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PLANT–POLLINATOR INTERACTIONS FROM FLOWER TO LANDSCAPE

The specialization continuum in pollination systems: diversity of concepts and implications for ecology, evolution and conservation

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Summary

1. Specialization in plant–pollinator relationships is a core concept in discussions of plant evolution and ecology; it is central to our thinking, not just about the ecology of plant–pollinator interactions and pollinator services, but also about reproductive isolation, speciation, extinction and assembly of communities. However, as reviewed here, the concept 'plant–pollinator specialization' has multiple definitions and uses, and these disparate uses have engendered confusion in the literature. Organizing these disparate uses into a comprehensive framework is an overdue task, prior efforts notwithstanding.

2. This contribution attempts to make clear the variation in meaning and usage of plant–pollinator specialization, including distinguishing between ecological specialization (interacting with few partners or resources), evolutionary specialization (genetic change associated with increased specialization) and phenotypic specialization (having specialized or derived phenotypic traits), with application of all three concepts to both plants and flower-visiting animals. These variations in interpretation of specialization affect how we view evolutionary and biogeographical trends, as well as extinction risk.

3. In the light of this conceptual diversity, I evaluate the relationships between specialization and possible trends in floral evolution and rates of speciation and extinction. I also address several implications of specialization for community ecology and resilience of pollination services in the face of environmental disturbance.

Key-words: community ecology, evolution, extinction, functional-group specialization, interaction networks, pollination, specialization, speciation

Introduction

Biological specialization is the tendency or ability of organisms to use only a subset of potential resources or habitats. Implicit in this concept is the idea that this subset of resources is used more effectively by specialists than by generalists. This, in turn, links the concept of specialization to competition and the ecological niche: competition drives the evolution of narrower niches (i.e. specialization), wherein competitive abilities are maximized. The interplay of these processes is thought to be a predominant theme in the evolution of life on Earth and, indeed, the primary source of biological diversity (species richness), phenotypic disparity (e.g. degree of morphological diversity) and community complexity (the number of species interactions) (Darwin 1872; MacArthur & Pianka 1966; Futuyma & Moreno 1988; Schluter 2000; Oyston *et al.* 2015).

Specialization has a long history as a topic of interest in the study of plants, especially with respect to floral morphology and function and effects on angiosperm diversity. However, despite its clear importance in plant evolution, floral specialization is poorly understood as a process, and it has multiple interpretations as a state, and unclear links to other processes such as diversification (see Ollerton 1996; Waser *et al.* 1996). For example, the association between specialization and diversity is generally thought to be the result of specialization increasing the likelihood of prezygotic reproductive isolation and, thereby, increasing rates of speciation (Grant 1949, 1971, 1994; see reviews in Kay & Sargent 2009 and Armbruster 2014). However, the

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association could also be generated in other ways (Armbruster & Muchhala 2009; Armbruster 2014).

How specialization is defined obviously affects how it is measured (e.g. Schluter 2000), and it also affects how we interpret the ecological and evolutionary significance of specialization. Here, I draw together and contrast all of the distinct definitions and uses of specialization of both flowers and their visitors. The goal is to explore both conceptual and empirical issues that relate to perceived links between floral specialization and angiosperm species diversity and disparity (phenotypic diversity), as well as the possible influences of floral specialization on the structure and resilience of ecological communities.

Ecological specialization of flowers

The commonest use of the specialization concept is 'ecological specialization', wherein fewer kinds of resources are used by specialists than by generalists (Table 1). For example, a plant species that presents nectar in a long nectar spur accessible to only one species of sphingid moth (see Darwin 1877; Nilsson 1988) has more specialized pollination than a plant species offering nectar in a shorter spur accessible to (and visited by) many species of noctuid and sphingid moths.

Ecological specialization of flowers is often referred to as 'specialized pollination'. Such specialization can be manifested in several ways, but the final result is pollination by relatively few species (or functional groups) of pollinators. Two initial questions must be addressed in defining and describing ecological specialization. First, is specialization treated as absolute (e.g. the number of pollinator species/functional groups) or relative to the total resource (proportion of available pollinator species/functional groups)? Secondly, what is the level of group or taxonomic resolution being used in defining resources (e.g. pollinator species vs. families or functionally similar ecological groups)?

FUNCTIONAL-GROUP SPECIALIZATION

With respect to the second question, group resolution, Robertson (1928), Fenster *et al.* (2004), Ollerton *et al.* (2007) and others have suggested that treating pollinators that interact with the flower similarly as a 'functional group' is often more informative than lower taxa as units. They proposed that these groups be higher-level categories, as in pollination syndromes (e.g. bats vs. hovering birds vs. short-tongued bees). Ollerton called this 'functional specialization', although I suggest that this be modified to 'functional-group specialization' for clarity. 'Functional specialization' has already been used extensively in the literature to refer to specialization in organ or tissue function, with nearly 2000 published papers in the biological sciences since 1970 (Web of Science search, 07.07.2016).

Traditionally, some mix of functional traits enter into functional-group classifications, such as mouthpart shape, or ability to hover, these groups converging on pollination-syndrome groupings (Faegri & van der Pijl 1979; Ollerton *et al.* 2007). The advantage of this approach is that classification into groups is easy. The disadvantage is that there is a risk of splitting apart two pollinators exerting similar selective pressures on certain floral traits (e.g. bee flies and bees) and grouping together pollinators potentially exerting different selective pressures (e.g. long-tongued bee flies and short-tongued bee flies).

Fenster *et al.* (2004) argued, in contrast, that functional groups should be defined as groups or guilds of species mediating (or inferred to mediate) similar selection on floral traits by virtue of their similarity in morphology and/or behaviour (consistent with the evolution of pollination syndromes). Thus, unrelated pollinator species could sometimes be in the same functional group, while taxonomically close pollinators might sometimes be in different functional groups, depending on the natural selection they generate. For example, male bees often exert very different selective pressures than conspecific females (Motten *et al.* 1981; Armbruster *et al.* 2002; Cane 2002; Pascarella 2010), as behaviour, body size and proboscis lengths generally differ (Michener 2007), while long-tongued flies might sometimes exert the same selection on floral tube length as bees with similar tongue lengths (as appears to be the case in pollination of *Linum* and *Stylidium*; Armbruster, Edwards & Debevec 1994; Armbruster *et al.* 2006, 2009).

