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Uni-directional consumer–resource theory characterizing transitions of interaction outcomes

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Abstract: A resource is considered here to be a biotic population that helps to maintain the population growth of its consumers, whereas a consumer utilizes a resource and in turn decreases its growth rate. Bi-directional consumer–resource (C–R) interactions have been the object of recent theory. In these interactions, each species acts, in some respects, as both a consumer and a resource of the other, which is the basis of many mutualisms. In uni-directional C–R interactions between two species, one acts as a consumer and the other as a material and/or energy resource, while neither acts as both. The relationship between insect pollinator/seed parasites and the host plant is an example of the latter interaction type of C–R, as the insect provides no material resource to the plant (though it provides a pollination service). In this paper we consider a different variation of the uni-directional C–R interaction, in which the resource species has both positive and negative effects on the consumer species, while the consumer has only a negative effect on the resource. A predator–prey system in which the prey is able to kill or consume predator eggs or larvae is an example. Our aim is to demonstrate mechanisms by which interaction outcomes of this system vary with different conditions, and thus to extend the uni-directional C–R theory established by Holland and DeAngelis (2009). By the analysis of a specific two-species system, it is shown that there is no periodic solution of the system, and the parameter (factor) space can be divided into six regions, which correspond to predation/parasitism, amensalism, and competition. The interaction outcomes of the system transition smoothly when the parameters are changed continuously in the six regions and/or initial densities of the species vary in a smooth fashion. Varying a pair of parameters can also result in the transitions. The analysis leads to both conditions under which the species approach their maximal densities, and explanations for phenomena in experiments by Urabe and Sterner (1996).

1. Introduction

Predator–prey interactions are pervasive in ecological systems, and models of predator–prey interactions have been a foundation for describing and understanding such interactions for several decades (e.g., MacArthur and Levins, 1967; MacArthur, 1972). These are a class of consumer–resource (C–R) interactions, which in basic terms relate the process of energy and/or nutrient transfer between a consumer organism and a resource. A resource is any biotic or abiotic factor that increases the population growth of its consumer, at least over some range of the availability or supply of the resource; consumers simultaneously change (and typically deplete) the availability or abundance of the exploited resource. A C–R interaction is characterized by (+ −), where the consumer gains some material benefit at the cost of the resource. Models such as the Rosenzweig–MacArthur (RM) model (Rosenzweig and MacArthur, 1963) have been highly successful in describing the properties of such interactions and have played a key role in the development of predator–prey theory over the last fifty years.

More recently, the fact that C–R interactions occur in other types of interactions has been incorporated in models. What this means is that even in other types of interaction, such as mutualism, amensalism, and commensalism, C–R interactions may be occurring, but the net result may not always be (+ −). For example, in mutualistic systems, a consumer (mutualist) exploits a resource (e.g. nutrient, nectar, shelter) supplied by another species (mutualist) and in the process provisions that species with another resource or a non-trophic service of dispersal or defense (Agrawal and Fordyce, 2000; Agrawal et al., 2007; Boukal et al., 2007; Chamberlain and Holland, 2008; Ferriere et al., 2007; Holland et al., 2005, 2009, 2010; Murdoch et al., 2003; Turchin, 2003; Wang and Wu, 2011). Mutualism is denoted by the outcome (+ +); that is, each interacting species benefits. However, because the underlying interactions are C–R in nature, the balance between benefit and

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cost for either or both of the species may shift, so that all other possible combinations of outcomes might occur under certain circumstances; that is, (+ −), (− 0), (+ 0) or (− −) (Anderson et al., 2004; Perhar and Arhonditsis, 2009; Wang et al., 2007).

Holland and DeAngelis (2009, 2010) denoted the generality of C–R interactions by writing the equations for two populations in the general form

$$\begin{aligned}\frac{dN_1}{dt} &= N_1[r_1 + c_1 f_1[R_2(N_1,N_2)] - q_1 g_1[R_1(N_1,N_2)] - d_1N_1],\\ \frac{dN_2}{dt} &= N_2[r_2 + c_2 f_2[R_1(N_1,N_2)] - q_2 g_2[R_2(N_1,N_2)] - d_2N_2],\end{aligned} \tag{1.1}$$

which they called a bi-directional C–R interaction. Here r_1 and r_2 are growth rates in the absence of the other species. In general, $r_1 > 0$, so the consumer can maintain itself without the resource. The ratios r_1/d_1 and r_2/d_2 can be thought of as carrying capacities in the absence of the other species. The equation for each population has a term, $f_i[R_j(N_i, N_j)]$, that represents its gain from the interaction, and a term, $g_i[R_j(N_i, N_j)]$, that represents the costs incurred to it by the interaction. Eq. (1.1) represent the model assumption that biomass or nutrients flow in both directions.

Mutualisms in which the resources are abiotic tend to be bi-directional. Some of the key mutualisms of this type include coral mutualisms, mycorrhizal mutualisms, nitrogen fixing mutualisms, and lichens. In corals, the photosynthetic zooxanthellae provide energy in the form of glucose to the coral animals, while the coral polyp passes nitrogen from captured prey to the zooxanthellae. Most terrestrial plants appear to have a mutualistic relationship with mycorrhizal fungi, which are usually found in the rhizosphere of the root system. The plant provides carbohydrate exudates to the fungi, which in turn, through their extensive network of hyphae in the soil, greatly increase the access of the plant to nutrients such as phosphorus. Nitrogen fixation mutualisms exist between leguminous host plants and rhizobial bacteria that reside in root nodules in the plant. The bacteria fix nitrogen that the plant uses, and receive carbohydrates from the plant in return. Lichens are a mutualistic association of a species of fungus and green or blue-green algae. The algae provide sugars and oxygen to the fungus, which provides the algae with nutrients that it absorbs from the substrate, such as a log or a rock, to which it is attached.

A special form of the model (1.1), noted by Holland and DeAngelis (2009), is uni-directional C–R interaction, represented by the equations

$$\begin{aligned}\frac{dN_1}{dt} &= N_1[r_1 + c_1 f_1[R_2(N_1,N_2)] - q_1 g_1[R_1(N_1,N_2)] - d_1N_1],\\ \frac{dN_2}{dt} &= N_2[r_2 + c_2 f_2[R_1(N_1,N_2)] - d_2N_2].\end{aligned} \tag{1.2}$$

In this model, there are positive effects occurring to both populations, but the population N_1 is the only one that incurs a loss due to a C–R interaction, reflecting that during the uni-directional C–R interaction, the consumer provisions the resource-supplying species with a non-trophic service of dispersal or defense. For example, as animals, N_2, consume nectar of plants, N_1, they pollinate the plants' flowers.

We believe that a another variation on these equations, which differs from both (1.1) and (1.2), is important to study; that is, the system

$$\begin{aligned}\frac{dN_1}{dt} &= N_1[r_1 + c_1 f_1[R_2(N_1,N_2)] - q_1 g_1[R_1(N_1,N_2)] - d_1N_1],\\ \frac{dN_2}{dt} &= N_2[r_2 - q_2 g_2[R_2(N_1,N_2)] - d_2N_2].\end{aligned} \tag{1.3}$$

In this model, N_2 is assumed to be the resource and N_1 the consumer. N_1 always has a negative effect on N_2, but the resource, N_2, can have a negative, as well as a positive, effect on the consumer, N_1. This system cannot represent a mutualism, because there is no possibility of N_2 receiving a positive effect from N_1. However, Eq. (1.3) constitute a general representation for some important types of interactions as discussed below.

