



How to be a good neighbour: Facilitation and competition between two co-flowering species



Mohsen B. Mesgaran^a, Juliette Bouhours^b, Mark A. Lewis^{b,c}, Roger D. Cousens^{a,*}

^a School of BioSciences, The University of Melbourne, Victoria 3010, Australia

^b Department of Mathematical and Statistical Sciences, University of Alberta, Alberta, T6G 2G1 Canada

^c Department of Biological Sciences, University of Alberta, Alberta, T6G2G1, Canada

ARTICLE INFO

Article history:

Received 27 November 2016

Revised 9 April 2017

Accepted 10 April 2017

Available online 15 April 2017

Keywords:

Breeding system

Selfing

Outcrossing

Functional response

Plant community

Pollination

Positive interactions

Mathematical model

Optimal foraging

ABSTRACT

Empirical evidence suggests that co-flowering species can facilitate each other through shared pollinators. However, the extent to which one co-flowering species can relieve pollination limitation of another while simultaneously competing for abiotic resource has rarely been examined. Using a deterministic model we explored the demographic outcome for one (“focal”) species of its co-occurrence with a species that shares pollinators and competes for both pollinator visitation and abiotic resources. In this paper we showed how the overall impact can be positive or negative, depending on the balance between enhanced fertilization versus increased competition. Our model could predict the density of co-flowering species that will maximize the pollination rate of the focal species by attracting pollinators. Because that density will also give rise to competitive effects, a lower density of co-flowering species is required for optimizing the trade-off between enhanced fertilization and competition so as to give the maximum possible facilitation of reproduction in the focal species. Results were qualitatively different when we considered attractiveness of the co-flowering species, as opposed to its density, because attractiveness, unlike density, had no effect on competition for abiotic resources. Whereas unattractive neighbours would not bring in pollinators, very attractive neighbours would captivate pollinators, not sharing them with the focal species. Thus optimal benefit to the focal species came at intermediate levels of attractiveness in the co-flowering species. This intermediate level of attractiveness in co-flowering species simultaneously maximized pollination and overall facilitation of reproduction for the focal species. The likelihood of facilitation was predicted to decline with the selfing rate of the focal species, revealing an indirect cost for an inbreeding mating system. Whether a co-flowering species can be facilitative depends on the way pollinators respond to the plant density: only a Type III functional response for visitation rate can result in facilitation. Our model provided both a conceptual framework and precise quantitative measures for determining the impacts of a neighbouring co-flowering species on reproduction.

© 2017 Elsevier Ltd. All rights reserved.

1. Introduction

Plant community theory is heavily biased toward negative interactions between plants, where the coexistence of species is explained mainly through competition avoidance mechanisms such as niche partitioning (Parrish and Bazzaz 1976) and spatiotemporal heterogeneity in limiting resources (Tilman 1982). However, plants also engage in positive interactions where the performance of at least one species is enhanced in the presence of another (Callaway 2007). While the notion of competition exclusion forms one of the main pillars of the discrepancy between the fundamental

niche and the realised niche (Hutchinson 1957), plant species can potentially expand the realised niches of other species through facilitative interactions (Bruno et al., 2003): some species may not exist where they do if they were alone. Despite the important role of facilitative interactions in determining the distribution, diversity and coexistence of plants, facilitation has received little attention in the ecological literature when compared with the competition.

Plants can directly improve the physical and chemical environments of their neighbours in a myriad of ways, such as providing shade under dry conditions (Holmgren 2000), increasing soil surface moisture for establishment of seedlings (Anderson et al., 2001), adding nutrients to the soil (Carlsson and Huss-Danell 2003), and providing shelter against disturbance (Bruno 2000). Facilitative interactions can also be driven indirectly through the involvement of a third party such as herbivores or pollinators. For

* Corresponding author.

E-mail addresses: mohsenm@unimelb.edu.au, mesgaran@gmail.com (M.B. Mesgaran), rcousens@unimelb.edu.au (R.D. Cousens).

example, sympatry with an unpalatable neighbour may protect a tasteful species against herbivores (Callaway et al., 2005) and co-flowering species may facilitate another by attracting shared pollinators (Ghazoul 2006).

Although shared pollinators have long been known as major structure-producing agents of plant communities (Feinsinger 1987), much of the focus has been on how plants compete for pollinator services (exploitation competition) or interfere with each other through interspecific ("improper") pollen transfer (interference competition) (Levin and Anderson 2016; Rathcke 1983; Waser 1978, 1983; Willmer 2011;). Evidence, however, is accumulating for pollination facilitation through multispecies floral displays (Ghazoul 2006; Johnson et al., 2012; Moeller 2004; Molina-Montenegro et al., 2008; Seifan et al., 2014; Sieber et al., 2011). Coexisting species may facilitate each other indirectly by maintaining populations of pollinators through the provision of food during the season or across years (Robson 2013; Moeller 2004; Waser and Real 1979;). Multispecies displays may also increase the diversity of pollinator fauna, which might be helpful for a rare species: the higher the richness of pollinators, the greater the chance of a rare species being visited by one of them (Ghazoul 2006). Co-occurrence with a highly rewarding species can increase visitation through the so-call "magnet" effect, where the conspicuous species attracts more pollinators, some of which then make visits to the other species (Laverty 1992; Molina-Montenegro et al., 2008; Thomson 1978).

Pollinators often show little interest in visiting low-density floral patches (Bernhardt et al., 2008; Elliott and Irwin 2009; Kunin 1997) as the costs of search and long flights between sparse plants may outweigh the rewards that are offered (Charnov 1976; Pyke et al., 1977). Outcrossing species occurring in small, sparse populations or with no attractive floral rewards are therefore expected to benefit from the presence of a co-flowering species as their joint floral display may make the mixed patch profitable enough to lure generalist pollinators (Duffy and Stout 2011; Ghazoul 2006; Seifan et al., 2014; Sieber et al., 2011). Using a mathematical model, Feldman et al. (2004) found that such a facilitation mechanism can occur when the visitation rate was an initially accelerating (sigmoidal) function of the combined number of plants from the two species in a patch. This facilitation mechanism assumes that pollinators do not discriminate between the species (i.e. the two species are equally attractive) and only respond to the collective floral display in a fashion similar to increasing intraspecific density (Ghazoul 2006). However, the two species may not be equally effective in attracting pollinators as pollinators often show constancy and preference for specific floral types (Kunin and Iwasa 1996; Jones 1997). The individual-based model of Hanoteaux et al. (2013) incorporates a difference in attractiveness and its interaction with the spatial distribution of species. Their study showed that when the less attractive species is highly abundant, it will be more successful if forms large monospecific patches than a uniform distribution while the opposite is true for a less attractive species that has a small population. Hanoteaux et al. (2013) model, however, assumes no competition for abiotic resources between co-flowering species. They found The degree of facilitation may also vary depending on the breeding system of species: the more an outcrossing mating system the plant species adopts, the more it becomes reliant on pollinator services and thus the more likely to be affected, either negatively or positively, by their co-flowering species that share pollinators. However, neither of the models mentioned above (Feldman et al., 2004; Hanoteaux et al., 2013) investigated the effects of breeding system differences on the outcome of the interaction between two co-flowering species.

The aim of this study was to delineate the suite of conditions where the existence of a second co-flowering species can be facilitative to its neighbouring species: *under what circumstances*

could a co-occurring species be a good neighbour? Are there optimal density and attractiveness values at which the co-flowering species is most facilitative to the focal species? Does the breeding system of the focal species affect its propensity for benefiting from the existence of a co-flowering species? Does the outcome of the interaction (either facilitative or competitive) rely on the shape of the pollination response function? We use the term "focal" here to refer to the species (A) that receives the researcher's main attention; since both species could facilitate the other, the choice of species is arbitrary. We use the term "co-flowering" for the other species (B) whose impact on species A is being considered.

Using a population dynamics model that incorporates mating systems, quantitative genetics, and pollinators, in our previous study we found that hybridization with a co-occurring species can facilitate the establishment of a colonizer that is experiencing pollen limitation due to its small population size (Mesgaran et al. 2016). Here, we used a modified version of that model to explore the possibility of facilitation between two co-flowering species that are not inter-fertile, so that cross-pollination will not produce hybrid lineages.

2. Model development

We made two major changes to Mesgaran et al. (2016) model. Firstly, the interspecific crossing does not result in hybridization. Secondly, there is only one density-dependent regulation whilst in the previous model there were two separate density-dependent sub-models: one for the ovules production and the other for seedling recruitment. The main reason for the latter modification was to simplify the model so that it can be approached more analytically. Briefly, the model is based on the life cycle of an annual, hermaphrodite plant with no persistent seedbank. Suppose a population of focal species A with n individuals in which each individual plant produces θ ovules, a fraction s of the ovules is self-fertilized whilst the remaining $1 - s$ fraction can potential produce seeds through outcrossing. However, not all non-selfed ovules, i.e. $\theta(1 - s)$, will be fertilized as the outcrossing requires the transfer of pollen from other individuals by means of pollinators or other agents such as wind, which may be inefficient. We assume in our model that animal pollinators are the only agent of pollen transfer and that their visitation rate is positively related to the population density, n , following the probability function $\phi(n)$. When there are two species the combined number of plants will determine the visitation rate (more details below). A positive density-dependent relationship between pollinator visitation rate and population density has been found in many empirical studies (Bernhardt et al., 2008; Feldman 2006; Elliott and Irwin 2009; Kunin 1997; Robson 2013) and has been used in several population models (e.g. Feldman et al., 2004; Morgan et al., 2005). Because of abiotic resource limitations, the performance of plants is reduced as the density increases, following a negative density-dependent function, $R(n)$, which can also be regarded as a recruitment function (Cheptou 2004). The dynamics of species A population over time, t , can be formulated as a recurrence equation:

$$n(t+1) = \underbrace{\theta}_{\text{fecundity No.}} \underbrace{n(t)R(n(t))}_{\text{adult plants}} \left(\underbrace{s}_{\text{selfing rate}} + \underbrace{(1-s)\phi(n(t))}_{\text{outcrossing rate}} \right) \quad (1)$$