In contrast, floral 'generalization' through pollination by one species of pollinator may sometimes occur when pollination by different conspecifics generates divergent selective pressures. For example, pollen-foraging bumblebees often generate different selective pressure than nectar-foraging bumblebees (e.g. Wilson *et al.* 2004; Armbruster, Shi & Huang 2014b; Cane 2014), as is the case for male and female bees. Thus, a flower pollinated by only one animal species may sometimes have 'generalized' pollination, as observed in *Dalechampia ilheotica* pollinated by both fragrance-foraging male and resin-foraging female euglossine bees (Armbruster 1993).

Use of the evolutionary approach to functional groups may sometimes broaden our concept of a functional group in ways that are unhelpful, so both caution and explicit description of any group classification must be applied. Counter-intuitive cases are probably rare, however, and the difference between morphological–taxonomic functional groups and evolutionary functional groups is probably small in most cases. Importantly, the definition of specialization based on evolutionary functional groups places specialization in an explicit evolutionary framework. This framework makes it clear that floral specialization is the evolutionary result of selective pressures generated by one to several selectively similar pollinator species.

PROPORTIONAL VS. ABSOLUTE SPECIALIZATION

Until recently, little attention has been focused on whether specialization should reflect the absolute number of

Table 1. Classificatory framework for specialization concepts as applied to plants and flower-visiting animals

Process/State	Subcategory	Scale	Scope	Basis	Units
Ecological specialization	Ecological	Absolute or proportional	Local or regional	Purely taxonomic	Species, genus, family, etc.
	Ecological functional group			Morphological/ecological/taxonomic	Morphology, behaviour, higher-level taxonomy
	Evolutionary functional group			Evolutionary	Shape of phenotypic selection surface
Phenotypic specialization	Advertisement, reward, mechanical fit				Floral morphology, colour, chemistry & function
Evolutionary specialization		Microevolution or macroevolution		Phenotypic selection or comparative	genetic or phenotypic variation/change

pollinator types vs. the proportion of potential pollinator types utilized. Use of one or few pollinator species as a result of the lack of other potential pollinators in a taxonomically depauperate environment ('imposed specialization') is not specialization in the usual ecological sense (specializing on a subset of resources). In contrast, 'proportional' or 'relative' specialization captures the degree to which a subset of potential pollinators are used. Although most authors do not emphasize this distinction, it becomes important when one works with the biota of islands (e.g. Marten-Rodriguez *et al.* 2015) or extreme environments, such as the Arctic (e.g. Armbruster 2006), and becomes an explicit methodological issue in network studies (Blüthgen, Menzel & Blüthgen 2006; Pauw & Stanway 2015). In terms of relative amounts of 'filtering', a species of *Pedicularis* (Orobanchaceae) pollinated primarily by one species of bumblebee in the Canadian High Arctic (where only a couple of bee species occur; Kevan 1972) is not more specialized than a *Pedicularis* species pollinated by several species of bees in montane California (where dozens of bee species are present). However, the evolutionary consequences, in terms of contemporary selection on traits promoting attraction of, and efficient pollination by those pollinators, are similar, whether the specialization is imposed or proportional.

SPECIALIZATION CONTINUA AND SCALES

Ecological specialization vs. generalization is an artificial dichotomy on an axis of continuous variation. Whether considering species or functional groups, a flower pollinated by one is clearly specialized, but at what number does one invoke generalized pollination? A focus on functional groups helps some, in that one could reasonably argue that a flower successfully employing pollinators in two or more functional groups is generalized. Another approach is to use quantitative indices of specialization based on comparing the list of observed interaction frequencies of a species with the expected frequencies under random visitation, given the observed diversity and relative importance of all interacting partners observed locally (Blüthgen, Menzel & Blüthgen 2006; see application in Pauw & Stanway 2015).

In thinking about flowers with ecologically generalized pollination ('generalist flowers'), it is useful to consider the origin and maintenance of generalized pollination. A generalist flower could be a 'cryptic specialist', because it has responded evolutionarily to a single selective pressure generated by a diversity of pollinators whose similarities in selection generated have escaped notice. Alternatively, a generalist flower may have originated by adapting to a balance of different selective pressures generated by a diversity of pollinator types. For example, *Stylidium* (Stylidiaceae) flowers exhibit several features that make them well adapted to using pollinators of a large range of sizes and taxa (Armbruster, Edwards & Debevec 1994; Armbruster *et al.* 2009). Some species of *Dudleya* (Crassulaceae) with semi-tubular corollas appear to be adapted to pollination by both bees and hummingbirds (Aigner 2004). Lastly, generalization could reflect a plant's limited capability in restricting access rewards by suboptimal floral visitors (i.e. evolutionary constraints).

An additional ambiguity accrues from the scale of ecological specialization. A plant species that is pollinated by one species of insect throughout its range is clearly a specialist, but what about a plant that is pollinated by several species across its range but only one species of pollinator in any one place? Such among-population differences in pollination ecology may be due to pollinator–environment differences (see Thompson 2005), or genetic differences between plant populations (i.e. different pollination ecotypes; see discussion in van der Niet, Peakall & Johnson 2014). Scale issues can also occur in time: a plant that blooms over an extended period may have multiple pollinator species across the year, but only one in a particular season (e.g. *Dalechampia brownsbergensis* in Suriname; Armbruster, Herzig & Clausen 1992).

ECOLOGICAL SPECIALIZATION WITH AND WITHOUT TRADE-OFFS

In a series of influential papers, Aigner (2001, 2004, 2006) pointed out the importance of assessing fitness trade-offs in attempting to understand the operation and evolution of specialized pollination. Fitness trade-offs occur when the positive effect of a floral trait on the pollination effectiveness of one pollinator creates a negative effect on pollination effectiveness of another. This can be assessed by considering the marginal increment in plant fitness generated by changes required to add a pollinator to the existing suite of effective pollinators in relation to the fitness cost incurred through those changes (Aigner 2001). Indeed, pollinator–effectiveness trade-offs are thought to have been critical in the origin and maintenance of specialized pollination (Schemske & Horvitz 1984; Wilson & Thomson 1996; Aigner 2001; Mayfield, Waser & Price 2001; but cf. Muchhala *et al.* 2010).

