ARTICLE

Macrosystems Ecology

Intensity, determinants, and impacts of liana load on tropical trees in central Africa

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Abstract

Lianas can create dense foliage that reduces the light available for the host trees on which they grow and can directly damage the host trees during their development. A better estimation of liana load and understanding of the determinants and impacts of liana load in tropical forests are both important in community ecology and ecosystem science. This has, however, never been studied to date in central Africa. Here, we evaluated the intensity, determinants, and impacts of liana load in three forest sites in central Africa. We determined the liana load categories for all trees belonging to 78 of the most dominant tree species (2683 trees in total), with tree diameters ranging from 10 to 250 cm. The liana load was visually estimated as the liana cover on host tree using simple scale indices, and the proportion of trees covered by lianas defined as the liana prevalence was estimated for each species. Overall, 42% of the 2683 trees were liana-loaded and the number of liana-loaded trees was higher for smaller diameter classes in the three forest sites. Within each forest site, there was a significant difference in liana prevalence among coexisting species. Taller trees with shallow crowns were less covered by liana at the tree level, whereas trees belonging to light-demanding and wind-dispersed species showed a lower liana prevalence rate at the species level. In each forest site, the liana load significantly affected tree height–diameter allometry, with liana-loaded trees being shorter for the same diameter. Lianas promote the structural complexity and influence tree diversity and ecosystem functioning of tropical forests.

KEYWORDS
central Africa, dispersal mode, height–diameter allometry, liana load, liana prevalence, light requirement, tree species

INTRODUCTION

Lianas or woody vines are an important component of forest communities and play a significant role in ecosystem processes (Schnitzer & Bongers, 2002, 2011). They use the architecture of trees to climb to the top of the canopy (Schnitzer & Bongers, 2002), but they frequently occur in both crown and stem (Ingwell et al., 2010; Putz, 1984a, 1984b; van der Heijden & Phillips, 2009). Once they reach the tree crown, lianas can create dense foliage that reduces the light available for the trees on which they grow (Clark & Clark, 1990; Fauset et al., 2017). The weight added by lianas on tree crowns can cause mechanical damages to branches and stems, and can directly damage host trees (Laurance et al., 2014; Phillips et al., 2005; Schnitzer et al., 2000; Schnitzer & Bongers, 2011; van der Heijden & Phillips, 2009). As a result, trees with a strong liana load are more prone to stem breakages, leading to mortality. Although ground-based measurements of lianas can be linked to remote sensing measurements, which provide a very-high-resolution view of liana distribution above the canopy over large extents and over time in tropical forests (Kaçamak et al., 2022), they nevertheless remain challenging and time-consuming. Many tropical foresters and ecologists have therefore sought shortcuts to describe the liana load carried by trees by using simple ordinal scale indices estimating "liana load" visually (Clark & Clark, 1990; Muller-Landau & Visser, 2019; Rutishauser et al., 2011; van der Heijden et al., 2010).

At the tree level, the crown of more than 50% of trees were liana-loaded in Amazonia (Reis et al., 2020; van der Heijden et al., 2008; van der Heijden & Phillips, 2009), but the intensity of liana load varied among potential host trees. It has been suggested that the characteristics of host trees may be more important than the direct effects of the physical environment in controlling the success of lianas in tropical forests (van der Heijden et al., 2008). Trees growing in close proximity to others already supporting lianas may be more prone to be liana-loaded as lianas often grow from one crown to another (Putz, 1984b; van der Heijden et al., 2008). The number of liana-loaded trees has been shown to increase with the size of the host trees in a tropical montane forest of southern Ecuador (Fadrique & Homeier, 2016). It was, in contrast, negatively associated with tree diameter in tropical lowland forests (Reis et al., 2020; van der Heijden et al., 2008). The light in the tree crown is also an important determinant and has been positively related to liana-loaded trees in Amazonia (Reis et al., 2020; van der Heijden et al., 2008). As most lianas seem to proliferate in high light conditions, well-lit tree crowns may present a higher risk of liana loads (Malizia & Grau, 2006).

Following Muller-Landau and Visser (2019), the proportion of trees covered by lianas was defined as the liana prevalence at the species level. Previous studies have identified that some tree species have a higher rate of liana prevalence than others (Alvira et al., 2004; Campbell & Newbery, 1993; Muller-Landau & Visser, 2019; Putz, 1984a, 1984b; Reis et al., 2020; Schnitzer et al., 2000; van der Heijden et al., 2008; Visser et al., 2018). This interspecific variation in liana prevalence was associated with tree species traits that prevent lianas from covering them, notably, having flexible stems, long leaves, long branch-free boles, and smooth bark (Campbell & Newbery, 1993; Carsten et al., 2002; Putz, 1984a). In central Africa, functional traits including wood density, light requirements, dispersal mode, and deciduous leaf habit provided insights into the life-history strategy of tropical tree species (Loubota Panzou, Ligot, et al., 2018). The liana prevalence was determined by species wood density in Amazonia, with heavy-wood density species having a high liana prevalence (Reis et al., 2020). Light requirement for regeneration that reflects a species strategy of light capture (Turner, 2001) was found to be negatively related to liana prevalence in Panama (Muller-Landau & Visser, 2019). The dispersal mode, which is crucial for the recruitment, distribution, and dynamics of plant populations (Nathan & Muller-Landau, 2000), was also found to be related to the liana prevalence, with animal-dispersed species showing higher liana prevalence (Ickes et al., 2005). In contrast, the deciduous leaf habit, which is a successful strategy to cope with dry season in tropical forests (Borchert et al., 2002), was not found to be associated with liana prevalence in Argentina (Malizia & Grau, 2006).

Lianas strongly influence forest structure at the stand level by competing with trees for below- and aboveground resources (Schnitzer & Bongers, 2011; van der Heijden & Phillips, 2009). Trees experiencing liana loads on their crowns may have fewer resources to increase in height and diameter, and consequently exhibit lower aboveground biomass than trees without those extra loads (Putz, 1984a). The liana load was found to significantly alter tree allometry, decreasing height–diameter ratio in Amazonian forests (Dias et al., 2017; Reis et al., 2020; van der Heijden et al., 2008) and to negatively affect plot-level aboveground biomass (Ledo et al., 2016; van der Heijden & Phillips, 2009), and thus diminish the carbon storage potential in tropical forests (Gerwing & Farias, 2000; Laurance et al., 2001).

Comparison of the intensity, determinants, and impacts of liana load among tropical forest species has barely been addressed (but see Reis et al., 2020 in Amazonia; Muller-Landau & Visser, 2019 in Central America), and, to our knowledge, never in Africa. The central Africa especially remains an understudied

region (Verbeeck et al., 2011) compared with the other tropical regions, where liana abundance and biomass have been shown to dramatically increase over the last decades (Schnitzer & Bongers, 2011). A better estimation of liana load, which is largely site-dependent in tropical forests (Muller-Landau & Visser, 2019), and understanding of the determinants and impacts of liana loads in tropical forests are both important in community ecology and ecosystem science (Schnitzer & Bongers, 2002, 2011).

