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Cite this article: Enock Bocko Y *et al.* 2026 Species-specific wood density improves biomass estimation in Congo Basin peatland forests. *Phil. Trans. R. Soc. B* **381**: 20240484.
https://doi.org/10.1098/rstb.2024.0484

Received: 6 March 2025
Accepted: 25 March 2026

One contribution of 17 to a discussion meeting issue 'African tropical peatlands: function, value and vulnerability'.

Subject Areas:
ecology, ecosystem, environmental science, plant science

Keywords:
Congo Basin, peat swamp forest, wood density, above ground biomass, functional traits

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Supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.8572124.

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Species-specific wood density improves biomass estimation in Congo Basin peatland forests

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The central Congo Basin hosts the world's largest tropical peat swamp forest (PSF), covering 167 600 km^2 and storing approximately 29 Pg of carbon below ground. However, estimates of above ground biomass (*AGB*) remain limited, partly owing to reliance on global wood density (*WD*) databases that may not reflect local species characteristics. This study assessed the impact of species-specific *WD* on *AGB* estimation in five PSF sites of the northern Republic of Congo. Specific *WD* was collected in one site, and these

data were then used to estimate *AGB* in four additional sites. We collected wood cores using an increment borer from 244 trees to measure the *WD* of the 20 most abundant species (93% of trees with diameters ≥10 cm). Using global *WD* values overestimated *AGB* by 24.7% ($p < 0.05$). The low average local *WD* (0.460 ± 0.12 g cm^{-3}) explained this difference. The *WD* variation was primarily species-driven (58%) and associated with functional traits; pioneer and evergreen species had lower *WD*. These findings highlight the importance of locally measured *WD* for accurate biomass and carbon stock estimation in tropical peatland forests. A French translation of this abstract is available in the supplementary material.

This article is part of the discussion meeting issue 'African tropical peatlands: function, value and vulnerability'.

1. Introduction

The Congo Basin is home to the world's largest tropical peatland complex covering approximately 167 600 km^2 and storing approximately 29.0 Pg of carbon below ground [1]. Although the peatland above ground carbon stocks are 13 times less than the below ground carbon stocks [1,2], good estimates of above ground biomass (*AGB*) for the peatlands are essential for understanding total carbon stocks, flows and potential losses. It is also important to note that today, only 17% of the world's peatlands are protected [3]. Furthermore, nearly half of those located in temperate and tropical zones still experience significant human pressure [3]. For the Republic of the Congo and the Democratic Republic of the Congo who are engaged in the reducing emissions from deforestation and forest degradation (REDD+) process, they require robust carbon accounting, including requirements for carbon reference levels [4].

For estimates of tree *AGB*, established allometric equations can be used, which use tree diameter at breast height (*DBH*), wood density (*WD*) and often height as measured parameters [5,6]. *DBH* and tree height are normally based on *in situ* measurements. For practical reasons, *WD*, despite being the second most important predictor variable of tree *AGB* after *DBH*, is rarely measured *in situ*. Instead, values are often obtained from databases of *WD*, such as the DRYAD database. As intraspecific and even intrageneric variations in *WD* are often low [7], the use of a global database can be a practical solution, but it can also have its limitations. For example, not all species are listed, or there are a limited number of individuals per species in the database. In the DRYAD database, of the 619 species found in tropical Africa, 264 (43%) are represented by a single sample [8]. Some studies have shown that the use of *WD* values from the DRYAD database can lead to a bias in local *AGB* estimations [9,10].

Interspecific variability in wood is strongly correlated with parameters both internal (functional characteristics) and external (environmental) to the species. An example of the correlation between functional characteristics and *WD* is the low specific *WD* of pioneer species compared to shade-bearing species [9,11–14]. This reflects the different ecological niches the species occupy and the different functional investments they make, for example in stem strength and construction and maintenance costs of the tree crown. In fact, shade-bearing species that invest in *WD* benefit from implosion-resistant hydraulic systems, chemical defences and a high ratio of trunk strength to tree surface [15]. By contrast, pioneer species tend to have larger leaves and faster volumetric growth, but lower *WD* and so are more likely to break [16].

Environmental factors, such as altitude, water gradient, average annual temperature, clay content and soil micronutrient content, influence the spatial variability of *WD* [17–19]. Although a negative influence of soil fertility on wood-specific density has been observed in some tropical forest sites [20,21], contrary results have been found at other sites [22,23]. The specific density of wood tends to decrease with increasing altitude [7,24] and to increase with soil fertility [22]. In addition, an increase in the amount of time when the soil is saturated with water influences the floristic composition of the environment [22,25]. For example, periodically flooded forests in the Amazon are made up of an assemblage of shade-tolerant species and, therefore, have a higher wood species density than on unflooded uplands [17]. Thus, in this region inundation and low soil fertility tend to reduce the specific density of wood [17]. However, for the central Congo peatlands, while it is known that certain species are common in this environment [2,25], it is not known how functional characteristics, soil fertility and high peatland water table affect *WD* and tree biomass estimation.

Although *WD* is a key parameter for the estimation and spatial variability of above ground tree biomass, little effort has been made to collect *WD* data for species or individuals within Central Africa [9], particularly in wetland forested ecosystems. Improving *WD* estimations and better understanding of the determinants of *WD* variation in peat swamp forests (PSFs) are important for improved knowledge of ecosystem functioning in Central Africa. Furthermore, future monitoring of the vegetation carbon sink/source in this system will require careful investigation if subtle changes in the carbon stocks of trees are to be detected; this will be contingent on robust estimates of *WD*. We addressed three research questions:

(i) what is the extent of variation in *WD* among coexisting tree species?
(ii) what are the determinants of interspecific variation in *WD*? and
(iii) how important are the impacts of interspecific variation in *WD* on the plot-level *WD* and *AGB*?

