

1 *Invited Tansley review*

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3 **Patterns and mechanisms of spatial variation in tropical forest productivity, woody residence**  
4 **time, and biomass**

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6 Helene C. Muller-Landau<sup>1</sup>, K. C. Cushman<sup>1</sup>, Eva E. Arroyo<sup>2</sup>, Isabel Martinez Cano<sup>3</sup>, Kristina J.  
7 Anderson-Teixeira<sup>1,4</sup>, and Bogumila Backiel<sup>1</sup>

8

9 <sup>1</sup>Center for Tropical Forest Science-Forest Global Earth Observatory, Smithsonian Tropical  
10 Research Institute, P.O. Box 0843-03092, Balboa, Ancón, Republic of Panamá;

11 <sup>2</sup>Columbia University, Department of Ecology, Evolution and Environmental Biology, 1200  
12 Amsterdam Avenue, New York, NY 10027, USA;

13 <sup>3</sup>Princeton University, Department of Ecology and Evolutionary Biology, Princeton, NJ 08544,  
14 USA;

15 <sup>4</sup>Conservation Ecology Center, Smithsonian Conservation Biology Institute and National  
16 Zoological Park, 1500 Remount Rd, Front Royal, VA 22630, USA.

17

18 Author for correspondence:

19 *Helene C. Muller-Landau*

20 *Tel: +507 212-8450*

21 *Email: [mullerh@si.edu](mailto:mullerh@si.edu)*

22

23 **Author ORCID IDS:**

24 Helene C. Muller-Landau: [0000-0002-3526-9021](https://orcid.org/0000-0002-3526-9021)

25 K. C. Cushman: [0000-0002-3464-1151](https://orcid.org/0000-0002-3464-1151)

26 Eva E. Arroyo: [0000-0002-8918-9721](https://orcid.org/0000-0002-8918-9721)

27 Isabel Martinez Cano: [0000-0003-4205-8596](https://orcid.org/0000-0003-4205-8596)

28 Kristina J. Anderson-Teixeira: [0000-0001-8461-9713](https://orcid.org/0000-0001-8461-9713)

29 Bogumila Backiel: [0000-0002-9429-2600](https://orcid.org/0000-0002-9429-2600)

30 **Social media:**

31 **Twitter:** @ForestGEO @stri\_panama @NGEETropics @K\_A\_Teixeira @bobackiel

32 **Facebook:** @ForestGEO @SmithsonianPanama

33 **Instagram:** @smithsonianpanama

34 **ResearchGate:** Helene C. Muller-Landau, KC Cushman, Isabel Martinez-Cano, Kristina J. Anderson-  
35 Teixeira

36

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54 **Summary:** Tropical forests vary widely in biomass carbon stocks and fluxes even after  
55 controlling for forest age. A mechanistic understanding of this variation is critical to accurately  
56 predicting responses to global change. We review empirical studies of spatial variation in  
57 tropical forest biomass, productivity, and woody residence time, focusing on mature forests.  
58 Woody productivity and biomass decrease from wet to dry forests and with elevation. Within  
59 lowland forests, productivity and biomass increase with temperature in wet forests, but  
60 decrease with temperature where water becomes limiting. Woody productivity increases with  
61 soil fertility, whereas residence time decreases, and biomass responses are variable, consistent  
62 with an overall unimodal relationship. Areas with higher disturbance rates and intensities have  
63 lower woody residence time and biomass. These environmental gradients all involve both  
64 direct effects of changing environments on forest carbon fluxes and shifts in functional  
65 composition – including changing abundances of lianas -- that substantially mitigate or  
66 exacerbate direct effects. Biogeographic realms differ significantly and importantly in  
67 productivity and biomass even after controlling for climate and biogeochemistry, further  
68 demonstrating the importance of plant species composition. Capturing these patterns in global  
69 vegetation models requires better mechanistic representation of water and nutrient limitation,  
70 plant compositional shifts, and tree mortality.

71 **Plain language summary:** Tropical forests vary widely in woody productivity, tree mortality, and  
72 biomass carbon stocks, even for forests of the same age. Reviewing previous studies, we find  
73 that productivity is highest in warm, wet forests on fertile soils, whereas mortality is higher at  
74 higher soil fertility and higher disturbance. This in turn means that biomass is higher at higher  
75 rainfall and temperature, lower disturbance, and intermediate soil fertility.

76 **Keywords:** Tropical forests, woody productivity, woody residence time, biomass carbon stocks,

77 precipitation, temperature, soil fertility, plant functional composition

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## 79 **I. Introduction**

80 Extant tropical forests vary widely in biomass density and thus carbon stocks, even  
81 when controlling for forest age (Becknell *et al.*, 2012; Lewis *et al.*, 2013; Poorter *et al.*, 2016;  
82 Alvarez-Davila *et al.*, 2017; Sullivan *et al.*, 2020). Much of this biomass variation is associated  
83 with climate and biogeochemistry, which influence woody productivity, residence time, and  
84 biomass both directly and indirectly via shifts in plant functional composition. However, our  
85 understanding of these patterns and their underlying mechanisms remains incomplete (Fig. 1).  
86 A mechanistic understanding of current variation in tropical forest carbon stocks and fluxes  
87 with climate, soils, and other factors is a critical precursor to accurately predicting forest  
88 responses to anthropogenic change.

89 Uncertainty about how tropical forest carbon pools will respond to global change is one  
90 of the largest sources of uncertainty in projecting future global carbon budgets and climate  
91 (Cavaleri *et al.*, 2015). Tropical forests currently account for two-thirds of terrestrial biomass  
92 carbon stocks (Pan *et al.*, 2013) and nearly a third of global soil carbon to 3 m depth (Jobbágy &  
93 Jackson, 2000). Increasing temperatures, changing precipitation patterns and disturbance  
94 regimes, increasing atmospheric carbon dioxide, and increasing nutrient deposition have the  
95 potential to greatly alter tropical forest carbon stocks and fluxes, and thus the global carbon  
96 budget (Lewis *et al.*, 2009; Wright, 2010). However, the combined impacts of these global  
97 change drivers on tropical forests remain unclear, with contrasting effects expected under  
98 different mechanisms and hypotheses, and mixed evidence to date of overall patterns (Lewis *et*  
99 *al.*, 2009; Wright, 2010). This uncertainty is reflected in highly divergent predictions for tropical

100 forest responses in different earth system models (Cavaleri *et al.*, 2015; Koven *et al.*, 2015;  
101 Rowland *et al.*, 2015).

102 Fundamentally, variation in mature forest aboveground biomass (AGB) arises from  
103 variation in aboveground woody productivity (AWP) and/or aboveground woody residence  
104 time (AWRT). AWP depends on NPP (net primary productivity) and allocation to wood, and  
105 ultimately on GPP (gross primary productivity) and carbon use efficiency (Malhi, 2012) (Fig. 1).  
106 In recent decades, as interest in forest carbon budgets has increased, many studies have  
107 investigated patterns and mechanisms of spatial variation in tropical forest AWP and AGB with  
108 abiotic and biotic factors (e.g., Levine *et al.*, 2016; Malhi *et al.*, 2017; Taylor *et al.*, 2017; Moore  
109 *et al.*, 2018; Sullivan *et al.*, 2020) (methods summarized in Box 1). This research builds naturally  
110 on an older literature on forest structure and composition (e.g., Richards, 1952; Gentry, 1988).  
111 Some consistent large-scale patterns have become clear; e.g., increasing dry season length (and  
112 decreasing precipitation) is associated with lower AWP and AGB (Becknell *et al.*, 2012; Poorter  
113 *et al.*, 2017; Taylor *et al.*, 2017). However, other patterns are inconsistent among studies; e.g.,  
114 AGB increases with soil fertility in some studies (Slik *et al.*, 2013; Lloyd *et al.*, 2015) and  
115 decreases in others (Lewis *et al.*, 2013; Schiatti *et al.*, 2016).

116 Mechanisms and patterns involving changes in tree mortality or shifts in plant functional  
117 composition remain poorly understood, whereas those involving changes in productivity of a  
118 given plant functional type along environmental gradients are relatively well-understood.  
119 Variation in tree mortality and thus AWRT is a key driver of spatial variation in AGB within the  
120 tropics (Johnson *et al.*, 2016), yet our understanding of tropical tree mortality remains  
121 extremely limited (McDowell *et al.*, 2018). Variation in plant functional composition also plays a

122 critical role in explaining large-scale variation in AWP, AWRT, and AGB. Different environments  
123 select for different plant functional composition, which in turn influences stand-level AWP,  
124 AWRT, and AGB in ways that may enhance or counter direct effects of environmental drivers  
125 (Fyllas *et al.*, 2009; Fyllas *et al.*, 2017; Turner *et al.*, 2018). For example, the abundance of lianas  
126 (woody climbing plants) varies strongly with environmental conditions (DeWalt *et al.*, 2015) and  
127 lianas negatively affect tree growth and survival and thus AWP, AWRT, and AGB (Ingwell *et al.*,  
128 2010; Duran & Gianoli, 2013; van der Heijden *et al.*, 2015; Lai *et al.*, 2017), with differential  
129 effects across tree species (Muller-Landau & Visser, 2019). Indeed, experimental liana removal  
130 increased AWP by 65% and AGB accumulation by 75% in a secondary moist tropical forest (van  
131 der Heijden *et al.*, 2015).

132 Earth system models (ESMs) are key tools for predicting the future of the global carbon  
133 cycle under global change, and for attributing temporal variation to different factors (Heavens  
134 *et al.*, 2013). These models are mechanistic, and attempt to capture hypothesized critical  
135 processes as gleaned from empirical studies (Heinze *et al.*, 2019). However, the most recent set  
136 of publicly released models completely fail to reproduce spatial variation in AGB, AWP, and  
137 AWRT in old-growth tropical forests (Fig. 2). This demonstrates that the models fail to  
138 adequately represent the mechanisms or capture the patterns of spatial variation in tropical  
139 forests today, and highlights the need for a more mechanistic understanding of these patterns.

140 Here we review empirical studies documenting how different environmental factors  
141 relate to tropical forest productivity, residence time, biomass, their proxies, and related  
142 variables. We first briefly describe the types of studies included, and their strengths and  
143 weaknesses. We then review empirical findings on tropical forest variation with climatic water



144 availability (precipitation regimes), elevation and temperature, soil fertility, disturbance, and  
145 biogeographic realm, and discuss hypothesized mechanisms underlying observed relationships.  
146 We discuss critical knowledge gaps and uncertainties in mechanistic understanding and in  
147 datasets, and key directions for future research.

## 148 **II. Methods**

149 We searched the literature for studies of among-site variation in our focal variables in  
150 mature, unlogged tropical forests, or in secondary forests when controlling for stand age, that  
151 included eight or more sites. We specifically searched for studies of variation in AGB, AWP,  
152 AWRT (Box 1), tree mortality rates, and tree turnover rates with respect to elevation,  
153 temperature, climatic measures of water availability (precipitation, dry season length, climatic  
154 water deficit, etc.), and/or soil fertility (soil phosphorus, cation exchange capacity, base cations,  
155 etc.). We also opportunistically tabulated studies reporting results for canopy height, basal  
156 area (BA), and basal area productivity (BAP), which serve as proxies for AGB and AWP (Box 1),  
157 as well as for the related productivity variables of ANPP, Litterfall NPP, and GPP (Fig. 1). Where  
158 a study included multiple analyses using different measures of the environmental factor of  
159 interest (e.g., precipitation and dry season length), we report the result for the independent  
160 variable showing a stronger relationship. Where both multivariate and bivariate analyses were  
161 reported, we report the multivariate analyses. Additional details on the literature search  
162 methods are given in Notes S1, the geographical distribution of data is shown in Figs. S1 and S9,  
163 and the resulting database is available at Dataset S1. In the remainder of this section, we  
164 discuss the main sources of error in our focal variables.

165 Most currently available information on our focal variables are based on tree plot  
166 census data. Because of high local spatial variability in the number and sizes of large trees,  
167 these plot-based estimates exhibit considerable sampling error, even for plots of 1 ha, and this  
168 error increases at smaller plot sizes (Muller-Landau *et al.*, 2014). We thus highlight studies  
169 based on plots with a median size of 1 ha or larger (124 of 201 results reviewed). Plot-based  
170 data may also have systematic errors, reflecting nonrandom plot placed. Some studies explicitly  
171 choose plot locations to avoid canopy gaps or areas of recent natural disturbance (e.g.,  
172 Kitayama & Aiba, 2002; Baez *et al.*, 2015), and plot locations tend to be biased towards taller  
173 forests even when methods do not explicitly state such criteria (Sheil, 1996; Marvin *et al.*,  
174 2014). Plots also tend to be located in more accessible areas, which have a stronger signature  
175 of past human land use (McMichael, CNH *et al.*, 2017) and current human impacts (McMichael,  
176 CH *et al.*, 2017).

