

1 **Biomass production efficiency controlled by management in temperate and boreal**  
2 **ecosystems**

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33

34 **Summary paragraph**

35 Plants acquire carbon through photosynthesis to sustain biomass production, autotrophic  
36 respiration, and production of non-structural compounds for multiple purposes<sup>1</sup>. The fraction  
37 of photosynthetic production used for biomass production, the biomass production  
38 efficiency<sup>2</sup>, 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 fertility<sup>2</sup>. 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.

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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)<sup>2</sup>. 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 compounds<sup>1</sup>.

59 Current knowledge about BPE is mainly derived from research on forests. Earlier work  
60 reported BPE to be conservative across forests<sup>3</sup>, whereas more recent syntheses suggest high  
61 inter-site variability<sup>2,4</sup>. The variation in BPE was first attributed to vegetation properties  
62 (forest age) and climate variables<sup>4</sup>. 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 driver<sup>2</sup>.

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<sup>2,5</sup>, management can indirectly affect BPE through effects on site fertility and  
76 related belowground dynamics<sup>2</sup>. 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  $0.46\pm 0.01$  (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

109 analysis confirmed that management was a significant explanatory variable for site fertility  
110 (likelihood ratio test of models with and without management as covariate: chi-square=17.33,  
111  $p=0.00017$ ), whereas the relationship between N deposition and fertility was weak (likelihood  
112 ratio test: chi-square=4.80,  $p=0.091$ ). This led us to model fertility as a function of  
113 management (taking into account that the fertility status was the result of both the impact of  
114 management operations on soil nutrient availability and the management choice of which  
115 land, e.g. high or low fertility, to manage) and to obtain model residuals for each site  
116 representing the ‘fertility status not explained by management’ and defined hereafter as  
117 ‘unexplained natural fertility’ (Methods). (3) Once the effect of fertility and management were  
118 disentangled, we evaluated their relative importance as controllers of BPE and compared them  
119 to other possible BPE drivers (e.g. vegetation and environmental characteristics, N  
120 deposition) within the forest dataset. This analysis revealed that management was the key  
121 determinant of the differences in BPE among forests, N deposition was the second most  
122 important driver, and the unexplained natural fertility was insignificant (Supplementary Table  
123 5, Supplementary Fig. 3). The analysis also showed that stand age had a significant (negative)  
124 impact on BPE which however became negligible when compared to the effect of  
125 management and N deposition (Supplementary Table 6). (4) We compared the BPE of key  
126 natural and managed ecosystem types (grasslands, forests and croplands) that typically share  
127 similar environmental characteristics and are regularly converted into one another, and  
128 observed that the BPE of managed sites was substantially greater than the BPE of natural sites  
129 (Figure 1, Figure 2; Supplementary Table 7). (5) Last, we studied the impact of the potential  
130 drivers of BPE on all natural ecosystems and found that BPE of natural unmanaged sites was  
131 independent not only of the observed site fertility (see above point 1) but also of N deposition  
132 and largely independent of all the vegetation and environmental drivers examined  
133 (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 uptake<sup>2</sup>. Our revised  
142 hypothesis relies on the fact that adaptation processes in natural ecosystems<sup>6</sup> 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 static<sup>7</sup> 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-analyses<sup>8</sup> 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 known<sup>9</sup>. Similarly, thinning can negatively affect the standing crop of mycorrhizal fungi<sup>10</sup> and  
155 ectomycorrhizal metabolic activity<sup>11,12</sup>, 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 ( $R_a$ ), thus lower  $R_a$ -to-GPP ratio<sup>2</sup>. However, as previous  
158 research does not support this hypothesis<sup>3,8</sup> and the variability of the  $R_a$ -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 processes<sup>13</sup>) 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 ecosystems<sup>14</sup>. 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<sup>3,4</sup> and provides important constraints for the  
182 global models that simulate high variability in BPE or NPP-to-GPP ratio.



