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**POLLINATORS, GEITONOLOGY
AND A MODEL OF POLLEN TRANSFER**

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ABSTRACT

A model of pollination that considers the amount of geitonogamous pollen transfer in different flowers and plants is presented. We assumed in this work self-incompatible plant species and we studied how pollination is affected by different round trips described by pollinator from its nest, taking into account the fraction geitonogamy and the fraction pollen export. A deterministic model and a stochastic model of pollen transfer were developed from which we found that when pollinators describe a uniform sequence (visit the same number of flowers in each plant), individuals receive the maximum outcross pollen or minimum self pollen. That is, from the point of view of fertilization, the optimal number of flowers visited in each plant depends on the number of flowers of the plant, the length of the visit and the number of individuals.

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1. Introduction

Pollen is produced for the fertilization of other plants, but it is also collected by pollinators as a protein resource. On the other hand, plants produce nectar in order to attract pollinators which find in flowers their only nectar sources. In this dynamic environment, pollinators visit different plants and flowers to collect nectar and pollen as food resources. After arrival at a plant, they constantly accumulate self pollen and lose outcross pollen (pollen of other plants). Each round trip of the pollinator from its nest is called a bout (Friedman & Shmida, 1995). This is important for plants since the pollination depends greatly on them. We will assume in this work self-incompatible plant species, which will also be called 'individuals'.

There are some studies (de Jong et al., 1992) that show that the proportion of self pollen delivered through geitonogamy (pollination between flowers of the same plant) increases with plant size. We will see how geitonogamy and pollen export are affected by different bouts, and how they are related to the flowers of the plant, to the individuals of the patch and to the length of the visit.

In this study, pollen deposition and removal are assumed to be fractions of the amount carried by the pollinator that will be called A and the pollen present in the anthers of a flower, called B . We will assume that, when a pollinator (such as a bee) visits a flower, a constant fraction of pollen on the anthers (k_2) adheres to it and deposits a constant fraction (k_1) of the pollen load on its body, on the stigma or other parts of the flower.

We assume no loss of pollen in the transfer from the pollinator to the stigma and viceversa. If this loss is considered important it should be included in the above mentioned fractions, generalizing them.

The model we are presenting in this paragraph is a deterministic one, in which we do not consider fluctuations in time, or these fluctuations are small enough to be rejected. If, on the other hand, we assume that the proportions k_1 and k_2 can vary and we associate these fluctuations with their probabilities of occurrence, a stochastic model should be applied. In the first part of this work, we will consider a deterministic model and in the second part a stochastic model. After comparing them, we will see that the results obtained for one of them also hold for the other.

2. Modeling sequences of visits

Pollinators often visit a fraction of the flowers of a plant during each approach (Klinkhamer et al., 1994). We are considering here that pollinators remain within one flower species during each bout. Field observations suggest that for example, bees, even when they change frequently flower species, they typically remain within one flower species during each bout (Friedman & Shmida, 1995). We will assume solitary pollinators in such a way that there is not exchange of information between them (Oster & Wilson, 1978).

In this work, we will also consider that the pollinator visits different flowers in different plants of the same species and it does not return to the same plant and flower in the same sequence, in such a way that the pollinator moves to a new plant carrying A outcross pollen, describing a movement as we can see in fig. 1, where we consider that the pollinator visits n plants and f_ℓ flowers in the plant ℓ , with $\ell = 1, 2, \dots, n$. The outcross pollen that the flowers receive is given by the terms where A appears, and the self pollen grains they receive correspond to the terms with B . We can also see in fig. 1, that the geitonogamy increases with the length of the flower visitation sequence in the same plant.

The pollinator leaves its nest with an empty nectar tank (crop) and visits the flowers in order to fill its crop with nectar and to collect pollen. We will assume that after leaving the nest the pollinator visits a plant where it collects A outcross pollen and then it starts the sequence of visits of our model. After leaving the plant n it goes to another plant with A outcross pollen before returning to the nest. Thus, this first and this last plant will not be considered in the sequence. We make this assumption only to clarify and simplify the definitions and calculations of this paragraph.