However, fitness trade-offs are not always observed. Aigner (2001, 2004, 2006) found that fitness trade-offs were absent in pollination of generalist *Dudleya greenei* flowers by large bees, small bees and hummingbirds. The absence of fitness trade-offs in the adaptation to a new pollinator disconnects ecological and phenotypic specialization (Aigner 2001). Experimental manipulation of corolla shape towards being more open resulted in hummingbirds being less effective, but bees becoming no more effective (Aigner 2004, 2006). Because most Crassulaceae have open flowers, these results can be interpreted as evidence of 'specialized' tubular morphology that better fits hummingbirds having evolved in response to marginal selection generated as hummingbirds were added to the plants' original pollinator repertoire (bees). The lack of trade-offs meant that bees were not lost as pollinators in the process, and net generalization increased. Due to the paucity of adequate studies, however, it remains unknown whether fitness trade-offs in pollination are rare or common (Aigner 2006).

A few studies are instructive in showing the range of outcomes and the importance of detailed understanding of the operation of trade-offs in pollination. Muchhala (2007) detected a strong trade-off between hummingbird and bat 'pollination' of artificial flowers of different widths, mimicking the floral morphologies of two species of *Burmeistera* (Campanulaceae). A perusal of published studies suggests that fitness trade-offs are more common in bilaterally symmetrical (zygomorphic) flowers than in radially symmetrical flowers (W. S. Armbruster, unpublished data). There are, of course, numerous interesting exceptions to this possible trend, such as Australian triggerplants, *Stylidium*, with zygomorphic flowers, but ecologically generalized pollination mostly lacking trade-offs. An 'opposite' exception is the shrubby wild flax *Linum suffruticosum*, which has radially symmetrical flowers, but has strong pollinator size-related trade-offs (Armbruster *et al.* 2006, 2009).

ECOLOGICAL SPECIALIZATION AS 'FILTERING'

Specialized pollination with trade-offs can also be viewed as the action of one or more 'filters' that exclude some potential pollinators and allow others 'through'. This is best understood if we consider pollination as a stepwise process. The first step is attraction of visitors through advertisements (e.g. colour, fragrance), rewards (e.g. accessible nectar) and the timing of floral receptivity (e.g. day vs. night). The second step is visitor contact with stamens, leading to pollen being picked up. The third step is visitor contact with stigmas, leading to that pollen being deposited on the stigma (Fig. 1a). Specializing 'filters' can act at any of these steps individually or in combination.

Attraction filters

Attraction filters operate at the first step by reducing the diversity of animals attracted to flowers (Fig. 1b), by, for example, when the flowers are open (day vs. night), what specific advertisements (colour, shape, scent) and rewards (nectar, pollen, oils, resin, etc.) are deployed (Armbruster 2012). Attraction filters operating through advertisement ('advertisement filters') exploit differential signalling and sensory biases. There is some evidence for the operation of advertisement filters through colour biases, for example white flowers being differentially attractive to nocturnal insects and red flowers reducing bee visitation sufficiently to promote specialization on bird pollination (see discussion in Chittka *et al.* 2001; Rodríguez-Gironés & Santamaría 2004; Wilson *et al.* 2004). Even more effective advertisement filtering is seen through diversification in floral fragrance chemistry, with certain compounds selectively attracting or repelling different kinds of animals (Faegri & van der Pijl 1979; Dressler 1982; Fenster *et al.* 2004; Raguso 2008).

Strong filtering effects are seen when filters operate through reward chemistry ('reward filters'). The chemistry of nectar and pollen can influence what animals are attracted (Faegri & van der Pijl 1979; Baker & Baker 1990; Baker, Baker & Hodges 1998). Rewards can also act directly through the inclusion of repellent components. For example, some nectars contain distasteful or poisonous components (e.g. Johnson, Hargreaves & Brown 2006).

'Specialized' pollinator rewards also act like filters; these include specialized brood sites, floral oils, reward fragrances and floral resins, materials not attractive to most flower-visiting animals (Armbruster 2012). The specificity of relationships between yuccas and yucca moths and figs and fig wasps, for example, is based on the various chemical and physical characteristics of the flower organs exploited by the pollinating seed predators. Oils secreted by flowers as rewards are collected only by members of a few small clades of bees in the Melittidae (e.g. *Macropis*, *Rediviva*) and Apidae (e.g. Tapinotaspidini + Ctenoplectrini, Tetrapediini, Centridini), which include oil in larval provisions (Buchmann 1987; Michener 2007). Other animals are not attracted by such rewards.

Another class of specialized reward that filters out all floral visitors but a few genera or species of bees is monoterpene or aromatic reward fragrances. Here, flowers offer no reward other than fragrances that are attractive to male euglossine bees (Apidae: Euglossini), a group of large, generally solitary, Neotropical bees. The males use the fragrances collected from flowers and other sources to attract females. Because these fragrances communicate species identity to the female bee (Zimmermann, Ramírez & Eltz 2009), as well as possibly signalling genetic quality, considerable specificity in attraction can occur. Several

