

Co-variation in biomass and environment at the scale of a forest concession in central Africa

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Abstract: Drivers of forest structure in central African rain forests are largely unknown. Using forest inventory data (3024 0.4-ha plots) in a forest concession of 154 456 ha in north-eastern Gabon covering an altitudinal gradient (from 485 to 1009 m asl), relationships between above-ground plot biomass and environmental variables (soil type, altitude, slope, aspect) and floristic composition (score given by an ordination method) were tested. After controlling for confounding variables, biomass was significantly related to altitude (with a modal response peaking at 346 Mg ha⁻¹ on western slopes at an altitude of 707 m asl) and to aspect (additional 18.3 Mg ha⁻¹ on eastern slopes) but not to floristic composition. Biomass and basal area responded differentially to the environment. Mean wood density was significantly related to soil, altitude and floristic composition, with a predicted minimum of 0.60 g cm⁻³ at an altitude of 1009 m asl in stands characterized by *Scorodophloeus zenkeri* and a maximum of 0.69 g cm⁻³ at an altitude of 458 m asl in monodominant *Gilbertiodendron dewevrei* stands. Variation in forest structure in the concession was primarily driven by altitude while floristic composition played a role in differentiating the variation in biomass and basal area.

Key Words: above-ground biomass, central Africa, environmental filter, floristic composition, forest structure, inventory data, tropical forest

INTRODUCTION

The drivers of tropical forest structure are complex and remain largely unknown (Toledo *et al.* 2011). When focusing on biomass, its relationship with environment is non-trivial and scale-dependent, yet important to understand to build large-scale biomass maps (Baccini *et al.* 2012). At the plot scale, an important determinant of the spatial distribution of biomass is its spatial autocorrelation (Réjou-Méchain *et al.* 2014). At the landscape level, the variation in biomass mainly parallels the variation in forest structure, i.e. basal area and height (Baraloto *et al.* 2011, Djomo *et al.* 2011). Lewis *et al.* (2013) showed that the biomass of tropical dense African forests was related at the continental scale to both climate and soil, with higher biomass where the rainfall in the driest nine months of the year was higher, where the rainfall in the wettest three months was lower, where temperature was lower, where soils were clay-richer,

where C:N ratio was lower, and where the sum of base cations was lower.

Biomass variation also has a degree of freedom that is independent of forest structure and that depends on floristic composition (Day *et al.* 2013). One question is whether the environment influences biomass by influencing forest structure (i.e. trees of the same floristic set vary in size), or by influencing floristic composition (i.e. tree sizes vary because they belong to different species with different potential stature) (Gonmadje *et al.* 2017). For instance, Gourlet-Fleury *et al.* (2011) showed a filtering effect of soil conditions on species composition with two opposite and almost cancelling effects on biomass: in unfavourable growing conditions, smaller average tree size was compensated by greater wood density due to slow growth, thus resulting in a biomass storage that was of the same level as in places with more favourable growing conditions.

The relative weight of variation in forest structure and floristic variation in biomass variation depends on the range of environmental variation and is thus scale-dependent. When environmental changes are so large that vegetation types vary across the studied area, floristic

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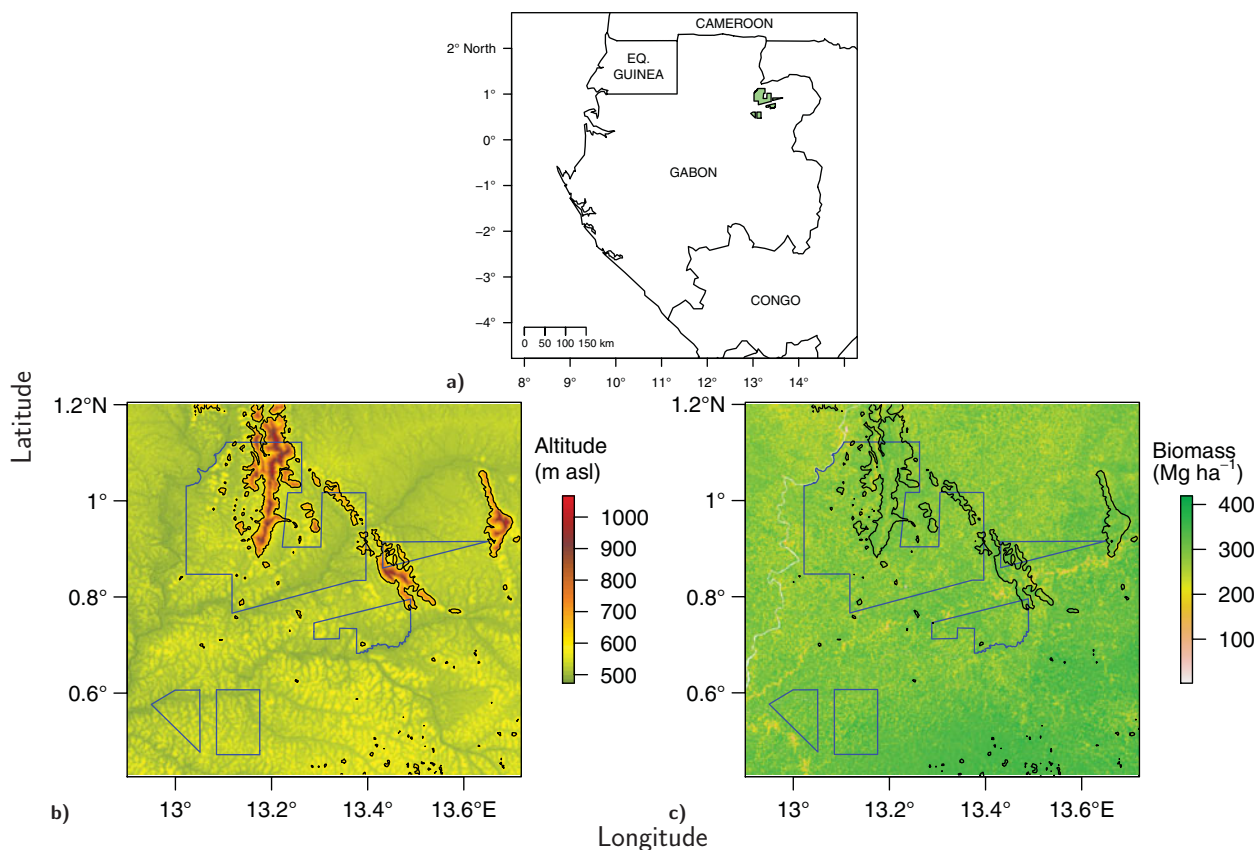


