

Forest Carbon Sequestration Peaks at Intermediate Elevations: Structural and Climatic Drivers of Aboveground Biomass in Bhutan's Temperate Forests

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Abstract

Altitudinal gradients are among Earth's steepest environmental gradients, yet forest carbon storage patterns along mountains remain poorly predicted by simple linear models. While some studies show biomass declining monotonically with elevation, others report mid-elevation peaks, a pattern critical for climate mitigation planning in montane regions. This study examined aboveground tree biomass (AGTB) and its environmental and structural drivers across three altitudinal bands (1,400–1,900 m, 2,000–2,500 m, 2,600–3,100 m) along the 37 km Lobesa-Dochula transect in Bhutan. We established 60 systematically distributed plots and measured all trees with diameter at breast height ≥ 10 cm, then employed Factor Analysis of Mixed Data (FAMD) and Generalized Additive Models (GAM) to identify biomass drivers. AGTB exhibited a pronounced unimodal distribution, with peak biomass at mid-elevation (146.82 ± 17.45 t/ha at 2,000–2,500 m), significantly higher than lower elevations (104.95 ± 17.45 t/ha; $p = 0.001$) and higher elevations (104.48 ± 28.56 t/ha; $p < 0.001$; $F(2,57) = 10.7$). The mid-elevation maximum reflects optimal overlap of temperature, precipitation, and structural complexity. Critically, altitude-dependent shifts in biomass drivers emerged: at low elevations, basal area dominated ($R^2 = 0.926$), while temperature-controlled biomass at high elevations ($R^2 = 0.931$). Mid-elevations displayed complex interactions between structural attributes (basal area, DBH) and spatial factors (altitude, longitude; $R^2 = 0.64$). This unimodal pattern, consistent with global montane forests, reveals that Bhutan's highest carbon sequestration capacity is concentrated at intermediate elevations, not continuously with forest area. We demonstrate that simple linear elevation-biomass relationships mask critical ecological thresholds. For climate mitigation policy, these findings argue for prioritizing mid-elevation forests in carbon accounting and conservation planning, as their disproportionate carbon storage makes them essential carbon infrastructure. This altitude-dependent vulnerability requires elevation-specific management strategies as climate change shifts the optimal biomass zone upslope.

Introduction

Forests have been globally recognized as crucial ecosystems for climate change mitigation due to their capacity to sequester atmospheric carbon dioxide (CO₂) and store it in biomass and soils (Augusto & Boča, 2022). Comprising approximately 30 percent of the land surface on Earth, forests contribute to 19 percent of the Earth's biomass and carbon stores and possess almost 45 percent of the carbon in land biomass (Thakur et al., 2024; Saeed et al., 2019). Since the concentration of atmospheric CO₂ has increased drastically over time (from 317 ppm in 1958 to 419.3 ppm in 2023), it has become increasingly critical to preserve forest biomass (NOAA, 2024) due to anthropogenic processes. Forest degradation and deforestation are now responsible for 17.4% of global greenhouse gas emissions, placing forests at the center of both climate impact and solution (Dani & Baniya, 2019). Biomass estimates in forests have shifted over time; the current emphasis is on carbon sequestration rather than timber productivity; hence, above-ground tree biomass (AGTB) is an important ecological indicator for assessing forest functioning (Edson & Wing, 2011). Forest carbon occurs in various pools, including above- and below-ground biomass, litter, dead wood, and soil organic matter, and the carbon component is retained about equally between trees and soil (Pan et al., 2011). The Intergovernmental Panel on Climate Change (IPCC)

acknowledges the existence of these pools and says they are the main carbon reservoirs that play a key role in controlling atmospheric carbon. It is estimated that forests contain $861 \pm 66 \text{ Mg C ha}^{-1}$ globally, of which 42 percent is found in the Above-ground biomass (Tadesse & Tamiru, 2024). In Bhutan, forests cover 2.68 million hectares, or approximately 69.71 percent of the national area (FMID, 2023a), a slight reduction from 71 percent in 2016. The national commitment to maintaining a carbon-neutral state, as demonstrated by Bhutan at COP21 in Paris, has also underscored national attention to biomass and carbon stock assessment (Tshering, 2024). According to FMID (2023b), Bhutan has an above-ground biomass of 296.04 million tonnes.

Forest biomass is a highly dynamic component that depends on biophysical factors, including altitude, slope, aspect, stem diameter, and species abundance (Urquiza Haas et al., 2007; Murthy et al., 2022). Altitude, in particular, can be regarded as the most significant factor, as it defines microclimates by altering temperature, precipitation, and exposure to solar radiation (Bhandari & Zhang, 2019). With altitude, forest type, productivity, and species composition also change, leading to spatially non-homogeneous biomass distributions (Xu et al., 2018; Moeslund et al., 2013). Light intensity, soil moisture, and temperature regimes are further influenced by slope and aspect, which affect tree growth and carbon accumulation (Boerner, 2006; Daryaei et al., 2019). Photosynthesis, respiration, and decomposition within forests are ecological processes that depend on the interaction of these five variables along altitudinal gradients, which ultimately determine the carbon stocks within forests.

In Bhutan, topography is steep, and elevation ranges are high; as a result, different forest zones have formed, from subtropical to alpine, each with varying levels and potential for biomass. The Lobesa-Dochula transect, with an altitude range of 1,400 to 3,100 meters above sea level (masl), is ideal for studying these dynamics because it represents both the dry west Himalaya and wet east Himalaya aspects of Bhutan (Wangda & Ohsawa, 2006). It encapsulates a microcosm of Bhutan's broader ecological range, providing a perfect area for studying biomass dynamics. Although there is worldwide concern about biomass dynamics, empirical studies on AGB dynamics across altitudinal gradients in Bhutan remain scarce. Even in places where such studies have been conducted worldwide, the results are not consistent. There is evidence that AGB decreases with altitude (Leuschner et al., 2007; Moser et al., 2008), and others point to a hump-shaped distribution with a maximum at intermediate altitudes (Ensslin et al., 2015). Some studies also find no noticeable correlation between biomass and altitude (Culmsee et al., 2010; Dossa et al., 2013).

Further, much research has focused on broad altitudinal ranges that typically extend above 2,000 meters, but few studies have examined steep, narrow altitudinal gradients like those between Lobesa and Dochula. When undertaken in separate areas, studies are usually constrained by confounding influences such as site-specific microclimates and anthropogenic impacts (Salvaña et al., 2019). In contrast, altitudinal sampling along a single transects, such as the Lobesa to Dochula transect, provides a clearer picture of how tree biomass varies with elevation under more uniform macroclimatic conditions (Sandoya et al., 2021; Klorner, 2007). This method can reveal both ecological transitions and species turnover and minimize the noise associated with external environmental variability. Since Bhutan has

varied geography and distinct climate regions, it is important to determine the factors influencing AGB along altitudinal gradients not only to develop a national carbon budget but also to enhance forest management practices under a changing climate regime.

