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RESEARCH PAPERS

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Old growth Afrotropical forests critical for maintaining forest carbon

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Abstract

Aim: Large trees [≥ 70 cm diameter at breast height (DBH)] contribute disproportionately to aboveground carbon stock (AGC) across the tropics but may be vulnerable to changing climate and human activities. Here we determine the distribution, drivers and threats to large trees and high carbon forest.

Location: Central Africa.

Time period: Current.

Major taxa studied: Trees.

Methods: Using Gabon's new National Resource Inventory of 104 field sites, AGC was calculated from 67,466 trees from 578 species and 97 genera. Power and Michaelis–Menten models assessed the contribution of large trees to AGC. Environmental and anthropogenic drivers of AGC, large trees, and stand variables were modelled using Akaike's information criterion (AIC) weights to calculate average regression coefficients for all possible models.

Results: Mean AGC for trees ≥ 10 cm DBH in Gabonese forestlands was 141.7 Mg C/ha, with averages of 166.6, 171.3 and 96.6 Mg C/ha in old growth, concession and secondary forest. High carbon forests occurred where large trees are most abundant: 31% of AGC was stored in large trees (2.3% of all stems). Human activities largely drove variation in AGC and large trees, but climate and edaphic conditions also determined stand variables (basal area, tree height, wood density, stem density). AGC and large trees increased with distance from human settlements; AGC was 40% lower in secondary than primary and concession forests and 33% higher in protected than non-managed areas.

Main conclusions: AGC and large trees were negatively associated with human activities, highlighting the importance of forest management. Redefining large trees as ≥ 50 cm DBH (4.3% more stems) would account for 20% more AGC. This study demonstrates that protecting relatively undisturbed forests can be disproportionately effective in conserving carbon and suggests that including sustainable forestry

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in programs like reduced emissions for deforestation and forest degradation could maintain carbon dense forests in logging concessions that are a large proportion of remaining Central African forests.

KEYWORDS

aboveground biomass, carbon, Central Africa, climate change, Gabon, large trees, tree height, tropical forest, wood density

1 | INTRODUCTION

Large trees dominate intact tropical ecosystems, bolstering global biodiversity and carbon storage (Lewis, Edwards, & Galbraith, 2015; Sullivan et al., 2017). Rising above the canopy, they modulate the understorey microclimate and provide habitat and resources for animals, invertebrates, and plants like epiphytes and lianas (Poulsen et al., 2017), while storing a large fraction of forest carbon (Bastin et al., 2015; Stegen et al., 2011; ter Steege et al., 2013). The world's tallest and densest forests are temperate rain forests, but tropical forests are the most widespread, accounting for two-thirds of all terrestrial biomass (Pan, Birdsey, Phillips, & Jackson, 2013). Large trees, often defined as ≥ 70 cm diameter at breast height (DBH), comprise on average 25–45% of aboveground carbon stock (AGC) in tropical regions while representing a small fraction of stems (Slik et al., 2013). Palaeotropical forests typically have larger trees than Neotropical forests, with African trees tending to have larger diameters and Asian trees tending to be taller than South American trees (Banin et al., 2012); but hotspots of biomass occur regionally, including the Guyana shield, intact forests of Borneo and Papua New Guinea, and central and western parts of the Congo Basin (Lewis et al., 2013; Slik et al., 2013; Xu et al., 2017). Given the importance of large trees for forest structure and functioning, and their sensitivity to disturbance, a primary goal of forest ecology is to identify the distribution, drivers and threats to the world's large forests (Lindenmayer, Laurance, & Franklin, 2012).

The influence of large trees on forest structure suggests that variables that affect the abundance of large stems could strongly influence ecosystem function and carbon storage. Multiple studies demonstrate that environmental variables, such as climate and soils, drive variation in tropical AGC, and to a lesser extent numbers of large trees, but their importance varies across regions and contexts. Forests in Africa, but not other regions, show a negative correlation between temperature and AGC (Lewis et al., 2013; Slik et al., 2013; Xu et al., 2017). The importance of annual precipitation and rainfall seasonality for AGC has been highlighted by several studies (Chave, Muller-Landau, et al., 2014; Malhi et al., 2006; Slik et al., 2010), including for African forests that often have lower average rainfall than other regions (Lewis et al., 2013; Slik et al., 2013), although precipitation in the wettest 3 months may be negatively associated with AGC above a certain point (Lewis et al., 2013; Xu et al., 2017). The positive effect of annual precipitation is consistent with reports that large trees are sensitive to water stress (Slik, 2004; Van Nieuwstadt & Sheil, 2005) due to a loss of hydraulic conductivity as the water deficit increases (Stegen et al., 2011). Using tree height as an indicator of large trees and AGC, a comparison of all humid tropical forests found that dry season precipitation and maximum annual water deficit are important determinants of height, but surface topography and topsoil texture also correlate strongly with the distribution of large trees (Yang et al., 2016). Generally, AGC increases with soil fertility in tropical forests (Quesada et al., 2012), although studies have found weak effects of soils, which have been partially attributed to the poor data quality of global soil databases (Lewis et al., 2013; Slik et al., 2013).

Rarely tested at large scales (regionally or nationally) in the humid tropics (Berenguer et al., 2014), human activities can have strong effects on large trees and AGC. Deforestation, usually caused by the conversion of forest to cropland and pasture, reduces the extent and biomass of the entire forest (Gibbs et al., 2010). Other forms of natural and anthropogenic disturbance disproportionately affect large trees. Logging is widespread across the tropics, occurring in 26% of Central Africa's remaining forests and up to 74% of some countries (Bayol et al., 2012). Timber operations harvest the largest most valuable trees, including many Central African biomass hyperdominants (Bastin et al., 2015). Land clearing for settlement and subsistence agriculture follows on the heels of logging, resulting in the intentional removal of large trees (Lindenmayer et al., 2012). While logging and subsistence agriculture clearly reduce carbon stocks (Medjibe, Putz, & Romero, 2013), their effects on large trees and AGC remain mostly unstudied at the landscape scale.

Here we report on one of the first modern forest inventories of a tropical forested country – the Gabonese Republic in Central Africa (Figure 1). Gabon is the second most forested country in the world, with 87% forest cover, a deforestation rate near zero, and 67% of its forests in timber concessions (Forêt Ressources Management, 2018). For economic development the government seeks increased investment in industrial agriculture and logging, while committing to reduce greenhouse gas emissions and preserve ecosystems and biodiversity. We use Gabon's national resource inventory (NRI) to characterize forest structure, quantify carbon stocks and identify areas of high carbon as priorities for conservation. We investigate: (a) the carbon density of forests across Gabon; (b) the contribution of large trees to AGC; and (c) the relative effects of environmental and