Figure 1. Map of the study area in north-eastern Gabon. Location of the Makokou concession (green polygon) in Gabon (a). Elevation (data from NASA's Shuttle Radar Topography Mission) (b). Biomass (data from Global Forest Watch) (c). The blue polygons delimit Olam's Makokou concession. The black polygons delimit the areas with an altitude greater than 600 m asl.

variation is expected to be the main driver of biomass variation. For instance, Ensslin *et al.* (2015) showed a change in forest biomass along an altitudinal gradient of 3700 m on Mount Kilimanjaro that followed a shift in vegetation type from savanna woodlands to afro-alpine vegetation. When environmental gradients are less marked, e.g. an altitudinal gradient of about 700 m like in Gonmadje *et al.* (2017), we hypothesize that variation in forest structure should be the main driver of biomass variation.

The current study aims at testing this hypothesis by investigating the relationship between forest above-ground biomass and the environment at the landscape scale for the tropical rain forests of Central Africa using data from a forest management inventory with an altitudinal gradient of 525 m. Forest biomass estimated from inventory data was related to environmental variables characterizing topography (altitude, slope) and soil. We aimed at disentangling the effect of forest structure and species composition on biomass variation by separately relating environmental variables and a floristic composition score to biomass, basal area and plot-level mean wood density.

MATERIALS AND METHODS

Study site

The study site was the Makokou logging concession sustainably managed by the Olam company, in the Ogooué-Ivindo province of north-eastern Gabon. The concession is 154 456 ha in area and is made of five disconnected blocks between 0°28'–1°07'N and 12°57'–13°39'E (Figure 1). Mean annual rainfall is between 1600–1700 mm with two dry seasons (July–August and February–March; Lérique 1983). Mean annual temperature in Makokou (487 m asl) is 23.9°C. The relief in the southern part of the concessions consists of an undulating plateau made up of many hills, at an altitude of about 500 m asl, on an Archean crystalline basement. In contrast, two mountain ranges are found in the northern part of the concession (Mount Belinga that reaches 1024 m asl and Mount Sassamongo that reaches 1001 m asl). These mountains are iron formations made of itabirites and quartzites. Soils are shallow yellow ferralsols (Martin *et al.* 1981). In the mountain ranges, ferruginous crusts often show on the surface.

The vegetation belongs to the dense forest of the Guineo-Congolian region, more precisely to the lower-Guinean continental forest (White 1986) and has been classified as a transition type between evergreen and semi-deciduous forests (Caballé 1978, De Namur 1990, Doumenge 1990, Doumenge *et al.* 2001). Representative species in terms of abundance are *Scyphocephalum mannii* (Benth.) Warb. (Myristicaceae), *Pycnanthus angolensis* (Welw.) Warb. (Myristicaceae), *Pentaclethra eetveldeana* De Wild. & T. Durand (Fabaceae), *Celtis* sp. (Cannabaceae), *Gilletiodendron pierreanum* (Harms) J. Léonard (Fabaceae) and *Gilbertiodendron dewevrei* (De Wild.) J. Léonard (Fabaceae).

Forest inventory

In 2007–2008, a management-oriented forest inventory was conducted in the Makokou concession. The sampling design was systematic using contiguous 0.4-ha (200 × 20 m) plots along equidistant transects. The distance between transects was 2 or 2.5 km, resulting in a planned sampling rate of 0.9%. In total, 3024 plots have been inventoried with an achieved sampling rate of 0.8% (TEREA 2010). The geographic coordinates of each plot were recorded. Each plot was classified into one of three soil types according to the soil classification by Martin *et al.* (1981), which differ by the depth of the organic and loose horizons: brachyapexols (depth ≥ 1.5 m), orthoapexols (depth < 1.5 m), or ferruginous crusts (no loose horizon). In each plot, all trees with diameter at breast height (dbh) ≥ 40 cm were inventoried and, in a subplot of half the plot (0.2 ha), all trees with 40 cm > dbh ≥ 20 cm were additionally inventoried. The species of each tree was recorded. Each tree was assigned to one of 14 dbh classes with 10 cm width starting from 20 cm dbh (with the last class gathering all trees ≥ 150 cm). Vernacular species names were converted into scientific names referring for nomenclature to the African Plant Database (version 3.4.0) of the Conservatoire et Jardin botaniques de la Ville de Genève and South African National Biodiversity Institute, sometimes resulting in lumping at the genus level (Réjou-Méchain *et al.* 2011). In total, 117 952 trees belonging to 253 species or genus and 49 families were inventoried. Three families or subfamilies alone represented almost half the number of inventoried trees: Caesalpinioideae (32.4% of the number of trees), Burseraceae (8.1%) and Euphorbiaceae (8.8%). Some species were not identified during the forest inventory and were not considered for the subsequent floristic analyses.

