Title
Aboveground Biomass Accumulation Over Two Decades Across a Gradient of Tropical Forest Restoration Interventions

Journal
Global Change Biology, 32(8)

ISSN
1354-1013

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Publication Date
2026-08-01

DOI
10.1111/gcb.71054

Peer reviewed

Title: Aboveground biomass accumulation over two decades across a gradient of tropical forest restoration interventions

Running title: Tree biomass in restored tropical forests

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Abstract

Tropical forest restoration is an important nature-based solution that can sequester carbon as a means to mitigate climate change. Restoration approaches range from natural regeneration to intensive tree planting, but few studies have compared aboveground biomass (AGB) stocks over decadal time scales across multiple restoration treatments implemented at the same sites. Here we leverage data from a two-decade restoration experiment in southern Costa Rica; in 2004-2006, we established restoration plots representing a gradient of intervention intensity: natural regeneration (no planting), applied nucleation (planting tree clusters), and plantation (full planting). We compare 18-20 years of AGB across treatments of the four planted tree species and naturally recruited trees. We also examine the relationships between AGB pools and structural metrics derived from UAV-borne LiDAR data collected after 16-18 years. Because most AGB was in planted trees, AGB was about 6.5 times greater in plantations compared to natural regeneration, and double in plantations compared to applied nucleation after two decades, despite substantial mortality of planted trees. However, the plantation treatment suppressed naturally recruited AGB and accumulated only half the amount of the natural regeneration treatment. Natural recruits comprised four times the proportion of AGB in applied nucleation compared to plantation. LiDAR-quantified LAI was more tightly correlated with total AGB in natural regeneration plots, whereas canopy height was more strongly correlated with planted biomass in plantation and applied nucleation. Our results highlight that tree planting accelerates AGB accumulation at degraded sites, and illustrate that practitioners should select species with complementary life history strategies that enable carbon to be sequestered beyond the first decade. Given the tradeoff between planted tree biomass and naturally-recruited biomass, spatially-patterned methods that plant fewer trees may better balance restoration goals beyond carbon accumulation, leading to more structurally and biologically diverse reforested systems.

Spanish-language abstract

La restauración de bosques tropicales es una importante solución basada en la naturaleza capaz de secuestrar carbono para mitigar el cambio climático. Los métodos de restauración abarcan desde la regeneración natural hasta la plantación intensiva de árboles; sin embargo, pocos estudios han comparado las reservas de biomasa aérea (AGB, por sus siglas en inglés) a lo largo de escalas temporales de décadas entre múltiples tratamientos de restauración implementados en los mismos sitios. En este estudio, utilizamos datos de un experimento de restauración de dos décadas de duración en el sur de Costa Rica; entre 2004 y 2006, establecimos parcelas de restauración que representaban un gradiente de intensidad de intervención: regeneración natural (sin plantación), nucleación aplicada (plantación de grupos o "islas" de árboles) y plantación (plantación total). Comparamos la AGB acumulada a lo largo de 18 a 20 años entre los tratamientos, considerando tanto las cuatro especies de árboles plantados como los árboles que reclutaron naturalmente. Asimismo, examinamos la relación entre las reservas de AGB y las métricas estructurales derivadas de datos detección y medición de distancias por luz (LiDAR, por sus siglas en inglés) obtenidos mediante vehículos aéreos no tripulados (UAV, por sus siglas en inglés) 16-18 años de iniciar la restauración. Dado que la mayor parte de la AGB residía en los árboles plantados, la AGB fue aproximadamente 6,5 veces mayor en las plantaciones que en la regeneración natural, y el doble en las plantaciones que en la nucleación aplicada tras dos décadas, a pesar de la considerable mortalidad de los árboles plantados. No obstante, el tratamiento de plantación inhibió la AGB proveniente de árboles que reclutaron naturalmente y acumuló solo la mitad de la cantidad observada en el tratamiento de regeneración natural. La proporción de AGB derivada de árboles reclutados naturalmente fue cuatro veces mayor en la nucleación aplicada que en la plantación. El índice de área foliar (LAI, por sus siglas en inglés) cuantificado mediante LiDAR mostró una correlación más estrecha con la AGB total en las parcelas de regeneración natural, mientras que la altura del dosel presentó una correlación más fuerte con la biomasa de árboles plantados en los tratamientos de plantación y nucleación aplicada. Nuestros resultados destacan que la plantación de árboles acelera la acumulación de AGB en sitios degradados e ilustran la necesidad de seleccionar especies con estrategias de historia de vida complementarias que permitan el secuestro de carbono más allá de la primera década. Ante la compensación existente entre la biomasa de árboles plantados y la de reclutamiento natural, los métodos con patrones espaciales que requieren plantar menos árboles podrían equilibrar mejor los objetivos de restauración más allá de la acumulación de carbono, dando lugar a sistemas reforestados con mayor diversidad estructural y biológica.

Keywords

applied nucleation, canopy height, carbon sequestration, leaf area index, LiDAR, plantation, forest recovery, reforestation, secondary forest, tropical forest.

Author Contributions

Francis H. Joyce: conceptualization, data curation, formal analysis, visualization, writing (original draft), writing (review & editing). **Rakan A. Zahawi:** conceptualization, funding acquisition, investigation, writing (review & editing). **Leland K. Werden:** investigation, writing (review & editing). **Sebastian Zarges:** conceptualization, investigation. **Matheus Pinheiro**

Ferreira: formal analysis, writing (review & editing). **Angélica M. Almeyda Zambrano**: investigation. **Eben Broadbent**: data curation, formal analysis, investigation, writing (review & editing). **Juan Abel Rosales**: investigation. **Karen D. Holl**: conceptualization, data curation, funding acquisition, investigation, writing (review & editing).

Data availability statement

The data and code that support the findings of this study are archived in the Dryad Digital Repository (https://10.5061/dryad.0p2ngf2gt).

1 | Introduction

Assessing patterns of biomass accumulation over time in tropical forest restoration is critically important to inform management practices for both carbon sequestration and biodiversity conservation and recovery. Previous syntheses have quantified aboveground biomass (AGB) accumulation in areas undergoing natural regeneration (Poorter et al., 2016, 2021), non-native monoculture plantations (Bukoski et al., 2022), and multi-species tree plantations (Feng et al., 2022) and have shown the importance of climate and species composition for AGB accumulation. However, replicated studies assessing multiple restoration treatments side-by-side are rare. Although synthetic studies are useful for understanding broad-scale patterns and for high-level planning of restoration initiatives at the scale of countries or subnational regions, making well-informed project-level decisions requires information on local-scale variation in biomass accumulation and direct observations of change over time.

