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Plant–pollinator interaction model with separate pollen and nectar dynamics

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ABSTRACT

The mutualism between plants and pollinators involves the exchange between plant resources and pollen dispersal services among con-specific plants. Since many pollinators are generalist foragers, the quality of pollination is compromised by inter-specific pollen transfer (IPT). This article proposes a mechanistic approach to model plant–pollinator interactions that considers the dynamics of pollen pick-up and its delivery to con-specific and hetero-specific targets, in parallel but separated from the consumption dynamics of plant rewards by the pollinators. This mechanism can model the interference effect caused by IPT on plant fitness, and predicts saturating effects on the quantity and efficiency of pollination. By coupling the mechanism with population dynamics, the resulting model demonstrates how plant–pollinator associations can shift between net mutualism and parasitism, depending on the ecological context and species traits.

1. Introduction

> *Il avait déjà peur de s'être trompé de planète*
>
> Le Petit Prince, Chapitre XVII – Antoine de Saint-Exupéry

Pollination by animal vectors is an important ecological service. Together with seed dispersal services, they support large plant–animal mutualistic communities upon which a multitude of terrestrial trophic networks depend. It is not surprising that pollination and seed dispersal have been subject to extensive research, empirically, experimentally and theoretically. This interest lead to the development of mathematical models of plant–pollinator interaction, where resources such as nectar, fruits or seeds are considered explicitly (Scheuring, 1992; Valdovinos et al., 2013; Encinas-Viso et al., 2014; Revilla, 2015) or implicitly (Holland and DeAngelis, 2010). These developments help remedy, partially, an inconvenient feature of Lotka–Volterra models of mutualism, which predicts unbounded growth whenever the strength of mutualistic interaction overcomes the strength of self-regulatory forces that keep populations in check (May, 1974; Vandermeer and Boucher, 1978; Moore et al., 2017).

In 2015, I suggested a mechanism for mutualism involving exchange of resources for mutualistic services, the kind of which occurs in the case of pollination or seed dispersal. In this mechanism plants provide energy rich resources such as nectar or fruits, and the consumption of these resources facilitates plant fertilization or seed dispersal, respectively. This general approach, with peculiar variations, has already been considered in several works (Scheuring, 1992; Valdovinos et al., 2013; Encinas-Viso et al., 2014; Revilla and Encinas-Viso, 2015). By assuming that plant resources are ephemeral compared with time scales of plant and animal population dynamics, the mutualistic interaction is described exclusively in terms of population densities. An emergent result from this separation of time scales, is that plant benefits saturate with animal abundances. This is a common feature of modern mutualistic models (Holland et al., 2006; Holland and DeAngelis, 2010) which prevents unbounded growth (but see Moore et al., 2017 for an alternative solution). Another result of combining resource dynamics and time scales separation is that concepts such "asymptotic pollination rates" can be linked with e.g., nectar production rates, while plant "handling times" (of using pollinators) are given meaning in terms of expected nectar (or flower) life times. In addition, the mechanism predicts pollinator self-regulation according to Schoener (1978) competition models based on energy partition. The resource-based approach in Revilla (2015) has been used to model a variety of ecological questions, such as competition between pollinators (Wang et al., 2018), spatial dynamics of plant–pollinator interactions (Wang, 2019), assembly of plant–pollinator communities (Becker et al., 2022), the effects of optimal foraging on plant coexistence (Revilla and Křivan, 2016, 2018, Revilla et al., 2021), and evolutionary diversification of pollination mutualisms (Marcou et al., 2024).

In the 2015 article, I did not consider a distinctive feature of animal pollination. A pollinator visiting multiple plant species can transfer pollen from e.g., plant species A to plant species B, leading to

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inter-specific pollen transfer (IPT).[1] The direct consequence of this accident is loss of the plant's male fitness component (wasted pollen), and potential loss of the female fitness component by stigma clogging, or germination of hetero-specific pollen (Waser, 1978, Murcia and Feinsinger, 1996, Morales and Traveset, 2008, Ashman and Arceo-Gómez, 2013). The pollen loss effect has been considered by some models in a probabilistic sense (e.g., Feldman et al., 2004, Benadi et al., 2012, Valdovinos et al., 2013), by assuming that pollination benefits correlate with the frequency of pollinator visits to con-specific plants (Vázquez et al., 2005, Vázquez et al., 2012). However, this assumption has been challenged (King et al., 2013), and pollen sampling reveals that IPT is widespread and asymmetric, i.e., some plants species are net sources of pollen to other plants, and some are net sinks instead (Fang and Huang, 2013, Morales and Traveset, 2008). The study of how pollen gets transferred between plants (Inouye et al., 1994) can improve our understanding of plant–pollinator networks beyond the limitations of visitation analyses (de Manincor et al., 2020).

In this article I propose a new model of plant–pollinator interaction, one that separates the (a) dynamics of nectar production and consumption from the (b) dynamics of pollen transfer, even though these two depend simultaneously on plant–pollinator visitation dynamics. A key difference between both types of dynamics is that pollen transfer involves two steps, (i) pollen pick-up by the pollinators and (ii) its delivery back to the same or a different plant species. This is unlike nectar dynamics, which is not expected to return to a plant once consumed. Using separation of time scales, between rapid pollen and nectar dynamics against slow plant and animal dynamics, it is possible to derive dynamical equations that predict mutualistic as well as antagonistic interactions between plants and pollinators. Some features of the 2015 model are maintained, such as saturating benefits for plants and resource limitation for animals. But more important, this mechanism links a plant's pollination efficiency with the reliability of pollen carriers, as well as traits from con-specific and hetero-specific targets. As a result, plant–pollinator interactions become context-dependent, spanning the mutualism–antagonism gradient in response to changes of the communities in which they are embedded.

2. Nectar and pollen dynamics

Consider a community of n plant and m pollinator species. Let P_i and A_j be plant $i = 1, \dots, n$ and pollinator $j = 1, \dots, m$ population densities, respectively. Encounters, i.e., visitations, follow mass action laws as in $V_{ij} = v_{ij} P_i A_j$, where v_{ij} are species-specific *visitation rates*. Pollinators visit plants to forage nectar, and plants could benefit from pollen dispersal services associated with these visits. Let N_i and G_i be respectively, total amounts of liquid nectar and pollen grains available from [all members of] plant i. Let's assume N_i and G_i are evenly spread across population i, i.e., individual plants hold N_i/P_i and G_i/P_i units (expected value). Nectar in flowers and pollen availability at anthers change with time t as follows

$$\frac{dN_i}{dt} = s_i P_i - w_i N_i - \sum_{j=1}^{m} b_{ij} v_{ij} A_j N_i, \tag{1}$$

$$\frac{dG_i}{dt} = p_i P_i - q_i G_i - \sum_{j=1}^{m} a_{ij} v_{ij} A_j G_i, \tag{2}$$

nectar is secreted by floral *nectaries*, at a rate s_i per plant and lost at a rate w_i (e.g., evaporation). Pollen is produced at a rate p_i per plant in floral organs called *anthers*, and is lost at a rate q_i (e.g., by wind or rain). Pollinators from species j remove $b_{ij} V_{ij} \times N_i/P_i = b_{ij} v_{ij} A_j N_i$ nectar units and $a_{ij} V_{ij} \times G_i/P_i = a_{ij} v_{ij} A_j N_i$ pollen grains, where b_{ij} is a specific nectar *consumption rate* and a_{ij} a specific pollen *attachment rate*.

Nectar dynamics (1) is sufficient to describe the consumer–resource aspect of plant–pollinator interactions that reward pollinators (Valdovinos et al., 2013, Revilla, 2015). Eq. (2) on the other hand, only accounts for the *pollen retrieval* phase of pollination. For plants to accrue pollination rewards, a subsequent *pollen delivery* phase has to take place, in which pollinators release pollen at con-specific flower *stigmas*. This second phase is modeled using *pollen loads* or *quotas* Q_{ij}, understood as total amount of pollen from plant i being carried by [all members of] pollinator j at a given time. Assume each individual pollinator carries Q_{ij}/A_j pollen grains (expected value). The dynamics of Q_{ij} obeys

$$\frac{dQ_{ij}}{dt} = a_{ij} v_{ij} G_i A_j - l_{ij} Q_{ij} - \sum_{k=1}^{n} d_{ijk} v_{kj} P_k Q_{ij}, \tag{3}$$

pollen loads accumulate through corresponding collection rates $a_{ij} v_{ij} G_i A_j$ that appear subtracting in Eq. (2). Pollinators deliver $d_{ijk} V_{kj} \times Q_{ij}/A_j = d_{ijk} v_{kj} P_k Q_{ij}$ pollen grains to plants of species k, where d_{ijk} is a *delivery* or *detachment rate* of pollen, specific with respect to pollen's origin (plant *i*), carrier (pollinator *j*) and destination (plant *k*). Pollination only occurs when delivery is con-specific, i.e., $k = i$. Hetero-specific deliveries, i.e., $k \neq i$, and *leak rates* l_{ij} (e.g., losses from grooming, fallout during flight), account for pollinator j inefficiency from plant i's standpoint.

