Optimal competitors: the balance of attraction and choices of mutualists, like pollinators, drives facilitation and may promote crop pollination

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Abstract

When two species use the same resource, this typically leads to competition, such as when different plants aim to attract the same mutualist pollinators. However, more flowers may also attract more pollinators to the area. Depending on which process dominates, one or both 'competitors' may actually benefit from the other's presence: a phenomenon called 'pollination facilitation' in plant ecology. For example, it has been argued that strips of wildflowers planted next to crops may attract pollinators who 'spill over' into the crop. Here we mathematically examine the tradeoff between facilitation and competition in consumer attraction. We show that contrary to previous claims, no accelerating benefits of density *per se* are necessary for facilitation. Instead, under very general assumptions, an imbalance between local competition and joint attraction of consumers can generate a benefit to at least one 'competitor'. This typically leads to maximal benefit to the crop at a low presence of highly attractive 'wildflowers' (i.e. plants that share pollinators with the crop). Our results generalize to many contexts where local competition may trade off with joint attraction of consumers. In such situations, the exact effect of competitor density on attraction of consumers can qualitatively shape outcomes, including facilitation or competition.

Introduction

Our views of ecology and evolution are frequently dominated by competition between individuals and species. However, it has become clear that in many cases, even organisms that depend on the same resource may facilitate each other's growth, within [1] or across species (in plants [2,3], animals [4,5], or microorganisms [6]). Individuals of other species may for example prepare habitats or provide additional resources, even while also competing for a joint resource [2,5]. It thus becomes important to understand under what conditions these positive effects outweigh the effects of competition, to yield an overall facilitative effect of one organism on another. Here we discuss this question in the context of species interactions, with the specific example of pollination facilitation.

Most flowering plants require animal pollinators in order to produce seeds, making pollination one of the most well-known mutualist interactions. Most plant species are visited by generalist pollinators, who have the potential to visit many species of plants [7–9]. Plants may thus compete for pollinator visits; on the other hand, large patches of flowers may attract more pollinators, potentially generating benefits from such high densities, in other words, facilitation [3,10–14]. While such facilitation has been argued for, empirical data have been inconclusive [5,15–18]. Our model provides some suggestions why this may be the case, i.e. why facilitation may depend the identity of the species involved and the scale of the study; it will thus allow progress in identifying the causes of context dependence [19].

The case of pollination facilitation in crops is also of particular applied importance [20–22]. Bees provide pollination services of importance to agriculture [23]. However, many bee species are declining [24,25], potentially leading to reduced pollination success [25,26]. This leads to a situation where crop yield may

be limited by the presence of pollinators [21,27]. One proposed solution has been to leave a small section of land next to crops uncultivated (or planted with wildflowers), to attract more pollinating insects, including bees, to the area [21,28]. This may have multiple benefits, including promoting endangered species of both pollinators and wild plant species [29,30] and reducing pests [21]. In particular however, it has been proposed that the presence of diverse plants that share pollinators with a crop may facilitate crop pollination via attraction of additional pollinators – but again with mixed empirical support ([20,21], and possibly [31,32]; no evidence found in [33,34] or a metaanalysis [28]). Some wildflowers are thought to be a natural competitor to crop plants over pollinator visits (sometimes termed the 'concentrator effect' because of concentration of bees at the field edge, [13]). If, on the other hand, crop and wildflowers jointly attract a higher total number of pollinators to the area, these might 'spill over' into the crop land (also termed the 'magnet effect', [10,28]). We use this scenario as the basis of our model, to explore the conditions under which two plants species who share a pollinator may facilitate or compete with each other over pollinator visits.

We derive general insights that apply to any situation in which two species attract the same consumers (whether these consumers are mutualists, as in pollination, or predators). In particular, we demonstrate that the tradeoff between consumer attraction and consumer choice can lead either to competition or facilitation. Our model is inspired by competition over pollinators in crops, but we expand on previous more general theory in plant ecology on pollination facilitation [14,35–37]. We add to these previous models by demonstrating that it is not necessary to assume a general Allee effect (i.e. an accelerating attraction of pollinators with plant density). That is, it is possible for another species to act as a facilitator even when increasing density of *con*specifics has negative (competitive) effects on individuals. We thus introduce a new general mechanism for facilitation, which depends on an imbalance between attraction of consumers to the area and local choices made by consumers (here, pollinators). This mechanism is likely to apply to other scenarios, including apparent competition, mass flowering, and mimicry, as well as outside of ecology to any situation in which two resource providers compete for consumers.

Model

Overview of our approach

We formulate a general model for the situation where two resources (which we term 'crop' and 'wildflowers') compete for consumers (for simplicity called 'bees'). 'Crop' and 'wildflowers' can be interpreted to be any two plant species sharing pollinators, such that we focus on the effect of the presence of the second of these two species on the first. We assume that 'more' of the wildflowers (w) increases the total number of bees in the area (N), but also leads a smaller fraction of these bees to visit the crop (D), creating a tradeoff (our notation is summarized in Tab. 1). We perform both analytical and numerical analyses to explore what determines the amount of wildflowers w^* that maximizes the number of bees on the crop, $F = ND$. We also analyze the amount by which pollinator visits to the crop increase with the presence of w, i.e. how much facilitation occurs.

D depends on the 'amount' w of wildflowers and the 'amount' c of the crop. Throughout, we assume that D is simply the fraction of the total resource that comes from the crop (i.e. input matching, [38,39]):

$$D(c, w) = c/[c + w]. \qquad [1]$$

This is also assumed in [14], their eq. 7, and implies only the ratio c/w is important in how bees divide up among resources locally). It can also be read to mean that our measure of 'value' of either species is

simply defined as the number of each that leads to bees choosing among the species equally at $c=w$ (thus for a species that is more attractive locally, the same 'value' may represent fewer individuals – our w represents the same as wm in [14], eq. 6). Note that (unlike [14,36]) we do not assume an ecological equilibrium, since we focus on a situation where both amount of crop and of wildflowers are the result of human decisions each year. This means our results do not depend on how exactly plant reproductive rate is determined by pollination, and makes our results applicable to other situations not in equilibrium (e.g. invasive species, [13,26,40,41]).

We specifically model (A) a situation in which the amount of wildflowers is independent of the (fixed) amount of crop c, and (B) one in which the total area available is fixed, and only a fraction of the area is devoted to wildflowers (with the rest taken up by the crop). This resembles a situation where the two plant types compete for a common resource other than the pollinators (as in [14,36]).

Model A: Independent w

In Model A we assume that c is fixed. To determine the optimal value of wildflowers, i.e. find w^* at which F is maximal, we first make a very general argument, which holds regardless of any specific assumptions about the shape of N other than that it is decelerating with w. F is maximal at

$$F'(w^*) = 0 \qquad [2]$$

So

$$\frac{\partial N}{\partial w}(c, w*)D(c, w*) + N(c, w*)\frac{\partial D}{\partial w}(c, w*) = 0 \qquad [3]$$

Given eq. [1], it follows that

$$\frac{\partial N}{\partial w} = \frac{N(c,w*)}{c+w*} \qquad [4]$$

Similarly to the graphical solution for the marginal value theorem [42], it can be graphically shown (Fig. 1a) that this implies that w^* increases as c increases.

Model A.1: N as decelerating function of w (power function)

For a more detailed analysis, we assume a particular shape of N (as [14]):

$$N(c, w) = Aw^a + N_c(c) \qquad [5]$$

$$0 < a < 1$$

This gives a relationship between N and w that is monotonically increasing but with diminishing returns (slope) as w increases (as Fig. 1d, f). In this case, the partial derivative of N at w^* (= $aAw^{*(a-1)}$ from eq. [5]) should be equal to

$$N(c, w^*)/(c + w^*) \qquad [6]$$

(cf. Fig. 1f).

It is reasonable to expect that the number of bees attracted to the area by the crop alone, i.e. with $w = 0$ ($N_c(c)$ in eq. [5]), increases with c. In the simple case of $N_c(c) = kc$, w^* satisfies

$$(w^*)^a (1 - a)/(a(w^*)^{(a-1)} - k/A) = c. \qquad [7]$$

Note that all combinations of k and A which have the same ratio k/A give the same w^*; this ratio relates the number of bees attracted to the area by the crop (relative to its 'amount', c) to that quantity for the wildflowers. For some parameter combinations, there is no positive w^*, i.e. wildflowers compete with the crop for pollinators at any amount (see Supplementary Information for numerical calculation of the effects of all parameters).

