

Whole-Leaf Shape and Venation-Loop Geometry Across Three Vein Scales

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Research Article

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Abstract

Leaf venation is hierarchical, but how the relationship between whole-leaf shape and venation-loop geometry varies with vein-width scale remains unclear. This study paired mask-derived leaf geometry with published species-level venation measurements for 102 plant species. Crofton circularity and log-transformed whole-leaf aspect ratio (AR) were compared with vein density, minimum-spanning-tree ratio, and loop elongation at three relative vein-width scales. Pearson correlations between $\ln(\text{AR})$ and corrected $\ln(\text{loop axis ratio})$ were 0.536, 0.667, and 0.940 from small to large scale ($R^2 = 0.288, 0.445,$ and 0.884). In exploratory paired-species bootstrap analyses, the large-scale correlation exceeded those at both smaller scales, although these comparisons did not account for phylogenetic relatedness. The large-scale log–log slope was 1.010 (conventional OLS 95% CI 0.937–1.082), and leave-one-out correlations ranged from 0.927 to 0.944. An exploratory hierarchical analysis found greater boundary representation and closer agreement between boundary-region and whole-leaf axis ratios at upper levels, potentially partly by construction. Associations involving vein density and minimum-spanning-tree ratio were weaker or inconsistent. Thus, in this observational species-level dataset, leaf elongation was most closely associated with loop elongation at the largest relative vein-width scale; the developmental basis and phylogenetic generality remain unresolved.

1. Introduction

Leaf venation forms a reticulate network spanning fine veins, enclosed regions, larger loops, and the leaf boundary. Its structure, development, function, and evolution have been widely investigated (Sack & Scoffoni, 2013). Hierarchical loop decomposition provides a way to quantify nested regions rather than treating the network as a single pattern (Katifori & Magnasco, 2012). Geometry at different network levels may therefore capture different aspects of leaf organization.

Whole-leaf aspect ratio measures global elongation, whereas areole or loop elongation describes regions enclosed by veins. The two measures concern different organizational levels despite their similar major-to-minor-axis definitions. Previous methods quantified spatial features of venation geometry (Rolland-Lagan et al., 2009). Studies comparing whole-leaf and areole elongation have found relationships that vary among plant groups and settings (Blonder et al., 2016, 2018). The relationship is not a new question; its dependence on vein-width scale remains worth testing explicitly.

Network scale matters because finer and coarser veins partition the leaf into differently sized regions. Multiscale venation statistics and automated extraction support analysis of this variation (Blonder et al., 2020; Xu et al., 2021). Matos et al. (2024) summarized venation properties at three species-relative vein-width scales in a public dataset of 122 fern and angiosperm species, and later work examined patterns across clades and scales (Matos et al., 2025). Species-relative categories do not imply identical absolute vein widths across taxa.

This study examines whether species-level correspondence between whole-leaf and venation-loop elongation varies across small, medium, and large relative vein-width categories. Comparing all three

categories tests whether the association is concentrated at particular network scales; it cannot by itself identify why the correspondence arises.

Whole-leaf circularity and aspect ratio (AR) were derived from public leaf masks and matched by species to published vein density (VD), minimum-spanning-tree ratio (MST ratio), and loop elongation (ER). The resulting complete-case sample comprised 102 species. The direct elongation-to-elongation comparison was treated as the central question, and the other network variables were used to evaluate whether any association was broader than shape alone.

The initial predictions were that greater whole-leaf elongation would be associated with little change or a modest decrease in VD, an increase in MST ratio, and greater loop elongation. The AR–ER association was also expected to be stronger at larger relative vein-width scales. These were directional expectations, not constraints imposed on the results; alternative patterns remained possible.

Finally, potential differences in fitted AR–ER relationships between woody and herbaceous species were examined. This was a secondary analysis because growth form is associated with taxonomic composition in this dataset.

