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Review

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How the switch to hummingbird pollination has greatly contributed to our understanding of evolutionary processes

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Summary

The evolutionary switch to hummingbird pollination exemplifies complex adaptation, requiring evolutionary change in multiple component traits. Despite this complexity, diverse lineages have converged on hummingbird-adapted flowers on a relatively short evolutionary timescale. Here, I review how features of the genetic basis of adaptation contribute to this remarkable evolutionary lability. Large-effect substitutions, large mutational targets for adaptation, adaptive introgression, and concentrated architecture all contribute to the origin and maintenance of hummingbird-adapted flowers. The genetic features of adaptation are likely shaped by the ecological and geographic context of the switch to hummingbird pollination, with implications for future evolutionary trajectories.

I. Introduction

Pollinators impose distinct selective pressures on flowers, due to differences in their morphologies, sensory systems, and behaviors. In response, flowering plants have converged on specific combinations of floral traits associated with particular pollinators, despite unique evolutionary starting points (Stebbins, 1970; Fenster *et al*., 2004). These trait combinations or 'syndromes' suggest that common phenotypic solutions evolve in response to similar pollinator-mediated selective pressures. A distinctive example is the floral syndrome associated with hummingbird pollination: bright red narrowly tubular flowers with elongated reproductive organs that produce copious amounts of nectar and lack a floral scent (Fig. 1). Evolutionary shifts from insect to hummingbird pollination are favored in circumstances where hummingbirds are common and efficient relative to ancestral insect pollinators. Indeed, hummingbirds may be more effective at conducting outcrossed pollination events relative to bees (e.g. Castellanos *et al*., 2003). The hummingbird syndrome includes adaptations to attract and specialize on hummingbirds (e.g. red color, large nectar

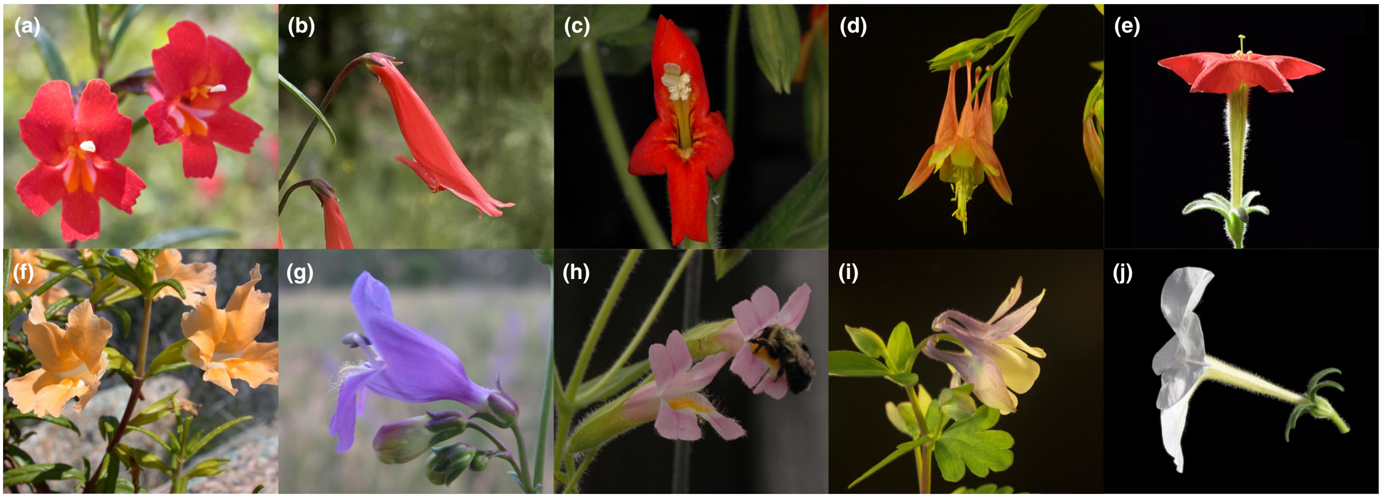

Fig. 1 Flowers adapted to hummingbird pollination (upper row), and their insect-pollinated relatives (lower row). (a) *Mimulus aurantiacus puniceus* (photograph: M. Streisfeld), (b) *Penstemon barbatus* (photograph: C. Wessinger), (c) *Mimulus cardinalis* (photograph: Y. Yuan), (d) *Aquilegia canadensis* (photograph: A. Ballerini), (e) *Petunia exserta* (photograph: R. Köpfli), (f) *Mimulus aurantiacus australis* (photograph: M. Streisfeld), (g) *Penstemon neomexicanus* (photograph: C. Wessinger), (h) *Mimulus lewisii* (photograph: Y. Yuan), (i) *Aquilegia brevistyla* (photograph: A. Ballerini), and (j) *Petunia axillaris* (photograph: R. Köpfli).