In this context, the study aimed to evaluate the intensity, determinants, and impacts of liana load in three forest sites in central Africa. We addressed three research questions:
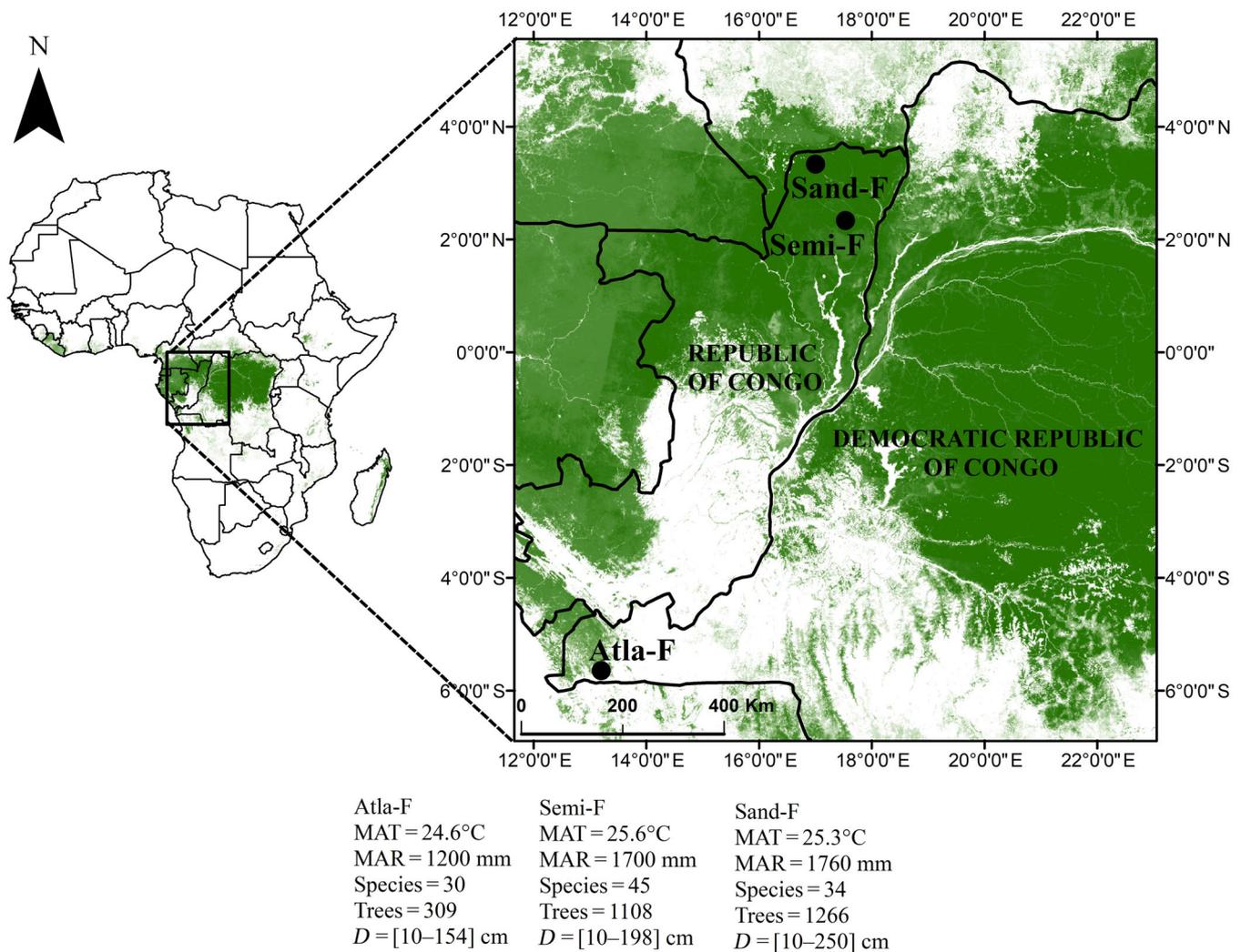
1. What is the extent of variation in liana load on host trees and liana prevalence among tree species?

2. What are the determinants of the liana load at the tree level and liana prevalence at the species level?

3. Does liana load impact forest structure, such as tree height–diameter allometry?

METHODS

Study sites

The study was conducted in three forest sites characteristic of three major forest types identified by Réjou-Méchain et al. (2021) in central Africa (Figure 1). The Luki site is representative of the Atlantic highland evergreen forest (Atla-F) in the southwest of the Democratic Republic of Congo and the forest in Luki was

Atla-F
MAT = 24.6°C
MAR = 1200 mm
Species = 30
Trees = 309
D = [10–154] cm

Semi-F
MAT = 25.6°C
MAR = 1700 mm
Species = 45
Trees = 1108
D = [10–198] cm

Sand-F
MAT = 25.3°C
MAR = 1760 mm
Species = 34
Trees = 1266
D = [10–250] cm

FIGURE 1 Location and characteristics of the three study sites in the southwestern Democratic Republic of the Congo (Atlantic highland evergreen forest [Atla-F]) and in the northern Republic of Congo (semideciduous forest [Semi-F] and evergreen-semideciduous forest on sandstone [Sand-F]) in central Africa on a background map of tree cover (Hansen et al., 2013). The mean annual temperature (MAT; in degrees Celsius), mean annual rainfall (MAR; in millimeters), number of species and trees sampled, and sampling effort in terms of diameter (D, in centimeters) range are provided for the three sites.

described in detail by Lubini (1997). Two other study sites, representative of the semideciduous forest (Semi-F) and the evergreen-semideciduous forest on sandstone (Sand-F), which were described by Fayolle et al. (2014), were inventoried in the northern Republic of Congo. The three forest sites show a slight topography with average altitudes varying between 430 and 530 m. On average, the annual rainfall is 1200 mm for the Atla-F and 1600 mm for both the Semi-F and Sand-F, and the mean annual temperature is 25°C in the three forest sites.

Sampling and tree measurements

Fieldwork was mostly conducted in permanent plots installed in old-growth forests in 8×1-ha plots for the southern site (Atla-F) and 18×1-ha plots for each of the two northern sites, Semi-F and Sand-F (Forni et al., 2019). In the plots, all trees with diameters ≥ 10 cm were inventoried and identified to species level, and plot data were used to select at least 30 abundant coexisting tree species (including $\geq 56\%$ of all trees ≥ 10-cm diameter) in each forest site. In the two northern sites (Semi-F and Sand-F), we additionally estimated liana abundance on all trees within two 1-ha plots and regularly over a 20×20 m grid for the other 16 plots. A total of 2683 trees belonging to 78 tree species were sampled in the three sites (309 trees belonging to 30 species for the Atla-F, 1108 trees belonging to 45 species for the Semi-F, and 1266 trees belonging to 34 species for the Sand-F) with five species shared by the three sites, and 21 shared by the closest northern sites (Semi-F and Sand-F). These 78 species belong to 64 genera and 31 families (Fabaceae is the most abundant family with 12 species, Appendix S1: Table S1). We aimed to sample 30 trees (range: 10–162) per species within each site to cover the species diameter range and establish species-specific allometric relationships (Loubota Panzou, Ligot, et al., 2018).

For each tree, the liana load was visually estimated by the same observer with the four categories proposed by Rutishauser et al. (2011), which were concordant with drone assessments in northern Republic of Congo (Kaçamak et al., 2022). The four liana load categories were as follows: 0 for no lianas in the crown, 1 for 1%–25% of the crown covered by lianas leaves, 2 for 26%–50% of the crown covered, and 3 for >51% of the crown covered. In addition, nondestructive quantitative measurements including tree diameter, total height, height of the first branch, the horizontal projection of four crown radii, and one qualitative measurement (crown exposure index described below) were performed for each tree following Loubota Panzou, Ligot, et al. (2018) and Loubota Panzou, Fayolle, et al. (2018). Tree diameter (D; in centimeters) was measured with a tape

at breast height or 30 cm above any deformation. Total tree height (H; in meters) and height of the first branch (H_{fb}, in meters) were measured using a VERTEX IV dendrometer, which is a valuable tool for nondestructive height measurements in central African forests (Fayolle et al., 2016). For crown measurements, we used the crown measurement protocol (Loubota Panzou & Feldpausch, 2020). Crown depth (C_{dept}) was defined as the length of the crown, which was calculated from the difference between H and H_{fb}. The crown diameter (C_{dia}) was defined from two times the mean of the crown radii measured according to the four cardinal directions. The crown exposure index (CEI) describing the crown position in the canopy and exposure to light (Dawkins, 1966) was visually estimated using the following five classes (Moravie et al., 1999): (1) for lower understory trees that are entirely shaded vertically and laterally by other crowns; (2) for upper understory trees that are entirely shaded vertically but with some direct side light; (3) for lower canopy trees that are partly exposed and shaded vertically by other crowns; (4) for upper canopy trees that are fully exposed from above but laterally complete with other crowns; and (5) for emergent trees that are free from competition for light, at least within the 90° inverted cone in which their crown lies. For the analyses, we used the three CEI groups adapted from Clark and Clark (1992) and representing trees in low light (trees with Code 1), in medium light (trees with Codes 2 and 3), and high light (trees with Codes 4 and 5) conditions.

