

# A MATHEMATICAL MODEL OF KIN SELECTION IN FLORAL DISPLAYS

SHAN SUN<sup>1</sup>, MARK BROOM<sup>2</sup>, MICHAL JOHANIS<sup>3</sup>, AND JAN RYCHTÁŘ<sup>\*4</sup>

**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 (Lavery, 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

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\*Corresponding author: rychartarj@vcu.edu.

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

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

42

## 2. MATHEMATICAL MODEL

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

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

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

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

53 The function  $P$  given in (1) has the following properties. The patch can attract between 0 and up to  
 54 1000 pollinators. If any plant increases its floral display, the whole patch will become more attractive  
 55 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  
 56 display has diminishing returns, i.e.  $\frac{\partial^2 P}{\partial f_i \partial f_j} \leq 0$  for all  $i, j = 1, \dots, N$ . Finally, all plants contribute in  
 57 the same way, i.e. the value of  $P$  is the same for all permutations of its arguments.

58 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  
 59 number of seeds produced by a plant with floral display  $f$  that gets completely pollinated (when there is  
 60 no pollen limitation). It illustrates a reasonable dependence of the number of seeds on the plant's floral  
 61 display. For small  $f$ ,  $S(f, P)$  is increasing in  $f$  because there are no serious resource limitations yet  
 62 and the chances of geitonogamy (Harder and Barrett, 1995) are also relatively small. It is plausible that  
 63 the increase is slowing down ( $\frac{\partial^2 S}{\partial f^2} \leq 0$ ) and eventually, there is a threshold  $f_t$  such that for  $f > f_t$ , the  
 64 function  $S(f, P)$  is decreasing in  $f$ . This is because a floral display increases the chances of geitonogamy  
 65 (Harder and Barrett, 1995), further reducing seed production (Finer and Morgan, 2003; Liao et al., 2009).  
 66 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  
 67  $P$ . Moreover, we will assume that the negative effect of allocating more to the floral display (and thus  
 68 less to seed production) is amplified by the increasing number of pollinators on the patch, i.e.  $\frac{\partial^2 S}{\partial f \partial P} \leq 0$   
 69 when  $f > f_t$  as well as of itself, i.e.  $\frac{\partial^2 S}{\partial f^2} \leq 0$  when  $f > f_t$ . This is because when more pollinators are  
 70 already attracted to the patch (and thus the plant), or when not enough is allocated to seed production,  
 71 allocating even less to seed production has larger negative consequences.

72 The magnet effect (Lavery, 1992; Molina-Montenegro et al., 2008) means that increasing the floral  
 73 display brings in more pollinators to the patch as a whole which benefits every plant in the patch. It  
 74 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  
 75 effect of  $P$  on  $S$  has diminishing returns, i.e.  $\frac{\partial^2 S}{\partial P^2} \leq 0$  (Bell, 1985; de Jong and Klinkhamer, 2005).  
 76 The assumption of benefits to every plant in the patch is in agreement with Klinkhamer et al. (2001);

