

Nutrient availability as the key regulator of global forest carbon balance

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Forests strongly affect climate through the exchange of large amounts of atmospheric CO₂ (ref. 1). The main drivers of spatial variability in net ecosystem production (NEP) on a global scale are, however, poorly known. As increasing nutrient availability increases the production of biomass per unit of photosynthesis² and reduces heterotrophic³ respiration in forests, we expected nutrients to determine carbon sequestration in forests. Our synthesis study of 92 forests in different climate zones revealed that nutrient availability indeed plays a crucial role in determining NEP and ecosystem carbon-use efficiency (CUEe; that is, the ratio of NEP to gross primary production (GPP)). Forests with high GPP exhibited high NEP only in nutrient-rich forests (CUEe = 33 ± 4%; mean ± s.e.m.). In nutrient-poor forests, a much larger proportion of GPP was released through ecosystem respiration, resulting in lower CUEe (6 ± 4%). Our finding that nutrient availability exerts a stronger control on NEP than on carbon input (GPP) conflicts with assumptions of nearly all global coupled carbon cycle–climate models, which assume that carbon inputs through photosynthesis drive biomass production and carbon sequestration. An improved global understanding of nutrient availability would therefore greatly improve carbon cycle modelling and should become a critical focus for future research.

The net ecosystem production (NEP) of an ecosystem represents its carbon (C) balance at daily to decadal scales. Despite considerable study, the main drivers of NEP are still unclear. Climate^{4,5}, climatic trends⁶, nitrogen deposition^{7,8}, disturbance and management^{8,9} have been suggested to influence NEP. These studies, however, either were unable to explain a substantial percentage of the spatial variability in NEP or collected data in a restricted subset of climatic space, indicating that it is not yet known what factor(s) most strongly govern NEP, one of the critical pathways by which terrestrial ecosystems feedback to climate.

At the ecosystem scale, nitrogen deposition has been suggested to enhance the NEP of forests^{3,7}. Nutrient availability is indeed a key variable explaining patterns of carbon allocation in forests; nutrient-rich forests exhibit higher biomass production, biomass production efficiency (defined as biomass production/gross primary production (GPP) ratio) and shoot-to-root biomass

production ratio². By converting a larger fraction of GPP to woody biomass and thereby increasing the residence time of the assimilated C, forests growing on more fertile soils can be expected to exhibit higher NEP. Carbon-use efficiency at the ecosystem level (CUEe), defined as NEP of an ecosystem per unit of GPP, measures the proficiency of an ecosystem to store C absorbed from the atmosphere. We thus suggest that both NEP and CUEe increase with increasing nutrient availability in forest ecosystems.

To test this hypothesis, we updated and analysed a global forest data set of mean annual carbon flux (GPP, ecosystem respiration (Re) and NEP), stand biomass, stand age and information on management. The resulting data set of 92 forests included scattered data from 1990 to 2010 from boreal, temperate, Mediterranean and tropical forests⁹ (Supplementary Fig. 1). We added all published information on the nutrient status of these forests and we classified them as forests with high nutrient availability (without apparent nutrient limitation) and low nutrient availability (apparently strongly nutrient-limited, in the sense of ref. 2, considering a holistic combination of availability of nutrients and soil characteristics). We based the nutrient availability classification on a multivariate factor analysis containing information about soil type, soil and foliar nutrient concentrations (N, P), soil pH, soil C/N ratio, nitrogen deposition and mineralization, history of the stand, specific reports of nutrient availability and an assessment by the principal investigator of the site (Supplementary Table 1). This analysis clearly separated nutrient-rich from nutrient-poor forests (Supplementary Fig. 2). We also established a medium category that was used for additional testing; it contained forests with information indicating moderate availability of nutrients or with little information about their nutrient status. Mean annual temperature and precipitation (MAT, MAP) from the WorldClim database¹⁰ and water deficit (WD) derived from Moderate Resolution Imaging Spectroradiometer (MODIS) evapotranspiration time series (MOD15A2 product) were used as climatic predictors. We then used generalized linear models to disentangle the effects of climate, management and stand age from those of nutrient availability on NEP and CUEe (see Methods for details on data sets and methodology).

