Global stability in consumer-resource cascades

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Abstract. Models of population growth in consumer-resource cascades (serially arranged containers with a dynamic consumer population, v, receiving a flow of resource, u, from the previous container) with a functional response of the form $h(u/v^b)$ are investigated. For $b \in [0, 1]$, it is shown that these models have a globally stable equilibrium. As a result, two conclusions can be drawn: (1) Consumer density dependence in the functional or in the per-capita numerical response can result in persistence of the consumer population in all containers. (2) In the absence of consumer density dependence, the consumer goes extinct in all containers except possibly the first. Several variations of this model are discussed including replacing discrete containers by a spatial continuum and introducing a dynamic resource.

Keywords: Global stability – Population dynamics – Bifurcation – Persistence

1 Introduction

In theoretical ecology, much controversy has surrounded the question: what is the correct form of the functional response (the instantaneous per-capita rate of resource consumption by the consumer population) in population models? In consumer-resource systems

$$\frac{du}{dt} = f(u)u - vg(u, v)$$

$$\frac{dv}{dt} = \theta vg(u, v) - \mu v \tag{1}$$

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where u is the resource density, v the consumer density, $f(u)$ the basal "per-capita" growth rate of the resource, θ the consumer's assimilation efficiency, and μ the consumer's respiration rate, the functional response, $g(u, v)$, plays an essential role. The simplest possible functional response, introduced by Lotka (1925) and Volterra (1926) and based on the law of mass action, is linear, $g(u, v) = au$. However, since unsaturated per-capita consumption rates (i.e., $\sup g(u, v) = \infty$) are a physiological impossibility, alternative resource-dependent, $g(u, v) = h(u)$, functional responses were introduced to increase realism (e.g., Ivlev 1961; Holling 1966), but even these suffered from unrealistic predictions such as the paradoxes of enrichment (Rosenzweig 1971) and biological control (Luck 1990).

As indicated in Equation 1, the functional response may also depend on the consumer density. Mutual interference may result in a decrease of searching efficiency as consumer density increases (Royama 1971; Hassell 1978). Alternatively, finite resources (even ones that regenerate instantaneously) discretely partitioned in space may have bounded extraction rates determined by resource density (i.e., there exists a $K > 0$ such that $Pg(N, P) \leqq KN$ for all $P > 0$). Watt (1968) developed a one-parameter family of functional responses to incorporate all of these effects. It is of the form $g(u, v) = h(u/v^b)$ with $h(x) = 1 - \exp(-x)$ and $b \in [0, 1]$. Although presented as an integrated functional response, Royama (1971) reinterpreted it as a instantaneous functional response that generalizes the toss-a-ring model: the area of the ring tossed by the consumer diminishes by a factor of $1/v^b$ due to mutual interference.

The special cases of $b = 1$ has received particular attention and has become known as a ratio-dependent functional response in the literature. This functional response was used in biologically detailed models for simulating agricultural ecosystems by Gutierrez et al. (1977, 1993). Its dynamics in food chains was investigated by Getz (1984) and Arditi and Ginzburg (1989) in the bitrophic setting, and by Gutierrez et al. (1994) in the tritrophic setting. The parameters of particular interest for $h(u/v)$ are $h_\infty = \lim_{x \to \infty} h(x)$, the maximal ingestion rate of the consumer, and $h'(0)$, the maximal resource extraction rate (i.e., $h(u/v) v \leqq h'(0) u$ and $\lim_{v \to \infty} h(u/v) v = h'(0) u$). Notice that if the intrinsic rate of increase for the resource exceeds the maximal extraction rate then both species of Equation 1 persist.

2 Main results

To compare the resource-dependent and ratio-dependent functional response models, Arditi et al. (1991) designed a set of experiments: Filter feeding cladocerans (the consumer) were reared in a flow-through system where water containing food particles (the resource) was pumped into serially arranged containers from which the consumer cannot escape. Starting with an inoculum in each container, the consumer populations were monitored until equilibrium was reached. To model these experiments, the following equations

were suggested by Arditi et al. (1991),

$$\frac{du_i}{dt} = \gamma(u_{i-1} - u_i) - v_i h(u_i/v_i^b) \tag{2}$$

$$\frac{dv_i}{dt} = \theta v_i h(u_i/v_i^b) - \mu v_i$$

$$i = 1, \ldots, n \tag{3}$$

where u_i is the concentration of resource in the i-th container, u_0 is the concentration of resource flowing into the first container, v_i is the biomass of consumer in the i-th container, γ is the flow rate, θ is the assimilation efficiency of the consumer, and μ is the respiration rate of the consumer. To keep the model biologically realistic and mathematically tractable, we place the following restrictions on h