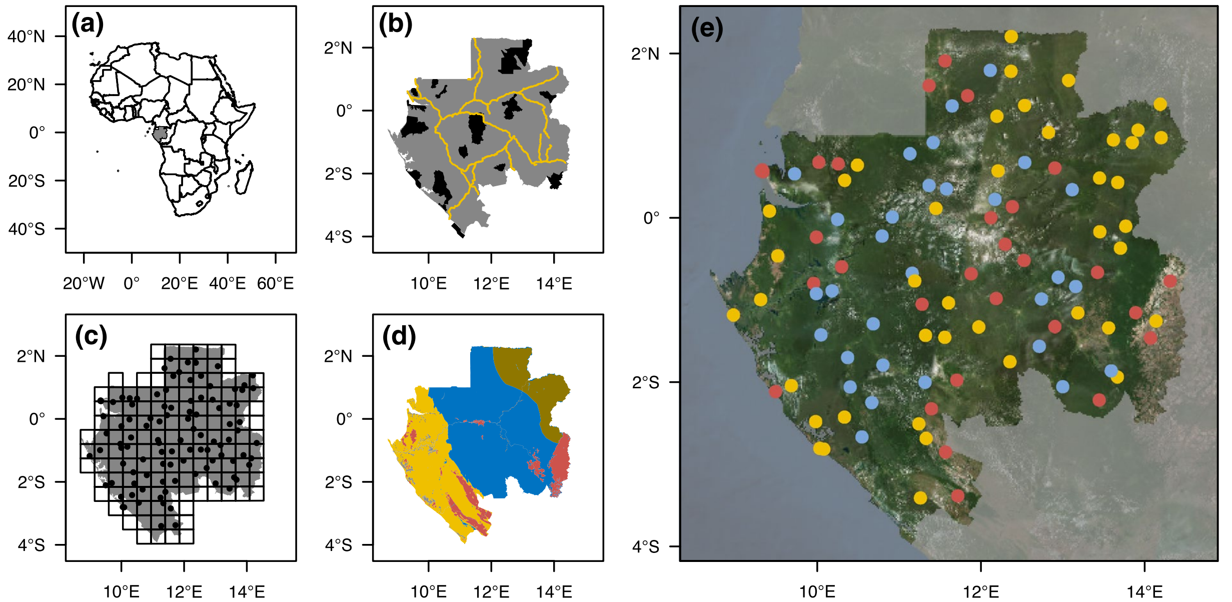

FIGURE 1 (a) Map of Gabon (grey polygon) within Africa. (b) Map of national roads (yellow lines) and national parks and presidential reserves (black polygons). (c) Map of Gabon overlain with a 50 km × 50 km grid, showing the systematic, random location of forest plots (black symbols). (d) Map of Gabon with major ecosystems (yellow = coastal forest; blue = central forest; brown = north-eastern forest; red = savanna). (e) Location of plot sites, coloured by disturbance type (yellow = primary forest; blue = concession forest; red = secondary forest)

anthropogenic variables on forest structure, with a focus on AGC and large trees.

2 | MATERIALS AND METHODS

Located on the western coast of equatorial Africa, Gabon is part of the Congo Basin forest, although its waters drain into the Ogooué Basin (Figure 1a). A strong precipitation gradient extends from the northern coast (3,200 mm annually) to the interior (1,300 mm) of the country. Land cover is dominated by rain forest (76%), followed by cropland (10%), grassland and savanna (7%), and flooded broadleaf forest (5%) (World Resources Institute, 2017). Four ecosystem types dominate (Figure 1d). *Coastal evergreen rainforest* in the west (0–300 m elevation) includes a mixture of terra firma, mangroves, flooded forest, and *Raphia* swamps. Coastal forests have been heavily harvested and reduced to secondary forest, with exceptions such as the Mondah and Mayumba forests and the Gamba Complex. Coastal forest transitions into low elevation *central forest*, where the sedimentary basin meets older geological types giving way to the Chaillu mountain chain – a block of sedimentary rock with a maximum elevation of 1,020 m. Central forest (300–1,000 m), often dominated by the long-lived pioneer timber species, *Aucoumea klaineana* (okoumé), covers most of central Gabon and is indicative of disturbance in the last 150 years (Born et al., 2011). The *north-eastern lowland forest* (300–1,000 m) extends east of the *A. klaineana* distribution. This semi-deciduous forest is characterized by a predominance of tree species such as *Terminalia superba* (limba), *Millettia laurentii* (wenge) and *Celtis* spp. The rest of the county is covered by *savanna* that is often interrupted by forest–savanna mosaic, with continuous savanna in the south-west and south-east.

Gabon's timber concessions include 14.7 million ha of forest, with 74% of the area under management plans and 16% certified for sustainable management (Forêt Ressources Management, 2018). Average harvest intensity is low, but varies with logging technique and history (Medjibe et al., 2013). In contrast, commercial agriculture is currently very limited in scope (Austin et al., 2017; Tyukavina et al., 2018). Secondary forests recovering from slash-and-burn agriculture or other forms of deforestation are located near towns and villages and along roads, particularly the paved national roads connecting regional capitals. Several types of formal land management exist in Gabon: `protected` refers to areas under strictest management, including national parks, presidential reserves and arboretums (15 parks, 3.3. million ha); 'reserve' designates Ramsar sites with lower levels of protection than national parks (6 sites, 2,215,954 ha); 'buffer' signifies 5-km buffer zones around national parks'; 'hunting' signifies designated hunting reserves (5 hunting reserves, 497,500 ha); and 'none' indicates no formal management.

2.1 | Inventory design, data collection, and estimation of AGC

Gabon's NRI is based on a semi-systematic sample of forestlands. We divided the country into one hundred and thirty-five 50 km × 50 km cells and randomly located an inventory site within each cell using the reverse randomized quadrant-recursive raster (RRQRR) algorithm in GIS (Figure 1c). The algorithm uses a spatially balanced design for sampling that maximizes the spatial independence among sample locations (Theobald et al., 2007). Stratified sampling is often more efficient than random sampling, but we lacked rigorous, a priori data for the selection of strata. Our semi-systematic approach does not depend on external data and samples can be added without disturbing the statistical integrity of the design.

Each inventory site consisted of one 1-ha (100 m × 100 m) plot and four 0.16-ha (40 m × 40 m) satellite plots spaced 250 m apart, with two satellite plots located to the east and west of the permanent plot. We employed this winged design to evaluate local variation in forest structure. Of 135 original sampling sites, we discarded 16 located in the ocean and did not sample 15 in savanna unlikely to have trees ≥ 10 cm DBH. At 16 sites, fewer than 4 satellite plots were established because they were in water bodies, open grassland, or the work was cut short for logistical reasons (e.g. sick field technician). Between 2012 and 2014 four field teams of five trained technicians inventoried the trees using standard protocols for plot establishment and measurement. Each tree ≥ 10 cm DBH was mapped, measured and identified. Measured trees in permanent plots, but not satellite plots, were marked with aluminium tags. Field teams measured tree diameters, *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 with a laser hypsometer (TruPulse 200 Hypsometer, Laser Technology, Inc., Centennial, CO), taking 3 measurements of 55 randomly selected trees per site with 10 trees from each of 5 DBH subclasses (10–20, 21–30, 31–40, 41–50, > 50 cm) and the five largest trees (e.g. Sullivan et al., 2018). Samples of unidentified trees were taken to the National Herbarium for identification. Of 67,466 trees, 80.9% were identified to species and 99.4% to genus; of 1,572 large trees, 92.1% were identified to species and 99.6% to genus.

We estimate AGC from tree measurements in 104 forest sites by converting tree diameters, *D*, to aboveground biomass (AGB) using allometric equations for moist forests (1,500–3,500 mm precipitation/year) that incorporate terms for wood density, ρ, and tree height, *H* (Supporting Information Appendix S1). In the case of multi-stemmed trees, we applied the model to each stem. These equations include the pantropical model (Chave, Réjou-Méchain, et al., 2014),

$$\mathrm{AGB}_{\mathrm{est}} = 0.0673 \times \left(\rho D^2 H\right)^{0.976} \tag{1}$$

and a Gabon-specific model (Ngomanda et al., 2014),

$$\mathrm{AGB}_{\mathrm{est}} = \exp\left(-2.5680 + 0.9517\ \ln D^2 \times H\ + 1.1891(\ln(\rho))\right). \tag{2}$$

Other allometric equations exist, but we focus on the pantropical model to facilitate comparison with other studies and because it is derived from many trees and species including 1,429 harvested trees from Africa. The Gabon-specific allometric model is based on 10 species (101 trees) from a single site in north-eastern Gabon (Ngomanda et al., 2014). Our study includes many families and species from across Gabon, making the pantropical equation more appropriate.