NEP in nutrient-rich forests averaged 33 ± 4% (mean ± s.e.m) of GPP, whereas nutrient-poor forests accumulated only 6 ± 4% of

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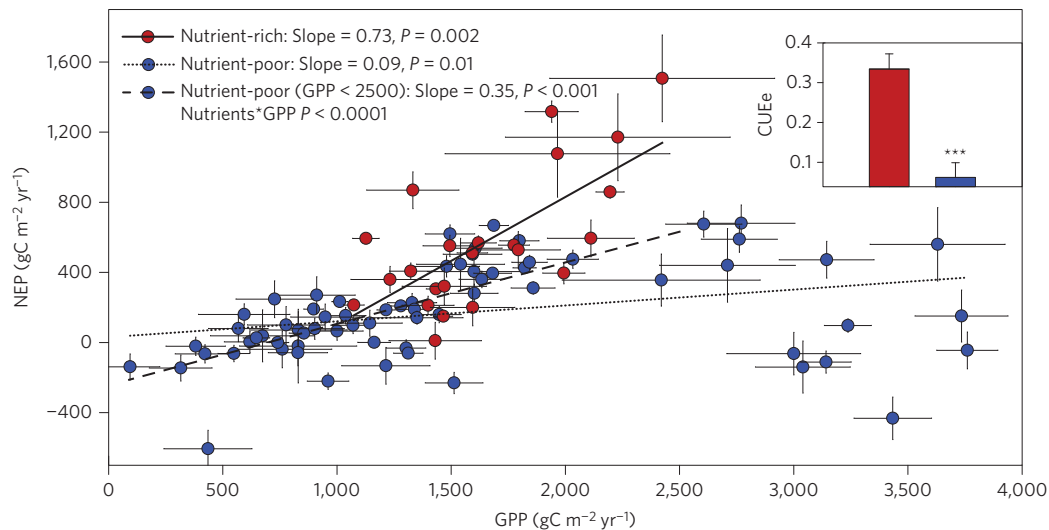


Figure 1 | Only nutrient-rich forests substantially increase carbon sequestration with increasing carbon uptake. The bar chart inside the main graph shows that carbon-use efficiency at the ecosystem level (CUEe) (net ecosystem production (NEP)/gross primary production (GPP) ratio) in nutrient-rich forests (red) is more than five times higher than in nutrient-poor forests (blue). We also present results for forests with $GPP < 2,500 \text{ gC m}^{-2} \text{ yr}^{-1}$, because values of $GPP > 2,500 \text{ gC m}^{-2} \text{ yr}^{-1}$ were available only for nutrient-poor forests. When considering only forests with $GPP < 2,500 \text{ gC m}^{-2} \text{ yr}^{-1}$, the $\text{Nutrients} \times \text{GPP}$ (where Nutrients = nutrient availability) interaction (where * indicates an interaction) was significant at the 0.006 level. In the bar chart, error bars indicate the s.e.m. and *** indicates significant differences at the $P < 0.001$ level.

the photosynthesized carbon (CUEe in Fig. 1, difference = $27 \pm 7\%$, analysis of variance $P < 0.001$). Only nutrient-rich forests showed a clear positive relationship between GPP and NEP (Fig. 1). In contrast, nutrient-poor forests channelled a larger proportion of GPP into Re (Fig. 2), with NEP being almost independent of GPP. Higher nutrient availability thus seems to channel C fixed by GPP towards storage in biomass and soils, rather than being respired back to the atmosphere.

A common protocol in eddy covariance CO_2 flux studies is to estimate GPP by adding Re (for example, extrapolated from nocturnal measurements) to the measured net ecosystem exchange (a proxy for short-term NEP). In this protocol any error in Re would therefore be directly propagated into a biased estimation of GPP, potentially imposing a spurious correlation between GPP and Re (refs 11,12). This correlation, however, in addition to being irrelevant on an annual scale¹³, was present in nutrient-poor forests but not in nutrient-rich forests (Fig. 2). The correlation between GPP and Re observed across nutrient-poor forests is thus unlikely an artefact from the processing of eddy-covariance data for separating these gross fluxes. We instead suggest that the positive relationship between Re and GPP only in nutrient-poor forests is due to different patterns of ecosystem functioning in nutrient-poor versus nutrient-rich forests.

