

RESEARCH ARTICLE

Goldilocks' quarter-hectare urban farm: An agent-based model for improved pollination of community gardens and small-holder farms

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Abstract

Industrial agriculture's expansive monocultures contrast against community farms of diverse crops in small allotments constrained by urban regulations. These human-controlled differences in scale, arrangement and crop diversity, may differently impact insect foraging and pollination. The relationship between human management and insect pollination is under-explored, especially regarding the implications of insect flower constancy—the tendency of insects to favour visits to a single rewarding flower species during a foraging bout. Although high flower-constancy is associated with reliable pollen transport, its impact on pollination depends also on planting regimes, the vicinity of neighbouring crops, weeds and wildflowers. This study explores the potential pollination impacts of insect flower constancy, heterospecific pollen transfer, and human-dictated crop patch size, using an agent-based model of insect pollinators foraging from two flowering plant species. Highly constant pollinators were most effective in the smallest patches when heterospecific pollen transfer was an issue. As patch size increased, pollination rates improved overall, but less constant insects produced better pollination rates for intermediate sized areas because they rapidly switched preferences between flower species. As patch size increased further, the influence of flower constancy on pollination rates was reduced. Study results suggest that typical community farms containing small single-crop patches operated by independent growers within an allotment, may be better pollinated if operated collaboratively to increase single-crop patch size. Crop patches needn't be large homogeneous agricultural monocultures, but neither should they be so small and heterogeneous as to inhibit pollination. We found a "Goldilocks zone" around 11m x 11m to be a good compromise for pollination, regardless of the level of flower constancy in local insects. As climate and human land use increasingly impact insect populations, the relationships between pollination systems, growers and policy makers must be continually examined to safeguard food supplies and native ecosystems.

Author summary

Most of the world's farms are very small, less than a hectare. As cities grow, even within developed nations, urban dwellers are increasingly turning to small community farms to grow food sustainably and for enjoyment. Many of the fruit and vegetable crops grown on small urban allotments and farms require pollination from a variety of local insects. In this study we used computer simulations to explore how insect species' different tendencies to visit single flower species when they forage, their *flower constancies*, influence crop pollination of small plots. We found that insects with high flower constancy, such as honeybees, are not fast pollinators of crops planted in small or intermediate sized patches common where growers each tend their own diversity of crops. For small patches, insects with low flower constancy pollinate more rapidly. While we found that plantings of a single crop in a quarter hectare or larger plot are ideal from a pollination perspective, given common urban and small-holder land constraints, our simulations found plots around 11m x 11m are a good compromise. These might be created between neighbours in a community farm, or by each grower dedicating their whole plot to a specific crop.

1 Introduction

Most of the world's farms are relatively small family/freeholder plots—in fact, 72% of the world's farms are smaller than 1 ha; 12% are 1–2 ha, 10% 2–5 ha and only 6% 5+ ha [1]. Despite this, the vast majority of research in agriculture overlooks small-holder farmers' circumstances, and therefore fails to tackle key issues in the sustainability of global food supplies [2]. With urban environments continuing to absorb the world's population growth [3], small-scale communal gardening has boomed, even in nations supported by industrial agriculture [4,5]. This trend has increased due to concerns about both food supply chains and community shopping during lockdowns associated with COVID-19 health measures [6]. Small plots of land in suburban yards, between apartment blocks, and alongside footpaths are consequently set aside in cities and urban environments to grow fruit, vegetables and herbs. Fig 1 shows a typical example of an urban communal garden from Edinburgh, Scotland, with tightly packed small plots in an area surrounded by housing. Fig 2B maps similar plots in Melbourne, Australia. This sort of arrangement can be found in urban areas worldwide.

On small-holder farms and urban allotments alike, spaces are frequently subdivided, even into areas of just a few metres across. Within these, an assortment of different crops are grown for personal consumption and/or for sale depending on the region and purpose of the farm [5,8]. At small spatial scales, optimisation of pollination, the subject of this paper, is potentially an important issue. The subdivision of land, and what is grown within a plot, are often subject to local policies, rules and regulations. Examples include the *Statutory allotments* sized up to “¼ of an acre” in the UK [9], and the *Schrebergarten* of Germany sized up to “400 square metres” [10]. However, these social and policy decisions may be at odds with biology. Hence, growers and gardeners may be aware of local climate and soil conditions, and the traits of the plants they grow, but their decision-making is subject to local policies and rules, and must navigate the space between human constraints and those of horticulture and the environment.

As well as providing valuable human amenities, green spaces provide ecosystem services that assist in biodiversity conservation [11,12]. This urban-ecological nexus highlights the importance of linking the provision of ecosystem services to urban planning and policy decisions [13].



Fig 1. A view of West Mains allotments, a typical community garden in Edinburgh, Scotland that provides 89 plots for rent to local residents. This is one of 44 allotment sites, providing 1,724 plots in total, across the city. The City of Edinburgh Council's Allotment Strategy 2017–2027 highlights the contribution these community gardens make to the health of local residents, to the sustainability and open-space of the city, and to promoting local biodiversity [7]. Plots such as these are common across world cities (e.g. see Fig 2B for a similar site in Melbourne, Australia). Photograph by author TT.

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Insect fauna also play multiple roles in urban agriculture, as plant pests, bio-control agents and pollinators [14,15]. Understanding these relationships with natural systems is key to reliable food production [14]. With the uptake of urban agriculture, and an increasing awareness of the importance of sustainable intensification on small-holder farms, studies of pollination at these scales in particular is of concern [14,16,17], but remains poorly researched [18]. One difficulty is the nature of small plots; it might be expected that data will be difficult to systematically acquire and analyse where land is intensely subdivided and managed by multiple parties. A solution to this dilemma can be the use of computer simulation to represent the complex scenario coherently and to improve understanding of the value of patches considering insects as pollen vectors. This is the approach adopted in the present research, and it has been adopted before to investigate the value of green spaces within the urban context from the perspective of its human inhabitants [19].

In this article, computer models are applied to answer specifically, *How does the subdivision of already small plots into tiny patches impact insect pollination? Are sub-plots, such as those*

