



## Specialized nursery pollination mutualisms as evolutionary traps stabilized by antagonistic traits

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### ABSTRACT

We examine the conditions for the transition from antagonism to mutualism between plants and their specialists nursery pollinators in a reference case which is the *Trollius europaeus*–*Chiastocheta* interaction. The mechanistic model we developed shows that a specialization of *T. europaeus* on *Chiastocheta* could be the result of an attempt to escape over-exploitation by closing its flower. The pressure for such an escape increases with the parasite's frequency and its pollination efficiency but decreases in the presence of alternative pollinators. The resulting specialization is a priori an unstable one, leading either to strong evolutionary oscillations, or to evolutionary suicide due to over-exploitation of the plants. It becomes stable if the plants develop a defense mechanism to regulate their parasite's population size and limit seed-exploitation. The development of a counter-measure by the latter can destabilize the mutualism depending on the costs linked to such a trait. On the other hand, we find that a specialization on a purely mutualistic basis would require a preexisting high diversity of flower-opening within the population.

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### 1. Introduction

Mutualism arises when interacting partners derive more reciprocal benefits than costs from the interaction. However, each partner being selected for increasing its net benefit by decreasing its costs, mutualisms are better seen as reciprocal exploitation mechanisms, which can lead to instability of the interaction (Bronstein, 2001a). Understanding the conditions that promote the transition from antagonism to mutualism and its stable persistence over evolutionary time scales has stimulated much empirical and theoretical work, including in nursery pollination systems. In these systems, the insect oviposits in the flower it pollinates, while its offspring develops by feeding on the developing seeds. Both species rely on the produced seeds for their reproduction, raising a plant–insect conflict of interest. The flower is the major interface between plant and insect, with selection acting on floral traits to increase pollination benefit, but also to reduce larval seed consumption. Indeed, several defense

mechanisms against mutualistic partners have been described in nursery pollination systems, including massive flower production followed by random abortion (Holland et al., 2004a), selective abortion of over-parasitized fruits (Pellmyr and Huth, 1995; Jolivet and Bernasconi, 2006; Burkhardt et al., 2009), chemical defense produced by plants to limit larval seed predation (Ibanez et al., 2009b; Gallet et al., 2007), but also pre-oviposition defense mechanisms such as short and curly stigmas obstructing corolla tube entrance in *Silene dioica* (Westerbergh, 2004) and long styles preventing oviposition in figs (Anstett et al., 1997). Given the widespread occurrence of antagonistic traits within mutualisms, one may wonder how these traits have evolved during the transition from parasitism to mutualism, and whether they are factors of stability or instability in mutualisms.

One of the aims of this work was to examine how the evolution of an antagonistic trait against a given nursery pollinator and the evolution of a counter-measure by the pollinator stabilize or destabilize the plant's specialization on that pollinator. Our reference case was the nursery pollination system involving the European globe-flower *Trollius europaeus*, in the following sections to be called *plant*, passively pollinated by *Chiastocheta* flies, in the following sections to be called *pollinators*, whose larvae develop only on globe-flower seeds. It is an example of a direct positive pseudoreciprocity mutualism (Bshary and Bronstein, 2011). The genus *Trollius* (Ranunculaceae) is a hermaphroditic, perennial species complex showing an extraordinary floral diversification across its geographical range. It grows in moist

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meadows in mountains in Europe, Asia and North America. Flowers can be flat, white and scentless (in North America), more or less bowl shaped, yellow, lilac or purple in different parts of Asia, or totally closed, yellow, and odorless in Europe. The closed shape of the flower in Europe is unique in the genus, and the European globeflower *T. europaeus* is the only species in the genus to be exclusively pollinated by *Chiastocheta* flies (Anthomyiidae). These small flies feed, mate, and lay eggs on *T. europaeus*, and the larvae develop only on the host-plant seeds. The *T. europaeus*–*Chiastocheta* flies interaction is, therefore, one of the few examples of extremely specialized reciprocal interaction. In contrast to other known nursery pollination mutualisms (e.g., the fig–fig wasps and the yucca–yucca moths mutualisms), this specialization is recent as all the other species in the genus did not evolve such specialization even though most are parasitized by *Chiastocheta* flies (Després et al., 2003). The traits involved in the specialization are the closed flower shape (Ibanez et al., 2009a) and the emission of volatile compounds (Ibanez et al., 2010). The antagonistic trait able to limit the costs imposed by the larvae is the accumulation of a chemical toxin in the carpel walls (Gallet et al., 2007; Ibanez et al., 2009b). Generalist *alternative pollinators* such as bumblebees and hoverflies are present in natural populations but cannot enter closed flowers (Jaeger et al., 2000; Ibanez et al., 2009a), thereby exerting a selection pressure towards flower opening (Ibanez and Després, 2009).

We wondered whether specialization took place on a mutualistic basis or rather resulted from an attempt on behalf of *T. europaeus* to avoid over-exploitation by *Chiastocheta* flies by closing its flower. We further tested the hypothesis that the evolution of a (chemical) defense stabilized this specialization on *Chiastocheta* flies because it reduces the predation costs imposed by its larvae. Finally, we tested how a counter-measure on behalf of the larvae such as toxin resistance could put this stability at stake. For our investigations, we modeled and simulated the coevolution of a nursery plant–pollinator system (referred to as *coalition*) with respect to five traits: first, flower morphology characterizing the degree of specialization of the plant to its specialized pollinator, second, a defense mechanism on behalf of the plant against larval seed-parasitism, third, resistance against this defense on behalf of the pollinators, fourth, pollinator flower-preference for feeding, mating and ovipositing and fifth, the degree of tolerance towards flowers with a morphology differing from the preferred one.

## 2. Material and methods

In the following, we present the general framework of the mathematical model, its specification to our system of interest and its numerical implementation in the evolutionary-dynamical simulations used to investigate the questions raised in the introduction. The model is in principle an ecological one, describing the population dynamics of the interacting partners. It obtains an evolutionary-dynamical meaning through the repeated introduction of new interaction partners, random mutants who descend from the already existing species and who may or may not invade the current populations. We provide a brief overview of the main assumptions made concerning the behavior of individuals and a list of all the parameters introduced into the model together with their biological or physical interpretation. A detailed definition and justification of the model, based on the assumptions presented in Section 2.2, is provided for the interested reader in Appendix A.

### 2.1. General framework of the ecological model

Our ecological model is a population-genetical one, built on the assumption of sexually reproducing, hermaphroditic, annual

populations of interacting species, each one comprising a finite number of genotypes. We note  $S$  the set of all considered species. Each genotype of a certain species  $s \in S$  was taken from an abstract genotype space  $G_s$ , fully defining the biology and behavior of the carrying individual. We supposed that at each time  $t \geq 0$ , the current environment influencing the ecological dynamics can be characterized by the current frequency  $\mathcal{N}_s(g)|_t \geq 0$  of each genotype  $g \in G_s$  of each species  $s \in S$ .

We chose a discrete-time model because an iterative map seemed more easily derivable from mechanistic considerations. The frequency  $\mathcal{N}_s(g)|_{t+1}$  of a genotype  $g \in G_s$  at time  $(t+1)$  depends solely on the frequencies  $\mathcal{N}_{\tilde{s}}(\tilde{g})|_t$  of every genotype  $\tilde{g} \in G_{\tilde{s}}$  of every interacting species  $\tilde{s} \in S$  at time  $t$ . We consider a stochastic dynamics and conduct a mean field approximation to arrive at expressions for the expected values of the vectors  $\mathcal{N}_s|_{t+1}$  at time  $(t+1)$  depending solely on their expected values at time  $t$ . Thus, the equations we present below describe the iterative dynamics in the phase space of all possible frequency vectors  $\mathcal{N}_s|_t$  with a finite-number of non-zero entries. In the following we shall note by  $\mathcal{N}|_t$  the ensemble of these frequency vectors.

Let  $\pi_s(g, \tilde{g}, \mathcal{N}|_t)$  denote the probability that a given offspring (e.g., egg, seed) of a given individual of genotype  $g \in G_s$  acting as female, results from the mating with another given individual of genotype  $\tilde{g} \in G_{\tilde{s}}$ , acting as male. Let  $\mu_s(g, \tilde{g}, h)$  denote the probability that a given offspring of two individuals of genotypes  $g, \tilde{g} \in G_s$  is of genotype  $h$  (in the simplest case given by Mendelian laws). Let  $v_s(g, \mathcal{N}|_t)$  be the expected number of offspring produced by an individual of genotype  $g \in G_s$  acting as a female. We decompose the life of an individual into a *juvenile phase*, during which its survival may depend on the current environment, its genotype and that of its *mother*, and an *adult phase* during which its survival, conditional upon the survival of its juvenile phase, depends solely on the environment and its own genotype. Let  $\sigma_s(g, h, \mathcal{N}|_t)$  be the probability that a given offspring of genotype  $h \in G_s$  of a female of genotype  $g \in G_s$  survives its juvenile phase. Let  $\tau_s(h, \mathcal{N}|_t)$  be the conditional surviving probability during its adult phase. Then the expected frequency  $\mathcal{N}_s(h)|_{t+1}$  of the genotype  $h \in G_s$  at time  $(t+1)$  is given by

$$\begin{aligned} \mathcal{N}_s(h)|_{t+1} = & \sum_{g, \tilde{g} \in G_s} \mathcal{N}_s(g)|_t \cdot \mathcal{N}_{\tilde{s}}(\tilde{g})|_t \cdot v_s(g, \mathcal{N}|_t) \\ & \cdot \pi_s(g, \tilde{g}, \mathcal{N}|_t) \cdot \mu_s(g, \tilde{g}, h) \\ & \cdot \sigma_s(g, h, \mathcal{N}|_t) \cdot \tau_s(h, \mathcal{N}|_t). \end{aligned} \quad (1)$$

For our special case, we considered a nursery pollination system, comprising a single-flowered *plant* pollinated by a specialist pollinator (in the following simply called *pollinator*) who oviposits its eggs into the flower and whose larvae feed on the fertilized seeds. We consider their interaction on a background of  $\mathcal{N}_{\text{pl}}(\text{str})$  identical *stranger flowers* and  $\mathcal{N}_{\text{po}}(\text{alt})$  identical *alternative pollinators*, occasionally visiting and pollinating the flower and competing with its specialized pollinator for resources. In view of the framework introduced above we thus considered  $S = \{\text{pl}, \text{po}\}$ , noting “pl” for plants and “po” for pollinators.

### 2.2. Model assumptions and parameters

Throughout this article we assume a large number of individuals, as some expressions are taken in the limit  $\mathcal{N} \rightarrow \infty$ . We suppose that ovule fertilization occurs solely by passive pollen transport of visiting pollinators and alternative pollinators and that all flowers blossom simultaneously. The *Trollius* flowering season lasts less than 2–3 weeks at a given elevation with a clear flowering peak, and each individual plant flowers for 6–9 days (Pellmyr, 1989; Després, 2003).

We suppose that each pollinator of genotype  $g_{po} \in G_{po}$  approaches plants randomly and independently of other pollinators, and that it chooses to enter the flower of an approached plant of genotype  $g_{pl} \in G_{pl}$  only with a probability  $\eta(g_{po}, g_{pl})$ . Here, the term *approach* should be interpreted loosely, standing for some way of inspecting flowers in order to decide whether or not to enter them, based solely on its own genotype and that of the flower. Even though punctual field observations have shown that large insects can chase *Chiastocheta* flies away from flowers (Ibanez and Després, 2009), *Chiastocheta* flies move mostly between flowers independently from the movement of other *Chiastocheta* flies or other small pollinators, the latter two being the more usual visitors (Pellmyr, 1989; Jaeger and Després, 1998). We suppose that flight time is so short that we can consider an insect to always be within a flower.

For simplicity, we suppose that the flowering period can be split into two consecutive parts: The *mating period* during which pollinators and alternative pollinators visit flowers in search of food and partners, and the *oviposition period* during which pollinators lay their eggs. We suppose the latter part to be so short as to be able to neglect any pollination by alternative pollinators.

We suppose that each pollinator starts from some random flower chosen according to its preferences and visits flowers during the mating period at a rate described by a homogeneous Poisson-process. Let  $n_{vis}$  denote the expected number of flowers visited during that period, each one chosen independently of the previous ones. We assume that the probability of a given pollinator of genotype  $g_{po}$  mating with a given pollinator of genotype  $\tilde{g}_{po}$  is proportional to the time spend together in a flower during that period. We assume that each pollinator of genotype  $g_{po} \in G_{po}$  always mates and lays a fixed number of eggs  $v_{po}$ . We suppose that pollinators lay their eggs during  $n_{ovi} := v_{po}/n_{cl}$  ovipositions, each time laying  $n_{cl}$  eggs. We suppose the time-distribution of the  $k$ -th oviposition to be the  $k$ -th order statistic of  $n_{ovi}$  ovipositions uniformly distributed within the oviposition period. Flowers are chosen at each oviposition randomly and independently of previous ovipositions or other pollinators, by the same principles as during the mating period.

We suppose that alternative pollinators visit plants and stranger flowers in the same fashion as pollinators, as determined by the probabilities  $\eta(alt, g_{pl})$  and  $\eta(alt, alt)$  of entering a plant of genotype  $g_{pl} \in G_{pl}$  or a stranger flower upon inspection respectively.

We suppose that any given unfertilized ovule of a given flower is fertilized by an entering pollinator (or alternative pollinator) with a fixed probability  $\pi_{fe}$ , to be called *pollination efficiency*, as soon as the pollinator enters the flower, on the condition that its previously visited flower was not a stranger one. We fixed the number of ovules per flower to  $n_{ovu}$ . See Appendices A.1.1 and A.1.2 for more information on the modeling of pollinator mating and ovule fertilization and in particular a derivation of the probabilities  $\pi_{po}$  and  $\pi_{pl}$  introduced in Section 2.1.

We suppose that the survival chance  $\sigma_{po}$  of a larva within a given flower, influenced by intraspecific competition for seeds and existing defense mechanisms on behalf of the plant, depends solely on the genotype of the larva, the genotype of the host-plant, the number of initial seeds (ovules fertilized) in the flower and the total number of larvae present. We introduce the parameters  $\omega_{la}$  and  $\omega_{re}$ , to be called *larva living cost* and *larva resistance cost* respectively. The term  $(\omega_{la} + \omega_{re} \cdot r_{po}^*)$  shall correspond to the number of seeds needed by one larva in order to survive with probability 1/2 in case of no defense mechanisms on behalf of the plant. The term  $\omega_{re} \cdot r_{po}^*$  corresponds to the fitness cost (Després et al., 2007a; McKenzie, 1996, Chapter 4) of a possible resistance  $r_{po}^*$  of the larva to the flower's defense (see Section 2.3), expressed in number of additional seeds required in

order to survive. See Appendices A.1.3 and A.2.1 for more on larva survival within flowers.

As seeds are parasitized by hatching pollinator larvae, the survival of the larval period by a given seed depends strongly on the presence of larvae and subsequently the oviposition behavior of pollinators with respect to the flower. A flower more appealing to pollinators will on the one hand have a higher initial seed number, on the other hand be hosting a greater number of hungry larvae. Additionally, a flower may activate various defense mechanisms, whose final effectivity depends on the susceptibility of each of the larvae. Concretely, we supposed that the survival probability of a seed depends solely on the genotype of the flower, the number  $X_{se}$  of initial seeds and the number of larvae  $X_{la}(g_{la})$  of each genotype  $g_{la} \in G_{po}$  present in the flower. In particular, we supposed the survival probability of a seed within a flower occupied by  $X_{la}(g_{la})$  larvae of genotype  $g_{la}$ , to be equal to the analogous probability in the case of a defenseless flower, occupied by the reduced number of larvae finally surviving any defense mechanisms. We thus implicitly supposed larvae to be the only threats to seeds and any defense mechanism against them to have an immediate effect. For the probability of a seed among  $X_{se}$  seeds within a defenseless flower to survive the threat posed by  $X_{la}$  larvae, we adopted the formula proposed by DeAngelis and Holland (2006), based on a model of seed-predators encountering seeds at a rate proportional to their frequency, spending a constant time consuming each seed found. The involved simulation parameters  $\tau_{ss}$  and  $\tau_{sc}$  represent the expected time needed to encounter a single seed and the time needed for the consumption of a single encountered seed respectively. See Appendices A.1.4 and A.2.2 for more on seed survival.

We suppose that each plant survives exactly one flowering period and dies immediately upon seed release. We suppose that the probability  $\tau_{pl}$  of a released seed becoming a plant and surviving adult phase until flowering depends solely on its genotype and the total number of new-generation plants competing for resources in an environment of fixed, limited *plant capacity*  $k_{pl}$ . That probability should tend to 1 in case of  $k_{pl}$  reaching infinity. The latter represents in our model the number of plants without defense mechanisms surviving the adult phase with a probability 1/2. The simulation parameter  $\omega_{de}$ , to be called *plant defense cost*, shall mediate the costs associated with any existing defense mechanism against larvae in terms of additional resources needed (Zavala et al., 2004; Lambers et al., 2008, Chapter 9B). See Appendices A.1.5 and A.2.4 for more on adult plant survival.

