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Spatial variability and controls over biomass stocks, carbon fluxes, and resource-use efficiencies across forest ecosystems

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1   **Spatial variability and controls over biomass stocks, carbon fluxes, and**  
2   **resource-use efficiencies across forest ecosystems**

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20   **Key message:** Stand age, water availability and the length of the warm period are the  
21   most influencing controls of forest structure, functioning and efficiency.

22   **Author contribution:** MFM, SV, IAJ and JP conceived the paper; MFM performed the  
23   analyses and wrote the paper; all authors contributed substantially to discussions and  
24   revisions.

25   **Conflict of interest:** The authors declare that they have no conflict of interest.

26

27    **Abstract**

28

29    We aimed to discern the distribution and controls of plant biomass, carbon fluxes, and resource-  
30    use efficiencies of forest ecosystems ranging from boreal to tropical forests. We analysed a global  
31    forest database containing estimates of stand biomass and carbon fluxes (400 and 111 sites,  
32    respectively) from which we calculated resource-use efficiencies (biomass production, carbon  
33    sequestration, light, and water-use efficiencies). We used the WorldClim climatic database and  
34    remote sensing data derived from the Moderate Resolution Imaging Spectroradiometer to analyse  
35    climatic controls of ecosystem functioning. The influences of forest type, stand age, management,  
36    and nitrogen deposition were also explored. Tropical forests exhibited the largest gross carbon  
37    fluxes (photosynthesis and ecosystem respiration), but rather low net ecosystem production, which  
38    peaks in temperate forests. Stand age, water availability, and length of the warm period were the  
39    main factors controlling forest structure (biomass) and functionality (carbon fluxes and efficiencies).  
40    The interaction between temperature and precipitation was the main climatic driver of gross  
41    primary production and ecosystem respiration. The mean resource-use efficiency varied little  
42    among biomes. The spatial variability of biomass stocks and their distribution among ecosystem  
43    compartments were strongly correlated with the variability in carbon fluxes, and both were strongly  
44    controlled by climate (water availability, temperature) and stand characteristics (age, type of leaf).  
45    Gross primary production and ecosystem respiration were strongly correlated with mean annual  
46    temperature and precipitation only when precipitation and temperature were not limiting factors.  
47    Finally, our results suggest a global convergence in mean resource-use efficiencies.

48

49    **Keywords:** Carbon cycle, budget, partitioning, allocation, climate, LUE, WUE, nitrogen deposition

50 **Commonly used abbreviations:**

51 Biomass and carbon-flux variables

52 LAI: leaf area index [ $\text{m}^2 \text{ m}^{-2}$ ]

53 SLA: specific leaf area [ $\text{m}^2 \text{ kg}^{-1}$ ]

54 GPP: gross primary production [ $\text{gC m}^{-2} \text{ year}^{-1}$ ]

55 Re: ecosystem respiration [ $\text{gC m}^{-2} \text{ year}^{-1}$ ]

56 NEP: net ecosystem production [ $\text{gC m}^{-2} \text{ year}^{-1}$ ]

57 TBP: total biomass production [ $\text{gC m}^{-2} \text{ year}^{-1}$ ]

58 ABP: aboveground biomass production [ $\text{gC m}^{-2} \text{ year}^{-1}$ ]

59 FNPP: foliage net primary production [ $\text{gC m}^{-2} \text{ year}^{-1}$ ]

60 WNPP: wood net primary production [ $\text{gC m}^{-2} \text{ year}^{-1}$ ]

61 BBP: belowground biomass production [ $\text{gC m}^{-2} \text{ year}^{-1}$ ]

62 *ABP%: ABP to GPP ratio [%]*

63 *FNPP%: FNPP to GPP ratio [%]*

64 *WNPP%: WNPP to GPP ratio [%]*

65 *BBP%: BBP to GPP ratio [%]*

66 Efficiency variables

67 CUEe: carbon use efficiency at the ecosystemic level [%]

68 BPE: biomass production efficiency [%]

69 LUE: light-use efficiency [ $\text{gC MJ}^{-1}$ ]

70 LUE%<sub>APAR</sub>: light-use efficiency relative to absorbed PAR [%]

71 LUE%<sub>PAR</sub>: light-use efficiency relative to incident PAR [%]

72 PAR: photosynthetically active radiation [ $\text{MJ m}^{-2}$ ]

73 LUE%<sub>TRad</sub>: light-use efficiency relative to total incident radiation [%]

74 WUE: water-use efficiency [ $\text{gC L}^{-1}$ ]

75 Climatic variables

76 AET: actual evapotranspiration [ $\text{mm year}^{-1}$ ]

77 PET: potential evapotranspiration [ $\text{mm year}^{-1}$ ]

- 78 WD: water deficit [%]
- 79 MAT: mean annual temperature [ $^{\circ}$ C]
- 80 MAP: mean annual precipitation [mm year $^{-1}$ ]

81 **1. Introduction**

82 The increasing atmospheric CO<sub>2</sub> concentration and its influence on global climate (IPCC 2007)  
83 highlight the necessity to better understand the mechanisms driving the global carbon cycle. Forest  
84 ecosystems sequester and store large amounts of carbon, both as living biomass and as dead  
85 organic matter (Dixon et al. 1994). Understanding how these ecosystems are structured and how  
86 they function is therefore of paramount importance for improving our knowledge of the global  
87 carbon cycle and for predicting future climate.

88 Previous studies (Margalef 1974; Dixon et al. 1994; Malhi et al. 1999; Gower et al. 2001; Litton et  
89 al. 2007; Luysaert et al. 2007; Keith et al. 2009; Pan et al. 2011) have reported estimates of the  
90 stocks and distribution of biomass among different ecosystemic compartments, carbon fluxes, or  
91 resource-use efficiencies for different regions and taxa, but most of the combined analyses of  
92 biomass distributions, carbon fluxes and resource-use efficiencies were based on limited subsets  
93 of climate space. Continuous efforts of the research community have rapidly increased data  
94 availability, and following methodological harmonisation has provided these data to be compared  
95 more easily.

96 Despite extensive literature on controls of resource-use efficiencies (Garbulsky et al., 2010; Gu et  
97 al., 2002; Jenkins et al., 2007; Landsberg and Waring, 1997; Wang et al., 2003 for light or radiation  
98 use efficiency and Field et al. 1983; Huxman et al. 2004; Yu et al. 2008; Troch et al. 2009; Lu and  
99 Zhuang 2010; Peñuelas et al. 2011 for water- or precipitation-use efficiency), differences in  
100 resource-use efficiency among biomes or forest types is seldom explicitly reported (but see Goetz  
101 and Prince, 1999 for LUE and Yu et al., 2008 for WUE), or the available data are insufficient for  
102 generalising the results to the entire biome or forest type under study. In this study, we will  
103 consider the resource-use efficiency for light (LUE), water (WUE), biomass production (BPE) and  
104 short term carbon sequestration at the ecosystemic level (CUEe).

105 Studies of climatic control concerning forest production or functioning have frequently tested the  
106 influence of temperature, precipitation, drought indices, or radiation (Kato and Tang, 2008; Law et

107 al., 2002; Luyssaert et al., 2007; Magnani et al., 2007; Valentini et al., 2000), although some other  
108 variables such as thermal amplitude, seasonality of precipitation, and actual or potential  
109 evapotranspiration may be key determinants of forest functioning (Garbulsky et al. 2010). In  
110 addition, the relative contributions to ecosystem structure and functioning of climate and forest  
111 characteristics such as stand age (Goulden et al., 2011; Magnani et al., 2007; Vicca et al., 2012),  
112 management (Luyssaert et al. 2007; Vicca et al. 2012), or nitrogen deposition (De Vries et al.,  
113 2009; Luyssaert et al., 2010; Magnani et al., 2007) are still debated.

114 In this study, we have updated a global database (Luyssaert et al. 2007) of forest carbon pools and  
115 fluxes and have extended this database with 45 new forests and data up to 2010, remote-sensing  
116 observations of actual evapotranspiration (AET) and the absorbed fraction of photosynthetically  
117 active radiation (fPAR) to calculate water-use and light-use efficiencies (WUE, LUE). Our aim was  
118 to update the analysis done by (Luyssaert et al. 2007) and to extend it with: i) an accurate and  
119 detailed description of the biomass stocks, annual carbon fluxes, and resource-use efficiencies of  
120 forest ecosystems in different biomes on a global scale based on field and remote-sensing data,  
121 and ii) a determination of the main drivers of the spatial variability in biomass stocks and in their  
122 distribution among ecosystem compartments, the annual carbon fluxes, and the resource-use  
123 efficiencies.

## 124 **2. Materials and Methods**

### 125 *2.1. Collection and selection of data*

#### 126 *2.1.1 Global forest database*

127 To characterise forest ecosystems, we used a publicly available database of global forests  
128 (Luyssaert et al. 2007). This database contains measurements, and in some cases their  
129 uncertainties, for several structural, functional, and bioclimatic characteristics and a compilation of  
130 simulated data such as, for example, nitrogen deposition for 558 forests around the world. To  
131 characterise forest ecosystems, we extracted from this database, for each forest, the following

132 variables (whenever available): i) maximum LAI, ii) stand biomass of living trees, comprising  
133 estimates of aboveground biomass (typically distinguishing between woody and foliar biomass)  
134 and of fine and coarse roots, iii) mean annual carbon fluxes, comprising estimates of GPP, Re,  
135 NEP (derived from eddy covariance towers), TBP, aboveground and belowground biomass  
136 production and NPP of wood and leaves, and iv) APAR (absorbed photosynthetically active  
137 radiation) used to calculate LUE (GPP:APAR; see section 2.1.4).

138 We also extracted several variables to use as predictors of the stand characteristics: i) nitrogen  
139 deposition derived from interpolated gridded maps based on ground observations (Holland et al.,  
140 2005) and model simulations (Galloway et al. 2004), ii) stand age, iii) leaf habit (evergreen or  
141 deciduous) and type (needleleaved or broadleaved), iv) management (managed, unmanaged,  
142 disturbed), and v) biome (boreal, temperate, Mediterranean, and tropical). The methodologies used  
143 to estimate all the variables within the database were reported by (Luyssaert et al. 2007). We  
144 selected these predictor variables since they have been previously suggested to influence carbon  
145 balance and functioning in terrestrial ecosystems (De Vries et al., 2009; Luyssaert et al., 2007;  
146 Janssens et al., 2010; Magnani et al., 2007; Peñuelas et al., 2012; Vicca et al., 2012).

#### 147 2.1.2 Geographical scale and forest types

148 All continents and biomes were represented in our database and analyses, but the available  
149 forests were distributed mostly around Europe and North America (Fig. S1 and Fig. S2 in  
150 Supporting Information), containing forests belonging to four different biomes (boreal [N=102],  
151 temperate [N=252], Mediterranean [N=11], and tropical [N=35] from which 10 were semi-arid  
152 forests and 25 were humid). Boreal and especially temperate forests were well represented in our  
153 database, but tropical and especially Mediterranean forests were underrepresented. The southern  
154 hemisphere was also poorly represented. The database contained evergreen, deciduous,  
155 needleleaved, broadleaved, and mixed (broadleaved-needleleaved) forests. Both leaf type and  
156 habit were well represented, but mixed forests were clearly in a minority.

157 2.1.3 *WorldClim database*

158 We used the WorldClim database (Hijmans et al. 2005) because, i) it has a high spatial resolution  
159 (30 arc seconds ~ 1 km at the equator), ii) it contains robust monthly climatic data derived from  
160 long time series (from 1950 to 2000), and iii) although only data for temperature and precipitation  
161 are available, the dataset provides several bioclimatic variables such as annual thermal amplitude  
162 or seasonality of temperature and precipitation.

163 2.1.4 *MODIS time series*

164 We downloaded the evapotranspiration time series (MOD16A2) from MODIS (Moderate Resolution  
165 Imaging Spectroradiometer) for the period between January 1, 2000 and December 27, 2009 to  
166 obtain climatic surrogates of potential and actual evapotranspiration (PET and AET respectively,  
167 Mu et al. 2007) to use them as climatic predictors and to calculate WUE (GPP divided by AET).  
168 The resolution of the data was 9 km<sup>2</sup> around the central coordinates of the forest. We selected  
169 such a coarse resolution because of the poor resolution of the coordinates provided by the  
170 database.

171 To calculate LUE relative to total PAR (GPP:PAR), we downloaded the fPAR (absorbed fraction of  
172 PAR) time series (MOD15A2) from MODIS (Fritsch et al. 2012) for the period between February  
173 18, 2000 and December 27, 2011 with a resolution of 9 km<sup>2</sup> around the central coordinates of the  
174 forest. Once we calculated the average fPAR for each forest during the entire time series, we  
175 calculated total PAR using the following equation: APAR=fPAR\*PAR, using APAR from the global  
176 forest database (see above).

