




RESEARCH ARTICLE

Structural and defensive roles of angiosperm leaf venation network reticulation across an Andes–Amazon elevation gradient

Benjamin Blonder^{1,2}  | Norma Salinas^{1,3} | Lisa Patrick Bentley^{1,4} |
 Alexander Shenkin¹  | Percy Orlando Chambi Porroa⁵ | Yolvi Valdez Teixeira⁵ |
 Tatiana Erika Boza Espinoza⁶ | Gregory R. Goldsmith⁷ | Lucas Enrico⁸ |
 Roberta Martin⁹ | Gregory P. Asner⁹ | Sandra Díaz^{1,8} | Brian J. Enquist¹⁰  |
 Yadvinder Malhi¹

¹Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK; ²School of Life Sciences, Arizona State University, Tempe, AZ, USA; ³Sección Química, Pontificia Universidad Católica del Perú, San Miguel, Lima, Perú; ⁴Department of Biology, Sonoma State University, Rohnert Park, CA, USA; ⁵Universidad Nacional de San Antonio Abad del Cusco, Cusco, Perú; ⁶Department of Systematic and Evolutionary Botany, University of Zurich, Zürich, Switzerland; ⁷Schmid College of Science and Technology, Chapman University, Orange, CA, USA; ⁸Instituto Multidisciplinario de Biología Vegetal (IMBIV, CONICET-UNC), and FCFyN, Universidad Nacional de Córdoba, Córdoba, Argentina; ⁹Department of Global Ecology, Carnegie Institution for Science, Stanford, CA, USA and ¹⁰Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, USA

Correspondence

Benjamin Blonder
 Email: bblonder@gmail.com

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Abstract

1. The network of minor veins of angiosperm leaves may include loops (reticulation). Variation in network architecture has been hypothesized to have hydraulic and also structural and defensive functions.
2. We measured venation network trait space in eight dimensions for 136 biomass-dominant angiosperm tree species along a 3,300 m elevation gradient in south-eastern Peru. We then examined the relative importance of multiple ecological and evolutionary predictors of reticulation.
3. Variation in minor venation network reticulation was constrained to three axes. These axes described reconnecting vs. branching veins, elongated vs. compact areoles compact vs. elongated and low vs. high-density veins. Variation in the first two axes was predicted by traits related to mechanical strength and secondary compounds, and in the third axis by site temperature.
4. *Synthesis*. Defensive and structural factors primarily explain variation in multiple axes of reticulation, with a smaller role for climate-linked factors. These results suggest that venation network reticulation may be determined more by species interactions than by hydraulic functions.

KEYWORDS

damage resilience, damage resistance, leaf performance, loop, redundancy, reticulation, trait space, tropical forest, venation network

1 | INTRODUCTION

Leaf function is important for determining plants' fitness across biotic and abiotic contexts. Venation mediates water and carbon fluxes (Brodrribb, Feild, & Jordan, 2007; Brodrribb, Feild, & Sack, 2010), may provide structural or defensive functions (Givnish, 1979; Méndez-Alonzo, Ewers, & Sack, 2013) and may influence whole-plant carbon construction cost (Sack & Scoffoni, 2013). The costs and the benefits of a leaf may be constrained by the architecture of the venation network (Blonder, Violle, Bentley, & Enquist, 2011; Brodrribb et al., 2007; Buckley, John, Scoffoni, & Sack, 2015; Sack & Scoffoni, 2013; Sack, Streeter, & Holbrook, 2004), which in turn maybe constrained by the evolution of novel venation phenotypes across clades (Brodrribb et al., 2010; Trivett & Pigg, 1996). As multiple functions map differently onto the same structure, not all function/cost axes can simultaneously be optimized by a network constrained to a planar geometry. For example, a network cannot simultaneously maximize efficiency and redundancy (Katifori, Szöllösi, & Magnasco, 2010). As a result, trade-offs may be necessary (Blonder et al., 2011; Katifori et al., 2010).

1.1 | Describing reticulation in minor venation networks

Venation networks vary widely in their geometry, with some that form extensive loops (closed interconnections of veins Roth-Nebelsick, Uhl, Mosbrugger, & Kerp, 2001) that enclose areoles and others that do not. This variation is reflected in the general term, "reticulation" (Roth-Nebelsick et al., 2001; Trivett & Pigg, 1996). As vein orders often smoothly transition into each other, we use "minor" to refer to the patterns' characteristic of the ultimate veins, although these patterns may include features created by higher order veins. Some leaves have areoles in their minor veins that are simple polygons, while others have freely ending veinlets (Ellis, Daly, & Hickey, 2009; von Ettingshausen, 1861). Reticulation patterns may be described by scale-dependent (with units) or scale-independent (dimensionless) statistics.

Scale-dependent reticulation patterns have been described by vein density, the length of veins per unit leaf area and by loopiness, the number of areoles per unit leaf area. Scale-independent reticulation patterns describe the shape of loops and other structures in the network (e.g. freely ending veinlets). Rapid evolution of minor venation across clades is also thought to be possible, consistent with functional roles of reticulation patterns (Blonder, Baldwin, Enquist, & Robichaux, 2016; Boyce et al., 2009; Givnish et al., 2005; Horn, Fisher, Tomlinson, Lewis, & Laubengayer, 2009).

Scale-dependent patterns in vein density have been shown to be predictive of transpiration and photosynthesis rates (Brodrribb et al., 2007), environmental change (de Boer, Eppinga, Wassen, & Dekker, 2012) and climate niches (Blonder & Enquist, 2014; Manze, 1967; Uhl & Mosbrugger, 1999). However, much less is known about the ecological significance of variation in scale-independent patterns of reticulation, about the drivers of this variation, or

about the evolutionary patterns and constraints underlying this variation. This is surprising, given the differences in reticulation readily observed across taxa, e.g. between *Ginkgo biloba* [maiden-hair tree], with no looping, and *Malus pumila* [orchard apple] with extensive looping.

1.2 | Functional hypotheses for reticulation

Empirical studies have shown that minor venation patterns reflect hydraulic functioning across environments (Blonder & Enquist, 2014; Blonder et al., 2017; Sack & Scoffoni, 2013). Higher vein density may occur in with warmer and drier abiotic conditions (Sack & Scoffoni, 2013). Sites with higher potential evapotranspiration or temperatures should select for species that achieve high carbon assimilation rates by transpiring either a high amount of water when water is temporarily abundant or that use the same amount of water more efficiently when water is not (Blonder, Violle, Bentley, & Enquist, 2014). Thus, higher vein density or water use efficiency should be associated with warmer environments (Blonder et al., 2014, 2016, 2017; Sack & Scoffoni, 2013; Uhl & Mosbrugger, 1999). As many scale-dependent reticulation metrics are necessarily correlated based on geometrical scaling considerations (Blonder, Violle, & Enquist, 2013; Carins Murphy, Jordan, & Brodrribb, 2016; Sack et al., 2012), warmer and less wet environments are expected to also have higher reticulation due to their direct impacts on vein density.

Reticulation may also mediate efficiency vs. redundancy trade-offs for leaf hydraulics. Theoretical models suggest that networks that only branch (no loops) provide the most efficient transport of such resources from a central point under constant conditions (Dodds, 2010; McKown, Cochard, & Sack, 2010; Price, Gilooly, Allen, Weitz, & Niklas, 2010; West, Brown, & Enquist, 1997), while networks that branch and also have loops provide alternate flow pathways that provide more resilience to fluctuating resource loads (Corson, 2010; Katifori et al., 2010; Nardini, Tyree, & Salleo, 2001; Price & Weitz, 2014; Sack, Dietrich, Streeter, Sanchez-Gomez, & Holbrook, 2008). Such fluctuating loads and damage could arise from the occurrence of sunflecks in shaded conditions (Givnish, 1979; Givnish et al., 2005; Zwieniecki, Melcher, Boyce, Sack, & Holbrook, 2002), drought stress and xylem cavitation (Brodrribb, Bienaimé, & Marmottant, 2016). Thus, reticulation could be associated with traits related to photosynthetic capacity and light environment.

Reticulation may also have multiple structural and defensive functions beyond these direct and indirect hydraulic functions (Sack & Scoffoni, 2013). Reticulation could increase damage resistance by offsetting other leaf anti-herbivore defence strategies (Roth-Nebelsick et al., 2001). More reticulation could provide higher damage resilience to herbivory or environmental stressors (e.g. wind-driven tearing) by providing alternate flow pathways that maintain hydraulic functioning (Sack et al., 2008). More reticulation could also provide more deterrence against chewing/cutting damage through increased mechanical strength and resistance to tearing (Choong et al., 1992; Wagner, 1979). Reticulation could also provide additional redundant pathways for latex flow, enabling successful

deployment of defence compounds after wounding (Agrawal & Konno, 2009). All of these strategies would provide an alternate solution offsetting investment in defence compounds. Thus, reticulation could be associated with traits related to secondary compound fractions (polyphenols, tannins, lignins) and toughness (force to punch or force to tear).