H1: $h: \boldsymbol{R} \rightarrow \boldsymbol{R}$ is C^1, $h(0) = 0$ and $h'(x) > 0$ for all $x \geqq 0$.
H2: The limit, $h_\infty = \lim_{x \rightarrow \infty} h(x)$, exists and is finite.
H3: $\lim_{x \rightarrow \infty} xh'(x) = 0$.

H1 asserts that per-capita consumption increases with resource density. H2 asserts that per-capita ingestion rates are bounded and H3 is chosen to ensure that there is a well defined flow given by Equation 2 when $b > 0$. Functions that satisfy H1–H3 include $ax^n/(c + x^n)$ with $n \geqq 1$, $a > 0$ and $c > 0$ (Holling 1966; Getz 1984; Arditi and Ginzburg 1989) and $h(x) = 1 - \exp(-ax)$ with $a > 0$ (Ivlev 1961; Watt 1968; Gutierrez et al. 1994).

Even in environments where abiotic factors are static, respiration rates and assimilation efficiencies are seldom constant. Overcrowding may result in behavioral changes that increase respiration rates or may result in the production of toxins that decrease assimilation efficiency. To capture these effects, we extend the model in Equation 2 by permitting θ and μ to be C^1 functions of v with following restrictions:

P1: $0 < \theta(v) \leqq 1$ and $\mu(v) > 0$ for all $v \geqq 0$.
P2: $\theta'(v) \leqq 0$ and $\mu'(v) \geqq 0$ for all $v \geqq 0$.
P3: $\theta(0) h_\infty - \mu(0) > 0$.

The biological interpretation of P1–P2 is clear. P3 asserts that the intrinsic rate of increase of the consumer is positive. When P3 is not satisfied, the consumer goes extinct.

Theorem 1 *Assume h is a function that satisfies H1–H3 and that θ and μ are functions that satisfy P1–P3. Let $b \in [0, 1]$, $\gamma > 0$ and $u_0 > 0$ be given. Then there exists an equilibrium, $S^* \in \boldsymbol{R}_+^{2n}$, of*

$$\frac{du_i}{dt} = \gamma(u_{i-1} - u_i) - v_i h(u_i/v_i^b) \tag{4}$$

$$\frac{dv_i}{dt} = \theta(v_i) \, v_i h(u_i/v_i^b) - \mu(v_i) v_i$$

$$i = 1, \ldots, n$$

that is globally stable (i.e., any solution $S(t)$ to Equation 4 with $S(0) > 0$ satisfies $S(t) \to S^*$ as $t \to \infty$).

Remark 1. Given a vector $v = (v_1, \ldots, v_n) \in R^n$, we write $v > 0$ if $v_i > 0$ for all i and $R_+^n = \{v \in R^n : v \geqq 0\}$.

A proof of Theorem 1 is found in Appendices A for $b > 0$ and B for $b = 0$ and is based upon two observations: (1) any container receiving a constant flow of resource has a globally stable equilibrium and (2) the only coupling between adjacent containers, say i and $i + 1$, is the flow of resource from the i-th container to the $i + 1$-th container. If we consider an initial consumer population distribution in a cascade of containers, then (1) implies that the first container in the cascade approaches a unique steady state. Furthermore, (1) and (2) imply that the second container eventually receives a constant flow of resource and is asymptotic to a system with a globally stable equilibrium. Thus, global stability moves down the cascade and the cascade dynamics are determined by the equilibria of Equation 4.

