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RESEARCH ARTICLE

Water availability modulates maximum canopy heights of low-elevation Amazonian second-growth forests

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Abstract

Tropical second-growth forests of the Amazon sequester large amounts of carbon and are important carbon sinks, contributing substantially to climate change mitigation, biodiversity conservation, and providing crucial ecosystem services. Deforestation due to selective logging and shifting cultivation is expanding second-growth forest areas in tropical forest regions, which if well managed, regenerate rapidly over time. Maximum forest canopy height is an important metric of biomass and carbon accumulation in second-growth forests and is strongly influenced by water availability. The water limitation hypothesis explains the positive influence of water availability on maximum tree heights and has been examined and demonstrated at a small-scale using field data, and at a global scale, with limited accuracy, using remote sensing data in tropical ecosystems. However, this hypothesis concerning maximum canopy height has not been much studied at regional and national scales for tropical second-growth forests. In this study, we leveraged NASA GEDI spaceborne lidar data across the Brazilian Amazon and derived second-growth forest relative height metrics for delineating the influence of water availability, second-growth forest age, and topographic elevation on maximum canopy height. Water availability was found to significantly influence the maximum canopy height of second-growth forest trees, of age range from 30 to 35 years, at elevations less than 500 m and maximum precipitation thresholds of 1500 mm. Our results indicate that changing precipitation patterns or increased drought conditions under different climate change regimes could impact forest structure, plant communities, ecosystem functioning, and carbon sequestration capabilities of tropical second-growth forests in the Amazon.

Keywords Forest regeneration · Carbon sequestration · Tropical forests · NASA GEDI · Secondary forests · Climate change impacts

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Introduction

Second-growth or secondary forests play an important role in carbon sequestration and climate regulation, in addition to biodiversity conservation, landscape connectivity, soil protection, and watershed management (Tito et al. 2022; Heinrich et al. 2021; Mohan et al. 2024). Their ability to sequester carbon is of particular significance in the Amazon, given the potential role of second-growth forests in climate change mitigation (Griscom et al. 2017). Second-growth forests cover over 129,000 km^2 of land area in the Brazilian Amazon in 2017 (Smith et al. 2020). Young second-growth forests of < 20 years were found to sequester ~19.0 Tg C yr^{-1} from 2017 until 2030, 11 to 20 times more carbon than mature old-growth forests (Asner et al. 2010; Poorter et al. 2016; Heinrich et al. 2021; Chazdon et al. 2016). Although they should not be treated as a replacement for old-growth forests, they help offset the carbon lost from deforestation in old-growth forests.

Maximum canopy height is correlated with biomass stocks in second-growth forests. The variability of the maximum canopy height of vegetation is explained by water and energy availability on a global scale (Koch et al. 2004; Klein et al. 2015). For most subtropical and tropical forest regions, water availability is found to have a positive influence on the maximum canopy height of trees, over energy availability, and this relationship is explained by the water or hydraulic limitation hypothesis (Ryan and Yoder 1997; Wang et al. 2022; Koch et al. 2004; Klein et al. 2015; Zhang et al. 2016). This theory states that one of the major limitations to terrestrial tree growth or survival is related to the transport of water through the tree's vascular system, especially in times of water stress. Various remote sensing studies have confirmed this connection for tropical forests at the global scale (Moles et al. 2009; Larjavaara 2014; Klein et al. 2015; Tao et al. 2016; Scheffer et al. 2018; Zhang et al. 2016), country level (Adrah et al. 2022), and regional level (Fricker et al. 2019; Wang et al. 2022). Nonetheless, the positive relationship between water availability and maximum canopy height is also moderated by biogeographic patterns and evolutionary history (Zhang et al. 2016).

Besides climate variables, other multiple abiotic factors such as topography and soil variables influencing plant rooting depth also influence maximum tree height. Trees growing on different topographical conditions of elevation and slope (e.g., steep slopes and valleys in mountainous regions, and those growing in lowland areas) are subjected to varying levels of water availability. Water availability has been found to have a positive influence on the maximum canopy height of trees in subtropical and tropical forests (Wang et al. 2022). However, the influence of topographic elevation on water availability and maximum canopy height becomes insignificant at variable elevation thresholds. For instance, the influence of topography and water availability on maximum canopy height was observed to be less significant at elevations higher than 1000 m for the mountainous tropical forest landscapes of Malaysia (Adrah et al. 2022). The subjecting effect of topography on maximum canopy height is stronger at fine spatial scales at elevations of less than 50–500 m while water availability is stronger at large spatial scales as measured by climate variables (Fricker et al. 2019). Soil type associated with geologic soil parent material influences soil water contents, organic matter, and pH, and determines maximum canopy height. The soil nutrient limitation, though important, has reduced influence on maximum canopy height at lower elevations and may vary with vegetation type because soil nutrient availability is strongly influenced by factors such as climate and topography. Thus, at lower elevations, water availability is the most limiting factor to tree height while the influence of soil characteristics and geologic parent material are marginally important and only at finer spatial scales (Fricker et al. 2019).

Although previous studies reported that water availability influences the maximum canopy height at the local scale in the tropics, this has not been explored in depth, and at larger temporal or spatial scales, for second-growth forests. One of the major reasons for this is the challenges associated with the quantification of the long-term increment, extent, and age of second-growth forests (Silva Junior et al. 2020). Nonetheless, it is known that water availability affects the growth rates and canopy heights of second-growth forests greatly as it is essential for carrying out major physiological processes such as photosynthesis, nutrient uptake, hormonal regulation, root development, and cell expansion (Anderegg et al. 2016; Coosme et al. 2017; McDowell et al. 2008; Hartmann et al. 2018). For instance, water stress can lead to the shrinkage of cells and thereby cause stunted growth and reduced plant height in regenerating forests (Ryan and Yoder 1997; Anderegg et al. 2016; Elias et al. 2020). Similarly, as plants need to take in water from roots to produce glucose and oxygen, limited water supply affects the photosynthesis rates resulting in shorter plants. Since water acts as a medium for efficient nutrient absorption, lack of water content can negatively impact metabolic processes—and in turn the overall health—of the emerging plants. During times of water scarcity, several hormonal changes occur in plants, which can force the plant to go to a water-saving mode through stomatal closure. Although this strategy helps the plant to survive, it can be detrimental to plant growth and height.

Most of the previous studies that explored the impact of water availability on second-growth forests canopy heights have utilized field data with microscale or macroscale plots (Lennox et al., 2018). For instance, Zarin et al. (2001)

showed that Amazon's second-growth forest was limited by water availability in terms of growing season days at a small plot scale. Chazdon et al. (2003) conducted a study to examine the relationship between soil water availability and second-growth forest growth in Costa Rica, and found that higher water availability resulted in increased rates of height and diameter growth of trees in second-growth forests. Similarly, studies focused on regeneration dynamics of second-growth forests have reported that areas receiving higher rainfall supported faster and more diverse vegetation recovery. Additionally, water availability has been found to influence the establishment, growth rates, density, and survival of tree seedlings (Lebrija-Trejos et al. 2010). However, these field-based studies are geographically and temporally scale-limited.

