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The effect of the Holling type II functional response on apparent competition

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Abstract

This article analyzes the classical 2-resource–1-consumer apparent competition community module with the Holling type II functional response. Two types of resource regulation (top-down vs. combined top-down and bottom-up) and two types of consumer behaviors (inflexible consumers with fixed preferences for resources vs. adaptive consumers) are considered. When resources grow exponentially and consumers are inflexible foragers, one resource is always outcompeted due to strong apparent competition. Density dependent resource growth relaxes apparent competition so that resources can coexist. As multiple attractors (either equilibria or limit cycles) coexist, population dynamics and community composition depend on initial population densities. Population dynamics change dramatically when consumers forage adaptively. In this case, the results both for top-down, and combined top-down and bottom-up regulation are similar and they show that species persistence occurs for a much larger set of parameter values when compared with inflexible consumers. Moreover, population dynamics will be chaotic when resource carrying capacities are high enough. This shows that adaptive consumer switching can destabilize population dynamics.

Keywords: Apparent competition; Optimal foraging; The ideal free distribution; Population dynamics; Evolutionary ecology; Patch dynamics; Chaos; Multiple attractors

1. Introduction

A consumer sharing two resources is one of the community modules that has received a lot of attention since the pioneering work of Holt (1977) on apparent competition (see also Holt, 1984; Holt and Lawton, 1994). In this module resources that can be spatially segregated, interact through shared consumers in a similar way as two predator species compete for a common prey. This is because apparent competition, as any other indirect density mediated interactions (e.g., trophical cascade), can strongly influence community composition (Holt and Lawton, 1994). A detailed mechanistic understanding of apparent competition is important, e.g., to asses the effect of alien species invasion on native ecosystems (e.g., Morris et al., 2004; Rand and Louda, 2004; Koss et al., 2004; Harmon and Andow, 2004; Koss and Snyder, 2005).

The negative effect of one resource on the other resource at a population equilibrium (or, more generally along a consumer isocline) was shown for a broad class of population dynamics (Holt, 1977). An excellent analysis for the Lotka–Volterra model with all species coexisting at an equilibrium was given in Holt (1977, 1984). In this case, an increase in one resource equilibrium density increases equilibrium consumer density which has a negative effect on the other resource equilibrium density. Understanding the role of apparent competition when species do not coexist at an equilibrium, or, multiple community states coexist, is more difficult. Holt (1997a) presents a time-averaging argument suggesting that if resources experience no direct density dependence, then even in fluctuating environments one resource will be outcompeted due to strong apparent competition. Such a situation often arises when the linear functional response is replaced by the

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Holling type II functional response which destabilizes the resource–consumer interaction via the MacArthur–Rosenzweig paradox of enrichment (e.g., Kretzschmar et al., 1993; Klebanoff and Hastings, 1994; Abrams et al., 1998; Abrams, 1999; Abrams and Holt, 2002).

Holt (1984) also showed that if consumers switch between resources optimally then apparent competition ceases at the population equilibrium. This is because apparent competition at the population equilibrium requires that the predator isocline in the resource 1–resource 2 phase space has a negative slope. However, when an optimally foraging consumer switches abruptly as resource densities change, the consumer isocline is rectangular (Holt, 1983). Křivan (1997) studied the effect of optimal predator switching on the Lotka–Volterra population dynamics (with exponential resource growth and linear functional response) in a two-patch environment. Consumers were assumed to be free to move between two resource patches while resources did not move. As predicted by Holt (1977, 1997a), fixed consumer preferences led to exclusion of one resource due to strong apparent competition. In contrast, if consumers moved between patches so that their fitness measured by the per capita population growth rate was instantaneously maximized, resources in both patches survived although the system dynamics did not tend to an equilibrium. Moreover, consumers drove resources to the levels where consumer fitness was independent of the consumer strategy, which led to the ideal free distribution (IFD) of consumers (Fretwell and Lucas, 1970).

In this article, we consider 2-resource–one consumer population dynamics with the Holling type II functional response. We compare the case where consumer preferences for either resource are independent from resource densities with population dynamics where consumers switch between the two prey optimally. We do this comparison both for exponential resource growth (top-down regulation) and logistic resource growth (combined top-down and bottom-up regulation). Following general predictions (Holt, 1977, 1997a) we expect that for inflexible consumers and top-down regulation only, one resource will be outcompeted from the community. When resource growth is also bottom-up regulated, apparent competition gets weaker as there is an upper limit on consumer densities (Holt, 1977), and resources can coexist. We analyze this case numerically and we show that bottom-up regulation can lead to non-equilibrium population dynamics (equilibria and/or limit cycles) and multiple attractors similarly as in the case of purely exploitative community module (Armstrong and McGehee, 1976, 1980). We analyze dependence of all attractors on resource carrying capacities.

Then we do the same analysis assuming that consumers behave as optimal foragers. We show that consumer switching promotes species coexistence without stabilizing population dynamics. In fact, optimal consumer foraging behavior can destabilize species coexistence and lead to chaotic population dynamics.