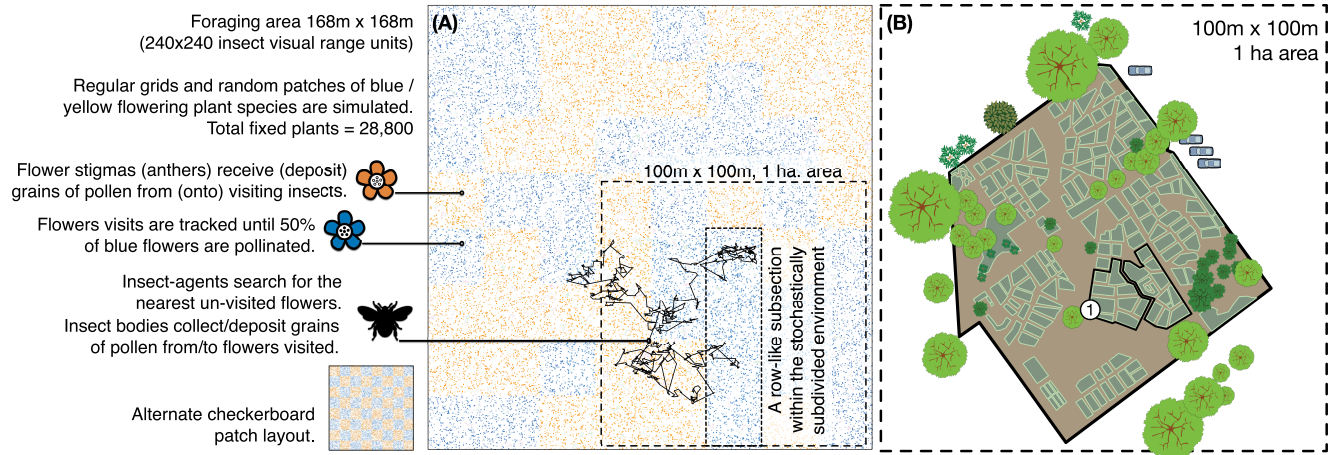


Fig 2. (A) Schematic representation of a simulated foraging environment with a stochastic distribution of blue/yellow flower patches, a sample insect pollinator path and a 1 ha boundary overlaid. One of many contiguous blocks of blue flowers arranged by chance along a row is outlined. A sample checkerboard flower patch subdivision is inset. Shown is an $S = 8$ square patch subdivision (Table 1). (B) Map of a community garden in suburban Melbourne, Australia. A boundary of 1 ha (10,000 m²) is overlaid (17 Dec. 2019, lat. 37.868574, lon. 144.977904, garden site area 3,500m²). Individual garden plots are outlined in pale green illustrating how small areas are subdivided to plots a few meters across. The irregularly shaped polygonal outlines labelled ① indicate collections of plots of total area ~125m² (= 11.2m x 11.2m)—cf. Fig 6. Map by AD.

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created in response to community practices and government policies, effectively pollinated by insects of different tendencies?

Some insects have evolved into specialists that visit particular species of flowering plants [20,21]. And whilst they too have innate preferences, some pollinators, such as honeybees (*Apis mellifera*), visit a variety of flowers [22] depending on availability and recent foraging experience. For centuries honeybees have been renowned for a learned “flower constancy”, a tendency to repeatedly visit a species of rewarding flower during a foraging bout that was observed over 2000 years ago [23, Bk IX, 624b (p. 971)]. From the insect’s perspective, such behaviour may be efficient [24,25], but other explanations might also hold [26]. Because it improves the reliability of pollen transfer between conspecifics, the tendency is also commonly understood to benefit flowers and consequently food and seed crop pollination. But how do these properties play out on land plots of different crop patch sizes, such as in subdivided urban community gardens?

In addition to their flower constancy, honeybees are easily managed and so support agriculture on a massive scale [27,28]. Still, honeybees are not the only insect pollinators of crops [29] and global wild bee population health generally is of ongoing concern due to numerous anthropogenic pressures [30,31]. As well as careful management of honeybees, it is therefore valuable to consider pollination by other insects, native bees or flies for instance [32], that might exhibit flower constancy different from honeybees [33]. Consideration must also be given to the fact that even honeybee flower constancy varies between individuals and situations [34]. So, what pollination differences might occur across degrees of flower-constancy and agricultural scales from urban allotments to small-holder farms? Additionally, what are the likely effects of heterospecific pollen transfer in these different farms?

Heterospecific pollen transfer by insect-pollinators requires that multiple species of flowers be collocated within the foraging range of an insect. An insect that is imperfectly flower constant may then visit both species of flower and incidentally transfer pollen from the anthers of one to the stigma of another. The smaller and more diverse the farms involved, the more likely heterospecific pollen transfer becomes. Variation in floral structure potentially enables co-

habiting, co-flowering species to avoid heterospecific pollen, since only if pollen is received by, and retrieved from, the same position on the body of the insect by each species' flowers is it likely to occur [35]. But, as explained below (section 1.1), many flowers do receive heterospecific pollen in practice, making this an important consideration for growers of diverse species on small plots.

Due to its importance to this study, in the following sections background on flower-constancy and heterospecific pollen transfer is provided, as well as an overview of earlier simulation-related research on the subject. Next, the article explains the agent-based model used to explore how flower constancy plays out across a range of plot sizes.

1.1 Flower constant and non-flower constant interactions

Although flower constancy is not the rule for all flower visits, nor flower visitors, it may be widespread [36]. Honeybees for example, are often flower constant. Once a honeybee has acquired experience it tends to continue foraging from a species whilst it remains profitable; bumblebees are perhaps less flower constant [24,25,37,38]. Yet even generally flower constant bees sometimes break it, and, many animals are not inclined towards constancy [24]. Consequently, even with honeybees, but especially when considering other insects, the implications of non- or low flower constancy need to be understood.

To a biotically pollinated flowering plant, flower constancy by generalist animal pollinators may maximise the value of metabolically expensive pollen. This is true especially if a plant species is abundant, since a rare species will be unlikely to retain a generalist insect's constancy [36]. Many flowers are designed to accept visits from generalist pollinators [39] which potentially expose them to pollen from other species transferred by an insect. This may not be desirable, since heterospecific pollen deposited on a flower's stigma can sometimes lower its reproductive potential through mechanical pollen-clogging, chemical allelopathy, or by usurping stilar conducting tissue or ovules [40]. Some plants have evolved tightly coupled relationships with specific insects [20,21]. In tight insect-plant couplings, rewards may be offered that are only accessible to that specific insect species through restrictions enforced by floral structures that place morphological and/or behavioural requirements on visitors [20,21,41–43]. In these cases, it would be natural to expect that insect-facilitated interspecific pollen transfer and its detrimental effects are subsequently lowered.

Largely for reasons of efficiency, industrial crops are planted in vast monocultures—many depend on insect pollination, often managed honeybees [44, pp. 67–99]. When in flower, a crop monoculture provides massive amounts of nutrition (but no variety). In the middle of such a field an insect, flower constant or not, has no choice but to only forage from the crop, and interspecific pollen transfer is low.

As already noted, most of the world's population though still depends on traditional farming using polycultures in small plots [1,2]. Polycultural farming is generally considered to be relatively beneficial for enhancing biodiversity [45] which implies also the presence of a range of insect pollinators with different flower constancies. Similarly, the practice of urban community gardening is becoming increasingly popular [4–6]. As in any area with multiple flowering plants, in these small subdivided plots, heterospecific pollen transfer by non-flower constant insects may be an issue too. Decreases in the pollination of any one crop brought about by heterospecific pollen transfer could then potentially reduce gains made through maintaining insect and crop biodiversity. Consequently, understanding the implications of insect flower constancy for small scale agriculture is relevant to pollination success.

While industrial agriculture might not, at first glance, share concerns about small-scale pollination issues with subsistence farmers, patches and verges between industrial fields and

along roads may be home to native flora [46] and fauna [47]. To counter some of the negative impacts of agricultural monocultures, these areas may be deliberately established to provide wildflower and insect habitat [48–50]. Some countries even reward farmers who turn land towards conservation [51], and the evidence suggests that the increase in wild insect numbers boosts crop pollination [52,53]. Although detailed studies are not known to be available in the current literature, these verges may become sources of pollen that can be carried into field edges by non-flower constant insects, possibly reducing yield. And *vice versa*, pollen from annually reseeded crops might swamp wildflower reproduction in areas intended to be conservation strongholds.

An additional concern of some industrial agriculture is the preservation of non-genetically modified status and the contamination of the environment by genetically modified (GM) material [54]. Then, even in enormous monocultures, pollen flow at field boundaries or between even distant fields, may be concerning between GM and non-GM crops [54]. Hence, heterospecific pollen transfer is relevant across all scales of agriculture.

