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Decline of pollinators and attractiveness of the plants

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Flowering plants rely mostly on pollinators to reproduce. A decline of pollinators puts an evolutionary pressure on the allocation of plants' resources towards attracting the few remaining pollinators. This may result in fewer resources available for the plants' survival and actual seed production. Moreover, due to the "magnet effect", attractive plants generally attract pollinators to all plants in their neighborhood, even the less attractive ones. To better understand the allocation trade-offs, we built a computer simulation and studied the evolution of resource allocation towards attracting pollinators. We observed that when pollinators are relatively abundant, there is not much incentive for the plants to allocate more energy to attract them. Only when pollinators are below a certain critical threshold is a relatively large investment in attracting the pollinators suddenly favored. The value of the critical threshold is quite low and further decreases with the increasing seed dispersal distance and the plant population size.

1. Introduction

Flowering plants, including plants that yield crops, are pollinated mainly by insects [Williams 2002]. Attractiveness of a plant's flowers is a major factor in the plant's reproductive success [Kunin and Iwasa 1996]. Flowers of different species may vary vastly in color, pattern, and size but they all retain a similar structure in order to appeal to the available insect pollinators [Endress 1994].

Pollinators thrive and depend on a nectar produced by the flowers [Gardener and Gillman 2002]. The nectar serves as an incentive to pick one plant over another [Faegri and Van Der Pijl 1979]. When a pollinator visits a flower to harvest its nectar, it helps the plant to reproduce: it deposits pollen collected earlier from other

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plants and it collects the plant's own pollen to be deposited in other flowers in the future [Johri 1984].

There is competition between plants for the same pollinators [Levin and Anderson 1970]. When the pollinators are rare, the plants tend to produce more and larger flowers and they allocate more resources to attract the pollinators [Ågren et al. 2013]. At the same time, when a plant is attractive, it increases the amount of pollinators in its immediate neighborhood [Faegri and Van Der Pijl 1979]. As a result, less attractive plants within a short distance of an attractive plant will also be visited and pollinated [Laverty 1992]. This "magnet effect" is observed across many species [Torices et al. 2018].

We study how the abundance of pollinators affects the evolution of plants' resource allocation. In Section 2, we describe a computer simulation to quantify the costs and benefits of allocating more resources to attract pollinators. The simulation follows a field of native plants that is invaded by a small number of potentially more attractive plants. We are interested in finding out the best allocation strategy for the invading plants. The results are presented in Section 3. We show that there is a critical threshold: when the number of pollinators is above the threshold, there is only a very small tendency to increase the attractiveness; when the number is below the threshold, a very large allocation to attract the pollinators is favored. The threshold is quite sharp, low and decreasing with the plant field size and seed dispersal distance. We conclude the paper in Section 4.

2. Methods: computer simulation

The basic structures and algorithm of the simulation are described below; see also Figure 2. The actual simulation was written in Matlab and the computations were done on the "teal" cluster in VCU's Center for High Performance Computing.

2.1. ***Plants.*** The plants are assumed to be annual. They grow from a seed, bloom, produce seeds, and die in one growing season. The plants can grow only from the seeds that were produced during the last season.

2.2. ***Plant field.*** The plants are assumed to grow in patches. The patches are arranged in an $N \times N$ square grid with periodic boundaries; see Figure 1. All patches on the field are identical and differ only in the number (and type) of plants that grow on them. Each patch can sustain up to C plants of any type. For simplicity, we assumed that each patch is either empty or consists of C plants.

2.3. ***Plant's attractiveness and seed production.*** We assume all plants have the same amount of resources (1 unit without loss of generality). The resources can be allocated to blooming and attracting pollinators, seed production, and survival. A plant's strategy is given by $a \in [0, 1]$, a proportion of resources allocated towards blooming and attracting the pollinators. When a plant using a strategy a is pollinated, it produces $S(a) = a(1-a)$ units of seeds. Plants growing from those seeds will have exactly the same allocation strategy a.

The function $S(a)$ was chosen as it is a simple function and the plants will not produce many seeds if either they do not allocate enough resources to blooming and attracting the pollinators or they allocate too much so that they will not have enough resources left for the actual seed production and their own survival.

