

## RESEARCH ARTICLE

# Size-Based Effects of Anthropogenic Pressures and Elephant Activity on Tropical Forest Carbon Stocks

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## ABSTRACT

**Aim:** To evaluate how elephant activity and anthropogenic disturbances (logging, secondary forest conversion, and proximity to villages) influence aboveground carbon (AGC) stocks in tropical forests and how their effects vary across tree size classes.

**Location:** Gabon.

**Time Period:** 2013–2023.

**Major Taxa Studied:** Gymnosperms and angiosperms.

**Methods:** Using 260 one-hectare forest plots across Gabon, we employed Bayesian modelling to quantify the effects of elephant activity and disturbances on AGC through changes in stand structure—that is, basal area (*BA*), tree height (*H*), and wood density (*WD*)—across three tree diameter (*D*) classes: small ( $10\text{ cm} \leq D < 30\text{ cm}$ ), medium ( $30\text{ cm} \leq D < 70\text{ cm}$ ) and large ( $D \geq 70\text{ cm}$ ). Environmental covariates (temperature, precipitation, and soil characteristics) were also incorporated in our models to account for broader climatic influences and to isolate disturbance effects.

**Results:** Anthropogenic disturbances, particularly secondary forest conversion and proximity to villages, were strongly associated with reductions in AGC, driven by declines in *BA*, *H*, and *WD*. By contrast, elephant activity increased *WD* in small and medium trees, suggesting long-term contributions to forest compositional shifts and carbon storage potential. Size-based analysis revealed divergent disturbance impacts across tree size classes that were not evident in whole-plot summaries.

**Main Conclusions:** Elephant activity and anthropogenic disturbances influence AGC through distinct, size-based pathways. While human activities reduce carbon stocks by altering forest structure, forest elephants enhance traits associated with carbon-dense composition. Conservation strategies that integrate faunal interactions with forest management are essential to maintaining tropical carbon stocks under ongoing environmental change.

## 1 | Introduction

Tropical forests are among the most carbon dense ecosystems on Earth, playing a critical role in climate regulation and biodiversity conservation through their ability to store vast amounts

of aboveground carbon (AGC; Poulsen et al. 2022; Berzaghi et al. 2018). However, carbon storage capacity in tropical forests is increasingly threatened by both environmental and anthropogenic disturbances (Muller-Landau et al. 2021; Heinrich et al. 2023) which alter forest structure—a key determinant of

AGC storage (Abbasi et al. 2023). Deforestation and forest degradation (e.g., land clearing, logging, and fragmentation) release roughly 1.1 gigatons of carbon per year from tropical forests (Brinck et al. 2017). Consequently, the carbon sink of tropical intact forests has declined by 31% in the 1900s and 2000s (Pan et al. 2024). Understanding how disturbances alter forest structure—and consequently AGC—can guide strategies to enhance carbon storage, promoting long-term ecological and climate resilience.

Both direct disturbances, such as, land use change and selective logging, and indirect disturbances, such as the loss of animals from a community, can reduce carbon storage in tropical forests (Jaureguiberry et al. 2022; Bello et al. 2015). Anthropogenic activity may drive the decline of both plant and animal species with high functional importance (Barlow et al. 2016), altering tree community composition and trait distributions (Ding et al. 2012). While biotic interactions are less often considered in forest carbon assessments, growing evidence highlights the role of animal communities in shaping AGC. Extensive research on African savanna elephants *Loxodonta africana* has shown their capacity to restructure vegetation, suppress tree regeneration across open ecosystems, and potentially reduce AGC (Guldmond and Van Aarde 2008; Rutina et al. 2005; O'Connor and Page 2014; Ferry et al. 2021). In contrast, forest elephants (*L. cyclotis*) remain underrepresented in ecological studies (Hyvarinen et al. 2021), despite increasing recognition of their influence on tropical forest structure and composition through selective browsing, trampling, and seed dispersal (Berzaghi et al. 2018, 2023; Poulsen et al. 2018; Beaune et al. 2013; Campos-Arceiz and Blake 2011a). Unlike their savanna counterparts, forest elephants affect closed-canopy systems by reducing stem density, maintaining canopy gaps, and suppressing regeneration (Berzaghi et al. 2018; Maicher et al. 2020). These selective effects may favor the recruitment and persistence of high wood density, carbon-rich tree species, potentially increasing long-term AGC despite immediate biomass removal (Berzaghi et al. 2023). Yet the broader implications of these impacts for forest carbon storage remain poorly understood (Guldmond and Van Aarde 2008), even as *L. cyclotis* populations have declined by over 60% from 2002 to 2012, including in protected areas (Maisels et al. 2013).

The age or size class distribution of the trees in a forest stand plays a crucial role in forest carbon dynamics (Piponiot et al. 2022). Large tropical trees, for example, are disproportionately important for carbon storage (Poulsen et al. 2022; Slik et al. 2013; Muller-Landau et al. 2021), but are also more vulnerable to both anthropogenic disturbances, such as logging, land conversion, and land management (Lindenmayer et al. 2012). However, the loss of large trees may not be offset by regeneration under current disturbance regimes, raising concerns about the long-term persistence of their carbon contributions. Such pressures have been linked to structural simplification in tropical forests—characterised by reduced size heterogeneity and compositional turnover (Hepner et al. 2025). Climate change may compound these threats by decreasing growth and survival in large trees, which are more prone to hydraulic failure during drought and more sensitive to thermal stress due to their high water demand and canopy exposure (Enquist et al. 2020; Bennett et al. 2015). Still, recent work suggests that vulnerability

is context dependent—with some large trees persisting under elephant and human disturbance due to their physical inaccessibility and resilience to damage (Kindermann et al. 2025).

While the decline of large trees is well-documented (Gora and Esquivel-Muelbert 2021), the role of smaller trees in forest productivity and carbon cycling remains less explored (Memighe et al. 2016; Johnson et al. 2017). Recent work increasingly recognizes the functional importance of smaller stems in maintaining carbon fluxes, structural resilience, and demographic turnover (Preece et al. 2012; Mugabowindekwe et al. 2023; Mensah et al. 2020; Hubau et al. 2019; Bartholomew et al. 2020). Furthermore, the impacts of disrupted plant–animal interactions—such as those caused by loss of animals from an ecosystem—on forest structure are likely to manifest over long time-scales (De Paula et al. 2018). Therefore, notwithstanding the widespread documentation of disturbance impacting large trees, the effects of disturbance may be more prominent in younger, small trees. Shifts in the composition and structure of small and medium-sized trees may signal early changes in forest function and long-term carbon trajectories (although see McLaren et al. 2024), highlighting the need for a nuanced understanding of size-based responses to disturbance.

