53

Woody Biomass Stocks and Fluxes in the Barro Colorado Island 50-ha Plot

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ABSTRACT. Tropical forest biomass is a globally important carbon stock with an uncertain future under climate change. Our understanding of tropical forest aboveground biomass stocks and fluxes has been advanced by studies on the Barro Colorado Island (BCI) 50-ha forest plot, where all trees larger than 1 cm in diameter have been measured approximately every five years since 1982. BCI studies introduced new methods for estimating biomass stocks as well as fluxes associated with tree growth and mortality and for quantifying associated uncertainty. Aboveground biomass stocks and fluxes on the BCI plot exhibited strong spatial variation in relation to gap dynamics and weak systematic variation among topographically defined habitats. Biomass fluxes varied strongly among census intervals, but there was no directional trend in biomass stocks. Compared with plot studies in other Latin American tropical forests, BCI is close to the median in stocks and woody productivity and in the 23rd percentile for net flux.

Keywords: aboveground biomass; woody productivity; tree mortality; tropical forest; carbon; forest monitoring plot; biomass allometry; buttressed trees; spatial structure; temporal variation

INTRODUCTION

Tropical forests constitute a globally important carbon stock, and uncertainty about the future of this carbon is one of the largest sources of uncertainty in projecting the future global carbon cycle (Cavaleri et al., 2015). Tree trunks and branches account for the large majority of forest biomass carbon stocks, as dry wood is approximately half carbon by weight (Thomas and Martin, 2012). The trajectory of tropical forest biomass carbon stocks thus depends on whether the total mass of wood in tropical forests increases or decreases, which in turn depends on land use as well as on how tree growth and mortality respond to changing atmospheric composition and climate (Mitchard, 2018). It is well understood that deforestation and forest degradation result in the release to the atmosphere of carbon previously stored in biomass as biomass burns or decomposes, whereas reforestation and forest regrowth result in net carbon uptake. What is less clear is how increasing atmospheric carbon dioxide and climate change are affecting carbon stocks in intact and otherwise undisturbed tropical forests.

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Manuscript received 14 November 2022; accepted 17 July 2023.

Carbon stocks per area in intact forests depend on the balance of two carbon fluxes—carbon uptake associated with tree growth, and carbon loss associated with tree mortality and branchfall—and both these fluxes can be influenced by global change (Muller-Landau et al., 2021). Increasing atmospheric carbon dioxide concentrations and increasing nitrogen deposition may increase photosynthetic rates, and thus potentially tree growth fluxes and forest carbon stocks (Norby et al., 2005; Quinn Thomas et al., 2010). At the same time, changing climates are increasing the frequency and intensity of droughts and major storms, and these and other factors may be increasing tropical tree mortality rates, thereby decreasing forest carbon stocks (McDowell et al., 2018).

The Barro Colorado Island (BCI) 50-ha plot was installed in 1980 to study forest composition and dynamics, and complete inventories of all stems larger than 1 cm in diameter have been conducted approximately every five years since then. These data are complemented by large datasets on tree height and wood density collected in central Panama. Together, these data can be used to quantify the aboveground biomass (AGB) of each tree measured. The BCI 50-ha plot is therefore an exceptional resource for studying spatial and temporal variation in carbon stocks and fluxes. The temporal coverage of forest inventories (40 years and growing) provides insight into long-term changes in biomass dynamics; the plot's large size limits sampling errors that can occur with smaller plots; and measurements of all trees from a small diameter upward provide crucial information on understory carbon dynamics.

In this chapter, we review previous research on woody biomass on the BCI 50-ha plot, including methodological studies as well as patterns of variation in woody biomass stocks and fluxes across space, time, tree size, and functional group. We also present updated analyses of these patterns in figures, and the associated supplemental material provides complete associated R code, extended tables of results, as well as additional information on the sensitivity of the results to methodological details. Other chapters in this volume address soil carbon stocks and fluxes (Cusack, 2024), woody debris carbon stocks and fluxes (Gora, 2024), and remote sensing of forest structure and dynamics, including estimated biomass stocks and fluxes (Cushman, 2024).

BACKGROUND

AGB can be measured directly by harvesting, drying, and weighing vegetation. Such destructive methods are expensive, preclude remeasurement over time in the same site, and have never been applied on BCI where destructive sampling is prohibited. AGB is thus more commonly estimated by combining local tree census data with allometric equations fitted to other destructive harvest data. These allometric equations enable estimation of the biomass of individual trees from their trunk diameters, and sometimes their heights and species wood densities. The estimated AGB is then summed across all trees to obtain the total AGB of the stand. This is often further converted to carbon stocks by multiplying by a conversion factor representing the proportion of dry biomass that is carbon, which is commonly taken to be a fixed value, although in reality it varies among species. Wood carbon fractions for 59 Panamanian tree species averaged 45.0% (range 42–48%) for oven-dried samples and 47.4% (range 42–52%) for freeze-dried samples that capture the volatile fraction (Martin and Thomas, 2011), compared with an average of 45.6% for 1,187 tropical angiosperms (Martin et al., 2018).