Airborne and satellite lidar (light detection and ranging) provide new opportunities for the study of second-growth forests. Vertical distribution of vegetation, canopy height, structural variations within forests, canopy gaps, and 3D canopy structure (Adrah et al. 2022; Wang et al. 2023) are useful to quantify aboveground biomass. Nonetheless, lidar studies that depend on aircraft to carry the sensors are expensive to conduct at large scales. With the availability of NASA's Global Ecosystem Dynamic and Investigation (GEDI) spaceborne lidar sampled measurements, we are now able to scale lidar work to regional, national, and global levels. GEDI offers a large number of sampled measurements that are near global scale between 51.6° north and south latitudes, making lidar data analysis possible at a much larger scale (Dubayah et al. 2020). Although research focusing applications of GEDI for studying second-growth forests is relatively new, a few recent studies—with some integrating GEDI with airborne lidar and satellite data—have looked into monitoring forest succession, canopy height variations, and biomass changes happening during regrowth in second-growth forests (Dubayah et al. 2022; Milenković et al. 2022; Adrah et al. 2022). A few other studies have also used the Geoscience Laser Altimeter System (GLAS) data—which was the first spaceborne lidar—to study biomass accumulation and change (Helmer et al. 2009) and interannual variability of carbon uptake of humid lowland second-growth forests in the Brazilian Amazon (Yang et al. 2020).

The main aim of our study is to explore how water availability impacts the canopy heights of second-growth forests in the Brazilian Amazon. Herein, water availability is defined as the difference between annual precipitation (P) and the annual potential evapotranspiration (PET), hereafter presented as P-PET. We quantified canopy heights for second-growth forests across the Brazilian Amazon using GEDI data, which allowed us to study the relationships at a larger scale that was not achieved by previous forest regeneration-based studies. Moreover, we examined the relationship between forest canopy height, forest age, and P-PET. Finally, the influence of topographic elevation on second-growth forest canopy height was evaluated.

Materials and methods

Study area

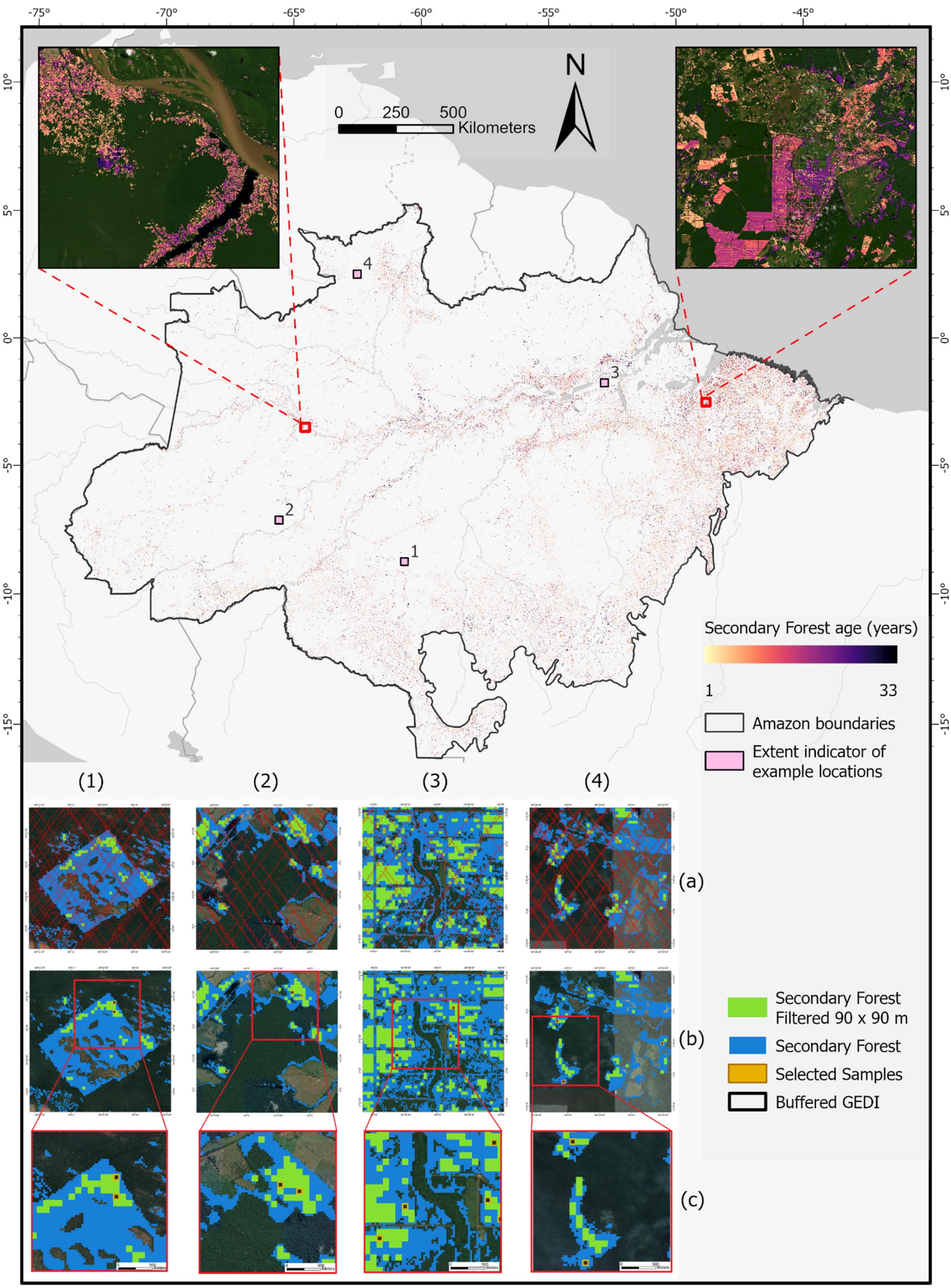
The study area is the Brazilian Amazon region, where we focused on the second-growth forest areas (Fig. 1). The average annual rainfall experienced by the region is around 1700–3000 mm, though this varied significantly based on the location and period considered. Areas in the southern and eastern fringe receive less rainfall, about 1700 mm, compared to other areas of the Brazilian Amazon. The elevation here varied from 1 to 1678 m asl, and in terms of slope, the minimum and maximum were 0 and 29, respectively.

Second-growth forest map

We considered the second-growth forest areas within the Brazilian Amazon region. The set of national-level second-growth forest growth maps of 30 m spatial resolution developed by Silva Junior et al. (2020) identified second-growth forest location and age (where age is defined as the time since the abandonment of agricultural or pastoral land use). The second-growth forest growth was located from Landsat-derived land-use and land-cover (LULC) data from the Brazilian Annual Land-Use and Land-Cover Mapping Project (MapBiomas Collection 4.1; https://mapbiomas.org/en/colecoes-mapbiomas-1) data. The second-growth forest map was based on how a pixel classified as anthropic cover for a given year changed to a pixel of forest cover in the following year. These annual maps provided second-growth forests increment, extent, age, and loss, for the years 1986 to 2018. This allowed us to investigate how second-growth forests of different ages were impacted by changes in environmental conditions. The ages of second-growth forests we observed ranged from 3 to 37 years. The MapBiomas LULC data that was used to derive the second-growth forest map was highly accurate at 86.40 ± 0.46% of average overall accuracy (Silva Junior et al. 2020).

