



Allometric models for liana aboveground biomass in old-growth and secondary tropical forests of Tanzania

Alain Senghor K. Ngute^{a,*}, Marion Pfeifer^b, David S. Schoeman^{c,d}, Roy E. Gereau^e, Hamidu R. Mnendo^f, Aloys Mwakisoma^f, Waziri Mhagawale^f, Exaud E. Kivambe^f, Gerard Kyasapa^f, Herman M. Lyatuu^f, Deo D. Shirima^{f,g,h}, Andrew R. Marshall^{a,f,i}

^a Forest Research Institute, University of the Sunshine Coast, Sippy Downs, Queensland, Australia

^b School of Natural and Environmental Sciences, Newcastle University, Newcastle upon Tyne, UK

^c Ocean Futures Research Cluster, School of Science, Technology and Engineering, University of the Sunshine Coast, Sippy Downs, Queensland, Australia

^d Centre for African Conservation Ecology, Department of Zoology, Nelson Mandela University, Gqeberha, South Africa

^e Missouri Botanical Garden, St. Louis, MO, USA

^f Reforest Africa, Mang'ula, Tanzania

^g Department of Ecosystems and Conservation, Sokoine University of Agriculture, Morogoro, Tanzania

^h National Carbon Monitoring Centre, Sokoine University of Agriculture, Morogoro, Tanzania

ⁱ Flamingo Land Ltd, North Yorkshire, UK

ARTICLE INFO

Keywords:

Vines
Woody climber
Allometry
Diameter
Equation
Carbon stocks
Climate change
Tropical forests
Magombera
Africa

ABSTRACT

Lianas are common in tropical forests, where they influence forest dynamics, thus impacting the global carbon sink, with implications for climate change mitigation. Despite their increasing competitiveness with trees at the global scale, robust measurements of liana aboveground biomass (AGB) have been limited. Here we use data from destructive sampling to develop two separate allometric equations for estimating liana AGB from stem diameter in old-growth ($n = 15$ lianas) and secondary forests ($n = 22$ lianas). We compared estimates of AGB using our equations for 3141 lianas (≥ 1 cm diameter) in Tanzania's Kilombero Valley against estimates from previously published equations in other tropical regions. Our equations demonstrated stronger correlations between diameter and destructively measured AGB, than those from previously published equations ($R^2 = 0.86$ – 0.89 , versus $R^2 = 0.82$ – 0.88). Across all stems, the average stem-level liana AGB estimated using the equation for old-growth forests was 52 % higher than that estimated by the equation for secondary forests, showing that lianas have lower biomass per unit diameter in forests impacted by disturbance. In such forests, liana stems are damaged, deformed, or cannot reach maximum height due to reduced structural support. At the scale of the forest stand, our equations estimated a mean liana AGB of 3.25 Mg ha^{-1} (95 % Confidence Interval: 1.52 – 6.96) in old-growth forests and 10.19 Mg ha^{-1} (5.91 – 17.64) in secondary forests. These estimates roughly aligned with estimates from other equations, although there was considerable variation. Depending on the equation used, mean stand-level estimates of liana AGB ranged from 2.49 – 9.76 Mg ha^{-1} in old-growth forests and 10.19 – 20.74 Mg ha^{-1} in secondary forests. Our findings show the variability in liana allometry and AGB with disturbance and successional stage, further underscoring a need for caution when comparing estimates of liana biomass across studies and regions.

1. Introduction

Lianas, or woody vines, play an integral role in tropical forests, greatly contributing to structural complexity (Phillips et al., 2002). They have a unique growth strategy, leveraging the mechanical support of host trees rather than investing in trunk thickness for self-support

(Rowe, 2018). This enables them to allocate more resources to leaf production and swift vertical growth towards the forest canopy (Schnitzer, 2018). Recently, lianas have gained attention due to their critical role in forest dynamics (Schnitzer and Bongers, 2011; Schnitzer, 2018; Marshall et al., 2020), biodiversity (DeWalt et al., 2010; Ledo and Schnitzer, 2014), and carbon cycling (van der Heijden et al., 2015; Dias

* Correspondence to: Forest Research Institute, University of the Sunshine Coast, 90 Sippy Downs Dr, Sippy Downs, QLD 4556, Australia.

E-mail addresses: alain.ngute@research.usc.edu.au, kamdoum.senghor@gmail.com (A.S.K. Ngute).

<https://doi.org/10.1016/j.foreco.2024.121962>

Received 22 October 2023; Received in revised form 25 April 2024; Accepted 29 April 2024

0378-1127/© 2024 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

et al., 2017). Indeed, the study of lianas in tropical forest ecosystems has become a vital aspect of global change ecology (Verbeek and Kearsley, 2016; di Porcia e Brugnera et al., 2019; van der Heijden et al., 2023) and ecological restoration (Marshall et al., 2023).

Lianas are known for significantly influencing tree recruitment, growth, and survival, which ultimately impact forest health and carbon storage (van der Heijden et al., 2015; Marshall et al., 2017). However, our understanding of their biomass and contribution to carbon storage is limited (Estrada-Villegas et al., 2022). This gap largely arises from the challenges posed by their unique growth habits and the difficulty of accurately measuring their biomass (Putz, 1983). Despite these obstacles, studies have begun highlighting the substantial contributions lianas make to tropical forests' total above-ground biomass (AGB), sometimes estimated to account for up to 25 % of the AGB (Schnitzer, 2005; Durán and Gianoli, 2013; Schnitzer et al., 2015). Lianas are especially abundant in disturbed forests, where measurement of biomass and associated competitive success relative to trees is most critical for assessing their influence on the global carbon sink (Ngute et al., 2024).

Developing allometric equations to estimate liana aboveground biomass in tropical forests is crucial for accurately quantifying carbon stocks and fluxes (Verbeek and Kearsley, 2016). Unlike trees, for which well-established allometric equations exist, lianas have been largely overlooked by studies estimating forest biomass-estimation studies (Schnitzer et al., 2006; Miao et al., 2016; di Porcia e Brugnera et al., 2019). Accurate estimation of the biomass of lianas is challenging due to their complex growth forms and reliance on host trees for support (Schnitzer and Bongers, 2011). Whilst terrestrial laser scanning may provide an emerging tool to obtain accurate estimates of liana volume and biomass (Krishna Moorthy et al., 2020), allometric equations that relate measurable traits such as ratios of stem diameter to biomass are typically the only viable approach for estimating liana biomass across regions without extensive destructive sampling (Schnitzer and Carson, 2010). However, these equations initially require a small amount of destructive sampling, where a subset of lianas representative of the study system is cut down, their diameter-biomass relationship is measured directly, and then used to estimate the biomass of other unharvested stems. However, the relationships between stem diameter and biomass vary among liana species due to differences in their growth patterns, forms and wood density (Krishna Moorthy et al., 2020).

Few studies have developed and tested allometric equations across different forest habitats (Addo-Fordjour and Rahmad 2013a; Miao et al., 2016). Yet the performance of allometric equations is expected to vary across different types of forests (Addo-Fordjour and Rahmad 2013a) due to differences in species composition, structure, and environmental conditions affecting liana and tree growth and carbon accumulation (Chave et al., 2014). As a result, equations developed for one type of forest may not provide accurate estimates when applied to another (Miao et al., 2016). In particular, previous modelling of liana allometry has not yet focussed on heavily disturbed secondary forests, where lianas have less structural support, and where there are increasing calls for more research to assess forest recovery and carbon accumulation (Marshall et al., 2023). There is also a lack of allometric equations for lianas in Africa, where the only liana allometric equations available are from Ghana (Addo-Fordjour and Rahmad, 2013a).