177 2.2. *Data analyses*

178 2.2.1 *Studied forest variables*

179 To describe the characteristics and analyse the functioning of forest ecosystems, we separated the  
180 variables under study into three groups: i) stand biomass, ii) annual carbon flux, and iii) resource-

181 use efficiency. The biomass variables were total, aboveground, belowground (coarse + fine roots),  
182 woody (trunk + branches), and foliar biomass. We also included the maximum LAI, a surrogate of  
183 SLA (maximum LAI · foliar biomass<sup>-1</sup>), and the percentage of foliar, woody, and belowground  
184 biomass relative to total biomass. The variables of carbon flux were GPP, TBP, aboveground,  
185 belowground, woody and foliar biomass production (~NPP), Re, NEP, and the percentage of GPP  
186 partitioned into aboveground (ABP%), belowground (BBP%), woody (WNPP%), and foliar NPP  
187 (FNPP%).

188 Finally, the variables of resource-use efficiency were i) carbon-use efficiency at the ecosystemic  
189 level (CUEe), defined as the percentage of NEP to GPP, ii) biomass production efficiency  
190 (TBP:GPP, see Vicca et al., 2012) in percentage (BPE), iii) light-use efficiency (LUE), as the ratio  
191 of GPP to APAR and, iv) water-use efficiency (WUE), as the ratio of GPP to AET. We additionally  
192 calculated LUE expressed as the percentage of the energy converted into organic matter (glucose)  
193 relative to the amount received as APAR, PAR, and total incident radiation, considering that: i) 1 g  
194 of glucose equals 4.1 kcal (Margalef 1974), ii) APAR equals PAR\*fPAR, and iii) PAR represents  
195 45% of the total incident radiation.

196 *2.2.2 Climatic predictors*

197 We extracted mean monthly and annual values for temperature (MAT) and precipitation (MAP)  
198 from the WorldClim database. We also extracted two key bioclimatic variables: annual thermal  
199 amplitude (mean maximum minus mean minimum temperature for the year, which provides  
200 information not only about the latitude of the forest but also about its continentality and elevation)  
201 and seasonality of precipitation (measured as the coefficient of variation of precipitation among  
202 months), which provides information about seasonal differences in the amount of precipitation.

203 We calculated the percentage of water deficit (WD) as an indicator of the intensity of water stress  
204 that the forests must tolerate. We calculated it from MODIS data as a percentage (WD = (1 –  
205 [AET/PET])\*100) rather than as an absolute value (Stephenson 1998) due to the large climatic

206 gradient included in our data that might lead to different sensitivities of the biological variables to  
207 absolute values of water deficit in forests from different biomes (e.g. a change of  $50 \text{ mm}^{-1} \text{ year}^{-1}$  in  
208 a boreal forest with a MAP =  $300 \text{ mm year}^{-1}$  may have a greater influence than in a tropical forest  
209 with MAP =  $2500 \text{ mm year}^{-1}$ ). We also calculated the length of the warm period, considered as the  
210 number of months whose mean temperature was above  $5 \text{ }^{\circ}\text{C}$ . We then extracted mean  
211 temperature, precipitation, potential and actual evapotranspiration, and water deficit during the  
212 warm period.

213 Summarising, we used 13 climatic predictor variables: PET, AET, WD, MAT, MAP (these five  
214 calculated both on an annual basis and for the warm period only), length of the warm period,  
215 annual thermal amplitude, and seasonality of precipitation. Correlations among the climatic  
216 variables are shown in Table S1, Supporting information.

217 *2.2.3 Statistical analyses*

218 To describe forest ecosystems, we first computed the averages of biomass, carbon flux and  
219 efficiency variables grouping forests according to biome and leaf type. As data were usually not  
220 normally distributed, we opted to perform bootstrapped ( $n=1000$ ) weighted means and to use the  
221 bias-corrected and accelerated 95% confidence intervals (Efron 1987) to test for differences  
222 between groups. We weighted cases according to the inverse of the uncertainty, except for  
223 biomass variables for which uncertainty was not reported in the database. We subsequently  
224 explored the possible relationships among different variables of biomass and flux via Pearson  
225 correlation analysis. We correlated the same dependent variable up to 10 times, so we controlled  
226 the rate of false discovery with Bonferroni corrections.

227 We performed stepwise forward-regression models to correlate the variables of biomass, carbon  
228 flux, and resource-use efficiency with climate, management, leaf habit and type, stand age, and  
229 nitrogen deposition. Predictor covariates were entered twice in the models, without transformation

230 and transformed into the natural logarithm, to check for possible nonlinearities. We excluded the  
231 variables from the models when presenting high collinearity (Variance Inflation Factor [VIF] > 5).

232 Because controls of GPP, Re, and NEP are of paramount importance in the carbon balance of  
233 ecosystems, we closely examined the relationships of these three variables of carbon flux with  
234 MAT and MAP. We thus classified forests according to MAT and MAP, defining thresholds based  
235 on the median of the distribution of our data. Forests with  $\text{MAP} \geq 827 \text{ mm year}^{-1}$  were considered  
236 wet forests, and forests with  $\text{MAP} < 827 \text{ mm year}^{-1}$  were classified as *dry*. Similarly, forests with  
237  $\text{MAT} \geq 8^\circ\text{C}$  were considered *warm* forests, whereas forests with  $\text{MAT} < 8^\circ\text{C}$  were classified as  
238 *cold*. Hence, forests were classified according to two-factor variables, each with two levels  
239 (wet/dry, warm/cold). This classification allowed us to test whether the relationships of the different  
240 variables of carbon flux with MAT depended on the *wetness* and whether the relationships  
241 between carbon fluxes and MAP depended on the *warmness*. To this end, we constructed  
242 multivariate generalised linear models (MGLM), including the interaction between *wetness* or  
243 *warmness* and MAT or MAP. Significant interactions would indicate changes in the relationships  
244 between carbon fluxes and climate according to *wetness* or *warmness*.

245 Finally, to analyse the direct, the indirect and the total effects of climate and nitrogen deposition on  
246 GPP, Re and NEP, we performed a path analysis using AET, MAT and nitrogen deposition as  
247 exogenous variables and GPP, Re and NEP as endogenous variables. The saturated model  
248 comprised all possible paths between exogenous and endogenous variables, a path from GPP to  
249 Re and a path from GPP and Re to NEP. We achieved the minimum adequate model by deleting,  
250 from the saturated model, those paths that were not found significant.

251 **3. Results**

252 *3.1. Global variation in biomass, carbon fluxes and efficiency*

253 *3.1.1. Characterisation of biomass stocks*

254 According to the bootstrapped 95% confidence intervals (which indicate significant differences  
255 when they do not overlap), the distribution of biomass among compartments revealed large  
256 differences among biomes (Fig.1 and Table S2, Supporting information) despite comprising forests  
257 of similar age, around 80 years old (Factorial ANOVA test: age ~ biome \* leaf type,  $P = 0.95$ ).  
258 Tropical and temperate forests presented the largest amounts of wood, aboveground biomass, and  
259 total-stand biomass, with values above  $10\,000 \text{ gC}\cdot\text{m}^{-2}$ , while Mediterranean broadleaved forests  
260 exhibited the lowest values (Fig. 1 and Table S2, Supporting information). Belowground biomass  
261 was lowest for boreal forests. A statistically significant difference was detected only for boreal  
262 versus temperate forests, although tropical forests also revealed a clear (and borderline significant)  
263 tendency of higher belowground biomass compared to boreal forests (Fig. 1 and Table S2,  
264 Supporting information).

265 The distribution of the biomass stocks among different plant organs also differed among biomes. In  
266 both the boreal and temperate zone, needleleaved forests presented higher percentages of foliar  
267 biomass than broadleaved forests (above 5.5% and below 2.5%, respectively, Table S2,  
268 Supporting information). However, the percentage of biomass represented by wood, about 70% in  
269 most cases, did not differ between biomes or type of leaf. Finally, almost half of the biomass in  
270 Mediterranean broadleaved forests occurred belowground, whereas root biomass did not exceed  
271 25% in all other forest types (Fig. 1 and Table S2, Supporting information).

272 The largest foliar biomass was found in temperate needleleaved and tropical broadleaved forests.  
273 The type of leaf was a crucial determinant of foliar biomass, because needleleaved forests had  
274 about 2.8 times more foliar biomass than did broadleaved forests across boreal and temperate  
275 biomes. Maximum LAI, however, did not significantly differ between leaf types within a single  
276 biome. The maximum values were found in temperate forests ( $\text{LAI} > 5$ ), whereas the lowest were  
277 reported in Mediterranean broadleaved forests ( $\text{LAI} < 2.7$ , Table S2, Supporting information). In  
278 broadleaved forests, the specific leaf area ( $\text{SLA} = \text{LAI}\cdot\text{foliar biomass}^{-1}$ ), decreased with decreasing  
279 latitude, ranging from about 36 in boreal forests to  $14 \text{ m}^2 \text{ kg}^{-1}$  in the tropics. Needleleaved boreal

280 forests showed the lowest SLA ( $12.6 \pm 1.2 \text{ m}^2 \text{ kg}^{-1}$ , mean  $\pm$  SE) and statistically differed from both  
281 boreal and temperate broadleaved forests (Table S2, Supporting information).

282 *3.1.2. Distribution of carbon fluxes*

283 All carbon fluxes and their partitioning variables revealed significant differences among biomes but  
284 not between needleleaved and broadleaved forests (Figs. 2 and 3 and Table S3, Supporting  
285 information). Tropical forests presented the highest rates for all fluxes, except for NEP (Figs. 2 and  
286 3a); the highest amount of NEP was observed at mid-latitudes (temperate and Mediterranean  
287 forests). Remarkably, tropical forests had rates of FNPP as high as the rates of TBP in boreal  
288 forests (Fig. 3a).

289 Boreal needleleaved forests partitioned about 6% of their carbon uptake (i.e. GPP) into the foliage  
290 compartment (FNPP), whereas temperate and tropical broadleaved forests partitioned almost 12%  
291 of GPP to foliage. Wood NPP ranged between 10% (boreal needleleaved and tropical broadleaved  
292 forests) and 16% (temperate broadleaved) of GPP, while roots received between 8% (tropical  
293 broadleaved) and 18% (temperate broadleaved) of total GPP (Fig. 3b).

294 *3.1.3. Resource-use efficiency of biomes*

295 CUEe followed the same pattern as NEP, being highest for temperate and lowest for tropical  
296 forests (Fig. 2, Table S4, Supporting information). On average, about 20% of GPP was  
297 sequestered (NEP) in temperate-forest ecosystems, whereas only  $3.3 \pm 2.8\%$  of the GPP of  
298 tropical broadleaved forests was actually stored. In contrast, BPE did not significantly differ among  
299 biomes, ranging from  $38 \pm 3.6\%$  to  $54 \pm 4.7\%$  (Table S4, Supporting information).

300 LUE ranged from  $2.0 \pm 0.2$  (in temperate and Mediterranean broadleaved forests) to  $2.6 \pm 0.1 \text{ gC}$   
301  $\text{MJ}^{-1}$  (in temperate needleleaved forests), with the former being significantly lower than the latter.  
302 When transforming this efficiency into the percentage of energy used, we found that forest  
303 ecosystems used between  $8.5 \pm 0.7\%$  and  $11.1 \pm 0.6\%$  of the absorbed light energy, between 5.5

304  $\pm 0.6\%$  and  $7.6 \pm 0.5\%$  of the total incident PAR, and between  $2.5 \pm 0.3\%$  and  $3.4 \pm 0.2\%$  of the  
305 total incident radiation (Table S4, Supporting information). Statistically, WUE did not differ among  
306 forest types due to high variability. On average, WUE ranged from  $2.1 \pm 0.2$  to  $3.1 \pm 0.6$  gC mm<sup>-1</sup> in  
307 Mediterranean broadleaved and needleleaved forests, respectively.

308 *3.2. Correlations with biomass stocks, carbon fluxes, and efficiencies*

309 *3.2.1. Biomass stocks and its distribution among ecosystem compartments*

310 Table 1 shows an overview of the results of the stepwise regression models for biomass stocks,  
311 carbon flux, and efficiency (see Table S5 in Supporting information for a more detailed description).  
312 Stand age, MAP, and the length of the warm period were the most correlated predictors with the  
313 spatial variability and distribution of the different compartments of biomass.

314 LAI and foliar biomass were positively correlated with indicators for water availability. Both were,  
315 respectively, 1.3 and 3 times higher in needleleaved than in broadleaved forests. Also, stand age  
316 and nitrogen revealed a significantly positive relation with LAI, whereas temperature during the  
317 warm period had a negative influence. Despite presenting a negative trend from boreal  
318 broadleaved to tropical broadleaved forests (Table S2, Supporting information), SLA was not  
319 significantly correlated with any of the predictor variables used in this study.