National carbon assessments often rely on aggregated metrics that obscure tree size-dependent responses of forest carbon to disturbance. In this study, we evaluate how natural and anthropogenic disturbances influence AGC through their effects on different tree size classes. Specifically, we evaluate how disturbances influence forest stand characteristics—basal area (*BA*), tree height (*H*), and wood density (*WD*)—and AGC across three tree size classes. These stand variables jointly determine AGC as reflected in widely used allometric models (Chave et al. 2014). *BA* reflects the total cross-sectional area of trees in a stand and is sensitive to disturbance-driven changes in tree density and size class structure. *H* and *WD* determine tree volume and wood mass, with *WD* capturing variation in species' life-history strategies and carbon density (Prado-Junior et al. 2016; Castillo-Figueroa et al. 2023). We focus on megaherbivore activity and anthropogenic activities that are directly measurable, including elephant activity, forest exploitation status, and proximity to villages. Our research takes place across 260 one-hectare plots throughout Gabon, a country predominantly covered by carbon-dense, broadleaf lowland rainforests (Poulsen et al. 2022). In the absence of long-term monitoring, we adopt a space-for-time substitution approach (Pickett 1989), inferring temporal dynamics from spatial variation in forest disturbance and structure. Forests retain structural legacies of past disturbance—such as shifts in tree size distributions or trait composition—that allow reconstruction of successional and carbon outcomes across gradients of land use and faunal activity (Kindermann et al. 2025; Stringer et al. 2012).

We hypothesize that disturbances alter AGC through size-based relationships with forest stand structure variables. Overall, we expect elephant activity to increase AGC, with observable effects on smaller tree size classes which are more likely to be damaged or killed by elephants. We expect timber harvest and tree felling for house construction, honey extraction, and canoe building near villages to reduce forest AGC, with observable effects on large trees which are more likely to be selectively harvested.

We also expect lower WD in plots near villages, since high-WD species are often selectively harvested for construction and fuel, while low-WD species are retained or regenerate more rapidly (Stringer et al. 2012; Woodward et al. 2021; Gotore et al. 2023).

Specifically, we make three plot-level predictions: (i) compared to stands without elephant activity, stands with elephant activity will have higher WD due to selective browsing and trampling of low WD trees and dispersal of high WD trees, (ii) compared to primary forest, secondary and logged forest will demonstrate higher BA of small trees and lower average H due to timber extraction and regeneration, and (iii) compared to tree stands far from villages, stands closer to villages will have higher BA in small tree size classes and lower WD, reflecting forest conversion near settlements.

## 2 | Methodology

### 2.1 | Study Sites and Data

The Republic of Gabon, situated on the western coast of equatorial Africa, is one of the most forested countries in the world, with about 89% of its land area covered by forest (Boucka et al. 2021). Although Gabon hosts a diversity of ecosystems, from mangroves to savanna woodlands (Goldstein et al. 2017), most forest is categorized as lowland broadleaf tropical forest known to store high levels of AGC (Poulsen et al. 2022). The country also hosts an estimated 95,000 elephants (Laguardia et al. 2021), the largest remaining number of forest elephants in any country (Maisels et al. 2013).

We employ data on 99,349 trees from 260 1-ha tree plots from Gabon's National Resource Inventory (NRI; a semi-systematic sampling of terrestrial ecosystems (Poulsen et al. 2022)). The Gabonese National Parks Agency (*Agence Nationale des Parcs Nationaux*; ANPN) established and inventoried all plots following standard methods (Poulsen et al. 2022). Within each plot, all trees  $\geq 10$  cm diameter at breast height,  $D$  (cm), were mapped, measured, and their species identified. Field teams measured  $D$  at a height of 1.3 m from the ground or 50 cm above any buttresses, stilt roots, or deformities. They measured tree heights,  $H$  (m), with a laser hypsometer (TruPulse 200 Hypsometer, Laser Technology Inc., Centennial, CO), taking three measurements of 55 randomly selected trees per site with 10 trees from each of five  $D$  subclasses (10–20, 21–30, 31–40, 41–50,  $> 50$  cm) and the five largest trees (e.g., Sullivan et al. 2018). Voucher specimens of trees species unidentified in situ were identified at the national herbarium. In the final dataset used in this study, 60.7% trees were identified to the species level, and 84.2% to the genus level.

Field teams collected metadata to describe plots in the field, including (1) *forest type*, whether the plot was composed of primary, logged, or secondary forest; (2) *habitat type*, whether the plot was located in forest, transitional, or savanna habitat; and (3) *elephant activity*, whether or not there was sign of elephant activity. Primary forest was defined as old growth forest showing no recent obvious signs of disturbance. Logged forest consisted of sites that retained forest cover but showed evidence of selective tree extraction such as stumps of harvested trees and skid trails. Secondary forest was defined as areas recovering from