We used the best taxonomic match of wood density for each stem (Zanne et al., 2009), substituting the mean wood density of the plot in the absence of species, genus or family level information. Of all inventoried trees, 41.9% had wood density values at the species level, and 24.1, 12.2 and 21.9% matched at the genus, family and plot levels, respectively. Of large trees, 63.7% had wood density values at the species level, and 20.8, 4.5 and 11.0% matched at the genus, family and plot levels, respectively. With height measurements for 7,036 trees, we built a series of diameter-height (D:H) regression models (linear, quadratic and polynomial) for each plot to predict the heights of the unmeasured trees (Beirne et al., 2019). For two plots without height measurements, we applied a national D:H model fitted to all the NRI data:

$$\hat{H} = 43.98 - 35.38 \times e^{-0.019D}. \tag{3}$$

AGC was calculated by summing the AGB of all the stems in a plot, dividing by plot area and multiplying by the assumed carbon content, 47.1%, of AGB (Thomas & Martin, 2012). Throughout, we present the area-weighted carbon density for each site (1-ha plot and satellite plots) as Mg C/ha.

2.1.1 | Importance of large trees to AGC

To assess the contribution of large trees to AGC, we applied Bastin et al.'s (2015) model to estimate plot-level AGB, $\mathrm{A\hat{G}B}_{\mathrm{TOT}}$, from the AGB of the largest trees, X:

$$\mathrm{A\hat{G}B}_{\mathrm{TOT}} = \alpha_i \times X^{\beta_i}. \tag{4}$$

The power model coefficient, α, is predicted from the number, *i*, of the largest trees using a power regression model with no intercept:

$$\alpha_i = a_1 x_i^{b_1}. \tag{5}$$

The exponent, β, is predicted from the number, *i*, of the largest trees using a Weibull model:

$$\beta_i = a_2 - b_2 e^{\left(c_2 * x_i^{d_2}\right)}. \tag{6}$$

We fit the models to the entire dataset and each disturbance type separately as forests might accumulate AGC from large trees at different rates (Supporting Information Appendix S2). To test whether the contribution of large trees differs among disturbance types, we modelled the relationship between the proportion of explained variation and cumulative number of trees with the Michaelis–Menten function:

$$\hat{R}^2 = \frac{f + (x_i + j)}{g\,(x_i + j)} \tag{7}$$

where *f*, *g*, and *j* are fitted parameters. We chose the asymptotic Michaelis–Menten (MONOD) growth function for its simplicity and use in assessments of biomass growth (McMahon, Parker, & Miller, 2010; Zhu, Zhang, Niu, Chu, & Luo, 2018). We fitted a single general model to the entire dataset, and then, compared its fits to data subsetted by disturbance type with individual models for each disturbance type using the small-sample corrected Akaike information criterion (AICc).

2.1.2 | Drivers of AGC, large trees, and stand variables

We downloaded bioclimatic variables from the WORLDCLIM dataset (http://www.worldclim.org/; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), defining the centre of a plot as its location, and compiling the following: average annual temperature (°C), temperature of the warmest quarter (°C), temperature of the coldest quarter (°C), temperature seasonality (standard deviation of temperature), annual rainfall (mm), rainfall in wettest quarter (mm), rainfall in the driest quarter (mm) and rainfall seasonality [coefficient of variation (CV) of rainfall]. Several climate variables were strongly correlated ($r \geq .70$), therefore, we used principal components analysis (PCA) to reduce them to three linearly uncorrelated variables that explained 95.0% of the variance in climate data (Supporting Information Appendix S3). Climate axis 1 (53.4% variance), *Pdryq*, was positively correlated with driest quarter and negatively related to all other variables. Axis 2 (22.2% variance), *Pseas*, was positively related to seasonality in temperature and precipitation and negatively related to all other variables. Axis 3 (19.3% variance), *Precip*, was strongly positively correlated with total precipitation and rainfall in wettest quarter.

Similarly, we selected 15 soil variables from the UN Food and Agriculture Organization (FAO) database (see FAO 2002 for exact definitions of variables). Using PCA, we summarized the soil data in three independent axes that explained 83.6% of the variance in soil data (Supporting Information Appendix S3). Soil axis 1 (47.1% variance), soil fertility, *Sfert*, was positively correlated with organic carbon topsoil, organic carbon subsoil, soil production, cation exchange capacity (CEC) soil and CEC clay. Axis 2 (21.7% variance), soil depth, *Sdepth*, was negatively correlated with nitrogen topsoil and C:N ratio topsoil, but positively correlated with soil depth, available water and pH topsoil. Axis 3 (14.8% variance), *Sdrain*, which we interpret as soil drainage and oxygen availability to roots, was positively correlated with soil drainage and textural classes of topsoil and subsoil, but negatively correlated to C:N ratio, base saturation topsoil and CEC clay topsoil.

We evaluated several indictors of disturbance, including disturbance type (concession, primary, secondary; Figure 1e), distance from nearest village (km) and presence of human trails. Primary, or old growth, forest was defined as having no recent obvious signs of disturbance. Concession forest included sites with obvious logging damage and within timber concessions. Secondary forest was defined as recovering from slash-and-burn agriculture or other forms of deforestation. Technicians recorded disturbance type and presence of human trails in the field, whereas the Euclidean distance from the plot centre to the nearest village was calculated in R. Finally, we classified plots into four major ecosystems (coastal forest, central forest, north-eastern forest, and savanna; Figure 1) and four habitats (highland, swamp, flooded, and terra firma).

We explored the data by examining bivariate relationships between independent variables and response variables (AGC, number of large trees, and stand variables; Figure 2). We used linear regression for all normally distributed response variables and generalized linear models for counts of large trees, accounting for overdispersion with a quasi-Poisson model. We then examined multivariate relationships among the above explanatory variables, standardized to facilitate comparison of effect sizes, and response variables using model averaging, implemented through the MuMIn package (Barton, 2019). Model averaging executes models for all possible combinations of variables (i.e. 4,095 combinations for our 12 variables) and ranks them from best to worst according to their AICc scores. We considered all models with Δ AICc < 4 as equally informative and determined the support for the explanatory variables by calculating their frequency of occurrence in the models (Galipaud, Gillingham, & Dechaume-Moncharmont, 2017). We used a cut-off of 60% support in our discussion of variables that drive numbers of large trees and AGC. Model-averaged regression coefficients based on AICc weights have been shown to be incorrect estimates of partial effects for individual predictors when there is multicollinearity among predictor variables (Cade, 2015); but, as described above, we minimized multicollinearity using PCA to reduce multiple correlated variables to fewer non-correlated predictors. All statistical analyses were conducted in R version 3.5.0 (R Core Team, 2019).

