

When can two plant species facilitate each other's pollination?

Tracy S. Feldman, William F. Morris and William G. Wilson

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Facilitation occurs when an increase in the density of one species causes an increase in the population growth rate or the density of a second species. In plants, ample evidence demonstrates that one species can facilitate another by ameliorating abiotic conditions, but the hypothesis that pollination facilitation – in which the presence of one flowering species increases pollinator visits to a second species – can also occur remains controversial. To identify the necessary conditions for pollination facilitation to occur, we constructed population models of two plant species that share the same pollinator and compete for establishment sites, and we assumed that heterospecific pollen can interfere with successful seed set. We found that facilitation for pollination occurs only when the pollinator visitation rate is an initially accelerating function of the combined numbers of flowering plants of both species in a patch. The presence of a second species can allow populations of a focal species either to persist for a longer amount of time before going extinct ("weak facilitation") or to persist indefinitely at a stable equilibrium density ("strong facilitation"). When only a single plant of either species can occupy a site, the plant species with the higher initial density can experience strong facilitation but will eventually out-compete the other species. However, when site occupancy was not exclusive, strong facilitation sometimes led to coexistence of the two species. Increasing the extent of pollen carryover increased the range of initial population densities leading to strong facilitation. In light of our theoretical results, we discuss the apparent rarity of pollination facilitation in nature.

T. S. Feldman, W. F. Morris and W. G. Wilson, Biology Dept, Duke Univ., Durham, NC 27708, USA (tsf@duke.edu).

Because most plants depend upon the same basic set of resources (i.e. light, water, and nutrients), interspecific competition between plant species is common. However, ecologists have increasingly come to recognize that plant species may also have positive effects on one another. For example, plants that arrive early in a primary successional sequence often improve soil conditions for later-arriving plant species (Wood and del Moral 1987, Williams 1990), a process Connell and Slatyer (1977) termed "facilitation". In desert and grassland environments, shading by so-called "nurse plants" may ameliorate harsh abiotic conditions, facilitating the recruitment of other plant species (Franco and Nobel 1989, Valiente-Banuet and Ezcurra 1991, Callaway 1992, Suzán et al. 1994, Tewksbury et al. 1998, Tewksbury and Lloyd 2001,

Nobel and Bobich 2002). In fact, there are myriad ways that one plant species may benefit another by altering environmental conditions (reviewed by Callaway 1995, Callaway and Walker 1997). In addition, defended plant species may protect less-defended species growing in their midst against attack by herbivores (Tahvanainen and Root 1972, Atsatt and O'Dowd 1976, Hay 1986, Pfister and Hay 1988, Hjaltnén et al. 1993, Tuomi et al. 1994). In some cases, these positive effects may be strong enough to outweigh any negative effects of competition, resulting in a net beneficial effect of one plant species on another.

For animal-pollinated plants, another way that one plant species could facilitate another is by increasing the number of pollinator visits received by the second

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species, thereby increasing its reproductive rate. Enhanced visitation might result if the presentation of flowers by the first species attracts pollinators to the neighborhood of the second species. The potential for pollination facilitation to occur was noted over two decades ago (Schemske 1981), but only a few examples of this phenomenon have yet been observed (Schemske 1981, Rathcke 1988, Lavery 1992). Does this scarcity of examples imply that the ecological conditions required for pollination facilitation to occur are so stringent as to make the phenomenon relatively rare in nature? In this paper, we use mathematical models to shed light on the ecological requirements for pollination facilitation to occur.

One factor that should play an important role in determining whether pollination facilitation is possible is how pollinators adjust the number of floral visits they make in an area to the total number of flowers of both species in that area. If the number of pollinator visits increases linearly as the combined number of flowers increases (and if pollinators do not discriminate between the two plant species), then the increased number of visits is exactly compensated for by the increased number of flowers. This compensation means that as the number of flowers of one species increases, the mean number of visits each flower of the second species will receive should not increase. On the other hand, if the number of visits increases in an accelerating fashion as total flower number increases, then one or both plant species may receive more visits per flower when both species are present. Hence, pollination facilitation occurs. While this argument sounds reasonable, no theoretical study has clearly demonstrated mathematically that a disproportionate increase in visit rate as total flower number increases is required for facilitation to occur. In a graphical model, Rathcke (1983) shows the number of pollinator visits increasing in an accelerating fashion as the total number of flowers increases, but doesn't explicitly discuss whether an accelerating pattern is necessary. Goulson (1994) comes closest to articulating the requirement for a disproportionate increase in visitation as the number of flowers increases, but states that visitation to the more common flowering species must increase as its density increases. Goulson's model makes the somewhat unrealistic assumption that pollinators always behave optimally, completely avoiding the rarer plant species until the reward level in the more common flowers drops below the density of rewards in the rarer flowers. In this paper, we demonstrate that facilitation can occur when the pollinator's visitation rate accelerates (at least initially) as the total number of plants (or flowers) in a patch increases, whereas facilitation does not occur with a strictly saturating visitation pattern.

