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Detecting tropical forest biomass dynamics from repeated airborne Lidar measurements

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Abstract

Reducing uncertainty of terrestrial carbon cycle depends strongly on the accurate estimation of changes of global forest carbon stock. However, this is a challenging problem from either ground surveys or remote sensing techniques in tropical forests. Here, we examine the feasibility of estimating changes of tropical forest biomass from two airborne Lidar measurements acquired about 10 yr apart over Barro Colorado Island (BCI), Panama from high and medium resolution airborne sensors. The estimation is calibrated with the forest inventory data over 50 ha that was surveyed every 5 yr during the study period. We estimated the aboveground forest biomass and its uncertainty for each time period at different spatial scales (0.04, 0.25, 1.0 ha) and developed a linear regression model between four Lidar height metrics and the aboveground biomass. The uncertainty associated with estimating biomass changes from both ground and Lidar data was quantified by propagating measurement and prediction errors across spatial scales. Errors associated with both the mean biomass stock and mean biomass change declined with increasing spatial scales. Biomass changes derived from Lidar and ground estimates were largely (36 out of 50 plots) in the same direction at the spatial scale of 1 ha. Lidar estimation of biomass was accurate at the 1 ha scale ($R^2 = 0.7$ and $RMSE_{\text{mean}} = 28.6 \text{ Mg ha}^{-1}$). However, to predict biomass changes, errors became comparable to ground estimates only at about 10-ha or more. Our results indicate that the 50-ha BCI plot lost a significant amount of biomass ($-0.8 \pm 2.2 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) over the past decade (2000–2010). Over the entire island and during the same period, mean AGB change is $-0.4 \pm 3.7 \text{ Mg ha}^{-1} \text{ yr}^{-1}$. Old growth forests lost biomass ($-0.7 \pm 3.5 \text{ Mg ha}^{-1} \text{ yr}^{-1}$), whereas the secondary forests gained biomass ($+0.4 \pm 3.4 \text{ Mg ha}^{-1} \text{ yr}^{-1}$). Our analysis demonstrates that repeated Lidar surveys, even with two different sensors, is able to estimate biomass changes in old-growth tropical forests at landscape scales ($>10 \text{ ha}$).

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1 Introduction

Tropical forests are a major focus for research because of the role they play in the global carbon cycle and recently in climate mitigation policies through REDD protocols (Reduced Emissions from Deforestation and Degradation). The study of forest dynamics is of particular interest because changes in carbon fluxes over time are caused by either natural or anthropogenic disturbances and by recovery from these disturbances. The study of carbon flux measurements in tropical forests has shown unprecedented progress in recent years, based on both ground and remote sensing techniques. For ground-based data, allometric equations have been developed from tree inventory data made across a range of tropical forest types (Chave et al., 2005; Higuchi et al., 1994; Chambers et al., 2001). These equations are key to converting tree diameter, height, and wood specific density into tree aboveground biomass (AGB, measured in oven-dry mass units) and to infer stand AGB across spatial scales (Chave et al., 2004). However, forest structure and biomass distribution are spatially variable and ground sampling and monitoring of tropical forest carbon dynamics is fraught with large uncertainties (Clark and Clark, 2000; Saatchi et al., 2011).

Remote sensing approaches, particularly from Lidar or low frequency radar sensors have been shown to provide relatively accurate estimates of above ground biomass over large areas (Asner et al., 2010; Drake et al., 2002a; Lefsky et al., 2002; Saatchi et al., 2011). High resolution Lidar data from airborne platforms have proven to be the most commercially available, cost effective, and accurate means of assessing forest above ground carbon stock for policy driven projects (Asner et al., 2011). Lidar measurements provide three dimensional forest structure at high enough spatial resolution to capture several important measures of forest dynamics: (1) tree size structure representing successional stages of the forest (Ni-Meister, et al., 2001), (2) gap size and light conditions in the forest capturing the disturbance dynamics and conditions for forest carbon dynamics (Lefsky et al., 2002; Kellner and Asner, 2009), and (3) spatial

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patterns representing changes of forest structure and biomass from tree to landscape scales (Dubayah et al., 2010).

The recent literature on this topic has mostly focused on measuring tropical forest carbon stocks. Comparatively limited research has been devoted to assessing the capability of remote sensing data to detect changes of forest biomass (but see Dubayah et al., 2010). The vertical height profiles can be used to develop algorithms for biomass change detection at various spatial scales using high resolution small footprint lidar or medium footprint waveform Lidar sensors (Dubayah et al., 2010). In this paper, we test this approach over the period 1998–2009 in the tropical forest of Barro Colorado Island (BCI), Panama. We seek to quantify the uncertainty for both AGB stocks and change at three different spatial scales (1 ha, 0.25 ha and 0.04 ha) using two different Lidar sensors. We then quantify the errors at different spatial scales and extend the analysis of local scale carbon dynamics in the 50 ha plot to the entire Barro Colorado Island. The analysis allows us to examine at what scale, we are able to detect the spatial patterns of forest biomass change while providing stable and accurate estimates.

