Shifts in pollinator population structure may jeopardize pollination service

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1   Plant-pollinator interactions are among the best known and ubiquitous plant-animal

2   mutualisms and are crucial for ecosystem functioning and the maintenance of biodiver-

3   sity. Most pollinators are insects with several life-stages (e.g. egg, larva, pupa, adult)

4   and the mutualistic interaction depends on the pollinator surviving these different life-

5   stages. However, to our knowledge, pollinator population structure has been ignored

6   in most theoretical models of plant-pollinator dynamics, and we lack understanding of

7   the role of different life-stages in determining the stability of the mutualism. Here we

8   therefore develop a simple plant-pollinator model with a facultative plant and an obli-

9   gate pollinator with stage-structure. Our model predicts a globally stable equilibrium

10   when pollinator demography is dominated by adults and a locally stable equilibrium

11   when the plants are strongly dependent on pollination and pollinator demography is

12   dominated by the larval stage. In the latter case, the mutualism is vulnerable to fluc-

13   tuations in the pollinator population size or structure caused by external factors (e.g.

14   pesticides) reducing larval development and increasing adult mortality. This may cause

15   a sudden collapse rather than gradual decrease of the mutualism, after which the polli-

16   nation service cannot be recovered by reducing these detrimental external factors, but

17   must be accompanied by large increases in pollinator populations. This highlights the

18   importance of considering population structure in plant-pollinator interactions.

19   KEYWORDS: mutualism; pollination service; population structure; pesticides; Allee

20   effect; insects

Introduction

Plant-pollinator interactions are essential for ecosystem functioning and the maintenance of biodiversity (Balvanera *et al.*, 2005). Many angiosperm plants depend on the service provided by pollinators to reproduce (Kearns *et al.*, 1998). Empirical studies of this type of mutualistic interaction are abundant (Waser, 2006). However, theoretical studies of plant-pollinator interactions are relatively scarce, originally focusing on very specific systems (e.g. fig-fig wasp) (Bronstein *et al.*, 2003; Wilson *et al.*, 2003) but more recently on mutualistic community dynamics (Bastolla *et al.*, 2009). Holland & DeAngelis (2010) have proposed to study plant-pollinator systems, and other types of mutualism (e.g. plant-mycorrhiza), in terms of consumer-resource interactions to develop more mechanistic models of mutualism. The theory of plant-pollinator interactions is progressing (Bronstein *et al.*, 2006; Bascompte & Jordano, 2007; Holland *et al.*, 2004, 2002), but a crucial component of this interaction is missing in many theoretical studies: the consideration of population structure. Many pollinators are insects with complex life-cycles, i.e. they have several life-stages (e.g. egg, larva, pupa, adult) and each life-stage is subject to different selective pressures (Wilbur & Rudolf, 2006; Herrera, 1984) and can have multiple indirect effects on their mutualistic partners (i.e. plants) (Adler & Bronstein, 2004).

In predator-prey models with population structure, indirect effects along the trophic chain can produce very different dynamics from unstructured populations (Abrams & Quince, 2005; Rudolf, 2007). For example, Rudolf (2007) found that behavioral interactions between predator stages (e.g. cannibalism) can alter the dynamics of predator-prey systems producing positive indirect effects that alter the strength of trophic cascades. Thus, we can expect different dynamics and stability conditions when considering population structure in plant-pollinator systems.

It is well known that mutualistic models with at least one obligatory mutualistic partner will show positive density-dependence (i.e. Allee effect) under certain conditions and therefore there will be regions of bistability where the obligate mutualist runs a risk of extinction (Vandermeer & Boucher, 1978; Dean, 1983; Wilson *et al.*, 2003). However, it is not yet known how population structure will affect the Allee effect and hence the stability of the plant-pollinator mutualism and thus the quality of the pollination service.

Here, we study a facultative-obligate plant-pollinator system with pollinator population structure and consumer-resource interactions (Holland & DeAngelis, 2010). This simple model assumes a more mechanistic plant-pollinator interaction (Soberón & Martínez del Río, 1981) than Lotka-Volterra models of mutualism (Addicott, 1981; Dean, 1983; May, 1976) by explicitly describing the resource and consumer dynamics between plants and pollinators, where there is an exchange of resources (i.e. nectar) for an ecological service (i.e. pollination). This allows us to go beyond the simple assumption of a mutualistic interaction coefficient that most mutualistic models make. This mutualistic coefficient usually does not reflect any biological mechanism or trait related to the specific mutualistic interaction, as for example in plant-pollinator interactions. Thus, by assuming the mechanism of nectar consumption we can incorporate more realism to the model and provide a better biological interpretation of the results. Our results indicate that population structure is highly important for the stability of plant-pollinator interactions and the management of pollination service.

