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

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

73   **Keywords:** Tropical forests, woody productivity, woody residence time, biomass carbon stocks,  
74 precipitation, temperature, soil fertility, plant functional composition

75

## 76   I. Introduction

77   Extant tropical forests vary widely in biomass density and thus carbon stocks, even when  
78 controlling for forest age (Becknell *et al.*, 2012; Lewis *et al.*, 2013; Poorter *et al.*, 2016; Alvarez-Davila  
79 *et al.*, 2017; Sullivan *et al.*, 2020). Much of this biomass variation is associated with climate and  
80 biogeochemistry, which influence woody productivity, residence time, and biomass both directly and  
81 indirectly via shifts in plant functional composition. However, our understanding of these patterns  
82 and their underlying mechanisms remains incomplete (Fig. 1). A mechanistic understanding of

83 current variation in tropical forest carbon stocks and fluxes with climate, soils, and other factors is a  
84 critical precursor to accurately predicting forest responses to anthropogenic change.

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

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

110           Mechanisms and patterns involving changes in tree mortality or shifts in plant functional  
111 composition remain poorly understood, whereas those involving changes in productivity of a given  
112 plant functional type along environmental gradients are relatively well-understood. Variation in tree  
113 mortality and thus AWRT is a key driver of spatial variation in AGB within the tropics (Johnson *et al.*,  
114 2016), yet our understanding of tropical tree mortality remains extremely limited (McDowell *et al.*,  
115 2018). Variation in plant functional composition also plays a critical role in explaining large-scale  
116 variation in AWP, AWRT, and AGB. Different environments select for different plant functional  
117 composition, which in turn influences stand-level AWP, AWRT, and AGB in ways that may enhance  
118 or counter direct effects of environmental drivers (Fyllas *et al.*, 2009; Fyllas *et al.*, 2017; Turner *et al.*,  
119 2018). For example, the abundance of lianas (woody climbing plants) varies strongly with  
120 environmental conditions (DeWalt *et al.*, 2015) and lianas negatively affect tree growth and survival  
121 and thus AWP, AWRT, and AGB (Ingwell *et al.*, 2010; Duran & Gianoli, 2013; van der Heijden *et al.*,  
122 2015; Lai *et al.*, 2017), with differential effects across tree species (Muller-Landau & Visser, 2019).  
123 Indeed, experimental liana removal increased AWP by 65% and AGB accumulation by 75% in a  
124 secondary moist tropical forest (van der Heijden *et al.*, 2015).

125           Earth system models (ESMs) are key tools for predicting the future of the global carbon cycle  
126 under global change, and for attributing temporal variation to different factors (Heavens *et al.*,  
127 2013). These models are mechanistic, and attempt to capture hypothesized critical processes as  
128 gleaned from empirical studies (Heinze *et al.*, 2019). However, the most recent set of publicly  
129 released models completely fail to reproduce spatial variation in AGB, AWP, and AWRT in old-  
130 growth tropical forests (Fig. 2). This demonstrates that the models fail to adequately represent the  
131 mechanisms or capture the patterns of spatial variation in tropical forests today, and highlights the  
132 need for a more mechanistic understanding of these patterns.

133           Here we review empirical studies documenting how different environmental factors relate to  
134 tropical forest productivity, residence time, biomass, their proxies, and related variables. We first  
135 briefly describe the types of studies included, and their strengths and weaknesses. We then review  
136 empirical findings on tropical forest variation with climatic water availability (precipitation regimes),

137 elevation and temperature, soil fertility, disturbance, and biogeographic realm, and discuss  
138 hypothesized mechanisms underlying observed relationships. We discuss critical knowledge gaps  
139 and uncertainties in mechanistic understanding and in datasets, and key directions for future  
140 research.

141 **II. Methods**

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

158 Most currently available information on our focal variables are based on tree plot census  
159 data. Because of high local spatial variability in the number and sizes of large trees, these plot-based  
160 estimates exhibit considerable sampling error, even for plots of 1 ha, and this error increases at  
161 smaller plot sizes (Muller-Landau *et al.*, 2014). We thus highlight studies based on plots with a  
162 median size of 1 ha or larger (124 of 201 results reviewed). Plot-based data may also have  
163 systematic errors, reflecting nonrandom plot placed. Some studies explicitly choose plot locations to

164 avoid canopy gaps or areas of recent natural disturbance (e.g., Kitayama & Aiba, 2002; Baez *et al.*,  
165 2015), and plot locations tend to be biased towards taller forests even when methods do not  
166 explicitly state such criteria (Sheil, 1996; Marvin *et al.*, 2014). Plots also tend to be located in more  
167 accessible areas, which have a stronger signature of past human land use (McMichael, CNH *et al.*,  
168 2017) and current human impacts (McMichael, CH *et al.*, 2017).

169       Estimation of AGB and AWP depend on biomass allometry equations (Box 1), which are a  
170 major source of error. These equations estimate individual tree aboveground woody biomass from  
171 measured tree diameter, and sometimes also tree height and/or wood density (e.g., (Chave *et al.*,  
172 2005; Chave *et al.*, 2014)). The key issue for analyses of among-site variation is that studies typically  
173 apply the same equation(s) across many sites. However, biomass allometries differ systematically  
174 among sites (e.g., Chave *et al.*, 2014), reflecting differences in height allometries (Feldpausch *et al.*,  
175 2012) and crown form (Ploton *et al.*, 2016), and potentially also rates of heartrot (Heineman *et al.*,  
176 2015) and crown breakage (Arellano *et al.*, 2019). Such differences are at best partially captured  
177 with generalized allometric equations which at best incorporate local height measurements and  
178 associated differences in diameter-height allometries, continuous terms for climate variation, and/or  
179 different equations for different regions or forest types (Chave *et al.*, 2005; Chave *et al.*, 2014).

180       AWP estimates suffer from additional sources of error. AWP estimates depend on diameter  
181 growth measurements, and thus are highly sensitive to diameter measurement errors and to data  
182 quality assurance quality control procedures, including procedures for estimating diameter change  
183 in buttressed trees (Sheil, 1995; Cushman *et al.*, 2014; Muller-Landau *et al.*, 2014). AWP is  
184 temporally variable (e.g., Rutishauser *et al.*, 2020), and thus sampling errors for short census  
185 intervals are high. At the same time, typical calculations underestimate AWP in longer census  
186 intervals because they increasingly miss AWP of trees that die between censuses (Kohyama *et al.*,  
187 2019). Finally, standard methods for estimating AWP entirely fail to capture wood production to  
188 compensate for branchfall, estimated at 15-45% of total AWP (Malhi *et al.*, 2014; Marvin & Asner,  
189 2016; Gora *et al.*, 2019). That is, as trees grow, they do not simply accrue biomass, they also shed old  
190 branches as they produce new ones.

191        Residence time variables have particularly high sampling errors, which may in part explain  
192    the dearth of published analyses. Because tree mortality is a binomial process and mortality rates  
193    are low, sampling errors in mortality rates are large, especially in small plots and shorter census  
194    intervals. Strong temporal variation in mortality – for example due to droughts (Bennett *et al.*,  
195    2015) – makes it yet more difficult to capture long-term mean mortality rates. Tree turnover rates,  
196    calculated as the average of mortality and recruitment rates, suffer these same problems. Syntheses  
197    of among-site patterns in mortality and turnover are further hindered by variability in methods for  
198    calculating mortality rates, inadequate reporting of calculation methods, and systematic biases in  
199    many estimators (Kohyama *et al.*, 2018) (see Notes S1). Calculating AWRT as the quotient AGB/AWP  
200    (Box 1) only partially avoids this issue, as AWP estimates also depend on mortality (because trees  
201    that die don't contribute to AWP). Such estimates of AWRT may also be biased by the equilibrium  
202    assumption that underlies them (see Notes S1).