2. Methods

2.1 Data source and study sample

This study used public leaf and venation data from the University of California Botanical Garden (UCBG) dataset associated with Matos et al. (2024). The source dataset contained 122 species, while the processed network table contained measurements for 120 species. Whole-leaf geometry was extracted independently in this project from the available leaf masks and then merged by species with the public metadata and multiscale venation measurements.

Candidate leaf masks were available for 117 species. Species without usable masks or complete geometry measurements were not reconstructed or assigned estimated values. After image-quality and completeness checks, 110 species had complete whole-leaf geometry measurements. Restricting the merge to species with all measurements required for the main analysis and to the woody/herbaceous comparison produced 102 unique species (76 woody, including trees and shrubs; 26 herbaceous). This was a complete-case, nonrandom subset of the available public data; the transition from 122 source species to 102 analyzed species should not be interpreted as a random sampling process. The unit of analysis was the species: a selected leaf mask per species provided geometry, and venation variables were published species-level summaries. Direct pairing of the geometry and venation measurements on the same individual leaf was not established.

2.2 Whole-leaf geometry

Whole-leaf geometry was quantified from binary leaf masks. Two complementary shape measures were retained: circularity and aspect ratio.

Circularity was calculated as

$$C = 4\pi A / P^2,$$

where A is leaf-mask area and P is Crofton perimeter, which was used for the primary circularity calculation.

Whole-leaf aspect ratio (AR) was calculated as

$$AR = \text{MajorAxisLength} / \text{MinorAxisLength}.$$

The major and minor axes were those of the equivalent ellipse derived from the second moments of the leaf region; AR was therefore not calculated from a bounding box. By definition, $AR \geq 1$, with values closer to 1 indicating less elongated global geometry and larger values indicating greater elongation.

Raw AR was strongly right-skewed in the final analysis set (skewness approximately 7.25). Natural-log transformation reduced this skewness substantially (to approximately 1.37), so $\ln(AR)$ was used as the primary whole-leaf elongation predictor. Circularity was retained without transformation, and extreme but valid geometry values were not removed solely because of their magnitude.

2.3 Multiscale venation variables

Three venation-network variables were analyzed: vein density (VD, vein length per leaf area; mm mm^{-2} , equivalently mm^{-1}), minimum-spanning-tree ratio (MST ratio, dimensionless), and loop elongation (ER, dimensionless), following the definitions in Matos et al. (2024). VD and MST ratio were analyzed as supplied in the processed table, without additional transformations in this study. MST ratio is the length of a minimum spanning tree connecting vein junctions divided by total vein length; higher values represent a more tree-like, less redundant network.

The processed GBM data contained $ER_GBM = \sqrt{ER_raw}$, where $ER_raw = a/b - 1$ and a/b is the major-to-minor axis ratio of a loop's equivalent ellipse. The final response reversed the GBM transformation before logarithmic scaling:

$$Y = \ln(1 + ER_GBM^2) = \ln(a/b).$$

Matos et al. (2024) define ER using the median loop-axis ratio minus 1. The corrected species-by-scale summary was modeled, rather than individual-loop measurements.

2.4 Venation scale

The small-, medium-, and large-scale venation measurements were taken from the relative vein-width processing of Matos et al. (2024). For each species, vein width was expressed relative to its species-specific maximum r_min :

$$s = r_min / \max(r_min).$$

The source-defined categories were small ($s \leq 0.3$), medium ($0.3 < s \leq 0.6$), and large ($s > 0.6$). The processed species-level variables summarized measurements by their median within each relative scale category. Thus, these labels refer to species-relative vein width, not the same absolute vein width across all species.

An additional hierarchical-loop-decomposition (HLD) diagnostic used $q = \text{widthThreshold} / \text{species-specific maximum widthThreshold}$. Boundary representation and boundary-region elongation were summarized in five q intervals (0–0.2, 0.2–0.4, 0.4–0.6, 0.6–0.8, and 0.8–1.0). This q coordinate is distinct from the three relative vein-width scales s in the primary analysis.

