


Testing for changes in biomass dynamics in large-scale forest datasets

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Abstract

Tropical forest responses to climate and atmospheric change are critical to the future of the global carbon budget. Recent studies have reported increases in estimated above-ground biomass (EAGB) stocks, productivity, and mortality in old-growth tropical forests. These increases could reflect a shift in forest functioning due to global change and/or long-lasting recovery from past disturbance. We introduce a novel approach to disentangle the relative contributions of these mechanisms by decomposing changes in whole-plot biomass fluxes into contributions from changes in the distribution of gap-successional stages and changes in fluxes for a given stage. Using 30 years of forest dynamic data at Barro Colorado Island, Panama, we investigated temporal variation in EAGB fluxes as a function of initial EAGB ($EAGB_i$) in 10×10 m quadrats. Productivity and mortality fluxes both increased strongly with initial quadrat EAGB. The distribution of EAGB (and thus $EAGB_i$) across quadrats hardly varied over 30 years (and seven censuses). EAGB fluxes as a function of $EAGB_i$ varied largely and significantly among census intervals, with notably higher productivity in 1985–1990 associated with recovery from the 1982–1983 El Niño event. Variation in whole-plot fluxes among census intervals was explained overwhelmingly by variation in fluxes as a function of $EAGB_i$, with essentially no contribution from changes in $EAGB_i$ distributions. The high observed temporal variation in productivity and mortality suggests that this forest is very sensitive to climate variability. There was no consistent long-term trend in productivity, mortality, or biomass in this forest over 30 years, although the temporal variability in productivity and mortality was so strong that it could well mask a substantial trend. Accurate prediction of future tropical forest carbon budgets will require accounting for disturbance-recovery dynamics and understanding temporal variability in productivity and mortality.

KEYWORDS

biomass dynamic, carbon fluxes, long-term change, tropical forests

1 | INTRODUCTION

Understanding tropical forest responses to atmospheric and climate change is critical to modeling the future global carbon cycle. Repeated censuses of forest inventory plots have found increasing

stocks of tree carbon in apparently undisturbed tropical forests in Amazonia (Baker et al., 2004; Phillips et al., 1998), Africa (Lewis et al., 2013), and Borneo (Qie et al., 2017). Globally, analysis of long-term forest inventories suggests that old-growth tropical forests are currently carbon sinks, sequestering an average

of 0.34 Mg C ha⁻¹ year⁻¹ (confidence intervals [CIs] = 0.17–0.47; Muller-Landau, Detto, Chisholm, Hubbell, & Condit, 2014), albeit with a reduction in sink strength over time (Brienen et al., 2015; Qie et al., 2017). The causes of this increase and its consistency in space and time remain uncertain (Lewis, Lloyd, Sitch, Mitchard, & Laurance, 2009; Wright, 2010, 2013). Current knowledge of changes in old-growth tropical forest carbon stocks is hampered by limited spatial and temporal coverage of monitoring plots, sensitivity to measurement errors and data correction procedures, and the confounding influences of disturbance-recovery dynamics (Clark, Clark, et al., 2017; Muller-Landau et al., 2014).

There are multiple pathways through which anthropogenic global change could increase or decrease carbon stocks and fluxes in old-growth tropical forests. Increasing atmospheric carbon dioxide could enhance tropical tree growth and forest productivity through increased photosynthesis and water use efficiency (Lloyd & Farquhar, 2008), and thereby increase forest carbon stocks (Figure 1a–c). Alternatively, rising temperatures and increasing drought frequency and/or intensity could increase tree mortality and thereby decrease forest carbon stocks (McDowell et al., 2018). The “Bigger and Faster” hypothesis proposes that growth, recruitment, and mortality are all increasing (Clark, Clark, et al., 2017); in this case, the net effect on biomass depends on the relative magnitude of the increases in productivity and mortality (Figure 1d–f). Some but not all studies have found evidence of increasing productivity (Brienen et al., 2015; Feeley, Wright, Supardi, Kassim, & Davies, 2007; Körner, 2015) and increasing mortality (Brando et al., 2014; Brienen et al., 2015; Liu et al., 2017; McDowell et al., 2018; Phillips et al., 2010).

It is also possible that the observed increase in tropical forest biomass is due not to global change influences but to long-lasting recovery from past disturbances in some (but not all) tropical forests (Figure 1g–i; Wright, 2010). There is growing evidence that past human-induced or climatic disturbances continue to profoundly shape current forest composition (Brncic, Willis, Harris, & Washington, 2006; Levis et al., 2017; Magnabosco Marra et al., 2018), functioning (Doughty et al., 2015; McMichael, Matthews-Bird, Farfan-Rios, & Feeley, 2017; Oslisly et al., 2013), and extent (Mayle, Burbridge, & Killeen, 2000) in tropical regions. Forest succession after disturbance would generate a pattern of increasing total biomass mortality and biomass productivity over time, similar to that expected under the “Bigger and Faster” hypothesis (Clark, Clark, et al., 2017), and constitutes a null hypothesis or non-global change hypothesis. Forest recovery post-disturbance poses a particular challenge, as it may act at various spatial and temporal scales, and in only a subset of tropical forests.

We propose to separate out the contributions of disturbance-recovery dynamics to temporal variation in forest carbon stocks by decomposing changes in whole-plot biomass fluxes into contributions from changes in the distribution of gap-successional stages and changes in fluxes for a given stage (Figure 2). An old-growth tropical forest is a shifting mosaic of patches at different stages of recovery (Watt, 1947; Whitmore, 1989), of which most are increasing in biomass at any given time (Körner, 2003a). Dividing a plot into small quadrats provides a simple operational way to characterize this mosaic of

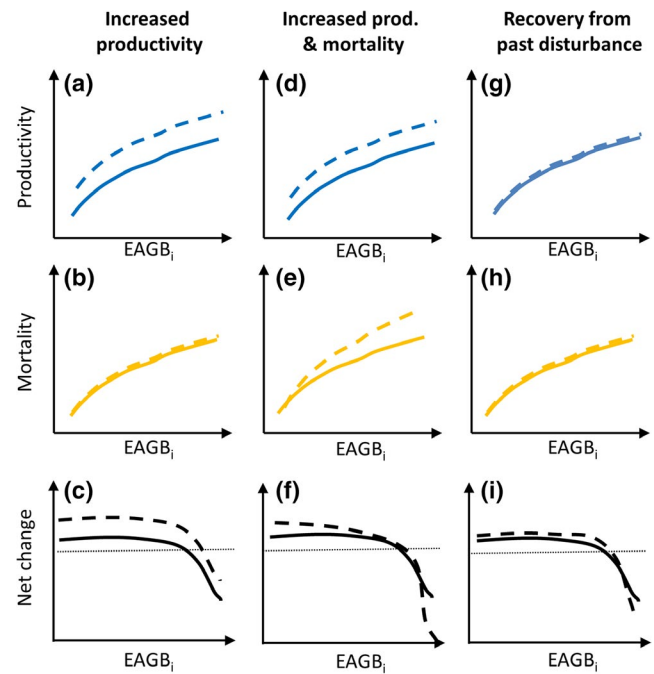


FIGURE 1 Expected patterns of quadrat biomass fluxes in relation to initial estimated above-ground biomass ($EAGB_i$) for three possible scenarios (columns) consistent with increasing biomass stocks in tropical forests. In every panel, the solid line shows the pattern expected for an earlier census interval, and the dashed line for a later census interval. Increasing productivity due to “fertilization” (first column), means higher productivity for a given $EAGB_i$ in the second census interval (a, dashed line) than in the first one (a, solid line), no systematic difference in mortality after controlling for $EAGB_i$ (b), and thus higher net change in $EAGB_i$ per $EAGB_i$ in the second census interval (c). Increasing productivity and mortality, as expected under “speeding up” (second column), means higher productivity and higher mortality in the second census interval (d, e) and diverse possible patterns for net change (f). Finally, recovery from disturbance (final column) is expected to show no systematic change in fluxes when controlling for $EAGB_i$ (g–i). Note that local quadrat productivity increases with initial quadrat $EAGB_i$ in all scenarios and census intervals (first row, blue), as does the local mortality flux (second row, yellow). Quadrat-level biomass net change (third row, black) is the difference between productivity and mortality fluxes, and is positive for low $EAGB_i$, and becomes negative for high $EAGB_i$.

stages, and quadrat initial $EAGB_i$ ($EAGB_i$) provides a useful proxy for age/time since disturbance (Bormann & Likens, 1979; Denslow, Ellison, & Sanford, 1998). Plot-level $EAGB_i$ fluxes (Figure 2c) then reflect the integration of functions for fluxes as a function of $EAGB_i$ (Figure 2a) with the distribution of $EAGB_i$ (Figure 2b). Both quadrat productivity and mortality fluxes (Mg/ha) are expected to increase with $EAGB_i$ (Figure 2a), and consistent global change influences should be evident in directional changes in these functions over time—that is, in increases or decreases in fluxes when controlling for $EAGB_i$. Climate variation could also contribute to temporal variation in productivity and mortality drivers, and thus in fluxes for a given $EAGB_i$ (Dong et al., 2012). In contrast, the distribution of quadrat $EAGB_i$ depends largely on the disturbance history at a site (Espírito-Santo et al., 2014; Fisher, Hurtt,

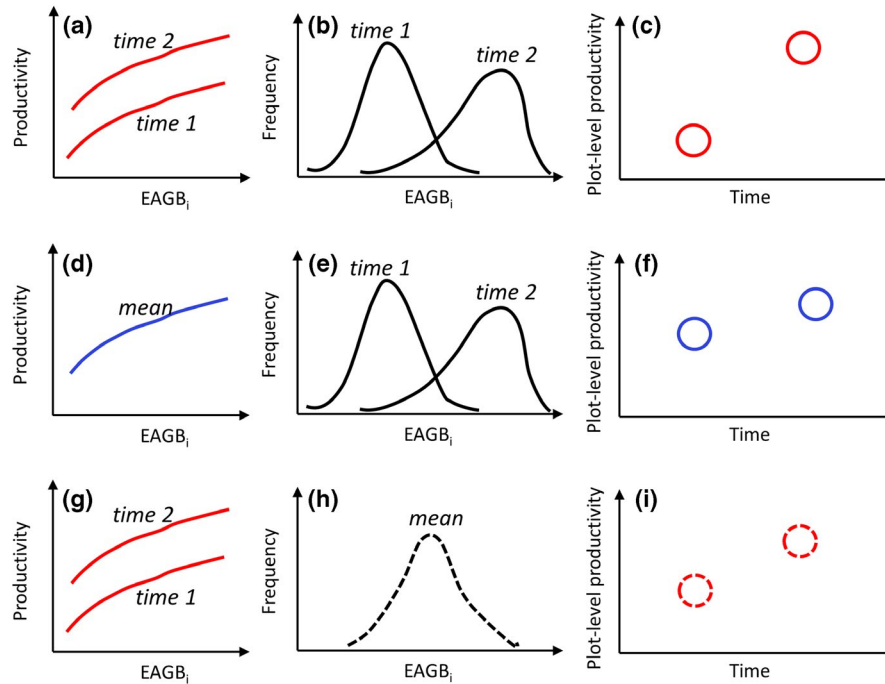


FIGURE 2 Whole plot estimated above-ground biomass (EAGB) fluxes (right column) in a given time period depends on the combination of how small-scale fluxes vary with initial EAGB ($EAGB_i$) (left column) and how $EAGB_i$ varies spatially across the plot and over time (middle column). Here, we illustrate this for productivity; the same integration holds for whole-plot mortality. To distinguish the contribution of flux– $EAGB_i$ relationships from the contribution of $EAGB_i$ distributions to plot-level biomass dynamics, we estimated what whole-plot fluxes would be in each census interval if either the flux– $EAGB_i$ relationship or the $EAGB_i$ distribution were constant across census intervals. To calculate a single constant flux– $EAGB_i$ relationship (d) and a single constant $EAGB_i$ distribution (h), we averaged across all census intervals weighted equally. We then integrated the empirical flux– $EAGB_i$ relationship over the $EAGB_i$ distribution for each census interval under three scenarios: (i) interval-specific flux– $EAGB_i$ relationships and interval-specific $EAGB_i$ distributions (a–c); (ii) the average flux– $EAGB_i$ relationship and interval-specific $EAGB_i$ distributions (d–f); (iii) interval-specific flux– $EAGB_i$ relationships and the average $EAGB_i$ distribution (g–i)

Thomas, & Chambers, 2008), and can fluctuate from a dominance of early successional (i.e., low $EAGB_i$) stages soon after disturbance (Figure 2b, time 1) to higher frequency of late successional quadrats longer after disturbance (Figure 2b, time 2).

Using a large-scale, long-term forest plot dataset for Barro Colorado Island (BCI), Panama, we seek to disentangle the influences of disturbance recovery from potential global change by quantifying how local biomass dynamics vary with initial biomass, and evaluating whether these relationships change over time. Specifically, we tested for temporal variation in quadrat productivity, loss, and net change in biomass when controlling for initial biomass. To assess the degree to which similar biomass patches were consistently associated with similar forest structure across census intervals, we also examined how quadrat initial biomass was related to tree density (per area) and mean tree size at each census and compared these relationships over time.

2 | METHODS

2.1 | Study site

Barro Colorado Island is located in central Panama (9°08' N, 79°510' W). Temperature averages 27°C and annual rainfall averages 2,657 mm (for 1926–2017; Paton, 2018), with a dry season between January and April. The vegetation is moist tropical

forest. The 50 ha forest dynamics plot was established in 1982 (Condit, 1998; Hubbell et al., 1999), and recensused in 1985 and every 5 years subsequently (Figure S1). All free-standing woody stems with a diameter at breast height (DBH) ≥ 1 cm were mapped, tagged, and identified to species, and were measured in diameter at every census in which they remained alive. Diameter measurements were taken at 1.3 m height or above any buttress or major stem deformity. We omitted the initial census of 1982–1983 from analyses of biomass and biomass dynamics due to major differences in the field measurement methods for large trees (Condit, 1998), leaving seven censuses and six 5 year intervals between 1985 and 2015. We omitted 1.2 ha of swamp and 1.9 ha of young forest from the analysis due to differences in species composition, structure, and dynamics (Condit, Hubbell, & Foster, 1996; Harms, Condit, Hubbell, & Foster, 2001), leaving 46.9 ha for analysis. (We note, however, that our results are robust to the inclusion of the young forest, as we would expect; see Supporting information C1). Supplemental materials provide additional details on the census methods (Supporting information A).

2.2 | Individual tree biomass calculation

For all stems of dicot (non-palm) species, we estimated above-ground biomass (EAGB) from individual DBH and species-specific

wood density (WD) using a generic tropical forest biomass equation (Chave et al., 2014). For stems measured at heights other than 1.3 m, we first calculated taper-corrected equivalent diameters at 1.3 m height using a generic taper correction equation for BCI:

$$DBH = D \times \exp(0.0247 \times (HOM - 1.3)),$$

where D is diameter measured at height of measurement (HOM; in m; equation 2, Cushman, Muller-Landau, Condit, & Hubbell, 2014). We applied this taper correction to avoid time-dependent biases in plot-level biomass stocks and fluxes associated with changes over time in the proportion of trees measured above 1.3 m and average measurement heights (Cushman et al., 2014). We also estimated missing diameter measurements (1,192 of the 2,607,014 records) by simple linear interpolation between consecutive measurements. We then EAGB (in Mg dry biomass) of each stem in each census from its DBH, using the updated version of equation 7 of Chave et al. (2014), incorporating species-level WD (in g/cm³) collected near the study site (Wright et al., 2010 and unpublished) and a climatic index that represents environmental influences on tree height allometries ($E = 0.05645985$ for BCI):

$$EAGB = \exp(-2.024 - 0.896 \times E + 0.920 \times \log(WD) + 2.795 \times \log(DBH) - 0.0461 \times \log(DBH)^2)$$

(see Supporting information S2 for details of wood density assignment).

For palms, we estimated biomass using a palm-specific allometric equation based on DBH. For palm species that do not grow in DBH (all local palm species except *Socratea exorrhiza*), we first assigned species-specific median DBH to each palm stem in each census (Table S1). We EAGB (in Mg dry biomass) of each palm stem as

$$AGB = 0.0417565 \times DBH^{2.7483},$$

based on the family-wise specific allometric equation of Goodman et al. (2013), modified to include the log-transformation correction factor (Baskerville, 1972). We recognize that this procedure results in systematic errors in biomass fluxes for palms that do not grow in diameter, because it fails to consider their height growth, and that better estimates would be possible if height data were available. Overall, palms other than *Socratea* account for 0.9% of the woody biomass and 1.8% of the estimated woody productivity on BCI.

For multi-stemmed trees, individual tree biomass was calculated as the sum of biomass of all live stems. Large (DBH > 50 cm) individuals of strangler fig species (*Ficus costaricana*, *Ficus obtusifolia*, *Ficus popenoei*, and *Ficus trigonata*), for which diameter measurements are unreliable measures of size, were excluded from the analysis by excluding associated quadrats (Table S2).

2.3 | Quadrat-level biomass stocks and fluxes

Biomass stocks and fluxes were analyzed at the scale of 10 m quadrats and for the plot as a whole. Analysis at the quadrat level aimed to quantify how local biomass fluxes vary with local initial biomass

for each census interval, and to compare these relationships across census intervals. Initial biomass was calculated as the sum of biomass of all trees alive at the initial census. We calculated biomass fluxes per time in productivity, mortality, and net change using simple arithmetic estimators. That is, we calculated fluxes for each quadrat by summing over relevant trees (i) and dividing by the time interval measured separately for each tree:

$$EAGB \text{ change} = \sum \frac{(EAGB_{\text{final } i} - EAGB_{\text{initial } i})}{\text{time}_i}$$

Productivity was calculated as the sum of the EAGB changes of surviving trees and the EAGB of recruits (including resprouts). Because the census dataset includes all stems >1 cm in diameter, biomass increment accounts for the vast majority of the woody productivity (97.5%; Figure S2). Biomass loss was calculated as the sum of EAGB_{*i*} of all trees that died by the next census, as well as of large individual stems that died on multi-stemmed individuals (see Supporting information A for details on the treatment of multi-stemmed trees). For recruits and dead stems, the time interval used was the mean time between measurements for that quadrat and census interval. These arithmetic estimators systematically underestimate fluxes because they miss contributions from trees that recruited and died during the census interval, with larger biases for longer census intervals (Kohyama, Kohyama, & Sheil, 2019). However, all our census intervals were very similar in length (Figure S1), and thus, these biases do not confound our analysis. Estimated biomass stocks and fluxes are expressed on a quadrat basis (100 m²), and can be converted to units of Mg/ha by multiplying by 100.

We quantified the relationship of quadrat-level biomass fluxes to initial biomass for each census interval using local regression and power function fits. We first illustrate the relationships for productivity, mortality, and net change using local polynomial regression, specifically the *locfit()* function in R (Loader, 1999) with smoothing parameter (alpha) set to 0.7. To formally test for variation in EAGB productivity and loss among census intervals, each of these fluxes was modeled as power functions of EAGB_{*i*}, with a power variance function structure (using package lme4; Bates, Mächler, Bolker, & Walker, 2015). We tested for differences among census intervals in power function “slopes” (exponents) and normalized intercepts, with these intercepts calculated as the predictions for the median EAGB value of 125.0 Mg/ha. CIs were computed by bootstrapping over quadrats (1,000 times). We evaluated the sensitivity of the results to different local regression models, and the consistency between the power function and local regression results.

For each census interval, our analyses of quadrat-level fluxes excluded quadrats affected by any one or more of three problems. First, analyses excluded quadrats if any stem had a change in HOM >10 cm during that census interval. Second, analyses excluded quadrats that ever had a strangler fig larger than 50 cm DBH. Finally, analyses excluded quadrats where an individual stem had an unreasonably large change in DBH in that census interval, such that its absolute biomass change was >0.98 Mg/ha (this threshold was

chosen because it is 20% of the mean productivity per hectare computed over all quadrats and census intervals that met the first two criteria). We excluded between 389 and 1,288 of the 4,669 possible quadrats (i.e., not in swamps or in young forest), depending on the census interval, mostly because of the first rule removing quadrats with a change in measurement height (Table S2). We did not remove or correct unlikely but less influential diameter changes, because in a dataset of this size, these random errors will tend to cancel out, whereas attempts to filter or correct such changes have strong potential to introduce systematic biases (because it is easier to detect some types of errors than others, Muller-Landau et al., 2014). The results were robust to varying filtering methods (Figure S7).

We evaluated consistency in or differences among censuses in the probability distribution of quadrat-level EAGB using empirical cumulative density functions. We specifically tested for differences among censuses in selected percentiles (5th, 10th, 25th, 50th, 75th, 90th, and 95th), by evaluating whether CIs overlapped. We estimated CIs on the percentiles by bootstrapping over quadrats.

We evaluated the sensitivity of our results to the spatial grain of quadrats, applying the same methods for smaller (8.33 m) and larger (12.5, 15.15 m) quadrats (Figures S8–S10).

2.4 | Disentangling sources of temporal variation in whole-plot fluxes

To distinguish the contribution of flux–EAGB_i relationships from the contribution of EAGB_i distributions to plot-level biomass dynamics, we estimated what whole-plot fluxes would be in each census interval if either the flux–EAGB_i relationship or the EAGB_i distribution was constant across census intervals. To calculate a single constant flux–EAGB_i relationship and a single constant EAGB_i distribution, we averaged across all census intervals weighted equally. We then integrated the empirical flux–EAGB_i relationship over the EAGB_i distribution (Figure 2) for each census interval under three scenarios: (a) interval-specific flux–EAGB_i relationships and the average EAGB_i distribution; (b) the average flux–EAGB_i relationship and interval-specific EAGB_i distributions; and (c) interval-specific flux–EAGB_i relationships and interval-specific EAGB_i distributions. For each flux–EAGB_i relationship, fluxes for the central 90% of the EAGB_i distribution (from the 5th to 95th percentile) were estimated from EAGB_i using fits of the *locfit* function to the full distribution, as above ($\alpha = 0.7$). In the tails of the distribution, fluxes were estimated as equal to the means for the corresponding interval (i.e., the 0–5th percentile interval or the 95th–100th percentile interval), to avoid undue influence of a few points.

2.5 | Forest structure

For each census interval, forest structure was quantified by analyzing the distributions over 10 × 10 m quadrats of the numbers of trees ≥ 1 , 10, and 60 cm, and of quadratic mean diameter ($D_g = \sqrt{\sum DBH^2/n}$, in cm). We quantified how these structure measures varied with quadrat EAGB in each census interval by fitting local regressions (R

function *locfit* with $\alpha = 0.7$), and calculating values expected for selected quadrat EAGB (corresponding to the 10th, 25th, 50th, 75th, and 90th percentiles computed for all censuses combined). We tested whether there were changes over time in the values expected for selected quadrat EAGB or in the plot-level means, by comparing CIs obtained by bootstrapping over quadrats.

3 | RESULTS

3.1 | Quadrat-level biomass fluxes

Mean quadrat EAGB productivity and EAGB mortality loss both increased with initial quadrat EAGB in each census interval, with uncertainty rising in parallel (Figures 3 and 4a,b; Figure S2). Both fluxes were well-fit by power functions of EAGB_i (Figure 4a,b; Figures S5 and S6). Mean EAGB net change was positive for low EAGB_i and became negative in quadrats with EAGB_i > ~3 Mg/100 m² (equivalently 300 Mg/ha; Figure 4c).

There was substantial variation among census intervals in EAGB fluxes as a function of EAGB_i. This is visually evident from examination of the differences in EAGB-specific fluxes from the mean flux over census intervals (Figure 4d–f), and is quantified by differences in parameter values of the power function fits (Figure 5; power functions were good fits to the data, as is evident from their concordance with local regressions in Figures S5 and S6). Productivity fluxes in the 1985–1990 census interval averaged 10%–30% higher than the mean over census intervals for all but the highest values of EAGB_i (Figure 4d, blue line). The next highest productivity fluxes were in the most recent census interval, and the lowest productivity fluxes were in 2000–2005 (Table S6). EAGB loss also varied among census intervals, with above-average EAGB loss for lower EAGB_i in some census intervals (2005–2010 and 2010–2015) and for higher EAGB_i in other intervals (1995–2000). The power function fits reflected these patterns, with significant variation among census intervals in the normalized intercepts, the estimated fluxes at the midpoint of the EAGB_i distribution (here 125 Mg/ha; Figure 5a,b; Table S6). For productivity, the first census interval had by far the largest intercept, with subsequent declines to 2000–2005, and then increases since 2005 (Figure 5a). For mortality, the intercept tended to increase after the 1990–1995 census interval. The slopes (exponents) of the power functions showed little variation among census intervals (mostly overlapping CIs, Figure 5c,d). CIs for EAGB loss and net flux were wide (Figures S3 and S4), limiting the power to test for significant differences among census intervals (Figure 4d–f; Figure S3 and S4). Results were qualitatively consistent for other quadrat sizes (Figures S8–S10).

3.2 | Whole plot biomass stocks and fluxes

The probability distribution of EAGB density over 10 × 10 m quadrats varied only slightly among censuses, and showed no clear directional change (Figure 6a). The 5th–50th percentiles of quadrat EAGB increased slightly from 1985 to 2000, and then decreased again to values similar to initial ones (Figure 6c). In contrast, the 90th percentile increased slightly over the study period (Figure 6c).

