be accessed by contacting the corresponding authors.

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Author contributions

E.D. conceived the project. R.B.J., C.T., A.F.A.P., A.A. and C.J.V.L. contributed ideas to the analysis. E.D., N.X., and X.W. compiled the database. E.D., X.Z., C.T. and C.J.V.L. analysed the data. E.D., R.B.J., C.T., A.F.A.P. and A.A. wrote and revised the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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