3 | RESULTS

3.1 | National assessment of AGC

NRI sites represented the forest types in Gabon (Table 1, Figure 3) and differed in AGC and stand variables (Supporting Information Appendix S1). Mean AGC across all 104 forestland sites was 141.7 ± 60.4 (*SD*) Mg C/ha (range: 3.6 to 292.5) (Table 1): the lowest AGC occurred in a coastal swamp, whereas 7 of the 9 lowest AGC sites occurred in savanna forest. Estimates of AGC from satellite plots were marginally less than adjacent 1-ha plots (linear mixed model: $\beta = 23.9$, $t = 1.77$, $p = .078$). The average distance between NRI sites was 31.9 km ± 12.6 and site-level AGC was not spatially autocorrelated (Moran's $I = -.005$, $p = .787$). When treated as independent replicates, satellite and permanent plots were significantly spatially autocorrelated (Moran's $I = .306$, $SD = 0.027$, $p < .001$), indicating that AGC is less variable within sites than among sites and that site is the appropriate level of replication. Primary and concession forest contained significantly more AGC than secondary forest (Table 1). AGC was highest in the north-east forest ecosystem and lowest in savanna forest and significantly higher on highlands

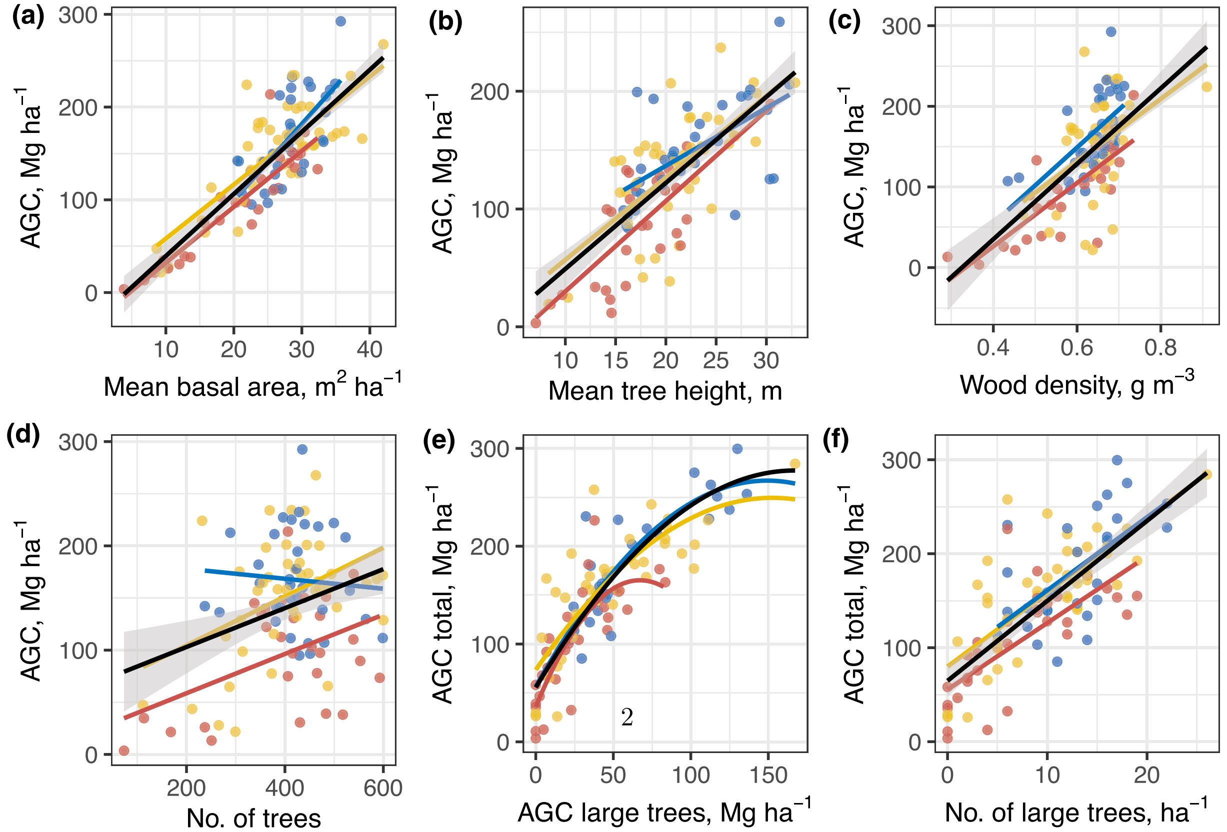

FIGURE 2 Aboveground carbon stock (AGC) for 104 national resource inventory (NRI) sites plotted against (a) mean basal area ($F_{1,102} = 232.8$, $p < .001$, $R^2 = .692$); (b) tree height ($F_{1,102} = 115$, $p < .001$, $R^2 = .525$); (c) wood mass density ($F_{1,102} = 74.04$, $p < .001$, $R^2 = .415$), (d) stem density ($F_{1,102} = 11.48$, $p = .001$, $R^2 = .092$), (e) total AGC of large trees at the site ($F_{2,101} = 138.6$, $p < .001$, $R^2 = .728$); and (f) number of large trees ($F_{1,101} = 132.8$, $p < .001$, $R^2 = .561$). Black lines represent the best-fit regression line for all disturbance types with their 95% confidence intervals (shading), and coloured lines are slopes from analyses of covariance testing the effect of the interaction between disturbance type (yellow = primary, blue = concession, red = secondary) and stand variables on AGC

than swamps and flooded forests. Protected areas held 46.3% more AGC than non-managed areas, but not significantly more than buffer zones, hunting zones, or reserves (Figure 3).

The best single predictor of site-level AGC was the AGC of large trees ($R^2 = .728$), followed by basal area ($R^2 = .692$), number of large trees ($R^2 = .561$) and tree height ($R^2 = .525$; Figure 2; Supporting Information Appendix S1). When combined, basal area, tree height, basal area-weighted wood density, and number of trees contributed significantly to site-level AGC ($F_{4,99} = 345.8$, $R^2 = .931$, $p < .001$; see results of large trees below), accounting for 93.6% of variation in AGC. Basal area, $\overline{BA}$, had the strongest positive effect on AGC, followed by mean tree height, $\overline{H}$, and wood density, $\overline{\rho}$; whereas the number of trees at a site, T, negatively affected AGC: ($y = 66.7 + 18.9X_{\overline{BA}} + 11.5_{\overline{H}} + 5.6_{\overline{\rho}} - 3.9_T$). High AGC occurred along the south-west coast of Gabon, stretching along the sedimentary basin from Port Gentil to Mayumba ($\overline{AGC}$= 209.1 Mg C/ha, $n = 8$; Figure 4) and in the north-east in and around the Ivindo and Mwagna National Parks ($\overline{AGC}$ = 193.8 Mg C/ha, $n = 11$; Figure 4). Highest numbers of large trees occurred in the north and north-east ($\overline{N}_{trees} = 22$, $n = 11$; Figure 4), whereas plots near the coast contained few large trees ($\overline{N}_{trees} = 11.6$, $n = 9$).

3.2 | Importance of large trees to AGC

Most AGC in Gabon's forests was stored in a limited number of large trees. Small trees (< 40 cm DBH) accounted for 88.5% of all trees, but only 36.3% of AGC, whereas large trees (≥ 70 cm DBH) made up 2.3% of trees and 30.6% of AGC, and the largest trees (> 100 cm DBH) represented 0.48% of trees and 12.1% of the AGC (Supporting Information Appendix S2). The proportion of AGC per site increased rapidly with the cumulative addition of the largest trees, reaching an average of 50 ± 27% for the 30 largest trees (*c.* 5% of stems) and 78 ± 36% for the 100 largest trees (*c.* 24% of the stems; Figure 5). The largest 10 and 20 trees explained 81 and 87% of the variance in AGC, respectively ($rRSE_{top10}$ = 20%; $rRSE_{top20}$ = 16%), and 69 trees, 16.6% of stems, explained 95% of the variation on average (Supporting Information Appendix S2). The largest 20 trees in a plot explained different levels of variation in AGC depending on disturbance type (concession = 84%, primary = 81% and secondary = 91%). Our Michaelis–Menten models similarly demonstrated that secondary forest accumulates AGC faster from large trees than primary and concession forest (Supporting Information Appendix S2).