In this study, we aim to determine the consequences of varying forest structures for estimating liana allometry and AGB. We develop allometric equations for estimating liana AGB from stem diameter separately in old-growth and secondary forests in Tanzania. To our knowledge, our study is the first attempt to develop allometric equations for lianas in East African forests. We explore the implications of these equations for estimates of liana AGB across forest stands. Using the same stem data, we compare the estimates of liana AGB from our local allometric equations to those from previously published equations derived for other tropical regions.

2. Materials and methods

2.1. Study site

The study was conducted in the Magombera Nature Forest Reserve in the Kilombero Valley, Tanzania (Fig. 1). The area is located at ~280 m elevation, with daily temperatures of 18–38°C and mean annual rainfall of approximately 1500 mm per year, with the peak of rains generally recorded between March and May. Soils mostly have a sandy clay loam texture ($3.7 \leq \text{pH} \leq 6.1$). The vegetation is dominated by seasonally flooded lowland forest, with an understorey comprising small herbs, vines, and evergreen shrubs, with lianas predominant in disturbed areas. Because of its proximity to the Udzungwa Mountains, the forest comprises a mix of both the Zanzibar-Inhumbane lowland forest and Eastern Afromontane forest (Marshall, 2008), making it uniquely representative of the broader East Africa region of moist forests and hence an excellent location for deriving regionally generalisable allometric equations.

Forests in the study sites (Fig. 1) have been impacted by varying intensities of historical disturbance, mostly from selective logging (ca. 30 years ago), ongoing fuelwood collection, and fires spreading from adjacent crop fields (Marshall, 2008). As a result, the remaining forests comprise a mosaic of habitats that we categorised into old-growth and secondary forests based on their structural attributes for trees (see Table 1). Old-growth forests constituted up to 80 % of the total forest area, with some understorey/mid-strata tree-cutting but with the canopy remaining largely intact. In contrast, secondary forests, which account for at least 20 %, are in heavily degraded areas without a continuous canopy and predominantly feature stunted/damaged trees (Marshall et al., 2017).

2.2. Data collection

A total of 15 and 22 liana stems were randomly sampled and harvested from old-growth and secondary forest areas, respectively. Randomised sampling was stratified by liana diameter (at a distance of 1.3 m from the rooting point) to ensure sampling across the full range of size classes in 1 cm increments from 1.0–1.9 cm to 9.0–9.9 cm. There were exceedingly few lianas beyond this size range (<1 % of stems). A larger number were sampled from secondary forests to account for variation in structure expected as a result of disturbance.

Harvested lianas belonged to 8 families and 9 species (Table 2). Harvested lianas comprised individuals with both single and multiple stems. Before harvesting, the diameter of each liana stem was measured following Gerwing et al. (2006) and Schnitzer et al. (2008). Stems were then harvested by cutting at the base of each individual. All samples, including any branches and leaves attached to each sample, were then oven-dried to constant weight at ~80°C. The total dry mass of each sample was then summed to determine aboveground biomass (hereafter AGB) for each stem.

2.3. Data analysis

All analyses were conducted in R statistical software, version 4.3–1 (R Core Team, 2023). To develop allometric equations for estimating liana total AGB from stem diameter in each type of forest, we fitted simple linear regression models of total oven-dry weight (AGB; kg) for each harvested liana as a function of its stem diameter (D ; cm). Allometric models were fitted using both untransformed data and data transformed by their natural logarithm. These approaches generally followed the methods of previous studies (Gehring et al., 2004; Schnitzer et al., 2006; Addo-Fordjour and Rahmad, 2013a; Addo-Fordjour and Rahmad, 2013b).

After checking the statistical assumptions of homoscedasticity and normality, the performance of fitted models was assessed using ordinary least-squares regression (OLS). We used Model Root Mean Squared Error (RMSE) and adjusted coefficient of determination (adj. R-squared) to

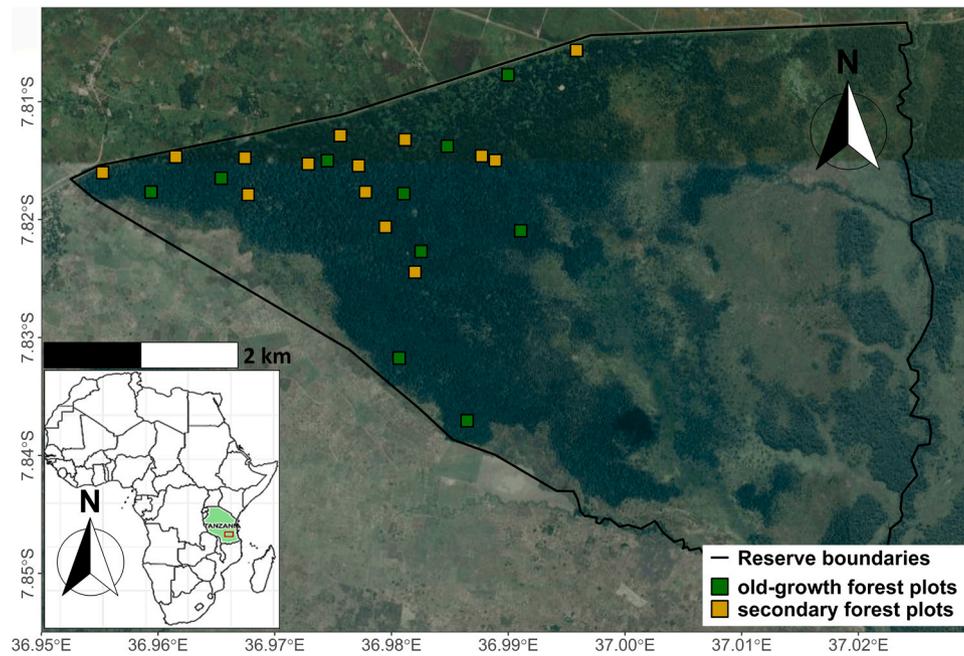


Fig. 1. Map of study site showing locations of vegetation sample plots (0.04-ha) across Magombera Nature Reserve in south-central Tanzania. Dark green areas within the reserve show the extent of moist forests. Google Satellite Imagery ©2023 TerraMetrics.

Table 1
Structural attributes for trees (DBH ≥ 1 cm) in old-growth and secondary forests.

	Old-growth forests	Secondary forests
N (20 m x 20 m plots)	10	14
DBH (cm)	8.6 (6.9–10.4) ^a	5.6 (4.1–7.1) ^b
Height (m)	5.9 (5.13–6.6) ^a	4.5 (3.9–5.2) ^b
Stem Density (stems ha ⁻¹)	2755(1488–4021) ^a	1813 (1312–2314) ^a
Basal Area (m ² ha ⁻¹)	26.5 (23.3–29.6) ^a	5.5 (3.6–7.4) ^b
Aboveground Biomass (Mg ha ⁻¹)	205.8 (179.5–232.2) ^a	25 (11.9–38.1) ^b
Liana crown occupancy (%)	3.3 (0–6.8) ^a	82.5 (73.0–92.3) ^b
Canopy loss (%) [‡]	<90	≥90

Note: Values refer to mean (95 % confidence intervals). Different superscript letters between columns mark significant differences detected by one-way Kruskal-Wallis tests ($p < 0.05$). DBH: Diameter at Breast Height. [‡]Marshall et al. (2017)

Table 2
Taxonomic details of liana stem harvested in each type of forest.

