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What maintains variation in flower accessibility to pollinators in plant communities? A simulation study

Tamar Keasar[1*] and Eric Wajnberg[2,3]

Abstract

Background Flowers in natural plant communities come in many shapes. Flowers with restrictive morphologies are considered complex, because only a subset of pollinators are able to learn how to access their nectar and pollen. Other flowers are easily accessible to diverse pollinating insects, and are regarded as simple. How and why do the two types of flowers coexist in natural plant communities?

We developed a spatially explicit evolutionary simulation framework to explore this question. We modeled the dynamics of two types of flowers ('complex' and 'simple') that differ in accessibility to their simulated pollinators and in food rewards. The flowers are visited by a population of pollinators, which initially possess heritable variation in their ability to learn to forage on the complex flowers. We manipulated the pollinators' flying distances and the flowers' overall density, spatial distribution, and starting proportion of simple flowers. We recorded the resulting dynamics of the two flower types in the community, and of the pollinators' learning rates, over 100 generations.

Results Complex and simple flowers coexisted under all simulated conditions. The steady-state community always contained more simple flowers than complex ones. Complex flowers attained higher frequencies when flowers were highly aggregated than when flower aggregation was low. Long-distance fliers evolved higher learning abilities than short-distance fliers. Pollinator learning abilities, in turn, were positively correlated with the frequency of complex flowers.

Conclusions Frequencies of complex flowers vary among natural plant communities. Our model predicts that this variation is shaped by the plants' spatial distribution as well as by the cognitive abilities of their pollinators. The model generates novel and testable hypotheses for understanding how diversity in flower shapes is maintained in natural plant communities.

Keywords Evolutionary simulation, Flying distance, Flower morphology, Learning, Monte Carlo simulation, Pollination, Spatial aggregation, Spatially explicit model

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Background

Plants and their insect pollinators have a long history of mutualistic, coevolutionary interactions. Multiple plant traits have evolved in response to pollinator-mediated selection over evolutionary time. Examples include flowering phenology, floral display size, scent, color, and shape that are adapted to the anatomical and physiological constraints of pollinating insects [2]. Flower anatomy has received particular attention within the framework

of 'pollination syndromes', which assumes convergent evolution of plant traits that attract specific functional groups of pollinators [8, 19]. For example, large, open, dish-shaped flowers are often associated with beetle pollination [27]. Similarly, the length of floral spurs (spiked projections) and corolla tubes predict the main pollinators of many plants [5].

Flower shapes have traditionally been classified according to their morphological features, such as symmetry and the fusion of floral parts [13]. From a functional standpoint, floral morphologies can be placed along a continuum according to their accessibility to insect visitors [1]. Radially symmetrical, upward-facing, dish-shaped flowers (*e.g.*, buttercups) are highly accessible, and the learning required by pollinators to handle them effectively is typically minimal. These highly accessible flowers are visited by numerous insect taxa or functional groups, and are therefore considered to be generalized. Bilaterally symmetrical flowers, with fused tube-like or lever-like parts, restrict their visitors' landing angle and require the insects to use specific motor routines to access their pollen and nectar. Inexperienced insect foragers require considerable time to interact with such flowers (*e.g.*, lupines), and sometimes fail to feed from them altogether [16, 25]. For pollinators visiting these specialized flowers, flower handling and consequently also foraging performance gradually improve through learning [16, 25]. Such flowers are at the low accessibility end of the continuum and are visited by fewer insect taxa (*e.g.*, [29, 31]). For brevity, we will use the terms 'simple' and 'complex', to denote flowers with high and low accessibility to visitors, respectively, as the extremes of a continuum of phenotypic specialization (*e.g.*, [1]).

Having fewer potential pollinators, complex flowers are predicted to be more rewarding to insect visitors than simple flowers [3]. This can result from stronger selection on complex flowers to produce nectar and pollen rewards that attract pollinators [3] and/or from fewer visitors that deplete the rewards. In support of this general predicted trend, nectar production increases with the flowers' corolla tube length in a worldwide phylogenetically controlled comparison across plant species. Nectar production is also higher in plants with bilateral floral symmetry than in radially symmetrical flowers (Bodner & Keasar, unpublished).

Although complex flowers generally produce higher rewards, it is not straightforward to understand how pollinators learn to handle them. Standard learning theory predicts that behaviors that are rewarding in the short-term are repeated more frequently by the learners [17], compared to when rewards are delayed. Simple flowers provide inexperienced foragers with higher short-term gains than complex flowers (owing to their easier

handling). This raises the question what mediates pollinators' persistence to visit and exploit complex flowers. Previous behavioral work found that bumble bees, which are important pollinators in temperate areas, have a mild innate preference for complex flowers over simple ones [18]. This preference increased when complex flowers provided higher rewards or had colors favored by the foragers [14, 18]. In addition, successful foraging on complex flowers induced bumble bees to try to feed from additional flower species with other complex shapes [15]. A modeling study further suggests that long-lived pollinators, and those active early in the flowering season, gain the highest reproductive success from foraging on complex flowers. Such visitors have sufficient time (in terms of life expectancy or of season length) to learn to handle the complex morphologies and to reap their benefits [12]. These additional mechanisms seem to promote foraging by pollinators on complex flowers.

