



# Invasibility of nectar robbers in pollination-mutualisms



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## ABSTRACT

Mutualisms play a crucial role in all natural communities. In pollination-mutualisms, a pollinator consumes nectar, pollen and other resources provided by a plant, while it transports pollen for the host plant and promotes reproduction of the plant. Nectar robbers are floral visitors that remove nectar without contacting the anthers and thus do not supply pollination service. The robbers are critical for the maintenance of mutualists. We have still few details on the maintenance and stability of plant-pollinator-exploiter systems. In this paper, based on analysis of a pollinator-plant-robber model, we demonstrate basic properties in robbers' invasibility and essential mechanisms by which nectar robbers can invade the pollinator-plant system and coexist with pollinators and plants. Moreover, some situations are exhibited in which the robbers' invasion can lead to extinction of pollination-mutualisms, which eventually leads to extinction of the robbers themselves.

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## 1. Introduction

Pollination mutualisms between flowering plants and their pollinators are important ecological interactions for the maintenance of both natural and agricultural communities [15]. In a plant-pollinator interaction, plants provide nectar, pollen and other resources for pollinators. The pollinators collect the food and contact the anthers and/or stigma of flowers and then transport pollen in their travel, which leads to reproduction of most flowering plants [25]. Nectar robbers are floral visitors who remove nectar via holes bitten on flowers without touching the anthers and stigma. Thus, the robbers consume resources from plants without providing pollination service in return, and are called cheaters in mutualisms [1,2,6]. Mutualism theory demonstrates that if there is no serious punishment or targeted deterrence of such cheaters, pollination mutualisms cannot persist [21]. However, although nectar robbing is ubiquitous and often costly in pollinator-plant systems, pollination seems to be a stable interaction in most natural communities [14]. Thus Irwin et al. [11] raised a challenging question (page 287, the 8th question) that why pollination mutualisms can persist in the widespread occurrence of nectar robbing.

Persistence of pollination-mutualisms in the presence of a third-species exploiter has been modeled in previous papers. Jang [13] considered a herbivore-pollinator-plant system in which a herbivore is the exploiter. The herbivore consumes plants and has a deleterious effect on pollinator visit rate. The pollinator-plant interaction is assumed to be facultative-obligate and is described by a Holling II functional response. Dynamics of the herbivore-pollinator-plant model demonstrated that the deleterious effect of herbivore lowers the pollinator population for the three species coexisting equilibrium, but has no effect on dynamics of the system.

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Ferrière et al. [5] considered co-evolution in obligate mutualisms between a host and its mutualist, where there are mutants in each species and the trait is the quantity of reward. Asymmetric competition for partners in favor of better mutualists means that an individual that provides more commodities is likely to obtain more commodities in return. Ferrière et al. [5] showed that the asymmetric competition is crucial to persistence of mutualisms: if it is too weak/strong, the obligate mutualisms go to extinction; if it is intermediate, the host and mutualist will co-evolve towards an evolutionary stable state (ESS). When there exists exploiter, Ferrière et al. [6] presented a host–mutualist–exploiter model, which is an extension of that by Ferrière et al. [5]. Based on analysis of the model, they demonstrated that when asymmetric competition in the host–mutualist mutualisms is strong, the presence of the exploiter can prevent evolutionary suicide of the mutualisms and drive the host–mutualist co-evolution towards a new ESS, in which the three species coexist.

Fishman and Hadany [7] considered the pollination of social bees and bumblebees, where the pollinators in pollinating the plants leave a mark on flowers that repel other pollinators. They showed that the plant–pollinator interaction can be approximated by a Beddington–DeAngelis functional response. Qualitative analysis and numerical simulations demonstrated that when the pollinators' efficiency in translating plant–pollinator interaction into fitness is large and initial densities of the two species are not so small, the plants and pollinators could persist at steady states. Wang et al. [24] presented a three-species model in which the pollination–mutualisms are uni-directional and a nectar robber is the third-species exploiter. The uni-directional mutualisms mean that a pollinator has both positive and negative effects on its host plant since its larvae eat seeds of the plant, while the plant has a positive effect on the pollinator. Dynamics of the model exhibited that the negative effect plays a role in invasion of robbers: when environmental conditions do not favor larval survival, the negative effect is small and the robbers' invasion will succeed. Otherwise, the robbers go to extinction. For other relevant work, we refer to Roubik [20], Inouye [12], Thompson [23], Sachs and Simms [21] and Georgelin and Loeuille [9]. While evolutionary persistence of host–mutualist systems in the presence of exploiters is demonstrated in previous works, ecological mechanisms by which nectar robbers can invade pollinator–plant systems, have not been shown.

Motivated by the work of Jang [13] and Fishman and Hadany [7], we form a three-species model characterizing interactions among pollinators, plants and nectar robbers. The model focuses on invasibility of robbers in pollination–mutualisms, where the pollinator–plant interaction is facultative–obligate and its functional response is of a Beddington–DeAngelis form. By global dynamics of the model, we demonstrate mechanisms by which nectar robbers can invade pollination–mutualisms and coexist with pollinators. We also exhibit that the invasion can lead to extinction of pollination–mutualisms, which consequently leads to extinction of the robbers themselves. Population densities of the species are shown to be crucial to the robbers' invasion in certain parameter ranges.

The manuscript is organized as follows. The pollinator–plant–robber model is characterized in Section 2. Section 3 exhibits its stability of the pollinator–plant subsystem. Section 4 shows dynamics of the pollinator–plant–robber model. Section 5 exhibits discussions.

## 2. A pollinator–plant–robber model

In this section, we describe a model characterizing pollinator–plant–robber systems we are concerned with, and examine boundedness of solutions of the model.

In the pollinator–plant system, pollinators transport pollen for plants and promote their reproduction. The plants supply nectar, pollen and other resources to the pollinators. Thus the relationship between them is mutualistic. Let  $u_1$  and  $u_2$  denote population densities of the pollinators and plants, respectively. As shown by Fishman and Hadany [7], the analytical expression for population-level plant–pollinator interactions can be approximated by a Beddington–DeAngelis functional response, where the interference among mutual pollinators is considered:

$$\frac{\alpha u_1 u_2}{1 + \alpha u_2 + \alpha \beta u_1},$$

where  $\alpha$  is the effective equilibrium constant for un-depleted flower/pollinator interactions, which combines travel and unloading times with individual-level pollinator–plant interactions.  $\beta$  represents the intensity of exploitation competition among pollinators [18].

We consider the situation in which pollinators can exploit other species for food [13]. Let  $r_1$  denote the intrinsic growth rate of the pollinators and  $d_1$  the intensity of intraspecific competition. Then the pollinators' growth can be depicted by

$$\frac{du_1}{dt} = u_1 \left( r_1 - d_1 u_1 + \frac{\mu \alpha u_2}{1 + \alpha u_2 + \alpha \beta u_1} \right),$$

where  $\mu$  represents the pollinators' efficiency in translating pollinator–plant interactions into fitness [7]. Let  $v$  be the corresponding value for the plants. Then the growth of plants can be depicted by

$$\frac{du_2}{dt} = u_2 \left( -d_2 + \frac{v \alpha u_1}{1 + \alpha u_2 + \alpha \beta u_1} \right),$$

where  $d_2$  is the mortality rate of plants (Lundberg and Ingvarsson [17]).

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