183 Finally, our findings have practical applications, particularly for Europe and North  
184 America. (i) The quantification of BPE for managed ecosystems can improve yield  
185 simulations by models (e.g. timber in forests, grains in crops), particularly for algorithms that  
186 derive BP as a proportion of GPP<sup>15,16</sup>. (ii) The land surface component of Earth system  
187 models currently does not take into account differences between natural and managed  
188 ecosystems which might introduce biases in BP projections. In fact, a case study based on the  
189 model ORCHIDEE<sup>17</sup> showed that taking into account a BPE difference of 8% between natural  
190 and managed ecosystems resulted in a 24% increment in BP for Europe (Supplementary  
191 Methods). (iii) Our study indicates new ways to indirectly derive BPE at regional and  
192 continental scales from maps of land use and human management. (iv) While C assimilation  
193 and BP are extensively studied, the ways to maximize BPE are less explored. However,  
194 substantial changes in yield are potentially associated with small changes in BPE. For  
195 instance, for a forest with a GPP of 1500 g C m<sup>-2</sup> y<sup>-1</sup>, an increase of 12% in BPE  
196 (Supplementary Table 7) would enhance BP by 180 g C m<sup>-2</sup> y<sup>-1</sup>, mainly in wood (Table 1).  
197 These examples show that our elucidation of BPE dynamics advances our understanding and  
198 quantification of the biomass production of terrestrial ecosystems.

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## 201 **References**

- 202 1 Luysaert, S. *et al.* CO<sub>2</sub> balance of boreal, temperate, and tropical forests derived from  
203 a global database. *Global Change Biol.* **13**, 2509-2537 (2007).
- 204 2 Vicca, S. *et al.* Fertile forests produce biomass more efficiently. *Ecol. Lett.* **15**, 520-  
205 526 (2012).
- 206 3 Waring, R. H., Landsberg, J. J. & Williams, M. Net primary production of forests: a  
207 constant fraction of gross primary production? *Tree Physiol.* **18**, 129-134 (1998).
- 208 4 DeLucia, E. H., Drake, J. E., Thomas, R. B. & Gonzalez-Meler, M. Forest carbon use  
209 efficiency: is respiration a constant fraction of gross primary production? *Global*  
210 *Change Biol.* **13**, 1157-1167 (2007).
- 211 5 Forrester, D. I. Growth responses to thinning, pruning and fertiliser application in  
212 Eucalyptus plantations: A review of their production ecology and interactions. *For.*  
213 *Ecol. Manage.* **310**, 336-347 (2013).