Eq. [7] is based on a non-decelerating relationship between c and $N_c(c)$. Since there are a finite number of bees in the world, this could not be true generally; but it is more likely to be a reasonable approximation if k (and thus $N_c(c)$) is small (the crop does not attract many pollinators to the area). Let

$$w_{\text{approx}}^* = ca/(1 - a), \qquad [8]$$

We note that for $N_c(c) = 0$, $w_{\text{approx}}^* = w^*$, as noted analogously by [43]. This suggests that eq. [8] gives a convenient approximation for w^* when $N_c(c)$ is small. Denoting the value of D if $w = w_{\text{approx}}^*$ by D_{approx}, it also suggests that for small N_c,

$$D_{\text{approx}} = c/[c + ca/[1 - a]] = 1 - a \qquad [9]$$

will be an approximation for $D(c, w^*)$. D_{approx} is an invariant [44–46], dimensionless in this case.

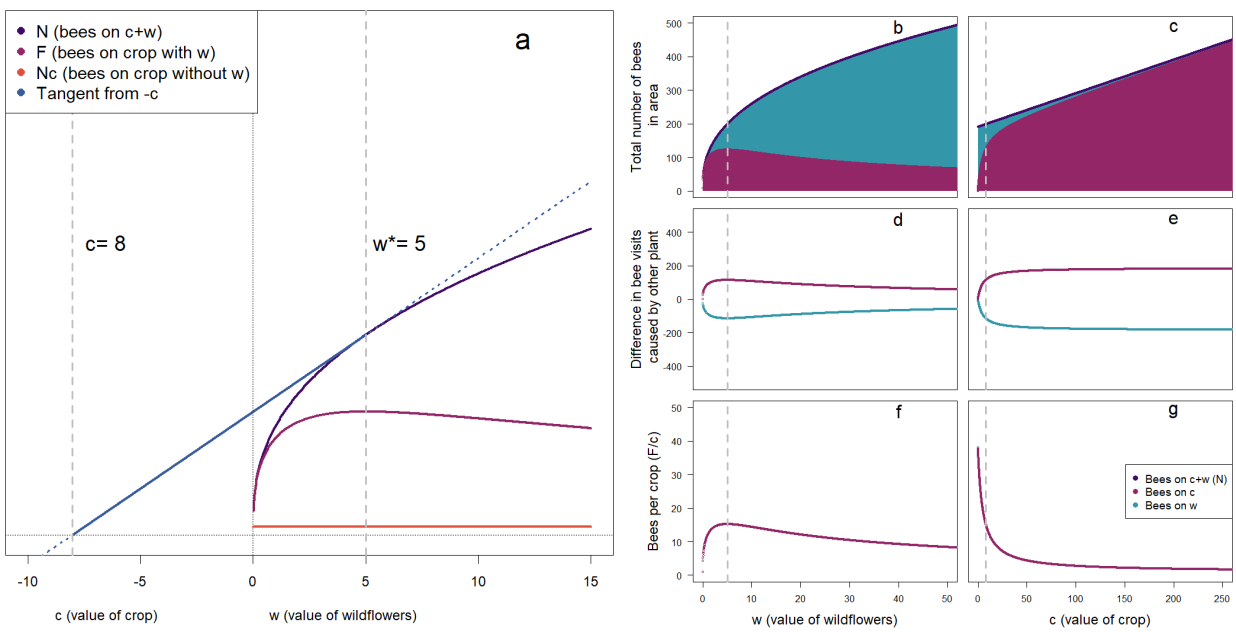

Fig. 1: The number of bees on the crop (F) peaks at a low but non-zero presence of the competitor (w), even when the number of bees attracted (N) is never accelerating with c+w. (a) Graphical solution to finding w^* (compare to marginal value theorem, [42]). We plot increasing w (value of wildflowers) on the right side of the x-axis, increasing c (value of crop) on the left. If we draw a tangent from the x-axis at -c on N, the tangent point gives w^*. This is because at this point, i.e. at (x=w^*, y=$N(w^*)$), both lines have the same slope, i.e. $N'(w)$ (slope of N) = $N(c, w)/(c+w)$ (slope of tangent), satisfying eq. [4] and thus maximizing F. N_c is the number of bees on the crop in the absence of w. In panels (b, d, f), c is kept fixed at 8, and in panels (c, e, g), w is kept fixed at 5. (b, c) Number of bees in total (N) and how they divide up between c and w. N increases with both w and c; here, we assume linear increase with c and decelerating with w (eq. [5] and [7]). F (bees on c) peaks at intermediate w. (d, e) The difference in the number of bees

on each species as a result of the presence of the other: bees gained by c (F-N_c, purple lines) are lost by w ((1-F)-N(c=0), blue lines) in this case. (f, g) The number of bees per value of w or c are by definition identical (eq. [1]), and monotonously decrease with c, but peak at intermediate w (because N decelerates with w but is linear in c, see Fig. 2). All panels: parameters a=0.4, and A=100.

The effect of attraction

While our solution above does not make very specific assumptions about the behavior of $N(c,w)$, it is based on a situation where N is decelerating with w (Fig. 1). That is, the number of bees attracted increases more and more slowly with an increasing amount of wildflowers. However, the outcome for either species depends critically on how exactly N behaves. If the number of bees is simply proportional to the sum of crop and wildflowers available ($N=g(c+w)$, where g is a positive constant, Fig. 2a), then there is neither competition nor facilitation: each plant attracts exactly the number of bees as visit it (F stays constant over w). If, in addition to the above, there is a constant number L of local bees, and the number of bees attracted to the area remains $N=g(c+w)$, then competition for these local bees occurs, and the number of bees visiting the crop is reduced by any presence of wildflowers (Fig. 2b). However, if wildflowers are disproportionately good at attracting pollinators ($N=Agw+gc$, Fig. 2c), or if either crop or wildflowers show diminishing returns in attracting pollinators (merely decelerating, $N=Aw^a + Ac^a$, Fig. 2d; or saturating, N=(1-exp(-aw)) + (1-exp(-ac)), Fig. 2e; we examine this case in more detail in the Supplementary Materials), then the number of bees attracted by wildflowers does not behave as the fraction of bees that then choose wildflowers once they arrive in the area. As a result, the number of bees visiting the crop (F) does not stay constant with the value of wildflowers present, and facilitation or competition may result. Past models have emphasized situations in which there is initially an acceleration of N with $g(c+w)$, [14,36], such as in a sigmoid relationship (cf. Holling type III functional response, $N=(r(c+w))^y/(1+((r(c+w))^y)$, Fig. 2f). In such a case both increasing density of conspecifics and heterospecifics leads to more bees attracted, also enabling facilitation (Fig. 2f). However, we as show here, such acceleration is not a necessary condition for facilitation (cf. Fig. 2c-e).