2. Material and methods

(a) Study area

Fieldwork was carried out in the Likouala Department, in the north of the Republic of Congo. The climate of the area is of the transitional equatorial type, marked by four seasons: a long dry season (December–March), a long rainy season

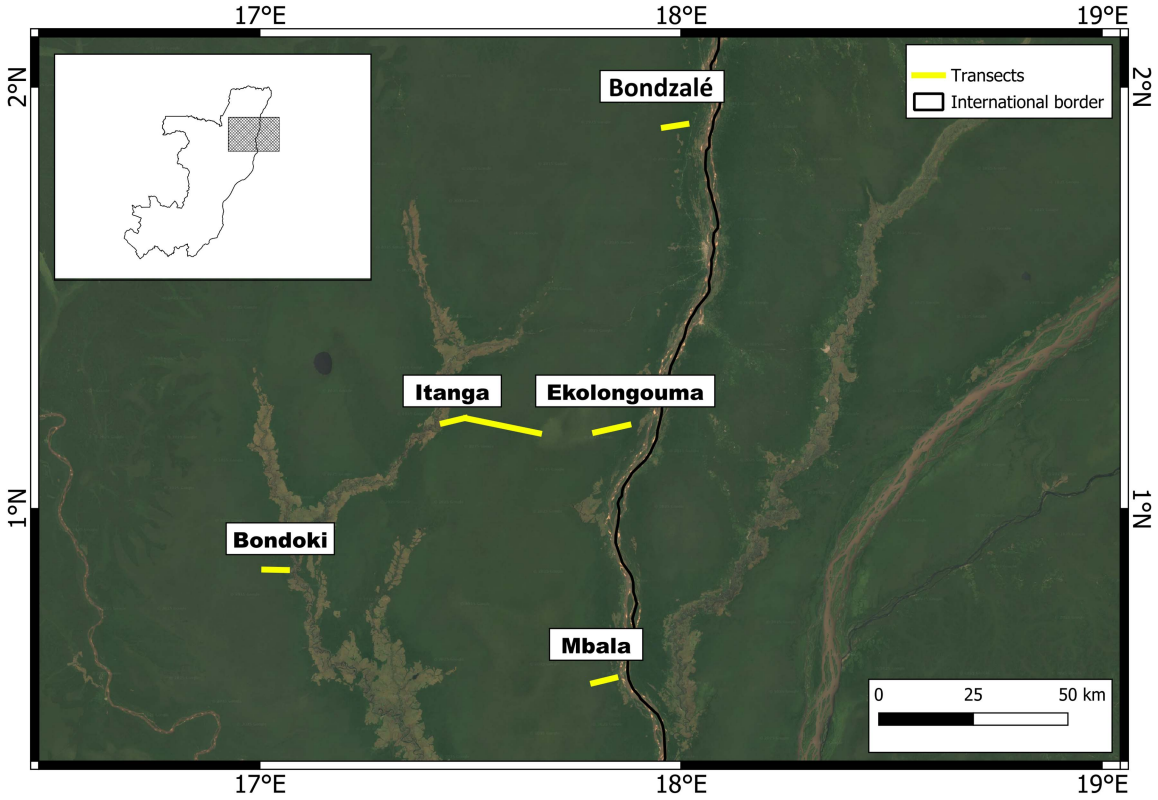

Figure 1. Location of the study sites in the peat swamp forest of the Likouala Department.

(August–November), a short dry season (July–August) and a short rainy season (April–June) [26]. The average temperature and rainfall are 25.6°C and 1556.5 mm, respectively [26]. The vegetation is dominated by two major communities: hardwood-dominated peat swamp vegetation and palm-dominated peat swamp vegetation [2,27]. The relief of the study area is flat, with an altitude varying between 300 and 400 m above see level (masl).

(b) Wood density measurements

We define *WD* as the ratio of the dry mass of a wood sample divided by its green volume [7]. Specific *WD* that was collected in one site (Ekolongouma), which was then applied to four other sites in a PSF (figure 1). The PSF in the northern Republic of Congo occupies an interfluvial basin, extending approximately 60 km between the black-water Likouala-aux-Herbes River and the white-water Oubangui River [2]. *WD* samples were collected from 273 individuals across 20 species (table 1) during the dry season, in February 2020. Only trees of the 20 dominant species of the peat-flooded forest in terms of frequency and relative density as observed in the work of Bocko *et al.* [25] were selected for sampling outside the plots for biomass estimation. In order to ensure that the trees were representative in terms of diameter, the sample trees were divided into six diameter classes: 10 to <20; 20 to <30; 30 to <40; 40 to <50; 50 to <60; and ≥60 cm. Three individuals per diameter class were sampled for each species, that is, 18 wood samples per species. However, for some tree species, not all diameter classes could be found. For this reason, only 244 wood samples were collected out of the 360 expected (table 1). *WD* samples were collected using a 5 mm increment borer at 1.30 m from the ground, unless the trunk had an abnormality at this point, in which case the sample was taken 50 cm above the abnormality. Each tree was hollowed out slightly beyond the pith of the stem, and the samples were placed into plastic drinking straws, sealed at the end, for transportation out of the field. In the laboratory, each sample was placed into water for 30 min to ensure measurement of the correct volume via adequate swelling. Green volume was calculated by measuring the wood sample's total length and the mean diameter from two measurements (one at each end of the sample) using digital callipers, while carefully avoiding any application of pressure on the wood sample with the calliper blades. Samples were subsequently dried at 100°C until constant mass in an electronic oven to give the dry mass.

(c) Species traits

We gathered data on four functional traits for the 20 species, for which we obtained *WD* values. These were maximum diameter (D_{max}), leaf habit (LH), dispersal mode (DM) and regeneration guild (RG) (supplementary material, table S1). We calculated D_{max} (range: 20–94 cm) as the 95-percentile stem diameter of the sampled trees for each species [28]. For LH, 18 species were considered evergreen, and two species were considered deciduous [29]. For DM, 12 were animal-dispersed, six were wind-dispersed and two species had unassisted DMs [30]. For RG, we followed the definitions of Hawthorne [31], with eight classified as shade-bearing (SB), five as non-pioneer light-demanding (NPLD) and six as pioneer (P) species.

Table 1. Characteristics of the wood density from local database for each study species: the samplings, including the number of trees and the diameter (cm) range, are also given for each study species.