Species	Family	Number of stems	
		Old-growth forest	Secondary forest
<i>Agelaea pentagyna</i> (Lam.) Baill.	Connaraceae	1	0
<i>Alafia microstylis</i> K.Schum.	Apocynaceae	2	0
<i>Dichapetalum ruhlandii</i> Engl.	Dichapetalaceae	3	4
<i>Keetia gueinzii</i> (Sond.) Bridson	Rubiaceae	0	4
<i>Landolphia kirkii</i> Dyer ex Hook.f.	Apocynaceae	1	2
<i>Microcos calymmatosepala</i> (K. Schum.) Burret	Malvaceae	4	7
<i>Salacia madagascariensis</i> (Lam.) DC.	Celastraceae	0	4
<i>Senegalia pentagona</i> (Schumach.) Kyal. & Boatwr.	Fabaceae	2	1
<i>Uvaria tanzaniae</i> Verdc.	Annonaceae	2	0

evaluate the goodness of fit (Wellek, 2021).

We accounted for bias resulting from the change in residual structure while back-log-transforming AGB estimates from logarithmic units by calculating a correction factor (CF) by which AGB should be multiplied to resorb the bias and avoid underestimating AGB (Baskerville, 1972; Beauchamp and Olson, 1973; Parresol, 1999). For each allometric model, CF was calculated as in Schnitzer et al. (2006), using the following formula:

$$CF = \exp^{(RMSE^2/2)} \tag{1}$$

Using Analysis of Covariance (ANCOVA), we tested the effects of forest categories on the relationship between liana AGB and D. We also computed least-squares means and used *post hoc* multiple pairwise tests with false discovery rate-adjusted *p*-values to compare estimates of liana AGB at the stem level from our new allometric models with those from other pre-existing allometric equations (Table 3).

Table 3
Existing equations for estimating liana aboveground biomass (kg) from stem diameter (D, cm) measured at 1.3 m from the rooting point.

Data region	Equation	Diameter range (cm)	Sample size
Ghana (primary forests) [†]	$10^{[1.077 + 0.85 \times \log(D)]}$	1.2–13.2	50
Ghana (secondary forests) [†]	$10^{[0.236 + 1.128 \times \log(D)]}$	1.2–13.0	50
Malaysia [‡]	$10^{[0.490 + 1.090 \times \log(D)]}$	1.3–14.2	60
China [‡]	$\exp^{[0.1498 + 1.7895 \times \ln(D)]}$	1.3–15.0	25
Pantropical [§]	$\exp^{[-1.484 + 2.657 \times \ln(D)]}$	1.0–23.0	424
Pantropical (no Venezuela) [§]	$\exp^{[-1.519 + 2.682 \times \ln(D)]}$	1.0–23.0	417
Tanzania (old-growth forests) [*]	NA	1.0–9.5	15
Tanzania (secondary forests) [*]	NA	1.0–9.0	22

[†]Addo-Fordjour & Rahmad (2013a)

[‡]Addo-Fordjour & Rahmad (2013b)

[§]Lü et al. (2009)

[§]Schnitzer et al. (2006)

* This study

Finally, we compared field-observed AGB values and estimates from newly developed and pre-existing allometric models (Table 3) using ANCOVA, analysis of variance (ANOVA), OLS and concordance correlation coefficient (CCC), which computes the agreement of two different methods on a continuous scale (Lin, 1989). CCC values range from -1 (perfect disagreement) to 1 (perfect agreement).

We applied our newly developed and published allometric equations to a dataset that comprised 3141 individual lianas (diameter ≥ 1 cm, at a distance of 1.3 m from the rooting point) to estimate their aboveground biomass and hence to compare the implications of using alternative allometric equations for landscape-level biomass/carbon estimation. These data were collected in a network of 24 permanent 0.04-ha sample plots, situated in old-growth (n = 10) and secondary (n = 14) forests across Magombera Nature Reserve (Fig. 1).

To compare estimates of liana AGB at the level of forest stand, we employed the ‘lme4’ R package (Bates et al., 2015) to fit a linear mixed-effects model, using liana AGB values—estimated by various equations (Table 3)—as the response. Before fitting the model, liana AGB values were transformed by their natural logarithm to meet the assumptions of normality and homoscedasticity. The model was predicted by two categorical variables: the type of forest (old-growth or secondary forest) and the equation used for AGB estimation. The equations for AGB estimation included eight different models originating from several studies: Addo-Fordjour and Rahmad (2013a, 2013b), Lü et al. (2009), Schnitzer et al. (2006), and our study (Table 3). We included plot locations as discrete random intercepts in the model to account for potential effects arising from sample plot distribution across the study site. Subsequently, we performed an ANOVA test and computed the estimated marginal means (also known as least-squares means) for each combination of equation and type of forest, followed by *post hoc* pairwise comparisons with Šidák adjustments from multiple comparisons using the ‘emmeans’ and ‘multcomp’ R packages (Hothorn et al., 2008; Lenth, 2023).

3. Results

3.1. Allometric models

In each of the forest categories we studied, all tested models demonstrated robust and significant linear relationships between stem diameter and liana AGB (Table 4). The models were formulated as follows:

$$\text{Model 1 : AGB} = \alpha_1 + \beta_1 \times D + \varepsilon_1 \tag{2}$$

$$\text{Model 2 : ln(AGB)} = \alpha_2 + \beta_2 \times \ln(D) + \varepsilon_2 \tag{3}$$

$$\text{Model 3 : ln(AGB)} = \alpha_3 + \beta_3 \times \ln(D^2) + \varepsilon_3 \tag{4}$$

Table 4

Parameters of fitted allometric models for estimating liana aboveground biomass (kg) from stem diameter (cm) in old-growth and secondary forests.

Forests	Model N°	d. f.	α ± se	β ± se	Adj. R ²	RMSE	p-value
Old-growth n = 15 stems	1	14	-17.85 ± 10.72	10.16 ± 4.11	0.67	19.43	<0.001
	2	14	-0.98 ± 0.21	2.46 ± 0.17	0.95	0.42	<0.001
	3	14	-0.98 ± 0.21	1.23 ± 0.08	0.95	0.42	<0.001
Secondary n = 22 stems	1	21	-13.83 ± 6.34	6.98 ± 2.16	0.70	10.09	<0.001
	2	21	-1.32 ± 0.12	2.43 ± 0.14	0.91	0.48	<0.001
	3	21	-1.32 ± 0.12	1.21 ± 0.07	0.91	0.48	<0.001

Note: d.f. = degrees-of-freedom; α = intercept; β = slope; se = standard error

where:

AGB is the aboveground biomass (in kg)

D is the diameter (in cm)

α₁, α₂ and α₃ are the model intercepts

β₁, β₂ and β₃ are the model slopes (exponents in the case of log-log models)

ε₁, ε₂ and ε₃ are the model residual error terms

We found that Model 2 was best suited for estimating liana biomass using stem diameter across both types of forests, because of its superior fit and better diagnostics (R² = 0.91–0.95; RMSE = 0.42–0.48; Fig. 2), as well as its simplicity relative to Model 3. Even though Model 3 had a comparable fit to Model 2 (see Table 4), it was more complex due to its reliance on squared diameter as the predictor. As a result, the following equations were derived for estimating liana AGB (in kg) in old-growth and secondary forests, respectively (Fig. 2):

$$\text{Old-growth forests : AGB} = \exp^{-0.98+2.46 \times \ln(D)} \times 1.092 \tag{5}$$

$$\text{Secondary forests : AGB} = \exp^{-1.32+2.43 \times \ln(D)} \times 1.121 \tag{6}$$

where D is the diameter (measured at 1.3 m from the rooting point) in cm.