320 Woody, aboveground, belowground, and total biomasses increased with the logarithm of stand  
321 age. Precipitation and the length of the warm period were also positively correlated with these  
322 variables of biomass, whereas mean temperature of the warm period negatively influenced total  
323 and belowground biomass; the latter was also about 1.5 times higher in needleleaved than in  
324 broadleaved forests (Table 1).

325 Younger evergreen forests showed higher proportion of leaf biomass than other forest types,  
326 particularly when seasonality of precipitation, nitrogen deposition, and water deficits were low  
327 (Table 1). The percentage of woody biomass increased with AET and the age of the forest.

328 Interestingly, the percentage of belowground biomass was negatively correlated with precipitation  
329 of the warm period, the opposite of the other variables of biomass. In addition, longer warm  
330 periods, higher age, and the evergreen leaf habit increased the percentage of biomass assigned to  
331 roots.

332 *3.2.2. Correlations with carbon fluxes*

333 On a global scale, most of the fluxes (except NEP) were strongly influenced by climate variables  
334 (Table 1 and Table S5b, Supporting information). GPP was positively correlated with water  
335 availability (precipitation and AET) during the warm period and also by stand age but was  
336 negatively correlated with annual thermal amplitude. Re was correlated by the variables of water  
337 availability and MAT (Table 1), with warm and wet forests presenting the highest rates of  
338 respiration. NEP, on the other hand, did not directly respond to climatic variables but was  
339 significantly correlated with nitrogen deposition and management. We tested whether this effect  
340 was not more prominent in North America and Europe than in the rest of the world, but the models  
341 indicated that the relationship did not vary among continents. The rates of NEP were about twice  
342 as high in managed as compared to unmanaged forests and 2.6 times higher in managed than in  
343 disturbed forests.

344 Comparison of warm versus cold forests and wet versus dry forests (Fig. 4), however, revealed  
345 that the relationships of GPP, Re, and NEP with MAP depended on warmness, whereas the  
346 relationships of GPP, Re, and NEP with MAT depended on wetness (MAP\*Warmness:  $P < 0.0001$ ;  
347 MAT\*Wetness:  $P < 0.001$ ; Fig. 4), and these relationships differed for each carbon flux. Warm  
348 forests revealed a significantly positive relation for both GPP and Re with MAP, both presenting a  
349 slope close to unity, while NEP was not correlated at all. Cold forests, instead, showed a lower  
350 slope for GPP versus MAP (single linear regression: 0.52;  $P < 0.01$ ), Re was not significantly  
351 correlated to MAP (0.17;  $P = 0.34$ ), and NEP revealed a significantly positive relationship with MAP  
352 (0.30;  $P = 0.03$ ). Similarly, wet forests showed a significant positive relationship of GPP and Re  
353 with MAT, whereas NEP was not significantly related to MAT. Dry forests showed a positive

354 relation between GPP and MAT albeit with a lower slope than the wet forests, whereas Re showed  
355 no significant relationship with MAT (Fig. 4). However, NEP was not significantly related to MAT.  
356 Even when excluding the tropical forests (which strongly influenced our regressions, see Fig. 4)  
357 from these analyses, similar patterns were observed (MAP\*Warmness:  $P < 0.05$ ; MAT\*Wetness:  $P$   
358  $< 0.05$  respectively) and remained significant despite presenting less evident changes in the slopes.  
359 With the exclusion of tropical forests, however, GPP presented a higher slope with MAP in cold  
360 forests than in warm forests, and NEP presented a significant relationship with MAT in wet forests  
361 whereas NEP was not longer related with MAP in cold forests.

362 The path analysis relating AET, MAT and nitrogen deposition with GPP, Re and NEP (Fig. 5, Table  
363 2) showed that AET and MAT only affected Re indirectly through their positive relationship with  
364 GPP. Also, nitrogen deposition presented a negative correlation with Re which, in turn, resulted in  
365 a positive and significant correlation with NEP (Table 2) just as the stepwise regression analysis  
366 revealed (Table 1). The relationship between GPP and Re was very tight (Fig. 5) and the  
367 calculated total effects for NEP revealed a greater sensitivity to Re (standardized coefficient for Re  
368 =  $-2.55 \pm 0.05$ ) than to GPP ( $0.26 \pm 0.11$ ) (Table 2).

369 High TBPs were correlated with low water deficit and long warm periods but decreased with  
370 increasing stand age (Table 1). Forests with long warm periods produced more foliage and  
371 aboveground biomass compared to forests with shorter warm periods. Also, aboveground biomass  
372 and wood biomass production were higher in forests presenting low water deficit and high nitrogen  
373 deposition compared to forests with high water deficit and low nitrogen deposition (Table 1).

374 Similarly, forests receiving higher nitrogen deposition assigned higher percentage of carbon to  
375 wood and aboveground biomass (Table 1). The percentage of carbon assigned to roots, on the  
376 other hand, was negatively correlated with precipitation during the warm period (as with the  
377 percentage of belowground biomass, mentioned in section 3.2.1) and by stand age. Finally, the  
378 percentage assigned to foliar NPP was positively correlated with annual thermal amplitude and the  
379 length of the warm period.

380 Forests with higher LAI and aboveground biomasses also had higher rates of GPP (LAI:  $R^2 = 0.14$ ,  
381  $P = 0.001$ ; aboveground biomass:  $R^2 = 0.26$ ;  $P < 0.001$ ). Also, Re was positively correlated with  
382 aboveground biomass ( $R^2 = 0.23$ ;  $P < 0.001$ ), and biomass production was positively correlated  
383 with woody biomass ( $R^2 = 0.62$ ;  $P = 0.004$ ). Other relationships emerged but were not significant  
384 after correction by Bonferroni procedures ( $\alpha = 0.005$ ).

385 *3.2.3. Correlations with forest resource-use efficiency*

386 Stepwise regressions showed that CUEe and WUE were positively correlated with stand age, while  
387 BPE was negatively correlated with stand age (Table 1, Table S5c, Supporting information). In  
388 addition, CUEe was affected by management in the same way as NEP (i.e. CUEe was higher in  
389 managed than in unmanaged forests), and the seasonality of precipitation was negatively  
390 correlated with BPE. LUE and WUE responded differently to temperature: lower values of WUE  
391 were detected in forests with high annual thermal amplitudes (which could also indicate a negative  
392 effect of temperature: see Table S1, Supporting information), whereas LUE decreased with the  
393 temperature of the warm period (although very little variance was explained by the model; Table 1  
394 and Table S5c, Supporting information). Also, WUE was negatively correlated with PET.

395 **4. Discussion**

396 The relationships found in our global analyses mostly agreed with previous meta-analyses or  
397 established ecophysiological principles. However, our analyses also uncovered novel global trends  
398 that deserve thoughtful discussion. We must also point out that, unfortunately, fertility could not be  
399 directly assessed in this paper and therefore, some relationships reported here might change  
400 according to the nutrient status of the forests.

401 *4.1. Forest functioning, characteristics, and endogenous drivers*

402 *4.1.1. Biomass stocks and carbon fluxes*

403 We have confirmed that the largest stocks of biomass are found in temperate and tropical forests  
404 (Fig. 1) (Keith et al., 2009). These forests also have the highest rates of biomass production and  
405 carbon uptake (Figs. 2 and 3a). In contrast, boreal and especially Mediterranean forests have the  
406 lowest stand biomasses. Because boreal forests are strongly limited by temperature and  
407 Mediterranean forests by water availability (Kramer et al. 2000), the low biomass stocks of these  
408 forests may be a consequence of their slow growth or conservative strategies imposed by strong  
409 constraints to growth (Ackerly and Stuart 2009). Our results agree with this hypothesis: indicators  
410 of water availability (MAP, AET, WD) and length of the warm period were the most influential  
411 climatic variables on forest structure and functioning (Table 1).

412 Logically, stand age was paramount in controlling woody, aboveground, and belowground  
413 biomasses, but its influence on foliage was negligible, suggesting the existence of a threshold to  
414 foliar biomass reached at young ages (Ryan et al. 1997; Chen et al. 2007, Table 1, Table S5a,  
415 Supporting information). This positive relationship of age with woody and root biomasses and the  
416 lack of a relationship with foliar biomass is surely the cause of the evident negative effect age has  
417 on the percentage of foliar biomass. Despite the positive relationship of age with root biomass, root  
418 NPP presented a negative response to aging. This result may indicate that the older the forest, the  
419 lower the resources required investing in roots, because the necessity to achieve a robust root  
420 system (strong anchor structure and large provisioning area) might be fulfilled by the progressive  
421 accumulation of root biomass. Furthermore, changes in the ratio fine-to-coarse roots to the  
422 belowground stock might change the belowground productivity as fine roots have different turnover  
423 rates than coarse roots.

424 The growth of some tropical forests is limited by solar radiation (Nemani et al. 2003). According to  
425 the functional equilibrium hypothesis (Poorter et al., 2012), the limitation of light may account for  
426 the high percentage, amount and production of foliar biomass in tropical broadleaved forests (Fig.  
427 1, Fig. 2a, Table S2 and Table S3 in Supporting information). Poorter et al. (2012), however,  
428 suggested that this limitation of light should also lead to high values of SLA more than to high  
429 values of the percentage of foliar biomass at the plant level, but this is exactly opposite to our

430 results at the ecosystem level (Table S2, Supporting information). This issue requires further  
431 examination as other evolutionary issues, such as herbivory, could be involved in SLA variation.  
432 On the other hand, needleleaved forests showed rather low values of SLA and higher amounts and  
433 percentages of foliar biomass, although GPP did not differ between leaf types within biomes. This  
434 observation agrees with the idea that needles photosynthesize less efficiently than broadleaves  
435 (Lusk et al. 2003).

436 The distribution of biomass among compartments is quite similar among forest biomes, with the  
437 exception of the Mediterranean forests, where roots represent ca. 50% of the total biomass  
438 (Pausas 1999). This exception is the result of evolutionary adaptations to withstand summer  
439 droughts or repeated fires by the accumulation of nonstructural carbohydrates in the lignotuber  
440 (Ackerly and Stuart 2009). Our results support this hypothesis; we found that the percentage of  
441 belowground biomass decreased with increasing amounts of precipitation during the warm period  
442 (Table 1 and Table S5a, Supporting information). Belowground biomass (or fraction), however, did  
443 not correlate with belowground biomass production (or carbon partitioning to roots), which may  
444 indicate that this higher amount of root biomass is more likely the result of a progressive  
445 accumulation than of higher carbon partitioning into roots. Because estimates of single-site root  
446 biomass stocks and production are very uncertain (as reported by Robinson [2004], for example),  
447 studies like ours that synthesise data represent a useful approach for acquiring reliable measures  
448 of belowground biomass (assuming that single-site uncertainty is random). However, forest biomes  
449 with few available data (see Fig. 1) may still require caution and further evaluation.

450 The positive relationship between GPP and stand age indicates that assimilation in forests is not  
451 only driven by climatic characteristics, as some models assume, and calls for a renewed attention  
452 from the forest carbon modeling community to the relationships between age and canopy or foliar  
453 characteristics. Despite the higher GPP of tropical forests than temperate forests, NEP is higher in  
454 temperate than in tropical forests. In fact, our data indicate that although tropical forests are most  
455 likely to be sinks of carbon (Stephens et al. 2007; Lewis et al. 2009), the average NEP in our study  
456 is not statistically significantly different from zero (Table S3, Supporting information) (Pan et al.

457 2011). Accordingly, tropical forests showed the lowest CUEe and BPE ratios of all forests (Figs. 2  
458 and 3b), indicating that they are the least efficient in the use of GPP, possibly because of the high  
459 temperatures and water availabilities that enhance both autotrophic and heterotrophic respiration  
460 more than rates of GPP (Fig. 4, Chambers et al., 2004; Kato and Tang, 2008) and/or because of  
461 the low nutrient availability that could enhance the production of root exudates or other  
462 unaccounted for components of NPP (Goulden et al., 2011; Vicca et al., 2012). On the other hand,  
463 our results indicated that spatial variability in NEP was more sensitive to changes in Re than in  
464 GPP (Table 2) which agrees with results from previous studies (Valentini et al. 2000).

465 The decrease of BPE with age was one of the foundations used by Goulden et al. (2011) to  
466 suggest that in boreal forests decreasing nutrient availability with increasing age could enhance  
467 carbon partitioning into the fine-root fraction. Our results support this negative relationship of stand  
468 age with BPE, but stand age also presented a negative relationship with the fraction of GPP  
469 partitioned to root (fine + coarse) biomass and a positive relationship with the amount and  
470 percentage of belowground biomass (Table 1). These results do not necessarily contradict the  
471 hypothesis presented by Goulden et al. (2011), because our data did not differentiate from the fine-  
472 root to the coarse-root fraction. An overall decrease in the production of belowground biomass  
473 could also be possible if an increase in the fine-root fraction is compensated for by a decrease in  
474 the production of coarse-root biomass. Also, Goulden et al. (2011) reported a negative effect of  
475 age on the ratio of NEP to TBP, indicating that old stands approach a steady state. We obtained a  
476 similar pattern for CUEe (as the ratio of NEP to GPP), as efficiency of carbon sequestration  
477 increased with age and tended to reach a steady state with positive values of CUEe (because of a  
478 logarithmic relationship; Table 1 and Table S5c, Supporting information). However, the predicted  
479 confidence intervals of CUEe did not differ from zero.

