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

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Summary

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

II. Introduction

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

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

date of overall patterns (Lewis *et al.*, 2009; Wright, 2010). This uncertainty is reflected in highly divergent predictions for tropical forest responses in different earth system models (Cavaleri *et al.*, 2015; Koven *et al.*, 2015; Rowland *et al.*, 2015).

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

Mechanisms and patterns involving changes in tree mortality or shifts in plant functional composition remain poorly understood, whereas those involving changes in productivity of a given plant

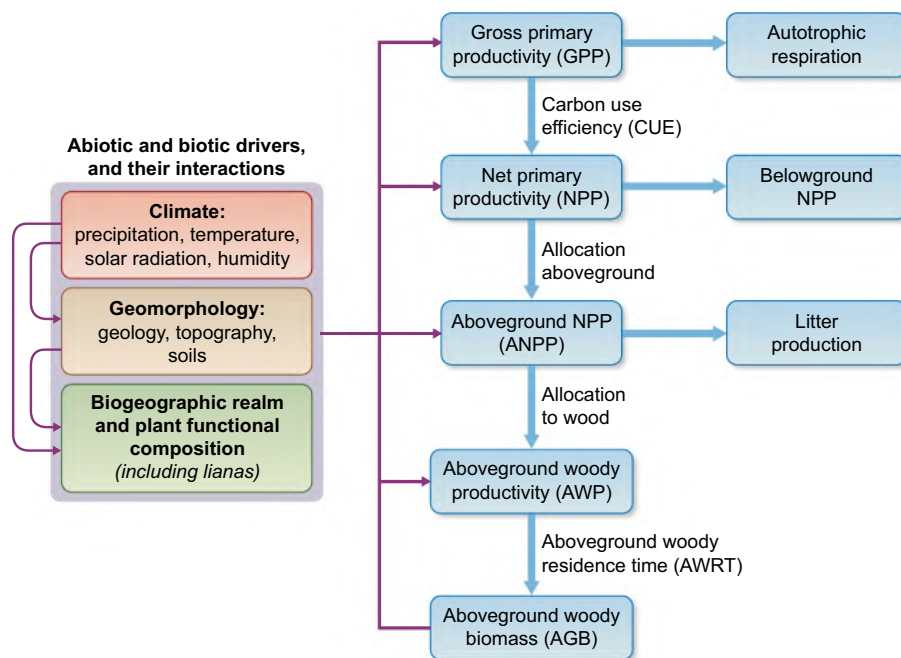


Fig. 1 Climate, geomorphology, biogeographic realm and plant functional composition interact to influence tropical forest aboveground woody productivity (AWP, units of mass area⁻¹ time⁻¹), aboveground woody residence time (AWRT, time) and thus aboveground woody biomass density (AGB, mass area⁻¹) via multiple pathways. Here blue boxes represent fluxes (mass area⁻¹ time⁻¹), blue arrows represent the factors by which the one quantity is multiplied to obtain another (e.g. NPP = GPP × CUE), and purple 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; Supporting Information Notes S1 provides additional details on these and related variables.

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

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

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

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

See Section II (Methods) and Supporting Information Notes S1 for details.

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

Earth system models (ESMs) are key tools for predicting the future of the global C cycle under global change, and for attributing

temporal variation to different factors (Heavens *et al.*, 2013). These models are mechanistic, and attempt to capture hypothesized critical processes as gleaned from empirical studies (Heinze *et al.*, 2019). However, the most recent set of publicly released models completely fail to reproduce spatial variation in AGB, AWP and AWRT in old-growth tropical forests (Fig. 2). This demonstrates that the models fail to adequately represent the mechanisms or capture the patterns of spatial variation in tropical forests today, and highlights the need for a more mechanistic understanding of these patterns.

Here we review empirical studies documenting how different environmental factors relate to tropical forest productivity, residence time, biomass, their proxies and related variables. We first briefly describe the types of studies included, and their strengths and weaknesses. We then review empirical findings on tropical forest variation with climatic water availability (precipitation regimes), elevation and temperature, soil fertility, disturbance and biogeographic realm, and discuss hypothesized mechanisms underlying observed relationships. We discuss critical knowledge gaps and uncertainties in mechanistic understanding and in datasets, and key directions for future research.

III. Methods

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

Most currently available information on our focal variables are based on tree plot census data. Because of high local spatial variability in the number and sizes of large trees, these plot-based estimates exhibit considerable sampling error, even for plots of 1 ha, and this error increases at smaller plot sizes (Muller-Landau *et al.*, 2014). We thus highlight studies based on plots with a median size of 1 ha or larger (124 of 201 results reviewed). Plot-