3.2. Estimation of liana AGB at the stem level

At the stem level, the mean AGB of lianas, when estimated using our newly developed old-growth forest allometric equation, was on average 52 % greater than that calculated with the new equation for secondary forests (Fig. 3). This discrepancy was further emphasised after adjusting for field-measured stem diameter, showing a statistically significant difference in stem-level estimates of liana AGB between the two equations (F_[1,35] = 2.098; p = 0.021, Appendix A, S1).

In both categories of forests, the estimates derived from our allometric equations did not significantly differ from those of existing models, except for models by Addo-Fordjour and Rahmad (2013a) from Ghana (p < 0.05, Fig. 4a). The allometric models by Addo-Fordjour and Rahmad (2013a) for primary and secondary forests showed the highest and lowest average stem-level liana AGB estimates for primary and secondary forests, respectively. Specifically, for old-growth forests, the liana AGB estimate was 38.6 kg stem⁻¹ (95 % confidence interval: 32.6–44.7 kg stem⁻¹), and for secondary forests, it was 8.2 kg stem⁻¹ (4.8–11.5 kg stem⁻¹). These estimates were significantly different (p < 0.001; Fig. 4a) from those produced by other models (Fig. 4a) in old-growth (F_[6,97] = 6.052; Appendix A, S2) and secondary forests (F_[6146] = 2.480; Appendix A, S3).

In both old-growth and secondary forests, the alternative allometric equations produced a wide range of AGB estimates for lianas of the same diameter. The variations in stem-level liana AGB were more pronounced as stem diameter increased (Fig. 4b). For instance, the pantropical allometric equations from Schnitzer et al. (2006) generally underestimated liana AGB by 17–18 % compared to our old-growth forest equation but overestimated by 15–16 % in comparison to our secondary forest equation (Fig. 4b). In contrast, equations for Ghana’s primary forest from Addo-Fordjour and Rahmad (2013a) overestimated liana AGB by a notable 53 % when compared to our equation for old-growth forests. However, their equation for the secondary forest underestimated the AGB of lianas by an average of 38 %, compared to our corresponding equation. These observations were made in individuals with a stem diameter greater than approximately 2.5 cm in old-growth forests and approximately 5 cm in secondary forests (Fig. 4b).

Estimates of stem-level liana AGB from our allometric equations more closely matched observed values than did estimates from other existing models (see Table 5). This close alignment is substantiated by high R² and CCC values for both old-growth (R² = 0.89; CCC = 0.88) and secondary forests (R² = 0.86; CCC = 0.89). Equations by Schnitzer et al. (2006) and Lü et al. (2009) also consistently showed strong correlation

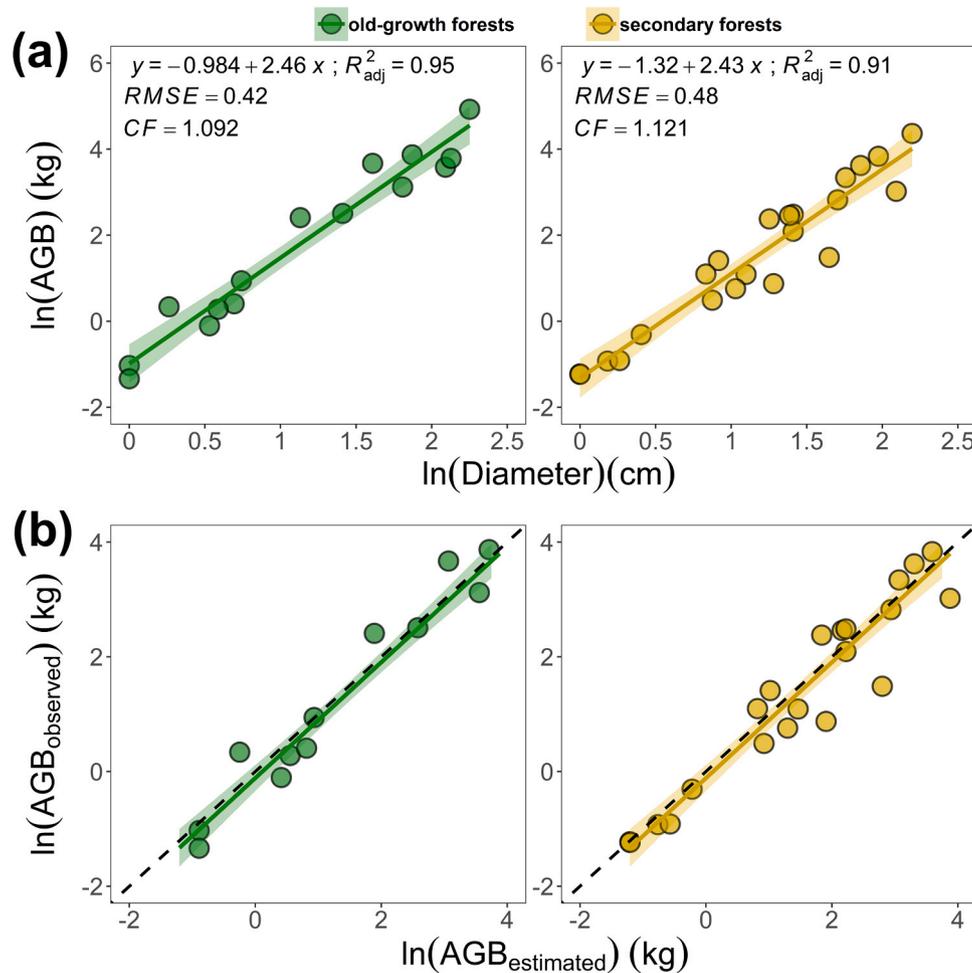


Fig. 2. Goodness-of-fit for the best models in both old-growth ($n = 15$ stems) and secondary ($n = 22$ stems) forests. (a) Allometric relationship between liana AGB and diameter. (b) Liana AGB as estimated from the model, versus observed AGB from the field, plotted against a reference line for a perfect fit (i.e., a line through the origin with unit slope —dashed line). RMSE = root mean square error. CF = correction factor. See Materials and Methods for details of calculations.

and concordance with observed liana AGB (Table 5). In contrast, equations from Addo-Fordjour and Rahmad (2013a, 2013b) often failed to closely match our stem-level field measurements of liana AGB ($\text{CCC} \leq 0.67$), even though their regressions produced high coefficients of determination ($R^2 = 0.82\text{--}0.87$; Table 5) relative to the data to which they were originally fit.

3.3. Estimation of liana AGB at the forest stand level

The performance of different allometric equations in estimating liana AGB at stand level varied significantly based on the type of forest ($p < 0.001$; Fig. 5). On average, old-growth forests had a significantly lower ($p < 0.001$; Fig. 5) liana AGB (3.61 Mg ha^{-1} , 95 % confidence interval: 2.04–6.36) compared to secondary forests (13.11 Mg ha^{-1} , 8.67–19.69). Our stand-level estimates of liana AGB for old-growth forests (3.25 Mg ha^{-1} , 1.52–6.96) and secondary forests (10.19 Mg ha^{-1} , 5.91–17.64) were not significantly different from those derived using other equations ($p \geq 0.05$; Fig. 5). However, there were some observed exceptions. In old-growth forests, the estimates from Ghana's primary forest equation (Addo-Fordjour and Rahmad, 2013a) were significantly higher than all others, including ours ($p < 0.001$, Fig. 5). In secondary forests, liana AGB estimates using equations from Malaysia (Addo-Fordjour and Rahmad, 2013b) and China (Lü et al., 2009) were the only ones significantly higher than those obtained by other equations, including ours ($p < 0.001$, Fig. 5).