As an artifact of choosing this function $S(a) = a(1-a)$, the pollinated plants achieve maximum seed production using strategy $a = 0.5$. However, as seen later, it does not necessarily mean that the strategy $a = 0.5$ is always the best strategy to use.

2.4. *Patch attractiveness.* We assume that the pollinators are attracted towards patches of plants rather than individual plants. The more attractive the patch is, the more likely it is to attract the pollinators. If a given patch P consists of $S_{P,\text{nat}}$ plants each allocating a_{nat} and $S_{P,\text{inv}}$ plants each allocating a_{inv} towards attractiveness, the attractiveness of a patch will be given by

$$A_P = S_{P,\text{nat}}\, a_{\text{nat}} + S_{P,\text{inv}}\, a_{\text{inv}} + r_P, \tag{1}$$

where $r_P \in (0, 0.001)$ is a small random number that is different for different patches and also changing every season. The purpose of r_P is to add a natural variation among patches occupied by plants using exactly the same strategies.

2.5. *Pollinators.* We assume that there is only one pollinator species. The abundance of the pollinators is represented by $p \in [0, 1]$. We assume that only pN^2 patches can be pollinated during one season. The pollinators will prefer patches with higher attractiveness. This is achieved by sorting all patches by their attractiveness and assuming that only the top pN^2 patches are visited. Once a patch is visited, all the plants on the patch are assumed to be pollinated regardless of their individual allocation strategies. This assumption allows us to account for the magnet effect.

2.6. *Seed dispersal.* Once a plant is pollinated, it produces seeds. The seeds then disperse over the field. We assume the seeds can disperse up to d patches away from their patch of origin. For simplicity, we assume that the seeds are equally likely to travel any distance $0, 1, \dots, d$ and move in any direction. This means that the probability of the seed staying at the origin is $1/(d+1)$. There are 8δ patches that are exactly $\delta \in \{1, 2, \dots, d\}$ away from the patch of the origin and so the probability that a seed will end up on a patch δ away is given by

$$\pi(\delta) = \begin{cases} (d+1)^{-1} & \text{if } \delta = 0, \\ (8\delta(d+1))^{-1} & \text{if } \delta \in \{1, 2, \dots, d\}, \\ 0 & \text{if } \delta > d; \end{cases} \tag{2}$$

see Figure 1.

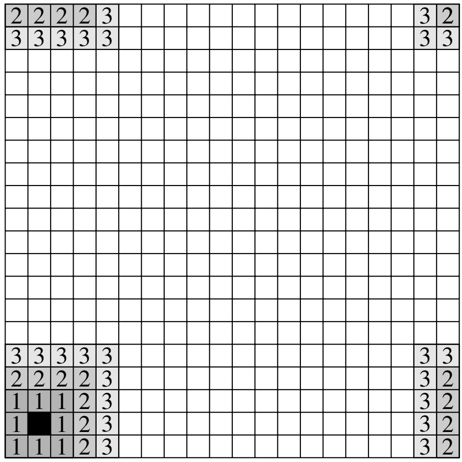

Figure 1. Visualization of the field and seed dispersal for $N = 20$ and $d = 3$. Each square represents a patch. In this case, the seeds originate from the black square. A fourth of all seeds produced there will stay there. The squares with the same shade of gray (and the same label representing its distance from the black square) will get the same number of seeds. In the sequence of increasing distance, there will be $\frac{1}{32}$, $\frac{1}{64}$ and $\frac{1}{96}$ of all seeds produced on the black patch. The boundaries are periodic.

Let $\rho(P, P_0)$ denote the distance between patches P and P_0 and let S_P be the number of seeds produced on patch P in a given season. Then, at the end of the season, after the seed dispersal, a patch P_0 will have

$$S'_{P_0} = \sum_{\delta \geq 0} \pi(\delta) \sum_{P, \rho(P, P_0) = \delta} S_P \tag{3}$$

seeds.

