



Landscape-scale lidar analysis of aboveground biomass distribution in secondary Brazilian Atlantic Forest

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ABSTRACT

Secondary forests account for more than half of tropical forests and represent a growing carbon sink, but rates of biomass accumulation vary by a factor of two or more even among plots in the same landscape. To better understand the drivers of this variability, we used airborne lidar to measure forest canopy height and estimate biomass over 4529 ha at Serra do Conduru Park in Southern Bahia, Brazil. We measured trees in 30 georeferenced field plots (0.25-ha each) to estimate biomass using allometry. Then we estimated aboveground biomass density (ABD) across the lidar study area using a statistical model developed from our field plots. This model related the 95th percentile of the distribution of lidar return heights to ABD. We overlaid this map of ABD on a Landsat-derived forest age map to determine rates of biomass accumulation. We found rapid initial biomass regeneration (~6 Mg/ha yr), which slowed as forests aged. We also observed high variability in both height and biomass across the landscape within forests of similar age. Nevertheless, a regression model that accounted for spatial autocorrelation and included forest age, slope, and distance to roads or open areas explained 62 and 77 percent of the landscape variation in ABD and canopy height, respectively. Thus, while there is high spatial heterogeneity in forest recovery, and the drivers of this heterogeneity warrant further investigation, we suggest that a relatively simple set of predictor variables is sufficient to explain the majority of variance in both height and ABD in this landscape.

Abstract in Portuguese is available with online material.

Key words: airborne laser scanning; second growth; Southern Bahia; topography; tropical moist forest.

SECONDARY TROPICAL FORESTS REPRESENT MORE THAN HALF OF THE WORLD'S TROPICAL FORESTS (FAO 2015) and are likely to increase in the future as deforestation and agricultural land abandonment continue (Chazdon 2014). Existing secondary tropical forests are an important carbon sink (Pan *et al.* 2011, Chazdon *et al.* 2016) and provide key habitat for tropical forest species (Chazdon *et al.* 2009, Dent & Wright 2009). In the Neotropics, studies from a network of plot-based chronosequences suggest that secondary forests recover quickly, reaching 90 percent of mature forest biomass in 66 yr (Poorter *et al.* 2016). However, forest regeneration rates are highly variable, and the drivers of this variation are both poorly understood and difficult to model based on the limited data available (Norden *et al.* 2015). Improving our understanding of this variability in biomass recovery rates will aid the modeling of terrestrial carbon uptake and inform forest restoration work.

We focus here on the Brazilian Atlantic forest, which once stretched over nearly the entire coast of Brazil but has been reduced to 12 percent of its original extent remaining by hundreds of years of logging and land use conversions (Ribeiro *et al.* 2009). Forest in this region has been harvested for wood products, cleared for swidden agriculture, converted to pasture or industrial crops such as sugar cane, or partially cleared for cacao cultivation. Selective logging has extensively affected remnant forest patches. Both hunting and fragmentation have contributed to severe defaunation (Canale *et al.* 2012). The remaining forest exists mostly as small, scattered fragments (Ribeiro *et al.* 2009), but efforts are underway to restore larger tracts and some natural regeneration has occurred in the past decades (Calmon *et al.* 2011).

The factors that affect variation in biomass regeneration in secondary forests depend on the spatial scale of interest. At global to continental scales, differences in total precipitation and its seasonality are important drivers of biomass recovery (Becknell *et al.* 2012, Poorter *et al.* 2016). At smaller scales, regrowth is also

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affected by topography, species composition, spatial structure (the size, shape, and distribution of patches across the landscape), and site history (Groeneveld *et al.* 2009). Topography has rarely been examined in tropical secondary forests but plays an important role in landscape-scale biomass distributions in mature forest sites (Clark & Clark 2000, Taylor *et al.* 2015) and is often correlated with tropical soil nutrient availability (Takyu *et al.* 2002, Vitousek *et al.* 2003, Porder *et al.* 2005, Osborne *et al.* 2017). Variation in soils affects productivity and biomass density at multiple sites (Davidson *et al.* 2004 Becknell & Powers 2014, Waring *et al.* 2015a), but soil properties also affect species composition and vice versa (John *et al.* 2007, Waring *et al.* 2015b). Species diversity and composition can play a role in biomass distributions (Finegan *et al.* 2015), as can the abundance of functional groups such as lianas or palms (Ledo *et al.* 2016, Scaranello *et al.* 2016). Whatever the scale, the extent and intensity of human land use are also likely important factors in determining rates of biomass recovery in secondary forests (Aide *et al.* 2000, Guariguata & Ostertag 2001).

The main source of data on secondary forest biomass regeneration comes from small plot-scale studies that use chronosequences to understand forest recovery (Chazdon 2014, Poorter *et al.* 2016). These chronosequences often rely on relatively small numbers of plots that may not capture the landscape-scale variation in biomass, nor be sufficient to elucidate the drivers of this variation across a landscape. While small plot-scale studies are crucial for measuring many important variables including species density and soil properties, airborne lidar offers an alternative for quantification of forest recovery at larger spatial scales (Leitold *et al.* 2015). Lidar data provide direct measurements of height, which can be used to generate estimates of forest biomass (Lefsky *et al.* 2002, Asner & Mascaro 2014). These height measurements and biomass estimates are used to study forest structure and dynamics (Longo *et al.* 2016, Silva *et al.* 2017) and are increasingly used to overcome the potential sampling error in plot-based studies of heterogeneous landscapes (Getzin *et al.* 2017, Asner *et al.* 2018). Similar to small plot-based chronosequences, lidar can be used to study forest recovery by combining the data with forest age maps derived from historical aerial photography or satellite imagery. Unlike small plot chronosequences, however, lidar can sample such a large area that in addition to age, the effects of landscape-scale factors such as slope, aspect, proximity to roads, and elevation on forest recovery can be assessed.