Reticulation could also directly provide mechanical strength to a leaf (Givnish, 1979; Givnish et al., 2005; Niinemets, Portsmouth, & Tobias, 2007; Sack & Frole, 2006), with loops providing reinforcing cross-linkages that increase stiffness and strength (Niklas, 1999; Read & Stokes, 2006) as well as reducing the potential for tearing and crack propagation (Vincent, 1982). Moreover, because it is more carbon efficient to have a single primary vein supporting a thin layer of lamina reinforced by reticulate veins than to have multiple primary veins supporting a thicker layer of lamina without minor vein reinforcements, thinner leaves should be mechanically supported by a single-large midvein and reticulate-veined lamina (Givnish, 1979). Such thin leaves are also found in the shade due to their higher light interception (Givnish, 1988). As a result, reticulation could be associated with variables related to leaf thickness, mechanical strength (force to punch and force to tear) and shaded light environment.

Venation networks also have construction costs, particularly due to this lignification of the veins (Mooney & Gulmon, 1982). Lignin-rich veins have a higher carbon cost for construction relative to other tissues (Lambers & Poorter, 1992) and also displace photosynthetic tissue, potentially reducing benefits per unit cost. The lignification of veins (or the presence of costly bundle sheath extensions) is variable across species and light levels (Ohtsuka, Sack, & Taneda, 2018), but in general, veins have higher construction costs than other leaf tissues. The contribution of minor veins to leaf construction cost remains controversial, but is potentially large (Blonder et al., 2011; Carins Murphy et al., 2016; John et al., 2017; Sack et al., 2013). Thus, reticulation could be associated with traits related to structural investment, including thickness, leaf mass per area, dry matter content and lignin concentration.

Finally, reticulation may also not have functional benefits due to the developmental constraints. Veins can complete development before leaf expansion ends (Sack & Scoffoni, 2013), such that cell expansion coordinates venation patterns (Carins Murphy, Jordan, & Brodribb, 2012; Jordan, Brodribb, Blackman, & Weston, 2013) and potentially also leaf area (Carins Murphy et al., 2016). Thus, variation in leaf form will also drive relationships between leaf shape, size and reticulation traits. For example, larger leaves may have fewer veins per unit area and potentially fewer loops as well (Blonder et al., 2013; Sack et al., 2012), while more elongated leaves may also cause more elongated areoles (Blonder et al., 2016). Thus, reticulation could be associated with leaf area and leaf aspect ratio.

1.3 | Evolutionary patterns of reticulation in angiosperms

There have been few studies pairing reticulation measurements with these potential predictors, limiting tests of these different functional

hypotheses. Previous studies using qualitative metrics of reticulation have focused on its origin across extant basal or extinct plant clades (Alvin & Chaloner, 1970; Hickey & Wolfe, 1975; Takhtajan, 1980; Trivett & Pigg, 1996). Quantitative data exist for a few hundred angiosperm species (Price & Weitz, 2014), while other quantitative data exist for focal subsets of monocots (Givnish et al., 2005; Horn et al., 2009). Similarly, there have been studies focusing on freely ending veinlets, but only for small numbers of species (Fiorin, Brodribb, & Anfodillo, 2016). Other intensive studies of loop topology have primarily examined mathematical questions, for example, Ronellenfitsch, Lasser, Daly, and Katifori (2015).

There also may be constraints on the evolution of reticulation. Qualitative reticulation traits like “open” and “closed” venation are often used to assign taxonomic position in plant systematics (Ellis et al., 2009), suggesting strong phylogenetic niche conservatism in network architecture. However, a contrasting viewpoint is provided by intraspecific data from *Arabidopsis thaliana*, where small changes in developmental processes or mutations in single genes can yield wide variation in network architecture (Carland, Defries, Cutler, & Nelson, 2015; Kang & Dengler, 2004; Steynen & Schultz, 2003). As a result, there remains a key opportunity to better quantify the taxonomic levels and clades in which reticulation shows the most variation.

1.4 | Present work

The aims of this study are to (1) quantitatively describe variation in reticulation, (2) test multiple ecological hypotheses for functions of reticulation and (3) examine evolutionary patterns and processes in reticulation. We explore several scale-dependent and scale-independent metrics for characterizing reticulation (Table 1) and then determine whether the above hypotheses are related to different functional traits or abiotic variables. Empirical data come from the dominant tree species occurring along a 3,300 m humid tropical forest elevation gradient in western Amazonia and the Andes (Blonder et al., 2017).

2 | MATERIALS AND METHODS

2.1 | Research site and sampling strategy

This study included 10 permanent 1-ha plots in the Departments of Cusco and Madre de Dios in southeastern Peru (Malhi et al., 2010; Table 2). Six of the plots are montane plots in the Kosñipata Valley of the Andes (elevation range 1,500–3,500 m a.s.l.), two are submontane plots located in the Pantiacolla front range of the Andes (range 600–900 m a.s.l.) and two are found in the Amazon lowlands in Tambopata National Park (range 200–225 m a.s.l.). Seasonal cloud immersion is common above 1,500 m asl elevation (Halladay, Malhi, & New, 2012). Plots were established in areas that have relatively homogeneous soil substrates and stand structure as well as minimal evidence of human disturbance (Girardin, Malhi, et al., 2014). All stems ≥ 10 cm diameter at breast height were tagged, sized and identified to species level.

TABLE 1 Summary of quantitative reticulation traits for the minor veins. Some traits are dimensional, that is, scale-dependent, while others are dimensionless, that is, scale-independent ratios. Example references that either defined or measured each metric are also given

Type	Trait name	Definition	Higher values indicate	Example reference
Scale-dependent	Vein density	Length of veins per unit leaf area	More veins	Brodribb et al. (2007)
Scale-dependent	Loopiness	Number of areoles per unit leaf area	More looping	Blonder et al. (2011)
Scale-independent	Areole loop index	Number of areoles per unit leaf area per squared vein density	More redundant pathways per vein	Blonder et al. (2013)
Scale-independent	Areole circularity ratio	Median of the distribution across areoles of 4π times the area divided by squared perimeter	Areoles with less infolding	Friel (2000)
Scale-independent	Areole elongation ratio	Median of the distribution across areoles of major axis length to minor axis length	Longer, more "stretched" areoles	Blonder et al. (2016)
Scale-independent	Minimum spanning tree ratio	Summed length of the minimum spanning tree connecting all vein segments divided by the summed length of all vein segments. The minimum spanning tree is defined as a subset of vein segments that maintains connectivity between all vein intersections but has less or no more total length than any other subset of vein segments.	More tree-like pathways	Price and Weitz (2014)
Scale-independent	Freely ending veinlet ratio	Number of vein segments that are only connected to other vein segments at one end divided by number of all vein segments	More non-redundant pathways per vein	Kang and Dengler (2004)
Scale-independent	Meshedness ratio	Number of loops in the network divided by the maximum possible number of loops given the number of vein intersections	Less tree-like pathways	Price and Weitz (2014)

TABLE 2 Summary of angiosperm branch collections at each site along the elevation gradient

Plot code	Latitude (°)	Longitude (°)	Elevation (m)	Mean annual temperature (°C)	Mean annual precipitation (mm)	No. of species sampled	No. of families sampled	No. of branches sampled
TAM-06	-12.8385	-69.296	215	24.4	1,900	22	13	82
TAM-05	-12.8309	-69.2705	223	24.4	1,900	25	16	91
PAN-02	-12.6495	-71.2626	595	23.0	2,366	12	10	55
PAN-03	-12.6383	-71.2744	859	21.9	2,835	14	10	59
SPD-02	-13.0491	-71.5365	1,494	18.8	5,302	23	17	92
SPD-01	-13.0475	-71.5423	1,713	17.4	5,302	26	21	114
TRU-04	-13.1055	-71.5893	2,719	13.5	2,318	15	11	95
ESP-01	-13.1751	-71.5948	2,868	13.1	1,560	15	11	107
WAY-01	-13.1908	-71.5874	3,045	11.8	1,560	13	9	78
ACJ-01	-13.1469	-71.6323	3,537	9.0	1,980	10	9	76

From April to November 2013, we measured plant traits of biomass-dominant tree species in these plots as part of the CHAMBASA (challenging attempt to measure biotic attributes along the slopes of the Andes) project. Sampling began at the

highest plots in April and moved to the lowest by November. This design may lead to some phenology biases in trait measurements but was necessary for logistical reasons. Based on data for the most recent census in each plot, we sampled species that

most contributed to plot basal area as a proxy for abundance. We aimed to sample the minimum number of species that contributed to 80% of basal area, although, in the diverse lowland forest plots, we only were able to sample species comprising 60%–70% of plot basal area. Within each species, 3–5 individual trees were chosen for climbing (five in upland sites and three in lowland sites). If three trees were not available in the chosen plot, we sampled additional individuals of the same species from an area immediately surrounding the plot. We sampled one sunlit canopy branch and one shaded (defined as occurring beneath other canopy layers) branch where possible, each at least 1 cm diameter, from each tree. From each branch, we measured five leaves from simple-leaved species or five individual leaflets from compound-leaved species (both referred to as “leaf” below) for trait measurements.