1.2 Agent-based simulations of insect-plant interaction

The use of agent-based models (ABM)—also known as individual-based models (IBM)—to explore the implications of bee behaviour is well established. Over forty years ago, Waser [55] used an ABM to study the impact of heterospecific pollen transfer on the coexistence of two flowering plant species. Campbell [56] extended this work modelling heterospecific pollen transfer for selected real flowering plants and insect pollinators. Around this time also, Hogeweg and Hesper [57] used an ABM to study in-hive bumblebee behaviour, demonstrating how the individual interactions of adult bees generated macro-level social structures and colony-level reproductive behaviour. There is therefore a long tradition of ABMs to help us understand bees.

More recently, ABMs have been applied to simulate honeybee foraging behaviour [58]. Also, the benefits of honeybee recruitment and its dependence on flower density has been investigated using ABMs [59] and they have been applied to model blueberry pollination [60]. ABMs have been used to investigate the impact of flower constancy under conditions where rewards are offered cyclically [34]; the impacts of bee visual scanning [61]; the effects of bee colour vision on flower colour evolution [62]; and, the implications of bee movement on greenhouse planting regimes to enhance pollination [63]. In each study since the 1970s, the key feature of bee ABMs is their generation of macro-level outcomes from individual foraging decisions. It is for this reason ABMs are adopted in the present study to research pollination in small plots that would otherwise be difficult to study.

2 Materials and methods

The ODD [64,65] is adopted to describe the ABM of this study. [Table 1](#) summarises parameters.

2.1 Purpose and patterns

The currently adopted model can be interpreted as a theoretical exposition with a predictive element. It was constructed to determine how crop patch size and insect pollinator flower constancy might impact pollination with or without heterospecific pollen deposition between crops.

As implemented, the model represents pollinators and the landscape abstractly with respect to the shape of land subdivisions and insect foraging's stochasticity ([Fig 2A](#)). However, its simulated patterns of insect decision-making are based on empirical flower constancy data

Table 1. Simulation parameters.

Parameter	Value	Parameter	Value
Environment size	240 pdu* x 240 pdu	Initial pollen on anther	100
Termination criterion	50% pollination of blue flowers	Anther to pollinator transfer per visit	1
Number of pollinators	400	Stigma pollen capacity	1
Number of plant species	2 (blue/yellow)	Pollinator to stigma transfer per visit	1
Plant density (mean plants per pdu ²)	0.5	Pollinator pollen carrying capacity	1
Pollinator Constancy parameter C values	0.1, 0.3, 0.5, 0.7, 0.9	Pollen carryover	1
Patch Size parameter S** values	2, 3, 4, 5, 6, 8, 10, 12, 15, 20, 24, 30, 40, 48, 60, 80, 120	Pollen-clogging (when enabled)	Yellow flower pollen clogs blue flower stigmas.
Patch distribution schemes	checkerboard, stochastic		

* pdu refers to perceptual distance units, the maximum range over which the simulated insect can perceive a target flower, 70 cm for a bumblebee (see section 2.2.1)

** Patch Size parameter S determines crop patch size as the divisor of the Environment along its boundaries. For example, S = 2 divides the overall environment (240 x 240 pdu²) into 2 patches along each axis, 4 patches in total, each of size 120 x 120 pdu².

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[24,25,37,38], and its land plot scales are based on data from the world's dominant farming practices. These particular model properties are sufficiently simple that apart from standard and graphical debugging, pattern-oriented modelling was not required to affirm their correct operation. Patterns that were used to assess the model were the rates of pollen collection and deposition and the time for flower constant insects to switch flower preferences under different experimental conditions. However, as full sweeps through the parameter spaces for these traits were conducted to address the study's theoretical research questions, the patterns were assessed for their general form, rather than their similarity to the patterns generated by specific insect species foraging from specific flowering plant species.

2.2 Entities, state variables and scales

In this study the entities are an environment containing two species of flowering plant set in a grid of species-specific patches of different size and arrangement; a set of insect pollinator agents that forage from the flowers with different flower constancies; and, pollen that is delivered between flowers by insects (Fig 2A, Table 1).

2.2.1 Environment model. The simulation environment is an area measured in “perceptual distance units” (pdu) based on insect vision similar to that of a bumblebee. As this is a key reference metric, it is explained first. Bumblebees, an important agricultural pollinator in many countries, can detect the presence of a cluster of 3–5 flowers (each of 2.5 cm diameter) at a distance of ~0.7 m, a distance that varies with lighting conditions, flower and background colour [66,67]. Nevertheless, detection appears to approximate a step function as a physiologically mediated perceptual threshold is crossed at approximately 0.7 m from a flower. This is modelled simply as flowers being undetected at distances >0.7 m and detected with certainty at distances <0.7 m. The model environment contains a 2D continuous region of 240 pdu x 240 pdu which consequently corresponds to 168 m x 168 m for an insect with bumblebee vision. This size was chosen due to the ease with which 240 can be evenly subdivided by an integer—space is subdivided into patches (Table 1) of dimension ranging from ½ the side length (resulting in 4 large patches, two of each plant species) through to 1/120th of the side length (giving 14,400 very small patches). Second, this size allows reproduction of plot

subdivisions of less than 1 hectare as used by the vast majority of the world's growers (sect. 1.0), including being typical of urban plots (Figs 1 and 2B). A parameter determines whether the model runs with environments of alternating checkerboard patches of the two crop species, or with patches stochastically allocated to one of the two crops (Fig 2A).

2.2.2 Pollinator agent model. Each pollinator maintains its current position and heading internally as it navigates through the continuous environment, collects, carries and delivers pollen between flowers. Each individual maintains a list of the 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 [68,69]. Each pollinator stores a constant parameter describing its flower constancy from 0.1 (low) to 0.9 (high) which impacts its foraging strategy as described in sect. 2.3.1.

2.2.3 Flower-plant agent model. Each plant in the environment is a unique entity assigned one of two plant species (blue/yellow) and a fixed location at creation. Although the colours are symbolic, the intention is for the two flower species to appear saliently different to the sensory systems of common crop insect pollinators including bees (Hymenoptera) [70] and flower-visiting flies (Diptera) [71] (To improve human-legibility of figures, yellow flowers are illustrated in orange).

Each plant is idealised as having one flower although in reality this may be an inflorescence which, from 1 pdu, will be perceived by insects as a unitary visual signal. For simplicity, it is also assumed that each flower colour is distinguishable from the background [72,73] to all insects from 1 pdu even though in reality this will depend on a number of factors beyond the study scope [66,67].

Each flower agent records the number of insect-collectable pollen grains currently available from its anthers—this is initialised with a fixed number when the flower is created and depleted as pollinators visit. During insect visits, a fixed number of anther pollen grains are transferred to the pollinator's body. The flower has a stigma pollen store (with a fixed maximum capacity) recording pollen grains deposited by visiting insects (sect. 2.3.2). Grains may be conspecific or heterospecific depending on the experimental configuration. The only differences between flower species are colour and pollen type.

2.2.4 Pollen agent model. Pollen grains record their individual parent flower, its species, and (when travelling on a pollinator's body), the number of flowers the pollinator has visited since grain collection. Pollen cannot move in any way other than from flower anther, to insect body, to flower stigma or to the environment where it becomes lost.