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

### 208    **III. Climatic water availability**

209        Precipitation patterns vary among tropical forests from those that receive abundant  
210    precipitation year-round (wet tropical forests) to those that experience limitations in water  
211    availability during one or two dry seasons (moist and dry tropical forests), variation we encompass  
212    under the term climatic water availability. This variability is evident in the large range of mean  
213    annual precipitation among tropical forests (Fig. S2). In general, the length and intensity of dry  
214    seasons are more important than total annual precipitation in determining forest carbon stocks and  
215    fluxes. Further, water limitation depends not only on precipitation, but also on potential  
216    evapotranspiration (itself dependent on temperature, solar radiation), as well as soil depth, soil  
217    water-holding capacity, and topographic position. Many analyses thus evaluate relationships with

218 more integrative measures of climatic water availability such as dry season length or maximum  
219 climatological water deficit, which are generally better predictors of forest structure and dynamics  
220 (e.g., Alvarez-Davila *et al.*, 2017). Here, we discuss how our focal variables vary with climatic water  
221 availability, and evaluate patterns in relation to the range of annual precipitation and temperature  
222 within studies (Figs. 3, S3).

223 **Productivity**

224 Productivity variables are positively associated with climatic water availability across lowland  
225 tropical forests over the range from dry to wet forests. Across lowland sites, AWP, litterfall, and  
226 ANPP are positively related to climatic water availability in most studies (Fig. 3a), with an initial fast  
227 increase slowing to a plateau or even a mild decrease for precipitation above ~3000 mm/yr (Poorter  
228 *et al.*, 2017; Taylor *et al.*, 2017). The positive effects of precipitation weaken and reverse in montane  
229 tropical forests (e.g., lowland Hofhansl15b vs. montane Hofhansl15c in Fig. 3a; (Hofhansl *et al.*,  
230 2015)). A meta-analysis of 145 tropical forests found that an increase in mean annual precipitation  
231 (MAP) from 1000 to 3000 mm was associated with a 2.3-fold increase in ANPP at 28°C, a 1-5 fold  
232 increase at 24°C, no change at 20°C, and a decrease in ANPP at temperatures below 20°C (Taylor *et*  
233 *al.*, 2017).

234 Lower forest productivity at lower precipitation reflects limitation by water availability  
235 and/or drought stress when potential evapotranspiration exceeds precipitation, combined with  
236 allocational changes and compositional shifts towards drought-tolerant species (Flack-Prain *et al.*,  
237 2019). Limited water availability translates into reduced gross primary production through both  
238 reduced leaf area maintained (including drought deciduous leaf phenology) and reduced  
239 photosynthesis per available leaf area as plants close their stomates and/or invest in more drought-  
240 tolerant organs with lower light use efficiency (Tan *et al.*, 2013; Guan *et al.*, 2015; Wu *et al.*, 2016;  
241 Pfeifer *et al.*, 2018). Higher precipitation is also associated with higher allocation of above-ground  
242 NPP to AWP (Hofhansl *et al.*, 2015) and taller trees for a given diameter (Banin *et al.*, 2012), further  
243 contributing to higher AWP. Compositional shifts also contribute: species found in drier forests have  
244 lower growth rates than those restricted to wetter forests (Baltzer & Davies, 2012; Brenes-Arguedas

245 *et al.*, 2013; Kupers *et al.*, 2019), because drought-tolerance traits, such as narrower xylem vessels,  
246 are costly (Gorel *et al.*, 2019), whereas the “drought-avoiding” deciduous strategy involves foregoing  
247 photosynthesis in part of the year (Brenes-Arguedas *et al.*, 2013).

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

257

#### 258 ***Residence time***

259       Few studies have evaluated how among-site variation in AWRT, mortality, or turnover relate  
260 to climatic water availability, and those that do have found at best weak relationships (e.g., Quesada  
261 *et al.*, 2012; Vilanova *et al.*, 2018). More studies have found trends for AWRT to be higher (and  
262 turnover lower) in wetter sites than the opposite, but overall patterns are inconsistent (Fig. 3b).  
263 This may reflect contrasting trends in different mortality threats with precipitation regimes. Drier  
264 sites are more likely to experience fire (Cochrane, 2011) and drought stress elevates mortality  
265 through hydraulic damage (Choat *et al.*, 2018), whereas higher rainfall is associated with greater  
266 risks of mortality from treefalls, lightning, and landslides (Espírito-Santo *et al.*, 2010; Yanoviak *et al.*,  
267 2020).

268       In contrast to the paucity of studies of spatial variation, there have been multiple studies of  
269 temporal variation. Many studies have documented elevated mortality in drought years (reviewed in  
270 (Phillips *et al.*, 2010; Bennett *et al.*, 2015)), whereas a few have found higher mortality in wetter  
271 years (Aubry-Kientz *et al.*, 2015) or wetter seasons (Brokaw, 1982; Fontes *et al.*, 2018). Patterns of

272 temporal variation in mortality with water availability do not necessarily predict among-site  
273 variation because compositional shifts at least partially compensate for shifts in mortality threats.  
274 For example, tree species common in drier sites have higher survival under drought than those  
275 common in wetter sites (Engelbrecht *et al.*, 2007; Baltzer & Davies, 2012; Brenes-Arguedas *et al.*,  
276 2013; Esquivel-Muelbert *et al.*, 2017).

### 277 **AGB**

278 AGB is positively related to climatic water availability in tropical forests in 16 of 16 studies  
279 finding a statistically significant relationship (Fig. 3c). The relationship of AGB with precipitation  
280 exhibits an initially steep increase below 2000 mm/yr gradually saturating at higher precipitation  
281 (Becknell *et al.*, 2012; Poorter *et al.*, 2016; Alvarez-Davila *et al.*, 2017). Increases are roughly parallel  
282 in old-growth and secondary forests: over 1000-3000 mm MAP, AGB increases 2-fold in 20-year  
283 secondary forests (Poorter *et al.*, 2016), and ~2.3-fold in mature forests (Alvarez-Davila *et al.*, 2017).  
284 Qualitatively the same patterns are found for tree basal area and canopy height, for both plot-based  
285 and remote sensing studies, and in both old-growth and secondary forests of a given age (Fig. 3c).  
286 Measures of drought stress such as dry season length or dry season water deficit are generally  
287 better predictors of AGB than precipitation alone, and exhibit more linear relationships with AGB  
288 (Poorter *et al.*, 2016; Alvarez-Davila *et al.*, 2017). At extremely high precipitation levels above ~4000  
289 mm/yr, AGB may decrease with further increases in precipitation, but there are few data for such  
290 sites, and spatial variation in precipitation may be confounded with solar radiation, soil fertility and  
291 other factors (Alvarez-Davila *et al.*, 2017). Overall the patterns in AGB parallel those in AWP,  
292 consistent with what would be expected given little variation in AWRT with precipitation (Fig. 4a).

### 293 **Synthesis**

294 Overall, patterns of variation in tropical forest productivity and biomass with climatic water  
295 availability are relatively well-documented and well-understood, and the underlying mechanisms are  
296 increasingly well-represented in forest and vegetation models (Christoffersen *et al.*, 2016; Levine *et*  
297 *al.*, 2016; Xu *et al.*, 2016). Additional data and analyses are needed to establish whether/how  
298 mortality rates vary spatially with climatic water availability, and to investigate the role of

299 compositional shifts in contributing to variation in carbon fluxes and stocks. The role of lianas  
300 deserves more attention, as lianas are more abundant in drier sites (DeWalt *et al.*, 2010), and could  
301 contribute to their lower tree productivity and possibly lower residence time.

302

#### 303 **IV. Temperature and elevation**

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

#### 315 **Productivity**

316 All productivity variables decline with elevation (Fig. 6a), suggesting a positive effect of  
317 temperature, but analyses with temperature find both positive and negative effects (Fig. 6a,d).  
318 Overall patterns seem consistent with a positive effect of temperature in wet sites, and a negative  
319 effect in dry sites. This is particularly apparent in studies that evaluate interactions of climatic water  
320 availability and temperature (Taylor *et al.*, 2017; Sullivan *et al.*, 2020). A meta-analysis found that  
321 ANPP (litterfall) decreased with temperature for precipitation below ~1400 mm/yr (1600 mm/yr),  
322 and increased with temperature for precipitation above that level, with ever faster increases for  
323 higher precipitation (Taylor *et al.*, 2017). At 2500 mm MAP, ANPP doubles between 10 and 22°C and  
324 triples by 28°C (Taylor *et al.*, 2017).