The Models

We consider two models of plant-pollinator interactions in which the pollinator has a population structure consisting of pollinating adults and non-interacting larvae. In both models the adults consume nectar, produced by the plants, in order to reproduce, and consumption leads to the plant being pollinated. In model (I) consumption follows a type I functional response and in model (II) a type II functional response (Holling's disc equation). Model (II) is biologically more realistic, but the predictions are qualitatively similar to those of model (I), which is analytically more tractable.

The general structure of both models describes the dynamics of plants and their insect pollinators with a system of ordinary differential equations for the plants biomass (P), the nectar provided by the plants (N), and the biomass densities of adult insects (A) and their larvae (L). Pollination is modeled as a consumer-resource interaction. In the absence of insect pollination, the plant biomass increases vegetatively according to the logistic model, but pollination by insects increases the growth rate by reproduction. The differential equations for plants and nectar are:

$$\frac{dP}{dt} = rP\left(1 - \delta_P P\right) + \sigma f(N)A \tag{1}$$

$$\frac{dN}{dt} = \rho P - \delta_N N - f(N)A \tag{2}$$

where in the first term in equation 1 r is the intrinsic growth rate and δ_P is a self-limitation coefficient, e.g. due to limiting nutrients. The second term accounts for the reproductive growth from pollination, which depends on the rate of nectar consumption, with a functional response $f(N)$. The parameter σ represents the pollination efficiency in terms of amount of plant biomass produced per nectar consumed, but it can also be taken as a proxy for the number of fertilized ovules per insect visit. Pollination efficiency can also be described by a plant trait (e.g. floral morphology), for example the anther exertion length, which determines the number of pollen grains removed by pollinators (Conner *et al.*, 1995). Evidently, the benefits of pollination for the plant lie in increasing its equilibrium abundance (Addicott, 1981; Wolin & Lawlor, 1984). Nectar increases in proportion to plant biomass with production rate per plant biomass ρ, and decreases with a first order decay rate δ_N and with the nectar consumption rate $f(N)A$.

Insects use nectar to produce eggs from which larvae emerge. Thus, the number of larvae produced is directly proportional to the amount of nectar consumed. Only the adult stage exploits resources (i.e. nectar), implying that larvae do not interact with the plant. This could be the case for some Hymenopteran pollinators (e.g. honey bees), which spend their larval stage in nest cavities without interacting with plants directly (Roulston & Goodell, 2011) or pollinators that feed on different plant species in their larval and adult stages. The equations describing pollinator dynamics are:

$$\frac{dL}{dt} = \epsilon f(N)A - \gamma L - \delta_L L \tag{3}$$

$$\frac{dA}{dt} = \gamma L - \delta_A A \tag{4}$$

where ϵ is the conversion efficiency for the transformation of nectar consumed into larvae, γ is the

per capita maturation rate and δ_L is the per capita larva mortality rate. Adult density increases by maturation of larvae and decreases by adult mortality at per capita rate δ_A.

Thus, the mutualistic interaction is assumed to be a facultative-obligatory mutualistic system. Plants are facultative mutualists because they can grow by means of vegetative growth, but insect pollinators are obligatory mutualists because they depend entirely on the consumption of nectar by the plants in order to produce larvae.

In model I, the pollinator functional response is of type I (linear):

$$f(N) = \alpha N \tag{5}$$

where α is the consumption rate per unit of nectar and per pollinator. In reality, a type I response is linear only up to a point $N = N^*$, after which it suddenly becomes constant. However, it is customary to assume that such point is not achieved during the dynamics, or that equilibrium states lie below it. In model II, pollination is modelled with a type II (saturating) functional response:

$$f(N) = \frac{\alpha N}{1 + t_h \alpha N} \tag{6}$$

where t_h is the handling time of the pollinators. Insect pollinators, like other consumers (e.g. herbivores), invest time in resource manipulation (i.e. handling time) (Holling, 1959; Ingvarsson & Lundberg, 1995; Herrera, 1989). Thus, the pollination benefits for both plants and pollinators do not grow linearly, but in a saturating fashion.

In the appendix we list the system parameters for both model alternatives (I and II) together with the values employed for the numerical analysis.