NASA GEDI spaceborne lidar data

NASA GEDI spaceborne lidar, which can provide structural metrics of forest ecosystems, was used for extracting canopy height estimates. With the support of three lasers, and four beams, split into eight tracks, ground transects are produced in this case. Each GEDI shot consists of a circular footprint of ~ 25 m in diameter, which is spaced 60 m


-75°
-70°
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N
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1
2
3
4
Secondary Forest age (years)
1
33
Amazon boundaries
Extent indicator of example locations
(1)
(2)
(3)
(4)
(a)
(b)
(c)
Secondary Forest Filtered 90 x 90 m
Secondary Forest
Selected Samples
Buffered GEDI

Fig. 1 Map of second-growth forest pixels, corresponding ages in the study area, and sample study sites for demonstrative purposes; four example locations are highlighted in pink; **a** filtered 90 × 90 m second-growth forests age map, **b** GEDI coverage for the corresponding area, **c** selected sample based on high quality GEDI shots overlapping filtered 90 × 90 m second-growth forests, and **d** zoomed in GEDI shots

and 600 m apart (approximately) in the track direction (i.e., along the track) and cross-track (i.e., between tracks) direction respectively. The recorded geolocated waveforms are further processed to elevation and relative height metrics (RH) in L2A product, and to cover and vertical profile metrics in L2B product. The algorithms used by GEDI to process the relative height, cover and vertical profile are described in detail in Hofton and Blair (2019). We used canopy relative height metrics (RH 0-100) from the L2A version 2 product available via Google Earth Engine (GEE) (Dubayah et al. 2021; Beck et al. 2021). The relative height is the height at which a certain quantile of returned energy is reached relative to the ground. We selected and evaluated all the relative height metrics commonly used in the literature as a proxy for the top of the canopy (RH90, RH95, RH98) as elaborated in section "Relative height metrics and water availability relationship" (Adrah et al. 2022; Dubayah et al. 2021; Potapov et al. 2021). We used all GEDI data available between 2019 and 2023 over the Brazilian Amazon. Next, we applied quality criteria filters to select the highest quality GEDI shots. We filtered GEDI L2A data based on the quality flag (equal to 1), degradation flag (equal to 0) and minimum accepted sensitivity of 0.98 (Dubayah et al. 2021). These flags can be interpreted as indicators of issues such as non-optimal operating conditions which affects geolocation performance, sub-optimal default algorithm settings for certain landscapes (e.g., high canopy), misclassification in coastal areas, waveforms of poor signal quality, waveforms affected by cloud/land surface conditions, etc. GEDI shots with no overlaps with the second-growth forest map from Silva Junior et al. (2020) were removed.

Climate and topographic data

Monthly climate and climate water balance for terrestrial surface were considered from 1988 to 2018 corresponding to the maximum second-growth forest age. The major climate variables used for this study are the annual mean precipitation and annual potential evapotranspiration. All these data were extracted monthly from the TerraClimate dataset, with spatial resolutions of approximately 5 km^2, also accessed through GEE (Abatzoglou et al. 2018). We defined the difference between P, the annual precipitation, and PET, the annual potential evapotranspiration (P-PET) as a proxy for water availability, which reflected the climatic water balance rather than direct measures of soil moisture or outputs from hydrological models (Klein et al. 2015; Adrah et al. 2022). We also evaluated the impact of two topographic variables; slope and elevation. These elevation data were obtained from the version four of hole-filled 90 m Shuttle Radar Topographic Mission Digital Elevation Model (SRTM-DEM) dataset and slope were derived using TAGEE package in GEE to derive the respective features at 90 x 90 m resolution (Jarvis et al. 2008; Safanelli et al. 2020). Although the SRTM-DEM is not corrected for vegetation bias, the vegetation bias is assumed to have minor impact on our results as we used the DEM to focus our study on elevation between 0 and 500 m and filter GEDI shots based on the slopes rather than modeling the relationship between heights and elevation. A summary of the data used can be found in Table S1 supplementary materials.

2Dataset preparation

Filtering was done for the following datasets: second-growth forest age map and GEDI shots; see Fig. 2 for the entire workflow. As a first step, we utilized a shapefile for the Brazilian Amazon boundary and created 90 m x 90 m grids. The grid size was selected to match 9 Landsat pixels (of 30 m x 30 m resolution each) per square grid. From this, we selected the grids where we could identify 100% second-growth forest pixel overlaps. Furthermore, as a means of cross-validation, we also checked the corresponding classes of the 90 m x 90 m grids in the Mapbiomas database and removed areas where the class was not a forest in both cases. This was done as an additional step to prevent misclassification and ensure that only pure second-growth forest areas are included in our analyses. We also removed grids where the within-grid second-growth forest age variation (i.e., maximum–minimum second-growth forest age) > 3 years to retain the homogeneity of the areas considered. After this, the mean second-growth forest age was estimated for all the existing grids.

GEDI shots overlapping the selected second-growth forest grids were extracted and points with RH90 < 3 m were removed, since GEDI measurements of short vegetation are less reliable (Li et al. 2023). This lower threshold was used as a quality filter. Further standard QA/QC (Quality Assessment/Quality Control) measures were applied as a cautious measure to eliminate potentially corrupted GEDI shots and were adopted as a reliability criteria for filtering GEDI data. In addition, shots where the slope is larger than 15 degrees were also removed to avoid uncertainties in GEDI measurements impacted by steep slopes (Adam et al. 2020; Fayad et al. 2021; Oliveira et al. 2023). For each remaining GEDI shot, a 45 m side buffer was created and the GEDI shots for which the buffer was not fully contained in the 90 m x 90 m were removed. This 45 m side buffer

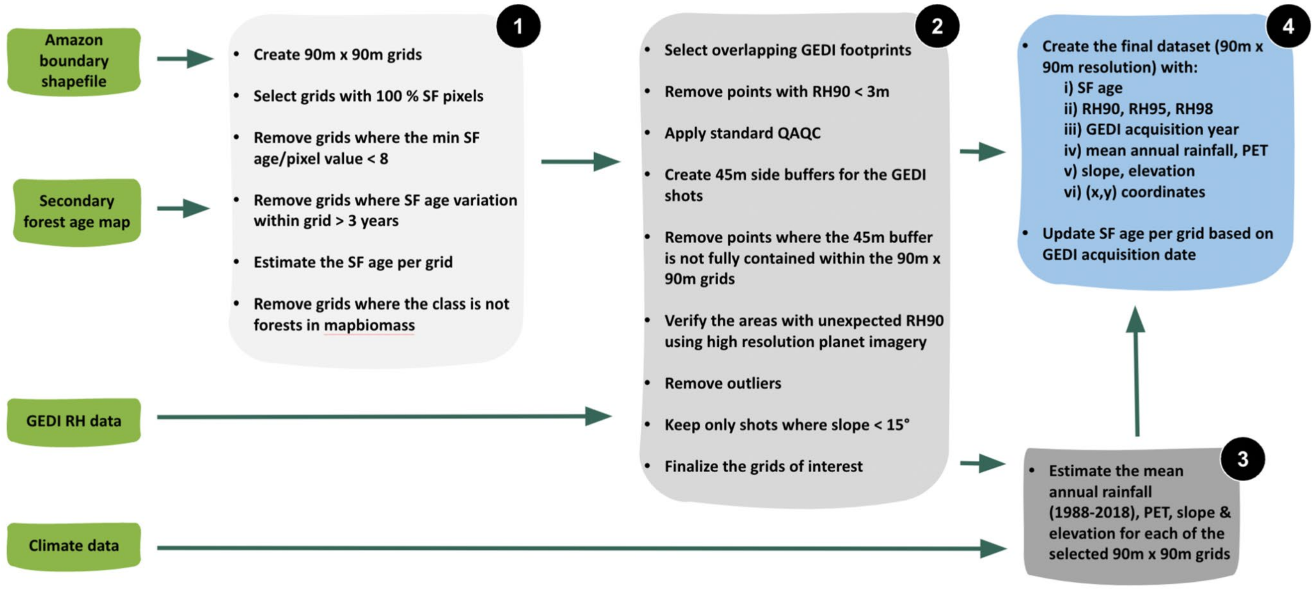

Fig. 2 Workflow diagram regarding the creation of the final dataset; the green boxes represent the input data; box 1 provides information about the grid generation and selection process; box 2 discussed various quality control quality assessment protocols; box 3 mentions about the rainfall data; box 4 includes information on the final dataset; RH: Relative Height: SF: Secondary Forest; QAQC: Quality Assurance and Quality Control

