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A discrete hierarchical model of intra-specific competition

S.R.-J. Jang [a,*] and J.M. Cushing [b]

[a] *Department of Mathematics and Statistics, Texas Tech University, Lubbock, TX 79409, USA*
[b] *Department of Mathematics, Interdisciplinary Program on Applied Mathematics, University of Arizona, Tucson, AZ 85721, USA*

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Abstract

A discrete hierarchical model with either age, size, or stage structure is derived. The resulting scalar equation for total population level is then used to study contest and scramble intra-specific competition. It is shown how equilibrium levels and resilience are related for the two different competition situations. In particular, scramble competition yields a higher population level while contest competition is more resilient if the uptake rate as a function of resource density is concave down. The conclusions are reversed if the uptake rate is concave up.

Keywords: Hierarchical population model; Contest and scramble competition; Equilibrium resilience; Discrete Dulac criterion; Uniform persistence

1. Introduction

Many ecological models assume homogeneity of individuals and study the dynamics of population density in response to ecological and environmental forces. However, the interactions of an individual organism with others or with the physical environment are likely to depend on its physiological features such as age, size, stage, etc. These differences among individuals consequently have a significant impact on the dynamics of populations.

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[*] Corresponding author. Present address: Department of Mathematics, University of Louisiana at Lafayette, Lafayette, LA 70504, USA.

E-mail address: jang@louisiana.edu (S.R.-J. Jang).

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One way to bridge this gap between individual organism and total population level is by using structured population models. If the vital rates of a structured population model are constant over time, it results in a linear model. Examples of linear structured models such as the Leslie matrix model and Usher matrix model give exponential growth or decay of the total population size [7]. The modification of this simple assumption led to the development of nonlinear structured models in which vital rates are density dependent.

Density dependent effects in many nonlinear structured models are incorporated in such a way that vital rates are functions of weighted total population size [1–5,13]. In many circumstances, however, vital rates depend on an individual's class rather than weighted total population size. We are interested in the class of structured models in which the vital rates of an individual depend on its position in a hierarchical ranking of the individuals in the population. This assumption is motivated by the frequent observation of a ranking among individuals in the population, based on either chronological age, size, or stage that affects an individual's vital rates through access to resources, mates, nesting sites, etc.

A continuous hierarchical age-structured model derived from the McKendrick equation was studied by Cushing [6], where the existence and uniqueness of a solution for the model was proved. Moreover, the global asymptotic dynamics of the total population size and the age distribution function were fully analyzed when the vital rates were assumed to be independent of time explicitly. Based on these results, an application to intra-specific competition and predation were also given in [6].

Intra-specific competition is one way that a population regulates its growth. For a population in which there is a hierarchical ranking among individuals there are two common forms of intra-specific competition: contest and scramble. Contest competition occurs when no individual in a class of lower rank can affect the amount of resource available to an individual of higher rank. Scramble competition, on the other hand, occurs when every individual can affect the amount of resource available to any other individual in the population [14].

By using simple discrete models, Lomnicki [14] asserts that contest competition in general is more advantageous to the population than scramble competition. The question of how equilibrium levels and resilience are related to the two forms of competition is discussed in the earlier study of Cushing [6] mentioned above. A continuous hierarchical model with intra-specific competition based on size-structure is also derived and analyzed by Cushing [7]. The results obtained in these studies support Lomnicki's conclusion that contest competition has a higher population equilibrium level and is also more resilient. In these models, the comparison between contest and scramble is by means of a homotopy of models connected one to the other.

In contrast to the modeling methodology used in [6,7], Henson and Cushing [11] derive a comparison criterion based upon the total amount of limiting resource available to the population. It was shown in [11] that the concavity of the uptake rate decides the outcome of the comparison. In particular, contest competition has a higher equilibrium level if the uptake rate is concave up and scramble competition yields a higher population equilibrium level if the uptake rate is concave down. The conclusion is reversed when equilibrium resilience is the basis of comparison.

There are many situations where population growth is a discrete process and the appropriate models are difference equations. In this work we adopt the modeling methodology used by Henson and Cushing [11] to study intra-specific competition of hierarchical-structured populations. While conclusions of [11] are valid only for age-structured models, our results obtained here make a significant generalization to arbitrary structured models. This includes, for example, consideration of age, size, life cycle, etc. It is shown in these discrete models that concavity of the uptake rate as a function of available resource is also the deciding factor between comparison. In Section 2, a basic hierarchical model will be described. Section 3 studies the asymptotic dynamics of the total population size and two forms of competition when resource level is assumed to be constant. A parallel discussion with a dynamically varying resource is given in Section 4. Section 5 provides a brief discussion.

2. Model derivation

The model derivation in this section follows that in [8]. Suppose that individuals in a population are categorized into a finite number m of classes. The classification can be based on any desired feature of the species (e.g., age, size, stage, etc.) so that the model includes virtually any type of structuring. Let $x_j(t)$ be the density of individuals in class j, $1 \leqslant j \leqslant m$, at time t for $t = 0, 1, 2, \ldots,$ and let $x(t) = \operatorname{col}(x_i(t))_{i=1}^m$ be the column of these densities, i.e., the class distribution vector at time t.

The transition among classes caused by death and growth is given by the transition matrix $\mathbf{T} = (\tau_{ij}\sigma_j)$, where σ_j is the probability that an individual in class j survives one unit of time and τ_{ij} is the fraction of those surviving individuals that move to class i so that $\sum_{i=1}^m \tau_{ij} = 1$ for $1 \leqslant j \leqslant m$.

In addition to intra-specific transition, a population can change through reproduction. Let $\mathbf{F} = (\phi_{ij}\beta_j)$ be the fertility matrix, where β_j is the average number of surviving offspring born to an individual in class j and ϕ_{ij} is the fraction of the offspring that lies in class i. Hence $\sum_{i=1}^m \phi_{ij} = 1$ for $1 \leqslant j \leqslant m$. Note that our assumption of $\mathbf{F}$ implies that newborns can lie in any classes. Let $\mathbf{P}$ denote the projection matrix, i.e., $\mathbf{P} = \mathbf{T} + \mathbf{F}$. Then the dynamics of class distribution vector are governed by the matrix equation

$$x(t+1) = \mathbf{P}x(t). \tag{2.1}$$

Let $p(t)$ be the total population size at time t. Since there is a hierarchy based on structuring variable, we let y_i be the density of individuals of rank less than i, i.e.,

$$y_i = \begin{cases} 0 & \text{if } i = 1, \\ \sum_{j=1}^{i-1} x_j & \text{if } 2 \leqslant i \leqslant m+1. \end{cases} \tag{2.2}$$

In particular, $y_{m+1} = p$. The submodels for the survival probabilities σ_j and the fertility rates β_j then depend on y_j in the following way.