The studies reviewed above indicate that learning is a key proximate mechanism that allows pollinators to visit and fertilize complex flowers, by reducing the flowers' handling times. This opens new questions at the evolutionary level, such as: how do the pollinators' foraging choices of simple *vs.* complex flowers affect the frequencies and dynamics of different flower morphologies in plant communities? In turn, how do these changes in flower frequencies drive the evolution of pollinator foraging behavior? Are the corresponding dynamics affected by the spatial distribution of the plants in their environment and by the pollinators' mobility?

Pollinator-plant coevolution involves heritable responses of plants to the trait distribution of their pollinators and *vice versa*. The fitness of each partner in the interaction depends on the phenotype of the other partner in a frequency-dependent manner. This interaction structure is readily modeled using evolutionary game theory [23]. Previous studies indeed used the game theoretical approach to predict the coexistence conditions in a two-plant-two-pollinator community [26], to understand why long-tongued bees tend to avoid short-tubed (simple) flowers [21], and to model the extinction risks of rare plant species [10]. The latter model, which incorporated flower morphology, predicts an increase in specialization of foraging pollinators on rare plants as their floral morphological complexity increases. This allows complex flowers to persist at low frequencies in plant communities.

In the present work, we take a similar modeling approach and develop an individual-based evolutionary spatially explicit simulation model. The model tracks the changes in the frequencies of simple and complex flowers in a plant community, and the changes in the capabilities of their pollinators to learn to forage on complex

flowers. This allows us to examine whether the initial frequencies of the two flower types, their density, their spatial patchiness and the pollinators' mobility, affect the plant-pollinator evolutionary dynamics. We tested the following specific hypotheses: (1) Higher encounter rates with complex flowers select for improved learning abilities in pollinators, and (2) floral specialization coevolves with pollinator learning ability, as good learners preferentially visit and pollinate complex flowers. We therefore predict that high pollinator flying abilities, flower densities, flower patchiness, frequencies of complex flowers, or a combination of these factors, will increase the pollinators' encounters with complex flowers and select for improved learning abilities. This, in turn, will lead to stable and robust higher abundances of complex flowers in the plant community.

Methods
Model framework
The time-scale: The model involves two time-scales, consisting of time steps (short term) and generations (long term). The length of each generation is determined by the pollinators' longevity, corresponds to a flowering season, and varies between generations. 100 generations are modeled.

The spatial scale: The pollinators' foraging environment is represented as a 2D square grid of 1000×1000 cells. Simple and complex flowers are placed in the grid, using a patchy distribution. Each cell can contain a simple flower, a complex flower, or remain empty.

Flower distribution
The locations of the flower patches are randomly determined all over the grid in each generation and the number of flowers is equal in all patches. Flower locations in each patch are drawn randomly from a Normal distribution with a standard deviation of 40 cells and centered on each patch location. The initial proportions p of simple flowers, the total number of flowers N, and the number of patches, are inputs to the model. At the beginning of each simulated generation, the numbers of simple and complex flowers in each patch are drawn from a Binomial distribution with probability equal to p, and we check that the overall proportions of simple and complex flowers in the environment correspond to p and $1 - p$, respectively. The total number of flowers, and the number of patches, do not change over the course of the generations.

Both simple and complex flowers produce a potential food reward that is completely collected by pollinators during a single visit. The potential rewards produced by the two flower types are parameters in the model. Simple flowers produce smaller amounts of food rewards than

complex flowers. Owing to their morphology, handling of simple flowers does not require learning. Thus, foragers that consecutively select rewarding simple flowers experience both constant food intake and handling times. Efficient handling of complex flowers, in contrast, involves a series of visits to the complex flower type. Therefore, handling time declines and the pollinators' ratio of energy intake per time invested increases as the foragers gain experience (see next section for details). Each visit by a pollinator contributes to a flower's reproductive success (see below). To facilitate the interpretation of the results, we model the floral rewards as non-replenishing. Additionally, the model does not include 'illegitimate' visits, such as by nectar robbers.

Pollinator behavior
One hundred insect pollinators of one species are placed randomly in the environment at the beginning of each generation. At the start of the first generation, there is inter-individual genetic variation, drawn from a Uniform distribution, in the pollinators' rate of learning how to forage on (*i.e.*, effectively extract resources from) complex flowers. This generates a neutral starting point for each simulation, where all possible genotypes are equally represented. As in previous work [12], the learning curve of the ability to exploit complex flowers follows a logistic curve. It starts at a lower resource intake compared to what is collected on simple flowers and attains a higher intake rate after the pollinator has visited several complex flowers and learning is completed. The logistic curve is based on the function $c(v) = \frac{K}{1+e^{-(\alpha v - \beta)}} + m$, in which $c(v)$ is the reward obtained from complex flowers after spending v visits on each of them, m is the minimal reward without learning, and K is the maximum additional reward that can be achieved through learning. Hence, $K + m$ is the maximum reward after the learning process is completed. α and β are the shape and position parameters defining the learning process, respectively. β corresponds to the inflexion point of the logistic curve, and the pollinators' learning rate is defined as $1/\beta$. The earlier the inflexion point, the faster are pollinators able to learn how to forage on complex flowers, as they require less time to reap the higher possible reward on such flowers.