2. One-consumer–two-resource population dynamics

We assume that resources are spatially distributed in two patch types. Resource abundance in patch i is R_i $(i = 1, 2)$ and the overall consumer abundance in both patches is C. Population dynamics that neglect consumer travel time are described by the following model:

$$\begin{aligned}
\frac{dR_1}{dt} &= r_1(R_1)R_1 - \frac{\lambda_1 R_1 u_1 C}{1 + h_1\lambda_1 R_1},\\
\frac{dR_2}{dt} &= r_2(R_2)R_2 - \frac{\lambda_2 R_2 u_2 C}{1 + h_2\lambda_2 R_2},\\
\frac{dC}{dt} &= \left(\frac{e_1\lambda_1 R_1}{1 + h_1\lambda_1 R_1} - m_1\right)u_1 C\\
&\quad + \left(\frac{e_2\lambda_2 R_2}{1 + h_2\lambda_2 R_2} - m_2\right)u_2 C. \qquad (1)
\end{aligned}$$

Here u_i denotes the fraction of lifetime an average consumer stays in patch i, r_i is the intrinsic per capita resource i growth rate, λ_i is the cropping rate, h_i is the handling time, e_i denotes the efficiency with which resources are converted to new consumers, and m_i is the per capita consumer mortality rate. Neglecting consumer travel time leads to $u_1 + u_2 = 1$, since every consumer is in either patch 1 or patch 2.

Assuming that consumer fitness is measured by the per capita instantaneous consumer population growth rate $dC/(Cdt)$, the consumer optimal strategy is

(a) If $e_1\lambda_1 R_1/(1 + h_1\lambda_1 R_1) - m_1 > e_2\lambda_2 R_2/(1 + h_2\lambda_2 R_2) - m_2$ then consumers maximize their fitness by feeding on resource 1 only ($u_1 = 1$ and $u_2 = 0$).
(b) If $e_1\lambda_1 R_1/(1 + h_1\lambda_1 R_1) - m_1 < e_2\lambda_2 R_2/(1 + h_2\lambda_2 R_2) - m_2$ then consumers maximize their fitness by feeding on resource 2 only ($u_1 = 0$ and $u_2 = 1$).
(c) If $e_1\lambda_1 R_1/(1 + h_1\lambda_1 R_1) - m_1 = e_2\lambda_2 R_2/(1 + h_2\lambda_2 R_2) - m_2$ then consumer fitness is independent of the consumer strategy. Thus, consumer strategy is not uniquely given by fitness maximization.

The equality in (c) defines a surface in the resource 1–resource 2-consumer density phase space. This surface (see the shaded surface in Fig. 1) is called the switching manifold. Along the switching manifold resource densities are such that consumer fitness is independent of the consumer strategy (u_i). If population dynamics together with the optimal consumer strategy are such that trajectories of model (1) tend to the switching manifold, the consumers will distribute among the two patches following the IFD (IFD; Fretwell and Lucas, 1970; Křivan, 1996).

