

Dynamical transitions in a pollination–herbivory interaction: a conflict between mutualism and antagonism

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Abstract

Plant-pollinator associations are often seen as purely mutualistic, while in reality they can be more complex. Indeed they may also display a diverse array of antagonistic interactions, such as competition and victim–exploiter interactions. In some cases mutualistic and antagonistic interactions are carried-out by the same species but at different life-stages. As a consequence, population structure affects the balance of inter-specific associations, a topic that is receiving increased attention. In this paper, we developed a model that captures the basic features of the interaction between a flowering plant and an insect with a larval stage that feeds on the plant’s vegetative tissues (e.g. leaves) and an adult pollinator stage. Our model is able to display a rich set of dynamics, the most remarkable of which involves victim–exploiter oscillations that allow plants to attain abundances above their carrying capacities, and the periodic alternation between states dominated by mutualism or antagonism. Our study indicates that changes in the insect’s life cycle can modify the balance between mutualism and antagonism, causing important qualitative changes in the interaction dynamics. These changes in the life cycle could be caused by a variety of external drivers, such as temperature, plant nutrients, pesticides and changes in the diet of adult pollinators.

Keywords: *mutualism, pollination, herbivory, insects, stage-structure, oscillations*

Introduction

Il faut bien que je supporte deux ou trois chenilles si je veux connaître les papillons

Le Petit Prince, Chapitre IX – Antoine de Saint-Exupéry

Mutualism can be broadly defined as an interaction where individuals two different species benefit from the activities of each other. Such beneficial activities are typically costly for their providers, in terms of resources, energy and time devoted to them, but the net balance is supposed to be a (+,+) in the final balance. However, there can be other kinds of costs, concerning detrimental interactions that run in parallel with mutualism, such as predation, parasitism or competition, involving the same parties. Moreover, some of these antagonistic interactions (e.g. competition) seem to be important for the evolution and stability of mutualism (Jones et al., 2012). In general, these costs have important consequences at the population and community level, because the net outcome of an interspecific association can turn out beneficial or detrimental, and perhaps more interestingly, variable (Bronstein, 1994). Variable interactions challenge the view that ecological communities are structured by well defined interactions at the species level such as competition (–,–), victim-exploiter (–,+) or mutualism (+,+).

Pollination is one of the most important mutualisms occurring between plants and animals. This form of trading resources for services greatly explains the evolutionary success of flowering plants in almost all terrestrial systems. It is responsible for the well being of ecosystem services. During the larval stage of many insect pollinators, such as Lepidopterans (butterflies and moths), the larvae feed on plant leaves to mature and become adult pollinators (Adler and Bronstein, 2004; Wäckers et al., 2007; Bronstein et al., 2009; Altermatt and Pearse, 2011). These ontogenetic diet shifts (Rudolf and Lafferty, 2011) are very common and important in understanding the ecological

and evolutionary dynamics of plant–animal mutualisms. Interestingly, in some cases larvae feed on the same plant species that they will pollinate as adults (Irwin, 2010; Bronstein et al., 2009). This shows that in several cases mutualistic and antagonistic interactions are exerted by the same species, and a potential conflict arises for the plant, between the benefits of mutualism and the costs of herbivory. One of the best known examples is the interaction between tobacco plants (*Nicotiana attenuata*) and the hawkmoth (*Manduca sexta*) (Baldwin, 1988; Kessler et al., 2010), whose larva is commonly called the tobacco hornworm. There are other examples of this type of interaction in the genus *Manduca* (Sphingidae), such as between the tomato plant (*Lycopersicon esculentum*) and the five-spotted hawkmoth (*Manduca quinquemaculata*) (Kennedy, 2003). These larvae have received a lot of attention due to their negative effects on agricultural crops (Campbell et al., 1991).

The interaction between *Manduca sexta* and *Datura wrightii* (Solanacea) (Bronstein et al., 2009; Alarcon et al., 2008) is another good example illustrating the costs and benefits of pollination mutualisms (Bronstein et al., 2009). *D. wrightii* provides high volumes of nectar and seems to depend heavily on the pollination service by *M. sexta* adults (Alarcon et al., 2008). However, *M. sexta* larvae, which feed on *D. wrightii* vegetative tissue, can have severe negative effects on plant fitness (McFadden, 1968; Barron-Gafford et al., 2012). We could assume that the benefits of pollination might outweigh the costs of herbivory for this mutualism to be relatively viable. The question is what are the conditions, in terms of benefits (pollination) and costs (herbivory), for this mutualistic interaction to be stable?

In the pollination–herbivory cases mentioned previously the benefits and costs for the plant are clearly differentiated. This is because the role of an insect as a pollinator or herbivore depends on the stage in its life cycle (Miller and Rudolf, 2011). Thus, whether mutualism or herbivory dominates the interaction is dependent on insect abundance and its population structure. In other words the *cost:benefit* ratio must be positively related with the insect’s *larva:adult* ratio. For a hypothetical scenario in which the costs of herbivory (–) and the benefits of pollination (+) are balanced for the plant (0), an increase in larval abundance relative to adults should bias the relationship towards a victim–exploiter one (–,+). Whereas an increase in adult abundance relative to larvae should bias the relationship towards mutualism (+,+). Under equilibrium conditions, one would expect transitions (bifurcations) from (–,+), to (0,+) to (+,+) and vice-versa as relevant parameters affecting the plant and the insect life-histories vary, such as flower production, mortalities or larvae maturation rates. However, under dynamic scenarios the outcome may be more complex: a victim–exploiter state (–,+) enhances larva development into pollinating adults, but this tips the interaction into a mutualism (+,+), which in turn contributes greater production of larva leading back to a victim–exploiter state (–,+). This raises the possibility of feedback between the plant–insect interaction and insect population structure, which can potentially lead to periodic alternation between mutualism and herbivory. Thus, when non-equilibrium dynamics are involved, questions concerning the overall nature (positive, neutral or negative) of mixed interactions may not have simple answers.

In this article we study the feedback between insect population structure, pollination and herbivory. We want to understand how the balance between costs (herbivory) and benefits (pollination) affects the interaction between plants (e.g. *D. wrightii*) and herbivore–pollinator insects (e.g. *M. sexta*)? Also what role does insect development have in this balance and on the resulting dynamics? We use a mathematical model which considers two different resources provided by the same plant species, nectar and vegetative tissues. Nectar consumption benefits the plant in the form of fertilized ovules, and consumption of vegetative tissues by larvae causes a cost. Our model predicts that the balance between mutualism and antagonism, and the long term stability of the plant–insect association, can be greatly affected by changes in larval development rates, as well as by changes in the diet of adult pollinators.