177 Estimation of AGB and AWP depend on biomass allometry equations (Box 1), which are  
178 a major source of error. These equations estimate individual tree aboveground woody biomass  
179 from measured tree diameter, and sometimes also tree height and/or wood density (e.g.,  
180 (Chave *et al.*, 2005; Chave *et al.*, 2014)). The key issue for analyses of among-site variation is  
181 that studies typically apply the same equation(s) across many sites. However, biomass  
182 allometries differ systematically among sites (e.g., Chave *et al.*, 2014), reflecting differences in  
183 height allometries (Feldpausch *et al.*, 2012) and crown form (Ploton *et al.*, 2016), and  
184 potentially also rates of heartrot (Heineman *et al.*, 2015) and crown breakage (Arellano *et al.*,  
185 2019). Such differences are at best partially captured with generalized allometric equations  
186 which at best incorporate local height measurements and associated differences in diameter-

187 height allometries, continuous terms for climate variation, and/or different equations for  
188 different regions or forest types (Chave *et al.*, 2005; Chave *et al.*, 2014).

189 AWP estimates suffer from additional sources of error. AWP estimates depend on  
190 diameter growth measurements, and thus are highly sensitive to diameter measurement errors  
191 and to data quality assurance quality control procedures, including procedures for estimating  
192 diameter change in buttressed trees (Sheil, 1995; Cushman *et al.*, 2014; Muller-Landau *et al.*,  
193 2014). AWP is temporally variable (e.g., Rutishauser *et al.*, 2020), and thus sampling errors for  
194 short census intervals are high. At the same time, typical calculations underestimate AWP in  
195 longer census intervals because they increasingly miss AWP of trees that die between censuses  
196 (Kohyama *et al.*, 2019). Finally, standard methods for estimating AWP entirely fail to capture  
197 wood production to compensate for branchfall, estimated at 15-45% of total AWP (Malhi *et al.*,  
198 2014; Marvin & Asner, 2016; Gora *et al.*, 2019). That is, as trees grow, they do not simply accrue  
199 biomass, they also shed old branches as they produce new ones.

200 Residence time variables have particularly high sampling errors, which may in part  
201 explain the dearth of published analyses. Because tree mortality is a binomial process and  
202 mortality rates are low, sampling errors in mortality rates are large, especially in small plots and  
203 shorter census intervals. Strong temporal variation in mortality – for example due to droughts  
204 (Bennett *et al.*, 2015) – makes it yet more difficult to capture long-term mean mortality rates.  
205 Tree turnover rates, calculated as the average of mortality and recruitment rates, suffer these  
206 same problems. Syntheses of among-site patterns in mortality and turnover are further  
207 hindered by variability in methods for calculating mortality rates, inadequate reporting of  
208 calculation methods, and systematic biases in many estimators (Kohyama *et al.*, 2018) (see

209 Notes S1). Calculating AWRT as the quotient AGB/AWP (Box 1) only partially avoids this issue,  
210 as AWP estimates also depend on mortality (because trees that die don't contribute to AWP).  
211 Such estimates of AWRT may also be biased by the equilibrium assumption that underlies them  
212 (see Notes S1).

213 Finally, most estimates of AGB, AWP, and AWRT omit smaller trees, lianas, epiphytes,  
214 herbaceous plants, and non-woody tissues, and (by definition) below-ground biomass; these  
215 are generally assumed to be relatively small and/or to vary proportionately. These assumptions,  
216 and other aspects of measurement methods and associated errors are discussed in more detail  
217 in Notes S1.

### 218 **III. Climatic water availability**

219 Precipitation patterns vary among tropical forests from those that receive abundant  
220 precipitation year-round (wet tropical forests) to those that experience limitations in water  
221 availability during one or two dry seasons (moist and dry tropical forests), variation we  
222 encompass under the term climatic water availability. This variability is evident in the large  
223 range of mean annual precipitation among tropical forests (Fig. S2). In general, the length and  
224 intensity of dry seasons are more important than total annual precipitation in determining  
225 forest carbon stocks and fluxes. Further, water limitation depends not only on precipitation, but  
226 also on potential evapotranspiration (itself dependent on temperature, solar radiation), as well  
227 as soil depth, soil water-holding capacity, and topographic position. Many analyses thus  
228 evaluate relationships with more integrative measures of climatic water availability such as dry  
229 season length or maximum climatological water deficit, which are generally better predictors of

230 forest structure and dynamics (e.g., Alvarez-Davila *et al.*, 2017). Here, we discuss how our focal  
231 variables vary with climatic water availability, and evaluate patterns in relation to the range of  
232 annual precipitation and temperature within studies (Figs. 3, S3).

### 233 **Productivity**

234 Productivity variables are positively associated with climatic water availability across  
235 lowland tropical forests over the range from dry to wet forests. Across lowland sites, AWP,  
236 litterfall, and ANPP are positively related to climatic water availability in most studies (Fig. 3a),  
237 with an initial fast increase slowing to a plateau or even a mild decrease for precipitation above  
238 ~3000 mm/yr (Poorter *et al.*, 2017; Taylor *et al.*, 2017). The positive effects of precipitation  
239 weaken and reverse in montane tropical forests (e.g., lowland Hofhansl15b vs. montane  
240 Hofhansl15c in Fig. 3a; (Hofhansl *et al.*, 2015)). A meta-analysis of 145 tropical forests found  
241 that an increase in mean annual precipitation (MAP) from 1000 to 3000 mm was associated  
242 with a 2.3-fold increase in ANPP at 28°C, a 1-5 fold increase at 24°C, no change at 20°C, and a  
243 decrease in ANPP at temperatures below 20°C (Taylor *et al.*, 2017).

244 Lower forest productivity at lower precipitation reflects limitation by water availability  
245 and/or drought stress when potential evapotranspiration exceeds precipitation, combined with  
246 allocational changes and compositional shifts towards drought-tolerant species (Flack-Prain *et*  
247 *al.*, 2019). Limited water availability translates into reduced gross primary production through  
248 both reduced leaf area maintained (including drought deciduous leaf phenology) and reduced  
249 photosynthesis per available leaf area as plants close their stomates and/or invest in more  
250 drought-tolerant organs with lower light use efficiency (Tan *et al.*, 2013; Guan *et al.*, 2015; Wu  
251 *et al.*, 2016; Pfeifer *et al.*, 2018). Higher precipitation is also associated with higher allocation of

252 above-ground NPP to AWP (Hofhansl *et al.*, 2015) and taller trees for a given diameter (Banin *et*  
253 *al.*, 2012), further contributing to higher AWP. Compositional shifts also contribute: species  
254 found in drier forests have lower growth rates than those restricted to wetter forests (Baltzer &  
255 Davies, 2012; Brenes-Arguedas *et al.*, 2013; Kupers *et al.*, 2019), because drought-tolerance  
256 traits, such as narrower xylem vessels, are costly (Gorel *et al.*, 2019), whereas the “drought-  
257 avoiding” deciduous strategy involves foregoing photosynthesis in part of the year (Brenes-  
258 Arguedas *et al.*, 2013).

259           Though the direct effects of water availability on productivity are positive, higher rainfall  
260 is also associated with increased cloudiness and decreased soil fertility, both of which depress  
261 productivity, and may explain declining productivity at very high rainfall and lower  
262 temperatures (Taylor *et al.*, 2017). Wetter sites on average have higher cloudiness and thus  
263 reduced light availability (Wagner *et al.*, 2016). High precipitation is also associated with soil-  
264 mediated reductions in productivity due to leaching of nutrients and reduced soil redox  
265 potential; these influences are relatively more important at cooler temperatures. Decreases in  
266 productivity with precipitation at the very highest levels of precipitation, especially in cooler  
267 sites (Taylor *et al.*, 2017) likely reflect these correlated increases in limitation by light and  
268 nutrients.

269

## 270 ***Residence time***

271           Few studies have evaluated how among-site variation in AWRT, mortality, or turnover  
272 relate to climatic water availability, and those that do have found at best weak relationships  
273 (e.g., Quesada *et al.*, 2012; Vilanova *et al.*, 2018). More studies have found trends for AWRT to

274 be higher (and turnover lower) in wetter sites than the opposite, but overall patterns are  
275 inconsistent (Fig. 3b). This may reflect contrasting trends in different mortality threats with  
276 precipitation regimes. Drier sites are more likely to experience fire (Cochrane, 2011) and  
277 drought stress elevates mortality through hydraulic damage (Choat *et al.*, 2018), whereas  
278 higher rainfall is associated with greater risks of mortality from treefalls, lightning, and  
279 landslides (Espirito-Santo *et al.*, 2010; Yanoviak *et al.*, 2020).

280 In contrast to the paucity of studies of spatial variation, there have been multiple  
281 studies of temporal variation. Many studies have documented elevated mortality in drought  
282 years (reviewed in (Phillips *et al.*, 2010; Bennett *et al.*, 2015)), whereas a few have found higher  
283 mortality in wetter years (Aubry-Kientz *et al.*, 2015) or wetter seasons (Brokaw, 1982; Fontes *et*  
284 *al.*, 2018). Patterns of temporal variation in mortality with water availability do not necessarily  
285 predict among-site variation because compositional shifts at least partially compensate for  
286 shifts in mortality threats. For example, tree species common in drier sites have higher survival  
287 under drought than those common in wetter sites (Engelbrecht *et al.*, 2007; Baltzer & Davies,  
288 2012; Brenes-Arguedas *et al.*, 2013; Esquivel-Muelbert *et al.*, 2017).

## 289 **AGB**

290 AGB is positively related to climatic water availability in tropical forests in 16 of 16  
291 studies finding a statistically significant relationship (Fig. 3c). The relationship of AGB with  
292 precipitation exhibits an initially steep increase below 2000 mm/yr gradually saturating at  
293 higher precipitation (Becknell *et al.*, 2012; Poorter *et al.*, 2016; Alvarez-Davila *et al.*, 2017).  
294 Increases are roughly parallel in old-growth and secondary forests: over 1000-3000 mm MAP,  
295 AGB increases 2-fold in 20-year secondary forests (Poorter *et al.*, 2016), and ~2.3-fold in mature

296 forests (Alvarez-Davila *et al.*, 2017). Qualitatively the same patterns are found for tree basal  
297 area and canopy height, for both plot-based and remote sensing studies, and in both old-  
298 growth and secondary forests of a given age (Fig. 3c). Measures of drought stress such as dry  
299 season length or dry season water deficit are generally better predictors of AGB than  
300 precipitation alone, and exhibit more linear relationships with AGB (Poorter *et al.*, 2016;  
301 Alvarez-Davila *et al.*, 2017). At extremely high precipitation levels above ~4000 mm/yr, AGB  
302 may decrease with further increases in precipitation, but there are few data for such sites, and  
303 spatial variation in precipitation may be confounded with solar radiation, soil fertility and other  
304 factors (Alvarez-Davila *et al.*, 2017). Overall the patterns in AGB parallel those in AWP,  
305 consistent with what would be expected given little variation in AWRT with precipitation (Fig.  
306 4a).

### 307 **Synthesis**

308 Overall, patterns of variation in tropical forest productivity and biomass with climatic  
309 water availability are relatively well-documented and well-understood, and the underlying  
310 mechanisms are increasingly well-represented in forest and vegetation models (Christoffersen  
311 *et al.*, 2016; Levine *et al.*, 2016; Xu *et al.*, 2016). Additional data and analyses are needed to  
312 establish whether/how mortality rates vary spatially with climatic water availability, and to  
313 investigate the role of compositional shifts in contributing to variation in carbon fluxes and  
314 stocks. The role of lianas deserves more attention, as lianas are more abundant in drier sites  
315 (DeWalt *et al.*, 2010), and could contribute to their lower tree productivity and possibly lower  
316 residence time.

