



Branch shape parameters for young open-grown *Carya laciniosa* (F.Michx.) G.Don (Juglandaceae)

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Abstract

Branch shape is a relevant tree morphological trait, representative of tree ontogenetic stage, successional status and resource-use strategy. However, branch-level studies have been limited due to tedious, time-consuming or costly measurement procedures. Here we applied a cost-efficient, quantitative framework for tree branch shape data collection and statistical evaluation, applied to young open-grown *Carya laciniosa*, an ecologically valuable but rare large-seeded deciduous tree species. After accounting for branch size and orientation, we fitted different polynomial models to photogrammetric points of 41 major branch axes belonging to four arboretum-grown leaf-off *C. laciniosa* trees, ranging from 6.1 to 8.7 m in height. Parametric branch shape was identified with great precision by the fourth-order polynomials ($R^2=0.96\pm0.07$ SD), but also acceptably by the third-order polynomials ($R^2=0.93\pm0.13$ SD). The shape parameters were weakly related to branch position within the crown ($R^2 < 0.40$), in contrast to branch size ($R^2=0.73$). The identified S-shaped branch type may be termed plagio-orthotropic, with the proximal part arching plagiotropically and the distal part ascending orthotropically. This type of shape was stable across canopy height strata, but the shape variation and the magnitude of branch curvature clearly decreased towards the upper canopy layers, revealing combined effects of branch age, gravitropism and bending strains induced by the seasonal loads. Our results corroborate the architectural similarity among the mid-successional *Carya* spp. This study highlights the relevance of branch shape, which can be feasibly recorded in terms of transferable parameters, possibly as a generic functional trait with a potential for quantification of ecosystem services, such as rainfall interception and retention, shading potential, thermal regulation and biodiversity support.

Keywords Tree architecture · Branch geometry · Posture control · Biomechanics · Intra-specific trait variation · Urban trees

Introduction

Branch shape conveys relevant information about the life history of a tree (Hallé et al. 1978; King 1998; Sterck et al. 2006), successional status (Millet et al. 1999) and ontogenetic stage (Laurans et al. 2024). For instance, tree species were sometimes grouped under branch shape category, as orthotropic or plagiotropic species (Hallé et al. 1978; King 1998; Givnish 2020). The former indicates a resource-acquisitive

strategy, with fast vertical branch development in the open, sun-exposed locations (such as in certain *Populus* spp. or *Pinus* spp.). The latter is linked with a resource-conservative strategy, with slow development of monolayer horizontal branches in shaded conditions (such as suppressed *Ulmus* spp. or *Tsuga* spp.). Nevertheless, many tree species elude these simple classifications (Fisher and Hibbs 1982). Particularly, the tree species with mixed life-history strategies are difficult to categorize, including large-seeded trees such as *Carya* spp. (McCarthy and Quinn 1990; Millet et al. 1999; White 1983). This is partly because the true variation in branch shapes may often exceed the available categories, even though a number of branch shape sub-categories have been proposed, such as secondary plagiotropy (Hallé et al. 1978; King 1998). Furthermore, it remains unclear whether branch shape may be accepted as a species-level functional trait, at least for a given ontogenetic stage (Laurans et al.

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2024), or is rather an ephemeral characteristic, which varies largely both within species and depending on the position within the crown of an individual tree (Moulia et al. 2019; Moulia and Fournier 2009). Despite the botanical and ecological relevance of branch shape, as well as considerable knowledge gaps, branch-level studies have been rare (Peng et al. 2025). This is due to the technological limitations of measurement methods: manual techniques are tedious, simplify branch form and are usually applicable to small trees or lower-located branches (Kint et al. 2010). Light Detection and Ranging (LiDAR) has contributed to automated branch quantification, but smaller branches and twigs are prone to occlusions and noise in the 3D point clouds, leading to large overestimations of size and volume (Demol et al. 2022). Photogrammetry seems best suited for measurement of fine branches, while high-resolution photos may capture detailed morphological markers, such as bud scale scars (Barthélémy and Caraglio 2007); however, the 2D nature of the more or less oblique images, in relation to a branch plane, adds uncertainty to the outcomes. In this work we propose and explore a novel framework for branch axis shape quantification using Single Image Photogrammetry (Kędra and Barbeito 2022) and a parametric statistical shape analysis. As a novel approach, we decompose the overall branch form into the shape, size and orientation components (Fig. 1), which allows for a straightforward comparison of branch shapes across branch sizes, but also reduces the scale-related effects of image obliquity (Maset and Fusiello 2024). The target trees are young open-grown *Carya lacini-osa* (F.Michx.) G.Don, which is a mid-successional species,

still awaiting a detailed analysis of the branching pattern (Millet et al. 1999).

To date studies that quantified tree branch shape have used several different shape descriptors, for instance: local branch angle (Bayer et al. 2013), average branch angle (Burkardt et al. 2020; Dorji et al. 2019; Seidel et al. 2019) and branch bending index (Bayer et al. 2013). Branch angle was most frequently used in tree-level studies that leveraged Terrestrial Laser Scanning (TLS or T-LiDAR) point clouds as the input data (Burkardt et al. 2020; Dorji et al. 2019; Seidel et al. 2019). In these studies, branch angles were derived from the orientation of cylinders fitted to local portions of a point cloud, and averaged over a specific order of branching, thus neglecting variation across individual branches but also the specific sequence of angles within a branch. These aspects of branch shape were highlighted by studies that measured local branch angle at two or several discrete locations along a branch (Bayer et al. 2013; King 1998). King (1998) measured branch angle of a whole branch and of a branch tip, in saplings of 61 tropical tree species, and noted that the latter angle best differentiated between the ascending orthotropic shapes and the arching plagiotropic shapes of branches and the associated species groups (King 1998). He also found that contrasting light environments always affected branch orientation (more upward in more sun-exposed individuals) but only some species shifted the overall branch shape pattern. Bayer et al. (2013) measured ten angles per each branch (from branch base to different decile distances along branch length, using a TLS point cloud). The authors found such detailed branch shape description useful in explaining differences between mature beech trees (*Fagus sylvatica*)