We assume the plants produce a large amount of seeds. With this assumption, if there is at least one seed on a patch, there are many more than C seeds on the patch. Since a patch can support only C plants, we renormalize: if on a given patch P_0 there is at least one seed and $S'_{P_0,\text{nat}}$ seeds come from native plants and $S'_{P_0,\text{inv}}$ seeds come from invasive plants, we will assume that there will be $C(S_{P'_0,\text{nat}}/(S'_{P_0,\text{nat}} + S'_{P_0,\text{inv}}))$ seeds of native plants and $C(S_{P'_0,\text{inv}}/(S'_{P_0,\text{nat}} + S'_{P_0,\text{inv}}))$ seeds of invasive plants that will germinate and grow into plants in the next season.

2.7. ***Summary of the simulation of one season.*** We will consider only a situation with two types of plants: native and invasive. Quantities related to native plants will have a subscript "nat", quantities related to invasive plants will have subscript "inv".

At the beginning of a season, each of the $N \times N$ patches P contains $S_{P,\,\mathrm{nat}}$ ($S_{P,\,\mathrm{inv}}$) seeds that will germinate and grow into $S_{P,\,\mathrm{nat}}$ ($S_{P,\,\mathrm{inv}}$) plants allocating a_{nat} (a_{inv}) towards attracting the pollinators where $0 \le S_{P,\,\mathrm{nat}}$, $0 \le S_{P,\,\mathrm{inv}}$, and $S_{P,\,\mathrm{nat}} + S_{P,\,\mathrm{inv}} \le C$.

The attractiveness of the patch P_0 is given by $A_{P_0} = S_{P_0,\mathrm{nat}}\, a_{\mathrm{nat}} + S_{P_0,\mathrm{inv}}\, a_{\mathrm{inv}} + r_{P_0}$, where $r_{P_0} \in (0, 0.001)$ is a small random number.

All plants on the patch P_0 are pollinated if and only if A_{P_0} is in the top pN^2 values of $\{A_P\}_{P=1}^{N^2}$. Only the plants that are pollinated produce seeds; new plants growing from those seeds during the next season will have exactly the same allocation strategy as the parent plant. Plants that are not pollinated do not produce any seeds.

The seeds disperse through the field. At the end of the season, all existing plants die and only the seeds remain on the patch to grow in the next season. We renormalize the seed count to keep the number of seeds, and consequently the plant count on each patch either 0 or C. If there was any seed on the patch at the end of the season, there will be C seeds after the at the end of the next season. We can consider this procedure to model the fact that out of possibly many seeds on the patch only some will survive to the next season and germinate and the patch itself can support at most C plants.

2.8. ***Overall simulation.*** The parameters of the simulation are as follows:

(1) The size, N, of the field. The field will have N^2 patches; each patch will have either 0 or C plants.

(2) The abundance, p, of the pollinators. Only pN^2 patches (the most attractive ones) will be visited by the pollinators. All plants on the visited patches will be pollinated.

(3) The allocation strategy of the native (a_{nat}) and invasive (a_{inv}) plants. A plant with strategy a will produce $S(a) = a(1-a)$ seeds if pollinated.

(4) The maximal distance, d, the seeds can disperse. The field is assumed to have periodic boundaries; see Figure 1.

For every set of the parameters specified above, we initialize the field by letting every patch be occupied by only native plants (using strategy a_{nat}). We let the simulation run for ten seasons to allow the population of plants to stabilize at the appropriate level. The number of occupied patches correlates with the pollinators' abundance p; see Figure 3.

At the end of the tenth season, we introduce invasive plants into one of the patches (we assume all plants on that patch now use strategy a_{inv}). We then let the simulation run for 100 seasons. At the end of the 100th season, we record the number of invasive and native plants in the field; see Figure 2. If there are no native plants left, we say that the invasive plants replaced the native plants.