Species traits

Here, we compiled seven traits including wood density, maximum height (H_{max}), maximum diameter (D_{max}), light requirement, leaf habit, dispersal mode, and regeneration guild for each species (Appendix S1: Table S1). We obtained the species average wood density (WD; in grams per cubic centimeter) from the global wood density database (Chave et al., 2009; Zanne et al., 2009) and species average varied from 0.29 to 0.89 g cm^{-3}. We respectively calculated D_{max} (range: 13–130 cm) and H_{max} (range: 11–61 m) as the 95th percentile of tree diameter and total height of the sampled trees for each species.

We quantified the crown exposure to light for juvenile plants (CEI$_{juv}$), which is a good indicator of species light requirement (Poorter et al., 2005, 2006). We fitted species-specific multinomial logistic regressions between the CEI and tree diameter, in agreement with Loubota Panzou, Ligot, et al. (2018) in central Africa. For each species, we obtained CEI$_{juv}$ (range: 1.03–4.22) using the CEI prediction of the species-specific multinomial logistic regression for 10 cm diameter as first proposed by Poorter et al. (2005, 2006).

We extracted the information on deciduous leaf habit (56 species were considered evergreen and 17 species were considered deciduous), dispersal mode (46 were animal-dispersed species, 16 were wind-dispersed species, and 7 had unassisted dispersed species), and regeneration guild (44 were classified as shade-bearer species, 25 as nonpioneer light-demanding species, and 9 as pioneer species) from the literature (Gillet & Doucet, 2012; Hawthorne, 1995; Meunier et al., 2015).

Data analysis

Following Muller-Landau and Visser (2019), we defined the liana prevalence as the proportion of trees covered by lianas using the four categories of liana load. We quantified three indices of liana prevalence for each species (Appendix S1). The first one (LI_{prop}) was simply the proportion of trees with lianas in the crown (trees with Codes 1, 2, or 3). The second one (LI_{heavy}) was the proportion of trees heavily covered by lianas (>25% of the crown covered by lianas, trees with Codes 2 and 3). Since the first two indices do not consider the tree size in the proportion of trees covered by lianas, a third index has been estimated using logistic regression (family = binomial) between liana load (presence and absence) and tree size. Tree height was the predictor variable since liana loads were related to tree height ($p < 0.001$) and not to tree diameter ($p = 0.633$) using linear relationships. We fitted species-specific relationships between liana loads and tree height, and for each species we calculated the third index (LI_{juv}), which is the estimated liana load for juvenile plants of 2 m height, in agreement with Poorter et al. (2006). Furthermore, we found that LI_{prop} and LI_{heavy} indices were positively correlated (Pearson $r = 0.71$, $p < 0.001$), as well as LI_{prop} and LI_{juv} indices (Pearson $r = 0.94$, $p < 0.001$). Thus, the first index defined as the proportion of trees covered by lianas (LI_{prop}, response variable) was used as the liana prevalence for the subsequent analyses.

To evaluate the most critical factors in determining liana load and prevalence, we developed general linear mixed effect models at the tree level (Equation 1 with liana presence and absence as response variable) and at the species level (Equation 2 with the proportion of trees covered by lianas as response variable). We used the characteristics of the host trees (tree diameter, tree height, crown depth, crown diameter, wood density, and crown exposure index) as determinants at the tree level, and species traits as determinants at the species level. Prior to this analysis, we removed possible collinearity among determinants (fixed effects of mixed linear models) using pairwise correlations. Because of

collinearity, we had to exclude tree diameter and maximum diameter at tree and species levels, respectively. After removing these variables, all pairwise correlations were weak enough not to cause collinearity problems (Pearson $r < 0.7$). At the tree level, the modeling approach of a tree i included tree height (H), wood density (WD), crown exposure index (CEI), crown diameter (C_{dia}), and crown depth (C_{dep}) as fixed effects and taxonomy (a nested design of family, genera within families, and species within genera within families) and site as random effects (Equation 1). Likewise, species traits including maximum height, wood density (WD), light requirement (CEI_{juv}), deciduous leaf habit (LH), guild regeneration (GR), and dispersal mode (DM) were included in the model as fixed effects and species clustered within site as random effects of a tree i belonging to species s (Equation 2).

$$
\begin{aligned}
\text{Liana load}_i = {} & \beta + \alpha_1 \times H_i + \alpha_2 \times \text{CEI}_i + \alpha_3 \times C_{\text{dia}i} \\
& + \alpha_4 \times C_{\text{dep}_i} + \alpha_5 \times \text{WD}_i + \beta_{\text{family}}[i] \\
& + \beta_{\text{genera−family}}[i] + \beta_{\text{species−genera−family}}[i] \\
& + \beta_{\text{site}}[i],
\end{aligned}
\tag{1}
$$

$$
\begin{aligned}
\text{Liana prevalence}_{is} = {} & \beta + \alpha_1 \times H_{\text{max}_{is}} + \alpha_2 \times \text{CEI}_{\text{juv}_{is}} \\
& + \alpha_3 \times \text{WD}_{is} + \alpha_4 \times \text{LH}_{is} + \alpha_5 \times \text{GR}_{is} \\
& + \alpha_6 \times \text{DM}_{is} + \beta_{\text{species}}[is] + \beta_{\text{site}}[is],
\end{aligned}
\tag{2}
$$

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

To examine the impacts of liana load on forest structure, we tested the variation in height–diameter allometry between liana-loaded trees and liana-free trees in each forest site. Asymptotic models have been demonstrated to better describe height–diameter allometry for aboveground estimation in tropical forests. The Michaelis–Menten model was found to provide a good fit for height–diameter data in central Africa (Fayolle et al., 2016; Loubota Panzou et al., 2021). In each forest site, the Michaelis–Menten model has been used to fit height–diameter allometric relationships for liana-loaded trees and liana-free trees using the following equation based on height (H) and diameter (D) of a tree i belonging to liana factor (liana-loaded trees and liana-free trees) l in each forest site:

$$
H_{il} = a_l \times D_{il} / (b_l + D_{il}),
\tag{3}
$$

where a and b are model parameters.

To test for significant differences in tree height–diameter allometry between liana-loaded trees and

liana-free trees, we fitted four models on the whole data set in each forest site: (1) a general model with fixed parameters (a and b), (2) varying a_l and b_l, (3) varying a_l and fixed b, and (4) fixed a and varying b_l. The model selection for each forest site was based on (i) the likelihood ratio test (a statistical test used to compare the goodness of fit of two statistical models); we considered the null model as a model with fixed coefficients without a liana factor effect (1), whereas the alternative models were the ones described above as (2), (3), and (4); and (ii) the model's Akaike information criterion (AIC) and Bayesian information criterion (BIC) values, with the lowest AIC and BIC indicating the best model (Burnham & Anderson, 2002).

All the statistical analyses were performed in the open source R environment (R Core Team, 2021), using the following packages: "ggplot2" for graphical output (Wickham, 2016) and "lme4" for the mixed linear model inference (Bates et al., 2015). Because the conditions of normality and homoscedasticity of residuals checked with Shapiro–Wilk and Breusch–Pagan tests, respectively, were not met, we used the nonparametric Kruskal–Wallis rank sum tests to test the differences among liana load categories in tree vertical structure (tree height and crown depth) at the tree level and among dispersal mode categories in liana prevalence at the species level. The null hypothesis for the nonparametric Kruskal–Wallis test was "no difference between medians for each qualitative variable" (Hollander & Wolfe, 1973). When the null hypothesis was rejected, we conducted post hoc Kruskal–Wallis multiple comparisons between medians (Siegel & Catellan, 1988) available in the PGIRMESS package (Giraudoux, 2013).

