

IDEA AND PERSPECTIVE

Venation networks and the origin of the leaf economics spectrum

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Abstract

The leaf economics spectrum describes biome-invariant scaling functions for leaf functional traits that relate to global primary productivity and nutrient cycling. Here, we develop a comprehensive framework for the origin of this leaf economics spectrum based on venation-mediated economic strategies. We define a standardized set of traits – density, distance and loopiness – that provides a common language for the study of venation. We develop a novel quantitative model that uses these venation traits to model leaf-level physiology, and show that selection to optimize the venation network predicts the mean global trait–trait scaling relationships across 2548 species. Furthermore, using empirical venation data for 25 plant species, we test our model by predicting four key leaf functional traits related to leaf economics: net carbon assimilation rate, life span, leaf mass per area ratio and nitrogen content. Together, these results indicate that selection on venation geometry is a fundamental basis for understanding the diversity of leaf form and function, and the carbon balance of leaves. The model and associated predictions have broad implications for integrating venation network geometry with pattern and process in ecophysiology, ecology and palaeobotany.

Keywords

Functional trait, leaf life span, leaf nitrogen content, LMA, loopiness, photosynthesis, physiological tradeoff, vein density, vein distance, venation network.

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INTRODUCTION

Leaves mediate the fluxes of resources and energy in all terrestrial ecosystems. They are a fundamental energetic unit of biology. Globally, it is estimated that terrestrial gross primary production exceeds 120×10^{12} kg C year⁻¹, approximately twice the contribution of the oceans (Field *et al.* 1998; Beer *et al.* 2010). Recent work has demonstrated that several key leaf functional traits that underlie leaf resource fluxes, such as peak carbon assimilation rate (A), leaf life span (LL), leaf mass per area ratio (LMA) and nitrogen concentration (N), scale with each other (Reich *et al.* 1997; Wright *et al.* 2004). This leaf economics spectrum is observed repeatedly across biomes, suggesting strong constraints on global resource fluxes that originate from similar selective pressures on leaf form and function (Reich *et al.* 1997, 1999; Wright *et al.* 2005).

Although the leaf economics spectrum is a fundamental component of understanding terrestrial ecosystem fluxes, its evolutionary and mechanistic basis is not fully understood. While mechanisms have been proposed to explain individual trait–trait correlations (Poorter & De Jong 1999; Tyree *et al.* 1999; Navas *et al.* 2003; Brodribb *et al.* 2007; Feng *et al.* 2008; Niklas *et al.* 2009; Brodribb & Feild 2010), we are aware of only one model that proposes an explanation for the leaf economics spectrum on the basis of physical and evolutionary tradeoffs (Shiple *et al.* 2006). This model remains largely untested.

Across plants, the high diversity in leaf form (Fig. 1) and function is mirrored by a high diversity in venation network geometry (Ellis *et al.* 2009). Moreover, there is evidence that the evolutionary convergence in leaf form is linked to the evolutionary convergence of venation traits such as reticulation (Carlquist 1959; Givnish *et al.* 2005). Here, we develop the hypothesis that leaf venation networks control the leaf

economics spectrum using a functional trait-based framework. Interest in functional traits has grown significantly in the last decade (Lavorel & Garnier 2002; McGill *et al.* 2006; Westoby & Wright 2006; Violle *et al.* 2007; Webb *et al.* 2010) but no comprehensive trait-based framework yet exists for leaf venation. Although some venation traits have been measured in a systematic way (Sack *et al.* 2008; Dunbar-Co *et al.* 2009; Brodribb & Feild 2010), there remains no standardization or proper definition of venation functional traits. Standardization of functional trait measurements enables the comparison of theoretical and empirical results from different studies across disciplines (Cornelissen *et al.* 2003). Moreover, most venation traits have never been measured concurrently and together with other leaf functional traits.

In this article, we argue that to understand the origin of the leaf economics spectrum and why leaf functional traits covary, one must first understand the costs and benefits of venation. We first present a quantitative framework for understanding leaf economic tradeoffs within the context of venation-mediated economic strategies. As part of this framework, we define three leaf venation traits (distance, density and loopiness) and develop standardized measurements for these traits. Next, we present a novel model to show how these venation traits are mechanistically linked to the leaf functional traits that define the leaf economics spectrum. We demonstrate that the mean global scaling functions that link several leaf functional traits (Wright *et al.* 2004) appear to vary with a small number of venation traits. Finally, we provide a preliminary test to assess if the model can predict the range of residual variation around the global scaling functions using empirical data drawn from 25 diverse plant species at a local scale. Our theoretical framework appears to offer the basis to understand mean global scaling functions as well as residual variation in leaf economics.

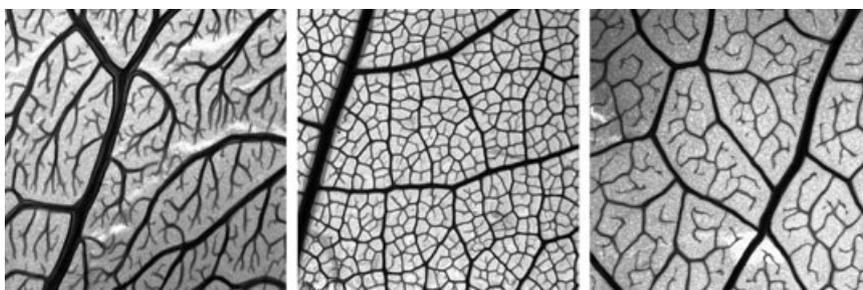


Figure 1 Venation networks are diverse and vary widely among species. As an example, three Angiosperm species exhibit high geometrical diversity in their terminal venation networks. Left to right: *Pistacia lentiscus*, *Baubinia variegata* and *Heteromeles arbutifolia*. All images are shown at the same scale of 3 mm × 3 mm.