Additional plot characteristics

In addition to the information collected during the forest inventory, external databases were used to complement

the plot description with biomass and environmental descriptors. Altitude, slope and aspect of each plot were obtained from the plot geographic coordinates using the SRTM 90 m digital elevation data (<http://srtm.csi.cgiar.org>). The altitude of the plots varied from 485 to 1009 m asl. Slope and aspect were computed from the digital elevation data using the 'terrain' function of the 'raster' package in the R software. Soil type (as given by the forest inventory), altitude, slope and sine and cosine of the aspect define the set of environmental variables of each plot.

Using two databases on wood density (that of CIRAD: <http://ur-biowoeb.cirad.fr>, and that of the World Agroforestry Centre: <http://db.worldagroforestry.org/wd>), a wood density was assigned to each species. When a species match was found in the databases, the mean of the wood densities was computed. If no match was found at the species level, the mean was computed across the genus (Slik 2006). If no match was found at the genus level, the mean was computed across the family. If no match was found at the family level, a default value of 0.58 g cm⁻³ was used (Brown 1997).

The above-ground dry biomass of each tree was predicted from its diameter and wood density using Chave *et al.* (2014) equation (7): $B = \exp[-1.803 - 0.976E + 0.976 \ln(\rho) + 2.673 \ln D - 0.0299 (\ln D)^2]$, where B is the tree biomass in kg, D is its dbh in cm, ρ is its wood density in g cm⁻³, and E is a climatic index that is related to the height-diameter allometry of trees. The data set used by Chave *et al.* (2014) included a subset of trees measured in the Makokou concession, with a E index equal to -0.106 for this site, which is the fixed value of E that we used for all plots. The alternative that consists in taking into account the spatial variation in E using the map of E provided by Chave *et al.* (2014) brought little difference in the predicted aboveground biomass (≤ 2 Mg ha⁻¹) and was dropped. Tree biomasses were summed up within each plot to obtain the plot-level biomasses.

Descriptive statistical analyses

A multivariate analysis of the 3024 × 253 table giving the abundance of each species in each plot was performed to ordinate the plots depending on their floristic characteristics. Correspondence analysis was not used because of its sensitivity to a few species like *Musanga cecropioides* R. Br. or *Tetrorchidium didymostemon* (Baill.) Pax & K. Hoffm. often found in secondary forests that were rare at the concession scale but locally abundant in a few plots. Instead, we used non-symmetrical correspondence analysis (NSCA), thus weighing the species by their total abundance (Couteron *et al.* 2003). The score of the plots along the first axis of the NSCA was used as a summary statistic of the floristic composition of each plot.

Prediction models for biomass

Plot-level biomass was predicted using the set of environmental variables and the floristic variable (score on the first axis of the NSCA) as predictors. The shape of the relationship between biomass and each predictor was explored using general additive models with thin plate regression splines as smooth functions. The effects of all predictors were then jointly tested using a linear model with linear dependence on all predictors except altitude for which a curvilinear relationship was observed and modelled using a second-order polynomial. The full model was:

$$B_i = \mu + \alpha_{(s_i)} + \beta h_i + \gamma h_i^2 + \delta p_i + \eta \sin(\theta_i) + \lambda \cos(\theta_i) + \nu F_i + \varepsilon_i \quad (1)$$

where B_i was the observed biomass of the i th plot, s_i its soil type (with the three types labelled as 1, 2, 3 for brachyapexols, orthoapexols, and ferruginous crusts, respectively), h_i its altitude (in m), p_i its slope, θ_i its aspect, F_i its score along the first axis of the NSCA, ε_i was the residual error of plot i , and μ , α_1 , α_2 , α_3 , β , γ , δ , η , λ and ν were parameters to estimate. The spatial distribution of plots resulted in spatial correlation between residuals ε_i , thus preventing the use of ordinary least squares to fit (1). Instead, generalized least squares fitting was used, using for the spatial correlation structure of the residuals an exponential model with a nugget effect (Banerjee *et al.* 2004):

$$\text{Cov}(\varepsilon_i, \varepsilon_j) = \sigma^2(1 - \tau)\exp(-d_{ij}/r) \quad (2)$$

where d_{ij} was the distance (in km) between plots i and j , σ the sill (in Mg ha⁻¹), τ the nugget effect (between 0 and 1), and r the range (in km). Model fitting was performed using the R software, including package 'nlme' for generalized least squares fitting and package 'mgcv' for general additive models.

Model (1) was also fitted using basal area as the response variable instead of biomass. To disentangle the variation of the forest structure from the variation of the expected biomass given the forest structure, the plot-level mean wood density was computed for each plot i as $W_i = (\sum_{j=1}^{n_i} G_{ij} \rho_{ij}) / (\sum_{j=1}^{n_i} G_{ij})$, where n_i is the number of trees in plot i , and G_{ij} and ρ_{ij} are the basal area and wood density of the j th tree of plot i , respectively. Model (1) was again fitted with biomass B_i replaced by mean wood density W_i as the response variable.

Comparison with biomass maps

To assess the consistency of biomass variation at the scale of the concession, the biomass estimates from the inventory plots were compared to the biomass data from

Global Forest Watch (http://data.globalforestwatch.org/datasets/8f93a6f94a414f9588ce4657a39c59ff_1, accessed on 6 September 2016) that expanded upon the methodology of Baccini *et al.* (2012) to produce a global 30-m resolution map of above-ground live woody biomass for circa the year 2000 (Figure 1c). Estimates of the total biomass in the Makokou concession from the ground inventory and from the map were compared. The biomass values at each plot location were extracted from the biomass map and correlated to their estimates from the forest inventory using Pearson's correlation coefficient.

Because an error in the geographic coordinates of the inventory plots could result in an undervalued correlation between biomass estimates, we also compared the broad-scale response of biomass to altitude according to inventory and to the biomass map. The altitudes of the plots were classified into three altitude ranges (< 600 m asl, between 600 and 800 m, and \geq 800 m), and the biomass difference between these three ranges was tested using an analysis of variance fitted by generalized least squares using (2) to model the spatial correlation structure of residuals. This method is appropriate for the biomass estimated from inventory plots but is only indicative for the biomass derived from the biomass map because the latter is a model prediction (including altitude as a predictor) rather than an observation from field measurements.

