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Biomass production efficiency controlled by management in temperate and boreal ecosystems

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34 **Summary paragraph**

35 Plants acquire carbon through photosynthesis to sustain biomass production, autotrophic
36 respiration, and production of non-structural compounds for multiple purposes¹. The fraction
37 of photosynthetic production used for biomass production, the biomass production
38 efficiency², is a key determinant of the conversion of solar energy to biomass. In forest
39 ecosystems, biomass production efficiency was suggested to be related to site fertility². Here
40 we present a global database of biomass production efficiency from 131 sites compiled from
41 individual studies using harvest, biometric, eddy covariance, or process-based model
42 estimates of production - dominated, however, by data from Europe and North America. We
43 show that instead of site fertility, ecosystem management is the key factor that controls
44 biomass production efficiency in terrestrial ecosystems. In addition, in natural forests,
45 grasslands, tundra, boreal peatlands and marshes biomass production efficiency is
46 independent of vegetation, environmental and climatic drivers. This similarity of biomass
47 production efficiency across natural ecosystem types suggests that the ratio of biomass
48 production to gross primary productivity is constant across natural ecosystems. We suggest
49 that plant adaptation results in similar growth efficiency in high and low fertility natural
50 systems, but that nutrient influxes under managed conditions favour a shift to carbon
51 investment from the belowground flux of non-structural compounds to aboveground biomass.

52

53

54 **Main text**

55 The fraction of gross primary production (GPP) used for biomass production (BP) of
56 terrestrial ecosystems has recently been coined biomass production efficiency (BPE)². BPE is
57 typically used as a proxy for the carbon-use efficiency or NPP-to-GPP ratio, where NPP refers
58 to net primary production i.e. BP plus the production of non-structural organic compounds¹.

59 Current knowledge about BPE is mainly derived from research on forests. Earlier work
60 reported BPE to be conservative across forests³, whereas more recent syntheses suggest high
61 inter-site variability^{2,4}. The variation in BPE was first attributed to vegetation properties
62 (forest age) and climate variables⁴. More recently, it was shown that forest BPE in a range of
63 natural and managed sites was correlated with site fertility, with management as a secondary
64 BPE driver².

65 Fertility and management are strongly correlated as management enhances
66 productivity by increasing plant-available resources, including nutrients. For instance,
67 fertilization of grasslands directly increases the ecosystem nutrient stock, whereas forest
68 thinning indirectly increases nutrient availability at the tree level by reducing plant-plant
69 competition. In addition, fertile sites are more likely than infertile sites to be managed.
70 Atmospheric deposition of nutrients, especially nitrogen (N), might further complicate the
71 relationship between BPE, fertility and management. The influence of site fertility and
72 management on BPE has not been disentangled in previous studies, and the impact of N
73 deposition on BPE is largely overlooked. Here, we postulate that the impact of management
74 on BPE is underestimated. In addition to a direct effect on BPE through selection of the most
75 efficient plants^{2,5}, management can indirectly affect BPE through effects on site fertility and
76 related belowground dynamics². Understanding of these dynamics not only will clarify the
77 controls of BPE but also elucidate the human impacts on BPE.

78 We compiled a new BPE dataset comprising 131 sites, including forests, grasslands,
79 croplands, wetlands (temperate marshes and boreal peatlands) and tundras (Methods). All
80 major climatic zones (from polar to tropical) were represented but managed sites were located
81 almost entirely in the temperate and boreal zone of North America and Europe
82 (Supplementary Fig. 1, Supplementary Table 1). For each site, our dataset also included
83 vegetation characteristics, environmental data and information on anthropogenic impacts such

