

## FLORAL ATTRACTIVENESS AND REWARDS AFFECT THE RESILIENCE OF HOST-POLLINATOR SYSTEMS: A GENETIC MODEL

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A genetic model was designed to depict what the resilience of host-pollinator interactions may be according to well known genetic rules and assuming an underlying genetic basis for (a) the attraction that flowers exert on pollinators, and (b) the fitness gain by the pollinator from visiting a flower. We explore the possible trajectories that a plant-pollinator system describes under certain bound conditions determined by a whole complex of attractiveness and reward scores. Such scores represent genetic relations between two diallelic loci assumed to control both traits. To see how the system would behave over time we created eight different scenarios, differing in the orientation they impose on the system. Half of these situations are of a reinforcing type (indicating a similar input both for attractiveness and rewards) and the remaining ones are conflicting (indicating opposite inputs). A numerical simulation was carried over seventy-five generations starting from Hardy–Weinberg equilibrium populations. We detected some general behavioral patterns in the final structure of frequencies. One of these may be viewed as a resilient type of structure (i.e., without memory of the initial population frequencies) which we hypothesize, may reflect the typical attraction-reward structure generally observed in nature. Another pattern is characterized by a pronounced loss of heterozygotes in the final structure, caused by the fixation of the most attractive phenotypes at the expense of the least attracting ones, independently of the pollinator genotype.

*Keywords:* Pollination; genetic models; ecological interactions.

### 1. Introduction

Plant-pollinator relationships are complex and fascinating, having received continued attention for the last two centuries [1, 24]. In a large part of the Angiosperms, plants typically display flower attractive to insects (or other pollinators) that visit flowers to gain some nourishing (mostly nectar and/or pollen). In the visiting process visitors deposit some pollen on stigmas and pick pollen grains from anthers,

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thus effecting plant-to-plant pollen transport along consecutive visits, a most important goal for cross-pollinated plants. The success of this mutualism lies in that plants get male gametes dispersed, and pollinators get a meal. Presentation of edible substances in flowers represents, from the plant “viewpoint”, an energy expenditure invested to reward an essential service.

There is evidence of intraspecific variation in plant attractiveness to pollen vectors, resulting from differences in flower design, flower display, and other factors. For instance, certain individuals are differentially visited because they are aggregated in denser stands [19], their inflorescences are larger-sized [9] or reach higher above ground [5], they display more flowers at a time [15, 21], the flowers have a distinct fragrance [7, 18]) or are more rewarding [14, 20, 28]. All the above plant traits are presumably under genetic control (see e.g., [28] for nectar rewards) and, therefore, are subject to selection because of the fitness consequences of optimizing gamete dispersal (but see [10] on the question of how often actual floral adaptations to pollination occur in nature, and [20] on inconstancy of trait expression).

The availability of rewards at individual flowers may vary both within and between individuals of the same plant species [14, 28]. Because reward availability is not the only factor determining flower attractiveness (see above), high attractiveness not necessarily implies high reward, as clearly exemplified by deceit flowers [6, 27]). On the other hand, visitors may vary in their ability to benefit from each visit, for instance as a consequence of differential tongue length [17], even if confronted with equally-rewarding flowers.

Although the plant-pollinator interaction has been studied in several ways, and some models have been published (e.g., [23] on effects on male reproductive success of some pollen- and pollinator type-related factors, [11] on effects on male fitness on plant’s adjustment of attractiveness; [8] on effects on female fitness of flower number) it seems that no analysis is available in which *both* plant’s and visitor’s point of view are taken into account.

Here we simulate a situation in which plants attract pollinators to varying degrees, and pollinators derive different levels of fitness gain from flower visits, with an emphasis on the populational consequences for both parties. A genetically-based model is formulated to simulate the development of a plant-pollinator community where both strongly and weakly attractive plants interact with high- and low-gaining visitors during several generations.

## 2. Models and Methods

Two reproductive traits, one in plants and the other in pollinators, were analyzed: (a) the *attraction* that flowers exert on pollinators, and (b) the *fitness* gained by the pollinator from visiting a flower. Two diallelic *loci* were assumed to rule those traits, one belonging to the plant genome and the other, to the pollinator genome. We have considered this simple genetic model (two *loci*) as an initial approach to the analysis of the interaction of such complex traits as floral attractiveness and floral

rewards. We are aware of the risks of oversimplification, but in a first exploration it seemed preferable to put emphasis in the diversity of interaction scenarios (see Sec. 2.4 below) while maintaining low the level of genetic complexity.

It has also been assumed that (a) there is one generation of host plant for each generation of pollinator (e.g., the plant species is a monocarpic annual and the pollinator species has 1 generation per year and does not overwinter), (b) plants are obligate zoophilic and xenogamous, and reproduce only by seed, (c) irrespective of how pollinators manage pollen after each visit to a flower, all genotypes of pollinators have the same per-visit efficiency as such, (d) all plant individuals in a given generation derive solely from seeds produced in the previous generation.

The plant-pollinator interaction has been modeled by means of two matrices, one of these ( $\mathbf{P}$ ) representing the attraction that flower phenotypes exert over the pollinator and the other ( $\mathbf{W}$ ) representing the fitness that a given pollinator gains from visiting a given flower. Thus — recalling that we are assuming 2 diallelic *loci* — we have two  $3 \times 3$  matrices. Each of the matrix  $\mathbf{P}$  entries ( $p_{ij}$ ) represents the attraction that a plant of genotype  $i$  exerts on a pollinator of genotype  $j$ . We denoted the host genotypes as  $A_1A_1$  ( $i = 1$ ),  $A_1A_2$  ( $i = 2$ ) and  $A_2A_2$  ( $i = 3$ ) and the pollinator genotypes as  $B_1B_1$  ( $j = 1$ ),  $B_1B_2$  ( $j = 2$ ) and  $B_2B_2$  ( $j = 3$ ). On the other hand, each of the matrix  $\mathbf{W}$  ( $w_{ij}$ ) entries represents the absolute gain in fitness derived by a pollinator of genotype  $j$  from visiting a plant of genotype  $i$ .

Clearly, each of both genes  $A$  and  $B$  is involved in the expression of two characters, one related to floral attractiveness and the other to pollinator fitness gain. For example, gene  $A$  may be controlling the intensity of floral scent emission and nectary depth, while gene  $B$  may be controlling the sensitivity of scent perception and tongue length. Both attractiveness and fitness gain are emergent properties of the host-pollinator interaction.