reward, and morphological fit to match hummingbirds) as well as traits that deter less efficient ancestral insect pollinators such as bees (e.g. absence of floral scent, absence of landing platform, and narrow floral tube).

The switch to hummingbird pollination is uniquely informative for considering the evolution of complex adaptations: Despite the complexity of this switch, requiring coordinated shifts in many types of traits, hummingbird pollination has evolved numerous times during the diversification of North American flora (Grant, 1994; Abrahamczyk & Renner, 2015), including repeated origins in some genera. In fact, many pairs of sister species with alternate floral syndromes (e.g. bee vs hummingbird) have been described (Thomson & Wilson, 2008), indicating that the hummingbird syndrome can evolve rapidly. Here, I discuss genetic features that may enable the origin and maintenance of this complex adaptation on a short evolutionary timescale.

II. Jumping toward a new phenotypic optimum through large-effect substitutions

The hummingbird syndrome is an evolutionary novelty that occupies a distinct adaptive peak in multi-trait space, widely separated from that of ancestral insect pollination (Fig. 2a). Theory predicts that an adaptive walk toward a new phenotypic optimum involves large mutational steps when the population is far from the new peak, followed by progressively smaller steps near the phenotypic optimum (Orr, 1998). Whether there is a predictable order to trait shifts during a switch to hummingbird pollination is unclear. We might expect that the initial steps are increased nectar and a shift to red flowers – key reward and signal traits to attract inquisitive hummingbirds – followed by later morphological adaptations to improve pollen transfer efficiency and deter less efficient pollinators (Fig. 2b; Thomson & Wilson, 2008). In this case, large-effect substitutions for reward and signal traits could allow a population to bridge fitness valleys between alternate floral syndromes and move the population rapidly toward a new adaptive peak.

Indeed, large-effect loci underpin reward and signal traits in diverse study systems. Pioneering QTL studies found large-effect loci contribute to floral divergence in bee-adapted *Mimulus lewisii* and hummingbird-adapted *M. cardinalis* (Bradshaw *et al.*, 1995, 1998). In this system, allelic differences in the flower color locus *YELLOW UPPER* (*YUP*) confer a major shift in pollinator attraction (Bradshaw & Schemske, 2003). Large-effect loci also underlie the evolution of red, hummingbird-adapted flowers in *Aquilegia canadensis* (Edwards *et al.*, 2021), *Jaltomata umbellata* (Kostyun *et al.*, 2019), *Mimulus aurantiacus* (Streisfeld *et al.*, 2013), *Penstemon barbatus* (Wessinger & Rausher, 2014), and *Petunia exserta* (Hermann *et al.*, 2013). Nectar production is not as easily or often measured as color and morphological traits. Yet, major-effect loci for nectar production have been characterized in several study systems, including *Mimulus* (Bradshaw *et al.*, 1995), *Penstemon* (Wessinger *et al.*, 2014), *Petunia* (Stuurman *et al.*, 2004), *Jaltomata* (Kostyun *et al.*, 2019), and *Rhytidophyllum* (Alexandre *et al.*, 2015). Thus, in many systems, large-effect loci for red color and increased nectar could help jumpstart an adaptive switch to hummingbird pollination.

