



# Coversheet

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**The relationship of woody plant size and leaf nutrient content to large-scale productivity for forests across the Americas**

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Manuscripts

1 **The relationship of woody plant size and leaf nutrient content to large-scale productivity**  
2 **for forests across the Americas**

3

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34

## 35 **Abstract**

- 36 1. Ecosystem processes are driven by both environmental variables and the attributes of  
37 component species. The extent to which these effects are independent and/or dependent  
38 upon each other has remained unclear. We assess the extent to which climate affects net  
39 primary productivity (NPP) both directly and indirectly via its effect on plant size and leaf  
40 functional traits.
- 41 2. Using species occurrences and functional trait databases for North and South America, we  
42 describe the upper limit of woody plant height within  $200 \times 200$  km grid-cells. In addition  
43 to maximum tree height, we quantify grid-cell means of three leaf traits (specific leaf area,  
44 and leaf nitrogen and phosphorus concentration) also hypothesized to influence  
45 productivity. Using structural equation modelling, we test the direct and indirect effects of  
46 environment and plant traits on remotely sensed MODIS- derived estimates of NPP, using  
47 plant size (canopy height and potential maximum tree height), leaf traits, growing season  
48 length, soil nutrients, climate and disturbances as explanatory variables.
- 49 3. Our results show that climate affects NPP directly as well as indirectly via plant size in  
50 both tropical and temperate forests. In tropical forests NPP further increases with leaf  
51 phosphorus concentration, whereas in temperate forests it increases with leaf nitrogen  
52 concentration. In boreal forests, NPP most strongly increases with increasing temperature  
53 and neither plant size nor leaf traits have a significant influence.
- 54 4. *Synthesis*: Our results suggest that at large spatial scales plant size and leaf nutrient traits  
55 can improve predictions of forest productivity over those based on climate alone.  
56 However, at higher latitudes their role is overridden by stressful climate. Our results  
57 provide independent empirical evidence for where and how global vegetation models  
58 predicting carbon fluxes could benefit from including effects of plant size and leaf  
59 stoichiometry.

60 **Key words:** BIEN database, biogeography and macroecology, biomass production, ecosystem  
61 function and services, leaf nitrogen, leaf phosphorous, MODIS, TRY database

## 62 **Introduction**

63 The composition of plant species assemblages is often cited as a significant driver of key  
64 ecosystem functions, such as carbon, nutrient and water cycles, and of the resulting ecosystem  
65 processes such as evapotranspiration, decomposition and biomass production (Cornwell et al.,  
66 2008; Grime, 1997; Lavorel & Garnier, 2002). As such, a key challenge for improving our  
67 ability to predict the ecological impacts of global climate change lies in understanding how  
68 environmental and land-use changes alter the composition of plant assemblages and how this  
69 in turn affects ecosystem processes (Chapin et al., 2000). Plant functional traits are  
70 increasingly emphasized as a way to link species composition to ecosystem function. For  
71 example, at the organismal and community scale, several studies have documented that  
72 variation in functional traits drives variation in ecosystem functions such as carbon or water  
73 cycles (Michaletz, Cheng, Kerkhoff, & Enquist, 2014; Reich, Walters, & Ellsworth, 1997;  
74 Stephenson et al., 2014; Violle et al., 2007). Nevertheless, how such relationships scale up  
75 from larger landscapes to continental scales remains unresolved. A way forward is to combine  
76 maps of functional traits of species assemblages with maps of ecosystem processes (e.g.  
77 satellite-derived productivity data) to allow the importance of plant traits in driving  
78 ecosystem processes at large spatial scales to be evaluated (Díaz et al., 2007; Lavorel et al.,  
79 2013).

80 Perhaps the most important trait affecting variation in ecosystem carbon, water and  
81 nutrient fluxes is plant size, which is often measured as height or stem diameter (Chapin,  
82 Bret-Harte, Hobbie, & Zhong, 1996; Niklas & Enquist, 2001; Stephenson et al., 2014).  
83 Metabolic scaling theory (MST) for forest structure and dynamics predicts that whole-stand  
84 resource use (e.g. carbon flux) should be proportional to the size of the largest individual  
85 present at the stand (Enquist, West, & Brown, 2009; West, Enquist, & Brown, 2009):

$$86 \quad B_{tot} \propto (M_{tot})^b \propto r_m, \quad [1]$$

87 where  $B_{tot}$  is the whole-stand metabolic rate or resource flux (e.g. carbon or water),  $M_{tot}$  is  
88 the total biomass of the stand,  $b$  is a mass-scaling exponent (which depends on the size  
89 structure of the stand, the scaling of resource use with plant size, and the scaling of stem  
90 radius and plant biomass), and  $r_m$  is the size (measured as stem radius) of the largest  
91 individual in the stand. MST predicts that the largest individual in the stand should be a  
92 central if not the primary predictor of variation in  $B_{tot}$  and  $M_{tot}$ . In agreement with theory,  
93 there is evidence that stand biomass of tropical and temperate forest plots, primarily  
94 determined by the size of the largest tree (Stegen et al., 2011), is one of the major drivers of  
95 forest productivity (Michaletz et al., 2014; Michaletz, Kerkhoff, & Enquist, 2018).  
96 Furthermore, given that tall trees sequester carbon at higher absolute rates compared to  
97 smaller trees (Stephenson et al., 2014), they are often strong contributors to the whole-stand  
98 carbon flux (Fauset et al., 2015; Gholz, 1982; but see Ligot et al., 2018). These theoretical  
99 predictions, however, are expected to be modified by human land-use or natural disturbances  
100 (Kerkhoff & Enquist, 2007; McDowell et al., 2018; see also Coomes, Holdaway, Kobe, Lines,  
101 & Allen, 2012; Muller-Landau et al., 2006).

102         Although some studies claim that variation in forest productivity is primarily  
103 determined by the direct effects of climate (Raich, Russell, Kitayama, Parton, & Vitousek,  
104 2006; Sankaran et al., 2005; Schuur, 2003), others suggest an indirect role of climate acting  
105 via local adaptations, soil nutrients, or regional land-use history mirrored in stand biomass  
106 (Chapin, Matson, & Vitousek, 2011; Michaletz et al., 2014, 2018) or a combination of these  
107 (Chu et al., 2016). Therefore, the unique contribution of stand biomass to rates of carbon flux,  
108 carbon sequestration, and productivity relative to factors such as climate, disturbances, and  
109 land-use intensity still needs to be evaluated.

110         Here, we test whether climate affects net primary productivity (NPP) directly or  
111 indirectly via its effect on tree size, a surrogate of stand biomass, as measured by maximum

112 tree height, in 200 x 200 km grid cells. As an NPP estimate, we used MODIS (Moderate  
113 Resolution Imaging Spectroradiometer) derived NPP (Running et al. 2004), defined as the  
114 total carbon that plants gain during photosynthesis minus the carbon lost by respiration. Our  
115 analyses utilized and compared two different measures of maximum tree height: 1) maximum  
116 canopy height per cell ('canopy height' hereafter), derived from remote sensing using a  
117 Geoscience Laser Altimeter System (GLAS), and 2) potential maximum tree height of all co-  
118 occurring plant species per cell, obtained by intersecting species occurrence records from that  
119 cell and species trait data.

