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ORIGINAL ARTICLE

Variation and Determinants of the Shape of Trees With Irregular Trunks in Central Africa

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ABSTRACT

Trees developing irregularities on their trunks have an influence on the estimation of above-ground biomass and carbon stocks in the tropics. This study aims to examine the variation and determinants of the shape of trees with irregular trunks in Central Africa. The study used close-range photogrammetric data and conventional data to analyze 275 trees belonging to 11 species. For each tree, the isoperimetric quotient (Q) at 1.30 m has been estimated from a cross-sectional disc. Between sites, we observed a significant variation in Q between two forest types, with trees tending to have lower Q values in the semi-deciduous forest (Semi-F) than in the evergreen forest (Ever-F), indicating trees in Semi-F had more irregular trunk shapes. Similar trends were reported for the three species shared by both forest types, suggesting an environmental control of the shape of trees with irregular trunks. Within sites, the lowest Q value was observed for *Triplochiton scleroxylon* in Semi-F and for *Pterocarpus soyauxii* in Ever-F, suggesting that these species had more irregular trunks than other species. The determinants of variations in Q were related to tree characteristics and species traits. At the tree level, Q was positively correlated with wood density and negatively correlated with crown volume, suggesting that trees with larger crowns and lower wood density are more likely to develop irregular trunks. At the species level, wind-dispersed species and deciduous species tended to have more irregular trunks. These results provide insight into the life cycle strategies of tropical tree species.

RÉSUMÉ

Les arbres présentant des irrégularités au niveau du tronc influencent l'estimation de la biomasse aérienne et des stocks de carbone dans les régions tropicales. Cette étude vise à analyser la variation et les déterminants de la forme des arbres à troncs irréguliers en Afrique centrale. Elle s'appuie sur des données issues de la photogrammétrie à courte portée ainsi que sur des mesures conventionnelles, portant sur 275 arbres appartenant à 11 espèces. Pour chaque arbre, le quotient isopérimétrique (Q) à 1,30 m de hauteur a été estimé à partir d'une section transversale du tronc. Entre les sites, une variation significative de Q a été observée entre deux types de forêts: les arbres présentaient des valeurs de Q plus faibles dans la forêt semi-décidue (Semi-F) que dans la forêt sempervirente (Ever-F), indiquant des formes de tronc plus irrégulières en Semi-F. Des tendances similaires ont été observées pour les trois espèces communes aux deux types de forêts, suggérant un effet du contrôle environnemental sur la forme des troncs. Au sein des sites, les valeurs les plus faibles de Q ont été enregistrées chez *Triplochiton scleroxylon* en Semi-F et *Pterocarpus soyauxii* en Ever-F, indiquant que ces espèces présentent des troncs plus irréguliers que les autres. Les déterminants des variations de Q sont liés à la fois aux caractéristiques individuelles des arbres et aux traits des espèces. À l'échelle individuelle, Q est. positivement corrélé à la densité du bois et négativement corrélé au volume de la couronne, suggérant que les arbres à couronnes plus volumineuses et à bois moins dense sont plus susceptibles de développer des troncs irréguliers. À l'échelle spécifique, les espèces à dispersion anémochore et à feuilles décidues présentent une tendance accrue à développer des troncs irréguliers. Ces résultats apportent un éclairage nouveau sur les stratégies de vie des espèces d'arbres tropicaux et contribuent à améliorer la précision des estimations de biomasse et de carbone.

1 | Introduction

Trees developing irregularities on the trunk have an influence on the estimation of above-ground biomass and carbon stocks in the tropics (Cushman et al. 2014, Cushman et al. 2021; Nölke et al. 2015; Bauwens et al. 2017, 2021). Recent studies have highlighted the role of trees with irregular trunks in nutrient uptake even at the adult stage, underlining their importance for tree physiology and the overall functioning of tropical ecosystems (Pandey et al. 2011; Tang et al. 2011). Understanding the determinants of the shape of trees with irregular trunks is therefore essential for refining our knowledge of tropical forest dynamics and improving the accuracy of biomass models.

The development of irregularities in tropical trees can be estimated using shape indices, estimated from cross-sections (Pulkkinen 2012; Ngomanda et al. 2012; Nölke et al. 2015; Bauwens et al. 2017; Cushman et al. 2021). These shape indices measure the deviation from an ideal circular shape, providing valuable information on trunk compactness and structural anomalies (Russ 1991). They have been widely applied in temperate forests, particularly in Europe, where these shape indices have been used to assess the effects of silvicultural practices and growing conditions on trunk morphology (Williamson 1975; Makinen 1998).

Studies on the shape of trees with irregular trunks remain limited in tropical forests. Two previous studies have shown significant variation in the shape of trees with irregular trunks within and between species in tropical forests, specifically in Central Africa (Ngomanda et al. 2012; Bauwens et al. 2017), in South America, and in Southeast Asia (Cushman et al. 2021). For example, 12%–51% of tree species develop irregularities at the base of the trunk in tropical Africa and South America (Chapman et al. 1998; Zhiyuan et al. 2013). Variation in the shape of trees with irregular trunks is determined by tree characteristics and abiotic factors. In particular, trees with larger diameters and greater heights tend to develop more pronounced trunk irregularities in tropical African forests (Chapman et al. 1998; Newbery et al. 2009; Bauwens et al. 2017), South America (Young and Perkocha 1994; Alencar et al. 2023), and South-East Asia (Mehedi et al. 2012; Zhiyuan et al. 2013). Likewise, it has also been positively associated with crown asymmetry (Young and Perkocha 1994; Chapman et al. 1998; Mehedi et al. 2012). Secondly, abiotic factors including soil properties, slope, and altitude have been found to explain the variation of the shape of trees with irregular trunks. For instance, trees with irregular trunks tended to be frequently observed on shallow and waterlogged soils (Navez 1930; Richards 1952). Similarly, they tended to occur at higher frequencies in areas of medium altitude and steep slopes compared with lower or flatter terrain (Alencar et al. 2023).

To our knowledge, few studies have examined how these determinants interact to influence variation of the shape of trees with irregular trunks (Alencar et al. 2023). Consequently, our understanding of the multiple interacting factors that together control the shape of trees with irregular trunks remains limited, particularly in Central Africa, a region that remains relatively understudied. Thus, the aim of this study was to examine the variation and determinants of the shape of trees with irregular trunks in Central Africa. We addressed two research questions: (i) does the shape of trees with irregular trunks vary among species and forest sites? and (ii) what are the determinants of the shape of trees with irregular trunks?