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

339        Allocational and compositional shifts also contribute to spatial variation in AWP with  
340    temperature. Cooler sites tend to have plant species with higher nutrient use efficiencies, longer-  
341    lived leaves, higher LMA (Asner & Martin, 2016) and other slow life history traits (Dalling *et al.*, 2016;  
342    Bahar *et al.*, 2017). These traits increase competitiveness in lower resource environments, while  
343    reducing light use efficiency and thus stand-level productivity (Reich, 2014). Cooler, higher elevation  
344    sites also tend to have higher allocation below-ground, a pattern consistent with increased nutrient  
345    limitation (Hofhansl *et al.*, 2015). This allocational shift could reconcile stronger elevational  
346    decreases in ANPP with weaker patterns in total NPP. Among water-limited sites, increasing  
347    temperature increases drought stress, potentially leading to the same types of allocational and  
348    compositional shifts expected under reduced climatic water availability.

349        Finally, correlated variation in other environmental factors also influences patterns with  
350    temperature among tropical sites. Cooler tropical forests are found overwhelmingly at higher  
351    elevations, where cloud cover is higher and fog is more frequent, thereby decreasing solar radiation  
352    and increasing light limitation (Bruijnzeel *et al.*, 2011). Cooler temperatures also slow decomposition

353 (Taylor *et al.*, 2017) and reduce biological N fixation (Houlton *et al.*, 2008), which tends to reduce  
354 nutrient availability, especially nitrogen availability (Wilcke *et al.*, 2008; Nottingham *et al.*, 2015).  
355 However, higher elevation and thus cooler forests tend to be found on geochemically young  
356 substrates with eroding slopes, which are associated with relatively higher availability of rock-  
357 derived nutrients (Porder *et al.*, 2007). Thus, for any given area, elevational variation in cloud cover,  
358 rainfall, and soils can magnify or counter the patterns expected based on temperature alone, and  
359 interact with compositional shifts (Peng *et al.*, 2020).

360 **Residence time**

361 Few studies have evaluated how AWRT, mortality, or turnover rates vary with temperature  
362 or elevation, and relationships were not statistically significant in most studies (Fig. 6b,e). Of the four  
363 studies finding significant relationships with elevation, three show higher AWRT (lower turnover) at  
364 higher elevation (Fig. 6b). This is consistent with the global pattern of a positive correlation between  
365 tree productivity and mortality (Stephenson & Mantgem, 2005), given that higher elevations tend to  
366 be associated with lower productivity and slower life histories (e.g., lower LMA Asner & Martin,  
367 2016).

368 **AGB**

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

377 **Synthesis**

378 The biochemical and physiological mechanisms by which temperature interacts with water  
379 availability to affect plant productivity are relatively well understood. These are central to responses

380 to short-term temporal variation in temperature within sites, which is reasonably well captured in  
381 mechanistic models (Schippers *et al.*, 2015). In contrast, responses to spatial variation in  
382 temperature regimes depend in large part on acclimation, allocational shifts, and compositional  
383 variation, and remain poorly understood. Compositional patterns, such as the decline in lianas and  
384 palms with elevation (e.g., Lieberman *et al.*, 1996), are likely to be major contributors to among-site  
385 variation in tropical forest carbon cycling with elevation and temperature; they deserve more  
386 attention. Finally, among-site patterns may vary not only with mean temperatures but also with  
387 extremes; e.g., relationships with maximum temperature were more often negative than those with  
388 mean temperature (Dataset S1).

## 389 **V. Soil fertility**

390 Tropical forests exhibit great heterogeneity in their biogeochemistry, reflecting wide  
391 variation in soil age, chemistry, and susceptibility to erosion or uplift, as well as high plant diversity;  
392 diversity matters because plants can affect soil properties under their crowns (Townsend *et al.*,  
393 2008; Waring *et al.*, 2015). Soil fertility is multi-dimensional, involving many different nutrients  
394 important in different ways (Kaspari & Powers, 2016), and available in different concentrations and  
395 forms at different soil depths, that covary across sites (e.g., Quesada *et al.*, 2010). Many studies thus  
396 evaluate patterns with respect to principal components axis or soil classes that reflect covariation in  
397 multiple nutrients (“Multi” in Fig. 7). In cases where individual studies investigated relationships  
398 with multiple soil fertility variables, we report results relative to the variable showing the strongest  
399 relationship with the dependent variable.

## 400 **Productivity**

401 AWP, BAP, ANPP, and litterfall are positively related to soil fertility in tropical forests. Of 22  
402 analyses of among-site variation, 21 showed a positive trend, and 16 were significantly positive (Fig.  
403 7a). Fertilization experiments further demonstrate that tropical forest productivity is limited by P  
404 and by N, and suggest that K and Ca might also be limiting –only one tropical forest fertilization  
405 experiment manipulated K or Ca (Wright, 2019). However, the range of AWP variation explained by  
406 fertility seems to be relatively smaller than that explained by climate; for example, AWP on high-

407 phosphorus soils averages ~20% higher than AWP on low-phosphorus soils in the Amazon and Sierra  
408 Leone (Quesada *et al.*, 2012; Jucker *et al.*, 2016). This may in part reflect shifts in allocation with  
409 fertility, with increased allocation to reproduction in more fertile sites (Wright *et al.*, 2011).

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

#### 425 ***Residence time***

426       Soil fertility is positively associated with tree mortality rates and thus negatively associated  
427 with AWRT across tropical forests (Fig. 7b). This pattern has been found at local (de Toledo *et al.*,  
428 2011; Sawada *et al.*, 2015), regional (Quesada *et al.*, 2012), and global (Galbraith *et al.*, 2013) scales.  
429 This variation is substantial, eclipsing both variation in productivity with soil fertility and variation in  
430 AWRT with climate. For example, across 59 sites in the Amazon, turnover increased 3-fold from low  
431 to high soil phosphorus (Quesada *et al.*, 2012). Pantropical analyses also found strong relationships,  
432 with median AWRT increasing~50% from young to old soils in Neotropical forests, and from  
433 intermediate to old soils in Paleotropical forests (Galbraith *et al.*, 2013).

434 Three classes of mechanisms likely contribute to higher mortality at higher soil fertility. First,  
435 higher growth at higher soil fertility speeds the rate of self-thinning, thereby increasing associated  
436 mortality rates (Stephenson & Mantgem, 2005). Second, more productive environments select for  
437 tree species with “fast” life history strategies such as low wood density (Quesada *et al.*, 2012), and  
438 given underlying tradeoffs, these species also have higher mortality rates (Stephenson & Mantgem,  
439 2005; Kraft *et al.*, 2010; Wright *et al.*, 2010; Reich, 2014). Third, higher soil fertility is associated with  
440 higher liana abundance (Putz & Chai, 1987; Laurance *et al.*, 2001; Schnitzer & Bongers, 2002; DeWalt  
441 *et al.*, 2006), and higher liana abundance is associated with higher tree mortality in observational  
442 and experimental studies (Ingwell *et al.*, 2010; van der Heijden *et al.*, 2015; Wright *et al.*, 2015).

#### 443 **AGB**

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

#### 457 **Synthesis**

458 It has long been clear that soil fertility plays a critical role in tropical forest structure and  
459 function (Vitousek & Sanford, 1986), and the broad outlines of its importance are evident in studies  
460 to date (Fig. 7). A central challenge is that tropical tree species display a wide diversity of strategies

461 for nutrient acquisition and use, strategies that are critical to compositional shifts and stand-level  
462 responses to soil fertility, and their regional variation (Laliberte *et al.*, 2017). Yet our understanding  
463 of these strategies – which include not only root morphology and foraging behavior but also  
464 chemical root exudates and interactions with microbial symbionts – remains very limited, reflecting  
465 the general paucity of data on roots and below-ground interactions.