480 *4.1.2. Light and water-use efficiency*

481 The similar values of LUE and WUE found across biomes (Table S4, Supporting information)  
482 suggest a convergence in the average of these resource-use efficiencies of forest ecosystems on a

483 global scale (Goetz and Prince, 1999; Huxman et al., 2004). On the other hand, the considerable  
484 variability observed within biomes and the lack of LUE data for tropical forests in particular, may  
485 obscure existing trends.

486 Binkley *et al.* (2004) stated that, at the ecosystemic level, an increase in efficiency modulated by  
487 an increase in a resource use could be due to an increased “*return on investment*” (e.g. a canopy  
488 with good hydric conditions would photosynthesise more carbon than another suffering stomatal  
489 closure for the same investment in canopy). Old forests had higher WUEs, possibly due to i) the  
490 positive relationship of stand age with LAI and GPP (given that we calculated  $\text{WUE} = \text{GPP} \cdot \text{AET}^{-1}$ ;  
491 Table 1, Magnani *et al.*, 2007) and ii) an increase in the resources (e.g. water, nutrients) provided  
492 by the root system to the canopy as a result of increasing root biomass with age (Table 1) (Binkley  
493 *et al.* 2004; Ackerly and Stuart 2009). In agreement with Binkley’s hypothesis, we found a  
494 significant relationship between LAI and GPP similar to that reported by other authors (Gower et  
495 al., 2001; Law *et al.*, 2002; Kato and Tang, 2008).

496 **4.2. Exogenous drivers of forest functioning and characteristics**

497 **4.2.1. The role of climate**

498 Our analyses confirm that water availability and the length of the warm period (~temperature) are  
499 paramount for controlling forest structure and functioning (Luyssaert *et al.* 2007; Keith *et al.* 2009).  
500 Only SLA, NEP, ABP%, WNPP%, and CUEe (5 of 26 variables studied) were not related to climate  
501 variables. Carbon pools and fluxes were generally higher in warm and wet forests (Table 1).

502 We have refined the analysis of Luyssaert *et al.* (2007), distinguishing dry from wet and cold from  
503 warm forests, and adding insights into the relationship between NEP and climate. Our results  
504 suggest that the interaction between MAT and MAP is of paramount importance for understanding  
505 the effect of climate on NEP (Fig. 4). The relationships of GPP and Re with MAP in warm forests  
506 are very similar and prevent a relationship between NEP and MAP, because most of the carbon  
507 assimilation is counterbalanced by the ecosystem respiration. In cold forests, however, the effect of

508 MAP on GPP is stronger than the effect of MAP on Re, and consequently NEP is positively  
509 influenced by MAP. These relationships suggest that, on a global scale, Re respond differently  
510 than GPP to the interaction between MAT and MAP, which is reflected by the correlation between  
511 NEP and MAP only in cold forests, where part of the production (GPP) is not respired due to  
512 limitations of temperature.

513 On the other hand, when looking for indirect relationships between climate and carbon fluxes, we  
514 found that Re does not present direct relationships neither with MAT nor with AET. Instead, the  
515 relation of Re with climate goes through the direct relationship with production (GPP, Fig. 5) as  
516 suggested by previous studies (Janssens et al. 2001). We found NEP to be directly correlated with  
517 MAT, but the correlation, although significant, was almost meaningless and was not significant  
518 when accounting for the total effects (Table 2).

519 The positive influence of water deficit during the warm period on WUE (Table 1)(Huxman et al.,  
520 2004; Yu et al., 2008; Troch et al., 2009) suggests an adaptive trait to maximise the efficiency of  
521 water use in those forests growing under water-limited conditions (Aranda et al. 2007; Ackerly and  
522 Stuart 2009). Our results also indicated that forests with lower thermal amplitudes can use water  
523 more efficiently, in terms of gross carbon fixation, than those exposed to wider oscillations in  
524 temperature. This relationship may be explained by several hypotheses: i) in evergreen forests,  
525 extremely cold episodes can provoke massive degradation of chloroplast, which can take up to  
526 eight weeks to recover (Malhi et al., 1999), ii) in warm forests presenting high thermal amplitude,  
527 elevated rates of evapotranspiration caused by extremely warm temperatures at the leaf and  
528 canopy levels can lead to higher photorespiration and thus lower GPP (Malhi et al., 1999), or iii)  
529 because warmer forests tend to have lower thermal amplitudes (Table S1, Supporting information),  
530 the longer periods of photosynthetic activity in warmer forests may enhance carbon uptake,  
531 whereas AET may remain constant on a yearly basis (if AET is limited by precipitation), thereby  
532 yielding higher WUEs. Additionally, lower thermal amplitudes also reduce the risk of damage from  
533 extremely cold or warm events.

534 On the other hand, WUE was negatively related to PET. In dry forests, higher PET creates larger  
535 water-potential gradients between the stomata and the atmosphere, higher rates of  
536 evapotranspiration per unit of carbon gained (lower WUE), and hence stomatal closure by leaf  
537 water depletion, leading to increased foliar temperature which, in addition, increases  
538 photorespiration (Malhi et al., 1999; Yu et al., 2008). Also, high levels of PET lead to high rates of  
539 evapotranspiration in forests without water restrictions (e.g. humid tropical forests), which could  
540 also reduce WUE. Similarly, forests with warmer growing seasons may have lower values of LUE  
541 (Table 1) due to enhanced photorespiration produced at higher temperatures or due to a higher  
542 probability of stomatal closure caused by the high evaporative demand, thereby reducing  
543 photosynthesis per unit of APAR.

544 *4.2.2. The role of management*

545 Previous studies (Shan et al., 2001 and references therein) have suggested that management can  
546 alter the patterns of carbon allocation through an increase in the available resources due to a  
547 relaxation of competition. Shan et al. (2001) reported increases in early volume growth and in the  
548 ratio of shoots to roots after elimination of the understory. Despite the potential effect that  
549 management can have in forest ecosystems, our analyses confer little importance to it. We have  
550 not detected changes in the patterns of carbon allocation, rates of production, or biomass stocks  
551 as a result of management (Table 1). This is maybe partially due to the fact that we used a global  
552 dataset of forests for which each variable had a wide range of variation. Thus, changes in these  
553 variables may depend more on the characteristics of the climate than on management. In the  
554 present study, only NEP and CUEe were directly related to management. Reducing biomass  
555 stocks and lowering competition for light, water, and nutrients seem a key for increasing NEP and  
556 CUEe, although management had no significant effect on carbon uptake or ecosystem respiration.

557 *4.2.3. The role of nitrogen deposition*

558 Nitrogen deposition also had a relevant influence on the functioning of forest ecosystems, as  
559 previously reported by other authors (see De Vries et al., 2009; Janssens et al., 2010; Luyssaert et  
560 al., 2010; Magnani et al., 2007). For example, the increased biomass production and carbon  
561 allocation to wood with increased nitrogen deposition (Table 1) agrees with the paradigm that  
562 partitioning to aboveground production increases with increasing belowground resources (Litton et  
563 al. 2007). Also, higher nitrogen availability allows to maintain higher nitrogen concentrations and  
564 consequently higher photosynthetic capacity per unit of leaf area (Field et al. 1983). We also found  
565 nitrogen deposition to positively influence LAI and NEP (Table 1). This influence may be related to  
566 an increase in the availability of nitrogen for plants, rendering nitrogen a less limiting factor to  
567 growth. Also, the negative influence of nitrogen deposition over the percentage of foliar biomass  
568 (Table 1) may indicate a shift towards more productive leaves when nitrogen is available.  
569 Regarding the effect on NEP, our path analysis revealed that the effect in NEP is, in fact, mediated  
570 by the effect of nitrogen deposition in Re (Fig. 5 and Table 2). In this sense, nitrogen deposition  
571 has also been suggested to reduce heterotrophic respiration (Janssens et al., 2010) by means of:  
572 i) changes in the saprotrophic community towards one more efficient in the use of carbon, which  
573 requires higher nitrogen availability, and ii) abiotic mechanisms of soil organic matter stabilisation,  
574 producing nitrogenous compounds that reduce the decomposability of soil organic matter. The  
575 maximum value of nitrogen deposition found in our forests was  $27.3 \text{ kg ha}^{-1} \text{ year}^{-1}$ ; higher amounts  
576 of nitrogen deposition may have opposite consequences in forest ecosystems (e.g. very high  
577 nitrogen deposition could cause negative impacts on carbon sequestration, De Vries et al., 2009).

578 Hence, this study provides an updated description of the structure, functioning, production, and  
579 resource-use efficiency of forests located in the main forest biomes of our planet. We also indicate  
580 the main controls of these properties, highlighting the paramount role of water availability,  
581 temperature and stand age. The results show a global positive synergic effect of MAP and MAT on  
582 forest production, growth and carbon accumulation. Although climate has globally affects BPE,  
583 LUE, and WUE, mean efficiencies differed very little among biomes, suggesting a global  
584 convergence of resource-use efficiencies across ecosystems.

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725

726

b)

727 **Figure captions**

728 **Figure 1:** Biomass distribution among compartments in different forest types and biomes. It is also  
729 shown the percentage of biomass that each compartment represents in relation to the total  
730 biomass. Letters indicate significant differences among groups at the 0.05 level (see Table S3 in  
731 Supporting information for average values and confidence intervals) followed by the number of  
732 replicates (between brackets). Missing letters indicate that the comparison was not possible due to  
733 the lack of replicates.

734 **Figure 2:** Mean values of carbon exchange between forest ecosystems and the atmosphere for  
735 different biomes. Letters indicate significant differences among groups at the 0.05 level (see Table  
736 S3 in Supporting information for average values and confidence intervals) followed by the number  
737 of replicates between brackets.

738 **Figure 3:** a) Net primary production (NPP) distribution (FNPP, WNPP, BBP) and b) partitioning of  
739 gross primary production (GPP) among compartments (FNPP%, WNPP%, BBP%) in different  
740 forest types and biomes. In graphs a and b, the total heights of the bars represent TBP and BPE,  
741 respectively (only forests with foliar, wood and root measurements available). Letters indicate  
742 significant differences among groups at the 0.05 level (see Table S3 in Supporting information for  
743 average values and confidence intervals) followed by the number of replicates between brackets.  
744 Missing letters indicate that the comparison was not possible due to the lack of replicates.

745 **Figure 4:** Scatter plots showing how mean annual precipitation (MAP) and mean annual  
746 temperature (MAT) are correlated with GPP, Re, and NEP, depending on the climatic  
747 characteristics of the stands (Wet: MAP >827 mm year<sup>-1</sup>; Warm: MAT >8 °C). Only significant  
748 slopes ( $P<0.05$ ) have been drawn. The levels of significance of the interaction MAP\*MAT are also  
749 indicated.

750 **Figure 5:** Resulting diagrams of the path analysis relating climate (AET and MAT) and nitrogen  
751 deposition as exogenous variables with carbon flux variables (GPP, Re and NEP) as endogenous  
752 variables. The “U” represents the non-explained variance of the endogenous variables, the arrows

753 show the standardized coefficients of the path (direct effects) and the boxes of the endogenous  
754 variables show the variability explained ( $R^2$ ). All paths shown are significant and models were  
755 simplified to achieve the Minimum Adequate Model according to AICc.