4. Discussion

Our results demonstrated robust and positive relationships between estimates of liana AGB and stem diameter. These relationships differed significantly between old-growth and secondary forests, utilising our newly developed models at both the individual stem and forest stand levels. This supports the notions that stem diameter is a strong predictor for liana biomass (Krishna Moorthy et al., 2020) and that individual liana AGB differs across old-growth and secondary forests (Miao et al., 2016; Addo-Fordjour and Rahmad, 2013a). Several factors, such as liana morphology, growth patterns, and wood density, could account for these discrepancies in estimated AGB between the two types of forests (Putz, 1983; Ledo and Schnitzer, 2014; Krishna Moorthy et al., 2020).

Upon comparing our estimates with those from other existing models, our equations demonstrated the strongest levels of agreement with observed liana AGB in both old-growth and secondary forests in Tanzania, where we collected the data for these models. High coefficients of determination and concordance in correlation coefficients between estimates from our equations and observed field values, signify their robust performance in predicting liana biomass at our study sites. The equations proposed by Schnitzer et al. (2006) and Lü et al. (2009) also consistently showed high correlation and concordance with observed liana AGB. However, the equations from Addo-Fordjour and Rahmad (2013a, 2013b) displayed weaker correlation and agreement, implying a discrepancy between the observed liana AGB and the estimates derived from these equations. Nonetheless, the regression still

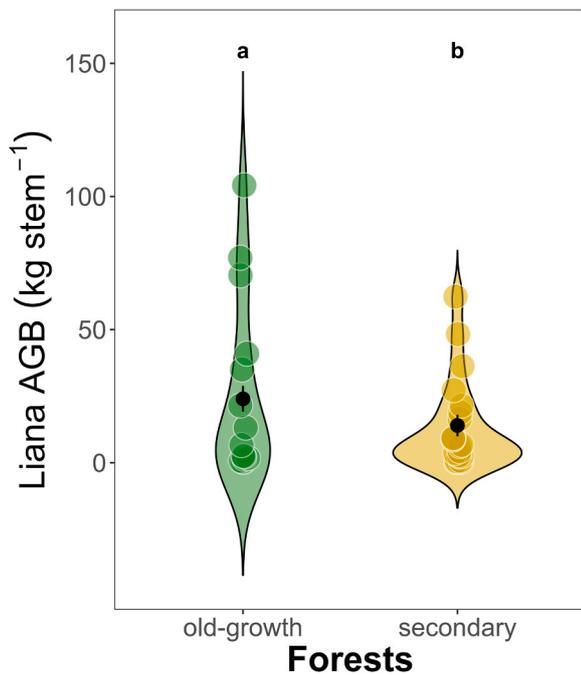


Fig. 3. Stem-level estimates of liana aboveground biomass (AGB) in old-growth ($n = 15$) and secondary ($n = 22$) forests at our study site, using our newly developed allometric equations tailored for each forest category. The black points indicate the mean AGB values estimated using least-squared regression models, with vertical lines representing the 95 % confidence intervals around these means. Superscript letters denote statistically significant differences between the forest types as shown by ANCOVA ($p < 0.05$). ANCOVA results can be found in Appendix A, S1.

yielded high coefficients of determination, indicating a good fit. These findings emphasise the need to consider both statistical fit and diagnostic measures when evaluating the performance of allometric equations (Chave et al., 2005).

Our results indicate that allometric equations produced a broad range of AGB estimates for lianas of the same diameter. We observed that the variations in stem-level AGB estimates became more pronounced as the stem diameter exceeded certain thresholds—specifically, around 2.5 cm and 5 cm in old-growth and secondary forests, respectively. This variance adds complexity to the task of selecting a particular equation for more accurate AGB estimation. We contend that future allometric models could be significantly improved by sampling a wider range of larger lianas. Such an approach will potentially refine AGB predictions and enhance precision across different forest types (Miao et al., 2016).

The capacity of various allometric equations in estimating stem-level liana AGB also varied considerably based on the types of forest, underscoring the necessity of suitable equations for differing conditions. This result indicates variability in growth patterns and liana biomass allocation across forest types and gradients of forest degradation (Gerwing and Farias, 2000).

Moreover, the equation for primary forest from Ghana (Addo-Fordjour and Rahmad, 2013a) overestimated liana AGB in Tanzania compared to our new equation for old-growth forests. Conversely, their equation for secondary forest underestimated liana AGB compared to our new equation for secondary forest. Furthermore, the equations derived from pantropical locations (except Africa) by Schnitzer et al. (2006) slightly underestimated liana AGB in Tanzania when compared to our estimates for old-growth forests and overestimated it relative to our secondary forest equation—although the observed differences were only marginal. These discrepancies emphasise the challenges of using pantropical (Schnitzer et al., 2006) or even relevant continental

(Addo-Fordjour and Rahmad, 2013a) equations for stem-level liana AGB estimation and the need for caution when applying allometric equations across different types of forests (Miao et al., 2016).

At the forest stand level, the performance of different allometric equations in estimating liana AGB also differed significantly based on the type of forest. Stand-level estimates of liana AGB varied greatly between old-growth and secondary forests, emphasising the need to consider the type of forest when estimating liana biomass (Addo-Fordjour and Rahmad, 2013a; Miao et al., 2016). Our equations estimated mean liana AGB values in old-growth and secondary forests that were comparable to those obtained from the pantropical equations (Schnitzer et al., 2006), but differed from estimates by other equations found in China (Lü et al., 2009) and Malaysia (Addo-Fordjour and Rahmad, 2013b), as well as Ghana's primary forests (Addo-Fordjour and Rahmad, 2013a), at the forest stand level. These observations suggest that our equations performed well in estimating stand-level liana AGB. However, there were considerable variations in liana AGB predictions depending on the allometric equation used. This difference was evident in both old-growth and secondary forests.

Interestingly, we found secondary forests consistently produced higher stand-level estimates of liana AGB per unit area, than old-growth forests across all equations, with the single exception being the equation for primary forests from Ghana (Addo-Fordjour and Rahmad, 2013a). These findings highlight the need for caution when comparing estimates of liana biomass across studies that use different allometric equations. Furthermore, the difference in liana AGB estimated by the allometric models for old-growth and secondary forests underscores the influence of forest structural disturbance on liana growth patterns. These results are in line with previous studies suggesting that forest structure and age can significantly impact liana biomass (Durán and Gianoli, 2013; van der Heijden et al., 2015). For example, secondary forests usually have greater light availability due to the absence of a closed canopy, which favours liana growth and results in higher individual biomass. Our findings echo this, as we found higher liana AGB in secondary forests across all equations. Nevertheless, we also speculate that the discrepancies observed in liana AGB estimates, both at stem and forest stand levels, across different forest categories and between allometric models could potentially be attributed to habitat and/or regional variations in liana species compositions.

In light of the observed differences between various models in estimating liana AGB at the forest stand level, our study suggests the need for more region-specific research across different forest types. The allometric models developed in our study, tailored to the ecological characteristics of Tanzanian forests, show promise for application in similar forest ecosystems within Tanzania and neighbouring East African countries. Given the potential for over- or underestimation when applying a pantropical model (Schnitzer et al., 2006) across various forest types and disturbance categories, our research encourages further investigations into liana AGB for forests in Tanzania and surrounding regions with analogous compositions. These studies are vital for identifying the most effective allometric models for specific forest ecosystems, enhancing the accuracy of AGB estimations, and aiding in effective forest management and conservation strategies.