RESULTS

Tree density was 146 stems of dbh \geq 20 cm ha⁻¹ on average (range = 2.5–362.5, SE = 43.7 ha⁻¹). The diameter distribution had a reverse-J shaped distribution that could be well approximated by a Weibull distribution with $146 \times \exp[-0.0589(D^{0.986} - 19.18)]$ giving the density of stems (in ha⁻¹) with a dbh greater than D (in cm) (Appendix 1). Basal area of stems \geq 20 cm dbh was 20.7 m² ha⁻¹ on average (range = 0.4–49.2, SE = 6.9 m² ha⁻¹). Above-ground dry biomass of stems \geq 20 cm dbh was 296 Mg ha⁻¹ on average (range = 5–820, SE = 113 Mg ha⁻¹).

The total above-ground biomass in the Makokou concession was estimated from the inventory data at 45.7 Tg with a 95% confidence interval of 45.1–46.3 Tg. However, spatial variation in biomass according to the map was not consistent with that of ground measurements. The correlation between the biomass estimated from inventory plots and that extracted from the biomass map was weak (Pearson correlation coefficient: 0.01; Figure 2). The response of biomass to altitude was not even the same for both biomass estimates. Whereas the biomass estimated from inventory plots peaked at intermediary altitudes (analysis of variance: F -value = 4.33, P = 0.013), the biomass extracted from the biomass

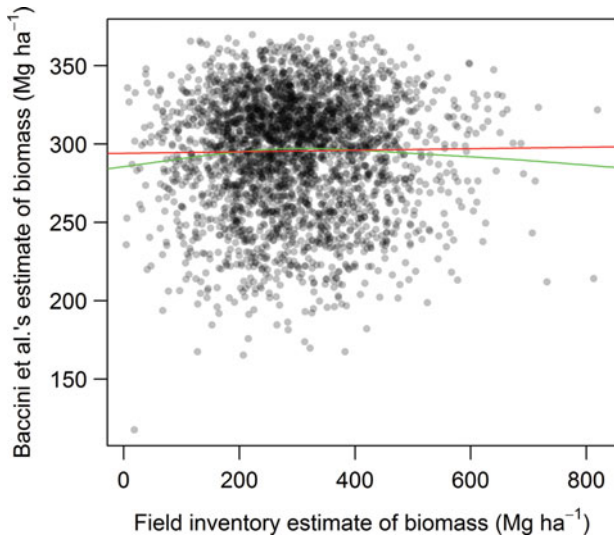


Figure 2. Above-ground biomass according to Baccini *et al.*'s (2012) map versus above-ground biomass in 0.4-ha plots in the Makokou forest concession, Gabon. The red line is the fit of a linear regression. The green line is the fit of a general additive model.

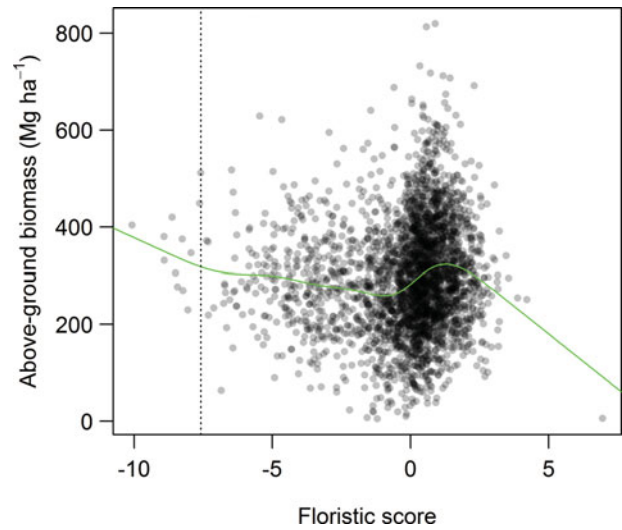


Figure 4. Above-ground biomass versus floristic score for 3024 0.4-ha plots in the Makokou forest concession, Gabon. The floristic score is the score along the first axis of the non-symmetrical correspondence analysis of the abundance table of the species in the plots. The dotted vertical line indicates monodominant *Gilbertiodendron dewevrei* plots (with a floristic score less than -7.6). The green line is the fit of a general additive model.

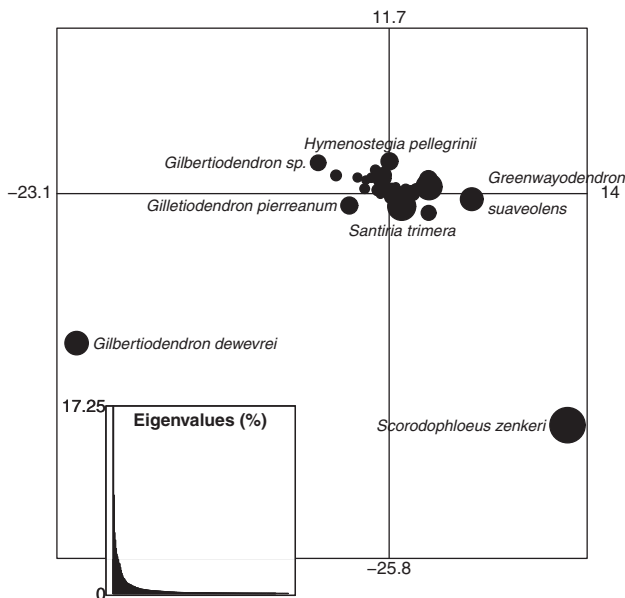


Figure 3. Projection of species on the factorial plane 1–2 of the non-symmetrical correspondence analysis (NSCA) of the abundance (≥ 20 cm) table of 253 species in 3024 0.4-ha plots in the Makokou forest concession, Gabon. The size of the symbols is proportional to the abundance of the species. The inset shows the eigenvalues of the NSCA.

map did not show any significant variation with altitude (F -value = 2.11, P = 0.120).