For fixed P_i and A_j, Eqs. (1)–(3) form a system of linear ordinary differential equations. Appendix A shows that this system attains the following unique steady-state asymptotically

$$\tilde{N}_i = \frac{s_i P_i}{w_i + \sum_{j=1}^{m} b_{ij} v_{ij} A_j}, \tag{4}$$

$$\tilde{G}_i = \frac{p_i P_i}{q_i + \sum_{j=1}^{m} a_{ij} v_{ij} A_j}, \tag{5}$$

$$\tilde{Q}_{ij} = \frac{a_{ij} v_{ij} \tilde{G}_i A_j}{l_{ij} + \sum_{k=1}^{n} d_{ijk} v_{kj} P_k} = \frac{a_{ij} p_i v_{ij} P_i A_j}{\left(l_{ij} + \sum_{k=1}^{n} d_{ijk} v_{kj} P_k\right)\left(q_i + \sum_{j=1}^{m} a_{ij} v_{ij} A_j\right)}, \tag{6}$$

From this point, we can start to relate pollen and nectar dynamics with the rewards received by plants and pollinators. Starting with the plants, it is reasonable to assume that reproduction scales with con-specific pollen delivery (Waites and Ågren, 2004), i.e., the contribution of pollinator j to plant i seed production *per capita* is proportional to $d_{iji} v_{ij} Q_{ij}$ (the $k = i$ element of the sum in (3)). This amount of pollen is translated into seed numbers $r_{ij} d_{iji} v_{ij} Q_{ij}$, by an appropriate *fertilization coefficient* r_{ij} that depends on the pollen carrier (pollinators could influence pollen quality). Summing over con-specific deliveries from all pollinators, birth rates (i.e., total rate of seed production) *per capita* are defined as

$$F_i := \sum_{j=1}^{m} r_{ij} d_{iji} v_{ij} Q_{ij}. \tag{7}$$

In the case of pollinators, nectar foraging rates *per capita*, $b_{ij} v_{ij} N_i$ in (1), are translated into newborns by specific *conversion efficiency* parameters e_{ij}. Thus, pollinator birth rates *per capita* are defined as

$$W_j := \sum_{i=1}^{n} e_{ij} b_{ij} v_{ij} N_i. \tag{8}$$

Birth rates can be cast as functions of population densities, by substituting Q_{ij} and N_i with corresponding steady-states, $\tilde{Q}_{ij}$ and $\tilde{N}_i$. For plants, using (6) in (7) we get

$$F_i = \sum_{j=1}^{m} p_i r_{ij} \underbrace{\left(\frac{a_{ij} v_{ij} A_j}{q_i + \sum_{\ell=1}^{m} a_{i\ell} v_{i\ell} A_\ell}\right)}_{R_{ij}} \underbrace{\left(\frac{d_{iji} v_{ij} P_i}{l_{ij} + \sum_{k=1}^{n} d_{ijk} v_{kj} P_k}\right)}_{T_{ij}}, \tag{9}$$

where

$$R_{ij} = \frac{a_{ij} v_{ij} A_j}{q_i + \sum_{\ell=1}^{m} a_{i\ell} v_{i\ell} A_\ell}, \tag{10}$$

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[1] Some articles also use the term *incorrect pollen transfer*, or *hetero-specific pollen transfer* (HPT).

is the relative *retrieval rate* (i.e., fraction taken) of pollen from plant i by pollinator j, and

$$T_{ij} = \frac{d_{iji} v_{ij} P_i}{l_{ij} + \sum_{k=1}^{n} d_{ijk} v_{kj} P_k}, \tag{11}$$

is the *transfer efficiency* of plant i pollen by pollinator j. R_{ij} and T_{ij} are in the $[0, 1)$ range. Pollen retrieval, and thus birth rates (9), saturate with A_j. The transfer efficiency of pollinator j saturates with con-specific plant density P_i, and decreases with hetero-specific density $P_{k \neq i}$.

For pollinators, using (4) in (8) we get

$$W_j = \sum_{i=1}^{n} \frac{e_{ij} b_{ij} v_{ij} s_i P_i}{w_i + \sum_{\ell=1}^{m} b_{i\ell} v_{i\ell} A_\ell}, \tag{12}$$

where the ℓ in the denominator represents all consumers, including $\ell = j$. This result predicts that pollinator births scale linearly with plant densities and decrease monotonically with pollinator densities.

Table 1
Model parameters, i and k denote plant species, j denotes pollinator species. The right column displays values used for Eqs. (15) and (16).

Symbol	Description	Value
r_{ij}	Fertilization coefficient (plants)	$r = 0.5$
K_i	Plant's carrying capacity	$K = 100$
c_{ik}	Plant inter-specific competition coefficient	$c = 0.2$ or $\gamma \geq 0$
e_{ij}	Foraging conversion efficiency (pollinator)	$e = 0.5$
m_i	Plant mortality rate	$m = 0.05$
k_j	Pollinator mortality rate	$k = 0.5$
p_i	Pollen production rate	$p = 1$
q_i	Pollen decay rate (on flowers)	$q = 1$
s_i	Nectar supply rate	$s = 1$
l_{ij}	Pollen loss rate (on animals)	$l = 1$
w_i	Nectar decay rate flowers	$w = 1$
v_{ij}	Plant–animal visitation rate	$v = 0.5$
a_{ij}	Plant→Pollinator pollen attachment rate	$a = 0.1$
d_{ijk}	Pollinator→Plant pollen detachment rate	$d = 0.5$ or $\delta \geq 0$
b_{ij}	Nectar consumption rate	$b = 0.1$ or $\beta \geq 0$
X	Density of alternative plant partners	$X \geq 0$
Y	Density of alternative pollinator partners	$Y \geq 0$

3. Plant and pollinator dynamics

To link plant and pollinator dynamics with the dynamics of pollen and nectar, appropriate dynamical equations for plant and pollinator densities are needed; for instance, differential equations styled like $dP_i/dt \propto F_i P_i$ and $dA_j/dt \propto W_j A_j$, using (7) and (8), together with mortality rates and density regulation terms. This would result in large coupled systems with five sets of equations for: nectar, pollen, loads, plants and pollinators. While the study of such large systems is relevant (e.g., Valdovinos et al., 2013: nectar–plants–pollinators), there is another productive alternative: we can assume that plant and pollinator demography is much slower than the dynamics of production, loss and consumption|transport, of nectar (1) and pollen (2), (3). Thus, F_i and W_i are replaced by their respective steady–state approximations (9) and (12). Changes of plant and pollinator populations can be modeled by

$$\frac{dP_i}{dt} := F_i(\mathbf{P}, \mathbf{A}) \left(1 - \frac{\sum_{k=1}^{n} c_{ik} P_k}{K_i} \right) P_i - m_i P_i \tag{13}$$

$$\frac{dA_j}{dt} := W_j(\mathbf{P}, \mathbf{A}) A_j - k_j A_j. \tag{14}$$

$\mathbf{P} = [P_1, \ldots, P_n], \mathbf{A} = [A_1, \ldots, A_m]$ serve to remind that *per capita* birth rates F_i (9) and W_j (12) now depend entirely on plant and pollinator densities. Still, interaction dynamics is influenced by multiple traits behind production (s_i, p_i), loss (w_i, q_i, l_{ij}) and transport $(a_{ij}, d_{ijk}, b_{ij})$ of pollen and nectar.

The $1 - \sum_k c_{ik} P_k / K_i$ factor multiplying F_i in (13) accounts for competition of adult plants against recruitment, where c_{ik} is the effect of plant species k on i relative to the effect of i on itself (thus $c_{ii} = 1$ by definition), and K_i is the plant's carrying capacity. In (14) pollinator birth rates W_j are regulated by competition for nectar, in the form proposed by Schoener (1978) for energy limited consumers. Plants and pollinators die out with mortality rates m_i and k_j *per capita*, respectively. Appendix B shows that the dynamics of system ((13), (14)) is bounded in the non-negative part of the $\mathbb{R}^{n+m}$ space.

