

1 Niche perspectives on plant-pollinator interactions

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15
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17 18 **Abstract**

19
20 While ecological niches are critical to species co-existence and diversification, the
21 niche concept has been under-utilized in studying the roles of pollinators in plant
22 evolution and reproduction. Pollination niches can be objectively characterized using
23 pollinator traits, abundance and distributions, as well as network topology. We review
24 evidence that floral traits represent adaptations to pollination niches, with trade-offs in
25 trait deployment reinforcing niche specialisation. In turn, specialised pollination
26 niches potentially increase speciation rates, foster species co-existence and constrain
27 species range limits. By linking studies of adaptation with those on speciation and co-
28 existence, the pollination niche provides an organising principle for research on plant
29 reproduction and conceptually unites these studies with fields of biology where the
30 niche perspective is already firmly established.

31
32 **The importance of the pollination niche**

33 Understanding the diversification of flowering plants remains one of the great
34 challenges in biology [1]. Fundamental to understanding the processes underpinning
35 diversification is the concept of the **niche** (see Glossary), the combination of
36 resources and environmental conditions that enable a population to establish positive
37 growth rates if individuals possess appropriate **functional traits** [2]. Niches are an
38 important driver of trait evolution, potentially leading to the origin of new species, but
39 are also critical for determining species' geographic range. Partitioning of niches also
40 reduces competition and is thus an important contributor to species co-existence [2,
41 3]. Resolving the functional traits associated with niche occupancy gives the niche
42 concept tremendous potential to integrate studies of trait adaptation and community
43 ecology [4]. While discussion of niches in plants has tended to focus on abiotic
44 factors, as most plant species are reliant on pollination for reproduction and therefore
45 population persistence, pollination is also a critical component of a plant's niche [5].

46

47 Using the concept of the **pollination niche**, we develop a framework that unites
48 studies of floral adaptation, species co-existence, plant distribution and speciation,
49 with the overall goal of understanding the origins and maintenance of diversity of
50 flowering plants. Having defined the pollination niche, we discuss approaches that
51 can be used for quantifying pollination niches, including potential opportunities for
52 using **plant-pollinator network** methodologies, before addressing the following
53 questions: (i) can the pollination niche act as a basis to understand functional traits?
54 (ii) do **trade-offs** explain occupancy of specialised pollination niches? (iii) what is the
55 role of the pollination niche in shaping community structure? (iv) to what extent does
56 the pollination niche determine geographic ranges? (v) do certain key floral
57 innovations increase speciation rates by enabling occupation of diverse pollination
58 niches?

59

60 **What is the pollination niche?**

61 We consider the **fundamental pollination niche** to be the vectors (biotic or abiotic)
62 that can potentially enable pollination for a given plant species, noting that the
63 fundamental niches at any given site may be expected to reflect the local temporal and
64 spatial variability of the pollinator assemblage. The **realised pollination niche** is
65 shaped by community level interactions affecting the effectiveness of pollen vectors
66 due to both the competition for pollinators among plants and the foraging preferences

67 of pollinators. Not all pollination niches in a community may be occupied at a given
68 point in time. For example, many species of hymenopteran use pheromone systems to
69 attract mates, yet only a tiny fraction of these insects are exploited for pollination by
70 plants that mimic insect sex pheromones [6]. Similarly, many generalist birds will
71 consume nectar if it is available, yet these birds are exploited for pollination only in
72 certain geographical regions [7].

73

74 The presence of a group of pollinators in a plant community and their relative
75 abundance clearly represents the most critical aspect of the pollination niche.
76 However, other axes of the pollination niche include seasonal opportunities for
77 pollination [8], variation in the lengths of the mouthparts with which pollinators
78 interact with flowers [9, 10], sites of pollen deposition on the pollinator [11-13], diel
79 opportunities for pollen release or pollinator visitation [14], and the type of floral
80 reward sought by animals [15, 16]. Each of these different niche axes has the potential
81 to drive floral trait diversification [17] and reduce interspecific pollen transfer [18],
82 both factors potentially reducing interspecific competition and maintaining
83 reproductive isolation.

84

85 **Quantifying pollination niches**

86 For pollination niches to be a useful tool for understanding the origins of plant
87 diversity, an objective approach for recognising and defining them is needed. In their
88 simplest form, niches can be described by niche position and niche breadth along an
89 axis. For example, in terms of a plant's edaphic preferences, there will be an optimal
90 soil pH for performance (niche position), but also a range of pH where population
91 growth rates are positive (niche breadth). When multiple variables are considered, the
92 niche becomes the area in multi-dimensional space where growth rates are positive
93 [19].

94

95 With regards to pollination, the niche would be the set of animal species or functional
96 group(s) and their associated traits that lead to positive population growth rates. For
97 example, for a hawkmoth-pollinated plant species, the tongue length of hawkmoth
98 pollinators can be used to identify niche position (median tongue length) and niche
99 breadth (range of tongue lengths for effective pollination) [9]. This approach can be
100 extended to the full plant community across multiple pollinators and their traits to

101 quantify areas of niche space that plants could potentially occupy (**Box 1**). However,
102 it is important to note that for those plant species reliant on biotic vectors, not all
103 visitors are part of the realised niche. For example, in a plant adapted to pollination by
104 sunbirds, the niche position critical for population persistence would include sunbirds
105 with particular bill lengths, but not incidental insect visitors that are ineffective
106 pollinators [20, 21].

107

108 There is a vast taxonomic and functional diversity of animals involved in pollination,
109 and for many of these we lack details of their behavioural responses to flowers and
110 their effect on plant fitness. As such, in pollination biology, the concept of niche
111 position is often expressed qualitatively in terms of **pollinator functional groups** - a
112 group of pollinators that are likely to exert similar selection pressures [16, 22] (most
113 often taxonomically related e.g. hawkmoths, sunbirds). The use of pollinator
114 functional groups is an effective tool in ecological and evolutionary studies when
115 large differences in the morphology and/or behaviour of the pollinators make the
116 pollinator niches relatively discrete. However, the inherently nested nature of
117 pollinator functional groups can make comparison between species or communities
118 challenging [5]. For example, sunbirds are nested within the broader category of bird
119 pollinators, but among the sunbirds there is also variation in beak length among
120 species [23]. Thus, a reliance on conventionally recognised functional groups may
121 completely overlook novel or subtle groupings leading to an underestimate of niche
122 specialisation. Therefore, visitation data for entire plant-pollinator networks could
123 provide a technique for more objective recognition of niches and the associated level
124 of specialisation.