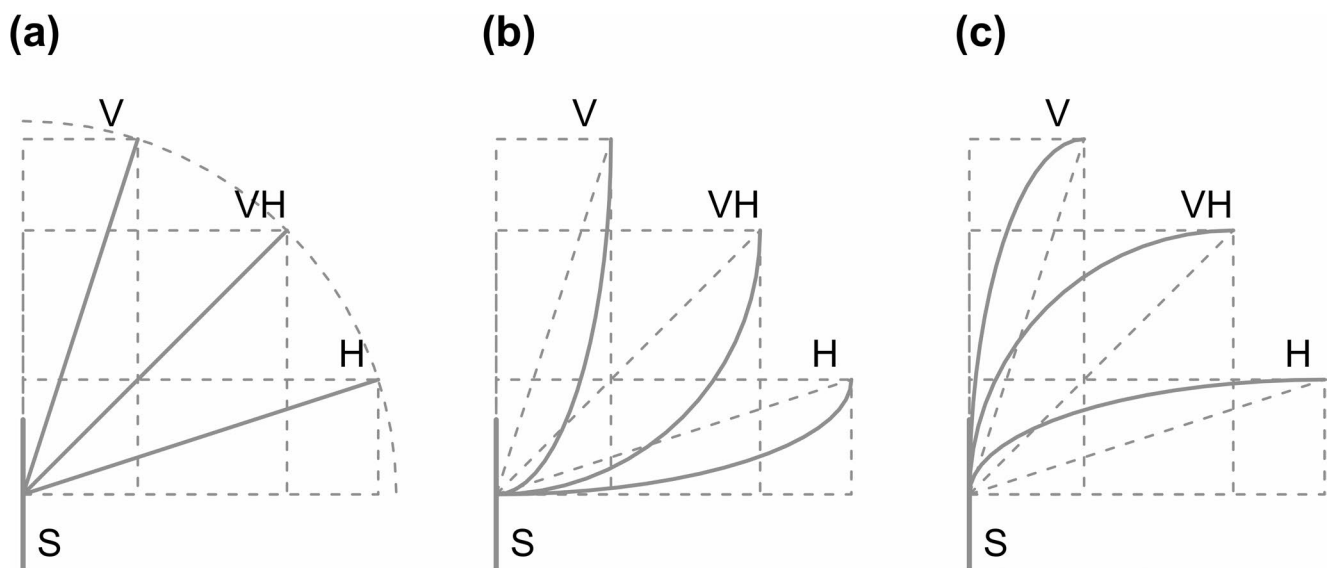


Fig. 1 Theoretical differentiation between branch axis shape, orientation and size features; (a)–(c) represent different branch shapes: linear (straight), orthotropic (ascending) and plagiotropic (arching), respectively; H, VH and V are horizontal, 1:1 diagonal and vertical

branch orientation, respectively; branch size, defined as a cord length stretched between branch base and branch tip (e.g. Kint et al. 2010), is constant across all branches; S denotes the location of the stem axis

growing in monospecific versus mixed stands with Norway spruce (*Picea abies*). The parametric models that could represent curvilinear shapes in trees in a continuous manner were so far applied to modeling crown envelope shape (Barbeito et al. 2017; Cattaneo et al. 2020), but to our knowledge no study used a similar approach to model individual branch axis shape.

The aim of this study was to provide a quantitative, parametric and transferable branch shape description of arboretum-grown *C. laciniosa* trees, using polynomial regression. By analogy to a taxonomically and ecologically similar *Carya* sp. (Millet et al. 1999) we could expect an orthotropic tendency in the branches of *C. laciniosa*, especially in the upper crowns of young open-grown trees. On the other hand, our study tree species is shade-tolerant, known to produce strong and very flexible wood, bears large compound leaves and produces the largest nuts among the *Carya* spp. (Burns and Honkala 1990). We therefore could further expect to find complex non-linear branch shapes in the lower crowns, affected by gravity (such as bending down in the proximal parts under its own weight, plus seed and

leaf mass seasonally), but also by tropism (such as upward growth at the distal ends). The specific objectives of this study were to:

- (1) evaluate branch shape and its complexity, in terms of the minimal number of required statistical parameters; and quantify the variation in branch shapes;
- (2) across individual trees;
- (3) within canopy height strata.

Materials and methods

Study trees

Four *Carya laciniosa* (F.Michx.) G.Don (Juglandaceae) trees were selected (Fig. 2), ranging from 6.1 m to 8.7 m in height and from 9 cm to 11.2 cm in stem Diameter at Breast Height (DBH) (Table 1). The trees grew in an open location (no considerable shading or competition) in the Kórnik Arboretum, Poland (52°14'46.7"N 17°06'05.9"E),

