

The Role of Local Species Abundance in the Evolution of Pollinator Attraction in Flowering Plants

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ABSTRACT: We present a population genetic model that incorporates aspects of pollinator efficiency and abundance to examine the effect of the local plant community on the evolution of floral trait specialization. Our model predicts that plant species evolve to be pollinator specialists on the most effective and common pollinators when their abundance is low relative to other plant species in the community (i.e., conspecific pollen is relatively rare) and evolve to be pollinator generalists when they are numerically dominant (i.e., conspecific pollen is abundant). Strong flower constancy also favors generalist floral traits. Furthermore, generalist species are predicted to differentiate when there is a concave trade-off in attracting pollinator species with different floral trait preferences. This result implies that populations that evolve toward a generalist strategy may be more prone to speciation. Ours is the first theoretical model to include local species abundance explicitly, despite the fact that it has been previously identified as an important factor in the evolution of plant specialization. Our results add a layer of ecological complexity to previous models of floral evolution and therefore have the potential to improve our power to predict circumstances under which specialized and generalized plant-pollinator interactions should evolve.

Keywords: generalization, flower constancy, pollination, specialization, species abundance, trait evolution.

That floral traits evolve for specialized pollination by certain types of animals is a central tenet in explanations for the diversity of angiosperms (Grant 1949, 1994; Hodges and Arnold 1995; Dodd et al. 1999; Sargent 2004). Specialized pollinators are thought to drive the evolution of phenotypic divergence between incipient plant species,

which leads to reproductive isolation and speciation. This concept is supported by evidence for pollinator syndromes in which suites of floral traits in species with similar pollinators exhibit convergent evolution (Faegri and van der Pijl 1979; Kay and Schemske 2003; Fenster et al. 2004). Indeed, plant-pollinator specialization has been identified as an important factor in studies of reproductive isolation in flowering plants (Hodges and Arnold 1994; Schemske and Bradshaw 1999; Ramsey et al. 2003).

In this article we develop a population genetic model to examine the forces affecting the tendency of flowers to evolve traits in order to attract a single type of pollinator (i.e., specialization) or a suite of several different pollinator species (i.e., generalization). We define specialization as a floral strategy to invest in particular traits that increase the relative preference of certain pollinators for the flower. In contrast, a generalist plant invests in a combination of traits so that a broader variety of pollinator species are attracted, but not as keenly. In our model, any pollinators whose preferences can be manipulated by a flower in a manner indistinguishable to floral evolution are grouped together. Hence, specialization can evolve to a pollinator species or to a functional group of pollinator species (Fenster et al. 2004). For example, a flower can evolve specialization to a group of different bee species if their preferences for certain floral traits are identical. The model addresses the evolution of plant specialization within a certain community of pollinators, not the evolution of pollinator preferences.

While plants with specialized pollination systems have traditionally been considered the rule in plant-pollinator interactions (reviewed by Johnson and Steiner [2000]), others have argued that rather than being specialized on one or a few pollinators, the majority of plant species are in fact pollinated by several pollinator species and should therefore be considered generalists (Ollerton 1996; Waser et al. 1996; Olesen and Jordano 2002). Whether specialist or generalist plant species prevail is currently under debate (reviewed by Fenster et al. [2004]). To further complicate matters, a flower that receives visits by many pollinator species may be effectively pollinated by only a few of the

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Table 1: Description of parameters used in the model

Parameter	Description
KK	Resident genotype
Kk	Invading heterozygote genotype
kk	Invading homozygote genotype
O	Other species
D	Frequency of KK resident
H	Frequency of invading Kk heterozygote
R	Frequency of invading kk homozygote
f	Frequency of focal species
$1-f$	Frequency of other species in the community
g	Frequency of pollinator A
$1-g$	Frequency of pollinator B
γ_A	Efficiency of pollinator A
γ_B	Efficiency of pollinator B
g_e	“Effective abundance” of pollinator A, a term that describes the relative abundance of pollinator A along with its pollination efficiency
$1-g_e$	“Effective abundance” of pollinator B
α_O (β_O)	Preference of pollinator A (B) for other species in the community
α_D (β_D)	Preference of pollinator A (B) for resident homozygote
α_H (β_H)	Preference of pollinator A (B) for invading heterozygote
α_R (β_R)	Preference of pollinator A (B) for invading homozygote
χ_{ij}	Degree to which a plant of genotype i attracts a pollinator of type j
T_A	Average strength of attraction of pollinator A to the plants in the community
T_B	Average strength of attraction of pollinator B to the plants in the community
C	Amount of plant resource available for attracting pollinators in the focal species
C_O	Amount of plant resource available for attracting pollinators averaged over all other plant species in the community
n	Curvature of the trade-off between attracting pollinators A and B (fig. 1)
$\left. \frac{d\lambda}{d\alpha_H} \right _{\alpha_H=\alpha_D}$	Selection gradient on a given floral trait
ω	Probability that the second flower visited by a pollinator is guaranteed to be the same species as the first (a measure of flower constancy)

visiting species. Thus, in spite of a high diversity of pollinator visitors, the plant species may in fact be a specialist (Schemske and Horvitz 1984). This insight makes it difficult to determine whether a plant species is functioning as a generalist or a specialist in the absence of quantitative data. While there are reliable examples of both extremes on the generalist and specialist spectrum, the relative frequency of such interactions is poorly known (Kay and Schemske 2004).

It is unclear which ecological conditions lead to the evolution of specialization or generalization in floral traits. Stebbins's (1970) “most effective pollinator principle” (MEPP) predicts that plants tend to evolve floral traits that promote specialization on those pollinators that “visit it most frequently and effectively in the region where it is evolving” (p. 318). Previous models have focused on examining the role pollinator effectiveness plays in shaping floral trait specialization in the absence of interspecific competition (e.g., Waser et al. 1996; Aigner 2001) despite

the fact that competition for pollinators has been recognized as important in floral evolution (Levin and Anderson 1970; Rathcke 1983; Caruso 2000, 2002; Bell et al. 2005).

In communities of coflowering plants, a species' relative local abundance has been shown to affect the frequency with which plants receive heterospecific pollen (Bell et al. 2005), which can be an important factor in the evolution of specialization. The motivation for predicting a relationship between a species' relative abundance and the evolution of specialization was communicated by Feinsinger (1983, pp. 287–288): “If a plant population is quite densely distributed, nearest neighbors are likely to be conspecific. Nearly any visitor, no matter how uncommitted, is likely to bring useful pollen to a plant and to disperse the plant's own pollen to nonspecific stigmas. Selection on plants to specialize is relaxed. Consider a population of widely dispersed plants with few flowers each, however. If these flowers invite all comers, then the pollinators may not distinguish the rare species from the more common ones.”

