

Commentary

Cheap and attractive: water relations and floral adaptation

Plant evolutionary ecologists spend their time searching for the causal mechanisms responsible for patterns in the green world. For example, plant hydraulics provide a host of patterns to be explained, such as the pervasive tendency for maximum vessel diameter to be narrower in drier areas (Pfausch *et al.*, 2016), the striking tendency for vessels to be solitary when the ground tissue is made up of true tracheids (Rosell *et al.*, 2007), and the potential tradeoff between vessel diameter and resistance to drought-induced embolism (Liu *et al.*, 2019). Students of plant hydraulics actively debate the causes, or even the reality, of all of these and many other patterns (Pittermann *et al.*, 2013; Rico *et al.*, 2013; Rodriguez-Zaccaro *et al.*, 2019). In the process of inferring explanations for such patterns, often unrecognized is the importance of understanding not only which trait combinations are commonly observed and why, but also whether unobserved or rare combinations can be produced by plants, and how the performance of these combinations compares with the common ones. A recent article in *New Phytologist* by Roddy *et al.* (2019, doi: 10.1111/nph.15749) on floral water relations admirably showcases this reasoning.

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The jumping off point for Roddy *et al.*'s study is in the diversity of leaves. For all the morphological variation across leaves, many of the functional features of leaves vary relatively little. Conduit diameters are predictable given leaf size (Sack *et al.*, 2012), and stomata–vein distances are constant within species (Fiorin *et al.*, 2016), for example. In Roddy *et al.*'s study, their sampling across a wide range of angiosperm leaves revealed a range in water potential at turgor loss point (Ψ_{tlp}) of only *c.* 1 MPa, from -0.76 to -1.88 MPa. The Ψ_{tlp} is an important indicator of drought resilience as it signals the start of wilting. (Whereas riparian or mesic-adapted plants will lose turgor at water potentials not far below 0 MPa, drought adapted species will wilt at more negative water potentials, primarily due to higher levels of cell osmoticity.) What keeps this and other leaf traits in such restricted ranges, and

why they fall within the absolute ranges that they do, are crucial questions demanding explanation.

Natural selection is a plausible possibility for the patterns that Roddy *et al.* document, but it could also be that plants are simply incapable of producing organs outside the range observed in leaves. Examples of such unoccupiable spaces abound in nature. Geophilomorph centipedes never produce even numbers of segments (Leśniewska *et al.*, 2009), mammals, from giraffes to whales, produce just seven cervical vertebrae (Galis *et al.*, 2006), and plants are trapped in a tradeoff making it impossible to produce wood that simultaneously is maximally stiff and provides maximal space for both storage and conduction (Pratt & Jacobsen, 2017). So, identifying selection as responsible for traits falling within a restricted range, such as the leaf traits of Roddy *et al.*, requires ruling out the inaccessibility of the empty spaces. Selection emerges as the result of performance, and thus fitness differences between heritable variants within species. Given any variation within a population of a species, variants with leaves that have higher leaf lifetime photosynthetic performance should be favored. Presumably only a narrow range of trait combinations within species corresponds to these optima. This means that, if the narrow range in Ψ_{tlp} across leaves is one favored by selection, then the range of trait values that plant developmental systems are capable of producing should be much wider. This assumption follows necessarily from the definition of natural selection, as the favoring of a subset from a wider pool of possible alternatives. But how, if selection acts so powerfully against these alternatives, can they be observed and this assumption tested?

One way is to examine the same traits in a differing selective context. If it is true that the range in the focal traits is maintained by selection, then examining a differing selective context should reveal a differing range of trait values. An excellent example of this reasoning is the comparison of domestic vs wild dogs of Drake & Klingenberg (2010). These authors examined geometric morphometric indices of skull shape across domestic dog breeds and compared them with the wolf, the wild ancestor of the dog. Their analyses found that over 70% of the variation in skull shape was described by the first three principal components (PCs), and we will focus on the first two here. PC1 described variation in how long or short the skull was, ranging from short-snouted lapdog breeds to the long-snouted wolf (space to the left of wolves in Fig. 1a). Presumably long snouts increase moment and thus bite force; somewhat shockingly, humans have bred dogs that are slightly *more* ferocious in this regard than wolves (space to the right of wolves in Fig. 1a). PC2 described how tall or short the skull was, from tall-headed breeds to those with long, sleek skulls. Plotting these first two PCs against one another shows that the domestic dog skull space includes the wolf space, but goes stunningly far beyond it (Drake & Klingenberg, 2010). There is a truly vast amount of heritable variation that selection can act on in skull shape, and it can

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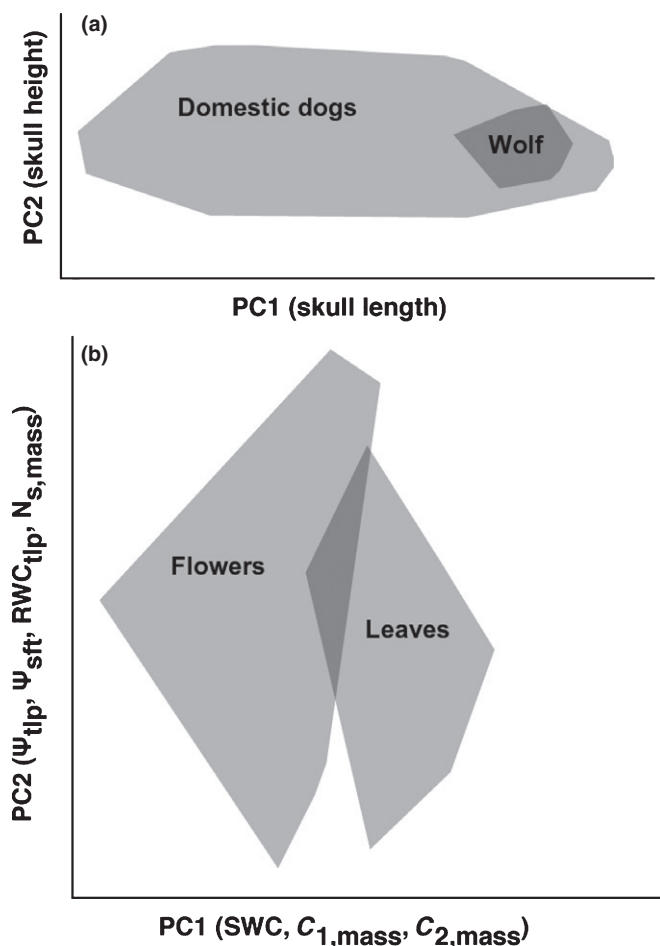