RESULTS

Variation in liana load and prevalence

At the tree level, 41.6% of the 2683 trees sampled in the three forest sites ranging from 10 to 250 cm diameters and belonging to 78 tree species were liana-loaded in the three forest sites. The number of liana-loaded trees was higher for smaller diameter classes in the three forest sites (Table 1).

At the species level, the liana prevalence varied from 0% to 90% (Appendix S1). Species particularly susceptible to liana prevalence were *Pentaclethra macrophylla* (Fabaceae) with 90% of trees were liana-loaded in the Atla-F, *Celtis tessmannii* (Cannabaceae) and *Garcinia punctata* (Clusiaceae) with 85% of trees were liana-loaded in the Semi-F, and *Carapa procera* (Meliaceae) with 70% of trees were liana-loaded in the Sand-F (Appendix S1).

TABLE 1 Number (with percentages in parentheses) of trees according to four liana load categories (0: 0%; 1: 1%–25%; 2: 25%–50%; and 3: >50% of the crown covered by lianas) and number (with percentages in parentheses) of liana-loaded trees for all tree diameters and according to three diameter (*D*) classes in three forests sites including the Atlantic highland evergreen forest (Atla-F), the semideciduous forest (Semi-F), and the evergreen-semideciduous forest on sandstone (Sand-F).

Category	Atla-F	Semi-F	Sand-F
Sampling			
No. species	30	45	34
No. trees	309	1108	1266
Diameter range (cm)	10–154	10–162	10–250
Liana load category			
0	179 (58)	544 (49)	845 (67)
1	78 (25)	293 (26)	244 (19)
2	33 (11)	87 (8)	95 (8)
3	19 (6)	184 (17)	82 (6)
Diameter class			
All tree diameters	130 (42)	564 (51)	421 (33)
$10 \leq D < 30$ cm	80 (62)	336 (59)	304 (72)
$30 \leq D < 70$ cm	42 (32)	171 (31)	97 (23)
$D \geq 70$ cm	8 (6)	57 (10)	20 (5)

Note: The three diameter size classes were as follows: the lower stratum with small trees (10 cm $\leq D <$ 30 cm), the middle stratum with large trees, most of which reach the canopy (30 cm $\leq D <$ 70 cm), and the upper stratum corresponding to the largest trees, which were either in the canopy or emergent, with diameter ≥70 cm, as shown in Loubota Panzou, Fayolle, et al. (2018).

Determinants of liana load and prevalence

At the tree level, the liana load (presence and absence) was most strongly related to tree height, crown depth, and crown exposure index (Figure 2a; Appendix S1: Table S2). We detected significant variation in tree height and crown depth among liana load categories, indicating that liana-loaded trees were smaller but showed deeper crown (Figure 2b,c). We found a potential difference of 4 m for tree height and 2 m for crown depth between liana-loaded trees and liana-free trees, indicating a reduction in tree height due to the liana presence. Indeed, the median and 95% confidence interval was 17.2 m (16.6–17.6 m) for tree height and 7.5 m (7.0–7.9 m) for crown depth for liana-loaded trees and 21.2 m (20.0–22.0 m) for tree height and 5.9 m (5.7–6.2 m) for crown depth for liana-free trees. In addition, the effect of light condition was also significant in the model.

At the species level, the liana prevalence was strongly related to species light requirement (CEI_{juv}) and species dispersal mode (Figure 3a; Appendix S1: Table S2).
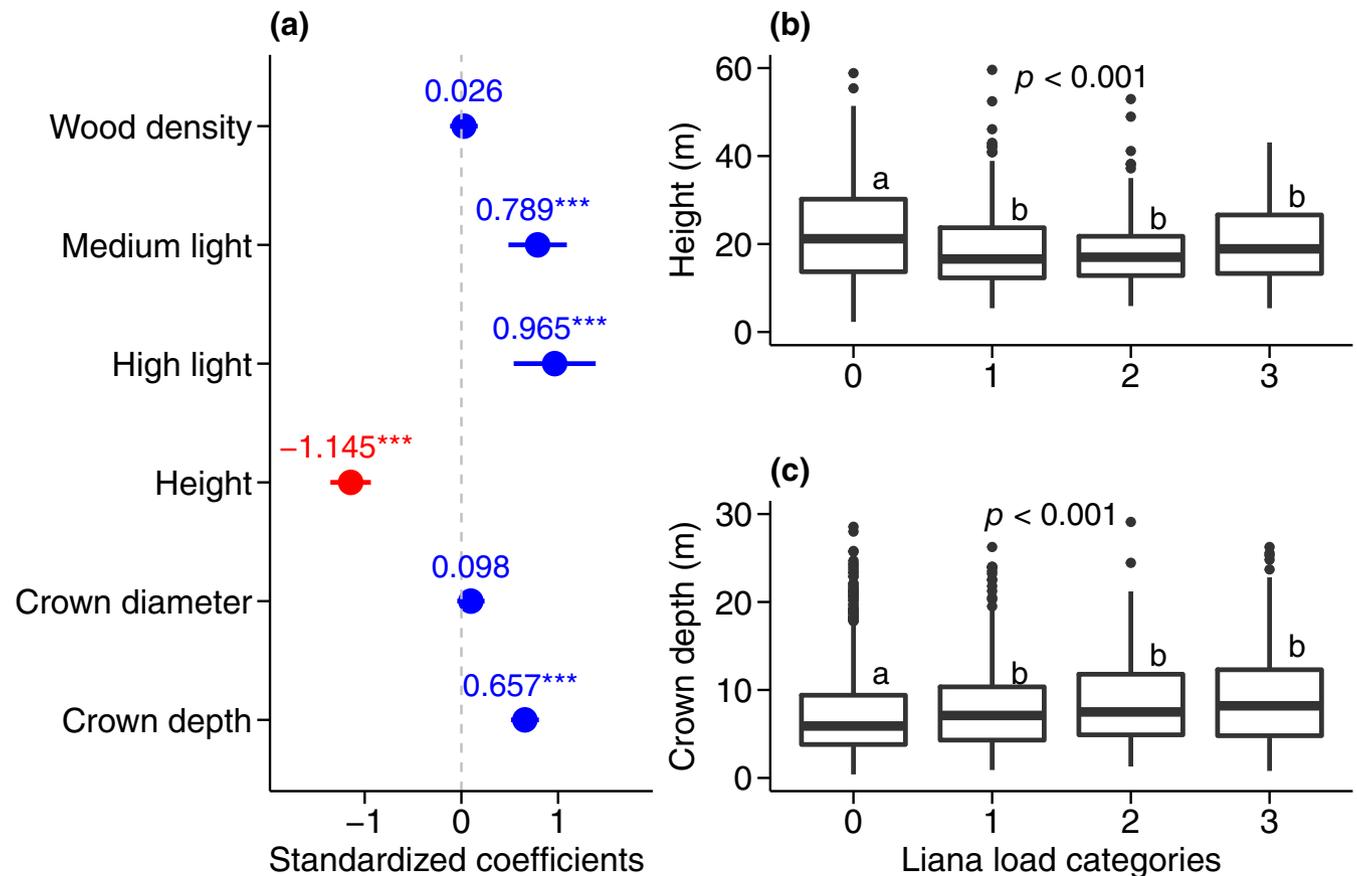
FIGURE 2 Tree-level determinants of liana load: (a) standardized coefficients of liana load with error bars showing confidence intervals (***$p < 0.001$) and all coefficients from fixed effects and random effects are shown in Appendix S1: Table S2; (b, c) bivariate relationships between the liana load categories and the significant variables with box plots showing tree height and crown depth for each of liana load categories (0: 0%; 1: 1%–25%; 2: 25%–50%; and 3: >50% of the crown covered by lianas) where the significant differences (nonparametric Kruskal–Wallis test) are shown by different letters using post hoc Kruskal–Wallis multiple comparisons between medians.

