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Using leaf shape to determine leaf size could be a game-changer

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Of all the attributes of plants, leaf size is one of the most widely considered – across evolutionary, ecological and biophysical contexts, and spanning back centuries. Yet despite comprehensive global repositories of collated plant traits (Kattge *et al*. 2020), measures of leaf size are surprisingly scant and difficult to estimate with sufficient accuracy, especially at scale. In a Technical Article in issue 128-4 of *Annals of Botany*, Schrader *et al*. (2021) present a simple shape-based classification scheme for accurately estimating leaf size with relative speed, which has the potential to fill vast gaps across taxa and ecosystems.

The prospect of filling these leaf size gaps is tantalising. Among the many reasons that leaf size is an important trait in ecology are its influence on leaf energy balance, thermoregulation, metabolic rate, photosynthesis, water relations, light interception, allometric scaling and associated structural trade-offs for optimising total plant productivity. Theory has long predicted relationships between leaf size and environment, notably, along temperature and rainfall gradients (Parkhurst and Loucks 1972). With our climate typified by ever greater extremes, the imperative to explore these relationships is stronger than ever. However, generalising leaf size-environment patterns at a global scale is less straightforward than we might expect. Across >7,000 species, Moles *et al*. (2014) found the correlation between leaf size and mean annual precipitation to be weaker than with mean annual temperature; whereas Wright *et al*. 2017 found that both temperature and rainfall were strong predictors, and rainfall is also strong for fossil leaves (Peppe *et al*. 2011).

Given that such studies represent robust analyses and large numbers of species, why are the relationships between leaf size and environment not as neat as we might predict? Among many, here are two plausible reasons.

1. Comprehensive and reliable data on leaf size are lacking. This means that we don't really know the extent to which the current gaps for certain taxa and biomes might influence relationships. For example, in research focused only on less represented extreme environments, leaf size-environment patterns are weak (e.g., tundra, Thomas *et al*. 2020).
2. Nature is messy. Leaf size is driven by multiple environmental variables, including temperature, rainfall, light environment, soil nutrient availability, seasonality and more, any or all of which may act in concert and/or vary across species distributions (Moles *et al.* 2014; Wright *et al*. 2017).

The presence of statistically detectable patterns in leaf size with environment begs deeper exploration. As climatic and other environmental data are increasingly available, a key step is to address the problem of point 1, above. The approach outlined by Schrader *et al*. (2021) opens up the possibility of filling large and/or critical gaps in data for leaf size, so that we can better explore the rich and enticing questions arising from point 2.

One reason that we don't have more comprehensive data on leaf size is that it's time-consuming to measure. Whether working on plants *in situ*, field-collected samples, fossils or herbarium specimens, scale-referenced images must first be made of the leaves, which are then processed using imaging software to extract the 2-dimensional area. This process contrasts the simpler, 1-dimensional measurements of leaf length and width, values for which, unlike leaf area, also are routinely reported in written descriptions of species. As Schrader *et al*. (2021) explain, back-calculating leaf size data theoretically is achievable with an allometric scaling function using these simpler parameters. Estimating leaf size as the product of length and width and a 2/3 correction factor to account for taper at each end is reasonably robust for ovate leaves and has been used since the 1950s. But of course, not all leaves are ovate – think about taxa or habitats in which bipinnate or pinnatisect leaves are common. When we're working with large datasets, we don't need perfection, but we want the variance around our means to be similar across comparative groups. The above conventional scaling function does not account for the breadth of leaf shapes, such that leaf size estimates for many leaf shapes can be highly inaccurate, potentially biasing certain taxa and even biomes.

Schrader *et al*. (2021) have developed a hierarchical, three-tiered system for classifying leaves into different groups based on a given suite of leaf shape attributes. Leaf shape-based correction factors associated with each group can then replace the conventional 2/3 correction factor in the scaling function for leaf size estimation. Being a tiered framework that includes progressively more detailed shape parameters, it is possible to classify leaves at only the highest tier, but accuracy markedly increases if the third and most detailed classification of leaf shape is used. The improved accuracy in leaf size estimates for highly dissected or oblate leaves relative to the conventional approximation is impressive, particularly at the highest tier (see Figure 3e vs 3f, Schrader *et al*. 2021). An important extension of the authors' approach is the exploration of family-specific correction factors, which they show to be robust, particularly for families in which leaf shapes are similar across lower taxa. For situations where genera vary in shape across a given family, it seems feasible that genus-specific factors could be generated. Using taxonomically-defined, shape-based correction factors would be particularly useful where very large datasets are required or for incomplete fossil specimens.

