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Biomass production efficiency controlled by management in temperate and boreal ecosystems

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Plants acquire carbon through photosynthesis to sustain biomass production, autotrophic respiration and production of non-structural compounds for multiple purposes[1]. The fraction of photosynthetic production used for biomass production, the biomass production efficiency[2], is a key determinant of the conversion of solar energy to biomass. In forest ecosystems, biomass production efficiency was suggested to be related to site fertility[2]. Here we present a database of biomass production efficiency from 131 sites compiled from individual studies using harvest, biometric, eddy covariance, or process-based model estimates of production. The database is global, but dominated by data from Europe and North America. We show that instead of site fertility, ecosystem management is the key factor that controls biomass production efficiency in terrestrial ecosystems. In addition, in natural forests, grasslands, tundra, boreal peatlands and marshes, biomass production efficiency is independent of vegetation, environmental and climatic drivers. This similarity of biomass production efficiency across natural ecosystem types suggests that the ratio of biomass production to gross primary productivity is constant across natural ecosystems. We suggest that plant adaptation results in similar growth efficiency in high- and low-fertility natural systems, but that nutrient influxes under managed conditions favour a shift to carbon investment from the belowground flux of non-structural compounds to aboveground biomass.

The fraction of gross primary production (GPP) used for biomass production (BP) of terrestrial ecosystems has recently been coined biomass production efficiency (BPE; ref. 2). BPE is typically used as a proxy for the carbon-use efficiency or NPP-to-GPP ratio, where NPP refers to net primary production—that is, BP plus the production of non-structural organic compounds[1]. Current knowledge about BPE is mainly derived from research on forests. Earlier work reported BPE to be conservative across forests[3], whereas more recent syntheses suggest high inter-site variability[2,4]. The variation in BPE was first attributed to vegetation properties (forest age) and climate variables[4]. More recently, it was shown that forest BPE in a range of natural and managed sites was correlated with site fertility, with management as a secondary BPE driver[2].

Fertility and management are strongly correlated as management enhances productivity by increasing plant-available resources, including nutrients. For instance, fertilization of grasslands directly increases the ecosystem nutrient stock, whereas forest thinning indirectly increases nutrient availability at the tree level by reducing plant–plant competition. In addition, fertile sites are more likely than infertile sites to be managed. Atmospheric deposition of nutrients, especially nitrogen (N), might further complicate the relationship between BPE, fertility and management. The influence of site fertility and management on BPE has not been disentangled in previous studies, and the impact of N deposition on BPE is largely overlooked. Here, we postulate that the impact of management on BPE is underestimated. In addition to a direct effect on BPE through selection of the most efficient plants[2,5], management can indirectly affect BPE through effects on site fertility and related belowground dynamics[2]. Understanding of these dynamics not only will clarify the controls of BPE but also elucidate the human impacts on BPE.

We compiled a new BPE data set comprising 131 sites, including forests, grasslands, croplands, wetlands (temperate marshes and boreal peatlands) and tundras (Methods). All major climatic zones (from polar to tropical) were represented, but managed sites were located almost entirely in the temperate and boreal zone of North America and Europe (Supplementary Fig. 1 and Supplementary Table 1). For each site, our data set also included vegetation characteristics, environmental data and information on anthropogenic impacts such as management and atmospheric N deposition (Supplementary Table 2). With regard to management, we adopted a binary classification (Methods), distinguishing natural sites (pristine sites or sites with a low human impact that largely reproduced naturally occurring processes—for example, grasslands with low grazing) from managed sites (sites dominated by human activity with impacts that would not occur in nature—for example, newly established and fertilized grasslands). The utility of this classification was tested against more complex classifications

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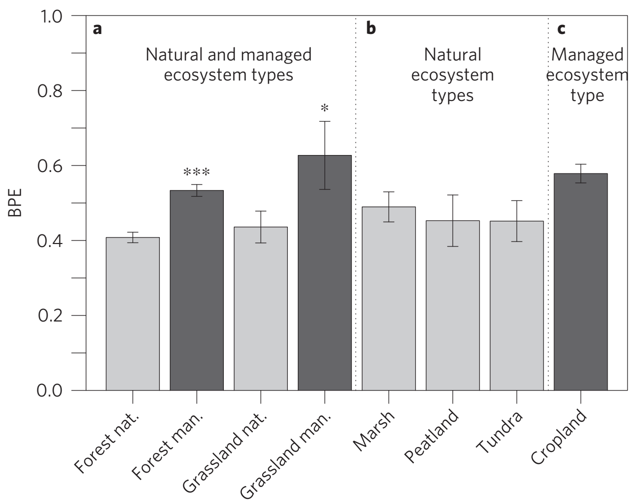

Figure 1 | BPE of natural and managed ecosystems. BPE (mean ± 1 s.e.m.) of (**a**) natural ecosystem types that can be regularly managed, such as forests and grasslands; (**b**) natural ecosystem types that are not commonly managed, such as temperate marshes, boreal peatlands and tundras; and (**c**) anthropogenic ecosystem types, such as croplands, that are not in a natural state but are maintained through management. Difference within forest types was significant at $p < 0.001$ (***), whereas difference within grassland types was significant at $p < 0.05$ (*). Light grey columns indicate natural (nat.) conditions and dark grey columns managed (man.) conditions.

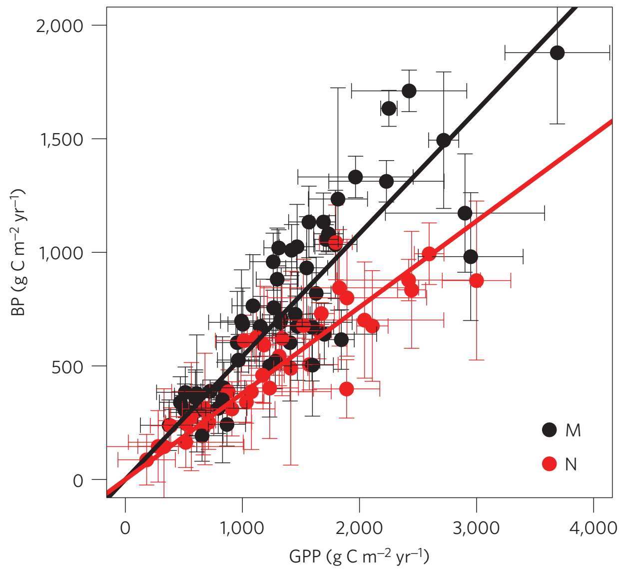

Figure 2 | Relationship between BP and GPP of natural and managed ecosystems. Annual values of BP and GPP with uncertainty intervals (s_{BPij} and s_{GPPij}) reflecting measurement uncertainty and sample size (Methods) for 93 sites worldwide comprising forests, grasslands and croplands, according to the management status: managed (black, M) or natural (red, N). The slope of the linear regressions equals the BPE.

(Methods), whereas its reproducibility was assured by the definition of several sub-categories within the 'managed' and 'natural' classes (Supplementary Table 3). The BPE data set, comprising the ancillary site information, is available in Supplementary Data. Our data analysis consisted of multinomial ordered logistic regressions to examine the relationship between fertility and management (code available in Supplementary Information), combined with linear (univariate analysis, multiple linear regressions) and nonlinear approaches (Random Forest) to extract emerging relationships between BPE and its potential predictors (Methods).

The analysis proceeded in five steps, using different subsets of our database. (1) We analysed all natural sites to test whether BPE is driven by natural variation in site fertility. The results showed that this hypothesis was not true. First, BPE did not differ significantly ($p = 0.83$) among natural ecosystem types of contrasting fertility status—that is, tundra and boreal peatlands (nutrient-poor), temperate marshes (nutrient-rich) and forests and grasslands (with variable but overall intermediate fertility status)—showing an average BPE (and s.e.m.) of 0.46 ± 0.01 (Fig. 1 and Supplementary Table 4). Second, the impact of fertility on the BPE of natural ecosystems remained nonsignificant when accounting for variation in fertility among forests ($p = 0.24$, $n = 43$), grasslands ($p = 0.72$, $n = 16$) or all natural sites lumped together ($p = 0.23$, $n = 75$; Supplementary Fig. 2). (2) We analysed the relationship between fertility and management in natural and managed forests to verify their correlation and disentangle the impact of management on fertility from the fertility status unrelated to management. This analysis confirmed that management was a significant explanatory variable for site fertility (likelihood ratio test of models with and without management as covariate: chi-square = 17.33, $p = 0.00017$), whereas the relationship between N deposition and fertility was weak (likelihood ratio test: chi-square = 4.80, $p = 0.091$). This led us to model fertility as a function of management (taking into account that the fertility status was the result of both the impact of management operations on soil nutrient availability and the management choice of which land, for example, high or low fertility, to manage) and to obtain model residuals for each site representing the 'fertility status not explained by management'—defined hereafter as 'unexplained natural fertility' (Methods). (3) Once the effect of fertility and management were disentangled, we evaluated their relative importance as controllers of BPE and compared them to other possible BPE drivers (for example, vegetation and environmental characteristics, N deposition) within the forest data set. This analysis revealed that management was the key determinant of the differences in BPE among forests, N deposition was the second most important driver, and the unexplained natural fertility was insignificant (Supplementary Table 5 and Supplementary Fig. 3). The analysis also showed that stand age had a significant (negative) impact on BPE, which, however, became negligible when compared to the effect of management and N deposition (Supplementary Table 6). (4) We compared the BPE of key natural and managed ecosystem types (grasslands, forests and croplands) that typically share similar environmental characteristics and are regularly converted into one another, and observed that the BPE of managed sites was substantially greater than the BPE of natural sites (Figs 1 and 2 and Supplementary Table 7). (5) Last, we studied the impact of the potential drivers of BPE on all natural ecosystems and found that BPE of natural unmanaged sites was independent not only of the observed site fertility (see above point 1) but also of N deposition, and largely independent of all the vegetation and environmental drivers examined (Supplementary Table 8 and Supplementary Fig. 3). Climate showed an influence on BPE, but this effect was weak ($0.05 < p < 0.10$) and not consistent across statistical methods (Supplementary Table 8 and Supplementary Fig. 3).

The observed positive impact of management on BPE does not come as a surprise in itself. Rather, the novelty of this study is the finding that management is by far the 'key' driver of BPE and more important than any other vegetation or environmental factors. This observation calls for a refinement of the hypothesis, which previously postulated that greater BPE in more fertile sites is related to reduced C allocation to symbiotic fungi, as plants in nutrient-rich conditions invest less in processes facilitating nutrient uptake[2]. Our revised hypothesis relies on the fact that adaptation processes in natural ecosystems[6] could allow plants in

Table 1 | Carbon allocation pattern in natural and managed forests as expressed by the ratio of BP to GPP.

BP:GPP ratio	Forests		
	Natural (%)	Managed (%)	*p* difference
Leaves	10 ± 1	10 ± 1	0.91
Wood	11 ± 1	24 ± 3	0.00019***
Other aboveground	6 ± 2	7 ± 3	0.61
Fine roots	12 ± 2	8 ± 2	0.083*
Coarse roots	3 ± 1	4 ± 1	0.29
Whole ecosystem (BPE)	41 ± 2	53 ± 3	0.020**

Values are mean ± 1 s.e.m., in percentage; replicates (*n*): 12 and 19 for natural and managed forests, respectively; other aboveground: reproductive organs and understory; ***$p < 0.001$; **$p < 0.05$ and *$0.05 < p < 0.10$.

both nutrient-poor and nutrient-rich environments to have similar growth efficiency. However, belowground C transfers to symbionts are not static[7], and the greater nutrient availability caused by management could make root symbiotic associations less important for plants, thus reducing the flux of C from plants to symbionts. This pattern would favour C investment in biomass production, particularly aboveground, as light may become the most limiting resource. This hypothesis is supported by the allocation pattern available for a subset of our forests, showing that management substantially increased allocation to aboveground wood BP (+13%, $p < 0.001$) and marginally decreased allocation to fine root BP (−4%, $p = 0.083$) (Table 1), and by forest C allocation meta-analyses[8] which reported increased C partitioning to aboveground BP and decreased partitioning to belowground C flux in response to fertilization. Declines in mycorrhizal fungi following fertilization are well known[9]. Similarly, thinning can negatively affect the standing crop of mycorrhizal fungi[10] and ectomycorrhizal metabolic activity[11,12], which is consistent with our new interpretation. In addition, the larger BPE in managed ecosystems might also reflect decreased allocation of GPP to autotrophic respiration (Ra), thus lower Ra-to-GPP ratio[2]. However, as previous research does not support this hypothesis[3,8] and the variability of the Ra-to-GPP ratio might be small, *ad hoc* experiments combining the assessment of C transfer to mycorrhizal fungi and ecosystem Ra will be needed to ascertain the importance of these dynamics in managed ecosystems. Similarly, further research should explore if the hypothesized reduction in C allocation to mycorrhizae (and exudates) might have a long-term negative feedback on the site nutrient availability where management does not include external input of nutrients, as well as the impact of ecosystem degradation on BPE, especially in tropical areas that are often overexploited.

Nitrogen deposition also seemed to have a positive effect on BPE. Like management, elevated N deposition represents an artificial change in natural fertility and a perturbation of the nutrient cycle. The apparently contrasting evidence that N deposition does not affect BPE of natural ecosystems (when considered separately from the managed ecosystems) is probably related to the intensity of the deposition and the fact that N deposition might influence BPE (like other ecosystem processes[13]) only at higher deposition rates. Natural sites are typically found in less urbanized locations, and in our data set they were characterized by deposition rates 43% lower than those of managed ecosystems. Furthermore, adaptation responses to N deposition are more likely to occur in natural ecosystems where succession is much longer than rotations in managed ecosystems.

Little information was previously available about BPE of non-forest ecosystems[14]. Our analysis showed that BPE of natural ecosystems is independent of ecosystem type, vegetation and environmental characteristics (including natural site fertility). The lack of sensitivity of BPE to these potential drivers points to a rather conservative BPE across natural ecosystems. Our study supports the physiological argumentation for a constant ratio between BP and GPP in natural ecosystems[3,4] and provides important constraints for the global models that simulate high variability in BPE or NPP-to-GPP ratio.

Finally, our findings have practical applications, particularly for Europe and North America. First, the quantification of BPE for managed ecosystems can improve yield simulations by models (for example, timber in forests, grains in crops), particularly for algorithms that derive BP as a proportion of GPP (refs 15,16). Second, the land surface component of Earth system models at present does not take into account differences between natural and managed ecosystems which might introduce biases in BP projections. In fact, a case study based on the model ORCHIDEE (ref. 17) showed that taking into account a BPE difference of 8% between natural and managed ecosystems resulted in a 24% increment in BP for Europe (Supplementary Methods). Third, our study indicates new ways to indirectly derive BPE at regional and continental scales from maps of land use and human management. Fourth, whereas C assimilation and BP are extensively studied, the ways to maximize BPE are less explored. However, substantial changes in yield are potentially associated with small changes in BPE. For instance, for a forest with a GPP of 1,500 $g\,C\,m^{-2}\,yr^{-1}$, an increase of 12% in BPE (Supplementary Table 7) would enhance BP by 180 $g\,C\,m^{-2}\,yr^{-1}$, mainly in wood (Table 1). These examples show that our elucidation of BPE dynamics advances our understanding and quantification of the biomass production of terrestrial ecosystems.

