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Title: Greater stem growth, woody allocation, and aboveground biomass in Paleotropical forests than in Neotropical forests

Running title: Carbon biogeography of tropical forests

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Abstract

Forest dynamics and tree species composition vary substantially between Paleotropical and Neotropical forests, but these broad biogeographic regions are treated uniformly in many land models. To assess whether these regional differences translate into variation in productivity and carbon (C) storage, we compiled a database of climate, tree stem growth, litterfall, aboveground net primary production (ANPP), and aboveground biomass across tropical rainforest sites spanning 33 countries throughout Central and South America, Asia and Australasia, but excluding Africa due to a paucity of available data. Though the *sum* of litterfall and stem growth (ANPP) did not differ between regions, both stem growth and the *ratio* of stem growth to litterfall were higher in Paleotropical forests compared to Neotropical forests across the full observed range of ANPP. Greater C allocation to woody growth likely explains the much larger aboveground biomass estimates in Paleotropical forests (~29%, or ~80 Mg DW ha^{-1}, greater than in the Neotropics). Climate was similar in Paleo- and Neotropical forests, thus the observed differences in C likely reflect differences in the evolutionary history of species and forest structure and function between regions. Our analysis suggests that Paleotropical forests, which can be dominated by tall-statured Dipterocarpaceae species, may be disproportionate hotspots for aboveground C storage. Land models typically treat these distinct tropical forests with differential structures as a single functional unit, but our findings suggest that this may overlook critical biogeographic variation in C storage potential among regions.

Keywords: Amazon Basin; biomass, carbon allocation, carbon cycle; climate; NPP; southeast Asia; synthesis, tropical rainforest

Introduction

Tropical rainforests exhibit relatively high rates of net primary productivity (NPP) and sequester more atmospheric CO_2 into plant biomass than most other terrestrial biomes (Bonan 2008, Beer et al. 2010, Pan et al. 2011). This productive biome also shows considerable state factor heterogeneity (e.g., climate, topography, and biological diversity) relative to most other biomes, which contributes to highly variable rates of aboveground net primary production (ANPP) and patterns of carbon (C) allocation (Townsend et al. 2008, Aragão et al. 2009, Banin et al. 2014, Hofhansl et al. 2014, Doughty et al. 2015, Taylor et al. 2017). This variation, in turn, could create substantial heterogeneity in aboveground biomass – and C storage – across the tropics.

Ultimately, spatial variations in NPP and C allocation likely reflect the influence of many factors on forest growth and turnover rates (Stephenson and van Mantgem 2005, Malhi et al. 2011, Banin et al. 2014). For example, differences in stem growth rates and the fractional allocation of ANPP to stem growth versus litterfall influence the amount of C stored in aboveground biomass (AGB), and previous work documents that both NPP and C allocation vary with climate (Malhi et al. 2009, Hofhansl et al. 2013, 2014, but see Aragão et al. 2009). Similarly, productivity and allocation to aboveground (stems, leaves) versus belowground (roots) biomass are also strongly influenced by climate and soil fertility (Giardina et al. 2003, Doughty et al. 2014, Reich et al. 2014). For example, relatively warm sites with fertile soils often achieve relatively high rates of ANPP, whereas relatively cool sites with infertile soils achieve much lower rates of plant growth (Quesada et al. 2012, Taylor et al. 2017). Differences in stem turnover rates could also help explain biogeographic variation in aboveground biomass between Paleotropical and Neotropical forests, but there is little evidence for strong differences (Banin et al. 2014 and references therein). Finally, previous work from the Amazon Basin shows that forest residence time correlates with changes in AGB (Brienen et al. 2015), suggesting that forest stand longevity also influences C storage. If so, AGB may, in turn, reflect the influence of factors that regulate forest residence time, such as landscape stability, soil fertility, disturbance regime, forest demographics, and species composition, among others (Galbraith et al. 2012, Becknell and Powers 2014, Finegan et al. 2014, Urrutia-Jalabert et al. 2015).

