Fast evolving flowers drive cactus diversification

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Abstract

The rise of biodiversity is shaped by variation in diversification rates. Across the Tree of Life, numerous forces are thought to influence these rates, including the evolution of adaptive traits, climate change, and interactions with other organisms. In the flowering plants, a longstanding hypothesis favoured by Darwin suggests that floral evolution is a driving force for plant diversity. However, this remains to be tested in detail across many diverse plant groups. Here, we test this in the cactus family, an iconic and rapidly diversifying plant family, by using the widely recorded but underexplored metric of floral length. Floral length itself shows no association with speciation rate. In contrast, the underlying rate of floral-length evolution is a strong positive predictor of speciation. The rate at which floral traits change is more important for generating new species than any particular floral form. Specific morphologies, which are shaped by adaptation to pollinators, are less important than previously thought. This work emphasises the role of “evolvability” in plant macroevolution and provides new evidence for the floral diversification hypothesis. Trait rate is more important than trait state.

Introduction

The cactus family, an iconic component of diverse ecosystems in the Americas, exhibits some of the fastest diversification rates across the plant Tree of Life (1). Some ~1,500-1,850 species have originated over the past 20-35 million years (Ma), which have evolved highly specific adaptations to often difficult environments, most notably arid ecosystems in which their species richness is highest (2). This is why a major hypothesis for the rapid diversification of cacti invokes aridification (3). As arid environments spread, succulent or succulent-pre-adapted plants are thought to have had a competitive advantage over others. However, recent work revealed the importance of other forces, identifying an interacting mixture of climate variables, plant height and geographic range size (4). This shift in perspective suggests we should explore the role of additional drivers of diversification, beyond aridification (5).

Cacti are perhaps best known for their succulent adaptations and unusual morphological variation, having evolved different forms from tiny globose species to giant columnars and sprawling epiphytes (6, 7). However, their floral variation, although greatly celebrated by collectors, also varies greatly in size, shape and colour (8). Floral variation plays a central role in plant reproduction and diversification, partly because flowers are the interface between plants and their pollinators (9). This is especially true for cacti, many of which have short-lived flowers and specific phenologies (e.g. night blooming (8)), suggesting that floral variation is under strong natural selection to ensure reproduction.

Differences in flower size, shape, and color can influence the specificity and efficiency of pollination, alter mating systems, and promote reproductive isolation between lineages (9). This has been a major focus in evolutionary biology since Darwin’s early work on orchids (10). In many angiosperm groups, shifts in floral traits are strongly associated with pollinator transitions, which in turn can drive bursts of speciation (11). In cacti, flowers vary from small and open flowers accessible to generalist insects to elongated, tubular or funnelform flowers specialised for hummingbirds, bats, or hawkmoths (8). The latter floral form is considered derived and was thought to have faster diversification rates, with bees the likely ancestral pollinators, and bee-pollinated cacti speciating at slower rates (12), although recent work found that pollinator variation is less important than other forces (4). Nevertheless, this predicts a positive association between overall flower size and diversification rate. By analysing flower length, we can overcome the scarcity of pollinator data for cacti (6, 12) and incorporate more variation than simple discrete statistical treatments previously used (4, 12). Moreover, a phylogenetic generalised least squares models (PGLS) using sparse pollinator data (6) confirms that flower length is strongly predictive of pollinator, with derived pollinator groups (bats, birds, moths) associated with significantly longer flowers than ancestral bee-pollination ($\beta = 0.5514 \pm 0.0917$, $t = 6.01$, $p < 0.00001$, $R^2 = 0.1094$).

We assembled and analysed a dataset of floral length for 774 species sampling 107/150 genera and all subfamilies except the paraphyletic Pereskioideae (for which only width data were available), and found ~185-fold variation. There is much more floral length variation in subfamily Cactoideae (mean = 6.51 cm, SD = 6.02 cm, n = 670) than in the less species rich Opuntioideae (mean = 5.09 cm, SD = 2.21 cm, n = 103), a similar pattern to the variation observed in growth forms and sizes (4). Floral length variation has strong phylogenetic signal (Pagel's lambda = 0.87, $P < 0.00001$), revealing that closely related species have similar morphologies, and highlighting the necessity for phylogenetic comparative methods to account for statistical non-independence (13). When associating variation in floral length with speciation rates estimated with Bayesian Analysis of Macroevolutionary Mixtures (BAMM, (14)), which has been shown to perform best in similar studies (15), we find there is no relationship. PGLS (16) detected no significant effect of log-transformed floral length on speciation rates ($\beta = 0.0173 \pm 0.0136$, $p = 0.204$, $R^2 = 0.0008$), and STRAPP permutation tests (17) similarly found no correlation (Pearson $r = -0.027$, $p = 0.855$) (Figure 1). Despite long-standing expectations that shifts toward specialised pollination syndromes with longer flowers should accelerate speciation (12), floral variation in cacti has little impact on their macroevolution.

