Persistence of pollination systems

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Abstract

Pollination systems are composed of flowering plants and flower visitors, engaging into mutualistic interactions. However, the flower visitors include true pollinators, which pollinate the flower by visiting it through the legitimate way, and also by cheaters, which use the flower’s resources (e.g. nectar and pollen) without pollinating it or been just marginally efficient on pollination. On the one hand, plants have different flower structures, as shallow and tubular flowers, which can provide some protection against the cheaters effects or higher efficiency when visited by pollinators. Even though cheaters can damage flowers, there is evidence that cheaters can have a positive effect on the pollination service. In fact, the existence of cheaters decreases the amount of reward provided by plants in a given environment. Therefore, pollinators travel further in order to visit more flowers or even spend a longer time in each flower to collect enough resources. It increases the cross-pollination rate and the pollination success, especially to auto-incompatible plant species. The presence of cheaters in these systems represent a delicate trade-off when mutualistic interactions when cheaters effects are taken into account. In this work, we are interested to understand how pollination systems allow the persistent coexistence of the two types of visitors and plants. We developed a mean field analytical model relying on game theory, with a bipartite network of two kinds of plants (shallow and tubular flowers) and two kinds of visitors (pollinators and cheaters). Our analytical and numerical results confirm the presence of metastable states of persistent coexistence of the above-mentioned visitors and plants. In order to better describe additional real-world features of pollination systems (i.e. the spatial distribution of flowers, the depletion of resources, and the crossing pollination effect) we also implement an agent-based model. In this case, we observed coexistence of the two visitors and two plants when we included the space. We are still studying the agent-based mode approach to understand, for instance, how spatial structures (as the ones resulting from mankind actions) can affect pollination systems.

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Introduction

Mutualisms are interactions between individuals of different species in which both have benefit in return (Bronstein, 1994). Many species are dependent on the mutualistic partners for defense (Rico-Gray & Oliveira, 2007), nutrition (Jordano, 2000) and reproduction (Bawa, 1990). However, the interactions among these mutualistic partners can vary in quality, in a gradient that goes from a pure mutualism (in which both are benefited by the interaction) to an antagonism (one is benefited while the other is harmed), passing by a commensalism (one is benefited while the other is not affected by the interaction). For instance, pollination systems are composed by plants and floral visitors. Among the flower visitors, there are true pollinators, which pollinate the flower visiting it by the legitimate way, and cheaters (Inouye, 1980). The cheaters use resources (e.g. nectar and pollen) from the flower without providing the pollination service. For example, nectar robbers reach the nectaries without touching the reproductive parts of the flower (Inouye, 1980).

The presence of cheaters can affect the behavior of the real mutualistic partners (Irwin & Brody, 1998; Maloof, 2001). One example of cheater is a species of bumblebee which robs the nectar of Ipomopsis aggregata (Polemoniaceae), making a hole in the base of the corolla of the flower, allowing easy access to the nectar on the basal nectaries (Irwin & Brody, 1998). By this way, the bumblebee does not touch the reproductive parts of the flower, and also leave the flower with no nectar for the next visitor. Some hummingbirds, which are the real pollinators of I. aggregata usually avoid flowers with a hole on the basal corolla (Irwin & Brody, 1998). This example shows how the harm caused by the cheater reflects on other species using the same plant as resource.

On the other hand, plants can also defend themselves against the action of the cheaters. Plants can avoid the attack of cheaters, cheating the visitors by chemical components, escaping in time or space and also by some kind of barrier (Irwin et al., 2004). In this context, the structure of flowers may play an important role over the attacks by flower-visitor. Plants with a shallow flower structure are less prone to be robbed or at least they suffer less harm caused by cheaters than the plants with flowers of tubular structure. Flowers with a tubular structure are usually more specialist in attracting and fitting their pollinators and they get a higher rate of pollination success due to the attraction of the right and specialist pollinator (Nilsson, 1988). However, when a non-specialist visitor tries to get a reward from this kind of flower, the larceny can be an easier and maybe the only way to reach it (Soberón & Martínez del Río, 1985).

The robbery has also its cost because it requires a time investment in constructing the hole or the slit (Irwin et al., 2010) and also to escape of other plant protections. Thus it
must compensate for the cheater to cheat the plant which flowers it can not get the reward by the legitimate way (i.e., as pollinators) (Lara & Ornelas, 2001). Pollinators might have higher reward visiting shallower flowers than tubular flowers (Galen, 1999). Thus, there is a trade-off in flower structure and behavior of plant visitors of pollination systems. This trade-off may be responsible for the coexistence of pollinators and cheaters/robbers and also the plants with different kinds of flower structure in real pollination systems.