At each time step during a generation, each forager perceives the location (and thus distance) of the closest simple and complex flower, regardless of the flowers' depletion level. Then, the tendency to visit a complex flower rather than a simple one increases probabilistically (1) with a decreasing flying distance to the complex flower; (2) if the pollinator evaluates complex flowers as more rewarding that simple flowers, based on its past reward harvesting; (3) if it had recently visited depleted

simple flowers, hence evaluates them as low in terms of the reward they provide; (4) if it had not recently visited a depleted complex flower. Appendix 1 details how the simulation calculates the probability of each pollinator being attracted by a complex or a simple flower at each time step of its foraging process. Once a target flower is identified, the pollinator moves in the direction of this flower, hence the location of the target flower determines the direction of flight. The flying distance, on the other hand, is drawn from a normal distribution, whose mean is an additional parameter of the model. If the drawn distance is equal to or larger than the distance to the target flower, the pollinator lands on the target flower. Otherwise, it lands on an empty grid cell, nearest to its pre-decided flying distance. The probabilistic flower selection process is then repeated in the next time step.

For the sake of simplicity, the pollinators are assumed to be solitary and not to be central place foragers. That is, they do not provision colony members with food and do not return to their original location after foraging. Upon arriving at a flower, the forager collects the food reward instantaneously in the arrival time step. If several individuals land simultaneously on the same flower, a single one, drawn randomly, collects all the food resources. A flower recently visited by a pollinator has a low chance to be revisited immediately, but progressively recovers its attraction to the pollinator after several other flowers have been visited. Marking visited flowers with repellent scents that decay non-linearly over time, a well-documented behavior of pollinators, is a potential mechanism that reduces such revisits [9, 28]. Each pollinator has a set foraging lifespan, after which it dies. It may visit numerous flowers during its lifetime. However, following experimental evidence demonstrating a trade-off between learning ability and longevity in bees [7, 11], we imposed a survival penalty on the pollinators in the model, which increases linearly with their learning rate. Each generation stops when the last pollinator has died at the end of its foraging lifespan.

Selection on flowers and on pollinators
The reward collected by each forager and the number of visits to each flower are recorded throughout each generation. Natural selection acts at the end of each simulated generation. It determines the distribution of pollinator learning genotypes in the next generation and the frequencies of simple and complex flowers, respectively. Individual pollinators that collect more food reproduce more, transmitting their learning genotype more frequently to their progeny. We implicitly assume asexual reproduction without recombination and mutation in the pollinator population. Therefore, learning genotypes that are eliminated by selection cannot be recreated later, and

the genetic variance in learning rate within the pollinator population thus progressively declines with time. Flowers fully depend on pollinators to reproduce. They produce progeny in proportion to the number of visits they receive (even if they were depleted when visited). Therefore, the relative frequencies of simple and complex flowers reflect the frequencies at which they are visited.

The genetic composition of the pollinator population and the frequency of both types of flowers at the end of each generation are used to build the following generations. In all simulations performed, 100 generations were always sufficient to attain stable equilibria in the proportion of the two flower types in the environment and in the number of learning genotypes.

The simulated scenarios: parameter settings
To assess how different parameters of the model influence the evolution of the plant-pollinator community, we varied the values of (1) the total number of flowers, (2) the initial proportion of simple flowers, (3) the number of flower patches (a few patches correspond to an aggregated flower distribution, while a large number of patches corresponds to a near-random distribution), and (4) the pollinators' average per-time-step flying distance. We selected two values for each of the four parameters. This resulted in 16 combinations of conditions (Table 1), each of which was replicated 100 times. This set of simulations always predicts coexistence of the two flower types, possibly driven by changes in the flower community composition, evolution of the pollinators' learning rates, the survival cost associated with learning rate, or reward depletion from the flowers (see the Results section). We thus ran additional simulations to disentangle the effects of these factors. The extra simulations were performed for the following scenario: 500 flowers with a 0.2 initial frequency of simple flowers, flowers distributed over five patches, and pollinators with an average flying distance of 5.0 (see Table 1). To assess whether the pollinators' learning-associated mortality might favor low learning rates and consequently increase their foraging on simple flowers, we eliminated the survival penalty. In a second set of simulations, we applied immediate refilling of visited flowers (*i.e.*, removed reward depletion) and found that the two flower types no longer coexisted (see Results). This raised the question whether reward depletion promotes coexistence by favoring rare flower types, by modifying the pollinators' learning rates, or both. We addressed this question through simulations that either fixed the frequencies of the two flower types (*i.e.*, prevented flower evolution) or eliminated evolution of the pollinators' learning abilities. Simulations were replicated 100 times for each of these additional combinations of conditions.

