Mathematical Biology

Dynamics of plant–pollinator–robber systems

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Abstract Plant–pollinator–robber systems are considered, where the plants and pollinators are mutualists, the plants and nectar robbers are in a parasitic relation, and the pollinators and nectar robbers consume a common limiting resource without interfering competition. My aim is to show a mechanism by which pollination–mutualism could persist when there exist nectar robbers. Through the dynamics of a plant–pollinator–robber model, it is shown that (i) when the plants alone (i.e., without pollination–mutualism) cannot provide sufficient resources for the robbers' survival but pollination–mutualism can persist in the plant–pollinator system, the pollination–mutualism may lead to invasion of the robbers, while the pollinators will not be driven into extinction by the robbers' invasion. (ii) When the plants alone cannot support the robbers' survival but persistence of pollination–mutualism in the plant–pollinator system is density-dependent, the pollinators and robbers could coexist if the robbers' efficiency in translating the plant–robber interactions into fitness is intermediate and the initial densities of the three species are in an appropriate region. (iii) When the plants alone can support the robbers' survival, the pollinators will not be driven into extinction by the robbers if their efficiency in translating the plant–pollinator interactions into fitness is relatively larger than that of the robbers. The analysis leads to an explanation for the persistence of pollination–mutualism in the presence of nectar robbers in real situations.

Keywords Acyclicity · Stability · Persistence · Mutualism · Invasion

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1 Introduction

Floral visitors attracted to flowers consist of pollinators and nectar robbers. Pollinators provide pollen transport service, while they consume nectar, pollen and other goods. Nectar robbers take nectar away through holes bitten in flowers, without providing pollination service. The robbers have been found in nature for hundreds of years. In 1793, Sprengel recorded that bumble bees perforate nectar spurs (Sprengel 1793). In 1859 and 1876, Darwin found that bumble bees steal nectar in clover flowers (Darwin 1859, 1876). Later researchers have shown that almost all plants, whose flowers are tubular or have nectar spurs, have been robbed. Thus, nectar robbing is a widespread and costly phenomenon in the growth of flowering plants. The plants may be able to resist nectar robbing through morphological and chemical traits, but many of the traits lead to deterrence to both the pollinators and robbers (McCall and Irwin 2006). While pollinators are often regarded as mutualists with plants, the nectar robbers are also called cheaters due to their adaptation in lowering robbing impact and frequency (Wootton 1994; Werner and Peacor 2003). Mutualism theory exhibits that cooperation cannot persist when there is no effective deterrence or serious punishment on cheaters. However in real situations, the plant–pollinator mutualism persists stably. Hence, an interesting question is raised by Irwin et al. (2010, page 287, the 8th question) asking why the plant–pollinator mutualism can persist when there exist nectar robbers (cheaters).

Dynamic systems theory may provide a way to answer the question. Indeed, there has been a growing literature on the study of plant–pollinator–herbivore systems (Freedman and Waltman 1984; Liou and Cheng 1988; Waltman 1991; Hsu et al. 2001; Wang et al. 2011, etc.). Jang (2002) characterized the interactions between plants and pollinators with the Holling II functional response. Based on her model, an interaction among herbivores, plants and pollinators is proposed. Strong analysis on global dynamics of the three-species model shows that an increasing pollination visitation rate due to the presence of herbivores can promote persistence of the system. In a recent study, Oña and Lachmann (2011) described plant–pollination systems by mutualism models with various functional responses. Analysis on the model with a linear functional response shows interesting thresholds of the ants' aggressiveness level, above which the pollinators will be driven into extinction. Fishman and Hadany (2010) concluded that an analytical expression for population-level plant–pollinator interactions can be approximated by the Beddington–DeAngelis functional response, where an exploitation competition among pollinators is considered and the interactions between the plants and pollinators are obligate. Qualitative analysis and numerical simulations demonstrated that when the pollinators' efficiency in translating plant–pollinator interactions into fitness is large and the initial population densities of the two species are not too small, the plants and pollinators could persist at a steady state. As far as we know, plant–pollinator–robber systems have not been analyzed in detail. Thus, formulating models and studying features of these systems is necessary.

In this paper, we consider biological systems consisting of plants, pollinators and nectar robbers, in which the interactions between the plants and pollinators are mutualistic with the Beddington–DeAngelis functional response, and the interactions between the plants and robbers are parasitic with the Holling II functional response.

Global dynamics of a plant–pollinator model with the Beddington–DeAngelis functional response are demonstrated. Based on the dynamics of a plant–pollinator–robber model, we show that (i) when the plants alone cannot provide sufficient resources for the robbers' survival but pollination–mutualism can persist in the plant–pollinator system, the pollination–mutualism promotes reproduction of the plants and may lead to invasion of the robbers, while the pollinators will not be driven into extinction by the robbers' invasion. (ii) When the plants alone cannot support the robbers' survival but persistence of pollination–mutualism in the plant–pollinator system is density-dependent, the pollinators and robbers could coexist if the robbers' efficiency is intermediate and the initial densities of the three species are in an appropriate region. Otherwise, if the efficiency is too small, the robbers will go to extinction while the plants and pollinators coexist; if the efficiency is too large and/or the initial densities are beyond a certain level, both the pollinators and robbers will go to extinction while the plants approach their carrying capacity. (iii) When the plants alone can support the robbers' survival, the robbers are always persistent in the plant–pollinator–robber system. The pollinators will not be driven into extinction by the robbers if their efficiency in translating plant–pollinator interactions into fitness is relatively larger than that of the robbers. Otherwise, the pollinators will go extinct. Numerical simulations show that when parameters (factors) in the system vary, interaction outcomes of the three species could transition among extinction of the robbers, persistence of the three species at a steady state, persistence of the three species in periodic oscillations, and extinction of the pollinators. The analysis provides an explanation for the persistence of pollinators and nectar robbers in real situations.

The paper is organized as follows. The plant–pollinator–robber model is characterized in Sect. 2. Section 3 exhibits dynamics of the subsystems. Section 4 shows persistence of the plant–pollinator–robber system. Discussions are in Sect. 5.

2 A plant–pollinator–robber model

In this section, we describe the plant–pollinator–robber system we are concerned with and show boundedness of solutions of the model.

Since the plants provide resources for the pollinators and the pollinators supply pollination service for the plants, the relationship between them is cooperative. Let x_1 and x_2 represent population densities of the plants and pollinators, respectively. Then the plant–pollinator interaction can be approximated by the Beddington–DeAngelis functional response (Fishman and Hadany 2010)

$$\frac{\alpha x_1 x_2}{1 + \alpha x_1 + \alpha \beta x_2}.$$

Here, the parameter α is the effective equilibrium value for un-depleted plant–pollinator interaction, which combines traveling and unloading times spent in central place pollinator foraging, with individual-level plant–pollinator interactions (Fishman and Hadany 2010). β denotes the intensity of exploitation competition among pollinators (Pianka 1974).

Let r_1 represent the intrinsic growth rate of the plants and d_1 their self-incompatible degree. We obtain the equation for the growth of the plants as given by

$$\frac{dx_1}{dt} = x_1 \left(r_1 - d_1 x_1 + \frac{\eta \alpha x_2}{1 + \alpha x_1 + \alpha \beta x_2} \right)$$

where the parameter η denotes the plants' efficiency in translating plant–pollinator interactions into fitness (see Beddington 1975; DeAngelis et al. 1975; Fishman and Hadany 2010 for details). Let μ denote the corresponding value for the pollinators and let r_2 be their death rate. Then we obtain the equation for the the growth of the pollinators as given by

$$\frac{dx_2}{dt} = x_2 \left(-r_2 + \frac{\mu \alpha x_1}{1 + \alpha x_1 + \alpha \beta x_2} \right).$$

For simplicity, we rewrite the plant–pollinator model as

$$\begin{aligned}
\frac{dx_1}{dt} &= x_1 \left(r_1 - d_1 x_1 + \frac{a_{12} x_2}{1 + \alpha x_1 + \beta x_2} \right) \\
\frac{dx_2}{dt} &= x_2 \left(-r_2 + \frac{a_{21} x_1}{1 + \alpha x_1 + \beta x_2} \right)
\end{aligned} \tag{2.1}$$

where $a_{12}(=\eta \alpha)$ can be regarded as the plants' efficiency when α is fixed in our discussion, and $a_{21}(=\mu \alpha)$ is the corresponding value for the pollinators.

Let x_3 represent the population density of the robbers. Since nectar robbers are predators to plants, the plant–robber system can be depicted by the predator–prey model with the Holling II functional response

$$\begin{aligned}
\frac{dx_1}{dt} &= x_1 \left(r_1 - d_1 x_1 - \frac{a_{13} x_3}{c + x_1} \right) \\
\frac{dx_3}{dt} &= x_3 \left(-r_3 + \frac{a_{31} x_1}{c + x_1} \right)
\end{aligned} \tag{2.2}$$

where the parameter a_{13} represents the saturation level in the Holling II functional response and c denotes the half-saturation constant, while a_{31} can be regarded as the robber' efficiency in translating plant–robber interactions into fitness. r_3 is the robbers' per-capita death rate.