Model ((13), (14)) is highly complex and involves many variables and parameters, see Table 1. In order to derive insights about the influence of pollen transport and nectar foraging upon plant–pollinator interactions, consider a small community with plant species i =P and k =X and pollinator species j =A and ℓ =Y. The dynamics of P and A are given by

$$\frac{dP}{dt} = \left\{ rp \frac{\left[\frac{\delta v P}{l + \delta v P + d v X}\right] a v A + \left[\frac{d v P}{l + d v P + d v X}\right] a v Y}{q + a v A + a v Y} \left(1 - \frac{P + cX}{K} \right) - m \right\} P \tag{15}$$

$$\frac{dA}{dt} = \left\{ es \left(\frac{\beta v P}{w + \beta v A + b v Y} + \frac{b v X}{w + b v A + b v Y} \right) - k \right\} A, \tag{16}$$

respectively. Pollen transport efficiencies (11) are indicated by square brackets. Pollen detachment rates are assumed uniform across plants and pollinators $d_{\mathrm{PAX}} = d_{\mathrm{PYX}} = d_{\mathrm{PYP}} = d$, except for con-specific delivery by pollinator A to plant P: $d_{\mathrm{PAP}} = \delta$. Similarly, nectar consumption rates are uniform across plants and pollinators $b_{\mathrm{XA}} = b_{\mathrm{PY}} = b_{\mathrm{XY}} = b$, except consumption of P's nectar by A: $b_{\mathrm{PA}} = \beta$. Populations of X and Y are assumed constant (no dynamics). Thus, X and Y are parameters which determine the ecological context of the P–A interaction. The rest of the parameters are set uniformly (e.g., $v_{ij} = v, a_{ij} = a, \ldots$), see Table 1. These assumptions facilitate description of the focal plant P–A interaction, by reference to interactions with non-focal, alternative plants and pollinators, i.e., X and Y values, the δ value relative to d, and that of β relative to b, as follows:

1. If $\delta > d$, pollinator A delivers P's pollen con-specifically more frequently that hetero-specifically, while pollinator Y delivers pollen P's pollen con- and hetero-specifically with the same frequency. We can say then that, in terms of service quality, A is a better pollinator than Y for plant P. If $\delta < d$ then Y is a better pollinator for P than A.
2. If $\beta > b$, plant P is a better nectar source than plant X for pollinator A, and also A is a better than pollinator Y at exploiting P's nectar. If $\beta < b$ on the other hand, plant X's nectar is better than P's, and also A and Y are equally good at exploiting X.
3. Y determines if the P–A interaction is obligate or facultative for plant P: a $P > 0$ equilibrium with $A = 0$ is (i) not feasible if $Y < Y^*$ or (ii) feasible if $Y > Y^*$. In the first case the interaction is obligate, in the second facultative. The critical value, $Y^* > 0$, increases with X.
4. X determines if the P–A interaction is obligate or facultative for pollinator P: a $A > 0$ equilibrium with $P = 0$ is (i) not feasible if $X < X^*$ or (ii) feasible if $X > X^*$. In the first case the interaction is obligate, in the second facultative. The critical value, $X^* > 0$, increases with Y.

The scenarios listed above can be combined, and the P–A dynamics can be studied by analyzing the stability around equilibrium states, where $dP/dt = dA/dt = 0$ for $P, A \geq 0$.

An equilibrium is locally asymptotically stable, if all eigenvalues of the jacobian matrix of the dynamical system have negative real parts (at that equilibrium). Stability for trivial $(P = A = 0)$, plant-only $(P > 0, A = 0)$ and pollinator-only $(P = 0, A > 0)$ equilibria are easy to derive by algebraic means, but not in the case coexistence equilibria $(P > 0, A > 0)$, which can be multiple and require numerical calculations. Thus, the dynamics was also studied by plotting plant and pollinator nullclines on the positive part of the PA plane, i.e., (P, A) points where $dP/dt = 0$ and $dA/dt = 0$, respectively, in system (15), (16). P–A equilibria correspond to nullcline intersections, and dynamics can

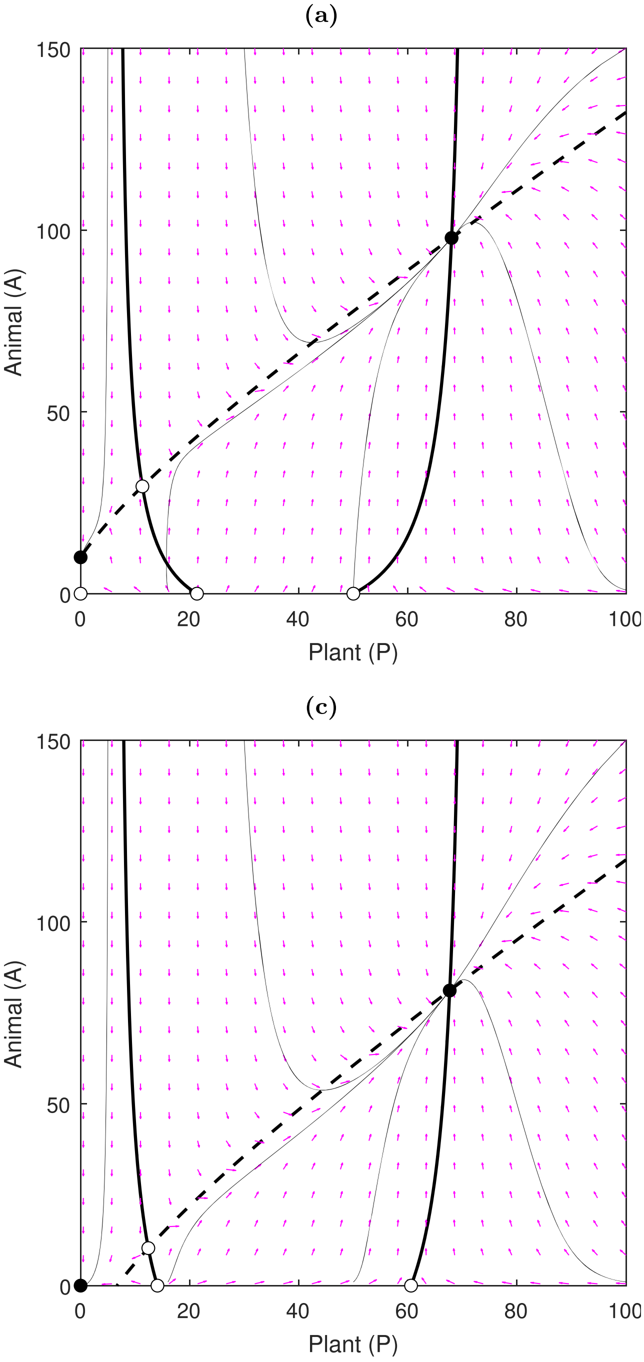

Fig. 1. Examples of plant P and pollinator A dynamics, when being best mutualists for one another ($\delta > d, \beta > b$) compared with alternatives (pollinator Y and plant X, respectively). Plant nullclines are solid curves, pollinator nullclines are dashed. A circle indicates equilibrium, black = stable, white = unstable. Trajectories (dots) follow the vector field (arrows). Parameters from Table 1 with $\delta = 0.7, \beta = 0.3$. The (X, Y) are $(60, 30)$, $(100, 30)$, $(60, 60)$, $(100, 100)$ in panels (a,b,c,d) respectively; these points are marked by "+" in Fig. 3(a).

be inferred from the direction field ($[dP/dt, dA/dt]$ vectors), as shown by Figs. 1 and 2. Be the reader aware about *trivial nullclines*, the P axis ($A = 0$) for pollinators and the A axis ($P = 0$) for plants. Their intersections give origin to plant-only and pollinator-only equilibria, and the mutual extinct state $(P, A) = (0, 0)$. For reasons of space, a lengthy account of equilibrium and stability conditions, as well as nullcline geometry, can be found in online Supplement file S1, sections 1.1 and 1.2. The nullclines, vector fields and numerical solutions depicted in Figs. 1 and 2 where produced using MATLAB R.2024 (system (15), (16) was solved using the ode45 function). The effect of X and Y variation on equilibria and their local stability (Fig. 3) was studied using XPPAUT (Ermentrout, 2002).

