Resource availability and disturbance shape maximum tree height across the Amazon

*Tall trees are key drivers of ecosystem process in tropical forest, but what controls the distribution of the very tallest trees remain poorly understood. The recent discovery of grove of trees over 80 meters tall in the Amazon rainforest requires a reevaluation of current thinking. We used high-resolution airborne laser surveys to measure canopy height across 282,750 ha of primary old-growth and secondary forests sampling the entire Brazilian Amazon. We first investigated how resources and disturbances shape the maximum height distribution across the Brazilian Amazon, and secondly the relationship between the occurrence of giant trees and the environmental factors that influence giant trees demography. We suggest that drivers of height development are fundamentally different from those influencing the occurrence of giant trees. Thus changes in wind and light availability shape their distribution as much as precipitation and temperature, altogether shaping the demographics and composition of forested biomes. The location of giant trees should be carefully considered by policy-makers when identifying important hotspots for the conservation of biodiversity in the Amazon.*

# Introduction

The Amazon is the largest rain forest on Earth, covering 5.5 million square kilometers, and storing ~ 17% of all vegetation carbon. Ecologists have long taken an interest in comparing forest structure across the tropics (Yang et al., 2016), and have reached a consensus that the Amazon supports shorter trees, and therefore stores a lower amount of carbon per hectare, than the forests of tropical Africa and Asia (Cao & Woodward, 1998; Feldpausch et al., 2012). Previous studies have showed the potential occurrence of tall canopy regions in the Amazon and debated the factors which governing Amazon tree growth (Lefsky 2010; Simard et al., 2011; Larjavaara, 2013; Tao et al., 2016). The recent confirmation of the existence of giant trees - up to 88 m tall - in the Amazon basin (Gorgens et al., 2019) challenges some paradigms and poses new questions about the drivers causing the spatial distribution of tall trees in the Amazon, and consequently about how maximum tree height is shaped across different regions in the Amazon.

To reach such immense sizes, trees must fulfill at least three conditions:  they must (1) have an evolutionary design that is capable of transporting water to great heights and overcome highly negative water potentials to deliver that water toward tissues in the upper canopy (Koch et al., 2004; Niklas, 2007; McDowell et al., 2008);  (2) inhabit an area with optimal environmental conditions (such as climate, soil properties, and water) that meet species-specific requirements (Simard et al., 2018; Scheffer et al., 2018) and (3) grow in regions with a low frequency of natural or anthropogenic disturbance events (Larjavaara, 2013; Lindenmayer & Laurance, 2016; Scheffer et al., 2018; Enquist et al., 2020).

Height growth is partly governed by local scale factors such as water availability, temperature, rooting depth, and soil type (Anderegg et al., 2016; McDowell & Allen, 2015; Coomes et al., 2006; Niklas, 2007), with precipitation and potential evapotranspiration consistently reported as key factors determining plant height across biomes (Moles et al., 2009; Larjavaara, 2013; Rueda et al., 2016). While resource availability (e.g. sunlight, nutrients, CO2, and water) controls a tree’s ability to produce biomass through photosynthesis and natural disturbances (e.g. wind-throw, drought, or lightning), the history of anthropogenic actions (e.g. selective logging, forest fragmentation) increase the likelihood of mortality and limit the time available for trees to grow taller (Bennett et al., 2015; Powers et al., 2020; Yanoviak et al., 2019; Almeida et al., 2019). Tall trees are likely to have developed strategies for surviving diseases and pathogens (van Gelder et al., 2006; Aleixo et al., 2019) as well as climatic fluctuations (Sakschewski et al., 2016) and resisting wind damage (Jagels et al., 2018).

The sheer size of the Amazon, its environmental heterogeneity and species diversity, pose challenges and practical difficulties to understand general ecological relationships and biogeographical patterns (Tuomisto et al., 2019). Forest plots provide many valuable insights to investigate the influences of the environment on tree height but they can only represent a minuscule fraction of the total forest area (Chave et al., 2020). Currently, a network of 5,351 forest inventory plots established across the Brazilian Amazon, of known and published sites recently compiled by (Tejada et al., 2019), represents only 0.0013% of the total forest area in this region. In addition, the plot distribution is spatially clustered in close proximity to major roads or large rivers (Stropp et al., 2020), implying a spatial distribution bias (Marvin et al., 2014) since about 42% of the total Brazilian Amazon lies over 50 km from the nearest forest inventory plots (Tejada et al., 2019). Remote sensing can remove sampling biases and uncertainty about ecological patterns (Schimel et al., 2015) and provides large datasets with which to uncover the environment controls of forest structure (Asner et al., 2010). In particular airborne LiDAR  (Light Detection and Ranging) generates valuable high-resolution 3D information of forest canopy structure (Görgens et al., 2016; Coomes et al., 2017), and can be used as an intermediary to integrate field data with satellite sources (Asner, 2009; Bae et al., 2019).

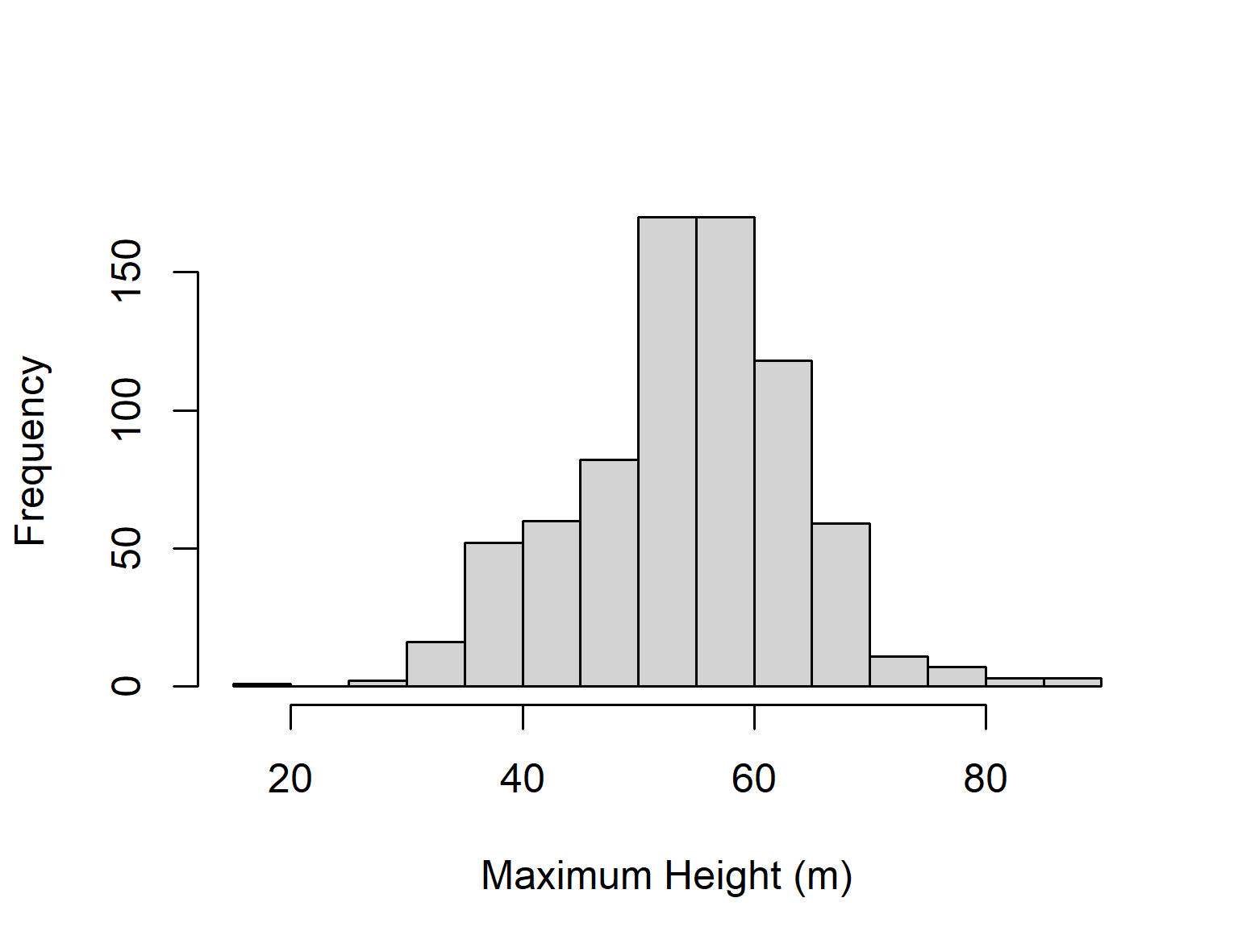
The question of how resources and disturbances determine maximum tree height across the Amazon has not been fully explored. In this study, we employed the largest airborne laser data collection in the Amazon to contribute to the understanding of (1) how resources and disturbances shape the maximum height distribution across the Brazilian Amazon, and (2) what drives the occurrence of giant trees (taller than 70 meters). We conducted an extensive analysis relating remotely sensed environmental variables to the maximum height recorded in the transects.