In practice, many restoration initiatives fall somewhere between the extremes of natural regeneration and monoculture plantations of non-native species. For example, mixed species plantings with native species are common (e.g., Rodrigues et al., 2011), and spatially patterned methods in which only a portion of a restoration site is planted are increasingly promoted to increase habitat heterogeneity and reduce labor and seedling requirements (e.g., Holl et al., 2024). Natural tree recruitment is crucial, even for methods that involve tree planting, because forest restoration seeks to create diverse, self-sustaining tree communities (Suding et al., 2015; C. Wang et al., 2022). Planting trees can quickly increase biomass in cleared tropical forests (Bonner et al., 2013). But whether the initial advantages of planting are sustained over time can be unclear because planted trees eventually die. Ideally the proportion of AGB from natural recruits would increase over time along with total AGB but most studies focus on planted tree growth. Fast-growing species that are typically planted at restoration sites for carbon capture tend to be shorter-lived (Brienen et al., 2020; Engert et al., 2020) and have lower wood density, so faster initial gains may not necessarily mean larger carbon stocks in the long run (Sugiyama et al., 2024). Furthermore, greater biomass of planted trees, which typically represent a limited suite of species, could be associated with lower biomass of naturally recruiting trees, challenging promises of win-win solutions for carbon sequestration and biodiversity. High variability of biomass outcomes among sites can confound comparisons of restoration treatment effects and lead to erroneous extrapolations in the absence of replicated experiments, with important implications for scaling up restoration initiatives (Reid et al., 2018).

Recent technological advances in remote- and near-sensing have led to the ability to calculate a wide range of forest structure metrics that can be used to characterize restored forests over time (de Almeida et al., 2025), provide insight into the structural differences underlying variation in AGB among stands (de Almeida et al., 2019), and model AGB over areas that lack direct tree measurements (Labrière et al., 2023). Whereas canopy height is a key variable for estimating AGB from remote sensing (Duncanson et al., 2022; Jucker et al., 2017) and is currently widely available (Lang et al., 2023; Tolan et al., 2024), LiDAR-derived metrics that capture forest structure below the top-of-canopy, such as leaf area index (LAI) and leaf area density profiles, are useful for discerning structural variation among forest stands of similar heights (de Almeida et al., 2025). Although space-borne systems are necessary for producing regional estimates and will be crucial for assessing the recovery of large-scale restoration initiatives, near-surface remote sensing (e.g., UAV-borne sensors) is more appropriate for assessing restoration projects where treatments have been applied to areas only slightly larger than the spatial resolution of moderate-resolution satellite data (e.g., 10 or 30 m).

Here, we assess time series of aboveground biomass accumulation over two decades in a multi-treatment forest restoration experiment that tests a gradient of intervention intensities replicated across a landscape in southern Costa Rica. The first decade of research in this system (Holl & Zahawi, 2014) showed that total biomass was strongly affected by the extent of planting, and that seedling height at 2 years explained about two-thirds of planted tree biomass at 6-8 years. Further, much of the variation in AGB ($R^2 = 0.81$) could be predicted by drone-based measurements of canopy height (Zahawi, Dandois, et al., 2015). Building on these initial insights, we asked: (1) How does aboveground woody biomass (AGB) after two decades of stand growth compare among a gradient of restoration interventions and to a reference forest benchmark? (2) Is there a tradeoff between planted AGB and naturally-recruited AGB? and (3) How well does drone-derived leaf area index (LAI) predict pools of AGB (total, planted, and recruit) compared to canopy height?

For question 1, we expected that total AGB would be positively related to the proportion of initial area planted (plantation > applied nucleation > natural regeneration). However, the influence of restoration treatments on the absolute and relative amount of AGB from naturally-recruited trees ("recruits") over time (question 2) was an open question, given that planted trees might either facilitate or suppress natural recruit AGB, by influencing the abundance and species composition of recruiting tree seedlings, and by affecting the growth and survival of recruits. For question 3, we expected both canopy height and LAI to be positively correlated to AGB, but that the correlation strengths would vary with AGB pool and restored forest type. Greater LAI could indicate a more complex canopy structure formed by trees in different strata, which could partition available resources and use light more efficiently for net primary productivity, resulting in greater overall biomass accumulation (Fahey et al., 2025; Gough et al., 2019; LaRue et al., 2019; Liu et al., 2024).

2 | Methods

2.1 | Study area

We conducted this study at 12 restoration sites in southern Costa Rica (Figure S1, 8º44′ – 8º47′ N, 82º56′ 82º57′ W). Sites range from 1100 to 1430 m in elevation, have a mean annual temperature of ~21ºC, and receive mean annual rainfall of 3500 to 4000 mm with a dry season from December to March. Forests in this region are at the boundary between Tropical Premontane Wet and Rain Forest life zones (Holdridge et al., 1971) and fall within the Talamancan montane forest and Isthmian-Pacific moist forest ecoregions (Olson et al., 2001). The landscape was largely deforested between 1960 and 1980 and is now a fragmented mosaic of remnant forest, secondary forest, cattle pastures, and agricultural fields (Zahawi, Duran, et al., 2015). All sites were farmed or grazed by cattle for at least 18 years and are separated by a minimum of 700 m (Table S1). Soils are volcanic in origin, mildly acidic (pH ~5.5), low in P and high in organic matter (Holl & Zahawi, 2014).

2.2 | Experimental design

At each restoration site, we established three 0.25-ha plots separated by a ≥5-m buffer. In 2004–2006, each plot received one of three randomized treatments: natural regeneration, applied nucleation, or plantation. Natural regeneration plots were not planted, whereas applied nucleation and plantation plots were planted with seedlings of four tree species (Figure S2): *Erythrina poeppigiana* (Walp.) O.F.Cook (Fabaceae), *Inga edulis* Mart. (Fabaceae), *Terminalia amazonia*

(J.F. Gmel.) Exell (Combretaceae) and *Vochysia guatemalensis* Donn. Sm. (Vochysiaceae). *E. poeppigiana* and *I. edulis* are naturalized species widely used in coffee intercropping. *T. amazonia* and *V. guatemalensis* are native to Costa Rica, planted as timber species, and typically found at elevations up to 1200 and 1500 m, respectively (Nichols et al., 1997; Orwa et al., 2009). Hereafter, we refer to the four planted species by their genera for simplicity. In applied nucleation plots, 86 trees were planted in six nuclei or patches, two each of 4 × 4 m, 8 × 8 m, and 12 × 12 m, whereas plantation plots were planted uniformly throughout with 313 trees. Seedlings were planted in alternating rows of *Erythrina*/*Inga* and *Terminalia*/*Vochysia,* with seedlings within rows spaced 4 m apart. Adjacent rows were offset by 2 m such that seedlings were separated by 2.8 m (Holl et al., 2011). In all plots, all herbaceous and ruderal vegetation was periodically cleared to ground level for the first 2.5 years to allow planted tree seedlings to grow above existing vegetation. Planted seedlings that died within 2 years were replaced.

Although the restoration experiment had a randomized complete block design, some plots and sites were lost to land use change by the end of this study (2024). Accordingly, the number of replicates for each treatment decreased over time: 11 to 9 natural regeneration plots, 11 to 9 applied nucleation plots, and 12 to 10 plantation plots. For brevity, in text we refer to the age of plots in a given survey year relative to the median year of plot initiation (2005). We also sampled plots in six areas of nearby remnant forest, which represent the best-available reference systems in the landscape (Figure S1).