Methods

Our model concerns the dynamics of the interaction between a plant and an insect. The insect life cycle comprises an adult phase that pollinates the flowers and a larval phase that feed on non-reproductive tissues of the same plant. Adults oviposit on the same species that they pollinate (e.g. *D. wrightii* – *M. sexta* interaction). Let denote the biomass densities of the plant, the larva, and the adult insect with P, L and A respectively. An additional variable, the total biomass of flowers F , enables the mutualism by providing resources to the insect (nectar), and by collecting services for the plant (pollination). The relationship is *facultative–obligatory*. In the absence of pollination plants do not reproduce, in the literal sense of giving rise to a new generation of plants. However, we assume that plant biomass can persist in time thanks to vegetative growth, e.g. root, stem and leave biomass are being constantly renewed. For the sake of simplicity, and because we want to focus on the plant–insect interaction, we describe this vegetative renewal by means of a logistic growth rate. In the absence of the plant however, the insect always goes extinct because larval development relies exclusively on herbivory, even if the adults pollinate other plant species. This is based on the biology of *M. sexta* (Bronstein et al., 2009). The mechanism of interaction between these four

variables (P, L, A, F), as shown in Figure 1, is described by the following system of ordinary differential equations (ODE):

$$\begin{aligned}
\frac{dP}{dt} &= rP(1 - cP) + \sigma aFA - bPL \\
\frac{dF}{dt} &= sP - wF - aFA \\
\frac{dL}{dt} &= \epsilon aFA + gA - \gamma bPL - mL \\
\frac{dA}{dt} &= \gamma bPL - nA
\end{aligned} \tag{1}$$

where r : plant intrinsic growth rate, c : plant intra-specific self-regulation coefficient (also the inverse its carrying capacity), a : pollination rate, b : herbivory rate, s : flower production rate, w : flower decay rate, m, n : larva and adult mortality rates, σ : plant pollination efficiency ratio, ϵ : adult consumption efficiency ratio. Like ϵ , parameter γ is also a consumption efficiency ratio, but we will call it the maturation rate for brevity since we will refer to it frequently. Our model assumes that pollination leads to flower closure (Primack, 1985), causing resource limitation for adult insects. Parameter g represents a reproduction rate resulting from the pollination of other plants species, which we do not model explicitly. Most of our results are for $g = 0$.

We now consider the fact that flowers are ephemeral compared with the life cycles of plants and insects. In other words, some variables (P, L, A) have slower dynamics, and others (F) are fast (Rinaldi and Scheffer, 2000). Given the near constancy of plants and animals in the flower equation of (1), we can predict that flowers will approach a quasi-steady-state (or quasi-equilibrium) biomass $F \approx sP/(w + aA)$, before P, L and A can vary appreciably. Substituting the quasi-steady-state biomass in system (1) we arrive at:

$$\begin{aligned}
\frac{dP}{dt} &= rP(1 - cP) + \sigma \left[\frac{asA}{w + aA} \right] P - bPL \\
\frac{dL}{dt} &= \epsilon \left[\frac{asP}{w + aA} \right] A + gA - \gamma bPL - mL \\
\frac{dA}{dt} &= \gamma bPL - nA
\end{aligned} \tag{2}$$

In system (2) the quantities in square brackets can be regarded as functional responses. Plant benefits saturate with adult pollinator biomass, i.e. pollination exhibits diminishing returns. The functional response for the insects is linear in the plant biomass, but is affected by intraspecific competition (Schoener, 1978) for mutualistic resources.

We non-dimensionalized this model to reduce the parameter space from 12 to 9 parameters, by casting biomasses with respect to the plant's carrying capacity ($1/c$) and time in units of plant biomass renewal time ($1/r$). This results in a PLA (plant, larva, adult) scaled model:

$$\begin{aligned}
\frac{dx}{d\tau} &= x(1 - x) + \sigma \frac{\alpha z}{\eta + z} x - \beta xy \\
\frac{dy}{d\tau} &= \epsilon \frac{\alpha x}{\eta + z} z + \phi z - \gamma \beta xy - \mu y \\
\frac{dz}{d\tau} &= \gamma \beta xy - \nu z
\end{aligned} \tag{3}$$

Table 1 lists the relevant transformations.

There is an important clarification to make concerning the nature and scales of the conversion efficiency ratios σ, ϵ involved in pollination, and γ for herbivory and maturation. This has to do with the fact that flowers *per se* are not resources or services, but *organs* that enable the mutualism to take place, and they mean different things in terms of biomass production for plants and animals. For insects, the yield of pollination is thermodynamically constrained. First of all, a given biomass F of flowers contains an amount of nectar that is necessarily less than F . More importantly, part of this nectar is devoted to survival, or wasted, leaving even less for reproduction. Similarly, not all the biomass consumed by larvae will contribute to their maturation to adult. *Ergo* $\epsilon < 1, \gamma < 1$. Regarding the returns from pollination for the plants, the situation is very different. Each flower harbors a large number of ovules, thus a potentially large number of seeds (Fagan et al., 2014), each of which will increase in biomass by consuming resources not considered by our model (e.g. nutrients, light). Consequently, a given biomass of pollinated flowers can produce a larger biomass of mature plants, making σ larger than 1.

Results

130 The PLA model (3) has many parameters, however here we focus on herbivory rates (β) and larvae maturation
132 (γ), because increasing β turns the net balance interaction towards antagonism, whereas increasing γ shifts insect
134 population structure towards the adult phase, turning the net balance towards mutualism. Both parameters also
136 relate to the state variables at equilibrium (i.e. $z/y = \beta\gamma x/\nu$ in (3) for $dz/d\tau = 0$). We studied the joint effects
of varying β and γ numerically (parameter values in Table 1) using XPPAUT (Ermentrout, 2003). ODE were
integrated using MATLAB (2010) or GNU/Octave (Eaton et al., 2008). We also present a simplified graphical
analysis of our model, in order to explain how different dynamics can arise, by varying other parameters. The
source codes supporting these results are provided as supplementary material (Appendix D).

138 Numerical results

Figure 2 shows interaction outcomes of the PLA model, as a function of β and γ for specialist pollinators ($\phi = 0$).
140 This parameter space is divided by a decreasing $R_o = 1$ line that indicates whether or not insects can invade when
rare. R_o is defined as (see derivation in Appendix A):

$$R_o = \frac{\epsilon\alpha\gamma\beta}{\eta\nu(\mu + \gamma\beta)} \quad (4)$$

142 and we call it the *basic reproductive number*, according to the argument that follows. Consider the following in
system (3): if the plant is at carrying capacity ($x = 1$), and is invaded by a very small number of adult insects
144 ($z \approx 0$), the average number of larvae produced by a single adult in a given instant is $\epsilon\alpha x/(\eta + z) \approx \epsilon\alpha/\eta$, and during
its life-time (ν^{-1}) it is $\epsilon\alpha/\eta\nu$. Larvae die at the rate μ , or mature with a rate equal to $\gamma\beta x = \gamma\beta$, per larva. Thus,
146 the probability of larvae becoming adults rather than dying is $\gamma\beta/(\mu + \gamma\beta)$. Multiplying the life-time contribution
of an adult by this probability gives the expected number of new adults replacing one adult per generation during
148 an invasion (R_o). More formally, R_o is the expected number of adult-insect-grams replacing one adult-insect-gram
per generation (assuming a constant mass-per-individual ratio).

150 Below the $R_o = 1$ line, small insect populations cannot replace themselves ($R_o < 1$) and two outcomes are
possible. If the maturation rate is too low, the plant only equilibrium ($x = 1, y = z = 0$) is globally stable
152 and plant–insect coexistence is impossible for all initial conditions. If the maturation rate is large enough, stable
coexistence is possible, but only if the initial plant and insect biomass are large enough. This is expected in models
154 where at least one species, here the insect, is an obligate mutualist. In this region of the space of parameters, the
growth of small insect populations increases with population size, a phenomenon called the Allee effect (Stephens
156 et al., 1999).