317



## 318 **IV. Temperature and elevation**

319           Most temperature variation across tropical forests is explained by elevation (Pearson  $r=$   
320 0.96 across 14,643 1-km pixels; Fig. 5a), and thus our understanding of temperature influences  
321 is based largely on elevational variation. However, it is important to keep in mind that  
322 elevational temperature variation is confounded with other factors. Atmospheric pressure  
323 decreases systematically with elevation, which affects photosynthesis both directly and  
324 indirectly by altering selection on photosynthetic traits (Wang *et al.*, 2017). Cloud cover (and  
325 thus solar radiation) and precipitation also change with elevation (Fig. 5b,c), as do other climate  
326 variables and geomorphology (Porder *et al.*, 2007). Indeed, across tropical forests globally,  
327 mean cloud cover increases from 57% at 29°C to ~89% at 8°C (Fig. S4). Here we synthesize  
328 results for the many observational studies of variation with elevation and the few with  
329 temperature, and graph results in relation to the ranges of temperature, elevation, and  
330 precipitation represented in each study (Figs. 6, S5).

### 331 ***Productivity***

332           All productivity variables decline with elevation (Fig. 6a), suggesting a positive effect of  
333 temperature, but analyses with temperature find both positive and negative effects (Fig. 6a,d).  
334 Overall patterns seem consistent with a positive effect of temperature in wet sites, and a  
335 negative effect in dry sites. This is particularly apparent in studies that evaluate interactions of  
336 climatic water availability and temperature (Taylor *et al.*, 2017; Sullivan *et al.*, 2020). A meta-  
337 analysis found that ANPP (litterfall) decreased with temperature for precipitation below ~1400  
338 mm/yr (1600 mm/yr), and increased with temperature for precipitation above that level, with

339 ever faster increases for higher precipitation (Taylor *et al.*, 2017). At 2500 mm MAP, ANPP  
340 doubles between 10 and 22°C and triples by 28°C (Taylor *et al.*, 2017).

341         Spatial variation in AWP with temperature can be explained in large part by the  
342 temperature responses of plant metabolic rates – photosynthesis and respiration. Across sites,  
343 the optimum temperature for photosynthesis is strongly positively correlated with mean  
344 growing season temperature (Tan *et al.*, 2017), and the photosynthetic rate at the temperature  
345 optimum increases with temperature, meaning warmer sites are expected to have higher  
346 photosynthetic rates, if water is not limiting (Farquhar *et al.*, 1980). Maintenance respiration  
347 rates also increase with temperature within sites -- but acclimation means that respiration rates  
348 at growth temperatures increase very little or not at all (Atkin *et al.*, 2015; Malhi *et al.*, 2017).  
349 Biomass accumulation rates increase with temperature in well-watered conditions (Cheesman  
350 & Winter, 2013), likely reflecting an increase in biosynthesis rates. In contrast, where water is  
351 limiting, photosynthesis decreases with temperature due to increased stomatal closure and  
352 higher respiratory costs (Schippers *et al.*, 2015). Overall, for any given plant and site, net  
353 photosynthesis is expected to be a unimodal function of temperature, reflecting biochemically  
354 determined unimodal responses of maximum photosynthetic rates in combination with  
355 stomatal conductance and respiration (Slot & Winter, 2017).

356         Allocational and compositional shifts also contribute to spatial variation in AWP with  
357 temperature. Cooler sites tend to have plant species with higher nutrient use efficiencies,  
358 longer-lived leaves, higher LMA (Asner & Martin, 2016) and other slow life history traits (Dalling  
359 *et al.*, 2016; Bahar *et al.*, 2017). These traits increase competitiveness in lower resource  
360 environments, while reducing light use efficiency and thus stand-level productivity (Reich,

361 2014). Cooler, higher elevation sites also tend to have higher allocation below-ground, a  
362 pattern consistent with increased nutrient limitation (Hofhansl *et al.*, 2015). This allocational  
363 shift could reconcile stronger elevational decreases in ANPP with weaker patterns in total NPP.  
364 Among water-limited sites, increasing temperature increases drought stress, potentially leading  
365 to the same types of allocational and compositional shifts expected under reduced climatic  
366 water availability.

367 Finally, correlated variation in other environmental factors also influences patterns with  
368 temperature among tropical sites. Cooler tropical forests are found overwhelmingly at higher  
369 elevations, where cloud cover is higher and fog is more frequent, thereby decreasing solar  
370 radiation and increasing light limitation (Bruijnzeel *et al.*, 2011). Cooler temperatures also slow  
371 decomposition (Taylor *et al.*, 2017) and reduce biological N fixation (Houlton *et al.*, 2008),  
372 which tends to reduce nutrient availability, especially nitrogen availability (Wilcke *et al.*, 2008;  
373 Nottingham *et al.*, 2015). However, higher elevation and thus cooler forests tend to be found  
374 on geochemically young substrates with eroding slopes, which are associated with relatively  
375 higher availability of rock-derived nutrients (Porder *et al.*, 2007). Thus, for any given area,  
376 elevational variation in cloud cover, rainfall, and soils can magnify or counter the patterns  
377 expected based on temperature alone, and interact with compositional shifts (Peng *et al.*,  
378 2020).

### 379 ***Residence time***

380 Few studies have evaluated how AWRT, mortality, or turnover rates vary with  
381 temperature or elevation, and relationships were not statistically significant in most studies  
382 (Fig. 6b,e). Of the four studies finding significant relationships with elevation, three show higher

383 AWRT (lower turnover) at higher elevation (Fig. 6b). This is consistent with the global pattern  
384 of a positive correlation between tree productivity and mortality (Stephenson & Mantgem,  
385 2005), given that higher elevations tend to be associated with lower productivity and slower life  
386 histories (e.g., lower LMA Asner & Martin, 2016).

### 387 **AGB**

388 AGB decreases with elevation in most studies, and canopy height decreases with  
389 elevation in almost all studies, but patterns of basal area variation are decidedly mixed, as are  
390 patterns of AGB with temperature (Fig. 6c, f). It's notable that some studies find very high or  
391 even the highest AGB at intermediate or high-elevation sites (e.g., Girardin *et al.*, 2010); the  
392 mechanisms underlying these exceptions are an important area for future research. In terms of  
393 the quantitative strength of these effects, regressions of AGB on elevation in Bolivia, Peru, and  
394 Ecuador find that AGB decreases 32, 34, and 50 Mg/ha per 1000 m elevation, respectively  
395 (Girardin *et al.*, 2014). Overall, the patterns in AGB with elevation and temperature largely  
396 mirror those in AWP.

### 397 **Synthesis**

398 The biochemical and physiological mechanisms by which temperature interacts with  
399 water availability to affect plant productivity are relatively well understood. These are central  
400 to responses to short-term temporal variation in temperature within sites, which is reasonably  
401 well captured in mechanistic models (Schippers *et al.*, 2015). In contrast, responses to spatial  
402 variation in temperature regimes depend in large part on acclimation, allocational shifts, and  
403 compositional variation, and remain poorly understood. Compositional patterns, such as the  
404 decline in lianas and palms with elevation (e.g., Lieberman *et al.*, 1996), are likely to be major

405 contributors to among-site variation in tropical forest carbon cycling with elevation and  
406 temperature; they deserve more attention. Finally, among-site patterns may vary not only with  
407 mean temperatures but also with extremes; e.g., relationships with maximum temperature  
408 were more often negative than those with mean temperature (Dataset S1).

## 409 **V. Soil fertility**

410 Tropical forests exhibit great heterogeneity in their biogeochemistry, reflecting wide  
411 variation in soil age, chemistry, and susceptibility to erosion or uplift, as well as high plant  
412 diversity; diversity matters because plants can affect soil properties under their crowns  
413 (Townsend *et al.*, 2008; Waring *et al.*, 2015). Soil fertility is multi-dimensional, involving many  
414 different nutrients important in different ways (Kaspari & Powers, 2016), and available in  
415 different concentrations and forms at different soil depths, that covary across sites (e.g.,  
416 Quesada *et al.*, 2010). Many studies thus evaluate patterns with respect to principal  
417 components axis or soil classes that reflect covariation in multiple nutrients (“Multi” in Fig. 7).  
418 In cases where individual studies investigated relationships with multiple soil fertility variables,  
419 we report results relative to the variable showing the strongest relationship with the  
420 dependent variable.

### 421 ***Productivity***

422 AWP, BAP, ANPP, and litterfall are positively related to soil fertility in tropical forests.  
423 Of 22 analyses of among-site variation, 21 showed a positive trend, and 16 were significantly  
424 positive (Fig. 7a). Fertilization experiments further demonstrate that tropical forest  
425 productivity is limited by P and by N, and suggest that K and Ca might also be limiting –only one

426 tropical forest fertilization experiment manipulated K or Ca (Wright, 2019). However, the range  
427 of AWP variation explained by fertility seems to be relatively smaller than that explained by  
428 climate; for example, AWP on high-phosphorus soils averages ~20% higher than AWP on low-  
429 phosphorus soils in the Amazon and Sierra Leone (Quesada *et al.*, 2012; Jucker *et al.*, 2016).  
430 This may in part reflect shifts in allocation with fertility, with increased allocation to  
431 reproduction in more fertile sites (Wright *et al.*, 2011).

432         The increase in woody productivity with soil fertility is consistent with our mechanistic  
433 understanding of the role of nutrients in plant function. Higher soil nutrients enable higher  
434 plant nutrient content (Fyllas *et al.*, 2009; Cleveland *et al.*, 2011; Asner & Martin, 2016), which  
435 in turn enables greater plant light use efficiency (Elser *et al.*, 2010). Higher soil nutrient  
436 availability also means plants need to spend fewer resources on nutrient acquisition, whether  
437 in constructing roots or supporting microbial symbionts, which enables higher fertility forests to  
438 turn a higher proportion of their GPP into aboveground biomass production (Vicca *et al.*, 2012;  
439 Doughty *et al.*, 2018). However compositional shifts partly compensate, as low-fertility sites  
440 have species with better nutrient acquisition abilities and higher nutrient use efficiencies,  
441 reducing productivity differences with soil fertility (Gleason *et al.*, 2009; Dalling *et al.*, 2016;  
442 Turner *et al.*, 2018). In addition, herbivory and liana abundance increase with soil fertility; it  
443 may be that these consumers and structural parasites capture a disproportionate share of the  
444 benefits of elevated nutrient availability (Schnitzer & Bongers, 2002; Campo & Dirzo, 2003). The  
445 consequence of these compositional shifts and biotic interactions is that the increase in stand-  
446 level AWP with fertility is lower than would be expected based on single-species responses in  
447 isolation, and may even be absent (e.g., Turner *et al.*, 2018).

448 **Residence time**

449           Soil fertility is positively associated with tree mortality rates and thus negatively  
450 associated with AWRT across tropical forests (Fig. 7b). This pattern has been found at local (de  
451 Toledo *et al.*, 2011; Sawada *et al.*, 2015), regional (Quesada *et al.*, 2012), and global (Galbraith  
452 *et al.*, 2013) scales. This variation is substantial, eclipsing both variation in productivity with soil  
453 fertility and variation in AWRT with climate. For example, across 59 sites in the Amazon,  
454 turnover increased 3-fold from low to high soil phosphorus (Quesada *et al.*, 2012). Pantropical  
455 analyses also found strong relationships, with median AWRT increasing ~50% from young to old  
456 soils in Neotropical forests, and from intermediate to old soils in Paleotropical forests (Galbraith  
457 *et al.*, 2013).

458           Three classes of mechanisms likely contribute to higher mortality at higher soil fertility.  
459 First, higher growth at higher soil fertility speeds the rate of self-thinning, thereby increasing  
460 associated mortality rates (Stephenson & Mantgem, 2005). Second, more productive  
461 environments select for tree species with “fast” life history strategies such as low wood density  
462 (Quesada *et al.*, 2012), and given underlying tradeoffs, these species also have higher mortality  
463 rates (Stephenson & Mantgem, 2005; Kraft *et al.*, 2010; Wright *et al.*, 2010; Reich, 2014). Third,  
464 higher soil fertility is associated with higher liana abundance (Putz & Chai, 1987; Laurance *et al.*,  
465 2001; Schnitzer & Bongers, 2002; DeWalt *et al.*, 2006), and higher liana abundance is associated  
466 with higher tree mortality in observational and experimental studies (Ingwell *et al.*, 2010; van  
467 der Heijden *et al.*, 2015; Wright *et al.*, 2015).