Starting from a set of population structures [12] in  $G_0$  (generation 0) the genetic system runs under fixed hereditary rules, thus the initial population structures become progressively transformed according to such rules until, finally, the genetic system reaches a given equilibrium state, being this a kind of steady equilibrium or a fixed trivial one [4]. We have denoted genotypic frequencies in generation  $t$  ( $G_t$ ) as  $P_{1t}, P_{2t}, P_{3t}, H_{1t}, H_{2t}$  and  $H_{3t}$  for genotypes  $A_1A_1, A_1A_2, A_2A_2, B_1B_1, B_1B_2$  and  $B_2B_2$ , respectively.

Other factors being equal, the probability of a given pollinator to meet a given plant in generation  $t$  arises solely from the nine ( $3 \times 3$ ) products of their respective probabilities in  $G_t$ . For example, the probability of a  $B_1B_1$  pollinator to meet an  $A_1A_1$  plant (in  $G_t$ ) is equal to  $P_{1t} \cdot H_{1t}$ , the probability of a  $B_2B_2$  pollinator to meet an  $A_1A_2$  plant (in  $G_t$ ) is equal to  $P_{2t} \cdot H_{3t}$ , and so on. Once the partners met, there is a probability for the pollinator to contact the flower and take the reward (and, then, of pollen removal and/or deposition) depending upon both genotypes. This last probability is given by the corresponding matrix  $\mathbf{P}$  entry:

$$\mathbf{P} = \begin{bmatrix} p_{11} & p_{12} & p_{13} \\ p_{21} & p_{22} & p_{23} \\ p_{31} & p_{32} & p_{33} \end{bmatrix}$$

where  $1 - p_{ij}$  is the probability for a pollinator of genotype  $j$  of no pollen removal at all from a flower of genotype  $i$  (including not even contacting the flower).

In all these reasonings it must be taken into account the asymmetric effects of interactions on gametes. The set of fitness gain ( $w_{ij}$ ) and attracting values ( $p_{ij}$ ) only affect the pollen transfer (ovules are not directly affected) while both types of gametes are equally affected in pollinators through their fitnesses.

**2.1. Average composition of pollinator’s pollen load**

In order to compute plant genotypic frequencies in the next generation, we first need to determine the average pollen load on the pollinator after visitation. Because of the different  $p_{ij}$  probabilities corresponding to each of the pollinators genotypes, we have to determine the frequencies of both types of pollen ( $A_1$  and  $A_2$ ) on each of the three types of pollinator ( $B_1B_1, B_1B_2$  and  $B_2B_2$ ) bodies:

$$B_1B_1 \text{ pollinators : } f_1(A_1) = \frac{P_{t1} \cdot p_{11} + \frac{1}{2}P_{t2} \cdot p_{21}}{\sum_{j=1}^3 P_{tj} \cdot p_{j1}}, \tag{1}$$

$$f_1(A_2) = \frac{P_{t3} \cdot p_{31} + \frac{1}{2}P_{t2} \cdot p_{21}}{\sum_{j=1}^3 P_{tj} \cdot p_{j1}}. \tag{2}$$

$$B_1B_2 \text{ pollinators : } f_2(A_1) = \frac{P_{t1} \cdot p_{12} + \frac{1}{2}P_{t2} \cdot p_{22}}{\sum_{j=1}^3 P_{tj} \cdot p_{j2}}, \tag{3}$$

$$f_2(A_2) = \frac{P_{t3} \cdot p_{32} + \frac{1}{2}P_{t2} \cdot p_{22}}{\sum_{j=1}^3 P_{tj} \cdot p_{j2}}. \tag{4}$$

$$B_2B_2 \text{ pollinators : } f_3(A_1) = \frac{P_{t1} \cdot p_{13} + \frac{1}{2}P_{t2} \cdot p_{23}}{\sum_{j=1}^3 P_{tj} \cdot p_{j3}}, \tag{5}$$

$$f_3(A_2) = \frac{P_{t3} \cdot p_{33} + \frac{1}{2}P_{t2} \cdot p_{23}}{\sum_{j=1}^3 P_{tj} \cdot p_{j3}}. \tag{6}$$

**2.2. Plant genotypic frequencies in the next generation**

The plant population will have in the next generation the following genotypic frequencies:

$$P_{t+1;1} = \frac{P_{t+1;1}^0}{S}, \tag{7}$$

$$P_{t+1;2} = \frac{P_{t+1;2}^0}{S}, \tag{8}$$

$$P_{t+1;3} = \frac{P_{t+1;3}^0}{S}, \tag{9}$$

where:

$$S = P_{t+1;1}^0 + P_{t+1;2}^0 + P_{t+1;3}^0, \tag{10}$$

$$P_{t+1;1}^0 = \sum_{j=1}^3 H_{tj} \cdot f_j(A_1) \left[ P_{t1} + \frac{1}{2}P_{t2} \right], \tag{11}$$

$$P_{t+1;2}^0 = \sum_{j=1}^3 H_{tj} \left\{ f_j(A_1) \left[ P_{t3} + \frac{1}{2}P_{t2} \right] + f_j(A_2) \left[ P_{t1} + \frac{1}{2}P_{t2} \right] \right\}, \tag{12}$$

$$P_{t+1;3}^0 = \sum_{j=1}^3 H_{tj} \cdot f_j(A_2) \left[ P_{t3} \cdot p_{3j} + \frac{1}{2}P_{t2} \cdot p_{2j} \right]. \tag{13}$$

**2.3. Pollinator genotypic frequencies in the next generation**

First we have to address the fitness gains obtained by pollinators. Each pollinator genotype will be affected in its fitness [22] by the reward got from the flower visited according to the matrix **W** entries ( $w_{ij}$ ). Therefore, the average fitness gained by each of the pollinator genotypes resulting from visiting flowers may be calculated as follows:

$$\bar{w}(B_1B_1) = \sum_{i=1}^3 P_{it} \cdot p_{i1} \cdot w_{i1} = \bar{w}_{1t}, \tag{14}$$

$$\bar{w}(B_1B_2) = \sum_{i=1}^3 P_{it} \cdot p_{i2} \cdot w_{i2} = \bar{w}_{2t}, \tag{15}$$

$$\bar{w}(B_2B_2) = \sum_{i=1}^3 P_{it} \cdot p_{i3} \cdot w_{i3} = \bar{w}_{3t}. \tag{16}$$