Table 2: Probability of and genetic contributions of four possible visit sequences by pollinators A and B

Visit sequence	Probability of sequence for A	Probability of sequence for B	Proportion of offspring <i>KK</i>	Proportion of offspring <i>Kk</i>	Proportion of offspring <i>kk</i>
<i>KK-KK</i>	$g\gamma_A(\alpha_D f D/T_A)^2$	$(1-g)\gamma_B(\beta_D f D/T_B)^2$	1	0	0
<i>KK-Kk</i> or <i>Kk-KK</i>	$2g\gamma_A(\alpha_D \alpha_H f^2 D H/T_A^2)$	$2(1-g)\gamma_B(\beta_D \beta_H f^2 D H/T_B^2)$	1/2	1/2	0
<i>KK-kk</i> or <i>kk-KK</i>	$2g\gamma_A(\alpha_D \alpha_R f^2 D R/T_A^2)$	$2(1-g)\gamma_B(\beta_D \beta_R f^2 D R/T_B^2)$	0	1	0
<i>Kk-Kk</i>	$g\gamma_A(\alpha_H f H/T_A)^2$	$(1-g)\gamma_B(\beta_H f H/T_B)^2$	1/4	1/2	1/4
<i>kk-Kk</i> or <i>Kk-kk</i>	$2g\gamma_A(\alpha_H \alpha_R f^2 H R/T_A^2)$	$2(1-g)\gamma_B(\beta_H \beta_R f^2 H R/T_B^2)$	0	1/2	1/2
<i>kk-kk</i>	$g\gamma_A(\alpha_R f R/T_A)^2$	$(1-g)\gamma_B(\beta_R f R/T_B)^2$	0	0	1

Indeed, recent studies have demonstrated that the strength and direction of pollinator-mediated selection on floral traits is influenced by the presence of heterospecific competitors for pollinator visitation (Caruso 2000). Thus, it seems critical to include species abundance in models of plant specialization, particularly considering that plant-pollinator interactions have profound implications for our understanding of floral adaptation and ultimately plant speciation (Johnson and Steiner 2000; Kay and Schemske 2004).

Here, we introduce a population genetic model that incorporates pollinator abundance and efficiency in order to explore the influence of local plant species' abundances on the evolution of specialization and generalization in animal-pollinated plant species.

The Model

The model describes the conditions under which a rare allele *k* spreads in a focal population of self-incompatible diploid floral morphs where *K* is the resident allele. Within the focal plant species, *KK*, *Kk*, and *kk* are three floral morphs that differ in the degree to which they attract the various pollinators in the community (table 1). The frequencies of these three diploid genotypes are *D* (*KK*), *H* (*Kk*), and *R* (*kk*). In the plant community at large, the frequency of the focal species is *f*, and the frequency of all other species of flowering plant (*O*) is $1 - f$. For clarity, we assume that there are two types of pollinator species, A and B, pollinating the community of flowering plants. It is straightforward, however, to extend the model to incorporate more pollinator types. In accordance with MEPP (Stebbins 1970), the two pollinators are allowed to differ in abundance and in their pollinating efficiency. To account for differences in abundance, we describe the frequency of pollinator A as *g* and the frequency of pollinator B as $1 - g$. In our model, the efficiency of pollen transport and deposition is proportional to γ_A for pollinator A and γ_B for pollinator B.

Visitation by a pollinator can only contribute to the male fitness of a self-incompatible genotype when subsequent visits by that pollinator are to a plant of the same

species. This consideration distinguishes our model from previous models of plant specialization, which implicitly assume that any pollen grain collected is equally likely to successfully fertilize an ovule (e.g., Waser et al. 1996) or use an optimality approach where plant fitness is not an explicit function of the mating rules (e.g., Aigner 2001). We simplify our model by assuming that the majority of pollen transfer occurs between one plant visit and the next. However, as long as pollen deposition is not affected by the type of plant species visited in interim steps, the results are the same regardless of whether the focal species is the next plant visited or the *x*th plant visited (see app. A). This assumption allows us to focus on pollinator visits as a sequence of two-stop trips, with the first stop representing pollen collection and the second stop representing pollen deposition. Each sequence of pollinator visits has a different probability, depending on the frequency of the morphs and the pollinators. The only sequence that contributes to the fitness of the focal species is one in which a pollinator collects pollen from a flower of the focal species (i.e., morphs *KK*, *Kk*, or *kk*) and subsequently deposits it on a flower of the same species.

The two pollinator species have different visitation preferences for the flowering plants in the community (table 1); these preferences are proportional to the investment, α_i , and β_j , by individual plants in the community in attracting pollinators A and B, respectively. We use a relative preference scheme as used by Kirkpatrick (1982) in models of sexual selection. Specifically, the degree to which a plant of genotype *i* attracts a pollinator of type *j*, χ_{ij} , is measured relative to the pollinator's overall attraction to other flowers in the local area, T_j . We define the probability that pollinator A visits a genotype (whose frequency, *i*, is *D*, *H*, or *R*) as $\chi_{iA} = \alpha_i f i / T_A$ and the probability of visitation by pollinator B as $\chi_{iB} = \beta_i f i / T_B$. The average strength of attraction of pollinators A and B to the plants in the community is represented by T_A and T_B :

$$T_A = f(\alpha_D D + \alpha_H H + \alpha_R R) + \alpha_O(1 - f), \quad (1)$$

$$T_B = f(\beta_D D + \beta_H H + \beta_R R) + \beta_O(1 - f). \quad (2)$$

Thus, pollinators shift their visitation patterns as the floral community evolves, becoming more likely to visit plants that have invested more in attracting them.

One major limiting assumption of our model is that we treat the relative frequency of pollinators A and B as constants. Clearly, these frequencies would respond to the local plant community through migration of pollinators as well as fitness differences among pollinators. Although further work allowing plant-pollinator coevolution is warranted, it seems a reasonable first step to assume that factors other than local flowering plant abundance, such as density regulation at the larval stage or plant abundance across a larger scale, may be more important determinants of pollinator density. Furthermore, our model provides important insight into the evolutionary forces in the presence of a fixed pollinator pool.

The number of *KK* individuals in the next generation, D' , is determined by summing over the probabilities that pollinators A and B gather and deposit pollen on flowers of the focal species times the probability of the visit sequence between a specific maternal genotype and a specific paternal genotype times the Mendelian probability of those parents producing *KK* offspring. From table 2, a set of recursions can be derived that describe the change in frequency of the three genotypes over a single generation:

$$D' = \frac{1}{\bar{w}} \left[g\gamma_A \chi_{DA}^2 + (1-g)\gamma_B \chi_{DB}^2 + g\gamma_A \chi_{DA} \chi_{HA} + (1-g)\gamma_B \chi_{DB} \chi_{HB} + g\frac{\gamma_A}{4} \chi_{HA}^2 + (1-g)\frac{\gamma_B}{4} \chi_{HB}^2 \right] \quad (3)$$

$$H' = \frac{1}{\bar{w}} \left[g\gamma_A \chi_{DA} \chi_{HA} + (1-g)\gamma_B \chi_{DB} \chi_{HB} + g\frac{\gamma_A}{2} \chi_{HA}^2 + (1-g)\frac{\gamma_B}{2} \chi_{HB}^2 + 2g\gamma_A \chi_{DA} \chi_{RA} + 2(1-g)\gamma_B \chi_{DB} \chi_{RB} + g\gamma_A \chi_{HA} \chi_{RA} + (1-g)\gamma_B \chi_{HB} \chi_{RB} \right] \quad (4)$$

$$R' = \frac{1}{\bar{w}} \left[g\gamma_A \chi_{RA}^2 + (1-g)\gamma_B \chi_{RB}^2 + g\frac{\gamma_A}{4} \chi_{HA}^2 + (1-g)\frac{\gamma_B}{4} \chi_{HB}^2 + g\gamma_A \chi_{HA} \chi_{RA} + (1-g)\gamma_B \chi_{HB} \chi_{RB} \right] \quad (5)$$

where \bar{w} represents the mean pollen fitness,

$$\bar{w} = g\gamma_A (\chi_{DA} + \chi_{HA} + \chi_{RA})^2 + (1-g)\gamma_B (\chi_{DB} + \chi_{HB} + \chi_{RB})^2. \quad (6)$$

Equations (1)–(6), as derived, assume that any pollen grain that is successfully collected and deposited on a stigma of the same species is able to fertilize an ovule. This assumption is only strictly true when pollen is limiting. Nevertheless, we also considered the opposite assumption, where ovules are limiting and all pollen landing on a stigma of a certain genotype must compete. Having ovule limitation rather than pollen limitation halved the strength of selection on new floral morphs, but it did not alter the direction of selection. Thus, the results reported below apply to either case.