466 New data, analyses, and modeling are needed to advance our understanding of soil fertility's  
467 role in structuring variation in tropical forests. More, better, and more consistent data on tropical  
468 soils is a critical component, especially in enabling better analyses of large-scale patterns (Hengl *et*  
469 *al.*, 2017). The ability to estimate foliar nutrients from airborne hyperspectral imaging has enabled  
470 large-scale data collection of these quantities and their relation to soils (e.g., Chadwick & Asner,  
471 2018); and satellite hyperspectral missions promise further advances (Schimel *et al.*, 2013). Earth  
472 system models are starting to incorporate nutrients mechanistically, and can provide useful tools to  
473 explore associated mechanisms and link them to patterns at different levels (Medvigy *et al.*, 2019;  
474 Sulman *et al.*, 2019).

## 475 VI. Disturbance

476 Tropical forests vary strongly in the frequency and intensity of natural disturbances, with  
477 important consequences for forest structure, dynamics, and composition. Here, we focus  
478 specifically on short-term natural disturbances such as storms, landslides, and wildfires, excluding  
479 disturbance by chronic stressors such as drought (addressed under water availability above) and  
480 flooding (addressed by (Daskin *et al.*, 2019)). Variation in natural disturbance rates across the  
481 tropics is substantial and systematic. The frequency and intensity of large-scale tropical cyclones  
482 (known regionally as hurricanes, typhoons, or cyclones) is near zero in tropical forests with latitudes  
483  $<10^\circ$ , and varies strongly among other areas (Ibanez *et al.*, 2019). Convective thunderstorms and  
484 lightning occur across the tropics; and both show strong geographic variation in frequency (Pereira-  
485 Filho *et al.*, 2015; Gora *et al.*, 2020). Within sites, storm impacts vary topographically, reflecting  
486 variation in wind exposure (highest on ridges, (Boose *et al.*, 1994)), soil saturation (highest in  
487 floodplains and concave topographies, (Margrove *et al.*, 2015)), and landslide risk (highest on steep

488 slopes, (Larsen & Torres-Sanchez, 1998).) Wildfire risk increases with dry season length and  
489 intensity, as well as with proximity to anthropogenic disturbance (Cochrane, 2011).

490 Disturbance directly increases tree mortality and decreases AWRT, thereby reducing AGB  
491 (Fig. 4d). Both large-scale cyclones and local convective storms increase tree mortality from treefalls  
492 (including landslides) (Larsen & Torres-Sanchez, 1998; Ostertag *et al.*, 2005; Negrón-Juárez *et al.*,  
493 2017; Hall *et al.*, 2020) and convective thunderstorms also kill trees via lightning (Yanoviak *et al.*,  
494 2020). Across tropical forests, higher lightning frequency is associated with higher biomass turnover  
495 rates and lower old-growth forest biomass (Gora *et al.*, 2020). Higher tropical cyclone frequency is  
496 associated with lower canopy height and higher stem density, reflecting an increasing number of  
497 smaller stems (Ibanez *et al.*, 2019). In humid tropical forests, median canopy height was 1.3-fold  
498 higher where cyclone frequency averaged less than one per century than where it averaged greater  
499 than one per decade (Ibanez *et al.*, 2019). Topographic variation in storm impacts is evident in  
500 mortality patterns; e.g., cyclone mortality rates are higher in areas with greater wind exposure  
501 (Negron-Juarez *et al.*, 2014). Fires directly kill trees and also increase mortality rates in subsequent  
502 years, especially in wetter forests (Barlow *et al.*, 2003), and areas that have experienced fires have  
503 lower biomass stocks than unburned areas for decades afterwards (Gerwing, 2002; Sato *et al.*,  
504 2016).

505 Disturbance also influences functional composition, as tropical tree species differ strongly in  
506 how they are affected by disturbances (Zimmerman *et al.*, 1994; Curran *et al.*, 2008; Slik *et al.*,  
507 2010b; Paz *et al.*, 2018; Staver *et al.*, 2019). In general, species with “faster” life histories are able to  
508 rebound more quickly following disturbances, and thus are more common in areas with recent  
509 disturbances (Paz *et al.*, 2018). Associated tradeoffs mean that disturbances generally increase the  
510 relative abundance of tree species with fast life histories, which tend to have low wood densities and  
511 achieve low biomass (Carreno-Rocabado *et al.*, 2012; Paz *et al.*, 2018). Lianas also proliferate after  
512 disturbances, and thus high disturbance frequency increases liana abundance (Schnitzer & Bongers,  
513 2011). Different disturbances can also favor particular traits; for example, species with higher wood  
514 density are less likely to suffer stem breaks during a hurricane (Zimmerman *et al.*, 1994). Whereas

515 shifts towards more disturbance-resistant species would tend to mitigate the direct effects of  
516 disturbance on mortality and biomass, increases in the abundance of lianas and of tree species with  
517 fast life history strategies would tend to further increase mortality and reduce biomass. Thus,  
518 compositional responses to disturbances also need to be considered to determine the total impacts  
519 of disturbance regimes on tropical forest structure and dynamics.

## 520 **VII. Biogeographic realm**

521 Tropical forests on different continents have significantly different productivity, residence  
522 time, and biomass. AWP is 25% higher in Asian than in Latin American forests (Taylor *et al.*, 2019).  
523 Mean AWRT in old-growth tropical forests is also higher in Asia and Africa than in Latin America, by  
524 22 and 33%, respectively (Galbraith *et al.*, 2013). Consistent with higher AWP and AWRT, AGB is  
525 higher in Paleotropical than in Neotropical forests, in both plot-based and satellite-based datasets  
526 (Lewis *et al.*, 2013; Slik *et al.*, 2013; Avitabile *et al.*, 2016; Sullivan *et al.*, 2017; Taylor *et al.*, 2019).  
527 For example, plot-based studies find that mean AGB is 29% higher in Asian than Latin American  
528 forests (Taylor *et al.*, 2019), and 26% higher in central Africa than in central Amazonia (Lewis *et al.*,  
529 2013). The dearth of studies of African forests is particularly concerning in light of these important  
530 biogeographic differences (Figs. S1, S9).

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

541 Differences in continental averages in part reflect differences in the frequencies of different  
542 climate regimes (Parmentier *et al.*, 2007), but substantial differences remain even after controlling  
543 for climate (Corlett & Primack, 2011). These can be explained by differences in the composition of  
544 plant and animal communities related to historical contingency and evolutionary legacy (Cavender-  
545 Bares *et al.*, 2016). Taxonomic composition of tropical forests varies strongly across biogeographic  
546 realms, which align to a large degree with continents (Slik *et al.*, 2018). Asian tropical forests are  
547 dominated by trees in the Dipterocarpaceae, a family that is almost absent in the Americas and  
548 Africa. Dipterocarp trees are distinctive in their combination of ectomycorrhizal associations, tall  
549 architecture, seed dispersal by wind, and mast fruiting (Ghazoul, 2016). Essentially, Asian tropical  
550 forests have a plant functional type that is substantially different from those in other tropical  
551 forests, and this leads to differences in stand-level AWP and AGB (Cavender-Bares *et al.*, 2016), as  
552 well as selective pressures on co-occurring trees to be similarly tall (Banin *et al.*, 2012). Differences  
553 among biogeographic regions may also in part reflect differences in the animal community (Corlett &  
554 Primack, 2011). For example, African elephants reduce the abundance of small stems and favor the  
555 growth of fewer larger trees of higher wood density, resulting in elevated forest carbon stocks  
556 (Berzaghi *et al.*, 2019).

