

# Optimal climate for large trees at high elevations drives patterns of biomass in remote forests of Papua New Guinea

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## Abstract

Our ability to model global carbon fluxes depends on understanding how terrestrial carbon stocks respond to varying environmental conditions. Tropical forests contain the bulk of the biosphere's carbon. However, there is a lack of consensus as to how gradients in environmental conditions affect tropical forest carbon. Papua New Guinea (PNG) lies within one of the largest areas of contiguous tropical forest and is characterized by environmental gradients driven by altitude; yet, the region has been grossly understudied. Here, we present the first field assessment of above-ground biomass (AGB) across three main forest types of PNG using 193 plots stratified across 3,100-m elevation gradient. Unexpectedly, AGB had no direct relationship to rainfall, temperature, soil, or topography. Instead, natural disturbances explained most variation in AGB. While large trees (diameter at breast height > 50 cm) drove altitudinal patterns of AGB, resulting in a major peak in AGB (2,200–3,100 m) and some of the most carbon-rich forests at these altitudes anywhere. Large trees were correlated to a set of climatic variables following a hump-shaped curve. The set of “optimal” climatic conditions found in montane cloud forests is similar to that of maritime temperate areas that harbor the largest trees in the world: high ratio of precipitation to evapotranspiration (2.8), moderate mean annual temperature (13.7°C), and low intra-annual temperature range (7.5°C). At extreme altitudes (2,800–3,100 m), where tree diversity elsewhere is usually low and large trees are generally rare or absent, specimens from 18 families had girths >70 cm diameter and maximum heights 20–41 m. These findings indicate that simple AGB-climate-edaphic models may not be suitable for estimating carbon storage in forests where optimal climate niches exist. Our study, conducted in a very remote area, suggests that tropical montane forests may contain greater AGB than previously thought and the importance of securing their future under a changing climate is therefore enhanced.

## KEYWORDS

carbon, elevation transect, forest biomass, large trees, natural disturbance, optimal climate condition, steep slopes, tropical montane forest

## 1 | INTRODUCTION

Accurate estimates of terrestrial carbon stocks underpin our ability to model current and future global carbon fluxes (Hansen et al., 2013). Tropical forests play an important role in the global carbon cycle, containing about half the carbon stored in terrestrial plant biomass (Pan et al., 2011). If intact tropical forests increase in biomass as the global climate changes, this will lower the rate of increase in atmospheric carbon dioxide, providing a negative feedback on global warming (Malhi et al., 2010). If the converse occurs, as predicted by some models (Huntingford et al., 2013), the loss of carbon from tropical forests will accelerate the pace of global climate change (Selmants, Litton, Giardina, & Asner, 2014). To improve existing models of global carbon stocks and fluxes, it is necessary to establish baseline data for the distribution of tropical forest biomass. Moreover, uncovering the relationship between environmental variables and forest biomass provides an empirical foundation for predicting the effects of changing climates on the global carbon cycle (Mitchard et al., 2013).

In the tropics, elevation gradients are well suited to these tasks, as they often present continuous unidirectional changes over short spatial scales in the environmental variables that are likely to affect forest biomass. These variables can include temperature, rainfall, insolation, and soil condition across a defined bio-geographic region (Malhi et al., 2010). Many studies have measured forest biomass in the tropics across a range of elevations, and most of these have demonstrated clear or direct relationships between forest biomass and climate (e.g., solar radiation, rainfall, temperature), edaphic variables (e.g., soil depth, soil type, nutrients), topographic variables (slope angle, aspect) or altitude as a surrogate for climate (Girardin et al., 2010; Girardin, Espejob, et al., 2013; Girardin, Farfan-Rios, et al., 2013; Homeier, Breckle, Gunter, Rollenbeck, & Leuschner, 2010; Kitayama & Aiba, 2002; Malhi et al., 2010; Vázquez & Givnish, 1998).

Recently, important insights have been gained through studies of elevation gradients in the Neotropics (Girardin et al., 2010; Girardin, Farfan-Rios, et al., 2013; Homeier et al., 2010; Vázquez & Givnish, 1998), South East Asia (Kitayama & Aiba, 2002), and in Africa (Marshall et al., 2012). Although some generic patterns in forest biomass have emerged from studies on elevation transects, such as a general decrease in forest biomass with increasing elevation and the effect of stand variables, such as tree size and wood specific gravity (WSG), little consensus yet exists on the relative importance of climate, edaphic conditions, or topography on forest biomass in tropical forests (Baraloto et al., 2011; Selmants et al., 2014).

The largest uncertainties in tropical forest carbon stocks come from areas that have had few direct field inventories of their above-ground biomass (AGB) (Mitchard et al., 2013). In particular, Papua New Guinea (PNG), the Democratic Republic of Congo, and the Central Amazon region of Brazil are the areas with the highest uncertainties in their forest carbon stocks because of the difficulty associated with performing field inventories in these remote forests (Mitchard et al., 2013). An improvement of these estimates will rely

upon gathering field variables that uncover the environmental drivers of AGB, such that the relationship between AGB and environmental variables can be extrapolated from field observations into modeled regional or global estimates of AGB (Chave et al., 2014; Clark & Kellner, 2012).

