Citation: Sun, S., Broom, M., Johanis, M. & Rychtar, J. (2021). A mathematical model of kin selection in floral displays. Journal of Theoretical Biology, 509, 110470. doi: 10.1016/j.jtbi.2020.110470

A MATHEMATICAL MODEL OF KIN SELECTION IN FLORAL DISPLAYS

SHAN SUN[1], MARK BROOM[2], MICHAL JOHANIS[3], AND JAN RYCHTÁŘ*[4]

ABSTRACT. Plants can adjust their competitive traits for acquiring resources in response to the relatedness of their neighbours. Recently, it has been found that plants can alter their investment in traits of attracting pollinators based on kin-interaction. We build a mathematical model to study the optimal floral display to attract pollinators in a patch with kin structure. We show that when plants can attract pollinators to a whole patch through the magnet effect, the floral display should increase with the increasing relatedness of the plants in the patch. Our model also indicates that increasing investment into attracting pollinators is a form of altruism, reducing a plant's own seed production but increasing the contribution of other plants to its fitness. We also predict that seed production should increase with increasing relatedness in the patch. Our model provides the explicit conditions when resource allocation to attract pollinators in response to neighbour relatedness can be favoured by kin selection, and a possible mechanism for the plants to deal with the consequent loss of pollinator diversity and abundance.

1. INTRODUCTION

Most plant-plant interactions occur in locally structured patches among close genetical relatives due to limited dispersal (Biernaskie, 2010; Ehlers and Bilde, 2019). Plants can alter the local environments directly and/or indirectly through the involvement of a third party such as herbivores or pollinators to modify the interactions between neighbouring plants (Mesgaran et al., 2017). In the context of resource competition, the relatedness of interacting plants could reduce competition based on kin selection theory (Hamilton, 1964a,b; West et al., 2007) and the focal plant's best strategy for acquiring resource can often depend on the identity of neighbours (Biernaskie, 2010). Some recent investigations have shown that plants could have the ability to identify their kin and could adjust their strategy in response to local relatedness of their neighbours, in particular reduce competitiveness towards kin neighbours relative to non-kin ones (Dudley and File, 2007; Bhatt et al., 2011; Crepy and Casal, 2015). These differential responses towards kin and non-kin neighbours showed kin selection as a process that can influence plant competitive interactions (Ehlers and Bilde, 2019). When the focal plant reduces its competitiveness toward to relatives, it reduces its direct fitness but gains indirectly by promoting the reproduction of relatives (Biernaskie, 2010; Ehlers and Bilde, 2019). As emphasized in numerous studies (West et al., 2002; Gardner et al., 2011; Ehlers and Bilde, 2019), to assess the circumstances under which kin selected responses can be expected it is necessary to measure the inclusive fitness of an individual plant rather than the mean fitness of the group.

Besides resource competition for nutrients, light and water, interactions among neighbouring plants are often mediated by the foraging choices of pollinators (Seifan et al., 2014). A plant with a large floral display increases the number of pollinators attracted to its vicinity, thus increasing visitation rates to neighbours (Moeller, 2004; Ghazoul, 2006; Seifan et al., 2014). This magnet effect (Laverty, 1992; Molina-Montenegro et al., 2008) has been observed in many different scenarios. For example, in mixed patches of individuals of *Echium vulgare* with low and high nectar production rates (NPR), plants with high NPR increase the average number of approaches to all plants in the group; therefore, plants with low NPR benefit from nectar-rich plants nearby (Klinkhamer et al., 2001). By introducing a highly conspicuous species into a species-rich meadow, Seifan et al. (2014) showed that the highly conspicuous species strongly contributed to the attractiveness of its local patch and thus benefited its neighbours in a certain range of plants' density.

Torices et al. (2018) provided clear evidence that a self-incompatible *Moricandia moricandioides* could alter their investment in floral display in response to kin neighbours in the same patch. Under

---

Key words and phrases. Magnet effect; pollinator attraction; optimal allocation; altruism; cooperation.

*Corresponding author: rychtarj@vcu.edu.

the facilitative interactions among plants in the same patch, the individuals of *M. moricandioides* growing with kin can produce larger floral displays than those growing with non-kin. Torices et al. (2018) interpreted the results as kin recognition, suggesting kin selection as a possible explanation for floral strategies. Ehlers and Bilde (2019) proposed that it is necessary for kin recognition to apply the inclusive fitness framework to assess whether kin selection occurs.

In this paper, we develop a theoretical model of the magnet effect among neighbouring plants to answer how the plant relatedness influences (on the patch scale) 1) the optimal floral display to attract pollinators and 2) the plant's own seed production and seed production of other plants.

2. MATHEMATICAL MODEL

We build the model based on the experimental paper Torices et al. (2018). The total number of seeds $S(f,P)$ produced by a plant depends on the following factors: (1) f, a size of the plant's floral display; and (2) $P = P(f_1,\dots,f_N)$, the total number of pollinators attracted to the patch which in turn depends on the floral displays f_i of each of the N plants in the patch. For an illustration we will consider the functions

$$P(f_1,\dots,f_N) = 1000\frac{f_1+\dots+f_N}{50+f_1+\dots+f_N}, \tag{1}$$

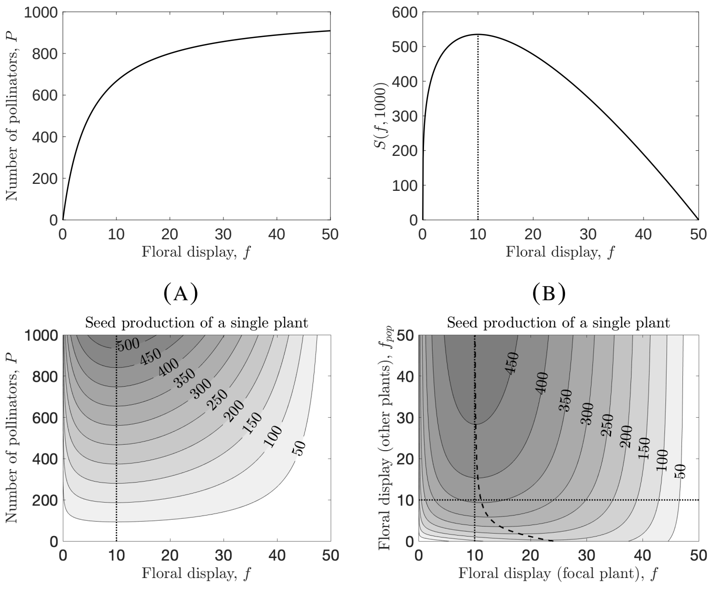
$$S(f,P) = \left(\frac{f}{50}\right)^{1/4}\cdot\left(1-\frac{f}{50}\right)P, \tag{2}$$

for the floral display f between 0 and 50 flowers per plant, see Figure 1. However, we stress that these functions are only for the illustration and they do not necessarily reflect all the details of plant reproduction. Unless stated otherwise, the results in the following sections hold for any functions P and S that satisfy quite general requirements listed below and with more mathematical details and precision in Appendix A.

The function P given in (1) has the following properties. The patch can attract between 0 and up to 1000 pollinators. If any plant increases its floral display, the whole patch will become more attractive and more pollinators will come to the patch, i.e. $\frac{\partial P}{\partial f_i} > 0$. At the same time, the investment into the floral display has diminishing returns, i.e. $\frac{\partial^2 P}{\partial f_i \partial f_j} \le 0$ for all $i,j = 1,\dots,N$. Finally, all plants contribute in the same way, i.e. the value of P is the same for all permutations of its arguments.