125

126 **Are network approaches a suitable first step for identifying pollination niches?**

127 *Recognising pollination niches using plant-pollinator networks*

128 Plant-pollinator networks describe the patterns of pollinator visits to plants for a
129 community of plants and pollinators (e.g. [24-27]). By characterising plant-pollinator
130 interactions at the community level, networks reveal not only interacting partners, but
131 also which potential interactions are absent among the species that are present in the
132 community. This has the potential to help researchers characterize the realised
133 pollination niche of individual species relative to the total pool of pollination niches
134 available. Further, analysing patterns of visitation for the entire community avoids

135 potential biases about which species are candidates for the use of particular niches,
136 and may even help to identify niches not previously suspected to exist.

137

138 The detection of **modularity**, where groups of species interact more frequently with
139 each other than with the remainder of the network, might offer an important first step
140 toward objectively identifying pollinator functional groups (niche position) and
141 relatively discrete pollination niches [27-29] **Figure 1**). While it can be tested if entire
142 networks exhibit significant modularity (see [28, 30] for methodology), recognition of
143 particular pollination niches requires identification of the specific modules to which
144 the plant and pollinator species have been assigned [27, 29]. Importantly, since
145 networks of plant-pollinator interactions are often nested, analysis of modularity can
146 be undertaken in a hierarchical fashion to test for modules within modules (e.g. long-
147 billed birds may be nested within a bird pollination module). However, given that
148 modularity is a consistent structural trait of plant-pollinator communities, and that it is
149 more likely to be detected in larger networks [28, 30], additional evidence may be
150 needed to test whether the modules identified are both biologically meaningful and
151 correspond to niches.

152

153 As a first step for testing the functional significance of modules, the plant members of
154 a given module must be shown to be interacting with any shared pollinators via the
155 same general pollination mechanism (e.g. exploitation of nectar foraging versus
156 sexually deceived insects). This is necessary to avoid inadvertently lumping plants
157 that actually occupy different niches. Once the basis of the interaction is known to be
158 consistent within a module, one can then test the expectation that pollinators from
159 within modules will be more effective than pollinators from other modules. If this
160 prediction is supported, and the module is indicative of a particular pollination niche,
161 one can test for an association between the module and specific floral traits. Finally,
162 testing functional significance of modules might involve experimentally establishing
163 whether the pollinators assigned to a module show similar responses to the flowers,
164 and if floral traits associated with the module influence pollinator attraction. As such,
165 the identification of network modules could represent a critical step towards testing
166 hypotheses to explain floral adaptation as well as community processes [24, 25, 27].

167

168 *Plant-pollinator networks and specialisation*

169 Since the study of interaction networks has become widely employed in pollination
170 biology, understanding specialisation has been a common topic of interest for
171 researchers taking this approach (see references in [31]). However, there are several
172 practical and statistical challenges to effectively implementing network studies, with
173 important consequences for quantifying the specialisation of pollination niches (**Box**
174 **2**). For example, absolute **ecological specialisation** cannot simply be measured by
175 metrics such as k (i.e. number of links - the number of other species that a given
176 species interacts with), as they partly reflect sampling effort [32]. Recognition of this
177 bias lead to the widespread usage of complementary specialisation d' [33], which
178 describes the deviation from a neutral pattern of associations [34]. However, rather
179 than down-weighting the specialisation of a species because it uses an abundant
180 pollinator, as in d' , we believe a more rigorous approach is to test whether the species
181 shows ecological specialisation and to identify the mechanism underpinning this
182 specialisation. Ecological specialisation is best quantified by identifying effective
183 pollinator species using methods such as single-visit pollen deposition and selective
184 exclusion experiments [35], and then using rarefaction approaches [36] to estimate the
185 level of sampling required to gain an accurate estimate of the number of interaction
186 partners [37]. Further, the proportion of pollination events by the most frequent of the
187 effective pollinator species, as an estimate of the reliance on a single species, is
188 potentially a useful metric for studies in both ecology and evolution. Once absolute
189 ecological specialisation is estimated, further data can be gathered to address whether
190 the plant attracts particular pollinators via specialised signals or rewards that are
191 adaptations to particular pollinators (i.e. is phenotypically specialised) or if
192 specialisation is merely imposed by an absence of other potentially suitable
193 pollinators [22].

194

195 **Functional floral traits**

196 In plant community ecology, functional traits, such as seed size, canopy height and
197 leaf mass per area, have been considered to represent adaptations to particular
198 environmental conditions or life history strategies, [4, 38]. Functional traits have the
199 ability to determine the structure of plant communities by imposing a mechanism that
200 filters out species that are not suitably equipped to occupy any of the available niches,
201 or are outcompeted by species already occupying certain niches. Functional traits
202 therefore ultimately affect which niches species can exploit and whether they can co-

203 exist [39]. For the best known pollination groups, it is clear that traits such as floral
204 colour, odour and morphology can be considered functional traits where certain
205 character states provide a fitness advantage for the occupation of particular pollinator
206 niches (**Table 1**). Manipulation of floral traits has demonstrated that divergence in
207 floral traits is associated with differences in pollinator attraction and plant fitness [17,
208 40-43]. Further, experimental studies have confirmed that heritable changes in floral
209 traits can occur in just a few generations when plants are exposed to different
210 pollinator environments [44, 45]. At the macroecological level, studies analysing
211 pollinator data and floral traits simultaneously in a phylogenetic context have
212 provided compelling evidence for associations between particular pollinators and sets
213 of floral traits [10, 46, 47]. For example, there has been convergent evolution of red
214 floral colouration and, in some cases large nectar quantities, exerted anthers and
215 changes in corolla shape and spur length, associated with shifts from bee to
216 hummingbird pollination in several plant genera in the North American flora such as
217 *Penstemon*, *Mimulus* and *Aquilegia* [10, 46, 48, 49].