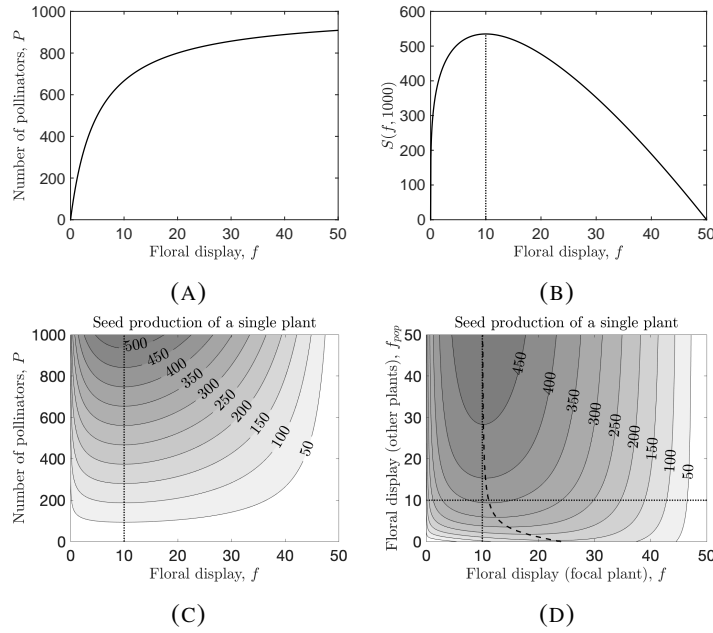


FIGURE 1. (A) The function  $f \mapsto P(f, \dots, f)$ , i.e. the number of pollinators attracted to the patch when each of the  $N = 10$  plants has a floral display  $f$ . (B) The function  $f \mapsto S(f, 1000)$ , i.e. the number of seeds the flower could produce if it has a floral display  $f$  and 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  $(f, f_{pop}) \mapsto S(f, P(f, f_{pop}, \dots, f_{pop}))$ , 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.

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

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

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

$$\tilde{S}(f, P) = (1 - \delta(r))S(f, P) \quad (3)$$

91 The total fitness of the plant  $i$  will depend not only on its own (viable) seed production, but also on the  
 92 (viable) seed production of related plants in the patch. Throughout the paper we refer to this total fitness  
 93 as simply the fitness, which is the sum of the contribution to this fitness of its own seed production, and

94 the contribution of the seed production of related plants through collective attractiveness of the patch.  
 95 We are investigating a very specific question in this paper, and, due to the complexity of our model,  
 96 deliberately avoid the terminology of inclusive fitness, which is the subject of quite a subtle debate  
 97 beyond the scope of this article.

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

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

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

### 109 3. RESULTS

110 The analysis of our model yields the following results. Mathematical proofs are provided in the Ap-  
 111 pendix B.

112 **The first result.** The optimal floral display is positively correlated with the average relatedness coef-  
 113 ficient, see Figure 2.

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

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

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

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

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

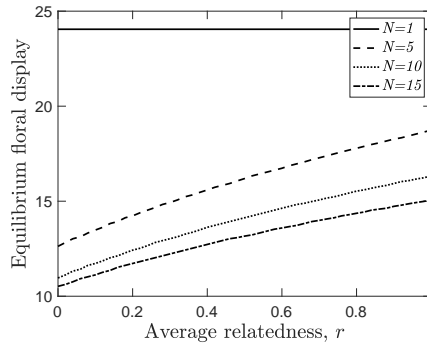


FIGURE 2. Nash equilibrium floral display as a function of the average relatedness coefficient for different patch sizes. Here, the results do not depend on the inbreeding depression  $\delta(r)$ . The optimal floral display is decreasing in the number of plants in the patch for the particular functions  $P$  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  $N$ .

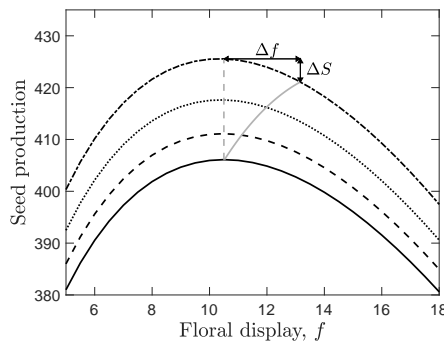


FIGURE 3. An individual plant pays a cost in terms of decreased its own seed production (by  $\Delta S$ ) as it increases its floral display (by  $\Delta f$ ) to attract pollinators for the whole patch. The graphs show the seed production of a focal plant as a function of its floral display  $f$  when 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.