2 Material and methods

2.1 Study area and inventory data

Barro Colorado Island (BCI) is a 1500 ha island located in the Panama Canal Zone in Central Panama. It was isolated from the mainland after the Chagres River was dammed in 1910 to complete the Panama Canal (McCullough, 1977, Fig. 1). The island is administered by the Smithsonian Tropical Research Institute (STRI) as part of the Barro Colorado Nature Monument (BCNM), a protected national biological reserve since 1923. Detailed description of climate, flora and fauna of BCI can be found in Croat (1978) and Leigh (1999). BCI is covered by moist tropical forest with half of the island dominated by old secondary forests (approximately 100 yr old), for the most part growing back from agricultural clearings, while the rest is covered by forests that

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large tree in a 0.04-ha subplot will strongly impact the AGB value of a subplot, leading to extremely low or extremely high AGB values (Chave et al., 2003).

AGB, estimated at the 1 ha scale, decreased both between 2000 and 2005 and between 2005 and 2010 census periods in the 50 ha plot (Fig. 2b, Table 3). The histograms show that changes between 2000 and 2005 were slightly skewed to negative values and had only few extreme values (mean = -2.4 Mgha^{-1} , std = 10.5 Mgha^{-1}), whereas during the second period between 2005 and 2010, there were more extreme values and the biomass loss was larger (mean = -5.5 Mgha^{-1} , std = 16.1 Mgha^{-1}). AGB in the 50 ha plot dropped by 7.8 Mgha^{-1} (std = 17.6 Mgha^{-1}) over the 10-yr period of study (i.e. an average value of $0.8 \text{ Mgha}^{-1} \text{ yr}^{-1}$).

The spatial scale analysis of AGB change (Table 3) confirms that at the 1 ha scale, the observed changes are more stable for a long-term analysis than smaller subplots (std_{change2000/2010.1 ha} = 17.6 Mgha^{-1} and std_{change2000/2010.0.04 ha} = 107.4 Mgha^{-1}). Here, stability refers to less variability and suggests that larger plots are individually more reliable for detecting long-term changes, whereas smaller plots individually represent changes associated with both natural gap dynamics (disturbance and recovery) and long term changes. Furthermore, 37 1 ha subplots lost AGB and the rest gained AGB over the same period. By further aggregating the subplots to larger scales, we find the forest is losing biomass more uniformly at 5-ha scale (std = 5.9 Mgha^{-1}), and at 10-ha scale (std = 4.2 Mgha^{-1}). At 25 ha, the two subplots lost -7.7 and -8.0 Mgha^{-1} of AGB for an average value of -7.8 Mgha^{-1} at 50 ha between 2000 and 2010.

3.2 Lidar-derived biomass estimation

Although the relative height (RH) metrics were individually correlated with ground-based AGB, using all four metrics improved the accuracy of the AGB estimation (see Supplement). Testing for the relative importance of each height metric, we found that all four metrics explained about 80 % of the variation in forest biomass at 1-ha scale,

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and relatively less variations at 0.25 ha (58 %) and 0.04 ha (32 %). The relative contribution of the height metrics at 1-ha were 16 %, 19 %, 30 %, and 15 % respectively for RH25, RH50, RH75, and RH100. The influence of spatial scale on AGB is examined here by again comparing the results obtained using 0.04 ha, 0.025 ha and 1 ha subplots, using the cross-validated data. Figure 3 shows that for both LVIS and DRL data, the accuracy of AGB estimation increases when larger subplots are used. We found a strong relationship between ground AGB and Lidar estimated AGB when using 1 ha subplots in the model, with similar results for both LVIS and DRL data ($R^2_{\text{LVIS}} = 0.62$ and $R^2_{\text{DRL}} = 0.70$, $\text{RMSE}_{\text{LVIS}} = 31.7 \text{ Mgha}^{-1}$ and $\text{RMSE}_{\text{DRL}} = 27.5 \text{ Mgha}^{-1}$). At the 0.04 ha scale, the estimation accuracy was lower than at the 1 ha scale ($R^2_{\text{LVIS}} = 0.19$ and $R^2_{\text{DRL}} = 0.29$, $\text{RMSE}_{\text{LVIS}} = 187.5 \text{ Mgha}^{-1}$ and $\text{RMSE}_{\text{DRL}} = 175.3 \text{ Mgha}^{-1}$). Bias is very low when using 1 ha plots ($B_{\text{LVIS}} = -1.1 \text{ Mgha}^{-1}$, $B_{\text{DRL}} = -0.2 \text{ Mgha}^{-1}$), while bias reaches between -23.9 Mgha^{-1} (for LVIS) and -20.4 Mgha^{-1} (for DRL) when using 0.04 ha subplots. When not using cross-validation, $R^2_{\text{LVIS}} = 0.71$ and $R^2_{\text{DRL}} = 0.75$ at the 1 ha scale.

