Faster speciating cacti have faster evolving flowers

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Faster speciating cacti have faster evolving flowers

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The rise of biodiversity is shaped by variation in speciation rates. Across many taxonomic groups, both trait values and the rates at which traits evolve have been proposed to influence diversification, but these factors can act independently. Here, we test two competing hypotheses in the cactus family, that speciation depends on flower length variation or on the rate of evolutionary change in flower length. Across >750 species in 107 genera, we find that flower length is only weakly related to speciation, whereas the rate of flower-length evolution is a strongly positive predictor. Moreover, flower length and rate of evolutionary change in flower length are only weakly correlated, indicating that rapid change, rather than any particular floral morphology, underlies cactus diversification. These results challenge expectations that specialized morphologies accelerate diversification, suggesting instead that in cacti, it is the tempo of floral change, rather than any particular floral form, that explains their extraordinary diversity.

1. Introduction

The cactus family, an iconic component of diverse ecosystems in the Americas, has undergone one of the fastest radiations in the plant Tree of Life, producing approximately 1850 species in the past 20–35 million years [1,2]. Popular explanations attribute this diversity to aridification, which gave succulent or pre-adapted lineages a competitive advantage [3]. Yet recent work suggests a more complex picture, involving climate, plant height and geographical range size, and points to additional drivers of speciation [4,5].

Cacti are best known for their succulent adaptations and unusual morphological variation, ranging from tiny globose species to giant columnars and sprawling epiphytes [6,7]. Their flowers, which are celebrated by collectors, are equally diverse, varying widely in length, shape and colour [8]. Owing to the fact that flowers mediate reproduction through interactions with pollinators, floral traits are central to plant speciation [9]. This is especially true for cacti, many of which produce short-lived and precisely timed flowers (e.g. night blooming [8]) that are subject to strong natural selection to secure pollination.

Differences in flower length, shape and colour can influence the specificity and efficiency of pollination, influence mating systems and promote reproductive isolation [9]. Since Darwin's studies of orchids, such shifts in floral traits have been recognized as potential drivers of speciation [10]. In many angiosperm groups, transitions between pollinators coincide with bursts of speciation [11]. In cacti, flowers vary from small and open flowers accessible to generalist insects to elongated, tubular or funnelform flowers specialized for hummingbirds, bats or hawkmoths [8]. The latter floral form is considered derived and was thought to have faster speciation 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 length and speciation rate.

To explicitly test these ideas, we evaluated two complementary hypotheses linking floral morphology and diversification. First, that flower length promotes speciation, if longer and more specialized flowers enhance pollinator specificity and reproductive isolation. To assess this, we first tested whether flower length predicts pollination mode across the cactus phylogeny, confirming that it can serve as a proxy for pollinator specialization, and then examined whether longer flowers are associated with faster speciation. Second, we tested whether the rate of flower-length evolution, rather than flower size itself, predicts speciation by generating rapid morphological change and new opportunities for isolation. We capture this relationship both with tip-rate dynamics in recent geological time and across the full evolutionary history of cacti, allowing us to evaluate the association across multiple evolutionary timescales.

2. Results and discussion

We assembled flower lengths for 774 species, representing 107 of 150 genera and all subfamilies except the paraphyletic Pereskioideae (for which only width data were available). Floral length spans approximately 185-fold variation across the family. More of this floral length variation occurs in the subfamily Cactoideae than in the less species-rich Opuntioideae (figure 1), echoing similar patterns in growth forms and plant height [4]. Floral length variation has strong phylogenetic signal (§3), revealing that closely related species have similar morphologies and highlighting the necessity for phylogenetic comparative methods [15].

Despite sparse pollinator data [6], a phylogenetic generalized least squares (PGLS) [16] analysis confirms that longer flowers strongly associated with derived pollination by bats, birds and moths, while shorter flowers correspond to ancestral bee pollination ($\beta = 0.55 \pm 0.09$, $t = 6.01$, $p = 5.62 \times 10^{-9}$, $R^2 = 0.11$, §3, figure 1). 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].

We then tested whether flower length is associated with speciation rates (§3), widely used in comparable studies [17]. In these tests, we investigated both the commonly used tip speciation rates [18], as well as pathwise rates that capture the full evolutionary history of diversification [17]. Using PGLS, we detected no significant effect of floral length on pathwise speciation rates ($\beta = 0.017 \pm 0.014$, $p = 0.20$, $R^2 = 0.0008$) or tip rates ($\beta = 0.002 \pm 0.005$, $p = 0.71$, $R^2 = 0.0002$). Similarly, structured rate permutations on phylogenies (STRAPP) tests [19] found no correlation with tip rates (Pearson $r = -0.027$, $p = 0.86$) (figure 1). Contrary to long-standing expectations that specialized, long-flowered lineages diversify more rapidly [12], flower length has little impact on cactus macroevolution.