Even though cheaters can cause many damages, there are some evidences that cheaters are not so harmful as described above. One of the benefits of the existence of cheaters is the fact that they decrease the amount of reward provided by plants to their visitors in the environment. As a consequence, the legitimate pollinator must travel further in order to visit more flowers and to reach enough reward. When the legitimate pollinator travels longer and visits more flowers, it carries the pollen from plants distant from each other (Pyke, 1982; Zimmerman & Cook, 1985; Singh et al., 2014). By this process, the crossing-pollination rate increases, which may result in higher fitness, specially to auto-incompatible plant species (Singh et al., 2014).

Thus, not only the trade-off, but also the indirect effects of the cheating on the interactions make mutualism a persistent interaction in Nature. In this work, we are interested to understand how a pollination system still exists in the presence of cheaters and in which conditions different kinds of visitors and plants of different flower structures may evolve. To explore this problem, we use a mean field approach using game theory in a bipartite network of the two kinds of plants and the two kinds of visitors. Because of the importance of the distance among flowers, depletion of resources, and the crossing pollination effect in the presence of cheaters, we also explored the problem in the space using an agent-based model.

**Analytical model**

We first introduce and discuss a model for the evolution of an pollination system in which the number of pollinators ($B_1$) and cheaters ($B_2$) co-evolve with the number of shallow ($F_1$) and tubular ($F_1$) flowers. The interactions between the two kinds of flower visitors and the two kinds of flower-plants can be modeled as a game with two-populations and two-strategies. Visitors and plants are then considered as evolutionary strategies of the game. The payoff matrix of this game can be expressed as:

\[
\begin{array}{c|cc}
& F_1 & F_2 \\
B_1 & (\alpha, \epsilon) & (\beta, \phi) \\
B_2 & (\gamma, -c\epsilon) & (\gamma, -c\phi) \\
\end{array}
\]
where the first value in each cell represents the payoff that a given visitor gets interacting with a given flower type, and the second value stands for the payoff that a flower obtains when it meets a given visitor. All the parameters in the payoff matrix are considered to be positive. The relationships between the payoffs of the species will determine the dynamics of the system. We also assume the following inequalities:

- A pollinator is more efficient and faster in collecting the nectar in an shallow flower than in a tubular flower. Thus, $\alpha > \beta$.

- A crucial parameter of the model that also characterizes its Nash Equilibria (Nash, 1950) and its evolutionary stable states (Hofbauer & Sigmund, 1998) is the payoff of the cheaters $\gamma$. In fact, when $\gamma < \beta$ the game becomes trivially solvable and the visitor dominant strategy is $B_1$, the pollinator. But, the cheater has some cost to get the nectar by the non-legitimate way and it must compensate only when cheating is the unique option. For shallower flowers, the legitimate visiting must provide a higher payoff. Then, we arrive at the relationship $\alpha > \gamma > \beta$, in which we observe more realistic pattern situations.

- Flowers only get a positive payoff when they meet a pollinator. We also assume that $\phi > \epsilon$, since a tubular flower obtain a higher payoff when interacting with a pollinator species than with a shallow flower. We assume this because tubular flowers have a more specialized structure and they attract specific pollinators, increasing their success in being pollinated. The parameter $c$ is also assumed to be a positive real number and it represents the normalization factor that regulates the importance of the negative interactions for the plants against cheaters in respect to the positive payoffs they obtain against pollinators.

Considering all the above assumptions, one may observe that it does not exist any Nash Equilibrium in pure strategies (Weibull, 1995). In particular, pollinators have a positive advantage with respect to other type of visitors when only shallow flowers exist ($\alpha > \gamma$), while cheaters prefer to live in an environment populated by tubular flowers ($\gamma > \beta$). On the other hand, tubular flowers obtain a higher payoff when only pollinators are present ($\phi > \epsilon$) but they also have a more negative payoff when cheaters replace pollinators.

**Basic treatment**

We introduce a simple version of the model described above in which we do not consider the positive effect that cheaters can produce in tubular flowers obligating pollinators to
visit more flowers. The absolute number of pollinators (cheaters) present in the ecosystem is given by the variable $B_1 (B_2)$. We also model the absolute number of shallow (tubular) flowers, $F_1 (F_2)$. Without loss of generality, all variables and parameters are considered to be real numbers. The basic treatment of the analytical model is given by the following differential equations:

$$
\dot{F}_1 = F_1 \left( r_F - \frac{F_1 + F_2}{K_F} + \epsilon \frac{B_1}{B_1 + B_2} - \frac{c \epsilon}{B_1 + B_2} B_2 \right)
$$

$$
\dot{F}_2 = F_2 \left( r_F - \frac{F_1 + F_2}{K_F} + \phi \frac{B_1}{B_1 + B_2} - \frac{c \phi}{B_1 + B_2} B_2 \right)
$$

$$
\dot{B}_1 = B_1 \left( r_B - \frac{B_1 + B_2}{F_1 + F_2 + K_B} + \alpha \frac{F_1}{F_1 + F_2} + \beta \frac{F_2}{F_1 + F_2} \right)
$$

$$
\dot{B}_2 = B_2 \left( r_B - \frac{B_1 + B_2}{F_1 + F_2 + K_B} + \gamma \right)
$$