All analyses were conducted on the same leaf (including reticulation measurements) except when other analyses were destructive, in which case, a replicate leaf from the same branch was used. Data from the campaign were accessed from the *GEMTraits* database and R package (Shenkin et al., 2017) and are archived on Dryad (Blonder et al., 2018).

2.2 | Predictor variables (traits)

We measured a wide range of functional traits to determine their predictive capacity for minor vein reticulation. The following four traits were measured on the same leaf for which reticulation response variables were later measured.

Leaf dry matter content (LDMC; g/g) was approximated as dry mass divided by fresh mass. Lamina thickness (mm) was measured at midpoint of lamina avoiding primary and secondary veins with a micrometer (Tresna). Lamina area (cm²) was calculated as the projected surface area of the whole leaf, including all leaflets if compound, measured at 300 pixels per inch resolution via digital scanner (Canon LiDE 110) and calculated from thresholded images in ImageJ. Leaf mass per area ratio (LMA; g/m²) was calculated as leaf dry mass divided by fresh leaf lamina area, not including the petiole or rachis. Light saturated maximum photosynthetic rate per unit area (A_{\max} ; $\mu\text{mol m}^{-2} \text{s}^{-1}$) was obtained with a portable photosynthesis system (6400XT; LiCor) during morning times under conditions of ambient humidity, saturating light (1,200–1,500 $\mu\text{mol m}^{-2} \text{s}^{-1}$), saturating [CO₂] (1,000–1,200 ppm) and ambient site temperature (16–26° interquartile range).

We also measured some traits on a different leaf from a branch of the same tree experiencing a similar light environment because of the destructive nature of some of these measurements. Force to punch (kN/m) was measured as the normalized force required to puncture the lamina, measured on fresh leaves with a penetrometer built according to the specifications of Onoda, Schieving, and Anten (2008), following the measurement guidelines of Pérez-Harguindeguy et al. (2013). Force to tear (kN/m) was measured as the normalized force required to tear the lamina, measured on fresh leaves with an apparatus designed by Hendry

and Grime (1993), following the measurement guidelines of Pérez-Harguindeguy et al. (2013).

Carbon isotope ratio ($\delta^{13}\text{C}$ —the ratio of ¹³C to ¹²C relative to Vienna PeeDee Belemnite [VPDB] per mil [‰]), used as a proxy for water use efficiency; Farquhar, Ehleringer, & Hubick, 1989) was measured by continuous flow gas ratio mass spectrometry. Samples were combusted using an elemental analyser (Costech) coupled to the mass spectrometer (Finnigan Delta PlusXL). Standardization is based on acetanilide for elemental concentration, NBS-22 and USGS-24 for $\delta^{13}\text{C}$.

Phenol and condensed tannin concentrations (mg) were determined as the per-dry mass concentration of phenol-containing compounds of molecular weight <500 and >500 respectively. Branches of mature leaves were sealed in polyethylene bags in the field to maintain moisture, stored on ice in coolers and transported to a local site for processing within 3 hr. Small leaf discs (at least 30 per leaf) were immediately taken from c. 6–12 randomly selected and cleaned leaves and transferred to –80°C cryogenic shipping containers. Frozen leaf disks were ground in 95% methanol on a high throughput tissue homogenizer. A portion of the solution was further diluted and incubated on an orbital shaker at room temperature (15–18°C) in the dark for 48 hr to ensure proper phenol extraction. A second portion of the solution was further diluted in a 2 ml centrifuge tube containing 10 mg polyvinylpyrrolidone (PVP) and incubated on ice for 30 min after vortexing. Following centrifugation, 75% of the supernatant was placed in a new centrifuge tube containing another 10 mg PVP for a second precipitation step. The total phenol concentration in solution was determined colorimetrically using the Folin–Ciocalteu method. Phenol concentrations were measured in gallic acid equivalents relative to an eight-point gallic acid standard curve. The tannin concentration was determined as the difference between total phenols and phenols in solution after PVP precipitation. Methods are described fully by Makkar, Blümmel, Borowy, and Becker (1993); Ainsworth and Gillespie (2007).

Lignin concentration (100 × g/g) was determined as the per-dry mass concentration of fibres resistant to strong acids, determined in 0.5 g dry ground leaf tissue through using sequential digestion of increasing acidity in a fibre analyser (Ankom Technology, Macedon, NY, USA). Methods follow Van Soest (1994).

Leaf aspect ratio (dimensionless) was calculated as leaf lamina length (not including petiole or rachis) divided by maximum leaf width, measured from a digital photograph in ImageJ. In the case of compound leaves, leaflets were used; in the case of palmate simple leaves, width was measured as lobe width.

2.3 | Predictor variables (climate)

Climate data were obtained using quality-controlled and gap-filled data from weather stations colocated with plots. Data were obtained from site-specific papers on TAM05 and TAM06 (Malhi et al., 2010), SPD01 and SPD02 (Huaraca Huasco et al., 2014), TRU04 (Girardin et al., 2013), ESP01 and WAY01 (Girardin, Silva-Espejo, et al., 2014) and ACJ01 (Oliveras et al., 2014), while climate data from PAN02

and PAN03 were collected in 2013–2014 and were processed using the same techniques described for the other sites. Data from ACJ01, PAN02, PAN03 and TRU04 were available since 2012 or 2013 and since 2009 for all others. Mean annual temperature (MAT; °C) was calculated as the mean of daily average temperatures. Annual precipitation (mm/year) was measured by a weather station. Values are reported in Table 2.

2.4 | Response variables (vein traits)

We chemically cleared, imaged and hand-traced a leaf venation network for one leaf from a sampled branch of a sunlit and (where possible) shaded light microenvironment from each tree, following standard protocol for dried leaves (Pérez-Harguindeguy et al., 2013). Images were made at a spatial resolution of 179 pixels/mm and avoided major veins whenever possible. We traced an average of $36 \pm 23 \text{ mm}^2$ of leaf area in order to capture a large number of areoles in each image ($n = 306 \pm 305 \text{ SD}$). These images and tracing methods are fully described in Blonder et al. (2017). This large image extent was necessary to robustly estimate reticulation traits, and therefore, necessarily included a small number of non-minor veins. We treated these equivalently to minor veins in tracing, as they often constituted integral boundaries of minor vein areoles, whose properties were of interest in this study.

We then calculated venation reticulation traits (Table 1) from these tracings, using MATLAB code available at https://github.com/bblonder/venation_programs/. Areoles that did not appear closed (i.e. partially lying outside the image) were not included in the analysis. We also added 1.0 to values of meshedness to make all values positive to permit log transformation in analyses. We corrected the two-dimensional reticulation traits (vein density, vein loopiness) for bias due to shrinkage of dried leaf samples. Shrinkage corrections were not required for dimensionless traits. We estimated the fraction of leaf area that was lost upon drying (S ; dimensionless). We calibrated a regression model for shrinkage using existing data for temperate and tropical species provided by Blonder et al. (2012) using both LMA and mean annual temperature (MAT) as predictors available in this dataset. The fitted model had coefficients $S = 0.3496 - 0.0005162 \text{ LMA} - 0.008316 \text{ MAT}$ ($R^2 = .36$, $df = 258$, $\text{RMSE} = 0.12$). We applied this model to each leaf in the current dataset to estimate S , which varied around a mean of $0.15 \pm 0.04 \text{ SD}$. We used these values to rescale vein density and loopiness values (with units per mm or per mm^2 respectively) by a factor of $\sqrt{(1 - S)}$ or $(1 - S)$, following Blonder et al. (2017).