- 214 6 Aerts, R. & Chapin, F. S., III. in *Advances in Ecological Research* Vol. 30 (eds A. H.  
215 Fittter & D. G. Raffaelli) 1-67 (Academic Press, 2000).
- 216 7 Heinemeyer, A. *et al.* Exploring the "overflow tap" theory: linking forest soil CO<sub>2</sub>  
217 fluxes and individual mycorrhizosphere components to photosynthesis.  
218 *Biogeosciences* **9**, 79-95 (2012).
- 219 8 Litton, C. M., Raich, J. W. & Ryan, M. G. Carbon allocation in forest ecosystems.  
220 *Global Change Biol.* **13**, 2089-2109 (2007).
- 221 9 Treseder, K. K. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and  
222 atmospheric CO<sub>2</sub> in field studies. *New Phytol.* **164**, 347-355 (2004).
- 223 10 Colgan, W., Carey, A. B., Trappe, J. M., Molina, R. & Thysell, D. Diversity and  
224 productivity of hypogeous fungal sporocarps in a variably thinned Douglas-fir forest.  
225 *Can. J. For. Res.* **29**, 1259-1268 (1999).
- 226 11 Buée, M., Vairelles, D. & Garbaye, J. Year-round monitoring of diversity and potential  
227 metabolic activity of the ectomycorrhizal community in a beech (*Fagus silvatica*)  
228 forest subjected to two thinning regimes. *Mycorrhiza* **15**, 235-245 (2005).
- 229 12 Mosca, E., Montecchio, L., Scattolin, L. & Garbaye, J. Enzymatic activities of three  
230 ectomycorrhizal types of *Quercus robur* L. in relation to tree decline and thinning. *Soil*  
231 *Biol. Biochem.* **39**, 2897-2904 (2007).
- 232 13 Magnani, F. *et al.* The human footprint in the carbon cycle of temperate and boreal  
233 forests. *Nature* **447**, 848-850 (2007).
- 234 14 Rocha, A. V. & Goulden, M. L. Why is marsh productivity so high? New insights from  
235 eddy covariance and biomass measurements in a *Typha* marsh. *Agric. For. Meteorol.*  
236 **149**, 159-168 (2009).
- 237 15 Landsberg, J. J. & Waring, R. H. A generalised model of forest productivity using  
238 simplified concepts of radiation-use efficiency, carbon balance and partitioning. *For.*  
239 *Ecol. Manage.* **95**, 209-228 (1997).
- 240 16 Running, S. W. & Coughlan, J. C. A general-model of forest ecosystem processes for  
241 regional applications. 1. Hydrological balance, canopy gas-exchange and primary  
242 production processes. *Ecol. Model.* **42**, 125-154 (1988).
- 243 17 Krinner, G. *et al.* A dynamic global vegetation model for studies of the coupled  
244 atmosphere-biosphere system. *Glob. Biogeochem. Cycles* **19**, GB1015 (2005).  
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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<sup>18,19</sup>) 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 uncertainty<sup>1</sup>; 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<sup>1,20-27</sup> or modelling<sup>28</sup> (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 observations<sup>25</sup>, whereas simulated values were used for the rest of the world<sup>22,23</sup>.

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 2012<sup>2</sup>.

394 *Production of reproductive organs in forests.* When missing, this BP component was  
395 derived from a relationship between reproductive BP versus aboveground BP<sup>2</sup> derived from  
396 the Global Forest Database<sup>1</sup>.

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 production<sup>2</sup>.

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 analysis<sup>2</sup>. However, the contribution of understory BP to total ecosystem BP

404 is more limited for temperate and tropical forests<sup>2</sup>. 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 studies<sup>2</sup>. 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 forests<sup>2</sup>.

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<sup>-1</sup>) and mesic tundra (0.42 years<sup>-1</sup>) 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 shrubs<sup>29</sup>.

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 forests<sup>2</sup>) 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  $0.52 \pm 0.03$  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 multicollinearity<sup>30</sup>: 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’<sup>30</sup>) 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  $\text{Logit } P(\text{fertility}=\text{L})=\text{intercept}_L + \beta_L \times \text{management} \text{ (1)}$

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

481

482 where  $\text{intercept}_L$  and  $\text{intercept}_M$  were -2.01 and -0.511, respectively, and  $\beta_L$  and  $\beta_M$  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 R<sup>31</sup>.

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 heteroskedasticity<sup>32</sup>).

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 variables<sup>33</sup>. 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)<sup>33</sup>. 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 algorithm<sup>34</sup>  
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 ( $l_{BPij}$ )<sup>1</sup>:

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

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 amount<sup>2</sup>:

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

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  $s_{BPij}$ :

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

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:

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

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 2007<sup>1</sup> and were reported in  
 562 Supplementary Table 9. For forest ecosystems, values of  $p_{BPi}$  and  $p_{GPPi}$  were from Luyssaert et  
 563 al 2007<sup>1</sup>, 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