2 | Materials and Methods

2.1 | Study Sites and Sampling

The study was conducted at two forest sites characteristic of two major forest types of the Congo Basin as described by Réjou-Méchain et al. (2021): semi-deciduous forests (Semi-F) and evergreen forests (Ever-F) in northern Republic of Congo (Figure 1). The Loundoungou site, located at 17°31′–17°34″ E, 02°18′–02°22″ N, belongs to Semi-F and is dominated by deciduous, light-demanding canopy tree species, notably from the *Celtis* genus (Fayolle et al. 2014). In contrast, the Ngombé site (15°20′–16°38′ E, 0°27′–1°48′N, Ever-F) is characterized by evergreen species, particularly from the Meliaceae and Fabaceae families (Lanfranchi and Schwartz 1990), typical of more humid and closed-canopy forests. Although both sites share similar climatic and topographic conditions—clay soils (Lanfranchi and Schwartz 1990; Fayolle et al. 2012), a humid tropical climate with mean annual rainfall between 1700 and 1900 mm, and elevations from 400 to 460 m (Freycon 2014; Verhegghen et al. 2016) —they differ in forest structure and species composition, reflecting a gradient from semi-deciduous to evergreen forest types.

In each forest site, the fieldwork was carried out within an 800-ha experimental set-up (DynAfFor project, www.dynaffor.org) which has been described by Forni et al. (2019). Using forest inventories from DynAfFor, we targeted 11 irregular trunk tree species ($n = 9$ species for Semi-F and $n = 5$ species for Ever-F, with three species shared among the two sites) belonging to 11 genera and 8 families (Table 1). These are mainly species with buttresses and flutes on both study sites. For each species, we sampled 20 individuals (range: 5–47 trees) on average, representing 307 trees in total (i.e., 181 trees in Semi-F and 126 trees in Ever-F).

2.2 | Photogrammetric Measurements and Processing

The image acquisition procedure consisted of removing all small plants and lianas around each tree within a radius of 3 m, prior to image acquisition. Four photogrammetric targets were placed at the four cardinal points around each tree at a distance of less than 1 m. The reference target was placed to the south to avoid backlighting. The targets were used to improve the alignment of the images and the scaling of the point cloud. The diameter at

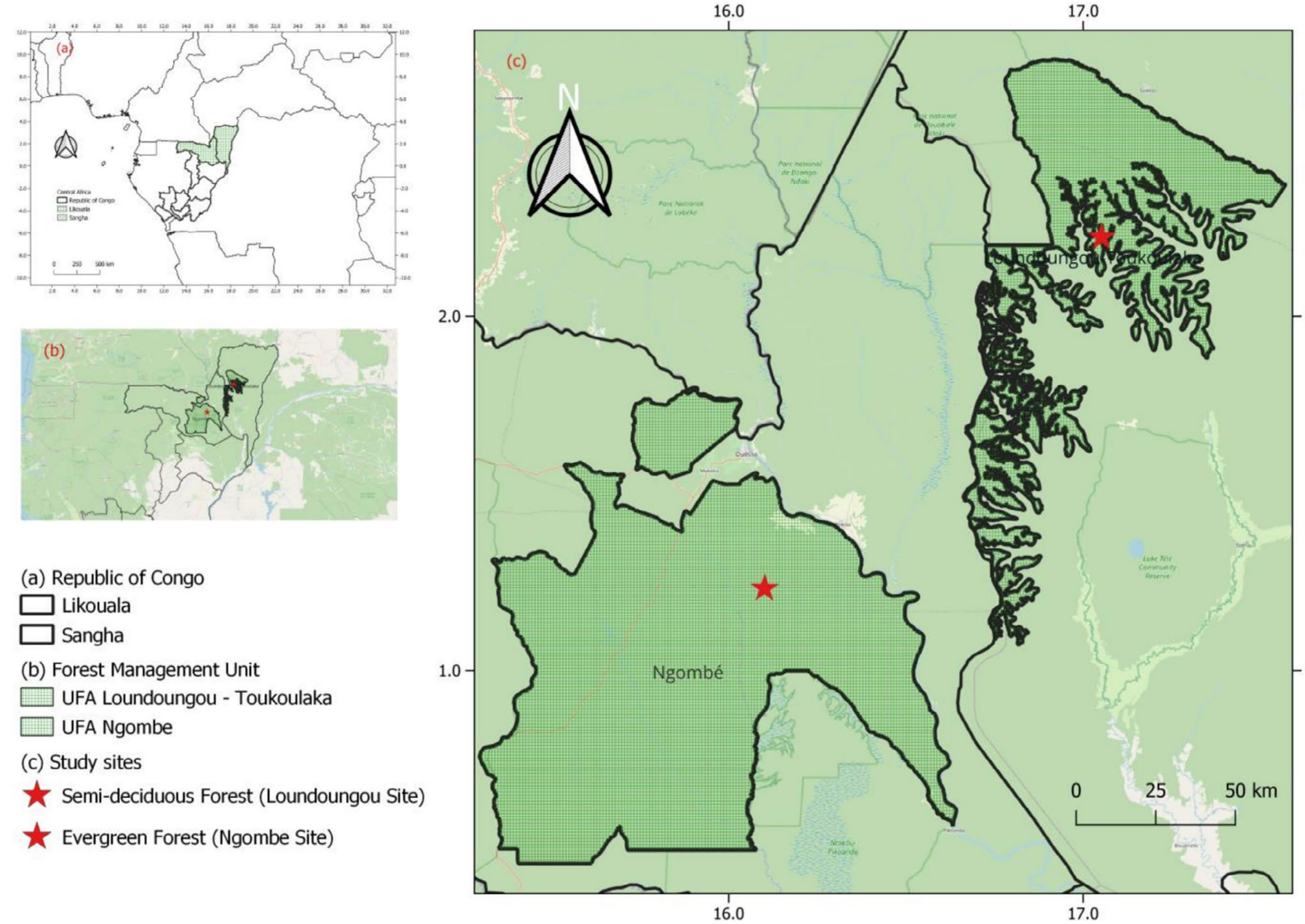

FIGURE 1 | Location of semi-deciduous forests (Loundoungou site) and evergreen forests (Ngombe site) in the north of the Republic of Congo.