Here we present such an assessment, using lidar-derived forest heights and biomass from the Brazilian Atlantic Forest in southern Bahia, Brazil. This is the first lidar-based study of biomass distribution in this floristically distinct and highly diverse region of Atlantic Forest (Thomas *et al.* 1998, Martini *et al.* 2007) and one of the few studies to use lidar to estimate secondary forest regeneration rates (Helmer *et al.* 2009, Mascaro *et al.* 2012). Specifically, we ask: (1) What is the distribution of forest height and biomass across forest age? (2) What is the relative influence on height or aboveground biomass density (ABD) of forest age, topography, and distance to roads and clearings? (3) How quickly

does height and biomass recover in the Southern Bahia Atlantic forest landscape?

METHODS

SITE DESCRIPTION.—This study was conducted in Serra do Conduru State Park in Southern Bahia, Brazil (14°30'16" S, 39°6'36" W). Serra do Conduru State Park houses a moist tropical forest with mean annual precipitation around 2000 mm distributed relatively evenly throughout the year and mean annual temperature of 24°C (Piotto *et al.* 2009). Elevation in Serra do Conduru ranges from under 100 m to just above 400 m asl. The park was established in 1997 to protect an area of intact Atlantic forest and restore the surrounding matrix of land previously used for pasture, swidden agriculture, cacao plantations, or cleared to harvest wood. The park bounds one of the largest contiguous areas of Atlantic forest in the northeast of Brazil (almost 10,000 ha) and includes patches of secondary forest at different stages of regeneration, active forest restoration sites, and areas of older forest that have been selectively logged in the past. Selective logging, hunting, and fiber harvesting are common throughout the park. Some small patches within the park remain occupied or used for grazing. Several frequently used roads bisect the park, and there are trails used by local inhabitants throughout the area.

FIELD MEASUREMENTS OF BIOMASS.—We measured tree diameters to estimate biomass in 30 plots (50 × 50 m each). To capture the variation in the landscape, the plots were established across gradients of slope (0–45%) and biomass. We measured the diameters at 1.3 m (dbh) of all trees above 10 cm (dbh) and trees below 10 cm (dbh) in 5 randomly located subplots (5 × 10 m) per plot.

We estimated tree biomass using a general tropical forest allometric equation using dbh, wood density, and a climate index that combines temperature seasonality, climate water deficit, and precipitation seasonality (Chave *et al.* 2014). We assigned each field plot a probable age as initiation of regeneration based on their location and forest age map produced with the Landsat analysis (see below; Table S1). Then we assigned trees within each plot a community-weighted mean wood density based on the time as abandonment (0.59–0.67 g/cm³) from plots of similar ages in the same park (Piotto *et al.* 2009). The biomass of palms was estimated using a general Arecaceae family-level allometric equation, which estimates biomass from diameter (Goodman *et al.* 2013). The estimated biomass for all trees was summed and divided by plot area to estimate ABD.

Field plots were geo-located using a Trimble Geo7x by taking an average of 65 position readings per plot corner. GPS readings were differentially corrected using a permanent base station located ~30 km from the field site. The postcorrection horizontal precision estimate for plot corners ranged from 0.1 to 1.8 m with an average of 1.2 m.

MAPPING FOREST AGE AND ANTHROPOGENIC FEATURES.—We used a time series of Landsat imagery to map forest age across the study

area (Fig. 1). In each year when cloud-free Landsat images were available, we conducted a supervised forest vs. non-forest classification using training areas in or around our study area that were consistently forested or not forested during entire range of the Landsat time series (1984–2016). We were able to find images with less than 20 percent clouds for 16 of the 32 yr: 1984, 1985, 1986, 1988, 1989, 1990, 1991, 1994, 1996, 2000, 2002, 2004, 2005, 2007, 2010, 2011, and 2016. Cloud-covered areas were identified by eye and were categorized as ‘no data’ for that year. For clouded areas, age determination was made based on the previous and subsequent years data. We combined these classified forest–non-forest layers for each year to produce estimates of forest age for each 30 m pixel in the study area.

We mapped the distance to current anthropogenic features (roads, and open areas) by combining lidar data with GPS data and imagery. We digitized roads using GPS data collected during fieldwork and 2011 Ikonos imagery. To find open areas, we first made a 1-m-pixel-scale canopy height model (CHM) using the lidar data. We took the maximum height measured in each 1×1 m pixel and then used a 5-pixel mean moving window smoothing function to remove anomalies. Next, we found all areas larger than 100 m^2 with a canopy height below 3 m. We combined these 100 m^2 open areas with the roads and calculated the distance from every point in the landscape to these anthropogenic features.