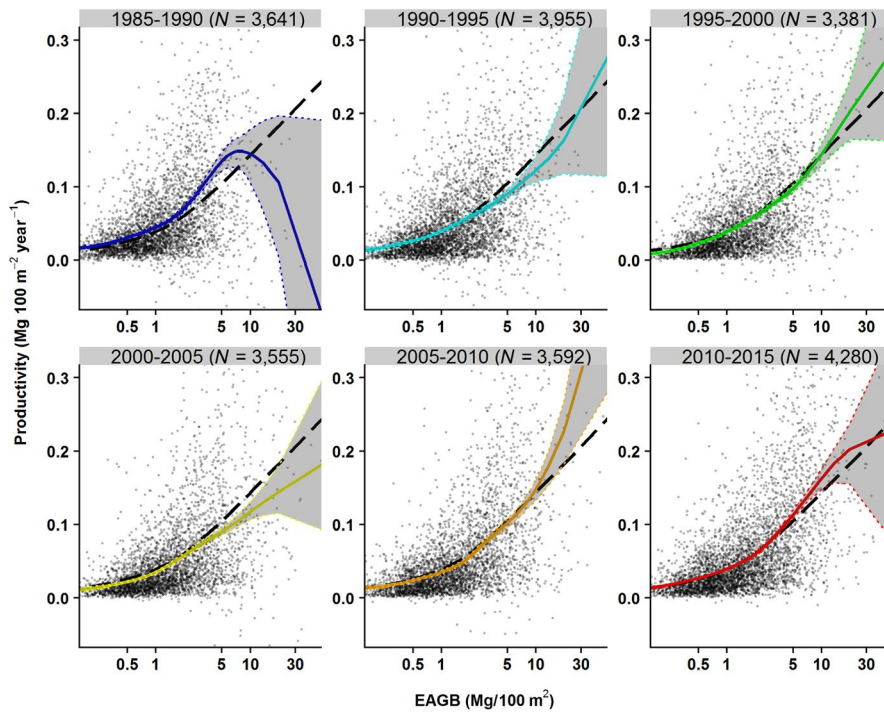


FIGURE 3 Quadrat-level mean annual estimated above-ground biomass (EAGB) productivity ($\text{Mg } 100 \text{ m}^{-2} \text{ year}^{-1}$) as a function of initial quadrat biomass (EAGB in $\text{Mg}/100 \text{ m}^2$) for each 5 year census interval, for individual $10 \times 10 \text{ m}$ quadrats (points), together with local polynomial regression lines for individual census intervals (colored solid lines) and for all census intervals combined (black dashed lines). Confidence envelopes were computed from bootstrapping over quadrats. For each census interval, analyses excluded quadrats with problematic EAGB change measurements (see Section 2 for details); N is the number of quadrats included for each census interval. The range of data shown here is truncated, but all points were included in the analyses. Note that EAGB stocks and fluxes can be converted to units of Mg/ha by multiplying by 100

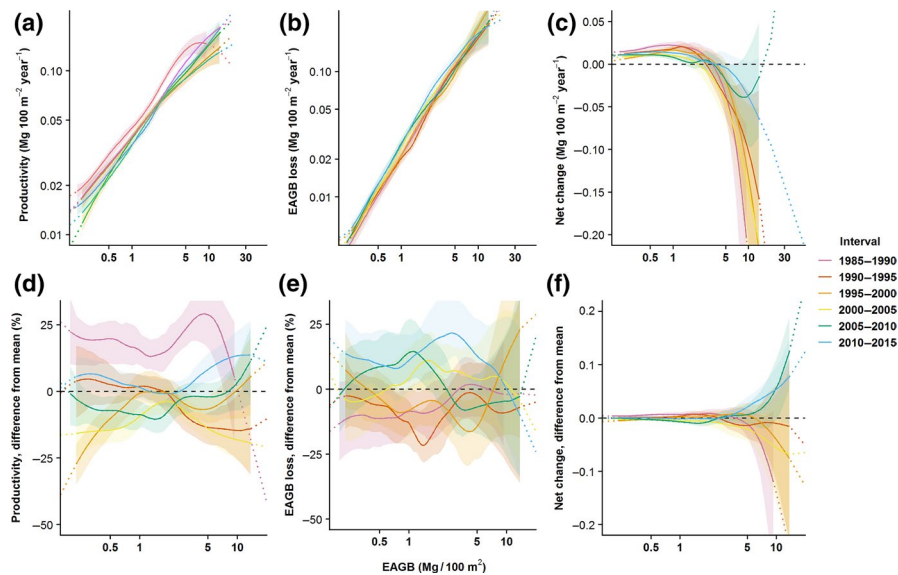


FIGURE 4 Variation among census intervals in quadrat estimated above-ground biomass (EAGB) productivity (a), loss (b), and net change (c) as a function of above-ground biomass (EAGB) at the initial census for $10 \times 10 \text{ m}$ quadrats, together with the corresponding differences from the mean (per initial EAGB) across all census intervals (d-f). Patterns were quantified using local polynomial regression; regression lines are displayed as solid lines for initial EAGB values spanning the 2nd–98th percentiles of the respective census interval, and as dotted lines outside this range. Confidence envelopes were computed by bootstrapping over quadrats, and are shown for the 2nd–98th percentiles of initial EAGB using shading. Analyses excluded quadrats with problematic EAGB change measurements (see methods for details). Note that productivity (a) and loss (b) are shown on log scales, and their differences from the mean are expressed in percentages (d,e) whereas the net change (c) and its difference from the mean (f) are shown on linear scales. Note that EAGB stocks and fluxes can be converted to units of Mg/ha by multiplying by 100

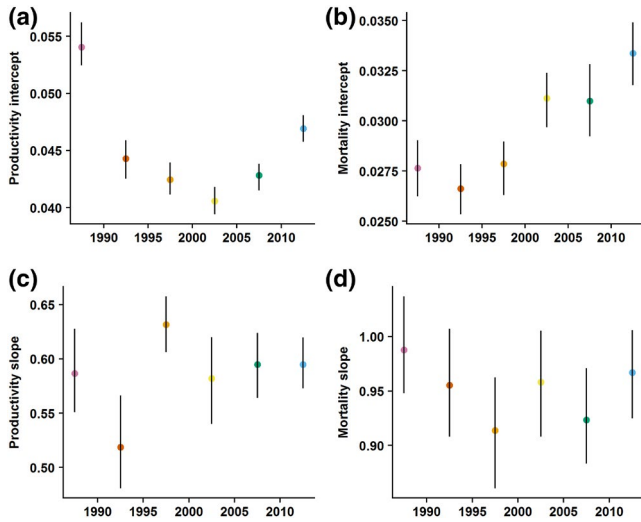


FIGURE 5 Variation among census intervals in the intercepts (a, b) and slopes (c, d) of power function relationships of quadrat-level productivity (a, c) and losses to mortality (b, d) to initial above-ground biomass. Intercepts are normalized, and represent the values at the overall midpoint estimated above-ground biomass (EAGB) value ($1.25 \text{ Mg}/100 \text{ m}^2$, i.e., an EAGB density of $125 \text{ Mg}/\text{ha}$). Confidence intervals were computed from bootstrapping over quadrats (see Table S2 for parameter values). Analyses excluded quadrats with problematic EAGB change measurements (see Section 2 for details)

Temporal variation in whole-plot EAGB fluxes as estimated by integrating temporal variation in flux–EAGB_i relationships and EAGB_i distributions was due almost entirely to temporal variation in flux–EAGB_i relationships for a given EAGB_i, with almost no contribution of temporal variation in the EAGB_i distribution (Figure 7; Table S4 scenario b). Temporal patterns in whole-plot fluxes thus roughly mirrored those in fluxes as a function of EAGB_i. Productivity flux was highest in 1985–1990, then dropped steeply, and has increased over the last three census intervals. Mortality loss flux dropped between the first and second census interval, and tended to increase since then, albeit CIs are wide. These patterns in estimated whole-plot fluxes mirrored calculated fluxes from summing over quadrats, although the exact pattern in productivity is highly sensitive to data cleaning and correction procedures (Figures S7–S17).

3.3 | Changes in forest structure

The mean density of stems $>1 \text{ cm dbh}$ increased modestly after the 1982–1983 drought, then thinned rapidly from 1990 to 2005, and was stable from 2005 to 2015 (Figure 8a, black points and lines). The same pattern was evident when controlling for focal quadrat biomass density (Figure 8a, colored lines). The density of stems $\geq 10 \text{ cm dbh}$ in the plot as a whole increased slowly to 1995 and then decreased to 2010, with parallel patterns in all but the lowest biomass quadrats (Figure 8b). The density of large stems ($\geq 60 \text{ cm dbh}$) remained essentially constant over time (Figure 8c; Table S5). Quadratic mean

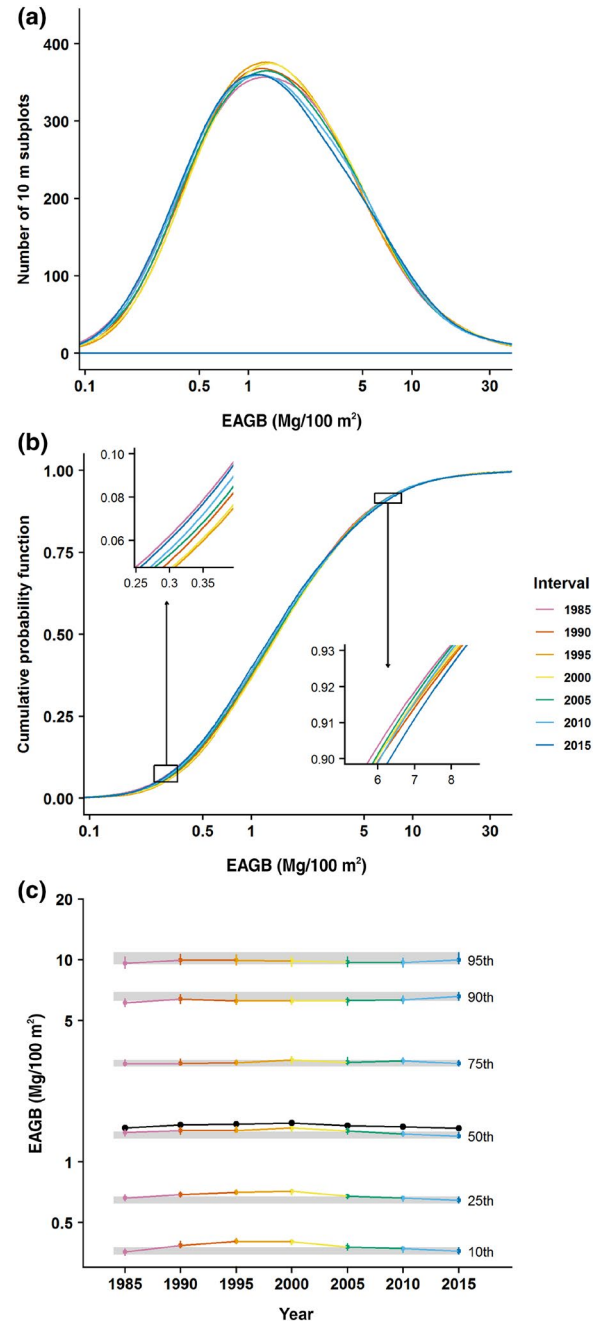


FIGURE 6 Probability density distribution (a) and cumulative probability distribution (b) of estimated above-ground biomass (EAGB) density across all $10 \times 10 \text{ m}$ quadrats, with insets in (b) magnified to show inter-census variation for cumulative probabilities of 0.05–0.1 and 0.9–0.95. (c) Variation over time in seven specific percentiles of the EAGB distribution over quadrats (colored points and lines) and in the overall mean EAGB density at the 50 ha scale (black solid points and lines). In panel (c), vertical lines show the 95% confidence intervals (CIs) from bootstrapping over quadrats, and horizontal gray shading shows the CIs for values in 2015 to enable easy visual assessment of how other years compare. The illustrated curves in panels (a) and (b) are truncated at the 0.2th and 99.8th percentiles of the distribution, but all values were included in analyses. Note that the EAGB densities can be converted to units of Mg/ha by multiplying by 100

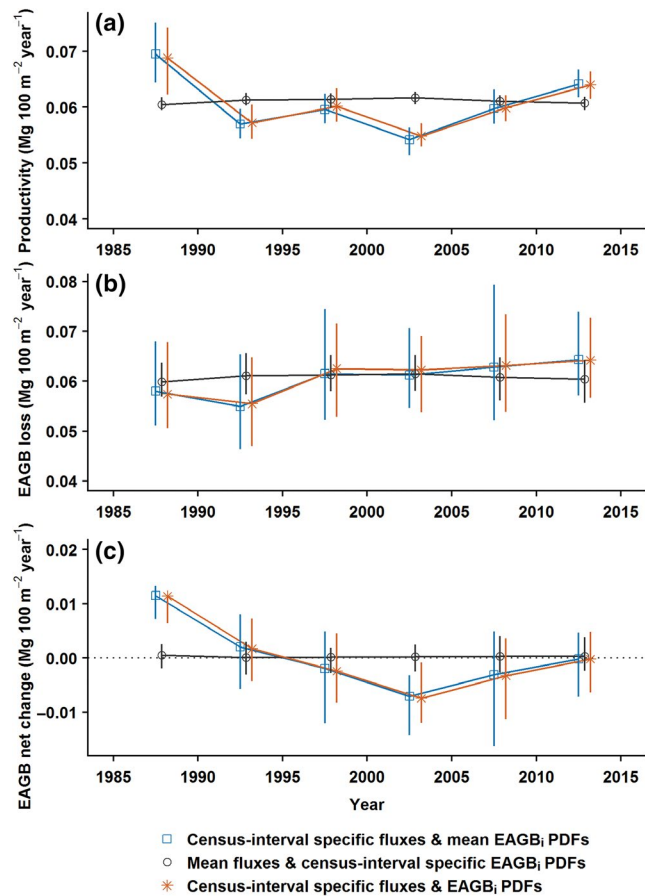


FIGURE 7 Time series of hypothetical whole-plot productivity (a), loss (b), and net change (c) expected with and without variation among census intervals in functions specifying how estimated above-ground biomass (EAGB) fluxes vary with initial biomass, and with and without variation among census intervals in initial EAGB distributions (EAGB_i). See Section 2 for details. Vertical lines show 95% confidence intervals obtained by bootstrapping over quadrats. The points are placed at the mid-points of the census intervals, and jiggered horizontally to increase readability. Values are given in Table S3. Note that EAGB stocks and fluxes can be converted to units of Mg/ha by multiplying by 100. PDF, probability density function

stem DBH increased from 1985 to 2000, and then leveled off, with parallel patterns for all quadrat biomass densities (Figure 8d).

4 | DISCUSSION

Here, we proposed and applied a straightforward way to control for successional stage in analyses of forest biomass change, by comparing forest patches at similar stages of gap recovery, as inferred by similar EAGB_i density. Our analyses revealed strong temporal variation in forest woody productivity and loss fluxes both at the whole plot level and when controlling for local (10 × 10 m) gap phase. There was no consistent long-term trend in productivity, mortality, or biomass in this forest over 30 years, although the interannual variability in productivity and mortality is so strong that it could well mask a substantial trend. Woody productivity varied ~25% among 5 year

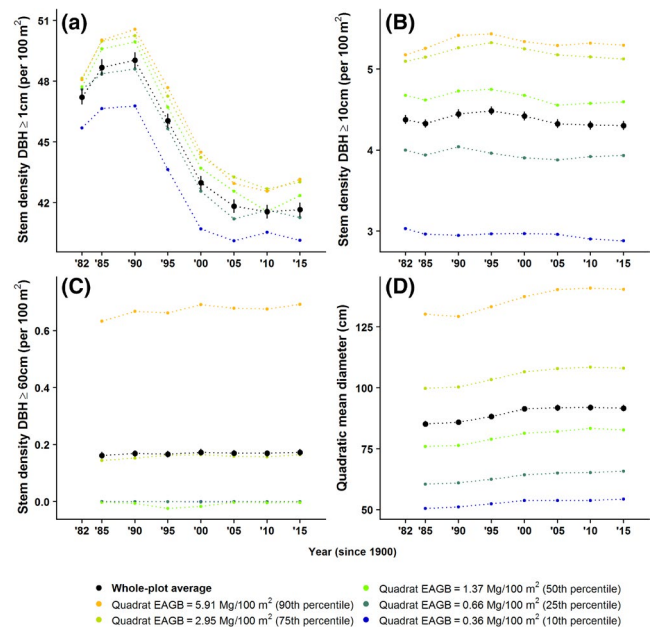


FIGURE 8 Variation among censuses in forest size structure at the whole plot level (black) and for different initial EAGB in 10 × 10 m quadrats (colors). 95% Confidence intervals (vertical lines) were obtained from bootstrapping over quadrats, but are generally smaller than the dot size. The density of large stems and mean diameter are not reported for 1982 due to inconsistencies in measurement methods (Condit, 1998). DBH, diameter at breast height

census intervals, and woody losses ~15%, between 1985 and 2015. Because this variability is consistent even after controlling for gap phase, we conclude it arises from interannual variation in driving factors, most obviously climate.

4.1 | Temporal climate variation in the tropics and its impacts

Tropical forests experience biologically important interannual climate variation in temperature, solar radiation, water availability, and the frequency and intensity of major storms. Interannual climate variation in tropical forests is related in part to irregularly periodic climate oscillations, including the El Niño Southern Oscillation (ENSO) and the Atlantic Multidecadal Oscillation (AMO). In much of the tropics, the El Niño phase of ENSO is associated with drier, sunnier, and hotter conditions, whereas the La Niña phase is associated with wetter, cloudier, and cooler conditions (Holmgren, Scheffer, Ezcurra, Gutiérrez, & Mohren, 2001; Marengo, Tomasella, Alves, Soares, & Rodriguez, 2011). The AMO also influences climate variation at our site and other areas in the region (Elder, Balling, Cerveny, & Krahenbuhl, 2014). Tropical tree recruitment, growth, and mortality all vary among years in relation to such local climate variation, and thus, stand-level productivity and mortality fluxes vary as well.

Extended periods of drier than normal conditions—that is, droughts—are associated with increased mortality and decreased

productivity in many tropical forests (Feldpausch et al., 2016; Phillips et al., 2009). The severe 1982–1983 El Niño made the dry season on BCI longer and harsher than normal, and was associated with higher tree mortality rates. Similarly, many sites in the Amazon and south-east Asia experienced elevated mortality during and after El Niño droughts (e.g., Brando et al., 2014; McDowell et al., 2018; Phillips et al., 2010; Qie et al., 2017; Rowland et al., 2015). El Niño droughts in the Amazon were also associated with decreased leaf area index, decreased photosynthesis (attributed to both stomatal closure and lower leaf area), and decreased woody productivity during the drought periods (Aguilos, Hérault, Burban, Wagner, & Bonal, 2018; Asner, Townsend, & Braswell, 2000; Rowland et al., 2014; Santos et al., 2018). Tree-ring studies generally find that woody productivity is positively correlated with annual precipitation (Alfaro-Sánchez, Muller-Landau, Wright, & Camarero, 2017; Schippers, Sterck, Vlam, & Zuidema, 2015), consistent with the idea that dry years are bad for productivity. Temporal variation in woody growth in relation to water availability could be explained in part by shifts in allocation (rather than simply differences in total GPP and NPP), with trees allocating to increased xylem growth in wet periods after droughts in order to replace drought-damaged xylem (Trugman et al., 2018).

Although most studies have emphasized the negative effects of drier periods, drier years also bring higher solar radiation, and this can lead to more favorable conditions for forest productivity and tree survival if the dryness is not too extreme. On BCI, the drier periods of the 1987–1988 and 1997–1998 El Niños (Figure S18) were associated with elevated fruit production (Detto, Wright, Calderón, & Muller-Landau, 2018), and the 5 year census periods encompassing these events featured above-average woody productivity (this study, Meakem et al., 2017). El Niño events are associated with reduced rainfall during the wet season across northern South American and southern Central America (Ropelewski & Halpert, 1987). Moisture availability remains ample and reduced cloud cover and great solar radiation relieves light limitation (Graham, Mulkey, Kitajima, Phillips, & Wright, 2003), providing a straightforward explanation for observed increases in productivity (Detto et al., 2018; Wright & Calderón, 2006). Consistent with these findings, a previous analysis of multiple moist and wet tropical forests, including BCI, found higher tree growth in census intervals with higher solar radiation (Dong et al., 2012). There are also reasons why dry years might exhibit lower rather than higher mortality. Reduced light limitation in sunnier years might reduce mortality rates for shaded understory tree, and fewer and smaller storms may reduce mortality due to windthrows, lightning, and landslides (Aubry-Kientz, Rossi, Wagner, & Hérault, 2015; Espírito-Santo et al., 2010; Guzzetti, Peruccacci, Rossi, & Stark, 2008; Yanoviak, Gora, Burchfield, Bitzer, & Detto, 2017).

Interannual variation in temperature may also contribute to interannual variation in tropical forest carbon dynamics. Warmer years have been associated with lower tropical tree growth in several studies (Clark, Piper, Keeling, & Clark, 2003; Dong et al., 2012;

Schippers et al., 2015). Temperature directly affects photosynthesis and respiration rates, with photosynthesis responding unimodally to temperature, and respiration increasing continuously with temperature (Lloyd & Farquhar, 2008; Slot & Winter, 2017). Furthermore, high leaf temperatures increase vapor pressure deficits and water demand, leading to stomatal closure, and it is this effect on water relations that appears to be the main contributor to temperature limitation on productivity (Aguilos et al., 2018; Slot & Winter, 2017). Higher atmospheric carbon dioxide concentrations increase plant water use efficiency, and may thereby partly mitigate the negative effects of higher temperatures and drier conditions on productivity (Holtum & Winter, 2010).

In addition to the direct effects of climate on plant physiological function and mortality risk, climate may also influence forest carbon cycles indirectly by causing shifts in allocation, stand structure, functional composition, and influences of interacting species. Plants may increase or decrease allocation to woody growth, including adding to or drawing down carbon stores, depending on past and current climate conditions (Clark, Clark, & Oberbauer, 2013; Doughty et al., 2014; Trugman et al., 2018). Past mortality events from climate alter tree age and size distributions, gap phase distributions, and thereby stand-level carbon budgets (Anderegg, Schwalm, et al., 2015; Chazdon, 2003; Clark, 2007). Differential recruitment, survival, and growth of plant functional types under particular climate conditions also alters functional composition, and thereby the response of forests to future climate. For example, mortality of drought-intolerant species under drought can shift composition toward more drought-tolerant species, with implications for forest carbon budgets and resilience to future droughts (Esquivel-Muelbert et al., 2019; McDowell et al., 2008; Ouédraogo, Mortier, Gourlet-Fleury, Freycon, & Picard, 2013). The proliferation of pathogens and insect herbivores, and thus their effects on trees, is also highly sensitive to climate conditions (Anderegg, Hicke, et al., 2015; Van Bael et al., 2004).

4.2 | Detecting and attributing long-term change

Tropical forests are experiencing global atmospheric and climate change. Mean atmospheric CO₂ concentration is increasing continuously, with an increase of 15% over the duration of our study (from 346 ppm in 1985 to 400 ppm in 2015, Figure S18g). Temperatures are increasing in most tropical regions, and precipitation patterns are changing in region-specific ways (Buckley & Huey, 2016; Malhi & Wright, 2004). At our site, the focal 30 year period exhibited trends of +0.15°C per decade in daily maximum temperature, +0.04°C per decade in daily minimum temperature, +5 mm/year in annual precipitation, +0.05% soil moisture per year, and -1.3 W m⁻² year⁻¹ in annual solar radiation. Trends in annual means of these BCI climate metrics over the 30 year period alone were not statistically significant after Bonferroni correction (individual *p*-values of .075, .44, .66, .033, and .48, respectively), reflecting the relative strength of interannual variation. This interannual variation limits the ability to detect long-term trends—but failure to reject the null hypothesis of

no increase should not be misinterpreted as support for constant climate conditions.

These atmospheric and climate changes are hypothesized to be changing tropical forest carbon dynamics (Lewis, Malhi, & Phillips, 2004). CO₂ is needed for photosynthesis, and physiological models suggest that the observed increase in CO₂ should increase growth (Phillips & Lewis, 2014), although there is uncertainty about the degree to which growth responses are limited by availability of other nutrients, and within-plant carbon demands (Körner, 2009, 2003b; Wright et al., 2011). Spatial variation in climate among tropical forests is associated with variation in tropical forest carbon stocks and fluxes (Álvarez-Dávila et al., 2017; Becknell, Kissing Kucek, & Powers, 2012; Poorter et al., 2016; Taylor et al., 2017), suggesting that directional climate changes should also change forest carbon budgets in the long term. As discussed above, tropical forests are also sensitive to temporal variation in climate conditions, further suggesting that climate change will matter. However, the relationship of short-term to long-term climate responses is not straightforward, because the importance of particular mechanisms shifts with the timescale. Allocational shifts to/from woody productivity, reproductive output, and carbohydrate stores play a large role in variation over seasonal to annual time scales (Dickman et al., 2018; Doughty et al., 2014), but are likely to play little role at decadal and longer time scales. In contrast, shifts in functional composition of the tree community are likely to play a large role in responses to long-term climate variation (van der Sande et al., 2016), but very little role in short-term responses. Such compositional shifts are in general expected to decrease the sensitivity of forest carbon fluxes to climate variation, as the forest becomes increasingly dominated by species that do relatively well in the new climate conditions (Esquivel-Muelbert et al., 2019; Fauset et al., 2015; Feldpausch et al., 2016).

However, evidence of long-term changes in tropical forest carbon cycling is mixed, with divergent patterns across studies. Increasing woody productivity and mortality were found in analyses of the RAINFOR network of Amazonian plots (Brienen et al., 2015), but not in site-specific studies of BCI (this study) or La Selva (Clark, Asao, et al., 2017; Clark et al., 2013; Clark, Clark, et al., 2017). On average, studies report increased biomass densities in old-growth tropical forests (Brienen et al., 2015; Chave et al., 2008, Lewis et al., 2009; Muller-Landau et al., 2014; Qie et al., 2017; Rutishauser, Wagner, Herault, Nicolini, & Blanc, 2010), but this pattern too is not universal (this study, Chave et al., 2008; Clark, Clark, et al., 2017; Feeley et al., 2007) and the causes of observed increases continue to be debated (Clark, 2004; Lewis et al., 2009; Muller-Landau, 2009; Wright, 2013). It is notable that two of the most intensive long-term studies of focal sites, this 30 year study of BCI and Clark, Clark, et al. (2017)'s 40 year study of La Selva, find multidecadal stability in forest structure and dynamics, in striking contrast to the "Bigger and Faster" hypothesis.

The large uncertainty surrounding estimated fluxes and their long-term trends observed here, even with such a large-scale long-term study, highlights the difficulty of accurately capturing

changes in forest dynamics from field data (Clark, Asao, et al., 2017). Wagner, Rutishauser, Blanc, and Herault (2010) calculated that estimating even the mean EAGB loss within 20% error with 95% confidence in a particular forest would require ~200 ha-years of monitoring, far more than the usual size and duration of most forest monitoring experiments. The effort required to accurately estimate a long-term trend is much higher still—even a trend as large as 1% a year amounts to only 10% a decade, within the error limits of the Wagner et al. (2010) calculation. Detection of long-term trends is further complicated by sensitivity of estimated trends to the precise methods of data quality assessment and quality control (QAQC; Figure S18). Many common QAQC procedures result in systematic biases in whole-plot statistics (Cushman et al., 2014; Muller-Landau et al., 2014). Our analysis followed current best practices for calculating EAGB fluxes, including standardizing effective POM (Cushman et al., 2014) and avoiding data "cleaning" procedures that can systematically bias whole-plot statistics (Muller-Landau et al., 2014).

4.3 | Conclusion and future directions

The tropical forest on BCI exhibited large temporal variability in stand-level productivity and mortality fluxes over 30 years, even after controlling for disturbance-recovery dynamics, but no long-term trend. Observed temporal variability was aligned to some degree with ENSO-related climate variation, but with a markedly different pattern than is usually reported, highlighting the complexity of tropical forest climate responses. While the drier conditions of El Niño events have been associated with increased tree mortality and reduced productivity in the Amazon (Feldpausch et al., 2016; Lewis, Brando, Phillips, Heijden, & Nepstad, 2011), the drier and sunnier conditions during El Niño events were associated with enhanced productivity and no change in mortality on BCI (Detto et al., 2018; Meakem et al., 2017). No long-term directional trend in productivity, mortality, or biomass was evident in our data, but such a trend could well be obscured by the strong interannual variation.

A better understanding of tropical forest responses to climate variation and long-term trends requires both more data and integration with mechanistic models. Although climate and atmospheric change is global, climate effects are locally variable, and forest responses are dependent on a myriad of other local factors, including species composition and disturbance history, resulting in highly variable EAGB dynamics (Clark et al., 2013). Future multisite analyses of large plot datasets using the methods developed here could provide insights into temporal and spatial variation in tropical forest carbon fluxes (Chave et al., 2008; van der Sande et al., 2016; Wagner et al., 2016). However, any studies based on extant plot datasets are likely to fall short of what is needed to quantify overall trends given high temporal and spatial variability, and the nonsystematic placement of sampling plots (Marvin et al., 2014; McMichael et al., 2017; Saatchi et al., 2015; Wright, 2006). Improvements in remote sensing ultimately promise more comprehensive and consistent measurements of tropical forest structure

and function, and their change over time (Bastin et al., 2018; Rödig et al., 2018; Saatchi et al., 2011), although the contribution of recovery from past disturbances remains to be resolved (McMichael et al., 2017; Palace et al., 2017). Studies integrating mechanistic models with data on climate drivers and forest dynamics are uniquely well suited to glean insights into the ultimate mechanisms behind observed patterns and to disentangling the roles of temperature, rainfall, atmospheric carbon dioxide, soils, species composition, and site history (Levine et al., 2016; Schippers et al., 2015).

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CONFLICT OF INTEREST

All authors declare no conflict of interest.

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SUPPORTING INFORMATION

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

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Supplemental information

“Testing for changes in biomass dynamics in large-scale forest datasets”

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Stuart J. Davies, and Helene C. Muller-Landau

Global Change Biology

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A. Details of census methods

In the first two censuses (1982 and 1985), diameters of stems with DBH < 55 mm were rounded down to the nearest 5 mm (10, 15, 20, 25, 30, 35, 40, 45, 50). To remove associated biases in tree growth measurements in the 1985-1990 interval, we substituted DBH values of trees DBH < 55 mm in 1985 and 1990, with median DBH values measured in 1990 for each rounding class. That is, trees recorded as 10 mm in 1985 or 10-14 mm in 1990 were analysed as having a diameter of 12 mm, and so forth. The medians by 5 mm diameter class were 12, 17, 22, 27, 32, 37, 42, 47 and 52 mm. This treatment affected 1990 data only for analysis of 1985-1990 growth, not for analysis of 1990-95 growth.

Before 2010, stems of multi-stemmed individuals were not individually tagged, making it impossible to unambiguously identify cases in which one stem died and another of similar size resprouted. We thus summed biomass over stems at the tree level, and treated most changes in total biomass of an individual tree as positive or negative growth (productivity). However, there were two types of cases in which we could confidently identify biomass losses and classify them as such. The first concerned cases in which main stems > 10 cm DBH died and resprouted, which we treated as a combination of biomass loss (mortality) fluxes of the stem that died and recruitment (productivity) fluxes of the resprouts. We classified cases as main stem deaths followed by resprouting if the DBH of the main stem was > 10 cm in one census, and at least 20% smaller in the next census (N=716). The second concerned cases in which multiple-stemmed individuals experienced a loss in biomass accompanied by a decrease in stem number; in these cases, the loss in biomass was counted entirely as mortality, with zero growth (productivity). We applied the same methods across all censuses, thereby avoiding a bias over time due to changing methods.

Table S1 Species-specific median DBH (cm) for palm species that do not grow in diameter. In these species, all changes in DBH over censuses are treated as measurement errors. To avoid associated errors in biomass fluxes, we assigned the species-specific median DBH to every stem at every census in these species.