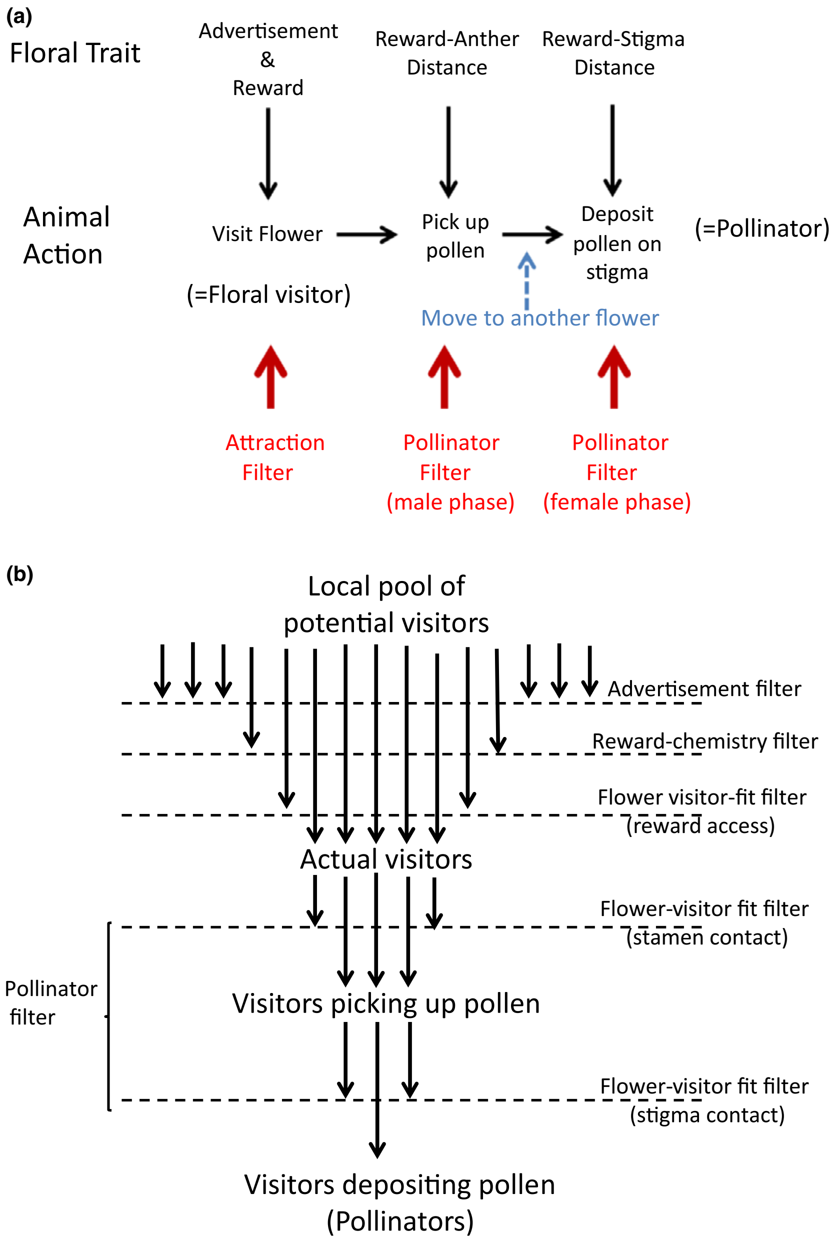

Fig. 1. Steps of pollination and filtering. (a) Flow diagram depicting the steps of pollination and points of pollinator 'filtering'. Sequential steps of pollination are in black, and sequential pollination 'filters' operating are in red. (b) Filter diagram depicting in more detail possible layers of specialization during pollination.

clades of orchids have independently evolved use of this reward system. The taxonomic diversity (e.g. Araceae, Clusiaceae, Solanaceae, Euphorbiaceae, Bignoniaceae; Dressler 1982; Armbruster 2012) of this reward system indicates multiple origins of the relationship on the plant side, but phylogenetic evidence suggests only one origin on the bee side (Ramírez *et al*. 2011).

Floral resins and waxes form a final class of specialized reward filter limiting pollinator diversity. Terpenoid and benzophenone resins are secreted by flowers of *Dalechampia* (Euphorbiaceae) and some Clusiaceae (*Clusia*, *Clusiella*, *Tovomitopsis*), respectively (see review in Armbruster 2012). Floral resin production is also reported in some species of *Maxillaria* (Orchidaceae; Whitten *et al*. 2007). These resins act as rewards to pollinating bees that use resin in nest construction, including euglossine, meliponine and megachilid bees. Waxes have also been reported in *Maxillaria* flowers, and they are thought to attract wax-using bees, such as Meliponini (Apidae; Armbruster 2012).

Pollinator filters

Pollinator filters can act at two stages in pollination: i) contact with anthers and ii) contact with stigmas (Fig. 1). An animal attracted to a flower by rewards and advertisements may still fail to be a pollinator if it does not contact the anthers and pick up pollen or does not contact the stigmas and deposit pollen (or both). For example, it is often the case that bees collect rewards without contacting the anthers. Although these are termed 'thieves' and may have negative effects on plant fitness, in some cases, they may represent plants adaptively filtering out of poor pollinators, thereby conserving pollen for pickup by better vectors. Whether adaptive or not, the failure of fertile floral parts to contact some floral visitors is clearly a form of *de facto* ecological specialization by plants on a subset of pollinators.

An extremely sophisticated and previously unrecognized type of pollinator filtering has been reported in *Heliconia tortuosa* (Heliconiaceae). Here, only a subset of pollinators, curve-billed trap-lining hummingbirds (which provide higher 'quality' in terms of pollen dispersal distance), stimulate stigma receptivity, pollen germination and thus fertilization. Flower visits by these curve-billed hummingbirds stimulated the growth of more than three times as many pollen tubes as visits by straight-billed hummingbirds and more than five times as many as visits by butterflies. The mechanism of plant 'choice' appears to be detection of nectar removal. Straight-billed, territorial hummingbirds do not drain the nectar, whereas curve-billed hummingbirds do (Betts, Hadley & Kress 2015).

ECOLOGICAL SPECIALIZATION OF POLLINATORS

Just as plants may specialize on a subset of potential pollinators, flower-visiting animals often specialize on a subset of plant species in their local environment. All the same theoretical issues apply, as well as some additional ones. There are again questions about specialization as a continuum and whether it is defined by the number of plant species, higher taxa or flower functional types visited. It should also be noted that animals, with specialized flower foraging, especially bees, are often no better or even worse than generalists as pollinators of those flowers (e.g. Neff & Simpson 1990; Michener 2007; Maldonado, Lomascolo & Vazquez 2013; but see Larsson 2005). Specialized, co-evolved pollinators attracted by oviposition opportunities in brood-site-reward flowers can act as antagonists when nectar-feeding co-pollinators are abundant (Thompson & Fernandez 2006).

As discussed for flowers, there is also an issue of imposed vs. proportional specialization (i.e. an animal species visiting flowers of only a few plant species because only few are in bloom, or because many are in bloom, but most are ignored, respectively). This ties into the temporal scale of specialization, where long-lived vertebrates and insect species with long 'flight seasons' (e.g. birds, bumblebees, honeybees) forage from more plant species than those with very short flight seasons. Indeed, the most specialized oligolectic bees usually have short flight seasons coinciding with the flowering of their specific host plants (Wcislo & Cane 1996).