(1)

All the previous differential equations are multiplied by their linear variable since we are considering linear growth rate functions. The parameters $r_i$ stand for the intrinsic growth rates. On the other hand, $K_j$ is related with the carrying capacity of the species. Then, $K_F$ bounds the number of both type flowers in a limited space, such a way that when the inequality $F_1 + F_2 > r_F K_F$ holds, the flowers start to grow much slower and to increasingly die out as the term $r_F - \frac{F_1 + F_2}{K_F}$ becomes negative. On the other hand, the number of visitors is bounded by a minimal carrying capacity $K_B$ that is given by the local environment (and not dependent on the flowers), and the current number of flowers $F_1 + F_2$ (which represents vital resources for the visitors). We can observe that $B_1 + B_2 > (F_1 + F_2 + K_B) r_B$ leads to a negative values for the visitor’s growth. The third and fourth term of the equations are given by the interactions of the flower (visitors) with the two types of visitors (flowers). It is equal to the probability which the flower (visitors) meets a type of visitor (flower) among the two types of visitors (flowers) multiplied by the corresponding payoff.

**Modified treatment**

Here, we modify the model described in the set of Eqs. 1 in order to include a more complex biological background.

In particular, we modify the way of interactions occur by also taking into account the fact that pollinators in shallow and tubular flowers must pollinate more when cheaters are also present in the environment: once a flower has been visited by a cheater, it partly
or completely looses its nectar; a pollinator that visits an empty-nectar flower must flies further a make more visits in order to find the required nectar. As a consequence the pollinator pollinates more. The differential equations that describes this dynamics are:

\[
\begin{align*}
\dot{F}_1 &= F_1 \left( r_F - \frac{F_1 + F_2}{K_F} + \epsilon \frac{B_1^2 + 2B_1B_2}{(B_1 + B_2)^2} - \epsilon \frac{B_2^2}{(B_1 + B_2)^2} \right), \\
\dot{F}_2 &= F_2 \left( r_F - \frac{F_1 + F_2}{K_F} + \phi \frac{B_1^2 + 2B_1B_2}{(B_1 + B_2)^2} - \phi \frac{B_2^2}{(B_1 + B_2)^2} \right), \\
\dot{B}_1 &= B_1 \left( r_B - \frac{B_1 + B_2}{F_1 + F_2 + K_B} + \alpha \frac{F_1}{F_1 + F_2} + \beta \frac{F_2}{F_1 + F_2} \right), \\
\dot{B}_2 &= B_2 \left( r_B - \frac{B_1 + B_2}{F_1 + F_2 + K_B} + \gamma \right)
\end{align*}
\]

(2)

The differential equations for the visitors remain the same than in Eq. 1, whereas the third term in the first and second equations are modified. In order to deduce this term, we consider now that a flower gets the negative payoff $-c\epsilon$ when it is visited by two cheaters with probability $\left( \frac{B_2}{B_1 + B_2} \right)^2$, and the positive payoff $\alpha$ when it is by at least one pollinator with probability $\frac{B_1^2 + 2B_1B_2}{(B_1 + B_2)^2}$.

**Results**

Both our simple and modified models represent 4-D dynamical systems. Performing a linear stability analysis (Strogatz, 2001) on them reveals the presence of 5 or 6 fixed points, i.e., 4-D points that are invariant under the system flow. In both the models, only one of these fixed points exhibit a strictly positive quantity for plants and visitors. Therefore, our models contemplate the presence of fixed points where pollinators, cheaters, shallow and tubular flowers all coexist together.

Computing the eigenvalues of the Jacobian matrix, derived from the system, in the fixed points highlights the presence of two complex conjugate eigenvalues and two real negative eigenvalues. Within the numerical investigation that we performed, with many different combinations of parameters $r_F, r_B, \alpha, \gamma, \beta$, the complex eigenvalues have a non-zero but rather small real part, of order $10^{-17}$, that is well above the machine precision and it is therefore not a numerical artifact.