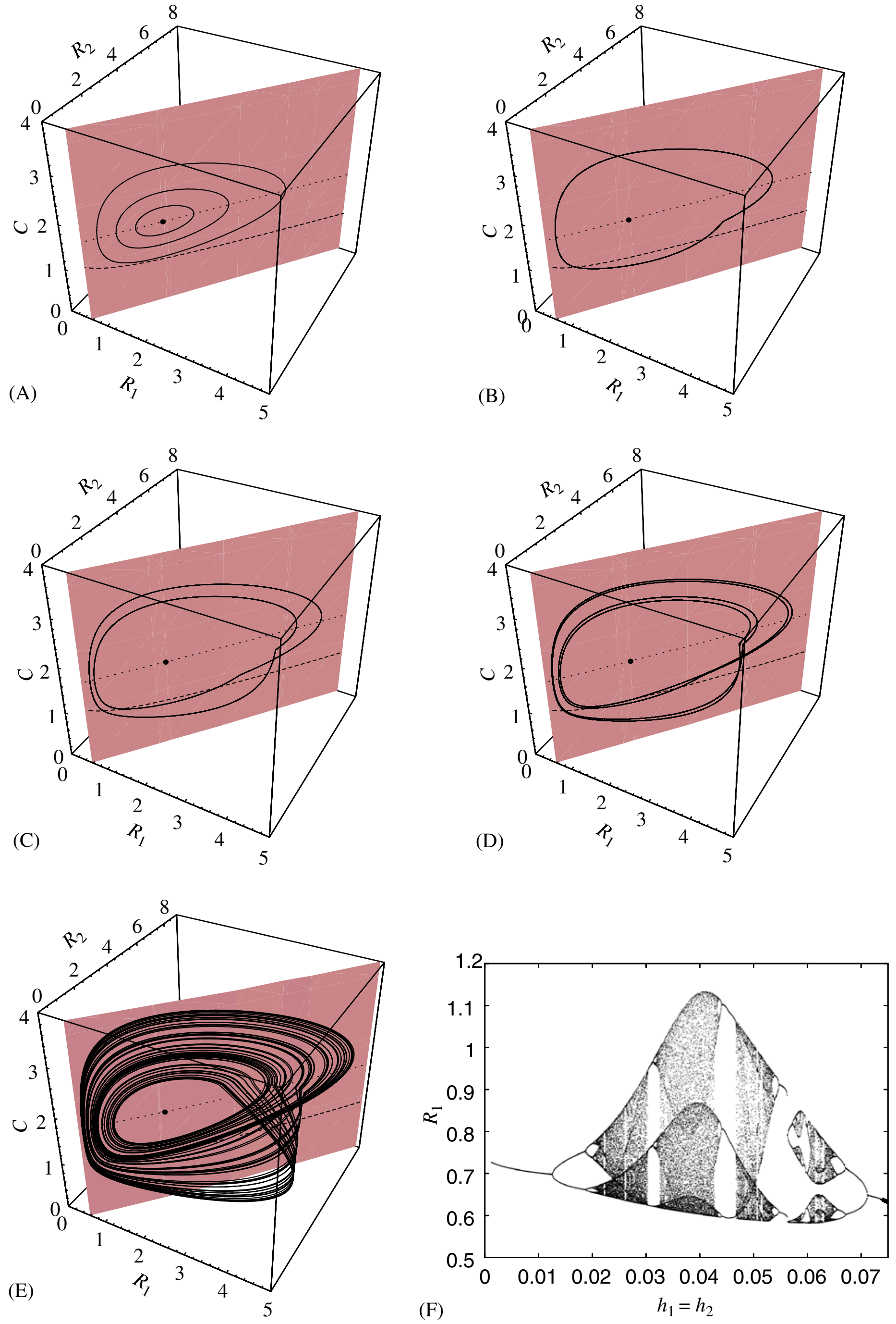

Fig. 1. The long term behavior of trajectories of model (1) with resources growing exponentially ($r_i(R_i) = r_i$) and adaptive consumers. For zero handling times (panel A, $h_1 = h_2 = 0$) a neutrally stable equilibrium exists. This equilibrium is surrounded by a family of Lotka–Volterra closed orbits. For positive handling times, the Lotka–Volterra cycles disappear and trajectories converge to a limit cycle (panel B, $h_1 = h_2 = 0.01$). As handling times increase, the limit cycle undergoes period doubling bifurcation (panel C shows a 2-cycle, $h_1 = h_2 = 0.015$, panel D shows a 4-cycle, $h_1 = h_2 = 0.019$) which is a well-known route to chaos (panel E, $h_1 = h_2 = 0.035$). A corresponding bifurcation diagram is shown in panel F. Other parameters: $r_1 = 1.5$, $r_2 = 0.5$, $m_1 = 0.3$, $m_2 = 0.2$, $e_1 = 0.15$, $e_2 = 0.1$ and $\lambda_1 = 1.2$, $\lambda_2 = 0.9$.

3. Top-down control only

Here we assume that resources grow exponentially and we set $r_i(R_i) = r_i$ in model (1). We will consider two cases: (i) consumer preferences for either resource are fixed and independent of the resource availability, or (ii) consumers adapt their preferences to changing resource densities.

3.1. Fixed preferences

We will show that, for small handling times, model (1) with fixed consumer preferences (u_i) is impermanent because the competitively weaker species (which is the species with lower ratio $r_i/(\lambda_i u_i)$) cannot invade the community consisting of the competitively stronger resource and consumers. Let us assume that resource j is missing. The present resource i-consumer population equilibrium is then

$$R_i^* = \frac{m_i u_i + m_j u_j}{\lambda_i u_i (e_i - m_i h_i) - \lambda_i h_i m_j u_j}$$

and

$$C^* = \frac{r_i e_i}{\lambda_i u_i (e_i - m_i h_i) - h_i \lambda_i m_j u_j}.$$

The missing resource j can invade at the above population equilibrium provided

$$\frac{r_j}{u_j \lambda_j} > \frac{r_i}{u_i \lambda_i - h_i \lambda_i / (e_i (m_i u_i + m_j u_j))}.$$

Similarly, the condition for invasibility of resource i at the resource j-consumer equilibrium is

$$\frac{r_i}{u_i \lambda_i} > \frac{r_j}{u_j \lambda_j - h_j \lambda_j / (e_j (m_i u_i + m_j u_j))}.$$

The above two inequalities cannot hold simultaneously when resource handling times are small, and, consequently, model (1) for non-adaptive consumers with fixed preferences for either patch is impermanent. When handling times are zero, model (1) has no interior equilibrium and the resource with higher ratio $r_i/(u_i \lambda_i)$ outcompetes the other resource through the shared consumers (Holt, 1977; Křivan, 1997). Numerical simulations show that the competitive exclusion holds also for small handling times (although for small positive handling times an interior equilibrium exists, but it is unstable). This is an excellent example of apparent competition in a highly unstable dynamics (Holt, 1977; Abrams et al., 1998; Brassil and Abrams, 2004).

3.2. *Optimal preferences*

Now we consider the case in which consumers behave as optimal foragers, by moving to the patch where their fitness maximizes. We show that consumer switching relaxes conditions for permanence, when compared with inflexible consumers, because the missing resource can always invade the remaining resource–consumer equilibrium. The optimal consumer strategy dictates that at such an equilibrium all consumers will be feeding in the patch that has a positive resource density. This is because in the resource free patch the consumer fitness is negative, while in the patch with a positive resource level the consumer fitness at the corresponding population equilibrium is zero, thus higher. Consequently, the missing resource, not being consumed, can always invade the consumer free patch and the necessary conditions for species permanence are trivially satisfied due to consumer adaptive behavior (see also Holt, 1977).

We show that model (1) with optimal consumers does not have any stable interior equilibrium. It is clear that there is no interior equilibrium off the switching manifold (because off the switching manifold one species is always exponentially growing). Now we consider population dynamics along the switching manifold. The switching manifold consists of two regions (Křivan, 1997; Boukal and Křivan, 1999): (i) the region where trajectories of model (1) tend to the switching manifold from both sides (this region is called the sliding domain because trajectories cannot leave the switching manifold and must "slide" along it), and (ii) the region where trajectories cross switching manifold transversally. In Fig. 1 these two regions of the switching manifold (shaded area) are separated by the dashed curve (the part of the switching manifold above the dashed curve is the sliding domain). Thus, if model (1) has an equilibrium in the switching manifold, the equilibrium must be in the sliding domain. The case where handling times are zero (Křivan, 1997) shows that such an equilibrium in the switching manifold exists (shown as the solid dot in Fig. 1A) and is neutrally stable. Numerical simulations reveal that small positive handling times destabilize this equilibrium and trajectories spiral away from it. When such a trajectory reaches the boundary of the sliding domain (the dashed curve in Fig. 1) it leaves the switching manifold and all consumers move to the patch that provides them with the highest fitness (which is patch 1 in Fig. 1). As resources in patch 1 decrease, there will be a time when consumer fitness equalizes in both patches. At this time, the trajectory hits again the switching manifold and moves along it until it reaches its boundary and so on. For small handling times a limit cycle appears (Fig. 1B). As handling times increase, the limit cycle undergoes a series of period doubling bifurcations (two-cycle in Fig. 1C, four-cycle in D), which is a well-known route to chaos (Fig. 1E). The corresponding bifurcation diagram is shown in Fig. 1F. This diagram shows, for each handling time, how points along the horizontal dotted line (Fig. 1) are mapped by the corresponding trajectories of model (1). More specifically, the points on the diagram show successive values of resource 1 at times when the corresponding trajectory of model (1) intersects with the dotted line while consumer density C decreases. Thus, for a given handling time, the number of points in Fig. 1F, corresponds to the multiplicity of the corresponding limit cycle of model 1 (i.e., a single point means that the corresponding trajectory follows a simple cycle, two points denote a 2-cycle as the one shown in Fig. 1C and so on). As handling times increase, multiplicity of the limit cycle first increases and then decreases via period reversal bifurcations leading finally to a single limit cycle for large handling times.