Above the $R_o = 1$ line the plant only equilibrium is always unstable against the invasion of small insect
158 populations ($R_o > 1$). Plants and insects can coexist in a stable equilibrium or via limit cycles (stable oscillations).
The zone of limit cycles occurs for intermediate values of the maturation rate (γ) and it widens with rate of herbivory
160 (β).

Plant equilibrium when coexisting with insects can be above or below the carrying capacity ($x = 1$). When
162 above carrying capacity the net result of the interaction is a mutualism (+,+). While in the second case we have
antagonism, more specifically net herbivory (-,+). As it would be expected, increasing herbivory rates (β) shifts
164 this net balance towards antagonism (low plant biomass), while decreasing it shifts the balance towards mutualism
(high plant biomass). The quantitative response to increases in the maturation rate (γ) is more complex however
166 (see the bifurcation plot in Appendix A).

Given that there is herbivory, we encounter victim–exploiter oscillations. However, the oscillations in the PLA
168 model are special in the sense that the plant can attain maximum biomasses above the carrying capacity ($x > 1$).
For an example see Figure 3. Instead of a stable balance between antagonism and mutualism, we can say that the
170 outcome in Figure 3 is a periodic alternation of both cases. This is not seen in simple victim–exploiter models,
where oscillations are always below the victim’s carrying capacity (Rosenzweig and MacArthur, 1963; Rosenzweig,
172 1971). The relative position of the cycles along the plant axis is also affected by herbivory: if β decreases (increases),
plant maxima and minima will increase (decrease) in Figure 3 (see bifurcation plot in Appendix A). In some cases
174 the entire plant cycle (maxima and minima) ends above the carrying capacity if β is low enough (see Appendix
C), but further decrease causes damped oscillations. We also found examples in which coexistence can be stable or
176 lead to limit cycles depending on the initial conditions (see example in Appendix C), but this happens in a very
restrictive region in the space of parameters (see bifurcation plot in Appendix A). Limit cycles can also cross the
178 plant’s carrying capacity under the original interaction mechanism (1), which does not assume the steady–state in
the flowers (see Appendix C, using parameters in the last column of Table 1).

180 Figure 4 shows the β vs γ parameter space of the model when the adults are more generalist. The relative
 182 positions of the plant-only, Allee effect, and coexistence regions are similar to the case of specialist pollinators
 (Figure 2). However, the region of limit cycles is much larger. The $R_0 = 1$ line is closer to the origin, because the
 expression for R_0 is now (see derivation in Appendix A):

$$R_0 = \frac{(\epsilon\alpha + \phi\eta)\gamma\beta}{\eta\nu(\mu + \gamma\beta)} \quad (5)$$

184 In other words, this means that the more generalist the adult pollinators (larger ϕ), the more likely they can
 invade when rare. There is also a small overlap between the Allee effect and limit cycle regions, i.e. parameter
 186 combinations for which the long term outcome could be insect extinction or plant–insect oscillations, depending on
 the initial conditions.

188 Graphical analysis

The general features of the interaction can be studied by phase-plane analysis. To make this easier, we collapsed
 190 the three-dimensional PLA model into a two-dimensional plant–larva (PL) model, by assuming that adults are
 extremely short lived compared with plants and larvae (see resulting ODE in Appendix B). The closest realization
 192 of this assumption could be *Manduca sexta*, which has a larval stage of approximately 20–25 days and adult stages
 of around 7 days (Reinecke et al., 1980; Ziegler, 1991). For a given parametrization (Table 1), the PL model has
 194 the same equilibria as the PLA model, but not the exact same global dynamics due to the alteration of time scales.
 Yet, this simplification provides insights about the outcomes displayed in Figures 2 and 4.

196 Figure 5 shows representative examples of plant and larva isoclines (i.e. non-trivial nullclines) and coexistence
 equilibria (intersections). They were numerically obtained with parameter values different from Table 1, but around
 198 with same orders of magnitude. Isocline properties are analytically justified (see Appendix B and supplemented
 Mathematica (2010) worksheet). The local dynamics around equilibria depends on the eigenvalues of the jacobian
 200 matrix of the PL model at the equilibrium. However, the highly non-linear nature of the PL model (see Appendix
 B), makes it pointless to try infer the signs of the eigenvalues by analytical means (except for trivial and plant-only
 202 equilibrium). Thus, we propose to use to local geometry of isocline intersections to infer local stability (Case, 2000).
 Plant isoclines take two main forms:

$$\begin{cases} \gamma\sigma\alpha < \eta\nu & \text{the isocline lies entirely below (to the left of) the carrying capacity} \\ \gamma\sigma\alpha > \eta\nu & \text{parts of the isocline lie above (to the right of) the carrying capacity} \end{cases} \quad (6)$$

204 In both cases, plants grow between the isocline and the axes, and decrease otherwise. Larva isoclines are simpler,
 they start in the plant axis and bend towards the right when insects tend towards specialization ($\phi < \nu$), as shown
 206 by Figure 5. When insects tend towards generalism ($\phi > \nu$), their isoclines increase rapidly upwards like the letter
 “J” (not shown here, see Appendix B). Insects grow below and right of the larva isocline, and decrease otherwise.

208 The $\gamma\sigma\alpha < \eta\nu$ case in Figure 5A exemplifies scenarios in which pollination rates (α), plant benefits (σ), adult
 pollinator lifetimes ($1/\nu$) and larva-to-adult transition rates (γ) are low. The plant’s isocline is a decreasing curve
 210 crossing the plant’s axis at its carrying capacity K ($x = 1, y = 0$). The intersection with the larva isocline creates a
 globally stable equilibrium, approached by oscillations of decreasing amplitude. The local stability of this equilibrium
 212 can be explained, in part, by the geometry of the intersection: Figure 5A shows that if plants increase (decrease)
 above (below) the intersection point, while keeping the insect density fixed, they enter a zone of negative (positive)
 214 growth; and the same behavior holds for the insects while keeping the plants fixed. In ecological terms, both species
 are self-limited around the equilibrium, a strong indication of stability (Case, 2000). Together with the fact that
 216 the trivial ($x = 0, y = 0$) and carrying capacity equilibrium ($x = 1, y = 0$) are saddle points, we conclude that
 plants and insects achieve a globally stable equilibrium after a period of transient oscillations (provided that insects
 218 are viable, e.g. β, γ, ϵ are large enough). This equilibrium is demographically unfavorable for the plant, because
 its biomass lies below the carrying capacity ($x < 1$). Indeed, for extreme scenarios of negligible plant pollination
 220 benefits (i.e. α and/or σ tend to zero), the plant’s isocline approximates a straight line with a negative slope, like
 the isocline of a logistic prey in a Lotka–Volterra model, which is well known to cause damped oscillations (Case,
 222 2000).