The above model can represent effective competitive (− −) systems when the negative effect of the resource on the consumer is greater than the positive effect. However, more importantly, the model can represent predator–prey systems in which the prey can also have a negative effect on the predator, and it may in general be possible for this negative effect to exceed the positive effect when the size of the resource becomes very large. Some ecological examples are as follows.

One case results from the fact that interacting species may switch predator and prey roles ontogenetically. For example, larval or juvenile piscivorous fish may be consumed by invertebrates and planktivorous fish that serve as the prey of the adult piscivores. For example, Polis et al. (1989) point out that 90 species of jellyfish and ctenophores eat fish eggs or larvae, while the older fish feed on these same species. Margalhães et al. (2005) noted that small juvenile 'predatory' mites may be killed by their thrips 'prey'. Barkai and McQuaid (1988) noted that on some South African islands, rock lobsters feed on whelks, but in other areas whelks may be in such high abundance that they overwhelm and consume the lobsters. For cases of this type to fit our model, the reversals of prey killing or eating predators should not constitute a major part of the prey's diet, as there is only a negative interaction term in the prey equation of (1.3). Such systems may be modeled by age-structured models, but the simple coupled system (1.3) can also yield insights.

Prey may have other, non-trophic, effects on predators. The interactions between grass and the herbivorous Brandt's vole in an Inner Mongolian grassland in China have been studied by Zhong et al. (1999). Grass is the main food of the vole, but when grass density is high, the grass is an obstacle for the voles' ability to communicate and interact. This leads to a decrease in mating opportunities, thus negatively affecting population growth. Thus in a model, the grass can be assumed to have two separate effects, one positive and one negative, on the voles.

Another general case in which positive and negative effects may simultaneously occur is the presence of chemicals in the edible biomass of many plant species that are toxic to herbivores (Dearing et al., 2005; Stamp, 2003). Herbivores may have behavioral mechanisms to avoid ingestion of toxins, but when toxic plants are present in high densities, the risk of ingestion and harmful effects or mortality to the herbivore may increase. Feng et al. (2008, 2009), Li et al. (2006) and Liu et al. (2008) have applied modeling to this interaction. However, their model does not have the form of (1.3), because they assumed that the toxin does not result in a mortality rate, but in a decrease in ingestion of the plant biomass. We suggest the model (1.3) may be a possible alternative for cases in which the toxin does not cause that herbivore to slow down its feeding rate, but instead leads to mortality of the herbivore.

As a final example that fits into the category of uni-directions C–R interactions, but may differ slightly in the form of Eq. (1.3), we mention the experiments of Urabe and Sterner (1996). In these experiments algae (the resource) is grown in batch culture, with zooplankton grazing on the algae. Phosphorus is the limiting nutrient. The experiments demonstrate that the population density of algae increases monotonically with increases in light intensity. The zooplankton increases monotonically as the biomass density of algae increases from small to medium levels. However, the growth rate of zooplankton decreases monotonically with further increases in algal biomass density. This is the result of light enrichment causing the phosphorus:carbon (P:C) ratio in the algae to decrease, lowering the nutritional value to the zooplankton and leading to their decline. This interaction has been modeled by Loladze et al. (2000), using an interaction term that changes from positive to negative as the P:C ratio exceeds a certain value. Although their model at first sight differs in mathematical form from model (1.3), we show later that (1.3) can be put in a similar form.

In the following section we describe our model in greater detail and analyze its steady state equilibria.

2. Model

In this section, we establish a differential equation system to describe the C–R population dynamics where the resource has both positive and negative effects on the consumer and the consumer has only negative effect on the resource. Then we introduce a specific model and exhibit features of its zero isoclines.

The uni-directional C–R system we consider is that of (1.3), which we write in slightly different form here;

$$\begin{aligned}\frac{dN_1}{dt} &= N_1[r_1 + c_1 f_1(N_1, N_2) - q_1 g_1(N_1, N_2) - d_1 N_1],\\ \frac{dN_2}{dt} &= N_2[r_2 - q_2 g_2(N_1, N_2) - d_2 N_2],\end{aligned} \tag{2.1}$$

where N_1 represents the population density of the consumer (species 1) while N_2 represents that of the resource (species 2).

In the first equation of (2.1), the parameter r_1 denotes the intrinsic growth rate of the consumer, and r_1/d_1 represents its carrying capacity when in isolation from the resource. The term '$+ c_1 f_1(N_1, N_2)$' denotes the increase in the growth of the consumer due to the resource (species 2) and '$f_1(N_1, N_2)$' describes how the positive effects from the resource vary with N_1 and N_2. The term '$- q_1 g_1(N_1, N_2)$' denotes the decrease in the growth of the consumer due to negative effects from the resource and '$- g_1(N_1, N_2)$' describes how the negative effects from the resource vary with N_1 and N_2. Coefficients c_1 and q_1 change f_1 and g_1 into the per capita growth rate of the consumer. In the second equation of (2.1), the parameter r_2 denotes the intrinsic growth rate of the resource while r_2/d_2 represents its carrying capacity. The term '$- q_2 g_2(N_1, N_2)$' is the negative effect on growth of the resource due to consumptions from the consumer (species 1). Hence, in the system (2.1), the consumer has only a negative effect, $-q_2 g_2$, on the resource (N_2), while the resource (N_2) has both positive $+c_1 f_1$ and negative, $-q_1 g_1$, effects on the consumer (N_1).

Without loss of generality, we suppose $c_1 = q_1 = 1$ and $q_2 = 1$ in this paper. In order to exhibit how and under what conditions interaction outcomes of (2.1) vary with different factors and/or initial densities of the species populations, we introduce the following specific system:

$$\begin{aligned}\frac{dN_1}{dt} &= N_1\left[r_1 + \frac{\alpha_{12} N_2}{b_2 + N_2} - \beta_1 N_2 - d_1 N_1\right]\\ \frac{dN_2}{dt} &= N_2[r_2 - \beta_2 N_1 - d_2 N_2],\end{aligned} \tag{2.2}$$

where N_i, r_i and d_i have the same meanings as those in model (2.1) and all parameters in the system are positive. Here, the response function (f_1) of the consumer is assumed to be proportional to $N_2/(b_2 + N_2)$: this displays a saturation effect for large N_2. The other functions, g_1 and g_2, are assumed to be linear. Thus the parameter α_{12} denotes the saturation level of the functional response of species 1 and b_2 denotes the half-saturation density of species 2. The parameter β_1 represents the negative effect level of species 2 on species 1, while β_2 denotes the consumption level of species 1 on species 2.