3.3 Lidar derived biomass change

Over the 50 ha plot, both ground and Lidar analyses indicate that on average, AGB decreased by 8 Mgha^{-1} between 2000 to 2010 ($\text{AGB}_{\text{Change.Ground}} = 7.8 \text{ Mgha}^{-1}$, $\text{AGB}_{\text{Change.Lidar}} = -7.7 \text{ Mgha}^{-1}$). At the 1 ha scale, the noise caused by estimation errors due to our regression model was large and only biomass changes greater than 22.6 Mgha^{-1} (standard deviation of Lidar-derived AGB change) could be detected unambiguously from Lidar data. Thirty-four of the fifty subplots showed the same direction (biomass gain or loss between the two dates) comparing the ground and Lidar-estimated AGB change (Fig. 4), with no regard of the 22.6 Mgha^{-1} threshold. For eleven of the remaining sixteen plots, AGB change between 2000 and 2010 is smaller than 22.6 Mgha^{-1} and therefore within the uncertainty threshold, in both ground and Lidar estimations. The remaining five 1 ha plots showed significantly opposite directions

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in Lidar and ground estimations. The difference between ground and Lidar estimation of AGB change was much larger with smaller subplots (Fig. 5). For example, 3 ha of the 50 ha plot have been classified as secondary forest (dominated by the tree species *Gustavia superba*). The ground data analysis indicates that AGB increased in these secondary plots between 2000 and 2010 (mean AGB change_(secondary) varies between +0.9 (0.04 ha scale) and +4.0 Mg ha⁻¹ (1 ha scale)). However, Lidar only had a positive AGB change for this area at a large scale (mean AGB change_(secondary) = +12.3 Mg ha⁻¹ at 1 ha scale) and did not show the same trend at finer spatial scales, with a mean AGB change_(secondary) of -13.1 Mg ha⁻¹ at 0.04 ha and -6.7 Mg ha⁻¹ at 0.25 ha. Hence even with small footprint Lidar, it is unlikely that quantitative changes in AGB will be accurately quantified at scales lower than 1 ha.

The ground and Lidar detection of changes had better agreements when the scale of analysis increased. At a 10 ha scale, the estimation of change could be predicted at about 6 Mg ha⁻¹ over 10 yr, or less than 1 Mg ha⁻¹ yr⁻¹. Table 4 shows how spatial scale affects Lidar-derived AGB change estimations at the plot level. Both Lidar-derived AGB change and the difference between Lidar and Field estimates decrease as the scale becomes coarser. The amplitude of differences between field-estimated change and Lidar-estimated change decreases quickly with increasing the scale of analysis, going from ±6.3 Mg ha⁻¹ yr⁻¹ at 1 ha to ±1.1 Mg ha⁻¹ yr⁻¹ at 25 ha. These results show that large spatial scales such as 10 ha or 25 ha give accurate AGB change estimations when looking at the 50 ha plot, but the 1 ha scale still seems to be a good option when looking for spatial patterns.

3.4 Whole-island estimates

Estimated AGB stocks and changes were then mapped across the entire island (1500 ha) using the equations developed at the plot level at 1 ha resolution, for both LVIS and DRL data. These two maps were then used to create an AGB change map (Fig. 6). A mask consisting of a one pixel erosion was applied to the final map to avoid

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errors induced by edge effects. Hence, all the pixels that were on the edges of the island and contained errors were removed. The AGB change map shows that 32 % of the island had gained biomass between 2000 and 2010, while 35 % lost biomass. The remaining 33 % did not show significant trends during the period (changes less than ±10.5 Mg ha⁻¹). Mean AGB change over the whole island was found to be -3.6 Mg ha⁻¹ (std = 37.2 Mg ha⁻¹), or -0.4 Mg ha⁻¹ yr⁻¹. Patterns related to the forest age (Fig. 7b) and stage of regeneration can be seen in the AGB change map. Combining the AGB change map and the age map shows that old growth forest areas lost a lot of AGB (change = -7.2 ± 34.9 Mg ha⁻¹) whereas secondary forests gained AGB (change = +3.9 ± 33.8 Mg ha⁻¹) between 2000 and 2010. Standard deviation remained high for both forest age classes.