Our statistical analyses using generalized linear models, including GPP, nutrient availability and stand age, explained 74%, 93% and 43% of the variance in NEP, Re (Table 1) and CUEe across sites, respectively (Supplementary Table 2). Nutrient availability alone explained 19% of the variance in NEP. When summed with its interactions with GPP (15%) and age (1%), nutrient availability accounted for 35% of the variance in NEP. GPP alone explained 18% of the cross-site variability in NEP. When additional interactions with nutrient availability and age (9%) were included, GPP explained 42% of the variability in NEP. The relationship between NEP and stand age, however, was significant only when GPP was previously included in the models, which emphasizes the smaller effect of stand age on NEP as compared with GPP (Supplementary Figs 3 and 4). Finally, MAT was positively correlated with NEP and explained 9% of its variance. In contrast to NEP, GPP alone explained 64% of

the variance in Re, with nutrient availability and its interactions explaining 9% and age and its interactions explaining only 5%. For CUEe, nutrient availability explained 12%, and GPP 14% of the variance in CUEe. Stand age also played an important role, interacting with GPP (reducing the positive effect of GPP on CUEe as forests matured) and explaining 17% of the variance in CUEe.

The relative contribution of explanatory variables thus differed among the NEP, Re and CUEe models, but the key and robust result is that nutrient status was a key factor for NEP and CUEe (Fig. 3 and Table 1 and Supplementary Table 2), despite the use of nutrient status as a binary variable (high versus low nutrient availability). Other possible predictors such as management and climate (MAP and WD) were not selected to enter in the general model by the stepwise model selection procedure; that is, they did not significantly affect NEP or Re (Table 1). Model-averaging techniques (see Supplementary Information) also indicated little importance of climate or management on NEP and Re. In contrast to NEP and Re, GPP was clearly climatically driven, being positively correlated with MAT and negatively correlated with WD, which accounted for 65% and 10%, respectively, of the variance in GPP.

The significant positive effect of nutrient availability on NEP proved to be robust in weighted models (Supplementary Fig. 5) and when controlling for effects of potentially confounding factors, for example: when using only data derived from eddy-covariance measurements (Table 1), when excluding forests with $GPPs > 2,500 \text{ gC m}^{-2} \text{ yr}^{-1}$ (that is, mostly tropical forests) from the analyses (no nutrient-rich forests were available for comparison at GPP higher than this threshold, Figs 1 and 2), when using only managed forests (Supplementary Figs 6 and 7), when using an alternative classification of nutrient status to analyse sensitivity to possible classification errors (Table 1 and Supplementary Table 2) and when using the first factor of the factor analysis for nutrient classification as a nutrient richness covariate (Table 1, nutrient richness factor). Furthermore, when including the moderate nutrient availability forests, this group showed an intermediate behaviour between the nutrient-rich and the nutrient-poor forests (Supplementary Fig. 8). On the other hand, when nutrient status was

