

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21

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

W Scott Armbruster^{1,2}

¹School of Biological Sciences, University of Portsmouth, Portsmouth PO1 2DY, UK; and

²Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775-7000, USA

22 **Summary**

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

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

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

41

42

43 **Key-words:** community ecology, evolution, extinction, functional-group specialization,
44 pollination, pollination networks, specialization, speciation

45

46

47 **Introduction**

48

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

59 Specialization has a long history as a topic of interest in the study of plants, especially
60 with respect to floral morphology and function and effects on angiosperm diversity.

61 However, despite its clear importance in plant evolution, floral specialization is poorly
62 understood as a process, and it has multiple interpretations as a state, and unclear links to
63 other processes such as diversification (see Waser et al. 1996, Ollerton 1996). For example,
64 the association between specialization and diversity is generally thought to be the result of
65 specialization increasing the likelihood of prezygotic reproductive isolation and, thereby,
66 increasing rates of speciation (Grant 1949, 1971, 1994; see reviews in Kay & Sargent 2009
67 and Armbruster 2014). However, the association could also be generated in other ways
68 (Armbruster & Muchhala 2009; Armbruster 2014; see below).

69 How specialization is defined obviously affects how it is measured (e.g. Schluter
70 2000), and it also affects how we interpret the ecological and evolutionary significance of
71 specialization. Here I draw together and contrast all of the distinct definitions and uses of

72 specialization of both flowers and their visitors. The goal is to explore both conceptual and
73 empirical issues that relate to perceived links between floral specialization and angiosperm
74 species diversity and disparity (phenotypic diversity), as well as the possible influences of
75 floral specialization on the structure and resilience of ecological communities.

76

77

78 **Ecological specialization of flowers**

79

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

86 Ecological specialization of flowers is often referred to as "specialized pollination".

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

94

95 **FUNCTIONAL-GROUP SPECIALIZATION**

96 With respect to the second question, group resolution, Robertson (1918), Fenster et al.
97 (2004), Ollerton et al. (2007), and others have suggested that treating pollinators that interact
98 with the flower similarly as a "functional group" is often more informative than lower taxa as
99 units. They proposed that these groups be higher-level categories, as in pollination-
100 syndromes (e.g. bats vs. hovering birds vs. short-tongued bees). Ollerton called this
101 "functional specialization", although I suggest that this be modified to "functional-group
102 specialization" for clarity. ("Functional specialization" has already been used extensively in
103 the literature to refer to specialization in organ or tissue function, with nearly 2000 published
104 papers in the biological sciences since 1970 (Web of Science search, 07.07.2016).

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

112 Fenster et al. (2004) argued, in contrast, that functional groups should be defined as
113 groups or guilds of species mediating (or inferred to mediate) similar selection on floral traits
114 by virtue of their similarity in morphology and/or behaviour (consistent with the evolution of
115 pollination syndromes). Thus unrelated pollinator species could sometimes be in the same
116 functional group, while taxonomically close pollinators might sometimes be in different
117 functional groups, depending on the natural selection they generate. For example, male bees
118 often exert very different selective pressures than conspecific females (Motten et al. 1981,
119 Armbruster et al. 2002, Cane 2002, Pascarella 2010), as behaviour, body size, and proboscis
120 lengths generally differ (Michener 2007), while long-tongued flies might sometimes exert the

121 same selection on floral-tube length as bees with similar tongue lengths (as appears to be the
122 case in pollination of *Linum* and *Stylidium*; Armbruster et al. 1994, 2006, 2009).

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

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

140

141 PROPORTIONAL VS. ABSOLUTE SPECIALIZATION

142 Until recently little attention has been focused on whether specialization should
143 reflect the absolute number of pollinator types vs. the proportion of potential pollinator types
144 utilized. Use of one or few pollinator species as a result of the lack of other potential
145 pollinators in a taxonomically depauperate environment ("imposed specialization") is not

146 specialization in the usual ecological sense (specializing on a subset of resources). In
147 contrast, "proportional" or "relative" specialization capture the degree to which a subset of
148 potential pollinators are used. Although most authors do not emphasize this distinction, it
149 becomes important when one works with the biota of islands (e.g. Marten-Rodriguez et al.
150 2015) or extreme environments, such as the Arctic (e.g. Armbruster 2006), and becomes an
151 explicit methodological issue in network studies (Blüthgen et al. 2006, Pauw et al. 2015). In
152 terms of relative amounts of "filtering" (see below), a species of *Pedicularis* (Orobanchaceae)
153 pollinated primarily by one species of bumble bee in the Canadian High Arctic (where only a
154 couple bee species occur; Kevan 1972) is not more specialized than a *Pedicularis* species
155 pollinated by several species of bees in montane California (where dozens of bee species are
156 present). However, the evolutionary consequences, in terms of contemporary selection on
157 traits promoting attraction of, and efficient pollination by those pollinators, are similar,
158 whether the specialization is imposed or proportional.

159

160 SPECIALIZATION CONTINUA AND SCALES

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

170 In thinking about flowers with ecologically generalized pollination ("generalist
171 flowers"), it is useful to consider the origin and maintenance of generalized pollination. A
172 generalist flower could be a "cryptic specialist", because it has responded evolutionarily to a
173 single selective pressure generated by a diversity of pollinators whose similarities in selection
174 generated have escaped notice. Alternatively, a generalist flower may have originated by
175 adapting to a balance of different selective pressures generated by a diversity of pollinator
176 types. For example, *Stylidium* (Stylidiaceae) flowers exhibit several features that make them
177 well adapted to using pollinators of a large range of sizes and taxa (Armbruster et al. 1994,
178 2009). Some species of *Dudleya* (Crassulaceae) with semi-tubular corollas appear to be
179 adapted to pollination by both bees and hummingbirds (Aigner 2004). Lastly, generalization
180 could reflect a plant's limited capability in restricting access rewards by suboptimal floral
181 visitors (i.e. evolutionary constraints).

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

192

193 ECOLOGICAL SPECIALIZATION WITH AND WITHOUT TRADE-OFFS

194 In a series of influential papers, Aigner (2001, 2004, 2006) pointed out the importance of
195 assessing fitness trade-offs in attempting to understand the operation and evolution of
196 specialized pollination. Fitness trade-offs occur when the positive effect of a floral trait on
197 the pollination effectiveness of one pollinator creates a negative effect on pollination
198 effectiveness of another. This can be assessed by considering the marginal increment in plant
199 fitness generated by changes required to add a pollinator to the existing suite of effective
200 pollinators in relation to the fitness cost incurred through those changes (Aigner 2001).
201 Indeed, pollinator-effectiveness trade-offs are thought to have been critical in the origin and
202 maintenance of specialized pollination (Schemske & Horvitz 1984; Wilson & Thomson
203 1996; Aigner 2001; Mayfield et al. 2001; but cf. Muchhala et al. 2010).

204 However, fitness trade-offs are not always observed. Aigner (2001, 2004, 2006)
205 found that fitness trade-offs were absent in pollination of generalist *Dudleya greenei* flowers
206 by large bees, small bees and hummingbirds. The absence of fitness trade-offs in the
207 adaptation to a new pollinator disconnects ecological and phenotypic specialization (Aigner
208 2001; see below;). Experimental manipulation of corolla shape towards being more open
209 resulted in hummingbirds being less effective, but bees becoming no more effective (Aigner
210 2004, 2006). Because most Crassulaceae have open flowers, these results can be interpreted
211 as evidence of "specialized" tubular morphology that better fits hummingbirds having
212 evolved in response to marginal selection generated as hummingbirds were added to the
213 plants' original pollinator repertoire (bees). The lack of trade-offs meant that bees were not
214 lost as pollinators in the process, and net generalization increased. Due to the paucity of
215 adequate studies, however, it remains unknown whether fitness trade-offs in pollination are
216 rare or common (Aigner 2006).