4 Discussion

The goal of our research was to study the ability of Lidar technology to estimate and map AGB changes when calibrated and combined with the field data. The relationship between Lidar-derived vertical canopy distribution and ground-based estimated AGB at plot level was used to create predictive equations for AGB at a landscape scale. A large number of studies have recently focused on AGB estimations in tropical forest using Lidar technology (Drake et al., 2002; Asner et al., 2011; Mascaro et al., 2011b) but to our knowledge, only one has been able to detect AGB changes from repeated Lidar measurements (Dubayah et al., 2010). Moreover, Dubayah et al. (2010) used the same sensor to detect AGB changes, whereas this study is the first to use two different sensors. Here we review our findings and discuss them in light of this recent literature and address the following questions associated with the biomass changes in old growth tropical forests: (1) can changes in biomass create a distinct and directional changes in vertical profile of the forest over time? (2) To what extent can these changes be detected by repeated measurements of the Lidar profiles?

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The loss of approximately $0.8 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ of forest biomass derived from both ground and Lidar data over the 50 ha BCI plot may not be surprising, but it runs against recently published results over both Amazonian (Baker et al., 2004) or African (Lewis et al., 2010) forests. The loss of biomass in the old growth forest in BCI has been attributed to short-term disturbance such as the droughts from El Niño and subsequent changes in forest composition (Chave et al., 2008; Feeley et al., 2011). The role of lianas, which have been shown to increase in dominance in this forest (Wright et al., 2004) may also help explain this trend as the liana distribution has been shown to be associated with stands with low stature and canopy heights (Dalling et al., 2012). Also, as lianas become more dominant (Phillips et al., 2000) they tend to impose a higher load on large trees, resulting in increasing the risk of the tree falling (Chao et al., 2010).

Droughts have been considered as the main culprit for the biomass loss in tropical forests (Nepsted et al., 2005; Phillips et al., 2009; Lewis et al., 2011). In most studies, it was hypothesized that the biomass from a severe drought event can be followed with recovery and biomass gain immediately or after few years (Phillips et al., 2009). However, here we show that the impact of the drought may be longer than a few years (about 10 yr).

A detailed analysis of the field inventory data suggest that the largest decline in biomass has been in DBH classes larger than 40 cm with the most significant loss (46.2 Mg ha^{-1}) in trees greater than 70 cm in diameter that include primarily the canopy or emergent trees (Fig. 7).

4.1 Use of Lidar height metrics

Differences in one height metric derived from Lidar waveforms (e.g. RH50, RH00, or Mean Canopy Height (MCH)) had no significant relationship with differences in forest biomass derived from the analysis of field surveys. This result suggested that we could not map the changes of forest biomass by directly analyzing the Lidar heights at 1-ha scale using two different sensors. Using the same sensor for both dates can

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potentially provide a more reliable and height difference to calculate AGB change directly from Lidar (Dubayah et al., 2010). The indirect estimate of biomass change from Lidar data, however provided similar results as the field observations at the landscape scales ($> 10 \text{ ha}$). By segmenting the Lidar derived biomass changes in the 50-ha plot into different biomass classes, the predicted changes point to regions of old growth with taller canopy trees ($> 40 \text{ cm}$) as the main contributor of the overall decline in forest biomass in the 50 ha plot (Fig. 8).

We tested the performance of the models against other common equations used in the literature and concluded that for our datasets, use of several height metrics always outperformed the use of a single height metric such as mean canopy height or height of the median energy (Asner et al., 2009; Mascaro et al., 2011; Drake et al., 2002). Although different height metrics are correlated, each may provide a slightly different slice of vertical structure of the forest canopy and together they improve detection of variation in basal area, tree density, and the structural representation of wood density (trees in different diameter classes or successional states). Indeed, each metric should give specific structural information about the forest. For example, RH25 may improve quantification of changes in biomass from regeneration of understory trees and young saplings. A low RH25 may indicate that there is a lot of understory vegetation in the forest; whereas a RH25 close to RH50 may indicate that the understory contains few individuals, and that the plot is mainly composed of tall trees. The dynamics of these combined height metrics, if accurately quantified, hence may provide a more accurate picture of how forests are growing than can be obtained with a single metric. More work studying the relationship between RH metrics and size classes of trees can test these relationships.