Papua New Guinea constitutes the eastern half of the island of New Guinea. The island is rugged, with a mountainous spine extending 2,500 km along its length, making it one of the world's great mountain systems (Hall, 1984). The region is ideal for the study of controls on AGB, with forests up to 4,000 m above sea level (asl) and extreme local relief causing abrupt changes in environmental conditions across much of the island (Paijmans, 1976). However, little is known about forest carbon stocks in PNG (Bryan, Kirkpatrick, Shearman, & Ash, 2011). For example, the best available global dataset of forest AGB used 4,000 field sites from across the tropics with not a single site from PNG (Saatchi et al., 2011). Most of PNG's forests lie beyond the reach of roads, coastal or river access, thereby imposing major logistic constraints on field surveys. Consequently, the forests of PNG remain some of the most under-researched areas of tropical forest worldwide (Bryan et al., 2011; Marshall & Beehler, 2007). Reducing uncertainties from important forest carbon stores such as those in PNG is an important first step toward improving global models of carbon stocks and fluxes (Mitchard et al., 2013).

We studied the relationship among forest structure attributes, AGB, climate, edaphic, and topographic variables along a 3,100-m elevation transect in PNG to determine the relationships between biomass and potential predictors.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

The study was conducted in the Saruwaged Range in Morobe Province, PNG (6°04'S, 146°48'E), in the Yopno-Uruwa-Som (YUS) Conservation Area, a region of 182,000 ha covered by 70% primary forest ranging from 50 m asl to 3,100 m asl. The climate is perhumid, with a mean annual precipitation (MAP) ranging between 2,600 mm in the lowlands and 4,200 mm in Upper-montane forests (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). Mean annual temperature (MAT) in the lowlands is 26°C, decreasing by about 5.4°C per 1,000 m of elevation gain, reaching 10°C at 3,100 m asl. The work for this study consisted of field surveys in a contiguous area of primary forest along on an elevation transect extending 35 km from near the Bismarck Sea coast at 50 m asl, (5°53.9'S, 146°52.0'E) to 3,115 m asl (6°5.7'S and 146°55.3'E) (Figure 1). The elevation gradient follows a SW-NE trending ridgeline that is covered by primary wet tropical forest, including Lowland (below 1,000 m), Montane (1,000–2,800 m asl), and Upper-montane (2,800–3,100 m asl) forests (Hothorn, Bretz, & Westfall, 2008).

In our study area, the cloud immersion zone, as defined by remote sensing (Gillieson, Silverman, Hopkinson, Quenzer, & Kuna, 2011), occurs between 2,200 m and 3,100 m. All soils at our sites have developed on limestone bedrock, with the exception of the



**FIGURE 1** Digital representation of the study sites along the elevation gradient. White dots represent study sites. Orange squares represent elevation zones, and the gray line represents the transect. Source: Google earth, image Landsat, TerraMetrics© 2014

**TABLE 1** Edaphic, climatic, and topographic variables along a 3,100-m elevation gradient in Papua New Guinea

Forest type <sup>a</sup>	Elevation zone	Altitude range (m asl)	Mean slope (° [95% C.I.])	MAT <sup>b</sup> (°C)	MAP (mm)	Soil type <sup>c</sup>	Mean soil depth <sup>d</sup> (cm)	No of plots
Lowland	50	50–150	2 [1–5]	26.3	2,598	Hapludolls	97	21
	500	470–610	15 [8–22]	23.4	2,806	Rendolls	92	16
	800	610–1,030	26 [17–45]	22.1	2,911	Troporthents	128	19
Montane	1,400	1,300–1,500	19 [12–25]	18.8	3,207	Troporthents	118	18
	1,800	1,750–1,930	13 [8–17]	16.2	3,484	Troporthents	134	21
	2,200	2,090–2,230	13 [9–17]	14.4	3,643	Troporthents	>200	29
	2,400	2,240–2,610	15 [11–19]	13.0	3,788	Troporthents	175	22
Upper-montane	2,800	2,720–2,886	12 [9–13]	10.5	4,090	Troporthents	180	25
	3,100	2,900–3,115	17 [14–21]	10.0	4,218	Cryorthents	194	22

<sup>a</sup>Forest types are based on Hothorn, Bretz, and Westfall (2008).

<sup>b</sup>Climatic variables are from BIOCLIM (Hijmans et al., 2005), MAT = mean annual temperature and MAP = mean annual precipitation.

<sup>c</sup>Soil types are from PNGRIS database.

<sup>d</sup>Soil depths are from Dieleman et al. (2013).

lowermost sites, where a limestone-colluvium derived soil with a 50-cm A-horizon overlies alluvial deposits (for more details about soils, see Table 1 and Dieleman, Venter, Ramachandra, Krockenberger, & Bird, 2013).

The entire study area lies within the YUS conservation area, which is named after the three major water catchments that drain a rugged, road-less mountain region of the Huon Peninsula. About 35 communities surround the YUS area, with a population of about 12,000, who have a subsistence lifestyle and depend on the forest for building material, food, and fuel (Bourke et al., 2002; Kocher-Schmid, 1991; Page, Murphy, Mizrahi, Cornelius, & Venter, 2016). The authority that issued the permit to work in

the YUS Conservation Area was the Tree Kangaroo Conservation Program.

