

# Orchard layout and plant traits influence fruit yield more strongly than pollinator behaviour and density in a dioecious crop

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## Abstract

Mutualistic plant-pollinator interactions are critical for the functioning of both non-managed and agricultural systems. Mathematical models of plant-pollinator interactions can help understand key determinants in pollination success. However, most previous models have not addressed pollinator behavior and plant biology combined. Information generated from such a model can inform optimal design of crop orchards and effective utilization of managed pollinators like honey bees, and help generate hypotheses about the effects of management practices and cultivar selection. We expect that honey bee density per flower and male to female flower ratio will influence fruit yield. To test the relative importance of these effects, both singly and simultaneously, we utilized a delay differential equation model combined with Latin hypercube sampling for sensitivity analysis. Empirical data obtained from historical records and collected in kiwifruit orchards in New Zealand were used to parameterize the model. We found that, at realistic bee densities, the optimal orchard had 65-75% female flowers, and the most benefit was gained from the first 6-8 bees/1000 flowers, with diminishing returns thereafter. While bee density significantly impacted fruit production, plant-based parameters—flower density and male:female flower ratio—were the most influential. The predictive model provides strategies for improving crop management.

## Introduction

Mutualistic plant-pollinator interactions play a vital role in plant reproduction in both natural systems and managed (i.e. agricultural) systems. Animal-mediated pollination

is important for 87.5% of angiosperms globally [1], and 75% of the most important crop species benefit significantly from this service [2], providing greater than US\$170 billion in economic value annually [3]. Functionally dioecious plants are especially reliant on pollination, as insects must cross from one plant to another. Even in well-studied systems, such as kiwifruit (*Actinidia chinensis*), the complexity of interacting variables limits the ability of researchers to provide clear recommendations to growers, with proposed stocking rates varying from 3-8 colonies per ha.

Mathematical modeling of plant-pollinator interactions can help understand key determinants in pollination success [5]. Such approaches could be valuable tools for designing optimal crop orchard layouts and for the effective use of managed pollinators in agricultural systems. This may be especially important in dioecious crops that have separate male and female plants which adds further complexity in conducting empirical field trials when these plants respond differently to environmental variables. Additionally, this modeling approach could be used to improve conservation practices for native pollinators and natural plant communities.

In spite of this, pollination models have tended to focus on plant biology [6–9] or insect behavior [10, 11] but few have examined both simultaneously [12, 13]. Including variables such as flower phenology, the ratio of male to female flowers, pollinator abundance, and flower handling behavior could assist in the generation of robust models. Combining information from both pollinators and plants in the same framework more realistically represents field conditions and enables us to directly compare their importance. A significant challenge in developing good models is sufficient data for parameterization. We chose kiwifruit as our model dioecious crop system as there are four decades of empirical data, examining many aspects of both insect behavior and plant biology [14].

We expected that male-female kiwifruit flower ratio and pollinator density will influence fruit yield, along with various parameters of pollinator behavior. To test the relative importance of these effects, both singly and simultaneously, we used a system of delay differential equations (DDEs) combined with Latin hypercube sampling for parameter sensitivity analysis [15]. The model explicitly tracks pollinators (parameterized here based on data from honey bees), with varying pollen loads as they preferentially visit male and female flowers, as well as the current number of open flowers over time. The delays incorporated into this model take into account the lifespan of open flowers, as male and female flowers open and close throughout the blooming period.

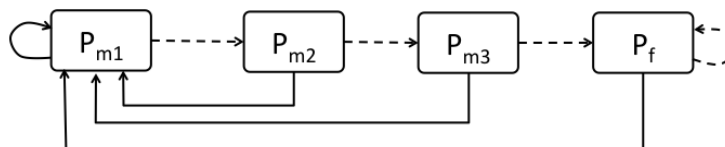
## Materials and methods

### Pollinator-flower model

We developed and analyzed a mathematical model of pollination dynamics. While the model incorporates both male and female flowers as well as insect pollinators it assumes homogeneous conditions across the field for both flower and pollinator densities. Pollinator dynamics are modeled with differential equations that divide the population into subcompartments based on their pollen load. Pollinators can have a high, medium, or low pollen load (denoted as  $P_{m1}$ ,  $P_{m2}$ , and  $P_{m3}$  respectively) or be carrying no pollen (denoted at  $P_f$ ). These states represent a division of empirical data on single-visit deposition, which often follows an exponential [16] or steeper than exponential decay [17].

We assume that pollinators load up on pollen with a visit to a male flower and deposit pollen with a visit to a female flower. A diagram depicting the movement of pollinators between the compartments is shown in Fig. 1. Pollinators that have just

visited a male flower have a high pollen load  $P_{m1}$ . These pollinators can either visit another male flower and remain in compartment  $P_{m1}$ , or visit a female flower, deposit some pollen and thus be transferred into compartment  $P_{m2}$ . Pollinators in compartment  $P_{m2}$  with a medium pollen load can either visit a male flower, acquire more pollen, and be transferred into compartment  $P_{m1}$ , or visit a female flower, deposit some pollen, and be transferred into compartment  $P_{m3}$ . Similarly, pollinators in compartment  $P_{m3}$  with a low pollen load can either visit a male flower, acquire more pollen, and be transferred into compartment  $P_{m1}$  or visit a female flower, deposit all their pollen, and be transferred into compartment  $P_f$ . Pollinators without any pollen in compartment  $P_f$  can either visit a female flower and remain in compartment  $P_f$ , or visit a male flower, acquire a full load of pollen, and be transferred into compartment  $P_{m1}$ .



**Fig 1.** Model flow diagram of pollinator types. Solid lines depict visits to a male flower. Dashed lines depict visits to a female flower.