2.5 Primary statistical analysis

The primary analysis crossed two whole-leaf predictors (Crofton circularity and $\ln(\text{AR})$), three venation outcomes (VD, MST ratio, and corrected ER), and three network scales (small, medium, and large), yielding 18 predictor-outcome-scale analyses.

For each relationship, Pearson correlation (r) and Spearman rank correlation (ρ) were computed, and ordinary least-squares (OLS) regression was fitted to obtain the slope, conventional OLS 95% confidence interval, and R^2 . HC3 heteroskedasticity-robust p -values, using t inference with residual degrees of freedom, assessed sensitivity to variance assumptions. Benjamini–Hochberg false-discovery-rate (BH-FDR) q -values across the 18 primary Pearson tests provided an exploratory multiplicity check.

2.6 Sensitivity and secondary analyses

Large-scale AR–ER robustness

The large-scale AR–ER association was assessed using leave-one-out Pearson correlations and separate correlations within six broad groups (asterids, basal angiosperms, basal eudicots, ferns, monocots, and rosids). These checks examined sensitivity to individual species and broad clade composition.

Exploratory paired-scale correlation comparison

To compare the three dependent AR–ER correlations, 102 species were resampled with replacement for 20,000 bootstrap replicates, retaining each species's scale-specific measurements together. Percentile 95% intervals were calculated for pairwise differences in Pearson r . A second, clade-stratified resampling analysis also used 20,000 replicates.

Zero-value exclusion sensitivity

To evaluate sensitivity to potentially ambiguous zero-valued network entries, the primary AR–ER correlations and growth-form interaction models were repeated after excluding species with zero corrected ER at each scale (small $n = 99$, medium $n = 100$, large $n = 102$). A stricter complete-positive restriction was also applied, excluding eight species with at least one zero across the nine scale-specific

VD, MST, and ER columns (n = 94). The frozen 102-species sample remained the primary analysis. Interaction sensitivity p-values used HC3 robust covariance; no multiple-testing correction was applied.

Exploratory hierarchy diagnostic

For each q interval, the fraction of HLD records flagged as boundary was calculated within each species and summarized across species by the median and interquartile range. Thus, species rather than individual HLD records received equal weight in the final cross-species summary. For species with valid boundary-region elongation, median boundary axis ratio was related to whole-leaf AR using Pearson correlations of their natural logarithms and the median boundary-to-leaf axis-ratio ratio. Contributing sample sizes could differ between the two panels when boundary-region elongation was unavailable.

Growth-form moderation

Growth form was evaluated as a secondary moderator of the AR–ER relationship. For each network scale, the interaction model was

$$Y = \beta_0 + \beta_1 X + \beta_2 G + \beta_3 (XG) + \varepsilon,$$

where $X = \ln(\text{AR})$, Y was corrected loop elongation, and $G = 0$ for herbaceous species and $G = 1$ for woody species. Under this coding, β_1 is the fitted herbaceous slope, $\beta_1 + \beta_3$ is the fitted woody slope, and β_3 represents the fitted difference between those slopes.

Because growth form was confounded with broad clade composition, a categorical clade-adjusted interaction model was used as a sensitivity analysis. HC3-robust p-values for both models used t inference; clade categories did not constitute a phylogenetic comparative model.

2.7 Reproducibility and provenance

Primary analyses were rerun from the frozen 102-species table. The HLD summaries were separately reproduced from local source files for 102 species (2,027,662 records); original and harmonized q-bin conventions yielded identical values. This verification did not reconstruct every upstream image-processing stage.

3. Results

3.1 Overall pattern across network variables

The 102-species sample comprised 76 woody and 26 herbaceous species. Among the measured network properties, associations with loop elongation were stronger and more consistent than those with VD or MST ratio.