Plant nullclines can take various shapes depending on parameter choices (see online Supplement file S1, section 1.2). Fig. 1 illustrates representative examples when P and A are best mutualistic partners for one another, compared with alternatives Y and X, respectively, i.e., $\delta > d$ and $\beta > b$. Plant nullclines show as concave-up curves (e.g., like a "bowl"), with $dP/dt > 0$ above ("inside the bowl") it and $dP/dt < 0$ below ("outside the bowl"). This means that increasing A enlarges the region of the plane where P increases, in other words the pollinator is good for the plant. The nullcline may intersect the P axis, giving rise to a pair of plant-only equilibria, making the P–A interaction facultative for the plant. However, the lowest intersection is a minimum viable density in the absence of A: below this point P goes extinct, above this point P

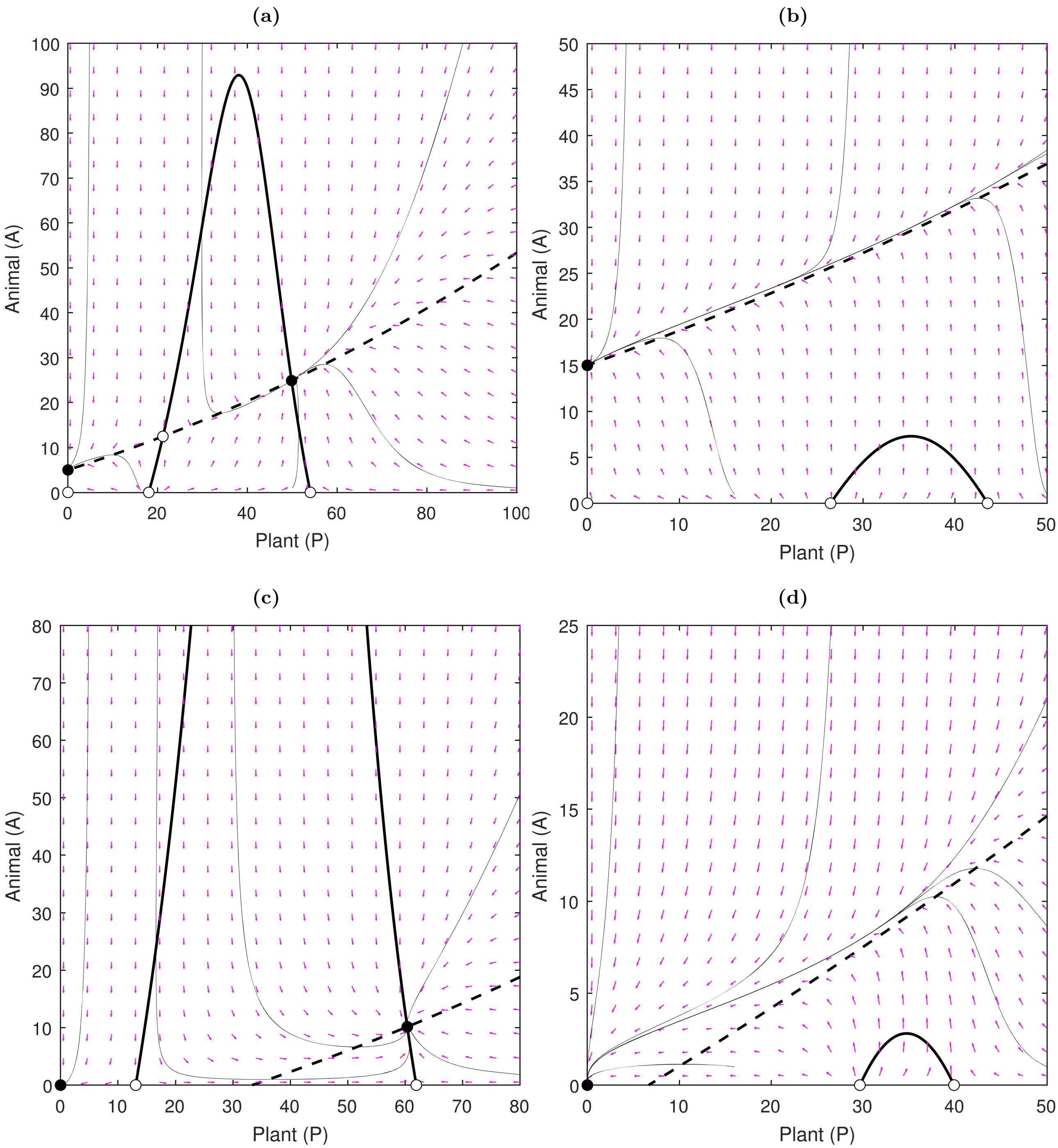

Fig. 2. Examples of plant P and pollinator A dynamics, when being worst mutualists for one another ($\delta < d, \beta < b$) compared with alternatives (pollinator Y and plant X, respectively). Plant nullclines are solid curves, pollinator nullclines are dashed. A circle indicates equilibrium, black = stable, white = unstable. Trajectories (dots) follow the vector field (arrows). Parameters from Table 1 with $\delta = 0.15, \beta = 0.03$. The (X, Y) are $(50, 25)$, $(60, 25)$, $(50, 40)$, $(88, 70)$ in panels (a,b,c,d) respectively; these points are marked by "+" in Fig. 3(b).

attains the highest intersection. If the nullcline does not intersect the P axis then P goes extinct in the absence of A. Pollinator nullclines are increasing curves provided $\beta > 0$, with $dA/dt < 0$ above it and $dA/dt > 0$ below. This means that increasing P enlarges the region where A increases. The nullcline may intersect the A axis at a single point, giving rise to a single locally stable pollinator-only equilibrium. If the pollinator nullcline does not intersect the A axis, it goes extinct in the absence of P. The panels of Fig. 1 correspond to cases in which the interaction is: (a) facultative for both P and A, (b) obligate for P and facultative for A, (c) facultative for P and obligate for A, (d) or obligate for both P and A.

In all cases shown by Fig. 1, stable coexistence depends on the initial conditions. There is always a stable point where $P = 0$, with $A > 0$ (panels a,b) or $A = 0$ (panels c,d). In other words, coexistence implies bi-stability: if initial P is large enough then plant and pollinator attain stable coexistence, but if initial P is too low the plant goes extinct (panels a,b, interaction is facultative for A) or both plant and pollinator go extinct (panels c,d, interaction is obligate for A). Although not shown in this figure, bi-stability also happens when the P and A nullcline intersect only once. To see how, picture a situation like in panel (c) but A's nullcline intersects the P axis in somewhere between the two intersections

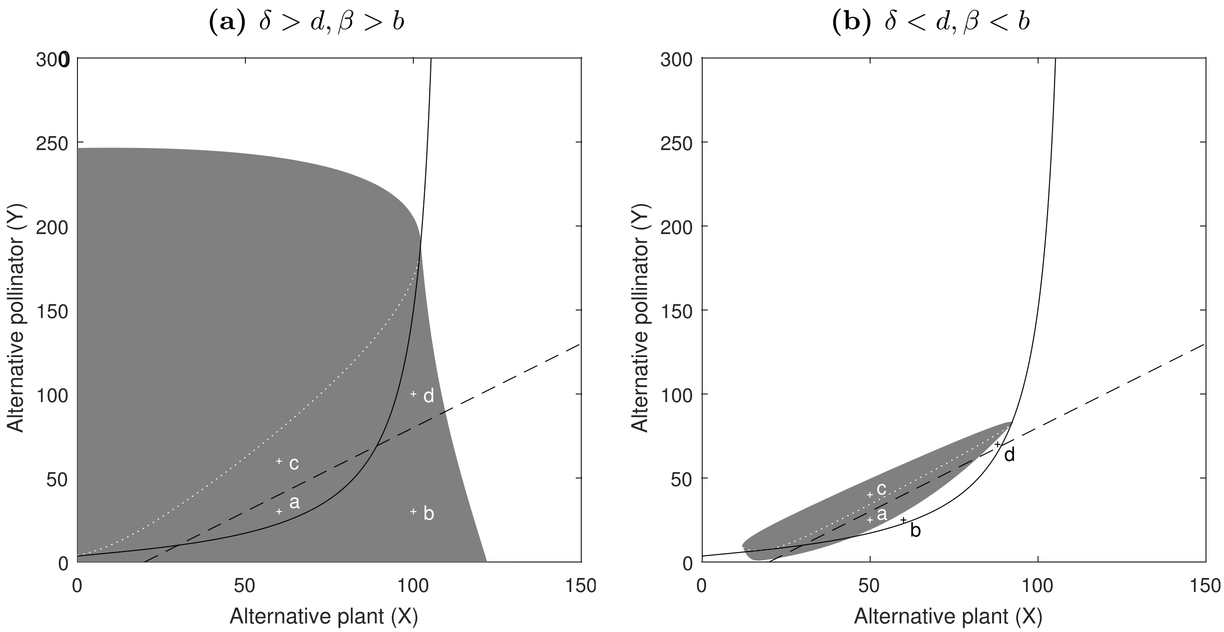

Fig. 3. Parameter plane of alternative mutualist abundances. Coexistence between plant P and pollinator A occurs in the dark area: as a single locally stable equilibrium in the part above the dots; or at two equilibria, one locally stable and the other unstable (saddle point) in the part below the dots. P is viable (not viable) without A in the region above and left (below and right) of the solid curve. A is viable (not viable) without P in the region below and right (above and left) of the dashed line. Parameters from Table 1; with $\delta = 0.7$ and $\beta = 0.3$ for panel (a), or $\delta = 0.15$ and $\beta = 0.03$ for panel (b). The global dynamics at the crosses are shown by corresponding labels in Figs. 1 and 2.

of P's nullcline on the same axis, the number of stable points is still two, one for coexistence and one for mutual extinction.