4. Bottom-up control

Now we consider a combined bottom-up and top-down regulation of resources. We assume the logistic resource growth rate $[r_i(R_i) := r_i(1 - R_i/K_i)]$ in model (1).

4.1. Fixed preferences

First we study the necessary conditions for species permanence. When compared to the case of top-down regulation only, we are in a more complex situation now, because when one resource is missing the other resource–consumer population dynamics may coexist along a limit cycle due to the paradox of enrichment. In this case, the invasibility condition for the missing species along the limit cycle cannot be derived analytically. In analyzing model (1) we will proceed in two steps. First, we derive conditions under which a missing species can invade the community that is at an equilibrium. These necessary conditions for species permanence can be derived analytically. Second, we will analyze qualitative behavior of model (1) numerically with respect to the resource carrying capacities.

4.1.1. Invasibility of the missing species at the community equilibrium

If one resource is missing the remaining resource–consumer population dynamics are described by the MacArthur–Rosenzweig system. If resource $j=(1,2)$ is missing the remaining resource i-consumer system has the following equilibrium:

$$R_i^* = \frac{m_i u_i + m_j u_j}{\lambda_i(u_i(e_i - m_i h_i) - h_i m_j u_j)},$$
$$C^* = \frac{r_i e_i}{\lambda_i u_i(e_i - m_i h_i) - h_i \lambda_i m_j u_j}\left(1 - \frac{R_i^*}{K_i}\right). \qquad (2)$$

This equilibrium is stable (as the equilibrium of the resource i-consumer system) if the present resource i carrying capacity meets the following two threshold conditions

$$\frac{m_i u_i + m_j u_j}{\lambda_i u_i(e_i - m_i h_i) - \lambda_i h_i m_j u_j} < K_i \leqslant \frac{e_i u_i + h_i(m_i u_i + m_j u_j)}{h_i \lambda_i(e_i u_i - h_i(m_i u_i + m_j u_j))}.$$

The first condition states that the carrying capacity must be high enough to support consumers at a positive density (this threshold for resource $i=1(2)$ is shown as the vertical (horizontal) dashed line in Fig. 2, left panel) while the second condition gives an upper bound below which the resource i-consumer equilibrium is stable (in the resource i-consumer phase space). This latter threshold for resource $i=1(2)$ is shown as the solid vertical (horizontal) line in Fig. 2, left panel. For high carrying capacities that meet the second threshold level, the resource i-consumer equilibrium is unstable and a stable (in resource i-consumer density phase space) limit cycle exists due to the paradox of enrichment.

The missing resource j can invade at population equilibrium (2) provided

$$K_i < R_i^* \bigg/ \left(1 - \frac{r_j}{u_j \lambda_j}\frac{\lambda_i}{r_i}\left(u_i - \frac{h_i(m_i u_i + m_j u_j)}{e_i}\right)\right). \qquad (3)$$

This threshold is shown for resource 1 (2) as the dotted vertical (horizontal) line in Fig. 2, left panel. For high resource i carrying capacity that do not satisfy the above inequality, the ith resource level is too high and the missing resource j cannot invade due to strong apparent competition (Holt, 1977).

When consumers are missing, the equilibrial resource densities are K_1 and K_2. Consumers can invade if

$$\left(\frac{e_1\lambda_1 K_1}{1 + h_1\lambda_1 K_1} - m_1\right)u_1 + \left(\frac{e_2\lambda_2 K_2}{1 + h_2\lambda_2 K_2} - m_2\right)u_2 > 0.$$

The expression on the left-hand side of the above inequality defines a curve in the resource carrying parameter space that separates regions A_0 from A_1 in Fig. 2, left panel.

Thus, the invasibility conditions for the missing species to invade at the community equilibrium are satisfied in regions of the resource carrying capacity parameter space that are bounded by the curve separating regions A_0 from A_1 and by dotted lines (Fig. 2, left panel). However, the problem is that for given resource carrying capacities the invasibility of the missing species at the community equilibrium does not guarantee indefinite coexistence of all species if the resource i-consumer limit cycle exists. For example, in Fig. 2C the paradox of enrichment threshold for resource 1 (solid vertical line) is to the left of the invasibility threshold (dotted vertical line). This means that for resource 1 carrying capacities that are to the right of the solid vertical line and to the left of the dotted vertical line a limit cycle in resource 1-consumer phase space exists. For species permanence, this limit cycle must also be invasible by missing resource 2, but the conditions for invasibility cannot be derived analytically. In the next section, we use numerical analysis to derive invasibility conditions along such a limit cycle. We remark, that for zero handling times no limit cycles with one resource missing exist.