Since we assume that there is no interfering competition between the pollinators and robbers, the plant–pollinator–robber system can be depicted by

$$\begin{aligned}
\frac{dx_1}{dt} &= x_1 \left(r_1 - d_1 x_1 + \frac{a_{12} x_2}{1 + \alpha x_1 + \beta x_2} - \frac{a_{13} x_3}{c + x_1} \right) \\
\frac{dx_2}{dt} &= x_2 \left(-r_2 + \frac{a_{21} x_1}{1 + \alpha x_1 + \beta x_2} \right) \\
\frac{dx_3}{dt} &= x_3 \left(-r_3 + \frac{a_{31} x_1}{c + x_1} \right).
\end{aligned} \tag{2.3}$$

We consider solutions of (2.3) under the initial value conditions

$$x_1(0) > 0, \quad x_2(0) > 0, \quad x_3(0) > 0. \tag{2.4}$$

First of all, the solutions to the initial value problem (2.3)–(2.4) are nonnegative. The main notion of persistence theory is permanence. Consider a dynamical system for n interacting biological species

$$\frac{dx_i}{dt} = x_i f_i(x_1, x_2, \ldots, x_n), \quad i = 1, 2, \ldots, n, \tag{2.5}$$

where x_i is the density of the ith species. Let $(x_1(t), x_2(t), \ldots, x_n(t))$ be the solution of (2.5) with positive initial values. System (2.5) is said to be *weakly persistent* if

$$\limsup_{t \to \infty} x_i(t) > 0, \quad i = 1, 2, \ldots, n,$$

persistent if

$$\liminf_{t \to \infty} x_i(t) > 0, \quad i = 1, 2, \ldots, n,$$

uniformly persistent if there is a constant $\delta_0 > 0$ such that

$$\liminf_{t \to \infty} x_i(t) \geq \delta_0, \quad i = 1, 2, \ldots, n,$$

and *permanent* if there are constants $\delta_0 > 0$ and $M_0 > 0$ such that

$$0 < \delta_0 \leq \liminf_{t \to \infty} x_i(t) \leq \limsup_{t \to \infty} x_i(t) \leq M_0, \quad i = 1, 2, \ldots, n.$$

Obviously, a permanent system is uniformly persistent and a uniformly persistent system is persistent, while a dissipative and uniformly persistent system is permanent. Moreover, positive solutions of a permanent system are not only uniformly bounded, but eventually uniformly bounded away from the boundary. For further discussion about persistence theory, we refer to Freedman and Moson (1990).

The following results show the boundedness of solutions of system (2.3).

Proposition 2.1 *System* (2.3) *is dissipative.*

Proof It follows from the first equation of (2.3) that

$$\frac{dx_1}{dt} \leq x_1 \left(r_1 + \frac{a_{12}}{\beta} - d_1 x_1 \right)$$

thus the comparison principle (Cosner 1996) implies that

$$\limsup_{t \to \infty} x_1(t) \leq \frac{\beta r_1 + a_{12}}{\beta d_1}.$$

Then for $\delta > 0$ small, we have $x_1(t) \leq \delta + (\beta r_1 + a_{12})/(\beta d_1)$ when t is sufficiently large. Let $r_0 = min\{r_2, r_3\}$. By the three equations in (2.3), we have

$$
\begin{aligned}
\frac{d}{dt}\left(x_1+\frac{a_{12}}{a_{21}}x_2+\frac{a_{13}}{a_{31}}x_3\right) &= x_1(r_1-d_1x_1)+\frac{2a_{12}x_1x_2}{1+\alpha x_1+\beta x_2}-\frac{a_{12}}{a_{21}}r_2x_2-\frac{a_{13}}{a_{31}}r_3x_3 \\
&< x_1\left(r_1+\frac{2a_{12}}{\beta}\right)-r_0\left(\frac{a_{12}}{a_{21}}x_2+\frac{a_{13}}{a_{31}}x_3\right) \\
&\leq \left(\frac{\beta r_1+a_{12}}{\beta d_1}+\delta\right)\left(r_0+r_1+\frac{2a_{12}}{\beta}\right) \\
&\quad -r_0\left(x_1+\frac{a_{12}}{a_{21}}x_2+\frac{a_{13}}{a_{31}}x_3\right).
\end{aligned}
$$

Citing the comparison theorem a second time, we have

$$
\limsup_{t\to\infty}\left(x_1+\frac{a_{12}}{a_{21}}x_2+\frac{a_{13}}{a_{31}}x_3\right)\leq\frac{1}{r_0}\left(\frac{\beta r_1+a_{12}}{\beta d_1}+\delta\right)\left(r_0+r_1+\frac{2a_{12}}{\beta}\right)
$$

which implies that system (2.3) is dissipative.   □

It follows from the second equation of (2.3) that $dx_2/dt \leq 0$ if $r_2 \geq a_{21}/\alpha$. By the Liapunov Theorem (Hofbauer and Sigmund 1998), we obtain $\lim_{t\to\infty} x_2(t) = 0$. Similarly, we obtain $\lim_{t\to\infty} x_3(t) = 0$ if $r_3 \geq a_{31}$. Since we focus on permanence of system (2.3) in this paper, we assume $a_{21} > r_2\alpha$, $a_{31} > r_3$.

3 Subsystems

In this section we examine the dynamics of subsystems of (2.3). When there are no plants in the system, we can see that both the pollinators and robbers will go to extinction. Thus, two two-species subsystems need to be considered.

3.1 Subsystem I: the plant–pollinator system

First we consider the plant–pollinator system (2.1). The boundedness of solutions of (2.1) can be obtained directly from Proposition 2.1, as shown in the following result.

Proposition 3.1 *System* (2.1) *is dissipative.*

Existence of periodic orbits can be excluded by the Bendixson–Dulac Theorem (Hofbauer and Sigmund 1998). Indeed, let $u(x_1, x_2)$ and $v(x_1, x_2)$ denote the functions on the right-hand sides of (2.1), respectively. Let $\vartheta(x_1, x_2) = 1/(x_1x_2)$, then

$$\frac{\partial(\vartheta u)}{\partial x_1} + \frac{\partial(\vartheta v)}{\partial x_2} = -\frac{d_1}{x_2} - \frac{\alpha a_{12} + \beta a_{21}}{(1 + \alpha x_1 + \beta x_2)^2} < 0.$$

Thus, we conclude the following result.

Proposition 3.2 *There is no periodic orbit of* (2.1) *in* R_+^2.

Stability of equilibria is considered as follows. Denote $f(x_1, x_2) = 1/(1 + \alpha x_1 + \beta x_2)$, then the Jacobian matrix $J(x_1, x_2)$ of (2.1) is

$$\begin{pmatrix} r_1 - 2d_1 x_1 + a_{12} x_2 f(1 - \alpha x_1 f) & a_{12} x_1 (1 + \alpha x_1) f^2 \\ a_{21} x_2 (1 + \beta x_2) f^2 & -r_2 + a_{21} x_1 f(1 - \beta x_2 f) \end{pmatrix}. \quad (3.1)$$

There are two equilibria on the axes, namely $O(0, 0)$ and $E_1(r_1/d_1, 0)$. O is a saddle point with eigenvalues r_1 and $-r_2$, while E_1 has eigenvalues $-r_1$, $-r_2 + a_{21} r_1/(d_1 + \alpha r_1)$.

The positive equilibrium is derived as follows. By (2.1), a straightforward computation shows that there are at most two positive equilibria $E_{12}^-(x_1^-, x_2^-)$ and $E_{12}(x_1^+, x_2^+)$, which can be expressed as follows when they exist

$$x_1^\pm = \frac{r_2(1 + \beta x_2^\pm)}{a_{21} - \alpha r_2} > \frac{r_1}{d_1}, \quad x_2^\pm = \frac{-B \pm \sqrt{\Delta}}{2A} \quad (3.2)$$

where

$$A = \frac{d_1 r_2 \beta^2}{(a_{21} - \alpha r_2)^2}, \quad B = -\frac{a_{12}}{a_{21}} - \frac{\beta r_1}{a_{21} - \alpha r_2} + \frac{2\beta d_1 r_2}{(a_{21} - \alpha r_2)^2},$$

$$C = -\frac{r_1}{a_{21} - \alpha r_2} + \frac{d_1 r_2}{(a_{21} - \alpha r_2)^2}, \quad \Delta = B^2 - 4AC.$$

For all we know, dynamical behavior of (2.1) has not been analyzed completely. The following result shows global dynamics of the system.