Let us consider the case described by Arditi et al. (1991) where θ and μ are held constant, say $\theta \equiv \theta_0$ and $\mu \equiv \mu_0$. In this case, the non-trivial equilibrium is given recursively by solutions to

$$\gamma u_{i-1} = \gamma v_i^b A + v_i \mu_0 / \theta_0 \tag{5}$$
$$u_i = A v_i^b,$$

where $A = h^{-1}(\mu_0/\theta_0)$. When $b > 0$, Equation 5 always admits a positive solution, $S^* = (u^*, v^*) > 0$ (see Appendix A). When $b = 0$, $S^* = (u^*, v^*)$ takes one of two forms:

$$(u^*, v^*) = \begin{cases} ((A, A, \ldots, A), (v_1^* > 0, 0, \ldots, 0)) & \text{if } u_0 \geqq A \\ ((u_0, \ldots, u_0), (0, \ldots, 0)) & \text{else} \end{cases}$$

(see Appendix B). In other words, when $b = 0$, the consumer populations goes extinct in all containers expect possibly the first. Alternatively, when $b > 0$, all containers sustain a positive consumer population. This surprising fact was first noticed by Arditi et al. (1991) in the special cases of $b = 0$ and $b = 1$. $b = 1$ is of particular interest as it produces an equilibrium of the form $(u_i^*, v_i^*) = c^{i-1}(u_1^*, v_1^*)$ for some $c \in (0, 1)$ and accurately describes several of the experimental results of Arditi et al. (1991).

Remark 2. To see how the equilibria vary as a function of the parameter b, we refer the reader to the PDE analog of Equation 4 discussed in the Concluding remarks.

As all containers asymptotically receive a constant concentration of resource, this bifurcation to persistence is best understood by examining the isocline structure of the first container. For all values of b, the resource isocline is given by a decreasing function of v_1 with a v_1-intercept at $u_1 = u_0$ and

a vertical asymptote at $u_1 < u_0$. When $b = 0$, the consumer's isocline is vertical and is given by $u_1 = A$. Therefore, if the incoming resource concentration remains at or below this threshold, (i.e., $u_0 \leqq A$), the consumer population is doomed, else it exploits the resource to this threshold. Either way, the incoming concentration into the second container approaches a value that is less than or equal to A. Consequently, all containers except the first receive insufficient resource to sustain a consumer population. This over exploitation occurs because the consumer is only resource-limited and has no negative self-feedbacks. When $b > 0$, a negative self-feedback is introduced in the consumer's functional response and the consumer's isocline, $u_i = v_i^b A$, bifurcates to a monotonically increasing curve that passes through the origin. Therefore, at any incoming resource concentration there are consumer densities with positive pre-capita growth rates and the consumer population is able to persist in all containers

An alternative mechanism that produces persistence in all containers is a negative self-feedback in the numerical response of the consumer (Ruxton and Gurney 1992). For example, assume respiration rates increase with consumer density (i.e., $\mu'(v) > 0$ for all $v > 0$) or assimilation efficiencies decrease with density (i.e., $\theta'(v) < 0$ for all $v < 0$) and $b = 0$. When the incoming resource concentration in the i-th container is constant, the resource isocline is as before, and the consumer isocline is monotonically increasing with a u_i-axis intercept to the right of the origin. This intercept determines a minimal threshold of resource concentration for the consumer but is balanced by the consumer's inability to exploit the resource to this threshold. Therefore, as long as the resource concentration that flows into the first container remains above this threshold, the consumers persist in all containers (see Appendix B).

3 Concluding remarks

Theorem 1 suggests two types of mechanisms that lead to the global stability of a strictly positive equilibrium for a consumer-resource cascade model. They involve negative self-feedbacks introduced into either the functional or numerical response. In the first case, resource acquisition is limited by the effects of mutual interference and interspecific competition. In the second case, resource allocation is limited by the effects of overcrowding on assimilation, conversion and respiration. In the absence of these feedbacks, the consumer population is driven to extinction in all containers except the first. Although specific formulations of these two effects were made in Theorem 1, other formulations of consumer dependence in the functional or numerical response are likely to produce similar results.

We conclude with two variations of the model presented in this manuscript.