III. The source of genetic variation for adaptive shifts

Rapid shifts to hummingbird pollination depend on the availability of relevant genetic variation, and a ready supply should accelerate adaptive shifts. *De novo* loss-of-function (LOF) mutations arise frequently due to a large mutational target size – there are many ways to inactivate a gene. Loss-of-function mutations are a surprisingly common ingredient in the switch to hummingbird pollination, particularly in the evolution of red flowers. In plants that produce anthocyanidin-based floral pigments, the resulting

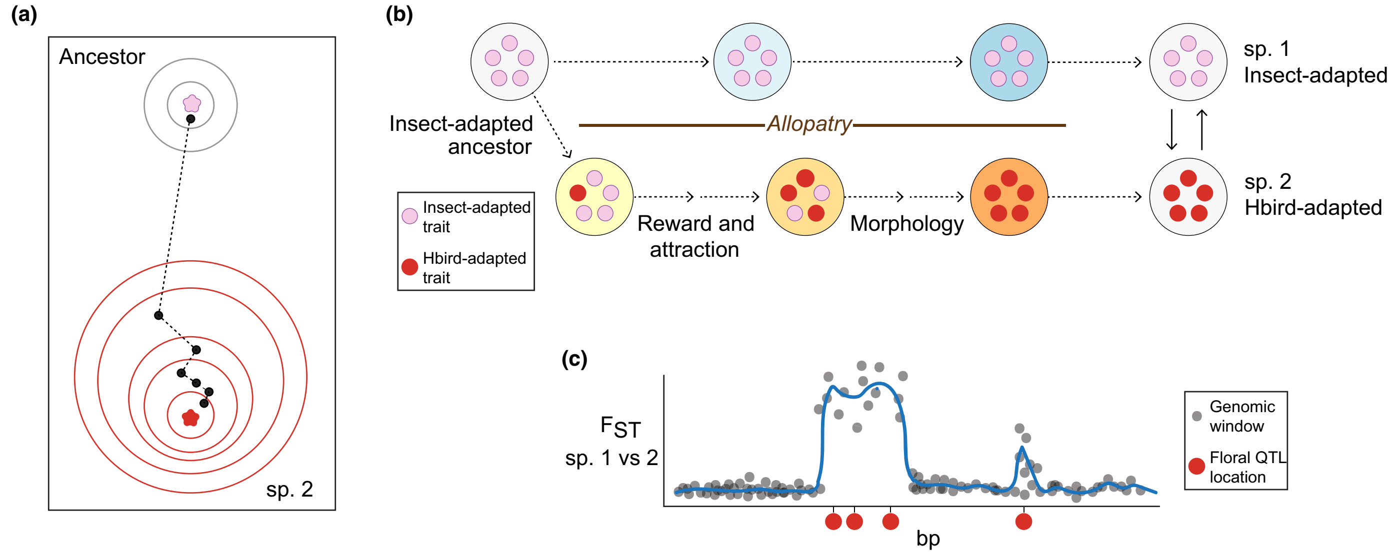

Fig. 2 Conceptual models of a switch to hummingbird pollination. (a) Adaptive landscape showing ancestral insect-pollination peak and derived hummingbird-pollination peak in multi-trait space, where dashed lines show mutational change with length corresponding to effect size. (b) Hypothesized order of trait evolution, where dashed arrows represent adaptive change, solid arrows represent gene flow, and background color of larger circle indicates differences in genetic backgrounds that accumulate in allopatry. (c) Expected genomic landscape of divergence (F_{ST}) between hummingbird-adapted and insect-adapted sister species in the face of gene flow. bp, base-pairs; hbird, hummingbird.

pigment hue is often determined by the number of hydroxyl groups attached to B ring of the anthocyanin molecule: a greater number of hydroxyl groups yields bluer pigment. A shift to red flowers from blue, purple, or pink may involve inactivation of hydroxylating enzymes. The genus *Penstemon* illustrates this mode of flower color evolution: repeated origins of red flowers in 12 different lineages have involved parallel but distinct LOF mutations to the coding sequence of *Flavonoid 3′,5′-hydroxylase* (Wessinger & Rausher, 2015). Recent studies have uncovered other, more exotic types of LOF mutations that underlie the evolution of red flowers. The *YUP* allele responsible for red flowers in *Mimulus cardinalis* involves a LOF mutation that disrupts a noncoding inverted repeat sequence that normally functions to silence the carotenoid pigment pathway (Liang *et al*., 2023). The shift from ancestral white to red flowers in *Petunia exserta* involved multiple genetic changes including a LOF mutation to the *MYB-FL* locus, which redirected flux in the flavonoid pathway from flavonol production to anthocyanin production and downregulation of an acyltransferase enzyme that causes bluish pigments to appear red (Berardi *et al*., 2021). These studies illustrate that LOF alleles can lead to red flowers regardless of the ancestral flower color.