Table 1 Parameter values used in the simulations. The number of flower patches defines the aggregation pattern of the flowers. Using the combination of parameters typed in bold letters, we performed additional simulations to identify the factors that allow coexistence of simple and complex flowers. These simulations involved fixed flower frequencies, fixed pollinator learning rates, no learning-survival trade-off, or no depletion of floral rewards

Parameter	Values used in the simulations
Parameters for which different values were tested	
Total number of flowers	**500**, 1000
Initial proportion of simple flowers	**0.2**, 0.8
Number of flower patches	**5**, 100
Mean of the distribution of the pollinators' flying distances at each time step (expressed in number of cells in the grid)	**5.0**, 20.0
Parameters that remained fixed	
Grid size	1000×1000 cells
Number of generations	100
Number of pollinators at each generation	100
Standard deviation of the distribution of the pollinators' flying distances at each time step (expressed in number of cells in the grid)	5
Reward on each simple flower (arbitrary unit)	50
Parameter of the learning curve describing the reward on complex flowers (see text)	$K = 100, \alpha = 0.45, m = 10$
Initial genetic variation in the parameter β	Uniform distribution in the $[1; 30]$ interval
Lifespan of each pollinator. Linearly correlated to the learning rate	Range $[68; 300]$ time steps

Analysis of the model's outputs

We calculated the mean values of the 100 replicates of each of the simulated scenarios with their associated standard errors across the simulated generations. We used a type I analysis of variance at the last generation of the simulation to evaluate how flower numbers, the initial proportion of simple flowers, the flowers' patchiness, and the pollinators' average flying distance affect the output variables. The ANOVA model included the main effects without interactions.

Results

Simple and complex flowers coexist in the environment

Both flower types persisted in all simulated scenarios, but simple flowers predominated: their average frequencies at generation 100 in the different scenarios ranged from 0.51 to 0.88 (Fig. 1). Since complex flowers can rapidly provide higher rewards than simple flowers, it is somewhat surprising that simple flowers were not outcompeted by the complex ones after several generations of selection. A possible explanation could be the fact that the learning rate of the pollinators is associated with a corresponding linear decrease in their survival in the model. In fact, removal of the survival penalty reduced the steady-state mean proportion of simple flowers from 0.60 to 0.50 (Fig. 2; 'baseline' *vs.* 'no learning penalty').

Another possible explanation concerns the role of an emergent negative frequency-dependent feedback loop in maintaining the coexistence of both flower types. Such

a process could operate through flower depletion that changes the profitability of simple and complex flowers and leads to modified flower preferences by the pollinators. For example, in a community dominated by simple flowers and by pollinators that specialize on them, depletion of the simple flowers' rewards can render them less profitable than the rare complex flowers. This would generate a selective advantage to pollinators with high learning abilities that are able to feed on complex flowers and that promote their pollination, increasing the frequencies of complex flowers in the community. A complementary process would then increase the fitness of simple flowers when rare and favor lower learning abilities for pollinators. Consistent with the possible contribution of reward depletion to coexistence, the proportions of reward-depleted flowers exceeded 0.7 after 200 time-steps in all simulated scenarios. Moreover, eliminating reward depletion prevented coexistence, as rare simple flowers (initial frequency 0.2) went extinct (Fig. 2). Conversely, when we eliminated flower depletion in a scenario with a high (0.8) initial frequency of simple flowers, these flowers became fixed in the plant community (data not shown). However, the fitness of the two flower types (determined by the number of pollinator visits) did not clearly correlate with their frequencies in the plant community (results not shown). This differs from what is expected under negative frequency dependence.

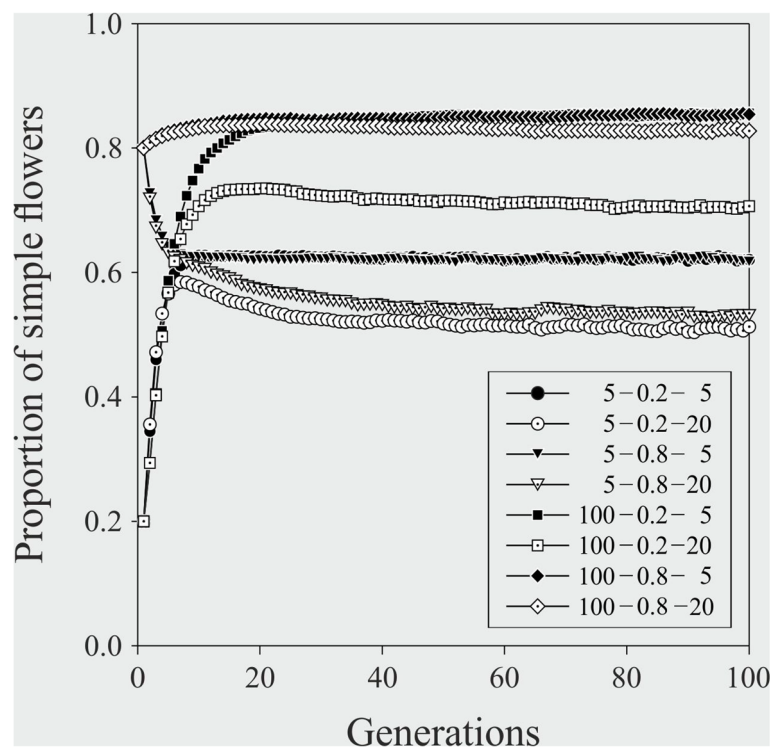Pollinator learning rates were higher when the frequency of simple flowers was fixed at their initial

Fig. 1 Mean proportions of simple flowers over 100 generations for the simulated scenarios. The numbers in the legend refer to the number of patches, the initial proportion of simple flowers, and the pollinators' mean flying distance. 5 and 100 patches correspond to high and low flower aggregation, respectively. The plots show average values for eight pairs of situations that differ in the total number of flowers (500 or 1000), and error bars are not plotted, for better readability

frequency than when flower frequencies were free to evolve (Fig. 3). When the pollinators' learning evolution was eliminated, the steady state learning parameter was fixed at ∼ 0.1. It increased to ∼ 0.3 when learning was allowed to evolve (Fig. 3). Nevertheless, complex and simple flowers coexisted even when learning abilities were fixed (Fig. 2), suggesting that flower depletion has a stronger effect on the coexistence of the two flower types than learning evolution.