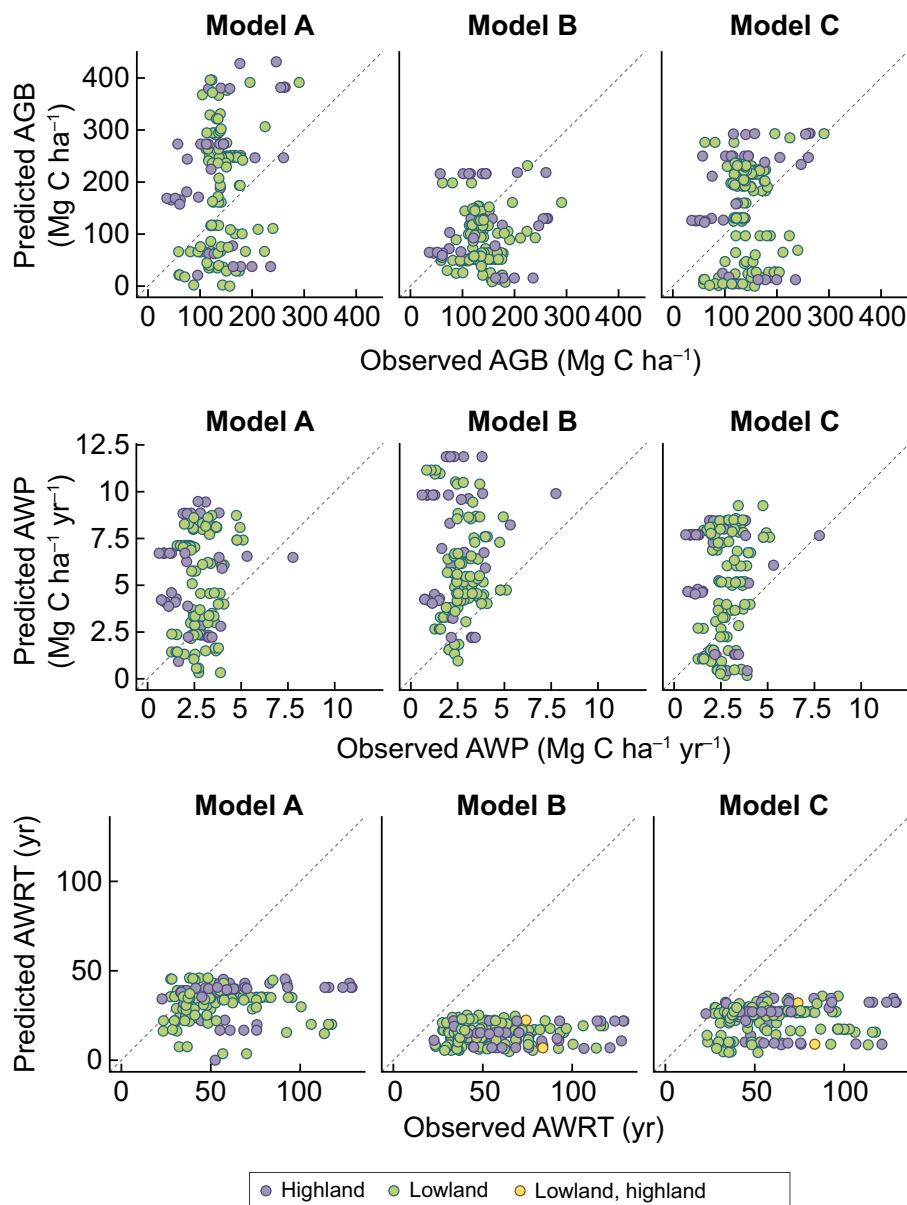


Fig. 2 Earth System Model (ESM) predictions of aboveground woody biomass (AGB, top row), aboveground woody productivity (AWP, middle row) and aboveground woody residence time (AWRT, bottom row) show little relation with observational data (Galbraith *et al.*, 2013) for 177 old-growth tropical forests. 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 Supporting Information Notes S1.

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

Estimation of AGB and AWP depend on biomass allometry equations (Box 1), which are a major source of error. These equations estimate individual tree aboveground woody biomass from measured tree diameter, and sometimes also tree height and/or wood density (e.g. Chave *et al.*, 2005; Chave *et al.*, 2014). The key issue for analyses of among-site variation is that studies typically apply the same equation(s) across many sites. However, biomass

allometries differ systematically among sites (e.g. Chave *et al.*, 2014), reflecting differences in height allometries (Feldpausch *et al.*, 2012) and crown form (Ploton *et al.*, 2016), and potentially also rates of heartrot (Heineman *et al.*, 2015) and crown breakage (Arellano *et al.*, 2019). Such differences are only partially captured with generalized allometric equations which at best incorporate local height measurements and associated differences in diameter-height allometries, continuous terms for climate variation and/or different equations for different regions or forest types (Chave *et al.*, 2005, 2014).

Estimates of AWP suffer from additional sources of error. They depend on diameter growth measurements, and thus are highly sensitive to diameter measurement errors and to data quality assurance quality control procedures, including procedures for estimating diameter change in buttressed trees (Sheil, 1995; Cushman *et al.*, 2014; Muller-Landau *et al.*, 2014). AWP is

temporally variable (e.g. Rutishauser *et al.*, 2020), and thus sampling errors for short census intervals are high. At the same time, typical calculations underestimate AWP in longer census intervals because they increasingly miss AWP of trees that die between censuses (Kohyama *et al.*, 2019). Finally, standard methods for estimating AWP entirely fail to capture wood production to compensate for branchfall, estimated at 15–45% of total AWP (Malhi *et al.*, 2014; Marvin & Asner, 2016; Gora *et al.*, 2019). That is, as trees grow, they do not simply accrue biomass, they also shed old branches as they produce new ones.

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

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

IV. Climatic water availability

Precipitation patterns vary among tropical forests from those that receive abundant precipitation year-round (wet tropical forests) to those that experience limitations in water availability during one or two dry seasons (moist and dry tropical forests), variation we encompass under the term climatic water availability. This variability is evident in the large range of mean annual precipitation among tropical forests (Fig. S2). In general, the length and intensity of dry seasons are more important than total annual precipitation in determining forest C stocks and fluxes. Further, water limitation depends not only on precipitation, but also on potential evapotranspiration (itself dependent on temperature, solar radiation), as well as soil depth, soil water-holding capacity and topographic position. Many analyses thus evaluate relationships with more integrative measures of climatic water availability such as dry season length or maximum climatological water deficit, which are generally better predictors of forest structure and dynamics (e.g. Alvarez-Davila *et al.*, 2017). Here, we discuss how our focal variables vary with climatic water availability, and evaluate patterns in relation to the range of annual precipitation and temperature within studies (Figs 3, S3).

1. Productivity

Productivity variables are positively associated with climatic water availability across lowland tropical forests over the range from dry to wet forests. Across lowland sites, AWP, litterfall and ANPP are positively related to climatic water availability in most studies (Fig. 3a), with an initial fast increase slowing to a plateau or even a mild decrease for precipitation above *c.* 3000 mm yr⁻¹ (Poorter *et al.*, 2017; Taylor *et al.*, 2017). The positive effects of precipitation weaken and reverse in montane tropical forests (e.g. lowland Hofhansl15b vs montane Hofhansl15c in Fig. 3a; Hofhansl *et al.*, 2015). A meta-analysis of 145 tropical forests found that an increase in mean annual precipitation (MAP) from 1000 to 3000 mm was associated 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 decrease in ANPP at temperatures below 20°C (Taylor *et al.*, 2017).

Lower forest productivity at lower precipitation reflects limitation by water availability and/or drought stress when potential evapotranspiration exceeds precipitation, combined with allocational changes and compositional shifts towards drought-tolerant species (Flack-Prain *et al.*, 2019). Limited water availability translates into reduced GPP through both reduced leaf area maintained (including drought deciduous leaf phenology) and reduced photosynthesis per available leaf area as plants close their stomata and/or invest in more drought-tolerant organs with lower light-use efficiency (LUE) (Tan *et al.*, 2013; Guan *et al.*, 2015; Wu *et al.*, 2016; Pfeifer *et al.*, 2018). Higher precipitation also is associated with higher allocation of aboveground NPP to AWP (Hofhansl *et al.*, 2015) and taller trees for a given diameter (Banin *et al.*, 2012), further contributing to higher AWP. Compositional shifts also contribute: species found in drier forests have lower growth rates than those restricted to wetter forests (Baltzer & Davies, 2012; Brenes-Arguedas *et al.*, 2013; Kupers *et al.*, 2019), because drought-tolerance traits, such as narrower xylem vessels, are costly (Gorel *et al.*, 2019), whereas the ‘drought-avoiding’ deciduous strategy involves foregoing photosynthesis in part of the year (Brenes-Arguedas *et al.*, 2013).

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

2. Residence time

Few studies have evaluated how among-site variation in AWRT, mortality or turnover relate to climatic water availability, and those