Plots could be ordinated along a floristic gradient determined by two species, *Gilbertiodendron dewevrei* and *Scorodophloeus zenkeri* Harms (Figure 3). Plots with a small score along the first axis of the NSCA had a high relative abundance of *G. dewevrei*, with a score less

than -7.6 corresponding to monodominant plots (i.e. $\geq 60\%$ of trees belonging to *G. dewevrei*). The relative density of *G. dewevrei* linearly decreased as the floristic score increased (Appendix 2), and a large score along the first axis indicated a high relative abundance of *S. zenkeri*. *Gilbertiodendron dewevrei*-monodominant plots had a significantly greater above-ground biomass than mixed plots (363 Mg ha^{-1} on average for monodominant plots versus 283 Mg ha^{-1} for mixed plots; one-way analysis of variance, P = 0.008). Nevertheless, the relationship between above-ground biomass and the floristic score was non-linear, with a decreasing trend for negative floristic scores and a hump-shaped response for positive floristic scores (Figure 4).

Among the five environmental and floristic predictors of above-ground biomass that were tested (soil type, altitude, slope, aspect and score on the first axis of the NSCA), only altitude and the sine of aspect were significant predictors according to the analysis of variance table (Table 1). The residual standard error of the fitted model was 110 Mg ha^{-1} and the spatial correlation of residuals had a range of 2.7 km and a nugget effect of 0.68 (Appendix 3). Because altitude and the sine of aspect were not significantly correlated (Pearson's correlation coefficient: 0.01), the effect of these two explanatory variables could be interpreted separately. The response of biomass to altitude had a modal shape with a maximum at an altitude of 707 m asl (predicted biomass of 367 Mg ha^{-1} on western slopes), and lower values at the lowest (241 Mg ha^{-1} on western slopes at the altitude of 485 m asl) and highest plot altitudes (133 Mg ha^{-1} on western

Table 1. Fit of the linear model predicting above-ground biomass from soil type, altitude (h), slope (p), aspect (θ) and floristic score (F) using data from 3024 inventory plots in the Makokou concession, north-eastern Gabon. The F -value and P -value are obtained from the analysis of variance table of the fitted model.

Predictor	Coefficient estimate	Std Error	F -value	P -value
Intercept for brachyapexols	-907.0	124.2	0.38	0.687
Difference of intercept between orthoapexols and brachyapexols	-7.98	16.6		
Difference of intercept between ferruginous crusts and brachyapexols	-24.1	18.7		
h	3.63	0.38	10.89	0.001
h^2	-0.0026	0.0003	86.83	< 0.001
p	2.44	36.02	0.04	0.846
$\sin(\theta)$	9.19	2.49	14.04	< 0.001
$\cos(\theta)$	2.27	2.90	0.77	0.380
F	-2.19	1.27	2.98	0.085

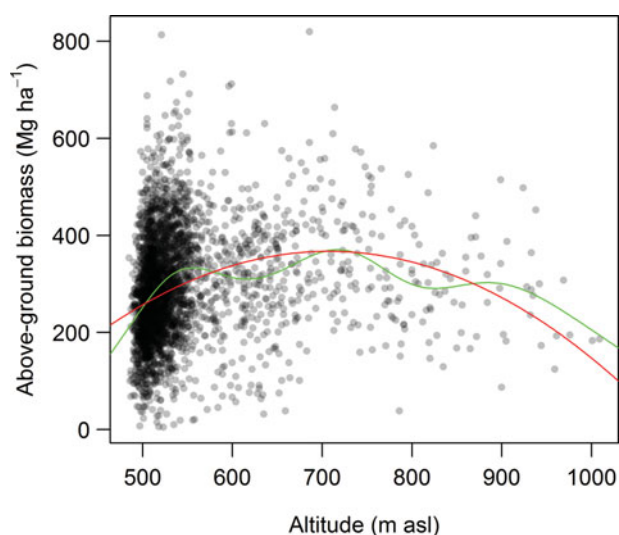


Figure 5. Above-ground biomass versus altitude for 3024 0.4-ha plots in the Makokou forest concession, Gabon. The red line is the fit of a linear regression with quadratic dependence on altitude for western slopes, brachyapexols, a null slope and a null floristic score. The green line is the fit of a general additive model.

slopes at the altitude of 1009 m; Figure 5). The sine of aspect defined a gradient from eastern slopes to western slopes. Thus, biomass was greater on the eastern slopes of the Mount Belinga and Mount Sassamongo mountain ranges than on their western slopes, with an additional predicted biomass of 18.4 Mg ha⁻¹ when moving from western to eastern slopes at the same altitude (Figure 6).

Basal area responded in exactly the same qualitative way to environmental and floristic predictors as above-ground biomass (Table 2): altitude and the sine of

aspect were the only two predictors with a coefficient significantly different from zero, with a modal response of basal area to altitude and a greater basal area on eastern slopes. The residual standard error of the fitted model was 6.60 m² ha⁻¹ and the spatial correlation of residuals had a range of 2.51 km and a nugget effect of 0.64.

When considering the mean wood density, among the five environmental and floristic predictors that were tested, only soil type, altitude (without its quadratic term) and floristic score were significant predictors according to the analysis of variance table (Table 3). The residual standard error of the fitted model was 0.05 g cm⁻³, with a range of 0.9 km and a nugget effect of 0.62. The interpretation of the parameter values depends on the collinearity among the predictors of the model. The floristic score presented a saturated relationship with altitude, with an increase of the floristic score with altitude up to a ceiling floristic score of about 0.8 for altitudes greater than about 540 m. Ferruginous crusts were predominantly found at high altitudes, whereas there was no significant difference in altitude between brachyapexols and orthoapexols. The floristic score was significantly different between soil types, with lower scores on brachyapexols, intermediate scores on orthoapexols, and higher scores on ferruginous crusts. These correlations among predictors and the sign of the model's parameters jointly brought the following interpretation: mean wood density decreased when altitude increased. Moreover, it was lower in forest stands characterized by *Scorodophloeus zenkeri* and greater in those characterized by *Gilbertiodendron dewevrei*. Soil slightly attenuated these differences.