Then, the overall average fitness in generation  $t$  is:

$$\bar{w}_t = \sum_{j=1}^3 H_{jt} \cdot \bar{w}_{jt}. \tag{17}$$

Finally, pollinator reproduction must be affected by its genotype fitness. Thus, we need to compute the new genotypic frequencies after selection ( $H_{jts}$ ) which are, simply, equal to:

$$H_{jts} = \frac{H_{jt} \cdot \bar{w}_{jt}}{\bar{w}_t}. \tag{18}$$

Then, the allelic frequencies are:

$$p_{t+1}(B_1) = H_{1ts} + \frac{1}{2}H_{2ts}, \tag{19}$$

$$p_{t+1}(B_2) = H_{3ts} + \frac{1}{2}H_{2ts}. \tag{20}$$

The next generation genotypic frequencies will be:

$$H_{1,t+1} = p_{t+1}^2(B_1), \tag{21}$$

$$H_{2,t+1} = 2 \cdot p_{t+1}(B_1) \cdot p_{t+1}(B_2), \tag{22}$$

$$H_{3,t+1} = p_{t+1}^2(B_2). \tag{23}$$

### 2.4. Numerical simulations

In order to visualize the behavior of the system over time until some sort of equilibrium is reached, we have constructed simulations upon the base of 8 combination of  $p_{ij}$  and  $w_{ij}$  values. We have designed four cases as *conflicting* (C), the remaining four being designed as *reinforcing* (R). The term “conflicting” refers to the situation when the values of attraction ( $p_{ij}$ ) and the values of fitness gain ( $w_{ij}$ ) orient the system in opposite directions, i.e., the former favor some host-pollinator combination of genotypes while the values of fitness gain ( $w_{ij}$ ) do with the opposite combinations (in other words, the most attractive hosts with respect to certain pollinator genotypes are those from which these genotypes derive the littlest fitness gains). The term “reinforcing” refers to the situation when the  $p_{ij}$  and  $w_{ij}$  values orient the system in the same direction. The  $p_{ij}$  values are probabilities while the  $w_{ij}$  ones are dimensionless integers representing the relative advantages in fitness obtained by the pollinators. The matrices corresponding to the 8 cases are the following:

(1) **Conflicting cases (C):**

$$\text{Case CA : } \mathbf{P} = \begin{bmatrix} 0.2 & 0.5 & 0.8 \\ 0.5 & 0.8 & 0.5 \\ 0.8 & 0.5 & 0.2 \end{bmatrix}; \quad \mathbf{W} = \begin{bmatrix} 8 & 5 & 2 \\ 5 & 8 & 5 \\ 2 & 5 & 8 \end{bmatrix}$$

$$\text{Case CB : } \mathbf{P} = \begin{bmatrix} 0.8 & 0.5 & 0.8 \\ 0.5 & 0.2 & 0.5 \\ 0.8 & 0.5 & 0.8 \end{bmatrix}; \quad \mathbf{W} = \begin{bmatrix} 2 & 5 & 2 \\ 5 & 8 & 5 \\ 2 & 5 & 2 \end{bmatrix}$$

$$\text{Case CC : } \mathbf{P} = \begin{bmatrix} 0.2 & 0.5 & 0.2 \\ 0.5 & 0.8 & 0.5 \\ 0.2 & 0.5 & 0.2 \end{bmatrix}; \quad \mathbf{W} = \begin{bmatrix} 8 & 5 & 8 \\ 5 & 2 & 5 \\ 8 & 5 & 8 \end{bmatrix}$$

$$\text{Case CD : } \mathbf{P} = \begin{bmatrix} 0.2 & 0.8 & 0.2 \\ 0.8 & 0.5 & 0.8 \\ 0.2 & 0.8 & 0.2 \end{bmatrix}; \quad \mathbf{W} = \begin{bmatrix} 8 & 2 & 8 \\ 2 & 5 & 2 \\ 8 & 2 & 8 \end{bmatrix}$$

(2) Reinforcing cases (R):

$$\text{Case RA : } \mathbf{P} = \begin{bmatrix} 0.2 & 0.5 & 0.8 \\ 0.5 & 0.8 & 0.5 \\ 0.8 & 0.5 & 0.2 \end{bmatrix}; \quad \mathbf{W} = \begin{bmatrix} 2 & 5 & 8 \\ 5 & 8 & 5 \\ 8 & 5 & 2 \end{bmatrix}$$

$$\text{Case RB : } \mathbf{P} = \begin{bmatrix} 0.8 & 0.5 & 0.8 \\ 0.5 & 0.2 & 0.5 \\ 0.8 & 0.5 & 0.8 \end{bmatrix}; \quad \mathbf{W} = \begin{bmatrix} 8 & 5 & 8 \\ 5 & 2 & 5 \\ 8 & 5 & 8 \end{bmatrix}$$

$$\text{Case RC : } \mathbf{P} = \begin{bmatrix} 0.2 & 0.5 & 0.2 \\ 0.5 & 0.8 & 0.5 \\ 0.2 & 0.5 & 0.2 \end{bmatrix}; \quad \mathbf{W} = \begin{bmatrix} 2 & 5 & 2 \\ 5 & 8 & 5 \\ 2 & 5 & 2 \end{bmatrix}$$

$$\text{Case RD : } \mathbf{P} = \begin{bmatrix} 0.2 & 0.8 & 0.2 \\ 0.8 & 0.5 & 0.8 \\ 0.2 & 0.8 & 0.2 \end{bmatrix}; \quad \mathbf{W} = \begin{bmatrix} 2 & 8 & 2 \\ 8 & 5 & 8 \\ 2 & 8 & 2 \end{bmatrix}$$

The figures were chosen somewhat arbitrarily but intending to reflect the factors playing into the system. Seventy five generations were simulated under the conditions established above starting from a generation ( $G_0$ ) in Hardy-Weinberg equilibrium, both for the  $A$  and the  $B$  loci, i.e. the initial allelic and genotypic frequencies were  $f(A_1)$  in  $G_0 = p_0$ ,  $f(A_2)$  in  $G_0 = q_0$ ,  $f(B_1)$  in  $G_0 = r_0$  and  $f(B_2)$  in  $G_0 = s_0$ . We have studied  $11 \times 11 = 121$  different population structures (i.e.,  $p_0 = 0, 0.1, 0.2, \dots, 0.9, 1$  and  $r_0 = 0, 0.1, 0.2, \dots, 0.9, 1$ ); they are represented in Fig. 1. We have plotted the  $G_{75}$  population structures considering almost the entire range of values (0.0001 through 0.9999) for  $p_0$  and  $r_0$  for each of the 8 cases (Figs. 2–9).