Previous models of pollination facilitation have been limited in two other regards. First, they have not taken a

population perspective on the question of pollination facilitation. That is, they have asked whether the presence of a second species will increase the rate of pollinator visitation to a focal species, but not whether increased pollination will elevate the growth rate or prolong the persistence of the focal population. In this paper, we define pollination facilitation as an increase in the population growth rate of one species caused by an increase in pollinator visitation due to the presence of a second flowering plant species. Using population models, we show that two species may facilitate each other's pollination, and yet be unable to coexist in the same patch. The second limitation of previous models (Bobi-sud and Neuhaus 1975) is that they do not account for the fact that plant species may compete for other resources even as they facilitate one another's pollination. By incorporating both pollinator visitation and competition for space into our models, we ask whether enhanced pollinator visitation caused by the presence of another species is strong enough to outweigh the negative effects of interspecific competition for space. Moreover, our models account for the negative effect of pollen loss to heterospecific flowers.

In summary, in this paper we used differential equation models describing a system of two self-incompatible species of plants that compete for space but share the same pollinator to answer the following questions:

- 1) is an acceleration in the pollinator visitation rate with an increase in the amount of floral resources in a patch necessary for pollination facilitation to occur?
- 2) when will two flowering plant species that facilitate each other's pollination but also compete for space be able to coexist locally, and when will facilitation be followed by competitive exclusion?
- 3) to what degree is the opportunity for pollination facilitation influenced by the loss of pollen to plants of the wrong species?

Methods

Derivation of the model

Seed production

We model two self-incompatible plant species and a pollinator population that visits the flowers of both plant species. We consider a patch of habitat that encompasses K sites, each of which can support at most a single individual of a given plant species. We explore interspecific competitive scenarios ranging from strong, in which a site occupied by one species cannot be colonized by the other to weak, in which individuals of the two species can co-occur in the same site. P_1 and P_2 represent the number of sites occupied by each species. Pollinators moving across the landscape may choose to visit the focal patch if it contains a sufficient amount of floral resources. Let N represent the number of sites,

distributed randomly among the K sites, that pollinators visit within the patch per unit time. The expected number of visits per site per unit time is thus N/K . To reflect pollinators that respond to the total number of flowers in the patch, we will allow N to depend upon $P_1 + P_2$. We assume that pollinators do not discriminate between the two plant species. Because both plant species are self-incompatible, a pollinator visit can be successful and effect seed set only if the pollinator is carrying pollen from another individual of the same plant species. Initially we assume that a pollinator will be carrying the appropriate pollen only if its last visit was to the same plant species; later we relax this assumption and allow more extensive pollen carryover. Because pollinators visit both plants, the total number of visits is limited, and a preceding visit to the ‘wrong’ species will prevent successful pollination, the two plants compete for the services of the pollinator.

Given the assumptions above, the expected number of successful, or good visits that each individual of species i receives is equal to:

$$\phi_i = \frac{N}{K} \left[\frac{P_i}{P_1 + P_2} \right] \quad (1)$$

where $P_i/(P_1 + P_2)$ is the probability that the preceding visit was to species i . We assume the actual number of good visits each individual of species i receives is drawn from a Poisson distribution with mean ϕ_i . Hence the probability that an individual of species i receives one or more good visits is $1 - e^{-\phi_i}$. We assume that if a plant of species i receives one or more good visits in a time interval, it will produce seeds at a fixed rate S_i ; specifically, we set the seed production rate of species 1 equal to $S_1(1 - e^{-\phi_1})$, and similarly for species 2. We assume the seeds each plant produces are distributed randomly among the K sites without regard to whether a site is presently occupied, so that the rate at which each individual of species i contributes seeds to each site equals $S_i(1 - e^{-\phi_i})/K$.

Competition for space

In addition to competing for pollinators, the two plant species also compete for establishment sites. We modeled competition for space using a modified Lotka–Volterra competition model. Let $0 \leq \alpha_{ij} \leq 1$ represent the ability of an established individual of species j to prevent the site it occupies from being colonized by a newly arriving propagule of species i . For example, if $\alpha_{12} = 1$, then individuals of species 1 cannot establish in sites occupied by species 2; if $\alpha_{12} = 0$, then an established individual of species 2 does not impede colonization of the site by species 1. At a given time, the fraction of sites that are ‘‘available’’ for colonization by species 1 (i.e. that are either empty or occupied by species 2, but weighted by

the ability of species 2 to impede colonization by species 1) is then $1 - (P_1 + \alpha_{12}P_2)/K$; similarly, the fraction of sites available for species 2 is $1 - (P_2 + \alpha_{21}P_1)/K$. By setting $\alpha_{12}, \alpha_{21} > 0$, we explore the conditions under which the positive effect of pollination facilitation outweighs the negative effect of competition for space. Finally, let the rates at which established individuals of the two species die equal δ_1 and δ_2 . Putting all these pieces together yields the model

$$\frac{dP_1}{dt} = \frac{S_1}{K} P_1 [1 - e^{(-\phi_1)}] \left[1 - \frac{P_1 + \alpha_{12}P_2}{K} \right] - \delta_1 P_1 \quad (2a)$$

$$\frac{dP_2}{dt} = \frac{S_2}{K} P_2 [1 - e^{(-\phi_2)}] \left[1 - \frac{P_2 + \alpha_{21}P_1}{K} \right] - \delta_2 P_2 \quad (2b)$$

In this model, it is mathematically possible for birth rates (i.e. the first terms on the right hand side of Eq. 2a and 2b) to become negative at high densities for some values of the competition coefficients in the range $0 \leq \alpha_{12}, \alpha_{21} \leq 1$. To prevent this biologically meaningless result, we set any negative birth rates to zero when solving the equations numerically. Moreover, because we are primarily interested in the behavior of this system at initially low densities, the possibility of negative birth rates at high densities is unlikely to affect our conclusions.