Another aspect of scale concerns whether we think about foraging specialization of species, populations or individuals. In some cases, an entire species utilizes flowers from a restricted set of plant species; in other cases, specialization may occur at the level of populations. Finally, floral specialization may occur, at least temporarily, at the level of individuals ('floral constancy'; see Waser 1986).

Within bees, specialization on certain species or families of plants when foraging pollen (for larval provisioning) is termed oligolecty. This is a common type of foraging strategy in solitary bees, especially in warm temperate regions (Michener 2007). Specialization of animals on flowers of particular plant species when foraging nectar is more rarely documented (but see Michener 2007), except in the cases of trait matching. Indeed, specialization of long-tongued animals on flowers with 'matching' long nectar tubes or spurs is expected under conditions of competitive resource depletion (Rodríguez-Gironés & Llandres 2008), but comparatively few data exist to evaluate this. That long-tongued insects may often be generalists even though their long-tubed flowers are pollination specialists (see Johnson & Raguso 2016) argues against co-evolutionary specialization in many cases of trait matching.

A striking case of apparently co-evolved 'trait matching' is seen in oil-foraging *Rediviva* bees and oil-reward *Diascia* flowers (Scrophulariaceae) in South Africa. Because the bees are highly specialized in where they obtain oil for larval provisioning (but not in nectar or pollen foraging), there is a tight among-population association between the length of the female bee's forelegs (the oil-collecting brushes are on the tarsi of the front legs) and the length of the corolla spurs containing oil (Steiner & Whitehead 1990, 1991). Similarly, dramatic trait matching is seen in other South African flowers and long-tongued flies (Johnson & Steiner 1997; Pauw, Stofberg & Waterman 2009; Newman, Manning & Anderson 2014) and in Neotropical flowers and pollinating hummingbirds (Maglianesi *et al.* 2014).

Phenotypic specialization

The concept of 'morphological specialization' dates back at least to Darwin (1859) and Cope (1896). Ollerton expanded the concept to 'phenotypic specialization', which includes any phenotypic trait that is highly modified from the 'usual' form (Ollerton *et al.* 2007), thus representing an evolved response apparently to selection for specialization. In contrast to ecological specialization in pollination, which is a characteristic of the interaction between plants and pollinators, phenotypic specialization is a characteristic of the organism.

PHENOTYPIC SPECIALIZATION OF FLOWERS

A seminal paper on floral variation and function in relation to phenotypic specialization was written by Berg (1960). She examined patterns of floral variation in plants with specialized vs. generalized pollination as inferred largely from floral symmetry and orientation. Monosymmetric (bilateral) flowers were assumed to be more specialized in pollination than polysymmetric (radial) flowers, and laterally oriented flowers were assumed to be more specialized than vertically oriented flowers. The phenotypic distinctions erected by Berg have largely stood the test of time, and the same traits continue to be used to infer ecological specialization (e.g. Armbruster *et al.* 1999; Sargent 2004; Fenster, Armbruster & Dudash 2009). Indeed, a recent study has shown that monosymmetric flowers are indeed pollinated by fewer functional groups of animals than are polysymmetric flowers (Gong & Huang 2009).

Extreme morphologies in both flowers and flower-visiting animals have been interpreted by Darwin (1877), and many biologists since, as evidence of both specialization and co-evolution (Thompson 1994; Schluter 2000). For example, the long nectar spurs of *Angraecum* orchids in Madagascar and the equally long proboscides of one sphinx moth *Xanthopan morgani* have been interpreted as indicative of mutual specialization (but see Wasserthal 1998). As noted above, the same is true of long nectar tubes and spurs of several South African flowers and long proboscides of their fly pollinators (e.g. Johnson & Steiner 1997; Pauw, Stofberg & Waterman 2009; Newman, Manning & Anderson 2014).

PHENOTYPIC SPECIALIZATION OF FLOWER-VISITING ANIMALS

Examples of phenotypic specialization of flower-visiting animals for effective foraging of floral rewards are numerous. For example, bees show phenotypic specializations for locating, harvesting and transporting floral resources: elongated proboscides for obtaining hidden nectar, scopae (pollen 'brushes') and corbiculae (pollen 'sacs') for transporting pollen (Thorp 1979); specialized scrapers for collecting floral oil (Buchmann 1987; Michener 2007); and the front-tarsal brushes, mid-tibial 'pads' and enlarged hind tibia of male euglossine bees for collecting, transferring and storing floral fragrances, respectively (Dressler 1982). As mentioned above, extremely long proboscides of most Lepidoptera, certain groups of flies and a large number of bee species are also specializations for obtaining floral nectar. Phenotypic specialization for pollen collection and transport is also seen in animals involved in obligate nursery mutualisms, for example the pollen-collecting tentacles of yucca moths (Pellmyr 2003) and pollen-storing concavities of fig wasps (Ramírez 1969).

PHENOTYPIC SPECIALIZATION MAY NOT BE ASSOCIATED WITH ECOLOGICAL SPECIALIZATION

Phenotypic specialization of flowers is usually thought to be associated with ecological specialization (e.g. Darwin 1877; Newman, Manning & Anderson 2014; but see Ollerton *et al.* 2009). However, because ecological generalization can itself be a derived state involving derived traits, one should not always assume that all derived traits are the product of specialization.

Apparently specialized phenotypes of flowers can sometimes evolve as a result of increasing the number of pollinator species rather than reducing their diversity, as already discussed. The same is true of flower-visiting animals, for which the evolution of long proboscides could reflect adding flowers with long tubes to a broad repertoire of nectar sources. Long proboscides in bees and lepidopterans allow such species to obtain nectar from both short- and long-tubed flowers often without large trade-offs (e.g. Borrell 2005; Johnson & Raguso 2016; Johnson *et al.* 2017; but see Bauder, Warren & Krenn 2015). Among hummingbirds, in contrast, handling trade-offs may be large enough to lead to specialization and bill length matching tube lengths of flowers visited (Maglianesi *et al.* 2014).