VENATION-LINKED LEAF ECONOMIC STRATEGIES

Carbon is a fundamental and universal currency in leaf economics. The energy gain associated with the assimilation of carbon dioxide drives plant growth, constrains plant demography and thus ultimately influences plant fitness (Kikuzawa 1995).

Across environments, natural selection has shaped the form and function of plants so that leaves will have a net positive return on resource investment (Westoby *et al.* 2002). In this context, the total mass of carbon assimilated by a leaf over its life span must be greater than the total mass of carbon invested in the leaf (Chabot & Hicks 1982; Williams *et al.* 1989). This can be expressed in terms of several key leaf functional traits as

$$\frac{A_a \cdot LL}{LMA} = A_m \cdot LL \geq \kappa, \quad (1)$$

where A_a is the peak net carbon assimilation rate per unit leaf area ($\text{mol C m}^{-2} \text{s}^{-1}$), A_m is the peak net carbon assimilation rate per unit leaf mass ($\text{mol C g}^{-1} \text{s}^{-1}$), LL is the leaf life span (s), LMA is the leaf mass per area ratio (g m^{-2}) and κ is a positive stoichiometric constant (mol C g^{-1}) representing minimum lifetime carbon gain. Empirical data indicate that eqn 1 likely sets a strong constraint on trait covariation because the value of κ appears to be largely independent of biome or leaf type (Kikuzawa & Lechowicz 2006). Below, we show how each component of eqn 1 is directly influenced by the geometry of the venation network.

Equation 1 indicates that selection to maximize the return on carbon investment can be achieved with three leaf-level economic strategies: (1) selection to increase A_m (or A_a), (2) selection to maximize LL by either minimizing leaf damage or by investing more in leaf structure and (3) selection to minimize LMA by minimizing the resource investment in leaf construction. As we discuss below, differing environments likely will determine which of these strategies are more favoured. Note, because the biochemistry of photosynthesis requires nitrogen-rich molecules, the value of A_m is positively linked to leaf nitrogen content per unit mass (N_m , %; $100 \times \text{g N g}^{-1}$) (Chapin 1980; Field & Mooney 1986). Nitrogen is a costly resource for plants (Field & Mooney 1986), hence the smallest N_m that can achieve a given A_m is optimal. Thus, the optimal leaf would have high A_m , high LL, low LMA and low N_m , but such leaves do not exist (Wright *et al.* 2004). We argue that constraints on the geometry of the venation network generate tradeoffs among these functional traits. Ultimately, differences in the environment determine how natural selection will shape the best economic strategy for a leaf. Thus, variability in the global spectrum of functional trait values should be the result of

selection for different combinations of economic strategies that are constrained and correlated by the geometry of the venation network. Below, we survey the influence of venation on each strategy, and then quantitatively show how variation in venation network geometry mediates leaf function.

Maximizing carbon assimilation

Selection to maximize carbon assimilation is shaped by venation-mediated constraints on water supply for photosynthesis and on carbon and nitrogen investment in structure. First, the physical structure of the venation network influences water transport rates, and ultimately, because of the photosynthesis–transpiration compromise, rates of carbon assimilation. Brodrribb *et al.* have found that across many species, closer spacing of terminal veins results in both higher water fluxes and carbon assimilation rates across many species (Brodrribb *et al.* 2007; Brodrribb & Feild 2010). Furthermore, intraxylem and extraxylem limits to rates of flow in leaves appear to be critically mediated by vein size (Tyree *et al.* 1999; Sack *et al.* 2003, 2004, 2008; Cochard *et al.* 2004), whereas the terminal veins limit water flux to a greater extent than do large veins (Sack & Holbrook 2006). Recent simulation work has also shown that high water flow rates are best achieved by varying the structure of the finest venation (McKown *et al.* 2010) and that terminal vein distance can influence rates of water diffusion (Noblin *et al.* 2008). Thus, we argue that terminal venation structure and geometry is the critical scale at which to understand limits to water flux, and subsequently encapsulate the tradeoff between transpiration and carbon assimilation.

Second, maximizing carbon assimilation requires a large carbon investment in vein construction and thus a high LMA. Ideally, resource transport networks minimize network construction cost and maximize resource supply rate (Murray 1926; West *et al.* 1997; Banavar *et al.* 2000; Tondeur & Luo 2004; Durand 2006; Katifori *et al.* 2010). Some studies suggest that networks that only branch hierarchically and do not reconnect have the highest supply rates for a given mass (Banavar *et al.* 1999; Durand 2007; Corson 2010; Dodds 2010). However, recent work has shown that reconnecting networks are likely selected for when there is heightened risk of herbivory or other damage or when spatially or temporally varying resource demands are experienced (Durand 2006; Katifori *et al.* 2010). Metabolic scaling theory, which describes hierarchical branching supply networks (West *et al.* 1997, 1999), has been applied to leaves (Price & Enquist 2007) but it is unclear if this theory appropriately accounts for reconnecting venation networks (Price & Enquist 2009).