Flower aggregation favors complex flowers

The steady-state frequencies of simple and complex flowers were mainly affected by the number of flower patches (Table 2). The lowest frequencies of simple flowers (< 0.55 at steady-state) occurred under high flower aggregation (5 patches) and high mean flying distances (20 units/time step). Their highest frequencies (> 0.75 at steady-state) were attained under low flower aggregation (100 patches), at both low (5) and high (20) mean flying distance. Intermediate frequencies of simple flowers (0.6–0.7) were mostly characterized by low (5) flying distances (Fig. 1).

Long-distance flights promote high learning abilities, which favor complex flowers

The pollinators' average flying distance was a significant predictor of the steady-state proportions of complex flowers, but explained a relatively low fraction (9.41%) of the variation in these proportions. On the other hand, flying distance was the main variable that affected learning rates in the last generation, accounting for almost 35% of the total variation (Table 2). Most of the initial 100 learning genotypes were eliminated by selection during the simulation, and only 1–2 genotypes remained in the last generation. The pollinators' mean ± SE learning abilities in the last simulated generation were 0.09 ± 0.03 and 0.44 ± 0.08 for short- and long-distance fliers, respectively (Fig. 4). Learning rate, in turn, was negatively correlated with the proportion of simple flowers ($r = -0.71$ in generation 100, $n = 1600$, Fig. 5). We infer that manipulating the pollinators' flying distance affected their learning abilities, and this in turn influenced the frequencies of complex and simple flowers.

Next, we explored how flying ability might promote the evolution of learning. Shorter-distance fliers initially spent more time in the simulation traveling between
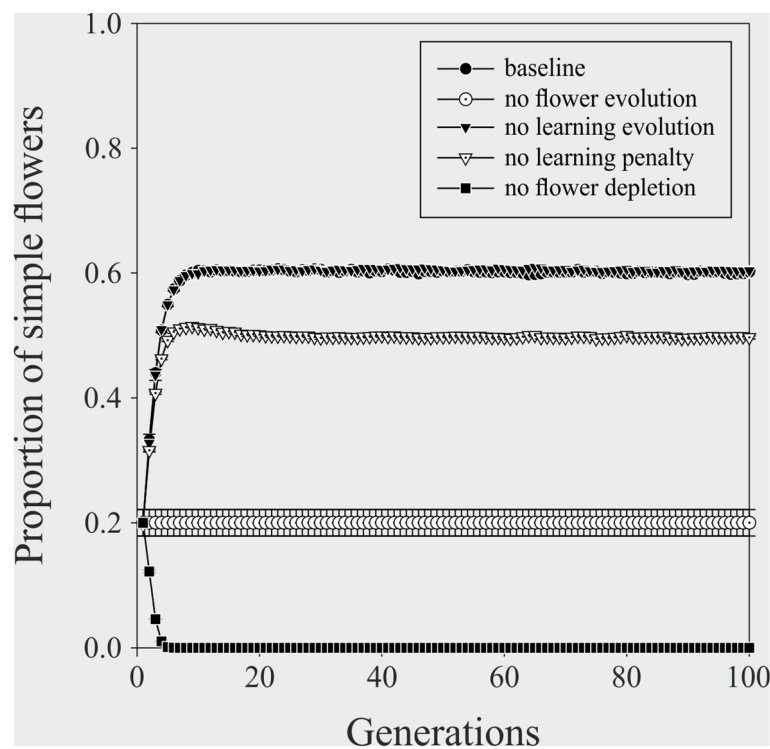
Fig. 2 Mean ± SE frequencies of simple flowers in the plant communities under a baseline set of conditions (500 flowers, initial proportion of simple flowers 0.2, 5 patches, flying distance 5 units/time step), compared with four modified models: fixed frequencies of simple and complex flowers, fixed learning genotypes, elimination of the survival penalty associated with learning rate, and elimination of flower depletion

flowers, with overall fewer visits to both simple and complex flowers. Longer-distance fliers, on the other hand, visited more flowers during their lifetime in the first generations of the simulation, providing the pollinators with more opportunities to learn to handle complex flowers (Fig. 6). Accordingly, the learning abilities of the long-distance fliers increased during the first 20 simulated generations, while the learning abilities of the short-distance fliers declined (Fig. 4). Over the subsequent generations, the evolution of higher learning abilities in the long-distance fliers was accompanied by a decrease in the number of flowers they visited. Similarly, in the short-distance fliers learning rates declined over the generations while the number of visited flowers increased (Figs. 4, 6). The decline in the number of visited flowers may reflect the survival penalty associated with improved learning. Consistent with this interpretation, removal of the survival penalty for pollinators in one of the simulated sets of conditions increased their learning abilities (Fig. 3) and also the number of flowers that they visited per generation (35.0 ± 1.5 flowers in generation 100 with a learning penalty, 69.3 ± 0.3 flowers after elimination of the penalty).

