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FORUM

Reconciling ecological processes with phylogenetic patterns: the apparent paradox of plant–pollinator systems

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To what extent do studies of the ecology of mutualistic interactions inform us about the evolution of such relationships? As I will show below, the evolution of floral diversity seems to be based upon specialized relationships with pollinators, yet (with some obvious exceptions) the majority of angiosperms appear to be promiscuously pollinated by a range of taxa. This apparent discrepancy between ecological process and phylogenetic pattern is worth exploring in some detail. Consider four facts regarding plant–pollinator interactions:

1 The vast majority of angiosperms are generalists in their pollinator requirements; a spectrum of taxonomically diverse animals can usually service the same plant species (Waser 1983; Renner & Feil 1983; Waser *et al.* 1996). For most plant species, this spectrum ranges across orders of insects (e.g. butterflies, bees, flies) but occasionally covers classes of animals, for example insects and birds or mammals.

2 The range of pollinators often varies over the course of an individual plant's flowering period as pollinator populations fluctuate (e.g. Gross & Werner 1983; Ashman & Stanton 1991). There may be a more or less predictable progression of taxa through the season, as is the case for British bumblebees (*Bombus* spp.) (Lack 1982; Fussell & Corbet 1992; Ollerton, unpublished data) or the sequence could be unpredictable.

3 Variation in the principal pollinators of a species can also occur between seasons, again because of fluctuating pollinator populations (Pettersson 1991; Fishbein & Venable 1996). This is much less likely to be predictable than intraseasonal fluctuations, unless pollinator numbers cycle in a regular manner.

4 Factors extrinsic to an individual plant, such as growing position, can influence the identity of pollinators (Herrera 1995). An aspect of this which does not seem to have been addressed in the literature is that the spectrum of pollinators could change over the lifetime of long-lived perennial species, in response to long-term fluctuations in pollinator populations, or because of differential attraction according to changes in size of floral display or nectar production.

Next, consider three facts about the evolution of angiosperms and their pollination systems:

1 Since their genesis in the Early Cretaceous, the flowering plants have diversified to become by far the most speciose group of plants ever to have existed. It is differences in floral morphology that are the mainstays of plant taxonomy, and are therefore used to separate species. From this it has been suggested that floral novelty (changes in the colour and relative size and arrangement of parts, differences in scent chemistry or reward type, etc.) must be a major promoter of speciation in the angiosperms (Darwin 1876; Baker 1959; Stebbins 1970).

2 A range of pollination systems operate within most families, tribes and genera of flowering plants. For example: palms are pollinated by beetles, bees and flies (Silberbauer-Gottsberger 1980); labiates by birds, bees, butterflies, moths and flies (Huck 1992); and orchids by beetles, wasps, ants, butterflies, bees, moths, flies and birds (Dafni & Bernhardt 1990). The phylogenetic basis of these patterns has been studied for only a few groups, for example: the families Pandanaceae (Cox 1990) and Asclepiadaceae (Ollerton & Liede, unpublished); the genera *Aphelandra* (Acanthaceae – McDade 1992), *Dalechampia* (Euphorbiaceae – Armbruster 1993) and *Yucca* (Agavaceae – Bogler *et al.* 1995). A similar pattern emerges in most studies – variation in pollination systems across the taxa concerned, often with multiple-origins for similar systems.

3 It appears from 2 (above) that pollination systems are labile and may evolve quite rapidly. Such flexibility of pollination systems might be mediated by the ease with which novel floral mutations can arise. It is known that rather little change in, for example, biochemical pathways (Armbruster 1993) or in a few genes controlling floral characteristics (Bradshaw *et al.* 1995) may precipitate a switch from one type of system to another. In addition, plant breeders can obtain a fantastic range of horticultural novelties through selective breeding over just a few generations. Convergent evolution resulting from multiple origins of similar adaptive morphologies in closely related taxa is frequently encountered – see the example of bird pollinated legumes presented by Crisp (1994). Thus floral lability, with concomitant switching between diverse pollinators, could be common in the angiosperms, though we lack the data to be sure if this applies across all taxa. Some groups of flowering plants may be more conservative (constrained?) in their tendencies to alter floral form. Also, the majority of angiosperms possess mixed-mating abilities, i.e. a mixture of out-crossing and selfing. Selfing is likely to retard the evolution of floral novelty by restricting the number of novel genetic combinations in a population and reducing the effect of pollinator-led selection on floral traits.