LIDAR DATA COLLECTION.—Lidar data were collected over a 4529-ha area encompassing the southern section of Conduru State Park in December 2015. The Brazilian firm GEOID Laser

Mapping obtained the small-footprint, multiple-return (up to 4 returns per pulse) data with an Optech Orion M300 sensor mounted on an airplane flying at an average altitude of 850 m above ground level with a field of view of 12° and a flight line overlap of 65 percent. The average lidar return density was 94 points/ m^2 . The digital terrain model (DTM) was generated from the lidar data by GEOID using a process previously described and shown to be accurate (Leitold *et al.* 2015). After subtracting ground height based on the DTM, mean canopy height at 30- and 50-m-pixel scales was calculated by first creating a 1-m canopy height map from the lidar data, then taking the average of this canopy height map over each 30 or 50 m pixel.

CALCULATION OF BIOMASS FROM LIDAR DATA.—To map estimated biomass across the landscape with lidar data, we used the area-based method where ABD measured in field plots is correlated with lidar metrics over the same area (Fig. 1A; White *et al.* 2013). We calculated a set of lidar metrics for each of our 30 field plots. These metrics included height percentiles and descriptive statistics (*e.g.*, mean, variance, skewness, and kurtosis). Next, we evaluated which metrics best explained the variation in field-measured biomass across the 30 field plots. We compared linear and sigmoidal models using automated variable selection algorithms and used the Akaike information criterion (AIC) for model selection. The best linear models predicted negative biomass for low mean canopy heights. To avoid this problem, we selected a sigmoidal model with a single variable (equation 1); the height of the 95th percentile (m) of lidar returns over the 0.25 ha plot (P95) based on AIC (Fig. 2; RSME= 44.85). This model had the smallest

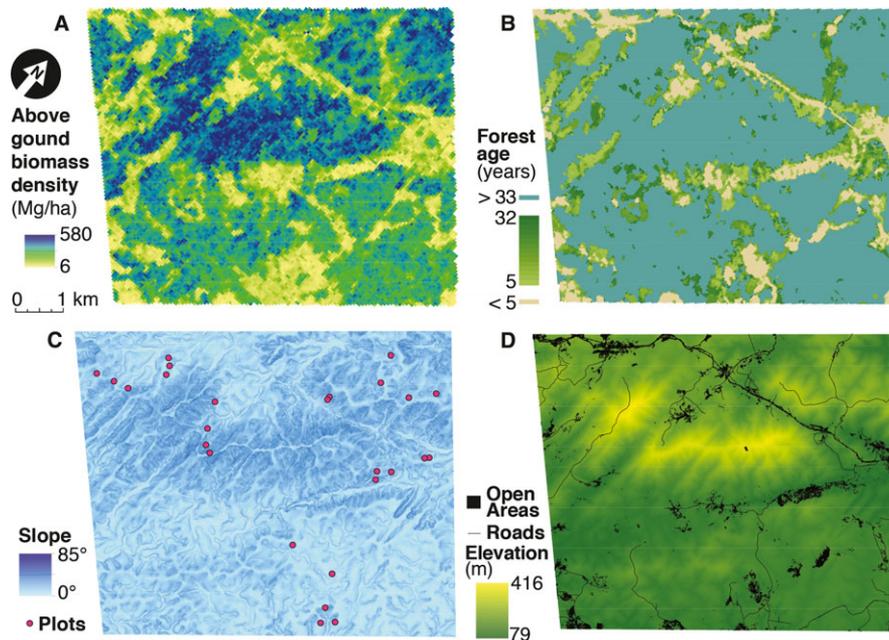


FIGURE 1. Maps of biomass (A), forest age (B), slope (C) and elevation, roads, and open areas (D). Maps have been rotated $\sim 40^\circ$ clockwise to better fit on the page. The aboveground biomass density map is at a 50-m-pixel scale, the forest age map is at a 30-m-pixel scale, and both slope and elevation are at the 1-m-pixel scale. The southeastern region of the study area with the highest elevations and steepest slopes also has the highest biomass density.

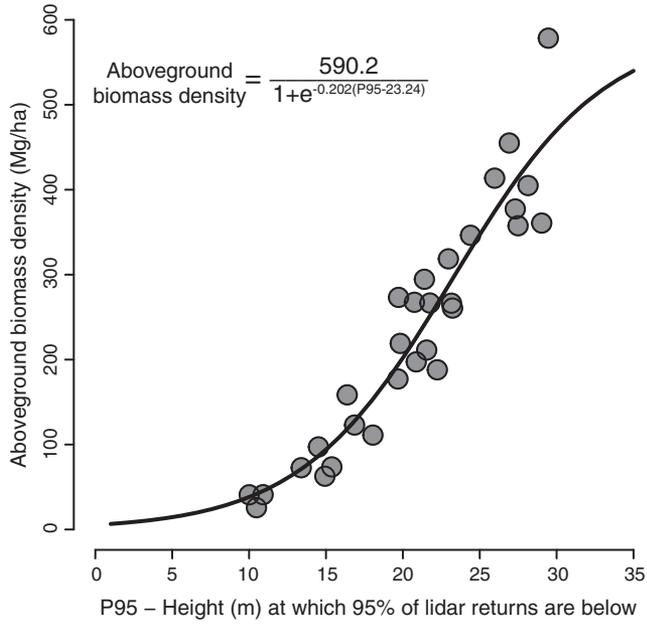


FIGURE 2. Aboveground biomass model. Points show the field-measured aboveground biomass density and lidar measured 95th percentile canopy height (P95) from thirty 0.25 ha field plots.