Further research is needed to deepen our understanding of liana biomass estimation and to address some limitations of our study. One such limitation is the sole focus on stem diameter as a predictor of liana AGB. While stem diameter is a reliable predictor (see Hozumi et al., 1969; Beekman, 1981; Putz, 1983), other variables, such as length, branching patterns, and wood density, could offer further insights into estimation of liana biomass, even though liana stem length has been shown to have only a very weak relationship with total AGB (Gehring et al., 2004; Addo-Fordjour and Rahmad, 2013b; Krishna Moorthy et al., 2020). Another important factor to consider is the potential impact of ontogenetic variation on estimates of liana biomass (Smith-Martin et al., 2020). Lianas exhibit dynamic growth patterns throughout their life cycles, and the relationship between stem diameter and biomass may

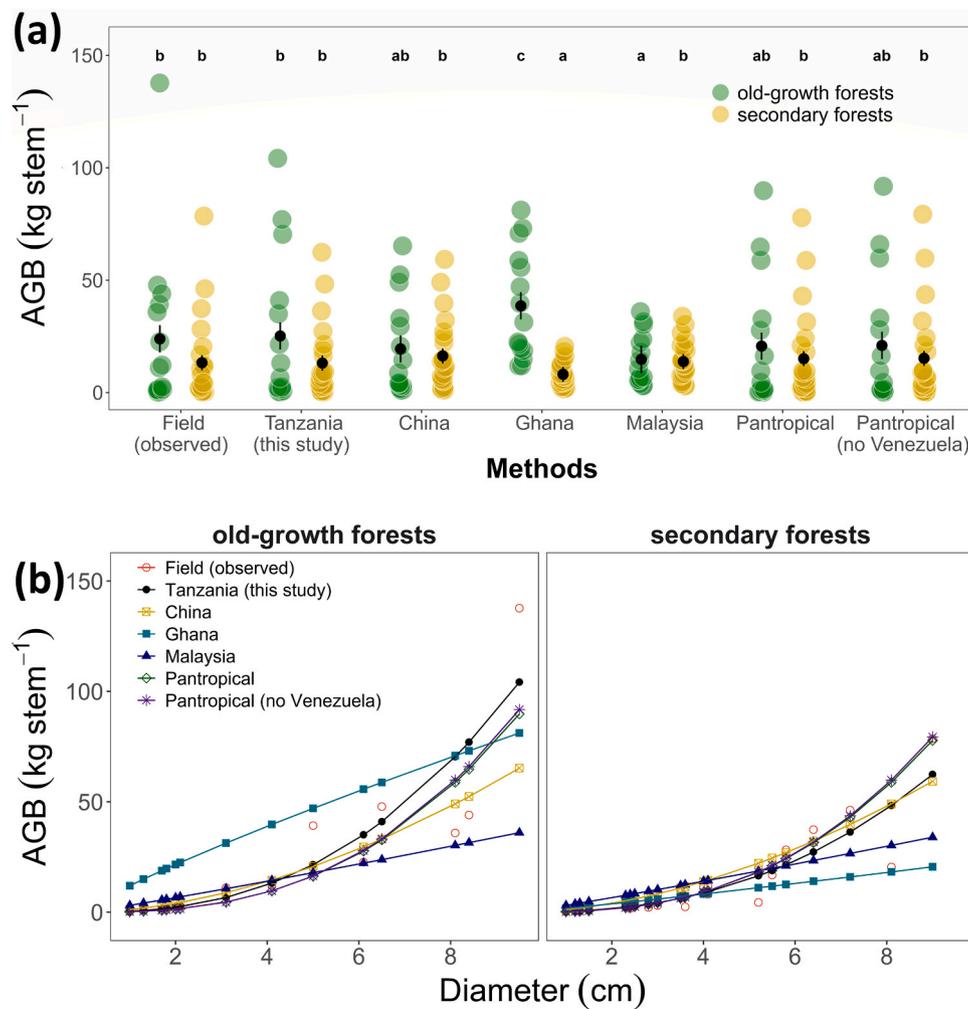


Fig. 4. Mean liana aboveground biomass for stems in old-growth ($n = 15$) and secondary ($n = 22$) forests at our study site. (a) Comparison of observed stem-level AGB from the field against estimates derived from various allometric equations within each forest category. Identical letters denote groupings with no significant difference ($p < 0.05$) by ANCOVA within each forest category. ANCOVA and *post hoc* test results can be found in Appendix A, S2–S3. (b) Relationships between liana diameter and AGB, as estimated through different allometric equations. China = Lü et al. (2009); Ghana = Addo-Fordjour and Rahmad (2013a); Malaysia = Addo-Fordjour and Rahmad (2013b); and Pantropical = Schnitzer et al. (2006).

Table 5

Summary of ordinary least-squares regression (R^2) and concordance correlation coefficients (CCC) between observed and estimated mean individual liana AGB derived from various existing equations in each type of forest.

Methods	Old-growth forests ($n = 15$)			Secondary forests ($n = 22$)		
	AGB \pm se (kg stem ⁻¹)	R^2	CCC	AGB \pm se (kg stem ⁻¹)	R^2	CCC
Field observation	23.9 \pm 9.3 ^{bc}	1	1	13.3 \pm 4.1 ^b	1	1
Tanzania (this study)	25.2 \pm 8.7 ^{bc}	0.89	0.88	13.1 \pm 3.6 ^b	0.86	0.89
China [‡]	19.5 \pm 4.6 ^b	0.88	0.75	16.4 \pm 3.5 ^b	0.85	0.86
Ghana [†]	38.6 \pm 6.2 ^c	0.86	0.67	8.2 \pm 1.2 ^a	0.82	0.42
Malaysia [¶]	14.8 \pm 2.9 ^b	0.87	0.45	13.8 \pm 1.9 ^b	0.82	0.65
Pantropical [§]	20.7 \pm 7.4 ^b	0.88	0.86	15.1 \pm 4.4 ^b	0.86	0.89
Pantropical (no Venezuela) [§]	21.0 \pm 7.6 ^b	0.88	0.87	15.3 \pm 4.5 ^b	0.86	0.89

Note: Different superscript letters denote significant differences ($p < 0.05$) across combinations of methods—forest categories (ANOVA results in Appendix A, S4).

[†]Addo-Fordjour and Rahmad (2013a)

[¶]Addo-Fordjour and Rahmad (2013b)

[‡]Lü et al. (2009)

[§]Schnitzer et al. (2006)

change as lianas age (Schnitzer et al., 2006). Including ontogenetic considerations and developing allometric equations specific to large lianas (diameter ≥ 10 cm, at a distance of 1.3 m from the rooting point) in future studies could provide more accurate estimates of stand-level liana AGB and a comprehensive understanding of liana AGB dynamics across forests (Miao et al., 2016; Verbeek and Kearsley, 2016).

Additionally, our study was limited to lowland old-growth and secondary forests, common types of forests in our study area. However, liana communities, structural types and allometry likely vary along elevational gradients and across different types of forests and regions, as already demonstrated for trees in our study region, which are tallest per unit diameter in mid-elevation moist forests (Marshall et al., 2012). Estimation of liana biomass may therefore require specific equations tailored to these contexts (Smith-Martin et al., 2020). Future research should therefore investigate the estimation of liana AGB in other forest ecosystems, such as tropical dry and montane forests, to broaden the applicability of allometric equations.