Pollinator visitation as a function of floral density

As noted in the introduction, we explore the consequences of two ways that pollinators might adjust their visitation rates to the total number of plants in a patch.

Saturating response to plant number

Many empirical studies have demonstrated that the rate of pollinator visitation to a patch is in fact an increasing function of the number of plants (or flowers) in the patch (Kunin 1993, 1997, Groom 1998). However, because the total number of pollinators is limited by other factors (e.g. nest sites, predation, etc.) and because floral visits involve a handling time, the total visitation rate N is likely to saturate as plant numbers reach high levels. Therefore, we chose to first model pollinator visitation as a saturating function of the total number of plants in the patch (Fig. 1; cf. the type II functional response of Holling 1959). The visitation rate depends upon the total number of plants because we assume pollinators do not discriminate among plant species. Thus, in the saturating case:

$$N = \frac{N_{\max}(P_1 + P_2)}{\beta + (P_1 + P_2)} \quad (3)$$

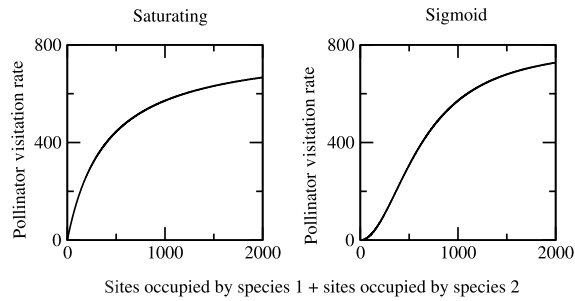


Fig. 1. Two patterns by which the pollinator visitation rate might respond to the total number of plants in a patch; left panel: saturating; right panel: sigmoidal.

where N_{\max} is the maximum visitation rate and β is the total number of plants at which the visitation rate equals one half its maximum value. Replacing Eq. 3 into Eq. 1 gives the following equations:

$$\frac{dP_1}{dt} = \frac{S_1}{K} P_1 \left\{ 1 - \exp \left[-\frac{N_{\max} P_1}{K(\beta + P_1 + P_2)} \right] \right\} \times \left[1 - \frac{P_1 + \alpha_{12} P_2}{K} \right] - \delta_1 P_1 \quad (4a)$$

$$\frac{dP_2}{dt} = \frac{S_2}{K} P_2 \left\{ 1 - \exp \left[-\frac{N_{\max} P_2}{K(\beta + P_1 + P_2)} \right] \right\} \times \left[1 - \frac{P_2 + \alpha_{21} P_1}{K} \right] - \delta_2 P_2 \quad (4b)$$

Sigmoidal response to an increase in plant number

If pollinators tend to avoid a patch that harbors few plants, but increasingly switch to using it as the number of plants increases, the visitation rate will initially accelerate as plant number increases. If the visitation rate also saturates as plant number becomes high, the visitation rate will be a sigmoidal function of plant number (Fig. 1; a Holling type III functional response). In general, this type of visitation response may arise if foragers use an area-restricted search strategy, in which individuals move shorter distances or increase their turning angles after encountering resources (Murdoch 1969, Lode 2000, but see Heimpel and Hough-Goldstein 1994). Many studies of pollinator behavior have demonstrated evidence for area-restricted searching in both invertebrate (Pyke 1978, Heinrich 1979, Zimmerman 1982, Waddington 1983, Zimmerman and Cook 1985, Zimmerman and Pyke 1986, Keasar et al. 1996) and vertebrate (Wolf and Hainsworth 1990) pollinator species. In the sigmoidal case:

$$N = \frac{N_{\max} (P_1 + P_2)^\sigma}{\beta + (P_1 + P_2)^\sigma} \quad (5)$$

where $\sigma > 1$. Here, we examine the case of $\sigma = 2$. If $\sigma = 1$, then this expression collapses to the saturating response (Eq. 3), and the full model equations (not shown) collapse to Eq. 4a and 4b.

Model analysis

The isoclines are found by setting the right hand sides of Eq. 2 to zero and solving for the value of P_2 as a function of P_1 . Because Eq. 2 is transcendental, we used numerical methods to find the roots. Equilibria occur where the isoclines cross. We determined the stability of equilibria using phase-plane methods.

Results

Similarities between the two models

The isoclines for the models with saturating and sigmoidal pollinator visitation responses are similar in many respects (Fig. 2). For example, in both models the isocline for species 1 is a hump-shaped curve; dP_1/dt is positive below this isocline and negative above it.