TABLE 1 | Characteristics of the study species including scientific names, family, and sampling effort (*n*, number of trees sampled, and diameter range).

		***n* [diameter range in cm]**	
Scientific name	**Family**	**Semi-F**	**Ever-F**
Antiaris toxicaria Lesch	Moraceae	5 [93.5–162]	—
Triplochiton scleroxylon K. Schum.	Malvaceae	8 [108–226]	—
Alstonia boonei De Wild.	Apocynaceae	9 [33.4–116]	—
Piptadeniastrum africanum (Hook. f.) Brenan	Fabaceae	38 [31.3–266]	—
Chrysophyllum lacourtianum De Wild.	Sapotaceae	—	5 [19–94]
Staudtia kamerunensis Warb.	Myristicaceae	—	47 [10.9–85.4]
Celtis mildbraedii Engl.	Cannabaceae	19 [41–153]	—
Manilkara mabokeensis Aubrev.	Sapotaceae	28 [42.6–113]	—
Pterocarpus soyauxii Taub.	Fabaceae	27 [24.2–158]	15 [27–139]
Entandrophragma cylindricum (Sprague) Sprague	Meliaceae	29 [58.5–215]	42 [10.5–174]
Erythrophleum suaveolens Brenan	Fabaceae	18 [54.4–142]	17 [22.4–109]

breast height (DBH) was marked with blue paint. For image acquisition, the Nikon D5600 digital SLR camera was used with a fixed zoom lens with a focal length of 16 mm. The camera (focus, ISO and shutter speed) was set to automatic mode. All the trees were photographed with these settings. A series of photographs was taken all around each tree following an image acquisition method similar to the "one panorama at each step" approach (Wenzel et al. 2013; Bauwens et al. 2017). At each step around the tree (1 m), photographs were taken with a high overlap (vertical panorama) and convergent images. The lateral shooting distance around the tree was 2–3 m.

We used Agisoft Metashape Professional software (Agisoft LCC, St Petersburg, Russia) to process the images. Each set of tree photos was loaded into the software without any additional information. The photogrammetric workflow of this software consists of six phases, namely, (1) target detection, (2) image alignment and sparse cloud generation, (3) scaling of the constructed 3D point clouds, (4) optimization of the sparse point clouds, (5) point cloud densification, and (6) mesh construction.

The photogrammetric workflow can be summarized as follows: after target detection (phase 1), the Metashape software automatically calculates the lens calibration parameters based on the SfM algorithm. The end product of phase 2 is a scattered point cloud of the tree trunk with the camera locations. In the third phase (3), the point cloud is scaled using the coded targets that are automatically detected on the photogrammetric test patterns detected in phase 1. The resulting 3D point cloud after scaling was optimized to adjust the camera's intrinsic and extrinsic parameters in the fourth phase (4). Phase 4 brings the scattered point cloud back along the trunk. Before the point clouds were densified to create the mesh, the poorly adjusted point clouds along the trunk were removed to reduce processing time. Then, thanks to the knowledge of the geometry of the image network, it was possible to produce the dense point cloud, which included the calculation of a corresponding 3D point for almost every pixel in the image using the Multi-View Stereo (MVS) algorithm (phase 5). Finally, the mesh (phase 6) was generated, saved and exported in the form of a "mesh" file containing the XYZ coordinates to obtain the cross-sections using Rstudio software.

The method used was carried out on a computer equipped with an AMD Ryzen 95,900X processor (12 cores—3.7/4.8 GHz—70 MB cache) with an Asus Prime X570-Pro—AMD X570 chipset and 64 GB DDR4 memory. From the 3D mesh, cross sections along the trunk were generated following the workflow detailed in (Bauwens et al. 2017) using the R packages "sp" (Pebesma et al. 2012), 'Raster' (Hijmans et al. 2013), "lidR" (Roussel et al. 2020). The workflow outputs 2-cm-thick cross-sections every 20 cm along the trunk Z-axis. Reconstruction for a given tree was considered failed and discarded from further analysis when one or more of the following automated quality criteria were met: (1) more than 20% of all extracted cross-sections returned missing or non-finite values for area or perimeter; (2) more than 10% of cross-sections had area = 0 or perim = 0; (3) the mesh contained large topological holes or multiple disconnected components resulting in non-contiguous trunk geometry; or (4) the extracted cross-section centroids exhibited non-monotonic vertical progression (indicative of segmentation errors or inverted geometry). These checks were implemented automatically and followed by a visual inspection for borderline cases. Based on inspection of failed cases, the most common causes were (i) incomplete or low-density meshes caused by insufficient image overlap or poor image focus during acquisition, and (ii) large occlusions from lianas or heavy understorey vegetation that produced non-manifold geometry. Using these criteria the workflow was successfully implemented on 88% ($n = 160$) of the 181 trees in Semi-F and 91% ($n = 115$) of the 126 trees in Ever-F; trees failing the quality control were excluded from analyses. For each cross-section, we calculated the area of the disc (area) and the perimeter of the disc (perim). A flow chart detailing the methods in this study is shown in Figure 2.

2.3 | Shape of Trees With Irregular Trunks

To describe the shape of tree species with irregular trunks, we first analyzed the distribution of trees according to trunk height classes (Figure 3). Trunk height was defined as the vertical distance from the base of the tree to the upper limit of the reconstructed 3D trunk model. This height did not necessarily reach the first large branch, but corresponded to the maximum height of the trunk section that could be accurately reconstructed from the 3D model. All trees exhibited an irregular structure with a bell-shaped profile. Trunk heights ranged from 1.9 to 16.3 m in the Semi-F and from 1.7 to 10.9 m in the Ever-F. Height class II [3–4.9 m] was the most represented, with 72 and 51 trees in the Semi-F and Ever-F respectively, followed by Height class IV [7–8.9 m] with 34 and 21 trees. Overall, height classes were more evenly represented in Semi-F than in Ever-F.