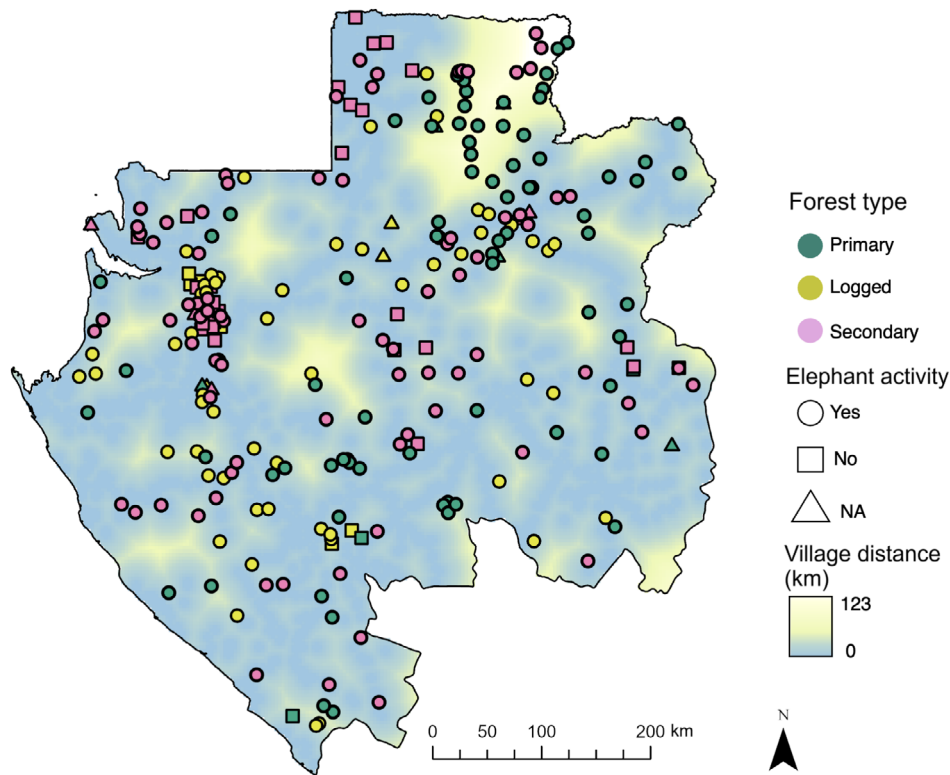
deforestation, typically from swidden agriculture. Secondary forest was identified largely by the species composition of the forest, such as the presence of tree species such as *Terminalia superba*, *Millettia laurentii*, *Triplochiton scleroxylon*, and *Musanga cecropioides*. The 260 plots in our study represent forest (at least 70% canopy cover) and transitional habitats, where the impact of forest elephants on trees is relevant, thus excluding savanna habitats (less than 10% canopy cover). Note that habitat type was based on visual estimation. For elephant activity, forest technicians assessed plots for presence of elephant dung, footprints, mud marks on trees, evidence of browsing, debarking of trees, and saplings broken in a distinctive manner (Terborgh et al. 2016). While technicians distinguished between recent and old elephant activity, we combined the two into a single category—elephant activity—because the effects of elephants on seed dispersal or browsing would take years to manifest in AGC (De Paula et al. 2018; see Figure 1).

### 2.2 | Plot-Specific Environmental Variables

We calculated or extracted environmental covariates for each plot, defining the center of each plot as its location. We measured the distance from the plot to the nearest village ( $DV$ ) (km) in R statistical software. We extracted historical climate data from the WORLDCLIM v2.1 database (Fick and Hijmans 2017) using the *raster* package (Hijmans 2023) and soil variables from Harmonised World Soil Database v1.2 (Fischer et al. 2008) using the *hwsdr* package (Hufkens 2021) in R (R Core Team 2024). We limited our examination of climatic and soil covariates to variables previously determined to influence AGC in Gabon, mean annual temperature ( $^{\circ}\text{C}$ ), annual precipitation (cm), specific soil cation exchange capacity (CEC;  $\text{cmol kg}^{-1}$ ), and soil organic carbon (OC; % weight; Table 1, Poulsen et al. 2022; Muller-Landau et al. 2021). OC was calculated as the mean of Topsoil OC and Subsoil OC, and CEC as the mean of Topsoil CEC (clay) and Subsoil CEC (clay).

### 2.3 | Plot Stand Structure and Aboveground Carbon by Tree Size Class

To investigate size-based contributions to forest structure and carbon storage, we stratified trees into three diameter classes:  $10 \text{ cm} \leq D < 30 \text{ cm}$  (small),  $30 \text{ cm} \leq D < 70 \text{ cm}$  (medium), and  $D \geq 70 \text{ cm}$  (large). These thresholds were defined based on the diameter range and distribution of trees in our study. Our dataset consisted of 75,495 small trees (76.0%), 21,122 medium trees (21.3%) and 2732 large trees (2.7%) across the 260 plots. For each size class and each plot, we calculated structural attributes—basal area, BA, mean height,  $\bar{H}$ , and mean wood density  $\bar{WD}$ . BA was calculated as the sum of cross-sectional stem areas ( $\pi D^2 / 4$ ) for all trees within a given size class and plot, and expressed in units of square meters per hectare ( $\text{m}^2 \text{ ha}^{-1}$ ). We used the best taxonomic match of WD for each individual tree (Zanne et al. 2009), substituting the plot mean  $\bar{WD}$  in the absence of WD values at species, genus, or family level. Of all inventoried trees, 42.5% were assigned WD values at the species level, 27.2% at the genus level, 12.3% at the family level, and 18% as the plot WD.  $\bar{WD}$  was calculated as the mean of individual tree WD. With height measurements



**FIGURE 1** | Map of the sampled plot network in Gabon ( $n = 260$ ). Point shape represents elephant activity: Circle = yes, square = no, triangle = NA; colour represents forest type: Teal = primary forest, yellow = logged, pink = secondary forest. Background represents distance to nearest village (km).

for 8525 trees—sampled equally across size classes—we modelled diameter-height ( $D:H$ ) relationships within each plot to predict the heights of the unmeasured trees. We used the `modelHD` function in the `BIOMASS` package (Rejou-Mechain et al. 2017), which fits five candidate models for  $D:H$  relationships in the tropics: three log–log polynomial models with order varying from 1 to 3, a three-parameter Weibull model (Feldpausch et al. 2012), and a two-parameter Michaelis–Menten model (Molto et al. 2014). Model selection was based on Residual Standard Error and average bias for the models.  $\bar{H}$  was calculated as the plot mean of individual tree heights.

We then estimated forest stand structure variables ( $BA$ ,  $\bar{H}$ , and  $\overline{WD}$ ) for each plot—overall and across size classes. We estimated plot-level aboveground biomass (AGB;  $\text{Mg ha}^{-1}$ ) using the `AGBmonteCarlo` function from the `BIOMASS` R package (Rejou-Mechain et al. 2017). This approach incorporates measurement uncertainty by propagating error in wood density and tree height through Monte Carlo simulation. AGC ( $\text{Mg ha}^{-1}$ ) was calculated by multiplying the plot AGB by the assumed carbon content, 47.1% (Thomas and Martin 2012).

## 2.4 | Bayesian Modelling of Size-Structured Forest Dynamics

We used Bayesian models to estimate the relationship between AGC, stand structure variables, environmental and disturbance predictors, and elephant activity. Our modelling framework assumes that AGC is determined by stand structure variables— $BA$ ,  $\bar{H}$ , and  $\overline{WD}$ —which in turn respond to environmental and disturbance predictors (Baraloto et al. 2011; Ali et al. 2019).