2.5 | Phylogenetic analysis

To examine evolutionary patterns of reticulation, we built a phylogenetic tree for all species for which reticulation measurements were available, using the *phylocom* function in *phylocom* 4.2 (Blonder et al., 2017). Clades were assigned using the “R20120829” plant megatree. Approximate crown ages were assigned via *phylocom*'s

bladj function, with constraints for internal nodes provided by Gastauer and Meira-Neto (2013).

2.6 | Statistical analysis

We conducted all analyses in the R statistical environment (<http://www.r-project.org>). We conducted analyses for all angiosperms and also for all angiosperms excluding palms (Arecaceae) because of the divergent morphology of this family.

To determine the overall reticulation trait space, we log transformed and scaled all reticulation traits, then made a principal components analysis. Based on the variance explained by each principal component, we then used the scores along the leading components as orthogonal reticulation axes (PC1, PC2 and PC3). These transformed variables and scores also were used for all subsequent analyses.

To examine evidence for phylogenetic niche conservatism, we first performed a variance partitioning analysis across taxonomic scales using standard mixed modelling methods (Messier, McGill, & Lechowicz, 2010). We also carried out an analysis of Blomberg's K , a metric of phylogenetic signal (Blomberg, Garland, Ives, & Crespi, 2003), within the *phytools* R package. All other phylogenetic analyses were made with the *ape* package. To examine evidence for directional shifts in reticulation traits over evolutionary time, we also performed a regression analysis of family age and family mean values of reticulation principal components. To examine variation in reticulation due to light microenvironment, we determined whether the difference between mean sun and shade leaf values, calculated for each species-site combination, was significantly different from zero according to a t test.

To separate the independent effects of environment and traits on the reticulation trait space, we analysed a series of Gaussian family generalized linear mixed models within a Bayesian framework for each reticulation principal component. This approach allows for hierarchical grouping of predictor data and phylogenetic non-independence of data.

Before carrying out this analysis, we gap filled the predictor data. Only 2.3% of the data were missing across all variables (Figure S1), but 32.3% of cases had at least one missing observation of at least one predictor. As deleting all incomplete observations would have vastly reduced the sample size and also have biased the analysis, we gap filled missing values in the matrix of predictor variables. We used multiple imputations via chained equations with predictive mean matching using the “mice” R package, which uses the distribution of observed data to predict the values of unobserved data. When data are missing at random, as is true here, this approach is asymptotically unbiased and asymptotically efficient (Buuren & Groothuis-Oudshoorn, 2011). We generated 10 independent imputations of the full dataset to account for uncertainty in the observed data. We then log transformed a subset of highly skewed predictor variables: (LMA, lamina area, thickness, force to puncture, force to tear, leaf aspect ratio) and then recentred and rescaled all predictor variables to put them on common scales.

Mixed models were constructed treating all of the trait and climate predictors as independent fixed effects because collinearity among predictors was low (mean Pearson's rho among all predictor variables, 0.04 ± 0.24 SD). These models incorporated a random effect of site (capturing nesting of climate measurements within sites) as a diagonal variance matrix and a random effect of species (capturing the nesting of multiple branches for each species). We also incorporated a random effect of evolutionary distance (capturing the relatedness of species) using an inverted phylogenetic covariance matrix. Prior distributions for each effect were chosen as inverse gamma with location and scale parameters set to 0.01 (Gelman, 2006). Models were implemented using a Markov chain Monte Carlo algorithm in the *MCMCglmm* R package (Hadfield, 2010). Each model was run for a burn-in period of 100,000 iterations, after which posterior distributions were characterized by taking 1,000 samples, each 100 iterations apart in the chain. Chain mixing was sufficient in all cases. We then repeated the modelling exercise for each imputation of the dataset and generated final posterior distributions by concatenating posterior samples across all models. To facilitate interpretation, approximate *p*-values for each fixed effect *a* were calculated as $p = 2 \times \min[P(a > 0), P(a < 0)]$, with statistical significance inferred at $p < .05$.

Because predictor variables were rescaled before analysis, the distribution of these fixed effects can be interpreted as effect sizes

(SD/SD). That is, a coefficient with value +1 indicates that a 1 standard deviation increase in the predictor variable directly causes a 1 standard deviation increase in the response variable, after accounting for any other predictor variable, and for any effects of shared evolutionary history among species, or of hierarchical structure in the data.

3 | RESULTS

We obtained reticulation traits and paired predictor variables for 849 branches from 136 angiosperm species (Table 2), of which 12 were from palm taxa. Most species were sampled only at a single site, with only eight species sampled in more than two plots (Blonder et al., 2017).

3.1 | Reticulation trait space

We found wide variation in every reticulation trait, with variation spanning up to two orders of magnitude across all taxa (Table 3). Two of the most variable traits were vein loopiness (90% quantile range, 0.8–54.1 per mm²) and freely ending veinlet ratio (90% quantile range, 0.086–0.43). Removing palms from this analysis had a negligible effect on trait ranges (Table S1).

TABLE 3 Ranges of variation for all unscaled reticulation traits and ecological predictors

Type	Variable	Units	5% quantile	50% quantile	95% quantile
Predictor (climate)	Light environment	—	Shade	Sun	Sun
Predictor (climate)	Mean annual precipitation	mm	1,560	1,980	5,302
Predictor (climate)	Mean annual temperature	°C	9.0	17.4	24.4
Predictor (trait)	Amax	nmol g s	0.849	7.607	18.94
Predictor (trait)	δ ¹³ C	per mil	-33.4	-30.3	-26.83
Predictor (trait)	Force to punch	kN/m	0.295	0.875	2.51
Predictor (trait)	Force to tear	kN/m	0.379	0.722	4.88
Predictor (trait)	Lamina area	cm ²	9.354	58.224	632.01
Predictor (trait)	Lamina thickness	mm	0.141	0.264	0.61
Predictor (trait)	LDMC	—	0.24	0.425	0.69
Predictor (trait)	Leaf aspect ratio	—	1.626	2.456	4.21
Predictor (trait)	Lignin	mg/g	9.064	23.76	39.55
Predictor (trait)	LMA	g/m ²	64.39	106.9	189.11
Predictor (trait)	Phenols	mg/g	0	88.145	166.01
Predictor (trait)	Tannins	100 g/g	0	38.52	83.55
Response (trait)	Areole circularity ratio	—	0.623	0.754	0.86
Response (trait)	Areole elongation ratio	—	1.373	1.502	1.77
Response (trait)	Areole loop index	—	0.023	0.074	0.15
Response (trait)	Freely ending veinlet ratio	—	0.086	0.212	0.43
Response (trait)	Meshedness ratio	—	-0.019	0.051	0.11
Response (trait)	Minimum spanning tree ratio	—	0.603	0.68	0.86
Response (trait)	Vein density	per mm	5.342	11.221	18.69
Response (trait)	Vein loopiness	per mm ²	0.882	9.154	54.06

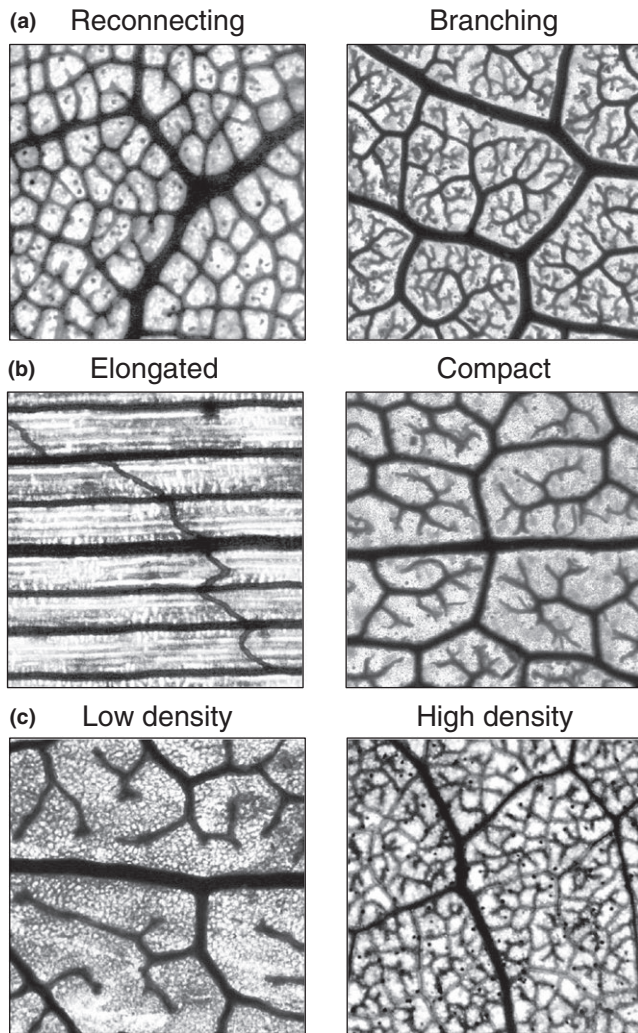


FIGURE 1 Illustration of major axes of variation in reticulation traits along low (left) and high (right) values of principal component axes. (a) Higher values of PC1 indicate networks with more branching for a given amount of reconnecting. (b) Higher values of PC2 indicate networks with more compact areoles. (c) Higher values of PC3 indicate networks with higher vein density

A small number of orthogonal axes characterized these reticulation traits (Figure 1). Three principal components (PC1–PC3) had variance fractions above 10%; these components explained 65.7%, 18.8% and 10.9% of the variation in the data respectively (additional components explained only <2% each; Figure 2). Higher values along PC1 described more branching and less reconnecting networks, with higher freely ending veinlet ratios and minimum spanning tree ratios. Higher values along PC2 described more compact, more circular and less elongated areoles. Higher values along PC3 described higher vein density and higher loopiness as well as lower meshedness. When palms were excluded from this analysis, the overall shape of the trait space and variance fractions were largely unchanged (Figure S2).