For $\ln(\text{AR})$ versus VD, Pearson correlations were -0.089 , -0.034 , and 0.201 at small, medium, and large scales, respectively. The large-scale Pearson association was nominally significant (unadjusted $p =$

0.043), but its BH-FDR q-value across 18 primary tests was 0.110. The corresponding Spearman correlation was 0.082 ($p = 0.415$), providing little evidence of a consistent monotonic relationship. For $\ln(\text{AR})$ versus MST ratio, Pearson correlations were -0.019 , -0.184 , and -0.136 across the three scales; none supported the prespecified prediction of a positive relationship.

3.2 Whole-leaf elongation and loop elongation across scales

Figure 2. Whole-leaf and venation-loop elongation across three relative vein-width scales. Associations between whole-leaf $\ln(\text{AR})$ and corrected loop elongation, $\ln(1 + \text{ER}_{\text{raw}}) = \ln(\text{loop axis ratio})$, at the small, medium, and large source-defined relative vein-width scales (Matos et al., 2024). Lines show ordinary least-squares fits; slopes and R^2 refer to OLS, and the three panels contain the same 102 species.

At the small scale, Pearson $r = 0.536$ and Spearman $\rho = 0.534$; the OLS slope was 0.666 (95% CI 0.458–0.874), with $R^2 = 0.288$. At medium scale, Pearson $r = 0.667$ and Spearman $\rho = 0.678$; the slope was 0.839 (95% CI 0.653–1.024), with $R^2 = 0.445$. At large scale, Pearson $r = 0.940$ and Spearman $\rho = 0.913$; the slope was 1.010 (95% CI 0.937–1.082), with $R^2 = 0.884$. The three AR–ER Pearson associations survived BH-FDR adjustment across the 18 primary comparisons (all $q < 0.001$).

In paired-species bootstrap analysis, the large-minus-small difference in Pearson r was 0.404 (95% percentile interval 0.210–0.650), and the large-minus-medium difference was 0.273 (0.120–0.467). The medium-minus-small difference was 0.131 (-0.037 –0.352), leaving that comparison uncertain. Clade-stratified resampling yielded the same qualitative pattern, although neither bootstrap approach accounted for phylogenetic relatedness.

The large-scale correlation ranged from 0.927 to 0.944 in leave-one-out analysis. It was also positive within each of six broad clades: asterids ($n = 26$, $r = 0.946$), basal angiosperms ($n = 10$, $r = 0.858$), basal eudicots ($n = 9$, $r = 0.937$), ferns ($n = 11$, $r = 0.987$), monocots ($n = 9$, $r = 0.963$), and rosids ($n = 37$, $r = 0.895$). The smaller groups warrant particular caution.

Excluding zero ER values separately at each scale yielded Pearson r values of 0.546 (small, $n = 99$), 0.738 (medium, $n = 100$), and 0.940 (large, $n = 102$). Restricting the sample to 94 species without any zero among the nine VD, MST, and ER columns gave $r = 0.655$, 0.818, and 0.947, respectively. The ordering of the three correlations was unchanged.

3.3 Exploratory hierarchical boundary diagnostic

Boundary representation increased toward higher levels of the q hierarchy (Fig. 3). At lower q , many measured regions were interior to the leaf; at upper q , the boundary-flagged fraction approached one. The numbers of contributing species varied among bins and between the boundary-fraction and boundary-elongation measures because some species lacked valid elongation measurements in particular intervals.

Across the five q intervals, median boundary fractions were 0.120, 0.590, 0.986, 1.000, and 1.000. Correlations between the log-transformed boundary and whole-leaf axis ratios were 0.420, 0.691, 0.720, 0.864, and 0.982; median boundary-to-leaf axis-ratio ratios were 0.915, 1.038, 1.005, 1.001, and 1.000, respectively. Both the rising boundary fraction and the approach of the ratio toward one describe a change in the geometry represented by upper hierarchical levels; neither statistic independently identifies a developmental process.