468 **AGB**

469           The combination of increasing AWP and decreasing AWRT with fertility would lead to  
470 the expectation of a unimodal relationship of AGB with fertility, with AWP limiting at the low  
471 end and AWRT at the high end (Fig. 4c). Empirical studies have variously found positive,  
472 negative and no relationships of tropical forest AGB to soil fertility (Fig. 7c). For example, AGB  
473 decreased 1.4-fold from low to high soil P across 59 plots in the Amazon (Quesada *et al.*, 2012),  
474 and decreased ~2 fold from the lowest to highest total base cations across 260 plots in Africa  
475 (Lewis *et al.*, 2013), whereas it increased 1.4-fold with soil nitrogen across 63 plots in the  
476 central Amazon (Laurance *et al.*, 1999). These different patterns are consistent with what we  
477 might expect if studies span different parts of an overall unimodal relationship. Because the  
478 decrease in AWRT is greater than the increase in AWP with fertility, we expect the peak to be  
479 located closer to the lower fertility end of the gradient. The location of the peak in AGB with  
480 respect to soil fertility is likely to vary across regions, reflecting compositional differences  
481 among regions and strong interspecific variation in mortality rates and responses to soil fertility  
482 (Condit *et al.*, 2006; Condit *et al.*, 2013).

483 **Synthesis**

484           It has long been clear that soil fertility plays a critical role in tropical forest structure and  
485 function (Vitousek & Sanford, 1986), and the broad outlines of its importance are evident in  
486 studies to date (Fig. 7). A central challenge is that tropical tree species display a wide diversity  
487 of strategies for nutrient acquisition and use, strategies that are critical to compositional shifts  
488 and stand-level responses to soil fertility, and their regional variation (Laliberte *et al.*, 2017). Yet  
489 our understanding of these strategies – which include not only root morphology and foraging



490 behavior but also chemical root exudates and interactions with microbial symbionts – remains  
491 very limited, reflecting the general paucity of data on roots and below-ground interactions.

492         New data, analyses, and modeling are needed to advance our understanding of soil  
493 fertility's role in structuring variation in tropical forests. More, better, and more consistent data  
494 on tropical soils is a critical component, especially in enabling better analyses of large-scale  
495 patterns (Hengl *et al.*, 2017). The ability to estimate foliar nutrients from airborne hyperspectral  
496 imaging has enabled large-scale data collection of these quantities and their relation to soils  
497 (e.g., Chadwick & Asner, 2018); and satellite hyperspectral missions promise further advances  
498 (Schimel *et al.*, 2013). Earth system models are starting to incorporate nutrients  
499 mechanistically, and can provide useful tools to explore associated mechanisms and link them  
500 to patterns at different levels (Medvigy *et al.*, 2019; Sulman *et al.*, 2019).

## 501 **VI. Disturbance**

502         Tropical forests vary strongly in the frequency and intensity of natural disturbances,  
503 with important consequences for forest structure, dynamics, and composition. Here, we focus  
504 specifically on short-term natural disturbances such as storms, landslides, and wildfires,  
505 excluding disturbance by chronic stressors such as drought (addressed under water availability  
506 above) and flooding (addressed by (Daskin *et al.*, 2019)). Variation in natural disturbance rates  
507 across the tropics is substantial and systematic. The frequency and intensity of large-scale  
508 tropical cyclones (known regionally as hurricanes, typhoons, or cyclones) is near zero in tropical  
509 forests with latitudes  $<10^\circ$ , and varies strongly among other areas (Ibanez *et al.*, 2019).  
510 Convective thunderstorms and lightning occur across the tropics; and both show strong  
511 geographic variation in frequency (Pereira-Filho *et al.*, 2015; Gora *et al.*, 2020). Within sites,

512 storm impacts vary topographically, reflecting variation in wind exposure (highest on ridges,  
513 (Boose *et al.*, 1994)), soil saturation (highest in floodplains and concave topographies,  
514 (Margrove *et al.*, 2015)), and landslide risk (highest on steep slopes, (Larsen & Torres-Sanchez,  
515 1998).) Wildfire risk increases with dry season length and intensity, as well as with proximity to  
516 anthropogenic disturbance (Cochrane, 2011).

517 Disturbance directly increases tree mortality and decreases AWRT, thereby reducing  
518 AGB (Fig. 4d). Both large-scale cyclones and local convective storms increase tree mortality  
519 from treefalls (including landslides) (Larsen & Torres-Sanchez, 1998; Ostertag *et al.*, 2005;  
520 Negrón-Juárez *et al.*, 2017; Hall *et al.*, 2020) and convective thunderstorms also kill trees via  
521 lightning (Yanoviak *et al.*, 2020). Across tropical forests, higher lightning frequency is associated  
522 with higher biomass turnover rates and lower old-growth forest biomass (Gora *et al.*, 2020).  
523 Higher tropical cyclone frequency is associated with lower canopy height and higher stem  
524 density, reflecting an increasing number of smaller stems (Ibanez *et al.*, 2019). In humid  
525 tropical forests, median canopy height was 1.3-fold higher where cyclone frequency averaged  
526 less than one per century than where it averaged greater than one per decade (Ibanez *et al.*,  
527 2019). Topographic variation in storm impacts is evident in mortality patterns; e.g., cyclone  
528 mortality rates are higher in areas with greater wind exposure (Negrón-Juárez *et al.*, 2014).  
529 Fires directly kill trees and also increase mortality rates in subsequent years, especially in  
530 wetter forests (Barlow *et al.*, 2003), and areas that have experienced fires have lower biomass  
531 stocks than unburned areas for decades afterwards (Gerwing, 2002; Sato *et al.*, 2016).

532 Disturbance also influences functional composition, as tropical tree species differ  
533 strongly in how they are affected by disturbances (Zimmerman *et al.*, 1994; Curran *et al.*, 2008;

534 Slik *et al.*, 2010b; Paz *et al.*, 2018; Staver *et al.*, 2019). In general, species with “faster” life  
535 histories are able to rebound more quickly following disturbances, and thus are more common  
536 in areas with recent disturbances (Paz *et al.*, 2018). Associated tradeoffs mean that  
537 disturbances generally increase the relative abundance of tree species with fast life histories,  
538 which tend to have low wood densities and achieve low biomass (Carreno-Rocabado *et al.*,  
539 2012; Paz *et al.*, 2018). Lianas also proliferate after disturbances, and thus high disturbance  
540 frequency increases liana abundance (Schnitzer & Bongers, 2011). Different disturbances can  
541 also favor particular traits; for example, species with higher wood density are less likely to  
542 suffer stem breaks during a hurricane (Zimmerman *et al.*, 1994). Whereas shifts towards more  
543 disturbance-resistant species would tend to mitigate the direct effects of disturbance on  
544 mortality and biomass, increases in the abundance of lianas and of tree species with fast life  
545 history strategies would tend to further increase mortality and reduce biomass. Thus,  
546 compositional responses to disturbances also need to be considered to determine the total  
547 impacts of disturbance regimes on tropical forest structure and dynamics.

## 548 **VII. Biogeographic realm**

549 Tropical forests on different continents have significantly different productivity,  
550 residence time, and biomass. AWP is 25% higher in Asian than in Latin American forests (Taylor  
551 *et al.*, 2019). Mean AWRT in old-growth tropical forests is also higher in Asia and Africa than in  
552 Latin America, by 22 and 33%, respectively (Galbraith *et al.*, 2013). Consistent with higher AWP  
553 and AWRT, AGB is higher in Paleotropical than in Neotropical forests, in both plot-based and  
554 satellite-based datasets (Lewis *et al.*, 2013; Slik *et al.*, 2013; Avitabile *et al.*, 2016; Sullivan *et al.*,  
555 2017; Taylor *et al.*, 2019). For example, plot-based studies find that mean AGB is 29% higher in

556 Asian than Latin American forests (Taylor *et al.*, 2019), and 26% higher in central Africa than in  
557 central Amazonia (Lewis *et al.*, 2013). The dearth of studies of African forests is particularly  
558 concerning in light of these important biogeographic differences (Figs. S1, S9).

559         Tropical forests in different biogeographic regions differ significantly in plant allocation,  
560 tree allometry, and forest structure. African forests have a larger proportion of their biomass in  
561 the largest trees than do Neotropical forests (Bastin *et al.*, 2018). Allocation of NPP to AWP is  
562 substantially higher in Asian than in Neotropical forests (Paoli & Curran, 2007; Malhi *et al.*,  
563 2011; Taylor *et al.*, 2019), which could contribute to the differences in AWP. Tropical trees in  
564 Asia are taller for the same diameter than those in other tropical regions (Feldpausch *et al.*,  
565 2012), with Africa intermediate and American trees shortest (Banin *et al.*, 2012). These  
566 differences in tree height persist even after controlling for differences in climate and soils, and  
567 even when comparing related taxa among regions; e.g., Asian trees in the family Fabaceae are  
568 taller than confamilials in Africa and the Americas (Banin *et al.*, 2012).

569         Differences in continental averages in part reflect differences in the frequencies of  
570 different climate regimes (Parmentier *et al.*, 2007), but substantial differences remain even  
571 after controlling for climate (Corlett & Primack, 2011). These can be explained by differences in  
572 the composition of plant and animal communities related to historical contingency and  
573 evolutionary legacy (Cavender-Bares *et al.*, 2016). Taxonomic composition of tropical forests  
574 varies strongly across biogeographic realms, which align to a large degree with continents (Slik  
575 *et al.*, 2018). Asian tropical forests are dominated by trees in the Dipterocarpaceae, a family  
576 that is almost absent in the Americas and Africa. Dipterocarp trees are distinctive in their  
577 combination of ectomycorrhizal associations, tall architecture, seed dispersal by wind, and mast

578 fruiting (Ghazoul, 2016). Essentially, Asian tropical forests have a plant functional type that is  
579 substantially different from those in other tropical forests, and this leads to differences in  
580 stand-level AWP and AGB (Cavender-Bares *et al.*, 2016), as well as selective pressures on co-  
581 occurring trees to be similarly tall (Banin *et al.*, 2012). Differences among biogeographic regions  
582 may also in part reflect differences in the animal community (Corlett & Primack, 2011). For  
583 example, African elephants reduce the abundance of small stems and favor the growth of fewer  
584 larger trees of higher wood density, resulting in elevated forest carbon stocks (Berzaghi *et al.*,  
585 2019).

## 586 **VIII. Discussion**

587         Our review of spatial variation in tropical forest carbon stocks and fluxes documented  
588 considerable qualitative consistency across studies, while also illuminating areas of divergent  
589 results and limited data. AWP and other measures of productivity examined here decrease  
590 strongly with seasonal water limitation and elevation, and increase weakly with soil fertility.  
591 This is consistent with our understanding of how water availability, temperature, and nutrients  
592 affect photosynthesis, allocation and functional composition. Favorable conditions for  
593 photosynthesis (i.e., moist, warm, and fertile) lead to greater allocation to AWP as well as  
594 functional shifts towards species with greater light use efficiency, such that these indirect  
595 effects reinforce the direct ones. This variation in AWP in turn contributes to AGB variation with  
596 the same factors, but AGB patterns with climate are much noisier than AWP patterns, and AGB  
597 variation with fertility does not necessarily align with AWP (Fig. 4). This reflects the importance  
598 of AWRT as a dominant driver of empirical variation in AGB (Johnson *et al.*, 2016), the limited  
599 variation in AWRT that is explained by climate, and the strong decrease in AWRT with soil

600 fertility. In general, our knowledge of AWRT drivers remains limited, although we know  
601 disturbance decreases AWRT. Overall, high tropical biodiversity challenges our ability to explain  
602 patterns in tropical forest carbon stocks and fluxes, most obviously in the substantial  
603 differences among biogeographic regions.

#### 604 ***Residence time***

605 AWRT is determined by tree mortality and branch turnover rates, both of which remain  
606 poorly understood, especially in comparison with productivity. Failure to better understand  
607 tree mortality is reflected in models, which currently have very limited and mostly  
608 phenomenological representations of tree mortality, and thus completely fail to reproduce  
609 empirical variation in mortality and AGB (Fig. 2) (Galbraith *et al.*, 2013; Friend *et al.*, 2014;  
610 Koven *et al.*, 2015). Our limited understanding of tropical tree mortality ultimately reflects the  
611 dearth of high-quality data on mortality patterns and mechanisms (McDowell *et al.*, 2018). The  
612 binomial nature of mortality, the low mortality rates in tropical forests, and the relatively high  
613 temporal variation in mortality mean that sampling errors in mortality and woody residence  
614 time are large, such that very large sample sizes (in area and time) are needed to quantify  
615 geographic variation with useful precision (McMahon *et al.*, 2019). Calculation of woody  
616 residence time as the quotient of AGB and AWP provides an alternative approach that  
617 circumvents some of these problems, but is of course dependent on high-quality estimates of  
618 AGB and AWP, and has its own pitfalls (Ge *et al.*, 2019). There is an urgent need for much more  
619 data on tropical tree mortality and woody residence time. Satellite-based methods have the  
620 potential to enable these to be estimated over much larger areas at much finer temporal  
621 resolution (Clark *et al.*, 2004), but this potential has yet to be realized.