2.3 | Tree measurements

To estimate woody aboveground biomass over time in restoration plots we used diameter at breast height (DBH) measurements collected between 2010-2025 during the first part of the wet season (June or July) for three categories of trees: (1) planted trees, (2) naturally recruited trees ≥10 cm DBH ("larger recruits"), and (3) naturally recruited trees 5.0-9.9 cm DBH ("smaller recruits"). Trees in all categories were identified to the lowest possible taxonomic resolution, permanently tagged, and measured for DBH on up to three stems. The sampling design and timeline varied by category (Table S2, Table S3, Figure S2).

We recorded survival for all planted trees in applied nucleation and plantation plots at 2-year intervals from 2010-2024 (planted tree age 3-5 to 18-20 years). At the same time, we measured DBH of all individuals ≥5 cm DBH in applied nucleation plots and of a subset comprising an equivalent number in plantation plots.

We measured all larger recruits within each restoration plot every year between 2010-2014, and thereafter every two years from 2016-2024. We measured all smaller recruits within four permanent subplots in each restoration plot every year from 2010-2019 and every other year from 2021-2025 (Table S2, Figure S2). In natural regeneration and plantation plots, the subplots were 8 × 8 m and located according to a stratified random design, with one subplot in each quarter of the plot. In applied nucleation plots, subplots were 8 × 16 m (double the sampling area), with half of the sampled area interior to the original planting area of medium and large nuclei, and half of the sampled area extending out from the planted area (Table S2, Figure S2).

In 2022, we measured all stems ≥5 cm DBH in the six remnant forests (Schubert et al., 2025) which we use as a benchmark for forest recovery. Each remnant forest site consisted of four 21 × 21 m plots (total 1764 m^2, Table S2). Tree measurement data sets included 4699 individuals of the four planted tree species, 2208 recruits of 99 taxa in restoration plots, and 1134 trees belonging to 147 taxa in remnant forests.

2.4 | Biomass estimates

To estimate woody AGB density (Mg per ha) from stem measurements for both planted and naturally-recruited trees in each year, we used a 5-step procedure:

1. We assigned wood density values (stem specific gravity, g cm^{-3}) to each species. We preferentially sourced values from previous local measurements (Holl & Zahawi, 2014; Werden et al., 2022) (n = 36 species with local values, including the four planted species). For species lacking local wood density measurements (n = 148 species), we extracted values from the global wood density data set (Chave et al., 2009; Zanne et al., 2009) using the BIOMASS package. When species-level values were unavailable (n = 125 species), we used genus-level or averages for the overall data set (see Table S4 for details).
2. We estimated AGB (Mg) for each measured stem ≥5 cm DBH using the pantropical allometric equation from Chave et al. (2014), as implemented by the computeAGB() function of R package 'BIOMASS' (Réjou-Méchain et al., 2017).
3. For each category of stem measurement (planted trees, larger recruits, and smaller recruits), we summed the individual stem AGB estimates and scaled to AGB density (Mg ha^{-1}) based on the sampled ground area in each treatment (see above and Table S2). As we measured DBH for a subset of planted trees in plantation plots, for each plantation plot we summed the tree-level AGB values by species, calculated the mean biomass for individuals of each species, and then multiplied the mean by the total number of surviving individuals of the same species. This scaling provided a species-level AGB density estimate for each tree measurement category in each treatment plot in each survey year (n = 174 planted tree plot ×

year combinations; n = 381 smaller recruit plot × year combinations; n = 325 larger recruit plot × year combinations). Because horizontally projected area differed among plots with varied slopes, the AGB density was likely slightly underestimated for smaller and larger recruits. However, the estimates for planted tree AGB density were unaffected by variation in plot sizes, because the number of trees planted in each treatment was standardized, such that using the nominal scaling factor was appropriate.

4. We estimated plot-level AGB density for years when a given tree category was not measured (Table S3) by linearly interpolating the values from the years immediately prior and following each missing value using the approx.na() function in the 'zoo' R package (Zeileis & Grothendieck, 2005). Smaller recruit data from 2025 were used to interpolate biomass of smaller recruits in 2024 but otherwise were not included in analyses.
5. Finally, for each combination of restoration plot and year, we summed larger and smaller recruit AGB density estimates to obtain overall recruit AGB density, and summed recruit and planted tree AGB density to obtain total AGB density.

The final data set of estimated AGB density contained time series (typically 15 years) for 34 restoration plots (481 total plot × year combinations). For brevity, hereafter all mentions of AGB are presented on a per-hectare basis (Mg ha^{-1}).

2.5| Drone data collection and processing

In July 2022, we flew the GatorEye Lite drone-LiDAR system (Broadbent et al., 2024) to characterize the physical structure of most restoration plots (n = 7 natural regeneration, 6 applied nucleation, 7 plantation plots). The Lite system is a DJI M300 flight platform and integrates multiple sensors, including a DJI L1 lidar system. We defined 600 × 600 m square flight areas (aka, 'big plots') centered over each site (block of 50 × 50 m field plots). Then we flew the area using flightlines spaced 25 m apart, at 100 m above ground level using terrain following, and at a speed of 10 m/s. This protocol was selected following visual inspection and quantitative analysis of point clouds over the denser forested plot areas to ensure sufficiently high ground point density would be collected throughout the plots, including in areas with dense LAI and on steep topography. The flightline azimuth was oriented to minimize vertical changes during individual flightlines. The L1 sensor was set to triple return mode with max point density collection. Data were processed to LAS format RGB colorized point clouds using DJI Terra software, using an on-site DJI D-RTK base station. The LAS points were then post-processed through the GatorEye MultiScalar workflow to create the final LAS file, and to also calculate digital elevation (DEM), surface (DSM), and height (CHM) rasters (see www.gatoreye.org for detailed system and workflow descriptions).

The LAS files were clipped to the plot boundaries and normalized using ground points classified by the cloth simulation filtering algorithm (Zhang et al., 2016). The normalized point cloud reflected the actual height of each LiDAR point relative to the ground surface. We produced the canopy height model (CHM) by rasterizing the height-normalized point cloud to a 1 × 1 m grid and taking the cell-wise maximum return as the top-of-canopy height. Using the high-density LiDAR point cloud, filtered to only include near-vertical laser pulses, we estimated the leaf area index (LAI), defined as the area of leaves per unit ground surface area (m^2/m^2), from laser transmittance via the Beer–Lambert law (Nilson, 1971), following the voxel-based method of Almeida et al. (2019). First, the point cloud was divided into canopy volume units (voxels) with dimensions of 5 × 5 × 5 m, and the leaf area density (LAD) was estimated using the first returns within each voxel. LAI was then derived by summing the vertical profiles (voxel columns) of LAD. The result was a raster in which each 5 × 5 m cell contained a corresponding LAI value. The entire process was implemented using the open-source 'leafR' R package (Almeida et al., 2019), and differs from the workflow suggested by Fischer et al. (2024). Specifically, our workflow did not use proprietary LAStools (the spikefree algorithm and specific ground classification methods). For statistical analyses, both the CHM and LAI rasters were summarized by calculating the mean of all grid cell values within each plot.