The lack of a relationship between ecological and floral phenotypic specialization is illustrated by triggerplants (*Stylidium*, Stylidiaceae). Flowers are phenotypically specialized in having fused staminate and pistillate tissues, which together form a flexible, motile column involved in forcibly placing pollen on, and retrieving pollen from pollinators (Fig. 2). Pollinators of a single *Stylidium* flower can include long- and short-tongued bees and long- and short-tongued bee flies, syrphid flies and beetles. These can all be effective pollinators because the flexible column conforms to the size shape of the different insect bodies during precise pollen placement and retrieval (Armbruster *et al.* 2009). This precision is important because often four to eight co-flowering species occur sympatrically, but fertile parts of sympatric species usually contact pollinators

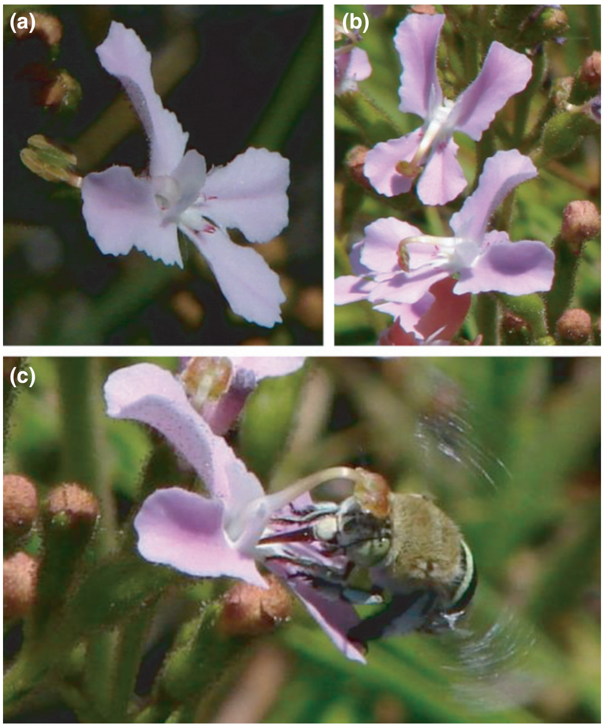

Fig. 2. Flowers and pollinator of *Stylidium maritimum.* (a) A flower with the column in the 'cocked' position. (b) Flowers with columns in the 'discharged' position. (c) A flower placing pollen on the head of a nectar-seeking *Amegilla* sp. (Apidae: Anthophorini).

consistently in different locations (Armbruster, Edwards & Debevec 1994; Armbruster *et al*. 2009; Armbruster 2012). The highly derived flowers of *Stylidium* allow efficient use of several functional groups of pollinators and also promote coexistence of multiple sympatric species (see Pauw 2013).

Evolutionary specialization and evolutionary trends

Evolutionary specialization in plant–pollinator interactions refers to the process or trend of evolving from ecologically or phenotypically less specialized to more specialized (Armbruster, Fenster & Dudash 2000; Fenster *et al*. 2004). Flowers may evolve more specialized pollination, and animals may evolve more specialized use of floral resources. If these occur concurrently, then they may indicate the operation of co-evolution *sensu* Janzen (1980). Usually, this is not the case (i.e. 1:1 co-evolved plant–pollinator specialization is rare). In fact, there appears to be a general tendency for specialized flower visitors to forage from generalist flowers and for specialized flowers to be associated with generalist pollinators ('network asymmetry'; Bascompte *et al*. 2003; Vazquez & Aizen 2004; Thebault & Fontaine 2008).

Specialization as a microevolutionary process is a genetic response to selection for more specialized ecology. Selection for specialization can be visualized as a narrow adaptive peak with steep sides (with base axes being resource use). The ability of the population to specialize is reflected in its ability to occupy the peak, with limits imposed by genetic constraints and developmental/environmental noise. Thus, the capacity for trait canalization becomes important, for example floral modularity (phenotypic independence from other traits; Berg 1960; Armbruster *et al*. 1999, 2014a; Murren 2012).

For example, consider pollinator-mediated selection imposed on an orchid that has recently evolved a floral fragrance attracting only one species of euglossine bee. Because all bees visiting are conspecific, they are of essentially the same size and have essentially the same behaviour. They will thus generate consistent, identical selection on traits that influence the fit of the bee in the flower relative to picking up and depositing pollinaria (e.g. flower size and shape). Floral phenotypes that fit the bee poorly are selected against, and if the variation has a genetic basis, those alleles will gradually disappear from the population.

One insight gained from studies of pollination trade-offs is that ecological specialization is more likely to evolve when there are strong trade-offs in pollinator effectiveness (e.g. Wilson & Thomson 1996; Aigner 2001; Muchhala 2007; Kay & Sargent 2009). However, Muchhala *et al*. (2010) showed convincingly with an individual-based model tracing the fates of pollen grains that selection through male fitness (the number of offspring sired on other plants) can drive the evolution of specialization on the best pollinators in the absence of any trade-offs in pollinator effectiveness. This is because those pollinators that are more efficient at transporting pollen to conspecific stigmas will be favoured over those losing a portion of their pollen load to, or *en route* to, heterospecific flowers.

FLORAL SPECIALIZATION, MACROEVOLUTION AND SPECIATION

Macroevolutionary questions can be addressed through comparative studies of plant–pollinator relationships. For example, there is long-standing interest in whether generalized ecology tends to evolve towards more specialized ecology (or vice versa) and whether specialists are evolutionary dead-ends (Futuyma & Moreno 1988; Armbruster & Baldwin 1998; Tripp & Manos 2008). The current conclusion is that there is not a strong effect of ecological specialization on either of the above evolutionary patterns (Barrett 2013), although more research is needed. Specialization commonly evolves from more generalized ancestors (evolutionary specialization), but the reverse (evolutionary generalization) is sometimes the case too (Armbruster & Baldwin 1998; Nosil & Mooers 2005; Tripp & Manos 2008; Barrett 2013).