3.4 Growth-form moderation

At the small scale, the fitted herbaceous slope was 0.957 and the woody slope was 0.169; the interaction coefficient was $\beta_3 = -0.788$ ($p = 1.86 \times 10^{-5}$). At the medium scale, the corresponding slopes were 1.117 and 0.494, with $\beta_3 = -0.623$ ($p = 8.35 \times 10^{-4}$). At the large scale, the fitted slopes were 1.028 and 0.994, and the interaction coefficient was small ($\beta_3 = -0.033$, $p = 0.657$).

After categorical clade adjustment, interaction coefficients were approximately -0.751 (small; conventional OLS $p = 1.14 \times 10^{-5}$), -0.609 (medium; $p = 0.00122$), and -0.047 (large; $p = 0.542$). Corresponding HC3-robust p -values were 0.0245, 0.00244, and 0.616.

For unadjusted models, HC3-robust interaction p -values were 0.00223, 0.00266, and 0.739 at the small, medium, and large scales. After restricting to 94 species without zero-valued network entries, the corresponding values were 0.0361, 0.00445, and 0.759. The small-scale evidence weakened after exclusion; these exploratory comparisons were not adjusted for multiplicity.

3.5 Circularity as a complementary shape measure

Circularity was negatively associated with corrected loop elongation at all three scales (Pearson $r = -0.241$, -0.250 , and -0.395 , respectively). Its relationships with VD and MST ratio were generally weak. Because circularity includes perimeter as well as area, this measure complements rather than duplicates the direct comparison of global and local elongation.

4. Discussion

The principal result is selective: whole-leaf elongation has a substantially clearer association with venation-loop elongation than with VD or MST ratio, particularly at the largest relative vein-width scale. The analysis does not therefore support a general claim that elongated leaves have uniformly altered network density or topology. Rather, the strongest correspondence concerns a geometric property measured at two organizational levels. The absence of the predicted positive MST relationship is also informative, because it separates geometric elongation from the degree to which a network is tree-like.

Previous studies considered whole-leaf and areole elongation, with findings that vary across study systems (Blonder et al., 2016, 2018). The present analysis explicitly compares three species-relative vein-width categories, enabled by hierarchical and multiscale methods (Katifori & Magnasco, 2012; Blonder et al., 2020; Matos et al., 2024). Differences in scale, spatial sampling, and measurement

definitions might account for discrepancies in earlier reports, but those datasets were not reanalyzed here.

At the largest relative scale, the fitted log–log slope was near one (1.010; conventional 95% CI 0.937–1.082). This is consistent with approximately proportional changes in whole-leaf and loop axis ratios within the observed dataset. Both are dimensionless shape measures, but one describes the leaf outline and the other enclosed venation regions. Their near-unit slope neither demonstrates identical shapes nor establishes a universal scaling law.

The large-scale association remained positive under leave-one-out and broad-clade checks. Paired-species bootstrap comparisons favored a larger correlation at this scale than at either smaller scale, while the medium-minus-small contrast remained uncertain. These analyses reduce concern about a single influential species but do not model shared evolutionary history. Phylogenetically explicit comparisons are therefore needed before attributing the pattern to general biological differences among network scales.

Growth-form moderation offers a secondary comparison. Woody and herbaceous fitted slopes differed at small and medium scales, while no interaction was detected at large scale. Because groups had unequal sample sizes and observed AR ranges, and growth form was confounded with broad clade composition, these contrasts cannot isolate the effect of growth form. The large-scale nonsignificant interaction also does not establish equal underlying slopes.

The separately reproduced hierarchy diagnostic (Fig. 3) adds geometric context. At higher q , boundary-flagged regions represented a larger fraction of observations, and their axis ratios approached whole-leaf AR. This pattern could partly arise by construction as upper-level regions incorporate the leaf boundary, rather than reflecting active developmental coordination. Moreover, the diagnostic's five q intervals differ from the three species-relative vein-width categories used in Fig. 2. Figure 3 therefore illustrates a plausible geometric constraint without directly testing the cause of the primary cross-scale association.