Cases A

This is a case of average advantage for heterozygotes, both for attractiveness and fitness gain (see matrices  $\mathbf{P}$  and  $\mathbf{W}$ ). The conflict (CA) induces the formation of  $A_1A_1-B_2B_2$  and  $A_2A_2-B_1B_1$  associations while in  $\mathbf{W}$  such combinations produce low aptitude values in the corresponding pollinator genotypes. For example,  $A_1A_1$  plants take advantage from high frequencies of  $B_2B_2$  pollinators because these pollinators are their most frequent visitors ( $p_{13}$ ). But  $B_2B_2$  pollinators, in turn, take advantage of high frequencies of  $A_2A_2$  plants because these are the most “rewarding” to them ( $w_{33}$ ). So, a dynamic equilibrium [22] is generated from that

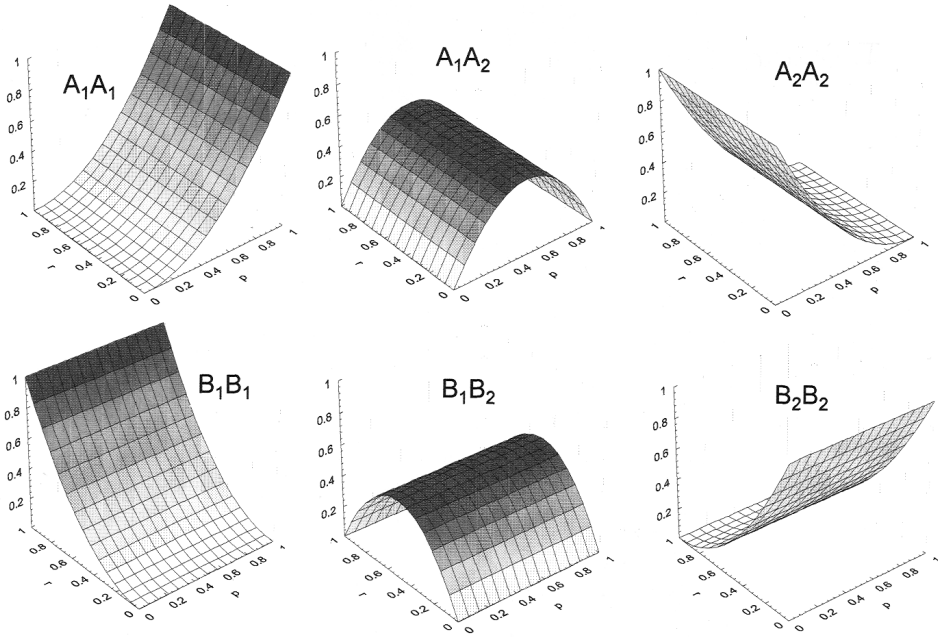


Fig. 1. Genotypic frequencies ( $z$  axis) at  $G_0$  (initial generation) as a function of the allelic frequencies both for plants ( $p_0$ ;  $x$  axis) and pollinators ( $r_0$ ;  $y$  axis).

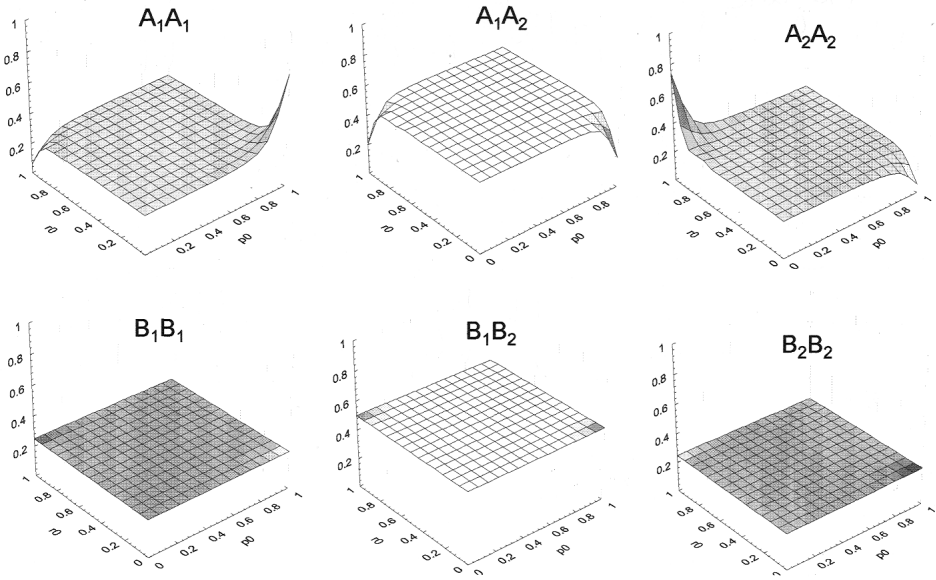


Fig. 2. Genotypic frequencies ( $z$  axis) at  $G_{75}$  (final generation) as a function of the allelic frequencies at  $G_0$  (initial generation) both for plants ( $p_0$ ;  $x$  axis) and pollinators ( $r_0$ ;  $y$  axis) corresponding to case CA.