This paper thus aims to determine the variation in above-ground biomass in trees across altitudinal zones along the Lobesa-Dochula gradient and the environmental and structural factors that could underlie these patterns. In particular, we aim at: (1) examining the change in biomass of trees in different altitudinal bands between Lobesa and Dochula and (2) determining what factors and their parameters influence above-ground (tree) biomass and identifying those parameters that cause the strongest influence in each of the altitudinal levels. The research will address the following research question: What is the variation in tree biomass among the different elevation bands in the study area? What are the effects of various environmental and structural characteristics and AGB? And, which of these variables have the most impact on AGB in both altitudinal zones?

Materials and Methods

Study Area

The study was conducted along the altitudinal gradient from Lobesa to Dochula Pass (Fig. 1). Lobesa is located at 27°31'13.62"N latitude and 89°52'1.63"E longitude at an altitude of 1,400 masl whereas Dochula pass is located at 27°29'23.41"N latitude and 89°45'4.48"E longitude at an altitude of 3,100 masl therefore, the altitudinal gradient of the study area ranged from 1,400 m to 3,100 m above sea level. The distance between Dochula and Lobesa is 37 km, with an altitude difference of 1,700 masl. Considering the wide range of climatic conditions that drive sharp changes in forest composition along an altitudinal gradient of less than 2,000 m, the study site was chosen to better understand the relationship between altitude and forest composition and biomass (Ahmad et al., 2021). The altitudinal range covered four forest types: chirpine forest, cool broadleaved forest, warm broadleaved forest, and mixed conifer forest (Dorji & Gurung, 2017). The vegetation composition transitioned from *Pinus roxburghii*-dominated forest in Lobesa to *Tsuga Dumosa*-dominated cloud forest in Dochula.

Sampling Method and Data Collection

To determine variation of above-ground biomass along an altitudinal gradient, a systematic random sampling method was used (Kirkpatrick & Hassall, 1985). The elevation was also classified into three transects: 1,400-1,900 m (T1), 2,000–2,500 m (T2), and 2,600-3,100 m (T3), separated by 100 m intervals to adequately depict changes in vegetation composition and structure. In each transect, a total of 20 circular plots with a radius of 12.62 m were set, starting with a randomly selected plot, followed by additional equally spaced plots at elevations of 26.32 m (Gashu et al., 2020). To reduce edge effects, all plots were geolocated at least 30 m from the nearest road and established with a Garmin GPS.

(a)

Tree measurements were conducted according to the National Forest Inventory (NFI, 2023) protocol, in which all living trees at 1.37 m height with DBH ≥ 10 cm were measured with a diameter tape, and tree heights were measured with a Suunto clinometer. Multistems over the breast line were counted as single stems, and stems that forked below the breast line were counted as individual ones. A densiometer was used to measure canopy cover, which affected the availability of light and biomass, and was categorized into four groups based on Dovciak & Brown (2014): sparse ($< 10\%$), moderately open (11–40%), moderately closed (41–70%), and closed canopy ($> 71\%$).

Figure 2

(a) Sampling and (b) plot design

Data Analysis

The above-ground tree biomass was calculated using an allometric model based on DBH, height, and wood density of the tree, following the methods of Chave et al. (2014) and Gonmadje et al. (2017).

$$AGTB = 0.0673 \times (\rho D^2 H)^{0.976}$$

Where, ρ – Wood density (g/cm^3)

D – DBH of the tree (cm)

H – Height of the tree (m)

Descriptive statistics were used to assess trends in above-ground biomass (AGTB) across altitudinal gradients. A normality test was conducted using the Shapiro-Wilk test. One-way ANOVA and Tukey's post hoc test were employed to determine significant differences among the gradients. The factors identified as important structural and environmental drivers were detected using Factor Analysis of Mixed Data (FAMD) (Davidow & Matteson, 2022), and Generalized Additive Models (GAMs) (Zhang et al., 2021) were used to model their non-linear effects via penalized regression splines. EDF, residual diagnostics, and collinearity were model diagnostics. All the analyses were conducted in R with the mgcv package (Pedersen et al., 2019).

Results

Above-Ground Biomass with Altitudinal Gradient

Aboveground tree biomass (AGTB) varied across the altitudinal gradient. The highest mean AGTB was observed in the 2000–2500 m altitude range (146.82 ± 17.45 t/ha). The AGTB in the 2600–3100 m and 1400–1900 m ranges were similar, measuring 104.48 ± 28.56 t/ha and 104.95 ± 17.45 t/ha, respectively. The above-ground tree biomass displayed a hump-shaped distribution corresponding to that of Chandragiri Hill, Kathmandu, Nepal, where above-ground tree biomass significantly increased up to

115.7 t/ha at 2200m before drastically decreasing to 43.39 t/ha at 2300m (Dani & Baniya, 2019). This is due to the presence of larger trees at mid–altitude, which are favoured by an optimal growth environment. Equivalent to that, the highest above–ground biomass was found in the mid–altitudinal zone (1560.01–1643m), followed by the lowest altitude (1435–1560 m), and the highest altitudinal class (1643.01–1704m) in Wacho Forest in Hawa Galan District, Kellem Wollega Zone, Oromia Region, Ethiopia (Gashu et al., 2020).

Table 1
Mean and standard deviation of AGTB (t/ha) along the altitudinal gradient

Altitudinal Gradient (masl)	AGTB (t/ha)
2600–3100	104.48 ± 28.56
2000–2500	146.82 ± 17.45
1400–1900	104.95 ± 17.45
Note: The values are represented as Mean ± Standard deviation. AGTB is expressed as tons per hectare (t/ha)	

Difference in Above–Ground Tree Biomass Along the Altitudinal Gradient

A one-way ANOVA revealed a significant effect of altitude on above-ground biomass, $F(2, 57) = 10.7, p < .001$. A Tukey's HSD post hoc test indicated that the 2000–2500 m altitude band (M difference = 41.9) had significantly higher biomass than the 1,400–1,900 m band, $p = .001$, 95% CI [16.58, 67.15]. There was no significant difference between the 2,600–3,100 m and 1,400–1,900 m bands (M difference = -0.47, $p = .999$, 95% CI [-25.76, 24.81]). However, the 2,600–3,100 m band had significantly lower biomass than the 2,000–2,500 m band (M difference = -42.3, $p < .001$, 95% CI [-67.62, -17.05]). These findings indicate that altitude has a nonlinear relationship with AGTB, with peak biomass at intermediate altitudes (2,000–2,500 m) and a dramatic decline at altitudes above 2,500 m. However, it contradicted the results of the study carried out by Suberi *et al.* (2018) in Khotokha, Wangdue Phodrang. The values for AGTB differed at low (90.45 ± 58.31), mid (200.56 ± 114.11), and higher (374.51 ± 142.64) altitudes due to differences in the altitudinal gradient, environment, and forest types. Such a result was found in other parts of the world; for example, a carbon stock analysis conducted in Gedo Forest found that altitude has a significant effect on aboveground biomass ($F = 5.172, p = .008$) (Yohannes et al., 2015).