3.2 | Patterns within clades

Species were not uniformly distributed within the reticulation trait space. While species were evenly spread along PC1 (skewness 0.65) and PC3 (skewness 0.28), variation along PC2 was uneven (skewness –5.9). PC2 was characterized by a small number of species with very high-areole elongation indices, generally in *Arecaceae* (palms). Individual families sometimes occupied distinct subsets of the overall reticulation trait space, for example, high loopiness within the *Urticaceae*, and high freely ending veinlet ratio within the *Clusiaceae* (Figure 3).

Reticulation traits showed strong variation in their level of phylogenetic niche conservatism (Figure 4a). A variance partitioning analysis indicated that some traits showed more than 50% of variation summed at the order or family level (areole elongation ratio, areole circularity ratio, vein density, vein loopiness and PC2). In contrast, other traits showed more than 30% of variation summed at the interspecific or intraspecific level (meshedness ratio, PC3, minimum spanning tree ratio, freely ending veinlet ratio, areole loop index). Thus, some aspects of the network are evolutionary labile (those primarily relating to branching patterns), while others are not (those primarily related to areole shape and scale). An analysis of phylogenetic signal showed that PC1 had a value of Blomberg's $K = 0.92$; PC2, $K = 1.2$; PC3, $K = 0.44$. Thus, PC2, reflective of areole shape, showed conservatism ($K > 1$) while PC1 and PC3, reflective of branching and scale, showed lability ($K < 1$). However, some of the phylogenetic signal in these patterns was due to the inclusion of palms. When these taxa were removed from the analysis, nearly all of the order- and family-scale variation in PC2, areole elongation ratio and areole circularity index were instead partitioned at genus scale (Figure S3). All other patterns remained consistent. Additionally, traits were observed to be much more evolutionary labile in non-palm taxa. PC1 had $K = 0.59$; PC2, $K = 0.44$; PC3, $K = 0.52$. Patterns of trait clustering are apparent on a phylogenetic tree showing species-mean trait values (Figure 4b).

We found that families with younger crown ages had lower values of PC1 and higher values of PC3, which was also reflected in higher values of areole circularity ratio, areole loop index, vein density and loopiness (Figure S4). However, variation in reticulation traits within families was high, leading to a weak overall trend for both all angiosperms and non-palm taxa.

3.3 | Patterns across environment

There were no effects of light microenvironment on reticulation principal components, except for PC3 ($p = .049$; Figure 5). Most individual reticulation traits showed a similar absence of pattern, with the exception of the two scale-dependent traits (vein density and vein loopiness) and areole loop index, for which sun leaves showed slightly higher trait values. When restricted to only non-palm taxa, results were largely consistent (Figure S5). Thus, scale-independent

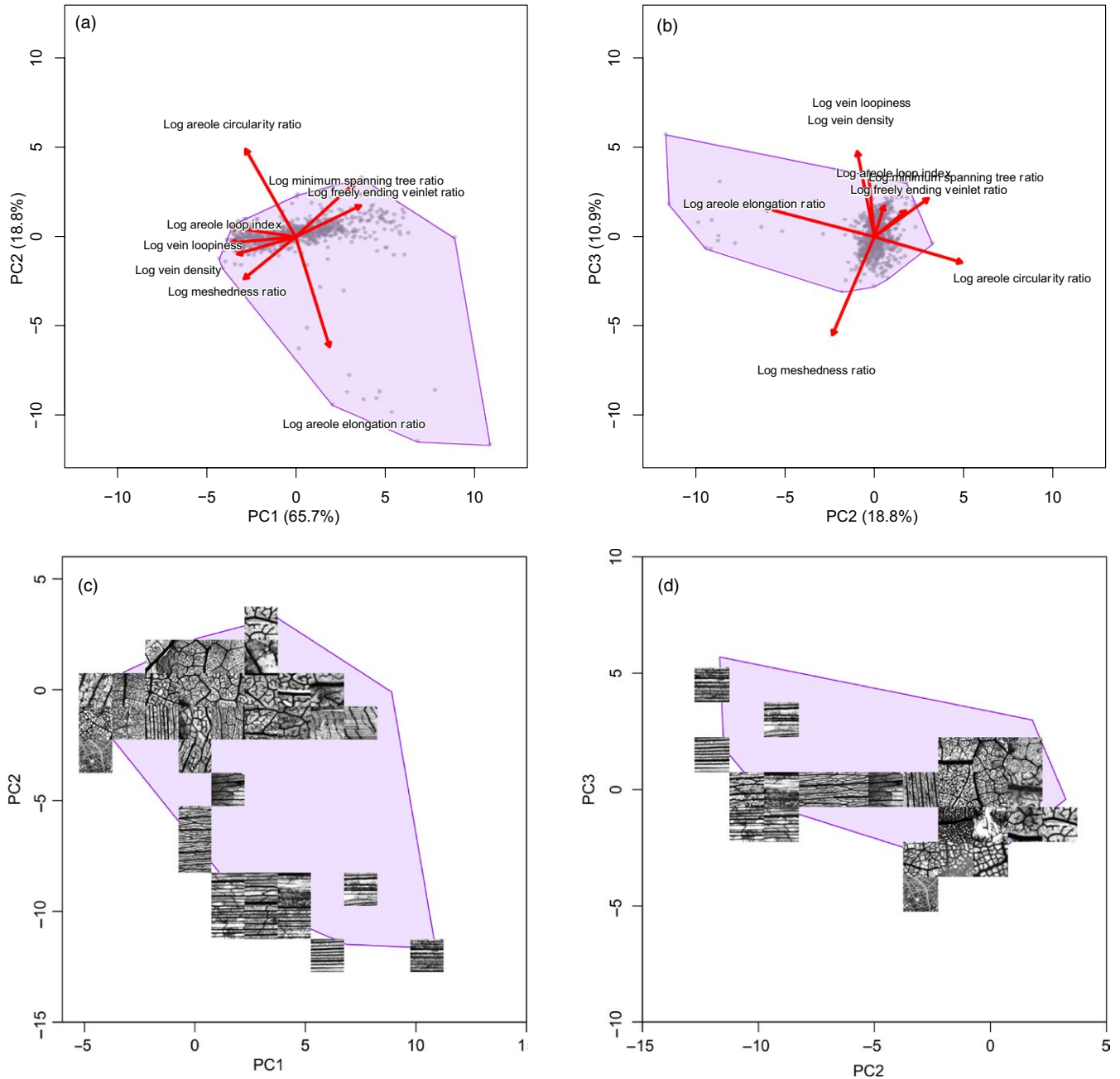


FIGURE 2 Minor vein reticulation trait space, as seen via principal components analysis of reticulation traits for the angiosperms. (a, b) Biplot of principal components 1 vs. 2 and 2 vs. 3. Individual leaves are shown as gray dots; axes as red arrows, with the overall trait space boundaries delineated via a purple convex hull. Labels indicate % variance explained by each axis. (c, d) Examples of venation networks corresponding to the same biplots. Grid cells show a randomly chosen venation network from a leaf with principal component scores within the grid ranges. The size of each image is 2.79×2.79 mm [Colour figure can be viewed at wileyonlinelibrary.com]

reticulation traits appear to be invariant to light environment, while scale-dependent traits were weakly dependent.