4.2 Spatial scale of forest dynamics

The linear relationship between Lidar metrics and biomass estimates was found to be stronger as the pixel scale became coarser. High coefficients of correlation ($R_{\text{LVIS}}^2 = 0.62$ and $R_{\text{DRL}}^2 = 0.70$), low RMSE ($\text{RMSE}_{\text{mean}} = 29.6 \text{ Mg ha}^{-1}$) indicate that

the 1 ha scale is the best spatial scale to use in this type of analysis, as it gives more accurate results and minimizes the errors related to both field data and remote sensing data. At a 0.04 ha scale, we found a poor correlation ($r_{LVIS}^2 = 0.19$ and $r_{DRL}^2 = 0.29$) between ground-estimated AGB and Lidar-estimated AGB because the relationship is affected by high AGB variation due to events such as tree falls, compositional variations and gap regeneration, not necessarily detected to the same accuracy in the field data and the Lidar data. Although one could argue that a 0.04 ha spatial scale would be useful in studies related to gap analysis, such a small scale is not necessary for our study and AGB change analyses.

Tree geolocation errors on the ground and tree crown position relative to trunk position are other sources of error. These issues are magnified as the subplot size decreases. The aggregate effects of these small-scale changes at larger plots or stand level define the forest carbon dynamics at annual or multi-year temporal scales.

An encouraging result of this study is that the level of accuracy for AGB estimates from DRL and LVIS are similar, despite the differences in sensor design, spatial resolution and footprint size. It opens possibilities in terms of biomass change detection using Lidar data for future studies. Although it is always preferable to perform a change analysis using matching datasets at two different dates, our study shows that it is possible to perform this type of analysis using different sensors without affecting the quality of the results.

Although field and Lidar AGB change estimates are similar over the 50 ha plot (mean change = -7.8 Mg ha^{-1} between 2000 and 2010), the noise at 1 ha scale is too large to assess biomass change accurately and quantitatively at the plot level. Small changes in biomass are difficult to model at this scale. As a result, average changes at the plot level may be difficult to establish accurately, unless the changes are large. Still, we were able to estimate the change qualitatively and predict the sign of the biomass change (biomass gain or biomass loss) in 68% of the 1-ha subplots.

In a recent study, Mascaro et al. (2011b) analyzed error predictions in terms of AGB and carbon stocks on BCI through two analyses using airborne Lidar data and ground

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inventory data. They first tested the prediction of Asner et al. (2010) that spatial errors would scale with the inverse of the square root of pixel area as spatial resolution changes. They then analyzed the importance of plot-edge discrimination errors in AGB estimations. At 1 ha scale, they found an RMSE of $11.1 \text{ Mg}_{\text{Carbon}} \text{ ha}^{-1}$, which corresponds to an RMSE of 22.2 Mg ha^{-1} in terms of AGB, when not using their stem-localized approach. This result is similar to ours, since we found a mean RMSE of 29.6 Mg ha^{-1} at the same scale. They further suggest that this RMSE could be reduced by accounting for canopy shape, which is essentially accounting for border effects in small subplots. Although this is a sensible approach, we refrained from implementing it because crown shape and size is seldom available in ground datasets, and we feel that the uncorrected RMSE reflects more accurately the inherent ability of the Lidar technology to infer tropical forest AGB. Further, at the 1 ha scale, this correction results only in a marginal reduction of the error (Mascaro et al., 2011a, Fig. S1), with $\text{RMSE}_{\text{corrected}} = 10.7 \text{ Mg}_{\text{Carbon}} \text{ ha}^{-1}$ against $\text{RMSE}_{\text{uncorrected}} = 11.1 \text{ Mg}_{\text{Carbon}} \text{ ha}^{-1}$.

Another difference of our study with that of Mascaro et al. (2011a) is that they used a calibration model between a single Lidar metric (MCH) and AGB, including early successional forest plots far away from BCI. Although this would be helpful to map AGB of the whole canal zone, it results in artificially inflating the R^2 of the model when just mapping BCI. Instead we used four Lidar-derived height metrics to estimate AGB directly from the 50-ha plot data, providing a more realistic error estimates for mapping the old growth forest biomass. Our approach also helps counter-balance the effects caused by the limited AGB range in the plot. Because the permanent plot is located in an old growth forest, there was no low biomass subplot. Using the four relative height metrics takes as much forest variation into account as possible. Thus, although the RH metrics are strongly correlated, we show in our analysis that using the four of them gives better results (see Supplement).

