Generalization versus specialization in plant pollination systems

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For a field that is more than two centuries old, pollination biology remains remarkably vigorous, with one of the current debates focusing on the degree of specialization in plant–pollinator relationships[1,2]. Ever since Darwin[3] infused pollination biology with the logic and explanatory power of evolutionary theory, there has been interest in the adaptive significance of floral traits in relation to pollinators. This found expression in the 'pollination syndromes' concept, which originated in the 19th century and developed into its modern form by the late 1960s (Ref. 4). In this view, the flowers of most angiosperms are sufficiently specialized for pollination by particular animal types for there to be recognizable convergent 'syndromes' of floral traits. Thus, for example, one might distinguish between butterfly-flowers and bee-flowers. The evidence to support the syndrome concept originated from a wide range of comparative studies encompassing many angiosperm families[4]. In one of the most influential studies, Grant and Grant concluded that 'a lock and key relation between flowers and pollinators … is widespread and probably universal in the phlox family'[5].

Recently, this traditional view has been counterbalanced by scepticism about the specialized nature of pollination systems[1,2,6,7]. Claiming evidence for widespread generalization in pollination systems, Waser and others[1,2] have questioned the view that specialization is the dominant evolutionary trend in the pollination systems of plants, and have proposed that the adaptive link between floral traits and observed pollinators might not be as simple as imagined previously [6,7].

The dichotomy between generalization and specialization in pollination systems is a simplification, for purposes of debate, of what is really a continuum between plants pollinated by literally hundreds of pollinator species and those pollinated by just one pollinator species[1]. Here, we briefly outline some of the methods used to measure specificity in pollination systems (Box 1), review the theory and empirical evidence, and then consider several implications for the evolution and conservation of plants.

Predictions

There is a surprising paucity of theory about the determinants of specificity in pollination systems. Pollinators influence the fitness of hermaphrodite plants through both a female component (seeds produced as a result of pollen

The long-standing notion that most angiosperm flowers are specialized for pollination by particular animal types, such as birds or bees, has been challenged recently on the basis of apparent widespread generalization in pollination systems. At the same time, biologists working mainly in the tropics and the species-rich temperate floras of the Southern hemisphere are documenting pollination systems that are remarkably specialized, often involving a single pollinator species. Current studies are aimed at understanding: (1) the ecological forces that have favoured either generalization or specialization in particular lineages and regions; (2) the implications for selection on floral traits and divergence of populations; and (3) the risk of collapse in plant–pollinator mutualisms of varying specificity.

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deposited on the stigma) and a male component (seeds sired as a result of pollen export to conspecific stigmas). According to Stebbin's 'most effective pollinator principle'[16], a plant should specialize on the most effective and/ or most abundant pollinator when pollinator availability is reliable. Conversely, generalization is favoured when the availability of even the most effective pollinator is unpredictable from year-to-year[1].

Plant life history, successional status, abundance and breeding system have all been considered to influence the evolution of floral specialization[17–24]. Plants that are long-lived or are capable of vegetative reproduction should be better able to risk specialization[1,17]. Conversely, generalization would be expected in short-lived plants, such as annuals, as well as other plants that have an obligate dependence on seeds for reproduction[17]. According to 'Baker's rule'[18], generalization (or a breeding system that does not require pollinators) would also be expected in colonizing weedy species, because these require a high degree of reproductive assurance.

Highly dispersed plants would be expected to specialize on pollinators that show fidelity, thus reducing pollen loss and clogging of stigmas with the pollen of more abundant plants[19,24]. This prediction is supported by studies in tropical forests that show that dispersed understorey shrubs and epiphytes tend to have relatively specialized pollination systems[24], while mass-blooming trees often are pollinated by a variety of generalist insects.

Bawa and Opler[21] predicted that plants with separate sexes (dioecy) would be more likely to have generalized pollination systems than hermaphrodite plants. Their prediction was based on the assumption that generalized systems carry a higher risk of intra-plant (geitonogamous) pollination by small insects and, therefore, would be more effective in plants with separate sexes. Support for the 'Bawa hypothesis' from broad surveys of tropical plants has been equivocal, with at least one study finding evidence for extensive specialization in the pollination systems of tropical dioecious plants[22].

Syndromes under siege?