2.6 | Statistical analysis

To assess treatment effects on total AGB and recruit AGB in the final year of the study (2024), after 18-20 years of recovery, we fitted a linear mixed effect model (LMM, Gaussian error distribution) with restoration treatment as a categorical fixed effect and site as a random effect. We also fit LMMs to compare the final (2024) total AGB in plantation plots to AGB in remnant forests, for both (a) the subset of five sites where both forest types were present, and (b) all available plantation plots (n = 10) and remnant forest sites (n = 6).

We compared planted tree survival 18-20 years after plots were established (i.e., in 2024, the final measurement year) for each species between applied nucleation and plantation using a binomial (proportional count) model with treatment, species, and their interaction as fixed effects and site as a random effect. We compared the per-individual accumulated AGB for the final year (2024) for the four planted species in applied nucleation and plantation by fitting an LMM (Gaussian error distribution) with treatment, species, and their interaction as fixed effects and site as a random effect.

To compare the effects of planted treatments on naturally recruiting AGB over time, we modeled recruit AGB as a proportion of total AGB using zero-inflated beta regression (0-1), with treatment, plot age (years), and their interaction as fixed effects and random intercepts and slopes for plots nested within sites. To assess whether there was a tradeoff between planted tree AGB and recruit AGB, we performed Pearson's correlations tests within each plot for every year. To explore the relationship between forest vertical structure and AGB pools, we performed Pearson's correlation tests between structural metrics (LAI and CHM height) and different AGB pools (total, planted, and recruit) for each treatment for the year 2022 (year 17).

We used R version 4.3.2 (R Core Team, 2023) for all analyses. We fit LMMs using the 'lme4' R package (Bates et al., 2015), and GLMs using the 'glmmTMB' package (Brooks et al., 2017) For mixed-effects models, we report conditional and marginal pseudo-R^2 values (R^2_C and R^2_M), which summarize goodness of fit for all predictors (fixed and random) and for only fixed predictors, respectively, calculated using package 'performance' v 0.11 (Lüdecke et al., 2021). We performed post-hoc comparisons to evaluate differences among treatment pairs using packages 'emmeans' v 1.8.9 (Lenth et al., 2023) and 'multcomp' v.1.4-25 (Hothorn et al., 2008).

3 | Results

3.1 | Total biomass

Total AGB in plantation plots (206.9 ± 20.4 Mg ha^{-1}, mean ± 1 SE) was approximately 6.5 times greater than in natural regeneration (31.7 ± 7.1 Mg ha^{-1}) and double that of applied nucleation (98.3 ± 17.1 Mg ha^{-1}; Figure 1a; $F = 69.61$, $p < 0.0001$, $R^2_C = 0.870$, $R^2_M = 0.693$) at the end of the study period (2024), when restored forests were 18-20 years old. Total AGB did not differ between remnant forest (276.4 ± 41.8 Mg ha^{-1}, Figure 1b) and plantation plots at year 18-20 in either model (5 paired sites: t = 0.7, p = 0.54; all sites: t = 1.7, p = 0.13).

3.2 | Planted tree AGB dynamics

Planted tree AGB after 18-20 years was much greater in plantation plots (188.7 ± 21.5 Mg ha^{-1}, mean ± SE) compared to applied nucleation plots (68.5 ± 17.9 Mg ha^{-1}) (Figure 1c, Figure 3, F = 73.03, p < 0.0001, R^2_C = 0.889, R^2_M = 0.527), which was expected given differences in number of trees planted. Distinct species-level patterns of AGB accumulation (Figure 2) underlie the temporal patterns of planted tree AGB (Figure 1c). In year 5, *Inga* comprised a mean of 62.7% and 48.9% of planted tree AGB in plantation and applied nucleation plots, respectively, but by year 11, *Inga* had dropped to 37.2% and 27.4% of planted AGB. Strikingly, *Inga* comprised only 6.3% and 4.4% of planted AGB by year 19, due to high mortality, whereas *Vochysia* increased to 73.4% and 64.9%, respectively (Figures 2 and 3). By year 19, mean plot-level survival was low for *Inga* (plantation: 12.1% ± 6.8% SE; applied nucleation: 21.8% ± 6.6%) and *Erythrina* (plantation: 23.8% ± 7.5%; applied nucleation: 32.7% ± 11.4%), whereas most *Terminalia* (plantation: 76.6% ± 6.0%; applied nucleation: 60.2% ± 9.3%) and *Vochysia* (plantation: 81.4% ± 4.9%; applied nucleation: 64.8% ± 8.1%) had survived (Figure S3). At that time, survival of the planted trees *Vochysia* and *Terminalia* was significantly greater in plantations compared to applied nucleation (p <0.0001, OR = 2.69 and 2.41, respectively), whereas survival lower in plantations for *Inga* (p = 0.006, OR = 0.51) and *Erythrina* (p = 0.048, OR = 0.65). Despite the high mortality of the two N-fixing species, overall planted tree biomass continued to increase over time (Figure 1c), due primarily to rapid growth of *Vochysia* (Figures 2 and 3). Per-individual AGB only differed significantly between planted treatments for *Erythrina*, which by 2024 had greater AGB per tree in applied nucleation compared to plantation plots (Figure S4).

3.3 | Natural recruit AGB

By 2024 (age 19), average recruit AGB in natural regeneration plots (32.2 ±5.1 Mg ha^{-1}) was almost double that of plantation plots (17.6 ± 4.9 Mg ha^{-1}, Figure 1d, Figure 3, $p = 0.03$), but no other pairwise treatment contrast was significant ($p > 0.2$), and overall treatment explained a relatively small proportion of recruit AGB ($R^2_C = 0.236$, $R^2_M = 0.153$) given the high within treatment variation. The percentage of total AGB comprised by natural recruits was greater in applied nucleation (~38%) than in plantation plots (10%) (Figure 4a, $z = -3.4$, $p = 0.003$). Moreover, the slope (annual change in proportion of total AGB) was marginally greater in applied nucleation plots ($z = -2.9$, $p = 0.004$). Correlations between recruit AGB and planted AGB were not significant due to high variance in outcomes across sites, but suggested an initial positive association that became moderately negatively associated over time (Figure 4b), with the initial positive relationship stronger in applied nucleation and the negative relationship stronger in plantation at the end of the study.

3.4 | Lidar metrics

Plot-level means of LAI and CHM in year 17 were strongly positively correlated ($r = 0.70$ to 0.87), with the strongest correlation in applied nucleation and the weakest in natural regeneration. Accordingly, relationships to AGB were similar between the two structural metrics (Figure 5). Plot-level LAI and CHM were positively correlated with total AGB (Table 1, Figure 5a,b), with the strongest correlation between mean LAI and total AGB in natural regeneration (r

= 0.90, Figure 5a,e) and the strongest correlation between canopy height and total AGB in applied nucleation (r =0.96, Figure 5b). Planted tree biomass was more strongly correlated with canopy height than with LAI (Table 1, Figure 5c,d). Neither LAI nor canopy height were correlated with recruit biomass in applied nucleation or plantation (Table 1, Figure 5e,f).

