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Uni-directional Interaction and Plant–Pollinator–Robber Coexistence

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Abstract A mathematical model for the plant–pollinator–robber interaction is studied to understand the factors leading to the widespread occurrence and stability of such interactions. In the interaction, a flowering plant provides resource for its pollinator and the pollinator has both positive and negative effects on the plant. A nectar robber acts as a plant predator, consuming a common resource with the pollinator, but with a different functional response. Using dynamical systems theory, mechanisms of species coexistence are investigated to show how a robber could invade the plant–pollinator system and persist stably with the pollinator. In addition, circumstances are demonstrated in which the pollinator's positive and negative effects on the plant could determine the robber's invasibility and the three-species coexistence.

Keywords Unidirectional consumer–resource interaction · Uniform persistence · Stability · Invasion · Extinction

1 Introduction

The relationship between flowering plants and animal pollinators has resulted from coevolution over tens of millions of years (Crane et al. 1986, 1995; Hu et al. 2008).

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The plants provide nectar, seeds, and other resources for the pollinators. The pollinators consume the resources and supply pollination as a service in return. This relationship can be termed mutualistic, as individuals of each species benefit from the interaction. Because cooperation of plants and pollinators is crucial to the maintenance of both natural and agricultural ecosystems (Kearns et al. 1998), it has been the object of much empirical research and many modeling studies.

In addition to the mutualistic pollinators that provide a service to plants, there are other visitors to flowers that are purely exploitative. A common tactic of these visitors is to remove nectar by biting holes on the plants, without contacting the anthers and/or stigma, and thus not transporting pollen (Sprengel 1793; Darwin 1859, 1876, etc.). These exploiters are referred to as “nectar robbers” since they consume nectar, but do not provide pollination service, or as “cheaters” because they take advantage of the mutualistic relationship between plants and pollinators. Since almost all plants whose flowers are tubular or have nectar spurs have robbers associated with them, nectar robbing is a widespread phenomenon. Usually, the nectar robbing has a detrimental effect on the plants by destruction of the flowers (e.g., González-Gómez and Valdivia 2005) or by deterring pollination by mutualist partners (e.g., Irwin and Brody 1998), though some cases have been studied in which the apparent net cost is either small or nonexistent (e.g., Richardson 2004).

Either because the costs of nectar robbing to the plant are generally small relative to the costs of effective morphological and chemical traits that would deter robbers, or because such defenses would reduce the efficiency of pollinators as well as robbers (McCall and Irwin 2006), plants have not evolved effective defenses against nectar robbing. Traditional mutualism theory would imply that mutualistic cooperation should not be able to persist when there is no targeted deterrence to the cheaters, because the cheaters, by avoiding pollen transfer, might also avoid some costs and would therefore be expected to drive the pollinators to extinction. Thus, it is a challenging problem to explain why pollination mutualism persists stably when there are nectar robbers/cheaters (Irwin et al. 2010).

The present work considers the question of whether a nectar robber and pollinator/seed parasite can coexist on one plant species, despite the apparent competitive advantages of the nectar robber. Our expectation is that mathematical models may play a useful role in the research of plant–pollinator–robber interaction, similar to their role in other areas of ecological theory (Williams 2008; Lonsdorf et al. 2009). Modeling of mutualistic relationships goes back at least as far as May (1976). More recently, mutualisms have been modeled as a special class of consumer–resource interactions, in which either resources or services are exchanged such that both interacting species populations profit from the interaction (Holland and DeAngelis 2009). The relationship between plants and pollinators is called a unidirectional consumer–resource (C–R) interaction, when one species acts as a resource and the other as both a resource and a consumer (Holland and DeAngelis 2009). Alternatively, a bidirectional C–R interaction means that both species exploit the other as a resource. In recent years, specific C–R models have shown a series of novel results (e.g., Neuhauser and Fargione 2004; Zhang et al. 2007; Holland and DeAngelis 2009; Wang et al. 2011; Li et al. 2011; Wang and DeAngelis 2011). For example, interaction outcomes of the C–R systems will transition among mutualism, amensalism, commensalism, neutralism, and parasitism when parameter values and/or initial densities are changed. Hence, considering the unidirectional C–R interaction between the plant and pollinator in the plant-pollinator-robber system is important.

Our present work was specifically stimulated by recent research by Fishman and Hadany (2010), who derived an analytical expression for population-level plant-pollinator interaction, showing that the functional response between the pollinator and plant can be approximated by the Beddington–DeAngelis (BD) functional response. Fishman and Hadany (2010) were modeling the interaction of a social insect, the honeybee, with a plant species. In that case, the “predator interference” of the BD functional response emerges because individual bees, after they have visited a plant and taken nectar, leave a temporary scent that warns other bees from the hive that the nectar supply of a flower is temporarily low. The existence of the BD functional response can have a fundamentally different effect on the plant–pollinator–robber system, than the more Holling type II functional response, which is more commonly assumed in consumer-resource interactions.

Here, we demonstrate global dynamics of this plant-pollinator model described by the BD functional response. Based on these global results, we extend the analysis to models of plant–pollinator–robber systems, assuming that unlike the pollinator, the robber interaction with the plant is a Holling type II functional response, since the robber removes nectar via biting holes and acts as a predator to the plant. The consumption of nectar by one robber may decrease that available to another individual, but that action is through depletion of resources, not interference. These two assumptions on functional responses lead to a three-species model that differs from any that we are aware of in the literature. We add the assumption that the plant has some pollination from sources other than the pollinator considered in this model, or there is some other mode of propagation, which is able to support the plant population at a lower level in the absence of the pollinator; thus it is nonobligate. Using this model, we demonstrate circumstances under which the three-species system can persist, while under other circumstances, the pollinator and/or robber will go to extinction.

The paper is organized as follows. The plant-pollinator-robber model is described in Sect. 2. Section 3 demonstrates dynamics of the subsystems, while Sect. 4 shows permanence of the three-species system. Discussion and application are given in Sect. 5.

2 A Plant–Pollinator–Robber Model

The model derivation is based on unidirectional interactions between plants and pollinators, and predator–prey relationship between plants and nectar robbers.

In the plant–pollinator system, pollinators travel from their nests to a foraging patch, collecting food, flying back to the nests, and unloading. In individual interactions with flowers, the pollinators remove nectar and contact pollen, and provide pollination service. Thus, the pollinators have both positive and negative effects on the plants, while the plants provide food and other resources for the pollinators.

Let N_1 and N_2 represent the population densities of plants and pollinators, respectively. As shown by Fishman and Hadany (2010), the positive effect of pollinators on plants can be described by $aN_1N_2/(1+aN_1+abN_2)$. The parameter a is the effective equilibrium constant for (undepleted) plant–pollinator interaction, which combines traveling and unloading times spent in central place pollinator foraging, with individual-level plant–pollinator interaction. b denotes the intensity of exploitation competition among pollinators (Pianka 1974). The negative effect of pollinators on plants can be described by $-B(N_1,N_2)N_1$. Since we know little of the appropriate functional forms for resource supply by mutualists, we simply assume a linear increase in cost of resource production with $B(N_1,N_2)=\beta_1 N_2$. Then β_1 denotes the per-capita negative effect.

In the plant–robber system, a nectar robber bites holes on plants it visits, and takes away nectar without providing pollination service. Thus, it acts as a predator to the plants and interactions between the plant and robber can be characterized by a predator–prey model with the Holling II functional response. In the pollinator-robber system, we assume that there is no interfering competition between the two species (Irwin et al. 2010). Then the plant-pollinator-robber interactions can be characterized by

$$\begin{aligned}\frac{dN_1}{dt}&=r_1N_1-d_1N_1^2+\frac{\alpha_{12}N_1N_2}{1+aN_1+bN_2}-\beta_1N_1N_2-\frac{\beta_2N_1N_3}{c+N_1},\\ \frac{dN_2}{dt}&=-d_2N_2+\frac{\alpha_{21}N_1N_2}{1+aN_1+bN_2},\\ \frac{dN_3}{dt}&=-d_3N_3+\frac{\alpha_{31}N_1N_3}{c+N_1},\end{aligned}\tag{1}$$

where N_1, N_2, and N_3 represent the population densities of plants, pollinators, and robbers, respectively. The parameter r_1 is the intrinsic growth rate of the plants and d_1 the self-incompatible degree. As mentioned above, a and b represent the effective equilibrium constant and the intensity of exploitation competition, while β_1 denotes the per-capita negative effect. Since a is fixed in the discussions of this paper, the parameter α_{12} can be regarded as the plants' efficiency in translating plant–pollinator interactions into fitness (Beddington 1975; DeAngelis et al. 1975; Fishman and Hadany 2010), and α_{21} is the corresponding value for the pollinators. β_2 denotes the saturation level in the Holling II functional response, while c is the half-saturation constant. d_2 (resp. d_3) is the pollinators' (resp. robbers') per-capita mortality rate, and α_{31} represents the robber' efficiency in translating plant-robber interactions into fitness.