We demonstrate the features of isoclines of (2.2) as follows. Let l_1 and l_2 denote the zero isoclines of N_1 and N_2, respectively:

$$\begin{aligned}l_1 &: N_1 = F_1(N_2) = \frac{1}{d_1}\left[r_1 + \frac{\alpha_{12} N_2}{b_2 + N_2} - \beta_1 N_2\right],\\ l_2 &: N_2 = F_2(N_1) = \frac{1}{d_2}(r_2 - \beta_2 N_1).\end{aligned} \tag{2.3}$$

On l_1, $P_1(r_1/d_1, 0)$ is an equilibrium of (2.2) and the point $(0, N_2^0)$ represents the intersection of l_1 and the N_2-axis, as shown in Fig. 1a. N_2^0 satisfies

$$\begin{aligned}N_2^0 &= \frac{r_1 + \alpha_{12} - b_2\beta_1 + \sqrt{\Delta_1}}{2\beta_1},\\ \Delta_1 &= (r_1 + \alpha_{12} - b_2\beta_1)^2 + 4 r_1 b_2 \beta_1.\end{aligned} \tag{2.4}$$

The isocline l_1 is concave left with maximum $\hat{N}(\hat{N}_1, \hat{N}_2)$ as shown in Fig. 1a. $\hat{N}_1$ and $\hat{N}_2$ are

$$\begin{aligned}\hat{N}_1 &= F_1(\hat{N}_2) = \frac{1}{d_1}\left[r_1 + \frac{\alpha_{12}\hat{N}_2}{b_2 + \hat{N}_2} - \beta_1 \hat{N}_2\right],\\ \hat{N}_2 &= \sqrt{\frac{\alpha_{12} b_2}{\beta_1}} - b_2.\end{aligned} \tag{2.5}$$

The reason is that $dF_1/dN_2|_{\hat{N}} = 0$ and $d^2F_1/dN_2^2 < 0$. Thus when $N_2 < \hat{N}_2$, the function $N_1 = F_1(N_2)$ is monotonically increasing; when $N_2 > \hat{N}_2$, the function becomes monotonically decreasing.

On l_2, $P_2(0, r_2/d_2)$ is an equilibrium of (2.2) and the point $(0, r_2/\beta_2)$ denotes the intersection of l_2 and the N_1-axis, as shown in Fig. 1a.

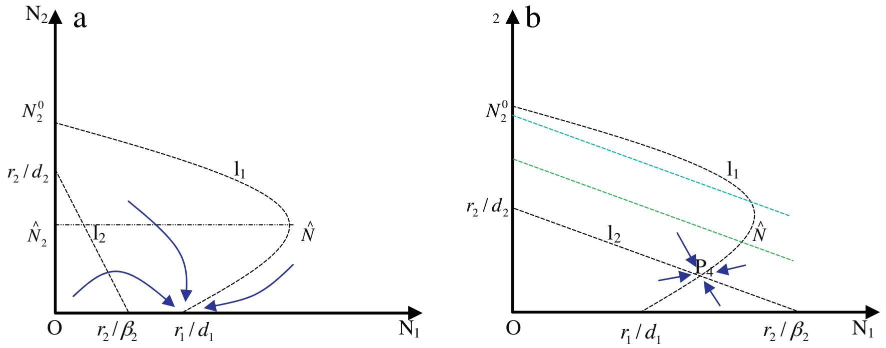

Fig. 1. In (a), $r_2/d_2 \le N_2^0$ and $r_2/\beta_2 \le r_1/d_1$. All positive solutions converge to equilibrium $P_1(r_1/d_1, 0)$ while $\hat{N}(\hat{N}_1, \hat{N}_2)$ denotes the maximum of l_1. In (b), $r_2/d_2 \le N_2^0$ and $r_2/\beta_2 > r_1/d_1$. All positive solutions converge to equilibrium $P_4(p_{41}, p_{42})$. When r_2 increases, l_2 moves upward in a parallel way from black, green to cyan color, and p_{41} increases as $p_{42} < \hat{N}_2$ while it decreases as $p_{42} > \hat{N}_2$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

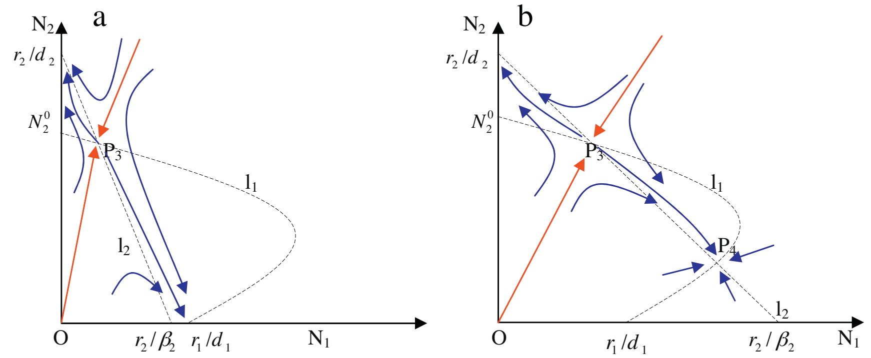

Fig. 2. In (a), $r_2/d_2 > N_2^0$ and $r_2/\beta_2 \leq r_1/d_1$. P_3 is a saddle with separatrix (the red line). Orbits under the red line converge to $P_1(r_1/d_1, 0)$ while those above the red line tend to $P_2(0, r_2/d_2)$. In (b), $r_2/d_2 > N_2^0$, $r_2/\beta_2 > r_1/d_1$, $\Delta_2 > 0$ and $AB > 0$. P_3 is a saddle and P_4 is a stable node, orbits under the separatrix (the red line) converge to P_4 while those above the red line tend to $P_2(0, r_2/d_2)$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

The intersection $\bar{N}(\bar{N}_1, \bar{N}_2)$ of l_1 and l_2 satisfies

$$A\bar{N}_1^2 - B\bar{N}_1 + C = 0, \qquad \bar{N}_2 = \frac{1}{d_2}(r_2 - \beta_2\bar{N}_1), \tag{2.6}$$

where

$$\begin{aligned} &A = \beta_2(\beta_1\beta_2 - d_1d_2), \qquad C = (\beta_1 r_2 - r_1 d_2)(b_2 d_2 + r_2) - d_2\alpha_{12} r_2, \\ &B = -(d_1d_2 - \beta_1\beta_2)(b_2d_2 + r_2) - \beta_2(r_1d_2 + d_2\alpha_{12} - \beta_1 r_2). \end{aligned} \tag{2.7}$$

The roots $\bar{N}_1$ in (2.6) and the corresponding values $\bar{N}_2$ are denoted by $P_i(p_{i1}, p_{i2})$, $i = 3, 4$:

$$\begin{aligned} p_{31} &= \frac{B - \sqrt{\Delta_2}}{2A}, \qquad p_{32} = \frac{1}{d_2}(r_2 - \beta_2 p_{31}), \\ p_{41} &= \frac{B + \sqrt{\Delta_2}}{2A}, \qquad p_{42} = \frac{1}{d_2}(r_2 - \beta_2 p_{41}), \qquad \Delta_2 = B^2 - 4AC. \end{aligned} \tag{2.8}$$

Thus the points $P_3(p_{31}, p_{32})$ and $P_4(p_{41}, p_{42})$ are equilibria of (2.2) if their components are positive. When the equilibria P_3 and P_4 coincide, l_2 is tangent to l_1 at $\bar{P}_3$, which corresponds to $\Delta_2 = 0$ and $AB > 0$.

