

Commentary

Pollinator-mediated selection and floral evolution: from pollination ecology to macroevolution

Pollination as an evolutionary process

Plant–pollinator relationships have been a central topic in the study of floral evolution ever since Darwin (1859, 1862); they have been cited as a classic example of evolution in response to selection mediated through biotic interactions (Grant, 1949; van der Pijl, 1961; Fægri & van der Pijl, 1979; Proctor *et al.*, 1996). Pollination biology is presently a major discipline that explores the mutualistic interactions among species. As an ecological discipline, it describes the association between floral traits and pollinator behaviour, the mechanical fit between the pollinator and the pollen-bearing and pollen-receiving structures, and the importance of biotic and abiotic interactions at the species to community levels (e.g. Dafni, 1992; Mitchell *et al.*, 2009; Vázquez *et al.*, 2009; Morris *et al.*, 2010). Moving beyond the mechanisms and patterns of interactions to the evolutionary processes that maintain or change them requires understanding the genetic basis of floral traits, the phenotypic basis of selection and the evolutionary consequences of these interactions. Indeed, many studies have attempted to place pollination ecology in an explicitly evolutionary framework (e.g. Grant, 1949; van der Pijl, 1961; Levin & Kerster, 1967; Schemske & Bradshaw, 1999; Armbruster *et al.*, 2005; Muchhala, 2007; Vereecken *et al.*, 2010). Nevertheless, there are very few studies in which the full path, from molecular patterns at the genome level and pollinator-mediated selection on phenotype, to the final evolutionary consequences, has been elucidated (Campbell *et al.*, 1991; Bradshaw & Schemske, 2003; Hoballah *et al.*, 2007). It is an ideal time to assess recent progress in taking evolutionary approaches to investigate pollination biology, with the aim of developing a cohesive framework for understanding the role of pollination in floral evolution. This issue of *New Phytologist* contains a special feature, based partly on a European Society for Evolutionary Biology symposium held in Turin in August 2009, that gathers together studies aimed at advancing our evolutionary understanding of pollination and setting a framework for future work.

Pollination genetics – prepollination processes

The genetic basis of floral traits is a key factor in determining evolutionary responses to pollinator-mediated selection on floral phenotype. There are two general approaches used to assess the genetic basis of floral phenotype. The first is to estimate the quantitative-genetic architecture of floral traits; this determines the evolvability and genetic constraints on trait evolution (Hansen *et al.*, 2003b; Hansen, 2006; Hansen & Houle, 2008). Heritability is the most common parameter estimated in quantitative genetic studies, and quantitative genetic studies of flowers show most traits to have significantly nonzero heritability values (Ashman & Majetic, 2006). Heritability is often not the best measure of evolutionary capacity, and a few studies use direct estimates of evolvability (Houle, 1992; Hansen & Houle, 2008) to predict the capacity of floral traits to respond to natural selection (Hansen *et al.*, 2003a,b; Lankinen *et al.*, 2007). Another important quantitative genetic parameter is the genetic correlation between floral traits; this estimates the effects of pleiotropy and/or linkage (e.g. Armbruster, 1991; Campbell *et al.*, 1994; Conner, 2002; Hansen *et al.*, 2003a). Bolstad *et al.* (pp. 370–384) take advantage of such quantitative-genetic information to disentangle the selection on signal from selection on reward.

The second approach used to assess the genetic basis of floral traits influencing pollination interactions is to identify the exact gene or genes and the molecular mechanisms that control floral traits (reviewed in Sapir, 2009b). The molecular variation of the exact gene that controls the phenotypic variation is not easy to determine for plants lacking full annotated genomes. Indeed, only a handful of studies have connected this variation to pollinator behaviour (Bradshaw & Schemske, 2003; Hoballah *et al.*, 2007; Kessler *et al.*, 2008; Martin *et al.*, 2008; Sapir, 2009a). This frontier seems promising, although demanding. The *New Phytologist* special feature does not cover this approach, but we look forward to future technological breakthroughs that will enable us to connect molecular plant genetics to pollinators' behaviour in nonmodel plants.

Pollinator-mediated selection and genetics

The two genetic components of floral evolution described above are largely prepollination phenomena. The evolutionary response to selection depends on heritability and genetic variation (prepollination), but also on selection and

processes following the pollination itself. Analysis of pollinator-mediated phenotypic selection is a powerful tool for assessing the potential evolutionary significance of a trait (reviewed in Harder & Johnson, 2009), and this approach has been taken by Sletvold *et al.* (pp. 385–392), Parachnowitsch & Kessler (pp. 393–402) and Bolstad *et al.* (pp. 370–384) in this issue. However, response to selection must be assessed in the next generation to ascertain the true evolutionary significance of trait variation. On a broader scale, gene flow mediated by pollinators can promote assortative mating among plants and lead to speciation (Jones, 2001; Sargent & Otto, 2006; Gegear & Burns, 2007). Correlation between mates can be estimated by comparing the regression of offspring phenotype over one parent, which is inflated by assortative mating, to the regression over mid-parent, which is not (Weis & Kossler, 2004). Overall, the distribution of traits in the offspring generation, at both phenotypic and genotypic levels, has not been studied in sufficient detail to draw conclusions about the effects of assortative mating mediated by pollinators.