217 A few studies are instructive in showing the range of outcomes and the importance of
218 detailed understanding of the operation of trade-offs in pollination. Muchhala (2007)

219 detected a strong trade-off between hummingbird and bat 'pollination' of artificial flowers of
220 different widths, mimicking the floral morphologies of two species of *Burmeistera*
221 (Campanulaceae). A perusal of published studies suggests that fitness trade-offs are more
222 common in bilaterally symmetrical (zygomorphic) flowers than in radially symmetrical
223 flowers (Armbruster, unpublished data). There are, of course, numerous interesting
224 exceptions to this possible trend, such as Australian triggerplants, *Stylidium*, with
225 zygomorphic flowers, but ecologically generalized pollination mostly lacking trade-offs (see
226 below). An "opposite" exception is the shrubby wild flax, *Linum suffruticosum*, which has
227 radially symmetrical flowers but has strong pollinator-size related trade-offs (Armbruster et
228 al. 2004, 2009).

229

230 ECOLOGICAL SPECIALIZATION AS "FILTERING"

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

239 **Attraction filters** operate at the first step by reducing the diversity of animals
240 attracted to flowers (Fig. 1B), by, e.g., when the flowers are open (day vs. night), what
241 specific advertisements (colour, shape, scent) and rewards (nectar, pollen, oils, resin, etc.) are
242 deployed (Armbruster 2012). Attraction filters operating through advertisement
243 ("advertisement filters") differential signalling and sensory biases. There is some evidence

244 for the operation of advertisement filters through color biases, e.g. white flowers being
245 differentially attractive to nocturnal insects and red flowers reducing bee visitation
246 sufficiently to promote specialization on bird pollination (see discussion in Chittka et al.
247 2001; Wilson et al. 2003; Rodríguez-Gironés & Santamaría 2004). Even more effective
248 advertisement filtering is seen through diversification in floral fragrance chemistry, with
249 certain compounds selectively attracting or repelling different kinds of animals (Dressler
250 1982, Faegri & van der Pijl 1979; Fenster et al. 2004; Raguso 2008).

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

256 "Specialize" pollinator rewards also act like filters; these include specialized brood
257 sites, floral oils, reward fragrances, and floral resins, materials not attractive to most flower-
258 visiting animals (Armbruster 2012). The specificity of relationships between yuccas and
259 yucca moths and figs and fig wasps, for example, is based on the various chemical and
260 physical characteristics of the flower organs exploited by the pollinating seed predators. Oils
261 secreted by flowers as rewards are collected only by members of a few small clades of bees
262 in the Melittidae (e.g. *Macropis*, *Rediviva*) and Apidae (e.g. Tapinotaspidini+Ctenoplectrini,
263 Tetrapediini, Centridini), which include oil in larval provisions (Buchmann 1987; Michener
264 2007). Other animals are not attracted by such rewards.

265 Another class of specialized reward that filters out all floral visitors but a few genera
266 or species of bees is monoterpene or aromatic reward fragrances. Here flowers offer no
267 reward other than fragrances that are attractive to male euglossine bees (Apidae: Euglossini),
268 a group of large, generally solitary, neotropical bees. The males use the fragrances collected

269 from flowers and other sources to attract females. Because these fragrances communicate
270 species identity to the female bee (Zimmermann et al. 2009), as well as possibly signalling
271 genetic quality, considerable specificity in attraction can occur. Several clades of orchids
272 have independently evolved use of this reward system. The taxonomic diversity (e.g.
273 Araceae, Clusiaceae, Solanaceae, Euphorbiaceae, Bignoniaceae, etc.; Dressler 1982;
274 Armbruster 2012) of this reward system indicates multiple origins of the relationship on the
275 plant side, but phylogenetic evidence suggests only one origin on the bee side (Ramírez et al.
276 2011).

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

285

286 "**Pollinator filters**" can act at two stages in pollination: i) contact with anthers and ii)
287 contact with stigmas (Fig. 1). An animal attracted to a flower by rewards and advertisements
288 may still fail to be a pollinator if it does not contact the anthers and pick up pollen or does not
289 contact the stigmas and deposit pollen (or both). For example, it is often the case that bees
290 collect rewards without contacting the anthers. Although these are termed "thieves" and may
291 have negative effects on plant fitness, in some cases, they may represent plants adaptively
292 filtering out of poor pollinators, thereby conserving pollen for pickup by better vectors.

293 Whether adaptive or not, the failure of fertile floral parts to contact some floral visitors is
294 clearly a form of *de facto* ecological specialization by plants on a subset of pollinators.

295

296

297 **Ecological specialization of pollinators**

298

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

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

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

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

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

342

343

344 Phenotypic specialization

345

346 The concept of "morphological specialization" dates back at least to Darwin (1859) and Cope
347 (1896). Ollerton expanded the concept to "phenotypic specialization", which includes any
348 phenotypic trait that is highly modified from the "usual" form (Ollerton et al. 2007), and thus
349 representing an evolved response apparently to selection for specialization. In contrast to
350 ecological specialization in pollination, which is a characteristic of the interaction between
351 plants and pollinators, phenotypic specialization is a characteristic of the organism.

352

353 PHENOTYPIC SPECIALIZATION OF FLOWERS

354 A seminal paper on floral variation and function in relation to phenotypic specialization was
355 written by Rissa Berg (1960). She examined patterns of floral variation in plants with
356 specialized vs. generalized pollination as inferred largely from floral symmetry and
357 orientation. Monosymmetric (bilateral) flowers were assumed to be more specialized in
358 pollination than polysymmetric (radial) flowers, and laterally oriented flowers were assumed
359 to be more specialized than vertically oriented flowers. The phenotypic distinctions erected
360 by Berg have largely stood the test of time, and the same traits continue to be used to infer
361 ecological specialization (e.g. Armbruster et al. 1999, Sargent 2000, Fenster et al. 2009).
362 Indeed, a recent study has shown that monosymmetric flowers are indeed pollinated by fewer
363 functional groups of animals than are polysymmetric flowers (Gong & Huang 2009).

364 Extreme morphologies in both flowers and flower-visiting animals have been
365 interpreted by Darwin (1877), and many biologists since, as evidence of both specialization
366 and coevolution (Thompson 1994, Schluter 2000). For example, the long nectar spurs of

367 *Angraecum* orchids in Madagascar and the equally long proboscides of one sphinx moth,
368 *Xanthopan morgani*, have been interpreted as indicative of mutual specialization (but see
369 Wasserthal 1998). As noted above, the same is true of long nectar tubes and spurs of several
370 South African flowers and long proboscides of their fly pollinators (e.g. Johnson & Steiner
371 1997, Pauw et al. 2009, Newman et al. 2014).

372

373 PHENOTYPIC SPECIALIZATION OF FLOWER-VISITING ANIMALS

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

386

387 PHENOTYPIC SPECIALIZATION MAY NOT BE ASSOCIATED WITH ECOLOGICAL 388 SPECIALIZATION

389 Phenotypic specialization of flowers is usually thought to be associated with ecological
390 specialization (e.g. Darwin 1877; Newman, Manning & Anderson 2014; but see Ollerton et al
391 2009). However, because ecological generalization can itself be a derived state involving

392 derived traits, one should not always assume that all derived traits are the product of
393 specialization.

394 Apparently specialized phenotypes of flowers can sometimes evolve as a result of
395 increasing the number of pollinator species rather than reducing their diversity, as already
396 discussed. The same is true of flower-visiting animals, for which the evolution of long
397 proboscides could reflect adding flowers with long tubes to a broad repertoire of nectar
398 sources. Long proboscides in bees and lepidopterans allow such species to obtain nectar
399 from both short- and long-tubed flowers often without large trade-offs (e.g. Borrell 2005;
400 Johnson & Raguso 2016; Johnson *et al.*, this volume; but see Bauder, Warren & Krenn
401 2015). Among hummingbirds, in contrast, handling trade-offs may be large enough to lead to
402 specialization and bill length matching tube lengths of flowers visited (Maglianesi *et al.*
403 2014).