DISCUSSION

The environmental variables that mostly explained biomass variation at the scale of the Makokou concession were altitude and aspect, with a modal response of biomass to altitude and a gradient from West- to East-oriented slopes. Both altitude and aspect do not directly influence forest structure but are summaries of local climate conditions with changing temperature, humidity and rainfall with altitude (Culmsee *et al.* 2010), and changing wind conditions with aspect. Changes of biomass with altitude have often been reported for tropical rain forests, but with contrasted trends. While Leuschner *et al.* (2007) reported a decrease of biomass along an altitudinal gradient of 2010 m in Ecuador, Culmsee *et al.* (2010) found no significant change of biomass along an altitudinal gradient of 1350 m in Sulawesi, and Alves *et al.* (2010) reported an increase of biomass along an altitudinal gradient of 1100 m in Brazil. When altitudinal gradients are so large, biomass changes are mostly explained by changes in floristic composition that go along (Ensslin

Table 2. Fit of the linear model predicting basal area from soil type, altitude (h), slope (p), aspect (θ) and floristic score (F) using data from 3024 inventory plots in the Makokou concession, north-eastern Gabon. The F -value and P-value are obtained from the analysis of variance table of the fitted model.

Predictor	Coefficient estimate	Std Error	F -value	P-value
Intercept for brachyapexols	- 52.3	7.5	0.95	0.385
Difference of intercept between orthoapexols and brachyapexols	- 0.28	1.0		
Difference of intercept between ferruginous crusts and brachyapexols	- 1.13	1.13		
h	0.22	0.02	20.24	<0.001
h^2	$- 1.52 \times 10^{-4}$	1.67×10^{-4}	88.31	<0.001
p	1.75	2.14	0.90	0.343
$\sin(\theta)$	0.60	0.15	17.16	<0.001
$\cos(\theta)$	0.12	0.17	0.56	0.455
F	$- 7.69 \times 10^{-2}$	0.08	1.04	0.309

Table 3. Fit of the linear model predicting wood density from soil type, altitude (h), slope (p), aspect (θ) and floristic score (F) using data from 3024 inventory plots in the Makokou concession, north-eastern Gabon. The F -value and P-value are obtained from the analysis of variance table of the fitted model.

Predictor	Coefficient estimate	Std Error	F -value	P-value
Intercept for brachyapexols	0.617	0.058	15.3	<0.001
Difference of intercept between orthoapexols and brachyapexols	0.0075	0.0049		
Difference of intercept between ferruginous crusts and brachyapexols	-0.0058	0.0058		
h	2.09×10^{-4}	1.80×10^{-4}	19.8	<0.001
h^2	-2.22×10^{-7}	1.33×10^{-7}	0.77	0.381
p	-0.016	0.016	0.85	0.357
$\sin(\theta)$	1.66×10^{-4}	11.2×10^{-4}	0.05	0.820
$\cos(\theta)$	6.49×10^{-4}	13.4×10^{-4}	0.42	0.518
F	-0.0016	0.0006	8.11	0.004

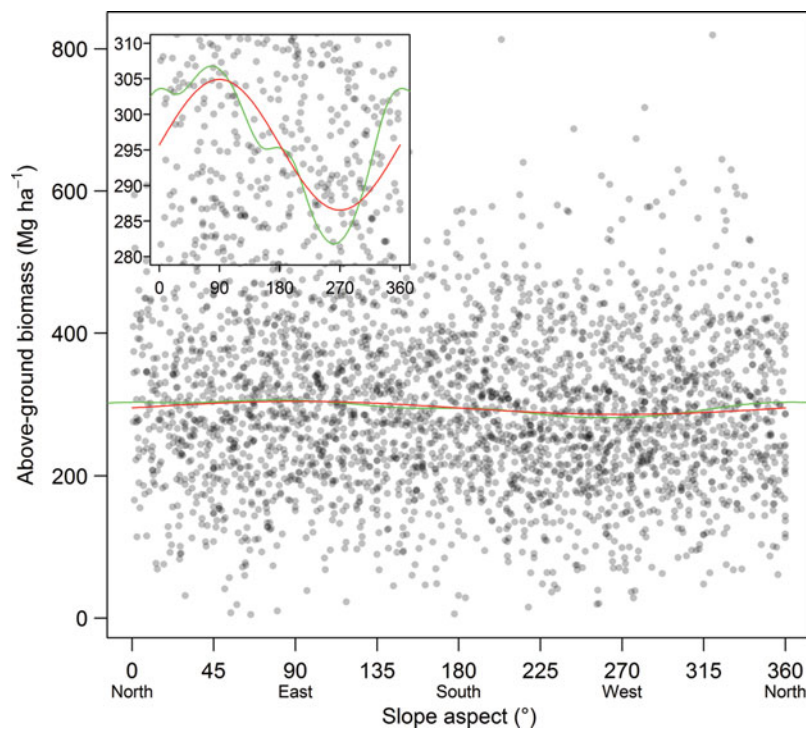


Figure 6. Above-ground biomass versus slope aspect for 3024 0.4-ha plots in the Makokou forest concession, Gabon. The red line is the fit of a linear regression with respect to the sine of aspect. The green line is the fit of a general additive model. The inset shows the same plot but with a restricted range on the y-axis.

et al. 2015) or compensate for (Culmsee *et al.* 2010) changes in forest structure. Along a smaller altitudinal gradient of 700 m in south-western Cameroon, Gonmadje *et al.* (2017) found a decrease in biomass that was also partially explained by a shift in species composition.