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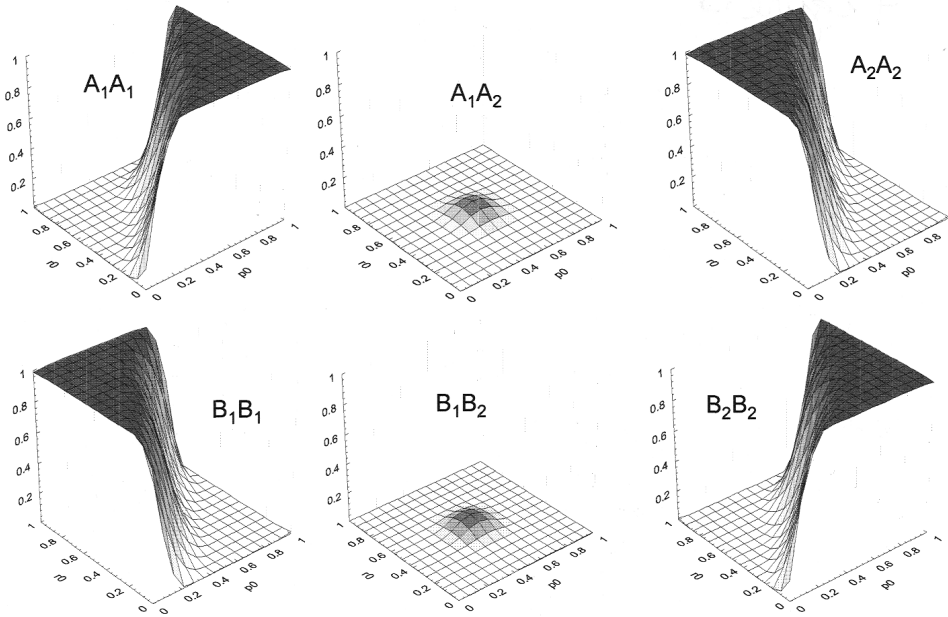


Fig. 3. Genotypic frequencies ( $z$  axis) at  $G_{75}$  (final generation) as a function of the allelic frequencies at  $G_0$  (initial generation) both for plants ( $p_0$ ;  $x$  axis) and pollinators ( $r_0$ ;  $y$  axis) corresponding to case RA.

conflicting trade-off directly affecting genotypic frequencies both of plants and pollinators. Leaving the system to operate under these rules over 75 generations stable structures are reached (Fig. 2). At first sight it may be observed a notorious similarity between the responses in plant populations and in pollinator populations. Comparing them with the initial structures (Fig. 1) it may be observed that all the populations stabilize in the same genotypic structure ( $[1/4; 1/2; 1/4]$ ) *no matter their respective initial structure*. Plant populations under the conflicting regime (CA) show a low degree of memory (i.e., some dependence on the initial conditions) especially for high allelic frequencies, say, for  $p_0 > 0.9$  and  $r_0 > 0.9$ . The main difference between plant and pollinator population is in the stabilization time, i.e., the generation in which the genotypic frequencies stop changing (we have taken a 5 decimal points accuracy). Plant populations stabilize in  $G_{57}$  (except for 2 extreme situations with different frequencies, also approaching the equilibrium structure  $[0.25; 0.50; 0.25]$  but at a much lesser rate). Pollinator populations, in turn, stabilize around  $G_{40}$ , i.e., they reach the steady structure before the plant populations do. There seems to be an attractor [16], i.e., a given genotypic structure attracting all trajectories without regard of their respective initial structures (Fig. 2).

The reinforcing case (RA) shows a similar behavior in both types of organisms; there is strong memory of the initial structure but it is modulated by each other species. It may also be observed a very strong decrease in the frequency of het-

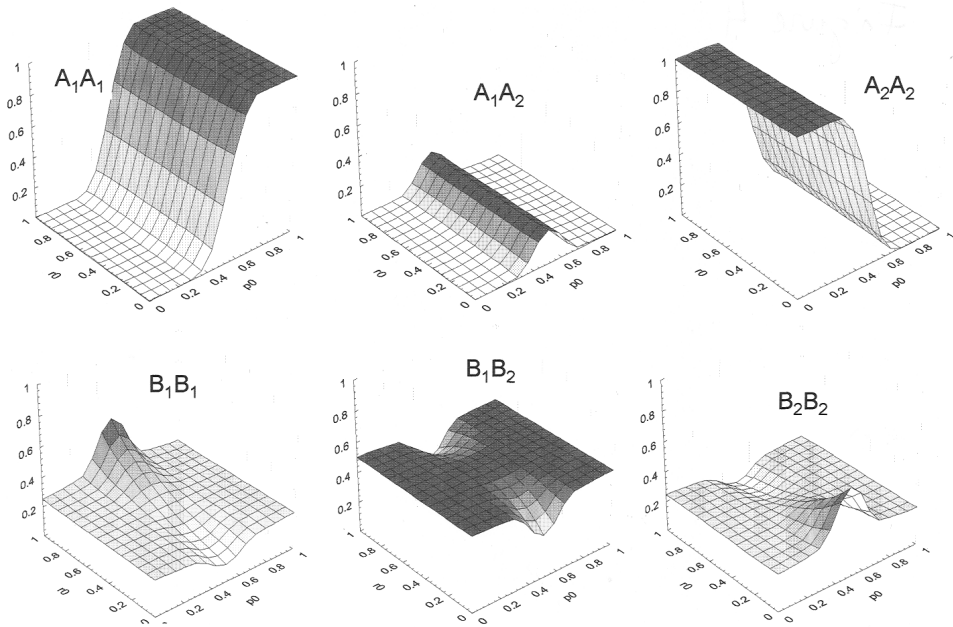


Fig. 4. Genotypic frequencies ( $z$  axis) at  $G_{75}$  (final generation) as a function of the allelic frequencies at  $G_0$  (initial generation) both for plants ( $p_0$ ;  $x$  axis) and pollinators ( $r_0$ ;  $y$  axis) corresponding to case CB.

erozygotes (Fig. 3). Only a tiny fraction of populations with plant allelic frequencies equalling those of pollinators remain in intermediate genotypic frequencies. Both species populations stabilize around  $G_{34}$ , i.e., they attain equilibrium at the same rate. The bound conditions given by matrices  $\mathbf{P}$  and  $\mathbf{W}$  tend to reinforce each other, i.e., when a pollinator is attracted by plants of a given genotype, the obtained fitness gain from those plants is directly proportional to that attraction (the figures in matrix  $\mathbf{W}$  are equal to those in matrix  $\mathbf{P}$  multiplied by 10 in all cases). Put another way, pollinators get their highest fitness gains from the flowers that most attract them. In all the cases of reinforcing effects (A, B, C and D), the matrix  $\mathbf{P}$  remains the same as in the corresponding conflicting cases. The differences between both situations take place in the matrix  $\mathbf{W}$ . This case represent, in Stuart Kauffman's words [13], a "freezing" strategy for the plant-pollinator interaction almost without any degree of resilience, even when heterozygote-heterozygote interactions (both for attraction and fitness gain) are high ( $p_{22} = 0.8$ ;  $w_{22} = 8$ ). Thus, the fact that heterozygote-heterozygote interactions are high does not determine per se a resilient behavior in the system.