Unrelated plants that share similar pollinators often show convergent suites of floral traits known as pollination syndromes[4]. For example, moth-pollinated flowers tend to be white with a long narrow corolla tube and are scented in

the evening, regardless of the plant family to which they belong. But syndromes are not always the tidy categories they are made out to be in introductory biology textbooks. In reality, convergence in floral traits is limited by phylogenetic constraints in floral design. A good example of this is a recent study[25] showing that the flowers of the South African milkweed, *Microloma sagittatum*, conform to the classic bird pollination syndrome[4] in most respects (red, scentless flowers with copious amounts of nectar), except that the corolla tube is short with a narrow entrance. What, at first, might seem to be a contradiction of the bird-pollination syndrome[26] is explained by the fact that the pollinia are attached, by means of a clasping mechanism, to the tip of the tongue of sunbirds, thus obviating the need for a long corolla tube and a broad entrance to the flowers. The existence of similar flowers in unrelated Asian milkweeds was used to predict that pollen transfer on bird tongues is more widespread in the family[25]. The utility of syndromes for generating such testable hypotheses was established by Darwin with his famous (and accurate) prediction that the long-spurred Malagasy orchid *Angraecum sesquipedale* is pollinated by a giant hawkmoth[3].

Pollination syndromes were intended to be used as a formal description of patterns of convergent evolution among unrelated plants, not as a substitute for field observations. Unfortunately, pollination syndromes have acquired a typological flavour, accentuated by abstruse terminology[4], which can lead researchers to focus only on floral visitors that conform to the 'correct' pollinator[1]. Some of the strongest objections to the syndrome concept have emanated from ecologists who stress the need for objective experimental investigation of pollination systems[1,6,12,26]. Flowers conforming to a particular syndrome, even one as distinctive as a 'moth-flower', can receive visits from opportunistic insects belonging to different orders, which, nevertheless, contribute to the fitness of the plant[11,12].

Specificity in plant pollination systems is usually achieved by combinations of advertising by specific scents and colours[4,19], floral morphology that restricts access to nectar[9,19,27] and, in some cases, unusual rewards (e.g. oils[15], fragrances and resins[28]). The role of colour in filtering floral visitors has almost certainly been overemphasized in the past, despite the fact that no botanist has made the radical claim that pollination syndromes can be defined by colour alone. Few pollinators appear to have fixed colour preferences[19] and even previous 'facts', such as red blindness in honeybees, have been called into question[29]. Studies of German wildflowers[1] and plants in lowland tropical forests[30] also show that flower colour by itself is not significantly correlated with pollination systems.

The syndrome concept can be tested effectively only by broad-scale correlations between multiple floral traits and pollinators. For example, a recent study in lowland tropical forests showed good support for the existence of pollination syndromes among 270 flowering plant species[30]. Only 37 of the 270 species were considered to have 'diverse' pollination systems[30].

Phylogenetic and geographical trends

Surveys of plant families[1,13,31] reveal strong differences in the degree of specificity in pollination systems, reflected by the median number of pollinators per plant species (in parentheses): Asteraceae (>25) (Ref. 23) and Ranunculaceae (10) (Ref. 1) occupy the generalist end of the continuum, while families such as Polemoniaceae (4) (Refs 1,5), Asclepiadaceae (3) (Ref. 13) and Orchidaceae (1) (Ref. 31) occupy the specialist end. Little attention has been devoted

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Box 1. Quantifying specificity in plant pollination systems

There is no single agreed upon method for measuring specificity in pollination systems. Simple lists of flower visitors, as provided by many earlier workers, are not useful as a measure of floral specialization because equal weighting is given to all visitors irrespective of any role they might play as pollen vectors. Distinguishing between visitors and pollen vectors (pollinators), therefore, is an essential prerequisite to any investigation of a pollination system[8–12].

Even the widespread use of numbers of pollinator species per plant species as a measure of specialization[1,13] is unsatisfactory because of the multiple taxonomic levels and functional differences that exist between pollinators. To illustrate, a plant pollinated by ten moth species could be considered more specialized than another plant pollinated by five insect species encompassing four orders. Reliance on a single functional type of pollinator, such as hawkmoths[14] or oil-collecting bees[15], is a far more widespread form of specialization than reliance on a single pollinator species.

Further confounding any attempts to use numbers of pollinators as a measure of floral specialization are differences in visitation rates and effectiveness among pollinators. Normally, these are assessed by direct observations of pollinator behaviour and by identification of pollen loads. A more elegant, though tedious, approach is to expose virgin flowers to a single visit and measure pollinator efficiency in terms of pollen deposition on the stigma, seed production and pollen removal[8,9,11]. In many cases, effective pollinators comprise only a small fraction of the total floral visitors[8,12].