Analysis and results

The analysis of the models consists of characterizing the equilibrium states $E = \{\hat{P}, \hat{N}, \hat{L}, \hat{A}\}$ and their stability. There are three classes of equilibrium states: the trivial equilibrium $E_0 = \{0, 0, 0, 0\}$ with plants and pollinators absent, the plant-only equilibrium $E_1 = \{\hat{P} > 0, \hat{N} > 0, \hat{L} = 0, \hat{A} = 0\}$

117 with the pollinators absent, and the plant-pollinator equilibrium with plants and pollinators present

118 $E_2 = \{\hat{P} > 0, \hat{N} > 0, \hat{L} > 0, \hat{A} > 0\}$. Because r is considered to be always positive, it immediately

119 follows that E_0 is always unstable, i.e. a small amount of plant biomass always leads from E_0 to

120 E_1 when all the other variables are $N = L = A = 0$. E_0 is also unstable when a small amount of

121 nectar and adult pollinators are initially present and $P = L = 0$. However, this scenario is ruled

122 out from all the analyses because there cannot be nectar without plants, as the plants provide the

123 flowers that make pollination possible in the first place.

124   The stability of E_1 and E_2 can be determined by the analysis of the eigenvalues of the Jacobian

125 matrix of the system evaluated at E_1 and E_2 (details in the Appendix).

Model I

127 In the absence of the pollinators, the plants grow logistically and a plant-only equilibrium is

128 attained: $E_1 = \{\hat{P} = \delta_P^{-1}, \hat{N} = \rho/(\delta_P \delta_N), \hat{L} = 0, \hat{A} = 0\}$. This equilibrium is unstable for invasion

129 by a low number of animals, if and only if:

$$R_0 = \frac{\epsilon \alpha \rho \gamma}{\delta_P \delta_N \delta_A (\gamma + \delta_L)} > 1 \tag{7}$$

130   We call R_0 the pollinator basic reproduction ratio. It is the expected number of adults produced

131 by one adult during its life-time. The rationale of Eq. 7 is as follows: from equation 3 the number

132 of larvae produced by an average adult during an arbitrary time span Δt must be equal to $\epsilon \alpha N \Delta t$.

133 During an invasion the amount of nectar available for the pollinators is $N = \rho/(\delta_P \delta_N)$, i.e. the

134 equilibrium level when pollinators are absent. If the time span is the same as the life-span of an

135 adult (i.e. $\Delta t = \delta_A^{-1}$), the average number of larvae produced by an adult during its life-time is

136 $\epsilon \alpha \rho/(\delta_P \delta_N \delta_A)$. According to equation 3, the fraction of larvae that become adults is $\gamma/(\gamma + \delta_L)$

137 while the complement $\delta_L/(\gamma + \delta_L)$ dies. Thus, after one life-time cycle, 1 adult is replaced by

138 $[\epsilon \alpha \rho/(\delta_P \delta_N \delta_A)] \times [\gamma/(\gamma + \delta_L)]$ new adults.

139   To obtain the plant-pollinator equilibrium E_2 we start by setting $dA/dt = 0$ in equation 4. This

140 shows that the pollinator adult:larva ratio at E_2 is:

$$\frac{\hat{A}}{\hat{L}} = \frac{\gamma}{\delta_A} \tag{8}$$

141 i.e., the pollinator population structure depends on the larval maturation rate and the adult
142 mortality rate. If maturation is fast relative to adult mortality $(\gamma \gg \delta_A)$ the system will shift to a
143 large proportion of adults versus larvae $(\hat{A} > \hat{L})$, and vice versa, slow maturation relative to adult
144 mortality $(\delta_A \gg \gamma)$ shifts the population towards a large proportion of larvae relative to adults
145 $(\hat{L} > \hat{A})$. Equation 8 also tells us that R_0 is proportional to the adult:larva ratio, if $\delta_L \gg \gamma$, but
146 in more general situations R_0 and the adult:larva ratio are just positively related.

147 We now set $dL/dt = 0$ in equation 3, where $\hat{L}$ and $\hat{A}$ can be eliminated using equation 8. This
148 gives us the nectar equilibrium abundance:

$$\hat{N} = \frac{(\gamma + \delta_L)}{\epsilon\alpha} \times \frac{\delta_A}{\gamma} \tag{9}$$

149 For the plant abundance we combine equations 1 and 2 with $dP/dt = dN/dt = 0$. This results
150 in a quadratic equation in $\hat{P}$, the solutions of which are:

$$\hat{P} = \frac{1+\omega}{2\delta_P}\left(1 \pm \sqrt{1 - \frac{4\omega}{(1+\omega)^2 R_0}}\right) \tag{10}$$

