

University of Nebraska - Lincoln
DigitalCommons@University of Nebraska - Lincoln

USGS Staff -- Published Research

US Geological Survey

8-15-2018

Global dynamics of a mutualism–competition model with one resource and multiple consumers

Yuanshi Wang

School of Mathematics, Sun Yat-sen University


Hong Wu

School of Mathematics, Sun Yat-sen University, wuhong@mail.sysu.edu.cn

Donald L. DeAngelis

U.S. Geological Survey, Wetland and Aquatic Research Center

Follow this and additional works at: <http://digitalcommons.unl.edu/usgsstaffpub>

 Part of the [Geology Commons](#), [Oceanography and Atmospheric Sciences and Meteorology Commons](#), [Other Earth Sciences Commons](#), and the [Other Environmental Sciences Commons](#)

Wang, Yuanshi; Wu, Hong; and DeAngelis, Donald L., "Global dynamics of a mutualism–competition model with one resource and multiple consumers" (2018). *USGS Staff -- Published Research*. 1073.

<http://digitalcommons.unl.edu/usgsstaffpub/1073>

This Article is brought to you for free and open access by the US Geological Survey at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in USGS Staff -- Published Research by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.



Global dynamics of a mutualism–competition model with one resource and multiple consumers

Yuanshi Wang¹ · Hong Wu¹ · Donald L. DeAngelis²

Received: 10 August 2017 / Revised: 15 August 2018
© Springer-Verlag GmbH Germany, part of Springer Nature 2018

Abstract

Recent simulation modeling has shown that species can coevolve toward clusters of coexisting consumers exploiting the same limiting resource or resources, with nearly identical ratios of coefficients related to growth and mortality. This paper provides a mathematical basis for such a situation; a full analysis of the global dynamics of a new model for such a class of n -dimensional consumer–resource system, in which a set of consumers with identical growth to mortality ratios compete for the same resource and in which each consumer is mutualistic with the resource. First, we study the system of one resource and two consumers. By theoretical analysis, we demonstrate the expected result that competitive exclusion of one of the consumers can occur when the growth to mortality ratios differ. However, when these ratios are identical, the outcomes are complex. Either equilibrium coexistence or mutual extinction can occur, depending on initial conditions. When there is coexistence, interaction outcomes between the consumers can transition between effective mutualism, parasitism, competition, amensalism and neutralism. We generalize to the global dynamics of a system of one resource and multiple consumers. Changes in one factor, either a parameter or initial density, can determine whether all of the consumers either coexist or go to extinction together. New results are presented showing that multiple competing consumers can coexist on a single resource when they have coevolved toward identical growth to mortality ratios. This coexistence can occur because of feedbacks created by all of the consumers providing a mutualistic service to the resource. This is biologically relevant to the persistence of pollination–mutualisms.

Keywords Principle of competitive exclusion · Cooperation · Global stability · Bifurcation · Coexistence

Mathematics Subject Classification 34C12 · 37N25 · 34C28 · 37G20

✉ Hong Wu
wuhong@mail.sysu.edu.cn

¹ School of Mathematics, Sun Yat-sen University, Guangzhou 510275, People's Republic of China

² U.S. Geological Survey, Wetland and Aquatic Research Center, Gainesville, FL 32653, USA

Published online: 04 September 2018

This document is a U.S. government work and is not subject to copyright in the United States.

Springer

1 Introduction

Competition is a ubiquitous, fundamental interaction that structures ecological communities and drives the evolution of natural selection. Exploitative competition can occur when two or more species compete for the same limiting resource and in the process reduce the abundance of that resource in the environment. Mathematical theory has shown that in general, two species competing for the same limiting resource cannot coexist, and n consumers competing for m resources with $n > m$ cannot subsist. Only the consumer species that can reduce the limiting resource to a lower level than any other consumer species will survive in the long run. This has been referred to as the R^* rule (Tilman 1982). This principle of competitive exclusion has been demonstrated in many mathematical studies where interspecific competition is greater than intraspecific competition of the consumers [e.g., Freedman and Waltman (1984), Hofbauer and Sigmund (1998), Cantrell et al. (2004), Li and Smith (2007), and Nguyen and Yin (2017)].

For example, Llibre and Xiao (2014) considered a Lotka–Volterra model of one prey and two predators in which the predators depend linearly on the prey, but growth of the prey is characterized by a logistic equation when in isolation. Using dynamical systems theory, they exhibited the phase portrait of the model near all equilibria at infinity and gave the global dynamical behavior of the three species in the first octant. The global dynamics demonstrate necessary and sufficient conditions under which competitive exclusion holds; that is, when one predator goes to extinction. They found that the two predators could persist only if the ratios of growth to mortality were exactly equal. Because the conditions for coexistence of two consumers on a resource appear to require the ‘knife-edge’ identity of ratios of growth to mortality, which seems initially to be unrealistic, ecologists have tried to explain biodiversity in terms of species having different niches, such as different resources, and when exploiting the same resources doing so in ways that did not overlap too much. This is despite the fact that many coexisting species seem to play very similar roles.

Recent research, however, has refuted previous theory that highly similar species could not coexist on the same resource. Scheffer and van Nes (2006) and, more robustly, Sakavara et al. (2018) have shown, through intensive simulations, that it is possible for multiple species competing on a set of common resources to coexist by coevolving into a ‘lumpy’ distribution in which different clusters of consumers self-organize towards similar sets of traits for exploiting different limiting resources. A given cluster of species in these simulations will evolve towards almost identical values of R^* for their limiting resource, and have nearly identical values of ratios of parameters related to propagation and mortality. Any competitive exclusion would require too long a time period to be relevant, which is an assumption in the neutral theory of Hubbell (2001). Scheffer et al. (2018) have termed the simulated lumpy distribution of clusters of species along a trait axis to be a step towards unifying biodiversity theory.

The results of Scheffer and van Nes (2006) and Sakavara et al. (2018) showing species coexistence of similar species are the result of simulations, and not mathematical analysis, and are for generic consumer–resource systems. Our goal is to both provide a mathematical basis for such coevolved multi-consumer systems, and to apply it in a new model of a system that is a specific system in which the consumers not only

compete for the common resource, but also provide the resource some benefit; that is, the relationships of the consumers to the resource can be mutualistic. For example, in pollination–mutualisms, the flowering plant provides food (e.g., nectar and pollen) for its pollinator, while the pollinator supplies pollination service for the plant in return. The act of pollination is a net benefit to the plant. But pollinator species are also competing exploitatively with each other for the nectar and pollen from the plants. This type of relationship occurs broadly in nature. Thus, it is natural to ask if the principle of competitive exclusion holds for consumers when two or more are mutualistic with the same resource.

A breakthrough in analyzing the effects of multiple species of mutualists, such as pollinators, interacting with a single resource, such as a species of flowering plant, was recently made by Revilla (2015). The model used in this case was based on the exchange of food for service. Thus, the relationship between the pollinator and plant is mutualism. Numerical simulations displayed that the mutualism between the species promotes persistence of the system. Then the two-species model was extended to that with one plant and $(n - 1)$ pollinators, in which pollinators compete for the same plant for food but each of them is mutualistic with the plant. It was also suggested that the resulting model could be generalized from species pairs to larger communities.

This model of Revilla (2015) has not been fully analyzed but has far-reaching implications. In this paper, we use Eqs. (5), (8–9) and (11) established by Revilla (2015) to study whether the principle of competitive exclusion holds for a particular case in which mutualism and competition are combined by analyzing the mutualism–competition model with one plant species and multiple pollinators established by Revilla (2015). The effects of one pollinator on another in the system are indirect since they are interacting through the intermediary plant. We are able to show that the indirect effects of competing pollinators through their mutualisms with the plant species can lead to coexistence of multiple pollinators. This appears to us to be a new result.

To review the basic interactions between species, the interaction outcomes between pollinators i and j are determined by positive (+), neutral (0), or negative (–) effects of one species on the other (Bronstein 1994; Wang and DeAngelis 2016). Assume that species i (resp. j) can approach a density of x_1 (resp. y_1) in the absence of j (resp. i), while in the presence of species j (resp. i), species i (resp. j) approaches a density of x_2 (resp. y_2). Here, the density of species represents the population abundance of the species. The outcomes are mutualism (+, +) if $x_2 - x_1 > 0$ and $y_2 - y_1 > 0$. Similar definitions can be given for outcomes of parasitism (+, –), competition (–, –), amensalism (–, 0), commensalism (+, 0), and neutralism (0, 0). When we replace the species i and j with communities Ω_i and Ω_j that have no common species, we obtain a similar set of definitions for interaction outcomes between communities Ω_i and Ω_j .

We first consider the system of one resource and two consumers. By applying the method in Llibre and Xiao (2014), we completely demonstrate the qualitative behavior of the model. It is shown that global dynamics of the model depend on the ratio of death rate and propagation rate of the consumer, while necessary and sufficient conditions can be obtained for the principle of competitive exclusion to hold (see Theorem 4.10). If the principle of competitive exclusion holds, then one consumer goes to extinction,

and the other consumer and the resource coexist at a positive steady state in R_+^2 . If the principle of competitive exclusion does not hold, then either the three species will coexist at a positive equilibrium in the positive octant R_+^3 or all competing consumers go to extinction and the resource persists. Then we study the system of one resource and multiple consumers, and the following cases are proven. (a) Assume that the ratios of death rate and propagation rate of the consumers are equal. When the coexistence of one consumer and the resource is density-dependent, the consumer goes to extinction if its initial population is small. However, in the presence of other consumers, all consumers can coexist because of the consumer–resource mutualisms, even though each of the consumers cannot coexist with the resource alone. Moreover, if one of the consumers (with a large initial density) can coexist with the resource alone, it can drive all other survivors into survival. (b) Assume that the ratios of consumers are different and coexistence of each consumer and resource is density-dependent. Then the consumer with a small initial density and the lowest ratio can drive all other consumers into extinction, even though each of the other consumers (with large initial densities) can coexist with the resource alone, which implies extinction of all consumers. Thus, the invasion of a competitive consumer could result in extinction of all consumers, including the invader itself. When the consumers come from different communities, similar discussions can be given for interactions between the communities.

The paper is organized as follows. In the next section, we describe the n -species model. Section 3 exhibits dynamics of subsystems of the three-species system, while the global stability of the three-species system is shown in Sect. 4. Section 5 is devoted to analysis of the n -species model, and Sect. 6 is the Discussion.

2 Model

Let us assume that species 1 is a plant and species 2 an animal that interacts mutually with the plant through pollination. As shown in Eqs. (8–9) of Revilla (2015), the dynamical model for the plant-animal system can be described by

$$\begin{aligned}\frac{dN_1}{dt} &= G_1(\cdot)N_1 + \sigma_1\beta_0FN_0 + \sigma_1\beta_2FN_2 \\ \frac{dN_2}{dt} &= G_2(\cdot)N_2 + \sigma_2\beta_2FN_2 \\ \frac{dF}{dt} &= \alpha N_1 - (\omega + \beta_0N_0 + \beta_2N_2)F\end{aligned}\quad (2.1)$$

where N_1 and N_2 represent population densities of the plant and animal, respectively. The function $G_i(\cdot)$ is the per-capita rate of change of species i when it does not interact with species j by means of the mutualism. The function F is the number of flowers or fruits produced by the plant. The parameter β_2 is the rate of pollination by the animal, and σ_2 its conversion ratio into biomass. The parameter σ_1 represents the plant's conversion ratio into new adult plants from a flower or fruit (Fagan et al. 2014). The term “ $\sigma_1\beta_0FN_0$ ” represents that pollination could be performed by abiotic factors like wind, where β_0 and N_0 would be proxies of, e.g. wind flux.

Since flowers or fruits are ephemeral compared with the lives of plant and animals, F will rapidly reach a steady state ($dF/dt \approx 0$) compared with the much slower demographics. Thus the number of flowers or fruits can be characterized by a function of plant and animal abundances:

$$F = \frac{\alpha N_1}{\omega + \beta_0 N_0 + \beta_2 N_2}$$

where α is the per-capita rate of the plant in producing resources, and ω is the loss or decay rate of the resources.

When there are $(n - 1)$ species of animals, the two-species model can be extended to the following n -species system by applying Eqs. (5) and (11) of Revilla (2015):

$$\begin{aligned} \frac{dN_1}{dt} &= G_1(\cdot)N_1 + \sigma_1\beta_0FN_0 + \sigma_1 \sum_{i=2}^n \beta_i FN_i \\ \frac{dN_i}{dt} &= G_i(\cdot)N_i + \sigma_i\beta_i FN_i, \quad 2 \leq i \leq n \end{aligned} \tag{2.2}$$

where N_i represents population density of the i th species of animals. The parameter β_i is the rate of pollination by the animal, σ_i its conversion ratio into biomass, and $F = \alpha N_1/(\omega + \beta_0 N_0 + \sum_{j=2}^n \beta_j N_j)$.