Table 2

One-way ANOVA for AGTB along the altitudinal gradient of 1,400–1,900 m, 2,000–2,500 m and 2,600–3,100 m

Source	df	SS	MS	F	p
Altitude Gradient	2	23637	11819	10.7	0.000113
Residuals	57	62935	1104		
Total	59				
Note: df = degree of freedom, SS = sum of squares, MS = mean squares, F = F-statistic, p = significance level. Statistical significance was evaluated at $p < 0.05$					

A unimodal trend is also observed in the results from Mexico, which peaks at 2,500 meters and ascends with altitude (Girón-Gutiérrez et al., 2024). Other studies have found mid-altitude peaks in AGTB (Culmsee et al., 2010; Marshall et al., 2012; Ensslin et al., 2015). Marshall et al. (2012) estimated that AGTB peaked above 1,500 m, although they suggest it could reach up to 540 t/ha. Although their estimate of 365 t/ha is lower than the AGTB of 2,500 m found in this study, Ensslin et al. (2015) note a peak at 2,200 m, a mid-altitude similar to the estimates made in this study. Alves et al. (2010) and Rosenfield & Souza (2014) also reported an increase in AGTB with increasing altitude, but only up to 1,500 m.

These findings suggest that peaks in AGTB around 2,200 to 2,500 m are common for temperate altitudinal transects. Such a pattern may result from optimal growth conditions in mid-altitudes (temperature, moisture, and nutrient availability) relative to higher and lower altitudes. The results indicate that mid-altitude forests are important for carbon sequestration and suggest that altitudinal thresholds are an important structuring process for biomass in montane ecosystems. However, a contrasting trend was also found, with differences not significant for above-ground biomass ($F = 1.344$, $p = .278$), despite an overall increase with altitude in Egdu Forest (Gubena & Soromessa, 2017).

Table 3

Post-hoc Tukey's test among the altitudinal gradients

Comparison	Difference	95% CI	Adjusted p-value
2000–2500 m vs 1400–1900 m	41.9	(16.58, 67.15)	0.001
2600–3100 m vs 1400–1900 m	– 0.47	(–25.76, 24.81)	0.999
2600–3100 m vs 2000–2500 m	– 42.3	(–67.62, – 17.05)	0
Note: The mean difference is significant at the adjusted p -value < 0.05 level			

Impact of Environmental Variables and Tree Structure on Above-Ground Biomass Along the Altitudinal Gradient

The Factor Analysis of Mixed Data (FAMD) has shown specific trends in the impact of environmental and tree structural variables on the biomass of the above-ground tree (AGTB) along the 1,400-3,100 meters altitudinal gradient. AGTB showed a positive correlation with altitude (loading = 0.93) in the lowest gradient (1,400-1,900 m). Mannan et al. (2019) support this trend, noting that biomass increases measured in the Himalayan forests of Pakistan increased with altitude from 70.80 Mg/ha to 474.08 Mg/ha. It, however, is opposite to findings in chirpine forests in Garhwal Himalaya where AGTB decreased between 1,000-1800 m (Kumar et al., 2019), which may be because the range was the highest in the research area.

The loading of basal area (0.83) was strong, which supported the core position of this variable in the accumulation of woody biomass, in compliance with Silk et al. (2013), who claimed that 86% of AGTB in Borneo forests could be explained by basal areas since it represents the cumulative cross-sectional area of all the stems in the given plot; it captures both the number of trees (density) and their sizes, especially favouring larger trees which contribute disproportionately to AGTB. Canopy cover was also positively related to biomass, but to a lesser degree (loading = 0.58), indicating that denser canopies with an overdominance of large trees increase biomass, as in Poorter et al. (2015) and Lutz et al. (2018). There was a significant positive effect (0.80) with slope that is probably attributable to lower human impact or more favorable microclimates on more rugged grounds (Miguel et al., 2018).

Figure 3

Factor analysis of mixed data (FAMD) of Environmental variables and Tree structural attributes of the lowest (1,500-1,900 m) and middle (2,000–2,500 m) altitudinal gradient of Lobesa to Dochula.

On the other hand, temperature was negatively associated with AGTB (-0.93), contrary to global trends, in which temperature positively affected biomass accumulation in coniferous systems (Chen et al., 2023). This disparity could be attributed to the blend of deciduous broadleaves at lower elevations that are highly susceptible to heat stress. In support of this, Way and Oren (2010) observed that evergreen species are less sensitive to high temperatures than deciduous species, whereas Gomez Apizarco et al. (2011) noted differences in temperature responses between angiosperms and conifers. The amount of precipitation each year showed a negative correlation with AGTB ($r = 0.78$). This could be attributed to nutrient leaching and reduced light availability in a cloudier, wetter environment (Poorter et al., 2015; Elbasiouny et al., 2022; Austin and Vitousek, 1998; Paoli et al., 2005).

The FAMD revealed intricate interactions in the mid-altitudinal range (2,000–2,500 m), with the first five dimensions accounting for a cumulative variance of 80.56 percent. In Dimension 1 (33.71%), AGTB correlated strongly with longitude, temperature, and aspect, and negatively with altitude. This trend reflects findings in the Qinling Daba Mountains, where AGTB reaches its peak at elevations of around 1,500-2,000 m and then declines (Yao, 2024). This trend of AGTB with elevation was also found in the Choco rainforest and Mexican dry forests (Abadla et al., 2025; SalinasMelgoza et al., 2018).

Dimension 2 (19.71%) placed importance on water availability and tree structure. AGTB was associated with mean DBH, basal area, and precipitation, indicating that biomass in this zone is driven by structural characteristics. Whereas precipitation adversely affected AGTB in hyper-humid regions such as Choc due to nutrient leaching (Wang et al., 2016; Abadia et al., 2025), moderate rainfall was favorable in subtropical forests (Yao, 2024). Dimension 3 (16.06%) showed interactions with latitude (0.61) and AGTB (0.45), and pointed to regional microclimatic effects. Dimension 4 (11.07%) showed a persistent positive association with canopy cover (1–0.72) and a negative association with precipitation (11.07–0.49), reaffirming the importance of forest structure and climate moderation. Topographic features were also found to be crucial, where the biomass was always much more significant on southerly aspects, which was attributed to increased productivity with solar radiation (Yao, 2024).