756

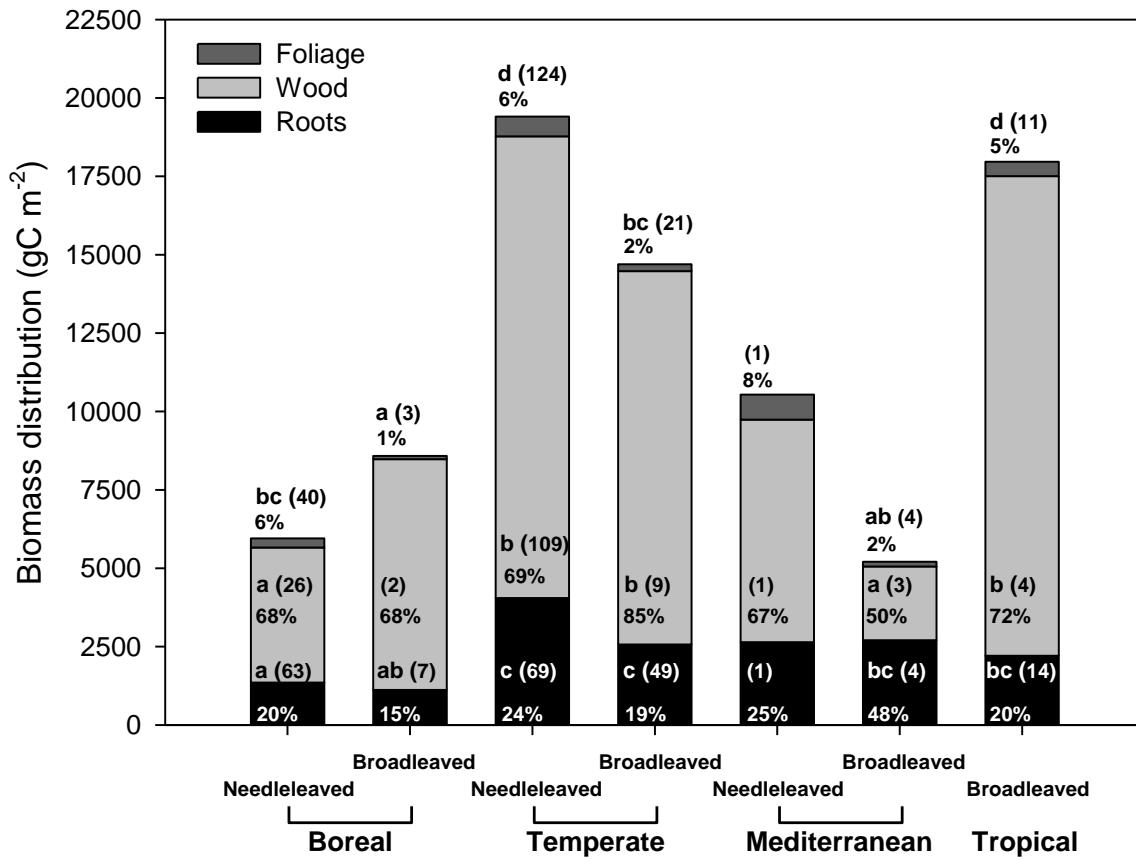
757 **Table captions**

758 **Table 1:** The influence of climatic variables, stand age, leaf habit, leaf type, and management  
759 (MNG) on the biomass, flux, and efficiency variables of the forests. Squares indicate  $\beta$  weights of  
760 the stepwise regression models using a color gradient where red indicates positive, blue indicates  
761 negative, and white indicates no correlation. In the table, "w" indicates that the relationship was  
762 with the variable calculated for the warm period. Otherwise, the relationship was with the annual  
763 variable. **Abbreviations:** actual and potential evapotranspiration (AET and PET), water deficit  
764 (WD), mean temperature (Temp), total precipitation sum (Prec), annual thermal amplitude (ThA),  
765 precipitation seasonality (PS), length of the warm period (LWP), nitrogen deposition (ND). Annual  
766 and warm-period variables of AET, PET, WD, Temp, and Prec are represented in single columns  
767 to compact the table. Factor codes: leaf habit (E: evergreen, D: deciduous); leaf type (N:  
768 needleleaved, B: broadleaved); management (M: managed, UM: unmanaged, D: disturbed).

769 **Table 1:** Total effects (mean  $\pm$  SE) resulting from the path analysis shown in Figure 5. Bold  
770 coefficients were significant at the 0.05 level.

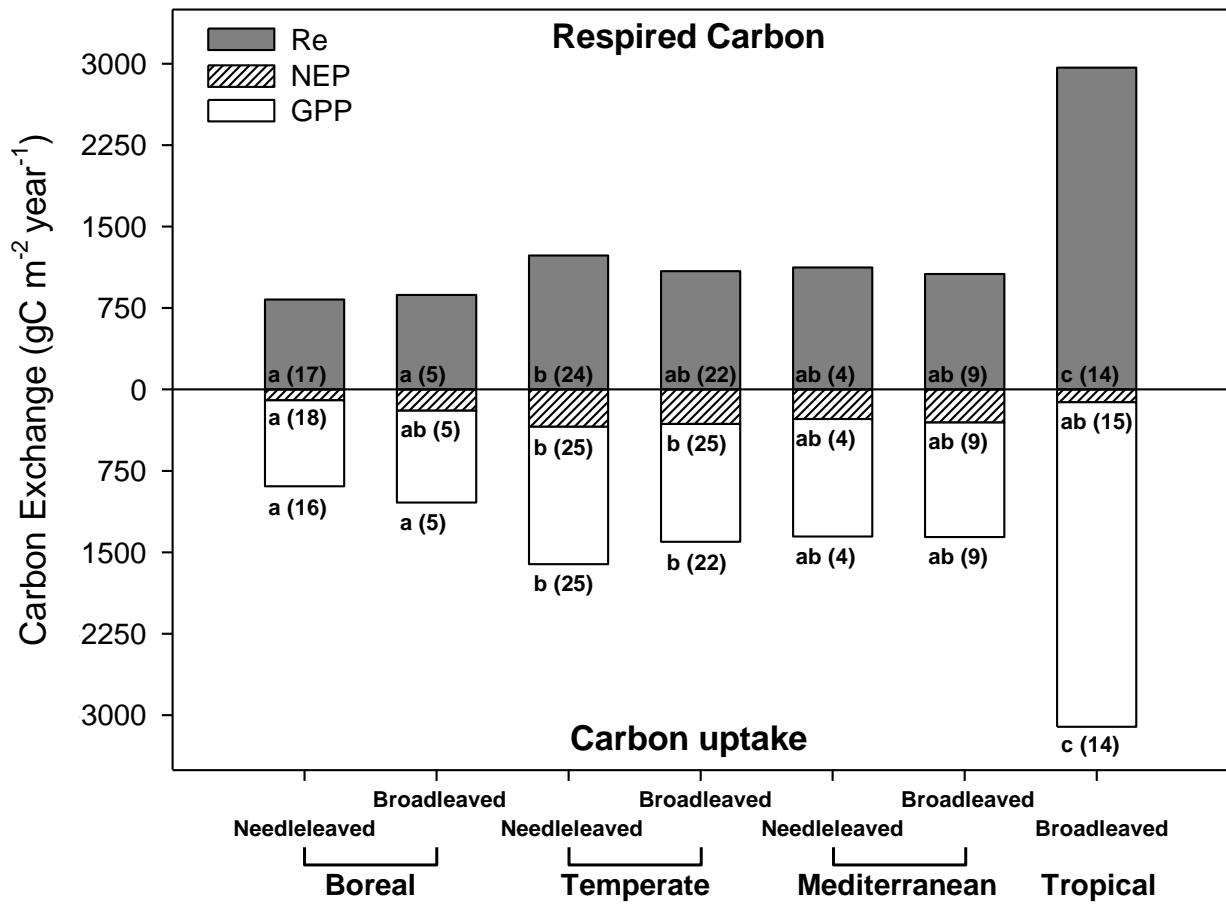
771

772 **Figure 1**

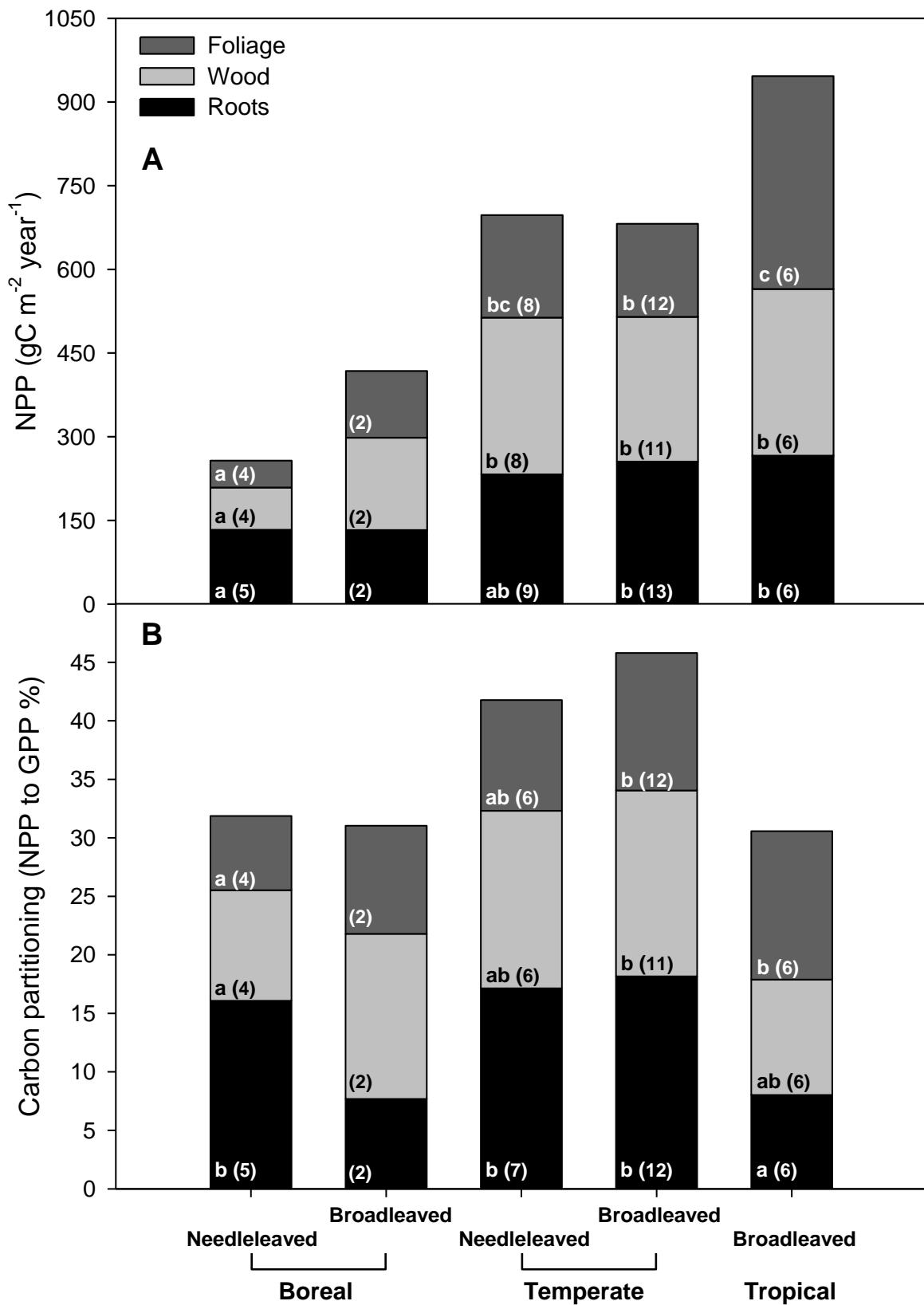


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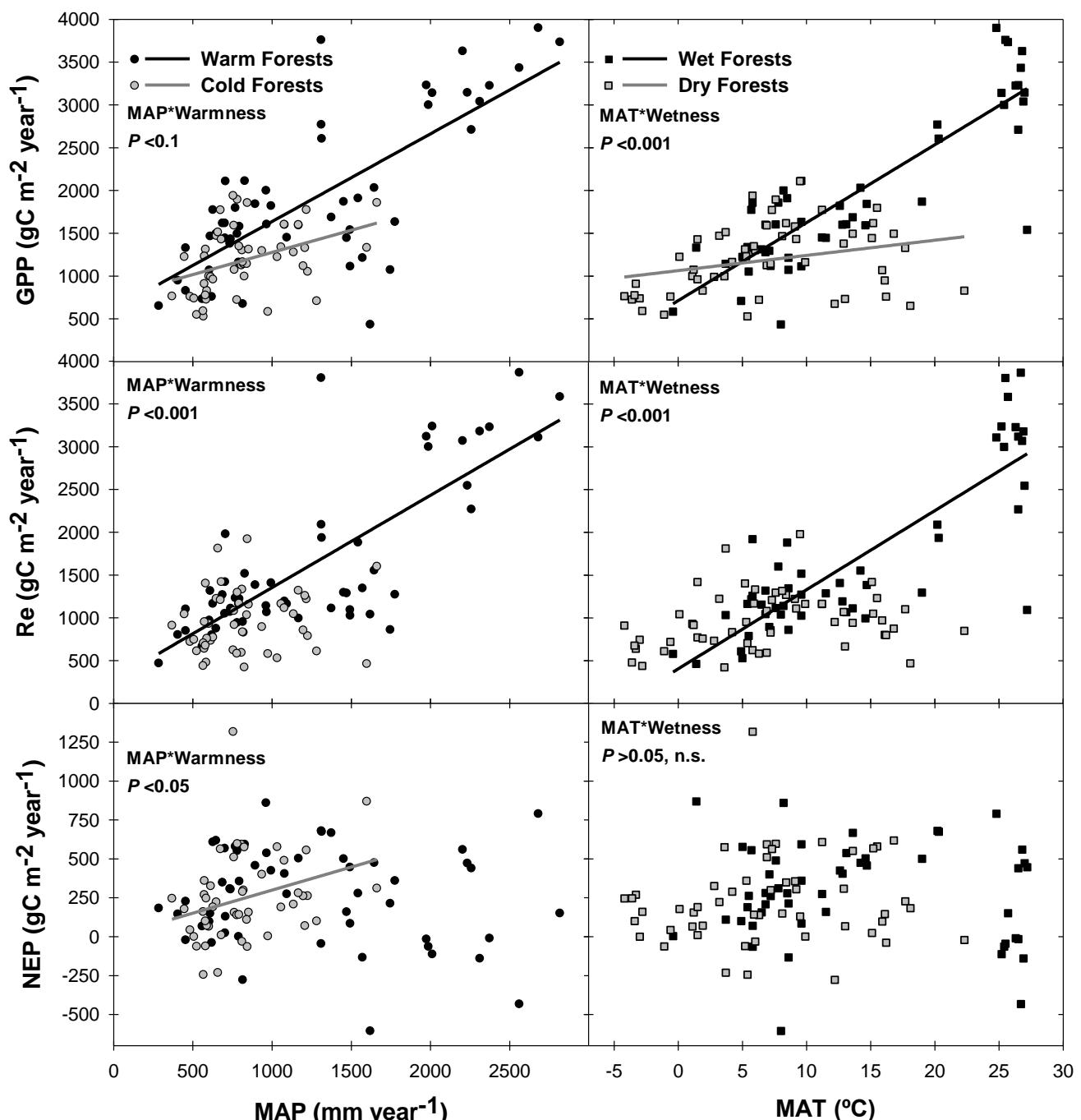
774 **Figure 2**