The irregular structure in the height classes is mainly due to branch and liana occlusions, as well as backlighting and image blur during image acquisition in the field. Forsman et al. (2016) indicates that capturing images in natural forests is much more difficult due to lighting conditions, tree density and occlusions by branches, shrubs, etc. The imbalance in trunk height meant that the shape of trees with irregular trunks along the trunk could not be adequately assessed. Moreover, it has already been shown that the shape of trees with irregular trunks varied within and among tree species (Bauwens et al. 2017). We therefore considered cross-sections at 1.30 m from the ground to describe the shape of trees with irregular trunks.

To describe the shape of trees with irregular trunks, the isoperimetric quotient (Q) was estimated from cross-sectional data obtained at 1.30 m from the ground at the Semi-F and Ever-F. The isoperimetric quotient characterizes the shape of the cross-section. The isoperimetric quotient (Q) is one of the most widely used of the large number of indices available to describe the shape of trees with irregular trunks (Pulkkinen 2012; Nölke et al. 2015; Cushman et al. 2021). The isoperimetric quotient (Q) is defined as a measure of compactness and describes the ratio between the area of the disc and the perimeter of each cross-section (Equation 1) (Pulkkinen 2012; Nölke et al. 2015; Cushman et al. 2021). The isoperimetric quotient (Q) ranges from 0 to 1, where a value of 1 corresponds to a perfect circular cross-section, and lower values indicate increasing deviation from circularity and thus greater trunk irregularity.

$$Q = \frac{4\pi \text{area}}{\text{perim}^2} \tag{1}$$

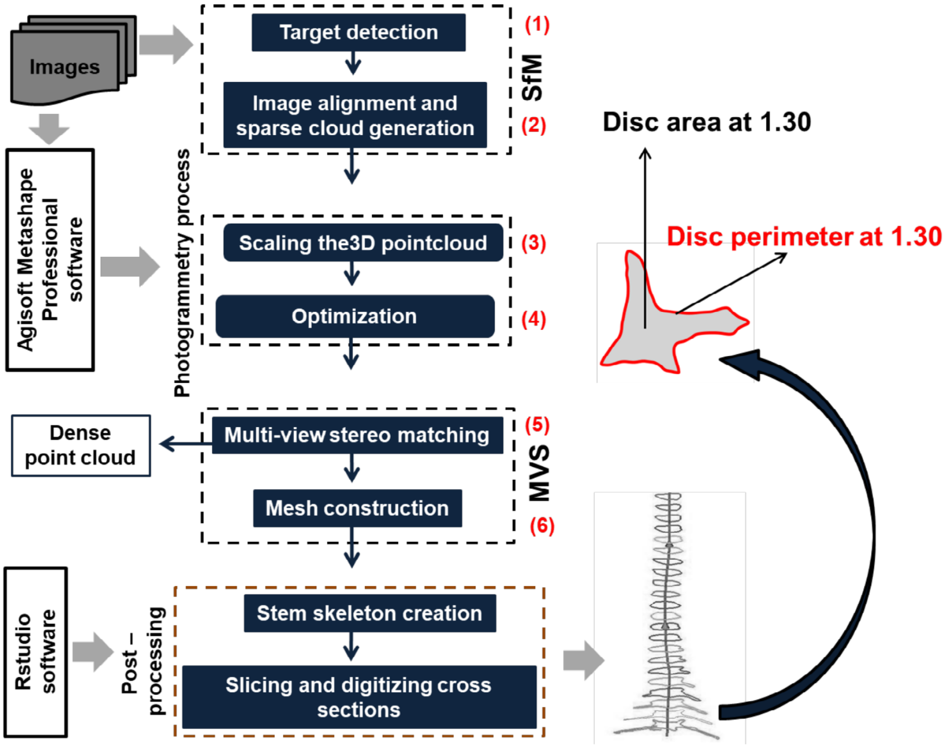

FIGURE 2 | Flowchart detailing the methods in this study.

where *Q*, the isoperimetric quotient; *area*: the area of the disc (in cm^2); perim, the perimeter of the disc (in cm^2).

2.4 | Tree Measurements and Species Traits

In addition to photogrammetric measurement, non-destructive quantitative measurements and species traits have been obtained at tree and species levels, respectively. At the tree level, we measured tree diameter, total height, first branch height, horizontal projection of four crown rays and a qualitative measure (crown exposure index described below). Tree diameter (D; in cm) was measured with a tape at breast height for less irregular trunks or 30 cm above any deformation. Total tree height (H, in metres) and first branch height (H_{fb}, in metres) were measured using a laser rangefinder device (VERTEX IV dendrometer). For crown measurements, we used the crown measurement protocol described in (Loubota Panzou and Feldpausch 2020). The crown depth (Cd, in m) was defined as the difference between H and H_{fb}. The crown radius (Cr, in m) was defined as the average of the four projected perpendicular crown radii, measured along 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), namely, (1) for lower canopy trees that are fully shaded vertically and laterally by other crowns; (2) for upper canopy trees that are fully shaded vertically but with some direct lateral light; (3) for lower canopy trees that are partially exposed and shaded vertically by other crowns; (4) for upper canopy trees that are fully exposed from above but complemented laterally by other crowns; and (5) for emergent trees that are free of competition for light, at least in the 90° inverted cone in which their crown is located.

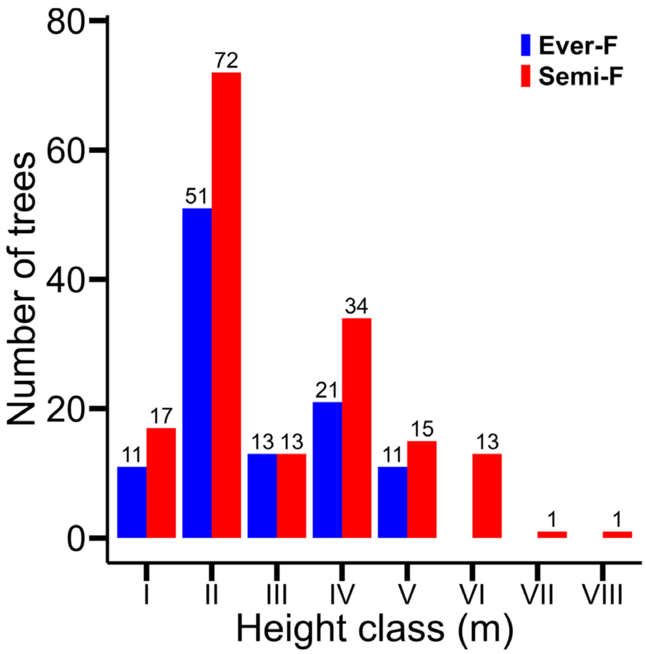

FIGURE 3 | Distribution of trees according to height classes in m at the Semi-F and Ever-F sites. With Class I: [1–2.9]; Class II: [3–4.9]; Class III: [5–6.9]; Class IV: [7–8.9]; Class V: [9–10.9]; Class VI: [11–12.9]; Class VII: [13–14.9]; Class VIII: [15–16.9].