However, this approximately 185-fold variation in flower length did not arise evenly across the family (figure 1). Bayesian phylogenetic model comparisons show strong support for variable rates of floral evolution (Bayes factor > 695, §3), with repeated accelerations in the Cacteae, Cereeae and Phyllocacteae of subfamily Cactoideae, while most Opuntioideae evolves at slower background rates (figure 1).

These species-specific rate estimates, derived from variable-rates models [13,20,21], quantify the tempo of floral evolution for each branch and thus can be directly compared with speciation rates [17,22]. Because evolutionary rates and trait magnitudes can covary, we first tested whether flower length and its rate of evolution are correlated. This relationship was weak, explaining only a minute proportion of variation (PGLS: $\beta = -0.26 \pm 0.12$, $p = 0.038$, $R^2 = 0.004$; electronic supplementary material), indicating that these predictors capture distinct orthogonal evolutionary processes. In contrast, the rate of floral evolution was strongly and positively associated with pathwise speciation (PGLS: $\beta = 0.72 \pm 0.06$, $p < 2.2 \times 10^{-16}$, $R^2 = 0.17$) and tip speciation (STRAPP: $r = 0.41$, $p = 0.022$; PGLS: $\beta = 0.18 \pm 0.04$, $p < 10^{-6}$, $R^2 = 0.034$). Multiple regression confirmed that this effect remains robust after accounting for flower length in pathwise speciation rates ($\beta = 0.73 \pm 0.06$, $p < 2.2 \times 10^{-16}$), while the independent contribution of length itself was minor ($\beta = 0.03 \pm 0.01$, $p = 0.01$; $\Delta R^2 = 0.006$; electronic supplementary material, figure S1). Using tip speciation rates, the rate of floral evolution remained a significant predictor ($\beta = 0.18 \pm 0.04$, $p = 2.63 \times 10^{-7}$), but flower length had no independent effect ($\beta = 0.003 \pm 0.005$, $p = 0.60$). Thus, the evolutionary tempo of floral change, not flower size itself, is the key predictor of speciation in cacti.

Despite striking floral diversity across the cacti tree, shaped in part by adaptation to pollinators, flower size itself is not linked to speciation. Instead, it is the rate of floral evolution that drives evolution of new species and predicts speciation. This challenges a long-standing expectation that the evolution of specialized flowers shapes the rise of plant biodiversity. Our results depart from previous work [12] but reinforce findings from recent studies using more nuanced approaches [4,5]. They also point to new hypotheses for cactus origins and diversity beyond aridification [3] and pollinator divergence [12].

Bursts of floral change, concentrated in several Cactoideae tribes, are associated with higher speciation. Novel floral forms may repeatedly generate reproductive isolation by engaging different pollinators, altering mating systems or opening ecological opportunities, even if no single morphology consistently confers an advantage. In the arid regions where cactus richness peaks, fluctuating ecological conditions and specialized pollinator communities may have further amplified the consequences of rapid floral evolution.

These findings provide new insights into the evolutionary origins of plant biodiversity and reframe long-standing hypotheses. Across angiosperms, growing evidence shows that while floral variation is great and pollinator shifts common, their macroevolutionary consequences are inconsistent or context-dependent [23–26]. By showing that evolutionary tempo rather than trait endpoints (in this case, flower length) explains speciation in cacti, we highlight the importance of rapid trait change in shaping plant radiations. Testing whether this pattern holds across other groups with extreme floral and pollinator diversity,