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to explaining these trends. Do they result from phylogenetic differences in floral construction or from the types of habitats and geographical regions that tend to be occupied by these families?
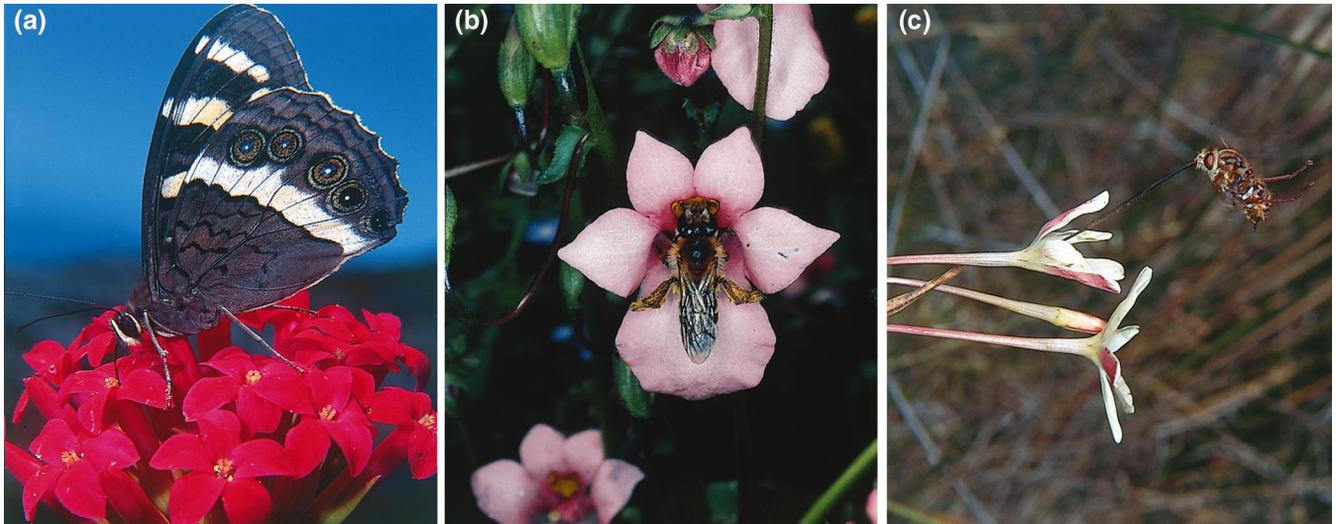
The existence of specialized pollination systems in tropical plants has been known for some time[4]. Among the classic pollination syndromes in the tropics are those involving bats, hawkmoths, crepuscular beetles, fig wasps, and resin-collecting, oil-collecting and euglossine bees[4,14,22,28,30,32].

Recent work in the species-rich temperate flora of South Africa has also revealed the existence of numerous highly specialized pollination systems, often involving just one pollinator[15,19,27,33,34] (Fig. 1a–c). Among these are several plant guilds that rely solely on one or two long-tongued fly species[27,33]. One guild consists of 20 plant species pollinated by *Moegistorhynchus longirostris,* a fly with a proboscis 60–100 mm in length, the longest of any known dipteran[27,33] (Fig. 1c). The plants pollinated by this fly have correspondingly long narrow corolla tubes and flower only during the few weeks of the year when this fly is active[27,33]. Another highly specialized guild of plants with large red flowers is pollinated solely by a satyriine butterfly, *Meneris tulbaghia*[19] (Fig. 1a). Oil-producing flowers occur in many southern African species belonging to the Scrophulariaceae and Orchidaceae, and these pollination systems frequently involve just one or two oil-collecting bee species[15] (Fig. 1b).

By contrast, relatively few specialized pollination systems are known from the floras of much of Europe and the eastern and northern parts of North America[1,2,6]. The pollinator fauna in these regions is dominated by opportunistic social bees, which might limit the possibilities for floral specialization[23]. In addition, generalized pollination systems might have been of ecological advantage for plants colonizing post-glacial landscapes as well as the modern agricultural–urban mosaics, which characterize much of these continents.