Now consider instead the case where Y is a better pollinator for plant P compared with A, i.e., $d > \delta$, while X is a better nectar source for pollinator A compared with P, i.e., $b > \beta$. In scenarios like this plant nullclines could be concave-up like in Fig. 1, but also concave-down as shown in Fig. 2 (e.g., like a "dome", maximum not seen in panel c because the vertical scale is too short). The concave-down shape is favored when Y is small and P has to rely more on A for pollination. Concave-down nullclines intersect the P axis twice. When the plant nullcline is like this, $dP/dt > 0$ in the region between the nullcline and the P axis, and $dP/dt > 0$ outside. The fact that increasing A narrows the width of the growth region, means that the net effect of A on P is antagonistic. In A's absence, P attains a viable equilibrium (highest nullcline intersection with P axis) provided initial densities are larger enough (above the lowest intersection between the nullcline and P axis).

Fig. 2 shows potential nullcline configurations when the net effect of pollinator A on plant P is antagonistic. The P–A interaction is facultative for P in all the panels. In panels (a,b) the interaction is facultative for A because the density of its competitor, pollinator Y, is sufficiently low. By contrast in panels (c,d), Y's density is large enough to make the P–A interaction obligate for A. This figure shows examples where the nullclines intersect twice (a) or once (c), and in both cases we can see that coexistence implies bi-stability: there is a stable coexistence point and a second stable point where the plant is extinct. Finally, this figure also shows two interesting scenarios, without nullcline intersection, leading to the plant's extinction. In the case of panel (a) the P–A interaction is facultative for P and for A, i.e., each can persist at stable densities in the absence of the other (provided minimum enough starting density for P), but the introduction of A causes the extinction of P. In the case of panel (b) the interaction is obligate for A, and its introduction ends up causing the extinction of both.

Changes in the ecological context in which the P–A interaction happens, i.e., density of alternative plant X or alternative pollinator Y, have consequences for mutualistic dependence and coexistence. This is illustrated in the XY parameter plane, Fig. 3:

- P–A interaction is facultative for P in the region above the j-shaped curve (solid) and obligate in the region below. This curve gives the critical Y^* value above of which plant-only equilibria are feasible.
- P–A interaction is facultative for A in the region below the straight line (dashes) and obligate in the region above. This line gives the critical X^* value above (or right of) which a pollinator-only equilibrium is feasible.
- If initial P is large enough (Allee effect), P–A coexistence is feasible in the dark region at
  - a single stable equilibrium in the part above the dotted line (like in Fig. 2c), or
  - two equilibria in the part below the dotted line, the equilibrium where P and A are higher is stable and the other equilibrium is unstable (like in Fig. 1a).

The coexistence regions in Fig. 3 are shown if (i) P and A are best mutualists for one another (panel a, where $\delta > d$ and $\beta > b$), or if (ii) Y is best for P and X is best for A (panel b, where $\delta < d$ and $\beta < b$). In the (i) first case coexistence spans well beyond regions where P or A are not viable when alone (below the solid line and above the dashed line), whereas in the (ii) second case coexistence is constrained close to the region where P and A are simultaneously viable when alone (above the solid line and below the dashed line).

There are many more patterns of nullcline intersections not shown in Figs. 1 and 2, e.g., cases of obligate–obligate mutualists in which nullclines don't intersect, leading to global extinction. All possible qualitative patterns and their locations in the XY parameter plane are shown in the online Supplement file S1, section 2. These are done for (i) $\delta > d, \beta > b$ and (ii) $\delta < d, \beta < b$, (iii) $\delta > d, \beta < b$ and (iv) $\delta < d, \beta > b$. All these indicate that coexistence between plant P and pollinator A is always conditional to plants starting with large enough initial densities (Allee effect).

4. Discussion

Plant–pollinator interactions can be modeled by a mechanism that disentangles resource (i.e., nectar) dynamics (1) from pollen transport

(2), (3). This new plant–pollinator model addresses the assumption that pollination services, which are hard to quantify, correlate with visitation rates (Vázquez et al., 2005, Vázquez et al., 2012), which are comparatively easier to account by observations and experiments. This assumption is implicit in Revilla (2015) resource-for-service exchange model, which does not consider pollen dynamics. In that model plant benefits are proportional to consumption of plant resources. In the present approach pollen and nectar dynamics are separate affairs, though linked by pollinator visitation. Thus, nectar consumption can go in parallel with variable levels of pollination service, from very efficient to mediocre (or no service at all, e.g., nectar robbing).

By assuming that pollen and nectar dynamics is fast compared with plant and pollinator demographics, low level details about pollen transfer and nectar consumption can be linked with dynamical Eqs. (13) and (14) to model plant–pollinator interactions at the population level. These equations are used predict plant–pollinator dynamics, which is done here graphically using the method of nullclines in simplified scenarios, e.g., system (15), (16). Note that in the Revilla (2015) paper plant benefits combine additively with logistic regulation (like e.g., Holland and DeAngelis 2010, Sauve et al. 2014), but here in this article the combination is multiplicative (like e.g., Benadi et al., 2012, Valdovinos et al., 2013, Revilla and Křivan, 2016). The multiplicative approach acknowledges that limiting factors implied by logistic regulation, such as competition for space, nutrient or light, impose upper limits to population density that cannot be overcome by producing more seeds.

Resource consumption dynamics (1) leads to pollinator competition just as in Revilla (2015) paper. This is Schoener (1978) approach to model competition, where resources are split among consumers according to specific consumption rates. The consumer fitnesses obtained with this approach can be used to derive, for instance, optimal foraging preferences for plants (Revilla and Křivan, 2016, 2018, Revilla et al., 2021). On the other hand, pollen dynamics (2), (3) makes pollination efficiency dependent on plant densities, leading to *Allee effects*, as well as interference by *inter-specific pollen transfer* (IPT). IPT allows plant–pollinator interactions to vary between net mutualism and net antagonistic exploitation of the plant by the pollinator, depending on the ecological context in which the interacting parts are embedded (i.e., availability of alternative interaction partners).

The interaction mechanism proposed in this paper implies that pollination and foraging benefits depend on traits influencing pollen attachment (a_{ij}) and detachment (d_{ijk}) rates, pollen losses during transit (l_{ij}) and nectar consumption rates (b_{ij}). Some traits are relatively conspicuous (e.g., flower tube lengths, mouthpart sizes, Fontaine et al., 2005; seasonality, Olesen et al., 2011) and are frequently used to parameterize interaction models (Encinas-Viso et al., 2012, Nuismer et al., 2013, Minoarivelo and Hui, 2015, Becker et al., 2022). Mechanistic models of the kind shown in this paper extend the dependencies to a microscopic realm. For instance, pollination benefits could be made dependent of physico-chemical properties of pollen grains and pollinator hairs (Stavert et al., 2016, Amador et al., 2017).

4.1. Pollination benefits, Allee effects and interference

Pollen transfer involves two steps: (i) pick-up followed by (ii) delivery. The first step (i) predicts that plant pollination benefits saturate with the abundance of pollinator j according to R_{ij} (10). The combined effect of all pollinators on plant's i birth rate (9) can be rewritten as

$$F_i = \frac{\sum_{j=1}^{m} \rho_{ij}\alpha_{ij}A_j}{1 + h_i \sum_{j=1}^{m} \alpha_{ij}A_j}, \tag{17}$$

where $\rho_{ij} = r_{ij}T_{ij}p_i/q_i$, $\alpha_{ij} = a_{ij}v_{ij}$ and $h_i = 1/q_i$. Eq. (17) resembles *Holling's type II* multi-species *functional response* in which α_{ij} is an "attack rate" and h_i as a "handling time" that is proportional to the expected lifetime of pollen waiting to be picked.[2] The reason for the saturation is that pollen production rate *per capita* (p_i) and its expected life time ($1/q_i$) are finite and don't scale with growing pollinator populations.