4 | Discussion

4.1 | Long-term effects of tree planting on AGB

In direct comparisons of three restoration treatments at the same sites, tree planting resulted in total AGB advantages that persisted after two decades of recovery. Most total AGB accumulation at these sites was driven by planted trees, even after substantial mortality of two of the planted species. At the same time, the full plantation treatment reduced recruit AGB compared to natural regeneration and applied nucleation, although the comparison was not significant for applied nucleation, given the high among-plot variance. Partial planting (applied nucleation) yielded less AGB than the full plantation treatment but offers two potential advantages. First, the ratio of total AGB in plantation relative to applied nucleation (2.1) was less than the ratio of planted trees in the two treatments (3.6 as many planted trees in plantations). Second, applied nucleation on average resulted in a fourfold greater proportion of biomass in naturally recruited trees compared to plantation, and in absolute values that approached those in natural regeneration. This means that AGB in applied nucleation is more evenly distributed across tree species and age classes and not concentrated in species-poor, single-aged stands. A likely driver for this greater recruit biomass accumulation in applied nucleation is higher growth rates in plots with less planted canopy cover (Caughlin et al., 2019; Kulikowski et al., 2023), likely due to greater light availability.

The amount of carbon sequestration needs to be considered in the light of the cost of the restoration methods. This study did not keep detailed record records of planting and maintenance costs during the initial 2.5 years of the experiment, so precise metrics of cost-effectiveness are unfortunately not possible. We previously estimated that the planting and maintenance costs of applied nucleation was approximately one third that of plantations (Holl et al., 2020), but the overall cost-effectiveness of a particular method for carbon sequestration depends on the cost structure and the relative importance of fixed costs such as land acquisition.

Our results emphasize the importance of careful selection of tree species to plant, especially when few species are available. The substantial mortality for two of the four planted species and resulting shift in AGB dominance to one species (*Vochysia*) highlights the need for a balanced approach to species selection based on growth rates and longevity, to ensure both early site capture ("fast carbon") and long-term, durable accumulation ("slow carbon") (Brancalion et al., 2018; Feng et al., 2022; Hulvey et al., 2013; Reich, 2014). Our limited species pool was not atypical of tree-planting efforts, but planting a greater diversity of species would be preferable. However, this requires seed collection and nursery capacity which can be expensive and labor intensive (Brancalion et al., 2012). Interestingly, *Terminalia amazonia*, which is one of the more widely planted native tropical timber tree species in Central America and has been suggested as an ideal species for long-term carbon storage because of its high wood density, low mortality, and large size potential species for reforestation (Hall & Ashton, 2016; Mayoral et al., 2017; Nichols et al., 1997; Sugiyama et al., 2024), had relatively high survival but low AGB even after nearly two decades, which may be due to shading from the faster growing species or the fact that we planted it at the high end of its natural elevation range.

4.2 | Recovery relative to local reference forest and the literature

Whereas an AGB recovery gap remains for natural regeneration and applied nucleation after 20 years, plantation plots reached comparable total AGB levels to reference sites in the study landscape. It is noteworthy that our remnant forest sites, although the best available near restoration sites, were (a) small samples (0.18 ha), (b) likely altered by past anthropogenic activities (selective logging, defaunation, fragmentation), and (c) quite variable among sites, ranging threefold in AGB (135 to 396 Mg ha^{-1}). AGB estimates from a single much larger (2.25 ha) old growth plot in the study landscape ranged from 318 to 386 Mg ha^{-1} over three censuses between 2010-2020 (San-José et al., 2021), which likely better represents AGB potential under less disturbed conditions and suggests that on average the plantation plot AGB is still below that of the most intact reference forest in the region. Notably, we did not quantify changes in root biomass or soil organic carbon, which is a major pool in old-growth forests, but much slower to recover than AGB (F. Wang et al., 2017).

The AGB accumulation we observed after 18-20 years in natural regeneration plots (31.7 ± 7.1 Mg ha^{-1}, range 6.5 to 66.7 Mg ha^{-1}) was low when compared to both our planted restoration treatments at the same sites, and also to recovery rates for tropical forests reported in the literature. For example, based on chronosequences at 45 sites in the tropical Americas, Poorter et al. (2016) reported average AGB of 122 Mg ha^{-1} after 20 years, approximately 4 times greater than AGB in our natural regeneration plots. Likewise, in lowland northeastern Costa Rica Rozendaal and Chazdon (2015) reported a mean AGB of 104.02 ± 3.72 Mg ha^{-1} for secondary forests 10-24 years old. Poorter et al. (2016) estimated that naturally regenerating forests require 66 years to recover 90% of old-growth AGB, but given the much lower AGB accumulation we observed over the first 20 years of regrowth, we would expect longer recovery times. This may be partly driven by climatic factors, given that the Poorter et al. (2016) sites were primarily in lowlands (< 1000 m vs. 1100–1430 m in our study), which generally have been considered to have greater biomass (Muller-Landau et al., 2021). However, recent evidence shows that biomass carbon accumulation actually peaks at 1000 m in the tropics (Su et al., 2024), and that montane forests can hold large aboveground carbon stocks (Cuni-Sanchez et al., 2021; Prada et al., 2025). Alternatively, our results may better represent AGB accumulation under conditions of high degraded sites (≥18 years of pasture or other prior agricultural use) where non-native grasses persist.

4.3 | Site variability

We also observed substantial (>3-fold) variability in total AGB across sites within restoration treatments. Some of this variability was related to climatic conditions, as two restoration sites were above 1300 m, pushing the upper limit of the elevational range for two of the planted species, which likely explains the overall lower biomass of planted trees and higher proportion of biomass comprised of recruits at these sites. At the same time, much of the variation (two-fold after excluding higher-elevation sites) is likely related to highly localized site conditions and land use history, which is a strong driver of rates of tropical forest recovery (Giles et al., 2024; Jakovac et al., 2021; Meli et al., 2017; Oberleitner et al., 2021). For example, the ranked duration of pasture use was previously found to be the best predictor of biomass accumulation among sites after 6-8 years (Holl & Zahawi, 2014). Results here highlight the amount of variation not captured within global maps of potential AGB accumulation from forest regrowth, even those with relatively fine-resolution (e.g., 1 km in Cook-Patton et al., 2020; Fesenmyer et al., 2025). The sites that are most likely to be used for tropical forest restoration are also those that are less productive for agriculture (Latawiec et al., 2015). Furthermore, when using tree planting approaches, the best-quality sites may not result in greater recruit AGB over time, because the restoration plantings performing the best in terms of planted tree AGB appear to suppress recruit AGB (Figure 4b).