The rate that pollinators visit male and female flowers is a crucial part of the model dynamics. We consider a pollinator visitation rate that depends on the search rate ( $\alpha$ ), the handling time ( $\beta$ ) and the densities of open male ( $m$ ) and female ( $f$ ) flowers. For pollinator visitation rates, previous work suggests that saturating functions of flower densities such as Holling type II functional responses are typical of oligolectic consumers that use only a few plant species [6]. Following previous studies [6, 18, 19] we defined the total pollinator visitation rate as:

$$\text{Total pollinator visitation rate} = \frac{\alpha(f + m)}{1 + \alpha\beta(f + m)} \quad (1)$$

which has the units of per time. This visitation rate includes visits to both male and female flowers. The movement of pollinators between male and female flowers depends on the proportion of male vs female flowers, as well as pollinator preferences. Previous studies suggest that honey bees have a preference to visits flowers of the same sex as the one they are currently on [20–23]. We define the preference parameter  $\delta$  such that a pollinator on a male flower can preferentially choose to next visit a female flower ( $0 < \delta < 1$ ). Similarly, we define the preference parameter  $\epsilon$  such that a pollinator on a female flower preferentially next visits a male flower ( $0 < \epsilon < 1$ ). Pollinators have no preference if  $\delta = \epsilon = 1$ . Then the movement of pollinators between flowers can be written as the following expressions:

$$\left(\frac{m}{f + m}\right)^\delta \quad \text{fraction on male flowers that move to a male flower} \quad (2a)$$

$$1 - \left(\frac{m}{f + m}\right)^\delta \quad \text{fraction on male flowers that move to a female flower} \quad (2b)$$

$$\left(\frac{f}{f + m}\right)^\epsilon \quad \text{fraction on female flowers that move to a female flower} \quad (2c)$$

$$1 - \left(\frac{f}{f + m}\right)^\epsilon \quad \text{fraction on female flowers that move to a male flower} \quad (2d)$$

The pollinator dynamics are described with the following system of ordinary differential

equations:

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$$\frac{dP_{m1}}{dt} = \underbrace{\left( \frac{\alpha(f+m)}{1+\alpha\beta(f+m)} \right)}_{\text{Total visitation rate}} \left[ \underbrace{\left( 1 - \left( \frac{f}{f+m} \right)^\varepsilon \right) (P_{m2} + P_{m3} + P_f)}_{\text{moves from female to male}} - \underbrace{\left( 1 - \left( \frac{m}{f+m} \right)^\delta \right) P_{m1}}_{\text{moves from male to female}} \right] \quad (3a)$$

$$\frac{dP_{m2}}{dt} = \underbrace{\left( \frac{\alpha(f+m)}{1+\alpha\beta(f+m)} \right)}_{\text{Total visitation rate}} \left[ \underbrace{\left( 1 - \left( \frac{m}{f+m} \right)^\delta \right) P_{m1}}_{\text{moves from male to female}} - \underbrace{\left( 1 - \left( \frac{f}{f+m} \right)^\varepsilon \right) P_{m2}}_{\text{moves from female to male}} - \underbrace{\left( \frac{f}{f+m} \right)^\varepsilon P_{m2}}_{\text{moves from female to female}} \right] \quad (3b)$$

$$\frac{dP_{m3}}{dt} = \underbrace{\left( \frac{\alpha(f+m)}{1+\alpha\beta(f+m)} \right)}_{\text{Total visitation rate}} \left[ \underbrace{\left( \frac{f}{f+m} \right)^\varepsilon P_{m2}}_{\text{moves from female to female}} - \underbrace{\left( 1 - \left( \frac{f}{f+m} \right)^\varepsilon \right) P_{m3}}_{\text{moves from female to male}} - \underbrace{\left( \frac{f}{f+m} \right)^\varepsilon P_{m3}}_{\text{moves from female to female}} \right] \quad (3c)$$

$$\frac{dP_f}{dt} = \underbrace{\left( \frac{\alpha(f+m)}{1+\alpha\beta(f+m)} \right)}_{\text{Total visitation rate}} \left[ \underbrace{\left( \frac{f}{f+m} \right)^\varepsilon P_{m3}}_{\text{moves from female to female}} - \underbrace{\left( 1 - \left( \frac{f}{f+m} \right)^\varepsilon \right) P_f}_{\text{moves from female to male}} \right] \quad (3d)$$

In order to incorporate the number of open male and female flowers we consider the total number of flower buds in the field to be fixed and assume the rate they open follows a normal distribution. Let  $B_m$  and  $B_f$  denote the total number of male and female flower buds. Initially all flower buds are closed. The rates that the male and female flowers open is modeled with

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$$\frac{dM}{dt} = \frac{B_m}{\sqrt{2\pi\sigma_m^2}} e^{-\frac{(t-t_m)^2}{2\sigma_m^2}} \quad (4a)$$

$$\frac{dF}{dt} = \frac{B_f}{\sqrt{2\pi\sigma_f^2}} e^{-\frac{(t-t_f)^2}{2\sigma_f^2}} \quad (4b)$$

where  $t_m$  and  $t_f$  are the times of peak flower opening rate and  $\sigma_m$  and  $\sigma_f$  are the variations in the rates of opening. We assume that each flower is only open for a fixed amount of time. Male flowers are open for  $\tau_m$  days and female flowers remain open for  $\tau_f$  days. The number of currently opened male and female flowers can be determined

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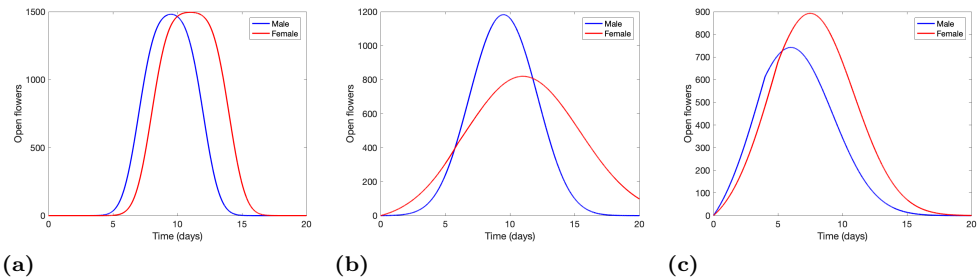
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with these fixed delays as follows:

$$m(t) = \begin{cases} M(t) - M(t - \tau_m) & \text{if } t > \tau_m \\ M(t) & \text{elsewhere} \end{cases} \quad (5a)$$

$$f(t) = \begin{cases} F(t) - F(t - \tau_f) & \text{if } t > \tau_f \\ F(t) & \text{elsewhere} \end{cases} \quad (5b)$$

Example simulated dynamics of open flowers over time are depicted in Fig 2.