138

#### 4. DISCUSSION

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

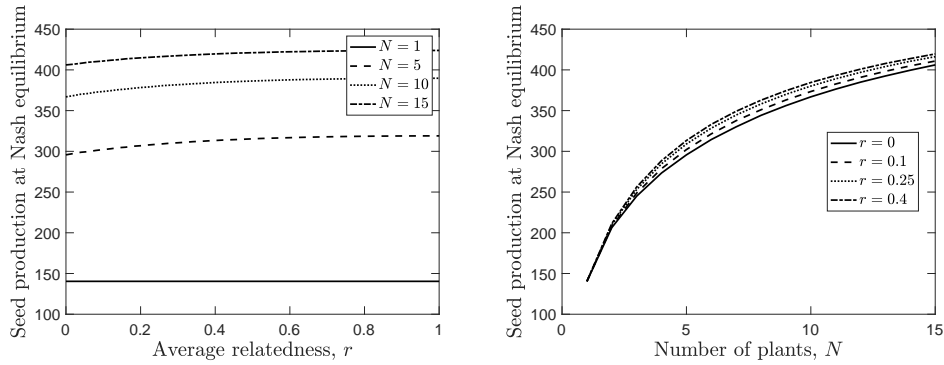


FIGURE 4. In the absence of inbreeding depression (when  $\delta(r) = 0$ ), individual seed production at equilibrium floral display is an increasing function of the average relatedness  $r$  within the patch. Also, we observe that individual seed production of each plant at the equilibrium is an increasing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

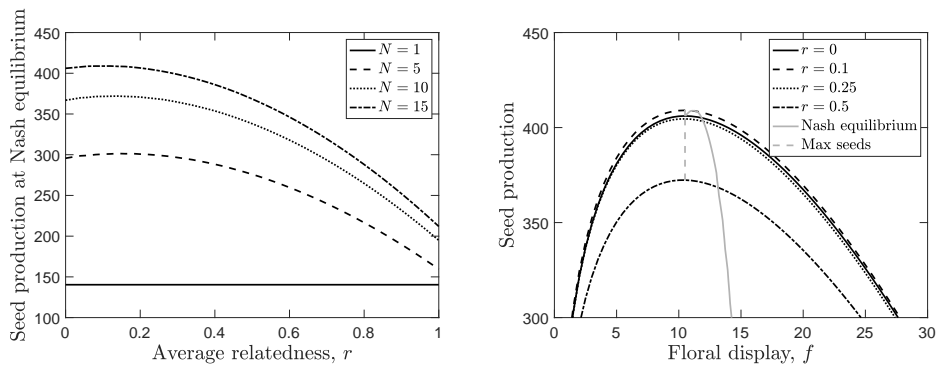


FIGURE 5. Left: In the presence of inbreeding depression (here  $\delta(r) = r^2/2$ ), individual seed production at Nash equilibrium display is an increasing function of the average relatedness  $r$  within the patch for small  $r$  and decreasing for large  $r$ . Right: individual seed production 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

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

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

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

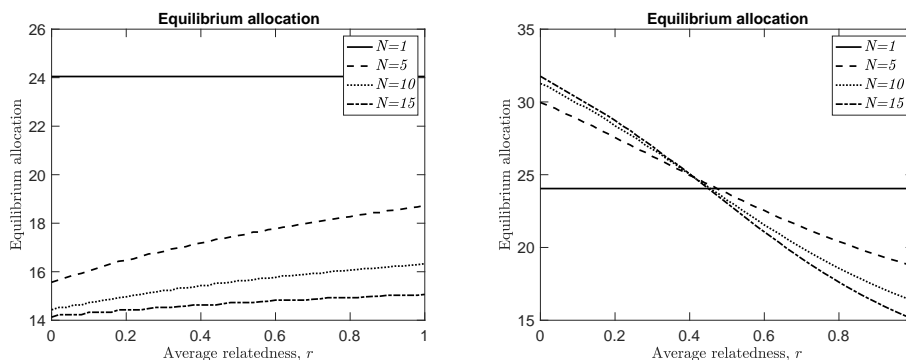


FIGURE 6. Equilibrium floral display when the seed production function is given by  $\hat{S}(f, f_{\text{avg}}, P) = S(f, P) \exp(z(f - f_{\text{avg}}))$ , where  $S$  and  $P$  are given as in (2) and (1). Due to the factor  $\exp(z(f - f_{\text{avg}}))$ , the plants whose floral display is above average 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.