In system (1), if $N_i(0)=0$, then $N_i(t)=0$ for all t, so that the three faces of the positive cone and, therefore, the positive cone itself, are invariant. Consider solutions of (1) with initial conditions $N_1(0)\geq 0$, $N_2(0)\geq 0$, $N_3(0)\geq 0$. Then solutions of (1) with these initial values are nonnegative. By the second equation of (1), we have $dN_2/dt\leq 0$ when $d_2\geq \alpha_{21}/a$. It follows from the Liapunov theorem (Hofbauer and Sigmund 1998) that $\lim_{t\to\infty}N_2(t)=0$, which implies extinction of pollinators. Similarly, when $d_3\geq\alpha_{31}$, we have $\lim_{t\to\infty}N_3(t)=0$, which implies extinction of nectar robbers. Since we consider coexistence of pollinators and robbers in this work, we assume

$$\alpha_{21} > ad_2, \qquad \alpha_{31} > d_3.$$

3 Two-Species Systems

We consider the dynamics of the three two-species subsystems of (1) in this section. The three subsystems are: the plant-pollinator system, the plant–robber system, and the pollinator–robber system. In the last system, it is easy to see that both pollinators and robbers will go to extinction, which comes from our assumption in (1) that the visitors rely on flowering plants for survival. Thus, we will focus on the first two systems.

In the absence of nectar robbers (i.e., $N_3 = 0$), system (1) becomes a plant-pollination model with unidirectional interactions

$$\begin{aligned}\frac{dN_1}{dt} &= r_1N_1 - d_1N_1^2 + \frac{\alpha_{12}N_1N_2}{1+aN_1+bN_2} - \beta_1N_1N_2,\\ \frac{dN_2}{dt} &= -d_2N_2 + \frac{\alpha_{21}N_1N_2}{1+aN_1+bN_2}.\end{aligned} \tag{2}$$

The following results exhibit dissipation and nonexistence of periodic orbits of (2).

Proposition 3.1

(i) *Solutions of* (2) *are bounded.*
(ii) *System* (2) *has no periodic orbits or cycle chains in the positive quadrant.*

Proof

(i) Note that $dN_1/dt < N_1(r_1 + \alpha_{12}/b - d_1N_1)$ shows that $\limsup_{t\to\infty} N_1(t) \le (r_1 + \alpha_{12}/b)/d_1$. Furthermore, since $dN_1/dt|_{N_1=(r_1+\alpha_{12}/b)/d_1} < 0$, we see that $N_1(t) \le (r_1 + \alpha_{12}/b)/d_1$ for t large. Thus, for all t large, $dN_2/dt < -d_2N_2 + \alpha_{21}(r_1+\alpha_{12}/b)/(bd_1)$. Hence $\limsup_{t\to\infty} N_2(t) \le \alpha_{21}(r_1+\alpha_{12}/b)/(bd_1d_2)$ for t large. This proves that solutions of (2) are forward bounded.
(ii) Let $U(N_1, N_2)$ and $V(N_1, N_2)$ denote the functions on the right-hand sides of (2), respectively. Denote $D(N_1, N_2) = 1/(N_1N_2)$, then we have $\partial(DU)/\partial N_1 + \partial(DV)/\partial N_2 = -d_1/N_2 - (a\alpha_{12} + b\alpha_{21})/(1+aN_1+bN_2)^2 < 0$. It follows from the Bendixson–Dulac theorem (Zhang et al. 1992) that system (2) has no periodic orbits or cycle chains in the positive quadrant. □

In order to show conditions under which the pollinators can persist in the plant-pollinator system, we consider stability of equilibria of (2), which is determined by the Jacobian matrix

$$J(N_1, N_2) = \begin{pmatrix} f_{11} & f_{12} \\ f_{21} & f_{22} \end{pmatrix} \tag{3}$$

where

$$
\begin{aligned}
f_{11} &= r_1 - 2d_1N_1 - \beta_1N_2 + \frac{\alpha_{12}N_2}{1+aN_1+bN_2} - \frac{a\alpha_{12}N_1N_2}{(1+aN_1+bN_2)^2},\\
f_{21} &= \frac{\alpha_{21}N_2(1+bN_2)}{(1+aN_1+bN_2)^2},\\
f_{12} &= -\beta_1N_1 + \frac{\alpha_{12}N_1(1+aN_1)}{(1+aN_1+bN_2)^2}, \qquad f_{22} = -d_2 + \frac{\alpha_{21}N_1(1+aN_1)}{(1+aN_1+bN_2)^2}.
\end{aligned}
$$

On the axes, there are two equilibria $O(0,0)$ and $P_1(r_1/d_1, 0)$. O is a saddle point since the Jacobian matrix $J(O)$ has eigenvalues r_1 and $-d_2$, while $J(P_1)$ has eigenvalues $-r_1$ and $-d_2 + \alpha_{21}r_1/(d_1 + ar_1)$. Let $P(N_1, N_2)$ be a positive equilibrium. By the right-hand side of (2), we obtain

$$
N_1 = \frac{d_2(1+bN_2)}{\alpha_{21}-ad_2}, \qquad a_0N_2^2 + a_1N_2 + a_2 = 0 \tag{4}
$$

where

$$
\begin{aligned}
a_0 &= \frac{b\beta_1}{\alpha_{21}-ad_2} + \frac{d_1d_2b^2}{(\alpha_{21}-ad_2)^2} > 0, \qquad a_1 = \frac{\beta_1 - br_1}{\alpha_{21}-ad_2} + \frac{2bd_1d_2}{(\alpha_{21}-ad_2)^2} - \frac{\alpha_{12}}{\alpha_{21}},\\
a_2 &= -\frac{r_1}{\alpha_{21}-ad_2} + \frac{d_1d_2}{(\alpha_{21}-ad_2)^2}.
\end{aligned}
$$

Thus, there may exist two positive equilibria $P_{12}(N_1^+, N_2^+)$ and $P_{12}^-(N_1^-, N_2^-)$ with

$$
N_1^{\pm} = \frac{d_2(1+bN_2^{\pm})}{\alpha_{21}-ad_2}, \quad N_2^{\pm} = \frac{-a_1 \pm \sqrt{\Delta_1}}{2a_0}, \ \Delta_1 = a_1^2 - 4a_0a_1. \tag{5}
$$

As a result, the global dynamics of (2) can be demonstrated by the following theorem, while the proof is in Appendix A.

Theorem 3.2

(i) *Suppose* $\alpha_{21} < d_2(d_1 + ar_1)/r_1$. *When* $-a_1 \le 0$ *or* $\Delta_1 < 0$, P_1 *is globally asymptotically stable in the positive quadrant.*

(ii) *When* $\alpha_{21} < d_2(d_1+ar_1)/r_1$, $-a_1 > 0$ *and* $\Delta_1 > 0$, *there exist two positive equilibria* P_{12}^- *and* P_{12}. P_{12}^- *is a saddle point, while* P_1 *and* P_{12} *are locally asymptotically stable. The positive quadrant is divided into two regions by the separatrices of* P_{12}^-. *The region above the separatrices is the basin of attraction of* P_{12}, *while the other is that of* P_1.

(iii) *When* $\alpha_{21} < d_2(d_1 + ar_1)/r_1$, $-a_1 > 0$ *and* $\Delta_1 = 0$, *there is a unique positive equilibrium* P_{12}. P_1 *is locally asymptotically stable and* P_{12} *is a saddle-node point. The positive quadrant is divided into two regions by the separatrices of* P_{12}^-. *The region above the separatrices is the basin of attraction of* P_{12}, *while the other is that of* P_1.

(iv) *When* $\alpha_{21} > d_2(d_1+ar_1)/r_1$, P_{12} *is the unique positive equilibrium of* (2), *which is globally asymptotically stable in the positive quadrant.*