3. Dynamic behavior

In this section, we exhibit the dynamic behavior of (2.2), which is shown in Figs. 2 and 3. The proofs are in Appendices A–D.

Theorem 3.1. *There is no periodic orbit in the system (2.2).*

Theorem 3.2. *When the intrinsic growth rate of the resource is small (i.e. $r_2 \leq d_2N_2^0$), we have the following results.*

(i) *If the consumption level of the consumer is large (i.e. $\beta_2 \geq r_2d_1/r_1$), the resource goes extinct while the consumer approaches its carrying capacity, as shown in Fig. 1a. That is, all positive solutions of (2.2) converge to equilibrium $P_1(r_1/d_1, 0)$.*

(ii) *If the consumption level of the consumer is small (i.e. $\beta_2 < r_2d_1/r_1$), the two species coexist at the steady state P_4, as shown in Fig. 1b. That is, all positive solutions of (2.2) converge to equilibrium P_4.*

Theorem 3.3. *When the intrinsic growth rate of the resource is large (i.e. $r_2 > d_2N_2^0$), we have the following results.*

(i) *If the consumption level of the consumer is large (i.e. $\beta_2 \geq r_2d_1/r_1$), then the initial densities of species populations determine the interaction outcomes: when the initial density of the consumer is relatively large, the resource goes extinct; otherwise, the consumer goes extinct, as shown in Fig. 2a. That is, orbits below the separatrix (the red line in Fig. 2a) of P_3 converge to $P_1(r_1/d_1, 0)$, while those above the separatrix tend to $P_2(0, r_2/d_2)$.*

(ii) *If the consumption level of the consumer is intermediate (i.e. $\beta_2 < r_2d_1/r_1$, but $\Delta_2 > 0$ and $AB > 0$), then the initial densities of species populations determine the interaction outcomes: when the initial density of the consumer is relatively small, the consumer goes extinct; otherwise, the two species coexist at the equilibrium P_4, as shown in Fig. 2b. That is, orbits above the separatrix (the red line in Fig. 2b) of P_3 tend to $P_2(0, r_2/d_2)$, while those below the separatrix converge to P_4.*

(iii) *If the consumption level of the consumer is at a critical value (i.e. $\Delta_2 = 0$, $\beta_2 < r_2d_1/r_1$ and $AB > 0$), then the initial densities of species populations determine the interaction outcomes: when the initial density of the consumer is relatively small, the*

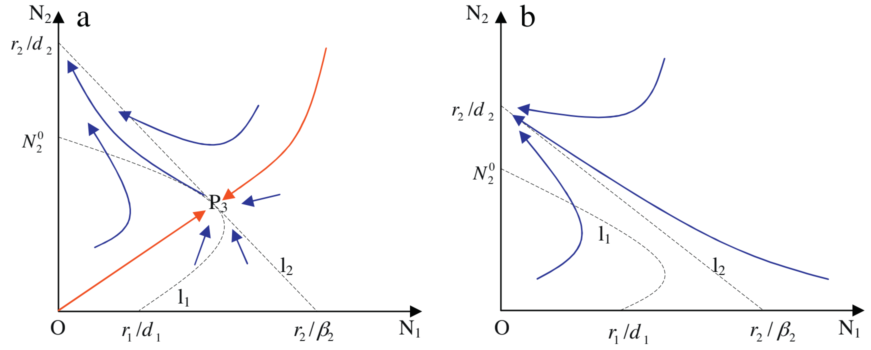

Fig. 3. In (a), $r_2/d_2 > N_2^0$, $r_2/\beta_2 > r_1/d_1$, $\Delta_2 = 0$ and $AB > 0$. Equilibrium P_3 is a saddle-node, and orbits under the separatrix (the red line) converge to P_3 while those above the red line tend to $P_2(0, r_2/d_2)$. In (b), $r_2/d_2 > N_2^0$, $r_2/\beta_2 > r_1/d_1$ and there is no interior equilibrium. All positive solutions converge to the equilibrium $P_2(0, r_2/d_2)$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

consumer goes extinct; otherwise, the two species coexist at equilibrium $\bar{P}_3$, *as shown in* Fig. 3a. *That is, orbits above the separatrix (the red line in* Fig. 2b) *of the saddle-node equilibrium* $\bar{P}_3$ *tend to* $P_2(0, r_2/d_2)$, *while those below the separatrix converge to* $\bar{P}_3$.

(iv) *If the consumption level of the consumer is small (i.e.* $\beta_2 < r_2d_1/r_1$, $\Delta_2 < 0$ *or* $AB \leq 0$), *the consumer goes extinct while the resource approaches its carrying capacity, as shown in* Fig. 3b. *That is, all positive solutions converge to the equilibrium* $P_2(0, r_2/d_2)$.

Therefore, dynamics of (2.2) are displayed in the following table:

Conditions	Equilibrium stability	Interaction outcomes
$r_2 \leq d_2N_2^0,\ \beta_2 \geq r_2d_1$	P_1 is stable	$(-\ 0)$
$r_2 \leq d_2N_2^0,\ \beta_2 < r_2d_1$	P_4 is stable	$(-\ +)$
$r_2 > d_2N_2^0,\ \beta_2 \geq r_2d_1$	P_1 and P_2 are stable	$(-\ 0)/(-\ -)/(0\ -)$
$r_2 > d_2N_2^0,\ \beta_2 < r_2d_1,\ \Delta_2 > 0, AB > 0$	P_2 and P_4 are stable	$(-\ +)/(-\ -)/(0\ -)$
$r_2 > d_2N_2^0,\ \beta_2 < r_2d_1,\ \Delta_2 > 0, AB > 0$	P_3 is a saddle-node	$(-\ +)/(-\ -)/(0\ -)$
$r_2 > d_2N_2^0,\ \beta_2 < r_2d_1,\ \Delta_2 < 0 \text{ or } AB \leq 0$	P_2 is stable	$(0\ -)$

The maximal population densities of the species are as follows. It follows from Theorems 3.2 and 3.3 that the maximal density of the resource is its carrying capacity r_2/d_2. The consumer could approach its maximal density at the maximum of l_1, $\hat{N}$, if the isocline l_2 passes through the point $\hat{N}$. By Theorem 3.2(ii) and Theorem 3.3(ii), we have the following result.

Corollary 3.4. *Let* $\hat{N}_2 > 0$ *and* $r_2 - \beta_2\hat{N}_1 - d_2\hat{N}_2 = 0$.

(i) *If the intrinsic growth rate of the resource is small (i.e.* $r_2 \leq d_2N_2^0$), *then the consumer approaches its maximum* $\hat{N}_1$ *while the resource reaches* $\hat{N}_2$.

(ii) *If the intrinsic growth rate of the resource is large (i.e.* $r_2 > d_2N_2^0$), *then the consumer approaches its maximum* $\hat{N}_1$ *and the resource reaches* $\hat{N}_2$ *if the initial density of the consumer is relatively large, i.e., the initial density point is below the separatrix of* P_3 *(the red line in* Fig. 2b).