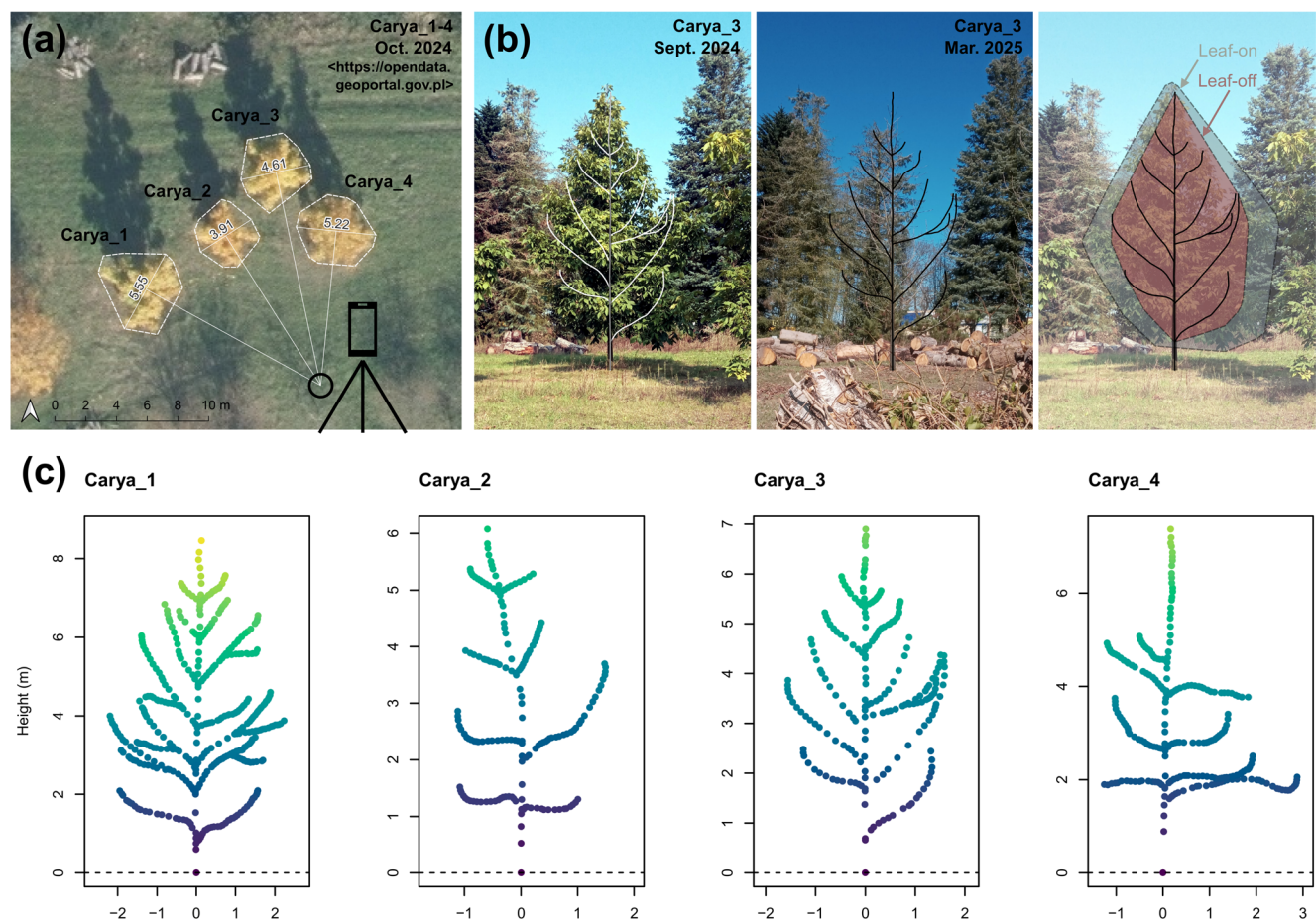


Fig. 2 Plan arrangement of the studied *Carya laciniosa* trees and location of the smartphone camera on a tripod (a); complete material for one tree (Carya_3): leaf-on (September 2024) image, leaf-off (March

2025) image, and the leaf-on image overlaid by digitized crown profiles and branching architecture (b); photogrammetric points for the major axes of the four *C. laciniosa* trees (c)

in a location with restricted visitor access. The target trees were not subject to any human-induced modifications of tree architecture, such as pruning and did not bear any signs of considerable wind damage, such as broken major branches. All four trees produced fruit (nut or karyon) in the year preceding branch measurements, thus sharing the same ontogenetic stage: the first period of maturation, when the reproductive efforts are increasing, possibly at some cost to the vegetative growth (Laurans et al. 2024). One of the trees (Carya_2) had two emerging competing stems in the middle crown (these axes were excluded from this study). The bark of all trees was still mostly smooth and only started peeling off near the bases of the main stems, thus bark roughness was not a limiting factor for photogrammetric measurements.

Photogrammetric data acquisition and processing

The four *C. laciniosa* trees were photographed twice, in September 2024 (leaf-on condition) and in March 2025 (leaf-off condition). The photogrammetric procedure followed (Kędra and Barbeito 2022). A standard smartphone device (LG LM-K410EMW) with a built-in high-resolution digital camera (3120×4160 pixels), mounted on a tripod, was placed at a spot from which all four individuals were well visible (Fig. 2a). The photographs were taken after adjusting the camera orientation (both camera roll and camera tilt set to 0°) using a clinometer application (“MultiClinometer” v.1.15; Calmatics 2021). The horizontal distance between the camera and the stem of each target tree (hereafter camera distance) was measured using a laser rangefinder (Bosh GLM80 Professional). The field-measured image parameters (camera tilt and camera distance) were further used to scale each image, using the geometric method and R code provided by Kędra and Barbeito (2022). The final metric images had a very high spatial resolution, with pixel size ranging between 3 mm and 4 mm. The leaf-off images were used for branch measurements, but the leaf-on images were stored as background information (Fig. 2b). The major axes of the four *C. laciniosa* trees were digitized in QGIS v.3.34.8 (in a projected coordinate system, using the advanced digitization tools), starting from the base of the stem of each tree, and from the tip of each branch axis.

Table 1 Characteristics of the individual *Carya laciniosa* trees studied: tree Height, stem Diameter at Breast Height (DBH) and Crown Width (leaf-on and leaf-off)

Tree ID	Height (m)	DBH (cm)	Leaf-on Crown Width (m)	Leaf-off Crown Width (m)
Carya_1	8.75	11.2	5.69	4.43
Carya_2	6.08	9.0	3.94	2.91
Carya_3	6.90	10.4	4.91	3.41
Carya_4	7.37	9.8	4.71	4.13

We excluded branches directed approximately parallel to the camera distance direction (appearing very short or steep in the image). The output geometries were stored as line shapefiles for each tree, including a unique identifier for every stem or branch axis.