**Fig 2.** Example simulations of open flowers over time following equations (5) starting with 1500 of each male and female flower buds  $B_m = B_f = 1500$  (modeling 5 meters by 5 meters orchard field) for (a)  $\sigma_m = 1$ ,  $\sigma_f = 1$ ,  $t_m = 7$ ,  $t_f = 8$ ,  $\tau_m = 5$ ,  $\tau_f = 6$  and (b)  $\sigma_m = 2$ ,  $\sigma_f = 4$ ,  $t_m = 7$ ,  $t_f = 8$ ,  $\tau_m = 5$ ,  $\tau_f = 6$  and (c)  $\sigma_m = 3$ ,  $\sigma_f = 3$ ,  $t_m = 4$ ,  $t_f = 5$ ,  $\tau_m = 4$ ,  $\tau_f = 5$ .

The incorporation of equations (5) into the system of differential equations for the pollinators model (3) results in a system of ordinary differential equations when  $t \leq \min\{\tau_m, \tau_f\}$ , before any open flowers begin to close, followed by a system of delay differential equations with a single delay  $\tau = \min\{\tau_m, \tau_f\}$  when  $\min\{\tau_m, \tau_f\} \leq t \leq \max\{\tau_m, \tau_f\}$ , and then by a system of delay differential equations with two fixed delays,  $\tau_m$  and  $\tau_f$ . This model tracks the number of open male and female flowers ( $m, f$ ) and the number of pollinators of each type ( $P_{m1}, P_{m2}, P_{m3}, P_f$ ) as they visit male and female flowers. The total number of different visits to female flowers is an important factor for pollination. The different classes of bees represent different pollen deposition potentials; we used empirical data to calculate the chance that each visit from each class of bee will produce a fully pollinated fruit. We then use the number of different visits and the chance of fruit set of each visit to determine the total number of fully pollinated fruit per hectare.

### Pollination measurement

We define the visit that results in transitioning a pollinator from group  $P_{m1}$  to  $P_{m2}$  as a type one visit, the visit that results in transitioning a pollinator from group  $P_{m2}$  to  $P_{m3}$  as a type two visit, and the visit that results in transitioning a pollinator from group  $P_{m3}$  to  $P_f$  as a type three visit. We then define fruit set for a day  $t$  denoted by  $P(t)$  as

$$P(t) = 1 - (1 - p_1)^{v_1(t)} \times (1 - p_2)^{v_2(t)} \times (1 - p_3)^{v_3(t)} \quad (6)$$

where  $v_n(t)$  for  $n = 1, 2, 3$  represents the total number of type  $n$  visits that each flower has received at the time of closing (day  $t$ ), and  $p_n$  represents the percent chance that a single visit will fully pollinate a flower to set fruit, for each visit type  $n$ . The total predicted yield is the fruit set for each day multiplied by the number of female flowers

closing on that day, summed over all the days,

$$\text{The total predicted yield} = \sum_t DFC(t) * P(t). \quad (7)$$

where  $DFC(t)$  denotes the daily number of female flowers closing at day  $t$ . The total predicted yield proportion over all days is the number of flowers closing on each day multiplied by the fruit set for that day divided by the total number of female flowers, in our calculation we use the number of total female flower buds,

$$\text{The total predicted yield proportion} = \frac{\sum_t DFC(t) * P(t)}{B_f}. \quad (8)$$

## Parameterization

All model parameters are listed in Table 1. In order to parameterize the visitation rate Eq. (1) we assume the pollinators are active in the field for only 4 hours per day. For the search rate  $\alpha$  we assume a pollinator encounters 2 flowers per min, or 480 visits per day, assuming they forage only 4 hours a day. For the handling time  $\beta$  it has been observed that the average time a pollinator spends on a flower is 16 sec, or 0.0011 days [24]. We use an odds ratio to parameterize the preference parameters,  $\delta$  and  $\epsilon$ . From the literature values, we calculated that pollinators on male flowers have a 0.957 probability of switching to a female flower and those on female flowers have a 0.951 probability of switching to a male [14, 22, 23]. Assuming an equal density of male and female flowers we take  $\delta = \ln(0.957)/\ln(0.5)$  and  $\epsilon = \ln(0.951)/\ln(0.5)$ . Once flowers begin to open, the peak day for flower openings occurs between days 2 and 9 [23, 25, 26] and we assume  $t_m = 6$  and  $t_f = 6$  days. Flowers remain open for 3–7 days [27] and we assume base values of 5 for  $\tau_m$  and 4 for  $\tau_f$ . Observed pollinator densities range from 0.2–20 per 1000 flowers [27], and we assume a baseline value of  $\rho = 6$  pollinators. We assume the percent chance that a single type one visit (transitions a pollinator from group  $P_{m1}$  to group  $P_{m2}$ ) will fully pollinate a flower to set fruit is  $p_1 = 66\%$ . A single type two visit (transitions from  $P_{m2}$  to  $P_{m3}$ ) will fully pollinate a flower with assumed  $p_2 = 55\%$  and a single type three visit (transitions from  $P_{m3}$  to  $P_f$ ) will fully pollinate a flower with assumed  $p_2 = 22\%$  [14]. For the total number of flowers we assume the number of flower buds follows  $B_m = B_f = 600,000$  per ha.

## Model simulations

All simulations were conducted using Matlab's differential equations solvers ode45 and dde23 with initial conditions such that 0% of pollinators were  $P_{m1}$ ,  $P_{m2}$ , and  $P_{m3}$ , and 100% of pollinators were  $P_f$  at time  $t = 0$  for an orchard of sample size of 1 ha. Parameter values for the total number of flower buds  $B_m$  (male) and  $B_f$  (female) along with the number of pollinators per 1000 female flowers  $\rho$  are used to determine the total number of pollinators for each simulation.

Model simulations for the set of baseline values given in Table 1 are shown in Fig. 3. Pollinators of type  $P_{m1}$  and  $P_f$  fluctuate during the blooming period while the number of pollinators of types  $P_{m2}$  and  $P_{m3}$  remain low (Fig. 3a). The accumulated number of visits to female flowers at the time of closing is almost identical across visit types (Fig. 3e), and is driven by the number of open female and male flowers, since the number of pollinators is fixed. Our model output measure (total predicted yield) is shown in Fig. 3f. Intuitively, type one visits have the highest fruit set rate while type three visits have the lowest fruit set rate, even though the total number of these visits are similar (Fig. 3f). The results in Fig. 3(f) multiplied by the daily number of female flowers closing yields the daily predicted yield. Then the summation of this yield returns the main output for our model; the total predicted yield (see Eq. (7)).

