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Running head. Simulation model for crop pollination

The costs and benefits of pollinator dependence: empirically-based simulations predict raspberry fruit quality

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Abstract

Globally, agriculture increasingly depends on pollinators to produce many seed and fruit crops. However, what constitutes optimal pollination service for pollinator-dependent crops remains unanswered. We developed a simulation model to identify the optimal pollination service that maximizes fruit quality in crops. The model depicts the pollination (i.e. autonomous self-fertilization, pollen deposition) and post-pollination (i.e. pollen germination, and time from germination to ovule fertilization) processes leading to fruit and seed set and allows for negative flower-pollinator interactions, specifically pistil damage. We This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1002/eap.01720

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parameterized and validated the model based on empirical observations of commercial raspberry in western Argentina. To assess the effects of pollination intensity for fruit production, we conducted simulations over a range of visit number per flower by the two primary managed pollinators worldwide, *Apis mellifera* and *Bombus terrestris*. Simulations identified that ~15-35 visits per flower by *A. mellifera* or ~10-20 visits by *B. terrestris* provide adequate pollination and maximize raspberry fruit quality (i.e. estimated as the proportion of ovules that develop into drupelets). Visits in excess of these optima reduce simulated fruit quality, and flowers receiving > 670 honey-bee visits or > 470 bumble-bee visits would produce fruits of poorer quality than those receiving no bee visits. The simulations generated consistent, unbiased predictions of fruit quality for 12 raspberry fields. This model could be adapted easily to other animal-pollinated crops and used to guide efficient pollinator management in any agro-ecosystem.

Keywords: simulation model, crop pollination, honey bees, bumble bees, raspberry, fruit quality.

Introduction

Globally, the area cultivated with pollinator-dependent crops is increasing proportionally faster than that of pollinator-independent crops in association with accelerated market demand (Aizen et al. 2008). Unfortunately, the continuous expansion of farmland threatens biodiversity in general (Robinson and Sutherland 2002, Benton et al. 2003), and pollinators in particular (Winfree et al. 2009, Garibaldi et al. 2011). For this reason, active management of pollinators to supplement the pollination service provided by wild flower visitors is a growing practice in most agroecosystems (Velthuis and Van Doorn 2006). Honey bees (*Apis*

mellifera L.) and, more recently, some species of bumble bees (*Bombus* spp.) are the most common species managed specifically for crop pollination (Velthuis and Van Doorn 2006).

Current management practices assume a monotonic increase in net pollination benefits (e.g. yield) with pollinator abundance (e.g. number of hives) (Dewenter 2003, King et al. 2013, Benjamin and Winfree 2014). However, such increases are possible only if ovule fertilization is incomplete and fewer zygotes are produced than can mature into seeds, given available resources (pollen limitation: Harder and Aizen 2010); otherwise ovule fertilization and seed set saturate with increasing pollen delivery. Furthermore, fruit/seed production can decline at high visitation rates if interaction costs (e.g. flower damage) grow faster than benefits (e.g. pollen deposition) above a certain visitation threshold (Morris et al. 2010, Aizen et al. 2014, Sáez et al. 2014). Therefore, optimization of critical yield components, such as fruit quantity and quality, can profit from detailed biological understanding of not only crop reproductive systems and pollination requirements, but also of the benefits and costs of animal pollination. Specifically, pollination management should be designed to prescribe ranges of pollinator abundance and mixtures of species that maximize target components of crop yield.

Female reproductive success of flowering plants depends on the outcomes of three sequential stages: pollination, ovule fertilization, and seed development. The outcomes of the first two stages depend on the quantity and quality of pollen deposited on stigmas, which determine pollen germination and pollen-tube development and hence the number of zygotes generated by ovule fertilization (Harder et al. 2012, 2016). Pollination can additionally influence seed development through effects of offspring quality (e.g., inbreeding versus outbreeding) on embryo survival (Husband and Schemske 1996, Harder et al. 2012) and demand for maternal resources (Ida et al. 2013). As a consequence of these effects,

pollination management based on basic principles of the limits on plant reproduction could enhance fruit and seed yield.