Branch shape modeling and statistical analyses

Branch geometry was imported into the R (R Core Team, 2024) statistical environment using the R package “sf” (Pebesma 2018) and further processed in the Cartesian coordinate system (Fig. 2c). The photogrammetric points for every major branch axis were separated by the unique identifier. Branch size (the horizontal extent or spread and the vertical spread) and branch position (height of the branch insertion point) information was recorded, and then the x (horizontal) and z (vertical) branch coordinates were scaled to a 0–1 range. This step removed the branch (absolute) size information but also integrated branch orientation (the proportion of branch vertical extent per unit horizontal extent) and provided a unified branch geometry description. We fitted simple linear models (Eq. 1) and second- to fourth-degree (Eq. 2) polynomial models to every set of photogrammetric points representing each branch axis, i.e.:

$$z \sim b_0 + x * b_1 \quad (1)$$

$$z \sim b_0 + x * b_1 + x^2 * b_2 + x^3 * b_3 + x^4 * b_4 \quad (2)$$

where: b_0 is model intercept and b_1 to b_4 are model slope parameters (in R notation).

For each branch, we compared the nested models in terms of the coefficient of determination (R^2) and by performing an ANOVA test, to check if adding a higher degree term significantly improved model fit (at the 0.05 alpha level). We selected the best performing model type across all branches, by evaluating the averaged R^2 and number and percent of improved models. The obtained model parameters were analyzed in terms of their probability distributions (by the means of standard histograms) and collinearity between them (Pearson’s product moment coefficients). We then investigated if the best performing branch shape model parameters were sensitive to branch position within a canopy. This was achieved by fitting new linear or polynomial models to the branch position versus branch shape parameters data. This analysis was followed by an attempt to provide generic branch shape parameters, either as a function of branch height (continuous change) or as a typical branch shape within a given canopy stratum (discrete change). Finally, we also investigated how branch size and orientation vary along branch height position, to provide a

basis for a broader discussion on the relevance of branch shape versus branch size and overall orientation.

Results

The shape and complexity of *Carya laciniosa* major branch axes

We identified 41 major branches distributed in tiers along the vertical height gradients in four *Carya laciniosa* trees (Fig. 3). There were 8 branches (Carya_2, Carya_4), 11 branches (Carya_3) and 14 branches (Carya_1) modeled per tree. The simple linear fits were generally poor and insufficient to capture the *C. laciniosa* branch shapes (mean $R^2=0.42\pm0.87$ SD; Table 2). The second-order (quadratic) models provided much better fits (mean $R^2=0.74\pm0.50$), significantly improving model performance for 90.2% of branches. Still, adding the third-order polynomial term improved most of the branch shape models (87.8%), and adding the fourth-order polynomial term improved nearly half of the branch models (46.3%). Notably, the fourth-order polynomial models had the highest and the most stable R^2 across all branches (mean $R^2=0.96\pm0.07$ SD). Both the third-order (Fig. 4a; Table 3a) and the fourth-order (Fig. 4b; Table 3b) polynomials identified characteristic S-shaped axes, which were proximally plagiotropic and shifting to distally orthotropic shapes, but not strictly sigmoid (the inflection point was clearly below 50% of branch height).

Inter-individual branch shape variation

The extracted model slope parameters of the best performing (fourth-order) polynomial models had unimodal, continuous distributions across all individuals (cf. Fig. S1 in Supplementary material), still with several outliers (in the cases of five branches). Two of the outlier branches were consistently identified by all four model parameters (b1–b4) and the b4 parameter identified three additional outlier branches. There were no outlier branch shapes in just one tree (Carya_1) and most of the outlier branch shapes (3) were found in Carya_4. The collinearity analysis (Fig. S2) revealed very high Pearson's correlation coefficients, between ±0.80 and ±0.96 for the third-order polynomial model parameters, and between ±0.80 and ±0.98 for the fourth-order polynomial model parameters.

Branch shape variation within canopy strata

The final branch shape parameters were weakly related to branch position within the crown (the highest $R^2=0.35$ and the lowest $R^2=0.09$, for b1 and b4 parameters, respectively),

even after removal of the five outlier branch parameters (Fig. S3). For parameters b1, b2 and b3 the best fits were provided by the quadratic models, with a steeper change in the lower branch positions (Fig. S3a–c). The fourth parameter (b4) was very weakly and linearly related to branch position, with a constant change but also with a large variation over the regression line (Fig. S3d). In contrast, the discrete analysis across three canopy strata revealed a clear pattern of decreasing variation in all shape parameters with increasing height of a canopy stratum (Fig. 5). Moreover, only one-sided (positive or negative) extreme values of the parameters differentiated the height strata: positive extremes of parameters b1 and b3 (Fig. 5a, c), and negative extremes of parameters b2 and b4 (Fig. 5b, d). These one-sided extremes (such as the positive extreme values of the parameter b1) drove the differences between the averaged branch shapes for a given canopy stratum (Table 3; Fig. 5). Overall, the branches were getting straighter and less variable in shape with increasing canopy position. In contrast to branch shape parameters, branch size (i.e. horizontal extent or spread) was strongly related to branch position within the canopy (Fig. 6). This relationship was weaker and linear ($R^2=0.63$) when the absolute measure of branch size was considered (Fig. 6a) and it was stronger ($R^2=0.73$) and non-linear (third-order polynomial) in the case of relative (height-normalized) branch size (Fig. 6b). Finally, branch orientation was not related to the relative height position within the crown and averaged approximately 45° (Fig. S4, S5).

Discussion

Branch shape type seasonally stable across individuals and canopy height strata

The prevailing branch shape parameterized in this study may be termed plagio-orthotropic (S-shaped), with the proximal part arching plagiotropically and the distal part ascending orthotropically. This implies that the local axis angle is steeply upward at the base, then plateaus and again steepens at the distal end. Qualitative observations of such mixed-axis branching patterns were reported for other species with an alternate phyllotaxy, when young branches grow out vertically and later lower gradually by the means of secondary growth and self-weight (Hallé et al. 1978). Branch shape in the young open-grown *Carya laciniosa* trees was generally stable across the four target individuals, which is evidenced by unimodal, continuous distributions of model parameters and high collinearity between them (cf. Fig. S1 and S2 in the Supplement). This further suggests that the identified branch shapes belong to a single family