At the simulations' last generation, the average total number of flowers visited per generation was similar for shorter-distance and longer-distance fliers (Fig. 6). It increased with total flower number (Table 2). This effect of flower density is actually not surprising, because foragers can encounter more flowers as the abundance of flowers in their environment increases.

Discussion

Variation in the accessibility of flowers to insect pollinators is a common feature in natural communities of entomophilous plants. We developed a spatially explicit Monte Carlo simulation model to explore how this variation is maintained, and whether pollinators play a role in its preservation. The simulations reproduce a stable and robust coexistence of complex and simple flowers in plant communities under numerous combinations of simulated parameter values. We predicted higher frequencies of complex flower under conditions that increase the pollinators' flower encounter rates and learning abilities. In agreement with our hypothesis, the relative abundance of complex flowers increased with high flower aggregation and with high pollinators' flying distances, which were associated with increased learning abilities. The remaining variables that we explored, the initial frequency of simple flowers and the total number of flowers, had much smaller effects on the frequencies of complex and simple flowers. In the next paragraphs, we discuss how flower
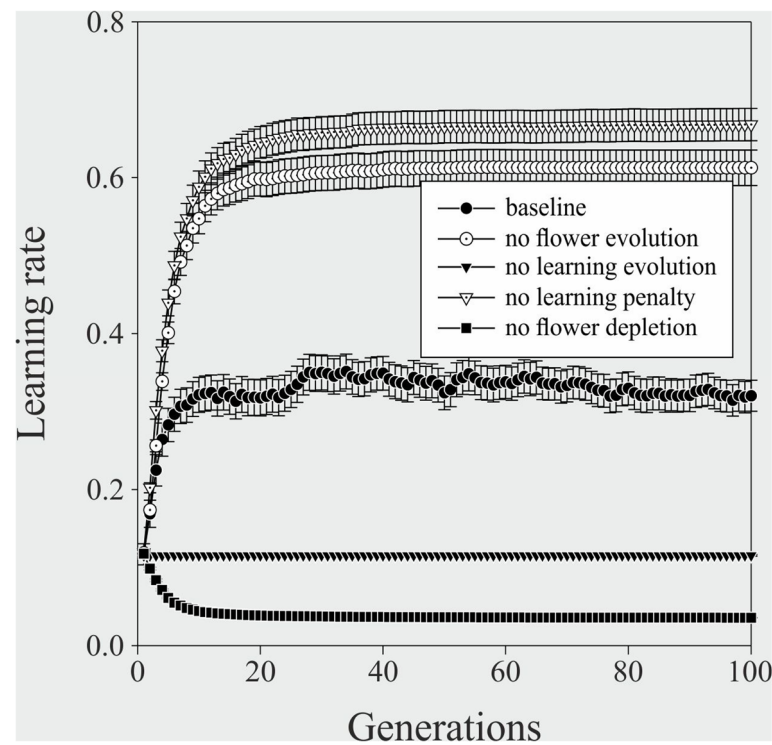
Fig. 3 Mean ± SE values of the learning rate parameter under a baseline set of conditions (500 flowers, initial proportion of simple flowers 0.2, 5 patches, flying distance 5 units/time step), compared with four modified models: fixed frequencies of simple and complex flowers, fixed learning genotypes, elimination of the survival penalty associated with learning rate, and elimination of flower depletion

Table 2 Model coefficients (± SE) of ANOVAs done at the last generation of simulations for the four independent variables, and the corresponding percentage of the variance in the model's output variables, explained by each independent variable (in brackets). ↑ and ↓ denote positive and negative effects, respectively. The number of flower patches defines the aggregation pattern of the flowers in the environment

Explanatory variables	Dependent variables		
	Proportion of simple flowers	Learning rate	Number of flowers visited
Total number of flowers	$1.05 \times 10^{-4} \pm 7.35 \times 10^{-6}$ (3.02) ↑	$-2.45 \times 10^{-4} \pm 2.01 \times 10^{-5}$ (4.19) ↓	2.57 ± 2.02 (25.71) ↑
Initial proportion of simple flowers	$5.87 \times 10^{-2} \pm 6.12 \times 10^{-3}$ (1.36) ↑	$-2.43 \times 10^{-1} \pm 1.68 \times 10^{-2}$ (5.94) ↓	14.55 ± 1.74 (3.09) ↑
Number of flower patches	$2.52 \times 10^{-3} \pm 3.87 \times 10^{-5}$ (62.63) ↑	$-1.95 \times 10^{-3} \pm 1.06 \times 10^{-4}$ (9.64) ↓	0.04 ± 0.01 (0.45) ↑
Mean flying distance of pollinators	$-9.27 \times 10^{-2} \pm 3.67 \times 10^{-3}$ (9.41) ↓	$3.53 \times 10^{-1} \pm 1.01 \times 10^{-2}$ (34.93) ↑	2.28 ± 1.05 (0.21) ↑
Residuals	(23.57)	(42.29)	(70.55)

aggregation and high pollinator learning abilities may increase the proportions of complex flowers in a plant community with both types of flowers. We also consider and discount the role of negative frequency selection in promoting coexistence.