2.3 Process overview and scheduling

At the beginning of each simulation run, crop patches are distributed across the environment in either a checkerboard or stochastic arrangement, depending upon the experimental configuration. In any given experiment, each patch in the environment is of the same size and each contains an equal number of plants determined by a plant density parameter (Table 1). Each patch consists of entirely blue or yellow species. A population of pollinator agents of identical flower constancy forage among the flower patches in discrete time-steps, making a single decision about flight direction and which flowers to land on (or not) per time-step. An insect landing on a flower may result in the transfer of pollen between it and the insect's body, potentially pollinating the flower.

A simulation run halts when 50% of the focal (blue) crop has been pollinated. The time at which this occurs is recorded to compare pollination outcomes between planting arrangements and pollinator constancy values. Multiple runs are conducted for each combination of patch arrangement and patch size, initialised with new pollinators and flowers populations each time.

2.3.1 Submodel pollinator dynamics. A simulation run begins with 400 insect pollinators distributed uniform-randomly throughout the environment. At each time step, pollinator update order is randomised. In turn, each pollinator executes a new behaviour iteration in each simulation time step during which it follows its foraging strategy to identify flowers and collect pollen from them, or deposit it to them (Fig 3). More than one pollinator can visit an individual flower within a time step. However, in the experiments described here there are no direct pollinator-pollinator interactions.

A pollinator will move to, and consider landing on, its nearest flower within a search radius of 1 pdu that does not appear on its recently visited flower list. This search radius of 1 pdu corresponds to the area over which the pollinator's visual system can detect nearby flowers (sect. 2.2.1). This style of foraging imitates movements common for honeybees and other bees also [74]. The probability of landing, $P(\text{landing})$, is decided using the pollinator agent's flower constancy parameter as follows:

```
FlowerConstancy = (0.1, 0.9)
If (Species (Newly Located Flower) NOT-EQUAL-TO Species (Most Recently
Visited Flower))
    Probability (landing) = 1.0 -FlowerConstancy
Else If (Species (Newly Located Flower) EQUAL-TO Species (Most
Recently Visited Flower))
    Probability (landing) = 0.9
Else (there hasn't been a previous flower visit recorded)
    Probability (landing) = 1.0
```

If no unvisited flower is available, or if the pollinator decides not to land on the unvisited flower it currently perceives, it moves a distance of 1 pdu in a uniform-random direction. In natural settings insects may employ a variety of foraging strategies [75]. Our previous work however, shows that when assessing relative pollen delivery rates between flower distributions and scenarios, foraging that is not directed towards the nearest flower can be successfully modelled using a random walk [61]. Pollen transfer processes potentially occur during any flower visit by a pollinator (sect. 2.3.3).

2.3.2 Submodel flower dynamics. At simulation commencement each flower has a fixed amount of anther pollen available for collection and a pollen-free stigma. As the simulation progresses, pollinators may collect anther pollen and deposit pollen on stigmas. Pollinators may deposit pollen from a different species onto the stigma (potentially pollen-clogging the flower) depending upon the experimental pollen-clogging configuration [76]. A parameter specifies the capacity for stigma pollen grains. In all experiments reported here, capacity = 1 so only a single pollen grain could be deposited—a simple proxy for real-world pollination that readily allows for interpretation of insect-agent facilitated pollen flow. If a deposited grain is from a conspecific, the flower is pollinated. The model was tested to explore the impact of a range of values for pollen transfer and/or stigma capacity (sect. 2.6), however the present study is only concerned with pollination considered as a binary property. The different scenarios explored are described in (sect. 2.3.3).

2.3.3 Submodel pollinator action on flowers. When a pollinator visits a flower each pollen grain it carries is randomly considered for transfer to the stigma, subject to the pollinator's fixed maximum number of transferrable grains per visit, the stigma's fixed maximum capacity for accepting grains per visit, and the stigma's overall capacity for pollen. Additionally, the anther species of origin and stigma species of destination are considered since the stigma may or may not be susceptible to receiving heterospecific pollen grains (sect. 2.2.3).

If the pollen grains randomly selected for transfer from the insect body to the stigma are of the same species as the current flower, they will be transferred to the flower if there is stigma capacity. However, if the pollen grains are of a different species to the current flower, one of

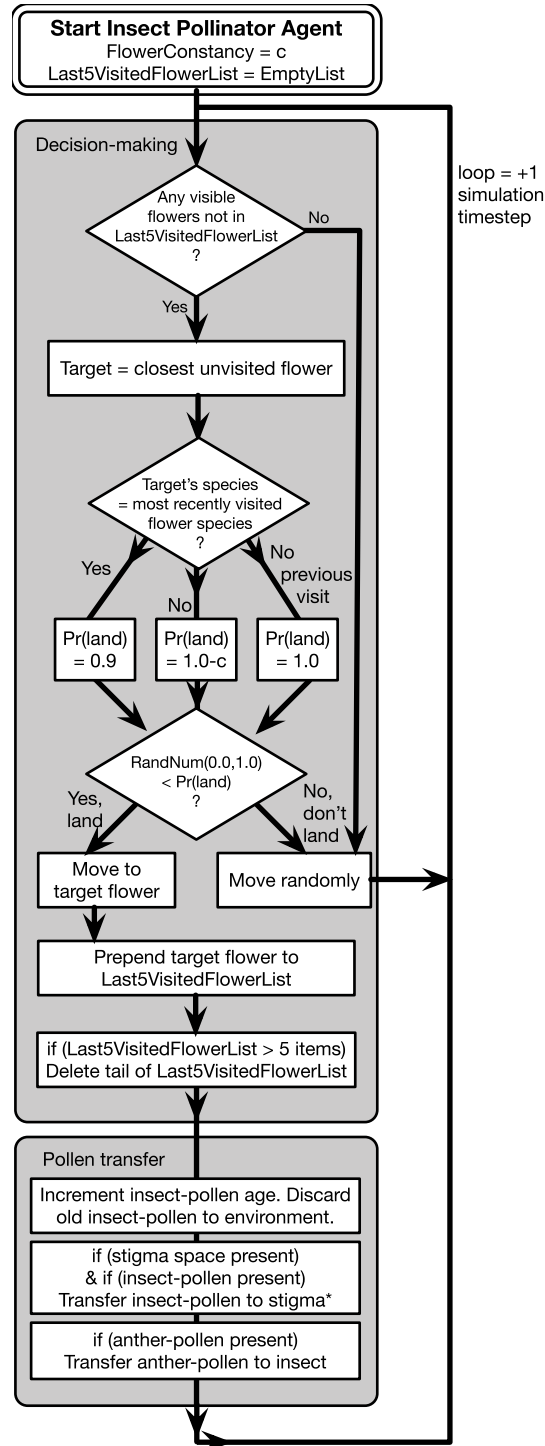


Fig 3. Individual pollinator agent behaviour. Insect-pollen is carried on the insect's body and available for deposition on a flower stigma. Anther-pollen is carried on a flower anther and available for deposition onto an insect's body. *Whether or not heterospecific pollen transfer is enabled determines whether pollen of one origin (blue/yellow anthers) can be transferred to a particular destination (blue/yellow stigmas). If heterospecific pollen transfer is disabled, when pollen is removed from an insect's body and there is insufficient stigma space, or when the pollen is of a different species to the stigma's flower, the pollen is lost to the environment.