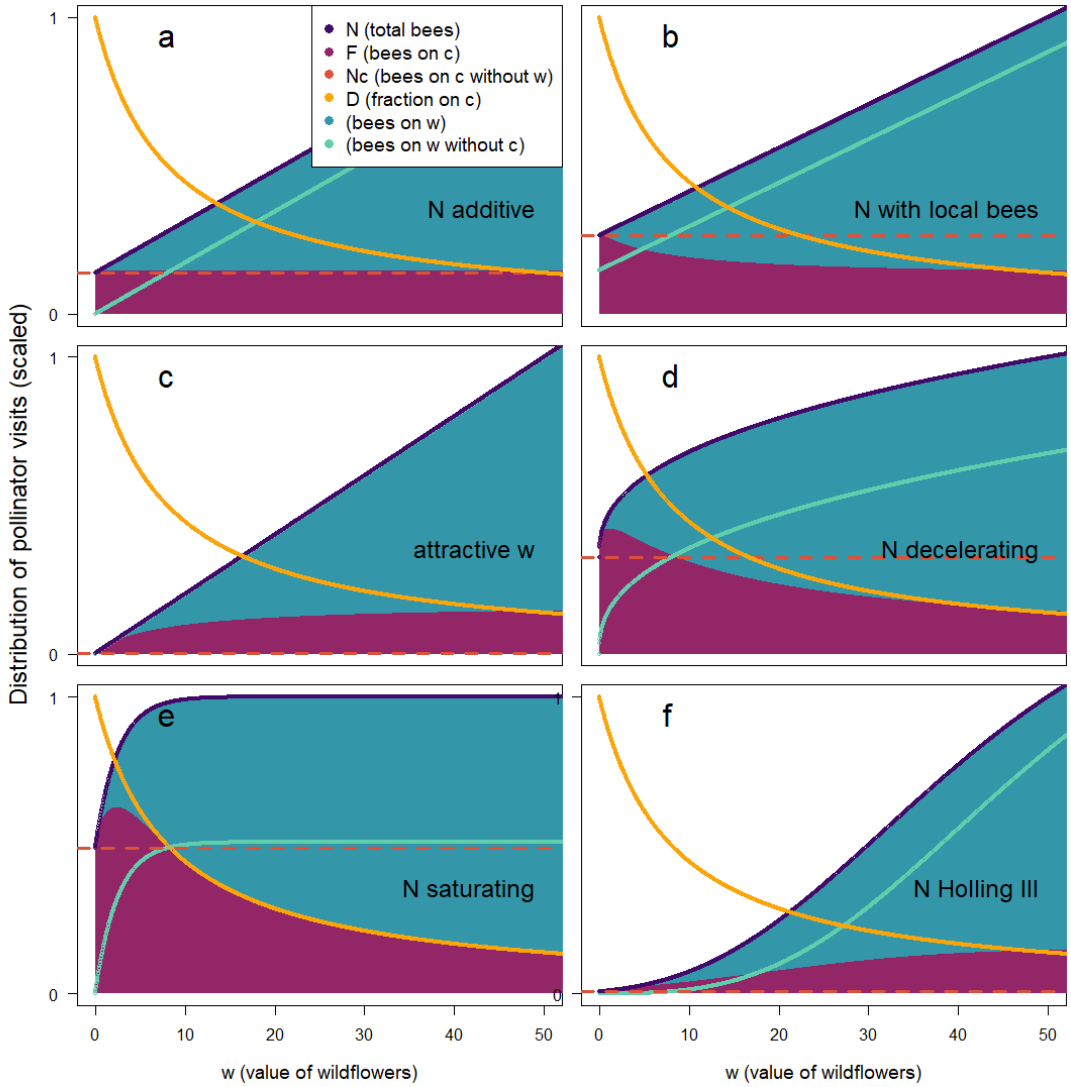

Fig. 2: The qualitative effect of different relationships of the number of bees attracted, N, with w. w has no effect in (a), competes with the crop (reduces F) in (b), facilitates the crop (increases F) in (c), and can have different effects at different w in (d,e,f). In all panels, N is scaled to 1 at w=50 (and F and the analogous number of bees on the wildflowers are scaled accordingly). Parameters are set to a=0.4, A=100, L=10, r=0.02, y=3, g=1. D, the fraction of pollinators on the crop, is the same in all panels as it only depends on c and w (not N). F is the product of D and N. Wherever F (bees on crop) is above N_c (bees on crop without w), facilitation is occurring.

<u>Model B: Fixed total area, such that *c* and *w* trade off</u>

Alternatively, we might assume that the total area in which either crop or wildflowers can be planted is fixed. Thus, increasing the amount of wildflowers requires a corresponding reduction in the amount of crop. We designate p as the proportion of total area devoted to wildflowers; the proportion of area devoted to crop is thus 1 - p. We further designate b as the relative value of wildflowers per area compared to the value of crop per area. If we standardize the 'value' of the crop at p = 0 to 1, then

$$c = 1 - p \quad [10a]$$

$$w = bp. \quad [10b]$$

The number of bees and the fraction on the crop are now functions of p so we change our notation to $N_p(p)$ and $D_p(p)$ to reflect this. We expect $b > 1$ as we assume that wildflowers are more attractive to bees than the crop is (per area). As a result, we expect that increasing p will increase N_p, decrease D_p, and decrease the area available for the crop. We want to maximize yield (f), which we take to depend linearly both on the number of bees visiting the crop (N_pD_p) and the crop area (total area multiplied by $(1 - p)$). Thus,

$$f = N_pD_p(1 - p)(\text{total area}). \quad [11]$$

At maximal f, $f' = 0$. Note that N_p and D_p both depend on p, but 'total area' is a scaling factor that does not affect the optimum. The differential (with respect to p) of the product of the three terms that depend on p is

$$N_p'D_p\,(1 - p) + N_pD_p'(1 - p) - N_pD_p\,. \quad [12]$$

This equals 0 at $p = p^*$, giving

$$\mathrm{d/dp}\,(N_pD_p\,) = N_pD_p\,/(1 - p^*). \quad [13]$$

Analogously to Model A, we assume a form for N that implies a decelerating effect of resource availability on the number of bees attracted:

$$N = A_w(bp)^a + A_c(1\text{-}p)^a \quad [14]$$

We numerically find f for different parameter values, as well as the resulting p^* (Fig. 3; see Supplementary Information for numerical calculation of the effects of all parameters, including the case where the exponents a corresponding to c and w are not the same).

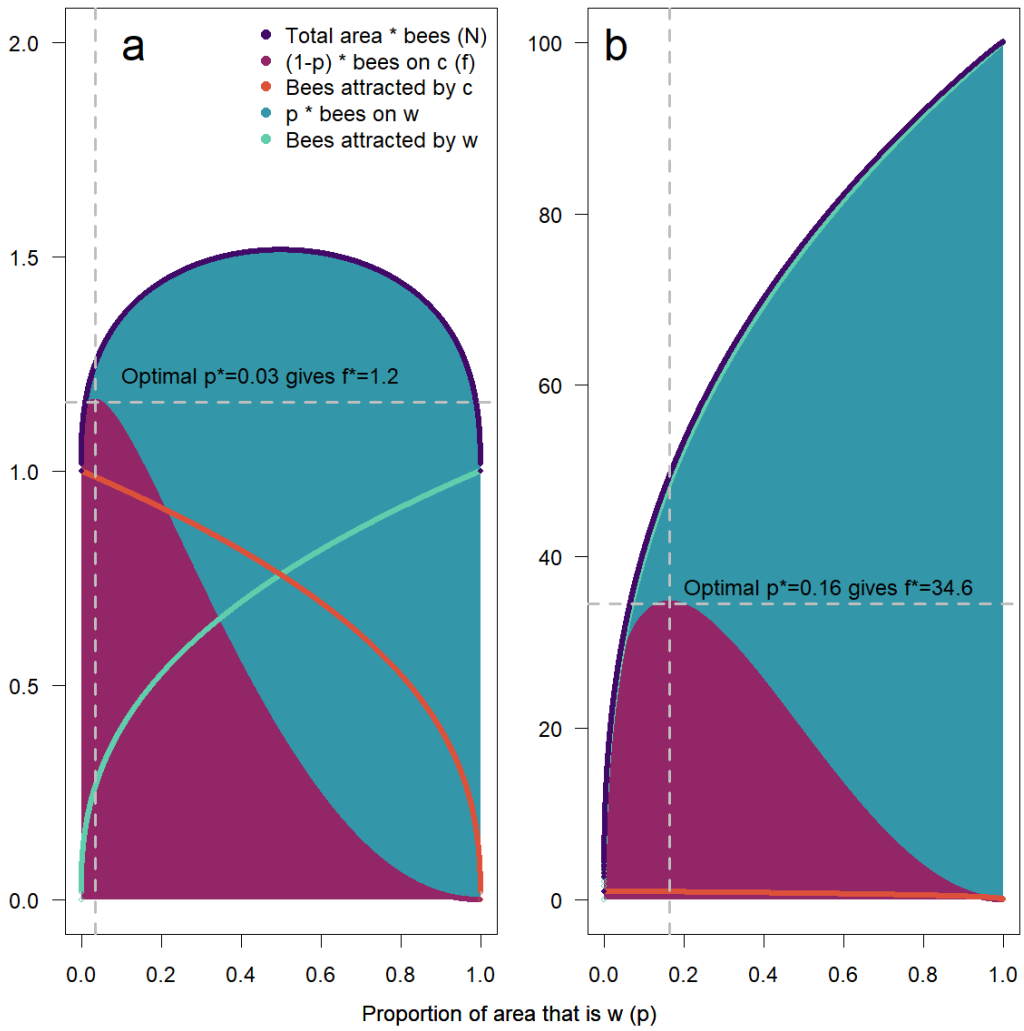

Fig. 3: The 'yield' (area multiplied by number of bees) for each resource in Model B (total area fixed). (a) Even assuming both resources are exactly equal in value (A_w=A_c=1, b=1, a=0.4), because of the decelerating returns in attraction from each resource individually (eq. [14]), the total number of bees (and thus yield) is highest at p=0.5. However, because bees choose both resources in proportion to their value, the more abundant resource achieves a net benefit from a small presence of the other resource (here, f peaks at p=0.03). (b) If w is much more attractive than c (A_w =100, A_c=1), the total number of bees attracted is almost exclusively driven by w (and thus increases with p). But because f is determined by 1-p as well as the number of bees on c, there is a tradeoff. Nonetheless, a more attractive w ultimately leads to a benefit for c (f* is higher for higher A_w).