Species traits were maximum diameter (Dmax), maximum height (Hmax), and maximum crown volume (Cvolmax) calculated as the 98th percentile of tree diameter, total tree height, and tree crown volume for each species. Species average wood density (WD, in $g.cm^{-3}$) which ranged from 0.32 to 0.88 $g.cm^{-3}$—were retrieved from the global wood density database (Chave et al. 2009; Zanne et al. 2009) and applied to each individual tree. These species-level mean values were assigned to individual trees and used in the analyses of trunk shape variation. We extracted light requirements using CEI for juvenile plants ($\mathrm{CEI}_{\mathrm{juv}}$) in Loubota Panzou et al. (2022). Leaf habit, dispersal mode, and regeneration guild were also extracted from the literature. Among the 11 species of trees with irregular trunks, three species were considered evergreen, and eight species were considered deciduous for leaf habit; two were animal-dispersed species, seven were wind-dispersed species, and 2 had unassisted dispersal modes (Beina 2011; Gillet 2013; Meunier et al. 2015; Lisingo 2016). Following (Hawthorne 1995) definitions in Ghana, the regeneration guild was assigned to each species according to existing literature (Meunier et al. 2015; Loubota Panzou et al. 2018). Of the 11 irregular trunk tree species, two were classified as shade-bearing (SB), five as non-pioneer light demanding (NPLD), and four as pioneer (P).

2.5 | Data Analysis

To detect differences in the shape of trees with irregular trunks between two forest sites, we performed an analysis of variance with one random factor (forest site) and the isoperimetric quotient as a fixed factor for all species and for shared species. Within each forest site, we used the one-sample Student's *t*-test to test for differences in the trunk shape of trees with irregular trunks among coexisting tree species.

To identify the most important factors in determining the shape of trees with irregular trunks, general linear mixed-effects models were fitted at tree and species level. At tree level, we used individual tree measurements (tree diameter, tree height, crown depth, crown radius, and crown exposure index), and species-level wood density values assigned to each tree as potential determinants of the shape of trees with irregular trunks, while species traits were used in the species-level model. Before fitting the models, we assessed multicollinearity among predictors using the variance inflation factor (VIF), applying a conservative threshold of $\mathrm{VIF} \geq 5$. Variables exhibiting strong collinearity were excluded to ensure the stability of parameter estimates and the independence of fixed effects. Consequently, tree diameter was removed from the tree-level model, while maximum diameter (Dmax) and regeneration guild (GR) were excluded from the species-level model due to their strong correlation with other traits, particularly maximum height (Hmax) and juvenile crown exposure index (CEIjuv). To further assess potential collinearity, we computed the full correlation matrix and VIF values for all predictors (Tables S1 and S2). Low to moderate correlations were observed among variables at the tree level, with the strongest being between diameter and height ($r = 0.60$), while height and crown volume were only weakly correlated ($r = 0.26$). All retained predictors exhibited acceptable collinearity ($\mathrm{GVIF}^{\wedge}(1/2\mathrm{Df}) < 5$), confirming the robustness and stability of the final models. Therefore, all selected variables were retained to preserve both statistical reliability and ecological interpretability. Hence, for a tree i belonging to a species j occurring at site s, the tree-level mixed-effect model accounted for tree height (H), crown volume (Cvol), crown exposure index (CEI), and wood density (WD) 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 2), while the species-level model accounted for including maximum height (Hmax), maximum crown volume (Cvolmax), light requirement (CEIjuv), wood density (WD), leaf habit (LH), and dispersal mode (DM) as fixed effects and site as random effect (Equation 3).

$$Q_i = \beta + \alpha_1 H_i + \alpha_2 C\mathrm{vol}_i + \alpha_3 \mathrm{CEI}_i + \alpha_4 \mathrm{WD}_i + \beta_{\mathrm{family}}[i] + \beta_{\mathrm{Genera-family}}[i] + \beta_{\mathrm{species-Genera-family}}[i] + \beta_{\mathrm{Site}}[i] \quad (2)$$

$$Q_{ij} = \beta + \alpha_1 H_{\mathrm{max}ij} + \alpha_2 \mathrm{Cvol}_{\mathrm{max}ij} + \alpha_3 \mathrm{CEI}_{\mathrm{juv}_{ij}} + \alpha_4 \mathrm{WD}_{ij} + \alpha_5 \mathrm{LH}_{ij} + \alpha_6 \mathrm{MD}_{ij} + \ \beta_{\mathrm{Site}}[ij] \quad (3)$$

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

Although the individual-level model accounted for species as a random intercept while including some species-level traits (e.g., wood density) as fixed effects, this approach may introduce a partial hierarchical inconsistency. To minimize this risk, we verified that the inclusion of species-level traits did not increase random variance or bias individual-level estimates.

All statistical analyses were performed with the open-source environment R version 4.2.1 (R Core Team 2022) using the packages “lme4” for linear mixed model analysis (Bates et al. 2014) and ‘ggplot2’ for graphical outputs. The conditions of normality and homogeneity of variances were tested using the Shapiro–Wilk and Bartlett tests respectively before proceeding with the analyses.

3 | Results

3.1 | Variation of the Shape of Trees With Irregular Trunks

Between sites, our results showed significant differences ($p < 0.001$) in the isoperimetric quotient (Q) for all species between the two forest sites (Figure 4a). Q (mean ± sd) was higher in Ever-F (0.77 ± 0.28) than in Semi-F (0.55 ± 0.29), suggesting that trees had more irregular trunks in Semi-F than Ever-F. For the three species shared to the two forest types, we identified a significant variation in Q between sites ($p < 0.001$; Figure 4b). This suggests that morphological contrasts among sites were driven by intra-specific variation in response to local environmental conditions such as soil characteristics, rainfall, and temperature.