was selected accounting for the maximum 10 m geolocation error estimated for enhanced geolocation GEDI version 2 and 12.5 m radius of the GEDI shot (i.e., 12.5 m + 12.5 m + 10 m + 10 m) (Beck et al. 2021; Schleich et al. 2023). We also verified areas with low second-growth forest age values and unexpected canopy height values using high resolution PlanetScope imagery (3 m spatial resolution) and however, none of the selected grids were marked as non-forest areas and hence no further data was removed. Moreover, trees with RH values above 70 m were removed, assuming these are outliers.

The final dataset had 8247 GEDI shots in total and comprised one shot per each grid cell of 90 m x 90 m. Climate and topographic information of these selected grid cells were then extracted. The variables of interest present included second-growth forest age for the selected 90 x 90 m grid cells, RH90, RH95, RH98, GEDI data acquisition year, geographic coordinates, mean annual rainfall, PET, elevation, slope, and P-PET. The mean age of corresponding grids was updated based on the GEDI data acquisition date (for example, 2 years was added to second-growth forest age if the GEDI data was acquired in 2020, given that the second-growth forest map was for 2018). RH refers to relative height metrics, specifically, the height above the ground at which a given percentage of the reflected laser energy is detected by the sensor.

Relative height metrics and water availability relationship

First, we evaluated the relation between second-growth forest age and three relative height metrics (RH90, RH95, RH98). Even though all the three height metrics showed a positive result in our analysis, RH90 had the best fitting and therefore, this metric was used in subsequent analyses. We aggregated the mean RH90 values for each 1 year second-growth forest age interval and plotted it against second-growth forest age to observe the relations more clearly. That is, for example, RH90 values of all the trees with ages > 1 year and <= 2 years, were pooled into one category (second-growth forest age = 2), and we estimated the mean RH90 for this range and allocated that as the RH90 value for the corresponding category. Second, we selected the grids where the mean second-growth forest age was between 30 years and 35 years (see Fig. 3). This criterion allows us to reflect typical growth patterns by making sure that the climate and other environmental impacts are spread out through a larger proportion of the tree lifespan, and that there exist minimum discrepancies arising from extreme conditions (e.g., the occurrence of drought, which might have a significant impact on tree heights, yet very difficult to interpret and/or isolate). Younger and smaller trees are more likely to be negatively affected by extreme events such as El Niño in tropical forests (Nakagawa et al. 2000). Younger second-growth forests were also excluded owing to their faster growth rate, since for a LiDAR-derived

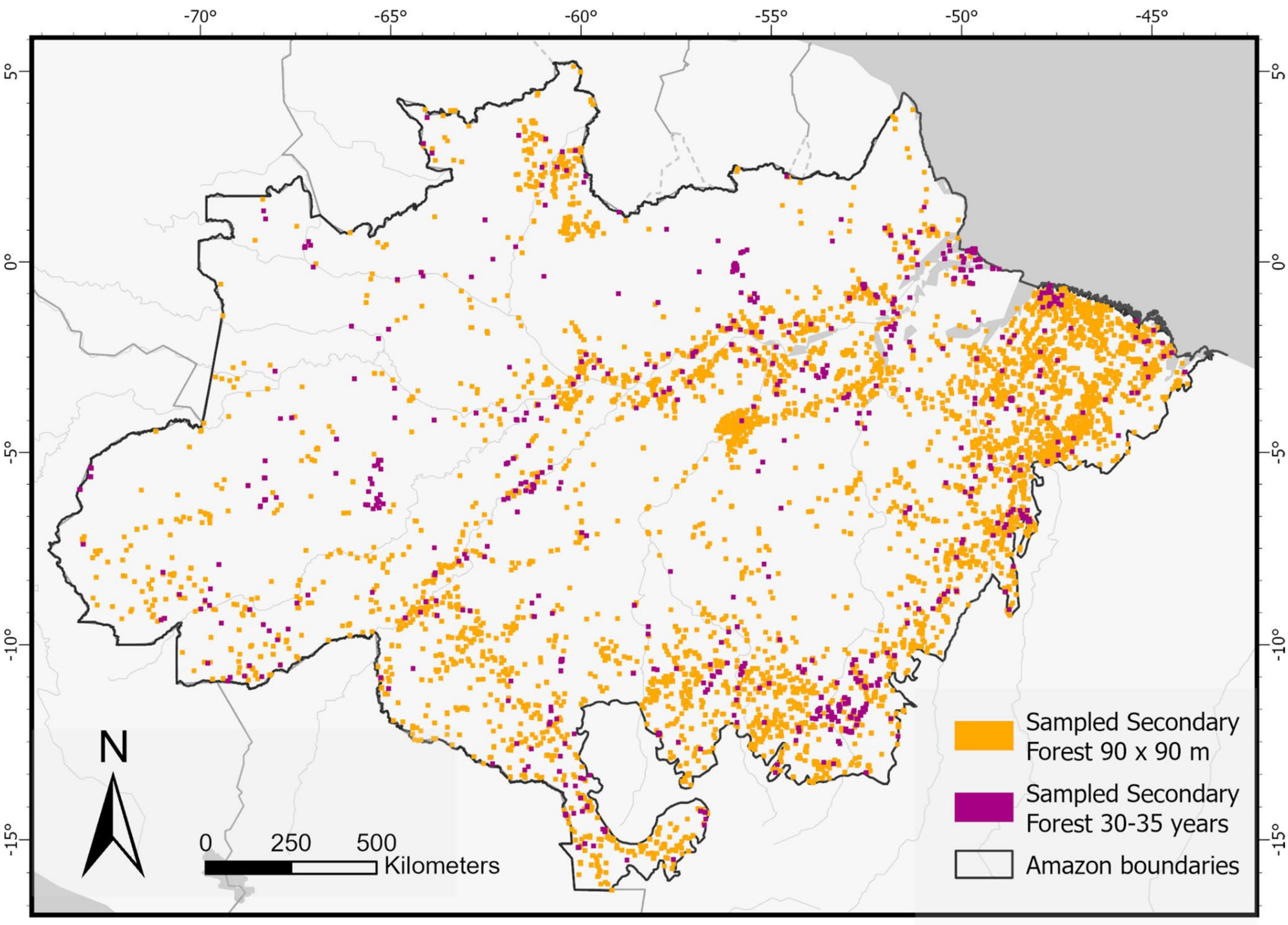

Fig. 3 Grids for the second-growth forest age range 30–35 years

canopy height estimate for biodiversity-related studies, an accuracy of ± 2 m is necessary. In young forests or shrub vegetation, even an absolute error of ± 1 meter can result in a disproportionately high relative error, making it difficult to obtain reliable height estimates (Bergen et al. 2009; Dhargay et al. 2022).