RMSE and made realistic (nonzero) predictions of biomass density across the landscape.

$$\text{Aboveground Biomass Density (Mg/ha)} = \frac{590.2}{1 + e^{-0.202(P95-23.24)}} \quad (1)$$

SPATIAL RESOLUTION OF DATA AND ANALYSES.—We used data with different spatial resolutions for different analyses. The age maps we developed from Landsat data are at the 30-m-pixel scale. Thus, any analysis involving these age maps was conducted at this scale or larger. Our maps of ABD are at the 50-m-pixel scale because the plots used to develop the lidar-AGD relationship were 50×50 m. We compared correlation coefficients and conducted regression analyses for canopy height at both 30- and 50-m-pixel scales to test for scale dependencies. We found very little differences between the results at these scales (Table 1), suggesting that the modeled relationships are not scale-dependent over this range. Raster data on slope or distance to anthropogenic features were developed at a 1-m scale and later scaled up to 30 or 50 m for statistical analyses.

RELATING HEIGHT AND BIOMASS TO LANDSCAPE VARIABLES.—We used an ordinary least squares-simultaneous autoregressive modeling (OLS-SAR) to explore the relationships between ABD or mean canopy height (the average of the 1 m CHM in each pixel) and forest age, topography, and distance to anthropogenic features. OLS-SAR allowed us to quantify the influence of the explanatory variables while simultaneously accounting for potential spatial autocorrelation and the spatial dependence of

TABLE 1. Regression coefficients for mean canopy height at the 30- and 50-m-pixel scale and for aboveground biomass density (ABD) at the 50-m-pixel scale. Variable coefficients are scaled for comparison so that larger coefficients indicate stronger effects. Lambda is the spatial autoregressive coefficient and is larger with more spatial autocorrelation. P-values for all coefficients were $< 2.2 \times 10^{-16}$.

| Explanatory variables | Height | Height | ABD |
|--|---------------------|---------------------|---------------------|
| | (30 m scale) | (50 m scale) | (50 m scale) |
| | Scaled coefficients | Scaled coefficients | Scaled coefficients |
| Age | 0.64 | 0.621 | 0.505 |
| Slope | 0.242 | 0.235 | 0.234 |
| Distance to roads and open areas >100 m ² | 0.196 | 0.232 | 0.211 |
| Model parameters | | | |
| <i>lambda</i> | 0.00024 | 0.000025 | 0.00025 |
| Nagelkerke pseudo-R ² | 0.75 | 0.77 | 0.62 |

unmeasured factors. All analyses were conducted using R (R Core Team 2017); to implement OLS-SAR regression, we used the *errrorsarlm* function from the R package *spdep* (Bivand *et al.* 2013). This function implements a spatial error model which accounts for spatial autocorrelation that variables in the model cannot explain (Kissling & Carl 2007).

To determine the OLS-SAR neighbor distance and weighting, we compared correlograms for Moran's I calculated using residuals of the non-spatial linear model and the OLS-SAR model. We tried neighbor distances between 100 and 2000 m and found that a neighbor distance of 1000 m minimized spatial autocorrelation of the OLS-SAR model residuals. We used a weighting function where the weight of a neighbor declines with distance at a rate that increases with distance. For each pixel, all other pixels with centers within 1000 m are given a weight. The closest pixels have the highest weight and the furthest have the lowest. The weights decline from 20 to 1 as the distance to a given pixel approaches 1000 m following an exponential decay function. This function was based on the shape of Moran's I correlograms which showed spatial autocorrelation at a maximum at the shortest distance and exponentially declining to zero at a distance of 1000 m. Before analysis, we scaled the variables to allow for the simple comparison of model coefficients. We did not include elevation, aspect, or other topographic variables in our analysis because they provided little additional explanatory power. Age was correlated with slope (Pearson correlation coefficient [PCC] = 0.15) and distance to anthropogenic features (PCC = 0.49). Slope and distance to anthropogenic features were correlated with each other (PCC = 0.25). For both height and ABD, we used random samples of 10,000 pixels for the OLS-SAR analyses because using the entire dataset was computationally prohibitive.

We used two approximations to examine rates of height and biomass change for forests less than 33 yr old. In a first linear

constant growth approximation, we divided height and biomass by age at each pixel. Alternatively, we estimated a variable rate over time from the derivative of the biomass or height vs. $\ln(\text{age})$ function. While each method highlights change at a different scale, together they give an approximation of the range of possible regeneration rates for forests at different ages.

RESULTS

AGE, HEIGHT, AND BIOMASS DISTRIBUTIONS.—In the thirty field plots (0.25 ha each), mean canopy height measured by lidar ranged from 4.9 to 26.4 m with an average of 17.3 m and a median of 17.5 m. Estimated ABD in the field plots ranged from 26 to 578 Mg/ha with a mean of 235 Mg/ha (Fig. 2). One field plot (ABD = 578 Mg/ha) had markedly higher biomass than other

plots because it included 10 trees above 50 cm dbh and one with dbh = 140 cm.

We mapped forest age across 4529 ha in our study area using a time series of Landsat images. We classified 395 ha (9%) as not forested and 1055 ha (23%) as secondary forest younger than 32 yr (in 2016). The remaining 3079 ha host secondary forests older than 33 yr or intact forests that may have been selectively logged in recent decades (Fig. 1B).