120         The relationship between tree height, climate and NPP can be supplemented or  
121 modified by other factors such as leaf traits that drive photosynthetic and whole plant growth  
122 rates (Enquist et al., 2015; S. Lavorel & Garnier, 2002; Reich, Walters, & Ellsworth, 1992;  
123 Reich et al., 1997; Violle et al., 2007) or intensity of disturbances. To reflect these influences,  
124 we have included fire frequency, human land-use, specific leaf area, leaf nitrogen  
125 concentration and leaf phosphorus concentration in our evaluation.

126         Building on the recent theoretical expectations and empirical evidence (Enquist et al.,  
127 2015; Michaletz et al., 2014), we predict that climate and other environmental variables such  
128 as fire frequency and human land-use (disturbances) affect NPP primarily *indirectly* via their  
129 effects on tree height (Prediction P1; see Fig. 1 for a conceptual schema) (McDowell et al.,  
130 2018). Specifically, we predict that tree height is limited by water availability. Larger trees are  
131 closer to hydraulic limits that are defined by local precipitation and temperature (Bennett,  
132 McDowell, Allen, & Anderson-Teixeira, 2015; Gholz, 1982; McDowell & Allen, 2015; Ryan  
133 & Yoder, 1997). The basic tenet of the 'hydraulic limitation hypothesis' is that taller trees  
134 exhibit increased stomatal closure due to an increase in hydraulic resistance with tree height  
135 combined with the need to maintain a minimum leaf water potential to avoid catastrophic  
136 embolism (Ryan & Yoder, 1997).

137           The derived values of potential maximum tree height for a cell may or may not be  
138 realized due to disturbance, climate stress, etc. Therefore, we predict (P2) that potential  
139 maximum tree height affects NPP indirectly, via its influence on canopy height, and that  
140 climate (P1a) and disturbances (P1b) and their interaction affect NPP indirectly by  
141 constraining the degree to which canopy height is a realization of potential tree height.  
142 Climate can also affect potential maximum tree height as an environmental filter that prevents  
143 establishment of species not adapted to local conditions.

144           Finally, we predict (P3) NPP to be affected by leaf traits that are driven by climate or  
145 soil nutrient concentration. Specifically, NPP should increase with increasing specific leaf  
146 area and leaf nitrogen concentration as these influence rates of photosynthesis and whole plant  
147 growth (Enquist et al., 2015; Reich et al., 1997; Violle et al., 2007; Wright et al., 2004). NPP  
148 should also increase with increasing leaf phosphorus concentration, particularly in tropical  
149 forests (Mercado et al., 2011; Tanner, Vitousek, & Cuevas, 1998). Leaf nitrogen and  
150 phosphorus concentration should be driven by the concentrations of these nutrients in the soil,  
151 which can be partly driven by climate (Hedin, 2004; Reich & Oleksyn, 2004). Specifically,  
152 we predict soil phosphorus availability to decrease with increasing precipitation because of  
153 higher leaching rates. Soil nitrogen availability should increase with increasing temperature  
154 due to the temperature-dependence of the forest nitrogen cycle (Brookshire et al., 2011). As  
155 for maximum potential tree height, climate can also affect leaf traits directly via  
156 environmental filtering.

157           To disentangle the relative importance of climate, disturbances, functional traits and  
158 soil properties in controlling large-scale forest productivity and to evaluate the interactions  
159 among these factors, we apply a path analysis framework (see Fig. 1a for a conceptual  
160 schema). Given the possibly different drivers of NPP in different forest biomes, we test the  
161 above-mentioned predictions for all forests together and for individual biomes separately.

162

163 **Methods**164 *Species and trait data*

165 We extracted species occurrence records from the BIEN 3.0 database  
166 (<http://bien.nceas.ucsb.edu>). Most of these data are publicly available via the *BIEN* R package  
167 (Maitner, 2017) with some exceptions such as endangered species and private records (see  
168 Maitner et al., 2018 for details). We included all plant occurrence records having their  
169 coordinates georeferenced within the mainland areas of the Americas, excluding occurrence  
170 data of cultivated species. We overlaid the occurrences with a 200 × 200 km grid (projection  
171 was Lambert Azimuthal Equal Area) to obtain a list of species for each grid cell. We included  
172 only cells with more than 80% of their area on land. We restricted our analyses to woody  
173 species following Engemann et al. (2016) (angiosperm and gymnosperm trees, shrubs and  
174 lianas; 6,107 species in total).

175 We obtained plant maximum height, specific leaf area, leaf nitrogen concentration and  
176 phosphorus concentration data for woody species from both the BIEN and TRY (Kattge et al.,  
177 2011) databases, resulting in 14,451 species-level trait values. We assigned the trait values to  
178 the species occurrences resulting in values for maximum height for 2,583 species, specific  
179 leaf area for 2,408 species, leaf nitrogen concentration for 2,615 species, and leaf phosphorus  
180 concentration for 1,754 species (see Fig. S1 in Appendix S2 for maps of showing spatial the  
181 distribution of trait values). MST predicts that the size (height) of the largest individual is a  
182 key predictor of whole-stand productivity. Therefore, to calculate potential maximum tree  
183 height, we estimated the per-cell 95<sup>th</sup> percentile of maximum tree height. We chose the 95<sup>th</sup>  
184 percentile over the maximum value as it reduces the possible effect of outliers. We used the  
185 mean of per-cell values of the specific leaf area (SLA), leaf nitrogen concentration (leaf N)  
186 and leaf phosphorus concentration (leaf P) (Fig. 2a-d) to characterize assemblage strategies

187 (Enquist et al., 2015; Garnier et al., 2004). Due to the low number of species with known trait  
188 values at some grid cells (mostly boreal forests; Fig. S1) we retained only those cells with > 3  
189 species with known values of each trait.

190

### 191 *Canopy height*

192 We used the canopy height map derived from the Geoscience Laser Altimeter System  
193 (GLAS) from collection periods between 2003-2007 (Lefsky, 2010). The map applies to  
194 forest patches identified with MODIS imagery. Although a more recent map of canopy  
195 vegetation height has been developed spanning a larger spatial extent including non-forest  
196 areas (Simard, Pinto, Fisher, & Baccini, 2011), it models canopy height using both GLAS  
197 measurements and climate variables (mean annual temperature, annual precipitation and their  
198 seasonality), and therefore is not appropriate for regression models incorporating those same  
199 climate variables (see also Tao, Guo, Li, Wang, & Fang, 2016). In this map, about 1/4 of all  
200 forest patches have direct measurements. Those were assigned a value equal to the 90<sup>th</sup>  
201 percentile of the GLAS-based canopy height estimate (Lefsky 2010). Canopy height of  
202 patches without direct measurements were estimated by statistical modeling using the values  
203 from the surrounding patches (Lefsky, 2010). We restricted our analyses to cells where >50  
204 percent of cell area was assigned with non-null canopy height values (i.e. cells with forest  
205 coverage > 50%). To estimate the canopy height variable, we used these non-null canopy  
206 height values to calculate per-cell 95<sup>th</sup> percentile (Fig. 2e).