Estimating the biomass of an individual tree using allometric equations involves multiple choices and approximations. Early allometric equations were calibrated on only a few harvested trees, usually at few sites, and used only diameter as a predictor variable (e.g., see Chave et al., 2003). Later equations included a larger number of sites spread across the tropics and incorporated tree height, or other environmental factors that affect height, and wood specific gravity (Chave et al., 2005, 2014). Tree height is more difficult to measure than diameter, especially in dense vegetation (Larjavaara and Muller-Landau, 2013); for plots such as BCI where heights are not available for all trees, it can be estimated using a height-diameter allometry equation (for BCI, see Martínez Cano et al., 2019). Wood specific gravity (defined as the oven-dry mass of wood per mass of water displaced by the fresh volume) is most often assigned by species from large databases (e.g., Zanne et al., 2009); it is often referred to as wood density in the ecological literature.

In addition to biomass stocks, ecologists are also interested in biomass fluxes associated with wood production and tree mortality, as well as their difference, which represents the net change in biomass over time. Aboveground woody productivity can be calculated simply by summing the increase in biomass of living trees between two censuses and the biomass of recruited trees (i.e., trees that were measured for the first time in the later census), and dividing by the total area and by the length of the time interval between the two censuses. Aboveground woody mortality is most simply calculated by summing the biomass of all trees that died between two censuses, and dividing by total area and time interval. These simple calculations underestimate the total flux of mass per area per time because they miss productivity of trees that died during the census interval, a bias that can be overcome by the use of somewhat more complicated equations (Kohyama et al., 2019).

METHODOLOGICAL STUDIES

Chave et al. (2004) presented one of the first studies estimating the contributions of different factors to uncertainty in biomass estimates, using the BCI 50-ha plot as a case study. They quantified uncertainty resulting from tree measurement error, choice of allometric model, sampling error associated with plot size, and representativeness of the larger forest landscape. Tree measurement errors can be exceptionally well quantified for BCI using double-blind remeasurements of 4,070 trees (Condit et al., 2017). Chave et al. (2004) estimated that the error associated with allometric models was the most important source of error in AGB at the plot level, around 13% of the mean AGB estimate. Subsequent studies have expanded on this pioneering work, and the BIOMASS package in R now includes tools for estimating and propagating these sources of uncertainty, including the BCI tree remeasurement data as an example (Réjou-Méchain et al., 2017). These studies all find that estimates of plot biomass stocks and fluxes depend strongly on the allometric equations and parameters that are chosen (Figure S1a, Table S1; Chave et al., 2003, 2004).

Studies on the BCI 50-ha plot have also developed improved methods of estimating biomass stocks and fluxes for trees with nonstandard diameter measurement heights and changes in measurement heights over time. The standard height for measuring tree diameter is 1.3 m (referred to as diameter at breast height, or dbh), but trees with trunk irregularities at 1.3 m typically are measured at another point, and buttressed trees are measured above the tops of buttresses (Condit, 1998). For these trees, diameter measurement height often varies among censuses, as buttresses grow upward and deformities and irregularities change over time. Because tree trunks decrease in diameter with height (i.e., they taper), this creates challenges to correctly estimate diameter and biomass growth of individual trees (Sheil, 1995). Furthermore, this can lead to biases in plot-level estimates of biomass change when there are systematic differences in measurement height methods among censuses, as on the BCI 50-ha plot, where the proportion of trees measured at higher points increased over time, especially in the early censuses (Muller-Landau et al., 2014). Cushman et al. (2014) measured trunk taper above buttresses on hundreds of trees on BCI and developed a taper correction equation that can be used to estimate equivalent diameter at 1.3 m height from measurements at nonstandard heights. Cushman et al. (2021) expanded on this work, quantifying trunk taper at multiple sites and developing generalized equations for taper correction in tropical forests. Muller-Landau et al. (2014) also explored the effects of alternative outlier detection and correction procedures for estimates of biomass change, showing that multiple reasonable alternative procedures can result in very different estimates.