Discussion

What makes a neighbor a competitor? When success depends on the attraction of consumers (such as mutualist pollinators), the presence of other individuals that contribute to such attraction may lead to benefits, whether they are conspecifics or heterospecifics. Previous theory had shown that as long as pollinator attraction accelerates with density of plants, higher density is beneficial to individuals [14,36]; this is a specific example of facilitation [2] or the Allee effect [5]. Here we show that such

disproportionate benefits of density (i.e. accelerating attraction of pollinators) are not necessary for one species to facilitate pollination of another. Instead, we show generally that the balance of competition and facilitation in pollination can be driven by the balance (or imbalance) between pollinator attraction-to-the-area and the choices-made-locally. This is because as the abundance of the potential competitor plant increases, it increases both the total number of pollinators attracted (a benefit) and draws such pollinators to itself (a cost) – but while these two processes trade off, they need not behave in the same way with increases in abundance (see also [18]).

The difference between attracting pollinators to the area and local choices of pollinators

The types of traits that make a flower attract pollinators to a local area are not necessarily the same ones that drive the proportion of visits to that flower type over another. First, how flowers are perceived from a distance is determined by different aspects than how flowers are perceived nearby (e.g. olfactory vs visual signals, [47,48]). Second, pollinators may often require and seek out micronutrients, which can attract them over some distance, even when the proportion of visits needed to flowers offering those nutrients is not large [49–51]. Third, 'attraction' may occur over different (longer) timescales than local choices, for example when bees are attracted to nest near particular species [22,52], or if bees make long foraging trips only to some patches but once there visit almost all available flowers [37,53,54]. In one system, extremely fast local reproduction combined with slow (if any) movement between patches of the pollinators may have led to extreme pollination facilitation (and concomitant evolution of mass flowering, [55]). While we don't explicitly model such temporal dynamics, they can lead to different effects of the abundance of a particular plant species on attraction of bees vs. choices of bees in the local area. Fourth, we frame the 'local area' that bees are attracted to as a spatial location, but it may be viewed as any set of flowers that bees, once attracted, are faithful to: for example, a learned color ('flower constancy', [56,57]). In this case 'attraction' is about how likely bees are to become flower-constant on the particular color or flower type, while 'choice' reflects (as before) how bees that are already committed (flower constant) on this type choose among the different species [57,58]. In all these cases, the number of pollinators available (N in our model) behaves differently than the proportion of bees visiting a focal plant species (D in our model), leading the 'neighboring' species to become either a competitor or facilitator. Moreover, a non-linear attraction of bees can lead to non-zero-sum effects, where both plant species may facilitate (or harm) each other (see Fig. 2).

In the context of promoting crop pollination, our model shows that other flower species that lead to strong attraction of pollinators (disproportionate to their 'value' or ability to concentrate pollinator visits locally) are most beneficial. These might be species offering particular micronutrients, species with prominent long-distance signals, or species that encourage pollinators to travel long distances to a patch (perhaps because their flower type is easy to learn to handle but does not yield a lot of nectar). Our model also shows that mutual facilitation is more likely the more pollinators seek balanced diets (i.e. behave as if each species individually yields diminishing returns, as Fig. 3). Empirical data are needed to better estimate the way attraction relates to abundance of different species in general [18,20] or in the specific cases relevant for increasing crop pollination.

Importantly, our model shows that subtle variations in the functional relationship of attraction and choice with density have qualitative effects on species interactions. As in other cases [59–61], such qualitative consequences can occur even when the relationships look quantitatively similar. For example, both we (Fig. 2d) and previous authors [14,36] modeled pollinator attraction as a decelerating power function of each species' abundance, but only in our model does this enable facilitation (because we allow an imbalance between attraction and choice).

'Apparent' facilitation

The model presented here also provides a more general framework for thinking about species interactions at different scales, a framework that applies in systems other than pollination mutualism. Most obviously it may apply to other mutualistic interactions, for example beneficial microbes and fungi [62]. However, it also applies to antagonistic interactions. If we imagine the 'bees' in our model as predators, the conclusions from our model hold: the bees play the role of 'shared predator' (whether or not they consume the flowers themselves or just the nectar and pollen within is, after all, immaterial to the bees' choices), and the different flower species are the 'prey'. Thus, both the attraction of bees to the area and the choices of bees between specific flowers should follow the same principles as for a predator on a food source (that is consumed). It follows that the presence of a second prey species in a patch may lead to either increased predation on a focal species (the equivalent of pollination facilitation) or decreased predation (the equivalent of pollination competition, which in this case would be a facilitative effect). Whether predation pressure is increased or decreased by additional prey species will thus depend, analogously, on the ability of these other species to attract predators to the area (or to the type of prey, analogous to flower constancy, discussed above) relative to how likely predators are to choose that prey once they encounter it [63].

In ecology, the term 'apparent competition' refers to the phenomenon that two (prey) species may affect each other's population dynamics by virtue of their effects on a shared predator [64]. Typically, however, models of apparent competition focus on the effects of the prey on the actual population growth of the predator (and in turn how this affects the growth of the prey populations), rather than the sub-population-level processes modeled here (of patch and item choice of predators). Nonetheless, even though our model does not consider population growth for either crop, wildflowers, or bees, the process described by our model can also explain an effect of one prey species on another via a shared predator. Our model thus implies that in cases where any two prey species share a predator that may be attracted to a local area, a process like 'apparent competition' or 'apparent facilitation' could occur, and would depend on the abundance of both prey types as well as how it relates to their ability to attract predators (as in [63]).

For the particular case of crops and wildflowers, it should be noted that our model also applies to herbivores, i.e. potential pests. That is, if wild plants share herbivore consumers with the crop, they may attract such herbivores 'spilling over' into the crop land. Empirical data is needed to determine the degree of such spillover; the attractiveness of any particular plant to herbivores is not likely to be the same, or even scale in the same way with abundance, as the attractiveness to pollinators. What also bears mentioning here is that previous empirical data show spillover at yet another trophic level: wildflower margins next to crops may lead to higher abundance of insect predators, i.e. pest control [21].

Conclusion

In plant ecology, pollination facilitation has been much discussed (e.g. in models [14,36,37,65] or empirically [10,15–17,35]). Our study demonstrates that facilitation can occur even under very minimal assumptions, namely, just two ecological principles: the numerical response [66,67] and an ideal free distribution [17,68,69], both standard approaches when describing how consumers select between resources. Facilitation or competition can thus occur without the need to assume more complex processes like resource competition [14,36], flower constancy [18,37,58], nonlinear relationship of pollination and reproduction [70], or specific spatial or temporal scales [28,30,37]; we also do not require that pollinator attraction is an accelerating function of plant abundance [14,36]. Nonetheless, such other processes may of course affect the balance of competition and facilitation; if one wishes to make a prediction for a particular case, the quantitative contributions of these different processes have to be estimated.

However, the key novel insight from our study is that an imbalance between attraction to the local area and choice of pollinators within the area alone can generate pollination facilitation between plant species. Ultimately this tension between attraction at the larger spatial scale (e.g. the field, the patch, or a set of preferred resources/prey) and competition at the smaller scale (e.g. individual plants or prey, wildflowers vs a crop plant) affects the way in which different resources affect each other's consumer visits, with implications not only in pollination but species interactions across ecology (predator-prey interactions, mimicry) as well as other fields interested in the relationship between resources and consumers.

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Tables and Figures

Table 1: Parameters and basic assumptions.

Parameter name	Definition in Model A	Equivalent in Model B	Explanation
w	'Amount' of wildflowers	bp	The 'amount' of the potential competitor species includes both its density or area covered and its nectar value relative to the crop (not distinguished in Model A). In Model B, b is the value (per area) of wildflowers relative to crop, and p the proportion of area occupied by wildflowers.
c	'Amount' of crop	$1 - p$	In Model A this can be thought of as the area of crop; in Model B it is the proportion of total area devoted to crop.
L	Local bees		Number of bees present regardless of c and w
$N(c, w)$	Number of bees attracted to local area	N_p	A numerical response, which we assume depends on the combined amount of wildflowers and crop. We examine different functional forms of $N(c, w)$.
N_c	Number of bees attracted by c alone		The number of bees attracted by c when w=0; if w>0, this is not necessarily the number of bees visiting c, as bees attracted to the area by either plant can end up visiting the other plant, depending on D.
D	Fraction of bees in local area that visit the crop	D_p	Connects consumer choices to c and w based on an ideal free distribution.
F	Pollinators on crop, for simplicity 'yield'	f	This is the quantity we want to maximize. In Model A, this is the number of bees that visit the crop; in Model B, this is modified by the fraction of area used for crop.
w^*	Optimal w	w^*	In Model A, this is the value of w that maximizes F for a given c; in Model B, the value of w that maximizes f for a given p. We are interested in determining under what conditions $w^*>0$, as well as its behavior under different model assumptions.
A, a	Constants modifying the form of N(c,w)	A_c, A_w, a	Essentially, the 'A' are multiplied with the 'amount' of the resource, and thus generally imply increasing long-range attraction of bees. We use the 'a' (eq. [5] and [14], with $0 < a < 1$) to modify how quickly N decelerates with c or w, i.e. how quickly the attraction of bees to the area decelerates.
k	The number of bees attracted per c		This constant in Model A plays a similar role to A_c in Model B, in that $N_c(c)=kc$, and higher k thus implies increased attractiveness of the crop.