# Methods

Between 2016 and 2018, an airborne mission (held by National Institute for Space Research - INPE and funded by Amazon Fund) collected airborne LiDAR data from 906 transects of 375 ha (12.5 x 0.3 km) each, randomly spread across primary and secondary forests defined by the PRODES database - layer mask of primary old-growth forests (**PRODES, INPE**, 2016) and by the TerraClass database - a layer mask of secondary forest (**TerraClass, INPE**, 2014). Details about LiDAR parameterization, processing, and the EBA project characteristics can be consulted in (Gorgens et al., 2019). Briefly, the average pulse density was set at 4 pulses m−2, the field of view equal to 30°, and flying altitude of 600 m. The pulse footprint was set to be below 30 cm, based on a divergence angle between 0.1 and 0.3 mrad. Each transect was processed by identifying the returns backscattered from the ground and interpolating a 1m spatial resolution digital terrain model (DTM) from them. Then, the DTM was employed to calculate the heights above ground from the returns backscattered from the vegetation (Görgens et al., 2016). The uppermost vegetation heights were then employed to compute a canopy height model CHM at the same spatial resolution as the DTM.

The terrain could also influence the extraction of the individual tree height. As the height is computed based on the difference between surface elevation and terrain elevation, difficulties in the true terrain determination could influence the height retrieval. Studies reported an underestimation of the tree height in hilly terrains, but in a similar way that other measurement approaches (e.g. field measurements). Results showed the LiDAR surveys with at least 4 points per square meters have high penetration into the canopy to height estimation (Clark et al., 2004; Glenn et al., 2011; Andrade et al., 2018).

A forest consists of superimposed groups that occur in different combinations over the landscape, and each unit is sensitive to certain special aspects of the environment (Vanclay, 1992). The soil (fertility, drainage), climate (temperature and rainfall patterns), topography (altitude, aspect), and other factors can only give a general indication of site productivity because they fail to account for any local variations in the site (e.g. the species present) (Binkley et al., 2004). Site comparison, like we are proposing here, should prefer indicators not unduly influenced by stand condition, use history, or diversity complexity. Maximum stand height for sites that are sufficiently large to reflect the maximum height that the nominated species is likely to attain is a perfect indicator (Daubenmire, 1976). Using the individual tree approach the emergent individual was located using a local minimum filter and the tree height determined. A single tallest tree was identified, located and isolated per transect. All the trees were manually inspected to exclude maximas not related to trees derived from artifacts, ensuring that all the largest heights indeed depicted a tall tree (Supplementary Figure 1). The height distribution of the tallest individual trees select for further analysis is present in Fig. 1.



*Figure 1. Maximum tree height distribution of the 906 trees extracted from the 906 airborne laser scanned transects dispersed across the Brazilian Amazon.*

## Environmental variables

To investigate drivers influencing the spatial distribution of giant trees, we initially considered a total of 18 environmental variables: (1) fraction of absorbed photosynthetically active radiation (FAPAR; in %); (2) elevation above sea level (Elevation; in m);  (3) the component of the horizontal wind towards east, i.e. zonal velocity (u-speed ; in m s-1); (4) the component of the horizontal wind towards north, i.e. meridional velocity (v-speed ; in m s-1); (5) the number of days not affected by cloud cover (clear days; in days yr-1); (6) the number of days with precipitation above 20 mm (days > 20mm; in days yr-1 ); (7) the number of months with precipitation below 100 mm (months < 100mm; in months yr-1 ) ; (8) lightning frequency (flashes rate); (9) annual precipitation (in mm); (10) potential evapotranspiration (in mm); (11) coefficient of variation of precipitation (precipitation seasonality; in %); (12) amount of precipitation on the wettest month (precip. wettest; in mm); (13) amount of precipitation on the driest month (precip. driest; in mm); (14) mean annual temperature (in °C); (15)  standard deviation of temperature (temp. seasonality; in °C); (16) annual maximum temperature (in °C); (17) soil clay content (in %); and (18) soil water content (in %).

The FAPAR was derived from land surface reflectance product calibrated and corrected from the National Oceanic and Atmospheric Administration’s (NOAA) Advanced Very High-Resolution Radiometer (AVHRR), which is a consistent time-series dataset spanning from the mid-1980s to present and suitable for climate studies (Tao et al., 2016). FAPAR is a primary vegetation variable controlling the photosynthetic activity of plants and is considered an essential climate variable (Mason et al., 2010).

The elevation was computed based on the third version of the Shuttle Radar Topography Mission (SRTM) provided by the National Aeronautics and Space Administration Jet Propulsion Lab (NASA JPL) (Farr et al., 2007; Liu et al., 2014). The SRTM mission collected data during ten days of operations, using two synthetic aperture radars: NASA’s C band system (5.6 cm wavelength) and an X band system by DLR (3.1 cm). C-band partially penetrates the vegetation canopy, with depth varying with vegetation structure. Since Amazonian vegetation is dense throughout, for the purposes of this study the C-band DEM is assumed to vary consistently with topography across the region.

We used the maximum daily mean wind speeds over the last 5 years from the fifth major global reanalysis (ERA5) produced by the European Centre for Medium-Range Weather Forecasts (ECMWF). The reanalysis combined model data with observations from across the world into a globally complete and consistent dataset (Olauson, 2018). Two wind velocities were considered: u-speed which is the zonal velocity (i.e. the component of the horizontal wind towards east), and v-speed which is the meridional velocity (i.e. the component of the horizontal wind towards north). These products are used extensively for modeling wind power both in academia and industry (Olauson, 2018; Albergel et al., 2019; Ramon et al., 2019).

The number of clear days was computed based on Moderate Resolution Imaging Spectroradiometer (MODIS) surface reflectance products. MODIS products provide an estimate of the surface spectral reflectance as it would be measured at ground level in the absence of atmospheric scattering or absorption (Kang et al., 2005; Bisht & Bras, 2010). We used the Terra MOD09GA Version 6 product, which provides an estimate of the surface spectral reflectance of MODIS, corrected for atmospheric conditions such as gases, aerosols, and Rayleigh scattering.

Temperature and precipitation were obtained from the WorldClim database of bioclimatic variables, which are derived from weather station data compiled for the 1950-2000 period (Hijmans et al., 2005; Fick & Hijmans, 2017). The main source of data was the Global Historical Climatology Network (GHCN), complemented with other global, national, regional, and local data sources, which were added if they were further than 5 km away from stations already included in the GHCN.

The lightning frequency was provided by Lightning Imaging Sensor (LIS) instrument onboard the Tropical Rainfall Measuring Mission provided by NASA Earth Observing System Data and Information System (EOSDIS) Global Hydrology Resource Center. The LIS provided the basis for the development of a comprehensive global thunderstorm and lightning climatology to detect the distribution and variability of total lightning occurring in the Earth (Albrecht et al., 2016).

The potential evapotranspiration was provided by the TerraClimate dataset, a global monthly climate and water balance for terrestrial surfaces spanning 1958–2015. The layer combined high-spatial-resolution climatological normals from WorldClim with Climate Research Unit (CRU) Ts4.0 and the Japanese 55-year Reanalysis (JRA-55) data. The Reference Evapotranspiration was calculated using the Penman-Monteith approach (Abatzoglou et al., 2018).

The number of months per year with precipitation below 100 mm and the number of days per year with precipitation above 20 mm was computed based on the Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS) dataset. CHIRPS incorporated 0.05° resolution satellite imagery with in-situ station data to create gridded rainfall time series for trend analysis and seasonal drought monitoring (Funk et al., 2015).

Edaphic variables were obtained from The OpenLandMap produced by the OpenGeoHub Foundation and contributing organizations. The clay content (fine particles < 2 μm) and water content layers, both with a spatial resolution of 250 m, were created based on machine learning predictions from a global compilation of soil profiles and samples (Arsanjani et al., 2014).

To help visualization of the regional-level, we used the division of the Brazilian Amazon into eight regions, according to the classification of (Morrone, 2014). This regionalization is based on biogeographic analyses of terrestrial plant and animal taxa of the Neotropical region and seeks to provide universality, objectivity, and stability, such that it can be applied when describing distributional areas of particular taxa or comparing different biogeographic analyses.