The term $\left(\frac{f}{50}\right)^{1/4}\cdot\left(1-\frac{f}{50}\right)$ in (2) is a hump-shaped function, see Figure 1(B). It may be seen as the number of seeds produced by a plant with floral display f that gets completely pollinated (when there is no pollen limitation). It illustrates a reasonable dependence of the number of seeds on the plant's floral display. For small f, $S(f,P)$ is increasing in f because there are no serious resource limitations yet and the chances of geitonogamy (Harder and Barrett, 1995) are also relatively small. It is plausible that the increase is slowing down ($\frac{\partial^2 S}{\partial f^2} \le 0$) and eventually, there is a threshold f_t such that for $f > f_t$, the function $S(f,P)$ is decreasing in f. This is because a floral display increases the chances of geitonogamy (Harder and Barrett, 1995), further reducing seed production (Finer and Morgan, 2003; Liao et al., 2009). Consequently, $\frac{\partial S}{\partial f}(f,P) > 0$ for each $f \in (0,f_t)$ and all P, and $\frac{\partial S}{\partial f}(f,P) < 0$ for each $f > f_t$ and all P. Moreover, we will assume that the negative effect of allocating more to the floral display (and thus less to seed production) is amplified by the increasing number of pollinators on the patch, i.e. $\frac{\partial^2 S}{\partial f \partial P} \le 0$ when $f > f_t$ as well as of itself, i.e. $\frac{\partial^2 S}{\partial f^2} \le 0$ when $f > f_t$. This is because when more pollinators are already attracted to the patch (and thus the plant), or when not enough is allocated to seed production, allocating even less to seed production has larger negative consequences.

The magnet effect (Laverty, 1992; Molina-Montenegro et al., 2008) means that increasing the floral display brings in more pollinators to the patch as a whole which benefits every plant in the patch. It means that S is an increasing function of P, i.e. $\frac{\partial S}{\partial P} > 0$. At the same time, we will assume that the effect of P on S has diminishing returns, i.e. $\frac{\partial^2 S}{\partial P^2} \le 0$ (Bell, 1985; de Jong and Klinkhamer, 2005). The assumption of benefits to every plant in the patch is in agreement with Klinkhamer et al. (2001);



(A) (B)

(C) (D)

FIGURE 1. (A) The function $f \mapsto P(f, \dots, f)$, i.e. the number of pollinators attracted to the patch when each of the $N = 10$ plants has a floral display f. (B) The function $f \mapsto S(f, 1000)$, i.e. the number of seeds the flower could produce if if has a floral display f and there are 1000 (max) pollinators on the patch. The vertical line signifies the optimal floral display $f = 10$ the plant can have. (C) The function $(f, P) \mapsto S(f, P)$, i.e. the seed production of a plant allocating f when the patch attracts P pollinators. (D) The function $(f, f_{\text{pop}}) \mapsto S\big(f, P(f, f_{\text{pop}}, \dots, f_{\text{pop}})\big)$, i.e. the seed production of a plant using f when every other plant uses f_{pop}. The dashed curve is the optimal floral display for a focal plant (i.e. the value of f for which the plant's seed production is maximal), the dotted vertical line is $f = f_t = 10$, the threshold value of the floral display where the seed production would be maximal if the floral display did not influence the number of pollinators, corresponding to (B). The difference between the dashed and dotted lines is larger the smaller the value of f_{pop}, as the effect of the plant's own display on attracting pollinators increases with decreasing f_{pop}. The horizontal line at $f_{pop} = f_t$ shows there is still incentive for an individual plant to increase the floral display.

however we can relax this assumption as later shown in the discussion and Figure 6 where we consider functions for which the more attractive plants in the patch receive a larger share of pollinators.

The above functions P and S nicely illustrate the public good dilemma associated with attracting the pollinators. It is in the interest of every plant to have a display of at least f_t (because for $f < f_t$, increasing f increases both the potential seed production as well as the number of pollinators P). If each plant allocates a substantial amount over f_t, many pollinators will come regardless of how much is allocated by the focal plant. It is therefore beneficial for the focal plant to allocate as little extra as possible and put any extra resources towards seed production. At the same time, if all plants have only the optimal floral display f_t, some pollinators will still come to the patch but each plant would benefit if it unilaterally changes its strategy and allocated a bit more to the floral display, see Figure 1(D).

The presence of related plants in the patch may decrease the proportion of viable seeds via inbreeding depression (Liao et al., 2009). To properly account for this phenomenon, we will use a non-decreasing function $\delta(r) \in [0, 1)$ of an average relatedness coefficient $r \in [0, 1]$ in the patch and define the amount of viable seeds of each plant as

$$\widetilde{S}(f, P) = \big(1 - \delta(r)\big)S(f, P) \tag{3}$$

The total fitness of the plant i will depend not only on its own (viable) seed production, but also on the (viable) seed production of related plants in the patch. Throughout the paper we refer to this total fitness as simply the fitness, which is the sum of the contribution to this fitness of its own seed production, and the contribution of the seed production of related plants through collective attractiveness of the patch. We are investigating a very specific question in this paper, and, due to the complexity of our model, deliberately avoid the terminology of inclusive fitness, which is the subject of quite a subtle debate beyond the scope of this article.

$$W_i(r, f_1, \dots, f_N) = \widetilde{S}\big(f_i, P(f_1, \dots, f_N)\big) + r \sum_{\substack{j=1 \\ j \neq i}}^{N} \widetilde{S}\big(f_j, P(f_1, \dots, f_N)\big). \tag{4}$$

Equation (4) gives the fitness, but models of altruism often consider acts of helping and associated costs and benefits. Taking the derivative of (4) with respect to f_i we can see that the cost associated with a small increase in f, Δf, is simply minus Δ times this derivative for the first component (an increase in floral display is associated with a reduction in fitness), and the benefit is Δ times the equivalent derivative for the second component (without the multiplier r). Thus the common comparison between cost, benefit and relatedness associated with Hamilton's rule (Hamilton, 1964a,b) is associated with the derivative of the fitness from (4) (see Taylor and Frank (1996), where W is the equivalent fitness and its derivative ΔW the associated cost-benefit equation).

In this paper, we will be looking for the symmetric Nash equilibrium strategy, i.e. a floral display f_{NE} such that if every plant in the patch adopt this value, no plant will benefit by unilaterally deviating from it. We shall refer to the Nash equilibrium as the optimal strategy in the rest of the paper.

3. RESULTS

The analysis of our model yields the following results. Mathematical proofs are provided in the Appendix B.

The first result. The optimal floral display is positively correlated with the average relatedness coefficient, see Figure 2.

The seed production of each plant is a trade-off between its floral display f and the allocation to reproduction. If all plants are unrelated this selfish optimisation would completely constitute its payoff. From equation (4) we see that there is a second component to the payoff, which increases with the number of attracted pollinators P, which increases with increasing f. Increasing relatedness does not affect the first component of the payoff but increases the second which is increasing in f. Thus, the overall increased relatedness pushes the optimal trade-off point to higher f.

We also believe that the optimal floral display is decreasing in the number of plants in the patch for all values of r and for all reasonable functions P and S, as demonstrated in Figure 2. This result is proved for small average relatedness r, see the Appendix. However, we cannot prove it for all r without adding significant restrictions on how P and S depend upon N, and we wish to maintain generality of our results.

The second result. The plants pay a cost in terms of decreasing their own seed production to increase their fitness by attracting pollinators to a whole patch and thus helping related plants produce more seeds, see Figure 3. This is analogous to the costs in Hamilton's rule (Hamilton, 1964a,b; Marshall, 2011).

The third result. In the absence of inbreeding depression, when all plants in the patch can adopt equilibrium floral display, increasing relatedness in the patch increases seed production of each plant in the patch, see Figure 4. This is a testable prediction of our model. Numerically, we can also see that increasing N, the number of plants in the patch, increases seed production of each plant by increasing the floral display of the patch as a whole.

When the inbreeding depression is present but low, then increasing the relatedness still increases seed production of each plant. However, when the inbreeding depression is large, increasing the relatedness decreases seed production. This is illustrated on Figure 5 for $\delta(r) = r^2/2$. There is a r_0 such that seed production is increasing for $r < r_0$ but decreasing for $r > r_0$. When $N = 15$, the change happens approximately at $r_0 = 0.25$. For smaller N, the change happens for slightly smaller r_0.