84 as management and atmospheric N deposition (Supplementary Table 2). With regard to
85 management, we adopted a binary classification (Methods), distinguishing natural sites
86 (pristine sites or sites with a low human impact that largely reproduced naturally occurring
87 processes, e.g. grasslands with low grazing) from managed sites (sites dominated by human
88 activity with impacts that would not occur in nature, e.g. newly established and fertilized
89 grasslands). The utility of this classification was tested against more complex classifications
90 (Methods), whereas its reproducibility was assured by the definition of several sub-categories
91 within the ‘managed’ and ‘natural’ classes (Supplementary Table 3). The BPE dataset,
92 comprising the ancillary site information, is available in Supplementary Data. Our data
93 analysis consisted of (i) multinomial ordered logistic regressions to examine the relationship
94 between fertility and management (code available in Supplementary Information) and (ii)
95 linear (univariate analysis, multiple linear regressions) and non-linear approaches (Random
96 Forest) to extract emerging relationships between BPE and its potential predictors (Methods).

97 The analysis proceeded in five steps, using different sub-sets of our database. (1) We
98 analyzed all natural sites to test whether BPE is driven by natural variation in site fertility. The
99 results showed that this hypothesis was not true. First, BPE did not differ significantly
100 ($p=0.83$) among natural ecosystem types of contrasting fertility status i.e. tundra and boreal
101 peatlands (nutrient-poor), temperate marshes (nutrient-rich) and forests and grasslands (with
102 variable but overall intermediate fertility status), showing an average BPE (and s.e.m) of
103 0.46 ± 0.01 (Figure 1; Supplementary Table 4). Second, the impact of fertility on the BPE of
104 natural ecosystems remained non-significant when accounting for variation in fertility among
105 forests ($p=0.24$, $n=43$), grasslands ($p=0.72$, $n=16$) or all natural sites lumped together ($p=0.23$,
106 $n=75$; Supplementary Fig. 2). (2) We analyzed the relationship between fertility and
107 management in natural and managed forests to verify their correlation and disentangle (i) the
108 impact of management on fertility from (ii) 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, e.g. high or low fertility, to manage) and to obtain model residuals for each site representing the ‘fertility status not explained by management’ and 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 (e.g. vegetation and environmental characteristics, N deposition) within the forest dataset. 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, 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 (Figure 1, Figure 2; 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, Supplementary Fig. 3). Climate showed an influence on BPE but this

134 effect was weak ($0.05 < p < 0.10$) and not consistent across statistical methods (Supplementary
135 Table 8, Supplementary Fig. 3).

136 The observed positive impact of management on BPE does not come as a surprise in
137 itself. Rather, the novelty of this study is the finding that management is by far the ‘key’
138 driver of BPE and more important than any other vegetation or environmental factors. This
139 observation calls for a refinement of the hypothesis, which previously postulated that greater
140 BPE in more fertile sites is related to reduced C allocation to symbiotic fungi, as plants in
141 nutrient-rich conditions invest less in processes facilitating nutrient uptake². Our revised
142 hypothesis relies on the fact that adaptation processes in natural ecosystems⁶ could allow
143 plants in both nutrient-poor and nutrient-rich environments to have similar growth efficiency.
144 However, belowground C transfers to symbionts are not static⁷ and the greater nutrient
145 availability caused by management could make root symbiotic associations less important for
146 plants and thus reduce the flux of C from plants to symbionts. This pattern would favor C
147 investment in biomass production, particularly aboveground, since light may become the most
148 limiting resource. This hypothesis is supported by (i) the allocation pattern available for a
149 subset of our forests showing that management substantially increased allocation to
150 aboveground wood BP (+13%, $p < 0.001$) and marginally decreased allocation to fine root BP
151 (-4%, $p = 0.083$) (Table 1) and by (ii) forest C allocation meta-analyses⁸ which reported
152 increased C partitioning to aboveground BP and decreased partitioning to belowground C flux
153 in response to fertilization. Declines in mycorrhizal fungi following fertilization are well
154 known⁹. Similarly, thinning can negatively affect the standing crop of mycorrhizal fungi¹⁰ and
155 ectomycorrhizal metabolic activity^{11,12}, which is consistent with our new interpretation. In
156 addition, the larger BPE in managed ecosystems might also reflect decreased allocation of
157 GPP to autotrophic respiration (Ra), thus lower Ra-to-GPP ratio². However, as previous
158 research does not support this hypothesis^{3,8} and the variability of the Ra-to-GPP ratio might be