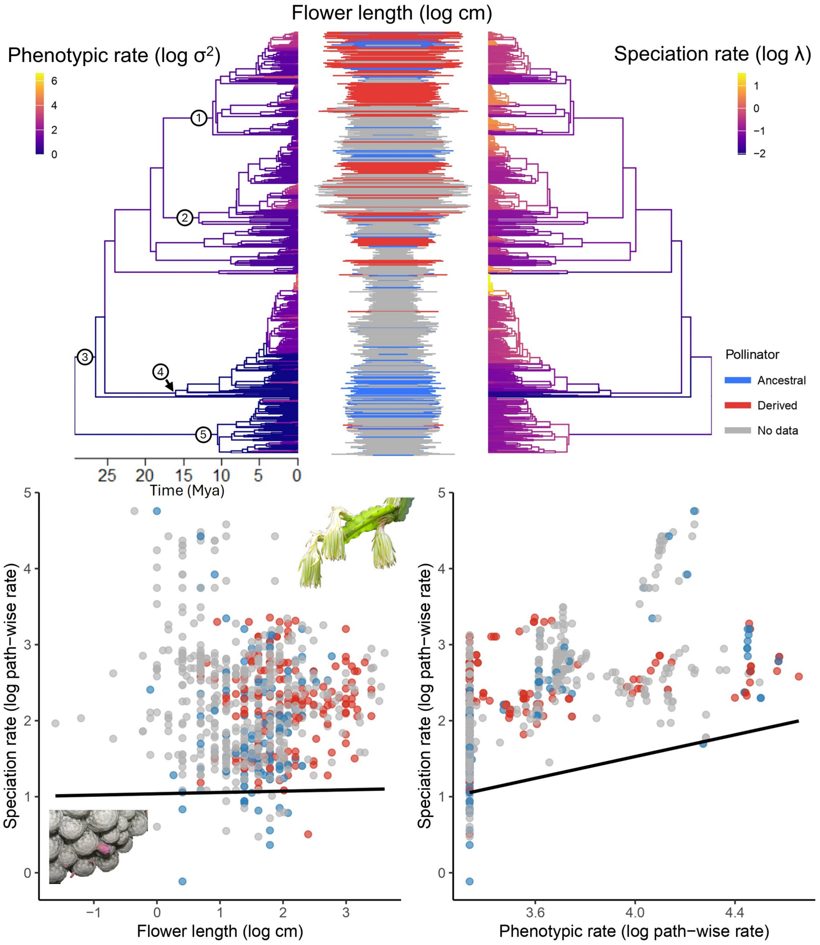

Figure 1. Evolutionary rates, not endpoints, predict cactus speciation. Top left: a phylogeny with branches coloured by phenotypic rate of floral-length evolution (log σ^2; BayesTraits [13]). The timescale is in units of million years. Numbers on branches indicate tribes and subfamilies highlighted in the results with elevated or depressed rates (1 = Cereeae; 2 = Phyllocacteae; 3 = Cactoideae; 4 = Cacteae; 5 = Opuntioideae). Top right: the mirrored phylogeny with branches coloured by speciation rate (log λ; BAMM [14]). Warmer colours indicate faster rates. Top centre: flower length (log for visualization ease), coloured by pollination state (ancestral = blue, derived = red, no data = grey). Flower length ranges from 0.2 to 37 cm. 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). Examples from genera with short and long flowers are displayed (Mammillaria and Hylocereus, mean 2.1 cm and 26.5 cm, respectively). Photographs are used under Creative Commons licences with modifications. Images of Mammillaria and Hylocereus are adapted from photographs by 阿橋花譜 KHQ Flower Guide (licensed under Creative Commons Attribution–ShareAlike 2.0) and Forest & Kim Starr (licensed under Creative Commons Attribution 3.0), respectively.

such as orchids, will be crucial for reassessing the mechanisms behind Darwin's floral speciation hypothesis [10,26]. With this in mind, Darwin's floral speciation hypothesis gains a new interpretation: it is not necessarily the new form flowers take, but the speed at which they evolve that drives the rise of biodiversity.

3. Material and methods

(a) Trait data and phylogenetic framework

Flower length variation was gathered largely from a comprehensive encyclopaedia of cactus diversity [8], with additional data from literature and online databases. We used maximum length to avoid issues associated with incomplete or diseased specimens. These data are to be made available for further analysis in the new Cactus Ecological Database (CactEcoDB) [6]. We retrieved pollinator data from CactEcoDB [6], which was originally compiled by Thompson *et al.* [4]. The v. 2 phylogeny from CactEcoDB was used, which is built from a supermatrix of 18 loci for 1063 species [4]. This has been remade since the original analyses of [4] and is now informed by a recently published phylogenomic backbone [27] (see [6,27] for a detailed description of the backbone).