404 The lack of a relationship between ecological and floral phenotypic specialization is
405 illustrated by triggerplants (*Stylidium*, Stylidiaceae). Flowers are phenotypically specialized
406 in have fused staminate and pistillate tissues, which together form a flexible, motile column
407 involved in forcibly placing pollen on, and retrieving pollen from pollinators (Fig. 2).
408 Pollinators of a single *Stylidium* flower can include long- and short-tongue bees and long- and
409 short-tongue bee flies, syrphid flies, and beetles. These can all be effective pollinators
410 because the flexible column conforms to the size shape of the different insect bodies during
411 precise pollen placement and retrieval (Armbruster *et al.* 2009). This precision is important
412 because often 4-8 co-flowering species occur sympatrically but fertile parts of sympatric
413 species usually contact pollinators consistently in different locations (Armbruster *et al.* 1994,
414 2009, Armbruster 2012). The highly derived flowers of *Stylidium* allow efficient use of
415 several functional groups of pollinators and also promote coexistence of multiple sympatric
416 species (see Pauw 2013).

417

418

419 Evolutionary specialization and evolutionary trends

420

421 Evolutionary specialization in plant-pollinator interactions refers to the process or trend of

422 evolving from ecologically or phenotypically less specialized to more specialized

423 (Armbruster et al. 2000, Fenster et al. 2004). Flowers may evolve more specialized

424 pollination, and animals may evolve more specialized use of floral resources. If these occur

425 concurrently, then they may indicate the operation of coevolution *sensu* Janzen (1980).

426 Usually this is not the case (i.e. 1:1 coevolved plant-pollinator specialization is rare). In fact,

427 there appears to be a general tendency for specialized flower visitors to forage from generalist

428 flowers and for specialized flowers to be associated with generalist pollinators ("network

429 asymmetry"; Bascompte et al. 2003; Vazquez & Aizen 2004; Thebault & Fontaine 2008).

430 Specialization as a microevolutionary process is a genetic response to selection for

431 more specialized ecology. Selection for specialization can be visualised as a narrow adaptive

432 peak with steep sides (with base axes being resource use). The ability of the population to

433 specialize is reflected in its ability to occupy the peak, with limits imposed by genetic

434 constraints and developmental/environmental noise. Thus, the capacity for trait canalisation

435 becomes important, e.g. floral modularity (phenotypic independence from other traits; Berg

436 1960; Armbruster et al. 1999, 2014a; Murren 2012).

437 For example, consider pollinator-mediated selection imposed on an orchid that has

438 recently evolved a floral fragrance attracting only one species of euglossine bee. Because all

439 bees visiting are conspecific, they are of essentially the same size and have essentially the

440 same behaviour. They will thus generate consistent, identical selection on traits that

441 influence the fit of the bee in the flower relative to picking up and depositing pollinaria (e.g.

442 flower size and shape). Floral phenotypes that fit the bee poorly are selected against, and if
443 the variation has a genetic basis, those alleles will gradually disappear from the population.

444 One insight gained from studies of pollination trade-offs is that ecological
445 specialization is more likely to evolve when there are strong trade-offs in pollinator
446 effectiveness (e.g. Wilson & Thomson 1996; Aigner 2001; Muchhala 2007; Kay and Sargent
447 2009). However, Muchhala et al. (2010) showed convincingly with an individual-based
448 model tracing the fates of pollen grains, that selection through male fitness (number of
449 offspring sired on other plants) can drive the evolution of specialization on the best
450 pollinators in the absence of any trade-offs in pollinator effectiveness. This is because those
451 pollinators that are more efficient at transporting pollen to conspecific stigmas will be
452 favoured over those losing a portion of their pollen load to, or *en route* to, heterospecific
453 flowers.

454

455 FLORAL SPECIALIZATION, MACROEVOLUTION, AND SPECIATION

456 Macroevolutionary questions can be addressed through comparative studies of plant-
457 pollinator relationships. For example, there is long-standing interest in whether generalized
458 ecology tends to evolve towards more specialized ecology (or vice versa), and whether
459 specialists are evolutionary dead-ends (Futuyma & Moreno 1988, Armbruster & Baldwin
460 1998, Tripp & Manos 2008). The current conclusion is that there is not a strong effect of
461 ecological specialization on either of the above evolutionary patterns (Barrett 2013), although
462 more research is needed. Specialization commonly evolves from more generalized ancestors
463 (evolutionary specialization), but the reverse (evolutionary generalization) is sometimes the
464 case too (Armbruster & Baldwin 1998, Nosil & Mooers 2005, Tripp & Manos 2008, Barrett
465 2013).

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

477 There are, however, additional possible evolutionary mechanisms that can generate an
478 association between specialization and clade diversity, and these have received attention only
479 recently (e.g. Armbruster and Muchhala 2009, Armbruster 2014, Armbruster et al. 2014b;
480 Givnish et al. 2015; O'Meara et al. 2016). Although these authors do not attempt to refute
481 differential speciation as a factor, they emphasize the possible operation of two additional
482 mechanisms. These are: i) differential extinction, where specialized flowers reduce
483 competition for pollination and/or increase pollination, outcrossing and successful
484 reproduction, and hence lower extinction rates; ii) co-occurrence with several relatives
485 (which increases with clade size) selects for specialized flowers (Armbruster and Muchhala
486 2009). The former mechanism receives support from observations of floral character
487 displacement and pollination-ecologically structured plant assemblages, where widespread
488 species diverge in pollination ecology from sympatric species in an "organised" fashion
489 (Armbruster et al. 1994, Pauw 2013). There is modelling evidence that such specialization

490 stabilizes community structure, hence reducing probabilities of extinction (Benadi *et al.*
491 2013).

492

493 POLLINATOR EVOLUTION

494 While many analyses of plant-pollinator relationships show evidence of flowers evolving in
495 response to selection mediated by pollinators, there are fewer examples of pollinators
496 evolving in response to selection mediated directly by the flowers with which they interact
497 (although diffuse coevolution between plants and flower-visiting animals is clearly
498 important). Examples of tight coevolution, best expressed in nursery pollination mutualisms
499 (see reviews in Thompson 1994, Pellmyr 2003), seem to be the exception rather than the rule
500 among free-living plants and pollinators, even when relationships are apparently quite
501 specialized (e.g. Ramírez *et al.* 2010).

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

509 There appears to be a coevolutionary relationship between length of the spur
510 containing oil in *Diascia* flowers and foreleg length in South Africa *Rediviva* (oil-collecting
511 brushes are on the tarsi of the front legs) (Steiner & Whitehead 1990, 1991), as noted above.
512 If these authors' interpretation is correct, this would be a rare example of 1:1 coevolution
513 amongst free-living mutualists (as opposed to diffuse coevolution, which is common). At the
514 very least, it is a good example of pollinators evolving in response to variation in their host-

515 flower's morphology. Other examples of local adaptation of pollinators to flower features
516 include long-tongued *Prosoeca* (Anderson & Johnson 2008) and *Moegistorhynchus* flies
517 (Nemestrinidae; Pauw et al. 2009), also in South Africa.

518

519 SPECIALIZATION AND PHENOTYPIC DISPARITY

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

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

535

536

537 **Influences of floral specialization on the structure of ecological** 538 **communities**

539

540 Numerous studies have suggested that excessive ecological overlap between sympatric
541 species leads to local exclusion or evolutionary divergence, and such effects are particularly
542 intense when “competitors” are closely related (Darwin 1872, Brown 1975). This is expected
543 to be the case for related, sympatric plants that have flowers similar enough potentially to
544 share pollinators (see reviews in Armbruster 1994; Pauw 2013; Beans 2014; but see Ollerton
545 *et al.* 2003). There is evidence that related sympatric species often bloom at different times
546 of day or season (e.g. Stiles 1977, Gleeson 1981, Stone *et al.* 1998, Aizen & Vasquez 2007),
547 attract different pollinators (e.g. Armbruster 1986), or place pollen in different locations on
548 shared pollinators (Dressler 1969, Armbruster *et al.* 1994, Muchhala & Potts 2007). For
549 example, in East Africa, species of *Acacia* trees (Fabaceae) share pollinator species, but tend
550 to release pollen at different times of day, minimising interspecific pollination (Stone *et al.*
551 1998). In Western Australia, sympatric species of triggerplants (*Stylidium*) share bee fly
552 pollinators, but usually place pollen in different locations on their bodies, reducing
553 interspecific pollen flow (Armbruster *et al.* 1994).