159 small, ad-hoc experiments combining the assessment of C transfer to mycorrhizal fungi and
160 ecosystem Ra will be needed to ascertain the importance of these dynamics in managed
161 ecosystems. Similarly, further research should explore (i) if the hypothesized reduction in C
162 allocation to mycorrhizae (and exudates) might have a long-term negative feedback on the site
163 nutrient availability where management does not include external input of nutrients and (ii)
164 the impact of ecosystem degradation on BPE, especially in tropical areas that are often
165 overexploited.

166 Nitrogen deposition also appeared to have a positive effect on BPE. Like management,
167 elevated N deposition represents an artificial change in natural fertility and a perturbation of
168 the nutrient cycle. The apparently contrasting evidence that N deposition does not affect BPE
169 of natural ecosystems (when considered separately from the managed ecosystems) is likely
170 related to the intensity of the deposition and the fact that N deposition might influence BPE
171 (like other ecosystem processes¹³) only at higher deposition rates. Natural sites are typically
172 found in less urbanized locations and in our dataset they were characterized by deposition
173 rates 43% lower than those of managed ecosystems. Furthermore, adaptation responses to N
174 deposition are more likely to occur in natural ecosystems where succession is much longer
175 than rotations in managed ecosystems.

176 Little information was previously available about BPE of non-forest ecosystems¹⁴. Our
177 analysis showed that BPE of natural ecosystems is independent of ecosystem type, vegetation
178 and environmental characteristics (including natural site fertility). The lack of sensitivity of
179 BPE to these potential drivers points to a rather conservative BPE across natural ecosystems.
180 Our study supports the (highly debated) physiological argumentation for a constant ratio
181 between BP and GPP in natural ecosystems^{3,4} and provides important constraints for the
182 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. (i) The quantification of BPE for managed ecosystems can improve yield simulations by models (e.g. timber in forests, grains in crops), particularly for algorithms that derive BP as a proportion of GPP^{15,16}. (ii) The land surface component of Earth system models currently 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 ORCHIDEE¹⁷ 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). (iii) Our study indicates new ways to indirectly derive BPE at regional and continental scales from maps of land use and human management. (iv) While 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 1500 g C m⁻² y⁻¹, an increase of 12% in BPE (Supplementary Table 7) would enhance BP by 180 g C m⁻² y⁻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.

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271

272 **Author contributions** MC, SV, SL and IAJ conceived the paper; MC performed the analyses
273 and wrote the text; SL provided ORCHIDEE simulations; JB developed the multinomial
274 ordered logistic regressions and the statistics; EC, DO, DP, PFS, XW, TZ provided field data
275 or contributed to data collection from external databases and literature; all authors contributed
276 substantially to discussions and revisions.

277

278 **Competing financial interests** The authors declare no competing financial interests.

279

280 **Figure captions**

281

282 Figure 1. Biomass production efficiency of natural and managed ecosystems. BPE (mean \pm 1
283 s.e.m.) of (a) natural ecosystem types that can be regularly managed such as forests and
284 grasslands; (b) natural ecosystem types that are not commonly managed such as temperate
285 marshes, boreal peatlands and tundras, and (c) anthropogenic ecosystem types, such as
286 croplands, that are not in a natural state but are maintained through management. Difference
287 within forest types was significant at $p < 0.001$ (***)^{*}, whereas difference within grassland
288 types was significant at $p < 0.05$ (*). Light grey columns indicate natural ('nat.') conditions and
289 dark grey columns managed ('man.') conditions.

290

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

297

298 Table 1

299 *Title.* Carbon allocation pattern in natural and managed forests as expressed by the ratio of BP
300 to GPP.