We assume that the survival probability  $\tau_{po}$  of adult pollinators is determined by two independent factors

1. Inter- and intraspecific competition for resources, in particular nectar and pollen, arising from a finite plant count.
2. The random occurrence of fatal events, such as attacks by predators.

The amount of resources available to each pollinator depends on the number of other pollinators or alternative pollinators interested in the same flowers. Regardless of the exact unit of measurement, we suppose that the amount of *quantifiable* resources offered by a plant is fixed and given by the model parameter  $\rho_{pl}$ . We conduct a time-average approximation and suppose that the rate of resources available to a pollinator entering the flower is inversely proportional to the expected number of visitors at any given time. The model parameter  $c_{alt}$  shall represent the amount of quantifiable resources consumed by an alternative pollinator in units of resources normally consumed by a pollinator. We suppose that the survival chance of a pollinator's adult phase until reproduction time, on the condition

of experiencing no fatal events during lifetime, depends solely on the amount of quantifiable resources available and the expected number of flights performed during lifetime. By fixing the expected total number of flowers visited by each pollinator to  $n_{\text{vis}} + n_{\text{ovi}}$ , the latter reduces to a dependency on the average number of flights  $\phi(g_{\text{po}})$  between each flower visit. The less tolerant a pollinator is with respect to the flowers it finds, the more flowers it needs to examine until finally entering one, increasing the amount of resources needed to survive. The quantity  $\phi(g_{\text{po}}) - 1$ , given by Eq. (A.17), thus corresponds to the expected number of rejected flowers between each visited one. We introduce the parameter  $\omega_{\text{po}}$ , to be called *pollinator living cost*, to be interpreted as the amount of quantifiable resources needed by a pollinator always landing on inspected flowers in order to have a survival chance of 1/2. We introduce the parameter  $\omega_{\text{se}}$ , to be called *pollinator search cost*, corresponding to the cost associated with each flight to a rejected flower.

On the other hand, we modeled lethal events (such as lethal predator attacks) occurring to a pollinator resting in a flower as a homogeneous Poisson process with a rate  $\delta(g_{\text{pl}})$  per time unit, depending solely on the genotype  $g_{\text{pl}} \in G_{\text{pl}}$  of the flower. More concretely, we supposed the rate  $\delta(g_{\text{pl}})$  of fatal events for a pollinator within a given flower of genotype  $g_{\text{pl}} \in G_{\text{pl}}$  to depend linearly on the accessibility  $o_{\text{pl}}^*$  of the flower to alternative pollinators (see Section 2.3), ranging between a fixed value  $\delta_{\text{cl}}$  for closed flowers and  $\delta_{\text{op}}$  for open flowers. The totality of lethal events occurring to a pollinator results from their cumulation in all the flowers visited by the pollinator during mating period. See Appendices A.1.6 and A.2.3 for more information on the modeling of adult pollinator survival.

### 2.3. Evolving traits

For plants we considered the following variable traits, abstracted as real numbers within the interval  $[0, 1]$ :

- Flower accessibility to alternative pollinators, in the following called *opening* and noted  $o_{\text{pl}}^*$ . We supposed that for alternative pollinators, all flowers (strangers or not) are of equal appeal, with their accessibility being the only factor reducing the chance of entering a flower. An opening  $o_{\text{pl}}^* \in [0, 1]$  can be interpreted as the probability that a given alternative pollinator approaching the flower, tries and manages to enter the flower. We thus set  $\eta(\text{alt}, g_{\text{pl}}) := o_{\text{pl}}^*$  and  $\eta(\text{alt}, \text{alt}) := 1$ , assuming all stranger flowers to be fully accessible.
- Intensity of flower-defense against seed consumers, noted  $d_{\text{pl}}^* \in [0, 1]$  and corresponding to the probability of eliminating a given non-resistant larva feeding on its seeds.

For pollinators we considered the following variable traits:

- Preferred flower opening, noted  $o_{\text{po}}^* \in [0, 1]$  and corresponding to the opening of the flower with highest probability of being entered upon examination (see Appendix A.1.1). We shall for simplicity call  $o_{\text{po}}^*$  the *pollinator opening*.
- *Tolerance* of flowers with different openings, noted  $s_{\text{po}}^* \in [0, 1]$ . Specifically, we supposed a probability  $\eta$  (see Appendix A.1.1) of the form

$$\eta(o_{\text{po}}^*, s_{\text{po}}^*; o_{\text{pl}}^*) = \exp \left[ -\frac{(o_{\text{po}}^* - o_{\text{pl}}^*)^2}{2\mathcal{V}(s_{\text{po}}^*)} \right],$$

where

$$\mathcal{V}(s_{\text{po}}^*) := s_{\text{po}, \text{min}} + \frac{s_{\text{po}}^*}{1 - s_{\text{po}}^*}, \quad (2)$$

merely serves at mapping the domain  $[0, 1]$  to  $[s_{\text{po}, \text{min}}, \infty)$ , with  $s_{\text{po}, \text{min}}$  as a fixed simulation parameter, corresponding to a minimum of flower-opening difference still *distinguishable* by pollinators.

- *Resistance* of larvae to the defense mechanisms of the flower, noted  $r_{\text{po}}^* \in [0, 1]$  and corresponding to the survival chance on the condition of an otherwise fatal flower defense. The probability of a larva surviving a flower's defense is thus given by  $(1 - d_{\text{pl}}^*) + d_{\text{pl}}^* r_{\text{po}}^*$ .

We mark trait variables with an asterisk “\*” to distinguish them from model parameters. Both pollinators and plants are considered as diploid, sexually reproducing hermaphrodites, with a genotype characterized by two values (*alleles*) for each one of the above mentioned genes. In this context, the abstract genotype spaces introduced in Section 2.1 take the explicit form  $G_{\text{pl}} = ([0, 1] \times [0, 1])^2$  and  $G_{\text{po}} = ([0, 1] \times [0, 1] \times [0, 1])^2$ . We supposed an additive genotype–phenotype mapping, that is, all functions of the genotype to depend solely on the arithmetic mean of the two corresponding alleles. In the following, we will be referring to this arithmetic mean when talking of the trait of an individual. The probability distribution  $\mu_c(g, \tilde{g}, \cdot)$  of child-genotypes resulting from a coupling of two genotypes  $g, \tilde{g} \in G_s$ , introduced in Section 2.1, was taken as purely Mendelian in nature while forbidding any recombinations.

### 2.4. Numerical simulation

The model introduced in Section 2.1 and elaborated on in Appendix A is an ecological one, describing the frequency-change of a given, finite number of plant and pollinator genotypes. Our numerical implementation is a direct translation of the model's formulas, in particular rule (1), to operations acting iteratively on the two frequency vectors  $\mathcal{N}_{\text{pl}}, \mathcal{N}_{\text{po}}$  of finite length.

Evolutionary change was introduced by mutating a random allele of a randomly chosen genotype around the original allele value after a fixed number of ecological iterations (collectively called an *evolutionary cycle*). The genotype to be mutated was chosen among all genotypes with a probability proportional to its frequency. The allele to be mutated was chosen among all possible alleles with a probability proportional to a fixed simulation parameter characteristic for the gene, henceforth called *mutability* of that gene. The distribution used for the mutation was a triangular one, with its mode at the original allele value and a span fixed as simulation parameter. An additional condition was that the probability of an allele value  $x \in [0, 1]$  to increase or decrease was proportional to the length of the intervals  $[x, 1]$  and  $[0, x]$  respectively. We chose this distribution because of its unimodality, its adjustable compact bounds and its simplicity. The newly resulting genotype was added to the existing frequency vector with an initial frequency 1 while equally reducing the frequency of the original genotype.

For optimization reasons, at the end of each evolutionary cycle genotypes with a frequency below a so called *extinction threshold* were removed, while rescaling the rest of the frequency vector in order to keep the total number of individuals unchanged. This operation proved to be essential to keeping computation times within reasonable limits and expresses the idea of keeping in the long-term only genes with a significant fitness.

Of special interest was the time-evolution of the distribution of allele values for various traits. These were computed for each allele independently of the allele-distributions of other genes and in particular by ignoring any possible linkage disequilibria. Model- and simulation-specific parameter values used in the simulations are summarized in Table 1. Ovule count  $n_{\text{ovu}}$  and clutch size  $n_{\text{cl}}$  were taken to be approximately the ones observed

**Table 1**

Default values for model and simulation-specific parameters (upper and lower part respectively) used throughout this article. Values marked with an asterisk were subject to variation between different simulations. Justifications for the chosen parameter values are given in Section 2.4.

Parameter	Symbol	Value
Ovule count	$n_{ovu}$	400
Flowers visited during mating period	$n_{vis}$	20
Total eggs laid	$v_{po}$	20
Eggs per oviposition	$n_{cl}$	4
Resources per flower	$\rho_{pl}$	1
Pollination efficiency	$\pi_{fe}$	0.2*
Relative seed search time	$\tau_{ss}$	1
Relative seed consumption time	$\tau_{sc}$	0.02
Larva living cost	$\omega_{la}$	10
Larva resistance cost	$\omega_{re}$	40*
Pollinator living cost	$\omega_{po}$	0.2*
Pollinator flower search cost	$\omega_{se}$	0.01*
Plant defense cost	$\omega_{de}$	1
Plant capacity	$k_{pl}$	1000
Flower opening distinguishability	$s_{po,min}$	0.01
Fatal events in open flowers	$\delta_{op}$	1
Fatal events in closed flowers	$\delta_{cl}$	0*
Resources consumed by strangers	$c_{alt}$	1
Alternative pollinator count	$N_{po}(alt)$	500*
Stranger flower count	$N_{pl}(str)$	1000
Iteration count per evolutionary cycle	–	500
Mutation count per evolutionary cycle	–	1 per species
Evolutionary cycle count	–	50–5000
Extinction threshold	–	1.0
Mutation span	–	0.2
Plant opening mutability	–	1.0
Plant defense mutability	–	1.0*
Pollinator opening mutability	–	1.0
Pollinator tolerance mutability	–	1.0
Pollinator resistance mutability	–	1.0

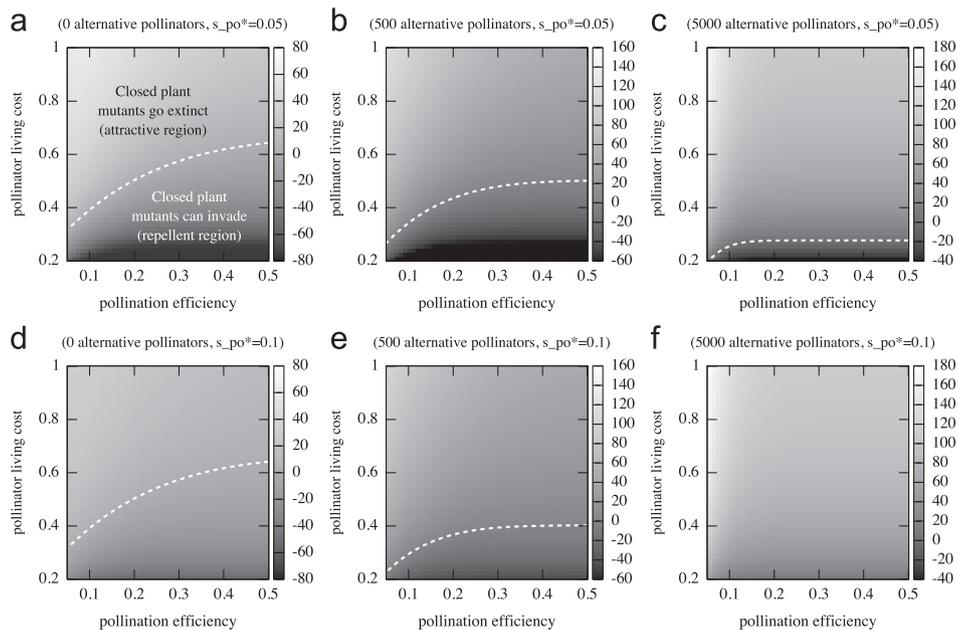
in natural *T. europaeus*–*Chiastocheta* populations (Jaeger and Després, 1998). Johannesen and Loeschcke (1996) estimated *Chiastocheta* fecundity between 10 and 60, we chose  $v_{po} = 20$ . The parameters  $\tau_{ss}$  and  $\tau_{se}$  introduced in Eq. (A.29) were chosen in the order of magnitude of values obtained through a least-squares fitting of Eq. (A.29) to data published by Després et al. (2007b, Table 1). The pollination efficiency  $\pi_{fe}$  was taken to be in the order of magnitude determined by Després (2003). Pollinator living cost  $\omega_{po}$  and larva living cost  $\omega_{la}$  were chosen so that in case of no defense or resistance, equilibrium plant and pollinator densities are in the same order of magnitude for coalitions consisting of totally closed flowers and pollinators. The flower search cost  $\omega_{se}$  was chosen so that lowering the flower acceptance probability from 1 to 1/2, approximately doubles the pollinator’s need for quantifiable resources (see Eq. (A.30)). We normalized the total amount of quantifiable resources  $\rho_{pl}$  offered by a plant by a choice of units to 1. The remaining parameter values are more or less *middle-of-the-road* choices.

The number of iterations per evolutionary cycle, predetermined from initial test-runs, was taken roughly to be the one needed for ecological equilibria to be established. We want to mention that in some cases we did observe some small-scale ecological oscillations, even after long runs. But these were in the order of less than 10% of the overall population sizes.

### 3. Simulation and analytical results

#### 3.1. Attraction and repulsion of plants

When starting with monomorphic plant populations and pollinator populations both sharing the same opening, while only allowing plant opening to evolve, two main types of behavior on

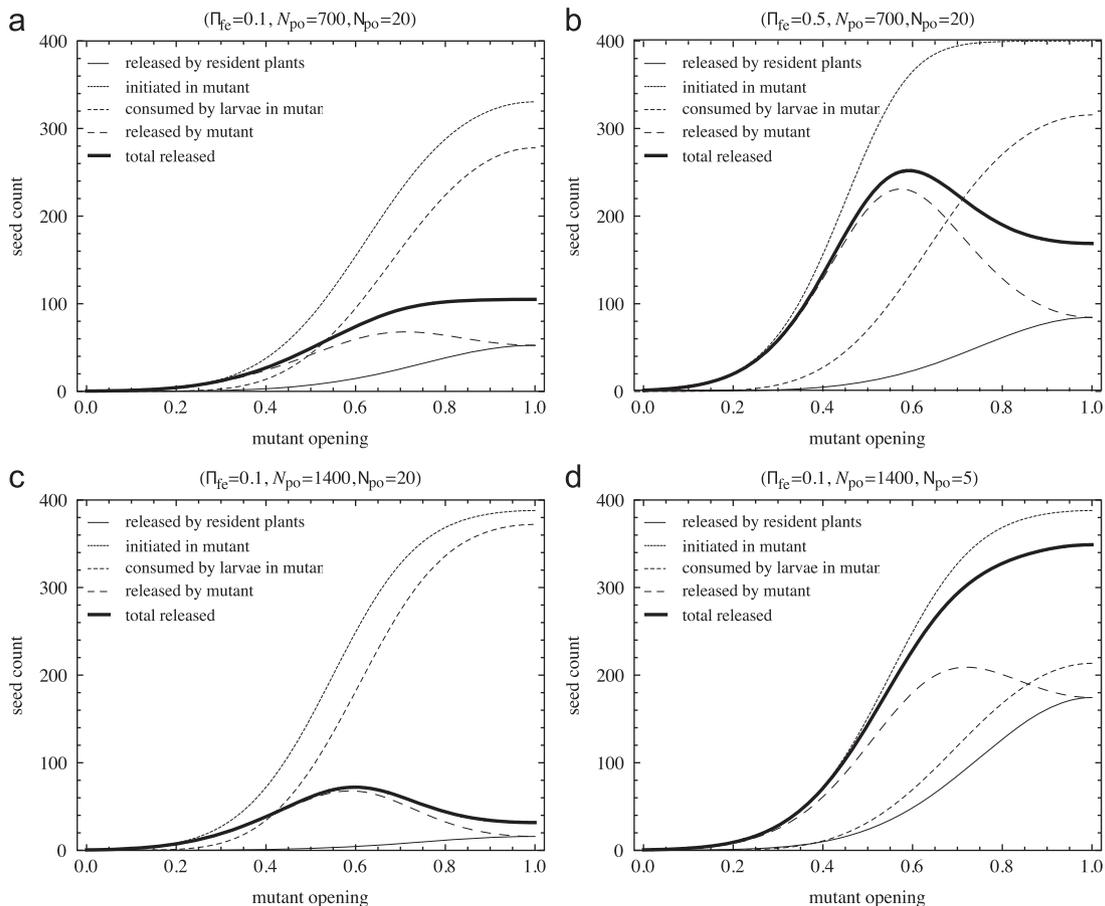


**Fig. 1.** Plant opening pressure maps in pure open coalitions for varying model parameters  $\omega_{po}$  and  $\pi_{fe}$ . As pressure a discrete approximation of the gradient of the Lyapunov exponent for more closed mutant plants (at  $\theta_{pl}^* = 0.9$ ) was taken, as described in Appendix C. A darker color signifies a greater evolutionary pressure on plants to close. Model parameter values common to all maps were  $\omega_{se} = 0.01$ ,  $\delta_{cl} = 0$ ,  $c_{alt} = 1$ . For the first row pollinator tolerance was  $s_{po}^* = 0.05$ , for the second one  $s_{po}^* = 0.1$ . For the maps (a) and (d) we supposed no alternative pollinators to be present, for maps (b) and (e)  $N_{po}(alt) = 500$ , for maps (c) and (f)  $N_{po}(alt) = 5000$ . The white dashed line separates the attractive (upper) from the repellent (lower) region.

the side of the plants were observed. In the first case, individual plants slightly differing in their opening from the rest of the population displayed an advantage and during time, the whole plant population gradually *avoided* specialist pollinators by evolving towards a different opening than preferred by them. In the second case, plant individuals differing in their opening from the rest of the population had a lower fitness and the genotype distribution was evolutionary stable. We shall subsequently call these two the *repellent* case and the *attractive* case respectively. They correspond to the cases where individual flowers have an interest in decreasing or increasing their interaction with pollinators respectively. In a broader sense, they correspond to an antagonistic interaction or mutualistic one. Simulations showed that the transition between the attractive and repellent cases was strongly influenced by the number of pollinators interacting with each flower as well as by their pollination efficiency. We varied the parameters that we found to be most affecting these factors and simulated the opening fitness gradient for totally open monomorphic plant populations pollinated by pollinators fully specialized on them. We assumed a complete absence of defense or resistance mechanisms and called these start configurations *pure open coalitions*. The obtained *parameter maps* of attractive and repellent regions are illustrated in Fig. 1. See Appendix C for details of this procedure.