**Table 1. Model parameters, base values and ranges used in simulations.**

Parameter	Meaning	Units	Base value	Range	References
$\alpha$	search rate	1/(day×flower)	480	120 – 3600	[14]
$\beta$	handling time	days	0.0011	0.00013– 0.0094	[20, 28–30]
$\delta$	switch preference from male to female flower	–	0.0634	0–1	[20–23], [14]
$\varepsilon$	switch preference from female to male flower	–	0.0725	0 –1	[20], [14]
$B_m$	number of male buds	flower	600000	300000–900000	[25, 31]
$B_f$	number of female buds	flower	600000	300000–900000	[25]
$t_m$	peak day of male flower opening	day	6	2 – 9	[23, 25, 26, 32]
$t_f$	peak day of female flower opening	day	6	2 – 9	[23, 25, 26, 32]
$\sigma_m$	spread of male flowering period		2.5	0.5–5.5	[23, 25, 26]
$\sigma_f$	spread of female flower period		2	1–4	[23, 25, 26]
$\tau_m$	life span of male flowering	day	4	3–5	[27]
$\tau_f$	life span of female flower	day	5	3–7	[22, 33, 34]
$\rho$	pollinators per 1000 flowers	pollinators/flower	6	1 – 20	[27, 31]
$p_1$	percent chance to set fruit from single type one visit		0.66	0.25– 0.75	[14]
$p_2$	percent chance to set fruit from single type two visit		0.55	0.1– 0.65	[14]
$p_3$	percent chance to set fruit from single type three visit		0.22	0– 0.5	[14]

### Parameter sensitivity analysis

In order to better assess the predictions of our model we investigate the uncertainty of the estimated parameter values using Latin Hypercube Sampling (LHS) with the statistical Partial Rank Correlation Coefficient (PRCC) technique, which provides a global parameter sensitivity analysis. LHS is a stratified Monte Carlo sampling method without replacement giving a global and unbiased selection of parameter values [15]. The PRCC technique is used to assess the importance of each parameter for a given output measure. It is appropriate when the parameters have a nonlinear and monotonic relationship with the output measures. Using a model orchard of 1 ha we used LHS to sample the parameters listed in Table 1 and used PRCC to investigate the output measure of the total predicted fully pollinated fruit per hectare (yield). Following [15] we performed a z-test on the resulting PRCC values and verified that, in general, higher magnitude PRCC values correspond with a stronger influence on the output measure. Most of the parameters had nonlinear and monotonic relationships to the total predicted yield. Additional investigation on parameter values that were nonmonotonic was done by truncating the parameter space to monotonic regions, details are presented in the appendix.

## Results

We varied key model input parameters and investigated model predictions with numerical simulations and sensitivity analysis. Model parameters are presented in Table 1. A major model output measure is the predicted yield, which is defined as the number of female flowers per ha that became fully pollinated fruit. A second important model output is the percentage of female flowers that became fully pollinated fruit.

To investigate the role of key plant parameters we varied the ratio of male to female



flowers in the orchard by fixing the total number of flowers and varying the percentage of flowers that are female, all other parameters were set to their base values shown in Table 1. Increasing the fraction of flowers that are female (versus male) per hectare first increases the total predicted yield (fruit per hectare), peaking near 0.66, and then decreasing rapidly as female flowers make up the majority of the orchard (Fig. 4). When the fraction of female flowers per hectare is low, nearly all female flowers produce fruit: predicted fruitset reaches above 97%. However, the total yield (fruit produced) is low due to the low quantity of female flower buds. On the other hand, when most flowers are female, predicted fruitset decreases to 20% along with an associated decline in yield. This is due to the fact that while the quantity of female flowers is high, the quantity of male flowers is low and the chances of successful pollination decreases substantially. The model predicts a maximum fruit yield when female flowers make up two thirds of the field with a fruitset (percent of open flowers that achieved successful pollination) of 78.3%.

Other key plant parameters influence the timing of when male and female flowers are open and receptive. The model assumes the rate that flowers open follow normal distributions with key parameters specifying the peak day of flower openings for both the male ( $t_m$ ) and female ( $t_f$ ) distributions. Varying the peak day that male and female flowers open influences the duration of time with both types of flowers open simultaneously as well as the number of flowers open during these times (Fig. 5a). In particular, differences between  $t_m$  and  $t_f$  shifts these distributions and affects the overlapping time when both flower types are open. In Fig. 5 we hold  $t_f = 6$  days constant and vary the peak day of male flowers opening from  $t_m = 3 - 9$  days. Predicted yield is maximized (with associated fruit set rates above 91%) when both flower types open concurrently with the same peak opening day (Fig. 5b).

To investigate the role of key pollinator parameters, we varied pollinator density based on data on observed honey bee densities. The total predicted yield increases rapidly as the number of bees increases from one to six bees per 1000 female flowers (Fig. 6). Here fruit set also increases from 39% with only one bee per 1000 female flowers to over 90% with six bees per 1000 female flowers. While continuing to increase the number of bees does increase fruit set rate and the total predicted yield, the increase slows down substantially above six bees per 1000 female flowers.

Pollinator behavior parameters also play important roles in the model. The model includes preference parameters for pollinators to switch the type of flower they are visiting, based again on data from honey bee observations. For the baseline values, a pollinator on a male flower preferentially chooses to visit a male flower next ( $\delta$ ), likewise a pollinator on a female flower preferentially chooses to visit a female flower next ( $\epsilon$ ). Total predicted yield increases as the pollinators increasingly prefer to switch between male and female flowers in sequential visits (Fig. 7a). The yield increases substantially when preference for switching is very small and saturates quickly after. The drastic increase in yield begins to plateau close to the baseline parameter values for the switch preferences,  $\epsilon$  and  $\delta$  (dashed lines in Fig. 7a). For a given switching probability, a preference for moving from female to male flowers ( $\epsilon$ ) leads to a higher yield compared with a preference for moving from male to female flowers ( $\delta$ ) (Fig. 7a). Another relevant pollinator behavior is the speed of foraging. Our model includes two parameters for this: the handling time and search rate. Our analyses indicate that of these two, the handling time is the most influential; the total predicted yield decreases quickly as the pollinators' handling time increases (Fig. 7b). When the handling time increases from 10 sec to 60 sec, fruit set rates decrease from 100% to 50%.