However, this ~185-fold variation in floral lengths evolved heterogeneously (Figure 1), and underlying rates of phenotypic evolution can be powerful predictors of speciation (15, 18). Comparing Bayesian models of variable rates and non-variable evolution (19) with BayesTraits (https://www.evolution.reading.ac.uk/), we find decisive evidence for variable rates throughout the history of cactus flower evolution (Bayes Factor = > 695). There are multiple accelerations in flower length evolution, found primarily in the Cacteae, Cereeae and Phylllocacteae tribes of subfamily Cactoideae, and relative stasis is recovered in subfamily Opuntioideae (Figure 1). The variable rates method provides estimates of species-specific phenotypic evolution (20, 21) and has been shown to perform best when assessing links with diversification rate (15). PGLS detected a strongly positive association between rates of floral length evolution and speciation rates ($\beta = 0.7151 \pm 0.0566$, $p < 0.00001$, $R^2 = 0.1709$, and STRAPP permutation tests found a significant correlation (Pearson $r = 0.410$, $p = 0.022$). This suggests that the tempo of floral evolution, rather than floral variation itself, plays a large role in accelerating speciation in the cactus family. Trait rate is more important than trait state.

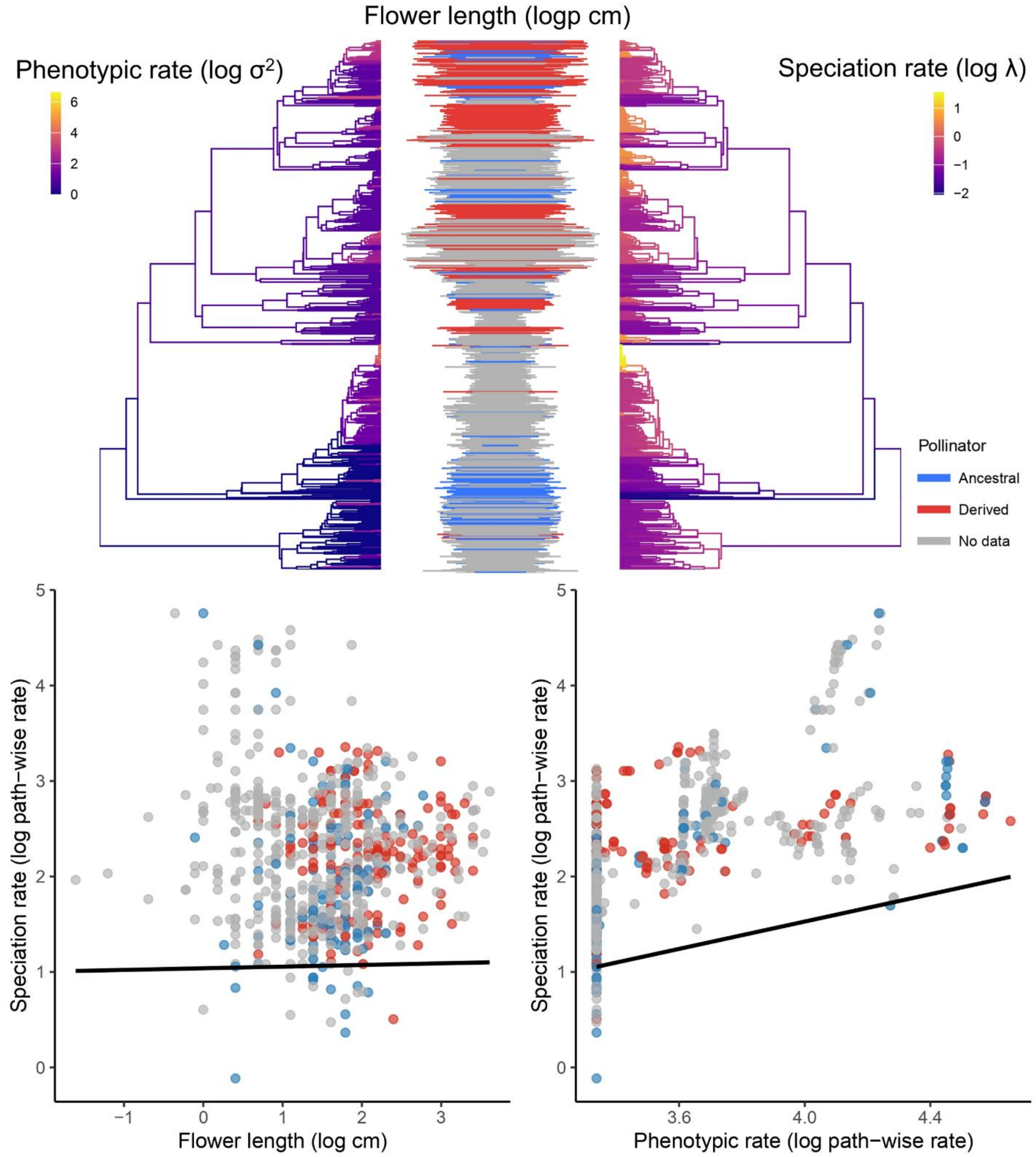

Figure 1: Evolutionary rates, not endpoints, predict cactus diversification. Top left: a phylogeny with branches coloured by phenotypic rate of floral-length evolution (log σ²; BayesTraits (19)). Top right: the mirrored phylogeny with branches coloured by speciation rate (log λ; BAMM (14, 19)). Warmer colours indicate faster rates. Top centre: flower length (logp for visualisation ease), coloured by pollination state (ancestral = blue, derived = red, no data = grey). Flower length ranges from 0.2-37cm. Bottom: phylogenetically controlled fits (black lines)

show no association between flower size and speciation (left), but a positive association between phenotypic rate and speciation (right). Species are coloured by pollination state. In the bottom figures, rates are modelled as path-wise (root-to-tip transformed phylogenetic distances).

Despite variation in floral morphology across the family that is shaped by pollinator adaptation, flower size itself is not linked to speciation rate, and it is the rate of floral evolution that drives speciation. This challenges a long-standing expectation that the evolution of specialised flowers shapes the rise of plant biodiversity. Our findings depart from previous work (12) but strengthen recent findings using more nuanced statistical methods (4, 5). This provides new hypotheses for cactus origins beyond aridification (3) and pollinator divergence (12), both of which have been questioned (4, 5).

Bursts of floral change, which are found primarily in Cactoideae tribes, are associated with higher speciation rates. A potential explanation linking floral evolution and repeated reproductive isolation is because novel floral forms may interact with different pollinators, undergo mating system changes, or exploit new ecological conditions, even if no single morphology is consistently advantageous. In arid ecosystems where cactus species richness is highest, fluctuating ecological conditions, previously linked to speciation (4), and specialised pollinator communities may further increase the impacts of evolvability.