code	species	family	number of trees	diameter range (cm)	mean wood density (g cm^{-3})	wood density range (g cm^{-3})
Car	*Carapa procera* DC.	Meliaceae	17	13.1–72.4	0.568	0.517–0.614
Cle	*Cleistopholis patens* (Benth.) Engl. & Diels	Annonaceae	7	25.8–60.0	0.202	0.139–0.272
Coe	*Coelocaryon preussii* Warb.	Myristicaceae	18	10.2–71.3	0.351	0.270–0.408
Dan	*Daniellia pynaertii* De Wild	Fabaceae	8	30.7–91.8	0.370	0.299–0.451
Dio	*Diospyros crassiflora* Hiern	Ebenaceae	5	11.3–20.7	0.680	0.655–0.701
Dry	*Drypetes occidentalis* (Müll. Arg.) Hutch.	Putranjivaceae	13	13.0–52.3	0.476	0.438–0.519
Ent	*Entandrophragma palustre* Staner	Meliaceae	19	12.5–79.8	0.475	0.356–0.657
Eri	*Eriocoelum microspermum* Gilg ex Radlk.	Sapindaceae	7	11.4–30.0	0.539	0.458–0.599
Gar	*Garcinia smeathmannii* (Planch. and Triana) Oliv	Clusiaceae	5	12.5–22.2	0.460	0.440–0.491
Gro	*Grossera macrantha* Pax	Euphorbiaceae	16	13.6–53.6	0.454	0.326–0.541
Mac	*Macaranga spinosa* Müll. Arg.	Euphorbiaceae	11	12.3–45.2	0.269	0.206–0.346
Manf	*Manilkara fouilloyana* Aubrév. & Pellegr.	Sapotaceae	18	16.3–74.7	0.667	0.447–0.820
Manl	*Manilkara letouzey* Aubrév.	Sapotaceae	12	13.9–47.0	0.470	0.417–0.584
Mit	*Mitragyna stipulosa* (DC) O. Kintze	Rubiaceae	4	20.8–60.8	0.396	0.386–0.414
New	*Newtonia devredii* G. C.C. Gilbert & Boutique	Fabaceae	11	17.6–60.3	0.520	0.428–0.585
Ste	*Sterculia tragacantha* Lindl.	Malvaceae	11	35.6–67.1	0.330	0.270–0.387
Sym	*Symphonia globulifera* L. f.	Clusiaceae	16	12.6–100.3	0.532	0.478–0.763
Uap	*Uapaca mole* Pax	Phyllanthaceae	18	11.2–69.0	0.551	0.478–0.623
Xylae	*Xylopia aethiopica* (Dunal) A. Rich.	Annonaceae	11	12.3–44.6	0.395	0.340–0.461
Xylru	*Xylopia rubescens* Oliv.	Annonaceae	17	15.2–57.5	0.325	0.246–0.681

(d) Above ground biomass plot censuses

To compare the effects of using local *WD* values versus the DRYAD database *WD* values on *AGB* estimates, we applied both sets of *WD* values to forest plot data collected at five different sites across the Likouala Department (figure 1): Itanga (1.205033 N, 17.447833 E), Bondoki (0.85444 N, 17.06425 E), Bondzalé (1.91242 N, 18.01296 E), Ekolongouma (1.225955 N, 17.911272 E) and Mbala (0.59886 N, 17.84406 E). At each study site, along a single transect that crossed *terra firme* forest, periodically flooded forest and flooded peat forest (FF), circular plots were installed every 100 m. As *WD* samples were collected from within an FF, we applied the two sets of *WD* values to the FF plots only across the five sites. A total of 94 nested circular plots were installed in the FF across the five sites: Bondoki, 16 plots, 6 km transect; Bondzalé, six plots, 6 km transect; Ekolongouma, six plots, 9 km transect;

Itanga, 60 plots, 20 km transect; Mbala, six plots, 6 km transect. The five sites were chosen in order to cover a large spatial area within the Likouala Department and to sample the different vegetation types found within the region. Accessing the peatlands can be challenging, and the transect length and the number of plots were determined by conditions on the ground at the time of sampling. The Itanga transect was installed during the main dry season, and its long length was intended to provide data points from near to the centre of a large area of flooded peat forest.

The circular plots were composed of three nested subplots of 6, 14 and 20 m radius, where all trees in the diameter ranges of 10 to <30, 30 to <60 and ≥60 cm, respectively, were measured. In total, across the 94 plots, 1075 individuals from 40 species were measured.

(e) Above ground biomass estimation

AGB for each tree was estimated using the following allometric equation taken from Chave *et al.* [5]:

$$AGB = \exp\left[-1.803 - 0.976 \times E + 0.976 \times \ln(WD) + 2.673 \times \ln(D) - 0.0299 \times (\ln(D))^2\right]. \tag{2.1}$$

Tree diameter (D; cm) was measured in the field. E represents an environmental stress factor, corresponding to the site locations, extracted from a climate map [4] (supplementary material, table S2). Each stem was assigned two *WD* values (*WD* in g cm^{-3}) corresponding to the species average from both the local database (this study), on the one hand, and the global *WD* DRYAD database, on the other [8,16]. For the DRYAD database *WD* values, we computed averages at species-level when possible, and if not, at a genus- or family-level for tropical Africa. For the DRYAD database, *WD* values were available at species level for 10 species, genus level for nine species and family level for one species (supplementary material, table S1). Thus, we estimated the biomass in two different ways. Firstly, we used the values of the specific *WD*s of the local species (AGB_{local}) collected in one site, which was then applied to 94 plots of five sites, and secondly, those of the global database (DRYAD), AGB_{DRYAD}.

(f) Data analysis

To test for significant differences in *WD* among species, one-way analysis of variance (ANOVA) was used, with species as a random factor and *WD* as a fixed factor. The coefficient of variation, which represents the ratio of the standard deviation to the mean, of *WD* was calculated for each species in order to quantify *WD* variation within each species. In addition, a nested ANOVA was used to determine the degree of variation explained by genus- and family levels. A multilevel model [32] was first fitted for *WD* according to the following equation:

$$WD = \mu + f/g/\text{sp} + \varepsilon, \tag{2.2}$$

where μ is the overall mean value of *WD*, $f/g/\text{sp}$ represents the taxonomic level of the data, that is, each species (sp) belongs to a genus (g), nested in a family (f), and ε is the residual term which includes natural variability as well as any measurement error. Furthermore, the coefficient of variation, which represents the ratio of the standard deviation to the mean, of *WD* was calculated for each genus and family in order to quantify how *WD* varies within each taxonomic level.

To evaluate the most important factors in determining *WD*, species traits, including $D_{\max}$, LH, DM and RG, were considered as determinants for each species. The general linear mixed effect model of a tree i belonging to species s has been developed using species traits (equation (2.3)). The inclusion of relevant random effects helped to ensure the accuracy of the model parameters while supporting the validity of the generalized conclusions [33]. Species traits, including $D_{\max}$, LH, RG and DM, were included in the model as fixed effects and taxonomy (a nested design of family, genera within families and species within genera within families) as random effects (equation (2.3)):

$$WD_{is} = \beta + \alpha_1 \times D_{\max_s} + \alpha_2 \times \text{LH}_s + \alpha_3 \times \text{RG}_i + \alpha_4 \times \text{DM}_s + \beta_{\text{family}}[i] \tag{2.3}$$

where α and β are the slope and intercept, respectively.