Third, we evaluated the relationship between RH90 and water availability in the selected grids using generalized linear regression. The relative height is treated as the response variable and water availability as the independent variable.

We conducted our analysis twice; first for all individual data points representing height-water availability, and second for bins of water availability and different corresponding canopy height percentiles. We considered water availability bins of 50 mm, 100 mm, 200 mm and 500 mm. This examination is advantageous to observe the trends across water availability gradients and examine the robustness of the relationship. For a bin to be considered, the minimum number of points per bin was predetermined to be 10; this helps reduce the effect of noise on the estimated model parameters. For each bin, we estimated the mean and 90th percentile of RH90; 10th, 25th, 75th and 95th percentile results were also evaluated. Both standard linear regression and generalized linear regression model were tested, and R^2 and *p*-values were taken into account, as they were the most commonly used models in previous studies. We considered only standard linear regression in further analysis as we did not observe any significant differences concerning the generalized linear regression model within the independent variable gradients we examined. Our primary goal here was to understand the influence of water availability on maximum canopy heights and average tree growth rates. The influence of elevation was also verified by plotting the RH90-water availability across different elevation thresholds as a recent study had underscored the significant change in RH90-water availability trends with changing elevations (Adrah et al. 2022; Jucker et al. 2018; Fricker et al. 2019). All the statistical and data analysis operations were carried out in R.

Results

The relationship between RH90 and second-growth forest age, when fitting all data and using the generalized linear regression is presented in Fig. 4. In Fig. 4a we have binned in the age classes as we were able to obtain a clearer relation when RH90 was aggregated to 1 year second-growth forest age intervals. While in Fig. 4b we have binned in both axes to further elucidate the canopy height-age relationship. Herein, Fig. 4b shows the effect size, and highlights the signals between RH90 and second-growth forest age we are observing at region scale, which is biologically meaningful.

By analyzing canopy heights of older second-growth forests, in relation to water availability, we are able to assess the growth dynamics. In our case, after selecting the grids with second-growth forest age between 30 and 35 years, RH90 values across the entire range of water availability were evaluated. Only the water availability range of 0–1500 mm was considered—as above 1500 mm, each of the 100 mm bins did not have the minimum number of data points (i.e., 10). Figure 5 shows the number of points per each 100 mm bin.

Regarding elevation, we decided to focus on the 0–500 m threshold as the relationships were not clear in higher elevations and our DEM elevation is not corrected for vegetation bias. Moreover, land use practices also vary drastically with higher elevations and hence the changes we might observe would be due to different anthropogenically impacted drivers other than water availability. Application of elevation cut-off resulted in removing 109 (1.3%) data points. The relationship between canopy height, water availability and elevation gradients for forests aged 30–35 years can be found in Supplementary Fig. S1. We also added boxplots showing canopy heights below and above these thresholds in Supplementary Fig. S2.

Both the 90th percentile (R^2: 0.784) and median (R^2: 0.724) of RH90 were found to be significantly influenced by water availability (Fig. 6). In Fig. 6 we can notice that RH90 (90th percentile) increases from an average of 17.6 m in the driest areas (20% lowest water availability) to 28.1 m in the most wettest areas (20% highest water availability) showing the significance of the effects. Likewise, in case of mean canopy heights, RH90 varies from 14.1 m (driest areas) to 20.6 m (wettest areas).

Discussion

Canopy heights of tropical second-growth forests change with time, controlled by several factors. Understanding the controlling influence of these factors is critical for sustainable management and conservation of second-growth forest ecosystems. GEDI-derived metrics were used to better understand the relationship between canopy height (RH90) and forest age for second-growth tropical forests in the Brazilian Amazon region, and to evaluate how canopy height of these forests are influenced by various topographic and environmental factors. We observed that water availability (P-PET)—at specific elevation, and slope thresholds—determined the canopy height-age distribution of second-growth forests of the 30–35 year age group. The relationship between second-growth forest canopy height change and water availability vary at different scales within the same geographical areas, as it is influenced by different topographic, climatic, and environmental factors (Elias et al. 2020).

Exploring the relationship between second-growth forest age and canopy height, by plotting all the points, we noticed a weak relationship between canopy height and second-growth forest mean age (–35 years). However, when we aggregated the mean canopy height values for each 1 year second-growth forest age interval (i.e., for each year, we calculated the corresponding mean canopy height) and plotted it against second-growth forest age, we observed an improvement in the relationship, evident by a higher R^2 value (Fig. 6). This suggests that second-growth forest canopy height change can be better explained by changes in the aggregated mean second-growth forest age. Herein, the ability of the present approach to predict variation in canopy height at any given location is very poor, however, we observe a tight relation between canopy height and mean age—which is biologically significant—at the region scale.

Uncertainties here associated with inferring the actual structure of the forests may arise from sensor type-related errors (which could be compounded by slope and/or ecosystem structure) and issues related to misclassification of second-growth forest pixels, which might affect interpretations, such as the presence of tall trees in the middle, pasture lands looking like forests, etc. Application of data fusion techniques–involving multiple remotely sensed data types–could help improve the results. We found that long-term water availability (P-PET) has a positive impact on the canopy height of second-growth forests at 500 m or less in elevation in gentle slopes (less than or equal to 15° slope conditions). Elevation and slope greater than 500 m and 15°, respectively, had less clear relationships and were not further explored in the study. This was in alignment to our previous study (Adrah et al. 2022) utilizing GEDI metrics, where we reported water availability and elevation to have a major influence on the canopy height across tropical forests of Malaysia. Moreover, at higher elevations, land use practices also vary more drastically in our study area and hence the changes we might observe would be due to