207

### 208 *NPP*

209 NPP is a product of the MODIS sensor (Running et al., 2004). It is calculated as gross  
210 primary productivity (GPP) minus autotrophic respiration. GPP is modeled as a function of  
211 photosynthetically active radiation (PAR), the fraction of PAR absorbed by plants, biome-

212 specific light-use efficiency, daily minimum temperature and vapor pressure deficit (Zhao,  
213 Heinsch, Nemani, & Running, 2005; Zhao & Running, 2010). Respiration combines  
214 maintenance respiration (a function of the daily average air temperature and leaf area index)  
215 and growth respiration (estimated as a constant proportion of total NPP). We averaged the  
216 NPP layer (available via <http://www.ntsg.umt.edu/>) over the years 2000-2012 and over each  
217 grid cell (Fig. 2f).

218

### 219 *Environmental data*

220 We included mean annual temperature and annual precipitation (1960-1990 means) extracted  
221 from the Worldclim database (version 1.4; [www.worldclim.org](http://www.worldclim.org); Hijmans, Cameron, Parra,  
222 Jones, & Jarvis, 2005). We selected these variables as both temperature (incorporated into  
223 potential evapotranspiration) and precipitation have been identified as strong predictors of  
224 forest canopy height (Tao et al., 2016), and temperature has been found to be the best  
225 predictor of mean height of woody species assemblages in 200 x 200 km grid squares in the  
226 Americas (Šímová et al., 2018). To reflect water limitation of plant growth, we included the  
227 yearly average of the fraction of soil water content available for evapotranspiration process  
228 ('soil water content' hereafter) obtained from CGIAR-CSI GeoPortal  
229 (<http://www.csi.cgiar.org>; Trabucco & Zomer, 2010). This variable is calculated as a  
230 difference between effective precipitation, actual evapotranspiration and water runoff where  
231 effective precipitation represents the total precipitation minus the precipitation intercepted by  
232 vegetation. We also included growing season length as another potentially important factor  
233 limiting forest NPP (Chapin et al., 2011; Michaletz et al., 2018) obtained from FAO (The  
234 Food and Agriculture Organization; <http://www.fao.org/geonetwork/srv/en/main.home>). This  
235 variable is defined as the period during the year when average temperatures are greater than or

236 equal to 5°C and precipitation plus moisture stored in the soil exceed half the potential  
237 evapotranspiration and the values are grouped into 16 zones.

238 As our first disturbance measure, we obtained fire frequency from Tansey et al.,  
239 (2008), and averaged this variable over years 2000-2007. As a second disturbance measure,  
240 we quantified human land use from the GlobCover 2009 land cover database  
241 ([http://due.esrin.esa.int/page\\_globcover.php](http://due.esrin.esa.int/page_globcover.php)). We chose the year 2009 to match the period of  
242 NPP data measurements (years 2000-2012) and canopy height measurements (year 2003-  
243 2007). We used the area covered by urban areas and all types of croplands (post-flooding or  
244 irrigated croplands, rain fed croplands, mosaic cropland and mosaic vegetation/cropland) in  
245 each grid cell as a measure of the intensity of human land use. We obtained soils data from  
246 ORNL DAAC (<https://daac.ornl.gov/>). We retrieved total soil phosphorus and organic soil  
247 phosphorus content from the Global Gridded Soil Phosphorus Distribution Maps (Yang, Post,  
248 Thornton, & Jain, 2014) and used these as surrogates of phosphorus available to plants. We  
249 retrieved topsoil organic carbon content from the RegridDED Harmonized World Soil Database  
250 (Wieder, Boehnert, Bonan, & Langseth, 2014) and used this as a negative surrogate for  
251 nitrogen available to plants. We calculated the mean of climate variables, fire frequency and  
252 soil variables at 200×200 km grid cell size using the package *raster* (Hijmans et al., 2016) in  
253 R (R Development Core Team, 2014). See Fig. S3 in Appendix S2 for maps and units of all  
254 variables.

255

### 256 *Forest biomes*

257 For the grid cells with >50% of forest coverage we assigned the forest biomes according to  
258 the following protocol. First, we grouped the major habitat types recognized by the WWF  
259 (World Wildlife Foundation; [www.worldwildlife.org](http://www.worldwildlife.org)) and obtained from The Nature  
260 Conservancy ([http://maps.tnc.org/gis\\_data.html](http://maps.tnc.org/gis_data.html)) into three main biomes: 1) tropical forests

261 (defined as area covered by Tropical and subtropical moist broadleaf forests, Tropical and  
262 subtropical dry broadleaf forests or Tropical and subtropical coniferous forests), 2) temperate  
263 forests (area covered by Temperate broadleaf and mixed forests or Temperate coniferous  
264 forest), and 3) boreal forests (defined as Boreal forests / Taiga). Second, for each grid cell, we  
265 considered the biome covering the largest area as the dominant biome (Fig. S2 in Appendix  
266 S2). Given the variability in canopy height values within tropical and temperate forest biomes,  
267 we further define four sub-biomes based on the WWF classification. These are 1) Temperate  
268 broadleaf and mixed forests, 2) Temperate coniferous forests, 3) Tropical and subtropical  
269 moist broadleaf forests and 4) Tropical and subtropical dry broadleaf forests. We omitted the  
270 tropical and subtropical coniferous forests sub-biome due to its limited spatial extent (four  
271 grid cells).

272

### 273 Data analyses

274 We fit structural equation models (package ‘lavaan’ in R) (Rosseel, 2011) to assess the  
275 distinct effects of potential maximum tree height, leaf traits, canopy height, length of the  
276 growing season, temperature, precipitation, human land-use and fire frequency on NPP. We  
277  $\log_e$ -transformed human land-use and fire frequency to improve normality. We checked for  
278 collinearity among variables using the variance inflation factor (VIF) where small VIF values  
279 indicate a low degree of collinearity. Some researchers recommend that the VIF of each  
280 variable entering the model be lower than 10 (Dormann et al., 2013), and others recommend  
281 VIF less than 5 (Hair, Ringle, & Sarstedt, 2011), or under ideal conditions even less than 3  
282 (Hair, Risher, Sarstedt, & Ringle, 2018). In tropical forests all variables had  $VIF < 10$  and  
283 most of them had  $VIF < 5$ . To meet similar VIF levels in temperate and boreal forests and  
284 across all forests we fit separate models using either temperature and water deficit (results  
285 presented in the main text) or precipitation and length of the growing season (results

286 presented in Appendix S3). Although not all variables were perfectly independent of each  
287 other, all of them were theoretically motivated and we aimed to avoid too many alternative  
288 models.