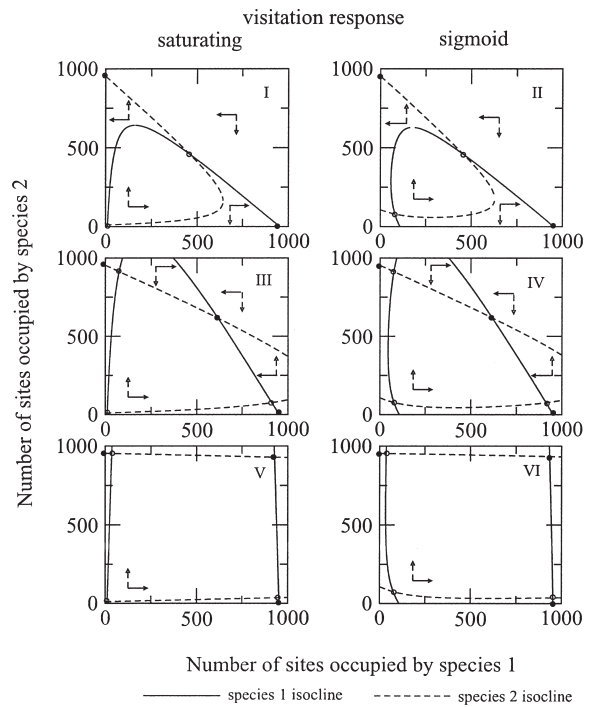


Fig. 2. Isoclines for the saturating (I, III, V) and sigmoidal (II, IV, VI) pollinator visitation models for three levels of competition for space. Competition coefficients: I and II: $\alpha_{12} = \alpha_{21} = 1.0$; III and IV: $\alpha_{12} = \alpha_{21} = 0.5$; V and VI: $\alpha_{12} = \alpha_{21} = 0$. Other parameter values: $K = 1000$, $S_1 = S_2 = 500$, $N_{\max} = 800$, $\beta = 400$, $\delta_1 = \delta_2 = 0.01$.

Similarly, the isocline for species 2 defines a region within which dP_2/dt is positive. In both models, when competition for space is intense (i.e. $\alpha_{12} = \alpha_{21} = 1$; Fig. 2: I and II), there is no stable equilibrium at which both plant species will persist in the patch. Depending upon the initial conditions, the system will go entirely to plant species 1, entirely to species 2, or to complete extinction of both plants. Extinction occurs when the total number of plants in the patch is initially low, so that few pollinators are attracted to the patch and seed production is not sufficient to compensate for the death of established individuals. Thus both plant species exhibit an Allee effect (Allee 1931). When competition for space is moderate (Fig. 2: III and IV) or absent (Fig. 2: V and VI), then in both models a stable equilibrium exists at which the two plant species coexist. Nevertheless, even when this equilibrium does exist, if the patch initially contains many individuals of one species but few individuals of the other, the rare species will be driven extinct. This is because most visits to the rare species will be immediately preceded by a visit to the common species, so that successful pollination of the rare species will be low.

Facilitation

The saturating and sigmoidal visitation models do, however, differ in one important respect. In the saturating model, the slope of the species 1 isocline is positive at its lower intersection with the P_1 axis (Fig. 2: I, III, and V). Similarly, the isocline for species 2 has a positive slope at its lower crossing of the P_2 axis (Fig. 2: II, IV, and VI). In contrast, these slopes are both negative in the sigmoidal visitation model. A negative slope indicates that facilitation is possible, for the following reason. For species 2 to facilitate species 1 when species 1 is at low density, there must exist a threshold density of species 2 below which the density of species 1 declines and above which it increases. The negative slope of the species 1 isocline assures that this will be the case. For example, consider how the growth rate of species 1 changes along a transect parallel to the P_2 axis starting at $P_2 = 0$ and a value of P_1 just to the left of the lower intersection of the species 1 isocline with the P_1 axis. Initially, dP_1/dt is negative, but once the isocline is crossed, it becomes positive. The isocline represents the threshold density of P_2 required for P_1 to increase. This graphical argument indicates that facilitation will be possible if the pollinator's visitation response to the total number of plants in a patch is sigmoidal, but not if it is saturating. In the appendix, we prove that facilitation is not possible in the saturating case, and that it is possible in the sigmoidal case.

In addition to the fact that the sigmoidal model allows facilitation but the saturating model does not, there are two other differences between the two models. First, for

comparable values of the other model parameters, the region where both species are increasing is smaller for the sigmoidal than for the saturating visitation response. Second, the Allee effect threshold is higher in the former, indicating that extinction will occur over a wider range of initial conditions.

Strong vs weak facilitation

Here, we define two types of facilitation between species. Strong facilitation occurs when the presence of one species enables a second species to increase from low numbers and persist in the system indefinitely, whereas when starting from the same initial number in the absence of the first species, the second species would go extinct. Weak facilitation occurs when, in the presence of the first species, the second species persists longer before going extinct than it would in isolation. We used Runge–Kutta numerical integration to determine which type of facilitation occurs in the model with a sigmoid pollinator visitation response.