301 *Footnote.* Values are mean \pm 1 s.e.m, in percentage; replicates (n): 12 and 19 for natural and
302 managed forests, respectively; notations: 'other aboveground': reproductive organs and
303 understory; +: $0.05 < p < 0.10$, *: $p < 0.05$, and ***: $p < 0.001$.

304

305 **Methods**

306

307 Dataset

308 Our analysis required site estimates of biomass production (BP), gross primary production
309 (GPP), and their uncertainty, to derive the biomass production efficiency (BPE) and its
310 uncertainty. The key rule for selecting the sites was the availability of site-specific estimates
311 of BP and GPP. Therefore, the dataset did not include values obtained from generic algorithms
312 (e.g. global models, remote sensing products). BP included above- and belowground growth.
313 In most cases, BP was obtained from harvest or biometric methods (comprising empirical
314 models as e.g. allometric relationships, root growth as function of soil conditions^{18,19}) and in
315 5% of the cases from process-based models with site-specific parameterization and/or
316 validation against growth or biomass data. Minor gap-filling was done for BP estimates at
317 some sites (see below). BP methodologies can be divided into broad classes according to
318 method uncertainty (i.e. low, medium or high uncertainty¹; Supplementary Table 9) related in
319 particular to the approach to determine fine root BP (the component of ecosystem BP most
320 difficult to assess; see Supplementary Methods) or the use of process-based models
321 (Supplementary Table 9). However, additional tests showed that the key results of our analysis
322 were independent of the BP methodology employed (Supplementary Table 10). GPP was
323 mostly estimated from eddy covariance (73% of the cases) or process-based models with site-
324 specific parameterization and/or validation (20% of the cases). Explanation about the
325 preference of these GPP methods instead of other approaches (e.g. GPP derived from the sum
326 of all carbon sinks within the ecosystem such e.g. BP, autotrophic respiration, carbon transfer
327 to mycorrhizal symbionts) is reported extensively in Supplementary Methods. Additional tests
328 showed that the alternative use of eddy covariance- or model-based estimates of GPP did not

329 affect the key results of our analysis (Supplementary Table 10). Detailed information on
330 uncertainty calculations are reported in Statistical analysis.

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

341 Ancillary data such as vegetation characteristics, climate, environmental conditions
342 and anthropogenic impacts were needed for each site to determine the possible effect of these
343 factors on BPE. Such information was retrieved mostly from the literature, open-access
344 databases^{1,20-27} or modelling²⁸ (Supplementary Table 2). For N deposition, data for Western
345 Europe and the conterminous USA were retrieved from interpolated gridded maps based on
346 ground observations²⁵, whereas simulated values were used for the rest of the world^{22,23}.

347

348 Management classification

349 The sites were divided into two categories: natural and managed. Natural sites are defined as
350 those characterized by none or low-to-moderate human impact, whereas managed sites are
351 heavily affected by human activity. We defined ‘low-to-moderate human impacts’ as human
352 activities that largely reproduce naturally occurring processes e.g. low grazing, occasional fire
353 in grasslands, forest regeneration. On the other hand, we considered sites ‘heavily affected by

354 human activity' to be those with impacts that would not occur in nature e.g. intense
355 fertilization of poor soils, sowing of cropland monocultures, thinning of healthy trees. The
356 classification was straightforward for marshes, peatlands and tundras (pristine or with
357 minimal human impact except in two managed wetlands) and for croplands (inherently
358 managed) (Supplementary Table 3). For forests and grasslands, the classification included
359 sub-categories for both the natural and managed classes (Supplementary Table 3). For
360 instance, for forests, we considered as natural the following types of forests: (i) old-growth
361 with minimal disturbance, (ii) natural succession due to fire/windthrow and at least 10 years
362 after the disturbance, (iii) unmanaged or with low human impact (e.g. understory grazing) in
363 the 50 years before measurement and (iv) planted forests without any intervention after
364 planting and at least 10 years old at the time of measurement. On the other hand, we
365 considered as managed forests: (i) forests with thinning/harvest in the 50 years before
366 measurement, (ii) newly (<10 years old) established plantations, (iii) forests fertilized in the
367 25 years before measurement, or (iv) forests managed for fruit/rubber production at time of
368 measurement. Similar sub-categories were defined for grasslands (Supplementary Table 3).