The presence of a non-zero real part in all the found eigenvalues and the smooth real mappings represented by our models allow for an application of the Hartman-Grobman theorem (Strogatz, 2001), according to which the phase space of the 4-D original dynamical systems is topologically equivalent to their linearized versions, respectively, in a
neighborhood of the fixed points. In other words, linear stability analysis is conclusive for asserting that these fixed points are stable along the eigendirections relative to the negative eigenvalues, while they are locally like stable or unstable spirals on the plane identified by the eigendirections of the two complex eigenvalues. Although the 4D case is extremely different from the 2D case, it is worth remembering that for dynamical flows on the real plane, complex conjugate eigenvalues $\lambda_{1,2} = \alpha \pm iw$ are relative to trajectories being spirals (when $\alpha \neq 0$) of the analytical form:

$$Ae^{\alpha t}(\cos wt + isin wt),$$

where $t$ is the time and the imaginary part $w$ represents the swirling rate of the spiral over time. Depending on the sign of $\alpha$ we can determine the stability of the fixed points. Positive real parts are relative to unstable spirals and negative real parts are relative to stable spirals (Strogatz, 2001). Despite it would be reasonable to expect for such a stable/unstable behavior on specific planes of our phase spaces, the higher dimensionality of our dynamical systems and the possible presence of intrinsically non-linear limit cycles (that cannot be captured by a linear stability analysis) require for us to corroborate our findings with extensive numerical simulations. Also the use of more advanced analytical techniques, such as manifold center reduction (Guo & Wu, 2013), would be an interesting further research direction.

We used the adaptive numerical integrators of Mathematica 10 in order to numerically integrate both our simple and modified models, respectively. In both cases, the integration on a time window of $10^4$ retrieves what seem to be attracting limit cycles. Extending the numerical integration windows to one order of magnitude more breaks the integration because of global numerical errors, as it is well known in these cases (Press et al., 1990).

It has to be underlined that, given the rather small real parts $\alpha \approx 10^{-17}$ in the time exponential of the spiral trajectories, the latter cannot modify noticeably their radiuses over our observed time windows. This implies that, despite not corresponding exactly to limit cycles, our fixed points can be treated as such. In other words, motivated by our analytical findings, we can approximate our numerical results to periodic orbits, an example being reported in Figure 2.

Therefore, at small observation scales ($t \propto 10^{-17}$), the total number of plants and the total number of visitors approximately swirl along a cycle, which lies entirely in the first quadrant of the real plane, see Figure 2. In other words, both our simple and modified models allow for metastable solutions (i.e., scenarios) where pollinators, cheaters and flowers persist together, fluctuating over time, for long periods.
Figure 1: Pollinator, cheater, shallow and tubular flowers number concentration over time for the simple (left) and the modified (right) models, respectively, with $r_F = r_B = 0.5$, $\alpha = 0.4$, $\gamma = 0.3$ and $\beta = 0.1$.

Figure 2: Total visitors vs total plants, over time for the simple (left) and the modified (right) models, respectively, with $r_F = r_B = 0.5$, $\alpha = 0.4$, $\gamma = 0.3$ and $\beta = 0.1$. Transient periods were omitted.
Figure 3: Discrete parameter sweep for many different combinations of parameters, $\alpha$, $\beta$ and $\gamma$ for the reproduction rates $r_F = r_B = 0.5$, for the simple (left) and the modified (right) models, respectively. Each parameter ranges from 0 to 1 with a discrete step of 1/25. In the $(\alpha, \beta)$ plane, $\gamma = 0.3$ and the region satisfying $\alpha > \gamma$ and $\beta < \gamma$ is highlighted in black.

Figure 4: Discrete parameter sweep for many different combinations of parameters, $\alpha$, $\beta$ and $\gamma$ for the reproduction rates $r_F = r_B = 0.5$, for the simple (left) and the modified (right) models, respectively. Each parameter ranges from 0 to 1 with a discrete step of 1/25. In the $(\alpha, \gamma)$ plane, $\beta = 0.1$ and the region satisfying $\alpha > \gamma$ and $\beta < \gamma$ is highlighted in black.
Interestingly, these scenarios are different in the two models for the very same combinations of parameters, as reported in Figure 1. Further numerical investigations show that these fixed points where coexistence is allowed appear only for very specific combinations of constraints. On the one hand, the reproduction rates $r_F$ and $r_B$ do not seem to display any evident effect on the qualitative existence of the above mentioned persisting states.