Supplementary Materials

The supplementary materials contain the following sections:

1. Effects of parameters on numerical results in Model A.1
2. Model A.2: Assuming a different shape of $N(c, w)$ (exponential, i.e. saturating, function)
3. Effects of parameters on numerical results in Model B

1. Effects of parameters on numerical results in Model A.1

Throughout our paper, we assume that local choices of consumers are directly proportional to the relative abundance or value of the resources, i.e. that $D(c, w) = c/[c + w]$ (eq. [1]).

The different models and different behaviors illustrated in the figures are explorations of different behavior of N (attraction of consumers to the area). Our analytical result (Fig. 1a) holds generally for any decelerating function of N with w. In Fig. 1b-g we assume that N is a power function of w but depends linearly on c; this can be seen as a special case of a power function with an exponent of 1. In Fig. 2d, we assume the same type of dependence (a power function), but with the same exponent (0.4) for both w and c.

Here, we explore numerically the distribution of bees across the two plant species for such a power-function for N that is symmetric with respect to w and c.

$$N(c, w) = N_w(w) + N_c(c) = A_w w^{a_w} + A_c c^{a_c} \qquad [S1]$$

A_w and A_c are parameters reflecting the (long-distance) attraction of pollinators to the patch by w and c respectively. The two exponents, a_w and a_c, are parameters that affect the degree of deceleration of N with w and c, respectively. In the following, we examine how the total N and the distribution of bees on w and c change with these parameters.

First, we examine how N, $F_c = F$ (bees on c), and $F_w = N\text{-}F_c$ (bees on w) change with the parameters and increasing w. As w and c are treated symmetrically, we only vary A_w (not A_c). We use the same default values as in the rest of the paper, namely c=8, A_w=100, A_c=1, a_w=0.4, a_c=0.4. At these values, the wildflowers are the main attractor for bees, and changing a_c matters very little (Fig. S1). The degree of facilitation depends primarily on A_w/A_c (and increases with this ratio). With a strongly decelerating N with w (i.e. low a_w), c benefits from very small amounts of w.

It is interesting to note that w^* generally maximizes not only the total number of bees on c but also the number of bees on each species per plant (panels g-i in Fig. S1). In other words, wildflowers experience an Allee effect (intraspecifically, benefits of higher density) at low density (low w), despite the fact that N/w never increases with increasing w.

Optimal amounts of wildflowers (w^*) generally increase with c (Fig. S2), but the benefits to the crop per c generally decrease with c.

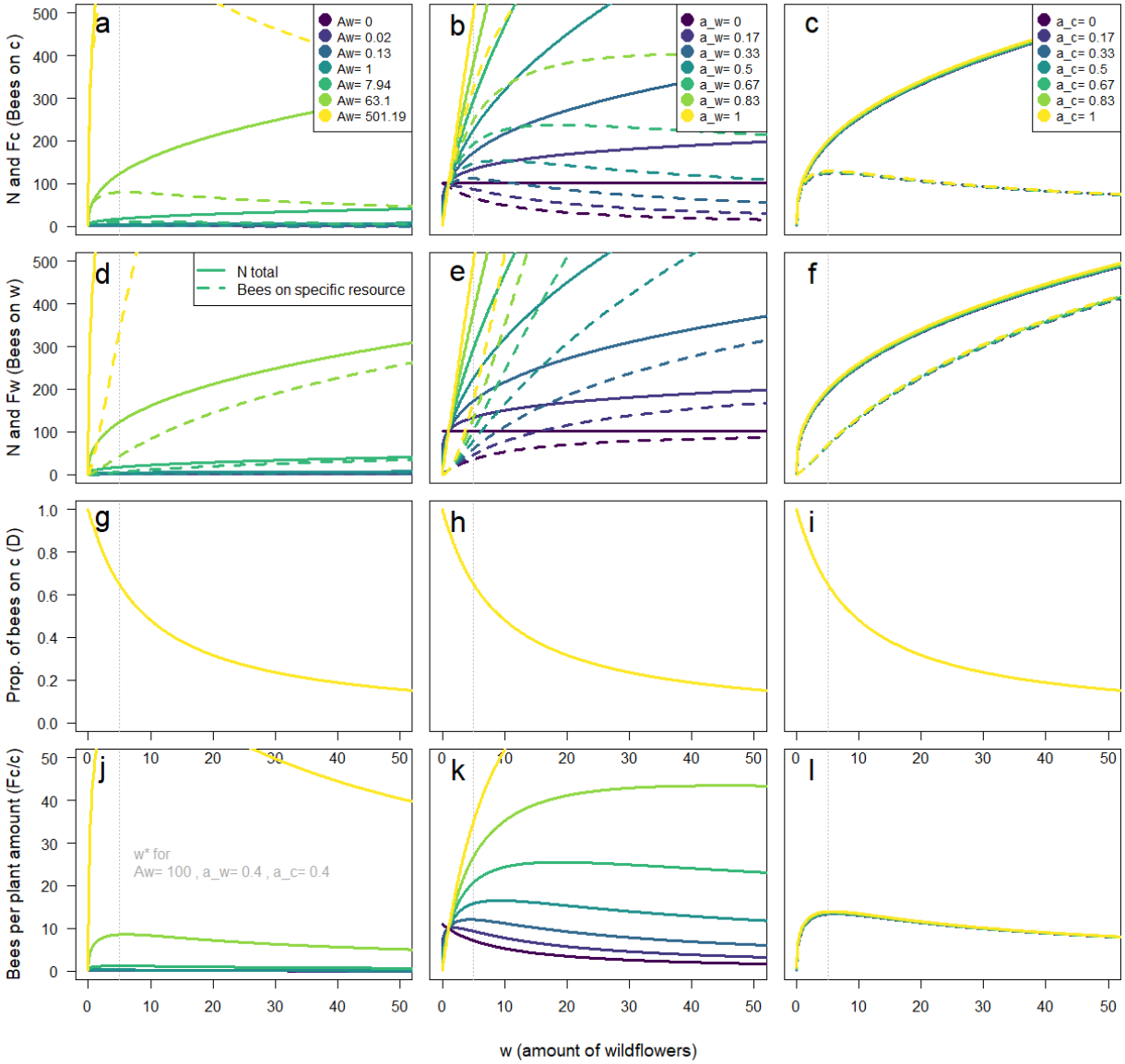

Fig. S1: The number of bees attracted to the patch in total (N, solid lines in a-f) and to the first species (F_c, dashed lines in a-c) and the second species (F_w, dashed lines in d-f). Colors indicate value for respective varied parameter (values for parameters not varied in a specific panel: c=8, A_w=100, A_c=1, a_w=0.4, a_c=0.4; vertical grey dashed lines indicate w* for these values, i.e. where Fc is maximal). Panels g-i show D, the fraction of bees on c: this does not depend on the parameters of N. Panels j-l show the number of bees per 'amount' of either species (F_c/c; this is by our definition for D identical to F_w/w). Note that since w increases on the x-axis but c is fixed, F_w generally increases but F_c decreases towards the right of the plot. Nonetheless, facilitation (increasing Fc with w) occurs for high A_w and low a_w, and regardless of a_c (consistent with our result that facilitation can occur regardless of the shape of N_c). Total N increases with A_w, and a_w for high w; at low w, a lower a_w means a steep increase in N with w that then quickly attenuates. N also increases with a_c, but since here A_w/A_c>>1, a change in a_c has a barely perceptible effect on N.