369 We tested the validity of our approach by comparing our binary management
370 classification to a more complex three-level classification According to the latter approach,
371 we considered 'pristine natural' the sites that were pristine or with minimal impacts and
372 'semi-natural' the sites with low-moderate human impacts (these classes were considered
373 jointly in the binary classification as 'natural'). For forests, for instance, we considered as
374 semi-natural the forests that were: (i) unmanaged or with low human impact (e.g. understory
375 grazing) in the 50 years before measurement and (ii) planted forests without any intervention
376 after planting and at least 10 years old (see above). The statistics of this additional test clearly
377 showed that (i) BPE of pristine natural and semi-natural forests did not differ and that (ii) the
378 BPE difference between pristine natural and semi-natural forests was considerably lower than

379 the difference between semi-natural and managed forests (Supplementary Fig. 4,
380 Supplementary Table 11). This confirmed that our standard binary classification is sound and
381 that our key result about the impact of management on BPE is robust. In addition, this
382 exercise revealed that the introduction of more levels in the management classification would
383 not be advantageous, but rather would make the entire statistical analysis more complex and
384 less robust. This was evident for grasslands, for which the three-level classification did not
385 alter the BPE pattern but substantially reduced the statistical power because of the smaller
386 sample size and associated higher uncertainties (Supplementary Fig. 4, Supplementary Table
387 11).

388

389 Gap-filling

390 Some of the selected sites lacked BP measurements of minor ecosystem biomass components
391 (e.g. nonvascular plants, understory) or were affected by minor systematic measurement
392 biases (e.g. neglecting litterfall decomposition in tropical forests). These missing BP portions
393 were gap-filled for completeness in analogy to Vicca et al 2012².

394 *Production of reproductive organs in forests.* When missing, this BP component was
395 derived from a relationship between reproductive BP versus aboveground BP² derived from
396 the Global Forest Database¹.

397 *Leaf biomass production in tropical forests.* Estimates of leaf BP in tropical forests are
398 systematically underestimated because of within-canopy decomposition of leaf litter during
399 the collection period. We estimated this missing portion of BP as 12% of total foliage
400 production².

401 *Understory biomass production in forests.* BP due to understory vegetation is
402 significant for boreal forests and thus boreal forests lacking this BP component were not
403 considered in our analysis². However, the contribution of understory BP to total ecosystem BP

404 is more limited for temperate and tropical forests². Thus, we did not discard temperate and
405 tropical forests lacking understory BP but gap-filled this missing BP component as done in
406 previous studies². In particular, understory BP was estimated as a fixed ratio of the forest tree
407 BP: 0.043 for temperate and 0.073 for tropical forests².

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

412 *Shrub biomass production due to stem secondary growth in peatland.* Missing BP due
413 to unaccounted shrub secondary growth (i.e. increase in stem/branch diameter) was estimated
414 to be 29% of the shrub aboveground primary growth (i.e. BP due to current-year leaves and
415 stem/branches) from data for subarctic shrubs²⁹.

416 The gap-filling concerned 31 forests of the 96 golden sites and 17 sites (14 forests, two
417 tundra and one peatland) of the additional 35 natural sites. For 69% of the cases, the gap-filled
418 BP differed by less than 5% than the original BP; for 13% of the cases the gap-filled and
419 original BP differed by 5-10%, whereas for 17% of the cases this difference was 10-15%.
420 Herbivory was not taken into account because it was negligible (e.g. for forests²) or because
421 BP measurements were from experiments that excluded large herbivores (e.g. for all
422 grasslands examined).

423 The gap-filling procedure avoided small secondary biases in the analysis but did not
424 alter the primary results (Supplementary Table 13). Overall, original BPE of managed and
425 natural forests (the ecosystem type most affected by gap-filling) was 0.52 ± 0.03 and $0.39 \pm$
426 0.02 (mean \pm s.e.m.), respectively, which was less than 2% smaller than gap-filled BPE
427 (Supplementary Table 7).