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two things will happen. When heterospecific pollen transfer is enabled the grain is transferred to the stigma where it occupies space, potentially blocking later pollination by a future conspecific grain. When heterospecific pollen transfer is disabled the grain ceases to be carried by the insect, it doesn't attach to the stigma, and it is lost to the environment for no reproductive benefit. This simulates the situation where co-flowering species deposit/receive pollen on different parts of an insect, e.g. [77]. In such cases, pollen deposited on other parts of the body besides the transfer point are often lost due to insect grooming, pollen collection into a bee's corbiculae, or brushed off by non-reproductive flower parts.

In the last stage of this submodel, the flower may transfer some of its anther pollen onto the pollinator's body. There is a fixed maximum number of grains that may be transferred from the anther in any one visit, and the anthers start with a specified amount of pollen in each run that is depleted by the insects. The values used in the current study for these various limits are shown in Table 1.

2.4 Design concepts

2.4.1 Basic principles. The basic principles and ecological hypotheses underlying the adopted modelling approach are specified for clarity and simplicity within each of the sub-sections describing the entities and their dynamics. These relate to: insect perception (how insects detect flowers, distinguish colour signals, scent-mark and memorise flowers and make foraging decisions); insect pollination (how pollen is transferred between flowers and insects, how heterospecific pollen interferes with pollination, how pollen is sometimes lost to the environment); and farmland subdivision (how small-holder farms and urban community gardens are sub-divided to plant diverse crops on small plots). These principles and practices are well established in the literature; the current model applies them to generate new understanding about how these factors interact to impact pollination.

2.4.2 Emergence. The emergent property of interest is the time taken for flowers to be pollinated when planted in different arrangements and scales, exposed to insects with different flower constancies and to heterospecific pollen.

2.4.3 Adaptation, objectives, learning and prediction. Insect agents follow a stochastic foraging strategy. They make a pseudo-decision to move randomly if they cannot see an unvisited flower from their present position. And, they make a stochastic decision to land on a local flower based on their current preference for its species and their flower constancy parameter. Agents do not learn or predict.

2.4.4 Sensing. Pollinator agents detect flowers of both species reliably within 1 pdu but not at all beyond this range. Their flower-memory/scent-marking and detection capabilities enable them to identify whether or not they have visited an individual flower in the last five visits.

2.4.5 Interaction. Any number of insects may visit a flower simultaneously, but insects don't interact with one another directly (sect. 2.3.1). At each visit pollen may be transferred from a flower anther to a visiting insect, from the insect to the flower's stigma (sect. 2.3.3), or pollen may be lost to the environment.

2.4.6 Stochasticity. Stochastic simulation elements are: the placement of flowers and initial pollinator location; the order in which pollinators and pollen transfer are updated; the pollinator's decision whether to land on a perceived flower (influenced by pollinator constancy parameter, the target flower species, and the presently perceived flower's species) and the direction a pollinator moves when unable to find a suitable flower target; the selection of pollen grains for transfer between insect, flower stigma or anther; and, in the stochastic planting arrangements, the allocation of a patch to a species.

2.4.7 Collectives. Insect pollinator collectives aren't modelled. Flowers and pollen of the same species are treated collectively for determining pollination and to generate simulation output data, but within the model they don't function collectively.

2.4.8 Observation. The main data values recorded are the absolute number of pollinated plants of each species at each time step, and the number of time steps until 50% pollination of blue flowers is achieved.

2.5 Initialization

The simulation is initialised with 28,800 flowering plants (mean density = 0.5 plants/pdu²). The environment is a square of size 240 pdu x 240 pdu divided into smaller square patches determined by the Patch Size *S* parameter (Table 1). Each patch contains flowers of either blue or yellow species distributed regularly (checkerboard) or stochastically (distributed randomly) (Fig 2A).

2.6 Testing–Verification, validation and sensitivity analysis

Software was written from scratch in C++ using standard software development tools and checked using standard engineering practices. Its operation was verified as follows. Simulations were run with real-time environment visualisation showing plant distributions, positions, paths of pollinators, and flower pollination status as a form of visual debugging [78] to eliminate gross errors in plant distribution and pollinator movement. Standard debugging tools and detailed logs were used to verify pollen transfer processors between pollinator and flower agents.

After confirming that the simulation behaved as expected, earlier experiments conducted by Waser [55] were replicated. Software behaviour was validated against the first three experiments described by Waser, which investigated the effects of duration of foraging bouts, whether heterospecific pollen could be deposited on stigmas, and the amount of pollen available on anthers, respectively. Large environment sizes, large populations and long runs were used, with parameters derived from the originals, to demonstrate a qualitative match.

After successfully replicating the results of Waser's first three experiments, the experiments were repeated with pollen-related parameters ten times his (original) values to check for sampling error effects caused by small parameter values. This uniform scaling preserves the ratios Waser noted were important for simulating pollination in the scenarios he described. The re-runs produced the same qualitative results as the originals, instilling confidence that the results were not suffering stochastic sampling issues.

A series of experiments were also conducted extending Waser's fourth experiment, which investigated the effect of introducing refugia for each plant species to reduce spatial competition. The replication of this experiment included a sweep through a wide range for the parameter specifying environment size. This acted as a sensitivity analysis with respect to the dimensions of the simulated foraging environment accessible to the insects and demonstrated that the results were not subject to variation caused by environment size.

2.7 Experiments

A full sweep through each combination of Pollinator Constancy *C* and Patch Size *S* values (Table 1) was conducted using checkerboard and stochastic patches. Runs were repeated with and without heterospecific pollen transfer. Simulation runs were conducted ($N = 100$) at each configuration, recording the time to 50% pollination of the blue (focal) crop with the yellow (non-focal) crop acting as a potential deposition site for blue pollen, and a source of heterospecific pollen.

3 Results

Results for checkerboard planting arrangements are provided in Fig 4A without heterospecific pollen transfer, and in Fig 4B with heterospecific pollen blocking blue flower reproduction. Fig 5A and 5B present results for the equivalent experiments conducted on stochastic planting arrangements.

The checkerboard provides a worst-case grid for pollinators showing any flower constancy since cell boundaries always demarcate a patch of a different species with respect to the current cell. For tiny patches (Fig 4, leftmost on the x-axes) the resulting impact on pollination is not highly pronounced since an insect can quickly locate its preferred flower type even when stationed in the centre of a non-favoured species' patch. In these cases, highly constant pollinators perform as well as (Fig 4A), or better than (Fig 4B), less constant pollinators. But as patch sizes increase through the intermediate ranges, highly constant insects pollinate more slowly than insects with low constancy (on the graphs, lower y-axis values indicate faster times to 50% pollination) until the largest subdivisions are reached. For large subdivisions, pollinator constancy doesn't matter at all.

A stochastic landscape lowers the probability of a patch boundary demarcating a non-preferred flower with respect to the current cell, in effect relaxing the patch size parameter randomly. The results (Fig 5) show that the blue flowers are more rapidly pollinated in the stochastic landscapes than on the worst-case checkerboards (Fig 4), indicating the potential value to manufacturing rows of contiguous crops (e.g., Fig 2A's coincidental row). This widely practiced planting arrangement simplifies human maintenance, but also reduces the navigational sophistication, spatial awareness and spatial memory requirements of an insect exploiting a patch. The benefits of even coincidental contiguous areas are made clear by comparing the faster small-patch pollination times of the stochastic arrangements: between Fig 4A (approx. 330–340 timesteps depending slightly on flower constancy) and Fig 5A (faster than 3A ranging between 240–280 timesteps), or between Fig 4B (widely varying at ~10 pdu² from 330–510 timesteps) and 4B (faster than 3B ranging between 260–270 timesteps).