Specifically, we modelled the stand structure variables as linear combinations of predictors including temperature, precipitation, elevation, distance to village, soil characteristics, forest type, and evidence of elephant activity. To identify the most relevant predictors for each stand variable, we compared models using leave-one-out cross-validation (LOO-CV). We modelled the AGC for plot,  $p$ , as a linear combination of the predicted stand structure variables:

$$AGC_p = \alpha_0 + \alpha_1 \times \widehat{BA}_p + \alpha_2 \times \widehat{H}_p + \alpha_3 \times \widehat{WD}_p \quad (1)$$

where  $\alpha_i$  are the model coefficients, and  $\widehat{BA}$ ,  $\widehat{H}$ , and  $\widehat{WD}$  are predicted values of the respective stand structure variables, calculated using the model:

$$X_p = \beta_0 + \beta_1 \times T_p + \beta_2 \times DV_p + \beta_3 \times EA_p + \dots \quad (2)$$

Here,  $X_p$  corresponds to each stand variable ( $BA$ ,  $\bar{H}$ ,  $\overline{WD}$ ) of plot  $p$ , while  $T_p$ ,  $DV_p$  and  $EA_p$  denote temperature, distance to village and evidence of elephant activity, and  $\beta_i$  are the model coefficients. We specified noninformative priors for the model parameters to minimise prior assumptions:  $\alpha_i \sim N(0, 10^6)$ ,  $\beta_i \sim N(0, 10^6)$ . Posterior distributions were obtained using Markov chain Monte Carlo (MCMC) methods, with 500,000 iterations following a burn-in of 50,000 iterations and a thinning interval of 500 to reduce autocorrelation. Convergence was assessed using the Gelman–Rubin diagnostic and visual inspection of trace plots.

To estimate the contribution of elephant activity and anthropogenic disturbances to AGC, we decomposed their effects through the structural pathways of  $BA$ ,  $H$ , and  $WD$ . Here,

**TABLE 1** | Summary statistics for the stand structure variables and predictors used in our models. For categorical variables (forest type and elephant activity), we present the levels with the number of plots per factor level.

Type	Variable	Mean	SD	Min	Max
Stand	AGC, Mg ha <sup>-1</sup>	137.7	51.6	14.5	315.9
	Height, m	19.3	3.8	9.0	33.0
	Basal area, m <sup>2</sup> ha <sup>-1</sup>	26.4	6.6	4.5	40.2
	Wood density, g cm <sup>-3</sup>	0.6	0.1	0.4	0.7
Predictor	Mean annual temperature, °C	24.6	1.1	21.9	26.4
	Annual precipitation, cm	188.5	29.4	136.6	310.2
	Soil CEC clay, cmol kg <sup>-1</sup>	12.2	5.3	3.5	23.5
	Soil OC, % weight	0.7	0.2	0.3	1.1
	Distance to village, km	13.8	17.4	0.4	93.4
	Forest type	Primary (115), Logged (65), Secondary (80)			
	Elephant activity	Yes (212), No (35), NA (13)			

structural pathways refers to indirect effects of predictors on AGC that are mediated by changes in key stand structure variables—specifically basal area (BA), canopy height (H), and wood density (WD). This framework allows us to partition the impact of predictors across stand structure variables, clarifying the mechanisms by which disturbances and elephant activity alter carbon stocks. While structural equation modelling (SEM) also provides a formal approach for analysing such effects, we have used a Bayesian regression-based decomposition to quantify each pathway's contribution. For instance, we computed the effect of elephant activity that was mediated through each structural pathway by estimating:

$$Y_{EA,j} = \beta_{EA,j} \times \alpha_j \quad (3)$$

where  $\beta_{EA,j}$  represents the effect of elephant activity on stand structure variable  $j$  (BA,  $\bar{H}$ ,  $\overline{WD}$ ) and  $\alpha_j$  represents the contribution of that variable to AGC. We then added the effect of EA through each of the three structural pathways to compute the total effect of EA on AGC. A similar approach was used to quantify the effect of logging and secondary forest conversion and DV on AGC. We estimated the changes in BA,  $\bar{H}$ ,  $\overline{WD}$  associated with different forest disturbances and propagated these effects through the AGC model to determine their cumulative impact.

To quantify size class-specific dependent effects of anthropogenic disturbances and megaherbivore activity, we re-fit the models within each tree size class (small, medium, large), yielding class-specific drivers of stand structure and AGC. All statistical analyses were performed using R version 4.4.1 (R Core Team 2024). Bayesian modelling was conducted using the rjags package (Plummer 2023) and figures were generated using ggplot2 (Wickham 2016).

## 3 | Results

### 3.1 | Plot Characteristics

Forest plots varied in their stand structure, natural and anthropogenic disturbance regimes, and environmental conditions (Table 1). Mean plot AGC was 137.7 Mg ha<sup>-1</sup> (95% CI: 131.3, 143.6). We observed evidence of EA in 83% of plots. Average DV was 13.8 km (95% CI: 11.6, 15.9). Additionally, 44% of plots were established in primary forest, 25% in logged forest, and 31% in secondary forest. On average, primary forest plots were located 7.2 km farther from villages than secondary forests (95% CI: 0.9, 13.5) and 6.0 km farther than logged forests (95% CI: 0.1, 11.9; Figure S8). These results confirm a spatial gradient in forest disturbance, with exploited forests more frequently located near villages.