Theorem 3.3   (i) (Wang et al. 2012) *If* $a_{21} > r_2(d_1 + \alpha r_1)/r_1$, *then there is a unique positive equilibrium* $E_{12}(x_1^+, x_2^+)$ *in* (2.1) *and solutions of* (2.1) *with positive initial values converge to* E_{12}.
   (ii) *Assume* $a_{21} < r_2(d_1 + \alpha r_1)/r_1$. *If* $B \geq 0$ *or* $\Delta < 0$, *then solutions of* (2.1) *with* $x_1(0) > 0$ *converge to* $E_1(r_1/d_1, 0)$.
  (iii) *If* $a_{21} < r_2(d_1 + \alpha r_1)/r_1$, $B < 0$ *and* $\Delta > 0$, *then* E_1 *is locally asymptotically stable and there are two positive equilibria* $E_{12}^-(x_1^-, x_2^-)$ *and* $E_{12}(x_1^+, x_2^+)$, *as shown in Fig.* 1. E_{12}^- *is a saddle point while* E_{12} *is locally asymptotically stable. The separatrices of* E_{12}^- *subdivide the interior of* (x_1, x_2)-*plane into two regions: the region below the separatrices is the basin of attraction of* E_1, *while the region above them is the basin of attraction of* E_{12}.
  (iv) *If* $a_{21} < r_2(d_1 + \alpha r_1)/r_1$, $B < 0$ *and* $\Delta = 0$, *then* E_1 *is locally asymptotically stable and there is a unique positive equilibrium* E_{12}, *which is a saddle-node point. The separatrices of* E_{12} *subdivide the interior of* (x_1, x_2)-*plane into two*
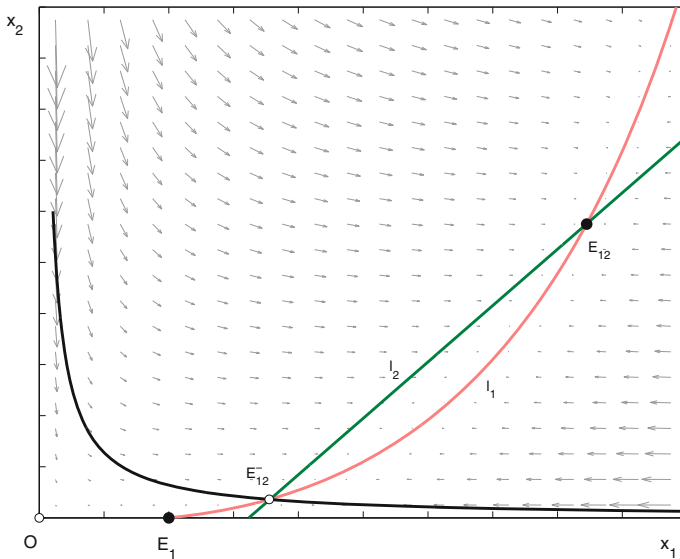
Fig. 1 Phase-plane diagram for the dynamics of (2.1) when there are two positive equilibria E_{12}^- and E_{12}. Stable and unstable equilibria are identified by *solid* and *open circles*, respectively. Vector fields are shown by *gray arrows*. The separatrices (the *black line*) of E_{12}^- subdivide the plane into two regions. The region below them is the basin of attraction of E_1 while the region above them is that of E_{12}

> *regions: one is the basin of attraction of E_1, while the other is the basin of attraction of E_{12}.*

Proof   (ii) Since $a_{21} < r_2(d_1 + \alpha r_1)/r_1$, E_1 is locally asymptotically stable and $C > 0$. If $B \geq 0$ or $\Delta < 0$, it follows from (3.2) that there is no positive equilibrium in (2.1). Then E_1 is globally asymptotically stable in the interior of the (x_1, x_2)-plane.

(iii) When $B < 0$ and $\Delta > 0$, there are two positive equilibria E_{12}^+ and E_{12}^-, as shown in (3.2). By (3.1), we can see that $\operatorname{tr}(J(E_{12})) < 0$. A long but straightforward computation shows that

$$\det J(E_{12}) = \frac{r_2 a_{21} x_2^+ (2A - \beta B)}{(a_{21} - \alpha r_2)^2} \left(x_2^+ - \frac{2\beta C - B}{2A - \beta B} \right).$$

A direct computation shows

$$(2A - \beta B)(-B + \sqrt{\Delta}) - 2A(2\beta C - B) = (2A - \beta B)\sqrt{\Delta} + \beta \Delta > 0$$

and then

$$x_2^+ = \frac{-B + \sqrt{\Delta}}{2A} > \frac{2\beta C - B}{2A - \beta B}.$$
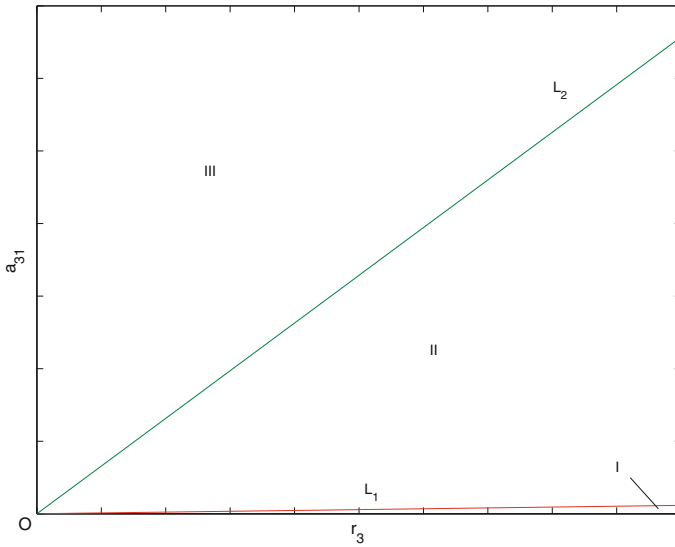
Fig. 2 Bifurcation diagram on the (r_3, a_{31})-parameter plane for the transition of dynamics. Denote L_1 : $a_{31} = 1.1583 * r_3$ (the *red line*) and L_2 : $a_{31} = 65.7222 * r_3$ (the *green line*). Then L_1 and L_2 divide the (r_3, a_{31})-plane into three regions. In region I, we have $a_{31} < 1.1583 * r_3$. That is, the robbers' efficiency a_{31} in translating plant–robber interactions into fitness is small. Thus the robbers cannot invade the plant–pollinator system and will go to extinction. In region II, we have $1.1583 * r_3 < a_{31} < 65.7222 * r_3$. That is, the efficiency is appropriate. Thus the robbers can invade the plant–pollinator system and will coexist with the pollinators. In region III, we have $a_{31} > 65.7222 * r_3$. That is, the efficiency is too large. Thus the robbers will invade the plant–pollinator system and drive the pollinators into extinction (color figure online)

Thus we have det $J(E_{12}^+) > 0$, which implies E_{12}^+ is locally asymptotically stable.

Since

$$\beta^2 \Delta - (2A - \beta B)^2 = -4A^2 + 4\beta AB - 4\beta^2 AC < 0,$$

then $\beta\sqrt{\Delta} - (2A - \beta B) < 0$ and

$$(2A - \beta B)[-B - \sqrt{\Delta}] - 2A(2\beta C - B) = \sqrt{\Delta}[\beta\sqrt{\Delta} - (2A - \beta B)] < 0.$$

Thus we have

$$x_2^- = \frac{-B - \sqrt{\Delta}}{2A} < \frac{2\beta C - B}{2A - \beta B}.$$

Hence, det $J(E_{12}^-) < 0$, which implies E_{12}^- is a saddle point. Thus the result in (iii) is proven.

(iv) When $B < 0$ and $\Delta = 0$, there is a unique positive equilibrium E_{22}, which is the overlapping point of equilibria E_{22}^- and E_{22}^+. By the criterion
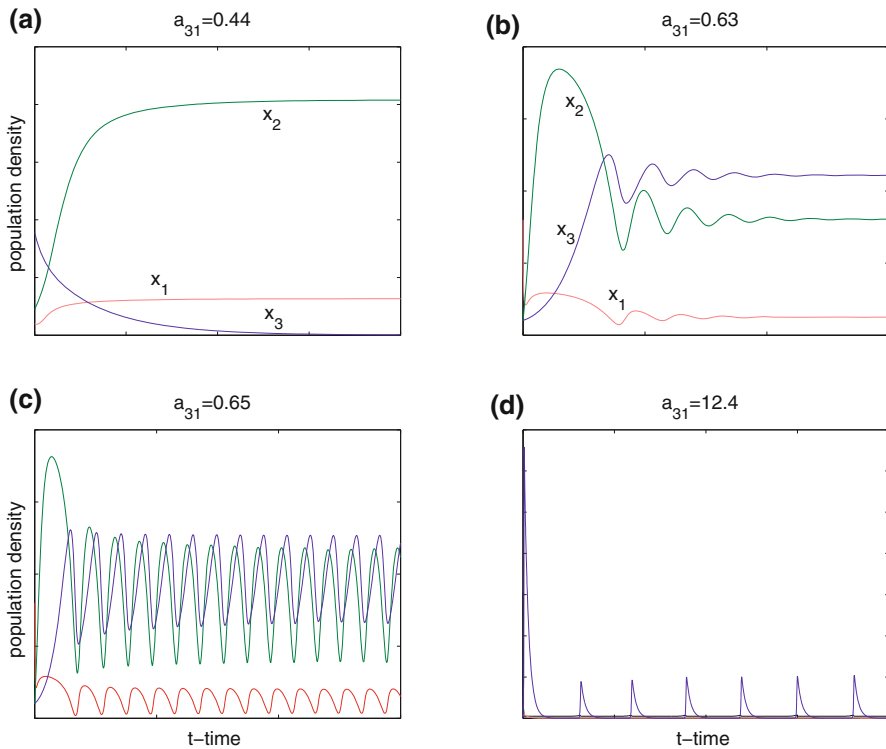
Fig. 3 **a** When $a_{31} = 0.44$, i.e., the robbers' efficiency in translating plant–robber interactions into fitness is small, the robbers with density x_3 go to extinction and the plants and pollinators with densities x_1 and x_2 coexist at a steady state. Here, the robbers can not invade the plant–pollinator system. **b** When $a_{31} = 0.63$, i.e., the robbers' efficiency is intermediate, the three species with densities x_1, x_2 and x_3 coexist at a steady state. Here, the robbers can invade the plant–pollinator system. **c** When $a_{31} = 0.65$, i.e., the robbers' efficiency is large, the three species with densities x_1, x_2 and x_3 coexist in periodic oscillations. **d** When $a_{31} = 12.4$, i.e., the robbers' efficiency is extremely large, the pollinators with densities x_2 go to extinction, while the plants and robbers with densities x_1 and x_3 coexist in periodic oscillations

for saddle-node points (e.g., Zhang et al. 1992), the equilibrium is a saddle-node point. Similar to the proof of (iii), the result in (iv) is proven.