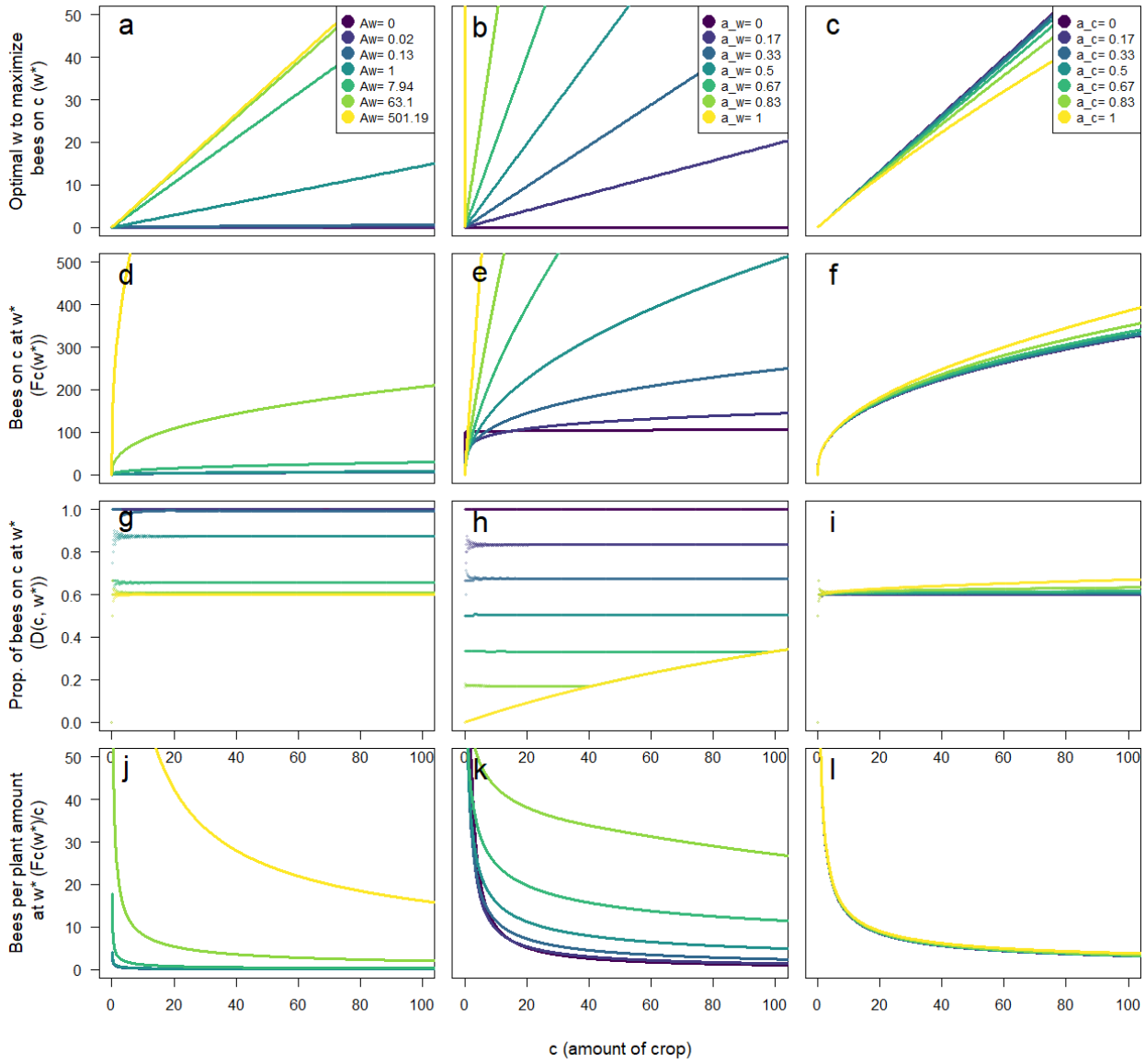

Fig. S2: The optimal amount of w with respect to maximizing bees on the crop generally increases with the amount of crop (i.e. w*, which maximizes F_c, panels a-c). However, since the facilitation effect we find here is based on the disproportionate attraction of bees by either species at low densities, the benefits of wildflowers per crop, even at the respective w*, decline with increasing amount of c. Highly attractive w (high A_w/A_c) yield the highest F_c (even per c). Values for parameters not varied in a specific panel: A_w=100, A_c=1, a_w=0.4, a_c=0.4. For high A_w/A_c, i.e. small N_c, $D(w^*)$ is approximately constant with w, and near to (1-a_w) (i.e. here near 0.6, panels g-i, as shown analytically in eq. [9]).

2. Model A.2: Assuming a different shape of $N(c, w)$ (exponential function)

In the main text, Model A, from equation [5] onwards, we assume that the number of bees attracted to the area, N, increases with w (and c) infinitely (albeit with diminishing returns). Alternatively, one might assume a shape of N that shows saturation, e.g. asymptotes with increasing w (a stronger condition than

just 'diminishing' returns). Which is the better description of the practical context will depend on what limits bee (or pollinator generally) population sizes, and their attraction to the area of the crop. Here we illustrate the behavior of N, F, and consequently w^* in the case that

$$N = M(1 - \exp(-qw)) + N_c \qquad [5\ \text{alt}]$$

Note that M plays a somewhat analogous role to A_w, in that it denotes the relative attraction of bees to the patch exerted by w; and q plays a role somewhat analogous to a (or a_w in Fig. S1), in that it controls the speed with which $N(w)$ decelerates (albeit here, higher q leads to reaching saturation faster).

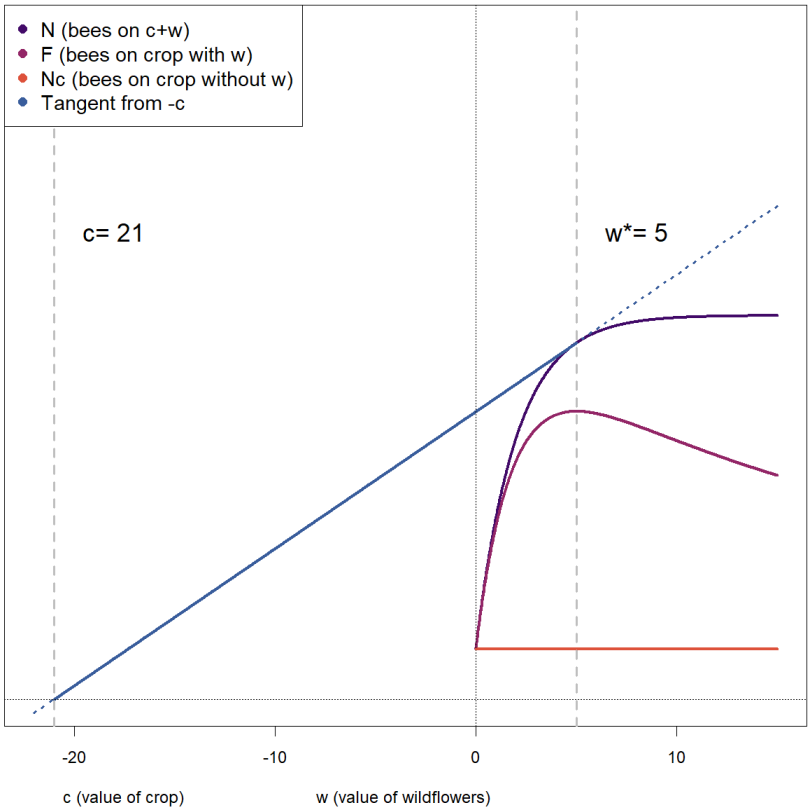

Fig. S3: An alternative expression for the behavior of N that asymptotes with increasing w. That is, N eventually stops increasing for high w. While this allows us to make the same argument about w^*, the specific relationship of c and w^* changes, as do the effects of parameters. Equivalent to Fig. 1a, we don't make assumptions here about the behavior of $N(c)$.

In this case, facilitation can occur (w^* is positive), if the amount of crop is equal to or larger than

$$c_{crit} = N_c/(qM). \qquad [6\ \text{alt}]$$

The optimal value w^* of w satisfies

$$c = (\exp(qw^*)(N_c/M + 1) - 1)/q - w^*. \qquad [7\ \text{alt}]$$

If $N_c = kc$ as in Fig. 1,

$$c = (\exp(qw^*) - qw^* - 1)/(q + (k/M)\exp(qw^*)) . \qquad [7a\ \text{alt}]$$

There is no longer an approximation for the fraction of bees on the crop at optimal w, $D(w^*)$, that is constant, even for N_c =0 (no bees on crop without wildflowers; see Fig. S5 g-i). We explore the effects of all parameters in Figs. S4 and S5.