151 where

$$\omega = \frac{\sigma\rho}{r} \tag{11}$$

152 is the "plant's mutualistic offset". The ω ratio indicates how much the plant's percapita growth
153 rate is raised due to the pollination services (σ) of the resources provided (ρ), in comparison with
154 the growth rate in the absence of the services. From equation 1 with $dP/dt = 0$ equation 9, and
155 equation 8, we can obtain the adult $\hat{A}$ and larval equilibrium $\hat{L}$ densities:

$$\hat{A} = \frac{\epsilon\rho\hat{P}(\delta_P\hat{P} - 1)}{\omega(\gamma + \delta_L)}\left(\frac{\gamma}{\delta_A}\right) \tag{12}$$

$$\hat{L} = \frac{\epsilon\rho\hat{P}(\delta_P\hat{P} - 1)}{\omega(\gamma + \delta_L)} \tag{13}$$

Given 10, 12 and 13, a mutualistic equilibrium is feasible (real and positive) if $\hat{P}$ is real and if it is larger than δ_P^{-1}, i.e. the plant's equilibrium in the absence of the pollinators. It turns out that both requirements are simultaneously are fulfilled if:

$$R_0 \geq \frac{4\omega}{(1 + \omega)^2} \tag{14}$$

In general 14 will be an inequality, where $\hat{P}$ exists as a real-valued pair $(\hat{P}_{HI}, \hat{P}_{LO})$ corresponding to the "+" and "-" cases in equation 10. Hence, $\hat{A}$ and $\hat{L}$ also exist as pairs $(\hat{A}_{HI}, \hat{A}_{LO})$ and $(\hat{L}_{HI}, \hat{L}_{LO})$ respectively. Thus, the plant-pollinator mutualism involves two real equilibria $E_{2,HI} = \{\hat{P}_{HI}, \hat{N}, \hat{L}_{HI}, \hat{A}_{HI}\}$ and $E_{2,LO} = \{\hat{P}_{LO}, \hat{N}, \hat{L}_{LO}, \hat{A}_{LO}\}$. The equality case in 14 corresponds to the coincidence of the two equilibria. In equations 12 and 13, we see that $E_{2,HI}$ or $E_{2,LO}$ will be biologically feasible (positive) if and only if $\hat{P}_{HI}$ or $\hat{P}_{LO}$, respectively, are larger than δ_P^{-1}, which is the plant equilibrium in the absence of the mutualism. In Figure 1 we sketch the plant equilibrium abundance (graph of 10) as a function of the pollinator's R_0, to illustrate the feasibility conditions of the mutualistic equilibrium. In this figure we can see that if the pollinator is able to invade when rare ($R_0 > 1$), there will be only one feasible plant-pollinator equilibrium ($E_{2,HI}$), corresponding to the upper branch of $\hat{P}$ in 10 (the "+" case). If the pollinator is not able to invade when rare ($R_0 < 1$), two plant-pollinator equilibria ($E_{2,HI}$ and $E_{2,LO}$, corresponding to the "+" and "-" cases in 10) are feasible if:

$$\frac{4\omega}{(1 + \omega)^2} < R_0 < 1 \tag{15}$$

and for $R_0 > 1$, only $E_{2,HI}$ is feasible.

The fact that the pollinator is always able to invade if there is a single feasible plant-pollinator

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174 equilibrium, and that the pollinator cannot invade if there are two plant-pollinator equilibria,
175 suggests the existence of a strong Allee effect, like in other models with at least one obligate
176 mutualist partner (Wilson *et al.*, 2003; Holland, 2002; Vandermeer & Boucher, 1978; Soberón &
177 Martínez del Río, 1981). With numerical stability analyses (see Appendix), we determined that if
178 $\omega > 1$ equilibrium $E_{2,HI}$ is always locally stable and $E_{2,LO}$ is always unstable, i.e. $E_{2,LO}$ must be
179 an extinction and invasion threshold for the pollinator. If $\omega < 1$ and $E_{2,LO}$ is not feasible, then
180 $E_{2,HI}$ is stable for $R_0 > 1$. Summarizing, from Figure 1 and the stability analysis, we can classify
181 three different mutualistic regimes:

$$
\omega
\begin{cases}
< 1: & \text{mutualism without Allee effect when: } R_0 > 1 \\
\\
> 1: & \text{mutualism}
\begin{cases}
\text{without Allee effect when: } \quad R_0 > 1 \\
\\
\text{with Allee effect when: } \qquad \frac{4\omega}{(1+\omega)^2} < R_0 < 1
\end{cases}
\end{cases}
\tag{16}
$$

182 The Allee effect can occur under ecological scenarios in which the plant's mutualistic offset ω
183 is greater than 1, i.e. when pollination is more important than vegetative growth for the plants.
184 The three regimes listed by 16 are represented in Figure 2.