Name	Median DBH (cm)	Name	Median DBH (cm)
<i>Astrocaryum standleyanum</i>	133	<i>Bactris major</i>	37
<i>Attalea rostrata</i>	376	<i>Chamaedorea tepejilote</i>	30
<i>Bactris barronis</i>	40	<i>Elaeis oleifera</i>	382
<i>Bactris coloniata</i>	35	<i>Geonoma interrupta</i>	35
<i>Bactris coloradonis</i>	40	<i>Oenocarpus mapora</i>	85

Table S2 Number of 10x10m quadrats meeting criteria for removal from the analyses by census interval and reason for removal. The reasons for removal are (i) presence of large (DBH>50 cm) strangler figs (*Ficus costaricana*, *F. obtusifolia*, *F. popenoei* or *F. trigonata*), (ii) at least one tree with change in POM > 10 cm, and (iii) at least one tree with an extreme productivity value (defined below). For consistency, quadrats containing at least one large strangler fig in any census were discarded from all analyses (N=13). Note that some quadrats are affected by more than one reason of removal and the total of quadrat excluded does not correspond to the sum of reasons of removal.

Census year	1990	1995	2000	2005	2010	2015
large strangler figs	4	5	7	5	5	4
change of POM > 10 cm	1010	701	1271	1104	1068	372
extreme productivity	20	12	18	10	10	15
Total quadrat excluded	1028	714	1288	1114	1077	389
(Total quadrat included	3641	3955	3381	3555	3592	4280)

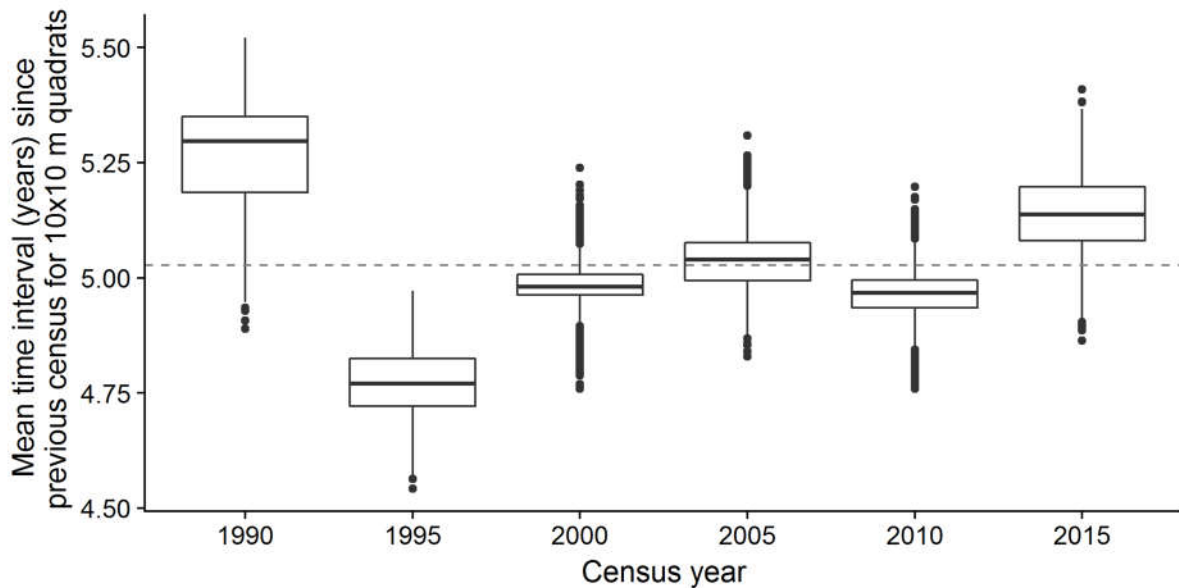


Figure S1 Variation in census interval length among census intervals and among 10x10 m quadrats. Biomass fluxes calculated with the simple formulas used here are increasingly biased downwards at longer census intervals (Kohyama et al. 2019). This would confound comparisons across census intervals if census interval lengths varied, but we show here that there is little variation among census intervals. Quadrat-level census intervals were computed as the means over each individual present in the quadrat in one or both censuses. For recruits, the initial date is the mean date at which other stems in the quadrat were censused. The boxes show medians, 25th, and 75th percentiles, the bars extend to $\pm 1.5 \times$ IQR below the first and third quartiles respectively, and additional outlying quadrats are shown individually. The analysis covers 48.8 ha of the BCI plot, excluding the 1.2 ha of swamp that were discarded from all analyses.

Table S3 Mean biomass increment per tree (in kg.yr⁻¹), sample size of trees used to calculate the mean (N), and the number of trees whose growth rates were substituted with these mean values (N_{sub}) for the analysis of whole-plot fluxes (Figure 7), by initial DBH class and census interval. Growth rates were substituted for trees that had a change in the point of measurement, or that had an unreasonably large change in dbh such that biomass growth $> t * \bar{P}$ (or $< -t * \bar{P}$), where t is a threshold (0.2 in our study) and \bar{P} is the mean productivity per hectare for all census intervals combined. The analysis covers 46.9 ha of the BCI plot, excluding 1.2 ha of swamp and 1.9 ha of young forest. Most substitutions were related to changes in POM (Table S2). Note that the analyses of quadrat-level fluxes (Figures 3, 4, 5) excluded quadrats with trees affected by any of these problems, and thus are not affected by these substitutions.

Census interval	< 5 cm			5-9.9 cm			10-19.9 cm			20-39.9 cm			40-59.9 cm			> 60 cm		
	mean	N	N _{sub}	mean	N	N _{sub}	mean	N	N _{sub}	mean	N	N _{sub}	mean	N	N _{sub}	mean	N	N _{sub}
1985-1990	0.13	144,282	3	1.16	21,402	51	4.57	9,414	23	19.22	3,920	380	70.63	803	408	146.90	350	392
1990-1995	0.09	147,457	1	0.88	24,347	67	4.14	9,953	72	16.98	4,114	321	44.19	1,031	211	87.74	599	199
1995-2000	0.09	137,564	277	0.77	23,867	290	3.98	9,794	365	17.43	4,147	357	44.58	1,031	215	92.81	637	168
2000-2005	0.09	129,288	140	0.83	23,402	206	3.86	9,559	295	16.35	4,094	336	45.31	973	260	77.62	581	235
2005-2010	0.12	124,829	206	0.90	23,061	234	3.94	9,451	266	15.96	3,824	479	46.31	1,056	166	101.28	667	149
2010-2015	0.12	123,822	90	1.00	23,485	129	4.29	9,476	87	17.31	4,085	87	48.63	1,169	22	109.56	748	48

B. Detailed results on analyses of biomass fluxes

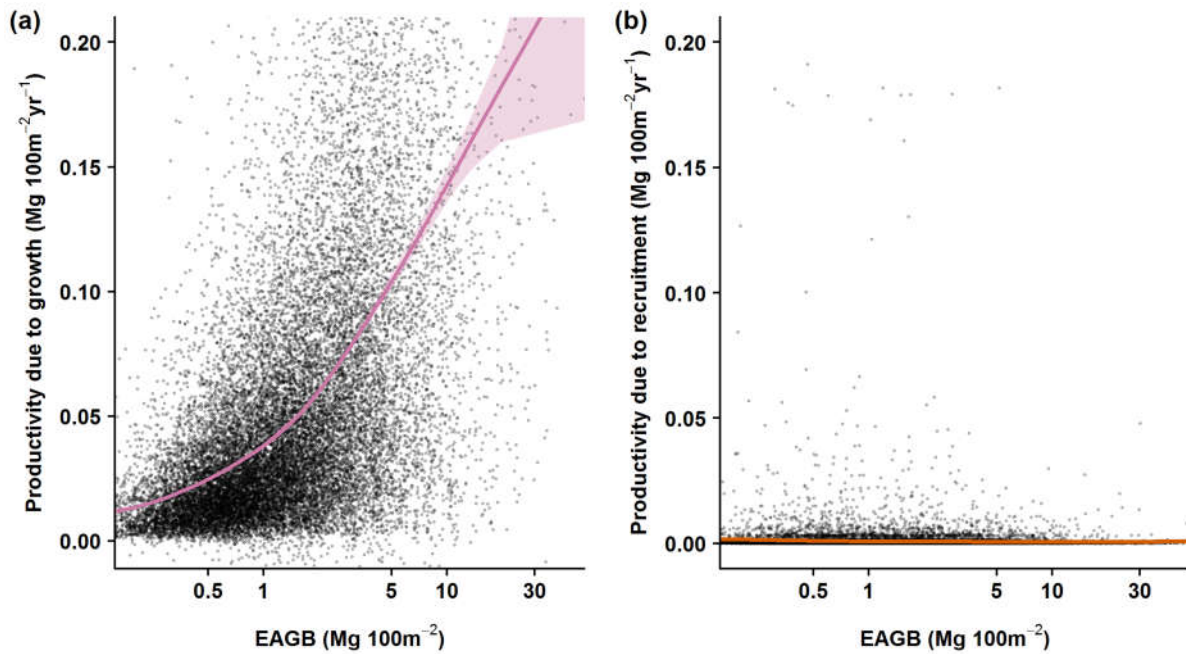


Figure S2 Quadrat-level annual EAGB productivity due to growth of surviving trees (a) and recruitment of new trees (b) (Mg.100m⁻².yr⁻¹) as a function of initial quadrat biomass for each 5-year census interval, for 10x10 m quadrats (points) with local polynomial regression lines for individual census intervals (colored solid lines) and for all census intervals combined (black dashed lines). For each census interval, analyses excluded quadrats containing one or more trees that (a) are large strangler figs, (b) have a change in POM, or (c) have an obvious major measurement error during the census interval (see methods for details; N is the number of quadrats included for each census interval). Regression lines are shown only for the ranges of the 2nd to 98th percentile values of the respective datasets (avoiding the distribution extremes where uncertainty increases). The range of data shown here is truncated for illustration purposes, but all points (including those outside the graphed range) were included in analyses.

Table S4 Time series of hypothetical whole-plot productivity, loss, and net change under three scenarios: (a) census-interval specific fluxes & mean EAGBi PDFs, (b) mean fluxes & census-interval specific EAGBi PDFs and (c) census-interval specific fluxes & EAGBi PDFs. Here “fluxes” refers to functions for quadrat biomass flux as a function of initial quadrat biomass, “EAGBi PDF” refers to the probability distribution of initial biomass density over quadrats, and means are based on combining data for all census intervals. Note that the analysis covers 46.9 ha of the BCI plot, excluding 1.2 ha of swamp and 1.9 ha of young forest.

Scenario	Census interval	Productivity	EAGB loss	Net change
a	1985-1990	0.070 (0.064-0.075)	0.058 (0.049-0.070)	0.012 (0.005-0.014)
a	1990-1995	0.057 (0.053-0.060)	0.054 (0.045-0.064)	0.003 (-0.004-0.009)
a	1995-2000	0.059 (0.057-0.061)	0.061 (0.051-0.069)	-0.002 (-0.008-0.006)
a	2000-2005	0.054 (0.051-0.056)	0.062 (0.055-0.071)	-0.008 (-0.015--0.003)
a	2005-2010	0.059 (0.056-0.062)	0.062 (0.052-0.071)	-0.003 (-0.009-0.004)
a	2010-2015	0.064 (0.061-0.066)	0.063 (0.057-0.070)	0.000 (-0.005-0.004)
b	1985-1990	0.060 (0.059-0.061)	0.059 (0.055-0.062)	0.001 (-0.001-0.003)
b	1990-1995	0.061 (0.060-0.062)	0.061 (0.057-0.065)	0.000 (-0.003-0.003)
b	1995-2000	0.061 (0.060-0.062)	0.061 (0.058-0.065)	0.000 (-0.002-0.002)
b	2000-2005	0.061 (0.060-0.062)	0.061 (0.057-0.065)	0.000 (-0.002-0.003)
b	2005-2010	0.061 (0.060-0.062)	0.060 (0.057-0.064)	0.001 (-0.002-0.003)
b	2010-2015	0.060 (0.059-0.062)	0.060 (0.057-0.064)	0.001 (-0.002-0.002)
c	1985-1990	0.069 (0.062-0.075)	0.057 (0.049-0.067)	0.012 (0.008-0.013)
c	1990-1995	0.057 (0.054-0.060)	0.055 (0.045-0.066)	0.002 (-0.006-0.009)
c	1995-2000	0.060 (0.057-0.062)	0.062 (0.054-0.072)	-0.002 (-0.009-0.003)
c	2000-2005	0.054 (0.052-0.057)	0.063 (0.055-0.071)	-0.008 (-0.015--0.003)
c	2005-2010	0.059 (0.057-0.063)	0.062 (0.052-0.072)	-0.003 (-0.010-0.005)
c	2010-2015	0.064 (0.061-0.066)	0.063 (0.056-0.072)	0.000 (-0.006-0.005)

Table S5 Plot-level average (value) and 95% confidence intervals for quadratic mean diameter and density of trees with DBH \geq 1, 10 and 60 cm by census (Figure 8). The density of large trees and mean diameter are not reported for 1982 due to inconsistencies in measurement methods (see Condit, 1998). Letters indicate significant differences within a given column. Note that the analysis covers 46.9 ha of the BCI plot, excluding 1.2 ha of swamp and 1.9 ha of young forest.

Census year	Quadratic mean diameter (cm)			Tree density DBH \geq 1 cm (ha ⁻¹)			Tree density DBH \geq 10 cm (ha ⁻¹)			Tree density DBH \geq 60 cm (ha ⁻¹)		
	value	5%CI	95%CI	value	5%CI	95%CI	value	5%CI	95%CI	value	5%CI	95%CI
1982	-	-	-	47.21a	46.85	47.63	4.38a	4.32	4.43	-	-	-
1985	85.2a	84.0	86.5	48.68b	48.27	49.09	4.33a	4.28	4.38	0.16a	0.15	0.17
1990	85.9a	84.8	87.0	49.04b	48.64	49.43	4.45b	4.39	4.50	0.17a	0.16	0.18
1995	88.3b	87.2	89.5	46.05c	45.69	46.39	4.49b	4.42	4.54	0.17a	0.15	0.18
2000	91.4c	90.3	92.6	42.98d	42.62	43.31	4.42b	4.39	4.48	0.17a	0.16	0.19
2005	91.9c	90.5	93.1	41.82e	41.50	42.16	4.33a	4.27	4.38	0.17a	0.16	0.18
2010	91.9c	90.7	93.1	41.55e	41.21	41.89	4.31a	4.25	4.36	0.17a	0.16	0.18
2015	91.7c	90.4	93.0	41.66e	41.31	42.00	4.30a	4.25	4.36	0.17a	0.16	0.18

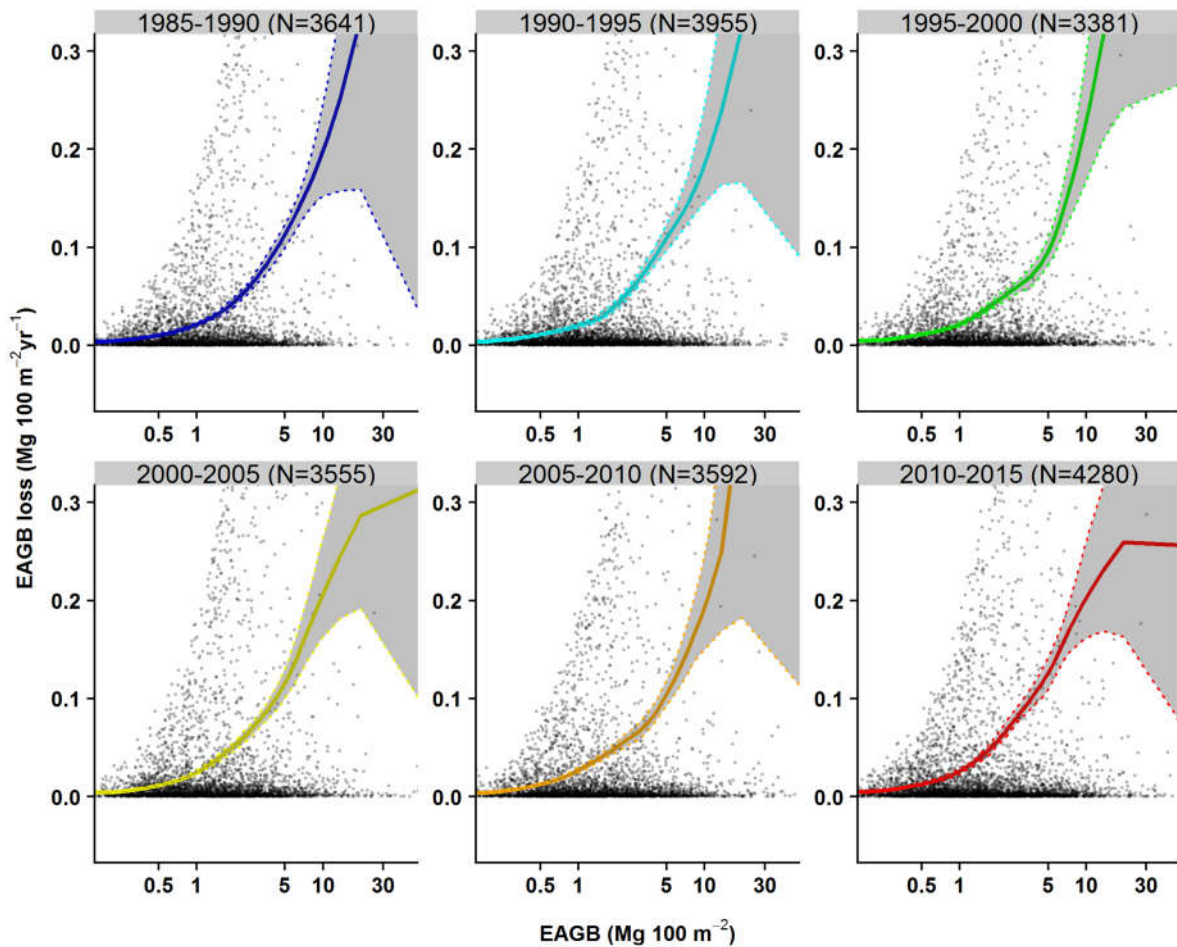


Figure S3 Quadrat-level annual EAGB mortality ($\text{Mg}\cdot 100\text{m}^{-2}\cdot\text{yr}^{-1}$) as a function of initial quadrat biomass for each 5-year census interval, for 10×10 m quadrats (points) with local polynomial regression lines for individual census intervals (colored solid lines) and for all census intervals combined (black dashed lines). For each census interval, analyses excluded quadrats containing one or more trees that (a) are large strangler figs, (b) have a change in POM, or (c) have an obvious major measurement error during the census interval (see methods for details; N is the number of quadrats included for each census interval). Regression lines are shown only for the ranges of the 2nd to 98th percentile values of the respective datasets (avoiding the distribution extremes where uncertainty increases). The range of data shown here is truncated for illustration purposes, but all points (including those outside the graphed range) were included in analyses.

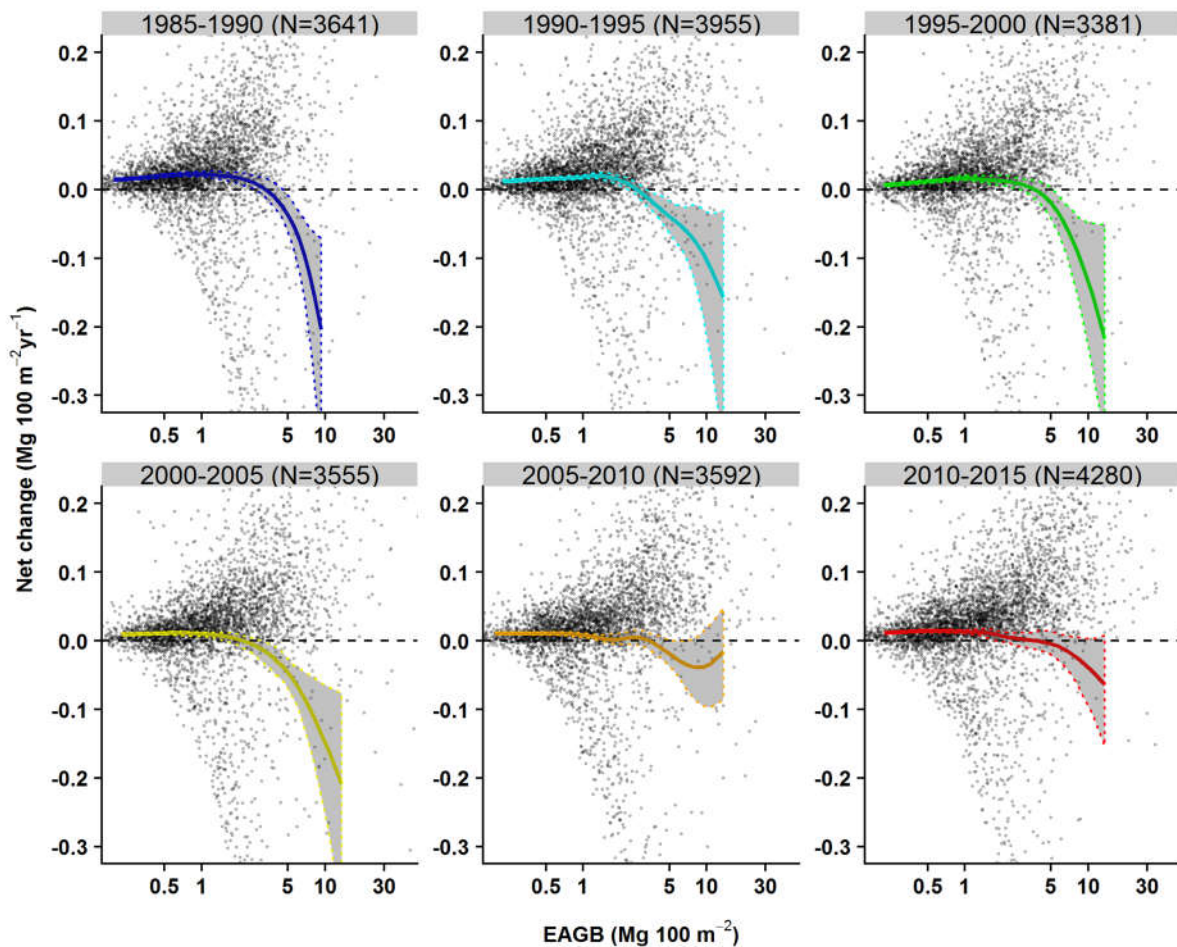


Figure S4 Quadrat-level annual EAGB net change ($\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) as a function of initial quadrat biomass for each 5-year census interval, for 10x10 m quadrats (points) with local polynomial regression lines for individual census intervals (colored solid lines) and for all census intervals combined (black dashed lines). Confidence envelopes (dotted lines) were computed from bootstrapping over quadrats. For each census interval, analyses excluded quadrats containing one or more trees that (a) are large strangler figs, (b) have a change in POM, or (c) have an obvious major measurement error during the census interval (see methods for details; N is the number of quadrats included for each census interval). Regression lines are shown only for the ranges of the 2nd to 98th percentile values of the respective datasets (avoiding the distribution extremes where uncertainty increases). The range of data shown here is truncated for illustration purposes, but all points (including those outside the graphed range) were included in analyses.

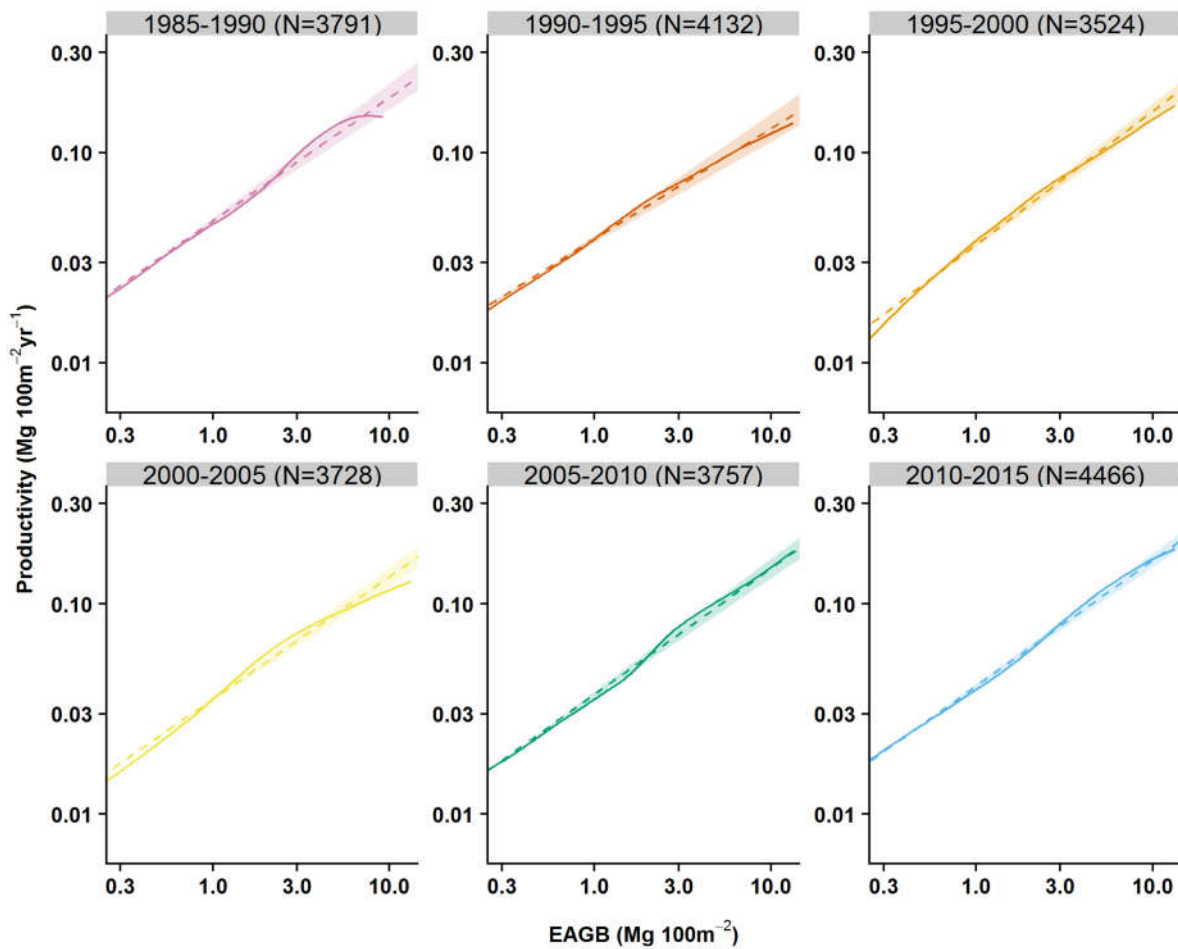


Figure S5 Comparisons of local polynomial regression lines (solid lines) and power function fits (dashed lines) for the relationships of quadrat-level mean annual EAGB productivity (Mg ha⁻¹ yr⁻¹) to initial quadrat biomass for each 5-year census interval (panels). Confidence envelopes for the power function fits (shading) were computed from bootstrapping over quadrats. Note that both axes are log-scaled. For each census interval, analyses excluded quadrats with problematic EAGB measurements (see methods for details). N is the number of quadrats included for each census interval. Regression lines are shown only for the ranges of the 2nd to 98th percentile values of the respective datasets, thereby avoiding the distribution extremes where uncertainty increases.