### Cases B

In case CB the matrix  $\mathbf{P}$  determines the homozygous plants ( $A_1A_1$  and  $A_2A_2$ ) to be the most attractive while the matrix  $\mathbf{W}$  determines that the greatest fitness

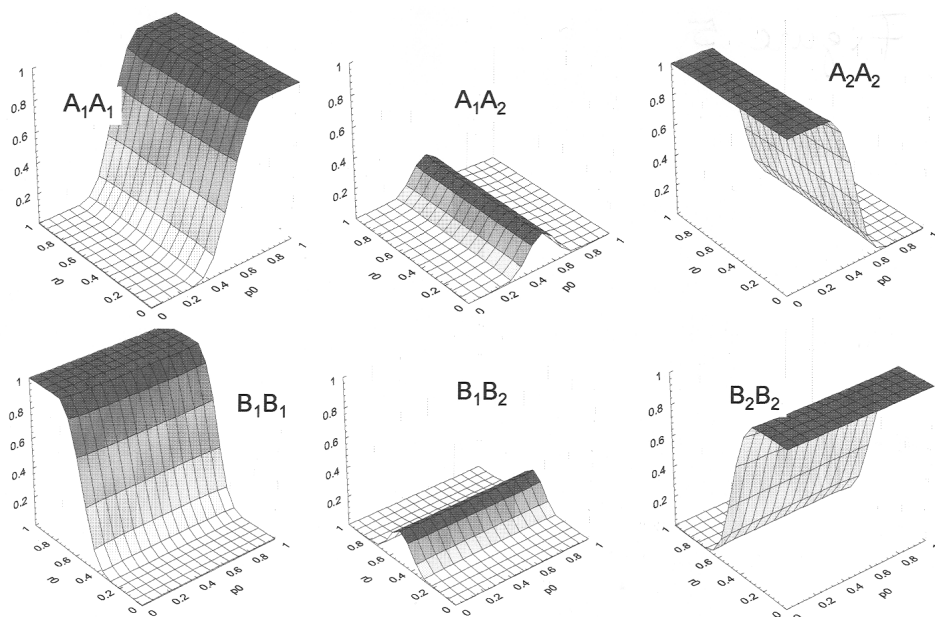


Fig. 5. Genotypic frequencies ( $z$  axis) at  $G_{75}$  (final generation) as a function of the allelic frequencies at  $G_0$  (initial generation) both for plants ( $p_0$ ;  $x$  axis) and pollinators ( $r_0$ ;  $y$  axis) corresponding to case RB.

gain is obtained by pollinators visiting heterozygous plants (especially if they are heterozygotes too), the heterozygous pollinators being the least “visiting” ones. Under these conditions structures are attained (Fig. 4) in which plant populations depend almost completely upon their initial structures and are fully independent upon the pollinator initial structures. Conversely, pollinator populations stabilize in starting-point-independent equilibrium structures (except for some dependence in intermediate values of  $p_0$  [ $0.4 < p_0 < 0.6$ ]). There is a strong tendency towards homozygosis in plant populations and they reach the equilibrium structure around  $G_{22}$ . Pollinator populations reach their equilibrium at  $G_{30}$  and there is an attractor structure around  $r_{30} = 0.5$  (recall that  $r_{30}$  is the frequency of allele  $B_1$  in  $G_{30}$ ). There are high fixation rates [4] for plant populations starting in allelic frequencies out of the intermediate points ( $p_0 < 0.4$  and  $p_0 > 0.6$ ). There is a complete independence from the starting structure of the pollinator population. The attractive effect of homozygous plants is stronger on the plant populations than on those of pollinators. The effect of fitness gain, in turn, is much stronger on the pollinator populations, which retain some memory of their starting structure in the cases of interaction with plant populations starting in a narrow strip of intermediate allelic frequencies (note the depressions and elevations in such coordinates in Fig. 4).

With respect to the reinforcing case (RB), plant populations show the same behavior as in CB. Plants reach their equilibrium frequencies around  $G_{22}$ . Pollinator

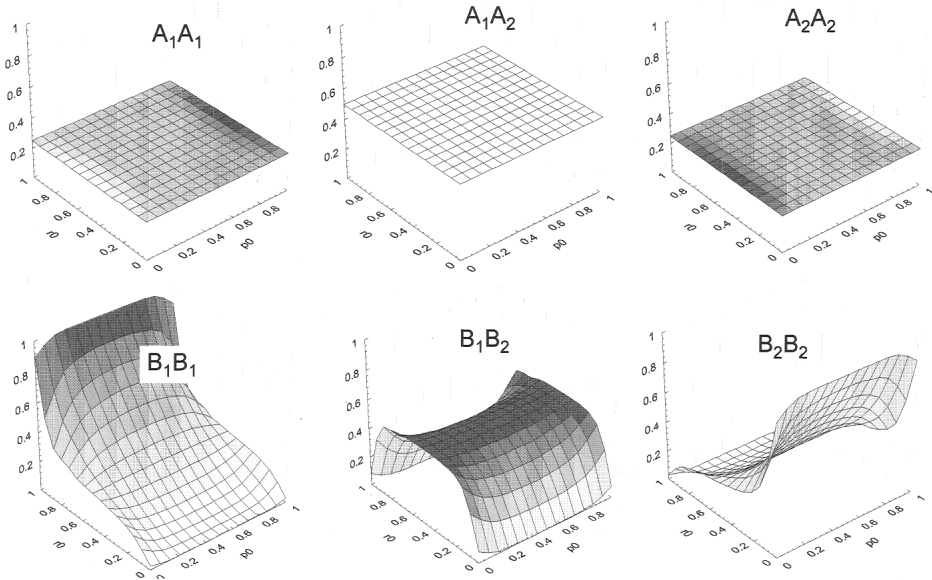


Fig. 6. Genotypic frequencies ( $z$  axis) at  $G_{75}$  (final generation) as a function of the allelic frequencies at  $G_0$  (initial generation) both for plants ( $p_0$ ;  $x$  axis) and pollinators ( $r_0$ ;  $y$  axis) corresponding to case CC.

populations also behave as the plants (Fig. 5): they show a neat tendency toward homozygosis (except for a narrow range in intermediate allelic frequencies) and they reach their “freezing” structures very rapidly ( $G_{12}$ ). It may be observed, by and large, behavior independence between plants and pollinators, the final structures depending strongly upon their initial structures. This is the strategy showing the highest degree of independence in the behavior of genotypic frequencies at equilibrium. The genotypic structures show a strong memory of the initial structure both for plants and insects and almost total independence of each other. The lack of association between plants and pollinator frequencies is greater than in cases A.