□

Theorem 3.3 provides criteria for persistence of the pollinators. (i) When the pollinators' efficiency in translating plant–pollinator interactions into fitness is large (i.e., $a_{21} > r_2(\alpha + d_1/r_1)$), the pollinators will persist while the plants approach a density larger than their carrying capacity when in isolation from the pollinators (i.e., $x_1^+ > r_1/d_1$). (ii) When the pollinators' efficiency is intermediate as shown in Theorem 3.3(iii)(iv), the pollinators can persist in the plant–pollinator system only if the initial densities of the two species are above the separatrices of E_{12}^-. (iii) When the pollinators' efficiency is small as shown in Theorem 3.3(ii), the pollinators cannot survive in the plant–pollinator system.

The following results (Propositions 3.4 and 3.5) show monotonicity of $x_1^{\pm}$ and $x_2^{\pm}$ when parameters in (3.2) vary, which is useful in applications of our results.

Proposition 3.4 *When E_{12}^{-} and/or E_{12} exist,*

$$\frac{\partial x_1^{-}}{\partial a_{12}} < 0, \quad \frac{\partial x_1^{-}}{\partial a_{21}} < 0, \quad \frac{\partial x_1^{-}}{\partial r_1} < 0, \quad \frac{\partial x_1^{-}}{\partial d_1} > 0, \quad \frac{\partial x_1^{-}}{\partial \alpha} > 0, \quad \frac{\partial x_1^{-}}{\partial \beta} > 0$$

$$\frac{\partial x_1^{+}}{\partial a_{12}} > 0, \quad \frac{\partial x_1^{+}}{\partial a_{21}} > 0, \quad \frac{\partial x_1^{+}}{\partial r_1} > 0, \quad \frac{\partial x_1^{+}}{\partial d_1} < 0, \quad \frac{\partial x_1^{+}}{\partial \alpha} < 0, \quad \frac{\partial x_1^{+}}{\partial \beta} < 0$$

where $x_1^{\pm}$ are given in (3.2).

Proof We prove the inequalities for x_1^{-}, while a similar proof can be given for x_1^{+}. It follows from (3.2) that $x_1^{-} > r_2/(a_{21} - \alpha r_2)$. By (2.1), we have

$$\bar{A}x_1^2 + \bar{B}x_1 + \bar{C} = 0 \tag{3.3}$$

where

$$\bar{A} = \frac{a_{21}\beta d_1 r_2}{\alpha} > 0, \quad \bar{B} = r_2[a_{12}r_2 - \frac{a_{21}}{\alpha}(a_{12} + \beta r_1)] < 0, \quad \bar{C} = \frac{a_{12}}{\alpha}r_2^2 > 0.$$

Denote $\bar{\Delta} = \bar{B}^2 - 4\bar{A}\bar{C}$. By taking partial derivatives on a_{12} in both sides of (3.3), we have

$$\frac{\partial x_1^{-}}{\partial a_{12}} = -\frac{r_2}{\alpha\sqrt{\bar{\Delta}}}(a_{21} - \alpha r_2)\left(x_1^{-} - \frac{r_2}{a_{21} - \alpha r_2}\right) < 0.$$

Similarly, we have

$$\frac{\partial x_1^{-}}{\partial a_{21}} = -\frac{\bar{C} + r_2^2 a_{21} x_1^{-}}{a_{21}\sqrt{\bar{\Delta}}} < 0, \quad \frac{\partial x_1^{-}}{\partial r_1} = -\frac{\beta r_2 a_{21} x_1^{-}}{\alpha\sqrt{\bar{\Delta}}} < 0, \quad \frac{\partial x_1^{-}}{\partial d_1} = \frac{\beta r_2 a_{21} x_1^{+2}}{\alpha\sqrt{\bar{\Delta}}} > 0,$$

$$\frac{\partial x_1^{-}}{\partial \alpha} = \frac{a_{12} r_2^2 x_1^{+}}{\alpha\sqrt{\bar{\Delta}}} > 0, \quad \frac{\partial x_1^{-}}{\partial \beta} = \frac{d_1 r_2 a_{21}}{\alpha\sqrt{\bar{\Delta}}} x_1^{-}\left(x_1^{-} - \frac{r_1}{d_1}\right) > 0.$$

Thus, Proposition 3.4 is proven. □

Proposition 3.5 *When E_{12}^{-} and/or E_{12} exist,*

$$\frac{\partial x_2^{-}}{\partial a_{12}} < 0, \quad \frac{\partial x_2^{-}}{\partial a_{21}} < 0, \quad \frac{\partial x_2^{-}}{\partial r_1} < 0, \quad \frac{\partial x_2^{-}}{\partial d_1} > 0, \quad \frac{\partial x_2^{-}}{\partial \alpha} > 0, \quad \frac{\partial x_2^{-}}{\partial \beta} > 0$$

$$\frac{\partial x_2^{+}}{\partial a_{12}} > 0, \quad \frac{\partial x_2^{+}}{\partial a_{21}} > 0, \quad \frac{\partial x_2^{+}}{\partial r_1} > 0, \quad \frac{\partial x_2^{+}}{\partial d_1} < 0, \quad \frac{\partial x_2^{+}}{\partial \alpha} < 0, \quad \frac{\partial x_2^{+}}{\partial \beta} < 0$$

where $x_2^{\pm}$ are given in (3.2).

Proof By (2.1), we have

$$\tilde{A}x_2^2 + \tilde{B}x_2 + \tilde{C} = 0 \tag{3.4}$$

where

$$\tilde{A} = d_1 r_2 \beta^2, \quad \tilde{B} = 2d_1 r_2 \beta - r_1 \beta(a_{21} - \alpha r_2) - a_{12}(a_{21} - \alpha r_2)^2/a_{21},$$
$$\tilde{C} = d_1 r_2 - r_1(a_{21} - \alpha r_2).$$

Denote $\tilde{\Delta} = \tilde{B}^2 - 4\tilde{A}\tilde{C}$. By taking partial derivatives on α in both sides of (3.4), we have

$$\frac{\partial x_2^-}{\partial \alpha} = \frac{r_1 r_2(1 + \beta x_2^-) + 2a_{12}r_2(a_{21} - \alpha r_2)/a_{21}}{\sqrt{\tilde{\Delta}}} > 0,$$

$$\frac{\partial x_2^+}{\partial \alpha} = -\frac{r_1 r_2(1 + \beta x_2^+) + 2a_{12}r_2(a_{21} - \alpha r_2)/a_{21}}{\sqrt{\tilde{\Delta}}} < 0.$$

By (3.2), we obtain

$$r_2(1 + \beta x_2^\pm) = (a_{21} - \alpha r_2)x_1^\pm. \tag{3.5}$$

By taking partial derivatives in both sides of (3.5), it follows from Proposition 3.4 that

$$\frac{\partial x_2^-}{\partial a_{12}} < 0, \quad \frac{\partial x_2^-}{\partial r_1} < 0, \quad \frac{\partial x_2^-}{\partial d_1} > 0, \quad \frac{\partial x_2^-}{\partial \beta} > 0,$$

$$\frac{\partial x_2^+}{\partial a_{12}} > 0, \quad \frac{\partial x_2^+}{\partial a_{21}} > 0, \quad \frac{\partial x_2^+}{\partial r_1} > 0, \quad \frac{\partial x_2^+}{\partial d_1} < 0, \quad \frac{\partial x_2^+}{\partial \beta} < 0.$$

By (3.4), we obtain

$$x_2^- x_2^+ = \tilde{C}/\tilde{A} = \frac{d_1 r_2 - r_1(a_{21} - \alpha r_2)}{d_1 r_2 \beta^2}.$$

By taking partial derivatives on a_{21} in both sides of the equation, we obtain

$$x_2^+ \frac{\partial x_2^-}{\partial a_{21}} + x_2^- \frac{\partial x_2^+}{\partial a_{21}} = \frac{-r_1}{d_1 r_2 \beta^2} < 0.$$

Since $\partial x_2^+/\partial a_{21} > 0$, then $\partial x_2^-/\partial a_{21} < 0$. Thus, Proposition 3.5 is proven. $\square$

3.2 Subsystem II: the plant–robber system

Second, we consider the plant–robber system (2.2). If $a_{31} > r_3(cd_1 + r_1)/r_1$, there is a positive equilibrium $E_{13}(x_1^\#, x_3^\#)$ in (2.2) where

$$x_1^\# = \frac{cr_3}{a_{31} - r_3}, \quad x_3^\# = \frac{a_{31}x_1^\#(r_1 - d_1 x_1^\#)}{a_{13}r_3}. \tag{3.6}$$

Dynamics of system (2.2) are well understood. We cite the results as follows.