554 Thus, natural assemblage may be structured by ecological or evolutionary processes
555 generated by reproductive interference), forming non-random assemblages of species (see
556 Waser 1983). Plant species that differ in their pollination niches through specialization may
557 be better able to maintain positive reproductive rates and coexist, thus allowing more species
558 to occur in communities than would otherwise be possible (Pauw 2013), and this may reduce
559 extinction rates. Such adaptation on the part of populations may contribute to ecological
560 stability and resilience in the face of environmental change or disturbance (Benadi *et al.*
561 2013; but cf. Waser *et al.* 1996).

562

563 NETWORK STUDIES OF ANIMAL-FLOWER INTERACTION WEBS

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

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

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

589

590

591 **Conclusions and recommendations for future research**

592

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

604 It seems advantageous to adopt a definition of specialization that incorporates both
605 ecology and evolution. In this regard, ecological specialization based on linkages with
606 evolutionarily defined functional groups (members of which generate similar selection
607 pressure) may sometimes be preferable to specialization defined by number of linkages with
608 interacting species or higher taxa, although this will not be practical for broad surveys. There
609 is a need for more phenotypic-selection studies to assess whether similar but unrelated
610 pollinators exert largely similar or very different selective pressures. Measurements of trade-
611 offs in the effectiveness of different kinds of pollinators are also needed in this context.

612 Evolutionary specialization, as defined here, involves, not only evolutionary trends,
613 but also processes. The relationships between floral phenotypic traits and trends of

614 increasing specialization need more investigation, especially using analytical methods that
615 afford insights into causality. Improvements in methods assessing rates of speciation and
616 extinction from phylogenetic data (cf. Fitzjohn et al. 2009, Rabosky 2016, and references
617 cited therein) would be especially valuable. Were these developed, we could gain better
618 insights into whether specialized flowers and pollinators enhance population viability and
619 reduce extinction or are instead drivers of speciation. It would be especially valuable to gain
620 such insights, because they would go a long ways towards resolving unanswered questions
621 about whether or not macroevolutionary trends are largely an extension of microevolution
622 (differential extinction is important) or instead largely independent of microevolution
623 (differential speciation is important; cf. Gould 1980; Mayr 1982; Pennell *et al.* 2014).

624

625

626 **Acknowledgements**

627

628 Funding for some of the research reviewed was provided by the US National Science
629 Foundation, the Norwegian Research Council, and the Royal Society (UK). I thank Jeri
630 Wright, Sue Nicolson, Jeff Ollerton, and Steve Johnson for valuable comments on earlier
631 drafts of this manuscript.

632

633

634 **References**

635

636 Aigner, P.A. (2001) Optimality modeling and fitness trade-offs: when should plants become
637 pollinator specialists? *Oikos*, **95**, 177–184.

- 638 Aigner, P.A. (2004) Floral specialization without trade-offs: optimal corolla flare in
639 contrasting pollination environments. *Ecology*, **85**, 2560–2569.
- 640 Aigner, P.A. (2006) The evolution of specialized floral phenotypes in a fine-grained
641 pollination environment. Pp. 23–46 in: Waser N.M., Ollerton J., eds. *Plant–pollinator*
642 *interactions: from specialization to generalization*, University of Chicago Press, Chicago.
- 643 Aizen, M.A. & Vázquez, D.P. (2006) Flowering phenologies of hummingbird plants from the
644 temperate forest of southern South America: is there evidence of competitive
645 displacement? *Ecography*, **29**, 357–366.
- 646 Anderson, B. & Johnson, S.D. (2008) The geographical mosaic of coevolution in a plant-
647 pollinator mutualism. *Evolution*, **62**, 220–225.
- 648 Armbruster, W.S. (1988) Multilevel comparative analysis of morphology, function, and
649 evolution of *Dalechampia* blossoms. *Ecology*, **69**, 1746–1761.
- 650 Armbruster, W.S. (2012) Evolution and ecological implications of “specialized” pollinator
651 rewards. Pp. 44–67 in, Patiny, S (ed.), *Evolution of Plant-Pollinator Relationships*,
652 Cambridge University Press, Cambridge, UK.
- 653 Armbruster, W.S. (2014) Floral specialization and angiosperm diversity: phenotypic
654 divergence, fitness trade-offs and realized pollination accuracy. *AoB PLANTS*, **6**, plu003
655 (doi: 10.1093/aobpla/plu003).
- 656 Armbruster, W.S., Di Stilio, V.S., Tuxil, J.D., Flores, T.C. & Velasquez Runk, J. L.. (1999)
657 Covariance and decoupling of floral and vegetative traits in nine neotropical plants: A
658 reevaluation of Berg’s correlation-pleiades concept. *American J. Botany*, **86**, 39–55.
- 659 Armbruster, W.S., Edwards, M.E. & Debevec, E.M. (1994) Character displacement generates
660 assemblage structure of Western Australian triggerplants (*Stylidium*). *Ecology*, **75**, 315-
661 329.

- 662 Armbruster, W.S., Fenster, C.B. & Dudash, M.R. (2000) Pollination “principles” revisited:
663 specialization, pollination syndromes, and the evolution of flowers. *Det Nor. Vidensk.*
664 *Acad. I. Mat. Natur. Kl. Skr. Ny Ser.*, **39**,179–200.
- 665 Armbruster, W.S., Hansen, T.F., Pélabon, C., Pérez-Barrales, R. & Maad, J. (2009) The
666 adaptive accuracy of flowers: Measurement and microevolutionary patterns. *Annals of*
667 *Botany*, **103**, 1529-1545.
- 668 Armbruster, W.S., Herzig, A.L. & Clausen, T.P. (1992) Pollination of two sympatric species
669 of *Dalechampia* (Euphorbiaceae) in Suriname by male euglossine bees. *American Journal*
670 *of Botany*, **79**, 1374–1381.
- 671 Armbruster, W.S. & Muchhala, N. (2009) Associations between floral specialization and
672 species diversity: cause, effect, or correlation? *Evolutionary Ecology*, **23**, 159–179.
- 673 Armbruster, W. S., C. P. H. Mulder, B. G. Baldwin, S. Kalisz, B. Wessa, and H. Nute. 2002.
674 Comparative analysis of late floral development and mating-system evolution in tribe
675 Collinsieae (Scrophulariaceae, s.l.). *American Journal of Botany*, **89**, 37-49.
- 676 Armbruster, W.S., Pélabon, C., Bolstad, G.H., Hansen, T.F. (2014a) Integrated phenotypes:
677 Understanding trait covariation in plants and animals. *Philosophical Transactions of the*
678 *Royal Society B*, **369**, 20130245.
- 679 Armbruster, W.S., Pérez-Barrales, R., Arroyo, J., Edwards, M.E. & Vargas, P. (2006) Three-
680 dimensional reciprocity of floral morphs in wild flax (*Linum suffruticosum*): A new twist
681 on heterostyly. *New Phytologist* **171**, 581–590.
- 682 Armbruster, W.S., Shi, X.-Q. & Huang, S.-Q. (2014b) Do specialized flowers promote
683 reproductive isolation? Realised pollination accuracy of three sympatric *Pedicularis*
684 species. *Annals of Botany*, **113**: 331-340.

