



# Shifts in pollinator population structure may jeopardize pollination service



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## AUTHOR HIGHLIGHTS

- A model of plant-pollinator mutualism with population structure is studied.
- The stability of the mutualism is highly sensitive to pollinator population structure.
- The interaction is at risk when external factors (e.g. pesticides) reduce larval development.
- A sudden collapse of pollination service can occur due to changes on pollinator population structure.

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## ABSTRACT

Plant–pollinator interactions are among the best known and ubiquitous plant–animal mutualisms and are crucial for ecosystem functioning and the maintenance of biodiversity. Most pollinators are insects with several life-stages (e.g. egg, larva, pupa, adult) and the mutualistic interaction depends on the pollinator surviving these different life-stages. However, to our knowledge, pollinator population structure has been ignored in most theoretical models of plant–pollinator dynamics, and we lack understanding of the role of different life-stages in determining the stability of the mutualism. Here we therefore develop a simple plant–pollinator model with a facultative plant and an obligate pollinator with stage-structure. Our model predicts a globally stable equilibrium when pollinator demography is dominated by adults and a locally stable equilibrium when the plants are strongly dependent on pollination and pollinator demography is dominated by the larval stage. In the latter case, the mutualism is vulnerable to fluctuations in the pollinator population size or structure caused by external factors (e.g. pesticides) reducing larval development and increasing adult mortality. This may cause a sudden collapse rather than gradual decrease of the mutualism, after which the pollination service cannot be recovered by reducing these detrimental external factors, but must be accompanied by large increases in pollinator populations. This highlights the importance of considering population structure in plant–pollinator interactions.

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## 1. 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,

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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 and 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 and 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 and Rudolf, 2006; Herrera, 1984) and can have multiple indirect effects on their mutualistic partners (i.e. plants) (Adler and Bronstein, 2004).

In predator–prey models with population structure, indirect effects along the trophic chain can produce very different dynamics from unstructured populations (Abrams and 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 and 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 and DeAngelis, 2010). This simple model assumes a more mechanistic plant–pollinator interaction (Soberón and 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.

## 2. 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 modelled 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

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

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

where in the first term in Eq. (1)  $r$  is the intrinsic growth rate and  $\delta_P$  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  $\sigma$  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 and Lawlor, 1984). Nectar increases in proportion to plant biomass with production rate per plant biomass  $\rho$ , and decreases with a first order decay rate  $\delta_N$  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 and Goodell, 2011) or pollinators that feed on different plant species in their larval and adult stages. The equations describing pollinator dynamics are

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

$$\frac{dA}{dt} = \gamma L - \delta_A A \quad (4)$$

where  $\epsilon$  is the conversion efficiency for the transformation of nectar consumed into larvae,  $\gamma$  is the per capita maturation rate and  $\delta_L$  is the per capita larva mortality rate. Adult density increases by maturation of larvae and decreases by adult mortality at per capita rate  $\delta_A$ .

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):

$$f(N) = \alpha N \quad (5)$$

where  $\alpha$  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  $f(N)$  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:

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

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 and Lundberg, 1995; Herrera, 1989). Thus, the pollination benefits for both plants and pollinators do not grow linearly, but in a saturating fashion.

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