The model gives rise to component Allee dynamics (*sensu* Stephens et al., 1999) as recruitment is negatively related to population density, $R(n)$, while visitation (pollination) probability, $\phi(n)$, and thus reproduction, is positively scaled with the density. For the recruitment function we use a Beverton-Holt type model:

$$R(n) = \frac{1}{1 + \beta n} \quad (2)$$

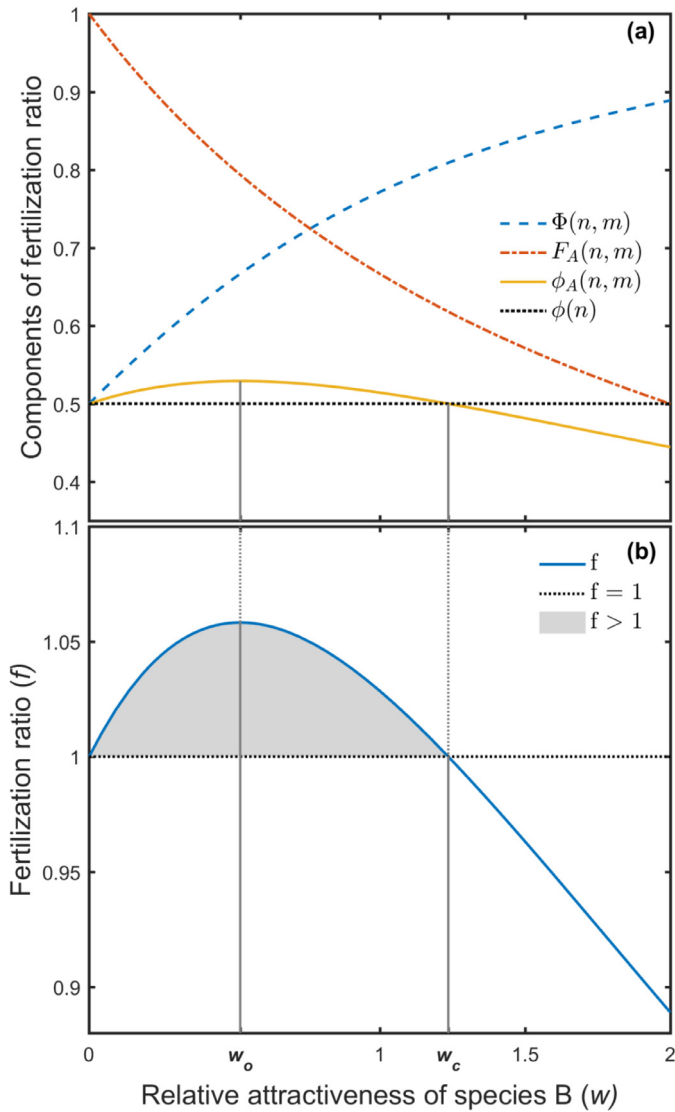


Fig. 1. The effect of the attractiveness (w) of a co-flowering species B on (a) various components of the fertilization ratio and (b) its consequences for the overall fertilization ratio (f) in the focal species A. w_o and w_c show the optimal and critical attractiveness levels respectively. The shaded area represents the range of w values with the fertilization ratio $f \geq 1$. Other parameters were: $\rho = 0.01$, $\gamma = 3$, $s = 0$, $n = 100$ and $m = 50$.

where β indicates the degree of competition between plants for (abiotic) resources. For pollination probability we used Holling's Type III functional response, also used by Morgan et al. (2005), to relate the probability of visitation to population density of species A:

$$\phi(n) = \frac{(\rho n)^\gamma}{1 + (\rho n)^\gamma}. \quad (3)$$

This type of functional response is expected for generalists that frequently switch between flower types (Willmer 2011: chapter 10) or if pollinators engage in an area-restricted search strategy (Tinbergen et al., 1967). A similar model was also used by Feldman et al. (2004). The reciprocal of ρ gives the population density at which 50% of flowers will be visited (and successfully pollinated) by pollinators. The parameter γ determines the shape of the curve: when γ is large there is little change in probability of pollination at low densities, compared to a small γ which gives a higher pollination rate at the same low densities (see Supple-

mentary Fig 1S). When $\gamma = 1$, the model reduces to a Type II functional response (Feldman et al., 2004).

The final model describing the population changes of focal species A over time is obtained by replacing, respectively, $R(n)$ and $\phi(n)$ in Eq. 1 by Eq. 2 and Eq. 3:

$$n(t+1) = \frac{n(t)\theta}{1 + \beta n(t)} \left(s + (1-s) \frac{(\rho n(t))^\gamma}{1 + (\rho n(t))^\gamma} \right). \quad (4)$$

Now suppose that there exists a co-flowering species, denoted by B, with a population size m in the habitat, which shares pollinators as well as competes for pollinators and abiotic resources with the focal species A. This second species, however, may facilitate the focal species by increasing the probability of pollination through the $\phi(n)$ function, which increases with the total density (i.e. $n + m$, see below). The two species can differ in competitiveness for pollinators, where αm individuals of species B are as competitive as n individuals of species A: the coefficient α is a scaling parameter that converts the competition load incurred by m individuals of species B to the equivalent amount measured in units of species A. The recruitment rate for the focal species A in the presence of co-flowering species B is:

$$R_A(n, m) = \frac{1}{1 + \beta(n + \alpha m)}. \quad (5)$$

Likewise, the two species may differ in their degree of attractiveness toward pollinators such that wm individuals of species B are as effective as n individuals of species A in attracting pollinators to the mixed patch of plants. Attractiveness is considered to be an intrinsic attribute of plant species derived from properties such as flower size, colour, the provision of nectar, etc. The probability of visitation (Eq. 3) for the two species model is therefore a function of the combined number of individuals from the two species adjusted for attractiveness:

$$\Phi(n, m) = \frac{(\rho(n + wm))^\gamma}{1 + (\rho(n + wm))^\gamma}. \quad (6)$$

The above equation gives the probability of visitation to the mixed patch. However, we need the proportion of total visits to the focal species A i.e. the species-specific visitation. The visitation probability for species A in the mixed population, ϕ_A , can be calculated by multiplying $\Phi(n, m)$ by its frequency (relative abundance) in the mixed population:

$$\phi_A(n, m) = \Phi(n, m) F_A(n, m), \quad (7)$$

where F_A is the frequency of species A in the mixed population as adjusted for its relative attractiveness:

$$F_A(n, m) = \frac{n}{n + wm}, \quad (8)$$

and that of species B is $F_B = 1 - F_A$, so that $F_A + F_B = 1$. If $w > 1$, then species B is more attractive than the focal species A and the number of visits that it receives is more than that would be expected from its frequency in the population, i.e. it is *as if* there are more plants from species B than their actual number. If $w < 1$, then species A is more attractive than species B and receives a greater proportion of visits than its actual frequency (see Mesgaran et al. 2016 for more details). Eq. 7 accommodates the two major components of the pollination process in a system of two co-flowering species: pollinator attraction to the mixed patch ($\Phi(n, m)$) and conspecific pollen removal and deposition (conspecific visitation). Eq. 7 therefore accounts for pollination facilitation, through $\Phi(n, m)$, as well as competition for shared pollinators, through F_A , concomitantly.

The difference equation describing the dynamics of population in our focal species A in the presence of the second species B can

be written as:

$$n(t + 1) = n(t)\theta R_A(n(t), m(t)) \times \{s + (1 - s)\Phi(n(t), m(t))F_A(n(t), m(t))\}, \tag{9}$$

which after respective substitutions from Eq. 5–8 gives:

$$n(t + 1) = \frac{n(t)\theta}{1 + \beta(n(t) + \alpha m(t))} \times \left\{ s + (1 - s) \frac{(\rho(n(t) + wm(t)))^\gamma}{1 + (\rho(n(t) + wm(t)))^\gamma} \cdot \frac{n(t)}{n(t) + wm(t)} \right\}. \tag{10}$$

We explored the potential consequences of adding a second species for our focal species A, mainly by comparing Eq.1 (focal species alone) with Eq. 9 (focal species with a co-flowering species). Both analytical solutions and numerical analyses were performed using MATLAB (version 2016a).

3. Results

Comparing the population dynamics of the focal species in the presence (Eq.9) and absence (Eq.1) of the second species, we can conclude a facilitative effect from the co-flowering species if the following inequality holds (note that we have dropped t from the equations):

$$\underbrace{n\theta R_A(n, m)(s + (1 - s)\phi_A(n, m))}_{\text{Eq. 9: species A in the presence of B}} > \underbrace{n\theta R(n)(s + (1 - s)\phi(n))}_{\text{Eq.1: species A alone}}, \tag{11}$$

which after eliminating the common factor $n\theta$ becomes:

$$R_A(n, m)(s + (1 - s)\phi_A(n, m)) > R(n)(s + (1 - s)\phi(n)). \tag{12}$$

After rearrangement we obtain:

$$\underbrace{\frac{(s + (1 - s)\phi_A(n, m))}{(s + (1 - s)\phi(n))}}_{\text{fertilization ratio (f)}} > \underbrace{\frac{R(n)}{R_A(n, m)}}_{\text{competition ratio (c)}}. \tag{13}$$

In this inequality, we will refer to the left ratio as the *fertilization ratio* f : the numerator and denominator in f show the fertilization rate of the focal species in the presence and absence of species B, respectively. So, when $f > 1$, it means that the co-flowering species can increase fertilization in the focal species A. However, $f > 1$ only represents the *necessary* condition for a facilitative interaction: as the *sufficient* condition for facilitation, the fertilization ratio f must also be larger than the *abiotic competition ratio* c i.e. $f > c$. Ratio c (left side in Eq.13) represents the recruitment of the focal species as it occurs alone (numerator) relative to that in the presence of co-flowering species. From Eq.2 and Eq.5, we can infer that the abiotic competition ratio c is always larger than 1:

$$c \equiv \frac{R(n)}{R_A(n, m)} = \frac{\frac{1}{1+\beta n}}{\frac{1}{1+\beta(n+\alpha m)}} = \frac{1 + \beta n + \beta \alpha m}{1 + \beta n}, \tag{14}$$

because the nominator has an additional, positive term: $\beta\alpha m$. The ratio c can be less than 1, only if α takes a negative value: $\alpha < 0$ may imply a mutualistic relationships whereby a co-occurring species increases the abiotic resources for the growth of its neighbouring species e.g. by fixing nitrogen as in legumes. This type of interaction is not addressed in this study. Therefore, facilitation is only warranted when $1 < f$ and $c < f$

We first attempt to identify circumstances that can lead to “pollination facilitation” satisfying the necessary condition $f > 1$, then explore whether the overall effect of species B on the focal species is positive, so that $f > c$ also holds.