The flowers' spatial distribution was the main factor that affected the relative abundances of the two flower types (Fig. 1, Table 2). We propose that this effect reflects two realistic choice rules that we incorporated into the model. First, pollinators do not perceive flowers that

they had visited recently, and this rule prevents foragers from revisiting the same flowers repeatedly. A pollinator that forages in small patches (5 or 10 flowers/patch) is expected to quickly visit all the complex flowers in the patch, because complex flowers are generally the less common morph (Fig. 1). The forager does not perceive these recently visited flowers as potential targets for revisits for the next few time steps. Instead, it faces a choice between a simple flower that it had not yet visited in its current patch and a complex flower in a different
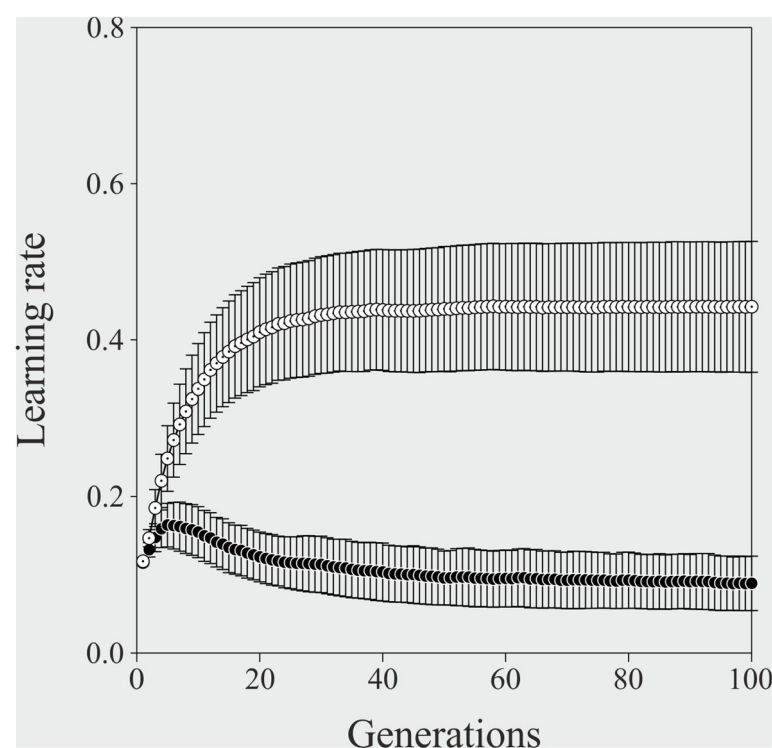
Fig. 4 Learning rate parameter of short- and long-distance fliers over the generations. Means (± SE) are pooled over all 8 combinations of conditions with either a low (5 units/time step; closed circles) or a high (20 units/time step; open circles) flying distances
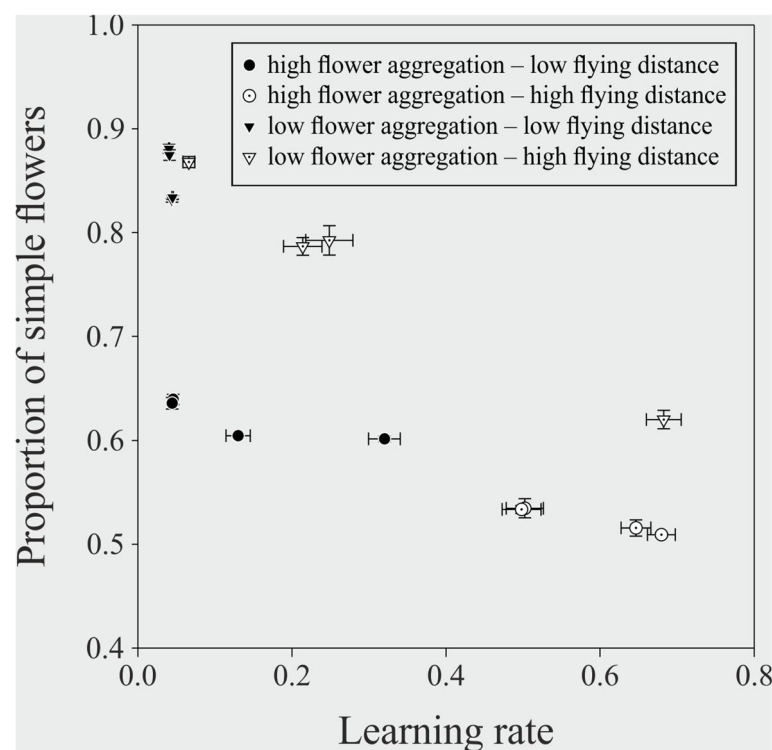