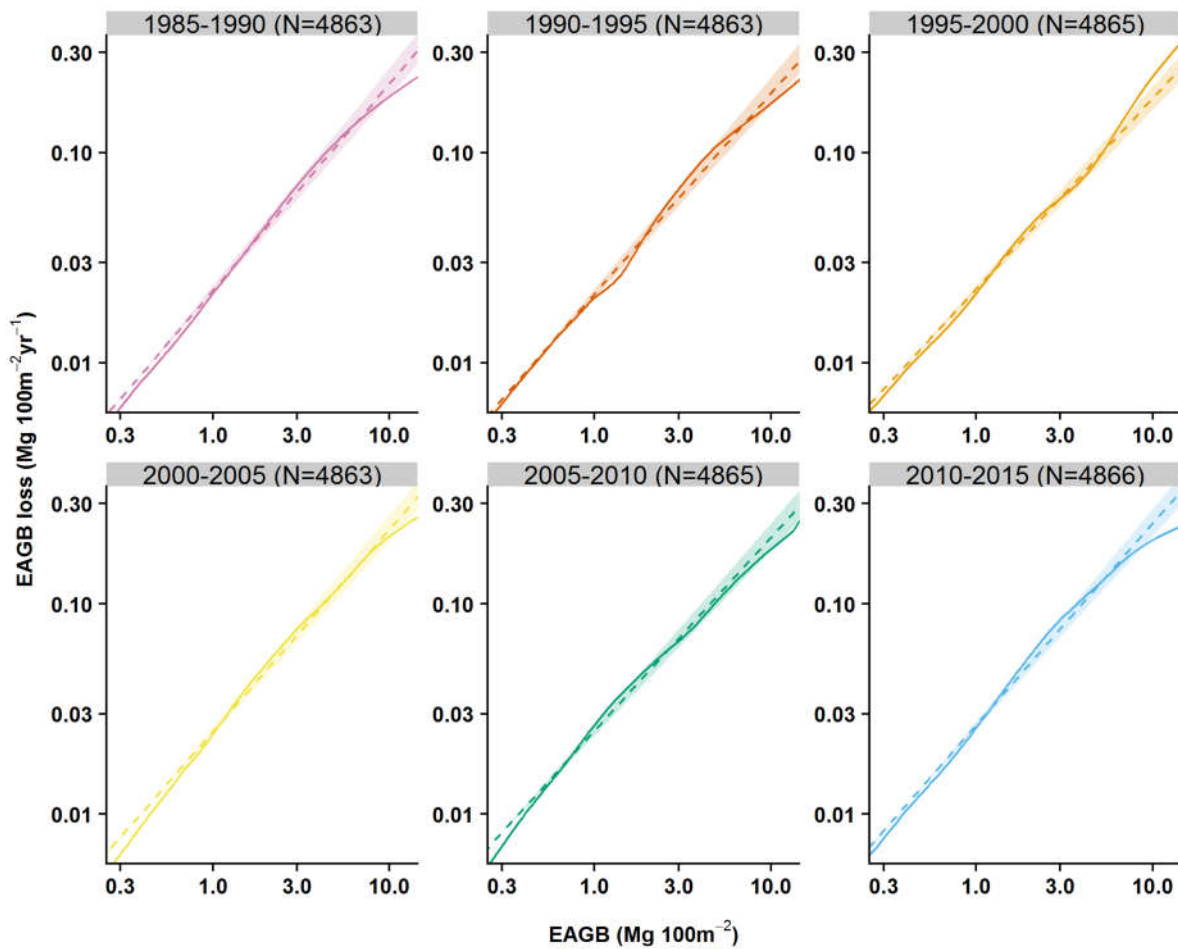


Figure S6 Comparisons of local polynomial regression lines (solid lines) and power function fits (dashed lines) for the relationships of quadrat-level mean annual EAGB loss (Mg ha⁻¹ yr⁻¹) to initial quadrat biomass for each 5-year census interval (panels). Confidence envelopes for the power function fits (shading) were computed from bootstrapping over quadrats. Note that both axis are log-scaled. For each census interval, analyses excluded quadrats with problematic EAGB measurements (see methods for details). N is the number of quadrats included for each census interval. Regression lines are shown only for the ranges of the 2nd to 98th percentile values of the respective datasets thereby avoiding the distribution extremes where uncertainty increases.

Table S6 The estimated normalized intercepts (or coefficients, alpha) and slopes (or exponents, beta) of power functions fitted to quadrat-level productivity and mortality as a function of initial quadrat biomass for each census interval, as shown in figure 5.

Flux	Census interval	Normalized intercepts	Slopes
Productivity	1985-1990	0.587 (0.553-0.629)	5.422 (6.333-6.779)
Productivity	1990-1995	0.525 (0.492-0.568)	4.387 (4.964-5.320)
Productivity	1995-2000	0.635 (0.612-0.667)	4.223 (4.983-5.314)
Productivity	2000-2005	0.583 (0.552-0.619)	4.032 (4.692-4.970)
Productivity	2005-2010	0.600 (0.573-0.635)	4.257 (4.996-5.272)
Productivity	2010-2015	0.598 (0.575-0.625)	4.659 (5.483-5.707)
Mortality	1985-1990	0.955 (0.896-1.024)	2.649 (3.349-3.804)
Mortality	1990-1995	0.910 (0.858-0.950)	2.755 (3.497-3.872)
Mortality	1995-2000	0.962 (0.918-1.008)	3.083 (3.987-4.345)
Mortality	2000-2005	0.923 (0.877-0.965)	3.072 (3.904-4.333)
Mortality	2005-2010	0.961 (0.906-0.994)	3.298 (4.196-4.696)
Mortality	2010-2015	0.587 (0.553-0.629)	5.422 (6.333-6.779)

C. Sensitivity analyses

Here we evaluate the robustness of our results to different data filtering methods and quadrat sizes.

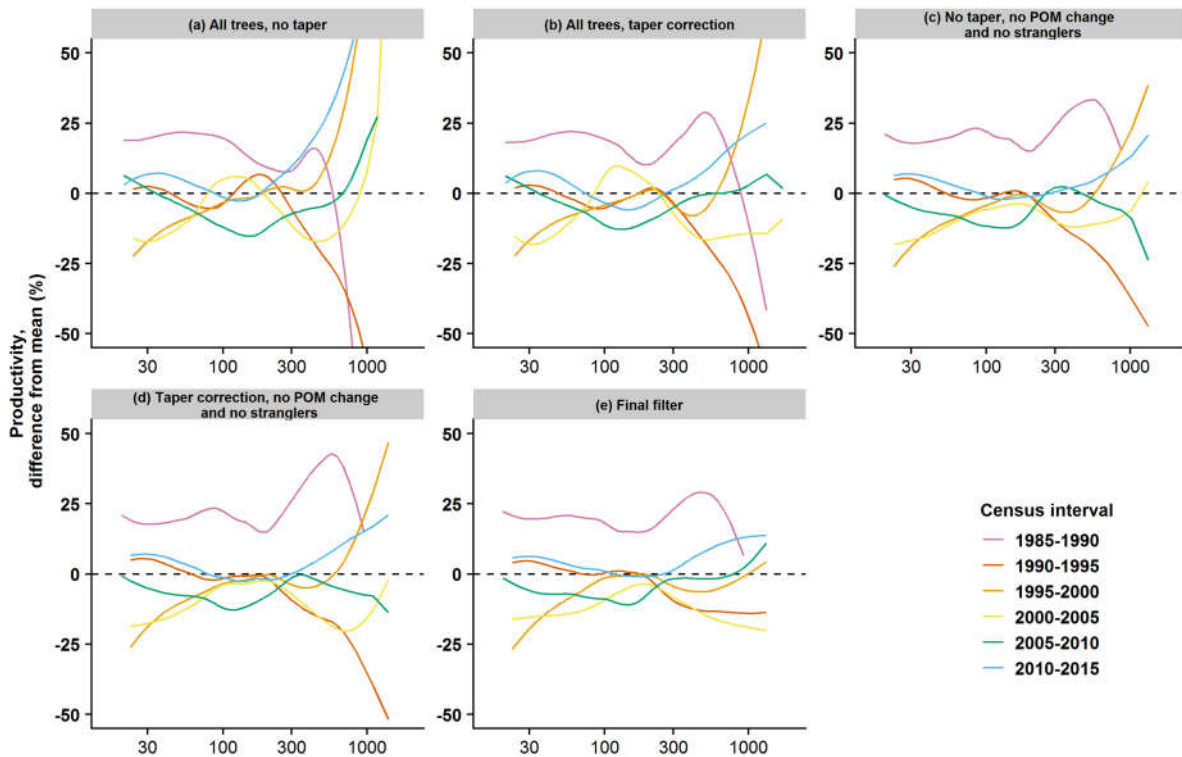
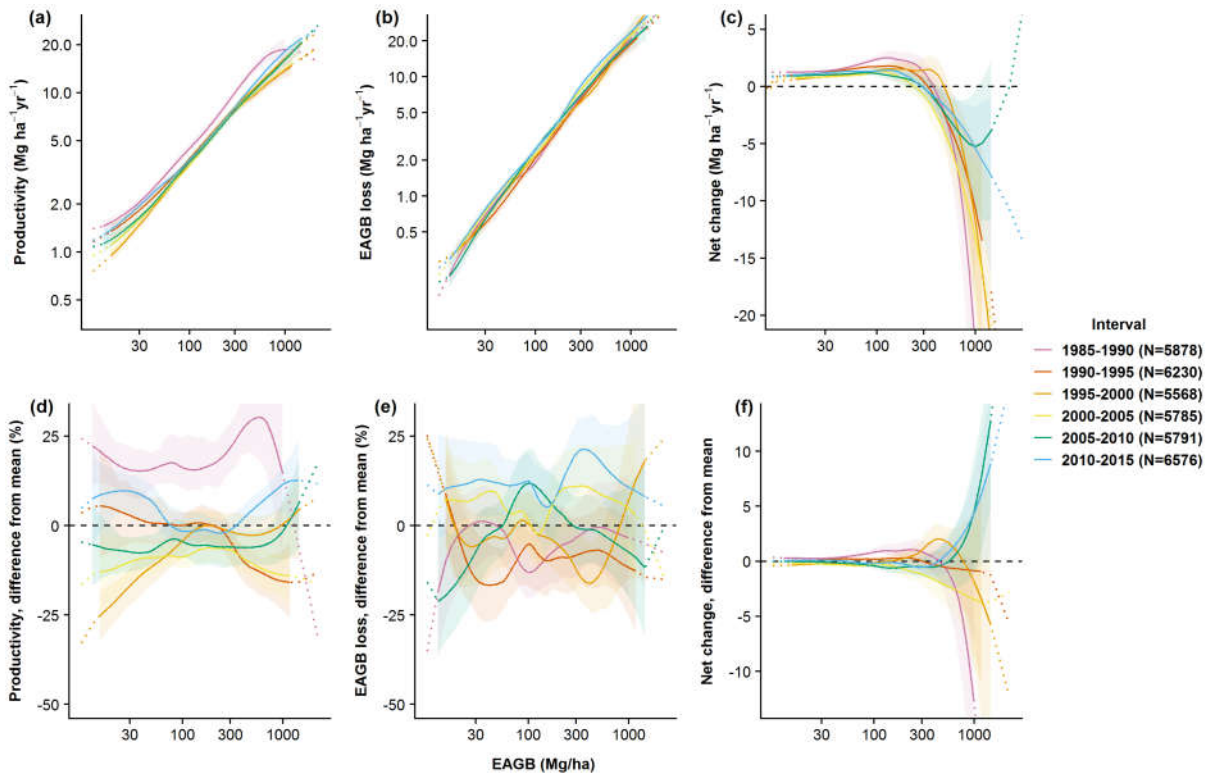
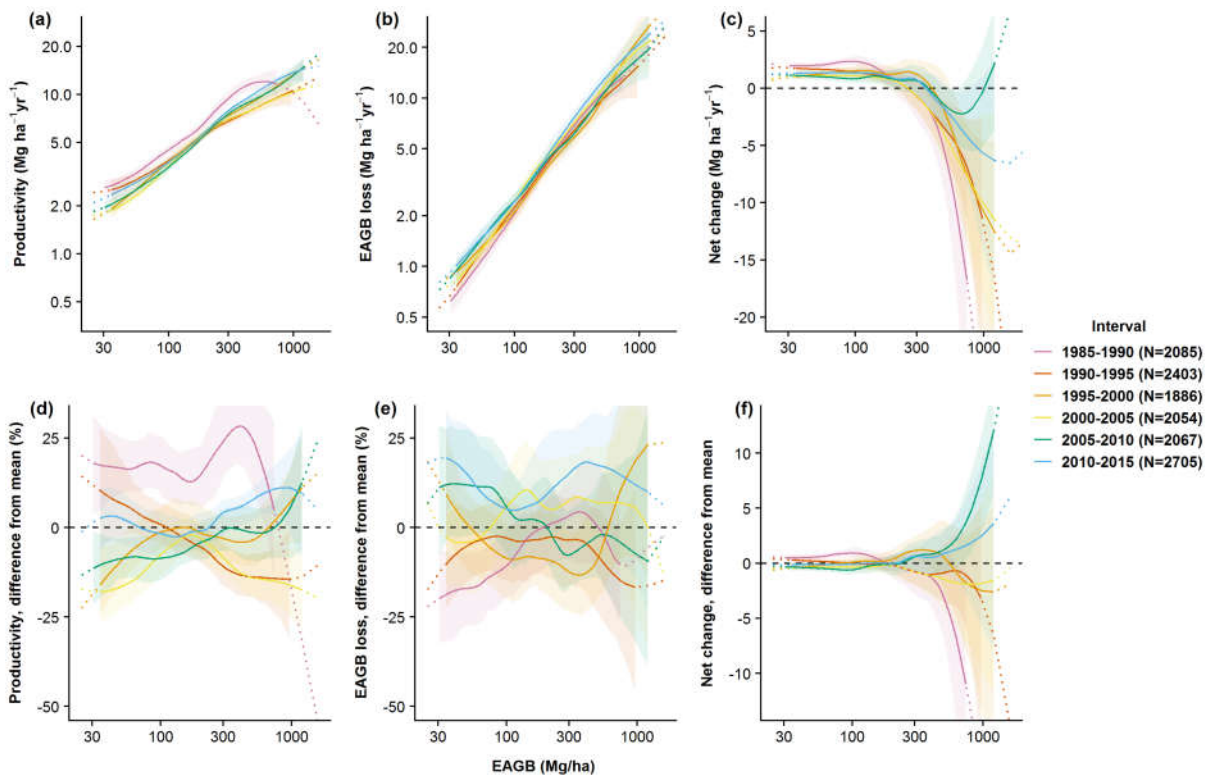


Figure S7 Effects of data filtering rules on variation among census intervals in patterns of productivity as a function of initial biomass for 10m quadrats. Alternative rule sets are: (a) all trees without taper correction, (b) all trees with taper correction, exclusion of quadrats with POM change and large strangler figs without (c) or with (d) taper correction, and (d) exclusion of quadrats with one or more trees with a highly suspicious and highly influential measurement error (i.e. productivity > 20% of mean productivity for 1 ha), large strangler figs and/or POM change. In all case, quadrats in swamps (1.2 ha) were discarded and POM changes were defined as a difference in POM greater than 10 cm.

A. Scale: 8.3 (500/60) m



B. Scale: 12.5 m



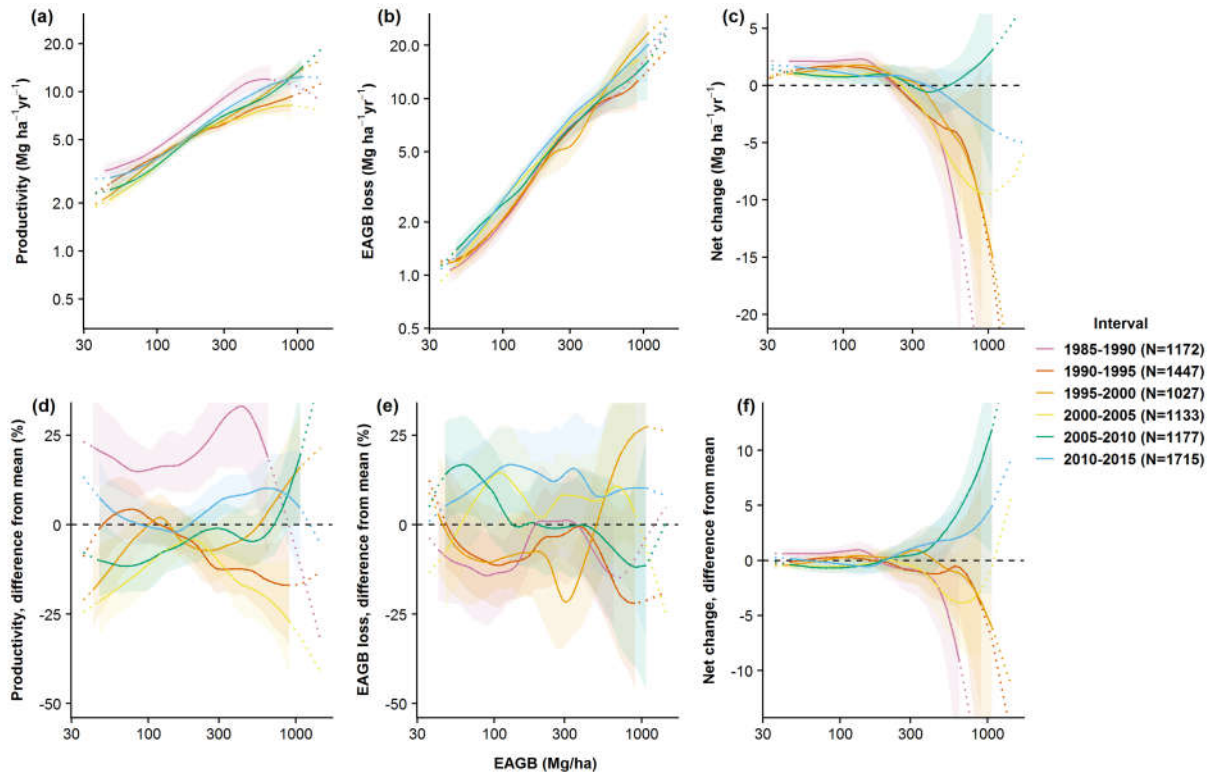
C. Scale: 15.15 m

Figure S8 Comparison of qualitative patterns of quadrat biomass fluxes across different quadrat sizes, for 8.93, 12.5 and 15.15-m square quadrats (A, B, and C respectively). Variation among census intervals in EAGB productivity (a), loss (b) and net change (c) as a function of aboveground biomass (EAGB) at the initial census for 10-m quadrats, computed using local polynomial regression, together with the corresponding differences from the mean (per initial EAGB) across all census intervals (d,e,f). Note that productivity (a) and loss (c) are shown on log scales, whereas the net change (e) is on a linear scale. Analyses excluded quadrats containing large strangler figs, one or more trees with a change in POM, or obvious major measurement error during the census interval (see methods). Regression lines are displayed for values spanning the 2nd to 98th percentiles of the respective census interval (solid lines), and outside this range (dotted lines). Note that extreme values (dotted lines) have large uncertainty and for (f), difference are not expressed as percentage. Confidence envelopes were computed by bootstrapping over quadrats. Number of quadrats included per census interval is given in the legend. Figures are given in Mg/ha to ease comparison among different quadrat sizes.

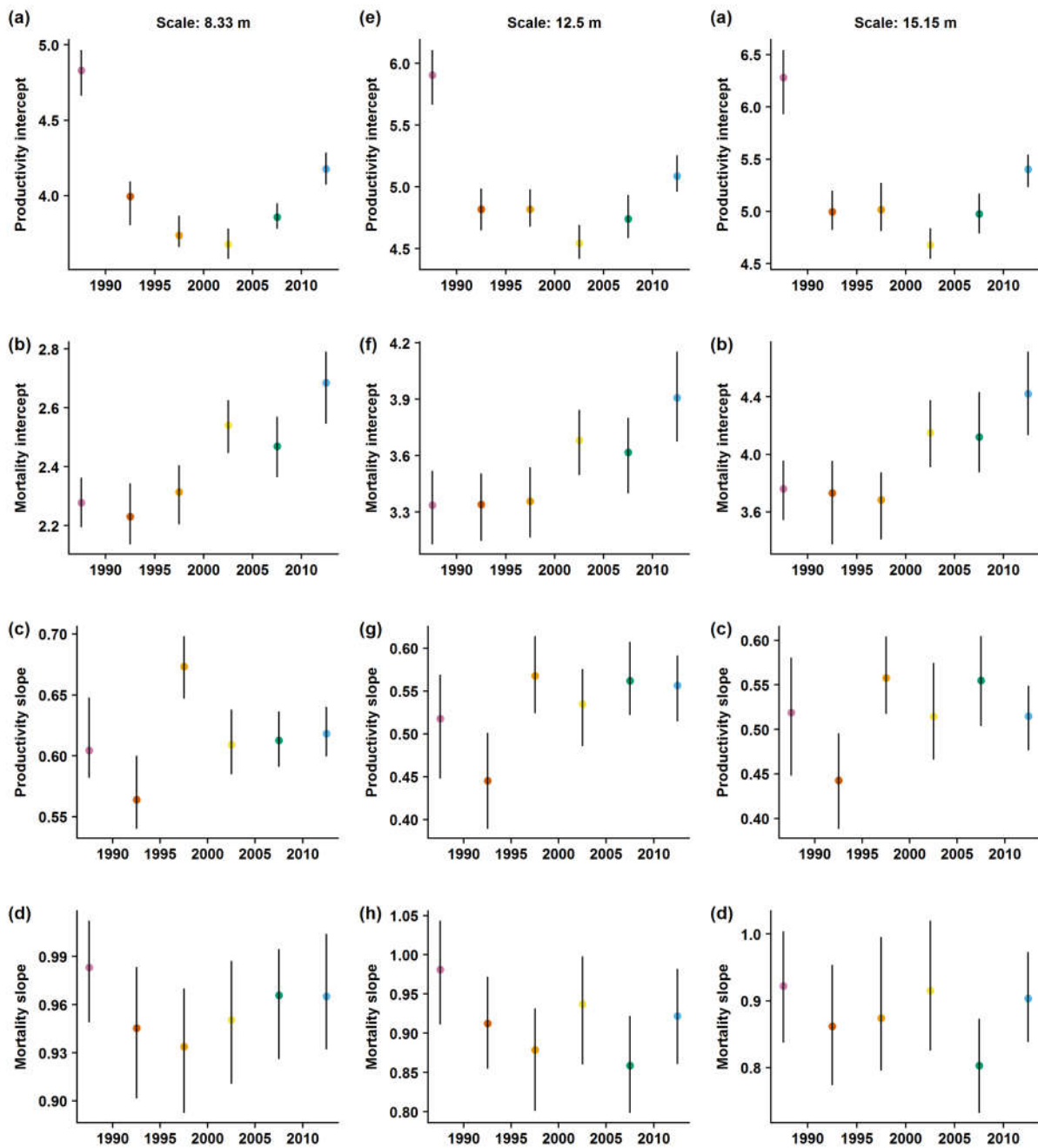


Figure S9 Intercept (a,b,e,f,i,j) and slope (c,d,g,h,k,l) of power function fits of quadrat-level productivity and mortality by census intervals, for quadrat sizes of 8.3, 12.5 and 15.15 m. The intercepts are normalized; they are the values at the midpoint EAGB value over all census intervals (125 Mg ha⁻¹). Points are placed at the mid-points of the census intervals Confidence intervals were computed from bootstrapping over quadrats.

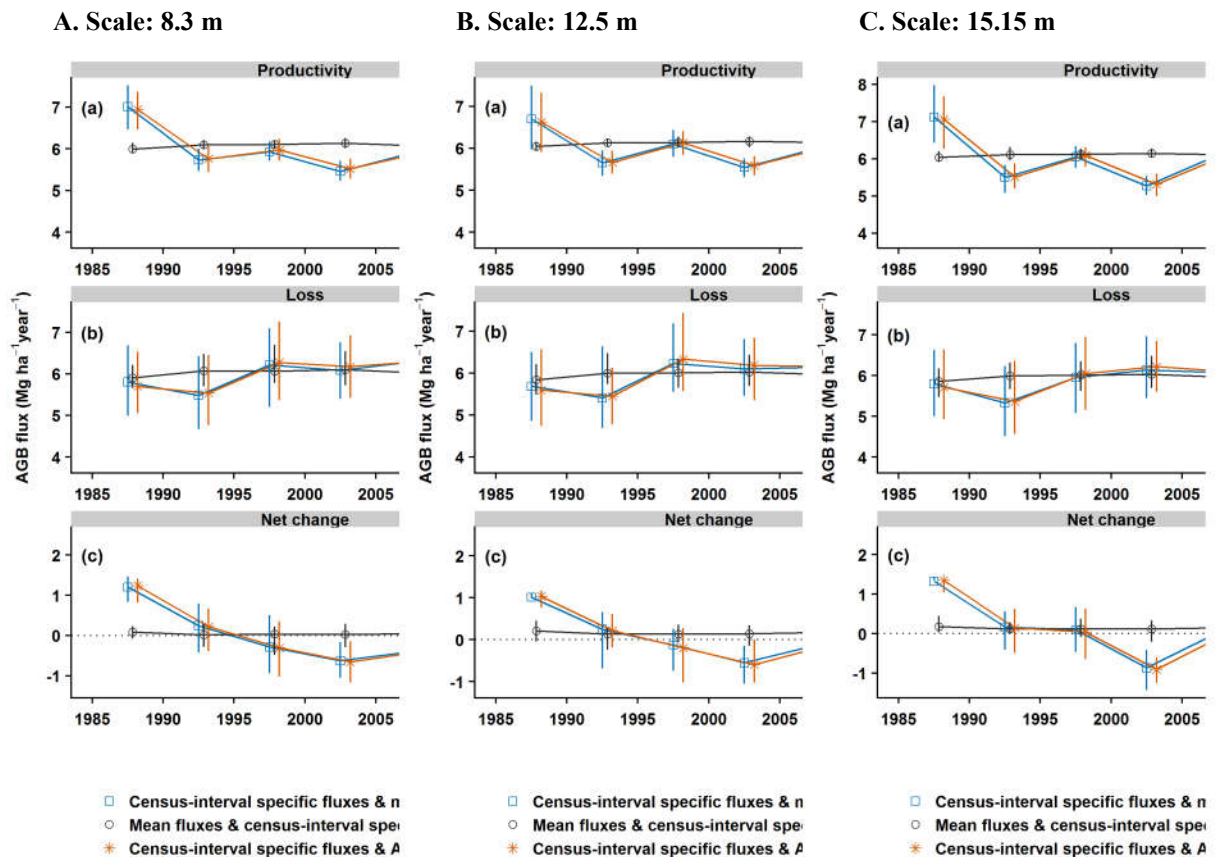


Figure S10 Comparison of qualitative patterns of hypothetical quadrat biomass fluxes across different quadrat sizes, for 8.93, 12.5 and 15.15-m square quadrats (A, B and C, respectively). Hypothetical fluxes were computed under three scenarios: census-interval fluxes and mean (i.e. across all census intervals) initial biomass (EAGBi) probability density functions (PDFs) (blue squares), mean fluxes and census-interval initial biomass PDFs (grey circles), and census-interval specific fluxes and initial biomass PDFs (red stars). Vertical lines show the 95% confidence intervals from bootstrapping over quadrats. The points are placed at the mid-points of the census intervals, and jiggered horizontally to increase readability. In all cases, missing diameter values (0.04%) were linearly interpolated, and EAGB calculations were based on equivalent diameters at 1.3 m estimated using a taper equation (see methods). In all cases, quadrats where a large strangler fig (DBH>50cm) occurred were excluded; these constituted less than 2.7% of quadrats. Note that difference in patterns are due to the substitution of extreme values (below 5th and above 95th percentiles of the overall EAGB distribution) in the hypothetical fluxes.

C1. Testing for the inclusion of 1.8 hectares of young forest at BCI

We tested for the robustness of our method and results in accounting for 1.8 hectare of ‘young forest’ regrowing from clear cutting about 120 years ago (Condit et al. 1996). We ran the same analysis and produce the same figures as presented in the manuscript and found no noticeable difference.

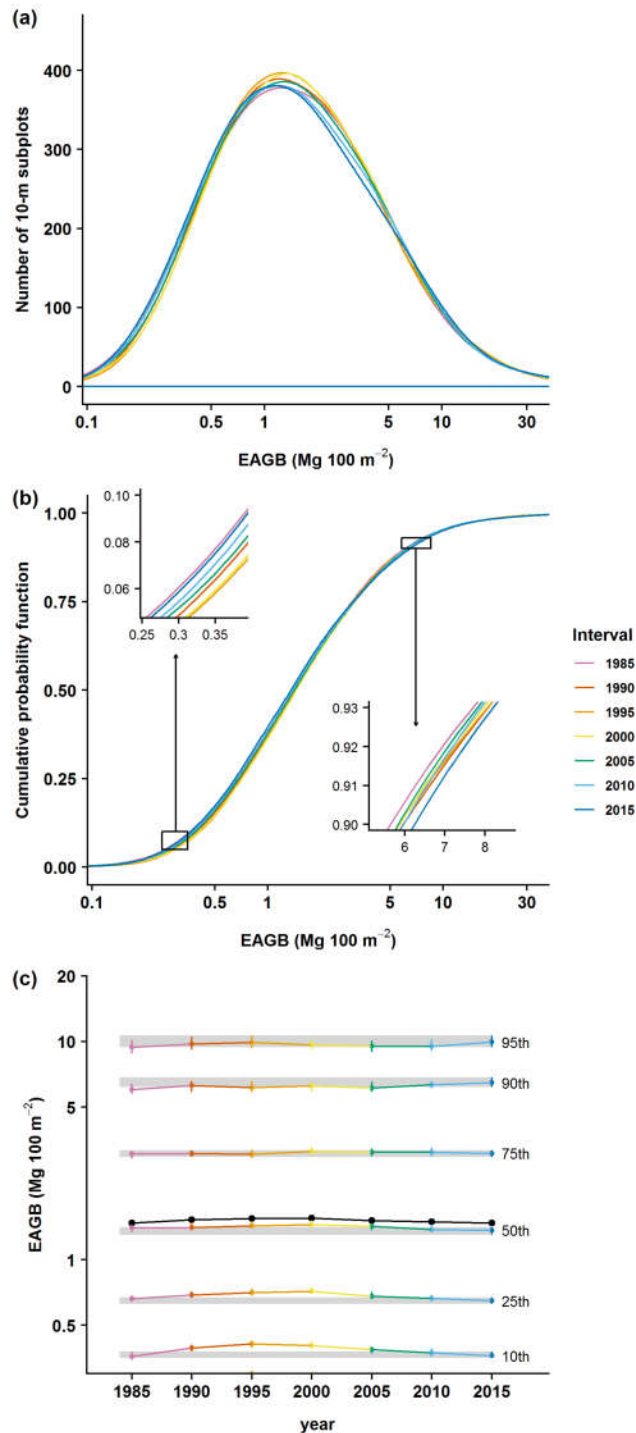


Figure S 11: Parallel figure to main text figure 6, except with secondary forest (1.8 ha) included. Probability density distribution (a) and cumulative probability distribution (b) of EAGB density across all 10 x 10 m quadrats, with insets in (b) magnified to show inter-census variation for cumulative probabilities of 0.05 to 0.1 and 0.9 to 0.95. (c) Variation over time in seven specific percentiles of the

EAGB distribution over quadrats (colored points and lines) and in the overall mean EAGB density at the 50-ha scale (black solid points and lines). In panel c, vertical lines show the 95% confidence intervals from bootstrapping over quadrats, and horizontal grey shading shows the confidence intervals for values in 2015 to enable easy visual assessment of how other years compare. The illustrated curves in panels a) and b) are truncated at the 0.2th and 99.8th percentiles of the distribution, but all values were included in analyses. Note that the EAGB densities can be converted to units of Mg ha⁻¹ by multiplying by 100.