Third, maximizing carbon assimilation requires a large nitrogen investment per unit mass (N_m , %), because photosynthetic biochemistry requires nitrogen-rich molecules (Chapin 1980). A general positive relationship between rates of carbon assimilation rates and nitrogen concentration has been observed globally (Field & Mooney 1986; Reich *et al.* 1997).

Minimizing mass per area ratio

Selection to balance carbon investment in leaf structure with carbon assimilation is complex. Carbon investment is necessary not only for constructing xylem conduits that supply water and nutrients, but also for ensuring that the leaf can support itself to intercept solar radiation. Primary and secondary veins act as cantilevered beams that support the weight of the leaf and provide resistance to mechanical loading. This ensures that the leaf presents a maximal effective surface area without sags or deformation (Niklas 1999). These mechanical considerations imply scaling relationships between leaf surface area and leaf mass, and between venation and non-venation tissue (Niklas *et al.* 2007). Theoretical work has suggested that larger leaves incur disproportionately large construction costs and LMA values (Niinemets *et al.* 2007; Price & Enquist 2007; Niklas *et al.* 2009). Leaves with a high proportion of carbon-dense molecules, such as cellulose and lignin, characteristic of leaves with high LMA, can also have a lower concentration of nitrogen-rich molecules (i.e. lower A_m). This inverse relationship is likely due to non-photosynthetic venation tissue displacing lamina tissue (Villar & Merino 2001; Poorter *et al.* 2006; Feng *et al.* 2008) but can be obscured by secondary variation in leaf thickness and bulk mass density.

Maximizing leaf life span

Long leaf life span can compensate for low carbon assimilation rates or high construction costs (Navas *et al.* 2003). Long life span can be achieved by reducing the risk of abiotic and biotic damage and is often accomplished by increasing the mechanical strength of leaf tissue (Coley 1983). Thick leaves can resist punctures and tears caused by herbivory or environmental factors like wind or cold (Niklas 1999). Denser venation may also resist damage in the same way. However, thicker leaves tend to have more widely spaced terminal veins (Noblin *et al.* 2008); hence the relationship between venation and life span is not simple. In general, increase in leaf thickness does tend to be associated with longer life span and decreased damage from herbivory (Wright & Cannon 2001). Long life span can also result from a leaf's ability to tolerate damage. Redundant flow pathways (high reticulation) in leaf venation ensure that damage to one section of tissue does not affect function in other sections of the leaf (Katifori *et al.* 2010). This may be important for conferring tolerance to herbivory and water stress-induced cavitation (Sack *et al.* 2008). Thus, reticulate venation networks that can reroute flow may be important for prolonging the lifetime of leaves.

Three venation functional traits

Next, we propose three functional traits that are closely linked to how selection maximizes leaf carbon gain in differing environments. Together, these three traits characterize properties of the terminal venation network: vein distance (d), density (σ) and loopiness (ξ)

(Fig. 2). The geometry of the venation network will determine a leaf's position on these three trait axes (Box 1). As argued above, we only consider the terminal veins because of their critical role in limiting resource fluxes. Distance, a measure of the spacing between veins, is defined as the diameter of the largest circle that can be inscribed in area of leaf that is closed by a continuous vein boundary. Distance has units of length. Low distance allows higher water and carbon fluxes because of shorter path lengths between veins and stomata (Brodribb *et al.* 2007). Density is defined as the total length of venation per unit area. Density has units of inverse length. High density implies high carbon investment in venation. Loopiness is defined as the number of closed loops per unit area. Loopiness has units of inverse length squared. High loopiness suggests more redundant paths for water to circumvent damage, and more ways to stop the propagation of a mechanical tear. Importantly, while these three traits are not strictly independent of each other, their values can vary within the constraints given by the planar geometry of leaves and the geometry of the venation network. Thus, leaf economic strategies are primarily set by how selection has shaped the different ways for spatially distributing terminal veins across the leaf (Box 1). Consequently, there should be characteristic relationships between d , σ and ξ within every species. Recent work within two angiosperm species appears to support this prediction for distance and density (Uhl & Mosbrugger 1999).

These three venation traits reduce the need for complex descriptions of leaf venation networks. Currently, taxonomic schemes for describing venation are categorical and must be assayed by an experienced investigator (Hickey 1973; Ellis *et al.* 2009). In contrast, just three venation traits can characterize the bulk properties of the terminal venation network. Furthermore, these traits can be measured on small sections of tissue (Fig. 2); they do not require complex measurements of multiple scales, angles or radii (Turcotte *et al.* 1998; Bohn *et al.* 2002; Couder *et al.* 2002), nor do they necessitate preparation of more labour-intensive tissue cross-sections (Brodribb *et al.* 2007). Rather, they can be automatically estimated using digital image analysis programs (Rolland-Lagan *et al.* 2009; Price *et al.* in press) and images of leaf venation (Fig. 2; Appendix S3 and Code S1).