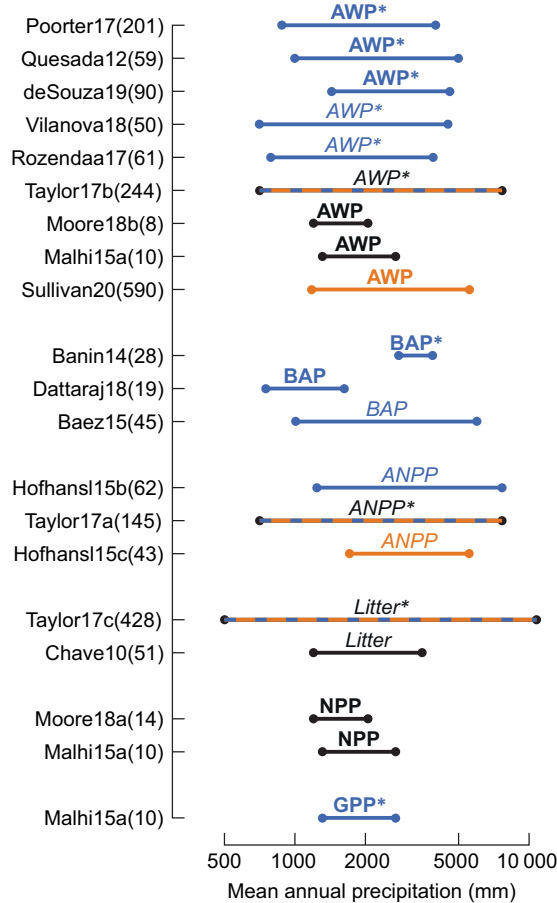
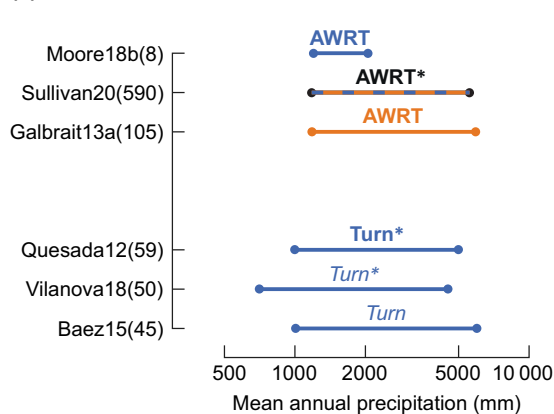
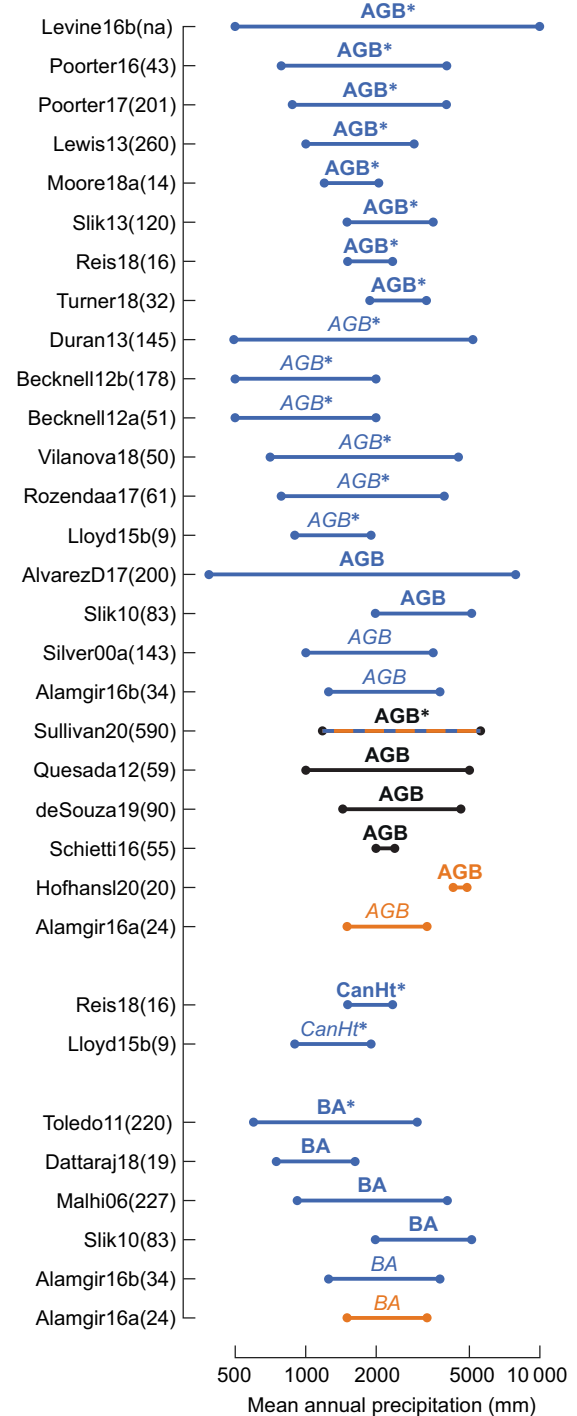
(a) Productivity vs moisture**(b) Residence time vs moisture****(c) Biomass vs moisture**

Fig. 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 variable pattern that depends on the range of the independent variable or on temperature; and black indicates no relationship. Asterisks indicate statistically significant effects. Bold highlights studies in which median plot area is ≥ 1 ha, whereas results for studies with smaller plot sizes are shown in italics. Note that the patterns always are 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 Supporting Information Fig. S3. AGB, aboveground biomass; ANPP, aboveground net primary productivity; AWP, aboveground woody productivity; AWRT, aboveground woody residence; BA, basal area; BAP, basal area productivity; CanHt, canopy height; GPP, gross primary productivity; Litter, litterfall; na, not available; NPP, net primary productivity; Turn, tree turnover rate. See Box 1, Fig. 1 and Notes S1 for definitions, measurement methods and inter-relationships of these response variables. Literature results are coded by the first eight letters of the first author's name, the last two 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).

that do have found at best weak relationships (e.g. Quesada *et al.*, 2012; Vilanova *et al.*, 2018). More studies have found trends for AWRT to be higher (and turnover lower) in wetter sites than the opposite, but overall patterns are inconsistent (Fig. 3b). This may reflect contrasting trends in different mortality threats with precipitation regimes. Drier sites are more likely to experience fire (Cochrane, 2011) and drought stress elevates mortality through hydraulic damage (Choat *et al.*, 2018), whereas higher rainfall is associated with greater risks of mortality from treefalls, lightning and landslides (Espirito-Santo *et al.*, 2010; Yanoviak *et al.*, 2020).

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

3. AGB

Aboveground biomass is positively related to climatic water availability in tropical forests in 16 of 16 studies finding a statistically significant relationship (Fig. 3c). The relationship of AGB with precipitation exhibits an initially steep increase below 2000 mm yr⁻¹ gradually saturating at higher precipitation (Becknell *et al.*, 2012; Poorter *et al.*, 2016; Alvarez-Davila *et al.*, 2017). Increases are roughly parallel in old-growth and secondary forests: over 1000–3000 mm MAP, AGB increases two-fold in 20-yr-old secondary forests (Poorter *et al.*, 2016) and *c.* 2.3-fold in mature forests (Alvarez-Davila *et al.*, 2017). Qualitatively the same patterns are found for tree basal area and canopy height, for both plot-based and remote sensing studies, and in both old-growth and secondary forests of a given age (Fig. 3c). Measures of drought stress such as dry season length or dry season water deficit are generally better predictors of AGB than precipitation alone, and exhibit more linear relationships with AGB (Poorter *et al.*, 2016; Alvarez-Davila *et al.*, 2017). At extremely high precipitation levels above *c.* 4000 mm yr⁻¹, AGB may decrease with further increases in precipitation, but there are few data for such sites, and spatial variation in precipitation may be confounded with solar radiation, soil fertility and other factors (Alvarez-Davila *et al.*, 2017). Overall the patterns in AGB parallel those in AWP, consistent with what would be expected given little variation in AWRT with precipitation (Fig. 4a).

4. Synthesis

Overall, patterns of variation in tropical forest productivity and biomass with climatic water availability are relatively well-documented and well-understood, and the underlying mechanisms are increasingly well-represented in forest and vegetation models (Christoffersen *et al.*, 2016; Levine *et al.*, 2016; Xu *et al.*, 2016).