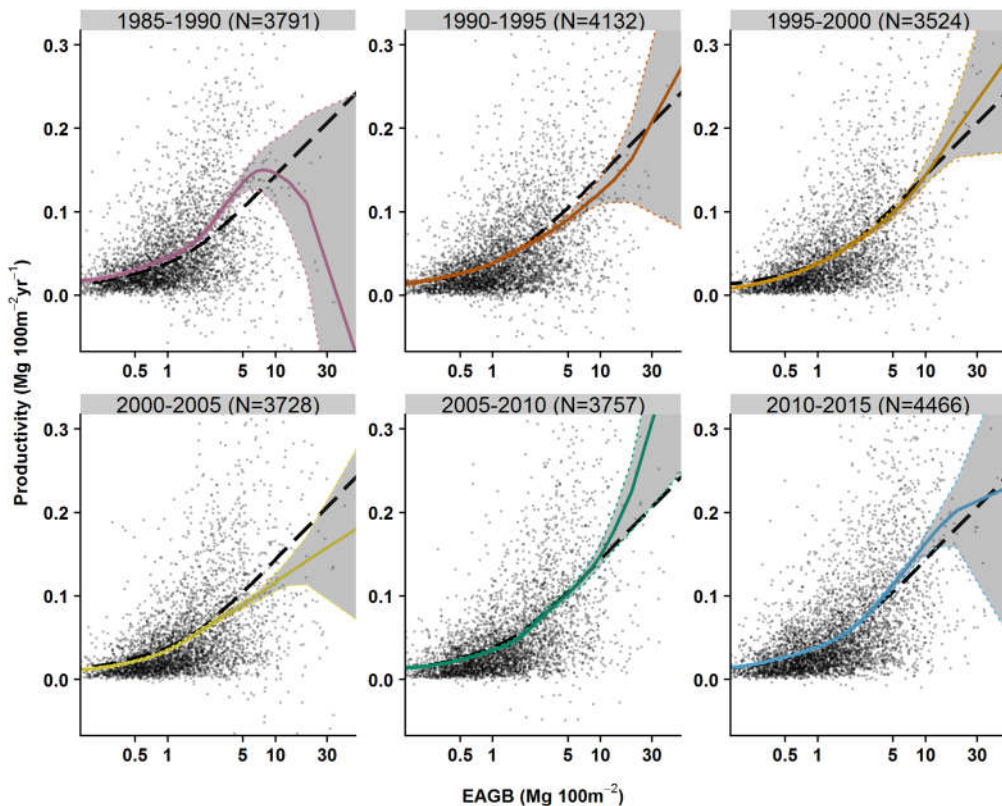


Figure S 12: Parallel figure to main text figure 3, except with secondary forest (1.8 ha) included. Quadrat-level mean annual EAGB productivity (Mg 100 m⁻² yr⁻¹) as a function of initial quadrat biomass (EAGB in Mg 100 m⁻²) for each 5-year census interval, for individual 10x10 m quadrats (points), together with local polynomial regression lines for individual census intervals (colored solid lines) and for all census intervals combined (black dashed lines). Confidence envelopes were computed from bootstrapping over quadrats. For each census interval, analyses excluded quadrats with problematic EAGB change measurements (see methods for details); N is the number of quadrats included for each census interval. The range of data shown here is truncated, but all points were included in the analyses. Note that EAGB stocks and fluxes can be converted to units of Mg ha⁻¹ by multiplying by 100.

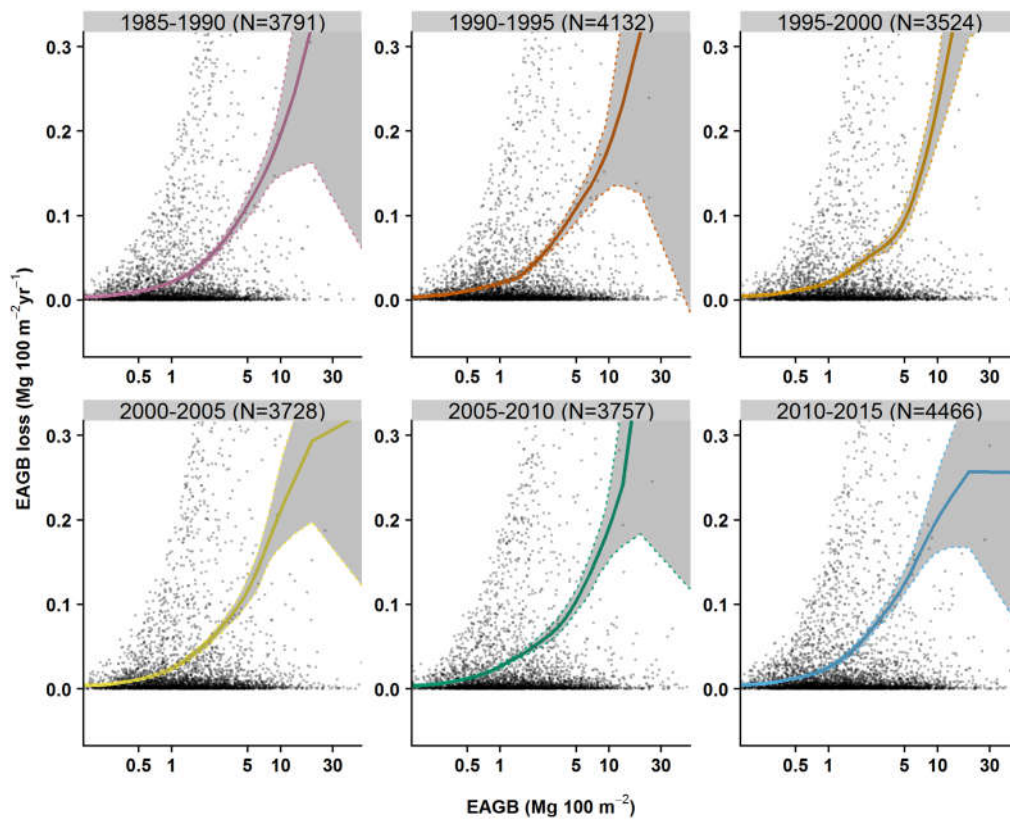


Figure S 13: Parallel figure to figure S3, except with secondary forest (1.8 ha) included. Quadrat-level annual EAGB mortality ($\text{Mg} \cdot 100 \text{m}^{-2} \cdot \text{yr}^{-1}$) as a function of initial quadrat biomass for each 5-year census interval, for 10x10 m quadrats (points) with local polynomial regression lines for individual census intervals (colored solid lines) and for all census intervals combined (black dashed lines). For each census interval, analyses excluded quadrats containing one or more trees that (a) are large strangler figs, (b) have a change in POM, or (c) have an obvious major measurement error during the census interval (see methods for details; N is the number of quadrats included for each census interval). Regression lines are shown only for the ranges of the 2nd to 98th percentile values of the respective datasets (avoiding the distribution extremes where uncertainty increases). The range of data shown here is truncated for illustration purposes, but all points (including those outside the graphed range) were included in analyses.

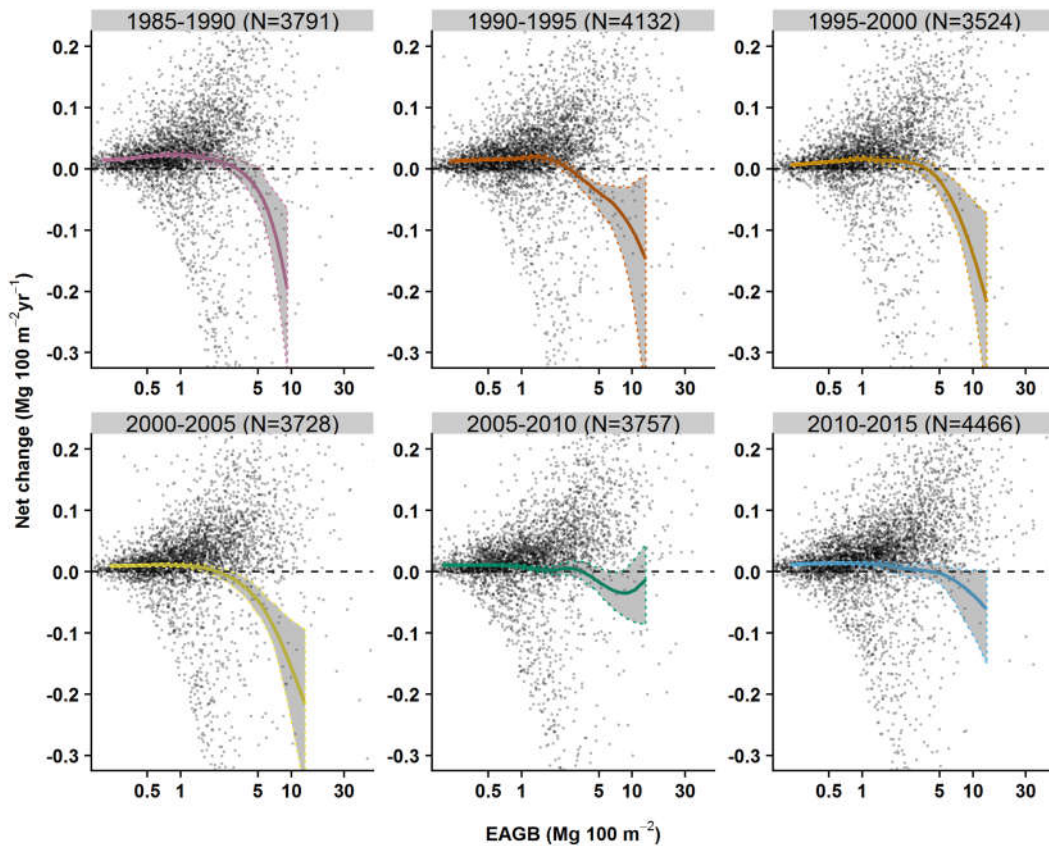


Figure S 14: Parallel figure to figure S4, except with secondary forest (1.8 ha) included. Quadrat-level annual EAGB net change ($\text{Mg}\cdot 100\text{m}^{-2}\cdot\text{yr}^{-1}$) as a function of initial quadrat biomass for each 5-year census interval, for 10x10 m quadrats (points) with local polynomial regression lines for individual census intervals (colored solid lines) and for all census intervals combined (black dashed lines). For each census interval, analyses excluded quadrats containing one or more trees that (a) are large strangler figs, (b) have a change in POM, or (c) have an obvious major measurement error during the census interval (see methods for details; N is the number of quadrats included for each census interval). Regression lines are shown only for the ranges of the 2nd to 98th percentile values of the respective datasets (avoiding the distribution extremes where uncertainty increases). The range of data shown here is truncated for illustration purposes.

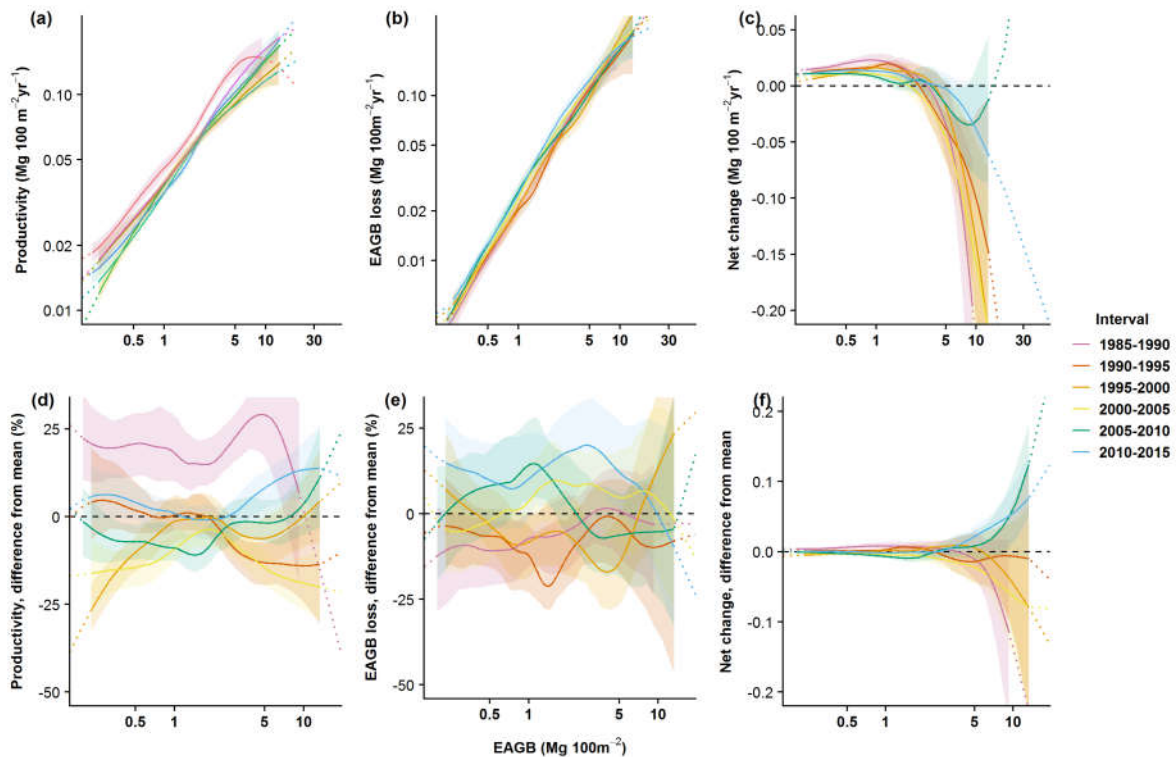


Figure S 15: Parallel figure to main text figure 4, except with secondary forest (1.8 ha) included. Variation among census intervals in quadrat EAGB productivity (a), loss (b) and net change (c) as a function of aboveground biomass (EAGB) at the initial census for 10x10 m quadrats, together with the corresponding differences from the mean (per initial EAGB) across all census intervals (d,e,f). Patterns were quantified using local polynomial regression; regression lines are displayed as solid lines for initial EAGB values spanning the 2nd to 98th percentiles of the respective census interval, and as dotted lines outside this range. Confidence envelopes were computed by bootstrapping over quadrats, and are shown for the 2nd to 98th percentiles of initial EAGB using shading. Analyses excluded quadrats with problematic EAGB change measurements (see methods for details). Note that productivity (a) and loss (b) are shown on log scales, and their differences from the mean are expressed in percentages (d,e) whereas the net change (c) and its difference from the mean (f) are shown on linear scales. Note that EAGB stocks and fluxes can be converted to units of Mg ha⁻¹ by multiplying by 100.

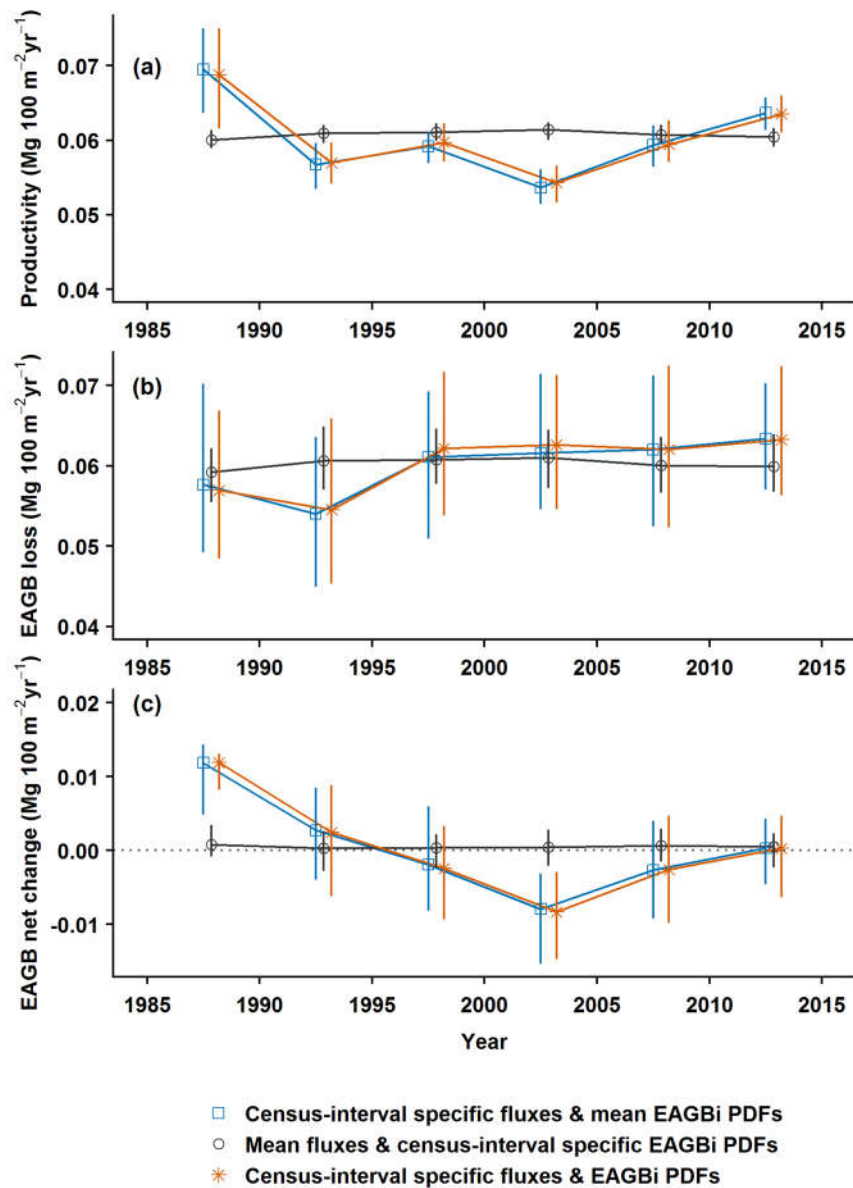


Figure S 16: Parallel figure to main text figure 7, except with secondary forest (1.8 ha) included. Time series of hypothetical whole-plot productivity (a), loss (b), and net change (c) expected with and without variation among census intervals in functions specifying how estimated above-ground biomass (EAGB) fluxes vary with initial biomass, and with and without variation among census intervals in initial EAGB distributions (EAGBi). See methods for details. Vertical lines show 95% confidence intervals obtained by bootstrapping over quadrats. The points are placed at the mid-points of the census intervals, and jiggered horizontally to increase readability. Values are given in Table S3. Note that EAGB stocks and fluxes can be converted to units of Mg ha^{-1} by multiplying by 100.

D. Empirical fluxes under different correction methods

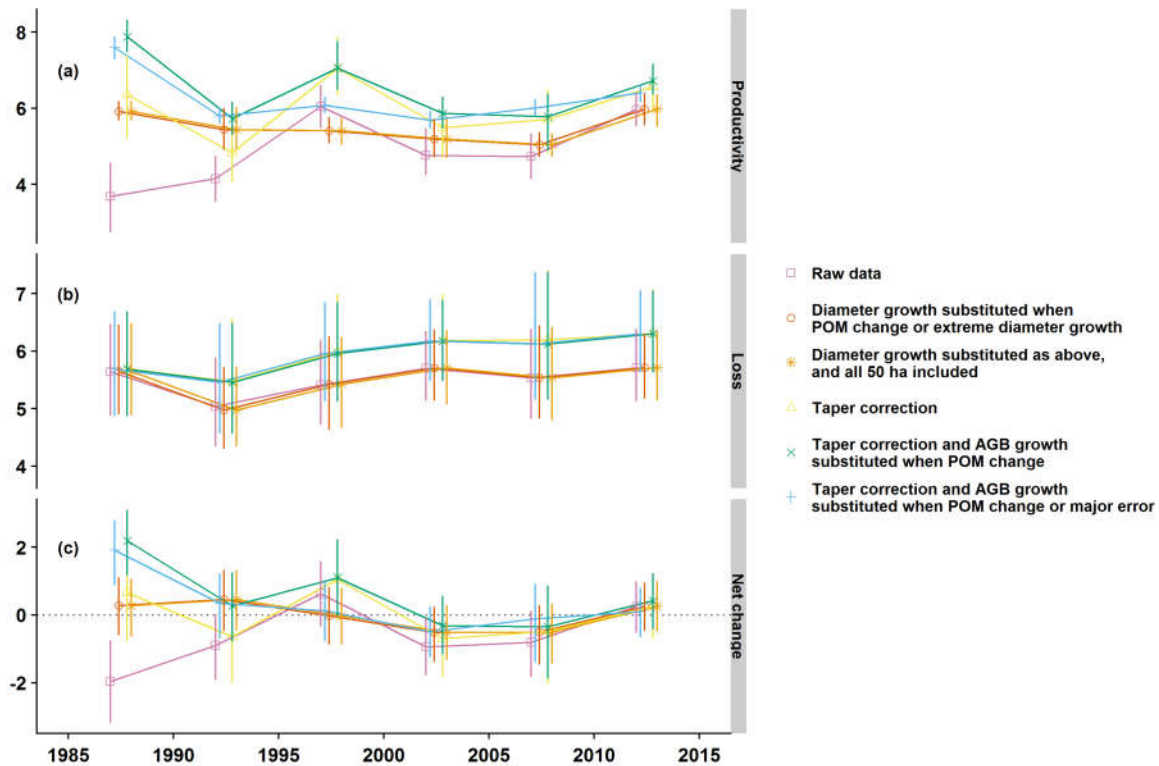


Figure S17 Estimated plot-level EAGB fluxes in woody productivity (a), loss (mortality) (b), and net change (c) for each census interval, calculated under alternative data correction procedures. (i) Original DBH data without any corrections (yellow squares). (ii) All trees that ever reached $\text{DBH} \geq 70$ cm and ever exhibited extreme diameter growth (increase > 45 mm/yr or decrease of more than 5 mm/yr) without a change in the point of measurement ($N=80$) were checked individually and corrected by linear interpolation/extrapolation between censuses, and all other individual census interval DBH records showing extreme diameter growth or with POM change were substituted with mean diameter growth for the same size classes following the methods of Chave et al. 2008 (diameter class limits were 10, 15, 20, 25, 30, 40, 50, 100, 200, 300, 400, 500, 600, 700, and 10,000 mm) (purple circles). (iii) As under the previous scenario, except all 50 ha were included for comparison with other studies, whereas all other scenarios shown here include data only for the 48.8 ha excluding the swamp (blue stars). (iv) DBHs were taper corrected and no other corrections were done (red stars). (v) DBHs were taper corrected and DBH records involving a POM change were substituted based on mean EAGB growth in the same diameter class (taper-corrected diameter class limits were 10, 50, 100, 200, 400, and 600 mm) (green triangles). (vi) DBHs were taper corrected and DBH records involving a POM change or highly suspicious and highly influential measurement error (i.e. productivity $> 20\%$ of mean productivity for 1 ha) were substituted based on mean EAGB growth in the same EAGB class, as in the previous scenario (black crosses). Vertical lines show the 95% confidence intervals from bootstrapping over quadrats. The points are placed at the mid-points of the census intervals, and jiggered horizontally to increase readability. In all cases, missing diameter values (0.04%) were linearly interpolated. In all cases except (iii), quadrats where a large strangler fig ($\text{DBH} \geq 50\text{cm}$) occurred were excluded; these constituted less than 2.7% of quadrats. Except in the case of the diameter series of large trees under (ii) and (iii), substitutions were done independently for each census interval, always affected the final diameter of the census interval, and did not carry over to the following census interval (e.g., a tree that had a change in point of measurement between 1990 and 1995 would have its 1995 diameter substituted for the 1990-1995 calculations, and its measured 1995

diameter used for 1995-2000 calculations). Size classes always included the upper bound (and for the smallest size class, also the lower bound). For cases (v) and (vi), we substituted size-class-specific mean EAGB growth rates for stems flagged for substitution. Mean EAGB growth rates were calculated for each census interval and diameter size class after excluding records with a change in measurement height or unrealistic diameter growth (Table S3), where unrealistic growth was defined as dbh growth > 75 mm/yr or second dbh measure more than 4 standard deviations in measurement error below the first (Rüger et al., 2011).

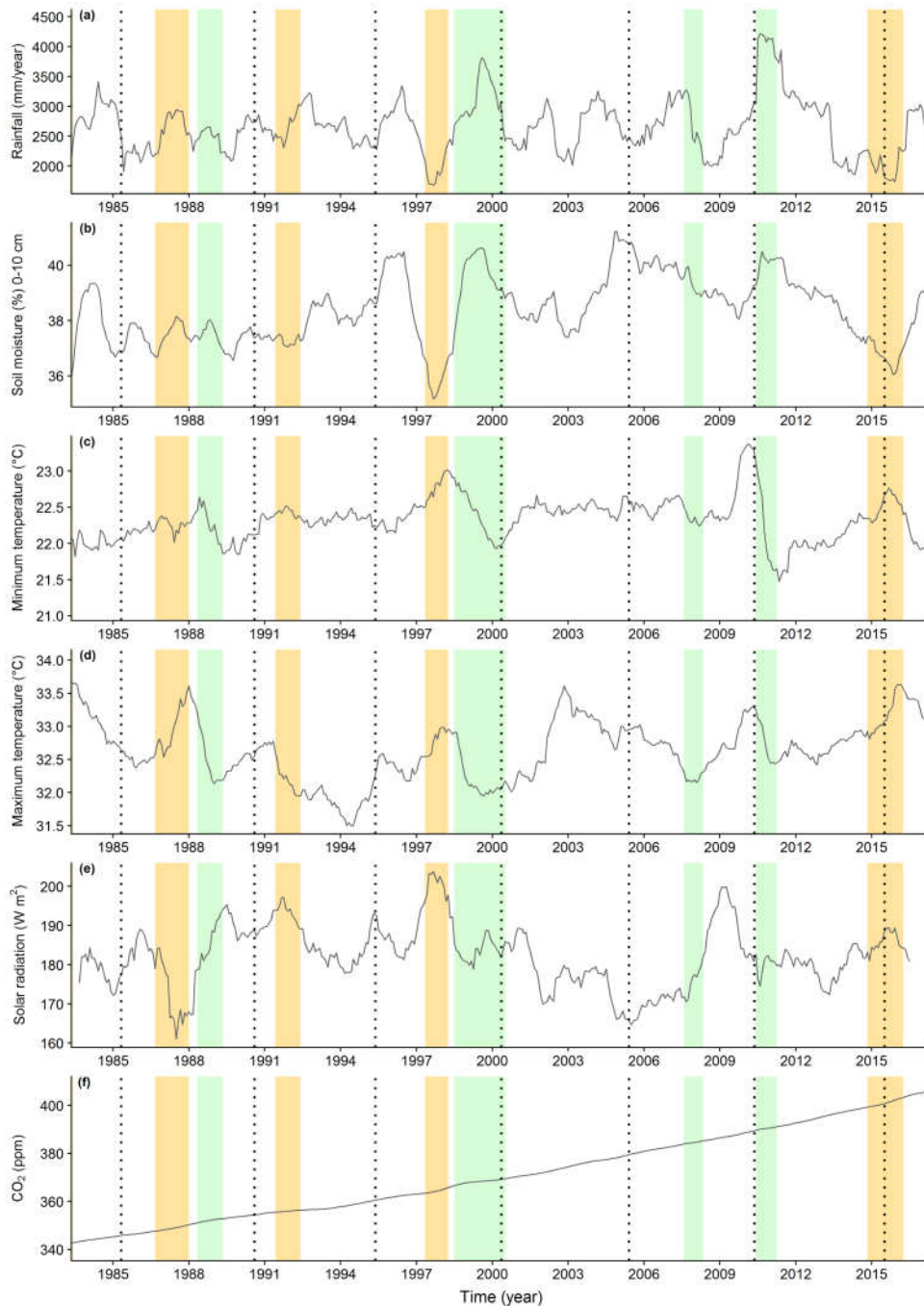


Figure S18 Temporal variation of potential drivers of biomass dynamics on BCI over the study period, including local climate drivers (a-e) and global atmospheric/climate drivers (f-g), as reflected in 12-month running sum (for a) and running means (for b to g) (grey lines). Vertical grey dashed lines indicate the mean date of each census of the 50 ha forest dynamics plot (the mean over trees of the measurement date for that census). Strong El Niño (orange) and La Niña (green) events are identified based on Oceanic Niño Index values >0.5 °C and less than -0.5 °C, respectively, for at least nine consecutive months. Local climate data were collected on Barro Colorado Island (see https://biogeodb.stri.si.edu/physical_monitoring/research/barrocolorado); Matteo Detto performed QAQC to identify errors and gap-fill missing and erroneous values of solar radiation using data from other nearby stations (Detto et al., 2018). Global mean annual atmospheric carbon dioxide (CO₂)

concentrations (ppm) were obtained from the NOAA ESRL (Earth Systems Research Laboratory) website <https://www.esrl.noaa.gov/gmd/ccgg/trends/full.html>.