Methods

Methods and any associated references are available in the online version of the paper.

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Author contributions

M.C., S.V., S.L. and I.A.J. conceived the paper; M.C. performed the analyses and wrote the text; S.L. provided ORCHIDEE simulations; J.B. developed the multinomial ordered logistic regressions and the statistics; E.C., D.O., D.P., P.F.S., X.W. and T.Z. provided field data or contributed to data collection from external databases and literature; all authors contributed substantially to discussions and revisions.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to M.C.

Competing financial interests

The authors declare no competing financial interests.

Methods

Data set. Our analysis required site estimates of biomass production (BP), gross primary production (GPP), and their uncertainty, to derive the biomass production efficiency (BPE) and its uncertainty. The key rule for selecting the sites was the availability of site-specific estimates of BP and GPP. Therefore, the data set did not include values obtained from generic algorithms (for example, global models, remote sensing products). BP included above- and belowground growth. In most cases, BP was obtained from harvest or biometric methods (comprising empirical models as, for example, allometric relationships, root growth as function of soil conditions[18,19]) and in 5% of the cases from process-based models with site-specific parameterization and/or validation against growth or biomass data. Minor gap-filling was done for BP estimates at some sites (see below). BP methodologies can be divided into broad classes according to method uncertainty (that is, low, medium or high uncertainty[1]; Supplementary Table 9) related in particular to the approach to determine fine root BP (the component of ecosystem BP most difficult to assess; see Supplementary Methods) or the use of process-based models (Supplementary Table 9). However, additional tests showed that the key results of our analysis were independent of the BP methodology employed (Supplementary Table 10). GPP was mostly estimated from eddy covariance (73% of the cases) or process-based models with site-specific parameterization and/or validation (20% of the cases). Explanation about the preference of these GPP methods instead of other approaches (for example, GPP derived from the sum of all carbon sinks within the ecosystem such as, for example, BP, autotrophic respiration, carbon transfer to mycorrhizal symbionts) is reported extensively in Supplementary Methods. Additional tests showed that the alternative use of eddy covariance- or model-based estimates of GPP did not affect the key results of our analysis (Supplementary Table 10). Detailed information on uncertainty calculations are reported in Statistical analysis.

The integrated data set provided BPE for 96 'golden' sites, for which BP and GPP were available from the same measuring period (53 forests, 14 grasslands, 24 croplands and 5 wetlands) and 35 additional natural sites for which BP and GPP were both available but not for the same measuring period (16 forests, 6 grasslands, 8 wetlands, 5 tundra). Wetlands were divided into marshes (herbaceous-dominated vegetation of the temperate zone mainly affected by flooding from river, sea or irrigation; 6 in total) and peatlands (ombrotrophic or minerotrophic inland boreal ecosystems rich in herbs, shrubs or mosses; 7 in total). An excerpt from the study data set is shown in Supplementary Table 1 and the geographical distribution of the sites in Supplementary Fig. 1. The key data used in the analysis are provided in Supplementary Data.

Ancillary data such as vegetation characteristics, climate, environmental conditions and anthropogenic impacts were needed for each site to determine the possible effect of these factors on BPE. Such information was retrieved mostly from the literature, open-access databases[1,20–27] or modelling[28] (Supplementary Table 2). For N deposition, data for Western Europe and the conterminous USA were retrieved from interpolated gridded maps based on ground observations[25], whereas simulated values were used for the rest of the world[22,23].

Management classification. Sites were divided into two categories. Natural sites are those characterized by none or low-to-moderate human impact, whereas managed sites are heavily affected by human activity. We defined 'low-to-moderate human impacts' as human activities that largely reproduce naturally occurring processes, for example, low grazing, occasional fire in grasslands, forest regeneration. We considered sites 'heavily affected by human activity' to be those with impacts that would not occur in nature—for example, intense fertilization of poor soils, sowing of cropland monocultures, thinning of healthy trees. The classification was straightforward for marshes, peatlands and tundras (pristine or with minimal human impact except in two managed wetlands) and for croplands (inherently managed) (Supplementary Table 3). For forests and grasslands, the classification included sub-categories for both the natural and managed classes (Supplementary Table 3). For forests, we considered as natural the following types of forests: old growth with minimal disturbance; natural succession due to fire/windthrow and at least 10 years after the disturbance; unmanaged or with low human impact (for example, understory grazing) in the 50 years before measurement; and planted forests without any intervention after planting and at least 10 years old at the time of measurement. We considered as managed forests: forests with thinning/harvest in the 50 years before measurement; newly (<10 years old) established plantations; forests fertilized in the 25 years before measurement; or forests managed for fruit/rubber production at time of measurement. Similar sub-categories were defined for grasslands (Supplementary Table 3).

We tested the validity of our approach by comparing our binary management classification to a more complex three-level classification In the latter approach, we considered 'pristine natural' the sites that were pristine or with minimal impacts, and 'semi-natural' the sites with low-moderate human impacts (these classes were considered jointly in the binary classification as 'natural'). For forests, we considered as semi-natural the forests that were: unmanaged or with low human impact (for example, understory grazing) in the 50 years before measurement, as well as planted forests without any intervention after planting and at least 10 years old (see above). The statistics of this additional test showed that BPE of pristine natural and semi-natural forests did not differ and that the BPE difference between pristine natural and semi-natural forests was considerably lower than the difference between semi-natural and managed forests (Supplementary Fig. 4 and Supplementary Table 11). This confirmed that our standard binary classification is sound. In addition, this exercise revealed that the introduction of more levels in the management classification would not be advantageous. This was evident for grasslands, for which the three-level classification did not alter the BPE pattern but substantially reduced the statistical power (Supplementary Fig. 4 and Supplementary Table 11).

Gap-filling. Some of the selected sites lacked BP measurements of minor ecosystem biomass components (for example, nonvascular plants, understory) or were affected by minor systematic measurement biases (for example, neglecting litterfall decomposition in tropical forests). These missing BP portions were gap-filled for completeness in analogy to ref. 2.

Production of reproductive organs in forests. When missing, this BP component was derived from a relationship between reproductive BP versus aboveground BP (ref. 2) derived from the Global Forest Database[1].

Leaf biomass production in tropical forests. Estimates of leaf BP in tropical forests are systematically underestimated because of within-canopy decomposition of leaf litter during the collection period. We estimated this missing portion of BP as 12% of total foliage production[2].

Understory biomass production in forests. BP due to understory vegetation is significant for boreal forests—thus, boreal forests lacking this BP component were not considered in our analysis[2]. However, the contribution of understory BP to total ecosystem BP is more limited for temperate and tropical forests[2]. Thus, we did not discard temperate and tropical forests lacking understory BP, but gap-filled this missing BP component, as done in previous studies[2]. In particular, understory BP was estimated as a fixed ratio of the forest tree BP: 0.043 for temperate and 0.073 for tropical forests[2].

Nonvascular biomass production in tundra. Missing nonvascular BP was derived from a nonvascular productivity ratio (BP-to-biomass ratio, the portion of biomass renewed every year). This ratio was calculated for wet ($0.50\,\mathrm{yr}^{-1}$) and mesic tundra ($0.42\,\mathrm{yr}^{-1}$) as the average of six observations for each tundra type (Supplementary Table 12).

Shrub biomass production due to stem secondary growth in peatland. Missing BP due to unaccounted shrub secondary growth (that is, increase in stem/branch diameter) was estimated to be 29% of the shrub aboveground primary growth (that is, BP due to current-year leaves and stem/branches) from data for subarctic shrubs[29].

The gap-filling concerned 31 forests of the 96 golden sites and 17 sites (14 forests, two tundras and one peatland) of the additional 35 natural sites. For 69% of the cases, the gap-filled BP differed by less than 5% than the original BP; for 13% of the cases the gap-filled and original BP differed by 5–10%, whereas for 17% of the cases this difference was 10–15%. Herbivory was not taken into account because it was negligible (for example, for forests[2]) or because BP measurements were from experiments that excluded large herbivores (for example, for all grasslands examined).

The gap-filling procedure avoided small secondary biases in the analysis but did not alter the primary results (Supplementary Table 13). Overall, original BPE of managed and natural forests (the ecosystem type most affected by gap-filling) was 0.52 ± 0.03 and 0.39 ± 0.02 (mean ± s.e.m.), respectively, which was less than 2% smaller than gap-filled BPE (Supplementary Table 7).

Statistical analysis. *Analysis overview and data set.* Our study consisted of five analyses, using different subsets of our database. (1) We analysed all natural sites ($n=75$; managed sites were not considered in this analysis) to test whether BPE is driven by natural variation in site fertility. In particular, we tested whether BPE differs among ecosystem types and sites of contrasting fertility. (2) We analysed the relationship between fertility and management in forests to verify their correlation and disentangle the impact of management on fertility from the fertility status not related to management. This analysis was performed on 53 managed and natural forests for which BP and GPP were measured during the same period. We focused this analysis on forests because they are the ecosystem type best represented in our data set and allow direct comparison with previous studies. (3) The relative importance of fertility, management and N deposition as controllers of BPE was compared to the importance of other possible BPE drivers. This analysis was performed on the forest data set considered in the second analysis after disentangling the effect of fertility and management. (4) We compared the BPE of key natural and managed ecosystem types (grasslands, forests and croplands) that typically share similar climatic and environmental characteristics and are regularly converted into one another. Only sites with BPE obtained from BP and GPP measured during the same period were used ($n=93$). (5) We studied the impact of the potential drivers of BPE in all natural ecosystems ($n=75$; this analysis did not include the managed sites).

For the analyses 1 and 5, we considered not only the sites for which BP and GPP were measured during the same period but also sites with BP and GPP measured during different (or only partially overlapping) periods (35 out of the 75 sites) to investigate a large set of ecosystem types (for example, from forest to tundra) and environmental conditions (for example, climate from tropical to polar, soil from waterlogged to very dry). For sites without management operations (and mostly at mature-old stage) the temporal mismatch in BP and GPP was less crucial, dampened at several sites by multi-year measurements (we used averages of BP and GPP for multi-year observations) and, most importantly, comparative tests revealed that the results of the analyses did not differ when all sites or only sites with temporal match in BP and GPP were considered (for example, Supplementary Table 14).

Relationship between fertility and management. Site fertility and site management are highly correlated factors that are both potentially crucial for BPE. For this study, we wanted to separate both drivers to test for BPE responses to the fertility status induced by management and the fertility status unrelated to management. To disentangle both effects, we applied an approach commonly used to deal with multicollinearity[30]: the observed fertility status was modelled as a function of management and the residuals from this model were used as explanatory variables of BPE (instead of the original fertility status). Hence, the residuals reflect the information on fertility not explained by management, which we termed 'unexplained natural fertility'. Initially, the model also included N deposition as an additional covariate, but we removed it in the final model as the relationship between N deposition and fertility was weak (see Main text).

A multinomial ordered logistic regression model (or 'proportional odds logistic regression model'[30]) was fitted with fertility as outcome (ordinal categorical variable with category high, H, medium, M, and low, L) and management (yes/no) as covariate. The model estimates the log odds of falling into or below a fertility category as a function of management:

$$\text{Logit P(fertility} = \text{L)} = \text{intercept}_{\text{L}} + \beta_{\text{L}} \times \text{management}$$

$$\text{Logit P(fertility} < \text{M)} = \text{intercept}_{\text{M}} + \beta_{\text{M}} \times \text{management}$$

where intercept_L and intercept_M were −2.01 and −0.511, respectively, and β_L and β_M were 2.84 and −0.0488, respectively. In other words, this model estimates the possible fertility distribution of each site according to its management status (given its management status, the probability to be H, M or L). Also three residuals were obtained for each site, which reflect the deviation of the fertility status of the site from the distribution estimated by the model. The independence of these three residuals on management (unlike the original fertility variable) was verified with t-tests (all p-values > 0.05).

BPE drivers. The relationships between BPE and its potential drivers were explored with three statistical approaches: univariate analysis, multiple linear regressions and Random Forest, which are described below. We used the following predictors: management status, observed natural fertility, climate zone, ecosystem type, growth form (five categorical variables) and N deposition, unexplained natural fertility (the three model residuals described above), soil available water content, annual precipitation and dry months per year (seven continuous variables) (Supplementary Table 2). All analyses were performed with R (ref. 31).

Univariate analysis tested the significance of the relationships between single predictors and BPE. For continuous variables, this was done with single linear regressions, whereas for categorical variables we used one-way analysis of variance (ANOVAs) with a *post hoc* Tukey's HSD test. Normality of residuals was tested with a Shapiro–Wilks' test and the assumption of homoscedasticity with Levene's test (for ANOVAs) or Breusch–Pagan test (for regressions). For the few cases for which these conditions were not met, data were transformed (for example, $\log(x)$, $1/x$ or x^2) or treated with alternative methods (Kruskal–Wallis test for non-normality and applications of White method for heteroskedasticity[32]).

Multiple linear regressions allow a comparison of the effect of the potential BPE predictors considering them all together. Whenever a given predictor was significant in the univariate analysis, but not in the multiple linear regressions, this indicated a lower importance of that predictor as compared to other predictors. In practice, we opted for backward stepwise regressions. Accordingly, the best BPE model was determined by starting from the model with all variables and successively removing the least important. The selection was done by comparing the new model (without the removed variable) with the original model (with the original variable) using Likelihood Ratio and Akaike Information Criterion (AIC). In practice, the new model was not accepted if the Likelihood Ratio was significant ($p < 0.05$) or the AIC increased. Stepwise multiple linear regression was a suitable methodology for our analysis, because it can be applied with both continuous and categorical variables. However, all factors of categorical variables need to be taken into consideration by introducing dummy variables. Prerequisites (or alternatives) for applying linear regressions (for example, residuals normality and homoscedasticity) were tested as described above for univariate analysis.

Random Forest is a partitioning method that we used to produce a large ensemble of regression trees considering always our complete BPE data set but random subsets of predictor variables[33]. This means that (in contrast to multiple linear regressions) Random Forest accounts also for nonlinear relationships and interactions, and evaluates each predictor variable (even the least important or redundant), providing a ranking of the predictors' importance. However, this analysis does not assign a significance label (contrary to linear regressions analysis). The importance of a given variable is instead indicated by the mean decrease in accuracy (or increase in mean squared error, %IncMSE) of model predictions when the value of that given variable was changed (permuted within the data set)[33]. The more important the variable, the larger the difference between original predictions and new predictions, and the larger the %IncMSE. We used the standard Random Forest algorithm[34] setting a large number of trees (50,000) to obtain stable results.