It follows from Theorems 3.2 and 3.3 that the sign of $N_2^0 - r_2/d_2$ plays a role in the transition of interaction of outcomes of the system (2.2). The variation of $N_2^0 - r_2/d_2$ with parameters α_{12} and β_1 is discussed as follows, while the related discussion is in Section 5 and the proof is in Appendix D.

Proposition 3.5. *For the saturation level* α_{12} *and negative effect level* β_1, *we have*

$$\frac{\partial(N_2^0 - r_2/d_2)}{\partial\alpha_{12}} > 0, \quad \frac{\partial(N_2^0 - r_2/d_2)}{\partial\beta_1} < 0.$$

Remark 3.6. It follows from Theorems 3.2 and 3.3 that the eight-dimensional parameter space, which consists of parameters r_1, r_2, $d_1, d_2, b_2, \alpha_{12}, \beta_1$ and β_2, is divided into six regions as follows, which is shown in Fig. 4:

(i) In region I, we have $r_2/d_2 \leq N_2^0$ and $r_2/\beta_2 \leq r_1/d_1$; in region II, we have $r_2/d_2 \leq N_2^0$ and $r_2/\beta_2 > r_1/d_1$; in region III, we have $r_2/d_2 > N_2^0$ and $r_2/\beta_2 \leq r_1/d_1$.

(ii) In region IV, we have $r_2/\beta_2 > r_1/d_1$, $\Delta_2 > 0$ and $AB > 0$; in region V, we have $r_2/\beta_2 > r_1/d_1$, $\Delta_2 = 0$ and $AB > 0$; in region VI, we have $r_2/\beta_2 > r_1/d_1$, $\Delta_2 < 0$ and/or $AB \leq 0$.

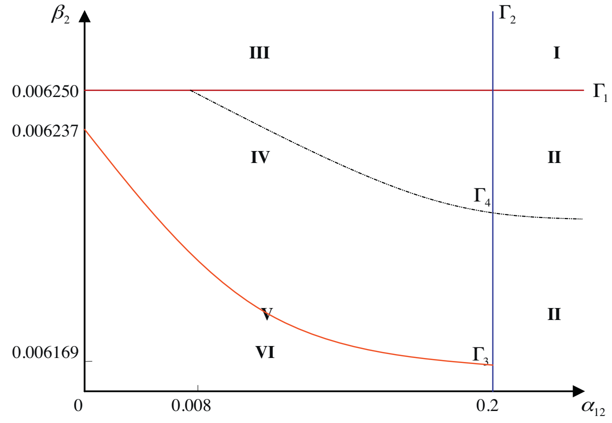

Fig. 4. Fix $r_1 = 0.8$, $r_2 = 0.5$, $b_2 = 0.4$, $\beta_1 = 0.02$ and $d_1 = d_2 = 0.01$. We denote curves $\Gamma_1 : \beta_2 = 0.00625$, $\Gamma_2 : \alpha_{12} = 0.2$, $\Gamma_3 : \Delta_2 = 0$ as $0 < \alpha_{12} < 0.2$, and $\Gamma_4 : p_{41} = 80$ as $\alpha_{12} > 0.008$. Then the $\alpha_{12}\beta_2$ plane is divided into six regions by Γ_1, Γ_2 and Γ_3. In region I, P_1 is globally stable and the interaction outcomes are $(-\ 0)$. In II, P_4 is globally stable and the outcomes are $(-\ +)$, $(-\ 0)$ and $(-\ -)$ when (α_{12}, β_2) is above, on and below Γ_4 respectively. In III, the unique interior equilibrium P_3 is a saddle and the outcomes are $(0\ -)$, $(-\ -)$ and $(-\ 0)$ when $N(0)$ is above, on and below the separatrix of P_3 respectively. In IV, there are two interior equilibria P_3 and P_4. The interaction outcomes are determined by both the factors and initial densities as described in Section 4, while similar situations emerge in region V where the unique interior equilibrium $\bar{P}_3$ is a saddle-node. In VI, P_2 is globally stable and the outcomes are $(0\ -)$.

4. Transition mechanism

In this section, we show how and under what conditions the interaction outcomes transition among predation/parasitism $(+\ -)$, amensalism $(-\ 0)$ and competition $(-\ -)$ as both the factors (parameters) and initial densities of the species vary. We also give an example to exhibit how and when the variance of two specific parameters leads to the transition of interaction outcomes.

We demonstrate the variance of interaction outcomes with all the eight parameters and initial densities as follows. As shown in Remarks 3.6, the parameter space is divided into six regions. When the parameters are in region I, we have $r_2/d_2 \leq N_2^0$ and $r_2/\beta_2 \leq r_1/d_1$. It follows from Theorem 3.2(i) that all positive solutions converge to $P_1(r_1/d_1, 0)$, which corresponds to the interaction outcomes $(-\ 0)$. Thus the resource (species 2) goes to extinction while the consumer (species 1) approaches its carrying capacity when in isolation from the resource. Hence the interaction outcomes of the system (2.2) are determined by the factors (parameters) in region I. The ecological meaning is that the small intrinsic growth rate of the resource ($r_2 \leq d_2N_2^0$) and large consumption level ($\beta_2 \geq r_2d_1/r_1$) lead to the extinction of the resource.

In region II, we have $r_2/d_2 \leq N_2^0$ and $r_2/\beta_2 > r_1/d_1$. It follows from Theorem 3.2(ii) that all positive solutions converge to $P_4(p_{41}, p_{42})$ and the two species coexist while p_{41} is given by (2.8). Then, if $p_{41} < r_1/d_1$, the interaction outcomes are $(-\ -)$; if $p_{41} = r_1/d_1$, the outcomes become $(-\ 0)$; if $p_{41} > r_1/d_1$, the outcomes become $(-\ +)$. Hence the interaction outcomes are also determined by the factors (parameters) in region II. The ecological meaning is that the small intrinsic growth rate of the resource ($r_2 \leq d_2N_2^0$) and small consumption level ($\beta_2 < r_2d_1/r_1$) lead to the coexistence of the two species.

In region III, we have $r_2/d_2 > N_2^0$ and $r_2/\beta_2 \leq r_1/d_1$. It follows from Theorem 3.3(i) that the N_1N_2 plane is divided into three regions by the separatrix of P_3 as shown in Fig. 2a: if the initial density point, $N(0)$, is above the separatrix of P_3, the solution $N(t)$ converges to P_2 as $t \to +\infty$, and the interaction outcomes are $(0\ -)$; if $N(0)$ is on the separatrix, the solution converges to P_3 and the outcomes become $(-\ -)$; if $N(0)$ is below the separatrix, the solution converges to P_1 and the outcomes become $(-\,0)$. Hence the interaction outcomes are determined by the initial population densities of the species in region III. The ecological meaning is that the large intrinsic growth rate of the resource ($r_2 > d_2 N_2^0$) and large consumption level ($\beta_2 > r_2 d_1 / r_1$) lead to the dependence on the initial population densities of the species.