FAMD results in the highest altitudinal band (2,600–3,100 m) revealed an evident shift in the biomass drivers. Dimension 1 (34.08%) showed positive correlations with AGTB and temperature (0.942), latitude (0.811), and mean DBH (0.826), and a negative correlation with altitude (0.942), implying that low altitude and warmer microclimates enhance growth in such elevated zones. This is consistent with the findings of Merganic et al. (2021) and Ferreira et al. (2023), which indicate that temperature was the most critical limitation of AGTB in montane forests.

The second dimension (18.10%) included slope (0.693) and longitude (0.637) as positive, significant variables, and precipitation had a negative effect (–0.692). This indicates that topography is a stronger determinant of biomass than moisture in these areas. Dimension 3 (14.57%) highlighted that structural features were important determinants of biomass, in particular basal area (0.700), and stem density (0.568). These structural associations replicate findings from KC et al. (2024), who highlighted DBH and basal area as key predictors of AGTB in the Terai region of Nepal.

There appeared to be a complex relationship between canopy cover and AGTB: biomass favored dense cover (> 71%), and low canopy cover that was excessively putrid was also observed in disturbed, low-biomass areas. This was also comparable to the complexity observed in the Atacora Mountains and the montane forests of Nepal (Avohou & Sinsin, 2009; KC et al., 2024), where canopy architecture and orientation combine with biomass to influence wind exposure and solar radiation. These trends indicate that in high-elevation ecosystems, temperature and altitude are the main limiting factors for AGTB, whereas structural features and ground topography serve as secondary factors. According to the FAMD results, the hierarchy differentiates site-specific, altitude-dependent biotic and abiotic drivers of forest biomass.

General Additive Model to Understand the Influence of Significant Variables on Above–Ground Biomass Along the Altitudinal Gradient.

The model contributed to AGTB variance explained 95.3% (adjusted $R^2 = 0.926$) at the lowest altitude (1,400–1,900 m). Basal area (BA/ha) showed a very significant nonlinear relationship with AGTB (edf = 3.985, $F = 12.999$, $p < .001$), hence confirming its dominant role in determining biomass accumulation. Conversely, climatic factors, temperature and annual rainfall, were not statistically significant. These

results imply that, at lower altitudes, forest structure exerts greater control than climate in determining biomass. This is unlike research such as Khan et al. (2019) and Qian & Qin (2006), which found climate to be a major driver of biomass. Nevertheless, their research focused on long-term climate (66 years), whereas the current paper used short-term data, which could explain the difference. Also, the positive relationship between AGTB and basal area has been confirmed in previous literature (Marklund, 1988; Jaakkola et al., 2005; Stephenson et al., 2014).

At the mid-altitude level (2,000–2,500 m), the GAM accounted for 79.8% of the deviance (adjusted $R^2 = 0.64$). In this case, basal area ($edf = 3.691$, $p = .031$) and average DBH ($edf = 1.0$, $p = .022$) showed significant positive effects on AGTB, indicating that stand structural attributes are important. Altitude also showed a significant linear relationship ($edf = 1.0$, $p = .036$) with AGTB, supporting its influence on vegetation dynamics. Longitude showed a trend of relative significance ($p = .064$), indicating spatial variation in biomass patterns. These findings align with earlier studies that highlight the importance of tree size in biomass accumulation (Silk et al., 2013; van der Sande et al., 2017; Cai et al., 2020). This is supported by data from pantropical forests, which indicate that 70% of the variation in above-ground biomass was attributed to the presence of numerous large trees with a DBH of approximately 70 cm (Silk et al., 2013). Not only in the Pantropical Forest, but the Atlantic moist forest in Brazil also showed that larger trees, with more aboveground biomass, were the main factor driving the increase and peak of biomass at mid-altitude (100–500 m), with the abundance of trees > 50 cm being the primary driver. According to the studies of Cai et al. (2020), van der Sande et al. (2017), Rodriguez-Hernandez et al. (2021), and Sanaei et al. (2021), the structural attributes of the trees have more input on above-ground biomass compared to other vegetation functionalities such as species richness, abundance, and evenness.

The GAM explained maximum variation (96.4% deviance explained; adjusted $R^2 = 0.931$) in the highest altitudinal range (2,500–3,100 m). The most important predictor of AGTB was temperature ($edf = 1.0$, $F = 44.208$, $p < .001$), whereas structural (basal area, canopy cover) and topographic (slope) factors were not relevant. It indicates that temperature is the primary driver of biomass at high altitudes due to its effects on physiological processes such as photosynthesis and growth rates (Carvalhais et al., 2014). The significant impact of temperature on biomass was also observed in other forests around the world, comparable to the highest altitudinal gradient in this study. The highest AGTB was found in tropical, subtropical, and temperate forests, with a declining trend when extending towards the northern and eastern parts of Eurasia and North America due to lower temperatures and greater temperature variation (Larjavaara et al., 2012). The mean above-ground biomass was found to be significantly in the southern region, followed by the tropics and then the northern temperate region (Krause et al., 2010; Corlett et al., 2011).

Contrary to the study's results, rising temperatures led to a dramatic fall in AGTB in the tropics, to almost 41%. Nevertheless, the boreal region experienced an increase in above-ground biomass with a temperature rise of almost 15%. This was, however, much less significant than a decrease in biomass; thus, global biomass was assumed to be negatively correlated with temperature (Larjavaara et al., 2021).

Conclusion

The findings of this study demonstrate a large altitude–dependent effect on biomass distribution, rather than AGB increasing or decreasing linearly with altitude. Instead, the biomass displayed a distinct hump-shaped pattern, peaking at mid-altitudes. It represents an ecological balance of temperature, precipitation, and tree structural complexity that favours most forest growth in the mid-elevation zones. These zones had very high species richness and were characterized by tree height and basal area, indicating the best climatic conditions and vegetation structure for biomass accumulation. The species composition changes with elevation, aligning with gradients in environmental variables such as temperature and precipitation.

Moreover, variables appearing at different altitudes were dominated by different variables. It was found that both at higher and lower altitudes, environmental parameters such as temperature and slope had a major effect, while structural attributes: DBH and basal area were more important at the mid elevations. The practical implications of these findings, in addition to their contribution to academic comprehension, are significant for forest carbon management in Bhutan. But as climate change affects forest ecosystems, this sort of study offers essential information to the adaptation decisions that will have to be made.