In fact, as showed in the Figures 3–5, the constraints coming from the game theoretic approach $\alpha > \gamma > \beta$ are reflected in some specific overlapping regions of the parameter space where persistence is admitted. It is worth noticing that our analysis focuses on the pairwise constraints $\alpha > \beta$ (Figure 3), $\alpha > \gamma$ (Figure 4), and $\gamma > \beta$ (Figure 5). Notice that there are other regions of the phase space that allow for the presence of coexistence, but they do not satisfy the constraints. Nonetheless, these other regions are not compatible with the three game theoretic inequalities at the same time. There is a small difference between the two models. In fact, the modified one allows for a moderate increase in the presence of stable spirals $+ (6 \pm 2)\%$. This stabilizing effect can ultimately be related to the presence of a positive effect coming from the interactions between pollinators and cheaters in our modified treatment.
The Agent-Based Simulation

Motivation

We introduce an agent-based model in order to capture the spatial dimension of the pollination problem. It will allow us not only to understand the importance of space between flowers, but also the importance of their distributions. We are therefore capable to study how the existence of different patches in the space affects the evolution of the populations under consideration.

Description of the setting

In the following, parameters of the model are written in font. A complete description of the model parameters can be found in the appendix. We define a continuous two dimensional space on which we initially allocate two types of flowers and two types of visitors. The allocation is random in the base case but can be modified in order to start with patches from the beginning. There are two types of flower plants, shallow flowers and tubular flowers. They differ only in the cost they bear on visitors consuming their nectar.

All flowers have the following characteristics: They have a maximum age and vanish after exceeding this age. Each flower has a certain amount of nectar, which it reproduces by a reproduction rate if the amount of nectar at the beginning of a turn is below a maximum nectar threshold. Similarly, each flower has a certain amount of pollen that reproduces the same way. Flowers reproduce if they get pollinated by a visitor. This means that every time a pollinator visits a flower, the flower takes all the similar pollen (i.e., pollen same type of itself) from the visitor. Each round, the flowers create offsprings within a reproduction radius, if the amount of pollen received through pollinators exceeds the flower reproduction threshold.

There are also different types of visitors, pollinators and cheaters. Visitors have a certain amount of energy. Moving around the space costs a certain amount of energy (cost). If the visitors reach an energy level of 0 (or reach their maximum age), they die. They can recover and store energy by consuming the nectar of the flowers: Each round a visitor is looking whether there is a flower inside its reachable radius. It moves randomly to one of the flowers within the radius. If there is no flower nearby, the visitor will reach a random point on the edge of its reachable circular area. If a visitor reaches a flower it enters the flower and pays a cost, depending on its own type and the type of the flower. In the base case, we have the following relation: cost pollinator shallow-flower < cost cheater < cost pollinator tubular-flower.
While it matters for the pollinator to crawl into a tubular or shallow flower, cheaters pay the same effort (for instance to make a hole) to get resources from shallow or tubular flowers. This procedure is completely analogous to the analytic model.

**Box 1: Summary of a round**

1. **The visitors reproduce:** For each visitor it is checked whether its energy is above the threshold for reproduction (reproduction threshold + initial energy). If this is the case, a visitor of the same type is added in a place near its parent and then the energy of the visitor is reduced by the threshold amount.

2. **The flowers reproduce:** For every flower it is checked whether its received pollen exceeds the reproduction threshold. If this is the case, the pollen is spent and a new flower of the same type is randomly allocated in the reproduction area of the flower.

3. **Increase the age:** The increment is of one for all visitors and flowers. If a visitor or flower exceeds their maximum age, they die and are removed from the simulation.

4. **Move of the visitors:** The visitors move and look for nectar: For each visitor, a list with all the flowers within its radius is created. If the list is empty, move to a random point on the edge of its reachable area. If the list is non-empty choose a flower at random and move to this flower. If the visitor has reached the flower, it enters the flower and extracts all the nectar and transforms it into energy according to the nectar to energy ratio.

5. **Only for pollinators that entered into a flower:** If it carries pollen of the same type, the pollen gets removed from the visitor and added to the received pollen of the flower. The visitor also takes the pollen from the flower and adds it to its pollen list.

6. **Renewal of pollen and nectar:** If the current amount of pollen/nectar is below the maximum value of pollen/nectar, the flower reproduces an amount according to the nectar/pollen reproduction rate. The visitor consumes the nectar in the flower and transforms it according to nectar to energy ratio into energy. The flower also attaches its pollen on the visitor and, if the visitor already carries pollen of the same type, takes this pollen for reproduction purposes off the visitor. Then the visitor leaves the flower and looks for another flower in the next round. If the visitor has an amount of energy larger than reproduction threshold + initial energy, it generates an offspring near to its location in the space and looses reproduction threshold amount of energy. The procedure of one round is summarized in Box 1.