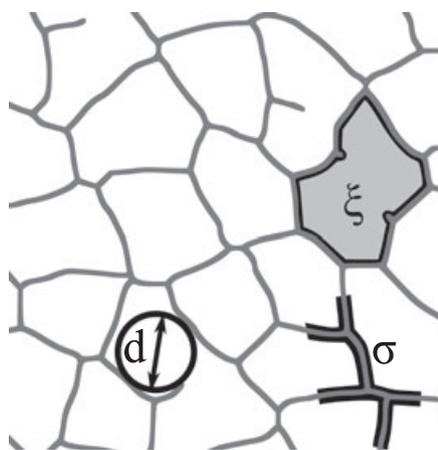


Figure 2 Venation traits can be easily estimated from skeletonized images of leaves (Code S1). Density (σ) is the total path length of veins in a region of interest (ROI) divided by the ROI area. Distance (d) is the mean diameter of the largest circular masks that fit in each areole (closed loop). This is equivalent to two times the regional maxima of the Euclidean distance transformation of the ROI. Loopiness (ξ) is the number of areoles in the ROI divided by the ROI area. Larger ROIs will produce more robust trait values and minimize edge effects.

Box 1 Geometrical constraints on leaf venation traits

Leaf venation reflects selection for multiple combinations of venation traits that result from different spatial geometries. Specifically, the size and shape of areoles (the areas enclosed by terminal veins) controls the coordination between the terminal venation traits density (σ), distance (d) and loopiness (ξ). As a first example, consider rectangular areoles with width Δx and length $k\Delta x$ (Figure S1). Assume without loss of generality that $k \geq 1$. For venation networks whose areoles are very long (monocotyledonous species) set $k = \infty$. For rectangular areoles, vein density is defined as the semi-perimeter of the areole divided by the area of the areole, or $\sigma = (k + 1)/(k\Delta x)$. Density is defined as the diameter of the largest circle that can be inscribed in the areole: $d = \Delta x$. Loopiness is defined as the inverse area of an areole: $\xi = 1/(k\Delta x^2)$. As k increases, ξ decreases, σ decreases and d is unaffected. Alternatively, as Δx increases, ξ decreases, σ decreases and d increases. These trends have several functional consequences. For example, A_m and LMA are predicted to depend on linear sums of d and σ . Maximal change in any of these traits requires simultaneously changing d and σ in the same direction, which is difficult to achieve by varying only Δx . Increasing k for a fixed value of Δx can solve this problem, at the cost of decreasing ξ . Thus, leaves that obtain the highest A_m and lowest LMA have areoles that are much longer than wide; effectively veins become unconnected and a branching architecture with no redundant flow pathways dominates. This potentially reduces LL. Conversely, maximization of ξ requires minimizing k or Δx . Because $k \geq 1$, maximum ξ is obtained for $k = 1$ (square areoles) or very small Δx (high σ and low d). This corresponds to leaves with potentially high LMA and A_m . More complex geometric features of venation networks, like freely ending veinlets that are only connected at one end, also influence relationships between venation traits. The presence of these veinlets does not change ξ , but does impact σ and d . Consider a unit square areole with and without a freely ending veinlet originating at the midpoint of one side and terminating at the centre of the areole. Without the veinlet, $\sigma = 2$ and $d = 1$. With the veinlet, $\sigma = 2.5$ and $d = 2 - \sqrt{2} = 0.58$. Thus, with only a 25% increase in σ , the leaf achieves a 42% decrease in d with no effect on ξ . This increases A_m without compromising LL and may explain the prevalence of freely ending veinlets in many species that have evolved to have high transpiration and carbon assimilation rates. Areoles with more complex shapes produce different venation trait combinations. For example, squares, equilateral triangles or regular hexagons can all tile the plane without requiring other tile shapes. Suppose each areole type has the same vein density: $\sigma = 2$. In this case, analytic geometry reveals that $d = 1$ for all shapes, but $\xi = 4/3\sqrt{3} = 0.77$ for the triangle, $\xi = 1$ for the square and $\xi = 2/\sqrt{3} = 1.15$ for the hexagon. In sum, the hexagon achieves higher potential loopiness for a fixed vein density and vein distance than either the square or the triangle. Interestingly, many minimal surfaces like soap films tend to have cells that are on average hexagonal (Weaire & Rivier 1984). Irregular polygons or tilings by multiple areole types will clearly have more complex effects on venation traits.

Trait abbreviation	Areole shape						
							
σ	2	3	2	2.50	2	2	
d	1	0.5	0.5	0.58	1	1	
ξ	1	2	0	1	0.77	1.15	

Importantly, they can also be related to the economics of the leaf, as developed below.

VENATION TRAITS AND THE LEAF ECONOMICS SPECTRUM

Next, we derive a model to illustrate how the three venation traits defined above can mechanistically predict key leaf functional traits. We start by modelling a leaf as a network of cylindrical terminal veins (Fig. S1). We assume that each vein has a radius r_V , and is embedded at a depth δ midway between the upper and lower surface of a lamina (i.e. the leaf thickness is 2δ). The veins have mass density ρ_V and the lamina has mass density ρ_L . Optimal resource transport implies that the distance between vein and evaporative surface should be proportional to the distance between terminal veins so that approximately

$$d = k_0 \delta. \quad (2)$$

Empirical data from 32 species support this relationship, with $k_0 \approx 1$ (Noblin *et al.* 2008) (Fig. S2). This relationship can be motivated by considering two extreme cases. Veins that are very closely spaced relative to leaf thickness oversupply water to points between veins and undersupply water to upper and lower leaf surfaces, whereas veins that are distantly spaced relative to leaf thickness oversupply water to leaf surfaces and undersupply water to points between veins. A compromise is achieved when the vein–vein distance and the vein–surface distance are roughly equal. Note also that venation traits cannot take arbitrarily large values, because veins can occupy no more than the entire volume of the leaf. An upper bound is when adjacent veins are touching, or

$$2r_V \leq d. \quad (3)$$

Because d is related by geometry to σ and ξ (Box 1), eqn 3 then implies a constraint on the range of variation of all other venation traits.