### 3.2 | Factors Associated With Increased Aboveground Carbon

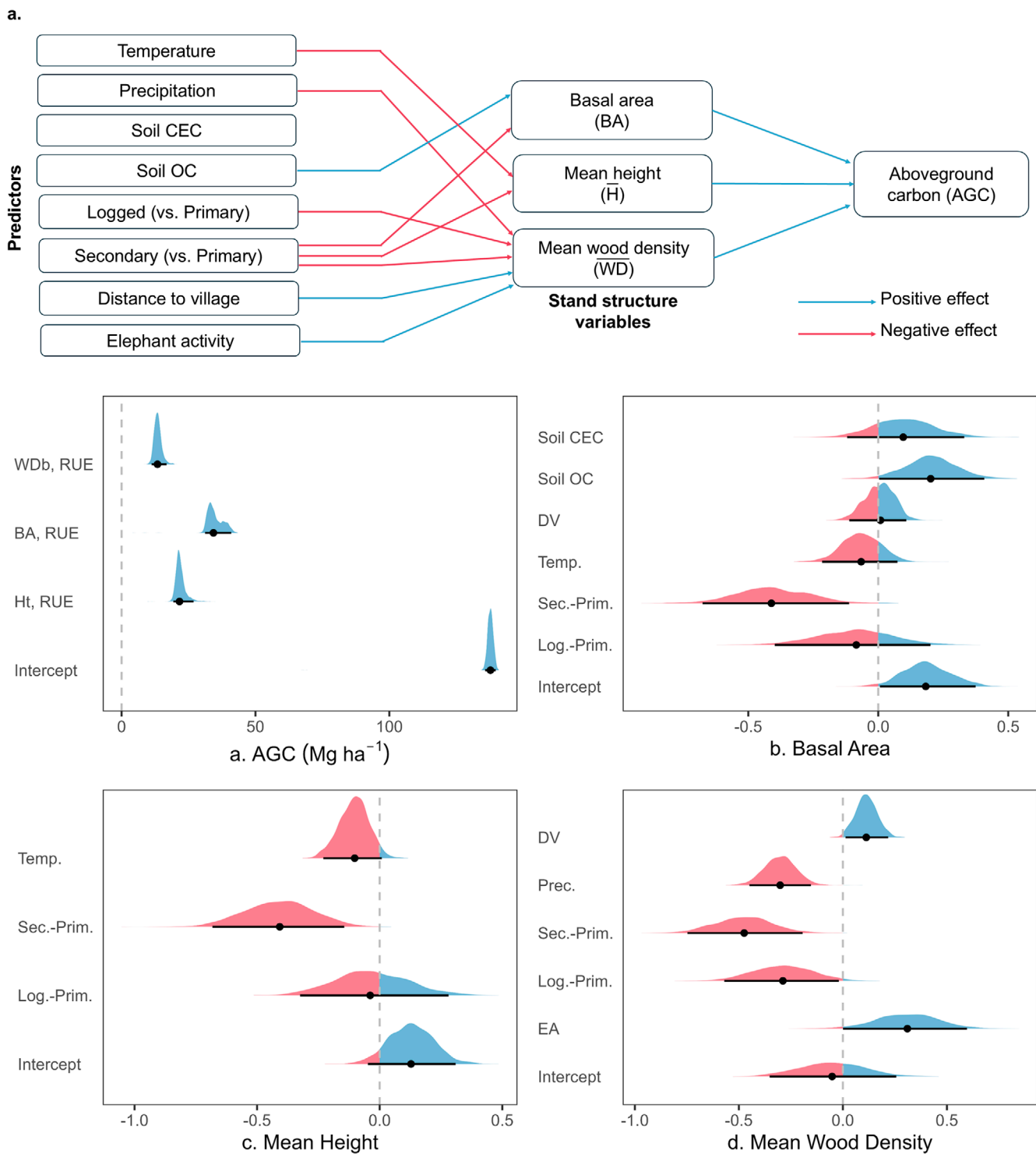
#### 3.2.1 | Stand Structure and AGC

We empirically assessed the role of environmental and disturbance factors in shaping forest stand structure and, consequently, AGC. BA,  $\bar{H}$ , and  $\overline{WD}$  were all significant structural determinants of AGC (Figure 2b). BA (95% CI = 31.2, 41.2) and  $\bar{H}$  (95% CI = 19.2, 27.7) had stronger effects on AGC than  $\overline{WD}$  (95% CI = 10.9, 16.7). An increase of one standard deviation,  $\sigma$ , in BA (7.5 m<sup>2</sup> ha<sup>-1</sup>) was associated with a 25.3% increase in AGC. Similarly, a one  $\sigma$  increase in  $\bar{H}$  (4.7 m) corresponded to a 15.8% increase in AGC, while a one  $\sigma$  increase in  $\overline{WD}$  (1.4 g cm<sup>-3</sup>) was associated with a 9.6% increase.

#### 3.2.2 | Predictor Effects on Stand Structure and AGC

To isolate the effects of anthropogenic disturbances and elephant activity on stand structure variables, we accounted for environmental characteristics such as temperature, precipitation and soil characteristics in our models. As expected, temperature was negatively associated with  $\bar{H}$  (95% CI: -0.2, 0.0), while precipitation was negatively correlated with  $\overline{WD}$  (95% CI: -0.4, -0.2). One  $\sigma$  increase in temperature (1.1°C) was associated with a 0.1 m decrease in  $\bar{H}$ , and one  $\sigma$  increase in annual precipitation (37.0 cm) was associated with a 0.3 g cm<sup>-3</sup> decrease in  $\overline{WD}$ . Soil characteristics, particularly higher CEC (95% CI: -0.1, 0.3) and OC (95% CI: 0.0, 0.4), were linked to increased BA.

Elephant activity was associated with increased  $\overline{WD}$ , which in turn contributed to higher AGC. There was no difference in BA



**FIGURE 2** | Structural and statistical relationships linking predictors to stand structure and aboveground carbon (AGC). (a) Conceptual pathway diagram showing effects of predictors on stand structure—basal area ( $BA$ ), mean height ( $\bar{H}$ ), and wood density ( $\bar{WD}$ )—and their influence on AGC. (b–e) Posterior effects of predictors on stand structure and AGC. Points show posterior means and horizontal lines show 95% credible intervals (CrI); vertical dashed lines denote zero. Blue shading indicates positive effects and red shading negative effects. All continuous predictors were standardised as z-scores, so coefficients are in units of one standard deviation ( $\sigma$ ). For categorical contrasts, Secondary–Primary (Sec.–Prim.) and Logged–Primary (Log.–Prim.), positive values indicate higher expected responses than primary forest. (b) Effects of  $BA$  ( $\text{m}^2 \text{ha}^{-1}$ ),  $\bar{H}$  (m), and  $\bar{WD}$  ( $\text{g cm}^{-3}$ ) on AGC ( $\text{Mg C ha}^{-1}$ ). (c–e) Effects of predictors—annual mean temperature (Temp.), annual precipitation (Prec.), soil organic carbon (Soil OC), soil cation exchange capacity (Soil CEC), distance to village (DV), forest type, and elephant activity (EA)—on stand structure. Intervals overlapping zero indicate weak or no effect at 95% CrI.