As can be seen from these maps, a lower pollinator living cost, essentially resulting in a higher pollinator density, always increases the pressure on plants to avoid interaction with pollinators by closing. What appears at first to be somewhat surprising was our finding that a higher pollination efficiency  $\pi_{fe}$  actually increases the pressure on plants to avoid interaction with pollinators. Furthermore, an increased tolerance  $s_{po}^*$  of the resident pollinators always reduces that same pressure and typically expands the attractive region. Only in the extreme case of zero alternative pollinators, does an increase in the pollinator's tolerance merely reduce evolutionary pressure without shifting the border between the attractive and repellent domain. The maps also show that a strong presence of alternative pollinators may even lead to the disappearance of repellent domains and thus, to a stabilization of the pure open coalition. Such effects have already been proposed by Ferdy et al. (2002).

Fig. 2 shows for typical parameter values the total number of seeds released, carrying the genes of some slightly closed, rare mutant of varying opening  $\sigma_{mu}^* < 1$ , appearing in a pure open coalition without alternative pollinators. It demonstrates how the mutant opening maximizing that number may shift away from the dominant opening 1, depending on pollinator frequency, fertilization efficiency and egg-count. The analytical calculations,



**Fig. 2.** Expected number  $X_{re,own}$  of seeds released by a mutant plant within a pure open coalition without alternative pollinators, expected number  $X_{re,res}$  of seeds released by resident plants fertilized by the mutant and their sum  $X_{re}$ , as functions of the mutant's opening  $\sigma_{mu}^*$  for different parameter values, as described in Appendix D. Also displayed are the expected number of seeds initialized and consumed by larvae within the mutant's flower. Resident pollinator tolerance was  $s_{po}^* = 0.05$ . All relevant simulation parameters were, if not stated otherwise, set to the values given by Table 1. (a) The pure open coalition is evolutionary stable with respect to flower opening, as closed mutants always have a disadvantage compared to their open relatives. (b) Even though the number of seeds  $X_{re}$  is overall higher than in the case  $\pi_{fe} = 0.1$ , they take on their maximum at  $\sigma_{mu}^* \approx 0.6$ . More closed plants benefit from a lower seed predation and show an advantage over their open counterparts. (c) The high number of pollinators keeps seed production low and gives an advantage to more closed flowers receiving less pollinator attention. (d) Despite the high number of pollinators, their low egg number  $v_{po} = 5$  keeps the pure open coalition stable against invasions by closed plants. Also note that for a fixed pollinator count, a lower egg number  $v_{po}$  is within our model equivalent to a defense mechanism on behalf of the plants, basically reducing the number of larvae feeding on their seeds.

based on the models proposed in Section 2.1 and Appendix A.2, are given in Appendix D.

### 3.2. Specialization in the attractive case

We simulated for different parameter values the evolution of initially pure open coalitions in the attractive case. We observed that as long as plant populations stayed adequately monomorphic and fixed in genotype space, no pressure was observed for pollinators to change their opening, who actually tended to prefer the most strongly represented flowers. Any temporary difference between plant and pollinator opening was attempted to be reduced by the pollinators, at a speed increasing with the flower search cost  $\omega_{se}$ . Even with a strong survival difference on more closed flowers ( $\delta_{cl} < \delta_{op}$ ) and a relatively small flower-search cost  $\omega_{se} \approx \omega_{po}/1000$ , a significant number of closed flowers was needed for pollinators to tend to change their preference towards them. Likewise, closed flower mutants in almost-pure open coalitions showed a strong disadvantage and a lower fitness with respect to their open counterparts, which received full attention from pollinators and possibly existing alternative pollinators.

As a consequence, we were not able to observe any parallel closing of plants and pollinators in the attractive case. This fixation was further enforced by the presence of alternative pollinators. It was loosened if pollinators had a higher fitness on closed plants due to less dangers or less interspecific competition ( $\delta_{cl} < \delta_{op}$  or  $c_{alt} > 0$ ). Furthermore, we introduced for different model parameters into pure open coalitions slightly more closed mutant plants and pollinators, simulating the final mean opening for each of the two partner species after ecological equilibrium for varying initial mutant frequencies. We thus obtained frequency maps of the *susceptibility* of pure open coalitions to invasion by closed mutants, as seen in Fig. 3. These maps not only illustrate the existence of a frequency threshold for a successful closed-mutant invasion, but also the inhibitory nature of alternative pollinators. The presence of alternative mutualists has already been suggested before as a factor in the evolution of more general mutualisms (Bronstein et al., 2006).

### 3.3. Specialization in the repellent case

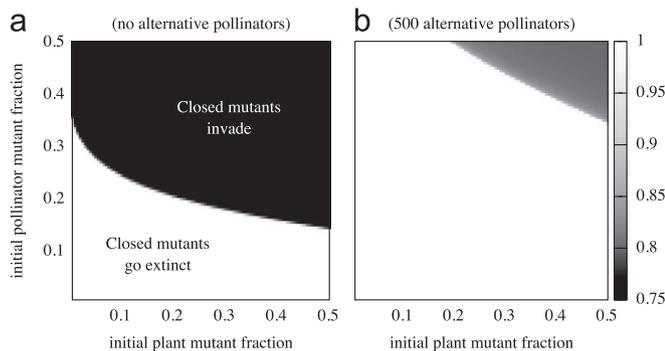
On the contrary, we observed rich evolutionary activity in the repellent case, where pure open coalitions become unstable as plants benefit from a lower interaction with pollinators. We

considered four scenarios, elaborated on below, all starting from a pure open coalition and in each one allowing for a different set of traits to coevolve. All four scenarios demonstrate a repellent character and it is only in the third and fourth scenario that a long-term stabilization of the gene pool appears.

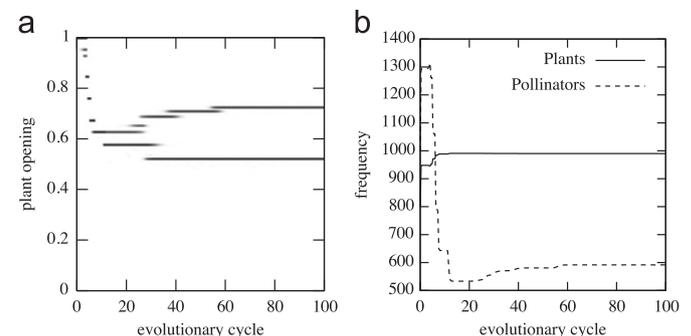
#### 3.3.1. Scenario 1: escape and chase

In the first scenario, we considered the coevolution of flower and insect opening by only allowing the genes  $o_{pl}^*$ ,  $o_{po}^*$  to mutate. Less open plants could easily invade and even replace the existing population as more closed plants interacted less with pollinators, eventually pulling the whole plant gene-pool towards closed flower shapes. This was observed regardless of whether pollinators were allowed to evolve or not (see Fig. 4), which confirmed the plants to be the drivers of this dynamic. Interestingly, for the rather artificial scenario of pollinators not being allowed to adapt to evolving flowers, disruptive divergence occurred at around  $o_{pl} \approx 0.6$ , leading to a stable coexistence of two plant genotypes at different openings. Furthermore, for a large enough thread reduction  $\delta_{cl} - \delta_{op}$  the closing of flowers actually led to an increase of the fitness and thus frequency of pollinators, which under certain conditions could overexploit plants and drive both partners to extinction, as illustrated in Fig. 5.

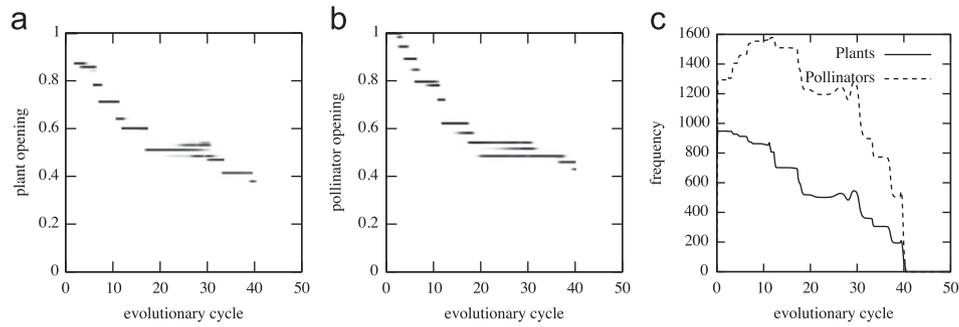
Even if allowed, pollinators would only adapt their preference to the gradually closing plant population if a flower search-cost  $\omega_{se} > 0$  was introduced. The reason for this apparent curiosity actually lies in the model itself. During their evolution towards more closed flowers, plant populations were due to high evolutionary pressure more or less monomorphic. Advantages for pollinators preferring more closed flowers do not appear if plant populations are insufficiently diversified, since eventually each pollinator will stick with what is available. This can be seen in Eqs. (A.8), (A.15) and (A.18). On the contrary, for  $\omega_{se} > 0$  pollinators quickly followed its closing partner, typically with some time-delay of a few (5–20) evolutionary cycles. As plant opening approached the minimum, evolution of  $o_{pl}^*$  slowed down, thus allowing for pollinator opening to approach it. As long as pollinator fitness does not significantly increase on closed flowers due to an equally high frequency  $\delta_{cl}$  of fatal events, an extinction as described above is avoided. On the contrary, this situation turned out to be highly unstable as the interaction was now at least as repellent as the one to begin with, stemming from the ever-existing advantage for plants avoiding an excessive interaction with pollinators. This led to a new *escape* and *chase* situation, this time towards open flowers. No halting of these oscillations, having periods in the order of 200 evolutionary cycles, could be



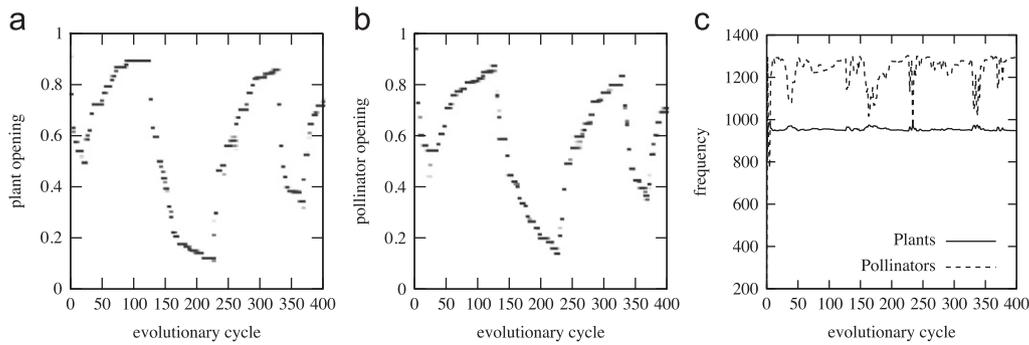
**Fig. 3.** Final mean plant opening of an initially pure open coalition after the introduction of closed plant and pollinator mutants ( $o_{pl}^* = 0.75$  and  $o_{po}^* = 0.75$ ) and 1000 subsequent ecological iterations, for various initial mutant frequencies: (a) No alternative pollinators present, (b) 500 alternative pollinators were present. Mutant frequencies are given as fractions of the total population. A darker color signifies a stronger invasion by the closed mutants, a white color means a total extinction of the latter. Simulation parameters were  $\omega_{po} = 1$ ,  $\omega_{se} = 0.001$ ,  $\delta_{cl} = 0$  and otherwise given by Table 1.



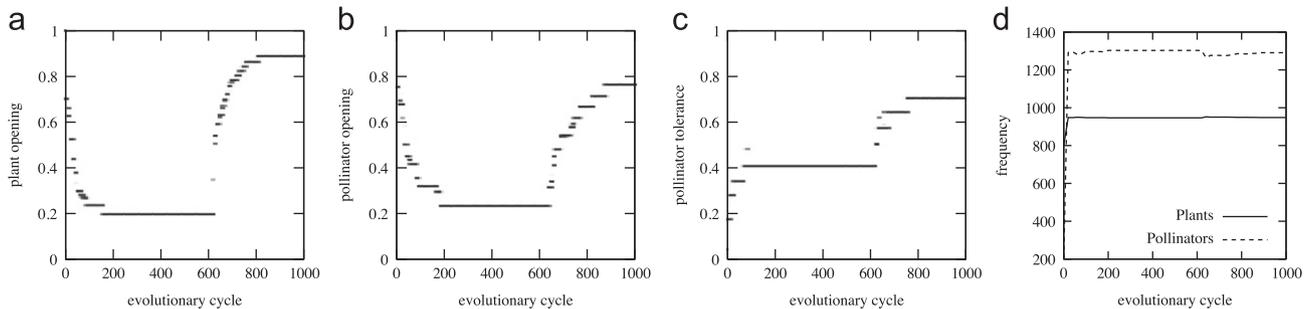
**Fig. 4.** Example simulation of evolution of an initially pure open coalition in the repellent case, with only plant opening allowed to mutate. Graphic (a) shows the evolution of allele frequency density over time for flower opening, a darker color signifying a higher frequency density. Graph (b) shows the evolution of population frequencies for both partners during the simulation. Model parameter values were  $\pi_{fe} = 0.2$ ,  $\omega_{po} = 0.2$ ,  $\omega_{se} = 0.01$ ,  $\delta_{cl} = 0$ ,  $c_{alt} = 1$  and  $\mathcal{N}_{po}(alt) = 500$ . Pollinator tolerance was fixed to  $s_{po}^* = 0.05$ .



**Fig. 5.** Example simulation of evolution of an initially pure open coalition, with only plant opening  $o_{pl}^*$  and pollinator opening  $o_{po}^*$  allowed to mutate. The graphics show the evolution of allele distribution over time for (a) flower opening and (b) pollinator opening, a darker color signifying a higher frequency density. Graph (c) shows the evolution of population frequencies for both partners during the simulation. Model parameter values were  $\pi_{fe} = 0.2$ ,  $\omega_{po} = 0.2$ ,  $\omega_{se} = 0.01$ ,  $\delta_{cl} = 0$ ,  $c_{alt} = 1$  and  $N_{po(alt)} = 500$ . Pollinator tolerance was fixed to  $s_{po}^* = 0.05$ . Both populations go extinct during the 40th evolutionary cycle.



**Fig. 6.** Example simulation of evolution of an initially pure open coalition, with only plant opening  $o_{pl}^*$  and pollinator opening  $o_{po}^*$  allowed to mutate. Graphics show the evolution of allele distribution over time for (a) flower opening and (b) pollinator opening, a darker color signifying a higher frequency density. Graph (c) shows the evolution of population frequencies for both partners during the simulation. Model parameter values were  $\pi_{fe} = 0.2$ ,  $\omega_{po} = 0.2$ ,  $\omega_{se} = 0.01$ ,  $\delta_{cl} = 1$ ,  $c_{alt} = 1$  and  $N_{po(alt)} = 500$ . Pollinator tolerance was fixed at  $s_{po}^* = 0.05$ .