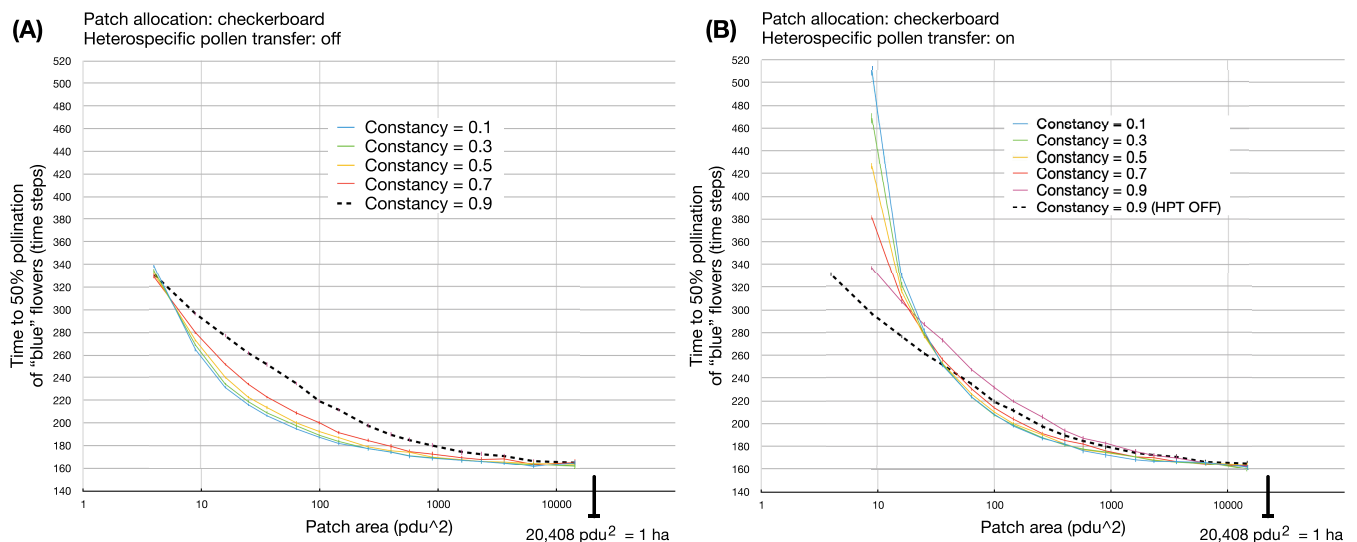


Fig 4. Plot of time to 50% pollination of blue flowers versus patch area (log scale) for checkerboard patch arrangements. Each line represents the performance of insect pollinators of different flower constancy. N = 100 simulation runs per datapoint, error bars = 95% conf. int. are barely visible. (A) Heterospecific pollen transfer disabled (B) Asymmetric heterospecific pollen transfer enabled from yellow to blue flowers; note the absence of data for very small patches since pollen clogging resulted in failure of the blue flowers to reach the target 50% pollination threshold. The line for Constancy = 0.9 from (A) in dashed-black is reproduced on graph (B) for direct comparison between scenarios.

<https://doi.org/10.1371/journal.pstr.0000021.g004>

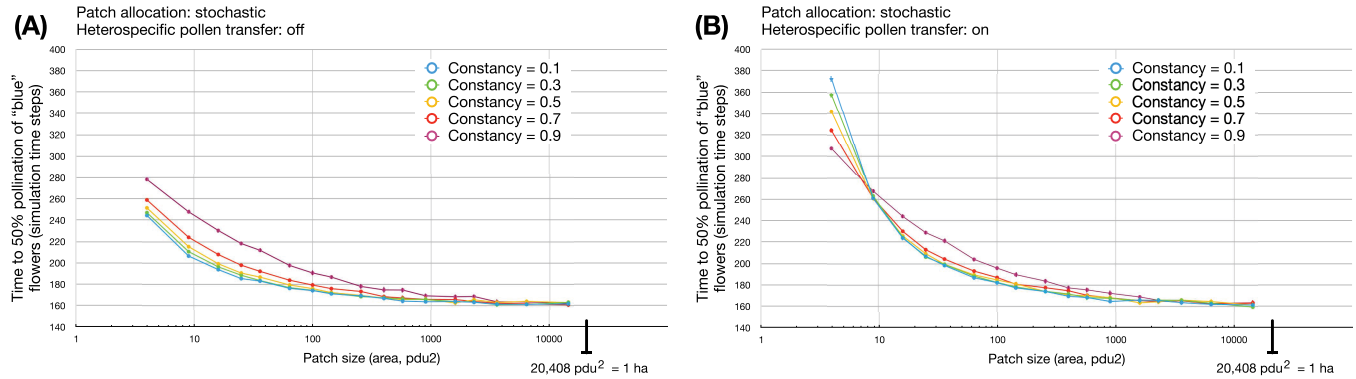


Fig 5. Plot of time to 50% pollination of blue flowers versus patch area (log scale) for stochastic patch arrangements. Each line represents the performance of insect pollinators of different flower constancy. N = 100 simulation runs per datapoint, error bars = 95% conf. int. are barely visible. (A) Heterospecific pollen transfer disabled (B) Asymmetric heterospecific pollen transfer enabled from the yellow to blue flowers.

<https://doi.org/10.1371/journal.pstr.0000021.g005>

In a comparison of Fig 4A to 4B, and Fig 5A to 5B, the effect of the heterospecific pollen transfer on blue flower pollination is evident. For the checkerboard arrangement (Fig 4), heterospecific pollen transfer completely prevents pollination of the smallest patches of blue flowers. But as patch sizes increase incrementally, the highly constant pollinators (which seldom carry heterospecific pollen) also seldom clog the blue flowers, resulting in them being the most effective pollinators in this scenario. This benefit is lost as patch sizes increase, since high flower constancy reduces flower visitation rate as it did in the non-pollen clogging scenarios. Although the stochastic patch arrangement did not suffer from the same complete pollination failure for tiny patches as the checkerboard, for the remainder of the patch sizes the two arrangements behave similarly. The checkerboard’s worst-case scenario resulted in slower times to 50% pollination in all but the largest patch sizes. For the large patches, pollinator constancy doesn’t matter in these circumstances either.

A one-hectare area is overlaid on Fig 2 for reference and marked on the x-axis of the plots in Figs 4 and 5. For clarity, Fig 6 presents pollination performance of square plots of side-length marked along the x-axis in metres relative to the largest plot size we explored. The planting arrangement used was the checkerboard, heterospecific pollen transfer was disabled, and pollinators had flower constancy = 0.9. Although we refer to patches towards the right-hand side of the x-axes in these figures as “large” (e.g. 120 pdu/84 m, 14,400 pdu², 7200 flowers), in fact these correspond to plots less than 100 m x 100 m. By industrial agricultural standards these might reasonably be considered very small! For instance, single “broadacre” crop fields in Australia (which include wind and insect-pollinated industrial canola *Brassica napus* (oilseed rape), grains and other crops) may be 25–100 ha and are frequently situated on farms with thousands of hectares of the same crop [79]. Nevertheless, as already indicated [1,2], over 70% of world farms are of the order simulated here. The plots mapped in Fig 2B are a few metres in length and typically include several co-planted crops—these configurations therefore are at the left-hand side of our x-axes which run only down to a 1.4 m x 1.4 m plot containing a single type of flowering crop. According to Fig 6, the 1.4 m x 1.4 m (1.96 m²) plots are slow to pollinate, taking over twice the time relative to 84 m x 84 m (7056 m²) plots. Yet 1.4 m x 1.4 m is seemingly around the area that community gardens (e.g., Fig 2B) might dedicate to a homogeneous flowering crop. The current study’s ABM shows that what is perhaps in some circumstances a manageable community plot size of 11.2 m x 11.2 m (125 m²) can achieve relatively efficient pollination—only ca. 20% less effective than a field approaching