There were strong direct relationships between reticulation traits and elevation when median values were analysed at plot level. Higher elevation plots were associated with higher PC1 and PC2 and lower PC3 (all $R^2 > .46$) which was in turn driven by associations with lower areole loop index, higher minimum spanning tree ratio, higher freely ending veinlet ratio, lower vein density and lower vein loopiness (all $R^2 > .58$; Figure 6). As such, there was a shift towards

leaves with more branched veins, more elongated areoles and lower vein densities at high elevations. These results were largely invariant when palms were excluded from the analysis (Figure S6).

3.4 | Predictors of reticulation

To better interpret these strong elevation and phylogenetic patterns, we used a generalized linear mixed model to interpret the climate and trait predictors of reticulation. After accounting for phylogenetic correlation

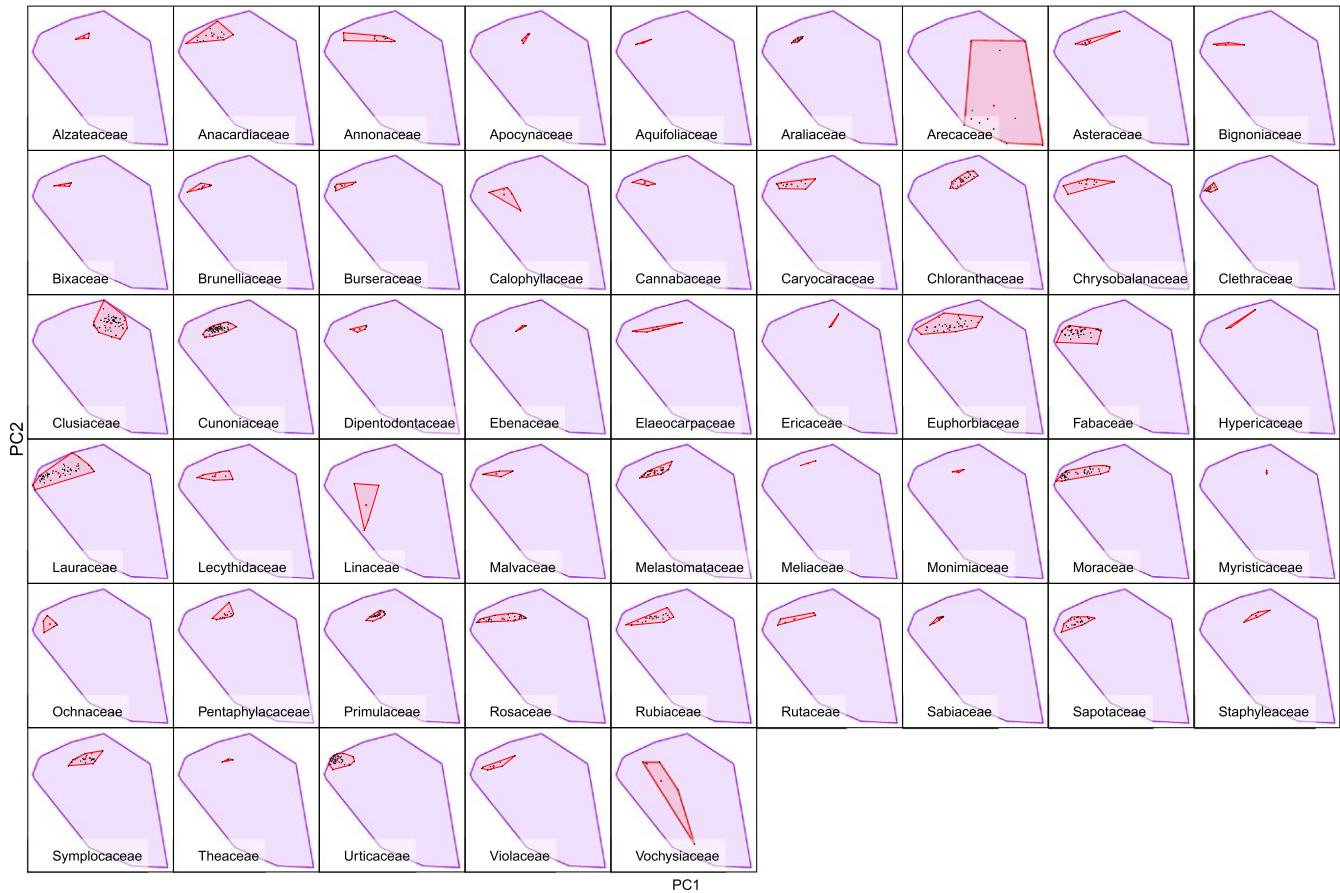


FIGURE 3 Variations in reticulation traits were grouped by family. The overall reticulation trait space for the first two principal components is shown in purple. Each family's distribution is shown via black points indicating individual leaves and red point their centroid and with red convex polygon outline [Colour figure can be viewed at wileyonlinelibrary.com]

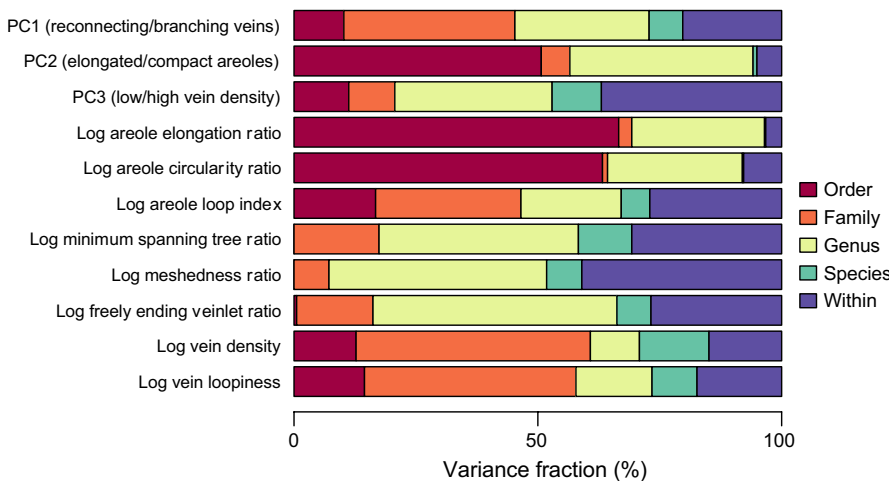


FIGURE 4 (a) Hierarchical variance partitioning of reticulation traits among taxonomic scales. (b) Distribution of reticulation principal components across the phylogenetic tree. Tips are labelled with circles whose colour indicates mean values for PC1, PC2 and PC3 [Colour figure can be viewed at wileyonlinelibrary.com]

structure, we found that different sets of predictors were associated with each reticulation axis (Figure 7). Higher values of PC1 were associated with lower values of lignins, phenols and LDMC, consistent with higher reticulation offsetting investment in secondary defence compounds and overall leaf structure. Higher values of PC2 were associated with lower values of force to punch, also consistent with higher reticulation

offsetting investments in mechanical strength. Higher values of PC3 were associated with higher mean annual temperature, consistent with transpiration supply-demand matching. No other predictors were significantly associated with any reticulation axis. When restricted to non-palm taxa, results were qualitatively unchanged, except that higher values of PC2 were also associated with lower tannins (Figure S7).