Implications for selection and speciation

Ollerton[2] has highlighted a seeming paradox: that many flowers show specialization in floral traits, yet often are visited by diverse assemblages of animals. This paradox can be resolved if only a small proportion of the visitor assemblage act as effective pollinators[8,10,11], if the members of the visitor assemblage are functionally equivalent and impose

Fig. 1. The flora of southern Africa is replete with examples of specialized pollination systems. (a) *Crassula coccinea* is a member of a guild of plants with large red flowers pollinated exclusively by the large satyriine butterfly *Meneris tulbaghia*[19]. *Photo reproduced, with permission, from S.D. Johnson.* (b) Oil-producing flowers in the Scrophulariaceae and Orchidaceae typically are pollinated by one or two bee species, such as this *Rediviva politiisima* collecting oil from the flowers of the twinspur *Diascia tugelensis*[15]. *Photo reproduced, with permission, from K.E. Steiner.* (c) Extreme specialization is evident in plants dependent on single long-tongued fly species, such as the 'mega-nosed' fly *Moegistorhynchus longirostris*[27,33]. *Photo reproduced, with permission, from S.D. Johnson and Ref. 33.*

similar selective pressures[35], or if selection has operated only at certain times in the past[2] (for example, when the visitor assemblage was depauperate and plants experienced severe pollen limitation[34]).

Studies of selection on floral traits have accumulated rapidly over the past five years[6,7,36–39]. In general, plants with generalist pollination systems might be less likely to experience strong directional selection on floral traits[36], whereas those with relatively specialized systems frequently show the effects of selection[37,39]. An exception is the study by Herrera[6] which found no significant selection on spur length in *Viola cazorlensis*, in spite of this species being pollinated almost exclusively by a single species of day-flying hawkmoth; however, the possibility of selection through the male component of fitness was not examined in this study. Other studies have shown strong selection on floral spur length in both moth- and long-tongued fly-pollinated species[33,39].

In spite of clear evidence linking animal pollination with high rates of speciation in plants[40], the relationship between floral adaptation to pollinators and speciation remains poorly understood[34,35]. Many authors have interpreted specialized pollination systems as isolating mechanisms[41], and even have argued that selection for reproductive isolation can favour the evolution of specialization[5]. However, the origins of reproductive isolation and speciation in plants often are uncoupled, with isolating mechanisms originating as an incidental consequence (or epiphenomenon) of the process of adaptive divergence in allopatric populations[34,35,42].

Adaptive radiation in many plant groups appears to have been a consequence of adaptive shifts between specialized pollination systems[16,28,43]. In a study of the large African orchid genus *Disa*, it was shown that cladogenesis has been associated with repeated shifts between various specialized pollination systems[43]. Similarly, in the tropical genus *Dalechampia* evolutionary transitions between pollination by euglossine, resin-collecting and pollen-collecting bees have been important for floral radiation[28]. Hodges[41] argued that the innovation of floral spurs has promoted radiation in many plant groups by promoting the development of more specialized pollination systems.

Pollination specificity and risk of extinction

There is increasing concern that human alteration of ecosystems will lead to widespread collapse in pollination systems[17,32,44]. The degree of specialization in the pollination systems of plants will undoubtedly influence the risk of such uncoupling of mutualisms[17,32]. At high risk are plants that depend on single pollinator species, while plants with relatively generalized pollination systems might be resilient to the loss of some pollinator species[17]. For example, it is hard to imagine that the loss of any one of the >26 moth species that pollinate *Silene vulgaris* would be of much ecological consequence for the plant populations, even though these moths differ in their effectiveness as agents of natural selection[9].

Collapse of a mutualism does not inevitably lead to the rapid extinction of the plant species involved. Bond[17] has pointed out that many plants with highly specialized pollination systems have compensatory mechanisms such as clonality, longevity and facultative self-pollination, which might allow a population to exist for hundreds of years without its mutualist partners. An example is the vegetative persistence of populations of the shrub *Ixianthes* despite the local absence of their sole pollinator, an oil-collecting bee[45]. Thus, loss of pollinators can lead to an insidious form of delayed extinction that is not readily detectable by managers of rare and threatened plant species.

Prospects

It is now abundantly clear that plants occupy virtually every point on the continuum from extreme generalization to extreme specialization in their pollination systems. Although some authors[2] have concluded that generalization is the rule rather than the exception for angiosperms on a global level, the reality is that little is known about the pollination systems of the vast majority of plants in the species-rich developing countries of the world. From a conservation standpoint, there is an urgent need to understand more about the ecological dependency of plants on pollinators, not just in terms of seed production, but also in terms of population viability[17,44].

Conceptually, pollination syndromes are sorely in need of more critical examination using field experiments. Are the floral traits that make up the various syndromes effective in filtering floral visitors, as shown convincingly in a recent study of *Mimulus* (monkeyflowers)[46], or is 'specificity' often merely a reflection of depauperate pollinator communities? Broad-scale community studies of the kind recently published by Momose *et al.*[30] are particularly valuable in this regard. At the population level, studies of pollinator effectiveness[8], although time-consuming and laborious, offer the most promise for attaining more meaningful estimates of floral specialization than the lists of floral visitors that have been used so often until now.

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