To evaluate the impacts of the interspecific variation in *WD* on the *AGB* and the difference between *WD* from the local database and from the global DRYAD database, we calculated the root mean square error (*RMSE*), the bias and the paired t-test. The *RMSE* (in g cm^{-3} for *WD* and in kg for *AGB*) was calculated as the square root of the mean square difference between *WD* obtained from the local database (referred to as *measured*) and *WD* from the global DRYAD database (referred to as *predicted*) or between *AGB* estimation using *WD* from the local database (referred to as *measured*) and *AGB* estimation using *WD* from the global DRYAD database (referred to as *predicted*) at the plot level (i):

$$RMSE = \sqrt{\frac{1}{n}\sum_{i=1}^{n}\left(measured_i - predicted_i\right)^2}, \tag{2.4}$$

where n is the number of sampled plots in each study site.

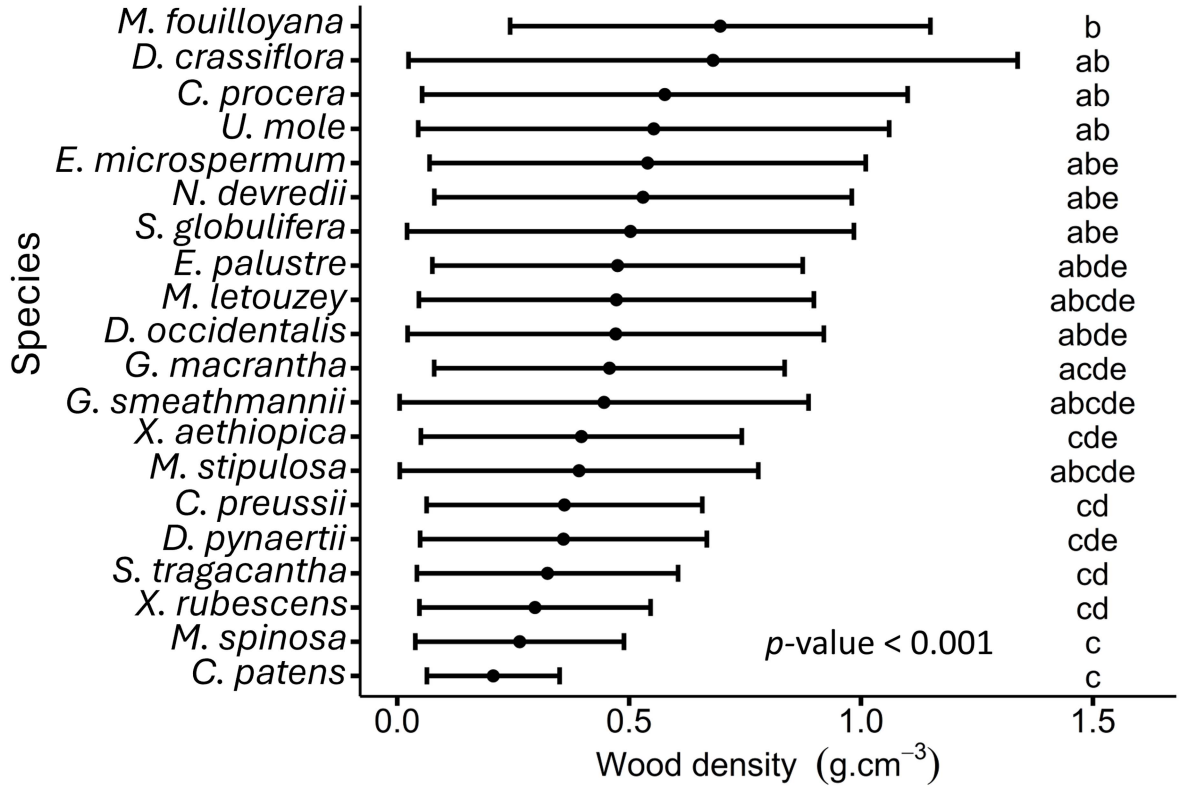

Figure 2. Distribution of wood density among study species. Lines with median (filled circle) indicate upper and lower 0.05 quantiles for crown depth and crown diameter or 0.5 quantiles for crown volume. Different letters and numbers indicate significant differences (p-value < 0.050 with Kruskal–Wallis test) among species. The species codes are given in table 1.

The bias (in %) was calculated as the difference between mean predicted and measured *WD* and *AGB* at the plot level (*i*) using equation (2.4):

$$\text{bias} = \frac{1}{n}\sum_{i=1}^{n}\left(predicted_i - measured_i\right)/measured_i, \tag{2.5}$$

where n is the number of sampled plots in each study site.

We used a paired *t*-test to identify significant differences between measured and predicted *WD* and *AGB*. Lastly, a one-way ANOVA, with site as a random factor, was used to test the spatial variation in both measured and predicted plot-level *WD* and *AGB*. A Pearson correlation test was carried out between the local *WD* values and those in the global DRYAD database for all the trees sampled.

When testing for differences in *WD* among species, conditions of normality and homoscedasticity of residuals (checked graphically and with Shapiro–Wilk and Breusch–Pagan tests) were violated, so a non-parametric test (Kruskal–Wallis rank sum test) was used. For the non-parametric Kruskal–Wallis test [34], the null hypothesis was 'no difference between medians of wood density'. When the null hypothesis was rejected, we conducted post hoc Kruskal–Wallis multiple comparisons between medians [35].

All the statistical analyses were performed with the open source R environment [36] using 'ggplot2' for graphical output [37].

3. Results

(a) Interspecific variation of wood density

WD values for the 20 species from the PSF had a mean of 0.460 g cm^{-3}, with a range of 0.202–0.680 g cm^{-3}. Notably, there were no very high *WD* species sampled in the PSF. *WD* was significantly different among coexisting species (ANOVA, p-value < 0.001). *Manilkara fouilloyana* Aubrév. & Pellegr. (Sapotaceae) and *Diospyros crassiflora* Hiern (Ebenaceae) had significantly higher *WD* values, whereas *Macaranga spinosa* Müll. Arg. (Euphorbiaceae) and *Cleistopholis patens* (Benth.) Engl. & Diels (Annonaceae) had significantly lower *WD* values compared to other species (figure 2).