3.1. Pollination facilitation: $f > 1$

3.1.1. Density and attractiveness of co-flowering species

Both competition and facilitation for pollination can occur simultaneously and this is accounted for by $\phi_A(n, m)$ (the numerator of f), which incorporates a facilitative effect of the second species through $\Phi(n, m)$ (Eq.6) and its competition through $F_A(n, m)$ (Eq.8). Both density m and relative attractiveness w play a dual role in pollination of focal species. Fig. 1 depicts these effects for the case of the relative attractiveness parameter w for an obligate outbreeder ($s = 0$). On the one hand, the increase in attractiveness (or equally the density of the second species, m) has a positive effect on the pollination of species A as it increases the overall visitation probability of the mixed population through the $\Phi(n, m)$ component (blue, dashed line in Fig 1a). On the other hand, it incurs negative effects on the pollination of the focal species A because it reduces the effective frequency of the focal species in the mixed population through $F_A(n, m)$ (red, dash-dotted line in Fig 1a). The product of these two functions, $\Phi(n, m) \times F_A(n, m)$, gives the probability of visitation to the focal species A in the presence of a second species i.e. $\phi_A(n, m)$. As shown in Fig 1a, this probability (orange, solid line in Fig 1a) and thus the fertilization ratio (blue, solid line in Fig 1b) increases with w before they reach their maxima at w_o (or m_o in the case of density). Beyond w_o , the probability of visitation to the focal species, $\phi_A(n, m)$, starts to decline until a critical value of attractiveness, denoted by w_c (or m_c for density) is reached, at which the probability of visitation to the focal species is the same whether the second species is present ($\phi_A(n, m)$) or absent ($\phi(n)$), hence yielding a fertilization ratio of $f = 1$ (i.e. $f|_{w=w_c} = 1$). That is, when $w > w_c$ (or $m > m_c$) the fertilization ratio becomes smaller than 1 indicating that the co-flowering species starts to compete with the focal species for pollinator services rather than aiding it. The optimal attractiveness w_o can be obtained by calculating the partial derivative of fertilization ratio f with respect to w i.e. $\frac{\partial f}{\partial w} = 0$:

$$w_o = \frac{(\gamma - 1)^{\frac{1}{\gamma}} - \rho n}{\rho m}, \tag{15}$$

Similarly, the fertilization ratio is maximized when the density of the co-flowering species is:

$$m_o = \frac{(\gamma - 1)^{\frac{1}{\gamma}} - \rho n}{\rho w}, \tag{16}$$

To obtain w_c we need to solve $f = 1$ for w :

$$w_c \equiv \left\{ f : \frac{s + (1 - s) \frac{(\rho(n+wm))^\gamma}{1 + (\rho(n+wm))^\gamma} \cdot \frac{n}{n+wm}}{s + (1 - s) \frac{(\rho n)^\gamma}{1 + (\rho n)^\gamma}} = 1 \right\},$$

which has no explicit solution, but it can be shown (see Appendix A) that w_c (and m_c) will become zero when the density of the focal species A is:

$$n_c = \frac{(\gamma - 1)^{\frac{1}{\gamma}}}{\rho}. \tag{17}$$

That is, when the focal species A occurs at a density equal to n_c , the density of the co-flowering species B (m) or its attractiveness (w) should be less than zero to be able to result in a fertilization ratio $f > 1$. Given that the density of co-flowering species cannot be less than zero, n_c represents a ceiling density for an Allee effect: below the n_c there exist a positive density-dependent relationship where additional individuals from the co-flowering species can enhance visitation to the focal species. However, above this ceiling density (hereafter referred to as the *Allee ceiling*) any additional individuals from the second species will incur competition for pollinators and hence will reduce the probability

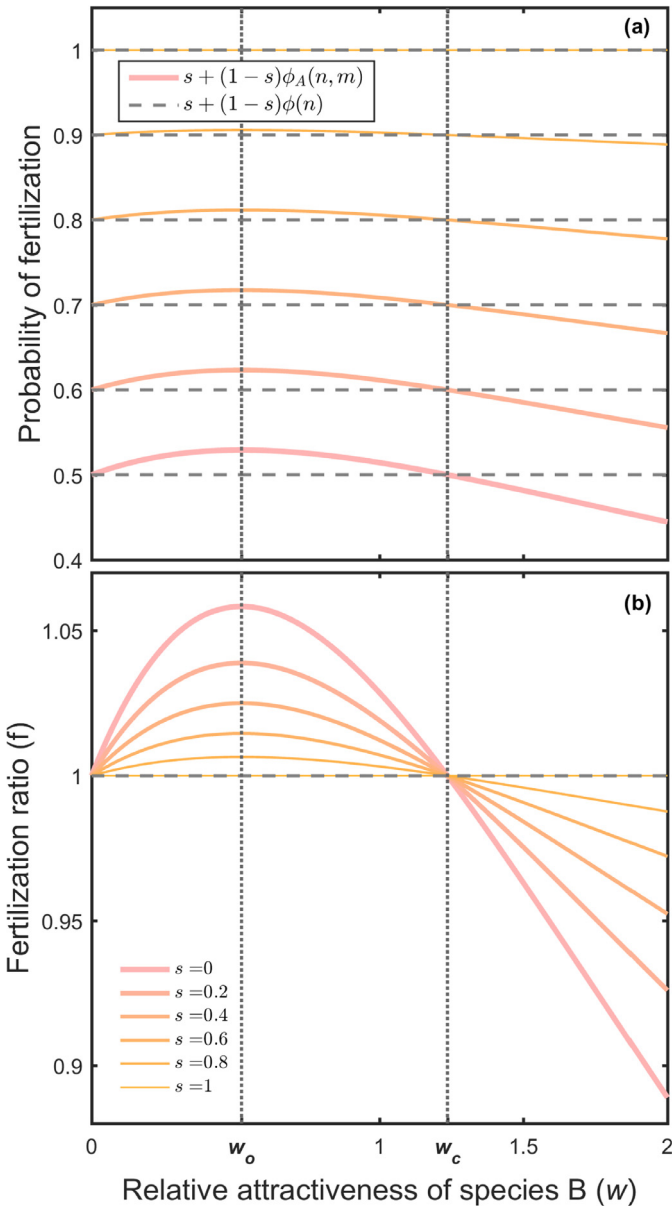


Fig. 2. Changes in (a) the probability of fertilization and (b) fertilization ratio (f) as a function of the attractiveness of the co-flowering species B (if present, solid lines) and the selfing rates (s) of the focal species A. As the focal species adopts a more selfing breeding system (the lines progressively becomes thinner), the probability of fertilization increases both in the absence (dashed lines) and presence (solid lines) of a co-flowering species but the gap between these two scenarios becomes smaller (a), which consequently reduces the fertilization ratio (b). As shown, the optimal (w_0) and critical (w_c) attractiveness values, dotted lines, are independent of selfing rate. Other parameters were: $\rho = 0.01$, $\gamma = 3$, $n = 100$ and $m = 50$.

of the focal species' pollination (i.e. negative density-dependence). Even if the density of the focal species is less than n_c , so that it is experiencing pollination limitation due to low density, the density (attractiveness) of the co-flowering species still needs to be less than m_c (w_c) to aid the pollination of the focal species (m_c and w_c cannot be written in explicit, closed form).

3.1.2. Breeding system of the focal species

As shown in Fig 2, the locations of both w_0 and w_c are independent of the selfing rate of the focal species, and selfing rate only changes the height of the f curve. Eq.15 (and Eq.16) analytically proves that the optimal attractiveness (optimal density) for maximum fertilization does not depend on the breeding system

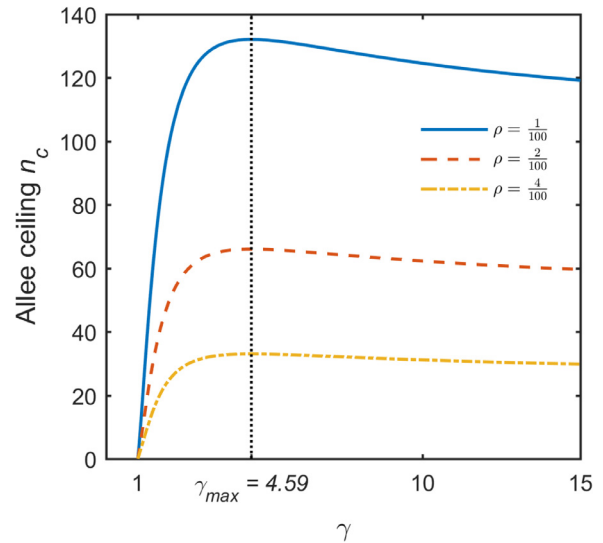


Fig. 3. Changes in Allee ceiling, n_c , as the value of shape parameter γ in pollination function (Eq. 3) increases. Regardless of ρ , the maximum value of Allee ceiling, n_c^{max} , occurs at $\gamma = 4.59$ (Eq. 18) and then declines to approach $\frac{1}{\rho}$ as γ approaches infinity (Eq. 19).

of the focal species. It is only the height of the fertilization ratio curve that decreases with the selfing rate of the focal species, which finally touches the unity line (dashed line in Fig 2b) at $s = 1$, yielding $f = 1$.

Beside these numerical simulations (Fig 2), it can be proven analytically that no pollination facilitation can be provided by the co-flowering species if the focal species is a fully selfing species. Let the focal species be a self-compatible species that self-fertilizes all its θ ovules such that $s \approx 1$. In this case the fertilization ratio becomes:

$$f = \frac{(1 + (1 - 1)\phi_A(n, m))}{(1 + (1 - 1)\phi(n))} = 1,$$

which does not satisfy the necessary condition of $f > 1$ i.e. the co-flowering species can no longer assist the focal species with the provision of pollination.