Development provides another possible explanation: models of venation patterning suggest that leaf shape and expansion may influence network formation (Fujita & Mochizuki, 2006). Yet similar observational patterns could reflect constraints imposed by the final leaf outline or traits shared through evolutionary history. With species-level summaries alone, these possibilities cannot be distinguished or assigned a causal direction.

Several limitations follow from the sampling and measurement design. Geometry from selected leaf masks was matched to published venation summaries by species, not necessarily measured on the same leaf. The 102-species sample is a nonrandom complete-case subset, with phylogenetic nonindependence that broad-clade checks cannot remove. Relative vein-width categories are not common absolute widths, and growth-form groups differ in sample size and AR distribution. A few zero-

valued network entries have uncertain upstream provenance, although exclusion did not change the principal correlation ordering. Boundary-related dependence also limits the HLD diagnostic.

Independent datasets with paired leaf-outline and venation measurements, explicit phylogenetic models, and sampling away from the enclosing boundary could test whether the scale-dependent association persists. Developmental measurements would be required to separate geometric constraints from biological coordination. These extensions, rather than additional interpretation of the current cross-sectional data, are needed to assess mechanism and generality.

In summary, whole-leaf and loop elongation corresponded most strongly at the largest species-relative vein-width scale in this dataset, while other venation properties showed less consistent relationships. The biological origin and generality of this scale dependence remain open.

Declarations

Competing Interests

The author declares no competing interests.

Use of Artificial Intelligence Tools

ChatGPT (OpenAI) assisted with research planning, Python code generation, statistical and reproducibility checks, and manuscript editing. The sole author is responsible for critically verifying the final analyses and interpretations and for reviewing and approving the manuscript.

Author Contributions

Alex Ziran Zhang conceived and led the study, defined its mathematical research focus, identified relevant public datasets, designed the analytical strategy, and selected statistical methods. He established and operated the computational workflow, reviewed and tested AI-generated Python code, validated analytical results, interpreted the findings, and wrote the manuscript.

Data Availability

The source leaf-mask and venation data were obtained from Matos et al. (2024) and are available through Dryad (<https://doi.org/10.5061/dryad.1g1jwsv36>). The derived 102-species analysis table, supplementary analysis results, and figure-level outputs are archived in Zenodo (version 1.0; <https://doi.org/10.5281/zenodo.23582574>). The complete upstream leaf-mask and hierarchical venation source files are not redistributed in the Zenodo archive.

Code Availability

The Python analysis scripts, supplementary statistical and validation code, software environment information, and reproducibility documentation are available in the same Zenodo archive (version 1.0; <https://doi.org/10.5281/zenodo.23582574>). Full source-to-figure reproduction additionally requires the original leaf masks and hierarchical venation files, which are not included in this archive.