The second step (ii) of pollen transfer leads to variable transfer efficiencies T_{ij} (11), affecting the conversion of pollinator services into fertilization. In the case of con-specific delivery, transfer efficiency T_{ij} saturates with con-specific plant density. This causes Allee effects in rare plants. To see why consider Eq. (15) with $X = Y = 0$. If A is very large and $P \ll K$, the plant's per capita rate of change is

$$\frac{dP}{Pdt} \approx \frac{rp\delta vP}{l + \delta vP} - m, \tag{18}$$

and is trivial to show that the derivative of the right-hand-side with respect to P is positive at $P = 0$. The reason for the Allee effect is that lower plant densities means low pollen production and insufficient con-specific targets. This is why plant–pollinator dynamics illustrated by Figs. 1 and 2 always include a stable point on the animal axis ($P = 0, A \geq 0$) corresponding to plant extinction, even if mutualism is facultative for the plants. It is important to remark that this Allee effect is different from the *mutualistic Allee effect* (Bronstein, 2015) that happens when plant and pollinator are obligate mutualists and both are at low densities.

In the case of hetero-specific delivery, pollination efficiency declines as the densities of competing delivery targets (other plants) increase. This enables indirect plant–plant antagonism through IPT. In the articles of Feldman et al. (2004), Benadi et al. (2012), Valdovinos et al. (2013) this effect is modeled with factors like

$$\frac{\mu_{ij}P_i}{\sum_{k=1}^{n} \mu_{kj}P_k}, \tag{19}$$

which relate pollinator j efficiency with the probability that the pollinator caries plant's i pollen. Here μ_{ij} is a parameter proportional to v_{ij}, and (19) could be derived from a general case that considers pollen retention across multiple flower visits (Benadi et al., 2012). Unlike T_{ij} (11), the (19) formulation implies that the pollination efficiency for a monoculture (when $P_{k\neq i} = 0$) is 1, regardless of its population size, i.e., there is no Allee effect caused by rarity of con-specific donors and targets.

4.2. Net mutualism versus net parasitism

System (13), (14) demonstrates mutualistic dynamics. If the interaction is facultative for plants and pollinators, mutualism allows higher equilibrium densities under coexistence in comparison with the situation where the population is alone. If the interaction is obligate for all, a plant is viable when pollinators exist with sufficient density, and vice-versa. Graphical analysis with a simplified version of the model (15), (16) indicates that plant–pollinator coexistence is always locally stable (Fig. 1). This is because plants experience the Allee effect discussed in the previous section, i.e., pollination efficiency increases with con-specific plant density.

For given appropriate ecological contexts, system (13), (14) also predicts antagonism of pollinators towards plants, due to inefficiencies caused by IPT. This is illustrated by the simplified system (15), (16), when the alternative pollinator Y is better than the focal pollinator A for the focal plant P, because $\delta < d$. What happens in this case is that P's pollen is competitively taken by the worst (A) and the best (Y) pollinators, and when the abundance of the worst pollinator increases relative to the best, a large fraction of pollen is wasted. In scenarios like these, the plant–pollination association is a net parasitism: pollinator A extract resource benefits while plant P pays the costs of pollen waste. It is interesting that under antagonism plant nullclines look like prey nullclines of the Rosenzweig and MacArthur (1963) model with a maximum (Fig. 2). In spite of that similarity, the limited numerical analysis in this article has not discovered limit cycle dynamics of the kind expected in conventional prey–predator associations.

The antagonistic setting was enabled by manipulating differences in pollen delivery/detachment rates (d_{ijk}), but similar outcomes could be

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[2] In a stricter sense what (17) actually models is the *numerical response*.

expected for differences in pollen loss rates (l_{ij}). The relevance of pollen losses by IPT was noted by Thomson (2003) in a colorful analogy (*sic*)

> "To understand why, think of pollination as a process of transferring water by bucket from a supply reservoir (i.e., pollen from a focal plant's anthers) to a receiving vessel (i.e., a set of stigmas). All pollinators are akin to leaky buckets; they vary with respect to the size of the bucket and the number of holes through which they leak. Imagine that your job is to transfer as much water as possible into the receptacle. As you work away with your bucket, which leaks moderately, a friend comes by with a leakier bucket and offers to help. Do you want his help or not? If your supply reservoir is Lake Ontario, you should say yes; anything he transfers will be effectively added to what you transfer. However, if the supply vessel is, say, a bathtub that you will be able to empty in the time allotted, you should decline the assistance. He will spill water that you would have been able to transfer if you were working alone."

The prediction of antagonism associated to low quality (e.g., "leaky") pollinators has important implications for natural and managed ecosystems (Morales and Traveset, 2008, 2009). Fig. 3 (see also parameter planes from supplementary file S1) imply that plant–pollinator coexistence in a local ecosystem can be altered in fundamental ways by changes in the abundances of alternative mutualists, which can be better or worse in their roles as resource providers or pollen carriers.

4.3. Limitations and extensions of the current approach

The pollen transfer mechanism proposed in this article (Eqs. (2) and (3)) treats pollen like uniform molecules following mass action laws, ignoring differences of form, size or accessibility (e.g., position in anthers or in pollinator bodies) that can be important for effective pollination. Although some of these details could be deal with using additional differential equations, doing so would make very difficult to derive plant birth rates like (9) analytically, for use in population dynamic models like (13).

An important assumption made here, is that the dynamics of pollen load Q_{ij} is coupled to pollen availability in flowers G_i,[3] but the dynamics of G_i is not coupled to Q_{ij}. In the model, pollen flows irreversibly from the G_i compartment into Q_{ij} compartments. In other words, G_i is a *source* for the Q_{ij}, which are *sinks* of the first. Also, there is no feedback that would slow down these flows. This ignores the finiteness of pollinator bodies, which are saturable by pollen, preventing further pickup. Thus, realistic attachment rates should be decreasing functions of loads ($a_{ij} = a_{ij}(Q_{ij})$, $da_{ij}/dt < 0$). This would couple G_i dynamics with Q_{ij}. That said, the position taken in this article is justified, if leak and delivery rates (l_{ij}, $d_{ijk}v_{kj}P_k$) are considered sufficiently high in comparison to attachment rates, thus preventing or delaying flows from Q_{ij} towards G_i, as well as pollinator saturation. This argument is frequently used in kinetic analyses (e.g., Briggs–Haldane mechanism for enzymatic reactions), in order to derive analytical results that are biologically interpretable (e.g., saturation by pollinators (10) and transfer efficiencies (11)).

The current approach considers only a fraction (yet important) of possible paths taken by pollen (e.g., see flowcharts in Inouye et al., 1994). Some paths bring pollen back to the same plant or even the same flower, promoting *selfing* instead of *outcrossing*. Modeling these phenomena using simple kinetics like (2), (3) may prove difficult, or just impractical for developing tractable population dynamic models. On the other hand, the current approach could modified to model *distylous* plants (Ganders, 1979): instead to considering several plant species, we deal with a single structured population with two *self-incompatible morphs*, each of which produces viable seeds only with pollen from the other morph.

Pollen is also an important food for many pollinators. The approach followed by this article can be adapted to account for pollen consumption. One way is to multiply each $a_{ij}v_{ij}A_jG_i$ term in equation (3) by $1 - \pi_{ij}$, where $0 \leq \pi_{ij} \leq 1$ is the fraction of acquired pollen that gets eaten. As a result, each element in the numerator of the plant birth rate (9) must be multiplied its corresponding $1 - \pi_{ij}$ fraction. On the pollinator side, eaten pollen ($\sum_{i=1}^{n} \pi_{ij}a_{ij}v_{ij}G_i$) and eaten nectar ($\sum_{i=1}^{n} b_{ij}v_{ij}N_i$) must be combined to produce birth rates like (12), taking into account the appropriate nutritional complementarity between nectar and pollen (Blüthgen and Klein, 2011).