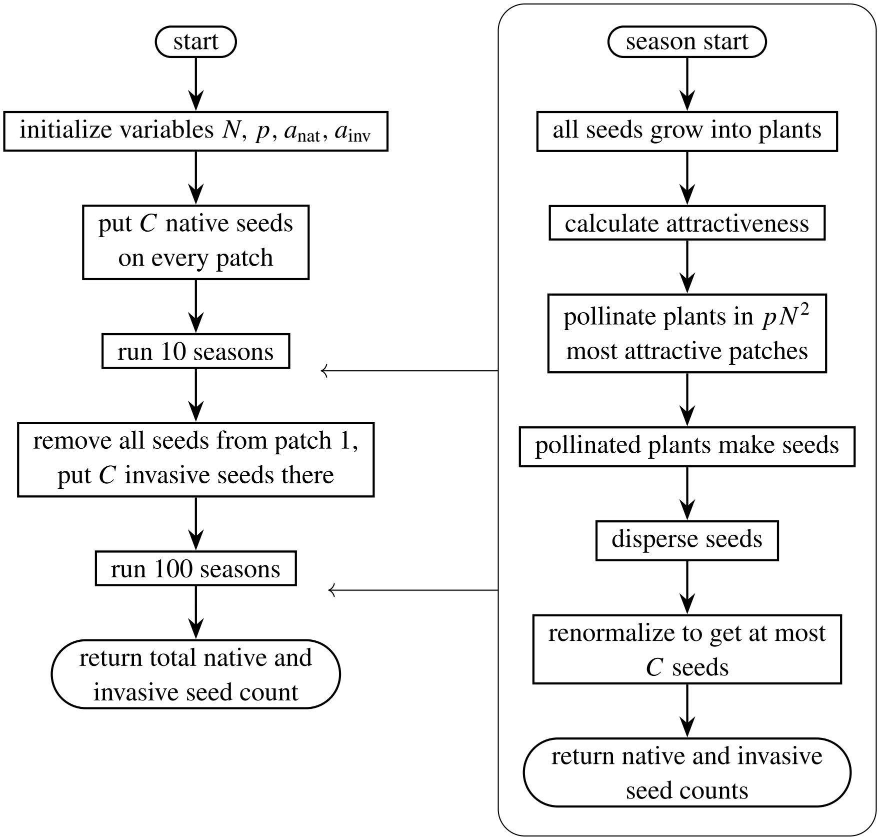

Figure 2. Scheme of the simulation described in more detail in Section 2.8.

We repeat the simulation 1000 times with the same parameters and record the probability of replacement and the average abundance of the invasive plants at the end of the 100th season.

2.9. ***Experiments.*** We are interested in what is the best invading strategy, i.e., a strategy that gives the highest chance of replacing the native plant population. If there are two (or more such values), we restrict our attention only to those values and the one yielding the largest final abundance is said to be the best. We run the following two experiments: we fixed $d = 1$ and used $N \in \{20, 30, 40, 50\}$ and we fixed $N = 20$ and used $d \in \{1, 2, 3, 4, 5\}$. For each such a pair N and d we used p between 0.01 and 0.4 in increments of 0.01. For given N, d and p, we run the simulation for all values a_{nat} from 0.5 to 1 (in increments of 0.01) and different values a_{inv} from a_{nat} to 1 (in increments 0.01).

To save computational time, we did not use $p > 0.4$ because our initial testing did not reveal any significant difference in the results between $p = 0.4$ and $p > 0.4$.

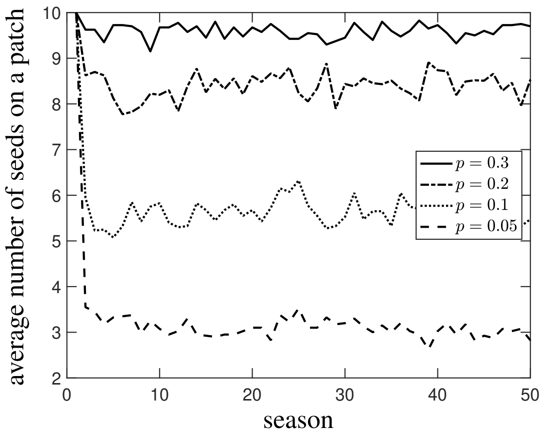

Figure 3. The time evolution of the seed count of native plants ($a_{\text{nat}} = 0.5$, $N = 20$, $d = 1$). The average seed count stabilizes within few seasons, we consider it stable at season 10.