Let $\beta \in C^0(R_+^2, R_+)$ and $\sigma \in C^0(R_+^2, [0,1])$ be functions such that the per capita birth rate of an individual is $\beta(z, p)$ and the probability an individual will survive one unit of time is $\sigma(z, p)$ when the total population size is p and the density of individuals of lower rank is z. We define β_j and σ_j to be the average per capita birth rate and survival probability for the jth class, respectively, i.e.,

$$\beta_j = \begin{cases} \frac{1}{x_j}\int_{y_j}^{y_j+x_j} \beta(z,p)\,dz & \text{if } x_j \neq 0, \\ \beta(y_j,p) & \text{if } x_j = 0, \end{cases} \tag{2.3}$$

and

$$\sigma_j = \begin{cases} \frac{1}{x_j}\int_{y_j}^{y_j+x_j} \sigma(z,p)\,dz & \text{if } x_j \neq 0, \\ \sigma(y_j,p) & \text{if } x_j = 0. \end{cases} \tag{2.4}$$

For example, if rank is determined by age, then the survival probability of individuals in the jth class ranges from $\sigma(y_j,p)$ for the youngest to $\sigma(y_{j+1},p)$ for the oldest in the class.

Under the above assumptions, if only birth and death processes are allowed, i.e., there is no migration, we have

$$x_i(t+1) = \sum_{j=1}^{m} \tau_{ij}\sigma_j x_j(t) + \sum_{j=1}^{m} \phi_{ij}\beta_j x_j(t) \tag{2.5}$$

for $1 \leqslant i \leqslant m$ and we can derive an equation for $y_i(t+1)$, where $y_1(t+1) = 0$ and

$$\begin{aligned} y_i(t+1) &= \sum_{k=1}^{i-1} x_k(t+1) \\ &= \sum_{j=1}^{m}\left(\sum_{k=1}^{i-1}\tau_{kj}\right)\int_{y_j}^{y_{j+1}} \sigma(z,p)\,dz + \sum_{j=1}^{m}\left(\sum_{k=1}^{i-1}\phi_{kj}\right)\int_{y_j}^{y_{j+1}} \beta(z,p)\,dz \end{aligned}$$

for $2 \leqslant i \leqslant m+1$. Thus if we let $y = (y_1, y_2, \ldots, y_m)^*$ and

$$f(y,p) = \begin{pmatrix} 0 \\ f_2(y_1, y_2, \ldots, y_m, p) \\ \vdots \\ f_m(y_1, y_2, \ldots, y_m, p) \end{pmatrix},$$

where $*$ denotes the transpose and

$$f_i = \sum_{j=1}^{m}\left(\sum_{k=1}^{i-1}\tau_{kj}\right)\int_{y_j}^{y_{j+1}} \sigma(z,p)\,dz + \sum_{j=1}^{m}\left(\sum_{k=1}^{i-1}\phi_{kj}\right)\int_{y_j}^{y_{j+1}} \beta(z,p)\,dz, \quad 2 \leqslant i \leqslant m,$$

then we have a system of difference equations

$$y(t+1) = f\bigl(y(t), p(t)\bigr) \tag{2.6}$$

for the cumulative densities $y_i(t)$, $1 \leqslant i \leqslant m$, and an uncoupled scalar equation for total population size

$$p(t+1) = s\bigl(p(t)\bigr) + b\bigl(p(t)\bigr), \tag{2.7}$$

where

$$s(p) = \int_0^p \sigma(z, p)\,dz, \qquad b(p) = \int_0^p \beta(z, p)\,dz$$

(recall $\sum_{k=1}^{m} \phi_{kj} = \sum_{k=1}^{m} \tau_{kj} = 1$ for $1 \leqslant j \leqslant m$). Consequently, (2.7) can be used to study intra-specific competition.

3. Intra-specific competition with constant resource

In this section we study the asymptotic dynamics of Eq. (2.7) for the total population size $p(t)$ derived in Section 2. We then compare scramble and contest competition using equilibrium level and resilience as comparison criteria. A discrete hierarchical model with intra-specific competition was studied in [17], where the modeling methodology used in [6,7] was adopted. Contrary to the modeling methodology used in [17], we assume that both populations have the same amount of available resource. In addition, it is assumed that both populations are identical in every aspect except in their mode of intra-specific competition.

Let R be the amount of a constant limiting resource available to the population and let c_s and c_c be the fractions of this amount that are available to an individual under scramble and contest competition, respectively. We assume these fractions are functions of some measure of population density z (to be specified below) and as such satisfy

$$c \in C^1\big(R_+, [0, 1]\big), \qquad c(0) = 1, \qquad c' < 0, \quad \text{and} \quad \lim_{z\to\infty} c(z) = 0. \tag{3.1}$$

Thus, the entire amount R of resource available to the population is available to each individual when the density is low, but the fraction available to an individual decreases as population density increases.

We assume the birth rate is proportional to the resource uptake rate u which, as a function of resource availablility, satisfies

$$u \in C^2(R_+, R_+), \qquad u(0) = 0, \quad \text{and} \quad u' > 0. \tag{3.2}$$

Thus resource uptake is zero in the absence of available resource and increases with increased resource availability.

Under scramble competition $Rc_s(p)$ is the per capita resource availability for an individual and thus the birth rate is $\beta = \beta_0 u(Rc_s(p))$. Under contest competition, on the other hand, the amount of resource available to an individual depends on its ranking. For individuals of rank class z the per capita resource availability is $Rc_c(p - z)$, so that $u(Rc_c(p - z))$ becomes the amount of resource consumed by an individual. (Note that $p - z$ is the density of individuals with equal or higher rank.) Thus the birth rate is $\beta = \beta_0 u(Rc_c(p - z))$. Here we have assumed that the number of offspring β_0 produced per unit resource per individual is the same in both models.

In this paper we concentrate on the effect on fertility of resource competition. To isolate this effect we assume the survival probability is a constant (i.e., is independent of resource consumption and population density), so that $\sigma(z, p) = \sigma_0 > 0$.

Our goal is to compare the dynamics effects of the two different modes of competition. To make the comparison accurate we assume both populations have the same amount of resource availability. We now show that this assumption requires a specific relationship between c_s and c_c. Since $Rc_s(p)$ is the per capita resource availability for an individual in scramble competition, $\sum_{i=1}^{m} Rc_s(p)x_i$ is the total amount of available resource for scramble population. For contest competition, by the biological interpretation of $Rc_c(p-z)$, the average per capita resource availability for an individual in the ith class is then

$$\begin{cases} \frac{1}{x_i}\int_{y_i}^{y_i+x_i} Rc_c(p-z)\,dz & \text{if } x_i \neq 0, \\ Rc_c(p-y_i) & \text{if } x_i = 0. \end{cases}$$

Thus our assumption of equal total resource availability requires

$$\sum_{i=1}^{m} Rc_s(p)x_i = \sum_{i=1}^{m} \int_{y_i}^{y_{i+1}} Rc_c(p-z)\,dz,$$

which leads to

$$c_s(p) = \frac{1}{p}\int_0^p c_c(z)\,dz \tag{3.3}$$

if R is independent of z. By using (3.3), Eq. (2.7) for total population size becomes

$$p(t+1) = \left[\sigma_0 + \beta_0 \frac{1}{p(t)} \int_0^{p(t)} u\big(Rc(z)\big)\,dz\right] p(t) \tag{3.4}$$

for contest competition and

$$p(t+1) = \left[\sigma_0 + \beta_0 u\left(\frac{1}{p(t)} R \int_0^{p(t)} c(z)\,dz\right)\right] p(t) \tag{3.5}$$

for scramble competition, where $c(z) = c_c(z)$ satisfies (3.1).