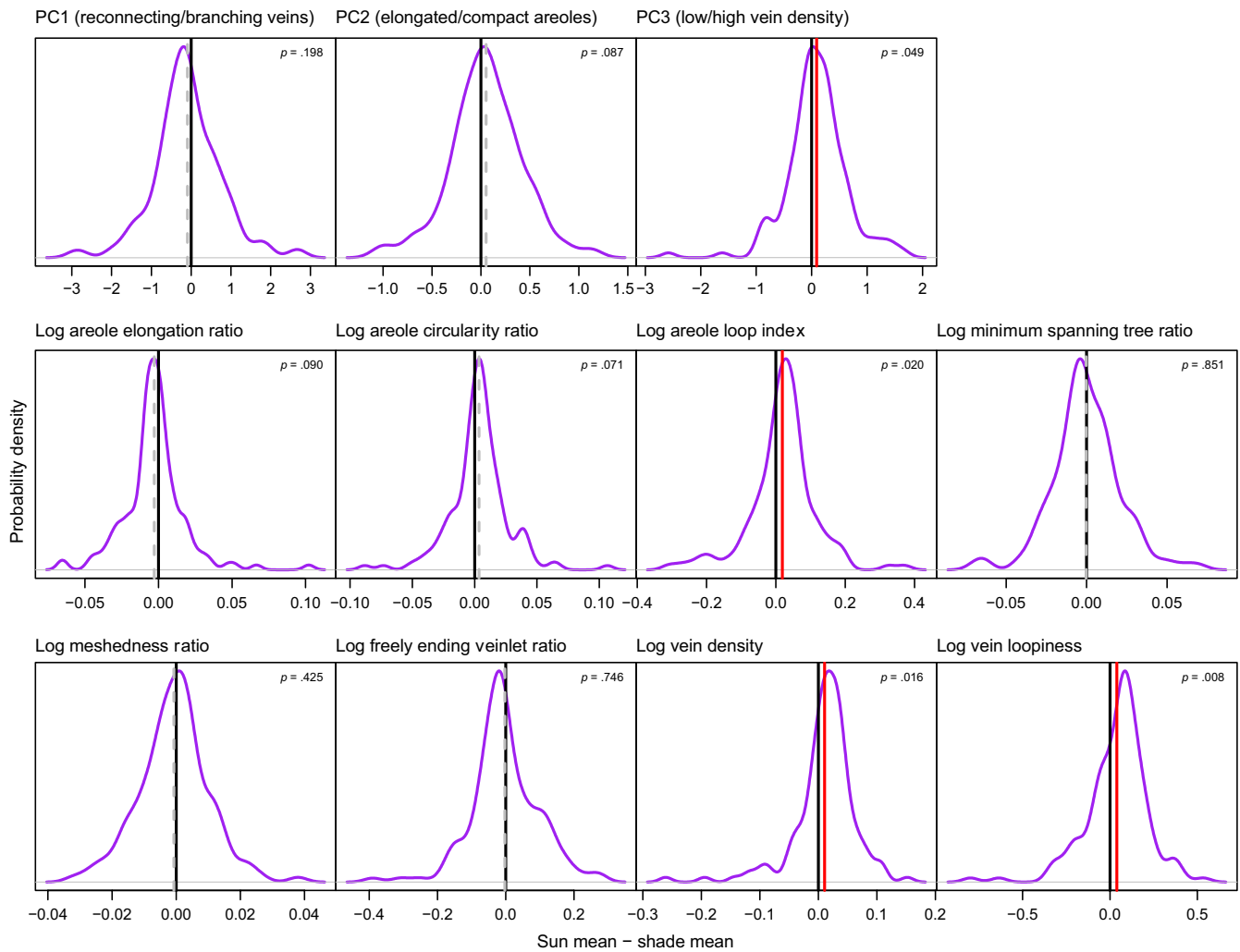


FIGURE 5 Effect of light availability on reticulation traits. Purple lines indicate the distribution of sun mean minus shade mean values within each species, across all species–sites combinations for the whole dataset. The null expectation of zero is shown as a black line. The mean of the observed distribution is shown as a solid red vertical line if significantly different from zero and dashed grey if not [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

While a large body of work has identified functions for leaf venation related to hydraulics (Brodribb et al., 2010, 2016; de Boer et al., 2012; Sack & Scoffoni, 2013), our results also suggest a key role for structural and defensive functions of venation reticulation (Sack & Scoffoni, 2013). We found that PC1 (reconnecting vs. branching) reflected lower investment in defence compounds and PC2 (elongated vs. compact areoles) reflected lower investment in structure. In contrast, PC3 (low vs. high density veins) reflected higher site temperature, consistent with hydraulic functions. Indeed, an earlier study along this elevation gradient showed that vein density responds strongly to temperature ($R^2 = .5$ at community-mean level; Blonder et al., 2017). However, the present study has now demonstrated that this finding is only a partial characterization for the phenotypic variation occurring along this elevation gradient. Other non-hydraulic aspects of network architecture, and consequently other non-climate predictors, play a more important role and also

have very strong community-weighted mean trait–environment relationships (e.g. $R^2 = .7$ for PC1 vs. elevation). A more complete understanding of network architecture may require parsing trade-offs amongst these multiple functions (de Boer et al., 2016), that is, the amount of hydraulic performance that can be sacrificed to enhance structural or defence performance.

There were only weak differences in traits between sunlit and shaded environments, especially for the scale-independent traits. It is possible that this pattern was driven by low within-species replication (an average of 3.8 ± 2.8 SD sun and 2.8 ± 2.1 SD shade branches per species). However, the lack of effects of consistent directionality suggests that the absence of a pattern is biologically real. One possible explanation is that vein patterning is set early during leaf development, such that only scale-dependent traits can vary plastically via variation in cell expansion. This perspective is consistent with extant knowledge for vascular development and leaf cellular physiology (Sack & Scoffoni, 2013). However, we did not find consistent support for a link between leaf elongation and areole elongation

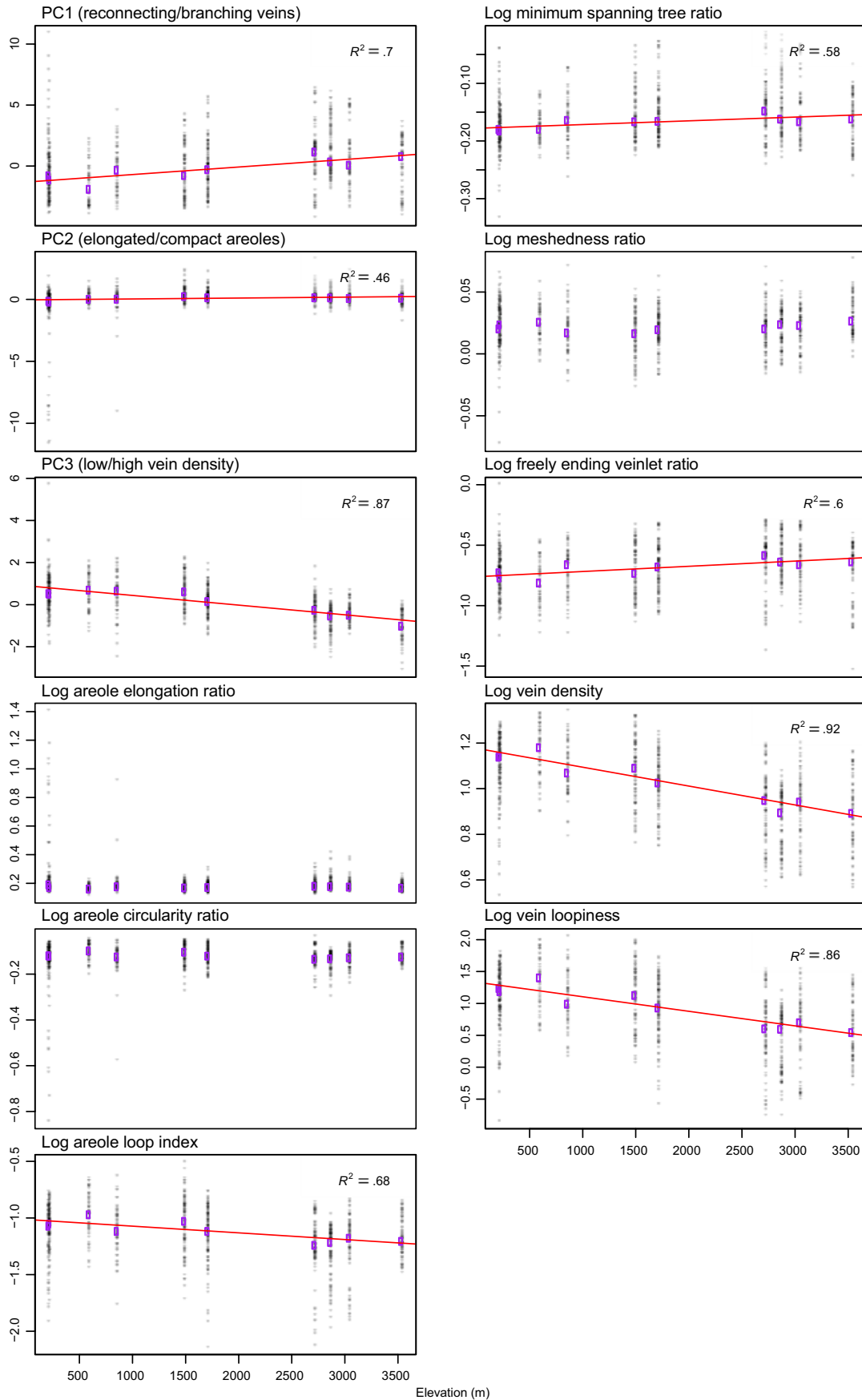


FIGURE 6 Elevation trends in principal component and individual reticulation traits for the entire dataset. Grey points represent individual leaves; open purple circle site medians. Regression lines (red) for site-median data are drawn when statistically significant [Colour figure can be viewed at wileyonlinelibrary.com]