Confounding factors. The response of BPE to N deposition and variables related to the water status (soil available water content, precipitation, dry months per year) could have been confounded by fertilization and irrigation/exceptional soil water conditions, respectively, at some sites. To check for the relevance of confounding factors, the analyses comprising N deposition and the variables related to the water status were performed both on the entire data set and on a subset that excluded sites with fertilization, irrigation, occasional flooding, minerotrophic conditions and permafrost. Overall, the impact of these sites was negligible (Supplementary Table 15)—therefore, they were not removed in the final analyses. Through the analysis, filtering for outliers was minimal and we removed only four sites with unrealistic BPE (0.84–0.94).

Uncertainty. The BP uncertainty for site i (s_{BPij}) depended on a typical range of uncertainty (p_{BPi}) based on ecosystem type, the experimental methodology j through a method-specific uncertainty reduction factor (RF_{BPj}) and the length of the measurement period in years (l_{BPij}; ref. 1):

$$s_{\text{BPij}} = \frac{(p_{\text{BPi}} \times RF_{\text{BPj}})}{(l_{\text{BPij}})^{0.5}}$$

In cases where BP needed to be gap-filled (see above), the uncertainty of the original BP estimate ($s_{\text{BPij original}}$) was increased by a factor equivalent to 100% of the gap-filling amount[2]:

$$s_{\text{BPij gapfilled}} = ((s_{\text{BPij original}})^2 + (\text{gapfilling})^2)^{0.5}$$

where $s_{\text{BPij gapfilled}}$ is the uncertainty of the gap-filled BP estimate. The uncertainty of GPP (s_{GPPij}) was calculated in the same way as s_{BPij}:

$$s_{\text{GPPij}} = \frac{(p_{\text{GPPi}} \times RF_{\text{GPPj}})}{(l_{\text{GPPij}})^{0.5}}$$

where p_{GPPi} is the typical range of GPP uncertainty, RF_{GPPj} the uncertainty reduction factor dependent on the experimental methodology j and l_{GPPij} the length of the measurement period in years. The uncertainty of BPE (s_{BPEij}) was calculated through error propagation:

$$s_{\text{BPEij}} = \left(\left(\frac{s_{\text{BPij}}}{BP_{\text{ij}}}\right)^2 + \left(\frac{s_{\text{GPPij}}}{GPP_{\text{ij}}}\right)^2\right)^{0.5}$$

where BP_{ij} and GPP_{ij} are values of BP and GPP, respectively, for site i and method j. Values of RF_{BPj} and RF_{GPPj} are reported in Supplementary Table 9 (ref. 1). For forest ecosystems, values of p_{BPi} and p_{GPPi} were available in the literature[1], whereas for non-forest ecosystems they were derived from the difference between the ninth and first decile of BP and GPP samples from about 20 to 110 sites according to ecosystem type (Supplementary Table 16).

Code availability. Code available in Supplementary Information.

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Biomass production efficiency controlled by management in temperate and boreal ecosystems

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1 Supplementary Methods

<u>*Methodology to estimate GPP*</u>

There are three common approaches to estimate annual gross primary production (GPP) at site level. (i) First, GPP as sum of all carbon sinks (sinks-sum) within the ecosystem (e.g. biomass production, (BP), autotrophic respiration (Ra), carbon transfer to mycorrhizal symbionts), which are normally measured with repeated stock inventories, plant growth monitoring and chamber based techniques[8]. (ii) Second, GPP derived from eddy covariance (EC) micro-meteorological measurements of the CO_2 exchange between the ecosystem and the atmosphere (net ecosystem production, NEP), with GPP obtained by summing NEP and the ecosystem respiration, which is commonly estimated by extrapolating the nighttime NEP during the day using temperature response functions[35,36]. (iii) Third, modelling of photosynthesis using process-based models with site-specific parameterization and/or validation[37,38]. Here, we preferred to use method (ii) and (iii) for the following reasons:

1. For our analysis, it was essential to have site estimates of both GPP and BP, as BPE is the BP-to-GPP ratio. Many EC sites are investigated for ecological measurements as well and measurements of BP are thus often done within the EC footprint area. On the other hand, sinks-sum methods do not consistently provide both GPP and BP estimates. In fact, there are two main types of sinks-sum approaches[8]: (i) methods estimating GPP by summing aboveground BP, aboveground Ra and total belowground carbon flux, and (ii) methods estimating GPP from aboveground BP and Ra and belowground BP and Ra. In the first approach, BP estimates are missing, as belowground BP is not measured. In the second approach, GPP estimates are incomplete for our analysis as carbon flux to mycorrhiza and exudation are not accounted for.

2. In the sinks-sum approach, BP and GPP are not independent as estimates of GPP are derived from measurements of BP. Therefore, any error in BP estimates would propagate into the GPP data, with a potential increase in the uncertainty of BPE. Eddy covariance and models provide GPP estimates independent on BP.

3. Eddy covariance and models can be used to estimate GPP in any type of terrestrial ecosystem, whereas sink-sums methods have been mainly used for forest ecosystems, but not for other ecosystem types. The use of different methods for different ecosystem types might introduce inconsistencies in the analysis.

4. The analysis of 20 forests with estimates of GPP available for both sinks-sum and EC methodology revealed that both approaches provide similar values of GPP with a mean difference of only 7% and GPP estimates based on sinks-sum non-significantly larger than GPP estimates based on EC (Campioli unpublished). This convergence does not imply that sinks-sum and EC are accurate as both approaches can be biased in a similar direction (e.g. EC-based GPP could be underestimated because of loss of nighttime fluxes, whereas GPP estimates from sinks-sum could be underestimated because of poor scaling). However, such convergence indicates that there is no evidence to rank one methodology lower than the other when performing synthesis studies across multiple sites.

5. As a consequence of the latter point, process-based models developed and calibrated using EC or sinks-sum data are not likely to produce unreliable numerical estimates of GPP. In fact, additional tests showed that the alternative use of EC- or model-based estimates of GPP had no impact on the key effect of management on BPE (Supplementary Table 10).

In conclusion, (i) sinks-sum methods are in general less suitable than EC and models for the BPE analysis performed here, (ii) EC and sinks-sum methods provide comparable estimates of GPP, and (iii) there is no evidence to consider unreliable the model-based estimates of GPP that we used in our analysis.

Uncertainty of fine root BP

Fine root production is commonly estimated with methods measuring root growth rather directly (e.g. ingrowth cores, minirhizotrons) or from less accurate methods (e.g. based on total belowground C flux, models). However, assessment of fine root BP is difficult and any method for estimating it has uncertainties and is prone to errors. Even we realize that fine root BP may be not wholly accurate for some of our site-year combinations, we do not see a possible source of bias that would systematically affect the comparison between natural and managed ecosystems and cast doubts on our key findings. Three reasons substantiate these considerations. (1) First, in general, the use of multiple years and sites minimizes major biases in synthesis studies (e.g. we used averages of fine root BP for multi-year observations). (2) Second, by examining the key forest dataset as an example (n=53; see Methods), we noted that for both the natural and managed category, fine root BP was measured with direct methods at about half of the sites (48-50%) and with less accurate methods for the other half (50-52% of the sites). Thus, the methods to asses fine root BP did not differ substantially between natural and managed ecosystems, avoiding systematic errors. (3) Third, 31 of the 53 forest sites considered at point 2 had detailed data on C allocation pattern and estimates of fine root BP available independent of the total belowground BP. For natural forests (n=12), this sub-set presented estimates of fine root BP, total BP and GPP of 163, 615 and 1549 gC m^{-2} y^{-1}, respectively. For managed forests (n=19), the same variables were 130, 888 and 1683 gC m^{-2} y^{-1}, respectively. The sub-set is therefore well representative as the BPE values of the natural and managed sites (0.41 and 0.53, respectively) are equal to the BPE values of the entire forest dataset (Supplementary Table 7). We calculated that such difference in BPE would be offset only if our data were affected by a 90-95% underestimation of fine root BP in natural sites concurrent to an opposite 90-95% overestimation of fine root BP in managed sites. Systematic biases of such opposite directions and degree are unrealistic given the similar methodologies employed for the determination of fine root BP in natural and managed forests. Moreover, assuming that fine root BP was measured correctly at natural sites and overestimated at managed sites, the BPE difference between natural and managed conditions would still hold even if actual fine root BP was close to zero in managed forests. Therefore, these additional considerations (point 1-3) confirm that the BPE difference between natural and managed ecosystems can not be due significantly to the uncertainty related to fine root BP.

Classification of site fertility

The soil nutrient classification is reported in Supplementary Table 17. The classification was developed following previous studies[2,39] and it was based on soil type, several physical-chemical proprieties of the soil (e.g. soil structure, nitrogen and carbon content, pH, cation exchange capacity) and fertilization. Data were from the literature (mostly) or directly provided by the site principal investigators (PIs). In 62% of the cases, the assigned soil nutrient availability level (high, medium or low) was explicitly confirmed by the site literature or PIs (in general, for the remaining cases, no information was available in the literature, PIs did not have additional information about site fertility or we were unable to have contact with the PIs). The reliability of this type of classification has been thoroughly evaluated[2,39].

ORCHIDEE modelling exercise

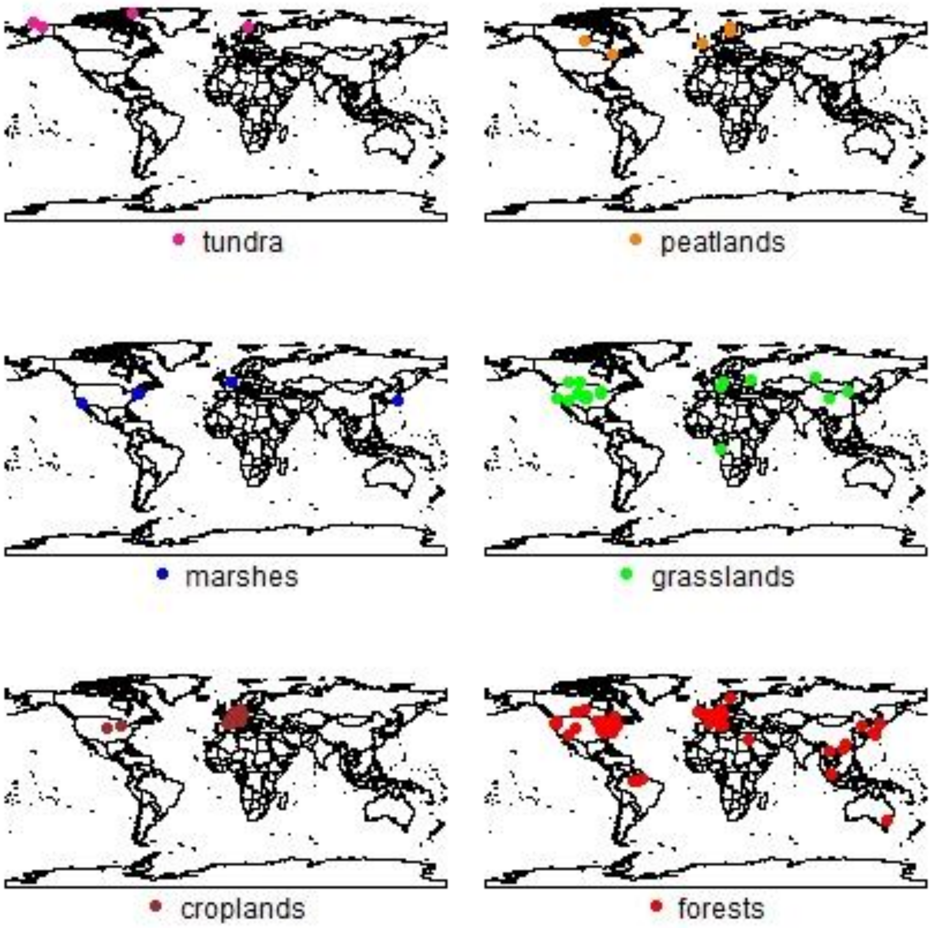
ORCHIDEE (Organizing Carbon and Hydrology in Dynamic Ecosystems) is a global land-surface model that calculates the C and H_2O cycle for major ecosystem types and ecosystem soil pools[17]. The current exercise was focused on the autotrophic component of the ecosystem and considered Europe as a case study (defined as the area between 10° W to 30° E and 35° to

75° N). Types and spatial distribution of the European ecosystems were derived from land cover and tree species maps[40,41].

The impact of BPE on the estimations of BP was derived by comparing a standard model simulation (assuming Europe covered by natural ecosystems, which is hypothetical but commonly done in land surface modeling) with a simulation with a BPE increase of 8% (representing Europe covered by managed ecosystems, which is realistic but seldom done). The simulations were done for a period of 150 years, driven by reiterated climatic conditions (NCC dataset 1951-2000[42]). The simulations showed that even a moderate BPE increment (actual BPE increment are expected to be larger; see Supplementary Table 7) resulted in a remarkable increase in BP for Europe (24%, from 2.50 to 3.10 Pg C y^{-1}) which was due not only to the increased BP per unit of photosynthates but also to the positive effect that the increment in leaf BP had on GPP.