Finally, this article only considers the male side of plant fitness. Foreign pollen can negatively affect the female side of fitness as well. One way to model effects on female fitness is to consider ovule dynamics, as in $dO_i/dt = \sigma_i P_i - \omega_i O_i - \sum_j \phi_{ij} O_i A_j - \sum_j \lambda_{ij} O_i A_j$, where O_i is the total number of unfertilized ovules from plant i, σ_i and ω_i are appropriate production and decay rates, ϕ_{ij} is the fertilization rate by pollinator j and λ_{ij} the abortion rate caused by foreign pollen brought by the same pollinator. If seed production is proportional to fertilization $\sum_j \phi_{ij} O_i A_j$, the steady-state for the suggested dynamics predicts *per capita* benefits like $\frac{\sigma_i \sum_j \phi_{ij} A_j}{\omega_i + \sum_j (\phi_{ij} + \lambda_{ij}) A_j}$. This results saturates with pollinator density like (9), and predicts that plant growth is bounded from above by foreign pollen deposition, accounted by the λ_{ij}. An important complication is that ϕ_{ij} and λ_{ij} may depend on population densities of con- and heterospecific pollen donors.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Tomás A. Revilla: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization.

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Appendix A

For given fixed $P_i, A_j \geq 0$, Eqs. (1) and (2) are of the form $dx/dt = \lambda - \mu x(t)$, which is separable. Solutions for initial value $x(0)$ are $x(t) = \lambda/\mu - [\lambda/\mu + x(0)]e^{-\mu t}$ and $\lim_{t\to\infty} x(t) = \lambda/\mu$. Thus,

$$\lim_{t\to\infty} N_i(t) = \tilde{N}_i = \frac{\lambda_n}{\mu_n} = \frac{s_i P_i}{w_i + \sum_{j=1}^{m} b_{ij} v_{ij} A_j} \tag{A.1}$$

$$\lim_{t\to\infty} G_i(t) = \tilde{G}_i = \frac{\lambda_g}{\mu_g} = \frac{p_i P_i}{q_i + \sum_{j=1}^{m} a_{ij} v_{ij} A_j} \tag{A.2}$$

the limits are approached monotonically.

Next, Eq. (3) is of the form $dQ_{ij}/dt = \gamma G_i(t) - \delta Q_{ij}(t)$ where $\gamma = a_{ij}v_{ij}A_j$ and $\delta = l_{ij} + \sum_{k=1}^{n} d_{ijk}v_{kj}P_k$. In view of (A.2) we can approximate $dQ_{ij}/dt \approx \gamma\tilde{G}_i - \delta Q_{ij}(t)$ for large t, which is separable, and $Q_{ij}(t) \approx (\gamma\tilde{G}_i - ke^{-\delta t})/\delta$. Thus,

$$\lim_{t\to\infty} Q_{ij}(t) = \tilde{Q}_{ij} = \frac{\gamma\tilde{G}_i}{\delta} = \frac{a_{ij}v_{ij}p_iP_iA_j}{(q_i + \sum_{j=1}^{m} a_{ij}v_{ij}A_j)(l_{ij} + l_{ij} + \sum_{k=1}^{n} d_{ijk}v_{kj}P_k)}. \tag{A.3}$$

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[3] That which is exposed at the anthers, not the pollen already delivered.

We conclude that $N_i(t), G_i(t)$ and $Q_{ij}(t)$ attain asymptotic steady states (4), (5) and (6), respectively.

Appendix B

Proposition: Solutions of (13), (14) are bounded in the non-negative $\mathbb{R}^{n+m}$ space.

Proof: Since $dP_i/dt|_{P_i=0} = dA_j/dt|_{A_j=0} = 0$, solutions satisfy $P_i(t), A_j(t) \geq 0$ for $t \geq 0$. From (9) we have $F_i < \sum_j p_i r_{ij}$ because $0 \leq R_{ij}, T_{ij} < 1$ (10), (11). Thus,

$$\begin{aligned} \frac{dP_i}{dt} &= \left\{ F_i \left(1 - \frac{P_i + \sum_{k\neq 1}^{n} c_{ik} P_k}{K_i} \right) - m_i \right\} P_i \\ &< \left\{ \sum_{j=1}^{m} p_i r_{ij} \left(1 - \frac{P_i}{K_i} \right) - m_i \right\} P_i \end{aligned} \tag{B.1}$$

($c_{ii} = 1$), which means that $\limsup_{t\to\infty} P_i(t) < K_i \left(1 - \frac{m_i}{p_i \sum_j r_{ij}} \right)$. (i) If $p_i \sum_j r_{ij} > m_i$ then $dP_i/dt|_{P_i=K_i} < 0$; (ii) if $p_i \sum_j r_{ij} < m_i$ then $dP_i/dt < 0$. From both cases we conclude that $P_i(t) < K_i$ for t large.

Next, from (12) we have

$$W_j = \sum_{i=1}^{n} \frac{e_{ij} b_{ij} v_{ij} s_i P_i}{w_i + b_{ij} v_{ij} A_j + \sum_{\ell\neq 1}^{m} b_{i\ell} v_{i\ell} A_\ell} < \sum_{i=1}^{n} \frac{e_{ij} s_i P_i}{A_j},$$

furthermore, since $P_i(t) < K_i$ for t large, we have

$$\frac{dA_j}{dt} = \{W_j - k_j\} A_j < \left\{ \sum_{i=1}^{n} \frac{e_{ij} s_i P_i}{A_j} - k_j \right\} A_j < \sum_{i=1}^{n} e_{ij} s_i K_i - k_j A_j, \tag{B.2}$$

hence $\limsup_{t\to\infty} A_j(t) \leq \sum_i e_{ij} s_i K_i / k_j$ and $dA_j/dt|_{A_j=\sum_i e_{ij} s_i K_i/k_j} < 0$. Thus, $A_j(t) < \sum_i e_{ij} s_i K_i / k_j$ for all t large.

We can then conclude that for all t large, solutions starting in the non-negative $\mathbb{R}^{n+m}$ space remain inside the $n+m$ dimensional rectangular parallelepiped

$$[0, K_1] \times \cdots \times [0, K_n] \times \left[0, \frac{\sum_i e_{i1} s_i K_i}{k_1}\right] \times \cdots \times \left[0, \frac{\sum_i e_{im} s_i K_i}{k_m}\right],$$

and system (13), (14) is bounded.

Supplementary material

Supplementary material associated with this article can be found in the online version at 10.1016/j.jtbi.2025.112096.

References

Amador, G.J., Matherne, M., Waller, D., Mathews, M., Gorb, S.N., Hu, D.L., 2017. Honey bee hairs and pollenkitt are essential for pollen capture and removal. Bioinspir. Biomim. 12 (2), 026015. https://doi.org/10.1088/1748-3190/aa5c6e

Ashman, T.-L., Arceo-Gómez, G., 2013. Toward a predictive understanding of the fitness costs of heterospecific pollen receipt and its importance in co-flowering communities. Am. J. Bot. 100 (6), 1061–1070. https://doi.org/10.3732/ajb.1200496

Becker, L., Blüthgen, N., Drossel, B., 2022. Stochasticity leads to coexistence of generalists and specialists in assembling mutualistic communities. Am. Nat. 200 (3), 303–315. https://doi.org/10.1086/720421

Benadi, G., Blüthgen, N., Hovestadt, T., Poethke, H.-J., 2012. Population dynamics of plant and pollinator communities: stability reconsidered. Am. Nat. 179 (2), 157–168. https://doi.org/10.1086/663685

Blüthgen, N., Klein, A.-M., 2011. Functional complementarity and specialisation: the role of biodiversity in plant–pollinator interactions. Basic Appl. Ecol. 12 (4), 282–291. https://doi.org/10.1016/j.baae.2010.11.001

Bronstein, J.L., 2015. Mutualism. Oxford University Press. first ed. edition.

Encinas-Viso, F., Revilla, T.A., Etienne, R.S., 2012. Phenology drives mutualistic network structure and diversity. Ecol. Lett. 15 (3), 198–208. https://doi.org/10.1111/j.1461-0248.2011.01726.x

Encinas-Viso, F., Revilla, T.A., Etienne, R.S., 2014. Shifts in pollinator population structure may jeopardize pollination service. J. Theor. Biol. 352, 24–30. https://doi.org/10.1016/j.jtbi.2014.02.030

Ermentrout, B., 2002. Simulating, Analyzing, and Animating Dynamical Systems: A Guide to XPPAUT for Researchers and Students. Society for Industrial and Applied Mathematics, Philadelphia. first ed.