Since survival probability σ_0 is a constant and $\beta_0 u(R)$ is the birth rate of an individual when the population density is zero,

$$n = \beta_0 u(R)(1 + \sigma_0 + \sigma_0^2 + \cdots) = \frac{\beta_0 u(R)}{1-\sigma_0}$$

is the *inherent net reproductive number* for both populations. It is the expected number of offspring per individual over its lifetime at low population density.

We are now ready to discuss the dynamics of Eqs. (3.4) and (3.5). Observe that trivial steady state 0 always exists for both equations. To address the existence of a positive steady state, we let

$$f_c(p) = \sigma_0 + \beta_0 \frac{\int_0^p u(Rc(z))\,dz}{p},$$

$$f_s(p) = \sigma_0 + \beta_0 u\left(R \frac{\int_0^p c(z)\,dz}{p}\right).$$

Then

$$\lim_{p\to 0^+} f_c(p) = \lim_{p\to 0^+} f_s(p) = \sigma_0 + \beta_0 u(R)$$

and

$$\lim_{p\to \infty} f_c(p) = \lim_{p\to \infty} f_s(p) = \sigma_0 < 1.$$

Furthermore,

$$f_c'(p) < 0, \quad f_s'(p) < 0 \quad \text{for } p \geqslant 0.$$

We conclude 0 is the only steady state if $n < 1$ and, if $n > 1$, there exists a unique positive steady state for both Eqs. (3.4) and (3.5). Let p_c and p_s denote the positive steady states of (3.4) and (3.5), respectively, when $n > 1$.

Theorem 3.1. *The dynamics of the contest competition model equation* (3.4) *are summarized as follows.*

(1) *If* $n < 1$, *then* $\lim_{t\to\infty} p(t) = 0$ *for any solution of* (3.4) *with* $p(0) \geqslant 0$.
(2) *If* $n > 1$, *then* $\lim_{t\to\infty} p(t) = p_c$ *for any solution of* (3.4) *with* $p(0) > 0$.

Proof. (1) Clearly if $p(0) = 0$, then $p(t) = 0$ for $t \geqslant 0$ and if $p(t_0) > 0$ for some $t_0 \geqslant 0$, then $p(t_0 + 1) > 0$. Thus we may assume that $p(t) > 0$ for all $t \geqslant 0$. Observe that

$$p(t+1) = \bigl(\sigma_0 + \beta_0 u\bigl(Rc(z^*)\bigr)\bigr) p(t)$$

for some $z^* \in (0, p(t))$ and since $u' > 0$ and $c' < 0$, we have

$$p(t+1) \leqslant \bigl(\sigma_0 + \beta_0 u(R)\bigr) p(t) < p(t).$$

Hence $\lim_{t\to\infty} p(t) = 0$ as 0 is the only steady state for (3.4).

(2) Let

$$F_c(p) = \sigma_0 p + \beta_0 \int_0^p u\bigl(Rc(z)\bigr)\, dz$$

and thus $f_c(p) = F_c(p)/p$. Since $f_c'(p) < 0$ for all $p \geqslant 0$ and $f_c(p_c) = 1$, we have

$$(p - p_c)\bigl(F_c(p) - p\bigr) = (p - p_c)\bigl(f_c(p) - 1\bigr) p < 0 \tag{3.6}$$

for $p > 0$ and $p \neq p_c$. By using (3.6) and the fact that $F_c'(p) > 0$ for all $p \geqslant 0$, we have that if $0 < p < p_c$, then $F_c(p) > p$ and $F_c(p) < p_c$. Consequently, $F_c^2(p) > F_c(p)$ and $F_c^2(p) < p_c$. Continuing in this fashion, we see that $\{F_c^t(p)\}_{t=0}^\infty$ is an increasing sequence of real numbers which is bounded above by p_c. Hence $\{F_c^t(p)\}_{t=0}^\infty$ converges to a positive steady state by the continuity of $F_c(p)$. Since the positive steady state is unique, $\lim_{t\to\infty} F_c^t(p) = p_c$ for $0 < p < p_c$.

On the other hand if $p > p_c$, then $F_c(p) < p$ and $F_c(p) > p_c$. Thus $\{F_c^t(p)\}_{t=0}^\infty$ is a decreasing sequence of real numbers which is bounded below by p_c. A similar argument can be applied to conclude that $\lim_{t\to\infty} F_c^t(p) = p_c$ if $p > p_c$. This completes the proof. □

To discuss the dynamics of (3.5), we let

$$F_s(p) = \left[\sigma_0 + \beta_0 u\left(\frac{R\int_0^p c(z)\,dz}{p}\right)\right]p$$

and

$$x = \frac{R\int_0^p c(z)\,dz}{p}$$

for notational convenience. Then

$$F_s'(p) = \sigma_0 + \beta_0 u(x) + \beta_0 R u'(x)\frac{pc(p) - \int_0^p c(z)\,dz}{p}$$

and

$$F_s''(p) = \beta_0 R^2 u''(x)\frac{(pc(p) - \int_0^p c(z)\,dz)^2}{p^3} + \beta_0 R u'(x) c'(p).$$

Moreover, if $u'' < 0$ on $(0, R)$ we have

$$F_s'(0) = \sigma_0 + \beta_0 u(R), \qquad \lim_{p\to\infty} F_s'(p) = \sigma_0 > 0, \qquad F_s''(p) < 0$$

for $p \geqslant 0$. Thus $F_s'(p) > 0$ for $p \geqslant 0$ if $u'' < 0$ on $(0, R)$. Therefore by a similar argument as in the proof of Theorem 3.1(2), the dynamics of (3.5) are easily understood if $n > 1$ and $u'' < 0$ on $(0, R)$.

If $u'' > 0$ on $(0, R)$, then $F_s(p)$ is no longer increasing on $[0, \infty)$. However, it can be easily shown that solutions of (3.5) are bounded. Indeed, since $u'' > 0$ on $(0, R)$, we apply Jensen's inequality derived in [11], i.e.,

$$\frac{1}{p}\int_0^p u\bigl(Rc(z)\bigr)\,dz > u\left(\frac{1}{p}\int_0^p Rc(z)\,dz\right)$$

for $p > 0$ and obtain

$$p(t+1) \leqslant \left(\sigma_0 + \beta_0\frac{1}{p(t)}\int_0^{p(t)} u\bigl(Rc(z)\bigr)\,dz\right)p(t).$$

It follows from Theorem 3.1 that $\limsup_{t\to\infty} p(t) \leqslant p_c$. Hence solutions of (3.5) with $p(0) \geqslant 0$ are bounded.

Let A be a subset of $[0, \infty)$ and $g : A \to A$ be continuous. For any $x \in A$, we consider the forward orbit $\{x, g(x), g^2(x), \ldots\}$. If there exists a sequence $n_j \to \infty$ such that $g^{n_j}(x) \to \bar{x}$ as $n_j \to \infty$, then $\bar{x}$ is called an *ω-limit point* of x. The collection of all ω-limit points is called the *ω-limit set* of x and is denoted by $\omega(x)$.

The well-known Dulac criterion for ordinary differential equations has been extended recently by McCluskey and Muldowney [16] for difference equations. The result obtained in [16] provides us a method for eliminating periodic solutions. For two-dimensional ordinary differential equations convergence to a steady state can then be determined by the Poincaré–Bendixon theorem. Similar to ordinary differential equations, elimination of periodic solutions for scalar difference equations may not lead to the convergence of steady states. The following theorem whose proof is postponed to Appendix A complements the discrete Dulac criterion derived in [16] giving us a tool for reaching such a conclusion.