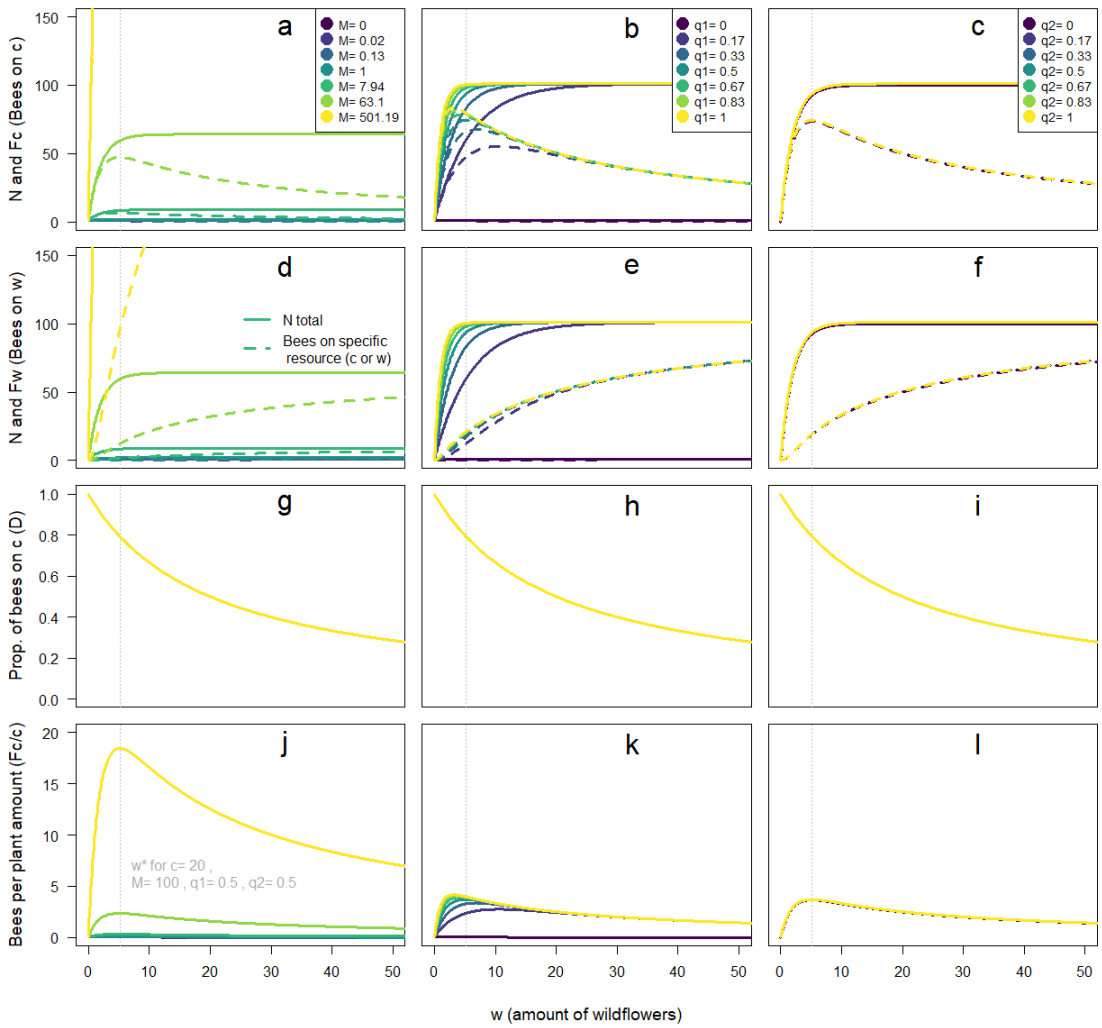

Fig. S4: Under the alternative behavior of N with w (a saturating, exponential function), the number of bees attracted to the area (panels a-f, solid lines; the total N plotted is the same in a and d, b and e, and e and f) and to the crop (panels a-c, dashed lines) and the wildflowers (panels d-f, dashed lines) asymptotes to a maximal value. For this figure, we assumed N_c=1-exp(q_2c) (i.e. equivalent behavior to $N(w)$). Colored lines show effects of different parameter values. Values for parameters not varied in a specific panel: M=100, q_1=0.5, q_2=0.5 and c=20. Vertical grey dashed lines show w^* for these default parameter values. Equivalent to Fig. S1, given that M=100 implies wildflowers are much more attractive than the crop, the parameter q_2 has little effect on total N or F. In fact, under the default parameters assumed here, N_c<1, meaning that practically all bees attracted to this species (the 'crop') are attracted by the other species (the 'wildflowers'). For the values of M plotted in panel a, c_{crit} is 100, 15, 2, 0.25, 0.03, 0.004 (in ascending order of M and excluding M=0, and these are the values of c where w^* becomes positive in panel a in Fig. S5).

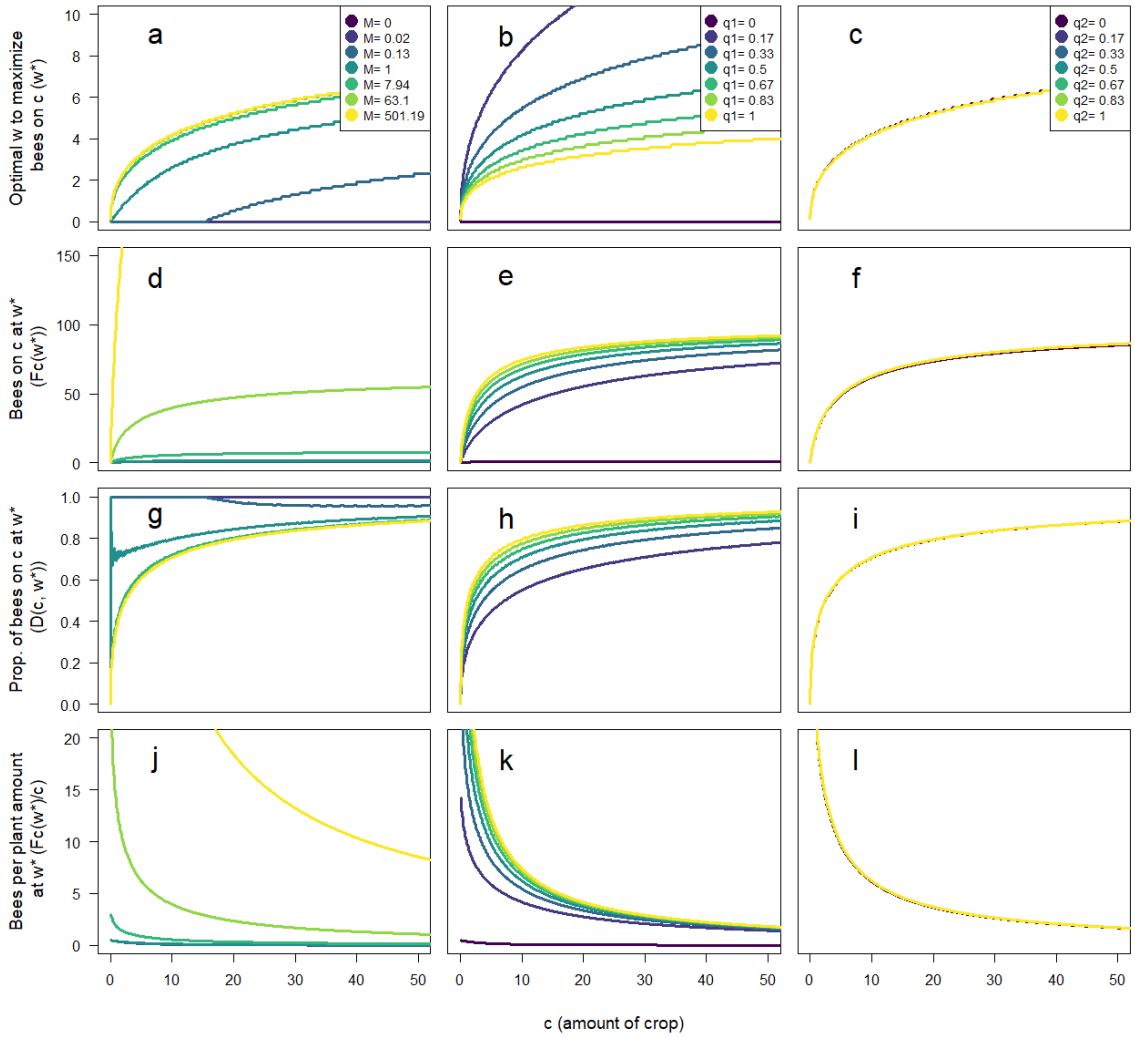

Fig. S5: Analogously to Fig. S2, under the saturating behavior of N (as in Fig. S4), w^* generally increases with c (panels a-c). Colored lines show effects of different parameter values. Values for parameters not varied in a specific panel: M=100, q_1=0.5, and q_2=0.5. As before, the benefit to the crop, F, is highest at high M (high attractiveness of wildflowers), across different amounts of c. Also as in Fig. S2, increasing amounts of crop generally have a negative effect on bees per crop (no intraspecific facilitation for c).