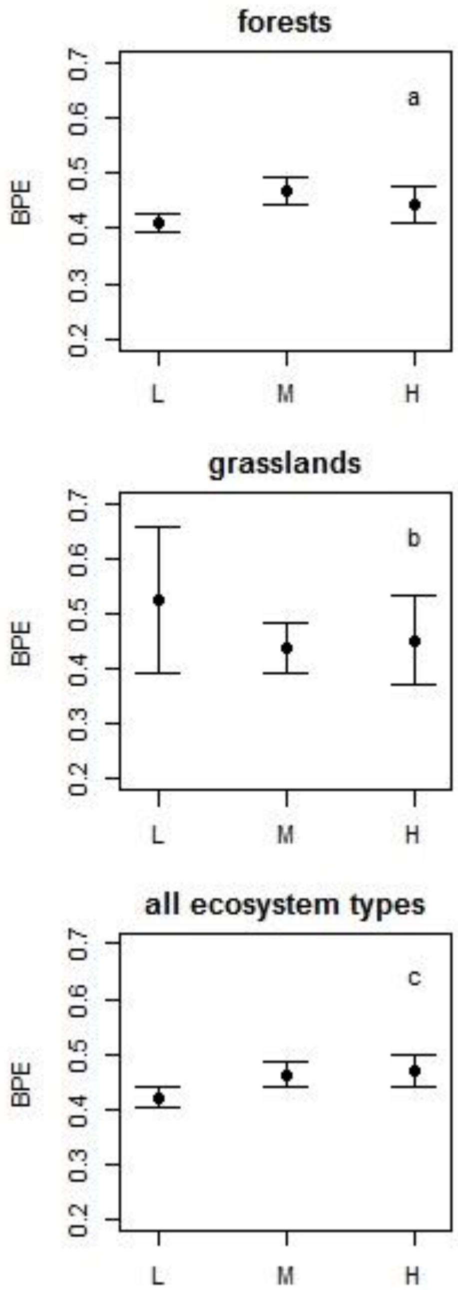
2 Supplementary Figures

Supplementary Figure 1



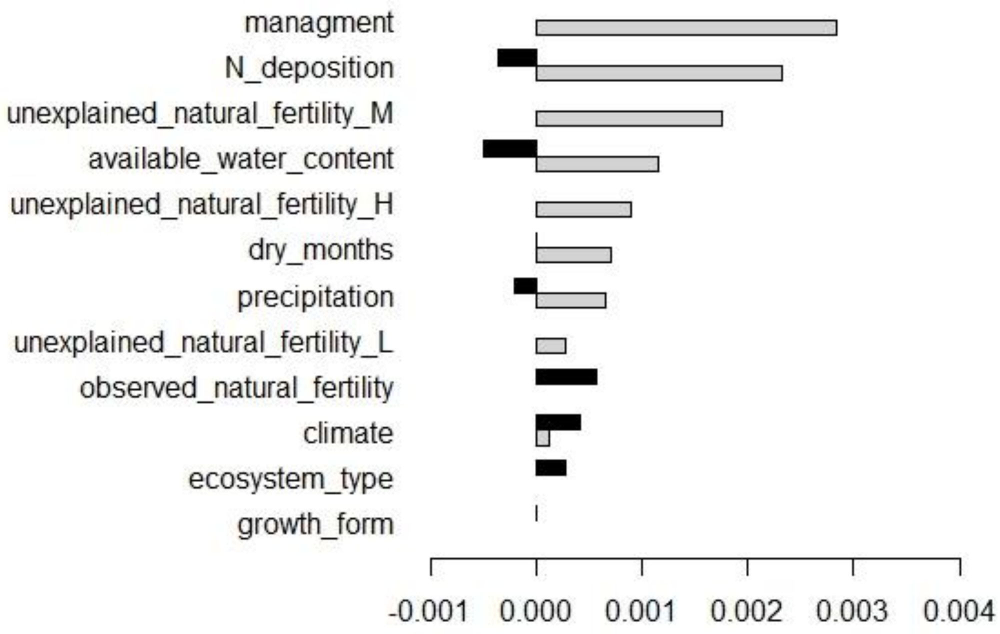
Supplementary Figure 1. Distribution of the study sites.

Supplementary Figure 2



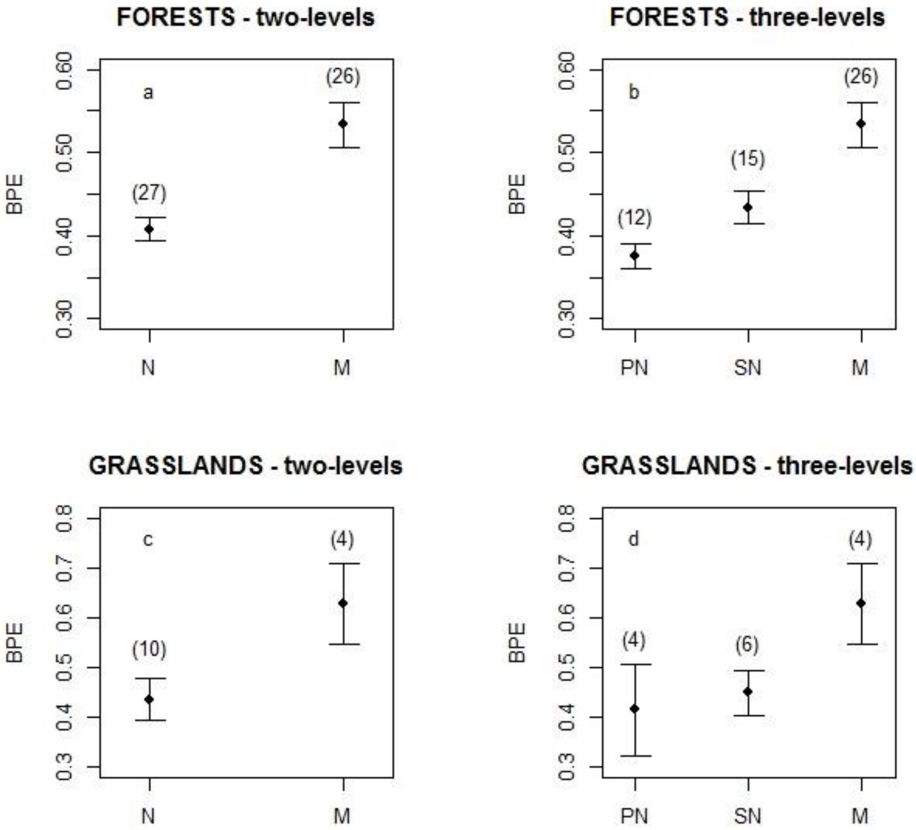
Supplementary Figure 2. Biomass production efficiency (BPE, mean ± 1 s.e.m.) according to site fertility (L: low, M: medium, H: high) for natural unmanaged ecosystems: (a) forests, (b) grasslands and (c) all ecosystem types lumped together (forests, grasslands, temperate marshes, boreal peatlands, tundras).

Supplementary Figure 3



Supplementary Figure 3. Ranking of vegetation, environmental, climatic and anthropogenic variables as predictors of biomass production efficiency from Random Forest analysis when considering forest sites (natural and managed; light grey bars, n=53) and natural unmanaged sites of all ecosystem types (dark grey bars, n=75). %IncMSE (mean decrease in model prediction accuracy resulting from a change in variable value) indicates the importance of a variable: the larger the %IncMSE, the larger the variable importance. Negative values of %IncMSE indicate that the variable has marginal explanatory power (for more information on Random Forest see Methods). Unexplained natural fertility H, unexplained natural fertility M and unexplained natural fertility L are the residuals of the model relating fertility to management and represent the ‘fertility status not explained by management’ for each of the three fertility classes: high fertility H, medium fertility M and low fertility L (see Methods). Observed natural fertility is the fertility status for natural, unmanaged sites. Dry months indicate the average number of months per year with potential evapotranspiration larger than precipitation.

Supplementary Figure 4



Supplementary Figure 4. Biomass production efficiency (BPE, mean ± 1 s.e.m.) of (a-c) natural (N) and managed (M) forests and grasslands when considering the two-level management classification and of (b-d) pristine natural (PN), semi-natural (SN) and managed forests and grasslands when considering a three-level management classification (numbers in parenthesis indicate site replicates).

3 Supplementary Tables

Supplementary Table 1. List of the study sites with value of biomass production (BP), gross primary production (GPP), biomass production efficiency (BPE) and information on ecosystem type, climate, management and measurement period.

Site name	Fluxnet[a]	climate [b]	BP [c]	period BP [d]	GPP	period GPP [d]	BPE	manag.[e]	management category [f] and reference
Croplands									
Auradé	FR-Aur	temp.	603	2006	956	2006	0.63	M	Fertilized[43-45]
Avignon	FR-Avi	temp.	932	2006	1549	2006	0.60	M	Fertilized[43,44,46]
Beano1	IT-Be1	temp.	1020	2007, 2008	1310	2007, 2008	0.78	M	Fertilized[47]
Gebesee	DE-Geb	cold	698	2007	992	2007	0.70	M	Fertilized[43-45]
Grignon	FR-Gri	temp.	765	2006	1090	2006	0.70	M	Fertilized[44,48]
Kellogg CRP-S	no	cold	308	2009	507	2009	0.61	M	Established same year of measurements on grasslands[49]
Kellogg CRP-P	no	cold	340	2009	470	2009	0.72	M	Established same year of measurements on grasslands[49]
Kellogg CRP-C	no	cold	370	2009	599	2009	0.62	M	Established same year of measurements on grasslands[49]
Kellogg Agr-C	no	cold	304	2009	615	2009	0.49	M	Established same year of measurements on agricultural land[49]
Kellogg Agr-S	no	cold	193	2009	655	2009	0.29	M	Established same year of measurements on agricultural land[49]
Kellogg Agr-P	no	cold	295	2009	552	2009	0.53	M	Fertilized[49]
Klingenberg	DE-Kli	cold	500	2006	1232	2006	0.41	M	Fertilized[43-45]
Lamasquère	FR-Lam	temp.	707	2007	1331	2007	0.53	M	Fertlized[43,44,46]
Lonzée winter wheat	BE-Lon	temp.	820	2005, 2007	1630	2005, 2007	0.50	M	Fertilized[50-52]
Lonzée sugar beet	BE-Lon	temp.	1010	2004	1420	2004	0.71	M	Fertilized[51,53]
Lonzée potato	BE-Lon	temp.	360	2006	600	2006	0.60	M	Fertilized[51,53]
Lutjewad	NL-Lut	temp.	882	2007	1297	2007	0.68	M	Fertilized[43,44,46]
Mead 1	US-Ne1	cold	1057	2001-2003	1715	2001-2003	0.62	M	Fertilized[54]
Mead 2 maize	US-Ne2	cold	1082	2001, 2003	1735	2001, 2003	0.62	M	Fertilized[54]
Mead 2 soybean	US-Ne2,	cold	526	2002	966	2002	0.54	M	Fertilized[54]
Mead 3 maize	US-Ne3	cold	728	2001, 2003	1451	2001, 2003	0.50	M	Fertilized[54]
Mead 3 soybean	US-Ne3	cold	404	2002	841	2002	0.48	M	Fertilized[54]

Oensingen	CH-Oe2	temp.	504	2007	1598	2007	0.32	M	Fertilized[43-45]
Risbyholm	DK-Ris	cold	684	2005, 2006	1003	2005, 2006	0.68	M	Fertilized[43-45]
Forests									
Bornhoved Alder	no	cold	878	1992-1993	2420	1992-1993	0.36	N	unmanaged or with low human impact in last 50 y[1]
Bornhoved Beech	no	cold	692	1992-1993	1324	1992-1993	0.52	M	thinning/harvest in last 50 y[1,55]
Caldaro	no	temp.	959	2010	1263	2010	0.76	M	managed for fruit/rubber production[56]
Cascade Head 1	no	temp.	702	1990	2043	1990	0.34	N	old-growth with minimal disturbance[1]
Cascade Head 1A	no	temp.	844	1990	1828	1990	0.46	N	unmanaged or with low human impact in last 50 y[1]
Caxiuana	BR-Cax	trop.	1214	2005	3820	1999-2003	0.32	N	old-growth with minimal disturbance[57,58]
Changbai Mountains	CN-Cha	cold	769	na (<2006)	1388	2003	0.55	N	old-growth with minimal disturbance[59-62]
Chibougamau EOBS	CA-Qfo	cold	310.5	2005	680	2005	0.46	N	natural successions after fire/windthrow and at least 10 y after disturbance[63,64]
Coastal plain North Carolina	US-NC2	temp.	1494	2005-2007	2719	2005-2007	0.55	M	fertilized in last 25 y[65]
Collelongo	IT-Col	cold	674	1996	1154	1996	0.58	M	thinning/harvest in last 50 y[1,66,67]
Dinghushan MF	CN-Din	temp.	678	2003-2004	1521	2003-2004	0.45	N	unmanaged or with low human impact in last 50 y[68,69]
Dooary	no	temp.	1634	2003-2009	2251	2003-2009	0.73	M	thinning/harvest in last 50 y[70]
Flakaliden C	SE-Fla	cold	530	2000-2002	1000	1997-1998	0.53	N	planted forests without any intervention after planting and at least 10 y old[1,71,72]
Frazer old	no	cold	472	na (<1996)	915	na (<1991)	0.52	N	old-growth with minimal disturbance[1,73]
Frazer young	no	cold	252	na (<1996)	977	na (<1991)	0.26	N	planted forests without any intervention after planting and at least 10 y old[1,73]
Fujiyoshida	JP-Fuj	cold	773.9	1999-2008	1802	2000-2008	0.43	N	unmanaged or with low human impact in last 50 y[74,75] (Ohtsuka Toshiyuki per. comm.)
Hainich	DE-Hai	cold	655	2000-2002	1651	2000-2002	0.40	N	old-growth with minimal disturbance[1,76]
Harvard	US-Ha1	cold	543	1999	1315	1999	0.41	N	natural successions after fire/windthrow and at least 10 y after disturbance[1]
Hesse	FR-Hes	temp.	757	1997	1267	1997	0.60	M	thinning/harvest in last 50 y[77,78]
Jacaranda K34	no	trop.	1046	2005	3040	1995-1996	0.34	N	old-growth with minimal disturbance[79 1]
Juniper	no	cold	145	1990	330	1990	0.44	N	unmanaged or with low human impact in last 50 y[1]
Kannenbruch Alder Ash	DE-Kan	cold	672	2002	1594	2002	0.42	M	thinning/harvest in last 50 y[1,80]
Kannenbruch Beech	DE-Kan	cold	675	2002	1470	2002	0.46	M	thinning/harvest in last 50 y[1,80]
Kannenbruch Oak	DE-Kan	cold	1035	2002	1794	2002	0.58	M	thinning/harvest in last 50 y[1,80]
Lochristi	BE-Lcr	temp.	521	2011	1281	2011	0.41	M	newly (<10 y) established plantation[81 82] (Berhongaray Gonzalo per. comm.)
Metolius	US-Me4	cold	449	1999-2001	1113	1996-2000	0.40	N	old-growth with minimal disturbance[1,83,84]
Metolius-young	US-Me5	cold	389	2000-2002	724	2000-2002	0.54	M	thinning/harvest in last 50 y[1,85]
Morgan Monroe	US-MMS	cold	1025	1998-1999	1467	1998-1999	0.70	M	thinning/harvest in last 50 y[1,86]
NAU Centennial Undisturbed	no	cold	387	2006-2007	879	2006-2007	0.44	N	unmanaged or with low human impact in last 50 y[87]
NAU Centennial thinned	no	cold	243	2006-2007	868	2006-2007	0.28	M	thinning/harvest in last 50 y[87]
Pasoh	no	trop.	1490	1971-2001	3230	2003-2005	0.46	N	old-growth with minimal disturbance [1,88]
Pierce Creek Forest C	no	temp.	981.4	1992-1993	2950	1992-1993	0.33	M	thinning/harvest in last 50 y[89]
Pierce Creek Forest IF	no	temp.	1879.	1992-1993	3690	1992-1993	0.51	M	fertilized in last 25 y[89]