Theorem 3.2. *Let* $g:[0,\infty)\to[0,\infty)$ *be continuous such that* g *has fixed points at* 0 *and at* $x_0>0$ *and* g *has no other periodic points. If every point has a bounded forward orbit, then the* ω*-limit set of each point is a subset of* $\{0,x_0\}$.

Using this theorem we can address the dynamics of (3.5).

Theorem 3.3. *The dynamics of the scramble competition model equation* (3.5) *are summarized as follows.*

(1) *If* $n<1$, *then* $\lim_{t\to\infty}p(t)=0$ *for any solution of* (3.5) *with* $p(0)\geqslant 0$.
(2) *If* $n>1$ *and*
  (a) *if* $u''<0$ *on* $(0,R)$, *then* $\lim_{t\to\infty}p(t)=p_s$ *if* $p(t)$ *is a solution of* (3.5) *with* $p(0)>0$;
  (b) *if* $u''>0$ *on* $(0,R)$ *and in addition* $1+\sigma_0\geqslant\beta_0Ru'(R)$, *then* $\lim_{t\to\infty}p(t)=p_s$ *for any solution* $p(t)$ *of* (3.5) *with* $p(0)>0$.

Proof. The proofs of (1) and (2)(a) are similar to the proof of Theorem 3.1. We only show our assertion for part (2)(b). We first review the discrete analogue of the Dulac criterion. Consider a scalar difference equation $x(t+1)=g(x(t))$, where $g:[0,\infty)\to[0,\infty)$ is continuously differentiable. If $1+g'(x)>0$ for $x\geqslant 0$, then the equation has no nontrivial periodic solution on $[0,\infty)$ [16]. The assumption $1+\sigma_0\geqslant\beta_0Ru'(R)$ implies that $1+F_s'(p)>0$ for all $p\geqslant 0$. Thus (3.5) has no nontrivial periodic solution on $[0,\infty)$. Since solutions of (3.5) are bounded, we apply Theorem 3.2 and conclude that the ω-limit set of any solution of (3.5) with $p(0)\geqslant 0$ is a subset of $\{0,p_s\}$. However, since $F_s'(0)>1$, 0 cannot be an ω-limit point of any solution with $p(0)>0$. Therefore, (2)(b) is shown. □

Theorem 3.3 suggests the concavity of the resource uptake function u plays a role in the dynamics of the scramble competition model (3.5). From a mathematical point of view, however, it is not clear from the statement of the theorem whether the added assumption in (2)(b) (namely, the inequality $1+\sigma_0\geqslant\beta_0Ru'(R)$) is necessary or not for the conclusion that $\lim_{t\to\infty}p(t)=p_s$. Figure 1 shows two examples with regard to this point. Consider the scramble competition model equation (3.5) with $u(z)=bz^4$ and $c(z)=e^{-az}$, where $a,b>0$, i.e., consider the difference equation

$$p(t+1)=\left(\sigma_0+\beta_0b\left(R\frac{1-e^{-ap(t)}}{ap(t)}\right)^4\right)p(t),\qquad p(0)>0.$$

Note $u''>0$ for all $z>0$. In the figure we see two bifurcation diagrams in which attractors are plotted against β_0. In both cases $a=b=1$.

In (a) we chose $\sigma_0=0.8$ and $R=1$. A calculation shows the two inequalities $n>1$ and $1+\sigma_0\geqslant\beta_0Ru'(R)$ needed for an application of Theorem 3.3(2)(b) hold for and only for $0.20<\beta_0<0.45$. We see from the bifurcation diagram in (a), however, that in fact

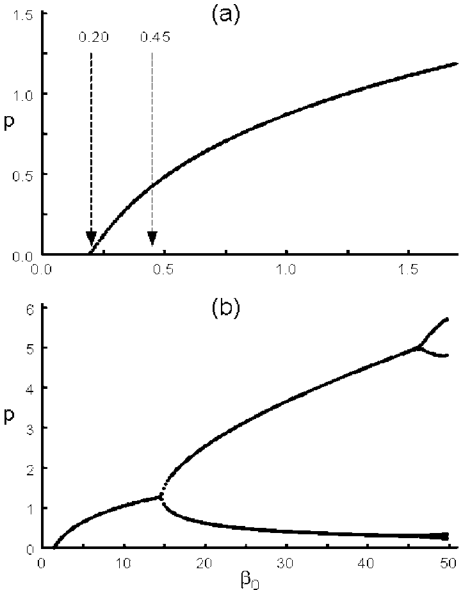

Fig. 1.

the positive equilibrium is a global attractor (with respect to positive initial conditions) for values of β_0 larger than 0.45 (i.e., where the second inequality fails to hold). Indeed, computer simulations suggest in this case that the positive equilibrium is attracting for all $\beta_0 > 0.45$.

In (b) we chose $\sigma_0 = 0.01$ and $R = 0.9$. A calculation shows $n > 1$ if and only if $1.5 < \beta_0$, but the inequality $1 + \sigma_0 \geqslant \beta_0 R u'(R)$ requires $\beta_0 \leqslant 0.38485$. Thus, Theorem 3.3(2)(b) does not apply to this case. Regardless, we see from the bifurcation diagram in (b) that for some such values of β_0 (approximately $1.5 < \beta_0 < 14.7$) the positive equilibrium is a global attractor (with respect to positive initial conditions) and the conclusion of Theorem 3.3(2)(b) holds nonetheless. However, this conclusion does not hold for all β_0, as is seen by the two period doubling bifurcations in (b).

Figure 1a shows that the added assumption in (2)(b) is in fact not a necessary condition for $\lim_{t\to\infty} p(t) = p_s$. On the other hand, Fig. 1b shows that if this assumption is dropped from (2)(b) the resulting assertion is false. Indeed, in Fig. 1b we see when the added assumption fails to hold, solutions of (3.5) may not equilibrate at all, but can approach other types of attractors (such as stable cycles). One way to view the added assumption in (2)(b) is that it provides a constraint on the size of the reproductive output of the population (i.e., on β_0). This is not a surprising constraint, when considering the well-know propensity of difference equations to undergo dynamic bifurcations and exhibit routes-to-chaos as fertility increases. From this point of view, Theorem 3.3(2)(a) (and Theorem 3.1) are more surprising in that they imply only equilibrium dynamics occur.

The most common assumption made in population dynamical models is that u is concave down, as in (2)(a). This reflects a decreasing rate change of the resource uptake rate as resource availability increases, a kind of “law of diminishing returns.” Indeed, many models assume that u increases to a horizontal asymptote in order to reflect a “saturation” level of resource consumption (e.g., this is true of the standard Holling II and III type uptake rates). Models with uptake rates that level off in this way cannot be concave up ($u'' > 0$), at least for all levels of resource abundance. In some models, however, the uptake rate u is concave up for low levels of resource abundance and concave down for high abundance levels (e.g., Holling III type uptake rates). Theorem 3.3(2)(b) can apply to such models.

Our next goal is to compare contest and scramble competition. The first comparison is based on equilibrium levels for total population size.