We found that 58% of the tree *WD* was explained by species-level variation, 24% by inter-genus variation and 13% by interfamily variation (table 2). There was a significant tendency towards more variability in species with a coefficient of variation of 23% and genera with a coefficient of variation of 21% than in family with a coefficient of variation of 13%. Yet, overall, there was little

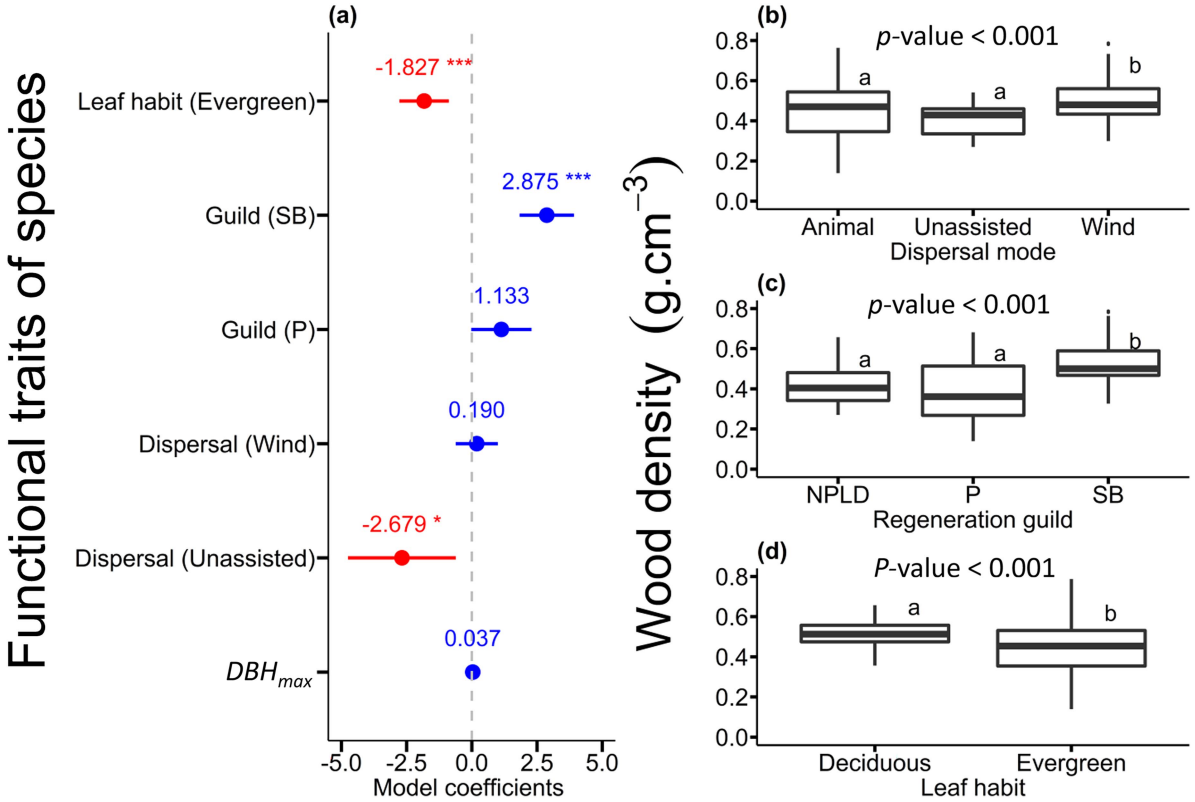

Figure 3. Species-level determinants of the wood density: (a) standardized coefficients of wood density with error bars showing confidence intervals (*p-value < 0.050, ***p-value < 0.001) with the blue as positive effect and the red as negative effect and all coefficients from fixed effects and random effects shown in the supplementary material, table S4; bivariate relationships between the wood density and the dispersal mode (b), bivariate relationships between the wood density and the regeneration guild (c), and bivariate relationships between the wood density and the leaf habit (d). Significant differences (non-parametric Kruskal–Wallis test) are shown by different letters using post hoc Kruskal–Wallis multiple comparisons between medians.

Table 2. Fraction of variance in wood density explained by various taxonomic levels (species, genus and family) for the full wood density dataset (244 trees): the sum of squares (SS), the mean squared (MS), explained variance (%) and coefficient of variation (CV, %) are given for each taxonomic level.

taxonomic level	SS	MS	explained variance (%)	CV (%)
species	0.314	0.155	58.50	22.87
genus	0.551	0.11	23.64	20.55
family	2.38	0.198	12.85	13.35
error	1.07	0.005	5.01	14.96

variation in *WD* within the 20 species studied, as evidenced by the coefficient of variation ranging from 3% to 31% (supplementary material, table S3).

For within-species variation, of the 20 study species, *Xylopia rubescens* Oliv. (Annonaceae) and *C. patens* (Benth.) Engl. & Diels (Annonaceae) were both species that had a large variation of *WD* values. Among the 18 genera, the within-genus coefficients of variation ranged from 3% (*Diospyros*) to 25% (*Xylopia*) (supplementary material, table S3). The most variable families were, in decreasing order, Annonaceae, Euphorbiaceae, Sapotaceae and Fabaceae (supplementary material, table S3). Finally, we did not detect any significant relationship between local tree *WD* and tree diameter for any species (supplementary material, figure S1).

(b) Determinants of interspecific variation in wood density

The *WD* from local data was strongly related to species traits, including RG, LH and DM (figure 3 and the supplementary material, table S4). There were significant variations in *WD* among RG, LH and DMs with SB species, deciduous and wind-dispersed species showing a higher *WD* (figure 3b–d).

The average *WD* of SB species (0.54 ± 0.10 g cm^{-3}) was significantly higher than that of P species (0.38 ± 0.13 g cm^{-3}) and NPLD (0.41 ± 0.09 g cm^{-3}) species. Similarly, those using wind as a means of seed dispersal had a significantly higher average *WD* (0.51 ± 0.12 g cm^{-3}) than those dispersing via animals (0.44 ± 0.13 g cm^{-3}) and controlled assistance (0.40 ± 0.08 g cm^{-3}). In