Additional data and analyses are needed to establish whether/how mortality rates vary spatially with climatic water availability, and to investigate the role of compositional shifts in contributing to variation in C fluxes and stocks. The role of lianas deserves more attention, as lianas are more abundant in drier sites (DeWalt *et al.*, 2010), and could contribute to their lower tree productivity and possibly lower residence time.

V. Temperature and elevation

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

1. Productivity

All productivity variables decline with elevation (Fig. 6a), suggesting a positive effect of temperature, but analyses with temperature find both positive and negative effects (Fig. 6a,d). Overall patterns seem consistent with a positive effect of temperature in wet sites and a negative effect in dry sites. This is particularly apparent in studies that evaluate interactions of climatic water availability and temperature (Taylor *et al.*, 2017; Sullivan *et al.*, 2020). A meta-analysis found that ANPP (litterfall) decreased with temperature for precipitation below *c.* 1400 mm yr⁻¹ (1600 mm yr⁻¹), and increased with temperature for precipitation above that level, with ever-faster increases for higher precipitation (Taylor *et al.*, 2017). At 2500 mm MAP, ANPP doubles between 10 and 22°C and triples by 28°C (Taylor *et al.*, 2017).

Spatial variation in AWP with temperature can be explained in large part by the temperature responses of plant metabolic rates – photosynthesis and respiration. Across sites, the optimum temperature for photosynthesis is strongly positively correlated with mean growing season temperature (Tan *et al.*, 2017), and the photosynthetic rate at the temperature optimum increases with temperature, meaning warmer sites are expected to have higher photosynthetic rates, if water is not limiting (Farquhar *et al.*, 1980). Maintenance respiration rates also increase with temperature within sites – but acclimation means that respiration rates at growth temperatures increase very little or not at all (Atkin *et al.*, 2015; Malhi *et al.*, 2017). Biomass accumulation rates increase with temperature in well-watered conditions (Cheesman & Winter, 2013), likely

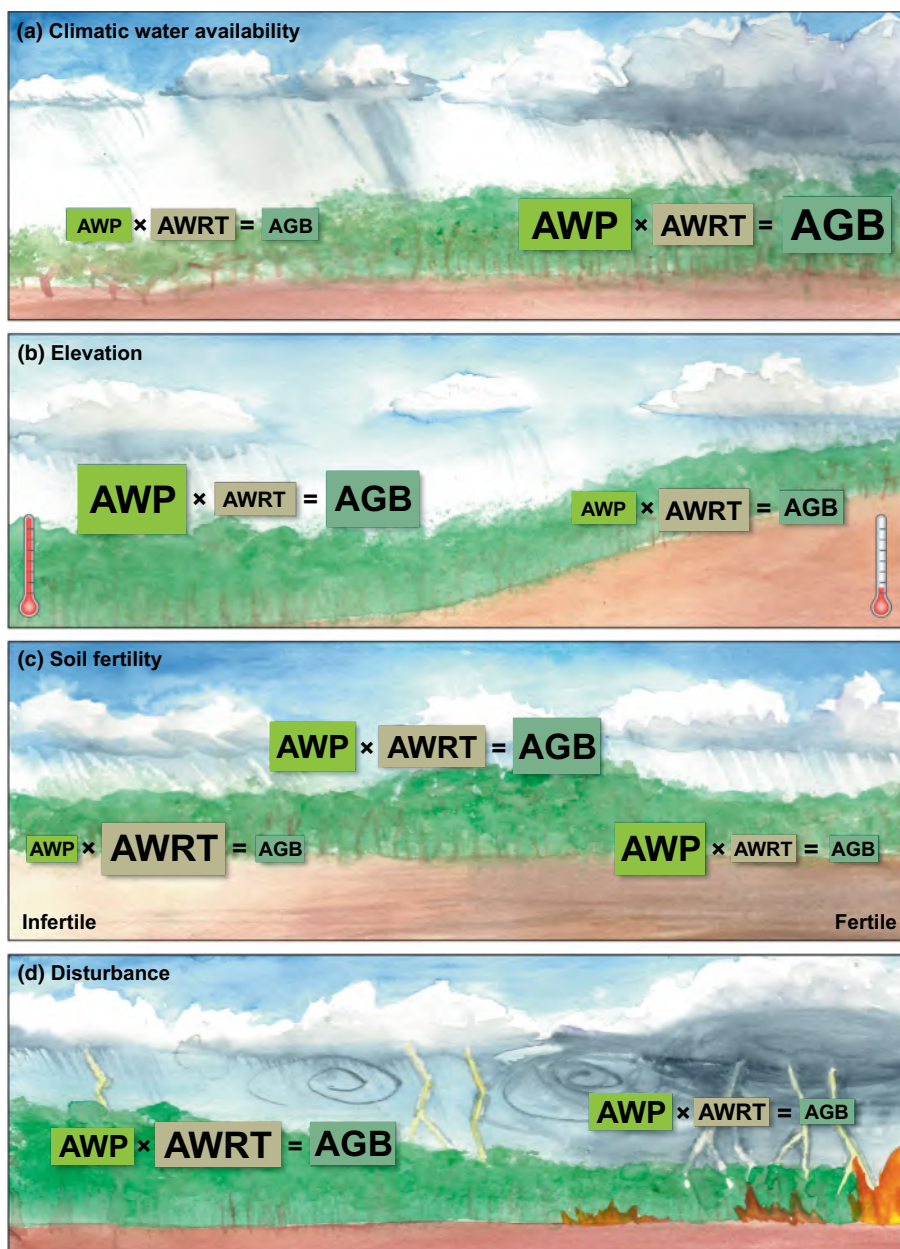


Fig. 4 Schematic of patterns of variation in tropical forest aboveground woody productivity (AWP), residence time (AWRT) and biomass (AGB) with climatic water availability (a), elevation in moist or wet sites (b), soil fertility (c) and disturbance (d). Text size reflects variation in a given variable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

reflecting an increase in biosynthesis rates. By contrast, where water is limiting, photosynthesis decreases with temperature as a result of increased stomatal closure and higher respiratory costs (Schipper *et al.*, 2015). Overall, for any given plant and site, net photosynthesis is expected to be a unimodal function of temperature, reflecting biochemically determined unimodal responses of maximum photosynthetic rates in combination with stomatal conductance and respiration (Slot & Winter, 2017).

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

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

Finally, correlated variation in other environmental factors also influences patterns with temperature among tropical sites. Cooler tropical forests are found overwhelmingly at higher elevations, where cloud cover is higher and fog is more frequent, thereby decreasing solar radiation and increasing light limitation