Within sites, Q varied considerably among tree species in Semi-F ($t = 7.52$, $\mathrm{df} = 8$, $p < 0.001$) and in Ever-F ($t = 8.90$, $\mathrm{df} = 4$, $p < 0.001$). The lowest Q value was observed for *Triplochiton scleroxylon* in Semi-F and for *Pterocarpus soyauxii* in Ever-F, suggesting that these tree species had more irregular trunks than other species within each site (Table 2, Figure S1).

3.2 | Determinants of the Shape of Tree With Irregular Trunks

At tree level, Q was most strongly related to wood density and crown volume (Figure 5a, Table S3). Q was significantly positively correlated with wood density (Figure 5b) and significantly

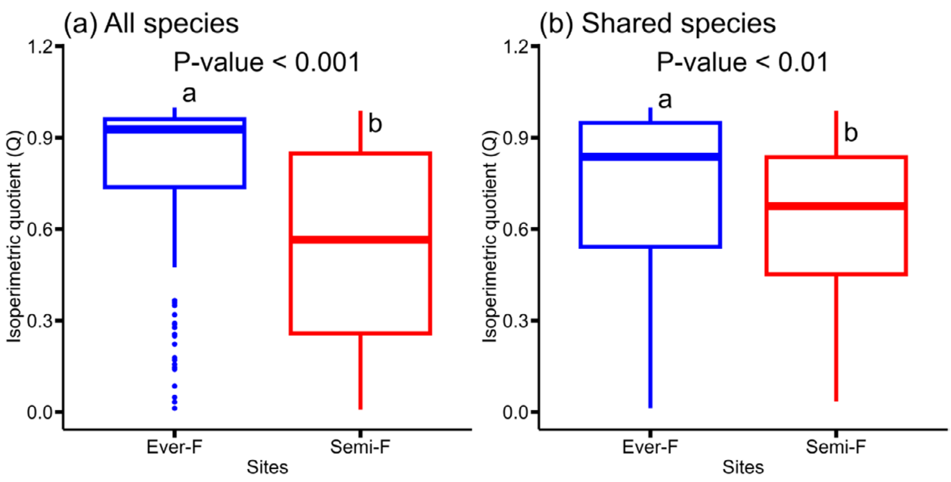

FIGURE 4 | Inter-site variation in the isoperimetric quotient (Q) of tree species with irregular trunks, (a) across all species in the study sites and (b) across shared species in the sites. P-value is given and the individual letters constitute the multiple comparison test.

TABLE 2 | Means and standard deviations of the isoperimetric quotient (Q) at 1.30 m above ground for semi-deciduous forest (Sem-F) and evergreen forest (Ever-F).

Sites	Scientific names	*n*	Mean ± Sd
Semi-F	*Antiaris toxicaria* Lesch	5	0.34 ± 0.15
	Triplochiton scleroxylon K. Schum.	7	0.29 ± 0.14
	Piptadeniastrum africanum (Hook. f.) Brenan	31	0.31 ± 0.25
	Alstonia boonei De Wild.	7	0.37 ± 0.16
	Celtis mildbraedii Engl.	19	0.47 ± 0.09
	Manilkara mabokeensis Aubrev.	24	0.88 ± 0.08
	Pterocarpus soyauxii Taub.	26	0.56 ± 0.30
	Entandrophragma cylindricum (Sprague) Sprague	27	0.62 ± 0.24
	Erythrophleum suaveolens Brenan	14	0.69 ± 0.17
Ever-F	*Chrysophyllum lacourtianum* De Wild.	4	0.66 ± 0.41
	Staudtia kamerunensis Warb.	42	0.89 ± 0.18
	Pterocarpus soyauxii Taub.	12	0.43 ± 0.29
	Entandrophragma cylindricum (Sprague) Sprague	39	0.75 ± 0.27
	Erythrophleum suaveolens Brenan	18	0.82 ± 0.23

negatively correlated with crown volume (Figure 5c). Trees with irregular trunks tended to have high crown volume and low wood density.

At the species level, Q was strongly related to leaf habit and dispersal mode (Figure 6a, Table S3). A significant variation was detected in the shape of tree species with irregular trunks among leaf habit and dispersal modes (Figure 6b,c), showing that tree species with irregular trunks tended to be deciduous and wind dispersed.

4 | Discussion

4.1 | A Site-Level Effect on the Shape of Trees With Irregular Trunks

Overall, trees in two study sites exhibited relatively low mean values of Q, indicating that the irregular trunks were particularly common in Central African forests. This study showed that the average shape of trees with irregular trunks was higher in Central Africa (two study sites) than in South America and Southeast Asia. This could be explained by the methodological difference observed in Cushman et al. (2021) that studied the shape of trees with irregular trunks in South America and Southeast Asia. However, our results are not directly comparable with those from Central Africa (Ngomanda et al. 2012; Bauwens et al. 2017), South America (Alencar et al. 2023), and Central America (Walsh and Dawson 2014), where the variation in the shape of trees with irregular trunks was explained using other shape indices.

The shape of trees with irregular trunks showed significant differences between two study sites, with higher levels of trunk irregularities (i.e., lower Q) found in Loundoungou (Semi-F) than in Ngombé (Ever-F). This result is consistent with the findings of Cushman et al. (2021), whom also found inter-site differences in the shape of trees with irregular trunks in South America and Southeast Asia. Similarly, significant differences between two forest sites in the shape of trees with irregular trunks were also observed for shared species. This suggests the environmental control through site-related environmental conditions rather than species turnover, in accordance with the results on the variation of the buttress formation in African tropical forests (Chapman et al. 1998). Although the two study sites are on clay soils and share a