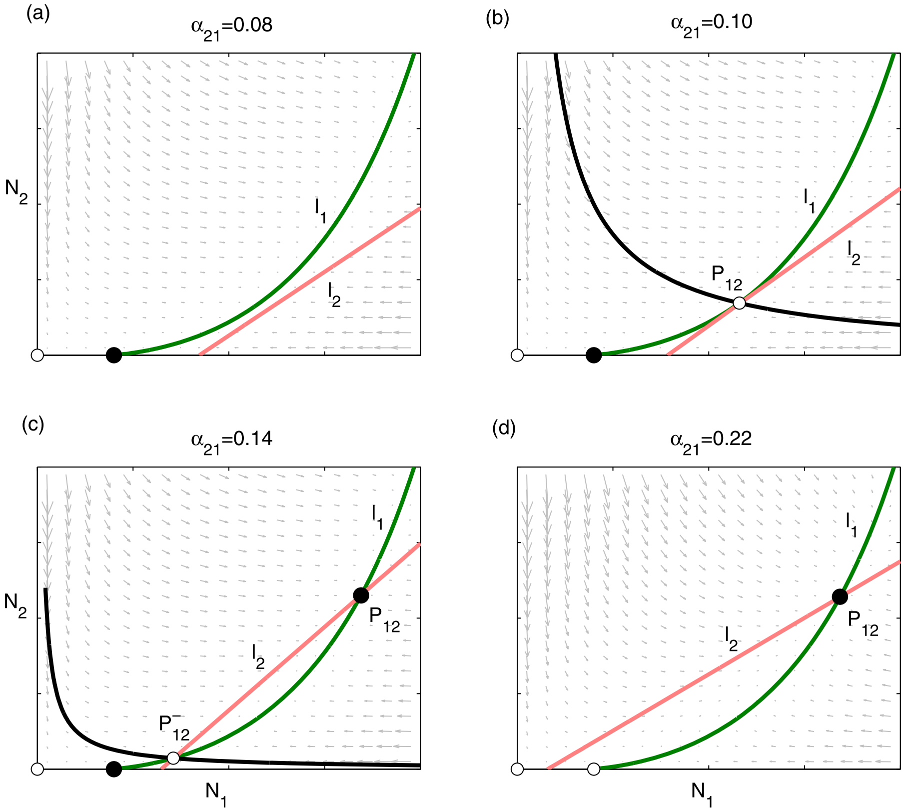

Fig. 1 Phase-plane panels for the population dynamics of the plant–pollinator system, in which l_1 and l_2 denote the isoclines of plants (N_1) and pollinators (N_2) in (2). Stable and unstable equilibria are identified by *solid* and *open circles*, respectively. Vector fields are shown by *gray arrows*, which represent the direction and speed of population trajectories. Fix $r_1 = 1.8, d_1 = 0.01, \alpha_{12} = 0.10, a = 0.35, b = 0.2, \beta_1 = 0.001, d_2 = 0.45$, and let α_{21} vary. (**a**) When pollinators' efficiency (α_{21}) in translating plant–pollinator interactions into fitness is small, they cannot survive in the plant–pollinator system and the plants approach the carrying capacity in the absence of pollinators. (**b**) When the pollinators' efficiency is intermediate and isoclines l_1 and l_2 are tangent at a saddle-node point P_{12}, the two species could coexist if their initial densities are sufficiently large. The separatrices (the *black line*) of P_{12} subdivide the plane into two regions. The region below it is the basin of attraction of $P_1(r_1/d_1, 0)$ while the region above it is that of P_{12}. A similar discussion can be given for (**c**), where isoclines l_1 and l_2 intersect at a saddle point P_{12}^- and a stable node P_{12}. (**d**) When the pollinators' efficiency is large, the plant-pollinator system persists at a steady state P_{12}, in which the plants approach a population density larger than the carrying capacity

Theorem 3.2 describes the global dynamics of system (2). (a) When their efficiency is small, the pollinators cannot survive in the plant-pollinator system, as shown in Theorem 3.2(i) and Fig. 1a. (b) When the efficiency is intermediate, the pollinators persist only if initial densities of the two species are above a threshold, as in Theorem 3.2(ii)(iii) and Fig. 1b–c. (c) When the efficiency is large, the pollinators will persist, as in Theorem 3.2(iv) and Fig. 1d.

When the two species coexist, the interaction outcomes may transition between mutualism and parasitism when the positive and negative effects α_{12} and β_1 vary, while the roles of the parameters are shown in the following proposition.

Proposition 3.3 *When $P_{12}(N_1^+, N_2^+)$ and/or $P_{12}^-(N_1^-, N_2^-)$ exist, we have*

$$\frac{\partial N_i^+}{\partial \beta_1} < 0, \qquad \frac{\partial N_i^-}{\partial \beta_1} > 0, \qquad \frac{\partial N_i^+}{\partial \alpha_{12}} > 0, \qquad \frac{\partial N_i^-}{\partial \alpha_{12}} < 0, \quad i = 1, 2$$

where $N_i^{\pm}$ are given in (5).

Proof We give a proof for N_i^-. A similar proof is possible for N_+^i. By (5), we obtain

$$N_2^- = \frac{\alpha_{21} - ad_2}{bd_2}\left(N_1^- - \frac{d_2}{\alpha_{21} - ad_2}\right).$$

Then $N_2^- > 0$ implies $N_1^- > d_2/(\alpha_{21} - ad_2)$. It follows from (2) that N_1^- satisfies

$$b_0 N_1^2 + b_1 N_1 + b_2 = 0, \qquad N_1^- = \frac{-b_1 - \sqrt{\Delta_2}}{2b_0}, \tag{6}$$

where

$$b_0 = \frac{\alpha_{21}}{a}\big[\beta_1(\alpha_{21} - ad_2) + bd_1 d_2\big] > 0, \qquad b_2 = \frac{\alpha_{12}}{a} d_2^2 > 0$$
$$b_1 = d_2\left[\alpha_{12} d_2 - \frac{\alpha_{21}}{a}(\alpha_{12} + br_1 + \beta_1)\right] < 0, \qquad \Delta_2 = b_1^2 - 4b_0 b_2.$$

By taking partial derivatives with respect to β_1 in both sides of (6), we have

$$\frac{\partial N_1^-}{\partial \beta_1} = \frac{\alpha_{21} N_1^-}{a\sqrt{\Delta_2}}(\alpha_{21} - ad_2)\left(N_1^- - \frac{d_2}{\alpha_{21} - ad_2}\right) > 0.$$

Similarly, we have

$$\frac{\partial N_1^-}{\partial \alpha_{12}} = -\frac{d_2}{a\sqrt{\Delta_2}}(\alpha_{21} - ad_2)\left(N_1^- - \frac{d_2}{\alpha_{21} - ad_2}\right) < 0.$$

Since $dN_2^-/dN_1^- = (\alpha_{21} - ad_2)/(bd_2) > 0$, the results for N_2^- exist. Thus, Proposition 3.3 is proved. □

Proposition 3.3 exhibits how the positive and negative effects of pollinators on the plants lead to transitions of interaction outcomes. Since $P_{12}(N_1^+, N_2^+)$ is asymptotically stable and N_1^+ represents the plant density at the equilibrium, Proposition 3.3 shows that the outcomes are mutualism when the negative effect (β_1) is small and/or the positive effect (α_{12}) is large. Otherwise, the outcomes would be parasitism. Equilibrium $P_{12}^-(N_1^-, N_2^-)$ is a saddle point and its separatrices determine the basin of attraction of the stable equilibrium P_{12}. Thus, when the negative effect is small and/or the positive effect is large, the interaction outcomes could be mutualism even if initial densities of the two species are small.

In the absence of pollinators (i.e., $N_2 = 0$), system (1) becomes a plant-robber model with the Holling II functional response

$$\begin{aligned} \frac{dN_1}{dt} &= r_1 N_1 - d_1 N_1^2 - \frac{\beta_2 N_1 N_3}{c + N_1}, \\ \frac{dN_3}{dt} &= -d_3 N_3 + \frac{\alpha_{31} N_1 N_3}{c + N_1}. \end{aligned} \tag{7}$$

When $d_3 < r_1\alpha_{31}/(r_1 + cd_1)$, there exists a positive equilibrium $P_{13}(N_1^\#, N_3^\#)$ of (7) with

$$N_1^\# = \frac{cd_3}{\alpha_{31} - d_3} < \frac{r_1}{d_1}, \qquad N_3^\# = \frac{\alpha_{31} N_1^\# (r_1 - d_1 N_1^\#)}{\beta_2 d_3}. \tag{8}$$

The following result exhibits the dynamics of system (7).

Proposition 3.4 (Kuang and Freedman 1988) *Assume* $\alpha_{31} > d_3$.

(i) *When*

$$\frac{r_1}{d_1} \le \frac{cd_3}{\alpha_{31} - d_3}$$

equilibrium $(r_1/d_1, 0)$ *of* (7) *is globally asymptotically stable in the positive quadrant.*

(ii) *When*

$$\frac{cd_3}{\alpha_{31} - d_3} < \frac{r_1}{d_1} \le \frac{c(\alpha_{31} + d_3)}{\alpha_{31} - d_3} \tag{9}$$

equilibrium P_{13} *is globally asymptotically stable in the positive quadrant.*

(iii) *When*

$$\frac{r_1}{d_1} > \frac{c(\alpha_{31} + d_3)}{\alpha_{31} - d_3} \tag{10}$$

there is a unique limit cycle $P_\phi(t) := (\phi_1(t), \phi_3(t))$ *of* (7), *which is globally asymptotically stable in the positive quadrant* (*except* P_{13}).

Proposition 3.4 describes the global dynamics of system (7). (a) When their efficiency is small, the robbers cannot survive in the plant-robber system, as shown in Proposition 3.4(i) and Fig. 2a. (b) When the efficiency is intermediate, the robbers and plants coexist at a steady state, as in Proposition 3.4(ii) and Fig. 2b–c. Here, the robbers' density at the steady state increases with their efficiency. (c) When the efficiency is large, the robbers and plants coexist in periodic oscillations, as in Proposition 3.4(iii) and Fig. 2d.