218

219 Floral functional traits may offer the same, or even better, predictive power for
220 assessing niche occupancy than do the vegetative traits that are traditionally used in
221 plant community ecology [4, 38]. This is evidenced by the extensive literature on
222 **pollination syndromes** that, despite being developed largely independently of niche
223 theory, has demonstrated the association of certain floral colours, shapes and rewards
224 with particular functional groups of pollinators [5, 47, 50-52]. For example, a recent
225 analysis of the South African flora, which focused on species with putatively
226 specialised pollination systems, showed that there is a close correspondence (c. 80%
227 matching) between Stefan Vogel's [51] assignments of plant species to floral
228 syndromes in the 1950s and the subsequently discovered pollinators of these species
229 [53]. However, support for pollination syndromes in some other floras, particularly
230 those in northern temperate regions, is more equivocal [54], suggesting that the
231 concept has less utility when pollination systems are relatively generalized.

232 Pollination syndromes may also be obscured when floral traits more strongly reflect
233 the bauplan of the plant lineage than adaptations to pollinators. In addition, most
234 floral syndrome classifications are based on qualitative trait categories, including
235 subjective human assessments of colour and scent. As such, there is a need for floral

236 functional traits to be standardized in the same quantitative manner as plant vegetative
237 traits [38] and validated across geographical regions and plant groups.

238

239 **Do trade-offs explain niche specialisation?**

240 If visitation from multiple pollinators (niche generalization) has the potential to
241 provide greater and more stable pollination service, it raises the question of how and
242 why niche specialisation arises? One potential explanation is that adaptation to the
243 most effective pollinator(s) involves trade-offs, where the functional traits that
244 increase visitation or effectiveness of one pollinator species reduce attraction of other
245 potential pollinator species or their pollination effectiveness [55]. Trade-offs in plants
246 are well known for traits related to survival, such as the trade-off between growth rate
247 and nutrient retention that leads to differences in growth rate between species
248 occurring in high and low nutrient conditions [56]. In pollination systems, such trade-
249 offs could act at multiple stages through the pollination process including long-
250 distance attraction to floral signals, behaviour on the flower, and morphological fit.
251 One obvious implication of strong-trade-offs is that hybrids between species with
252 different specialised pollination systems will often have reduced pollination success,
253 thus resulting in at least a partial barrier to gene flow between species.

254

255 The strongest evidence for the presence of trade-offs underpinning specialised
256 pollination niches comes from systems where divergent floral traits associated with
257 the attraction of two pollinator species are manipulated to test whether a change to
258 intermediate floral traits is associated with reduced pollinator attraction or
259 effectiveness. For example, trade-offs have been demonstrated for floral signals
260 involved in pollinator attraction [42] and in floral traits affecting the morphological fit
261 of the pollinator [57] (**Figure 2**). However, **bimodal pollination** has been reported for
262 some plant species (e.g. involving mammals and hummingbirds with parallel
263 adaptations to both groups [58]) and many plants have relatively generalist pollination
264 systems, suggesting that trade-offs are not always strong enough to enforce
265 specialisation. Nonetheless, the few experimental tests of trade-offs have generally
266 provided strong evidence in support of their existence [41, 42, 57, 59], but see [60,
267 61]. Should future experiments confirm that trade-offs are a key mechanism
268 underpinning specialisation, this would also support the hypothesis that trait trade-offs

269 contribute to the process of speciation and to the persistence of diverse plant
270 communities.

271

272 **Pollination niches and species co-existence**

273 The occupation of different niches as a mechanism that alleviates interspecific
274 competition is often critical for species co-existence [3]. For example, in plants,
275 different drought and water-logging tolerance can lead to the exploitation of different
276 microsites, thereby fostering co-occurrence [19, 62]. Given the large diversity of co-
277 flowering plant species in many plant communities, it is expected that at least some
278 level of partitioning of the available pool of potential pollinators between plants
279 occurs through the use of different pollinator species, thereby reducing interspecific
280 pollen transfer [18] and competition for pollinators [63]. Indeed, in a fascinating
281 recent example, it was shown that two colour morphs of a bromeliad persist through
282 different foraging preferences between males and females of a hummingbird
283 pollinator species, thus preventing competitive exclusion of one of the morphs [64].

284

285 Pollination niches are unusual in the niche context for not only providing scope for
286 interspecific competition, but also for ecological facilitation. Rewarding plants often
287 exhibit Allee effects where small populations produce a lower total reward to
288 pollinators and therefore achieve lower per plant visitation [65-67]. A corollary of this
289 is that a plant can benefit from the presence of other co-occurring rewarding “magnet”
290 plant species that attract a greater number of pollinators into the plant community
291 because of an effective increase in the total number of rewarding plants. While
292 perhaps best known in deceptive orchids, where non-rewarding plants receive a
293 benefit from co-occurring with rewarding plants [68, 69], facilitation by attracting
294 additional pollinators has also been demonstrated among different rewarding plant
295 species [70, 71]. However, experiments with the self-incompatible herb *Raphanus*
296 *raphanistrum* demonstrated the context dependence of such effects [72]. Using
297 experimental plots with plants that shared pollinator species, it was shown that
298 facilitative effects transitioned to competitive effects as the abundance of the focal
299 species was reduced relative to the co-occurring plant species.

300

301 While using different pollinators clearly reduces the potential for competition between
302 plants, the question remains whether partitioning of the pollination niche is a major

303 contributor to co-existence of closely related or ecological similar plants. Pauw [63]
304 hypothesised that when reproduction is pollen limited and the abundance of a plant
305 species is limited by intraspecific competition for pollinators, a new colonist (or
306 mutation) in the community is more likely to establish if it occupies a different
307 pollination niche. Using a model of plant and pollinator dynamics, Benadi [73]
308 showed that the occupation of different pollination niches is most likely to contribute
309 to species co-existence when the costs of searching for flowers are low, pollinator
310 populations are strongly limited by resources other than floral rewards, and plant-
311 pollinator interactions are specialised. There is some empirical evidence that the rate
312 of per flower pollinator visits declines at both low and particularly high levels of plant
313 abundance [74, 75], suggesting the potential for competition between plant species
314 that share pollinators [76].