A growing body of evidence points to substantial biogeographic differences in forest composition and function that may also strongly influence tropical forest C fluxes and stocks. For example, there appear to be systemic differences in forest C storage and turnover attributes between Paleotropical (i.e., Asia and Australia) and Neotropical (Central, South American, and Caribbean) forests. Some evidence suggests that Paleotropical forests have higher stem growth rates than Neotropical forests with comparable soil fertility and climate conditions (Banin et al. 2014). Additional lines of evidence suggest that, in general, when compared to Neotropical forests, lowland forests of southeast Asia are characterized by trees that are on average taller (Feldpausch et al. 2011), invest a greater fraction of photosynthate into wood versus leaf production (Paoli and Curran 2007), less into roots (Malhi et al. 2011), and that may achieve greater aboveground C storage (Slik et al. 2013). In addition, large biogeographic differences in forest C cycling between Paleotropical and Neotropical forests might reflect differences in the evolutionary history of species behavior and forest function. One notable tree family, the Dipterocarpaceae, is widely distributed across much of the Asian lowland tropics and includes members known for their tall stature and rapid woody biomass accrual (Slik et al. 2003, Banin et al. 2014). It has been suggested that the dominance of Dipterocarpaceae has also created a competitive environment that promotes the co-existence of a diversity of larger-statured species in the region (Banin et al. 2012).

Here, we report findings from a data synthesis effort conducted to explore potential biogeographic differences in aboveground C cycling between Neotropical and Paleotropical forests. Such differences, if they exist, could have important implications for our understanding of the C cycle at global scale. Indeed, many land models currently assume a strong, continuous increase of biomass C storage with increases in tropical forest NPP (Negrón-Juárez et al. 2015), despite evidence to the contrary (Keeling and Phillips 2007), highlighting uncertainties in simulating plant productivity, allocation, and mortality across the tropics. At the same time, ecosystem demography models are only beginning to consider potential biogeographic differences in plant traits and plant community-level dynamics that will determine which species – and thus which set of forest traits – may emerge in the transient scenarios of a shifting environment (Reichstein et al. 2014, Butler et al. 2017, Feng et al. 2018, Fisher et al. 2018).

Methods

We synthesized data available in the peer-reviewed literature through 2016 to explore biogeographic patterns of climate, plant productivity, C allocation, and standing biomass in tropical forests globally (Appendix S2). The database includes field-measured climate (temperature and rainfall) and ANPP (the sum of two other measured variables, litterfall and stem growth) collected in primary tropical forests with no reported evidence of recent large-scale natural or human disturbance, and is explained in detail in Taylor et al. (2017). For example, work that specifically focused on successional forest dynamics in sites immediately (1 – 2 y) following large-scale natural (e.g., cyclones; Gleason et al. 2008) or anthropogenic events (e.g., clearcuts; Davidson et al. 2004) were not included in the analysis. We expanded this database to include measurements of aboveground biomass (AGB), typically quantified by applying allometric scaling equations to census data that may include information on DBH as well as metrics of wood density and tree height (Chave et al. 2005, Feldpausch et al. 2011). Consistent with other recent syntheses (Malhi 2012, Hofhansl et al. 2014, Taylor et al. 2017), we did not attempt to standardize allometric models for estimating woody growth, primarily due to the impracticality of coalescing raw plot data.

Altogether, the final database contains plot measurements from > 30 countries (Appendix S1: Figure S1) and includes measurements of total annual net primary productivity ANPP (n = 98, litterfall + woody growth), litterfall (n = 440) and stem growth (n = 254) and ABG (n = 421) (Appendix S1: Figure S1). However, our extensive literature search only revealed a handful of sites in Africa where stand-level C cycling data were available. We deemed it insufficient to include these few sites in our assessment of large-scale, regional differences, and thus excluded African sites from the analyses. Since the database was assembled and analyzed, at least one new analyses of forest dynamics in Africa has been published (Moore et al. 2017), but few of those data are publicly accessible. Thus, for the purposes of this analysis, Neotropical forests include those found in Central and South America (and include the Caribbean and Hawaii), and Paleotropical forests include those in Asia and Australasia.