For simplicity, we assume

$$G_1(N_1) = r_1 - d_1 N_1, \quad G_i(N_i) = -r_i, \quad 2 \leq i \leq n$$

where parameter r_1 represents the intrinsic growth rate of the plant, and d_1 its intraspecific competition degree. For $i \geq 2$, parameter r_i represents the death rate of the i th species. We consider solutions of (2.2) under the initial value conditions $N(0) = (N_1(0), N_2(0), \dots, N_n(0)) \geq 0$.

Before considering the general n -species system (2.2), we focus on the case of $n = 3$, i.e., there are one plant and two animal species. Let

$$\bar{r}_1 = r_1 + \sigma_1\alpha, \quad b_{12} = \frac{\sigma_1\alpha\omega}{\omega + \beta_0 N_0}, \quad \alpha_{i1} = \frac{\alpha\sigma_i\beta_i}{\omega + \beta_0 N_0}, \quad \hat{N}_i = \frac{\beta_i}{\omega + \beta_0 N_0}N_i, \quad i = 2, 3.$$

By dropping hats in \hat{N}_i , system (2.2) becomes

$$\begin{aligned} \frac{dN_1}{dt} &= N_1 \left(\bar{r}_1 - d_1 N_1 - \frac{b_{12}}{1 + N_2 + N_3} \right) \\ \frac{dN_2}{dt} &= N_2 \left(-r_2 + \frac{a_{21}N_1}{1 + N_2 + N_3} \right) \\ \frac{dN_3}{dt} &= N_3 \left(-r_3 + \frac{a_{31}N_1}{1 + N_2 + N_3} \right). \end{aligned} \tag{2.3}$$

Then $\bar{r}_1 > b_{12}$ and solutions of system (2.3) are nonnegative. Boundedness of the solutions is shown as follows, the proof of which is in Appendix A.

Proposition 2.1 *Solutions of system (2.3) are bounded in R^3_+ .*

3 Subsystems

System (2.3) has three invariant planes $N_i = 0, i = 1, 2, 3$. On the invariant plane $N_1 = 0$ (i.e., the (N_2, N_3) -plane), system (2.3) has a unique equilibrium $O(0, 0, 0)$, which is globally asymptotically stable for all parameters. The biological reason is that it is assumed that pollinators depend on the plant for survival. Thus we need to consider dynamics of system (2.3) on the (N_1, N_2) -plane and (N_1, N_3) -plane.

On the invariant (N_1, N_2) -plane, the restricted system of (2.3) can be written as

$$\begin{aligned} \frac{dN_1}{dt} &= N_1 \left(\bar{r}_1 - d_1 N_1 - \frac{b_{12}}{1 + N_2} \right) \\ \frac{dN_2}{dt} &= N_2 \left(-r_2 + \frac{a_{21} N_1}{1 + N_2} \right). \end{aligned} \tag{3.1}$$

Dynamics of system (3.1) have been studied by Jang (2002) except two cases. Now we cite the results and consider the two cases.

Proposition 3.1 Jang (2002) *Solutions of system (3.1) in R^2_+ are nonnegative and bounded, and there is no periodic orbit of (3.1) in R^2_+ .*

Stability of equilibria of (3.1) is as follows. Let $g = 1/(1 + N_2)$. Then the Jacobian matrix of (3.1) is

$$J = \begin{pmatrix} \bar{r}_1 - 2d_1 N_1 - b_{12}g & b_{12} N_1 g^2 \\ a_{21} N_2 g & -r_2 + a_{21} N_1 g - a_{21} N_1 N_2 g^2 \end{pmatrix}. \tag{3.2}$$

There are two equilibria on the axes, namely $O(0, 0)$ and $E_1(\bar{N}_1, 0)$ with

$$\bar{N}_1 = (\bar{r}_1 - b_{12}) / d_1. \tag{3.3}$$

By (3.2), equilibrium O is a saddle point with eigenvalues $\bar{r}_1 - b_{12}$ and $-r_2$, and E_1 has eigenvalues

$$\lambda_1^{(1)} = -(\bar{r}_1 - b_{12}), \quad \lambda_1^{(2)} = -r_2 + a_{21} \bar{N}_1. \tag{3.4}$$

There are at most two positive equilibria $E_{12}^-(N_1^-, N_2^-)$ and $E_{12}^+(N_1^+, N_2^+)$, which satisfy the following conditions when they exist:

$$\begin{aligned} N_1^\pm &= \frac{\bar{r}_1}{2d_1} \pm \frac{\sqrt{\Delta}}{2d_1 a_{21}}, \quad N_2^\pm = \frac{a_{21}}{r_2} \left(N_1^\pm - \frac{r_2}{a_{21}} \right) \\ \Delta &= \bar{r}_1^2 a_{21}^2 - 4d_1 r_2 b_{12} a_{21}. \end{aligned} \tag{3.5}$$

Then system (3.1) has positive equilibria if $N_1^- > r_2/a_{21}$ or $N_1^+ > r_2/a_{21}$. Let

$$a_{21}^0 = \frac{4d_1r_2b_{12}}{\bar{r}_1^2}, \quad a_{21}^* = \frac{r_2d_1}{\bar{r}_1 - b_{12}}, \quad a_{21}^1 = \frac{2r_2d_1}{\bar{r}_1}. \tag{3.6}$$

From (3.4) and (3.5), we obtain that $\Delta > 0$ corresponds to $a_{21} > a_{21}^0$; $\lambda_1^{(2)} > 0$ corresponds to $a_{21} > a_{21}^*$; $a_{21} > a_{21}^1$ corresponds to $\frac{\bar{r}_1}{2d_1} > \frac{r_2}{a_{21}}$. A direct computation shows that $a_{21}^* \geq a_{21}^0$, in which the equality holds if $b_{12} = \bar{r}_1/2$.

The following result was given by Jang (2002) except the case of $\lambda_1^{(2)} = 0$. In order to obtain the necessary and sufficient conditions, we prove the whole result.

Proposition 3.2 (i) E_{12}^- is a positive equilibrium of (3.1) if and only if

$$\lambda_1^{(2)} < 0, \quad \Delta \geq 0, \quad a_{21} > a_{21}^1. \tag{3.7}$$

(ii) E_{12}^+ is a positive equilibrium of (3.1) if and only if one of the following conditions is satisfied: (1) $\lambda_1^{(2)} > 0$; (2) $\Delta > 0$ and $a_{21} \geq a_{21}^1$; (3) $\Delta = 0$ and $a_{21} > a_{21}^1$.

Proof (i) Assume that E_{12}^- is a positive equilibrium. Then $a_{21} > a_{21}^1$ and $\Delta \geq 0$, which implies $a_{21} \geq a_{21}^0$. If $a_{21} > a_{21}^0$, then $a_{21} < a_{21}^*$ by $N_1^- > r_2/a_{21}$. Thus $\lambda_1^{(2)} < 0$. If $a_{21} = a_{21}^0 > a_{21}^1$, then $b_{12} > \bar{r}_1/2$, which implies that $a_{21} = a_{21}^0 < a_{21}^*$. Thus $\lambda_1^{(2)} < 0$. The reverse is similar.

(ii) Assume that E_{12}^+ is a positive equilibrium. Then $\Delta \geq 0$, which implies $a_{21} \geq a_{21}^0$. If $a_{21} > a_{21}^0$ and $a_{21} < a_{21}^1$, then $a_{21} > a_{21}^*$ by $N_1^+ > r_2/a_{21}$. From $a_{21}^* \geq a_{21}^0$, we obtain the condition of $a_{21}^* < a_{21} < a_{21}^1$, which can be written as $a_{21} > a_{21}^*$ (i.e., $\lambda_1^{(2)} > 0$). The reason is that if $a_{21} > a_{21}^*$ and $a_{21} \geq a_{21}^1$ then $N_1^+ > r_2/a_{21}$. When $a_{21} > a_{21}^0$ and $a_{21} \geq a_{21}^1$, it is clear that $N_1^+ > r_2/a_{21}$. If $a_{21} = a_{21}^0$, then $a_{21} > a_{21}^1$ by $N_1^+ > r_2/a_{21}$. The reverse is similar. \square

Dynamics of system (3.1) were given by Jang (2002) except the cases of $\lambda_1^{(2)} = 0$ and $\lambda_1^{(2)} < 0, \Delta = 0, a_{21} > \alpha_{21}^1$. We exhibit the dynamics as follows and give the proof for the two cases in Appendix B.

Theorem 3.3 (i) Assume $\lambda_1^{(2)} > 0$. There is a unique positive equilibrium $E_{12}^+(N_1^+, N_2^+)$ in system (3.1), which is globally asymptotically stable in $\text{int}R_+^2$.

(ii) Assume $\lambda_1^{(2)} = 0$. If $a_{21} > a_{21}^1$, the unique positive equilibrium E_{12}^+ is globally asymptotically stable in $\text{int}R_+^2$. If $a_{21} \leq a_{21}^1$, there is no positive equilibrium in system (3.1) and the boundary equilibrium $E_1(\bar{N}_1, 0)$ is globally asymptotically stable in $\text{int}R_+^2$.

(iii) Assume $\lambda_1^{(2)} < 0$. Then equilibrium E_1 is locally asymptotically stable in $\text{int}R_+^2$. When $a_{21} \leq a_{21}^1$, E_1 is globally asymptotically stable. When $a_{21} > a_{21}^1$, saddle-node bifurcation occurs at $\Delta = 0$: (I) If $\Delta > 0$, there are two positive equilibria E_{12}^- and E_{12}^+ : E_{12}^- is a saddle point while E_{12}^+ is asymptotically stable. (II) If $\Delta = 0$, the equilibria E_{12}^- and E_{12}^+ coincide and form a saddle-node point. In

cases (I–II), the separatrices of E_{12}^- subdivide $\text{int}R_+^2$ into two regions: one is the basin of attraction of E_1 , while the other is that of E_{12}^+ . (III) If $\Delta < 0$, there is no positive equilibrium and E_1 is globally asymptotically stable in $\text{int}R_+^2$.

Theorem 3.3 provides criteria for persistence of the pollinator. Recall that $\Delta < 0$ can be written as $a_{21} < a_{21}^0$. When the energetic reward for the pollinator is small (e.g., $a_{21} < a_{21}^0$), the benefit for searching such a plant is small in comparison with other plants, which implies extinction of the pollinator in this system. When the energetic reward is intermediate (e.g., $\max\{a_{21}^0, a_{21}^1\} < a_{21} < a_{21}^*$), there are two fates for the pollinator. The system has two positive equilibria and the stable manifold of the unstable one becomes the threshold condition for persistence of the pollinator. The plant and pollinator can survive if their initial densities are not below the threshold. Otherwise, the pollinator goes to extinction. When the energetic reward is large (i.e., $a_{21} > a_{21}^*$), the pollinator can be attracted by the plant and both species persist in the system. That is, the pollinator will increase rapidly when rare because of the rich reward. Even when the pollinator is not rare, it will persist in the plant-pollinator system because of the rich reward and pollination–mutualisms as shown by Theorem 3.3(i).

On the invariant (N_1, N_3) -plane, the restricted system of (2.3) is

$$\begin{aligned} \frac{dN_1}{dt} &= N_1 \left(\bar{r}_1 - d_1 N_1 - \frac{b_{13}}{1 + N_3} \right) \\ \frac{dN_3}{dt} &= N_3 \left(-r_3 + \frac{a_{31} N_1}{1 + N_3} \right) \end{aligned} \tag{3.8}$$

where $b_{13} = b_{12}$.