3.1.3. Shape of visitation response to plant density

We found that if the relationship between plant density and probability of visitation follows the Holling's Type II function, no pollination facilitation can be provided by the co-flowering species. A Type II functional response is obtained when $\gamma = 1$, which gives a fertilization ratio:

$$f_{(\gamma=1)} = \frac{s + (1 - s) \frac{\rho(n+wm)}{1+\rho(n+wm)} \cdot \frac{n}{n+wm}}{s + (1 - s) \frac{\rho n}{1+\rho n}},$$

and after expansion we obtain:

$$f_{(\gamma=1)} = \frac{s\rho^2 m n w + \rho^2 n^2 + \rho m s w + \rho n s + \rho n + s}{\rho^2 m n w + \rho^2 n^2 + \rho m s w + \rho n s + \rho n + s}.$$

The numerator and denominator of the above equation are identical with the only exception of an additional multiplier s (the selfing rate) in the numerator. Given that s cannot be larger than 1, this ratio is always smaller than or equal to 1, hence defying the necessary condition (i.e. $f > 1$) for a facilitative interaction.

From Eq.17, representing the Allee ceiling n_c , we could also infer that a saturating function cannot facilitate pollination because plugging $\gamma = 1$ into this equation gives $n_c = 0$, meaning that the density of the focal species should be zero (also see Fig 3) to be facilitated by its co-flowering species: something that is logically not possible. The two parameters defining the visitation function,

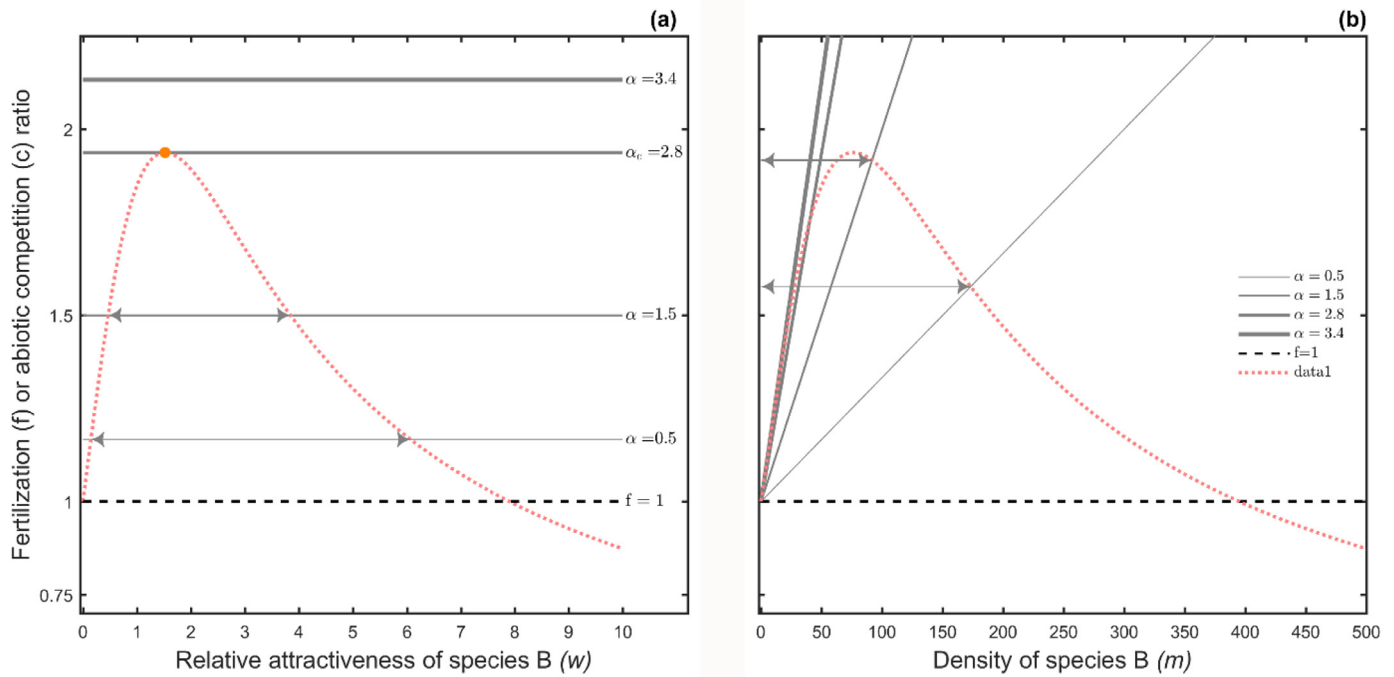


Fig. 5. Fertilization ratio (f) and abiotic competition ratio (c) as a function of the (a) attractiveness and (b) density of the co-flowering species B. Solid lines indicate c for various values of α (relative competitiveness of species B for abiotic resources) while the dotted line is f , which is independent of α . For attractiveness (a), the increase in α shifts the intercept of the c line and at $\alpha = \alpha_w$, the c line is tangent to the f curve (solid circle shows the f maximum and if $\alpha > \alpha_w$ abiotic competition ratio will exceed the fertilization ratio). For density (b), the slope of the c line increases with α ; in both cases the range where f is larger than c decreases with increase in α as shown by arrows. Parameter values used were: $m = 50$ only in (a), $n = 50$, $\rho = 0.01$, $\gamma = 3$, $s = 0.05$, $\beta = 0.01$, $\alpha = 1$ in both (a) and (b), and $w = 1$ only in (b).

the degree of second species' competitiveness relative to that of the focal species (Fig 5). As c is independent of w , increasing α only moves up the c line (increases the intercept) and this upward shift narrows the $f > c$ domain (as shown by arrows in Fig 5a) until a critical value of α , denoted by α_c , at which the c line touches the maximum value of f (shown by solid circle in Fig 5a). Regardless of the attractiveness (w) of the co-flowering species, any further increases in its competitiveness beyond the α_w , will place the c line above the f curve, eliminating the possibility of facilitation by the co-flowering species (see Appendix B for analytical derivation of α_w).

When c is plotted against the density of co-flowering species, the increase in α makes the slope of c line steeper while having no effect on the intercept (Fig 5b) as contrasted to w (Fig 5a). As the c line becomes steeper the range of m over which $f > c$ becomes narrower (shown by arrows in Fig 5b). (see Appendix C for analytical derivation of α_m i.e. the critical α value such that the c line stands above the f curve regardless of the value of m). Contrary to attractiveness, for which both maximum f and maximum $\frac{f}{c}$ occur at the same value of w i.e. w_o , the density that maximizes f , i.e. m_o , does not result in maximum $\frac{f}{c}$ (Fig 6): w_o is therefore a global optimum that maximizes both f and $\frac{f}{c}$ ratios whereas m_o is a local optimum that only maximizes the f ratio (the global optimal density of co-flowering species cannot be written in closed form).

3.2.3. Breeding system of the focal species

The mediating role of the focal species' selfing rate in shaping the facilitation domain, i.e. the parameter space satisfying $f > c$, is shown in Fig. 7. As shown, the facilitation domain shrinks as the focal species adopts more a selfing breeding system. When the focal species has a selfing rate of 1% and the attractiveness of the co-flowering species is optimal for pollination (in this example $w_o = 1.52$), the focal species can tolerate the highest degree of competition from its neighbouring species (in this example α as

large as ≈ 3.7) and yet attain $f > c$. However, when the selfing rate of the focal species increases to 50%, the co-flowering species should have a small relative competitiveness of $\alpha < 0.5$ (i.e. $2m = n$) to be able to provide facilitation (Fig 7a). A high density of co-flowering species will not be facilitative unless the species is a weak competitor with a small α (Fig 5b). Even so, increasing the selfing rate of the focal species from 1% to 50% can reduce the area of facilitation domain by 85% (Fig 7b).

4. Discussion

By comparing the reproduction and survival of a focal species as it occurs alone vs. in the presence of a co-flowering species, we have been able to delineate the suite of conditions that can give rise to a facilitative interaction. Unlike the new facilitation mechanism proposed by Mesgaran et al. (2016) and Bouhours et al. (2017), hybridization with a co-occurring congener is not required to allow an outcrossing colonizer to overcome pollen limitation. Our previous models showed that the individuals of the co-flowering species can assist the colonizer in two ways: by increasing the total size of the mixed population, which in turn increases the visitation rate, and by acting as potential compatible mates for the outcrosser (Bouhours et al., 2017; Mesgaran et al. 2016). Following Kunin (1993), we may refer to the former facilitation mechanism as an improvement in the "quantity" of pollination while the latter can be described as an improvement in the "quality" of pollination. In this study, we only examined the *quantity* component of the facilitation mechanism whilst the study of Bouhours et al. (2017) showed that improving the *quality* of pollination through hybridization can also result in facilitation. A non-hybridization scenario, as with this study, would apparently reflect a broader ecological context as many co-flowering species do not hybridize. Our analytical and numerical analyses showed that there is a high chance for the focal species to benefit from the company of a co-flowering species that shares pollinator services.