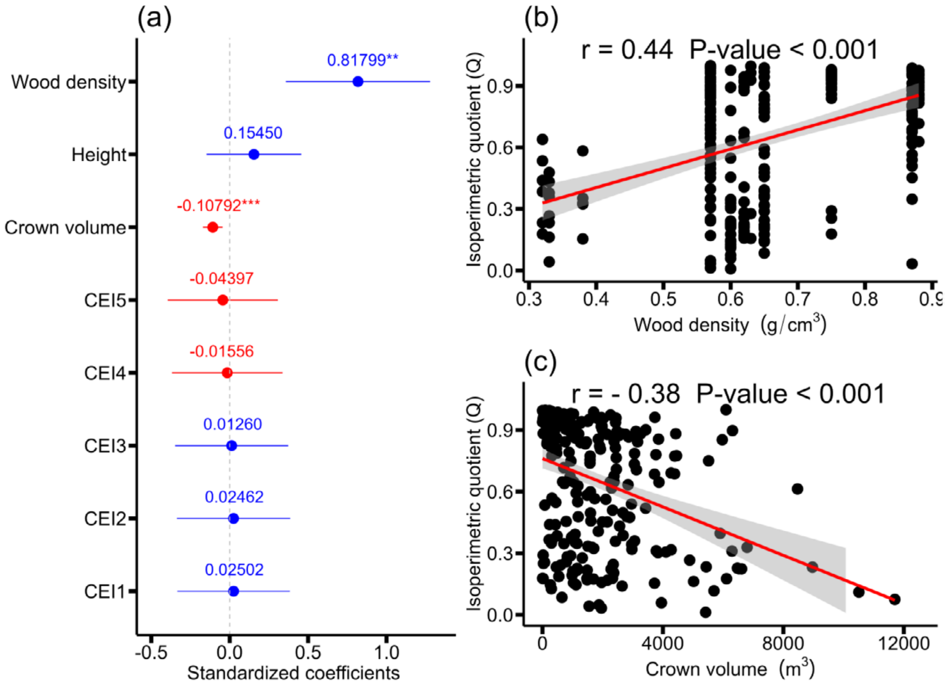

FIGURE 5 | Determinants of the isoperimetric quotient (Q) at tree level: (a) standardized coefficients of the isoperimetric quotient (Q) with error bars indicating confidence intervals (*$p < 0.05$) and all coefficients of fixed and random effects are presented in Table S3 (red indicates negative coefficient and blue indicates positive coefficient); (b, c) bivariate relationships between isoperimetric quotients (Q) and significant variables with Pearson correlation coefficients (r). With CEI: Crown exposure index.

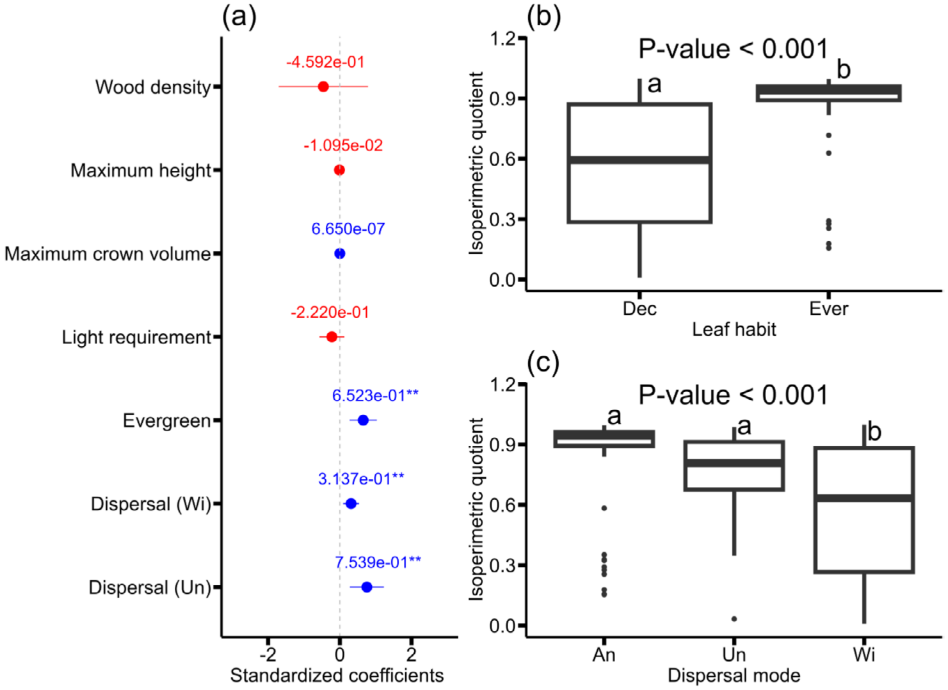

FIGURE 6 | Site-level determinants of isoperimetric quotient (Q): (a) standardized coefficients of isoperimetric quotient (Q) with error bars indicating confidence intervals (***$p < 0.001$) and all coefficients for fixed and random effects are presented in Table S3 (red indicates negative coefficient and blue indicates positive coefficient); (b, c) variations in leaf area and dispersal pattern for which significant differences were found using the non-parametric Wilconox and Kruskal–Wallis tests, respectively. Differences are indicated by different letters (Kruskal–Wallis post hoc multiple comparisons between medians). Leaf habit (evergreen or deciduous), dispersal mode (Un, unassisted; An, animal dispersal; and Wi, wind).

fairly similar climate, we cannot exclude an impact of environmental conditions on Q when considering larger environmental gradients nor any structural difference between forest types (Fayolle et al. 2016), but results from compositional differences. *Triplochiton scleroxylon* and *Piptadeniastrum africanum* species for instance, two tall canopy trees species with deciduous leaf habits, displayed the most irregular trunk shapes and were only present in the deciduous forest site.

The diameter of trees with irregular trunks cannot be measured at the standard measurement height during forest inventories, which leads to systematic errors on trees and stands carbon stocks when a general biomass allometry model is used (Bauwens et al. 2021). The presence of a spatial structure in average shape of trees with irregular trunks (i.e., inter-site effect) could thus propagate systematic errors latter on the forest carbon modeling chain, for instance when extrapolating field-derived carbon estimates using remote-sensing data or when assessing average carbon stock per forest stratum (e.g., evergreen vs. deciduous forests) in the frame of national carbon accounting schemes (e.g., REDD+). We thus argue that the impact of irregular trunks on tree and stand carbon stock estimates should be more thoroughly studied and accounted for when developing biomass allometry equations.