Lidar-derived mean forest canopy height at 30-m-pixel scale ranged from 0.1 to 35.1 m with a median of 17.9 m. Younger secondary forests (<33 yr old) had a mean canopy height of 11.0 m while forests 33 yr and older had a mean canopy height of 21.2 m. The median of the height distribution within a 5-yr age class increases as plots age (Fig. 3A) but there is considerable overlap among the height distributions of different age classes.

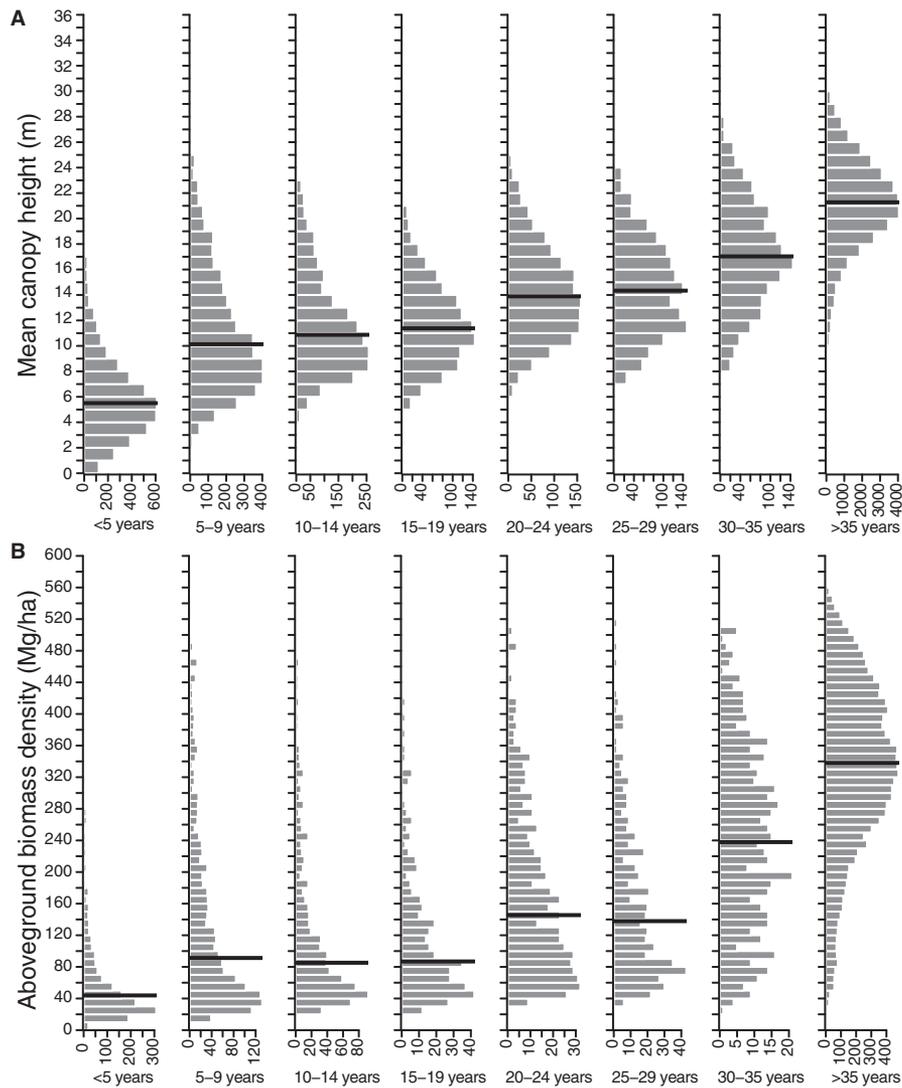


FIGURE 3. Distributions of height (A) and aboveground biomass density (B) in forests of different age. The thin black lines represent the median canopy height or aboveground biomass density for each age class. Median biomass and height generally increase with age and the distributions change from being skewed toward lower numbers toward being relatively normal as forest age.

Aboveground biomass density was mapped at the 50-m-pixel scale (the scale of our calibration plots) across 4529 ha based on a model of biomass (equation 1) calibrated by 30 forest inventory plots (Fig. 1A). ABD had a mean of 267 Mg/ha and ranged from 7 to 574 Mg/ha. Biomass distributions for young forest pixels (<30 yr) are mostly low, but have a long tail toward higher ABD (Fig. 3B). Older plots show a more symmetrical distribution of height and biomass.

REGRESSION OF MEAN CANOPY HEIGHT AND ABOVEGROUND BIOMASS DENSITY.—An OLS-SAR model of ABD including age, slope, and distance to roads and open areas explains 75 and 77 percent of mean canopy height variation at the 30- and 50-m-pixel scales, respectively (Table 1; Fig. 4A–B). Similarly, it explains ~62 percent of the variation in biomass at the 50-m-pixel scale (Table 1; Fig. 4C–D). For both height and biomass, age had the strongest effect followed by slope and distance to roads and open areas. The scaled coefficients show that age had at least twice the effect as slope for both height and biomass. Slope and distance to roads and open areas had similar-sized effects. Repeating the OLS-SAR analyses using a single explanatory variable shows that age, slope, and distance to anthropogenic features explains 70, 55, and 51 percent of the variation in canopy height, and 59, 40, and 47 percent of the variation in ABD.