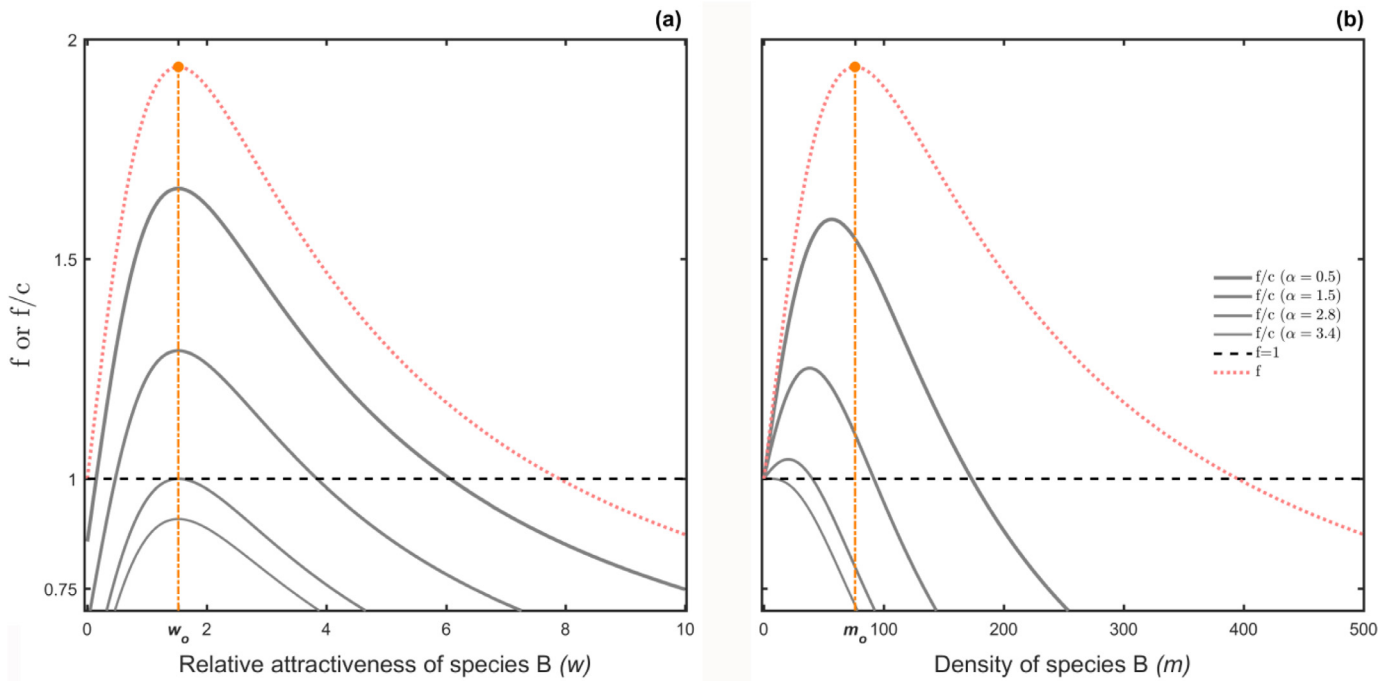


Fig. 6. Fertilization ratio (f) and ratio of fertilization to abiotic competition ($\frac{f}{c}$) as a function of the (a) attractiveness and (b) density of the co-flowering species B. Solid lines indicate $\frac{f}{c}$ ratios for various values of α (competitiveness of species B for abiotic resources) while the dotted line is f , which is independent of α . The attractiveness value that maximizes f , i.e. w_0 , also maximizes $\frac{f}{c}$ but the density at which fertilization ratio f peaks, i.e. m_0 , is not a global maximum. Other parameter values used were: $m = 50$ only in (a), $n = 50$, $\rho = 0.01$, $\gamma = 3$, $s = 0.05$, $\beta = 0.01$ in both (a) and (b), and $w = 1$ only in (b).

The existence of a co-flowering species affects the two major components of the pollination process, i.e. pollinator attraction and conspecific visitation (pollen removal and pollen deposition), in a contrasting way. Competition and facilitation, in fact, occur at the same time but whether the net outcome for the focal species is positive (facilitation) or negative (competition) depends on a multitude of factors such as the density and attractiveness of the interacting species, the behaviour of pollinators (e.g. how they respond to plant density) as well as the breeding system of the focal species. At either very low or very high densities, the co-flowering species is less likely to facilitate the population growth of the focal species. At low density, the co-flowering species may not be effective enough in attracting pollinators to the mixed patch while at high density it can reduce the conspecific pollen deposition and removal in the focal species (Morales and Traveset 2008): at such high densities, the competition from co-flowering species for pollinators outweighs the facilitation (as measured by a reduction in fertilization ratio f). Further, the high density of co-flowering species intensifies the competition for abiotic resources (as measured by an increase in abiotic competition ratio c). Empirical studies also suggest that facilitation diminishes at high heterospecific densities or is more likely to occur in small patches of the focal species (Dauber et al., 2010; Duffy et al., 2013; Ghazoul 2006; Moeller 2004), but none of these studies have factored in the competition for abiotic resources. It is therefore unclear whether the observed reduction in the performance (e.g. seed set) of the focal species has been driven by the competition for pollinators or by the exploitation of abiotic resources (e.g. nutrients).

For a fixed value of density \times attractiveness i.e. $wm = K$, where K is a constant, our model suggests that a co-flowering species that possess high attractiveness (large w) but occurs at low numbers (small m) is more likely to result in facilitation than the opposite combination (i.e. small w with large m). This situation represents the so-called magnet effect (Thomson 1978) where the existence of a highly attractive co-flowering species could increase

the visitation rate to the mixed patch (e.g. Johnson et al., 2003; Molina-Montenegro et al., 2008). However, if the co-flowering species is *too magnetic* (i.e. $w > w_c$), it will attract pollinators away from visiting the focal species to the extent that the visitation rate to the focal species in the mixed population can become smaller than that of the monoculture. Alternatively, when the density of co-flowering species is very high, its attractiveness should be low to avoid interspecific competition for pollination resources, but competition for abiotic resources can still be a hindrance to facilitation at these high densities. That explains why with large attractiveness w facilitation is a more plausible outcome than it is with a large density m . Overall, we found that there are optimal values for the density and attractiveness of the co-flowering species. We were able to present the global optimum for attractiveness (w_0) as in Eq.15 but global optimum for density cannot be expressed in closed form (Eq.16 is a local optimum density which only maximizes the fertilization ratio f but not the overall facilitation).

Our analysis showed that the shape of response curves must be *convex* to result in facilitation. This conclusion was derived from both the Allee ceiling (Eq.17) and fertilization ratio (Eq.13) equations. That is, a $\gamma \leq 1$, which produces a *concave* curve, gave an Allee ceiling $n_c \leq 0$ and fertilization ratio $f \leq 1$. While the former implies an impossible outcome i.e. zero or negative density for the focal species to be facilitated, the latter fails to meet the necessary condition of $f > 1$. Using a different modelling approach but with a similar pollination functional curve, Feldman et al. (2004) also found that facilitation cannot be derived from a saturating, concave function (i.e. when $\gamma \leq 1$ or a $\sigma = 1$ in their model) but will be possible if the relationship between visitation rate and the total number of plants in a patch is sigmoidal (i.e. when $\gamma > 1$ or $\sigma = 2$ in their model). However, there is no consensus about the shape of the response curve as this relationship depends on a multitude of interacting factors including the characteristics of the plant species (e.g. reward offer) and those of the pollinators (e.g. specialist vs. generalist) that can vary over time and space. Various

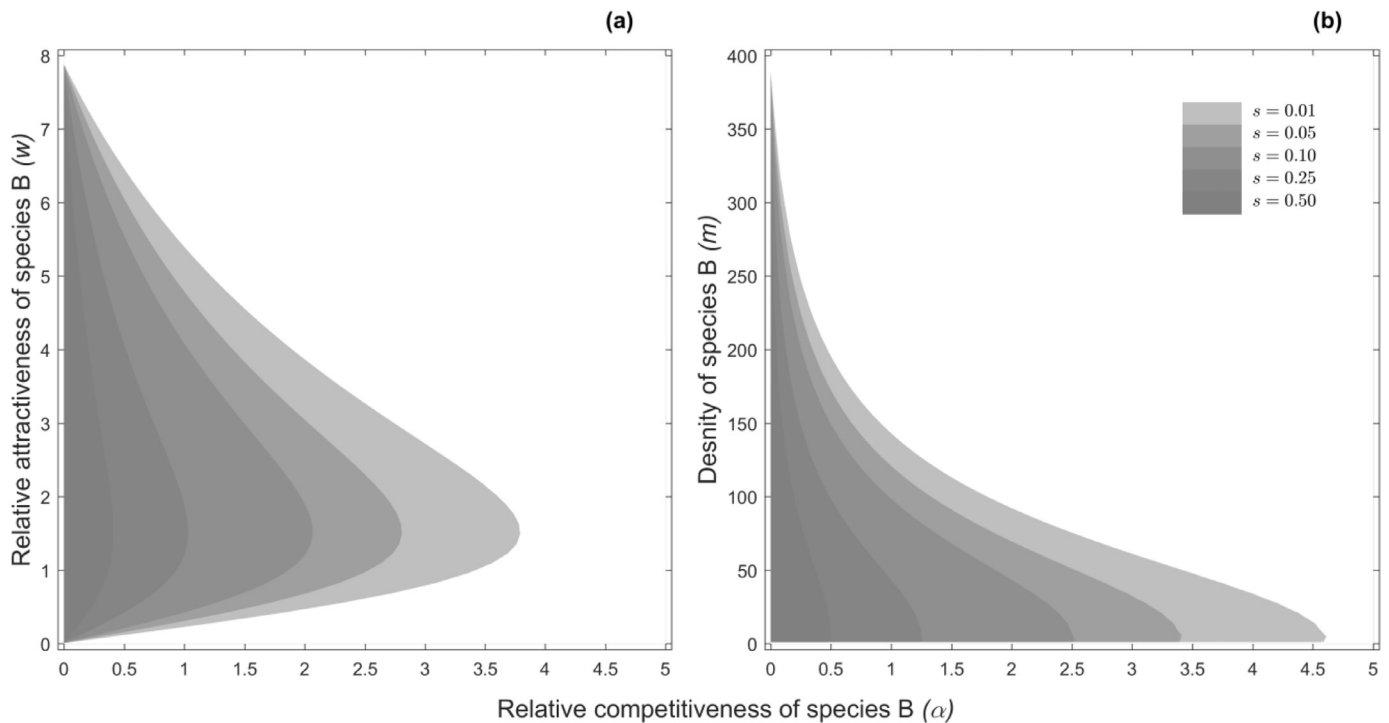


Fig. 7. Facilitation domain as determined by a fertilization ratio f that is larger than the abiotic competition ratio c (grey areas) over the parameter spaces of (a) competitiveness α and attractiveness w , and (b) competitiveness and density m of the co-flowering species B. Note the contraction of the facilitation domain as the selfing rate s in the focal species increases. The white area indicates the competition domain where $f < c$. Other parameters were $\beta = 0.01$, $\gamma = 3$, $\rho = 0.01$, $n = 50$ with $m = 50$ in (a) and $w = 1$ in (b).

shapes of visitation response have been detected in different studies e.g. the relationship between patch size and number of visits (per unit time) was convex (Duffy et al., 2013), linear (Johnson et al., 2012) and concave (Feldman 2006; Robson 2013). Both Rathcke (1983) and Feinsinger (1987) proposed a graphical model (without any specific formula) where the probability of pollination increases in an accelerating fashion with the density of flowers but then declines at very high floral densities, giving rise to a hump-shaped response curve. Such a response curve is expected (e.g. Brys et al., 2008) where the visitation rate is measured by the number of flowers visited per unit of time: when flower density is very high the pollinator pool becomes saturated so that there are more flowers than can be served by the community of pollinators (Feinsinger 1987). The models of both Rathcke (1983) and Feinsinger (1987) considers a transition from a facilitative effect to a competitive effect that corresponds with low and high floral densities respectively, meaning that competition and facilitation are operating at different times (Rathcke 1983). What seems to be more realistic, however, is that they are both acting simultaneously and it is the relative magnitude of these two processes that changes with density (Callaway 2007). If the pollination success is measured at the population level, as in our model and that of Feldman et al. (2004), then the response curve should not be hump shaped. At this scale, there should be no decline in the probability of pollination (of population) even at the very high densities. That is, the pollination probability of individual plants may follow the hump-shaped density relation, but that of the whole population should increase with density and reach a plateau where the plateau reflects the maximum capacity for pollination services.