Literature cited

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Wood densities arise from a local data base (Wright et al. 2010 and unpublished) and a global data base (Zanne et al. 2009). Level of assignment (level) was done first at species level using the local data base, or the global database if not present in the local data base. If the species was not present, wood density was averaged at genus level (merging both bases) or across all assigned species (stand-level) instead.

genus	species	family	WD (g/cm ³)	level	source
Abarema	barbouriana	Fabaceae	0.512	genus	genus average
Abarema	macradenia	Fabaceae	0.438	species	local data base
Abarema	idiopoda	Fabaceae	0.512	genus	genus average
Acacia	mangium	Fabaceae	0.507	species	global data base
Acalypha	diversifolia	Euphorbiaceae	0.300	genus	genus average
Acalypha	macrostachya	Euphorbiaceae	0.300	genus	genus average
Acanthocereus	tetragonus	Cactaceae	0.592	stand-level average	
Acidoton	nicaraguensis	Euphorbiaceae	0.592	stand-level average	
Acrocomia	aculeata	Arecaceae	0.592	stand-level average	
Adelia	triloba	Euphorbiaceae	0.574	species	local data base
Adenaria	floribunda	Lythraceae	0.592	stand-level average	
Aegiphila	anomala	Lamiaceae	0.657	genus	genus average
Aegiphila	panamensis	Lamiaceae	0.657	genus	genus average
Agonandra	brasiliensis	Opiliaceae	0.818	species	global data base
Agouticarpa	curviflora	Rubiaceae	0.592	stand-level average	
Agouticarpa	williamsii	Rubiaceae	0.592	stand-level average	
Aiouea	vexatrix	Lauraceae	0.370	genus	genus average
Aiphanes	hirsuta	Arecaceae	0.592	stand-level average	
Albizia	adinocephala	Fabaceae	0.556	genus	genus average
Albizia	niopoides	Fabaceae	0.555	species	global data base
Albizia	procera	Fabaceae	0.573	species	local data base
Alchornea	costaricensis	Euphorbiaceae	0.301	species	local data base
Alchornea	grandis	Euphorbiaceae	0.340	species	global data base
Alchornea	latifolia	Euphorbiaceae	0.425	species	local data base
Alibertia	edulis	Rubiaceae	0.760	species	local data base
Alibertia	dwyeri	Rubiaceae	0.733	genus	genus average
Allenanthus	erythrocarpus	Rubiaceae	0.592	stand-level average	
Allophylus	gentryi	Sapindaceae	0.518	genus	genus average
Allophylus	psilospermus	Sapindaceae	0.518	genus	genus average
Allophylus	racemosus	Sapindaceae	0.518	genus	genus average
Alseis	blackiana	Rubiaceae	0.536	species	local data base
Amaioua	corymbosa	Rubiaceae	0.625	genus	genus average
Amaioua	magnicarpa	Rubiaceae	0.625	genus	genus average
Amaioua	pedicellata	Rubiaceae	0.625	genus	genus average
Amanoa	guianensis	Phyllanthaceae	0.843	species	global data base
Ampelocera	edentula	Ulmaceae	0.700	species	local data base
Ampelocera	macphersonii	Ulmaceae	0.726	genus	genus average
Amphitecna	latifolia	Bignoniaceae	0.460	genus	genus average

genus	species	family	WD (g/cm ³)	level	source
Amphitecna	spathicalyx	Bignoniaceae	0.460	genus	genus average
Amphitecna	isthmica	Bignoniaceae	0.460	genus	genus average
Anacardium	excelsum	Anacardiaceae	0.391	species	local data base
Anacardium	occidentale	Anacardiaceae	0.447	species	global data base
Anaxagorea	allenii	Annonaceae	0.530	genus	genus average
Anaxagorea	panamensis	Annonaceae	0.530	genus	genus average
Anaxagorea	crassipetala	Annonaceae	0.480	species	global data base
Andira	inermis	Fabaceae	0.643	species	local data base
Aniba	hostmanniana	Lauraceae	0.619	species	local data base
Annona	acuminata	Annonaceae	0.524	genus	genus average
Annona	cherimola	Annonaceae	0.524	genus	genus average
Annona	glabra	Annonaceae	0.500	species	global data base
Annona	hayesii	Annonaceae	0.524	genus	genus average
Annona	montana	Annonaceae	0.524	genus	genus average
Annona	muricata	Annonaceae	0.360	species	global data base
Annona	pittieri	Annonaceae	0.524	genus	genus average
Annona	purpurea	Annonaceae	0.570	species	local data base
Annona	reticulata	Annonaceae	0.550	species	global data base
Annona	spraguei	Annonaceae	0.559	species	local data base
Annona	mucosa	Annonaceae	0.524	genus	genus average
Annona	papilionella	Annonaceae	0.524	genus	genus average
Apeiba	hybrid	Malvaceae	0.255	genus	genus average
Apeiba	tibourbou	Malvaceae	0.200	species	local data base
Apeiba	membranacea	Malvaceae	0.255	genus	genus average
Aphelandra	campanensis	Acanthaceae	0.592	stand-level average	
Aphelandra	gracilis	Acanthaceae	0.592	stand-level average	
Aphelandra	scabra	Acanthaceae	0.592	stand-level average	
Aphelandra	sinclairiana	Acanthaceae	0.592	stand-level average	
Appunia	seibertii	Rubiaceae	0.592	stand-level average	
Arachnothryx	buddleioides	Rubiaceae	0.560	species	global data base
Ardisia	bartlettii	Primulaceae	0.591	genus	genus average
Ardisia	dukei	Primulaceae	0.591	genus	genus average
Ardisia	glomerata	Primulaceae	0.591	genus	genus average
Ardisia	guianensis	Primulaceae	0.620	species	local data base
Ardisia	opegrapha	Primulaceae	0.591	genus	genus average
Ardisia	revoluta	Primulaceae	0.591	genus	genus average
Ardisia	solanacea	Primulaceae	0.620	species	global data base
Ardisia	standleyana	Primulaceae	0.591	genus	genus average
Ardisia	compressa	Primulaceae	0.591	genus	genus average
Artocarpus	altilis	Moraceae	0.431	species	local data base
Aspidosperma	desmanthum	Apocynaceae	0.610	species	global data base
Aspidosperma	excelsum	Apocynaceae	0.792	species	global data base
Astrocaryum	alatum	Arecaceae	0.508	genus	genus average
Astrocaryum	standleyanum	Arecaceae	0.508	genus	genus average

genus	species	family	WD (g/cm ³)	level	source
Astronium	graveolens	Anacardiaceae	0.868	species	local data base
Attalea	rostrata	Arecaceae	0.326	genus	genus average
Avicennia	bicolor	Acanthaceae	0.685	genus	genus average
Avicennia	germinans	Acanthaceae	0.776	species	global data base
Bactris	barronis	Arecaceae	0.592	stand-level average	
Bactris	coloniata	Arecaceae	0.592	stand-level average	
Bactris	coloradonis	Arecaceae	0.592	stand-level average	
Bactris	gasipaes	Arecaceae	0.592	stand-level average	
Bactris	major	Arecaceae	0.592	stand-level average	
Bactris	maraja	Arecaceae	0.592	stand-level average	
Bactris	panamensis	Arecaceae	0.592	stand-level average	
Banara	guianensis	Salicaceae	0.610	species	local data base
Bauhinia	ungulata	Fabaceae	0.755	genus	genus average
Beilschmiedia	sulcata	Lauraceae	0.563	genus	genus average
Beilschmiedia	aff.tilaranensis	Lauraceae	0.563	genus	genus average
Beilschmiedia	tovarensis	Lauraceae	0.563	genus	genus average
Bellucia	pentamera	Melastomataceae	0.485	species	local data base
Bertiera	guianensis	Rubiaceae	0.592	stand-level average	
Besleria	formicaria	Gesneriaceae	0.592	stand-level average	
Besleria	robusta	Gesneriaceae	0.592	stand-level average	
Billia	rosea	Sapindaceae	0.690	genus	genus average
Bixa	orellana	Bixaceae	0.360	species	global data base
Blighia	sapida	Sapindaceae	0.762	species	global data base
Bocconia	frutescens	Papaveraceae	0.592	stand-level average	
Bonellia	macrocarpa	Primulaceae	0.592	stand-level average	
Bourreria	costaricensis	Boraginaceae	0.730	genus	genus average
Brosimum	alicastrum	Moraceae	0.600	species	local data base
Brosimum	costaricanum	Moraceae	0.665	species	local data base
Brosimum	guianense	Moraceae	0.844	species	local data base
Brosimum	lactescens	Moraceae	0.656	species	local data base
Brosimum	rubescens	Moraceae	0.825	species	global data base
Brosimum	utile	Moraceae	0.506	species	local data base
Brownea	macrophylla	Fabaceae	1.210	genus	genus average
Buchenavia	tetraphylla	Combretaceae	0.617	species	global data base
Bunchosia	dwyeri	Malpighiaceae	0.695	genus	genus average
Bunchosia	macrophylla	Malpighiaceae	0.695	genus	genus average
Bunchosia	nitida	Malpighiaceae	0.695	genus	genus average
Bunchosia	odorata	Malpighiaceae	0.695	genus	genus average
Bursera	simaruba	Burseraceae	0.305	species	local data base
Bursera	tomentosa	Burseraceae	0.311	genus	genus average
Byrsonima	crassifolia	Malpighiaceae	0.586	species	local data base
Byrsonima	crispa	Malpighiaceae	0.580	species	local data base
Byrsonima	dressleri	Malpighiaceae	0.649	genus	genus average
Byrsonima	spicata	Malpighiaceae	0.614	species	local data base

genus	species	family	WD (g/cm ³)	level	source
Calatola	costaricensis	Icacinaceae	0.566	species	local data base
Calliandra	laxa	Fabaceae	0.816	genus	genus average
Calliandra	aff.grandifolia	Fabaceae	0.816	genus	genus average
Callicarpa	acuminata	Lamiaceae	0.350	genus	genus average
Calophyllum	brasiliense	Calophyllaceae	0.589	species	local data base
Calophyllum	inophyllum	Calophyllaceae	0.585	species	global data base
Calophyllum	longifolium	Calophyllaceae	0.542	species	local data base
Calycolpus	warszewiczianus	Myrtaceae	0.800	genus	genus average
Calycophyllum	candidissimum	Rubiaceae	0.702	species	local data base
Calypttranthes	chytraculia	Myrtaceae	0.783	genus	genus average
Calypttranthes	pulchella	Myrtaceae	0.783	genus	genus average
Calypttranthes	tumidonodia	Myrtaceae	0.783	genus	genus average
Calyptrogyne	costatifrons	Arecaceae	0.592	stand-level average	
Camposperma	panamense	Anacardiaceae	0.376	genus	genus average
Capparidastrum	frondosum	Capparaceae	0.592	stand-level average	
Capparidastrum	discolor	Capparaceae	0.592	stand-level average	
Capparidastrum	aff.osmanthum	Capparaceae	0.592	stand-level average	
Carapa	guianensis	Meliaceae	0.530	species	local data base
Carica	papaya	Caricaceae	0.188	genus	genus average
Caryodaphnopsis	burgeri	Lauraceae	0.592	stand-level average	
Caryodaphnopsis	tomentosa	Lauraceae	0.592	stand-level average	
Casearia	aculeata	Salicaceae	0.660	species	local data base
Casearia	arguta	Salicaceae	0.517	species	local data base
Casearia	commersoniana	Salicaceae	0.621	genus	genus average
Casearia	coronata	Salicaceae	0.621	genus	genus average
Casearia	corymbosa	Salicaceae	0.621	genus	genus average
Casearia	guianensis	Salicaceae	0.742	species	local data base
Casearia	nigricans	Salicaceae	0.621	genus	genus average
Casearia	sylvestris	Salicaceae	0.705	species	local data base
Casearia	arborea	Salicaceae	0.574	species	local data base
Cassia	grandis	Fabaceae	0.736	genus	genus average
Cassia	moschata	Fabaceae	0.805	species	local data base
Cassipourea	enana	Rhizophoraceae	0.650	genus	genus average
Cassipourea	hoja_grande	Rhizophoraceae	0.650	genus	genus average
Cassipourea	elliptica	Rhizophoraceae	0.650	genus	genus average
Castilla	elastica	Moraceae	0.524	species	local data base
Cavanillesia	platanifolia	Malvaceae	0.360	species	local data base
Cecropia	garciae	Urticaceae	0.340	genus	genus average
Cecropia	heterochroma	Urticaceae	0.340	genus	genus average
Cecropia	insignis	Urticaceae	0.318	species	local data base
Cecropia	longipes	Urticaceae	0.340	genus	genus average
Cecropia	obtusifolia	Urticaceae	0.307	species	local data base
Cecropia	peltata	Urticaceae	0.300	species	local data base
Cecropia	hispidissima	Urticaceae	0.340	genus	genus average

genus	species	family	WD (g/cm ³)	level	source
Cedrela	fissilis	Meliaceae	0.467	species	global data base
Cedrela	odorata	Meliaceae	0.447	species	local data base
Ceiba	pentandra	Malvaceae	0.305	species	local data base
Celtis	schippii	Cannabaceae	0.616	species	local data base
Centropogon	tortilis	Campanulaceae	0.592	stand-level average	
Cespedesia	spathulata	Ochnaceae	0.613	species	local data base
Cestrum	latifolium	Solanaceae	0.592	stand-level average	
Cestrum	racemosum	Solanaceae	0.592	stand-level average	
Cestrum	schlechtendahlii	Solanaceae	0.592	stand-level average	
Chamaedorea	pinnatifrons	Arecaceae	0.592	stand-level average	
Chamaedorea	tepejilote	Arecaceae	0.592	stand-level average	
Chamguava	schippii	Myrtaceae	0.592	stand-level average	
Cheiloclinium	cognatum	Celastraceae	0.592	stand-level average	
Chimarrhis	parviflora	Rubiaceae	0.707	genus	genus average
Chimarrhis	latifolia	Rubiaceae	0.707	genus	genus average
Chionanthus	panamensis	Oleaceae	0.680	genus	genus average
Chloroleucon	mangense	Fabaceae	0.990	species	global data base
Chomelia	spinosa	Rubiaceae	0.530	species	local data base
Chromolucuma	aff.rubriflora	Sapotaceae	0.730	genus	genus average
Chrysobalanus	icaco	Chrysobalanaceae	0.753	species	global data base
Chrysochlamys	eclipes	Clusiaceae	0.430	genus	genus average
Chrysochlamys	glauca	Clusiaceae	0.430	genus	genus average
Chrysochlamys	grandifolia	Clusiaceae	0.430	genus	genus average
Chrysophyllum	brenesii	Sapotaceae	0.665	genus	genus average
Chrysophyllum	cainito	Sapotaceae	0.655	species	local data base
Chrysophyllum	colombianum	Sapotaceae	0.665	genus	genus average
Chrysophyllum	hirsutum	Sapotaceae	0.665	genus	genus average
Chrysophyllum	venezuelanense	Sapotaceae	0.665	genus	genus average
Chrysophyllum	argenteum	Sapotaceae	0.777	species	local data base
Cinnamomum	triplinerve	Lauraceae	0.467	genus	genus average
Cinnamomum	tonduzii	Lauraceae	0.467	genus	genus average
Citharexylum	caudatum	Verbenaceae	0.667	genus	genus average
Citrus	sinensis	Rutaceae	0.780	species	local data base
Clarisia	biflora	Moraceae	0.498	species	local data base
Clarisia	racemosa	Moraceae	0.585	species	local data base
Clavija	biborrana	Primulaceae	0.592	stand-level average	
Clavija	costaricana	Primulaceae	0.592	stand-level average	
Clavija	mezii	Primulaceae	0.592	stand-level average	
Clethra	mexicana	Clethraceae	0.550	species	global data base
Clidemia	crenulata	Melastomataceae	0.592	stand-level average	
Clidemia	densiflora	Melastomataceae	0.592	stand-level average	
Clidemia	dentata	Melastomataceae	0.592	stand-level average	
Clidemia	hammelii	Melastomataceae	0.592	stand-level average	
Clidemia	octona	Melastomataceae	0.592	stand-level average	

genus	species	family	WD (g/cm ³)	level	source
Clidemia	septuplinervia	Melastomataceae	0.592	stand-level average	
Clidemia	discolor	Melastomataceae	0.592	stand-level average	
Clitoria	glaberrima	Fabaceae	0.592	stand-level average	
Clusia	cretosa	Clusiaceae	0.676	genus	genus average
Clusia	divaricata	Clusiaceae	0.676	genus	genus average
Clusia	pratensis	Clusiaceae	0.676	genus	genus average
Clusia	rosea	Clusiaceae	0.605	species	global data base
Clusia	stenophylla	Clusiaceae	0.676	genus	genus average
Cnidioscolus	urens	Euphorbiaceae	0.427	genus	genus average
Coccoloba	acuminata	Polygonaceae	0.580	species	global data base
Coccoloba	ascendens	Polygonaceae	0.687	genus	genus average
Coccoloba	caracasana	Polygonaceae	0.430	species	global data base
Coccoloba	coronata	Polygonaceae	0.687	genus	genus average
Coccoloba	johnstonii	Polygonaceae	0.687	genus	genus average
Coccoloba	lasseri	Polygonaceae	0.687	genus	genus average
Coccoloba	manzinellensis	Polygonaceae	0.687	genus	genus average
Coccoloba	mollis	Polygonaceae	0.675	species	local data base
Coccoloba	padiformis	Polygonaceae	0.800	species	local data base
Coccoloba	tuerckheimii	Polygonaceae	0.687	genus	genus average
Coccoloba	uvifera	Polygonaceae	0.700	species	global data base
Coccoloba	obovata	Polygonaceae	0.687	genus	genus average
Cochlospermum	vitifolium	Bixaceae	0.218	species	global data base
Cocos	nucifera	Arecaceae	0.592	stand-level average	
Coffea	arabica	Rubiaceae	0.620	species	global data base
Cojoba	hoja_grande	Fabaceae	0.592	stand-level average	
Cojoba	rufescens	Fabaceae	0.592	stand-level average	
Colpothrinax	aphanopetala	Arecaceae	0.592	stand-level average	
Colubrina	glandulosa	Rhamnaceae	0.739	species	local data base
Colubrina	heteroneura	Rhamnaceae	0.970	species	local data base
Colubrina	spinosa	Rhamnaceae	0.495	species	global data base
Compsoeura	rigidifolia	Myristicaceae	0.592	stand-level average	
Compsoeura	mexicana	Myristicaceae	0.592	stand-level average	
Conceveiba	pleiostemona	Euphorbiaceae	0.266	species	local data base
Conchocarpus	nicaraguensis	Rutaceae	0.592	stand-level average	
Condaminea	corymbosa	Rubiaceae	0.592	stand-level average	
Conocarpus	erectus	Combretaceae	0.845	species	global data base
Conostegia	bracteata	Melastomataceae	0.592	stand-level average	
Conostegia	cinnamomea	Melastomataceae	0.592	stand-level average	
Conostegia	cuatrecasii	Melastomataceae	0.592	stand-level average	
Conostegia	rufescens	Melastomataceae	0.592	stand-level average	
Conostegia	speciosa	Melastomataceae	0.592	stand-level average	
Conostegia	xalapensis	Melastomataceae	0.592	stand-level average	
Conostegia	montana	Melastomataceae	0.592	stand-level average	
Copaifera	aromatica	Fabaceae	0.620	species	local data base

genus	species	family	WD (g/cm ³)	level	source
Cordia	alliodora	Boraginaceae	0.520	species	local data base
Cordia	bicolor	Boraginaceae	0.475	species	local data base
Cordia	collococca	Boraginaceae	0.420	species	global data base
Cordia	cymosa	Boraginaceae	0.538	genus	genus average
Cordia	dentata	Boraginaceae	0.500	species	global data base
Cordia	eristigma	Boraginaceae	0.538	genus	genus average
Cordia	lasiocalyx	Boraginaceae	0.397	species	local data base
Cordia	lucidula	Boraginaceae	0.538	genus	genus average
Cordia	megalantha	Boraginaceae	0.390	species	global data base
Cordia	panamensis	Boraginaceae	0.330	species	local data base
Cordia	porcata	Boraginaceae	0.538	genus	genus average
Cordia	dwyeri	Boraginaceae	0.538	genus	genus average
Cordia	correae	Boraginaceae	0.538	genus	genus average
Cordia	garapatica	Rubiaceae	0.592	stand-level average	
Cornutia	pyramidata	Lamiaceae	0.600	genus	genus average
Cosmibuena	macrocarpa	Rubiaceae	0.592	stand-level average	
Couepia	chocolate	Chrysobalanaceae	0.798	genus	genus average
Couratari	guianensis	Lecythidaceae	0.507	species	local data base
Coussarea	cerroazulensis	Rubiaceae	0.618	genus	genus average
Coussarea	curvigemma	Rubiaceae	0.618	genus	genus average
Coussarea	latifolia	Rubiaceae	0.618	genus	genus average
Coussarea	loftonii	Rubiaceae	0.618	genus	genus average
Coutarea	hexandra	Rubiaceae	0.600	species	local data base
Crateva	tapia	Capparaceae	0.519	species	local data base
Cre mastosperma	panamense	Annonaceae	0.592	stand-level average	
Crescentia	cujete	Bignoniaceae	0.634	species	global data base
Crossopetalum	parviflorum	Celastraceae	0.592	stand-level average	
Croton	billbergianus	Euphorbiaceae	0.510	genus	genus average
Croton	draco	Euphorbiaceae	0.510	genus	genus average
Croton	pachypodus	Euphorbiaceae	0.510	genus	genus average
Croton	schiedeanus	Euphorbiaceae	0.510	genus	genus average
Croton	smithianus	Euphorbiaceae	0.510	genus	genus average
Croton	matourensis	Euphorbiaceae	0.388	species	global data base
Crudia	acuminata	Fabaceae	0.777	genus	genus average
Cryosophila	warscewiczii	Arecaceae	0.400	species	local data base
Cryptocarya	panamensis	Lauraceae	0.561	genus	genus average
Cupania	cinerea	Sapindaceae	0.500	species	local data base
Cupania	guatemalensis	Sapindaceae	0.688	species	local data base
Cupania	latifolia	Sapindaceae	0.618	genus	genus average
Cupania	rufescens	Sapindaceae	0.618	genus	genus average
Cupania	scrobiculata	Sapindaceae	0.628	species	local data base
Cupania	seemannii	Sapindaceae	0.618	genus	genus average
Curatella	americana	Dilleniaceae	0.650	species	global data base
Cyathea	multiflora	Cyatheaceae	0.592	stand-level average	

genus	species	family	WD (g/cm ³)	level	source
Cyathea	petiolata	Cyatheaceae	0.592	stand-level average	
Cybianthus	schlimii	Primulaceae	0.593	genus	genus average
Cymbopetalum	lanugipetalum	Annonaceae	0.552	genus	genus average
Cymbopetalum	costaricense	Annonaceae	0.552	genus	genus average
Cynometra	bauhiniifolia	Fabaceae	0.812	genus	genus average
Cynophalla	flexuosa	Capparaceae	0.592	stand-level average	
Cynophalla	verrucosa	Capparaceae	0.592	stand-level average	
Cyrilla	racemiflora	Cyrrillaceae	0.590	species	global data base
Dalbergia	retusa	Fabaceae	0.863	species	local data base
Damburneya	umbrosa	Lauraceae	0.592	stand-level average	
Damburneya	martinicensis	Lauraceae	0.592	stand-level average	
Daphnopsis	americana	Thymelaeaceae	0.520	genus	genus average
Daphnopsis	correae	Thymelaeaceae	0.520	genus	genus average
Delonix	regia	Fabaceae	0.579	species	global data base
Dendropanax	sessiliflorus	Araliaceae	0.420	genus	genus average
Dendropanax	arboreus	Araliaceae	0.420	species	local data base
Dendropanax	punctatus	Araliaceae	0.420	genus	genus average
Dendropanax	globosus	Araliaceae	0.420	genus	genus average
Desmopsis	maxonii	Annonaceae	0.764	genus	genus average
Desmopsis	panamensis	Annonaceae	0.764	species	local data base
Dialium	guianense	Fabaceae	0.896	species	local data base
Dichapetalum	axillare	Dichapetalaceae	0.761	genus	genus average
Dilodendron	costaricense	Sapindaceae	0.592	stand-level average	
Diospyros	artanthifolia	Ebenaceae	0.683	genus	genus average
Diphysa	americana	Fabaceae	1.080	genus	genus average
Diploporis	purpurea	Fabaceae	0.762	species	global data base
Dipteryx	oleifera	Fabaceae	0.848	species	local data base
Discophora	guianensis	Stemonuraceae	0.560	species	local data base
Drypetes	standleyi	Putranjivaceae	0.675	species	local data base
Drypetes	coba	Putranjivaceae	0.695	genus	genus average
Drypetes	aff.amazonica	Putranjivaceae	0.695	genus	genus average
Duguetia	confusa	Annonaceae	0.729	genus	genus average
Duguetia	panamensis	Annonaceae	0.729	genus	genus average
Dussia	atropurpurea	Fabaceae	0.553	genus	genus average
Dussia	macrophyllata	Fabaceae	0.563	species	local data base
Dussia	tessmannii	Fabaceae	0.553	genus	genus average
Dystovomita	paniculata	Clusiaceae	0.592	stand-level average	
Ecclinusa	lanceolata	Sapotaceae	0.580	species	local data base
Elaeagia	auriculata	Rubiaceae	0.592	stand-level average	
Elaeagia	nitidifolia	Rubiaceae	0.592	stand-level average	
Elaeis	oleifera	Arecaceae	0.592	stand-level average	
Endlicheria	browniana	Lauraceae	0.495	genus	genus average
Enterolobium	cyclocarpum	Fabaceae	0.391	species	local data base
Enterolobium	schomburgkii	Fabaceae	0.699	species	local data base