Geitonogamy, has been estimated in the case of one individual (de Jong et al., 1993); we generalize the concept for n individuals. In this study, the fraction

geitonogamy of the whole visit is defined as a ratio of the sum of the total number of self pollen grains that every flower visited receives in every plant visited and the total number of grains (outcross and self pollen grains) that the same groups of flowers receive in the whole visit. In other words:

$$G = \frac{\sum_{\ell=1}^n \sum_{i=1}^{f_\ell} k_i B k_2 \sum_{j=1}^{i-1} (1-k_1)^{j-1}}{\sum_{\ell=1}^n \sum_{i=1}^{f_\ell} (k_i (1-k_1)^{i-1} A + k_i B k_2 \sum_{j=1}^{i-1} (1-k_1)^{j-1})}$$

We will consider n , the number of individuals in the model, as the minimum between the number of individuals of the patch and the number of changes (an average) that the pollinator can make in a bout, moving from one plant to another. This fraction also depends on the length of the total sequence m (the bout), the number of plants visited ℓ , with $\ell = 1, 2, \dots, n$, and the numbers of flowers visited in each plant, named f_ℓ . We can easily see that $m = f_1 + f_2 + \dots + f_n$. Notice the validity of the relation $m \leq n f$, where f is the number of flowers in each plant. It could be estimated as the mean number of flowers of the plants, and such that $f_\ell \leq f$, with $\ell = 1, 2, \dots, n$.

We assume that the pollen grains the pollinator deposits, is the same quantity that the pollinator picks up, this is named "pollinator saturation" and written as follows

$$(1) \quad k_1 A = k_2 B$$

In this case, results depend on the pollen deposition fraction k_1 . We can see it below, with $m = f_1 + f_2 + \dots + f_n$

$$G = 1 - \frac{\sum_{\ell=1}^n [1 - (1-k_1)^{f_\ell}]}{m k_1}$$

The number of pollen grains exported by the pollinator from one plant ℓ to another plant visited in the same sequence is given as follows (male fitness for individual ℓ (Klinkhamer et al., 1994)):

$$P_{\ell} = \sum_{i=1}^k k_2 B (1-k_i)^{i-1}$$

Consequently, the total number of pollen grains exported by the pollinator from one plant to another, from this to the next one, and so on, is given as the following sum, that, in a sense, could be interpreted as the male fitness of the sequence:

$$P = \sum_{\ell=1}^n \sum_{i=1}^k k_2 B (1-k_i)^{i-1} = \sum_{\ell=1}^n \frac{k_2 B [1 - (1-k_i)^k]}{k_i}$$

In a sequence of visits, $f_1 k_2 B + \dots + f_n k_2 B = m k_2 B$ pollen grains adhere to the pollinator. Therefore, the fraction of pollen export equals

$$F = \frac{P}{m k_2 B} = \frac{\sum_{\ell=1}^n [1 - (1-k_i)^k]}{m k_i}$$

Note that under the assumption of "pollinator saturation", $G = 1 - F$.

The i -th flower of plant ℓ in a sequence of visits receives $k_i (1-k_i)^{i-1} A$ outcross pollen grains while the whole plant (female fitness of individual ℓ)

$$H_{\ell} = \sum_{i=1}^k k_i (1-k_i)^{i-1} A$$

Analogously we can define, and interpret as the female fitness of the sequence:

$$H = \sum_{\ell=1}^n \sum_{i=1}^k k_i (1-k_i)^{i-1} A = \sum_{\ell=1}^n \frac{k_i A [1 - (1-k_i)^k]}{k_i}$$

In a sequence of visits, $f_1 k_2 B + \dots + f_n k_2 B = m k_2 B = m k_1 A$ pollen grains adhere to the pollinator. Therefore, the fraction outcross pollen which the plants receive equals:

$$T = \frac{H}{m k_1 A} = \frac{\sum_{\ell=1}^n [1 - (1-k_i)^k]}{m k_i}$$

Notice that under the condition of "pollinator saturation" (1), which will be used in the next paragraphs, and from the definitions we have just seen, we obtain $P_{\ell} = H_{\ell}$, $P=H$, and $F=T$.