Our study also showed that the breeding system of the focal species is a major determinant of the outcome of the interaction between two co-flowering plant species. Whereas selfing can benefit the plant species through reproductive assurance (Baker 1955) and two-fold gene transmission (Fisher 1941), it brings along

large costs such as inbreeding depression and the loss of genetic diversity (Charlesworth 2003; Wright et al., 2013). If an outcrossing species can overcome the problem of pollination limitation because of “good neighbours”, then there can be little or no advantage for a selfing mating system as a means of reproductive assurance. Indeed, the cost for a selfer is lack of facilitation gain. The advantage of an outbreeding system is that, through pollination facilitation, an outcrosser can become as reproductive as a selfer and yet avoid all the costs associated with an inbreeding mating system, though outbreeding depression can sometimes be costly. Outbreeding is the most common mode of reproduction, with more than 80% of plant species reproducing through outcrossing (Iqic and Kohn 2006). Can this high frequency of outcrossing in plant taxa be explained by evolutionary grounds alone? Clearly, there is no benefit for increased diversity, the well-known advantage of an outcrossing system, if the outcrosser fails to reproduce in the first place. An inbreeding mode of reproduction may then appear to be more successful as it solves the first problem (i.e. poor reproduction) and then embarks on dovetailing genotype and environment. An outcrossing system is only successful and prevails if its bearer has already assured reproduction. This raises the question of how an outcrosser can achieve reproductive success to benefit from the evolutionary eminence of its breeding system? Since many plant communities are composed of several plant species that overlap in flowering timing and share pollinators (Carvalho et al., 2014; Ghazoul 2006; Janovský et al., 2013; Moreira et al., 2015), we believe that facilitative interactions could be common and sufficient to provide the required reproductive assurance. Pollination facilitation may therefore offer a complementary explanation as to why outcrossing is very common amongst plant species.

While our model incorporated several key aspects pertinent to plant and pollination ecology, some simplifications were implemented to make the model tractable. First, although the model incorporated competition for pollination quantity (Kunin 1993)

through $F_A(n, m)$ in Eq.7, it did not include interference through interspecific pollen transfer (IPT) (Morales and Traveset 2008; Waser 1978) where the deposition of improper pollen (*sensu* Rathcke 1983) on the stigma can reduce the fertilization rate in the recipient flower (e.g. Caruso and Alfaro 2000; Jakobsson et al., 2008; Randall and Hilu 1990;). The facilitation domain may decrease should competition for the pollination quality (i.e. IPT) be incorporated into the model. Second, our model allows for a facilitative interaction only through pollinator sharing; however, the second species can assist its neighbouring species in multifarious ways such as providing shade under dry and hot conditions (Holmgren 2000), protection against enemies (Callaway et al., 2005) and fixing nitrogen (Carlsson and Huss-Danell 2003). One possible way to incorporate these alternative facilitative effects into the model is by assigning negative values to the α parameter in the denominator of Eq.5 i.e. $\beta(n + \alpha m)$: an $\alpha < 0$ means that the second species improve the abiotic conditions for the focal species. As our primary interest was the net effects of pollination in driving facilitation, the other facilitation mechanisms that can be envisaged from $\alpha < 0$ were not investigated. Third, our model is non-spatial and thus assumes that the two plant species are mixed homogeneously over space, so that the probability of plant-pollinator encounter is proportional to their respective frequency. However, the spatial arrangement of plants can affect their interaction with visitors, so there can be the possibility for a facilitative (or competitive) interaction (de Waal et al. 2015; Geslin et al., 2014; Seifan et al., 2014). For example, the results of both theoretical models and manipulative experiments suggest that aggregation of plants in dense patches can increase fecundity or reduce extinction risk when the focal species occurs at low relative densities (de Waal et al. 2015; Hanoteaux et al., 2013). Fourth, a more realistic model needs to make a link between the population dynamics of plant and the pollinator(s) (see Song and Feldman 2014). For example, if the population size of pollinators increases with the size of the plant population (because of ample food supply), then the visitation response curve (Eq.3) is not expected to level off at high densities. Such a direct link may exist for a strong mutualistic relationship as in the fig and fig wasps complex where the pollinators live inside the inflorescence (Wiebes 2009). However, with such specialist pollinators the visitation rate is not expected to depend (or only weakly depend) on the population size of host plant. Nonetheless, generalist bees are more likely to be constrained by the availability of nest sites than floral resources (Pauw 2007). Finally, our model was based on the unidirectional effects where we only considered the effects of the second species on the focal species but the not the reverse effects.

5. Conclusion

Our model predicted that a co-flowering plant species can enhance reproduction of its neighbouring species by sharing pollinators. However, the overall impact of a co-flowering species on its neighbour can be negative or positive depending on the degree of interspecific competition for abiotic resources, the pollinator's response to plant density, the density and attractiveness of the interacting species and the breeding system of the focal species. Our model predicted that the optimal density of co-flowering species required for an overall facilitative outcome is smaller than the density at which the focal species receives the maximum pollination. However, attractiveness in the co-flowering species had a global optimum for both pollination and the overall facilitation because attractiveness has no effect on competition for abiotic resources. A selfing breeding system can deprive the focal species of potential benefits provided by a co-flowering species highlighting an indirect cost for this mode of reproduction. Only when pollinators

respond to plant density following a type III functional response, can a co-flowering species increase pollination in its neighbour.

As reviewed by Callaway (2007) there is ample empirical evidence for positive interactions and their pivotal role in plant communities. Here, our mathematical model provided further theoretical instances of facilitative interactions between two plant species.

Acknowledgments

R.D.C. and M.B.M acknowledge funding from Australian Research Council Discovery Grant DP140100608. JB was funded by a PIMS Postdoctoral Fellowship and the University of Alberta. M.A.L. acknowledges funding from the Natural Sciences and Engineering Research Council and a Canada Research Chair.

Appendix A

As discussed in the Result (Section 3.1.1.), there are critical values for the attractiveness (w_c) and density (m_c) of the co-flowering species at which the fertilization ratio f in the focal species will become unity (i.e. no facilitation can be obtained when $w = w_c$ or $m = m_c$). We also noted that when the density of the focal species reaches the so-called critical value of Allee ceiling (n_c), the negative effects of the second species will start to outweigh its positive effects, so to maintain $f = 1$, the second species should not exist i.e. $w = w_c = 0$ or $m = m_c = 0$ should hold. When $n = n_c$, the fertilization ratio f will become < 1 if $w_c > 0$ or $m_c > 0$. Here we present the derivation of n_c by finding $w_c = 0$ for which we first need to obtain w_c (the procedure is the same for m_c so we only show the results for w_c). w_c is the critical attractiveness w at which the fertilization ratio $f = 1$. We therefore need to solve the following equation for w :

$$f = \frac{s + (1 - s) \frac{(\rho(n+wm))^\gamma}{1+(\rho(n+wm))^\gamma} \cdot \frac{n}{n+wm}}{s + (1 - s) \frac{(\rho n)^\gamma}{1+(\rho n)^\gamma}} = 1, \tag{1a}$$

which does not have an explicit, closed solution. However, we can solve Eq.1a iteratively for various integer values of γ parameter.

Let $\gamma = 2$; now, solving Eq.1a for w returns the following positive, non-zero solution:

$$w_c = -\frac{n - \frac{1}{\rho^2 n}}{m}.$$

Note that we did not use $\gamma = 1$ as we already know that no facilitation can be provided by a saturating, Hetering Type II function (see the Result Section 3.1.3).