289 We first ran the model with all solid black and dashed links as presented in Fig. 1a.  
290 Here, solid black lines represent our predictions (P1-P4) about the indirect effect of climate,  
291 human land-use and fire on NPP via tree size and leaf traits. Dashed lines represent alternative  
292 direct effects of climate, human land-use and fire. To obtain the best-fit model we took a  
293 stepwise approach and removed weak and non-significant links and evaluated the model  
294 parameters at each step. Specifically, we aimed to 1) identify non-significant p-values of the  
295 Chi-squared test reflecting the probability of failing to reject the model given the data, 2)  
296 minimize the  $BIC_c$  (sample size-adjusted Bayesian Information Criterion) and the Root Mean  
297 Square Error of Approximation (RMSEA), and 3) maximize the Comparative Fit Index (CFI)  
298 and Tucker-Lewis Index (TLI) (Bollen, Harden, Ray, & Zavisca, 2014). We also checked for  
299 possible missing paths in the model according to the modification indices ( $\mu$ ) that represent  
300 the reduction in the Chi-squared value after adding the missing path; paths with  $\mu > 3.84$   
301 (corresponding to the Chi-square statistic value of  $p = 0.05$ ) were retained. We tested for  
302 missing paths between traits and disturbances (fire frequency, human land-use). These two  
303 predictors were not included in our original model because of mismatched temporal scales;  
304 plant species occurrence records were collected over a much longer time period than were the  
305 data underpinning the disturbance layers. Also, given that satellite data estimate of canopy  
306 height can be biased (Mitchard et al., 2014), we additionally explored a direct effect of  
307 potential maximum tree height on NPP acting independently of canopy height. We performed  
308 these analyses for all forests and then for tropical, temperate and boreal forest biomes  
309 individually.

310 In analyses focused on tropical and temperate forests, we accounted for a sub-biome  
311 effect (moist and dry tropical forests, coniferous and deciduous temperate forests). We predict  
312 (P4) the sub-biome to mirror climate effects, in part, and to also reflect differences in  
313 evolutionary history, topography or edaphic conditions that can affect NPP directly or  
314 indirectly via their effects on canopy height or the traits of species assemblages (Fig. 1b).

315

## 316 **Results**

317 Across all forest biomes (Fig. 3a, see also Fig. S4 in Appendix S3), NPP increased with  
318 increasing canopy height (in accordance with P1). Also, potential maximum tree height  
319 affected NPP indirectly via canopy height (in accordance with P2) and there was a positive  
320 link between potential maximum tree height and both soil water content (P2) and temperature.  
321 Still, the strongest NPP determinant was leaf N (in accordance with P3), while both  
322 temperature (with positive effect) and soil water content (with negative effect) affected NPP  
323 indirectly via leaf N (P3b). Unexpectedly (P3a), we did not find a support for a link between  
324 leaf N and soil nutrients. NPP further increased with increasing soil water content and  
325 temperature. When growing season length and precipitation were substituted for temperature  
326 and soil water content (Fig. S5a in Appendix S3), the growing season length became the  
327 strongest predictor of NPP (with positive effect) and of canopy height (with negative effect).  
328 Also, precipitation became the strongest determinant of potential maximum tree height (in  
329 accordance with P2) and there was a new negative link between topsoil organic carbon  
330 content and leaf N (in accordance with P3a). Other relationships were consistent with the first  
331 model.

332 In tropical forests (Fig. 3c, Fig. S6 in Appendix S3), NPP increased with increasing  
333 canopy height (in accordance with P1), and also, potential maximum tree height affected NPP  
334 indirectly via canopy height (in accordance with P2). NPP further increased with increasing

335 leaf P (in accordance with P3). As predicted (P1, P2 and P3b), climate had an indirect effect  
336 on NPP via plant traits. Specifically, potential maximum tree height increased with increasing  
337 soil water content, leaf P increased with decreasing precipitation, and both canopy height and  
338 leaf P increased with decreasing temperature. Leaf P further increased with increasing total  
339 soil phosphorus concentration (in accordance with P3a). Still, besides the indirect effect of  
340 climate, NPP of tropical forests strongly increased with increasing soil water content and  
341 growing season length while it also decreased with increasing precipitation. After accounting  
342 for moist and dry tropical sub-biome, sub-biome became an important predictor of NPP,  
343 canopy height, potential maximum tree height and leaf P as expected (P4), and the link  
344 between NPP and growing season length disappeared (Fig. 3d); otherwise relationships were  
345 consistent with the first model.

346         When analyzed across temperate forests (Figs 3e, see also S7 in Appendix S3), we did  
347 not find support for our prediction of the positive link between NPP and canopy height (P1).  
348 Also, the effect of leaf traits on NPP was unimportant. Instead, NPP increased with increasing  
349 temperature and soil water content. Lack of support for P1, however, was largely driven by  
350 the difference between broadleaf and coniferous sub-biome. Support for P1 was observed  
351 after controlling for the effect of sub-biome, when we found a significant positive missing  
352 path between NPP and potential maximum tree height (Fig. 3f). The nonsignificant effect of  
353 canopy height on NPP was largely driven by coniferous sub-biome (Fig S7) where canopy  
354 height often exceeded potential maximum tree height (Fig. S8 in Appendix S3) possibly due  
355 to the increasing uncertainty of satellite-based canopy height measurements with increasing  
356 terrain rugosity (Lefsky, 2010). Furthermore, both leaf N (with positive effect) and leaf P  
357 (with negative effect) became important predictors of NPP in temperate forests, and climate  
358 had an indirect effect on NPP via these traits (P3b). Specifically, leaf N increased with  
359 increasing temperature and both leaf N and leaf P decreased with increasing soil water

360 content. Contrary to our expectation (P3a), soil variables had no significant effects on leaf  
361 traits. Still, sub-biome became the strongest determinant of NPP, canopy height and potential  
362 maximum tree height. When using growing season length and precipitation instead of  
363 temperature and soil water content, precipitation became an important predictor of leaf N, leaf  
364 P and potential maximum tree height (Figs S5c-d); otherwise results remained qualitatively  
365 similar to the first model.

366 In boreal forests, temperature was the only predictor of both NPP (with positive effect)  
367 and canopy height (with negative effect) (Fig. 3b, see also Fig. S9 in Appendix S3) and none  
368 of our predictions concerning plant traits (P1, P2 and P3) were supported. These results could  
369 be affected by the low sample size ( $n=25$ ) caused by the low number of cells with  $>3$  species  
370 with known values of all traits. Therefore, we repeated the analysis without traits using all  
371 grid cells with boreal forest cover  $>50\%$  ( $n=58$ ). Still, the results remained qualitatively  
372 similar, except that NPP also increased with increasing total soil phosphorus concentration  
373 (Fig. S10a in Appendix S3). When growing season length and precipitation were substituted  
374 for temperature and soil water content, NPP strongly increased with increasing growing  
375 season length. It also weakly increased with increasing precipitation (Figs S5b and S10b).