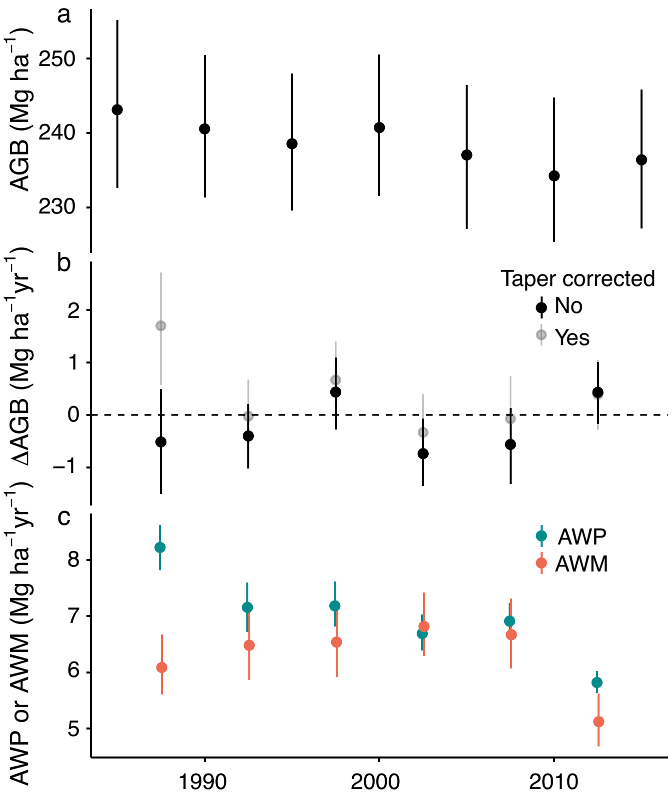

FIGURE 1. Aboveground biomass (AGB) stocks and fluxes in the Barro Colorado Island (BCI) 50-ha plot. (**a**) AGB (Mg ha^{-1}) by census; (**b**) changes in AGB stocks (ΔAGB, Mg ha^{-1} yr^{-1}), by census interval; (**c**) AGB fluxes (Mg ha^{-1} yr^{-1}), by census interval: aboveground woody productivity (AWP) in blue and aboveground woody mortality (AWM) in red. Points represent the total plot value, and segments represent the 95% confidence interval obtained by bootstrapping over 20 × 20 m quadrats. Individual stem AGB values were obtained using the biomass allometry equation from Chave et al. (2014) including height and the local height allometry from Martínez Cano et al. (2019). See Table S1 for exact values, and Appendix S1 for R code and methodological details.

For the Barro Colorado Nature Monument (BCNM), we currently recommend use of the Chave et al. (2014) pantropical equation including height, in combination with the generalized local height allometry of Martínez Cano et al. (2019) and species-specific wood-specific gravity values from regional measurements, where available (Condit et al., 2019, species list; Rutishauser et al., 2020, supplementary material). This produces an AGB estimate for 2015 of 236 Mg ha^{-1} (Fig. 1a; Table S1). The Chave et al. (2014) allometric equation is based on the largest existing dataset of harvested trees (4,004, including 1,481 with height) and is widely used in tropical studies, simplifying comparison of biomass values across studies and sites. The use of a local height allometry (Martínez Cano et al., 2019) ensures that the allometry is adapted to local environmental conditions in the BCNM. In contrast, the use of the Chave et al. (2014) allometry without height results in a 10% higher value, likely overestimating biomass at BCI. For comparisons over time within the BCI 50-ha plot that include censuses before 1995, we recommend use of the taper correction to avoid biases resulting from changes in the distribution of measurement heights across censuses. When comparing BCI with other sites, especially if using data from 1995 and after, we recommend not using the taper correction unless it can be applied across all sites. For comparisons of variation in biomass stocks and fluxes at many sites across the regional rainfall gradient for which local height data are not available (e.g., Muller-Landau et al., 2024), we recommend the use of the Chave et al. (2014) pantropical equation without height, as its environmental factor implicitly captures climate-related variation in height allometries. We note that the preferred allometric equations are expected to change in the future as equations incorporating more data and more regional data become available. Many additional biomass allometry studies have been published since Chave et al. (2014), including Duque et al. (2017), which is based on 392 trees harvested in the Pacific coast of Colombia, an area with similar floristics and forest structure to the BCI 50-ha plot.

EMPIRICAL PATTERNS

Spatial Variation

Woody biomass stocks and fluxes exhibit high small-scale spatial variability (e.g., tens of meters; Réjou-Méchain et al., 2014). This is especially true when all stocks and fluxes for a tree are assigned to the location of the trunk, as is typical in such analyses; the noisiness decreases when they are instead distributed across the estimated crown area (Mascaro et al., 2011b). Because forest inventories are expensive and therefore limited in area (typically 0.1–1 ha), this fine-scale variability results in sampling errors. These can be well-quantified on large plots like the BCI 50-ha plot by quantifying the spatial variation within the plot. Chave et al. (2003) calculated that estimating the total plot's AGB within a 20% error with 95% confidence would require 481 subplots of 10 × 10 m (4.81 ha total), 160 of 20 × 20 m (6.4 ha total), or nine of 100 × 100 m (9 ha total). A single 1-ha subplot is within 10% of the mean value of the plot as a whole only 40% of the time (Hetzer et al., 2020). In general, the standard deviation (SD) of variation among subplots declines with increasing area approximately as SD~1/sqrt(area), for both biomass (Chave et al., 2003; Réjou-Méchain et al., 2014) and biomass change (Muller-Landau et al., 2014), as expected for independent samples, but with deviations indicative of spatial autocorrelation in biomass as subplot size exceeds 1 ha (Réjou-Méchain et al., 2014). Variograms and wavelet variance analyses show a lack of statistically significant local spatial autocorrelation of biomass or biomass change within the BCI 50-ha plot for smaller subplots of 5 × 5 to 100 × 100 m (Muller-Landau et al., 2014; Réjou-Méchain et al., 2014), supporting the treatment of subplots as independent samples.