4.4 | Insights from UAV-derived metrics

Even though mean LAI and canopy height were highly correlated with each other at the plot-level, the strength of their correlation with AGB varied by restoration treatment and AGB pool. As expected, LAI was more informative at explaining AGB than canopy height in contexts where recruits were proportionally more important (i.e., natural regeneration), as natural regrowth should develop a more complex, multi-strata structure compared to uniform single-aged plantations. However, because LAI generally saturates during succession, is less likely to be useful as a predictor of AGB at older secondary forest stands or those with faster recovery. By contrast, mean canopy height was more strongly correlated with total AGB for applied nucleation plots, and with planted AGB in both applied nucleation and plantation plots. This finding is consistent with previous studies demonstrating the value of calculating multiple, complementary structural metrics from remotely-sensed data for monitoring restored forests (de Almeida et al., 2025). Continuing to better link field-based data on species composition to increasingly sophisticated remote sensing methods is critical (Labrière et al., 2023), given that failing to account for systematic shifts in wood density composition results in spatially-biased estimates of AGB (Mo et al., 2024; Sullivan et al., 2025). This is especially true if restoration goals encompass not just carbon accumulation but also biodiversity (Brancalion et al., 2025). In successional forests monitoring assemblages of seedlings, saplings, and small trees that occur below the canopy is important because they represent the future canopy layer, as well as structural complexity that is critical for faunal habitat.

4.5 | Management Recommendations

The most appropriate forest restoration approach at a given site depends on a host of factors, including the project goal, resources available, past land use history, and rate of natural recovery (Busch et al., 2024; Holl & Aide, 2011). Our and other results (Bonner et al., 2013) show that more extensive tree planting is likely to maximize aboveground carbon sequestration, if that is a primary goal, although that may not be the case in sites with more rapid natural regeneration than our study sites (Busch et al., 2024), which had been used for at least two decades prior for agriculture or pasture and were mostly dominated at the outset by aggressive forage grasses. In contrast, applied nucleation comprises an intermediate intervention approach that has multiple benefits. It can require substantially less planting material, given limited funding and the highly constrained seed and seedling supply chain for restoration globally (Fargione et al., 2021; National Academies of Sciences, Engineering, and Medicine., 2023; Valette et al., 2020). Moreover, it results in a substantially large proportion of AGB comprised of a diversity of recruiting species, which is likely to improve long-term carbon resilience (Warner et al., 2023) and faunal habitat value (C. Wang et al., 2022). We recommend that people leading reforestation projects not immediately assume that extensive tree planting is necessary, but rather consider various forest restoration interventions to evaluate which is the best fit with project goals, rate of natural regeneration, and resource availability (Busch et al., 2024). If full or partial tree planting is part of the approach, projects should include a mix of species that represent a range of growth and longevity traits, as well as potential benefits to wildlife and humans.

Acknowledgments

Financial support for the Islas restoration project was provided by NSF (DEB 0515577; DEB 09-18112; DEB 14-56520; DEB 20-16623) to K.D.H. and R.A.Z. We thank the USDA McIntire-Stennis program for supporting the development and maintenance of the GatorEye program. We are also grateful to Daniella Schweizer for providing logistical support during drone flights, and to Google for funding contributions toward data collection. We thank landowners of restoration sites, the many field assistants who helped with data collection, and Federico Oviedo Brenes for invaluable botanical expertise.

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Table 1. Correlations between LiDAR-derived structural metrics and AGB pools.

AGB pool	LiDAR Metric	Restoration treatment	Correlation coefficient (r)	p-value
Total	Mean LAI	Natural regeneration	0.90	0.006
		Applied nucleation	0.79	0.063
		Plantation	0.49	0.27
	Mean canopy height	Natural regeneration	0.52	0.23
		Applied nucleation	0.96	0.002
		Plantation	0.62	0.13
Planted	Mean LAI	Natural regeneration	-	-
		Applied nucleation	0.80	0.058
		Plantation	0.46	0.29
	Mean canopy height	Natural regeneration	-	-
		Applied nucleation	0.92	0.009
		Plantation	0.73	0.065
Recruit	Mean LAI	Natural regeneration	0.90	0.006
		Applied nucleation	-0.25	0.63
		Plantation	-0.01	0.98
	Mean canopy height	Natural regeneration	0.52	0.23
		Applied nucleation	-0.06	0.90
		Plantation	-0.42	0.34