RATES OF HEIGHT AND BIOMASS INCREASE.—The highest rates of height increase or biomass accumulation are in the youngest age groups (Fig. 5). These rates decline in the first 15 yr of succession and stabilize thereafter. Using a linear approximation, the median height increase is 1.7 m/yr in forests under 10 yr old,

0.9 m/yr to 0.6 m/yr as forests age increases from 10 to 20 yr old. 20- to 30-yr-old forests grow ~0.5 m/yr. A logarithmic model produces a similar pattern but accentuates the differences between age classes, resulting in estimates of 2.9, 0.29, 0.15, and 0.10 m/yr for 1-, 10-, 20-, and 30-yr-old forests, respectively. Similarly, a linear approximation suggests that median biomass increases 15 Mg/ha yr in secondary forest less than 10 yr old and declines to 6 Mg/ha yr in secondary forest between 10 and 32 yr old. In the logarithmic model, the biomass accumulation rate declines from ~41.7 Mg/ha yr at the start of regeneration to a tenth of that, 4.2 Mg/ha yr at 10 yr, 2.1 Mg/ha yr at 20 yr, and 1.4 Mg/ha yr at 30 yr.

DISCUSSION

Studies of secondary forests have shown wide variation in aboveground biomass recovery at both regional and landscape scales (Becknell & Powers 2014, Rozendaal & Chazdon 2015, Poorter *et al.* 2016). This reported variation may reflect the true distribution of biomass in a secondary forest landscape, or it may result from typical small plot chronosequences having too few plots to capture the landscape mean trajectory. Distinguishing between these two possibilities and elucidating the effects of the other variables have only recently become possible with landscape-scale assessments of height and biomass in forests of different ages (Helmer *et al.* 2009, Mascaro *et al.* 2012). Like small plot chronosequences, our lidar data reveal wide variation in forest height and biomass recovery even in secondary forests of similar age. This suggests that the ranges observed in ground-based studies are not an artifact of limited sampling, at least in and

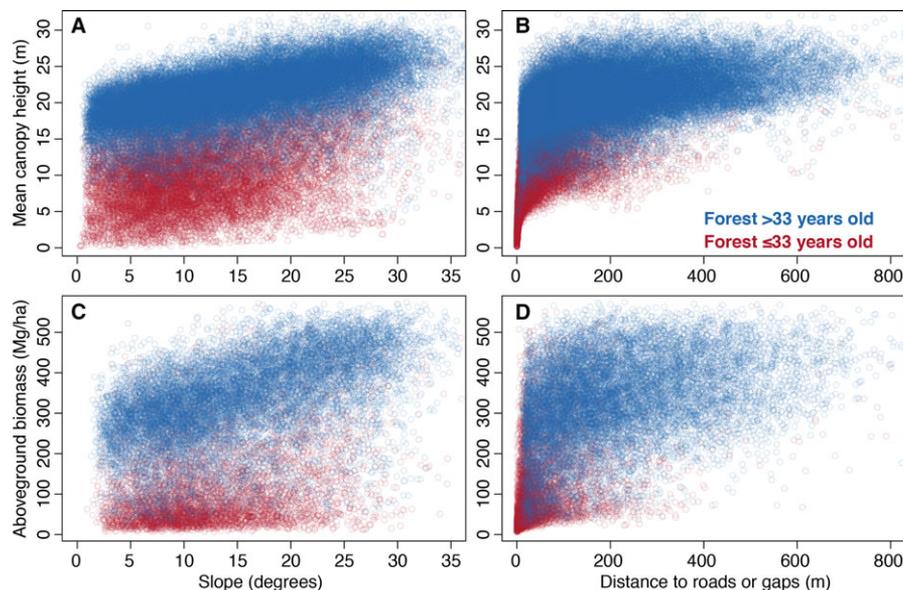


FIGURE 4. The relationship between mean canopy height and aboveground biomass density with slope (A, C) and distance to roads or open areas (B, D). Red dots are sites with forest >33 yr of age and blue dots are sites 33 yr of age or younger. Height and biomass have positive relationships with both height and distance to roads and clearings. The positive slope relationships are much clearer in forests older than 33 yr compared to younger forest. The positive relationships with distance to roads or open areas relationship appear to disappear as distance to roads gets beyond 400 m.