The BCI 50-ha plot includes some topographic variation and can be divided into distinct habitats based on slope and elevation, with an additional separation of a small patch of younger forest in the north central part of the plot (Harms et al., 2001; Harms, 2024). These topographically defined habitats differ systematically in biomass and woody productivity (Fig. 2, Table S2; Chave et al., 2003). The slope habitat has the highest estimated biomass per area (274 ± 15 Mg ha^{-1}), while the swamp has the highest estimated woody productivity flux (9.2 ± 2.4 Mg ha^{-1} yr^{-1}). Conversely, young forest has the lowest estimated biomass (193 ± 18 Mg ha^{-1}) and woody productivity (6.4 ± 1.0 Mg ha^{-1}). These differences among habitats, combined with the large-scale spatial structure of habitats within the plot, can explain why variation among 1-ha and larger subplots is larger than expected based on variation among smaller subplots (Réjou-Méchain et al., 2014).

Temporal Variation

Productivity and mortality fluxes varied significantly among census intervals in the BCI 50-ha plot, yet biomass stocks remained relatively constant between 1985 and 2015 (Fig. 1; Chave et al., 2003, 2008; Feeley et al., 2007a; Cushman et al., 2014; Muller-Landau et al., 2014; Meakem et al., 2018; Rutishauser et al., 2020). The exact temporal patterns vary considerably depending on methodological details regarding allometric equations and approaches for dealing with changes in the point of measurement height and outlying growth records, especially for productivity (Table S1), leading to differences in results among studies. Because tree measurement points were moved substantially upward on many trees from 1985 to 1990, the estimated net flux for 1985–1990 is particularly sensitive; for example, it is significantly positive if a taper correction is applied, and slightly negative without one (Fig. 1b; Cushman et al., 2014).

Temporal variation in wood productivity and mortality has been explained in part by the effects of climate on tree growth and mortality, although making such links is challenging given the five-year census intervals. Both mortality and diameter growth rates were elevated during the first census interval of 1982–1985, especially for larger trees; this interval included a major drought associated with a strong El Niño event (Condit, 1995; Feeley et al., 2007b; Condit et al., 2017; Meakem et al., 2018). Most studies do not attempt to calculate biomass stocks or fluxes for the first census (1982) and first census interval, because all of the trees, including buttressed trees, were measured in diameter at 1.3 m in the first census, but the one study that does so estimates both productivity and mortality fluxes were highest in this census interval (Meakem et al., 2018). Diameter growth rates and woody productivity were also elevated in the following census interval of 1985–1990 relative to later intervals (Chave et al., 2003; Condit et al., 2017; Meakem et al., 2018; Rutishauser et al., 2020). Feeley et al. (2007b) and Dong et al. (2012) examine how temporal variation in growth on BCI (through 2005) and one or three (respectively) other large tropical plots relates to climate, with both finding that growth was negatively correlated with mean daily minimum temperature and positively correlated with solar radiation among census intervals within sites.

Testing for changes in growth, mortality, and biomass within mature forests can be challenging because these forests are mosaics of areas in different stages of gap-phase regeneration (succession after canopy gap formation) and thus of areas with different forest structure, biomass, growth, and mortality. Several studies have taken advantage of the large size of the BCI 50-ha plot to test whether there have been changes over