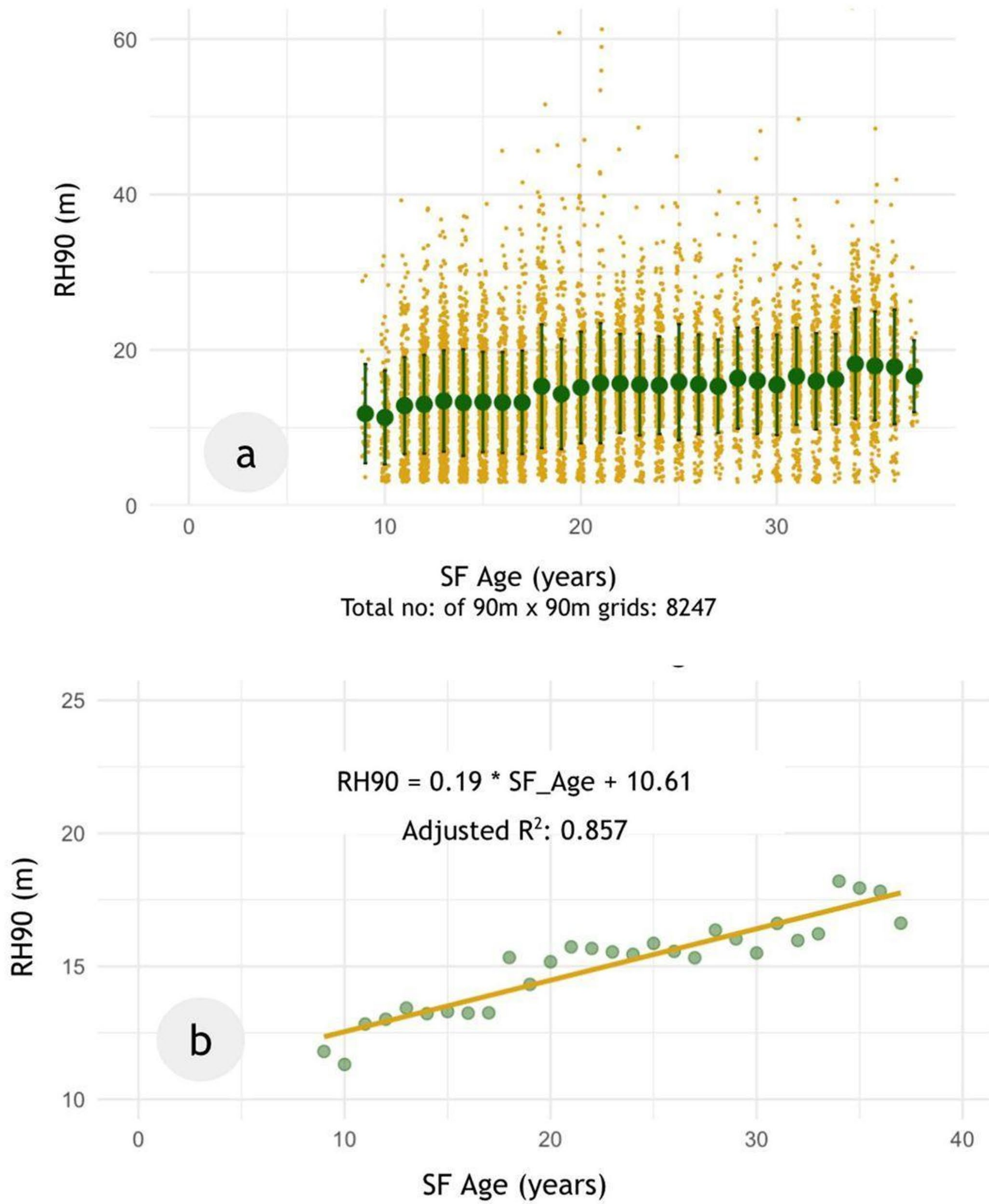

Fig. 4 Canopy height changes with respect to age: **a** RH90 across individual second-growth forest age; **b** mean RH90 versus second-growth forest age

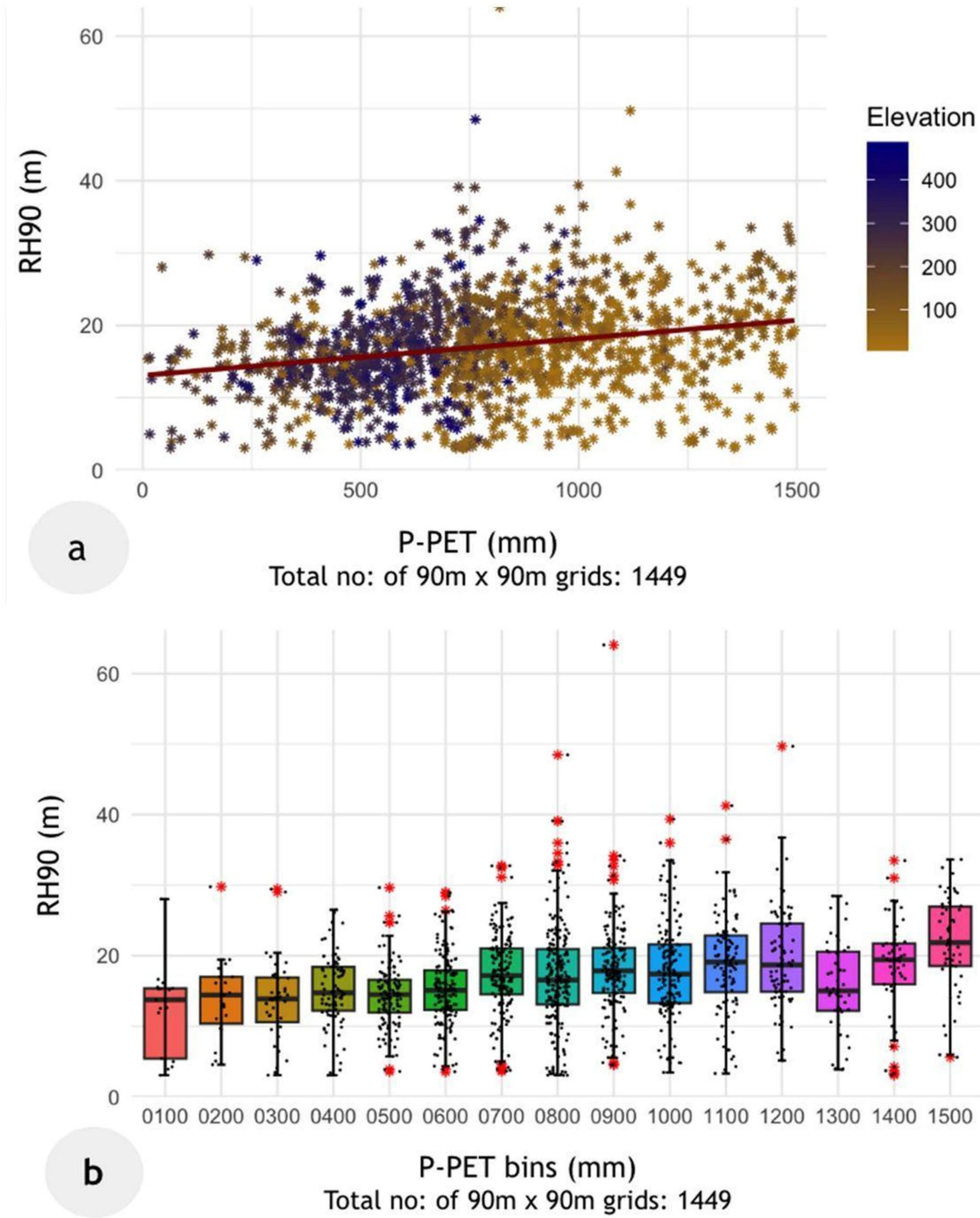

Fig. 5 **a** RH90 across water availability (P-PET) gradients; **b** RH90 across P-PET bins of 100 mm (e.g., 0–100, 100.1–200, 200.1–300, etc.)