We now solve for $w_c = 0$, which gives us:

$$\rho_2 = \frac{1}{n}.$$

Now let $\gamma = 3$; the positive, non-zero solution for Eq.1a is:

$$w_c = -\frac{n - \frac{(4\rho^3 n^3 + 1)^{\frac{1}{2} + 1}}{2\rho^3 n^2}}{m},$$

which after solving for $w_c = 0$ gives us:

$$\rho_3 = \left(\frac{2}{n^3}\right)^{\frac{1}{3}}.$$

Finally, let $\gamma = 4$; the positive, non-zero solution for Eq.1a is:

$$-w_c = \frac{\frac{1}{3\rho^4 n^2} + \frac{1}{9\rho^8 n^6}}{\left(\left(\frac{1}{2\rho^4 n} + \frac{1}{6\rho^8 n^5} + \frac{1}{27\rho^{12} n^9} \right)^2 - \left(\frac{1}{3\rho^4 n^2} + \frac{1}{9\rho^8 n^6} \right)^3 \right)^{\frac{1}{2}} + \frac{1}{2\rho^4 n} + \frac{1}{6\rho^8 n^5} + \frac{1}{27\rho^{12} n^9}} + \frac{1}{3\rho^4 n^2}$$

$$n + \left(\left(\frac{1}{2\rho^4 n} + \frac{1}{6\rho^8 n^5} + \frac{1}{27\rho^{12} n^9} \right)^2 - \left(\frac{1}{3\rho^4 n^2} + \frac{1}{9\rho^8 n^6} \right)^3 \right)^{\frac{1}{2}} + \frac{1}{3\rho^4 n^2}$$

which after solving for $w_c = 0$ gives us:

$$\rho_4 = \left(\frac{3}{n^4} \right)^{\frac{1}{4}}$$

A list of solutions for a range of γ (integer) values is given in the table below:

$\gamma = 2$	$\rho_2 = 1/n$
$\gamma = 3$	$\rho_3 = (2/n^3)^{1/3}$
$\gamma = 4$	$\rho_4 = (3/n^4)^{1/4}$
$\gamma = 5$	$\rho_5 = (4/n^5)^{1/5}$
$\gamma = 6$	$\rho_6 = (5/n^6)^{1/6}$
$\gamma = 7$	$\rho_7 = (6/n^7)^{1/7}$
$\gamma = 8$	$\rho_8 = (7/n^8)^{1/8}$
$\gamma = 9$	$\rho_9 = (8/n^9)^{1/9}$
$\gamma = 10$	$\rho_{10} = (9/n^{10})^{1/10}$

From the observed pattern we can derive the general formula, which is valid at least $\forall \gamma \in \{2, \dots, 10\}$:

$$\rho_c = \frac{(\gamma - 1)^{\frac{1}{\gamma}}}{n} \tag{2a}$$

For example, if $\gamma = 2$, then $\rho_c = \frac{\sqrt{2-1}}{n} = \frac{1}{n}$, as shown in the table above. Now, from Eq.2a, we derive the Allee ceiling, which is the density of the focal species that gives the $w_c = 0$:

$$\forall \gamma \in \{2, \dots, 10\}: n_c = \frac{(\gamma - 1)^{\frac{1}{\gamma}}}{\rho} \tag{3a}$$

Eq.3a is also a solution to $m_c = 0$ i.e. when $n = n_c$ and $m = 0$ then $f = 1$ and if $m > 0$ then $f < 1$. In biological terms, if the density of the focal species is equal to n_c , the density and/or attractiveness of a second species should be less than zero to be able to facilitate the pollination of the focal species.

Appendix B

To obtain the critical value of α at which the competition ratio c is equal to the maximum fertilization ratio, f_0 , we first substitute the w in the f equation:

$$f = \frac{s + (1 - s) \frac{(\rho(n+wm))^\gamma}{1+(\rho(n+wm))^\gamma} \cdot \frac{n}{n+wm}}{s + (1 - s) \frac{(\rho n)^\gamma}{1+(\rho n)^\gamma}} \tag{1b}$$

with the optimal attractiveness w_0 (Eq.15 in the main text):

$$w \equiv w_0 = \frac{(\gamma - 1)^{\frac{1}{\gamma}} - \rho n}{\rho m} \tag{2b}$$

to obtain:

$$f_0 = \frac{s + (1 - s) \frac{\left(\rho \left(n + \left(\frac{(\gamma - 1)^{\frac{1}{\gamma}} - \rho n}{\rho m} \right) m \right) \right)^\gamma}{1 + \left(\rho \left(n + \left(\frac{(\gamma - 1)^{\frac{1}{\gamma}} - \rho n}{\rho m} \right) m \right) \right)^\gamma} \cdot \frac{n}{n + \left(\frac{(\gamma - 1)^{\frac{1}{\gamma}} - \rho n}{\rho m} \right) m}}{s + (1 - s) \frac{(\rho n)^\gamma}{1 + (\rho n)^\gamma}} \tag{3b}$$

which after simplification gives:

$$f_0 = \frac{\left(s - \frac{\rho n(s-1) \left((\gamma - 1)^{\frac{1}{\gamma}} \right)^b}{\left((\gamma - 1)^{\frac{1}{\gamma}} + 1 \right) (\gamma - 1)^{\frac{1}{\gamma}}} \right) ((\rho n)^\gamma + 1)}{s + (\rho n)^\gamma} \tag{4b}$$

Now we need to find α such that the competition ratio c (Eq.14) equals f_0 i.e. $\{\alpha : c = f_0\}$:

$$\alpha_w \equiv \left\{ \alpha : \frac{\left(s - \frac{\rho n(s-1) \left((\gamma - 1)^{\frac{1}{\gamma}} \right)^b}{\left((\gamma - 1)^{\frac{1}{\gamma}} + 1 \right) (\gamma - 1)^{\frac{1}{\gamma}}} \right) ((\rho n)^\gamma + 1)}{s + (\rho n)^\gamma} = \frac{1 + \beta n + \beta \alpha m}{1 + \beta n} \right\} \tag{5b}$$

which gives:

$$\alpha_w = \frac{\left(\frac{\left(s - \frac{\rho n(s-1) \left((\gamma - 1)^{\frac{1}{\gamma}} \right)^b}{\left((\gamma - 1)^{\frac{1}{\gamma}} + 1 \right) (\gamma - 1)^{\frac{1}{\gamma}}} \right) ((\rho n)^\gamma + 1)}{s + (\rho n)^\gamma} - 1 \right) (\beta n + 1)}{\beta m} \tag{6b}$$

where α_w is relative competitiveness of the co-flowering species at which the maximum fertilization ratio, f_0 , equals the abiotic competition from the co-flowering species, suggesting that the co-flowering species will not provide any facilitation if its relative competitiveness α equals α_w (Eq.6b).

Appendix C

To obtain the critical value of α for which the c line stands above the f curve regardless of the value of m , we first notice that f stands below its tangent at 0. Indeed computing the first derivative of f with respect to m , we obtain

$$\frac{\partial f}{\partial m} = Constant \cdot \frac{wn(\rho(n+wm))^\gamma (\gamma - 1 - (\rho(n+wm))^\gamma)}{[(1 + (\rho(n+wm))^\gamma)^2]}$$

where the $Constant := \frac{1-s}{s+(1-s) \cdot \frac{(\rho n)^\gamma}{1+(\rho n)^\gamma}}$ is positive and independent

of m . One can thus conclude that f as a function of m , is increasing for all $m < \frac{(\gamma - 1)^{1/\gamma} - \rho n}{\rho w}$ and decreasing for larger values of m . Now computing the second derivative of f with respect to m , we obtain:

$$\frac{\partial^2 f}{\partial m^2} = Constant \cdot \frac{(\rho(n+wm))^\gamma \cdot wn \cdot w}{[(1 + (\rho(n+wm))^\gamma)(n+wm)]^3} \cdot (\gamma - 1 - (\rho(n+wm))^\gamma) [\gamma(1 + (\rho(n+wm))^\gamma) - 2\gamma(\rho(n+wm))^\gamma - 2(1 + (\rho(n+wm))^\gamma)]$$

where $Constant$ is the same positive constant independent of m defined above. The terms on the first line of this equation are all positive, and the terms in the second and third lines are positive

for all $m < \frac{(\gamma - 1)^{1/\gamma} - \rho n}{\rho w}$ as soon as $\gamma \geq 2$. This implies that f , as a function of m , is concave for all $m < \frac{(\gamma - 1)^{1/\gamma} - \rho n}{\rho w}$. From these two

facts (f increasing concave for all $m < \frac{(\gamma - 1)^{1/\gamma} - \rho n}{\rho w}$ and f decreasing for all $m > \frac{(\gamma - 1)^{1/\gamma} - \rho n}{\rho w}$) we can conclude that f as a function of m

stands below its tangent at 0. Thus to compute the critical α value such that the c line stands above the f curve regardless of the value of m , we define $\alpha_m := \{\alpha > 0 : \alpha = \partial f / \partial m(m = 0)\}$ and thus

$$\alpha_m = \frac{(1 - s) \cdot w \cdot (\rho n)^\gamma (\gamma - 1 + (\rho n)^\gamma)}{(s + (\rho n)^\gamma)(1 + (\rho n)^\gamma)n}$$

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.jtbi.2017.04.011](https://doi.org/10.1016/j.jtbi.2017.04.011).