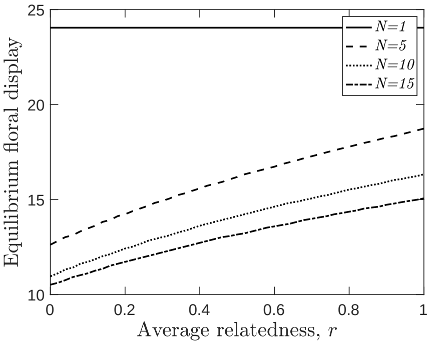


FIGURE 2. Nash equilibrium floral display as a function of the average relatedness coefficient for different patch sizes. Here, the results do not depend on the inbreeding depression $\delta(r)$. The optimal floral display is decreasing in the number of plants in the patch for the particular functions P and S given in (1) and (2). However, we cannot prove this result for all values of r without adding significant restrictions on how P and S depend upon N.

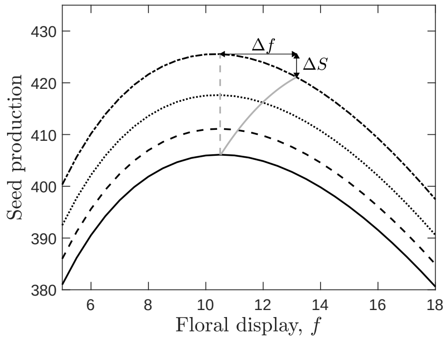


FIGURE 3. An individual plant pays a cost in terms of decreased its own seed production (by ΔS) as it increases its floral display (by Δf) to attract pollinators for the whole patch. The graphs show the seed production of a focal plant as a function of its floral display f when all other plants use the optimal (Nash equilibrium) value f_{NE} for various r (f_{NE} is such a value that if every plant in the patch adopt it, no plant will benefit by unilaterally deviating from it). From the bottom to the top, $r = 0$ (solid), $r = 0.1$ (dashed), $r = 0.25$ (dotted), $r = 0.5$ (dash-dotted). The vertical gray dashed line represents the floral display at which the plant achieves the maximum S. The short gray solid curve shows the seed production if the focal plant display is at the equilibrium (as r varies). This figure illustrates the situation without inbreeding depression ($\delta(r) = 0$) and with $N = 15$. However, the situation with inbreeding depression is similar, see Figure 5.

4. DISCUSSION

We built a theoretical model of interactions between neighbouring plants mediated through their pollinators and identified conditions that can result in the plants' increased investment in attracting pollinators. When plants are closely surrounded by other plants within the patch, and neighbours could benefit from the focal plants with a highly floral display by the magnet effect, our analytical analyses showed: 1) that the optimal floral display can increase with the increased relatedness of plants in the patch; 2) that the increased floral display can be a cost to the focal plant in terms of its own seed production; and 3) each plant can gain in terms of increased seed production by sharing more collective attractiveness of the patch if the patch consists of more related plants (or a larger number of plants). Our model provides

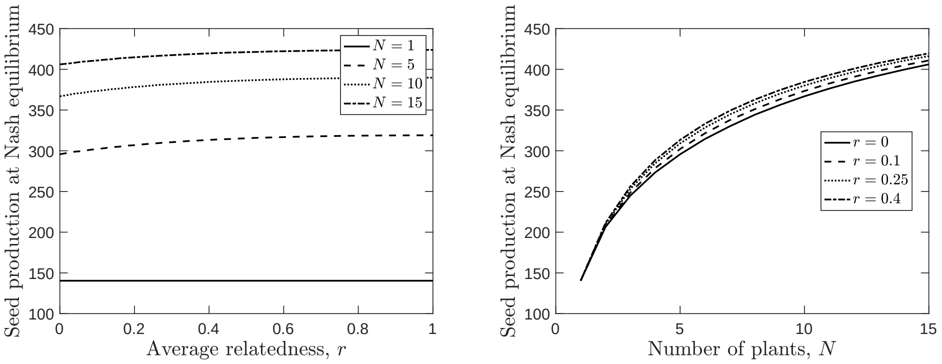


FIGURE 4. In the absence of inbreeding depression (when $\delta(r) = 0$), individual seed production at equilibrium floral display is an increasing function of the average relatedness r within the patch. Also, we observe that individual seed production of each plant at the equilibrium is an increasing function of N.

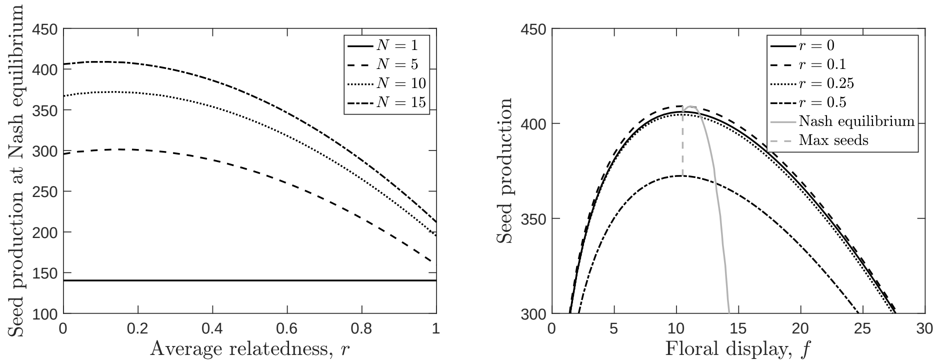


FIGURE 5. Left: In the presence of inbreeding depression (here $\delta(r) = r^2/2$), individual seed production at Nash equilibrium display is an increasing function of the average relatedness r within the patch for small r and decreasing for large r. Right: individual seed production $S(f, P(f, \ldots, f))$ is still a decreasing function of f but the dependence of r and the Nash equilibrium curve is not simple as for $\delta(r) = 0$.

a theoretical framework and the testable predictions for determining the impact of kin selection on the traits that depend on the interactions between neighbouring plants.

Our model showed that increase of floral display due to magnet effect depends on the relatedness and the number of plants within the patch. In agreement with Torices et al. (2018), we showed that the plants increase floral display when surrounded by relatives. We also showed that when the relatedness is small, the optimal floral display decreases with the number of plants in the patch. This seems to contradict results of Milla et al. (2009). They reported that *Lupinus angustifolius* plants growing with non-kin neighbours produced significantly more flowers than those growing with siblings. However, the example of *L. angustifolius* is not consistent with the assumptions of our model. The mating system of this species is predominantly selfing and its reproduction is scarcely dependent on the local community of pollinators (Milla et al., 2009). The observed phenomenon could be explained as a by-product of self/non-self-recognition in resource allocation - the plants grown with non-kin tended to be larger (Klemens, 2008; Milla et al., 2009). This illustrates that the magnet effect depends on the mating system of species: the more outcrossing the mating system that the plant species adopts, the more it becomes reliant on pollinator services and thus the more likely it is to be affected (Mesgaran et al., 2017).

In our model, every plant in the patch benefits equally from the increased investment in floral display by any other plant in the patch. We note that the benefits increase only asymptotically due to limits on either ovule number or the resources available for seed production (Aizen and Harder, 2007; Morris et al., 2010). There is a cost incurred from attracting pollinators associated with a resource depletion. For example, the plants need to replenish the nectar after its removal by pollinators (Morris et al., 2010;

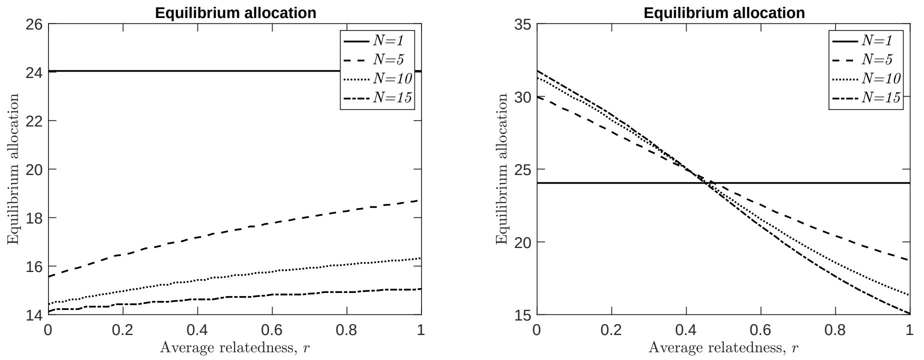


FIGURE 6. Equilibrium floral display when the seed production function is given by $\widehat{S}(f, f_{\mathrm{avg}}, P) = S(f, P)\exp(z(f - f_{\mathrm{avg}}))$, where S and P are given as in (2) and (1). Due to the factor $\exp(z(f - f_{\mathrm{avg}}))$, the plants whose floral display is above average produce more seeds (presumably because they are visited by pollinators more often). Increasing the scaling parameter $z \geq 0$ makes the effect more profound. Left: $z = 0.01$, right: $z = 0.05$. The switch from increasing to decreasing display happens around $z \approx 0.013$ when the Nash equilibrium display is almost constant.