The liana prevalence was negatively correlated with the species light requirement for the three forest sites (Pearson $r = -0.51$, $p < 0.001$), indicating that light-demanding species showed a lower liana prevalence rate (Figure 3b), potentially due to their greater height. A significant variation was identified in the liana prevalence among dispersal mode types, with wind-dispersed species showing a lower rate of liana prevalence (Figure 3c).

## Impacts of liana load on forest structure

In each forest site, we identified a significant variation in height–diameter allometry between liana-loaded and liana-free trees (Figure 4). Based on AIC and BIC values, we selected the Michaelis–Menten models with different a coefficient values (H_{max}) between liana-loaded and liana-free trees (Table 2). For a given diameter, liana-free trees were taller than liana-loaded trees (Figure 4, Table 2).

DISCUSSION

This study provides important insights into the intensity, the determinants, and the impacts of liana load in central African moist forests. Among the 2683 trees sampled in three forest sites, 42% were liana-loaded and the liana prevalence was highly variable among species within each forest site. The main determinants of liana load at the tree level were related to the tree vertical structure (tree height and crown depth), and the main determinants of liana prevalence at the species level were species dispersal mode and to a lesser extent species light requirement. Furthermore, our results indicated that liana load altered tree height–diameter allometry.

Intensity of liana load and prevalence

Our results showed that less than half of all trees studied with diameter ≥10 cm were liana-loaded in the
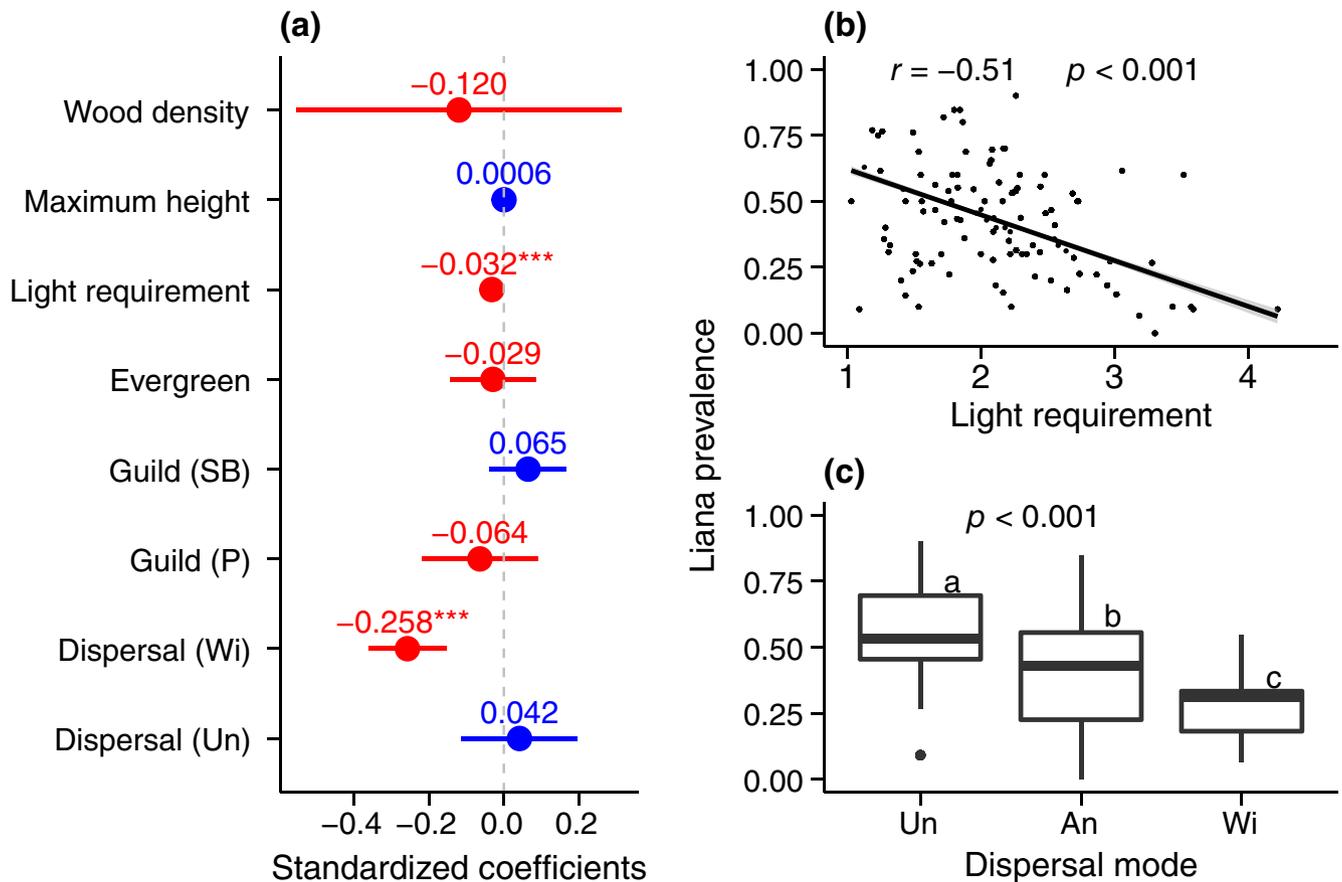
FIGURE 3 Species-level determinants of liana prevalence: (a) standardized coefficients with error bars showing confidence intervals (***$p < 0.001$) and all coefficients from fixed effects and random effects shown in Appendix S1: Table S2; (b, c) bivariate relationships between the liana prevalence and light requirement with the Pearson correlation coefficient (r) and the dispersal mode where the significant differences (nonparametric Kruskal–Wallis test) are shown by different letters using post hoc Kruskal–Wallis multiple comparisons between medians. Deciduous leaf habit (evergreen vs. deciduous), regeneration guild (SB, shade-bearer and P, pioneer), and dispersal mode (Un, unassisted; An, animal dispersal; and Wi, wind).

three forest sites. This is the first time such an estimation of liana load intensity has been performed in central Africa. The number of liana-loaded trees is lower in central Africa than in Amazonia, as reported in the previous studies of Putz (1984a, 1984b), van der Heijden et al. (2008), and Reis et al. (2020). Apparently, the dominance of liana observed in the Neotropics (>50% of trees) appears less important in central Africa. In addition, the number of liana-loaded trees gradually decreased with increasing diameter classes, as previously reported by van der Heijden et al. (2008) in Amazonia. Trees of smaller size classes may be more prone to liana loads since lianas generally climb on successively taller trees to reach the canopy (Putz, 1995).