4.1.2. Numerical analysis

For numerical analysis we parameterize model (1) so that resource 1 will be outcompeted by resource 2 when resource carrying capacities K_1 and K_2 are infinite (i.e., if resource growth is density independent). Fig. 2 (left panel) and Table 1 show results of numerical stability analysis of model (1). Panel A assumes zero handling times while panels C and E assume positive handling times ($h_1 = h_2 = 0.02$ and $h_1 = h_2 = 0.08$, respectively). Table 1 lists all equilibria and limit cycles that we found by numerical analysis. The equilibria and limit cycles with one species missing are classified as unstable and invasible (UI), unstable and non-invasible (UN), or stable (S). We remark that every boundary equilibrium that is stable (S) is automatically non-invasible. Interior equilibria and limit cycles are classified as stable (S) or unstable (U). Using continuation package XPPAUT (Ermentrout, 2002), we split the K_1–K_2 parameter space in regions with qualitatively different predictions for population dynamics. The curves separating these regions are described in Appendix.

Inspection of Table 1 shows that model (1) is permanent in the following regions: A_1, A_2, A_5, B_1, B_2, B_5, D_1, D_2, D_4

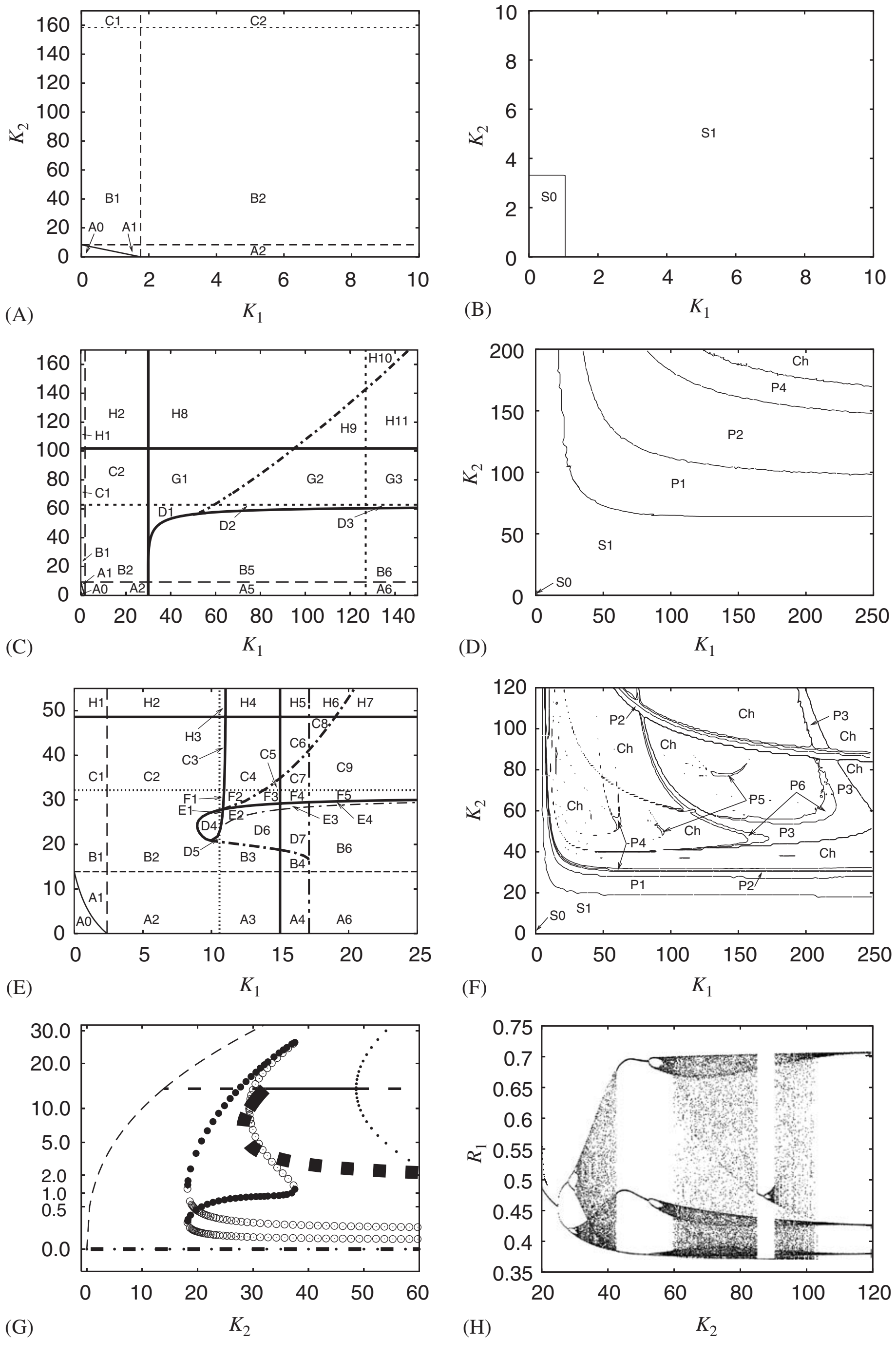

Fig. 2. Results of numerical analysis of model (1) with bottom-up regulation and non-adaptive consumers (left panel, with equal consumer preferences for either patch, $u_1 = u_2 = 0.5$) and adaptive consumers (right panel). The upper three rows show bifurcation diagrams in the carrying capacity parameter space (K_1–K_2) for increasing handling times ($h_1 = h_2 = 0$ in A and B; $h_1 = h_2 = 0.02$ in C and D; $h_1 = h_2 = 0.08$ in E, F). List of all attractors corresponding to various regions is given in Table 1 (for the left panel) and 2 (for the right panel), respectively. Detailed description of curves is in the Appendix. The bottom row shows bifurcation diagrams at a fixed carrying capacity ($K_1 = 16$ in panel G and $K_1 = 200$ in panel H). In panel G, the number of coexisting species is indicated by the line thickness (thick line = 3 species, medium thick line = 2 species, thin line = single species), or the diameter of the circle (large diameter circle = 3 species, small diameter circle = 2 species). Solid (dashed) lines and filled (open) circles denote locally stable (unstable) equilibria and limit cycles, respectively. Parameters: $r_1 = 1.5$, $r_2 = 0.5$, $m_1 = 0.3$, $m_2 = 0.2$, $e_1 = 0.15$, $e_2 = 0.1$, $\lambda_1 = 1.9$, $\lambda_2 = 0.6$.