We used equations (1)–(6) to investigate the spread of a new allele k that alters the allocation of floral resources invested in the attraction of one or both pollinator species.

Invasion Criteria

To assess the evolutionary forces acting on the allocation of floral resources to attracting different pollinators, we examined when a resident genotype (*KK*, $\hat{D} = 1$) could be invaded by a rare mutant allele (k) that differs from the resident in its attractiveness to the two pollinators (table 1). To do so, we performed a local stability analysis of the equilibrium, $\hat{D} = 1$, assuming that *Kk* and *kk* were rare. Because of the assumption that k is rare and that selfing does not occur, the frequency of *kk* individuals does not influence the invasion criteria. Therefore, the population at the time of invasion effectively contains only *Kk* individuals (invading morph) and *KK* individuals (resident morph).

If there were no constraints on floral attractiveness, flowers would evolve to be infinitely attractive to all pollinators. In consideration of this we have included a trade-off between investments in attracting one pollinator versus the other such that $(\alpha_i/C)^n + (\beta_i/C)^n = 1$, where C is the maximum amount of plant resource available for attracting pollinators in the focal species and n describes the curvature of the trade-off function (fig. 1). This trade-off

function has the useful property that it differentiates between cases where intermediate combinations of β and α are more attractive, on average, than the extremes (when $n > 1$) or, conversely, where the two extremes are more attractive, on average, than intermediate allocation strategies (when $n < 1$). When $n = 1$, the trade-off function is linear, and all combinations of α and β are equally attractive. Studies examining the nature of the trade-off between attracting different species of pollinators are rare; interestingly, however, the limited data that exist suggest that all three types of trade-off functions arise in natural systems (e.g., Fulton and Hodges 1999; Schemske and Bradshaw 1999; Bradshaw and Schemske 2003; Aigner 2004). Other species in the community may invest more or less in floral structures C_o , and we take α_o and β_o to be the average level of investment over all other plant species in attracting pollinators A and B, respectively. We assume that these parameters for other species satisfy the same trade-off function (fig. 1)

Assuming that the frequency of the k allele is rare (on the order of ϵ , a small term), we determined the leading eigenvalue, λ , where $H' = \lambda H + 0(\epsilon)$, and

$$\lambda = \frac{\frac{g_e \alpha_D \alpha_H}{[(1-f)\alpha_o + f\alpha_D]^2} + \frac{(1-g_e)\beta_H \beta_D}{[(1-f)\beta_o + f\beta_D]^2}}{\frac{g_e (\alpha_D)^2}{[(1-f)\alpha_o + f\alpha_D]^2} + \frac{(1-g_e)(\beta_D)^2}{[(1-f)\beta_o + f\beta_D]^2}} + 0(\epsilon^2). \quad (7)$$

The term $g_e = g\gamma_A/[g\gamma_A + (1-g)\gamma_B]$ is the effective abundance of pollinator A, which describes the relative abundance of pollinator A along with its pollination efficiency.

Assuming that the effect of the allele on the floral trait is small and performing a Taylor series, the leading eigenvalue is approximately $\lambda = 1 + (d\lambda/d\alpha_H)|_{\alpha_H=\alpha_D}(\alpha_H - \alpha_D)$, where $(d\lambda/d\alpha_H)|_{\alpha_H=\alpha_D}$ is defined as the ‘‘selection gradient’’ on the floral trait, and we take into account the trade-off in resource allocation by setting $\beta_H = C[1 - (\alpha_H/C)^n]^{1/n}$. The selection gradient describes how the spread of the allele depends on its effect; when the selection gradient is positive, alleles that increase α_H are able to invade and vice versa.

By definition, an evolutionarily stable strategy (ESS; denoted by an asterisk) cannot be invaded by any other strategy. Thus, to be an ESS, an intermediate strategy that allocates resources to attracting both pollinators must satisfy $d\lambda/d\alpha_H|_{\alpha_H=\alpha_D} = 0$ (Maynard Smith 1982). In addition, an ESS must also satisfy $d^2\lambda/d^2\alpha_H|_{\alpha_H=\alpha_D} < 0$ so that a mutant with the same allocation strategy as the resident maximizes rather than minimizes λ . If the first but not the second derivative condition is satisfied, any mutant allele can spread through a population at the potential ESS, a phenomenon known as evolutionary branching (Dieckmann et al. 2003). As will be shown in a later section,

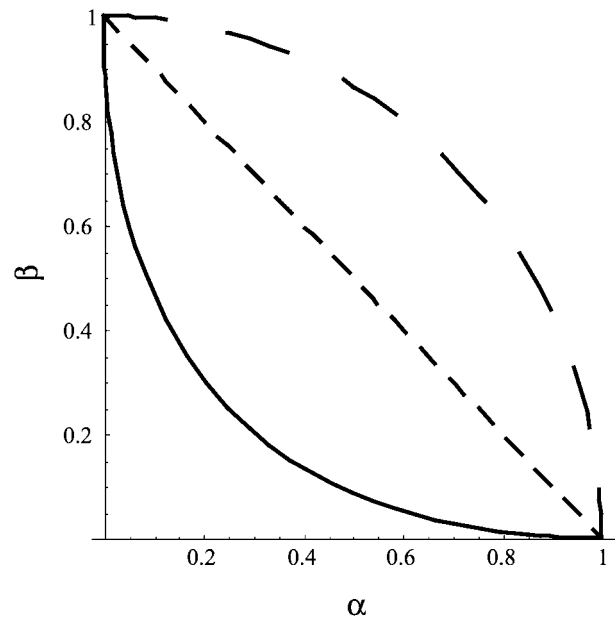


Figure 1: Illustration of possible curves describing the trade-off function between allocation to attracting the A pollinator (α) and the B pollinator (β). Each curve illustrates a different value of n ; linear trade-off, $n = 1$ (short-dashed line), a case where intermediates are more attractive than extremes, $n = 2$ (long-dashed line), and a case where intermediates are less attractive than the extremes, $n = 1/2$ (solid line).

whether or not evolutionary branching occurs at a potential ESS depends on the shape of the resource trade-off function (with $n < 1$ favoring branching).

Results

Our goal is to examine how the spread of the invading genotype, Kk , changes with respect to its relative allocation to attracting the two pollinator species under different conditions.