Estimates of ANPP are most commonly generated using estimates of stem growth and litterfall. Litterfall estimates were generated by common methods (Clark et al. 2001) with data collection spanning a minimum of 12 months. For most studies, litter collections occurred at ~ 2-week intervals, though in certain cases (especially at tropical dry forest sites), greater collection intervals reflected reduced risk of litter decomposition during the dry season. When reported, twigs (< 2 mm diameter), fruits, flowers, and other plant material accumulated in traps were classed as fine litterfall and included in estimates (Clark et al. 2001). Subsequent C losses resulting from herbivory, leaching, volatile organic compound emissions and *in situ* decomposition are typically not accounted for in field measurements (Clark et al. 2001), which may lead to systematic underestimates of total ANPP (Metcalfe et al. 2013). However, since these fluxes are rarely estimated and are thought to account for only a relatively small portion of ANPP (Greenberg et al. 2004, Kuhn et al. 2007), we did not correct for them. Stem growth estimates are typically generated by repeated measurements of tree biomass in field plots. In the majority of cases, data is collected only for stems >10 cm diameter at breast height (DBH), which typically account for >90% of the standing biomass in a field plot (Aiba and Kitayama 1999). Because branch fall is a poorly defined component of woody growth and data are seldom available (Malhi et al. 2011), we did not attempt to correct for it in ANPP calculations.

Research has shown that belowground production (e.g., via coarse and fine roots) may represent 20 – 30% of total forest NPP (Malhi et al. 2011). Similarly, branchfall represents a smaller but still important component of ANPP (Malhi et al. 2011). In this study we did not account for either as published data on these important but rarely measured components of NPP were scarce. Unfortunately, a truly comprehensive description of the C cycle has only been produced for a very small number of sites (e.g., Malhi et al. 2009). Several new efforts (e.g., the RAINFOR network) and published studies (e.g., Malhi et al. 2011) are beginning to address this shortcoming, but given the paucity of data from most sites – especially Paleotropical forests – we excluded belowground NPP and instead focused on aboveground NPP as is commonly done elsewhere (e.g., Banin et al. 2014; Hofhansl et al. 2015).

Statistical Analyses

The data used in this analysis were derived from 62 unique publications. We compared publication dates of studies conducted in the Neotropics against those conducted in the Paleotropics to assess if there were biases associated with publication date. Because these data were skewed, we used a Wilcoxon – Mann-Whitney two sample test (unpaired samples) to assess whether the publication dates shared similar distributions.

We similarly used Wilcoxon – Mann-Whitney test to assess whether the distribution of mean annual temperature (MAT), mean annual precipitation (MAP), ANPP, litterfall, woody biomass and allocation ratios varied between Neotropical and Paleotropical forests. We chose non-parametric tests because most of the variables had skewed distributions that would have required data transformations to meet the assumptions of parametric tests.

Next, we used standardized major axis estimation (SMA) to explore the bivariate relationships between ANPP, litterfall, stem growth and AGB and assessed whether these relationships varied between the Paleotropics and the Neotropics in terms of their slopes and intercepts (e.g., Reiss 1989, Warton et al. 2012). In all cases, we initially tested for differences in slopes between the biogeographic regions. If no difference was found in slope we then tested for differences in intercepts between the bivariate relationships by region. SMA assumes linearity in the relationship between covariates and normally distributed residuals. Consequently, we transformed most of the covariates using a square root transformation and then visually assessed whether our models met the assumptions of the approach using plots of residual vs. fitted values and normal-quantile plots (Warton et al. 2012). We implemented SMA using the SMATR package in R (Warton et al. 2012).

Results

The data contained in the database span more than five decades, from the 1960s through the early 2010s. While we were unable to specifically evaluate when data from Paleotropical and Neotropical forest sites were collected, we did confirm the absence of bias resulting from possible differences in publication dates of the Paleotropical and Neotropical studies ($P = 0.58$; data not shown). With respect to climate, mean annual temperature (MAT) was slightly higher in Neotropical forests than in Paleotropical forests (by an average of 0.6°C; $P = 0.01$), but MAP did not differ among regions (Table 1; $P = 0.57$).