and D_5. This is because in these regions the missing species can invade two-species equilibria and two-species limit cycles, provided they exist. However, species can coexist even if the system is impermanent. Inspection of Table 1 shows that, in addition to regions where model (1) is permanent, all species can coexist (either at an equilibrium, or along a limit cycle) in regions A_6, B_6, C_5, C_7, C_9, D_3, D_6, D_7, E_1–E_4, F_1–F_5, G_2, G_3 and H_7, H_9, H_{11} (see Table 1 and Fig. 2C, E). However, in these regions species coexistence depends on the initial densities.

Table 1
The results of numerical analysis of model (1) for inflexible consumers and logistically growing resources

Region	Equilibria			Limit cycles		
	R_1C	R_2C	R_1R_2C	R_1C	R_2C	R_1R_2C
A_0	–	–	–	–	–	–
A_1	–	–	S	–	–	–
A_2	UI	–	S	–	–	–
A_3	S	–	–	–	–	–
A_4	UN	–	–	S	–	–
A_5	UI	–	U	UI	–	S
A_6	UN	–	–	UI	–	S
B_1	–	UI	S	–	–	–
B_2	UI	UI	S	–	–	–
B_3	S	UI	–	–	–	–
B_4	UN	UI	–	S	–	–
B_5	UI	UI	U	UI	–	S
B_6	UN	UI	–	UI	–	S
C_1	–	S	–	–	–	–
C_2	UI	S	–	–	–	–
C_3	S	S	U	–	–	–
C_4	S	S	U	–	–	U
C_5	S	S	U	–	–	S, U, U
C_6	UN	S	U	S	–	U
C_7	UN	S	U	S	–	S, U, U
C_8	UN	S	U	UI	–	–
C_9	UN	S	U	UI	–	S, U
D_1	UI	UI	S	UI	–	–
D_2	UI	UI	S	UI	–	S,U
D_3	UN	UI	S	UI	–	S, U
D_4	UI	UI	U	–	–	S
D_5	UI	UI	U	–	–	S, U
D_6	S	UI	–	–	–	S, U
D_7	UN	UI	–	S	–	S, U
E_1	S	UI	U, U	–	–	S
E_2	S	UI	U, U	–	–	S, U
E_3	UN	UI	U, U	S	–	S, U
E_4	UN	UI	U, U	UI	–	S
F_1	S	UI	S, U	–	–	–
F_2	S	UI	S, U	–	–	U
F_3	S	UI	S, U	–	–	S, U, U
F_4	UN	UI	S, U	S	–	S, U, U
F_5	UN	UI	S, U	UI	–	S, U
G_1	UI	S	–	UI	–	–
G_2	UI	S	–	UI	–	S, U
G_3	UN	S	–	UI	–	S, U
H_1	–	UN	–	–	S	–
H_2	UI	UN	–	–	S	–
H_3	S	UN	U	–	S	–
H_4	S	UN	U	–	S	U
H_5	UN	UN	U	S	S	U
H_6	UN	UN	U	UI	S	–
H_7	UN	UN	U	UI	S	S, U
H_8	UI	UN	–	UI	S	–
H_9	UI	UN	–	UI	S	S, U
H_{10}	UN	UN	–	UI	S	–
H_{11}	UN	UN	–	UI	S	S, U

The two-species equilibria and boundary cycles are denotes as R_iC ($i = 1, 2$) and the three-species equilibria and limit cycles are denoted as R_1R_2C, respectively. For the boundary equilibria and limit cycles their invasibility by the missing species is indicated (UN = Unstable and Non-invasible, UI = Unstable and Invasible). Stable (unstable) equilibria and limit cycles are denotes by S (U). Regions of the carrying capacity parameter space correspond to those shown in Fig. 2, left panel.

Table 2
List of the regions corresponding to Fig. 2, right panel and their attractors for adaptive consumers

	Stable attractors
S_0	consumers extinct
S_1	interior equilibrium (no limit cycle)
P_1	interior limit cycle
P_2	interior double limit cycle
P_3	interior triple limit cycle
P_4	interior quadruple limit cycle
P_5	interior 5-limit cycle
P_6	interior 6-limit cycle
Ch	chaotic behavior

Our numerical analysis shows that model (1) behaves qualitatively similarly as the two-dimensional predator-prey MacArthur–Rosenzweig model. For low carrying capacities species coexist at an equilibrium (e.g., regions A_1, A_2, B_1, B_2) while at high carrying capacities either one resource is outcompeted (e.g., regions H_6, H_{10}), or species coexistence is achieved along a locally stable limit cycle (e.g., regions C_9, G_3, H_7, H_{11}). Thus, we observe the paradox of enrichment. In contrast to its two-species counterpart, the three species model can have multiple attractors.