315

316 Several community studies have tested if some plant communities are structured such
317 that there is much lower pollination niche overlap than expected by chance. For
318 example, there is evidence of interspecific competition being avoided by differential
319 pollen placement [11, 13], the use of different pollinator species [12, 77], and
320 differences in pollen release [14] and flowering time [8]. However, there are also
321 several studies that have not found any strong signature of competition for pollinators
322 in terms of community structure [78]. Interestingly, this includes research on the
323 coexistence of species in the hyper-diverse assemblages of *Erica* in the Cape Floristic
324 Region of South Africa where evidence of strong niche partitioning was anticipated
325 [79, 80]. An unresolved issue in systems where competition does appear to be
326 important, is whether competition mainly results in *in situ* **character displacement** or
327 filtering (ecological sorting) of plants that can enter the community.

328

329 **The pollination niche and species range limits**

330 While the spatial distribution of plants is strongly correlated with edaphic and climatic
331 niche components [81, 82], pollinators also have the ability to limit the spatial
332 distribution of plants. Indeed, at broader spatial scales there is evidence that the
333 pollination niche can limit the geographic range of plant species [83]. Using niche
334 modelling, Duffy & Johnson [84] showed that for 21 of 32 South African plant
335 species with relatively specialised pollination systems, pollinator distribution was the
336 best predictor of their geographic range. Though pollinator constraints on plant

337 geographic ranges would intuitively be more likely to apply in plants with specialised
338 niches, one of the most compelling cases of pollinators contributing to natural range
339 limits comes from a plant species pollinated by several generalist bee species. In the
340 Californian endemic *Clarkia xantiana* the abundance of generalist bees is lower and
341 more variable at the more arid range margin leading to overall lower pollinator
342 availability [85]. Additional evidence for pollinator limitation on geographic ranges
343 comes from anthropogenic dispersal of plants, where of the 1000s of plant
344 introductions, there are few cases of plants with highly ecologically specialised
345 pollination systems becoming invasive [86, 87]. For example, of the 60 species of
346 *Ficus* introduced to Florida, beyond the natural geographic range of their specific
347 pollinator species, the only three to become invasive did so after the introduction of
348 their pollinator [86]. Similar processes appear to operate at the landscape scale, where
349 scarcity of pollinator species can lead to low levels of reproduction, potentially
350 leading to reduced occupancy of otherwise suitable patches of habitat [88, 89].

351

352 **The pollination niche and evolutionary diversification**

353 Pollination has long been hypothesised to be a key contributor to the diversification of
354 flowering plants [90-92]. Indeed, there is abundant evidence that pollinators drive
355 phenotypic diversification among populations [92]. Due to the link between pollinator
356 adaptation and the evolution of reproductive isolation, these microevolutionary
357 processes are expected to result in a macroevolutionary pattern of adaptive radiations
358 in pollination systems [5, 47, 93]. The niche perspective is central for understanding
359 the role of pollination in plant diversification at two levels. Firstly, the evolution of a
360 particular pollination strategy or even a single floral trait may greatly increase the
361 number of niches available for exploitation, which may, in turn, promote diversity of
362 the lineage. As such, key innovations such as zygomorphy [94] or nectar spurs [95]
363 have been linked to increased diversification rate. The process underlying this
364 increased rate is thought to be the exploitation of an increased number of relatively
365 discrete pollination niches, but this has not been tested in detail. Key innovations can
366 also include chemical traits; for example, the evolution of pollination by sexual
367 deception can lead to a large number of new pollination niches, each involving
368 exploitation of the males of particular insect species [6, 96], potentially leading to an
369 overall increase in plant diversification rate [97]. Secondly, some pollination niches
370 may be indirectly associated with elevated levels of plant speciation. For example, it

371 has been predicted that in some plant groups diversification rates will be higher in
372 bee-pollinated than in bird-pollinated lineages due to birds reducing genetic
373 differentiation through long-distance pollen dispersal [49]. In some lineages and some
374 geographic regions there is compelling evidence that shifts in the pollination niche are
375 often associated with speciation. Indeed, in an analysis of plant lineages where
376 phylogenetic and pollination strategy data are available, Van der Niet & Johnson [93]
377 showed that approximately 25% of speciation events were associated with a shift in
378 pollinator type. However, it remains poorly understood how frequently shifts in
379 pollinator assemblages are associated with speciation in generalist lineages, and if any
380 such differences arise from evolution of floral traits or as a simple by-product of
381 related plant species occupying habitats or geographic regions with different
382 pollinator assemblages [98, 99].

383

384 **Concluding remarks and future perspectives**

385 Studies of plant-pollinator interactions are typically conducted according to two very
386 different traditions: classical adaptationist studies [17] and community-level network
387 studies [31]. There has been little cross-talk between these two approaches, with the
388 adaptationist approach emphasizing trait functions and factors that impact on plant
389 fitness, and the network approach emphasizing metrics that describe the ecological
390 properties of whole communities. The niche perspective has potential to integrate
391 these two approaches to help explain the community context of specialisation in
392 pollination systems and its implications for trait evolution, lineage diversification, and
393 species persistence. Likewise, the evolution of floral traits in generalist lineages could
394 potentially be explained through using community data for the complex task of
395 defining generalist niches, and by experiments that test for variation between
396 pollinator species in both their response to floral traits and their consequences for
397 plant fitness [61].

398

399 While objective recognition of niches is becoming a cornerstone of studies using the
400 pollination niche concept, there is a need to expand beyond using only network
401 summary analyses of patterns of plant-pollinator interactions at a particular point in
402 space and time. For example, experimental manipulation of the flowering or
403 pollinating community (e.g. [100-102]) is a potentially powerful, but currently
404 underutilised, approach to improve understanding the fundamental niche.