genus	species	family	WD (g/cm ³)	level	source
Erblichia	odorata	Passifloraceae	0.592	stand-level average	
Erismia	blanca	Vochysiaceae	0.571	genus	genus average
Erythrina	costaricensis	Fabaceae	0.289	genus	genus average
Erythrina	fusca	Fabaceae	0.299	species	global data base
Erythrina	poeppigiana	Fabaceae	0.305	species	global data base
Erythrina	rubrinervia	Fabaceae	0.289	genus	genus average
Erythroxyllum	citrifolium	Erythroxyllaceae	0.710	species	local data base
Erythroxyllum	panamense	Erythroxyllaceae	0.790	genus	genus average
Erythroxyllum	macrophyllum	Erythroxyllaceae	0.710	species	local data base
Eschweilera	amplexifolia	Lecythidaceae	0.825	genus	genus average
Eschweilera	calyculata	Lecythidaceae	0.825	genus	genus average
Eschweilera	jacquelyniae	Lecythidaceae	0.825	genus	genus average
Eschweilera	pittieri	Lecythidaceae	0.860	species	local data base
Eschweilera	sessilis	Lecythidaceae	0.825	genus	genus average
Eschweilera	panamensis	Lecythidaceae	0.825	genus	genus average
Eschweilera	aff.compressa	Lecythidaceae	0.825	genus	genus average
Esenbeckia	panamensis	Rutaceae	1.077	genus	genus average
Eugenia	coloradoensis	Myrtaceae	0.721	genus	genus average
Eugenia	crimolensis	Myrtaceae	0.721	genus	genus average
Eugenia	galalonensis	Myrtaceae	0.721	genus	genus average
Eugenia	nesiotica	Myrtaceae	0.721	genus	genus average
Eugenia	oerstediana	Myrtaceae	0.721	genus	genus average
Eugenia	venezuelensis	Myrtaceae	0.820	species	local data base
Eugenia	principium	Myrtaceae	0.721	genus	genus average
Eugenia	austin-smithii	Myrtaceae	0.721	genus	genus average
Eugenia	octopleura	Myrtaceae	0.721	genus	genus average
Eugenia	hiraeifolia	Myrtaceae	0.721	genus	genus average
Euphorbia	sinclairiana	Euphorbiaceae	0.457	genus	genus average
Euterpe	preclatoria	Arecaceae	0.388	species	local data base
Exostema	mexicanum	Rubiaceae	0.995	genus	genus average
Fairchildia	panamensis	Fabaceae	0.592	stand-level average	
Faramea	eurycarpa	Rubiaceae	0.585	genus	genus average
Faramea	luteovirens	Rubiaceae	0.585	genus	genus average
Faramea	multiflora	Rubiaceae	0.585	genus	genus average
Faramea	occidentalis	Rubiaceae	0.585	species	local data base
Faramea	papillata	Rubiaceae	0.585	genus	genus average
Faramea	papirifolia	Rubiaceae	0.585	genus	genus average
Faramea	suerrensensis	Rubiaceae	0.585	genus	genus average
Faramea	coba	Rubiaceae	0.585	genus	genus average
Faramea	parvibractea	Rubiaceae	0.585	genus	genus average
Faramea	calophylla	Rubiaceae	0.585	genus	genus average
Ferdinandusa	panamensis	Rubiaceae	0.725	genus	genus average
Ficus	citrifolia	Moraceae	0.400	species	local data base
Ficus	colubrinal	Moraceae	0.406	genus	genus average

genus	species	family	WD (g/cm ³)	level	source
Ficus	costaricana	Moraceae	0.406	genus	genus average
Ficus	insipida	Moraceae	0.377	species	local data base
Ficus	maxima	Moraceae	0.361	species	local data base
Ficus	nymphaeifolia	Moraceae	0.415	species	local data base
Ficus	obtusifolia	Moraceae	0.406	genus	genus average
Ficus	pertusa	Moraceae	0.420	species	local data base
Ficus	popenoei	Moraceae	0.406	genus	genus average
Ficus	tonduzii	Moraceae	0.406	genus	genus average
Ficus	yoponensis	Moraceae	0.406	genus	genus average
Ficus	apollinaris	Moraceae	0.406	genus	genus average
Ficus	brevibracteata	Moraceae	0.406	genus	genus average
Ficus	benamina	Moraceae	0.459	species	global data base
Ficus	unidentified	Moraceae	0.406	genus	genus average
Ficus	trigonata	Moraceae	0.430	species	global data base
Ficus	matiziana	Moraceae	0.406	genus	genus average
Fissicalyx	fendleri	Fabaceae	0.592	stand-level average	
Flacourtia	jangomas	Salicaceae	0.923	species	global data base
Flemingia	strobilifera	Fabaceae	0.592	stand-level average	
Freziera	calophylla	Pentaphylacaceae	0.580	genus	genus average
Galipea	panamensis	Rutaceae	0.997	genus	genus average
Garcinia	madruno	Clusiaceae	0.727	species	local data base
Garcinia	magnifolia	Clusiaceae	0.742	genus	genus average
Garcinia	recondita	Clusiaceae	0.742	genus	genus average
Genipa	americana	Rubiaceae	0.634	species	local data base
Geonoma	congesta	Arecaceae	0.592	stand-level average	
Geonoma	cuneata	Arecaceae	0.592	stand-level average	
Geonoma	deversa	Arecaceae	0.592	stand-level average	
Geonoma	interrupta	Arecaceae	0.592	stand-level average	
Gliricidia	sepium	Fabaceae	0.618	species	global data base
Gloeospermum	blakeanum	Violaceae	0.592	stand-level average	
Gloeospermum	sphaerocarpum	Violaceae	0.592	stand-level average	
Gloeospermum	eneidense	Violaceae	0.592	stand-level average	
Gmelina	arborea	Lamiaceae	0.430	species	local data base
Godmania	aesculifolia	Bignoniaceae	0.520	species	global data base
Gonzalagunia	panamensis	Rubiaceae	0.592	stand-level average	
Gonzalagunia	rudis	Rubiaceae	0.592	stand-level average	
Gordonia	fruticosa	Theaceae	0.519	species	local data base
Gordonia	brenesii	Theaceae	0.589	genus	genus average
Gossypium	barbadense	Malvaceae	0.680	genus	genus average
Graffenrieda	galeottii	Melastomataceae	0.592	stand-level average	
Grias	cauliflora	Lecythidaceae	0.620	genus	genus average
Guapira	campochagres	Nyctaginaceae	0.671	genus	genus average
Guapira	standleyana	Nyctaginaceae	0.671	genus	genus average
Guapira	costaricana	Nyctaginaceae	0.671	genus	genus average

genus	species	family	WD (g/cm ³)	level	source
Guarea	glabra	Meliaceae	0.478	species	local data base
Guarea	arbusto	Meliaceae	0.607	genus	genus average
Guarea	sherman	Meliaceae	0.607	genus	genus average
Guarea	grandifolia	Meliaceae	0.545	species	local data base
Guarea	guidonia	Meliaceae	0.565	species	local data base
Guarea	pterorhachis	Meliaceae	0.770	species	local data base
Guarea	bullata	Meliaceae	0.607	genus	genus average
Guarea	kunthiana	Meliaceae	0.616	species	local data base
Guarea	rhopalocarpa	Meliaceae	0.607	genus	genus average
Guarea	cf.macrophylla	Meliaceae	0.607	genus	genus average
Guarea	hoffmanniana	Meliaceae	0.607	genus	genus average
Guatteria	amplifolia	Annonaceae	0.511	species	local data base
Guatteria	aberrans	Annonaceae	0.577	genus	genus average
Guatteria	alata	Annonaceae	0.577	genus	genus average
Guatteria	allenii	Annonaceae	0.577	genus	genus average
Guatteria	dolichopoda	Annonaceae	0.577	genus	genus average
Guatteria	jefensis	Annonaceae	0.577	genus	genus average
Guatteria	sessilicarpa	Annonaceae	0.577	genus	genus average
Guatteria	lucens	Annonaceae	0.577	genus	genus average
Guatteria	ucayalina	Annonaceae	0.577	genus	genus average
Guazuma	ulmifolia	Malvaceae	0.519	species	local data base
Guettarda	crispiflora	Rubiaceae	0.728	genus	genus average
Guettarda	foliacea	Rubiaceae	0.728	genus	genus average
Guettarda	odorata	Rubiaceae	0.728	genus	genus average
Guettarda	ramuliflora	Rubiaceae	0.728	genus	genus average
Gustavia	dubia	Lecythidaceae	0.638	genus	genus average
Gustavia	fosteri	Lecythidaceae	0.638	genus	genus average
Gustavia	hexapetala	Lecythidaceae	0.716	species	global data base
Gustavia	nana	Lecythidaceae	0.638	genus	genus average
Gustavia	superba	Lecythidaceae	0.580	species	local data base
Gyranthera	dariensis	Malvaceae	0.370	genus	genus average
Hamelia	axillaris	Rubiaceae	0.618	species	local data base
Hamelia	patens	Rubiaceae	0.763	species	local data base
Hampea	appendiculata	Malvaceae	0.245	species	local data base
Hampea	micrantha	Malvaceae	0.318	genus	genus average
Handroanthus	guayacan	Bignoniaceae	0.592	stand-level average	
Handroanthus	impetiginosus	Bignoniaceae	0.592	stand-level average	
Handroanthus	ochraceus	Bignoniaceae	0.592	stand-level average	
Hasseltia	floribunda	Salicaceae	0.530	species	local data base
Hedyosmum	bonplandianum	Chloranthaceae	0.450	genus	genus average
Hedyosmum	scaberrimum	Chloranthaceae	0.450	genus	genus average
Heisteria	acuminata	Olacaceae	0.696	genus	genus average
Heisteria	concinna	Olacaceae	0.640	species	local data base
Heisteria	costaricensis	Olacaceae	0.696	genus	genus average

genus	species	family	WD (g/cm ³)	level	source
Helicostylis	tovarensis	Moraceae	0.669	genus	genus average
Helicteres	guazumifolia	Malvaceae	0.592	stand-level average	
Heliocarpus	americanus	Malvaceae	0.221	species	global data base
Henriettea	succosa	Melastomataceae	0.690	genus	genus average
Henriettea	fascicularis	Melastomataceae	0.690	genus	genus average
Henriettea	tuberculosa	Melastomataceae	0.690	genus	genus average
Henriettea	trachyphylla	Melastomataceae	0.690	genus	genus average
Hernandia	didymantha	Hernandiaceae	0.280	species	local data base
Hernandia	stenura	Hernandiaceae	0.292	genus	genus average
Herrania	nycterodendron	Malvaceae	0.592	stand-level average	
Herrania	purpurea	Malvaceae	0.592	stand-level average	
Hevea	brasiliensis	Euphorbiaceae	0.467	species	local data base
Hieronyma	oblonga	Phyllanthaceae	0.592	stand-level average	
Hieronyma	alchorneoides	Phyllanthaceae	0.592	stand-level average	
Hippomane	mancinella	Euphorbiaceae	0.500	species	global data base
Hippotis	panamensis	Rubiaceae	0.592	stand-level average	
Hirtella	americana	Chrysobalanaceae	0.793	genus	genus average
Hirtella	guatemalensis	Chrysobalanaceae	0.793	genus	genus average
Hirtella	latifolia	Chrysobalanaceae	0.793	genus	genus average
Hirtella	racemosa	Chrysobalanaceae	0.775	species	local data base
Hirtella	triandra	Chrysobalanaceae	0.683	species	local data base
Hirtella	tubiflora	Chrysobalanaceae	0.793	genus	genus average
Homalium	racemosum	Salicaceae	0.795	species	global data base
Hortia	brasiliana	Rutaceae	0.901	genus	genus average
Humiriastrum	diguense	Humiriaceae	0.690	genus	genus average
Hura	crepitans	Euphorbiaceae	0.367	species	local data base
Hybanthus	denticulatus	Violaceae	0.670	genus	genus average
Hymenaea	courbaril	Fabaceae	0.792	species	local data base
Hymenandra	pittieri	Primulaceae	0.592	stand-level average	
Hymenolobium	mesoamericanum	Fabaceae	0.642	genus	genus average
Hyperbaena	tonduzii	Menispermaceae	0.592	stand-level average	
Ilex	guianensis	Aquifoliaceae	0.563	genus	genus average
Inga	ciliata	Fabaceae	0.578	genus	genus average
Inga	alba	Fabaceae	0.586	species	local data base
Inga	bella	Fabaceae	0.578	genus	genus average
Inga	capitata	Fabaceae	0.592	species	local data base
Inga	chocoensis	Fabaceae	0.578	genus	genus average
Inga	multijuga	Fabaceae	0.578	genus	genus average
Inga	dwyeri	Fabaceae	0.578	genus	genus average
Inga	edulis	Fabaceae	0.587	species	global data base
Inga	filiformis	Fabaceae	0.578	genus	genus average
Inga	goldmanii	Fabaceae	0.578	genus	genus average
Inga	jefensis	Fabaceae	0.578	genus	genus average
Inga	marginata	Fabaceae	0.552	species	local data base

genus	species	family	WD (g/cm ³)	level	source
Inga	mucuna	Fabaceae	0.578	genus	genus average
Inga	pauciflora	Fabaceae	0.578	genus	genus average
Inga	pezizifera	Fabaceae	0.607	species	local data base
Inga	polita	Fabaceae	0.578	genus	genus average
Inga	portobellensis	Fabaceae	0.578	genus	genus average
Inga	punctata	Fabaceae	0.560	species	local data base
Inga	ruiziana	Fabaceae	0.578	genus	genus average
Inga	sapindoides	Fabaceae	0.578	genus	genus average
Inga	sertilifera	Fabaceae	0.650	species	local data base
Inga	spectabilis	Fabaceae	0.578	genus	genus average
Inga	cocleensis	Fabaceae	0.578	genus	genus average
Inga	umbellifera	Fabaceae	0.724	species	local data base
Inga	urceolata	Fabaceae	0.578	genus	genus average
Inga	venusta	Fabaceae	0.578	genus	genus average
Inga	vera	Fabaceae	0.577	species	local data base
Inga	acuminata	Fabaceae	0.578	genus	genus average
Inga	laurina	Fabaceae	0.661	species	local data base
Inga	nobilis	Fabaceae	0.560	species	local data base
Inga	oerstediana	Fabaceae	0.425	species	local data base
Inga	thibaudiana	Fabaceae	0.578	genus	genus average
Inga	acrocephala	Fabaceae	0.513	species	local data base
Inga	leiocalycina	Fabaceae	0.560	species	local data base
Inga	sierrae	Fabaceae	0.578	genus	genus average
Inga	aff.stenophylla	Fabaceae	0.578	genus	genus average
Inga	mortoniana	Fabaceae	0.578	genus	genus average
Inga	unidentified	Fabaceae	0.578	genus	genus average
Iriartea	deltoidea	Arecaceae	0.267	species	local data base
Iryanthera	juruensis	Myristicaceae	0.633	species	global data base
Isertia	haenkeana	Rubiaceae	0.548	genus	genus average
Isertia	laevis	Rubiaceae	0.520	species	global data base
Ixora	floribunda	Rubiaceae	0.793	genus	genus average
Jacaranda	caucana	Bignoniaceae	0.473	genus	genus average
Jacaranda	copaia	Bignoniaceae	0.351	species	local data base
Jacaratia	spinosa	Caricaceae	0.265	genus	genus average
Jatropha	curcas	Euphorbiaceae	0.170	species	global data base
Jatropha	gossypifolia	Euphorbiaceae	0.325	genus	genus average
Jatropha	integerrima	Euphorbiaceae	0.325	genus	genus average
Khaya	senegalensis	Meliaceae	0.626	species	global data base
Klarobelia	anomala	Annonaceae	0.592	stand-level average	
Koanophyllon	wetmorei	Compositae	0.592	stand-level average	
Lacistema	aggregatum	Lacistemataceae	0.506	species	local data base
Lacmellea	panamensis	Apocynaceae	0.472	species	local data base
Lacmellea	speciosa	Apocynaceae	0.513	genus	genus average
Ladenbergia	brenesii	Rubiaceae	0.490	genus	genus average

genus	species	family	WD (g/cm ³)	level	source
Ladenbergia	macrocarpa	Rubiaceae	0.490	genus	genus average
Laetia	procera	Salicaceae	0.648	species	local data base
Laetia	thamnia	Salicaceae	0.660	species	local data base
Lafoensia	punicifolia	Lythraceae	0.705	species	local data base
Lagerstroemia	speciosa	Lythraceae	0.595	species	global data base
Laguncularia	racemosa	Combretaceae	0.610	species	global data base
Lantana	camara	Verbenaceae	0.592	stand-level average	
Laxoplumeria	tessmannii	Apocynaceae	0.592	stand-level average	
Leandra	roja	Melastomataceae	0.592	stand-level average	
Leandra	dichotoma	Melastomataceae	0.592	stand-level average	
Leandra	granatensis	Melastomataceae	0.592	stand-level average	
Lecointea	amazonica	Fabaceae	0.893	species	local data base
Lecythis	ampla	Lecythidaceae	0.750	species	local data base
Lennea	viridiflora	Fabaceae	0.592	stand-level average	
Leonia	glycyarpa	Violaceae	0.600	species	local data base
Leptolobium	panamense	Fabaceae	0.592	stand-level average	
Libidibia	coriaria	Fabaceae	0.592	stand-level average	
Licania	affinis	Chrysobalanaceae	0.820	genus	genus average
Licania	arborea	Chrysobalanaceae	0.622	species	local data base
Licania	cruegeriana	Chrysobalanaceae	0.820	genus	genus average
Licania	fasciculata	Chrysobalanaceae	0.820	genus	genus average
Licania	hypoleuca	Chrysobalanaceae	0.909	species	local data base
Licania	morii	Chrysobalanaceae	0.820	genus	genus average
Licania	platypus	Chrysobalanaceae	0.620	species	local data base
Licania	coba	Chrysobalanaceae	0.820	genus	genus average
Licania	macrocarpa	Chrysobalanaceae	0.820	genus	genus average
Licania	kallunkiae	Chrysobalanaceae	0.820	genus	genus average
Licaria	guianensis	Lauraceae	0.748	species	global data base
Licaria	excelsa	Lauraceae	0.787	genus	genus average
Licaria	misantlae	Lauraceae	0.787	genus	genus average
Licaria	cannella	Lauraceae	0.939	species	global data base
Lindackeria	laurina	Achariaceae	0.560	genus	genus average
Lisianthus	jefensis	Gentianaceae	0.592	stand-level average	
Lonchocarpus	atropurpureus	Fabaceae	0.758	genus	genus average
Lonchocarpus	sericeus	Fabaceae	0.705	species	global data base
Lonchocarpus	velutinus	Fabaceae	0.750	species	global data base
Lonchocarpus	heptaphyllus	Fabaceae	0.687	species	local data base
Lonchocarpus	oliganthus	Fabaceae	0.758	genus	genus average
Lonchocarpus	ferrugineus	Fabaceae	0.758	genus	genus average
Lozania	pittieri	Lacistemataceae	0.592	stand-level average	
Luehea	seemannii	Malvaceae	0.417	species	local data base
Luehea	speciosa	Malvaceae	0.440	species	local data base
Lunania	mexicana	Salicaceae	0.580	species	global data base
Lunania	parviflora	Salicaceae	0.635	species	local data base

genus	species	family	WD (g/cm ³)	level	source
Lycianthes	maxonii	Solanaceae	0.440	genus	genus average
Mabea	occidentalis	Euphorbiaceae	0.608	genus	genus average
Machaerium	biovulatum	Fabaceae	0.732	genus	genus average
Maclura	tinctoria	Moraceae	0.794	species	local data base
Macoubea	mesoamericana	Apocynaceae	0.414	genus	genus average
Macrocnemum	roseum	Rubiaceae	0.450	species	local data base
Macrolobium	pittieri	Fabaceae	0.619	genus	genus average
Macrolobium	costaricense	Fabaceae	0.619	genus	genus average
Malmea	dimera	Annonaceae	0.390	genus	genus average
Malouetia	quadricasorum	Apocynaceae	0.527	genus	genus average
Malpighia	albiflora	Malpighiaceae	0.592	stand-level average	
Malpighia	romeroana	Malpighiaceae	0.592	stand-level average	
Mammea	immansueta	Calophyllaceae	0.779	genus	genus average
Mangifera	indica	Anacardiaceae	0.553	species	local data base
Manihot	esculenta	Euphorbiaceae	0.592	stand-level average	
Manilkara	bidentata	Sapotaceae	0.873	species	local data base
Manilkara	zapota	Sapotaceae	0.810	species	local data base
Manilkara	chicle	Sapotaceae	1.040	species	global data base
Maprounea	guianensis	Euphorbiaceae	0.588	species	local data base
Maquira	guianensis	Moraceae	0.766	species	local data base
Maranthes	panamensis	Chrysobalanaceae	0.830	genus	genus average
Margaritaria	nobilis	Phyllanthaceae	0.616	species	local data base
Marila	lactogena	Calophyllaceae	0.592	stand-level average	
Marila	laxiflora	Calophyllaceae	0.592	stand-level average	
Marila	pluricostata	Calophyllaceae	0.592	stand-level average	
Marila	domingensis	Calophyllaceae	0.592	stand-level average	
Matayba	apetala	Sapindaceae	0.771	genus	genus average
Matayba	glaberrima	Sapindaceae	0.771	genus	genus average
Matayba	scrobiculata	Sapindaceae	0.771	genus	genus average
Matisia	aff.idroboi	Malvaceae	0.535	genus	genus average
Matisia	bracteolosa	Malvaceae	0.535	genus	genus average
Matisia	jefensis	Malvaceae	0.535	genus	genus average
Matisia	obliquifolia	Malvaceae	0.535	genus	genus average
Matisia	sanblasensis	Malvaceae	0.535	genus	genus average
Matisia	exalata	Malvaceae	0.535	genus	genus average
Mayna	grandifolia	Achariaceae	0.592	stand-level average	
Mayna	odorata	Achariaceae	0.592	stand-level average	
Maytenus	schippii	Celastraceae	0.713	genus	genus average
Melicoccus	bijugatus	Sapindaceae	0.980	genus	genus average
Meliosma	glabrata	Sabiaceae	0.479	genus	genus average
Meliosma	grandiflora	Sabiaceae	0.479	genus	genus average
Meliosma	idiopoda	Sabiaceae	0.479	genus	genus average
Meliosma	occidentalis	Sabiaceae	0.479	genus	genus average
Meliosma	hoja_grande	Sabiaceae	0.479	genus	genus average

genus	species	family	WD (g/cm ³)	level	source
Meliosma	frondosa	Sabiaceae	0.479	genus	genus average
Miconia	affinis	Melastomataceae	0.634	genus	genus average
Miconia	argentea	Melastomataceae	0.589	species	local data base
Miconia	centronioides	Melastomataceae	0.634	genus	genus average
Miconia	centrosperma	Melastomataceae	0.634	genus	genus average
Miconia	chrysophylla	Melastomataceae	0.620	species	global data base
Miconia	dodecandra	Melastomataceae	0.634	genus	genus average
Miconia	elata	Melastomataceae	0.470	species	local data base
Miconia	hondurensis	Melastomataceae	0.634	genus	genus average
Miconia	impetiolaris	Melastomataceae	0.747	species	local data base
Miconia	lacera	Melastomataceae	0.634	genus	genus average
Miconia	ligulata	Melastomataceae	0.634	genus	genus average
Miconia	minutiflora	Melastomataceae	0.634	genus	genus average
Miconia	multispicata	Melastomataceae	0.634	genus	genus average
Miconia	nervosa	Melastomataceae	0.634	genus	genus average
Miconia	oinochrophylla	Melastomataceae	0.634	genus	genus average
Miconia	pileata	Melastomataceae	0.634	genus	genus average
Miconia	poepigii	Melastomataceae	0.597	species	local data base
Miconia	prasina	Melastomataceae	0.699	species	local data base
Miconia	punctata	Melastomataceae	0.634	genus	genus average
Miconia	reducens	Melastomataceae	0.620	species	local data base
Miconia	rubiginosa	Melastomataceae	0.634	genus	genus average
Miconia	serrulata	Melastomataceae	0.634	genus	genus average
Miconia	simplex	Melastomataceae	0.634	genus	genus average
Miconia	stenostachya	Melastomataceae	0.634	genus	genus average
Miconia	trinervia	Melastomataceae	0.620	species	local data base
Miconia	dorsiloba	Melastomataceae	0.634	genus	genus average
Miconia	umbriensis	Melastomataceae	0.634	genus	genus average
Miconia	doniana	Melastomataceae	0.634	genus	genus average
Micropholis	guyanensis	Sapotaceae	0.657	species	global data base
Micropholis	melinoniana	Sapotaceae	0.530	species	local data base
Micropholis	venulosa	Sapotaceae	0.670	species	local data base
Mimosa	tenuiflora	Fabaceae	1.120	species	global data base
Mimusops	elengi	Sapotaceae	0.849	species	global data base
Minuartia	guianensis	Olacaceae	0.787	species	local data base
Mollinedia	viridiflora	Monimiaceae	0.592	stand-level average	
Morella	cerifera	Myricaceae	0.592	stand-level average	
Morinda	panamensis	Rubiaceae	0.490	species	global data base
Morinda	citrifolia	Rubiaceae	0.630	species	global data base
Mortoniendron	anisophyllum	Malvaceae	0.510	genus	genus average
Mosannona	garwoodii	Annonaceae	0.592	stand-level average	
Mosquitoxylum	jamaicense	Anacardiaceae	0.592	stand-level average	
Mouriri	gleasoniana	Melastomataceae	0.840	genus	genus average
Mouriri	myrtilloides	Melastomataceae	0.840	genus	genus average

genus	species	family	WD (g/cm ³)	level	source
Mouriri	panamensis	Melastomataceae	0.840	genus	genus average
Mouriri	coba	Melastomataceae	0.840	genus	genus average
Mouriri	aff.exilis	Melastomataceae	0.840	genus	genus average
Mouriri	cf.completens	Melastomataceae	0.840	genus	genus average
Muntingia	calabura	Muntingiaceae	0.300	species	global data base
Myrcia	splendens	Myrtaceae	0.800	species	global data base
Myrcia	panamensis	Myrtaceae	0.816	genus	genus average
Myrcia	fosteri	Myrtaceae	0.816	genus	genus average
Myrcia	zetekiana	Myrtaceae	0.816	genus	genus average
Myrciaria	floribunda	Myrtaceae	0.785	species	global data base
Myriocarpa	longipes	Urticaceae	0.592	stand-level average	
Myrospermum	frutescens	Fabaceae	0.830	species	local data base
Myrsine	coriacea	Primulaceae	0.647	species	global data base
Naucleopsis	naga	Moraceae	0.651	genus	genus average
Naucleopsis	ulei	Moraceae	0.670	species	local data base
Naucleopsis	straminea	Moraceae	0.651	genus	genus average
Naucleopsis	capirensis	Moraceae	0.651	genus	genus average
Nectandra	bicolor	Lauraceae	0.562	genus	genus average
Nectandra	cissiflora	Lauraceae	0.590	species	local data base
Nectandra	cuspidata	Lauraceae	0.518	species	local data base
Nectandra	fuzzy	Lauraceae	0.562	genus	genus average
Nectandra	lineata	Lauraceae	0.562	genus	genus average
Neea	roja	Nyctaginaceae	0.640	genus	genus average
Neea	amplifolia	Nyctaginaceae	0.640	genus	genus average
Neea	delicatula	Nyctaginaceae	0.640	genus	genus average
Neea	laetevirens	Nyctaginaceae	0.640	genus	genus average
Ochoterena	colombiana	Anacardiaceae	0.592	stand-level average	
Ochroma	pyramidale	Malvaceae	0.158	species	local data base
Ocotea	arcuata	Lauraceae	0.542	genus	genus average
Ocotea	atirrensis	Lauraceae	0.480	species	local data base
Ocotea	cernua	Lauraceae	0.454	species	local data base
Ocotea	dendrodaphne	Lauraceae	0.530	species	local data base
Ocotea	endresiana	Lauraceae	0.542	genus	genus average
Ocotea	insularis	Lauraceae	0.542	genus	genus average
Ocotea	leucoxyton	Lauraceae	0.462	species	local data base
Ocotea	meziana	Lauraceae	0.390	species	global data base
Ocotea	oblonga	Lauraceae	0.386	species	local data base
Ocotea	rubrinervis	Lauraceae	0.542	genus	genus average
Ocotea	tonduzii	Lauraceae	0.542	genus	genus average
Ocotea	veraguensis	Lauraceae	0.735	species	local data base
Ocotea	puberula	Lauraceae	0.433	species	local data base
Ocotea	whitei	Lauraceae	0.542	genus	genus average
Ocotea	hartshorniana	Lauraceae	0.380	species	global data base
Ocotea	jorge-escobarii	Lauraceae	0.542	genus	genus average