Since equations in (3.8) have the same form as those in (3.8), their dynamics can be described by Theorem 3.3 with the following replacements:

$$\begin{aligned} r_2 &\rightarrow r_3, \quad a_{21} \rightarrow a_{31}, \quad b_{12} \rightarrow b_{13}, \quad \lambda_1^{(2)} \rightarrow \lambda_1^{(3)}, \quad \Delta \rightarrow \check{\Delta} \\ N_1^\pm &\rightarrow \check{N}_1^\pm, \quad N_2^\pm \rightarrow \check{N}_3^\pm, \quad E_{12}^\pm(N_1^\pm, N_2^\pm) \rightarrow E_{13}^\pm(\check{N}_1^\pm, \check{N}_3^\pm). \end{aligned}$$

Denote

$$a_{31}^0 = \frac{4d_1 r_3 b_{13}}{\bar{r}_1^2}, \quad a_{31}^* = \frac{r_3 d_1}{\bar{r}_1 - b_{13}}, \quad a_{31}^1 = \frac{2r_3 d_1}{\bar{r}_1}. \tag{3.9}$$

A direct computation shows that

$$\frac{r_2}{a_{21}^0} = \frac{r_3}{a_{31}^0}, \quad \frac{r_2}{a_{21}^*} = \frac{r_3}{a_{31}^*}, \quad \frac{r_2}{a_{21}^1} = \frac{r_3}{a_{31}^1}. \tag{3.10}$$

From (3.10), we conclude the following result.

Proposition 3.4 Assume $\frac{r_2}{a_{21}} = \frac{r_3}{a_{31}}$. Then we obtain $\Delta = r_2^2 \check{\Delta} / r_3^2$. Moreover, $a_{21} > a_{21}^0$ if and only if $a_{31} > a_{31}^0$; $a_{21} > a_{21}^*$ if and only if $a_{31} > a_{31}^*$; $a_{21} > a_{21}^1$ if and only if $a_{31} > a_{31}^1$.

4 Global dynamics

In this section, we completely characterize global dynamics of the three-species system (2.3) in R_+^3 . We show that for some values of parameters, mutualism between the consumer and resource can lead to survival of one or both consumers, while the invasion of a competitive consumer could result in extinction of all consumers that include the invader itself. For other values of parameters, the principle of competitive exclusion holds, which implies that one of the consumers goes to extinction and the other consumer and the resource coexists at a positive steady state in R_+^2 .

Proposition 4.1 *If $\frac{r_2}{a_{21}} = \frac{r_3}{a_{31}}$, system (2.3) has a first integral $V(N_1, N_2, N_3) = N_2^{-a_{31}} N_3^{a_{21}}$.*

Proof Since $\frac{r_2}{a_{21}} = \frac{r_3}{a_{31}}$, we have

$$\frac{dV(N_1, N_2, N_3)}{dt} \Big|_{(2.3)} = a_{21}a_{31} \left(\frac{r_2}{a_{21}} - \frac{r_3}{a_{31}} \right) V(N_1, N_2, N_3) = 0,$$

which implies that the function $V(N_1, N_2, N_3)$ is a first integral of (2.3). □

On the invariant surface

$$V(N_1, N_2, N_3) = c_0$$

with $c_0 = N_2^{-a_{31}}(0)N_3^{a_{21}}(0) > 0$, we obtain $N_3 = cN_2^s$ with $c = c_0^{1/a_{21}}$, $s = a_{31}/a_{21}$. Without loss of generality, we assume $s \geq 1$. Then system (2.3) on the invariant surface can be written as

$$\begin{aligned} \frac{dN_1}{dt} &= N_1 \left(\bar{r}_1 - d_1N_1 - \frac{b_{12}}{1 + N_2 + cN_2^s} \right) \\ \frac{dN_2}{dt} &= N_2 \left(-r_2 + \frac{a_{21}N_1}{1 + N_2 + cN_2^s} \right). \end{aligned} \tag{4.1}$$

The boundedness of solutions of (4.1) can be obtained directly from Proposition 2.1. Existence of periodic orbits can be excluded by the Bendixson–Dulac Theorem. Indeed, let $\hat{F} = (\hat{F}_1, \hat{F}_2)^T$ be the right-hand side of (4.1). Let $\phi(N_1, N_2) = 1/(N_1N_2)$. Then we have

$$\frac{\partial(\phi\hat{F}_1)}{\partial N_1} + \frac{\partial(\phi\hat{F}_2)}{\partial N_2} = -\frac{d_1}{N_2} - \frac{a_{21}(1 + csN_2^{s-1})}{(1 + N_2 + cN_2^s)^2} < 0.$$

Thus, we conclude the following results.

Proposition 4.2 *Solutions of system (4.1) are bounded and there is no periodic orbit of (4.1) in R_+^2 .*

Stability of equilibria of (4.1) is as follows. Let $\hat{g} = (1 + N_2 + cN_2^s)^2$. The Jacobian matrix of (4.1) is

$$J = \begin{pmatrix} \bar{r}_1 - 2d_1N_1 - b_{12}\hat{g} & b_{12}N_1(1 + scN_2^{s-1})\hat{g}^2 \\ a_{21}N_2\hat{g} & -r_2 + a_{21}N_1\hat{g} - a_{21}N_1N_2(1 + scN_2^{s-1})\hat{g}^2 \end{pmatrix}. \tag{4.2}$$

There are two equilibria on the axes, namely $O(0, 0)$ and $E_1(\bar{N}_1, 0)$ where \bar{N}_1 is defined in (3.3). O is a saddle point with eigenvalues $\bar{r}_1 - b_{12}$ and $-r_2$, and E_1 has eigenvalues $\lambda_1^{(1)}$ and $\lambda_1^{(2)}$ defined in (3.4).

There are at most two positive equilibria $\hat{E}_{12}^-(N_1^-, \hat{N}_2^-)$ and $\hat{E}_{12}^+(N_1^+, \hat{N}_2^+)$, which satisfy the following conditions when they exist

$$N_1 = \hat{h}(N_2) = \frac{r_2}{a_{21}}(1 + N_2 + cN_2^s), \quad N_1^\pm = \frac{\bar{r}_1}{2d_1} \pm \frac{\sqrt{\Delta}}{2d_1a_{21}}, \tag{4.3}$$

where Δ is defined in (3.5). Since the function $\hat{h}(N_2) \geq r_2/a_{21}$ is monotonically increasing, system (4.1) has positive equilibria if $N_1^- > r_2/a_{21}$ or $N_1^+ > r_2/a_{21}$.

Let a_{21}^0, a_{21}^* and a_{21}^1 be those defined in (3.6). By a proof similar to that for Proposition 3.2, we conclude the following result.

- Proposition 4.3** (i) \hat{E}_{12}^- is a positive equilibrium of (4.1) if and only if $\lambda_1^{(2)} < 0, \Delta \geq 0, a_{21} > a_{21}^1$.
 (ii) \hat{E}_{12}^+ is a positive equilibrium of (4.1) if and only if one of the following conditions is satisfied: (1) $\lambda_1^{(2)} > 0$; (2) $\Delta > 0$ and $a_{21} \geq a_{21}^1$; (3) $\Delta = 0$ and $a_{21} > a_{21}^1$.

Dynamics of system (4.1) are shown as follows, the proof of which is in Appendix C.

Theorem 4.4 (i) Assume $\lambda_1^{(2)} > 0$. There is a unique positive equilibrium $\hat{E}_{12}^+(N_1^+, \hat{N}_2^+)$ in system (4.1), which is globally asymptotically stable in $\text{int}R_+^2$, as shown in Fig. 1a.

- (ii) Assume $\lambda_1^{(2)} = 0$. If $a_{21} > a_{21}^1$, the unique positive equilibrium \hat{E}_{12}^+ is globally asymptotically stable in $\text{int}R_+^2$. If $a_{21} \leq a_{21}^1$, then the boundary equilibrium $E_1(\bar{N}_1, 0)$ is globally asymptotically stable in $\text{int}R_+^2$.
 (iii) Assume $\lambda_1^{(2)} < 0$. Then equilibrium E_1 is locally asymptotically stable. When $a_{21} \leq a_{21}^1$, E_1 is globally asymptotically stable in $\text{int}R_+^2$. When $a_{21} > a_{21}^1$, saddle-node bifurcation occurs at $\Delta = 0$: (I) If $\Delta > 0$, there are two positive equilibria \hat{E}_{12}^- and \hat{E}_{12}^+ . \hat{E}_{12}^- is a saddle point while \hat{E}_{12}^+ is asymptotically stable, as shown in Fig. 1b. (II) If $\Delta = 0$, \hat{E}_{12}^- and \hat{E}_{12}^+ coincide and form a saddle-node point, as shown in Fig. 1c. In cases (I–II), the separatrices of \hat{E}_{12}^- subdivide $\text{int}R_+^2$ into two regions: one is the basin of attraction of E_1 , while the other is that of \hat{E}_{12}^+ . (III) If $\Delta < 0$, then E_1 is globally asymptotically stable in $\text{int}R_+^2$, as shown in Fig. 1d.

In the three-dimensional system (2.3), there exist equilibria $O(0, 0, 0)$ and $P_1(\bar{N}_1, 0, 0)$ for all values of the parameters. Apart from the two boundary equilibria, system (2.3) may have other boundary equilibria and positive equilibria in R_+^3

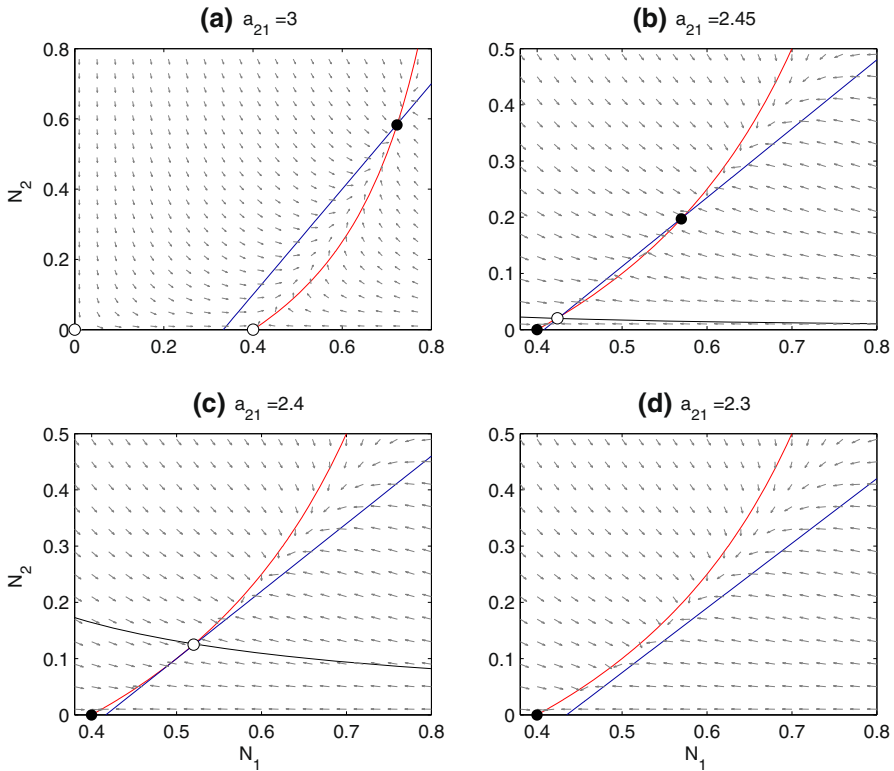


Fig. 1 Phase-plane diagram of system (4.1). Stable and unstable equilibria are identified by solid and open circles, respectively. Vector fields are shown by gray arrows. Let $\bar{r}_1 = r_2 = r_3 = d_1 = s = c = 1, b_{12} = 0.6$. Then $a_{21}^0 = 2.4, a_{21}^1 = 2, a_{21}^* = 2.5$. **a** Let $a_{21} = 3$. All positive solutions of (4.1) converge to equilibrium $E_{12}^+(0.723, 0.583)$. **b, c** Let $a_{21} = 2.45$ and $a_{21} = 2.4$, respectively. There are two positive equilibria E_{12}^- and E_{12}^+ . 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}^+ . **d** Let $a_{21} = 2.3$. All positive solutions of (4.1) converges to equilibrium $E_1(0.4, 0)$

for some parameter values. Doing easy algebra calculations and citing Proposition 3.4, Theorems 3.3 and 4.4, we obtain the following result.