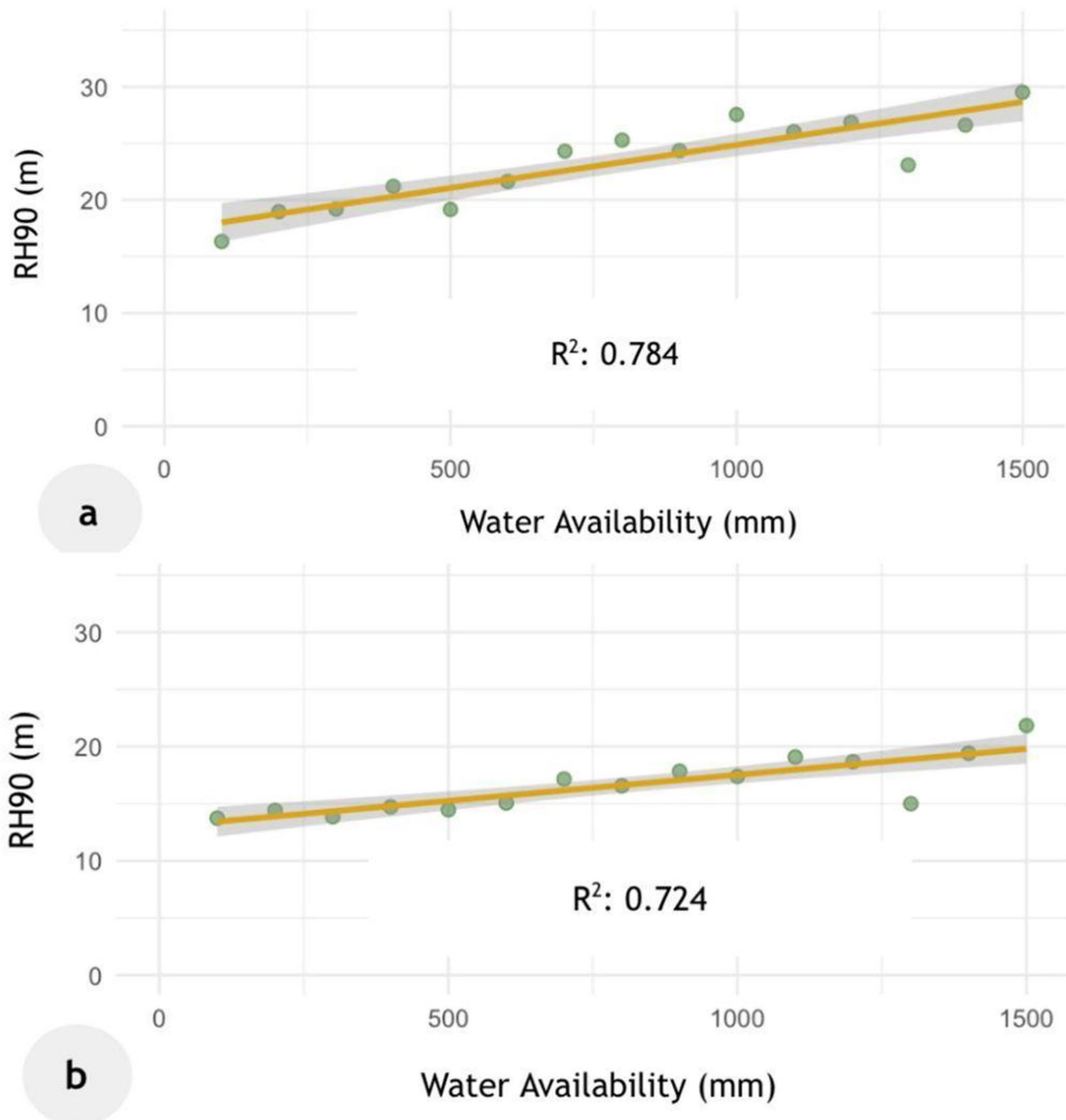

Fig. 6 **a** RH90 90th percentile versus water availability; **b** RH90 50th percentile versus water availability; the gray area represents the confidence interval. Fitted linear regression and R^2 are shown in the figures

different anthropogenically impacted drivers other than water availability.

The relation between forest canopy height and climatic and environmental factors as its predictors may vary across forest types and geographical locations. In our study, second-growth forest mean age, aggregated mean age, and elevation and slope environmental factors were observed to be second-growth determinants of canopy heights based on linear regression analysis results, which is in alignment with other similar studies. For instance, Tao et al. (2016) reported that annual mean temperature beyond 25 °C with variation of 4 °C halts canopy height increase mainly due to varying water availability by as much as 3000 mm in forest areas of all types. Gorgens et al. (2021) found that precipitation and temperature influence the distribution of giant trees in the Brazilian Amazon. Likewise Adrah et al. (2022) observed that water availability, elevation, and slope mainly influenced the canopy height across tropical forests of Malaysia. Additionally, Helmer and Lefsky (2006) noted that second-growth forest age was strongly associated with canopy heights in Rondonia, Brazil, similar to our results where aggregated second-growth forest mean age did predict canopy height. Our results highlight the importance of water availability in modulating 30–35 years second-growth forest canopy height, consistent with the hydraulic limitation hypothesis proved in previous ground based studies. However, it should be noted that over the last 40 years, the Amazon has become warmer and it has also seen several strong drought events (1983–1984, 1997–1998, 2005, 2010, 2015–2016, and 2023). These affected the region with different intensities and different locations. In future studies, it is important to evaluate if they all have measurable effects on second growth height and analyze how climate change is affecting the pace of forest regeneration.

Our result that water availability exerts a strong controlling influence on second-growth forest canopy height and tree growth rates is highly consistent with that of other studies using various remote sensing date types at different spatial scales (Klein et al. 2015; Tao et al. 2016; Adrah et al. 2022; Wang et al. 2022). Similarly, forest canopy heights increased with increase in water availability (P-PET) only up to a threshold. In our study, for second-growth forests aged 30–35 years, canopy heights increased starting at 100 mm and peaking at 900 mm (maximum canopy height values were observed with water availability between 700 and 1200 mm), and remained high with water availability up to 1500 mm and above. This result is consistent with that of Tao et al. (2016), who reported that forest canopy heights initially increased, then peaked or saturated at 680 mm of water availability, and then finally decreased regardless of increasing moisture for all forest types across continents. However, our result is in contrast with that of other studies, which reported that forest canopy heights increased continuously with increasing moisture (Givnish et al. 2014) or that canopy heights peaked at high water availability levels (Klein et al. 2015). This could be due to differences in the ages of the forests considered or because of the chosen estimation method, topography, spatial and temporal scale of the study, regression model, and/or remote sensing data type used to obtain the forest metrics (e.g., canopy height, age, species composition, length of growing season, and type of forests).

Climate models and the IPCC report that the Amazon region is likely to become drier and more drought-prone in the 21st century. AR6 (WGI) specifically notes that tropical regions including the Amazon basin are projected to experience increased aridity (Douville et al., 2021). High confidence is assigned to the projection that Amazon soil moisture will decline and dry-season intensity will rise under continued warming. Likewise, AR6 (WG2) emphasizes Amazon drought vulnerability: unprecedented droughts already occurred in 1998, 2005, 2010 and 2015/16, and models project more frequent and intense droughts in eastern Amazonia (Castellanos et al., 2022). If Amazon precipitation regimes shift in this way, the ~ 1500 mm canopy-height threshold becomes critically relevant, as regions currently near this threshold could slip below it. Forests historically sustaining tall canopies may find themselves in more water-limited environments. In practice this could lead to reduced maximum tree height and shifts in canopy structure: without enough rainfall, trees cannot develop or maintain the tallest crowns. This is consistent with Giardina et al. (2018) showing taller Amazon forests being more sensitive to vapor-pressure deficits and drought than shorter, younger forests. Moreover, increased drought frequency can cause higher mortality and slower growth for large trees. In ecological terms, a shift in climate could effectively raise the canopy-saturation threshold. Even if some areas technically still receive > 1500 mm/year, elevated temperatures and seasonality might mean trees behave as if in a drier regime, which could lower the Amazon's canopy height ceiling (Castellanos et al., 2022).