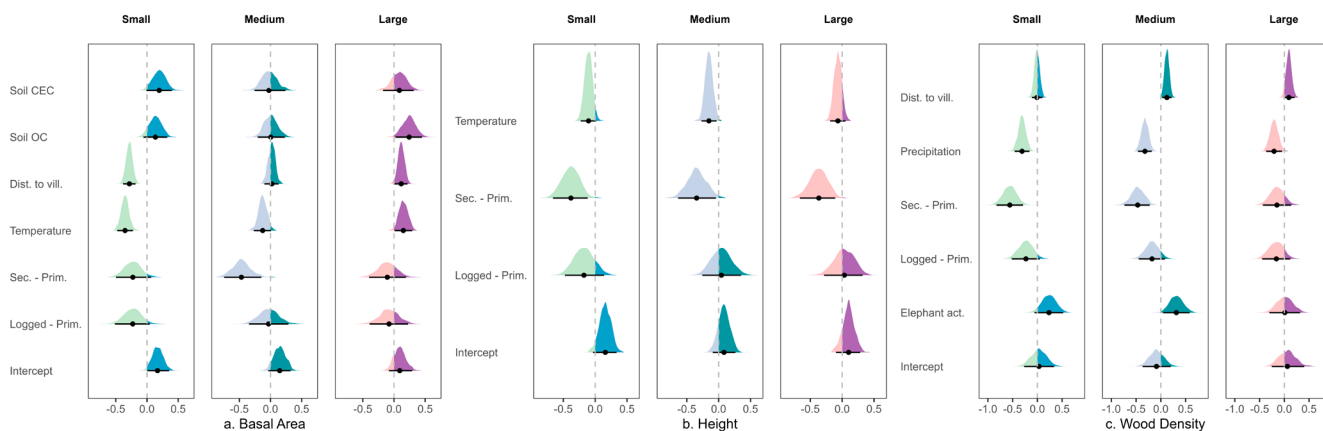
and  $\bar{H}$  of plots with and without evidence of *EA*. Plots with evidence of *EA* had  $0.3 \text{ g cm}^{-3}$  higher  $\bar{WD}$  (95% CI: 0.0,  $0.6 \text{ g cm}^{-3}$ ) than plots with no evidence of elephant activity, contributing to an average increase of  $0.3 \text{ Mg ha}^{-1}$  in AGC (95% CI: 0.0, 0.7). These effects were comparable in magnitude to those of other anthropogenic and environmental variables influencing plot  $\bar{WD}$  (Figure 2e).

The impact of anthropogenic disturbance on AGC was more pronounced. Logged forests exhibited lower AGC than primary forest mainly due to lower  $\bar{WD}$  (95% CI:  $-0.6, 0.0$ ), manifesting in  $0.3 \text{ Mg ha}^{-1}$  (95% CI:  $-0.4, 0.0$ ) less AGC. The AGC difference between secondary and primary forests was greater than that between logged and primary forests, with losses occurring across all three structural pathways. Reduced *BA* contributed a median of  $-91.7 \text{ Mg ha}^{-1}$  (95% CI:  $-140.1, -28.7$ ), lower  $\bar{H}$  contributed  $-34.3 \text{ Mg ha}^{-1}$  (95% CI:  $-54.7, -15.3$ ), and reduced  $\bar{WD}$  contributed  $-0.43 \text{ Mg ha}^{-1}$  (95% CI:  $-0.6, -0.2$ ). These cumulative reductions in stand characteristics resulted in an average of  $35.7 \text{ Mg ha}^{-1}$

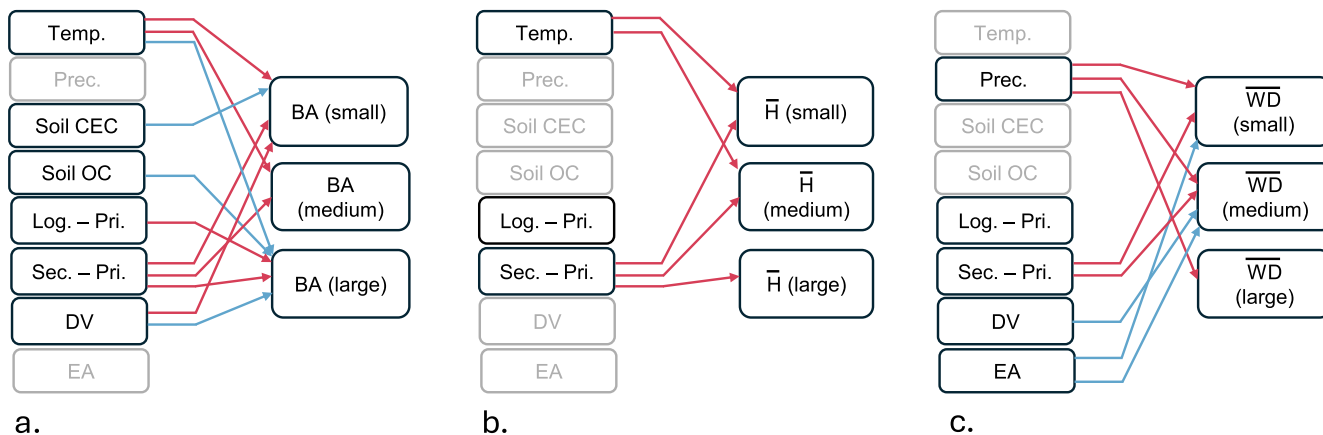
less AGC in secondary forests compared to primary forests (95% CI:  $-49.8, -11.7$ ). The effect of *DV* on AGC operated primarily through the  $\bar{WD}$  pathway. With every 1 km increase in *DV*,  $\bar{WD}$  increased by  $0.1 \text{ g cm}^{-3}$  (95% CI: 0.0, 0.2), contributing to an average of  $0.1 \text{ Mg ha}^{-1}$  higher AGC per km (95% CI: 0.0, 0.2).

### 3.3 | Size-Based Effects of Predictors on Forest Stand Structure

Size-specific responses to environmental predictors, disturbance factors, and elephant activity revealed distinct patterns across tree classes. While total *BA* showed no relationship with temperature, small-tree *BA* was negatively associated with higher temperature (95% CI:  $-0.5, -0.2$ ), and the *BA* of large trees had a positive relationship with temperature (95% CI: 0.0, 0.3). Small-tree *BA* also increased with soil CEC (95% CI: 0.0, 0.4); while soil OC only had a positive effect for the large tree class (95% CI: 0.0, 0.5; Figures 3a and 4a).  $\bar{H}$  tended



**FIGURE 3** | Posterior effects of predictors on (a) basal area ( $\text{m}^2 \text{ ha}^{-1}$ ), (b) mean height (m), and (c) mean wood density ( $\text{g cm}^{-3}$ ) for small, medium, and large trees. Points show posterior means and horizontal lines show 95% credible intervals (CrI); vertical dashed lines denote zero. Blue shading indicates positive effects and red shading negative effects. The predictors include annual mean temperature (Temp.), annual precipitation (Prec.), soil organic carbon (Soil OC), soil cation exchange capacity (Soil CEC), distance to village (*DV*), forest type, and elephant activity (*EA*)—on stand structure. All continuous predictors were standardised as z-scores, so coefficients are in units of one standard deviation ( $\sigma$ ). For categorical contrasts, Secondary–Primary (Sec.–Prim.) and Logged–Primary (Log.–Prim.), positive values indicate higher expected responses than primary forest. Intervals overlapping zero indicate weak or no effect at 95% CrI.