## 557 **VIII. Discussion**

558 Our review of spatial variation in tropical forest carbon stocks and fluxes documented  
559 considerable qualitative consistency across studies, while also illuminating areas of divergent results  
560 and limited data. AWP and other measures of productivity examined here decrease strongly with  
561 seasonal water limitation and elevation, and increase weakly with soil fertility. This is consistent with  
562 our understanding of how water availability, temperature, and nutrients affect photosynthesis,  
563 allocation and functional composition. Favorable conditions for photosynthesis (i.e., moist, warm,  
564 and fertile) lead to greater allocation to AWP as well as functional shifts towards species with  
565 greater light use efficiency, such that these indirect effects reinforce the direct ones. This variation in  
566 AWP in turn contributes to AGB variation with the same factors, but AGB patterns with climate are  
567 much noisier than AWP patterns, and AGB variation with fertility does not necessarily align with

568 AWP (Fig. 4). This reflects the importance of AWRT as a dominant driver of empirical variation in  
569 AGB (Johnson *et al.*, 2016), the limited variation in AWRT that is explained by climate, and the strong  
570 decrease in AWRT with soil fertility. In general, our knowledge of AWRT drivers remains limited,  
571 although we know disturbance decreases AWRT. Overall, high tropical biodiversity challenges our  
572 ability to explain patterns in tropical forest carbon stocks and fluxes, most obviously in the  
573 substantial differences among biogeographic regions.

574 ***Residence time***

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

591 Branch turnover rates also contribute to woody residence time and are even less well  
592 understood than mortality. Branch turnover encompasses both “planned” branchfall as trees drop  
593 old branches and build new ones, and “unplanned” branchfall, e.g., due to damage when a  
594 neighboring tree falls. Relatively few studies directly measure branchfall rates (but see Palace *et al.*,

595 2008; Malhi *et al.*, 2017; Moore *et al.*, 2018), and spatiotemporal variability in branchfall is so high  
596 that sampling errors in such data are invariably large (Gora *et al.*, 2019). Most AWP estimates from  
597 plot recensuses include only net increases in standing woody biomass without considering branch  
598 turnover, and thus are systematic underestimates. Branchfall is also ignored by most AWRT  
599 calculations, which are thus systematic overestimates. These AWP and AWRT estimates are  
600 mutually consistent, but a poor basis for modeling, because they underestimate the cost of tree  
601 growth. Incorporating the cost of branch turnover to dynamic vegetation models reduces tree  
602 biomass accumulation rates, improving estimates of forest size structure (Martínez Cano *et al.*,  
603 2020). More measurements of branch turnover are needed to provide information on this critical  
604 parameter, including its variation among tree species and with environmental conditions.

605 **Community ecology**

606 To understand spatial variation in tropical forest carbon stocks and fluxes it is critical to  
607 understand the drivers of variation in plant *functional* composition – in the relative abundance of  
608 plants varying in life history strategy and functional traits. As detailed in this review, every major  
609 environmental gradient in tropical forests is characterized by shifts in tree functional composition  
610 that influence patterns of productivity, mortality and biomass along these gradients (e.g., Gleason *et*  
611 *al.*, 2009; Dalling *et al.*, 2016). Understanding functional composition is a complex problem involving  
612 historical biogeographic influences on species pools, species sorting by environmental filters,  
613 competition among species, and phenotypic variation within species (McGill & Brown, 2007).  
614 Empirical research provides considerable information on spatial variation in tropical tree species and  
615 functional composition, how species traits relate to performance under different environmental  
616 conditions, and on associated tradeoffs (e.g., Poorter & Markestijn, 2008; Gleason *et al.*, 2009;  
617 Brenes-Arguedas *et al.*, 2013; Asner & Martin, 2016; Staver *et al.*, 2019). Better representation of  
618 the diversity of tropical plant physiology and life history strategies in models is critical to capturing  
619 turnover in functional composition and associated shifts in forest functioning along environmental  
620 gradients (Levine *et al.*, 2016) and among floristic realms (Slik *et al.*, 2018; Taylor *et al.*, 2019), as

621 well as the diversity of locally coexisting functional types that determines functioning and responses  
622 to temporal climatic variation (Verheijen *et al.*, 2015; Sakschewski *et al.*, 2016; Powell *et al.*, 2018).

623 Liana abundance varies greatly among tropical forests, and strongly influences forest carbon  
624 stocks and fluxes. Liana abundance increases with soil fertility and disturbance, and decreases with  
625 rainfall and elevation (Schnitzer & Bongers, 2002); it also varies greatly within individual tropical  
626 forest sites (e.g., Schnitzer *et al.*, 2012). Multiple hypotheses have been proposed to explain these  
627 patterns, yet the mechanisms underlying variation in liana abundance remain little understood  
628 (Schnitzer, 2018; Muller-Landau & Pacala, 2020). Trees with heavy liana infestations had  
629 approximately half the growth and twice the mortality rates of liana-free trees in observational  
630 studies (Ingwell *et al.*, 2010; Wright *et al.*, 2015; Visser *et al.*, 2018), and experimental liana removal  
631 increased tree growth 25–372% (Estrada-Villegas & Schnitzer, 2018). Thus, lianas decrease AWP,  
632 AWRT, and thereby AGB. Mean AGB decreases more than two-fold with increasing liana abundance  
633 across sites (Duran & Gianoli, 2013), and experimental liana removal increased AGB accumulation in  
634 secondary forests by 75% (van der Heijden *et al.*, 2015). Further, lianas differentially affect trees of  
635 different species (Muller-Landau & Visser, 2019), and thus likely influence tree community functional  
636 composition, which may magnify or mitigate the direct effects of lianas. Tropical lianas are  
637 themselves very diverse, with local species richness typically on the order of a third to half of that of  
638 trees, and thus liana functional composition may also play a role. Liana species vary in their traits  
639 and effects on trees (Ichihashi & Tateno, 2011), and shifts in liana composition among sites may thus  
640 contribute to variation in forest carbon dynamics (Muller-Landau & Visser, 2019). The incorporation  
641 of lianas in models involves unique challenges because of the complexities of their interactions with  
642 host trees, but may be critical to reproducing major changes in forest structure and functioning  
643 associated with variation in liana abundance along successional, climate, and disturbance gradients  
644 (Brugnera *et al.*, 2019).

645 Most research on variation in plant functional composition has focused on direct  
646 environmental influences on plant performance. However, environmental conditions may also  
647 influence plants via changes in antagonistic and mutualistic interactions with microbes,  
648 invertebrates, and vertebrates. For example, there is some evidence of higher herbivory in sites with

649 higher soil fertility, where plant tissue nutrient concentrations are higher (Campo & Dirzo, 2003).  
650 Differences in vertebrate abundance and community composition contribute to savanna-forest  
651 boundaries and possibly differences in forest structure among biogeographic regions (Corlett, 2016).  
652 And it has long been hypothesized that pest pressures is higher at wetter sites, and may drive  
653 compositional shifts and higher plant diversity (Janzen & Schoener, 1968; Givnish, 1999), although  
654 evidence to date remains limited (but see (Spear *et al.*, 2015)). The influences of biotic interactions  
655 have been assumed to be secondary to more direct environmental influences, and have been  
656 ignored in vegetation models; however, they may be critical to predicting future forest carbon  
657 dynamics under global change, including defaunation (Dirzo *et al.*, 2014).

658 ***Conclusions and future directions***

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

674 We also critically need a mechanistic understanding of the emergence of observed empirical  
675 patterns, so that we can reproduce them in models for the right reasons and have some hope of

676 correctly predicting responses to future novel climate conditions (Wright *et al.*, 2009). Research to  
677 date provides considerable support for various hypotheses regarding contributing mechanisms.  
678 However, every environmental pattern involves multiple mechanisms, and we lack an understanding  
679 of the relative importance of different mechanisms and their interactions. A combination of  
680 mechanistic empirical studies and mechanistic modeling is key to resolving this uncertainty, yet  
681 many of the hypothesized underlying processes are not yet represented in models, which currently  
682 fail to reproduce key patterns (Fig. 2). This is not surprising considering the models' very limited  
683 representation of tree mortality (Galbraith *et al.*, 2013; Johnson *et al.*, 2016), tropical tree functional  
684 diversity (Sakschewski *et al.*, 2016), and many other processes.