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4.3 Variation of forest dynamics across the island

Landscape-level AGB changes at 1 ha resolution of the old-growth and younger forest match changes expected from forest succession theory (Shugart, 1984). Mean AGB change over the whole island is -3.6 Mgha^{-1} between 2000 and 2010, with most of the old growth forest being neutral or losing AGB (average change = -7.2 Mgha^{-1}) while secondary forests gained AGB (average change = $+3.9 \text{ Mgha}^{-1}$). Previous ground-based studies over the BCI plot already reported this trend for the 2000–2005 interval (Chave et al., 2008). The fact that 100-yr old secondary forests still are aggrading carbon also is an important finding of this study.

Mascaró et al. (2011a) recently published an AGB map of BCI based on a similar approach. They found that AGB was lower in young forests than in mature forests. Here, we provide the first map of AGB changes and we show that young forests are increasing in AGB as expected.

Dubayah et al. (2010) performed the first AGB change study in a tropical forest. Their study was conducted at La Selva research station, Costa Rica. Their study presents some major differences with our study in terms of methodology. Dubayah et al. (2010) compared two LVIS datasets for the change analysis, while we are comparing one small footprint DRL and one LVIS dataset. In their study, Dubayah et al. (2010) performed a footprint-to-footprint comparison of the data and of height metrics. Their approach made it simpler to conduct an AGB change analysis by directly using change in Lidar-derived height between two dates, and change in ground estimated AGB between two dates. Our approach was less direct, but we avoided the issue of DEM location in LVIS. In doing so, we set the stage for many forthcoming Lidar studies based on a range of operating instruments. Despite these differences, the results of Dubayah et al. (2010) and ours are comparable in terms of AGB change trends. Indeed, Dubayah et al. (2010) showed that old growth forest was mostly neutral (average AGB change between 1998 and 2005 is 1.9 Mgha^{-1}), while secondary forests are gaining biomass (average change between 1998 and 2005 is 25.2 Mgha^{-1}).

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4.4 Sources of errors

This study assumes Lidar height metrics can be used to detect biomass changes in old-growth and undisturbed tropical forest. An underlying hypothesis is that changes in biomass in the forest are related to changes in forest height or vertical structure. Unfortunately, this hypothesis is difficult to test based on literature data. Long-term studies in BCI and other sites have revealed that changes in forest structure and dynamics have complex trajectories and are often driven by many factors including random population fluctuations, climate disturbance, large scale successional or gap phase processes, and increasing resource availability or carbon fertilization (Feeley et al., 2011; Chave et al., 2008; Baker et al., 2004; Lewis et al., 2004, 2010; Clark et al., 2003, 2010). Over the past 25 yr the BCI plot has seen a high turnover, with almost 50 % of the initial individuals dying and being replaced. However, BCI forest structure studies include trees $> 1 \text{ cm DBH}$ while most similar studies only include trees $> 10 \text{ cm DBH}$. This difference could explain BCI's apparently high turnover.

Some limitations related to both field data and Lidar data need to be discussed to better understand our results and the errors that we reported. First, the time difference between the field inventory and the acquisitions of Lidar data is a source of error that is hard to quantify in our analysis. Events such as tree falls might have happened between 1998 (LVIS data acquirement) and 2000 and between 2009 (DRL data acquirement) and 2010, causing error in model calibration, particularly at smaller scales, where the whole subplot would be affected.

The error associated with field data is also difficult to quantify. Although outliers in trunk diameter measurement are corrected before they are used in allometric equations, other errors related to fieldwork, such as tree geolocation errors, cannot be backtracked. Tree location errors can cause ambiguity in relating Lidar metrics to forest structure and biomass around the edges of plots and may introduce error in estimating the forest biomass and uncertainty in detecting small changes of biomass. This effect is minimized in the BCI dataset because of the intensive effort paid in the field.

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1980

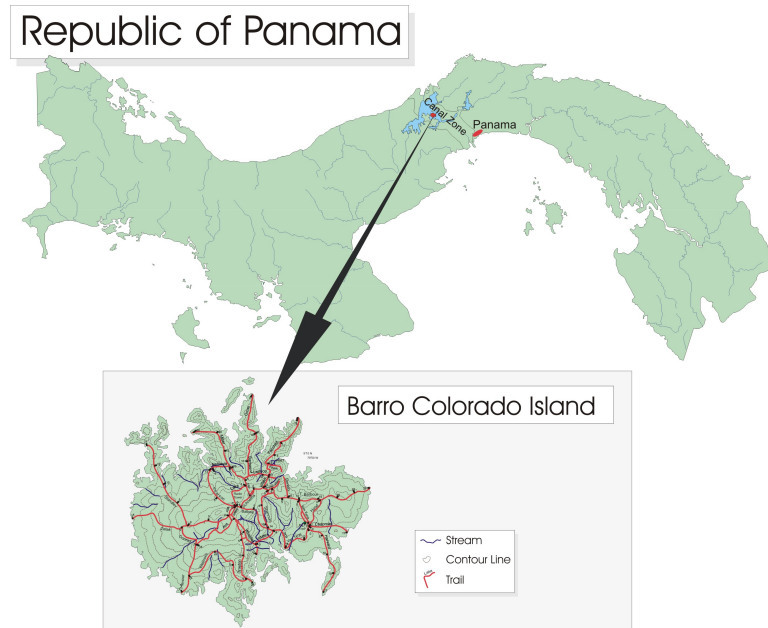


Fig. 1. Panama and Barro Colorado Island Map (Smithsonian Tropical Research Institute website).