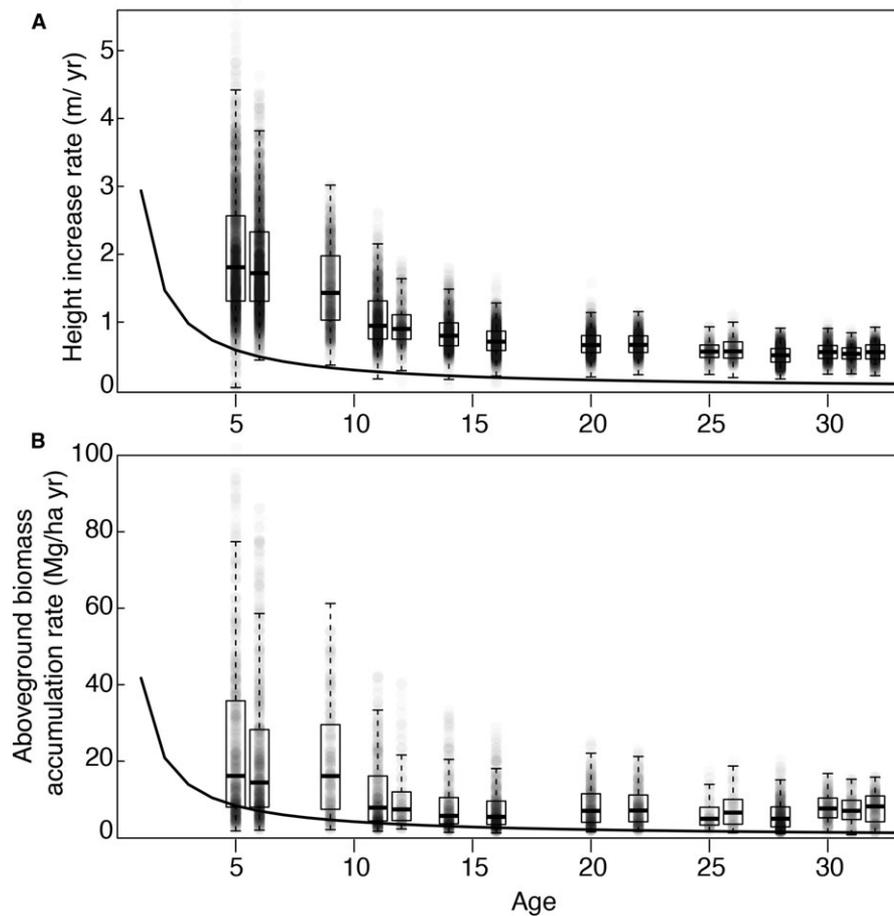


FIGURE 5. Height increase (A) and biomass accumulation (B) rates and in secondary forest <33 yr old. The black curve is the derivative of the statistical relationship between aboveground biomass and the natural logarithm of forest age. The gray dots and the boxplots represent the linear change in biomass until that age, calculated by dividing biomass by stand age. The boxes represent first and third quartiles and the black center line in the box is the median for each age group.

around Serra do Conduru. Across the park landscape, we observed forests ranging in mean height by ~ 20 m *within* an age class (and similar scale variation in biomass; Fig. 3). This wide variation poses a problem for plot-scale chronosequence studies. If the level of variation found in our study is common across secondary tropical forests, then larger ground-based chronosequence sample sizes may be needed to properly characterize the regeneration of these forests. This also underscores the need for studies that supplement plot work with remote sensing methods that estimate biomass at a landscape scale.

Despite the complexity of the landscape, we were able to explain a high percentage of the variation in both height and biomass recovery with relatively few variables: age, slope, and distance to anthropogenic features. After age, slope had the strongest effect on the distribution of biomass and mean canopy height across Serra do Conduru. In fact, slope alone explains 55 percent of the variation in mean canopy height and 40 percent of the variation in ABD. There was a clear positive relation between slope and both canopy height and biomass; this was most evident in forests 33 yr or older (Fig. 4).

In this landscape, lower biomass forests occur on low slopes, *e.g.*, in valleys, even in ‘old’ forests (>33 yr; Fig. 4A,C). Broad flat uplands are not found in this study area. In the tropics, low slopes and valleys are typically more fertile than uplands (Takyu *et al.* 2002, Vitousek *et al.* 2003, Porder *et al.* 2005, Osborne *et al.* 2017) and are preferentially cleared where steep lands are not, or alternatively steep lands are more readily abandoned. Thus, we believe that past land use likely explains the lower biomass at low slopes that we observe in this highly disturbed forest landscape. There is evidence throughout the Atlantic forest that higher elevations and steeper slopes have remained forested while lower, flatter areas were more likely to be cleared (Silva *et al.* 2007, Ribeiro *et al.* 2009). In our study area, there is extensive evidence of past and some ongoing selective logging, including trails, stumps, and wood scraps from field milling. The steepest slopes are more challenging places from which to remove trees, leaving more large trees standing and more aboveground biomass.

In addition to age and slope, the distributions of mean canopy height and biomass density are also significantly related to distance to anthropogenic features (roads and open areas larger

than 100 m²). The strength of this effect was marginally smaller than the slope effect, but these two variables are correlated (PCC = 0.25). The distance effect likely results from a combination of past farming and selective tree harvest. Farms were located in areas with access roads, potentially leading to associated soil degradation or erosion that could in turn have slowed forest regeneration. Forest clearing and selective harvest also likely took place where forests were accessible or adjacent to farms. Sites far from any road or existing farm or pasture were less likely to experience significant clearing or selective harvesting. Together with the effect of age, the significance of slope and distance to human features demonstrates the strong dependency of forest structure on human activities (both past and present) in Serra do Conduru.

RATES OF HEIGHT CHANGE AND BIOMASS REGENERATION.—Our analysis demonstrates that biomass accumulates rapidly in the secondary Atlantic forest in Southern Bahia. Despite a long history of human use of forests in the region, regrowth is at least as fast as the average secondary forest in a recently synthesized Neotropical plot network (Poorter *et al.* 2016). We find the median biomass for forest between 15 and 25 yr was 120 Mg/ha (the mean was 149 Mg/ha) and the mean rate of biomass accumulation based on the linear approximation was 6 Mg/ha yr for forests between 10 and 32 yr old. The mean accumulation rate derived from the biomass-ln(age) function for forests age 1–20 was 7.5 Mg/ha yr. Other studies have reported lidar-based secondary forest biomass regeneration rates from repeat lidar measurements at La Selva, Costa Rica and in Central Panama. At La Selva, regeneration averages 3.6 Mg/ha yr (Dubayah *et al.* 2010) while in Panama, the rate was only 1.8 Mg/ha yr (Meyer *et al.* 2013). However, the secondary forests in Panama included substantial areas older than 30 yr. A lidar chronosequence study in Rondônia, Brazil reported an average biomass accumulation rate of 8.4 Mg/ha yr for forest between 3 and 16 yr old (Helmer *et al.* 2009). While methods and site history vary among these studies, together they suggest that forest regeneration in Southern Bahia is relatively rapid.