2.1 A COMPUTATIONAL APPROACH

As a first step, to explore how pollination vary with the different bouts, we developed a computational program. The program simulates all possible sequences the pollinator can follow when it visits m flowers in n individuals that have an average of f flowers each one, and appoints the one which gives the greatest movement of outcross pollen. Consequently, the geitonogamy fraction, the fraction pollen export, the number of pollen grains exported by the pollinator (P_{ℓ}) and the number of outcross pollen grains which the plants receive (H_{ℓ}) are given for each individual and for each sequence and, in particular, for the sequence that gives the maximum of F (or minimum of G). From the computational analysis, we can see that, if $m \leq f$, the sequence corresponding to the visit of only one plant gives the maximum of the geitonogamy fraction and the minimum of the fitness. If $m > f$, these values are obtained when the insect visits m different flowers with the minimum changes of plants.

The interesting fact we found is that the maximization of fitness and minimization of geitonogamy was found when the number of flowers visited does not vary with individuals, or it changes only minimally. According to this, it can result that m/n , (that is the equal number of flowers visited in each plant), is not an integer number, in this case, an approximation is given in practice. That is, m/n is approximated with the minimum integer number smaller than itself, let's call it w . So, we obtain s plants with w flowers and $n-s$ with $w+1$ flowers, such as $m=sw+(n-s)(w+1)$. These results do not depend on which particular plant has been visited k or $k+1$ times. Consequently the conclusions do not change. These considerations are also taken into account in the analytic analysis, where the variables that represent numbers of flowers are seen as continuous variables in order to study them with mathematical tools of calculus. We want to analyze all of these facts from an analytical point of view in order to see the extension of the approach we found.

2.2 MATHEMATICAL ANALYSIS

Thus, we will see that a mathematical development confirms the results we have seen with computational methods. From a mathematical point of view, this can be seen as a problem of maxima and minima with constraint conditions. The method of Lagrange multipliers gives us a useful tool to calculate extreme values, or equivalently, in our case, the maximum that the individuals receive of outcross pollen. In this case, the problem is reduced to calculate, the minimum geitonogamy fraction (G) or the maximum fraction of pollen export (F).

We can go on considering G as a function continuously differentiable on an open set, depending on f_1, f_2, \dots, f_n , which, for our purposes, are assumed to be continuous variables and such that

$$f_1 + f_2 + \dots + f_n = m.$$

The basic result used in the method of Lagrange multipliers is given in the Appendix I. Following this method for $G(f_1, f_2, \dots, f_n)$, with the constraint

$f_1 + f_2 + \dots + f_n = m$, we obtain the minimum in (f_1, f_2, \dots, f_n) such that $f_1 = f_2 = \dots = f_n = \frac{m}{n}$. Particular cases for $n=2$ and $n=3$ are calculated in

Appendix II.

Thus, from the point of view of fertilization the optimal number of flowers visited in each plant depends on the number of flowers of the plant, the length of the visit and the number of individuals.

Since $G=1-F$, we conclude that, whenever G has a minimum, F has a maximum in the same point. We could analogously study the maximum for function F with this method, without considering G . Moreover, since the denominator of F does not depend on the values of the variables f_1, f_2, \dots, f_n , only on its fixed sum m , a maximum for F is a maximum for P , thus a similar analysis can be made for $P=H$. Conclusions do not change if different values for A, B, k_1 and k_2 are considered, keeping in mind our condition of pollinator saturation (1).

3. A stochastic model

Up to now we have been considering the proportions k_1 and k_2 as fixed values. However, in practice, they can vary. Thus, if these values are assumed to be random variables with the corresponding probabilities, a stochastic model can be studied. The proportions k_1 and k_2 vary between 0 and 1 and depend on different facts such as, width or length of the style. We could also define coefficients of difficulty or aptitude, to study the stochastic variation of the proportions. In this work, we will consider the width of the style (a) or length of the style (b), that can be estimated as an average of real data. We can see that these assumptions correspond to a Beta Distribution that depends on parameters a and b , where k_{1i} means the stochastic fraction the pollinator deposits on the flower i and k_{2i} the stochastic fraction of pollen on the anthers of flower i that adheres to it.