## 2.2 | Study design

Nine elevation zones were selected prior to the commencement of fieldwork using remotely sensed images with the aims of (1) capturing the range of forest types and the changes in forest structural attributes along the elevation gradient and (2) sampling in areas far from present-day human disturbance (i.e., requiring more than one day's return walk from a village). The lowermost sites did not satisfy the second criterion as villagers could access the forest within a



**FIGURE 2** Photograph of a steep sample plot with an average slope of 68.0°

day's walk; therefore, they were excluded from analyses investigating natural disturbance.

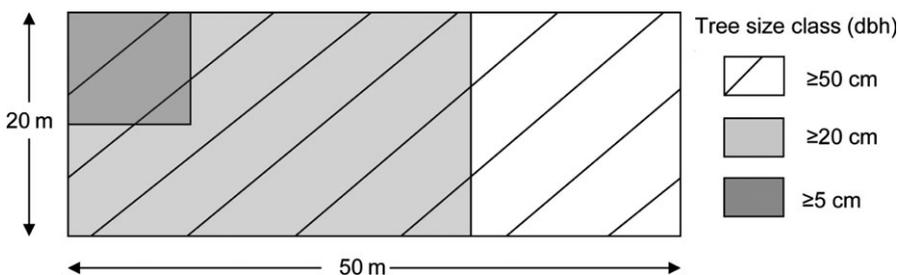
Elevation zones ( $N = 9$ ) were further stratified to include three slope categories (gentle 0°–15°, moderate 16°–25°, and steep 26°–80°) and three aspect categories (east, west, and ridge top), where possible. In plots established on very steep slopes, ranging from 45° to 80°, climbing equipment was used to establish the plot and to measure the trees (Figure 2).

A total of 193 rectangular plots (20 × 50 m) were established (Figure 3), with each of the nine elevation zones containing 16–29 sites with a minimum of 120-m distance between plots. Methods for biomass inventories and plot establishment were based on the widely used Land Use, Land-Use Change, and Forestry protocols (Pearson, Walker, & Brown, 2005). We chose to sample many small plots across the landscape, instead of fewer larger plots, to capture more landscape variability (Laumonier, Edin, Kanninen, & Munandar, 2010). The southwest corner of each plot was selected randomly by throwing a spear into the air. From the point where the spear landed, we followed a random compass bearing for 15 m. This technique was employed to ensure that sites were sampled regardless of disturbance. Natural disturbance was recorded for a site if a landslide or windthrow resulted in visible damage to forest structure causing at least six tree-falls within the site. The plots were delineated using compasses and survey tapes and pegs were used to mark the corners.

General parameters measured in the field to estimate AGB included diameter at breast height (DBH), tree height (H) and WSG and tree taxa. DBH values were measured to the nearest millimeter with a diameter tape at 1.3 m above the ground. For trees with

buttresses, bush ladders were built to measure the diameter from a point immediately above the buttress with distance to the ground recorded. Height was measured by standing directly below the crown and measuring the highest point visible in the canopy with a rangefinder (LaserAce® hypsometer) multiple times until the highest point was reliably identified (Feldpausch et al., 2011). Heights were measured for 75.4% of the stems; for the remainder, heights were estimated using a taxon- and altitude-specific height-diameter model (Appendix S1). Canopy height was determined using the mean of all stems >50 cm DBH. The height of emergent trees is reported as the mean of the tallest tree of each plot, reported for each elevation zone (Girardin, Farfan-Rios, et al., 2013). WSG values were derived from several rainforest datasets (Chave et al., 2006; Eddowes, 1977; IPCC, 2006; Zanne et al., 2009) and from wood cores taken for 25 tree species with high contributions to AGB (for details on WSG sampling methods, see Torello Raventos, 2014). For trees without WSG values, average WSG for the elevation zone was used (Fox et al., 2010). We measured lianas, palms, pandanus, and lying dead trees according to protocols in Pearson et al. (2005).

Tree identification was carried out from the collection of fertile vouchers, pictures of fertile botanical specimens, DNA-barcoding analysis from leaf tissue, and from local knowledge of tree names. DNA-barcoding analysis was performed for 50 of the most common trees in the study area (Costion et al., 2011). For the 6,791 stems recorded in this study, 71% of stems were identified to family level or below, with more than half of the sites having 85% or more of their stems identified. In total, we identified 75 families and 140 genera. However, botanical surveys are ongoing and taxonomy is still being refined.



**FIGURE 3** Diagram of a forest biomass inventory plot

## 2.3 | Biomass estimates

Trees, as a broad category, included woody broadleaf and conifers, palms, woody lianas, tree ferns, and pandanus. For woody trees (broadleaf and conifers), which comprised 80.2% of the stems, we used equations from Chave et al. (2005) to estimate AGB as they have been shown to perform well across a broad range of tropical forests (Rutishauser et al., 2013). For other stem types, including standing and lying dead trees, we used allometric equations outlined in Appendix S2. All AGB estimates on slopes were transformed to a horizontal projection (Pearson et al., 2005).