685 Fortunately, a new generation of models has been developed in the last decade that better  
686 captures some spatial variation in tropical forest biomass. Whereas older models represented forest  
687 vegetation as a “big leaf”, new vegetation demographic approaches explicitly model the growth,  
688 survival, and reproduction of trees or cohorts of trees (Fisher *et al.*, 2018). When run with prescribed  
689 meteorological conditions, these models have succeeded in reproducing a multitude of patterns  
690 within individual tropical sites, as well as general patterns of among-site variation along some  
691 environmental gradients (Seiler *et al.*, 2014; Levine *et al.*, 2016; Xu *et al.*, 2016; Longo *et al.*, 2019;  
692 Medvigy *et al.*, 2019; Koven *et al.*, 2020; Martínez Cano *et al.*, 2020). However, most still contain  
693 large systematic errors; e.g., predicting too many large trees (Koven *et al.*, 2020), and/or excessively  
694 high tree mortality rates (Longo *et al.*, 2019). Further, they mostly lack the mechanisms needed to  
695 capture temporal responses to drought or spatial variation with soil fertility, disturbance, and  
696 biogeographic region.

697 Tree mortality, branch turnover, tree functional composition, and biotic interactions of trees  
698 with lianas and other organisms are key areas for further research, both for empirical data collection  
699 as well as modeling. Advances in remote sensing promise to yield much more and more widely  
700 distributed data on tropical forest structure and function (Schimel *et al.*, 2019), but adequate  
701 investment in concurrent ground data collection in the tropics is vital if these missions are to fulfill  
702 their promise (Chave *et al.*, 2019). Every type of evidence on its own has key limitations;  
703 triangulation across multiple lines of evidence is needed to reach robust conclusions (Munafo &

704 Smith, 2018). We must integrate empirical studies and mechanistic modeling to make progress on  
705 the big questions of the mechanisms of extant variation in tropical forests today and the implications  
706 for their future trajectories (Hofhansl *et al.*, 2016; Fisher *et al.*, 2018).

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712 **Author contributions**

713 HCM planned and designed the research. HCM, KCC, and EEA conducted the literature review. HCM,  
714 KCC, IMC, and BB analyzed data. HCM, KCC, IMC, KAT, and BB prepared figures. HCM drafted the  
715 manuscript. All authors contributed to revisions.

716

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

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

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

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

740       See Methods and Notes S1 for details.

741 **Figure Legends**

742

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

754

755 Figure 2. Earth System Model (ESM) predictions of aboveground woody biomass (AGB, top row),  
756 aboveground woody productivity (AWP, middle row), and aboveground woody residence time  
757 (AWRT, bottom row) show little relation with observational data (Galbraith *et al.*, 2013) for 177 old-  
758 growth tropical forests. Both observed and modeled residence times are calculated as AGB/AWP  
759 (Box 1). ESMs simulate vegetation dynamics in tropical forests around the globe as part of their  
760 simulation of the entire earth system, including the atmosphere, ocean, and land surface, and their  
761 interactions. Spatial variation in predicted climates in these models translates to spatial variation in  
762 predicted vegetation because of modeled effects of climate on photosynthesis and respiration, and  
763 thus on woody productivity and potentially the dominant plant functional type, with effects that  
764 vary depending on the details of model structure and parameterization. Model predictions are from  
765 the most recent set of publicly released ESM models and simulation results, from the Coupled Model

766 Intercomparison Project 5 (Taylor *et al.*, 2012). Further details are given in Supporting Information  
767 Notes S1.

768 Figure 3. Literature results on spatial variation in productivity (a), residence time (b), and  
769 aboveground biomass (c) with precipitation, dry season length, and other measures of climatic water  
770 availability, graphed in relation to the range of precipitation in the study sites (on a log scale). Blue  
771 indicates that productivity, residence time, or biomass tend to be higher in wetter sites; orange  
772 indicates that they tend to be higher in drier sites; dashed blue and orange variable pattern that  
773 depends on the range of the independent variable or on temperature; and black indicates no  
774 relationship. Asterisks indicate statistically significant effects. Bold highlights studies in which  
775 median plot area is 1 ha or larger, whereas results for studies with smaller plot sizes are shown in  
776 italics. Note that the patterns are always reported here in terms of the response of productivity,  
777 residence time, or biomass, even if the response metric is inversely related to these (e.g., a blue  
778 turnover result indicates that in wetter sites tree turnover is lower implying residence time is  
779 higher). These results are graphed in relation to temperature range in Supporting Information Fig.  
780 S3. AWP = aboveground woody productivity, BAP = basal area productivity, ANPP = aboveground  
781 net primary productivity, Litter = litterfall; NPP = net primary productivity, GPP = gross primary  
782 productivity, AWRT = aboveground woody residence, Turn = tree turnover rate, AGB = aboveground  
783 biomass, CanHt = canopy height, BA = basal area. See Box 1, Fig. 1, and Notes S1 for definitions,  
784 measurement methods, and interrelationships of these response variables. Literature results are  
785 coded by the first 8 letters of the first author's name, the last 2 digits of the year, a letter indicating  
786 which set of sites within the publication (if there is more than one set of sites for the study in the  
787 database), and the number of sites included within parentheses (Dataset S1).

788

789 Figure 4. Schematic of patterns of variation in tropical forest aboveground woody productivity  
790 (AWP), residence time (AWRT), and biomass (AGB) with climatic water availability(a), elevation in  
791 moist or wet sites (b), soil fertility (c), and disturbance (d). Text size reflects variation in a given

792 variable along the environmental gradient; e.g., AWP and AGB increase with climatic water  
793 availability. (Watercolors by K. T. Anderson-Teixeira.)

794

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

808

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

818 Supporting Information Fig. S8. AWP = aboveground woody productivity, BAP = basal area  
819 productivity, ANPP = aboveground net primary productivity, Litter = litterfall; NPP = net primary  
820 productivity, GPP = gross primary productivity, AWRT = aboveground woody residence, Mort = tree  
821 mortality rate, Turn = tree turnover rate, AGB = aboveground biomass, CanHt = canopy height, BA =  
822 basal area. Literature results are coded by the first 8 letters of the first author's name, the last 2  
823 digits of the year, a letter indicating which set of sites within the publication, and the number of sites  
824 included within parentheses (Dataset S1). These Response variable and study abbreviations as in  
825 Fig. 3 (Dataset S1).

826

827 Figure 7. Literature results on spatial variation in productivity (a), residence time (b), and  
828 aboveground biomass (c) with soil fertility, graphed in relation to the soil fertility measure used  
829 (Multi = a soil fertility axis or classification that encompassed multiple nutrients; P = phosphorus;  
830 CEC = cation exchange capacity; Bases = total soil bases; Other includes studies using nitrogen,  
831 potassium, magnesium, and calcium. Green indicates that productivity, residence time, or biomass  
832 tend to be higher in more fertile sites; brown indicates that they tend to be higher in less fertile  
833 sites, and black indicates no relationship or an inconsistent relationship. Asterixes indicate  
834 statistically significant effects. Bold highlights studies in which median plot area is 1 ha or larger,  
835 whereas results for studies with smaller plot sizes are shown in italics. For studies that investigate  
836 multiple soil fertility measure, the text denoting the response variable is graphed in the column  
837 corresponding to the variable that exhibited the strongest relationship; additional results for other  
838 types of soil variables are indicated with an asterix for significant results, and a tilde for others. In  
839 some cases results for secondary variables reflect weaker tests of effects (e.g., correlations) than the  
840 main results (e.g., multiple regression), and thus the secondary results can be significant while the  
841 primary results are not (e.g., turnover results for Quesada et al. 2012). AWP = aboveground woody  
842 productivity, BAP = basal area productivity, ANPP = aboveground net primary productivity, Litter =  
843 litterfall; NPP = net primary productivity, GPP = gross primary productivity, AWRT = aboveground  
844 woody residence, Mort = tree mortality rate, Turn = tree turnover rate, AGB = aboveground biomass,

845 CanHt = canopy height, BA = basal area. Literature results are coded by the first 8 letters of the first  
846 author's name, the last 2 digits of the year, a letter indicating which set of sites within the  
847 publication, and the number of sites included within parentheses (Supporting Information Dataset  
848 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.