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

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

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

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

195 As in Klinkhamer et al. (2001), we assumed in the model that the attractiveness of a plant only  
 196 contributes to attracting a pollinator to the patch, and that the pollinator visits all plants equally once  
 197 entering the patch. However, this may not always be the case (Biernaskie and Elle, 2007). Within a  
 198 patch, pollinators can preferentially or more frequently visit plants offering high rewards (Cartar, 2004;  
 199 Lefebvre et al., 2007). Thus, the plants with an above average floral display have a competitive advantage  
 200 in attracting pollinators (Biernaskie and Elle, 2007). In order to explicitly incorporate variability within

201 a patch, we can expand the assumptions that the seed production of a plant depends not only on (1) the  
 202 floral display, and (2) the total attractiveness of the plant patch, but also on (3) the average floral display  
 203 in the patch. In this way, the model can capture the likelihood that, within a given patch, more attractive  
 204 plants attract more pollinators and in turn produce more seeds. We found that our results would not  
 205 change when the effect of the variability of floral display on seed production within the patch is small,  
 206 see Figure 6. However, when the effect is larger, there are differences. The equilibrium display becomes  
 207 decreasing in  $r$ . Moreover, the equilibrium display is increasing in  $N$  for small  $r$  and decreasing in  $N$   
 208 for large  $r$ . We note that the results of Torices et al. (2018) also showed that for small  $r$  ( $k = 0.25$ ), the  
 209 equilibrium display is increasing in  $N$ .

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

218 Recently, Ollerton (2017) assessed the current diversity of pollinators and suggested that there is  
 219 a reduction of the different types of pollinator richness and density in some regions. Thomann et al.  
 220 (2013) proposed that plant reproductive strategies can adapt to this pollinator decline by reinforcing  
 221 interactions with pollinators. Our model suggests that an increasing investment in floral display by kin  
 222 selection could provide the mechanism to deal with the pollination crisis. Further works need to show  
 223 how evolution of reinforced interactions can avoid an evolutionary trap if pollinators keep declining and  
 224 plants continue increasing investment in floral display.

#### 225 APPENDIX A. MATHEMATICAL SETUP OF THE MODEL

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

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

231 We assume that  $S$  has the following properties:

- 232 •  $S : [0, f_{\max}] \times [0, P_{\max}] \mapsto [0, S_{\max}]$ , i.e. the plants can make up to (a very large)  $f_{\max}$  flowers,  
 233 up to  $P_{\max}$  pollinators can potentially come to the patch and if all goes well, the plant can make  
 234 up to  $S_{\max}$  seeds.
- 235 •  $S(f, 0) = 0$  for all  $f \in [0, f_{\max}]$  (in practice  $f > 0$  will likely imply  $P > 0$ , but this assumption  
 236 is needed for mathematical completeness to have  $S$  defined properly on its whole domain),
- 237 •  $S(f_{\max}, P) = 0$  for all  $P \in [0, P_{\max}]$ , i.e. when the plant makes way too many flowers, it will  
 238 not be able to produce any seeds
- 239 • 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)  
 240  $\frac{\partial S}{\partial f}(f, P) < 0$  for  $f \in (f_t, f_{\max})$  and  $P \in (0, P_{\max})$ . Haig and Westoby (1988) assumed: 1) the  
 241 resources allocation only between plant attraction and seed provisioning could ensure enough  
 242 pollen capture to fertilize ovules that would mature to seed; 2) ovule fertilizations increasing  
 243 with the amount of resources allocation to pollinator attraction but at a diminishing rate, and  
 244 predicted that the optimal resources allocation to pollinator attraction should gain just the num-  
 245 ber of ovule fertilizations needed to consume the available seed-provisioning resources (Burd,  
 246 2008). Also, Liao et al. (2009) showed that the rate of pollinator visitation varied positively with  
 247 display size, but seed production decreased with floral display increasing due to geitonogamous  
 248 pollination in four *Aconitum kusnezoffii* populations.
- 249 •  $\frac{\partial S}{\partial P}(f, P) > 0$  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  
 250  $P \in (0, P_{\max})$ , see for example Garibaldi et al. (2013).