The $\gamma\sigma\alpha > \eta\nu$ case in Figures 5B,C,D cover scenarios in which pollination rates (α), pollination benefits (σ),
 224 adult pollinator lifetimes ($1/\nu$) and larva-to-adult (harm-to-benefit) transition rates (γ) are high. One part of the
 plant’s isocline lies above the carrying capacity, which means that coexistence equilibria with plant biomass larger
 226 than the carrying capacity ($x > 1$) are possible; which is favorable for the plant. Figure 5B, shows an example
 where the larva isocline intersects the plant’s twice above the carrying capacity. The right intersection is a locally

228 stable equilibrium, whereas the left intersection is a saddle point. The saddle point belongs to a boundary that
separates regions of initial conditions leading to insect persistence or insect extinction. This can explain the Allee
230 effect, i.e. insect growth rates increase (go from negative to positive) with insect density when insect populations
are very small.

232 As the second inequality of (6) widens ($\gamma\sigma\alpha \gg \eta\nu$), the plant’s isocline takes a mushroom-like shape (or “anvil” or
letter “ Ω ”), as in Figure 5C,D. The plant’s isocline displays a very prominent “hump”, like in the prey isocline of the
234 Rosenzweig–MacArthur model (Rosenzweig and MacArthur, 1963). As a “rule of thumb”, intersections at the right
of the hump would lead to damped oscillations, for the reasons explained before (Figure 5A, for $\gamma\sigma\alpha < \eta\nu$). Also as
236 a “rule of thumb”, intersections at the left of the hump (like in Figure 5B) are expected to result in reduced stability.
This is because a small increase (decrease) along the plant’s axis leaves the plant at the growing (decreasing) side of
238 its isocline, promoting further increase (decrease). This means that plants do not experience self-limitation, which
is an indication of instability (Case, 2000), and we infer that interactions will not dampen. As we can see Figure
240 5C shows is an exception of this prediction; but in 5D we have an example where an intersection at the left of the
hump cause instability, leading to limit cycles. In both examples the intersection occurs above the plants carrying
242 capacity, thus revealing oscillations alternating above and below the plant’s carrying capacity. We want to stress
one more time, that these predictions based on isocline intersection configurations (left vs right of the hump) must
244 be taken as “rules of thumb”.

Figure 5C also reveals an important consequence of the dual interaction between the plant and the insect. As
246 we can see, the presence of a saddle point leads to the Allee effect explained before. But this figure also shows that
large larval densities can lead to insect extinction. This can be explained by the fact that at large initial densities,
248 the larva overexploits the plant, and this is followed by an insect population crash from which it cannot recover,
due to the Allee effect.

250 As γ, σ, α increase and/or η, ν decrease more and more, the decreasing segment of the plant isocline (the part at
the right of the hump) approximates a decreasing line (actually a straight asymptotic line, see Appendix B), while
252 the rest of the isocline is pushed closer and closer to the axes. In other words, when pollination rates (α), benefits
(σ), adult lifetimes ($1/\nu$) and larva development rates (γ) increase, plant isoclines would resemble the isocline of
254 a logistic prey, with a “pseudo” carrying capacity (the rightmost extent of the isocline) larger than the intrinsic
carrying capacity ($x = 1$). Figure 5D is an example of this. These conditions would promote stable coexistence
256 with large plant equilibrium biomasses.

Discussion

258 We developed a plant–insect model that considers two interaction types, pollination and herbivory. Ours belongs to
a class of models (Hernandez, 1998; Holland and DeAngelis, 2010) in which balances between costs and benefits cause
260 continuous variation in interaction strengths, as well as transitions among interaction types (mutualism, predation,
competition). In our particular case, interaction types depend on the stage of the insect’s life cycle, as inspired
262 by the interaction between *M. sexta* and *D. wrightii* (Bronstein et al., 2009; Alarcon et al., 2008) or between *M.*
sexta and *N. attenuata* (Baldwin, 1988). There are many other examples of pollination–herbivory in Lepidopterans,
264 where adult butterflies pollinate the same plants exploited by their larvae (Wäckers et al., 2007; Altermatt and
Pearse, 2011). We assign antagonistic and mutualistic roles to larva and adult insect stages respectively, which
266 enable us to study the consequences of ontogenetic changes on the dynamics of plant–insect associations, a topic
that is receiving increased attention (Miller and Rudolf, 2011; Rudolf and Lafferty, 2011). Our model could be
268 generalized to other scenarios, in which drastic ontogenetic niche shifts cause the separation of benefits and costs
in time and space. But excludes cases like the yucca/yucca moth interaction (Holland et al., 2002), where adult
270 pollinated ovules face larval predation, i.e. benefits themselves are deducted.

Instead of using species biomasses as resource and service proxies (Holland and DeAngelis, 2010), we consider a
272 mechanism (1) that treats resources more explicitly (Encinas-Viso et al., 2014). We use flowers as a direct proxy of
resource availability, by assuming a uniform volume of nectar per flower. Nectar consumption by insects is concomi-
274 tant with service exploitation by the plants (pollination), based on the assumption that flowers contain uniform
numbers of ovules. Pollination also leads to flower closure (Primack, 1985), making them limiting resources. Flowers
276 are ephemeral compared with plants and insects, so we consider that they attain a steady-state between production
and disappearance. As a result, the dynamics is stated only in terms of plant, larva and adult populations, i.e.
278 the PLA model (3). The feasibility of the results described by our analysis depends on several parameters. The
consumption, mortalities and growth rates, and the carrying capacities (e.g. a, b, m, n and r, c in the fourth column
280 of Table 1), have values close to the ranges considered by other models (Holland and DeAngelis, 2010; Johnson
and Amarasekare, 2013). Oscillations, for example, require large herbivory rates, but this is usual for *M. sexta*

282 (McFadden, 1968).

Mutualism–antagonism cycles

284 The PLA model displays plant–insect coexistence for any combination of (non-trivial) initial conditions where insects
can invade when rare ($R_o > 1$). Coexistence is also possible where insects cannot invade when rare ($R_o < 1$), but
286 this requires high initial biomasses of plants and insects (Allee effect). Coexistence can take the form of a stable
equilibrium, but it can also take the form of stable oscillations, i.e. limit cycles.

288 Previous models combining mutualism and antagonism predict oscillations, but they are transient ones (Holland
et al., 2002; Wang and Deangelis, 2012), or the limit cycles occur entirely below the plant’s carrying capacity
290 (Holland et al., 2013). We have good reasons to conclude that the cycles are herbivory driven and not simply a
consequence of the PLA model having many variables and non-linearities. First of all, limit cycles require herbivory
292 rates (β) to be large enough. Second, given limit cycles, an increase in the maturation rate (γ) causes a transition
to stable coexistence, and further increase in β is required to induce limit cycles again (Figure 2). This makes sense
294 because by speeding up the transition from larva to adult, the total effect of herbivory on the plants is reduced,
hence preventing a crash in plant biomass followed by a crash in the insects. Third, when adult pollinators have
296 alternative food sources ($\phi > 1$), the zone of limit cycles in the space of parameters becomes larger (Figure 4).
This also makes sense, because the total effect of herbivory increases by an additional supply of larva (which is not
298 limited by the nectar of the plant considered), leading to a plant biomass crash followed by insect decline.