Proposition 4.5 *System (2.3) always has the boundary equilibria $O(0, 0, 0)$ and $P_1(\bar{N}_1, 0, 0)$ in R_+^3 .*

- (i) *If $\lambda_1^{(2)} > 0$, system (2.3) has additional boundary equilibria $P_{12}^+(N_1^+, N_2^+, 0)$ in R_+^3 . If $\lambda_1^{(3)} > 0$, system (2.3) has additional boundary equilibria $P_{13}^+(\check{N}_1^+, 0, \check{N}_3^+)$ in R_+^3 . If $\frac{r_2}{a_{21}} = \frac{r_3}{a_{31}}$ and $\lambda_1^{(2)} > 0$, then system (2.3) has infinitely many positive equilibria $P^+(N_1, N_2, N_3)$ in $\text{int}R_+^3$, which fill up a segment L^+ with endpoints at the boundary equilibria P_{12}^+ and P_{13}^+ ; more precisely,*

$$L^+ = \left\{ (N_1, N_2, N_3) \geq 0 : N_1 = \frac{\bar{r}_1}{2d_1} + \frac{\sqrt{\Delta}}{2d_1 a_{21}}, \quad \frac{a_{21} N_1}{1 + N_2 + N_3} = r_2 \right\}.$$

- (ii) If $\lambda_1^{(2)} < 0$, $a_{21} > a_{21}^1$ and $\Delta \geq 0$, then system (2.3) has additional boundary equilibria $P_{12}^\pm(N_1^\pm, N_2^\pm, 0)$. If $\lambda_1^{(3)} < 0$, $a_{31} > a_{31}^1$ and $\check{\Delta} \geq 0$, then system (2.3) has additional boundary equilibria $P_{13}^\pm(\check{N}_1^\pm, 0, \check{N}_3^\pm)$.
- (iii) Assume $\frac{r_2}{a_{21}} = \frac{r_3}{a_{31}}$, $\lambda_1^{(2)} < 0$, $a_{21} > a_{21}^1$ and $\Delta \geq 0$. Then system (2.3) has infinitely many positive equilibria $P^\pm(N_1, N_2, N_3)$ in $\text{int}R_+^3$, which fill up two segments L^\pm with endpoints at the boundary equilibria P_{12}^\pm and P_{13}^\pm ; more precisely,

$$L^\pm = \left\{ (N_1, N_2, N_3) \geq 0 : N_1 = \frac{\bar{r}_1}{2d_1} \pm \frac{\sqrt{\Delta}}{2d_1 a_{21}}, \quad \frac{a_{21} N_1}{1 + N_2 + N_3} = r_2 \right\}.$$

Summarizing Theorems 3.3, 4.4 and Proposition 4.5, we conclude global dynamics of system (2.3) as follows.

Theorem 4.6 *Let $\frac{r_2}{a_{21}} = \frac{r_3}{a_{31}}$.*

- (i) Assume $\lambda_1^{(2)} > 0$, or $\lambda_1^{(2)} = 0$ and $a_{21} > a_{21}^1$. System (2.3) has infinitely many positive equilibria P^+ filling up a segment L^+ which attract all solutions of system (2.3) with positive initial conditions, the endpoints of L^+ attract all solutions of system (2.3) with initial conditions $(N_1, N_2, 0)$ or $(N_1, 0, N_3)$ satisfying $N_1 N_2 N_3 > 0$, equilibrium $P_1(\bar{N}_1, 0, 0)$ attracts all solutions of system (2.3) with initial conditions $(N_1, 0, 0)$ satisfying $N_1 > 0$, and the origin $O(0, 0, 0)$ attracts all solutions of system (2.3) with nonnegative initial conditions $(0, N_2, N_3)$. The phase portrait is sketched in Fig. 2.
- (ii) Assume $\lambda_1^{(2)} < 0$, $\Delta \geq 0$ and $a_{21} > a_{21}^1$. The equilibrium P_1 is locally asymptotically stable in $\text{int}R_+^3$ and system (2.3) has infinitely many positive equilibria P^\pm filling up two segments L^\pm . The separatrices of equilibria on L^- form a 2-dimensional separatrix surface S^- , which subdivides $\text{int}R_+^3$ into two regions: one is the basin of attraction of P_1 , while the other is that of L^+ . The separatrices of endpoints of L^- subdivide the corresponding plane in $\text{int}R_+^2$ into two regions: one is the basin of attraction of P_1 , while the other is that of the endpoints of L^+ . P_1 also attracts all solutions of system (2.3) with initial conditions $(N_1, 0, 0)$ satisfying $N_1 > 0$, while the origin O attracts all solutions of system (2.3) with nonnegative initial conditions $(0, N_2, N_3)$. The phase portrait is sketched in Fig. 3.
- (iii) Assume $\Delta < 0$, or $\lambda_1^{(2)} \leq 0$ and $a_{21} \leq a_{21}^1$. System (2.3) has only two equilibria O and P_1 , the equilibrium P_1 attracts all solutions of system (2.3) in R_+^3 except the orbits in the (N_2, N_3) -plane, and the origin O attracts all solutions of (2.3) in the (N_2, N_3) -plane. The phase portrait is sketched in Fig. 4.

Theorem 4.6 reveals that two competing consumers either coexist or coextinct if they have the same ratio of death rate and propagation rate. Recall that $\lambda_1^{(2)} > 0$ can be

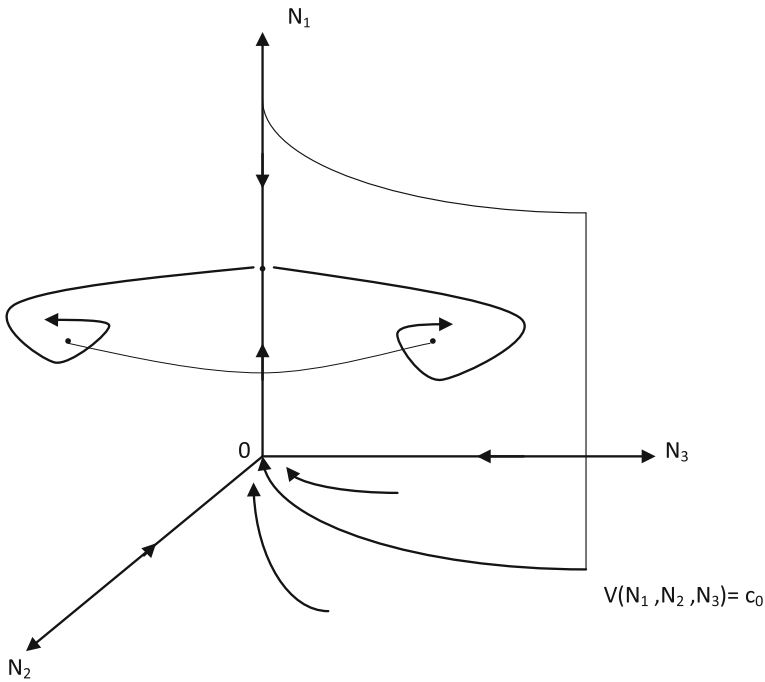


Fig. 2 Global diagram of system (2.3) when $\frac{r_2}{a_{21}} = \frac{r_3}{a_{31}}$ and $a_{21} > a_{21}^*$

written as $\frac{r_2}{a_{21}} < \bar{N}_1$, where \bar{N}_1 is the carrying capacity of the resource in the absence of consumers. Thus, when the ratio of death rate and propagation rate of the consumer is less than the carrying capacity of the resource (i.e., $\frac{r_2}{a_{21}} < \bar{N}_1$), two competing consumers coexist at a positive equilibrium. When the ratio is large (e.g., $\frac{r_2}{a_{21}} > \frac{r_2}{a_{21}^*}$), the two competing consumers eventually go to extinction even though the resource persists.

When the ratio is intermediate (e.g., $\bar{N}_1 < \frac{r_2}{a_{21}} < \min\{\frac{r_2}{a_{21}^*}, \frac{r_2}{a_{21}^*}\}$), the competing consumers could coexist at a steady state if initial densities of the three species are not small, i.e., not below the stable manifold of L^- . However, if the densities are below the threshold, both consumers go to extinction and the resource persists. This delicate threshold phenomenon is also observed by Lundberg and Ingvarsson (1998) for which an obligate plant-pollinator model is considered. Moreover, the resource approaches a density larger than \bar{N}_1 when in coexistence with consumers, which would promote survival of more consumers in the n -species system as shown in Sect. 5.

From Theorem 4.6(ii), we obtain conditions under which interaction outcomes between the consumers can transition between mutualism, parasitism, competition and neutralism as the initial population densities vary.

Theorem 4.7 Assume $\frac{r_2}{a_{21}} = \frac{r_3}{a_{31}}$. Let $\lambda_1^{(2)} < 0$, $\Delta \geq 0$ and $a_{21} > a_{21}^1$.

- (i) Interaction outcomes between species N_2 and N_3 are mutualism if and only if the initial values $(N_1(0), N_2(0), 0)$ and $(N_1(0), 0, N_3(0))$ are below the sepa-

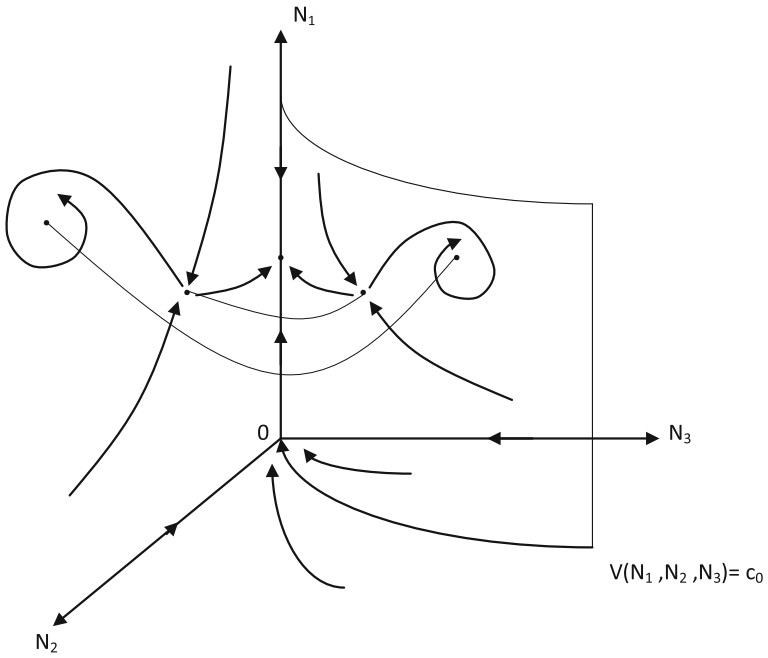


Fig. 3 Global diagram of system (2.3) when $\frac{r_2}{a_{21}} = \frac{r_3}{a_{31}}, a_{21}^0 < a_{21} < a_{21}^*$ and $a_{21} > a_{21}^1$

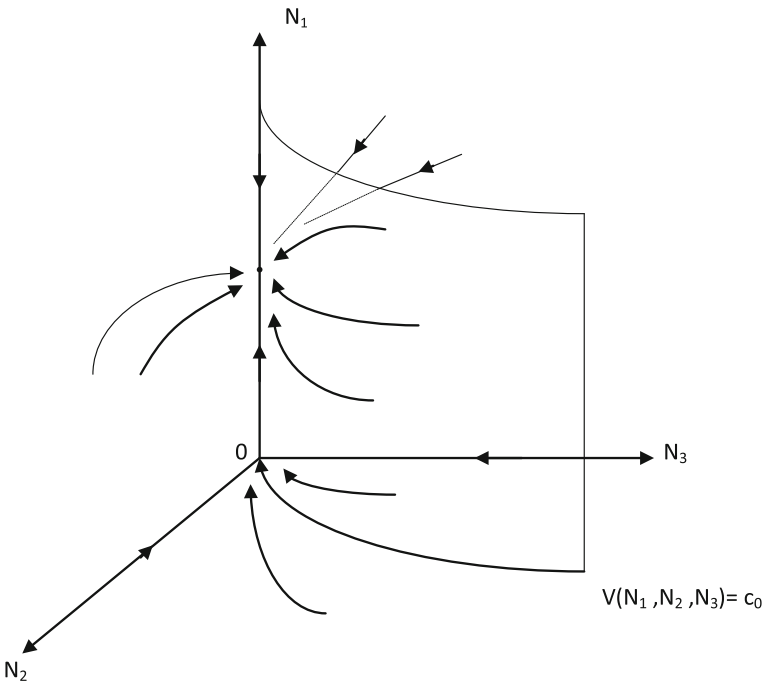


Fig. 4 Global diagram of system (2.3) when $\frac{r_2}{a_{21}} = \frac{r_3}{a_{31}}$ and $a_{21} < a_{21}^0$