Theorem 3.6 (Kuang and Freedman 1988)

 (*i*) *If*

$$\frac{r_1}{d_1} \leq \frac{cr_3}{a_{31} - r_3},$$

 solutions of (2.2) *with* $x_1(0) > 0$ *converge to equilibrium* $(r_1/d_1, 0)$.
 (*ii*) *If*

$$\frac{cr_3}{a_{31} - r_3} < \frac{r_1}{d_1} \leq \frac{c(a_{31} + r_3)}{a_{31} - r_3}, \tag{3.7}$$

 solutions of (2.2) *with positive initial values converge to* E_{13}.
 (*iii*) *If*

$$\frac{r_1}{d_1} > \frac{c(a_{31} + r_3)}{a_{31} - r_3}, \tag{3.8}$$

 E_{13} *is unstable and there is a unique limit cycle* $E_\phi(\phi_1(t), \phi_3(t))$. *Solutions of* (2.2) *with positive initial values* (*except* E_{13}) *converge to* E_ϕ.

4 Permanence

In this section, we consider permanence of system (2.3). Since the system is dissipative, we need to show the uniform persistence of (2.3), that is, we need to study dynamics of (2.3) on the boundaries of the positive cone.

Let $g(x_1) = x_1/(c + x_1)$. The Jacobian matrix $J(x_1, x_2, x_3)$ of (2.3) is

$$\begin{pmatrix} r_1 - 2d_1 x_1 + a_{12}x_2 f(1 - \alpha x_1 f) - a_{13}x_3 \dot{g} & a_{12}x_1(1 + \alpha x_1)f^2 & -a_{13}g \\ a_{21}x_2(1 + \beta x_2)f^2 & a_{21}x_1 f(1 - \beta x_2 f) - r_2 & 0 \\ ca_{31}x_3 \dot{g} & 0 & a_{31}g - r_3 \end{pmatrix} \tag{4.1}$$

Then the equilibrium $O(0, 0, 0)$ is a saddle point with eigenvalues r_1, $-r_2$ and $-r_3$. The equilibrium $P_1(r_1/d_1, 0, 0)$ has eigenvalues

$$\lambda_1^{(1)} = -r_1, \quad \lambda_2^{(1)} = -r_2 + \frac{a_{21}r_1}{d_1 + \alpha r_1}, \quad \lambda_3^{(1)} = -r_3 + \frac{a_{31}r_1}{cd_1 + r_1}. \tag{4.2}$$

Here, $\lambda_i^{(j)}$ denotes the eigenvalue of equilibrium P_j in the x_i-direction.

The persistence of (2.3) is considered in the following three cases: $\lambda_2^{(1)} > 0, \lambda_3^{(1)} > 0$; $\lambda_2^{(1)} > 0, \lambda_3^{(1)} < 0$; $\lambda_2^{(1)} < 0$.

Case 1 $\lambda_2^{(1)} > 0, \lambda_3^{(1)} > 0$.

In this case, P_1 is a saddle point. It is asymptotically stable in the x_1-direction and is unstable in the x_2- and x_3-directions. Since $\lambda_2^{(1)} > 0$, the equilibrium $P_{12}(x_1^+, x_2^+, 0)$ is globally asymptotically stable in the interior of the (x_1, x_2)-plane by Theorem 3.3(i). Its eigenvalue in the x_3-direction is

$$\lambda_3^{(12)} = -r_3 + \frac{a_{31}x_1^+}{c + x_1^+}. \tag{4.3}$$

Since $\lambda_2^{(1)} > 0$ and $x_1^+ > r_1/d_1$, it follows from the monotonicity of function $x_1/(1 + x_1)$ that $\lambda_3^{(12)} > 0$. Then P_{12} is a saddle point. It is globally asymptotically stable in the interior of the (x_1, x_2)-plane by Theorem 3.3(i), and is unstable in the x_3-direction.

Since $\lambda_3^{(1)} > 0$, $P_{13}(x_1^\#, 0, x_3^\#)$ is an equilibrium of (2.3). By (4.1), its eigenvalue in the x_2-direction is

$$\lambda_2^{(13)} = -r_2 + \frac{a_{21}x_1^\#}{1 + \alpha x_1^\#}. \tag{4.4}$$

Thus, if $\lambda_2^{(13)} > 0$ and condition (3.7) holds, P_{13} is a saddle point. It is globally asymptotically stable in the interior of the (x_1, x_3)-plane by Theorem 3.6(ii) and is unstable in the x_2-direction. If $\lambda_2^{(13)} > 0$ and condition (3.8) holds, P_{13} is unstable in R_+^3.

The periodic orbit $P_\phi(\phi_1(t), 0, \phi_3(t))$ exists when condition (3.8) holds, where $\phi_1(t)$ and $\phi_3(t)$ are shown in Theorem 3.6. Since $P_\phi(t)$ is asymptotically stable on the (x_1, x_3)-plane, we only need to deal with its stability in the x_2-direction, which is determined by the Floquet multipliers of the variational system

$$\frac{d\Phi(t)}{dt} = J(\phi_1(t), 0, \phi_3(t))\Phi(t), \quad \Phi(0) = I$$

where $J(x_1, x_2, x_3)$ is given in (4.1) and I is the 3×3 identity matrix. Let T denote the period of $P_\phi(t)$. The Floquet multiplier in the x_2-direction is

$$\exp\left[\frac{1}{T}\int_0^T \left(-r_2 + \frac{a_{21}\phi_1(t)}{1 + \alpha\phi_1(t)}\right) dt\right].$$

Thus, if

$$\lambda_2^{(\phi)} = -r_2 + \frac{1}{T}\int_0^T \frac{a_{21}\phi_1(t)}{1 + \alpha\phi_1(t)} dt > 0, \tag{4.5}$$

then $P_\phi(t)$ is unstable in the x_2-direction. If $\lambda_2^{(\phi)} < 0$, it is locally asymptotically stable.

It follows from the proof of Proposition 2.1 that there is a constant $H > 0$ (e.g., $H = [\delta + (\beta r_1 + a_{12})/(\beta d_1)](r_0 + r_1 + 2a_{12}/\beta)/r_0$) such that $\frac{d}{dt}(x_1 + a_{12}x_2/a_{21} + a_{13}x_3/a_{31}) < 0$ as $x_1 + a_{12}x_2/a_{21} + a_{13}x_3/a_{31} \geq H$. Thus, the set

$$\Omega = \left\{ (x_1, x_2, x_3) \in R_+^3 : 0 \leq x_1 + \frac{a_{12}}{a_{21}}x_2 + \frac{a_{13}}{a_{31}}x_3 \leq H \right\}$$

is forward invariant and includes all ω-limit points of (2.3).

Theorem 4.1 *Assume $\lambda_2^{(1)} > 0$ and $\lambda_3^{(1)} > 0$.*

- (i) *If $\lambda_2^{(13)} < 0$ and condition (3.7) holds, every solution of (2.3) with $x_3(0) > 0$ converges to $P_{13}(x_1^\#, 0, x_3^\#)$.*
- (ii) *If $\lambda_2^{(13)} > 0$ and condition (3.7) holds, system (2.3) is permanent.*
- (iii) *If $\lambda_2^{(13)} < 0, \lambda_2^{(\phi)} < 0$ and condition (3.8) holds, every solution of (2.3) with $x_2(0) > 0$ satisfies $\lim_{t\to\infty} x_2(t) = 0$.*
- (iv) *If $\lambda_2^{(13)} > 0, \lambda_2^{(\phi)} > 0$ and condition (3.8) holds, system (2.3) is permanent.*
- (v) *If $\lambda_2^{(13)}\lambda_2^{(\phi)} < 0$ and condition (3.8) holds, system (2.3) is not persistent.*

Proof   (i) When $\lambda_2^{(13)} < 0$, there is no positive equilibrium of (2.3). Indeed, suppose $P^*(x_1^*, x_2^*, x_3^*)$ is a positive equilibrium of (2.3). Then $x_1^* = x_1^\#$ by the third equation of (2.3). It follows from (4.4) that

$$-r_2 + \frac{a_{21}x_1^*}{1 + \alpha x_1^* + \beta x_2^*} < -r_2 + \frac{a_{21}x_1^\#}{1 + \alpha x_1^\#} < 0$$

which is a contradiction by the second equation of (2.3).

Since $\lambda_2^{(13)} < 0$ and condition (3.7) holds, P_{13} is globally asymptotically stable in the interior of the (x_1, x_3)-plane and is locally asymptotically stable in R_+^3. Let Ω_{13} be the basin of attraction of P_{13} in Ω. Then Ω_{13} is open and forward invariant and $\Omega - \Omega_{13}$ is closed and forward invariant in Ω. Suppose the interior of $\Omega - \Omega_{13}$ (i.e., $\text{int}(\Omega - \Omega_{13})$) is not empty, then orbits of (2.3) in $\text{int}(\Omega - \Omega_{13})$ will not converge to P_{13} since they are not in the basin of attraction of P_{13}. Let $(x_1(t), x_2(t), x_3(t))$ be a solution of (2.3) with $(x_1(0), x_2(0), x_3(0)) \in \text{int}(\Omega - \Omega_{13})$, then we have $\limsup_{t\to\infty} x_i(t) > 0, i = 1, 2, 3$. Indeed, if $\lim_{t\to\infty} x_2(t) = 0$, then the ω-limit set of the orbit lies on the (x_1, x_3)-plane. On the (x_1, x_3)-plane, P_{13} is globally asymptotically stable while O and P_1 are hyperbolic saddle points. We apply a result of Thieme (1992) and conclude that this orbit converges to P_{13}, which is a contradiction. Similar discussions could show that $\limsup_{t\to\infty} x_i(t) > 0, i = 1, 3$. Hence system (2.3) is weakly persistent on $\Omega - \Omega_{13}$. Since the boundary equilibria O, P_1 and P_{12} are hyperbolic saddle points and can not form a heteroclinic cycle, hypotheses of (H-1) to (H-4) derived by Butler et al. (1986) are satisfied on $\Omega - \Omega_{13}$. Thus, system (2.3) restricted on $\Omega - \Omega_{13}$ is uniformly persistent and has a positive equilibrium P^* as a result of Butler et al. (1986) (see also Butler and Waltman 1986; Freedman et al. 1994; Yang and Ruan 1996). This forms a

contradiction since there is no positive equilibrium. Thus, int($\Omega - \Omega_{13}$) is empty and the result in (i) is proven.