We also did not consider $a_{\text{nat}} < 0.5$ because such native plants would be always replaced by invasive plants using $a_{\text{inv}} = 0.5$. Indeed, if $a_{\text{nat}} < 0.5$ and $a_{\text{inv}} = 0.5$, then patches with invasive plants will be more attractive than patches with native plants only. Moreover, the invasive plants will produce more seeds than the native plants. Finally, we did not use $a_{\text{inv}} < a_{\text{nat}}$, because such invasive plants never stay in the population for too long (their initial patch is the least attractive patch in the field so it very rarely gets chosen by the pollinators).

For each of the above combinations of $N, d, p, a_{\text{nat}}, a_{\text{inv}}$ we ran the simulation 1000 times. Each time, we recorded the total number of native and invasive plants at the end of the 100th season. We calculated $\text{Repl}(N, d, p, a_{\text{nat}}, a_{\text{inv}})$, the probability of replacement as the proportion of simulations that ended with some invasive but no native plants. We then identified a set

$$A_{\text{best}}(N, d, p, a_{\text{nat}}) = \text{argmax}_{a_{\text{inv}}}(\text{Repl}(N, d, p, a_{\text{nat}}, a_{\text{inv}})) \tag{4}$$

of values that yielded the highest replacement probability. The best invasive strategy, $a_{\text{best}} = a_{\text{best}}(N, d, p, a_{\text{nat}})$, was determined as a strategy in $A_{\text{best}}(N, d, p, a_{\text{nat}})$ that yielded the maximal final abundance of invasive plants.

3. Results

We identified $a_{\text{best}} = a_{\text{best}}(N, d, p, a_{\text{nat}})$, the best invading strategy. We found that there is a critical value $p_{\text{crit}} = p_{\text{crit}}(N, d)$ and constants $M_{N,d}$ and $B_{N,d}$ such that

$$a_{\text{best}}(N, d, p, a_{\text{nat}}) \approx \begin{cases} a_{\text{nat}} + \Delta & \text{if } p \geq p_{\text{crit}}(N, d), \\ M_{N,d}a_{\text{nat}} + B_{N,d} & \text{if } p < p_{\text{crit}}(N, d), \end{cases} \tag{5}$$

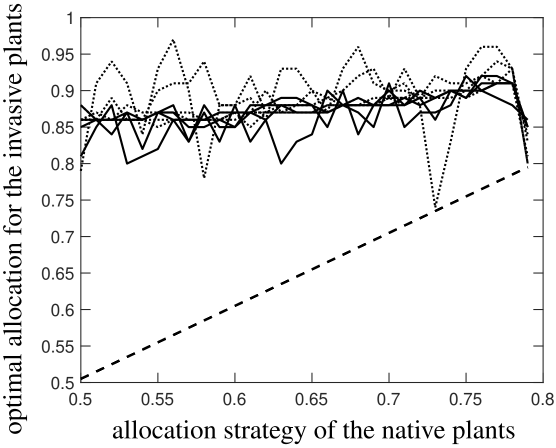

Figure 4. The optimal allocation strategy $a_{\text{best}}(N, d, p, a_{\text{nat}})$ as a function of the allocation of the native plants a_{nat}. Full lines are for $p \leq 0.1$, dotted lines for p between 0.11 and 0.18, dashed line is for $p \geq 0.19$. In this figure, $N = 20,\ d = 1$.

where $\Delta = 0.01$ is the increment in our values of a_{inv}. As seen in Figure 4, regardless of the value of p, $a_{\text{best}}(N, d, p, a_{\text{nat}})$ exhibits a linear trend in a_{nat}. For $p \geq p_{\text{crit}}(N, d)$, the best strategy follows the line $a_{\text{nat}} + \Delta$ exactly. For $p < p_{\text{crit}}(N, d)$, the slope of the linear trend is around 0.13 and the outcome is much noisier. While the coefficients $M_{N,d}$ and $B_{N,d}$ varied in N and d ($M_{N,d}$ was generally slightly decreasing in N and d; $B_{N,d}$ was generally slightly increasing in N and d), the variation could be contributed to random fluctuation and was not substantial. Overall, $M_{N,d} \approx 0.13$ and $B_{N,d} \approx 0.79$ are good approximations (with R^2 around 0.8). Since the significance of formula (5) is the existence of a critical value of p_{crit} and the two distinct behaviors of a_{best}, we did not investigate the best values of the coefficients $M_{N,d}$ and $B_{N,d}$ in greater detail.