**Fig. 7.** Example simulation of evolution of an initially pure open coalition, with only plant opening, pollinator opening and pollinator tolerance allowed to mutate. The graphics show the evolution of allele distribution over time for (a) flower opening, (b) pollinator opening and (c) pollinator tolerance, a darker color signifying a higher frequency density. Graph (d) shows the evolution of population frequencies for both partners during the simulation. Model parameter values were  $\pi_{fe} = 0.2$ ,  $\omega_{po} = 0.2$ ,  $\omega_{se} = 0.01$ ,  $\delta_{cl} = 1$ ,  $c_{alt} = 1$  and  $N_{po(alt)} = 500$ . Initial pollinator tolerance was  $s_{po}^* = 0.05$ .

observed within the simulated time of up to 5000 evolutionary cycles. See Fig. 6 for an example simulation of this scenario.

### 3.3.2. Scenario 2: escape and chase with metastability

In the second scenario, we considered the coevolution of flower and pollinator opening by allowing the genes  $o_{pl}^*$ ,  $o_{po}^*$  as well as  $s_{po}^*$  to mutate. Just as in the first scenario, closed plants easily invaded and replaced resident populations, thus initially driving the coalition towards closed flowers. But parallel to adapting their preferred opening to their evolving partner, pollinators also increased their tolerance  $s_{po}^*$  as to accept a larger spectrum of flower opening and effectively reduce the number of

useless flights. We found that this increase in tolerance reduced the advantage for flowers deviating from the mainstream opening, thus reducing evolutionary pressure to escape. This resulted in *metastable* states were plants would have only a minimal advantage of escaping pollinators, thus resting fixed and specialized on the pollinators for a long time, occasionally falling into sudden *escape* and *chase* phases. The (temporarily) attained opening of both partners depended on the speed with which pollinators adapted their tolerance and thus on the flower search cost  $\omega_{se}$ . Fig. 7 shows a typical simulation of this scenario, where the metastable specialization lasts only for a limited period of time. Notice how pollinators become more tolerant every time plants undergo a change in their opening.

3.3.3. Scenario 3: stable closing

In the third scenario, we simulated the coevolution of flower opening  $o_{pl}^*$ , pollinator opening  $o_{po}^*$  and plant defense  $d_{pl}^*$ . Initially, over-exploitation of the plants by pollinators allowed for more closed flowers to invade the resident population and drive the whole plant gene-pool towards more closed flowers in order to avoid interaction with pollinators. Simultaneously, defense started to evolve within flowers against seed-consumers up to a certain value, which was higher for the cases where closed flowers offered a direct advantage to pollinators ( $\delta_{cl} < \delta_{op}$ ). The development of a defense, eventually constrained by the associated costs, led to a sharp decrease of the pollinator population, eventually shifting the situation from a repellent to an attractive one. Once pollinator frequency surpassed a certain threshold, flowers had no longer an interest to avoid pollinators and kept their current opening, settling down on an evolutionary stable strategy. Furthermore, this reduction of pollinator density saved both partners from a possible evolutionary extinction they would otherwise be subject to (see first scenario). The actually attained opening depended on the speed (mutability) with which defense

could evolve. In particular, for a sufficiently low defense mutability evolutionary oscillations (or evolutionary extinction for that matter) could still make an appearance until a certain degree of defense was reached. See Fig. 8 for a typical simulation of this scenario, in which defense mechanisms develop quickly enough to stabilize plant and pollinator openings at an early state.

3.3.4. Scenario 4: conditionally stable closing

In the fourth scenario, we simulated the coevolution of flower opening  $o_{pl}^*$ , pollinator opening  $o_{po}^*$ , plant defense  $d_{pl}^*$  and pollinator resistance  $r_{po}^*$  to the plant's defense mechanisms. Simulations such as the one illustrated in Fig. 9 showed that the possibility of pollinators developing a resistance to the plant's defense mechanisms, can prevent the stabilization of the mutualism otherwise achieved by that defense, by canceling out any effects the latter could have had. It was only for relatively high resistance costs  $\omega_{re} \geq 100$  that any resistance would be so limited as to allow for the plant's defense mechanisms to keep parasitism low and the mutualism stable. Fig. 10 shows an example

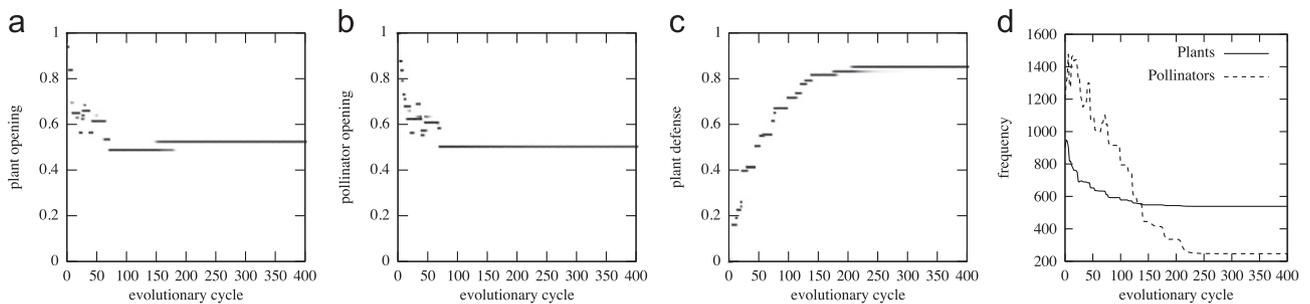


Fig. 8. Example simulation of evolution of an initially pure open coalition, with only plant opening  $o_{pl}^*$ , pollinator opening  $o_{po}^*$  and plant defense  $d_{pl}^*$  allowed to mutate. Graphics show the evolution of allele distribution over time for (a) flower opening, (b) pollinator opening and (c) plant defense, a darker color signifying a higher frequency density. Graph (d) shows the evolution of population frequencies for both partners during the simulation. Model parameter values were  $\pi_{fe} = 0.2$ ,  $\omega_{po} = 0.2$ ,  $\omega_{se} = 0.01$ ,  $\delta_{cl} = 0$ ,  $c_{alt} = 1$  and  $N_{po}(alt) = 500$ . Pollinator tolerance was fixed to  $s_{po}^* = 0.05$ , defense mutability equal to 1.

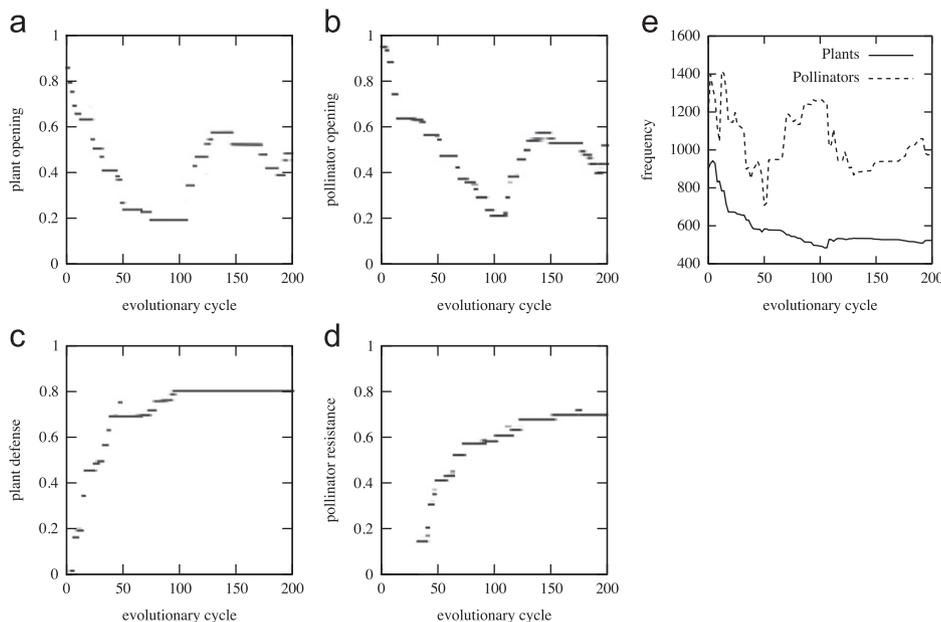
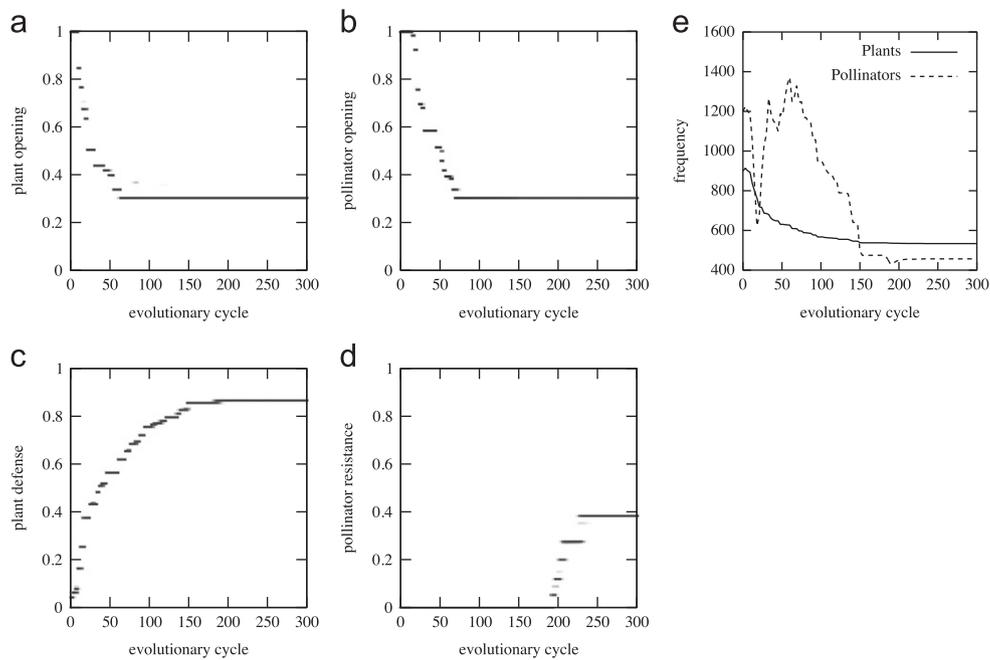


Fig. 9. Example simulation of evolution of an initially pure open coalition, with plant opening  $o_{pl}^*$ , pollinator opening  $o_{po}^*$ , plant defense  $d_{pl}^*$  and pollinator resistance  $r_{po}^*$  allowed to mutate. The graphics show the evolution of allele distribution over time for (a) flower opening, (b) pollinator opening, (c) plant defense and (d) pollinator resistance, a darker color signifying a higher frequency density. Graph (e) shows the evolution of population frequencies for both partners during the simulation. Model parameter values were  $\pi_{fe} = 0.2$ ,  $\omega_{po} = 0.2$ ,  $\omega_{se} = 0.01$ ,  $\delta_{cl} = 0$ ,  $c_{alt} = 1$ ,  $\omega_{re} = 20$  and  $N_{po}(alt) = 500$ . Pollinator tolerance was fixed to  $s_{po}^* = 0.05$ , defense mutability equal to 1.



**Fig. 10.** Example simulation of evolution of an initially pure open coalition, with plant opening  $\sigma_{pl}^*$ , pollinator opening  $\sigma_{po}^*$ , plant defense  $d_{pl}^*$  and pollinator resistance  $r_{po}^*$  allowed to mutate. The graphics show the evolution of allele distribution over time for (a) flower opening, (b) pollinator opening, (c) plant defense and (d) pollinator resistance, a darker color signifying a higher frequency density. Graph (e) shows the evolution of population frequencies for both partners during the simulation. Model parameter values were  $\pi_{re} = 0.2$ ,  $\omega_{po} = 0.2$ ,  $\omega_{se} = 0.01$ ,  $\delta_{cl} = 0$ ,  $c_{alt} = 1$ ,  $\omega_{re} = 150$  and  $N_{po}(alt) = 500$ . Pollinator tolerance was fixed to  $s_{po}^* = 0.05$ , defense mutability equal to 1.

**Table 2**

Synopsis of main encountered evolutionary scenarios as described in Section 3.3, starting from a pure open coalition in the repellent case.

Sc.	Evolving traits	Remarks	Evolutionary behavior
1	$\sigma_{pl}^*$ , $\sigma_{po}^*$	$\delta_{op} - \delta_{cl}$ large	Plants close, pollinators follow and both go extinct due to over-exploitation of plants (Fig. 5).
1	$\sigma_{pl}^*$ , $\sigma_{po}^*$	$\delta_{op} - \delta_{cl}$ small	Plant and pollinator openings undergo strong oscillations consisting of escape-chase phases (Fig. 6).
2	$\sigma_{pl}^*$ , $\sigma_{po}^*$ , $s_{po}^*$		Plant and pollinator openings alternate between escape-chase phases and metastable states (Fig. 7).
3	$\sigma_{pl}^*$ , $\sigma_{po}^*$ , $d_{pl}^*$		Plants close and pollinators follow. Defense mechanisms develop and stabilize the coalition by shifting it to the attractive case (Fig. 8).
4	$\sigma_{pl}^*$ , $\sigma_{po}^*$ , $d_{pl}^*$ , $r_{po}^*$	$\omega_{re}$ low	Plant and pollinator openings undergo strong oscillations. Plants develop defense mechanism. The coalition rests unstable due to high resistance developed by pollinators (Fig. 9).
4	$\sigma_{pl}^*$ , $\sigma_{po}^*$ , $d_{pl}^*$ , $r_{po}^*$	$\omega_{re}$ high	Plants close, pollinators follow. Plants develop defense mechanism, which stabilizes the coalition by shifting it to the attractive case. The resistance developed by pollinators is too low to destabilize the coalition (Fig. 10).

simulation, in which a defense develops on behalf of plants against larvae, which in turn develop a resistance only when plant-defense gets strong enough. The strong limitation of developed resistance eventually ensures that pollinator frequency and larval seed-exploitation stays low and the preceding specialization stable. As can be seen, plant defense tended to undergo disruptive selection as soon as pollinators became resistant to it, resulting in two streamlines of different defense degrees. Occasionally, similar branching occurred with respect to the pollinator's resistance as well. See Table 2 for a summary of the above described scenarios.

## 4. Discussion

### 4.1. Distinguishing between attractive and repellent cases

The results presented in Section 3.1 show that for adequately small pollinator populations, flowers have an advantage to attract as many pollinators as possible, leading to the evolutionary

stability of the pure open coalition. For an increasing number of pollinators, seed-predation becomes too costly to accept and flowers seek to reduce interaction with pollinators by closing and thus becoming less attractive for them.

The results also demonstrate that, more *net-beneficial* interactions between two partners, as is the case for higher fertilization efficiencies, do not generally increase the pressure for the benefited partner to maintain the highest possible interaction frequency with its benefiter. What is more crucial to the stability of a mutualism in which costs and pay-off are frequency-dependent, is the existence or not of an advantage of lowering interaction with respect to the rest of the population, by means of weighting the additional benefits and costs of such an avoidance. A higher pollination efficiency means that fewer pollinators are actually needed to achieve a (nearby) *complete* fertilization of ovules. This ensures that lowering the interaction is a lucrative way of reducing larval seed consumption, since fewer seeds are left unfertilized as a downside.

This interplay is best explained in the case of a closed mutant within a pure open coalition without alternative pollinators, as

illustrated in Fig. 2. It shows that the number of seeds released by resident plants carrying the mutant's genes, always increases with the mutant approaching the resident population. Thus, with respect to a mutant's *male function*, it is always in the flower's interest to stay attractive in order to disperse its pollen to as many resident flowers as possible. It also shows that a mutant's ovules are always better fertilized with increased opening as the flower is more often visited by pollinators. Then again, seed survival within the mutant's flower decreases with increasing opening as more larvae occupy the flower. The total number  $X_{re}$  of seeds released within the population, carrying the genes of the mutant, can be considered within our model as a direct measure of the mutant's *fitness*, as all other factors determining survival of offspring are common for all plants (see Appendix A.2.4). It results from a superposition of all three mentioned effects.

Nonetheless, a potential shift of the maximum of  $X_{re}$  away from a total opening is always linked to the mutant's *female success* as seed releaser, trying to maximize the final number of seeds released. Similarly shaped seed-specific costs and benefits for the *female function* of *Ficus aurea* depending on the number of visits by its parasitic pollinator *Pegoscapus mexicanus* were observed by Bronstein (2001b). It is noteworthy that only in two of the four cases (Fig. 2(b), (c)) does a pressure to close exerted on females actually overcome the pressure to stay open exerted on males. This shows that of at least equal importance is the success at pollen dispersal, which can play a significant role at keeping plants close to their parasitic pollinator's preferences (Ibanez et al., 2009a).