			2						
Popface alba	no	temp.	1313	2000-2001	2230	2000-2001	0.59	M	newly (<10 y) established plantation[90]
Popface euamericana	no	temp.	1332	2000-2001	1966	2000-2001	0.68	M	newly (<10 y) established plantation [90]
Popface nigra	no	temp.	1711	2000-2001	2424	2000-2001	0.71	M	newly (<10 y) established plantation[90]
Prince Albert SSA SOAS	CA-Oas	cold	459	1994	1172	1994	0.39	N	natural successions after fire/windthrow and at least 10 y after disturbance[1]
Prince Albert SSA SOBS	CA-Obs	cold	311	1994	910	1994	0.34	N	natural successions after fire/windthrow and at least 10 y after disturbance[1]
Prince Albert SSA SOJP	CA-Ojp	cold	252	1994	710	1994	0.35	N	natural successions after fire/windthrow and at least 10 y after disturbance[1]
Puechabon	FR-Pue	temp.	490	2001-2002	1413	2001-2002	0.35	N	unmanaged or with low human impact in last 50 y[1,91-93]
Qianyanzhou Ecological Station	CN-Qia	temp.	1044	2003-2005	1798	2003-2005	0.58	N	planted forests without any intervention after planting and at least 10 y old[94,95]
Santiam Pass	no	cold	387	1990	1077	1990	0.36	N	unmanaged or with low human impact in last 50 y[1]
Saskatchewan HJP75	CA-SJ3	cold	277	2004	564	2004	0.49	N	planted forests without any intervention after planting and at least 10 y old[37,96]
Scio	no	temp.	1173	1990	2901	1990	0.40	M	fertilized in last 25 y[1,97]
Soroe	DK-Sor	cold	1134	2000-2002	1692	2000-2002	0.67	M	thinning/harvest in last 50 y[1,67,98,99]
Sylvania hardwood	US-Syv	cold	341	2002-2003	1034	2002-2003	0.33	N	old-growth with minimal disturbance[1,100,101]
Takayama	JP-Tak	cold	626	1999-2006	1120	1999-2006	0.56	N	planted forests without any intervention after planting and at least 10 y old[1,102,103]
Tapajos67	no	trop.	1673	1999-2005	3149	2002-2005	0.53	N	old-growth with minimal disturbance[57]
Tapajos83	no	trop.	876	2000	3000	2000	0.29	N	old-growth with minimal disturbance[1]
Teshio CCLaG	JP-Tef	cold	850.75	1997-2004	1439	2002	0.59	N	old-growth with minimal disturbance[104,105]
Tharandt	DE-Tha	cold	616	2000-2002	1845	2000-2002	0.33	M	thinning/harvest in last 50 y[1,67]
Thompson NSA NOBS	CA-NS1	cold	226	2001-2004	665	2001-2004	0.34	N	natural successions after fire/windthrow and at least 10 y after disturbance[106,107]
Thompson d71	CA-NS2	cold	354	2001-2004	574	2003-2004	0.62	N	natural successions after fire/windthrow and at least 10 y after disturbance[107]
Thompson d37	CA-NS3	cold	261	2001-2004	633	2003-2004	0.41	N	natural successions after fire/windthrow and at least 10 y after disturbance[107]
Thompson d20	CA-NS5	cold	347	2001-2004	652	2003-2004	0.53	N	natural successions after fire/windthrow and at least 10 y after disturbance[107]
Thompson d15	CA-NS6	cold	220	na (<2005)	443	2003-2004	0.50	N	natural successions after fire/windthrow and at least 10 y after disturbance[107]
Tumbarumba	AU-Tum	temp.	640	2003	1700	2003	0.38	M	thinning/harvest in last 50 y[108]
Turkey Point TP02	CA-TP1	cold	379	2005-2008	610	2005-2008	0.62	M	newly (<10 y) established plantation[109,110]
Turkey Point TP89	CA-TP2	cold	835	2005-2008	2445	2005-2008	0.34	N	planted forests without any intervention after planting and at least 10 y old[109,110]
Turkey Point TP74	CA-TP3	cold	593	2005-2008	1184	2005-2008	0.50	N	planted forests without any intervention after planting and at least 10 y old[109,110]

Turkey Point TP39	CA-TP4	cold	603	2005-2008	1407	2005-2008	0.43	M	thinning/harvest in last 50 y[109,110]
University of Michigan	no	cold	675	2004	1350	1999	0.50	N	unmanaged or with low human impact in last 50 y[1]
Walker Branch	US-WBW	temp.	731	1995-1998	1674	1995-1998	0.44	N	unmanaged or with low human impact in last 50 y [1]
Warings Woods	no	temp.	800	1990	1893	1990	0.42	N	planted forests without any intervention after planting and at least 10 y old[1]
Wind River	US-Wrc	temp.	622	1999	1338	1999	0.47	N	old-growth with minimal disturbance[111,112]
Wytham Woods	no	temp.	676	2007-2008	2110	2007-2008	0.32	N	unmanaged or with low human impact in last 50 y[1,113]
Xishuangbanna	CN-Xsh	temp.	994	2003-2006	2595	2003-2006	0.38	N	old-growth with minimal disturbance[114]
Xishuangbanna plantation	no	temp.	1235	2011	1816	2011	0.68	M	managed for fruit/rubber production[115]
Yatir	IL-Yat	temp.	351	2001-2006	830	2001-2006	0.42	M	thinning/harvest in last 50 y[116]
Grasslands									
Beano2	IT-Be2	temp.	1134	2007, 2008	1568	2007, 2008	0.72	M	established same year of measurements on fertilized agricultural land[47]
Cheyenne	no	cold	179	na-1991	626	1997, 1998	0.29	N	low-moderate grazing and/or annual burning[117,118]
Grillenburg	DE-Gri	cold	403	2004	1233	2004	0.33	N	mowing (not intensive)[119]
Haibei	CN-Hab	cold	493	2008, 2009	634	2002-2004	0.78	N	low-moderate grazing and/or annual burning[120,121]
Hakasija 1	RU-Ha1	cold	246	2003, 2004	519	2003, 2004	0.47	N	low-moderate grazing and/or annual burning[43,122,123]
Hakasija 3	RU-Ha3	cold	259	2004	526	2004	0.49	N	established/restored grassland (5-20 y before measurements)[123]
Inner Mongolia	no	cold	87	2006	182	2006	0.48	N	low-moderate grazing and/or annual burning[124,125]
Kellogg CRP-Ref	no	cold	612	2010	1015	2010	0.60	N	established/restored grassland (5-20 y before measurements)[49,126]
Kellogg CRP-S	no	cold	384	2010	512	2010	0.75	M	fertilized[126,127]
Kellogg Agr-S	no	cold	239	2010	374	2010	0.64	M	fertilized[126,127]
Kellogg Agr-P	no	cold	314	2010	793	2010	0.40	M	established same year of measurements on fertilized agricultural land[126,127]
Jasper	US-Jas	temp.	164	1994	516	1994	0.32	N	minor human impact in the past and protected since at least 15 y[128,129]
Konza	US-Kon	cold	597	1983-1987	1151	1987	0.52	N	low-moderate grazing and/or annual burning[130-133]
Kursk	no	cold	898	1972, 1973, 1981-1983	1611	na-1983	0.56	N	pristine[134 135,136]
Lethbridge	CA-Let	cold	146	1999, 2000	280	1999, 2000	0.52	N	minor human impact in the past and protected since at least 15 y[137,138]
Matador	no	cold	233	1971	786	na-1995	0.30	N	minor human impact in the past and protected since at least 15 y[135,137,139]
NAU Coconito Burned	no	cold	237	2006, 2007	387	2006,2007	0.61	N	natural successions after fire and at least 10 y after disturbance[87]
Osage	no	temp.	399	1970-1972	1890	1970-1972	0.21	N	minor human impact in the past and protected since at least 15 y[140,141]
Tchizalamou	CG-Tch	trop.	506	2007	1572	2007	0.32	N	low-moderate grazing and/or annual burning[43,142,143]
Woodward	no	temp.	449	1995-1997	829	1997	0.54	N	low-moderate grazing and/or annual burning[135,144]

Marshes									
Burcht	no	temp.	708	1996-1998	1453	1996-1998	0.49	N	mowing (not intensive)[145]
Flax Pond	no	cold	400	na (<1979)	814	1974	0.49	N	no disturbance[146]
Great Sippewissett	no	cold	1000	na (<1985)	1700	na (<1984)	0.59	N	no disturbance[147,148]
Mase	JP-Mas	temp.	678	2002, 2003	1049	2002, 2003	0.65	M	fertilization and irrigation[149,150]
Saeftinghe	no	temp.	494	1996-1998	1261	1996-1998	0.39	N	mowing (not intensive)[145]
San Joaquin	US-SJ1	temp.	867	1999-2007	1428	1999-2007	0.61	M	irrigation[151]
Peatlands									
BOREAS collapse bog	no	cold	150	na (<1996)	296	1996	0.51	N	pristine[152]
BOREAS intermediate fen	no	cold	380	na (<1996)	623	1996	0.61	N	pristine[152]
BOREAS rich fen	no	cold	340	na (<1996)	481	1996	0.71	N	pristine[152]
Bog End, Moor House	no	temp.	223	1970	891	2007	0.25	N	minimal disturbance (grazing)[153,154 155]
Degerö	SE-Deg	cold	152	2001, 2002, 2004-2006	331	2001, 2002, 2004-2006	0.47	N	pristine[43,156]
Mer Bleue	CA-Mer	cold	231	1999, 2007	528	1998, 2005	0.44	N	pristine[157-160]
Stordalen palsa	no	cold	42	na (<1996)	211	2008, 2009	0.20	N	pristine[161,162]
Tundra									
Alexandra Fiord, wet meadow	no	cold	62	1980-1983	264	2000, 2001	0.23	N	pristine[163,164]
Barrow	US-Brw	cold	105	1970-1974	211	1971	0.50	N	pristine[165-167]
Imnavait Creek	no	cold	153	2011, 2012	288	2012	0.53	N	pristine (Sullivan PF unpublished)
Paddus	no	cold	103	2005, 2007	209	1999	0.49	N	pristine[168,169]
Toolik Lake	no	cold	156	1982-2004	311	1993-2000	0.50	N	pristine[38,170-172]

Notes: [(a)] indicates if site in Fluxnet (http://www.fluxdata.org/default.aspx) or *European Fluxes Database Cluster* (http://gaia.agraria.unitus.it/home/sites-list) with code; [(b)] climate: from simplified Köppen-Geiger classification: temp.: temperate, and trop.: tropical (see Supplementary Table 2 for more details); [(c)] gap-filled value (see Methods); [(d)] indicate the period with data availability not necessarily coinciding with the number of experimental years; [(e)] manag.: management status: N: natural, M: managed, and [(f)] management category: management classification (see Extended Data Table 1 for more details).

Supplementary Table 2. Variables tested as predictors of the biomass production efficiency.

Variable	Source: description	Source: reference	Categories/range values
Categorical			
Management	Literature, Global Forest Database[1]	this study (Supplementary Table 1) www.lsce.ipsl.fr/Pisp/sebastiaan.luyssaert/ (Global Forest Database)	2 categories: natural, managed
Observed natural fertility	Literature, ISRIC-WISE global data set[20]	http://www.isric.org/ (ISRIC-WISE) this study (Supplementary Table 17)	3 categories: high, medium, low
Unexplained natural fertility	Modelled	this study (Statistical analysis)	3 indexes per site (high, medium, low fertility used as reference)
Ecosystem type	Literature, Global Forest Database[1]	this study (Supplementary Table 1) www.lsce.ipsl.fr/Pisp/sebastiaan.luyssaert/ (Global Forest Database)	6 categories: forest, grassland, cropland, marsh, peatland and tundra
Climate zone	Simplified Köppen-Geiger classification [(a)] using WorldClim data[21]	www.worldclim.org/ (WorldClim)	3 categories: cold, temperate, tropical
Growth form	Literature, Global Forest Database[1]	this study (Supplementary Table 1) www.lsce.ipsl.fr/Pisp/sebastiaan.luyssaert/ (Global Forest Database)	2 categories: herbaceous, woody (dominant species)
Continuous			
Nitrogen deposition	Data and model[1,22-25]	webmap.ornl.gov/ogcdown/dataset.jsp?ds_id=830 webmap.ornl.gov/ogcdown/dataset.jsp?ds_id=730	values from 1.4 to 27.3 kg N ha^{-1} y^{-1}
Available water content	Calculated with model Rosetta[28] from soil texture and density from literature or ISRIC-WISE global data set[20]	http://www.cals.arizona.edu/research/rosetta/index.html (model Rosetta) this study (Supplementary Table 17) http://www.isric.org/ (ISRIC-WISE)	values from 0.05 to 0.5
Precipitation	WorldClim[21]	www.worldclim.org/ (WorldClim)	values from 115 to 2724 mm y^{-1}
Dry months	Index of drought calculated using CRU TS3.10 as the number of months per year when potential evapotranspiration is larger than precipitation[26,27]	http://catalogue.ceda.ac.uk/uuid/ac3e6be017970639a9278e64d3fd5508 (CRU TS3.10)	values from 0.9 to 12 month y^{-1}

Notes: [(a)] Fundamental Köppen-Geiger classification comprises five climatic zones: tropical, arid, temperate, cold and polar[173]; here, we have merged arid and polar to other categories because of the few arid and polar sites.

Supplementary Table 3. Management classification of the sites investigated.

Ecosystem type and management categories	n
Natural forests	
old-growth with minimal disturbance	14
natural succession due to fire/windthrow and at least 10 y after disturbance	10
unmanaged or with low human impact (e.g. understory grazing) in last 50 y	11
planted forests without any intervention after planting and at least 10 y old	8
Managed forests [(a)]	
thinning/harvest in last 50 y	16
newly (<10 y) established plantation	5
fertilization in last 25 y	3
managed for fruit/rubber production	2
Natural grasslands	
pristine	1
natural succession due to fire and at least 10 y after disturbance	1
minor human impact in the past and protected for at least 15 y	4
low-moderate grazing and/or annual burning	7
established/restored grassland (10-20 y before measurements)	2
mowing (not intensive)	1
Managed grasslands [(a)]	
established same year of measurements on agricultural land	2
fertilization	2
Natural marshes	
no disturbance	2
mowing (not intensive)	2
Managed marshes [(a)]	
Fertilized and/or flooded	2
Peatlands (only natural)	
pristine	6
minimal disturbance (grazing)	1
Tundra (only natural)	
Pristine	5
Croplands (only managed) [(a)]	
Fertilization	19
Established same year of measurements on agricultural land	2
Established same year of measurements on grasslands	3

Notes. [(a)] the main management operations / regimes were used for the classification; however, other operations (e.g. irrigation, soil preparation, pest-control) might also have been performed concurrently. n: site replicates.

Supplementary Table 4. Values (mean±s.e.m; replicates in parenthesis) of biomass production efficiency (BPE) for natural unmanaged sites of key terrestrial ecosystem types.

Ecosystem type	BPE
forest	0.43±0.01 (43)
grassland	0.46±0.04 (16)
marsh	0.49±0.04 (4)
peatland	0.45±0.07 (7)
tundra	0.45±0.05 (5)
difference among ecosystem types	p=0.826
mean across ecosystem types	0.46±0.01

Notes: Significance value p tested with ANOVA analysis.

Supplementary Table 5. Results of univariate analysis and multiple linear regressions (backward stepwise regressions) to detect the effect of climatic and environmental conditions (climate zone, fertility, available water content, precipitation, drought index) and human impact (management status, N deposition) on biomass production efficiency (BPE) when considering 53 globally distributed forest sites.