Theorem 3.4. *Let* $n > 1$. *Then each of the following is true.*

(1) *If* $u'' < 0$ *on* $(0, R)$, *then* $p_s > p_c$.
(2) *If* $u'' > 0$ *on* $(0, R)$, *then* $p_s < p_c$.

Proof. The idea employed here is similar to that of the continuous hierarchical model [11]. We apply Jensen’s inequality which states that if $u'' < 0$ on $(0, R)$, then

$$\frac{1}{p}\int_0^p u\bigl(Rc(z)\bigr)\,dz < u\left(\frac{1}{p}\int_0^p Rc(z)\,dz\right) \quad \text{for all } p > 0,$$

with the above inequality reversed if $u'' > 0$ on $(0, R)$.

We only prove (1) as (2) can be shown similarly. Observe that

$$\sigma_0 + \beta_0 u\left(R\frac{1}{p_s}\int_0^{p_s} c(z)\,dz\right) = 1$$

$$= \sigma_0 + \frac{\beta_0}{p_c}\int_0^{p_c} u\bigl(Rc(z)\bigr)\,dz < \sigma_0 + \beta_0 u\left(R\frac{1}{p_c}\int_0^{p_c} c(z)\,dz\right),$$

i.e.,

$$u\left(R\frac{1}{p_s}\int_0^{p_s} c(z)\,dz\right) < u\left(R\frac{1}{p_c}\int_0^{p_c} c(z)\,dz\right).$$

Since $u(R(1/p)\int_0^p c(z)\,dz)$ is a strictly decreasing function of p, we immediately see that $p_s > p_c$. $\Box$

We conclude that with respect to equilibrium levels, scramble competition yields a higher population level if the uptake rate u is concave down on $(0, R)$ and contest competition has a higher equilibrium level if the uptake rate u is concave up on $(0, R)$.

We next turn to study the comparison between contest and scramble competition by means of equilibrium resilience. Recall that equilibrium resilience is a measure of how fast a population is returned to its equilibrium level if the population is perturbed from its equilibrium. If the perturbation is small, by ignoring higher order perturbation terms, it is easy to see that whether the perturbation will die out or not depends on $F_c'(p_c)$ and $F_s'(p_s)$ for contest and scramble competition, respectively. Let $\lambda_s(n) = F_s'(p_s(n))$ and $\lambda_c(n) = F_c'(p_c(n))$. Observe that $\lambda_c(n) > 0$ for $n \geqslant 1$. Also, since

$$\lambda_s(1) = \sigma_0 + \beta_0 u(R) = 1 > 0,$$

we see that $\lambda_s(n) > 0$ for $n > 1$ but sufficiently close to 1. We consider $\lambda_s(n) - \lambda_c(n)$ for $n > 1$ but close to 1.

We rewrite $\lambda_s(n) - \lambda_c(n)$ as $\lambda_s(n) - \lambda_c(n) = \beta_0[\tilde{\lambda}_s(n) - \tilde{\lambda}_c(n)]$. Then

$$\operatorname{sign}\bigl[\lambda_s(n) - \lambda_c(n)\bigr] = \operatorname{sign}\bigl[\tilde{\lambda}_s(n) - \tilde{\lambda}_c(n)\bigr] = \operatorname{sign}\bigl[u^{-1}\bigl(\tilde{\lambda}_s(n)\bigr) - u^{-1}\bigl(\tilde{\lambda}_c(n)\bigr)\bigr].$$

By using a second-order Taylor expansion about $n = 1$ for $u^{-1}(\tilde{\lambda}_s(n)) - u^{-1}(\tilde{\lambda}_c(n))$ and after some lengthy computations, we have that for $n > 1$ but close to 1,

$$u^{-1}\bigl(\tilde{\lambda}_s(n)\bigr) - u^{-1}\bigl(\tilde{\lambda}_c(n)\bigr) \approx -\frac{(u(R))^2 u''(R)}{6(u'(R))^3}(n-1)^2.$$

We summarize our discussion into the following

Theorem 3.5. *Let $n > 1$. Then each of the following is true.*

(1) $\lambda_c < \lambda_s$ *if $u''(R) < 0$ and n is sufficiently close to* 1.
(2) $\lambda_c > \lambda_s$ *if $u''(R) > 0$ and n is sufficiently close to* 1.

Recall that p_c is always globally asymptotically stable for (3.4) and $\lambda_c(n) > 0$ for $n \geqslant 1$. Moreover, $\lambda_s(n) < 1$ for all $n > 1$ and $\lambda_s(1) = 1$. Thus $0 < \lambda_s(n) < 1$ for $n > 1$ and close to 1, i.e., p_s is locally asymptotically stable if n is close to 1. We conclude that when $n > 1$ but close to 1 contest competition is more resilient if $u''(R) < 0$ and scramble competition is more resilient if $u''(R) > 0$. Therefore there is a trade off between the two forms of intra-specific competition.

4. Intra-specific competition with dynamic resource

Suppose now that the resource level R is not constant in time. We first derive a system of difference equations for the dynamics of the resource level and total population size. We then discuss its dynamics and compare two forms of intra-specific competition, as in the previous section.

We assume in the absence of the population, the dynamic of resource R is governed by the chemostat law $R(t+1) = (1-k_0)R(t) + k_0 R^0$, where $R^0 > 0$ is the equilibrium resource level for self-renewal and k_0 denotes both the input and washout rate with $0 < k_0 < 1$. The dynamics of this equation are very simple: $R(t)$ always asymptotically stabilizes at $R^0 > 0$. In the presence of the population, the dynamics of R are governed by

$$R(t+1) = (1-k_0)\bigl[R(t) - F\bigl(p(t), R(t)\bigr)\bigr] + k_0 R^0,$$

where $F(p(t), R(t))$ describes the resource consumption rate by the population. Hence it is assumed that, during one unit of time, consumption occurs first and then washout. The model derivation here is parallel to that of the discrete chemostat model given by Smith [15].

We now describe $F(p, R)$. Recall that for scramble competition, $u(Rc_s(p))$ is the amount of resource consumed by an individual when total population size is p. We assume both populations have the same amount of resource, and thus

$$c_s(p) = \frac{1}{p}\int_0^p c_c(z)\,dz.$$

Therefore

$$u\bigl(Rc_s(p)\bigr)p = u\left(R\frac{1}{p}\int_0^p c(z)\,dz\right)p$$

is the total amount of resource consumed by the population. Similarly, as $u(Rc_c(p-z))$ is the amount of resource consumed by an individual for contest competition when total population size is p and population density of lower rank is z, we see that the average resource consumed by an individual in the jth class is

$$\begin{cases} \frac{1}{x_j}\int_{y_j}^{y_j+x_j} u(Rc(p-z))\,dz & \text{if } x_j \neq 0, \\ u(Rc(p-y_j)) & \text{if } x_j = 0. \end{cases} \tag{4.1}$$

Thus the total amount of resource consumed by the population is $\int_0^p u(Rc(z))\,dz$. Consequently, the dynamics of total population size and resource level are described by the following system of difference equations

$$\begin{aligned} p(t+1) &= \left(\sigma_0 + \beta_0\frac{1}{p(t)}\int_0^{p(t)} u\bigl(R(t)c(z)\bigr)\,dz\right)p(t), \\ R(t+1) &= (1-k_0)\left(R(t) - \int_0^{p(t)} u\bigl(R(t)c(z)\bigr)\,dz\right) + k_0R^0 \end{aligned} \tag{4.2}$$

for contest competition and

$$\begin{aligned} p(t+1) &= \left(\sigma_0 + \beta_0 u\left(R(t)\frac{1}{p(t)}\int_0^{p(t)} c(z)\,dz\right)\right)p(t), \\ R(t+1) &= (1-k_0)\left(R(t) - u\left(R(t)\frac{1}{p(t)}\int_0^{p(t)} c(z)\,dz\right)p(t)\right) + k_0R^0 \end{aligned} \tag{4.3}$$

for scramble competition.