When the pollinators are relatively abundant ($p \geq p_{\text{crit}}$), there is very little incentive for the plants to allocate too much energy towards attracting them. If the invasive plants attract more pollinators, the patches with them will be pollinated with very high probability. If the invasive plants allocate a'_{inv} instead of a_{inv} (for $a'_{\text{inv}} > a_{\text{inv}} > a_{\text{nat}}$), the increase in attractiveness will not increase the probability of their patches to be visited. However, many of these patches will contain native plants as well. The native plants will be pollinated too and will, in fact, produce more seeds than the invasive plants (because for $0.5 < a_{\text{nat}} < a_{\text{inv}} < a'_{\text{inv}}$ and $S(a_{\text{nat}}) > S(a_{\text{inv}}) > S(a'_{\text{inv}})$). This means that in the next generation, there will again be a lot of patches with a mix of native and invasive plants. Moreover, if the invasive plants allocate a'_{inv} instead of a_{inv} (for $a'_{\text{inv}} > a_{\text{inv}} > a_{\text{nat}}$), there will be even fewer invasive plants in the next generation (because $S(a_{\text{nat}}) > S(a_{\text{inv}}) > S(a'_{\text{inv}})$).

d	$p_{\text{crit}}(20, d)$
1	0.19
2	0.14
3	0.12
4	0.10
5	0.07

Table 1. The critical value p_{crit} as a function of the seed displacement distance d. Here, $N = 20$.

Consequently, the invasive plants should allocate as little as possible above the native plants' allocation.

When the pollinators are rare ($p < p_{\text{crit}}$), the pollinators are visiting only very few patches. This provides a strong incentive for the invasive plants to invest many more resources to attracting the pollinators because then only the patches with no (or very few) native species get visited.

What makes our result surprising is that there is a relatively sharp cut off point between the two kinds of allocation strategies; see Figure 4.

The critical value $p_{\text{crit}}(N, d)$ is decreasing in the seed dispersal distance d; see Table 1. As d increases (and p stays constant), the number of patches containing only invasive plants decreases and many patches contain a mix of invasive and native plants. If the plants on a mixed patch are all pollinated, a native plant will produce more seeds than an invasive plant. Consequently, the proportion of invasive plants can be decreasing in time. However, for a fixed d, as p decreases, only the patches with decreasing proportion of native plants get pollinated, which means that it is actually the proportion of native patches that is decreasing in time.

The critical value $p_{\text{crit}}(N, d)$ also decreases with the increasing field size, N; see Table 2. We do not fully understand the reason for this decrease. However, we believe that the critical value decreases to $p = 1/(d + 1)^2$. For such p and large N, pollinating $N^2/(d + 1)^2$ patches means that in the next generation, almost all patches will be occupied again. More simulation trials are needed to confirm or reject this hypothesis.

field size N	$p_{\text{crit}}(N, 1)$
20	0.19
30	0.16
40	0.14
50	0.12

Table 2. The critical value p_{crit} as a function of N. Here $d = 1$.

4. Conclusions

The lives of pollinators and plants are interconnected in many ways [Corbet 1996]. A decline of pollinators puts many plant species at a serious risk of extinction [Lernnartsson 2002] and under pressure to evolve strategies that will help them deal with the decline.

We built a computer simulation to study the effect of pollinators' decline on the plants' resource allocation. We saw that plants with more attractive flowers are able to replace plants with less attractive flowers; however, we saw this happening only when pollinators were truly very rare. When the pollinators' numbers are above this relatively sharp threshold, the incentive to evolve more attractive flowers is still there but it seems to be kept in check by the associated costs, such as being left with fewer resources towards seed production and survival. This finding seems to be in line with results of previous studies such as [Rathcke 1983; Kunin and Iwasa 1996].

We note that evolving more attractive flowers is not the only option. Plants can evolve a decreased dependence on the pollinators by allowing their flowers to be pollinated by wind and other means [Culley et al. 2002].

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