Darwin (1877), Grant (1949) and many others since have argued that floral specialization influences plant diversification, and this concept continues to hold intuitive appeal (see reviews in Kay & Sargent 2009; Armbruster 2014). The most commonly invoked mechanism is that specialized pollination increases the likelihood of prezygotic reproductive isolation and hence speciation rates and clade diversity (Grant 1949, 1994). One early study demonstrated that clades whose members bore spurred (specialized) flowers contained more species than their sister clades whose members lacked nectar spurs (Hodges & Arnold 1995). They interpreted this to be likely the result of differential speciation rates. Differential speciation has been invoked as the mechanism explaining associations between specialized flowers and species diversity in most subsequent papers (e.g. Hodges 1997; Sargent 2004; Schiestl & Schlueter 2009).

There are, however, additional possible evolutionary mechanisms that can generate an association between specialization and clade diversity, and these have received attention only recently (e.g. Armbruster & Muchhala 2009; Armbruster 2014; Armbruster, Shi & Huang 2014b; Givnish *et al*. 2015; O'Meara *et al*. 2016). Although these authors do not attempt to refute differential speciation as a factor, they emphasize the possible operation of two additional mechanisms. These are (i) differential extinction, where specialized flowers reduce competition for pollination and/or increase pollination, outcrossing and successful reproduction and hence lower extinction rates, and (ii) co-occurrence with several relatives (which increases with clade size) selects for specialized flowers (Armbruster & Muchhala 2009). The former mechanism receives support from observations of floral character displacement and pollination ecologically structured plant assemblages, where widespread species diverge in pollination ecology from sympatric species in an 'organized' fashion (Armbruster, Edwards & Debevec 1994; Pauw 2013). There is modelling evidence that such specialization stabilizes community structure, hence reducing probabilities of extinction (Benadi *et al.* 2013).

POLLINATOR EVOLUTION

While many analyses of plant–pollinator relationships show evidence of flowers evolving in response to selection mediated by pollinators, there are fewer examples of pollinators evolving in response to selection mediated directly by the flowers with which they interact (although diffuse co-evolution between plants and flower-visiting animals is clearly important). Examples of tight co-evolution, best expressed in nursery pollination mutualisms (see reviews in Thompson 1994; Pellmyr 2003), seem to be the exception rather than the rule among free-living plants and pollinators, even when relationships are apparently quite specialized (e.g. Ramírez *et al.* 2011).

Bee oligolecty (collection of pollen only from related plants) has originated multiple times from generalized pollen use, forming tight associations between certain bee species and certain plant families (Wcislo & Cane 1996). This indicates evolutionary specialization on the part of the bees probably independent of plant evolution. I know of no examples, however, of oligolectic bees being co-evolved pollinators of their host plants (see also Michener 2007). The transition from oligolecty to polylecty has also occurred in some bee lineages (e.g. Muller 1996).

There appears to be a co-evolutionary relationship between length of the spur containing oil in *Diascia* flowers and foreleg length in South Africa *Rediviva* (oil-collecting brushes are on the tarsi of the front legs) (Steiner & Whitehead 1990, 1991), as noted above. If these authors' interpretation is correct, this would be a rare example of 1:1 co-evolution among free-living mutualists (as opposed to diffuse co-evolution, which is common). At the very least, it is a good example of pollinators evolving in response to variation in their host flower's morphology. Other examples of local adaptation of pollinators to flower features include long-tongued *Prosoeca* (Anderson & Johnson 2008) and *Moegistorhynchus* flies (Nemestrinidae; Pauw, Stofberg & Waterman 2009), also in South Africa.

SPECIALIZATION AND PHENOTYPIC DISPARITY

In the history of life, evolution of increasing disparity (degree of phenotypic diversity) is probably associated with evolution of phenotypic specialization. One pattern observed in the deep evolutionary history of various groups is the early rise in disparity followed by stability (e.g. Hughes, Gerber & Wills 2013; Oyston *et al.* 2015). This presumably reflects early increases in specialization, followed by stabilization or even declines. Virtually, no research directly addresses this hypothesized relationship, and it deserves further investigation (Matthew Wills, pers. comm.).

There is persuasive correlative evidence that specialization on different pollinators has contributed to increases in the phenotypic diversity (disparity) of flowers, at least in some cases (van der Niet & Johnson 2012; Gomez *et al.* 2016). Across the major groups of flowering plants, however, increases in floral disparity and current frequencies of floral character combinations appear to be the result of complex interactions between differential diversification and non-equilibrium historical effects, with only limited input from evolutionary transitions between states as mediated by pollinators and other selective agents (O'Meara *et al.* 2016).

Influences of floral specialization on the structure of ecological communities

Numerous studies have suggested that excessive ecological overlap between sympatric species leads to local exclusion or evolutionary divergence, and such effects are particularly intense when 'competitors' are closely related (Darwin 1872, Brown 1975). This is expected to be the case for related, sympatric plants that have flowers similar enough potentially to share pollinators (see reviews in Armbruster, Edwards & Debevec 1994; Pauw 2013; Beans 2014; but see Ollerton *et al.* 2003). There is evidence that related sympatric species often bloom at different times of day or season (e.g. Stiles 1977; Gleeson 1981; Stone, Willmer & Rowe 1998; Aizen & Vázquez 2006), attract different pollinators (e.g. Armbruster 1986) or place pollen in different locations on shared pollinators (Dressler 1969; Armbruster, Edwards & Debevec 1994; Muchhala & Potts 2007). For example, in East Africa, species of *Acacia* trees (Fabaceae) share pollinator species, but tend to release pollen at different times of day, minimizing interspecific pollination (Stone, Willmer & Rowe 1998). In Western Australia, sympatric species of triggerplants (*Stylidium*) share bee fly pollinators, but usually place pollen in different locations on their bodies, reducing interspecific pollen flow (Armbruster, Edwards & Debevec 1994).

Thus, natural assemblage may be structured by ecological or evolutionary processes generated by reproductive interference, forming non-random assemblages of species (see Waser 1983). Plant species that differ in their pollination niches through specialization may be better able to maintain positive reproductive rates and coexist, thus allowing more species to occur in communities than would otherwise be possible (Pauw 2013), and this may reduce extinction rates. Such adaptation on the part of populations may contribute to ecological stability and resilience in the face of environmental change or disturbance (Benadi *et al.* 2013; but cf. Waser *et al.* 1996).