1985

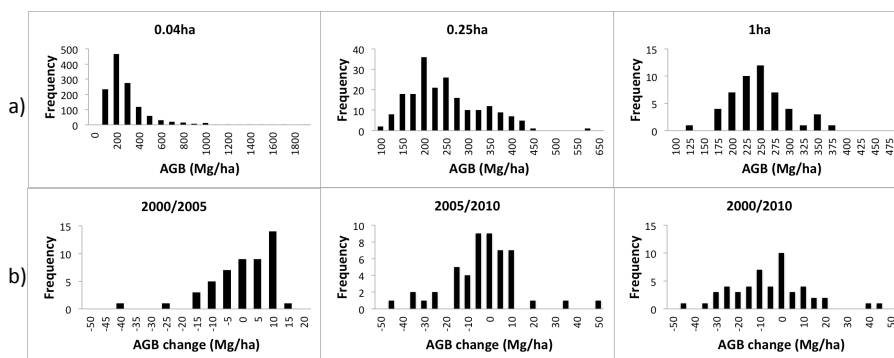


Fig. 2. (a) Histograms of AGB distribution in the permanent plot at three spatial scales. AGB distribution is skewed to the left when using 0.04 ha subplots. AGB distribution becomes normal when working with larger subplots, especially at 1 ha. **(b)** Histograms of AGB Change between 2000, 2005 and 2010 in the 50 ha plot (1 ha scale) . There are more extreme values (positive and negative) between 2005 and 2010, than between 2000 and 2005.

1986

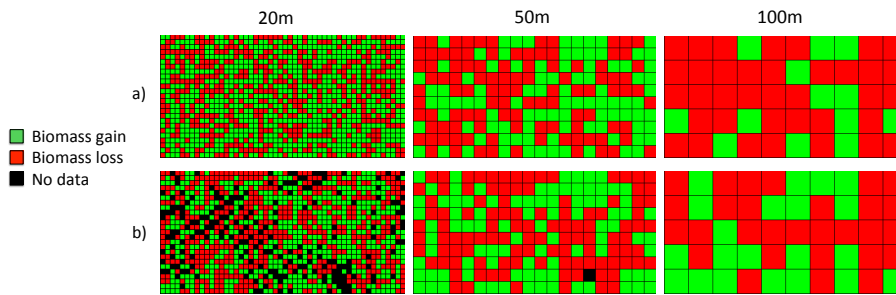


Fig. 5. AGB change (in $Mg\,ha^{-1}$) from Ground estimations (a) and from Lidar estimations (b) in the 50 ha plot, at 0.04 ha, 0.25 ha and 1 ha spatial scales. At these scales and at the plot level, Lidar estimates do not show the same AGB change trends as the ground estimates, although patterns can be seen at the 1 ha scale.

1989

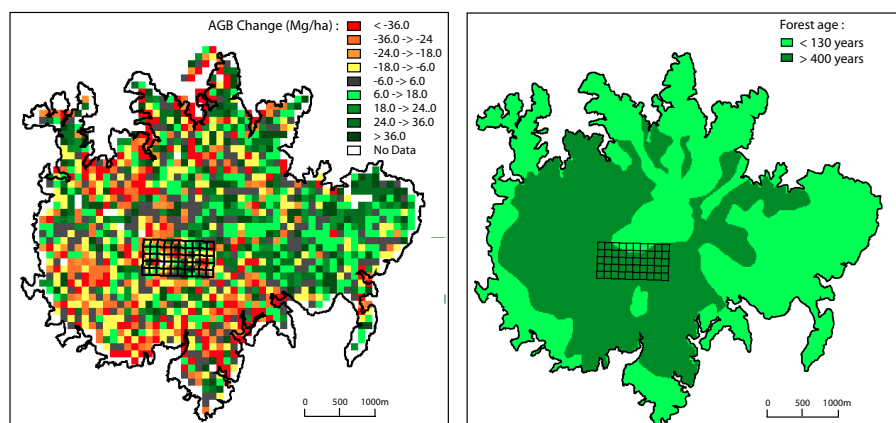


Fig. 6. AGB change map between 2000 and 2010 (left) and forest age map (right). AGB decreased in old growth forest (dark green in the age map), whereas the forest gained biomass in younger, regenerating forest (light green in the age map).