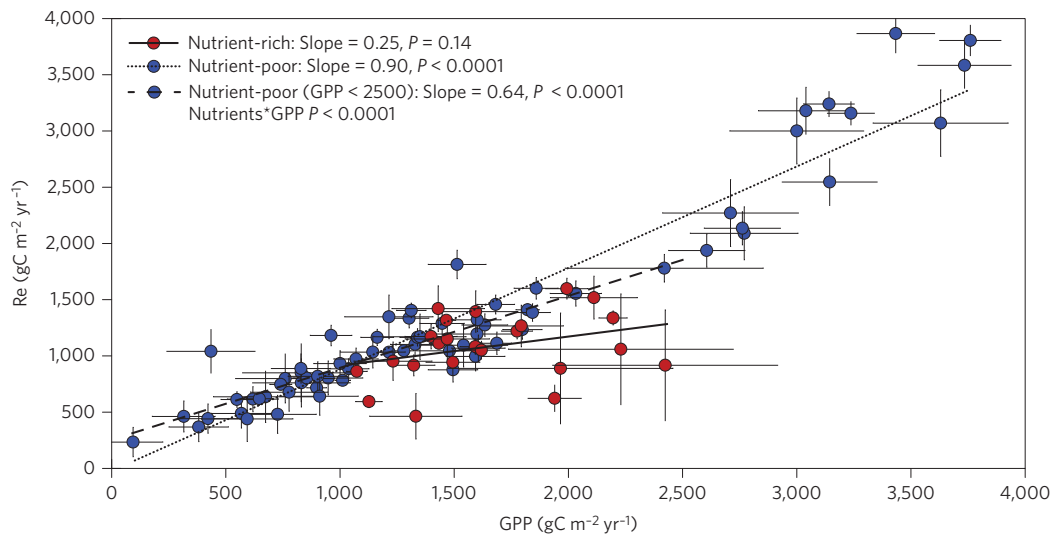


Figure 2 | The coupling between ecosystem respiration (Re) and gross primary production (GPP) is weak in nutrient-rich forests and very strong in nutrient-poor forests. Nutrient-rich forests decouple Re from GPP, resulting in an increase in carbon accumulation with increasing GPP. When considering only forests with $GPP < 2,500 \text{ gC m}^{-2} \text{ yr}^{-1}$, the Nutrients * GPP (where Nutrients = nutrient availability) interaction (where * indicates an interaction) is significant at the 0.005 level. Error bars indicate the uncertainty of the estimate on both the x and y axes (s.e.m.).

excluded from the analyses, management played the role of nutrients in our models, albeit the models explained less of the variance than did the models containing nutrient availability (Table 1), and the second-order Akaike information criterion increased considerably (by 18.6 and 17.2 points for NEP and Re, respectively). These results were expected because managed forests are mostly nutrient-rich forests (Supplementary Fig. 7) for the generation of profits from fertile lands.

The positive effect of nutrient availability on a more efficient use of photosynthates and a larger sequestration of carbon at the ecosystem level is probably not driven by a single mechanism or a single compartment of the ecosystem but rather by a combination of autotrophic and heterotrophic processes. Autotrophic processes are mainly related to different patterns of carbon allocation in nutrient-rich and nutrient-poor forests^{2,14}, whereas mechanisms related to heterotrophic processes involve primarily changes in substrate quality and the composition of the community of decomposers (mainly fungal and bacterial)^{3,15}.

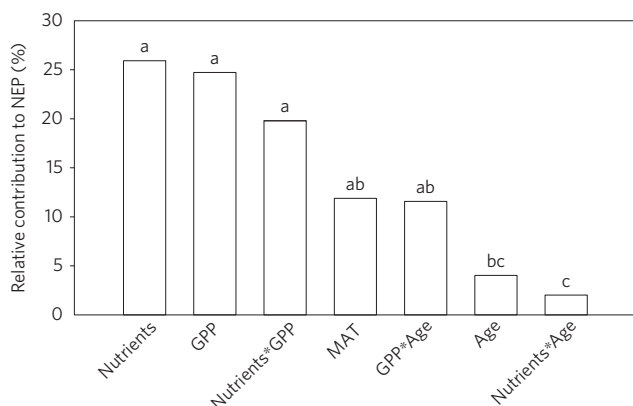


Figure 3 | Relative contribution of predictor variables in the model explaining variability in net ecosystem production (NEP). Letters indicate significant differences according to the bootstrapped confidence intervals computed for the differences among variables (relaimpo R package³⁰). Nutrients = nutrient availability. All variables and interactions shown were statistically significant ($P < 0.05$). The * symbol indicates an interaction.

For the autotrophic compartment, we detected two differences in the distribution of biomass across different organs between the different nutrient classes, despite also considering other factors such as climate and management. First, although only marginally significant, the ratio of fine-root biomass to total biomass was almost three times higher in nutrient-poor forests than in nutrient-rich forests ($P = 0.06$, $N = 17$; Supplementary Fig. 9a), indicating a higher proportional investment of GPP into fine roots for increasing access to nutrients^{16,17}. Second, the leaf area index per unit of fine-root biomass was twice as large in nutrient-rich forests ($P = 0.013$, $N = 19$; Supplementary Fig. 9b), indicating a shift in carbon allocation towards photosynthetic tissues when nutrients are not limiting growth and trees need to invest less in nutrient-acquiring structures. Accordingly, an earlier study, using a subset of our database, pointed out that nutrient-rich forests allocate larger proportions of their photosynthates to wood production compared with nutrient-poor forests at the cost of producing less root biomass². These changes in allocation patterns thus suggest enhanced carbon fixation in nutrient-rich forests.