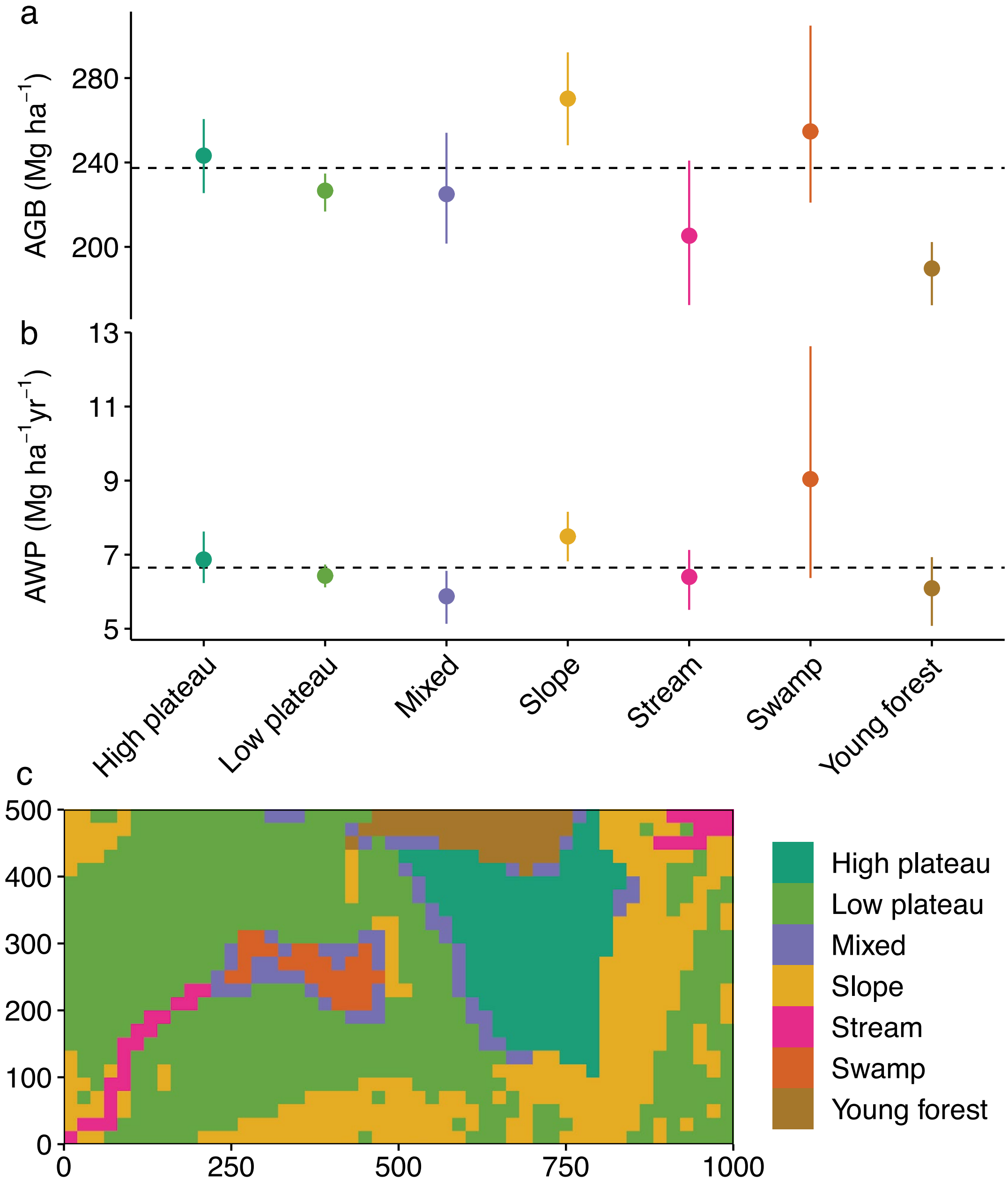

FIGURE 2. Spatial variation in (**a**) aboveground biomass (AGB, Mg ha^{-1}) and (**b**) aboveground woody productivity (AWP, Mg ha^{-1} yr^{-1}) among habitats, as defined by Harms et al. (2001). (**c**) The location of habitats in the 50-ha plot. In (a) and (b), points represent the habitat-specific means, averaged over censuses or census intervals (starting in 1995), and segments represent the 95% confidence interval obtained by bootstrapping over 20 × 20 m quadrats. The horizontal lines represent the mean value for the plot. Habitat-specific values for AGB, AWP, aboveground woody mortality (AWM) and net changes in AGB between censuses are provided in Table S2.

time in the distribution of gap dynamic stages or changes in biomass dynamics for a given gap dynamic stage (Feeley et al., 2007a; Muller-Landau et al., 2014; Rutishauser et al., 2020). Although differing in their methods and the census intervals included, all of these studies have concluded that the distribution of gap dynamic stages does not vary significantly among censuses and that biomass stocks and fluxes as a function of gap stage show no long-term directional trend across all