The graphical analysis provides another indication that oscillations are herbivory driven. On the one hand
300 insect isoclines (or rather larva isoclines) are always positively sloped, and insects only grow when plant biomass
is large enough (how large depends on insect’s population size, due to intra-specific competition). Plant isoclines,
302 on the other hand, can display a hump (Figure 5B,C,D), and they grow (decrease) below (above) the hump.
These two features of insect and plant isoclines are associated with limit cycles in classical victim–exploiter models
304 (Rosenzweig and MacArthur, 1963). If there is no herbivory or another form of antagonism (e.g. competition) but
only mutualism, the plant’s isocline would be a positively sloped line, and plants would attain large populations
306 in the presence of large insect populations, without cycles. However, mutualism is still essential for limit cycles:
if mutualistic benefits are not large enough ($\gamma\sigma\alpha < \eta\nu$), plant isoclines do not have a hump (Figure 5A) and
308 oscillations are predicted to vanish. The effect of mutualism on stability is like the effect of enrichment on the
stability in pure victim–exploiter models (Rosenzweig, 1971), by allowing the plants to overcome the limits imposed
310 by their intrinsic carrying capacity.

Classification of outcomes: mutualism or herbivory?

312 Interactions can be classified according to the net effect of one species on the abundance (biomass, density) of
another (but see other schemes Abrams 1987). This classification scheme can be problematic in empirical contexts,
314 because reference baselines such as carrying capacities are usually not known and because stable abundances make
little sense under the influence of unpredictable external fluctuations (Hernandez, 2009).

316 Our PLA model illustrates the classification issue when non-equilibrium dynamics are generated endogenously,
i.e. not by external perturbations. Since plants are facultative mutualists and insects are obligatory ones, one
318 can say the outcome is *net mutualism* (+,+) or *net herbivory* (-,+), if the coexistence is stable, and the plant
equilibrium ends up respectively above or below the carrying capacity (Hernandez, 1998; Holland and DeAngelis,
320 2010). If coexistence is under non-equilibrium conditions and plant oscillations are entirely below the carrying
capacity (e.g. for large β), the outcome is detrimental for plant and hence there is net herbivory (-,+); oscillations
322 may in fact be considered irrelevant for this conclusion (or may further support the case of herbivory, read below).
However, when the plant oscillation maximum is above carrying capacity and the minimum is below, like in Figure
324 3, could we say that the system alternates periodically between states of net mutualism and net herbivory? Here
perhaps a time-based average over the cycle can help up us decide. The situation could be more complicated if
326 plant oscillations lie entirely above the carrying capacity (see an example in Appendix C): one can say that the
net outcome is a mutualism due to enlarged plant biomasses, but the oscillations indicates that a victim–exploiter
328 interaction exists. As we can see, deciding upon the net outcome require consideration of both equilibrium and
dynamical aspects.

330 Factors that could cause dynamical transitions

Environmental factors

332 The parameters in our analyses can change due to external factors. One of the most important is temperature
(Gillooly et al., 2001). It is well known for example, that warming can reduce the number of days needed by larvae
334 to complete their development (Bonhomme, 2000), making γ higher. Keeping everything else equal but γ , for
insects that cannot invade when rare (i.e. displaying Allee effects, $R_o < 1$), a cooling of the environment will cause
336 the sudden extinction of the insect and a catastrophic collapse of the mutualism, which cannot be simply reverted
by warming. For insects that can invade when rare ($R_o > 1$), by slowing down larva development, cooling would
338 increase the burden of herbivory over the benefits of pollination making the system more prone to oscillations and
less stable (even less under strong herbivory, large β). Flowering, pollination, herbivory, growth and mortality rates
340 (e.g. s, a, b, r, m and n in equations 1) are also temperature-dependent, and they can increase or decrease with
warming depending on the thermal impacts on insect and plant metabolisms (Vasseur and McCann, 2005). This
342 makes general predictions more difficult. However, we get the general picture that warming or cooling can change
the balance between costs and benefits impacting the stability of the plant–insect association.

344 Dynamical transitions can also be induced by changes in the chemical environment, often as a consequence of
human activity. Some pesticides, for example, are hormone retarding agents (Dev, 1986). This means that their
346 release can reduce γ altering the balance of the interaction towards more herbivory and less pollination and finally
endangering pollination service (Potts et al., 2010; Kearns et al., 1998). In other cases, the chemical changes are
348 initiated by the plants: in response to herbivory, many plants release predator attractants (Allmann and Baldwin,
2010), which can increase larval mortality μ . If the insect does nothing but harm, this is always an advantage.
350 If the insect is also a very effective pollinator, the abuse of this strategy can cost the plant important pollination
services because a dead herbivore today is one less pollinator tomorrow.

352 Another factor that can increase or decrease larvae maturation rates (γ), is the level of nutrients present in the
plant’s vegetative tissue (Woods, 1999; Perkins et al., 2004). On the one hand, the use of fertilizers rich in phosphorus
354 could increase larvae maturation rates (Perkins et al., 2004). On the other hand, under low protein consumption
M. sexta larvae could decrease maturation rate, although *M. sexta* larvae can compensate this lack of proteins by
356 increasing their herbivory levels (i.e. compensatory consumption) (Woods, 1999). Thus, different external factors
related to plant nutrients could indirectly trigger different larvae maturation rates that will potentially modify the
358 interaction dynamics.

Pollinator’s diet breadth

360 An important factor that can affect the balance between mutualism and herbivory is the diet breadth of pollinators.
Alternative food sources for the adults could lead to apparent competition (Holt, 1977) mediated by pollination, as
362 predicted for the interaction between *D. wrightii* (Solanacea) and *M. sexta* (Sphingidae) in the presence of *Agave*
palmieri (plant) (Bronstein et al., 2009): visitation of *Agave* by *M. sexta* does not affect the pollination benefits
364 received by *D. wrightii*, but it increases oviposition rates on *D. wrightii*, increasing herbivory. As discussed before,
such an increase in herbivory could explain why oscillations are more widespread when adult insects have alternative
366 food sources ($\phi > 0$) in our PLA model.

Although we did not explore this with our model, the diet breadth of the larva could also have important
368 consequences. In the empirical systems that inspired our model, the larva can have alternative hosts (Alarcon
et al., 2008), spreading the costs of herbivory over several species. The local extinction of such hosts could increase
370 herbivory on the remaining ones, promoting unstable dynamics. To explore these issues properly, models like ours
must be extended to consider larger community modules or networks, taking into account that there is a positive
372 correlation between the diet breadths of larval and adult stages (Altermatt and Pearse, 2011).

From the perspective of the plant, the lack of alternative pollinators could also lead to increased herbivory and
374 loss of stability. The case of the tobacco plant (*N. attenuata*) and *M. sexta* is illustrative. These moths are nocturnal
pollinators, and in response to herbivory by their larvae, the plants can change their phenology by opening flowers
376 during the morning instead. Thus, oviposition and subsequent herbivory can be avoided, whereas pollination can
still be performed by hummingbirds (Kessler et al., 2010). Although hummingbirds are thought to be less reliable
378 pollinators than moths for several reasons (Irwin, 2010), they are an alternative with negligible costs. Thus, a
decline in hummingbird populations will render the herbivore avoidance strategy useless and plants would have no
380 alternative but to be pollinated by insects with herbivorous larvae that promote oscillations.