Floral specialization and adaptive radiations in pollination are among the most widely discussed concepts in the field, dating back to at least Sprengel (1793) and Darwin (1862, 1877). Recent interest has focused on the role of pollinator differences in driving speciation and hence diversification (e.g. Grant, 1949; Schemske & Bradshaw, 1999; Kay & Sargent, 2009; Venail *et al.*, 2010). However, there remains uncertainty in just how floral specialization relates to species diversification – through cause (e.g. Dodd *et al.*, 2000; Sargent, 2004), effect, or spurious correlation (Armbruster & Muchhala, 2009). There is also uncertainty in just how common ecological specialization is in pollination, and how important it is in speciation (Waser *et al.*, 1996; Johnson & Steiner, 2000; Fenster *et al.*, 2004). It is also not clear whether generalization in pollination leads to specialization during pollinator-mediated adaptive divergence, or vice versa (Martén-Rodríguez *et al.*, pp. 403–417).

Diversifications in pollination systems are usually driven by adaptation to new pollinators (e.g. Armbruster & Baldwin, 1998; Kay & Sargent, 2009; Schluter, 2009; Alonso *et al.*, 2010). Alternatively, diversification in floral traits may not be adaptive in that floral diversification can occur for reasons not associated with their present function in pollination (nonadaptive radiations; Levin, 2000; Armbruster, 2002). Distinguishing among the various possible causes of diversification in pollination systems within a discrete clade is challenging but important for understanding adaptation, speciation and the macro-evolutionary patterns generated by these processes. As phylogenies become available for more groups, our ability to trace evolutionary change in pollination ecology will

improve. It will soon be possible to assess evolutionary patterns of diversification in a large sample of clades with fully elucidated phylogenies and pollination ecologies (Smith *et al.*, 2008), as exemplified by four papers in this volume (see the following section).

An evolutionary approach to pollination ecology

It is clear from the preceding discussion that much can be gained by approaching pollination in an evolutionary-genetic framework. We emphasize the need for more knowledge about the genetic basis of traits influencing pollinator behaviour, as well as the genetic responses to pollinator-mediated selection. These effects together determine the course of future evolutionary change in floral traits and plant–pollinator interactions. We emphasize studying pollination as an evolutionary process, and the importance of injecting evolutionary genetics into pollination studies, above and beyond evolution's direct ecological significance (see Thompson, 1998).

This *New Phytologist* special feature brings together several examples of this approach. Vallejo-Marin *et al.* (pp. 418–425) examine the correlations of floral traits associated with reward and advertisement, using a phylogenetic perspective to ascertain evolutionary origins. Three papers in this issue examine the selection exerted on floral traits. Sletvold *et al.* (pp. 385–392) and Parachnowitsch & Kessler (pp. 393–402) show experimentally that floral traits are indeed under pollinator-mediated selection, and Bolstad *et al.* (pp. 370–384) partition this selection into its effect on advertisement vs reward traits. In order to detect the postpollination outcome, Rymer *et al.* (pp. 426–436) used maternal and paternal fitness to assess assortative mating that may isolate sympatric *Gladiolus* morphs. Surprisingly, they found a lack of assortative mating and predicted that the morphs will introgress. This study in particular raises the need for more tests of the paradigm of pollinator-mediated ecological speciation. The use of phylogenetic analyses provide a basis to associate speciation in deceptive orchids with the diversification of chemical odours (Peakall *et al.*, pp. 437–450), and to show the direction of evolution from specialization to generalization in the Caribbean flora (Martén-Rodríguez *et al.*, pp. 403–417). Finally, the use of phylogenetic analyses to study the evolution of pollination systems is reviewed by Smith (pp. 354–363).

We think that, despite the extensive literature on the effects of floral traits on pollinators and vice versa, the field is still in the early stages of moving from describing patterns to understanding processes. The full integration of molecular and/or quantitative genetics as prepollination processes with measures of phenotypic selection and postpollination

processes is a promising direction for future studies of evolutionary pollination ecology.

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The invasion of the land by plants: when and where?

The origin of land plants was one of the most important events in the history of life on Earth. It was a major macro-evolutionary event in its own right, with profound ecological consequences, but it also had enormous effects on the environment of planet Earth, altering atmospheric composition, weathering and soil formation, etc., and hence climate and biogeochemical cycles. Understanding the timing of the origin of land plants is a long term goal. In this issue of *New Phytologist*, Rubinstein *et al.* (pp. 365–369) provide new evidence that this event occurred 8–12 million yr earlier than previously accepted.

‘Thus, although reports are currently few, attention is turning to the possibility that the centre of origin of land plants may have been located on Gondwana.’

The land plants (Embryophytes) are a monophyletic group that evolved as an adaptive response to the migration from a freshwater aquatic to terrestrial subaerial habitat. Phylogenetic analysis of extant plants suggests that charophycean green algae share a sister group relationship with the Embryophytes, that is, the land plants probably evolved from a freshwater aquatic multicellular green alga similar to extant *Chara* and *Coleochaete* (Graham, 1993). Within the Embryophytes liverworts are the most basal group, followed by mosses, and then hornworts and vascular plants sharing a sister group relationship (Qiu *et al.*, 2006). However, it is to the fossil record we must turn if we are to understand what the first land plants were like and when and where they evolved.

Traditionally the earliest evidence for land plants was actual megafossils (fossils representing a significant portion of the plant). Until the late 1950s the simple rhyniophytoid plant *Cooksonia* provided this benchmark (Lang, 1937), and it is still the oldest generally accepted megafossil, being reported from the Late Silurian (late Wenlock) (Edwards *et al.*, 1983). However, evidence from a new technique called palynology became widely available from the late 1950s. This technique involves dissolving rock to release