## Random Forest and Maximum Entropy

To explore the influence and importance of the environmental variables for development in tree height, we employed Random Forest modeling, which consists of generating a large number of regression trees, each constructed considering a random data subset. The regression trees are used to identify the best sequence for splitting the solution space to estimate the output. To visualize how the environmental variables relate to the maximum height we used marginal plots, estimating the maximum height by one variable per time, keeping others constant at average. Among the initial 18 environmental variables, two of them (precipitation on driest month and months < 100mm) were excluded due to high correlation (> 0.80) to other independent variables. Using the coordinates of the tallest tree within each lidar transect, we performed a simple extraction of the values for all the variable layers. Tree height was then modeled against the factors using a random forest algorithm, which recursively computes classification and regression trees (CART) from random subsets, a k-fold (k = 15) cross-validation method, and 500 as the number of CART. The number of variables randomly sampled as candidates at each split was set to 10. The adjusted model was evaluated considering the mean absolute error (MAE), root mean squared error (RMSE), and coefficient of determination (R²) of cross-validated predicted versus observed values. To assess the overall relative variable importance we used the mean increase in accuracy. For further information about the variables importance, see in Supplementary Figure 2 a plot considering the mean decrease in accuracy and the mean decrease in node impurity for all the variables. The resulting Random Forest model was finally implemented using the environmental variables to deliver a map of estimated maximum heights across the Amazon.

Then we focused on the tallest trees only - those over 70 m in height - to determine the conditions which allow them to occur. We employed a maximum entropy envelope approach (MaxEnt) commonly applied to modelling species geographic distributions with presence-only data and indicate better discrimination of suitable versus unsuitable areas for the species (Phillips et al., 2006). The variable importance of the MaxEnt model was used to indicate the most relevant characteristics sustaining extreme height individuals and the potential location for new occurrence.  The observations higher than 70 m were filtered out and used to adjust an envelope model based on maximum entropy. In its optimization routine, the algorithm tracked how much the model gain was improved when small changes were made to each coefficient value associated with a particular variable.  Each variable was then ranked based on the proportion of all contributions. The resulting MaxEnt model was finally implemented using the environmental variables to deliver a map of probability of occurrence for trees taller than 75 m across the Amazon.

# Results

Trees exceeding 50 m were registered in 54 0 transects, widely distributed across many parts of the Brazilian Amazon. Within those transects, only 23 showed trees above 70 m and only 6 registered trees above 80 m. The distribution of these tall trees is concentrated in the eastern Amazon in the Roraima and Guianan Lowlands biogeographic regions (Fig 2).

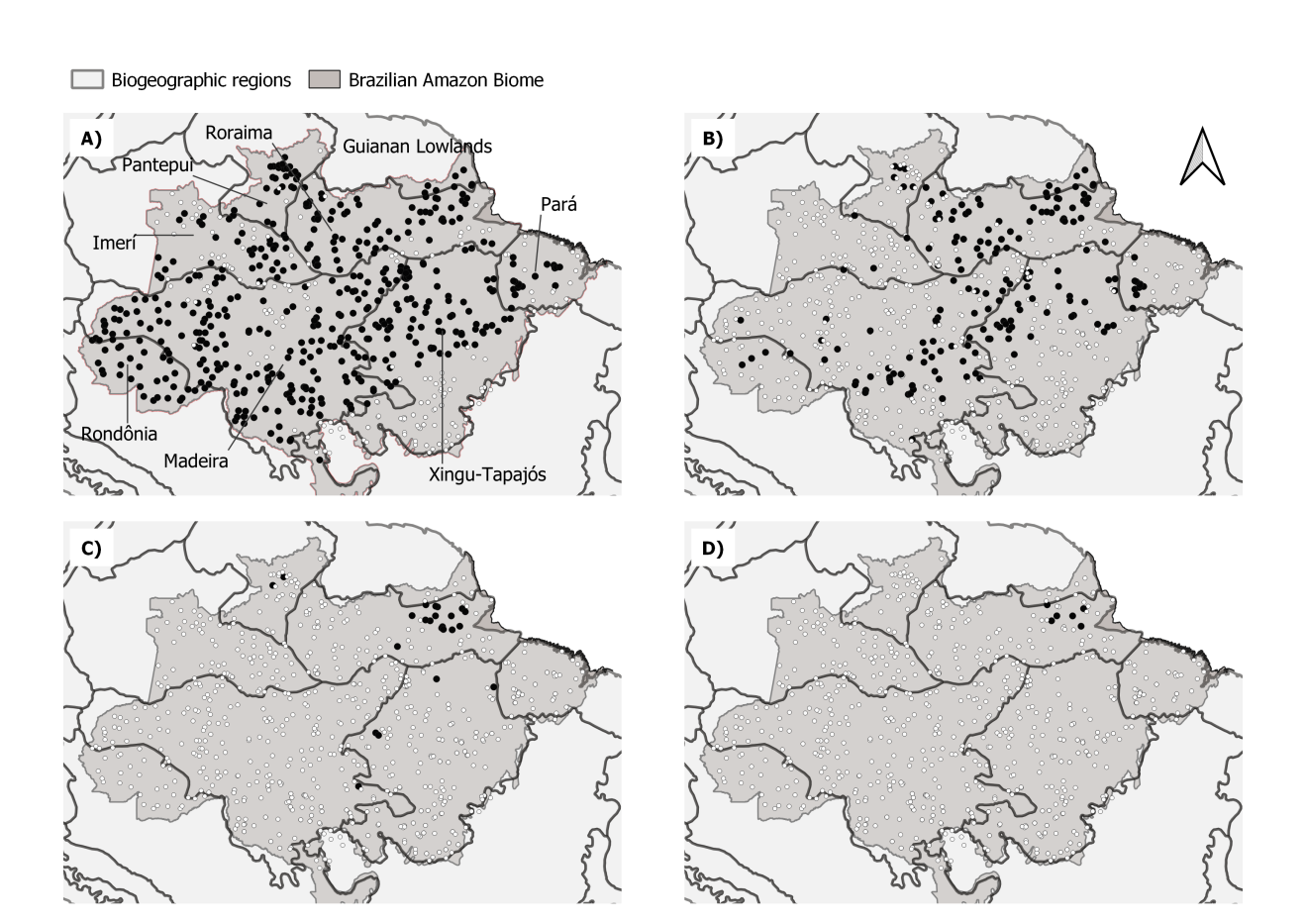


Figure 2. Maps of the Brazilian Amazon showing the location of transects considering height thresholds: 50 m, 60 m, 70 m, and 80 m in height. Black circles indicate transects with trees taller then the threshold, white circles indicate remaining transects.

The variables with the most explanatory power in the Random Forests model were (1st) the number of clear days, followed by (2nd) clay content in the soil and (3rd) elevation. The difference between the 4th and the 15th of the importance rank less than 6 units, ranging from 22.4 to 15.6. The variable soil water content (16th) was the weakest predictor (Table 1). The variable importance could also be measured by alternative metrics from a Random Forest Model like node purity and mean squared error (see Supplementary Figure 2 for alternative importance metrics).

Table 1. Variables used to estimate maximum height distribution and evaluate its distribution, ranked by variable importance results in the Random Forest model