376 To evaluate whether models including traits improve predictions of NPP over those  
377 based on climate alone, we additionally compared three sets of models: 1) Partial mediation  
378 models where climate affects NPP both directly and indirectly via functional traits, 2) No  
379 mediation models where traits do not explain the association between climate and NPP, and 3)  
380 Complete mediation models where traits completely explain the variation in NPP and climate  
381 has only indirect effect (see Fig. S11 as an example). We performed this analysis only for  
382 those biomes where traits were selected as important productivity predictors, specifically  
383 where Partial mediation models were selected by the model evaluation procedure (Figs. 3a,c-  
384 d,f, S5a,d). For the No mediation model we used the Partial mediation model structure and set

385 all parameters between traits and NPP to zero. To build the Complete mediation models we  
386 removed all direct links between climate (temperature, precipitation, soil water concentration  
387 and growing season length) and NPP. We compared the model fit according to the AIC and  
388 Chi-square statistics. In all cases Partial mediation models provided the best explanation of  
389 the data (Table S3).

390

### 391 **Discussion**

392 We found that productivity of American tropical and temperate forests is jointly affected by  
393 climate, plant size and leaf nutrient traits, but through differing direct and indirect paths. In  
394 boreal forests neither tree size nor leaf traits appeared as important predictors of productivity.  
395 Instead, productivity in boreal forests was driven by a direct role of temperature. Together,  
396 these results are largely consistent with theoretical expectations and recent empirical evidence  
397 (Enquist et al., 2015; Michaletz et al., 2014) where tree size is a central trait affecting carbon  
398 flux and biomass production in mature forests. Our results further underscore that more  
399 stressful climates likely modify these theoretical predictions at higher latitudes. Our results  
400 also agree with recent evidence of nutrient availability as another important regulator of forest  
401 carbon flux (Fernández-Martínez et al., 2014).

402 The finding that productivity of tropical forests increased with the height of the tallest  
403 trees is consistent with the previous observations that tree size is an important predictor of  
404 biomass production in this biome (Bastin et al., 2015; Fauset et al., 2015; Finegan et al.,  
405 2015). Our findings also agree with Michaletz et al. (2014, 2018) who concluded that climate  
406 affects productivity of forest plots indirectly, acting via stand biomass (see also Enquist,  
407 2011). Here, we found a positive indirect link between water availability (expressed as  
408 precipitation and soil water content) and productivity acting via potential maximum tree  
409 height, and a negative indirect link between temperature and productivity acting via canopy

410 height. This is consistent with the hydraulic limitation hypothesis (Ryan & Yoder, 1997) as  
411 decreasing water availability and increasing temperature increase the probability of drought  
412 embolism in tree hydraulic pathways (McDowell & Allen, 2015).

413 Our results indicate that tropical forest productivity is strongly influenced by water  
414 availability. Soil water content had a direct positive effect on tropical productivity and this  
415 link was stronger than the indirect path via plant size. In addition to the role of tree size and  
416 soil water content, tropical productivity increased with increasing leaf phosphorus  
417 concentration, driven by both climate and soil phosphorus concentration. This agrees with our  
418 prediction and with evidence of phosphorus as a key nutrient influencing productivity in  
419 warm and wet tropical lowland forests (Quesada et al., 2012; Vitousek, 1984). Unexpectedly,  
420 productivity of tropical forests further decreased with increasing precipitation. This  
421 relationship is, however, largely driven by the sites of high precipitation (>3m) that are not  
422 the most productive (Fig. S6). The highest precipitation occurs in northern part of the Amazon  
423 (Fig. S3) whereas the most productive sites are in the foothills of the Andes (Fig. 2). Such  
424 NPP patterns could result from the lower plant respiration rates caused by the lower  
425 temperature in higher altitudes. Lower productivity at sites of highest rainfall can also result  
426 from higher rates of soil weathering and nutrient leaching (Quesada et al., 2012). At the same  
427 time, higher tree mortality and turnover rates may lead to higher rates of carbon flux at sites  
428 with lower rainfall as a result of higher soil disturbances and episodic drought (Malhi et al.,  
429 2015; Quesada et al., 2012). Still, the variation explained in productivity of tropical forests  
430 was rather low compared to temperate and boreal forests, suggesting that we were missing  
431 some other important factor such as climatic or topographic heterogeneity, climate velocity or  
432 the effect of tree plantations.

433 In temperate forests, we found support for our prediction that tree size positively  
434 affects productivity only when we accounted for coniferous and deciduous sub-biomes. Still,

435 whereas productivity increased with increasing potential maximum tree height, the link  
436 between canopy height and productivity was unexpectedly not significant. It is, therefore,  
437 possible that other factors than realized tree height, such as past land-use legacies, leaf area  
438 index or nutrient limitation play, important role in carbon cycle of temperate forests (Coomes  
439 et al., 2012; Waring, 1983).

440 Consistent with the observation that nitrogen limitation on productivity is more  
441 pronounced in temperate than tropical regions (but see LeBauer & Treseder, 2008; Reich &  
442 Oleksyn, 2004), we found a strong positive link between leaf nitrogen concentration and  
443 temperate forest productivity. Our finding that leaf nitrogen concentration strongly increased  
444 with increasing temperature is consistent with the temperature-dependence of the forest  
445 nitrogen cycle (Brookshire et al., 2011). In contrast to tropical forests, productivity of  
446 temperate forests decreased with increasing leaf phosphorus, a relation largely driven by the  
447 deciduous sub-biome (Fig S7). Although phosphorus availability certainly limits plant growth  
448 in temperate forests (Wardle, Walker, & Bardgett, 2004), this finding can be interpreted as an  
449 adaptive response of plants to selection on fast growth rate (thus on high phosphorus demand)  
450 during the short vegetation season at high latitudes and altitudes (Kerkhoff, Enquist, Elser, &  
451 Fagan, 2005) where the productivity is generally low (Fig. 2f). Also, younger soils of  
452 temperate forests are richer in phosphorus relative to nitrogen available to plants, with the  
453 consequence that nitrogen availability generally drives production in this subbiome (Vitousek,  
454 Porder, Houlton, & Chadwick, 2010; Walker & Syers, 1976). Alternatively, this finding could  
455 result from an indirect effect of precipitation leaching soil phosphorus on older soils at lower  
456 latitudes (see also Šímová, Rueda, & Hawkins, 2017). Besides the indirect effect of climate  
457 (acting via potential maximum tree height and leaf traits), productivity of temperate forests  
458 also increased with increasing mean annual temperature, suggesting the direct effect of  
459 stressful climate on photosynthetic rates. Still, the strongest productivity predictor was the

460 effect of the sub-biome. This indicates that coniferous forests are on average less productive,  
461 given their canopy height, in comparison to deciduous forests (except of the relatively small  
462 area of highly productive forests of the North American pacific coast), which also  
463 corresponds to their relatively low carbon-use efficiency (DeLucia, Drake, Thomas, &  
464 Gonzalez-Meler, 2007).

