Floral advertisement and the competition for pollination services

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ABSTRACT

Flowering plants are a major component of terrestrial ecosystems, and most of them depend on animal pollinators for reproduction. Thus, the mutualism between flowering plants and their pollinators is a keystone ecological relationship in both natural and agricultural ecosystems. Though plant–pollinator interactions have received considerable amount of attention, there are still many unanswered questions. In this paper, we use methods of evolutionary game theory to investigate the co-evolution of floral advertisement and pollinator preferences.

Our results indicate that competition for pollination services among plant species can in some cases lead to specialization of the pollinator population to a single plant species (oligolecty). However, collecting pollen from multiple plants – at least at the population level – is evolutionarily stable under a wider parameter range. Finally, we show that, in the presence of pollinators, plants that optimize their investment in attracting vs. rewarding visiting pollinators outcompete plants that do not.

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1. Introduction

Flowering plants (angiosperms) number in excess of 350,000 species (cf., Cardinal and Danforth, 2013) and dominate many terrestrial ecosystems. Most angiosperm species (78–94%) rely on animal pollinators (Ollerton et al., 2011). Pollinators visit flowers, transporting pollen in the process, because plants have evolved means to attract and reward such activities. The reward is a critical component of non-deceptive biotic pollination because effective pollen transfer depends on the duration of a visit (Jones and Reithel, 2001), which increases with the magnitude of the reward (Chittka et al., 1997; Cresswell, 1999; Howell and Alarcon, 2007).

Moreover, many pollinator species are capable of classifying flower types as unrewarding vs. rewarding, and avoiding the former. Mechanisms for such classification probably include remembering, to some extent, the rewards obtained on previous visits to the same flower type or location (Amaya-Marquez, 2009). On the other hand, the magnitude of the reward is irrelevant for plants that fail to attract pollinator visitors.

Consequently, zoophilous plants have to balance their investment in attracting pollinator visits – *advertisement* vs. the investment in rewarding these visitors. Roughly speaking, plants that under-invest in advertisement will not be visited enough. In

contrast, plants that invest too much in advertisement at the expense of reward get few repeat visits – and the visits that they do get are unproductive in terms of pollen transfer (Chittka et al., 1997; Howell and Alarcon, 2007; Heil, 2011).

Let us define floral advertisement as any attribute of a flowering plant that increases the probability of a pollinator's visit (Fenster et al., 2006; Raguso et al., 2007). Pollinators can be affected by many types of floral attributes e.g., color schemes (Wilbert et al., 1997; Wesselingh and Arnold, 2000; Johnson and Midgley, 2001), floral scents (Knudsen et al., 2001; Raguso, 2008), flower or inflorescence shapes (Möller and Sorci, 1998; Wignall et al., 2006; Whitney and Glover, 2007) and size (Spaethe et al., 2001; Davis et al., 2008). In this paper we focus on plants' relative investment in *quantitative* signals – such as the intensity of scent/coloration or flower/inflorescence size.

Previously (Fishman and Hadany, 2013), we investigated the effects of plants' *relative investment in advertisement* (RIA) on plant-pollinator interactions. In particular, we have shown that the allocation of resources between advertisement and pollinators' reward can be optimized. Moreover, such optima are *evolutionarily attractive* in the sense that the plants' RIA evolves to these optima through a sequence of small effect variation/selection steps.

However, these results were derived in the context of pollinators' exclusive interactions with a single plant species. Here we use a complementary approach of modeling floral RIA evolution in the context of the competition for pollination services among plant species. That is, we do not restrict the modeled

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pollinators to foraging on single plant species. This approach allows us to obtain a more realistic picture of pollinator preferences and plant species' competition.

This paper is organized as follows. In Section 1, we formulate an evolutionary game that addresses competition among plant strategies that differ in their RIA values in the context of pollinator strategies that are not restricted to foraging on modeled plants. The technical details of the evolutionarily stability analysis are given in Appendix A. In Section 2, we present and review the results. Some of the alternatives to the formulations in the main model are presented and analyzed in the Appendix B and Appendix C. Finally, some of the necessary background for the paper – the results of our previous work, is reviewed in the online supplement.

The central aspect of the current paper is that some of the modeled pollinators can choose to forage on plants other than the modeled ones. Thus, our results can be summarized in terms of the relative magnitude of the benefits available to pollinators that "switch allegiance". It turns out that these benefits fall into three quantitative classes – each associated with a unique (and globally attractive) evolutionarily stable solution.

(i) When the benefits are small, all pollinators forage on modeled plants – among which plants that optimize allocation of resources between attracting and rewarding visiting pollinators outcompete plants that do not.

(ii) For intermediate benefits, only a fraction of pollinators forage on modeled plants. However, plants with optimal allocation of resources still outcompete the rest.

(iii) When the benefits are large, all pollinators "switch allegiance". In this case the pertinent plant strategies become interchangeable. That is, we have a continuum – rather than a point – evolutionarily stable solution (Cressman, 1992).

2. The model

Let us define plants' relative investment in advertisement as a fraction of a total investment in cross-pollination assurance. That is, RID is given by

$$\xi = \frac{I_T - I_F}{I_T}. \tag{1a}$$

Here $I_T > 0$ is the plant's total investment in cross pollination, whereas $0 < I_F < I_T$ represents the investment in food reward for visiting pollinators.