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Figures

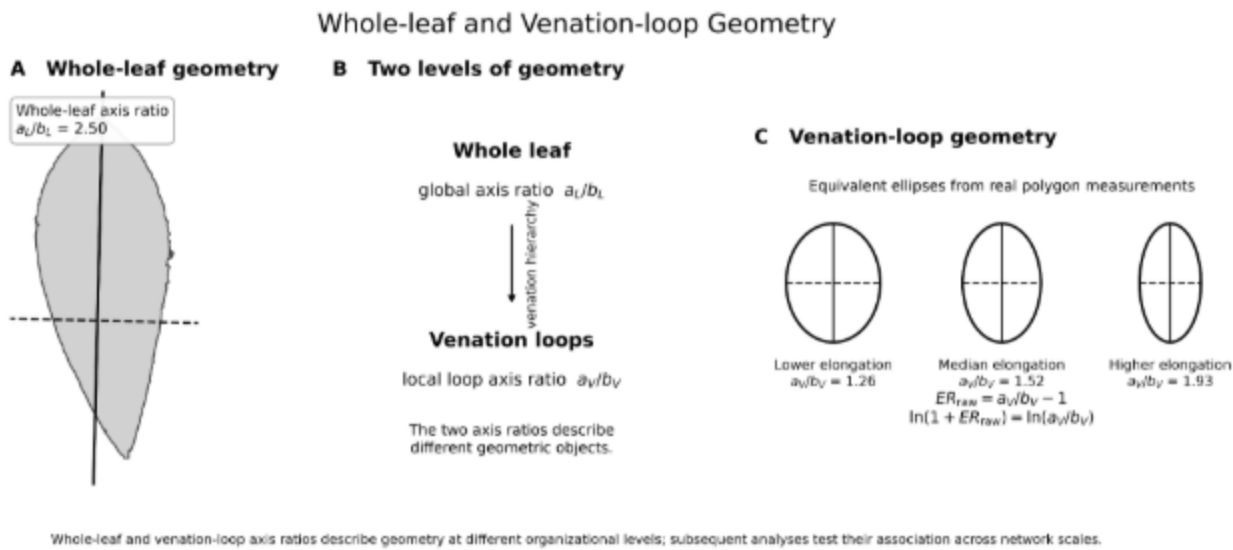


Figure 1

Whole-leaf and venation-loop geometry. The diagram distinguishes whole-leaf equivalent-ellipse aspect ratio from local loop elongation; loop examples derive from measured polygons of a representative source species.

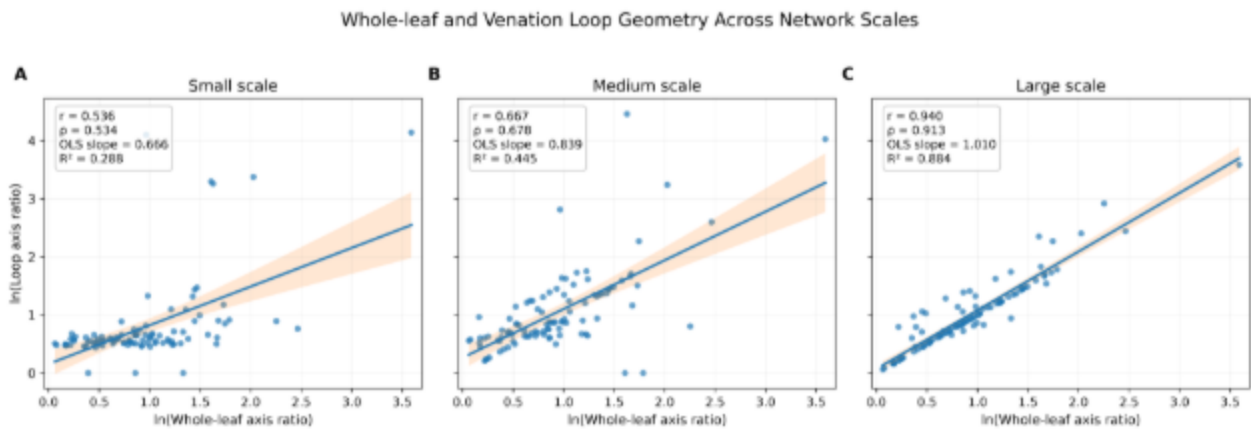


Figure 2

Whole-leaf and venation-loop elongation across three relative vein-width scales. Associations between whole-leaf $\ln(AR)$ and corrected loop elongation, $\ln(1 + ER_{raw}) = \ln(\text{loop axis ratio})$, at the small, medium, and large source-defined relative vein-width scales (Matos et al., 2024). Lines show ordinary least-squares fits; slopes and R^2 refer to OLS, and the three panels contain the same 102 species.