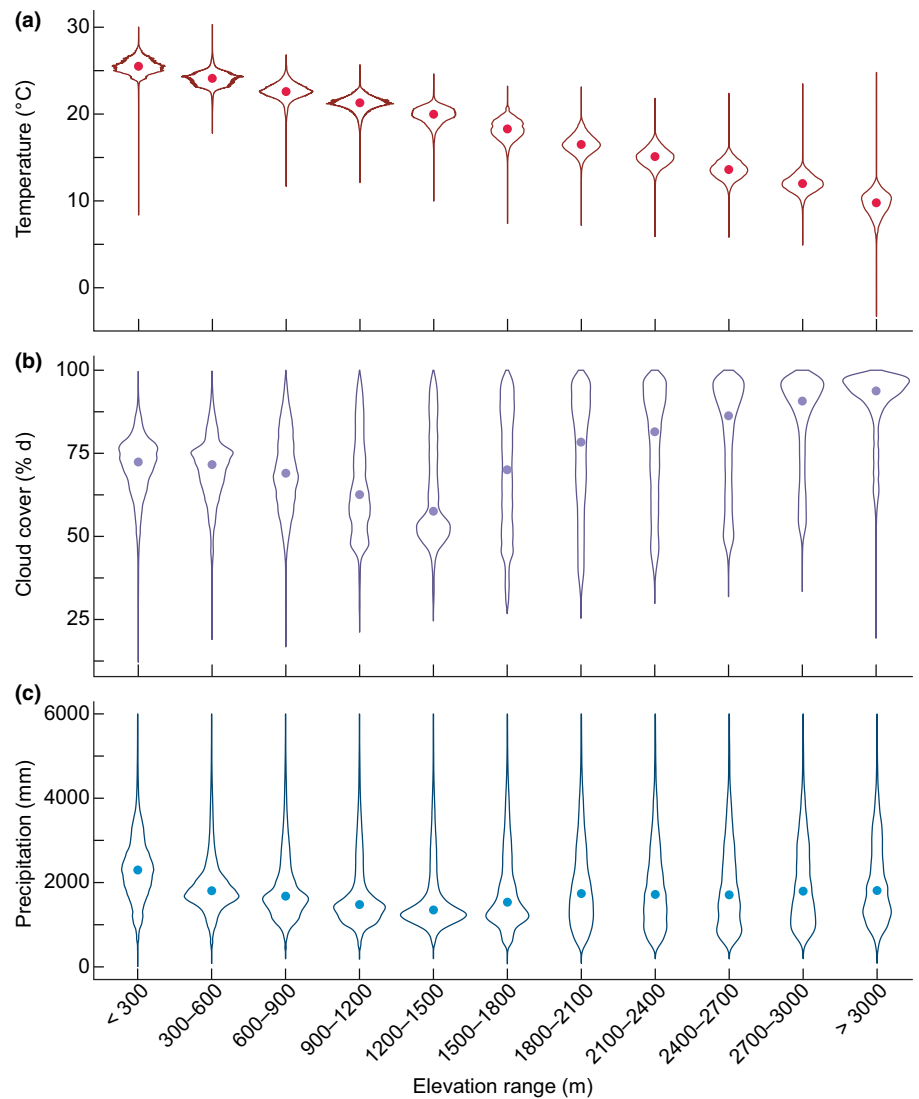


Fig. 5 Variation in the distributions of mean annual temperature (a), mean cloud cover (b) and mean annual precipitation (c) in relation to elevation in tropical forests. Panels show violin plots of the distribution across 1-km pixels, with the red dots indicating medians. Tropical forest area was defined 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 Supporting Information Fig. S6; see also Figs S7, S8 for versions including additional land-cover types). Mean elevation data from SRTM (<https://cgiarcsi.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 & 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.

(Bruijnzeel *et al.*, 2011). Cooler temperatures also slow decomposition (Taylor *et al.*, 2017) and reduce biological nitrogen (N) fixation (Houlton *et al.*, 2008), which tends to reduce nutrient availability, especially N availability (Wilcke *et al.*, 2008; Nottingham *et al.*, 2015). However, higher elevation and thus cooler forests tend to be found on geochemically young substrates with eroding slopes, which are associated with relatively higher availability of rock-derived nutrients (Porder *et al.*, 2007). Thus, for any given area, elevational variation in cloud cover, rainfall and soils can magnify or counter the patterns expected based on temperature alone, and interact with compositional shifts (Peng *et al.*, 2020).

2. Residence time

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

is consistent with the global pattern of a positive correlation between tree productivity and mortality (Stephenson & Mantgem, 2005), given that higher elevations tend to be associated with lower productivity and slower life histories (e.g. lower LMA; Asner & Martin, 2016).

3. AGB

Aboveground biomass decreases with elevation in most studies, and canopy height decreases with elevation in almost all studies, but patterns of basal area variation are decidedly mixed, as are patterns of AGB with temperature (Fig. 6c,f). It is notable that some studies find very high or even the highest AGB at intermediate or high-elevation sites (e.g. Girardin *et al.*, 2010); the mechanisms underlying these exceptions are an important area for future research. In terms of the quantitative strength of these effects, regressions of AGB on elevation in Bolivia, Peru and Ecuador found that AGB decreases 32, 34 and 50 Mgha⁻¹ per 1000 m elevation, respectively (Girardin *et al.*, 2014). Overall, the patterns