Now that the leaf network has been defined in terms of venation functional traits, we use these traits to derive equations for four major leaf functional traits: LMA, LL, A_m and N_m . We make the simplifying assumption that these venation traits are independent of leaf size or area. To arrive at an equation for LMA, we partition leaf volume and mass between terminal venation and lamina (a full derivation is provided in Appendix S1). Accounting for the different mass densities of venation and lamina tissue, and the relationship between leaf thickness and vein distance, the total mass of a unit area of leaf is:

$$\text{LMA} = \pi r_V^2 (\rho_V - \rho_L) \sigma + \frac{2\rho_L}{k_0} d. \quad (4)$$

This equation shows that venation networks with high terminal vein density or high terminal vein distance produce high LMA. However, the geometric linkages between these traits (Box 1) will produce further nonlinear effects on LMA.

Leaf life span is determined by the interactions between physiological leaf life span maxima (LL_{\max}) and programmed death and external causes. External causes include complete herbivory or damage to the venation network due to partial herbivory, pathogens, weather, etc. Evidence exists that thicker (δ) leaves are more resistant to such damage (Chabot & Hicks 1982). We also suggest that leaves with loopier venation networks (high ξ) can reroute flow after damage, improving survivorship. A reasonable expectation is that $LL = LL_{\max} - g(\delta, \xi)$, where the form of g is unknown. A reasonable first approximation for the relationship between leaf life span and leaf network geometry is that LL is directly proportional to δ , so that:

$$\begin{aligned} LL &= k_1 \delta \\ &= k_1 d \end{aligned} \quad (5)$$

where k_1 is an undetermined constant of proportionality and the second equality is from eqn 2. Although it is difficult to be more precise without optimality arguments (Kikuzawa 1995) or more detailed knowledge of the environment, eqn 5 represents the simplest model for how LL relates to leaf network geometry. A more detailed model could also explicitly incorporate ξ .

Next, we model peak per-mass carbon assimilation rate (A_m). Due to the transpiration–photosynthesis compromise, variation in A_m must then be directionally proportional to whole-leaf conductance to water vapour. As we detail in Appendix S1, assuming a rectangular venation network, and that water moves by steady-state diffusion out of the venation network through intercellular spaces and finally through stomata, we derive the following relationship predicting leaf net photosynthesis, A_m :

$$A_m = \frac{[\pi a_0 D (1 - b) k_0 n_s a_s \text{WUE}] \sigma}{[2\rho_L d + k_0 \pi r_V^2 (\rho_V - \rho_L) \sigma][\pi t_s + \sqrt{\pi a_s} \sigma + 2a_s n_s \log \frac{d}{k_0 r_V}]}. \quad (6)$$

where a_s is the maximum aperture of a stomate, n_s is the number density of open stomata, t_s is the thickness of a stomatal pore, D is the temperature and pressure dependent diffusion constant of water in air, a_0 is the temperature and pressure dependent saturation vapour concentration of water in air, WUE is water-use efficiency and b is the relative humidity (Buck 1981; Nobel 1999). Equation 6 explicitly shows how numerous environmental factors, leaf functional traits and venation traits combine to govern A_m .

Next, we can incorporate how the per-mass nitrogen concentration, N_m , can also be determined by venation traits. Nitrogen is ultimately

partitioned into two categories: photosynthetic (allocated to Rubisco, chlorophyll, etc.) and non-photosynthetic (allocated to structural molecules, shared biochemical pathways not directly involved in electron transport or carbon fixation, etc.). Here, we assume that the photosynthetic nitrogen pool is proportional to peak carbon assimilation rate, because Rubisco and chlorophyll availability can limit photosynthesis (Field & Mooney 1986). We also assume that non-photosynthetic nitrogen is proportional to the mass of leaf lamina because the venation network is lignified and does not contain large concentrations of nitrogen. Summing these two contributions we obtain

$$N_m = k_2 A_m + \frac{k_3 2d - k_0 \pi r_V^2 \sigma}{k_0 \text{LMA}} \quad (7)$$

where k_2 and k_3 are species-specific stoichiometric constants that control the relative allocation of nitrogen to photosynthetic and non-photosynthetic tissue. A full derivation is provided in Appendix S1. Similar to eqn 6, eqn 7 shows how the environment and functional traits interact nonlinearly to govern leaf nitrogen concentration.

We have focused on four functional traits related to leaf carbon flux because they are fundamental to leaf economics and are commonly measured. However, the leaf economics spectrum does involve many other traits (e.g. respiration rate, phosphorus content) and may be coordinated with resource partitioning in other plant tissues (Kerkhoff *et al.* 2006; Freschet *et al.* 2010). While beyond the scope of this paper, a further elaboration of our model could potentially account for how these additional traits covary with the central traits covered here.

