NEWS AND COMMENTARY

Adaptive evolution

The ecological genetics of floral traits

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Floral traits have fascinated evolutionary biologists since Darwin published 'The various contrivances by which orchids are fertilized by insects' in 1862. Because flowers are remarkably diverse and important for sexual reproduction in plants, floral traits are excellent subjects for studies of adaptive microevolution. In addition, floral traits are unique among plant traits because they can directly influence pollinator-mediated reproductive isolation between species. Consequently, floral traits can provide a direct link between patterns of evolution within species and rates of divergence between species.

A study recently published in *Heredity* (Ashman and Majetic, 2006) provides the first review of empirical studies on the quantitative genetics of floral traits. Their results indicate that floral evolution can be genetically constrained and point to the ecological conditions where these constraints will be more or less important. At the same time, this review highlights areas where more research is needed.

Quantitative genetics points to two possible constraints on adaptive evolution: first, natural selection on a trait will not result in adaptive evolutionary change if there is little genetic variation for that trait, and second, genetic covariation between traits can constrain their adaptive evolution if there is an indirect response to natural selection via correlated traits. Ashman and Majetic (2006) review estimates of genetic variation and covariation for floral traits of 41 species from 21 families, using heritabilities (h^2) and genetic correlations (r_g) as estimates of genetic variation and covariation, respectively. Their most interesting results address the effect of mating system, floral symmetry, and resource allocation on the quantitative genetics of floral traits.

Heritabilities for all classes of floral traits were lower in self-compatible species compared to self-incompatible ones, supporting Stebbins' (1957) 'evolutionary dead end' hypothesis for why self-pollination is relatively uncommon in angiosperms. Stebbins argued that because evolution in response to natural selection is slower for species with lower h^2, self-pollinating angiosperm species will not be able to respond to novel selection pressures and consequently may have elevated extinction rates. The evolution of selfing species from outcrossing ancestors is one of the most common evolutionary transitions in angiosperms and, as such, Stebbins' hypothesis has dominated the field of plant evolutionary biology. Despite the importance of Stebbins' hypothesis, empirical data supporting the reduction of h^2 in selfing species are scarce (Takebayashi and Morrell, 2001), making the review a significant contribution. Because self-compatible plant species can have mixed mating systems (both self-pollination and outcrossing), future studies should correlate the realized selfing rate with h^2 of floral traits to more definitively test whether adaptive evolution is genetically constrained in selfing species.

The review also supports Berg's (1960) hypothesis that traits of zygomorphic (bilaterally symmetrical) flowers with specialized pollinators are more strongly correlated than traits of actinomorphic (radially symmetrical) flowers with generalist pollinators. Berg predicted that floral integration (correlated variation in floral traits) should be stronger in zygomorphic species because it promotes precise pollination by restricting which pollinators can visit a flower, the direction from which they can approach, and their movement within the flower. Although widely cited in studies of floral evolution, the empirical data for some of Berg's (1960) hypotheses are weak (Armbruster *et al*, 1999). However, Ashman and Majetic (2006) found that r_g among floral traits of species with zygomorphic flowers were strong and positive relative to species with actinomorphic flowers, and suggest that high r_g among floral traits may constrain the adaptive evolution of zygomorphs. Interestingly, lineages with zygomorphic flowers are more speciose than those with actinomorphic flowers (Sargent, 2004), implying that high r_g among floral traits of

zygomorphs does not represent a long-term constraint on angiosperm evolution. Studies that focus on lineages with both actinomorphic and zygomorphic species could be useful in resolving this contradiction between patterns of genetic variation within species and speciation within clades.

Finally, mean r_g between flower size and number was not significantly different from zero, which does not support the hypothesis that the evolution of floral displays is genetically constrained by a trade-off between the size and number of flowers produced by a plant. This is a significant result because the inverse relationship between flower size and number is the type of resource allocation trade-off that underlies much of life history and sex allocation theory and is an assumption of many theoretical models of floral evolution. Ashman and Majetic's (2006) findings differ from three recent empirical studies (Caruso, 2004; Delph *et al*, 2004a, b), which found convincing evidence for negative r_g between flower size and number. These contrary results suggest that trade-offs between flower size and number may be more apparent in some angiosperm lineages than in others, but more estimates of genetic (or even phenotypic) correlations would be needed to test this hypothesis.

Ashman and Majetic (2006) tested an impressive number of hypothesized constraints on floral evolution, but the quality and quantity of studies included in the review suggest that their analyses need to be interpreted with caution. They analyzed h^2 and r_g because they were the most commonly reported parameters, but both are problematic. Heritabilities are ratios and thus can reflect changes in genetic variation, phenotypic variation, or both (Houle, 1992). Bivariate r_g may under- or overestimate constraints on evolution caused by indirect responses to natural selection (Blows and Hoffmann, 2005). In addition, the sample sizes for certain hypotheses, particularly those related to sexually dimorphic species, were as low as $N = 3$. Even though floral traits have been much more intensively studied than many other classes of plant traits, our ability to generalize about genetic constraints on floral evolution is still limited by a lack of quality data.

Although Ashman and Majetic's (2006) review indicates that the evolution of floral traits can be genetically constrained, it also highlights the difficulty of relating these intraspecific constraints to patterns of angiosperm

speciation. In particular, this relationship assumes that the same genes are responsible for intra- and interspecific differences in floral traits, an assumption that cannot be tested using estimates of h^2 and r_g. Fortunately, techniques such as quantitative trait locus (QTL) mapping may make it easier to relate the genes responsible for intra- and interspecific variation. For example, Hall *et al* (2006) found that many of the QTL underlying variation in floral traits within the wildflower *Mimulus gutttus* were also responsible for differences in floral traits between *Mimulus* species. Ashman and Majetic's (2006) review should inspire more such attempts to use modern molecular techniques to dissect the genetics of floral traits and their implications for angiosperm evolution.

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