428

429

430 Statistical analysis

431

432 *Analysis overview and dataset*

433 Our study consisted of five analyses, using different sub-sets of our database. (1) First, we
434 analyzed all natural sites (n=75; managed sites were not considered in this analysis) to test
435 whether BPE is driven by natural variation in site fertility. In particular, we tested whether
436 BPE differs among ecosystem types and sites of contrasting fertility. (2) Second, we analyzed
437 the relationship between fertility and management in forests to verify their correlation and
438 disentangle (i) the impact of management on fertility from (ii) the fertility status not related to
439 management. This analysis was performed on 53 managed and natural forests for which BP
440 and GPP were measured during the same period. We focused this analysis only on forests
441 because they are the ecosystem type best represented in our dataset and allow direct
442 comparison with previous studies. (3) Third, the relative importance of fertility, management
443 and N deposition as controllers of BPE was compared to the importance of other possible
444 BPE drivers. This analysis was performed on the same forest dataset considered in the second
445 analysis after disentangling the effect of fertility and management. (4) Fourth, we compared
446 the BPE of key natural and managed ecosystem types (grasslands, forests and croplands) that
447 typically share similar climatic and environmental characteristics and are regularly converted
448 into one another. Only sites with BPE obtained from BP and GPP measured during the same
449 period were used (n=93). (5) Five, we studied the impact of the potential drivers of BPE in all
450 natural ecosystems (n=75; this analysis did not include the managed sites).

451 For the analyses 1 and 5, we considered not only the sites for which BP and GPP were
452 measured during the same period but also sites with BP and GPP measured during different
453 (or only partially overlapping) periods (35 out of the 75 sites) to investigate a large set of

454 ecosystem types (e.g. from forest to tundra) and environmental conditions (e.g. climate from
455 tropical to polar, soil from waterlogged to very dry). For sites without management operations
456 (and mostly at mature-old stage) the temporal mismatch in BP and GPP was less crucial,
457 dampened at several sites by multi-year measurements (we used averages of BP and GPP for
458 multi-year observations) and, most importantly, comparative tests revealed that the results of
459 the analyses did not differ when all sites or only sites with temporal match in BP and GPP
460 were considered (e.g. Supplementary Table 14).

461

462 *Relationship between fertility and management*

463 Site fertility and site management are highly correlated factors that are both potentially crucial
464 for BPE. For this study, we wanted to separate both drivers to test for BPE responses to (1)
465 the fertility status induced by management and (ii) the fertility status unrelated to
466 management. To disentangle both effects, we applied an approach commonly used to deal
467 with multicollinearity³⁰: the observed fertility status was modeled as a function of
468 management and the residuals from this model were used as explanatory variables of BPE
469 (instead of the original fertility status). Hence, the residuals reflect the information on fertility
470 not explained by management, which we termed ‘unexplained natural fertility’. Initially, the
471 model also included N deposition as an additional covariate, but we removed it in the final
472 model as the relationship between N deposition and fertility was weak (see Main text).

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

478

479 Logit $P(\text{fertility}=\text{L}) = \text{intercept}_L + \beta_L \times \text{management}$ (1)

480 Logit $P(\text{fertility}=\text{M}) = \text{intercept}_M + \beta_M \times \text{management}$ (2)

481

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

489

490 *BPE drivers*

491 The relationships between BPE and its potential drivers were explored with three statistical
492 approaches: univariate analysis, multiple linear regressions and Random Forest, which are
493 described below. We used the following predictors: management status, observed natural
494 fertility, climate zone, ecosystem type, growth form (five categorical variables) and N
495 deposition, unexplained natural fertility (the three model residuals described above), soil
496 available water content, annual precipitation and dry months per year (seven continuous
497 variables) (Supplementary Table 2). All analyses were performed with R³¹.