In region IV, we have $r_2/d_2 > N_2^0$, $r_2/\beta_2 > r_1/d_1$, $\Delta_2 > 0$ and $AB > 0$. It follows from Theorem 3.3(ii) that the N_1N_2 plane is divided into three regions by the separatrix of P_3 as shown in Fig. 2b: if the initial density point, $N(0)$, is above the separatrix of P_3, the solution $N(t)$ converges to P_2 as $t \to +\infty$, and the interaction outcomes are $(0\,-)$. If $N(0)$ is on the separatrix, the solution converges to P_3 and the outcomes are: $(-\,-)$ as $p_{31} < r_1/d_1$; $(-\,0)$ as $p_{31} = r_1/d_1$; $(-\,+)$ as $p_{31} > r_1/d_1$, while p_{31} is given by (2.8). If $N(0)$ is below the separatrix, the solution converges to $P_4(p_{41}, p_{42})$ and the outcomes are: $(-\,-)$ as $p_{41} < r_1/d_1$; $(-\,0)$ as $p_{41} = r_1/d_1$; $(-\,+)$ as $p_{41} > r_1/d_1$, while p_{41} is given by (2.8). Hence the interaction outcomes are determined by both the factors (parameters) and initial population densities in region IV. The ecological meaning is that the large intrinsic growth rate of the resource ($r_2 > d_2 N_2^0$) and intermediate consumption level ($\beta_2 < r_2 d_1 / r_1$ but $\Delta_2 > 0$ and $AB > 0$) lead to the dependence on both factors and initial population densities.

In region V, we have $r_2/d_2 > N_2^0$, $r_2/\beta_2 > r_1/d_1$, $\Delta_2 = 0$ and $AB > 0$. It follows from Theorem 3.3(iii) that the N_1N_2 plane is divided into two regions by the separatrix of $\bar{P}_3$, as shown in Fig. 3a: if the initial density point, $N(0)$, is above the separatrix of $\bar{P}_3$, the solution $N(t)$ converges to P_2 as $t \to +\infty$, and the interaction outcomes are $(0\,-)$. If $N(0)$ is on or below the separatrix, the solution converges to $\bar{P}_3$ and the outcomes are: $(-\,-)$ as $\bar{p}_{31} < r_1/d_1$; $(-\,0)$ as $\bar{p}_{31} = r_1/d_1$; $(-\,+)$ as $\bar{p}_{31} > r_1/d_1$, while $\bar{p}_{31}$ is given by (2.8). Hence the interaction outcomes are also determined by both the factors (parameters) and initial population densities in region V. The ecological meaning is that the large intrinsic growth rate of the resource ($r_2 > d_2 N_2^0$) and intermediate consumption level ($\beta_2 < r_2 d_1 / r_1$ but $\Delta_2 = 0$ and $AB > 0$) lead to the dependence on both factors and initial population densities.

In region VI, we have $r_2/d_2 > N_2^0$, $r_2/\beta_2 > r_1/d_1$, $\Delta_2 < 0$ and/or $AB \le 0$. It follows from Theorem 3.3(iv) that all positive solutions converge to $P_2(0, r_2/d_2)$, as shown in Fig. 3b, and the interaction outcomes are $(0\,-)$. Thus the consumer goes to extinction, while the resource approaches its carrying capacity when in isolation from the consumer. Hence the interaction outcomes are determined by the factors (parameters) in region VI. The ecological meaning is that the large intrinsic growth rate of the resource ($r_2 > d_2 N_2^0$) and small consumption level ($\beta_2 < r_2 d_1 / r_1$, $\Delta_2 < 0$ and/or $AB \le 0$) lead to the extinction of the consumer.

As an example, we show how a pair of parameters and the initial densities of species populations affect the interaction outcomes of the system (2.2) as follows. We fix all parameters but α_{12} and β_2, while similar discussions can be given for other parameters.

Let

$$r_1 = 0.8, \qquad r_2 = 0.5, \qquad \beta_1 = 0.02, \qquad b_2 = 0.4,$$
$$d_1 = d_2 = 0.01.$$

Let Γ_1 denote the line $r_2/\beta_2 = r_1/d_1$, we have

$$\Gamma_1 : \beta_2 = 0.00625.$$

Let Γ_2 denote the curve $N_2^0 = r_2/d_2$. Since $N_2^0 \approx (0.8 + \alpha_{12})/0.02$, we have

$$\Gamma_2 : \alpha_{12} = 0.2.$$

We denote

$$\Gamma_3 = \{(\alpha_{12}, \beta_2) : 0 < \alpha_{12} < 0.2, \Delta_2 = 0, AB > 0\},$$

and

$$\Gamma_4 = \{(\alpha_{12}, \beta_2) : \alpha_{12} > 0.008,\ p_{41} = 80\},$$

which are shown in Fig. 4 based on numerical simulations. Here, A, B, Δ_2 and p_{41} are given by (2.7) and (2.8).

It follows from Theorems 3.2 and 3.3 that the $\alpha_{12}\beta_2$ parameter plane is divided into six regions by the curves Γ_1, Γ_2 and Γ_3, which are shown in Fig. 4. As discussed above, in region I = $\{(\alpha_{12}, \beta_2) : \alpha_{12} \ge 0.2, \beta_2 \ge 0.00625\}$, all positive solutions converge to the equilibrium P_1, which corresponds to the interaction outcomes $(-\,0)$. In region II = $\{(\alpha_{12}, \beta_2) : \alpha_{12} \ge 0.2, \beta_2 < 0.00625\}$, and all positive solutions converge to the equilibrium P_4. Furthermore, when (α_{12}, β_2) is above Γ_4, we have $p_{41} > r_1/d_1$ and the interaction outcomes are $(-\,+)$; when (α_{12}, β_2) is on Γ_4, we have $p_{41} = r_1/d_1$ and the outcomes are $(-\,0)$; when (α_{12}, β_2) is below Γ_4, we have $p_{41} < r_1/d_1$ and the outcomes are $(-\,-)$. That is, the interaction outcomes are determined by the factors (parameters) in both regions I and II.

In region III = $\{(\alpha_{12}, \beta_2) : 0 < \alpha_{12} < 0.2, \beta_2 \ge 0.00625\}$, the unique equilibrium P_3 is a saddle, while the dynamical behavior of (2.2) is shown in Fig. 2a. It follows from the monotonicity of l_2 that $p_{31} < r_1/d_1$. Hence when the initial density point, $N(0)$, is above the separatrix of P_3, the solution $N(t)$ converges to P_2, which corresponds to the interaction outcomes $(0\,-)$. When $N(0)$ is on the separatrix, the solution converges to P_3, which corresponds to the outcomes $(-\,-)$. When $N(0)$ is below the separatrix, the solution converges to P_1, which corresponds to the outcomes $(-\,0)$. That is, the interaction outcomes are determined by the initial population densities of the species in region III.