Our analysis showed no overall differences in rates of ANPP between Neotropical (10.8 ± 4.8 Mg DW ha^{-1} y^{-1}; mean ± 1 S. D.) and Paleotropical forests (12.4 ± 5.7 Mg DW ha^{-1} y^{-1}) (Table 1; $P < 0.1$). Of the components of ANPP, litterfall did not differ significantly between biogeographic regions (Table 1; $P = 0.46$), and frequency plots of litterfall values indicate roughly similar distribution of litterfall rates in Neotropical and Paleotropical forests (Fig. 1A). By contrast, Paleotropical forests had higher rates of stem growth than Neotropical forests (6.4 ± 4.2 Mg DW ha^{-1} y^{-1} and 5.1 ± 2.7 Mg DW ha^{-1} y^{-1}, respectively) (Table 1; $P < 0.07$). This was also indicated by the higher mode of stem growth in Paleotropical versus Neotropical forests (Fig. 1B).

Differences in stem growth (Fig. 1B; Table 1) resulted in large differences in the ratio of stem growth to litterfall between Paleotropical and Neotropical forests ($P < 0.001$; Table 1; Fig. 1C). On average, Paleotropical forests allocate a much greater proportion of photosynthate to stem growth than litterfall than Neotropical forests (ratio 1.13 ± 0.74 versus 0.73 ± 0.75 for Neotropical forests; Table 1; $P < 0.001$). Higher allocation of C to stem growth persisted across the entire range of litterfall inputs and ANPP rates in Paleotropical forests compared to Neotropical forests (Fig. 2A). For example, for a given litterfall amount, Paleotropical forests have significantly higher stem growth than Neotropical forests (Fig. 2A; Table 2). Similarly, for any given ANPP rate, Paleotropical forests showed a higher ratio of stem growth:litterfall in Paleotropical forests relatively to Neotropical forests (Fig. 2B; Table 2).

Reflecting their greater allocation to stem growth, on average, Paleotropical forests have substantially higher aboveground biomass (~ 80 Mg DW ha^{-1} more, a difference of ~29%) relative to Neotropical forests (Table 1). Combined, this results in distinct biogeographic patterns in biomass–productivity relationships observed across Paleotropical and Neotropical forests (Fig.

2C). The highest levels of aboveground biomass occur in Paleotropical forests, where AGB values in excess of 400 Mg ha^{-1} were common (Fig. 2C). By contrast, none of the Neotropical forest sites achieved such high biomass values, including sites where ANPP rates were as high as the highest rates observed in Paleotropical forests (Fig. 2C). In addition, our analysis showed that the slope of the relationship between ANPP and aboveground biomass was greater in Paleotropical forests ($P < 0.001$; Table 2). That is, as ANPP increases, a greater amount of woody biomass accumulates in Paleotropical versus Neotropical forests.

Discussion

Although ANPP did not differ significantly between major biogeographic forest regions (Table 1), our analysis revealed some important nuance: Paleotropical forests have higher stem growth and allocate a greater proportion of fixed C to stem growth than to litterfall compared with their Neotropical counterparts (Table 1; Fig. 2B). Over time, these relatively high stem growth:litterfall ratios likely contribute to the higher levels of aboveground biomass – both in absolute terms and per unit ANPP – in Paleo- versus Neotropical forests (Table 1; Fig. 2C). Though not assessed in this analysis, a recent survey of African Paleotropical forests suggested that they also maintain greater AGB than their Neotropical counterparts (Lewis et al. 2013). Thus, our results add to this emerging body of evidence, suggesting that on a per area basis, Paleotropical rainforests may be important hotspots of terrestrial C storage.