Together, eqns 1–7 provide insight into how venation traits mediate different economic strategies across environments. For example, our model predicts that selection for increased rates of transpiration (e.g. in low temperature environments where the diffusion constant, D , is small; or in humid environments with a low water vapour concentration gradient) should result in morphological convergence of vein geometry. Our model predicts that in both environments, leaves should be characterized by very dense or closely spaced (low d) veins, which then implies shorter life spans. Similarly, if water-use efficiency is fixed, then selection for increased carbon assimilation rates will result in increased venation conductance and thus an increase in vein density or decrease in vein distance. Alternatively, leaves adapted to higher environmental CO_2 concentrations should be characterized by lower transpiration rates, lower water-use efficiencies and lower vein densities to achieve the same carbon assimilation rate. There is some support for these predictions. Over evolutionary time scales, falling atmospheric CO_2 concentrations in the late Cretaceous are likely linked to higher transpiration rates and the high vein densities that characterize the Angiosperms (Brodribb & Feild 2010). Thus, the environment-dependent predictions of the model have the potential to provide insights into leaf form and function across broad climatic gradients as well as broad biogeographic patterns of plant species distributions (Chabot & Hicks 1982; Kikuzawa & Ackerly 2002).

PREDICTIONS AND PRELIMINARY EVIDENCE

Our model quantitatively predicts how leaf functional traits vary with the geometry of the leaf venation network. To assess our model predictions at global and local scales, we used two different approaches.

Our first approach was to predict the global leaf economics spectrum using species-level data. Specifically, we determined trait–trait relationships between A_m , LL, LMA and N_m by allowing values of d , σ and ξ to covary for given venation geometries, then constructed ordered pairs of \log_{10} -transformed predicted functional trait values for the same range of σ values. For this approach, we set non-venation model parameters to interspecific mean values reported in the literature (Appendix S2). We compared predicted trait–trait relationships to empirical relationships from the GLOPNET database (Wright *et al.* 2004), a compilation of functional trait values for 2548 taxonomically diverse plant species. We examined the effects of both reticulate and open venation by considering the extreme cases of rectangular venation networks with reticulate venation and square-like areoles (e.g. *Quercus* sp.) and parallel venation with open areoles (e.g. *Poa* sp. or *Ginkgo biloba*). Our model correctly predicts the directionality and magnitude of all examined leaf functional trait scaling relationships represented in the leaf economics spectrum (Fig. 3). The low predicted values of A_m that lay outside of the range of the GLOPNET data may be reasonable because GLOPNET does not have extensive coverage of the more basal Tracheophyte clades that are known to have very low vein densities and low carbon assimilation rates (Boyce *et al.* 2009). Furthermore, model predictions for global functional trait scaling relationships are similar for reticulate

and open venation. Thus, d and σ seem to play a fundamental role in predicting the leaf economics spectrum, while ξ does not. Reticulate venation, which is related to ξ , has evolved multiple times but we still have limited understanding of its functional consequences (Katifori *et al.* 2010). Reticulation of the venation network does vary across species, however, so the functional effects of ξ certainly deserve further study. According to our model, the form of functional trait scaling relationships can thus be determined with only one of these venation traits. These results are consistent with two observations. First, a high proportion of variance in leaf functional traits is explained by a single axis in the GLOPNET dataset (Wright *et al.* 2004). Second, previous structural equation modelling work has identified a single latent variable that can explain the leaf economics spectrum (Shipley *et al.* 2006). While Shipley *et al.* (2006) identified this variable as the ratio of cytoplasmic to cell wall volume (i.e. a ratio of metabolically active to inactive tissue), an interpretation of this latent variable as the mass of the entire venation network (i.e. metabolically inactive xylem described in part by σ) is also consistent with their results.

Our second approach was to assess if our model could account for residual variation around the mean global scaling relationships. We conducted a preliminary experiment, sampling 25 woody species near Tucson, AZ (Data S1, full dataset and species list). For each leaf, we measured A_m , LMA and N_m directly using standard methodology,