## 2.4 | Climate and edaphic variables

Site latitude and longitude were obtained by handheld GPS. Mean annual precipitation (MAP), MAT, and intra-annual temperature range (maximum temperature of the warmest month minus the minimum temperature of the coldest month) were derived from BIOCLIM (Hijmans et al., 2005) with a spatial resolution of 10' for temperature and 5' for rainfall variables. Evapotranspiration (E) was obtained from CGIAR-CSI Global-PET and Global Aridity Index (Global-Aridity) database (<http://www.cgiar-csi.org>) and the ratio of precipitation to E (P/E) was used as a measure of water availability for plants (Bowman, Williamson, Keenan, & Prior, 2014). Solar radiation (insolation) was derived from topographic position calculated without taking into account cloud cover (Kriticos et al., 2012; Ramachandran Nair, Mohan Kumar, & Nair, 2009). Soil organic carbon, soil pH, root mass, carbon-to-nitrogen ratios, and soil depth were extracted from Dieleman et al. (2013) who analyzed 497 samples from 87 plots covering all nine elevation zones in the study area.

## 2.5 | Data analysis

### 2.5.1 | Exploratory analyses

We undertook a range of exploratory analyses that directed subsequent analysis. We inspected pairwise plots to confirm that the various slope and aspect categories were well represented in each of the nine elevation zones along the altitudinal gradient; elevation zone 50-m asl was omitted from this test as sites in this zone had zero aspect and slope (Appendix S3). We also examined pairwise relationships between AGB, altitude, climatic, and edaphic variables (Appendix S4). This revealed two results relevant to our subsequent analyses: (1) The relationship between AGB and altitude was bimodal rather than linear and (2) most of the climate and edaphic variables were strongly correlated with altitude and with each other. We therefore tailored our various subsequent analyses to accommodate these preliminary findings.

### 2.5.2 | Models of disturbance

We were interested in how natural disturbances affect AGB along the altitudinal gradient. For the first analysis, we used mixed-effects

generalized additive models (GAMs) to fit nonlinear spline functions to the relationship between ln-transformed AGB and altitude (Wood, 2006). GAMs are semi-parametric tests that are based on generalized linear models but provide smooth response to the explanatory variable without setting a priori relationships (e.g., linear, logarithmic, power). Two models were fitted; one with separate splines for disturbed and intact sites and the other with the same spline fitted to disturbed and intact sites, with an additive disturbance effect. In both models, elevation zone was included as a random effect to account for clustered sampling within each zone. The two models had similar explanatory power, but since the simpler model that included the same spline function for disturbed and intact sites had a lower Akaike information criterion (134.8 vs. 140.2), we present this model.

### 2.5.3 | Models of biomass potential

For the remaining analyses we excluded disturbed sites, as our interest was in the determinants of AGB potential along the altitudinal gradient. Our exploratory analyses revealed that AGB was not linearly related to altitude or to any of the climate or edaphic variables (Appendix S4). In fact these relationships tended to be bimodal. We therefore adopted a three-stage approach for analyzing AGB data.

First, we fitted a basic GAM (without random effects) to the bimodal relationship between ln-transformed AGB and a key climate variable (moisture availability: MAP/MAPET). We then extracted the residuals from this model to test whether the AGB variation could be explained by moisture availability or by edaphic variables (Appendix S5). To do this, the residuals of this model were treated as the response variable in a linear mixed-effects model, with soil depth (plot-scale) and mean pH (per elevation zone) included as fixed effects and elevation zone included as a random effect. Second, we investigated how key forest structural attributes were related to AGB using linear mixed-effects models. Because large trees contribute substantially to AGB in our study, we modeled ln-transformed AGB as a function of the number of stems >50 cm DBH per hectare and the average height-diameter ratio (of stems >50 cm DBH). Again, elevation zone was included as a random effect to account for clustered sampling within zones. Third, we investigated how these key structural attributes were related to key climate and edaphic variables using GAMs. Because these environmental variables were strongly correlated with each other, we fitted them one at a time.

Statistical analyses were executed in R 3.0.3 (R Core Team, 2013). The *nlme* package (Pinheiro, Bates, DebRoy, & Sarkar, 2009) was used to fit linear mixed-effects models, the *lme4* package (Bates, Maechler, Bolker, & Walker, 2014) was used to fit mixed effects logistic regressions and the *gam4* package (Wood & Scheip, 2012) was used to fit generalized additive mixed models. Post hoc multiple comparisons were conducted for the model of disturbance probability using the *glht* function in the Multcomp package (Hothorn, Bretz, & Westfall, 2008).

### 3 | RESULTS

#### 3.1 | Forest structure and exploratory results

Aboveground biomass exhibited a bimodal relationship with altitude. The first AGB peak was at elevation zone 50 m asl (604 Mg/ha  $SD \pm 258$ ) and the second at elevation zones 2,200 and 2,400 m asl (458 Mg/ha  $SD \pm 140$ ). These two peaks had significantly higher AGB than the other elevation zones (Table 2; ANOVA  $F_{8, 185} = 11.1$ ,  $p < .0001$ , Tukey's post hoc). The lowest AGB was found at elevation zones 1,400 and 3,100 m asl; both having approximately 270 Mg/ha (Table 2). The AGB also had a bimodal relationship with climate and edaphic variables because these were highly correlated with altitude (Appendix S6). For this reason, there was no clear direct relationship between AGB and climatic/edaphic variables.