251 •  $\frac{\partial^2 S}{\partial f^2}(f, P) \leq 0$ ,  $\frac{\partial^2 S}{\partial P^2}(f, P) \leq 0$  for  $f \in (0, f_{\max})$  and  $P \in (0, P_{\max})$  and these second deriva-  
 252 tives are never all zero at the same point of  $(0, f_{\max}) \times (0, P_{\max})$ , see for example Devaux et al.  
 253 (2014).

254 •  $\frac{\partial^2 S}{\partial f \partial P}(f, P) \leq 0$  for  $f \in [f_t, f_{\max})$  and  $P \in (0, P_{\max})$ , see for example Liao et al. (2009).

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

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

258 We assume that  $P$  has the following properties:

259 •  $P : [0, f_{\max}]^N \mapsto [0, P_{\max}]$ ,

260 •  $P(0, \dots, 0) = 0$ ,

261 • the value of  $P$  is the same for all permutations of its arguments.

262 •  $\frac{\partial P}{\partial f_i}(f_1, \dots, f_N) > 0$  for each  $f_i \in (0, f_{\max})$ ,  $f_j \in [0, f_{\max}]$ ,  $j \in \{1, \dots, N\} \setminus \{i\}$ , and this  
 263 holds for all  $i = 1, \dots, N$ ,

264 •  $\frac{\partial^2 P}{\partial f_i \partial f_j}(f_1, \dots, f_N) \leq 0$  for each  $\mathbf{f} \in (0, f_{\max})^N$ ,  $i, j = 1, \dots, N$ ,

265 •  $\frac{\partial^2 P}{\partial f_i^2}(f_1, \dots, f_N) \leq 0$  for  $f_i \in (0, f_{\max})$ ,  $f_j \in [0, f_{\max}]$ ,  $j \in \{1, \dots, N\} \setminus \{i\}$ ,  $i = 1, \dots, N$ .

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

## 267 APPENDIX B. PROOFS

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

$$F_{r,\mathbf{e}}(x) = \frac{1}{1 - \delta(r)} W_1(r, x, \mathbf{e}) \quad (5)$$

$$= S(x, P(x, e_1, \dots, e_{N-1})) + r \sum_{j=1}^{N-1} S(e_j, P(x, e_1, \dots, e_{N-1})) \quad (6)$$

270 Note that from the symmetry of  $P$  it follows that

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

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

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

275 Let  $\mathbf{e} \in [0, f_{\max}]^{N-1}$ . By differentiating at  $x \in (0, f_{\max})$  (note that by our assumptions  $P(x, \mathbf{e}) \in$   
 276  $(0, P_{\max})$ ) we obtain

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

277 and

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

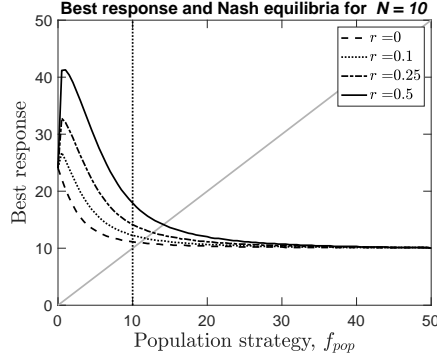


FIGURE 7. Best responses for different values of relatedness coefficients  $r$ . The vertical dotted line represents  $f_t$ .

278 Our assumptions on partial derivatives of  $S$  and  $P$  imply that  $F'_{r,e}(x) > 0$  for  $x \in (0, f_t)$  and that  
 279 the maximum of  $F_{r,e}$  occurs in  $[f_t, f_{\max}]$ . Moreover,  $F''_{r,e}(x) < 0$  for each  $x \in [f_t, f_{\max}]$ . Since  $F_{r,e}$  is  
 280 clearly continuous on  $[0, f_{\max}]$ , it is strictly concave there. Thus it attains a unique maximum on  $[0, f_{\max}]$   
 281 at some point which we denote by  $\varphi(r, e)$ . This is the best response of (any) plant when the other plants  
 282 have floral display  $e = (e_1, \dots, e_{N-1})$ . We note that  $\varphi(r, e) \in [f_t, f_{\max}]$  because  $F_{r,e}$  is increasing on  
 283  $(0, f_t)$ . Since  $W_1$  is continuous and the maximum is attained uniquely, the Berge Maximum Theorem  
 284 (Aliprantis and Border, 2006, Theorem 17.31, Lemma 17.6) implies that the best response function  $\varphi$  is  
 285 continuous on  $[0, f_{\max}) \times [0, f_{\max}]^{N-1}$ .