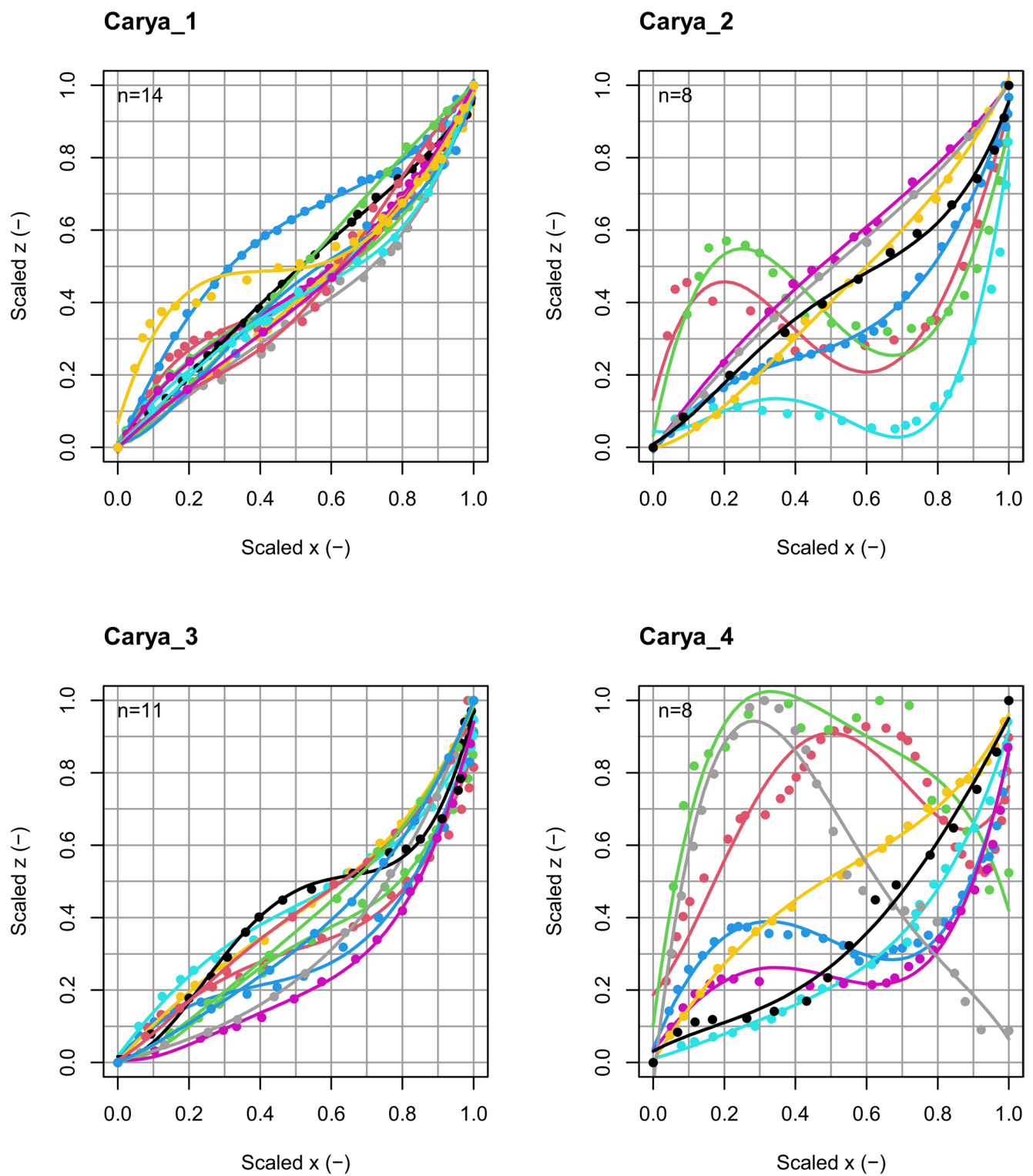


Fig. 3 Branch shape models (fourth-order polynomials) fitted to the scaled photogrammetric points of 41 branches belonging to four *Carya lacini-osa* individuals (Carya_1–4); different colors denote different branches

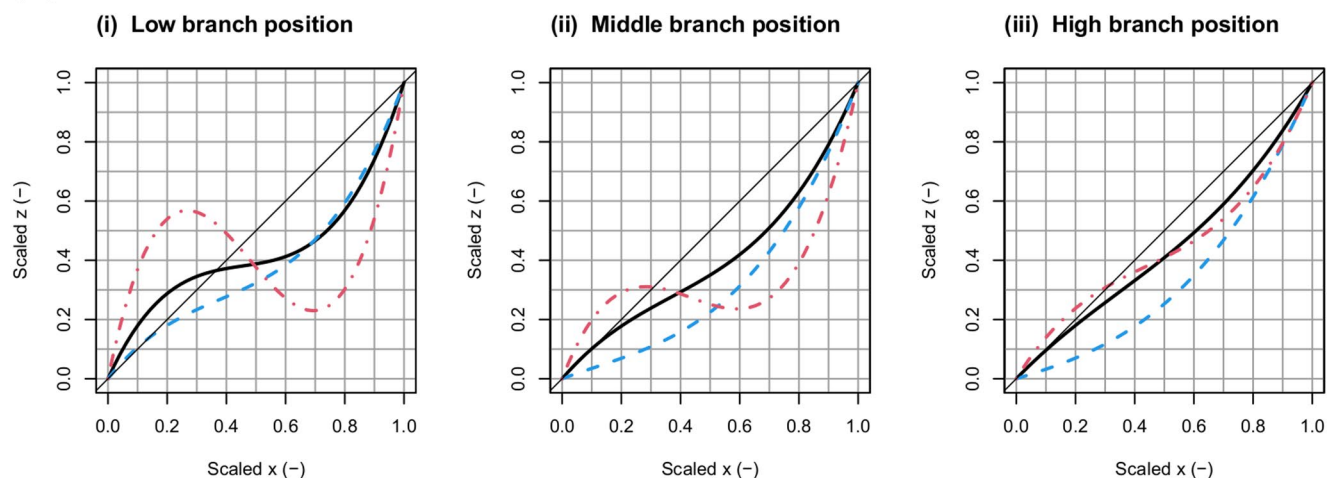
Table 2 Comparison of polynomial model fitting to the photogrammetric points of 41 branches belonging to four *Carya laciniosa* individuals; the last two columns indicate number of (#) or percent of (%) models that improved significantly (according to an ANOVA test) after adding a higher polynomial term