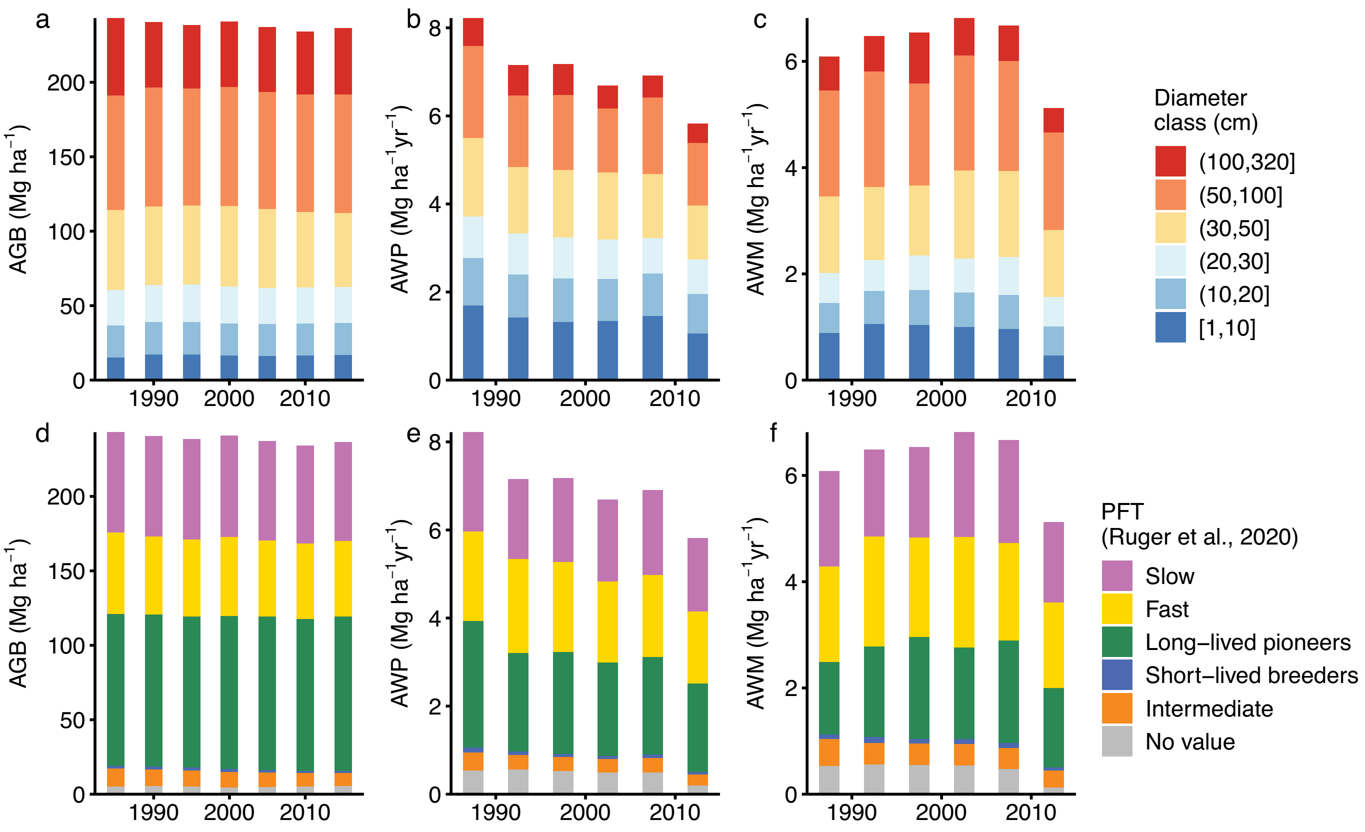

FIGURE 3. Contributions of (**a–c**) diameter classes and (**d–f**) functional groups to aboveground biomass (AGB, Mg ha^{-1}), aboveground woody productivity (AWP, Mg ha^{-1} yr^{-1}), and aboveground woody mortality (AWM, Mg ha^{-1} yr^{-1}). AGB, AWP, and AWM values as well as intercensus changes in AGB by size class and functional group are provided in Table S3.

census intervals. Mortality rates and fluxes, however, decreased from the initial censuses to the 1990-1995 interval and have increased since (Condit et al., 2017; Meakem et al., 2018; Rutishauser et al., 2020).

Contributions by Size Class, Functional Type, and Species

Biomass is highly unequally distributed among trees of different sizes and species. These distributions affect the plot's biomass fluxes, as trees of different sizes and functional traits have different growth and mortality rates, and respond differently to environmental variation. Intermediate diameter classes contained the greatest proportion of AGB: more than half of the total live AGB was in trees 10–60 cm in diameter (Chave et al., 2003; Piponiot et al., 2022). Woody productivity fluxes also peak at intermediate-diameter classes in BCI, but their value is relatively higher in small stems compared with AGB: stems ≥50 cm accounted for on average 59% of AGB, but only 45% of woody productivity (Meakem et al., 2018; Piponiot et al., 2022). The distribution of AGB stocks and fluxes among diameter classes varies little over time (Fig. 3a–c; Table S3). Classifying species by the functional groups defined by Rüger et al. (2020), we find that long-lived pioneers are the most important group, contributing an average of 43% of the AGB and 32% of woody productivity, with these proportions increasing over time (Fig. 3c–e; Table S4). The distribution of biomass stocks and fluxes among species is highly uneven. Just 10 species contribute 41% of AGB, and the distribution of contributions to aboveground woody productivity is only somewhat less skewed (Table S5).

THE BCI 50-HA PLOT IN A REGIONAL AND GLOBAL CONTEXT

The BCI 50-ha plot is intermediate in climate, soils, biomass stocks, productivity, and mortality in comparison with other forest sites in central Panama (Chave et al., 2004; Muller-Landau et al., 2024). Remote sensing studies suggest the forest structure