These findings provide new insights into the evolutionary origins of plant biodiversity and reframe longstanding hypotheses. Across angiosperms, growing evidence shows that while floral variation is great and pollinator shifts common, their macroevolutionary consequences are inconsistent or context-dependent (22–24). By revealing the strong power of trait rates, instead of trait states, our findings support the power of “evolvability” in shaping plant macroevolution. It is not the endpoint of floral evolution, but the ability to evolve floral variation rapidly, that drives rapid plant radiations. Testing whether this pattern extends to other angiosperm groups, especially those with great floral and pollinator diversity such as orchids, will be informative for reassessing the prevalence and mechanism of Darwin’s floral diversification hypothesis (10).

Materials and Methods

Flower length variation was gathered largely from a comprehensive encyclopedia of cactus diversity (8), with additional data from literature and online databases. These data, along with sparser data on flower widths and descriptive data on floral colour and shape, are now available for further analysis in the new Cactus Ecological Database (CactEcoDB) (6). The version 2 phylogeny of CactEcoDB was used, which was reconstructed using a supermatrix of 18 loci for 1063 species (4). It has been remade since the original analyses of (4), and is now informed by a phylogenomic backbone (25). Speciation rates were re-estimated using BAMM (14) and are also available in CactEcoDB, replacing those calculated from the version 1 phylogeny (4). Here, we used the median root-to-tip distance (path-wise) on a phylogeny with branch lengths scaled by speciation rate. A PGLS assessed whether pollinator mode (ancestral vs derived pollinator, as in (12)) shapes floral lengths (16, 26), with pollinator data from CactEcoDB. The phylogenetic signal of log transformed floral lengths was calculated using Pagel’s lambda (13) with the R package phytools (27). Contrasting models of floral trait evolution, either with or without rate variation (19), were estimated with the package BayesTraits (https://www.evolution.reading.ac.uk/), and Bayes Factor support calculated with log marginal likelihoods calculated by stepping stone sampling. The output from the variable rates model was processed using scripts from BayesTraitR (https://github.com/joannabaker/BayesTraitR) and the median path-wise distance was calculated as a measure of species-specific phenotypic evolution (19–21). Relationships between floral length and rates of floral length evolution were assessed with PGLS and STRAPP (17, 28).

Data availability

All code will be made available in GitHub (https://github.com/jamie-thompson/cactus_flowers) and data will be made available in CactEcoDB (6) upon acceptance for publication.

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