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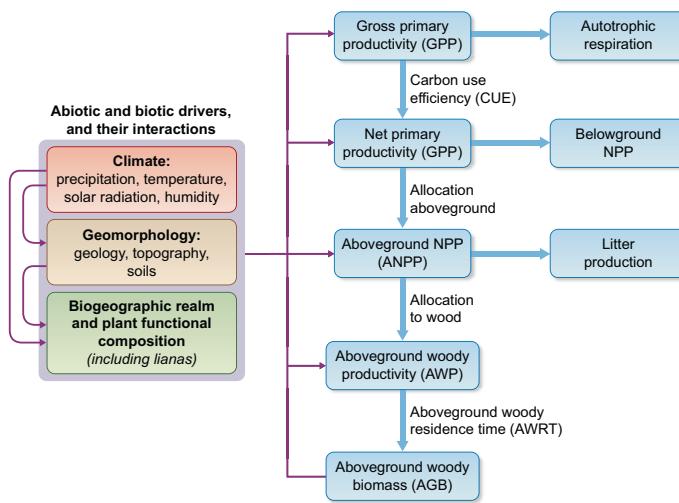
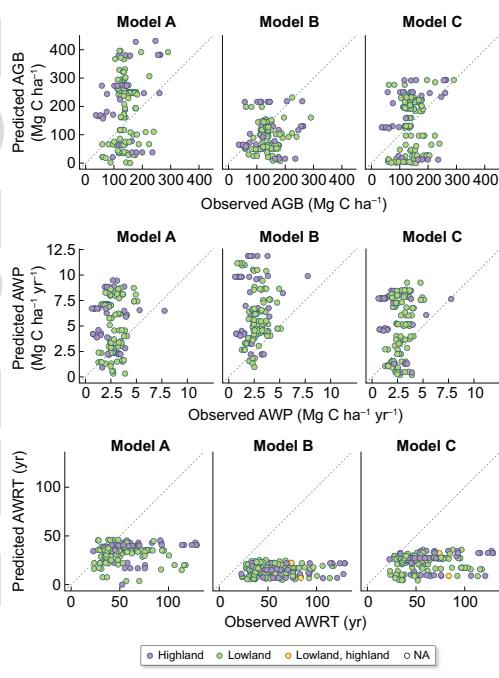


Figure 1

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Figure 2  
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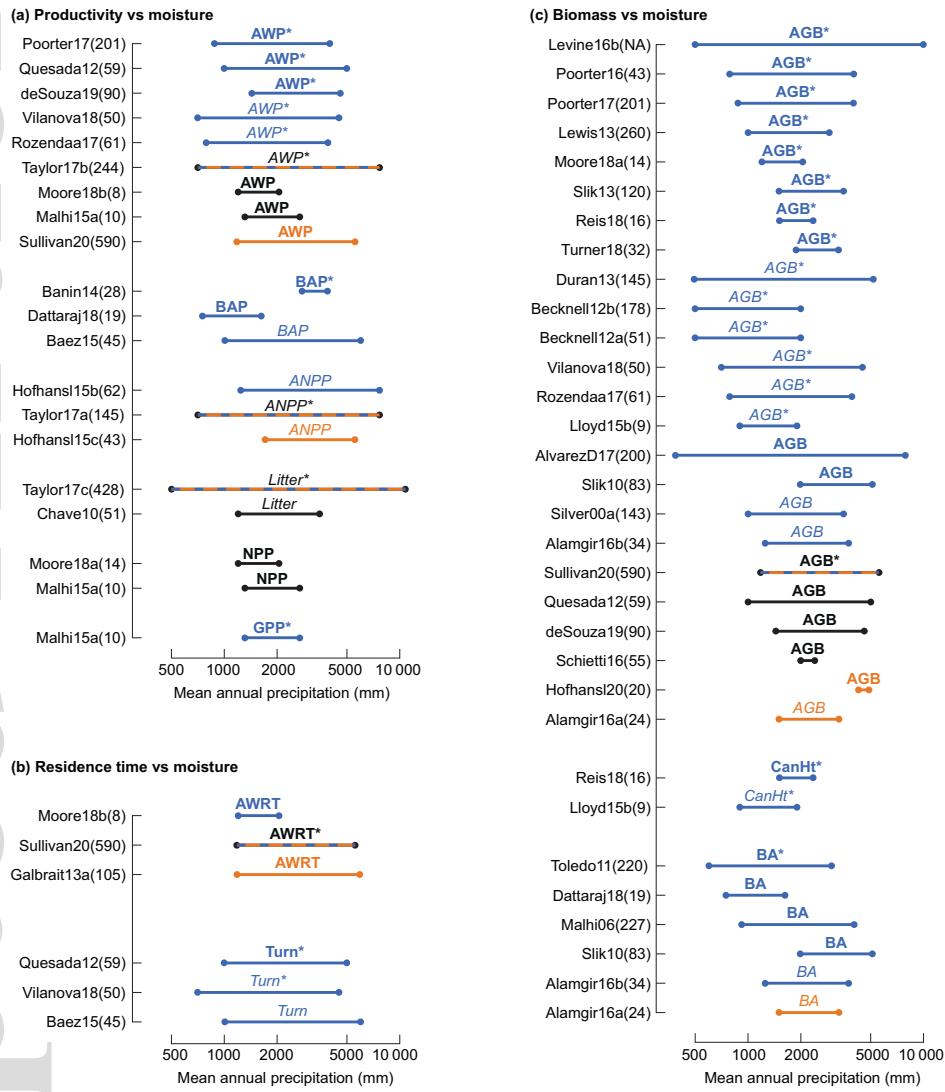


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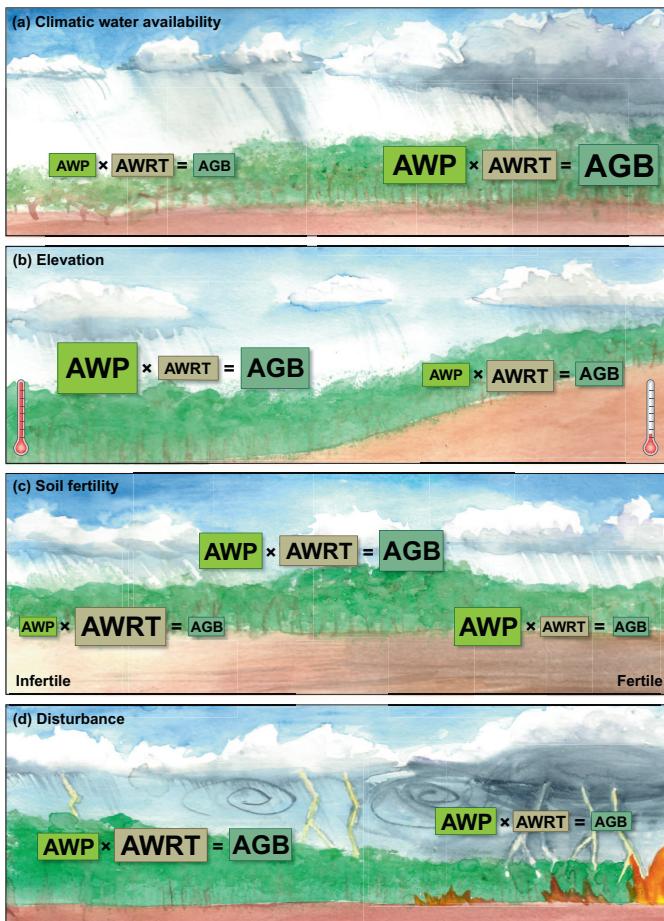