When competition for space is strong (i.e. $\alpha_{12} = \alpha_{21} = 1$), facilitation is (with one unrealistic exception) weak. In Fig. 3 (I and II), we start species 1 at a single initial number of plants (100) but we vary the initial number of species 2. When species 2 is absent (case a), species 1 goes extinct. An initially low number for species 2 (case b) elicits insufficient pollinator visitation, and although species 1 persists longer than in the absence of species 2, both species go extinct. When the initial density species 2 is higher but not as high as the initial density of species 1 (cases c, d, and e), species 1 is facilitated by, but eventually out-competes, species 2. Only if the two species start with sufficiently high but identical initial densities (case f) – an unlikely case in nature – do they both persist. However, in this case, the system approaches an unstable, saddle-point equilibrium (the upper unstable equilibrium in Fig. 2, I and II); any forces that displace the system from this equilibrium (except for displacements that land the system precisely along the stable manifold) will result in the extinction of one of the two species. Lastly, if there are initially more plants of species 2 than species 1 (case g), species 1 will be out-competed by species 2. In summary, when facilitation is weak, whichever species has the higher initial number of plants out-competes the other species.

If competition for space is weaker (i.e. $\alpha_{12}, \alpha_{21} < 1$), both weak and strong facilitation can occur (Fig. 3, III and IV). At the parameter values in Fig. 3 (I and II), species 1 still goes extinct in the absence of species 2 (case a). In case b, both species ultimately go extinct, but species 1 persists for longer than it does when competition is stronger. In cases c and d, species 2 is driven extinct by species 1, but in all other cases, both species coexist at a stable equilibrium (Fig. 2: IV and VI). Thus,

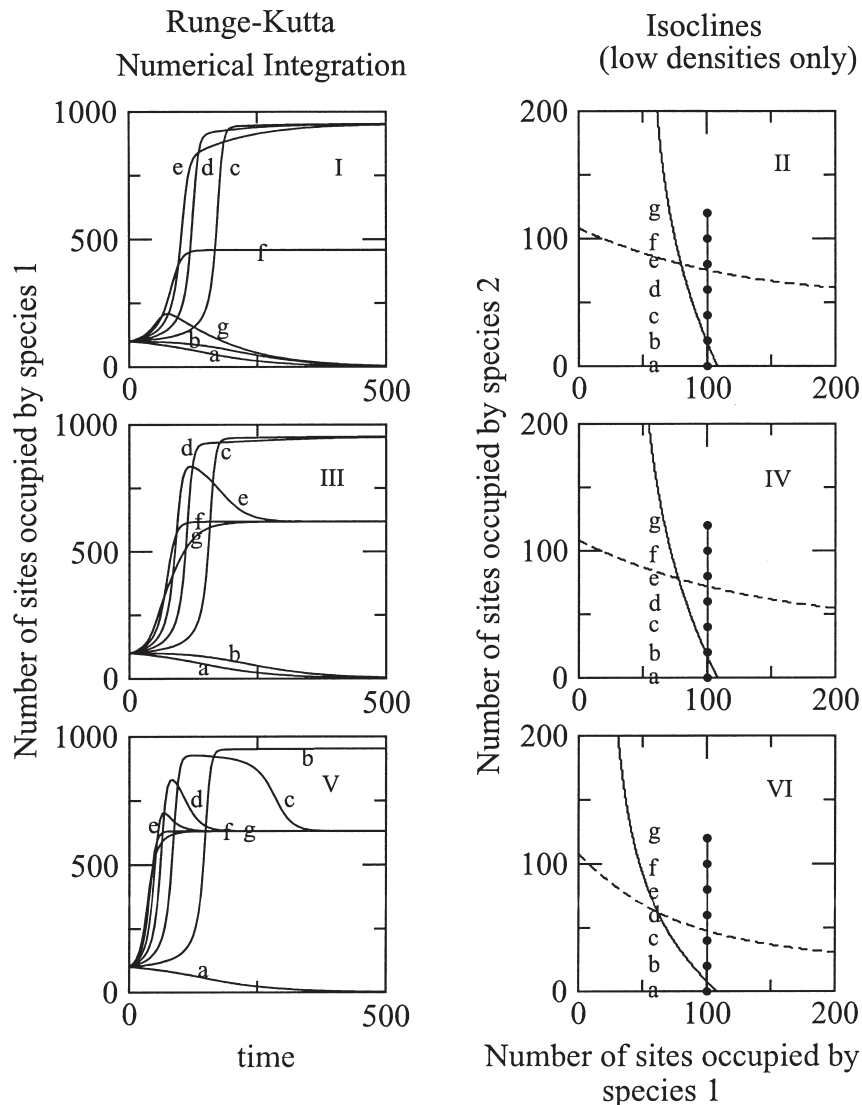


Fig. 3. I, III, and V denote population trajectories predicted by the sigmoidal visitation model for species 1 starting at low numbers as the initial number of species 2 increases, under strong competition for space (I and II; $\alpha_{12} = \alpha_{21} = 1.0$), or weak competition for space (III-VI; $\alpha_{12} = \alpha_{21} = 0.5$). II, IV, and VI denote low density regions of isoclines in Fig. 2. In all cases, initial density for species 1 was 100 sites, and initial densities for species 2 were: a) 0, b) 20, c) 40, d) 60, e) 80, f) 100, or g) 120 sites occupied (denoted as the dots on II, IV, and VI; the vertical line denotes the starting population size of species 1). Other parameter values as in Fig. 2. V. and VI. Population trajectories and isoclines predicted by the sigmoidal visitation model, but with more extensive pollen carryover ($\Psi = 2$).

in this simple two-species system, there are two conditions that must be met for mutual strong facilitation to occur:

- 1) Pollinators must respond to resources with a sigmoidal response (i.e. at low densities, visitation must increase at an accelerating rate as floral density increases).
- 2) Interspecific competition for space must be sufficiently weak that the two plant species have the potential to coexist (i.e. interspecific competition must be weaker than intraspecific competition).