An increase in the production of leaves in nutrient-rich forests, at the expense of producing fewer fine roots, could decrease the benefit of increasing above-ground allocation in terms of CUE if that above-ground carbon is not stabilized. On the other hand, although some studies have reported higher root respiration per unit mass at high root nutrient concentrations^{18,19}, a substantial decrease in root biomass may counterbalance this increase in autotrophic respiration and even reduce it at the ecosystem level³. In addition, when soil nutrients are poorly available, plants engage in active nutrient transport through the cell to increase nutrient uptake, spending energy for nutrient acquisition and therefore reducing energy available for plant growth²⁰. The net effect of root physiological adjustments to nutrient supply is unclear.

Changes in patterns of photosynthate allocation are also relevant for the heterotrophic compartment. For example, the higher proportion of GPP in nutrient-rich forests partitioned to tissues with long turnover times such as wood^{2,14} may decrease heterotrophic respiration, because wood is generally composed of rather recalcitrant molecules that decompose slowly²¹. Furthermore, numerous studies suggest that under high nutrient availability, forests allocate less C to fungal root symbionts², and to exudation

Table 1 | Summary of the percentage of variance explained by the significant variables of the models relating net ecosystem production (NEP) and ecosystem respiration (Re) with gross primary production (GPP), nutrient availability (NA), management (MNG) and stand age and their second-order interactions.

Model	GPP	NA	GPP*NA	MAT	GPP*Age	Age	Age*NA	MNG	WD	GPP*MNG	Model R ² (percentage)
General											
NEP (Fig. 1)	18 (1.8)	19 (1.3)	15 (−1.9)	9 (0.5)	9 (−1.0)	3 (1.1)	1 (−0.4)				74
Re (Fig. 2)	64 (0.1)	3 (−0.7)	5 (1.1)	16 (−0.2)	3 (0.5)	1 (−0.6)	1 (0.2)				93
CUEe	14 (0.9)	12 (−0.3)			17 (−1.2)	0 (1.1)					43
Weighted (Supplementary Fig. 2)											
NEP	20 (1.6)	14 (1.0)	8 (−1.4)	8 (0.4)	6 (−1.0)	2 (1.2)	3 (−0.5)				61
Re	65 (0.3)	2 (−0.5)	3 (0.8)	15 (−0.2)	2 (0.5)	0 (−0.6)	1 (0.3)				88
CUEe	1 (0.5)	16 (−0.1)			9 (−0.8)	3 (0.9)	5 (−0.4)				34
Eddy-covariance data alone											
NEP	18 (1.5)	11 (0.8)	6 (−1.5)	9 (0.5)				4 (0.6)		11 (−0.8)	59
Re	67 (0.4)	1 (−0.4)	1 (0.7)	19 (−0.2)				1 (−0.2)		2 (0.4)	92
CUEe	12 (0.9)	9 (−0.3)			15 (−1.2)	2 (1.2)					38
Without nutrient availability											
NEP	31 (1.1)							8 (0.6)	5 (0.3)	15 (−1.8)	59
Re	70 (0.6)							2 (−0.3)	11 (−0.2)	4 (0.5)	87
CUEe	15 (0.9)							0 (0.8)		2 (−1.1)	46
GPP <2500 gC m^{−2} yr^{−1}											
NEP (Fig. 1)	44 (1.2)	17 (0.6)	6 (−0.9)						5 (0.2)		72
Re (Fig. 2)	55 (0.3)	3 (−0.6)	6 (0.8)						10 (−0.2)		74
CUEe	38 (0.8)				7 (−0.8)	1 (0.9)					46
GPP <2500 gC m^{−2} yr^{−1} weighted (Supplementary Fig. 2)											
NEP	34 (0.9)	11 (0.7)	5 (−0.9)	12 (0.3)							62
Re	58 (0.9)	3 (0.2)							11 (−0.2)		72
CUEe		15 (−0.2)		19 (0.3)							34
Managed forests (Supplementary Fig. 6)											
NEP	52 (1.1)	14 (0.3)	4 (−0.7)						9 (0.3)		79
Re	57 (0.4)	3 (−0.4)	5 (0.7)						17 (−0.3)		82
CUEe	37 (0.7)	9 (−0.3)			5 (−0.6)	3 (0.8)					54
Alternative classification											
NEP	25 (1.6)	12 (1.2)	11 (−1.5)	11 (0.5)	1 (−1.1)	4 (1.2)	2 (−0.4)				75
Re	67 (0.3)	2 (−0.8)	4 (0.9)	13 (−0.3)	4 (0.6)	1 (−0.7)	1 (0.2)				92
CUEe	12 (0.6)	7 (−0.3)		6 (0.4)	18 (−1.2)	0 (1.2)					43
Nutrient richness factor											
NEP	25 (0.9)	23 (−0.4)	5 (0.8)					5 (0.4)		9 (−0.7)	67
Re	79 (0.7)	4 (−0.2)						1 (−0.3)		3 (0.4)	87
CUEe	14 (0.8)	10 (0.2)						0 (0.8)		17 (−1.0)	41