In region IV = $\{(\alpha_{12}, \beta_2) : 0 < \alpha_{12} < 0.2, \beta_2 < 0.00625$ and (α_{12}, β_2) is above $\Gamma_3\}$, there are two interior equilibria P_3 and P_4, where P_3 is a saddle and P_4 is a stable node as shown in Fig. 2b. Numerical simulations show that $p_{31} < r_1/d_1$ in region IV. Then when the initial density point $N(0)$ is above the separatrix of P_3, the solution $N(t)$ converges to P_2, which corresponds to the interaction outcomes $(0\,-)$. When $N(0)$ is on the separatrix, the solution converges to P_3, which corresponds to the outcomes $(-\,-)$. When $N(0)$ is below the separatrix, the solution converges to P_4 and the interaction outcomes are $(-\,+)$, $(-\,0)$ and $(-\,-)$, as (α_{12}, β_2) is above, on and below Γ_4, respectively. That is, the interaction outcomes are determined by both the factors (parameters) and initial population densities in region IV.

In region V = $\{(\alpha_{12}, \beta_2) : 0 < \alpha_{12} < 0.2$ and (α_{12}, β_2) is on $\Gamma_3\}$, the unique interior equilibrium P_3 is a saddle-node, as shown in Fig. 3a. Numerical simulations display that $p_{31} < r_1/d_1$ in region V. Then when the initial density point $N(0)$ is above the separatrix of P_3, the solution $N(t)$ converges to P_2, which corresponds to the interaction outcomes $(0\,-)$. When $N(0)$ is on or below the separatrix, the solution converges to P_3, which corresponds to the outcomes $(-\,-)$. That is, the interaction outcomes are determined by both the factors (parameters) and initial population densities in region V.

In region VI = $\{(\alpha_{12}, \beta_2) : 0 < \alpha_{12} < 0.2$ and (α_{12}, β_2) is below $\Gamma_3\}$, all positive solutions converge to equilibrium P_2 as shown in Fig. 3b, which corresponds to the interaction outcomes $(0\,-)$. That is, the interaction outcomes are determined by the factors (parameters) in region VI.

5. Application and discussion

In this paper we have considered a uni-directional C–R system in which the resource has a negative, as well as a positive, effect on the consumer. Using the analysis of a specific system, we demonstrated the mechanisms by which and circumstances under which interaction outcomes of the system vary with both different factors and initial densities of the species populations. We also showed conditions under which the maximal population densities of the species can be approached. Our work extends the C–R theory established by Holland and DeAngelis (2009).

In the specific uni-directional C–R system that we considered, factors (parameters) play an important role in the transition of interaction outcomes. We focused on the saturation level (α_{12}) and consumption level (β_2) of the consumer (species 1), and noted that similar descriptions can be given for the resource (species 2), as well as for other factors than the two just mentioned. *First*, when both the saturation level and consumption level of the consumer are large (i.e., $N_2^0 > r_2/d_2$ and $\beta_2 > r_2 d_1/r_1$), it follows from Theorem 3.2(i) and Proposition 3.5 that the consumer is 'dominant' in the two species system. Thus, for any initial population densities, the consumer will approach its carrying capacity, while the resource goes to extinction. *Second*, when the saturation level is large but the consumption level is intermediate, it follows from Theorem 3.2(ii) and Proposition 3.5 that the two species coexist and species 1 would approach a density larger than its carrying capacity, as the two levels are well balanced, which is described by the inequality $p_{41} > r_1/d_1$ (see Fig. 1b). *Finally*, when both the saturation level and consumption level are small, it follows from Theorem 3.3(iv) and Proposition 3.5 that the consumer goes to extinction while the resource approaches its carrying capacity.

The initial population densities of the species are crucial in the transition of interaction outcomes. When the saturation level is small, but the consumption level is large, it follows from Theorem 3.3(i) and Proposition 3.5 that, if its initial population density is large, the consumer will approach its carrying capacity, while the resource goes to extinction. Otherwise, if its initial density is small, the consumer will go to extinction, while the resource approaches its carrying capacity. Hence it is the initial population densities of the species that determine the interaction outcomes of the system in this situation.

The balance of the factors and initial population densities are also vital in the transition of interaction outcomes. When both the saturation level and consumption level of the consumer are intermediate in value, it follows from Theorem 3.3(ii) and (iii) that, if its initial density is small, the consumer will go to extinction, while the resource approaches its carrying capacity. However, if the initial density of the consumer is large, the two species coexist and the consumer will approach a density larger than its carrying capacity, if the two levels are well balanced, which is described by the inequality $p_{41} > r_1/d_1$ (see Fig. 1b).

The interesting phenomena shown in the experiments of Urabe and Sterner (1996), as mentioned in the Introduction, can be explained using our model. First, recall that Loladze et al. (2000) developed a model for this phenomenon, using a function for the efficiency of conversion of algae to zooplankton biomass that can decrease to zero when the algal density increases to large values, as a result of the phosphorus: carbon ratio, and hence food quality, decreasing. Although the mathematical function that Loladze et al. use looks different from mathematical form of model (2.2), it is easy to show that the two terms

$$\frac{\alpha_{12}N_2}{b_2+N_2} - \beta_1 N_2$$

can be rewritten, with introduction of some new parameters, as

$$\frac{\eta_1 N_2}{b_2+N_2}(1-\eta_2 N_2),$$

where $\eta_1 = \alpha_{12} - \beta_1 b_2$ and $\eta_2 = \beta_1/(\alpha_{12} - \beta_1 b_2)$. This represents a trophic interaction term in which the conversion efficiency, $1 - \eta_2 N_2$, decreases with increasing algae biomass. Hence this is similar in form to the model of Loladze et al. From this model (2.2), it is easy to explain the experimental results. When light intensity increases from low, to medium, then to high levels in the experiments, the intrinsic growth rate of the algae (i.e., r_2 in (2.2)) monotonically increases from small, to medium, to large values (Urabe and Sterner, 1996). Consider the situation in which the algae and zooplankton coexist, that is, in which $P_4(p_{41}, p_{42})$ is a stable equilibrium of (2.2) in Theorem 3.3(ii). The variation of p_{41} with increases of r_2 can be shown geometrically as follows. By the concave principle and monotonicity of l_1, as shown in Fig. 1b, isocline l_2 moves upward in a parallel way when r_2 increases. Then p_{41} increases monotonically with the increase of r_2, as long as $p_{42} < \hat{N}_2$ holds, where l_1 corresponds to a monotonically increasing function, and p_{41} decreases monotonically with the increase of r_2 when $p_{42} > \hat{N}_2$, where l_1 then corresponds to a monotonically decreasing function. Hence when r_2 increases from small to intermediate values (i.e., $p_{42} \le \hat{N}_2$), the population density of the zooplankton, p_{41}, increases from a small value to its maximum $\hat{N}_1$. However, when r_2 increases from intermediate to large values, such that $\hat{N}_2 < p_{42} < \bar{p}_{32}$, p_{41} decreases monotonically from its maximum $\hat{N}_1$ to $\bar{p}_{31}$ where $\bar{p}_{31}$ and $\bar{p}_{32}$ are given in (2.8). Hence our model provides explanations for the phenomena in the experiments. Furthermore, the model predicts new situations: when the light intensity continues to increase, such that the condition in Theorem 3.3(iv) is satisfied (i.e., the equilibrium $\bar{P}_3(\bar{p}_{31}, \bar{p}_{32})$ disappears), it follows from Theorem 3.3(iii) and (iv) that the density (i.e., the steady state) of the zooplankton will jump from a positive value ($\bar{p}_{31}$) to zero; that is, as a discrete jump rather than a continuous transition. Therefore, when the growth rate, r_2, of algae increases, there are three stages in the zooplankton's growth. In the first stage, its density increases monotonically from small values to its maximal value; in the second stage, its density decreases monotonically from its maximum to a positive value ($\bar{p}_{31}$); in the third stage, its density (i.e., in steady state) suddenly jumps from the positive value ($\bar{p}_{31}$) to zero, where it goes to extinction.