Figures

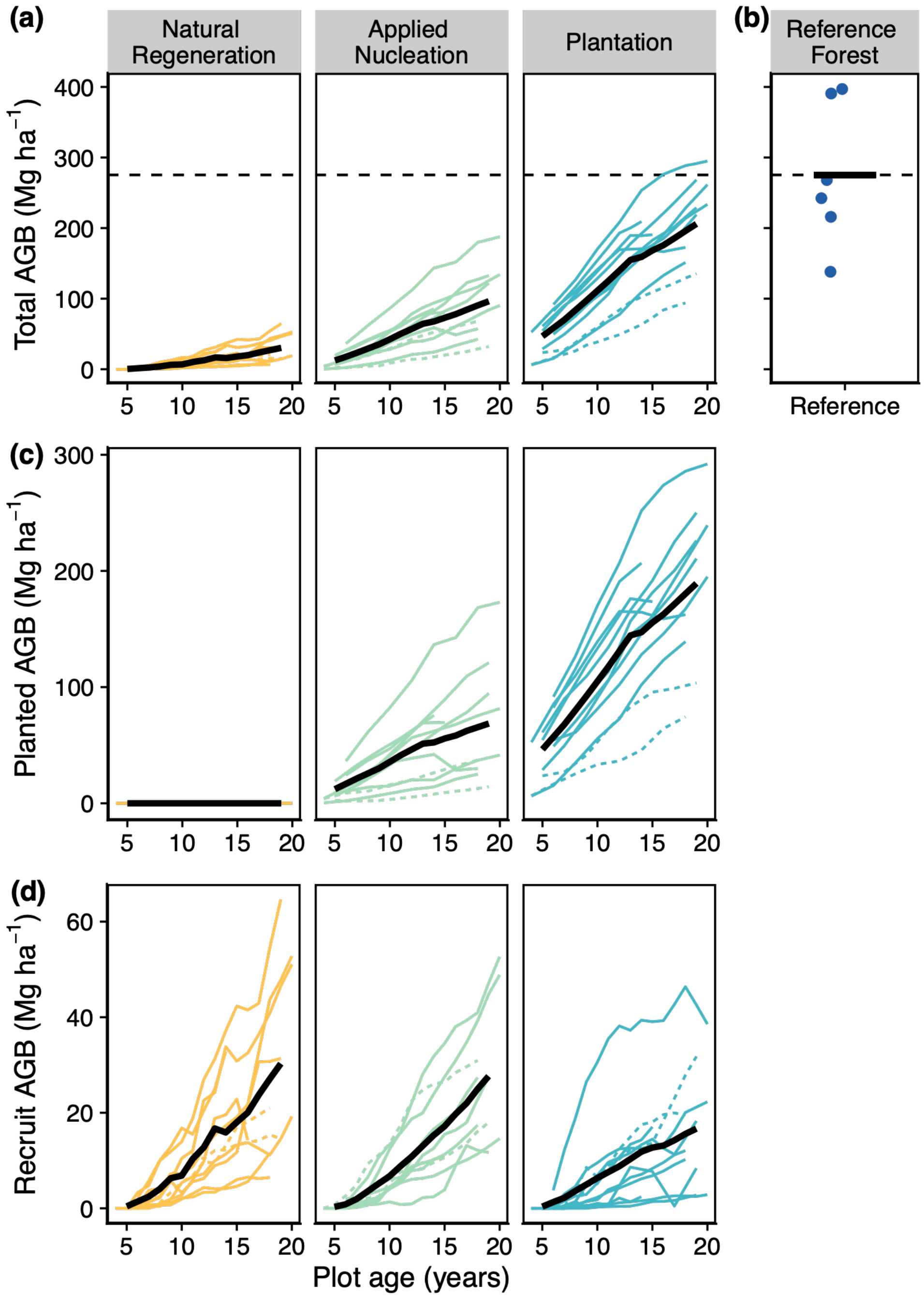

Figure 1. Total AGB in restoration treatments (a), total AGB in remnant forest (b), planted AGB (c), and natural recruit AGB (d). Note different y-axis scales. Thick lines represent mean values. The dashed line in panel a represents remnant forest mean total AGB. Dotted lines represent sites with elevation >1300 m.

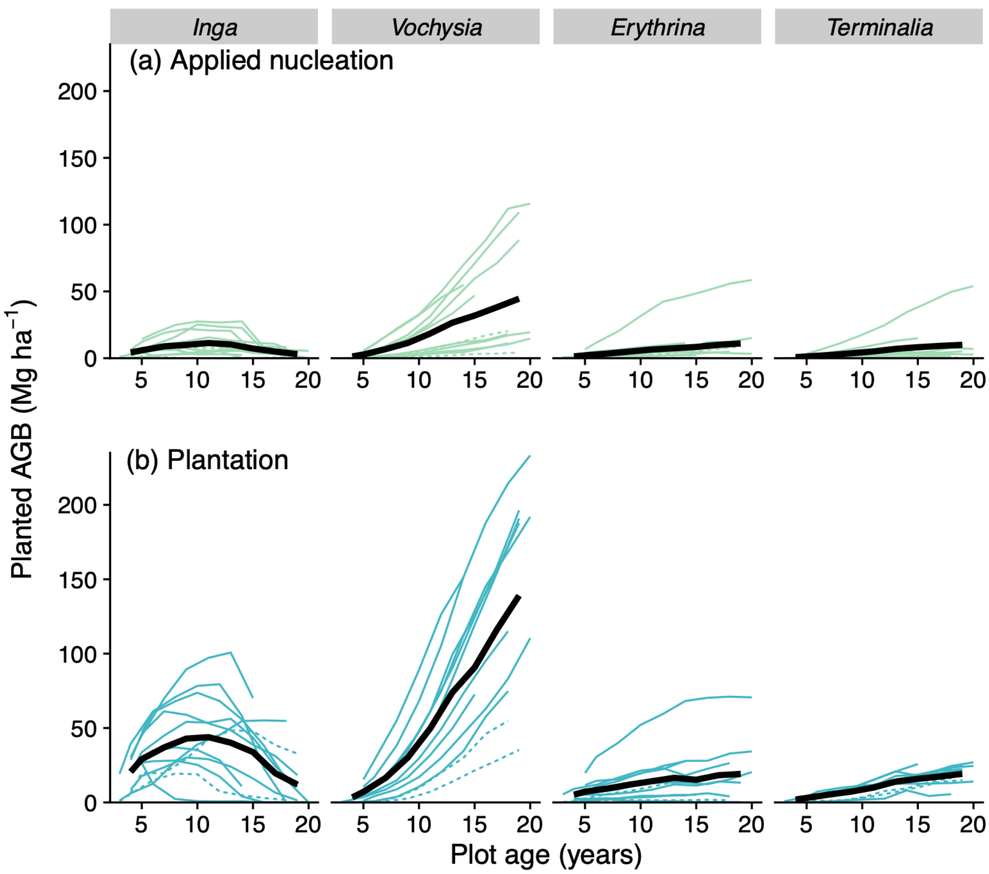

Figure 2. Planted tree AGB over time by species in applied nucleation (a) and plantation (b) plots**.** Thick black lines represent treatment means for each species, where plot age corresponds to the median plot age in a given census year. Thin lines represent AGB in individual plots. Dotted lines represent sites with elevation >1300 m.

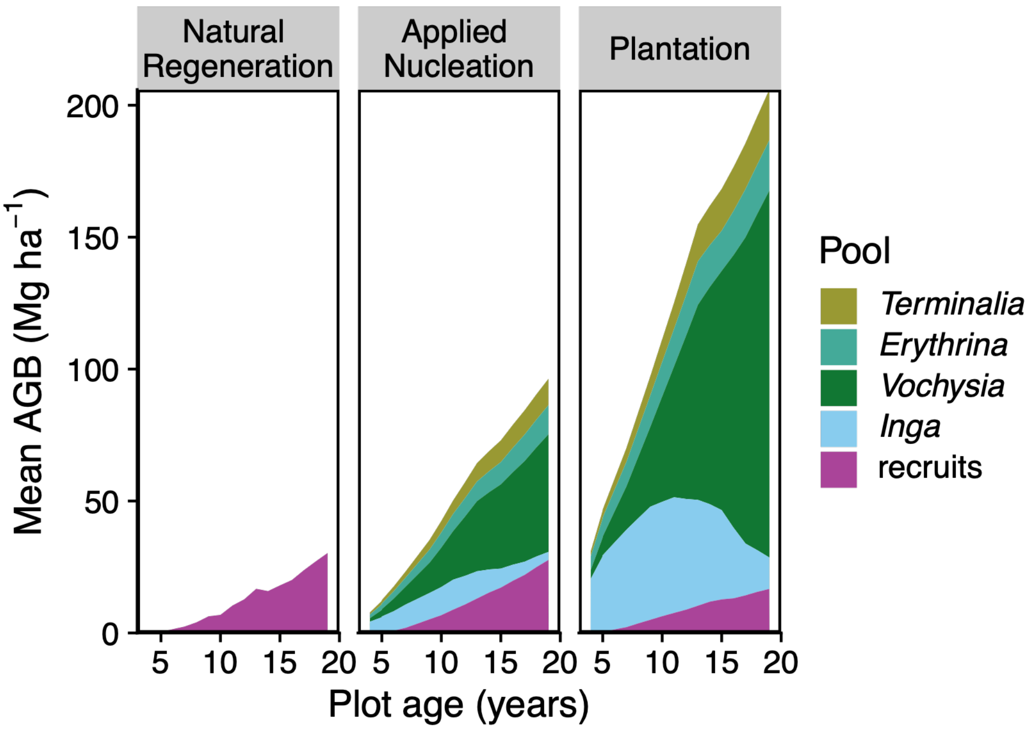

Figure 3. Mean AGB for planted species and natural recruits over time (n = 9-12 plots per age)**.** Recruits include all other species of naturally recruited trees ≥5-cm DBH within restoration plots. Plot age is the median plot age in a given survey year (i.e., years since 2005).