In addition to describing Arditi et al. (1991)'s experiments, Equation 4 may be used to describe consumer populations in ponds and lakes along a river's

path. However, a simpler and more common scenario are rivers and streams, themselves, with a sessile consumer (e.g., diatoms, substrate feeders) and a freely flowing resource. In this case, discrete "containers" are replaced by a spatial continuum. If we let $u(t, x)$ and $v(t, x)$ represent the resource and consumer distributed over one dimensional space, $\boldsymbol{R}_+$, then the dynamics of this system can be represented as

$$
\begin{aligned}
u_t &= -\gamma u_x - vh(u/v^b) \\
v_t &= \theta vh(u/v^b) - \mu v
\end{aligned}
\tag{6}
$$

with initial conditions $u(t, 0) = u_0$ for all $t \geq 0$ and $v(0, x) = f(x)$ for some continuous function, $f: \boldsymbol{R}_+ \to \boldsymbol{R}_+$. Equation 6 is the PDE analog of Equation 4. When θ and μ are constants, the non-trivial steady states for the consumer of Equation 6 are given by:

$$
v(x) = \begin{cases}
0 & b = 0 \\
((1 - b)Ax + f(0)^{b-1})^{1/(b-1)} & b \in (0, 1) \\
f(0)e^{-Ax} & b = 1
\end{cases}
$$

where $A = \dfrac{\mu}{\gamma b \theta h^{-1}(\mu/\theta)}$. When $b = 0$ or $b = 1$, these steady states naturally correspond to the equilibria of Equation 2 and prompt the question: Are they globally stable?

Until now, the resource in the cascade models has not been dynamic. Including the effects of growth, reproduction and respiration of the resource will produce more interesting dynamics. For example, consider

$$
\begin{aligned}
u_t &= -\gamma u_x + au - bu^2 - vh(u/v^b) \\
v_t &= \theta vh(u/v^b) - \mu v
\end{aligned}
$$

where $au - bu^2$ is the logistic population dynamics of the resource. It is well known that for $\gamma = 0$ we can get limit cycles. But, do these limit cycles propagate down the cascade for $\gamma > 0$? If they do propagate, will they spatially dampen out and be in phase? Or will they produce spatial-temporal chaos?

Appendix A: Proof of Theorem 1 ($b > 0$)

The strategy behind the proof of Theorem 1 is to prove global stability of $(\dot{u}_1, \dot{u}_2)$ of Equation 4, induct on $(\dot{u}_i, \dot{v}_i)$ by viewing these equations as an asymptotically autonomous differential equation and apply results of Benaïm and Hirsch (1995).

First assume $b > 0$. In this case we need three lemmas to accomplish our task. The first lemma shows that Equation 4 extends in a continuously differentiable manner to certain coordinate planes.

Lemma 1 *Let $h: \mathbf{R}_+ \to \mathbf{R}_+$ be a function that satisfies H1–H3. If $b \in [0, 1]$, then Equation 4 extends in a C^1 fashion to*

$$\{(\boldsymbol{u}, \boldsymbol{v}) \in \boldsymbol{R}^{2n}: \boldsymbol{u} > 0, \boldsymbol{v} \geqq 0\}.$$

Proof. Left to the reader.

Remark 3. One can show Equation 4 extends continuously to $\boldsymbol{R}_+^{2n}$ (but not in a Lipschitz manner) and has unique solutions.

Lemma 2 *Let $b \in (0, 1]$, $\gamma > 0$ and $C > 0$ be given. Assume the function h satisfies H1–H3 and the functions, θ and μ satisfy P1–P3. Then there exists $S^* \in \boldsymbol{R}^2$ with $S^* > 0$ such that if $S(t)$ is a solution to*

$$\frac{du}{dt} = \gamma(C - u) - vh(u/v^b)$$

$$\frac{dv}{dt} = \theta(v)vh(u/v^b) - \mu(v)v \tag{7}$$

with $S(0) > 0$, then

$$\lim_{t \to \infty} S(t) = S^*.$$

Proof. The only equilibria of Equation 7 are $(C, 0)$ and the solutions to

$$u = v^b h^{-1}\left(\frac{\mu(v)}{\theta(v)}\right) \tag{8}$$

$$\gamma C = v^b \gamma h^{-1}\left(\frac{\mu(v)}{\theta(v)}\right) + v\frac{\mu(v)}{\theta(v)}. \tag{9}$$