**FIGURE 4** | Conceptual pathway diagram showing effects of predictors on stand structure: (a) basal area (*BA*), (b) mean height ( $\bar{H}$ ), and (c) wood density ( $\bar{WD}$ )—across size classes. Arrows are coloured by effect direction: Blue for positive and red for negative effects. Only relationships with 95% credible intervals that exclude zero are shown; predictors not included in the corresponding model are faded for clarity.

to be higher in plots with lower temperature (Figure 2), but there was no effect of temperature on  $\bar{H}$  in the large trees size class (Figures 3b and 4b).

Wood density ( $\overline{WD}$ ) exhibited consistent negative associations with precipitation across all size classes. However, the effect of elephant activity on  $\overline{WD}$  was dependent on size class.  $\overline{WD}$  of small and medium trees, but not large trees, increased in plots with observed elephant activity (Figures 3c and 4c).

Proximity to villages also had divergent effects by size: small-tree BA increased closer to villages ( $0.02 \text{ m}^2 \text{ ha}^{-1}$  per km; 95% CI: 0.01, 0.03), while large-tree BA increased with distance (95% CI: 0.0, 0.1). Overall  $\overline{WD}$  was higher farther from villages, but this effect was driven by medium and large trees (Figures 3c and 4c). There was no difference in BA of large trees between secondary and primary forests.

Forest type also showed size-based variation. Both logged and secondary forest plots had lower  $\overline{WD}$  than primary forest plots (Figure 2e). While  $\overline{WD}$  of small and medium trees was lower in secondary forest plots than primary forest plots by  $0.5 \text{ g cm}^{-3}$ , there was no significant effect for large trees at the 95% credible interval (Figures 3c and 4c). Small trees in logged forests had lower  $\overline{WD}$  than small trees in primary forest plots, but medium and large trees did not.

## 4 | Discussion

Our findings demonstrate that anthropogenic disturbances and elephant activity affect forest carbon stocks through distinct, size-specific structural pathways. Anthropogenic disturbances—secondary forest conversion and proximity to villages—were associated with substantial reductions in AGC, mediated by declines in basal area (BA), height ( $\bar{H}$ ), and wood density ( $\overline{WD}$ ). By contrast, elephant activity can indirectly enhance carbon storage by increasing  $\overline{WD}$  in small and medium trees, consistent with selective feeding and dispersal that aggregate high-WD species in the community. By disaggregating AGC by tree size class, we reveal that these impacts are not uniformly distributed across trees of different diameters: while human activities disproportionately reduce AGC in larger trees, elephants likely enhance the long-term carbon storage potential of recruiting cohorts (i.e., small–medium size classes within forest stands). These results underscore the importance of considering size-based forest dynamics and biotic interactions in carbon assessments.

### 4.1 | Anthropogenic Disturbance Effects

Anthropogenic disturbances lowered AGC by altering structural characteristics of forest stands. Consistent with (Poulsen et al. 2022), secondary forests exhibited the lowest AGC, reflecting their early successional status following deforestation from swidden agriculture (Figure S1). These stands have lost many large, high-carbon trees and are dominated by fast-growing, low-WD species (Poulsen et al. 2022; Barlow et al. 2016), contributing to low AGC (Figures S3–S6).

Size-based analyses revealed important heterogeneity in forest response and clarified several patterns masked in whole-plot summaries. For example, using a smaller sample of 104 forest plots, Poulsen et al. (2022) found that logged forests in Gabon retained high overall AGC—comparable to or even exceeding that of primary forests. Our size-based decomposition, however, revealed a more nuanced structural response. Specifically, we find that logging caused declines in  $\overline{WD}$  among small trees, suggesting long-term compositional shifts toward fast-growing, low-density species. These changes may not manifest in total AGC immediately, but compromise long-term carbon storage due to the higher mortality and reduced residence time of low-WD trees (Gora and Esquivel-Muelbert 2021). Even if selective logging targets a small number of large stems, collateral damage of logging (i.e., through felled trees, soil disturbance, and edge effects) may disproportionately affect smaller size classes. The lack of an observed effect of logging on large-tree basal area might be because they represent legacy individuals established prior to disturbance or reflect variation in logging intensity and time since logging, which were not measured in this study. Our results suggest that failing to assess effects of logging on different size classes masks subtle but potentially important structural changes, with long-term consequences for AGC. These findings are consistent with previous work showing that logging alters forest structure through both removal and regeneration (Keith et al. 2014; Cazzolla Gatti et al. 2015).

Similarly, proximity to villages was associated with decreased AGC: plots closer to villages had more small trees and fewer large trees, consistent with selective harvesting of larger individuals.  $\overline{WD}$  was associated with increased  $DV$ , particularly among medium and large trees. This pattern suggests that human disturbance near settlements favours low-WD species, either due to selective extraction of high-WD trees or greater recruitment of fast-growing pioneer species or both (Ding et al. 2012). These structural shifts reflect not only direct extraction pressures but also the spatial coupling between forest type and settlement. Logged and secondary forests tended to be located closer to villages than primary forests (Figure S8), likely reflecting a feedback loop in which forest degradation and settlement expansion co-occur. As a result,  $DV$  is not an independent driver, but a composite indicator of chronic disturbance—capturing agricultural encroachment and selective logging. Although our models included both  $DV$  and forest type, future work should disentangle these drivers to clarify causal pathways. Nevertheless, our results highlight how forest degradation unfolds not only through biomass loss, but through compositional and structural change—marked by the loss of large carbon-dense trees and their replacement with smaller, lower-carbon individuals (Lewis et al. 2013).

### 4.2 | Effects of Elephant Activity

Elephant activity likely indirectly increased AGC by facilitating the dominance of high-WD species (Figure 2). This aligns with previous studies showing that forest elephants damage seedlings and saplings and preferentially browse on species with low-WD (Terborgh et al. 2016; Rosin et al. 2020), suppressing

their regeneration, while dispersing seeds of large-seeded, high-*WD* species (Berzaghi et al. 2023; Blake et al. 2009; Poulsen et al. 2021; Campos-Arceiz and Blake 2011b). These filtering effects may promote the persistence and recruitment of high-*WD* trees, enhancing long-term carbon storage. *WD* is associated with structural strength, lower mortality, and resistance to decay—traits which stabilise forest carbon stocks.