Declarations

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Figures

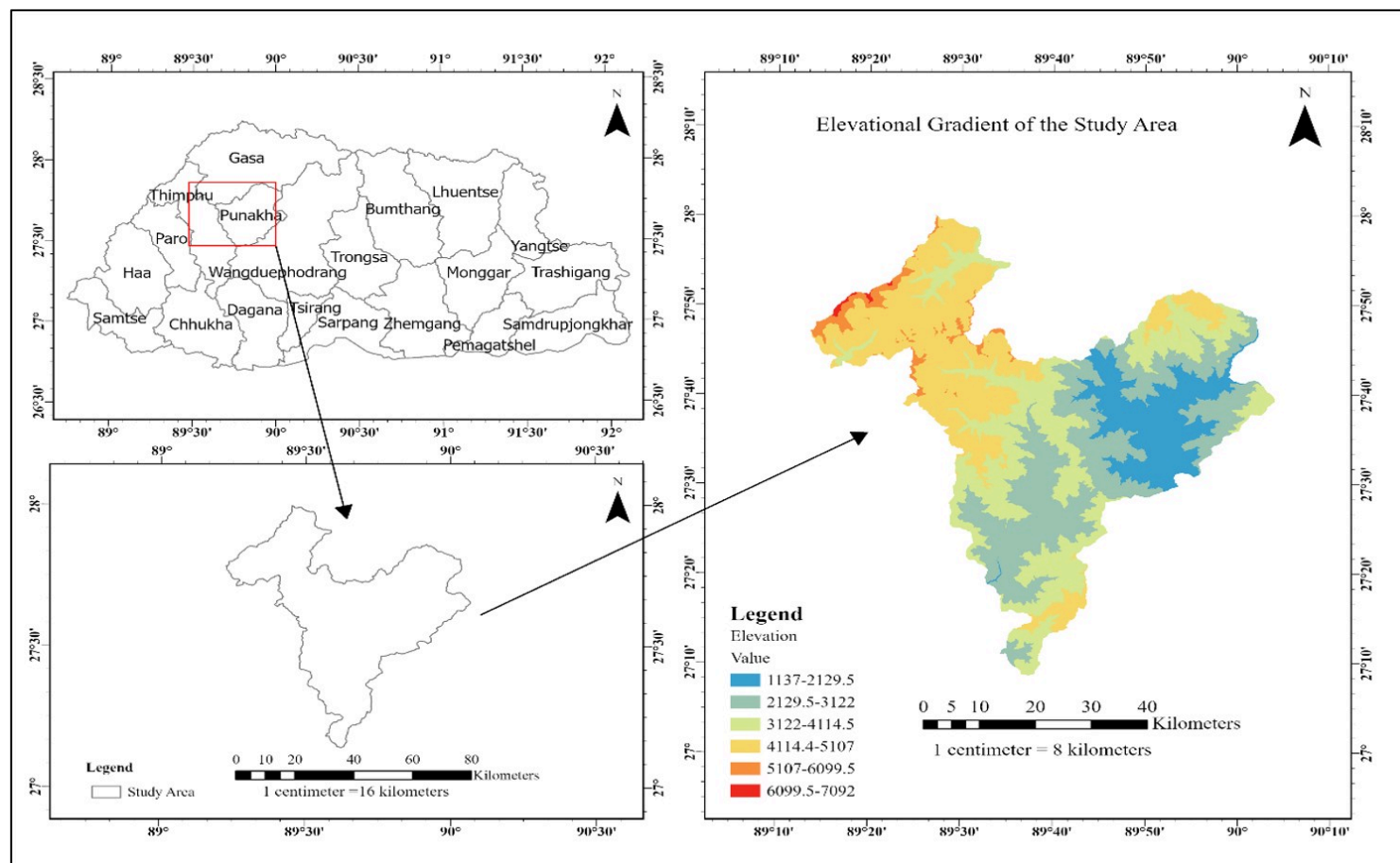


Figure 1

Study area map along the altitudinal gradient of Lobesa to Dochula

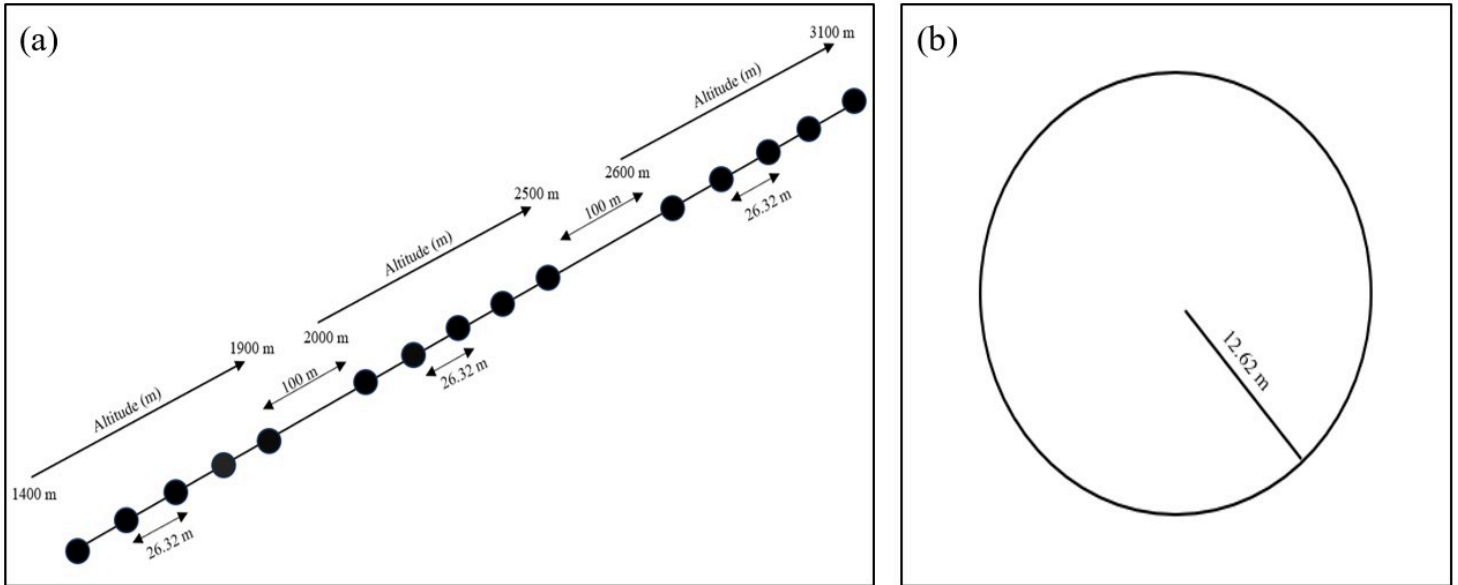


Figure 2

(a) Sampling and (b) plot design

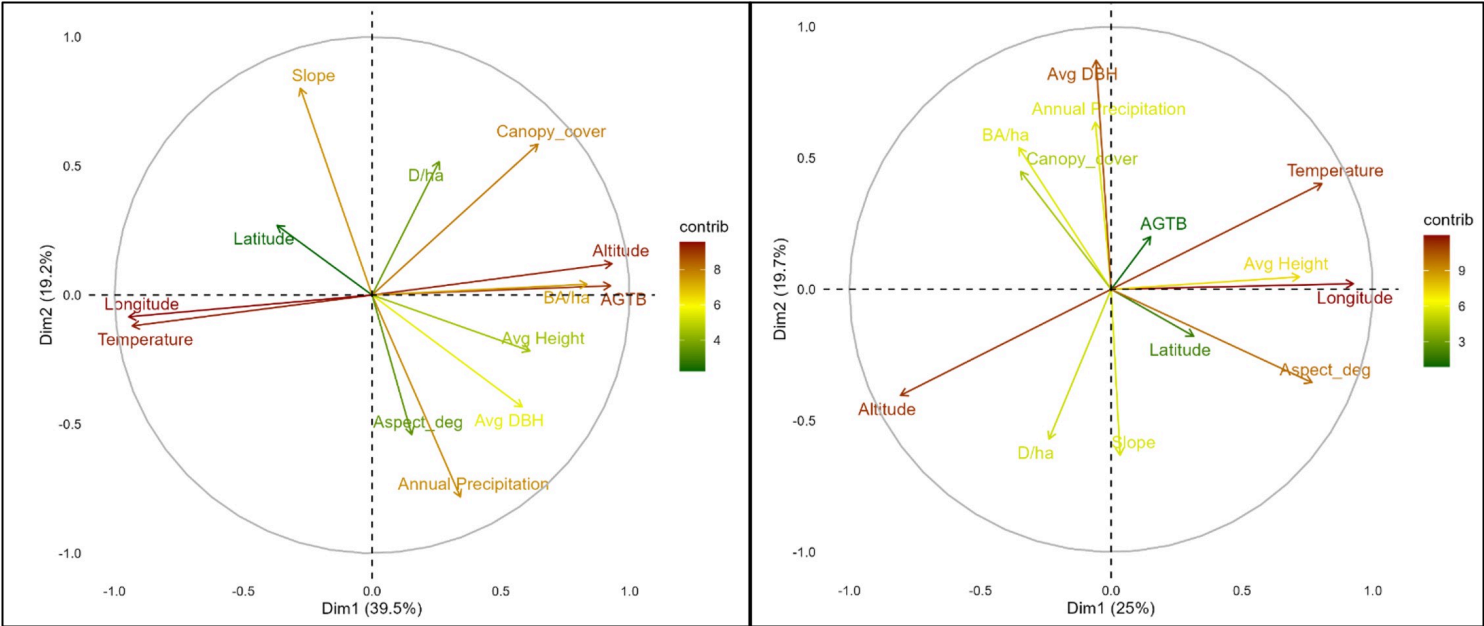


Figure 3