To illustrate this approach to pollination management we developed a mechanistic simulation model to identify the optimal pollination service (visit frequency and pollinator identity) for maximizing fruit quality (i.e. proportion of ovules that develop into drupelets) in raspberry (*Rubus idaeus* L.) fields. The model is based on field experiments designed both to identify functions describing the pollination and post-pollination processes that determine the number of drupelets per fruit and to estimate their key parameters. Specifically, these experiments estimated: (1) the extent of autonomous self-fertilization; (2) the relation of pollen deposition to the number of visits by flower visitors; (3) the minimum number of pollen grains on the stigma needed for pollen-grain germination and pollen-tube growth; (4) the time between pollen germination and ovule fertilization; and (5) the relation of flower damage to the number of visits of floral visitors. In raspberry, style breakage that interrupts pollen-tube growth, the most important interaction cost, increases with bee density (Aizen et al. 2014, Sáez et al. 2014).

After estimating the model parameters and the consequences of visitation rates, we evaluated the utility of the model by checking its ability to predict fruit quality in actual field situations. For this, we used previously published data of the relation of drupelet set to variation in visitation by managed *A. mellifera* and invasive *Bombus terrestris* (L.) among raspberry fields (see Sáez et al. 2014). Although this model was derived specifically to predict pollination-related benefits and costs in raspberry, it depicts most key biological processes needed to model the pollination dynamics of any pollinator-dependent crop or wild plant.

Materials and Methods

Field site and study crop

Experiments to estimate model functions and parameters (see below and Appendices) were conducted during the 2013 austral summer (January–March) in a raspberry field (*Rubus idaeus*, Autumn bliss variety) at Arroyo Claro Farm (41° 56.700 S; 71° 31.200 W), El Bolson, Río Negro, Argentina. Raspberry flowers are bisexual and completely self-compatible, but their structure (i.e. 80–100 clustered pistils surrounded by many stamens) precludes complete autonomous self-pollination. Specifically, pollen from the peripheral ring of anthers cannot contact the centermost pistils of the flower in the absence of a pollen vector (Cane 2005). Thus, even though most raspberry flowers can set fruit without bee visits, unvisited flowers set more malformed fruits with fewer drupelets than open-pollinated flowers (Cane 2005, Morales 2009). Consequently, most, if not all, of a flower's many ovules have to be fertilized to produce market-quality fruits (Cane 2005). Therefore, honey-bee or bumble-bee hives are commonly deployed in raspberry fields to ensure adequate pollination (Velthuis and Van Doorn 2006). Although honey bees and bumble bees can forage very differently, leading to different rates of self and outcross pollen deposition, pollen quality has no effect on drupelet set or fruit mass, as raspberry is fully self-compatible (Tuohimetsä et al. 2014). In NW Patagonia, raspberry flowers are mostly visited by two introduced bees: the managed honey bee, *A. mellifera*, and the feral bumble bee, *B. terrestris* (see Morales 2009, Sáez et al. 2014). While visiting flowers, these bees usefully transfer pollen, but they can also break flower styles, hindering ovule fertilization by precluding or interrupting pollen-tube growth (Aizen et al. 2014, Sáez et al. 2014).

Pollination model

We developed a stochastic simulation model of the pollination and post-pollination processes that occur during a raspberry flower's lifespan (Figure 1). To link pollinator abundance and fruit development mechanistically, we simulated scenarios of increased visitation frequencies. The model simulates events occurring while individual flowers are exposed to pollinator activity (2.5-day floral lifespan with ~8 h of visitation day⁻¹: A. Sáez, personal observation). For every simulated hour the model recorded and updated the number of visits received by each replicated flower, pollen deposition and style damage caused by pollinator visits, pollen germination and pollen tube growth. At the end of a simulation, expected drupelet set was calculated based on the number of pistils with sufficient pollen tubes reaching ovaries of replicated flowers. Pollination and post-pollination processes were simulated using functions describing mean outcomes, with parameters estimated from field experiments (see Appendices S1-S5) and published data. Given the mean of a particular process, stochasticity was introduced based on an appropriate probability distribution. Parameters were estimated using Maximum Likelihood with the *mle2* function from *bbmle* R package (Bolker et al. 2012). Below we summarize the pollination and post-pollination processes and functions represented in the model, whereas Appendices S1-S5 describe the field experiments and parameter estimation procedures.