The modeling framework enables us to vary key plant and pollinator parameters simultaneously. For a given percentage of female flower buds that make up the orchard, predicted yield increases as the number of bees per 1000 female flowers increases



(Fig. 8). When the female flower buds percentage is high (between 50% and 90%), maintenance of bee densities over 6 bees per 1000 female flowers will lead to better pollination and therefore ensure a high predicted yield.

Parameter sensitivity analysis shows that the percentage of female flowers, the total number of buds, and the bee density have the most significant effect on the total predicted yield (Fig. 9) with a positive correlation. Bee density, the pollinators' preference to switch from female to male flowers ( $\epsilon$ ), the male flowering period ( $\sigma_m$ ), and the pollinator's preference to switch from male to female flowers ( $\delta$ ) are the next most important parameters that are positively correlated with the predicted yield, while pollinator handling time is the only parameter with a strongly negative effect on the total predicted yield.

## Discussion

Flower density and the percentage of female flowers were highly influential parameters in predicting final fruit yield. Also important was the width of the male blooming window. Managed honey bees are the primary mode of kiwifruit pollination globally [2], and several pollinator-related factors were found to influence yield, with bee density, flower handling time, and preference for moving between flowers of different sexes all highlighted by our sensitivity analysis.

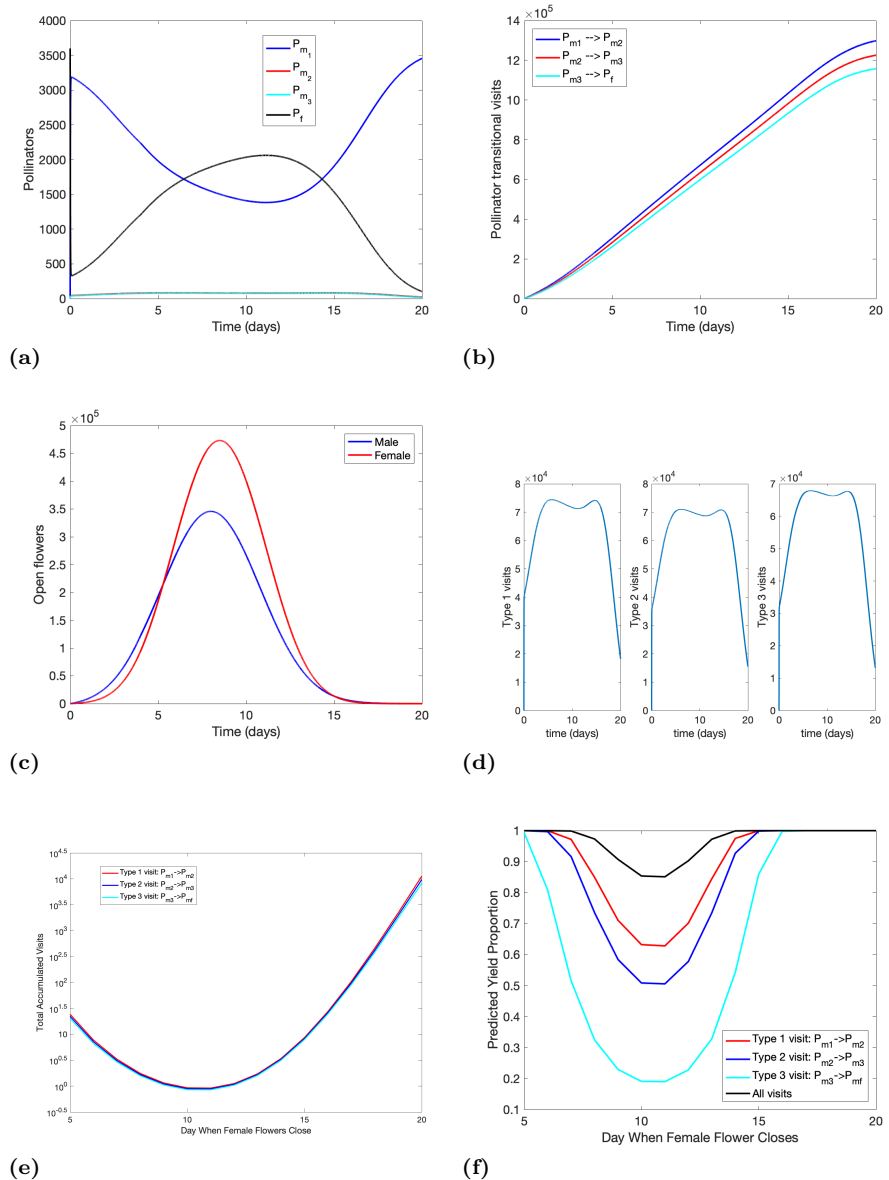
Kiwifruit flowers may take up to 40 honey bee visits to be fully pollinated [35], but this is partially due to the large numbers of bees which deposit little or no pollen. We found that increasing bee density will increase fruit production, but that there is a point of diminishing returns after the first 6-8 bees per 1000 female flowers and buds. This finding broadly agrees with the literature, which reports that densities of around 3-6 bees per 1000 flowers are sufficient for full pollination [36-38], with sustained higher bee numbers being unusual, though sustained densities of 14 bees per 1000 flowers have been reported in cages [37] and densities of 30-60 bees per 1000 flowers may occur for a very brief period of time in rare circumstances [4, 22]. We found that a longer flower handling time was negatively correlated with fruit production in this model. Although empirical data show that honey bee flower handling time is not correlated with pollen deposition [14], the rate of flower visitation is a well-known factor in limiting the effectiveness of pollinators independently of pollen deposition. [39].