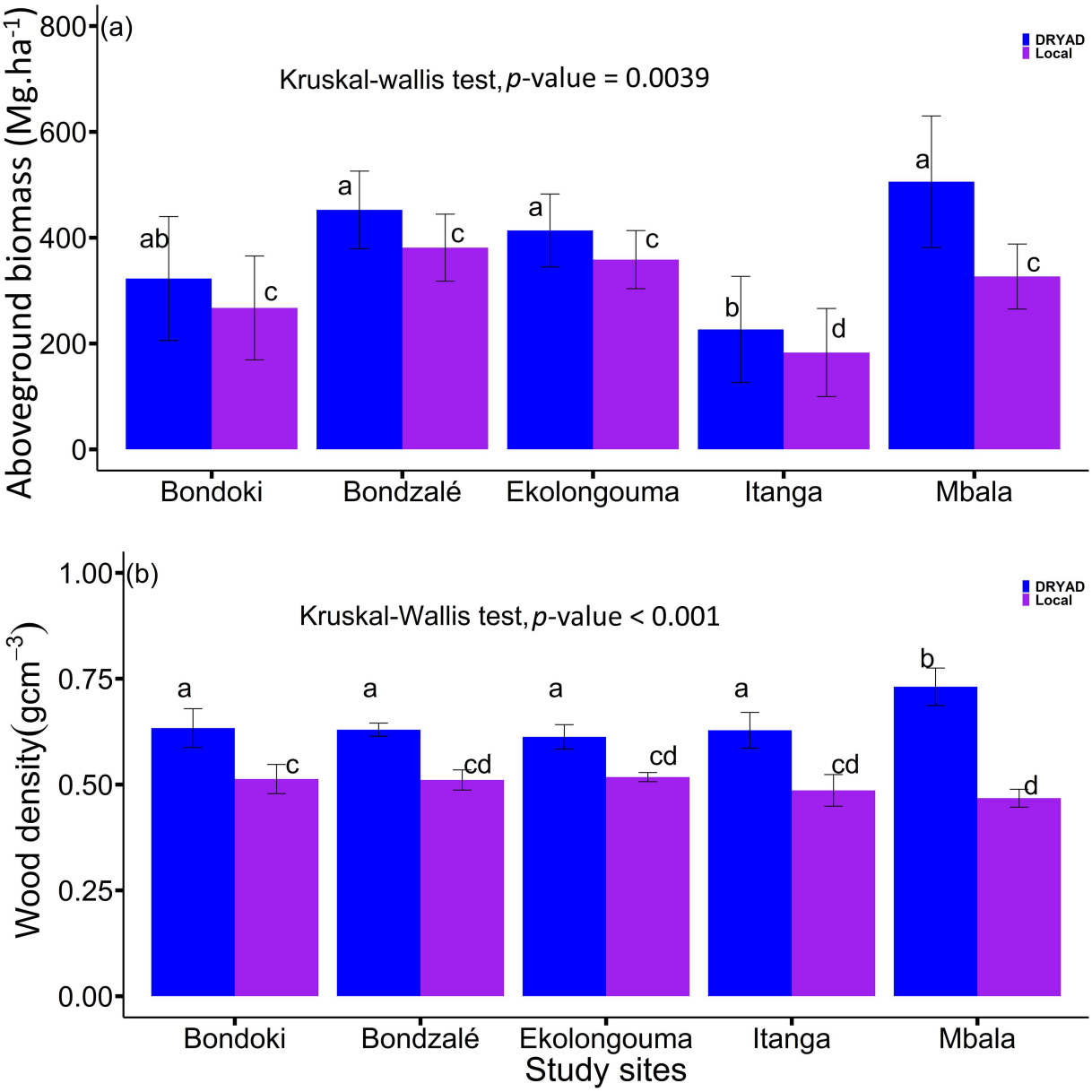

Figure 4. Differences among study sites in above ground biomass (a) and wood density (b) for DRYAD and local databases. Boxplots that show values of above ground biomass (Mg ha^{-1}) and wood density (g cm^{-3}) are given at the plot level in each study site. Statistical comparisons among above ground biomass are based on the non-parametric Kruskal–Wallis rank sum test and different letters indicate a significant difference ($p < 0.05$) according to Dunn post hoc tests.

addition, deciduous forest species had a mean *WD* value (0.51 ± 0.06 g cm^{-3}) that was significantly different from the 0.45 ± 0.13 g cm^{-3} of evergreen forest species (supplementary material, table S5).

(c) Above ground biomass estimation

Calculating *AGB* using local *WD* values gave a mean (±s.d.) of 230.28 ± 106.48 Mg dry mass ha^{-1}, which was significantly less than the *AGB* value calculated using the DRYAD database, at 287.16 ± 135.73 Mg dry mass ha^{-1} (Kruskal–Wallis test, *p*-value = 0.003). In all five transects, the AGB_{local} was lower than AGB_{dryad}, showing the importance of local and habitat-specific *WD* measurements (figure 4a). The mean values of *AGB* obtained per site, after using local *WD*, were 182.88 ± 83.19, 267.26 ± 98.22, 326.61 ± 61.48, 358.49 ± 54.82 and 381.11 ± 63.20 Mg dry mass ha^{-1}, respectively, for Itanga, Bondoki, Mbala, Ekolongouma and Bondzalé. The values obtained using the *WD* from the DRYAD database were 226.64 ± 100.27, 322.75 ± 117.13, 413.66 ± 68.86, 452.49 ± 73.31 and 505.67 ± 124.31 Mg of dry mass ha^{-1} for the Itanga, Bondoki, Ekolongouma, Bondzalé and Mbala sites, respectively. On average, AGB_{local} was overestimated by 24.7% after using *WD* from the DRYAD database.

There is a significant variation in *WD* and *AGB* among sites, but the patterns differed between data derived from the global DRYAD database and data from the local database (figure 4a,b). For example, when using local *WD* values, the Bondoki transect had significantly higher *WD* values (0.51 ± 0.03 g cm^{-3}) than at Itanga (0.49 ± 0.009 g cm^{-3}), but when using DRYAD *WD* values,