405 Incorporating morphology and pollinator behaviour into studies of interaction
406 networks enables a direct test of whether floral traits are associated with network
407 modules (e.g. [24]), thereby identifying traits that can be tested experimentally for
408 their role in pollinator attraction (see **Outstanding Questions**). The identification of
409 functional traits is critical as this forms the basis of understanding specialisation and
410 how shifts in niches may occur - one of the most fundamental unanswered questions
411 in pollination biology. Indeed, the evidence for numerous shifts in pollination strategy
412 in many plant lineages [93] highlights the importance of understanding how
413 transitions arise between pollination niches. A key aim for future studies will be to
414 identify the pollination niche axes that are most often associated with plant speciation
415 and to determine whether these are the same or different from the axes that are most
416 effective at fostering ecological co-existence. We expect that the incorporation of
417 niche theory into pollination biology will enable much better integration of this
418 discipline into the general fields of ecology and evolutionary biology.

419

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430

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682

683

684 **Glossary:**

685 **Bimodal pollination:** where for a given plant species pollination is achieved by two
686 different functional groups of animals normally associated with different sets of
687 functional traits.

688 **Character displacement:** evolution through natural selection for traits that reduce
689 competition or reproductive interference.

690 **Ecological specialisation:** in the context of pollination, the use of one or few
691 pollinator species.

692 **Functional trait:** a trait that strongly affects organismal performance. As such, they
693 are expected to have a large affect on fitness in any given niche.

694 **Fundamental niche:** In the context of biotic pollination, the pollen vectors capable of
695 supporting positive population growth rates in the absence of competition.

696 **Modularity:** A consistent pattern in interaction networks where groups of species
697 tend to interact with each other more regularly than with the members of other groups.

698 **Niche:** the resources and environmental conditions that enable a population of a
699 species to maintain a net reproductive rate of ≥ 1 . Each variable contributing towards
700 the overall niche is referred to as a niche axis. The niche of a species is commonly
701 articulated as the n -dimensional hyper-volume generated from the suitable conditions
702 across n niche axes.

703 **Plant-pollinator network:** the set of pollination interactions in a community of
704 plants and pollinators.

705 **Pollinator functional group:** a group of pollinator species that are likely to exert
706 similar selection pressures. These pollinator species are often phylogenetically
707 related.

708 **Pollination niche:** the abiotic or biotic vectors and their associated traits providing
709 effective pollination at the time and place that a plant species flowers.

710 **Pollination syndrome:** a suite of floral traits shared across plant species that
711 primarily use the same pollinator functional group.

712 **Realised niche:** In the context of biotic pollination, the pollination service from the
713 pollen vectors that can support positive population growth rates, as shaped by
714 competition and facilitation.

715 **Trade-offs:** when adaptation to a particular niche lowers performance in another
716 niche.

717

719 **Box 1. Using pollinator traits to recognise pollination niches**

720

721 *Overview*

722 Plotting the frequency distribution of variation in hawkmoth tongue length across a
723 pollinator community can aid identification of the potential pollination niches
724 available to the plant species pollinated by nectar foraging hawkmoths in a given
725 community. Subsequently, an independent assessment of plant functional traits
726 associated with hawkmoth pollination, such as flower tube length, can reveal if plants
727 show adaptation to a particular pollination niche [9].

728

729 *Pollination niche position, breadth and availability*

730 In this example, pollination niche position is the median tongue length for a given
731 functional pollinator group (Figure I, panel C and D). Pollination niche breadth is the
732 range of effective tongue lengths (panel C and D). Pollination niche availability at a
733 given site is indicated by the abundance of pollinator individuals (panel D). In this
734 community, there are two pollination niches, corresponding to short-tongued and
735 long-tongued hawkmoths. Furthermore, the moth-pollinated plant species in the
736 community show strong evidence for floral tube length adaptation to one or other of
737 the two pollination niches (panel E).

738

739 *Advantages of using pollinator traits to recognise pollination niches*

740 This approach allows one to test for floral adaptation to particular niches, and enables
741 development of clear predictions of niche availability to understand niche occupancy.
742 While illustrated here with a univariate pollinator trait, this approach can be extended
743 to include multiple niche axes in the same way as multi-dimensional quantifications
744 of abiotic niches. For example, other pollinator traits could include food preference,
745 flight time, body size, and floral odour preference.

746

747 *Challenges for testing plant adaptation to the pollination niche*

748 *A priori* evidence is needed to identify niche axes that may represent functional traits.
749 Many plant traits that may be adaptations to their pollination niche are multi-variate
750 (e.g. nectar composition) and may require variable reduction methods (e.g. Principal
751 Co-ordinates Analysis), making clear ecological interpretations more difficult.
752 Detailed sampling of the functional group of pollinators, either to determine

753 availability or to measure pollinator traits potentially relevant for pollination, can be
754 challenging.
755

756 **Box 2. Challenges for using networks to understand pollination niches.**

757 Plant-pollinator networks may allow objective quantification of the pollination niches
758 in any given community. For a given plant species, niche position would be the
759 module, with the discreteness of the niche measured by Modularity Q [30], and niche
760 breadth would be the number of links, or the number of species with more than N
761 number of visits (to remove incidental visitors). Niche availability would be the
762 abundance of effective pollinator individuals summed across species within a module.

763

764 *Visitation vs pollination:* Quantifying visitation rather than pollination underestimates
765 specialisation of the pollination systems [103, 104]. This has been partly addressed by
766 quantifying contact with the reproductive structures, but evidence suggests that this
767 still can underestimate specialisation compared with quantifying pollen deposition
768 [105].

769 *Detecting pollinators with low visitation rates:* Studies that conduct observations
770 based purely on transects rather than equal observation time across plant species bias
771 the data towards lower visitation and increased specialisation for rarer plant species
772 [34].

773 *Bias of metrics towards specialisation:* Using simulations of networks generated
774 under a quantitative niche model, Frund *et al.* [32] found that 48 metrics of
775 specialisation and network structure are biased towards overestimating specialisation,
776 and advocated at least 20 observations per plant species to accurately estimate
777 specialisation.