## 568 **References only in Methods**

- 569 18 Aber, J. D., Melillo, J. M., Nadelhoffer, K. J., McClaugherty, C. A. & Pastor, J. Fine  
 570 roots turnover in forest ecosystems in relation to quantity and form of nitrogen  
 571 availability- a comparison of 2 methods. *Oecologia* **66**, 317-321 (1985).  
 572 19 Baret, F., Olioso, A. & Luciani, J. L. Root biomass fraction as a function of growth  
 573 degree days in wheat. *Plant Soil* **140**, 137-144 (1992).  
 574 20 Batjes, N. H. *ISRIC-WISE global data set of derived soil properties on a 0.5 by 0.5*  
 575 *degree grid (Version 3.0)*. Vol. Report 2005/08 (ISRIC - World Soil Information,  
 576 Wageningen (with data set), 2005).  
 577 21 Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. Very high  
 578 resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**,  
 579 1965-1978 (2005).  
 580 22 Dentener, F. J. *Global maps of atmospheric nitrogen deposition, 1860, 1993, and*  
 581 *2050*. (Data set. Available on-line [<http://www.daac.ornl.gov>] from Oak Ridge  
 582 National Laboratory Distributed Active Archive Center, 2006).  
 583 23 Galloway, J. N. *et al.* Nitrogen cycles: past, present, and future. *Biogeochemistry* **70**,  
 584 153-226 (2004).



585 24 Holland, E. A., Braswell, B. H., Sulzman, J. & Lamarque, J. F. Nitrogen deposition  
586 onto the United States and western Europe: Synthesis of observations and models.  
587 *Ecol. Appl.* **15**, 38-57 (2005).

588 25 Holland, E. A., Braswell, B. H., Sulzman, J. M. & Lamarque, J. F. *Nitrogen deposition*  
589 *onto the United States and Western Europe*. (Data set. Available on-line  
590 [<http://www.daac.ornl.gov>] from Oak Ridge National Laboratory Distributed Active  
591 Archive Center, 2005).

592 26 Harris, I., Jones, P. D., Osborn, T. J. & Lister, D. H. Updated high-resolution grids of  
593 monthly climatic observations - the CRU TS3.10 Dataset. *Int. J. Climatol.* **34**, 623-642  
594 (2014).

595 27 Jones, P. D. & Harris, I. *CRU TS3.10: Climatic Research Unit (CRU) Time-Series (TS)*  
596 *version 3.10 of high resolution gridded data of month-by-month variation in climate*  
597 *(Jan. 1901 - Dec. 2009)*. University of East Anglia Climatic Research Unit. (NCAS  
598 British Atmospheric Data Centre, 2013).

599 28 Schaap, M. G., Leij, F. J. & van Genuchten, M. T. ROSETTA: a computer program for  
600 estimating soil hydraulic parameters with hierarchical pedotransfer functions. *J.*  
601 *Hydrol.* **251**, 163-176 (2001).

602 29 Campioli, M., Leblans, N. & Michelsen, A. Stem secondary growth of tundra shrubs:  
603 impact of environmental factors and relationships with apical growth. *Arct. Antarct.*  
604 *Alp. Res.* **44**, 16-25 (2012).

605 30 Agresti, A. *An Introduction to Categorical Data Analysis*. (John Wiley & Sons, Inc.,  
606 2002).

607 31 Team, R. D. C. *R: A language and environment for statistical computing*. (R  
608 Foundation for Statistical Computing, 2013).

609 32 Zeileis, A. Object-oriented computation of sandwich estimators. *J. Stat. Softw.* **16**, 9  
610 (2006).

611 33 Breiman, L. Random forests. *Mach. Learn.* **45**, 5-32 (2001).

612 34 Liaw, A. & Wiener, M. Classification and regression by Random Forest. *R news* **2**, 5  
613 (2002).