TABLE 1 Summary statistics of Gabon's national resource inventory (NRI), including sites consisting of one 1-ha plot and four 0.16-ha satellite plots (see Materials and Methods, 16 sites have fewer than four satellite plots) and 1-ha plots for comparison with other studies. Aboveground carbon stock (AGC) is calculated with Chave, Réjou-Méchain, et al.'s (2014) pantropical equation, except Gabon* is calculated using the Gabon-specific equation that estimated AGC as 26% lower (range = 6.2–48.3%)

Variable	NRI sites mean per ha [95% CI]	NRI 1-ha plots mean per ha [95% CI]
No. sites	104	104
Area, ha	164.3	104
No. plots by size, ha	377 x 0.16-ha, 104 x 1-ha	104 x 1-ha
No. trees/ha	407.5 [387.7, 427.2]	415.8 [393.6, 438.0]
DBH (*D*), cm	23.3 [22.8, 23.8]	23.5 [22.9, 24.1]
DBH max, cm	125.2 [118.3, 132.1]	117.6 [111.2, 123.9]
Wood density (ρ), g/cm^3	0.628 [0.612, 0.644]	0.630 [0.613, 0.647]
Height (*H*), m	20.4 [19.4, 21.5]	20.5 [19.5, 21.6]
Height max, m	39.7 [37.9, 41.4]	38.9 [37.2, 40.7]
BA, m^2/ha	25.3 [23.8, 26.7]	26.0 [24.5, 27.6]
Aboveground carbon, Mg/ha		
Gabon	141.7 [130.1, 153.3]	146.4 [133.6, 159.3]
Gabon*	112.3 [103.1, 121.6]	116.1 [105.9, 126.3]
Primary forest (*n* = 43)	151.9 [134.8, 169.0]	156.6 [138.1, 175.2]
Primary, terra firma forest (*n* = 27)	166.6 [150.2, 183.1]	168.6 [151.1, 186.1]
Concession forest (*n* = 31)	171.3 [154.8, 187.7]	178.5 [158.5, 198.4]
Secondary forest (*n* = 30)	96.6 [77.0, 116.2]	98.7 [77.3, 120.0]
Parks/reserves (*n* = 21)	170.9 [139.3, 202.4]	174.7 [140.1, 209.4]
Non-park/reserve forests (*n* = 83)	134.3 [122.3, 146.4]	139.3 [125.8, 152.7]
Central forest (*n* = 51)	144.9 [130.9, 159.0]	148.6 [132.4, 164.7]
Coastal forest (*n* = 29)	152.8 [126.2, 179.3]	157.7 [127.9, 187.4]
North-east forest (*n* = 15)	155.1 [132.3, 178.0]	161.9 [137.1, 186.7]
Savanna forest (*n* = 9)	65.6 [23.5, 107.7]	72.1 [28.2, 116.1]

BA = basal area; CI = confidence interval; DBH = diameter at breast height.

Thirty-five tree species (6.1% of identified species) made up 50% of total AGC. Species of large trees varied by ecosystem: *Aucoumea klaineana* (13–23% of large trees) is the most abundant species in coastal, central and savanna forests, whereas *Gilbertiodendron dewevrei*, *Scyphocephalium* spp., *Petersianthus macrocarpus* and *Maranthes glabra* make up 18.6% of Congolian forest (Supporting Information Appendix S2). The composition of large tree species was generally the same across disturbance types, except secondary forest had significantly higher average numbers of *Musanga cecropioides* (16.5 stems versus 3.5 in concession and 1.1 in primary forest) and *A. klaineana* (19.2 stems versus *c*. 5.8 in concession and primary forest). Biomass hyperdominants included *A. klaineana*, *Scyphocephalium mannii*, *Desbordia glaucescens*, *Pycnanthus angolensis* and *Piptadeniastrum africanum*. *Aucoumea klaineana*, which comprises 80% of Gabon's timber exports (Lescuyer, Cerutti, Manguiengha, & bi Ndong, 2011), represented 4.7% of total AGC and 9.1% of the AGC of large trees. Several of the 10 most abundant large tree species are harvested for timber (Supporting Information Appendix S2).

3.2.1 | Drivers of large trees and AGC

Using model averaging to evaluate the leading climatic, environmental and human determinants of forest structure (AGC, number of large trees, and stand variables; Figure 6; Supporting Information Appendix S3), the independent variables most frequently retained in the top models included: distance from village, disturbance type (five response variables), ecosystem type (four response variables), slope and precipitation (three response variables). Human activity negatively affected stand variables. Apart from stem density, all stand variables had lower values in secondary than primary and concession forest and increased with distance from village. Annual precipitation positively affected most stand variables, but wood density decreased with precipitation. Mean wood density and basal area increased with slope, whereas tree height decreased with slope. Here we focus on AGC and large trees (see Supporting Information Appendix S3 for other response variables).

Variation in site-level AGC across Gabon was explained by 29 equally likely models (mean $R^2 = .346$) and was most frequently positively correlated with distance from village and soil fertility (Figure 6, Supporting Information Table S3.8). Secondary and savanna forests had significantly lower AGC than other disturbance and ecosystem types.

Variation in site-level number of large trees was explained by 51 equally likely models (mean $R^2 = .508$). The number of large trees was positively related to distance from village (Figure 6). The number of large trees was significantly lower in secondary forest (7.8 large trees/ha) than concession (12.4 trees/ha) and primary forest (10.5 trees/ha).

4 | DISCUSSION

4.1 | National assessment of AGC

Gabon has one of the highest densities of aboveground forest carbon among forested nations (Saatchi et al., 2011), with a national average of 141.7 Mg C/ha (95% confidence interval (CI): 130.1, 153.3).

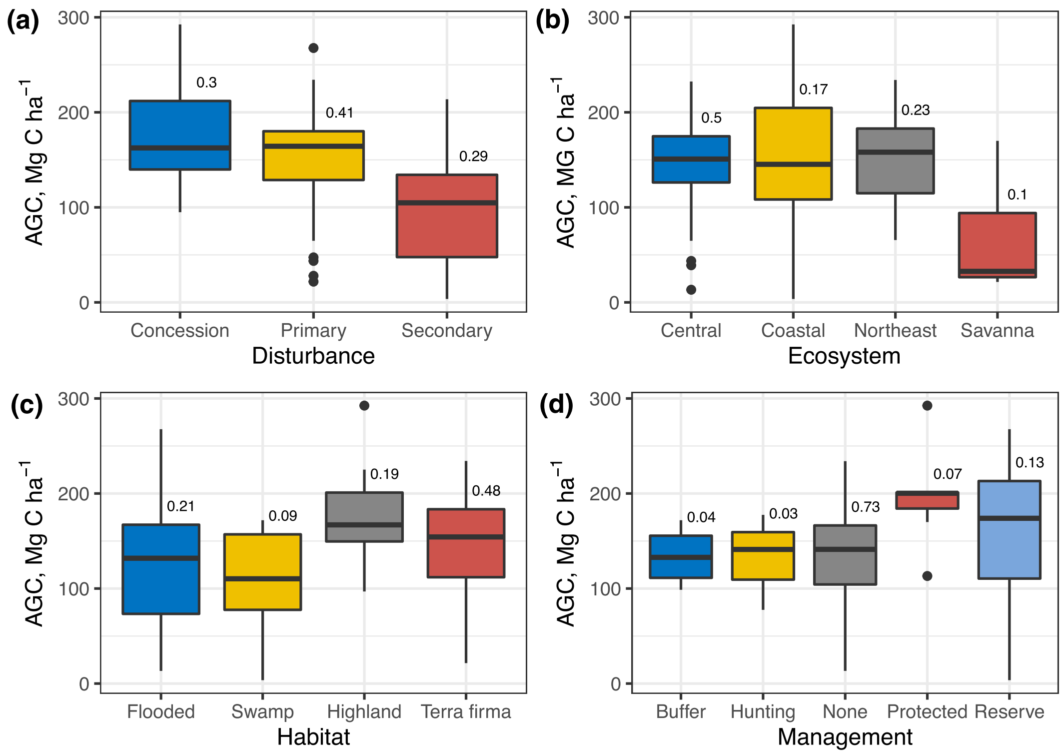

FIGURE 3 Aboveground carbon stock (AGC) of national resource inventory (NRI) sites by (a) disturbance type: plots in secondary forest have significantly lower AGC than primary and concession forest ($F_{2,101} = 16.5$, $p < .001$); (b) ecosystem: plots in savanna hold significantly lower AGC than all other ecosystem types ($F_{3,100} = 8.0$, $p < .001$); (c) forest type: highland plots contain significantly higher AGC than swamps and flooded forests ($F_{3,97} = 4.04$, $p = .009$), and (d) management: plots in protected areas contain significantly higher AGC than areas with no management ($F_{4,99} = 2.1$, $p = .0865$), and plots in protected and reserve areas contain significantly higher AGC than other management types ($F = 6.47_{1,102}$, $p = .0125$). The number to the right of each boxplot is the proportion of all sites belonging to that category (e.g. 30% of sites were in concession forests)