Aizen et al., 2014). For any behaviour to evolve and be evolutionarily stable, the cost of such a behaviour must be compensated by increased benefits to itself or to relatives. In the context of our model, result 2 shows that the plants pay a cost to increase the fitness of their relatives.

We note that there are a number of different ways that cooperative behaviour can be fostered within populations. In particular Lehmann and Keller (2006) identified four distinct scenarios, two of which they termed cooperation (direct benefit or reciprocation) and two altruism (kin selection or greenbeard), and in their Table 3 they classified many of the existing models into these categories (often models were in more than one). Our model involves a suboptimal investment into the floral display (larger than needed to achieve the maximal seed production) to benefit relatives at the expense of individual fitness, and so is firmly within the altruism/kin selection category.

We showed that increased investment in floral display can be seen as an altruistic behaviour of providing costly help to recipients (Lehmann and Keller, 2006; West et al., 2007; Dudley, 2015), which could be favoured by kin selection. In the experimental results of *L. angustifolius*, the groups of plants consisting of all non-kin individuals could produce more flowers than groups of siblings or moderate non-kin ones (Milla et al., 2009). Torices et al. (2018) did not report the negative effects of allocation to attractive traits on the fitness of the focal plant; however, there is accumulating evidence for the reduction of attractiveness structures to increase seed production (Andersson, 2000, 2005). The occurrence of traits that benefit relatives is crucial for kin selection (Lehmann and Keller, 2006), either through local dispersal (high population viscosity), kin recognition or greenbeard effects (West et al., 2007). In plants, the seed dispersal is stochastic, and greenbeard effects are unlikely or unimportant due to their vulnerability to falsebeards mimicking the signals of altruists without providing the altruistic behaviour (Gardner and West, 2010). Therefore, for plants, kin recognition is probably crucial for the evolution of altruism towards relatives (File et al., 2011).

In result 3, we demonstrated that in an environment where the relatedness among neighbours varies, the collective attractiveness of the patch can reduce the cost of altruism through increasing seed production. Our model suggested that the collective attractiveness of a more related patch can improve the fitness (in terms of equation (4)) of plants within the patch, depending on how individual plants modulate their floral display in response to the relatedness of neighbours.

As in Klinkhamer et al. (2001), we assumed in the model that the attractiveness of a plant only contributes to attracting a pollinator to the patch, and that the pollinator visits all plants equally once entering the patch. However, this may not always be the case (Biernaskie and Elle, 2007). Within a patch, pollinators can preferentially or more frequently visit plants offering high rewards (Cartar, 2004; Lefebvre et al., 2007). Thus, the plants with an above average floral display have a competitive advantage in attracting pollinators (Biernaskie and Elle, 2007). In order to explicitly incorporate variability within a patch, we can expand the assumptions that the seed production of a plant depends not only on (1) the floral display, and (2) the total attractiveness of the plant patch, but also on (3) the average floral display in the patch. In this way, the model can capture the likelihood that, within a given patch, more attractive plants attract more pollinators and in turn produce more seeds. We found that our results would not change when the effect of the variability of floral display on seed production within the patch is small, see Figure 6. However, when the effect is larger, there are differences. The equilibrium display becomes decreasing in r. Moreover, the equilibrium display is increasing in N for small r and decreasing in N for large r. We note that the results of Torices et al. (2018) also showed that for small r ($k = 0.25$), the equilibrium display is increasing in N.

For future research, one needs to incorporate the competition for pollinator services (exploitation competition) and the optimal foraging behaviour of pollinators in the patch with kin structure. For example, investment in alternative attractiveness traits could influence competition for access to pollinators (Biernaskie and Elle, 2007). Pollinators preferentially visit plants with higher nectar production rates (Cartar, 2004) and the patch-leaving mechanism of pollinators (Lefebvre et al., 2007) could thus prevent some plants being visited within the patch. By combining the magnet effect studied in this paper with competition for pollinators within the patch and between the patches, we expect to gain a better understanding of conditions that favour altruistic allocation of resources towards floral display.

Recently, Ollerton (2017) assessed the current diversity of pollinators and suggested that there is a reduction of the different types of pollinator richness and density in some regions. Thomann et al. (2013) proposed that plant reproductive strategies can adapt to this pollinator decline by reinforcing interactions with pollinators. Our model suggests that an increasing investment in floral display by kin selection could provide the mechanism to deal with the pollination crisis. Further works need to show how evolution of reinforced interactions can avoid an evolutionary trap if pollinators keep declining and plants continue increasing investment in floral display.

APPENDIX A. MATHEMATICAL SETUP OF THE MODEL

We assume that all the functions considered are continuous and of class C^2 in the interior of the domain.

The total number of seeds $S(f, P)$ produced by a plant depends on (1) the plant's floral display f, and (2) the number of pollinators P attracted to the plant patch; the number of pollinators depends on the floral display of each plant in the patch. We may assume that $f \in [0, f_{\max}]$, $P \in [0, P_{\max}]$.

We assume that S has the following properties:

- $S : [0, f_{\max}] \times [0, P_{\max}] \mapsto [0, S_{\max}]$, i.e. the plants can make up to (a very large) $f_{\max}$ flowers, up to $P_{\max}$ pollinators can potentially come to the patch and if all goes well, the plant can make up to $S_{\max}$ seeds.
- $S(f, 0) = 0$ for all $f \in [0, f_{\max}]$ (in practice $f > 0$ will likely imply $P > 0$, but this assumption is needed for mathematical completeness to have S defined properly on its whole domain),
- $S(f_{\max}, P) = 0$ for all $P \in [0, P_{\max}]$, i.e. when the plant makes way too many flowers, it will not be able to produce any seeds
- There is $f_t \in (0, f_{\max})$ such that (a) $\frac{\partial S}{\partial f}(f, P) > 0$ for $f \in (0, f_t)$ and $P \in (0, P_{\max})$, and (b) $\frac{\partial S}{\partial f}(f, P) < 0$ for $f \in (f_t, f_{\max})$ and $P \in (0, P_{\max})$. Haig and Westoby (1988) assumed: 1) the resources allocation only between plant attraction and seed provisioning could ensure enough pollen capture to fertilize ovules that would mature to seed; 2) ovule fertilizations increasing with the amount of resources allocation to pollinator attraction but at a diminishing rate, and predicted that the optimal resources allocation to pollinator attraction should gain just the number of ovule fertilizations needed to consume the available seed-provisioning resources (Burd, 2008). Also, Liao et al. (2009) showed that the rate of pollinator visitation varied positively with display size, but seed production decreased with floral display increasing due to geitonogamous pollination in four *Aconitum kusnezoffii* populations.
- $\frac{\partial S}{\partial P}(f, P) > 0$ for $f \in (0, f_{\max})$ and $P \in (0, P_{\max})$, and $\frac{\partial S}{\partial P}(0, P) \geq 0$, $\frac{\partial S}{\partial P}(f_{\max}, P) \geq 0$ for $P \in (0, P_{\max})$, see for example Garibaldi et al. (2013).

- $\frac{\partial^2 S}{\partial f^2}(f,P) \le 0$, $\frac{\partial^2 S}{\partial P^2}(f,P) \le 0$ for $f \in (0, f_{\max})$ and $P \in (0, P_{\max})$ and these second derivatives are never all zero at the same point of $(0, f_{\max}) \times (0, P_{\max})$, see for example Devaux et al. (2014).
- $\frac{\partial^2 S}{\partial f \partial P}(f,P) \le 0$ for $f \in [f_t, f_{\max})$ and $P \in (0, P_{\max})$, see for example Liao et al. (2009).

Note that it follows that $S(f,P) > 0$ for all $f \in (0, f_{\max})$, $P \in (0, P_{\max})$.