Factor analysis of mixed data (FAMD) of Environmental variables and Tree structural attributes of the lowest (1,500-1,900 m) and middle (2,000–2,500 m) altitudinal gradient of Lobesa to Dochula.

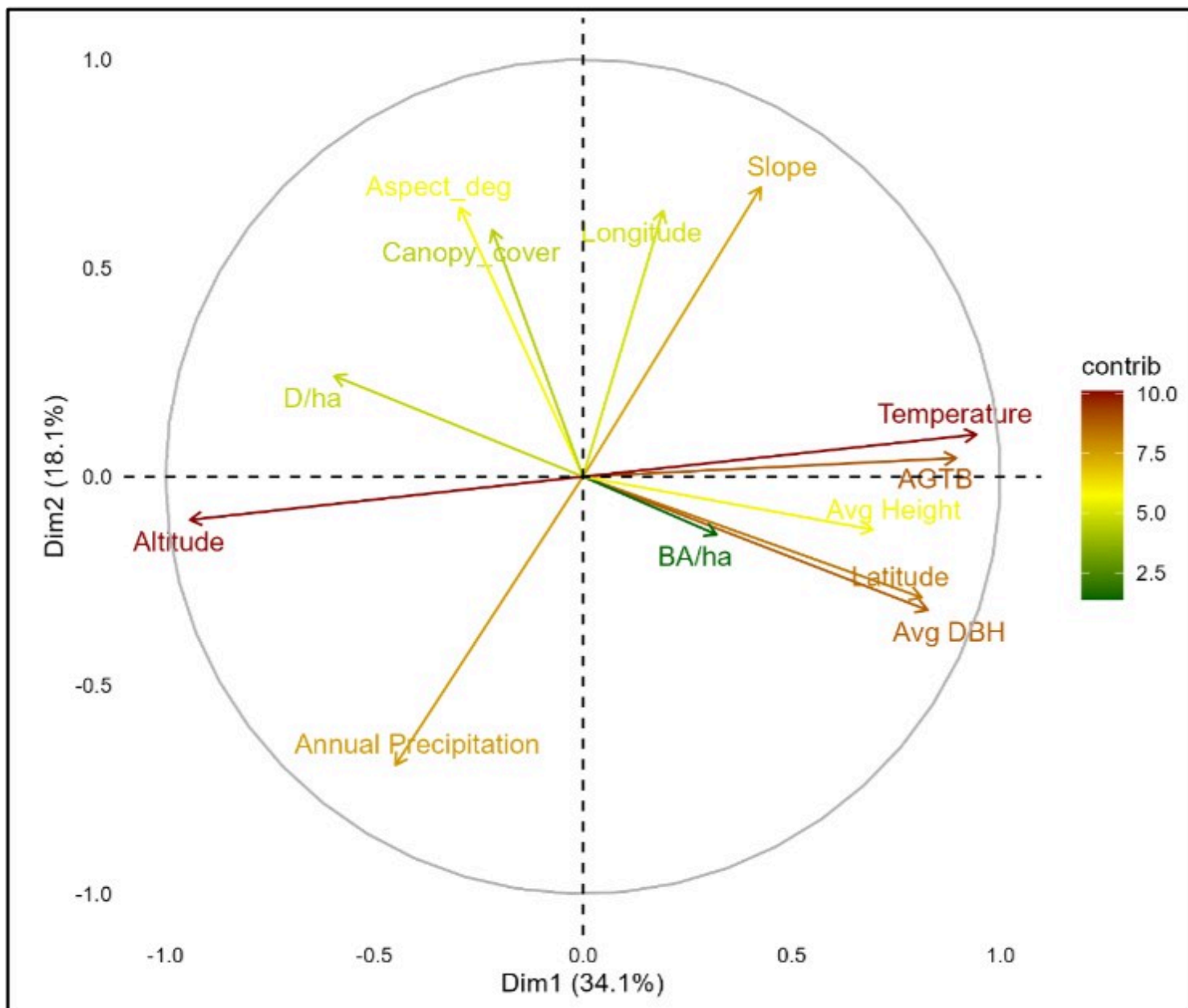


Figure 4

Factor analysis of mixed data (FAMD) of Environmental variables and Tree structural attributes of the highest (2,600–3,100 m) altitudinal gradient of Lobesa to Dochula.