778 *d' does not measure ecological specialisation:* Ecological specialisation of a
779 pollination system is the number of species that an organism interacts with (or
780 primarily with). However, d' , which provides a measure of the complementarity (or
781 exclusiveness) of species interactions [34], is frequently used as a measure of
782 ecological specialisation. Pauw & Stanaway [26] illustrated the shortcoming of this
783 approach in a community where a specialist *Gladiolus* species visited by one species
784 of *Anthophora* bee species had a d' value of only 0.3 (scale from 0 to 1) while a
785 generalist *Crassula* species with 10 pollinator species had a $d' = 0.99$, because nine of
786 its pollinators were not recorded on other plant species.

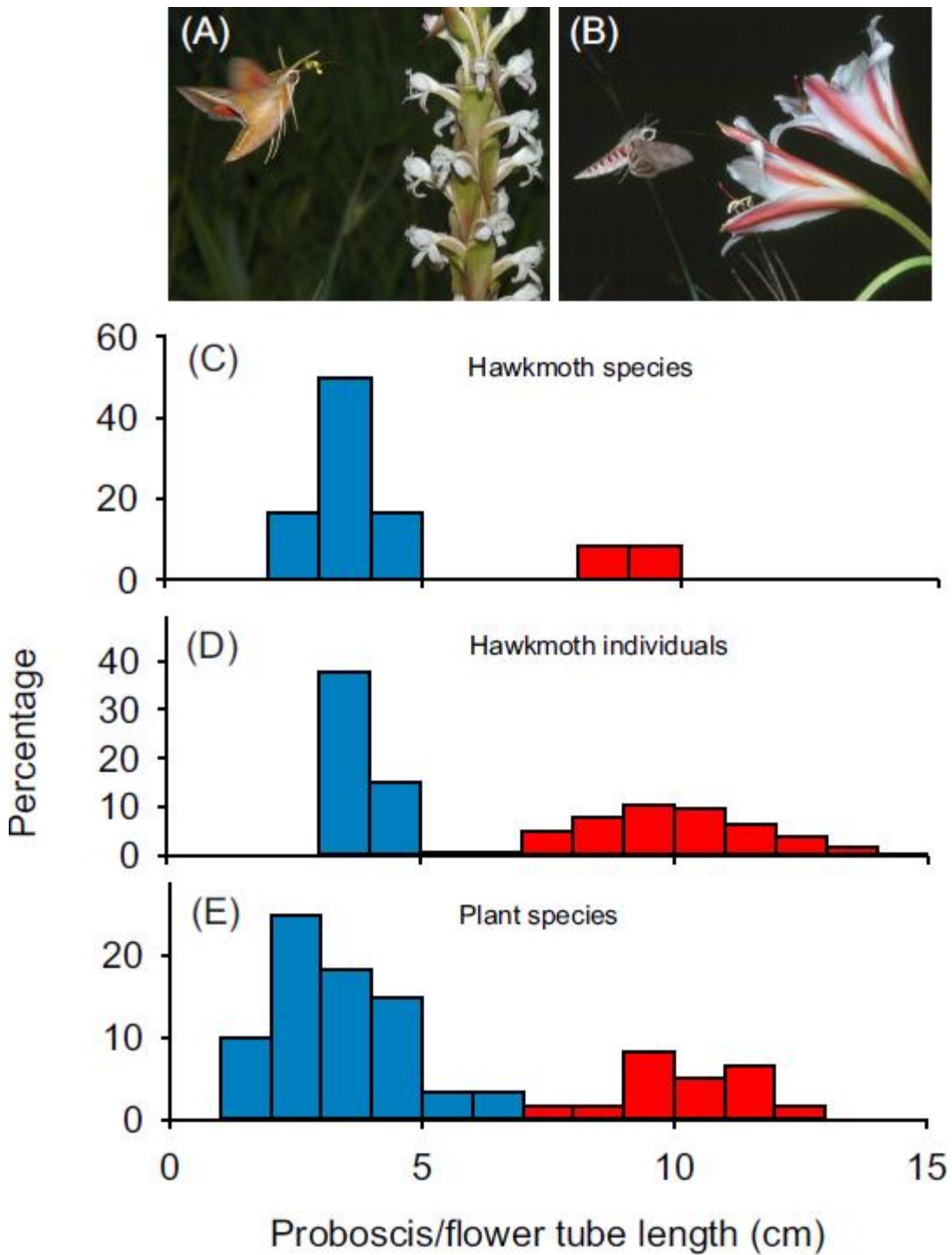
787 *Geography of specialisation:* If pooling data across sites, species absent from a site
788 are interpreted as not interacting with particular species when in fact there was no

789 opportunity to interact (forbidden links), resulting in erroneously high specialisation
790 estimates.

791 *Temporal/seasonal variation:* Networks can change properties over the course of a
792 year and/or flowering season [106].

793 *Pollinators can be attracted via different mechanisms:* Not accounting for the
794 mechanism of attraction underestimates the number of pollination niches as the same
795 pollinator could be attracted to two different species through two different
796 rewards/mechanisms.