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Layer | Definition | Related to | Unit | Source | Spatial resolution (Time interval) | Expected influence in max. height | Importance  (increase accuracy) |
| clearDays | number of clear days per year | energy balance - water balance - radiation | Days | MODIS | 500 meters  (2014 - 2018) | Negative | 25.5 |
| clayContent | fraction of clay content | soil structure - physical properties - water availability | % | OpenLandMap | 250 meters | Positive | 23.4 |
| topography | elevation above sea level | distance to water - flooding zones - soil | M | SRTM | 30 meters | Positive | 23.3 |
| pannual | average annual precipitation | precipitation - precipitation intensity - precipitation distribution | Mm | WorldClim | 30 arc seconds | Positive | 22.4 |
| pseason | precipitation seasonality | precipitation - precipitation intensity - precipitation distribution | Mm | WorldClim | 30 arc seconds | Positive | 21.3 |
| tseason | temperature seasonality | temperature - temperature distribution | C | WorldClim | 30 arc seconds | Negative | 21.3 |
| uspeed | zonal speed (W-E) | storms - convective winds | m/s | ECM-RWF | 0.25 degrees  (2014-2018) | Negative | 21.1 |
| pet | potential evapotranspiration | energy balance - water balance - radiation - vegetation health - anthropic regions - soil exposure | Mm | TerraClimate | 2.5 arc minutes  (1990 - 2016) | Positive | 20.2 |
| fapar | fraction of absorbed photosynthetically active radiation | radiation - vegetation health - anthropic regions - soil exposure | % | NOAA AVHRR | 0.05 degrees  (2016 - 2018) | Positive | 20.0 |
| pwettest | precipitation of the wettest month | precipitation - precipitation intensity - precipitation distribution | Mm | WorldClim | 30 arc seconds | Negative | 19.9 |
| tmax | maximum temperatura | storms - convective winds | C | WorldClim | 30 arc seconds | Negative | 19.8 |
| vspeed | meridional speed (N-S) | storms - convective winds | m/s | ECM-RWF | 0.25 degrees  (2014-2018) | Negative | 18.1 |
| lightning | lightining rate | storms - convective winds | flashes rate | LIS TRMM | 0.1 degrees  (1998 - 2018) | Negative | 18.0 |
| days20 | days with precipitasion higher then 20 mm | storms - convective winds - precipitation | Days | CHIRPS | 0.05 degrees  (2014-2018) | Negative | 16.4 |
| tannual | daily average annual temperature | temperature - temperature distribution | C | WorldClim | 30 arc seconds | Negative | 15.6 |
| waterContent | fraction of water content | soil structure - physical properties - water availability | % | OpenLandMap | 250 meters | Positive | 9.7 |
| month100 | month with precipitation below 100 mm | precipitation - precipitation intensity - precipitation distribution | Months | CHIRPS | 0.05 degrees  (2014-2018) | Negative | Removed by high correlation |
| pdriest | precipitation of the driest month | precipitation - precipitation intensity - precipitation distribution | Mm | WorldClim | 30 arc seconds | Positive | Removed by high correlation |

The Random Forest model obtained MAE = 3.62 m, RMSE  = 4.92 m, and R² = 0.735 (observed versus predicted height plot is available in Supplementary Figure 3). The Random Forest model predicted maximum tree height above 70 meters in 56,747 km² (1.03% of the Amazon). Those regions are concentrated in Eastern Amazon, with trees specifically achieving the greatest heights in the Northeastern part of Roraima biogeographic region (Fig. 3).

The LiDAR sampling design included all forested areas: mature, secondary and degraded. Given the difficulties to detect the exact boundaries of secondary/degraded and mature forests and the large nature of the sampling unit (12,5 km), before excluding those areas, we investigated the influence of secondary/degraded areas in the results. To perform the investigation, we removed low values of FAPAR (< 80%) that are related to degraded forests and anthropogenic regions - eliminating 133 transects. Besides the spatial distributions for maximum tree height persisted similarly after removing these potential anthropogenic effects, the variables importance kept similar and consistent (Supplementary Table 1). The comparison demonstrated that the underlying patterns we report are naturally driven by the environmental factors and maximum tree height of the transects are robust enough to the implemented analysis.

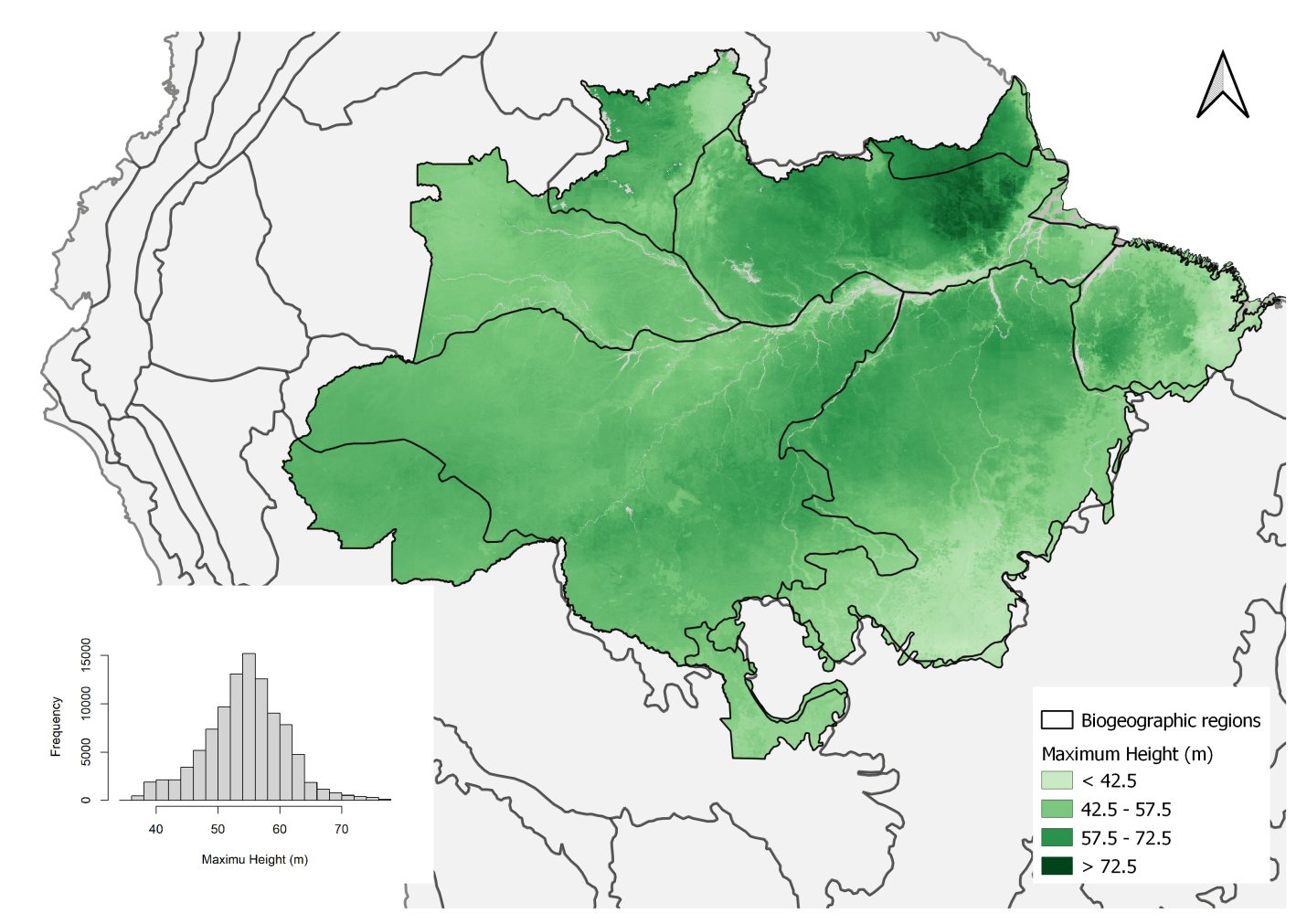


Figure 3. The maximum tree height distribution estimated by the Random Forest model based on the environmental variables. Available at https://doi.org/10.5281/zenodo.4036988.

The number of clear days was the strongest predictor of maximum height (Table 1). The shape of this relationship resembles a step function (Fig. 4), in which regions with the number of clear days below 130 days per year support tall trees, with an abrupt decline in maximum height above this level. Elevation was also a key predictor of tree height, with low-lying forests growing 7 m lower than trees in terrains above 40 m above sea level. An increase in soil clay content from 20% to 40% translated into a 7 m increase in maximum height.  Our results also demonstrate that mean annual precipitation was a key factor related to maximum height, with a tolerance curve peaking at around 2,300 mm yr-1 as optimal annual precipitation across the Brazilian Amazon. In comparison to these areas, we observe a 4 m decline in maximum tree height in regions with annual precipitation below 1,500 mm yr-1 or above 3,000 mm yr-1. From the intermediate importance variables, we highlight the zonal velocity (u-speed) and FAPAR influencing height variation in ranges around 6 m.