465 In contrast to tropical and temperate forests, temperature was the only productivity  
466 determinant in boreal forests and we did not find any evidence for the effect of plant size or  
467 leaf traits. This finding deviates from a previous plot-based study showing that biomass  
468 production increases with the stand biomass, particularly in low-productivity boreal and  
469 montane forests (Keeling & Phillips, 2007). We suspect that the correlation between stand  
470 biomass and productivity of boreal forests observed by other studies (Jenkins, 2015; Keeling  
471 & Phillips, 2007) may be only indirect and could result from the effect of temperature limiting  
472 both these variables, but more studies are needed to confirm this hypothesis.

473 Despite the comprehensive datasets, our results may be affected by several important  
474 potential biases. First, our study is based on relatively coarse spatial grain leading to the  
475 relatively low number of cells with at least 50% forest coverage, in turn resulting in omitting  
476 some forest areas such as Rocky Mountains and Sierra Nevada in USA and Sierra Madre in  
477 Mexico. Also, at such spatial grain we cannot capture fine-scale influences, such as  
478 topography and forest development stages, which are key determinants of productivity (e.g.  
479 Michaletz et al., 2014). Nevertheless, this resolution avoids the false absence problem caused  
480 by the clumped distribution of species occurrence data and is generally recommended in  
481 macroecological studies (Hurlbert & Jetz, 2007).

482 A second potential issue is sampling bias; there were gaps in spatial coverage of tree  
483 occurrences in both the Amazon Basin and Canada (Fig. S1), which may have generated some  
484 of the outlying values in grid-cell 95<sup>th</sup> percentile and average of trait values. A possible

485 solution to avoid the sampling bias would be to use modelled species range maps.  
486 Nevertheless, the disadvantage of species range maps is that they are modelled in part using  
487 climate variables (Goldsmith et al., 2016), which could generate some level of circularity in  
488 analyses with climate as an explanatory variable. Also, for trait values, we were missing many  
489 records, especially from the Amazon Basin, which could also have biased our results. Still, as  
490 we showed in a previous study (Šímová et al., 2018), the trait-climate correlations of woody  
491 species are robust to this sampling bias. Some uncertainty also concerns canopy height due to  
492 the necessary extrapolation of the spatially separated point measurements (Tao et al., 2016),  
493 and also due to its inaccurate estimate with increasing terrain rugosity (Lefsky, 2010; Simard  
494 et al., 2011). Moreover, the ability of satellite-based canopy height in predicting above ground  
495 biomass (and thus also NPP) may be biased due to missing information of variation in wood  
496 density and tree allometry (Mitchard et al., 2014).

497         We suggest that our findings should be reexamined when better, large-scale trait and  
498 canopy data becomes available. Similar problems may also affect the MODIS-based  
499 productivity estimate, which is modelled based on remote sensing, solar radiation,  
500 temperature and water vapor deficit (Running et al., 2004; Zhao et al., 2005), potentially  
501 leading to some circularity in analyses with climate. Moreover, the MODIS-based  
502 productivity model does not explicitly account for the effect of soil nutrients as one of the  
503 factors limiting plant growth, which leads to some uncertainty of the productivity estimates,  
504 especially in tropical regions (Cleveland et al., 2015; Šímová & Storch, 2017). Large-scale  
505 soil data also can be problematic as they are generated with relatively high uncertainty (Yang,  
506 Post, Thornton, & Jain, 2013), which can be responsible for the overall weak support for the  
507 links between leaf and soil nutrients. Another potential problem concerns the data analysis.  
508 Although structural equation modelling (SEM) is a powerful data-analytic technique,  
509 selecting the model that best fits the data can result in some degree of selection uncertainty

510 (Whittingham, Stephens, Bradbury, & Freckleton, 2006). This is due to the dependency of  
511 model rankings on sample size (Preacher & Merkle, 2012). Consequently, it is important that  
512 our results be reevaluated when more data are available, especially from other parts of the  
513 world. Lastly, as our study is restricted to forests, we recommend future studies explore the  
514 link between plant functional traits and large-scale ecosystem processes in non-forest biomes.

515 In summary, our results point to the importance of tree size as a driver of forest  
516 productivity. We found that water availability limits productivity of tropical and temperate  
517 forests, both directly and indirectly via the maximum size to which tree species can grow.  
518 This finding agrees with the Metabolic Scaling Theory (West et al., 2009) and with recent  
519 evidence for tall trees as important drivers of forest carbon flux (Fauset et al., 2015;  
520 Stephenson et al., 2014). Further, we found that productivity of tropical and temperate forests  
521 strongly depends on the leaf nutrient concentration, which is also largely driven by climate.  
522 Our results support recent attempts to include information on plant functional traits in models  
523 predicting dynamics of the global carbon cycle (Reichstein, Bahn, Mahecha, Kattge, &  
524 Baldocchi, 2014). Nevertheless, the importance of plant traits is not universal, or is at least  
525 context dependent, as different processes matter more in different environmental contexts.

526

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550

#### 551 **Data Accessibility Statement**

552 The reference list for BIEN and TRY data is available in Appendix S1. The species  
553 occurrence table and raster maps of mean leaf traits are available via Šimová et al., (2018).  
554 The raster map of maximum plant height and aggregated data frame is available online at  
555 TRY file archive [link to be added after acceptance]. Trait data are available via the BIEN  
556 package (Maitner, 2017) and TRY (www.try-db.org).

557 **Author contributions:** IS, JC-S, BS and BJE conceived the study; IS analyzed the data and  
558 led the writing with major contributions from JC-S, BS and STM; BJE, RKP, BBoyle, J-CS,

559 SKW, CV, NJBK, NM-H and BJM developed the BIEN database  
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561 commented on the manuscript.