Forest structure attributes used to calculate AGB such as DBH, height, and WSG generally decreased with altitude, with the exception of stand density, which increased with altitude (Table 2). The strong relationship between altitude and stem density was caused by the increase in smaller stems (DBH < 50 cm), as the number of large stems (DBH  $\geq$  50 cm) was not related to altitude (Table 2). It is important to note the height of tallest trees found in elevation zones above 2,200 m asl (Table 2)

#### 3.2 | Disturbance effects on AGB

Natural disturbance, caused by landslides and windthrows, explained more variation in AGB than any other environmental variable considered in this study (Appendix S6). The model with same spline fitted to disturbed and intact sites, with an additive disturbance effect, had the strongest explanatory power (Figure 4). Despite the same spline function being fitted to disturbed and intact sites, the two fitted curves followed a similar bimodal trend (Figure 4). However, they were not parallel: Disturbance caused greater reductions in AGB at lower altitudes. On average, disturbed sites had around 20% (75 Mg/ha) less AGB than intact sites.

#### 3.3 | Models of biomass potential

##### 3.3.1 | Edaphic factors

Soil depth and soil pH were poor predictors of AGB variation, after taking into account the bimodal relationship between AGB and moisture availability (soil depth:  $t = 1.62$ ,  $p = .164$ ; mean soil pH:  $t = 0.45$ ,  $p = .671$ ).

##### 3.3.2 | Incidence of large trees

To examine how plot level forest structure attributes related to AGB, we modeled ln-transformed AGB as a function of these. This model revealed a strong, positive linear relationship between ln-transformed AGB and the number of large stems (Figure 5,  $t = 7.25$ ,  $p < .001$ ). The model was improved when accounting for the additive effect of the median height:DBH (H:D) ratio of large trees per plot, which was also significantly positively related to AGB (Figure 5,  $t = 2.55$ ,  $p = .012$ ). This model explained 43% of AGB variation among elevation zones and 39% within. While it is likely that taller trees for a given diameter have larger AGB, these results demonstrate the importance of tree height as a driver of AGB within and among elevation zones.

We found the highest stand density (per hectare) of large trees in forests 2,200–2,400 m asl (Table 2). However, even at the extreme altitudes of 2,800–3,100 m, 18 families were represented by individuals having >70 cm DBH, and these individuals ranged in height from 20 to 41 m (Table 3). The tallest angiosperms were *Dryadodaphne crassa* (40 m), *Nothofagus starkenborghii* (41 m), *Elaeocarpus sp.* (40 m), *Caldcluvia nymanii* (39 m), *Endospermum medullosum* (33 m), and *Saurauia capitulata* (30 m), while the tallest gymnosperms were *Dacrydium nidulum* (35 m) and *Libocedrus papuana* (31 m).

##### 3.3.3 | Climate and the density of large stems

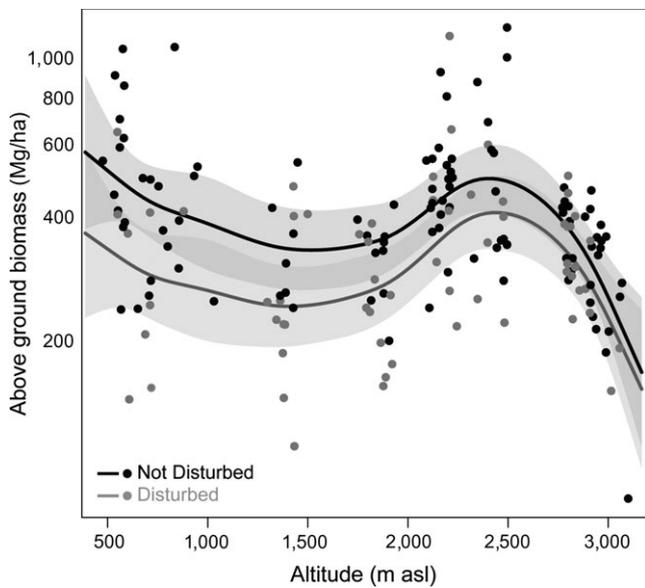
The abundance of large trees (DBH > 50 cm) followed a similar hump-shaped relationship when plotted against moisture availability

**TABLE 2** Mean forest structure attributes for the nine elevation zones ranging 50–3,100 m asl in primary forests of PNG ( $N = 193$ )

Elevation zone	AGB (Mg/ha)	Canopy height (m)	Tallest tree (m)	WSG <sup>a</sup> (g/cm)	DBH (cm)	Stand density (per hectare)	Large tree density (per hectare)
50	604.1	44	64	0.58	37.3	914	62
500	451.3	37	49	0.62	30.1	1,095	45
800	324.2	35	46	0.54	31.4	824	40
1,400	268.7	30	48	0.54	35.8	736	57
1,800	273.2	30	38	0.49	31.0	1,194	55
2,200	458.1	32	45	0.51	35.0	1,382	86
2,400	427.5	31	40	0.50	33.3	1,612	83
2,800	335.2	26	41	0.51	27.0	2,205	58
3,100	266.8	24	31	0.48	28.5	1,703	52

AGB, aboveground biomass; DBH, diameter at breast height; PNG, Papua New Guinea.