(ii) Since $\lambda_2^{(13)} > 0$ and condition (3.7) holds, P_{13} is a saddle point. It is globally asymptotically stable in the interior of the (x_1, x_3)-plane and is unstable in the x_2-direction. Since the boundary equilibria are hyperbolic saddle points and can not form a heteroclinic cycle, hypotheses of (H-1) to (H-4) derived by Butler et al. (1986) are satisfied. Thus, system (2.3) is uniformly persistent. By Proposition 2.1, (2.3) is permanent.

(iii) Since $\lambda_2^{(\phi)} < 0$ and condition (3.8) holds, P_ϕ is locally asymptotically stable. Let Ω_ϕ be the union of basins of attraction of P_{13} and P_ϕ in Ω. Similar to the proof in (i), int($\Omega - \Omega_\phi$) is empty and the result in (iii) is proven.

(iv) Since $\lambda_2^{(13)} > 0$, P_{13} is unstable in the x_2-direction. Since $\lambda_2^{(\phi)} > 0$ and condition (3.8) holds, P_ϕ is unstable, while it is globally asymptotically stable in the interior of the (x_1, x_3)-plane (except P_{13}) by Theorem 3.6(iii). Thus, the boundary equilibria and periodic orbits are hyperbolic and can not form a heteroclinic cycle. Similar to the proof of (ii), system (2.3) is permanent.

(v) When $\lambda_2^{(13)} > 0$ and $\lambda_2^{(\phi)} < 0$, P_ϕ is locally asymptotically stable in Ω. When $\lambda_2^{(13)} < 0$ and $\lambda_2^{(\phi)} > 0$, P_{13} is asymptotically stable in the x_2-direction, and there is a positive solution of (2.3) which converges to P_{13}. Thus, system (2.3) is not persistent.

□

Theorem 4.1 provides criteria for pollinators' persistence in the presence of robbers' invasion. In this paper, our discussion focuses on the animals' efficiencies (i.e., a_{21}, a_{31}) in translating plant-animal interactions into fitness, while a similar discussion can be given for other parameters. Here, condition $\lambda_3^{(1)} > 0$ implies that the plants alone can provide sufficient resources for the robbers' survival. Thus, the robbers can always invade the plant–pollinator system since the pollinators have an indirect positive effect on the robbers through the plants. Although condition $\lambda_2^{(1)} > 0$ implies that the plants and pollinators can coexist in the absence of robbers, the pollinators may be driven into extinction by the robbers' invasion. Indeed, Theorem 4.1(i) shows that the pollinators will be driven into extinction when the robbers' efficiency is intermediate (e.g., $r_3(1 + cd_1/r_1) < a_{31} \leq r_3(1 + cd_1/r_1)/(1 - cd_1/r_1)$) as $c < r_1/d_1$) but the pollinators' efficiency is small (i.e., $a_{21} < r_2(\alpha + 1/x_1^\#)$).

Theorem 4.1(ii) shows that the pollinators can persist when the robbers' efficiency is intermediate but the pollinators' efficiency is large (i.e., $a_{21} > r_2(\alpha + 1/x_1^\#)$). Theorem 4.1(iii) shows that the pollinators will be driven into extinction when the robbers' efficiency is large (e.g., $a_{31} > r_3(1 + cd_1/r_1)/(1 - cd_1/r_1)$ as $c < r_1/d_1$) but the pollinators' efficiency is extremely small (i.e., $a_{21} < r_2(\alpha + 1/x_1^\#)$ and $\lambda_2^{(\phi)} < 0$). Theorem 4.1(iv) shows that the pollinators can persist when the robbers' efficiency is large but the pollinators' efficiency is extremely large (i.e., $a_{21} > r_2(\alpha + 1/x_1^\#)$ and $\lambda_2^{(\phi)} > 0$). Theorem 4.1(v) shows that the pollinators may be driven into extinction when the robbers' efficiency is large but the pollinators' efficiency is not extremely large (i.e., $\lambda_2^{(13)}\lambda_2^{(\phi)} < 0$).

Therefore, when the plants alone could support the robbers' survival, the pollinators can persist only if their efficiency is relatively larger than that of the robbers as shown in Theorem 4.1(ii)(iv). On the other hand, since the pollinators can persist in the plant–pollinator system, it is the robbers' invasion that leads to the pollinators' extinction in the situations of Theorem 4.1(i)(iii)(v).

Case 2 $\lambda_2^{(1)} > 0, \quad \lambda_3^{(1)} < 0.$

In this case, P_1 is globally asymptotically stable in the interior of the (x_1, x_3)-plane, and is unstable in the x_2-direction.

Theorem 4.2 *Assume* $\lambda_2^{(1)} > 0$ *and* $\lambda_3^{(1)} < 0.$

(i) *If* $\lambda_3^{(12)} < 0$, *every solution of* (2.3) *with* $x_2(0) > 0$ *converges to* $P_{12}(x_1^+, x_2^+, 0).$
(ii) *If* $\lambda_3^{(12)} > 0$, *system* (2.3) *is permanent.*

Proof (i) Since $\lambda_3^{(12)} < 0$, then $-r_3 + a_{31}x_1^+/(c + x_1^+) < 0$. By the monotonicity of function $x_1/(c + x_1)$, there are constants $\delta > 0, \epsilon > 0$ such that when $0 \leq x_1 < x_1^+ + \delta$, we have

$$-r_3 + \frac{a_{31}x_1}{c + x_1} < -\epsilon < 0.$$

Let $x(t)$ be a solution of (2.3) with $x_i(0) > 0, i = 1, 2, 3$. Let $\bar{x}(t)$ be a solution of (2.1) with $\bar{x}_i(0) = x_i(0), i = 1, 2$. By (2.3), $x(t)$ satisfies

$$\frac{dx_1}{dt} \leq x_1\left(r_1 - d_1x_1 + \frac{a_{12}x_2}{1 + \alpha x_1 + \beta x_2}\right)$$
$$\frac{dx_2}{dt} \leq x_2\left(-r_2 + \frac{a_{21}x_1}{1 + \alpha x_1 + \beta x_2}\right).$$

It follows from the comparison theorem (Cosner 1996) that $x_i(t) \leq \bar{x}_i(t)$ as $t > 0, i = 1, 2$.
Since $\lambda_2^{(1)} > 0$, P_{12} is globally asymptotically stable in the interior of the (x_1, x_2)-plane by Theorem 3.3(i). Thus, there is $T > 0$ such that when $t > T$, $\bar{x}_1(t) < x_1^+ + \delta$. Then $x_1(t) < x_1^+ + \delta$ as $t > T$. Hence, $dx_3/dt < -\epsilon x_3$ as $t > T$, which implies $\lim_{t\to\infty} x_3(t) = 0$. As a result of Thieme (1992), systems (2.3) and (2.1) have the same asymptotic dynamics. Thus, (i) is proven.

(ii) Since $\lambda_3^{(12)} > 0$, the equilibrium $P_{12}(x_1^+, x_2^+, 0)$ is a saddle point. It is globally asymptotically stable in the interior of the (x_1, x_2)-plane and is unstable in the x_3-direction. Since the boundary equilibria O, P_1 and P_{12} are hyperbolic saddle points, hypotheses of (H1) to (H4) derived by Freedman and Waltman (1984) are easily satisfied. Thus, system (2.3) is persistent as a result of Freedman and Waltman (1984). It follows from Proposition 2.1 that compactness criteria $(c_{1.1})$ and $(c_{4.1})$ derived by Thieme (1993) are satisfied. Thus, system (2.3) is permanent as a result of Thieme (1993). $\square$

Theorem 4.2 provides criteria for the robbers' invasion. Here, condition $\lambda_3^{(1)} < 0$ implies that the plants alone cannot provide sufficient resources for the robbers' survival. Thus, the robbers can persist only if there exists pollination–mutualism. Since $\lambda_2^{(1)} > 0$, pollination–mutualism can persist in the absence of robbers. However, the mutualism cannot guarantee the robbers' survival. Indeed, Theorem 4.2(i) shows that when the robbers' efficiency is small (i.e., $a_{31} < r_3(1+c/x_1^+)$), they cannot invade the plant–pollinator system and will go to extinction. Moreover, Theorem 4.2(ii) shows that when the robbers' efficiency is large (i.e., $a_{31} > r_3(1 + c/x_1^+)$), they can invade the plant–pollinator system and persist. Since the robbers cannot survive in the plant–robber system, it is the pollination–mutualism that leads to the robbers' persistence in the situation of Theorem 4.2(ii), where the pollinators will not be driven into extinction by the robbers' invasion.

Case 3 $\lambda_2^{(1)} < 0$.

Theorem 4.3 *Assume* $\lambda_2^{(1)} < 0$ *and* $\lambda_3^{(1)} > 0$. *Every solution of* (2.3) *with* $x_2(0) > 0$ *satisfies* $\lim_{t\to\infty} x_2(t) = 0$.