286 Now put  $\psi_r(f) = \varphi(r, f, \dots, f)$ , i.e.  $\psi_r(f)$  is the unique best response of a focal plant in a group  
 287 where all other plants allocate  $f$ . We will prove that  $\psi_r$  is non-increasing on  $[f_t, f_{\max}]$ ; more exactly,  
 288 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  
 289 illustrated in Figure 7.

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

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

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

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

299 So,  $\psi_r$  is non-increasing on  $[f_t, f_{\max}]$  and it follows from above that  $\psi_r(f_t) > f_t$  (if  $\psi_r(f_t) =$   
 300  $f_t$ , then  $\psi_r(f) < f_t$  for  $f > f_t$  which is not possible). Also,  $W_1(r, f_{\max}, \dots, f_{\max}) = 0$ , while  
 301  $W_1(r, x, f_{\max}, \dots, f_{\max}) > 0$  for any  $x \in (0, f_{\max})$ , so  $\psi_r(f_{\max}) < f_{\max}$ . Since  $\psi_r$  is continuous,  
 302 the Darboux property implies that  $\psi_r$  has a fixed point  $f_{\text{NE}}^r \in (f_t, f_{\max})$ , i.e.  $\psi_r(f_{\text{NE}}^r) = f_{\text{NE}}^r$ . More-  
 303 over, because  $\psi_r$  is non-increasing, this fixed point is unique. This means, that  $f_{\text{NE}}^r$  is the best response to  
 304 all other plants allocating  $f_{\text{NE}}^r$ , i.e.  $(f_{\text{NE}}^r, \dots, f_{\text{NE}}^r)$  is the unique symmetric Nash equilibrium. Further,  
 305 given that the best response is unique, this Nash equilibrium is strict, and so is the unique symmetric  
 306 Evolutionarily Stable Strategy (ESS), i.e. a strategy which, if adopted by a population, cannot be invaded  
 307 by an initially rare alternative strategy (Maynard Smith and Price, 1973). Also, we note that this strategy

308 is likely attracting in the adaptive dynamics sense and hence continuously stable strategy (CSS), see for  
 309 example Brännström et al. (2013); Metz (2011).

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

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

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

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

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

320 Let  $\tilde{r} > r \geq 0$ . We show that  $\psi_{\tilde{r}}(f) > \psi_r(f)$  whenever  $f \in (f_t, f_{\max})$  is such that  $\psi_r(f) \in (f_t, f_{\max})$ .  
 321 Indeed, in this case  $F'_{r,\mathbf{f}}(\psi_r(f)) = 0$  (we set  $\mathbf{f} = (f, \dots, f)$ ) and hence  $F'_{\tilde{r},\mathbf{f}}(\psi_r(f)) > F'_{r,\mathbf{f}}(\psi_r(f)) =$   
 322  $0$ . The concavity of  $F_{\tilde{r},\mathbf{f}}$  then implies that  $\psi_{\tilde{r}}(f) > \psi_r(f)$ . The continuity of  $\psi_r$  and the monotonicity  
 323 of  $\psi_r, \psi_{\tilde{r}}$  together with the fact that  $\psi_r(f_{\text{NE}}^r) \in (f_t, f_{\max})$  now imply that  $\psi_{\tilde{r}}(f) \geq \psi_r(f)$  for each  
 324  $f \in [f_t, f_{\max}]$ .