Boundary Dominance and Geometric Convergence Across the Venation Hierarchy

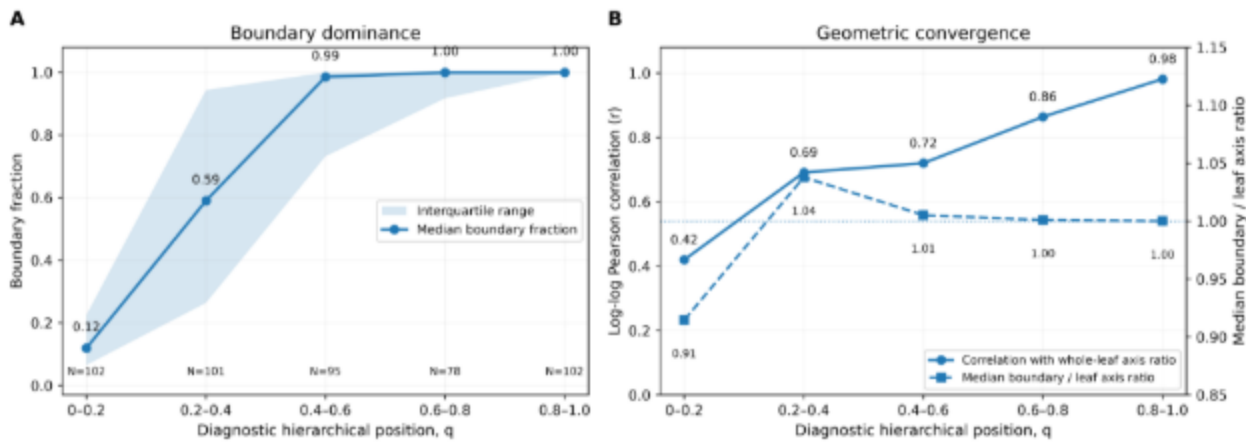


Figure 3

Boundary representation and shape correspondence across the HLD hierarchy. (A) Median within-species fraction of records flagged as boundary (line), interquartile range (shading), and contributing-species counts (N). (B) Pearson r between $\ln(\text{boundary-region axis ratio})$ and $\ln(\text{whole-leaf AR})$ (solid line; $N = 102, 99, 94, 78$, and 102 across the five bins) and median boundary-to-leaf axis-ratio ratio (dashed line, right axis). The q intervals represent an exploratory hierarchy diagnostic, not the three vein-width categories in Figure 2.

Growth-form Moderation of Whole-leaf and Venation-loop Geometry

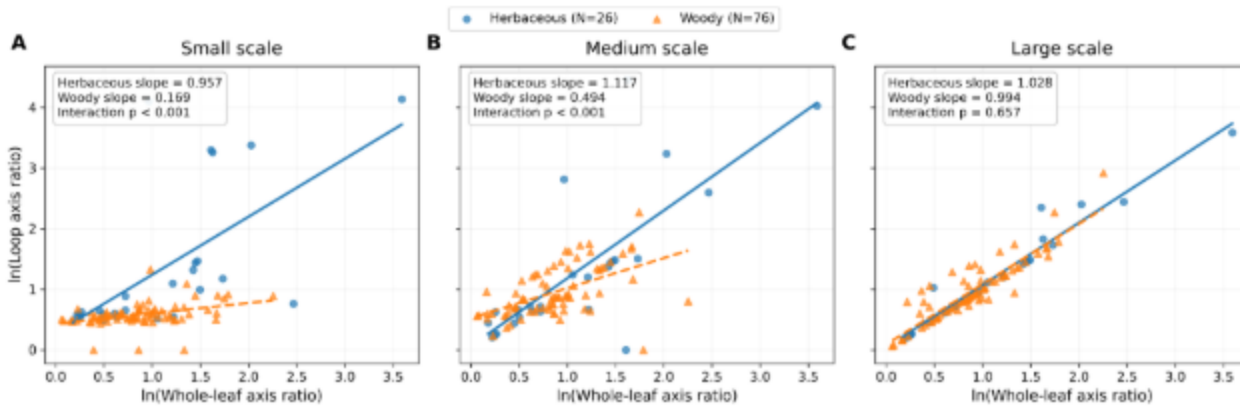


Figure 4

Growth-form moderation of whole-leaf and venation-loop elongation. Herbaceous ($n = 26$) and woody ($n = 76$) species are shown at each relative vein-width scale. Figure labels report conventional OLS interaction p -values; HC3-robust p -values are given in Results.