Note that system (4.2) as well as system (4.3) may not be biologically meaningful as the consumption rate $F(p(t), R(t))$ may exceed the available resource $R(t)$ at time t. On the other hand, in the derivation of models (4.2) and (4.3), we tactically assumed that the resource level $R(t)$ is unchanged during one unit of time, i.e., $F(p(t), R(t))/R(t)$ is small if $R(t) > 0$. In order to incorporate these observations, we shall restrict ourselves to Holling II uptake rate as in [15]

$$u(R) = \frac{mR}{a + R}, \tag{4.4}$$

where a is the half saturation constant and m is the maximal uptake rate. In addition, we make the following assumption. Fix any $\eta \in (0, 1 - k_0)$ and some appropriate upper bound M $(\geqslant \beta_0 R^0)$ of $(1 - k_0)p + \beta_0 R$, we assume that

$$\frac{m}{a} M < \eta. \tag{4.5}$$

We shall see that under constraint (4.5), the consumption rate $F(p(t), R(t))$ will never exceed $R(t)$ for $t = 0, 1, \ldots$. Indeed, let

$$D = \bigl\{(p, R) \in R_+^2\colon\ (1 - k_0)p + \beta_0 R \leqslant M\bigr\}. \tag{4.6}$$

We show that D is positively invariant for both systems, so that each of the systems defines a discrete semidynamical system on D.

Proposition 4.1. *Assume* (4.5) *is satisfied. If* $\sigma_0 + k_0 \leqslant 1$, *then* D *is positively invariant for systems* (4.2) *and* (4.3), *respectively.*

Proof. We show our assertion for (4.2), a similar analysis applying to (4.3). Let $(p(0), R(0)) \in D$ be given. Clearly, $p(1) \geqslant 0$ and if $R(0) = 0$, then $R(1) = k_0 R^0 > 0$. If $R(0) > 0$, (4.5) implies

$$\frac{\int_0^{p(0)} u(R(0)c(z))\,dz}{R(0)} \leqslant \frac{u(R(0))p(0)}{R(0)} < \frac{\eta p(0)}{M} < \frac{\eta}{1 - k_0} < 1,$$

i.e., $F(p(0), R(0)) < R(0)$ and thus $R(1) > k_0 R^0$. Furthermore, by using (4.2),

$$\begin{aligned}
(1 - k_0)p(1) + \beta_0 R(1) &= (1 - k_0)\sigma_0 p(0) + \beta_0(1 - k_0)R(0) + \beta_0 k_0 R^0 \\
&\leqslant (1 - k_0)M + (1 - k_0)(\sigma_0 + k_0 - 1)p(0) + k_0\beta_0 R^0 \leqslant M
\end{aligned}$$

as $\sigma_0 + k_0 \leqslant 1$. Thus $(p(1), R(1)) \in D$ and consequently D is positively invariant for (4.2). □

We assume $\sigma_0 + k_0 \leqslant 1$ for the remainder of the discussion. The inherent net reproductive number for both populations with dynamic resource is given by

$$n = \frac{\beta_0 u(R^0)}{1 - \sigma_0}.$$

It is easy to see that trivial steady state $E_0 = (0, R^0)$ always exists for both systems. For the existence of a positive steady state (p^*, R^*), p^* must satisfy

$$\frac{1}{p}\int_0^p u\left(\left(R^0 - \frac{1}{k_0 n}(1-k_0)u(R^0)p\right)c(z)\right)dz = \frac{u(R^0)}{n} \tag{4.7}$$

for contest competition and

$$u\left(\left(R^0 - \frac{1}{k_0 n}(1-k_0)u(R^0)p\right)\frac{1}{p}\int_0^p c(z)\,dz\right) = \frac{u(R^0)}{n} \tag{4.8}$$

for scramble competition. Let $g_c(p)$ and $g_s(p)$ denote the left-hand sides of (4.7) and (4.8), respectively. Clearly,

$$\lim_{p\to 0^+} g_s(p) = u(R^0) = \lim_{p\to 0^+} g_c(p),$$
$$g_c'(p) < 0, \qquad g_s'(p) < 0$$

for $p \in [0, \hat{p})$, where

$$\hat{p} = \frac{nk_0R^0}{(1-k_0)u(R^0)}$$

and $g_c(\hat{p}) = g_s(\hat{p}) = 0$. Therefore, we conclude that $E_0 = (0, R^0)$ is the only steady state if $n \leqslant 1$ and a positive steady state (p^*, R^*) exists if $n > 1$. In this case, the positive steady state is unique. Let $E_c = (p_c, R_c)$ and $E_s = (p_s, R_s)$ be the corresponding positive steady states for system (4.2) and (4.3), respectively. It can be shown that $E_c, E_s \in D$.

Let J_c and J_s denote the Jacobian matrices associated with systems (4.2) and (4.3), respectively. A straightforward calculation shows that the Jacobian matrix at E_0 is given by

$$J_c(E_0) = J_s(E_0) = \begin{pmatrix} \sigma_0 + \beta_0 u(R^0) & 0 \\ -(1-k_0)u(R^0) & 1-k_0 \end{pmatrix}.$$

Therefore, E_0 is locally asymptotically stable for both systems if $n < 1$. If $n > 1$, then E_0 is a saddle point with local stable manifold lying in the R-axis. The following theorem shows that E_0 is indeed globally asymptotically stable if $n < 1$.

Theorem 4.2. *Assume* (4.5) *and* $\sigma_0 + k_0 \leqslant 1$. *If* $n < 1$, *then* E_0 *is a global attractor in* D *for both systems, i.e.,* $\lim_{t\to\infty} p(t) = 0$ *and* $\lim_{t\to\infty} R(t) = R^0$ *if* $(p(t), R(t))$ *is a solution for either* (4.2) *or* (4.3) *with* $(p(0), R(0)) \in D$.

Proof. We show our assertion for system (4.3). The same argument applies to system (4.2). Note

$$R(t+1) \leqslant (1-k_0)R(t) + k_0R^0$$

and hence $\limsup_{t\to\infty} R(t) \leqslant R^0$. Since

$$n = \frac{\beta_0 u(R^0)}{1-\sigma_0} < 1,$$

there exists $\epsilon > 0$ such that

$$\frac{\beta_0 u(R^0+\epsilon)}{1-\sigma_0} < 1.$$

For this $\epsilon > 0$, there exists $t_1 > 0$ such that $R(t) \leqslant R^0 + \epsilon$ for $t \geqslant t_1$. Thus if $t \geqslant t_1$, then

$$p(t+1) \leqslant \bigl(\sigma_0 + \beta_0 u\bigl(R(t)\bigr)\bigr)p(t) \leqslant \bigl(\sigma_0 + \beta_0 u(R^0+\epsilon)\bigr)p(t).$$

Hence $\limsup_{t\to\infty} p(t) \leqslant 0$ and $\lim_{t\to\infty} p(t) = 0$ is shown. It remains to show that $\lim_{t\to\infty} R(t) = R^0$.