- 685 Ashman, T.-L. & Arceo-Gomez, G. (2013) Toward a predictive understanding of the fitness
686 costs of heterospecific pollen receipt and its importance in co-flowering communities.
687 *American Journal of Botany*, **100**, 1061-1070 .
- 688 Baker, H.G. & Baker, I. (1990) The predictive value of nectar chemistry to the recognition of
689 pollinator types. *Israel Journal of Botany*, **39**, 157-166.
- 690 Baker H.G., Baker, I. & Hodges, S.A. (1998) Sugar composition of nectars and fruits
691 consumed by birds and bats in the tropics and subtropics. *Biotropica*, **30**, 559-586.
- 692 Barrett, S.C.H. (2013) The evolution of plant reproductive systems: how often are transitions
693 irreversible? *Proceedings of the Royal Society B-Biological Sciences*, **280**, no. 20130913.
- 694 Bauder, J.A.-S., Warren, A.D. & Krenn, H.W. (2015) The ecological role of extremely long-
695 proboscid Neotropical butterflies (Lepidoptera: Hesperiiidae) in plant-pollinator networks.
696 *Arthropod-Plant Interactions*, **9**, 415-424.
- 697 Beans, C.M. (2014) The case for character displacement in plants. *Ecology and Evolution*, **4**,
698 862–875.
- 699 Bascompte, J., Jordano, P., Melian, C.J. & Olesen J.M. (2003) The nested assembly of plant-
700 animal mutualistic networks. *Proceedings of the National Academy of Sciences USA*, **100**,
701 9383-9387.
- 702 Benadi, G., Blüthgen, N., Hovestadt, T. & Poethke, H.J. 2013. Contrasting specialization-
703 stability relationships in plant-animal mutualistic systems. *Ecological Modelling* **258**, 65-
704 73.
- 705 Berg, R.L. (1960) The ecological significance of correlation pleiades. *Evolution*, **14**, 171–
706 180.
- 707 Blüthgen, N., Menzel, F. & Blüthgen, N. (2006) Measuring specialization in species
708 interaction networks. *BMC Ecology*, **6**, 9.

- 709 Borrell, B.J. (2005) Long tongues and loose niches: Evolution of euglossine bees and their
710 nectar flowers. *Biotropica*, **37**, 664-669.
- 711 Brown, J.H. (1975) Geographical ecology of desert rodents. Pp. 315-341 in Cody, M.L. &
712 Diamond, J.M. (eds.) *Ecology and evolution of communities*. Harvard University Press,
713 Cambridge, MA.
- 714 Buchmann, S.L. (1987) The ecology of oil flowers and their bees. *Annual Review of Ecology*
715 *and Systematics*, **18**, 343-369.
- 716 Cane, J.H. (2002) Pollinating bees (Hymenoptera : Apiformes) of US alfalfa compared for
717 rates of pod and seed set. *Journal of Economic Entomology*, **95**, 22-27.
- 718 Cane, J.H. (2014) The oligolectic bee *Osmia brevis* sonicates *Penstemon* flowers for pollen: a
719 newly documented behavior for the Megachilidae. *Apidologie*, **45**, 678-684.
- 720 Chittka, L., Spaethe, J., Schmidt, A. & Hickersberger, A. (2001) Adaptation, constraint, and
721 chance in the evolution of flower color and pollinator color vision. *Cognitive Ecology of*
722 *Pollination* (eds., Chittka, L. & Thomson, J.D.), pp. 106–126. Cambridge Univ. Press,
723 Cambridge UK.
- 724 Cope, E.D. (1896) *The Primary Factors of Organic Evolution* (547pp). Open Court
725 Publishing Co, Chicago IL.
- 726 Darwin, C. (1859 & 1872) *The Origin of Species*, 1st & 3rd eds. Murray, London, UK.
- 727 Darwin, C. (1877) *The Various Contrivances by Which Orchids Are Fertilised by Insects*, 2nd
728 Ed. Murray, London, UK.
- 729 Dressler, R.L. (1969) Pollination by euglossine bees. *Evolution*, **22**, 202-210.
- 730 Dressler R.L. (1982) Biology of the orchid bees (Euglossini). *Annual Review of Ecology and*
731 *Systematics*, **13**, 373-394.
- 732 Faegri, K. & van der Pijl, L. (1979) *Principles of Pollination Ecology* 3rd ed. Pergamon,
733 London, UK.

- 734 Fang, Q. & Huang, S.-Q. (2013) A directed network analysis of heterospecific pollen transfer
735 in a biodiverse community. *Ecology*, **94**, 1176-1185.
- 736 Fenster, C.B., Armbruster, W.S. & Dudash, M.R. (2009) Specialization of flowers: Is floral
737 orientation an overlooked first step? *New Phytologist*, **183**, 502-506.
- 738 Fenster, C.B., Armbruster, W.S., Wilson, P., Dudash, M.R. & Thomson, J.T. (2004)
739 Pollination syndromes and floral specialization. *Annual Review of Ecology, Evolution, &*
740 *Systematics*, **35**, 375-403.
- 741 FitzJohn, R.G., Maddison, W.P. & Otto, S.P. (2009) Estimating trait-dependent speciation
742 and extinction rates from incompletely resolved phylogenies. *Systematic Biology* **58**, 595-
743 611.
- 744 Futuyma, D.J. & Moreno, G. (1988) The evolution of ecological specialization. *Annual*
745 *Review of Ecology & Systematics*, **19**, 207-233.
- 746 Givnish, T.J., Spalink, D., Ames, M., Lyon, S.P., Hunter, S.J., Zuluaga, A., Iles, W.J.D.,
747 Clements, M.A., Arroyo, M.T.K., Leebens-Mack, J., Endara, L. Kriebel, R., Neubig,
748 K.M., Whitten, W.M., Williams, N.H., Cameron, K.M. (2015) Orchid phylogenomics and
749 multiple drivers of their extraordinary diversification. *Proceedings of the Royal Society B-*
750 *Biological Sciences*, **282**, 171-180.
- 751 Gleason, S.K. (1981) Character displacement in flowering phenologies. *Oecologia*, **51**, 294-
752 295.
- 753 Gomez J.M., Torices, R., Lorite, J., Klingenberg, C.P. & Perfectti, F. (2016) The role of
754 pollinators in the evolution of corolla shape variation, disparity and integration in a highly
755 diversified plant family with a conserved floral bauplan. *Annals of Botany*, **117**, 889-904.
- 756 Gong, Y.-B. & Huang, S.-Q. (2009). Floral symmetry: pollinator-mediated stabilizing
757 selection on flower size in bilateral species. *Proceedings of the Royal Society London B*,
758 **276**, 4013-4020.

- 759 Grant, V. (1949) Pollination systems as isolating mechanisms in flowering plants. *Evolution*,
760 3, 82–97.
- 761 Grant, V. (1971) *Plant Speciation*. Columbia University Press, New York, NY.
- 762 Grant, V. (1994) Modes and origins of mechanical and ethological isolation in angiosperms.
763 *Proceedings of the National Academy of Sciences of the USA*, **91**, 3–10.
- 764 Gould, S.J. (1980) Is a new and general theory of evolution emerging? *Paleobiology* **6**, 119-
765 130.
- 766 Hodges, S.A. (1997) Floral nectar spurs and diversification. *International Journal of Plant*
767 *Sciences*, **158**, S81-S88.
- 768 Hodges, S.A. & Arnold, M.L. (1995) Spurring plant diversification: Are floral nectar spurs a
769 key Innovation? *Proceedings Royal Soc London, Ser B. Biological Sciences*, **262**, 343-
770 348.
- 771 Hughes M., Gerber S. & Wills M.A. (2013) Clades reach highest morphological disparity
772 early in their evolution. *Proceedings of the National Academy of Sciences of the USA* **110**,
773 13875–13879.
- 774 Janzen, D.H. (1980) When is it coevolution? *Evolution*, **34**, 611-612.
- 775 Johnson, S.D., Hargreaves, A. & Brown, M. (2006) Dark bitter-tasting nectar functions as a
776 filter of flower visitors in a bird-pollinated plant. *Ecology*, **87**, 2709-2716.
- 777 Johnson, S.D. & Raguso, R. (2016) The long-tongued hawkmoth pollinator niche for native
778 and invasive plants in Africa. *Annals of Botany*, **117**, 25-36.
- 779 Johnson, S.D. & Steiner, K.E. (1997) Long-tongued fly pollination and evolution of floral
780 spur length in the *Disa draconis* complex (Orchidaceae). *Evolution*, **51**, 45-53.
- 781 Kay, K.M. & Sargent, R.D. (2009) The role of animal pollination in plant speciation:
782 integrating ecology, geography, and genetics. *Annual Review of Ecology, Evolution, &*
783 *Systematics*, **40**, 637–656.