The β coefficients of the models are shown in brackets. For NA, MNG or their interactions with covariates, the β coefficients of the factors and the interactions indicate differences from the reference level (for example, the slope of nutrient-rich forests of the general model is 1.8, and the slope, β , of the nutrient-poor forests is $1.8 - 1.9 = -0.1$). The model nutrient richness factor shows the model including the factors used in the nutrient classification (see Supplementary Methods, information on nutrient availability, and Supplementary Fig. 2) as a nutrient richness covariate instead of the binary variable nutrient availability. For this model, NA indicates the effect of the first factor extracted. The * symbol indicates an interaction.

that stimulates heterotrophic respiration in the rhizosphere³. Together, these nutrient effects would reduce microbial biomass and respiration, relative to nutrient-poor forests. In addition, communities of microbes and detritivores that consume nutrient-rich organic matter have higher growth efficiencies (less respiration per unit of organic matter decomposed) than do communities that decompose nutrient-poor organic matter^{15,22}. This difference could reduce heterotrophic respiration in nutrient-rich forests^{3,15} and potentially enhance carbon sequestration and accumulation in nutrient-rich forests.

Our results indicate a key effect of nutrient availability on forest carbon balance and particularly on the capacity of forests to sequester carbon. Only when nutrient availability is high can

forests sequester large amounts of carbon. This knowledge is crucial, especially given the human-induced alterations of nutrient availability and stoichiometry in many regions of the planet^{23,24}. Earth system models should evolve from considering only the effects of nitrogen on plant growth^{25,26} to considering the interactions of nitrogen as well as other nutrients with the entire carbon cycle²⁷. The relationship between GPP and NEP seems to be strongly controlled by the nutrient status of the forest, which implies that Earth system models will be unable to accurately predict the carbon balance of forest ecosystems without information on both background (pre-industrial) and regional changes in nutrient availability²⁸ resulting from direct human activities (for example, nitrogen deposition) and from indirect human activities (for

example, climate change and elevated CO₂ altering soil and plant nutrient cycling). Moreover, because GPP and surrogates are widely available from remotely sensed data, the assessment of nutrient status could allow estimation of NEP with remote sensing of GPP and ground-based measurements of CUEe. This way, estimates of global terrestrial carbon sequestration could be improved, and guidance for improved management of forest carbon could be provided. Finally, experimental research and environmental monitoring would benefit substantially by considering nutrient availability as carefully as climate.

Methods

Sources of data. We used data of mean annual carbon flux from a global forest database⁹. This data set contains complete measurements of carbon balance and uncertainties of GPP, Re and NEP of forests around the world. The WorldClim database¹⁰ (resolution ~1 km at the Equator) and MODIS evapotranspiration time series (MOD15A2 product) provided climatic data (MAT and MAP from WorldClim and potential and actual evapotranspiration from MODIS). The reliability of the data from the WorldClim database was tested with the available observed climatic values from the forests ($N = 123$). Results indicated a strong correlation between observed and WorldClim values for annual temperature and precipitation ($R^2 = 0.96$, $P < 0.001$ and $R^2 = 0.84$, $P < 0.001$ respectively).