Polynomial function	Mean R -squared	SD R -squared	# models improved	% models improved
poly(x, 1)	0.423	0.867	-	-
poly(x, 2)	0.741	0.495	37	90.2
poly(x, 3)	0.926	0.128	36	87.8
poly(x, 4)	0.959	0.068	19	46.3

of shapes, with only a few outliers. Still, there was a clear pattern of decreasing magnitude of branch curvature and shape variation with an increasing canopy height layer, suggesting a large importance of branch age. Interestingly, we found very smooth shapes of the major branch axes, despite

a predominantly sympodial developmental pattern in *Carya* spp. (Millet et al. 1999). The smooth (not gnarled) shape was evidenced by very high coefficients of determination in the final fourth-order polynomial models, but also in the simpler third-order models, with the fitted S-shaped curves adhering very well to the photogrammetric points. This may suggest an active mechanism of axis smoothing, governed by the gravitropic tendencies, and by the laws of the theory of elasticity (Jirasek et al. 2000; Moulia et al. 2006, 2022), due to branch bending strain induced by seasonal biomass loads (Huang et al. 2005; Van Rooij et al. 2023). Notably, the plagio-orthotropic branch shape applies only to the leaf-off state, according to our corroborating leaf-on state images (cf. Fig. S6), when the branch shape was apparently fully plagiotropic, or nearly so. This suggests that the major branch axes are mechanically stressed in the leaf-on season

(a)



(b)

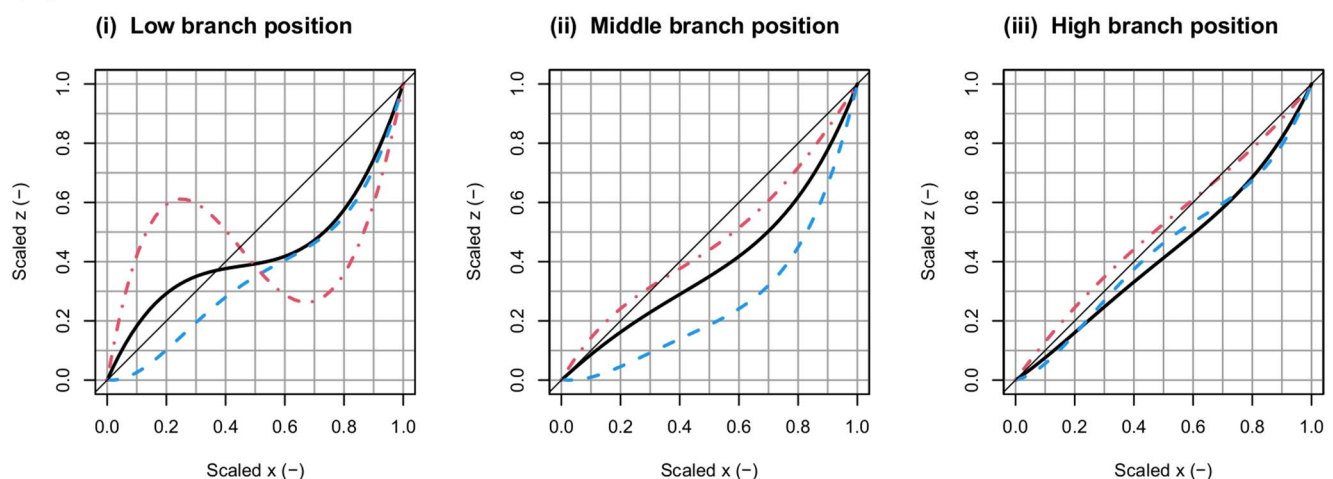


Fig. 4 Third-order polynomial (a) and fourth-order polynomial (b) scaled averaged branch shape (thick black lines) for low (i), middle (ii) and high (iii) branch position within the canopy; blue dashed lines and

red dash-dotted lines represent individual branch shapes which were extreme in terms of the b_1 parameter values (minimal or maximal, respectively) within a stratum; the thin black lines are 1:1 diagonals

Table 3 Third-order polynomial (a) and fourth-order polynomial (b) averaged branch shape parameter values and standard deviations (SD) for three strata within the canopy: low, middle or high branch position; see Fig. 4 for graphical representations of the polynomials

(a)				
Branch position	b1 (SD)	b2 (SD)	b3 (SD)	
Low	2.01 (0.87)	-4.13 (2.76)	3.02 (1.91)	
Middle	1.11 (0.55)	-1.62 (1.62)	1.46 (1.16)	
High	1.02 (0.40)	-0.82 (0.89)	0.79 (0.59)	
(b)				
Branch position	b1 (SD)	b2 (SD)	b3 (SD)	b4 (SD)
Low	2.06 (1.40)	-4.32 (5.60)	3.33 (6.92)	-0.17 (2.83)
Middle	0.86 (0.60)	-0.42 (1.98)	-0.40 (3.15)	0.91 (1.83)
High	0.66 (0.37)	1.01 (1.54)	-2.15 (2.77)	1.46 (1.52)

and bend strongly upward when the leaf and nut weight is released. The biological and biomechanical causes of the relatively low intra-seasonal variation in the identified branch shapes may lie in a specific combination of some extreme functional traits of *C. laciniosa* (at least for temperate trees): large leaf and seed mass, and a heavy and dense, yet very flexible wood (Burns and Honkala 1990). Such a combination of traits may leave little room for other young branch shapes to be viable in this stress-tolerant, resource-conservative species. However, the present study only provides an external, descriptive analysis of branch shape, and future research may aim at elucidating the particular contributions of the morphospace bio-physical constituents (Moullia et al. 2022), including the still little-known mechanical role of the bark (Clair et al. 2019).