- 784 Kevan, P.G. 1972. Insect pollination of high arctic flowers. *Journal of Ecology*, **60**, 831-847.
- 785 Larsson M (2005) Higher pollinator effectiveness by specialist than generalist flower-visitors
786 of unspecialized *Knautia arvensis* (Dipsacaceae). *Oecologia*, 146, 394–403.
- 787 MacArthur, R.H. & Pianka, E.R. (1966) On the optimal use of a patchy environment.
788 *Evolution*, **100**, 603-609.
- 789 Maglianesi, M.A., Blüthgen, N., Bohning-Gaese, K. & Schleuning, M. (2014) Morphological
790 traits determine specialization and resource use in plant-hummingbird networks in the
791 neotropics. *Ecology*, **95**, 3325-3334.
- 792 Marten-Rodriguez, S., Quesada, M., Castro, A.A., Lopezaraiza-Mikel, M. & Fenster, C.B.
793 (2015) A comparison of reproductive strategies between island and mainland Caribbean
794 Gesneriaceae. *Journal of Ecology*, **103**, 1190-1204.
- 795 Mayfield, M.M., Waser, N.M. & Price, M.V. (2001) Exploring the “most effective pollinator
796 principle” with complex flowers: bumblebees and *Ipomopsis aggregata*. *Annals of Botany*,
797 **88**, 591–596.
- 798 Mayr, E. (1982) Speciation and macroevolution. *Evolution*, **36**, 1119-1132.
- 799 Michener, C.D. (2007) *The Bees of the World*, 2nd Ed. Johns Hopkins University Press,
800 Baltimore.
- 801 Motten, A.F., Campbell, D.R., Alexander, D.E. & Miller, H.L. (1981) Pollination
802 effectiveness of specialist and generalist visitors to a North Carolina population of
803 *Claytonia virginica*. *Ecology*, **62**, 1278-1287.
- 804 Muchhala, N. (2007) Adaptive trade-off in floral morphology mediates specialization for
805 flowers pollinated by bats and hummingbirds. *American Naturalist*, **169**, 494–504.
- 806 Muchhala, N., Brown, Z., Armbruster, W.S. & Potts M.D. (2010) Competition drives
807 specialization in pollination systems through costs to male fitness. *American Naturalist*,
808 **176**, 732-743.

- 809 Muchhala, N. & Potts, M.D. (2007) Character displacement among bat-pollinated flowers of
810 the genus *Burmeistera*: analysis of mechanism, process and pattern. *Proceedings Royal*
811 *Society London B. Biological Sciences*, **274**, 2731–2737.
- 812 Muller, A. (1996) Host-plant specialization in western palearctic Anthidiine bees
813 (Hymenoptera: Apoidea: Megachilidae). *Ecological Monographs*, **66**, 235-257.
- 814 Murren, C.J. (2012) The integrated phenotype. *Integrative and Comparative Biology*, **52**, 64–
815 76.
- 816 Neff, J.L. & Simpson, B.B. (1990) The roles of phenology and reward structure in the
817 pollination biology of wild sunflower (*Helianthus annuus* L, Asteraceae). *Israel Journal*
818 *of Botany*, **39**, 197-216.
- 819 Newman, E., Manning, J. & Anderson, B. (2014) Matching floral and pollinator traits
820 through guild convergence and pollinator ecotype formation. *Annals of Botany*, **113**, 373-
821 384.
- 822 Nilsson, L.A. (1988) The evolution of flowers with deep corolla tubes. *Nature*, **334**, 147-149.
- 823 Nosil, P. & Mooers, A.O. (2005) Testing hypotheses about ecological specialization using
824 phylogenetic trees. *Evolution*, **59**, 2256-2263.
- 825 Olesen, J.M., Bascompte, J., Dupont, Y.L. & Jordano, P. (2007) The modularity of
826 pollination networks. *Proc. Natl. Acad. Sci. U. S. A.*, **104**, 19891–19896.
- 827 Ollerton, J. (1996) Reconciling ecological processes with phylogenetic patterns: The apparent
828 paradox of plant-pollinator systems. *Journal of Ecology*, **84**, 767-769.
- 829 Ollerton J., Johnson S.D., Cranmer, L. & Kellie, S. (2003) The pollination ecology of an
830 assemblage of grassland asclepiads in South Africa. *Annals of Botany*, **92**, 807-834
- 831 Ollerton, J., Johnson, S.D. & Hingston, A.B. (2006) Geographical variation in diversity and
832 specificity of pollination systems. *Plant-Pollinator Interactions. From Specialization to*

- 833 *Generalization* (eds. Waser, N.M. & Ollerton J.), pp. 283-308, Chicago University Press,
834 Chicago, IL.
- 835 Ollerton, J., Killick, A., Lamborn, E., Watts, S. & Whiston, M. (2007) Multiple meanings and
836 modes: on the many ways to be a generalist flower. *Taxon*, **56**, 717–728.
- 837 Ollerton, J., Masinde, S. Meve, U. Picker, M. & Whittington, A. (2009) Fly pollination in
838 *Ceropegia* (Apocynaceae: Asclepiadoideae): biogeographic and phylogenetic
839 perspectives. *Annals of Botany*, **103**, 1501-1514.
- 840 O’Meara BC, Smith SD, Armbruster WS, Harder LD, Hardy CR, Hileman LC, Hufford L,
841 Litt A, Magallón S, Smith SA, Stevens PF, Fenster CB, Diggle PK. 2016. Non-
842 equilibrium dynamics and floral trait interactions shape extant angiosperm diversity.
843 *Proceedings Royal Society B*, **283**, 20152304.
- 844 Oyston, J.W., Hughes, M., Wagner, P.J., Gerber, S. & Wills, M.A. (2015) What limits the
845 morphological disparity of clades? *Interface Focus*, **5**, 20150042
846 (<http://dx.doi.org/10.1098/rsfs.2015.0042>).
- 847 Pascarella, J.B. (2010) Pollination biology of *Gelsemium sempervirens* L. (Ait.)
848 (Gelsemiaceae): do male and female *Habropoda laboriosa* F. (Hymenoptera, Apidae)
849 differ in pollination efficiency? *Journal of Apicultural Research*, **49**, 170-176.
- 850 Pauw, A. (2013) Can pollination niches facilitate plant coexistence? *Trends in Ecology &*
851 *Evolution*, **28**, 30-37.
- 852 Pauw, A. & Stanway, R. (2015) Unrivalled specialization in a pollination network from
853 South Africa reveals that specialization increases with latitude only in the Southern
854 Hemisphere. *Journal of Biogeography*, **42**, 652-661.
- 855 Pauw, A., Stofberg, J. & Waterman, R.J. (2009) Flies and flowers in Darwin's race.
856 *Evolution*, **63**, 268-279.

