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# Competition and pollen wars: simulations reveal the dynamics of competition mediated through heterospecific pollen transfer by non-flower constant insects

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## Abstract

Heterospecific pollen transfer by insect pollinators has the potential to drive inter-species competition between flowering plants. This phenomenon may newly arise in a region if insect pollinator or flowering plant populations change. An agent-based simulation is presented to assess the potential impact of heterospecific pollen transfer by insects on two co-flowering plant species within an environment consisting of a shared central region and species-specific refugia. Where heterospecific pollen asymmetrically suppressed the reproduction of one competitor, the pollen recipient was rapidly ousted from shared regions. If pollinators made deep, repeated, forays into and out of plant refugia, the clogged species was even unseated from its own refugium. When heterospecific pollen symmetrically suppressed plant reproduction, the same effects were observed, but with one or the other species excluded at random by the pollen clogging mediated interaction. We conclude that both symmetrical and asymmetrical heterospecific pollen transfer may be important elements of inter-species dynamics. In particular, our simulation shows pollen and pollinator visits lost to heterospecific flowers may not always be wasted from the producer's standpoint. Instead, heterospecific pollen delivery may convey a competitive advantage even when the recipient has a refuge safe from direct invasion. This is possible because the pollen producer may use pollinators to clog a competitor's stigmas in a refugium without entering into competition there for space, nutrients, light, pollinators, or other resources. Consequently, the evolution of plant signals to promote pollinator constancy may not be the only effective strategy in inter-species competition.

**Keywords** Insect pollination · Heterospecific pollen transfer · Agent-based model · Flower constancy

**Author summary** Once honeybees learn to associate nectar or pollen rewards with a specific type of flower, they often prefer to keep visiting the same species whilst foraging to maintain their own efficiency. This also has the benefit for the flower's reproductive cycle, of making honeybees a reliable pollen vector and key partner in plant fitness. Sometimes, however, this insect "flower constancy" breaks down, and not all flower visitors are so constant in their behaviours. A flower visitor may thus incidentally take pollen from one flower species and deliver it to a different species. Considering the plant that provided the pollen, this is potentially a wasted opportunity for reproduction since its pollen is seemingly lost for no reproductive gain. Our simulations reveal, however, how lost pollen may actually provide a competitive advantage by inhibiting the reproduction of a plant's competitors, even if the competitor occupies a refuge zone immune from physical invasion by the pollen donor at that time. Our results demonstrate the potential impact of this interaction on plant community assembly and provide key insights with implications for wildflower conservation, field margin maintenance, and pollination-dependent food production.

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## Introduction

Flowering plant species may compete against one another for nutrients, water, light, space, and pollinators (Chittka and Schürkens 2001). Competition might also occur through heterospecific pollen transfer. For this transfer to be facilitated by an insect, some basic conditions must be met. These include that the flowers be collocated within the foraging range of an individual pollinator; that the two plants share that visitor; that there is overlap in the species' flowering periods; and that pollen is deposited on, and retrieved from, the same position on the body of the insect by each species' flowers. Finally, the likelihood of interspecies pollen transfer is potentially high if the insect is imperfectly flower-constant, but visits both species of flower on a bout or within a period during which pollen from a heterospecific visit stays on its body.

The non-flower-constancy of insects potentially has a significant impact on plant reproduction for the pollen producer (Wilcock and Neiland 2002; Morales and Traveset 2008). However, impacts may also be felt indirectly by the recipient of heterospecific pollen.

Heterospecific pollen deposition is known to be common, with one meta-analysis finding that of 77 angiosperm species from 31 families, all received at least some pollen from co-flowering species, and more than a half of them received it in more than a half of their flowers (Ashman and Arceo-Gómez 2013). It was noted by Ashman and Arceo-Gómez that sometimes heterospecific pollen loads were low, but that it has been shown previously that even low percentages may biochemically suppress the reproduction of the recipient (Thomson et al. 1981). Several studies have assessed the impact of heterospecific pollen from mixed communities of flowering plants in nature, and in hand pollination experiments, but clear effects have been difficult to ascertain and outcomes vary from case to case (See survey (Morales and Traveset 2008), especially their summary Table 2, and (McLernon et al. 1996)). Given this variation in the empirical evidence, helpful clarity might come from a mathematical model (Levin and Anderson 1970), or, as we present here, a simulation (Waser 1978; Campbell 1986). For the purposes of our study, we identify two ways in which the presence of heterospecific plants and non-constant pollinators may represent a reproductive cost to donors and recipients of heterospecific pollen:

i. *Undelivered pollen/wasted pollen.* This may occur because pollen is deposited on heterospecific stigmas by an inconstant pollinator, a direct loss which we model, or because more pollen is mechanically dislodged, actively groomed, or consumed between floral visits when another plant species is present. Although such indirect losses can occur even during flight between conspecific plants, the presence of heterospecific flowers is known to alter pollinator travel times or behaviours between visits (Flanagan et al. 2009). We do not model these latter phenomena here.

ii. *Stigma and ovule interference.* Pollen from one species deposited onto the stigma of another species may mechanically block stigmatic surface from access by reproductively useful conspecific pollen (pollen clogging), induce stigma closure, usurp stylar conducting tissue or ovules if heterospecific pollen tubes develop before conspecific tubes do, or cause chemical inhibition of pollination even when conspecific pollen arrives (allelopathy) (Thomson et al. 1981; Waser and Fugate 1986; Harder et al. 1993; Wilcock and Neiland 2002).

These are costs, the first to the source and the second to the recipient, of a heterospecific pollinator visit. Heterospecific pollen transfer is (presumably) always detrimental or neutral to the recipient, and a pollen loss to the donor. It can be, however, that the donor benefits competitively over the heterospecific pollen recipient, despite the lost opportunity for conspecific pollen transfer. This mechanism of interference competition has been examined experimentally for specific species (e.g. Waser and Fugate (1986) and Caruso and Alfaro (2000)) but its potential to impact a spatially distributed community of plants with shared pollinators has not yet been thoroughly explored. This is therefore the main aim of the present study.