For weak facilitation to occur, the system needs to meet only the first criteria.

More extensive pollen carryover

Finally, we extended the model to examine the case in which pollinators may carry pollen for more than one visit. Denote Ψ as the number of subsequent visits over which pollinators retain pollen. That is, a visit to species 1 will result in successful pollination if any of the preceding Ψ visits was to species 1. If $P_2/(P_1 + P_2)$ is the probability that a given visit is to species 2, then:

$$\begin{aligned}
 & \text{(Probability of 1 or more visits to species 1 in preceding } \Psi \text{ visits)} \\
 &= 1 - \text{(Probability of no visits to species 1 in } \Psi \text{ visits)} \\
 &= 1 - \left(\frac{P_2}{P_1 + P_2} \right)^\Psi \quad (6)
 \end{aligned}$$

In the case where $\Psi = 1$, Eq. 6 collapses to $P_1/(P_1 + P_2)$, which is the probability of a “good” visit in Eq. 1. We substituted expression (6) with $\Psi = 2$ into Eq. (1) in place of $P_1/(P_1 + P_2)$, substituted this new expression for ϕ_i into the sigmoidal visitation model, and determined the isoclines numerically. Compared to the case of more limited pollen carryover, the region where the population growth rates of both species are positive is larger, the Allee effect thresholds are lower, and the slopes of the isoclines at low numbers are more negative, indicating greater opportunities for facilitation (Fig. 3, VI).

Fig. 3V shows population trajectories from Runge–Kutta numerical integration of the model with $\Psi = 2$. We used the same initial population sizes as before. In case a (absence of species two), species one goes extinct. In case b, species one out-competes species two. In all other cases, both species co-exist. Thus, facilitation occurs over a wider range of initial population densities with increased pollen carryover.

Discussion

Our model shows that one species of flowering plant can facilitate the pollination of another species and thereby increase its population growth rate, provided that pollinator visitation responds in an initially accelerating fashion to the number of plants in a patch. Strong facilitation occurs when competition coefficients are less than 1, and weak facilitation occurs when competition coefficients are equal to 1 (competitive displacement). In addition, increasing the number of visits over which pollinators carry pollen increases the range of initial population sizes over which facilitation occurs. With a sigmoid visitation response, the Allee effect threshold density (below which populations go extinct) increases, because pollinators do not respond to lower plant densities. Increased pollen carryover decreases this threshold because it causes more visits to be effective, which is especially important when plant numbers (and therefore pollinator visitation rates) are low. In the following paragraphs, we review caveats about our model, highlight advantages of our approach, and discuss implications of our results for how often and under what conditions we should expect to see pollination facilitation in nature.

Three important assumptions underlie our results. The first assumption is that pollinators do not distinguish between the two plant species either when deciding whether to enter a patch, or when choosing which individuals to visit once they have entered the patch. Whether this is the case may depend upon whether the flowers of the two species are perceived as similar by the pollinators, whether the pollinators are generalists, and whether the pollinators exhibit floral constancy (i.e. whether they are more likely to revisit the last plant

species visited, Bobisud and Neuhaus 1975). If pollinators are attracted to a patch by total flower number but then exhibit floral constancy, facilitation may be easier to achieve than our models indicate (assuming both species are visited by some individual pollinators).

The second assumption of our models is that spatial structure can safely be ignored. Spatial arrangement of patches and arrangement of plants within patches may influence whether or not facilitation occurs. Among patches, relative isolation of a patch may influence pollinator visitation response – more isolated patches may receive fewer visits (Groom 1998). Within a patch, plant species may be interspersed or clumped relative to one another. Clumping of individuals within a species may make facilitation more likely, by inducing behavioural floral constancy on pollinators that move between nearest neighbors during foraging bouts (as in Campbell 1985, Fenster 1991, Karron et al. 1995).

The third assumption of our models is that when pollen is carried for more than one visit, heterospecific pollen does not decrease plant siring success of subsequently deposited conspecific pollen, either by clogging stigmas (Waser and Fugate 1986) or by usurping ovules. The greater the “pollen precedence effect”, the more the results for this modified version of the pollen carryover model would be similar to those of the original model, in which only the immediately preceding visit can effect pollination.