The liana prevalence, corresponding to the proportion of trees covered by lianas (Muller-Landau & Visser, 2019), varied among coexisting tree species within each forest site in central Africa, in agreement with previous studies in the Neotropics (Alvira et al., 2004; Campbell & Newbery, 1993; Muller-Landau & Visser, 2019; Putz, 1984a, 1984b; Reis et al., 2020; Schnitzer et al., 2000; van der Heijden et al., 2008; Visser et al., 2018). High rates of liana prevalence were always related to particular species. *P. macrophylla* was in the Atla-F consisting of a mixture of evergreen and deciduous species (Lubini, 1997), *C. tessmannii* was in the semideciduous forest that is dominated by light-demanding tree species such as *Celtis* spp. (Fayolle et al., 2014), and *Carapa procera* was in the evergreen-semideciduous forest on sandstone that is enriched by many slow-growing shade-tolerant species (Fayolle et al., 2014). These species with a high rate of liana prevalence in one site had not necessarily a high rate of liana prevalence in the other sites, which suggests that the same tree species is not always colonized by liana in the same way, with the same liana load.
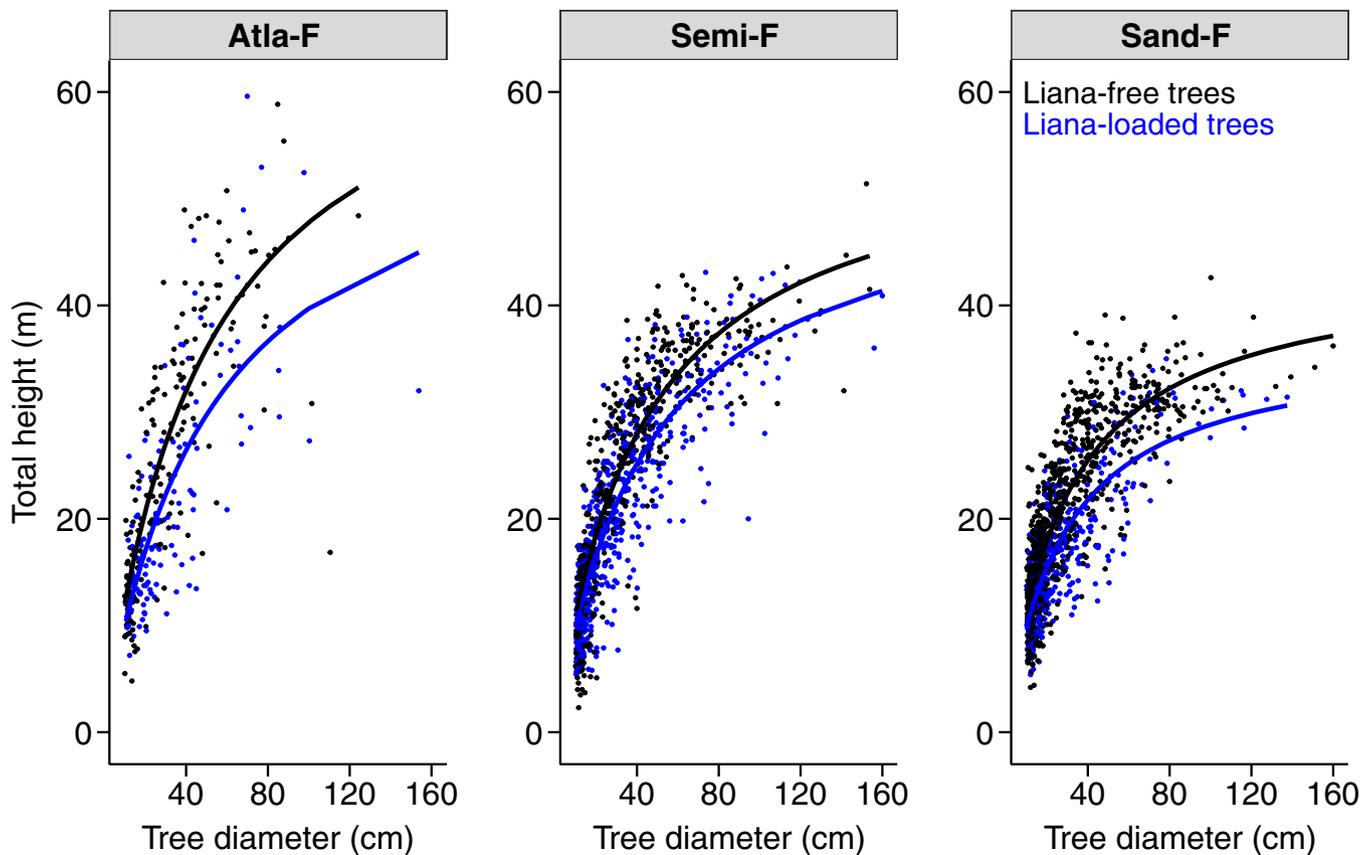
FIGURE 4 Height–diameter allometric relationships between liana-loaded trees and liana-free trees in three forests sites (Atlantic highland evergreen forest [Atla-F]; semideciduous forest [Semi-F]; and evergreen-semideciduous forest on sandstone [Sand-F]).

Liana load and prevalence determined by tree vertical structure and species traits

At the tree level, the factors that determine the liana load were the tree height and crown depth. Liana-loaded trees were smaller and had a larger crown depth. Most lianas were loaded on a tree trunk by surrounding it, but are restricted by a maximum host diameter that they can encircle (Dewalt et al., 2000; Putz, 1984b). In contrast, for the crowns, large crowns favor liana colonization, and trees experiencing liana loads on their crowns may have fewer resources to increase in height (Putz, 1984b). Liana loads thus significantly alter tree allometry as reported in Amazonia (Dias et al., 2017; Reis et al., 2020) by decreasing slenderness (tree height–diameter ratio).

Species traits including light requirement and dispersal mode significantly influenced the liana prevalence, suggesting that light-demanding and wind-dispersed species had a low level of susceptibility to lianas, in agreement with the results of Visser et al. (2018) and Muller-Landau and Visser (2019) in Panama. The liana prevalence was also influenced by wood density and maximum height in Amazonian moist forest (van der Heijden et al., 2008). In central Africa, we found that wind-dispersed species had a low rate of liana prevalence. The wind-dispersed species may be inclined to grow up fast, having less liana prevalence (Wright et al., 2007) and being larger statured (Loubota Panzou, Ligot, et al., 2018).

Impact of liana load on forest structure

We found that the *a* coefficient (H_{max}) of the Michaelis–Menten model varied significantly between liana-loaded and liana-free trees in each forest site. This result suggests that at small diameters, liana-loaded and liana-free trees show similar allometries, but they diverge in their resource allocation strategies at larger diameters (Hulshof et al., 2015). Liana-loaded trees were significantly shorter in height than liana-free trees, in agreement with the results of Dias et al. (2017) in Amazonia. Given that lianas cause mechanical stress on trees due to the additional weight added to the tree crown, they reduce the total height of tree host and might enhance the probability of the tree trunk bends and breaks (Putz et al., 1983). For adult trees, liana loads result in a greater decrease in height than in diameter (Dias et al., 2017). Lianas can over-compete trees because of

TABLE 2 Impact of liana load on tree height–diameter allometry in three forests sites (Atlantic highland evergreen forest [Atla-F]; semideciduous forest [Semi-F], and evergreen-semideciduous forest on sandstone [Sand-F]).

Model	AIC	BIC	*p*
Atla-F			
General model (without effect)	2106	2117	
Varying a_l and b_l	2084	2099	<0.001
Fixed a and varying b_l	2075	2099	<0.001
Varying a_l and fixed b	**2073**	**2088**	**<0.001**
Semi-F			
General model (without effect)	6434	6449	
Varying a_l and b_l	6376	6396	<0.001
Fixed a and varying b_l	6354	6374	<0.001
Varying a_l and fixed b	**6351**	**6371**	**<0.001**
Sand-F			
General model (without effect)	7181	7196	
Varying a_l and b_l	7072	7093	<0.001
Fixed a and varying b_l	7050	7071	<0.001
Varying a_l and fixed b	**7034**	**7054**	**<0.001**

Note: We compared a general model with fixed parameters and three alternative models including a liana factor (*l*) effect on the model parameters (varying a_l and b_l, fixed a and varying b_l, and varying a_l and fixed b) using the Akaike information criterion (AIC) and Bayesian information criterion (BIC) values and likelihood ratio tests (*p* value). The best model is shown in boldface.

their lower investment in supporting tissues and, once at the canopy, because they overshadow and displace host tree leaves, rivaling with them on aboveground resources (Putz, 1984a; Putz et al., 1983; Schnitzer et al., 2005).

Lianas significantly impact the capacity of tropical forests to store and sequester carbon in trees (van der Heijden et al., 2015). Several studies have already demonstrated that liana load decreases tree growth rates (Campanello et al., 2007; Clark & Clark, 1990; Putz, 1984b) and affects the carbon stocks (van der Heijden et al., 2008). In response to this reduction of tree height, areas with larger values of aboveground biomass were negatively associated with the presence of lianas (Ledo et al., 2016; van der Heijden & Phillips, 2009).