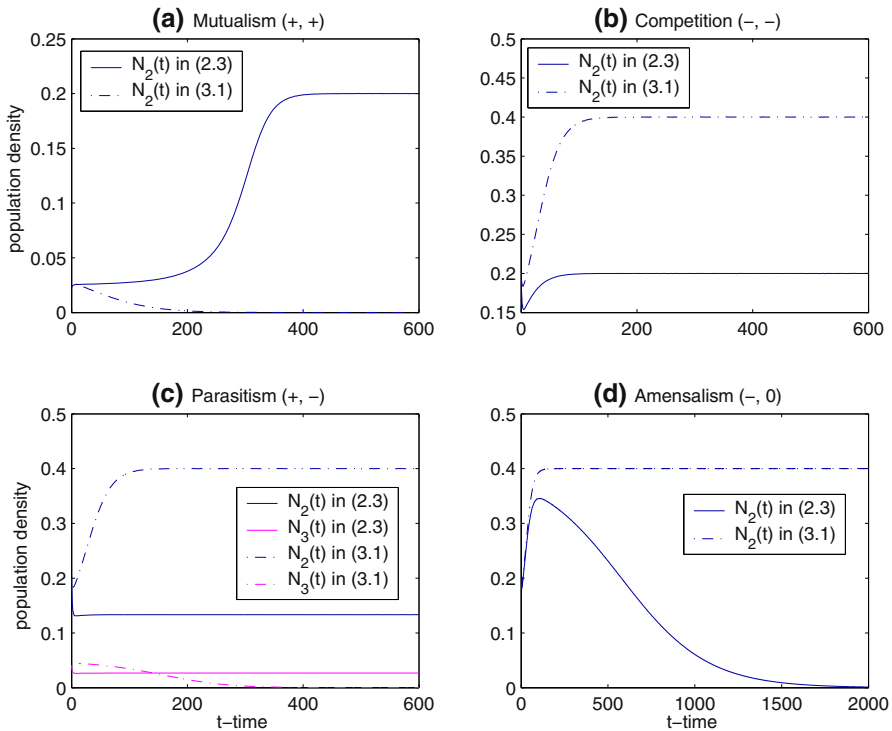


Fig. 5 Transition of interaction outcomes between species N_2 and N_3 in system (2.3). Let $\bar{r}_1 = r_2 = r_3 = d_1 = 1, b_{12} = 0.6$. Thus $a_{21}^0 = 2.4, a_{21}^1 = 2, a_{21}^* = 2.5$. **a, b** Let $a_{21} = a_{31} = 2.45$. When $N(0) = (0.45, 0.023, 0.023)$, neither species N_2 nor N_3 can survive in the absence of the other, while they can coexist and each species approaches a density 0.2. Thus their relationship is mutualism. When $N(0) = (0.45, 0.2, 0.2)$, each species of N_2 and N_3 can approach a density 0.4 in the absence of the other. However, when they coexist, each species approaches a density 0.2. Thus their relationship is competition. **c** Let $a_{21} = a_{31} = 2.45$. When $N(0) = (0.45, 0.2, 0.04)$, species N_2 approaches a density 0.4 in the absence of N_3 , while species N_3 goes to extinction in the absence of N_2 . When they coexist, species N_2 approaches the density 0.14 and species N_3 persists at 0.028. Thus their relationship is parasitism. **d** Let $a_{21} = 2.45, a_{31} = 2.46, N(0) = (0.45, 0.2, 0.02)$. Species N_2 approaches a density 0.4 in the absence of N_3 , while it goes to extinction in the presence of N_3 . Species N_3 always goes to extinction. Thus their relationship is amensalism

atrices of E_{12}^- and E_{13}^- respectively, but $(N_1(0), N_2(0), N_3(0))$ is not below the separatrix surface S^- of L^- , as shown in simulations of Fig. 5a.

- (ii) Interaction outcomes between species N_2 and N_3 are competition if and only if the initial values $(N_1(0), N_2(0), 0)$ and $(N_1(0), 0, N_3(0))$ are not below separatrices of E_{12}^- and E_{13}^- respectively, and $(N_1(0), N_2(0), N_3(0))$ is also not below S^- , as shown in simulations of Fig. 5b.
- (iii) Interaction outcomes between species N_2 and N_3 are neutralism if and only if the initial values $(N_1(0), N_2(0), 0)$ and $(N_1(0), 0, N_3(0))$ are below the separatrices of E_{12}^- and E_{13}^- respectively, and $(N_1(0), N_2(0), N_3(0))$ is also below S^- .
- (iv) Interaction outcomes between species N_2 and N_3 are parasitism if and only if one of the initial values $(N_1(0), N_2(0), 0)$ and $(N_1(0), 0, N_3(0))$ is below the

corresponding separatrices of E_{12}^- or E_{13}^- , the other is not below that separatrices, and $(N_1(0), N_2(0), N_3(0))$ is also not below S^- , as shown in simulations of Fig. 5c.

Proof (i) In this case, neither species N_2 nor N_3 can survive in the absence of the other, while they coexist at $P^+(N_1^+, N_2^+, N_3^+)$. Thus their relationship is mutualism.

(ii) In this case, species N_2 and N_3 can respectively approach positive densities N_2^+ and N_3^+ in the absence of the other, while they coexist at $P^+(N_1^+, \hat{N}_2^+, \hat{N}_3^+)$. Since

$$N_1^+ = h(N_2^+) = \frac{r_2}{a_{21}}(1 + N_2^+), \quad N_1^+ = \hat{h}(\hat{N}_2^+) = \frac{r_2}{a_{21}}\left(1 + \hat{N}_2^+ + c(\hat{N}_2^+)^s\right),$$

we obtain $N_2^+ > \hat{N}_2^+$. A similar discussion can show $N_3^+ > \hat{N}_3^+$. Thus their relationship is competition.

(iii) In this case, both species cannot survive in the absence of the other, and cannot survive in the presence of the other. Thus their relationship is neutralism.

(iv) Without loss of generality, we assume that in the absence of species N_3 , species N_1 and N_2 can approach positive densities N_1^+ and N_2^+ respectively, while species N_3 goes to extinction in the absence of species N_2 . When species N_2 and N_3 coexist at $P^+(N_1^+, \hat{N}_2^+, \hat{N}_3^+)$, we have $N_2^+ > \hat{N}_2^+$ by a proof similar to that in (ii). Thus their relationship is parasitism. \square

By a proof similar to that for Theorem 4.7, we conclude the following result.

Theorem 4.8 Assume $N(0) > 0$ and $\frac{r_2}{a_{21}} = \frac{r_3}{a_{31}}$.

(i) Interaction outcomes between species N_2 and N_3 are competition if $\lambda_1^{(2)} > 0$, or $\lambda_1^{(2)} = 0$ and $a_{21} > a_{21}^1$.

(ii) Interaction outcomes between species N_2 and N_3 are neutralism if $\Delta < 0$, or $\lambda_1^{(2)} = 0$ and $a_{21} \leq a_{21}^1$.

Now we consider conditions under which the principle of competitive exclusion holds for system (2.3). We focus on the case of $\frac{r_2}{a_{21}} < \frac{r_3}{a_{31}}$, while a similar discussion can be given for the case of $\frac{r_2}{a_{21}} > \frac{r_3}{a_{31}}$. We first give the dynamics of system (2.3) in $\text{int}R_+^3$.

Theorem 4.9 If $\frac{r_2}{a_{21}} < \frac{r_3}{a_{31}}$, the principle of competitive exclusion may hold for system (2.3). More precisely, orbits of system (2.3) in $\text{int}R_+^3$ are asymptotic to the orbits on the (N_1, N_2) -plane in forward time.

Proof Let

$$V_1(N_1, N_2, N_3) = N_2^{-a_{31}} N_3^{a_{21}}.$$

Since $\frac{r_2}{a_{21}} < \frac{r_3}{a_{31}}$, we have

$$\frac{dV_1(N_1, N_2, N_3)}{dt} \Big|_{(2.3)} = a_{21}a_{31} \left(\frac{r_2}{a_{21}} - \frac{r_3}{a_{31}} \right) V_1(N_1, N_2, N_3) \leq 0.$$

Let $\frac{dV_1(N_1, N_2, N_3)}{dt}|_{(2.3)} = 0$, we obtain $N_3 = 0$. By the LaSalle principle, all solutions of system (2.3) in $\text{int}R_+^3$ are asymptotic to the orbits on the (N_1, N_2) -plane in forward time, which leads to the statement. \square

When $\frac{r_2}{a_{21}} < \frac{r_3}{a_{31}}$ and $\lambda_1^{(2)} < 0$, we obtain $\lambda_1^{(3)} < 0$ by (3.10) and the saddle point E_{12}^- has a two-dimensional stable manifold S^- in $\text{int}R_+^3$. Summarizing Theorems 3.3, 4.9, we obtain the following result.

Theorem 4.10 *Assume $\frac{r_2}{a_{21}} < \frac{r_3}{a_{31}}$. The principle of competitive exclusion holds for system (2.3) if and only if one of the following conditions is satisfied.*

- (i) $\lambda_1^{(2)} > 0$, or $\lambda_1^{(2)} = 0$ and $a_{21} > a_{21}^1$; $\lambda_1^{(3)} > 0$, or $\lambda_1^{(3)} = 0$ and $a_{31} > a_{31}^1$. In this case, orbits of system (2.3) in $\text{int}R_+^3$ converge to P_{12}^+ , which implies that species N_3 goes to extinction and species N_2 survives. Thus, interaction outcomes between the species is amensalism $(-, 0)$.
- (ii) $\lambda_1^{(2)} > 0$, $\lambda_1^{(3)} < 0$, $a_{31} > a_{31}^1$ and $\check{\Delta} \geq 0$, while the initial value of $(N_1(0), N_3(0))$ is not below the separatrix of E_{13}^- . In this case, orbits of system (2.3) in $\text{int}R_+^3$ converge to P_{12}^+ . Thus species N_3 goes to extinction and species N_2 survives.
- (iii) $\lambda_1^{(2)} < 0$, $\Delta \geq 0$, $a_{21} > a_{21}^1$; $a_{31} > a_{31}^1$ and $\check{\Delta} \geq 0$, $(N_1(0), N_2(0))$ and $(N_1(0), N_3(0))$ are not below the separatrix of E_{12}^- and E_{13}^- respectively, while $(N_1(0), N_2(0), N_3(0))$ is also not below the stable manifold S^- of E_{12}^- in $\text{int}R_+^3$. In this case, orbits of system (2.3) in $\text{int}R_+^3$ converge to P_{12}^+ . Thus species N_3 goes to extinction and species N_2 survives.

When the principle of competitive exclusion does not hold for system (2.3), both competing consumers go to extinction, and all orbits of system (2.3) converge to the equilibrium P_1 except the orbits in the (N_2, N_3) -plane.

5 The n -dimensional system

In this section, we thoroughly demonstrate global dynamics of the one-plant and $(n - 1)$ -pollinator system, which shows that all of the results for the one-plant and two-pollinator system can be extended to the n -species system.

Let

$$G_1(N_1) = r_1 - d_1N_1, \quad G_i(N_i) = -r_i, \quad a_{i1} = \frac{\sigma_i\alpha\beta_i}{\omega + \beta_0N_0}$$

$$\bar{r}_1 = r_1 + \sigma_1\alpha, \quad b_{12} = \frac{\sigma_1\alpha\omega}{\omega + \beta_0N_0}, \quad \hat{N}_i = \frac{\beta_i}{\omega + \beta_0N_0}N_i, \quad 2 \leq i \leq n.$$

By dropping hats in \hat{N}_i , system (2.2) becomes

$$\frac{dN_1}{dt} = N_1 \left(\bar{r}_1 - d_1N_1 - \frac{b_{12}}{1 + \sum_{j=2}^n N_j} \right)$$

$$\frac{dN_i}{dt} = N_i \left(-r_i + \frac{a_{i1}N_1}{1 + \sum_{j=2}^n N_j} \right), \quad 2 \leq i \leq n. \tag{5.1}$$

Then $\bar{r}_1 > b_{12}$ and solutions of system (5.1) in R_+^n are nonnegative.

By a proof similar to that for Proposition 2.1, we conclude the following result.

Proposition 5.1 *Solutions of system (5.1) are bounded in R_+^n .*

Without loss of generality, we assume that there is $3 \leq m \leq n$ such that

$$\frac{r_2}{a_{21}} = \frac{r_i}{a_{i1}}, \quad \frac{r_2}{a_{21}} < \frac{r_j}{a_{j1}}, \quad 3 \leq i \leq m, \quad m + 1 \leq j \leq n.$$

By a proof similar to that for Theorem 4.9, we conclude the following result by constructing Lyapunov function $V_j(N) = N_2^{-a_{j1}} N_j^{a_{21}}$.