The attractive and repellent cases introduced in Section 3.1 correspond for pure open coalitions to the cases where the maximum of  $X_{re}$  is situated at full or lower opening respectively. Of course the arguments presented here concerning the stability of pure open coalitions are valid for coalitions of any arbitrary common opening. It should be mentioned that this susceptibility of pure open coalitions to the invasion of closed plants in the repellent case has little to do with the long-term effects on the plant's population size, as demonstrated in Fig. 5. Closed plants invade because they have an advantage over their still-open counterparts, even if seed-exploitation might increase when finally all plants get to be more closed.

#### 4.2. Conditions for a mutualistic specialization

As suggested by the results presented in Section 3.2, mutualistic specialization of plants to pollinators starting from a pure open coalition is not an evolutionary convergent strategy in the attractive case. Plants seeking to maximize their pollen-dispersal will be subject to strong evolutionary pressure to stay attractive and accessible for as many potential visitors as possible. Any noteworthy deviation of the plant's genotype distribution from a full opening would require a significant number of pollinators already willing to concentrate on these more closed flowers. On the other hand, the advantages for pollinators preferring closed flowers (i.e. less competition with alternative pollinators or less dangers) only appear when the flower genotypic distribution differs adequately from the pure open one, as otherwise pollinators would either mostly stick with flowers available, or spend a large amount of time and energy searching for flowers hard to find.

Consequently, a certain critical mutant density needs to be overcome for at least one of the two partners in order for both mutants to invade the pure open coalition in the long run, as can be seen in Fig. 3. See Appendix E for an illustration of these coupled invasion dynamics. These minimum densities were much higher than one could expect from fluctuations arising simply from mutations occurring once in a while. A strong dispersal within the population would furthermore increase its

homogeneity and reduce the probability of strong, local density fluctuations. Indeed, both direct field observation of *Chiastocheta* fly behavior (Després, 2003) and more indirect measurements of fly movement across *Trollius* populations through the analysis of genetic population structuring (low genetic differentiation, Després et al., 2002), suggest that *Chiastocheta* flies are able to fly long distances and that spatial structuring is weak. In fig–fig wasp systems long-range pollinator flight distances were also documented by Harrison (2003).

Intraspecific competition between larvae, as described in Appendix A.2.1, seemed to play only a minor role even for living costs  $\omega_{la}$  reducing survival chances in the flower to well below 1/10. Note that the only trait allowing an avoidance of competition through speciation, would within our model be the preferred flower opening. We attribute the lack of such speciations to the tendency of the plant gene pool to stay monomorphic with respect to flower opening, in both the attractive and the repellent cases. Nonetheless, the model-framework presented in Section 2.1 and Appendix A.1 allows for other traits such as egg count, known to be affected by intraspecific competition (Després and Cherif, 2004), to be included for further investigation in future research.

The scenario of plants closing because of pollinators learning to prefer closed flowers and plants seeking to increase their interaction with them, could as a consequence not to be verified within the context of our model. This constitutes an escape-driven closing of the *T. europaeus* as suggested by the results in Section 3.3 and described in Section 4.3 an attractive alternative explanation.

It should, however, be noted that this double-mill is not an issue in mutualisms where an *anticipation* of one of the two partners for an approach by the second is not costly or already present in some way, as is the case for aphid–ant mutualisms, where honeydew is a byproduct of the consumed phloem sap by aphids (Stadler and Dixon, 2005). Furthermore, in mutualistic systems with limited dispersal, like plant–mycorrhizal fungi or symbiotic systems, local fluctuations of globally rare phenotypes might allow the evolution of specialization in otherwise *invasion-resistant* coalitions similar to our case. It should also be mentioned that it could still be possible for a specialization of the *T. europaeus* on the *Chiastocheta* flies to have taken place on a mutualistic basis as has already been suggested by Ibanez and Després (2009), if for some external reason flower opening was kept highly diversified, long enough for *Chiastocheta* flies to recognize the benefits of and adapt to closed flowers. The reasons or even the possibility for such a diversity to be maintained despite the above mentioned hurdles, remain to be investigated.

#### 4.3. Specialization as an evolutionary trap

The results in Section 3.3 show that closing of the *T. europaeus* could result from a desperate and eventually pointless attempt of plants to avoid over-exploitation by seed-eaters by becoming less attractive. This density-dependent pressure of avoidance could be triggered by a sudden increase in the pollinators population due to environmental changes such as the extinction of a natural enemy. This could explain why in many *Trollius*–*Chiastocheta* coalitions closing of the flowers has not taken place (Després et al., 2003). We propose that closed globes, being a heritable trait strongly independent on environmental factors, could be a simple means of quickly avoiding their parasites. Of course for this to work, pollinators need to be specialized on open flowers, not yet having known the benefits closed flower might provide. An empirical way of testing this hypothesis would be to artificially close individuals in naturally open *Trollius* species and observe the visits they receive from *Chiastocheta* flies. Alternatively, one

could compare visiting rates between flowers within *Trollius* populations with naturally variable opening, as is the case in certain Japanese taxa (Pellmyr, 1992). Similar experiments on the globular morphology have already been performed on *T. europaeus*–*Chiastocheta* coalitions in the French Alps by Ibanez et al. (2009a), where *T. europaeus* flowers are closed and effectively specialized on *Chiastocheta* flies. These field works showed that artificially opened flowers were much less frequented by *Chiastocheta* flies than their naturally closed relatives.

As more and more plants close, pollinators quickly adapt their preference to the newly appearing and finally prevailing more closed flowers. Depending on the exact background environmental conditions and biological factors, this could in time lead to an increase of pollinator population sizes and finally a coevolutionary suicide due to over-exploitation, which can be interpreted as a harmful feedback of the environment to the changing trait of plants (Haldane, 1990; Parvinen, 2005; Jones et al., 2009). But even if plants could withstand the presumably increasing pollinator frequency, without any other regulatory mechanisms the outcome genotype distribution is highly unstable, as over-exploitation is still at least equally harmful to the plants, leading to strong evolutionary oscillations of plant and pollinator openings as described in Section 3.3 and seen in Fig. 6. Similar behavior has been described by Dieckmann et al. (1995) for predator–prey systems and can be seen as a special case of Red Queen dynamics (Van Valen, 1973). An increase of pollinator tolerance towards a broader spectrum of flowers, triggered by the appearing costs of rejecting an increasing number of flowers, generally only establishes a metastability of the attained genotype distribution. As shown paradigmatically in Fig. 7 that distribution is subject to sudden *escape-attempts* of still overexploited plants.

#### 4.4. Stabilization of the specialization

We argue that an effective stabilizing mechanism must be one passing the coalition over to an attractive state, in which individual plants actually have an interest in receiving full attention from pollinators. Such a mechanism could be one reducing the negative effects of interaction or keeping the population of the parasitic partner low, as can be seen by comparing Fig. 2(c) with (d) or (a) with (c) respectively. They show how a lower exploitation by pollinators (lower egg-count  $v_{po}$ ) or simply a lower pollinator frequency  $N_{po}$  can keep fitness maximal for plants preferred the most by pollinators. Similar interspecific population-regulatory mechanisms on behalf of host plants have been proposed by Holland et al. (2004b) for the stabilization of the senita cactus and senita moth mutualism. A stabilization of the *T. europaeus*–*Chiastocheta* interaction by means of a chemical defense has been hypothesized by Gallet et al. (2007). Our simulations, particularly scenarios three and four (Figs. 8 and 10), make this hypothesis a plausible one. The constant (or even increasing) exploitation of plants by their partner eventually leads to the development of strong defense mechanisms against seed-consumers. With the resulting decrease of the pollinator's population and a limitation of larvae consuming seeds comes a stabilization of the genotype distribution attained after an escape–chase phase, whose duration and outcome depend on the costs and time needed to develop such a defense. A combination of a defense mechanism along with some sort of metastabilization through an increase of pollinator tolerance, would further improve the chances of flowers eventually staying closed, as defense mechanisms would have more time to develop during metastable states.

As suggested by our simulations (see Fig. 9), an antagonistic trait on behalf of the pollinators fully or partially reducing the efficiency of the plant's defense in regulating the pollinator's

population size and larva count, could prevent the specialization from stabilizing. Whether or not these counter-measures on behalf of the pollinators lead to a frequency increase that jeopardizes evolutionary stability, strongly depends not only on the possibility of developing such measures but also on the associated costs, as indicated by a comparison of Figs. 9 and 10. Thus, whether or not a chemical defense on behalf of the *T. europaeus* really stabilizes the currently observed specialization, depends on whether developing a truly efficient toxin resistance turned out to be too costly for *Chiastocheta* larvae.

#### 4.5. Final remarks on the model

It should be noted that, in this article, all species were modeled as annual ones. To verify the compatibility with the perennial character of *Trollius*, we subsequently modified our simulations to allow for plants to live during more than one fly lifetime, by including in the next generation a fraction of the previous one. The probability of an individual plant being kept in the next cycle, was taken independently of previous cycles to be  $1-1/L$ , with  $L \geq 1$  being the expected lifetime of an individual. Increasing  $L$  to values greater than 1, decreased small-scale temporal population fluctuations in the ecological dynamics but did not seem to have any long-term effects, in particular evolutionary ones.

Though derived from elementary mechanistic and stochastic considerations, our model was built hierarchically upon various abstraction levels as we hoped this might allow other authors to adapt it to nursery plant–pollinator systems similar to the *T. europaeus*–*Chiastocheta* one. In particular, a defense mechanism against larvae needs not be a chemical one and flower morphology needs not necessarily refer to the corolla opening but rather the degree of exclusion of alternative pollinators. In the case of the yucca–yucca moth system, setting  $\rho = 1$  instead of Eq. (A.15) would eliminate competition for pollen and nectar (moths do not feed on them Powell, 1992). Setting the number  $n_{vis}$  of flowers visited during mating to zero, would account for the moths only pollinating yucca flowers during oviposition (see Appendix A.1.2). Infestation-dependent, selective fruit abortion documented for some yuccas (Pellmyr and Huth, 1994; Richter and Weis, 1995), could be accounted for by an appropriate modification of the survival probabilities in Eqs. (A.27) and (A.29).

## 5. Conclusion

The highly specialized *T. europaeus*–*Chiastocheta* mutualism probably results from the coevolution of two antagonistic traits of the plant, namely globe closure as an attempt to avoid interaction with its parasitic pollinators and chemical defense to prevent seed over-exploitation. In that sense, globe closure should be seen as an initially antagonistic behavior on behalf of the plant, eventually leading to an obligate mutualism stabilized by the parallel evolution of a *real* defense mechanism. This counter-intuitive mechanism not only provides an original explanation of specialization in nursery pollination systems, it also shows, one step beyond the parasitism–mutualism continuum paradigm, how antagonism and mutualism can be entangled in the evolution of interspecific interactions.

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**Appendix A. Construction of the model**

In the following we provide a complete definition and justification of the model used throughout the article, as a specification of the general framework presented in Section 2.1 for nursery plant/pollinator systems. This appendix is meant, together with Sections 2.1, 2.3 and 2.4, to be self-consistent and can be worked through by anyone merely interested in understanding the model and adapting it to his own needs.

We give concrete expressions for the factors  $v_s, \pi_s, \mu_s, \sigma_s, \tau_s$ , where  $s \in S = \{pl, po\}$ , determining the iteration map (1). We derive these expressions from simple assumptions about the underlying behavior of the interacting partners expressed by a number of certain functional responses and parameters. We then concretize this model by proposing specific shapes for these functional responses, either adopted from the existing literature or justified by heuristic considerations. All the parameters introduced in the model bear some physical or biological interpretation.

For any given functions (vectors)  $\varphi, \vartheta : G_s \rightarrow \mathbb{R}, s \in S$  we shall denote in the following

$$\langle \varphi, \vartheta \rangle := \sum_{g \in G_s} \varphi(g) \cdot \vartheta(g),$$

whenever the sum is well-defined. We shall write  $\varphi|_t$  instead of  $\varphi(\mathcal{N}|_t)$  for any function  $\varphi$  depending on the current populations.

**A.1. Mean field approximations**

**A.1.1. Pollinator mating**

We suppose that each pollinator of genotype  $g_{po} \in G_{po}$  approaches plants randomly and independently of other pollinators, and that it chooses to enter the flower of an approached plant of genotype  $g_{pl} \in G_{pl}$  only with a probability  $\eta(g_{po}, g_{pl})$ . Here, the term *approach* should be interpreted loosely, standing for some way of inspecting flowers in order to decide whether or not to enter them, based solely on its own genotype and that of the flower. Supposing that flight time is so short that we can suppose an insect to always be within a flower, we arrive at the probability

$$\hat{\eta}(g_{po}, g_{pl})|_t := \frac{\eta(g_{po}, g_{pl})}{\langle \eta(g_{po}, \cdot), \mathcal{N}_{pl}|_t \rangle}, \tag{A.1}$$

of a given pollinator of genotype  $g_{po} \in G_{po}$  to be found within a given flower of genotype  $g_{pl} \in G_{pl}$  at any given time. It depends not only on the personal preference of the pollinator for the flower as given by  $\eta(g_{po}, g_{pl})$ , but also on the actual number of flowers available for each genotype. The probability that two given pollinators of genotypes  $g_{po}, \tilde{g}_{po} \in G_{po}$  are within the same flower at any given moment of time is given by

$$\gamma_{po}(g_{po}, \tilde{g}_{po})|_t := \langle \hat{\eta}(g_{po}, \cdot)|_t \cdot \hat{\eta}(\tilde{g}_{po}, \cdot)|_t, \mathcal{N}_{pl}|_t \rangle.$$

Thus, supposing that the probability of a given pollinator of genotype  $g_{po}$  mating with a given pollinator of genotype  $\tilde{g}_{po}$  is proportional to the time spend together, we arrive at the expression

$$\pi_{po}(g_{po}, \tilde{g}_{po})|_t = \frac{\gamma_{po}(g_{po}, \tilde{g}_{po})|_t}{\langle \gamma_{po}(g_{po}, \cdot)|_t, \mathcal{N}_{po}|_t \rangle},$$

for the probability of an egg carried by the first to be fertilized by the second. We suppose that each pollinator of genotype  $g_{po} \in G_{po}$  always mates and lays a fixed number of eggs  $v_{po}(g_{po})$ .

**A.1.2. Plant ovule fertilization**

We suppose that ovule fertilization occurs solely by passive pollen transport of visiting pollinators and alternative pollinators and that all flowers blossom simultaneously. We suppose that the flowering period can be split into two consecutive parts: the

*mating period* during which pollinators and alternative pollinators visit flowers in search of food and partners, and the *oviposition period* during which pollinators lay their eggs, while always choosing flowers independently and in the same way as described in Appendix A.1.1. Furthermore, we suppose the latter part to be so short as to be able to neglect any pollination by alternative pollinators. We suppose that any given unfertilized ovule of a given flower of genotype  $g_{pl} \in G_{pl}$  is fertilized by an entering pollinator of genotype  $g_{po} \in G_{po}$  with a fixed probability  $\pi_{fe}(g_{po}, g_{pl})$ , to be called *pollination efficiency*, as soon as the pollinator enters the flower, on the condition that its previously visited flower was not a stranger one.

For notational reasons, we extend the genotype space  $G_{po}$  and frequency vector  $\mathcal{N}_{po}$  to the genotype space  $G_{po}^* := G_{po} \cup \{\text{alt}\}$  and frequency vector  $\mathcal{N}_{po}^*$  to include alternative pollinators as well, indexed by “alt”. Similarly, we extend  $G_{pl}$  and  $\mathcal{N}_{pl}$  to  $G_{pl}^*$  and  $\mathcal{N}_{pl}^*$  to include stranger flowers as well, indexed by “str”. We suppose that alternative pollinators visit plants and stranger flowers in the same fashion as pollinators, as given by the probabilities  $\eta(\text{alt}, g_{pl})$  and  $\eta(\text{alt}, \text{alt})$  of entering a plant of genotype  $g_{pl} \in G_{pl}$  or a stranger flower upon inspection respectively. Thus, the probability of a given alternative pollinator to be found within a given flower of genotype  $g_{pl} \in G_{pl}$  is given by

$$\hat{\eta}(\text{alt}, g_{pl})|_t := \frac{\eta(\text{alt}, g_{pl})}{\langle \eta(\text{alt}, \cdot), \mathcal{N}_{pl}^*|_t \rangle}, \tag{A.2}$$

similar to expression (A.1) seen for pollinators.

We suppose that each pollinator of genotype  $g_{po} \in G_{po}$  (alternative pollinator) starts from some random flower chosen with probability (A.1) (or (A.2) for alternative pollinators) and visits flowers during the mating period at a rate described by a homogeneous Poisson-process. Let  $n_{vis}(g_{po})$  ( $n_{vis}(\text{alt})$ ) denote the expected number of flowers visited during that period, each one chosen independently of the previous ones. Let  $n_{ovi}(g_{po})$  be the number of ovipositions performed by the given pollinator, whereas we suppose the time-distribution of the  $k$ -th oviposition to be the  $k$ -th order statistic of  $n_{ovi}(g_{po})$  ovipositions uniformly distributed within the oviposition period. Finally, we assume a large number of plants that is  $\hat{\eta} \ll 1$ . Starting from the above assumptions, we now seek an expression for the probability  $\pi_{pl}(g_{pl}, \tilde{g}_{pl})|_t$  of a given ovule of a first plant of genotype  $g_{pl}$  to be fertilized by some second plant of genotype  $\tilde{g}_{pl}$ , conditional upon its fertilization. For notational simplicity we shall temporarily suppress the index “|<sub>t</sub>”.