498 *Univariate analysis.* This analysis tested the significance of the relationships between
499 single predictors and BPE. For continuous variables, this was done with single linear
500 regressions, whereas for categorical variables we used one-way ANOVAs with post-hoc
501 Tukey's HSD test. Normality of residuals was tested with Shapiro-Wilks' test and the
502 assumption of homoscedasticity with Levene's test (for ANOVAs) or Breusch-Pagan test (for
503 regressions). For the few cases for which these conditions were not met, data were

504 transformed (e.g. $\log(x)$, $1/x$ or x^2) or treated with alternative methods (Kruskal-Wallis test for
505 non-normality and applications of White method for heteroskedasticity³²).

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

521 *Random Forest.* We used this partitioning method to produce a large ensemble of
522 regression trees considering always our complete BPE dataset but random subsets of predictor
523 variables³³. This means that (in contrast to multiple linear regressions) Random Forest
524 accounts also for non-linear relationships and interactions, and evaluates each predictor
525 variable (even the least important or redundant), providing a ranking of the predictors'
526 importance. However, this analysis does not assign a significance label (contrary to linear
527 regressions analysis). The importance of a given variable is instead indicated by the mean
528 decrease in accuracy (or increase in mean squared error, %IncMSE) of model predictions

529 when the value of that given variable was changed (permuted within the dataset)³³. The more
530 important the variable, the larger the difference between original predictions and new
531 predictions, and the larger the %IncMSE. We used the standard Random Forest algorithm³⁴
532 setting a large number of trees (50000) to obtain stable results.

533

534 *Confounding factors*

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

544

545 *Uncertainty*

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

549
$$s_{BPij} = \frac{(p_{BPi} \times RF_{BPj})}{(l_{BPij})^{0.5}} \quad (3)$$

550 In case BP needed to be gap-filled (see above), the uncertainty of the original BP estimate
551 ($s_{BPij \text{ original}}$) was increased by a factor equivalent to 100% of the gap-filling amount²:

552
$$s_{BPij \text{ gapfilled}} = \left((s_{BPij \text{ original}})^2 + (\text{gapfilling})^2 \right)^{0.5} \quad (4)$$

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

555
$$s_{GPPij} = \frac{(p_{GPPi} \times RF_{GPPj})}{(l_{GPPij})^{0.5}} \quad (5)$$

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

559
$$s_{BPEij} = \left(\left(\frac{s_{BPij}}{BP_{ij}} \right)^2 + \left(\frac{s_{GPPij}}{GPP_{ij}} \right)^2 \right)^{0.5} \quad (6)$$

560 where BP_{ij} and GPP_{ij} are values of BP and GPP, respectively, for site i and method j . Values
561 of RF_{BPj} and RF_{GPPj} were determined following Luyssaert et al 2007¹ and were reported in
562 Supplementary Table 9. For forest ecosystems, values of p_{BPi} and p_{GPPi} were from Luyssaert et
563 al 2007¹, whereas for non-forest ecosystems they were derived from the difference between
564 the ninth and first decile of BP and GPP samples from ca. 20 to 110 sites according to
565 ecosystem type (Supplementary Table 16).