Proof Let $x(t)$ be a solution of (2.3) with $x_i(0) > 0$, $i = 1, 2, 3$. Since $\lambda_2^{(1)} < 0$, P_1 is locally asymptotically stable in the interior of the (x_1, x_2)-plane. By Theorem 3.3, either there is no positive equilibrium, or there are two positive equilibria of system (2.1).

When there is no positive equilibrium of system (2.1) as discussed in Theorem 3.3 (ii), P_1 is globally asymptotically stable in the interior of the (x_1, x_2)-plane. Thus, for the solution $\bar{x}(t) = (\bar{x}_1(t), \bar{x}_2(t))$ of (2.1) with $\bar{x}_i(0) = x_i(0)$, $i = 1, 2$, we have $\lim_{t\to\infty} \bar{x}_2(t) = 0$. Similar to the proof of Theorem 4.2(i), we have $x_2(t) \leq \bar{x}_2(t)$. Thus, $\lim_{t\to\infty} x_2(t) = 0$.

When there are two positive equilibria of system (2.1) as discussed in Theorem 3.3(iii), the stable manifold of equilibrium $E_{12}^-(x_1^-, x_2^-)$ subdivides the (x_1, x_2)-plane into two regions: one is the basin of attraction of P_1, which is denoted by Π_1; the other is that of P_{12}^+, which is denoted by Π_{12}. Then for any solution $\bar{x}(t) = (\bar{x}_1(t), \bar{x}_2(t))$ of (2.1) with $(\bar{x}_1(0), \bar{x}_2(0)) \in \Pi_1$, we have $\lim_{t\to\infty} \bar{x}_2(t) = 0$. Similar to the proof above, we have $\lim_{t\to\infty} x_2(t) = 0$ for any solution of (2.3) with $(x_1(0), x_2(0)) \in \Pi_1$ and $x_3(0) > 0$. Let $\Omega_3 \subseteq \Omega$ denote the set in which solutions of (2.3) with $x(0) \in \Omega$ satisfy $\lim_{t\to\infty} x_2(t) = 0$, then Ω_3 is open and forward invariant, and $\Omega - \Omega_3$ is closed and forward invariant in Ω.

Since $\lambda_3^{(1)} > 0$ and $x_1^{\pm} > r_1/d_1$, the eigenvalues of equilibria $P_{12}^-(x_1^-, x_2^-, 0)$ and $P_{12}(x_1^+, x_2^+, 0)$ in the x_3-direction satisfies $\lambda_3^{(12)} > \lambda_3^{(12-)} > 0$ by (4.3). Thus, the boundary equilibria are hyperbolic saddle points and cannot form a heteroclinic cycle. Similar to the proof of Theorem 4.1(i), the set int$(\Omega - \Omega_3)$ is empty. Thus, solutions of (2.3) with $x_2(0) > 0$ satisfy $\lim_{t\to\infty} x_2(t) = 0$. Similar discussion can be given for the situation in Theorem 3.3(iv).   □

Theorem 4.3 demonstrates a situation in which the pollinators are driven into extinction by the robbers' invasion. Here, condition $\lambda_3^{(1)} > 0$ implies that the plants alone can provide sufficient resources for the robbers' survival. Thus, the robbers can always

invade the plant–pollinator system. Since $\lambda_2^{(1)} < 0$, the pollinators can persist in the plant–pollinator system only if their initial population density is large and efficiency is intermediate as shown in Theorem 3.3(ii)(iii). This persistence will not happen in the presence of the robbers' invasion. As shown in Theorem 4.3, for any initial density of the pollinators, the pollinators will go to extinction due to the robbers' invasion. Since the pollinators with a large initial density can survive in the plant–pollinator system, it is the robbers' invasion that leads to the pollinators' extinction.

Theorem 4.4 *Assume $\lambda_2^{(1)} < 0$ and $\lambda_3^{(1)} < 0$. Let M_{12}^- denote the stable manifold of the saddle point $P_{12}^-(x_1^-, x_2^-, 0)$ when it exists.*

(i) *If $B \geq 0$ or $\Delta < 0$, every solution of (2.3) with $x_1(0) > 0$ converges to P_1.*
(ii) *If $B < 0$, $\Delta > 0$ and in addition*

    (a) *If $\lambda_3^{(12)} < 0$, then M_{12}^- subdivides R_+^3 into two invariant subsets S_1 and S_{12} such that $P_1 \in S_1$ and $P_{12} \in S_{12}$. Except on a set of initial conditions of Lebesgue measure zero, solutions of (2.3) with $x(0) \in S_1$ and $x_1(0) > 0$ converge to P_1, while solutions of (2.3) with $x(0) \in S_{12}$ and $x_1(0) > 0$ converge to P_{12}.*

    (b) *If $\lambda_3^{(12-)} < 0$ and $\lambda_3^{(12)} > 0$, then M_{12}^- subdivides R_+^3 into two invariant subsets S_1 and S_{12} such that $P_1 \in S_1$ and $P_{12} \in S_{12}$. Except on a set of initial conditions of Lebesgue measure zero, solutions of (2.3) with $x(0) \in S_1$ and $x_1(0) > 0$ converge to P_1, while solutions of (2.3) with $x(0) \in S_{12}$ and $x_1(0) > 0$ satisfy $\liminf_{t \to \infty} x_i(t) \geq \epsilon_0$ for some $\epsilon_0 > 0$.*

    (c) *If $\lambda_3^{(12-)} > 0$, every solution of (2.3) with $x_1(0) > 0$ converges to P_1.*

Proof Since $\lambda_3^{(1)} < 0$, it follows from Theorem 3.6(i) that P_1 is globally asymptotically stable in the interior of the (x_1, x_3)-plane.

  (i) Since $B \geq 0$ or $\Delta < 0$, P_1 is globally asymptotically stable in the interior of the (x_1, x_2)-plane by Theorem 3.3(i). Similar to the proof of Theorems 4.2(i) and 4.3, we obtain $\lim_{t \to \infty} x_i(t) = 0$, $i = 2, 3$.

  (ii) Since $B < 0$ and $\Delta > 0$, there are two equilibria $P_{12}^-(x_1^-, x_2^-, 0)$ and $P_{12}(x_1^+, x_2^+, 0)$ in the interior of the (x_1, x_2)-plane.

    (a) Since $\lambda_3^{(12)} < 0$, it follows from the monotonicity of function $x_1/(c + x_1)$ that $\lambda_3^{(12-)} < \lambda_3^{(12)} < 0$. Thus P_{12}^- is a saddle point whose stable manifold M_{12}^- is two-dimensional, while P_{12} is locally asymptotically stable. By Theorem 3.3(iii) and the comparison theorem, solutions of (2.3) with $x_1(0) > 0$ satisfy either $\limsup_{t \to \infty} x_1(t) \leq r_1/d_1$, $\limsup_{t \to \infty} x_2(t) \leq 0$, or $\limsup_{t \to \infty} x_1(t) \leq x_1^+$, $\limsup_{t \to \infty} x_2(t) \leq x_2^+$. For the former situation, we have $\lim_{t \to \infty} x_2(t) = 0$ and then $\lim_{t \to \infty} x_3(t) = 0$. For the latter situation, similar to the proof of Theorem 4.2(i), we have $\lim_{t \to \infty} x_3(t) = 0$. Since S_1 and S_{12} are forward invariant, the result in (a) is proven by Theorem 3.3(iii).

    (b) Similar to the proof in (a), solutions of (2.3) with $x(0) \in S_1$ and $x_1(0) > 0$ converge to P_1. In the subset S_{12}, since $\lambda_3^{(12)} > 0$, P_{12} is unstable in the x_3-direction. Thus, system (2.3) restricted on S_{12} is uniformly persistent.

(c) Since $\lambda_3^{(12-)} > 0$, then $\lambda_3^{(12)} > \lambda_3^{(12-)} > 0$. Here, P_1 is locally asymptotically stable in R_3^+. Let Ω_1 be the basin of attraction of P_1 in Ω. Then Ω_1 is open and forward invariant, and $\Omega - \Omega_1$ is closed and forward invariant in Ω. Suppose int$(\Omega - \Omega_1)$ is not empty. Since the equilibria P_{12}^- and P_{12} are saddle points, similar to the proof of Theorem 4.1(ii), system (2.3) is uniformly persistent and has a positive equilibrium $P^*(x_1^*, x_2^*, x_3^*)$ in $\Omega - \Omega_1$.