For the results it is not important whether visitors or flowers reproduce first.
Results

ABM without space

We first consider the results of the ABM without the consideration of space. We identified two core parameter sets for the dynamics of the model: (i) the costs for the extraction of the nectar for the visitors and (ii) a potential carrying capacity for the visitors. While these core parameters do influence the dynamics of the model in an important and interesting way, the remaining parameters are of minor interest and turned out to be of minor importance for the dynamics. We therefore focus on the core parameters of the model. We used the results of the analytical model (see Analytical model section) to define the costs for the pollinators and cheaters. When cheaters extract the nectar of a flower, their energy decreases by 0.33, when pollinators enter an shallow or tubular flower, their energy level decreases by 0.25 and 1.0 respectively. While a greater change of the parameters has a severe influence on the resulting dynamics, the behavior of the model is not too sensitive to moderate changes of these parameters, with the obvious effect that an increased of the costs results in a decreasing number of the respective

Figure 6: Average results for the case with 100 runs and 2,500 time steps. Dynamics do not change after 600 time steps. The carrying capacity for the flowers is 2,000. No explicit carrying capacity for the visitors is set.
species. The base case, without taking the space in consideration, is shown in Figure 6, which shows the average behavior of 100 simulations with 600 time steps. We start with an initial number of shallow and tubular flowers of 500 flowers each. The initial number of each kind of visitor was 600.

<table>
<thead>
<tr>
<th>Species</th>
<th>Extinction</th>
<th>Min</th>
<th>Max</th>
<th>Average</th>
<th>Std.dev</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shallow Flowers</td>
<td>0.0%</td>
<td>485</td>
<td>1515</td>
<td>1027</td>
<td>313</td>
</tr>
<tr>
<td>Tubular Flowers</td>
<td>0.0%</td>
<td>484</td>
<td>1514</td>
<td>971</td>
<td>313</td>
</tr>
<tr>
<td>Pollinators</td>
<td>0.0%</td>
<td>9660</td>
<td>11970</td>
<td>10541</td>
<td>459</td>
</tr>
<tr>
<td>Cheaters</td>
<td>100%</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Table 1: Asymptotic results for the ABM without space defined and without explicit carrying capacity for the visitors.

This result is somehow different to the one from the analytical model as there never is a coexistence of all visitors and plants. It turns out that coexistence in the ABM model without space requires the specification of a separate carrying capacity for the visitors. The results for a carrying capacity of 1,000, i.e., the half or the carrying capacity of the flowers, is shown in Figure 7. This time, average results may, however, be misleading. A look on the statistics provided in table 2 reveals that a variety of qualitative different dynamics result from this configuration. Now, there are scenarios in which all visitors and plants go extinct, and in only 16% of the runs, coexistence of all of them could be observed.

The underlying mechanism suggested by the model is straightforward: If there is no separated carrying capacity for the visitors, their populations increase dramatically in the beginning, they consume too much nectar so that the flowers cannot reproduce fast enough, and then the visitors die out. A separate carrying capacity suppresses this effect and might yield a coexistence of all visitors and plants in most of the cases. But yield the danger that the number of cheaters increases too much compared with the number of pollinators, the former start to dominate the (now restricted) visitor population and make the system go extinct. Additional simulations have shown that this kind of dynamics is not very dependent on the initial conditions.

### ABM with space

While the analytical model does not allow to consider the role of space explicitly, we now study how the dynamics of the two cases change, if space is introduced explicitly into the ABM. Introducing space with a random initial configuration does not change the
dynamics significantly. Although we can observe the mechanisms that lead to this result graphically now. Two possible dynamics can be observed: Either visitors and plants focus locally in the space and form a big, growing patch with a very high density of flowers. While the frontiers between the patches stay empty for a very long time, in the center visitors visit nearby flowers in an almost entirely random manner, as the whole flower population is locally very dense. The other possibility is that there form small, nearby patches where one of the types starts to dominate.

In the patches where tubular flowers start to grow, the number of cheaters increase faster than that of the pollinators. This leads, in the medium run, to the extinction

![Graph showing population dynamics](image)

Figure 7: Average results for the coexistence case with 100 runs. The carrying capacity for the flowers is 2,000, the carrying capacity for the visitors is 1,000.