Loss-of-function mutations arise relatively frequently – helpful for rapid evolutionary shifts – yet there is a catch: They tend to be recessive. In theory, new beneficial recessive alleles are unlikely to fix in randomly mating populations, a disadvantage known as Haldane's sieve (Haldane, 1927). Self-pollination can weaken the effects of Haldane's sieve, improving the conditions where a beneficial recessive mutation can contribute to pollinator adaptation (Charlesworth, 1992; Wessinger & Kelly, 2018). Thus, at least occasional selfing might be one explanation for the preponderance of recessive alleles contributing to the switch to hummingbird pollination (e.g. Bradshaw *et al*., 1998). Pollinator movement between flowers on the same plant can lead to incidental self-pollination in seemingly outcrossing species, whether they be insect- or hummingbird-adapted (e.g. Grant & Grant, 1968). While occasional selfing may facilitate adaptation via recessive alleles, selfing often carries a fitness cost in the form of inbreeding depression (Abrahamczyk *et al*., 2022). This cost of selfing is why specialization on effective pollinators is favored in the first place.

Another potential source of variation for rapid evolutionary shifts is pre-existing variation, for example standing genetic variation. In fact, the fixation probability of a newly beneficial allele from standing variation at mutation-selection balance is independent of dominance (Orr & Betancourt, 2001). Thus, recessive alleles could quickly be favored, particularly if occasional selfing accompanies a change in pollinator adaptation. In addition to standing variation, introgression of pre-existing hummingbird-adapted alleles from other taxa could bypass the long waiting times expected for sequential *de novo* mutations, a process that Stebbins (1989) speculated might fuel multiple origins of hummingbird pollination seen in genera such as *Aquilegia*, *Delphinium*, *Mimulus*, and *Penstemon*. Adaptive introgression is only plausible if reproductive isolating barriers are weak between hybridizing taxa. Moreover, alleles with large effects (whether that be large effects on individual traits or pleiotropic effects on multiple traits) or haplotypes of linked adaptive alleles should introgress more efficiently than polygenic traits specified by many unlinked loci. Our best example of adaptive introgression fueling a switch to hummingbird pollination comes from the *Mimulus aurantiacus* species complex: A major-effect regulatory mutation to the *MaMyb2* gene that confers red flowers has been transferred between lineages through introgression, facilitating repeated switches from yellow to red flowers (Stankowski & Streisfeld, 2015; Short & Streisfeld, 2023). Future phylogenomic studies using whole genome data could reveal whether introgression facilitated repeated shifts to hummingbird pollination in other systems.

IV. The maintenance of polygenic differences in recently diverged species

Gene flow between closely related taxa can break apart favorable combinations of alleles that build up during polygenic adaptation, a potential issue for sister species with alternate floral syndromes that co-occur in secondary contact. However, if alleles for hummingbird syndrome traits are 'concentrated' in the genome – underlying loci have large effects or are tightly linked so that they are inherited as a single locus – pollinator-mediated selection for divergent floral phenotypes will be more efficient at resisting the homogenizing effects of gene flow (Yeaman, 2022). Such regions should be detectable as genomic islands of elevated genetic divergence between hybridizing sister species (Fig. 2c).

In key study systems, adaptive alleles conferring hummingbird adaptation are bundled together in regions of low recombination, facilitating their joint inheritance. The switch to hummingbird pollination in *Petunia exserta* involved major-effect alleles specifying red color, UV-absorbing pigments, lack of floral scent, and elongated reproductive organs that are clustered in a supergene-like region of low recombination (Hermann *et al.*, 2013). This region also includes a locus involved in hybrid incompatibility with *P. axillaris* (Li *et al.*, 2023), an arrangement that may help to maintain floral differences in sympatry. A similarly concentrated architecture is found in the *M. lewisii* – *M. cardinalis* system, where *YUP* is located in a region of suppressed recombination with loci affecting anthocyanin content, nectar production, and floral organ length, along with a hybrid lethality factor (Bradshaw *et al.*, 1995, 1998; Fishman *et al.*, 2013). The genomic landscape of divergence between *M. lewisii* and *M. cardinalis* suggests this region has resisted gene flow between species and is detectable as a genomic island of differentiation above the genome-wide average (Nelson *et al.*, 2021).