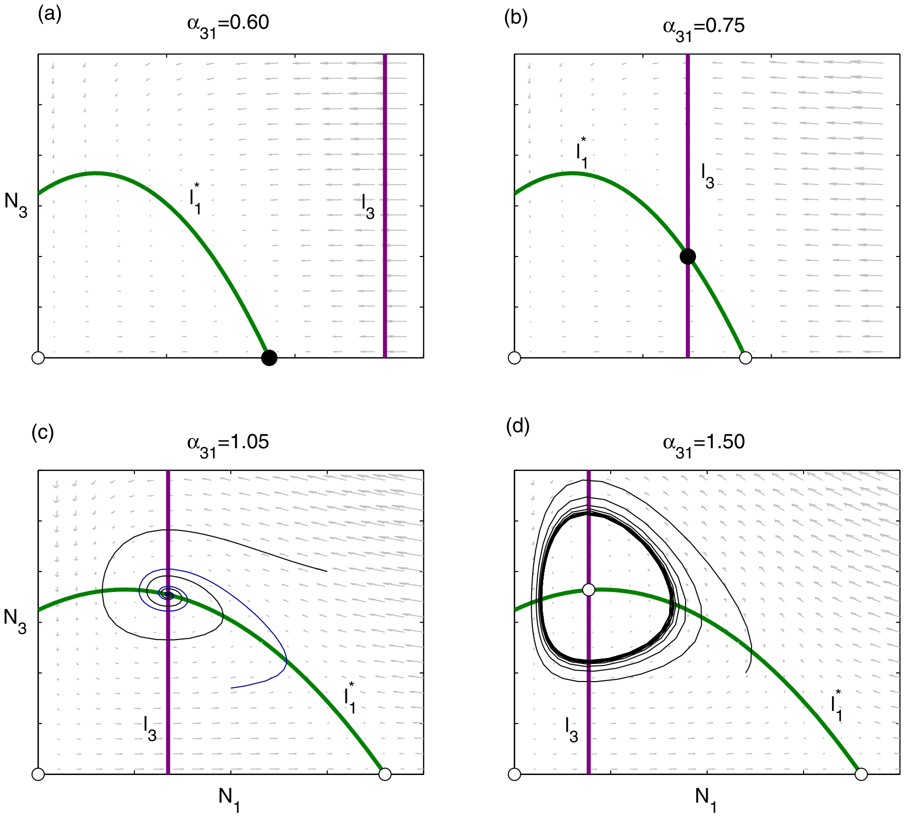

Fig. 2 Phase-plane panels for the population dynamics of the plant–robber system, in which l_1^* and l_3 denote the isoclines of plants (N_1) and nectar robbers (N_3) in (7). *Solid* and *open circles* represent stable and unstable equilibria, respectively. Vector fields are displayed by *gray arrows*, which denote the direction and speed of population trajectories. Fix $r_1 = 1.8, d_1 = 0.01, c = 90, \beta_2 = 0.5, d_3 = 0.45$, and let α_{31} vary. (**a**) When the robbers' efficiency (α_{31}) in translating plant–robber interactions into fitness is small, they cannot survive in the plant–robber system and the plants would approach the carrying capacity in the absence of robbers. (**b**) When the robbers' efficiency is intermediate, the two species coexist at a steady state, in which the plants approach a population density less than the carrying capacity. A similar discussion can be given for (**c**), in which the robbers' density in the steady state increases with their efficiency. (**d**) When the robbers' efficiency is large, the plant–robber system persists in periodic oscillations

4 Coexistence

In this section, we are concerned about permanence of the plant-pollinator-robber system, i.e., the dissipation and uniform persistence of (1) in the positive cone.

The dissipation of (1) is shown as follows. By the first equation of (1), we have $dN_1/dt < N_1(r_1 - d_1N_1 + \alpha_{12}/b)$, thus the comparison principle (Cosner 1996) implies that $\limsup_{t\to\infty} N_1(t) \le (br_1 + \alpha_{12})/(bd_1)$. Since $dN_1/dt|_{N_1=(r_1+\alpha_{12}/b)/d_1} < 0$, we obtain $N_1(t) \le (br_1 + \alpha_{12})/(bd_1)$. Denote $d_0 = \min\{d_2, d_3\}$. By (1), a straightforward computation shows that when t is large

$$\begin{aligned}
&\frac{d}{dt}\left(N_1+\frac{\alpha_{12}}{\alpha_{21}}N_2+\frac{\beta_2}{\alpha_{31}}N_3\right)\\
&\quad=N_1(r_1-d_1N_1)+\frac{2\alpha_{12}N_1N_2}{1+aN_1+bN_2}-\beta_1N_1N_2-\frac{\alpha_{12}}{\alpha_{21}}d_2N_2-\frac{\beta_2}{\alpha_{31}}d_3N_3\\
&\quad<N_1\left(r_1+\frac{2\alpha_{12}}{b}\right)-d_0\left(\frac{\alpha_{12}}{\alpha_{21}}N_2+\frac{\beta_2}{\alpha_{31}}N_3\right)\\
&\quad<\left(d_0+r_1+\frac{2\alpha_{12}}{b}\right)\frac{br_1+\alpha_{12}}{bd_1}-d_0\left(N_1+\frac{\alpha_{12}}{\alpha_{21}}N_2+\frac{\beta_2}{\alpha_{31}}N_3\right). \qquad (11)
\end{aligned}$$

Then the comparison principle (Cosner 1996) implies that

$$\limsup_{t\to\infty}\left(N_1+\frac{\alpha_{12}}{\alpha_{21}}N_2+\frac{\beta_2}{\alpha_{31}}N_3\right)\le\frac{1}{d_0}\left(\delta+\frac{br_1+\alpha_{12}}{bd_1}\right)\left(d_0+r_1+\frac{2\alpha_{12}}{b}\right).$$

Thus, we conclude the following result.

Theorem 4.1 *The plant-pollinator-robber system* (1) *is dissipative.*

To examine the uniform persistence of (1), we need to analyze the dynamics on the boundaries of the positive cone, which consist of three coordinate planes. As mentioned in Sect. 2 of this paper, the coordinate planes are forward invariant. Stability of equilibria of (1) on the boundaries is determined by the Jacobian matrix

$$J(N_1,N_2,N_3)=\begin{pmatrix} f_{11}-\frac{c\beta_2N_3}{(c+N_1)^2} & f_{12} & -\frac{\beta_2N_1}{c+N_1}\\ f_{21} & f_{22} & 0\\ -\frac{c\alpha_{31}N_3}{(c+N_1)^2} & 0 & \frac{\alpha_{31}N_1}{c+N_1}\end{pmatrix} \qquad (12)$$

where f_{ij} are given in (3).

(a) On the axes, there are two equilibria $O(0,0,0)$ and $E_1(r_1/d_1,0,0)$. O is a saddle point since the Jacobian matrix $J(O)$ has eigenvalues r_1, $-d_2$ and $-d_3$. Thus, the (N_2,N_3)-plane is the stable manifold and the N_1-axis is the unstable manifold. $J(E_1)$ has eigenvalues

$$\mu_1^{(1)}=-r_1,\qquad \mu_2^{(1)}=\frac{\alpha_{21}r_1}{d_1+ar_1}-d_2,\qquad \mu_3^{(1)}=\frac{\alpha_{31}r_1}{cd_1+r_1}-d_3,$$

where $\mu_j^{(1)}$ denotes the eigenvalue of equilibrium E_1 with the eigenvector in the N_j-axis direction, $j=1,2,3$. In the following analysis of this paper, let $\mu_j^{(i)}$ denote the eigenvalue of equilibrium E_i with the eigenvector in the N_j-axis direction.

(b) On the (N_1,N_2)-plane, there may exist equilibria $E_{12}:=(N_1^+,N_2^+,0)$ and $E_{12}^-:=(N_1^-,N_2^-,0)$, in which $N_i^\pm$ are given in (5). When they exist, E_{12} is locally asymptotically stable and E_{12}^- is a saddle point (Theorem 3.2). Their eigenvalues with the eigenvector in the N_3-axis direction are

$$\mu_3^{(12)} = \frac{\alpha_{31}N_1^+}{c+N_1^+} - d_3, \qquad \mu_3^{(12-)} = \frac{\alpha_{31}N_1^-}{c+N_1^-} - d_3.$$

(c) On the (N_1, N_3)-plane, equilibrium $E_{13} := (N_1^\#, 0, N_3^\#)$ exists if $\mu_3^{(1)} > 0$ (Proposition 3.4), while $N_i^\#$ are given in (8). E_{13} is globally asymptotically stable when condition (9) holds, and is unstable when condition (10) holds. By (12), its eigenvalue with the eigenvector in the N_2-axis direction is

$$\mu_2^{(13)} = \frac{\alpha_{21}N_1^\#}{1+aN_1^\#} - d_2. \tag{13}$$

It follows from Proposition 3.4 that when $\mu_2^{(13)} > 0$ and condition (10) holds, there exists a periodic orbit $(\phi_1(t), 0, \phi_3(t))$, which is denoted by $E_\phi(t)$. By Proposition 3.4(iii), $E_\phi(t)$ is asymptotically stable on the (N_1, N_3)-plane. Thus, we only need to consider its stability in the N_2-axis direction. It follows from the Floquet multipliers (cf. Perko 2001) that when

$$\mu_2^{(\phi)} = \frac{1}{T}\int_0^T \frac{\alpha_{21}\phi_1(t)}{1+a\phi_1(t)}\,dt - d_2 < 0 \tag{14}$$

$E_\phi(t)$ is locally asymptotically stable in R_+^3. When $\mu_2^{(\phi)} > 0$, $E_\phi(t)$ is unstable in the N_2-axis direction.

By (11), there exists a constant $G > 0$ (e.g., $G = [(br_1 + \alpha_{12})/(bd_1)](d_0 + r_1 + 2\alpha_{12}/b)/d_0$), which satisfies that $\frac{d}{dt}(N_1 + \alpha_{12}N_2/\alpha_{21} + \beta_2 N_3/\alpha_{31}) < 0$ when $N_1 + \alpha_{12}N_2/\alpha_{21} + \beta_2 N_3/\alpha_{31} \geq G$. Denote

$$\varpi = \left\{(N_1, N_2, N_3) : 0 \leq N_1 + \frac{\alpha_{12}}{\alpha_{21}}N_2 + \frac{\beta_2}{\alpha_{31}}N_3 \leq G,\, N_i \geq 0,\ i = 1, 2, 3\right\}$$

then the set ϖ is forward invariant and all ω-limit points of (1) are in ϖ.

The following result (Theorem 4.2) exhibits the plant-pollinator-robber coexistence when pollinators (resp. robbers) can persist in the absence of robbers (resp. in the absence of pollinators), while the proof is in Appendix B.

Theorem 4.2 *Let* $r_1/d_1 > \max\{d_2/(\alpha_{21} - ad_2), cd_3/(\alpha_{31} - d_3)\}$.