As regards slope aspect, its effect on species composition and height-diameter allometry when the mountain ridges protect from winds is documented (Chen *et al.* 1997, Thomas *et al.* 2015), and in dry ecosystems it has been identified as a factor explaining biomass variation (Sternberg & Shoshany 2001). In the present study, the North-South orientation of the Belinga mountain range and the prevailing West-South-West direction of winds in the Makokou region (as reported in IRENA, 2016, on-line global wind atlas by the Danmarks Tekniske Universitet, <http://irena.masdar.ac.ae/?&tool=dtu:gwa>) may explain why this effect was observed.

Variation in biomass at Makokou partially depended on the floristic score, reflecting on one part of the variation range a decreasing gradient of abundance of the species *Gilbertiodendron dewevrei* going in hand with a decrease in biomass. Like Makana *et al.* (2011) and contrary to Peh *et al.* (2011b), we found that biomass in *G. dewevrei*-monodominant stands at Makokou was on average 80 Mg ha⁻¹ larger than that in mixed stands. Nevertheless, the overall dependence of biomass on the floristic score was non-linear, with some confounding effect of altitude, so that the floristic score was not identified as a significant predictor of biomass on the whole range of biomass change.

The confounding effects of correlated predictors may explain why no unique response of biomass to altitude has been found (Kitayama & Aiba 2002). In the present study for instance, soil type that was correlated to altitude may have contributed to the biomass response to altitude, with ferruginous crusts being dominantly found at high altitudes.

To understand the biomass response to environmental variables, it may be important to disentangle the effect of forest structure and species composition on biomass variation. Diameter-height allometry that is one component of the forest structure that may influence plot-level biomass was disregarded in the current study by using a fixed *E* index. Should the spatial map of *E* by Chave *et al.* (2014) be used instead of a fixed *E*, the resulting variation in diameter-height allometry would not be consistent with the observed biomass response to altitude. At the scale of the Makokou concession, the spatialized *E* decreases indeed with altitude, implying greater tree height and biomass at higher altitude. This dependence contradicts field observations that tree height for the same dbh decreases with altitude in tropical rain forests (Clark *et al.* 2015, Culmsee *et al.* 2010). Tree height measurements in the Makokou concession would be needed to check if Chave's map of *E*, although correctly

representing the variation of *E* at large scale, fails to capture the variation of diameter-height allometry at the scale of a few square kilometres.

As a consequence, plot-level biomass in the Makokou concession was mainly driven by the plot-level basal area and mean wood density. Therefore, at first approximation, we can interpret the variation in mean wood density as the variation of the conditional biomass knowing basal area. Biomass at Makokou paralleled basal area in its response to altitude and aspect that are the most influencing environmental factors, indicating that the forest structure was the main driver of biomass change at the scale of the concession. However, after controlling for this main trend, biomass did depart from its expected value given the basal area depending on other environmental factors. Several authors have already highlighted that biomass and basal area responded differentially to the environment (Slik *et al.* 2010). Gourlet-Fleury *et al.* (2011) showed that the mean wood density increased along a gradient from rich to poor soil type. Culmsee *et al.* (2010) showed that the mean wood density increased with altitude. In both cases, the variation of *W* compensated for the variation in basal area so that biomass remained approximately constant across soil types or over the elevational gradient. In the current study, we also found that the mean wood density varied with soil type and altitude, but with a decreasing wood density at higher altitude. Moreover, wood density decreased on average by 0.03 g cm⁻³ from monodominant *Gilbertiodendron dewevrei* stands to stands characterized by *Scorodophloeus zenkeri*. Aspect did not influence the mean wood density as it did for biomass, thus suggesting that changes in biomass with aspect directly followed from changes in basal area.

When turning back to the average standing stock of the forest in the Makokou concession, the comparison of stand density (146 ha⁻¹), basal area (20.7 m² ha⁻¹), biomass (296 Mg ha⁻¹) with other published values for African lowland moist forests using 20 cm as a minimum dbh for inventory showed little difference: basal area between 17.8–22.3 m² ha⁻¹ (Gourlet-Fleury *et al.* 2011), and biomass between 217.5–273.3 Mg ha⁻¹ (Gourlet-Fleury *et al.* 2011).

To compare with published values using 10 cm as minimum dbh, we can consider that the dbh distribution at Makokou was close to a Weibull distribution with parameters 0.0589 and 0.986 (Appendix 1), which brings an estimated contribution of trees in the dbh range 10–20 cm of an additional 109.7 trees ha⁻¹ for stand density, 1.9 m² ha⁻¹ for basal area, and 14.9 Mg ha⁻¹ for biomass. Tree density (256 ha⁻¹), basal area (22.7 m² ha⁻¹) and above-ground biomass (311 Mg ha⁻¹) in the Makokou concession were then significantly lower than those reported by Lewis *et al.* (2013) for permanent sample plots in intact closed-canopy tropical forests of central Africa (density of 426 ha⁻¹, basal area of 30.3 m² ha⁻¹,

biomass of 395.7 Mg ha⁻¹), but similar to those reported by Maniatis *et al.* (2011) using forest inventory data in Gabon (biomass between 312–333 Mg ha⁻¹), by FAO (2005) for the semi-deciduous moist forests in Cameroon based on the data of the national forest inventory (296.3 Mg ha⁻¹), or by Kearsley *et al.* (2013) in eastern Democratic Republic of Congo (324 ± 40 Mg ha⁻¹).