(b) Estimation of speciation and phenotypic rates

Speciation rates estimated using BAMM [14] were also retrieved from CactEcoDB [6], where they were run for 50 million generations, sampling every 5000 and discarding the first 10% as burn-in. We used the R package BAMMtools [28] to calculate tip speciation rates to capture contemporary evolutionary dynamics, as is common in evolutionary research [18]. We also calculated root-to-tip patristic phylogenetic distance (described as path-wise [20]), on a phylogeny with branch lengths scaled by the median speciation rate of the posterior sample [17]. Contrasting models of floral trait evolution, either with or without rate variation [13], were estimated with the package BayesTraits v. 4 (https://www.evolution.reading.ac.uk/), and Bayes Factor support assessed with log marginal likelihoods calculated by stepping stone sampling. These analyses were run for 50 million Markov chain Monte Carlo (MCMC) generations each, sampling every 5000, with the first 10% discarded as burn-in. The output from the variable rates model was processed using scripts from BayesTraitR (https://github.com/joannabaker/BayesTraitR), and the median pathwise distance was calculated as a measure of species-specific phenotypic evolution [13,20,21].

(c) Comparative analyses of floral evolution and speciation

A PGLS assessed whether pollinator mode (ancestral versus derived pollinator, as in [12]) shapes log-transformed floral lengths [16,29]. The phylogenetic signal of log-transformed floral lengths was calculated using Pagel's lambda [15] with the R package phytools [30]. Relationships between floral length, rates of floral length evolution and speciation (both pathwise and tip) were assessed using PGLS [29]. Pearson correlations involving tip speciation rates were additionally performed using STRAPP [19] in BAMMtools [28], which accounts for uncertainty in speciation-rate estimates across the posterior sample estimated with BAMM. All underlying data and results are available at Figshare [31].

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Underlying data, code and results are available from GitHub (https://github.com/jamie-thompson/cactus_flowers) and Figshare [31]. Flower length data are also made available in CactEcoDB [6].

Supplementary material is available online [32].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. J.B.T.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, validation, visualization, writing—original draft, writing—review and editing; C.V.: conceptualization, formal analysis, investigation, methodology, project administration, resources, software, supervision, visualization, writing—original draft, writing—review and editing.

Both authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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References

1. Magallón S, Sánchez-Reyes LL, Gómez-Acevedo SL. 2019 Thirty clues to the exceptional diversification of flowering plants. *Ann. Bot*. **123**, 491–503. (doi:10.1093/aob/mcy182)
2. Griffiths H, Males J. 2017 Succulent plants. *Curr. Biol*. **27**, R890–R896. (doi:10.1016/j.cub.2017.03.021)
3. Arakaki M, Christin PA, Nyffeler R, Lendel A, Eggli U, Ogburn RM, Spriggs E, Moore MJ, Edwards EJ. 2011 Contemporaneous and recent radiations of the world's major succulent plant lineages. *Proc. Natl Acad. Sci. USA* **108**, 8379–8384. (doi:10.1073/pnas.1100628108)
4. Thompson JB, Hernández-Hernández T, Keeling G, Vásquez-Cruz M, Priest NK. 2024 Identifying the multiple drivers of cactus diversification. *Nat. Commun*. **15**, 7282. (doi:10.1038/s41467-024-51666-2)
5. Thompson J, Ramírez-Barahona S, Priest N, Hernández-Hernández T. 2023 Did succulents diversify in response to aridity? Evolutionary analyses of major succulent lineages around the world. *bioRxiv*. (doi:10.1101/2023.05.23.541957)
6. Thompson JB *et al*. 2026 CactEcoDB: trait, spatial, environmental, phylogenetic and diversification data for the cactus family. *Sci Data* (doi:10.1038/s41597-026-06936-7)
7. Hernández-Hernández T, Hernández HM, De-Nova JA, Puente R, Eguiarte LE, Magallón S. 2011 Phylogenetic relationships and evolution of growth form in Cactaceae (Caryophyllales, Eudicotyledoneae). *Am. J. Bot*. **98**, 44–61. (doi:10.3732/ajb.1000129)
8. Anderson EF. 2001 *The cactus family*. Portland, OR: Timber Press.
9. Soltis PS, Soltis DE. 2014 Flower diversity and angiosperm diversification. In *Flower development*, pp. 85–102. New York, NY: Humana Press. (doi:10.1007/978-1-4614-9408-9_4)
10. Darwin C. 1862 *On the various contrivances by which British and foreign orchids are fertilised by insects: and on the good effects of intercrossing*. London, UK: J. Murray. (doi:10.1017/CBO9780511910197)
11. Van der Niet T, JohnsonSD. 2012 Phylogenetic evidence for pollinator-driven diversification of angiosperms. *Trends Ecol. Evol.* **27**, 353–361. (doi:10.1016/j.tree.2012.02.002)
12. Hernández-Hernández T, Brown JW, Schlumpberger BO, Eguiarte LE, Magallón S. 2014 Beyond aridification: multiple explanations for the elevated diversification of cacti in the new world succulent biome. *New Phytol*. **202**, 1382–1397. (doi:10.1111/nph.12752)
13. Venditti C, Meade A, Pagel M. 2011 Multiple routes to mammalian diversity. *Nature* **479**, 393–396. (doi:10.1038/nature10516)
14. Rabosky DL. 2014 Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. *PLoS One* **9**, e89543. (doi:10.1371/journal.pone.0089543)
15. Pagel M. 1999 Inferring the historical patterns of biological evolution. *Nature* **401**, 877–884. (doi:10.1038/44766)
16. Freckleton RP, Harvey PH, Pagel M. 2002 Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat*. **160**, 712–726. (doi:10.1086/343873)
17. Cooney CR, Thomas GH. 2020 Heterogeneous relationships between rates of speciation and body size evolution across vertebrate clades. *Nat. Ecol. Evol*. **5**, 101–110. (doi:10.1038/s41559-020-01321-y)
18. Title PO, Rabosky DL. 2019 Tip rates, phylogenies and diversification: what are we estimating, and how good are the estimates? *Methods Ecol. Evol*. **10**, 821–834. (doi:10.1111/2041-210x.13153)
19. Rabosky DL, Huang H. 2016 A robust semi-parametric test for detecting trait-dependent diversification. *Syst. Biol*. **65**, 181–193. (doi:10.1093/sysbio/syv066)
20. Baker J, Meade A, Pagel M, Venditti C. 2015 Adaptive evolution toward larger size in mammals. *Proc. Natl Acad. Sci. USA* **112**, 5093–5098. (doi:10.1073/pnas.1419823112)
21. Baker J, Meade A, Pagel M, Venditti C. 2016 Positive phenotypic selection inferred from phylogenies. *Biol. J. Linn. Soc*. **118**, 95–115. (doi:10.1111/bij.12649)