The relationship between plants exchanging hetrospecific pollen might conceivably be symmetrical, with pollen of each species interfering with female reproductive success of the other species. Or, it may be asymmetrical, with only one species' pollen lowering reproductive success of the other's female flowers (see Table 1) (Morales and Traveset 2008; Fang and Huang 2013; Moreira-Hernández and Muchhala 2019). How do the dynamics of these scenarios differ? How do they differ from the case in which neither species directly interferes with the reproduction of the other?

By operating within a simulation framework consistent with that of earlier authors (Waser 1978; Campbell 1986), we seek to understand how interspecies dynamics generated by pollen dispersal and receipt might drive relationships between two populations of flowering plants. Our new contribution facilitates a direct comparison of the dynamics of the interactions between the flowering plants competing for an insect pollinator under symmetrical and asymmetrical pollen clogging and non-pollen clogging scenarios. We test if, and under what conditions, these interactions might enable one plant to exclude another, and how the dynamics of the scenarios differ.

Agent-based and computer models of search movements are an established technique to study the implications of animal foraging and navigation (Mueller et al. 2011) and flower selection through different visual systems (Gegear and Burns

**Table 1** The possibilities for pollen clogging of two co-flowering, self-incompatible plant species (X and Y)

|  |  | **X clogs Y** |  |
|---|---|---|---|
|  |  | Yes | No |
| **Y clogs X** | Yes | Case 1<br>Symmetrical clogging | Case 2b<br>Asymmetrical |
|  | No | Case 2a<br>Asymmetrical | Case 3<br>Symmetrical non-clogging |

2007; Bukovac et al. 2017). Here, as is often done, we will use such a model for theoretical explorations (Edmonds et al. 2019). An early agent-based simulation sets a precedent for unravelling some potential implications of heterospecific pollen delivery (Waser 1978). Following Waser, Campbell (1986) detailed a specific case of insect-mediated pollen transfer between co-flowering herbs.

The simulation we present here explores theoretical questions modelled on Waser's (1978) section *(4) Effects of Refugia* arising from experimental configurations unaddressed in the earlier study. Specifically, we explore the potential for a competitive advantage to be gained by a pollen-losing species over the heterospecific pollen recipient, and the population dynamics of these situations in cases where species have refugia safe from direct invasion by competitors, but through which a shared pollinator may move.

## Materials and methods

The following section is based on the ODD protocol for agent-based models (Grimm et al. 2010).

### Purpose

Our goal was to explore the potential for inter-species competition between plants, mediated through heterospecific pollen deposition by insect pollinators, within habitat that is impervious to direct invasion by the pollen producer. To this end, we constructed a simulation of two species of self-incompatible flowering plants, blooming simultaneously, and sharing a single insect pollinator species.

### Entities, state variables, and scales

Pollen distribution is inherently spatial, density dependent and affected by pollinator behaviour. In this study, we model a plant population within a shared zone, bordered by two species-specific refugia. We explore the resulting population dynamics when the region is subject to pollen distribution by non-flower constant insects. Parameters are summarised in Table 1-Sup and detailed in the relevant subsections below.

### The environment model

Distances within our simulated environment are specified in pollinator-neutral "perceptual distance units" (pdu) and are not specific to any particular insect. We model flowers within the environment as undetected by insects at distances > 1 pdu and certainly detected at < 1 pdu. This is based on what is known of bumblebee vision, where detection approximates a step function as a physiologically mediated perceptual threshold is crossed at a distance of approximately 0.7 m from a flower (Dyer et al. 2008; Wertlen et al. 2008). This scale is used as the reference measure in our model environment, which contains a large 2D continuous central region of 120 × 200 pdu shared by the two plant species. Waser (1978) introduced two peripheral refugia in his experiment (4) *Effects of Refugia*, which we replicated. On either side of the central region are two refuge strips (40 × 200 pdu), each assigned to one or the other species, making the entire environment 200 × 200 pdu.

### Pollinator agent model

Each pollinator tracks its current position and heading as it moves. It carries pollen collected from flower visits and maintains a memory of its five most recently visited flowers. It will not revisit any flower on this list, in keeping with empirical data on bee short-term memory, scent marking, and foraging behaviour (Brown and Demas 1994; Giurfa et al. 1994). Each pollinator has a foraging strategy, either *Forage Nearest* flower or *Forage Any* flower (sect. Process overview and scheduling – Pollinator dynamics).

### Flower/plant agent model

Each modelled plant is assigned to one of the two species and a fixed position. For simplicity, plants have a single flower that acts as a proxy for an inflorescence. An insect may view this from a distance as a unitary colour signal for many temperate zone herbaceous plants (Dyer et al. 2008). Flowers begin with a fixed number of collectable pollen grains and the depletion from pollinator visits is tracked. During insect visits, a fixed number of anther pollen grains are transferred to the pollinator's body. The flower's stigma records pollen that visitors deposit (either conspecific or heterospecific grains) up to the capacity set by a parameter for stigma space. Each conspecific grain received is assumed to fertilise one available ovule of the fixed number of ovules per flower and so in our model, stigma space and ovule count are equivalent (Table 1-Sup).

## Pollen agent model

Pollen grains record the individual flower that produced them, their species, and (when travelling on a pollinator's body) the number of flowers the pollinator has visited since collecting the grain. In our simulation, pollen can be transferred only from anther, to pollinator body, to stigma, or lost to the environment.

## Process overview and scheduling

**Overview of dynamics: Foraging and reproduction phases** The simulation cycles through two distinct phases. These are an *insect foraging-pollination phase*, which in reality spans the course of a flowering season, and the resultant *plant reproduction phase* which may take months. One iteration through both phases constitutes a generation; thus, plants in the model are monocarpic. During a foraging-pollination phase, insects forage from the fixed population of flowers, transferring pollen between them as they visit. This proceeds in discrete steps and ends after a specified limit. At this point, the plant reproduction phase begins.