Based on a regional model, secondary Neotropical forests with 2000 mm of year per year such as those in our study should accumulate about 120 Mg/ha of biomass in the first 20 yr of regeneration (Poorter *et al.* 2016). This suggests that Atlantic forests in this area should reach 90 percent of mature levels of biomass as fast as or faster than the average Neotropical forest (66 yr; Poorter *et al.* 2016) and that regeneration has not been significantly inhibited by the legacy of past land use or ongoing disturbance compared to other sites.

Secondary forests in other areas of the Atlantic forest have been studied for structural and floristic changes with age, but biomass regeneration estimates are rare. Toward the northern limit of the Atlantic forest range, in a moist tropical secondary forest (mean annual precipitation 1687 mm/yr), regeneration rates appear rapid, with 20-yr-old forest attaining 83 percent of mature forest levels of basal area (do Nascimento *et al.* 2014). In southern tropical Atlantic forest with mean annual precipitation over 2000 mm/yr, basal area

recovery is slower (biomass estimates are not available) and takes closer to 35 or 50 yr to attain mature levels of biomass (Marques *et al.* 2014, Martins *et al.* 2015). In southern seasonally dry tropical Atlantic forest, regeneration is also slow and potentially arrested by shrub species (Robinson *et al.* 2015). In subtropical Atlantic forest, at its most southern extent, there appear to be moderate rates of regeneration with 26- to 45-yr-old forest attaining roughly 65 percent of mature forest basal area (Zanini *et al.* 2014). In contrast, our study shows that north-central moist Atlantic forest reaches 70 percent of older forest biomass and 80 percent of older forest height after 30 yr. The explanation for these regional differences is unknown but is likely a combination of ecological and human factors.

REMAINING UNCERTAINTIES.—While our OLS model was able to explain much of the variance in the height and biomass of forests in this landscape, the correlation of driving variables (*e.g.*, steep slopes are further from roads and are more likely to host older forests) makes truly disentangling causation difficult even with a landscape-scale view. In addition, there are other potentially important factors that we were unable to include in our analysis. First among these is soil variation, as the coarse-scale soil maps available for this region do not elucidate differences in our comparably small study area. Soil nutrient status and texture have been found to explain both patterns in biomass regeneration (Moran *et al.* 2000, Zarin *et al.* 2001, Becknell & Powers 2014) and landscape-scale variation in aboveground biomass in mature tropical forest (Laurance *et al.* 1999). Additionally, species richness and functional composition may play a role in biomass regeneration and distribution in the Atlantic Forest, as they do in other regions (Lebrija-Trejos *et al.* 2010, Becknell & Powers 2014, Lasky *et al.* 2014). While we know that diversity is remarkably high in the region of our study area (Thomas *et al.* 1998, Martini *et al.* 2007), we do not have landscape-scale data on diversity or species composition with which to test this here. Ideally, we would also have better information on the intensity and type of past land use that has been shown to affect biomass regeneration (Uhl *et al.* 1988). Another possibility is that our study area does not include a sufficient sample size of certain explanatory factors (or combinations of factors). This could be remedied in future studies with a larger study area or by replicating the study area at multiple locations in the region.

It is also possible that some of the unexplained variation in forest properties results from a misclassification of forest age, which would lead us to over- or underestimate its importance in determining height and biomass. Estimating forest age in secondary forest landscapes is a problem for both small plot and remote sensing-based studies. Remnant trees or tiny patches of forest in and around cleared land complicate age classification. In addition, as the resolution of Landsat data is 30 m, there are likely pixels within which multiple ages of forest co-occur. There is also the potential for additional uncertainty because of the differences between the 30-m-scale age map and the 50-m-scale biomass map. However, when we analyzed canopy height at both 30 and 50 m scales, the results were unchanged, suggesting that the mismatch between pixel sizes does not produce additional

uncertainty. Regardless, mixed pixels and other factors may combine to masking the true forest age and add error to our model. Despite this potential additional error, age alone can explain 70 percent of the variation in height and 59 percent of the variation in ABD.

CONCLUSIONS

Our analysis of ~45 km² of Atlantic forest in Southern Bahia suggests that secondary forest regenerates quickly after land clearing and fragmentation. Furthermore, we find the extent of recovery can be predicted from just a few explanatory variables (age, slope, distance to human activity), an encouraging result given the need to quantify carbon uptake if payments for carbon sequestration become widespread. While a small fraction of the variance in forest canopy height and ABD remains unexplained, our results highlight the promise of remote sensing to understand the drivers, and extent of, variation in tropical secondary forest regrowth across the Neotropics.

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DATA AVAILABILITY

The lidar dataset used in this study are archived at Embrapa’s Sustainable Landscapes project (Paisagens Sustentáveis) and are available to download at the website: <https://www.paisagenslidar.cnpqia.embrapa.br/webgis>.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

TABLE S1. *Data from 30 forest inventory plots (0.25-ha each).*

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