By comparison, the mean AGC of the Democratic Republic of Congo (DRC), also from a systematic sampling of forests, is 113 ± 9 Mg C/ha (Xu et al., 2017). On average, the primary forests of Gabon have a carbon density (*c*. 150 Mg C/ha) similar to the DRC and much higher than old growth forests in Amazonia and Southeast Asia (Feldpausch et al., 2012; Lewis et al., 2013; Sullivan et al., 2017). Most of Gabon's AGC is stored in large trees: trees ≥ 50 cm DBH account for 6.6% of stems and 51.3% of AGC and trees ≥ 70 cm DBH account for 2.3% of trees and 30.6% of AGC. Here, we also establish baseline estimates of old growth (166.6 Mg C/ha), concession (171.3 Mg C/ha) and secondary (96.6 Mg C/ha) forests (Table 1). Note that both the mean AGC and AGC in primary terra firma, closed canopy forest (168.6 Mg C/ha; 95% CI: 151.1, 186.1) in Gabon are significantly lower than the value reported for African humid tropical forests from research plots (202 Mg C/ha; Lewis et al., 2013). This difference is likely attributable to the NRI's probabilistic sampling design (Figure 1) that captures a combination of intact and partially disturbed forests, unlike research plots concentrated in undisturbed, old growth forest (e.g. Xu et al., 2017).

Despite being one of the world's most forested countries, with a very low population density and deforestation rate, in Gabon human activities are the dominant drivers of variation in AGC and numbers of large trees. Of environmental variables, only soil fertility positively influenced AGC and no variables strongly affected numbers of large trees, whereas climate and soils contributed importantly to variation in mean basal area, tree height, wood density, and stem density. In many tropical countries, tackling climate change by reducing carbon emissions depends on working at the deforestation front and promoting reforestation. In Gabon, conservation of its stable, majestic forests ought to be a priority, while also carefully managing high carbon, degraded forests and promoting regeneration of secondary forests. Protecting forests that are not already significantly disturbed and that contain abundant large trees can conserve carbon, biodiversity, and ecosystem services (Funk et al., 2019).

Gabon's NRI is one of the most rigorous national inventories of tropical forest to date. The inventory employs internationally recognized data collection methods, relatively large plots to increase precision (Chave et al., 2004), and samples forest and disturbance types relative to their representation while avoiding the 'majestic forest' bias. With funding from the Central African Forest Initiative (CAFI), additional sites are being added to the NRI and the sampling sites reported here are being remeasured to monitor carbon dynamics over time. The NRI data are important nationally and regionally for reporting on greenhouse gas emissions. Nations that are parties to the United Nations Framework Convention on Climate Change (UNFCCC) must report on emissions and removals for climate change mitigation efforts, and the reducing emissions from deforestation and forest degradation (REDD+) policy framework will

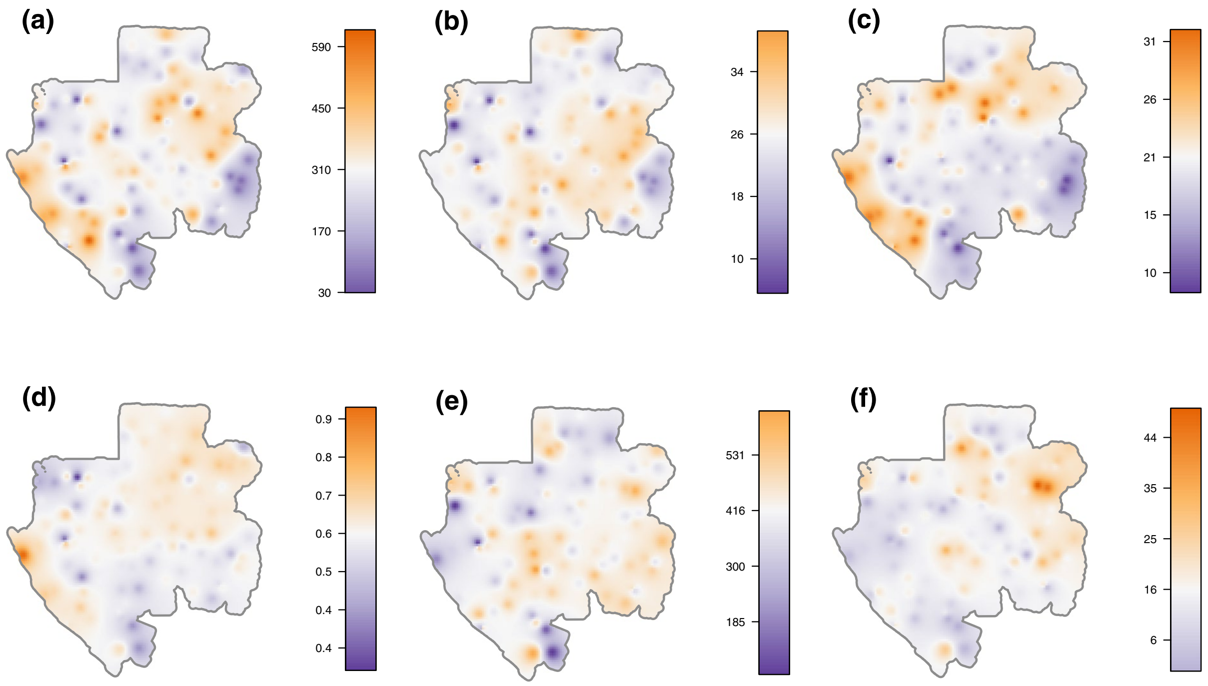

FIGURE 4 Extrapolation maps showing the predicted distribution of (a) aboveground carbon, Mg/ha; (b) mean basal area, m^2/ha; (c) tree height, m; (d) wood density, g/cm^3; (e) numbers of stems/ha; and, (f) numbers of large trees [stems ≥ 70 cm diameter at breast height (DBH)] in field plots across Gabon. The colour scale for each map is mean-centred so that white areas are average, shades of orange are above and shades of purple are below average. Forests with high carbon and tall trees occur largely along the coast and north-eastern section of Gabon. Forests with high numbers of large trees also occur in the north-east, which was opened up relatively late to industrial logging, agriculture, and mining compared to the western and southern sections of the country. Gabon's high carbon forests are also relatively isolated from the national road network along which most villages lie (Figure 1)

require establishment of reference emission levels for comparison against future emissions measured by a monitoring, reporting and verification (MRV) system. With limited forest monitoring in the tropics, many countries rely on default values in Intergovernmental Panel on Climate Change (IPCC) guidelines (IPCC, 2006) to estimate emissions, rather than country-specific data (Tier 2) or higher-level methods like repeated measurements of permanent plots (Tier 3). Gabon's NRI is on track to achieve Tier 3 reporting and contribute to improving IPCC default rates (Suarez et al., 2019). By making its data openly accessible, Gabon could advance the development of regional and global policies to fight climate change.