22. Rabosky DL, Santini F, Eastman J, Smith SA, Sidlauskas B, Chang J, Alfaro ME. 2013 Rates of speciation and morphological evolution are correlated across the largest vertebrate radiation. *Nat. Commun*. **4**, 1958. (doi:10.1038/ncomms2958)
23. Gravendeel B, Smithson A, Slik FJW, Schuiteman A. 2004 Epiphytism and pollinator specialization: drivers for orchid diversity? *Phil. Trans. R. Soc. Lond. B* **359**, 1523–1535. (doi:10.1098/rstb.2004.1529)
24. Givnish TJ *et al*. 2015 Orchid phylogenomics and multiple drivers of their extraordinary diversification. *Proc. R. Soc. B* **282**, 20151553. (doi:10.1098/rspb.2015.1553)
25. Herting J, Schönenberger J, Sauquet H. 2023 Profile of a flower: how rates of morphological evolution drive floral diversification in Ericales and angiosperms. *Am. J. Bot*. **110**, e16213. (doi:10.1002/ajb2.16213)
26. Thompson JB, Hagen ER, Forward EA, Pérez-Escobar OA, Clark JW, Priest NK. 2025 Frequent shifts in pollination strategy are decoupled from diversification in the terrestrial orchids. *EcoEvoRxiv*. (doi:10.32942/X21P97)
27. de Vos JM, Eggli U, Nyffeler R, Larridon I, McGinnie C, Epitawalage N, Maurin O, Forest F, Baker WJ. 2025 Phylogenomics and classification of Cactaceae based on hundreds of nuclear genes. *Plant Syst. Evol.* **311**, 28. (doi:10.1007/s00606-025-01948-z)
28. Rabosky DL, Grundler M, Anderson C, Title P, Shi JJ, Brown JW, Huang H, Larson JG. 2014 BAMMtools: an R package for the analysis of evolutionary dynamics on phylogenetic trees. *Methods Ecol. Evol*. **5**, 701–707. (doi:10.1111/2041-210x.12199)
29. Orme D. 2013 The CAPER package: comparative analysis of phylogenetics and evolution in R. R package version 5. Vienna, Austria: R Foundation for Statistical Computing. See https://cran.r-project.org/web/packages/caper/index.html.
30. Revell LJ. 2012 Phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol*. **3**, 217–223. (doi:10.1111/j.2041-210x.2011.00169.x)
31. Thompson JB, Venditti C. 2026 Data from: Faster speciating cacti have faster evolving flowers. *Figshare*. (doi:10.6084/m9.figshare.31241725)
32. Thompson J, Venditti C. 2026 Supplementary material from: Faster speciating cacti have faster evolving flowers. Figshare. (doi:10.6084/m9.figshare.c.8340073)