1990

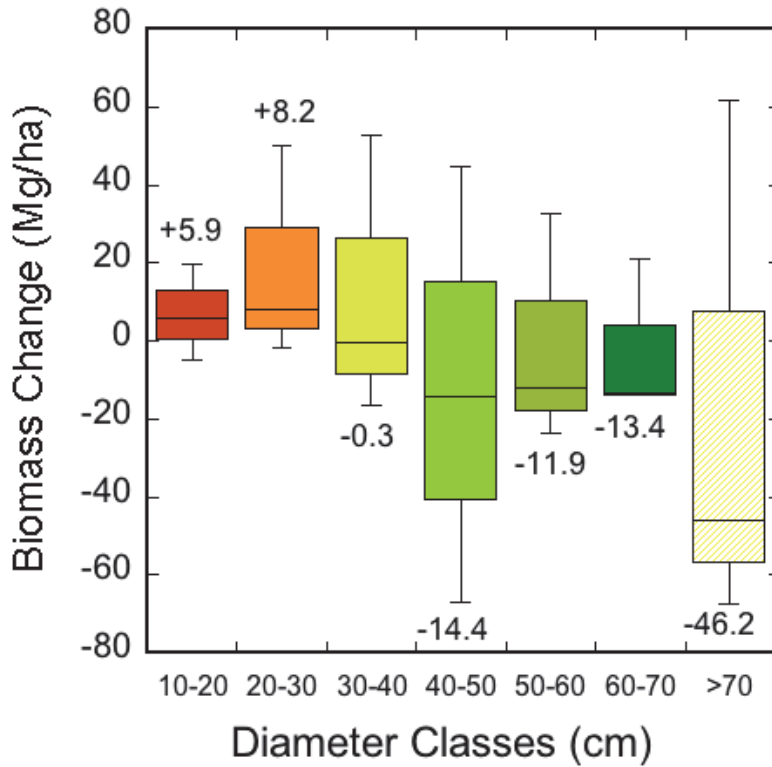


Fig. 7. DBH classes and AGB change (20 m spatial scale). AGB is increasing in small DBH classes while trees having DBH higher than 40m are losing biomass.

1991

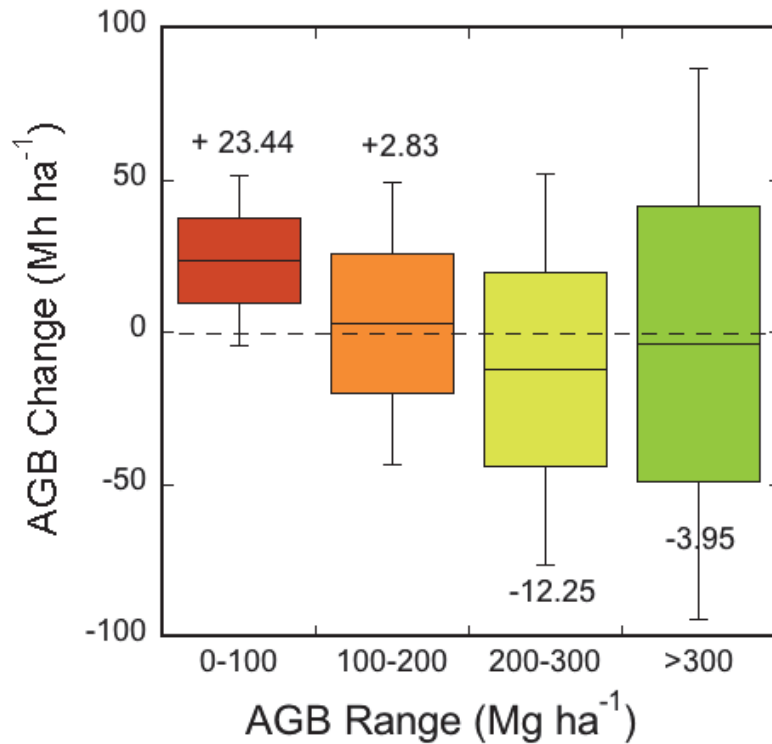


Fig. 8. Lidar-derived AGB range and AGB Change (20 m spatial scale). AGB in subplots with low biomass is increasing, while subplots with high biomass are losing biomass and contribute to the overall loss of biomass in BCI.

1992