BPE predictors	Univariate analysis		Stepwise regression
Categorical variables	*p ANOVA*	*post-hoc* [h]	*included*
Management (M, N) [a]	0.000702 ***	n.a.	yes
Climate (C, Te, Tr) [b]	0.152	n.s.	yes
Continuous variables	*p regression*	*Adj R^2*	*included*
Unexplained natural fertility (reference L) [c]	0.25	0.0068	yes
Unexplained natural fertility (reference M) [d]	0.815	-0.018	yes
Unexplained natural fertility (reference H) [e]	0.229	0.0091	yes
Nitrogen deposition	0.00478 **	0.13	yes
Available water content	0.542	-0.012	yes
Precipitation	0.579	-0.013	yes
Dry months [f]	0.245	0.007373	yes
Age [g]	0.0313 *	0.0772	no
Variables final model stepwise regression			
Management	n.a.	n.a.	0.00145 **
Nitrogen deposition	n.a.	n.a.	0.02942 *
Adj R^2 initial model	n.a.	n.a.	0.25
Adj R^2 final model	n.a.	n.a.	0.28

Notes: For categorical variables, we report p value of one-way ANOVA (post-hoc information (Tukey's HSD test) not applicable (n.a.) or non-significant with p>0.05 (n.s)). For continuous variables, the p value of the linear regression and adjusted R^2 are reported. [a] M: managed, N: natural; [b] C: cold, Te: temperate, Tr: tropical; [c] [d] and [e] fertility status not explained by management for low (L), medium (M) and high (H) fertility class (see Methods for more information); [f] average number of months per year with potential evapotranspiration larger than precipitation; [g] not available for all sites; significant differences are indicated with '*' when 0.01<p<0.05, with '**' when 0.001<p<0.01 or with '***' when p < 0.001

Supplementary Table 6. Univariate analysis and multiple linear regressions (backward stepwise regressions) to investigate the importance of management, nitrogen deposition and stand age on biomass production efficiency (BPE) when considering 48 forest sites globally distributed (i.e. all forests with BPE derived from biomass production and gross primary production measured during the same period and with concurrent information on management, nitrogen deposition and age).

BPE predictors	Univariate analysis		Stepwise regression
	p value	*adj R^2*	*included*
Management	0.00204 ** [(a)]	n.a.	yes
Nitrogen deposition	0.00696 ** [(b)]	0.1293 [(b)]	yes
Age	0.0313 * [(b)]	0.0772 [(b)]	yes
Variables final model stepwise regression			
Management	n.a.	n.a.	0.00403 **
Nitrogen deposition	n.a.	n.a.	0.03393 *
Adj R^2 initial model	n.a.	n.a.	0.27
Adj R^2 final model	n.a.	n.a.	0.27

Notes: [(a)] one-way ANOVA, [(b)] linear regression

Supplementary Table 7. Values (mean±s.e.m; replicates in parenthesis) of biomass production efficiency (BPE) for key terrestrial ecosystem types according to their management status.

Ecosystem type	BPE		
	natural	managed	p difference
forest	0.41±0.01 (27)	0.53±0.03 (26)	0.000702 ***
grassland	0.44±0.04 (10)	0.63±0.08 (4)	0.0413 *
cropland	n.a.	0.58±0.03 (24)	n.a.

Notes: Acronym 'n.a.' indicates no data available / not applicable; significance value p tested with ANOVA analysis.

Supplementary Table 8. Results of univariate analysis and multiple linear regressions (backward stepwise regressions) to detect the most important environmental, climatic and vegetation variables in predicting biomass production efficiency (BPE), when considering 75 globally distributed natural unmanaged sites.

BPE predictors	Univariate analysis		Stepwise regression
Categorical variables	*p ANOVA*	*post-hoc* [f]	*included*
Biome (F, G, M, P, T) [a]	0.826	n.s.	yes
Climate (C, Te, Tr) [b]	0.052	n.s.	yes
Growth form (H, W) [c]	0.447	n.s.	yes
Fertility (L, M, H) [d]	0.234	n.s.	yes
Continuous variables	*p regression*	*Adj R^2*	*included*
Nitrogen deposition	0.729	-0.012	yes
Available water content	0.555	-0.0088	yes
Precipitation	0.338	-0.00093	yes
Dry months [e]	0.339	-0.00098	yes
Variables final model stepwise regression			
Climate	n.a.	n.a.	p=0.051[g] p=0.079[h]
Adj R^2 initial model	n.a.	n.a.	-0.0053
Adj R^2 final model	n.a.	n.a.	0.053

Notes: [a] F: forests, G: grasslands, M: marshes, P: peatlands, T: tundra; [b] C: cold, Te: temperate, Tr: tropical; [c] H: herbaceous, W: woody; [d] H: high, M: medium, L: low; [e] average number of months per year with potential evapotranspiration larger than precipitation; [f] post-hoc information (Tukey's HSD test) non-significant with p>0.05 (n.s); [g] factor: temperate, reference: cold; [h] factor: tropical, reference: cold; n.a. 'not applicable'; significant differences are indicated with '*' when 0.01<p<0.05, '**' when 0.001<p<0.01 and '***' when p < 0.001.

Supplementary Table 9. Methodologies used to assess biomass production (BP) and gross primary production (GPP) with their uncertainty reduction factor (RF[1]; the lower RF, the lower the methodology uncertainty).

method	RF
BP	
Isotope turnover	0.3
Series aboveground biomass and belowground growth	0.3
Series aboveground and belowground biomass	0.6
Site-specific model or estimates partially derived from literature	0.6
Flux component based	1.0
GPP	
Eddy covariance and data assimilation	0.2
Eddy covariance	0.3
Chamber-based	0.6
Site-specific model	0.6
Flux component based	1.0

Supplementary Table 10. Impact of different methodologies to estimate gross primary production (GPP; i.e. eddy covariance or process-based models) and biomass production (BP; i.e. methods with 'low uncertainty', LU, or 'medium uncertainty', MU; see footnotes) on the difference in biomass production efficiency (BPE) between natural (N) and managed (M) forests.

	GPP method	BP method	site	BPE		
				N	M	p difference
Impact GPP methodology on BPE						
case 1	eddy	all	38	0.41	0.55	0.0010
case 2	model	all	15	0.40	0.50	0.096
Impact BP methodology on BPE						
case 3	eddy	LU [a]	19	0.40	0.56	0.024
case 4	eddy	MU [b] [c]	19	0.42	0.54	0.025

Notes: [a] temporal series of aboveground biomass (e.g. from sequential harvests or inventories of standing biomass) and belowground growth (e.g. ingrowth-cores or minirhizotrons), [b] temporal series of aboveground biomass (see in (a)) and belowground biomass (e.g. sequential root coring), and [c] site-specific models (e.g. empirical models relating soil conditions to root growth, process-based models with site calibration against growth and biomass data) or with BP estimates partially derived from the literature from similar sites (see also Supplementary Table 9).

Supplementary Table 11. Significance level 'p' of the difference in biomass production efficiency between natural (N) and managed (M) forest and grassland ecosystems (two-level management classification) or between pristine natural (PN), semi-natural (SN) and managed forest and grassland ecosystems (three-level management classification); see Supplementary Figure 4.

	Forests management classification		Grasslands management classification	
	Two-level	Three-level	Two-level	Three-level
1 way ANOVA	0.00070***	0.00083***	0.041*	0.13
Tukey's HSD test	N-M 0.00070***	PN-M 0.00072*** SN-M 0.079+ SN-PN 0.21	N-M 0.041*	PN-M 0.15 SN-M 0.19 SN-PN 0.93

Notes: +: 0.05 <p<0.10, *: p<0.05, ***: p<0.001

Supplementary Table 12. The ratio of annual biomass production (BP) to standing biomass (B) for the nonvascular component of various high latitude plant communities (BP-to-B ratio or the portion of biomass renewed every year; year^{-1}) for gap-filling of biomass production efficiency of tundra ecosystems (see Methods for details).

Location and reference	Community type	BP-to-B ratio
wet systems		
Central Norway[174]	wet meadow	0.99
Northern Alaska[175]	wet tundra	0.78
Northern Canada[176,177]	hummocky sedge-moss meadow	0.19
Northern Canada[176,177]	wet sedge-moss meadow	0.20
Northern Sweden[178]	subarctic mire	0.23
Western Siberia[179]	eutrophic swamp (sedge-*Sphagnum*)	0.64
dry systems		
Central Alaska[180]	moist acidic tussock	0.27
Central Alaska[181]	tussock tundra	0.41
Central Norway[182]	dry meadow	0.95
Northern Alaska [170,171]	moist acidic tussock tundra	0.20
Northern Sweden[169]	moderately exposed heath	0.41
Northern Sweden[169]	tree-line heath	0.25
Mean wet systems	-	0.50
Mean dry systems	-	0.42

Supplementary Table 13. Comparison of the statistical analyses using gap-filled and original (not gap-filled) values of biomass production efficiency (BPE), considering all forest sites (natural and managed, For.) and natural unmanaged sites of all ecosystem types investigated (Nat.).

BPE predictors	Gap-filled BPE						Original BPE					
	For.			Nat.			For.			Nat.		
	U	M	P	U	M	P	U	M	P	U	M	P
Management			1						1			
Nitrogen deposition			2			7			2			7
Natural fertility			3			1			3			2
Available water content			4			8			4			8
Dry months			5			5			5			5
Precipitation			6			6			6			6
Climate			7			2			7			1
Age												
Ecosystem type						3						3
Growth form						4						4

Notes: U: univariate analysis, M: multiple linear regressions and P: partitioning with Random Forest. Colors: (i) orange filling indicates a significant relationship ($p<0.05$); (ii) yellow filling indicates a trend ($0.05<p<0.10$), and (iii) grey filling indicates that the predictor variable was not used in the analysis. Numbers indicate the ranking of the variables from the most (1) to the least (7 or 8) influential. Natural fertility was observed for natural sites. For managed sites, the modeled unexplained natural fertility (see Statistical analysis) was used as a proxy of natural fertility.

Supplementary Table 14. Univariate analysis and multiple linear regressions (backward stepwise regressions) to evaluate the impact of different datasets of biomass production efficiency (BPE, which is the ratio between annual biomass production (BP) and gross primary production (GPP)) on the relationship between BPE and its potential environmental, climatic and vegetation drivers for natural unmanaged sites: Dataset 1, comprising sites (n=75) with BP and GPP not necessarily measured during the same period, and Dataset 2, comprising only sites (n=40) with BP and GPP measured during the same period.

BPE predictors	Dataset 1			Dataset 2		
	Univariate analysis		Stepwise regression	Univariate analysis		Stepwise regression
Categorical variables	*p ANOVA*	*post-hoc* [f]	*included*	*p ANOVA*	*post-hoc*	*included*
Biome (F, G, M, P, T) [a]	0.826	n.s.	yes	0.800	n.s.	yes
Climate (C, Te, Tr) [b]	0.052	n.s.	yes	0.096	n.s.	yes
Growth form (H, W) [c]	0.447	n.s.	yes	0.324	n.s.	yes
Fertility (L, M, H) [d]	0.234	n.s.	yes	0.269	n.s.	yes
Continuous variables	*p regression*	*Adj R^2*	*included*	*p regression*	*Adj R^2*	*included*
Nitrogen deposition	0.729	-0.012	yes	0.485	-0.013	yes
available water content	0.555	-0.0088	yes	0.479	-0.013	yes
Precipitation	0.338	-0.00093	yes	0.899	-0.026	yes
Dry months [e]	0.339	-0.00098	yes	0.889	-0.026	yes
Variables final model stepwise regression						
climate	n.a.	n.a.	p=0.051[g] p=0.079[h]	n.a.	n.a.	p=0.22[g] p=0.048* [h]
Adj R^2 initial model	n.a.	n.a.	-0.0053	n.a.	n.a.	0.0098
Adj R^2 final model	n.a.	n.a.	0.053	n.a.	n.a.	0.071

Notes: [a] F: forests, G: grasslands, M: marshes, P: peatlands, T: tundra; [b] C: cold, Te: temperate, Tr: tropical; [c] H: herbaceous, W: woody; [d] H: high, M: medium, L: low; [e] average number of months per year with potential evapotranspiration larger than precipitation; [f] post-hoc information (Tukey's HSD test) non-significant with $p>0.05$ (n.s); [g] factor: temperate, reference: cold; [h] factor: tropical, reference: cold; n.a. 'not applicable'; significant differences are indicated with '*' when $0.01<p<0.05$.

Supplementary Table 15. Univariate analysis (linear regression) for forest sites (natural and managed) and natural unmanaged sites of all ecosystem types (forests, grasslands, marshes, peatlands, tundra) to evaluate the importance of (i) fertilization on the relationship between biomass production efficiency (BPE) and nitrogen deposition and of (ii) irrigation, flooding, minerotrophic and permafrost conditions on the relationship between BPE and variables related to the water status (available water content, precipitation, dry months per year).

BPE predictors	natural and managed forests				all natural ecosystems			
	all sites		sites without confounding effects [(a)]		all sites		sites without confounding effects [(b)]	
	p value	adj R^2	p value	adj R^2	p value	adj R^2	p value	adj R^2
nitrogen deposition	0.00478 **	0.13	0.00653 **	0.15	n.a.	n.a.	n.a.	n.a.
available water content	0.542	-0.012	0.351	-0.0024	0.555	-0.0088	0.873	-0.016
precipitation	0.579	-0.013	0.985	-0.022	0.338	-0.00093	0.325	-0.00025
dry months	0.245	0.0074	0.0765	0.046	0.339	-0.00098	0.688	-0.011

Notes: [(a)] without considering fertilized sites for analysis on nitrogen deposition and without considering irrigated sites for analysis on soil water content, precipitation and dry months (i.e. average number of months per year when potential evapotranspiration is larger than precipitation); [(b)] without considering sites with occasional flooding (e.g. marshes), minerotrophic conditions (e.g. some peatlands) and sites with permafrost (tundra).

Supplementary Table 16. Values of standard uncertainty (p) for non-forest ecosystem types for the uncertainty assessment of biomass production (BP) and gross primary production (GPP) of each site i (see Methods for more details).

Ecosystem type	p_{BPi} (gC m^{-2} y^{-1})	p_{GPPi} (gC m^{-2} y^{-1})
grassland	371	818
cropland	375	597
marsh	687	793
peatland	232	344
tundra	88	93

Supplementary Table 17. Classification of soil nutrient availability.