By the assumptions made,  $\eta_{on pl}(g_{po}) := 1$  and

$$\eta_{on pl}(\text{alt}) := \frac{\langle \eta(\text{alt}, \cdot), \mathcal{N}_{pl} \rangle}{\langle \eta(\text{alt}, \cdot), \mathcal{N}_{pl}^* \rangle},$$

give the probability that a given pollinator of genotype  $g_{po} \in G_{po}$  or a given alternative pollinator is on some plant at a given time respectively. As implied by the theory of thinning of Poisson processes (see for example Resnick, 1992, Chapter 4.4), one arrives at the probability

$$\pi_{pl,fe}^{\text{mat}}(g_{pl}) = 1 - \exp[-\langle n_{vis}(\cdot) \cdot \hat{\eta}(\cdot, g_{pl}) \cdot \pi_{fe}(\cdot, g_{pl}) \cdot \eta_{on pl}(\cdot), \mathcal{N}_{po}^* \rangle], \tag{A.3}$$

of a given ovule of a plant of genotype  $g_{pl} \in G_{pl}$  being fertilized during the mating period. Furthermore, it is straightforward to show that the probability of a given, yet unfertilized ovule of a plant of genotype  $g_{pl} \in G_{pl}$  being fertilized during the oviposition period takes the form

$$\begin{aligned} \pi_{pl,fe}^{\text{ov}}(g_{pl}) &= 1 - \prod_{g \in G_{pl}} [1 - \hat{\eta}(g_{po}, g_{pl}) \cdot \pi_{fe}(g_{po}, g_{pl})]^{n_{ovi}(g_{po}) \cdot \mathcal{N}_{po}} \\ &\approx 1 - \exp[-\langle n_{ovi}(\cdot) \cdot \hat{\eta}(\cdot, g_{pl}) \cdot \pi_{fe}(\cdot, g_{pl}), \mathcal{N}_{po} \rangle], \end{aligned}$$

with the latter approximation holding under the assumption of a large number of plants. The overall probability of a given ovule being fertilized during the flowering period is given by

$$\pi_{\text{pl,fe}}(\mathbf{g}_{\text{pl}}) := \pi_{\text{pl,fe}}^{\text{mat}}(\mathbf{g}_{\text{pl}}) + [1 - \pi_{\text{pl,fe}}^{\text{mat}}(\mathbf{g}_{\text{pl}})] \cdot \pi_{\text{pl,fe}}^{\text{ov}}(\mathbf{g}_{\text{pl}}), \quad (\text{A.4})$$

and the expected number of fertilized ovules within a flower of genotype  $\mathbf{g}_{\text{pl}}$  at the end of the flowering season takes the form

$$v_{\text{pl}}(\mathbf{g}_{\text{pl}})|_t = \pi_{\text{pl,fe}}(\mathbf{g}_{\text{pl}})|_t \cdot n_{\text{ovu}}(\mathbf{g}_{\text{pl}}). \quad (\text{A.5})$$

We claim that the probability that a given fertilized ovule of a plant of genotype  $\mathbf{g}_{\text{pl}} \in G_{\text{pl}}$  was fertilized by pollen of a given plant of genotype  $\tilde{\mathbf{g}}_{\text{pl}} \in G_{\text{pl}}$ , takes in the above mentioned limits the approximate form

$$\begin{aligned} \pi_{\text{pl}}(\mathbf{g}_{\text{pl}}, \tilde{\mathbf{g}}_{\text{pl}})|_t &\approx \frac{\pi_{\text{pl,fe}}^{\text{mat}}(\mathbf{g}_{\text{pl}})|_t}{\pi_{\text{pl,fe}}(\mathbf{g}_{\text{pl}})|_t} \\ &\times \frac{\langle n_{\text{vis}}(\cdot) \cdot \hat{\eta}(\cdot, \mathbf{g}_{\text{pl}})|_t \cdot \hat{\eta}(\cdot, \tilde{\mathbf{g}}_{\text{pl}})|_t \cdot \pi_{\text{fe}}(\cdot, \mathbf{g}_{\text{pl}}), \mathcal{N}_{\text{po}}^*|_t \rangle}{\langle n_{\text{vis}}(\cdot) \cdot \hat{\eta}(\cdot, \mathbf{g}_{\text{pl}})|_t \cdot \pi_{\text{fe}}(\cdot, \mathbf{g}_{\text{pl}}) \cdot \eta_{\text{on pl}}(\cdot)|_t, \mathcal{N}_{\text{po}}^*|_t \rangle} \\ &+ [1 - \pi_{\text{pl,fe}}^{\text{mat}}(\mathbf{g}_{\text{pl}})|_t] \cdot \frac{\pi_{\text{pl,fe}}^{\text{ov}}(\mathbf{g}_{\text{pl}})|_t}{\pi_{\text{pl,fe}}(\mathbf{g}_{\text{pl}})|_t} \\ &\times \frac{\langle n_{\text{ovi}}(\cdot) \cdot \hat{\eta}(\cdot, \mathbf{g}_{\text{pl}})|_t \cdot \hat{\eta}(\cdot, \tilde{\mathbf{g}}_{\text{pl}})|_t \cdot \pi_{\text{fe}}(\cdot, \mathbf{g}_{\text{pl}}), \mathcal{N}_{\text{po}}|_t \rangle}{\langle n_{\text{ov}}(\cdot) \cdot \hat{\eta}(\cdot, \mathbf{g}_{\text{pl}})|_t \cdot \pi_{\text{fe}}(\cdot, \mathbf{g}_{\text{pl}}), \mathcal{N}_{\text{po}}|_t \rangle}. \end{aligned}$$

**Proof.** It suffices to show that conditional upon its fertilization during the mating period, the probability of being fertilized by the second plant is given by

$$\frac{\langle n_{\text{vis}}(\cdot) \cdot \hat{\eta}(\cdot, \mathbf{g}_{\text{pl}}) \cdot \hat{\eta}(\cdot, \tilde{\mathbf{g}}_{\text{pl}}) \cdot \pi_{\text{fe}}(\cdot, \mathbf{g}_{\text{pl}}), \mathcal{N}_{\text{po}}^* \rangle}{\langle n_{\text{vis}}(\cdot) \cdot \hat{\eta}(\cdot, \mathbf{g}_{\text{pl}}) \cdot \pi_{\text{fe}}(\cdot, \mathbf{g}_{\text{pl}}) \cdot \eta_{\text{on pl}}(\cdot), \mathcal{N}_{\text{po}}^* \rangle}, \quad (\text{A.6})$$

and that conditional upon its fertilization during the oviposition period, the probability of being fertilized by the second plant is given by

$$\frac{\langle n_{\text{ovi}}(\cdot) \cdot \hat{\eta}(\cdot, \mathbf{g}_{\text{pl}}) \cdot \hat{\eta}(\cdot, \tilde{\mathbf{g}}_{\text{pl}}) \cdot \pi_{\text{fe}}(\cdot, \mathbf{g}_{\text{pl}}), \mathcal{N}_{\text{po}} \rangle}{\langle n_{\text{ov}}(\cdot) \cdot \hat{\eta}(\cdot, \mathbf{g}_{\text{pl}}) \cdot \pi_{\text{fe}}(\cdot, \mathbf{g}_{\text{pl}}), \mathcal{N}_{\text{po}} \rangle}. \quad (\text{A.7})$$

Since the proof for expression (A.7) is based on similar arguments as for expression (A.6), we shall here restrict ourselves to the first one. Suppose that at some (random) point in time an insect (pollinator or alternative pollinator) sets off to visit a new flower. Then the probability of the ovule being fertilized by that insect is given by

$$\begin{aligned} \pi_{\text{at}}^{\text{mat}}(\mathbf{g}_{\text{pl}}) &:= \sum_{\mathbf{g}_{\text{po}} \in G_{\text{po}}} \frac{n_{\text{vis}}(\mathbf{g}_{\text{po}}) \cdot \mathcal{N}^*(\mathbf{g}_{\text{po}})}{\langle n_{\text{vis}}(\cdot), \mathcal{N}_{\text{po}}^* \rangle} \\ &\times \hat{\eta}(\mathbf{g}_{\text{po}}, \mathbf{g}_{\text{pl}}) \cdot \pi_{\text{fe}}(\mathbf{g}_{\text{po}}, \mathbf{g}_{\text{pl}}) \cdot \eta_{\text{on pl}}(\mathbf{g}_{\text{po}}). \end{aligned}$$

On the other hand, the probability of being fertilized by the second plant via that insect, is given by

$$\begin{aligned} \pi_{\text{at,by}}^{\text{mat}}(\mathbf{g}_{\text{pl}}, \tilde{\mathbf{g}}_{\text{pl}}) &:= \sum_{\mathbf{g}_{\text{po}} \in G_{\text{po}}} \frac{n_{\text{vis}}(\mathbf{g}_{\text{po}}) \cdot \mathcal{N}^*(\mathbf{g}_{\text{po}})}{\langle n_{\text{vis}}(\cdot), \mathcal{N}_{\text{po}}^* \rangle} \\ &\times \hat{\eta}(\mathbf{g}_{\text{po}}, \mathbf{g}_{\text{pl}}) \cdot \hat{\eta}(\mathbf{g}_{\text{po}}, \tilde{\mathbf{g}}_{\text{pl}}) \cdot \pi_{\text{fe}}(\mathbf{g}_{\text{po}}, \mathbf{g}_{\text{pl}}), \end{aligned}$$

whereas  $\hat{\eta}(\mathbf{g}_{\text{po}}, \mathbf{g}_{\text{pl}}) \cdot \hat{\eta}(\mathbf{g}_{\text{po}}, \tilde{\mathbf{g}}_{\text{pl}})$  is the probability of an insect of genotype  $\mathbf{g}_{\text{po}}$  to be coming from the second flower and landing on the first one. Conditional upon its fertilization at a certain time during mating period, the probability of the ovule being fertilized by the second plant is given by

$$\frac{\pi_{\text{at,by}}^{\text{mat}}(\mathbf{g}_{\text{pl}}, \tilde{\mathbf{g}}_{\text{pl}})}{\pi_{\text{at}}^{\text{mat}}(\mathbf{g}_{\text{pl}})}$$

and thus indeed equal to expression (A.6).  $\square$

### A.1.3. Survival of pollinator larvae

We suppose that each pollinator of genotype  $\mathbf{g}_{\text{po}} \in G_{\text{po}}$  lays its eggs during  $n_{\text{ovi}}(\mathbf{g}_{\text{po}})$  ovipositions, each time laying  $n_{\text{cl}}(\mathbf{g}_{\text{po}})$  eggs. Flowers are chosen at each oviposition randomly and independently of previous ovipositions or other pollinators, in the same manner as described in Appendix A.1.1. We suppose that the survival chance of a larva within a given flower of genotype  $\mathbf{g}_{\text{pl}} \in G_{\text{pl}}$ , depends solely on the genotype  $\mathbf{g}_{\text{la}} \in G_{\text{po}}$  of the larva, the genotype  $\mathbf{g}_{\text{pl}}$  of the host-plant, the number  $X_{\text{se}}$  of initial seeds (ovules fertilized) in the flower and the total number  $X_{\text{la}}$  of larvae present, as given by the function value  $\sigma_{\text{po,o}}(\mathbf{g}_{\text{pl}}, \mathbf{g}_{\text{la}}, X_{\text{se}}, X_{\text{la}})$ . We claim (see proof below) that the survival probability of a larva of genotype  $\mathbf{g}_{\text{la}} \in G_{\text{po}}$ , hatching from an egg laid by a pollinator of genotype  $\mathbf{g}_{\text{po}} \in G_{\text{po}}$  is, within a mean-field approximation and for a large flower number, given by

$$\begin{aligned} \sigma_{\text{po}}(\mathbf{g}_{\text{po}}, \mathbf{g}_{\text{la}})|_t &\approx \sum_{\mathbf{g}_{\text{pl}} \in G_{\text{pl}}} \mathcal{N}_{\text{pl}}(\mathbf{g}_{\text{pl}})|_t \cdot \hat{\eta}(\mathbf{g}_{\text{po}}, \mathbf{g}_{\text{pl}})|_t \\ &\cdot \sigma_{\text{po,o}}(\mathbf{g}_{\text{pl}}, \mathbf{g}_{\text{la}}, n_{\text{ovu}}(\mathbf{g}_{\text{pl}}) \\ &\cdot [\pi_{\text{pl,fe}}(\mathbf{g}_{\text{pl}})|_t \cdot (1 - \pi_{\text{fe}}(\mathbf{g}_{\text{po}}, \mathbf{g}_{\text{pl}})) + \pi_{\text{fe}}(\mathbf{g}_{\text{po}}, \mathbf{g}_{\text{pl}})], \\ &X_{\text{lar}}(\mathbf{g}_{\text{pl}})|_t + n_{\text{cl}}(\mathbf{g}_{\text{po}})). \end{aligned} \quad (\text{A.8})$$

The probability  $\pi_{\text{pl,fe}}(\mathbf{g}_{\text{pl}})|_t$  is given by Eq. (A.4) and

$$X_{\text{lar}}(\mathbf{g}_{\text{pl}})|_t := \langle v_{\text{po}}(\cdot) \cdot \hat{\eta}(\cdot, \mathbf{g}_{\text{pl}})|_t, \mathcal{N}_{\text{po}}|_t \rangle$$

is the expected number of larvae (i.e. eggs laid) within a given flower of genotype  $\mathbf{g}_{\text{pl}} \in G_{\text{pl}}$ .

**Proof.** In the following, let  $I_{\text{po}}$  be the set of individual pollinators and  $I_{\text{pl}}$  the set of individual plants. For notational reasons, we shall omit all indices “|<sub>t</sub>” and consider functions on  $G_{\text{po}}$  and  $G_{\text{pl}}$  as functions on  $I_{\text{po}}$  and  $I_{\text{pl}}$  respectively. Let  $Y_{ijk}$  be the random number of eggs laid by pollinator  $i \in I_{\text{po}}$  into flower  $j \in I_{\text{pl}}$  during its  $k$ -th oviposition and  $A_{ijk}$  the event that this number is not zero. Note that  $Y_{ijk}$  is the product of the constant  $n_{\text{cl}}(i)$  with a Bernoulli-trial of probability  $\hat{\eta}(i, j)$  and that for each fixed  $j \in I_{\text{pl}}$  the random variables  $\{Y_{ijk}\}_{i,k}$  are independent. Let

$$Y_j := \sum_{i \in I_{\text{po}}} \sum_{k=1}^{n_{\text{ovi}}(i)} Y_{ijk} \quad (\text{A.9})$$

be the total number of eggs laid by pollinators into flower  $j$ . Let  $X_j$  be the total number of ovules fertilized within flower  $j$ . Then for given values of  $X_j, Y_j$ , the survival probability of a larva of genotype  $\mathbf{g}_{\text{la}}$  is within flower  $j$  given by  $\sigma_{\text{po,o}}(j, \mathbf{g}_{\text{la}}, X_j, Y_j)$ . Consequently, the survival chance of a larva of genotype  $\mathbf{g}_{\text{la}}$  laid by pollinator  $i$  is given by

$$\begin{aligned} \sigma(i, \mathbf{g}_{\text{la}}) &= \sum_{k=1}^{n_{\text{ovi}}(i)} \frac{1}{n_{\text{ovi}}(i)} \sum_{j \in I_{\text{pl}}} \hat{\eta}(i, j) \cdot \sum_{x_j, y_j} \\ P(X_j = x_j, Y_j = y_j | A_{ijk}) \cdot \sigma_{\text{po,o}}(j, \mathbf{g}_{\text{la}}, x_j, y_j) \\ &= \sum_{j \in I_{\text{pl}}} \hat{\eta}(i, j) \cdot \mathbb{E}\{\sigma_{\text{po,o}}(j, \mathbf{g}_{\text{la}}, X_j, Y_j) | A_{ij1}\}. \end{aligned} \quad (\text{A.10})$$