Figure 4

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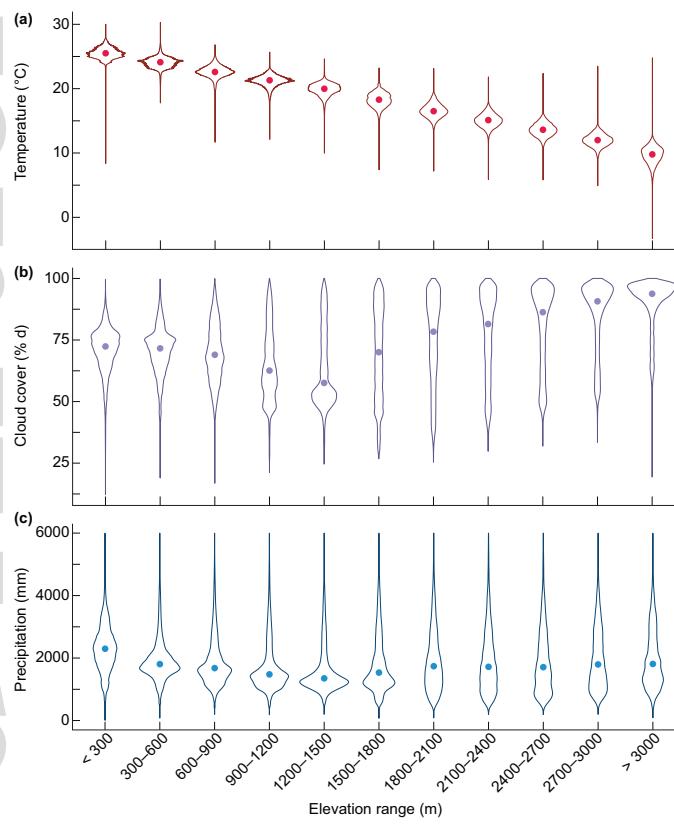


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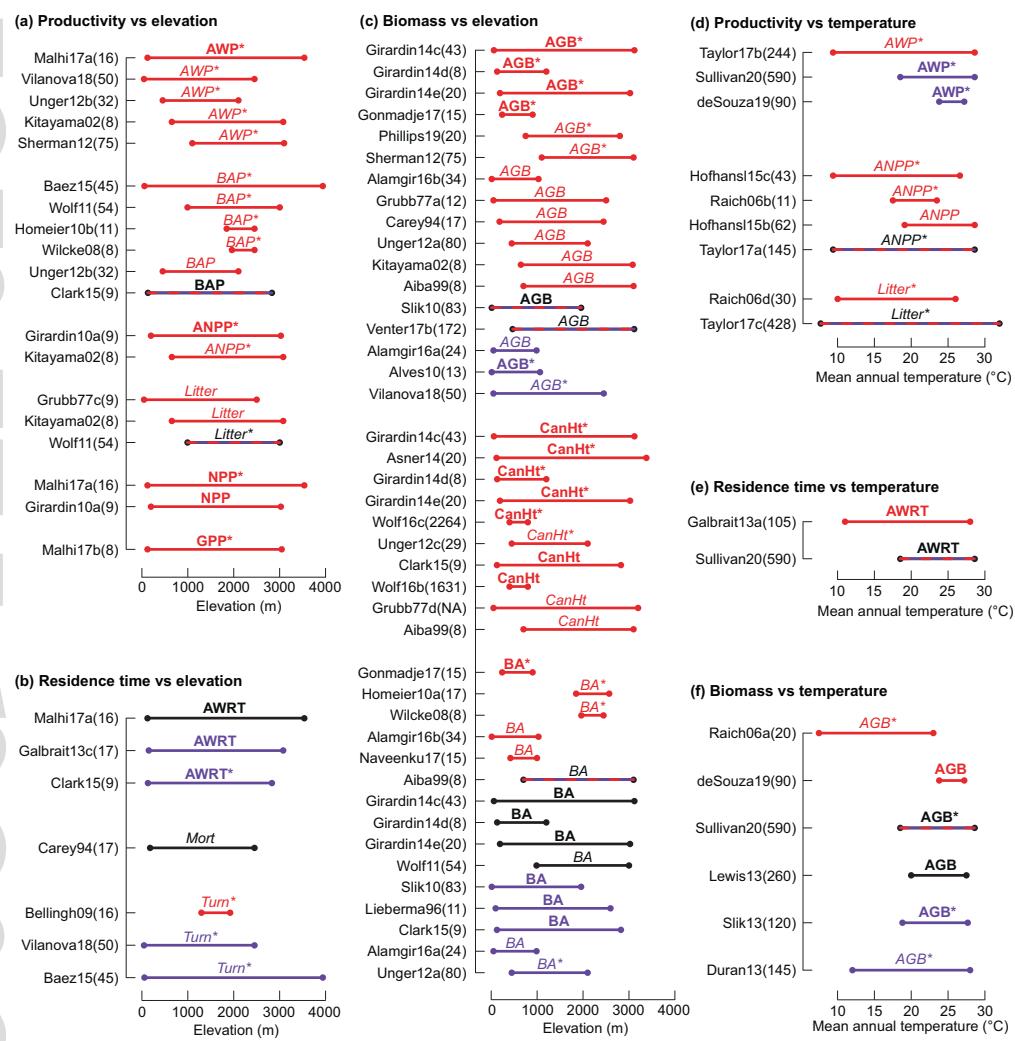


Figure 6

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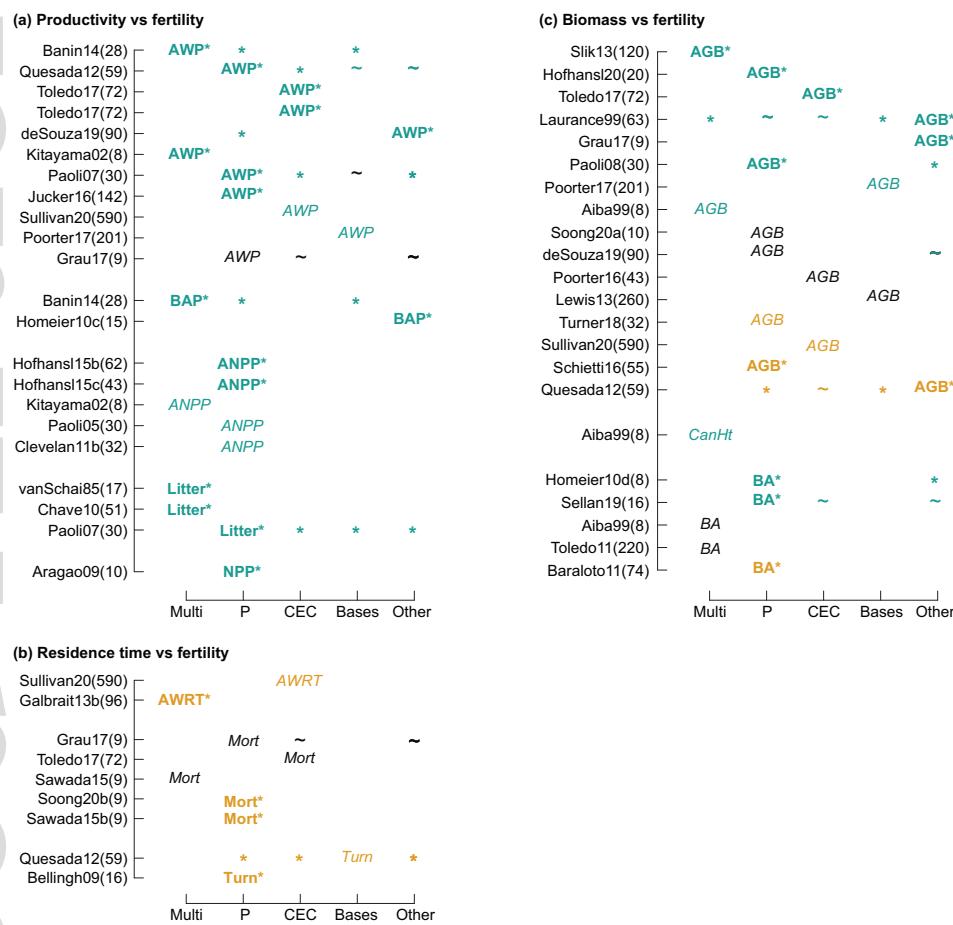


Figure 7  
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