Theorem 5.2 *Orbits (N_1, N_2, \dots, N_n) of system (5.1) in $\text{int}R_+^n$ satisfy $\lim_{t \rightarrow \infty} N_j(t) = 0$ with $m + 1 \leq j \leq n$, and are asymptotic to the (N_1, N_2, \dots, N_m) -space in forward time.*

Now we focus on the m -dimensional subsystem of (5.1) consisting of (N_1, N_2, \dots, N_m) :

$$\begin{aligned} \frac{dN_1}{dt} &= N_1 \left(\bar{r}_1 - d_1 N_1 - \frac{b_{12}}{1 + \sum_{j=2}^m N_j} \right) \\ \frac{dN_i}{dt} &= N_i \left(-r_i + \frac{a_{i1}N_1}{1 + \sum_{j=2}^m N_j} \right), \quad 2 \leq i \leq m \end{aligned} \tag{5.2}$$

where $\frac{r_2}{a_{21}} = \frac{r_i}{a_{i1}}$.

By a proof similar to that for Proposition 4.1, we conclude the following result.

Proposition 5.3 *System of (5.2) has first integrals $V_i(N) = N_2^{-a_{i1}} N_i^{a_{21}}$, $3 \leq i \leq m$.*

Let $s_i = a_{i1}/a_{21}$. Without loss of generality, we assume $s_i \geq 1$ for $3 \leq i \leq m$. On the invariant set $N_i = c_i N_2^{s_i}$ with $c_i > 0$, system (5.2) can be written as

$$\begin{aligned} \frac{dN_1}{dt} &= N_1 \left(\bar{r}_1 - d_1 N_1 - \frac{b_{12}}{1 + N_2 + \sum_{i=3}^m c_i N_2^{s_i}} \right) \\ \frac{dN_2}{dt} &= N_2 \left(-r_2 + \frac{a_{21}N_1}{1 + N_2 + \sum_{i=3}^m c_i N_2^{s_i}} \right). \end{aligned} \tag{5.3}$$

Dynamics of system (5.3) can be obtained by a proof similar to that for (4.1). Thus we exhibit the results in Propositions 5.4 and 5.5 and Theorem 5.6, but omit their proofs.

Proposition 5.4 *Solutions of system (5.3) are bounded in R_+^2 and there is no periodic orbit of (5.3) in R_+^2 .*

There are two equilibria on the axes, namely $O(0, 0)$ and $E_1(\bar{N}_1, 0)$ where \bar{N}_1 is defined in (3.3). O is a saddle point with eigenvalues $\bar{r}_1 - b_{12}$ and $-r_2$, and E_1 has eigenvalues $\lambda_1^{(1)}$ and $\lambda_1^{(2)}$ defined in (3.4).

There are at most two positive equilibria $\tilde{E}_{12}^-(N_1^-, \tilde{N}_2^-)$ and $\tilde{E}_{12}^+(N_1^+, \tilde{N}_2^+)$, which satisfy the following conditions when they exist

$$N_1 = \tilde{h}(N_2) = \frac{r_2}{a_{21}} \left(1 + N_2 + \sum_{i=3}^m c_i N_2^{s_i} \right), \quad N_1^\pm = \frac{\bar{r}_1}{2d_1} \pm \frac{\sqrt{\Delta}}{2d_1 a_{21}}, \quad (5.4)$$

where Δ is defined in (3.5).

Let a_{21}^0, a_{21}^* and a_{21}^1 be those defined in (3.6). Then we have:

- Proposition 5.5** (i) \tilde{E}_{12}^- is a positive equilibrium of (5.3) if and only if $\lambda_1^{(2)} < 0, \Delta \geq 0, a_{21} > a_{21}^1$.
 (ii) \tilde{E}_{12}^+ is a positive equilibrium of (5.3) if and only if one of the following conditions is satisfied: (1) $\lambda_1^{(2)} > 0$; (2) $\Delta > 0$ and $a_{21} \geq a_{21}^1$; (3) $\Delta = 0$ and $a_{21} > a_{21}^1$.

- Theorem 5.6** (i) Assume $\lambda_1^{(2)} > 0$. There is a unique positive equilibrium $\tilde{E}_{12}^+(N_1^+, \tilde{N}_2^+)$ in system (5.3), which is globally asymptotically stable in $\text{int}R_+^2$.
 (ii) Assume $\lambda_1^{(2)} = 0$. If $a_{21} > a_{21}^1$, the unique positive equilibrium \tilde{E}_{12}^+ is globally asymptotically stable in $\text{int}R_+^2$. If $a_{21} \leq a_{21}^1$, then the boundary equilibrium $E_1(\bar{N}_1, 0)$ is globally asymptotically stable in $\text{int}R_+^2$.
 (iii) Assume $\lambda_1^{(2)} < 0$. Then equilibrium E_1 is locally asymptotically stable. When $a_{21} \leq a_{21}^1$, E_1 is globally asymptotically stable in $\text{int}R_+^2$. When $a_{21} > a_{21}^1$, saddle-node bifurcation occurs at $\Delta = 0$: (a) If $\Delta > 0$, there are two positive equilibria \tilde{E}_{12}^- and \tilde{E}_{12}^+ . \tilde{E}_{12}^- is a saddle point while \tilde{E}_{12}^+ is asymptotically stable. (b) If $\Delta = 0$, then \tilde{E}_{12}^- and \tilde{E}_{12}^+ coincide and form a saddle-node point. In cases (a–b), the separatrices of \tilde{E}_{12}^- subdivide $\text{int}R_+^2$ into two regions: one is the basin of attraction of E_1 , while the other is that of \tilde{E}_{12}^+ . (c) If $\Delta < 0$, then E_1 is globally asymptotically stable in $\text{int}R_+^2$.

From Proposition 5.5, we obtain existence of the boundary and positive equilibria of (5.2).

Proposition 5.7 System (5.2) always has the boundary equilibria $O(0, 0, \dots, 0)$ and $P_1(\bar{N}_1, 0, \dots, 0)$ in R_+^m .

- (i) If $\lambda_1^{(2)} > 0$, system (5.2) has infinitely many positive equilibria \tilde{P}^+ in $\text{int}R_+^m$, which fill up an $(m - 2)$ -dimensional superplane \tilde{L}^+ with endpoints at the corresponding boundary; more precisely,

$$\tilde{L}^+ = \left\{ (N_1, N_2, \dots, N_m) \geq 0 : N_1 = \frac{\bar{r}_1}{2d_1} + \frac{\sqrt{\Delta}}{2d_1 a_{21}}, \quad \frac{a_{21} N_1}{1 + N_2 + \sum_{j=3}^m N_j} = r_2 \right\}.$$

(ii) If $\lambda_1^{(2)} < 0$, $a_{21} > a_{21}^1$ and $\Delta \geq 0$, then system (5.2) has infinitely many positive equilibria \tilde{P}^\pm in $\text{int}R_+^m$, which fill up two $(m - 2)$ -dimensional superplane \tilde{L}^\pm with endpoints at the corresponding boundary; more precisely,

$$\tilde{L}^\pm = \left\{ (N_1, N_2, \dots, N_m) \geq 0 : N_1 = \frac{\bar{r}_1}{2d_1} \pm \frac{\sqrt{\Delta}}{2d_1 a_{21}}, \frac{a_{21} N_1}{1 + N_2 + \sum_{j=3}^m N_j} = r_2 \right\}.$$

From Theorem 5.6, we obtain global dynamics of system (5.2):

- Theorem 5.8** (i) If $\lambda_1^{(2)} > 0$, or $\lambda_1^{(2)} = 0$ and $a_{21} > a_{21}^1$, then system (5.2) has infinitely many positive equilibria \tilde{P}^+ filling up an $(m - 2)$ -dimensional superplane \tilde{L}^+ which attract all solutions of system (5.2) with positive initial conditions.
- (ii) If $\lambda_1^{(2)} < 0$, $a_{21} > a_{21}^1$ and $\Delta \geq 0$, then equilibrium P_1 is locally asymptotically stable and system (5.2) has infinitely many positive equilibria \tilde{P}^\pm filling up two $(m - 2)$ -dimensional superplane \tilde{L}^\pm . The separatrices of equilibria on \tilde{L}^- form an $(m - 1)$ -dimensional separatrix surface \tilde{S}^- , which subdivides $\text{int}R_+^m$ into two regions: one is the basin of attraction of P_1 , while the other is that of \tilde{L}^+ .
- (iii) If $\lambda_1^{(2)} \leq 0$, $a_{21} \leq a_{21}^1$ or $\Delta < 0$, then system (5.2) has only two equilibria O and P_1 , the equilibrium P_1 attracts all solutions of system (5.2) in R_+^m except the orbits in the $(0, N_2, \dots, N_m)$ -plane, and the equilibrium O attracts all solutions of system (5.2) in the $(0, N_2, \dots, N_m)$ -plane.
- (iv) On the boundary $N_1 = 0$, the origin O is globally asymptotically stable. On the boundary $N_{i_0} = 0$ for $2 \leq i_0 \leq m$, system (5.2) becomes $(m - 1)$ -dimensional, and its dynamics can be described by those similar to (i)–(iii) in this theorem. Similar discussions can also be given for the boundary of system (5.2) with dimensions smaller than $m - 1$.

Theorem 5.8 provides criteria for persistence of pollination–mutualisms when pollinators have the same ratio of death rate and propagation rate. Notice that $\lambda_1^{(2)} > 0$ is equivalent to $\frac{r_2}{a_{21}} < \bar{N}_1$. If the ratio of death rate and propagation rate of the pollinator is less than the carrying capacity of the plant (i.e., $\frac{r_2}{a_{21}} < \bar{N}_1$), all competing pollinators coexist at a positive steady state, which implies the persistence of pollination–mutualisms. If the ratio is large (e.g., $\frac{r_2}{a_{21}} > \frac{r_2}{a_{21}^1}$), all pollinators eventually go to extinction even though the plant persists, which implies the extinction of pollination–mutualisms.

If the ratio is intermediate (e.g., $\bar{N}_1 < \frac{r_2}{a_{21}} < \min\{\frac{r_2}{a_{21}^0}, \frac{r_2}{a_{21}^1}\}$), there are two fates for pollinators. The system has infinite positive equilibria and the stable manifold \tilde{L}^- of the unstable positive equilibria becomes the threshold condition for persistence of pollination–mutualisms. When initial densities of the m species are not small, i.e., not below the threshold, the competing pollinators will coexist at a positive steady state. However, when the densities are below the threshold, all pollinators go to extinction and the plant persists. This conflicts with the principle of competitive exclusion but coincides with our intuition. Here, we can see that varying one initial population density of the species can lead to survival/extinction of all consumers.

Let $m-1 \rightarrow \infty$, i.e., the kinds of pollinators are sufficiently large. Then the Eq. (5.4) implies that some of the pollinators would approach an extremely small density that the species can be regarded as going to extinction (e.g., the number of individuals of a pollinator is less than one). This is because their competition for the same plant. Thus, extremely large kinds of pollinators would imply extinction of some pollinators under the condition of pollinators' coexistence in the above cases of small and intermediate ratios.

Let Ω_i be the community of animals without species i . It is clear that system (5.2) restricted on (N_1, N_i) -plane has the dynamics as shown in Theorem 3.3, which implies that it has separatrices of the saddle point E_{1i}^- when E_{1i}^- exists. Similarly, system (5.2) restricted on the superplane $N_i = 0$ has the dynamics similar to those described in Theorem 5.8, which implies that it has separatrix surface \tilde{S}_i^- when the corresponding \tilde{L}^- exists. Thus, transition of interaction outcomes between species i and community Ω_i can be described by Theorems 4.7, 4.8 when the following replacements are taken:

$$\text{species } N_2 \rightarrow \text{species } i, \quad \text{species } N_3 \rightarrow \text{community } \Omega_i, \quad E_{12}^- \rightarrow E_{1i}^-, \quad E_{13}^- \rightarrow \tilde{L}^-.$$

The principle of competitive exclusion for system (5.1) can be described by Theorem 4.10 when we regard the competing species N_i and N_j in (5.1) as species N_2 and N_3 in (2.3), \tilde{S}^- as S^- , and $(N_1(0), N_2(0), \dots, N_n(0))$ as $(N_1(0), N_2(0), N_3(0))$, etc.