Under a mean-field approximation with respect to  $X_j$  and  $Y_j$ , Eq. (A.10) takes the form

$$\sigma(i, \mathbf{g}_{\text{la}}) \approx \sum_{j \in I_{\text{pl}}} \hat{\eta}(i, j) \cdot \sigma_{\text{po,o}}(j, \mathbf{g}_{\text{la}}, \mathbb{E}\{X_j | A_{ij1}\}, \mathbb{E}\{Y_j | A_{ij1}\}), \quad (\text{A.11})$$

with  $\mathbb{E}\{X_j | A_{ij1}\}$  and  $\mathbb{E}\{Y_j | A_{ij1}\}$  as expected seed and larva count within flower  $j$ , conditional on the event of the flower being chosen by pollinator  $i$  for its first oviposition. From Eq. (A.9) it follows that

$$\begin{aligned} \mathbb{E}\{Y_j | A_{ij1}\} &= \sum_{l \in I_{\text{po}} \setminus \{i\}} n_{\text{ovi}}(l) \cdot n_{\text{cl}}(l) \cdot \hat{\eta}(l, j) \\ &+ (n_{\text{ovi}}(i) - 1) \cdot n_{\text{cl}}(i) \cdot \hat{\eta}(i, j) + n_{\text{cl}}(i) \\ &= \langle v_{\text{po}}(\cdot) \cdot \hat{\eta}(\cdot, j), \mathcal{N}_{\text{po}} \rangle + n_{\text{cl}}(i) \cdot (1 - \hat{\eta}(i, j)), \end{aligned}$$

which under the assumption of a large plant number, that is  $\hat{\eta}(i, j) \ll 1$ , takes the simpler form

$$\mathbb{E}\{Y_j | A_{ij1}\} \approx \langle \nu_{po}(\cdot) \cdot \hat{\eta}(\cdot, j), \mathcal{N}_{po} \rangle + n_{cl}(i). \quad (A.12)$$

On the other hand, the probability that a given ovule of flower  $j$  is not fertilized, conditional upon  $A_{ij1}$ , takes the form

$$\prod_{l \in I_{po}(i)} \prod_{k=1}^{n_{ov}(l)} [1 - \hat{\eta}(l, j) \cdot \pi_{fe}(l, j)] \cdot \prod_{k=2}^{n_{ov}(i)} [1 - \hat{\eta}(i, j) \cdot \pi_{fe}(i, j)] \cdot [1 - \pi_{fe}(i, j)] \cdot [1 - \pi_{pl,fe}^{mat}(j)] = [1 - \pi_{pl,fe}(j)] \cdot \frac{[1 - \pi_{fe}(i, j)]}{1 - \hat{\eta}(i, j) \pi_{fe}(i, j)}, \quad (A.13)$$

with  $\pi_{pl,fe}^{mat}(j)$  and  $\pi_{pl,fe}(j)$  given by Eqs. (A.3) and (A.4) and (A.4) respectively. Assuming again a large number of plants, expression (A.13) simplifies to

$$[1 - \pi_{pl,fe}(j)] \cdot [1 - \pi_{fe}(i, j)],$$

so that finally

$$\mathbb{E}\{X_j | A_{ij1}\} \approx n_{ovu}(j) \cdot [\pi_{pl,fe}(j) \cdot (1 - \pi_{fe}(i, j)) + \pi_{fe}(i, j)]. \quad (A.14)$$

Inserting Eqs. (A.12) and (A.14) into Eq. (A.11) finally yields formula (A.8).  $\square$

#### A.1.4. Seed survival

As seeds are parasitized by hatching pollinator larvae, the survival of the larval period by a given seed depends strongly on the presence of larvae and subsequently the oviposition behavior of pollinators with respect to the flower. A flower more appealing to pollinators will on the one hand have a higher initial seed number, on the other hand be hosting a greater number of hungry larvae. Additionally, a flower may activate various defense mechanisms, whose final effectivity depends on the susceptibility of each of the larvae. Concretely, we supposed that the survival probability of a seed depends solely on the genotype  $g_{pl} \in G_{pl}$  of the flower, the number  $X_{se}$  of initial seeds and the number of larvae  $X_{la}(g_{la})$  of each genotype  $g_{la} \in G_{po}$  present in the flower, as given by the function value  $\sigma_{pl,o}(g_{pl}, X_{se}, X_{la}(\cdot))$ . A mean field approximation leads to the expression

$$\sigma_{pl}(g_{pl}, g_{se})|_t = \sigma_{pl,o}(g_{pl}, \nu_{pl}(g_{pl})|_t, X_{la}(g_{pl}, \cdot)|_t),$$

for the survival probability of a seed within a given flower of genotype  $g_{pl} \in G_{pl}$ . Here,  $X_{la}(g_{pl}, g_{la})|_t$  is the expected number of larvae of genotype  $g_{la} \in G_{po}$  hatching in a given flower of genotype  $g_{pl} \in G_{pl}$ . It is given by

$$X_{la}(g_{pl}, g_{la})|_t = \langle \nu_{po}(\cdot) \cdot \hat{\eta}(\cdot, g_{pl})|_t \cdot \pi_{po,la}(\cdot, g_{la})|_t, \mathcal{N}_{po}|_t \rangle,$$

whereas

$$\pi_{po,la}(g_{po}, g_{la})|_t := \langle \pi_{po}(g_{po}, \cdot)|_t \cdot \mu_{po}(g_{po}, \cdot, g_{la}), \mathcal{N}_{po}|_t \rangle$$

is the probability that an egg of a given pollinator of genotype  $g_{po} \in G_{po}$  is of genotype  $g_{la} \in G_{po}$ . The expected initial seed count  $\nu_{pl}(g_{pl})|_t$  in the flower is given by Eq. (A.5).

#### A.1.5. Adult plant survival

We suppose that each plant survives exactly one flowering period and dies immediately upon seed release. We suppose that the probability of a released seed becoming a plant and surviving adult phase until flowering depends solely on its genotype  $g_{pl} \in G_{pl}$  and the total number of new-generation plants competing for resources in an environment of fixed, limited capacity. The expected number of the latter is for each genotype  $g_{pl}$  given by

$$\mathcal{N}_{pl}(g_{pl})|_{t+1/2} := \sum_{g, \tilde{g} \in G_{pl}} \mathcal{N}_{pl}(g)|_t \cdot \mathcal{N}_{pl}(\tilde{g})|_t \cdot \nu_{pl}(g)|_t \cdot \pi_{pl}(g, \tilde{g})|_t \cdot \mu_{pl}(g, \tilde{g}, g_{pl}) \cdot \sigma_{pl}(g, g_{pl})|_t,$$

with the index “ $|_{t+1/2}$ ” indicating that this number is an intermediate one, taken right before the plant’s adult phase. By performing a mean field approximation we arrive at a surviving probability of the form

$$\tau_{pl}(g_{pl})|_t = \tau_{pl,co}(g_{pl}, \langle 1, \mathcal{N}_{pl}|_{t+1/2} \rangle),$$

where  $\tau_{pl,co}$  is some function to be specified later on in Appendix A.2.4, a priori depending on the genotype of the plant and the total number of plants competing for a limited number of resources.

#### A.1.6. Adult pollinator survival

We assume that the survival probability of adult pollinators is determined by competition for resources arising from a finite plant count, as well as the random occurrence of fatal events such as attacks by predators. The amount of resources available to each pollinator depends on the number of other pollinators or alternative pollinators interested in the same flowers. Regardless of the exact unit of measurement, we suppose that the amount of *quantifiable* resources offered by a plant of genotype  $g_{pl} \in G_{pl}$  is fixed and given by  $\rho_{pl}(g_{pl})$ . We conduct a time-average approximation and suppose that the rate of resources available to a pollinator entering the flower is inversely proportional to the expected number of visitors

$$X_{po}(g_{pl})|_t = \langle \hat{\eta}(\cdot, g_{pl})|_{t+1/2}, \mathcal{N}_{po}|_{t+1/2} \rangle + c_{alt} \cdot \hat{\eta}(alt, g_{pl})|_{t+1/2} \cdot \mathcal{N}_{po}(alt)$$

at any given time. The constant factor  $c_{alt}$  accounts for the amount of quantifiable resources consumed by an alternative pollinator in units of resources consumed by a pollinator, considered as a model parameter. The frequency vector  $\mathcal{N}_{po}|_{t+1/2}$  is defined for pollinators in the same way as for plants in Appendix A.1.5. The function  $\hat{\eta}|_{t+1/2}$  is defined in the same manner as  $\hat{\eta}|_t$  in Appendix A.1.1, this time with respect to the frequency vectors  $\mathcal{N}_{po}|_{t+1/2}$  and  $\mathcal{N}_{pl}|_{t+1}$ . Therefore, the expected number of quantifiable resources available to a pollinator of genotype  $g_{po} \in G_{po}$  is given by

$$\rho_{po}(g_{po})|_t = \left\langle \hat{\eta}(g_{po}, \cdot)|_{t+1/2} \cdot \frac{\rho_{pl}(\cdot)}{X_{po}(\cdot)|_t}, \mathcal{N}_{pl}|_{t+1} \right\rangle. \quad (A.15)$$

We suppose that the survival chance of a pollinator’s adult phase until reproduction time, on the condition of experiencing no fatal events during lifetime, depends solely on the amount of quantifiable resources available and the expected number of flights performed during lifetime. By fixing the expected total number of flowers visited for each pollinator, the latter reduces to a dependency on the average number of flights between each flower visit. By applying a mean field approximation with respect to the amount of quantifiable resources available and the number of between-flower flights, we took

$$\tau_{po,co}(g_{po}, \rho_{po}(g_{po})|_t, \phi_{po}(g_{po})|_t) \quad (A.16)$$

as probability of an emerging pollinator surviving until reproduction, on the condition of experiencing no fatal events during lifetime. Here,  $\tau_{po,co}$  is a priori some function to be specified later on, depending on the pollinator genotype, positively on the amount of quantifiable resources available and negatively on the average number of between-flower flights, whose expected value is given by

$$\phi(g_{po})|_t := \frac{\langle 1, \mathcal{N}_{pl}|_{t+1/2} \rangle}{\langle \eta(g_{po}, \cdot), \mathcal{N}_{pl}|_{t+1/2} \rangle}, \quad (A.17)$$

as implied by our flower visiting model described in Appendix A.1.1. The less tolerant a pollinator is with respect to the flowers it finds, the more flowers it needs to examine until finally entering one.

The difference  $\phi(g_{po})|_t - 1$  thus corresponds to the expected number of rejected flowers between each visited one.

On the other hand, we modeled external threats (such as predators) to a pollinator resting in a flower as a homogeneous Poisson process with a rate  $\delta(g_{pl})$  per time unit, depending solely on the genotype  $g_{pl} \in G_{pl}$  of the flower. For simplicity, we identified the adult phase of a pollinator with its mating period, here taken without loss of generality to last one time unit. During that period, flowers are visited as described by a Poisson process of constant rate (see Appendix A.1.1), each time chosen independently of previously visited flowers. If  $\mathbf{T}_{g_{po}} \in [0, 1]^{G_{pl}}$  is the random vector whose component  $T_{g_{po}}(g_{pl})$  gives the time spend by a given pollinator of genotype  $g_{po}$  on flowers of genotype  $g_{pl}$  during adult phase, then the probability of experiencing no fatal events at all during adult phase is given by  $\mathbb{E} \exp[-\langle \delta(\cdot), \mathbf{T}_{g_{po}} \rangle]$ , with the operator  $\mathbb{E}$  denoting the expected value. In the limit of an infinite visiting rate this probability takes the form (to be proven below)

$$\begin{aligned} \tau_{po,fa}(g_{po})|_t &:= \exp[-\langle \delta(\cdot), \mathbb{E} \mathbf{T}_{g_{po}} \rangle] \\ &= \exp[-\langle \hat{\eta}(g_{po}, \cdot) |_{t+1/2} \cdot \delta(\cdot), \mathcal{N}_{pl}|_{t+1} \rangle], \end{aligned} \quad (\text{A.18})$$

which was adopted in our model. By combining the factors (A.16) and (A.18), we took

$$\tau_{po}(g_{po})|_t := \tau_{po,co}(g_{po}, \rho_{po}(g_{po})|_t, \phi_{po}(g_{po})|_t) \cdot \tau_{po,fa}(g_{po})|_t,$$

as the overall probability of the pollinator surviving adulthood.

**Proof of approximation (A.18).** We shall demonstrate that the probability of a given pollinator of genotype  $g_{po}$  not experiencing any fatal events during adult phase, goes as postulated above for a high visiting rate over to the limit  $\exp[-\langle \delta(\cdot), \mathbb{E} \mathbf{T}_{g_{po}} \rangle]$ . For notational reasons we shall write

$$\hat{\eta}(g) := \hat{\eta}(g_{po}, g) |_{t+1/2} \cdot \mathcal{N}_{pl}(g) |_{t+1} = \mathbb{E} T_{g_{po}}(g)$$

for the probability of finding the pollinator in some flower of genotype  $g_{pl}$  at a given time and  $n := n_{vis}(g_{po})$  for the flower visiting rate.

Let  $\gamma(\tau) \in G_{pl}$  be the random genotype of the hosting flower at time  $\tau$  and  $T$  the random occurrence time of the first fatal event. We shall write  $p(\tau) := P(T \geq \tau)$  for the probability of the pollinator surviving up until time  $\tau$  and  $p_g(\tau) := P(T \geq \tau, \gamma(\tau) = g)$  for the probability that the pollinator can be found within a flower of genotype  $g$  at time  $\tau$ . We shall derive and solve a differential equation for  $p$  under the start conditions  $p(0) = 1$  and  $p_g(0) = \hat{\eta}(g)$ . Suppose that for a given time  $\tau$ , the pollinator lives within a flower of genotype  $g$ . Then, the event of being found alive at some later time  $\tau+s$  within a different flower of genotype  $\tilde{g} \neq g$  corresponds to the event that the pollinator has survived the time span  $[\tau, \tau+s]$  and at some point flew to the new flower. Thus one finds that the probability  $P(\gamma(\tau+s) = \tilde{g} | \gamma(\tau) = g, T \geq \tau+s)$  has the behavior  $\hat{\eta}(\tilde{g}) \cdot ns + o(s)$ . The event of being found alive at time  $\tau+s$  within the same flower type corresponds to the event of surviving the time-span  $[\tau, \tau+s]$  and either not changing the flower at all, or at some point flying to the same type of flower. One finds that the probability  $P(\gamma(\tau+s) = g | \gamma(\tau) = g, T \geq \tau+s)$  is given by

$$1 - \delta(g)s - (1 - \hat{\eta}(g)) \cdot ns + o(s),$$

so that

$$\begin{aligned} v_g(\tau+s) &= \sum_{\tilde{g} \in G_{pl}} v_{\tilde{g}}(\tau) \cdot P\left(\gamma(\tau+s) = \tilde{g} | \gamma(\tau) = g, T \geq \tau+s\right) \\ &= v_g(\tau) [(1 - \delta(g)s - (1 - \hat{\eta}(g)) \cdot ns)] \\ &\quad + \sum_{\tilde{g} \neq g} v_{\tilde{g}}(\tau) \hat{\eta}(\tilde{g}) \cdot ns + o(s). \end{aligned} \quad (\text{A.19})$$

Taking the limit  $s \rightarrow 0^+$  in Eq. (A.19) and using  $v(\tau) = \sum_{g \in G_{pl}} v_g(\tau)$  leads to the differential equation

$$\frac{dv_g}{d\tau}(\tau) = -(\delta(g) + n) \cdot v_g(\tau) + n \hat{\eta}(g) v(\tau), \quad (\text{A.20})$$

which after summation over  $g$  leads to

$$\frac{dv}{d\tau}(\tau) = - \sum_{g \in G_{pl}} \delta(g) \cdot v_g(\tau). \quad (\text{A.21})$$

The solution of Eq. (A.20) is given by

$$v_g(\tau) = \hat{\eta}(g) \cdot e^{-(\delta(g)+n)\tau} + n \hat{\eta}(g) \int_0^\tau v(s) e^{-(\delta(g)+n)(\tau-s)} ds, \quad (\text{A.22})$$

whereas we considered the function  $v$  as given. Inserting Eq. (A.22) into Eq. (A.21) yields the differential equation

$$\begin{aligned} v'(\tau) &= - \sum_{g \in G_{pl}} \hat{\eta}(g) \delta(g) e^{-(\delta(g)+n)\tau} \\ &\quad - \sum_{g \in G_{pl}} \hat{\eta}(g) \delta(g) n \int_0^\tau v(s) e^{-(\delta(g)+n)(\tau-s)} ds. \end{aligned} \quad (\text{A.23})$$

Note that from Eq. (A.23) follows that

$$\sup_{\substack{\tau \in [0,1] \\ n \geq 0}} |v'(\tau)| < \infty. \quad (\text{A.24})$$

By substituting  $u := \tau - s$  and performing a partial integration, Eq. (A.23) can be rewritten as

$$v'(\tau) = - \sum_{g \in G_{pl}} \hat{\eta}(g) \delta(g) \cdot \left[ v(\tau) + \int_0^\tau e^{-nu} \frac{d}{du} [v(\tau-u) e^{-\delta(g)u}] du \right]. \quad (\text{A.25})$$

From Eqs. (A.24) and (A.25) it follows that

$$\sup_{\tau \in [0,1]} \left| v'(\tau) - \sum_{g \in G_{pl}} \hat{\eta}(g) \delta(g) v(\tau) \right| \xrightarrow{n \rightarrow \infty} 0,$$

which implies that

$$\sup_{\tau \in [0,1]} \left| v(\tau) - \exp \left[ - \sum_{g \in G_{pl}} \hat{\eta}(g) \delta(g) \tau \right] \right| \xrightarrow{n \rightarrow \infty} 0.$$

In particular, one finds

$$P(T \geq 1) = v(1) \xrightarrow{n \rightarrow \infty} \exp \left[ - \sum_{g \in G_{pl}} \hat{\eta}(g) \delta(g) \right]$$

as claimed.  $\square$

## A.2. Concrete genotype spaces and functional responses

In the previous section we reduced the ecological dynamics of an arbitrary finite number of plant and pollinator genotypes, via mean field approximations to a set of basic response functions. These functions should describe the biology of single individuals as well as any considered micro-dynamics, such as competition of larvae within single flowers. The explicit form of these functions and in particular their dependence on the model parameters and interacting genotypes, as presented below, is inspired from similar models in the literature (DeAngelis and Holland, 2006; Verhulst, 1838) as well as mechanistic considerations. The concrete genotypes used for the plants and pollinators were already defined in Section 2.3.