Site name	Fluxnet	Status	soil type	structure	N	C	C:N	pH	CEC	Fert.	Extra info	Rep.	summary remarks and reference
Croplands													
Auradé	FR-Aur	H	Luvisol	clay loam; sand 21%, clay 32%	0.094	0.87	9.3	6.9	14	yes	Al, Ca, Mg, Mn, P_2O_5, K, Na	X	Fertile soil type, suitability for agriculture, fertilization[183-185] (Ceschia Eric, per. com.)
Avignon	FR-Avi	H	Calcaric Fluvisol		0.14	1.33	9.6			yes			Fertile soil type, suitability for agriculture, fertilization[186]
Beano1	IT-Be1	H	Chromi-Endoskeletic Cambisol	sand 27%, clay 15%	0.19	1.85	9.8	7.1		yes		X	Fertile soil type, suitability for agriculture, fertilization[47] (Alberti Giorgio, Delle Vedove Gemini per. com.)
Gebesee	DE-Geb	H	Chernozerm	silty clay loam; sand 4%, clay 36%	0.14	1.2	9	6.7		yes			Fertile soil type, suitability for agriculture, fertilization[187,188]
Grignon	FR-Gri	H	Luvisol	silt loam; sand 10%, clay 19%	0.14	1.6	11.2	7.2	16	yes		X	Fertile soil type, suitability for agriculture, fertilization[185,187] (Loubet Benjamin per. com)
Kellogg CRP-S	no	M	Typic Hapludalfs	sand 70%, clay 27%	0.20	2.4	11.7	5.9	6.0	yes	K, P, Ca, Mg	X	Marginal land with low soil quality; history of agriculture (with fertilization) but nutrient leaching; however, 20 y grassland land use improved soil status[49,127,189]
Kellogg CRP-P	no	M	Typic Hapludalfs	sand 68%, clay 27%	0.23	2.6	11.6	6.2	5.5	yes	K, P, Ca, Mg	X	Marginal land with low soil quality; history of agriculture (with fertilization) but nutrient leaching; however, 20 y grassland land use improved soil status[49,127,189]
Kellogg CRP-C	no	M	Typic Hapludalfs	sand 67%, clay 27%	0.28	3.1	11.1	6.1	6.0	yes	K, P, Ca, Mg	X	Marginal land with low soil quality; history of agriculture (with fertilization) but nutrient leaching; however, 20 y grassland land use improved soil status[49,127,189]
Kellogg Agr-C	no	M	Typic Hapludalfs	sand 64%, clay 30%	0.13	1.4	10.8	6.4	8.1	yes	K, P, Ca, Mg	X	Marginal land with low soil quality; history of agriculture (with fertilization) but nutrient leaching[49,127,189]

Kellogg Agr-S	no	M	Typic Hapludalfs	sand 62%, clay 33%	0.13	1.4	10.2	6.4	7.1	yes	K, P, Ca, Mg	X	Marginal land with low soil quality; history of agriculture (with fertilization) but nutrient leaching[49,127,189]
Kellogg Agr-P	no	M	Typic Hapludalfs	sand 54%, clay 36%	0.16	1.6	10.1	5.8	8.6	yes	K, P, Ca, Mg	X	Marginal land with low soil quality; history of agriculture (with fertilization) but nutrient leaching[49,127,189]
Klingenberg	DE-Kli	H	Gleysoil (drained)	clay loam; sand 21%, clay 56%	0.33	4.3	13	6.2		yes		X	Fertile soil type, suitability for agriculture, fertilization[186] (Grünwald Thomas per. com.)
Lamasquère	FR-Lam	H	Brunisol	clay; sand 12%, clay 54%	0.18	1.6	8.9	7.0	19	yes	Al, Ca, Mg, Mn, P_2O_5, K, Na	X	Fertile soil type, suitability for agriculture, fertilization[184,185] (Ceschia Eric, per. com.)
Lonzée winter wheat	BE-Lon	H	Luvisol	Sand 8%, clay 20%						yes			Fertile soil type, suitability for agriculture, fertilization[50]
Lonzée sugar beet	BE-Lon	H	Luvisol	Sand 8%, clay 20%						yes			Fertile soil type, suitability for agriculture, fertilization[50]
Lonzée potato	BE-Lon	H	Luvisol	Sand 8%, clay 20%						yes			Fertile soil type, suitability for agriculture, fertilization[50]
Lutjewad	NL-Lut	H	Calcaric Epigleyic Fluvisol							yes		X	Fertile soil type, suitability for agriculture, fertilization[185]
Mead 1	US-Ne1	H	Mollic Hapludalfs, Pachic Argialbolls, Vertic Argialbolls	sand 11%, clay 37%			11.0	6.3		yes	P, K, Na, Ca, Mg	X	Fertile soil type, suitability for agriculture, fertilization[54] (Andy Suyker per. com.)
Mead 2 maize	US-Ne2	H	Mollic Hapludalfs, Pachic Argialbolls, Vertic Argialbolls	sand 12%, clay 33%			10.8	5.7		yes	P, K, Na, Ca, Mg	X	Fertile soil type, suitability for agriculture, fertilization[54,190](Andy Suyker per. com.)
Mead 2 soybean	US-Ne2	H	Mollic Hapludalfs, Pachic Argialbolls, Vertic Argialbolls	sand 12%, clay 33%			10.8	5.7		yes	P, K, Na, Ca, Mg	X	Fertile soil type, suitability for agriculture, fertilization[54,190](Andy Suyker per. com.)
Mead 3 maize	US-Ne3	H	Mollic Hapludalfs,	sand 8%, clay 35%			11.0	5.8		yes	P, K, Na, Ca, Mg	X	Fertile soil type, suitability for agriculture, fertilization[54,190](Andy

			Pachic Argialbolls, Vertic Argialbolls										Suyker per. com.)
Mead 3 soybean	US-Ne3	H	Mollic Hapludalfs, Pachic Argialbolls, Vertic Argialbolls	sand 8%, clay 35%			11.0	5.8		yes	P, K, Na, Ca, Mg	X	Fertile soil type, suitability for agriculture, fertilization[54,190](Andy Suyker per. com.)
Oensingen	CH-Oe2	H	Eutri-Stagnic Cambisol	sandy clay; sand 30%, clay 42%	0.39	3.1	8	6.7		yes		X	Fertile soil type, suitability for agriculture, fertilization[191]
Risbyholm	DK-Ris	H	Histosol, (drained)			3.5				yes			Soil improvement (drainage), suitability for agriculture, fertilization[186]
forest													
Bornhoved Alder	no	L	Fibric Histosol	organic	1.5	26	17	5.8		no	N_2 fixation	X	Wet and nutrient-poor soil; substantial C allocated belowground to N_2-fixing bacteria to increase N availability[192,193]
Bornhoved Beech	no	L	dystri-cambic Arenosol	sandy texture	0.19	2.9	15	3.3		no			Poor soil type[192,193]
Caldaro	no	H	Calcaric cambisol	Sand 45%, clay 11%	0.20	1.74	8.7	7.4		yes			Fertile soil type, fertilization, area with intense agriculture[56] (Zanotelli Damiano per. comm.)
Cascade Head 1	no	H								no		X	nitrogen-rich[194]
Cascade Head 1A	no	H								no	N_2 fixation	X	nitrogen-rich and N_2 fixation by vegetation[194]
Caxiuana	BR-Cax	L	oxisol	sand 33%, clay 54%	0.13	1.68	12.3	3.8	2.3	no	P, micronutrients	X	Forest soil extremely nutrient limited, with low P and CEC[57,195]
Changbai Mountains	CN-Cha	H	Mollisols	upper organic-rich horizon, clay-loam	0.89	7.5	8.5	5.8		no	P		Soil type and organic layer indicate good fertility status [60,61] (Wu Jianbing per. comm.)
Chibougamau EOBS	CA-Qfo	L	ferro-humic podzol	Organic layer 15-40 cm, deeper silty-sand texture; mostly well-drained	0.66	46.5				no			Poor soil type[64,196,197]

Coastal plain North Carolina	US-NC2	M	histosol	peat soil	1	26	26			yes			Fertilized poor soil[65]
Collelongo	IT-Col	H	Humic alfisol	Silty loam	0.4-1.8	5-15	13	5.9-5.9	15-41	no	Micronutrients, base saturation		Fertile soil type and good soil chemical properties[198]
Dinghushan MF	CN-Din	L	lateritic red soil / yellow soil	18% sand, 19% clay		2.2		3.8		no			Poor soil type, with increase fertility with forest age[68,69]
Dooary	no	H	Gleysols	sand 9%, clay 53%	0.42	4.7	11	4.8		no	P,K		planted on former fertilized grasslands and relative high yield class[199-201]
Flakaliden C	SE-Fla	L	iron podzol	sand 56%, clay 6%						no		X	Nutrient limited[202,203]
Frazer old	no	L	typic cryochrepts (Inceptisols)	sandy loams				4.5-6.1	20	no		X	Soil with low fertility and particularly low N[73,204]
Frazer young	no	L	typic cryochrepts (Inceptisols)	sandy loams				4.5-6.1	20	no		X	Soil with low fertility and particularly low N[73,204]
Fujiyoshida	JP-Fuj	L	Lava flow	no mineral soil			35-53 humus			no			Lava flow (1000 y old), no mineral soil, deep layer litter (Ohtsuka Toshiyuki per. comm.)
Hainich	DE-Hai	H	Cambisol	sand 4%, clay 40%			11.8	5.7	10-12	no	Base saturation, micronutrients	X	Fertile soil [76,205]
Harvard	US-Ha1	L	inceptisols	sandy loam, well drained				<7		no	N mineralization	X	Nutrient-poor with low N mineralization[206]
Hesse	FR-Hes	H	luvisol / stagnic luvisol	sand 6%, clay 26%				3.9-4.1	5-7	no	Base saturation	X	Soil type typically nutrient-rich; stand among the best fertility site classes [77,207,208]
JacarandaK34	no	L	oxisols	sand 63%, clay 3%	0.08-0.15	1.3-2.6	17	3.9-4.7	1.3	no	P, micronutrients		Soil heavily leached and nutrient-poor [57,195,209]
Juniper	no	L								no	Foliar N		Typical N limitation in region[97]; dry site: availability of nutrients inherently low in such ecosystem type[97,210-212]
Kannenbruch AlderAsh	DE-Kan	H								no		X	Soil very fertile[80]
Kannenbruch Beech	DE-Kan	H								no		X	Soil very fertile[80]
Kannenbruch Oak	DE-Kan	H								no		X	Soil very fertile[80]
Lochristi	BE-Lcr	H		sand with a clay-enriched deep soil layer; sand	0.14	1.6	11.7	5.6		yes	K, P, Mg, Na, Ca	X	Suitability for agriculture, former intensive fertilization[81]

				86%, clay 11%									
Metolius	US-Me4	M	Inceptisol	65% sand, 10% clay	0.04-0.09	0.6-2.3	18-26	6.8-7.1		no	Presence N_2 fixers, details N cyle	X	Poor soil type but N_2 fixing shrubs in understory improve nutrient status [213-215]
Metolius-young	US-Me5	M	Inceptisol	65% sand, 10% clay	0.04-0.09	0.8-2.3	19-26	6.5-6.9		no	Presence N_2 fixers, details N cyle	X	Poor soil type but N_2 fixing shrubs in understory improve nutrient status[213-215]
Morgan Monroe	US-MMS	M	typic Dystrochrept (Inceptisols)	34% sand, 40% clay				5.2		no			Poor soil type but relative high N mineralization[206]
NAU Centennial Undisturbed	no	M	Typic Eutroboralf	sand 19%, clay 29%	0.12	2.6	21.7	5.5		no		X	Medium nutrient status[87,216] (Dore Sabina per. comm.)
NAU Centennial thinned	no	M	Mollic Eutroboralf/ Typic Argiboroll	sand 33%, clay 31%	0.17	3.4	19.7	5.5		no		X	Medium nutrient status[87,216] (Dore Sabina per. comm.)
Pasoh	no	L	laterite					3.5–4.8		no	P, exchangeable cataions and bases	X	Poor soil[217,218]
Pierce Creek Forest C	no	M	Podzol	A horizon: sand (40 cm); B horizon: clay and gravel (60 cm)						no		X	Low N but P not limiting[89]
Pierce Creek Forest IF	no	H	Podzol	A horizon: sand (40 cm); B horizon: clay and gravel (60 cm)						yes		X	Fertilization (and irrigation) till N appeared in excess[89]
Popface alba	no	H	Alfisol	sand 38%, clay 18%	0.13	1.1	9.3	5	26.4	yes		X	Plantation on former agricultural land with high nutrient availability[219-221]
Popface euamericana	no	H	Alfisol	sand 38%, clay 18%	0.13	1.1	9.3	5	26.4	yes		X	Plantation on former agricultural land with high nutrient availability[219-221]
Popface nigra	no	H	Alfisol	sand 38%, clay 18%	0.13	1.1	9.3	5	26.4	yes		X	Plantation on former agricultural land with high nutrient availability [219-221]
Prince AlbertSSA SOAS	CA-Oas	M	Orthic Gray Luvisol	Loam-clay loam,	0.021					no	Mg, Ca, dominant species		N_2 fixation moderate the nutrient limitation typical of cold biomes

				moderately drained							N2 fixer, vegetation nutrient analysis		with slow decomposition rates [222-224]
Prince Albert SSA SOBS	CA-Obs	L	20-30 cm peat over sand	poorly drained	0.007					no	Mg, Ca, vegetation nutrient analysis		Nutrient limitation because of slow decomposition rates [222,223]
Prince Albert SSA SOJP	CA-Ojp	L	Eutric Brunisol/Orthic Eutric Brunisol	Well drained	0.005					no	Mg, Ca, vegetation nutrient analysis		Nutrient limitation because of slow decomposition rates [222,223]
Puechabon	FR-Pue	M	Rendzina	14% sand, 40% clay	0.25	3.8	14.8	7.6	26.9	no	Leaf nutrients	X	Sufficient N, low P[92,93]
Qianyanzhou Ecological Station	CN-Qia	L	red earth	17% sand, 15% clay						no			Poor soil type[225,226]
Santiam Pass	no	L								no	Foliar N		Typical N limitation in region[97]; vegetation properties indicate relatively nutrient-poor status[227]
Saskatchewan HJP75	CA-SJ3	L		Organic layer and mineral (sand 86%, clay 4%); well drained			44 (organic)			no		X	Nutrient-poor[228]
Scio	no	H								no	Foliar N	X	Relative high nutritional status and biomass production not limited by nutrient availability[227]
Soroe	DK-Sor	H	Luvisol	sand 74%, clay 12%	high				14	no		X	Nutrient rich soil[198,229]
Sylvania hardwood	US-Syv	L	spodosols	57% sand, 6% clay	0.18	3.4	19	4.5		no	N mineralization, details N cycle	X	Infertile soil type[100,230]
Takayama	JP-Tak	H	brown forest soil	sand 41%, clay 38%						no			Soil type very fertile[231-233]
Tapajos67	no	L	Oxisols	Sand 3%, clay 89% (with sandier patches)	0.17	2.54	15.2	3.84	3.0	no	P, micronutrients		Nutrient-poor soil type[57,195]
Tapajos83	no	L	Ferralsol							no			Nutrient-poor soil type [57,195]
Teshio CCLaG	JP-Tef	H	Gleyic Cambisol							no			Fertile soil type[105]
Tharandt	DE-Tha	M	Dystric Cambisol	Sand 12%, clay 15%				3.9	5.6	no	Base saturation		Fertile soil type but low pH and ion exchange capacity[208,234]
Thompson NSA	CA-NS1	L	30-50 cm Peat	poorly	0.006					no	Mg, Ca,		Nutrient limitation because of slow