- 857 Pellmyr, O. (2003) Yuccas, yucca moths, and coevolution: A review. *Annals of the Missouri*
858 *Botanical Garden*, **90**, 35-55.
- 859 Pennell, M.W., Harmon, L.J. & Uyeda, J.C. (2014) Is there room for punctuated equilibrium
860 in macroevolution? *Trends in Ecology & Evolution*, **29**, 23-32.
- 861 Rabosky, D.L. (2016) Challenges in the estimation of extinction from molecular phylogenies:
862 A response to Beaulieu and O'Meara. *Evolution*, **70**, 218-228.
- 863 Raguso, R.A. (2008) Wake up and smell the roses: The ecology and evolution of floral scent.
864 *Annual Review of Ecology Evolution and Systematics*, **39**, 549-569.
- 865 Ramírez, S.R., Eltz, T., Fujiwara, M.K., Gerlach, G., Goldman-Huertas, B., Tsutsui, N.D. &
866 Pierce, N.E. (2011) Asynchronous diversification in a specialized plant-pollinator
867 mutualism. *Science*, **333**, 1742-1746.
- 868 Ramírez, W. (1969) Fig wasps: Mechanism of pollen transfer. *Science*, **163**, 580-581.
- 869 Robertson, C. (1928) *Flowers and Insects. Lists of Visitors of Four Hundred and Fifty-Three*
870 *Flowers*. Charles Robertson, Carlinville, IL. 221 pp.
- 871 Rodríguez-Gironés, M.A. & Llandres, A.L. (2008) Resource competition triggers the co-
872 evolution of long tongues and deep corolla tubes. *PLOS One*, **3**, e2992.
- 873 Rodríguez-Gironés, M.A. & Santamaría, L. (2004) Why are so many bird flowers red? *PLOS*
874 *Biology*, DOI: 10.1371/journal.pbio.0020350.
- 875 Sargent, R.D. (2004) Floral symmetry affects speciation rates in angiosperms. *Proceedings*
876 *Royal Society London B Biological Sciences*, **271**, 603–608.
- 877 Schemske D.W. & Horvitz CC. 1984. Variation among floral visitors in pollination ability—a
878 precondition for mutualism specialization. *Science*, **225**, 519–521.
- 879 Schiestl, F.P. & Schlueter, P.M. (2009) Floral isolation, specialized pollination, and
880 pollinator behavior in orchids. *Annual Review of Entomology*, **54**, 425–446.

- 881 Schluter, D. (2000) *The Ecology of Adaptive Radiation*. Oxford University Press, Oxford,
882 UK.
- 883 Simpson, G.G. (1953) *The Major Features of Evolution*. Columbia University Press, New
884 York, NY.
- 885 Steiner, K.E. & Whitehead, V.B. (1990) Pollinator adaptation to oil-secreting flowers --
886 *Rediviva* and *Diascia*. *Evolution*, **44**, 1701-1707.
- 887 Steiner, K.E. & Whitehead, V.B. (1991) Oil flowers and oil bees -- further evidence of
888 pollinator adaptation. *Evolution*, **45**, 1493-15501.
- 889 Stiles, F.G. (1977) Coadapted competitors - flowering seasons of hummingbird-pollinated
890 plants in a tropical forest. *Science*, **198**, 1177-1178.
- 891 Stone, G.N., Willmer, P. & Rowe, J.A. (1998) Partitioning of pollinators during flowering in
892 an African *Acacia* community. *Ecology*, **79**, 2808–2827.
- 893 Svensson E. & Calsbeek R. (2012) *The Adaptive Landscape in Evolutionary Biology*, Oxford
894 University Press, Oxford, UK.
- 895 Thebault, E. & Fontaine, C. (2008) Does asymmetric specialization differ between
896 mutualistic and trophic networks? *Oikos*, **117**, 555-563.
- 897 Thompson, J.N. (1994) *The Coevolutionary Process*. University of Chicago Press, Chicago,
898 IL.
- 899 Thompson, J.N. (2005) *The Geographic Mosaic of Coevolution*. University of Chicago Press,
900 Chicago, IL.
- 901 Thompson, J.N. & Fernandez, C.C. (2006) Temporal dynamics of antagonism and mutualism
902 in a geographically variable plant-insect interaction. *Ecology*, **87**, 103-112.
- 903 Thorp, R.W. (1979) Structural, behavioral, and physiological adaptations of bees (apoidea)
904 for collecting pollen. *Annals of the Missouri Botanical Garden*, **66**, 788-812.

- 905 Traveset, A., Chamorro, S., Olesen, J.M. & Heleno, R. (2015) Space, time and aliens:
906 charting the dynamic structure of Galapagos pollination networks. *AOB PLANTS* **7**,
907 plv068.
- 908 Tripp, E.A. & Manos, P.S. (2008) Is floral specialization an evolutionary dead-end?
909 Pollination system transitions in *Ruellia* (Acanthaceae). *Evolution*, **62**, 1712-1736.
- 910 van der Niet, T. & Johnson, S.D. (2012) Phylogenetic evidence for pollinator-driven
911 diversification of angiosperms. *Trends in Ecology & Evolution*, **27**, 353-361.
- 912 van der Niet, T., Peakall, R. & Johnson, S.D. (2014) Pollinator-driven ecological speciation
913 in plants: new evidence and future perspectives. *Annals of Botany*, **113**, 199-211.
- 914 van der Pijl, L. & Dodson, C.H. (1966) *Orchid flowers: Their pollination and evolution*.
915 University of Miami Press, Miami, FL.
- 916 Vazquez, D.P. & Aizen, M.A. (2004) Asymmetric specialization: A pervasive feature of
917 plant-pollinator interactions, *Ecology* **85**, 1251-1257.
- 918 Waser, N.M. (1983) Competition for pollination and floral character differences among
919 sympatric plant species: a review of the evidence. Pp. 277-293 in Jones, C.E. & Little,
920 R.J. (eds). *Handbook of Experimental Pollination Biology*. Academic Press, New York.
- 921 Waser, N.M. (1986) Floral constancy —definition, cause, and measurement. *American*
922 *Naturalist*, **127**, 593–603.
- 923 Waser, N.M., Chittka, L., Price, M.V., Williams, N.M. & Ollerton J. (1996) Generalization in
924 pollination systems, and why it matters. *Ecology*, **77**, 1043-1060.
- 925 Wasserthal, L.T. (1998) Deep flowers for long tongues. *Trends in Ecology & Evolution*, **13**,
926 459-460.
- 927 Wcislo, W.T. & Cane, J.H. (1996) Floral resource utilization by solitary bees (Hymenoptera:
928 Apoidea) and exploitation of their stored foods by natural enemies. *Annual Review of*
929 *Entomology*, **41**, 257-286.

- 930 Whitten, W.M., Blanco, M.A., Williams, N.H., Koehler, S., Carnevali, G., Singer, R.B. ,
931 Endara, L. & Neubig, K.M. (2007). Molecular phylogenetics of *Maxillaria* and related
932 genera (Orchidaceae: Cymbidieae) based on combined molecular data sets. *American*
933 *Journal of Botany*, **94**, 1860–1889.
- 934 Wilson, P. & Thomson, J.D. 1996. How do flowers diverge? Pp. 88-111 in: Lloyd, D.G. &
935 Barrett, S.C.H., eds. *Floral Biology*. Chapman and Hall, New York, NY.
- 936 Wilson, P., Castellanos, M.C., Hogue, J.N., Thomson, J.D. & Armbruster, W.S. (2004) A
937 multivariate search for pollination syndromes among penstemons. *Oikos*, **104**, 345–361.
- 938 Zimmermann, Y., Ramírez S.R. & Eltz, T. (2009) Chemical niche differentiation among
939 sympatric orchid bees. *Ecology*, **90**, 2994-3008.
- 940
- 941
- 942

943

944 **Tables**

945

946 Table 1. Classificatory framework for specialization concepts as applied to plants and flower-
 947 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

948

949

950 **Figure Captions**

951

952 Figure 1. Steps of pollination and filtering. A. Flow diagram depicting the steps of pollination
953 and points of pollinator "filtering". Sequential steps of pollination are in black and sequential
954 pollination "filters" operating are in red. B. Filter diagram depicting in more detail possible
955 layers of specialization during pollination.