Ecological consequences of the identified branch shape

The plagio-orthotropic branch shape type was stable across branch height and among the studied individuals, suggesting that the shape is indeed species-specific (Nauber et al. 2024). This may have implications for ecological and biological modeling. Branch shape information may indeed be indicative of the successional potential (Millet et al. 1999) and foliage display of a given tree species, as well as the range of ecosystem services that it can provide (Silva Luz et al. 2024; Tülek et al. 2024). For instance, the parameterized branch shape may be useful for quantification of rainfall interception and retention, shading potential, thermal regulation and biodiversity support (Silva Luz et al. 2024). Further research is needed to evaluate these effects, but the proposed photogrammetric framework opens promising avenues for such studies. Specifically, a large proportion of horizontally oriented branch segments (especially in the leaf-on season) and large compound leaves, should contribute to increased rainfall interception and water storage at the cost of stem-flow (Herwitz 1987; Ahmed et al. 2015). Similarly, the wider leaf-on crowns, due to outward-bending of branches near the crown peripheries (cf. Fig. S6), may efficiently increase

the shading effects and a favorable regulation of the local climate (Berry et al. 2013). Moreover, our results suggest branch shape as a possible source of variation in the stem size-crown size allometry (Pretzsch et al. 2015), while the branch shape-driven inter-seasonal crown size differences were large and varied between individual trees (cf. Table 1). Furthermore, the plagio-orthotropic branch axis shape may support wind-pollination (Niklas 1985) and the initial reproductive efforts of the young large-seeded trees, by securing a safe bending margin for the seasonally loaded branch tips.

Advances in photogrammetric branch measurements

In this study we revealed that a quantitative decomposition of branch form, into shape, size and orientation components may support consistent and conclusive results. Here, branch shape parameters and the branch size indicator (branch horizontal spread) displayed different patterns in relation to the height position within *C. laciniosa* crowns. Branch orientation was the most variable and not related to height position (cf. Fig. S4, S5). Therefore, the proposed approach definitely strengthened and clarified the shape information signal in the data. It seems feasible to apply the proposed quantitative framework to a broader range of tree species, especially when the photogrammetric method of data collection is cost-efficient and accurate (Penanhoat et al. 2024). Such observations can complement LiDAR data and measurements, and contribute to a botanical library of branch shape parameters, a potentially useful alternative to the conventional discrete angular measures, e.g. as input or validation for functional-structural tree models (de Reffye et al. 1988; O'Sullivan et al. 2021; Bekkers et al. 2025). We also showed that the photographs of several solitary trees can be taken from a single location, which reduces the time needed for fieldwork. This procedure, however, may not be applicable in denser urban stands or forest conditions, where more asymmetrical crowns may constrain a particular image direction (Kędra et al. 2019). Still, in arboreta, parks and other urban settings, permanent photogrammetric