The effects of visitation frequency were assessed with a series of simulations that depicted a range of mean visitation frequency from 0 to 35 visits · flower⁻¹ · h⁻¹ in increments of 0.01 visits · flower⁻¹ · h⁻¹. During a flower's lifespan, this range is equivalent to 0 to 700 visits, the range observed in 16 fields (Sáez et al. 2014). Each simulation considered 1000 replicated flowers, with the number of pistils per flower, each containing a single ovule, drawn from a Poisson distribution with mean = 95 (the average for ~500 flowers sampled from the same 16 fields). The number of visits, v , received by each flower during each

simulated hour was drawn from a Poisson distribution with a mean equal to the visit frequency (i.e., from 0 to 35, see above).

Raspberry flowers develop some drupelets independently of flower visitation (Cane 2005). Autonomous self-pollination, s , was incorporated in the model by sampling the number of self-pollen grains deposited on each stigma per hour from a Poisson distribution with a mean of 0.135. This self-deposition rate equates to an average of 65% of pistils developing into drupelets, the observed mean drupelet set in the absence of pollinator visitation (see Appendix S1).

Pollen deposition on stigmas accumulates with successive pollinator visits. The number of pollen grains per stigma or pollen receipt, p , was modelled with a negative binomial distribution with the expected value being an asymptotic function of the number of bee visits, v ,

$$\text{Eq. 1: } p = \alpha \cdot (1 - e^{-\beta \cdot v}).$$

Field experiments estimated $\alpha = 88.22$, and $\beta = 0.0082$ and 0.0164 for *A. mellifera* and *B. terrestris*, respectively. The estimated dispersion parameter of the negative binomial distribution was 3.54 (see Appendix S2).

After pollen is deposited on a stigma, grains germinate and tubes start growing towards the ovary. Pollen germination followed a binomial distribution with germination success, g , modeled as an asymptotic function of pollen receipt, p ,

$$\text{Eq. 2: } g = 1 - e^{-\gamma p},$$

with γ estimated to be 0.56 (see Appendix S3). In the model, we assumed that at least five pollen grains had to germinate on the stigma for one pollen tube to reach the ovule and fertilize it (Harder et al. 2016a).

Bee visits to raspberry flowers can break styles, interfering with ovule fertilization if damage occurs before pollen tubes have passed the point of breakage (Aizen et al. 2014, Sáez

et al. 2014). We incorporated this effect by representing both the probability of style damage and the period between pollination and pollen-tube passage beyond the breakage point. The probability of style damage per pistil, d , was modeled as a modified asymptotic function of the number of bee visits, v ,

$$\text{Eq. 3: } d = 1 - e^{-\mu v^\theta},$$

with $\mu = 0.00021$ and 0.00035 for *A. mellifera* and *B. terrestris*, respectively, and $\theta = 1.32$ for both species. Variation around this expected damage probability was modelled with a beta-binomial distribution, with an estimated dispersion parameter of 2.26 (see Appendix S4). If styles are broken, the damage occurs ~ 0.2 mm below the stigma, which represents 10% of the style length. We estimated the period required for pollen tubes to pass this point using a sigmoidal relation of drupelet set, D , to time since pollination, t ,

$$\text{Eq. 4: } D = \frac{D_{\max}}{1 + \omega e^{-\psi t}},$$

with $D_{\max} = 95$ drupelets, $\omega = 45.42$, and $\psi = 0.26$. Based on this function, if style breakage occurred before either any pollen deposition or < 4.1 h after initial pollination it prevented ovule fertilization and drupelet development (Appendix S5).

The preceding processes were implemented for each simulated hour of the 20-h period that flowers receive bee visits during their lifespan, after which the model calculated the proportion of pistils that developed into drupelets (i.e. drupelet set) per flower (Fig. 1). This model assumes no resource limitation (i.e. either water or nutrients), so that only variation in pollination and post-pollination processes affected fruiting success.

The two most abundant visitors of raspberry flowers in the studied fields, *A. mellifera* and *B. terrestris*, differ in their efficiency of pollen deposition per visit and the likelihood of style damage (see Appendices S2 and S5). Therefore, we simulated three scenarios: (i) visits by only *A. mellifera*; (ii) visits by only *B. terrestris*; and (iii) mixed visitation. For the latter

case, we kept the total number of visits (i.e. from 0 to 700) constant and varied the proportion of visits by the two pollinators.