As already mentioned in Section 2.2, we fixed the number of ovules  $n_{ovu}$  created within each flower, the total number of eggs  $v_{po}$  laid by a pollinator and the number of eggs  $n_{cl}$  laid at each oviposition (see Appendices A.1.2 and A.1.3) as parameters of the

simulation. Similarly, we fixed the total amount of quantifiable resources  $\rho_{pl}$  offered by a plant (see Appendix A.1.6) and normalized it by a choice of units to 1. We considered the fertilization probability  $\pi_{fe}$  of a given ovule during an insect visit as well as the expected number of flowers visited  $n_{vis}$  during mating period (see Appendix A.1.2) as fixed simulation parameters for pollinators as well as alternative pollinators.

#### A.2.1. Larval survival chance

We supposed the survival chance  $\sigma_{po,o}(g_{pl}, g_{la}, X_{se}, X_{la})$  of a larva of genotype  $g_{la} \in G_{po}$  within a flower of genotype  $g_{pl} \in G_{pl}$  (see Appendix A.1.3), occupied by  $X_{la}$  larvae competing for  $X_{se}$  seeds, to be a product of the following two probabilities:

- The probability  $1 - \varepsilon_{de}(g_{pl}, g_{la})$  of surviving the defense mechanism of the flower, with the so called defense effectivity  $\varepsilon_{de}(g_{pl}, g_{la})$  itself given by

$$\varepsilon_{de}(g_{pl}, g_{la}) = d_{pl}^* \cdot (1 - r_{po}^*). \quad (A.26)$$

It is zero if the flower has no defense at all or if the larva is totally resistant to any existing defense.

- The probability  $\sigma_{po,co}(g_{la}, X_{se}, X_{la})$  of surviving the larval period within a defenseless flower, expressing the (negative) effects of competition for a limited number of seeds. We used the form

$$\sigma_{po,co}(g_{la}, X_{se}, X_{la}) := \left[ 1 + \frac{(\omega_{la} + \omega_{re} \cdot r_{po}^*) \cdot X_{la}}{1 - \sigma_{pl,nd}(X_{se}, X_{la}) \cdot X_{se}} \right]^{-1}, \quad (A.27)$$

justified in Appendix B as an interpretation of the logistic growth equation (Verhulst, 1838). The term  $X_{se} \cdot [1 - \sigma_{pl,nd}(X_{se}, X_{la})]$  corresponds to the number of seeds eaten by  $X_{la}$  larvae within a defenseless flower with initially  $X_{se}$  seeds, given below by Eq. (A.29). The term  $(\omega_{la} + \omega_{re} \cdot r_{po}^*)$  corresponds to the number of seeds needed by one larva in order to survive with probability 1/2. The coefficients  $\omega_{la}$  and  $\omega_{re}$ , to be called *larva living cost* and *larva resistance cost*, were taken to be fixed simulation parameters. The term  $\omega_{re} \cdot r_{po}^*$  corresponds to the fitness cost (Després et al., 2007a; McKenzie, 1996, Chapter 4) of a possible resistance  $r_{po}^*$  of the larva to the flower's defense, expressed in number of additional seeds required in order to survive.

#### A.2.2. Seed survival chance

We supposed the survival probability  $\sigma_{pl,o}(g_{pl}, X_{se}, X_{la}(\cdot))$  of a seed within a flower of genotype  $g_{pl}$  with  $X_{se}$  seeds, occupied by  $X_{la}(g_{la})$  larvae of genotype  $g_{la}$ , to be equal to the analogous probability  $\sigma_{pl,nd}(X_{se}, X_{la})$  in the case of a defenseless flower, occupied by the reduced number of larvae finally surviving any defense mechanisms. We thus implicitly supposed larvae to be the only threats to seeds and any defense mechanism against them to have an immediate effect. Consequently, we set

$$\sigma_{pl,o}(g_{pl}, X_{se}, X_{la}(\cdot)) := \sigma_{pl,nd} \left[ X_{se}, \sum_{g_{la} \in G_{la}} (1 - \varepsilon_{de}(g_{pl}, g_{la})) \cdot X_{la}(g_{la}) \right]. \quad (A.28)$$

The term  $\varepsilon_{de}(g_{pl}, g_{la})$  is exactly the defense effectivity of the flower against a larva of genotype  $g_{la}$ , given by Eq. (A.26). The sum in Eq. (A.28) is the expected total number of larvae surviving the defense mechanisms of the flower. Finally, we took

$$\sigma_{pl,nd}(X_{se}, X_{la}) := \exp \left[ - \frac{X_{la}}{\tau_{ss} + \tau_{sc} \cdot X_{se}} \right] \quad (A.29)$$

as the probability of a seed among  $X_{se}$  seeds within a defenseless flower to survive the threat posed by  $X_{la}$  larvae. See DeAngelis and

Holland (2006) for a justification of this formula, based on a model of seed-predators encountering seeds at a rate proportional to their frequency, spending a constant time consuming each seed found. The fixed simulation parameter  $\tau_{ss}$  represents the expected time needed to encounter a single seed,  $\tau_{sc}$  the time needed for the consumption of a single encountered seed.

#### A.2.3. Adult pollinator survival chance

In Appendix A.1.6 the survival chance  $\tau_{po,co}(g_{po}, \rho, \phi)$  of a pollinator of genotype  $g_{po}$  was introduced, with  $\rho$  quantifiable resources available,  $\phi$  expected flights between flower visits and no external threats. Similar to expression (A.27), we adopted the form presented in Appendix B and set

$$\tau_{po,co}(g_{po}, \rho, \phi) := \frac{1}{1 + [\omega_{po} + \omega_{se}(\phi - 1)(n_{vis}(g_{po}) + n_{ovi}(g_{po}))] \cdot \frac{1}{\rho}}. \quad (A.30)$$

The term  $(n_{vis}(g_{po}) + n_{ovi}(g_{po}))$  corresponds to the total number of flowers visited by a pollinator during lifetime. The parameter  $\omega_{po}$ , to be called *pollinator living cost*, can be interpreted as the amount of quantifiable resources needed by a pollinator always landing on inspected flowers and having a survival chance of 1/2. The simulation parameter  $\omega_{se}$ , to be called *pollinator search cost*, corresponds to the cost associated with each flight to a rejected flower.

We supposed the rate  $\delta(g_{pl})$  of fatal events for a pollinator within a given flower of genotype  $g_{pl} \in G_{pl}$  (see Appendix A.1.6) to depend linearly on the accessibility of the flower to alternative pollinators, ranging between a fixed value  $\delta_{cl}$  for closed flowers and  $\delta_{op}$  for open flowers. We thus set

$$\delta(g_{pl}) = \delta_{cl} + (\delta_{op} - \delta_{cl}) \cdot o_{pl}^*,$$

with  $o_{pl}^*$  being the opening of the flower in question.

#### A.2.4. Adult plant survival

We supposed emerging adult plants to be competing with each other for a limited, fixed amount of quantifiable resources, surviving with the probability 1 in case of the latter reaching infinity. In any other case, plants survive with a probability  $\tau_{pl,co}(g_{pl}, N)$  (see Appendix A.1.5) depending solely on their genotype  $g_{pl}$  and on the total number of plants  $N$  in a fashion described in Appendix B. We thus posed

$$\tau_{pl,co}(g_{pl}, N) := \frac{1}{1 + (1 + \omega_{de} \cdot d_{pl}^*) \cdot \frac{N}{k_{pl}}},$$

with the *plant capacity*  $k_{pl}$  as fixed simulation parameter, representing the number of plants without defense mechanisms surviving the adult phase with a probability 1/2. The simulation parameter  $\omega_{de}$ , to be called *plant defense cost*, stands for the cost associated with any existing defense mechanism against larvae (Zavala et al., 2004; Lambers et al., 2008, Chapter 9B).

## Appendix B. Surviving intraspecific competition

We shall here present an interpretation of the logistic growth equation (Verhulst, 1838)

$$\frac{dN}{dt} = \ln(r) \cdot N \cdot \left( 1 - \frac{N}{k} \right), \quad (B.1)$$

for single-species populations of size  $N$  with discrete time dynamics within an environment of limited carrying capacity, in terms of produced offspring and density dependent offspring survival chance. Suppressing the term  $-N/k$  in Eq. (B.1) corresponds to a population with no premature-mortality and constant relative growth rate. Such a population with initial size  $N_0$ , would

reach the size  $N_o \cdot v$  after unit time (one-generation time), thus permitting to interpret  $v$  as number of offspring per individual. As the full Eq. (B.1) results in the size

$$N(1) = \frac{kN_o v}{k + N_o \cdot (v-1)},$$

one can interpret the fraction

$$\frac{N(1)}{N_o r} = \frac{1}{1 + \frac{1}{k} N_o \cdot (v-1)}, \quad (\text{B.2})$$

as the survival probability of a given offspring. Supposing a big number of offspring per individual, that is  $v \gg 1$ , the probability (B.2) takes the form

$$\frac{N(1)}{N_o r} = \frac{1}{1 + \frac{N_o v}{k}},$$

depending solely on the carrying capacity  $k$  of the environment and the number of offspring  $N_o v$  competing for available resources.

### Appendix C. On the computation of plant-opening pressure

In Section 3.1 we mentioned the computation of maps such as the ones in Fig. 1, displaying regions of attractiveness and repulsion by means of evolutionary pressure exerted on flower opening. This pressure was computed for pure open coalitions by introducing slightly more closed mutant plants ( $\sigma_{pl}^* = 0.9$ ) with initial frequency 1 into the equilibrated resident population and computing the ecological equilibrium of the new coalition. Both resident and new populations were each equilibrated through 500 ecological iterations. If  $r_{ini}$  and  $r_{fin}$  denote the fraction of plant-opening alleles with value  $\sigma_{po}^* = 0.9$  in the initial resident and the final population respectively, then

$$p := \frac{1}{(0.9-1.0)} \cdot \ln \frac{r_{fin}}{r_{ini}} \quad (\text{C.1})$$

was taken as an approximation of the fitness gradient with respect to plant opening, for the supposed simulation parameters. A negative value signifies that closed mutants can invade the resident population, a positive one that such mutants tend to go extinct. Note how expression (C.1) can be interpreted as gradient of the Lyapunov exponent for the population growth of an invading mutant of opening  $\sigma_{pl}^*$ , taken at the resident opening.

### Appendix D. Seed production in pure open coalitions

We shall consider in this appendix the seeds initiated in and released (that is, being fertilized and surviving the larval period) by a rare mutant flower of opening  $\sigma_{mu}^* < 1$ , appearing in a pure open coalition without alternative pollinators. Supposing a large number of resident open plants, it is straightforward to show from the models proposed in Section 2.1 and Appendix A.2 that the expected number of seeds released by such a mutant plant is

$$X_{re,own} := n_{ovu} \cdot \pi_{pl,fe}(\text{mut}) \cdot \sigma_{pl,nd}(n_{ovu} \cdot \pi_{pl,fe}(\text{mut}), X_{la}(\text{mut})), \quad (\text{D.1})$$

with

$$\pi_{pl,fe}(\text{mut}) := 1 - \exp \left[ -\pi_{fe} \frac{N_{po}}{N_{pl}} (n_{vis} + n_{ovi}) \cdot \eta(\text{mut}) \right],$$

as probability of a given ovule being fertilized (*initiated*) and

$$X_{la}(\text{mut}) := v_{po} \frac{N_{po}}{N_{pl}} \cdot \eta(\text{mut}),$$

as the expected number of larvae hatching within the mutant plant's flower. Here,  $N_{po}$  and  $N_{pl}$  denote the number of resident pollinators and resident plants respectively at ecological equilibrium,  $s_{po}^*$  the tolerance of the resident pollinators and

$$\eta(\text{mut}) := \exp \left[ -\frac{(1 - \sigma_{mu}^*)^2}{2\mathcal{V}(s_{po}^*)} \right],$$

the probability of a resident pollinator entering a mutant flower upon inspection, as introduced in Appendix A.1.1 and elaborated on in Section 2.3. The functions  $\sigma_{pl,nd}$  and  $\mathcal{V}$  are given by Eq. (A.29) and Eq. (2) respectively. The factor

$$\sigma_{pl,nd}(n_{ovu} \cdot \pi_{pl,fe}(\text{mut}), X_{la}(\text{mut})),$$

in expression (D.1) corresponds to the probability of an initiated seed of a mutant plant not being consumed by larvae. Similarly, one finds the expected number of seeds released by resident plants and fertilized by the mutant to be

$$X_{re,res} := n_{ovu} \cdot \pi_{pl,fe}(\text{mut}) \cdot \eta(\text{mut}) \cdot \sigma_{pl,nd}(n_{ovu} \cdot \pi_{pl,fe}(\text{res}), X_{la}(\text{res})),$$

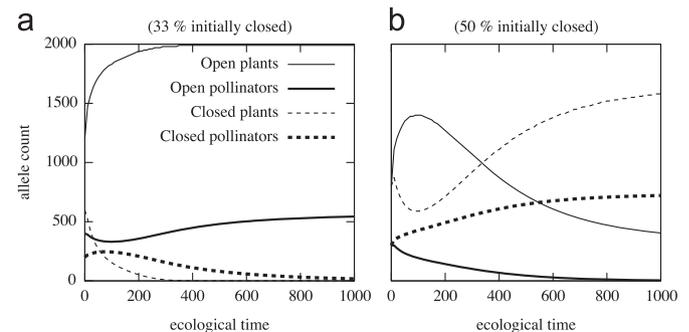
with

$$\pi_{pl,fe}(\text{res}) := 1 - \exp \left[ -\pi_{fe} \frac{N_{po}}{N_{pl}} (n_{vis} + n_{ovi}) \right],$$

as probability of a given resident ovule being initialized and  $X_{la}(\text{res}) := v_{po} \cdot N_{po}/N_{pl}$  as the expected number of larvae hatching within a resident flower. The total number of seeds released within the population, carrying the genes of the mutant, is the sum  $X_{re} := X_{re,own} + X_{re,res}$ . Note that we neglect the small possibility of the mutant fertilizing other rare mutants. As a rare mutant plant does not significantly distort ecological equilibrium, we can suppose  $N_{po}$  and  $N_{pl}$  to be fixed for various values of  $\sigma_{mu}^*$ , thus obtaining  $X_{re,own}$ ,  $X_{re,res}$  and  $X_{re}$  as functions of  $\sigma_{mu}^* \in [0, 1]$  with all simulation parameters as shape parameters.

### Appendix E. Invasion of pure open coalitions

Fig. E1 illustrates the ecological dynamics describing the invasion or extinction of mutant closed plants and pollinators introduced simultaneously into a pure open coalition, for two different initial mutant frequencies. In the first and second case, closed mutants each make up initially 33% and 50% of the total population respectively. In the first case, closed pollinators rise at



**Fig. E1.** Population dynamics for a pure open coalition (*resident population*) starting alongside with more closed plants ( $\sigma_{pl}^* = 0.75$ ) and pollinators ( $\sigma_{po}^* = 0.75$ ) (*mutants*). The graphs show the change of open and closed allele frequencies in the population as it approaches its equilibrium after approximately 1000 ecological iterations. Model parameters used were  $\omega_{po} = 1$ ,  $\omega_{se} = 0.001$ ,  $\delta_{cl} = 0$ ,  $N_{po}(\text{alt}) = 500$  and otherwise given by Table 1. (a) Closed plants and pollinators each initially make up 33% of the total plant and pollinator population respectively but still go extinct. (b) Closed plants and pollinators each initially make up 50% of the total plant and pollinator population respectively and invade the resident coalition.

first in numbers but finally go extinct as resident plants prevail too quickly, annulling any initial advantage closed pollinators may have had. In the second case, closed pollinators manage to multiply quickly enough for closed plants to find an advantage over their open relatives as well, so that closed mutants eventually invade the resident population. Note the high frequency thresholds needed for mutants to be able to invade.

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