All continents were represented in our analyses (Supplementary Fig. 1), although most of the forests were located in Europe and North America. Boreal ($N = 31$) and especially temperate ($N = 68$) sites outnumbered Mediterranean ($N = 14$) and tropical ($N = 16$) sites. Of the forests included, 61 were coniferous, 57 were broadleaved and 11 were mixed.

Information on nutrient availability. For each forest, we compiled all available information from the published literature (carbon, nitrogen and phosphorus concentrations of soil and/or leaves, soil type, soil texture, soil C/N ratio, soil pH, measures of nutrients, and so on.) related to nutrient availability. Then we followed the criteria shown in Supplementary Table 3 to code these variables as three-level factors indicating high, medium or low nutrient availability. Next, we transformed these factors into dummy variables and performed a factor analysis. The first factor extracted explained 14.8% of the variance in the data set and was related to nutrient-rich dummy variables whereas the second factor explained 8.7% of the variance and was related to nutrient-poor dummy variables (Supplementary Fig. 2a). Then, on the basis of the aggregations across the two main factors extracted (Supplementary Fig. 2b) we classified the forests as having clearly high or clearly low nutrient availabilities. The remaining forests, for which empirical evidence was insufficient to classify them as nutrient-rich or nutrient-poor or indicated moderate nutrient availability, were classified as medium nutrient availability. To maximize robustness, we included only the forests with clearly high ($N = 23$) and clearly low ($N = 69$) nutrient availabilities in the main analysis, discarding data from the 37 remaining forests with medium nutrient availability. We also present the analysis with all of the available data (including the medium nutrient availability category) in Supplementary Fig. 8 and in Supplementary Models.

Statistical analyses. We ran generalized linear models to test for differences in CUEe, NEP, Re and GPP between forests of high and low nutrient availability, accounting for the possible effects of GPP, mean stand age, management (as a binary variable: managed or unmanaged) and climate (MAT, MAP and $WD = 1 - (AET/PET) * 100$), where AET and PET represent actual and potential evapotranspiration, respectively. That is, $NEP \sim GPP + \text{nutrient availability} + \text{Age} + \text{Management} + \text{MAT} + \text{MAP} + \text{WD}$. We tested for interactions up to the second order among GPP, nutrient availability, age and management. The significant variables of the final model (minimum adequate model) were selected using stepwise backward variable selection and the Akaike information criterion of the respective regression models. To evaluate the variance explained by each predictor variable, we used the averaged over orderings method (the lmg metric, similar to hierarchical partitioning) to decompose R^2 from R (ref. 29) with the package relaimpo (Relative Importance for Linear Regression³⁰). Finally, we tested whether nutrient status, management, age and climatic variables could lead to changes in patterns of biomass allocation with stepwise forward regressions. Model residuals met the assumptions required in all analyses (that is, normality and homoscedasticity).

The robustness of our analyses was tested by five different methods: running weighted models using the inverse of the uncertainty of the estimates as a weighting factor; using only data derived from eddy-covariance towers; restricting comparison of nutrient-rich and nutrient-poor forests to a common rank of GPP ($GPP < 2,500 \text{ gC m}^{-2} \text{ yr}^{-1}$ in Figs 1 and 2, thus excluding most of the tropical forests and using forests presenting GPPs above 1,000 and below

$2,500 \text{ gC m}^{-2} \text{ yr}^{-1}$ in Supplementary Fig. 10); using an alternative classification of nutrient availability (the second most plausible classification) as an analysis of sensitivity; and using the factors extracted for the classification of nutrients as nutrient richness covariates instead of using the binary factor nutrient availability. Detailed information about the methods used in this paper is presented in the Supplementary Information.

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Author contributions

M.F.-M., S.V., I.A.J. and J.P. conceived the paper and analysed the data. All authors contributed substantially to the discussion and the text writing.

Additional information

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Competing financial interests

The authors declare no competing financial interests.

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Nutrient availability as the key regulator of global forest carbon balance

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