<sup>a</sup>WSG means are weighted by basal-area.

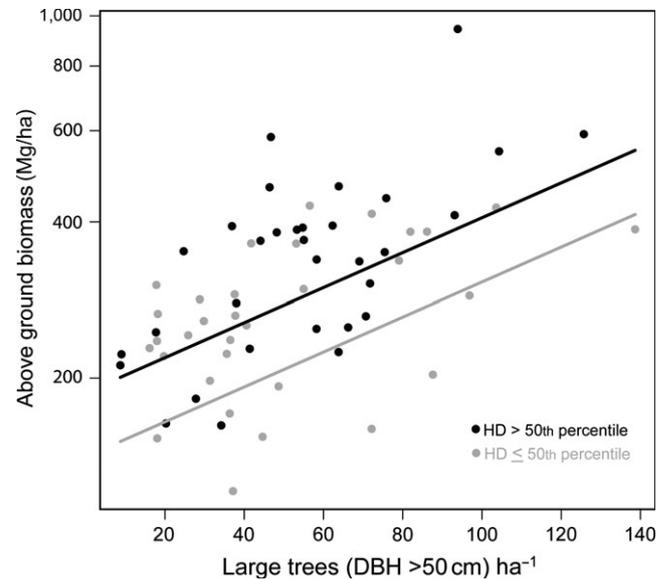


**FIGURE 4** Relationship between aboveground biomass (AGB) and altitude demonstrating the effect of natural disturbance in primary forests of the Huon Peninsula, Papua New Guinea (PNG). Sites with disturbance are shown as gray dots and without disturbance as black dots. Curves are fitted splines from generalized additive models (GAMs) for both undisturbed plots (black line) and disturbed plots (gray line). Shading indicates the 95% confidence interval for each spline. We omitted the lowermost sites (50 m) from this analysis because of the high probability of human disturbance. Note the y-axis has been square root transformed

(P/E), MAT, and intra-annual temperature range. However, here, we report the results for moisture availability (Figure 6) as it has been demonstrated to be a good predictor of tree height and AGB (Bowman et al., 2014). In the elevation zones where the peak in large stem density occurred (2,200 and 2,400 m asl), the ratio of P/E was 2.8, the average MAT was 13.7°C, and the intra-annual temperature range was 7.5°C. These conditions were found in the cloud immersion zone.

## 4 | DISCUSSION

Contrary to expectations, AGB of primary forests along a 3,100-m elevation gradient in PNG did not vary directly with a number of environmental variables collected in the field, including forest structure, soil characteristics, and topographic variables, nor with those derived from various global datasets on climate and topography. Although natural disturbances were ubiquitous across the study area and explained most of the variation in AGB (Figure 4), the altitudinal pattern of AGB exhibited a major secondary peak at high altitude as a result of dense stands of unusually large trees for those elevations (Figure 5). The abundance of large trees was related to a set of climatic variables, but the relationships were unimodal following hump-shaped curves, rather than a simple linear relationship. This set of “optimal” climatic conditions identified in this study (Figure 6) is



**FIGURE 5** Relationship between aboveground biomass (AGB) and the number of large trees (>50 cm DBH) in primary forest in the study area. Black dots and the black fitted line represent sites with large trees having height-to-diameter ratio (HD) greater than the median (0.7). Gray dots and the gray fitted line represent sites with HD equal or lesser than the median. The model explains 43% of AGB variation among elevation zones and 39% within elevation zones. Fitted lines are from a linear mixed-effects model with elevation site included as a random effect. Note the log-scale on the y axis. Sites with signs of natural disturbances have been omitted

similar to those found in foggy maritime temperate areas that harbor the largest trees in the world. Our study presents the first assessment of AGB in PNG’s high altitude forests, revealing that they are among the world’s most carbon-rich montane forests (Culmsee, Leuschner, Moser, & Pitopang, 2010; Girardin, Espejob, et al., 2013).

One of our most striking observations was that large trees, the major driver of AGB patterns in our study, were associated with a set of optimal climatic conditions: high water availability, moderate temperatures, and small intra-annual temperature variations (Figure 6). These conditions, found in high elevation forests in PNG, are remarkably similar to those which occur in regions identified as the most important for carbon storage in forests around the world (Keith, Mackey, & Lindenmayer, 2009). These areas are found in temperate maritime areas with substantial fog cover (Larjavaara, 2014). For example, the foggy mid-west coast of the USA boasts the largest gymnosperm (*Sequoiadendron sempervirens*) and the moist southeastern coast Australia is where the tallest angiosperm is found (*Eucalyptus regnans*). This climate envelope has been identified outside of temperate regions in tropical montane areas covered in cloud. However, most studies report tropical montane forests having smaller trees than at lower elevations (Girardin, Espejob, et al., 2013; Girardin, Farfan-Rios, et al., 2013; Raich, Russel, Kanehiro, Parton, & Vitousek, 2006). The abundance of large trees followed a hump-shaped relationship with high moisture availability (P/E). Givnish, Wong, Stuart-Williams, Holloway-Phillips, and Farquhar (2014) found