185 The analysis so far indicates that the stable branch of $\hat{P}$ in equation 10 (the "+" case) is positively
186 related with the pollinator's R_0, which is in turn is related to the adult to larva equilibrium ratio,
187 as mentioned earlier. This means that plant population abundances increase when pollinator
188 maturation rates γ are very large compared with adult mortalities δ_A. This is because the faster
189 the maturation and the slower the adult mortality, the larger the proportion of adults in the
190 pollinator population, the ones providing the services for the plant. A relation between plant
191 equilibrium abundance and the equilibrium adult:larva ratio can be obtained by substituting the
192 definition of R_0 (equation 7) in the stable branch of 10 and substituting the γ/δ_A ratio by the
193 adult:larva ratio from the equation 8:

$$
\hat{P} = \frac{1+\omega}{2\delta_P} \left(1 + \sqrt{1 - \frac{4\omega}{(1+\omega)^2} \frac{\delta_P \delta_N (\gamma + \delta_L)}{\epsilon \alpha \rho \left(\hat{A}/\hat{L} \right)}} \right)
\tag{17}
$$

194 Figure 3 shows $\hat{P}$ as a function of $\hat{A}/\hat{L}$ for several values of the mutualistic offset. This relation-

ship permit us to make a prediction for real systems. For real plant-pollinator systems, one could find positive relationships between the abundance of plant populations and the relative ratio of adults versus larva in the populations of their pollinators. This prediction involves the $\hat{L}$, $\hat{A}$ and $\hat{P}$, which are in principle easier to quantify in the field (censuses) than the parameters of the model, which involve physiology and metabolism (ussualy measured under artificial conditions). In systems where pollinators have little or no influence one would expect to see little variation in plant abundances against large variations in the relative ratio of adults in the pollination populations, whereas for plants that depending strongly on pollination, one would expect to see abrupt changes in population abundances caused by small changes the relative abundance of adult pollinators. The last case exemplifies how an mutualistic interaction can become very sensitive to changes in the life cycles in one of the mutualistic populations.

Model II

The model with type II functional response exhibits the same qualitative behavior with respect to stability and coexistence of plant-pollinator mutualism as model I (see Appendix for details). The condition of pollinator growth when rare in this model is that the basic reproduction ratio is again higher than 1:

$$R_0 = \frac{\epsilon \rho \alpha \gamma}{\delta_A (\delta_P \delta_N + t_h \alpha \rho)(\gamma + \delta_L)} > 1 \tag{18}$$

The main difference between the models is related to the effect of the pollinator's handling time, as can be seen in the basic reproductive ratio (equation 18). An increase in handling time produces a saturating effect in the pollination service and the equilibrium density of the animals. The condition for the Allee effect (eq. 14) is exactly the same as in model I and the stability conditions for the plant-pollinator coexistence are qualitatively similar to the previous model (see Appendix). Interestingly, pollinators with larger handling times ($t_h \gg 0$) and therefore relatively low R_0 are able to exist in the Allee effect region as long as pollination service is highly rewarding ($\omega > 1$). This is because there is no relationship between handling time (t_h) and pollination efficiency (σ) . R_0 is only affected by t_h (eq. 18) while the lower bound to R_0 is only affected by

σ (see equation 16). Thus, many but short visits to flowers can be viable as well as with efficient pollination of only few flowers that takes a long time per visit.

Discussion

Determining the stability of mutualistic interactions has been the main interest of classical theoretical studies. May (1976) found that obligate mutualistic interactions are very unstable and prone to extinction. Later, several studies showed that mutualism can be stable when intraspecific competition is strong relative to the mutualistic interaction (Dean, 1983; Addicott, 1981). Addicott (1981) argued that if mutualistic interaction coefficients are decreasing functions of density (Vandermeer & Boucher, 1978), then a locally unstable equilibrium does not necessarily imply that the system is globally unstable (Travis & Post, 1979). Recently, theoretical research has mainly focused on more mechanistic models of obligatory plant-pollinator interactions (e.g. fig-fig wasp) on eco-evolutionary dynamics (Ferriere *et al.*, 2007; Ferdy *et al.*, 2002) and on other types of ecological interactions mediating mutualism (Bronstein *et al.*, 2006); for example, antagonistic interactions (e.g. herbivores, parasites) in mutualistic systems (Wilson *et al.*, 2003; Bronstein *et al.*, 2003) can make mutualism more unstable and prone to extinction under certain conditions.

In mutualisms in which one or both partners are obligate, coexistence depends on partners attaining minimum abundance thresholds. Below such threshold, net population growth is negative and leads to extinction, whereas above the threshold, growth is positive leading to preservation. This is commonly interpreted as an Allee effect of mutualism (Wilson *et al.*, 2003; Wolin & Lawlor, 1984). Thus, models of obligate mutualisms will display bi-stability and Allee effects in some region of the space of parameters, whether we explicitly consider population structure or not. However, we consider it because larval stages, by being idle and not taking direct a role in pollination, reduce the effective abundance of the pollinator population making more difficult to achieve the necessary numbers that prevent a plant-insect mutualism from collapsing.