During the plant reproduction phase, viable seeds from pollinated plants form the seed bank for a new plant generation. All plants and pollinators from the previous generation are removed, and new plants are created based upon parent seeds picked at random (without replacement) from the seed bank. New plants are distributed locally using a uniform random distribution to compute the angle of dispersal in the horizontal plane, and a Gaussian distribution to compute radial distance from the parent. If a seed of one plant species lands in the refugium of the other, it is removed from the simulation (it is inviable). New plants are drawn until the seed bank is exhausted, or until the maximum carrying capacity of the refugia and environment are reached. A new population of pollinators is then created and distributed to random starting positions in the environment. Then the foraging-pollination phase of a new generation commences. The simulation loop cycles through a specified number of generations.

**Pollinator dynamics** Each foraging-pollination phase begins with a population of pollinators distributed uniform-randomly across the environment. At each time step, during the foraging-pollination phase, the update order of pollinators is randomised. Each pollinator executes a new foraging behaviour iteration in each simulation time step to collect pollen from flowers as it follows a foraging strategy. Multiple pollinators may land on a single flower within a time step, but pollinators do not directly interact with one another.

A pollinator following the Forage Nearest flower strategy (Fig. 1a) moves to and lands on the nearest flower within a search radius of 1 pdu from its current position that does not appear on its recently visited flower list. This style of foraging imitates movements common for honeybees and other bees also (Anderson and Symon 1988). If no suitable flower is available, the pollinator moves 1 pdu in a uniform-random direction. This is not a movement pattern of real insects, but since we are interested in the relative success of flowering plants, as long as we are consistent this is sufficient (Bukovac et al. 2013).

A pollinator following the Forage Any flower strategy (Fig. 1b) picks a flower to visit at random from all flowers in the entire environment, excluding those on its recently visited list. This strategy was introduced to assess the potential impact of the spatial cohesiveness of insect movement. Bouts that bypass many flowers are typical of trap-lining insects (for instance globally significant pollinators, *Amegilla* spp., Anthophorini: Hymenoptera) whose behaviour has, for some species, been contrasted against that of bees tending to explore locally (Anderson and Symon 1988). Long movements have also been observed in bumblebees (*Bombus* spp., Bombini: Hymenoptera) when making decisions to switch flower species during a bout (Chittka et al. 1997). We do not model the repetition characteristic of trap-lining, or decision-making based on rewards, only the range over which bee movements potentially spread pollen. Behaviours in which flowers of the most recently visited flower species are bypassed in order to visit next a more distant flower of a different species are complex and may be related to the salience of the flower species and other factors (Chittka et al. 1997). We comment on this further in the "Discussion" section.

Pollen transfer occurs during pollinator flower visits (sect. Pollinator action on flowers).

**Flower dynamics** Each flower begins a simulation foraging phase with a fixed amount of pollen available in its anthers for collection and a stigma free from pollen. As the foraging phase progresses, visiting pollinators may deposit pollen on its stigma. Pollinators may be allowed to deposit pollen from a different species onto the stigma (potentially pollen clogging the flower) depending upon experimental configuration (Table 1). A parameter specifies the capacity for pollen grains on a stigma (which, for simplicity, we take as equal to the ovule number per flower, although in nature this may not be the case). At the end of a

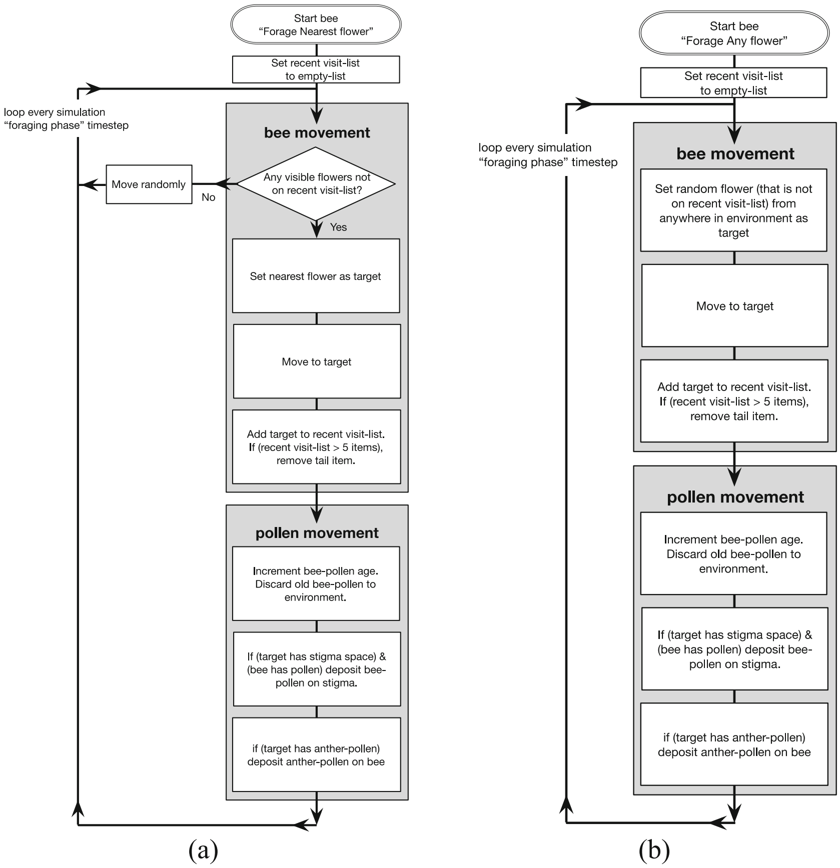

**Fig. 1** Flow charts for individual pollinator agents following Forage Nearest flower strategy (**a**) and Forage Any flower strategy (**b**). Bee-pollen refers to pollen carried on the body of the insect and potentially available for deposition on the stigma of a flower for pollination or pollen clogging. Anther-pollen refers to pollen carried on a flower anther and potentially available for deposition on the body of a bee

foraging phase, every conspecific pollen grain on the stigma forms a viable seed that enters the seed bank.