NETWORK STUDIES OF ANIMAL–FLOWER INTERACTION WEBS

Studies of animal–flower interaction networks have contributed in important ways to our understanding of generalized and specialized pollination (e.g. Bascompte *et al.* 2003; Olesen *et al.* 2007). However, missing from most of these analyses is the biological detail about how effective floral visitors are as pollinators; most interaction network studies have not assessed pollination success. This is fine as a trophic network (animals exploiting food resources), but it is inadequate as a measure of specialized vs. generalized pollination from the plant perspective. Improvements include building networks based on identifying pollen on stigmas (Ashman & Arceo-Gomez 2013; Fang & Huang 2013) and direct assessment of pollinator effectiveness (e.g. Ollerton *et al.* 2003; Traveset *et al.* 2015).

Another shortcoming of most network studies is that they fail to assess what resources animals are collecting from flowers, and this can cause misinterpretation of the degree of animal specialization. For example, when a bee visits several kinds of flower, it would normally be treated as a generalist. However, to reproduce, bees need several kinds of resources from their environment, and these may have to be harvested from a variety of flowers.

Female euglossine bees, for example, depend on some flowers for nectar, others for pollen and still other flowers (or other plant parts) for resin. Male euglossine bees visit some flowers for nectar, and they collect fragrances (used for attracting females) from yet other plants (Ramírez *et al.* 2011). Using a network analysis ignoring resources collected, euglossine bees would appear to be generalists, yet they are better described as ecologically generalized in some foraging activities (pollen and nectar foraging), but potentially highly specialized in others (resin and fragrance foraging; Fig. 3). Such complex interrelationships may be especially vulnerable to loss of local plants diversity. Yet analyses concluding that such bees are generalists could easily lead to the opposite conclusion. Thus, both pollination effectiveness and resources collected will need to be incorporated into future network studies if we are to make inferences about ecosystem resilience.

Conclusions and recommendations for future research

The specialization concept in plant–pollinator interactions has been used in a variety of ways, ranging from ecological and phenotypic to evolutionary. All are valid, but in any study, they need to be defined, because different interpretations of specialization have different evolutionary and ecological implications. There are indeed many ways that flowers evolve towards ecological specialization. Counter-intuitively, highly ‘specialized’ (derived) floral morphologies can also evolve to promote the efficacy of generalized pollination. Some flower-visiting animals can be misinterpreted as generalists because they visit many kinds of flowers, when in fact they have actually specialized on different hosts for different essential resources. Thus, more detailed studies of the webs of interactions between flowers and pollinators will be needed for accurate assessment of ecosystem resilience and vulnerability in the face of changing climate and other environmental challenges.

It seems advantageous to adopt a definition of specialization that incorporates both ecology and evolution. In this regard, ecological specialization based on linkages with evolutionarily defined functional groups (members of which generate similar selection pressure) may sometimes be preferable to specialization defined by the number of linkages with interacting species or higher taxa, although this will not be practical for broad surveys. There is a need

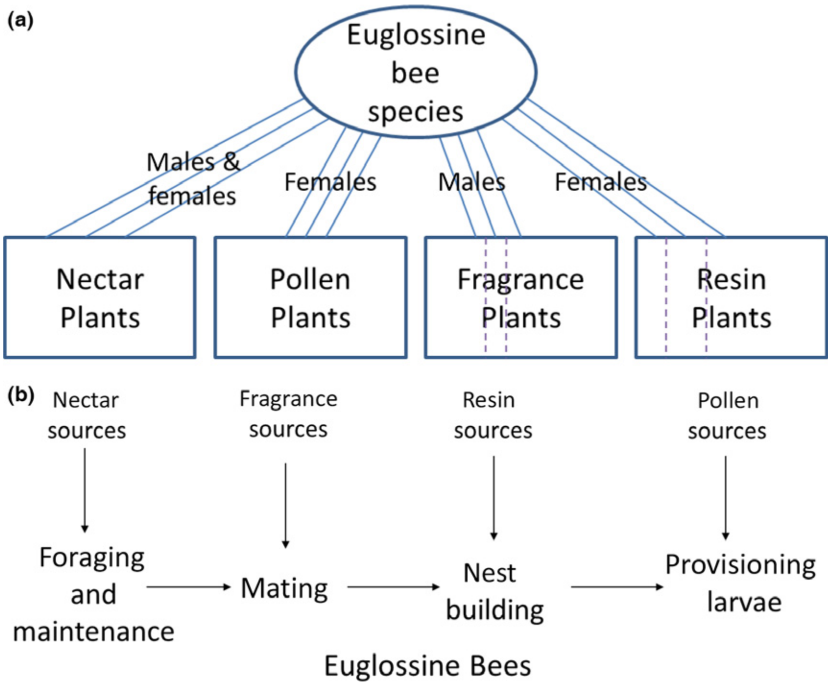

Fig. 3. Euglossine bees (Apidae: Euglossini) are serial foragers using multiple plant species for various resources. They are dependent on all these resources. Flower resources in different categories (boxes) are not alternatives; all are necessary for bee survival and reproduction. (a) Network diagram suggesting generalization (a misleading conclusion) with members of one species of bee visiting a number of different plant species for resources. Note that fragrances and resins are modelled as coming from three non-interchangeable plant species, denoted by dotted partitions. (b) Series diagram emphasizing multiple dependencies.

for more phenotypic selection studies to assess whether similar but unrelated pollinators exert largely similar or very different selective pressures. Measurements of trade-offs in the effectiveness of different kinds of pollinators are also needed in this context.

Evolutionary specialization, as defined here, involves not only evolutionary trends, but also processes. The relationships between floral phenotypic traits and trends of increasing specialization need more investigation, especially using analytical methods that afford insights into causality. Improvements in methods assessing rates of speciation and extinction from phylogenetic data (cf. FitzJohn, Maddison & Otto 2009; Rabosky 2016 and references cited therein) would be especially valuable. Were these developed, we could gain better insights into whether specialized flowers and pollinators enhance population viability and reduce extinction or are instead drivers of speciation. It would be especially valuable to gain such insights, because they would go a long way towards resolving unanswered questions about whether or not macroevolutionary trends are largely an extension of microevolution (differential extinction is important) or instead largely independent of microevolution (differential speciation is important; cf. Gould 1980; Mayr 1982; Pennell, Harmon & Uyeda 2014).

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