References

- Anderson, L.J., Brumbaugh, M.S., Jackson, R.B., 2001. Water and tree-understorey interactions: a natural experiment in a savanna with oak wilt. *Ecology* 82, 33–49.
- Baker, H.G., 1955. Self-compatibility and establishment after “long-distance” dispersal. *Evolution* 9, 347–349.
- Bernhardt, C.E., Mitchell, R.J., Michaels, H.J., 2008. Effects of population size and density on pollinator visitation, pollinator behavior, and pollen tube abundance in *Lupinus perennis*. *Int. J. Plant Sci.* 169, 944–953.
- Bouhours, J., Mesgaran, M.B., Cousens, R.D., Lewis, M.A., 2017. Neutral hybridization can facilitate invasion by improving pollination quality. *Theor. Ecol.* doi:10.1007/s12080-017-0333-4.
- Bruno, J.F., 2000. Facilitation of cobble beach plant communities through habitat modification by *Spartina alterniflora*. *Ecology* 81, 1179–1192.
- Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003. Inclusion of facilitation into ecological theory. *Trends Ecol. Evol.* 18, 119–125.
- Brys, R., Jacquemyn, H., Hermy, M., 2008. Pollination efficiency and reproductive patterns in relation to local plant density, population size, and floral display in the rewarding *Listera ovata* (Orchidaceae). *Bot. J. Linn. Soc.* 157, 713–721.
- Callaway, R.M., 2007. Positive Interactions and Interdependence in Plant Communities. Springer, The Netherlands.
- Callaway, R.M., Kikodze, D., Chiboshvili, M., Khetsuriani, L., 2005. Unpalatable plants protect neighbors from grazing and increase plant community diversity. *Ecology* 86, 1856–1862.
- Carlsson, G., Huss-Danell, K., 2003. Nitrogen fixation in perennial forage legumes in the field. *Plant Soil* 253, 353–372.
- Caruso, C.M., Alfaro, M., 2000. Interspecific pollen transfer as a mechanism of competition: effect of *Castilleja linariaefolia* pollen on seed set of *Ipomopsis aggregata*. *Can. J. Bot.* 78, 600–606.
- Carvalho, L.G., Biesmeijer, J.C., Benadi, G., Fründ, J., Stang, M., Bartomeus, I., Kaiser-Bunbury, C.N., et al., 2014. The potential for indirect effects between co-flowering plants via shared pollinators depends on resource abundance, accessibility and relatedness. *Ecol. Lett.* 17, 1389–1399.
- Charlesworth, D., 2003. Effects of inbreeding on the genetic diversity of populations. *Phil. Trans. R. Soc. B. Discipline Biology* 358, 1051–1070.
- Charnov, E.L., 1976. Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* 136, 129–136.
- Cheptou, P.-O., 2004. Allee effect and self-fertilization in hermaphrodites: reproductive assurance in demographically stable populations. *Evolution* 58, 2613–2621.
- Corless, R.M., Gonnert, G.H., Hare, D.E.G., Jeffrey, D.J., Knuth, D.E., 1996. On the Lambert W function. *Adv. Comput. Math.* 5, 329–359.
- Dauber, J., Biesmeijer, J.C., Gabriel, D., Kunin, W.E., Lamborn, E., Meyer, B., Nielsen, A., et al., 2010. Effects of patch size and density on flower visitation and seed set of wild plants: a pan-European approach. *J. Ecol.* 98, 188–196.
- de Waal, C., Anderson, B., Ellis, A.G., 2015. Relative density and dispersion pattern of two southern African Asteraceae affect fecundity through heterospecific interference and mate availability, not pollinator visitation rate. *J. Ecol.* 103, 513–525.
- Duffy, K.J., Patrick, K.L., Johnson, S.D., 2013. Does the likelihood of an Allee effect on plant fecundity depend on the type of pollinator? *J. Ecol.* 101, 953–962.
- Duffy, K.J., Stout, J.C., 2011. Effects of conspecific and heterospecific floral density on the pollination of two related rewarding orchids. *Plant Ecol.* 212, 1397–1406.
- Elliott, S.E., Irwin, R.E., 2009. Effects of flowering plant density on pollinator visitation, pollen receipt, and seed production in *Delphinium barbeyi* (Ranunculaceae). *Am. J. Bot.* 96, 912–919.
- Feinsinger, P., 1987. Effects of plant species on each other's pollination: Is community structure influenced? *Trends Ecol. Evol.* 2, 123–126.
- Feldman, T.S., 2006. Pollinator aggregative and functional responses to flower density: does pollinator response to patches of plants accelerate at low-densities? *Oikos* 115, 128–140.
- Feldman, T.S., Morris, W.F., Wilson, W.G., 2004. When can two plant species facilitate each other's pollination? *Oikos* 105, 197–207.
- Fisher, R.A., 1941. Average excess and average effect of a gene substitution. *Ann. Eugen.* 11, 53–63.
- Geslin, B., Baude, M., Mallard, F., Dajoz, I., 2014. Effect of local spatial plant distribution and conspecific density on bumble bee foraging behaviour. *Ecol. Entomol.* 39, 334–342.
- Ghazoul, J., 2006. Floral diversity and the facilitation of pollination. *J. Ecol.* 94, 295–304.
- Hanoteaux, S., Tielbörger, K., Seifan, M., 2013. Effects of spatial patterns on the pollination success of a less attractive species. *Oikos* 122, 867–880.
- Holmgren, M., 2000. Combined effects of shade and drought on tulip poplar seedlings: trade-off in tolerance or facilitation? *Oikos* 90, 67–78.
- Hutchinson, G.E., 1957. Concluding remarks. *Cold. Spring. Harb. Symp. Quant. Biol.* 22, 415–427.
- Igic, B., Kohn, J.R., 2006. The distribution of plant mating systems: study bias against obligately outcrossing species. *Evolution* 60, 1098–1103.
- Jakobsson, A., Padrón, B., Traveset, A., 2008. Pollen transfer from invasive *Carpobrotus* spp. to natives – a study of pollinator behaviour and reproduction success. *Biol. Cons.* 141, 136–145.
- Janovský, Z., Mikát, M., Hadrava, J., Horčíčková, E., Kmecová, K., Požárová, D., Smyčka, J., et al., 2013. Conspecific and heterospecific plant densities at small-scale can drive plant-pollinator interactions. *PLoS ONE* 8, e77361.
- Johnson, S.D., Hollens, H., Kuhlmann, M., 2012. Competition versus facilitation: conspecific effects on pollinator visitation and seed set in the iris *Lapeirousia oreogena*. *Oikos* 121, 545–550.
- Johnson, S.D., Peter, C.I., Nilsson, L.A., Ågren, J., 2003. Pollination success in a deceptive orchid is enhanced by co-occurring rewarding magnet plants. *Ecology* 84, 2919–2927.
- Jones, K.N., 1997. Analysis of pollinator foraging: tests for non-random behaviour. *Func. Ecol.* 11, 255–259.
- Kunin, W., 1993. Sex and the single mustard: population density and pollinator behavior effects on seed-set. *Ecology* 74, 2145–2160.
- Kunin, W.E., 1997. Population size and density effects in pollination: pollinator foraging and plant reproductive success in experimental arrays of *Brassica kaber*. *J. Ecol.* 85, 225–234.
- Kunin, W., Iwasa, Y., 1996. Pollinator foraging strategies in mixed floral arrays: density effects and floral constancy. *Theor. Popul. Biol.* 49, 232–263.
- Laverty, T.M., 1992. Plant interactions for pollinator visits: a test of the magnet species effect. *Oecol.* 89, 502–508.
- Levin, D.A., Anderson, W.W., 2016. Competition for pollinators between simultaneously flowering species. *Am. Nat.* 104, 455–467.
- Mesgaran, M.B., Lewis, M.A., Ades, P.K., Donohue, K., Ohadi, S., Li, C., Cousens, R.D., 2016. Hybridization can facilitate species invasions, even without enhancing local adaptation. *Proc. Natl. Acad. Sci. U.S.A.* 113, 10210–10214.
- Moeller, D.A., 2004. Facilitative interactions among plants via shared pollinators. *Ecology* 85, 3289–3301.
- Molina-Montenegro, M.A., Badano, E.I., Cavieres, L.A., 2008. Positive interactions among plant species for pollinator service: assessing the “magnet species” concept with invasive species. *Oikos* 117, 1833–1839.
- Morales, C.L., Traveset, A., 2008. Interspecific pollen transfer: magnitude, prevalence and consequences for plant fitness. *Crit. Rev. Plant. Sci.* 27, 221–238.
- Moreira, E.F., Boscolo, D., Viana, B.F., 2015. Spatial heterogeneity regulates plant-pollinator networks across multiple landscape scales. *PLoS ONE* 10, e0123628.
- Morgan, M.T., Wilson, W.G., Knight, T.M., 2005. Plant population dynamics, pollinator foraging, and the selection of self-fertilization. *Am. Nat.* 166, 169–183.
- Parrish, J.A.D., Bazzaz, F.A., 1976. Underground niche separation in successional plants. *Ecology* 57, 1281–1288.
- Pauw, A., 2007. Collapse of a pollination web in small conservation areas. *Ecology* 88, 1759–1769.
- Pyke, G.H., Pulliam, H.R., Charnov, E.L., 1977. Optimal foraging: a selective review of theory and tests. *Q. Rev. Biol.* 52, 137–154.
- Randall, J., Hilu, K., 1990. Interference through improper pollen transfer in mixed stands of *Impatiens capensis* and *I. pallida* (Balsaminaceae). *Am. J. Bot.* 69, 1022–1031.
- Rathcke, B., 1983. Competition and facilitation among plants for pollination. In: Real, L.A. (Ed.), *Pollination Biology*. Academic Press, Orlando, pp. 305–329.
- Robson, D.B., 2013. An assessment of the potential for pollination facilitation of a rare plant by common plants: *Symphytotrichum sericeum* (Asteraceae) as a case study. *Botany* 91, 34–42.
- Seifan, M., Hoch, E., Hanoteaux, S., 2014. The outcome of shared pollination services is affected by the density and spatial pattern of an attractive neighbour. *J. Ecol.* 102, 953–962.
- Sieber, Y., Holderegger, R., Waser, N.M., Thomas, V.F.D., Braun, S., Erhardt, A., Reyher, H.U., et al., 2011. Do alpine plants facilitate each other's pollination? Experiments at a small spatial scale. *Acta Oecol.* 37, 369–374.
- Song, Z., Feldman, M.W., 2014. Adaptive foraging behaviour of individual pollinators and the coexistence of co-flowering plants. *Proc. R. Soc. B.* 281, 20132437.
- Stephens, P.A., Sutherland, W.J., Freckleton, P.R., 1999. What is the Allee effect? *Oikos* 87, 185–190.
- Thomson, J.D., 1978. Effects of stand composition on insect visitation in two-species mixtures of *Hieracium*. *Am. Midl. Nat.* 100, 431–440.
- Tilman, D., 1982. Resource competition and community structure. *Monographs in Population Biology*, Vol. 17. Princeton University Press, Princeton, NJ, U.S.A.
- Tinbergen, N., Impeken, M., Franck, D., 1967. An experiment on spacing-out as a defence against predation. *Behaviour* 28, 307–320.
- Waser, N.M., 1978. Interspecific pollen transfer and competition between co-occurring plant species. *Oecology* 36, 223–236.
- Waser, N.M., 1983. Competition for pollination and floral character differences among sympatric plant species: a review of the evidence. In: Jones, C.E., Little, R.J. (Eds.), *Handbook of Experimental Pollination Biology*. Van Nostrand Reinhold, New York, pp. 277–293.
- Waser, N.M., Real, L.A., 1979. Effective mutualism between sequentially flowering plant species. *Nature* 281, 670–672.
- Wiebes, J.T., 2009. Coevolution of figs and fig wasps. *Annu. Rev. Ecol. Evol. Syst.* 10, 1–12.
- Willmer, P., 2011. *Pollination and Floral Ecology*. Princeton University Press, NJ, U.S.A.
- Wright, S.I., Kalisz, S., Slotte, T., 2013. Evolutionary consequences of self-fertilization in plants. *Proc. R. Soc. B.* 280, 20130133.