**Pollinator action on flowers** Each pollen grain carried by a pollinator visiting a flower is considered for transfer to a stigma subject to these limiting factors: the pollinator has a fixed maximum number of grains it can transfer to the stigma per visit; the stigma has a fixed capacity for accepting pollen grains, and the stigma may or may not be susceptible to receiving heterospecific grains (above, sect. Flower dynamics). If any grains on the pollinator are eligible, the determined number are picked at random and transferred to the stigma. If heterospecific transfer is disabled in an experiment, selected heterospecific grains are lost to the environment instead. Finally, the flower may transfer pollen it has remaining in its anthers to the pollinator up to the fixed transfer limit per visit.

## Design concepts

**Basic principles** Parameter values relating to pollen production, transportation, and deposition match those of Waser as determined from biological data (Waser 1978, p. 233) except that in the earlier work, absolute values for pollen produced per flower were small due to limitations of 1970s computers. We tested our simulations with larger absolute values for these parameters whilst retaining the same ratios, to determine that our runs did not suffer from sampling error effects mentioned by Waser (sect. Testing -Verification, validation, and sensitivity analysis), before we used these values in our experiments.

Other notable differences between our model and Waser's are our use of a continuous spatial environment and that our use of modern computers allows us to simulate much larger environments than was feasible in 1978. We have determined empirically that the values we use both generate model behaviour matching that of Waser's simulations and robust system behaviour for exploration of our own hypotheses (sect. Testing - Verification, validation, and sensitivity analysis).

**Emergence** The key emergent properties of interest are the timespans and interaction dynamics of plant species' coexistence under different pollen clogging configurations.

**Adaptation, objectives, learning, and prediction** Insect agents follow their foraging strategy, only making a pseudo-decision to move randomly if they cannot see an unvisited flower from their present position whilst conducting the Forage Nearest flower strategy. Alternative decisions are not evaluated. Agents have no learning or predictive capabilities.

**Sensing** Insect agents can perceive flowers within a single perceptual distance unit (pdu). They maintain a flower-memory/scent marking and detection capability enabling them to identify if an individual flower has been visited by them in the last five visits.

**Interaction** Multiple insects may visit a flower within a time step, but insects do not interact with one another directly (sect. Pollinator dynamics). At each visit, pollen may be transferred from insect to flower stigma and from flower anther to insect (sect. Pollinator action on flowers), or the pollen may be lost to the environment.

**Stochasticity** Stochastic elements of the simulation are the following: placement of flowers and pollinators at the start of a foraging phase; order of pollinator update and pollen transfer during the foraging phase; direction a pollinator moves if it is unable to find a suitable flower target; choice of target for the Forage Any flower strategy; selection of individual pollen grains for transfer from insect to stigma or from anther to insect body upon landing; and, in the reproduction phase, the order in which viable seeds are selected for the next generation and the distribution of seeds from a parent plant.

**Observation** In our experiments, the main data recorded are the number of plants of each species at the end of a generation.

## Initialisation

Table 1-Sup provides the parameters used to initialise each of the experiments. Table 1 presents the simulated pollen clogging scenarios. Whether or not pollen clogging occurs in any specific (real) ecological case will depend on floral and insect morphology and insect behaviours that affect pollen transfer. For instance, a plant species X might require precise pollen placement and retrieval while species Y may deposit and remove pollen from many locations on a visitor's body. In this case, species Y could be susceptible to pollen clogging by species X while X is less susceptible to clogging by Y (Table 1, case 2a or, vice versa, case 2b). If both plant species are specialists and deposit pollen onto a particular part of an insect body unused by co-flowering plants, pollen clogging need not occur, even with non-constant pollinators (case 3). Or perhaps both are generalists that clog one another (case 1). Our simulation explores how each case affects population dynamics as plants reproduce across multiple seasons.

We ran 100 replicates of the experimental cases (Table 1) for foraging strategy Forage Nearest flower or Forage Any flower, depending on the experiment, to ensure reliable separation of mean performance within the stochastic variability of the simulation as reported in the "Results" section. Simulations were run with and without plant refugia (Sect. The environment model), and depending on the experiment, with 1, 5, or 50 ovules per flower to understand sensitivity of results to this parameter.

**Testing—Verification, validation, and sensitivity analysis** Standard software-engineering procedures ensured code was checked during development. Correct operation was verified as follows. We ran the simulation with real-time environment visualisation showing plant species distributions, flower pollination status, and pollinator movement trails. We used this facility for visual debugging (Dorin and Geard 2014) and to "sanity check" plant and pollinator behaviour. We wrote the software ourselves from scratch in C++ using standard software debugging tools and logs to verify pollen transfer.

To validate the basic flower species fixation behaviour of our agent-based pollination model against a purely stochastic model, we executed Stochastic Fixation Control experiments (see Sup). After confirming that the simulation behaved as expected, we validated its behaviour against Waser's experiments 1, 2, and 3 (Waser 1978) and tested its sensitivity to large environment and population sizes, and its performance over long runs, with parameters detailed in Table 1-Sup and explained above. Our simulation generated the same qualitative results as Waser's—fixation by one plant species occurred after a small number of generations.

## Results

### No refugia, forage nearest flower, ovules = 5

This configuration represents a situation with two co-flowering, co-habiting species, and no refugia (Table 2). In the no clogging scenario, 86% of the time the two species co-existed for the full 1000 generations. In the remaining 14% of runs, X fixated 9 times, Y 5 times. This small number of fixations each took over 400 generations to arrive (Fig. 2a). As illustrated in the corresponding sample run (Fig. 2d), the inter-species dynamics are not forced in any particular direction; instead, plant populations fluctuate stochastically. Similar stochastic fluctuations occur with symmetrical two-way clogging (Fig. 2c and f) for which 87% of runs did not end in fixation, with X fixated 4% of the remaining runs and Y fixated in 9% of runs.