Preference factors are less well-known, but highlighted here. Honey bees are able to differentiate between male and female kiwifruit flowers without landing on them [22], and they must travel from a male flower to a female flower to deposit viable pollen. This chance of switching can potentially be affected by other pollinators in the field [40], as well as the attractiveness of the male and female cultivars. Increasing the chance of switching between plant sexes may be a critical factor for kiwifruit pollination, as the baseline values in our model are right on the edge of a steep decline—if less switching happens than currently reported in the literature (as indicated by the base parameter values), there could be very significant, negative impacts on pollination.

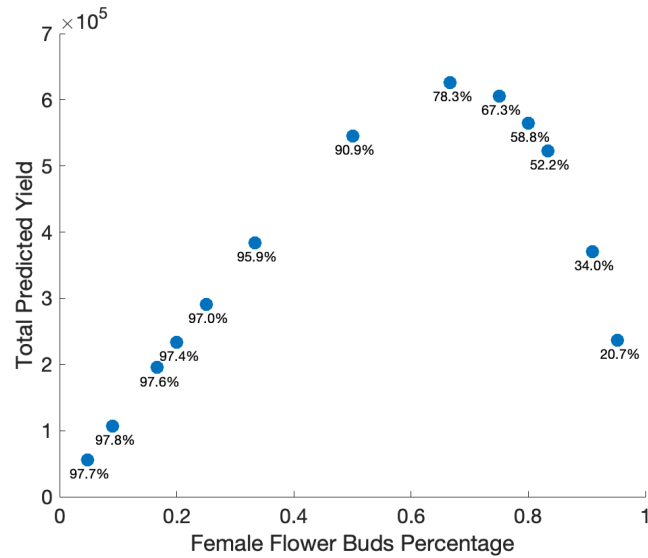
When examining the interaction of bee density and the proportion of female flowers, we found that, at typical bee densities ( $< 12$  bees per 1000 flowers), the optimum proportion of female flowers was 65-75% of total flowers, representing a 'sweet spot' between having more possibilities for fruit development and risk from insufficient movement of bees between the two flower sexes. Current orchard plantings have an approximately 50:50 ratio between male and female flowers [4], highlighting an opportunity to increase yield by changing pruning practices to increase the proportion of female flowers—an easily achievable intervention compared with changing pollinator behavior.

Our model takes advantage of over 30 years of field-based data in New Zealand and

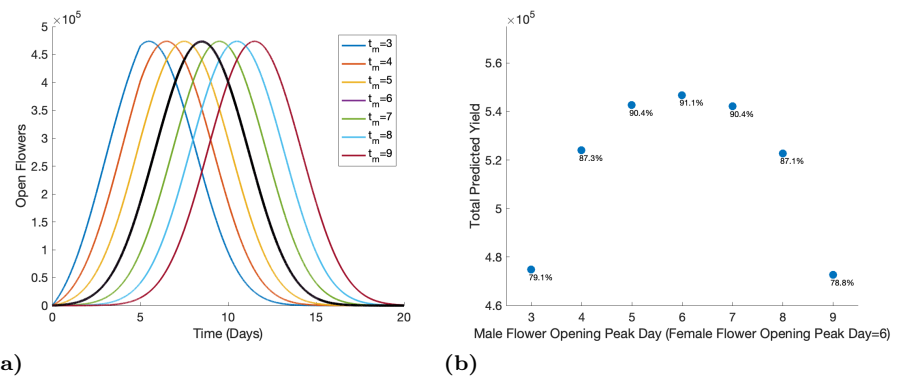
other parts of the world and provides a way to quantitatively assess how different plant- 286  
and insect-related factors interact and their importance for final fruit set. Our results 287  
suggest that choosing cultivars which have their peak bloom on the same day, planting 288  
and pruning to achieve approximately 70% female flowers in the orchard, having as 289  
many flowers as the vine can support to full fruit size, and placing enough hives to 290  
maintain more than 6 bees per 1000 flowers will optimize yield. There is the potential 291  
for future work to improve the predictive power of this model by accounting for multiple 292  
pollinators and spatial scale and pattern. 293



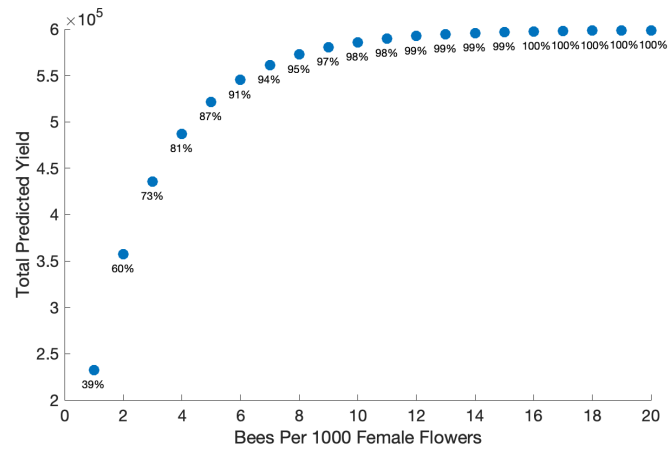
**Fig 3.** Model simulations presenting (a) number of pollinators during the bloom period, (b) accumulated number of transitional visits of different types, (c) number of open male and female flower during the bloom period, (d) daily number of transitional visits of different types, (e) daily number of transitional visits of different types per female flower at the time of closing, (f) predicted number of fully pollenated fruit for each type visit and all visits for female flowers at the time of closing. All parameter values are base values in Table 1 with initial conditions that pollinators haven't collected any pollen yet (*i.e.*,  $P_{m1} = P_{m2} = P_{m3} = 0$  and  $P_f = \rho * B_f/1000$ )



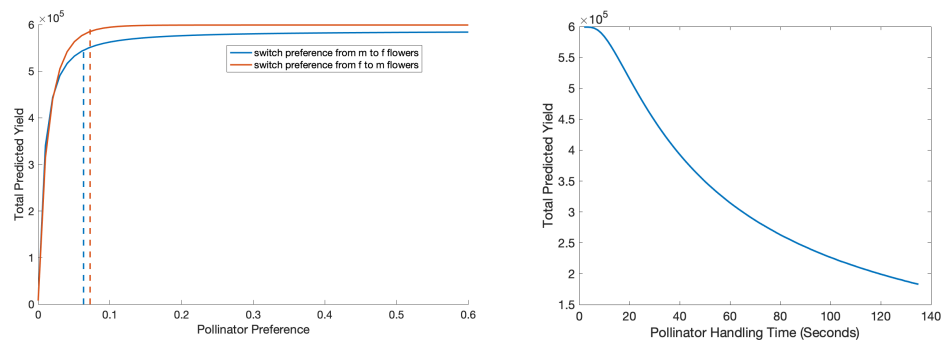
**Fig 4.** Total predicted yield (fruit per ha) as a function of the fraction of flowers that are female. The total number of buds was kept constant at 1.2 million/ha and the fraction of female flowers varied. Other parameters are baseline values in Table 1. The fruitset (percentage of open female flowers that achieved full pollination) is listed under each data point.