(i) *When* $\alpha_{21} > d_2(a + 1/N_1^\#)$, $\alpha_{31} > d_3(1 + c/N_1^\#)$ *and condition* (9) *holds, system* (1) *is permanent.*

(ii) *When* $\alpha_{21} > d_2(a + 1/N_1^\#)$, $\alpha_{31} > d_3(1 + c/N_1^\#)$, $\mu_2^{(\phi)} > 0$ *and condition* (10) *holds, system* (1) *is permanent.*

(iii) *When* $\alpha_{21} < d_2(a + 1/N_1^\#)$ *and condition* (9) *holds,* $E_{13}(N_1^\#, 0, N_3^\#)$ *is globally asymptotically stable in the positive cone.*

(iv) *When* $\alpha_{21} < d_2(a + 1/N_1^\#)$, $\mu_2^{(\phi)} < 0$ *and condition* (10) *holds, every solution of* (1) *with* $N_2(0) > 0$ *satisfies* $\lim_{t\to\infty} N_2(t) = 0$.

(v) *When* $\alpha_{21} < d_2(a + 1/N_1^{\#})$ *and* $\mu_2^{(\phi)} > 0$, *or, when* $\alpha_{21} > d_2(a + 1/N_1^{\#})$ *and* $\mu_2^{(\phi)} < 0$, *system* (1) *is not persistent.*

In circumstances considered by Theorem 4.2, conditions $r_1/d_1 > \max\{d_2/(\alpha_{21} - ad_2), cd_3/(\alpha_{31} - d_3)\}$ imply that the plants alone (i.e., without pollination mutualisms) can provide sufficient resources for the robbers' survival, while the pollinators can persist in the absence of robbers. In this work, our discussions focus on indirect interactions between pollinators and robbers through the host plants, i.e., the animals' efficiencies α_{21} and α_{31}, and the negative effect β_1. Similar discussions can be given for other parameters. In Theorem 4.2, the robbers can invade the plant-pollinator system although the pollinators have a negative effect on the plants. The underlying reason derived from the proof of Theorem 4.2 is that the pollinators' negative effect β_1 is small such that the plants can still support the robbers' survival (i.e., $N_1^+ > N_1^{\#}$ with $\partial N_1^+/\partial \beta_1 < 0$).

The condition $\mu_2^{(\phi)} > 0$ can be explained as follows. $\mu_2^{(\phi)}$ could be calculated by (14) when $E_\phi(t)$ is obtained. Since (14) can be rewritten as

$$\alpha_{21} > d_2 T \left[\int_0^T \frac{\phi_1(t)}{1 + a\phi_1(t)} dt \right]^{-1}$$

the biological meaning of $\mu_2^{(\phi)} > 0$ is that the pollinators' efficiency should be sufficiently large for their persistence in the presence of robbers, as shown in Theorem 4.2(ii). Otherwise, when $\mu_2^{(\phi)} < 0$, the pollinators will be driven into extinction by the robbers' invasion, as in Theorem 4.2(iv).

Theorem 4.2 demonstrates that the pollinators can persist (i) when the pollinators' efficiency is large ($\alpha_{21} > d_2(a + 1/N_1^{\#})$ but the robbers' efficiency is intermediate ($d_3(1 + cd_1/r_1) < \alpha_{31} \le d_3(1 + cd_1/r_1)/(1 - cd_1/r_1)$), or (ii) when the pollinators' efficiency is extremely large ($\alpha_{21} > d_2(a + 1/N_1^{\#})$ and $\mu_2^{(\phi)} > 0$) but the robbers' efficiency is large ($\alpha_{31} > d_3(1 + cd_1/r_1)/(1 - cd_1/r_1)$). The pollinators would be driven into extinction by the robbers' invasion (iii) when the pollinators' efficiency is small ($\alpha_{21} < d_2(a + 1/x_1^{\#})$) but the robbers' efficiency is intermediate; (iv) when the pollinators' efficiency is extremely small ($\alpha_{21} < d_2(a + 1/x_1^{\#})$ and $\mu_2^{(\phi)} < 0$) but the robbers' efficiency is large. Theorem 4.2(v) shows that when the pollinators' efficiency is not extremely large ($\mu_2^{(13)}\mu_2^{(\phi)} < 0$) but the robbers' efficiency is large, the pollinators go to extinction. In all circumstances of Theorem 4.2, we assume the plant–pollinator system persists in the absence of robbers. Thus, the pollinators' extinction in Theorem 4.2(iii)(iv)(v) is caused by the robbers' invasion.

Nectar robbers are not always able to invade the plant–pollinator system. The following result (Theorem 4.3) exhibits criteria for the robbers' invasion, while the proof is in Appendix C.

Theorem 4.3 *Let* $r_1/d_1 > d_2/(\alpha_{21} - ad_2)$, $r_1/d_1 < cd_3/(\alpha_{31} - d_3)$.

(i) *When* $\alpha_{31} > d_3(1 + c/N_1^+)$, *system* (1) *is permanent.*
(ii) *When* $\alpha_{31} < d_3(1 + c/N_1^+)$, *equilibrium* $E_{12}(N_1^+, N_2^+, 0)$ *is globally asymptotically stable in the positive cone.*

In the circumstance considered by Theorem 4.3, condition $r_1/d_1 < cd_3/(\alpha_{31} - d_3)$ implies that plants alone cannot provide sufficient resources for the robbers' survival. That is, the robbers' persistence depends on pollination mutualisms. On the other hand, condition $r_1/d_1 > d_2/(\alpha_{21} - ad_2)$ implies that pollination mutualisms can persist in the absence of robbers. Theorem 4.3(i) shows that when the robbers' efficiency is large ($\alpha_{31} > d_3(1 + c/N_1^+)$), the robbers can invade the plant–pollinator system but will not drive the pollinators into extinction. The underlying reason is that the plants alone cannot support the robbers' survival. When the robbers' efficiency is small ($\alpha_{31} < d_3(1 + c/N_1^+)$), Theorem 4.3(ii) exhibits that the robbers cannot invade the plant-pollinator system and will go to extinction, while the plants and pollinators persist.

The unidirectional interactions between plants and pollinators could determine the three-species coexistence. Our discussion focuses on the negative effect β_1, while a similar discussion is possible for the positive effect α_{12}. Indeed, condition $\alpha_{31} > d_3(1 + c/N_1^+)$ can be rewritten as $N_1^+ > cd_3/(\alpha_{31} - d_3)$. Since $\partial N_1^+/\partial\beta_1 < 0$ (Proposition 3.3), Theorem 4.3 shows that when the negative effect is small such that $N_1^+ > cd_3/(\alpha_{31} - d_3)$, the robbers can invade the plant–pollinator system and the three species coexist. Otherwise, when the negative effect is large such that $N_1^+ < cd_3/(\alpha_{31} - d_3)$, the robbers will go to extinction.

The following result (Theorem 4.4) demonstrates a circumstance in which the robbers' invasion will lead to the pollinators' extinction, while the proof is in Appendix D.

Theorem 4.4 *Let* $r_1/d_1 < d_2/(\alpha_{21} - ad_2)$, $r_1/d_1 > cd_3/(\alpha_{31} - d_3)$. *Solutions of* (1) *with* $N_2(0) > 0$ *satisfy* $\lim_{t\to\infty} N_2(t) = 0$.

In the circumstance considered by Theorem 4.4, condition $r_1/d_1 < d_2/(\alpha_{21} - ad_2)$ implies that the pollinators can persist in the plant-pollinator system only if their initial density is sufficiently high and efficiency is as large as those in Theorem 3.2(ii)(iii). On the other hand, condition $r_1/d_1 > cd_3/(\alpha_{31} - d_3)$ implies that the plants alone can support the robbers' survival. Thus the robbers can invade the plant-pollinator system and the pollinators cannot persist in the presence of robbers. This is because the pollinators' efficiency is relatively small (i.e., the robbers' efficiency is relatively large) since the two conditions in Theorem 4.4 can be rewritten as $\alpha_{21} < ad_2 + d_1d_2/r_1$, $\alpha_{31} > d_3(1 + cd_1/r_1)$. Because pollinators with high initial densities can survive in the absence of robbers, their extinction is caused by the robbers' invasion.

The following result (Theorem 4.5) displays a circumstance in which the three-species coexistence is density-dependent, while the proof is in Appendix E.

Theorem 4.5 *Let* $r_1/d_1 < d_2/(\alpha_{21} - ad_2)$, $r_1/d_1 < cd_3/(\alpha_{31} - d_3)$. *Let* S_{12}^- *be the stable manifold of* $E_{12}^-(N_1^-, N_2^-, 0)$ *as it is a boundary equilibrium of* (1).

(i) *When* $\Delta_1 < 0$ *or* $a_1 \geq 0$, E_1 *is globally asymptotically stable in the positive cone.*

(ii) *When* $\Delta_1 > 0$, $a_1 < 0$ *and* $\alpha_{31} < d_3(1 + c/N_1^+)$, *the two-dimensional manifold* S_{12}^- *divides* intR_+^3 *into two regions: one is the basin of attraction of* E_1, *while the other is that of* E_{12}.