With 1-way clogging, in all runs, the species that clogged its competitor went rapidly to fixation (Table 2) with a mean of 10.49 generations (s.d. 7.09) (Fig. 2b and e). In none of these runs did the clogged species survive beyond 66 generations (Fig. 2b).

The above scenarios describe simulations with five ovules per plant (Table 1-Sup). These experiments were re-run with one and fifty ovules per plant to explore the impact of this parameter. With one ovule per plant, neither species survived to the conclusion of any run, regardless of pollen clogging scenario. The limited reproductive scope afforded by a single ovule would

**Table 2** Fixation and dominance time statistics for simulation configuration with Forage Nearest flower strategy, local seed dispersal (radius s.d. = 3 pdu), 5 ovules/flower, 200 × 200 pdu central shared region, no refugia, run length = 1000 gens, $N$ = 100 runs. Mean values were computed only from runs in which fixation/dominance occurred

| No refugia ovules = 5 | Fixation time (generations) | | Dominance time (generations) | | Species X vs Y | | | |
|---|---|---|---|---|---|---|---|---|
| | Mean | std. dev. | Mean | std. dev. | $N$ | Runs X fixated | Runs Y fixated | Runs no fixation |
| No clogging | 764.21 | 170.53 | 40.21 | 40.28 | 100 | 9 | 5 | 86 |
| 1-way clogging | 10.49 | 7.09 | 1.00 | 0.00 | 100 | 100 | 0 | 0 |
| 2-way clogging | 805.46 | 148.59 | 84.38 | 116.51 | 100 | 4 | 9 | 87 |

not allow persistence in the model environment. With fifty ovules per plant, results qualitatively matched those for five ovules. That is, for the symmetrical conditions of no clogging and 2-way clogging, each species was observed to have approximately even chances of drifting to extinction/fixation in a fraction of the total runs. With 1-way clogging, the clogged species was rapidly excluded—albeit less rapidly and with greater variability than with five ovules per plant (Table 2-Sup).

Together these experiments with different ovule numbers per flower give weight to our standard configuration of five ovules providing reproductive scenarios unconstrained by pollen, pollinator or ovule availability. Instead, the loss of a

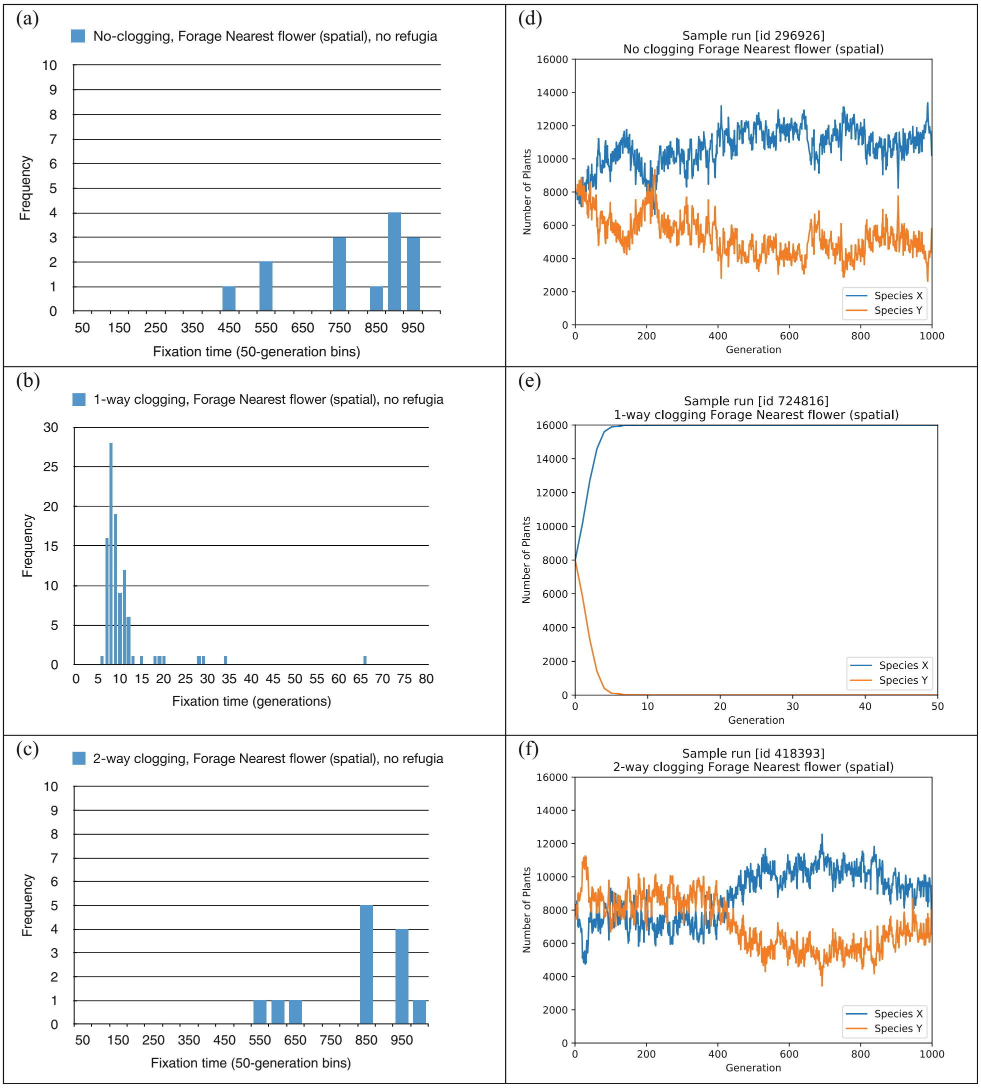

**Fig. 2** Simulation configurations with Forage Nearest flower strategy, local seed dispersal (radius s.d. = 3 pdu), 5 ovules/flower, 200 × 200 pdu shared region, no refugia, run length = 1000 gens, $N$ = 100 runs. Frequency plots of runs vs fixation time for pollen clogging configurations: no clogging (**a**), 1-way clogging (**b**), 2-way clogging (**c**). Sample runs demonstrating plant population dynamics over the simulation period illustrating no clogging stochastic behaviour (**d**), 1-way clogging driven exclusion (**e**), and 2-way clogging stochastic behaviour (**f**)