We assume that the patch consists of N plants. The total attractiveness $P(f_1, \dots, f_N)$ of the patch depends on floral display of each plant in the patch; here f_i is the floral display of a plant i.

We assume that P has the following properties:

- $P : [0, f_{\max}]^N \mapsto [0, P_{\max}]$,
- $P(0, \dots, 0) = 0$,
- the value of P is the same for all permutations of its arguments.
- $\frac{\partial P}{\partial f_i}(f_1, \dots, f_N) > 0$ for each $f_i \in (0, f_{\max})$, $f_j \in [0, f_{\max}]$, $j \in \{1, \dots, N\} \setminus \{i\}$, and this holds for all $i = 1, \dots, N$,
- $\frac{\partial^2 P}{\partial f_i \partial f_j}(f_1, \dots, f_N) \le 0$ for each $\boldsymbol{f} \in (0, f_{\max})^N$, $i, j = 1, \dots, N$,
- $\frac{\partial^2 P}{\partial f_i^2}(f_1, \dots, f_N) \le 0$ for $f_i \in (0, f_{\max})$, $f_j \in [0, f_{\max}]$, $j \in \{1, \dots, N\} \setminus \{i\}$, $i = 1, \dots, N$.

Finally, we consider a non-decreasing function $\delta : [0,1] \mapsto [0,1]$ to model the inbreeding depression.

APPENDIX B. PROOFS

First we look at the best response of the plant i when all other plants allocate fixed f_j, $j \neq i$. For $\boldsymbol{e} = (e_1, e_2, \dots, e_{N-1}) \in [0, f_{\max}]^{N-1}$, representing the floral displays of the other plants, denote

$$
\begin{aligned}
F_{r,\boldsymbol{e}}(x) &= \frac{1}{1-\delta(r)} W_1(r, x, \boldsymbol{e}) && (5)\\
&= S\big(x, P(x, e_1, \dots, e_{N-1})\big) + r \sum_{j=1}^{N-1} S\big(e_j, P(x, e_1, \dots, e_{N-1})\big) && (6)
\end{aligned}
$$

Note that from the symmetry of P it follows that

$$
\frac{1}{1-\delta(r)} W_i(r, f_1, \dots, f_{i-1}, x, f_{i+1}, \dots, f_N) = F_{r,\boldsymbol{e}}(x) \tag{7}
$$

when $\boldsymbol{e} = (f_1, \dots, f_{i-1}, f_{i+1}, \dots, f_N)$. Thus we may investigate only $F_{r,\boldsymbol{e}}$.

In the following calculations, we will see expressions like $\frac{\partial S}{\partial f}\big(x, P(x, \boldsymbol{e})\big)$. Note that S is a function of two variables, f and P. Consequently, $\frac{\partial S}{\partial f}\big(x, P(x, \boldsymbol{e})\big)$ means that we differentiate S with respect to its first variable (f) and then evaluate the derivative at the point $(f, P) = (x, P(x, \boldsymbol{e}))$.

Let $\boldsymbol{e} \in [0, f_{\max}]^{N-1}$. By differentiating at $x \in (0, f_{\max})$ (note that by our assumptions $P(x, \boldsymbol{e}) \in (0, P_{\max})$) we obtain

$$
F'_{r,\boldsymbol{e}}(x) = \frac{\partial S}{\partial f}\big(x, P(x, \boldsymbol{e})\big) + \frac{\partial S}{\partial P}\big(x, P(x, \boldsymbol{e})\big) \frac{\partial P}{\partial f_1}(x, \boldsymbol{e}) + k \sum_{j=1}^{N-1} \frac{\partial S}{\partial P}\big(e_j, P(x, \boldsymbol{e})\big) \frac{\partial P}{\partial f_1}(x, \boldsymbol{e}) \tag{8}
$$

and

$$
\begin{aligned}
F''_{r,\boldsymbol{e}}(x) = {} & \frac{\partial^2 S}{\partial f^2}\big(x, P(x, \boldsymbol{e})\big) + \frac{\partial^2 S}{\partial f \partial P}\big(x, P(x, \boldsymbol{e})\big) \frac{\partial P}{\partial f_1}(x, \boldsymbol{e}) \\
& + \left(\frac{\partial^2 S}{\partial f \partial P}\big(x, P(x, \boldsymbol{e})\big) + \frac{\partial^2 S}{\partial P^2}\big(x, P(x, \boldsymbol{e})\big) \frac{\partial P}{\partial f_1}(x, \boldsymbol{e}) \right) \frac{\partial P}{\partial f_1}(x, \boldsymbol{e}) \\
& + \frac{\partial S}{\partial P}\big(x, P(x, \boldsymbol{e})\big) \frac{\partial^2 P}{\partial f_1^2}(x, \boldsymbol{e}) \\
& + k \sum_{j=1}^{N-1} \left(\frac{\partial^2 S}{\partial P^2}\big(e_j, P(x, \boldsymbol{e})\big) \left(\frac{\partial P}{\partial f_1}(x, \boldsymbol{e}) \right)^2 + \frac{\partial S}{\partial P}\big(e_j, P(x, \boldsymbol{e})\big) \frac{\partial^2 P}{\partial f_1^2}(x, \boldsymbol{e}) \right).
\end{aligned}
$$

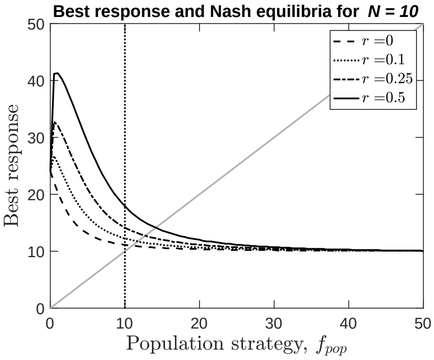


FIGURE 7. Best responses for different values of relatedness coefficients r. The vertical dotted line represents f_t.

Our assumptions on partial derivatives of S and P imply that $F'_{r,\boldsymbol{e}}(x) > 0$ for $x \in (0, f_t)$ and that the maximum of $F_{r,\boldsymbol{e}}$ occurs in $[f_t, f_{\max}]$. Moreover, $F''_{r,\boldsymbol{e}}(x) < 0$ for each $x \in [f_t, f_{\max})$. Since $F_{r,\boldsymbol{e}}$ is clearly continuous on $[0, f_{\max}]$, it is strictly concave there. Thus it attains a unique maximum on $[0, f_{\max}]$ at some point which we denote by $\varphi(r, \boldsymbol{e})$. This is the best response of (any) plant when the other plants have floral display $\boldsymbol{e} = (e_1, \ldots, e_{N-1})$. We note that $\varphi(r, \boldsymbol{e}) \in [f_t, f_{\max}]$ because $F_{r,\boldsymbol{e}})$ is increasing on $(0, f_t)$. Since W_1 is continuous and the maximum is attained uniquely, the Berge Maximum Theorem (Aliprantis and Border, 2006, Theorem 17.31, Lemma 17.6) implies that the best response function φ is continuous on $[0, f_{\max}) \times [0, f_{\max}]^{N-1}$.

Now put $\psi_r(f) = \varphi(r, f, \ldots, f)$, i.e. $\psi_r(f)$ is the unique best response of a focal plant in a group where all other plants allocate f. We will prove that ψ_r is non-increasing on $[f_t, f_{\max}]$; more exactly, it can be constant $f_{\max}$ for $f \leq f_c$ for some $f_c \in [f_t, f_{\max}]$ and then decreasing on $(f_c, f_{\max}]$. This is illustrated in Figure 7.

