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Competition, trait–mediated facilitation, and the structure of plant–pollinator communities

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ABSTRACT

In plant–pollinator communities many pollinators are potential generalists and their preferences for certain plants can change quickly in response to changes in plant and pollinator densities. These changes in preferences affect coexistence within pollinator guilds as well as within plant guilds. Using a mathematical model, we study how adaptations of pollinator preferences influence population dynamics of a two-plant–two-pollinator community interaction module. Adaptation leads to coexistence between generalist and specialist pollinators, and produces complex plant population dynamics, involving alternative stable states and discrete transitions in the plant community. Pollinator adaptation also leads to plant–plant apparent facilitation that is mediated by changes in pollinator preferences. We show that adaptive pollinator behavior reduces niche overlap and leads to coexistence by specialization on different plants. Thus, this article documents how adaptive pollinator preferences for plants change the structure and coexistence of plant–pollinator communities.

The pedigree of honey
Does not concern the bee;
A clover, any time, to him
Is aristocracy.
Poems (1890) – Emily Dickinson

1. Introduction

Many mutualistic interactions feature direct resource-for-resource (e.g., plant–mycorrhizae, lichens), or resource-for-service (e.g., pollination, seed dispersal) exchanges between species, but this fact was not explicitly considered by the first models of mutualism based on the Lotka–Volterra equations (Gause and Witt, 1935; Vandermeer and Boucher, 1978). As a result, positive feedbacks between mutualists predicted infinite population growth. Later models considered negative density dependence at high population densities (Boucher, 1988; Gerla and Mooij, 2014; Hernandez, 1998) that stabilizes population dynamics. Increased awareness about the consumer–resource aspects of mutualisms (Holland and DeAngelis, 2010) provides some mechanistic underpinnings for density dependence (e.g., mutualistic benefits saturate, just like plant growth saturates with nutrients or predator feeding saturates with prey). More recently, differentiation between non-living mutualistic resources (e.g., mineral nutrients, nectar, fruits) and their living providers (e.g., fungi, plant) led to several mechanistic models (Benadi et al., 2012; Revilla, 2015; Valdovinos et al., 2013). These are very relevant for studies of plant–animal mutualisms, like pollination and seed dispersal, for two reasons. First, competition between animals for nectar or fruits can be treated using concepts from consumer–resource theory (Grover, 1997). Second, competition between plants for pollination or seed dispersal can result from plants influencing the preferences of animals, according to optimal foraging theory (Pyke, 2016).

In an earlier work (Revilla and Křivan, 2016) we analyzed coexistence conditions for two plants competing for a single pollinator. If the pollinator is a generalist, plants can facilitate each other by making the pollinator more abundant. Facilitation is an example of an indirect density-mediated interaction (sensu Bolker et al., 2003) between the two plants. However, if pollinators have adaptive preferences, a positive feedback between plant abundance and pollinator preferences predicts exclusion of the rare plant, which gets less pollination as pollinators specialize on the common plant. In other words, when pollinator preferences respond to plant densities, plants will experience competition for pollination services (in addition to competition for other factors such as nutrients, light or space) because an increase in pollination of one plant exerts

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a negative effect on the other plants that gets less pollination. In Revilla and Křivan (2016) we found that plant coexistence depends on the balance between plant facilitation via increasing abundance of the common pollinator, and competition for pollinator preferences, which adapt in response to the relative abundance of plant resources. Pollinator preferences were described by the ideal free distribution (IFD; Fretwell and Lucas, 1969) that predicts pollinator distribution between the two plants in such a way that neither of the two plants provides pollinators with a higher payoff. For a single pollinator, the IFD is also an evolutionarily stable strategy (ESS, Křivan et al., 2008), i.e., once adopted by all individuals no mutant with a different strategy can invade the resident population (Maynard Smith and Price, 1973).

In many real life settings however, plants compete for pollination services provided by several pollinator species, which in turn compete for plant resources. Pollinator preferences for plants respond not only to plant abundances, but also to inter- and intra-specific competition between pollinators. Simulations of large plant–pollinator communities indicate that plant coexistence is promoted when generalist pollinators specialize to reduce competition for resources, i.e., to decrease niche overlap (Valdovinos et al., 2016, 2013). This is the classic competitive exclusion principle which states that n competing species (i.e., pollinators) cannot coexist at a population equilibrium if they are limited by less than n limiting factors (i.e., plants) (Levin, 1970).

In this article we study a mutualistic–competitive interaction module consisting of two plants and two pollinators where pollinators behave as adaptive foragers that maximize their fitness depending on plant resource quality and abundance. This means that depending on plant and pollinator densities, pollinators switch between generalism and specialism. These behavioral changes also change the topology of the interaction network. Thus, we focus on two questions: Under what conditions the two plants and two pollinators can coexist at an equilibrium, and what are the corresponding community network configurations.