Conclusions

382 Many insect pollinators are herbivores during their larval phases. If pollination and herbivory targets the same plant
(e.g. as between tobacco plants and hawkmoths), the overall outcome of the association depends on the balance
384 between costs and benefits for the plant. As predicted by our plant-larva-adult (PLA) model, this balance is affected
by changes in insect development: the faster larvae turns into adults the better for the plant, and the more stable
386 the interaction; the slower this development the poorer the outcome for the plant, and the less stable the interaction
(oscillations). Under plant–insect oscillations, this balance can be dynamically complex (e.g. periodic alternation
388 between mutualism and antagonism). Since maturation rates play an essential role in long term stability, we predict
important qualitative changes in the dynamics due to changes in environmental conditions, such as temperature
390 and chemical compounds (e.g. toxins, hormones, plant nutrients). The stability of these mixed interactions can
also be greatly affected by changes in the diet generalism of the pollinators.

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Tables and Figure legends

Symbol	Description	Value	$c = 0.01, r = 0.05$
$x = cP, y = cL, z = cA$	plant, larval and adult biomass	variable	
$\tau = rt$	time	variable	
$\alpha = s/r$	asymptotic pollination rate	5	$s = 0.25$
$\eta = wc/a$	half-saturation constant of pollination	0.1	$w = 0.5$ & $a = 0.05$
$\beta = b/rc$	herbivory rate	0 to 100	$b = 0$ to 0.05
$\mu = m/r$	larva mortality rate	1	$m = 0.05$
$\nu = n/r$	adult mortality rate	2	$n = 0.1$
$\phi = g/r$	insect intrinsic reproduction rate	0 or 1	$g = 0$ or 0.05
σ	plant pollination conversion ratio	5	
ϵ	insect pollination conversion ratio	0.5	
γ	maturation rate (herbivory conversion ratio)	0 to 0.1	

Table 1: Variables and parameters of the scaled PLA model (3) and values used for numerical analyses. The last column shows a corresponding set of parameter values in the unscaled version of the same model (2), for plant carrying capacities of $c^{-1} = 100$ biomass units, and $r^{-1} = 20$ time units.

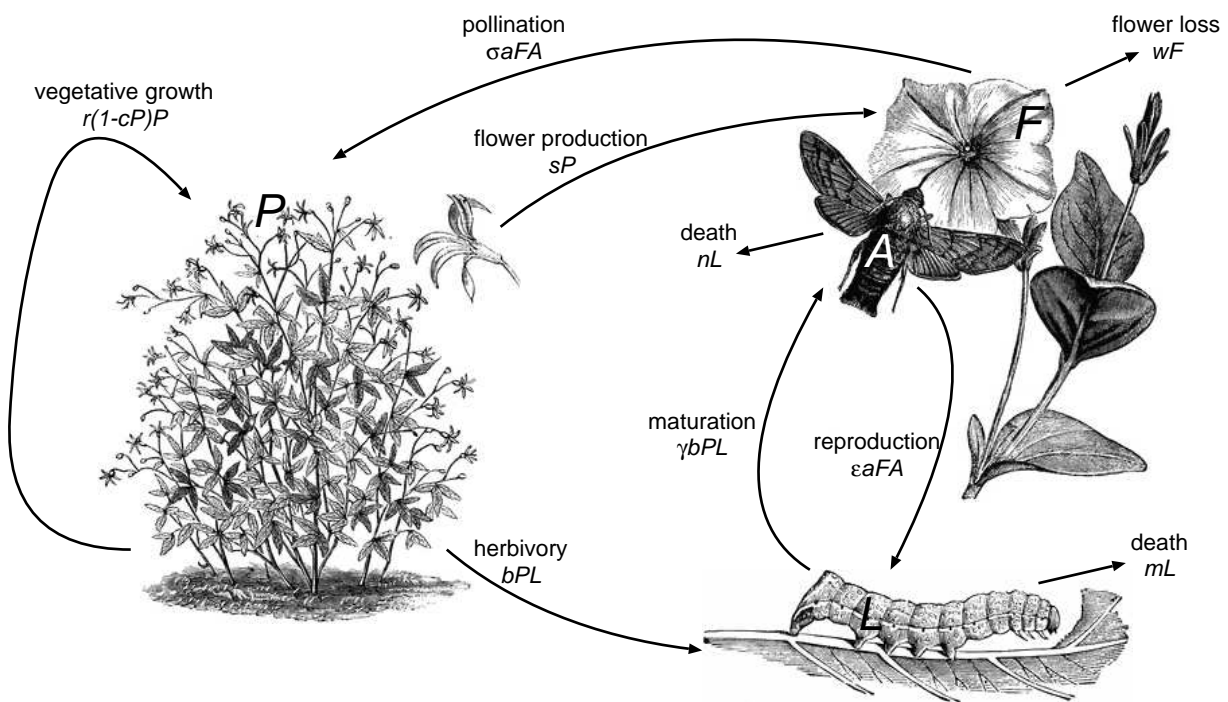


Figure 1: Interaction mechanism between plants (P), flowers (F), larva (L), adult insects (A) and associated biomass flow rates in equations (1). Clipart sources: <http://etc.usf.edu/clipart/>