4.2 | Importance of large trees to AGC

In Gabon, like in tropical forests in other countries, large trees are the major constituents of live AGC. Intact African forests are characterized by their large trees (Feldpausch et al., 2012; Lewis et al., 2013), and we found the largest 5% of trees store 50% of AGC on average similar to Central Africa in general (Bastin et al., 2015). However, the proportional contribution of large trees to AGC varied with disturbance type: secondary forest, with a lower average AGC, accumulates AGC at a faster rate from large trees than primary and concession forest. Loss of the largest trees drastically changes forest structure and diameter distributions; thus understanding the relative importance of large trees to AGC in different forest types could help characterize forest degradation, which accounts for a large fraction of carbon loss world-wide (Pan et al., 2013). Large tree biomass in Gabon is also correlated with high densities of coarse woody debris (Carlson, Koerner, Medjibe, White, & Poulsen, 2017) and large liana biomass (Poulsen et al., 2017); thus, the loss of large trees could affect multiple pools of carbon.

Large trees are typically defined as having diameters ≥ 70 cm, but Meyer et al. (2018) determined that a threshold of > 50 cm DBH was more reliable for quantifying the number and distribution of large trees in old growth Neotropical forests. Rethinking the definition of large trees could have several advantages. First, defining only 2.3% of stems as 'large' seems extreme. In Gabon, trees ≥ 50 cm make up 6.6% of all stems and 51.3% of AGC – still a small proportion of trees but *c.* 20% more in measured AGC. If 'large trees' were protected by law in industrial agricultural fields, for example, more carbon could be preserved with the conservation of only 4.3% more stems. Second, in our study, basal area and tree height explain AGC; therefore, relaxing the definition of 'large' might capture some smaller diameter, tall trees that contribute to AGC. Third, in Gabon selective logging starts at a minimum cutting diameter of 40 cm for *Diospyros crassiflora*, with minimum harvest diameters of 60–90 cm for 60 species and 70 cm for all others (Ministère des eaux et forêts 2014). Accounting for large trees of ≥ 50 cm DBH would more thoroughly capture the effects of logging.

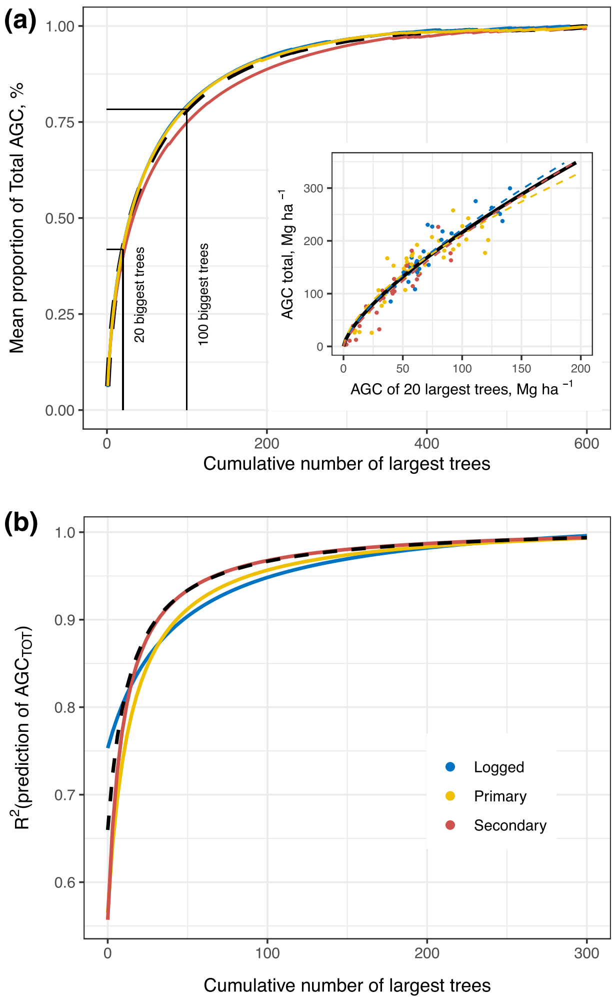

FIGURE 5 (a) The mean proportion of total aboveground carbon stock (AGC) represented by the cumulative addition of the largest trees. Black dashed line shows all data; coloured lines depict each disturbance type (yellow = primary forest, blue = concession forest, red = secondary forest). (inset) AGC of the largest trees versus the total AGC of 1-ha plots for each disturbance type and all disturbance types combined (black dashed line). (b) Fits of models predicting variation in total AGC explained by the cumulative addition of large trees: different forest types have different accumulation curves

4.3 | Drivers of large trees and AGC

Precipitation, soil types and ecosystems vary spatially across Gabon, yet our results indicate that anthropogenic disturbance (disturbance type and distance from villages) is the primary driver of numbers of large trees and AGC and strongly influences other stand variables (Figure 6). Soil fertility was the only environmental variable to influence AGC. Like previous studies, stand variables including number of large trees, basal area and tree height explained most of the variation in plot-level AGC. Interestingly, basal-area weighted wood density also explained a relatively high level of variation in AGC compared to other studies (Bastin et al., 2018; Lewis et al., 2013). Florist species composition may, therefore, be an important factor influencing AGC in Gabon. Wood density was marginally correlated with distance from villages ($r = .184$, $df = 102$, $p = .06$), suggesting a floristic gradient of pioneer to old growth species explained by distance from the road network.

Although environmental variables exerted weak control over large trees and AGC, climate, soil and topography influenced stand variables that explain most of the spatial variation in AGC. Environmental variables can strongly affect stand variables while explaining little overall variation in AGC because they covary negatively in their responses to climate, soils and topography (Baraloto et al., 2011). In fact, the environmental variables considered here often differentially affected forest stand variables. For example, basal area and number of trees increased with slope, whereas tree heights declined (Figure 6). Because stand variables are components of AGC, identifying the drivers of individual stand variables is important for understanding the mechanisms of temporal–spatial variation in AGC (Bastin et al., 2018).

In Gabon, secondary forests have significantly lower carbon stocks than primary forests, but with an average of 96.6 Mg C/ha, they are on the high side of AGC estimates from other tropical countries like Costa Rica (82.2 Mg C/ha) and Sierra Leone, where old fallows with residual trees have 80 Mg C/ha (Cuni-Sanchez & Lindsell, 2017; Fonseca, Rey Benayas, & Alice, 2011). In Cameroon, forest fallows contain 50% of the carbon stocks of an old growth forest (Njomgang, Yemefack, Nounamo, & Moukam, & Kotto-Same, 2011), whereas in Gabon they hold 63%. Gabon's secondary forests have important conservation value because of their relatively high carbon stocks, as well as for their carbon sequestration potential: secondary forests can uptake carbon 11 times as fast as old growth forests (Poorter et al., 2016).

Regeneration of secondary and disturbed forests to their natural state can sequester more carbon than agroforestry and plantations (Lewis, Wheeler, Mitchard, & Koch, 2019); thus, highly forested, developing countries like Gabon must carefully balance development and climate change mitigation. In the Congo Basin, small-scale, non-mechanized forest clearing for agriculture doubled between 2000 and 2014 (Tyukavina et al., 2018). Although this type of slash-and-burn farming contributes less to forest clearing in Gabon than other countries, it undoubtedly explains increasing AGC with distance from villages. Slash-and-burn farming converts forest to fields every 3–5 years to maintain productivity. Reducing the expansion of secondary forest, therefore, will require crops with longer rotation times, application of expensive fertilizers, or a transition to high intensity agriculture. Currently, industrial production of oil palm and rubber makes up just 0.8% of the land area in Gabon (Tyukavina et al., 2018), but this is projected to increase as the Congo Basin goes through a new wave of agroindustry development (Austin et al., 2017; Feintrenie, 2014). Most secondary forests in Gabon surpass the carbon threshold (75 Mg C/ha) above which the High Carbon Stock approach discourages development (HCS Technical Committee, 2015), indicating that plantation siting must consider AGC, and offsets or other measures may be required to mitigate planned deforestation (Burton et al., 2017).