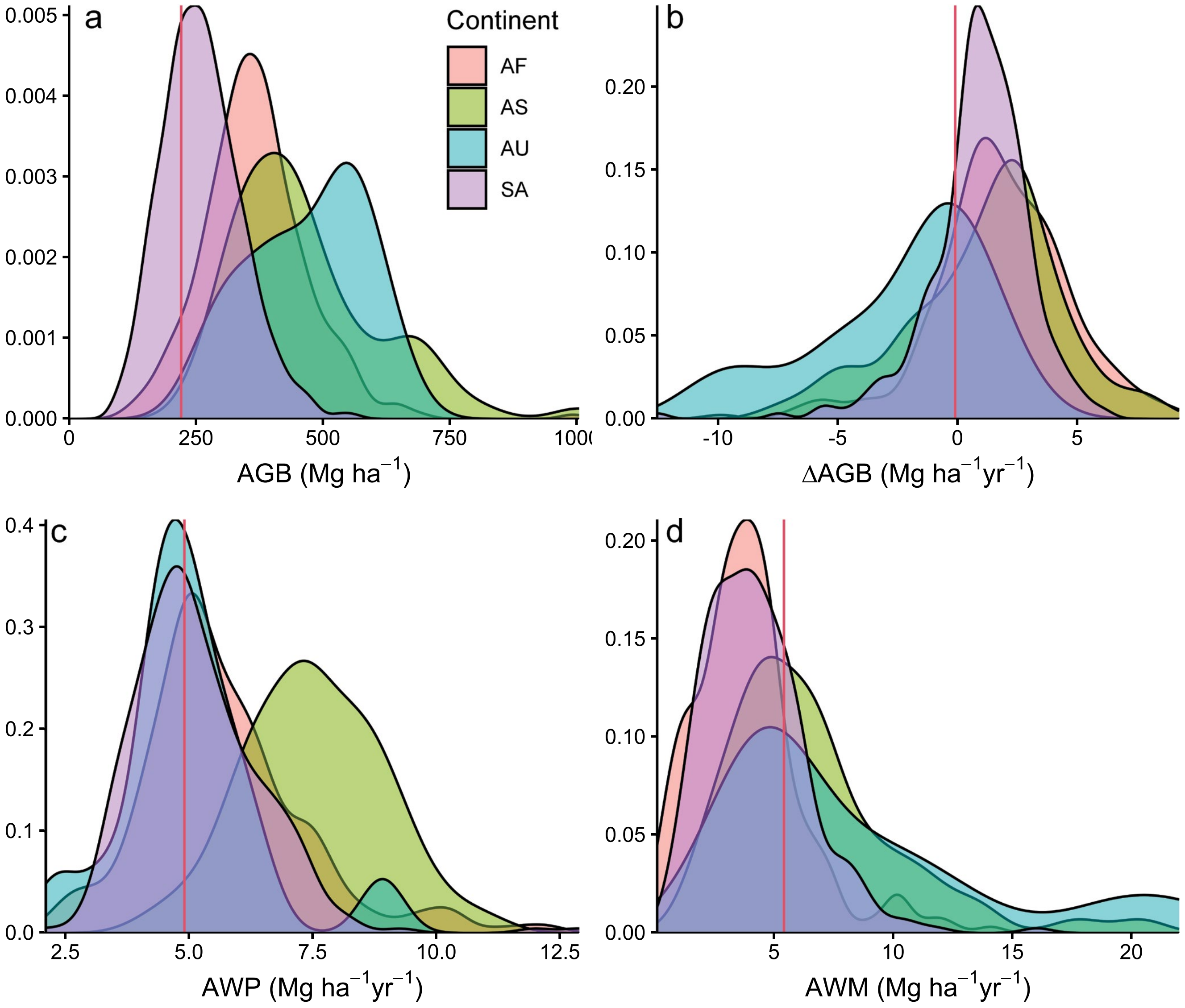

FIGURE 4. Density plots of distributions of aboveground biomass (AGB, Mg ha^{-1}), changes in AGB (ΔAGB, Mg ha^{-1} yr^{-1}), aboveground woody productivity (AWP, Mg ha^{-1} yr^{-1}), and aboveground woody mortality (AWM, Mg ha^{-1} yr^{-1}) in mature tropical forests on four continents: Africa (AF), Asia (AS), Australia (AU), and South America (SA); data are from Sullivan et al. (2020). Mean values for BCI (using the same methods) are indicated by red vertical lines.

and biomass of the 50-ha plot are fairly typical for old-growth forest in the central area of the island (Mascaro et al., 2011a), and its biomass, productivity, and mortality are similar to those found in other old-growth plots on BCI, even though the plot is in the flattest, highest elevation part of the island (chapter 8, Meakem et al., 2024).

Compared with other old-growth tropical forest plots in Latin America included in Sullivan et al. (2020), the BCI 50-ha plot is fairly typical in its values of biomass stocks, productivity, and mortality and is lower than most (23rd percentile) in net biomass change (Fig. 4). The contrast between multiple high-profile studies reporting increasing biomass stocks in other plot-based studies of tropical forest (Baker et al., 2004; Lewis et al., 2009; Sullivan et al., 2020) and the relatively stable biomass stocks on the BCI 50-ha plot over more than 30 years has led many to ask if there is something different about BCI, in biology or methods. However, a recent remote sensing study finds that intact moist tropical forests in South America were on average approximately carbon neutral between 2000 and 2019 (Xu et al., 2021). Specifically, 18% of the area was estimated to be gaining carbon at a rate of 0.19 Mg C ha^{-1} yr^{-1}, 20% losing carbon at a rate of 0.18 Mg C ha^{-1} yr^{-1}, and the remaining area had no significant trend. This suggests that, far from being an outlier, BCI is similar to the median intact moist tropical forests of South America in the relative stability of its forest carbon stocks. Variation among sites in forest carbon stocks, productivity, and net flux is expected because of underlying heterogeneity. Tropical forests are highly heterogeneous in climate, soils, anthropogenic pressures, forest structure, and species composition, and these differences can all contribute to variation in their carbon stocks and fluxes, including biomass trajectories over recent decades (Muller-Landau and Wright, 2024).