956

957 Figure 2. Flowers and pollinator of *Stylidium maritimum*. A. A flower with the column in the
958 "cocked" position. B. Flowers with columns in the "discharged" position. C. A flower
959 placing pollen on the head of a nectar-seeking *Amegilla* sp. (Apidae: Anthophorini).

960

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

968

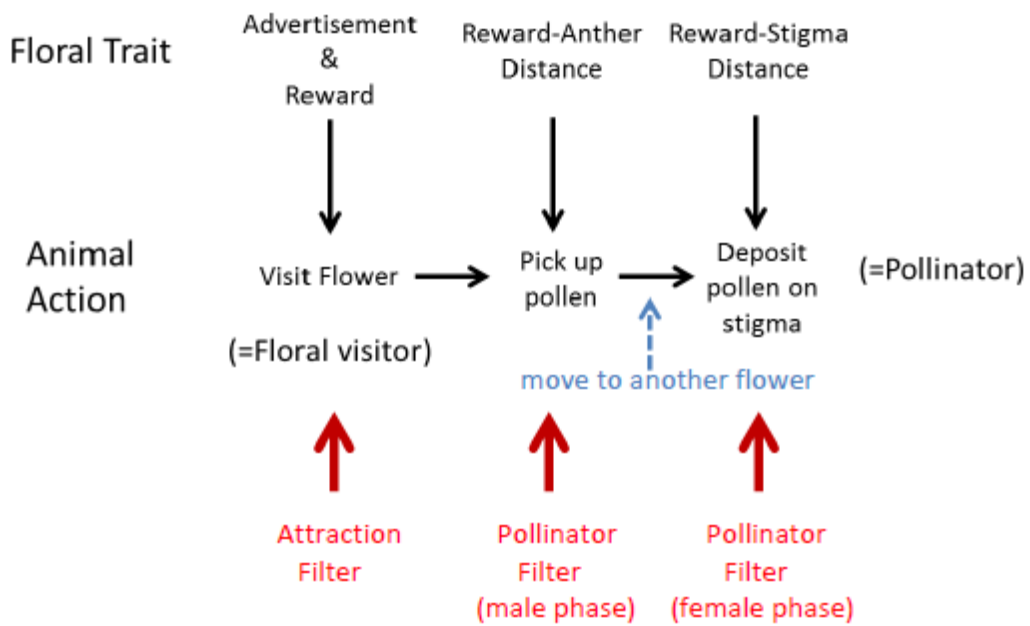
969

970

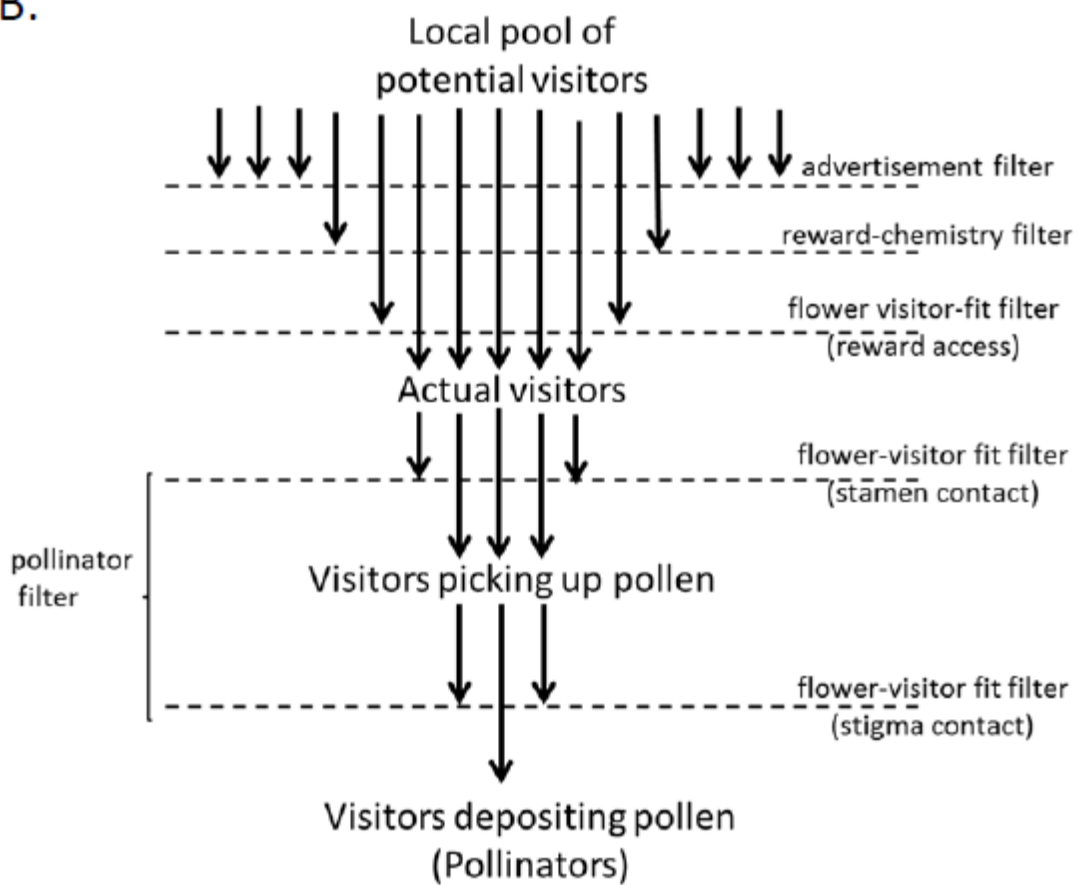
971

972 Figure 1.

A.



B.



974

975 Figure 2.



976

977

978

979

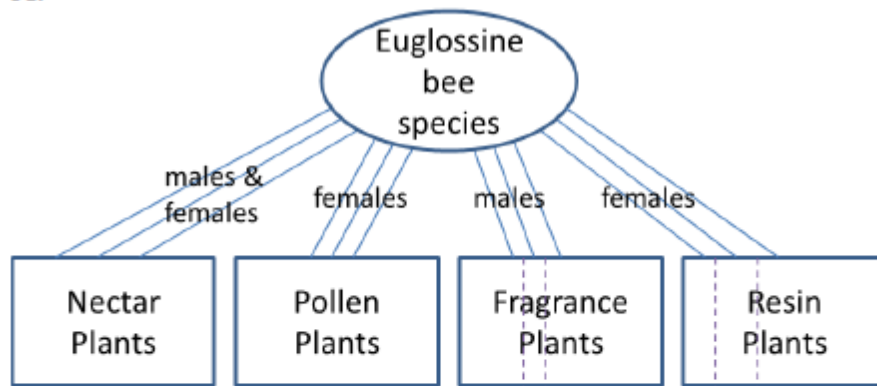
980

981

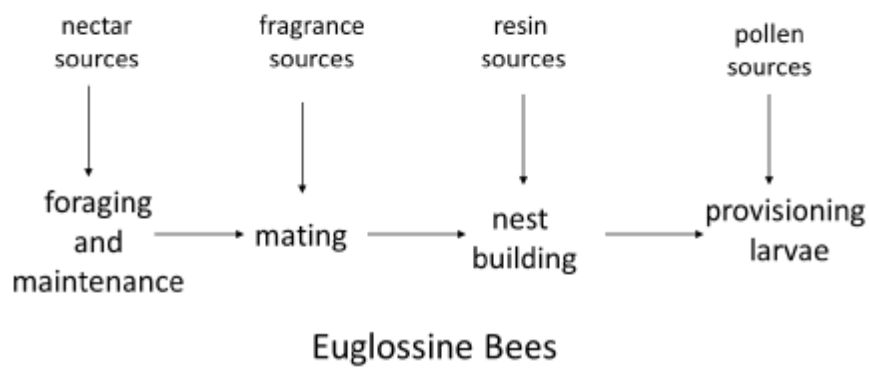
982

983 Figure 3.

A.



B.



984