We focus our investigation on the role of the relative abundance of the focal species on the ability of the rare floral morph allele to invade a population of resident alleles. The intuition behind the results becomes most clear at the extremes, when the focal species is common relative to other species in the community and when the focal species is rare relative to other species. We therefore commence our discussion of the results at these extremes.

Focal Species Is Locally Abundant

When plants are surrounded primarily by conspecifics (e.g., when a species occurs in dense patches), there is an increased probability that pollen received will be genetically compatible, and we expect relaxed selection for spe-

cialization (Feinsinger 1983). Substituting $f = 1 - \xi$, where ξ is a small quantity, into (7), we find that the selection gradient equals

$$\frac{d\lambda}{d\alpha_H} \Big|_{\alpha_H=\alpha_D} \approx \frac{C^n g_e - \alpha_D^n}{\alpha_D^n (C^n - \alpha_D^n)} + 0(\xi). \quad (8)$$

By solving $d\lambda/d\alpha_H|_{\alpha_H=\alpha_D} = 0$, we find that a potential ESS occurs at $\alpha_D^*/C = g_e^{1/n}$. Using (8), it can be shown that when $\alpha_D < \alpha_D^*$, a rare allele can invade only if it increases α , with the converse holding when $\alpha_D > \alpha_D^*$. In other words, selection favors mutant alleles that bring the population closer to $\alpha_D^*/C = g_e^{1/n}$ (this point is thus convergence stable; fig. 2).

When the function describing the trade-off between attracting each pollinator is linear (i.e., when $n = 1$), the potential ESS occurs at $\alpha_D^*/C = g_e$. At this point, the proportion of available resources invested in attracting the A pollinator equals the effective abundance of the A pollinator, which in turn is proportional to the abundance and efficiency of the pollinator. Consequently, evolution favors plants that invest in attracting all available pollinators in proportion to each pollinator's effective abundance rather than specializing on the most effective pollinator. Thus, we expect specialist plants to evolve to be more generalist in their attraction of pollinators when a focal species is numerically dominant within the plant community.

Focal Species Is Locally Rare

At the other extreme, when the focal species is rare relative to other species in the community, incoming pollen is less

likely to be genetically compatible, and we expect strong selection on plants to specialize on a pollinator (Feinsinger 1983). Substituting $f = \xi$ into (7), we obtain an equation that describes selection on the rare *Kk* morph,

$$\frac{d\lambda}{d\alpha_H} \Big|_{\alpha_H=\alpha_D} = \frac{g_e \beta_0^2 \alpha_D^2 \beta_D^n - (1 - g_e) \alpha_0^2 \alpha_D^n \beta_D^2}{\alpha_D \beta_D^n [g_e \alpha_D^2 \beta_0^2 + (1 - g_e) \alpha_0^2 \beta_D^2]} + 0(\xi). \quad (9)$$

There is no explicit ESS solution to (9). However, substituting $n = 1$ into (9) indicates that for this special case, a potential ESS occurs when

$$\frac{\alpha_D^*}{C} = \frac{(1 - g_e) \alpha_0^2}{(1 - g_e) \alpha_0^2 + g_e \beta_0^2}. \quad (10)$$

Contrary to the previous case, here we find that invasion occurs when $\alpha_D < \alpha_D^*$ if the invading allele invests less in attracting pollinator A, while invasion occurs when $\alpha_D > \alpha_D^*$ if the allele causes the flower to be more attractive to pollinator A (fig. 3). Thus, populations not initially at (10) evolve away from it (this strategy is convergence unstable), and the system evolves toward specialization on pollinator A (if $\alpha_D > \alpha_D^*$) or B (if $\alpha_D < \alpha_D^*$) through a series of small mutational steps. Importantly, plants do not always specialize on the most effective or most abundant pollinator as measured by g_e . Instead, they can specialize on the least effective (or least abundant) pollinator if the plant is initially more attractive to that pollinator. Nevertheless, specialists on pollinator A are able to invade a broader range of generalists (i.e., species with a broader range of α_D) when pollinator A has a higher efficiency or higher abun-

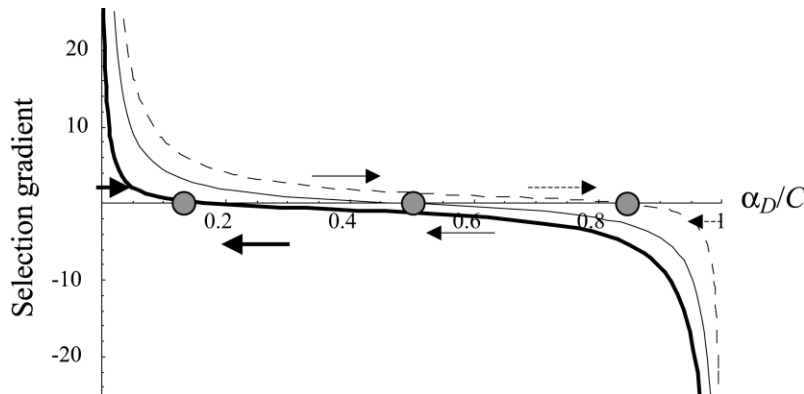


Figure 2: Selection gradient ($d\lambda/d\alpha_H$) on the *k* allele in a resident population that invests a proportion α_D/C (*X*-axis) of its resources in attracting pollinator A when the frequency of the focal species is high ($f \approx 1$) and $n = 1$. Circles indicate the convergence stable generalist ESS for each curve. Arrows indicate the direction selection is expected to drive a population. Each curve and set of arrows represents a different effective abundance of pollinator A: $g_e = 0.85$ (dashed line), $g_e = 0.5$ (thin line), and $g_e = 0.15$ (thick line).

dance (fig. 3, *dashed curve*), and vice versa (fig. 3, *thick curve*). When the other plant species are equally attractive to the two pollinators (i.e., $\alpha_o = \beta_o$), plants tend to evolve toward specialization on whichever pollinator was initially more attracted to the focal species (i.e., pollinator A if $\alpha_D/C > 1 - g_e$ and pollinator B otherwise). In contrast, when the other species in the community are specialized on pollinator A (i.e., $\beta_o = 0$), the focal species is more likely to specialize on the underutilized pollinator, B.

Focal Species Occurs at Intermediate Abundance

When the abundance of the focal species, f , is between 0 and 1, there are two or three strategies toward which a population might evolve. When the abundance of the focal species is low, the population evolves toward specialization on either pollinator A or pollinator B, depending on the initial floral trait (assuming $0 < n < 2$). When the abundance of the focal species is high, however, evolution toward a generalist strategy can also occur (fig. 4). As f varies from 0 to 1, there comes a point, f_{crit} , at which the potential generalist ESS switches from being repelling (convergence unstable) to attracting (convergence stable) from nearby points. To determine f_{crit} , we found the value of f where the slope of the selection gradient switches from being positive to negative at the potential generalist ESS. For f below this point, floral traits evolve toward extreme specialization (either $\alpha_D = 0$ or $\alpha_D = C$), and the generalist strategy is repelling (convergence unstable). For f above f_{crit} however, evolution proceeds toward a generalist strategy, at least for flowers that are not too highly specialized (fig. 5).