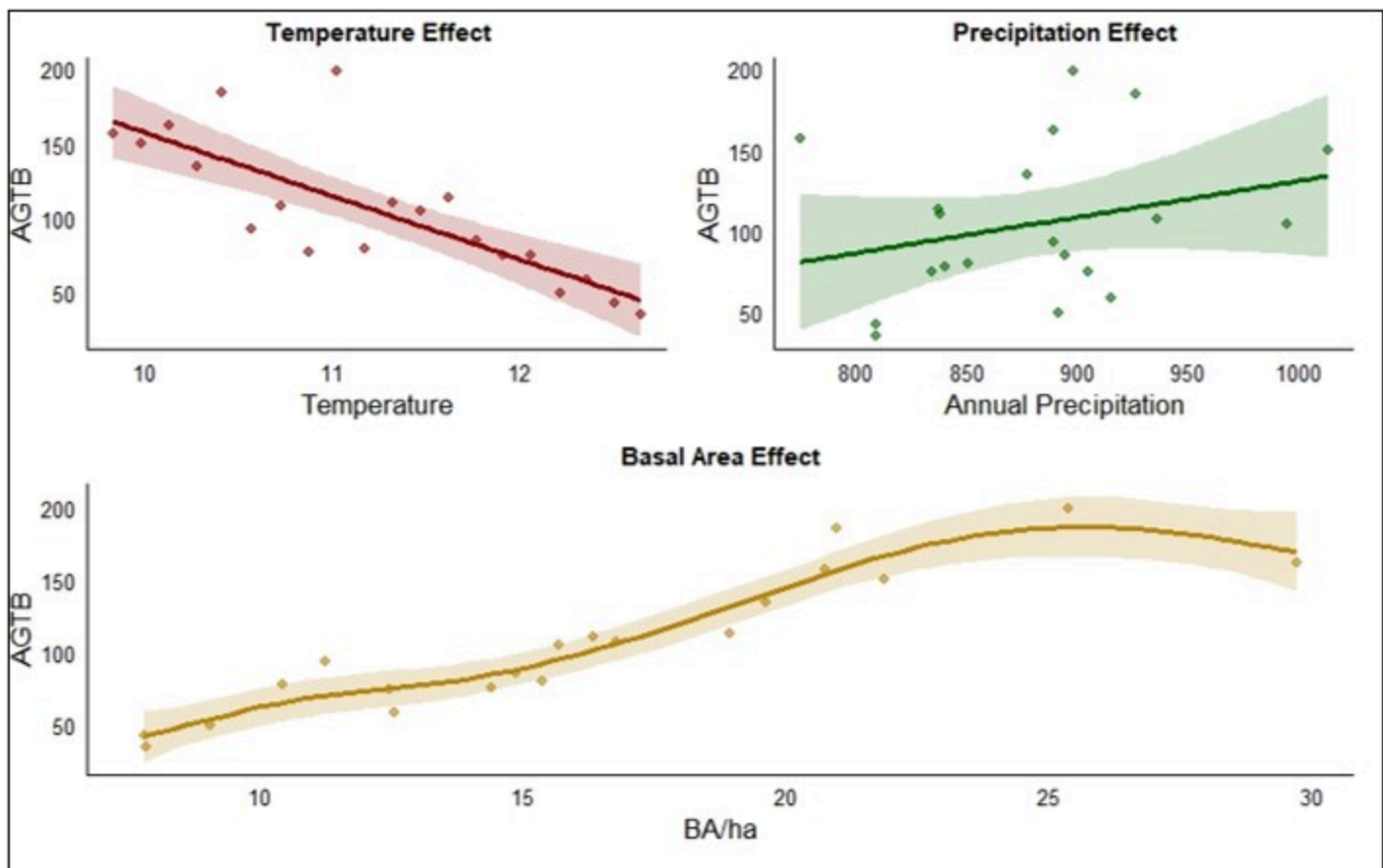


Figure 5

General Additive Model (GAM) of the highest correlated environmental and structural variables (Temperature, Annual precipitation, and Basal area per hectare) with above-ground biomass in the lowest altitudinal gradient (1,400–1,900 m).