797

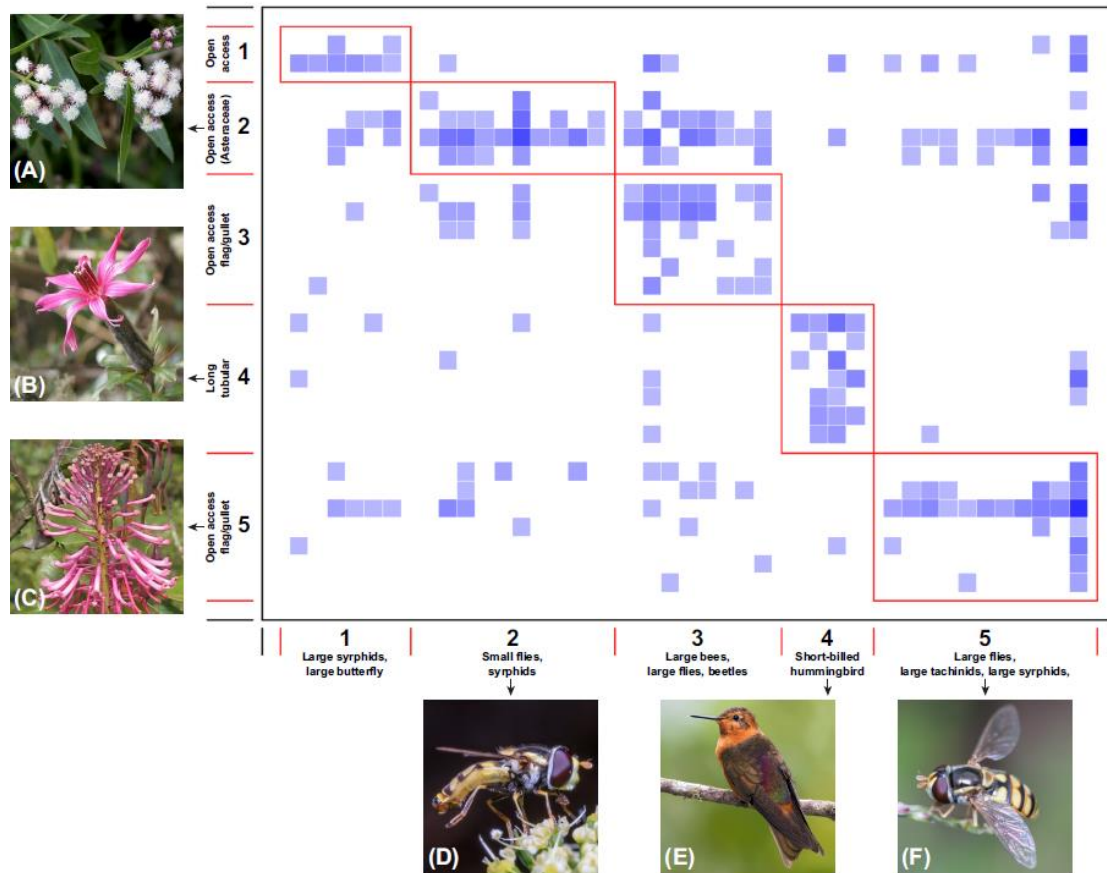


799

800 **Figure I, Box 1:** Subtropical South Africa has numerous species of plant pollinated
 801 by hawkmoths, including (A) *Satyrium longicauda* pollinated by the short-tongued
 802 hawkmoth *Basiothia schenki* and (B) *Crinum bulbispermum* pollinated by the long-
 803 tongued hawkmoth *Agrius convolvuli*. Plots illustrate the correspondence between
 804 hawkmoth tongue lengths [(C) species means; (D) individual measurements] and (E)
 805 mean floral tube lengths [9]. Blue bars in the histogram illustrate the niche involving

806 short-tongued hawkmoths, red bars illustrate the niche involving long-tongued
807 hawkmoths. Photos by Steve Johnson.