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

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

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

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

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

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

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

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

337 Consequently, since we have

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

338 we get that, at least for  $r$  small enough,

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

339 Thus,  $f_{\text{NE}}^{r,N} < f_{\text{NE}}^{r,N-1}$ .

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

343 To see this, for a fixed  $r$  and  $N$  denote  $g(x) = S(x, P(x, \mathbf{f}_{\text{NE}}^r))$ . Then

$$g'(x) = \frac{\partial S}{\partial f}(x, P(x, \mathbf{f}_{\text{NE}}^r)) + \frac{\partial S}{\partial P}(x, P(x, \mathbf{f}_{\text{NE}}^r)) \frac{\partial P}{\partial f_1}(x, \mathbf{f}_{\text{NE}}^r) \quad (9)$$

$$= F'_{r, \mathbf{f}_{\text{NE}}^r}(x) - (N-1)r \frac{\partial S}{\partial P}(f_{\text{NE}}^r, P(x, \mathbf{f}_{\text{NE}}^r)) \frac{\partial P}{\partial f_1}(x, \mathbf{f}_{\text{NE}}^r) \quad (10)$$

$$< F'_{r, \mathbf{f}_{\text{NE}}^r}(x) \quad (11)$$

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

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

348 First we need to show that the mapping  $\omega: r \mapsto f_{\text{NE}}^r$  is continuous, which implies that  $I = \omega([0, 1])$  is  
 349 an interval. So, fix any  $r \in [0, 1]$  and let  $\varepsilon > 0$ . The continuity of  $\varphi$  in particular implies the continuity  
 350 of the mapping  $\tilde{r} \mapsto \psi_{\tilde{r}}(f_{\text{NE}}^r)$ . Hence there is  $\sigma > 0$  such that  $|\psi_{\tilde{r}}(f_{\text{NE}}^r) - \psi_r(f_{\text{NE}}^r)| < \varepsilon$  whenever  
 351  $|\tilde{r} - r| < \sigma$ . So suppose that  $\tilde{r} \in [0, 1]$  is such that  $|\tilde{r} - r| < \sigma$ . We use the fact that  $\psi_{\tilde{r}}$  is non-  
 352 increasing: if  $f_{\text{NE}}^r < f_{\text{NE}}^{\tilde{r}}$ , then  $f_{\text{NE}}^{\tilde{r}} = \psi_{\tilde{r}}(f_{\text{NE}}^r) \leq \psi_{\tilde{r}}(f_{\text{NE}}^r) < \psi_r(f_{\text{NE}}^r) + \varepsilon = f_{\text{NE}}^r + \varepsilon$ , and if  
 353  $f_{\text{NE}}^r > f_{\text{NE}}^{\tilde{r}}$ , then  $f_{\text{NE}}^{\tilde{r}} = \psi_{\tilde{r}}(f_{\text{NE}}^r) \geq \psi_{\tilde{r}}(f_{\text{NE}}^r) > \psi_r(f_{\text{NE}}^r) - \varepsilon = f_{\text{NE}}^r - \varepsilon$ . Hence  $|f_{\text{NE}}^{\tilde{r}} - f_{\text{NE}}^r| < \varepsilon$ .

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

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

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

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465 <sup>1</sup>STATE KEY LABORATORY OF GRASSLAND AGRO-ECOSYSTEMS, SCHOOL OF LIFE SCIENCES, LANZHOU UNIVER-  
466 SITY, LANZHOU 730000, PEOPLE'S REPUBLIC OF CHINA

467 <sup>2</sup>DEPARTMENT OF MATHEMATICS, CITY, UNIVERSITY OF LONDON, NORTHAMPTON SQUARE, LONDON, EC1V  
468 OHB, UK

469 <sup>3</sup>DEPARTMENT OF MATHEMATICAL ANALYSIS, FACULTY OF MATHEMATICS AND PHYSICS, CHARLES UNIVERSITY,  
470 SOKOLOVSKÁ 83, 186 75 PRAHA 8, CZECH REPUBLIC

471 <sup>4</sup>DEPARTMENT OF MATHEMATICS AND APPLIED MATHEMATICS, VIRGINIA COMMONWEALTH UNIVERSITY, RICH-  
472 MOND, VA 23284-2014, USA