**TABLE 3** Heights of tropical montane trees of the Huon Peninsula, PNG, from families with specimens of DBH >70 cm DBH

Family	Genus	Max tree height (m)			
		50–800 m asl	800–2,000 m asl	2,000–2,800 m asl	2,800–3,100 m asl
Fabaceae	<i>Pterocarpus</i>	64			
Hernandiaceae	<i>Hernandia</i>	56			
Tetramelaceae	<i>Octomeles</i>	55			
Elaeocarpaceae	<i>Sloanea, Elaeocarpus</i>	49		24	40
Sapindaceae	<i>Pometia</i>	47	26		
Melastomataceae	<i>Melastoma</i>	46	29	32	
Cunoniaceae	<i>Caldcluvia, Davidsonia, Schizomeria</i>	45	33	37	39
Moraceae	<i>Ficus</i>	43	35	36	
Escalloniaceae	<i>Quintinia, Carpodetus</i>	41	18	29	28
Anacardiaceae	<i>Dracontomelon</i>	40			
Meliaceae	<i>Chisocheton</i>	37			
Achariaceae	<i>Pangium</i>	36			
Myrtaceae	<i>Syzygium</i>	33	40		27
Nothofagaceae	<i>Nothofagus, Lithocarpus</i>	30	33	30	41
Myristicaceae	<i>Myristica, Horsfeldia</i>	36	33	36	30
Rubiaceae	<i>Neonauclea, Timonius</i>	37	46	15	20
Euphorbiaceae	<i>Endospermum, Cleidion, Homalanthus, Macaranga</i>	31	33	39	29
Lauraceae	<i>Cryptocarya</i>		34	32	27
Sapotaceae	<i>Pouteria</i>		33	31	
Urticaceae	<i>Dendrocnide</i>		32	30	30
Cupressaceae	<i>Libocedrus</i>		30	27	31
Monimiaceae	<i>Dryadodaphne</i>			45	30
Apocynaceae	<i>Alstonia</i>			39	
Podocarpaceae	<i>Dacridium, Podocarpus</i>		28	36	31
Staphyleaceae	<i>Staphylea</i>			31	
Actinidiaceae	<i>Saurauia</i>			28	30
Icacinaceae	<i>Platea</i>			27	
Proteaceae	<i>Helicia</i>				29
Theaceae	<i>Eurya</i>				26
Rutaceae	<i>Zanthoxylum, Melicole</i>	42	32	36	27
Rosaceae	<i>Prunus</i>				25

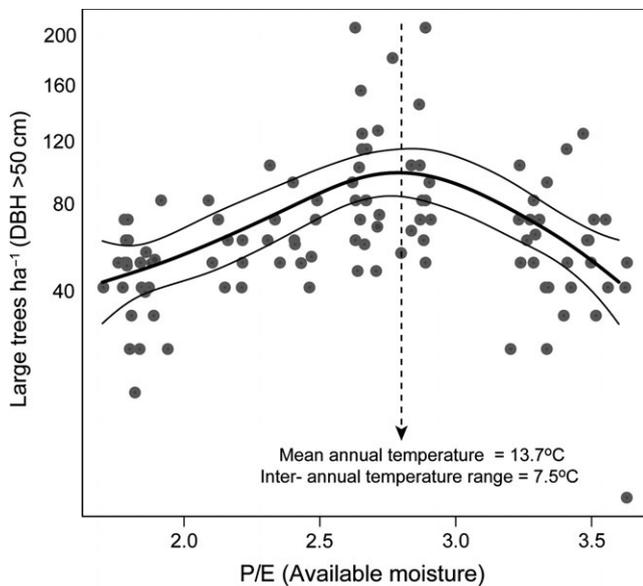
DBH, diameter at breast height; PNG, Papua New Guinea.

that tree height showed a strong positive relationship with P/E along an environmental gradient.

In the cloud immersion zone, trees were of unusually tall stature for those elevations. Some of our sites contained individuals reaching over 40 m tall at 2,800 m asl (Table 3, e.g., *N. starckenborghii*, *D. crassa*, *C. nymanii*) and over 30 m tall up to altitudes of 3,100 m asl (e.g., *D. nidulum*, *L. papuana*, *Elaeocarpus* sp., and *Myrtaceae* sp.). To our knowledge, canopies have seldom been reported to exceed 15–20 m above 2,400 m asl in other parts of the world (Raich et al., 2006) and this despite the steep earthquake and landslide prone terrain of PNG. Low intra-annual range and moderate MAT have been shown to provide optimal conditions for tree growth (Bowman et al., 2014). It is possible that the cloud immersion zones in our study

area coincide with moderate intra-annual temperature variations, leading to a lower energy requirement for acclimating metabolism to varying thermal regimes (Larjavaara & Muller-Landau, 2012). Cloud cover could also cause rainfall to be more evenly spread throughout the year, thereby minimizing seasonal droughts that might lead to hydraulic failure in tall trees, a known limiting factor of tree height (Zhang et al., 2009).