It can be shown (Fishman and Hadany, 2010) that both the degree of cross-fertilization achieved by plants and the quantity of food collected – and therefore, survival and recruitment of new pollinator cohorts – can be productively approximated by the familiar Beddington–DeAngelis function (Beddington, 1975; Deangelis et al., 1975). That is, for uniform populations of flowers and their pollinators, the benefits to both mutualists are related to RIA via the following function:

$$\Phi(\xi) = \frac{\alpha(\xi)N}{1 + \alpha(\xi) + \alpha(\xi)b}. \tag{1b}$$

Here $\alpha(\xi)$ represents the functional relation between RIA and pollinators' "affinity" to modeled flowers – see Fishman and Hadany (2010) for details, whereas $b > 0$ is the coefficient for interference competition among pollinators. Finally, $N > 0$ is pollinators' population density. It is easy to see that to maximize $\Phi(\xi)$, plants have to maximize $\alpha(\xi)$.

In the current paper, we define $\alpha(\xi)$ in the most general terms possible. That is, we identify the minimal set of attributes that such a function must have and analyze our model(s) in these terms.

For convenience in subsequent analysis, let us rewrite $\alpha(\xi) = a\theta(\xi)$ where a is a positive constant (incorporating such factors as total investment in cross-pollination as well as the mutualists' population densities, etc . . .), whereas $\theta : [0,1] \mapsto [0,1]$ is a function possessing the following attributes.

(Q1) Since $\theta(\cdot)$ describes biological phenomena, we shall assume that it is "well-behaved" in a sense of being – at least – twice continuously differentiable on the unit interval. Formally, $\theta \in C^2([0,1])$. We shall further assume that pollinators' are sensitive to the relative, rather than absolute, variation in RIA i.e., $\theta''(\xi) < 0$.

(Q2) As discussed above, plants that do not invest in advertisement will not be visited. Whereas, plants that invest only in advertisement will not get repeat visits – and the visits that they do get will be unproductive in terms of pollen transfer (Chittka et al., 1997; Howell and Alarcon, 2007; Heil, 2011). Formally, $\theta(0) = \theta(1) = 0$. Finally, it is reasonable to assume that plants with RIA values between these two extremes receive some productive visits i.e., $\theta(\xi) > 0$ for $0 < \xi < 1$.

(Q3) An immediate consequence of (Q1) and (Q2) is that there exists unique $0 < \xi_0 < 1$ such that $\theta(\xi_0) = \max\{\theta(\xi) | 0 \leq \xi \leq 1\} > 0$. And therefore, Eq. (1b), ξ_0 maximizes the plant payoff, $\Phi(\xi)$.

Some discussion of the possible forms of $\theta(\xi)$ is given in the online supplement. Accordingly, we define two plant strategies

$\mathbf{F_O}$ plants whose relative investment in advertisement is optimal.

$\mathbf{F_S}$ plants whose relative investment in advertisement is suboptimal i.e., $\xi_S \neq \xi_0$. (Note: in the present context it does not matter whether $0 < \xi_S < \xi_0$ or $\xi_0 < \xi_S < 1$. Since ξ_0 is the maximum, in either case $\alpha(\xi_S) < \alpha(\xi_0)$)

Let the frequency of the $\mathbf{F_O}$ strategists in the population be given by $0 \leq x \leq 1$.

There are two logical possibilities for the relevant pollinator strategies: pollinators cannot discriminate between $\mathbf{F_O}$ and $\mathbf{F_S}$ plants except by direct comparison; pollinators can consistently select the optimal plants.

Here, we assume that pollinators do not "consciously" discriminate between $\mathbf{F_O}$ and $\mathbf{F_S}$ plants. In Appendix B, we show that this assumption does not affect the principal properties of the model. Accordingly, we postulate two pollinator strategies:

$\mathbf{P_V}$ = pollinators that forage on both types indiscriminately.

$\mathbf{P_A}$ = pollinators that avoid both $\mathbf{F_O}$ and $\mathbf{F_S}$ plants – foraging elsewhere.

Let us define the frequency of $\mathbf{P_V}$ strategists by $0 \leq y \leq 1$.

Using the methods defined in our previous work (Fishman and Hadany, 2010, 2013), see the online supplement for details, we obtain the following payoff matrixes for the interactions between plants and their pollinators.

$$\begin{array}{c} \\ \mathbf{F_O} \\ \mathbf{F_S} \end{array} \begin{pmatrix} \mathbf{P_V} & \mathbf{P_A} \\ \dfrac{\kappa_F a\theta(\xi_O)N}{\Delta(x) + a\theta(\xi_O)by} & 0 \\ \dfrac{\kappa_F a\theta(\xi_S)N}{\Delta(x) + a\theta(\xi_S)by} & 0 \end{pmatrix}$$

and

$$\begin{array}{c} \\ \mathbf{P_V} \\ \mathbf{P_A} \end{array} \begin{pmatrix} \mathbf{F_O} & \mathbf{F_S} \\ \dfrac{\kappa_P a\theta(\xi_O)N}{\Delta(x) + a\theta(\xi_O)by} & \dfrac{\kappa_P a\theta(\xi_S)N}{\Delta(x) + a\theta(\xi_S)by} \\ C & C \end{pmatrix} \tag{2a}$$

Here the payoffs are those of the row players, and

$$\Delta(x) = 1 + a\theta(\xi_O)x + a\theta(\xi_S)(1 - x). \tag{2b}$$

Whereas κ_F and κ_P are the terms that translate plant/pollinator interactions into their respective fitness benefits. Finally, we