808

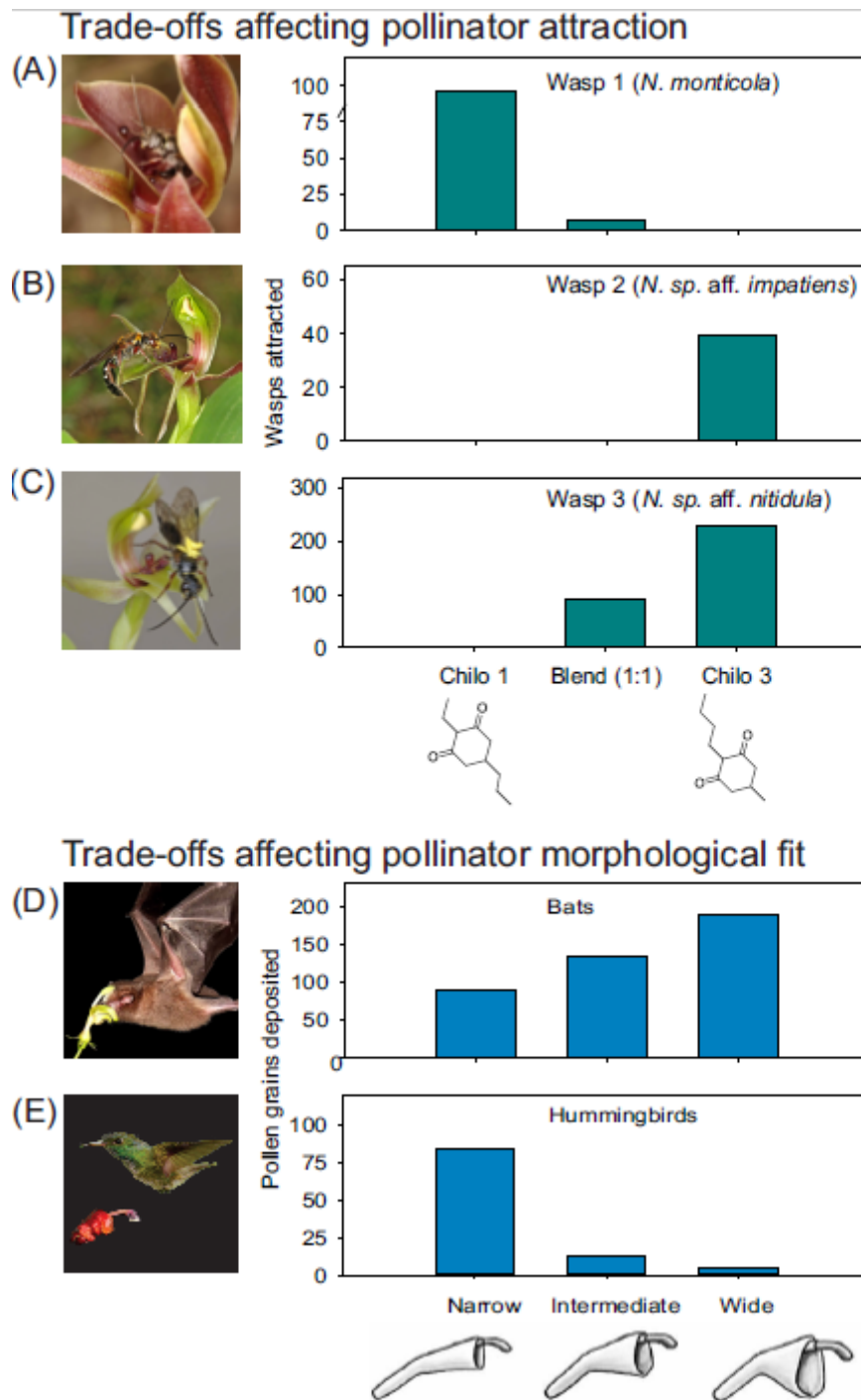


809

810 **Figure 1:** The use of a plant-pollinator network to objectively test for pollinator
811 niches. Potential pollination niches are recognised through the identification of
812 modules, which are then overlaid with data on floral and pollinator traits to test for
813 adaptation by plants to groups of pollinators, and the identification of candidate
814 functional traits. In this example, Watts *et al.* [27] collected data on potential
815 pollinators for several communities in the Peruvian Andes and identified modules
816 using the software *QuantBiMo* [30]. This figure illustrates the objective identification
817 of a module of hummingbirds (e.g. Shining Sunbeam) associated with long tubed
818 flowers (e.g. *Fuchsia apetala*). Other modules mostly correspond to varying groups of
819 insects, particularly flies. This dataset illustrates that some plant species attract
820 pollinators from more than one module, and therefore the potential for individual
821 pollinator species to contribute to more than one pollination niche. For a given plant
822 species, comparing the effectiveness of floral visitors within its module with visitors

823 from other modules (e.g. for module 4, short-billed hummingbirds vs syrphid flies)
824 could provide a basis for understanding specialisation of the pollination niche. Further
825 work would involve experimental approaches to test if members of these modules
826 respond similarly to floral traits, and if there is evidence for corresponding floral
827 adaptation. Members of modules illustrated are: (A) *Baccaris salcifolia* (Asteraceae);
828 (B) *Barnadesia horrida* (Asteraceae); (C) *Oreocallis grandiflora* (Proteaceae); (D)
829 Syphid species (E) *Aglaeactis cupripennis* (Trochilidae) (F) Syphid species. Note that
830 the syrphid photos are illustrative and do not represent actual members of this
831 community. Photographs: (A) Lynn Watson, (B & C) Stella Watts, (D & F) Thomas
832 Semple, (E) Supreet Sahoo.

833



834

835 **Figure 2:** Fitness trade-offs as a mechanism underpinning the specialisation of
 836 pollination systems. *Trade-offs in pollinator attraction* (Panel A, B and C): In
 837 sexually deceptive orchids, each orchid species is primarily pollinated by a single
 838 pollinator species [42, 96], which is attracted through mimicry of the sex pheromone
 839 of the female of the pollinator species [6]. Related orchids typically attract related
 840 pollinators using different blends of compounds, often with some overlap of the
 841 constituent compounds [42]. Here, three species of *Chiloglottis* use one of two
 842 different chiloglottones (chiloglottone 1 and 3) to attract sexually deceived





843 *Neozeleboria* thynnine wasps. When these compounds are experimentally presented
844 to pollinators either by themselves or in a 1:1 blend, the single compounds attract
845 individuals of different pollinator species, while the blend attracts few or no
846 pollinators (Panel A, B and C) (data from [42]). *Trade-offs in morphological fit*: Some
847 neotropical plant genera have undergone shifts in pollination strategy between
848 pollination by hummingbirds and bats [47]. Using flowers with artificial corollas in a
849 flight cage experiment, Muchhala [57] demonstrated that narrow corollas guided bills
850 of the hummingbird *Adelomyia melanogenys* (illustrated here by a similar
851 hummingbird species) more effectively than did wide corollas, leading to greater
852 pollen deposition (Panel E). Alternatively, wide corollas guided snouts of the bat
853 *Anoura geoffroyi* more effectively than did narrow corollas, leading to more pollen
854 deposition from bats, but less from hummingbirds (Panel D). A model based on this
855 experiment predicted that intermediate corollas are never favoured. Photos by Rod
856 Peakall, Nathan Muchhala and Steven Johnson.

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860 **Table 1:** Examples of pollination niches and functional traits related to niche occupancy^a

				
Plant species	<i>Satyrium pumilum</i> (Orchidaceae)	<i>Disa pulchra</i> (Orchidaceae)	<i>Mimulus cardinalis</i> (Phrymaceae)	<i>Gladiolus longicollis</i> (Iridaceae)
Pollination niche – vector	Flesh flies (Sarcophagidae)	<i>Philoliche aethiopica</i> (tabanid fly)	Anna’s hummingbird	various hawkmoth species (Sphingidae)
Pollination niche – basis for pollinator attraction	Deception of flies through carrion mimicry	Batesian mimicry of nectar producing <i>Watsonia</i>	Mutualism involving nectar reward	Mutualism involving nectar reward
Functional traits	Pollinator attraction by specific emission rates of floral odour (exp), Matching of carrion odour through production of oligosulfides, 2-heptanone, p-cresol and indole (obs), Dull floral colouration (obs) Prostrate flowering (obs)	Pink floral colour that matches the model species (exp), Petaloid shape (exp), Floral nectar guides that match the model species (exp), summer flowering (obs)	Red floral colour (exp), Tubular corolla (obs), Large nectar volume (exp), Exserted anthers (obs)	Long nectar spurs (fit), Greater inflorescence height (fit), flowers open at night (obs)
Reference	[107]	[43]	[40]	[108, 109]

861 ^aFor functional traits; (exp) denotes when the importance of the trait has been tested experimentally for that species; (fit) denotes when variation
 862 in plant fitness in response to the trait has been measured in wild populations; (obs) denotes when the importance of the trait has been inferred
 863 through observation (e.g. observation of nectar consumption).