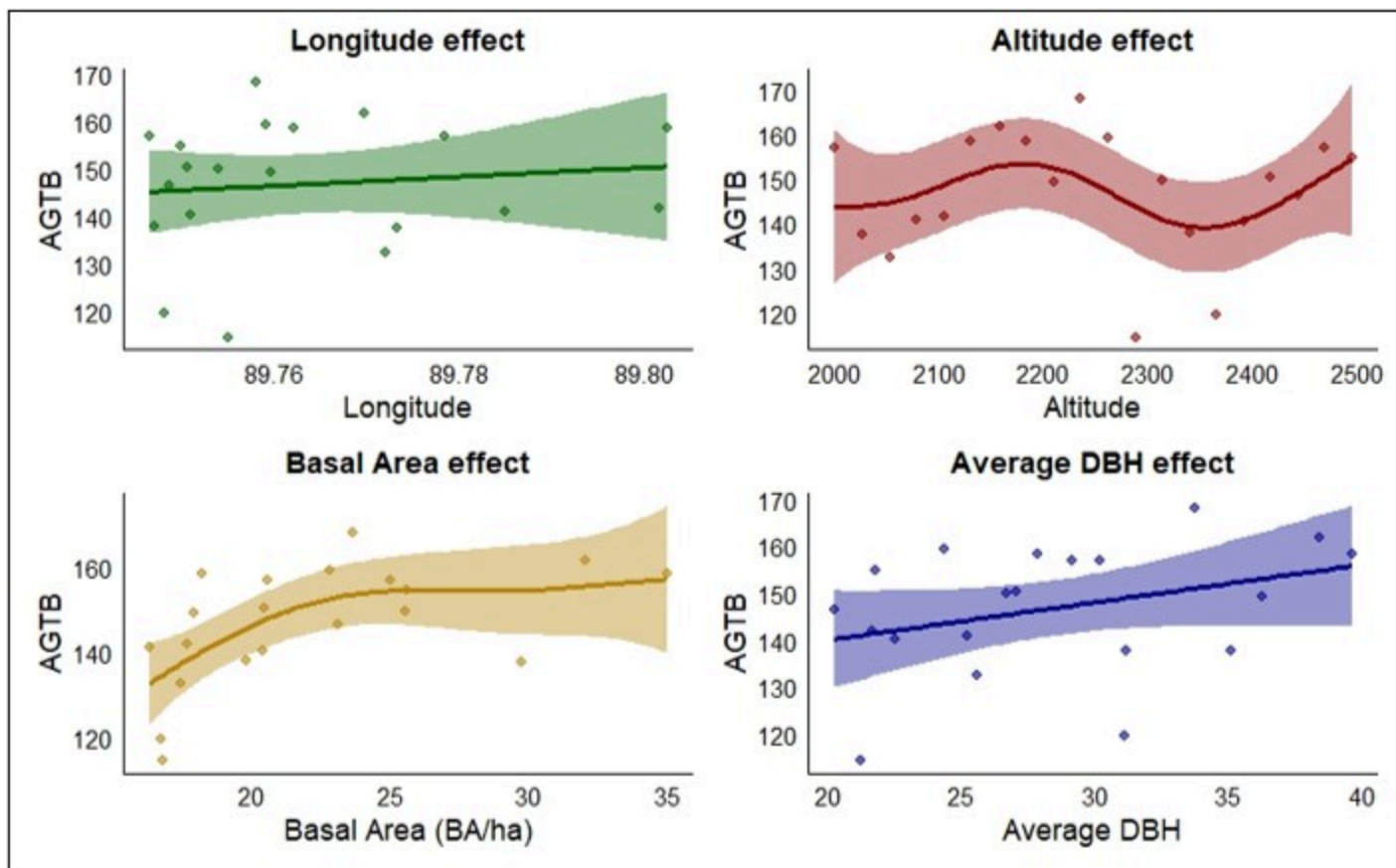


Figure 6

General Additive Model (GAM) of the highest correlated environmental and structural variables (Longitude, Altitude, Average DBH, and Basal area per hectare) with above-ground biomass in the middle altitudinal gradient (2,000–2,500 m).

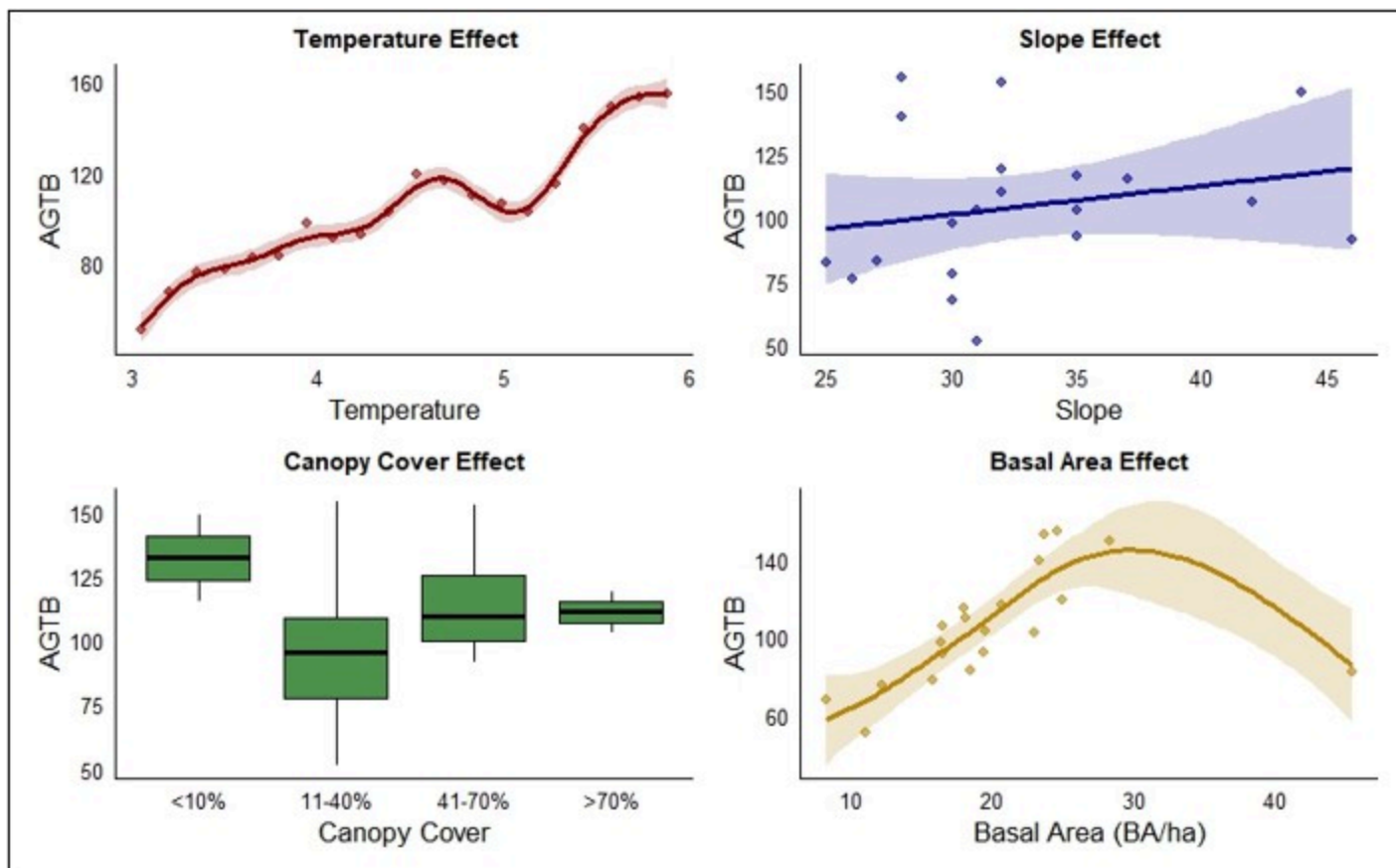


Figure 7

General Additive Model (GAM) of the highest correlated environmental and structural variables (Temperature, slope, Canopy cover, and Basal area per hectare) with above-ground biomass in the highest altitudinal gradient (2,600–3,100 m)