(iii) *When* $\Delta_1 > 0$, $a_1 < 0$ *and* $d_3(1 + c/N_1^+) < \alpha_{31} < d_3(1 + c/N_1^-)$, *the two-dimensional manifold* S_{12}^- *divides* $intR_+^3$ *into two regions*: *one is the basin of attraction of* E_1, *while system* (1) *is uniformly persistent in the other region.*

(iv) *When* $\Delta_1 > 0$, $a_1 < 0$ *and* $\alpha_{31} > d_3(1 + c/N_1^-)$, E_1 *is globally asymptotically stable in the positive cone.*

In circumstances considered by Theorem 4.5, condition $r_1/d_1 < cd_3/(\alpha_{31} - d_3)$ implies that plants alone cannot provide sufficient resources for the robbers' survival. That is, the robbers' persistence depends on pollination mutualisms. However, condition $r_1/d_1 < d_2/(\alpha_{21} - ad_2)$ implies that the pollination mutualisms persist only if the pollinators' efficiency is large and the initial densities of the plants and pollinators are above a threshold (Theorem 3.2(ii)(iii)). Theorem 4.5(i) shows that when the pollination mutualisms do not persist, the robbers cannot survive. Theorem 4.5(ii) exhibits that when the pollination mutualisms could persist in the absence of robbers, the robbers cannot invade the plant–pollinator system if their efficiency is too small ($\alpha_{31} < d_3(1 + c/N_1^+)$). However, if the efficiency is too large ($\alpha_{31} > d_3(1 + c/N_1^-)$), Theorem 4.5(iv) displays that the robbers can invade the plant-pollinator system, but they will drive the pollinators into extinction and eventually lead to extinction of themselves. This is because the plants alone cannot support the robbers' survival. Theorem 4.5(iii) shows that when the robbers' efficiency is intermediate ($d_3(1 + c/N_1^+) < \alpha_{31} < d_3(1 + c/N_1^-)$), the three species coexist if their initial densities are in an appropriate region.

The unidirectional interactions between plants and pollinators are crucial to the three-species coexistence. Indeed, the condition $d_3(1 + c/N_1^+) < \alpha_{31} < d_3(1 + c/N_1^-)$ in Theorem 4.5(iii) can be rewritten as $N_1^- < cd_3/(\alpha_{31} - d_3) < N_1^+$. Since $\partial N_1^-/\partial \beta_1 > 0$ and $\partial N_1^+/\partial \beta_1 < 0$ (Proposition 3.3), the three species can coexist when β_1 is intermediate such that the above inequalities are satisfied. On the other hand, if β_1 is too large such that $N_1^- < N_1^+ < cd_3/(\alpha_{31} - d_3)$, Theorem 4.5(ii) shows that the robbers cannot invade the plant-pollinator system, while the plants and pollinators persist. If β_1 is too small such that $cd_3/(\alpha_{31} - d_3) < N_1^- < N_1^+$, Theorem 4.5(iv) shows that the robbers' invasion will lead to extinction of both the pollinators and robbers. A similar discussion is possible for the positive effect α_{12}.

5 Discussion and Application

In this paper, we considered the plant–pollinator–robber system, where the plant–pollinator subsystem is described by a unidirectional C–R model and the plant–robber subsystem is described by a predator–prey model. Pollinators and robbers interact indirectly through consumption of the same limiting resource. By qualitative analysis on the model, we showed global dynamics of the system, which lead to circumstances under which the three species could coexist.

Persistence of the plant–pollinator–robber system consists of persistence of all three species. The plant is always persistent in our analysis since it is assumed that both the pollinator and robber rely on the plant for survival. This is assured through the assumption of a source of propagation other than pollination from the pollinator in the model. There are three circumstances under which the plant–pollinator–robber system is persistent, which are described as follows. (i) When a pollination mutualism can persist in the plant–pollinator subsystem, and when the plants alone (in the absence of the pollinator) can support the robbers' survival, the pollinators could coexist with the robbers if their efficiency in translating plant-pollinator interaction into fitness is relatively larger than that of the robbers. (ii) When the pollination mutualism can persist but the plants alone cannot support the robbers' survival, the pollination mutualism may lead to invasion and persistence of the robbers, and the pollinators will not be driven into extinction by the robbers' invasion. (iii) When persistence of the pollination mutualism depends on initial population densities and the plants alone cannot support the robbers' survival, the robbers and pollinators could coexist if the robbers' efficiency is intermediate and initial density is small.

Unidirectional interactions between plants and pollinators could determine the robbers' invasibility. We focus on the circumstances in Theorem 4.3, while similar discussions can be given for the others. In Theorem 4.3, the plants alone cannot support the robbers' survival, while the pollination mutualism can persist in the absence of robbers. Thus, when the pollinators' negative effect on the plants is small, the robbers could survive. Otherwise, the robbers would go to extinction. For example, as mentioned in Sect. 1 in this paper, larvae might be abundant over the short term. When their negative effect on the plants is large, the robber cannot invade the plant-pollinator system and will go to extinction. Conversely, in the situation when the environmental conditions do not favor larval survival, the negative effect is small and the robber's invasion would succeed (Holland and DeAngelis 2006).

Initial population densities of the three species may be crucial to their coexistence. As shown in Theorem 4.5, when the plants alone cannot support the robbers' survival and persistence of the pollination mutualism is density-dependent, the three-species system persists only if their initial densities are in an appropriate region. Otherwise, (a) if initial densities of the plants and pollinators are too small, the pollinators cannot survive, which will lead to extinction of the robbers. (b) If the initial densities are large but the robbers' initial density is too large, the robbers will drive the pollinators into extinction, which eventually leads to extinction of the robbers themselves. Thus, only when the initial densities of the plants and pollinators are large and the robbers' initial density is relatively small, the three species could coexist.

When in coexistence, the three species may be at a steady state or in oscillations. Indeed, the dissipation of solutions and uniform persistence of (1) guarantee that the system has a unique positive equilibrium (Butler et al. 1986). When the equilibrium is asymptotically stable, the system persists at a steady state. If the equilibrium loses its stability, a stable limit cycle emerges by the Hopf bifurcation theorem and the three species persist in a form of periodic oscillations, as shown in Fig. 3. Thus, the results in this paper can be used to show more complex dynamics of the system. Since our focus is on plant-pollinator-robber coexistence, we do not extend the discussion further.

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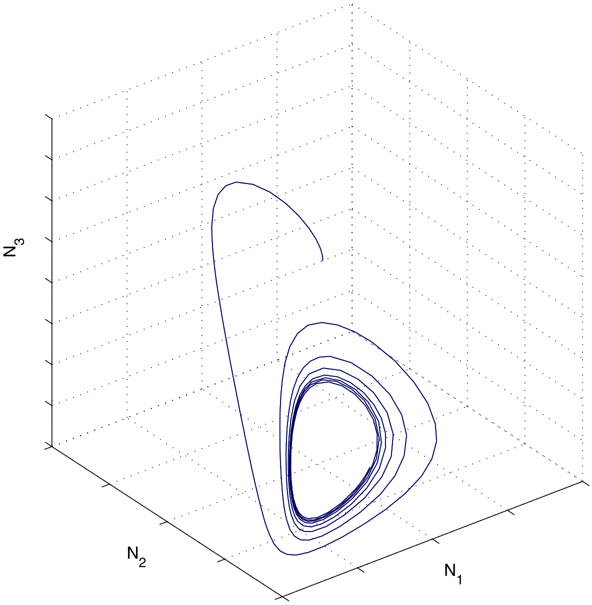

Fig. 3 Population dynamics of the plant–pollinator–robber system (1). Fix $r_1 = 1.8$, $d_2 = d_3 = 0.45$, $d_1 = 0.01$, $\alpha_{12} = 0.10$, $\alpha_{21} = 0.25$, $\alpha_{31} = 1.25$, $a = 0.35$, $b = 0.2$, $c = 90$, $\beta_1 = 0.001$, $\beta_2 = 0.5$. Numerical simulations show that the three-species system persists in periodic oscillations

Appendix A

Proof of Theorem 3.2

(i) Since $\alpha_{21} < d_2(d_1 + ar_1)/r_1$, we obtain $a_2 > 0$ and P_1 is locally asymptotically stable. Thus, if $-a_1 \leq 0$ or $\Delta_1 < 0$, it follows from (5) that there is no positive root. By Proposition 3.1, P_1 is globally asymptotically stable.

(ii) It follows from $a_1 < 0$ and $\Delta_1 > 0$ that there are two positive equilibria P_{12}^- and P_{12}. By (3), we obtain $\mathrm{tr}(J(P_{12})) < 0$. A long but straightforward computation shows that

$$\det J(P_{12}) = \frac{d_2 N_2^+}{b(\alpha_{21} - ad_2)^2}\Lambda, \quad \Lambda = \alpha_{21} a_0 \big(1 + bN_2^+\big)^2 - \alpha_{12} b.$$

By (5), we have

$$\Lambda = b\alpha_{21}(2a_0 - ba_1)\left(N_2^+ - \frac{2ba_2 - B}{2a_0 - ba_1}\right).$$

It follows from $a_1 < 0$ that

$$2a_0 - ba_1 = b\left(\frac{\alpha_{12}}{\alpha_{21}} + \frac{\beta_1 + br_1}{\alpha_{21} - ad_2}\right) > 0, \qquad 2ba_2 - a_1 = \frac{\alpha_{12}}{\alpha_{21}} - \frac{\beta_1 + br_1}{\alpha_{21} - ad_2} > 0.$$

Since

$$(2a_0 - ba_1)(-a_1 + \sqrt{\Delta_1}) - 2a_0(2ba_2 - a_1) = (2a_0 - ba_1)\sqrt{\Delta_1} + b\Delta_1 > 0,$$

then

$$N_2^+ = \frac{-a_1 + \sqrt{\Delta_1}}{2a_0} > \frac{2ba_2 - a_1}{2a_0 - ba_1}.$$

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

While $b^2\Delta_1 - (2a_0 - ba_1)^2 = -4a_0^2 + 4ba_0a_1 - 4b^2a_0a_2 < 0$, we obtain $b\sqrt{\Delta_1} - (2a_0 - ba_1) < 0$, and

$$\begin{aligned}(2a_0 - ba_1)\big(-a_1 - \sqrt{\Delta_1}\big) - 2a_0(2ba_2 - a_1) &= -(2a_0 - ba_1)\sqrt{\Delta_1} + b\Delta_1 \\ &= \sqrt{\Delta_1}\big[b\sqrt{\Delta_1} - (2a_0 - ba_1)\big] \\ &< 0.\end{aligned}$$

Hence, we have

$$N_2^- = \frac{-a_1 - \sqrt{\Delta_1}}{2a_0} < \frac{2ba_2 - a_1}{2a_0 - ba_1}.$$

Thus, $\det J(P_{12}^-) < 0$, which implies P_{12}^- is a saddle point. By Proposition 3.1, (ii) is proved.