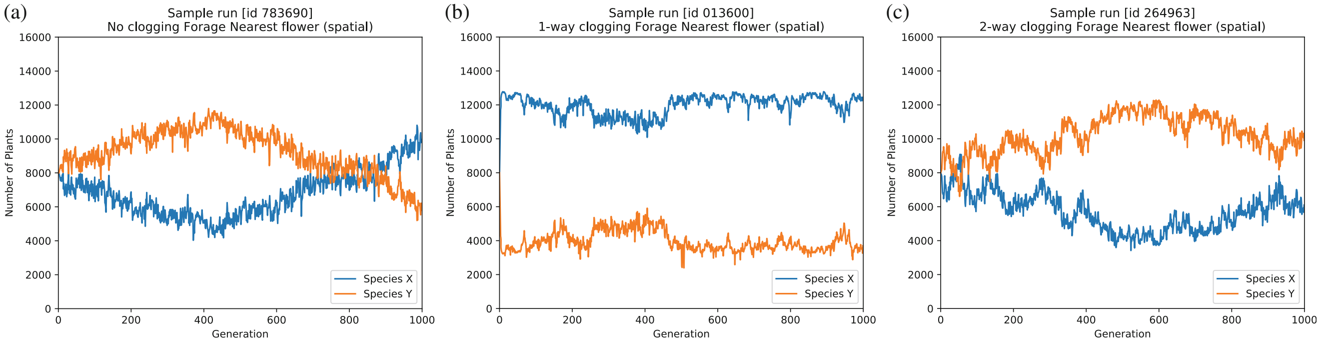

**Fig. 3** Sample runs for simulation configurations with Forage Nearest flower strategy, local seed dispersal (radius s. d. = 3 pdu), 5 ovules/flower, 120 × 200 pdu central shared region, 2 species-specific plant refugia of 40 × 200 pdu, run length = 1000 gens, and pollen clogging configurations: no clogging (**a**), 1-way clogging (**b**), 2-way clogging (**c**). Sample runs demonstrate plant population dynamics over the simulation period illustrating the highly stochastic dynamics with refugia of no clogging (**a**) and 2-way clogging (**c**). This can be compared here to the driven reduction in female reproductive success of the clogged species in the 1-way clogging scenario (**b**). Within the shared central region, the clogged species is outcompeted within the very first few generations. From then on, the majority of its population is maintained in its refugium (around its maximum capacity of 3200 plants)

species when it occurs in our runs is due to stochastic drift or pollen clogging.

## Refugia, forage nearest flower, ovules = 5

This configuration represents the situation with two co-flowering, co-habiting species occupying a central region bordered on two opposing sides by species-specific refugia. In no case did a plant species go to fixation. As shown in the sample runs (Fig. 3 a–c), stochastic fluctuations occur in the populations. However, in the 1-way clogging scenario, although fluctuations still occur and the clogging species dominates the shared central region (carrying capacity 9600 plants based on density parameter of 0.4 plants/pdu$^2$) and its refuge (capacity 3200 plants), the clogged species remains safe in its own refuge (capacity 3200 plants).

## Refugia, forage any flower, ovules = 5

This configuration represents a situation like that described immediately above except that the insects here conduct the Forage Any flower strategy which distributes pollen randomly across the foraging space within the refugia and central shared region (Table 3). The no clogging scenario (Fig. 4a) plays out much as it did before (Fig. 3a), but the 1-way and 2-way clogging scenarios (Fig. 4b and c) differ from their spatially coherent foraging counterparts. In the a-spatial case, pollen flow across refuge boundaries excludes one or the other species in every run from both the central region *and* its refuge. This exclusion occurs consistently, smoothly, and rapidly with means of 16.62 (s.d. 1.36) and 19.45 (s.d. 2.29) generations for 1-way and 2-way clogging respectively.

# Discussion

Our results support the hypothesis that heterospecific pollen deposition has the potential to act as an “infertility bomb”. Under some circumstances, this may drive the exclusion of a competitor from a region that both plant species could otherwise potentially coinhabit.

The model we have implemented captures key aspects of heterospecific pollen transfer that allow us to draw such conclusions to a point, but extension in a number of ways would be worthwhile. In particular, the likelihood of bees switching from one floral species to another is known to be related to

**Table 3** Fixation and dominance time statistics for simulation configuration with the a-spatial Forage Any flower strategy, local seed dispersal (radius s.d. = 3 pdu), 5 ovules/flower, 120 × 200 pdu central shared region, 2 species-specific plant refugia of 40 × 200 pdu, run length = 1000 gens, $N$ = 100 runs

| With refugia ovules = 5 | Fixation time (generations) | | Dominance time (generations) | | Species X vs Y | | | |
|---|---|---|---|---|---|---|---|---|
| | Mean | std. dev. | Mean | std. dev. | $N$ | Runs with X fixated | Runs with Y fixated | Runs with no fixation |
| No clogging | n/a | n/a | n/a | n/a | 100 | 0 | 0 | 100 |
| 1-way clogging | 16.62 | 1.36 | 1.00 | 0.0 | 100 | 100 | 0 | 0 |
| 2-way clogging | 19.45 | 2.29 | 1.77 | 1.55 | 100 | 53 | 47 | 0 |