622           Branch turnover rates also contribute to woody residence time and are even less well  
623 understood than mortality. Branch turnover encompasses both “planned” branchfall as trees  
624 drop old branches and build new ones, and “unplanned” branchfall, e.g., due to damage when a  
625 neighboring tree falls. Relatively few studies directly measure branchfall rates (but see Palace  
626 *et al.*, 2008; Malhi *et al.*, 2017; Moore *et al.*, 2018), and spatiotemporal variability in branchfall  
627 is so high that sampling errors in such data are invariably large (Gora *et al.*, 2019). Most AWP  
628 estimates from plot recensuses include only net increases in standing woody biomass without  
629 considering branch turnover, and thus are systematic underestimates. Branchfall is also  
630 ignored by most AWRT calculations, which are thus systematic overestimates. These AWP and  
631 AWRT estimates are mutually consistent, but a poor basis for modeling, because they  
632 underestimate the cost of tree growth. Incorporating the cost of branch turnover to dynamic  
633 vegetation models reduces tree biomass accumulation rates, improving estimates of forest size  
634 structure (Martínez Cano *et al.*, 2020). More measurements of branch turnover are needed to  
635 provide information on this critical parameter, including its variation among tree species and  
636 with environmental conditions.

### 637 ***Community ecology***

638           To understand spatial variation in tropical forest carbon stocks and fluxes it is critical to  
639 understand the drivers of variation in plant *functional* composition – in the relative abundance  
640 of plants varying in life history strategy and functional traits. As detailed in this review, every  
641 major environmental gradient in tropical forests is characterized by shifts in tree functional  
642 composition that influence patterns of productivity, mortality and biomass along these  
643 gradients (e.g., Gleason *et al.*, 2009; Dalling *et al.*, 2016). Understanding functional composition

644 is a complex problem involving historical biogeographic influences on species pools, species  
645 sorting by environmental filters, competition among species, and phenotypic variation within  
646 species (McGill & Brown, 2007). Empirical research provides considerable information on  
647 spatial variation in tropical tree species and functional composition, how species traits relate to  
648 performance under different environmental conditions, and on associated tradeoffs (e.g.,  
649 Poorter & Markesteijn, 2008; Gleason *et al.*, 2009; Brenes-Arguedas *et al.*, 2013; Asner &  
650 Martin, 2016; Staver *et al.*, 2019). Better representation of the diversity of tropical plant  
651 physiology and life history strategies in models is critical to capturing turnover in functional  
652 composition and associated shifts in forest functioning along environmental gradients (Levine  
653 *et al.*, 2016) and among floristic realms (Slik *et al.*, 2018; Taylor *et al.*, 2019), as well as the  
654 diversity of locally coexisting functional types that determines functioning and responses to  
655 temporal climatic variation (Verheijen *et al.*, 2015; Sakschewski *et al.*, 2016; Powell *et al.*, 2018).

656         Liana abundance varies greatly among tropical forests, and strongly influences forest  
657 carbon stocks and fluxes. Liana abundance increases with soil fertility and disturbance, and  
658 decreases with rainfall and elevation (Schnitzer & Bongers, 2002); it also varies greatly within  
659 individual tropical forest sites (e.g., Schnitzer *et al.*, 2012). Multiple hypotheses have been  
660 proposed to explain these patterns, yet the mechanisms underlying variation in liana  
661 abundance remain little understood (Schnitzer, 2018; Muller-Landau & Pacala, 2020). Trees  
662 with heavy liana infestations had approximately half the growth and twice the mortality rates  
663 of liana-free trees in observational studies (Ingwell *et al.*, 2010; Wright *et al.*, 2015; Visser *et al.*,  
664 2018), and experimental liana removal increased tree growth 25-372% (Estrada-Villegas &  
665 Schnitzer, 2018). Thus, lianas decrease AWP, AWRT, and thereby AGB. Mean AGB decreases



666 more than two-fold with increasing liana abundance across sites (Duran & Gianoli, 2013), and  
667 experimental liana removal increased AGB accumulation in secondary forests by 75% (van der  
668 Heijden *et al.*, 2015). Further, lianas differentially affect trees of different species (Muller-  
669 Landau & Visser, 2019), and thus likely influence tree community functional composition, which  
670 may magnify or mitigate the direct effects of lianas. Tropical lianas are themselves very diverse,  
671 with local species richness typically on the order of a third to half of that of trees, and thus liana  
672 functional composition may also play a role. Liana species vary in their traits and effects on  
673 trees (Ichihashi & Tatenno, 2011), and shifts in liana composition among sites may thus  
674 contribute to variation in forest carbon dynamics (Muller-Landau & Visser, 2019). The  
675 incorporation of lianas in models involves unique challenges because of the complexities of  
676 their interactions with host trees, but may be critical to reproducing major changes in forest  
677 structure and functioning associated with variation in liana abundance along successional,  
678 climate, and disturbance gradients (Brugnera *et al.*, 2019).

679         Most research on variation in plant functional composition has focused on direct  
680 environmental influences on plant performance. However, environmental conditions may also  
681 influence plants via changes in antagonistic and mutualistic interactions with microbes,  
682 invertebrates, and vertebrates. For example, there is some evidence of higher herbivory in sites  
683 with higher soil fertility, where plant tissue nutrient concentrations are higher (Campo & Dirzo,  
684 2003). Differences in vertebrate abundance and community composition contribute to  
685 savanna-forest boundaries and possibly differences in forest structure among biogeographic  
686 regions (Corlett, 2016). And it has long been hypothesized that pest pressures is higher at  
687 wetter sites, and may drive compositional shifts and higher plant diversity (Janzen & Schoener,

688 1968; Givnish, 1999), although evidence to date remains limited (but see (Spear *et al.*, 2015)).  
689 The influences of biotic interactions have been assumed to be secondary to more direct  
690 environmental influences, and have been ignored in vegetation models; however, they may be  
691 critical to predicting future forest carbon dynamics under global change, including defaunation  
692 (Dirzo *et al.*, 2014).

### 693 ***Conclusions and future directions***

694 An overview of decades of empirical research in tropical forests suggests general  
695 patterns in productivity, residence time, and estimated AGB variation, but studies to date have  
696 important limitations. First, essentially all studies have sizable sampling errors (see Methods),  
697 and these are especially large for studies with smaller plot sizes, smaller numbers of sites, and  
698 shorter measurement periods (Clark *et al.*, 2017). Second, studies to date all rest on the  
699 application of one or a few allometric equations across multiple sites, and almost none involve  
700 site-specific measurements of branch turnover. Systematic differences in biomass allometries  
701 and/or branch turnover along environmental gradients could lead patterns in true AGB, AWP,  
702 and AWRT to diverge substantially from those estimated by current methods. Third, study sites  
703 are not well-distributed across tropical forests, due to local and global bias in plot placement  
704 and research effort (Fig. S1, S9). There is a critical need and opportunity for future empirical  
705 research that overcomes these limitations by taking advantage of new technologies like laser  
706 scanning to more directly measure biomass allometries, branch turnover, and their variation  
707 among sites (Stovall *et al.*, 2018), and of new and forthcoming satellite remote sensing products  
708 that will provide much larger and better distributed datasets on forest carbon cycling (Schimel  
709 *et al.*, 2019).

710 We also critically need a mechanistic understanding of the emergence of observed  
711 empirical patterns, so that we can reproduce them in models for the right reasons and have  
712 some hope of correctly predicting responses to future novel climate conditions (Wright *et al.*,  
713 2009). Research to date provides considerable support for various hypotheses regarding  
714 contributing mechanisms. However, every environmental pattern involves multiple  
715 mechanisms, and we lack an understanding of the relative importance of different mechanisms  
716 and their interactions. A combination of mechanistic empirical studies and mechanistic  
717 modeling is key to resolving this uncertainty, yet many of the hypothesized underlying  
718 processes are not yet represented in models, which currently fail to reproduce key patterns  
719 (Fig. 2). This is not surprising considering the models' very limited representation of tree  
720 mortality (Galbraith *et al.*, 2013; Johnson *et al.*, 2016), tropical tree functional diversity  
721 (Sakschewski *et al.*, 2016), and many other processes.

722 Fortunately, a new generation of models has been developed in the last decade that  
723 better captures some spatial variation in tropical forest biomass. Whereas older models  
724 represented forest vegetation as a "big leaf", new vegetation demographic approaches  
725 explicitly model the growth, survival, and reproduction of trees or cohorts of trees (Fisher *et al.*,  
726 2018). When run with prescribed meteorological conditions, these models have succeeded in  
727 reproducing a multitude of patterns within individual tropical sites, as well as general patterns  
728 of among-site variation along some environmental gradients (Seiler *et al.*, 2014; Levine *et al.*,  
729 2016; Xu *et al.*, 2016; Longo *et al.*, 2019; Medvigy *et al.*, 2019; Koven *et al.*, 2020; Martínez  
730 Cano *et al.*, 2020). However, most still contain large systematic errors; e.g., predicting too many  
731 large trees (Koven *et al.*, 2020), and/or excessively high tree mortality rates (Longo *et al.*, 2019).

732 Further, they mostly lack the mechanisms needed to capture temporal responses to drought or  
733 spatial variation with soil fertility, disturbance, and biogeographic region.

734 Tree mortality, branch turnover, tree functional composition, and biotic interactions of  
735 trees with lianas and other organisms are key areas for further research, both for empirical data  
736 collection as well as modeling. Advances in remote sensing promise to yield much more and  
737 more widely distributed data on tropical forest structure and function (Schimel *et al.*, 2019), but  
738 adequate investment in concurrent ground data collection in the tropics is vital if these  
739 missions are to fulfill their promise (Chave *et al.*, 2019). Every type of evidence on its own has  
740 key limitations; triangulation across multiple lines of evidence is needed to reach robust  
741 conclusions (Munafo & Smith, 2018). We must integrate empirical studies and mechanistic  
742 modeling to make progress on the big questions of the mechanisms of extant variation in  
743 tropical forests today and the implications for their future trajectories (Hofhansl *et al.*, 2016;  
744 Fisher *et al.*, 2018).

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750 **Author Contributions**

751 HCM planned and designed the research. HCM, KCC, and EEA conducted the literature review.

752 HCM, KCC, IMC, and BB analyzed data. HCM, KCC, IMC, KAT, and BB prepared figures. HCM

753 drafted the manuscript. All authors contributed to revisions.

754

755 **Box 1. Estimating aboveground biomass, woody productivity, and residence**  
756 **time**

757 **Aboveground biomass (AGB, mass area<sup>-1</sup>)**, our central measure of biomass carbon stocks, is  
758 estimated aboveground woody biomass per area, typically of trees above some threshold  
759 diameter, omitting smaller trees and lianas (woody vines). Individual tree aboveground biomass  
760 is estimated from tree census data with allometric equations and summed to obtain plot-level  
761 totals. AGB is also estimated from lidar and radar measurements of canopy structure using  
762 phenomenological relationships with plot-based AGB estimates. Tree basal area (BA, basal area  
763 of trunks per ground area) and mean canopy height are generally well-correlated with AGB  
764 across sites, and thus are reasonably good proxies for evaluating among-site variation.

765 **Aboveground woody productivity (AWP, mass area<sup>-1</sup> time<sup>-1</sup>)**, our central measure of  
766 productivity, is typically estimated from repeat tree censuses as the sum of the growth in  
767 estimated AGB of surviving trees plus the AGB of recruits (trees newly above the size  
768 threshold), per area per time. Such calculations ignore branch production that merely  
769 compensates for branchfall (see Methods). Like AGB, AWP is based on allometric equations and  
770 generally omits lianas and smaller trees. Parallel calculations of basal area productivity (BAP)  
771 are good proxies for among-site variation in AWP.

772 **Aboveground woody residence time (AWRT, time)** is the average time carbon remains in  
773 aboveground woody biomass before it becomes dead wood. AWRT is determined by the  
774 mortality rates of woody plants and branches, with large tree mortality rates disproportionately  
775 important. In mature forests, AWRT is most often estimated as the quotient of biomass and  
776 productivity (AWRT = AGB / AWP), because productivity fluxes are more constant in time than  
777 mortality fluxes and assumed equal over the long-term. When AWP calculations ignore  
778 branchfall, AWRT misses it as well. AWRT is inversely related to tree mortality rates and tree  
779 turnover rates across sites.