We remark, that the interior locally stable limit cycle exists even for large values of carrying capacities (e.g., for carrying capacities in regions H_7 and H_{11}). As we know that there is no interior attractor when resource growth is exponential, we can ask what happens to the locally stable limit cycle as the carrying capacities tend to infinity (in which case model with density-dependent resource growth converges to the model with exponentially growing resources). Numerical simulations suggest that as the carrying capacities increase, the amplitude of the interior limit cycle increases too and the limit cycle approaches the plane $R_1 = 0$, which means that the stronger competitor (which is resource 2 in our case) outcompetes the weaker competitor exactly as predicted by the model without resource density dependence.

To understand better dynamics of model (1), we consider a vertical cross-section of Fig. 2E at $K_1 = 16$. The structure of corresponding attractors along this cross-section is shown in Fig. 2G. Since resource 1 carrying capacity $K_1 = 16$ meets the threshold for the paradox of enrichment (i.e., $K_1 = 16$ is to the right of the vertical solid line in Fig. 2E), there is a stable limit cycle (denoted by small solid dots for $R_2 = 0$ in Fig. 2G) in resource 1-consumer density phase space. For $K_1 = 16$, resource 2 cannot invade along this two species limit cycle (the threshold for the invasibility of resource 2 along resource 1-consumer limit cycle is possible for $K_1 > 18.2$, see the vertical dash–double-dotted line in Fig. 2E) and the boundary limit cycle is an attractor (Table 1). This attractor exists for any value of K_2. The unstable resource 1-consumer equilibrium is shown as the medium thick dashed line at $R_2 = 0$ in Fig. 2G. Thus, for low values of $K_2 < 18.2$ resource 2 is necessarily outcompeted from the system. For higher values of K_2 ($18.2 < K_2 < 29.2$) there are two attractors, because a locally stable interior limit cycle (shown as the large solid dots in Fig. 2G) exists. Whether resource 2 is outcompeted or not depends now on the initial values of all species. For yet higher values of K_2 ($29.2 < K_2 < 32.2$) a third attractor appears. This is a locally stable interior equilibrium shown as the thick solid line in Fig. 2G. In this parameter range all species can coexist either at the interior equilibrium, or at the limit cycle, or resource 2 can be outcompeted. For $K_2 = 32.2$, the interior equilibrium disappears and a new resource 2-consumer equilibrium (the medium thick solid horizontal line in Fig. 2G) becomes the third attractor. In this case either resource can outcompete the other resource, or both resources can coexist along a limit cycle. For $K_2 = 37.5$, the interior stable limit cycle disappears and coexistence of both resources is impossible. We get a bistable case where one resource outcompetes the other resource. Which resource will survive depends on the initial population densities. For $K_2 > 48.7$, we still have the bistable situation but the coexistence of resource 2 with consumers is possible only along a limit cycle due to the paradox of enrichment (Table 2).

4.2. *Optimal preferences*

Now we consider the case where consumers behave as optimal foragers. First we show that invasibility conditions for species permanence are relaxed when compared with inflexible consumers for the same reason as in the case of exponentially growing resources. We consider two qualitatively different cases. First, let us assume that consumer mortality rates in both patches are the same ($m_1 = m_2$) and one resource is missing. The optimal foraging strategy then dictates that all consumers will be in the patch with the resource and the missing resource can always invade in the consumer free patch. This shows that the missing resource can invade regardless if the other resource–consumer system is at an equilibrium or fluctuates along a limit cycle (see also Holt, 1997a). Second, let us consider the case where consumer mortality rates are patch-dependent. Again we assume that one resource is missing from the system. In this case, however, it is not true that consumers will not move to the empty patch. Indeed, if the resource level in the other patch is low and/or the consumer mortality rate in that patch is high, the empty patch can serve as a refuge (or as a sink Holt, 1997b). This shows that the argument used in the case where consumer mortality rates are equal cannot be applied in the present situation and the invasibility conditions along a limit cycle with one missing resource cannot be verified analytically.

For species persistence we have to ensure that consumers can invade the resource 1–resource 2 equilibrium $(K_1, K_2, 0)$. Let us assume that this equilibrium lies in the part of the species density phase space where consumers feed on resource i only. Then consumers can invade at this equilibrium provided resource i is abundant enough to support consumers at positive density, i.e.,

$$K_i > \frac{m_i}{\lambda_i(e_i - m_i h_i)}. \tag{4}$$

First, we consider the case of zero handling times (Fig. 2B) which was studied in detail by Křivan and Schmitz (2003). There are two possibilities. Either both resource carrying capacities meet the threshold given by (4) in which case consumers will occupy both patches and the corresponding population equilibrium is globally asymptotically stable, or, only one carrying capacity meets the threshold condition given by (4) in which case all consumers will occupy a single patch only. Both of these cases correspond to the region S_1 in Fig. 2B. In region S_0, neither of the two resource carrying capacities meets condition (4) and consumers go extinct.

Second, let us consider positive handling times (Figs. 2D, F). Numerical simulations lead to population dynamics that are very similar to those with top-down regulation only (Fig. 1). At very low carrying capacities (region S_0 in Fig. 2, right panel) resources are not able to support consumers at positive densities. At higher values (region S_1) species coexist at a globally stable equilibrium that undergoes a series of period doubling bifurcations as the carrying capacities continue to grow (P-regions), eventually leading to a chaotic behavior (region Ch). The chaotic region is punctuated by regions where coexistence occurs along a limit cycle (Fig. 2F, H). Fig. 2H shows bifurcation of the Poincaré return map as a function of K_2. This diagram was constructed similarly as the bifurcation diagram in Fig. 1F.

5. Discussion

In this article, we studied population dynamics of the apparent competition community module (Holt, 1977, 1984, 1997a) with the Holling type II function responses. We considered two types of consumer foraging behavior (inflexible or optimal) and two types of resource growth (exponential or logistic).