There is also a need for more comprehensive field sampling to validate the performance of allometric equations and assess their generalisability. Our study constructed allometric equations using a limited number of liana individuals, and may not fully capture the variation in liana biomass across different forest conditions. Increasing the sample size and encompassing a broader range of forest ecosystems and

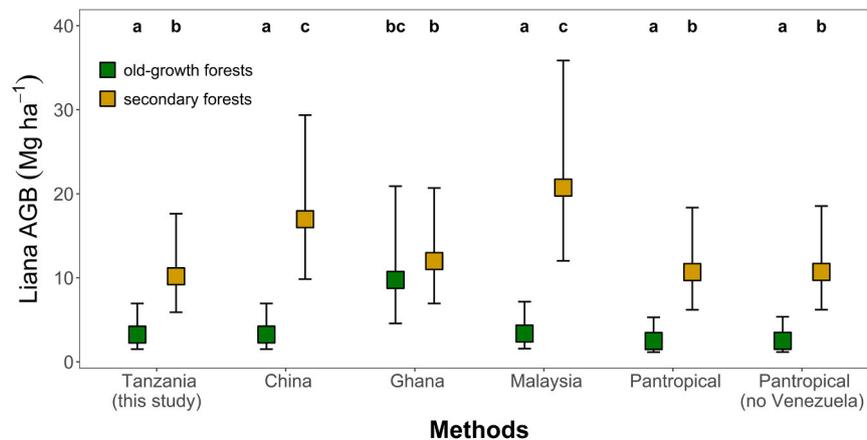


Fig. 5. Liana AGB (Mean \pm 95 % CI) at the plot level, estimated using different allometric equations, for old-growth ($n = 10$) and secondary ($n = 14$) forests in Tanzania. Identical letters denote groups with no statistically significant differences (as shown by ANOVA: $p < 0.05$) in liana AGB estimates across combinations of equations and types of forests. References: China = Lü et al. (2009); Ghana = Addo-Fordjour and Rahmad (2013a); Malaysia = Addo-Fordjour and Rahmad (2013b); Pantropical = Schnitzer et al. (2006). Note: Our estimates and those from Addo-Fordjour and Rahmad (2013a) were derived using separate equations for old-growth and secondary forests. Estimates from Lü et al. (2009) and Schnitzer et al. (2006) use a single equation regardless of the forest category.

geographical locations would improve the robustness and applicability of the developed equations.

5. Conclusion

In summary, our study enriches the body of knowledge on liana AGB with new allometric equations tailored to specific forest types for Tanzania. Our findings suggest that the allometric equation selected and the forest type play crucial roles in AGB estimation, with secondary forests showing lower AGB per unit diameter than old-growth counterparts. These observations underscore the key influence of forest disturbance legacies on liana AGB estimation and point to the necessity of incorporating forest types in biomass assessments. Furthermore, they highlight the need for comprehensive research on liana AGB estimation, taking into account other potential predictors such as length, branching patterns, and wood density.

CRedit authorship contribution statement

Alain Senghor K. Ngute: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Formal analysis, Data curation. **Andrew R. Marshall:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Deo D. Shirima:** Writing – review & editing, Project administration. **David S. Schoeman:** Writing – review & editing, Validation, Supervision. **Marion Pfeifer:** Writing – review & editing, Validation, Supervision, Methodology, Funding acquisition, Conceptualization. **Hamidu R. Mnendendo:** Writing – review & editing, Investigation. **Roy E. Gereau:** Writing – review & editing, Investigation. **Waziri Mhagawale:** Writing – review & editing, Investigation. **Aloys Mwakisoma:** Writing – review & editing, Investigation. **Gerard Kyasapa:** Writing – review & editing, Investigation. **Exaud E. Kivambe:** Writing – review & editing, Investigation. **Herman M. Lyatuu:** Writing – review & editing, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We extend our sincere gratitude to the two anonymous reviewers for their time and effort in reviewing our manuscript. We are deeply grateful to the Tanzania Commission for Science and Technology (COSTECH), the Tanzania Wildlife Research Institute (TAWIRI), and the Tanzania Forest Service Agency (TFS) for providing the necessary permits and permissions to perform this research. ASKN was supported by the University of the Sunshine Coast through an Australian Government International Research Training Program (RTP) Scholarship (1125098). The work formed part of the Forest Restoration and Climate Experiment (FoRCE), funded by an Australian Research Council Future Fellowship (ARM, FT170100279), with match-funding from the University of the Sunshine Coast. We are highly indebted to the staff of Reforest Africa and the populations Mang'ula and of Katurukila villages for their kind logistic support during field campaigns.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2024.121962](https://doi.org/10.1016/j.foreco.2024.121962).

References

- Addo-Fordjour, P., Rahmad, Z.B., 2013a. Mixed species allometric models for estimating above-ground liana biomass in tropical primary and secondary forests, Ghana. *ISRN For.* 2013, 1–9. <https://doi.org/10.1155/2013/153587>.
- Addo-Fordjour, P., Rahmad, Z.B., 2013b. Development of allometric equations for estimating above-ground liana biomass in tropical primary and secondary forests, Malaysia. *Int. J. Ecol.* 2013, 1–8. <https://doi.org/10.1155/2013/658140>.
- Baskerville, G.L., 1972. Use of logarithmic regression in the estimation of plant biomass. *Can. J. For. Res.* 2, 49–53. <https://doi.org/10.1139/x72-009>.
- Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67 <https://doi.org/10.18637/jss.v067.i01>.
- Beauchamp, J.J., Olson, J.S., 1973. Corrections for bias in regression estimates after logarithmic transformation. *Ecology* 54, 1403–1407. <https://doi.org/10.2307/1934208>.
- Beekman, F., 1981. *Structural and dynamic aspects of the occurrence and development of lianas in the tropical rainforest* (PhD Dissertation). Agricultural University, Wageningen, The Netherlands.
- Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., et al., 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145, 87–99. <https://doi.org/10.1007/s00442-005-0100-x>.