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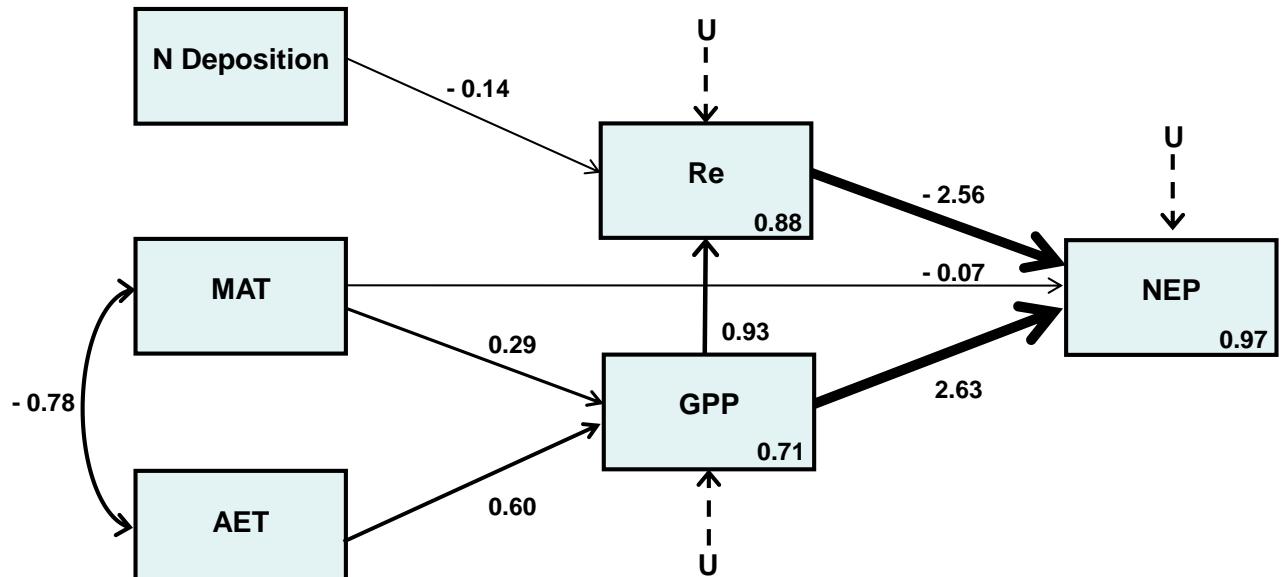


779 **Figure 4**



780

781 Figure 5

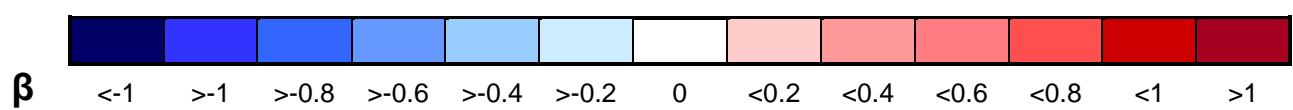


782

783 Table 1

	AET	PET	WD	Temp	Prec	ThA	PS	LWP	Age	ND	L Habit	L Type	MNG
LAI	w			w								N > B	
SLA													
FB			blue									N > B	
WB					red								
AB					red								
BB				w	red							N > B	
TB				w	red								
%FB				w								E > D	
%WB	red												
%BB					w							E > D	
GPP	w				w	blue							
TBP			blue										
ABP			w										
FNPP									red				
WNPP			w										
BBP						blue							
Re		blue		red	w								
NEP												M > UM M > D	
ABP%													
BBP%					w								
FNPP%								red					
WNPP%										red			
CUEe										red			M > UM
BPE							blue						
LUE				w									
WUE		blue	w				blue			red			

784



785

786

787 **Table 2**

Total Effects	N dep	AET	MAT	GPP	Re
GPP		1.60 ± 0.23	27.44 ± 8.08		
Re	-19.06 ± 4.58	1.46 ± 0.22	25.01 ± 7.42	0.91 ± 0.03	
NEP	18.44 ± 4.44	0.16 ± 0.31	0.22 ± 10.74	0.09 ± 0.04	-0.96 ± 0.02
<b>Standardized total effects</b>					
GPP		0.60 ± 0.09	0.29 ± 0.09		
Re	-0.14 ± 0.05	0.55 ± 0.08	0.27 ± 0.08	0.93 ± 0.03	
NEP	0.37 ± 0.14	0.16 ± 0.31	0.01 ± 0.30	0.26 ± 0.11	-2.55 ± 0.05

788

789 **Supporting information**

790 **Figure S1:** Global map of the forest sites in the study containing estimates for stand biomass,  
791 carbon flux, or both.

792 **Figure S2:** Pie plots showing the number and percentage (graphic) of forests per management  
793 regime in each one of the biomes of our final dataset. **Abbreviations:** managed forests (M),  
794 unmanaged (UM), recently disturbed (RD) and forests without available information on  
795 management (NI).

796 **Figure S3:** Relationship of GPP, Re and NEP (plots A, B and C respectively) with MAT and MAP  
797 of the warm period. The response surface was obtained using spline functions to smooth the data  
798 within a Generalized Additive Models (GAM).

799 **Table S1:** Pearson correlation coefficients for climatic variables, stand age and nitrogen  
800 deposition. Bold coefficients are significant at the 0.05 level. **Abbreviations:** mean annual actual  
801 evapotranspiration (AET), mean annual potential evapotranspiration (PET), mean annual  
802 percentage of water deficit (WD), mean annual temperature (MAT), mean annual precipitation  
803 (MAP), mean annual thermal amplitude (ThA), mean precipitation seasonality (PS), mean  
804 temperature of the warm period (TWP), mean length of the warm period (LWP), mean precipitation  
805 of the warm period (PWP), actual evapotranspiration of the warm period (AET WP), mean potential  
806 evapotranspiration of the warm period (PET WP), mean percentage of water deficit of the warm  
807 period (WD WP), mean annual nitrogen deposition (ND).

808 **Table S2:** Stand age, mean biomass and its distribution among boreal, temperate, Mediterranean,  
809 and tropical biomes, separating forests by leaf type. The table shows the mean value (in  $\text{gC} \cdot \text{m}^{-2}$ ,  
810 except for LAI and SLA, whose units are  $\text{m}^2 \text{m}^{-2}$  and  $\text{m}^2 \text{kg}^{-1}$ , respectively) followed by the lower and  
811 upper 95% bootstrapped (bias accelerated) confidence intervals and the number of replicates (in  
812 parentheses). “NA” indicates not available data. Notice that the percentages of foliar, woody, and  
813 belowground biomasses are calculated relative to total biomass. Mixed forests were excluded.

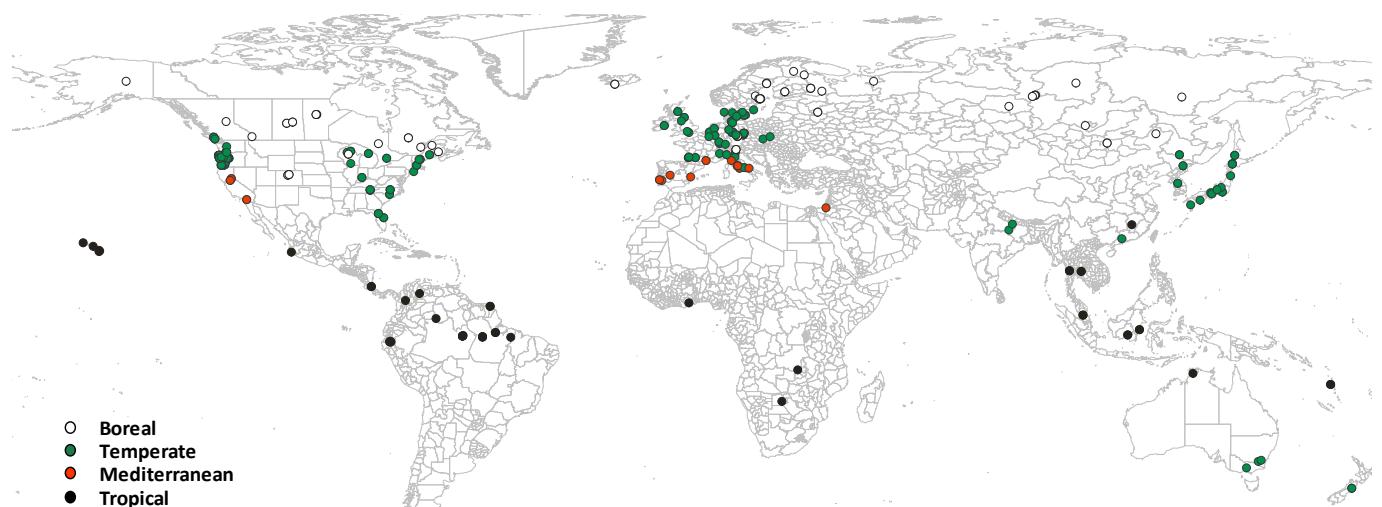
814   **Table S3:** Weighted values of mean carbon flux and partitioning percentages for boreal,  
815   temperate, Mediterranean, and tropical biomes, grouping forests according to leaf type. The table  
816   shows the mean value (in  $\text{gC} \cdot \text{m}^{-2} \text{ year}^{-1}$ ) followed by the lower and upper 95% bootstrapped (bias  
817   accelerated) confidence intervals and the number of replicates (in parentheses). “NA” indicates not  
818   available data The ABP%, BBP%, FNPP%, and WNPP% percentages are NPP fluxes relative to  
819   GPP. The weighting factor was calculated as the inverse of the uncertainty. Mixed forests were  
820   excluded.

821

822 **Table S4:** Weighted mean values of resource-use efficiency for boreal, temperate, Mediterranean,  
823 and tropical biomes, grouping forests according to leaf type. The table shows the mean value of  
824 each efficiency variable, followed by the lower and upper 95% bootstrapped (bias accelerated)  
825 confidence intervals and the number of replicates (in parentheses). “NA” indicates not available  
826 data. The CUEe and BPE percentages correspond to the ratio of NEP to GPP and of TBP to GPP,  
827 respectively. LUE units are gC MJ<sup>-1</sup>, and WUE units are gC L<sup>-1</sup>. The weighting factor was  
828 calculated as the inverse of the uncertainty. Mixed forests were excluded.

829 **Table S5:**  $\beta$  coefficients ( $\pm$  SE) of the stepwise regressions for the a) structural, b) functional, and  
830 c) efficiency variables studied. The adjusted  $R^2$  of the entire model and the number of replicates  
831 are also noted. “Ln” after a dependent variable indicates that a logarithmic transformation was  
832 required to achieve the model’s assumptions. “Ln” after a  $\beta$  coefficient indicates the variable  
833 entered the model in its logarithmic form. For management, leaf habit, and leaf type, a capital letter  
834 is designated to express differences between levels (management: U = unmanaged, M =  
835 managed, D = disturbed; leaf habit: E = evergreen, D = deciduous; leaf type: N = needleleaved, B  
836 = broadleaved). All regression models were significant at the 0.001 level or lower. **Abbreviations:**  
837 mean annual actual evapotranspiration (AET), mean annual potential evapotranspiration (PET),  
838 mean annual percentage of water deficit (WD), mean annual temperature (MAT), mean annual  
839 precipitation (MAP), mean annual thermal amplitude (ThA), mean precipitation seasonality (PS),  
840 mean temperature of the warm period (TWP), mean length of the warm period (LWP), mean  
841 precipitation of the warm period (PWP), actual evapotranspiration of the warm period (AET WP),  
842 mean potential evapotranspiration of the warm period (PET WP), mean percentage of water deficit  
843 of the warm period (WD WP), mean annual nitrogen deposition (ND).