Our results points at the important, but currently ignored role, that population structure has on this Allee effect and therefore on the stability and conservation of mutualisms. In our model pollination is performed by adult pollinators, that is, a fraction of the population of one of the

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mutualistic partners is performing the service. Consequently, alterations of the pollinator life-cycle such as the decrease of the maturation rate can lead to large numbers of larvae relative to pollinating adults, thus decreasing the mutual benefit received by both partner species. In the particular case of the plant this can lead to lower abundances, but in the case of the pollinator this could mean sudden extinction.

The question is what could cause such a detrimental effect in plant-pollinator interactions. The current global pollinator decline, particularly specialist bees (i.e. oligolectic bees) (Larsson & Franzén, 2007; Biesmeijer *et al.*, 2006), has stimulated research aiming at understanding the multiple causes that impair pollinator population growth (Potts *et al.*, 2010). Apart from natural pathogens (Pettis *et al.*, 2012), pesticides are among the most important causes, slowing the larval maturation rate and increasing the adult mortality rate, particularly in Hymenopteran pollinators (Wu *et al.*, 2011; Roulston & Goodell, 2011; Krupke *et al.*, 2012). Pesticides have various negative effects on the survivorship and development of bee colonies: they can impair foraging behavior, decrease egg production, delay larval development and shorten adult longevity (Wu *et al.*, 2011; Roulston & Goodell, 2011; Krupke *et al.*, 2012; Pettis *et al.*, 2012; Morandin & Winston, 2003). Our model predicts that these effects of pesticides can produce a shift in the pollinator population structure to higher larva to adult ratios and decrease the population growth ($R_0 < 1$) putting the pollinators in the Allee effect region (i.e. bistability region). Furthermore, due to hysteresis (Scheffer & Carpenter, 2003), after a perturbation a pollinator population that was close to the fold bifurcation point (i.e. critical transition (Scheffer *et al.*, 2009)) will not recover by, for example, an increase of nectar production rate (ρ) to the values where the transition occurred, i.e. it will not return to the alternative stable state of coexistence with plants (E_{HI}). Such a return requires a large increase not just in pollinator abundance (adults and larvae), but also in the relative proportion of adults, which cannot be achieved by restoring the nectar production rate alone. This has important consequences for the management of pollination service in crop-pollinated fields because these critical transitions might be detectable before the population collapses (Scheffer *et al.*, 2009).

Our model only explores the dynamics between a facultative plant and an obligate pollinator.

That is, strictly speaking we only investigate a case of specialist pollinators, such as oligolectic bees. However, this type of pollinators is at a higher risk of collapse (Biesmeijer *et al.*, 2006). Furthermore, our model allows one to draw some conclusions also in the case of generalist pollinators, such as honey bees (Zayed *et al.*, 2005; Biesmeijer *et al.*, 2006). Honey bees, which often depend on a limited number of pollen/nectar resources because of habitat fragmentation (Kremen *et al.*, 2002; Roulston & Goodell, 2011; Franzén & Nilsson, 2009) or suffer from a reduction in larval maturation rate due to pesticides (Wu *et al.*, 2011), show the same catastrophic consequences as specialist pollinators. Thus, we believe that our results are relevant for plant-pollinator systems in general. Our model only studied a pair-wise interaction and not a community. Although simple models provide much insight, it is essential that future theoretical studies incorporate population structure into mutualistic community dynamics models (Bastolla *et al.*, 2009) to generate predictions for the management of pollination services and conservation of threatened species. We also advocate the future consideration of models that consider the conflict between mutualistic and antagonistic effects from different pollinator life-stages on the plants. This is particularly common in Lepidopteran pollinators (Adler & Bronstein, 2004; Kessler *et al.*, 2010)

Adding a nectar handling time does not change qualitatively the conditions for an Allee effect, but it quantitatively directly affects the stability of the mutualism, as has been found in other models (Soberón & Martínez del Río, 1981; Ingvarsson & Lundberg, 1995). Increases in handling time decrease the pollinator basic reproductive ratio (R_0); hence longer handling times will drive pollinators to extinction or to the Allee effect region if pollination efficiency is high enough (see condition 15). In our model, pollination efficiency is independent of the pollinator's handling time. Thus, in the Allee effect region we can find 'slow' pollinators if there is high pollination efficiency. Several studies have found a negative correlation between pollination efficiency and handling time (Pattersson, 1991; Mitchell & Waser, 1992). Other studies report that pollination efficiency and handling time can be positively correlated (Conner *et al.*, 1995; Ivey *et al.*, 2003). These differences seem to depend on the plant and pollinator species studied and the components of pollination efficiency measured (Herrera, 1989; Ivey *et al.*, 2003). For the plants, there is a clear advantage in having an efficient pollination service and different floral traits might evolve

to increase flower-handling time (e.g. evolution of flexible pedicels (Hurlbert *et al.*, 1996)), but stability of this interaction essentially will depend on the cost-benefit balance (Holland, 2002) and the community context (i.e. structure and composition of the community).