- DeWalt, S.J., Schnitzer, S.A., Chave, J., Bongers, F., Burnham, R.J., Cai, Z., et al., 2010. Annual rainfall and seasonality predict pan-tropical patterns of liana density and basal area. *Biotropica* 42, 309–317. <https://doi.org/10.1111/j.1744-7429.2009.00589.x>.
- di Porcia e Brugnera, M., Meunier, F., Longo, M., Krishna Moorthy, S.M., De Deurwaerder, H., Schnitzer, S.A., et al., 2019. Modelling the impact of liana infestation on the demography and carbon cycle of tropical forests. *Glob. Change Biol.* 25, 3767–3780. <https://doi.org/10.1111/gcb.14769>.
- Dias, A.S., dos Santos, K., dos Santos, F.A.M., Martins, F.R., 2017. How liana loads alter tree allometry in tropical forests. *Plant Ecol.* 218, 119–125. <https://doi.org/10.1007/s11258-016-0671-0>.
- Durán, S.M., Gianoli, E., 2013. Carbon stocks in tropical forests decrease with liana density. *Biol. Lett.* 9. <https://doi.org/10.1098/rsbl.2013.0301>.
- Estrada-Villegas, S., Pedraza Narvaez, S.S., Sanchez, A., Schnitzer, S.A., 2022. Lianas significantly reduce tree performance and biomass accumulation across tropical forests: a global meta-analysis. *Front. For. Glob. Change* 4, 1–9. <https://doi.org/10.3389/ffgc.2021.812066>.
- Gehring, C., Park, S., Denich, M., 2004. Liana allometric biomass equations for Amazonian primary and secondary forest. *For. Ecol. Manag.* 195, 69–83. <https://doi.org/10.1016/j.foreco.2004.02.054>.
- Gerwing, J.J., Farias, D.L., 2000. Integrating liana abundance and forest stature into an estimate of total aboveground biomass for an eastern Amazonian forest. *J. Trop. Ecol.* 16, 327–335. <https://doi.org/10.1017/s0266467400001437>.
- Gerwing, J.J., Schnitzer, S.A., Burnham, R.J., Bongers, F., Chave, J., DeWalt, S.J., et al., 2006. A standard protocol for liana censuses. *Biotropica* 38, 256–261. <https://doi.org/10.1111/j.1744-7429.2006.00134.x>.
- Hothorn, T., Bretz, F., Westfall, P., 2008. simultaneous inference in general parametric models. *Biom. J.* 50, 346–363. <https://doi.org/10.1002/bimj.200810425>.
- Hozumi, K., Yoda, K., Kokawa, S., Kira, T., 1969. Production ecology of tropical rain forests in southwestern Cambodia: I. Plant biomass. *Nat. life Southeast Asia* 6, 1–51.
- Krishna Moorthy, S.M., Raunonen, P., Van den Bulcke, J., Calders, K., Verbeeck, H., 2020. Terrestrial laser scanning for non-destructive estimates of liana stem biomass. *For. Ecol. Manag.* 456, 117751. <https://doi.org/10.1016/j.foreco.2019.117751>.
- Ledo, A., Schnitzer, S.A., 2014. Disturbance and clonal reproduction determine liana distribution and maintain liana diversity in a tropical forest. *Ecology* 95, 2169–2178. <https://doi.org/10.1890/13-1775.1>.
- Lenth, R., (2023). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.8.6..
- Lin, L.I., 1989. A concordance correlation coefficient to evaluate reproducibility. *Biometrics* 45, 255. <https://doi.org/10.2307/2532051>.
- Lü, X.T., Tang, J.W., Feng, Z.L., Li, M.H., 2009. Diversity and aboveground biomass of lianas in the tropical seasonal rain forests of Xishuangbanna, SW China. *Rev. Biol. Trop.* 57, 211–222. <https://doi.org/10.15517/rbt.v57i1-2.11316>.
- Marshall, A.R. (2008). Ecological Report on Magombera Forest. WWF–Tanzania Programme Office. 65p.
- Marshall, A.R., Coates, M.A., Archer, J., Kivambe, E., Mnendo, H., Mtoka, S., et al., 2017. Liana cutting for restoring tropical forests: a rare palaeotropical trial. *Afr. J. Ecol.* 55, 282–297. <https://doi.org/10.1111/aje.12349>.
- Marshall, A.R., Platts, P.J., Chazdon, R.L., Seki, H., Campbell, M.J., Phillips, O.L., et al., 2020. Conceptualising the global forest response to liana proliferation. *Front. For. Glob. Change* 3. <https://doi.org/10.3389/ffgc.2020.00035>.
- Marshall, A.R., Waite, C.E., Pfeifer, M., Banin, L.F., Rakotonarivo, S., Chomba, S., et al., 2023. Fifteen essential science advances needed for effective restoration of the world's forest landscapes. *Philos. Trans. R. Soc. B Biol. Sci.* 378. <https://doi.org/10.1098/rstb.2021.0065>.
- Marshall, A.R., Willcock, S., Platts, P.J., Lovett, J.C., Balmford, A., Burgess, N.D., et al., 2012. Measuring and modelling above-ground carbon and tree allometry along a tropical elevation gradient. *Biol. Conserv.* 154, 20–33. <https://doi.org/10.1016/j.biocon.2012.03.017>.
- Miao, Z., Koerner, S.E., Medjibe, V.P., Poulsen, J.R., 2016. Wanted: new allometric equations for large lianas and African lianas. *Biotropica* 48, 561–564. <https://doi.org/10.1111/btp.12353>.
- Ngute, A.S.K., Schoeman, D.S., Pfeifer, M., van der Heijden, G.M.F., Phillips, O.L., van Breugel, M., et al., 2024. Global dominance of lianas over trees is driven by forest disturbance, climate and topography. *Glob. Change Biol.* 30, e17140. <https://doi.org/10.1111/gcb.17140>.
- Parresol, B.R., 1999. Assessing tree and stand biomass: a review with examples and critical comparisons. *For. Sci.* 45, 573–593.
- Phillips, O.L., Vásquez Martínez, R., Arroyo, L., Baker, T.R., Killeen, T., Lewis, S.L., et al., 2002. Increasing dominance of large lianas in Amazonian forests. *Nature* 418, 770–774. <https://doi.org/10.1038/nature00926>.
- Putz, F.E., 1983. Liana biomass and leaf area of a “Tierra Firme” forest in the Rio Negro Basin, Venezuela. *Biotropica* 15, 185. <https://doi.org/10.2307/2387827>.
- R Core Team, 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rowe, N., 2018. Lianas. *Curr. Biol.* 28, R249–R252. <https://doi.org/10.1016/j.cub.2018.01.028>.
- Schnitzer, S.A., Bongers, F., 2011. Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. *Ecol. Lett.* 14, 397–406. <https://doi.org/10.1111/j.1461-0248.2011.01590.x>.
- Schnitzer, S.A., Carson, W.P., 2010. Lianas suppress tree regeneration and diversity in treefall gaps. *Ecol. Lett.* 13, 849–857. <https://doi.org/10.1111/j.1461-0248.2010.01480.x>.
- Schnitzer, S.A., 2005. A mechanistic explanation for global patterns of liana abundance and distribution. *Am. Nat.* 166, 262–276. <https://doi.org/10.1086/431250>.
- Schnitzer, S.A., 2018. Testing ecological theory with lianas. *New Phytol.* 220, 366–380. <https://doi.org/10.1111/nph.15431>.
- Schnitzer, S.A., DeWalt, S.J., Chave, J., 2006. Censusing and measuring lianas: a quantitative comparison of the common methods. *Biotropica* 38, 581–591. <https://doi.org/10.1111/j.1744-7429.2006.00187.x>.
- Schnitzer, S.A., Putz, F.E., Bongers, F., Kroening, K., 2015. The past, present, and potential future of liana ecology. *Ecology of Lianas*. John Wiley & Sons, Ltd, Chichester, UK, pp. 1–10. <https://doi.org/10.1002/9781118392409.ch1>.
- Schnitzer, S.A., Rutishauser, S., Aguilar, S., 2008. Supplemental protocol for liana censuses. *For. Ecol. Manag.* 255, 1044–1049. <https://doi.org/10.1016/j.foreco.2007.10.012>.
- Smith-Martin, C.M., Xu, X., Medvigy, D., Schnitzer, S.A., Powers, J.S., 2020. Allometric scaling laws linking biomass and rooting depth vary across ontogeny and functional groups in tropical dry forest lianas and trees. *New Phytol.* 226, 714–726. <https://doi.org/10.1111/nph.16275>.
- van der Heijden, G.M.F., Powers, J.S., Schnitzer, S.A., 2015. Lianas reduce carbon accumulation and storage in tropical forests. *Proc. Natl. Acad. Sci. U. S. A.* 112, 13267–13271. <https://doi.org/10.1073/pnas.1504869112>.
- van der Heijden, G.M.F., Schnitzer, S.A., Meunier, F., 2023. Editorial: Lianas, ecosystems, and global change. *Front. For. Glob. Change* 6, 1079620. <https://doi.org/10.3389/ffgc.2023.1079620>.
- Verbeeck, H., Kearsley, E., 2016. The importance of including lianas in global vegetation models. *Proc. Natl. Acad. Sci.* 113. <https://doi.org/10.1073/pnas.1521343113>.
- Wellek, S., 2021. Testing for goodness rather than lack of fit of continuous probability distributions. *PLoS One* 16, e0256499. <https://doi.org/10.1371/journal.pone.0256499>.