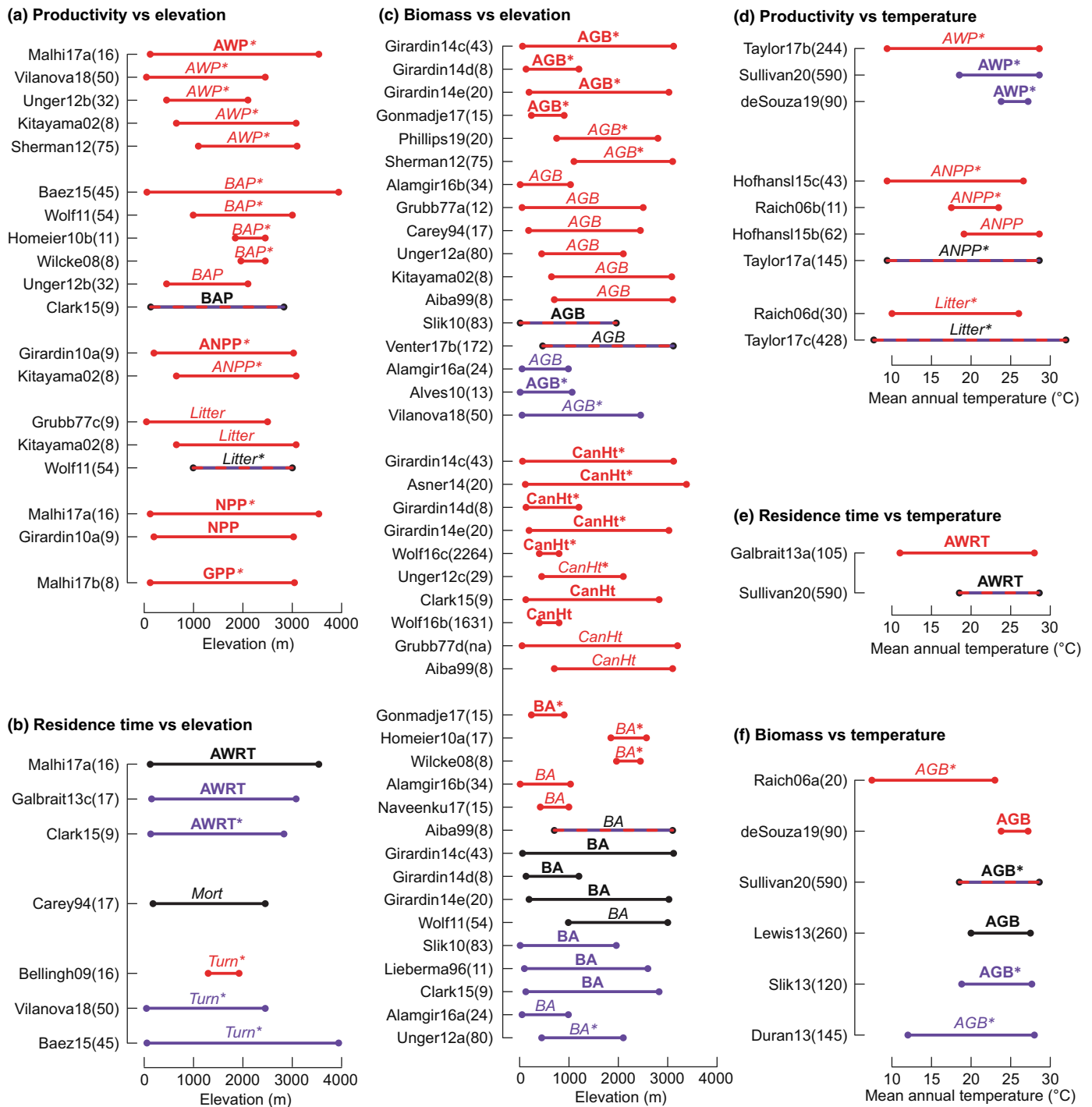


Fig. 6 Literature results on spatial variation in productivity (a, d), residence time (b, e) and aboveground biomass (c, f) with elevation (a–c) or temperature (d–f), graphed in relation to the range in elevation or temperature, respectively, in the study sites. Red indicates that productivity, residence time or biomass tend to be higher in lower elevation or warmer sites; 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, whereas results for studies with smaller plot sizes are shown in italics. These results are graphed in relation to precipitation range in Supporting Information Fig. S8. AGB, aboveground biomass; ANPP, aboveground net primary productivity; AWP, aboveground woody productivity; AWRT, aboveground woody residence; BA, basal area; BAP, basal area productivity; CanHt, canopy height; GPP, gross primary productivity; Litter, litterfall; na, not available; NPP, net primary productivity; Turn, tree turnover rate. Literature results are coded by the first eight letters of the first author's name, the last two digits of the year, a letter indicating which set of sites within the publication, and the number of sites included within parentheses (Dataset S1). Response variable and study abbreviations as in Fig. 3 (Dataset S1).

in AGB with elevation and temperature largely mirror those in AWP.

4. Synthesis

The biochemical and physiological mechanisms by which temperature interacts with water availability to affect plant productivity are relatively well understood. These are central to responses to short-term temporal variation in temperature within sites, which is reasonably well captured in mechanistic models (Schippers *et al.*, 2015). By contrast, responses to spatial variation in temperature regimes depend in large part on acclimation, allocational shifts and compositional variation, and remain poorly understood. Compositional patterns, such as the decline in lianas and palms with elevation (e.g. Lieberman *et al.*, 1996), are likely to be major contributors to among-site variation in tropical forest C cycling with elevation and temperature; they deserve more attention. Finally, among-site patterns may vary not only with mean temperatures, but also with extremes (e.g. relationships with maximum temperature were more often negative than those with mean temperature) (Dataset S1).

VI. Soil fertility

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

1. Productivity

Values for AWP, BAP, ANPP and litterfall are positively related to soil fertility in tropical forests. Of 22 analyses of among-site variation, 21 showed a positive trend and 16 were significantly positive (Fig. 7a). Fertilization experiments further demonstrate that tropical forest productivity is limited by P and by N, and suggest that potassium (K) and calcium (Ca) also might be limiting – only one tropical forest fertilization experiment manipulated K or Ca (Wright, 2019). However, the range of AWP variation explained by fertility seems to be relatively smaller than that explained by climate; for example, AWP on high-P soils averages *c.* 20% higher than AWP on low-P soils in the Amazon and Sierra Leone (Quesada *et al.*, 2012; Jucker *et al.*, 2016). This may in part reflect shifts in allocation with fertility, with increased allocation to reproduction in more fertile sites (Wright *et al.*, 2011).

The increase in woody productivity with soil fertility is consistent with our mechanistic understanding of the role of

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

2. Residence time

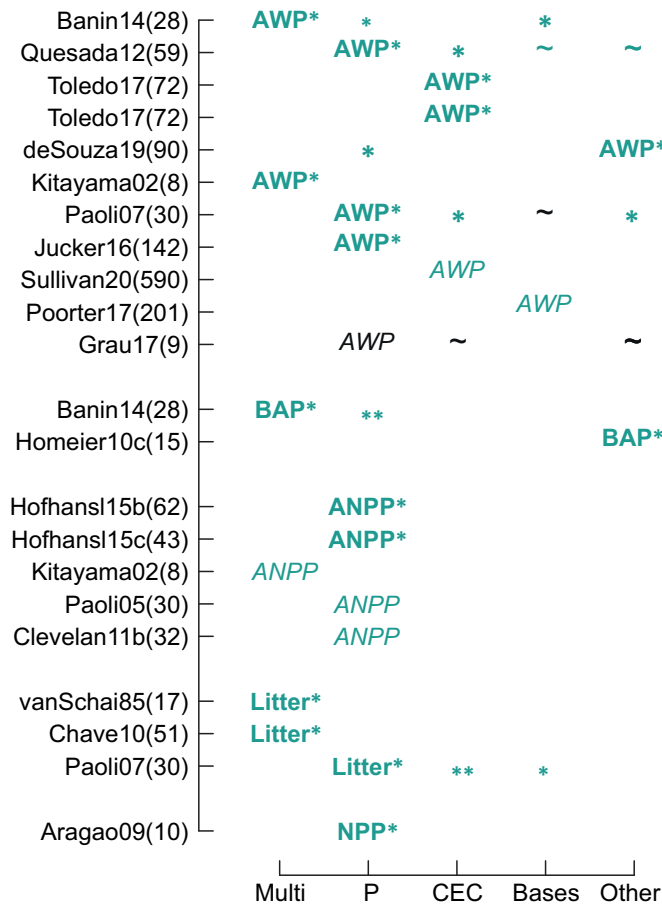
Soil fertility is positively associated with tree mortality rates and thus negatively associated with AWRT across tropical forests (Fig. 7b). This pattern has been found at local (de Toledo *et al.*, 2011; Sawada *et al.*, 2015), regional (Quesada *et al.*, 2012) and global (Galbraith *et al.*, 2013)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

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

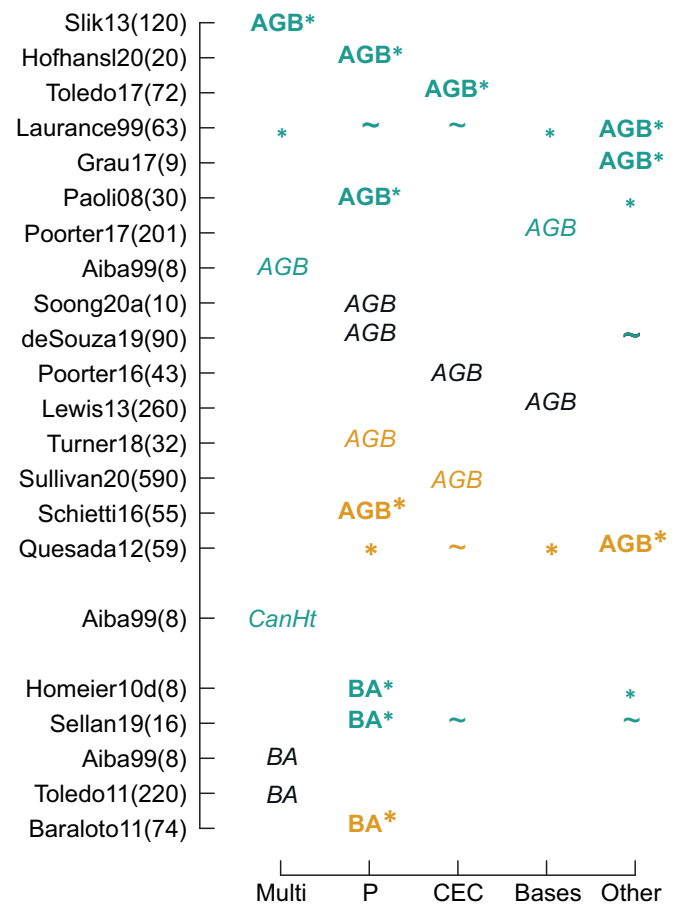
3. AGB

The combination of increasing AWP and decreasing AWRT with fertility would lead to the expectation of a unimodal relationship of