In general, stem growth and litterfall – the latter a proxy for canopy production – scaled together in similar ways biogeographically (i.e., had comparable slopes), although for any given litterfall value, stem growth was greater in Paleotropical forests (i.e. had different intercepts, Fig. 2A). Robust relationships between litterfall and stem growth have been observed previously in individual sites (Clark et al. 2001, Malhi et al. 2004); here we show that the relationship between the two components of ANPP is fairly constrained at large scales, but with higher stem growth per unit litterfall in Paleotropical forests (Fig 2A). This greater allocation of Paleotropical ANPP to stem growth (Fig. 2B) mirrors observations of relatively high rates of woody growth documented across dipterocarp-dominated lowland forests in Borneo (Paoli and Curran 2007). More recently, Banin et al. (2014) compared forest woody growth rates in Northern Borneo and north-western Amazonia using a standardized methodological approach (Feldpausch et al. 2012, Quesada et al. 2012) and showed that SE Asian forests had much higher rates of woody growth than Neotropical forests under generally similar climate and soil fertility conditions. The distinct differences we observed provide strong additional evidence in support of a broad biogeographic difference in allocation between Neotropical forests and their wood-rich Paleotropical counterparts.

Our analysis showed only small differences in MAT between Paleotropical and Neotropical forest sites (Table 1). Previous studies have shown correlations between AGB and/or tree height and specific climatic variables, including maximum and minimum temperature, precipitation seasonality and degree of solar radiation (Banin et al. 2012, Slik et al. 2013), but broad biogeographic differences persist even after these factors are corrected for (Banin et al. 2012). Instead, local-, regional- and continental-scale differences in allocation and AGB may more strongly reflect biogeographic differences in centers of species origin, phylogenetic history, disturbance regimes and/or selective pressures over geologic timescales (Feldpausch et al. 2011, Lewis et al. 2013, Banin et al. 2014). In Southeast Asia, members of the Dipterocarpaceae are renowned for their high biomass and tall, emergent architecture and include the world's tallest tropical tree (genus *Shorea* in Borneo, G. Asner, *pers. comm.*). In some of these southeast Asian sites, dipterocarps dominate the composition of forests, and by virtue of their large size, contribute to AGB levels that are among the highest observed in tropical forests (Slik et al. 2008, 2013). The contribution of tall trees has been documented in biomass assessments in the field (Slik et al. 2013), which show that Asian Paleotropical forests are generally taller than their African and New World counterparts (Feldpausch et al. 2011). Banin et al. (2014) attributed differences in woody growth between Borneo and Amazonia to the abundance of large trees and different height-diameter allometry in dipterocarp forests in Borneo. The species-effect of dipterocarps may be similar to the influence of *Sequioa, Fitzroya, and Gilbertiodendron* in supporting C-rich forests in Northern California, Patagonia, and Africa (Busing and Fujimori 2005, Djuikouo et al. 2010, Makana et al. 2011, Urrutia-Jalabert et al. 2015), respectively, with the addition of potential competitive factors that may promote greater average height of co-existing species in non-mono-dominant stands (Banin et al. 2012).

The differential partitioning of NPP to stem growth versus litterfall that we observed (Table 1; Fig. 2B) also has important implications for understanding the biogeographic differences in AGB. Proportionally greater allocation of NPP to stem growth creates more woody biomass, which serves as a much longer-term terrestrial sink for atmospheric CO_2 (ca. 60-100 y in the Amazon, Vieira et al. 2005), whereas litterfall turns over on much shorter timescales in tropical forests (1-2 y; Brown and Lugo 1982). Stand-level AGB integrates the combined effects of woody growth rates, as well as tree recruitment and forest mortality (Johnson et al. 2016). Forests that allocate proportionally more NPP to wood growth and live longer (i.e. have a higher C residence time) should, in theory, accumulate greater amounts of AGB (Johnson et al. 2016), which is indeed true for Paleotropical forests (Table 1; Galbraith et al. 2012, Banin et al. 2014).