As with all good tools, which give the best result when we know when and how to use them, carefully defining the context for our question about leaf size matters here. For example, implicit in using the leaf size estimation scheme is the recognition that leaf shape varies widely across species (Figure 1). Leaf shape is a critical moderator of leaf size-temperature relationships. When referring to leaf 'size', we generally are talking about the 2-dimensional area of the lamina, but there are many features of leaves that influence their thermoregulation (Michaletz *et al*. 2015). Aside from reflective properties, thickness and angle, how the lamina of a leaf is geometrically and structurally arrayed is a key determinant of the adjacent leaf-air boundary layer, which in turn influences the rate of temperature convection to and from the leaf. Relative to entire leaves of comparable area, leaves that are lobed often have a reduced effective width, which is a better predictor than area of leaf temperature (Leigh *at al*. 2017). So, if the context for our question was exploring leaf size-environment relationships based on leaf temperature, we would be wanting to incorporate information on leaf shape. Happily, because information on leaf shape is a necessary pre-requisite for generating accurate correction factors for size (lobed *vs* entire is the minimum allocation required; Schrader *et al*. 2021), this information could readily be included in analyses.

It also is important to acknowledge that leaf size – and indeed, shape – can vary greatly within some species across their distribution and even within individual plant canopies. For example, sun *vs* shade leaves in certain rainforest groups have large, lobed leaves at the bottom of the canopy and very small, often entire leaves at the top. Such within-species variation has been ever thus, but with a new-found capacity for greatly increased accuracy in leaf size estimates, overconfidence in our data could blind us to this potentially large source of error. Again, proper use of the tool simply requires an awareness of this possibility and the associated implications within our research context. For instance, it may be appropriate to include more than one leaf morph for species with marked heterophylly. Or perhaps we might include leaves from the wettest and driest edges of a species distribution. For a raft of well-framed questions, this new scheme for accurate and rapid assessment of leaf size for filling large and critical data gaps could be a game-changer.

References

Kattge J, Diaz S, Tautenhahn S, *et al*. 2020. TRY plant trait database – enhanced coverage and open access. *Global Change Biology* **26**: 119–188.

Leigh A, Sevanto S, Close JD, Nicotra AB. **2017**. The influence of leaf size and shape on leaf thermal dynamics: does theory hold up under natural conditions? *Plant Cell and Environment* **40**: 414 237–248.

Michaletz ST, Weiser MD, Zhou J, Kaspari M, Helliker BR, Enquist BJ. 2015. Plant thermoregulation: energetics, trait–environment interactions, and carbon economics. *Trends in Ecology and Evolution* **30**: 714-724.

Moles AT, Perkins SE, Laffan SW, *et al*. 2014. Which is a better predictor of plant traits: temperature or precipitation? *Journal of Vegetation Science* **25**: 1167–1180.

Parkhurst DF, Loucks OL. 1972. Optimal leaf size in relation to environment. *Journal of Ecology*, **60**: 505-537.

Peppe DJ, Royer DL, Cariglino B, *et al.* 2011. Sensitivity of leaf size and shape to climate: Global patterns and paleoclimatic applications. *New Phytologist* **190**: 724–739.

Schrader J, Shi P, Royer DL, Peppe DJ, Gallagher RV, Li Y, Wang R, Wright IJ. 2021. Leaf size estimation based on leaf length, width and shape. *Annals of Botany* 128: 395–406.

Thomas HJD, Bjorkman AD, Myers-Smith IH. 2020. Global plant trait relationships extend to the climatic extremes of the tundra biome. *Nature Communications* **11**: 1351.

Wright IJ, Dong N, Maire V, *et al.* 2017. Global climatic drivers of leaf size. *Science* **357**: 917–921.

Figure 1. Leaf shape varies widely with environment, across and within plant species. Incorporating information on leaf shape is important in framing questions about and gathering data on leaf size.