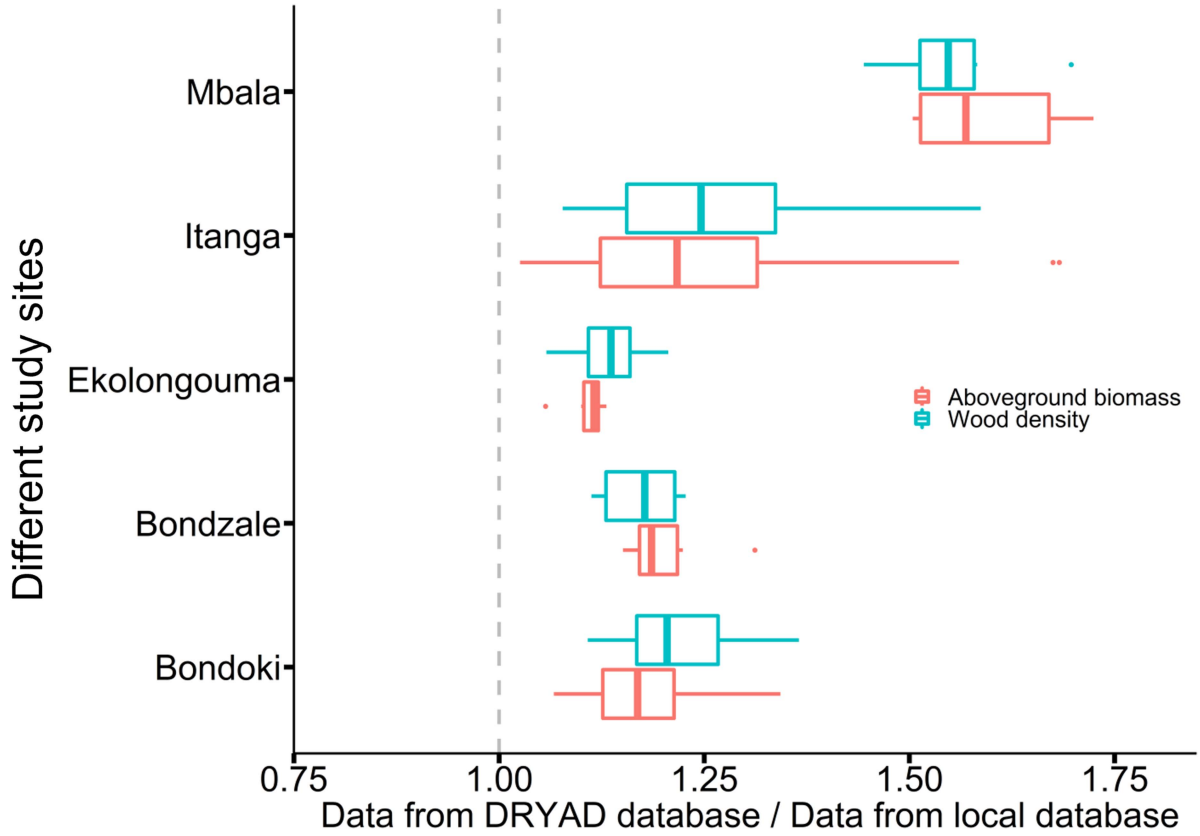

Figure 5. Wood density and above ground biomass errors between data from the DRYAD database and data from the local database at the plot level in five study sites. The grey dotted line represents the 1 error for plot wood density and aboveground biomass.

Table 3. Root mean square error (*RMSE*, in g cm^{-3} for wood density, *WD* and kg for above ground biomass, *AGB*), bias (%) and paired *t*-tests (*p*-value) in wood density and *AGB* between data from the global DRYAD database and data from the local database at the plot level within each study site.

		paired *t*-test				
variable	site	d.f.	statistic	*p*-value	bias (%)	*RMSE*
WD	Bondoki	15	13.514	<0.001	21.3	0.115
	Bondzalé	5	9.6066	<0.001	17.1	0.091
	Ekolongouma	5	6.3365	0.001	13.39	0.076
	Itanga	59	20.03	<0.001	24.97	0.129
	Mbala	5	16.589	<0.001	55.38	0.262
AGB	Bondoki	15	7.925	<0.001	17.07	3355
	Bondzalé	5	5.461	0.002	20.42	5226
	Ekolongouma	5	10.548	<0.001	10.51	3242
	Itanga	59	12.346	<0.001	19.36	2049
	Mbala	5	6.001	0.002	64.55	11 849

there was no significant difference (figure 4b). It should also be noted that the correlation between local *WD* values and those of the global database was weak (Pearson test, $r = 0.20$) for all 976 trees sampled.

The values of *RMSE* and bias in *WD* and *AGB* varied strongly among study sites with high values of *RMSE* and bias of *WD* and *AGB* in Mbala (table 3). For all study sites, the results of a *t*-test demonstrated significant differences in *WD* and *AGB* between the values from the local database and those from the global DRYAD database (table 3). The *WD* of study species from the global

DRYAD database tended to overestimate the mean plot-level *WD* and *AGB* values in all study sites (figure 5). This suggests that the use of *WD* from the local database improved the accuracy of plot-level *WD* and *AGB* estimation.

4. Discussion

(a) Wood density varies among coexisting tree species

WD values of tree species varied from 0.20 to 0.68 g cm^{-3} in Central African PSFs, in agreement with the results of previous studies in tropical forests [8,16,38]. The average *WD* found in the present study (0.460 g cm^{-3}) was roughly equal to that presented by Reyes *et al.* [38] and Lewis *et al.* [39] for African tropical forest tree species (0.5 and 0.65 g cm^{-3}, respectively). However, it was lower than the mean value of 0.645 g cm^{-3} found by Chave *et al.* [7] for tree species from the tropical forests of America (Central and South). Since the range of mean density values of wood used in the pulp industry is 0.4–0.6 g cm^{-3} [40], wood from some larger-statured species in the central Congo Basin peatland forests could be a viable resource for timber industries in the future, if strict conservation measures are not taken. For example, *Daniellia pynaertii* De Wild. is already used in the swamp forest of the Congo Basin [41]. Therefore, it seems to indeed be the case that logging is one of the main threats to the largest forested tropical peatland complex in the world [42].

Tree *WD* variability was better explained at the species level than at the genus and family levels. This finding, which was also made by Chave *et al.* [7], implies that a precise identification at the species level tree inventories is required to estimate *WD* and *AGB* in the tropics. The significant differences in mean *WD* values of the different species studied reveales the need to consider species and ecosystem diversity when estimating the biomass and thus the carbon storage of tropical peatland forests.

(b) Drivers of species wood density

The mode of seed regeneration, the mode of seed dispersal and growth habitat explained the interspecific variation in *WD* values observed between the 20 species investigated in this study. This finding is owing to *WD* being related to the ecological preferences of tree species [43]. For example, the regeneration mode of the studied species revealed that SB species had the highest *WD* values compared to NPLD species. This observation has previously been made in Central Africa [9,12], America [43] and Asia [13] and is related to the classic trade-off between rapid growth which favours low *WD* and the increased risks of damage and death that co-occur with low *WD*. However, there may be factors beyond wood strength and the cost of construction. For example, tree species with high *WD* have a lower trunk surface area for a given trunk strength, all else being equal, and a lower surface area means lower maintenance respiration, incurring a lower cost to the tree, thereby advantaging longer lived trees with higher *WD* [44]. If this is correct, the typically lower *WD* of the species growing in the PSF may imply that these trees are less long-lived than the average tree in a *terra firme* tropical forest system. Long-term inventory plot observations in PSFs would allow an assessment of this hypothesis and the prediction that stem and biomass turnover rates should be high in PSFs.