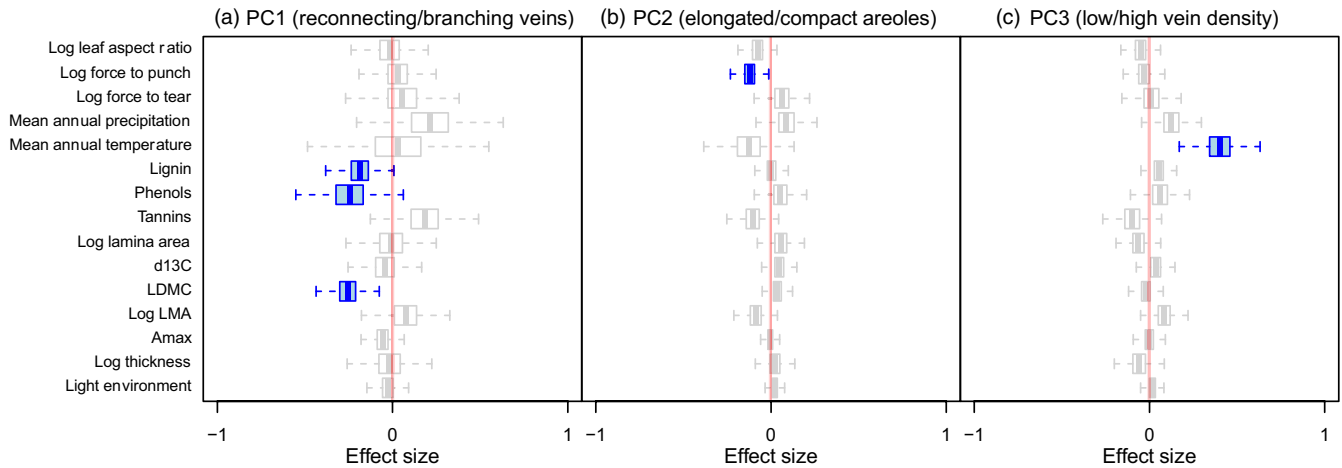


FIGURE 7 Relationships between reticulation trait axes and multiple trait and climate predictor variables. Boxes indicate the posterior distribution of fixed effects for Bayesian GLMM models. The analysis is scaled such that a value of +1 indicates that a 1 standard deviation (SD) change in a predictor results in a 1 standard deviation (SD) change in the reticulation principal component, after accounting for all phylogenetic effects and hierarchical structure in the data. Distributions are concatenated across 10 resampled imputations of the dataset. Significant fixed effects are highlighted in dark blue and otherwise shown in light grey. Estimates are shown for (a) PC1, (b) PC2 and (c) PC3 [Colour figure can be viewed at wileyonlinelibrary.com]

in this dataset, which would also be expected under such a cellular expansion process. This pattern has only been shown in a small clade of Hawaiian species (Blonder et al., 2016). It may be that leaf size and shape and venation patterns can become decoupled via multiple developmental processes.

Additionally, we found no evidence that higher reticulation leads to lower maximum per-mass photosynthesis rates, as might have been expected by an efficiency vs. redundancy trade-off (Corson, 2010; Katifori et al., 2010). This result probably arises because the increase in hydraulic conductance from increasing minor vein density is larger than the increase in cost from increasing the number of redundant veins and (thus reticulation traits like loopiness). It may be that the costs of redundant veins become more important only when considering larger-scale loops in the network, for example, in primary and secondary veins.

Herbivory may also directly influence reticulation traits. Previous work has suggested that reticulation can enhance damage resistance. Leaf venation patterns have been demonstrated to influence leaf mechanical strength (Enrico, Díaz, Westoby, & Rice, 2016; Roth-Nebelsick et al., 2001; Zhang, Hongo, & Akimoto, 2004), which in turn are negatively related to herbivory (Coley, 1983; Grubb et al., 2008; Nichols-Orians & Schultz, 1990; Pérez-Harguindeguy et al., 2003). Additionally, reticulation can enhance damage resilience, as demonstrated by experimental wounding of species with or without loops in their veins (Katifori et al., 2010). However, direct measurements of herbivore attack and success rates would be needed to determine whether reticulation axes are directly linked to performance in contemporary biotic contexts.

4.1 | Quantifying variation in reticulation

Our results also help clarify the dimensionality of reticulation trait space. We found that three axes captured more than 95% of the

variation for the 50 families on this Andes–Amazon transect. These axes also have a clear interpretation: the first described a continuum of scale-independent branching, the second axis a continuum of scale-independent areole compactness and the third axis the scale-dependent density of the network. While the importance of network scale and minor vein density (PC3) in plant functioning and community assembly has been widely acknowledged (e.g. Sack & Scoffoni, 2013), we found that scale-independent axes of reconnecting/branching veins (PC1) and elongated/compact areoles (PC2) showed more variation in this dataset. Palms, which are dominant in several sites, occupy an extreme set of values along these axes. However, the exclusion of palms did not qualitatively change our findings except those based on evolutionary position.

Variation generally was phylogenetically conserved at the genus level and above, but also varied consistently at community scale along the elevation gradient. This suggests that reticulation traits drive species sorting into local communities across environments and/or that historical biogeographic processes have led to the radiation of clades with certain reticulation traits only in some regions.

We also found only limited evidence for directional shifts in reticulation traits over evolutionary time, as most family-age vs. reticulation trait relationships were not statistically significant. While increases in vein density have been observed in more recently derived clades within the angiosperms (Boyce et al., 2009), reticulation metrics showed weak patterns. Thus, it appears that high values of reticulation traits are possible in both new and old angiosperm clades.

The strong niche conservatism of reticulation is surprising, given the apparent ease of evolution in these traits. The transition between purely branching and reconnecting venation is apparently not difficult (Takhtajan, 1980) and has occurred independently in both directions many times over macroevolutionary time (Wagner,

1979). Rapid transitions in reticulation are seen via qualitative metrics within the monocots (Givnish et al., 2005) and with quantitative traits within the Hawaiian silversword alliance (Asteraceae; Carlquist, 1959; Blonder et al., 2016). Transitions may occur quickly because reticulation can be under simple genetic control. In *A. thaliana*, knockouts of single genes are sufficient to shift from a wild-type reticulate pattern to an open pattern (Carland & Nelson, 2004; Steynen & Schultz, 2003). Similarly, studies of vascular network formation in the same species show that small developmental changes in auxin gradients and canalization can lead to dramatically different reticulation trait values (Berleth, Mattsson, & Hardtke, 2000). We do not yet understand how to reconcile these observations with this study.

There are likely to be additional axes required to fully characterize reticulation trait space. The traits we surveyed are focused only on the minor veins and do not contain information related to branching angles and diameters, or to the nesting of loops across vein orders, which are also important components of transportation network architecture. Loops in secondary or tertiary veins may show different patterns than the minor veins. Potential benefits include reinforcement of leaf edges against tearing (Niklas, 1999) or tolerance of large-scale hydraulic failure (Sack et al., 2008). Potential carbon costs arise because of the large mass investment in major veins (John et al., 2017). Such variation could be measured via recently proposed hierarchical metrics that quantify how areoles are nested within other areoles (Katifori & Magnasco, 2012; Mileyko, Edelsbrunner, Price, & Weitz, 2012; Ronellenfisch et al., 2015).

There have been many hypotheses for the functions of leaf venation (Sack & Scoffoni, 2013). This study now demonstrates that multiple hypotheses are supported: our data show that venation can have structural and defensive functions as well as hydraulic functions. Thus, patterns of reticulation may indicate the outcome of selection for multiple functions. However, patterns of reticulation still remain unmeasured for the vast majority of plant taxa, despite the importance of venation networks in mediating plant carbon uptake and water loss worldwide. Systematic studies of reticulation across the evolutionary tree will further unravel the drivers and consequences of leaf venation network architecture.

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AUTHORS' CONTRIBUTIONS

Y.M. conceived and received funding for the field campaign; N.S., L.P.B., A.S. and T.E.B.E. led the implementation of the field campaign; G.P.A., S.D., B.J.E. and Y.M. designed the field campaign; B.B., N.S., Y.V.T. and P.O.C.P. contributed venation analyses; B.B. led the statistical analysis and writing. All authors contributed to generating other datasets, to writing and to fieldwork.

DATA ACCESSIBILITY

Data are deposited in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.33bf108> (Blonder et al., 2018). Venation network images are archived at <http://www.clearedleavesdb.org/> (collection "Kosñipata Valley (CHAMBASA elevation transect)") and can be searched using the branch and tree codes in the data file.

ORCID

Benjamin Blonder  <http://orcid.org/0000-0002-5061-2385>

Alexander Shenkin  <http://orcid.org/0000-0003-2358-9367>

Brian J. Enquist  <http://orcid.org/0000-0002-6124-7096>

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