(a) Productivity vs fertility



(c) Biomass vs fertility



(b) Residence time vs fertility

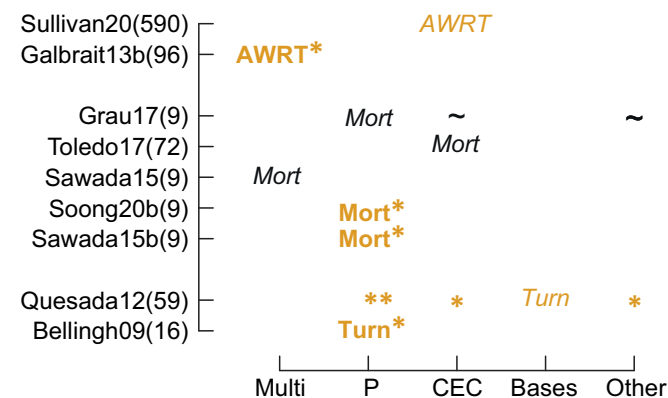


Fig. 7 Literature results on spatial variation in productivity (a), residence time (b) and aboveground biomass (c) with soil fertility, graphed in relation to the soil fertility measure used (Multi, a soil fertility axis or classification that encompassed multiple nutrients; P, phosphorus; CEC, cation 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; brown indicates that they tend to be higher in less fertile sites, and black indicates no relationship or an inconsistent relationship. Asterisks indicate statistically significant effects. Bold highlights studies in which median plot area is ≥ 1 ha, 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). AGB, aboveground biomass; ANPP, aboveground net primary productivity; AWP, aboveground woody productivity; AWRT, aboveground woody residence; BA, basal area; BAP, basal area productivity; CanHt, canopy height; GPP, gross primary productivity; Litter, litterfall; NPP, net primary productivity; Turn, tree turnover rate. Literature results are coded by the first eight letters of the first author's name, the last two digits of the year, a letter indicating which set of sites within the publication, and the number of sites included within parentheses (Supporting Information Dataset S1).

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

4. Synthesis

It has long been clear that soil fertility plays a critical role in tropical forest structure and function (Vitousek & Sanford, 1986), and the broad outlines of its importance are evident in studies to date (Fig. 7). A central challenge is that tropical tree species display a wide diversity of strategies for nutrient acquisition and use, strategies that are critical to compositional shifts and stand-level responses to soil fertility, and their regional variation (Laliberte *et al.*, 2017). Yet our understanding of these strategies – which include not only root morphology and foraging behavior, but also chemical root exudates and interactions with microbial symbionts – remains very limited, reflecting the general paucity of data on roots and belowground interactions.

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

VII. Disturbance

Tropical forests vary strongly in the frequency and intensity of natural disturbances, with important consequences for forest structure, dynamics and composition. Here, we focus specifically on short-term natural disturbances such as storms, landslides and wildfires, excluding disturbance by chronic stressors such as drought (addressed under water availability above) and flooding (addressed by Daskin *et al.*, 2019). Variation in natural disturbance rates across the tropics is substantial and systematic. The frequency

and intensity of large-scale tropical cyclones (known regionally as hurricanes, typhoons or cyclones) is near zero in tropical forests with latitudes $< 10^\circ$, and varies strongly among other areas (Ibanez *et al.*, 2019). Convective thunderstorms and lightning occur across the tropics, and both show strong geographical variation in frequency (Pereira-Filho *et al.*, 2015; Gora *et al.*, 2020). Within sites, storm impacts vary topographically, reflecting variation in wind exposure (highest on ridges; Boose *et al.*, 1994), soil saturation (highest in floodplains and concave topographies; Margrove *et al.*, 2015), and landslide risk (highest on steep slopes; Larsen & Torres-Sanchez, 1998). Wildfire risk increases with dry season length and intensity, as well as with proximity to anthropogenic disturbance (Cochrane, 2011).

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

Disturbance also influences functional composition, as tropical tree species differ strongly in how they are affected by disturbances (Zimmerman *et al.*, 1994; Curran *et al.*, 2008; Slik *et al.*, 2010b; Paz *et al.*, 2018; Staver *et al.*, 2019). In general, species with 'faster' life histories are able to rebound more quickly following disturbances, and thus are more common in areas with recent disturbances (Paz *et al.*, 2018). Associated tradeoffs mean that disturbances generally increase the relative abundance of tree species with fast life histories, which tend to have low wood densities and achieve low biomass (Carreno-Rocabado *et al.*, 2012; Paz *et al.*, 2018). Lianas also proliferate after disturbances, and thus high disturbance frequency increases liana abundance (Schnitzer & Bongers, 2011). Different disturbances also can favor particular traits; for example, species with higher wood density are less likely to suffer stem breaks during a hurricane (Zimmerman *et al.*, 1994). Whereas shifts towards more disturbance-resistant species would tend to mitigate the direct effects of disturbance on mortality and biomass, increases in the abundance of lianas and of tree species with fast life-history strategies would tend to further increase mortality and reduce biomass. Thus, compositional responses to

disturbances also need to be considered to determine the total impacts of disturbance regimes on tropical forest structure and dynamics.

VIII. Biogeographic realm

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

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

Differences in continental averages in part reflect differences in the frequencies of different climate regimes (Parmentier *et al.*, 2007), but substantial differences remain even after controlling for climate (Corlett & Primack, 2011). These can be explained by differences in the composition of plant and animal communities related to historical contingency and evolutionary legacy (Cavender-Bares *et al.*, 2016). Taxonomic composition of tropical forests varies strongly across biogeographic realms, which align to a large degree with continents (Slik *et al.*, 2018). Asian tropical forests are dominated by trees in the Dipterocarpaceae, a family that is almost absent in the Americas and Africa. Dipterocarp trees are distinctive in their combination of ectomycorrhizal associations, tall architecture, seed dispersal by wind and mast fruiting (Ghazoul, 2016). Essentially, Asian tropical forests have a plant functional type that is substantially different from those in other tropical forests, and this leads to differences in stand-level AWP and AGB (Cavender-Bares *et al.*, 2016), as well as selective pressures on co-occurring trees to be tall also (Banin *et al.*, 2012). Differences among biogeographic regions may also in part reflect differences in the animal community (Corlett & Primack, 2011). For example, African elephants reduce

the abundance of small stems and favor the growth of fewer larger trees of higher wood density, resulting in elevated forest C stocks (Berzaghi *et al.*, 2019).