4.2 | Tree Characteristics and Species Traits Determine the Shape of Trees With Irregular Trunks

At tree level, the determinants of the shape of trees with irregular trunks were crown volume and wood density. Trees with irregular trunks had large crown volumes and low wood density. Canopy trees developing large crown volumes have been observed in Central Africa, South America (Loubota Panzou et al. 2021), and Southeast Asia (Antin et al. 2013). Large canopy trees have the advantage of increasing carbon uptake, intercepting light, and eliminating competition with neighboring canopies (Shenkin et al. 2020). Most of these canopy trees have low wood density values in tropics (Poorter et al. 2006). These low wood density values indicate the heliophilic nature of the wood in these trees (Morel et al. 2018).

The shape of trees with irregular trunks of coexisting species varied in each forest site, in agreement with previous studies in tropical Africa (Chapman et al. 1998; Ngomanda et al. 2012; Bauwens et al. 2017), South America (Alencar et al. 2023), and South-East Asia (Mehedi et al. 2012; Zhiyuan et al. 2013). Species traits, notably leaf habit and dispersal mode, significantly influenced the shape of trees with irregular trunks, suggesting that species with irregular trunks tend to be deciduous and wind dispersed. In Central Africa, deciduous and wind-dispersed species are mainly found among large canopy species (Loubota Panzou et al. 2018).

Among species, deciduous species presented a much wider gradient of the shape of trees with irregular trunks (i.e., Q) than evergreen species, with a much lower distribution mean (i.e., more irregular trunk shapes). Apart from the advantage of reducing hydraulic stress through leaf fall during the dry season (Santiago et al. 2004), the predominance of large deciduous canopy species in seasonal rainforests could also be explained by their higher photosynthetic capacity compared with evergreen species (Brodribb et al. 2002).

Among species, animal-dispersed species presented a much wider gradient of the shape of trees with irregular trunks (i.e., Q) than wind-dispersed species, with a much lower distribution mean (i.e., more irregular trunk shapes). Wind dispersed species with large canopies could be favored because of their seed mass and ability to colonize environments disturbed by windthrow (Muller-Landau et al. 2008; Adiko et al. 2020). Wind dispersal over long distances could play a disproportionately important role for seeds that colonize open spaces, enabling them to avoid distance- or density-related mortality (Augspurger et al. 2017).

4.3 | Study Limitations

To our knowledge, this is the first study to quantify the shape of trees with irregular trunks in Central Africa. The study evaluated the use of the photogrammetric approach in tropical forests with a limit based on an imbalance in the height of trees generated by three dimensions (3D) in two study sites. Several authors have described the limitations of image acquisition in natural or planted forests for the reconstruction of trees in three dimensions (Forsman et al. 2016; Surový et al. 2016; Bauwens et al. 2017; Fang and Strimbu 2017; Cushman et al. 2021). According to Bauwens et al. (2017), the limitation of the height of trees reconstructed in 3D in tropical forests is due to the backlighting on some images, the low resolution, and the strong inclination of the images of the upper part of the tree. The authors suggest that if a 3D model of the upper part of the trunk is required, the effect of backlighting can be mitigated by taking photos early in the morning or at the end of the day.

To minimize this risk of irregular tree heights generated in 3D, two image acquisition techniques have been proposed in the literature (Bauwens et al. 2017; Mulverhill et al. 2019). Bauwens et al. (2017) proposed photographing trees at two different heights (at eye level and at a height of 4 m using a pole) in Central Africa. Mulverhill et al. (2019) suggested photographing trees at three different heights (2 m, 3 m, and 5 m) in North America.

In addition to these technical constraints, this study was limited by the relatively small number of shared species between the two forest sites. This limited sample size may reduce the statistical power of inter-forest comparisons and restrict the detection of subtle intraspecific differences in trunk shape. Nevertheless, the consistent trends observed between analyses including all species and those restricted to shared species suggest that our main conclusions remain robust.

Additionally, only one large plot (800 ha) was sampled per forest type. This limited spatial replication may confound site-specific characteristics with forest-type effects and thus restrict the generality of conclusions. Nevertheless, these two well-characterized sites are representative of the main forest types of the Congo Basin, providing a relevant baseline for future studies.

5 | Conclusion

This study provided new information on the variation and determinants of the shape of trees with irregular trunks in Central

African forests. The shape of trees with irregular trunks varied between two forest sites and among coexisting tree species within each forest site. We found that trees with large crown size and low wood density as well as deciduous tree species and wind-dispersed species were more likely to develop irregular trunks. These results provide valuable insights into the life-history strategy of tropical tree species. Future studies on the variation in the shape of trees with irregular trunks could be carried out in other forest types for a better understanding in Central Africa.

Author Contributions

M.M.N.B., G.J.L.P., P.P., P.L., and J.J.L. designed the study and developed the methodology. M.M.N.B. and E.F. collected the study data. M.M.N.B. and P.L. contributed to the analysis of the 3D data. M.M.N.B. and G.J.L.P. performed the statistical analysis of the data. All authors read and approved the published version of the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from Laboratory of Biodiversity, Ecosystem and Environment Manage. Restrictions apply to the availability of these data, which were used under license for this study. Data are available from the author(s) with the permission of Laboratory of Biodiversity, Ecosystem and Environment Manage.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Correlation matrices of structural and functional variables at the tree level and species level prior to mixed-effects modeling. With CEI: Crown exposure index, Hmax: maximum height, Cvolmax: maximum Crown volume, $\mathrm{CEI}_{\mathrm{juv}}$, light requirements using CEI for juvenile plants, LH, leaf habit (deciduous and evergreen), DM, dispersal mode (unassisted dispersal, wind dispersal and animal dispersal), RG: regeneration guild (pioneer, P, nonpioneer light-demanding, NPLD, and shade-bearer, SB). **Table S2:** Generalized Variance Inflation Factors (GVIF) for tree-level and species-level predictors included in the mixed-effects models. With CEI: Crown exposure index, Hmax: maximum height, Cvolmax: maximum Crown volume, $\mathrm{CEI}_{\mathrm{juv}}$: light requirements using CEI for juvenile plants, LH, leaf habit (deciduous and evergreen), DM, dispersal mode (unassisted dispersal, wind dispersal and animal dispersal). **Table S3:** Determinants of the isoperimetric quotient at tree and species levels according to the results of two linear mixed models. With CEI: Crown exposure index, Hmax: maximum height, Cvolmax: maximum Crown volume, $\mathrm{CEI}_{\mathrm{juv}}$: light requirements using CEI for juvenile plants, WD, Wood density, Dispersal (Unassisted, Wind), Guild (Pionner).