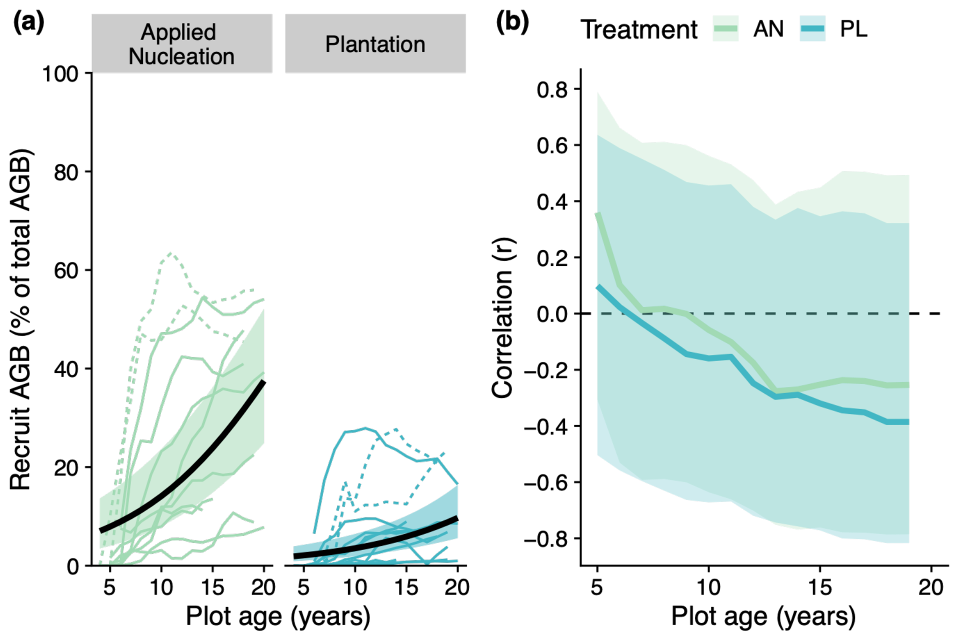

Figure 4. Recruit biomass relative to planted biomass over time. (a) Naturally recruited biomass as a proportion of total biomass. Black line and error band depict model predictions and confidence interval from a zero-inflated beta regression with both a random intercept and a random slope for each plot nested within site. (b) Pearson's correlation coefficient between planted and recruit AGB in applied nucleation and plantation ($n = 9–12$ plots per treatment). Error band represents 95% CIs. Treatment codes: AN = applied nucleation, PL = plantation.

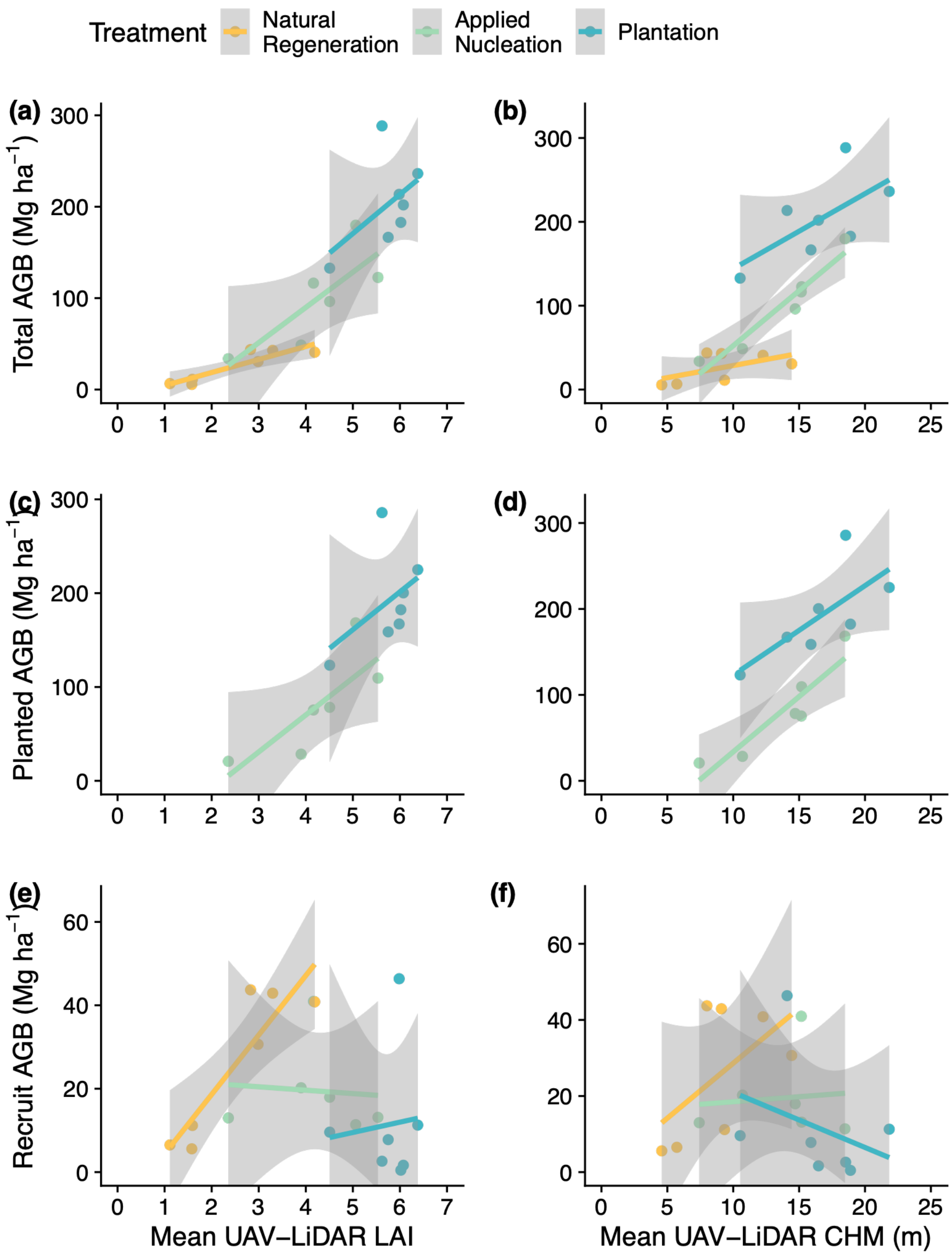

Figure 5. Total (a, b), planted (c, d), and recruit (e, f) AGB vs. plot-level mean leaf area index (LAI) and canopy height derived from UAV-LiDAR in year 17 (2022) (n = 7 natural regeneration plots, 6 applied nucleation plots, and 7 plantation plots).