844 **Figure S1**

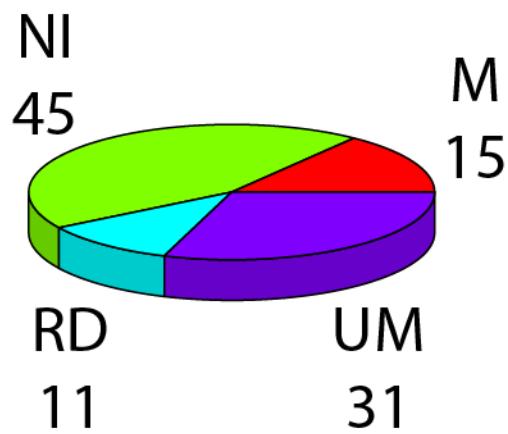


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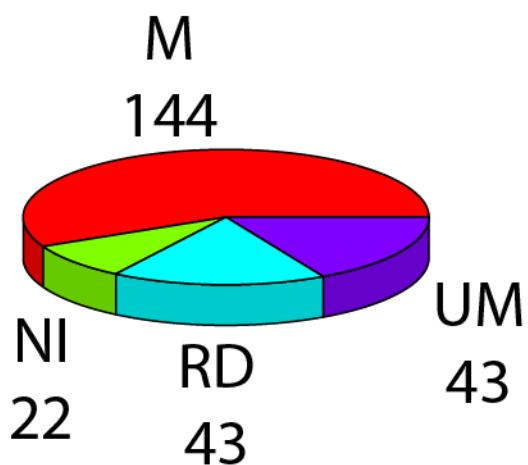
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**Figure S2**

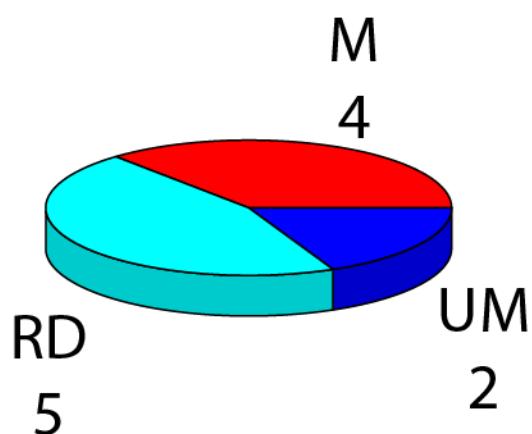
## Boreal Forests



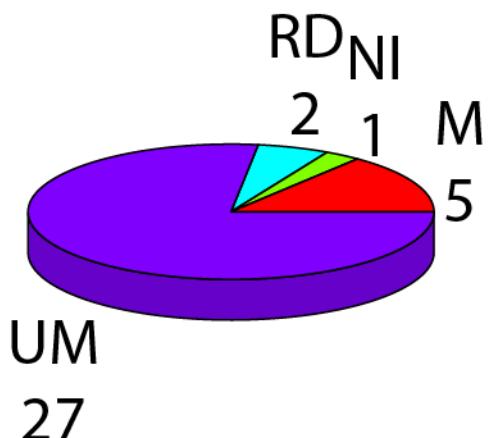
## Temperate Forests

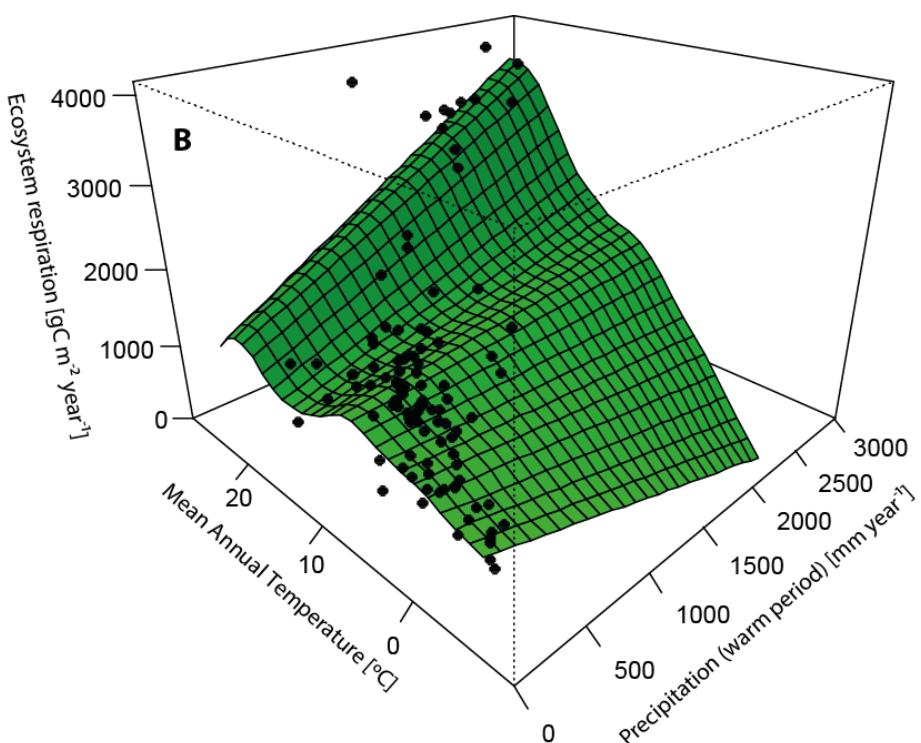
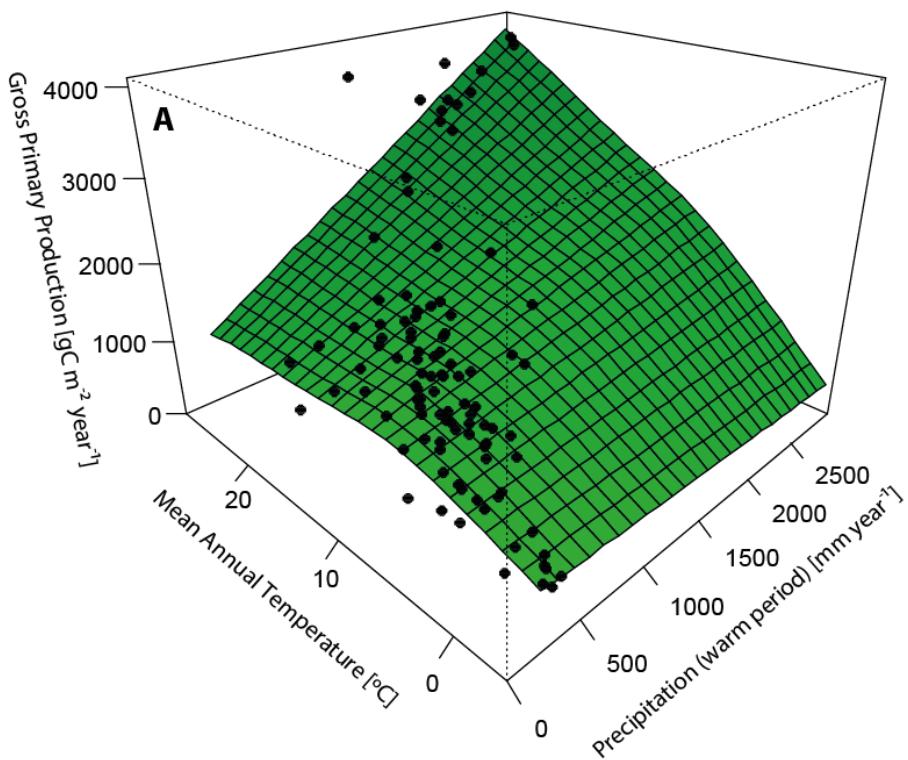


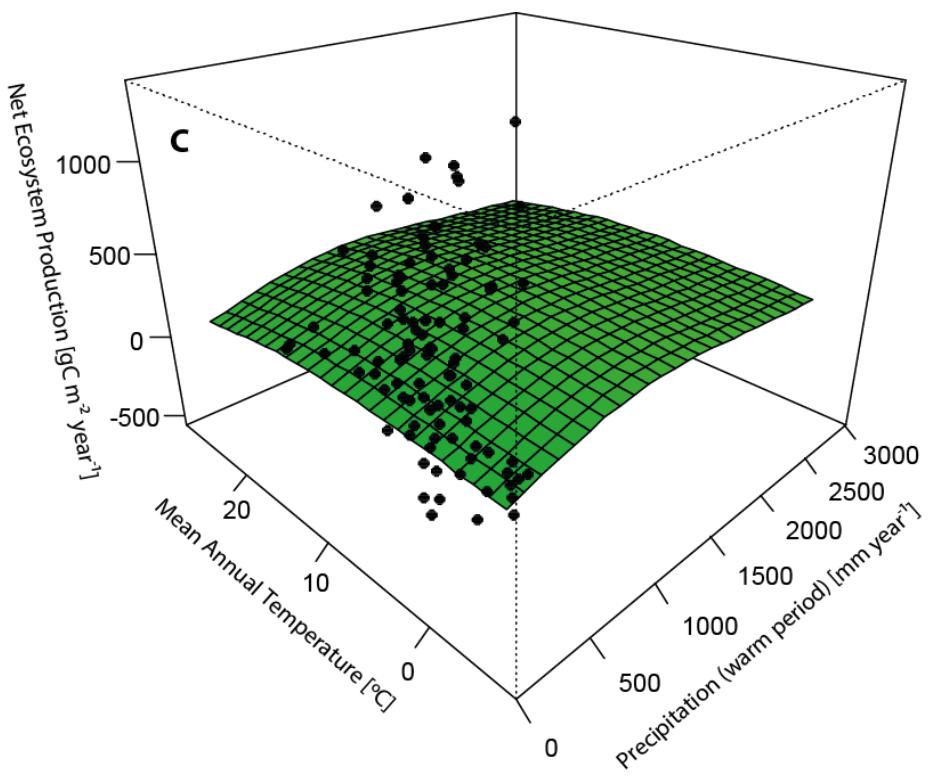
## Mediterranean Forests



## Tropical Forests



**Figure S3**



852

853

**Table S1**

	AET	PET	WD	MAT	MAP	ThA	PS	TWP	PWP	LWP	AET WP	PET WP	WD WP	Age	ND
<b>AET</b>	0.24	-0.62	0.77	0.74	-0.54	0.11	0.80	0.81	0.62	1.00	0.28	-0.59	-0.04	0.05	
<b>PET</b>	0.24		0.50	0.58	0.09	-0.24	0.54	0.48	0.23	0.65	0.26	0.99	0.51	-0.15	-0.13
<b>WD</b>	-0.62	0.50		-0.25	-0.52	0.32	0.29	-0.33	-0.49	-0.05	-0.61	0.44	0.99	-0.08	<b>-0.18</b>
<b>MAT</b>	0.77	0.58	-0.25		0.62	-0.76	0.22	0.88	0.79	0.91	0.80	0.64	-0.20	-0.23	0.01
<b>MAP</b>	0.74	0.09	-0.52	0.62		-0.55	0.05	0.65	0.91	0.40	0.72	0.11	-0.49	0.04	-0.12
<b>ThA</b>	-0.54	-0.24	0.32	-0.76	-0.55		0.10	-0.49	-0.59	-0.65	-0.56	-0.30	0.25	0.21	-0.11
<b>PS</b>	0.11	0.54	0.29	0.22	0.05	0.10		0.34	0.13	0.22	0.12	0.52	0.28	0.14	<b>-0.42</b>
<b>TWP</b>	0.80	0.48	-0.33	0.88	0.65	-0.49	0.34		0.84	0.71	0.82	0.52	-0.31	-0.10	-0.13
<b>PWP</b>	0.81	0.23	-0.49	0.79	0.91	-0.59	0.13	0.84		0.63	0.82	0.28	-0.45	-0.06	-0.10
<b>LWP</b>	0.62	0.65	-0.05	0.91	0.40	-0.65	0.22	0.71	0.63		0.67	0.72	0.01	<b>-0.26</b>	0.01
<b>AET WP</b>	1.00	0.26	-0.61	0.80	0.72	-0.56	0.12	0.82	0.82	0.67		0.30	-0.58	-0.07	0.05
<b>PET WP</b>	0.28	0.99	0.44	0.64	0.11	-0.30	0.52	0.52	0.28	0.72	0.30		0.47	<b>-0.20</b>	-0.12
<b>WD WP</b>	-0.59	0.51	0.99	-0.20	-0.49	0.25	0.28	-0.31	-0.45	0.01	-0.58	0.47		-0.10	<b>-0.21</b>
<b>Age</b>	-0.04	-0.15	-0.08	<b>-0.23</b>	0.04	<b>0.21</b>	0.14	-0.10	-0.06	<b>-0.26</b>	-0.07	<b>-0.20</b>	-0.10		-0.08
<b>ND</b>	0.05	-0.13	<b>-0.18</b>	0.01	-0.12	-0.11	<b>-0.42</b>	-0.13	-0.10	0.01	0.05	-0.12	-0.21	-0.08	