Fig. 5 The mean (± SE) frequencies of simple flowers at generation 100, plotted as a function of the mean (± SE) learning abilities, in the 16 combinations of simulated conditions. Symbols and shading denote different combinations of flower aggregation (low: 100 patches, high: 5 patches) and pollinator mean flying distances (low: 5 units/time step, high: 20 units/time step)
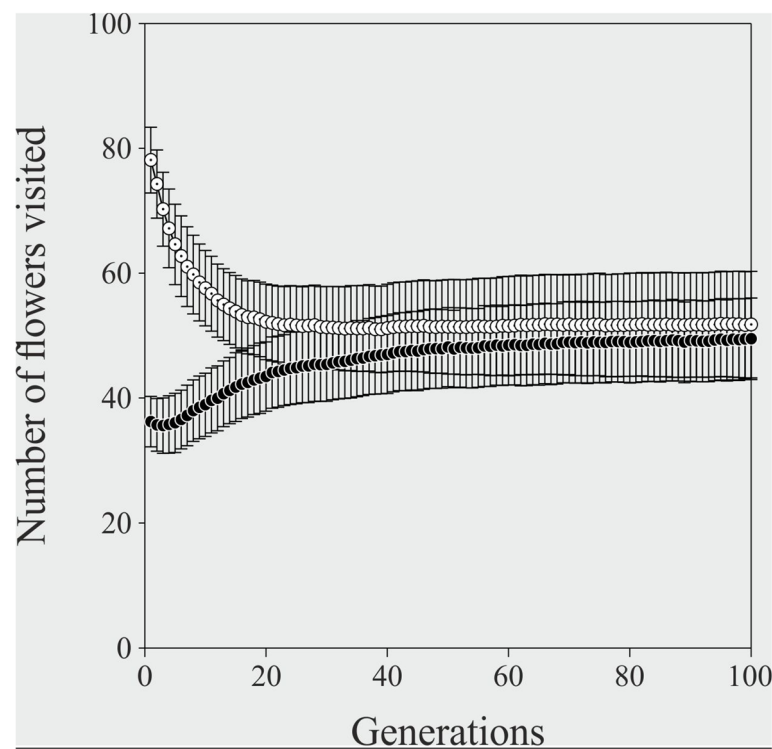
Fig. 6 The number of flowers visited by short-distance and long-distance fliers over the generations. Means (± SE) are pooled over all 8 combinations of conditions with either a low (5 units/time step; closed circles) or a high (20 units/time step; open circles) flying distances

patch. According to another decision rule implemented in the model, pollinators consider both previous reward and flying distance when choosing which flower type to visit. This favors the nearby simple flowers over the complex, more distant ones, under low flower aggregation. This selective advantage of simple flowers is predicted to decline when flowers are aggregated into large patches, because of the larger number of complex flowers available within each patch.

We also considered a negative frequency-dependent selection process, driven by faster reward depletion in the common flower type than in the rare one, as a mechanism of coexistence. In support of this possibility, elimination of flower depletion led to extinction of the rare flower type. However, the fitness of both flower types did not show a clear negative correlation with their frequency in the plant community, as would be expected under negative frequency dependence. This suggests a stronger role for reward depletion than for negative frequency dependence in promoting coexistence of simple and complex flowers.

The frequencies of complex flowers also increased when the pollinators' flying distance was high. This effect seems to be indirect, and mediated through an increase in learning abilities of long-distance fliers. Higher learning abilities, in turn, result in more visits to complex flowers and increase their fitness (Fig. 5).

Figure 5 illustrates, among other things, combined effects of flower aggregation and learning rate on the steady-state frequencies of the two flower types. A possible interpretation is that high learning rates reduce the reward-based preference to simple flowers, while high flower aggregation reduces the distance-based preference to these flowers. Hence, simple flowers are least favored when flower aggregation and learning abilities are high, and most favored under conditions of low flower aggregation and learning abilities. When the two effects act in opposite directions (high flower aggregation and low learning rates, or low flower aggregation and high learning rates), intermediate frequencies of simple flower evolve.

Life-history trade-offs may impose constraints on learning abilities in pollinators. For example, brain size was proposed as a limiting factor of associative learning in bees [4]. This can prevent fixation of the highest learning genotypes in the pollinator population, and of the complex flowers in the plant community. Our model implements the trade-off by coupling learning rate with a survival cost, as observed in real situations [7, 11]. Other costs of learning ability (*e.g.*, in terms of

foraging speed [30], or performance in resource-poor environments [24]) would probably have similar effects.

Finally, our model currently includes simplifying assumptions that limit its realism, and that can be relaxed in future work. Further potential development of the model may incorporate more than one pollinator type (*e.g.*, a specialist and a competing generalist species), explicit modeling of nectar *vs.* pollen foraging [20], reward replenishment (nectar) or staggered presentation (pollen), constraints on morphology-reward relationships [6], and central place foraging.

Conclusions

We present a modeling framework to help understand how simple and complex flowers coexist in plant communities. The model generates evolutionary predictions that can be evaluated against observations from natural plant-pollinator communities, as well as behavioral predictions that can be tested in controlled laboratory experiments. At the evolutionary level, the model predicts the frequency of complex flowers to increase with spatial aggregation and pollinator flying distances. These predictions can be tested by comparing floral accessibility features (such a symmetry and depth) and pollinator flight ranges between increasingly fragmented habitats. At the behavioral level, increasing learning abilities are expected to improve pollinators' success in foraging on complex flowers. This prediction can be tested by exposing pollinators to metabolites that interfere with learning and memory (*e.g.*, neonicotinoids; [22]) and measuring the resulting change in their foraging performance on simple *vs.* complex flowers. Such tests will provide further insights on the selective processes that mold flower shapes.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12862-025-02380-0.

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│ Supplementary Material 1   │
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Authors' contributions
T.K. conceived the project, E.W. designed and coded the model, both authors analyzed and interpreted the results, and wrote the paper.

Data availability
All simulation results are available at https://tamarkeasarlab.weebly.com/data-sets.html.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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Publisher's Note

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