Model validation and sensitivity

To assess the validity of the simulation model for predicting the effects of pollinator visitation on drupelet set, we simulated 12 scenarios representing particular visitation frequencies and proportions of *A. mellifera* and *B. terrestris* observed during the 2012 flowering season. This dataset is well balanced, as similar proportions of honey bees and bumble bees visited flowers (mean \pm SD = 0.42 ± 0.37 , and 0.44 ± 0.41 , respectively: see Table S1 in Sáez et al. 2014 for more details). We assessed the model's predictive capability by regressing the observed drupelet set on the simulation mean. The r^2 of the linear regression represents the proportion of the overall variation in observed mean drupelet set explained by the simulation predictions, whereas the intercept and slope describe model bias and consistency, respectively (Piñeiro et al. 2008). As both observed and predicted drupelet set are random variables, the intercept and slope were estimated from model II regression using the lmodel2 package, R software version 3.0.2 (Legendre 2014; R Core Team 2016). We specifically used major-axis regression as both variables were measured in the same units (Sokal and Rohlf 1981). For each of the 12 fields, we simulated the same number of fruits as we harvested during 2012 to enable comparisons based on equivalent sample sizes.

We estimated the relative influence of the different input parameters on the output (drupelet set) of the simulation model using Monte Carlo estimation of Sobol's Indices (Sobol et al. 2007; Saltelli et al. 2010) with the "sobol2007" function of the "Sensitivity" R package (Pujol et al. 2012) (Table 1). Sobol's method estimates both first-order and total indices. The first-order indices represent the direct contribution of each factor (parameter) to the model output variance (i.e. percentage of the output variance associated with each input factor independently of any other factor), whereas the total indices measure the variance due

to each factor and all of its interactions with other input factors. We varied the parameters for the functions that controlled autonomous self-pollination (see Appendix S1), pollen deposition (see Appendix S2), pollen germination (see Appendix S3), style damage (see Appendix S4), and the period during which pollen-tube growth could be interrupted by style damage (see Appendix S5).

Results

In the simulations, both pollinator density and identity affected the proportion of drupelets set per raspberry fruit. At low pollinator densities, increased visitation by either *A. mellifera* or *B. terrestris* strongly enhanced drupelet set above the ~ 65% that occurs autonomously for isolated flowers (Fig. 2). For visitation by either *A. mellifera* or *B. terrestris* alone, drupelet set increased rapidly with increasing visits, being maximized at 99% success for flowers that received between ~15 - 35 or ~10 - 20 visits, respectively (Fig. 2). However, additional visitation by either pollinator caused drupelet set to decline. With > 670 *A. mellifera* visits or > 470 *B. terrestris* visits, drupelet set fell below that expected from autonomous self-pollination in the absence of pollinators (Fig. 2, left panel). When both pollinators visited raspberry flowers, about 10 visits per flower by each pollinator maximized drupelet set (Fig. 3). Slightly fewer total visits were required to maximize drupelet set if *B. terrestris* dominated the pollinator fauna.

Analysis of model goodness-of-fit detected a significant positive relation of the observed proportion of drupelets per fruit in different fields to that predicted by the model ($r^2 = 0.52$, $n = 12$, $P = 0.007$: Fig. 4), with estimated major-axis intercept = -0.08 and slope = 1.02. The 95% confidence interval for the intercept [-0.99, 0.34] included 0, indicating that the simulation predictions were not significantly biased (Piñeiro et al. 2008). The 95% confidence interval for the slope [0.49, 2.16] included 1, indicating that the predictions were consistent with the observations (Piñeiro et al. 2008). Approximately 75% of the predicted

means for drupelet set deviated from the observed means by < 10 % and the remainder differed by 10 to 25% (Fig. 4).

Sensitivity analysis identified three model parameters with particularly strong influences on variation in predicted drupelet set (see Table 1). These parameters respectively describe the approach to the asymptotes of the exponential functions of pollen deposition (β), pollen germination (γ), and style damage (μ). The germination parameter primarily affected drupelet set directly (large first-order sensitivity compared to total sensitivity), whereas the pollen-deposition and style-damage parameters had more extensive indirect effects (i.e. interactive effects with other factors).