Let $f_t < f < e < f_{\max}$ and denote $\boldsymbol{f} = (f, \ldots, f) \in [f_t, f_{\max}]^{N-1}$ and $\boldsymbol{e} = (e, \ldots, e) \in [f_t, f_{\max}]^{N-1}$. Let $x \in [f_t, f_{\max})$ be arbitrary. Since P is increasing separately in each coordinate, it easily follows by induction that $0 < P(x, \boldsymbol{f}) < P(x, \boldsymbol{e}) < P_{\max}$. Consequently, since by our assumptions the partial derivatives of S are non-increasing separately in each coordinate,

$$\begin{aligned}
&\frac{\partial S}{\partial f}\big(x, P(x, \boldsymbol{f})\big) \geq \frac{\partial S}{\partial f}\big(x, P(x, \boldsymbol{e})\big),\\
&\frac{\partial S}{\partial P}\big(x, P(x, \boldsymbol{f})\big) \geq \frac{\partial S}{\partial P}\big(x, P(x, \boldsymbol{e})\big),\\
&\frac{\partial S}{\partial P}\big(f, P(x, \boldsymbol{f})\big)\ \frac{\partial S}{\partial P}\big(f, P(x, \boldsymbol{e})\big) \geq \frac{\partial S}{\partial P}\big(e, P(x, \boldsymbol{e})\big).
\end{aligned}$$

Similarly, since $\frac{\partial P}{\partial f_1}$ is non-increasing separately in each coordinate, by induction we get $\frac{\partial P}{\partial f_1}(x, \boldsymbol{f}) \geq \frac{\partial P}{\partial f_1}(x, \boldsymbol{e})$. Applying the above inequalities to (8) we obtain $F'_{r,\boldsymbol{f}}(x) > F'_{r,\boldsymbol{e}}(x)$ and this holds for any $x \in [f_t, f_{\max})$.

Now if $\psi_r(f) \in [f_t, f_{\max})$, then $F'_{r,\boldsymbol{f}}\big(\psi_r(f)\big) = 0$ and so $F'_{r,\boldsymbol{e}}\big(\psi_r(f)\big) < F'_{r,\boldsymbol{f}}\big(\psi_r(f)\big) = 0$. Hence the concavity of $F_{r,\boldsymbol{e}}$ implies that $\psi_r(e) < \psi_r(f)$. If $\psi_r(f) = f_{\max}$, then clearly $\psi_r(e) \leq f_{\max} = \psi_r(f)$.

So, ψ_r is non-increasing on $[f_t, f_{\max}]$ and it follows from above that $\psi_r(f_t) > f_t$ (if $\psi_r(f_t) = f_t$, then $\psi_r(f) < f_t$ for $f > f_t$ which is not possible). Also, $W_1(r, f_{\max}, \ldots, f_{\max}) = 0$, while $W_1(r, x, f_{\max}, \ldots, f_{\max}) > 0$ for any $x \in (0, f_{\max})$, so $\psi_r(f_{\max}) < f_{\max}$. Since ψ_r is continuous, the Darboux property implies that ψ_r has a fixed point $f^r_{\mathrm{NE}} \in (f_t, f_{\max})$, i.e. $\psi_r(f^r_{\mathrm{NE}}) = f^r_{\mathrm{NE}}$. Moreover, because ψ_r is non-increasing, this fixed point is unique. This means, that f^r_{NE} is the best response to all other plants allocating f^r_{NE}, i.e. $(f^r_{\mathrm{NE}}, \ldots, f^r_{\mathrm{NE}})$ is the unique symmetric Nash equilibrium. Further, given that the best response is unique, this Nash equilibrium is strict, and so is the unique symmetric Evolutionarily Stable Strategy (ESS), i.e. a strategy which, if adopted by a population, cannot be invaded by an initially rare alternative strategy (Maynard Smith and Price, 1973). Also, we note that this strategy is likely attracting in the adaptive dynamics sense and hence continuously stable strategy (CSS), see for example Brännström et al. (2013); Metz (2011).

We remark that there may be other, non-symmetric equilibria present (and consequently, if thinking in terms of adaptive dynamics, we cannot rule out branching points), but we focus our analysis solely on the symmetric one. This is for two main reasons. Firstly, if strategies are heritable and patches composed of related individuals, it is reasonable that such symmetric solutions would occur, and as our solution is evolutionarily stable, then evolution will not lead us away from such a solution. Secondly, practically it would not be possible to consider all of the possible asymmetric equilibria for arbitrary N.

Now, we can proceed with the proofs of the main results.

The first result. The optimal floral display is increasing in r. Moreover, at least for small r, the optimal display is decreasing in N.

To prove the optimal display is increasing in r, fix N and note that

$$F'_{\widetilde{r},\boldsymbol{f}}(x) = F'_{r,\boldsymbol{f}}(x) + (\widetilde{r} - r) \sum_{j=1}^{N-1} \frac{\partial S}{\partial P}\big(f_j, P(x, \boldsymbol{f})\big) \frac{\partial P}{\partial f_1}(x, \boldsymbol{f}).$$

Let $\widetilde{r} > r \geq 0$. We show that $\psi_{\widetilde{r}}(f) > \psi_r(f)$ whenever $f \in (f_t, f_{\max})$ is such that $\psi_r(f) \in (f_t, f_{\max})$. Indeed, in this case $F'_{r,\boldsymbol{f}}\big(\psi_r(f)\big) = 0$ (we set $\boldsymbol{f} = (f, \dots, f)$) and hence $F'_{\widetilde{r},\boldsymbol{f}}\big(\psi_r(f)\big) > F'_{r,\boldsymbol{f}}\big(\psi_r(f)\big) = 0$. The concavity of $F_{\widetilde{r},\boldsymbol{f}}$ then implies that $\psi_{\widetilde{r}}(f) > \psi_r(f)$. The continuity of ψ_r and the monotonicity of ψ_r, $\psi_{\widetilde{r}}$ together with the fact that $\psi_r(f^r_{\text{NE}}) \in (f_t, f_{\max})$ now imply that $\psi_{\widetilde{r}}(f) \geq \psi_r(f)$ for each $f \in [f_t, f_{\max}]$.

Finally, since $f^r_{\text{NE}} \in (f_t, f_{\max})$ is the unique fixed point of ψ_r, $\psi_{\widetilde{r}}(f) \geq \psi_r(f) > f$ whenever $f_t \leq f < f^r_{\text{NE}}$, and by the above $\psi_{\widetilde{r}}(f^r_{\text{NE}}) > \psi_r(f^r_{\text{NE}}) = f^r_{\text{NE}}$. Thus the fixed point $f^{\widetilde{r}}_{\text{NE}}$ of $\psi_{\widetilde{r}}$ is bigger than f^r_{NE}.

Second part of the first result For the purpose of this section, we will use index N or $N-1$ to study the dependence on the number of plants explicitly. For example, $f^{r,N}_{\text{NE}}$ is the optimal floral display in the patch of N plants and $f^{r,N-1}_{\text{NE}}$ is the optimal display in the patch of $N-1$.

To see $f^{r,N}_{\text{NE}}$ is decreasing in N (at least for small r), let $\boldsymbol{f}^{r,N-1}_{\text{NE}} \in [f_t, f_{\max}]^{N-1}$ be the optimal display for patch with $N-1$ plants. Denote $P_{N-1} = P(0, \boldsymbol{f}^{r,N-1}_{\text{NE}})$ the number of pollinators attracted to the patch with $N-1$ plants all behaving optimally. Since $\frac{\partial P}{\partial f_i} > 0$, we get that $P(x, \boldsymbol{f}^{r,N-1}_{\text{NE}}) > P_{N-1}$ for any $x \in (f_t, f_{\max})$. Since $\frac{\partial^2 S}{\partial f \partial P} < 0$, we get

$$\frac{\partial S}{\partial f}(f^{r,N-1}_{\text{NE}}, P_{N-1}) > \frac{\partial S}{\partial f}\big(f^{r,N-1}_{\text{NE}}, P(f^{r,N-1}_{\text{NE}}, \boldsymbol{f}^{r,N-1}_{\text{NE}})\big)$$

Since $\frac{\partial^2 S}{\partial P^2} < 0$, we get

$$\frac{\partial S}{\partial P}(f^{r,N-1}_{\text{NE}}, P_{N-1}) > \frac{\partial S}{\partial P}\big(f^{r,N-1}_{\text{NE}}, P(f^{r,N-1}_{\text{NE}}, \boldsymbol{f}^{r,N-1}_{\text{NE}})\big)$$

Finally, since $\frac{\partial^2 P}{\partial f_i \partial f_j} < 0$, we get

$$\frac{\partial P}{\partial f_1}(0, \boldsymbol{f}^{r,N-1}_{\text{NE}}) > \frac{\partial P}{\partial f_1}(f^{r,N-1}_{\text{NE}}, \boldsymbol{f}^{r,N-1}_{\text{NE}})$$