562

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840

#### 841 **Supporting information**

842 Additional Supporting Information may be found in the online version of this article:

843 Appendix S1 – Reference list for BIEN and TRY data

844 Appendix S2 – Spatial maps of forest biomes and sampling coverage of trait values

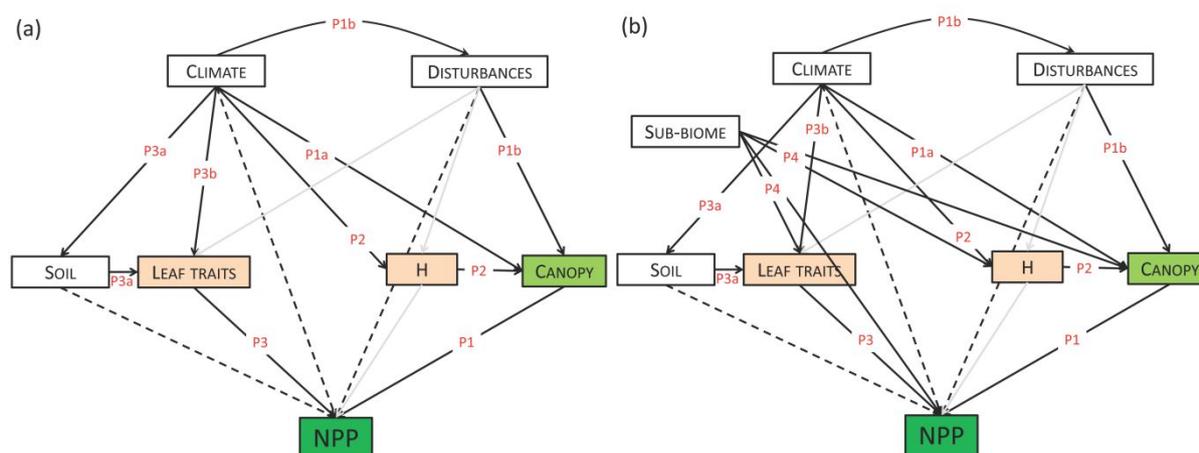
845 Appendix S3 – Supplementary models, maps and full model outputs

846 **Table 1:** Results from the structural equation models for different forest biomes and for all forests together. ‘Sub-biome’ indicates whether the  
 847 variable Sub-biome is included in the model (1) or not (0), Chi-sq contains the values of the Chi-square statistics, p-value (Chi) is the p-value of  
 848 the Chi-square test, CFI is Comparative Fit Index, TLI is Tucker-Lewis Index, RMSEA is Root Mean Square Error of Approximation, BICc is  
 849 sample-size-adjusted Bayesian Information Criterion, K is the number of free parameters, n is number of samples (grid cells) and  $r^2_{NPP}$ ,  
 850  $r^2_{Canopy}$ ,  $r^2_H$ ,  $r^2_{Leaf P}$ ,  $r^2_{Leaf N}$ ,  $r^2_{Fire}$  show variation explained for NPP, Canopy height, Potential maximum tree height (H), leaf phosphorus and  
 851 nitrogen concentration (Leaf P, Leaf N) and fire frequency. See Fig. 3 for the model diagrams.

Biome	Sub-biome	Chi-sq	df	p-value (Chi)	CFI	TLI	RMSEA	K	n	$r^2_{NPP}$	$r^2_{Canopy}$	$r^2_H$	$r^2_{Leaf P}$	$r^2_{Leaf N}$	$r^2_{Fire}$
All forests	0	1.54	2	0.46	1.00	1.00	0.00	16	258	0.50	0.31	0.19	-	0.70	-
Tropical	0	14.66	15	0.48	1.00	1.00	0.00	19	181	0.44	0.44	0.26	0.57	-	-
Tropical	1	17.36	13	0.18	0.99	0.98	0.04	21	177	0.50	0.51	0.36	0.58	-	-
Temperate	0	6.52	6	0.37	0.99	0.99	0.04	12	52	0.49	0.55	0.11	-	-	0.20
Temperate	1	5.02	7	0.66	1.00	1.03	0.00	23	52	0.70	0.69	0.28	0.44	0.56	-
Boreal	0	0.00	0	0.00	1.00	1.00	0.00	5	25	0.84	0.20	-	-	-	-

853 **Figure legends**

854



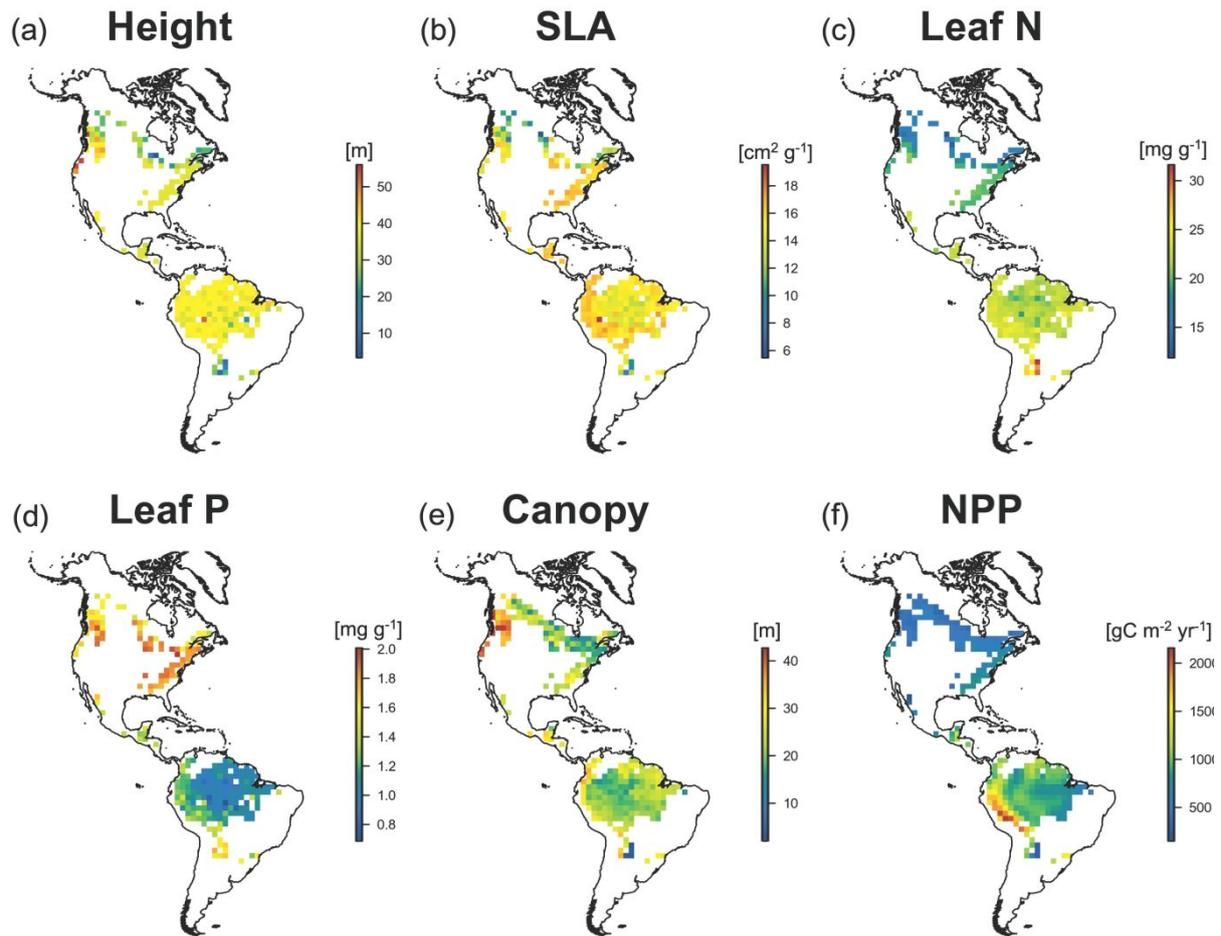
855

856 Figure 1: The conceptual path diagram for the structural equation modelling demonstrating  
 857 the hypothesized causal relationships of climate, disturbances, canopy height ('Canopy'),  
 858 potential maximum tree height ('H'), leaf traits, and soil nutrient concentration ('Soil') in  
 859 explaining net primary productivity ('NPP') of forest assemblages. Solid black lines represent  
 860 our predictions about the indirect effect of climate, disturbances and soil nutrient  
 861 concentration on NPP via tree size and leaf traits, whereas dashed lines represent alternative  
 862 direct effects of these variables on NPP. We further tested for the possible missing paths in  
 863 the model, highlighted in grey. Besides the original model (a), we added an effect of Sub-  
 864 biome (b), separating tropical and subtropical moist broadleaf forests from tropical and  
 865 subtropical dry broadleaf forests and temperate broadleaf and mixed forests from temperate  
 866 coniferous forests.