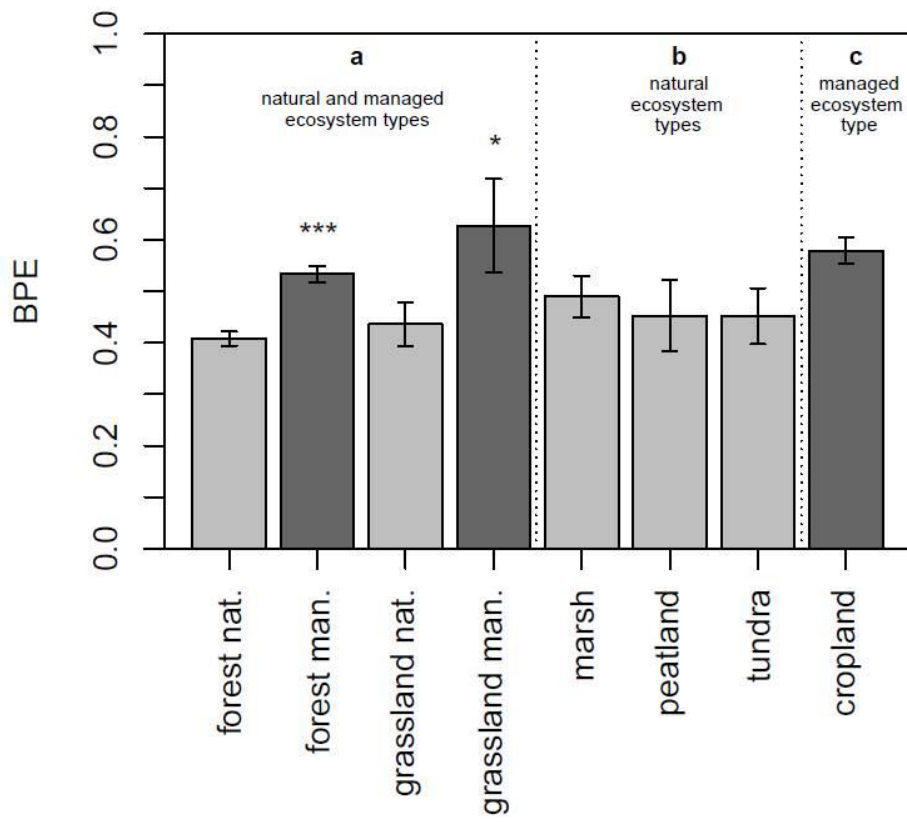
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Figure 1

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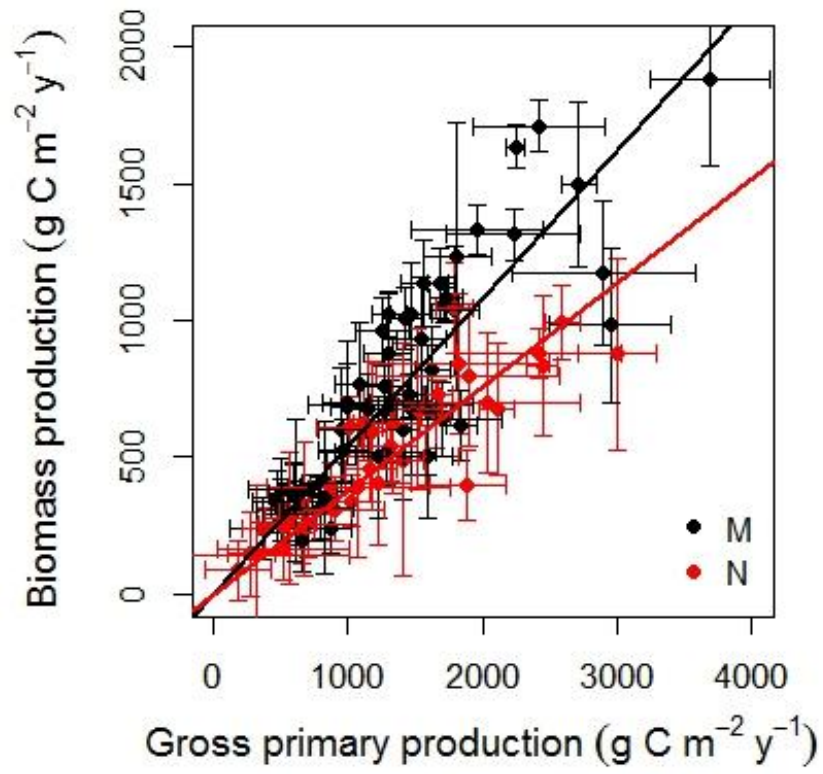
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Figure 2

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622

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