Consequently, since we have

$$\begin{aligned} F'_{r,N,\boldsymbol{f}^{r,N-1}_{\text{NE}}}(x) = {} & \frac{\partial S}{\partial f}\big(x, P(f^{r,N-1}_{\text{NE}}, \boldsymbol{f}^{r,N-1}_{\text{NE}})\big) + \frac{\partial S}{\partial P}\big(x, P(x, \boldsymbol{f}^{r,N}_{\text{NE}})\big) \frac{\partial P}{\partial f_1}(x, \boldsymbol{f}^{r,N-1}_{\text{NE}}) \\ & + (N-1) r \frac{\partial S}{\partial P}\big(f^{r,N-1}_{\text{NE}}, P(x, \boldsymbol{f}^{r,N-1}_{\text{NE}})\big) \frac{\partial P}{\partial f_1}(x, \boldsymbol{f}^{r,N-1}_{\text{NE}}) \end{aligned}$$

we get that, at least for r small enough,

$$F'_{r,N,\boldsymbol{f}^{r,N-1}_{\text{NE}}}(f^{r,N}_{\text{NE}}) < F'_{r,N-1,\boldsymbol{f}^{r,N-1}_{\text{NE}}}(f^{r,N-1}_{\text{NE}}) = 0$$

Thus, $f^{r,N}_{\text{NE}} < f^{r,N-1}_{\text{NE}}$.

The second result. The plants in the patch pay cost in terms of decreased seed production to increase their fitness by attracting pollinators to a whole patch and thus helping related plants produce more seeds, see Figure 3.

To see this, for a fixed r and N denote $g(x) = S\big(x, P(x, \boldsymbol{f}^r_{\mathrm{NE}})\big)$. Then

$$\begin{aligned} g'(x) &= \frac{\partial S}{\partial f}\big(x, P(x, \boldsymbol{f}^r_{\mathrm{NE}})\big) + \frac{\partial S}{\partial P}\big(x, P(x, \boldsymbol{f}^r_{\mathrm{NE}})\big)\frac{\partial P}{\partial f_1}(x, \boldsymbol{f}^r_{\mathrm{NE}}) && (9)\\ &= F'_{r,\boldsymbol{f}^r_{\mathrm{NE}}}(x) - (N-1)r\frac{\partial S}{\partial P}\big(f^r_{\mathrm{NE}}, P(x, \boldsymbol{f}^r_{\mathrm{NE}})\big)\frac{\partial P}{\partial f_1}(x, \boldsymbol{f}^r_{\mathrm{NE}}) && (10)\\ &< F'_{r,\boldsymbol{f}^r_{\mathrm{NE}}}(x) && (11) \end{aligned}$$

for $x \in (f_t, f_{\max})$. In particular, $g'(f^r_{\mathrm{NE}}) < F'_{r,\boldsymbol{f}^r_{\mathrm{NE}}}(f^r_{\mathrm{NE}}) = 0$, i.e. allocating little less than f^r_{NE} would increase the seed production.

The third result. When $\delta(r) = 0$ for all r, increasing relatedness in the patch increases the seed production of each plant in the patch, see Figure 4.

First we need to show that the mapping $\omega\colon r \mapsto f^r_{\mathrm{NE}}$ is continuous, which implies that $I = \omega([0,1))$ is an interval. So, fix any $r \in [0,1)$ and let $\varepsilon > 0$. The continuity of φ in particular implies the continuity of the mapping $\widetilde{r} \mapsto \psi_{\widetilde{r}}(f^r_{\mathrm{NE}})$. Hence there is $\sigma > 0$ such that $|\psi_{\widetilde{r}}(f^r_{\mathrm{NE}}) - \psi_r(f^r_{\mathrm{NE}})| < \varepsilon$ whenever $|\widetilde{r} - k| < \sigma$. So suppose that $\widetilde{r} \in [0,1)$ is such that $|\widetilde{r} - r| < \sigma$. We use the fact that $\psi_{\widetilde{r}}$ is non-increasing: if $f^r_{\mathrm{NE}} < f^{\widetilde{r}}_{\mathrm{NE}}$, then $f^{\widetilde{r}}_{\mathrm{NE}} = \psi_{\widetilde{r}}(f^{\widetilde{r}}_{\mathrm{NE}}) \le \psi_{\widetilde{r}}(f^r_{\mathrm{NE}}) < \psi_r(f^r_{\mathrm{NE}}) + \varepsilon = f^r_{\mathrm{NE}} + \varepsilon$, and if $f^r_{\mathrm{NE}} > f^{\widetilde{r}}_{\mathrm{NE}}$, then $f^{\widetilde{r}}_{\mathrm{NE}} = \psi_{\widetilde{r}}(f^{\widetilde{r}}_{\mathrm{NE}}) \ge \psi_{\widetilde{r}}(f^r_{\mathrm{NE}}) > \psi_r(f^r_{\mathrm{NE}}) - \varepsilon = f^r_{\mathrm{NE}} - \varepsilon$. Hence $|f^{\widetilde{r}}_{\mathrm{NE}} - f^r_{\mathrm{NE}}| < \varepsilon$.

Now, the seed production when all the plants allocate the same is given by $s(f) = S\big(f, P(\boldsymbol{f})\big)$, where $\boldsymbol{f} = (f, \dots, f) \in [f_t, f_{\max}]^N$, and this does not depend on r. Thus

$$\begin{aligned} s'(f) &= \frac{\partial S}{\partial f}\big(f, P(\boldsymbol{f})\big) + \frac{\partial S}{\partial P}\big(f, P(\boldsymbol{f})\big)\sum_{i=1}^{N}\frac{\partial P}{\partial f_i}(\boldsymbol{f}) = \frac{\partial S}{\partial f}\big(f, P(\boldsymbol{f})\big) + N\frac{\partial S}{\partial P}\big(f, P(\boldsymbol{f})\big)\frac{\partial P}{\partial f_1}(\boldsymbol{f})\\ &= F'_{r,\boldsymbol{f}}(f) + (N-1)(1-r)\frac{\partial S}{\partial P}\big(f, P(\boldsymbol{f})\big)\frac{\partial P}{\partial f_1}(\boldsymbol{f}) > F'_{r,\boldsymbol{f}}(f) \end{aligned}$$

for $f \in (f_t, f_{\max})$. In particular, since $F'_{r,\boldsymbol{f}^r_{\mathrm{NE}}}(f^r_{\mathrm{NE}}) = 0$, we get $s'(f^r_{\mathrm{NE}}) > 0$. Thus $s'(f) > 0$ for each $f \in I$, so s is increasing on I. In combination with the first result we obtain that $r \mapsto s(f^r_{\mathrm{NE}})$ is increasing.

ACKNOWLEDGEMENTS

SS was financially supported by the National Natural Science Foundation of China (31870357).

REFERENCES

Aizen, M. A. and Harder, L. D. (2007). Expanding the limits of the pollen-limitation concept: effects of pollen quantity and quality. *Ecology*, 88(2):271–281.

Aizen, M. A., Morales, C. L., Vázquez, D. P., Garibaldi, L. A., Sáez, A., and Harder, L. D. (2014). When mutualism goes bad: density-dependent impacts of introduced bees on plant reproduction. *New Phytologist*, 204(2):322–328.

Aliprantis, C. D. and Border, K. C. (2006). *Infinite dimensional analysis: a hitchhiker's guide*. Springer.

Andersson, S. (2000). The cost of flowers in *Nigella degenii* inferred from flower and perianth removal experiments. *International Journal of Plant Sciences*, 161(6):903–908.

Andersson, S. (2005). Floral costs in *Nigella sativa* (Ranunculaceae): compensatory responses to perianth removal. *American Journal of Botany*, 92(2):279–283.

Bell, G. (1985). On the function of flowers. *Proceedings of the Royal society of London. Series B. Biological sciences*, 224(1235):223–265.

Bhatt, M. V., Khandelwal, A., and Dudley, S. A. (2011). Kin recognition, not competitive interactions, predicts root allocation in young *Cakile edentula* seedling pairs. *New Phytologist*, 189(4):1135–1142.