genus	species	family	WD (g/cm ³)	level	source
Ocotea	helicterifolia	Lauraceae	0.542	genus	genus average
Oenocarpus	mapora	Arecaceae	0.713	species	local data base
Opuntia	elatior	Cactaceae	0.592	stand-level average	
Oreopanax	capitatus	Araliaceae	0.520	genus	genus average
Ormosia	amazonica	Fabaceae	0.579	genus	genus average
Ormosia	macrocalyx	Fabaceae	0.579	genus	genus average
Ormosia	coccinea	Fabaceae	0.625	species	local data base
Ormosia	velutina	Fabaceae	0.579	genus	genus average
Ossaea	spicata	Melastomataceae	0.592	stand-level average	
Osteophloeum	platyspermum	Myristicaceae	0.466	species	local data base
Otoba	acuminata	Myristicaceae	0.389	genus	genus average
Otoba	latialata	Myristicaceae	0.389	genus	genus average
Otoba	novogranatensis	Myristicaceae	0.350	species	local data base
Otoba	parvifolia	Myristicaceae	0.426	species	local data base
Ouratea	knappiae	Ochnaceae	0.743	genus	genus average
Ouratea	lucens	Ochnaceae	0.743	genus	genus average
Ouratea	prominens	Ochnaceae	0.743	genus	genus average
Ouratea	sulcatinervia	Ochnaceae	0.743	genus	genus average
Oxandra	longipetala	Annonaceae	0.737	genus	genus average
Oxandra	panamensis	Annonaceae	0.737	genus	genus average
Oxandra	venezuelana	Annonaceae	0.737	genus	genus average
Pachira	aquatica	Malvaceae	0.377	species	local data base
Pachira	sessilis	Malvaceae	0.420	species	local data base
Palicourea	allenii	Rubiaceae	0.550	genus	genus average
Palicourea	guianensis	Rubiaceae	0.540	species	local data base
Palicourea	triphylla	Rubiaceae	0.550	genus	genus average
Palicourea	crocea	Rubiaceae	0.560	species	global data base
Palicourea	umbelliformis	Rubiaceae	0.550	genus	genus average
Palicourea	hondensis	Rubiaceae	0.550	genus	genus average
Palicourea	acuminata	Rubiaceae	0.550	genus	genus average
Palicourea	brachiata	Rubiaceae	0.550	genus	genus average
Palicourea	capitata	Rubiaceae	0.550	genus	genus average
Palicourea	cyanococca	Rubiaceae	0.550	genus	genus average
Palicourea	deflexa	Rubiaceae	0.550	genus	genus average
Palicourea	elata	Rubiaceae	0.550	genus	genus average
Palicourea	glomerulata	Rubiaceae	0.550	genus	genus average
Palicourea	gracilentata	Rubiaceae	0.550	genus	genus average
Palicourea	hoffmannseggiana	Rubiaceae	0.550	genus	genus average
Palicourea	longicuspis	Rubiaceae	0.550	genus	genus average
Palicourea	luxurians	Rubiaceae	0.550	genus	genus average
Palicourea	tomentosa	Rubiaceae	0.550	genus	genus average
Palicourea	pubescens	Rubiaceae	0.550	genus	genus average
Palicourea	racemosa	Rubiaceae	0.550	genus	genus average
Palicourea	suerrensis	Rubiaceae	0.550	genus	genus average

genus	species	family	WD (g/cm ³)	level	source
Panopsis	suaveolens	Proteaceae	0.512	genus	genus average
Parathesis	amplifolia	Primulaceae	0.620	genus	genus average
Parinari	chocoensis	Chrysobalanaceae	0.713	genus	genus average
Parkia	nitida	Fabaceae	0.383	species	local data base
Parkinsonia	aculeata	Fabaceae	0.622	species	global data base
Parmentiera	cereifera	Bignoniaceae	0.592	stand-level average	
Parmentiera	macrophylla	Bignoniaceae	0.592	stand-level average	
Pavonia	dasyptala	Malvaceae	0.592	stand-level average	
Pelliciera	rhizophorae	Tetrameristaceae	0.592	stand-level average	
Pentagonia	gymnopoda	Rubiaceae	0.592	stand-level average	
Pentagonia	macrophylla	Rubiaceae	0.592	stand-level average	
Pentagonia	parvifolia	Rubiaceae	0.592	stand-level average	
Pentagonia	wendlandii	Rubiaceae	0.592	stand-level average	
Pentagonia	costaricensis	Rubiaceae	0.592	stand-level average	
Pera	arborea	Peraceae	0.730	species	local data base
Pera	oppositifolia	Peraceae	0.666	genus	genus average
Perebea	angustifolia	Moraceae	0.517	species	local data base
Perebea	guianensis	Moraceae	0.560	species	local data base
Perebea	xanthochyma	Moraceae	0.560	species	local data base
Pereskia	bleo	Cactaceae	0.592	stand-level average	
Persea	americana	Lauraceae	0.549	species	global data base
Photinia	microcarpa	Rosaceae	0.724	genus	genus average
Phyllanthus	acuminatus	Phyllanthaceae	0.613	genus	genus average
Phytelephas	seemannii	Arecaceae	0.592	stand-level average	
Picramnia	latifolia	Picramniaceae	0.592	stand-level average	
Pinus	caribaea	Pinaceae	0.571	species	global data base
Piper	hispidum	Piperaceae	0.393	species	local data base
Piper	aduncum	Piperaceae	0.393	genus	genus average
Piper	aequale	Piperaceae	0.393	genus	genus average
Piper	amalago	Piperaceae	0.393	genus	genus average
Piper	arboresum	Piperaceae	0.393	genus	genus average
Piper	augustum	Piperaceae	0.393	genus	genus average
Piper	auritum	Piperaceae	0.393	genus	genus average
Piper	cordulatum	Piperaceae	0.393	genus	genus average
Piper	fimbriulatum	Piperaceae	0.393	genus	genus average
Piper	grande	Piperaceae	0.393	genus	genus average
Piper	hirtellipetiolum	Piperaceae	0.393	genus	genus average
Piper	longispicum	Piperaceae	0.393	genus	genus average
Piper	marginatum	Piperaceae	0.393	genus	genus average
Piper	perlasense	Piperaceae	0.393	genus	genus average
Piper	phytolaccifolium	Piperaceae	0.393	genus	genus average
Piper	reticulatum	Piperaceae	0.330	species	local data base
Piper	colonense	Piperaceae	0.393	genus	genus average
Piper	schiedeanum	Piperaceae	0.393	genus	genus average

genus	species	family	WD (g/cm ³)	level	source
Piper	imperiale	Piperaceae	0.393	genus	genus average
Piptocoma	discolor	Compositae	0.470	species	global data base
Pithecellobium	hymenaeifolium	Fabaceae	0.502	genus	genus average
Pithecellobium	lanceolatum	Fabaceae	0.502	genus	genus average
Pithecellobium	unguis-cati	Fabaceae	0.502	genus	genus average
Pittoniotis	trichantha	Rubiaceae	0.592	stand-level average	
Platymiscium	pinnatum	Fabaceae	0.721	species	local data base
Platypodium	elegans	Fabaceae	0.806	species	local data base
Pleuranthodendron	lindenii	Salicaceae	0.680	species	local data base
Pleurothyrium	aff.hexaglandulosum	Lauraceae	0.470	genus	genus average
Pleurothyrium	racemosum	Lauraceae	0.470	genus	genus average
Plinia	povedae	Myrtaceae	0.950	genus	genus average
Plumeria	rubra	Apocynaceae	0.500	species	global data base
Pochota	quinata	Malvaceae	0.592	stand-level average	
Podocarpus	guatemalensis	Podocarpaceae	0.400	species	global data base
Podocarpus	oleifolius	Podocarpaceae	0.453	species	local data base
Pogonopus	exsertus	Rubiaceae	0.592	stand-level average	
Pombalia	prunifolia	NA	0.592	stand-level average	
Posoqueria	latifolia	Rubiaceae	0.570	species	local data base
Posoqueria	coriacea	Rubiaceae	0.575	genus	genus average
Potalia	turbinata	Gentianaceae	0.592	stand-level average	
Poulsenia	armata	Moraceae	0.350	species	local data base
Pourouma	bicolor	Urticaceae	0.353	species	local data base
Pourouma	minor	Urticaceae	0.436	species	local data base
Pouteria	glomerata	Sapotaceae	0.679	species	local data base
Pouteria	buenaventurensis	Sapotaceae	0.560	species	local data base
Pouteria	bulliformis	Sapotaceae	0.688	genus	genus average
Pouteria	calistophylla	Sapotaceae	0.688	genus	genus average
Pouteria	campechiana	Sapotaceae	0.790	species	local data base
Pouteria	cuspidata	Sapotaceae	0.900	species	local data base
Pouteria	fossicola	Sapotaceae	0.688	genus	genus average
Pouteria	foveolata	Sapotaceae	0.688	genus	genus average
Pouteria	leptopedicellata	Sapotaceae	0.688	genus	genus average
Pouteria	aff.sclerocarpa	Sapotaceae	0.688	genus	genus average
Pouteria	stipitata	Sapotaceae	0.688	genus	genus average
Pouteria	torta	Sapotaceae	0.769	species	local data base
Pouteria	reticulata	Sapotaceae	0.794	species	local data base
Pouteria	congestifolia	Sapotaceae	0.688	genus	genus average
Pouteria	durlandii	Sapotaceae	0.690	species	local data base
Pouteria	silvestris	Sapotaceae	0.688	genus	genus average
Pouteria	sapota	Sapotaceae	0.855	species	global data base
Preslianthus	panamensis	NA	0.592	stand-level average	
Preslianthus	pittieri	NA	0.592	stand-level average	
Prestoea	decurrens	Arecaceae	0.250	species	local data base

genus	species	family	WD (g/cm ³)	level	source
Prioria	copaifera	Fabaceae	0.414	species	local data base
Prockia	crucis	Salicaceae	0.580	species	local data base
Prosopis	juliflora	Fabaceae	0.794	species	global data base
Protium	tenuifolium	Burseraceae	0.570	species	local data base
Protium	aff.guianense	Burseraceae	0.568	genus	genus average
Protium	costaricense	Burseraceae	0.568	genus	genus average
Protium	glabrum	Burseraceae	0.568	genus	genus average
Protium	panamense	Burseraceae	0.452	species	local data base
Protium	trifoliolatum	Burseraceae	0.685	species	local data base
Protium	confusum	Burseraceae	0.568	genus	genus average
Pseudima	frutescens	Sapindaceae	0.800	species	global data base
Pseudobombax	septenatum	Malvaceae	0.212	species	local data base
Pseudolmedia	spuria	Moraceae	0.713	species	local data base
Pseudolmedia	laevigata	Moraceae	0.629	species	local data base
Pseudosamanea	guachapele	Fabaceae	0.592	stand-level average	
Psidium	friedrichsthalianum	Myrtaceae	0.855	genus	genus average
Psidium	guajava	Myrtaceae	0.652	species	global data base
Psychotria	calophylla	Rubiaceae	0.496	genus	genus average
Psychotria	chagrensis	Rubiaceae	0.496	genus	genus average
Psychotria	graciliflora	Rubiaceae	0.496	genus	genus average
Psychotria	grandis	Rubiaceae	0.295	species	local data base
Psychotria	horizontalis	Rubiaceae	0.496	genus	genus average
Psychotria	limonensis	Rubiaceae	0.496	genus	genus average
Psychotria	marginata	Rubiaceae	0.496	genus	genus average
Psychotria	micrantha	Rubiaceae	0.496	genus	genus average
Psychotria	nervosa	Rubiaceae	0.496	genus	genus average
Psychotria	panamensis	Rubiaceae	0.496	genus	genus average
Psychotria	psychotriifolia	Rubiaceae	0.496	genus	genus average
Psychotria	remota	Rubiaceae	0.496	genus	genus average
Psychotria	tenuifolia	Rubiaceae	0.496	genus	genus average
Pterocarpus	acapulcensis	Fabaceae	0.627	genus	genus average
Pterocarpus	officinalis	Fabaceae	0.383	species	local data base
Pterocarpus	hayesii	Fabaceae	0.627	genus	genus average
Quadrella	cynophallophora	Capparaceae	0.592	stand-level average	
Quadrella	antonensis	Capparaceae	0.592	stand-level average	
Quadrella	indica	Capparaceae	0.592	stand-level average	
Qualea	polychroma	Vochysiaceae	0.647	genus	genus average
Quararibea	asterolepis	Malvaceae	0.454	species	local data base
Quararibea	platyphylla	Malvaceae	0.488	genus	genus average
Quararibea	pumila	Malvaceae	0.488	genus	genus average
Quararibea	pterocalyx	Malvaceae	0.488	genus	genus average
Quassia	amara	Simaroubaceae	0.470	species	local data base
Quetzalia	occidentalis	Celastraceae	0.592	stand-level average	
Quiina	schippii	Ochnaceae	0.862	genus	genus average

genus	species	family	WD (g/cm ³)	level	source
Randia	campo_chagres	Rubiaceae	0.671	genus	genus average
Randia	aculeata	Rubiaceae	0.671	genus	genus average
Randia	armata	Rubiaceae	0.668	species	local data base
Randia	grandifolia	Rubiaceae	0.671	genus	genus average
Randia	lasiantha	Rubiaceae	0.671	genus	genus average
Randia	hondensis	Rubiaceae	0.671	genus	genus average
Raphia	taedigera	Arecaceae	0.592	stand-level average	
Raritebe	palicoureooides	Rubiaceae	0.592	stand-level average	
Rauvolfia	littoralis	Apocynaceae	0.486	genus	genus average
Rauvolfia	purpurascens	Apocynaceae	0.476	species	global data base
Rhizophora	mangle	Rhizophoraceae	0.898	species	global data base
Richeria	grandis	Phyllanthaceae	0.577	species	global data base
Ricinus	communis	Euphorbiaceae	0.592	stand-level average	
Rinorea	apiculata	Violaceae	0.681	genus	genus average
Rinorea	crenata	Violaceae	0.681	genus	genus average
Rinorea	dasyadena	Violaceae	0.681	genus	genus average
Rinorea	lindeniana	Violaceae	0.681	genus	genus average
Rinorea	squamata	Violaceae	0.681	genus	genus average
Rinorea	sylvatica	Violaceae	0.681	genus	genus average
Rinorea	hummelii	Violaceae	0.681	genus	genus average
Rogiera	amoena	Rubiaceae	0.592	stand-level average	
Ronabea	latifolia	Rubiaceae	0.592	stand-level average	
Rondeletia	hameliifolia	Rubiaceae	0.500	genus	genus average
Rondeletia	panamensis	Rubiaceae	0.500	genus	genus average
Rosenbergiodendron	formosum	Rubiaceae	0.592	stand-level average	
Roupala	montana	Proteaceae	0.783	species	local data base
Roupala	percoriacea	Proteaceae	0.837	genus	genus average
Roystonea	regia	Arecaceae	0.592	stand-level average	
Rudgea	cornifolia	Rubiaceae	0.570	genus	genus average
Rudgea	isthmensis	Rubiaceae	0.570	genus	genus average
Rudgea	pittieri	Rubiaceae	0.570	genus	genus average
Rudgea	skutchii	Rubiaceae	0.570	genus	genus average
Ruprechtia	costata	Polygonaceae	0.653	genus	genus average
Ruptiliocarpon	caracolito	Lepidobotryaceae	0.592	stand-level average	
Ryania	speciosa	Salicaceae	0.592	stand-level average	
Sacoglottis	ovicarpa	Humiriaceae	0.775	genus	genus average
Sacoglottis	trichogyna	Humiriaceae	0.775	genus	genus average
Salacia	juhuana	Celastraceae	0.760	genus	genus average
Salacia	petenensis	Celastraceae	0.760	genus	genus average
Samanea	saman	Fabaceae	0.592	stand-level average	
Sapindus	saponaria	Sapindaceae	0.712	species	local data base
Sapium	broadleaf	Euphorbiaceae	0.419	genus	genus average
Sapium	glandulosum	Euphorbiaceae	0.415	species	local data base
Sapium	laurifolium	Euphorbiaceae	0.419	genus	genus average

genus	species	family	WD (g/cm ³)	level	source
Sarcaulus	brasiliensis	Sapotaceae	0.615	species	local data base
Saurauia	yasicae	Actinidiaceae	0.411	genus	genus average
Schefflera	morototoni	Araliaceae	0.456	species	local data base
Schizolobium	parahyba	Fabaceae	0.347	species	local data base
Schoenobiblus	panamensis	Thymelaeaceae	0.592	stand-level average	
Sciadodendron	excelsum	Araliaceae	0.530	species	local data base
Senegalia	riparia	Fabaceae	0.592	stand-level average	
Senna	bicapsularis	Fabaceae	0.603	genus	genus average
Senna	reticulata	Fabaceae	0.450	species	global data base
Senna	dariensis	Fabaceae	0.603	genus	genus average
Sideroxylon	capiri	Sapotaceae	0.760	species	global data base
Sideroxylon	celastrinum	Sapotaceae	0.849	genus	genus average
Sideroxylon	persimile	Sapotaceae	0.849	genus	genus average
Sideroxylon	cf.contrerasii	Sapotaceae	0.849	genus	genus average
Simaba	cedron	Simaroubaceae	0.474	species	global data base
Simaba	polyphylla	Simaroubaceae	0.410	genus	genus average
Simarouba	amara	Simaroubaceae	0.383	species	local data base
Simira	maxonii	Rubiaceae	0.615	species	global data base
Siparuna	conica	Siparunaceae	0.662	genus	genus average
Siparuna	cuspidata	Siparunaceae	0.655	species	local data base
Siparuna	grandiflora	Siparunaceae	0.662	genus	genus average
Siparuna	guianensis	Siparunaceae	0.662	genus	genus average
Siparuna	pauciflora	Siparunaceae	0.662	genus	genus average
Siparuna	thecaphora	Siparunaceae	0.662	genus	genus average
Siparuna	cristata	Siparunaceae	0.662	genus	genus average
Sloanea	laurifolia	Elaeocarpaceae	0.816	species	local data base
Sloanea	megaphylla	Elaeocarpaceae	0.609	genus	genus average
Sloanea	meianthera	Elaeocarpaceae	0.609	genus	genus average
Sloanea	zuliaensis	Elaeocarpaceae	0.609	genus	genus average
Sloanea	terniflora	Elaeocarpaceae	0.609	genus	genus average
Sloanea	medusula	Elaeocarpaceae	0.609	genus	genus average
Sloanea	obtusifolia	Elaeocarpaceae	0.609	genus	genus average
Socratea	exorrhiza	Arecaceae	0.230	species	local data base
Solanum	enves_purpura	Solanaceae	0.412	genus	genus average
Solanum	arboreum	Solanaceae	0.412	genus	genus average
Solanum	asperum	Solanaceae	0.412	genus	genus average
Solanum	hayesii	Solanaceae	0.412	genus	genus average
Solanum	jamaicense	Solanaceae	0.412	genus	genus average
Solanum	circinatum	Solanaceae	0.412	genus	genus average
Solanum	cordovense	Solanaceae	0.412	genus	genus average
Solanum	lepidotum	Solanaceae	0.412	genus	genus average
Sorocea	pubivena	Moraceae	0.605	genus	genus average
Sorocea	affinis	Moraceae	0.605	genus	genus average
Spachea	correae	Malpighiaceae	0.595	genus	genus average

genus	species	family	WD (g/cm ³)	level	source
Spachea	membranacea	Malpighiaceae	0.595	genus	genus average
Spathodea	campanulata	Bignoniaceae	0.351	species	global data base
Spondias	dulcis	Anacardiaceae	0.370	species	local data base
Spondias	mombin	Anacardiaceae	0.391	species	local data base
Spondias	purpurea	Anacardiaceae	0.330	species	global data base
Spondias	radlkoferi	Anacardiaceae	0.434	species	local data base
Stachyarrhena	heterochroa	Rubiaceae	0.820	genus	genus average
Stauranthus	perforatus	Rutaceae	0.592	stand-level average	
Stemmadenia	alfaroi	Apocynaceae	0.500	genus	genus average
Sterculia	costaricana	Malvaceae	0.405	genus	genus average
Sterculia	apetala	Malvaceae	0.392	species	local data base
Sterculia	recordiana	Malvaceae	0.490	species	local data base
Stylogyne	turbacensis	Primulaceae	0.483	genus	genus average
Swartzia	simplex	Fabaceae	0.849	genus	genus average
Swartzia	aff.sumorum	Fabaceae	0.849	genus	genus average
Swietenia	macrophylla	Meliaceae	0.520	species	local data base
Symphonia	globulifera	Clusiaceae	0.600	species	local data base
Symplocos	panamensis	Symplocaceae	0.534	genus	genus average
Synechanthus	warscewiczianus	Arecaceae	0.592	stand-level average	
Syzygium	jampos	Myrtaceae	0.700	species	global data base
Syzygium	malaccense	Myrtaceae	0.562	species	global data base
Tabebuia	rosea	Bignoniaceae	0.531	species	local data base
Tabebuia	striata	Bignoniaceae	0.762	genus	genus average
Tabernaemontana	arborea	Apocynaceae	0.526	genus	genus average
Tabernaemontana	longipes	Apocynaceae	0.526	genus	genus average
Tabernaemontana	panamensis	Apocynaceae	0.526	genus	genus average
Tabernaemontana	undulata	Apocynaceae	0.585	species	local data base
Tabernaemontana	grandiflora	Apocynaceae	0.526	genus	genus average
Tachigali	panamensis	Fabaceae	0.577	genus	genus average
Tachigali	costaricensis	Fabaceae	0.577	genus	genus average
Talauma	gloriensis	Magnoliaceae	0.592	stand-level average	
Talauma	sambuensis	Magnoliaceae	0.592	stand-level average	
Talipariti	tiliaceum	Malvaceae	0.543	species	global data base
Talisia	nervosa	Sapindaceae	0.833	genus	genus average
Talisia	croatii	Sapindaceae	0.833	genus	genus average
Tamarindus	indica	Fabaceae	0.978	species	global data base
Tapirira	guianensis	Anacardiaceae	0.457	species	local data base
Tapura	cubensis	Dichapetalaceae	0.640	genus	genus average
Tecoma	stans	Bignoniaceae	0.466	species	global data base
Tectona	grandis	Lamiaceae	0.601	species	global data base
Terminalia	amazonia	Combretaceae	0.674	species	local data base
Terminalia	catappa	Combretaceae	0.478	species	global data base
Terminalia	oblonga	Combretaceae	0.694	species	local data base
Terminalia	bucidoides	Combretaceae	0.630	genus	genus average

genus	species	family	WD (g/cm ³)	level	source
Terminalia	buceras	Combretaceae	0.630	genus	genus average
Ternstroemia	tepezapote	Pentaphylacaceae	0.616	genus	genus average
Tetragastris	panamensis	Burseraceae	0.717	species	local data base
Tetrathylacium	johansenii	Salicaceae	0.620	genus	genus average
Tetrathylacium	macrophyllum	Salicaceae	0.620	species	local data base
Tetrorchidium	euryphyllum	Euphorbiaceae	0.455	genus	genus average
Tetrorchidium	robledoanum	Euphorbiaceae	0.455	genus	genus average
Theobroma	bernoullii	Malvaceae	0.532	genus	genus average
Theobroma	cacao	Malvaceae	0.420	species	local data base
Theobroma	simiarum	Malvaceae	0.532	genus	genus average
Theobroma	speciosum	Malvaceae	0.630	species	local data base
Theobroma	bicolor	Malvaceae	0.532	genus	genus average
Thevetia	ahouai	Apocynaceae	0.720	genus	genus average
Tococa	guianensis	Melastomataceae	0.592	stand-level average	
Tocoyena	pittieri	Rubiaceae	0.620	genus	genus average
Tovomita	longifolia	Clusiaceae	0.695	genus	genus average
Tovomita	stylosa	Clusiaceae	0.695	genus	genus average
Tovomita	weddelliana	Clusiaceae	0.695	genus	genus average
Trattinnickia	aspera	Burseraceae	0.424	species	local data base
Trattinnickia	burserifolia	Burseraceae	0.460	species	local data base
Trema	micrantha	Cannabaceae	0.319	species	local data base
Trema	integerrima	Cannabaceae	0.300	species	global data base
Trema	unidentified	Cannabaceae	0.342	genus	genus average
Trichanthera	gigantea	Acanthaceae	0.450	species	local data base
Trichilia	hirta	Meliaceae	0.569	species	local data base
Trichilia	martiana	Meliaceae	0.470	species	local data base
Trichilia	pleeana	Meliaceae	0.675	species	local data base
Trichilia	poepigii	Meliaceae	0.645	genus	genus average
Trichilia	quadrijuga	Meliaceae	0.548	species	local data base
Trichilia	septentrionalis	Meliaceae	0.645	genus	genus average
Trichilia	trifolia	Meliaceae	0.800	species	global data base
Trichilia	pallida	Meliaceae	0.700	species	local data base
Trichilia	tuberculata	Meliaceae	0.628	species	local data base
Trichospermum	galeottii	Malvaceae	0.270	species	local data base
Triplaris	cumingiana	Polygonaceae	0.520	species	local data base
Triumfetta	bogotensis	Malvaceae	0.592	stand-level average	
Trophis	racemosa	Moraceae	0.659	species	local data base
Trophis	caucana	Moraceae	0.470	species	local data base
Turnera	panamensis	Passifloraceae	0.592	stand-level average	
Turpinia	occidentalis	Staphyleaceae	0.342	species	local data base
Unidentified	pubescente	NA	0.592	stand-level average	
Unidentified	species	NA	0.592	stand-level average	
Unonopsis	panamensis	Annonaceae	0.534	genus	genus average
Unonopsis	pittieri	Annonaceae	0.368	species	local data base

genus	species	family	WD (g/cm ³)	level	source
Unonopsis	theobromifolia	Annonaceae	0.534	genus	genus average
Unonopsis	aff.veneficiorum	Annonaceae	0.534	genus	genus average
Unonopsis	peludo	Annonaceae	0.534	genus	genus average
Unonopsis	bullata	Annonaceae	0.534	genus	genus average
Unonopsis	storkii	Annonaceae	0.534	genus	genus average
Urera	baccifera	Urticaceae	0.220	species	local data base
Urera	caracasana	Urticaceae	0.316	species	global data base
Urera	laciniata	Urticaceae	0.342	genus	genus average
Vachellia	melanoceras	Fabaceae	0.592	stand-level average	
Vachellia	collinsii	Fabaceae	0.592	stand-level average	
Vantanea	depleta	Humiriaceae	0.837	genus	genus average
Varronia	curassavica	Boraginaceae	0.592	stand-level average	
Vasconcellea	cauliflora	Caricaceae	0.592	stand-level average	
Vatairea	erythrocarpa	Fabaceae	0.673	genus	genus average
Verbesina	gigantea	Compositae	0.592	stand-level average	
Verbesina	lanata	Compositae	0.592	stand-level average	
Vernonia	patens	Compositae	0.330	genus	genus average
Virola	elongata	Myristicaceae	0.523	species	local data base
Virola	koschnyi	Myristicaceae	0.408	species	local data base
Virola	macrocarpa	Myristicaceae	0.484	genus	genus average
Virola	megacarpa	Myristicaceae	0.484	genus	genus average
Virola	sebifera	Myristicaceae	0.445	species	local data base
Virola	multiflora	Myristicaceae	0.458	species	local data base
Virola	guatemalensis	Myristicaceae	0.520	species	global data base
Virola	nobilis	Myristicaceae	0.484	genus	genus average
Vismia	baccifera	Hypericaceae	0.430	species	local data base
Vismia	billbergiana	Hypericaceae	0.493	genus	genus average
Vismia	jefensis	Hypericaceae	0.493	genus	genus average
Vismia	macrophylla	Hypericaceae	0.494	species	local data base
Vitex	cooperi	Lamiaceae	0.565	genus	genus average
Vitex	cymosa	Lamiaceae	0.563	species	local data base
Vochysia	ferruginea	Vochysiaceae	0.410	species	local data base
Vochysia	jefensis	Vochysiaceae	0.486	genus	genus average
Vochysia	guatemalensis	Vochysiaceae	0.353	species	local data base
Waltheria	glomerata	Malvaceae	0.592	stand-level average	
Warszewiczia	coccinea	Rubiaceae	0.557	species	local data base
Welfia	regia	Arecaceae	0.400	species	local data base
Wettinia	quinaria	Arecaceae	0.592	stand-level average	
Witheringia	solanacea	Solanaceae	0.592	stand-level average	
Ximenia	americana	Olcaceae	0.856	species	local data base
Xylopia	aromatica	Annonaceae	0.561	species	local data base
Xylopia	bocatorena	Annonaceae	0.591	genus	genus average
Xylopia	frutescens	Annonaceae	0.593	species	local data base
Xylopia	macrantha	Annonaceae	0.874	species	local data base

genus	species	family	WD (g/cm ³)	level	source
Xylopia	sericea	Annonaceae	0.591	genus	genus average
Xylopia	roubik	Annonaceae	0.591	genus	genus average
Xylosma	chlorantha	Salicaceae	0.661	genus	genus average
Xylosma	oligandra	Salicaceae	0.661	genus	genus average
Xylosma	panamensis	Salicaceae	0.661	genus	genus average
Zamia	fairchildiana	Zamiaceae	0.592	stand-level average	
Zanthoxylum	acuminatum	Rutaceae	0.618	genus	genus average
Zanthoxylum	panamense	Rutaceae	0.490	species	local data base
Zanthoxylum	setulosum	Rutaceae	0.469	species	local data base
Zanthoxylum	ekmanii	Rutaceae	0.618	genus	genus average
Ziziphus	chloroxylon	Rhamnaceae	0.778	genus	genus average
Ziziphus	mauritiana	Rhamnaceae	0.618	species	global data base
Zuelania	guidonia	Salicaceae	0.583	species	local data base
Zygia	dinizii	Fabaceae	0.820	genus	genus average
Zygia	englesingii	Fabaceae	0.820	genus	genus average
Zygia	latifolia	Fabaceae	0.750	species	global data base
Zygia	longifolia	Fabaceae	0.710	species	global data base