NOBS			over clay	drained							vegetation nutrient analysis		decomposition rates [222,224]
Thompson d71	CA-NS2	M	Gray Luvisols							no	Full physical and chemical analysis		Decomposition limited by cold climate but likely benefited from a ‘fire fertilization’ effect[235-237]
Thompson d37	CA-NS3	M	Gray Luvisols							no	Full physical and chemical analysis		Decomposition limited by cold climate but likely benefited from a ‘fire fertilization’ effect[235-237]
Thompson d20	CA-NS5	M	Gray Luvisols							no	Full physical and chemical analysis		Decomposition limited by cold climate but likely benefited from a ‘fire fertilization’ effect[235-237]
Thompson d15	CA-NS6	M	Gray Luvisols							no	Full physical and chemical analysis		Decomposition limited by cold climate but likely benefited from a ‘fire fertilization’ effect[235-237]
Tumbarumba	AU-Tum	M	Red dermosol					<7		no		X	Moderate nutrient status[108]
Turkey Point TP02	CA-TP1	H	Brunisolic Gray Brown Luvisol	80-90% sand, <5% clay	0.06	0.68	11.4	6.3		yes	macronutrients(P, K, Ca, Mg)		Relatively fertile soil with likely improved nutrient status from previous farming activities[109,110]
Turkey Point TP89	CA-TP2	H	Gleyed Brunisolic Gray Brown Luvisol	80-90% sand, <5% clay	0.07	0.99	14.2	4.3		no	macronutrients(P, K, Ca, Mg)		Relatively fertile soil with likely improved nutrient status from previous farming activities[109,110]
Turkey Point TP74	CA-TP3	M	Brunisolic Gray Brown Luvisol	80-90% sand, <5% clay	0.05	0.97	19.4	3.7		no	macronutrients(P, K, Ca, Mg)		Relatively fertile soil with moderate nutrient availability[109,110]
Turkey Point TP39	CA-TP4	M	Brunisolic Gray Brown Luvisol	80-90% sand, <5% clay	0.05	0.77	15.4	4.1		no	macronutrients(P, K, Ca, Mg)		Relatively fertile soil with moderate nutrient availability[109,110]
University of Michigan	no	L	Podzols (Entic Haplothods)	Well drained, 92% sand, 1% clay				3.5-4.5		no	N mineralization		Poor soil type with N limitation [238,239]
Walker Branch	US-WBW	L	typic Paleudult	sand 34%, clay 63%				<7	2.9	no	exchangeable bases, N and P		Soil low in exchangeable bases, N, and P[206,240,241]
Warings Woods	no	H		well-drained						no		X	High fertility[242]
Wind River	US-Wrc	M	Andisols (Entic Vitrands)	Well drained, loam, 5-8% clay	1.4-1.9	3.4-5.3	25-28	4.9-5.7		no		X	Fertile soil type but with moderate nutrient limitation[243,244]
Wytham Woods	no	H	Cambisols	clay (60% land surface),	0.40	5.3	13.5			no	Vegetation survey, P, Ca, K, Mg		Fertile soil type and vegetation typical for relatively nutrient-rich soils[113,245,246]

				silty clay (22%), clay loam (15%)									
Xishuangbanna	CN-Xsh	L	laterite/latosol	sandy loam	0.21	1.9	9	4.5-5.5		no	P, K		Classification based on poor soil type but nutrient concentrations upper range reported for tropical forests[114,247]
Xishuangbanna plantation	no	M								yes			Area of poor soil type (see Xishuangbanna) but fertility amended by fertilization[115]
Yatir	IL-Yat	L	Rendzina (above chalk and limestone)	Sand 30%, Clay 44%	0.10	1.14	11.4	8.4		no		X	N limitation in arid environment[248,249]
Grasslands													
Beano2	IT-Be2	H	Chromi-Endoskeletic Cambisol	sand 27%, clay 15%	0.19	1.92	10.1	7.1		yes		X	Fertile soil type, suitability for agriculture, fertilization[47] (Alberti Giorgio, Delle Vedove Gemini per. com.)
Cheyenne	no	M	Aridic Argiustolls	sandy loam; sand 63%, clay 19%		1.2-2.3		6	28	no			Soil type of moderate fertility[117,250,251]
Grillenburg	DE-Gri	M	pseudogley	sand 10%, clay 9%			11.3	6.4		no		X	N limitation possible but plant composition and historical use (agriculture >50 y before measurements) point to a medium status[119] (Bernhofer Christian, Grünwald Thomas per. com.)
Haibei	CN-Hab	L	Mat Cry-gelic Cambisol	clay loam	0.42	4.3	10.2	7.3	30	no	P, K; foliar nutrients	X	Nutrient-poor soil, typical of cold biomes[252]
Hakasija 1	RU-Ha1	M	calcic chernozem	silty clay	0.24	2.2	9			no		X	Fertile soil but mineralization limited by cold climate[122,123]
Hakasija 3	RU-Ha3	M	calcic chernozem	silty clay			9			no		X	Fertile soil and agriculture 10 y before measurements (with limited fertilization) but mineralization limited by cold climate[123]
Inner Mongolia	no	L	Calcic Chernozems	sand 49%, clay 18%	0.24	2.3	9.6	6.6	15.7	no		X	Nutrients limiting in wet conditions (in dry conditions water is limiting)[124,253]
Kellogg CRP-Ref	no	M	Typic Hapludalfs	sand 60%, clay 35%	0.27	3.1	11.4	6.2	6.5	no	K, P, Ca, Mg	X	Marginal land with low soil quality; history of agriculture (with fertilization) but nutrient leaching; however, 20 y grassland land use

													improved soil status[49,126,127,189]
Kellogg CRP-S	no	M	Typic Hapludalfs	sand 70%, clay 27%	0.20	2.4	11.7	5.9	6.0	yes	K, P, Ca, Mg	X	Marginal land with low soil quality; history of agriculture (with fertilization) but nutrient leaching; however, 20 y grassland land use improved soil status[49,126,127,189]
Kellogg Agr-S	no	M	Typic Hapludalfs	sand 62%, clay 33%	0.13	1.4	10.2	6.4	7.1	yes	K, P, Ca, Mg	X	Marginal land with low soil quality; history of agriculture (with fertilization) but nutrient leaching[49,126,127,189]
Kellogg Agr-P	no	M	Typic Hapludalfs	sand 54%, clay 36%	0.16	1.6	10.1	5.8	8.6	yes	K, P, Ca, Mg	X	Marginal land with low soil quality; history of agriculture (with fertilization) but nutrient leaching[49,126,127,189]
Jasper	US-Jas	M	sandstone-derived soil (Dibble Series, Millsholm variant)	Silty clay loam; sand 10%, clay 40%	0.10	3.0	30	5.5	3.8	no	P, K	X	Soil moderately fertile likely limited in N and P[129,254]
Konza	US-Kon	H	Typic Natrustolls	silty clay loam						no			Fertile soil type[130]
Kursk	no	H	chernozem	sand 32%, clay 37%			11.9	6.3	53	no		X	Rich soil and productive site[134]
Lethbridge	CA-Let	H	orthic dark-brown chernozems	clay-loam; sand 29%, clay 31%	0.48	6.1	12.7	7.1		no		X	Soil type is very fertile[137,255]
Matador	no	M	Rego Brown Chernozemic	clay						no		X	Study site similar to Lethbridge but colder climate likely limiting decomposition [137,139]
NAU Coconito Burned	no	M	Mollic Eutroboralf	24% sand, 20% clay						no			Fertile soil type but great loss of organic matter in fire 10 y before measurements[87]
Osage	no	H	mollisols	loam / silty clay loam	0.17	0.90	5.3	5.9		no	P, K, Ca, Mg; base saturation available	X	Nutrient-rich[141]
Tchizalamou	CG-Tch	L	Ferralic Arenosols	sand					0.5	no		X	Low ionic content, unsuitable for agriculture[256,257]
Woodward	no	M	Psammentic Haplustalfs , Typic Ustipsamments	sandy						no			Soil type of moderate fertility[144]
Marshes													

Burcht	no	H								no		X	Nutrient-rich conditions[145]
Flax Pond	no	M								no			General N limitation within this type of ecosystem; P is not limiting[258,259]
Great Sippewissett	no	H								no		X	No nutrient limitation at the site[260]
Mase	JP-Mas	H	Typic Endoaquepts	clay loam	0.20	2.30	11.5			yes			Fertile soil and fertilizer application[149]
Saeftinghe	no	H								no		X	Nutrient-rich conditions[145]
San Joaquin	US-SJ1	H								no		X	Nutrient-rich site[151]
Peatlands													
BOREAS collapse bog	no	L	peat	organic + clays			97.6	3.9		no		X	Poor nutrient status[152]
BOREAS intermediate fen	no	M	peat	organic + clays			43.2	5.8		no		X	Intermediate nutrient status[152]
BOREAS rich fen	no	H	peat	organic + clays			26.5	7.2		no		X	Rich nutrient status[152]
Bog End, Moor House	no	L	peat							no			Lack of site specific info; global map of soil fertility indicates low fertility[20]
Degerö	SE-Deg	L	peat					acid		no		X	Low nutrients[156]
Mer Bleue	CA-Mer	L	peat					acid		no		X	Nutrient poor[157]
Stordalen palsa	no	L	histel	peat + silt	0.48-0.58	46-47	8-10	4.2-4.6		no	N mineralization	X	Nutrient poor[162,261,262]
Tundra													
Alexandra Fiord, wet meadow	no	L		organic + silty loam	1.7	15	8.8	6.3		no	K, P, Ca, Mg	X	Low nutrient status[164]
Barrow	US-Brw	L		organic horizon + silty clay/silty loam +buried peat			20	4-5.5	95	no	C:P; foliar nutrients analysis	X	Very nutrient poor: N and P most deficient (with N more deficient than P), then, order deficiency K> Ca>Mg[165]
Imnavait Creek	no	L			0.12	4.2	35	4.5	18	no	Ca, Mg, Al, Mn, Fe; N mineralization	X	Nutrient limitation[263]
Paddus	no	L			1.85	43	23.2	7.1		no		X	Nutrient-poor[264,265]
Toolik Lake	no	L	histic pergelic cryaquept	Organic + silt	0.14	4.4	31	5	29	no	Ca, Mg, Al, Mn, Fe; N mineralization	X	Productivity is limited by N and secondary by P [170,263,266]

Notes: Information about the column heads: Fluxnet: indicates if site is in Fluxnet (http://www.fluxdata.org/default.aspx) or *European Fluxes Database Cluster* (http://gaia.agraria.unitus.it/home/sites-list) with code; status: soil nutrient availability or site fertility (H: high, M: medium, L: low); soil type: nomenclature follows the site literature and not a single system; structure: proportion of sand and clay, texture class and other soil physical characteristics; N: nitrogen content (%); C: carbon content (%); C:N: C:N ratio; pH: when available pH in $CaCl_2$ was reported, otherwise from water solution; CEC: cation exchange capacity (in cmol kg^{-1}); Fert.: fertilized site (yes or no); Extra info: supplementary information on the nutrient status available in the literature (e.g. phosphorous, micronutrients, foliar nutrient analysis, nitrogen mineralization, base saturation); rep. (report): the 'X' indicates whether the fertility category (high, medium, or low) was specifically confirmed in the literature or by the site PI.

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5 Column heads of data file

site: site name

ecosystem_type: C: cropland, F: forest, G: grassland, M: marsh, P: boreal peatland, T: tundra

latitude: positive: northern hemisphere, negative: southern hemisphere

longitude: positive: East, negative: West

BPo: original biomass production, gC m^{-2} y^{-1}

BPo_u: uncertainty original biomass production, gC m^{-2} y^{-1}

BPgf: gap-filled biomass production, gC m^{-2} y^{-1}

BPgf_u: uncertainty gap-filled biomass production, gC m^{-2} y^{-1}

GPP: gross primary production, gC m^{-2} y^{-1}

GPP_u: uncertainty gross primary production, gC m^{-2} y^{-1}

BPEo: biomass production efficiency derived from BPo, dimensionless

BPEgf: biomass production efficiency derived from BPgf, dimensionless

time_code: A: BP and GPP measured during the same period, B: BP and GPP measured during different periods

growth_form: dominant functional type: W: woody, H: herbaceous

age_forest: only for forests with BP and GPP measured during the same period (NA: not available), y

climate: cold, temperate, tropical

precipitation: annual precipitation, mm y^{-1}

dry_month: number of months per year with potential evapotranspiration larger than precipitation, month y^{-1}

available_water_content: soil available water

fertility: I: infertile, M: medium fertility status, F: fertile nitrogen_deposition: atmospheric nitrogen deposition, kg N ha^{-1} y^{-1}

management: N: natural sites, M: managed sites

For details and data sources see Methods and Supplementary Table 2.

6 R code of multinomial ordered logistic regressions

```
#################################################################################
#Load libraries
#################################################################################
library('mlogit')
require(foreign)
require(ggplot2)
require(MASS)
require(Hmisc)
require(reshape2)
require(car)


#################################################################################
#Read data + data management
#################################################################################
matteodatat=read.table('Campioli_Data.txt',header=T,dec='.',stringsAsFactors=FALSE)
matteodatat2=subset(matteodatat,matteodatat$biome=='F' & matteodatat$time_code='1')
matteodata=matteodatat2[,c('BPEgf,'fertility',' management')]
colnames(matteodata)=c('bpe','fertility','management')

matteodata$fertilityf=as.factor(ifelse(matteodata$fertility=='I',1,ifelse(matteodata$fertility=='
M',2,3)))
matteodata$managementf=as.factor(ifelse(matteodata$management=='N',0,1))

#################################################################################
#Model fertility as a function of management ASSUMING FERTILITY CLASSES
ORDERED
#################################################################################
fertmodord=polr(matteodata$fertilityf~matteodata$management,method='logistic') #cfr
Agresti's cumulative link model
summary(fertmodord)
fertmodord$fitted.values

fertmodordfitI=fertmodord$fitted.values[,1]
fertmodordfitM=fertmodord$fitted.values[,2]
fertmodordfitF=fertmodord$fitted.values[,3]
#residuals – to be used in further analysis as 'unexplained natural fertility' – see main text
fertilityordIres=ifelse(matteodata$fertility=='I',1-fertmodordfitI,0-fertmodordfitI)
fertilityordMres=ifelse(matteodata$fertility=='M',1-fertmodordfitM,0-fertmodordfitM)
fertilityordFres=ifelse(matteodata$fertility=='F',1-fertmodordfitF,0-fertmodordfitF)

cor(as.matrix(cbind(fertilityordFres,fertilityordIres,fertilityordMres))) #correlated!

#tests to check if residuals depend on management (they should not!)
cor(cbind(fertilityordFres,fertilityordIres,matteodata$managementf)) #correlation between
management and residuals should be low
```

```
t.test(fertilityordIres~ matteodata$management) #not significant
t.test(fertilityordMres~ matteodata$management) #not significant
t.test(fertilityordFres~ matteodata$management) #not significant
```