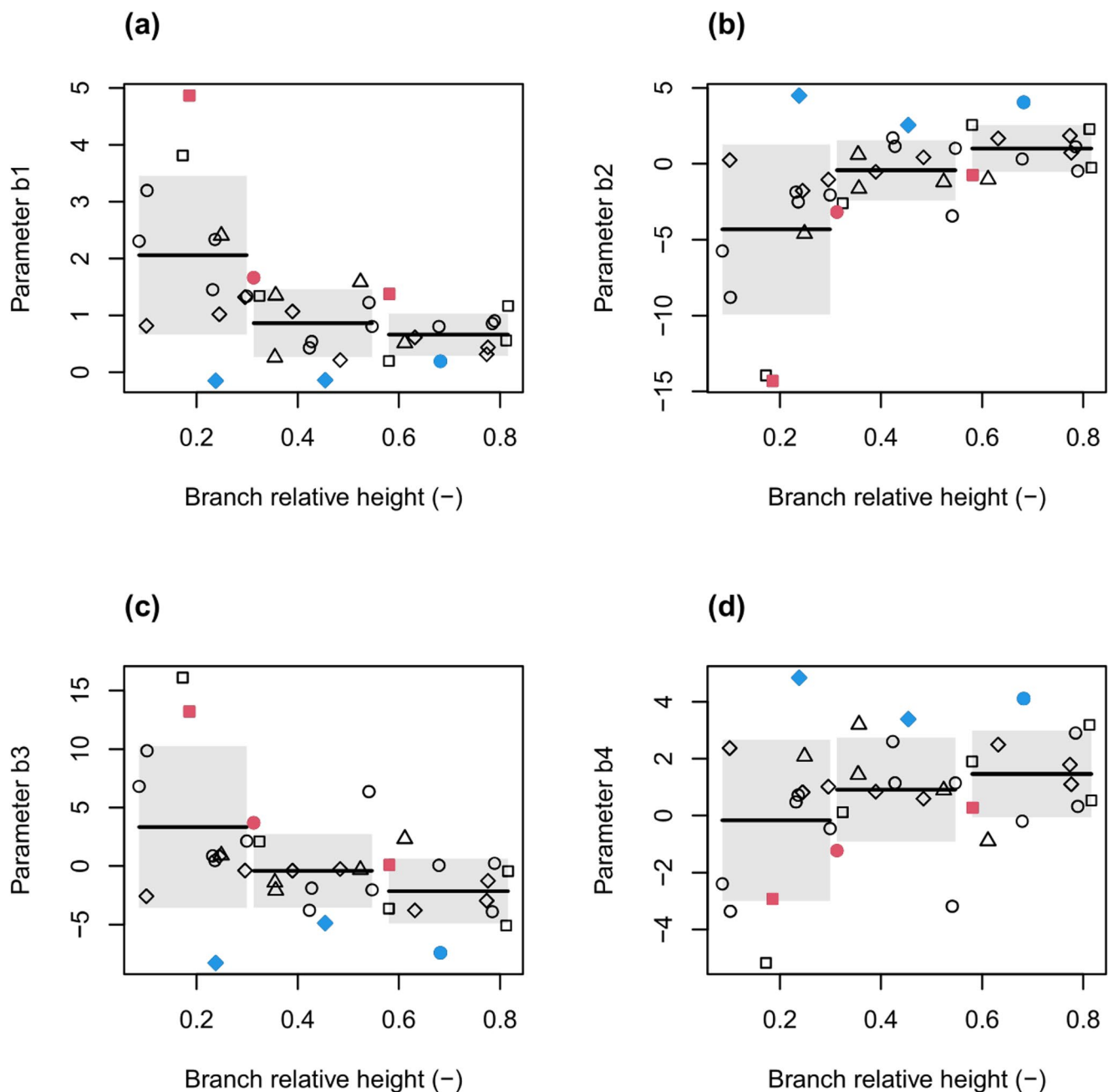


Fig. 5 The fourth-order polynomial branch shape parameters (b1 (a), b2 (b), b3 (c), b4 (d)) plotted against branch relative height; the thick horizontal lines represent mean parameter values within three canopy strata: low, middle and high branch position; the gray filled areas reach ± 1 SD from the mean; different point symbols denote different

Carya laciniola trees: circles – Carya_1, squares – Carya_2, diamonds – Carya_3, triangles – Carya_4; blue and red filled points indicate six individual branch shapes which were extreme in terms of the b1 parameter values (minimal or maximal, respectively) within a stratum

data collection points for monitoring tree architecture can be established in spots with good visibility. We showcased here that photographs may be easily repeated over time, such as in different seasons, and precisely overlaid for change analysis (cf. Fig. S6).

Conclusion

In this study we applied a cost-efficient, quantitative framework for photogrammetric data collection and statistical evaluation of tree branch shape, providing transferable branch axis shape parameters for young open-grown *Carya laciniola*. The studied tree species is an ecologically valuable

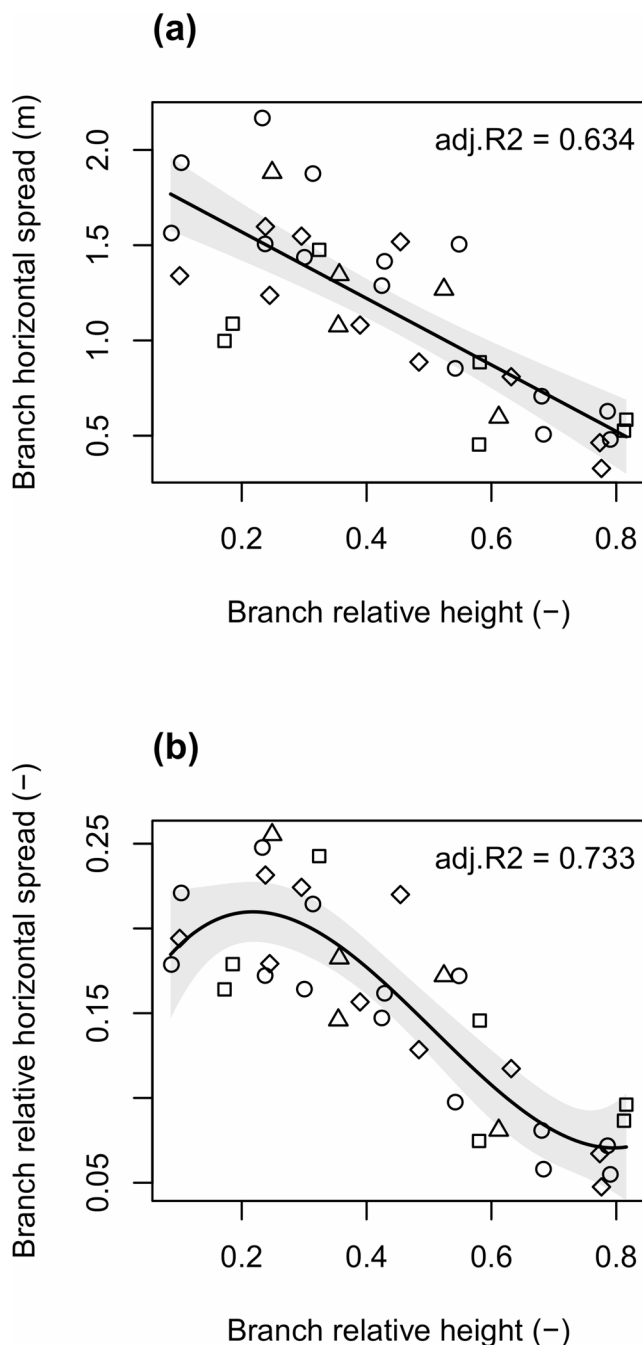


Fig. 6 Branch absolute horizontal spread **(a)** and branch relative (height-normalized) horizontal spread **(b)** plotted against branch relative height; the fitted models are simple linear fit in **(a)** and third-order polynomial in **(b)**, with the 95% CIs in gray; the adjusted R-squared values for the respective fits were given in each plot legend (adj.R2); different point symbols denote different *Carya laciniosa* trees: circles – Carya_1, squares – Carya_2, diamonds – Carya_3, triangles – Carya_4

component of native communities in North America and rare throughout the distribution, but with a considerable potential as a useful urban tree for provision of ecosystem services in many European cities. This tree species has been very poorly studied in terms of its architectural development and branching pattern. We corroborate the architectural similarity among the large-seeded *Carya* spp., with a generally upward branch orientation in the open, but a complex plagio-orthotropic branch shape during the leaf-off season. We provided evidence that such a branch shape, after accounting for size and orientation, may be stable along tree height and across conspecific individuals. Therefore, the branch shape may be a relevant generic or species-level functional trait, informative of the successional potential and the range of delivered ecosystem services. Future studies may aim at extending the library of branch shape parameters by applying the proposed framework to other tree species, thus building a botanically faithful foundation for automated tree architecture reconstruction and prediction efforts.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00468-026-02765-8>.

Author Contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Kamil Kędra. The first draft of the manuscript was written by Kamil Kędra and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The data generated and analyzed during this study are included in this published article and its supplementary files.

Declaration

Competing Interests We declare that there are no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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