IX. Discussion

Our review of spatial variation in tropical forest C stocks and fluxes documented considerable qualitative consistency across studies, while also illuminating areas of divergent results and limited data. AWP and other measures of productivity examined here decrease strongly with seasonal water limitation and elevation, and increase weakly with soil fertility. This is consistent with our understanding of how water availability, temperature and nutrients affect photosynthesis, allocation and functional composition. Favorable conditions for photosynthesis (i.e. moist, warm and fertile) lead to greater allocation to AWP as well as functional shifts towards species with greater LUE, such that these indirect effects reinforce the direct ones. This variation in AWP in turn contributes to AGB variation with the same factors, but AGB patterns with climate are much noisier than AWP patterns, and AGB variation with fertility does not necessarily align with AWP (Fig. 4). This reflects the importance of AWRT as a dominant driver of empirical variation in AGB (Johnson *et al.*, 2016), the limited variation in AWRT that is explained by climate and the strong decrease in AWRT with soil fertility. In general, our knowledge of AWRT drivers remains limited, although we know disturbance decreases AWRT. Overall, high tropical biodiversity challenges our ability to explain patterns in tropical forest C stocks and fluxes, most obviously in the substantial differences among biogeographic regions.

1. Residence time

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

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

2. Community ecology

In order to understand spatial variation in tropical forest C stocks and fluxes it is critical to understand the drivers of variation in plant functional composition – in the relative abundance of plants varying in life-history strategy and functional traits. As detailed in this review, every major environmental gradient in tropical forests is characterized by shifts in tree functional composition that influence patterns of productivity, mortality and biomass along these gradients (e.g. Gleason *et al.*, 2009; Dalling *et al.*, 2016). Understanding functional composition is a complex problem involving historical biogeographical influences on species pools, species sorting by environmental filters, competition among species and phenotypic variation within species (McGill & Brown, 2007). Empirical research provides considerable information on spatial variation in tropical tree species and functional composition, how species traits relate to performance under different environmental conditions, and on associated tradeoffs (e.g. Poorter & Markesteijn, 2008; Gleason *et al.*, 2009; Brenes-Arguedas *et al.*, 2013; Asner & Martin, 2016; Staver *et al.*, 2019). Better representation of the diversity of tropical plant physiology and life-history strategies in models is critical to capturing turnover in functional composition and associated shifts in forest functioning along environmental gradients (Levine *et al.*, 2016) and among floristic realms (Slik *et al.*, 2018; Taylor *et al.*, 2019), as well as the diversity of locally coexisting functional types that determines functioning and responses to temporal climatic variation (Verheijen *et al.*, 2015; Sakschewski *et al.*, 2016; Powell *et al.*, 2018).

Liana abundance varies greatly among tropical forests, and strongly influences forest C stocks and fluxes. Liana abundance increases with soil fertility and disturbance, and decreases with rainfall and elevation (Schnitzer & Bongers, 2002); it also varies greatly within individual tropical forest sites (e.g. Schnitzer *et al.*, 2012). Multiple hypotheses have been proposed to explain these

patterns, yet the mechanisms underlying variation in liana abundance remain little understood (Schnitzer, 2018; Muller-Landau & Pacala, 2020). Trees with heavy liana infestations had approximately half the growth and twice the mortality rates of liana-free trees in observational studies (Ingwell *et al.*, 2010; Wright *et al.*, 2015; Visser *et al.*, 2018), and experimental liana removal increased tree growth by 25–372% (Estrada-Villegas & Schnitzer, 2018). Thus, lianas decrease AWP, AWPRT and, thereby, AGB. Mean AGB decreases more than two-fold with increasing liana abundance across sites (Duran & Gianoli, 2013), and experimental liana removal increased AGB accumulation in secondary forests by 75% (van der Heijden *et al.*, 2015). Further, lianas differentially affect trees of different species (Muller-Landau & Visser, 2019), and thus likely influence tree community functional composition, which may magnify or mitigate the direct effects of lianas. Tropical lianas are themselves very diverse, with local species richness typically on the order of a third to half of that of trees, and thus liana functional composition also may play a role. Liana species vary in their traits and effects on trees (Ichihashi & Tateno, 2011), and shifts in liana composition among sites may thus contribute to variation in forest C dynamics (Muller-Landau & Visser, 2019). The incorporation of lianas in models involves unique challenges because of the complexities of their interactions with host trees, but may be critical to reproducing major changes in forest structure and functioning associated with variation in liana abundance along successional, climate and disturbance gradients (Brugnera *et al.*, 2019).

Most research on variation in plant functional composition has focused on direct environmental influences on plant performance. However, environmental conditions also may influence plants via changes in antagonistic and mutualistic interactions with microbes, invertebrates, and vertebrates. For example, there is some evidence of higher herbivory in sites with higher soil fertility, where plant tissue nutrient concentrations are higher (Campo & Dirzo, 2003). Differences in vertebrate abundance and community composition contribute to savanna–forest boundaries and possibly differences in forest structure among biogeographic regions (Corlett, 2016). In addition it has long been hypothesized that pest pressures are higher at wetter sites, and may drive compositional shifts and higher plant diversity (Janzen & Schoener, 1968; Givnish, 1999), although evidence to date remains limited (but see Spear *et al.*, 2015). The influences of biotic interactions have been assumed to be secondary to more direct environmental influences, and have been ignored in vegetation models; however, they may be critical to predicting future forest C dynamics under global change, including defaunation (Dirzo *et al.*, 2014).

3. Conclusions and future directions

An overview of decades of empirical research in tropical forests suggests general patterns in productivity, residence time, and estimated AGB variation, but studies to date have important limitations. First, essentially all studies have sizable sampling errors (see Section II, Methods), and these are especially large for studies with smaller plot sizes, smaller numbers of sites and shorter measurement periods (Clark *et al.*, 2017). Second, studies to date

all rest on the application of one or a few allometric equations across multiple sites, and almost none involve site-specific measurements of branch turnover. Systematic differences in biomass allometries and/or branch turnover along environmental gradients could lead patterns in true AGB, AWP and AWRT to diverge substantially from those estimated by current methods. Third, study sites are not well-distributed across tropical forests, owing to local and global bias in plot placement and research effort (Figs S1, S9). There is a critical need and opportunity for future empirical research that overcomes these limitations by taking advantage of new technologies such as laser scanning to more directly measure biomass allometries, branch turnover and their variation among sites (Stovall *et al.*, 2018), and of new and forthcoming satellite remote sensing products that will provide much larger and better distributed datasets on forest C cycling (Schimel *et al.*, 2019).

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

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

Tree mortality, branch turnover, tree functional composition, and biotic interactions of trees with lianas and other organisms are key areas for further research, both for empirical data collection as well as modeling. Advances in remote sensing promise to yield much more and more widely distributed data on tropical forest structure and function (Schimel *et al.*, 2019), but adequate investment in concurrent ground data collection in the tropics is

vital if these missions are to fulfill their promise (Chave *et al.*, 2019). Every type of evidence on its own has key limitations; triangulation across multiple lines of evidence is needed to reach robust conclusions (Munafò & Smith, 2018). We must integrate empirical studies and mechanistic modeling to make progress on the big questions of the mechanisms of extant variation in tropical forests today and the implications for their future trajectories (Hofhansl *et al.*, 2016; Fisher *et al.*, 2018).







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Author contributions

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

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

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.

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

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

Fig. 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.

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

Fig. 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.

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

Fig. 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'.

Fig. 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'.

Fig. 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.

Notes S1 Additional information on methods.

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