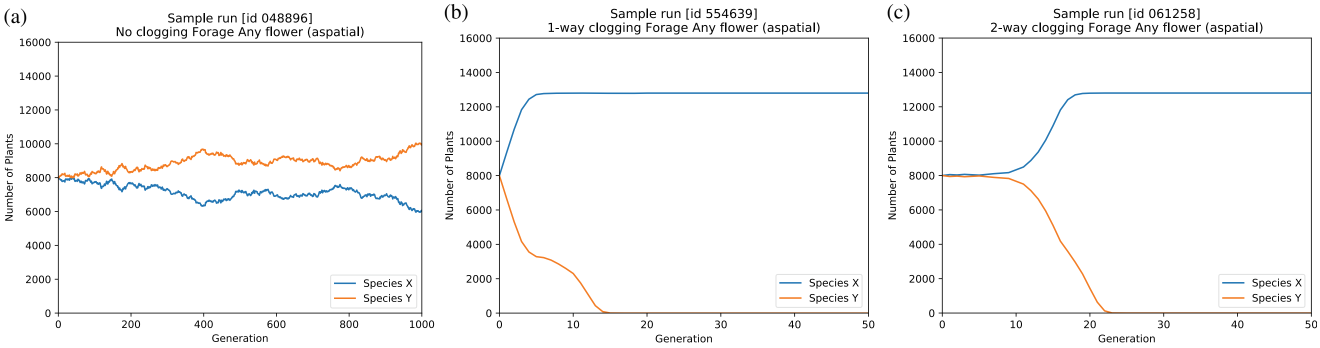

**Fig. 4** Sample runs for simulation configurations with the a-spatial Forage Any flower strategy, local seed dispersal (radius s.d. = 3 pdu), 5 ovules/flower, 120 × 200 pdu central shared region, 2 species-specific plant refugia of 40 × 200 pdu, and pollen clogging configurations: no clogging (plotted over 1000 generations) (**a**), 1-way clogging (plotted only over 50 generations since fixation occurs after 15 gens) (**b**), 2-way clogging (plotted only over 50 generations since fixation occurs after 21 gens) (**c**). The sample runs demonstrate the impact of the wide pollen dispersal by the a-spatial insects in this simulation when compared to the conventional spatial Forage Nearest flower (cf. Fig. 3 which, apart from foraging strategy, is parameterised identically to this experiment). In a run with no clogging (**a**), plant population dynamics over the simulation period remain stochastic as for the Forage Nearest strategy. But with both 1-way (**b**) and 2-way clogging (**c**), exclusion of one species from the central region is rapid (population of one species drops to 3200 plants), and this is shortly followed by its complete exclusion even from its refuge

complex factors that include past foraging success, flower handling time, and the salience of the difference in floral signals the species exhibit (Chittka et al. 1997). We have modelled flower choice and insect navigation as partially random processes, an obvious place from which to start. But further studies to elucidate the different impacts of more elaborate, realistic, and species-specific processes of insect floral selection (based on insect colour vision and cognition for example) and navigation (such as occurs in trap-lining) would be worthwhile also. We note too that whilst our model focuses on insects, birds are also important floral pollinators that may distribute pollen much further than insects. A comparison of the simulated impacts of such long-range foraging to that of insects would allow us to better understand the potential implications of pollen clogging between species that might not be close neighbours.

As they are currently implemented, our simulations without refugia and with symmetrical situations where both or neither species suffered pollen clogging resulted in a stochastic drift in the populations of the two plants with no clear statistical or qualitative differences apparent between the situations (Table 2 and Fig. 2). Still, almost 15% of the time this scenario resulted in exclusion of one or the other species at random with the population and environment sizes we described. In the remainder of the runs, the two plant species co-existed to the end of their 1000-generation run. Whilst stochastic, undriven dynamics link exclusion simply to environment size and/or carrying capacity, in the case of asymmetrical 1-way clogging, our simulations behaved differently. The clogged species was consistently and rapidly excluded from the environment within very few generations (compare *x*-axis scales for Fig. 2e against Fig. 2d and f) in a dynamic that appears driven.

With plant refugia of the capacity we implemented, the clogged species maintained a viable population in its refuge in all scenarios in which a Forage Nearest flower pollinator strategy was acting, even when species suffered reproductive loss associated with 1-way heterospecific pollen receipt and clogging. But under clogging, the clogged species was unable to use its refugium as a base from which to make inroads into the shared region where it was always outcompeted.

The exclusory action of pollen clogging intensified when pollen dispersal by insects was widened through the Forage Any flower strategy. This is expected since the local dispersal of seeds from parent plants has the effect of creating buffer zones within which conspecific pollen is more likely to be delivered than heterospecific pollen. The bigger and denser the zone, the lower the chance it will be infiltrated by heterospecific pollen. Refugia are an environmentally enforced example of this buffering, but local seed dispersal generates patchy buffers too. Any tendency of insects to hop between flower patches, as we simulate with the Forage Any flower strategy, reduces the impact of spatial buffering on heterospecific pollen transfer.

With the a-spatial Forage Any flower insect behaviour, pollen delivery caused the rapid, smooth decline, and elimination of clogged plants, even from refugia (Table 3). In the 1-way clogging scenario, the clogged species was always immediately rapidly excluded. The sample run (Fig. 4b) shows the population's initial rapid loss from the central shared region. This is slowed slightly as the clogged species retains some hold on its refuge with a capacity of 3200 plants, but then even this falls away as the competitor has its "pollen bombs" delivered by non-flower constant insects across the refuge boundary into its competitor's territory. Ultimately the clogged species is lost even from the refuge.

In the symmetrical 2-way case, one or the other species at random gained the upper hand and then rapidly excluded its competitor from the shared region and its refuge in all runs also. Without pollen clogging as a contributing factor, neither species was ever eliminated from the environment within the 1000 generations of our runs, giving further credence to the idea that heterospecific pollen transfer, even if it is bilateral, changes the interaction dynamics of plant populations, especially when insects are poorly flower-constant.

The rates at which interactions mediated by pollen clogging act in the real world would need to be determined for specific plant-pollinator scenarios. Rates would be expected to vary depending on the tendencies and the mechanisms by which pollen might clog fertilisation of ovules from one species or another. Rates would also vary with the tendencies of insects to be flower constant, something which in turn relates to their behaviours and sensory capabilities (Chittka et al. 1999). However, the simulations tend to indicate that we might expect relative rates of exclusion to be marked in the real world, since clear qualitative distinctions and quantitative values differing by an order of magnitude were found under simulated non-clogging and pollen clogging scenarios.