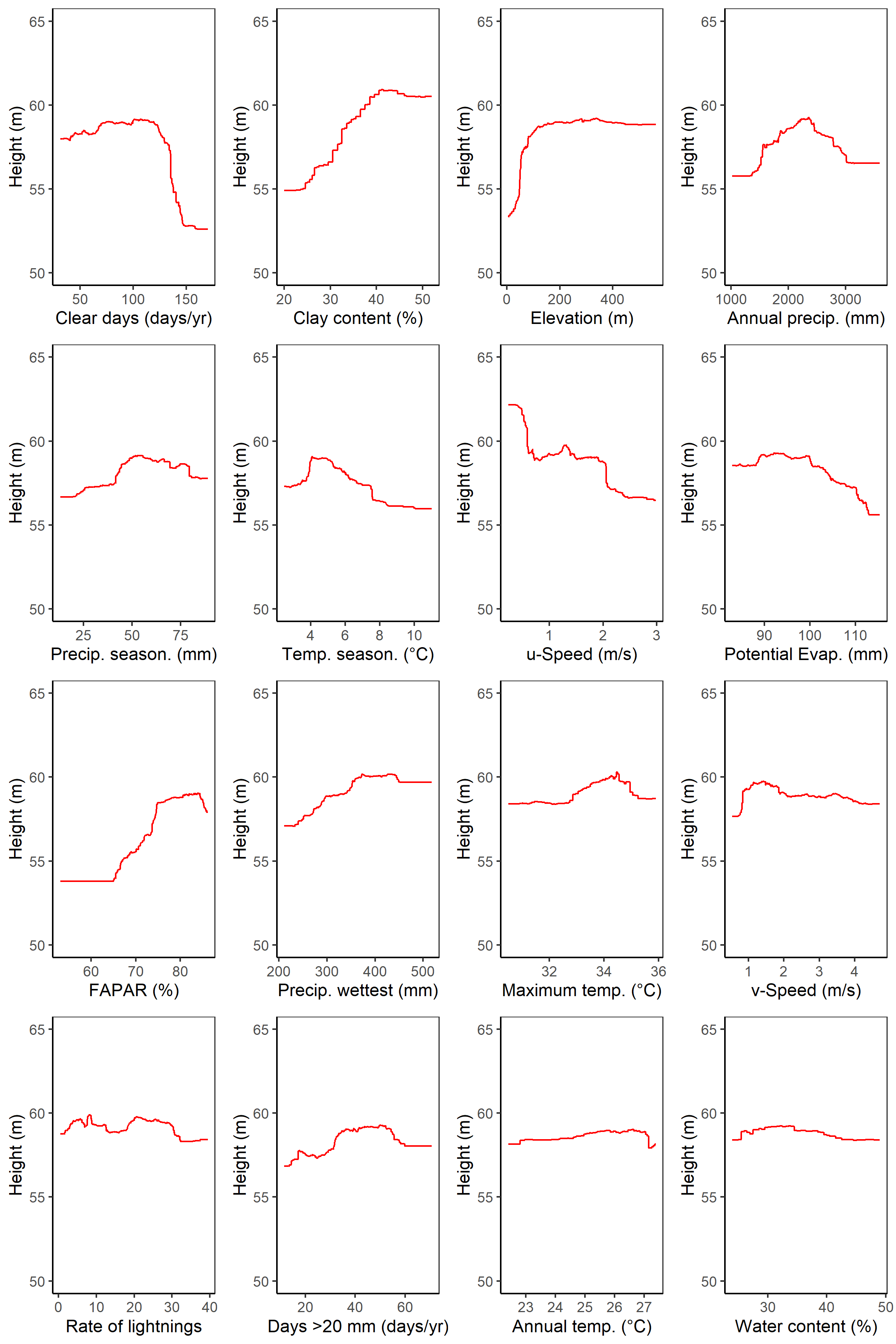


Figure 4. The marginal plot obtained for each environmental variable in the random forest model, keeping others constant on the average. Lines close to horizontal indicate a given environmental factor having little effect on the height of tall trees.

The results of the MaxEnt approach are focusing on the occurrence of trees taller than 70 m in height. The extraordinarily tall trees were found in conditions characterized by a much smaller set of environmental variables from those which drove the large-scale patterns of maximum height (Fig. 5). The maximum entropy model shows that the niche is dominated mostly by wind speed (relative importance of 67.7 %). The second most important driver of tall tree occurrence was the elevation above sea level (relative importance of 12.3 %). The resulting map of predicted occurrence of the tallest trees in the Amazon from the MaxEnt model shows that the probability of maximum tree height occurrence is highest in northeastern Amazon (Fig. 6), more specifically in the Roraima and Guianan Lowlands biogeographic regions.

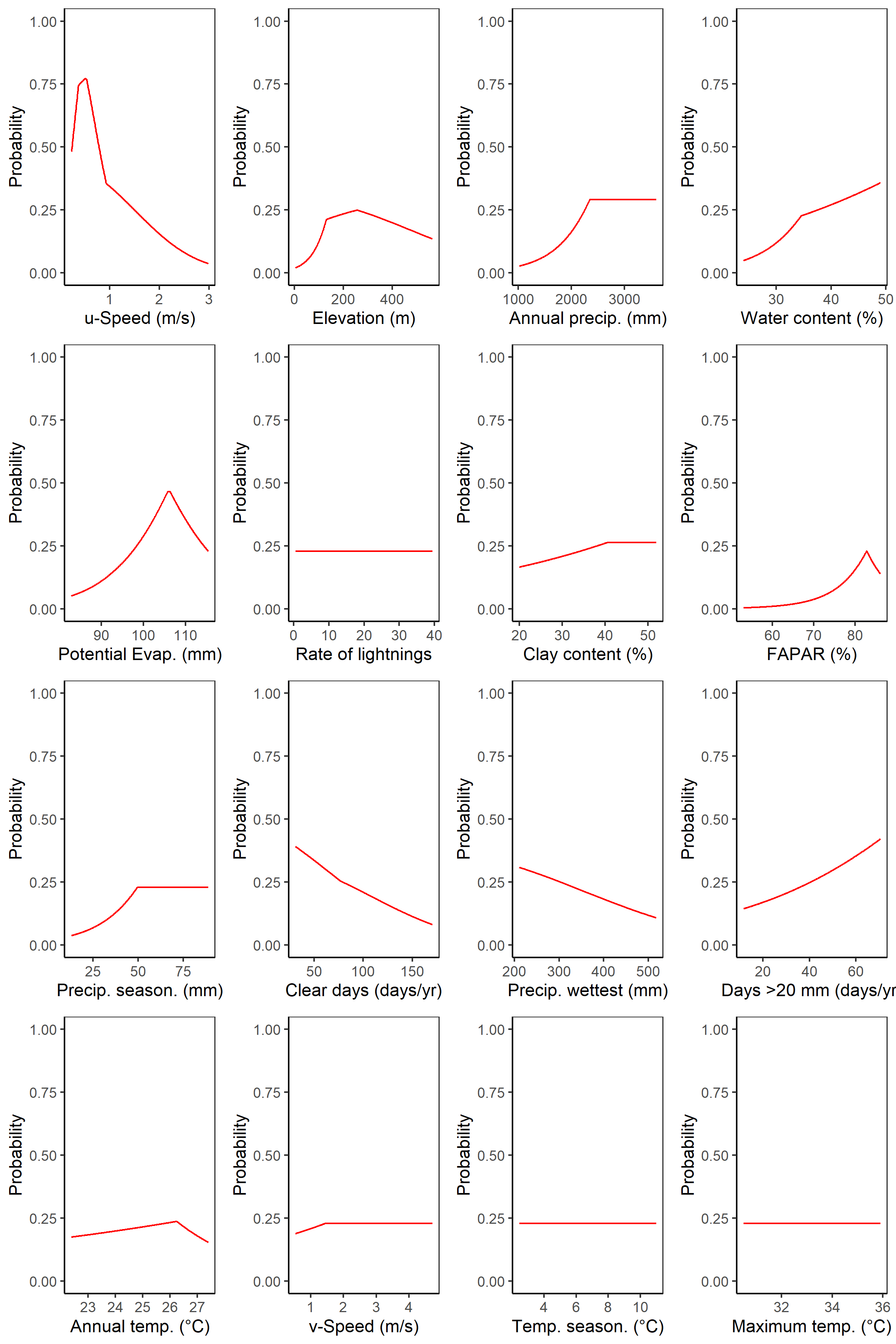


Figure 5. The marginal plot obtained for each environmental variable in the Maximum Entropy model, keeping others constant on the average. Lines close to horizontal indicate a given environmental factor having little effect on the probability of tall trees.