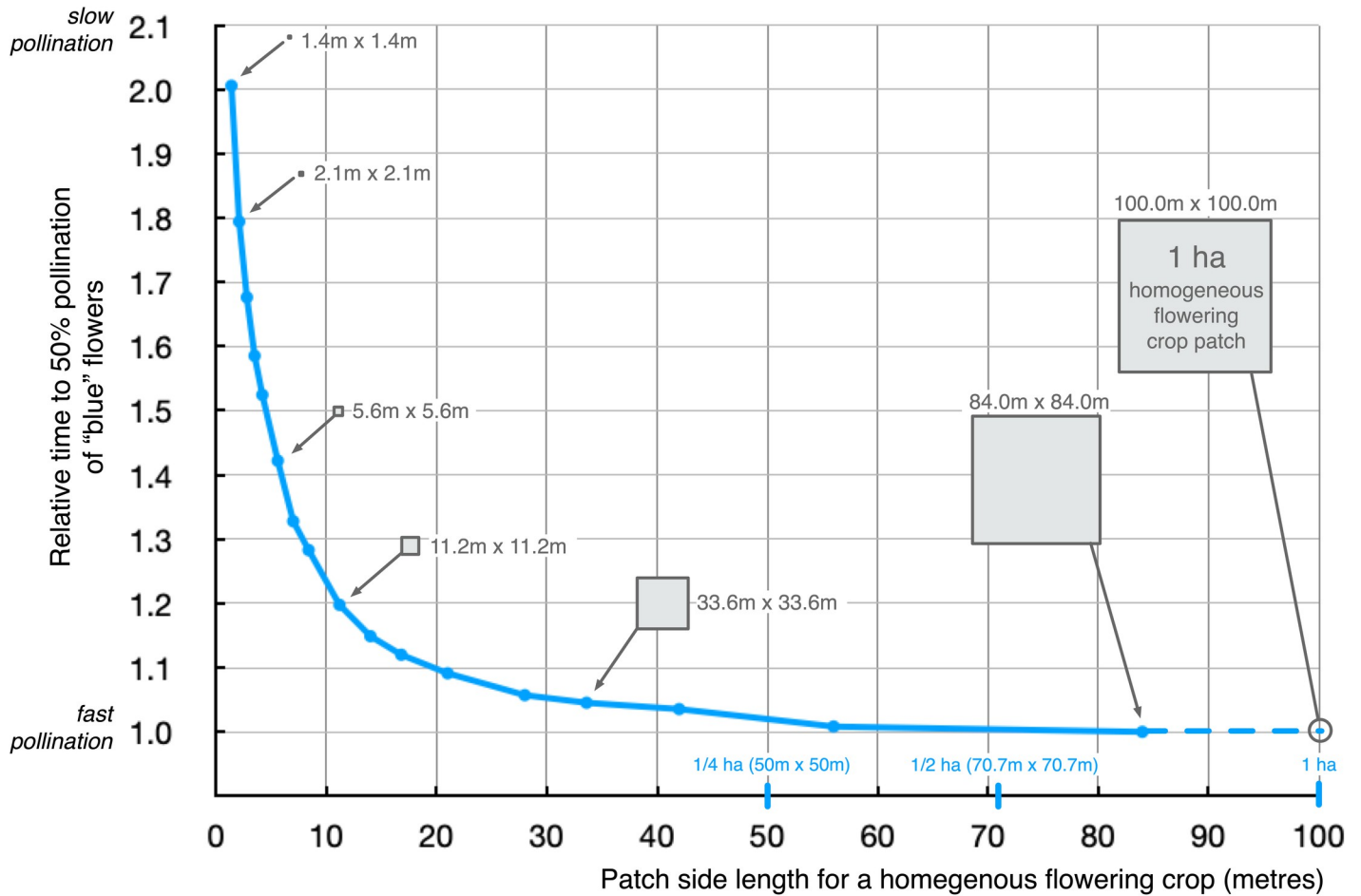


Fig 6. Relative time to 50% pollination of the “blue” crop with respect to the largest plot size. (Checkerboard; heterospecific pollen transfer off; pollinator flower constancy 0.9). For clarity, plot side lengths are given in metres with illustrations of areas relative to 1 ha. The 1.4 m x 1.4 m plots (approximately the area of homogeneous crops planted within urban community gardens, Fig 2B) take over twice the time to pollinate relative to the largest contiguous plots of 84 m x 84 m. A compromise size is shown at the bend of the curve sized at 11.2 m x 11.2 m (Note: This data is normalised, for error bars see Figs 4 and 5).

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a hectare. If land is available, this configuration might be realised with strategic urban planning or collaboration between existing holders of smaller plots (Fig 2B-①).

4 Discussion

Flower-constant insects appear to benefit agricultural pollination, since they boost the reliability of pollen delivery [80]. But the consequences of flower constancy are difficult to unravel [24,26,81,82]. Despite the apparently intuitive benefits of flower-constant insects, studies document the simple fact that many crops and flowering plants benefit from visitation by a wide variety of insects [83,84]. As indicated above, disruptions to climate and ecosystems may also require farmers to diversify dependence on insect pollinators to improve the security and sustainability of food production. And this is why simulations such as those of the current study are so important. For proper pollination management, the implications of insect diversity and flower-constancy must be understood.

The simulations reported here are scaled in insect-relative perceptual distance units to account for differences in insect visual range. Scaling is derived from bumblebee vision experiments indicating 1 pdu = 0.7m for this common agriculturally-relevant insect (sect. 2.2.1).

Simulated floral density had a mean of 0.5 flowers per unit area (pdu^2). (For notes on the impact of varying floral density see [S1 Text](#)) From these figures patch length can be computed in pdu or metres, area in pdu^2 , and the expected number of flowers in a patch. These values are all quoted below in a tuple (patch side length pdu/metres, patch area pdu^2 , patch average flower number) to facilitate discussion of simulation results in relation to real-world scenarios.

When single-species flower patches are small (3 pdu /2.1 m, 9 pdu^2 , 4.5 flowers) then flowers appear to an insect to be comingled ([Fig 4](#)). This models situations where different flowering plants are adjacent, or on some farms, where patches of co-flowering weeds grow among crops. In this case, if heterospecific pollen transfer is not a concern, for instance because there are structural incompatibilities between co-flowering species that prevent it, then insect constancy levels don't impact pollination rate ([Fig 4A](#)). But, an abundance of highly flower constant insects may be important for reliable pollination where this isolation does not occur, since non-flower constant insects may deposit heterospecific pollen onto target flowers ([Fig 4B](#)). This results in poor pollination outcomes—the very smallest patches (2 pdu/1.4 m, 4 pdu^2 , 2 flowers) failed to reach 50% pollination and were completely clogged by heterospecific pollen (*cf.* [Fig 4A and 4B](#)).