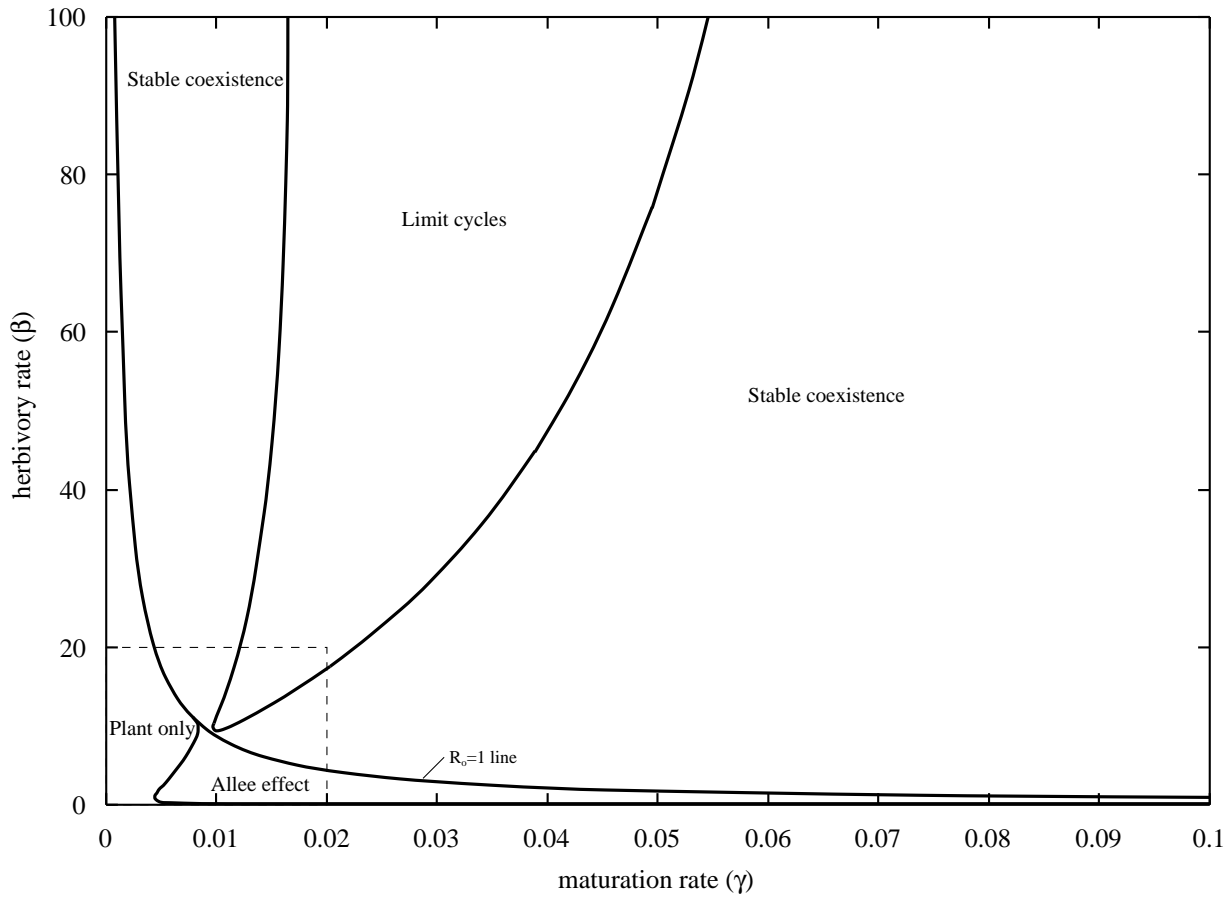


Figure 2: Outcomes of the PLA model as a function of the larval maturation and herbivory rates for specialist pollinators ($\phi = 0$). The rectangular region in the bottom left is analyzed with more detail in Appendix A.

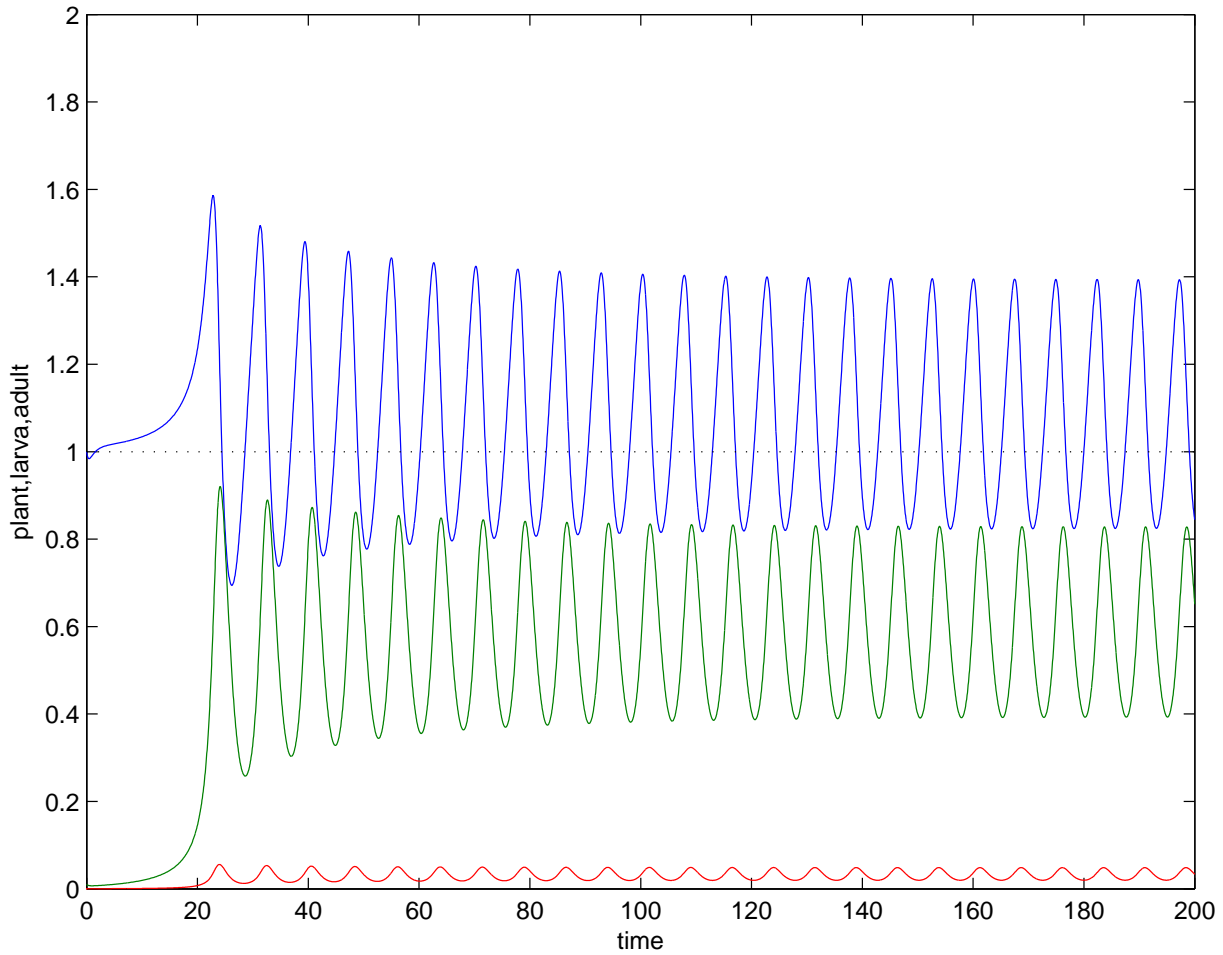


Figure 3: Limit cycles in the PLA model (3) with plant biomasses alternating above and below the carrying capacity (dotted line). Parameters as in Table 1, with $\gamma = 0.01, \beta = 10$. Blue:plant, green:larva, red:adult.