So, from the assumptions we have considered, we have that the variable k_{1j} is distributed as a Beta distribution with parameters a and b , where the density function of the Beta distribution, is given as follows

$$g_i(k_{1j}) = \frac{1}{B(a,b)} k_{1j}^{a-1} (1-k_{1j})^{b-1}$$

where, $a > 0$, $b > 0$ and $0 < k_{1j} < 1$.

The function $B(a,b) = \int_0^1 k_{1j}^{a-1} (1-k_{1j})^{b-1} dk_{1j}$ is called the beta function.

The expected value in the case of the Beta Distribution (Freund & Walpole, 1980; Dudewicz & Mishra, 1988) is

$$E(k_{1j}) = \frac{a}{a+b} \quad \text{and} \quad E(1-k_{1j}) = \frac{b}{a+b}.$$

Note that if the length of the style (b) increases, the expected proportion the flower receives, decreases. Analogously, when the width of the style (a) increases, the expected proportion of pollen also increases.

In order to make this stochastic analysis, we will consider the variables as follows: k_{1j} is a stochastic variable that represents the proportion of pollen that the pollinator deposits on the stigma, or on other parts of the flower i , whilst for each individual ℓ the multidimensional density function g , can be given as a function depending on the f_ℓ flowers visited or, in other words, on f_ℓ variables, namely $k_{11}, k_{12}, \dots, k_{1f_\ell}$. We assume that the proportion of pollen the pollinator deposits on one flower, does not depend on the proportion which is deposited on another flower. Thus, these variables can be considered as independent variables in such a way that the multivariate density function can be given by

$$g(k_{11}, k_{12}, \dots, k_{1f_\ell}) = g_1(k_{11}) g_2(k_{12}) \dots g_{f_\ell}(k_{1f_\ell})$$

These assumptions are used in the following analysis, where we will study the fraction outcross pollen which the plants receive (that is the equality we called T). The other relations we have defined can be studied analogously.

So, we are now interested in the expected value of the total proportion of outcross pollen which the plant ℓ receives. Taking into account the definition of g , its properties, the expected values we have written above and the mentioned hypothesis of independence of variables, the expected value for individual ℓ can be written as follows:

$$\begin{aligned} E(k_{11} + k_{12}(1-k_{11}) + k_{13}(1-k_{11})(1-k_{12}) + \dots + k_{1f_\ell}(1-k_{11}) \dots (1-k_{1(f_\ell-1)})) &= \\ = \frac{a}{a+b} + \frac{a}{a+b} \frac{b}{a+b} + \frac{a}{a+b} \left(\frac{b}{a+b}\right)^2 + \dots + \frac{a}{a+b} \left(\frac{b}{a+b}\right)^{f_\ell-1} &= \\ = \frac{a}{a+b} \frac{1 - \left(\frac{b}{a+b}\right)^{f_\ell}}{1 - \left(\frac{b}{a+b}\right)} = 1 - \left(\frac{b}{a+b}\right)^{f_\ell} \end{aligned}$$

In a sequence of visits $m \frac{a}{a+b} A$ gives the expected pollen grains that adhere to the pollinator. Consequently, the stochastic analogy to the fraction outcross pollen which the plants receive (T), will be called T_S , and it may be estimated as

$$T_S = \frac{\sum_{i=1}^n \left[1 - \left(\frac{b}{a+b}\right)^{f_i} \right]}{m \frac{a}{a+b}}$$

We can see that the functions we obtain in this stochastic case are similar to the functions we obtained in the deterministic case. Thus we can make the same analysis as for the study of the extreme points in the deterministic case with the method of Lagrange, and the constraint condition $f_1 + f_2 + \dots + f_n - m = 0$.

After calculating the partial derivatives we conclude that (f_1, f_2, \dots, f_n) , such that $f_1 = f_2 = \dots = f_n = \frac{m}{n}$, gives a maximum or a minimum, in this case we can see that it is a maximum.