Discrepancies between biomass estimates from permanent sample plots and those from large-scale forest inventories question the understanding that we currently have of the biomass distribution in central African rain forests. Comparisons between field estimates and biomass maps obtained by remote sensing, or comparisons between different biomass maps (Avitabile *et al.* 2016, Mitchard *et al.* 2014), show similar levels of discrepancy. In this study, the field estimate of the total above-ground biomass in the Makokou concession was consistent with the estimate of 45.1 Tg given by the biomass map by Baccini *et al.* (2012), but the spatial variation in biomass was not. Part of the explanation for this discrepancy relies on the differences of scale used by the different studies. Trends in biomass that are captured at the global level may not be correct when the resulting global map is cropped to a few square kilometres. The same could be true for the *E* index or climate variables, and it justifies why we used altitude and aspect as proxies for climate rather than using global climate data. It further calls for a better understanding of the relationship between biomass and environmental variables at the scale of a few thousand hectares.

Based on the results of the current study, we conclude that, in Makokou, variation in forest structure (both basal area and biomass) was primarily driven by altitude and aspect while soil type and floristic composition (in particular the relative abundance of *Gilbertiodendron dewevrei*) played a role in differentiating the variation in biomass from the variation in basal area.

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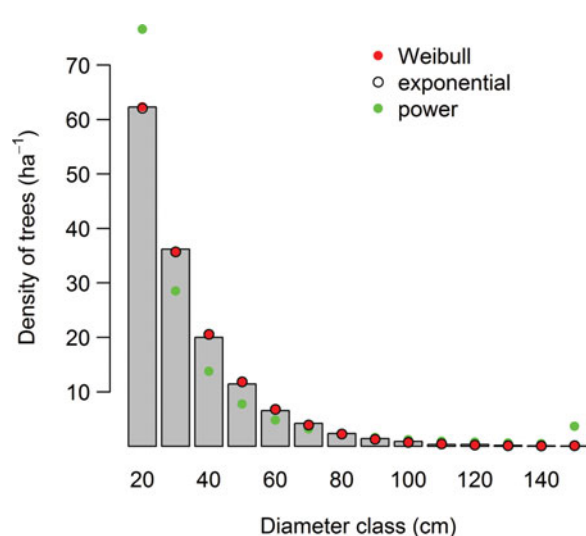
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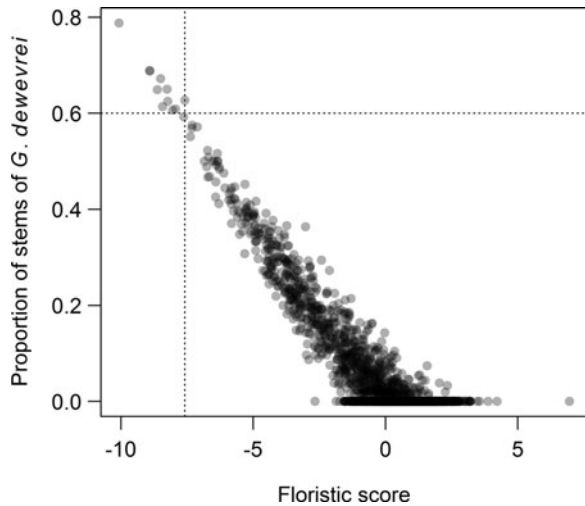
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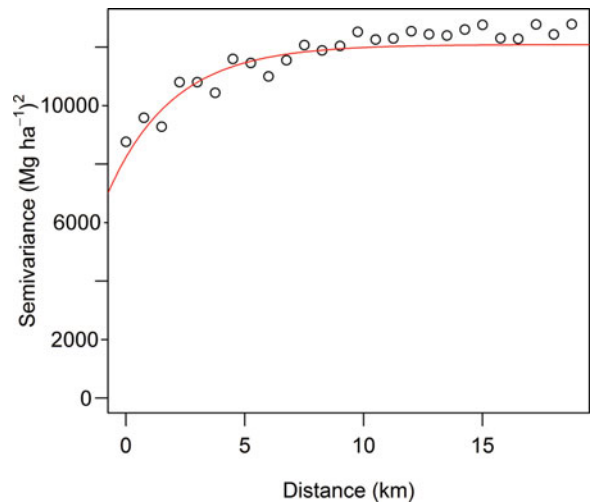
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Appendix 1. Fit of a truncated exponential, a truncated power and a truncated Weibull distribution to the diameter distribution observed in the Makokou concession using the method described by Taubert *et al.* (2013, based on the binned number of trees in 14 diameter classes ranging from 20 cm to 150 cm with a width of 10 cm, except the last class that includes all trees ≥ 150 cm dbh). The distribution functions of the fitted distributions are: $F(x) = 1 - \exp[-0.0553(x - 20)]$ for the truncated exponential (AIC = 433), $F(x) = 1 - (x/20)^{2.830}$ for the truncated power (AIC = 22 627), and $F(x) = 1 - \exp[-0.0589(x^{0.986} - 20^{0.986})]$ for the truncated Weibull (AIC = 432).



Appendix 2. Relationship between the floristic score (score on the first axis of the non-symmetrical correspondence analysis of the table of abundances of 253 tree species in 3024 inventory plots in the Makokou forest concession, north-eastern Gabon) and the proportion of stems in the plot belonging to *Gilbertiodendron deweyrei* (De Wild.) J.Léonard. Each dot corresponds to an inventory plot. Following Peh *et al.* (2011a), the minimal proportion of 60% (horizontal dotted line) was taken as the threshold for monodominant plots.



Appendix 3. Empirical variogram (dots) of the residuals of the model that predicts above-ground biomass from environmental and floristic predictors in the Makokou concession, north-eastern Gabon, and modelled spatial structure of the residuals (red line) using an exponential model with nugget: $\gamma(d) = (109.9)^2 \{0.68 + 0.32 [1 - \exp(-d/2.7)]\}$, where $\gamma(d)$ is the semivariance of above-ground biomass in two plots a distance d apart.