**Fig 5.** Open male (colored) and female (black) flowers (a) and total predicted yield (b) for varying peak day of male flower opening from day 3 to day 9. The total amount of buds was kept constant at 1.2 million/ha with a male to female flower ratio of 1:1 and 6 bees per 1000 female flowers. Other parameters are baseline values in Table 1. The percentage of open female flowers that achieved sufficient pollination to set fruit is listed under each data point.



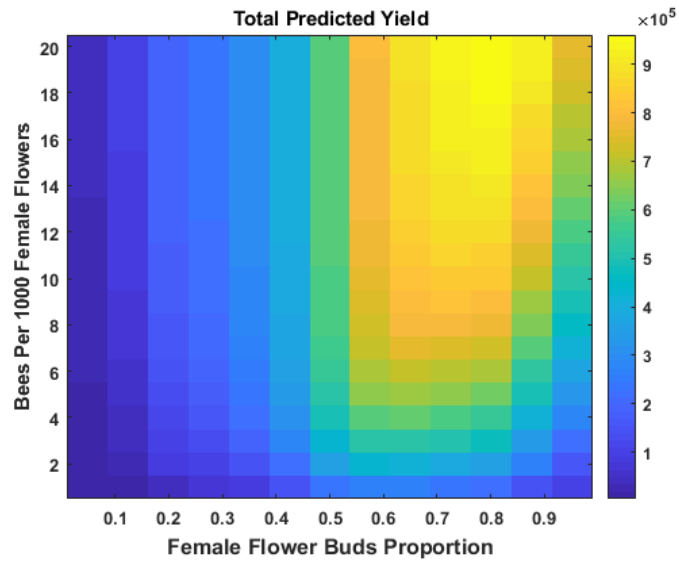
**Fig 6.** Total predicted yield as a function of the number of bees per 1000 female flowers. The bee density varies from 1 bee per 1000 female flowers to 20 bees per 1000 female flowers, and the total amount of buds was kept constant at 1.2 million/ha with a male to female flower ratio of 1:1. Other parameters are baseline values in Table 1. The percentage of open female flowers that achieved sufficient pollination to set fruit is listed under each data point.



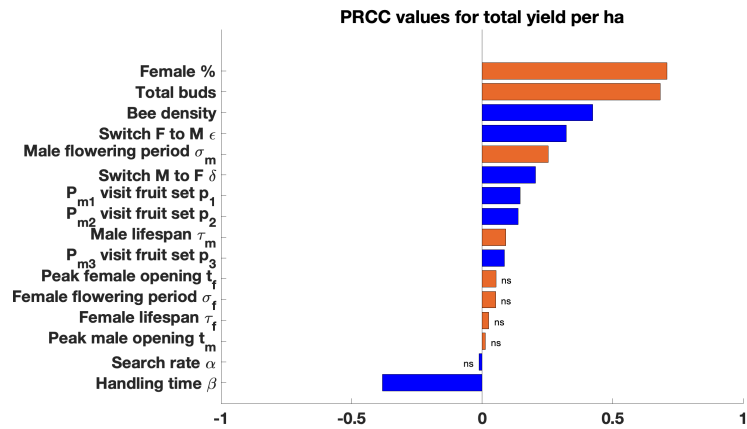
(a)

(b)

**Fig 7.** Total predicted yield for varying pollinators' preference of flowers (a) and for varying pollinators' handling time (b). Other parameters are baseline values in Table 1. Pollinators prefer flowers of the same sex in sequential visits; preference values of 0 mean pollinators never switch and preference values of 1 mean pollinators choose their next flower without regard to its sex. Blue dashed line in (a) depict baseline values of  $\delta$  (switch preference from male to female flower) and red dashed lines depict values of  $\epsilon$  (switch preference from female to male flower).



**Fig 8.** Total predicted yield for varying the proportion of female flower buds and the number of bees per 1000 female flowers. The total amount of buds was kept constant at 1.2 million/ha. Other parameters are baseline values in Table 1.



**Fig 9.** Sensitivity analysis of the Delay Differential Equation model using partial rank correlation coefficient (PRCC) values for each parameter in the Latin hypercube sampling. PRCC values marked as ns are not significant ( $P < 0.05$ ). Flower traits are in orange and pollinator traits are in blue.

## Supporting information

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**S1 Appendix.** Many of the parameters have monotonic relationships with the output measure (Fig. 10a) and the PRCC statistics for those are reliable. However, we note that parameters  $\sigma_m, \sigma_f, t_m, t_f$  and the proportion of female flower buds in the field exhibit nonmonotonic behaviors. Therefore, we conducted additional LHE sampling by truncating the ranges of these parameters to monotonic regions. Figures 10b and c depict the monotonicity of the truncated parameter space. The resulting PRCC results for the entire parameter space as well as the truncated parameter spaces are compared in Fig 11. Parameters for the total number of buds, percentage of female buds, bee density, and handling time are consistently identified as important parameters in all cases. We note that in the truncated case we split the percentage of female flower buds into the cases of 5–76% and 76–96%. In the first half this parameter shows a highly influential positive relationship with predicted yield (large positive PRCC value) and in the second half the parameter is inversely related to the predicted yield. This is as expected as saturating the field with only female buds will eventually cause a decrease in yield. These dynamics are observed in the monotonicity plots as well.