### Cases C

The conflicting case (CC) results in a final structure somewhat inverse to that in case CB: all plant populations reach the same dynamic equilibrium around  $G_{33}$ . The pollinator populations retain some memory of their initial structure, except for some extreme values accounting for less than 10% of the total values; so early as  $G_5$  the population frequencies are much the same as in  $G_{75}$ . The superiority of heterozygotes in attracting pollinators has a much stronger effect on the plant populations than on the pollinator ones. Values of fitness gain, in turn, have a little effect (Fig. 6). As in all other cases, memory of past states indicates lack, or low degree of resilience; in case the system suffers from an injury event modifying its genetic structure, the tendency over next generations will be to “recall” this new

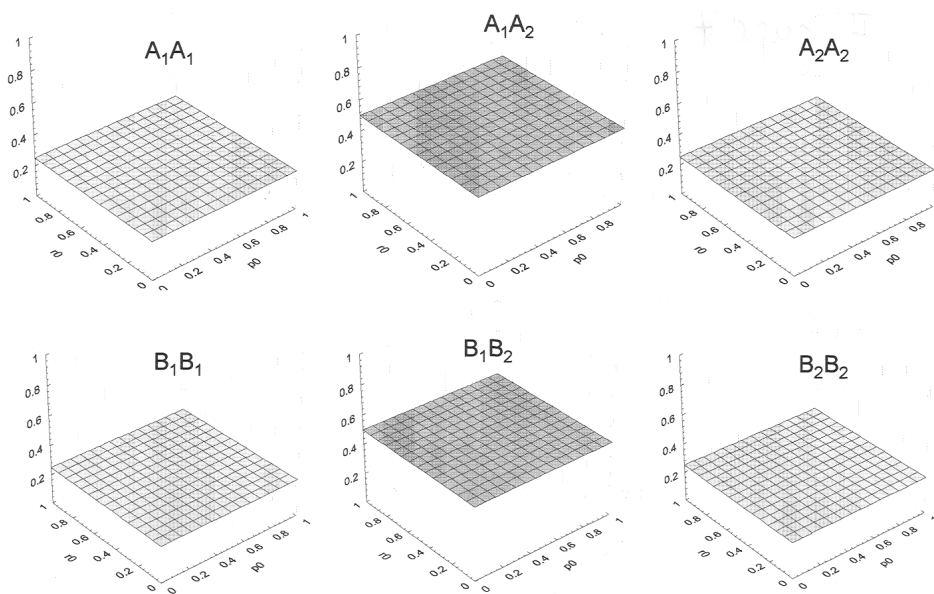


Fig. 7. Genotypic frequencies ( $z$  axis) at  $G_{75}$  (final generation) as a function of the allelic frequencies at  $G_0$  (initial generation) both for plants ( $p_0$ ;  $x$  axis) and pollinators ( $r_0$ ;  $y$  axis) corresponding to case RC.

starting structure.

In case RC both groups of organisms reach a dynamic equilibrium; the plants in  $G_{33}$  and the pollinators in  $G_{16}$  (Fig. 7) stabilizing in a  $[0.25; 0.50; 0.25]$  structure. It would be worth to figure out what the behavior of the system may be in case of a severe environmental injury; it would be a genetic resilience proof.

RC is the most polymorphism-conservative strategy. Both populations reach equilibrium in intermediate genotypic frequencies and a true and clear reinforcing effect takes place between probabilities of attraction and fitness gained, as may be expected from  $p_{ij}$  and  $w_{ij}$  that clearly support heterozygote-heterozygote interactions (Fig. 7). Therefore, this is a very resilient strategy.

### Cases D

Also here there is a tendency to intermediate frequency equilibrium both for plants and pollinators, but at a much lower rate; in all cases populations of both species stabilize around  $G_{65}$  (Figs. 8 and 9). The memory of the system is higher than in Case C. There also seems to be here a strong influence of the attraction probabilities (matrix  $\mathbf{P}$ ) on both kinds of organisms. Fitness gains, with their marked support to homozygote-homozygote interactions, do not make important differences with respect to the final equilibrium frequencies. Thus, even though these cases lead the system to a dynamic equilibrium state, the low rate of progress toward such state decreases the resilience of the system.

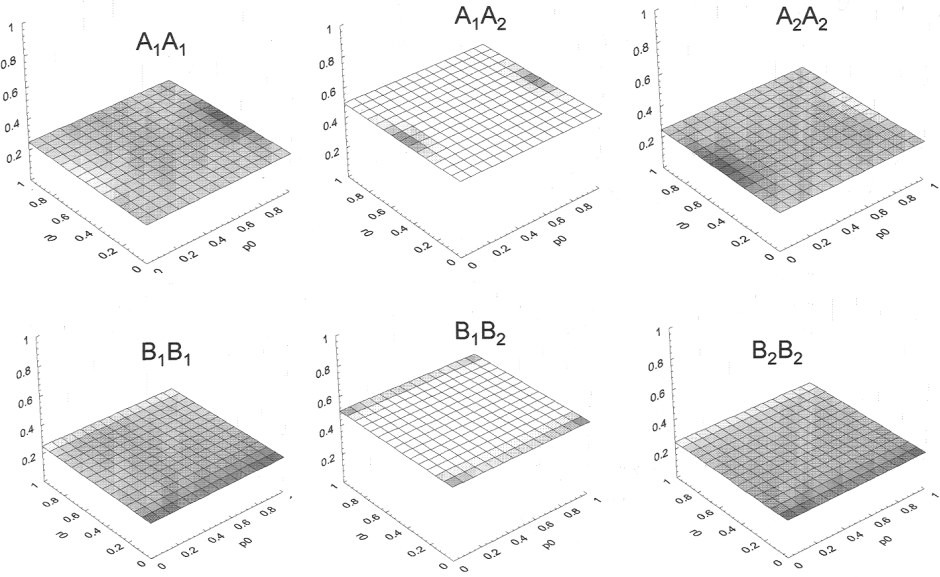


Fig. 8. Genotypic frequencies ( $z$  axis) at  $G_{75}$  (final generation) as a function of the allelic frequencies at  $G_0$  (initial generation) both for plants ( $p_0$ ;  $x$  axis) and pollinators ( $r_0$ ;  $y$  axis) corresponding to case CD.