From the density function of k_{1i} , that is the beta distribution, we can deduce the density function of k_{2i} , knowing that $k_{2i}B = k_{1i}A$, with a simple change of variables

$$p(k_{2i}) = \frac{B}{A} \frac{1}{B(a,b)} \left(k_{2i} \frac{B}{A}\right)^{a-1} \left(1 - k_{2i} \frac{B}{A}\right)^{b-1}$$

The condition of "pollinator saturation" can be seen in terms of the expected value, that is $E(k_{2i}B) = E(k_{1i}A)$, from which we have $E(k_{2i}) = \frac{A}{B} \frac{a}{a+b}$

Then, the total number of pollen grains exported by the pollinator, which is to be called P_S in the stochastic case, can be written as:

$$P_S = \sum_{i=1}^n \sum_{j=1}^l A \frac{a}{a+b} \left(\frac{b}{a+b}\right)^{ji} = \sum_{i=1}^n A \left(1 - \left(\frac{b}{a+b}\right)^l\right)$$

as before $P_S = H_S$.

The fraction pollen export is estimated to be

$$F_S = \frac{P_S}{mA \frac{a}{a+b}} = \frac{\sum_{i=1}^n \left(1 - \left(\frac{b}{a+b}\right)^l\right)}{m \frac{a}{a+b}}$$

The fraction geitonogamy of the whole visit in the stochastic case is written as:

$$G_S = 1 - \frac{\sum_{i=1}^n \left(1 - \left(\frac{b}{a+b}\right)^l\right)}{m \frac{a}{a+b}}$$

We can see that with the deterministic and stochastic analysis, our conclusions do not change, since functions have the same shape. However, the solution obtained with the deterministic model agrees with the solution obtained with the stochastic model only in the case when the deposition fraction and the adherence fraction vary independently in each flower.

4. Discussion

When a pollinator visits successive plants and flowers it loses outcross pollen and accumulates self pollen. When flower visitation sequences in one individual are longer, a smaller fraction of the removed pollen is actually exported to other plants and a larger fraction is deposited on the plant itself. In this round trip, the pollinator can follow different movements.

Our focus is on the different sequences that the pollinators can describe and how pollination is affected by them. The model presented in this work provides a means of examining the dynamics of the pollination, and shows how the individuals, the flowers and the length of the visits influence greatly the pollination. We considered the geitonogamy fraction as a measure of pollen transfer among flowers on the same plant and the fraction of outcross pollen to estimate the compatible pollen, which the plant receives. We studied all bouts that pollinators can follow and the sequence in which individuals receive the maximum outcross pollen or minimum self pollen. This was found when pollinators visit the same number of flowers in each plant. Thus, we can talk about a constant or uniform sequence. If the number of flowers in each plant obtained is not an integer number, an approximation is needed in practice. In this case, different sequences can be obtained depending on the flowers visited in each plant, however, all of them give the same results related to outcross pollen and the conclusion is the same.

According to the deterministic model, if the following parameters vary in different sequences: the amount of pollen carried by the pollinator (A) or present in the anthers of a flower (B), the proportions of the pollen on the anthers that adheres to pollinators (k_2) and the proportions that deposits (k_1), then our conclusions do not change under the assumption of "pollinator saturation". Analogously, if in the stochastic model A and B vary, as well as the parameters a and b that can describe for example morphological characteristics of flowers, but are constant values in a bout, results do not change.

As a conclusion we can say that, from the point of view of successful fertilization of plants, the optimal number of flowers visited in each plant is proportional to the total number of flowers visited and to the number of individuals and depends on the number of flowers of the plant. From these results, one can expect that, if the number of individuals n increases and $n \leq m$, the optimal value will be found to be an equal number of flowers visited in n individuals. If the number of flowers in each plant decreases, the optimal number would vary correspondingly.

We have presented a model in which pollinators and flowers interact in a dynamic environment. We assume that individuals are distributed in a patch in such a way that pollinators can visit one plant and then go to another plant without returning. Some studies show that the pollinator visits many flowers from few individuals in order to fill its crop with nectar and to collect pollen (O'Toole & Raw, 1991). Once the insect visits a plant, one can expect it visits close flowers in that plant and when it is near a new plant it reaches it and goes on visiting close flowers in the new individual and so on. In this dynamics one can expect a regular behavior regarding number of flowers visited in each plant, assuming that there are not great differences in the individuals. Furthermore, we assume that any environmental factors that may influence this dynamics are the same for all plants.