When flower patches are large (120 pdu/84m, 14,400 pdu^2 , 7200 flowers) then insect flower constancy doesn't matter ([Fig 4A and 4B](#)). Away from field margins the centre of a target crop is buffered from heterospecific pollen. There's only conspecific pollen nearby and no opportunity for pollen loss to other species. Hence, pollen-carrying insects of all flower-constancy levels are potentially useful pollinators in this scenario, even if the pollen carryover range is short.

In the wide middle range of patches from (5 pdu /3.5 m, 12.5 flowers) up to (60 pdu/42 m, 1800 flowers) highly constant insects are consistently the slowest to pollinate the target flowers, regardless of whether heterospecific pollen transfer is a factor ([Fig 4A and 4B](#)). On a checkerboard planting arrangement of anything other than the largest patches, these insects will often encounter the edges of their preferred floral resource. Therefore, when they leave their preferred patch they consume valuable time traversing patches of the alternate species without landing. Some insects may switch preferences to the alternate species. But the higher their flower constancy, by definition, the longer this typically takes. As shown above, if patches are small the wasted time is short since flowers of the preferred type are always close. Also shown above, if the patches are large patch boundaries are far apart, so many flowers will be pollinated before a boundary is encountered. It is in the mid-range that highly flower-constant insects' reluctance to switch preferences lowers their pollination value.

Although checkerboard and stochastic farm subdivisions have been explored here to discover the implications of worst-case and random conditions at different scales, these cases also help to deduce the performance of alternatives. For example, as noted, single-species rows the length of a plot are a simple improvement. These effectively reduce patch number (with respect to random and checkerboard arrangements) whilst maintaining crop quantities. In this case a flower-constant insect might follow a row end to end for effective foraging and pollination. In our model of two crop species (a focal crop and a non-focal source and sink for heterospecific pollen), a row arrangement would be best consolidated into two large rectangular patches, each occupying half of the area (rather than many alternating stripes of blue and yellow). This will result in pollination times like those at the righthand side of the x-axes in [Figs 4 and 5](#). However, with higher crop diversity, effective pollination is still maintained by flower-constant insects. But non-constant insects that move transversely across rows will transfer heterospecific pollen causing pollination times to approach those for checkboard plantings.

As with the number of patches, within limits tolerated by the crop plant density can be grower-controlled. Additional pilot simulations (see [S1 Text](#)) confirm the intuitive result that increasing flower density increases time to pollination, having the effect of lifting the curves of

Figs 4–6 up the y-axis. I.e., a fixed-size land plot having more flowers than the reference experiments takes longer to pollinate if the number of insects remains constant. But, since the lengths of the borders shared with neighbouring patches remains constant in this alternative scenario, and so does the speed of insect movement and the insect's visual range, there is no change in the fact that small patches are less rapidly pollinated than larger ones. The impact of increased pollinator numbers was also tested with respect to the reference simulations. As expected, this reduces the time to pollination, having the effect of dropping the curves of Figs 4–6 down the y-axis. The broad conclusions drawn from Fig 6 though, that homogeneous plots around 11.2 m x 11.2 m are a good compromise, and that sizes over one quarter of a hectare are as effectively pollinated as large plots, both hold even if floral density and/or pollinator numbers are increased.

Overall, allowing for the generalisation to uniform floral density and insect pollinator vision, the study results suggest that crop patches smaller than approximately one quarter of a hectare may be less effectively pollinated than larger plots (Fig 6). There are many reasons besides pollination though why planting a diversity of crops on a single small farm is highly desirable [45]. But all pollination times reported by the simulations of the current study drop as patch area increases, regardless of pollinator flower-constancy. So, if pollination performance is the aim, then larger patches give better outcomes. Given the difficulty of establishing homogeneous crop plots of a quarter hectare in urban and community gardens, a plot of 11.2 m x 11.2 m. may be achievable in constrained urban spaces and appears to be a good compromise.

In any real scenario, pollinator abundance, variations in flowering times and flower structures determine the extent that pollen-clogging, pollen- or pollinator-limitation impact food production. But the simulations presented here suggest that whatever these values might be on a specific farm, small plot sizes lower pollination rates. This leads to the proposal that in community gardens and small-holder farms, it may be helpful if growers requiring insect pollination establish cooperatives analogous to those recommended for gardeners to create multi-garden patches for urban biodiversity maintenance [11]. For food production, each grower could set their plot toward production of a single flowering crop, whilst neighbours assign land to a different one. Or neighbours could grow the same crops adjacent to one another. This would allow individuals to specialise cropping skills, farm conditions and procedures to boost success.

5 Recommendations and study limitations

To assist in making the results general, the range of insect flower constancies and defined crop plot dimensions was simulated in perceptual distance units (pdu). But whether or not specific insects with visual perception and acuity different to bumblebees [66] will be effective on specific farms must remain an exercise for future lab experiments and field trials well beyond the scope of this study.

As described in section 2.3.1, insect movement was simulated using a nearest unvisited neighbour foraging strategy that exploits local resources, supported by a random movement made when no recognisably unvisited flowers remain in view. The local exploitation strategy is supported by the ways many insects forage, but not all insects make completely random hops between distant patches [74,85]. For instance, some insects navigate between distant patches using landmarks spread across large open environments [86,87]. This tendency is not simulated in this study as it is not relevant to the focus on the pollination of a particular collection of plots making up a typical urban community garden.

Even within patches of around 5 m in side length, individual bumblebees have been shown to develop repeated foraging traplines, courses they optimise over repeated bouts [88]. Such

behaviours influence the rate and distribution of flower visits by an individual bee [89], and ultimately impact pollination. However, there are observable variations in trapline construction, use and optimisation between bumblebee colonies, and between individual worker bumblebees from a single colony [88]. Bumblebees differ from honeybees who may trapline under some circumstances [90], but also communicate resource locations using their dance language [91]. They also differ from observations of blue-banded bee foraging since these insects may visit a single flower on a plant before making a long trip to a distant plant to visit another single flower there [74].

In all of the above situations, traplines made by selected insect species vary from individual to individual. They are influenced heavily by the rewards each insect encounters and removes from flowers, the rates at which flowers replenish nectar, the rates at which flowers bud and wither over days, and by the risk aversion of some bee species to predation. As the current study is intended to explore pollination of patches foraged by a wide variety of insects, the adopted approach is arguably a suitable and simple way to grasp the overall impact of this inter- and intra-species diversity. Future work could investigate foraging behaviours of specific insects on the pollination of specific crops.

6 Conclusion

The simulations of this study modelled a range of sizes of single-crop patches with which to subdivide farms of less than a hectare, a range of insect flower constancies, and explored the impact of heterospecific pollen transfer between two crops. In all cases, larger patch sizes were more rapidly pollinated with rates seeing little improvement above a quarter hectare. High insect flower constancy benefitted pollination rate only for the very smallest patches when heterospecific pollen transfer was an issue. As patch size increased towards the middle of the ranges the study explored, highly flower constant insects were consistently found to be less effective pollinators than fickle insects. The latter insects rapidly changed preferences to favour any flower patch they discovered. For sizes of a quarter hectare and above, pollinator flower constancy made no discernible difference to pollination rate.

The study's findings indicate that from an insect pollination perspective, human decisions to subdivide small farms into tiny plots are not ideal. Where possible, working with neighbours to consolidate crops into larger patches is a more effective strategy for improved pollination.

Supporting information

S1 Text. Supplementary Materials: Impact of increased floral density and increased pollinator numbers.

(DOCX)

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