(iii) It follows from $B < 0$ and $\Delta_1 = 0$ that there exists a unique positive equilibrium P_{12}, which is the coincide of equilibria P_{12}^- and P_{12}. By the criterion for saddle-node points (Theorem 7.1, Zhang et al. 1992), P_{12} is a saddle-node point. By Proposition 3.1, (iii) is proved.

(iv) It follows from $\alpha_{21} > d_2(d_1 + ar_1)/r_1$ that $C < 0$ and P_1 is a saddle. By (5), there is at most one interior equilibrium (N_1^+, N_2^+). It follows from Proposition 3.1 that there exists a unique interior equilibrium $P_{12}(N_1^+, N_2^+)$ of system (2), which is globally asymptotically stable in the positive quadrant. □

Appendix B

Proof of Theorem 4.2 By $r_1/d_1 > \max\{d_2/(\alpha_{21} - ad_2), cd_3/(\alpha_{31} - d_3)\}$, we obtain $\mu_2^{(1)} > 0$ and $\mu_3^{(1)} > 0$. Thus, E_1 is a saddle point, and equilibria E_{12} and E_{13} exist. Since $\mu_2^{(1)} > 0$, $E_{12}(N_1^+, N_2^+, 0)$ is globally asymptotically stable in the interior of the (N_1, N_2)-plane (Theorem 3.2). We show $\mu_3^{(12)} > 0$ as follows. By the second equation of (2), we have

$$-d_2 + \frac{\alpha_{21}N_1^+}{1 + aN_1^+} > -d_2 + \frac{\alpha_{21}N_1^+}{1 + aN_1^+ + bN_2^+} = 0$$

then

$$-d_2 + \frac{\alpha_{21}N_1^+}{1 + aN_1^+} > -d_2 + \frac{\alpha_{21}N_1^\#}{1 + aN_1^\#}.$$

By the monotonicity of function $N_1/(1+aN_1)$ that $N_1^+ > N_1^\#$. It follows from the monotonicity of function $N_1/(c+N_1)$ that

$$\mu_3^{(12)} = -d_3 + \frac{\alpha_{31}N_1^+}{c+N_1^+} > -d_3 + \frac{\alpha_{31}N_1^\#}{c+N_1^\#} = 0$$

which implies $\mu_3^{(12)} > 0$, i.e., E_{12} is unstable in the N_3-axis direction.

When $\alpha_{21} < d_2(a + 1/N_1^\#)$, we obtain $\mu_2^{(13)} < 0$. Then there is no positive equilibrium of (1). Indeed, suppose $E^*(N_1^*, N_2^*, N_3^*)$ is a positive equilibrium of (1). By the third equation of (1), we obtain $N_1^* = N_1^\#$. It follows from (13) that

$$-d_2 + \frac{\alpha_{21}N_1^*}{1+aN_1^*+bN_2^*} < -d_2 + \frac{\alpha_{21}N_1^\#}{1+aN_1^\#} = \mu_2^{(13)} < 0$$

which forms a contradiction by the second equation of (1).

(i) It follows from $\mu_3^{(12)} > 0$ that E_{12} is a saddle point: the (N_1, N_2)-plane is the stable manifold and the N_3-axis is the unstable manifold. Since $\mu_2^{(13)} > 0$ and condition (9) holds, E_{13} is a saddle point: the (N_1, N_3)-plane is the stable manifold and the N_2-axis is the unstable manifold. Thus, the boundary equilibria can not form a heteroclinic cycle. It follows from the acyclicity theorem of Butler et al. (1986) that uniform persistence of (1) is guaranteed.

(ii) It follows from $\mu_2^{(13)} > 0$, $\mu_2^{(\phi)} > 0$ and (10) that, E_{13} is unstable; E_ϕ is also unstable: the (N_1, N_3)-plane is the stable manifold, and the N_2-axis is the unstable manifold. Thus, the boundary equilibria and periodic orbits cannot form a heteroclinic cycle. Similar to the proof of (i), (ii) is proved.

(iii) It follows from $\mu_2^{(13)} < 0$ and (9) that E_{13} is locally asymptotically stable in R_+^3. Let ϖ_{13} be the basin of attraction of E_{13} in ϖ. Then ϖ_{13} is open and forward invariant, and $\varpi - \varpi_{13}$ is closed and forward invariant in ϖ. Suppose the interior of $\varpi - \varpi_{13}$ (i.e., $\mathrm{int}(\varpi - \varpi_{13})$) is not empty. Since the boundary equilibria O, E, and E_{12} are hyperbolic saddle points and cannot form a heteroclinic cycle, hypotheses of (H-1) to (H-4) derived by Butler et al. (1986) are satisfied in $\varpi - \varpi_{13}$. Thus, system (1) restricted on $\varpi - \varpi_{13}$ is uniformly persistent and has a positive equilibrium E^* as a result of Butler et al. (1986). This forms a contradiction since there is no positive equilibrium when $\mu_2^{(13)} < 0$. Thus, $\mathrm{int}(\varpi - \varpi_{13})$ is empty and (iii) is proved.

(iv) It follows from $\mu_2^{(\phi)} < 0$ and (10) that E_ϕ is locally asymptotically stable. Let ϖ_ϕ consist of basins of attraction of E_{13} and E_ϕ in ϖ. Similar to the proof in (iii), $\mathrm{int}(\varpi - \varpi_\phi)$ is empty and (iv) is proved.

(v) It follows from $\mu_2^{(13)} > 0$ and $\mu_2^{(\phi)} < 0$ that E_ϕ is locally asymptotically stable in ϖ. When $\mu_2^{(13)} < 0$ and $\mu_2^{(\phi)} > 0$, E_{13} is stable in the N_2-axis direction, and there is a positive solution of (1) which converges to E_{13}. Thus, system (1) is not persistent. □

Appendix C

Proof of Theorem 4.3 It follows from $r_1/d_1 > d_2/(\alpha_{21} - ad_2)$ and $r_1/d_1 < cd_3/(\alpha_{31} - d_3)$ that $\mu_2^{(1)} > 0$ and $\mu_3^{(1)} < 0$. Then E_1 is globally asymptotically stable in the interior of the (N_1, N_3)-plane, and is unstable in the N_2-axis direction; E_{12} is globally asymptotically stable in the interior of the (N_1, N_2)-plane.

(i) It follows from $\alpha_{31} > d_3(1 + c/N_1^+)$ that $\mu_3^{(12)} > 0$. Then the equilibrium $E_{12}(N_1^+, N_2^+, 0)$ is unstable in the N_3-axis direction. Since the boundary equilibria O, E_1, and E_{12} are hyperbolic and cannot form a heteroclinic cycle, system (1) is uniformly persistent as a result of Butler et al. (1986).

(ii) It follows from $\alpha_{31} < d_3(1 + c/N_1^+)$ that $\mu_3^{(12)} < 0$ and $-d_3 + \alpha_{31}N_1^+/(c + N_1^+) < 0$. Then E_{12} is locally asymptotically stable in R_+^3. Let ϖ_{12} be the basin of attraction of E_{12} in ϖ. Then ϖ_{12} is open and forward invariant, and $\varpi - \varpi_{12}$ is closed and forward invariant in ϖ. Suppose $\mathrm{int}(\varpi - \varpi_{12})$ is not empty. Since the boundary equilibria O and E_1 are hyperbolic and cannot form a heteroclinic cycle, hypotheses of (H-1) to (H-4) derived by Butler et al. (1986) are satisfied in $\varpi - \varpi_{12}$. Thus, system (1) restricted on $\varpi - \varpi_{12}$ is uniformly persistent and has a positive equilibrium $E^*(N_1^*, N_2^*, N_3^*)$ as a result of Butler et al. (1986). By the first two equations of (1), $E^*(N_1^*, N_2^*, N_3^*)$ satisfies

$$r_1 - d_1N_1^* + \frac{\alpha_{12}N_2^*}{1 + aN_1^* + bN_2^*} - \beta_1N_2^* > 0,$$
$$-d_2\big(1 + aN_1^* + bN_2^*\big) + \alpha_{21}N_1^* = 0.$$

One the other hand, the equilibrium $P_{12}(N_1^+, N_2^+)$ of (2) satisfies

$$r_1 - d_1N_1^+ + \frac{\alpha_{12}N_2^+}{1 + aN_1^+ + bN_2^+} - \beta_1N_2^+ = 0,$$
$$-d_2\big(1 + aN_1^+ + bN_2^+\big) + \alpha_{21}N_1^+ = 0.$$

It follows from the monotonicity of the functions (about N_1) in the right-hand sides of the above equations that $N_1^* \le N_1^+$. By $N_1^* = N_1^\#$, we obtain $N_1^\# \le N_1^+$. Since

$$-d_3 + \alpha_{31}N_1^+/\big(c + N_1^+\big) < 0, \qquad -d_3 + \alpha_{31}N_1^\#/\big(c + N_1^\#\big) = 0$$

it follows from the monotonicity of function $N_1/(c + N_1)$ that $N_1^\# > N_1^+$, which forms a contradiction. Thus, $\mathrm{int}(\varpi - \varpi_{12})$ is empty and (ii) is proved. □

Appendix D

Proof of Theorem 4.4 Since $r_1/d_1 < d_2/(\alpha_{21} - ad_2)$ and $r_1/d_1 > cd_3/(\alpha_{31} - d_3)$, we obtain $\mu_2^{(1)} < 0$ and $\mu_3^{(1)} > 0$. Then E_1 is asymptotically stable on the (N_1, N_2)-plane. It follows from Theorem 3.2 that, system (2) either has no positive equilibrium, or has two positive equilibria.