However, the reasons for the occurrence of much larger trees, compared to other studies at those elevations, are still unclear (Larjavaara, 2014). Deeper soils recorded in our study may have helped large trees persist despite high disturbance rates (Givnish et al., 2014). We suspect that soil depth and other soil attributes had significant impacts on biomass and the occurrence of large trees



**FIGURE 6** Relationship between the number of large stems and the ratio of precipitation to evapotranspiration (P/E), a measure of moisture available for trees. Optimal mean annual temperature (MAT) and inter-annual T range are also shown. Each dot represents a site. Note the square-root transformation of the y axis

(Ashton & Hall, 1992), but we were not able to demonstrate the magnitude of these impacts because soil depths were measured to a maximum of 200 cm and 80% of the soil plots above 2,200 m asl reached that maximum. Thus, it was not possible to fully define the effect of soil depth on AGB and forest structure above this elevation.

In tropical forests, large trees store most of the carbon and control the bulk of the variation in forest biomass (Slik et al., 2013). However, predicting patterns in the occurrence of large trees in tropical forests is still a great source of uncertainty in modeling forest carbon (Slik et al., 2013). Compared to temperate regions, little is known about the drivers of large tree occurrence in tropical forests (Larjavaara, 2014). Moreover, large trees may introduce significant errors in forest biomass assessments (Venter, Venter, Edwards, & Bird, 2015). Given the disproportionately large contribution of large trees to forest biomass, understanding the environmental factors that promote their growth and distribution is essential to better predict patterns of forest biomass (Larjavaara & Muller-Landau, 2012). This study suggests that improving our understanding by identifying factors that lead to the presence and persistence of large trees is a key component required to improve forest carbon stock assessments and management of forests. It would be essential to map the extent of “optimal” climate niches for the growth of trees, and this would prioritize further field campaigns and potentially reveal other remote and significant carbon-rich forests.

Variation caused by disturbances, natural or anthropogenic, can be significant and can obscure the effect of climatic or edaphic variables (Fox, Vieilledent, Yosi, Pokana, & Keenan, 2011; Stegen et al., 2011). In our analysis, we only considered lowermost sites to be affected by human disturbances, based on our selection

criteria. However, it is likely that montane forests far from villages without obvious signs of human disturbances may still have been shaped by a legacy of long human presence in the region that includes evidence of very early montane forest occupation and long sequences of human modification of landscapes in this general region (Groube, Chappell, Muk, & Price, 1986; Summerhayes et al., 2010).

Very few studies have recorded AGB on very steep slopes, even though most tropical montane forests are on steep terrain (Spracklen & Righelato, 2014). We gained novel insight into the disproportionate effects of natural disturbances on AGB using rappelling equipment to sample very steep terrain. Natural disturbances, as defined in our study, were mostly caused by localized landslides and windthrows. When present, natural disturbances reduced biomass by an average of 20% (Figure 5), with greater reductions in AGB at lower altitudes. This finding indicates that slope should be taken into consideration when modeling AGB across a mountainous landscape.

Our study had a number of limitations. Better insights into the relationship between AGB and climate could be obtained if local weather station data were available because these are more accurate than global syntheses and do not conceal local variation. This may become possible in the future as four weather stations have recently been installed in the area. Moreover, our study design, which consisted of sampling many smaller plots instead of fewer larger plots in order to stratify our samples, may have led to heightened correlations of AGB to large trees (Stegen et al., 2011). Finally, tropical montane forests are under-represented in research; thus, large trees may not be as uncommon as we suggest but simply under-reported (Malhi et al., 2010).

The most useful models are those with a parsimonious set of explanatory variables that are readily available and that have strong predictive power. However, our study suggests that simple AGB-climate-edaphic models may not be suitable for the forests in PNG or in areas where natural disturbances are prominent and niche climates exist. Instead, process-based models that take into account local disturbances may be more suitable (Stegen et al., 2011). Recently, the global relationship between maximum canopy height and water availability (P/E) has been validated (Klein, Randin, & Körner, 2015), and advances in metabolic scaling theory and water–energy balance equations have provided models of large-scale patterns of maximum forest canopy height in the USA (Choi et al., 2016). Therefore, geo-predictors such as water availability (P/E) could potentially be used to locate remote tropical forests with high biomass to help guide research and conservation priorities.

The value of tropical montane forests for their carbon and biodiversity is increasingly being recognized, particularly as they may act as biodiversity refugia for commonly endemic species that have evolved within stable climate niches (Keppel et al., 2012). The predicted effects of changes in temperature and rainfall in montane forests could have severe consequences for the persistence of the large, old trees found in these regions, potentially threatening

important carbon stores and biodiversity (Ponce-Reyes, Nicholson, Baxter, Fuller, & Possingham, 2013). However, tropical montane forests remain some of the most understudied forest ecosystems, partly because they are remote and because of their difficult topography (Homeier et al., 2010). Tropical montane forests are often typified as squat and gnarly, which may be a misconception, as we have shown here. Therefore, the importance of securing their future under a changing climate is enhanced.

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## SUPPORTING INFORMATION

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

# Graphical Abstract

The contents of this page will be used as part of the graphical abstract of html only. It will not be published as part of main article.



Montane cloud forests are often thought to be squat and gnarly with little carbon benefit, a misconception we show in this study. Optimal climate conditions for large trees drive forest biomass patterns along a 3000m elevation gradient in Papua New Guinea. These optimal climate niches, similar to those also found in the temperate coastal climates that are home to the largest trees in the world, are also found at high elevations in remote tropical forests of Papua New Guinea.