<table>
<thead>
<tr>
<th>Species</th>
<th>Extinction</th>
<th>Min</th>
<th>Max</th>
<th>Average</th>
<th>Std.dev</th>
</tr>
</thead>
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<tr>
<td>Shallow Flowers</td>
<td>37.3%</td>
<td>0</td>
<td>1985</td>
<td>1027</td>
<td>949</td>
</tr>
<tr>
<td>Tubular Flowers</td>
<td>50.9%</td>
<td>0</td>
<td>1987</td>
<td>971</td>
<td>732</td>
</tr>
<tr>
<td>Pollinators</td>
<td>9.8%</td>
<td>0</td>
<td>1000</td>
<td>10541</td>
<td>591</td>
</tr>
<tr>
<td>Cheaters</td>
<td>39.2%</td>
<td>0</td>
<td>917</td>
<td>310</td>
<td>344</td>
</tr>
</tbody>
</table>

Table 2: Asymptotic results for the ABM without space defined and with explicit carrying capacity for the visitors.
Figure 8: Transition in space with random initial configuration where one big path is formed as small patches dominated by cheaters and tubular flowers die out. Cheaters are colored in red, pollinators in blue, shallow flowers in yellow, and tubular flowers in green.

of this patch. Patches with a domination of shallow flowers and pollinators continue to grow until the overall carrying capacity for flowers is reached. While the first dynamics without the space leads to a coexistence of pollinators and the two flower types, the latter yields a coexistence of pollinators and shallow flowers. The transition is illustrated in Figure 9.

The dynamics become more interesting if one accounts for different patches of flowers rights from the beginning of the simulation, as it is shown in Figure 9a. Initially, both tend to grow. After 17 time steps, the cheaters start to dominate the patch with the tubular flowers (fig. 9b), which leads to an extinction of this patch after about 60 time steps (fig. 9c). In the other patch there are only shallow flowers. Because of their (small) advantage over the cheaters in the patch with shallow flowers, pollinators now dominate this patch and the number of flowers grows until it reaches the carrying capacity, as it is shown in Figure 9d.

Further statistical analysis is necessary to establish the results more rigorously, the ABM suggests that if the system does not receive exogenous shocks, all possible configurations of space tend to approximate the behavior without space in the limit. This is particularly true if one considers random initial configuration in the space. If one starts with different patches, it takes some time until patches merge and the results for the non-spatial model is approximated. The mechanisms leading to the overall results, can be observed explicitly. An overall coexistence is more likely for the spatial model, at least
as long patches have not yet merged. It seems to be the case, however, that a survival of cheaters for longer time horizons is impossible until they create new strategies that close the efficiency gap between pollinators and shallow flowers and the cheaters.

![Initial configuration.](image1)

![Situation after 17 time steps.](image2)

![Situation after 60 time steps.](image3)

![Situation after 110 time steps.](image4)

Figure 9: Transition in space with initial patches.

**Discussion and future directions**

In this study we show how the stability of coexistence points in pollination system can change depending on the consequences of cheater behavior. Cheaters in pollination system are usually considered as generators of harm and promoters of the decreasing success of pollination events. We analyzed the situation in which the very presence of cheaters increases the pollinators efficiency to the plants. It can be thought of as an increase in the distance pollinators must fly to reach enough resource or as a consequent increment
in the time spent by the pollinator in each flower to get enough resource as well.

We further believe that the distance among plants (or among resources, in the point of view of the flower visitors) press an important role in this systems. Pollinators and cheaters cannot fly indefinitely through the space. The best for auto-incompatible plants is to be pollinated by unrelated pollen, i.e. by pollen from an plant of different ancestors. Because the un-relatedness among plants increases with distance, the pollen coming from further plants would increase the success of a pollination event and a consequent success to the fitness of the plant. In order to study the role of space, we considered a agent based model in which we included a spatial structure and where flower visitors must move and reach the resource among the flowers.

The ABM suggests that the space consideration brings up new possibilities of coexistence of the two visitors and two plants, something that was possible in a respective non-spacial agent based model only if we included the carrying capacity for the visitors. The carrying capacity in the model without the explicit space makes the space role, forcing a limitation to visitor’s indefinitely growth. However the carrying capacity term is broad and it can accomplish many effects we do not understand completely. The space and distances among partners seems to be an important generator factor for the pollination systems. The ABM also suggested some explicit mechanisms that lead to the extinction of coexistence of the species. Further attention must be put on the importance of the visitor payoffs and the consequences of its values for the ABM. We are still working on this project, making these considerations and analyzing the ABM results statistically.