Remarks The relationship between two communities of animals in system (5.2) can transition in a way similar to that in Theorems 4.7 and 4.8. Indeed, assume that the animals in system (5.2) come from two communities: Ω_1 and Ω_2 . Then consider two subsystems: one consists of species 1 and Ω_1 while the other consists of species 1 and Ω_2 . System (5.2) restricted on the two subsystems has the dynamics similar to those described in Theorem 5.8, which implies that it has separatrix surface \tilde{S}_i^- when the corresponding \tilde{L}_i^- exists, $i = 1, 2$. Thus, Theorems 4.7 and 4.8 hold for system (5.2) in two communities after taking the following replacements:

$$\text{species } N_2 \rightarrow \text{community } \Omega_1, \quad \text{species } N_3 \rightarrow \text{community } \Omega_2, \quad E_{12}^- \rightarrow \tilde{L}_1^-, \quad E_{13}^- \rightarrow \tilde{L}_2^-.$$

6 Discussion

In this paper, we consider a mutualism–competition system with one resource and multiple consumers, in which consumers compete for the same resource and each consumer is mutualistic with the resource. We assume, consistent with Scheffer and van Nes (2006) and Sakavara et al. (2018), that clusters of consumers can coexist on the same limiting resources, with nearly identical propagation to mortality ratios.

The most important result is that multiple consumers can coexist on a single resource. But the detailed results for the system consumer-mutualist system studied are complex and coexistence is not guaranteed. Global dynamics of the model demonstrate that interaction outcomes between the consumers can transition between mutualism, parasitism, competition, amensalism and neutralism, while in the previous literature, interaction outcomes between competitive consumers could transition

only between competition, amensalism and neutralism (e.g., Hofbauer and Sigmund 1998; Llibre and Xiao 2014). Moreover, it is shown here that mutualism between the consumer and resource tends to promote the survival of one or more consumers, while competition between the consumers could result in extinction of one or all consumers. Thus, our analysis implies interesting biological results, which are described as follows.

In the one-plant and two-pollinator system, as shown in Theorem 4.7 and Fig. 5, (a) when the initial density of each pollinator is intermediate, one pollinator cannot coexist with the plant in the absence of the other, while the three species can coexist and pollination–mutualisms persist. The underlying reason is that each of the pollinators promotes growth of the plant and thus benefits the other pollinator. However, when the initial density of one pollinator is small, both pollinators go to extinction. Thus, varying the initial density can lead to survival/extinction of both pollinators. (b) When both of the initial densities are large, each pollinator can coexist with the plant in the absence of the other, while the three-species system persists at an equilibrium in which each pollinator approaches a low density. The underlying reason is that the plant can approach its maximal density in the presence of one pollinator and the existence of the other cannot increase the plant's population density any further. (c) When one of the initial densities is large but the other is small, the first pollinator can coexist with the plant in the absence of the second, while the second one cannot in the absence of the first. When they coexist, the first one approaches a high density. The underlying reason is that the plant can approach its maximal density in the presence of the first pollinator, which leads to survival of the second, while the existence of the second pollinator cannot increase the plant's density further. (d) As shown in Theorem 4.9 and Fig. 5d, species N_3 dominates N_2 in their competition for the plant. When the initial density of N_2 is large but that of N_3 is small, species N_2 can coexist with the plant in the absence of species N_3 , while species N_3 cannot. However, in the presence of species N_3 , species N_2 is driven into extinction by species N_3 , followed by species N_3 finally going to extinction. The underlying reason is that species N_3 has a competitive ability stronger than N_2 , which drives species N_2 into extinction, but its initial density is not large enough for its own persistence. Moreover, further numerical simulations show that when $a_{31} = a_{21} = 2.45$ and $N(0) = (0.45, 0.2, 0.02)$, the three species coexist at a steady state $P^+ = (0.5714, 0.3637, 0.0364)$, which means that the relationship between the consumers returns to parasitism as shown in Fig. 5c. Thus, varying one parameter (i.e., a_{31}) can lead to survival/extinction of both consumers.

In the one-plant and multi-pollinator system as shown in Sect. 5, global dynamics of the model demonstrate that results for the three-species system can be extended to the n -species system. If the principle of competitive exclusion holds, then one consumer and the resource coexist at a positive steady state in R_+^n , and other consumers go to extinction. If the principle of competitive exclusion does not hold, then either more than one consumer and the resource will coexist at a positive equilibrium in the positive octant R_+^n or all competing consumers go to extinction and the resource persists. Here, mutualism between the consumer and resource can lead to survival of all consumers, while competition between the consumers could result in extinction of one or all consumers. Interaction outcomes between one consumer and the other consumers could transition between mutualism, parasitism, competition, amensalism and neutralism,

while varying one parameter or initial density can lead to survival/extinction of all consumers. When the consumers come from two different groups Ω_1 and Ω_2 , then similar phenomena would occur in interactions between the groups.

Of course, such an n -species system is only a part, or a module, within real pollinator-plant networks that exist in nature. Plant-pollinator networks in nature have been studied for decades (e.g., Gilbert 1980) and continue to be an area of active research (e.g., Vanbergen et al. 2017). The larger networks consist of many interacting plant host and pollinator species. However, study of such parts, or modules, within the overall community is valuable. Plant-pollinator networks are not randomly assembled, but consist of tightly interacting modules that are weakly linked to the larger community (e.g., Oleson et al. 2007). Some of these modules are similar to that studied here. For example, studies of the cycad (*Macrozamia communis*), which has a several pollinators, the two most effective of which are specialist pollinating beetles, *Cycadotheripschadwicki* and *Traneslyterioides* (Terry 2001). Therefore, there exist pollinator-plant modules that are at least qualitatively similar to that which we studied, and might possibly even be used to test some of our results.

With pollinators under threat world-wide Vanbergen (2013), better understanding of how various disturbances affect existing plant-pollinator networks is needed. For example, how tolerant are particular specialist pollinators, and larger networks, to the extinction of other pollinators (e.g., Memmott et al. 2004)? Alternatively, how stable are models and larger networks to invasion by a new plant or pollinator (e.g., Traveset and Richardson 2006)? Is it possible to manipulate systems, by actions that favor a plant or pollinator species, to promote the coexistence of other pollinators (e.g., Albrecht et al. 2014; Bascompte et al. 2003; Campbell et al. 2015)? All of these questions can at least be partially addressed through modeling. It is our hope that theoretical studies like ours can provide the mathematical basis for insights into the conditions influencing coexistence or extinction of pollinators.

Acknowledgements We would like to thank the anonymous reviewers for their helpful comments on the manuscript. Yuanshi Wang and Hong Wu were supported by NSF of People's Republic of China (11571382). D. L. DeAngelis acknowledges the support of the US Geological Survey's Greater Everglades Priority Ecosystem Sciences program. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

Appendix A. Proof of Proposition 2.1

Proof Let $N(t) = (N_1(t), N_2(t), N_3(t))$ be a solution of (2.3) with a fixed initial value $N(0) \geq 0$. It follows from the first equation of (2.3) that

$$\frac{dN_1}{dt} \leq N_1 (\bar{r}_1 - d_1 N_1).$$

Let $K_1 = \bar{r}_1/d_1$. The comparison principle (Hale 1969) implies $\limsup_{t \rightarrow \infty} N_1(t) \leq K_1$. Then for $\delta_0 > 0$ small, there is $T_1 > 0$ such that if $t > T_1$, then $N_1(t) \leq K_1 + \delta_0$.

It follows from the second equation of (2.3) that if $t > T_1$, then

$$\begin{aligned} \frac{dN_2}{dt} &= \frac{N_2}{1 + N_2 + N_3} [-r_2(1 + N_2 + N_3) + a_{21}N_1] \\ &\leq \frac{N_2}{1 + N_2 + N_3} [-r_2(1 + N_2 + N_3) + a_{21}(K_1 + \delta_0)] \\ &\leq \frac{N_2}{1 + N_2 + N_3} [a_{21}(K_1 + \delta_0) - r_2 - r_2N_2]. \end{aligned}$$

Let $K_2 = [a_{21}(K_1 + \delta_0) - r_2]/r_2$. If $K_2 \leq 0$, then $\lim_{t \rightarrow \infty} N_2(t) = 0$, which implies that there is $T_{21} > T_1 > 0$ such that when $t > T_{21}$, we have $N_2(t) < \delta_0$. If $K_2 > 0$, then

$$\frac{dN_2}{dt} \leq \frac{N_2}{r_2(1 + N_2 + N_3)} (K_2 - N_2) < 0 \quad \text{as } N_2 > K_2$$

which implies $\limsup_{t \rightarrow \infty} N_2(t) \leq K_2$. Then there is $T_{22} > T_1 > 0$ such that when $t > T_{22}$, we have $N_2(t) < K_2 + \delta_0$. Thus, there exists $T_2 > 0$ such that if $t > T_2$, then $N_2(t) < |K_2| + \delta_0$.

Let $K_3 = [a_{31}(K_1 + \delta_0) - r_3]/r_3$. By the third equation of (2.3) and a discussion similar to that for K_2 , we obtain that there is $T_3 > T_2$ such that if $t > T_3$, then $N_3(t) < |K_3| + \delta_0$.

Let $T = T_3$. If $t > T$, then $\|N(t)\| = \sum_{i=1}^3 N_i(t) \leq \sum_{i=1}^3 M_i$ with $M_i = |K_i| + \delta_0$. Thus solutions of (2.3) are bounded. \square

Appendix B. Proof of two cases in Theorem 3.3

Proof (ii) The case of $\lambda_1^{(2)} = 0$.

From $\lambda_1^{(2)} = 0$, we have $a_{21} = a_{21}^*$. If $a_{21}^* < a_{21}^1$, there is no positive equilibrium in system (3.1) by Proposition 3.2. If $a_{21}^* = a_{21}^1$, we have $b_{12} = \bar{r}_1/2$ and $a_{21} = a_{21}^0$, which implies that $\Delta = 0$ and there is no positive equilibrium in system (3.1). Thus, E_1 is globally asymptotically stable.

If $a_{21} > a_{21}^1$, E_{12}^+ is the unique positive equilibrium by Proposition 3.2. We apply the central manifold theorem to show that E_1 has no stable manifold in $\text{int}R_+^2$, which implies that E_{12}^+ is globally asymptotically stable. The following transformation can change system (3.1) into a standard form near E_1 :

$$\begin{pmatrix} x_1 \\ x_2 \end{pmatrix} = \begin{pmatrix} N_1 - \bar{N}_1 \\ N_2 \end{pmatrix}, \quad \begin{pmatrix} y_1 \\ y_2 \end{pmatrix} = \frac{1}{d_1} \begin{pmatrix} d_1 & -b_{12} \\ 0 & 1 \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}.$$

Then system (3.1) can be written as

$$\begin{aligned} \frac{dy_1}{dt} &= \lambda_1^{(1)} y_1 - d_1 (y_1 + b_{12}y_2)^2 + b_{12}d_1 (y_1 + b_{12}y_2) y_2 \\ &\quad - b_{12}d_1^2 \bar{N}_1 y_2^2 - \frac{b_{12}r_2 y_2}{\bar{N}_1} [y_1 + y_2 (2b_{12} - \bar{r}_1)] + o(|y|^2) \end{aligned}$$

$$\begin{aligned} \frac{dy_2}{dt} &= r_2 y_2 \left[-1 + \frac{(y_1 + b_{12} y_2 + \bar{N}_1) d_1}{\bar{N}_1 (d_1 + y_2)} \right] \\ &= \frac{r_2 y_2}{\bar{N}_1} [y_1 + y_2 (2b_{12} - \bar{r}_1)] + o(|y|^2) \end{aligned} \tag{6.1}$$

which implies that the solution $y_2 = 0$ is a stable manifold of equilibrium $(0, 0)$ in system (6.1). Let $y_1 = \phi(y_2) = ay_2^2 + o(y_2^2)$ be the central manifold of (6.1) at $(0, 0)$. From $a_{21} = a_{21}^* > a_{21}^1$, we have $b_{12} = \hat{r}_1 - r_2 d_1 / a_{21} > \hat{r}_1 / 2$. A long but straightforward computation shows that

$$a = \frac{b_{12}}{\lambda_1^{(1)} \bar{N}_1} \left[d_1^2 \bar{N}_1^2 + r_2 (2b_{12} - \bar{r}_1) \right] < 0.$$

Thus equilibrium $(0, 0)$ is a saddle-node point. On the central manifold $y_1 = \phi(y_2)$, we have $dy_2/dt > 0$. Then equilibrium $(0, 0)$ has no stable manifold in $\text{int}R_+^2$. Thus, E_1 has no stable manifold in $\text{int}R_+^2$ and E_{12}^+ is globally asymptotically stable.

(iii) The case of $\lambda_1^{(2)} < 0$, $\Delta = 0$ and $a_{21} > a_{21}^1$.

From $\lambda_1^{(2)} < 0$, we have $a_{21} < a_{21}^*$ and equilibrium E_1 is locally asymptotically stable.