Discussion

Reproductive consequences of pollinator dependence

This study characterizes the benefits and costs of pollinator dependence for female reproductive success of flowering plants. The adopted approach involves two components: a set of experiments and observations needed to characterize functions describing the fundamental pollination and post-pollination processes linking pollination and fruit development; and a simulation model that integrates the empirically-parameterized functions to predict reproductive success based on pollinator abundance and identity. The simulation model, parameterized specifically based on the reproductive biology of raspberry, predicted among-field variation in independently-collected observations consistently and without significant bias. Furthermore, the model predicted a peaked response of the quality of raspberry fruits with increasing pollinator visitation, in agreement with the conceptual cost-benefit models of Simms and Rausher (1987), Morris et al. (2010), and Aizen et al. (2014). Unlike these conceptual models, the empirically-based mechanistic simulations predict the quantitative reproductive outcomes expected from specific densities and mixtures of pollinators. For example, it identified that maximal yield of high-quality raspberries requires

a density of honey bees and/or bumble bees sufficient for individual flowers to receive ~15–20 visits during their receptive lifespan: less frequent visitation causes pollen limitation, whereas more frequent visitation causes flower damage. Thus, this combination of empirical and simulation methods reveals key features of plant-pollinator interactions and their reproductive consequences, and provides scientifically-informed predictions that can be used to manage plant populations, including crops.

The mechanistic approach implemented in this study incorporates four empirical functions describing key pollination and post-pollination processes. First, drupelet set arising from autonomous self-pollination provides a baseline against which to evaluate the net benefits of pollinator visits. In raspberry, fruit set can occur without pollinator visits because of extensive autogamy and limited pre-dispersal inbreeding depression (Cane 2005).

However, animal-pollination enhances fruit quality, specifically the number of drupelets per fruit, which positively affects fruit size. Second, pollen deposition on stigmas increases in a saturating relation with pollinator visitation (Fig. A2: also see Morris et al. 2010). Thus, at least the quantitative benefits of animal pollination are subject to diminishing returns: once enough pollinators have visited a flower to saturate the stigma more pollinator visits do not increase pollen deposition (see also Morris et al. 2010). Third, ovule fertilization did not vary linear with pollination success because of a decelerating relation of pollen germination to pollen deposition (Fig. A3). Consequently, poorly pollinated flowers set fewer seeds than expected from the number of pollinator visits they received. In contrast to the preceding beneficial effects of pollinator visitation, the fourth function described a potential cost, namely the relation of style damage to visitation (Fig. A4). Style damage imposes a reproductive cost that depends on the time elapsed since effective pollination, as determined by both pollinator visitation, which affected the timing of damage, and pollen-tube growth rate, which governed whether pollen tubes passed the breakage point before breakage

occurred. This cost function is instrumental in causing reproductive success to decline at high visitation frequencies and, hence, in determining the optimal visitation frequency.

The simulation model based on these processes effectively predicted observed variation in average drupelet set among raspberry fields with differing bee abundance and proportions of honey bees and bumble bees. This effectiveness was realized even though some parameters were inferred (see M & M), rather than estimated, and the observations used for model validation were sampled during just one day per field (see Sáez et al. 2014). The general correspondence between predictions and observations, despite these limitations, provides convincing evidence that the simulation model incorporated essential reproductive processes.

Although the simulation model incorporated most processes responsible for seed production, several relevant processes were not represented explicitly, which could have affected model predictions. We assumed that ovule fertilization required germination of at least five pollen grains, whereas the probability that a particular pollen tube reaches the ovary generally declines with increasing stigmatic pollen receipt owing to pollen-tube competition (Harder et al. 2016). Such density-dependent pollen-tube success has two consequences. First, ovule fertilization can occur with just a few germinated pollen grains, so the simulations may underrepresent reproductive success following very poor pollination. Second, with many germinated grains ovule fertilization depends on the stylar capacity to support pollen tubes (and ovule number in species with multi-ovulate ovaries), which may occur with less pollen receipt than that needed to saturate the stigmatic pollen load. If so, fewer pollinator visits are required to maximize ovule fertilization than predicted by the simulation model. Two other related features of reproductive success not included in the simulation model are the effects of pollen quality on ovule fertilization and of zygote quality on seed development. These qualitative components probably have little relevance for

raspberry reproduction, as it is fully self-compatible and exhibits little pre-dispersal inbreeding depression; however, they may be germane for other species.