When resources grow exponentially, handling times are zero, and consumer preferences for resources are fixed, apparent competition always leads to exclusion of the competitively weaker resource (Holt, 1977; Křivan, 1997). In contrast, when consumers are optimal foragers, both resources do coexist in the system and coexistence occurs along a limit cycle centered at a neutrally stable equilibrium (Fig. 1A; Křivan, 1997). In this article, we demonstrated that positive handling times do not qualitatively change predictions obtained for zero handling times and inflexible consumers. However, for optimally foraging consumers, positive handling times destroy the neutral stability of the population equilibrium and a globally stable limit cycle appears for small handling times. As handling times increase, this cycle undergoes a series of period doubling bifurcations which leads to chaos (Fig. 1).

Then we studied the effect of the logistic resource growth on apparent competition. First, we considered the case where consumers have fixed preferences for either resource. Similar models have been extensively studied in literature (e.g., Vance, 1978; Gilpin, 1979; Kretzschmar et al., 1993; Klebanoff and Hastings, 1994; Abrams et al., 1998; Abrams, 1999). These models, however, study different systems. Either, functional responses are linear, or the two resource species occur in a fine-grained environment where they can also compete for common resources. In this article, we focused on numerical analysis of the model that assumes a coarse-grained environment where resources cannot compete directly. We analyzed this model with respect to environmental productivities measured by the carrying capacities. It has been argued in literature (e.g., Holt and Lawton, 1993; Holt, 1997a; Křivan and Sikder, 1999; Křivan and Diehl, 2005) that resource enrichment (modeled as an increase in resource carrying capacity) typically makes resource coexistence less likely. These predictions are often based on conditions for species invasibility when rare, which are necessary conditions for species permanence (Butler and Waltman, 1986). Violation of the invasibility conditions does not necessarily mean that species cannot survive as survival depends on initial population densities. We showed that in the case of inflexible predators, species permanence is guaranteed for intermediate levels of resource carrying capacities (i.e., in regions A_1, A_2, A_5, B_1, B_2, B_5, D_1, D_2, D_4 and D_5 in Fig. 2). However, species can coexist even if invasibility conditions for species persistence do not hold, i.e., when one or both species cannot invade the community when initially rare. Armstrong and McGehee (1976) (see also Armstrong and McGehee, 1980; Abrams and Holt, 2002) showed that two competing species can survive on a single resource. In our case, the Armstrong and McGehee mechanism requires that the missing resource can invade the community which fluctuates along a limit cycle, but it cannot invade when the community is in unstable two-species equilibrium.Table 1 shows that this happens in regions A_6, B_6, D_3, E_4, F_5 of the resource carrying capacity parameter space. In all these cases all species will coexist for almost all initial conditions, although the system is impermanent because there are initial conditions for which one resource goes to extinction. Even if a boundary attractor exists (which happens in regions C_5, C_7, C_9, D_6, D_7, E_1, E_2, E_3, F_1–F_4, G_2–G_3, H_7, H_9, H_{11}), species can still coexist indefinitely at an interior attractor depending on the initial data. Thus, the set of enrichment levels at which all species can coexist is much larger than the set where the system is permanent.

The case where consumer preferences for resources are fixed corresponds to the classical apparent competition module that considers passive non-directional dispersal of consumers between two resource patches. Since the highly productive patches support more consumers than the less productive patches, passive non-directional dispersal leads to consumer "spill-over" from the highly productive patches to the less productive patches. This spill-over causes a negative effect of high productive patches on less productive patches which is the mechanisms leading to apparent competition. This effect is stronger if resources grow exponentially, while logistic resource growth weakens the spill-over effect and the apparent competition (Holt, 1977).

Holt (1977) predicted that strong consumer switching relaxes apparent competition. In fact, optimal foraging prevents the spill-over effect because consumers do not disperse from the patch where their fitness maximizes. In addition, our numerical simulations show that optimal foraging (i) increases range of parameters for which all species coexist, and (ii) leads to chaotic population dynamics (Figs. 1 and 2, right panel). This clearly shows that adaptive behavior can lead to chaotic population dynamics.

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Appendix A. The bifurcation analysis of model (1) for non-adaptive consumers

Here we describe various curves shown in Figs. 2C and E. These curves were obtained using XPPAUT continuation software (Ermentrout, 2002). The dashed-double dotted vertical line shown in Fig. 2E is the invasibility threshold for resource 2 along resource 1-consumer limit cycle. For resource 1 carrying capacities that meet this threshold (i.e., they are to the right of this threshold in Fig. 2), resource 2 can invade resource 1-consumer limit cycle. The solid thick curve in Figs. 2C, E is the Hopf bifurcation curve along which an interior limit cycle bifurcates from an interior equilibrium. An example of such a bifurcation is given in Fig. 2G at the point $K_2 = 29.3$, $R_2 = 10.0$ where the curve of interior equilibria (the thick curve) changes its stability and an unstable limit cycle emerges. The dash-dotted thick curve in Fig. 2E is the turning point of a branch of interior limit cycles (i.e., along this curve two interior limit cycles collide). An example of this bifurcation type is shown in Fig. 2G at $K_2 = 18.2$ where to the left of this carrying capacity no interior limit cycle exists while to the right two interior limit cycles (one stable and one unstable) exist. Similarly, the thin dash-dotted curve in Fig. 2E is the turning point of an interior equilibrium curve (i.e., along this curve two interior equilibria collide into a single equilibrium). An example is given in Fig. 2G where to the left of $K_2 = 28$ no interior equilibrium exists while to the right of this point two interior equilibria exist.

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