In this paper, we take a population perspective, allowing us to model population-level consequences (i.e. change in persistence time or population growth rate) of changes in the pollinator visitation rate. Our model accounts for the Allee effect inherent in obligate pollination mutualisms involving self-incompatible plants (e.g. Soberon and Martinez Del Rio 1981, Ferdy et al. 1999). The Allee effect has been demonstrated empirically in a few plant-pollinator systems (Lamont et al. 1993, Groom 1998). Also, our results demonstrate that facilitation among plant species does not inevitably lead to coexistence, especially when competitive displacement is possible. If this is the case, then under some circumstances, one species facilitating another may even bring about its own competitive displacement from a patch. However, even if coexistence is impossible, one species may prolong the population persistence of the other species (i.e. weak facilitation). Several theoretical studies have demonstrated the importance of pollinator visitation-response in shaping the population dynamics of plant–pollinator systems (Soberon and Martinez Del Rio 1981, Ingvarsson and Lundberg 1995). However, these models did not examine effects of a sigmoid pollinator response on these systems. In addition, models of competition for pollination (Levin and Anderson 1970, Goulson 1994, Ishii and Higashi 2001) did not incorporate saturating or sigmoidal responses of pollinator visitation to floral density.

Our results have important implications for persistence of small or sparse populations. If pollinators respond in an accelerating fashion to patches of floral resources, then plant populations in degraded or fragmented habitat or newly established plant populations may be more likely to persist if other plant species bloom nearby. Thus, populations may be more likely to persist at smaller sizes or at lower densities in the presence of co-occurring plants than in their absence.

Few empirical studies have demonstrated pollination facilitation (Schemske 1981, Laverty 1992, Lamont et al. 1993). While other types of facilitation (e.g. nurse plant effects) involve direct effects of one plant species on another, pollination facilitation involves a third species (the pollinator), which may make conditions under which it occurs more restrictive. Thus, pollination facilitation may be harder to detect. However, many studies document associational plant refuges, which occur when palatable plant species gain protection from herbivores when growing in association with unpalatable plants (Tahvanainen and Root 1972, Atsatt and O'Dowd 1976, Hay 1986, Pfister and Hay 1988, Hjältén et al. 1993). Although this type of facilitation can also be mediated through a third species (the herbivore), herbivore damage to palatable plant species need only decrease as the density of nearby unpalatable plant species increases. Thus, the functional form of herbivore responses resulting in associational plant refuges is likely to be less restrictive than the functional form of pollinator responses resulting in facilitation (i.e. a sigmoidal pollinator response).

It may be that the sigmoid pattern of visitation response is rare. Few studies have actually measured the visitation response of pollinators to increasing plant density (Kunin 1993, Sih and Baltus 1987). To test for a sigmoidal visitation response, researchers must quantify how visitation rate of all effective pollinators increases as plant density increases. This is not the same as measuring how the visitation rate (i.e. the number of flowers visited per unit time) of individual pollinators increases with plant density (Pyke 1978, Heinrich 1979, Zimmerman 1982, Waddington 1983, Zimmerman and Cook 1985, Zimmerman and Pyke 1986, Wolf and Hainsworth 1990, Keasar et al. 1996). In fact, the visitation response we have modeled is a combination of an aggregative response to the number of plants in a patch manifested at the level of the pollinator population and a functional response of individual pollinators. Thus, empiricists should measure visitation rate of the entire effective pollinator community (measured as visits per unit time) to equal-sized patches with different numbers of individual plants of 2 or more species. Pollination facilitation is possible if visitation rate of pollinators responds to patches of plants as a sigmoid function of increasing plant density, and if the effective pollinator community responds as if each plant species were substitutable.

Goulson (1994) argued that facilitation would occur only if insect visitation increases disproportionately, depleting the nectar/pollen rewards in a preferred plant species and causing pollinators to switch to another plant species, or if pollinators that exhibit constancy switch to two plant species that they cannot distinguish. He discounted the importance of facilitation under either of these conditions, arguing that the first case was unlikely, and that even if two plants were indistinguishable to pollinators, negative effects of interspecific pollen transfer on seed production would likely outweigh benefits of facilitation (Goulson 1994). Because our models assume that pollinators do not distinguish among the two plant species, we cannot fully address Goulson's first point. However, pollinators may instead respond disproportionately to increasing total density of floral resources when choosing among patches on a landscape. If pollinator visitation to a patch increases as an accelerating function of plant density, then unless all pollinators that have entered a patch are constant to the same plant species, facilitation may be more likely than Goulson proposes. Further, our results indicate that facilitation still occurs when there is no pollen carryover beyond one visit (this is akin to strong negative effects of heterospecific pollen). Thus, the benefits of facilitation can sometimes outweigh the costs of interspecific pollen transfer.

Our model clarifies the conditions under which benefits of facilitation may outweigh negative effects of competition between two plant species. According to the model, the conditions under which one plant species can facilitate another's pollination are somewhat restrictive, but it is still unclear how common these conditions are in nature. Further empirical study is necessary to determine whether the paucity of evidence for pollination facilitation in nature is due to lack of adequate studies, difficulty of detection, rarity of conditions under which facilitation occurs, or a combination of these factors.

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Appendix. Facilitation can occur with an accelerating but not a saturating pollinator response

The potential for pollination facilitation to occur is perhaps of the greatest interest when the total number of plants in the patch is low, for in that case only the combined numbers of both plant species might elicit sufficient pollinator visits to cause the birth rate of either species to exceed its respective death rate. Here we derive an analytical approximation for Eq. (2) that is valid when the number of plants in the patch is small (i.e. $P_1 + P_2 \ll K$), and we use it to show that pollination facilitation requires an accelerating pollinator response to the total number of plants in the patch.