Implications for plant communities and plant evolution

When pollen availability limits plant reproduction, pollen loss would be expected to play an important role in interspecies competition. Consequently, increasing the reliability of pollen delivery to conspecifics may increase an individual's reproductive success in these scenarios. We might therefore expect to find that plants have evolved characteristics to support pollinator flower-constancy including the presence of rewards, and colours or forms detectable to pollinators and distinguishable from other co-flowering species (Goulson 1994). However, nature's complexity can mean that in practice it can be difficult to identify direct evidence of such floral evolution within the timeframe of typical studies. Among many confounding factors, three are particularly relevant.

First, the presence of floral mimics demonstrates the viability of a floral species imitating, instead of diverging from, the appearance of other species (Dafni 1984).

Second, although at first glance, heterospecific pollen transfer represents a reproductive cost to pollen donor and recipient, especially when pollen is limited, two species may balance this against the benefits of facilitating each other's pollination by attracting more pollinators to a region than either could alone (Feldman et al. 2004). Our simulation results suggest that one species may benefit if it can unilaterally pollen clog its competitor via shared pollinator visits.

Third, in most environments, a range of potential beneficial and pest insects, each with its own perceptual and cognitive system, is present. The result can be multiple pressures on flower traits that may push in different directions. For instance, some flowers must reduce the impact, and possible physical damage, caused by non-pollinators, including floral herbivores (Kemp and Ellis 2019) or even nectar-robbing bees. This may introduce pressure to evolve colours cryptic to non-pollinator insect visual systems or floral morphology that excludes some kinds of visitors. This pressure may be counter-balanced against the need for pollinators to clearly identify and distinguish between co-flowering species to be reliably flower-constant. Hence, with the characteristics of local animal visual systems affecting floral colour distributions within plant communities in a variety of ways (Shrestha et al. 2016; Shrestha et al. 2019), a flower is unlikely to consistently prevent heterospecific pollen transfer.

Our simulation results suggest the extent that pollen misdelivery might need to be factored into our understanding of plant competition, even though the periods available for typical ecological studies might be too short to capture the entire sequence of events directly. For example, Figs. 2e, 3b, and 4b and c show that for annually blooming plants, pollen clogging-driven phenomena may unfold relatively rapidly, within say 20 generations in our model. But this is still far longer than the period over which typical ecological studies are currently funded. Yet over this time period, the phenomena we study here might conceivably impact human food production or wildflower conservation, for instance. If pollen loss can reduce the reproductive success of a competitor, especially one ensconced within an otherwise impenetrable refuge, the pollen loser might gain a net benefit by reducing competition in the habitat shared with its competitor in these time frames. If so, then non-flower constant pollinators would play a key role in this relationship to mediate species interactions and potentially modulate species abundance.

Implications of non-constancy on flowering crops and roadside conservation zones

In cases where flowers from a single species bloom in large clusters or patches, in expansive agricultural monocultures, or on large trees, non-constant pollinators may be of little impact due to the absence of nearby sources of heterospecific pollen (Feinsinger et al. 1986). In these situations, even an insect making random flower visits may be an effective pollinator. However, random foraging potentially interferes with conspecific pollen delivery and successful reproduction of flowering plants where several sympatric species tend to pollen clog one another (Tscheulin and Petanidou 2013). In agricultural settings, this might lower yield where roadside weeds or abundant wildflowers border crops (Kremen 2008), although usually this boosts crop yield, perhaps through an increase in pollination services rendered by native insects, or due to wild and managed honeybee interactions (Greenleaf and Kremen 2006; Blaauw and Isaacs 2014). Our simulation results suggest that the impact might be reversed—multi-season crops could swamp nearby wildflowers over many years with pollen loads deposited by insects into roadside verges. This might be a factor in cases where such spaces are set aside for wildflower conservation (Fekete et al. 2017), or to provide flowers for insect conservation (Feltham et al. 2015; Grant et al. 2018).

Even flower-constant pollinator behaviour can break down. For example, when flowers that bloom together look alike, honeybees make mistakes, inadvertently breaking flower-constancy (Dyer et al. 2012). In some cases, for instance after receiving low or infrequent rewards, bees may break flower-constancy to search for alternatives (Chittka et al. 1997; Dyer et al. 2014). As already noted, many insect pollinators are generalists and choose any rewarding flower if it appears similar in colour and/or olfactory signal (Sanchez et al. 2015) to one encountered earlier. Flower visitors such as flies and butterflies may not exhibit flower-constancy to the same degree as bees (Goulson et al. 1997; Goulson and Wright 1998; Chittka et al. 1999). Hence, based on the findings presented here, it would be worthwhile to explore pollen deposition by insects in roadside verges and to assess the flower-constancy of the insects that forage between these conservation verges and nearby flowering crops.

As our climate shifts, pollinator ranges change, we reduce pollinator habitat, spread chemical pollutants, and wildfires rage, some insect species will decline in number, possibly to extinction. We should be careful about drawing global conclusions on insect declines from limited data (Saunders et al. 2019), but especially at local levels, we can expect dramatic perturbations in the populations of insects that visit crops and wildflowers. To mitigate against these, we must understand the consequences of their behaviour on crop and wildflower pollination. Our study reveals the potential for strong competitive effects that may impact fragile plant communities and lower the efficiency of human food production. Only field studies will reveal the extent to which the scenarios our simulations document play out in specific ecological contexts.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s12080-020-00490-7.

**Code availability** Simulation source code is available Open Access via GitHub: https://github.com/tim-taylor/evobee.

**Author contributions** AD conceived the idea; AD, MB, JG, MS, and AGD refined it; AD and TT designed the simulations; TT programmed the simulations, ran the experiments, and statistically analysed the data; AD and TT wrote the manuscript; all authors edited and provided editorial advice on the manuscript.

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**Data availability** Simulation output data and configuration files are available Open Access via GitHub: https://github.com/tim-taylor/evobee.

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflicts of interest.

**Ethics approval** N/A

**Consent to participate** N/A

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