We conclude that population structure is crucial for the stability of plant-pollinator interactions. The inclusion of population, temporal (i.e. phenology) and spatial structure is fundamental to properly conserve and manage plant-pollinator communities.

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Figure captions

Figure 1   Plant equilibrium densities as a function of animal basic reproductive ratio R_0 in model type I. The horizontal line at $\hat{P} = \delta_P^{-1}$ corresponds to the plant-only equilibrium, which is locally stable for $R_0 \leq 1$ and unstable for $R_0 > 1$. The plant-animal equilibria are represented by a curve starting with two symmetric branches $\hat{P}_{HI}$ and $\hat{P}_{LO}$ above and below $P = \frac{1+\omega}{2\delta_P}$ respectively. The upper branch $\hat{P}_{HI}$ corresponds to the plant-animal mutualism, and is stable (numerically determined); the lower branch $\hat{P}_{LO}$ is unstable and corresponds to a saddle point. Equilibrium values in the hatched region are unfeasible (i.e. they correspond with negative pollinator densities). (A) If $\sigma\rho < 1$ the system shows mutualism for $R_0 > 1$ without Allee effect. (B) If $\omega > 1$ the system shows mutualism with Allee effect for $\frac{4\omega}{(1+\omega)^2} < R_0 < 1$ and without Allee effect for $R_0 > 1$.   21

Figure 2   Parameter space of the plant-pollinator mutualism model type I, animal basic reproductive ratio (R_0) vs. plant's mutualistic offset (ω). The parameter space is divided into three regions of coexistence and stability: i) *Pollinator extinction*: $R_0 < 1$ for $\omega < 1$ and $R_0 < \frac{4\omega}{(1+\omega)^2}$ for $\omega > 1$; this is the region where animal pollinators cannot survive under any condition and consequently the mutualism is not possible. ii) *Allee effect*: $\frac{4r\sigma\rho}{(1+\omega)^2} < R_0 < 1$; this is the Allee effect area for animal pollinators, which increases with the plant's mutualistic offset $(\omega > 1)$. This region is unstable for the plant-pollinator mutualism, only pollinators above the extinction threshold can survive. iii) *Plant-pollinator coexistence*: $R_0 > 1$. In this region, the plant-pollinator mutualism is globally stable. For parameters values used , see the appendix.   22

Figure 3   Relationship between the plant equilibrium abundances ($\hat{P}$) and the equilib-

rium adult to larva ratio ($\hat{A}/\hat{L}$) for different amounts of the plant mutualistic

offset (ω), in model I. In the absence of benefits from pollination ($\omega = 0$),

plant abundances are not affected. When plants experience benefits from pol-

lination ($\omega > 0$), an increase in the relative proportion of adults causes an

increase in plant abundance. If the relative benefits of pollination for growth

are low ($\omega < 1$), the plant equilibrium decreases continuously towards its

condition without benefits, as the proportion of adults in the pollinator pop-

ulation decreases. But if the benefits are high ($\omega > 1$) the decrease can be

abrupt rather than continuous. For parameters values used, see the appendix.   23
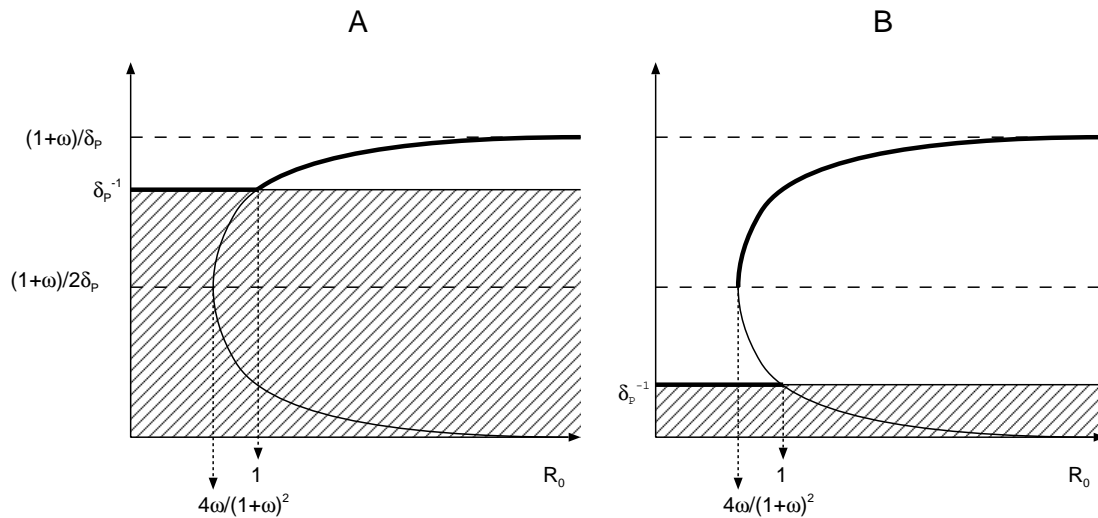
Figures