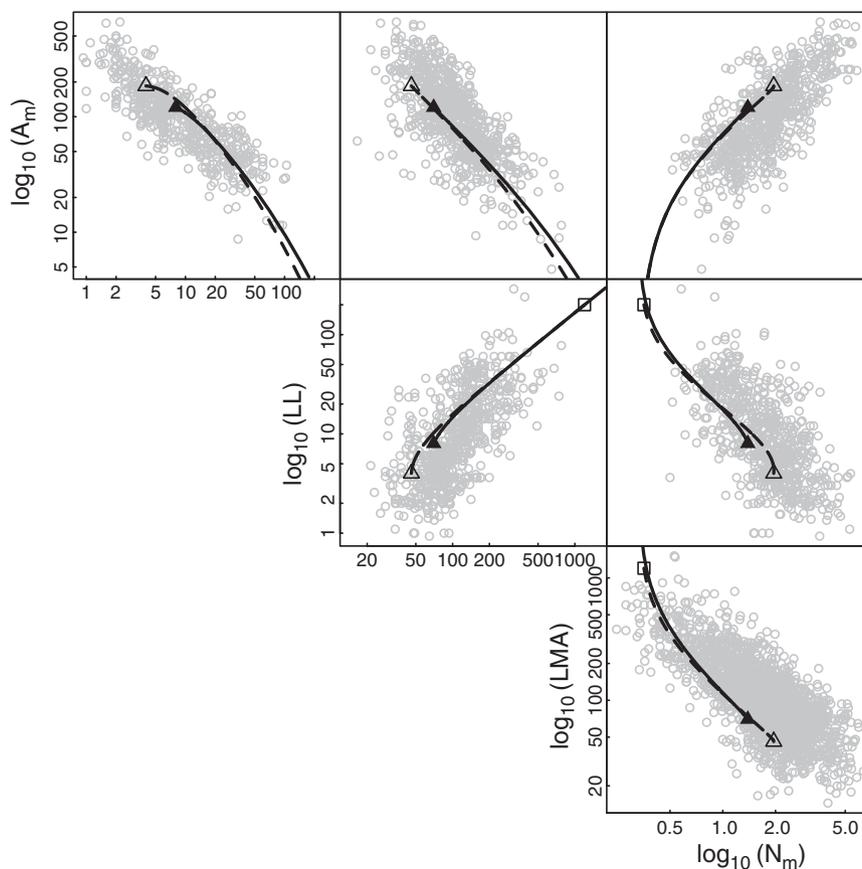


Figure 3 The leaf economics spectrum can be directly predicted using three venation traits. Functional trait correlations between maximum carbon assimilation rate (A_m , $\text{nmol C g}^{-1} \text{ s}^{-1}$), leaf life span (LL, months), leaf mass per area ratio (LMA, g m^{-2}) and leaf nitrogen content (N_m , %; $100 \times \text{g N g}^{-1}$). Open grey circles represent data from 2548 species in the global GLOPNET database (Wright *et al.* 2004). Solid lines represent model predictions for reticulate venation (square areoles); dashed lines represent model predictions for parallel venation (open areoles). These correspond to $d = 2/\sigma$ and $d = 1/\sigma$, respectively. Minimum and maximum empirical values of vein densities are also shown (Boyce *et al.* 2009): solid squares are vein densities of $\sigma = 500 \text{ m}^2 \text{ m}^{-2}$; open triangles are $\sigma = 25\,000 \text{ m}^2 \text{ m}^{-2}$.

and obtained species-mean LL values from GLOPNET when available. We then calculated σ , d and ξ on images of chemically cleared leaf tissue (see Appendix S3 and Code S1 for detailed methods). Measured vein density ranged from 1.5×10^3 to $2.2 \times 10^4 \text{ m}^{-1}$, distance from 6.7×10^{-5} to $5.0 \times 10^{-4} \text{ m}$ and loopiness from 6.4×10^5 to $5.1 \times 10^7 \text{ m}^{-2}$. We also directly measured several other model parameters including leaf temperature, D , b , WUE and k_0 (for all other model parameters, we used species-mean values – details in Appendix S2). We found that broad trends in the empirical data were consistent with the global leaf economics spectrum, falling within the range of global trait variation (Fig. 4). These results demonstrate that the model can capture some sources of variability in the leaf economics spectrum. Nevertheless, these more detailed local-scale predictions from the model appear to over-predict the magnitude of scaling relationships for photosynthesis, and produce weak scaling relationships involving leaf life span. We suggest that the life span patterns are unclear because this was the only trait we were not able to directly measure on individual leaves. Other deviations suggest that additional parameters in the model (such as stomatal density and lamina mass density; see Appendix S2) should also be measured to account for further residual variation. In sum, the model seems to successfully explain mean trends in the leaf economics spectrum and may eventually be able to explain residual variation. A more complete statistical treatment and discussion of these results are found with Figure S3.

In order for our model to account for more of the variation in leaf traits observed at local scales, the inclusion of other traits will likely be necessary. Local predictions from our model are likely skewed by the assumption that venation networks are comprised wholly of identical terminal veins. In reality, larger and numerous primary and secondary veins will account for additional leaf mass. Accounting for this mass would predict lower A_m and N_m but higher LMA, as these large veins contain large amounts of carbon but do not themselves photosynthesize. Additionally, these considerations also suggest that absolute leaf size may play an important role: large leaves require disproportionately more mass allocated to petioles and primary or secondary veins for mechanical support (Niklas 1999). Thus, to account for additional residual variation, additional traits like leaf area and secondary vein density may be necessary to more completely describe venation networks. For example, LMA could be influenced by variation in terminal vein radius or tissue mass density. Empirically lower tissue mass density or smaller radius veins than assumed could decrease LMA values. LL, understood as a function of damage resistance, could also be influenced by the presence of larger primary and secondary veins or variation in vein radius and tissue mass density. We also suggest that variation in stomatal density could account for the lower accuracy of our A_m prediction. We assumed the same stomatal density for all leaves, when it is reasonable to assume coordination between stomatal and venation traits. It is known that vein radius, stomatal number density and