CONCLUSIONS AND FUTURE DIRECTIONS

The 50-ha plot tree censuses have greatly improved our knowledge of tropical forest biomass stocks and dynamics, as well as the underlying processes driving spatial and temporal variation in tree growth and mortality. They have led to a better understanding of the multiple sources of uncertainty in estimating woody biomass stocks and fluxes. Although woody biomass fluxes have varied among censuses, including in relation to El Niño events, there were no long-term directional changes in woody biomass stocks. However, there are still critical gaps in this knowledge, particularly with respect to temporal variation in biomass fluxes in relation to climate variation and global change, and the degree to which estimates of biomass stocks and fluxes based on allometric equations capture true patterns of variation.

The five-year census interval length for the complete tree censuses on the 50-ha BCI plot limits the ability to investigate temporal variation in woody productivity and mortality, as these intervals average over annual and intra-annual variation, and provide few data points for links to climate. Annual censuses of subsets of trees for mortality and damage (Arellano et al., 2021; Zuleta et al., 2022) and for diameter growth with dendrometers (Ramos et al., 2022) now provide higher temporal resolution data for quantifying temporal and testing associated hypotheses. Monthly drone flights over the 50-ha plot since October 2014 provide even higher temporal resolution data on canopy disturbance, including treefalls, branchfalls, and standing dead trees (Araujo et al., 2021).

Estimates of biomass stocks and fluxes on the 50-ha plot to date all rely on generalized allometric equations, which have large errors on individual trees and systematic errors across sites, species, and tree condition, including liana infestation. A key question is the degree to which these indirect methods correctly capture spatial and temporal variation in biomass stocks and fluxes, especially considering increasing liana abundance and infestation (Wright et al., 2004; Ingwell et al., 2010; Schnitzer et al., 2021) and changes in tree species composition (Katabuchi et al., 2017). Furthermore, standard estimates of biomass loss fluxes ignore branchfalls, which are an important part of AGB turnover in tropical forests and account for about a fourth of the area of canopy gaps in BCI (Araujo et al., 2021). Terrestrial laser scanning can provide nondestructive measurements of stem and branch volume, which greatly increase the precision of forest biomass estimates, and can capture local variation in biomass allometries (Disney, 2019). Repeat terrestrial or drone-based laser scanning now provides the means to more directly measure aboveground woody stocks and fluxes (Cushman et al., 2024), and the collection of such datasets should be a high priority for future research.

ACKNOWLEGMENTS

We thank Alvaro Duque and Stuart Davies for helpful comments on an earlier draft. We gratefully acknowledge the contributions of the many people who have assisted in measuring trees and entering data over the years, as well as Robin Foster for his role as one of the founding principal investigators; Robin Foster, Jeff Klahn, and Sue Williams for supervising the first, second, and third censuses, respectively; and Steve Dolins for designing the tree census database. The BCI Forest Dynamics Research Project was made possible by National Science Foundation grants to Stephen P. Hubbell (DEB-0640386, DEB-0425651, DEB-0346488, DEB-0129874, DEB-00753102, DEB-9909347, DEB-9615226, DEB-9615226, DEB-9405933, DEB-9221033, DEB-9100058, DEB-8906869, DEB-8605042, DEB-8206992, DEB-7922197), support from the Forest Global Earth Observatory (ForestGEO), the Smithsonian Tropical Research Institute, the John D. and Catherine T. MacArthur Foundation, the Mellon Foundation, the Small World Institute Fund, and numerous private individuals.

AUTHOR CONTRIBUTIONS

H.C.M. and C.P. conceived the manuscript and reviewed the literature. C.P. conducted the analyses and produced the tables and graphs. C.P. and H.C.M. drafted the text. S.P.H. designed the plot census and obtained funding for initial censuses. R.C., R.P., and S.A. oversaw data collection. R.P. and S.A. identified plant species. R.C. and S.L. managed the data.

ONLINE SUPPLEMENTARY MATERIAL

Appendix S1. R code for running analyses. https://doi.org/10.25573/data.22718599

Tables S1–S7. Stocks and fluxes of aboveground biomass, basal area and number of trees in the BCI 50-ha plot by size class, habitat, plant functional type, species, and under alternative calculation methods. https://doi.org/10.25573/data.22780166

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