Another issue we are going to analyze in more depth is how the space structure can affect the coexistence of plants and visitors and how the forced spatial structure, as a mankind effect owing to the habitat fragmentation or deforestation, affect the existence or extinction of species in pollination systems. Because the ABM allows us making the space explicit, new studies concerning distances among patches, space structure of plant distributions, and moving potential differences between the two types of visitors become possible. Our preliminary results suggest that these mechanisms play an important role for the persistence of pollination systems and we hope to contribute with the new studies, providing the ABM model online in the future.
References


### Appendix

<table>
<thead>
<tr>
<th>Name in Script</th>
<th>Explanation</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>General</strong></td>
<td></td>
</tr>
<tr>
<td>number_of_timesteps</td>
<td>The number of iterations for the simulation</td>
</tr>
<tr>
<td>space_size</td>
<td>The size of the two-dimensional, continuous space</td>
</tr>
<tr>
<td>flowersize</td>
<td>How flowers are represented graphically</td>
</tr>
<tr>
<td>visitorsize</td>
<td>How visitors are represented graphically</td>
</tr>
<tr>
<td>patch_center</td>
<td>The list of positions of the initial patches</td>
</tr>
<tr>
<td>patch_radius</td>
<td>The list of sizes of initial patches</td>
</tr>
<tr>
<td>patch_shallow_flowers</td>
<td>The number of shallow flowers in each patch</td>
</tr>
<tr>
<td>patch_tubular_flowers</td>
<td>The number of tubular flowers in each patch</td>
</tr>
<tr>
<td>use_patches</td>
<td>Specifies whether to start with initial patches</td>
</tr>
<tr>
<td><strong>Flowers</strong></td>
<td></td>
</tr>
<tr>
<td>num_shallowflowers</td>
<td>Initial number of shallow flowers</td>
</tr>
<tr>
<td>num_tubularflowers</td>
<td>Initial number of tubular flowers</td>
</tr>
<tr>
<td>init_nectar</td>
<td>Initial amount of nectar for the flowers</td>
</tr>
<tr>
<td>init_pollen</td>
<td>Initial amount of nectar for the flowers</td>
</tr>
<tr>
<td>pollen_thrh</td>
<td>Threshold above which flowers start to reproduce</td>
</tr>
<tr>
<td>numflowertype</td>
<td>Number of flower types: Reproduction is possible only if the flower gets pollen indirectly from flowers of the same type</td>
</tr>
<tr>
<td>maxflowerage</td>
<td>Maximum age for the flowers</td>
</tr>
<tr>
<td>max_total_flowers</td>
<td>Maximum amount of flowers that can reside in the space</td>
</tr>
<tr>
<td>nectar_reprod</td>
<td>the amount of nectar that will be renewed in one round for each flower</td>
</tr>
<tr>
<td>pollen_reprod</td>
<td>the amount of pollen that will be renewed in one round for each flower</td>
</tr>
<tr>
<td>max_nectar</td>
<td>Threshold for nectar carried by the flower; flower reproduces pollen if actual amount of nectar is less</td>
</tr>
<tr>
<td>max_pollen</td>
<td>Threshold for pollen carried by the flower; flower reproduces pollen if actual amount of pollen is less</td>
</tr>
<tr>
<td>dispersal_rad</td>
<td>Radius around the parent into which new flowers are born</td>
</tr>
<tr>
<td><strong>Visitors</strong></td>
<td></td>
</tr>
<tr>
<td>num_pollinators</td>
<td>Initial number of pollinators</td>
</tr>
<tr>
<td>num_cheaters</td>
<td>Initial number of cheaters</td>
</tr>
<tr>
<td>init_energy</td>
<td>Initial amount of energy of the visitors</td>
</tr>
<tr>
<td>visitor_reprod_thrh</td>
<td>The amount ( \text{visitor	extunderscore reprod	extunderscore thr} \times \text{initial	extunderscore energy} ) is the threshold above which visitors reproduce and ( \text{visitor	extunderscore reprod	extunderscore thr} ) is the cost the parent visitor pays for reproduction</td>
</tr>
<tr>
<td>nectar2energy</td>
<td>The rate according to which visitors change nectar into energy</td>
</tr>
<tr>
<td>maxvisitorage</td>
<td>Maximum age for the visitors</td>
</tr>
<tr>
<td>visitor_radius</td>
<td>The radius in which a visitor can see and move within one round</td>
</tr>
<tr>
<td>visitor_born_rad</td>
<td>Radius around the parent into which new visitors are born</td>
</tr>
<tr>
<td>cost_pollinator_shallow_flower</td>
<td>The cost for the pollinator to enter an shallow flower</td>
</tr>
<tr>
<td>cost_pollinator_tubular_flower</td>
<td>The cost for the pollinator to enter an tubular flower</td>
</tr>
<tr>
<td>cost_cheater</td>
<td>The cost for the cheater to drill a hole on any flower</td>
</tr>
<tr>
<td>visitor_nectar_thr</td>
<td>Maximum amount of nectar a visitor can carry</td>
</tr>
</tbody>
</table>