Let $f(v)$ be the right hand side of Equation 9. Since $(h^{-1})'(v) > 0$ (by H2 and the inverse function theorem), P2 implies that f is strictly monotone and increasing. Furthermore, $f: \boldsymbol{R}_+ \to \boldsymbol{R}_+$ is surjective since $f(0) = 0$ and $f(v) \to \infty$ as $v \to \infty$. Therefore Equations 8 and 9 have a unique positive solution, (u^*, v^*). The variational matrix of Equation 7 is

$$\begin{pmatrix} -\gamma - v^{1-b}h'(u/v^b) & -h(u/v^b) + buv^{-b}h'(u/v^b) \\ \theta v^{1-b}h'(u/v^b) & h(u/v^b)(\theta + v\theta') - \theta uv^{-b}bh'(u/v^b) - v\mu' - \mu \end{pmatrix}$$

and evaluated at (u^*, v^*) has positive determinant and negative trace. Thus (u^*, v^*) is an asymptotically stable equilibrium. By H3, the variational matrix evaluated at $(C, 0)$ is

$$\begin{pmatrix} -\gamma & -h_\infty \\ 0 & \theta(0)h_\infty - \mu(0) \end{pmatrix}$$

and has eigenvalues with positive (by P3) and negative real parts. By Lemma 1, $(C, 0)$ is an unstable equilibrium with its stable manifold lying in the u-axis.

Let

$$f(u, v) = \frac{1}{vh(u/v^b)}$$

Since $f(u, v)$ is positive for positive u and v, the integral curves of

$$\frac{du}{dt} = f(u, v)(\gamma(C - u) - vh(u/v^b))$$

$$\frac{dv}{dt} = f(u, v)(\theta(v)vh(u/v^b) - \mu(v)v)$$

(10)

in the positive orthant are equivalent to those of Equation 7. The divergence of Equation 10,

$$\frac{-\gamma h(u/v^b)v - \gamma(C - u)h'(u/v^b)v^{1-b}}{(h(u/v^b)v)^2} + \theta' - \frac{\mu'h(u/v^b) + h'(u/v^b)uv^{-1-b}b}{h(u/v^b)^2}$$

is strictly negative for all $u < C$. Therefore Equation 7 has no periodic solutions in $(0, C) \times (0, \infty)$. As $(0, C) \times (0, \infty)$ is forward invariant and contains all equilibria of Equation 7, the Poincaré–Hopf index theorem implies that Equation 7 has no periodic solutions in $\mathbf{R}_+^2$.

Let $S(t)$ be a solution to Equation 7 such that $S(0) > 0$. Since $\dot{u} < 0$ for $(u, v) \in (C, \infty) \times \mathbf{R}_+$ and $\dot{v} < 0$ whenever $0 < v^b h^{-1}(\mu(0)/\theta(0)) < u$, $S(t)$ is bounded in forward time. As $S(t)$ is bounded, not periodic, and the equilibrium $(C, 0)$ is unstable, Poincaré–Bendixson theory implies $S(t)$ approaches (u^*, v^*) as $t \to \infty$. □

Lemma 3 *Assume h, θ, γ and μ are as in Lemma 2 and $C(t)$ is a continuous function such that*

$$\lim_{t - \infty} C(t) = C_\infty < \infty .$$

If $S(t) = (u(t), v(t))$ is a solution to

$$\frac{du}{dt} = \gamma(C(t) - u) - vh(u/v^b)$$

$$\frac{dv}{dt} = \theta(v)vh(u/v^b) - \mu(v)v$$

(11)

with $S(0) > 0$, then

$$\lim_{t \to \infty} S(t) = S^*$$

where S^* is given by Lemma 2 with $C = C_\infty$.

Proof. Since $C(t) \to C_\infty$ as $t \to \infty$, Equation 11 is uniformly asymptotic (with respect to u and v) to Equation 7 with $C = C_\infty$. Let $S(t)$ be a solution to Equation 11 with $S(0) > 0$. Define the limit set of $S(t)$ as

$$S_+ = \bigcap_{m > 0} \overline{\bigcup_{t > m} S(t)} .$$

(12)

As $S(t)$ is bounded, S_+ is a compact set. A theorem of Benaïm and Hirsch (1995) implies S_+ is an internally chain recurrent set of the flow to Equation 7 with $C = C_\infty$. The only internally chain recurrent sets of Equation 7 are the two equilibria one of which is a saddle with its stable manifold on the u-axis. Therefore $S_+ = S^*$ where S^* is given by Lemma 2.   □