Given slow vegetation dynamics, recent selective browsing and seed dispersal by elephants may not affect old, large trees (Berzaghi et al. 2018). Consistent with this, we found positive associations between *EA* and  $\overline{WD}$  only among small and medium trees (Figure 3). Size-based *EA* effects reflect the longer time-scales required for faunal interactions to manifest at higher canopy strata. Older individuals, particularly large trees, may persist both because they are physically resistant to elephant damage, and as legacies of past ecological conditions, including historical elephant abundance (Lindenmayer et al. 2012; Kindermann et al. 2025; Moncrieff et al. 2011). Elephant poaching in Gabon was most severe in the early 2000s (Maisels et al. 2013; Poulsen et al. 2017), so the structural consequences of reduced elephant activity might not yet be apparent. Overall, our results suggest that forest elephants contribute to long-term carbon resilience by promoting carbon-dense composition through size- and trait-based filtering.

#### 4.3 | Predictors Interact to Impact Forest Carbon

Anthropogenic and natural disturbances likely interact to influence forest structure and AGC. Secondary forests, which tend to have a higher abundance of fast-growing, low-*WD* species (Maicher et al. 2020), could experience greater elephant browsing pressure than primary forests. In secondary forests, elephants may consume and remove a larger proportion of vegetation, potentially accelerating shifts in species composition and forest succession. Elephants may also visit secondary forests due to fruit/crop availability and logged forests as they provide access to human-dominated areas through logging roads (Mbamy et al. 2024). Elephant effects on carbon storage could therefore be stronger in secondary than primary forests. However, compared to primary forests, secondary forests in Gabon tend to have fewer trees with fruits that are consumed and dispersed by frugivores such as elephants (DeSisto et al. 2026). Other factors, including direct anthropogenic effects, may therefore be stronger drivers of elephant activity in secondary forests. For example, poaching can drive declines in elephant populations and alter their spatial distribution, leading to sub-regional heterogeneity in activity levels (Maisels et al. 2013; Poulsen et al. 2017). Human-driven defaunation of frugivores has been widely associated with decreased carbon stocks in tropical forests (Bello et al. 2015; Chanthorn et al. 2019). Climate change may also shape biotic disturbance pathways. In Gabon, increased temperatures and reduced precipitation have reduced tree fruit production, contributing to poor body condition among forest elephants, and likely altering their foraging behaviour and spatial use (Bush et al. 2020). As a result, climate stress and megaherbivore activity may not act independently, but interactively—potentially compounding impacts on forest composition and regeneration.

#### 4.4 | Limitations

Our study substitutes space for time to investigate how anthropogenic disturbances and megaherbivore activity alter patterns of forest structure, but temporal studies are needed to fully capture long-term effects. For example, the observed patterns of elephant activity may not reflect historical elephant ranges and movement patterns that have shaped current forest structure. The identified differences in forest structure could be caused by elephants or, conversely, elephants could prefer forests with higher *WD*. Another limitation of our study is its focus on adult trees; elephant browsing likely has the strongest effects on understory vegetation. To definitively quantify the effect of disturbance on forest structure and AGC, we need large-scale experiments in which vegetation dynamics are monitored over time in forest stands protected and unprotected from disturbances. Additionally, we consider binary presence or absence of elephants, but results likely differ depending on variation in elephant population densities. While valuable elephant density estimates exist for some sites across Gabon (Laguardia et al. 2021), campaigns to collect additional elephant density data across the country will enable future investigation of the relationship between elephant density and forest carbon. Further, while the locations of the plots used in our analysis are widespread across Gabon and part of a semi-systematic sampling design, we cannot rule out the presence of some sampling bias in our dataset. Lastly, although we detected significant effects of logging, secondary forest conversion, and proximity to settlements, we do not explicitly model the underlying socio-economic drivers of these disturbances. Future work integrating remote sensing with socio-economic data could reveal how land-use policies, local livelihoods, and infrastructure development shape forest carbon outcomes and ecological resilience.

#### 5 | Conclusions

Forest carbon stocks are shaped by both human pressures and natural disturbances, each operating through size-dependent structural pathways. In Gabon, we find that anthropogenic activities—such as logging, forest conversion, and proximity to human settlements—were associated with reduced forest carbon, primarily through reductions in *WD* and *BA* among small and medium trees rather than direct loss of large trees. In parallel, declining forest elephant populations threaten the ecological processes that sustain carbon-dense forests over time. Our study reveals the size-dependent pathways linking soil, climate, anthropogenic pressures, and megaherbivore activity to forest stand structure and, ultimately, AGC. Effective carbon management must move beyond simple biomass metrics to consider how ecological interactions and size-specific changes in forest composition and structure shape carbon outcomes over space and time. In Central Africa and beyond, we advocate for conservation and research approaches that jointly address defaunation, forest degradation, and forest structure. Protecting ecological processes—alongside preventing deforestation—will be essential to maintaining carbon stocks and biodiversity in the world's tropical forests.

## Author Contributions

Conceptualization, A.G., C.D., and J.R.P.; Data Collection, D.M.I., A.N., and J.R.P.; Formal Analysis, A.G., C.D. and J.R.P.; Data Curation, A.G., C.D., V.M., H.M., and J.R.P.; Writing – Original Draft, A.G., C.D., J.R.P.; Writing – Revising and Writing, all authors; Visualisation, A.G. and C.D.; Supervision, J.R.P.

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The authors have nothing to report.

## Conflicts of Interest

The authors declare no conflicts of interest.

## Data Availability Statement

Restrictions apply to the availability of data, which were used under licence for this study. Raw data are available from the corresponding author with the permission of Le Ministère des Eaux, de la Forest, de la Mer, de l'Environnement, Gabon. To allow the replication of our analysis, our manuscript is accompanied with a data repository. We provide the dataset used in our analysis with basal area, wood density, tree heights and aboveground carbon aggregated at plot level. In order to respect the confidentiality of the data, we have removed the plot coordinates. We have also provided the climatic and soil variables extracted for the plots with original plot identifiers. The original plot identifiers can be linked to the plot coordinates if access to the raw data is granted. The aggregated plot-level data and code are openly available in Zenodo at <https://doi.org/10.5281/zenodo.15660360>.

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### Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** geb70207-sup-0001-AppendixS1.pdf.