	Boreal		Temperate		Mediterranean		Tropical
	Needleleaved	Broadleaved	Needleleaved	Broadleaved	Needleleaved	Broadleaved	Broadleaved
<b>Stand Age</b>	84.9	69.5	84.6	75.3	24.0	32.0	78.5
	73.8 - 98.3 (81)	47.5 - 103.9 (10)	68.7 - 106.1 (157)	63.2 - 95.1 (74)	NA - NA (2)	11.9 - 54.7 (7)	60.2 - 95.6 (22)
<b>LAI</b>	3.9	3.5	6.6	5.6	4.1	2.1	4.9
	3.3 - 4.8 (56)	2.8 - 4.5 (9)	6.0 - 7.1 (151)	5.0 - 6.6 (73)	NA - NA (2)	1.4 - 2.7 (9)	4.3 - 5.4 (22)
<b>SLA</b>	12.6	35.9	18.9	26.2	6.9	20.3	13.5
	10.4 - 15.3 (21)	33.9 - 37.1 (3)	12.9 - 41.3 (118)	21.7 - 30.9 (20)	NA - NA (1)	11.0 - 28.5 (4)	10.7 - 18.7 (9)
<b>Foliar Biomass</b>	292	103	629	223	800	152	458
	254 - 335 (40)	76 - 125 (3)	558 - 700 (124)	188 - 276 (21)	NA - NA (1)	40 - 248 (4)	341 - 705 (11)
<b>Woody Biomass</b>	4310	7359	14727	11907	7100	2351	15294
	3240 - 5936 (26)	NA - NA (2)	12331 - 17518 (109)	10609 - 13428 (9)	NA - NA (1)	667 - 3483 (3)	9839 - 18302 (4)
<b>Aboveground B.</b>	5332	6699	13630	10557	7960	3245	10256
	4511 - 6239 (67)	4286 - 8667 (7)	11652 - 15717 (141)	9146 - 12170 (51)	NA - NA (1)	1120 - 4941 (4)	8396 - 12348 (27)
<b>Belowground B.</b>	1353	1120	4047	2568	2640	2704	2210
	1155 - 1583 (63)	735 - 1663 (7)	3124 - 5153 (69)	2130 - 3878 (49)	NA - NA (1)	1613 - 4747 (4)	1659 - 3372 (14)
<b>Total Biomass</b>	6900	7818	17724	13162	10600	5950	11923
	5988 - 7980 (63)	5094 - 10119 (7)	14062 - 22452 (69)	11285 - 15506 (48)	NA - NA (1)	3351 - 9417 (4)	9095 - 15090 (13)
<b>% Foliar</b>	5.8%	1.1%	5.7%	2.2%	7.5%	2.3%	5.2%
	4.2% - 8.6% (35)	0.7% - 1.5% (3)	4.6% - 7.1% (57)	1.6% - 3.4% (18)	NA - NA (1)	1.2% - 3.2% (4)	3.0% - 10.3% (10)
<b>% Woody</b>	68.1%	67.8%	69.3%	85.1%	67.0%	50.0%	72.2%
	59.0% - 74.0% (23)	NA - NA (2)	65.4% - 72.8% (47)	71.5% - 111.2% (9)	NA - NA (1)	26.5% - 64.2% (3)	67.2% - 75.1% (3)
<b>% Belowground</b>	20.1%	15.2%	24.0%	19.4%	24.9%	47.9%	19.9%
	18.8% - 21.7% (63)	11.4% - 20.6% (7)	22.3% - 26.3% (69)	17.6% - 23.3% (48)	NA - NA (1)	28.9% - 61.9% (4)	15.5% - 24.7% (13)

**Table S3**

	Boreal		Temperate		Mediterranean		Tropical
	Needleleaved	Broadleaved	Needleleaved	Broadleaved	Needleleaved	Broadleaved	Broadleaved
<b>GPP</b>	892	1041	1609	1403	1354	1359	3106
	788 - 1027 (17)	769 - 1200 (5)	1419 - 1743 (24)	1283 - 1533 (22)	813 - 1647 (4)	1152 - 1560 (9)	2596 - 3414 (14)
<b>TBP</b>	349	500	775	797	NA	NA	1232
	255 - 506 (5)	NA - NA (2)	581 - 1077 (9)	703 - 939 (13)	NA - NA (NA)	NA - NA (NA)	1055 - 1444 (5)
<b>ABP</b>	130	285	504	434	NA	NA	718
	107 - 148 (5)	NA - NA (2)	311 - 870 (9)	363 - 522 (13)	NA - NA (NA)	NA - NA (NA)	514 - 948 (6)
<b>FNPP</b>	48	120	184	167	NA	NA	382
	45 - 52 (4)	NA - NA (2)	106 - 370 (8)	146 - 190 (12)	NA - NA (NA)	NA - NA (NA)	319 - 551 (6)
<b>WNPP</b>	76	166	281	260	NA	NA	299
	57 - 98 (4)	NA - NA (2)	163 - 556 (8)	192 - 353 (11)	NA - NA (NA)	NA - NA (NA)	164 - 380 (6)
<b>BBP</b>	133	133	232	255	NA	NA	266
	103 - 201 (5)	NA - NA (2)	188 - 300 (9)	210 - 318 (13)	NA - NA (NA)	NA - NA (NA)	232 - 314 (6)
<b>Re</b>	828	870	1234	1090	1124	1063	2964
	704 - 1040 (16)	586 - 1002 (5)	1097 - 1348 (25)	965 - 1238 (22)	567 - 1305 (4)	925 - 1243 (9)	2396 - 3289 (14)
<b>NEP</b>	99	196	343	317	271	305	118
	16 - 216 (18)	154 - 265 (5)	254 - 431 (25)	239 - 416 (25)	175 - 411 (4)	120 - 478 (9)	-23 - 304 (15)
<b>ABP%</b>	17.3%	23.4%	26.0%	31.1%	NA	NA	24.2%
	16.1% – 20.7% (5)	NA - NA (2)	17.3% – 50.2% (7)	24.5% – 39.3% (12)	NA - NA (NA)	NA - NA (NA)	15.0% – 31.8% (6)
<b>BBP%</b>	16.1%	7.7%	17.1%	18.2%	NA	NA	8.0%
	14.1% – 20.1% (5)	NA - NA (2)	11.8% – 29.2% (7)	14.2% – 22.7% (12)	NA - NA (NA)	NA - NA (NA)	7.0% – 9.1% (6)
<b>FNPP%</b>	6.3%	9.2%	9.5%	11.8%	NA	NA	12.7%
	4.9% – 6.8% (4)	NA - NA (2)	6.0% – 23.4% (6)	11.0% – 12.6% (12)	NA - NA (NA)	NA - NA (NA)	9.2% – 19.0% (6)
<b>WNPP%</b>	9.5%	14.1%	15.2%	15.9%	NA	NA	9.9%
	8.8% – 10.1% (4)	NA - NA (2)	9.4% – 33.2% (6)	11.2% – 22.2% (11)	NA - NA (NA)	NA - NA (NA)	4.4% – 12.8% (6)

	<b>Boreal</b>		<b>Temperate</b>		<b>Mediterranean</b>		<b>Tropical</b>
	<b>Needleleaved</b>	<b>Broadleaved</b>	<b>Needleleaved</b>	<b>Broadleaved</b>	<b>Needleleaved</b>	<b>Broadleaved</b>	<b>Broadleaved</b>
<b>CUEe%</b>	9.7%	17.9%	21.8%	21.7%	19.4%	20.8%	3.3%
	-0.2% - 21.3% (16)	14.5% - 25.6% (5)	17.0% - 26.0% (24)	16.9% - 27.9% (22)	12.3% - 23.6% (4)	8.9% - 30.0% (9)	-2.0% - 9.1% (14)
<b>BPE%</b>	<b>43.7%</b>	<b>40.6%</b>	<b>50.8%</b>	<b>54.8%</b>	<b>NA</b>	<b>NA</b>	<b>38.2%</b>
	35.5% - 54.7% (5)	NA - NA (2)	41.4% - 72.0% (7)	46.3% - 64.0% (12)	NA - NA (NA)	NA - NA (NA)	33.0% - 48.2% (5)
<b>LUE</b>	<b>2.2</b>	<b>NA</b>	<b>2.6</b>	<b>2.0</b>	<b>2.3</b>	<b>2.0</b>	<b>NA</b>
	1.7 - 2.6 (9)	NA - NA (NA)	2.4 - 2.9 (10)	1.7 - 2.3 (11)	NA - NA (2)	1.6 - 2.2 (7)	NA - NA (NA)
<b>LUE%<sub>APAR</sub></b>	<b>9.4%</b>	<b>NA</b>	<b>11.1%</b>	<b>8.5%</b>	<b>9.8%</b>	<b>8.5%</b>	<b>NA</b>
	7.1% - 11.0% (9)	NA - NA (NA)	10.1% - 12.5% (10)	7.0% - 9.9% (11)	NA - NA (2)	7.2% - 9.7% (7)	NA - NA (NA)
<b>LUE%<sub>PAR</sub></b>	<b>6.2%</b>	<b>NA</b>	<b>7.6%</b>	<b>5.8%</b>	<b>5.8%</b>	<b>5.5%</b>	<b>NA</b>
	4.2% - 7.5% (9)	NA - NA (NA)	6.7% - 8.6% (10)	4.9% - 6.8% (11)	4.0% - 7.1% (2)	4.2% - 6.4% (7)	NA - NA (NA)
<b>LUE%<sub>TRad</sub></b>	<b>2.8%</b>	<b>NA</b>	<b>3.4%</b>	<b>2.6%</b>	<b>2.6%</b>	<b>2.5%</b>	<b>NA</b>
	2.0% - 3.4% (9)	NA - NA (NA)	3.0% - 3.8% (10)	2.2% - 3.1% (11)	1.8% - 2.6% (2)	1.9% - 2.9% (7)	NA - NA (NA)
<b>WUE</b>	<b>2.6</b>	<b>2.5</b>	<b>2.8</b>	<b>2.3</b>	<b>3.1</b>	<b>2.1</b>	<b>2.7</b>
	2.3 - 2.9 (17)	2.0 - 2.9 (5)	2.5 - 3.2 (24)	1.9 - 2.7 (22)	2.3 - 4.3 (4)	1.7 - 2.5 (9)	2.4 - 2.8 (14)

**Table S5**

b) Fluxes	GPP	TBP	ABP (Ln)	FNPP	WNPP (Ln)	BBP	Re	NEP	ABP%	BBP%	FNPP%	WNPP%
R <sup>2</sup> adj	0.81	0.76	0.73	0.64	0.47	0.28	0.76	0.18	0.22	0.30	0.42	0.24
N	83	30	34	32	30	30	103	109	32	28	29	29
<b>AET</b>												
<b>PET</b>												
WD			-0.33 ± 0.12					-0.28 ± 0.06Ln				
MAT								0.22 ± 0.09				
MAP												
ThA		-0.33 ± 0.06				-0.39 ± 0.16					1.12 ± 0.29Ln	
PS												
TWP												
LWP		0.56 ± 0.12Ln	0.45 ± 0.13	0.80 ± 0.11							1.36 ± 0.29Ln	
PWP	0.40 ± 0.09						0.49 ± 0.10			-0.53 ± 0.16Ln		
AET WP	0.36 ± 0.10											
PET WP												
WD WP			-0.34 ± 0.14		-0.48 ± 0.14							
Stand Age	0.23 ± 0.05 Ln	-0.32 ± 0.09Ln				-0.37 ± 0.16Ln				-0.41 ± 0.16Ln		
ND		0.41 ± 0.10		0.41 ± 0.14				0.23 ± 0.10	0.50 ± 0.16Ln			0.51 ± 0.16Ln
Leaf Habit												
Leaf Type												
Management								M > UM - M > D				

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c) Efficiencies	CUEe	BPE	LUE	WUE
R <sup>2</sup> adj	0.18	0.33	0.13	0.43
N	82	27	42	83
AET				
PET			-0.41 ± 0.10Ln	
WD				
MAT				
MAP				
ThA			-0.66 ± 0.10	
PS		-0.40 ± 0.16		
TWP			-0.39 ± 0.15Ln	
LWP				
PWP				
AET WP				
PET WP				
WD WP			0.60 ± 0.10	
Stand Age	0.39 ± 0.15Ln	-0.42 ± 0.16Ln	0.35 ± 0.09Ln	
ND				
Leaf Habit				
Leaf Type				
Management	M > UM			

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