Previous research has pointed to residence time and forest mortality rate as being more important drivers of AGB than stem growth (Johnson et al. 2016), at least within Amazonia. Elsewhere, greater biomass in some African forests, even those with low stem density, may arise from longer biomass residence time compared with Amazon forests (Lewis et al. 2013). Our results suggest that in addition to forest residence time, broad biogeographic differences in aboveground C allocation also have important implications for tropical forest biomass. Thus, accurate information of whole-plant function may still be critical to understanding forest C cycling. For example, while dipterocarps and dipterocarp-dominated forests have relatively high above ground wood:leaf allocation they also may allocate far less NPP to root growth than other tropical forests (Niiyama et al. 2010, Malhi et al. 2011), thus contributing to higher aboveground biomass stocks in the Paleotropics (Table 1). Though this root-to-shoot tradeoff would align with expectations of resource-investment along a trait-tradeoff spectrum (Reich 2014), it remains unclear how a large tree could live long and grow tall and simultaneously reduce investment in its root system. Finally, some uncertainty in analysis is introduced by the paucity of accurate height-based allometric equations for estimating biomass, which has been a significant obstacle in the field (Hunter et al. 2013). Although much progress has been made on this issue in the past 5-10 years, especially via the RAINFOR network (e.g., Feldpausch et al. 2011), insufficient geographic data precluded the use of more sophisticated standardized allometric scaling in this study. On balance, strong regional differences in woody C allocation and biomass (Table 2) highlight clear biogeographic heterogeneity in forest C cycling.

It remains unclear why the structure and function of Paleotropical Asian forests differ from tropical forests elsewhere. Some hypothesize that the relatively plentiful water in the region has led to the evolutionary emergence of species that maximize height because long-term hydraulic constraints on tree growth are reduced (Niklas 2007). Evidence for this comes from positive correlations between forest stem densities and AGB in Amazonia and Borneo with wetter conditions. Feldpausch et al. (2011, 2012) and Banin et al. (2014) also found that forest height for a given tree diameter is maximized in wet regions. Regional differences in AGB across the Amazon are linked to spatial variation in forest architecture and allometry associated with distinct floristic communities that inhabit different environmental zones of the basin (Johnson et al. 2016). Similar forest dynamics are also likely important, though connection between species composition and forest function is far less understood in Asian and especially African Paleotropical forests.

Implications for Modeling Tropical Forest C Cycling

Broadly, regional variations in NPP allocation to woody versus canopy growth influence AGB stocks, and this has implications for understanding, mapping, and predicting vegetation C stocks. For example, the biogeographic differences in aboveground C allocation reported here suggest that lowland forests in Asia have a greater potential for C storage on a per area basis than do forests in the New World. Such knowledge could shape conservation goals for maximizing areas of high C storage, as well as our fundamental understanding of how to represent tropical rainforest in land models.

Recent studies suggest that it is critically important to parameterize elements of forest function to accurately model the behavior of the tropical C cycle (Delbart et al. 2010, Castanho et al. 2013). Yet, NPP, allocation of NPP to stem growth, forest residence time, and mortality are often treated as fixed values most land models (Negrón-Juárez et al. 2015), despite the increasing availability of parameterizing field data from pantropical observations (Malhi et al. 2009, Feldpausch et al. 2012, Lewis et al. 2013). Building in biogeographic differences in forest C dynamics is very likely to be important for characterizing the behavior and response of different forest regions to future change (Fisher et al. 2018). For example, while land models typically assume a strong positive correlation between NPP and biomass (Negrón-Juárez et al. 2015), observational support for this relationship is weak, at least across the Amazon basin (Johnson et al. 2016). Though we find evidence for a positive relationship in our study, we provide strong evidence that the *slope* of this relationship is distinct between geographic regions (Fig. 2C). As ANPP increases, AGB increases more rapidly in the Paleotropics than in the Neotropics, although the mechanisms underpinning this difference remain unclear. Finally, under climate change scenarios, any simulated gains in NPP (*e.g.*, from CO_2 fertilization) that are allocated to woody biomass would increase the strength of the land C sink, making allocation a key model consideration. We acknowledge these dynamics remain highly uncertain (Koven et al. 2015), but our results suggest that in the Paleotropics, a greater proportion of this C is likely to be allocated to slow-turnover woody pools with relatively long residence times.