566

567

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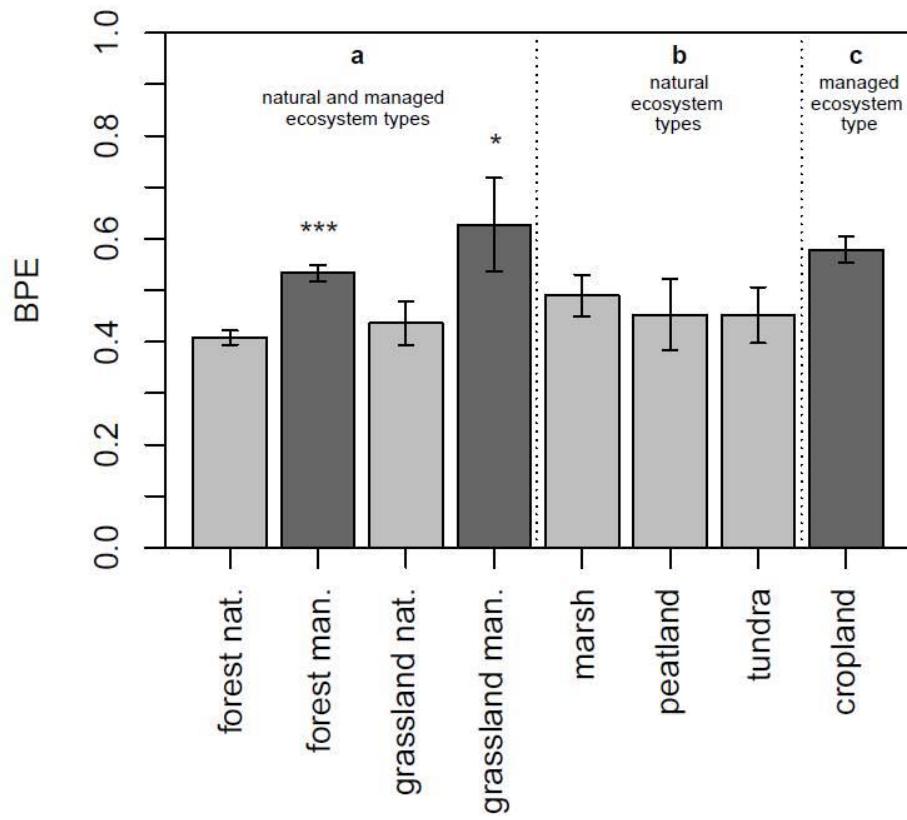
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615

Figure 1

616

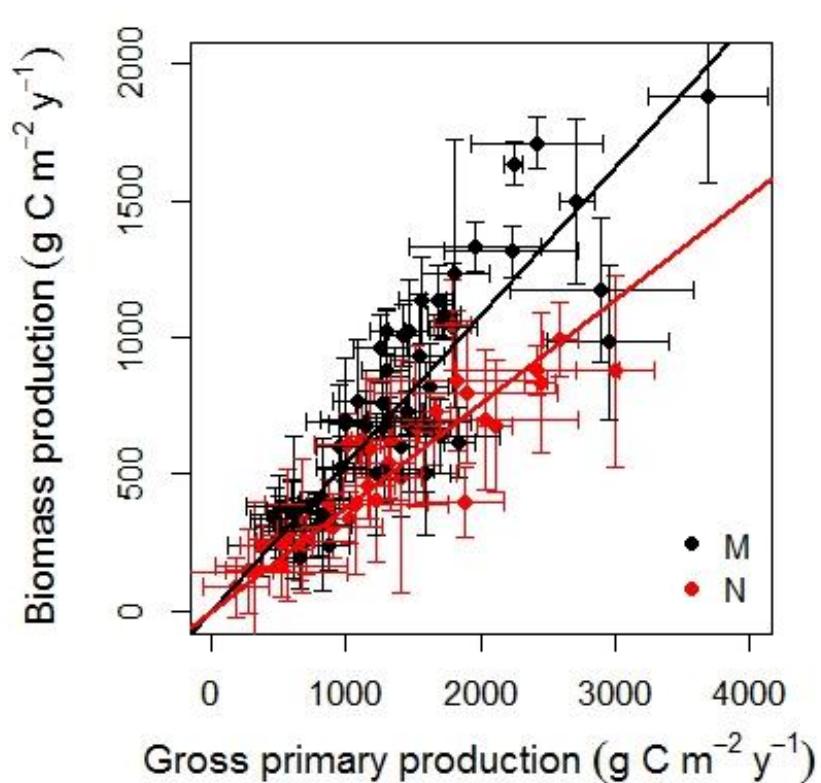
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619

Figure 2



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621

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623

624

Table 1

625

BP-to-GPP ratio	N (n=12)	M (n=19)	p diff N-M
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*

626

627