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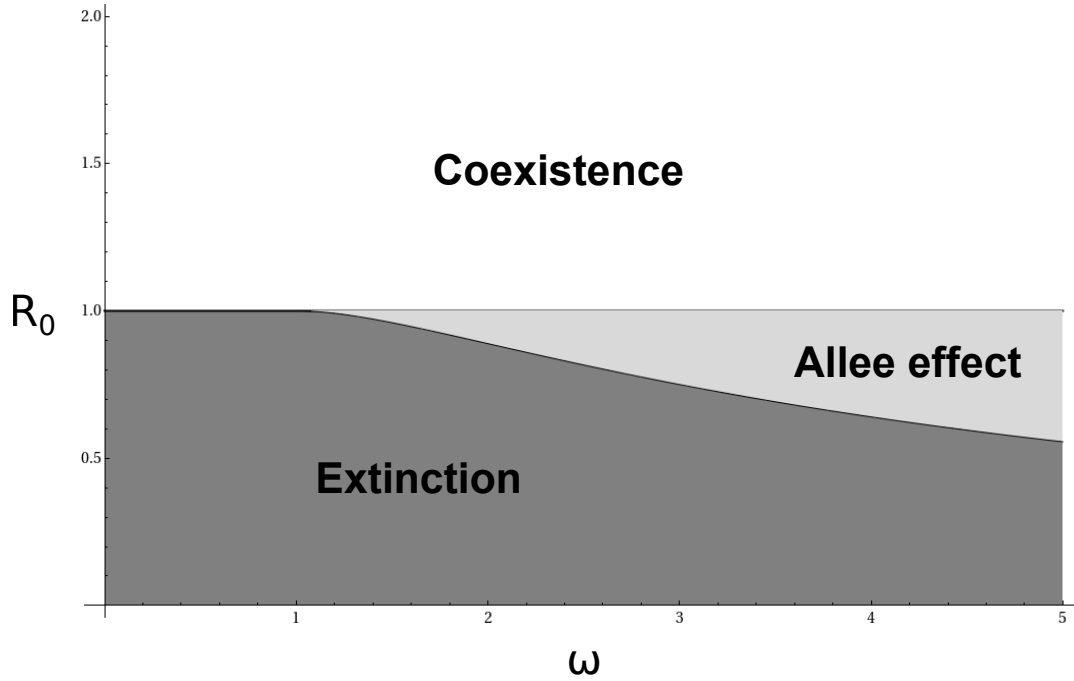
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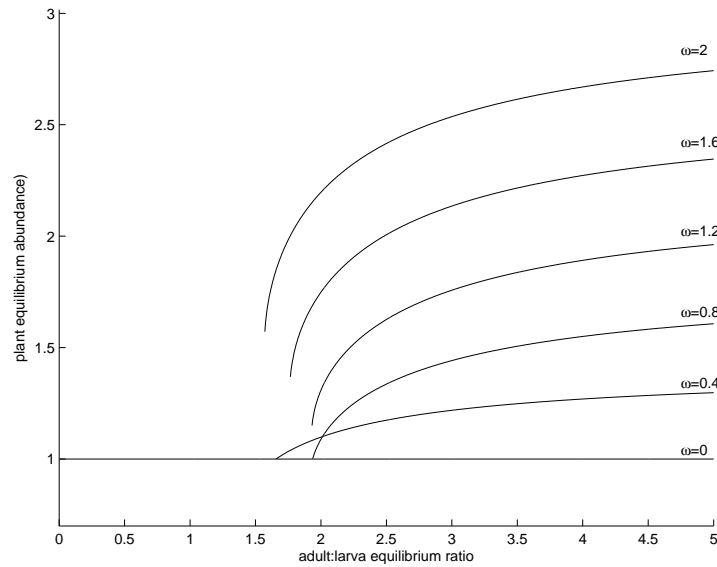
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