Biernaskie, J. M. (2010). Evidence for competition and cooperation among climbing plants. *Proceedings of the Royal Society B: Biological Sciences*, 278(1714):1989–1996.

Biernaskie, J. M. and Elle, E. (2007). A theory for exaggerated secondary sexual traits in animal-pollinated plants. *Evolutionary Ecology*, 21(4):459–472.

Brännström, Å., Johansson, J., and Von Festenberg, N. (2013). The hitchhiker's guide to adaptive dynamics. *Games*, 4(3):304–328.

Burd, M. (2008). The Haig-Westoby model revisited. *The American Naturalist*, 171(3):400–404.

Cartar, R. V. (2004). Resource tracking by bumble bees: responses to plant-level differences in quality. *Ecology*, 85(10):2764–2771.

Crepy, M. A. and Casal, J. J. (2015). Photoreceptor-mediated kin recognition in plants. *New Phytologist*, 205(1):329–338.

de Jong, T. and Klinkhamer, P. (2005). *Evolutionary ecology of plant reproductive strategies*. Cambridge University Press.

Devaux, C., Lande, R., and Porcher, E. (2014). Pollination ecology and inbreeding depression control individual flowering phenologies and mixed mating. *Evolution*, 68(11):3051–3065.

Dudley, S. A. (2015). Plant cooperation. *AoB Plants*, 7:plv113.

Dudley, S. A. and File, A. L. (2007). Kin recognition in an annual plant. *Biology Letters*, 3(4):435–438.

Ehlers, B. K. and Bilde, T. (2019). Inclusive fitness, asymmetric competition and kin selection in plants. *Oikos*, 128(6):765–774.

File, A. L., Murphy, G. P., and Dudley, S. A. (2011). Fitness consequences of plants growing with siblings: reconciling kin selection, niche partitioning and competitive ability. *Proceedings of the Royal Society B: Biological Sciences*, 279(1727):209–218.

Finer, M. S. and Morgan, M. T. (2003). Effects of natural rates of geitonogamy on fruit set in *Asclepias speciosa* (Apocynaceae): evidence favoring the plant's dilemma. *American Journal of Botany*, 90(12):1746–1750.

Gardner, A. and West, S. A. (2010). Greenbeards. *Evolution: International Journal of Organic Evolution*, 64(1):25–38.

Gardner, A., West, S. A., and Wild, G. (2011). The genetical theory of kin selection. *Journal of Evolutionary Biology*, 24(5):1020–1043.

Garibaldi, L. A., Steffan-Dewenter, I., Winfree, R., Aizen, M. A., Bommarco, R., Cunningham, S. A., Kremen, C., Carvalheiro, L. G., Harder, L. D., and Afik, O. (2013). Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *science*, 339(6127):1608–1611.

Ghazoul, J. (2006). Floral diversity and the facilitation of pollination. *Journal of Ecology*, 94(2):295–304.

Haig, D. and Westoby, M. (1988). On limits to seed production. *The American Naturalist*, 131(5):757–759.

Hamilton, W. D. (1964a). The genetical evolution of social behavior, I. *Journal of Theoretical Biology*, 7(1):1–16.

Hamilton, W. D. (1964b). The genetical evolution of social behaviour. II. *Journal of Theoretical Biology*, 7(1):17–52.

Harder, L. D. and Barrett, S. C. (1995). Mating cost of large floral displays in hermaphrodite plants. *Nature*, 373(6514):512–515.

Klemens, J. A. (2008). Kin recognition in plants? *Biology Letters*, 4(1):67–68.

Klinkhamer, P. G., De Jong, T. J., and Linnebank, L. A. (2001). Small-scale spatial patterns determine ecological relationships: an experimental example using nectar production rates. *Ecology Letters*, 4(6):559–567.

Laverty, T. M. (1992). Plant interactions for pollinator visits: a test of the magnet species effect. *Oecologia*, 89(4):502–508.

Lefebvre, D., Pierre, J., Outreman, Y., and Pierre, J.-S. (2007). Patch departure rules in bumblebees: evidence of a decremental motivational mechanism. *Behavioral Ecology and Sociobiology*, 61(11):1707–1715.

Lehmann, L. and Keller, L. (2006). The evolution of cooperation and altruism–a general framework and a classification of models. *Journal of Evolutionary Biology*, 19(5):1365–1376.

Liao, W.-J., Hu, Y., Zhu, B.-R., Zhao, X.-Q., Zeng, Y.-F., and Zhang, D.-Y. (2009). Female reproductive success decreases with display size in monkshood, *Aconitum kusnezoffii* (Ranunculaceae). *Annals of Botany*, 104(7):1405–1412.

Marshall, J. A. (2011). Group selection and kin selection: formally equivalent approaches. *Trends in Ecology & Evolution*, 26(7):325–332.

Maynard Smith, J. and Price, G. (1973). The logic of animal conflict. *Nature*, 246(5427):15–18.

Mesgaran, M. B., Bouhours, J., Lewis, M. A., and Cousens, R. D. (2017). How to be a good neighbour: Facilitation and competition between two co-flowering species. *Journal of Theoretical Biology*, 422(7):72–83.

Metz, J. H. (2011). Thoughts on the geometry of meso-evolution: collecting mathematical elements for a postmodern synthesis. In *The Mathematics of Darwin's legacy*, pages 193–231. Springer.

Milla, R., Forero, D. M., Escudero, A., and Iriondo, J. M. (2009). Growing with siblings: a common ground for cooperation or for fiercer competition among plants? *Proceedings of the Royal Society B: Biological Sciences*, 276(1667):2531–2540.

Moeller, D. A. (2004). Facilitative interactions among plants via shared pollinators. *Ecology*, 85(12):3289–3301.

Molina-Montenegro, M. A., Badano, E. I., and Cavieres, L. A. (2008). Positive interactions among plant species for pollinator service: assessing the 'magnet species' concept with invasive species. *Oikos*, 117(12):1833–1839.

Morris, W. F., Vázquez, D. P., and Chacoff, N. P. (2010). Benefit and cost curves for typical pollination mutualisms. *Ecology*, 91(5):1276–1285.

Ollerton, J. (2017). Pollinator diversity: distribution, ecological function, and conservation. *Annual Review of Ecology, Evolution, and Systematics*, 48:353–376.

Seifan, M., Hoch, E.-M., Hanoteaux, S., and Tielbörger, K. (2014). The outcome of shared pollination services is affected by the density and spatial pattern of an attractive neighbour. *Journal of Ecology*, 102(4):953–962.

Taylor, P. D. and Frank, S. A. (1996). How to make a kin selection model. *Journal of Theoretical Biology*, 180(1):27–37.

Thomann, M., Imbert, E., Devaux, C., and Cheptou, P.-O. (2013). Flowering plants under global pollinator decline. *Trends in Plant Science*, 18(7):353–359.

Torices, R., Gómez, J. M., and Pannell, J. R. (2018). Kin discrimination allows plants to modify investment towards pollinator attraction. *Nature Communications*, 9(1).

West, S. A., Griffin, A. S., and Gardner, A. (2007). Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *Journal of Evolutionary Biology*, 20(2):415–432.

West, S. A., Pen, I., and Griffin, A. S. (2002). Cooperation and competition between relatives. *Science*, 296(5565):72–75.

[1]STATE KEY LABORATORY OF GRASSLAND AGRO-ECOSYSTEMS, SCHOOL OF LIFE SCIENCES, LANZHOU UNIVERSITY, LANZHOU 730000, PEOPLE'S REPUBLIC OF CHINA

[2]DEPARTMENT OF MATHEMATICS, CITY, UNIVERSITY OF LONDON, NORTHAMPTON SQUARE, LONDON, EC1V 0HB, UK

[3]DEPARTMENT OF MATHEMATICAL ANALYSIS, FACULTY OF MATHEMATICS AND PHYSICS, CHARLES UNIVERSITY, SOKOLOVSKÁ 83, 186 75 PRAHA 8, CZECH REPUBLIC

[4]DEPARTMENT OF MATHEMATICS AND APPLIED MATHEMATICS, VIRGINIA COMMONWEALTH UNIVERSITY, RICHMOND, VA 23284-2014, USA