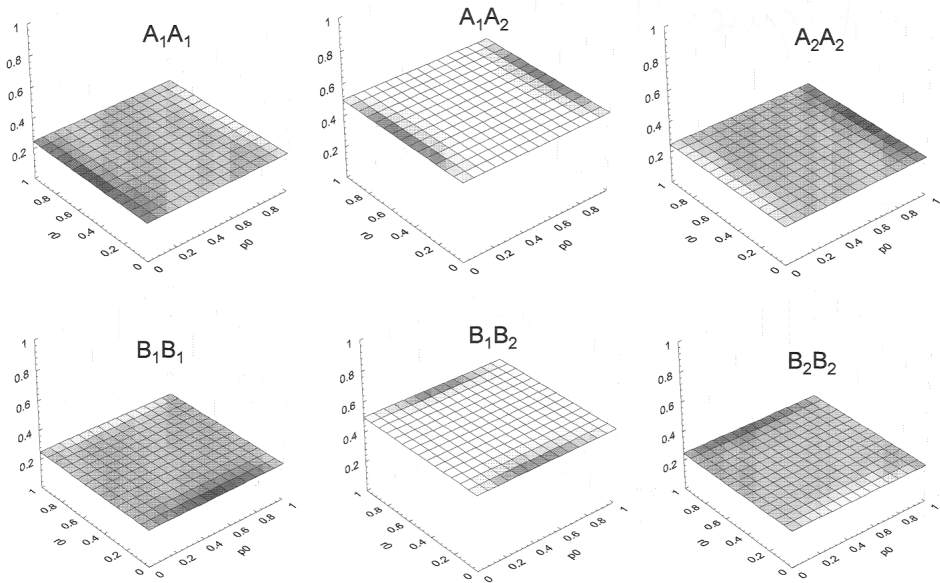


Fig. 9. Genotypic frequencies ( $z$  axis) at  $G_{75}$  (final generation) as a function of the allelic frequencies at  $G_0$  (initial generation) both for plants ( $p_0$ ;  $x$  axis) and pollinators ( $r_0$ ;  $y$  axis) corresponding to case RD.

### 3. Discussion and Conclusions

In the words of Harder and Barrett [9], “. . . the isolation of pollination and mating system biology hinders comprehensive understanding of the function and evolution of floral characters that influence fertility”. In the present study we contribute to revert this situation by dealing with floral attractiveness and floral reward-derived fitness gain of pollinator, i.e., two characters emergent from the flower-pollinator interaction, in a context that enables the assessment of the reproductive value that such traits have for both interacting populations. Even in the limited framework established by our assumptions and by the use of a simple genetic model, as an outcome of our simulations we were able to generate an array of population structures different enough as to reach some conclusions.

*System resilience.* One very important aspect of these integrated host-pollinator systems is their degree of resilience and, especially, their genetic resilience, i.e., their genetically-based ability to return to a previous state when disturbed. Assuming a genetic system determining the expression of traits such as floral attractiveness or pollinator fitness gain, it is the dynamics of the population genotypic structures that will determine the capability of the system to override fluctuations.

In this respect, we detected some general behavioral patterns in the structure of frequencies obtained at the end of the simulation. One of these may be viewed as a resilient type of structure, which is best represented by the case RC. In it, frequencies are stabilized in intermediate values both for plants and pollinators no matter what the initial allelic frequencies were. Frequencies stabilize near Hardy–Weinberg equilibrium values — when we say “Hardy–Weinberg” values we are not meaning true Hardy–Weinberg equilibrium (we are in the presence of selection, thus violating one of the assumptions of the Hardy–Weinberg postulate) but values numerically equivalent to that of Hardy–Weinberg equilibrium — [22] around  $p(G_{33}) = r(G_{16}) = 0.5$ . This state is clearly induced by the advantageous  $p_{ij}$  and  $w_{ij}$  values corresponding to heterozygotes.

Other similarly resilient structures (i.e., without memory of the initial population frequencies) were obtained in cases CD, RD, CA (for pollinators especially) and CC (for plants only). Overall, in this pattern the  $p_{ij}$  and  $w_{ij}$  seem to determine the populations final fate (genotypes prevail in a way directly proportional to their average attractiveness and pollinators do the same, in a way directly proportional to the average fitness gain). We hypothesize that this type of pattern reflects the typical attraction-reward structure generally observed in nature.

Another pattern is characterized by a pronounced loss of heterozygotes in the final structure, caused by the fixation of the most attractive genotypes at the expense of the least attractive ones, independently of the pollinator’s genotype. The cases CB and RB show this type of pattern. RA shows a strong decrease in the heterozygote’s frequencies — even though both,  $p_{22}$  and  $w_{22}$  are high — probably because (i) the starting frequencies of heterozygotes are never higher than 0.5 and, (ii) the segregation of heterozygotes giving homozygous offspring. There are other

cases in which the  $p_{ij}$  and  $w_{ij}$  values are high (and that for this reason they lead the population to the stable structure above mentioned) but in such cases the  $p_{ij}$  and  $w_{ij}$  values corresponding to the homozygote-homozygote interaction are not as high as in RA. As shown in the previous section, cases CB, RA and RB represent the least resilient situations.

*Future prospects.* As genetic determination of floral characters gains more and more experimental support [2, 3, 25, 26], and as the amount and quality of rewards taken by pollinators affects, no doubt, their fitness, any speculation about the genetic basis of resilience will be worth to test in the field.

In this work we put our focus on the structure of host- and pollinators populations, i.e., we only dealt with genotypic frequencies. Another important aspect we feel is worth studying is how population size will be affected by floral attractiveness and reward values. This, we hope, will be achieved through very different sets of  $p_{ij}$  and  $w_{ij}$  values.

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