For any given $\delta > 0$, there exist $t_0 > 0$ such that $p(t) < \delta$ for $t \geqslant t_0$. We choose $\delta > 0$ such that

$$\delta(1-k_0)u\left(\frac{M}{\beta_0}\right) < k_0 R^0.$$

Thus for $t \geqslant t_0$,

$$\begin{aligned} R(t+1) &\geqslant (1-k_0)R(t) - (1-k_0)u\bigl(R(t)\bigr)p(t) + k_0 R^0 \\ &> (1-k_0)R(t) - (1-k_0)\delta u\left(\frac{M}{\beta_0}\right) + k_0 R^0. \end{aligned}$$

Let $x^0 = k_0 R^0 - (1-k_0)\delta u(M/\beta_0)$ and consider the difference equation

$$x(t+1) = (1-k_0)x(t) + x^0, \qquad x(0) = R(t_0).$$

Then $\lim_{t\to\infty} x(t) = x^0/k_0$ if $x(0) \geqslant 0$. This shows that

$$\liminf_{t\to\infty} R(t) \geqslant \frac{x^0}{k_0} = R^0 - \frac{1-k_0}{k_0}\delta u\left(\frac{M}{\beta_0}\right).$$

Letting $\delta \to 0^+$, we obtain $\liminf_{t\to\infty} R(t) \geqslant R^0$. Therefore $\lim_{t\to\infty} R(t) = R^0$ and the proof is complete. □

Let $n > 1$. Then both $E_c = (p_c, R_c)$ and $E_s = (p_s, R_s)$ exist. In the following we verify that E_c and E_s are local attractors for systems (4.2) and (4.3), respectively.

Proposition 4.3. *Assume* (4.5) *and* $\sigma_0 + k_0 \leqslant 1$. *Let* $n > 1$. *Then* E_c *and* E_s *are locally asymptotically stable for systems* (4.2) *and* (4.3), *respectively.*

Proof. We apply the Jury condition. We only treat system (4.2), the same analysis working for system (4.3) as well.

The Jacobian matrix for (4.2) is

$$J_c = \begin{pmatrix} \sigma_0 + \beta_0 u(Rc(p)) & \beta_0 \int_0^p u'(Rc(z))c(z)\,dz \\ -(1-k_0)u(Rc(p)) & (1-k_0) - (1-k_0)\int_0^p u'(Rc(z))c(z)\,dz \end{pmatrix}.$$

Replace p by p_c and R by R_c in J_c and rewrite

$$J_c = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}.$$

The eigenvalues λ of J_c satisfy

$$\lambda^2 - (a_{11} + a_{22})\lambda + (a_{11}a_{22} - a_{12}a_{21}) = 0.$$

A sufficient criterion based on the Jury condition for eigenvalues λ to lie inside a unit circle, where λ satisfies $\lambda^2 + a_1\lambda + a_0 = 0$, is $|a_0| < 1$ and $|a_1| < 1 + a_0$ [9].

Note

$$\begin{aligned} a_0 &= a_{11}a_{22} - a_{12}a_{21} \\ &= (1-k_0)\big(\sigma_0 + \beta_0 u\big(R_c c(p_c)\big)\big) - (1-k_0)\sigma_0 p_c u'\big(R_c c(z^*)\big)c(z^*) \end{aligned}$$

for some $z^* \in (0, p_c)$. Since $R_c c(z^*) > 0$ and $u'' < 0$, we see that

$$u'\big(R_c c(z^*)\big) < u'(0) = \frac{m}{a}.$$

Thus constraint (4.5) implies $a_0 > 0$. To show $a_0 < 1$, observe that since $u(R_c c(z))$ is a decreasing function of z, we have

$$\sigma_0 p_c + \beta_0 p_c u\big(R_c c(p_c)\big) < p_c,$$

i.e., $\sigma_0 + \beta_0 u(R_c c(p_c)) < 1$. Hence $a_0 < 1 - k_0 < 1$ and $|a_0| < 1$ follows.

We show that $|a_1| < 1 + a_0$ by showing $-(1 + a_0) < a_1 < 1 + a_0$. Clearly,

$$\begin{aligned} a_1 - 1 - a_0 &= -(2-k_0)\big(\sigma_0 + \beta_0 u\big(R_c c(p_c)\big)\big) - (2-k_0) \\ &\quad + (1-k_0)(\sigma_0 + 1)\int_0^{p_c} u'\big(R_c c(z)\big)c(z)\,dz \\ &< -(2-k_0)\big(\sigma_0 + \beta_0 u\big(R_c c(p_c)\big)\big) - (2-k_0) + \eta(1+\sigma_0) < 0. \end{aligned}$$

On the other hand,

$$a_1 + 1 + a_0 > (1-k_0)(1-\sigma_0)\int_0^{p_c} u'\big(R_c c(z)\big)c(z)\,dz > 0.$$

We conclude that $|a_1| < 1 + a_0$ and therefore E_c is a local attractor for system (4.2). □

We suspect E_c and E_s are indeed globally asymptotically stable in D for systems (4.2) and (4.3), respectively. Consequently, both populations can persist in a positive steady state fashion. Another useful tool in showing survivability of populations without investigating global stability is the concept of persistence. In the following, we briefly discuss the terminology derived by Hofbauer and So [12]. Let (H, d) be a metric space and $h : H \to H$ be continuous with a closed subspace Y such that $h(H \setminus Y) \subset H \setminus Y$. It is assumed that H has a global attractor X. Let M be the maximal compact invariant set in Y. Then h is uniformly persistent (with respect to Y), i.e., there exists $\gamma > 0$ such that $\liminf_{t\to\infty} d(h^t(x), Y) > \gamma$ for all $x \in H \setminus Y$ if and only if M is isolated in X and $W^s(M) = \{x \in H\colon\ h^t(x) \to M \text{ as } t \to \infty\} \subset Y$ [12, Theorem 4.1].

Theorem 4.4. *Assume* (4.5) *and* $\sigma_0 + k_0 \leqslant 1$. *Let* $n > 1$. *Then systems* (4.2) *and* (4.3) *are uniformly persistent, i.e., there exists* $\delta > 0$ *such that* $\liminf_{t\to\infty} p(t) \geqslant \delta$ *and* $\liminf_{t\to\infty} R(t) \geqslant \delta$ *for all solutions of* (4.2) *and* (4.3) *with* $(p(0), R(0)) \in D$ *and* $p(0) > 0$.

Proof. Clearly, $R(t+1) \geqslant k_0 R^0$ for $t \geqslant 0$. Hence $\liminf_{t\to\infty} R(t) \geqslant k_0 R^0$. Let $Y = \{(0, R) \in D\colon\ R \geqslant 0\}$, i.e., Y is the nonnegative R-axis in D. It is sufficient to show that systems (4.2) and (4.3) are uniformly persistent with respect to Y. We only show our assertion for system (4.2) as system (4.3) can be treated similarly. In doing so, we first observe that the map defined by system (4.2) is point dissipative and asymptotically smooth [10]. Therefore, there exists a global attractor X [10, Theorem 2.4.6] and $D \setminus Y$ is forward invariant. Clearly, $\{E_0\}$ is the maximal compact invariant set in Y and $E_0 \in X$. It remains to show that $\{E_0\}$ is isolated in X and $W^s(\{E_0\}) \subset Y$.