3. Effects of parameters on numerical results in Model B

Using numerical calculations, we explored the effects of different parameter values on the model presented as Model B in eqs. [10-14] (Figs. S6 and S7). As in all previous examples in this paper, high A_w maximizes facilitation (highest f^*, see Fig. S7 panel e), although p^* asymptotes with high A_w (Fig. S7, panel a). In Fig. S6, panels a-d, because of the decelerating relationship of N with density of either species, in all cases except where a_w or a_c=0, the total number of bees is always higher at an intermediate amount of c and w. In panels e-h, wildflowers are so much more attractive that the total number of bees is always maximized at p=1 (all wildflowers). As in Fig. S1, with Aw =100, the value of a_c is essentially irrelevant (panel g).

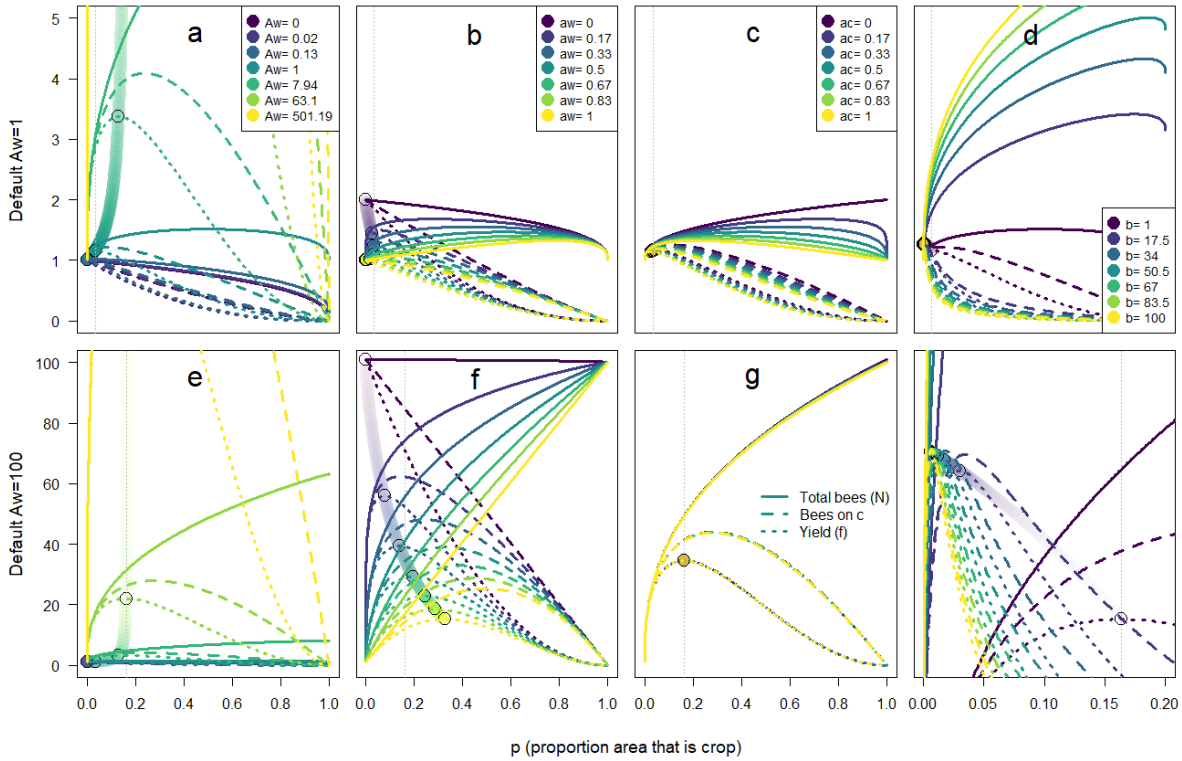

Fig. S6: Numerical solutions for Model B, where total area is held constant, and thus, along the x-axis, w increases and c decreases (with p). On the y-axis, solid lines show the total number of bees at the patch, N; dashed lines show the fraction of those bees on the crop; and dotted lines show resulting yield, f. Circles (and transparent thick line) denote p^* (i.e. where f is maximized). All plots assume a decelerating relationship of N with w and c respectively (eq. [S1]). Default parameter values are b=1, A_c=1, a_w=a_c=0.4. In panels a-d, A_w=1, and thus both resources attract bees equally. In panels e-h, A_w=100, and thus wildflowers attract more bees to the patch (as in Fig. 3a and b, respectively). Grey vertical lines indicate p^* for default parameter values (where total yield is maximal).

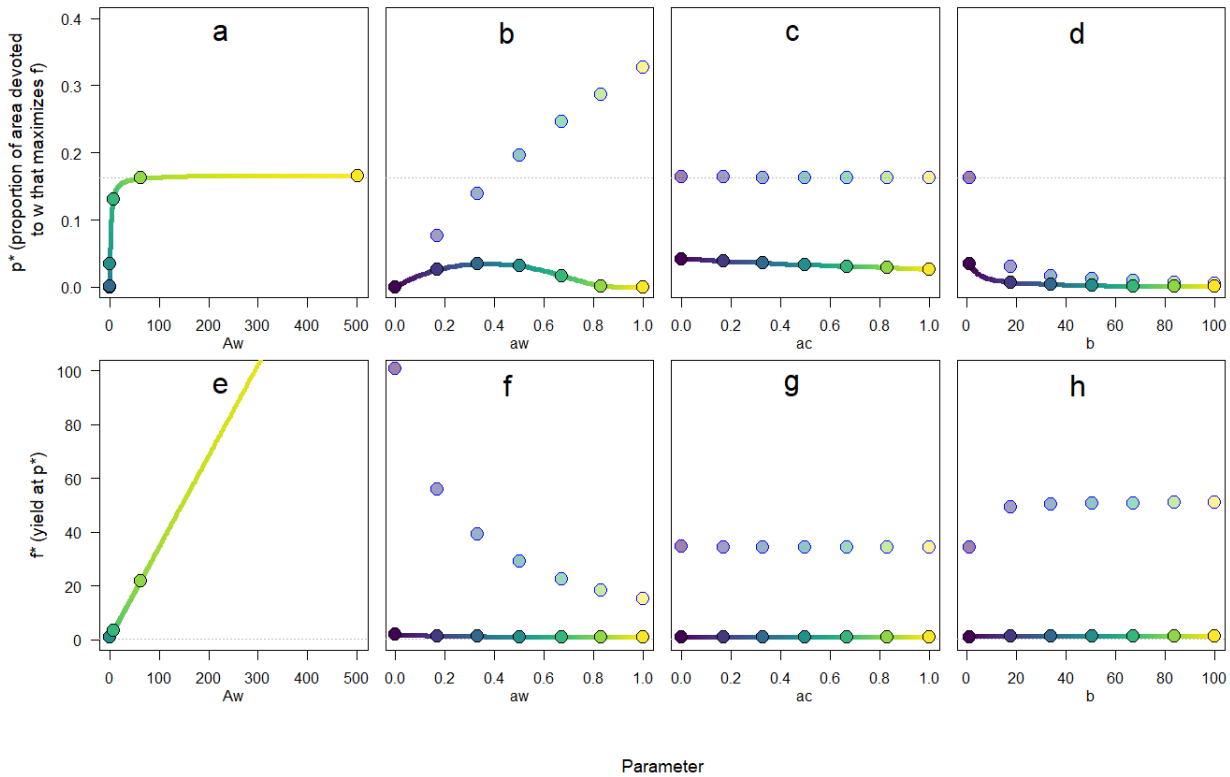

Fig. S7: In the numerical solution to Model B, we calculate the p at which f is maximal (p* with its resulting f*). Here, p* (panels a-d) and f* (panels e-h) are shown for A_w=1 (darker color dots and line) and A_w=100 (lighter colors). The dots are at parameter values also represented in Fig. S6. Default parameter values are b=1, A_c=1, a_w=a_c=0.4. Note that for a_w, p* (the optimal proportion of w) may trade off with f*, i.e. the highest f* is achieved for low a_w, which have a low p*; at high a_w, a higher p* is optimal but still leads to a lower f*.