780 See Methods and Notes S1 for details.

781

## Figures

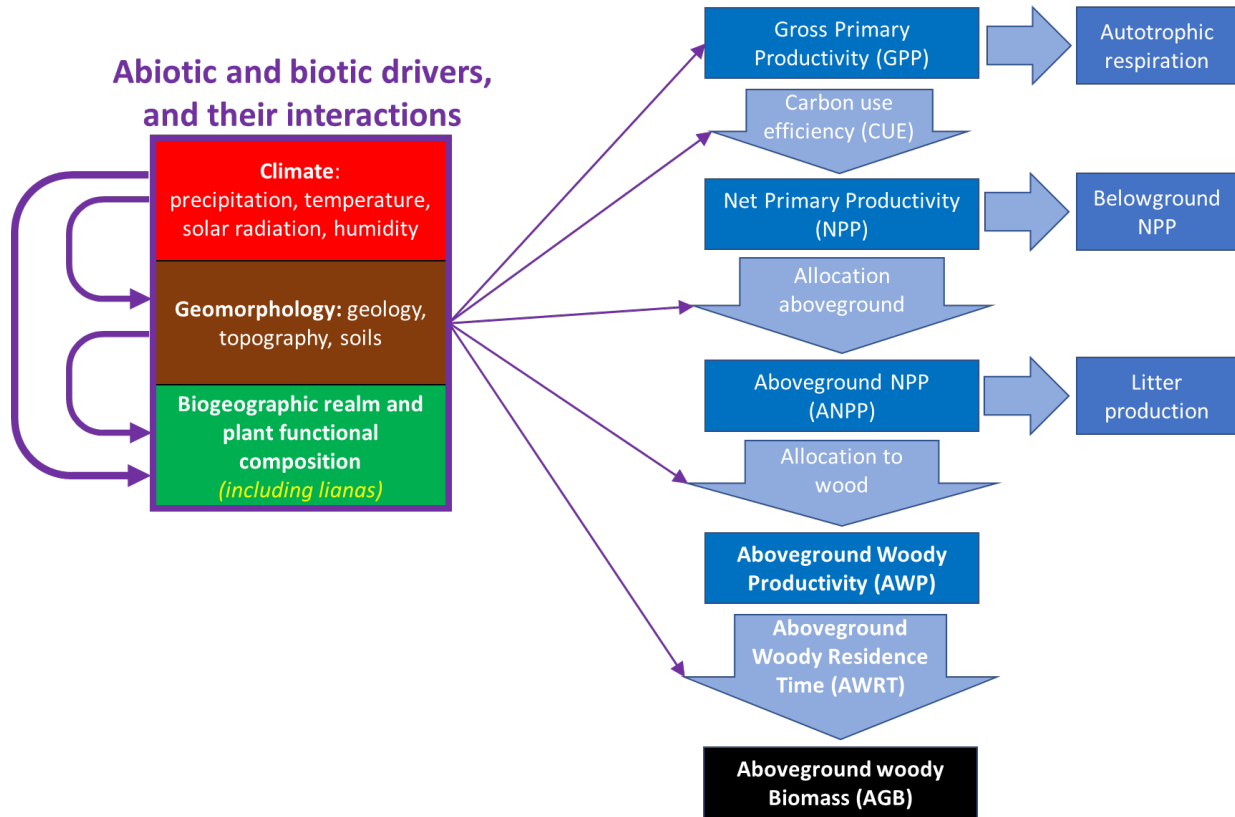


Figure 1. Climate, geomorphology, and biogeographic realm and plant functional composition interact to influence tropical forest aboveground woody productivity (AWP, units of mass area<sup>-1</sup> time<sup>-1</sup>), aboveground woody residence time (AWRT, time) and thus aboveground woody biomass density (AGB, mass area<sup>-1</sup>, black box) via multiple pathways. Here blue boxes represent fluxes (mass area<sup>-1</sup> time<sup>-1</sup>), fat light blue arrows represent the factors by which the one quantity is multiplied to obtain another (e.g., NPP = GPP\*CUE), and thin arrows represent causal influences. Note that GPP (gross primary productivity) is the sum of NPP (net primary productivity) and autotrophic respiration; NPP is the sum of aboveground NPP (ANPP) and belowground NPP (root production); and ANPP is the sum of AWP and canopy productivity (leaves, fruits, fine woody branches, all measured as litterfall). Box 1 gives basic information on measurement methods for AGB, AWP, and AWRT; Notes S1 provides additional details on these and related variables.

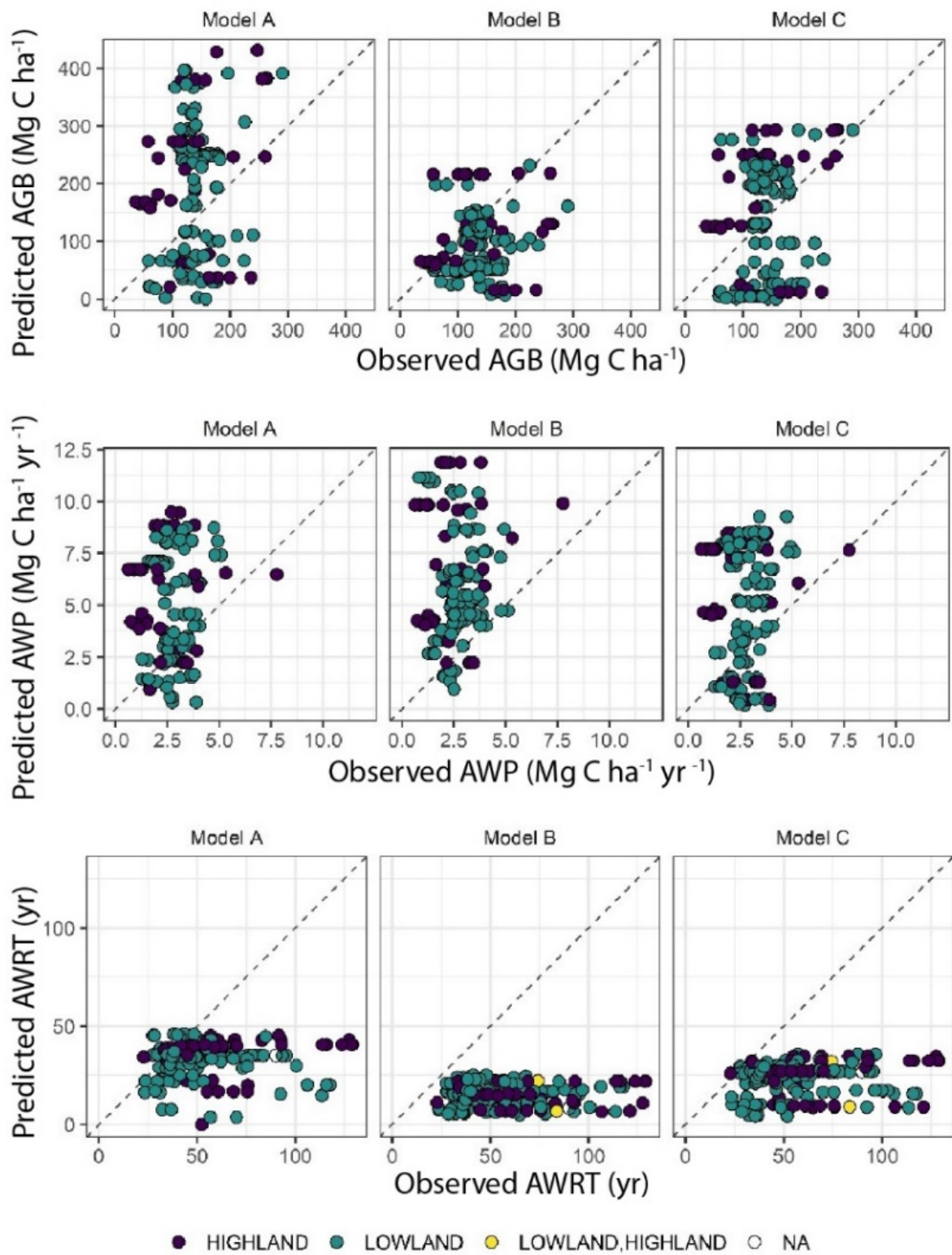
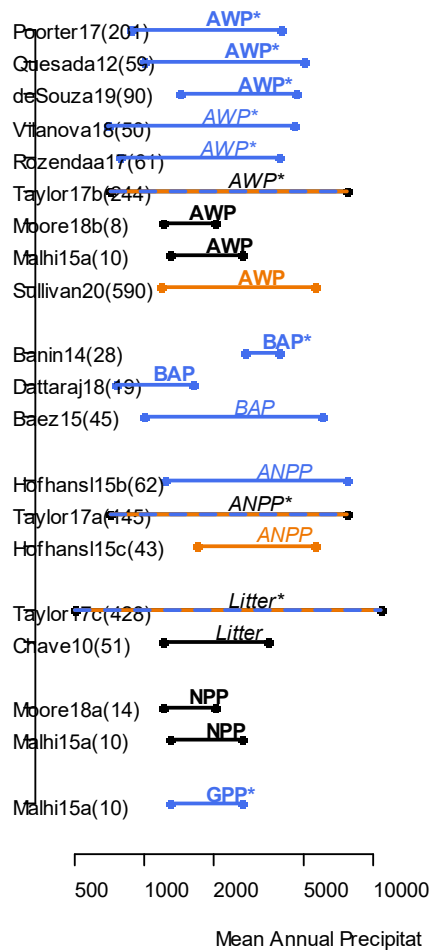


Figure 2. Earth System Model (ESM) predictions of aboveground woody biomass (AGB, top row), aboveground woody productivity (AWP, middle row), and aboveground woody residence

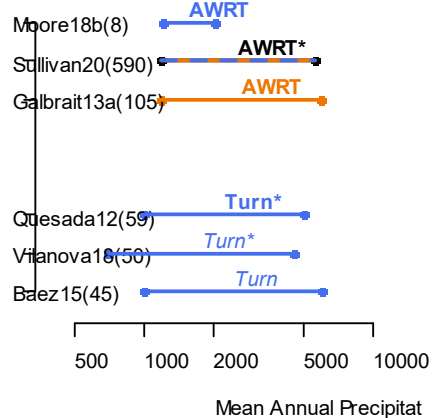


time (AWRT, bottom row) show little relation with observational data (Galbraith *et al.*, 2013) for 177 old-growth tropical forests. Both observed and modeled residence times are calculated as AGB/AWP (Box 1). ESMs simulate vegetation dynamics in tropical forests around the globe as part of their simulation of the entire earth system, including the atmosphere, ocean, and land surface, and their interactions. Spatial variation in predicted climates in these models translates to spatial variation in predicted vegetation because of modeled effects of climate on photosynthesis and respiration, and thus on woody productivity and potentially the dominant plant functional type, with effects that vary depending on the details of model structure and parameterization. Model predictions are from the most recent set of publicly released ESM models and simulation results, from the Coupled Model Intercomparison Project 5 (Taylor *et al.*, 2012). Further details are given in Notes S1.