We encounter an apparent paradox when trying to reconcile what we know of plant–pollinator ecology with phylogenetic information about the evolution of plant–pollinator relationships: pollination systems can (and do) evolve rapidly in response to consistent selection on floral novelty by pollinators (e.g. Galen 1996) but where does this consistent selection come from? Not, apparently, from the temporally variable, taxonomically diverse array of pollinators possessed by the majority of plant species. Given the range of floral cues (colour, patterning, scent, shape) to which different pollinators respond, specialization to a taxonomically narrow array of pollinators would appear to be a prerequisite for the evolution of floral novelty. Otherwise, the spread of conflicting behavioural and physical attributes of the pollinators would negate any possible selection – mutants would not be selected for because they could not engage the services of a committed pollinator.

How can this paradox be resolved? I can think of a number of possible resolutions; hopefully others can think of more:

1 There is evidence that in some systems all pollinators are not equal in their ability to pollinate and, despite a wide spectrum of visitors, a plant is effectively a specialist. For example, although both Lepidoptera and Hymenoptera pollinated *Calathea ovandensis* (Marantaceae), it was the Hymenoptera which were responsible for 99% of the fruits set (Schemske & Horvitz 1984). Similarly, bees were much more effective pollinators of *Asclepias tuberosa* (Asclepiadaceae) than butterflies (Fishbein & Venable 1996). This kind of differential pollinating ability is probably quite common, though it has been little studied. Thus plant species that are apparently generalists in their pollination requirements may prove to be much more specialized than a simple study of their pollinator spectrum would suggest. This would result in more consistent selection on floral mutations. However, it should be noted that the Hymenoptera which pollinated *Calathea ovandensis* in Schemske & Horvitz's study spanned five genera in three tribes of the family Apidae; thus the extent to which these bees would exert similar selection pressures on floral traits is debatable. Not only that, but the observations were restricted to 20 days (during peak flowering) in one year; given what we know of temporal variation in pollinator spectra (see above), the true taxonomic range of hymenopteran pollinators is likely to be even larger. We simply do not have enough information to judge this hypothesis.

2 Micro-selection pressures exerted by pollinators, and which are measurable over short time scales, might not equate with the macro-selection pressures needed to promote the evolution of floral diversity. This is really a reiteration of the microevolution/macroevolution debate which has enlivened evolutionary theory, and need not be exhumed here. Though the adaptive value of floral traits is well established (Waser 1983) and pollinator-mediated selection on floral variation has been measured (Nilsson 1988; Cresswell & Galen 1991) we do not know whether the evolution of one species from another (by relatively minor changes in floral form) is qualitatively the same (just a quantitatively smaller effect) as the evolutionary transition from one genus to another, or between other higher taxa.

3 Does present floral diversity represent periods of pollinator specialization, either sometime in the past, or at the edge of a species' range, or following long-distance dispersal of individuals? Could it be that during the lifetime of a particular plant genus or species, there will be periods of specialization and of generalization? At times of specialization, floral features may evolve under consistent selection from a taxonomically restricted range of pollinators; during times of generalization (the norm?) such selection pressures are dissipated across a spectrum of pollinators. Thus the present-day diversity of floral form is a result of the periods of pollinator specialization within a lineage; the period of specialization, from the plant's perspective, is broken when its pollinator becomes extinct (globally or locally) and the role of pollen vector must be filled by other organisms. It is worth noting that periods when a pollinator is likely to become locally extinct are the same times as when new potential pollinators may enter the arena, e.g. climatic fluctuations, species' range extensions, disease epidemics, or other perturbations, when local exclusion competition by the original pollinator is negated.

4 Were Darwin, Baker, Stebbins *et al.* wrong in their view of floral novelty inducing speciation? Processes such as hybridization, and possibly ploidy changes, may be more important in generating and maintaining floral novelty than spontaneous mutation and pollinator-mediated selection. Hybridization is a common phenomenon in plant taxa and it can give rise to 'extreme or novel characters' (Rieseberg & Ellstrand 1993) or even new taxa (Abbott 1992). But its importance in evolutionary processes, relative to natural selection, is unknown. It is important to note here that, although taxonomic information tells us that there is a link between speciation and floral novelty, it says nothing about the order of events; speciation (via hybridization, ploidy changes, etc.)

may precede floral divergence, not vice versa (Scott Armbruster, personal communication 1996).

These resolutions are not necessarily mutually exclusive, and there may well be alternative possibilities that I have not considered. Deciding which are correct (or perhaps easier, which are definitely incorrect) will take time and effort and not a little luck. Information must be garnered from disciplines as diverse as palaeontology (is anyone looking at pollen-loads of bees and other pollinators in amber?), morphological and molecular systematics (phylogenetic trees for more plant groups), evolutionary theory (are micro and macro-evolutionary patterns the same or different?) and field ecology (more data on relative pollinator effectiveness and temporal variation in pollinator spectra). Such a multidisciplinary approach is the only way to square ecological process with phylogenetic pattern.

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