The work in this paper differs from that of Holland and DeAngelis (2009) on their uni-directional model. *First*, the model is a different variation from their model (see Section 1). Second, the method of analysis is different. While the results of Holland and DeAngelis (2009) are obtained by numerical simulations and are powerful in predicting novel transitions of outcomes, mathematical proofs were not shown, but the analysis were performed using symbolic math and specified parameter values. In this paper, we deduce our results in a rigorous way. *Furthermore*, our conditions under which the interaction outcomes undergo transitions are given quantitatively, which is helpful in understanding which factor or initial density is important. *Finally*, the results have some differences: (a) The interaction outcomes ($- \, -$) display that both of the consumer and resource would approach population densities below their carrying capacities; (b) The interaction outcomes ($0 \, -$) demonstrate a novel situation that the consumer may go extinct in the C–R system as shown in Fig. 3; (c) The transitions in this paper are among the interaction outcomes ($- \, +$), ($0 \, -$), ($- \, 0$) and ($- \, -$), while the transitions are among ($+ \, -$), ($0 \, +$), ($+ \, 0$) and ($+ \, +$) in the paper by Holland and DeAngelis (2009) in their uni-directional C–R model.

The situation that resources have a negative effect on the consumers exists widely in nature. For example, our everyday experience tells us that many kinds of human food have both healthy and unhealthy effects on human bodies. Despite the simplicity of our assumptions, our model is helpful in understanding the transitions between different interaction outcomes that can occur during changes of different factors in uni-directional C–R systems.

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Appendix A

Proof of Theorem 3.1. Let

$$D(N_1,N_2)=\frac{1}{N_1N_2},$$

then we have

$$\frac{\partial[D(d_1G_1-d_1N_1)]}{\partial N_1}+\frac{\partial[D(d_2G_2-d_2N_2)]}{\partial N_2}=-\frac{d_1}{N_2}-\frac{d_2}{N_1}<0.$$

By the Bendixson–Dulac Theorem (Hofbauer and Sigmund, 1998), there is no periodic orbit in system (2.2). ☐

Appendix B

Proof of Theorem 3.2. When $r_2/d_2\le N_2^0$ and $r_2/\boldsymbol{\beta}_2\le r_1/d_1$ as shown in Fig. 1a, l_1 is above l_2 and there is no intersection between them in the interior of R_+^2 where $R_+^2=\{(N_1,N_2):N_1\ge 0,N_2\ge 0\}$. Then there is no interior equilibrium of (2.2). It follows from the phase portrait analysis (Hofbauer and Sigmund, 1998) that all positive solutions of 2.2 converge to equilibrium P_1 as shown in Fig. 1a. That is, species 1 reaches its carrying capacity when in isolation from species 2, while species 2 goes to extinction. When $r_2/\boldsymbol{\beta}_2>r_1/d_1$ as shown in Fig. 1b, l_1 and l_2 intersect at P_4. It follows from Theorem 3.2 and the phase portrait analysis that all positive solutions of (2.2) converge to P_4 as shown in Fig. 1b. ☐

Appendix C

Proof of Theorem 3.3. When $r_2/d_2>N_2^0$ and $r_2/\boldsymbol{\beta}_2\le r_1/d_1$ as shown in Fig. 2a, l_1 and l_2 intersect at P_3. It follows from Theorem 3.1 and the phase portrait analysis that P_3 is a saddle and orbits below the separatrix of P_3 converge to the equilibria P_1 while those above the separatrix converge to P_2, which is shown in Fig. 2a.

When $r_2/\boldsymbol{\beta}_2>r_1/d_1$, $\boldsymbol{\Delta}_2>0$ and $AB>0$ as shown in Fig. 2b, l_1 and l_2 intersect at P_3 and P_4. It follows from Theorem 3.1 and the phase portrait analysis that P_3 is a saddle while P_4 is a stable node, and orbits below the separatrix of P_3 converge to the equilibria P_4 while those above the separatrix converge to P_2, which is shown in Fig. 2b.

When $r_2/\boldsymbol{\beta}_2>r_1/d_1$, $\boldsymbol{\Delta}_2=0$ and $AB>0$ as shown in Fig. 3a, l_1 and l_2 are tangent at the saddle-node $\bar{P}_3(P_{31},P_{32})$ (Zhang et al., 1992)

$$P_{31}=\frac{B}{2A},\qquad P_{32}=\frac{1}{d_2}(r_2-\beta_2p_{31}).\tag{C.1}$$

It follows from Theorem 3.1 and the phase portrait analysis that orbits below the separatrix of P_3 converge to the equilibria P_3 while those above the separatrix converge to P_2, which is shown in Fig. 3a.

When $r_2/\boldsymbol{\beta}_2>r_1/d_1$, $\boldsymbol{\Delta}_2<0$ (or $AB\le 0$) as shown in Fig. 3b, l_1 is below l_2. Then there is no interior equilibrium of (2.2) and all positive solutions converge to P_2. ☐

Appendix D

Proof of Proposition 3.5. It follows from (2.4) that

$$\frac{\partial(N_2^0-r_2/d_2)}{\partial\alpha_{12}}=\frac{r_1+\alpha_{12}-b_2\beta_1+\sqrt{\Delta_1}}{2\beta_1\sqrt{\Delta_1}}>0.$$

By the definition of N_2^0, we have

$$r_1+\alpha_{12}\frac{\alpha_{12}b_2}{b_2+N_2^0}-\beta_1N_2^0=0.$$

By taking partial derivatives with respect to $\boldsymbol{\beta}_1$ on both sides of the equation, we have

$$\left[\frac{\alpha_{12}b_2}{(b_2+N_2^0)^2}-\beta_1\right]\frac{\partial N_2^0}{\partial\beta_1}=N_2^0.\tag{D.1}$$

It follows from (2.4) that

$$b_2+N_2^0=\frac{r_1+\alpha_{12}+b_2\beta_1+\sqrt{\Delta_1}}{2\beta_1}>\frac{r_1+\alpha_{12}+b_2\beta_1}{\beta_1}.$$

Therefore, we have $(b_2+N_2^0)^2>\alpha_{12}b_2/\beta_1$. That is, $\alpha_{12}b_2/(b_2+N_2^0)^2-\beta_1<0$. By (D.1), we have $\partial N_2^0/\partial\beta_1<0$. That is, $\partial(N_2^0-r_2/d_2)/\partial\beta_1<0$. ☐

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