Let $N(t)$ be a solution of (1) with $N_i(0) > 0, i = 1, 2, 3$. If there is no positive equilibrium of (2) as shown in Theorem 3.2(i), E_1 is globally asymptotically stable in the interior of the (N_1, N_2)-plane. Let $\bar{N}(t) = (\bar{N}_1(t), \bar{N}_2(t))$ be a solution of (2) with $\bar{N}_i(0) = N_i(0), i = 1, 2$, then $\lim_{t\to\infty} \bar{N}_2(t) = 0$. By a proof similar to that of Theorem 4.3(ii), we obtain $N_2(t) \le \bar{N}_2(t)$ for $t > 0$, which implies $\lim_{t\to\infty} N_2(t) = 0$.

For the case that both $P^-_{12}(N^-_1, N^-_2)$ and $P_{12}(N^+_1, N^+_2)$ are positive equilibria of (2) as shown in Theorem 3.2(iii), the stable manifold of equilibrium P^-_{12} divides the (N_1, N_2)-plane into two regions. The region below the manifold, which is denoted by Ω_1, is the basin of attraction of P_1, while the other one, which is denoted by Ω_{12}, is the basin of attraction of P_{12}. Let $\bar{N}(t) = (\bar{N}_1(t), \bar{N}_2(t))$ be a solution of (2) with $(\bar{N}_1(0), \bar{N}_2(0)) \in \Omega_1$, then $\lim_{t\to\infty} \bar{N}_2(t) = 0$. By a proof similar to that of Theorem 4.3(ii), we obtain $\lim_{t\to\infty} N_2(t) = 0$ for solutions of (1) with $(N_1(0), N_2(0)) \in \Omega_1$.

Let $\varpi_1 \subseteq \varpi$ be a set such that solutions of (1) with $N(0) \in \varpi$ satisfy $\lim_{t\to\infty} N_2(t) = 0$. Then ϖ_1 is open and forward invariant, and $\varpi - \varpi_1$ is closed and forward invariant in ϖ. It follows from $\mu^{(1)}_2 < 0$ and $N^\#_1 < r_1/d_1$ that $\mu^{(13)}_2 < 0$. Similar to the proof of Theorem 4.2, we obtain $N^\pm_1 > N^\#_1$ and $\mu^{(12)}_3 > \mu^{(12-)}_3 > 0$. Then the boundary equilibria of (1) are hyperbolic and cannot form a heteroclinic cycle. By a proof similar to that of Theorem 4.2(iii), the set $\mathrm{int}(\varpi - \varpi_1)$ is empty. That is, solutions of (1) with $N_2(0) > 0$ satisfy $\lim_{t\to\infty} N_2(t) = 0$. A similar proof can be given for the case in Theorem 3.2(ii). □

Appendix E

Proof of Theorem 4.5 It follows from $r_1/d_1 < d_2/(\alpha_{21} - ad_2)$ and $r_1/d_1 < cd_3/(\alpha_{31} - d_3)$ that $\mu^{(1)}_i < 0, i = 2, 3$. Then E_1 is globally asymptotically stable in the interior of the (N_1, N_3)-plane by Theorem 3.4(i).

(i) When $\Delta_1 < 0$ or $a_1 \ge 0$, it follows from Theorem 3.2(i) that equilibrium E_1 is globally asymptotically stable in the interior of the (N_1, N_2)-plane. By a proof similar to that of Theorem 4.3(ii) and Theorem 4.4, we have $\lim_{t\to\infty} N_i(t) = 0, i = 2, 3$.

(ii) It follows from $\alpha_{31} < d_3(1 + c/N^+_1)$ that $\mu^{(12)}_3 < 0$. When $\Delta_1 > 0$ and $a_1 < 0$, $E^-_{12}(N^-_1, N^-_2, 0)$ and $E_{12}(N^+_1, N^+_2, 0)$ are boundary equilibria of (1). Since function $N_1/(c+N_1)$ is monotonic, we obtain $\mu^{(12-)}_3 < 0$ by $\mu^{(12-)}_3 < \mu^{(12)}_3$ and $\mu^{(12)}_3 < 0$. Thus, E_{12} is asymptotically stable, while E^-_{12} is a saddle point with a two-dimensional stable manifold S^-_{12}. It follows from Theorem 3.2(iii) and the comparison theorem that, every solution of (1) with $N_1(0) > 0$ satisfies either $\limsup_{t\to\infty} N_1(t) \le r_1/d_1, \limsup_{t\to\infty} N_2(t) \le 0$, or $\limsup_{t\to\infty} N_1(t) \le N^+_1, \limsup_{t\to\infty} N_2(t) \le N^+_2$. For the first case, we have $\lim_{t\to\infty} N_2(t) = 0$ and then $\lim_{t\to\infty} N_3(t) = 0$. For the second case, by a proof similar to that of Theorem 4.3(ii), we obtain $\lim_{t\to\infty} N_3(t) = 0$. By Theorem 3.2(iii), S^-_{12} divides $\mathrm{int}R^3_+$ into two regions. One region, which is denoted by ϖ_1, is the basin of attraction of E_1. The other region, which is denoted by ϖ_{12}, is that of E_{12}. Since ϖ_1 and ϖ_{12} are forward invariant, (ii) is proved.

(iii) By a proof similar to that of (ii), ϖ_1 is the basin of attraction of E_1. In ϖ_{12}, E_{12} is unstable in the N_3-axis direction since $\mu_3^{(12)} > 0$. Thus, system (1) is uniformly persistent in ϖ_{12}.

(iv) Since function $N_1/(c + N_1)$ is monotonic, we obtain $\mu_3^{(12)} > 0$ by $\mu_3^{(12)} > \mu_3^{(12-)}$ and $\mu_3^{(12-)} > 0$. Then equilibria E_{12}^- and E_{12} are saddle points. Since E_1 is locally asymptotically stable, we denote the basin of attraction of E_1 in ϖ by ϖ_1. Then ϖ_1 is open and forward invariant, and $\varpi - \varpi_1$ is closed and forward invariant in ϖ. By a proof similar to that of Theorem 4.2(i), system (1) is uniformly persistent and has a positive equilibrium $E^*(N_1^*, N_2^*, N_3^*)$ in $\varpi - \varpi_1$ as a result of Butler et al. (1986).

We denote the solution of (2) with $\bar{N}_i(0) = N_i^*$ by $\bar{N}(t), i = 1, 2$. By a proof similar to that of Theorem 4.3(ii), we have $\bar{N}_i(t) \geq N_i^*$ for $t > 0$. It follows from $\mu_3^{(12-)} > 0$ that $-d_3 + \alpha_{31}N_1^-/(c + N_1^-) > -d_3 + \alpha_{31}N_1^*/(c + N_1^*) = 0$. As shown in Fig. 1c, we denote the N_1-isocline of (2) by $l_1 : r_1 - d_1N_1 + \alpha_{12}N_2 f = 0$, and the N_2-isocline of (2) by $l_2 : -d_2 + \alpha_{21}N_1 f = 0$. The isocline l_1 (resp. l_2) and the N_1-axis intersects at $P_1(r_1/d_1, 0)$ (resp. $Q_1(d_2/(\alpha_{21} - ad_2), 0)$).

Since $\mu_2^{(1)} < 0$, we have $r_1/d_1 < d_2/(\alpha_{21} - ad_2)$. Thus, Q_1 is at the right-hand side of E_1. Since there is no intersection of l_1 and l_2 as $N_1 < N_1^-$, l_2 is below l_1 as $N_1 < N_1^-$. Since $r_1 - d_1N_1 + \alpha_{12}N_2/(1 + aN_1 + bN_2)|_{Q_1} < 0$, the vector field of (2) satisfies $dN_1/dt < 0$ in the region below l_1. Then l_2 is below the stable manifold of P_{12}^- when $N_1 < N_1^-$, as shown in Fig. 1c. Since the point (N_1^*, N_2^*) with $N_1^* < N_1^-$ is on l_2, it is below the stable manifold. By Theorem 3.2(iii), we obtain $\lim_{t\to\infty} \bar{N}_2(t) = 0$. That is, $N_2^* = 0$, which forms a contradiction. □

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