Let $\bar{x}(t)$ be the solution of (2.1) with $\bar{x}_i(0) = x_i^*, i = 1, 2$. Similar to the proof of Theorem 4.2(i), we obtain $\bar{x}_i(t) \geq x_i^*$ as $t > 0, i = 1, 2$. Since $\lambda_3^{(12-)} > 0$, then $-r_3 + a_{31}x_1^-/(c + x_1^-) > -r_3 + a_{31}x_1^*/(c + x_1^*) = 0$. It follows from the monotonicity of function $x_1/(c + x_1)$ that $x_1^* < x_1^-$. On the (x_1, x_2)-plane, we denote the x_1-isocline of (2.1) by $l_1 : r_1 - d_1x_1 + a_{12}x_2 f = 0$, and denote the x_2-isocline of (2.1) by $l_2 : -r_2 + a_{21}x_1 f = 0$, as shown in Fig. 1. The intersection of l_1 (resp. l_2) with the x_2-axis is $Q_1(0, -r_1/(a_{12} + r_1\beta))$ (resp. $Q_2(0, -1/\beta)$). Thus, Q_2 is below Q_1. Since there is no intersection of l_1 and l_2 as $x_1 < x_1^-$, l_2 is below l_1 as $x_1 < x_1^-$. By the monotonicity of function $x_2 f$ on the variable x_2, the vector field of (2.1) satisfies $dx_1/dt < 0$ in the region below l_1. Thus, l_2 is below the stable manifold of E_{12}^- as $x_1 < x_1^-$, as shown in Fig. 1. While the point (x_1^*, x_2^*) with $x_1^* < x_1^-$ is on l_2, it is below the stable manifold. It follows from Theorem 3.3(iii) that $\lim_{t \to \infty} \bar{x}_2(t) = 0$. Then $x_2^* = 0$, which is a contradiction.   □

Theorem 4.4 displays a situation in which persistence of the three species is density-dependent. Here, condition $\lambda_3^{(1)} < 0$ implies that the plants alone cannot support the robbers' survival. Thus, the robbers could survive only if there exists pollination–mutualism. Since $\lambda_2^{(1)} < 0$, the pollination–mutualism can persist only if the initial densities of the plants and pollinators are above the stable manifold of E_{12}^- [Theorem 3.3(ii)]. Theorem 4.4(i) shows that when pollination–mutualism in the plant–pollinator system cannot persist, the robbers will go to extinction.

Theorem 4.4(iia) shows that when pollination–mutualism in the plant–pollinator system can persist, the robbers cannot invade the plant–pollinator system and will go to extinction if the robbers' efficiency is too small (i.e., $a_{31} < r_3(1 + c/x_1^+)$). Theorem 4.4(iib) shows that the system is permanent when the initial densities of the three species are in the region S_{12} and the robbers' efficiency in translating plant–robber interactions into fitness is intermediate (i.e., $r_3(1 + c/x_1^+) < a_{31} < r_3(1 + c/x_1^-)$). Thus, the permanence is density-dependent while the two-dimensional stable manifold M_{12}^- is the threshold for the initial population densities. That is, when the densities are beyond M_{12}^-, the three species coexist; otherwise, both the pollinators and robbers go to extinction. Theorem 4.4(iic) shows that when the robbers' efficiency is too large (i.e., $a_{31} > r_3(1 + c/x_1^-)$), the robbers can invade the plant–pollinator system but will drive the pollinators into extinction, and then lead to extinction of themselves since the plants alone cannot support the robbers' survival. On the other hand, it follows from Proposition 3.4 that $\partial x_1^-/\partial a_{21} < 0$ and $\partial x_1^+/\partial a_{21} > 0$. Thus, an increase of the pollinators' efficiency enlarges the coexistence interval $r_3(1 + c/x_1^+) < a_{31} < r_3(1 + c/x_1^-)$, and promotes persistence of the three species. A similar discussion can be given for other parameters in Propositions 3.4 and 3.5.

5 Discussion

In this paper, we consider systems of flowering plants, pollinators and nectar robbers. Global dynamics of the plant–pollinator–robber model show mechanisms by which the robbers can invade the plant–pollinator system, and by which the pollinators would not be driven into extinction by the robbers' invasion.

Properties of the pollinators play a role in the robbers' invasion. As shown in Theorem 4.2(ii), when the plants alone cannot provide sufficient resources for the robbers' survival (i.e., $r_1/d_1 < cr_3/(a_{31} - r_3)$), pollination–mutualism enhances reproduction of the plants, which leads to the robbers' invasion. Here, the enhanced density (x_1^+), which is expressed in (3.2), is determined by the pollinators' properties. As shown in Proposition 3.4, an increase of pollinators' efficiency (a_{21}), a decrease of the competition degree (β), or a decrease of the pollinators' death rate (r_2), will enhance the plants' reproduction and may lead to the robbers' persistence (invasion). After the invasion, it is worth noticing that the pollinators will not be driven into extinction. Indeed, when the pollinators' density is so small that the pollination–mutualism cannot lead to sufficient resources for the robbers' survival, the robbers will decrease and go to extinction. At that time, the pollinators' density will increase. Hence, the pollinators will not go to extinction. The underlying reason is that the plants alone cannot support the robbers' survival. A similar discussion can be given for the situation in Theorem 4.4(iib).

Properties of the robbers are crucial to the pollinators' persistence. When the plants alone can provide sufficient resources for the robbers' survival (i.e., $r_1/d_1 > cr_3/(a_{31}-r_3)$), the robbers can always invade the plant–pollinator system. If the plant–pollinator subsystem can persist, Theorem 4.1(ii)(iv) shows that the pollinators can be persistent if the robbers' efficiency is relatively less than that of the pollinators. Otherwise, the pollinators will be driven into extinction as shown in Theorem 4.1(i)(iii)(v). Moreover, if persistence of pollination–mutualism in the plant–pollinator system is density-dependent as shown in Theorem 4.4(iib), the pollinators and robbers would coexist when the robbers' efficiency is intermediate and the initial densities of the three species are in an appropriate region. Otherwise, both the pollinators and robbers will go to extinction as shown in Theorem 4.4(iic). On the other hand, when the plants alone cannot support the robbers' survival but the plants-pollinator subsystem can persist as shown in Theorem 4.2(ii), the pollinators and robbers would coexist if the robbers' efficiency is large. Hence, the situations shown in Theorem 4.1(ii)(iv), Theorem 4.2(ii) and 4.4(iib) provide possible answers to the question raised by Irwin et al. (2010).

Properties of the plants are important to both the robbers' invasion and pollinators' persistence. As shown in Proposition 3.4, an increase of the plants' intrinsic growth rate (r_1) and/or efficiency (a_{12}), or a decrease of the plants' death rate (d_1), will enhance the plants' reproduction, which promotes both of the robbers' invasion and pollinators' persistence (Theorems 4.1, 4.2 and 4.4). On the other hand, properties of the plants may reduce the robbers' efficiency and promote the pollinators' persistence (Theorems 4.1(ii), 4.4(iib)). For example, in *Pavonia dasypetala*, nectar robbing by *T. ferricauda* is both energetically expensive and time consuming due to the thickened tissue of the flower's calyx (Roubik 1982; Inoue 1983). Hence the trait of

Pavonia dasypetala reduces the efficiency of *T. ferricauda* and promotes the pollinators' persistence.

Varying parameters in the system may lead to interesting transitions of interaction outcomes of the three species. *First,* we show that varying two parameters would lead to the transition through a bifurcation diagram on the (r_3, a_{31})-parameter plane, while similar discussions can be given for other pairs of parameters. Fix $r_1 = 1.0, r_2 = 0.45, d_1 = 0.01, a_{12} = 0.55, \alpha = 0.35, \beta = 0.2, a_{13} = 0.3, a_{21} = 0.74, c = 50$, and let r_3 and a_{31} vary. Denote lines

$$L_1 : a_{31} = 1.1583 * r_3, \quad L_2 : a_{31} = 65.7222 * r_3.$$

As shown in Fig. 2, L_1 and L_2 subdivide the (r_3, a_{31})-plane into three regions. In region I, we have $a_{31} < 1.1583 * r_3$. That is, $\lambda_2^{(1)} > 0$ and $\lambda_3^{(1)} < \lambda_3^{(12)} < 0$. It follows from Theorem 4.2(i) that the robbers will go to extinction since their efficiency in translating plant–robber interactions into fitness is relatively small ($a_{31} < 1.1583 * r_3$). In region II, we have $1.1583 * r_3 < a_{31} < 65.7222 * r_3$. It follows from Theorems 4.1(ii) and 4.2(ii) that the robbers can invade the plant–pollinator system and will coexist with the pollinators since their efficiency is appropriate ($1.1583 * r_3 < a_{31} < 65.7222 * r_3$). In region III, we have $a_{31} > 65.7222 * r_3$. It follows from Theorem 4.1(i) that the robbers will invade the plant–pollinator system and drive the pollinators into extinction since their efficiency is too large ($a_{31} > 65.7222 * r_3$).

Second, we show that varying one parameter could also lead to the transition. We focus on the robbers' efficiency (a_{31}), while similar discussions can be given for other parameters. In the following numerical simulations, we fix $r_1 = 1.0, r_2 = 0.45, r_3 = 0.45, d_1 = 0.01, a_{12} = 0.55, \alpha = 0.35, \beta = 0.2, a_{13} = 0.3, a_{21} = 0.74, c = 50$, and let a_{31} vary. When their efficiency is small (i.e., $a_{31} = 0.44$), the robbers will go to extinction (Fig. 3a). When the efficiency is intermediate ($a_{31} = 0.63$), the three species will coexist at a steady state (Fig. 3b). When the efficiency is large ($a_{31} = 0.65$), the three-species system is permanent in periodic oscillations (Fig. 3c). When the robbers' efficiency is extremely large ($a_{31} = 12.4$), the pollinators will be driven into extinction by the robbers' invasion and the plant–robber system persists (Fig. 3d).

It follows from the boundedness of solutions and uniform persistence that system (2.3) has a unique positive equilibrium. Hence, our analysis here could be used to obtain more results about the dynamics of the systems. For example, varying parameter values may change stability of the positive equilibrium and lead to emergence of three-dimensional periodic solutions via Hopf bifurcation as shown in Fig. 3c. Since our aim in this paper is to establish permanence of the three-species system, we do not consider the point further.

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