To identify f_{crit} and determine when convergence to a generalist strategy is possible, we focus on two floral at-

traction strategies of the other plants in the community. In the first case, the attractiveness of the flowers in the community matches the pollinators' effective abundance; in the second, the plants in the community are highly specialized to one of the pollinators. In both cases, the analysis simplifies and sheds light on the conditions favoring the evolution of specialization.

No Underutilized Pollinators. In order to find f_{crit} , we first make the simplifying assumption that pollinator investment among the nonfocal species (α_o, β_o) is proportional to the effective abundance of the pollinators with $\alpha_o/g_e = \beta_o/(1 - g_e)$. In other words, the rest of the plant community is well matched to the pollinator community, and there is no underutilized pollinator. In this case, there is again a potential generalist ESS at $\alpha_D^*/C = g_e^{1/n}$. Evolution proceeds toward this generalist strategy, however, only when the abundance of the focal species, f , is above $f_{crit} = C_o / \{C_o + C[n/(2 - n)]\}$. Interestingly, because f_{crit} decreases as a function of C and increases as a function of C_o , there is a larger range of communities that favor the evolution of a generalist strategy when the focal species allocates more to floral attraction than other species (cf. fig. 6). Not surprisingly, f_{crit} also decreases as a function of n , implying that evolution is more likely to lead to a generalist strategy when there is a relaxed trade-off between attracting different pollinators (n high).

An Underutilized Pollinator. In this second case, we explored a scenario where other species in the community are specialists on only one pollinator (pollinator B, for the purposes of this description) such that there is an underutilized pollinator (pollinator A). Substituting $\alpha_o = 0$

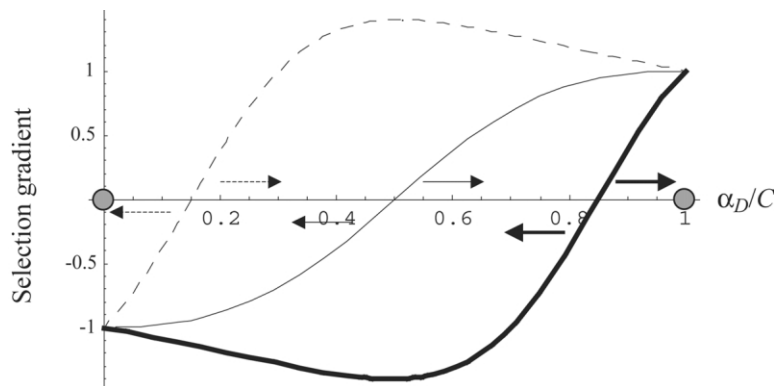


Figure 3: Selection gradient ($dN/d\alpha_H$) on the k allele in a resident population that invests a proportion (α_D/C) of its resources in attracting pollinator A when the frequency of the focal species is low ($f \approx 0$) and $n = 1$. We assume that the other species invest equally in attracting pollinators A and B ($\alpha_o = \beta_o = C/2$) and have equal resources available for investment in pollinator attraction ($C_o = C$). The circles indicate the convergence stable specialist ESS for each curve. Arrows indicate the direction selection is expected to drive a population. Each curve and set of arrows represents different effective abundance of pollinator A: $g_e = 0.85$ (*dashed line*), $g_e = 0.5$ (*thin line*), and $g_e = 0.15$ (*thick line*).

into the selection gradient, we determined that, in this extreme case, specialization on pollinator A is always an attracting ESS but that specialization on pollinator B never is. Furthermore, when there is a linear trade-off ($n = 1$), there can be evolution toward a generalist strategy when the effective abundance of pollinator A is sufficiently low, $g_e < g_{e_{crit}} = C^2 f^2 / [2C_o(1 - f) + Cf]^2$. Again, this condition becomes easier to satisfy (i.e., $g_{e_{crit}}$ increases) with increasing f ; in other words, convergence toward a generalist strategy is possible over a broader range of parameters when the relative abundance of the focal species increases. It is also possible to show that, for nonlinear trade-off functions, $g_{e_{crit}}$ increases with n , at least for values of n near 1 (analysis available from either author on request). In short, when all other plants in the focal species' community are specialists on pollinator B, the focal species either evolves specialization on pollinator A or evolves a generalist strategy, the latter being more likely when pollinator A is rare (g_e low), when the focal species is common (f high), or when there is a relaxed trade-off between attracting pollinators A and B (n high).

Evolution of Specialization versus Generalization. We should note that specialists on A and specialists on B are attracting ESS except under extreme conditions (e.g., when the community is dominated by the focal species, $f \approx 1$). Therefore, it is critical to ask whether plants evolve toward the generalist strategy over a broad or narrow range of initial levels of investment in attracting pollinator A. In figure 6, we show that when the generalist strategy is convergence stable, the conditions under which evolution proceeds toward the generalist strategy are quite broad.

Two Types of Generalists

In the above analysis, we focused on the strategies toward which a population converges over evolutionary time. Importantly, once a population has reached a convergence stable state, the population may or may not be stable to invasion by mutant strategies. In particular, a plant species that has evolved a generalist strategy may or may not be stable to the invasion of more specialized mutant strategies. If it is stable, then all flowers become attractive to both pollinators (a fixed generalist strategy). If it is unstable, the population diversifies, with some plants specializing on pollinator A and some on pollinator B (a polymorphic generalist strategy). This second scenario is particularly interesting because such polymorphic floral traits generate partial reproductive isolation, representing a first step toward speciation. We can assess whether a fixed or polymorphic strategy is expected in the long run by examining whether branching occurs at the potential generalist ESS.

A potential ESS must satisfy $d\lambda/d\alpha_H|_{\alpha_H=\alpha_D} = 0$. Unfortunately, there is no explicit solution to $d\lambda/d\alpha_H|_{\alpha_H=\alpha_D} = 0$. However, given that a potential generalist ESS exists, we can determine whether it is stable to invasion by any mutant strategy (i.e., an ESS that maximizes λ) or unstable (i.e., a branching point that minimizes λ) using the second derivative condition:

$$\frac{d^2\lambda}{d^2\alpha_H} \Big|_{\alpha_H=\alpha_D} = \frac{C^n(1 - g_e)(1 - n)\alpha_D^{n-2}\beta_D^2}{(C^n - \alpha_D^n)^2[(1 - f)\beta_o + f\beta_D]^2 \left\{ \frac{g_e\alpha_D^2}{[(1 - f)\alpha_o + f\alpha_D]^2} + \frac{(1 - g_e)\beta_D^2}{[(1 - f)\beta_o + f\beta_D]^2} \right\}} \quad (11)$$

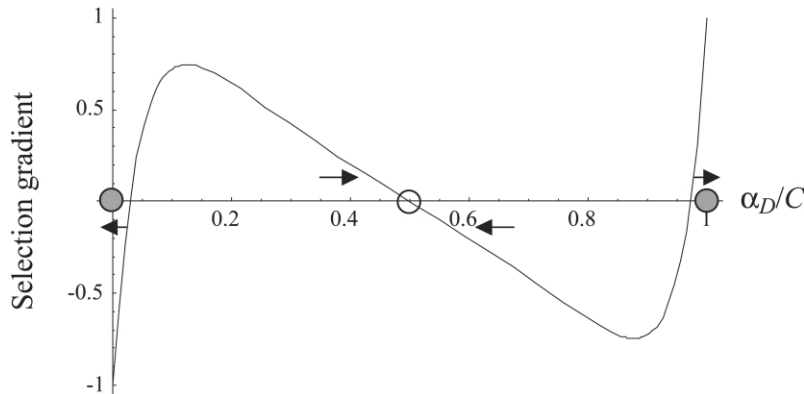


Figure 4: Selection gradient ($d\lambda/d\alpha_H$) on the k allele in a resident population that invests a proportion of α_D/C of its resources in attracting pollinator A when $f = 3/4$ and $n = 1$. The open circle indicates the generalist ESS at $\alpha_D^* = Cg_e$. We assume that the other species invest equally in attracting pollinators A and B ($\alpha_o = \beta_o = C/2$) and have equal resources available for investment in pollinator attractions ($C_o = C$). The shaded circles indicate the two specialist ESSs ($\alpha_D = 0$ and $\alpha_D = C$). Arrows indicate the direction selection is expected to drive a population.