Overall, our analysis adds to emerging evidence for important biogeographic differences in tropical forest C allocation that influence aboveground C storage. These differences seem to be rooted in patterns of floristic composition that ultimately influence patterns of tropical forest C cycling and storage. However, we argue that future research efforts should focus on quantifying the variation, spatial distribution and controls over NPP allocation with explicit consideration of floristic control of forest function (Asner et al. 2013, Doughty et al. 2017). In particular, more information is needed for Africa, to investigate the variation and central tendencies of forest C dynamics in its extensive tropical forests. Next, aboveground C cycling tells only part of the story: Belowground measurements of NPP and biomass are notably lacking, but can represent upwards of 30% of total NPP in some tropical forests (Malhi et al. 2011). More data are needed to examine patterns and variation in belowground C allocation in this productive, heterogeneous biome. Branchfall also represents a relatively minor but still significant portion of ANPP, but is seldom measured or reported (Malhi et al. 2011). More comprehensive synthesis of information from a larger, representative sample of sites across the tropics are critical for more accurate representation of tropical forests in a range of modeling applications.

Acknowledgments

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Table 1. Carbon cycling metrics in Neotropical and Paleotropical forests. ANPP is aboveground net primary production, and SG:LIT is the ratio of stem growth to litterfall. Values are means ± 1 S.D, with sample size (*n*) in parentheses. ANPP, litterfall, stem growth, and aboveground biomass are expressed as megagrams (10^6 g) dry weight (DW) of biomass. Differences in the distributions of the variables between geographic regions were assessed using Wilcoxon rank sum tests (equivalent to a Mann – Whitney test) with *P*-values presented below.

	Neotropical Forests	Paleotropical Forests	*P*-value
MAT (°C)	23.6 ± 4.0 (*n* = 476)	23.0 ± 4.3 (*n* = 203)	0.01
MAP (mm y^{-1})	2617 ± 1062 (*n* = 511)	2828 ± 1742 (*n* = 216)	0.57
Litterfall (Mg DW ha^{-1} y^{-1})	7.4 ± 2.7 (*n* = 248)	7.3 ± 2.8 (*n* = 192)	0.46
Stem Growth (Mg DW ha^{-1} y^{-1})	5.1 ± 2.7 (*n* = 196)	6.4 ± 4.2 (*n* = 58)	0.07
ANPP (Mg DW ha^{-1} y^{-1})	10.8 ± 4.8 (*n* = 98)	12.4 ± 5.7 (*n* = 51)	0.10
Stem growth:Litterfall	0.73 ± 0.75 (*n* = 96)	1.13 ± 0.74 (*n* = 51)	< 0.001
Aboveground Biomass (Mg DW ha^{-1})	277.3 ± 94.9 (*n* = 349)	356.7 ± 200.3 (*n* = 72)	< 0.001

Table 2. Summary of Standardized Major Axis models (SMA) including formulas, limits, goodness of fits, and *P*-values for relationships depicted in Figure 2. AGB = aboveground biomass; ANPP = aboveground net primary production; sqrt = square root; geog = geographic region (i.e., paleotropical or neotropical).