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST
The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT
Data (Loubota Panzou, 2022) are available from ORBI: https://hdl.handle.net/2268/294508.

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REFERENCES
Alvira, D., F. E. Putz, and T. S. Fredericksen. 2004. "Liana Loads and Post Logging Liana Densities after Liana Cutting in a Lowland Forest in Bolivia." *Forest Ecology and Management* 190: 73–86.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67: 1–45.

Borchert, R., G. Rivera, and W. Hagnauer. 2002. "Modification of Vegetative Phenology in a Tropical Semi-Deciduous Forest by Abnormal Drought and Rain." *Biotropica* 34(1): 27–39.

Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Multimodel Inference. A Practical Information-Theoretic*

Approach (Second Edition). New York: Springer-Verlag New York.

Campanello, P. I., M. G. Gatti, A. Ares, L. Montti, and G. Goldstein. 2007. "Tree Regeneration and Microclimate in a Liana and Bamboo-Dominated Semideciduous Atlantic Forest." *Forest Ecology and Management* 252: 108–17.

Campbell, E. J. F., and D. M. Newbery. 1993. "Ecological Relationships between Lianas and Trees in Lowland Rain Forest in Sabah, East Malaysia." *Journal of Tropical Ecology* 9: 469–90.

Carsten, L. D., F. A. Juola, T. D. Male, and S. Cherry. 2002. "Host Associations of Lianas in a South-East Queensland Rain Forest." *Journal of Tropical Ecology* 18: 107–20.

Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. "Towards a Worldwide Wood Economics Spectrum." *Ecology Letters* 12: 351–66.

Clark, D. A., and D. B. Clark. 1992. "Life History Diversity of Canopy and Emergent Trees in a Neotropical Rain Forest." *Ecological Monographs* 62: 315–44.

Clark, D. B., and D. A. Clark. 1990. "Distribution and Effects on Tree Growth of Lianas and Woody Hemiepiphytes in a Costa Rican Tropical Wet Forest." *Journal of Tropical Ecology* 6: 321–31.

Dawkins, H. C. 1966. *The Productivity of Tropical High-Forest Trees and Their Reaction to Controllable Environment*. Oxford, UK: Commonwealth Forestry Institute.

Dewalt, S. J., S. A. Schnitzer, and S. Julie. 2000. "Density and Diversity of Lianas along a Chronosequence in a Central Panamanian Lowland Forest." *Journal of Tropical Ecology* 16: 1–19.

Dias, A. S., K. dos Santos, F. A. M. dos Santos, and F. R. Martins. 2017. "How Liana Loads Alter Tree Allometry in Tropical Forests." *Plant Ecology* 218: 119–25.

Fadrique, B., and J. Homeier. 2016. "Elevation and Topography Influence Community Structure, Biomass and Host Tree Interactions of Lianas in Tropical Montane Forests of Southern Ecuador." *Journal of Vegetation Science* 27: 958–68.

Fauset, S., M. U. Gloor, M. P. M. Aidar, H. C. Freitas, N. M. Fyllas, M. A. Marabesi, A. L. C. Rochelle, A. Shenkin, S. A. Vieira, and C. A. Joly. 2017. "Tropical Forest Light Regimes in a Human-Modified Landscape." *Ecosphere* 8: e02002.

Fayolle, A., G. J. Loubota Panzou, T. Drouet, M. D. Swaine, S. Bauwens, J. Vleminckx, A. Biwole, P. Lejeune, and J.-L. Doucet. 2016. "Taller Trees, Denser Stands and Greater Biomass in Semi-Deciduous Than in Evergreen Lowland Central African Forests." *Forest Ecology and Management* 374: 42–50.

Fayolle, A., N. Picard, J. L. Doucet, M. Swaine, N. Bayol, F. Bénédet, and S. Gourlet-Fleury. 2014. "A New Insight in the Structure, Composition and Functioning of Central African Moist Forests." *Forest Ecology and Management* 329: 195–205.

Forni, E., V. Rossi, J.-F. Gillet, F. Bénédet, G. Cornu, V. Freycon, I. Zombo, et al. 2019. "Dispositifs permanents de nouvelle génération pour le suivi de la dynamique forestière en Afrique centrale: bilan en République du Congo." *Bois et Forêt des Tropiques* 341: 55–70.

Gerwing, J. J., and D. L. Farias. 2000. "Integrating Liana Abundance and Forest Stature into an Estimate of Total Aboveground Biomass for an Eastern Amazonian Forest." *Journal of Tropical Ecology* 16: 327–35.

Gillet, J., and J. Doucet. 2012. "A Commented Checklist of Woody Plants in the Northern Republic of Congo." *Plant Ecology and Evolution* 145: 258–71.

Giraudoux, P. 2013. "Pgirmess: Data Analysis in Ecology." R Package. https://CRAN.R-project.org/package=pgirmess.

Hansen, M. C., P. V. Potapov, R. Moore, M. Hancher, S. A. Turubanova, A. Tyukavina, S. V. Stehman, et al. 2013. "High-Resolution Global Maps of 21st-Century Forest Cover Change." *Science* 342: 850–3.

Hawthorne, W. 1995. *Ecological Profiles of Ghanaian Forest Trees*. Oxford, UK: Department of Plant Sciences, University of Oxford, Oxford Forestry Institute.

Hollander, M., and D. A. Wolfe. 1973. *Nonparametric Statistical Methods*. New York: John Wiley & Sons.

Hulshof, C. M., N. G. Swenson, and M. D. Weiser. 2015. "Tree Height–Diameter Allometry across the United States." *Ecology and Evolution* 5: 1193–204.

Ickes, K., C. J. Paciorek, and S. C. Thomas. 2005. "Impacts of Nest Construction by Native Pigs (*Sus scrofa*) on Lowland Malaysian Rain Forest Saplings." *Ecology* 86(6): 1540–7.

Ingwell, L. L., S. J. Wright, K. K. Becklund, S. P. Hubbell, and S. A. Schnitzer. 2010. "The Impact of Lianas on 10 Years of Tree Growth and Mortality on Barro Colorado Island, Panama." *Journal of Ecology* 98: 879–87.

Kaçamak, B., N. Barbier, M. Aubry-Kientz, E. Forni, S. Gourlet-Fleury, D. Guibal, J.-J. Loumeto, et al. 2022. "Linking Drone and Ground-Based Liana Measurements in a Congolese Forest." *Frontiers in Forests and Global Change* 5: 803194.

Laurance, W. F., A. S. Andrade, A. Magrach, J. L. C. Camargo, J. J. Valsko, M. Campbell, P. M. Fearnside, W. Edwards, T. E. Lovejoy, and S. G. Laurance. 2014. "Long-Term Changes in Liana Abundance and Forest Dynamics in Undisturbed Amazonian Forests." *Ecology* 95: 1604–11.

Laurance, W. F., D. Perez-Salicrup, P. Delamonica, P. M. Fearnside, S. D'Angelo, A. Jerozolinski, L. Pohl, and T. E. Lovejoy. 2001. "Rain Forest Fragmentation and the Structure of Amazonian Liana Communities." *Ecology* 82: 105–16.

Ledo, A., J. B. Illian, S. A. Schnitzer, S. J. Wright, J. W. Dalling, and D. F. R. P. Burslem. 2016. "Lianas and Soil Nutrients Predict Fine-Scale Distribution of above-Ground Biomass in a Tropical Moist Forest." *Journal of Ecology* 104: 1819–28.

Loubota Panzou, G. J., Y. E. Bocko, A. Y. Mavoungou, and J. J. Loumeto. 2021. "Height–Diameter Allometry in African Monodominant Forest Close to Mixed Forest." *Journal of Tropical Ecology* 37(2): 98–107.

Loubota Panzou, G. J., A. Fayolle, T. R. Feldpausch, G. Ligot, J. L. Doucet, E. Forni, I. Zombo, M. Mazengue, J. J. Loumeto, and S. Gourlet-Fleury. 2018. "What Controls Local-Scale Aboveground Biomass Variation in Central Africa? Testing Structural, Composition and Architectural Attributes." *Forest Ecology and Management* 429: 570–8.