Interestingly, when $n > 1$, (11) is negative, and a generalist strategy is therefore stable, whereas when $n < 1$, (11) is positive, and a generalist strategy is unstable. This makes sense in light of the fact that the trade-off is beneficial to generalists when $n > 1$ but to specialists when $n < 1$ (fig. 7). Hence, when the trade-off function favors generalists, we expect the evolution of a fixed trait where each individual in the population exhibits floral traits intermediately attractive to the two pollinators. However, when the trade-off function favors specialization, we expect the evolution of a polymorphism where some individuals specialize on one pollinator type and other individuals specialize on another pollinator type.

Flower Constancy

Some studies suggest that pollinating animals display “a propensity to visit the same type of flower as last visited irrespective of the value of alternatives” (Waser 2001, p. 322), a behavior known as flower constancy (Chittka et al. 1999; Waser 2001). In the above analyses, the type of flower first visited by a pollinator does not alter a flower’s probability of being subsequently visited. We examine the effect of flower constancy in appendix B. Essentially, when pollinators display flower constancy, generalization is favored under a larger range of parameter space. This finding is intuitive because in essence, flower constancy acts to increase a species’ effective local abundance by increasing the probability that incoming pollen is genetically compatible. Hence, increasing flower constancy has the effect of lowering the minimum abundance of a focal species (f_{crit}) necessary for the evolution of a generalist strategy. Nevertheless, empirical studies suggest that strong flower constancy is uncommon and that many insects are weakly constant at best (Heinrich 1976; Chittka et al. 1997). Overall, in a community with multiple floral species competing for pollinators, strong flower constancy, when it exists, will weaken selection for specialization because the focal species will be less affected by the receipt of heterospecific pollen.

General Predictions

The main prediction stemming from our model is that a species that is numerically rare relative to other animal-pollinated plant species in its vicinity is more likely to evolve specialist floral traits that are attractive to only one or a few species of pollinators. In contrast, a species that is relatively common will be more likely to exhibit generalist pollinator traits that are attractive to many species of pollinators. Furthermore, the nature of the trade-off function between attracting different pollinators affects whether generalization evolves as a fixed trait or a poly-

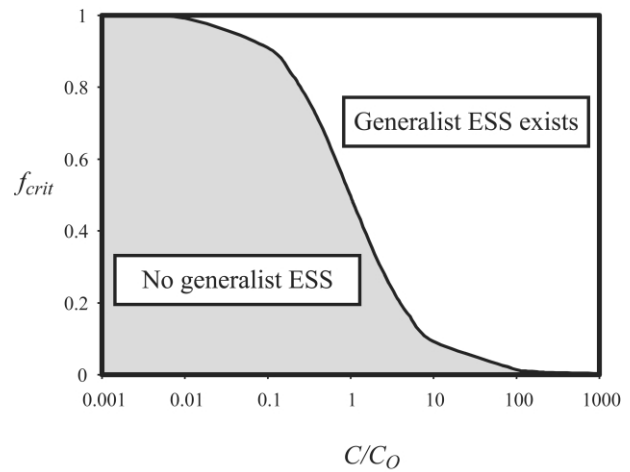


Figure 5: Relative values of C_0 and C affect the evolution of a generalist ESS when $n = 1$, based on the case where there are no underutilized pollinators. The term f_{crit} (Y-axis) represents the frequency of the focal species above which a generalist ESS exists at $\alpha_D = Cg_e$ for a given set of values of C_0 and C (X-axis, log scale).

morphism. Generally, a polymorphic strategy is favored when intermediate investment is penalized with lower overall visitation relative to investment in only one flower type or the other (figs. 1, 7). This result is significant because polymorphic populations for these floral traits are partially reproductively isolated and may be more prone to speciate (Dieckmann et al. 2003).

When a species exists at an intermediate frequency, we predict that the initial state of the population influences whether a generalist or specialist strategy evolves (fig. 6). A plant that finds itself at an intermediate frequency in a new environment is more likely to become a specialist if it already invests heavily in attracting a pollinator that is locally abundant but a generalist if it tends to attract several local pollinators or attracts a locally rare pollinator.

Discussion

Our model of the evolution of floral morphology makes a clear prediction linking local species abundance and the evolution of floral traits that influence pollinator specificity. Our results indicate that plants evolve to be pollinator specialists in communities where the focal species is relatively rare due to the increased probability that random pollinator visits result in the deposition of heterospecific pollen (Caruso and Alfaro 2000).

In communities where the focal species occurs at a high density, we found that plants evolve to be pollinator generalists because most pollinators carry conspecific pollen. In this case, there is an advantage to mutations that attract