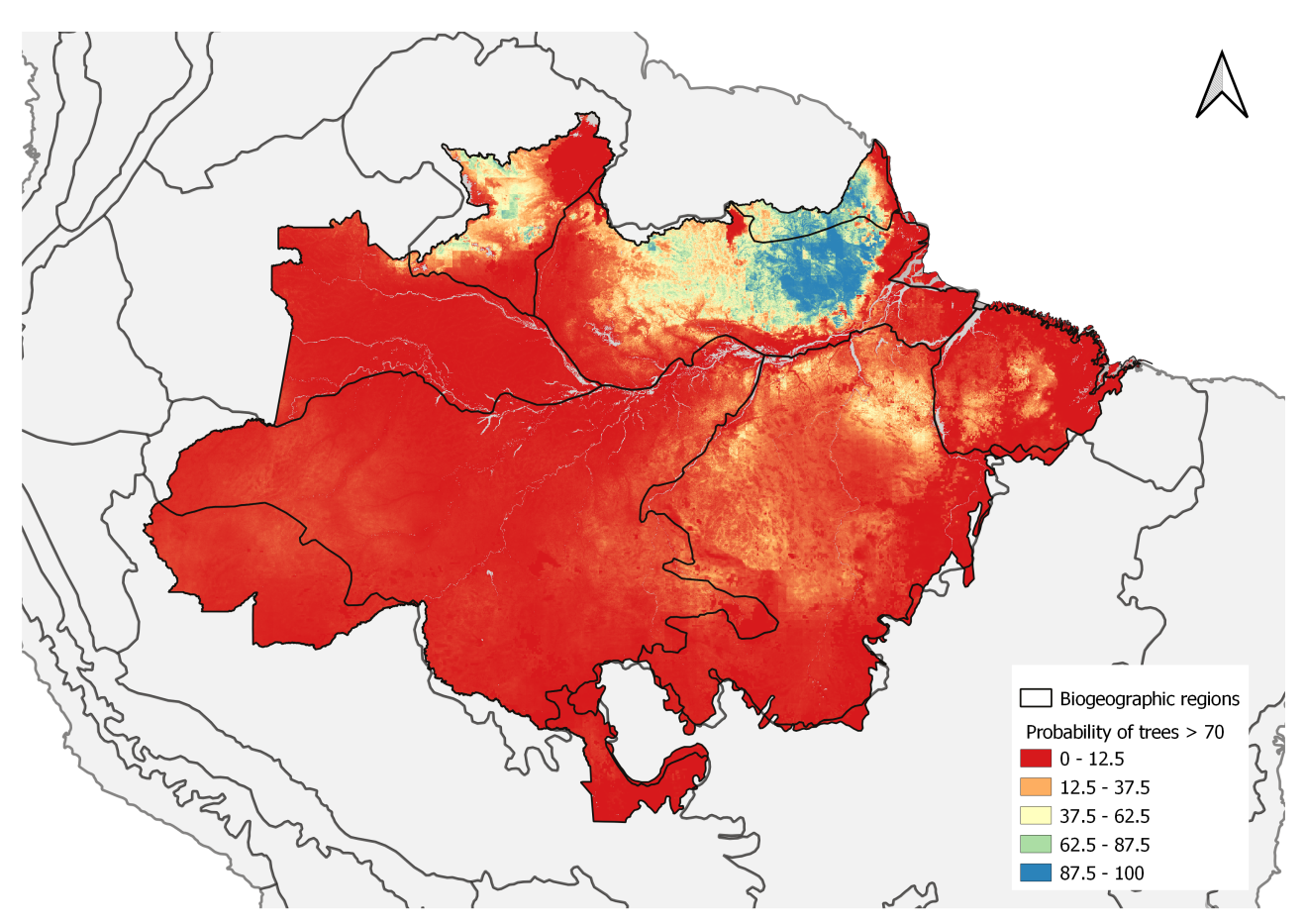


Figure 6. The probability of tall tree occurrence based on environmental conditions estimated by the Maximum Entropy model. Available at https://doi.org/10.5281/zenodo.4037101.

# Discussion

We found that maximum tree height across the Brazilian amazon was related to a number of environmental variables but the distribution of giant trees >70 m was driven almost entirely by wind speed. The number of cloud days stands out as the most relevant variable to explain maximum height distribution, followed closely by wind speed, soil clay content, elevation, precipitation and temperature seasonality, potential evapotranspiration, and maximum temperature.

## Maximum height distribution

A myriad of environmental variables with complementary effects on species composition, as well as on their physiological and structural traits, play a crucial role in the tree lifespan (Muller-Landau, 2004) and, consequently, on height development. Previous studies have observed two large-scale gradients in the Amazon: one from the Guiana Shield to the Southwestern Amazon, related to variation in soil fertility, and another gradient from Colombia to the Southeastern Amazon, related to the length of the dry season (ter Steege et al., 2006).

Maximum height was strongly related to the number of cloudy days, followed by soil clay content, elevation, annual precipitation and precipitation seasonality. An increase in cloud-free days goes together with an increase in direct solar radiation (Barkhordarian et al., 2019), which, along with changes in the Vapor Pressure Deficit, or atmospheric dryness, drive changes in the physiological function of trees (Williams et al., 2012; Nunes et al., 2019). The increase in diffuse radiation led by cloudy conditions induces an increase in photosynthetic activity (Gu, 2003). Tall trees have direct exposure to sunlight and high temperatures lead to higher stomatal control to avoid excessive water loss (Drake et al., 2018; Rowland et al., 2015). Tree responses to direct solar radiation are dependent on the species and developmental stage, with physiological and structural changes to maximize either growth or survival (Wright et al., 2004; Nunes et al., 2019; Poorter & Bongers, 2006). As trees grow taller, increasing leaf water stress due to gravity and path length resistance may limit leaf expansion and photosynthesis, and consequently height growth (Koch et al., 2004).

An increase in soil clay content also translated into an increase in maximum height. Clay content is usually higher on flat terrain (Laurance et al., 1999) decreasing from 75% to 5% when moving from the plateau areas to the valleys (Ferraz et al., 1998; Toledo et al., 2016). A previous study showed an increase in wood density from stands on sandy soils in valleys to clayey soils on plateaus at a local scale in Central Amazon, and lower tree mortality rates in clayey soils (Toledo et al., 2016). We suggest that the structured soils allow trees to obtain an additional volume of water during the dry season towards eastern Amazon, where soils tend to be richer in clay compared to central and western Amazon (Fisher et al., 2008; Hodnett et al., 1997). The dimorphic root systems associated with structured, clayey soils can redistribute water from deep layers to the soil surface during periods of drought (Broedel et al., 2017).

Elevation was also a key predictor of tree height, with low-lying forests growing potentially less than trees in terrains over 40 m a.s.l.. The topographic gradient is likely to be related to the likelihood of flooding in the low elevation transects on the lowlands. Rivers erode the *terra firme* terraces and create floodplains of variable sizes dating to the Miocene, with terrace–floodplain elevation differences decreasing eastwards from the Andes (Hamilton et al., 2007). The terrace and floodplain forests in the Amazon also have differences related to species turnover, which reveals the micro-topography effects on the survival rate in Amazonian forests (Asner et al., 2015). Species from the plateaus may be more susceptible to prolonged periods with lower soil water content, and, therefore, they invest in higher hydraulic safety with higher wood density, lower mean vessel hydraulic diameter, lower mean vessel area and smaller stem cross-sectional sapwood area than species in valley forests (Cosme et al., 2017).

Mean annual precipitation was also a key factor for trees to grow taller. A tolerance curve associated the height of tall trees with precipitation, peaking at  2,300 mm  yr-1 as optimal, but also showing that areas too dry or too wet may both inhibit the growth of tall trees. Thus, we observed a decline in maximum tree height in regions with annual precipitations below 1,500 mm yr-1 or above 3,000 mm yr-1. The availability of soil water depends on both precipitation and evapotranspiration, and our results suggest that below 1,500 mm yr-1 evapotranspiration may exceed precipitation in the Amazon (Scheffer et al., 2018), and mortality by the hydraulic failure may occur for trees near their maximum height (McDowell et al., 2008). Mean annual precipitation above 2,300 mm  year-1 may be related to exceeding water, and the combination of high precipitation and poorly drained soils may result in anaerobic conditions with negative effects on tree growth and survival (Quesada et al., 2009). Furthermore, higher precipitation tends to be related to the occurrence of storms and stronger winds with increases in tree mortality (Aleixo et al., 2019).

## Conditions supporting tall trees

In our study, low wind speed was determined as the single most important predictor of the occurrence of the tallest trees in the Brazilian Amazon. The fact that trees adapt to their wind environment and are shorter in windy locations has been widely observed in temperate regions (Telewski, 2006, Bonnesoeur et al., 2016). We observed a similar effect across the Amazon, with trees over 70 m tall having a 50-75% likelihood of surviving in the calmest areas but a sharply decreasing probability with stronger winds. This agrees with previous findings that disturbance rates are three times higher in the Western Amazon (Espírito-Santo et al., 2014) and may demonstrate how significant the role of wind is in shaping the niche for extraordinarily tall trees. The importance of wind speed was also apparent in the Random Forest model which showed a 9 m reduction in the estimated tree height from the calmest to the windiest areas. The zonal velocity (i.e. the eastward component), which is the prevailing wind direction in the region, drives this pattern.