Loubota Panzou, G. J., and T. R. Feldpausch. 2020. *Measuring Crown Dimensions for Tropical Forest Trees a Field Manual*. Exeter: NERC.

Loubota Panzou, G. J., G. Ligot, S. Gourlet-Fleury, J. L. Doucet, E. Forni, J. J. Loumeto, and A. Fayolle. 2018. "Architectural Differences Associated with Functional Traits among 45 Coexisting Tree Species in Central Africa." *Functional Ecology* 32: 2583–93.

Loubota Panzou, G. J. 2022. "Intensity, Determinants, and Impacts of Liana Load on Tropical Trees in Central Africa." Dataset. ORBI. https://hdl.handle.net/2268/294508.

Lubini, C. A. 1997. *La vegetation de la Réserve de Biosphère de Luki au Mayombe (Zaïre)*. Meise, Belgium: Jardin Botanique National de Belgique.

Malizia, A., and H. R. Grau. 2006. "Liana–Host Tree Associations in a Subtropical Montane Forest of North-Western Argentina." *Journal of Tropical Ecology* 22: 331–9.

Meunier, Q., C. Moumbogou, and J.-L. Doucet. 2015. *Arbres utiles du Gabon*. Gembloux, Belgium: Presses Agronomiques de Gembloux.

Moravie, M. A., M. Durand, and F. Houllier. 1999. "Ecological Meaning and Predictive Ability of Social Status, Vigour and Competition Indices in a Tropical Rain Forest (India)." *Forest Ecology and Management* 117: 221–40.

Muller-Landau, H. C., and M. D. Visser. 2019. "How Do Lianas and Vines Influence Competitive Differences and Niche Differences among Tree Species? Concepts and a Case Study in a Tropical Forest." *Journal of Ecology* 107: 1469–81.

Nathan, R., and H. C. Muller-Landau. 2000. "Spatial Patterns of Seed Dispersal, their Determinants and Consequences for Recruitment." *Trends in Ecology & Evolution* 15(7): 278–85.

Phillips, O. L., R. Vasquez Martinez, A. Monteagudo Mendoza, T. R. Baker, and P. Nunez Vargas. 2005. "Large Lianas as Hyperdynamic Elements of the Tropical Forest Canopy." *Ecology* 86: 1250–8.

Poorter, L., F. Bongers, F. J. Sterck, and H. Wöll. 2005. "Beyond the Regeneration Phase: Differentiation of Height-Light Trajectories among Tropical Tree Species." *Journal of Ecology* 93: 256–67.

Poorter, L., L. Bongers, and F. Bongers. 2006. "Architecture of 54 Moist-Forest Tree Species: Traits, Trade-Offs, and Functional Groups." *Ecology* 87: 1289–301.

Putz, F. E. 1984a. "How Trees Avoid and Shed Lianas." *Biotropica* 16: 19–23.

Putz, F. E. 1984b. "The Natural History of Lianas on Barro Colorado Island, Panama." *Ecology* 65: 1713–24.

Putz, F. E. 1995. "Vines in Treetops: Consequences of Mechanical Dependence." In *Forest Canopy*, edited by M. D. Lowman and N. M. Nadkami, 311–24. London, UK: Academic Press Limited.

Putz, F. E., P. D. Coley, K. Lu, A. Montalvo, and A. Aiello. 1983. "Uprooting and Snapping of Trees: Structural Determinants and Ecological Consequences de la Recherche." *Canadian Journal of Forest Research* 13: 1011–20.

R Core Team. 2021. *R: A Language and Environment for Statistical Computing (R Version 4.1.1)*. Vienna: R Foundation for Statistical Computing.

Reis, S. M., B. S. Marimon, P. S. Morandi, E. Fernando, A. Esquivel-muelbert, B. Hur, B. H. Marimon junior, et al. 2020. "Causes and Consequences of Liana Infestation in Southern Amazonia." *Journal of Ecology* 108: 2184–97.

Réjou-Méchain, M., F. Mortier, J. Bastin, G. Cornu, N. Barbier, N. Bayol, F. Bénédet, et al. 2021. "Unveiling African Rainforest Composition and Vulnerability to Global Change." *Nature* 593: 90–4.

Rutishauser, E., D. Barthélémy, L. Blanc, and N. Eric-André. 2011. "Crown Fragmentation Assessment in Tropical Trees: Method, Insights and Perspectives." *Forest Ecology and Management* 261: 400–7.

Schnitzer, S. A., and F. Bongers. 2002. "The Ecology of Lianas and Their Role in Forests." *Trends in Ecology & Evolution* 17: 223–30.

Schnitzer, S. A., and F. Bongers. 2011. "Increasing Liana Abundance and Biomass in Tropical Forests: Emerging Patterns and Putative Mechanisms." *Ecology Letters* 14: 397–406.

Schnitzer, S. A., J. W. Dalling, and W. P. Carson. 2000. "The Impact of Lianas on Tree Regeneration in Tropical Forest Canopy Gaps: Evidence for an Alternative Pathway of Gap-Phase Regeneration." *Journal of Ecology* 88: 655–66.

Schnitzer, S. A., M. E. Kuzee, and F. Bongers. 2005. "Disentangling Above- and Below-Ground Competition between Lianas and Trees in a Tropical Forest." *Journal of Ecology* 93: 1115–25.

Siegel, S., and N. J. Catellan. 1988. *Nonparametric Statistics for the Behavioural Sciences*. New York: McGrawHill.

Turner, I. M. 2001. *The Ecology of Tree in the Tropical Rain Forest*. Cambridge: Cambridge University Press.

van der Heijden, G. M. F., T. R. Feldpausch, A. F. de la Herrero, N. K. van der Velden, and O. L. Phillips. 2010. "Calibrating the Liana Crown Occupancy Index in Amazonian Forests." *Forest Ecology and Management* 260: 549–55.

van der Heijden, G. M. F., J. R. Healey, and O. L. Phillips. 2008. "Infestation of Trees by Lianas in a Tropical Forest in Amazonian Peru." *Journal of Vegetation Science* 19: 747–56.

van der Heijden, G. M. F., and O. L. Phillips. 2009. "Liana Infestation Impacts Tree Growth in a Lowland Tropical Moist Forest." *Biogeosciences* 6: 2217–26.

van der Heijden, G. M. F., J. S. Powers, and S. A. Schnitzer. 2015. "Lianas Reduce Carbon Accumulation and Storage in Tropical Forests." *Proceedings of the National Academy of Sciences* 112: 13267–71.

Verbeeck, H., P. Boeckx, and K. Steppe. 2011. "Tropical Forests: Include Congo Basin." *Nature* 479(7372): 179.

Visser, M. D., S. A. Schnitzer, H. C. Muller-landau, E. Jongejans, H. de Kroon, L. S. Comita, S. P. Hubbell, and S. J. Wright. 2018. "Tree Species Vary Widely in their Tolerance for Liana Infestation: A Case Study of Differential Host Response to Generalist Parasites." *Journal of Ecology* 106: 781–94.

Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. New York: Springer-Verlag New York.

Wright, S. J., K. E. Stoner, N. Beckman, R. T. Corlett, R. Dirzo, H. C. Muller-Landau, G. Nunez-lturri, C. A. Peres, and B. C. Wang. 2007. "The Plight of Large Animals in Tropical Forests and the Consequences for Plant Regeneration." *Biotropica* 39: 289–91.

Zanne, A. E., G. Lopez-Gonzalez, D. A. Coomes, J. Illic, S. Jansen, S. L. Lewis, R. B. Miller, N. G. Swenson, M. C. Wiemann, and J. Chave. 2009. "Data from: Towards a Worldwide Wood Economics Spectrum." Dryad Dataset. https://hdl.handle.net/10255/dryad.235.

SUPPORTING INFORMATION

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