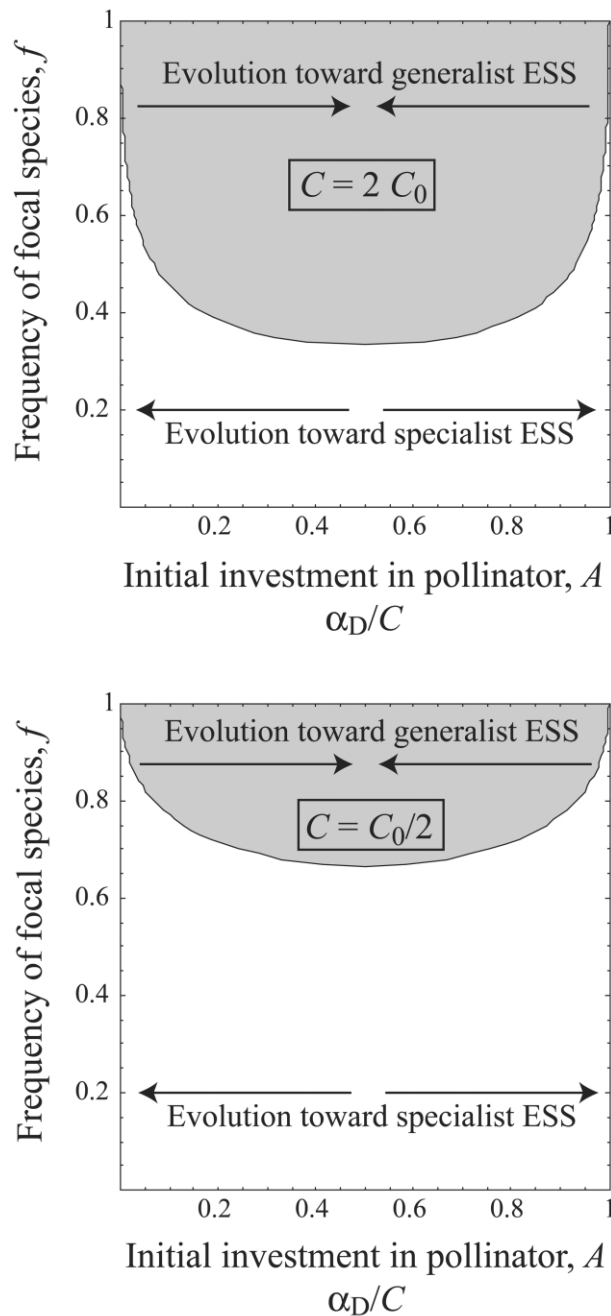


Figure 6: Focal species evolves toward a generalist or a specialist ESS depending on its frequency in the community, f (Y-axis), and the initial investment by the focal species in attracting the A pollinator, α_D/C (X-axis). We assumed that $g_e = 1/2$, $\alpha_D/g_e = \beta_D/(1 - g_e)$, and $n = 1$, in which case the generalist ESS is $\alpha_D^* = Cg_e$. The focal species is predicted to evolve toward the generalist ESS (shaded area), except where the focal species is rare or has a high initial investment in one pollinator over the other (unshaded area). Top, $C = 2C_0$. Bottom, $C = C_0/2$. A focal species evolves a generalist floral strategy over a broader parameter range when it invests more in pollinator attraction relative to other species in the community (top).

underutilized pollinators because they preferentially visit the mutant plant but are still likely to carry conspecific pollen. Generalization is also favored when plants investing in intermediate floral trait combinations receive a higher frequency of pollinator visitation ($n > 1$) and when pollinators exhibit flower constancy (app. B). Furthermore, when a generalist strategy is favored, the population is more likely to evolve generalization in the form of a polymorphism (i.e., a population with more than one type of specialist) when the trade-off between investing in two pollinators penalizes intermediate floral trait combinations. Our results suggest that this form of generalization can lead to evolutionary branching, which can lead to speciation (Dieckmann et al. 2003).

We found that in communities with an intermediate density of the focal species, multiple evolutionarily stable strategies (ESS) are possible. According to our model, in such communities specialization evolves over a broader set of conditions in a focal species that invests less in pollinator attraction than surrounding species ($C < C_0$) while generalization is more often favored in a focal species that invests more in pollinator attraction than its neighbors (figs. 5, 6). Interestingly, not all populations can reach any particular ESS, because the direction of evolution depends on the initial level of floral investment in attracting different pollinators, which indicates that the history of floral evolution affects the evolution of plant specialization to pollinators.

Most studies of plant-pollinator interactions focus on the relationship between a single plant species and its pollinator(s). As a consequence, our current understanding of how the plant community affects the evolution of generalization or specialization is underdeveloped (Olesen and Jordano 2002). Our results are distinct from the predictions of previous models in several important ways. As in the most effective pollinator principle (MEPP), we predict that when specialization is favored, floral traits should be selected to increase the plant's attractiveness to the most effective and/or abundant pollinator, but only if the species already tends to be more attractive to that pollinator. In contrast to MEPP, our model predicts that selection can drive a plant toward specialization on the least effective and/or abundant pollinator if the species already possesses traits that are attractive to that pollinator (fig. 4). Furthermore, we expect specialization to evolve primarily when the species is rare relative to other species in the community.

Interestingly, our results suggest that a species' relative abundance should be a better predictor of the degree of floral specialization versus generalization than the efficiency and/or abundance of pollinators. We found that plants should evolve to specialize on the most effective and/or abundant pollinator only when the focal species is

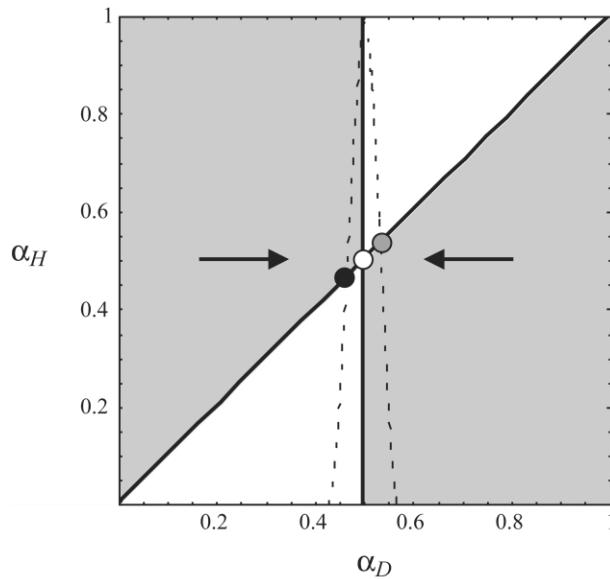


Figure 7: Phase diagram showing the parameter space under which a rare mutant that allocates α_H to attracting pollinator A (Y-axis) spreads in a resident population allocating α_D (X-axis) for the parameters $g_c = 1/2$, $C = 1$, and $f = 1$. The diagonal line indicates $\alpha_H = \alpha_D$, and the vertical solid line indicates the investment in α_D that cannot be invaded by any mutant strategy (ESS) when $n = 1$ (open circle). The two dashed lines indicate how the potential ESS shifts and the placement of the vertical line when $n \neq 1$. For $n < 1$, the potential ESS shifts toward $\alpha_D = 0$ (solid circle) and the vertical line shifts clockwise, indicating that this ESS is an evolutionary branching point. For $n > 1$, the ESS shifts toward $\alpha_D = 1$ (shaded circle) and the vertical line shifts counterclockwise, indicating convergence without branching.

rare, and even then only when the current allocation to attracting that pollinator is already reasonably high. If a species is numerically dominant, our model predicts the evolution of floral traits that are of intermediate attractiveness to all available pollinators, with the most effective/abundant pollinators being attracted more often (in proportion to their efficiency and abundance). For example, when a plant species that is numerically dominant in its community is visited by both bees that prefer pink corollas and hummingbirds that prefer red corollas, we predict corolla color will evolve to some intermediate trait combination determined by the effectiveness and abundance of the two pollinators. Conversely, where this same plant species is rare we predict specialization on the corolla color that is initially most effective in attracting pollinators and transferring pollen to conspecifics.

The ecological correlates of plant-pollinator specialization and generalization are topics of long-standing interest. Some recent studies (e.g., Olesen and Jordano 2002; Vázquez and Aizen 2003, 2004) use data from plant-pollinator networks to look for patterns in the degree of

specialist and generalist interactions across communities. In addition, network theory is being used to determine whether plant-pollinator communities exhibit the same topologies as other related types of networks (e.g., Bascompte et al. 2003; Jordano et al. 2003). Most ecological networks tend to follow a scale-free topology, indicating that a large number of species with few interactions coexist with relatively few species that have many interactions (generalists). In contrast, Jordano et al. (2003) report that the cumulative distribution of links (number of other species with which a plant or pollinator interacts) in plant-pollinator networks tends to lack many of the super-generalists predicted by a scale-free topology. Our model predicts that the lack of generalist plants should be particularly striking in species-rich communities.