A balance between tree structural strength and wind shearing forces contributes to set an upper limit to tree height development (Klein et al., 2015). Trees adapt their growth rates to their local wind environment, although the scale of this effect is unknown (Telewski, 2006; Bonnesoeur et al., 2016). Large-scale wind patterns in the Amazon are dominated by the easterly trade winds. Wind damage is most common from September to February (Negrón-Juárez et al., 2017) and taller trees have higher rates of mortality in wind storms (Rifai et al., 2016).

Besides the ERA5 wind product does not show a magnitude technically associated to tree damage, its long-term mean speed could indicate variability and trends between regions, which seems to be relevant in our amazonian-scale analysis. To compute the wind speed map, ERA5 does not ingest surface winds from land stations. As a result, ERA5 is parametrized in planetary boundary layer schemes from surface characteristics resulting in lowering the inland speed (Ramon et al., 2019).

Removing wind components from the maximum entropy model, the importance of zonal wind speed shifts to lightning (importance changes from 3 to 34), potential evapotranspiration (importance changes from 4 to 18) and precipitation seasonality (importance changes from 0.5 to 15). Secondary factors such elevation, annual precipitation and water content did not change after removing wind speed. This shifts indicates that wind speed is indeed adding information which is scattered in others factors, and related to anomalous events (i.e. lightning and seasonality).

Interestingly, our data showed that the lightning rate was only weakly related to maximum forest height patterns in both the Random Forests and MaxEnt models. Despite being relevant to the death of individual trees (Marra et al., 2014; Niklas, 1998) and being the key factor causing tree deaths in tropical forests of Panama (Yanoviak et al., 2019), lightning and storms do not seem to impact the potential dominant tree of a region, nor to limit the survival of the tallest trees, in light of our results.

The locations of the tall trees (> 70 m) in the eastern Amazon coincide with forests that have a high basal area predicted by statistical modeling of permanent plot data (Malhi et al., 2006; ter Steege et al., 2006). Young soils nearer the Andes, as well as the sedimented and flooded lowlands, are richer in nutrients, thereby supporting fast-growing, low wood density species with high turnover rates and, as a result, the trees do not reach extremely large sizes (Marra et al., 2014; Quesada et al., 2011; Phillips et al., 2004). The Fabaceae family which contains most of the large trees, grows successfully in low-dynamics environments such as the Guiana Shields. Higher occurrence of the Fabaceae in these low-fertility soils may occur due to the ability to fix nitrogen in the soil and ectomycorrhizal association (Webb & Sprent, 2002; Sprent, 2009). Soil physical properties combined with limited nutrient supply in eastern Amazon favor slow-growing species that invest their resources in structures that can support taller and bigger trees with a long lifespan (Malhi et al., 2004; Quesada et al., 2009).

Plant size distributions can be understood as the demographic consequence of size‐dependent variation in growth and mortality in old-growth forests, and the mortality of large trees is independent of resource availability and competition (Coomes et al., 2003). Understanding the spatial distribution of maximum tree height in tropical forests and how it is associated with environmental conditions and tree functional traits is of fundamental importance. Emergent trees that reach their maximum height are responsible for a significant amount of the transpired water flux and the above-ground carbon storage. Trees which reach these extraordinary heights are rare and only a small proportion of species have the necessary adaptions to achieve this. However, these adaptations are not sufficient alone, and maximum tree height is strongly influenced by environmental conditions.

Current climate models differ in their predictions of large-scale changes in wind patterns, although warmer temperatures will mean that the air can hold more moisture, which will likely make convective storms more intense. Whatever the change in environmental conditions, it is likely to occur faster than trees can adapt. Our results showed that precipitation and temperature have a lower importance than expected from previous studies. Nevertheless, changes in the precipitation and radiation regimes (strongly linked to the number of cloudy days) could reshape our forest biomes. Ultimately, the association between environmental conditions and mechanisms of natural selection, where some traits have some advantages in comparison to others influencing the survival of the most adaptable, are key to understanding the complexity of this process in a changing climate.