### a. Productivity vs. Moisture



### b. Residence Time vs. Moisture



### c. Biomass vs. Moisture

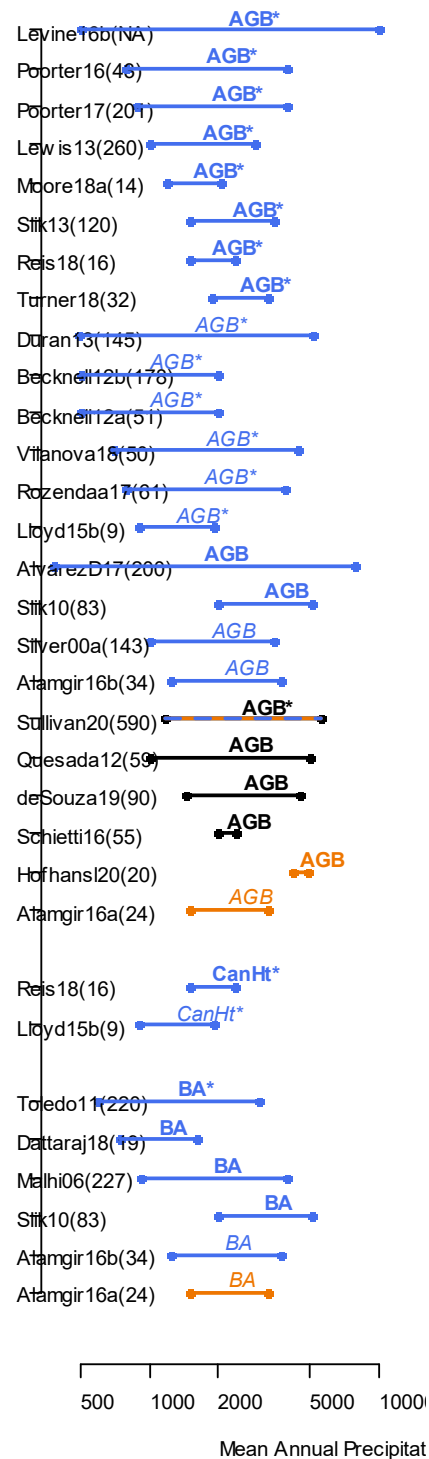


Figure 3. Literature results on spatial variation in productivity (a), residence time (b), and aboveground biomass (c) with precipitation, dry season length, and other measures of climatic

water availability, graphed in relation to the range of precipitation in the study sites (on a log scale). Blue indicates that productivity, residence time, or biomass tend to be higher in wetter sites; orange indicates that they tend to be higher in drier sites; dashed blue and orange a variable pattern that depends on the range of the independent variable or on temperature; and black indicates no relationship. Asterixes indicate statistically significant effects. Bold highlights studies in which median plot area is 1 ha or larger, whereas results for studies with smaller plot sizes are shown in italics. Note that the patterns are always reported here in terms of the response of productivity, residence time, or biomass, even if the response metric is inversely related to these (e.g., a blue turnover result indicates that in wetter sites tree turnover is lower implying residence time is higher). These results are graphed in relation to temperature range in Fig. S3. Abbreviations: AWP = aboveground woody productivity, BAP = basal area productivity, ANPP = aboveground net primary productivity, Litter = litterfall; NPP = net primary productivity, GPP = gross primary productivity, AWRT = aboveground woody residence, Turn = tree turnover rate, AGB = aboveground biomass, CanHt = canopy height, BA = basal area. See Box 1, Fig. 1, and Notes S1 for definitions, measurement methods, and interrelationships of these response variables. Literature results are coded by the first 8 letters of the first author's name, the last 2 digits of the year, a letter indicating which set of sites within the publication (if there is more than one set of sites for the study in the database), and the number of sites included within parentheses (Dataset S1).

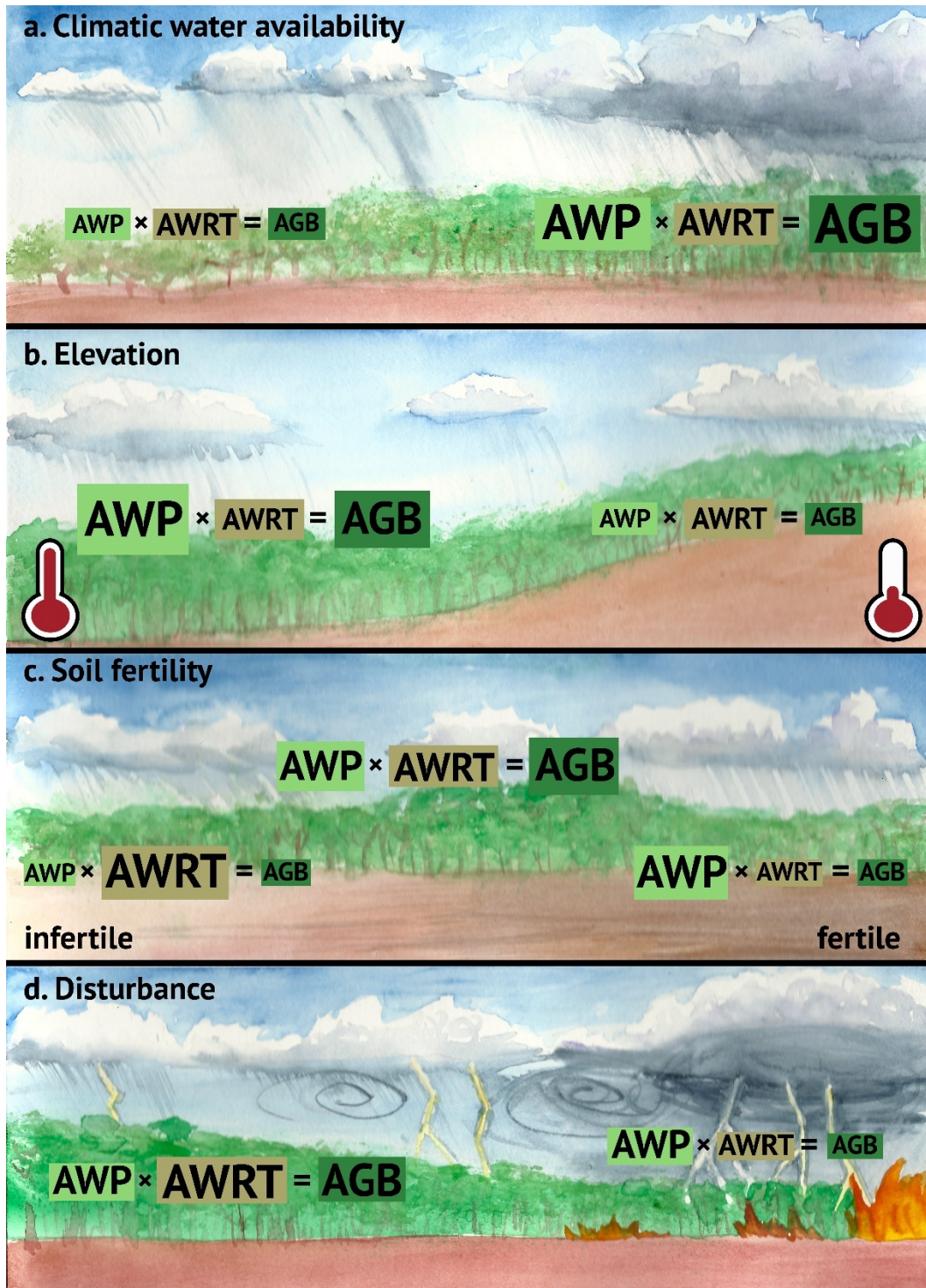


Figure 4. Schematic of patterns of variation in tropical forest aboveground woody productivity (AWP), residence time (AWRT), and biomass (AGB) with climatic water availability(a), elevation in moist or wet sites (b), soil fertility (c), and disturbance (d). Text size reflects variation in a given variable along the environmental gradient; e.g., AWP and AGB increase with climatic water availability. (Watercolors by K. T. Anderson-Teixeira.)

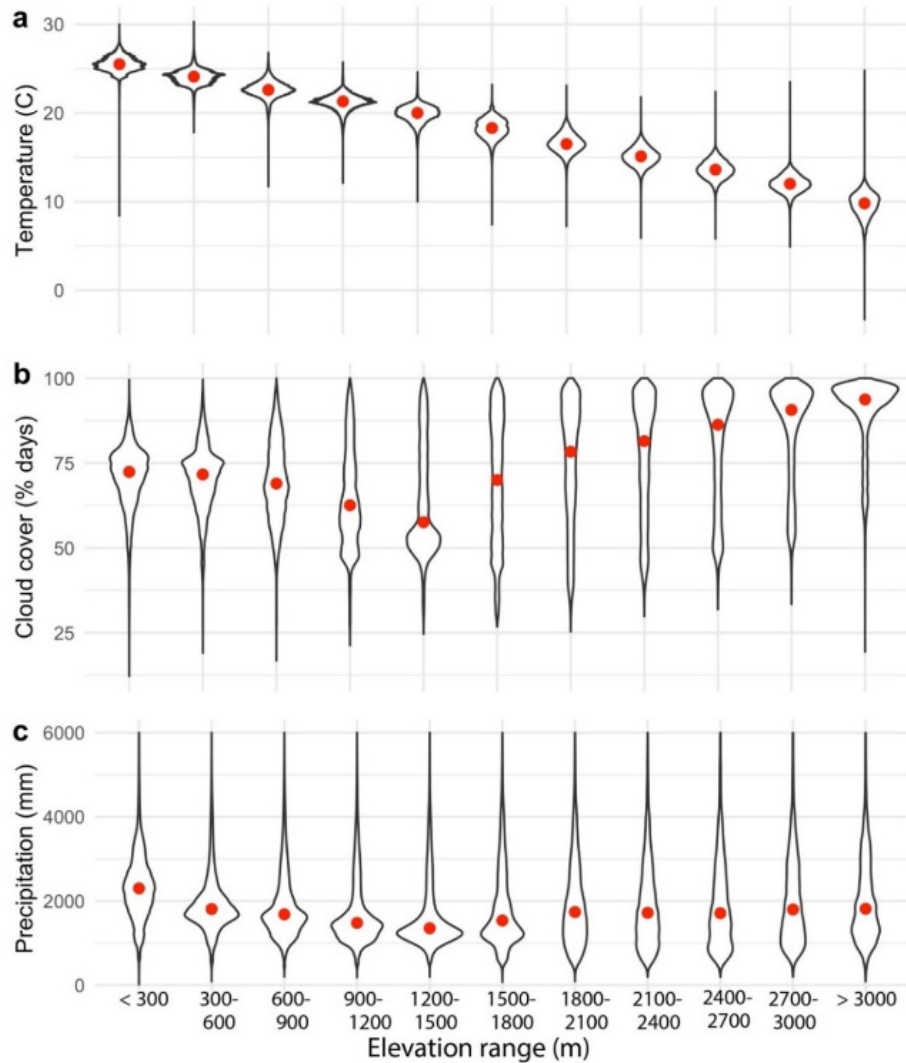


Figure 5. Variation in the distributions of mean annual temperature (a), mean cloud cover (b), and mean annual precipitation (c) in relation to elevation in tropical forests. Panels show violin plots of the distribution across 1-km pixels, with the red dots indicating medians. Tropical forest area was defined based on SYNMAP (Jung *et al.*, 2006) as land between 23.44 S and 23.44 N latitude, in land cover types classified as “trees” (see Fig. S6; see also Figs. S7, S8 for versions including additional land cover types). Mean elevation data from SRTM (<https://cgiasi.community/data/srtm-90m-digital-elevation-database-v4-1/>); mean annual temperature and precipitation from CHELSA (<http://chelsa-climate.org/>); and cloud cover from Wilson and Jetz (Wilson & Jetz, 2016) (<https://journals.plos.org/plosbiology/article?id=10.1371/journal.pbio.1002415>). The violin plots for annual precipitation are truncated at 6000 mm for graphing (at most 0.7% of data were above 6000 mm in any elevation class); the form of the plots and the location of the medians are based on the complete untruncated datasets.