To complete the proof of Theorem 1 for $b > 0$, we proceed inductively. Let $S(t) = (\mathbf{u}(t), \mathbf{v}(t))$ be a solution to Equation 4 with $S(0) > 0$. Lemma 2 applies to $(u_1(t), v_1(t))$ and therefore

$$\lim_{t \to \infty} (u_1(t), v_1(t)) = (u_1^*, v_1^*)$$

where (u_1^*, v_1^*) is determined by Lemma 2 with $C = u_0$. Applying Lemma 3 to $(u_2(t), v_2(t))$ with $C(t) = u_1(t)$, we get

$$\lim_{t \to \infty} (u_2(t), v_2(t)) = (u_2^*, v_2^*) .$$

Applying Lemma 3 $n - 2$ more times completes the proof.   □

Appendix B: Proof of Theorem 1 ($b = 0$)

We use the same strategy as for $b > 0$ and begin by demonstrating solutions are bounded.

Lemma 4 *Let h, θ, γ and μ be as in Lemma 2 and $C(t)$ be a continuous bounded function. If $S(t) = (u(t), v(t))$ is a solution to*

$$\frac{du}{dt} = \gamma(C(t) - u) - vh(u)$$

$$\frac{dv}{dt} = \theta(v)vh(u) - \mu(v)v$$

(13)

with $S(0) \geqq 0$, then $\sup_{t > 0} | S(t) |$ is finite.

Proof. Let $S(t)$ be a solution to Equation 13 with $S(0) \geqq 0$. Pick $D > \sup_{t > 0} C(t)$. Let $\tilde{S}(t) = (\tilde{u}(t), \tilde{v}(t))$ be a solution to

$$\dot{u} = \gamma(D - u) - vg(u)$$

$$\dot{v} = \theta(0)vg(u) - \mu(0)v$$

(14)

with $S(0) = \tilde{S}(0)$. By choice of D and P2, it sufficient to show that $\tilde{S}(t)$ is bounded for all positive t.

Let $A = h^{-1}(\mu(0)/\theta(0))$. In Equation 14, $\dot{u} < -D$ for all $u \geqq 2D$. Consequently there exists a positive $\tilde{t}$ such that $\tilde{u}(t) \leqq 2D$ for all $t \geqq \tilde{t}$. In Equation 14, $\dot{v}$ is negative for all $u \leqq A$ and otherwise positive. Therefore, if $2D \leqq A$, then $\tilde{v}(t) \leqq \tilde{v}(\tilde{t})$ for all $t \geqq \tilde{t}$ and we are done. On the other hand, suppose $2D > A$. Let $S^*(t) = (u^*(t), v^*(t))$ be a solution to Equation 14 with $u^*(0) = 2D$ and $v^*(0) > \tilde{v}(\tilde{t})$. By choosing $v^*(0)$ sufficiently large, there exists a $t^* > 0$ such

that $u^*(t^*) = A$. The Poincaré-Bendixson theorem implies that $\tilde{S}(t)$ remains in the bounded region defined by the v-axis, u-axis, the line $u = 2D$, the arc defined by $\{S^*(t):0 \leqq t \leqq t^*\}$ and the line segment defined by $\{(u, v^*(t^*)):0 \leqq u \leqq A\}$.   □

Lemma 5 *Let h, θ, γ, C and μ be as in Lemma 2. If $S(t)$ is a solution to*

$$\frac{du}{dt} = \gamma(C - u) - vh(u)$$

$$\frac{dv}{dt} = \theta(v)\, vh(u) - \mu(v)v$$

(15)

with $S(0) > 0$, then

$$\lim_{t \to \infty} S(t) = (u^*, v^*)$$

where

$$(u^*, v^*) = \begin{cases} >0 & \text{if } C > A \\ (C, 0) & \text{else} \end{cases}.$$

and $A = h^{-1}(\mu(0)/\theta(0)))$.

Proof. The equilibria of Equation 15 are $(C, 0)$ and the solutions of

$$v\mu(v)/\theta(v) + \gamma h^{-1}(\mu(v)/\theta(v)) = \gamma C$$

(16)

$$u = h^{-1}(\mu(v)/\theta(v)) .$$

(17)

The left hand side of Equation 16 is strictly monotone increasing as a function of v and maps $[0, \infty)$ onto $[\gamma A, \infty)$. Thus, if $C > A$, there is a unique positive solution, $S^* = (u^*, v^*)$, to Equations 16 and 17.