Effects of pollinator visitation and pollination management

Simulations of visitation by the two main pollinators (*A. mellifera* and *B. terrestris*) in the sampled raspberry fields produced qualitatively similar relations between reproductive success and number of visits; however, quantitative differences were evident. These species differed somewhat in the range of visitation that maximized drupelet set and more so in the visitation threshold for which interaction costs exceed pollination benefits (Fig. 2).

Simulation of fruit quality in raspberry when *A. mellifera* was the sole flower visitor predicted maximum benefits, in terms of the proportion of drupelets per fruit, between 15 - 35 visits during a flower's lifespan (i.e. 0.75 - 1.75 visits·h⁻¹). This predicted optimal visitation is close to Chagnon et al.'s (1991) estimated the minimum number of visits to raspberry flowers to maximize fruit quality and production in European raspberry fields. In contrast to the relatively limited range of visitation rate needed to maximize raspberry quality, the simulation predicted beneficial effects of honey-bee visitation for up to 670 visits during a flower's lifespan. Above this number, bees become antagonists, rather than mutualists (see also Chagnon et al. 1991, Aizen et al. 2014) and autonomous self-pollination would be preferable.

Compared to *A. mellifera*, fewer *B. terrestris* visits (i.e. ~10 - 20 visits during a flower's lifespan or 0.5 - 1 visits·h⁻¹) are needed to maximize fruit quality, but they are more damaging than honey-bee visits. Specifically, the model predicted that *B. terrestris* is antagonistic if flowers receive > 470 visits (i.e. 23.5 visits·h⁻¹). Such frequencies occurred in at least two of the 16 raspberry fields that we surveyed (see Sáez et al. 2014). Paradoxically, although this bumble bee was introduced in neighboring Chile for crop pollination, it has

since become so invasive (Torreta et al. 2006, Morales et al. 2013) that management practices to control its density are badly needed (Aizen et al. in press).

Given the ability of the empirically-based simulations to predict yield components, this approach provides a valuable tool both for evaluating the utility of current pollination regimes using short-term pollinator surveys, and for designing optimal strategies for active pollinator management (also see Velthuis and Van Doorn 2006). For example, sensitivity analysis revealed that variation in reproductive success depends mainly on parameters related to pollen deposition, pollen germination, and style damage. Thus, for a plant species with slow pollen germination effective pollinator management would recommend stocking with pollinators with high rates of pollen deposition and low incidence of flower damage.

General applicability

Active management of honey bees and, to a lesser extent, other insects for crop pollination is a growing practice in most agroecosystems (Aizen and Harder 2009). Pollinator supplementation involves financial expense associated with buying or renting beehives, supplementing bee nutrition, and maintaining healthy bees. Therefore, pollination management requires economic optimization governed by the (marginal) yield improvement and countervailing (marginal) expense of each increment of pollinator abundance (Garibaldi et al. 2016). This study illustrates that optimal stocking densities can also depend on ecological costs if yield declines at high densities of flower visitors. However, these costs have not been recognized or considered in pollinator management before. For example, in the study area, beekeepers place their hives near raspberry fields to increase honey yield because raspberry flowers produce considerable nectar (Sáez et al. 2017). Also, the farmers of these fields held the opinion that more bees are better. However, honey-bee visitation in all 16 raspberry fields sampled during 2012 (some stocked with honey-bee hives) exceeded the 1.75

visits h⁻¹ frequency beyond which yield decreases. This suggests that optimum management should have involved fewer hives.

Although specific features of the pollinator dependence of raspberry fruit production motivated the development of this model and supporting experiments, the processes that it depicts are largely general features of female reproduction by pollinator-dependent angiosperms. The most obvious exception involves the effect of visitation on flower damage, which is not known to occur widely. Nevertheless, other processes could cause reduced reproductive success following intense pollination (see Young and Young 1992, Morris et al. 2010, Harder et al. 2016a). With the incorporation of relevant cost functions, this model could be applied readily to any pollinator-dependent crop, or non-cultivated species.