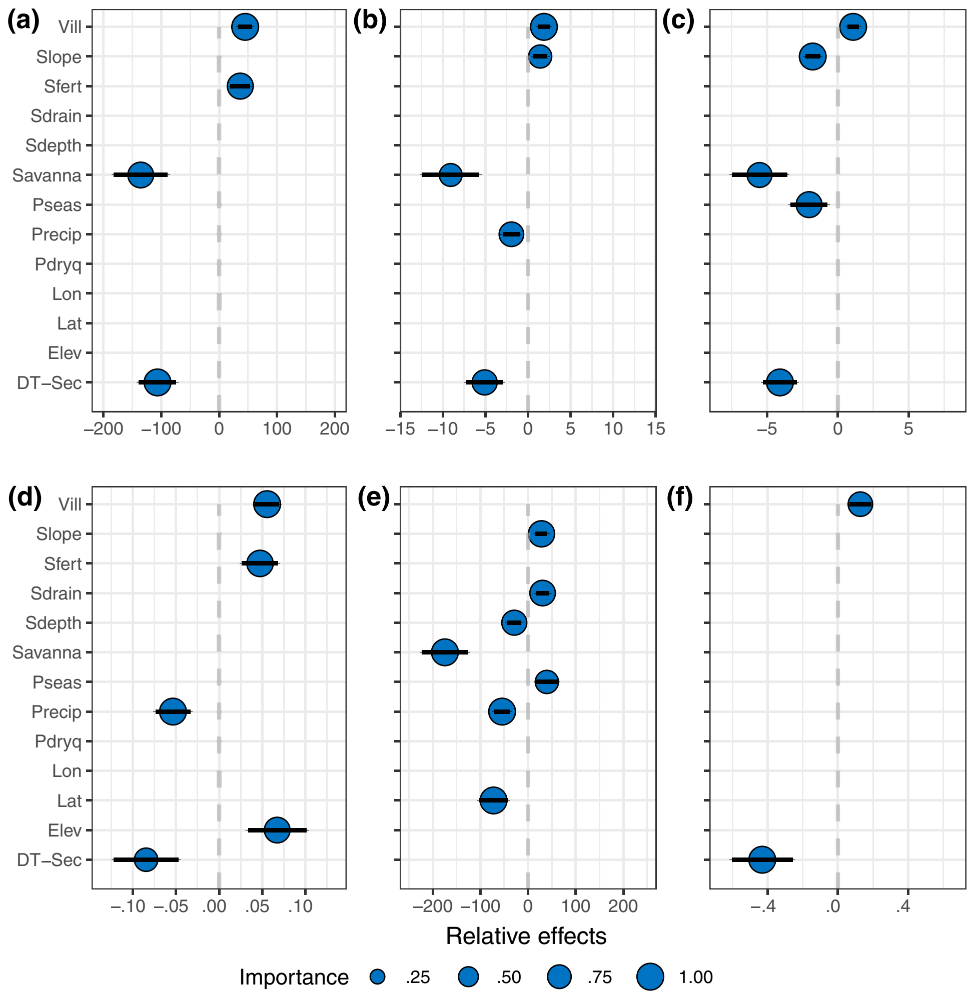

FIGURE 6 Relative effects of independent variables on stand variables, including (a) aboveground carbon stock (AGC), Mg/ha; (b) basal area, m^2/ha; (c) tree height, m; (d) wood density, g/cm^3; (e) number of trees/ha; and (f) number of large trees/ha. The size of the symbols represents model support for the effects. The position of the symbols on the *x* axis represents the relative effect size of the standardized coefficients, calculated as $E_{Rel,i} = E_i / \sum E_i$. Independent variables include distance from villages (Vill), slope (Slope), soil fertility (Sfert), soil drainage (Sdrain), soil depth (Sdepth), savanna (Savanna), seasonality of precipitation (Pseas), total annual precipitation (Precip), precipitation in the driest quarter (Pdryq), longitude (Lon), latitude (Lat), elevation (Elev) and secondary forest (DT-Sec). Here we present independent variables with model support of .60 and higher (see Supporting Information Appendix S3 for all independent variables) [Colour figure can be viewed at wileyonlinelibrary.com]

Selective logging, Gabon's primary land use activity, constitutes 61.6% of forest loss (Tyukavina et al., 2018). Concession forest contains slightly higher AGC than primary forest even though significant carbon losses follow conventional and reduced impact logging (Medjibe et al., 2013). Excluding savanna, swamps and flooded forests, where logging would not occur, primary forests store 166.6 Mg C/ha on average, nearly the same as concession forest (171.3 Mg C/ha). High AGC in concession forests is likely a result of grouping all sites that occurred in timber concessions together, whether they had been logged or not, or possibly by landscape-level high grading, where forests with the largest trees are selected for timber harvest. Low harvest intensity in Central Africa, rarely exceeding 10–13 m^3 per hectare or 4–8% of standing timber volume (Karsenty, 2016), might also allow logged forests to recover rapidly (Rutishauser et al., 2015). If our results hold up under additional study, they argue for including sustainable forestry in programmes like REDD+.

Protected areas world-wide store 15.2% of global terrestrial carbon stocks and reduce carbon emissions (Bebber & Butt, 2017). Gabon's national parks and reserves, 18.4% of the country's landmass, store significantly higher densities of AGC than forests outside of parks. The 49,256 km^2 of forested lands in parks and reserves store approximately 0.84 Gt C or 25.4% of AGC. Gabon's protected areas, therefore, are an important component of its climate mitigation strategy. At the same time, most terrestrial carbon (2.47 Gt C) lies outside of protected areas and requires concerted management as the government grows its agricultural sector (Austin et al., 2017). Two areas of high carbon density occur along the south-western coast and in the north-eastern part of the country. Both areas include parks separated by logging concessions. With careful management, these concessions could contribute to Gabon's timber industry, capture carbon through forest regrowth, and conserve biodiversity.

5 | CONCLUSION

Based on a rigorous national inventory of forestlands in Gabon, we demonstrate that Central African forests can hold high densities of AGC in secondary and concession forests, as well as old growth forests. Combatting climate change, therefore, will require a combined approach that includes measures for conserving, managing and regenerating tropical forests. The international community proposes to pay developing nations to reduce greenhouse gas emissions from deforestation and forest degradation (REDD+). Additional policies will be necessary. Agricultural development or other activities that necessitate deforestation should only occur in secondary forests with low AGC. Importantly, international mechanisms should also include provisions for promoting the permanence of stable, intact old growth forests like those in Gabon (Funk et al., 2019). Similar attention should be given to logging concessions in carbon dense forests that represent a large proportion of remaining Central African forests. Protecting forests that are not already significantly disturbed will require considerable international financial assistance to promote low emissions development and policies such as country-wide forest certification. The preservation of the world's large primary forests will conserve carbon, biodiversity, and ecosystem services now, and avoid the rush to save the remnants of diminished, low carbon secondary forest later.

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DATA AVAILABILITY STATEMENT

The data are subject to third party restrictions. The data that support the findings of this study are available from Le Ministère des Eaux, de la Forest, de la Mer, de l'Environnement. Restrictions apply to the availability of these data, which were used under licence for this study. Data are available from the corresponding author with the permission of Le Ministère des Eaux, de la Forest, de la Mer, de l'Environnement.

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BIOSKETCHES

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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