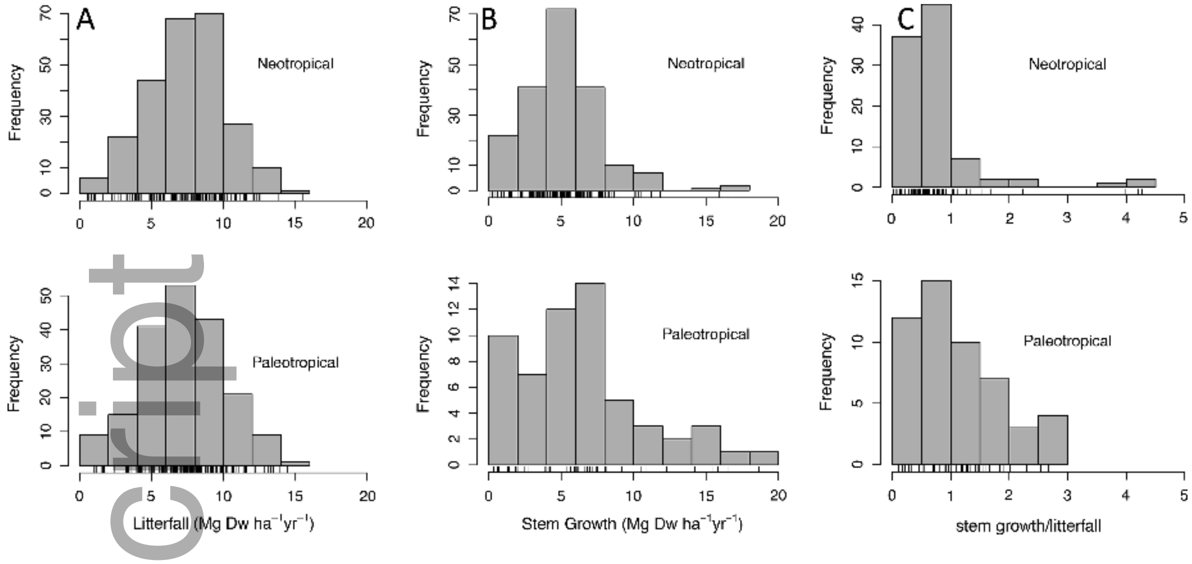
Model	Slope/Elevation	Lower Limit	Upper Limit	R^2	*P*-value
sqrt(stem growth) ~ litterfall + geog	Slope				
	Elevation Elevation				
Neotropical	-0.21	-0.58	0.15	0.16	< 0.001
Paleotropical	0.474	0.07	0.87	1.10	0.02
sqrt(stem growth-to-litterfall ratio) ~ sqrt(ANPP) + geog	Slope				0.55
	Elevation Elevation				0.07
Neotropical	0.46	0.40	0.54	0.02	0.16
Paleotropical	-0.58	-0.86	-0.31	0.26	< 0.001
sqrt(AGB) ~ sqrt(temp$ANPP) * temp$geog	Slope				< 0.001
	Elevation Slope				
Neotropical	5.31	4.57	6.16	0.56	< 0.001
Paleotropical	8.28	6.93	9.89	0.66	< 0.001

Figure Legends

Fig. 1. Frequency distributions and rug plots of A) litterfall; B) stem growth; and C) stem growth to litterfall ratio in neotropical and paleotropical forests in the database. Outliers in the

Neotropics with exceptionally high stem growth and stem growth:litterfall are from three sites in Hawaii.

Fig. 2. Bivariate relationships between aboveground carbon fluxes (litterfall and stem growth), the components of aboveground net primary productivity (ANPP), and aboveground biomass (AGB) differs between Neotropical (red) and Paleotropical (blue) forests. Panels show the: (A) Relationship between litterfall and stem growth; (B) Ratio of stem growth:litterfall and ANPP; and (C) Relationship between AGB and ANPP for each region. Slopes, intercepts, and their confidence intervals for the bivariate relationships by region are presented in Table 2.



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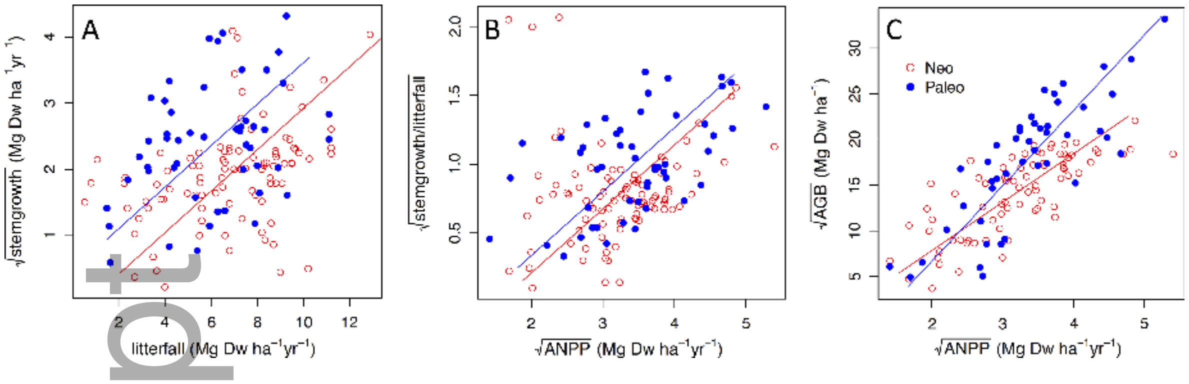

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