Implementation of the model for other species requires only to carry out experiments to estimate model parameters (see Appendices 1-5) and to verify that the modelled relations describe trends adequately. For many important pollinator dependent crops (e.g. apples, almonds, coffee, mango, etc.), much information on parameters and processes can be found in the literature. Failing that, relevant experiments could be conducted by pollination biologists at the request of growers' associations and agricultural agencies. In addition to providing key information about the reproductive implications of pollinator dependence and the contributions of specific pollinators, this approach provides a scientific foundation for efficient and effective pollinator management in agro-ecosystems.

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Supporting Information

Additional supporting information may be found in the online version of this article at
<http://onlinelibrary.wiley.com/doi/10.1002/eap.xxxx/suppinfo>

Data Availability

Data available from Figshare:

Appendix S1 data – <https://doi.org/10.6084/m9.figshare.5971495.v1>

Appendix S2 data - <https://doi.org/10.6084/m9.figshare.5971492.v1>

Appendix S3 data - <https://doi.org/10.6084/m9.figshare.5971498.v1>

Appendix S4 data - <https://doi.org/10.6084/m9.figshare.5971504.v1>

Appendix S5 data - <https://doi.org/10.6084/m9.figshare.5971507.v1>

Apis-Bombus Simulation data - <https://doi.org/10.6084/m9.figshare.5930362.v1>

Bombus simulation data - <https://doi.org/10.6084/m9.figshare.5930350.v1>

Apis simulation data - <https://doi.org/10.6084/m9.figshare.5930329.v1>

Observed vs Predicted data - <https://doi.org/10.6084/m9.figshare.5930275.v1>

Table 1. Description of parameters of the simulation model and their estimated first-order and total sensitivities based on Sobol's analysis. Large sensitivity values are in bold.

Parameter	Description	Range	First order sensitivity ± SE	Total sensitivity ± SE
s	Self-pollination	0-1	0.027 ± 0.018	0.090 ± 0.016
α	Asymptotic pollen deposition	30-200	0.053 ± 0.021	0.143 ± 0.020
β	Rate of the asymptotic function for pollen deposition	0-0.1	0.180 ± 0.029	0.318 ± 0.028
γ	Rate of the exponential function for pollen germination	0-1	0.311 ± 0.030	0.414 ± 0.030
μ	Rate of the exponential function for style damage	0-0.1	0.180 ± 0.033	0.342 ± 0.031
θ	Shape of the exponential function for style damage	0.5-2	0.004 ± 0.018	0.103 ± 0.017
t	Period after pollen deposition for style damage to interfere with ovule fertilization	1-8	0.026 ± 0.019	0.123 ± 0.017

Figure 1. Flowchart describing the structure of the raspberry benefit-cost pollination model.

Squares and diamonds represent deterministic functions of key variables governing stochastic pollen deposition, pollen germination, and pistil damage processes, whereas the ellipse represents the model output.

Figure 2. Relations of the simulated proportions of pistils that develop into drupelets (i.e. drupelet set) to the numbers of visits per flower by *Apis mellifera* (left panel) and *Bombus terrestris* (right panel). Black circles indicate the mean prediction of the simulation model and red lines depict the 0.025 and 0.975 quantiles of the simulation outcomes. Black dashed lines indicate the expected drupelet set owing to autonomous self-pollination alone. Net benefits from interacting with bees occur when drupelet set exceeds that resulting from autonomous selfing.

Figure 3. Contour plot of the simulated proportions of pistils that developed into drupelets (i.e. drupelet set) for combinations of numbers of visits by *Apis mellifera* and *Bombus terrestris* (from 0 to 170 visits by each bee species). The square at the lower-left corner of panel A denotes the region illustrated in panel B.

Figure 4. Relation of the observed mean (\pm 95% CI) proportion of pistils that developed into drupelets (i.e. drupelet set) to the mean predicted by the simulation model for 12 raspberry fields. The black line depicts equality between observation and prediction (intercept = 0, slope = 1), whereas the red dashed lines represent \pm 10% error estimation in drupelet set.