Fang, Q., Huang, S.-Q., 2013. A directed network analysis of heterospecific pollen transfer in a biodiverse community. Ecology 94 (5), 1176–1185. https://doi.org/10.1890/12-1634.1

Feldman, T.S., William, F.M., William, G.W., 2004. When can two plant species facilitate each other's pollination? Oikos 105 (1), 197–207. https://doi.org/10.1111/j.0030-1299.2004.12845.x

Fontaine, C., Dajoz, I., Meriguet, J., Loreau, M., 2005. Functional diversity of plant–pollinator interaction webs enhances the persistence of plant communities. PLoS Biol. 4 (1), e1. https://doi.org/10.1371/journal.pbio.0040001

Ganders, F.R., 1979. The biology of heterostyly. N.Z. J. Bot. 17 (4), 607–635. https://doi.org/10.1080/0028825X.1979.10432574

Holland, J.N., DeAngelis, D.L., 2010. A consumer-resource approach to the density-dependent population dynamics of mutualism. Ecology 91, 1286–1295. https://doi.org/10.1890/09-1163.1

Holland, J.N., Okuyama, T., DeAngelis, D.L., 2006. Comment on "Asymmetric coevolutionary networks facilitate biodiversity maintenance". Science 313 (5795), 1887. https://doi.org/10.1126/science.1129547

Inouye, D.W., Gill, D.E., Dudash, M.R., Fenster, C.B., 1994. A model and lexicon for pollen fate. Am. J. Bot. 81 (12), 1517–1530. https://doi.org/10.1002/j.1537-2197.1994.tb11462.x

King, C., Ballantyne, G., Willmer, P.G., 2013. Why flower visitation is a poor proxy for pollination: measuring single-visit pollen deposition, with implications for pollination networks and conservation. Methods Ecol. Evol. 4 (9), 811–818. https://doi.org/10.1111/2041-210X.12074

de Manincor, N., Hautekèete, N., Mazoyer, C., Moreau, P., Piquot, Y., Schatz, B., Schmitt, E., Zélazny, M., Massol, F., 2020. How biased is our perception of plant-pollinator networks? A comparison of visit- and pollen-based representations of the same networks. Acta Oecol. 105, 103551. https://doi.org/10.1016/j.actao.2020.103551

Marcou, T., Revilla, T.A., Křivan, V., 2024. Evolutionary emergence of plant and pollinator polymorphisms in consumer-resource mutualisms. J. Theor. Biol. 594, 111911. https://doi.org/10.1016/j.jtbi.2024.111911

May, R.M., 1974. Stability and complexity in model ecosystems. Princeton Landmarks in Biology, Princeton University Press, Princeton.

Minoarivelo, H.O., Hui, C., 2015. Trait-mediated interaction leads to structural emergence in mutualistic networks. Evol. Ecol. 30, 105–121. https://doi.org/10.1007/s10682-015-9798-z

Moore, C.M., Catella, S.A., Abbott, K.C., 2017. Population dynamics of mutualism and intraspecific density dependence: how θ-logistic density dependence affects mutualistic positive feedback. Ecol. Model. 368, 191–197. https://doi.org/10.1016/j.ecolmodel.2017.11.016

Morales, C.L., Traveset, A., 2008. Interspecific pollen transfer: magnitude, prevalence and consequences for plant fitness. CRC Crit. Rev. Plant Sci. 27 (4), 221–238. https://doi.org/10.1080/07352680802205631

Morales, C.L., Traveset, A., 2009. A meta-analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants. Ecol. Lett. 12, 716–728. https://doi.org/10.1111/j.1461-0248.2009.01319.x

Murcia, C., Feinsinger, P., 1996. Interspecific pollen loss by hummingbirds visiting flower mixtures: effects of floral architecture. Ecology 77 (2), 550–560. https://doi.org/10.2307/2265629

Nuismer, S.L., Jordano, P., Bascompte, J., 2013. Coevolution and the architecture of mutualistic networks. Evolution 67 (2), 338–354. https://doi.org/10.1111/j.1558-5646.2012.01801.x

Olesen, J.M., Bascompte, J., Dupont, Y.L., Elberling, H., Rasmussen, C., Jordano, P., 2011. Missing and forbidden links in mutualistic networks. Proc. R. Soc. B 278 (1706), 725–732. https://doi.org/10.1098/rspb.2010.1371

Revilla, T.A., 2015. Numerical responses in resource-based mutualisms: a time scale approach. J. Theor. Biol. 387, 39–46. https://doi.org/10.1016/j.jtbi.2015.04.012

Revilla, T.A., Encinas-Viso, F., 2015. Dynamical transitions in a pollination–herbivory interaction: a conflict between mutualism and antagonism. PLoS One 10 (2), e0117964. https://doi.org/10.1371/journal.pone.0117964

Revilla, T.A., Křivan, V., 2016. Pollinator foraging adaptation and the coexistence of competing plants. PLoS One 11 (8), e0160076. https://doi.org/10.1371/journal.pone.0160076

Revilla, T.A., Křivan, V., 2018. Competition, trait-mediated facilitation, and the structure of plant-pollinator communities. J. Theor. Biol. 440, 42–57. https://doi.org/10.1016/j.jtbi.2017.12.019

Revilla, T.A., Marcou, T., Křivan, V., 2021. Plant competition under simultaneous adaptation by herbivores and pollinators. Ecol. Model. 455, 109634. https://doi.org/10.1016/j.ecolmodel.2021.109634

Rosenzweig, M.L., MacArthur, R.H., 1963. Graphical representation and stability conditions of predator-prey interactions. Am. Nat. 97, 209–223. http://www.jstor.org/stable/2458702.

Sauve, A., Fontaine, C., Thébault, E., 2014. Structure–stability relationships in networks combining mutualistic and antagonistic interactions. Oikos 123 (3), 378–384. https://doi.org/10.1111/j.1600-0706.2013.00743.x

Scheuring, I., 1992. "The orgy of mutualism" as an artefact: a stage structured model of plant-pollinator and seed-dispersal systems. Abstr. Bot. 16 (1), 65–70. https://doi.org/10.2307/43519288

Schoener, T.W., 1978. Effects of density-restricted food encounter on some single-level competition models. Theor. Popul. Biol. 13 (3), 365–381. https://doi.org/10.1016/0040-5809(78)90052-7

Stavert, J.R., Liñán Cembrano, G., Beggs, J.R., Howlett, B.G., Pattemore, D.E., Bartomeus, I., 2016. Hairiness: the missing link between pollinators and pollination. PeerJ 4, e2779. https://doi.org/10.7717/peerj.2779

Thomson, J., 2003. When is it mutualism? Am. Nat. 162 (S4), S1–S9. https://doi.org/10.1086/378683

Valdovinos, F.S., Moisset de Espanés, P., Flores, J.D., Ramos-Jiliberto, R., 2013. Adaptive foraging allows the maintenance of biodiversity of pollination networks. Oikos 122 (6), 907–917. https://doi.org/10.1111/j.1600-0706.2012.20830.x

Vandermeer, J., Boucher, D.H., 1978. Varieties of mutualistic interaction in population models. J. Theor. Biol. 74, 549–558. https://doi.org/10.1016/0022-5193(78)90241-2

Vázquez, D.P., Lomáscolo, S.B., Maldonado, M.B., Chacoff, N.P., Dorado, J., Stevani, E.L., Vitale, N.L., 2012. The strength of plant–pollinator interactions. Ecology 93 (4), 719–725. https://doi.org/10.1890/11-1356.1

Vázquez, D.P., Morris, W.F., Jordano, P., 2005. Interaction frequency as a surrogate for the total effect of animal mutualists on plants. Ecol. Lett. 8, 1088–1094. https://doi.org/10.1111/j.1461-0248.2005.00810.x

Waites, A.R., Ågren, J., 2004. Pollinator visitation, stigmatic pollen loads and among-population variation in seed set in lythrum salicaria. J. Ecol. 92 (3), 512–526. https://doi.org/10.1111/j.0022-0477.2004.00893.x

Wang, Y., 2019. Pollination-mutualisms in a two-patch system with dispersal. J. Theor. Biol. 476, 51–61. https://doi.org/10.1016/j.jtbi.2019.06.004

Wang, Y., Wu, H., DeAngelis, D.L., 2018. Global dynamics of a mutualism-competition model with one resource and multiple consumers. J. Math. Biol. 78, 683–710. https://doi.org/10.1007/s00285-018-1288-9

Waser, N.M., 1978. Interspecific pollen transfer and competition between co-occurring plant species. Oecologia 36 (2), 223–236. https://doi.org/10.1007/BF00349811