There are some studies (de Jong et al., 1992) that show that flowers on small and large plants receive equal amounts of outcross pollen (pollen of other plants), whereas flowers on large plants receive more self pollen, so that the proportion of self pollen delivered through geitonogamy increases with plant size. If plants are homogeneous, one can expect that they receive equal amounts of outcross and self pollen grains that, under the "pollinator saturation", means that the pollinator visits equal number of flowers in each individual.

Moreover, from the results of our model, one can deduce that, if experimental data that show a uniform behavior of pollinators are obtained in any patch, a best fertilization would be expected.

This work could prove helpful in studying the field pollination if more data could be obtained to fit the model and to support the results that our model predicts. Furthermore, the case of no pollinator saturation should be studied, in order to generalize the model without restricted conditions.

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APPENDIX I

The Method of Lagrange allows us to find maximum or minimum values with constraint conditions. The basic result used in it is this:
 Suppose G a function continuously differentiable on an open set that contains the differentiable curve C , e.g. $R(t) = x(t) \mathbf{i} + y(t) \mathbf{j} + z(t) \mathbf{k}$.

If \mathbf{x}_0 minimizes (or maximizes) $G(\mathbf{x})$ on C , then $\nabla G(\mathbf{x}_0)$ is perpendicular to C at \mathbf{x}_0 . This is the key to why the method of Lagrange multipliers works as we shall see now.

Suppose that h is a continuously differentiable function defined on a subset of the domain of G . \mathbf{x}_0 is a point on the surface $h(\mathbf{x})=0$, where G has a local maximum or minimum value relative to its other values on the surface.

We can write, in general for vectors \mathbf{x} the following result

If \mathbf{x}_0 minimizes (or maximizes) $G(\mathbf{x})$, subject to the constraint condition $h(\mathbf{x})=0$ then $\nabla G(\mathbf{x}_0)$ and $\nabla h(\mathbf{x}_0)$ are parallel, where $\nabla G(\mathbf{x}_0)$ and $\nabla h(\mathbf{x}_0)$ are the gradients of the corresponding functions.

Thus, if $\nabla h(\mathbf{x}_0) \neq 0$, then there exists a scalar λ such that

$$\nabla G(\mathbf{x}_0) = \lambda \nabla h(\mathbf{x}_0)$$

in our case using the relation we have seen, that is $f_1 + f_2 + \dots + f_n = m$ the function h is

$$h(f_1, f_2, \dots, f_n) = f_1 + f_2 + \dots + f_n - m = 0$$

APPENDIX II

We now see the method of Lagrange in a particular case for two individuals, that is $n=2$, in this case we want to minimize

$$G(f_1, f_2) = 1 - \frac{[1 - (1 - k_1)^{f_1}] + [1 - (1 - k_1)^{f_2}]}{mk_1}$$

subject to the constraint condition $h(f_1, f_2) = f_1 + f_2 - m = 0$

$$\text{The gradient is defined } \nabla G(f_1, f_2) = \frac{\partial G}{\partial f_1} \mathbf{i} + \frac{\partial G}{\partial f_2} \mathbf{j}$$

where the first partial derivative is given in the following equality with $f=f_1$ and the second one with $f=f_2$

$$\frac{\partial G}{\partial f} = \frac{-(1-k_1)^f \ln(1-k_1) (f_1+f_2) - [1-(1-k_1)^{f_1}] - [1-(1-k_1)^{f_2}]}{(f_1+f_2)^2 k_1}$$

Setting $\nabla G(f_1, f_2) = \lambda \nabla h(f_1, f_2)$ we obtain

$$\frac{\partial G}{\partial f_1} = \lambda \quad , \quad \frac{\partial G}{\partial f_2} = \lambda$$

and we can conclude that $f_1 = f_2$. the constraint condition gives us $f_1 = f_2 = \frac{m}{2}$, then this (f_1, f_2) is by the method of Lagrange a maximum or a minimum.