Our model fits were better with second-growth forest of 30–35 years, with tree age less than 8 years and trees shorter than 3 m were removed, even though greater than 20 years second-growth forest are reported to have reached their peak stage in terms of maximum carbon intake (null carbon intake rate). In addition, the water availability data was limited to 1500 mm, which could be attributed to challenges to data collection arising from cloudiness in the tropical regions. As a consequence, we were unable to examine the relationship between canopy height and tree growth rate at higher water availability or moisture indices values. Based on our observations, water availability associated with low elevation and slope conditions was found to be an influential determinant of canopy height in the second-growth tropical forest landscape of the Brazilian Amazon. In future studies, other important factors determining second-growth forest tree growth rate and canopy height such as soil type, wind, temperature, nutrient availability, tree species type, seed availability, and actual evapotranspiration at different spatial scales, could be integrated into our current approach to evaluate if the relationship still holds.

We observed that second-growth forest growth is affected by nearby deforestation and forest fragmentation activities, depicted by low height trees of higher age closer to such human-disturbed areas, such that second-growth forest regrowth might be slower closer to deforested and fragmented forest disturbed areas, consistent with the observations globally and in other tropical forests (Klein et al. 2015; Ranglong et al. 2025). Anthropogenic-induced forcing factors such as deforestation, climate change and widespread use of fires will degrade second-growth forest regrowth and the hydrological cycle of the Amazon due to reduced rainfall and water availability for second-growth forest growth. Thus, reducing deforestation to less than 20% and achieving 12 million ha reforestation will help build back a margin of safety against the Amazon hydrological tipping point (Lovejoy and Nobre 2018). Our study results highlight the need for future studies that investigate and model how second-growth forest growth (maximum canopy height and regrowth rate) might be affected by reduced water availability driven by nearby deforestation and forest fragmentation in disturbed tropical forest biomes or ecosystems.

The quality of GEDI data on canopy height is highly affected by steeper slopes in montane forests (Adrah et al. 2022; Adam et al. 2020; Dorado-Roda et al. 2021; Lang et al. 2022). GEDI is less efficient in detecting the top height of short vegetation below ~ 2.5 m theoretical minimum owing to its LiDAR pulse width (Dubayah et al. 2020; Li et al. 2023), and at slopes greater than 15 degrees (Adam et al. 2020; Fayad et al. 2021; Oliveira et al. 2023). Therefore, we removed trees less than 8 years (for making sure that RH90 is > 3 m) and did not consider slopes greater than 15 degrees and elevation greater than 500 m in our analysis, since our study area was focused on lowland second-growth forests. The GEDI's inefficiency to detect and identify shorter trees (< 3 m) at high elevation > 500 m and slopes (> 15 degrees) could be attributed to the moderate spatial resolution of 25 m, which could also decrease the accuracy of estimating average canopy height growth and regrowth rate and increase the magnitude of calibration error. GEDI takes samples rather than continuous measurements of vegetation structural characteristics, such that GEDI-derived RH canopy height values often overestimated lower forest heights and underestimated higher forest heights of 25 years or older second-growth forests, which required robust calibration. Thus, omitting either the calibration step or the removal of second-growth-forest-border pixels would result in an underestimation of the regrowth rate by more than 20% (Milenković et al. 2022).

The TerraClimate dataset that we used for extracting the climate and climate water balance data had a coarse spatial resolution at 5 km^2, which assumes that for a distance of 5 km within the Brazilian Amazon, there is not a highly significant spatial variability in precipitation or evapotranspiration. This assumption is supported by findings that spatial correlation in precipitation trends extends across the Amazon over distances of at least half a degree of latitude or longitude equivalent to 55–60 km (Buarque et al. 2010). In addition, we did not consider the influence of water availability beyond the 1500 mm threshold due to limited data points; a known significant change in canopy height-water availability trends with changing elevations (Hofhansl et al. 2011), and negative impact of excessive water availability at 680 mm P-PET gradient on maximum canopy height have also been reported in previous studies (Tao et al. 2016). This collectively limited the possibility of us investigating the influence of water availability on different second-growth forest ages and different topographic slopes and elevations on average canopy height and tree growth rate in this study. However, in our previous study (Adrah et al. 2022) we found that a significant steep decline in maximum canopy height occurs only at a much higher threshold of approximately 2700 mm water availability (P-PET), after an initial gradual decline after approximately 800 mm water availability.

Our study is limited by the use of the SRTM-DEM which is not a true vegetation corrected digital elevation model and would therefore contain an impact of forest vegetation on elevation data. This is because the C-band radar used by SRTM could not fully penetrate the forest canopy (O'Loughlin et al., 2016). However, since we used SRTM solely to limit our study area within low elevation zones below 500 m, the influence of vegetation canopy is likely to be minimal over such high elevation threshold. Additionally, filtering slopes using the SRTM-DEM for GEDI shots was also used purely as a quality filter to ensure that we selected the highest-quality lidar data—an extra precaution rather than a basis for drawing conclusions. However, future studies could benefit from using vegetation corrected DEM products for a more accurate result.

Conclusions

In this study, we leveraged NASA GEDI spaceborne lidar technology data and derived second-growth forest metrics for delineating the influence of water availability, second-growth forest age, and topographic elevation on canopy height across the Brazilian Amazon to test the water availability hypothesis. We found that water availability significantly influenced maximum canopy height of second-growth forest trees in elevations lower than 500 m and maximum precipitation thresholds of 1500 mm, beyond which the effect reached saturation. Mean RH90 was also found to be associated with second-growth forest age ranges from 30 to 35 years, especially when RH90 was aggregated to 1 year second-growth forest age intervals across the entire range (0–1500 mm) of water availability. Although previous plot level field-based studies and global satellite-based studies have justified the influence of water availability on plant growth for old growth tropical forests, its influence on maximum canopy heights of tropical second-growth forests is less explored at regional scales due to data limitations. Our study underscores how advances in remote sensing technology such as the GEDI spaceborne lidar could help in detecting second-growth forest characteristics in relation to water availability and topography, and contribute to our understanding of forest structure, plant physiology, species distribution patterns, carbon sequestration potential, and ecosystem dynamics while advancing scientific research. Future studies should evaluate the impact of extreme drought events and additional factors (such as seed availability, soil type, distance from fragmented forests, etc.) on secondary forest growth and incorporate data fusion techniques for minimizing forest classification errors, and thereby address some of the limitations faced in our work.

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Author contributions M.M., G.Z.P., J.Q.C., and E.A. conceptualized the study and designed the methodology. M.M. and E.A. performed data analysis with contributions from G.Z.P, Y.F., M.K., A.D.R., J.Q.C. and M.L. Model development and implementation were led by M.M. and E.A. G.Z.P, A.D.R., J.Q.C, M.K. and M.L. provided critical inputs on statistical analyses and visualization. G.Z.P. supervised the project, and J.Q.C. provided overall guidance and secured funding. M.M. drafted the manuscript, with critical revisions and editing provided by all co-authors including E.B.E., O.C., A.F, and L.M. All authors reviewed and approved the final manuscript.

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Declarations

Conflict of interest The authors declare that they have no known conflict of financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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