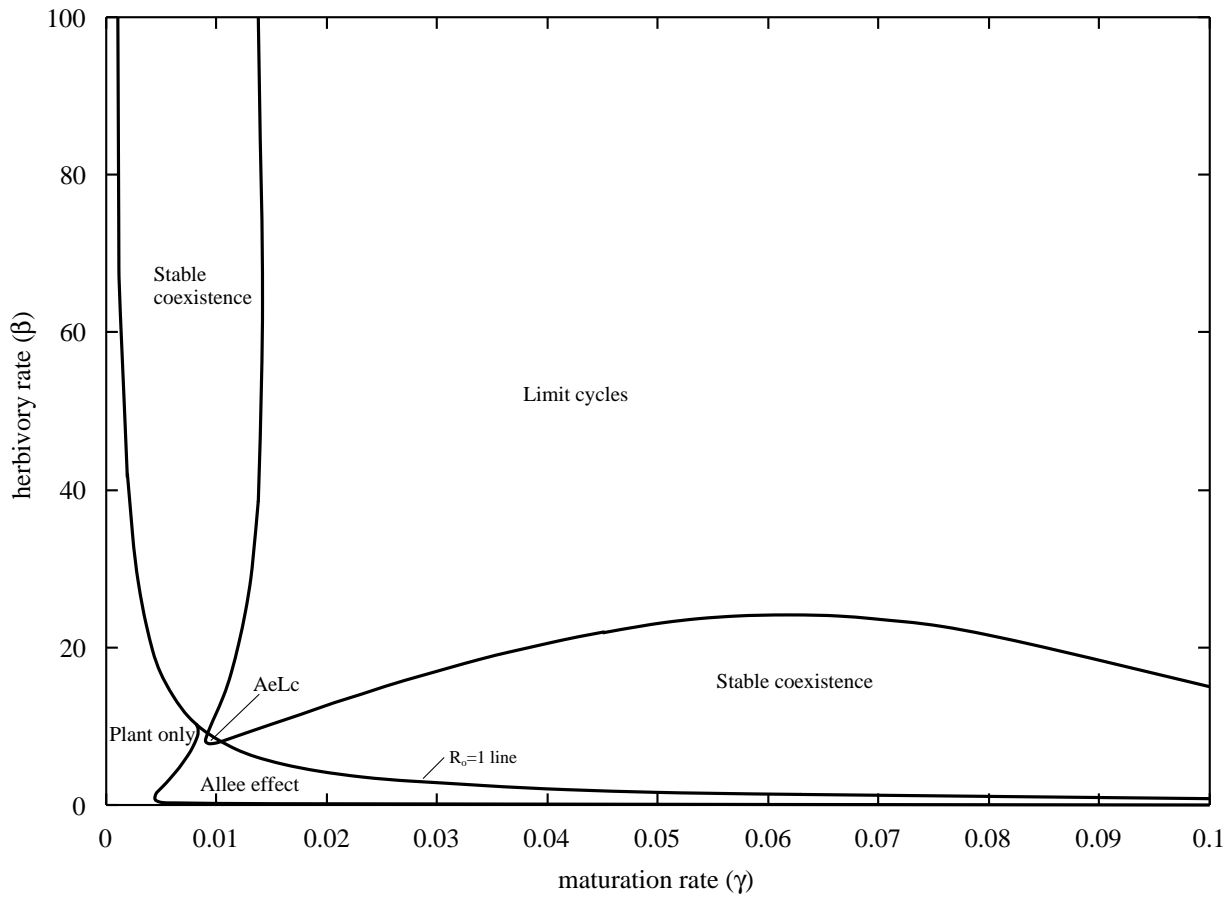


Figure 4: Outcomes of the PLA model as a function of the larval maturation and herbivory rates for generalist pollinators ($\phi = 1$). AeLc: intersection of the Allee effect and Limit cycle zones.

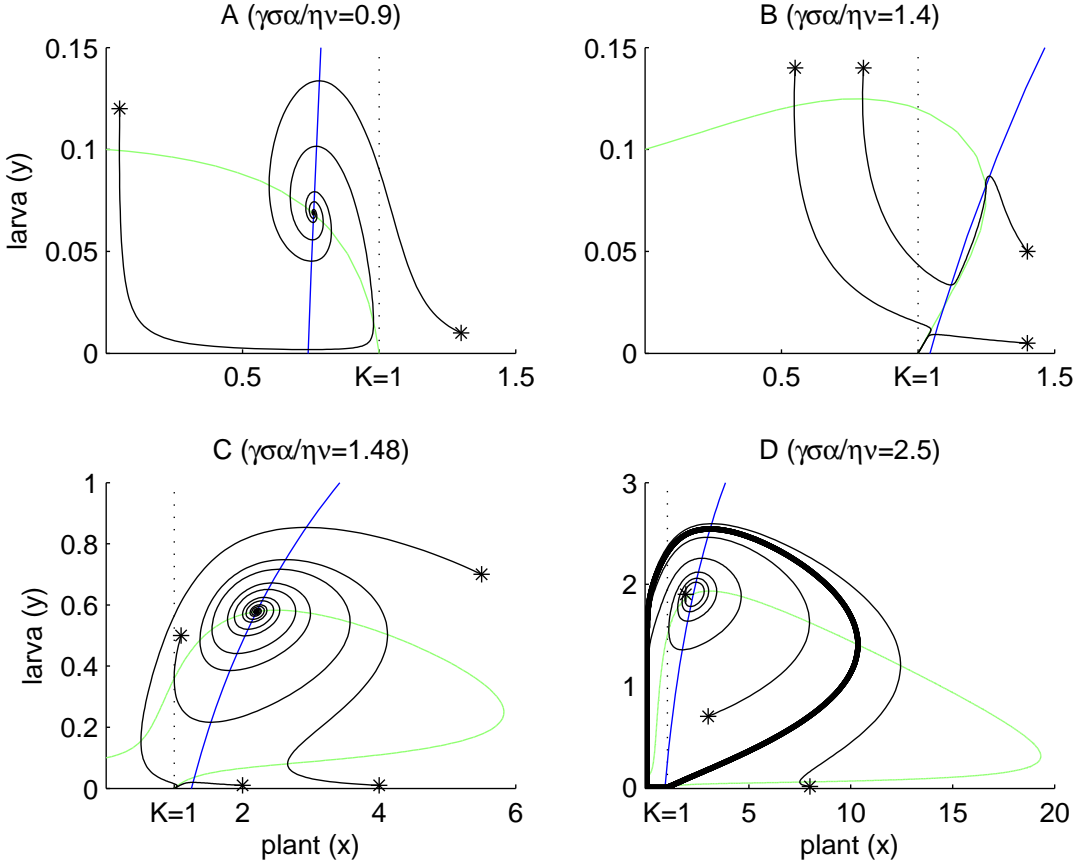


Figure 5: Plant (green) and larva (blue) isoclines of the simplified version of the PLA model. Several trajectories are shown (starting with *). The dotted line at $x = 1$ is the plant's carrying capacity. When $\gamma\sigma\alpha/\eta\nu < 1$ the plant's isocline always decreases, when $\gamma\sigma\alpha/\eta\nu > 1$, it bulges above the carrying capacity, and displays a hump. (A) Damped oscillations leading to globally stable coexistence. (B) The isoclines intersect as a locally stable equilibrium and as a saddle point. Insects can coexist with the plant or go extinct depending on the initial conditions. (C) When $\gamma\sigma\alpha/\eta\nu$ the plant's isocline displays a mushroom shape. The larva isocline intersects the plant's at the left of the hump, and the equilibrium is locally stable, oscillations vanish. There is also a saddle point, some trajectories lead to extinction due to the Allee effect or because of overexploitation (D) Another intersection the left of plant's hump, this time oscillations approach a limit cycle (thick loop). Common parameters in all panels are $\beta = 10, \eta = 0.1, \mu = 1, \phi = 0$. For the other parameters; in (A): $\sigma = 3, \epsilon = 0.7, \alpha = 3, \gamma = 0.02, \nu = 2$; in (B): $\sigma = 2.1, \epsilon = 0.21, \alpha = 2, \gamma = 0.05, \nu = 1.5$; in (C): $\sigma = 3.7, \epsilon = 0.2, \alpha = 3, \gamma = 0.02, \nu = 1.5$; in (D): $\sigma = 5, \epsilon = 0.3, \alpha = 5, \gamma = 0.02, \nu = 2$.