867

868

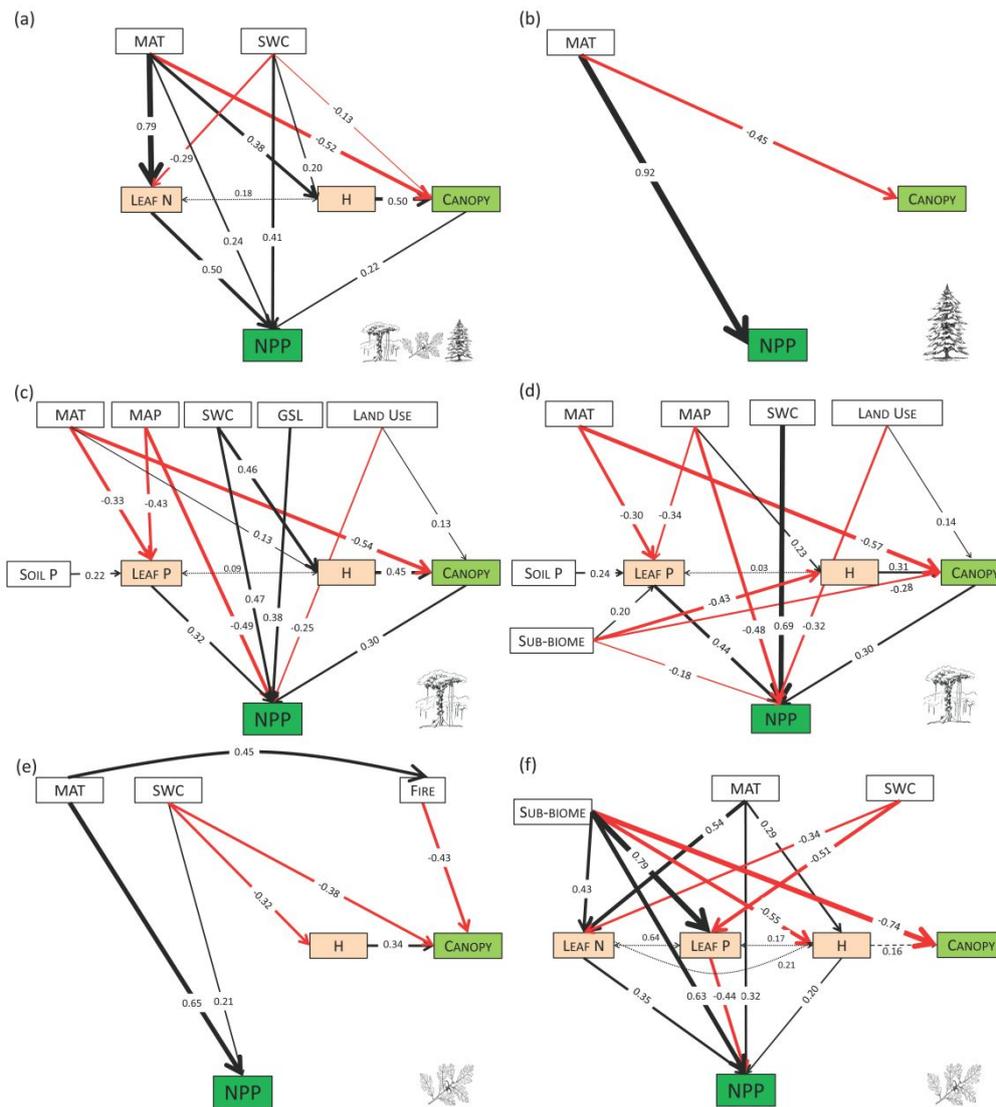
869



870

871 Figure 2: Maps of the productivity, canopy height and assemblage functional trait values of  
 872 the forest biomes estimated over the  $200 \times 200$  km grid-cells. (a) Potential maximum tree  
 873 height ('Height'), (b) specific leaf area ('SLA'), (c-d) leaf nitrogen and phosphorus  
 874 concentration ('Leaf N' and 'Leaf P') estimated from woody species occurrences, (e) canopy  
 875 height ('Canopy') estimated from the Geoscience Laser Altimeter System, and (f) net primary  
 876 productivity ('NPP') derived from the MODIS data. Note that panels a-d show only those  
 877 cells with  $>3$  species with known values of all four traits and with at least 50% of forest  
 878 coverage whereas cells on panels e-f are restricted only to at least 50% of forest coverage (see  
 879 also Fig. S1 in Appendix S2 for the sampling coverage). See Fig. S3 in Appendix S2 for maps  
 880 of all variables used in our models.

881



882

883 Figure 3: Structural equation models representing connections between productivity, canopy  
 884 height, and assemblage functional traits values for all forests together (a), boreal forests (b),  
 885 tropical forests without (c) or with (d) sub-biomes included, and temperate forests without (e)  
 886 or with (f) sub-biomes included. ‘MAT’ is temperature, ‘MAP’ is precipitation, ‘SWC’ is soil  
 887 water content, ‘GSL’ is growing season length, ‘Land-use’ is human land-use, ‘Fire’ is fire  
 888 frequency, ‘Canopy’ is canopy height, ‘H’ is potential maximum tree height, ‘Leaf N’ is leaf  
 889 nitrogen concentration, ‘Leaf P’ is leaf phosphorus concentration, ‘Soil P’ is total soil  
 890 phosphorus concentration and ‘NPP’ is net primary productivity. Sub-biome is coded as 0/1  
 891 for moist/dry tropical forests and for coniferous/broadleaf temperate forests respectively.

892 Significant links are represented by solid arrows, non-significant links ( $p > 0.05$ ) are  
893 represented by dashed arrows and error covariance is represented by dotted arrows. Positive  
894 links are black, negative links are red. The numbers next to each arrow are standardized  
895 coefficients. See Table 1 for the model results summary and Figs S4, S6-7, S9 for bi-variate  
896 relationships of each variable plotted against NPP. See also Fig. S5 for models with growing  
897 season length and precipitation instead of temperature and soil water content.  
898