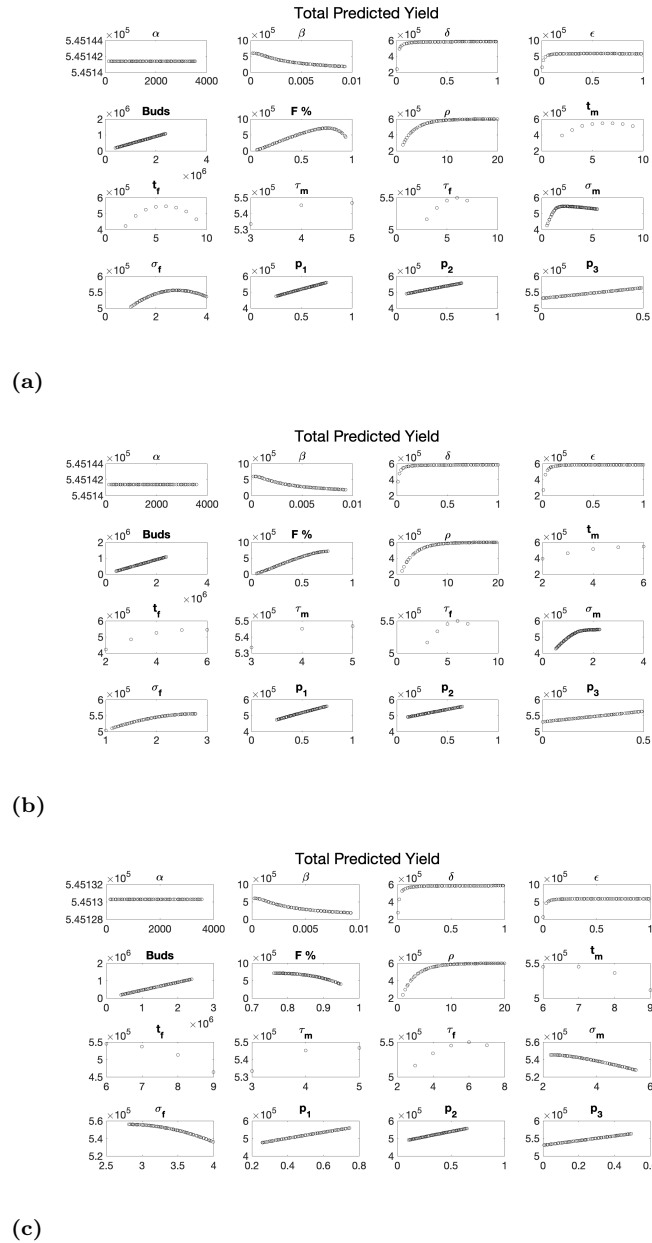
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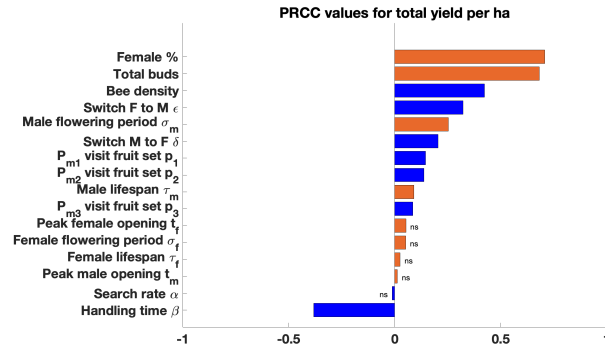
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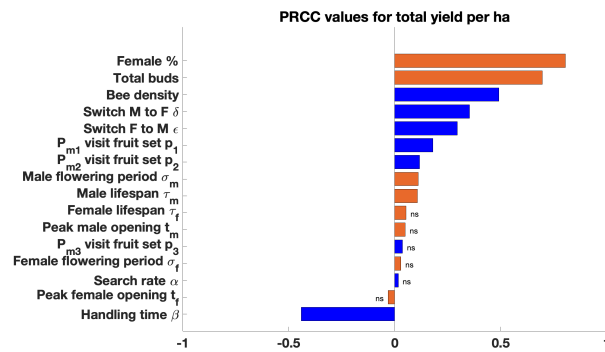




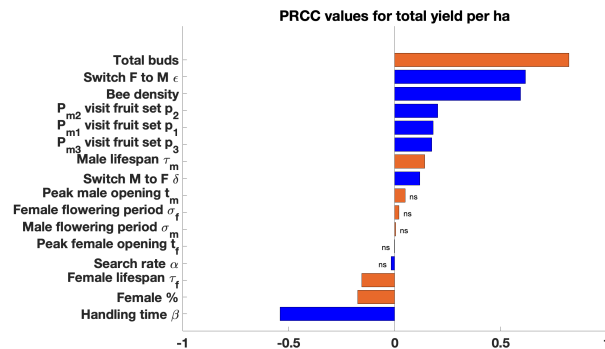
**Fig 10.** Latin hypercube sampling monotonicity plots for the (a) original parameter ranges listed in Table 1 with the percentage of female buds  $\in (5\%, 95\%)$ , (b) truncated parameter ranges including  $\sigma_m \in (.05, 2.27)$ ,  $\sigma_f \in (1, 2.8)$ ,  $t_m \in (2, 6)$ ,  $t_f \in (2, 6)$  and percentage of female buds  $\in (5\%, 76\%)$ , and (c) truncated parameter ranges including  $\sigma_m \in (2.27, 5.5)$ ,  $\sigma_f \in (2.8, 4)$ ,  $t_m \in (6, 9)$ ,  $t_f \in (6, 9)$  and percentage of female buds  $\in (76\%, 96\%)$ .



(a)



(b)



(c)

**Fig 11.** Latin hypercube sampling Partial rank correlation coefficient values for each parameter in the (a) original parameter ranges listed in Table 1 with the percentage of female buds  $\in$  (5%, 95%), (b) truncated parameter ranges including  $\sigma_m \in (.05, 2.27)$ ,  $\sigma_f \in (1, 2.8)$ ,  $t_m \in (2, 6)$ ,  $t_f \in (2, 6)$  and percentage of female buds  $\in$  (5%, 76%), and (c) truncated parameter ranges including  $\sigma_m \in (2.27, 5.5)$ ,  $\sigma_f \in (2.8, 4)$ ,  $t_m \in (6, 9)$ ,  $t_f \in (6, 9)$  and percentage of female buds  $\in$  (76%, 96%). Flower traits are in orange and pollinator traits are in blue.

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