Since $\Delta = 0$ and $a_{21} > a_{21}^1$, the two positive equilibria E_{12}^- and E_{12}^+ coincide by Proposition 3.2. By (3.2), the Jacobian matrix of (3.1) at a positive equilibrium (N_1, N_2) is

$$J = \begin{pmatrix} -d_1 N_1 & b_{12} N_1 g^2 \\ a_{21} N_2 g & -a_{21} N_1 N_2 g^2 \end{pmatrix}, \tag{6.2}$$

which implies $\text{tr}J(E_{12}^\pm) < 0$. A direct computation shows that

$$\det J(E_{12}^\pm) = \pm N_1 N_2 g^2 \sqrt{\Delta} = 0, \tag{6.3}$$

which implies that there is a simple zero eigenvalue of $J(E_{12}^-)$. We apply Sotomayor’s theorem Perko (2001) to show that saddle-node bifurcation occurs at E_{12}^- when $\Delta = 0$. For the simple zero eigenvalue, we have the left and right eigenvectors of $J(E_{12}^-)$ by (6.2):

$$w = (a_{21} N_2 g, d_1 N_1)^T, \quad v = (b_{12} g^2, d_1)^T.$$

Let $\mu = a_{21}$ be the parameter in Sotomayor’s theorem. Let $F = (F_1, F_2)^T$ be the righthand side of (3.1). Then we have $F_\mu = (0, N_1 N_2 g)^T$. Thus $w^T F_\mu = d_1 N_1^2 N_2 g > 0$ at E_{12}^- and $\mu = a_{21}^0$. Direct computations show that

$$\begin{aligned} \frac{\partial^2 F_1}{\partial N_1^2} &= -2d_1, & \frac{\partial^2 F_1}{\partial N_1 \partial N_2} &= b_{12} g^2, & \frac{\partial^2 F_1}{\partial N_2^2} &= -2b_{12} N_1 g^3, \\ \frac{\partial^2 F_2}{\partial N_1^2} &= 0, & \frac{\partial^2 F_2}{\partial N_1 N_2} &= a_{21} g [1 - N_2 g], & \frac{\partial^2 F_2}{\partial N_2^2} &= 2r_2 g (-1 + N_2 g). \end{aligned}$$

A long but straightforward computation shows that

$$w \cdot D^2F(v, v) = -2d_1^2 a_{21} b_{12} N_1 N_2 g^4 < 0.$$

Thus, the Sotomayor’s theorem implies that saddle-node bifurcation occurs at E_{12}^- when $a_{21} = a_{21}^0$: (1) If $a_{21} > a_{21}^0$, then $\det J(E_{12}^+) > 0$ and $\det J(E_{12}^-) < 0$, which implies that E_{12}^+ is a stable node and E_{12}^- is a saddle point. (2) If $a_{21} = a_{21}^0$, E_{12}^- is a saddle-node point. (3) If $a_{21} < a_{21}^0$, there is no positive equilibrium and E_1 is globally asymptotically stable.

It follows from Proposition 3.1 that when E_{12}^- and E_{12}^+ exist, the separatrices of E_{12}^- subdivide the interior of (N_1, N_2) -plane into two regions: one is the basin of attraction of E_1 , while the other is that of E_{12}^+ . Thus, the result in the second case is proven. □

Appendix C. Proof of Theorem 4.4

Proof Since the proof for (ii) is similar to that for (ii) in Theorem 3.3, we omit the details.

- (i) Since $\lambda_1^{(2)} > 0$, equilibrium E_1 is a saddle point and has no stable manifold in $\text{int}R_+^2$. From $\lambda_1^{(2)} > 0$ we have $a_{21} > a_{21}^*$ and $a_{21} > a_{21}^0$. By Proposition 4.3, \hat{E}_{12}^+ is the unique positive equilibrium. By Proposition 4.2, \hat{E}_{12}^+ is globally asymptotically stable.
- (ii) It follows from $\lambda_1^{(2)} < 0$ that the equilibrium E_1 is asymptotically stable. From $\lambda_1^{(2)} < 0$ we obtain $a_{21} < a_{21}^*$. When $a_{21} \leq a_{21}^1$, there is no positive equilibrium in system (4.1) by Proposition 4.3. Thus E_1 is globally asymptotically stable.

Assume $a_{21} > a_{21}^1$. If $\Delta \geq 0$, then $a_{21} \geq a_{21}^0$ and there are two positive equilibria \hat{E}_{12}^- and \hat{E}_{12}^+ by Proposition 4.3. Let $\hat{g}(N_2) = 1/(1 + N_2 + cN_2^s)$. By (4.2), the Jacobian matrix of (4.1) at a positive equilibrium (N_1, N_2) is

$$J = \begin{pmatrix} -d_1 N_1 & b_{12} (1 + csN_2^{s-1}) N_1 \hat{g}^2 \\ a_{21} N_2 \hat{g} & -a_{21} N_1 N_2 (1 + csN_2^{s-1}) \hat{g}^2 \end{pmatrix}, \tag{6.4}$$

which implies $\text{tr}J(\hat{E}_{12}^\pm) < 0$. A direct computation shows that

$$\det J(\hat{E}_{12}^\pm) = \pm N_1 N_2 (1 + csN_2^{s-1}) \hat{g}^2 \sqrt{\Delta}. \tag{6.5}$$

Thus, if $\Delta > 0$, then \hat{E}_{12}^- is a saddle point and \hat{E}_{12}^+ is asymptotically stable.

When $\Delta = 0$, equilibria \hat{E}_{12}^- and \hat{E}_{12}^+ coincide and $\det J(\hat{E}_{12}^-) = 0$, which implies that there is a simple zero eigenvalue of $J(\hat{E}_{12}^-)$. We apply Sotomayor’s theorem to show that saddle-node bifurcation occurs at \hat{E}_{12}^- when $\Delta = 0$, i.e., $a_{21} = a_{21}^0$. For the simple zero eigenvalue, we have the left and right eigenvectors of $J(\hat{E}_{12}^-)$ by (6.4):

$$w = (a_{21}N_2\hat{g}, d_1N_1)^T, \quad v = (b_{12}(1 + csN_2^{s-1})\hat{g}^2, d_1)^T.$$

Let $\mu = a_{21}$ be the parameter in Sotomayor’s theorem. Let $\hat{F} = (\hat{F}_1, \hat{F}_2)^T$ be the righthand side of (4.1). Then $\hat{F}_\mu = (0, N_1N_2\hat{g})^T$, which implies that $w^T \hat{F}_\mu = d_1N_1^2N_2\hat{g} > 0$ at \hat{E}_{12}^- and $\mu = a_{21}^0$. Direct computations show that

$$\begin{aligned} \frac{\partial^2 \hat{F}_1}{\partial N_1^2} &= -2d_1, & \frac{\partial^2 \hat{F}_2}{\partial N_1^2} &= 0, & \frac{\partial^2 \hat{F}_1}{\partial N_2^2} &= b_{12}N_1\hat{g}^2 \left[cs(s-1)N_2^{s-2} - 2\hat{g}(1 + csN_2^{s-1})^2 \right], \\ \frac{\partial^2 \hat{F}_1}{\partial N_1 \partial N_2} &= b_{12}(1 + csN_2^{s-1})\hat{g}^2, & \frac{\partial^2 \hat{F}_2}{\partial N_1 N_2} &= a_{21}\hat{g} \left[1 - N_2\hat{g}(1 + csN_2^{s-1}) \right], \\ \frac{\partial^2 \hat{F}_2}{\partial N_2^2} &= 2r_2\hat{g}(1 + csN_2^{s-1}) \left[-1 + N_2\hat{g}(1 + csN_2^{s-1}) \right] - r_2\hat{g}cs(s-1)N_2^{s-2}. \end{aligned}$$

A long but straightforward computation shows that

$$w \cdot D^2 \hat{F}(v, v) = -2d_1^2 a_{21} b_{12} N_1 N_2 \hat{g}^4 (1 + csN_2^{s-1}) < 0.$$

Thus, the Sotomayor’s theorem implies that saddle-node bifurcation occurs at \hat{E}_{12}^- when $\Delta = 0$. By a discussion similar to the proof for Theorem 3.3(iii), the result in (iii) is proven. □

References

Albrecht M, Padrn B, Bartomeus I, Traveset A (2014) Consequences of plant invasions on compartmentalization and species’ roles in plant–pollinator networks. *Proc R Soc Lond B* 281:20140773

Bascompte J, Jordano P, Melián CJ, Olesen JM (2003) The nested assembly of plant–animal mutualistic networks. *Proc Natl Acad Sci* 100:9383–987

Bronstein JL (1994) Conditional outcomes in mutualistic interactions. *Trends Ecol Evol* 9:214–217

Campbell C, Yang S, Albert R, Shea K (2015) Plant–pollinator community network response to species invasion depends on both invader and community characteristics. *Oikos* 124:406–413

Cantrell RS, Cosner C, Ruan S (2004) Intraspecific interference and consumer–resource dynamics. *Discrete Cont Dyn Syst B* 4:527–546

Fagan WF, Bewick S, Cantrell S, Cosner C, Varassin IG, Inouye DW (2014) Phenologically explicit models for studying plant–pollinator interactions under climate change. *Theor Ecol* 7:289–297

Freedman HI, Waltman P (1984) Persistence in models of three interacting predator–prey populations. *Math Bios* 68:213–231

Gilbert LE (1980) Food web organization and conservation of neotropical diversity. In: Soule Michael, Wilcox Bruce A (eds) *Conservation biology. An evolutionary-ecological perspective*. Sinauer Associates, Sunderland, pp 11–34

Hale JK (1969) *Ordinary differential equations*. Wiley, New York

Hofbauer J, Sigmund K (1998) *Evolutionary games and population dynamics*. Cambridge University Press, Cambridge

Hubbell SP (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton University Press

Jang SR-J (2002) Dynamics of herbivore–plant–pollinator models. *J Math Biol* 44:129–149

Li B, Smith HL (2007) Global dynamics of microbial competition for two resources with internal storage competition model. *J Math Biol* 55:481–511

Llibre J, Xiao D (2014) Global dynamics of a Lotka–Volterra model with two predators competing for one prey. *SIAM J Appl Math* 74:434–453

- Lundberg S, Ingvarsson P (1998) Population dynamics of resource limited plants and their pollinators. *Theor Popul Biol* 54:44–49
- Memmott J, Waser NM, Price MV (2004) Tolerance of pollination networks to species extinctions. *Proc R Soc Lond B* 271:2605–2611
- Nguyen DH, Yin G (2017) Coexistence and exclusion of stochastic competitive Lotka–Volterra models. *J Differ Equ* 262:1192–1225
- Olesen JM, Bascompte J, Dupont YL, Jordano P (2007) The modularity of pollination networks. *Proc Natl Acad Sci* 104:19891–19896
- Perko L (2001) *Differential equations and dynamical systems*. Springer, New York
- Revilla T (2015) Numerical responses in resource-based mutualisms: a time scale approach. *J Theor Biol* 378:39–46
- Sakavara A, Tsirtsis G, Roelke DL, Nancy R, Spatharis S (2018) Lumpy species coexistence arises robustly in fluctuating resource environments. *Proc Natl Acad Sci* 115:738–743
- Scheffer AM, van Nes EH (2006) Self-organized similarity, the evolutionary emergence of groups of similar species. *Proc Natl Acad Sci* 103:6230–6235
- Scheffer M, van Nes EH, Vergnon R (2018) Toward a unifying theory of biodiversity. *Proc Natl Acad Sci* 115:639–641
- Terry I (2001) Thrips and weevils as dual, specialist pollinators of the Australian cycad *Macrozamia communis* (Zamiaceae). *Int J Plant Sci* 162:1293–1305
- Tilman D (1982) *Resource competition and community structure*. Princeton University Press, Princeton
- Traveset A, Richardson DM (2006) Biological invasions as disrupters of plant reproductive mutualisms. *Trends Ecol Evol* 21:208–215
- Vanbergen AJ (2013) Threats to an ecosystem service: pressures on pollinators. *Front Ecol Environ* 11:251–259
- Vanbergen AJ, Woodcock BA, Heard MS, Chapman DS (2017) Network size, structure and mutualisms dependence affect the propensity for plant–pollinator extinction cascades. *Funct Ecol*. <https://doi.org/10.1111/1365-2435.12823>
- Wang Y, DeAngelis DL (2016) Stability of an intraguild predation system with mutual predation. *Commun Nonlinear Sci Numer Simul* 33:141–159