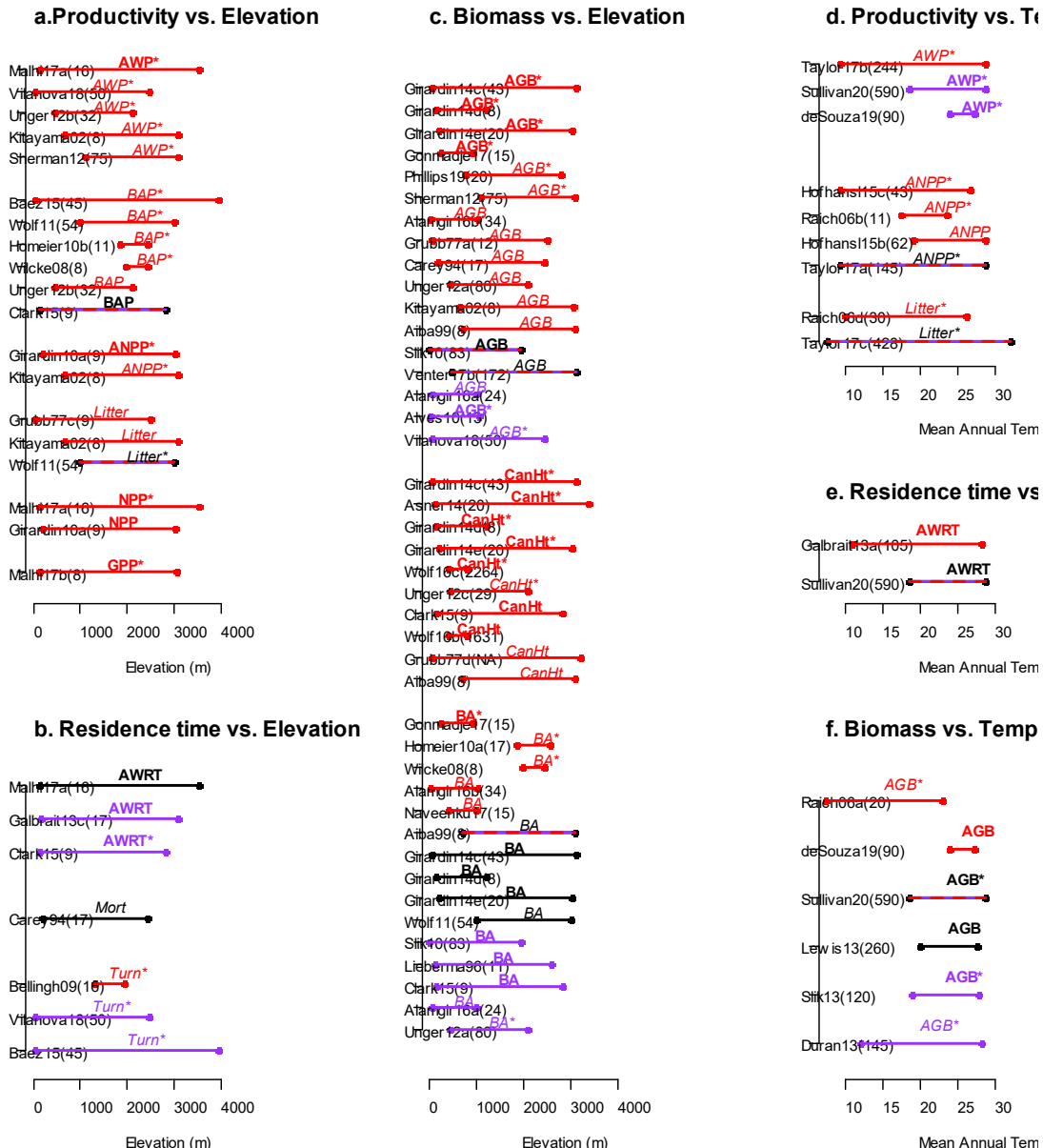
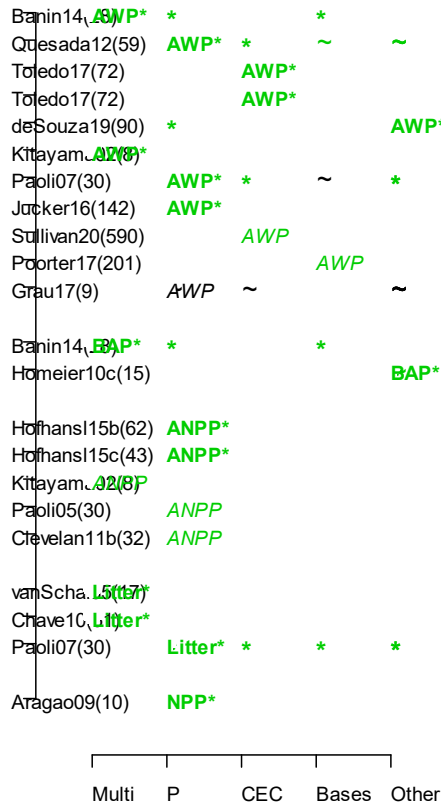


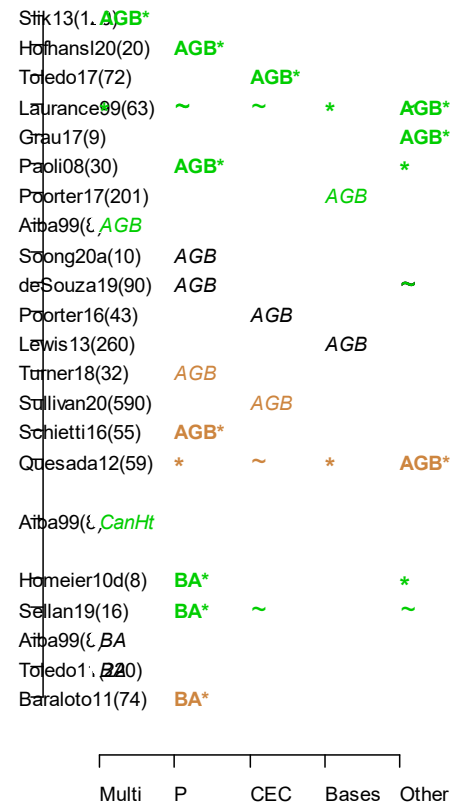
Figure 6. Literature results on spatial variation in productivity (a,d), residence time (b, e), and aboveground biomass (c, f) with elevation (a-c) or temperature (d-f), graphed in relation to the range in elevation or temperature, respectively, in the study sites. Red indicates that productivity, residence time, or biomass tend to be higher in lower elevation sites or warmer; purple indicates that they tend to be higher in higher elevation or cooler sites; black indicates no relationship; and dashed red and purple that they exhibit a variable relationship depending either on the range of the independent variable or on a precipitation variable. Asterisks indicate statistically significant effects. Bold highlights studies in which median plot area is 1 ha or larger, whereas results for studies with smaller plot sizes are shown in italics. These results are graphed in relation to precipitation range in Fig. S8. Abbreviations: AWP = aboveground woody productivity, BAP = basal area productivity, ANPP = aboveground net primary

productivity, Litter = litterfall; NPP = net primary productivity, GPP = gross primary productivity, AWRT = aboveground woody residence, Mort = tree mortality rate, Turn = tree turnover rate, AGB = aboveground biomass, CanHt = canopy height, BA = basal area. Literature results are coded by the first 8 letters of the first author's name, the last 2 digits of the year, a letter indicating which set of sites within the publication, and the number of sites included within parentheses (Dataset S1). These Response variable and study abbreviations as in Fig. 3 (Dataset S1).

**a. Productivity vs. Fertility**



**c. Biomass vs. Fertility**



**b. Residence Time vs. Fertility**

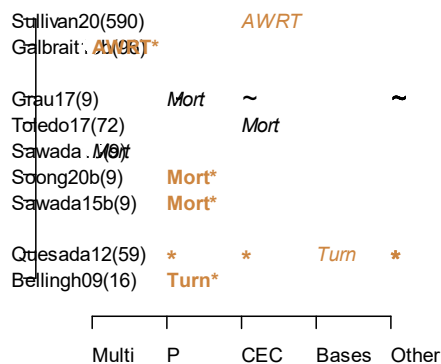


Figure 7. Literature results on spatial variation in productivity (a), residence time (b), and aboveground biomass (c) with soil fertility, graphed in relation to the soil fertility measure used (Multi = a soil fertility axis or classification that encompassed multiple nutrients; P = phosphorus; CEC = cation exchange capacity; Bases = total soil bases; Other includes studies using nitrogen, potassium, magnesium, and calcium. Green indicates that productivity, residence time, or biomass tend to be higher in more fertile sites; tan indicates that they tend to be higher in less fertile sites, and black indicates no relationship or an inconsistent relationship. Asterixes indicate statistically significant effects. Bold highlights studies in which



median plot area is 1 ha or larger, whereas results for studies with smaller plot sizes are shown in italics. For studies that investigate multiple soil fertility measure, the text denoting the response variable is graphed in the column corresponding to the variable that exhibited the strongest relationship; additional results for other types of soil variables are indicated with an asterisk for significant results, and a tilde for others. In some cases results for secondary variables reflect weaker tests of effects (e.g., correlations) than the main results (e.g., multiple regression), and thus the secondary results can be significant while the primary results are not (e.g., turnover results for Quesada et al. 2012). Abbreviations: AWP = aboveground woody productivity, BAP = basal area productivity, ANPP = aboveground net primary productivity, Litter = litterfall; NPP = net primary productivity, GPP = gross primary productivity, AWRT = aboveground woody residence, Mort = tree mortality rate, Turn = tree turnover rate, AGB = aboveground biomass, CanHt = canopy height, BA = basal area. Literature results are coded by the first 8 letters of the first author's name, the last 2 digits of the year, a letter indicating which set of sites within the publication, and the number of sites included within parentheses (Dataset S1).

## Supporting Information

**Notes S1.** Additional information on methods.

**Figure S1.** Global distribution of data underlying the studies of tropical forest productivity, woody residence time, and biomass reviewed here.

**Figure S2.** Distribution of tropical land area and forest area with respect to mean annual precipitation and mean annual temperature.

**Figure S3.** Literature results on spatial variation in productivity, residence time, aboveground biomass, and associated variables with precipitation, dry season length, and other measures of climatic water availability, graphed in relation to the range of temperature in the study sites.

**Figure S4.** Mean annual cloud cover in relation to temperature in tropical forests.

**Figure S5.** Literature results on spatial variation in productivity, residence time, aboveground biomass, and associated variables with elevation or temperature, graphed in relation to the range in precipitation in the study sites.

**Figure S6.** Map of relevant SYNMAP land cover classes in the tropics.

**Figure S7.** Variation in the distributions of mean annual temperature, mean cloud cover, and mean annual precipitation in relation to elevation in tropical forests, when tropical forests are defined to include land cover type 'trees and shrubs' in addition to 'trees'.

**Figure S8.** Variation in the distributions of mean annual temperature, mean cloud cover, and mean annual precipitation in relation to elevation in tropical forests, when tropical forests are defined to include land cover types 'trees and shrubs' and 'trees and grasses' in addition to 'trees'.

**Figure S9.** Interactive version of Fig. S1, showing the global distribution of data underlying the studies of tropical forest productivity, woody residence time, and biomass reviewed here.

**Dataset S1.** Database of the literature results on environmental variation in tropical forest productivity, woody residence time, and biomass that appear in Figs. 3, 6 and 7.

Citations corresponding to entries in Figures 3, 6, and 7. This is a placeholder to insure that they appear in the references.

(Grau *et al.*, 2017)  
(Gonmadje *et al.*, 2017)  
(Girardin *et al.*, 2014)  
(Carey *et al.*, 1994)  
(Alves *et al.*, 2010)  
(de Souza *et al.*, 2019)  
(Alamgir *et al.*, 2016)  
(Paoli *et al.*, 2008)  
(Quesada *et al.*, 2012)  
(Lewis *et al.*, 2013)  
(Aiba & Kitayama, 1999)  
(Laurance *et al.*, 1999)  
(Levine *et al.*, 2016)  
(Moore *et al.*, 2018)  
(Alvarez-Davila *et al.*, 2017)  
(Slik *et al.*, 2013)  
(Soong *et al.*, 2020)  
(Lloyd *et al.*, 2015)  
(Hofhansl *et al.*, 2020)  
(Turner *et al.*, 2018)  
(Becknell *et al.*, 2012)  
(Toledo *et al.*, 2017)  
(Duran & Gianoli, 2013)  
(Slik *et al.*, 2010a)  
(Rozendaal *et al.*, 2017)  
(Kitayama & Aiba, 2002)  
(Schietti *et al.*, 2016)  
(Sherman *et al.*, 2012)  
(Phillips *et al.*, 2019)  
(Poorter *et al.*, 2016)  
(Poorter *et al.*, 2017)  
(Silver *et al.*, 2000)  
(Raich *et al.*, 2006)  
(Unger *et al.*, 2012)  
(Reis *et al.*, 2018)  
(Grubb, 1977)  
(Sullivan *et al.*, 2020)  
(Vilanova *et al.*, 2018)

(Venter *et al.*, 2017)  
(Hofhansl *et al.*, 2015)  
(Taylor *et al.*, 2017)  
(Paoli *et al.*, 2005)  
(Cleveland *et al.*, 2011)  
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(Jucker *et al.*, 2016)  
(Banin *et al.*, 2014)  
(Paoli & Curran, 2007)  
(Malhi *et al.*, 2017)  
(Malhi *et al.*, 2015)  
(Clark *et al.*, 2015)  
(Galbraith *et al.*, 2013)  
(Naveenkumar *et al.*, 2017)  
(Sellan *et al.*, 2019)  
(Toledo *et al.*, 2011)  
(Homeier *et al.*, 2010)  
(Lieberman *et al.*, 1996)  
(Baraloto *et al.*, 2011)  
(Wilcke *et al.*, 2008)  
(Wolf *et al.*, 2011)  
(Malhi *et al.*, 2006)  
(Dattaraja *et al.*, 2018)  
(Baez *et al.*, 2015)  
(Wolf *et al.*, 2016)  
(Asner *et al.*, 2014)  
(van Schaik & Mirmanto, 1985)  
(Chave *et al.*, 2010)  
(Sawada *et al.*, 2015)  
(Aragao *et al.*, 2009)  
(Bellingham & Sparrow, 2009)



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