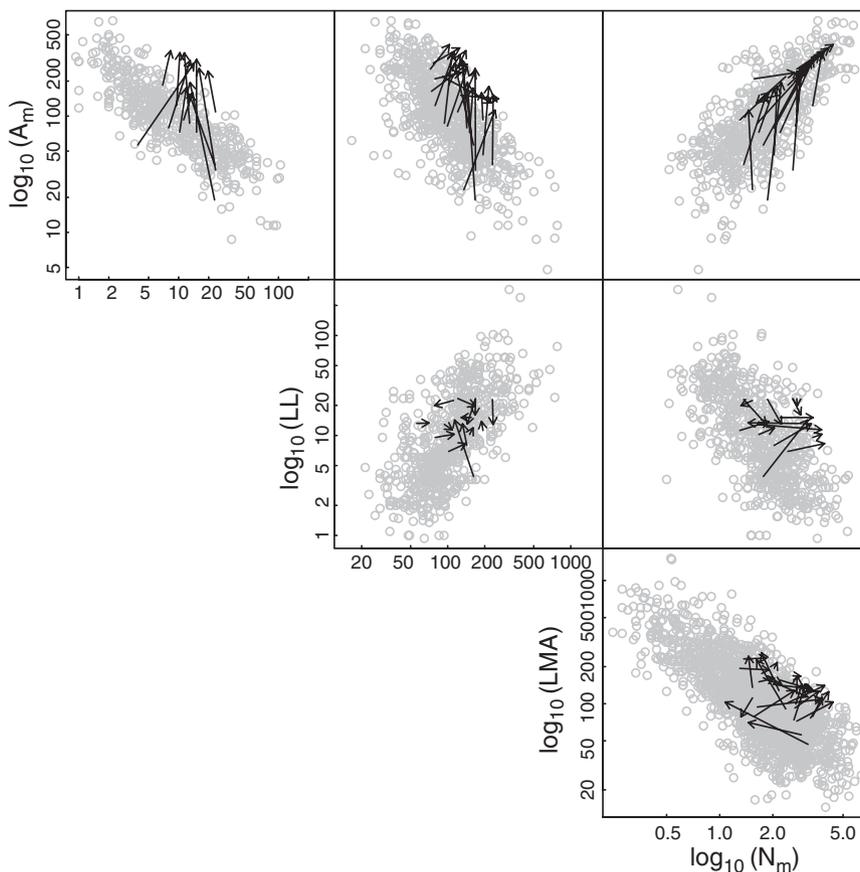


Figure 4 Observed and predicted values of leaf functional traits lie on the global leaf economics spectrum. Observations are for 25 species in Tucson, AZ. Predictions are based on observed venation traits and the modelling framework developed in the text. Arrow bases denote measured values for functional traits; arrow points denote model predictions based on measurements of venation network geometry. Grey circles represent global species-mean observations from GLOPNET (Wright *et al.* 2004).

lamina tissue mass density can vary among species, particularly in response to environmental drivers (Dunbar-Co *et al.* 2009). Finally, our equation for A_m is approximate; more advanced modelling approaches may produce a more accurate equation (Appendix S1). Altogether, deviations from the model highlight important physical processes, opportunities for further work and non-constant parameters that should be measured in the future. Although single-vein leaves like needles are already well understood from a hydraulic perspective (Zwieniecki *et al.* 2004), more detailed modelling of very complex and very simple leaf venation networks will improve our understanding of leaf function.

FUTURE DIRECTIONS AND CONCLUSIONS

We have advanced a new hypothesis for the origin of the leaf economics spectrum and defined a standardized set of traits that provides a common language for future studies of venation. Future experimental work should provide a more rigorous test of the domains of applicability of our modelling framework involving these venation traits. For example, model extensions should more fully include the effects of leaf size since biomechanical constraints on large leaves may play an important role in leaf mass allocation. However, the model as it currently stands provides a useful starting point for applications in ecophysiology, ecology and palaeobotany. For example, the model implies linkages between leaf venation and biochemistry that can be further explored to allow for a better understanding of how venation traits influence biochemical limitations to photosynthesis (Farquhar *et al.* 1980). The model framework also has the potential to connect genetic processes and ecosystem functioning by linking the functional implications of different leaf developmental processes and genes influencing venation (Haritatos *et al.* 2000; Koizumi *et al.* 2000; Kang & Dengler 2004). Additionally, the model offers new approaches for the estimation of palaeoclimate and extinct plant function using fossil leaves (Uhl & Mosbrugger 1999; Huff *et al.* 2003; Wilf 2008). Venation traits can be used as correlates for climatic variation or directly interpreted through this model as predictors of plant function (Brodrribb *et al.* 2010). Finally, the model's coupling to environmental and climatic variables may make it possible to understand historical conditions that have selected for a broad range of leaf form and function. For example, by distinguishing between single-veined needle-like leaves found in many Gymnosperms, the parallel-veined Monocots, and many of the densely veined Angiosperms, the model could provide a useful understanding of the macroevolutionary trajectory of vascular plants (Brodrribb & Feild 2010).

Our venation model provides a useful 'zeroth-order' approximation for understanding the origin of the leaf economics spectrum. We hope that further extensions of this theory, coupled with more detailed experimental measurements of the traits and parameters identified in such a model, will enable venation networks to become robust predictors of leaf function.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Derivations of model predictions.

Appendix S2 Abbreviations, definitions, units, ranges, mean values and references for all parameters used in the model involving venation traits.

Appendix S3 Experimental methods.

Code S1 MATLAB codes to automatically calculate venation traits.

Data S1 Species list and measurements for 25 Tucson species.

Figure S1 Structure of a model leaf including terminal veins.

Figure S2 Vein spacing and leaf thickness.

Figure S3 Empirically measured venation and functional traits.

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