Correspondingly, Olesen and Jordano (2002) report an exponential decline in the degree of connectance (i.e., the fraction of observed interactions relative to the total possible) with increasing species richness, which they interpret as evidence for increased specialization in species-rich communities. This is consistent with our model prediction that plant species in communities with high species richness should evolve toward specialization. However, Kay and Schemske (2004) point out that some of these results need to be interpreted cautiously because Olesen and Jordano's (2002) index of connectance is confounded by network size. Furthermore, Kay and Schemske (2004) point out that the presence or absence of observed interactions is a coarse measurement and tends to be a poor index of specialization.

In a comparative study of several datasets of pollen limitation and species richness, Vamasi et al. (2006) report that pollen limitation increases with angiosperm species richness within a community. They attribute this result to increased competition for pollinators in species-rich communities. Moreover, they found that plant-pollinator specialization is positively correlated with local species richness, which is consistent with our key prediction. Thus, existing studies provide some support for the predictions of our model. However, we feel that more direct tests are warranted, for example, experiments that vary the abundance of a focal plant species and examine the relative fitness of floral variants.

The present model also has implications for predicting the establishment of introduced plant species. The natural enemy escape hypothesis purports that an invasive plant should be able to invest more resources into traits such as pollinator attraction because in its new habitat it has escaped from the requirement of investing in antiherbivory defenses (Myers and Bazely 2003). Our model predicts that plants with more resources invested in pollinator attraction (higher C) should more easily evolve to be pollinator generalists. Indeed, the invasive species *Impatiens glandulifera* has been

shown to exert increased competition for pollinators on coflowering plants in the vicinity (Chittka and Schurkens 2001). The findings suggest that it would be worth exploring empirically whether plant species such as *I. gladiifera* with increased allocation to pollinator attraction also have a greater tendency to evolve generalization.

Our model demonstrates that a plant's relative abundance may play an important role in the evolution of floral traits that influence pollinator specificity. Furthermore, we determined that a locally abundant species evolves toward a polymorphic population of specialists when there is a strong trade-off between attracting different pollinators ($n < 1$), suggesting that a plant's local abundance plays a role in determining the direction of floral trait evolution and the potential for speciation. These results highlight the importance of considering plant local abundance when constructing hypotheses and experiments to explore the role of pollinator preference in floral trait evolution.

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APPENDIX A

Visitation Sequence

To prove that the model applies regardless of the number of visits, we consider a pollinator that makes v visits after picking up pollen from a focal plant and deposits a proportion, $f[x]$, at the x th flower stop after the pollen grains are picked up. The overall probability of pollen transfer from a KK to another KK individual (table 2) is

$$P[KK \rightarrow KK] = g\gamma_A \frac{\alpha_D f D}{T_A} \times \left(f[1] \frac{\alpha_D f D}{T_A} + f[2] \frac{\alpha_D f D}{T_A} + \dots + f[v] \frac{\alpha_D f D}{T_A} \right) \quad (\text{A1})$$

(see "The Model" section of the main text for a description of terms). The term $f[x]$ represents a probability distribution, where by definition $\sum_{x=1}^v f[x] = 1$. Thus, assuming that the proportion of pollen deposited, $f[x]$, does not depend on the sequence of flowers visited, the probability distribution factors out of equation (A1). This indicates that the results of this article hold regardless of whether the focal species is the next plant visited or the x th plant visited, as long as pollen deposition rates are independent of which exact flowers are visited.

APPENDIX B

Flower Constancy

Here we examine the effects of flower constancy on the evolution of specialist and generalist flowers. Flower constancy is "a propensity to visit the same type of flower as last visited irrespective of the value of alternatives" (Waser 2001, p. 322; see also Chittka et al. 1999). We assumed that the first plant visited was chosen according to the relative preferences described in table 2 but that the second plant visited was, with probability ω , guaranteed to be of the same species as the first flower, with visitation to a particular genotype being proportional to the genotype's frequency as well as its attractiveness. With probability $1 - \omega$, the second plant was visited as outlined before (i.e., according to the probabilities outlined in table 2). Adding flower constancy to equations (3)–(6), the leading eigenvalue became

$$\lambda_c = \frac{(1 - \omega) f \left\{ \frac{g_e \alpha_H \alpha_D}{[f \alpha_D + (1-f) \alpha_O]^2} + \frac{(1-g_e) \beta_H \beta_D}{[f \beta_D + (1-f) \beta_O]^2} \right\}}{\nu} + \frac{\omega \left\{ \frac{g_e \alpha_H}{[f \alpha_D + (1-f) \alpha_O]} + \frac{(1-g_e) \beta_H}{[f \beta_D + (1-f) \beta_O]} \right\} + O(\epsilon^2)}{\nu}, \quad (\text{B1})$$

where

$$\nu = (1 - \omega) f \left\{ \frac{g_e \alpha_D^2}{[f \alpha_D + (1-f) \alpha_O]^2} + \frac{(1-g_e) \beta_D^2}{[f \beta_D + (1-f) \beta_O]^2} \right\} + \omega \left\{ \frac{g_e \alpha_D}{[f \alpha_D + (1-f) \alpha_O]} + \frac{(1-g_e) \beta_D}{[f \beta_D + (1-f) \beta_O]} \right\}.$$

Here we focus on the linear trade-off curve ($n = 1$) and explore how conditions allowing for the existence of a convergence stable generalist strategy are altered by flower constancy. As in the main text, we analyze two cases: in the first case the attractiveness of the flowers in the community matches the pollinators' effective abundance (no underutilized pollinator); in the second, the plants in the community are highly specialized to one of the pollinators (one pollinator is underutilized).

No underutilized pollinator. An analysis of the derivative $d\lambda_c/d\alpha_H$ indicates that when the flowers of the other species match the effective abundance of the various pollinators (i.e., $\alpha_O/g_e = \beta_O/[1 - g_e]$), a potential ESS exists at $\alpha_D^*/C = g_e$. Again, the generalist strategy is convergence stable as long as f is greater than a critical value, $f_{crit,\omega}$, where $df_{crit,\omega}/d\omega$ is always negative. Thus, a stable generalist strategy is more likely to occur with increasing flower constancy. Furthermore, we found that a convergence stable generalist strategy exists regardless of the abundance of the focal species, f , as long as $\omega > 1/2$.

An underutilized pollinator. When the other species is a specialist on pollinator B (i.e., $\alpha_O = 0$), we found that $\alpha_D^* = C$ is always a potential ESS. However, when flower constancy, ω , is sufficiently strong, $\alpha_D^* = C$ becomes convergence unstable, and the system converges on a generalist strategy. When the abundance and efficiency of the A pollinator (g_e) is less than $g_{e,crit} = [C_O\omega(1 - f) + Cf]^2/[C_O(2 - \omega)(1 - f) + Cf]^2$, the generalist strategy is guaranteed to be convergence stable. Increasing ω makes this condition easier to satisfy, and therefore the generalist strategy is more likely to be convergence stable when ω is large. Nevertheless, when the focal species is very rare (f near 0), evolution always proceeds away from the generalist strategy, regardless of the strength of flower constancy.

In summary, increasing the strength of flower constancy, ω , tends to increase the parameter range over which the system converges on a generalist strategy. Essentially, increasing flower constancy acts in a manner similar to increasing a plant species' local abundance by reducing the probability of receiving incompatible pollen.

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