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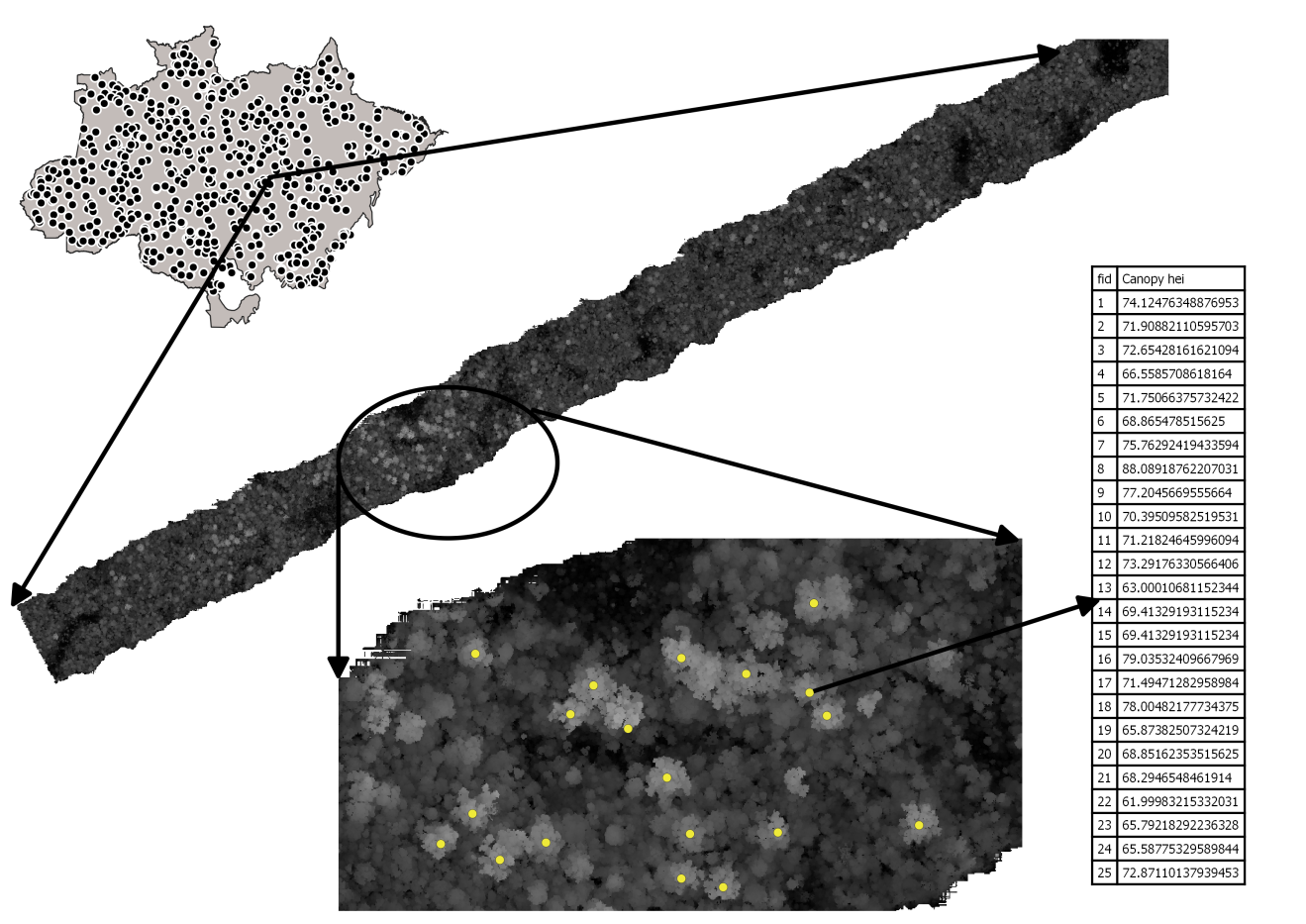
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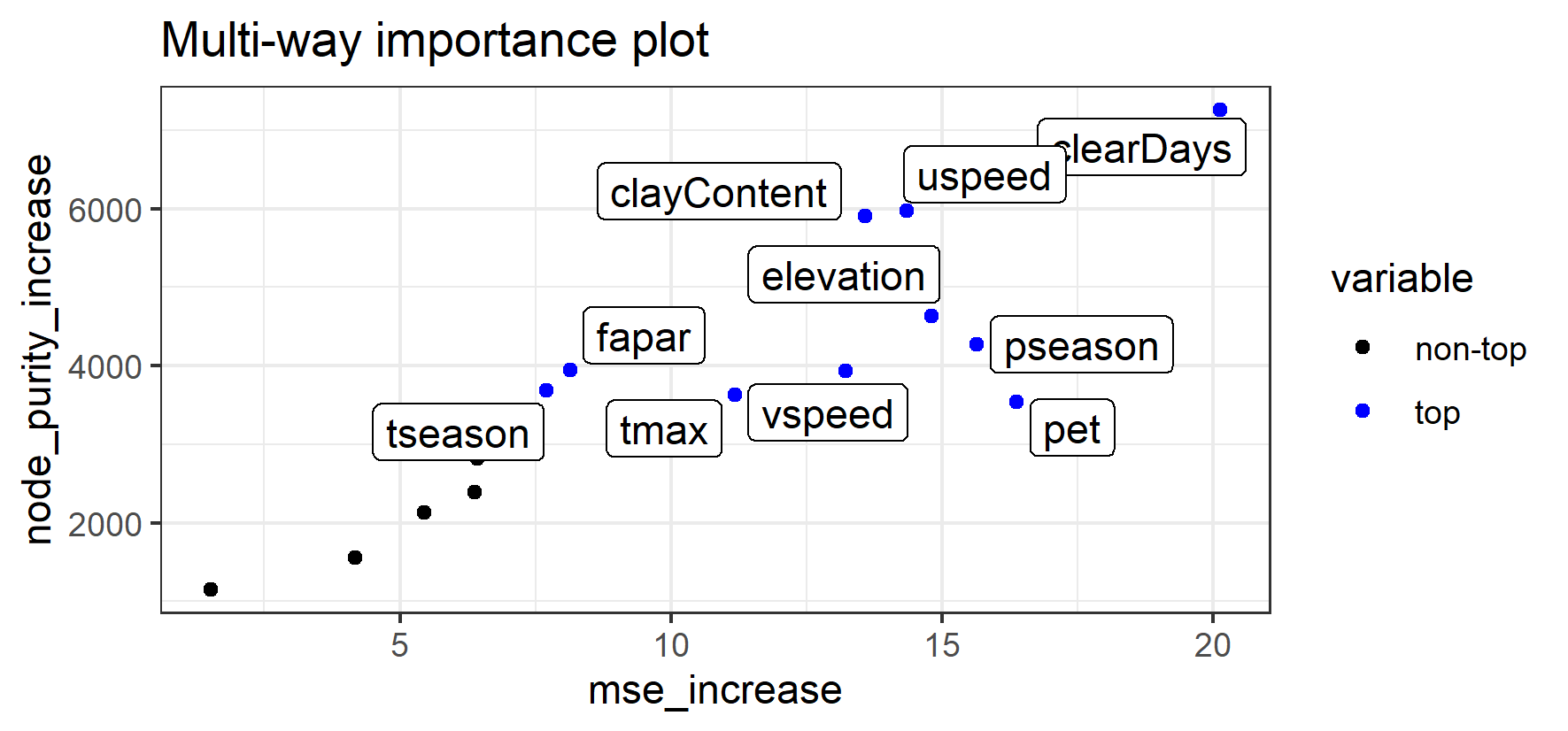
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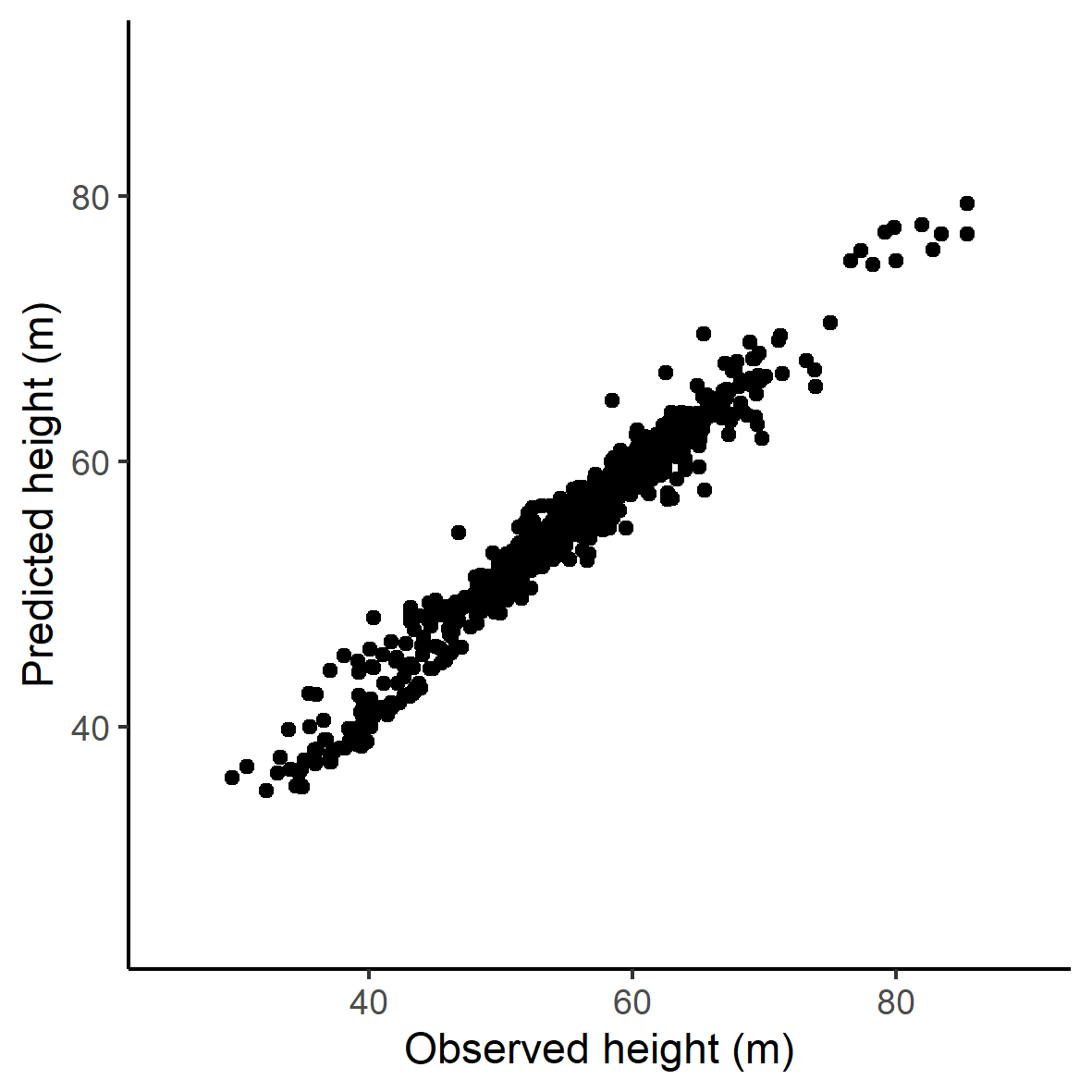
# Supplementary Figures



Supplementary Figure 1. The uppermost vegetation heights were then employed to compute a canopy height model CHM. A single tallest tree was identified, isolated and located per transect.



Supplementary Figure 2. Variable importance considering the mean increase in accuracy (mse\_increase) and the mean decrease in node impurity for all the variables (node\_purity\_increase).



Supplementary Figure 2. Observed versus predicted maximum height by the Random Forest model.

Supplementary Table 1. Variable importance results for the Random Forest model adjusted considering all the transects, and removing transects located in secondary and degraded forests (i.e. intact forest).

|  |  |  |
| --- | --- | --- |
| Layer | Importance including all transects  (increase accuracy) | Importance considering only intact forest  (increase accuracy) |
| clearDays | 25.5 | 22.5 |
| clayContent | 23.4 | 21.8 |
| topography | 23.3 | 20.9 |
| pannual | 22.4 | 21.4 |
| pseason | 21.3 | 19.3 |
| tseason | 21.3 | 19.4 |
| uspeed | 21.1 | 18.4 |
| pet | 20.2 | 17.4 |
| fapar | 20.0 | 17.3 |
| pwettest | 19.9 | 18.3 |
| tmax | 19.8 | 18.9 |
| vspeed | 18.1 | 18.4 |
| lightning | 18.0 | 17.2 |
| days20 | 16.4 | 18.9 |
| tannual | 15.6 | 15.3 |
| waterContent | 9.7 | 9.6 |