(c) Impact of wood density on above ground biomass estimation

We reveal significant differences between *AGB* calculated using local *WD*s and *AGB* calculated using *WD*s from the global DRYAD database. *AGB* is much lower when using local values, with impacts on the assessment of forest carbon stocks. In fact, using global *WD* values overestimated *AGB* by 24.7% ($p < 0.05$). This observation emphasizes the importance of deriving location-specific values for *WD* that take account of variation between species, sites, biomes and regions [7,20,45]. Indeed, such is the importance of *WD* that it has been shown to be the primary control of the spatial variation in *AGB* in some tropical forest regions [22,39,45–47]. The high bias and *RMSE* values obtained in the present study are related to the overestimation of wood-specific gravity and biomass obtained from the DRYAD database. This finding, echoing Loubota Panzou *et al.* [48], demonstrates that the biomass values obtained in Central Africa suffer from a large uncertainty. Thus, taking into account the individual identity of the species (the specific density of the wood) will lead to a reduction in the biases and uncertainties associated with the estimation of forest biomass in the tropics [45].

The high mean values of specific *WD* obtained from the DRYAD database compared with those of the present study (for the same species) were also observed in a moist Central African forest [9] and a mangrove ecosystem in Tanzania [49]. For example, the average specific densities of wood of species, such as *Carapa procera* (0.604 g cm^{-3}), *Coelocaryon preussii* (0.495 g cm^{-3}), *Diospyros crassiflora* (0.858 g cm^{-3}), *Symphonia globulifera* (0.589 g cm^{-3}) and *Uapaca mole* (0.652 g cm^{-3}) [8,16], are 3.6%–17.6% higher than in the present study (table 1). Within the DRYAD database, for our 20 dominant species for the central Congo peatlands, there were between 2 and 19 *WD* values, from 2 to 7 different references, for each individual tree species. The use of *WD*s from the DRYAD database to estimate the biomass of forested peatlands will contribute to an overestimation of their carbon storage capacity in the vegetation. In particular, the present study and that of Manuri *et al.* [50] revealed a weak correlation between the density of the local wood in the trees and that of the global DRYAD database. It is unlikely that the discrepancies observed between the local *WD* values and those in the DRYAD database are owing to differences in the age of the trees sampled or to soil type. As indicated by Chave *et al.* [16] and as observed in the present study, *WD* varies from one individual to another (table 1). In addition, the work of Besnard *et al.* [51] highlights the great variability in forest age, particularly in the tropical region of the Amazonia and Congo Basin. It is important to note that soil type explains around 11%–16% of the variability in *WD* [19]. This could, therefore, justify

the differences observed between the values in the DRYAD database and those in our study, in which the trees sampled grew on peaty soil.

The results of this study have a potential impact on the implementation of REDD+ in Central Africa. Indeed, within the framework of the REDD+ measurement, reporting and verification mechanism, the findings reveal that it is necessary to integrate the collection of local *WD* data into national forest inventories. This will enable accurate estimates of biomass and therefore forest carbon. Despite the relevance of this study, it has some limitations, mainly owing to the complexity of the ecosystem. In fact, it should be noted that *WD* data were collected at only one site in the central basin forest peatland in the Republic of Congo. Hence, there is a need to broaden the geographical scope of this study. Furthermore, an increase in the number of biomass sampling plots and the length of the Bondoki, Bondzalé, Ekolongouma and Mbala transects will enable better consideration of the spatial variability of *WD* and therefore biomass across the Congo Basin.

5. Conclusion

Estimates of *AGB* using the most commonly used global database of *WD* overestimates *AGB* by 24.70% in the central Congo Basin forests. This is because the *WD* of trees in the world's largest tropical peatland complex in the central Congo Basin is lower than those found in the global database and lower than trees from nearby *terra firme* forest. The PSFs, overall, have much lower *AGB* than Central African *terra firme* forests. *AGB* and *WD* were influenced by the species found in the PSFs. This suggests that the use of *WD* from a local database will improve the accuracy of plot-level *WD* and *AGB* estimation. Accurate estimation of *WD* of species across sites and biomes will reduce errors in estimating tree biomass and forest carbon storage in the tropics. It therefore seems essential to continue measuring the *WD* of species present in tropical peatlands and surrounding ecosystems. This will enable the creation of databases specific to local forest ecosystems and provide accurate carbon estimates.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. All data used to produce the figures and tables in this paper are provided as the supplementary material [52].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Author's contributions. Y.E.B.: conceptualization, data curation, formal analysis, methodology, project administration, supervision, validation, visualization, writing—original draft, writing—review and editing; G.J.L.P.: data curation, formal analysis, validation, visualization, writing—review and editing; G.D.: methodology, validation, visualization, writing—review and editing; J.A.B.-L.: methodology, validation, visualization, writing—review and editing; Y.E.W.M.: validation, visualization, writing—review and editing; M.M.: validation, visualization, writing—review and editing; D.E.C.: validation, visualization, writing—review and editing; N.G.: validation, visualization, writing—review and editing; D.H.: validation, visualization, writing—review and editing; M.S.: validation, visualization, writing—review and editing; B.C.: validation, visualization, writing—review and editing; S.G.: validation, visualization, writing—review and editing; D.Y.: validation, visualization, writing—review and editing; S.C.: validation, visualization, writing—review and editing; A.B0.: validation, visualization, writing—review and editing; P.C.: validation, visualization, writing—review and editing; R.B.: validation, visualization, writing—review and editing; E.S.: validation, visualization, writing—review and editing; E.B.: validation, visualization, writing—review and editing; P.G.: validation, visualization, writing—review and editing; A.Ba.: validation, visualization, writing—review and editing; P.M.: validation, visualization, writing—review and editing; C.E.N.E.: validation, visualization, writing—review and editing; A.J.J.-S.: validation, visualization, writing—review and editing; S.I.: validation, visualization, writing—review and editing; Y.G.: validation, visualization, writing—review and editing; I.L.: validation, visualization, writing—review and editing; S.S.: validation, visualization, writing—review and editing; S.E.P.: validation, visualization, writing—review and editing; J.J.L.: conceptualization, validation, visualization, writing—review and editing; S.L.L.: conceptualization, funding acquisition, methodology, project administration, supervision, validation, visualization, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. This work was funded by a Natural Environment Research Council large grant [NE/R016860/1, http://gotw.nerc.ac.uk/list_full.asp?pcode=NE%2FR016860%2F1&cookieConsent=A] awarded to S.L.L.

Acknowledgements. We thank the villages of Bolembe, Ekolongouma, Bondoki, Bondzalé, Itanga and Mbala, for their assistance during the field data collection period. Thanks to the Ministry of Environment, Sustainable Development and the Congo Basin, the Ministry of Forestry Economy, the Ministry of Higher Education, Scientific Research and Technological Innovation, Republic of the Congo, Marien Ngouabi University and the Likouala Department governor for the research permits. We thank the fieldworker team. At the end of this work, we would also like to thank Helen Plante for the logistics.

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