Fig. 1 Finding that differing selective conditions lead to differing trait distributions is consistent with trait distributions being shaped by selection. (a) Dog skull shape morphometric indices vary vastly more than in their ancestor, the wolf (after Drake & Klingenberg, 2010). This dramatically shows that skull shape can vary widely beyond that seen in the wild, and is strongly consistent with the notion that wolf skull proportions are maintained by selection relative to the other shapes possible. (b) Similarly, Roddy *et al.* (2019; doi: 10.1111/nph.15749) recently published in *New Phytologist* show that an array of leaf and flower pressure–volume curve variables differ markedly, with flowers covering a wider and largely nonoverlapping area of trait space. As in the dog example, Roddy *et al.*'s finding is consistent with the expectation that leaf water relations can vary well beyond the values normally observed, and that the restricted range occupied is the result of selection, with flowers demonstrating that other configurations are possible, but likely not favored in leaves. PC, principal component; SWC, saturated water content; $C_{1, \text{mass}}$ and $C_{2, \text{mass}}$, hydraulic capacitance before turgor loss, per dry mass; Ψ_{tip} , water potential at the turgor loss point, Ψ_{sft} , osmotic potential at full turgor; RWC_{tip} , relative water content at the turgor loss point; $N_{s, \text{mass}}$, moles of osmotically active solutes, per dry mass.

be favored under differing (in this case artificial) selective conditions. This also is manifestly consistent with the hypothesis that wolf skull shape is one favored by selection in the wild. Roddy *et al.* apply similar reasoning to flowers vs leaves.

Flowers are a ubiquitous sight in daily life, but being mostly nonphotosynthetic and generally lacking transpiration, basic floral physiology has only recently attracted attention. Yet the flowers of some species do mimic leaves in some respects, albeit rarely. For

example, some species have pronounced petal venation, and stomata may be present on the petals or even pistils, while the green spathes of *Arum* lilies probably make significant photosynthetic contributions. But for the most part, the vast majority of flowers have none of this despite their shared developmental origins with leaves. Instead, it is selection for effective floral display (Chwil, 2009; Zhang *et al.*, 2018), and pollinator attraction that explains this diversity of floral form and function. From a plant's point of view, flowers are disposable organs that should be sufficiently appealing to get the job done but built as cheaply as possible. Given this 'Topshop' strategy, it is reasonable to expect that water relations must ultimately underpin the success of the floral display in attracting pollinators; nothing good can come from flaccid flowers.

Recognizing that both flowers and leaves occupy a similar canopy microclimate, Roddy *et al.* wondered how the water relations of these organs compare given that leaves are persistent autotrophs as opposed to flowers, which are ephemeral heterotrophs, the evolution of which is shaped primarily by factors other than metabolic activity. On the one hand, selection favors specific floral morphology but on the other hand, the physiological demands of producing and maintaining the floral display may counteract particular possible phenotypes. Roddy *et al.* discovered that flowers had significantly higher saturated water content and capacitance than leaves, along with a higher (less negative) turgor loss point. When coupled with a lower bulk modulus of elasticity (flexible cells), the data overwhelmingly support the hypothesis that flowers rely on capacitance to buffer water loss and maintain turgor. Simply put, flowers, in contrast to leaves, are delicate mechanical hydrostats, the physiology of which is attuned to their inherent expendability. Roddy *et al.*'s results (Fig. 1b) highlight the way that different parts of the same organism can have radically different characters.

Just as the very different selective contexts of domestic dogs lead to a much wider array of variation in skull shape, so too the very wide range of floral selective contexts might lead to a much wider, and largely non-overlapping, array of trait combinations as compared to leaves (Fig. 1b). This result is consistent with the expectation that, if the trait combinations found in leaves are the product of selection, then alternatives that differ in performance should be developmentally possible, and that these variants should be heritable and capable of responding to selection. Whereas Drake & Klingenberg (2010) used the results of artificial selection in their study, Roddy *et al.* leveraged the variation in selective contexts in natural situations across flowers and leaves. But the reasoning is the same: if a given pattern is the result of adaptation, then by definition heritable variants are (or were at one time) producible, and these variants should have lower fitness than the commonly observed ones.

Studying the interaction between adaptation, contingent events in evolution, and the dynamics of development requires adducing many layers of evidence, and there is no one 'smoking gun' (Pigliucci, 2007). These layers of evidence come from three main sources (Olson & Arroyo-Santos, 2015), which are optimality models, population biology, and the comparative method, as used by Roddy *et al.* So, while additional theory and empirical data are needed to build our understanding of the causes behind many, perhaps most, of the patterns of trait association in plant–water relations, Roddy *et al.* showcase the way forward in testing the


central and often overlooked assumption of the existence of developmental alternatives, and this is indeed cause for much admiration.

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