We can easily see that, in fact, it is a minimum.

In a particular case for three individuals, that is $n=3$, we want to minimize

$$G(f_1, f_2, f_3) = 1 - \frac{[1-(1-k_1)^{f_1}] + [1-(1-k_1)^{f_2}] + [1-(1-k_1)^{f_3}]}{mk_1}$$

subject to the constraint $h(f_1, f_2, f_3) = f_1 + f_2 + f_3 - m = 0$

By a similar analysis we can conclude that $f_1 = f_2 = f_3 = \frac{m}{3}$. As before, we can

see that, in fact (f_1, f_2, f_3) is a minimum.

For a greater number of variables, the method can be applied analogously.

Thus, for $G(f_1, f_2, \dots, f_n)$, with the constraint condition $f_1 + f_2 + \dots + f_n - m = 0$,

we obtain the minimum in (f_1, f_2, \dots, f_n) such that $f_1 = f_2 = \dots = f_n = \frac{m}{n}$

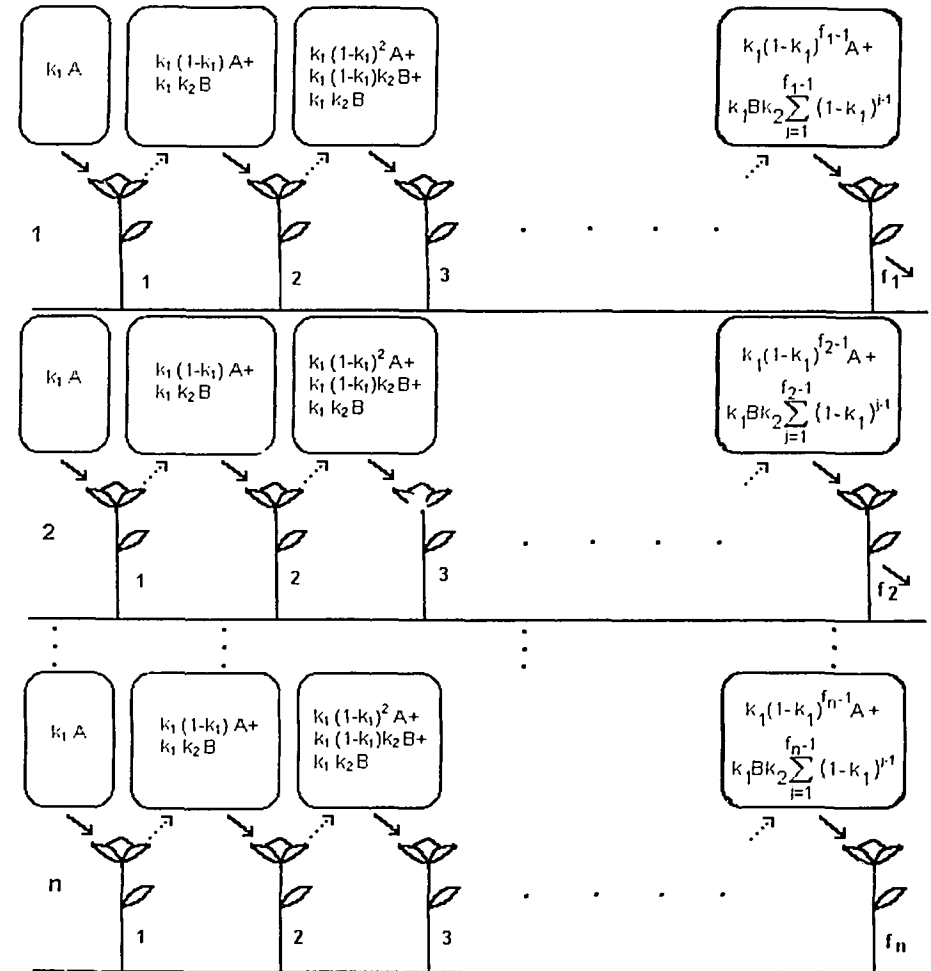


Fig 1. Pollinators and the pollen transfer