We first consider the saturating pollinator response model (Eq. 4a, 4b). If we assume that plant numbers are low and pollinator visits are correspondingly infrequent such that $\phi_1 = N_{\max} P_1 / (K(\beta + P_1 + P_2))$ is small, we can use the expression $\exp(\phi_1) \approx 1 + \phi_1$, $\phi \ll 1$, to derive an approximation for Eq. (5a):

$$\frac{dP_1}{dt} = \frac{S_1 N_{\max} P_1^2}{K^2(\beta + P_1 + P_2)} \left[1 - \frac{P_1 + \alpha_{12} P_2}{K} \right] - \delta_1 P_1 \quad (\text{A.1})$$

The zero net growth isocline is found by setting the right hand side of Eq. (A.1) to zero and solving the resulting expression for P_2 as a function of P_1 :

$$P_2 = \frac{-P_1^2 + (K - \gamma)P_1 - \gamma\beta}{\alpha_{12}P_1 + \gamma} \quad (\text{A.2})$$

where $\gamma = K^3 \delta_1 / S_1 N_{\max}$.

Following the argument we presented in the text, in order for either strong or weak facilitation to occur, the

$$\frac{dP_2}{dP_1} = \frac{-2P_1 - \gamma + K}{\alpha_{12}P_1 + \gamma} - \frac{\alpha_{12}[-P_1^2 + (K - \gamma)P_1 - \gamma\beta]}{(\alpha_{12}P_1 + \gamma)^2} \quad (\text{A.4})$$

Because the second term on the right hand side of (A.4) equals $\alpha_{12}P_2 / (\alpha_{12}P_1 + \gamma)$ (see A.2) and because $P_2 = 0$, (A.4) simplifies to

$$\frac{dP_2}{dP_1} = \frac{-2P_1 - \gamma + K}{\alpha_{12}P_1 + \gamma} \quad (\text{A.5})$$

As the denominator of (A.5) is always positive, facilitation requires that $P_1 > (K - \gamma)/2$ at $P_1 = P_1^*$. However, from (A.3), P_1^* is actually less than $(K - \gamma)/2$. We conclude that facilitation is not possible with a saturating pollinator response.

We now repeat the preceding analysis for an accelerating pollinator response. Substituting the approximation for the exponential function and the sigmoid pollinator response into Eq. (4a), then setting the resulting expression to zero yields an implicit function for the species 1 isocline

$$P_1^3 + [\gamma - K + (1 + \alpha_{12})P_2]P_1^2 + [2\gamma - K + \alpha_{12}P_2]P_2P_1 + \gamma(\beta + P_2^2) = 0 \quad (\text{A.6})$$

As it is difficult to solve the cubic (A.6) for P_2 as a function of P_1 , we instead solve for dP_2/dP_1 using implicit differentiation and the chain rule. Let the left-hand side of (A.6) be represented by the function $F(P_1, P_2)$, and let $P_2 = P_2(P_1)$ represent P_2 as a function of P_1 . By the chain rule, $dP_2/dP_1 = -(dF/dP_1)/(dF/dP_2)$, so from (A.6):

$$\frac{dP_2}{dP_1} = \frac{-(3P_1^2 + 2[\gamma - K + (1 + \alpha_{12})P_2]P_1 + [2\gamma - K + \alpha_{12}P_2]P_2)}{((1 + \alpha_{12})P_1^2 + (2\gamma - K)P_1 + 2\alpha_{12}P_1P_2 + 2\gamma P_2)} \quad (\text{A.7})$$

slope of the isocline at its lower crossing with the species 1 axis must be negative. That is, we require that

$$\left. \frac{dP_2}{dP_1} \right|_{(P_1, P_2) = (P_1^*, 0)} < 0 \text{ where}$$

$$P_1^* = \frac{1}{2}(K - \gamma - \sqrt{(K - \gamma)^2 - 4\gamma\beta}) \quad (\text{A.3})$$

is the lower intercept of the isocline (A.2) with the species 1 axis (i.e. the smaller root obtained by setting [A.2] to zero and solving for P_1). From Eq. A.2,

Facilitation requires that the right-hand side of (A.7) be negative at $(P_1, P_2) = (P_1^*, 0)$ (where P_1^* is again the lower intercept of the species 1 isocline with the species 1 axis), i.e. that

$$\frac{-(3P_1^{*2} + 2(\gamma - K))}{(1 + \alpha_{12})P_1^{*2} - (2\gamma - K)} < 0 \quad (\text{A.8})$$

(A.8) implies that if $(1 + \alpha_{12})P_1^* - (2\gamma - K) > 0$, facilitation will occur if $P_1^* > \frac{2}{3}(K - \gamma)$, and that if $(1 + \alpha_{12})P_1^* - (2\gamma - K) < 0$, facilitation will occur if $P_1^* <$

$\frac{2}{3}(K - \gamma)$. Numerical calculation of the isoclines indicates that these conditions can be met. For example, for the parameter values $K = 1000$, $\gamma = 25$, and $\alpha_{12} = 0.5$, (A.9) will be satisfied if $P_1^* < 650$.

Inspection of the intercept of the species 1 isocline for these parameter values indicates that $P_1^* \approx 110$, so that facilitation can indeed occur under these conditions.