The variational matrix for Equation 15 is

$$\begin{pmatrix} -\gamma - vh'(u) & -h(u) \\ \theta vh'(u) & h(u)(\theta + \theta'v) - \mu - \mu'v \end{pmatrix}.$$

Evaluated at $(C, 0)$ the variational matrix becomes

$$\begin{pmatrix} -\gamma & -h(C) \\ 0 & \theta(0)h(C) - \mu(0) \end{pmatrix}.$$

As $C > A$ and h is increasing (by H1), we have $\theta(0)\, h(C) - \mu(0) > 0$. Therefore $(C, 0)$ is a saddle with its stable manifold lying in the u-axis. When $C > A$, the variational matrix evaluated at (u^*, v^*) is

$$\begin{pmatrix} -\gamma - v^*h'(u^*) & -h(u^*) \\ \theta(v^*)v^*h'(u^*) & h(u^*)\theta'(v^*) - \mu'(v^*)v^* \end{pmatrix}.$$

which has positive determinant and negative trace. Therefore (u^*, v^*) is an asymptotically stable equilibrium.

Assume $C > A$. Let

$$f(u, v) = \frac{1}{vh(u)}$$

Since $f(u, v)$ is positive for positive u and v,

$$\frac{du}{dt} = f(u, v)(\gamma(C - u) - vh(u))$$

$$\frac{dv}{dt} = f(u, v)(\theta(v)vh(u) - \mu(v)v) \tag{18}$$

has the same integral curves in the positive orthant as Equation 15. The divergence of Equation 18,

$$\frac{-\gamma h(u) - \gamma(C - u)h'(u)}{vh(u)^2} + \theta'(v) - \frac{\mu'(v)}{h(u)} \tag{19}$$

is strictly negative for all $0 < u < C$. Therefore Equation 15 has no periodic solutions contained in $[0, C] \times [0, \infty)$. As all the equilibria of Equation 15 lie in the forward invariant region $[0, C] \times [0, \infty)$, the Poincaré-Hopf index theorem implies there are no periodic solutions to Equation 15. Lemma 4 and the Poincaré-Bendixson theorem imply that $S(t)$ approaches S^* as $t \to \infty$.

If $C \leqq A$, then the only equilibrium of Equation 15 is $(C, 0)$. As $\mathbf{R}_+^2$ is invariant, the Poincaré-Hopf index theorem implies that Equation 15 has no periodic solutions. The Poincaré-Bendixson theorem and Lemma 4 implies that all solutions approach $(C, 0)$. □

Lemma 6 *Assume* h, θ, γ *and* μ *are is in Lemma 2. let* $C(t)$ *be a continuous function such that*

$$\lim_{t \to \infty} C(t) = C_\infty < \infty.$$

If $S(t)$ *is a solution to*

$$\frac{du}{dt} = \gamma(C(t) - u) - vh(u)$$

$$\frac{dv}{dt} = \theta(v)\, vh(u) - \mu(v)\, v \tag{20}$$

with $S(0) > 0$, *then*

$$\lim_{t \to \infty} S(t) = S^*$$

where S^* *is given by Lemma 5 with* $C = C_\infty$.

Proof. When $C_\infty > A = h^{-1}(\mu(0)/\theta(0))$, the proof is analogous to Lemma 3. Assume $C_\infty \leqq A$. Equation 20 is uniformly asymptotic to Equation 15 with $C = C_\infty$. By Benaïm and Hirsch (1995), we need to show the only internally chain recurrent set in the positive orthant of Equation 15 (with $C = C_\infty$) is the fixed point $(C_\infty, 0)$. If $C_\infty < A$ then $(C_\infty, 0)$ is a stable equilibrium (see proof of Lemma 5) and it is the only internally chain recurrent set. If $C_\infty = A$, then by the Poincaré-Bendixson theory the only other candidates for an internally chain recurrent set are the homoclinic loops in an elliptic sector of $(C_\infty, 0)$. However, by Equation 19 there is a neighborhood of this point that admits no homoclinic loops and hence no elliptic sectors. □

To complete the proof of the theorem, proceed inductively as in the conclusion of Appendix A.

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