To gain insight, we study separately plant population dynamics at fixed pollinator densities, and pollinator population dynamics at fixed plant densities, respectively. In both cases we compare population dynamics for inflexible pollinators with those for adaptive pollinators. Under fixed pollinator preferences (Section 2), stable coexistence of plants, or pollinators, is possible at a unique equilibrium. It is also possible that at this population equilibrium both pollinators are generalists. Both these predictions change when pollinator preferences for plants are adaptive (Section 3). First, when pollinator densities are fixed, plants can coexist at alternative stable states characterized by different interaction topologies given by pollinator strategy. However, there is no plant stable coexistence when both pollinators are generalists. Second, when plant densities are fixed, pollinators can coexist at an equilibrium only if they specialize on different plants (Section 3.3). We show how these conclusions can explain some recent experimental and simulated results, as well as predict the effects of pollinator adaptation in real communities.

2. Population dynamics when pollinator preferences for plants are fixed

Consider two plant populations P1 and P2 interacting with two pollinator populations A1 and A2. Mutualism is mediated by resources R1 and R2 produced by plants P1 and P2, respectively. We assume that pollination is concomitant with pollinator resource consumption. Since resources like nectar or pollen have much faster turnover dynamics (hours, days) than plants and pollinators (weeks, months), we assume they attain a quasi-steady-state at current plant and animal densities (Revilla, 2015). As a result, population dynamics follow the Revilla and Křivan (2016) model for a single pollinator, extended for two pollinators

$$\frac{dP_1}{dt} = \left(\frac{a_1(r_{11}u_1b_{11}A_1 + r_{12}v_1b_{12}A_2)}{w_1 + u_1b_{11}A_1 + v_1b_{12}A_2}\left(1 - \frac{P_1 + c_2P_2}{K_1}\right) - m_1\right)P_1 \tag{1a}$$

$$\frac{dP_2}{dt} = \left(\frac{a_2(r_{21}u_2b_{21}A_1 + r_{22}v_2b_{22}A_2)}{w_2 + u_2b_{21}A_1 + v_2b_{22}A_2}\left(1 - \frac{P_2 + c_1P_1}{K_2}\right) - m_2\right)P_2 \tag{1b}$$

$$\frac{dA_1}{dt} = \left(\frac{a_1e_{11}u_1b_{11}P_1}{w_1+u_1b_{11}A_1+v_1b_{12}A_2} + \frac{a_2e_{21}u_2b_{21}P_2}{w_2+u_2b_{21}A_1+v_2b_{22}A_2} - d_1\right)A_1 \tag{1c}$$

$$\frac{dA_2}{dt} = \left(\frac{a_1e_{12}v_1b_{12}P_1}{w_1+u_1b_{11}A_1+v_1b_{12}A_2} + \frac{a_2e_{22}v_2b_{22}P_2}{w_2+u_2b_{21}A_1+v_2b_{22}A_2} - d_2\right)A_2, \tag{1d}$$

where P_i $(i = 1, 2)$ is plant Pi population density, and A_j $(j = 1, 2)$ is pollinator Aj population density. Here a_i is a plant resource production rate, w_i is its spontaneous decay rate, and b_{ij} is a pollinator specific consumption rate. In the plant equations (1a,1b), pollinator consumption rates translate into seed production rates with efficiency r_{ij}. Plant growth is reduced by intra-specific competition, with carrying capacity K_i, and by inter-specific competition, where c_i is the relative effect of plant i on the other plant. In the absence of pollinators, plants die with per-capita rates m_i, so plants are obligate mutualists. In the pollinator equations (1c,1d), consumption translates into growth with efficiency ratios e_{ij}. Without plants, pollinators die with per-capita rates d_j, so pollinators are obligate mutualists too.

Pollinator A1 (A2) preferences are u_1 (v_1) for plant P1 and $u_2 = 1 - u_1$ $(v_2 = 1 - v_1)$ for plant P2. Preferences can be interpreted as fractions of foraging time that individual pollinators spend on plant P1 or P2, or the proportion of a pollinator population which is visiting P1 or P2 at a given time. Preferences allows us to categorize pollinators as generalists or specialists. For example, if $(u_1, u_2) = (3/4, 1/4)$ and $(v_1, v_2) = (0, 1)$, then A1 is a generalist (biased towards P1) and A2 is a P2 specialist. In this section we assume that pollinator preferences for plants are fixed and we derive conditions for plant stable coexistence that are compared in Section 3 with the case where pollinator preferences are adaptive. Unfortunately, the many variables and parameters of model (1) do not allow us to analyze it at this generality. In order to gain insights, we assume that either plants or pollinators are kept at fixed densities and employing isocline analysis (Case, 2000) we characterize coexistence between plants (1a,1b), or between pollinators (1c,1d).

2.1. Plant coexistence

First, we consider plant-only dynamics. Let us consider a community consisting of a single plant Pi $(i = 1, 2)$ and two pollinators. At fixed pollinator densities A_1 and A_2, the necessary condition for plant Pi to survive is that its pollinator-dependent per-capita birth rate is higher than its mortality rate, i.e.,

$$r_i = \frac{a_i(r_{i1}u_ib_{i1}A_1 + r_{i2}v_ib_{i2}A_2)}{w_i + u_ib_{i1}A_1 + v_ib_{i2}A_2} > m_i, \tag{2}$$

in which case the plant will attain its pollinator-dependent carrying capacity

$$H_i = K_i\left(1 - \frac{m_i}{r_i}\right). \tag{3}$$