While a concentrated genetic architecture involving tightly linked large-effect loci is the most efficient genetic architecture to keep adaptive combinations of alleles together, this arrangement is not required. Linkage disequilibrium among unlinked adaptive alleles can arise through strong selection and assortative mating. For example, in *M. aurantiacus*, hummingbird- vs hawkmoth-adapted ecotypes hybridize where ranges overlap. Although flower color differences between ecotypes involve a major-effect locus (Streisfeld *et al.*, 2013), divergence in other floral traits involves many loci of small effect that are scattered throughout the genome (Stankowski *et al.*, 2023). Genomic intervals that overlap floral QTLs do not exhibit elevated differentiation between ecotypes, suggesting these regions do not strongly resist gene flow relative to the genome-wide average (Stankowski *et al.*, 2023). Louisiana Irises show similar patterns: Admixture mapping in natural hybrid zones formed by the bee-adapted *Iris hexagona* and hummingbird-adapted *I. fulva* revealed most floral traits have a polygenic architecture of small-effect loci distributed throughout the genome that, again, are not particularly resistant to gene flow compared with genome-wide background patterns (Sung *et al.*, 2018). The patterns observed in *M. aurantiacus* and Louisiana Iris systems seem counterintuitive: Although floral syndromes are maintained despite gene flow between species, individual loci do not appear as outlier barriers to gene flow. Perhaps in these systems, divergent selection acting on a highly polygenic architecture of small-effect loci results in weak selection opposing gene flow at any individual locus.

V. Outlook

The switch to hummingbird pollination has been a particularly useful area to investigate the genetics of complex adaptations, since closely related species with divergent syndromes can easily be crossed for genetic analysis. Overall, results from genetic studies agree with theoretical predictions regarding the evolution of complex polygenic adaptations, including the distribution of effect sizes during an adaptive walk toward a new optimum, a bias toward mutations with large target sizes, and the role of genetic architecture in maintaining polygenic adaptation in the face of gene flow. Although comparatively fewer studies have examined the genetic basis of evolutionary shifts to other specialized pollination systems, these features are likely general to evolutionary shifts to a novel pollinator. For example, a shift to hawkmoth pollination in *Petunia* involves both a mix of large- and small-effect loci, including LOF alleles responsible for the evolution of white flowers (Stuurman *et al.*, 2004; Hoballah *et al.*, 2007). Although characterizing the genetic details of floral syndrome switches is relatively straightforward, we are still missing important details. For example, the genetic features of a pollinator switch should critically depend on the ecological and geographic context (Stebbins, 1989), which is currently mysterious for most of the study systems discussed here. Moreover, evolutionary genetic details will depend on whether selection acts on individual traits or trait combinations, which, in turn, may depend on the pollinator environment.

We also remain in the dark concerning how the genetic and ecological features of complex adaptation may scale up to shape macroevolutionary patterns. For example, a directional bias favoring shifts from insect to hummingbird pollination has been suggested, at least for western North American taxa (Grant & Grant, 1968; Thomson & Wilson, 2008). *Penstemon* shows enough evolutionary replication to detect this pattern, with at least 20 separate switches to hummingbird pollination and no obvious cases of reversals back to insect pollination (Wilson *et al.*, 2007; Wessinger *et al.*, 2019). However, studies in Neotropical groups find 'reversals' from hummingbird to insect pollinators are not rare (Stephens *et al.*, 2023). Perhaps there simply has not yet been enough time for reversals in North American groups to have left a macroevolutionary signature. Alternatively, perhaps in some groups, a switch to hummingbird pollination is relatively easy, but is difficult to reverse. Possible explanations include genetic constraints on reversals – LOF mutations underlying the switch to hummingbird pollination may be difficult to reverse through gene repair. However, the diversity of genetic mechanisms for phenotypic change suggests nature might find workarounds to genetic constraints. Ecological factors might be more important than genetic constraints in explaining why gains of hummingbird pollination are more common than losses in some groups of plants:

adaptation to highly efficient hummingbird pollinators can lead to the evolution of exclusionary traits that deter ancestral pollinators, so it would be difficult for these ancestral pollinators to once again exert selection on floral traits (Thomson & Wilson, 2008). In fact, such selective epistasis among traits may commonly shape patterns of complex adaptation. Accumulating studies of the switch to hummingbird pollination will help us begin to understand the relationships between ecological context, the genetics of adaptation, and macroevolutionary trends.

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Competing interests

None declared.

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