Let $\epsilon > 0$ be given such that

$$\sigma_0 + \beta_0 u\big((R^0 - \epsilon)c(\epsilon)\big) > 1.$$

If $\{E_0\}$ is not isolated in X, then there exists a maximal invariant set M in $\overline{B(E_0, \epsilon)} \cap X$ with $M \neq \{E_0\}$. Let $p_0 = \sup\{p\colon\ (p, R) \in M\}$. Then there exists at least one R_0 such that $(p_0, R_0) \in M$ and $0 < p_0 \leqslant \epsilon$. Let $(p(0), R(0)) = (p_0, R_0)$. Then

$$p(1) > \big[\sigma_0 + \beta_0 u\big(R(0)c\big(p(0)\big)\big)\big]p(0) \geqslant \big[\sigma_0 + \beta_0 u\big((R^0 - \epsilon)c(\epsilon)\big)\big]p(0) > p(0),$$

i.e., $(p(1), R(1)) \notin M$, a contradiction. We conclude that $\{E_0\}$ is isolated in X.

Suppose now there exists $(p(0), R(0)) \in D$ with $p(0) > 0$ such that $\lim_{t\to\infty} p(t) = 0$ and thus $\lim_{t\to\infty} R(t) = R^0$. Let $\epsilon > 0$ be given as above. There exists $t_0 > 0$ such that $R(t) > R^0 - \epsilon$ and $p(t) < \epsilon$ for $t \geqslant t_0$. Thus for $t \geqslant t_0$,

$$\begin{aligned} p(t+1) &> \left(\sigma_0 + \beta_0 \frac{1}{p(t)} \int_0^{p(t)} u\big((R^0 - \epsilon)c(z)\big)\,dz\right) p(t) \\ &> \big(\sigma_0 + \beta_0 u\big((R^0 - \epsilon)c(\epsilon)\big)\big) p(t) > p(t) \end{aligned}$$

shows that $\lim_{t\to\infty} p(t) = p^* > 0$ exists. We arrive at a contradiction. Hence $W^s(\{E_0\}) \subset Y$ and system (4.2) is uniformly persistent by [12, Theorem 4.1]. □

To compare equilibrium levels p_c and p_s for contest and scramble populations, we recall (4.7) and (4.8), where $g_c'(p) < 0$ and $g_s'(p) < 0$ for $p \in [0, \hat{p})$. Since $u'' < 0$, it follows from Jensen's inequality that $g_c(p) < g_s(p)$ for $p \in (0, \hat{p})$. We immediately see that $p_c < p_s$ and consequently $R_c > R_s$.

Theorem 4.5. *Assume* (4.5) *and* $\sigma_0 + k_0 \leqslant 1$. *Let* $n > 1$. *Then* $p_c < p_s$ *and* $R_c > R_s$.

Therefore scramble competition yields a higher equilibrium level than contest competition in the dynamically varying resource environment.

5. Discussion

Since Lomnicki's assertion that contest competition is more advantageous to population [14], several models have been derived in an attempt to justify this tenet. In this manuscript we use discrete models to study such a comparison. In particular, a discrete version of hierarchical model is derived. Similar to its continuous counterpart, the total population size can be decoupled from those of lower cumulative densities. Consequently, this decoupled scalar difference equation can be used to study the comparison between contest and scramble competition. In doing so, it is necessary to assume that both populations are identical in every way except in their mode of intra-specific competition.

It is shown that if the inherent net reproductive number n is less than 1, then both populations become extinct with either a constant or a dynamically varying resource level. Populations can survive only if $n > 1$. This survivability is characterized in terms of the global asymptotic stability of the positive equilibrium when the resource level is assumed to be constant. If resource level is modeled dynamically, uniform persistence is used as a measure of survivability.

When comparison between contest and scramble intra-specific competition is based on the level of the positive equilibrium, then concavity of the resource uptake rate u as a function of resource availability is the deciding factor for comparison. Indeed, if u is concave up then contest competition has a larger equilibrium size while scramble competition has a larger population size if u is concave down. When resource level is dynamically varying, we restrict ourselves to Michaelis–Menton uptake rate. It is again demonstrated that scramble competition is more advantageous, as u is concave down. If comparison is based on equilibrium resilience, the above conclusions are reversed. Specifically, for $n > 1$ but close to 1, contest competition is more resilient if u is concave down while scramble competition is more resilient if u is concave up.

Although our results obtained here are consistent with those demonstrated in continuous hierarchical age-structured models [11], the main conclusions apply to arbitrary discrete structured models. We conclude that the tenet made by Lomnicki has to be more carefully stated. On the other hand, if submodels of vital rates are modeled differently, it is plausible that a different conclusion may be reached. Therefore, whether scramble or contest competition yields a higher population equilibrium level or is more resilient to the population depends not only on the modeling methodology and comparison method used but also on the submodels of vital rates involved.

Aside from these biological conclusions, the mathematical result in this paper complements the discrete Dulac criterion derived in [16] by providing a sufficient condition for which scalar difference equations do converge to equilibria after elimination of nontrivial periodic solutions. This result gives rise to a new mathematical tool for understanding the asymptotes of scalar difference equations.

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Appendix A

Lemma A.1. *If $f:[a,b]\to[a,b]$ is continuous and surjective with a single fixed point $\bar{x}$, then f has a periodic point of period* 2.

Proof. Observe that since f has a unique fixed point $\bar{x}$, there are c and d with $c<\bar{x}<d$ such that $f(c)=b$ and $f(d)=a$. Then there is a point $c^*<\bar{x}$ such that $f(c^*)=d$. Note that $f^2(c^*)=a$. Thus either $f^2(a)=a$ or f^2 has a fixed point between a and c^*. In either case, f has a periodic point of period 2. □

Theorem A.2. *Suppose $f:[0,\infty)\to[0,\infty)$ is continuous such that f has fixed points at* 0 *and at $x_0>0$ and f has no other periodic points. If every point has a bounded forward orbit, then the ω-limit set of each point is a subset of* $\{0,x_0\}$.

Proof. Let $M=\max\{f(x)\colon 0\leqslant x\leqslant x_0\}$ and let m be the first point of $[0,x_0]$ such that $f(m)=M$.

Observe that if $x>x_0$, then the orbit of x decreases until some point of the orbit is in $[0,M]$. To see this suppose that $f^n(x)>M$ for all n. If $f^i(x)<f^{i+1}(x)$ for each i, then this bounded sequence converges to a fixed point $p>x_0$ and if there is an integer n such that $f^n(x)<f^{n+1}(x)$ but $f^{n+2}(x)<f^{n+1}(x)$ then f has a fixed point p in $[f^n(x),f^{n+1}(x)]$. We obtain contradictions. On the other hand, if $f^n(x)$ decreases but is bounded below by a number greater than M, then again f has a fixed point greater than x_0. Therefore it is sufficient to consider the orbit of f on $[0,M]$.

If $M=x_0$, then the curve of f on $(0,x_0)$ must either lie above $y=x$ or below $y=x$. If it lies above $y=x$, then every point of $[0,x_0]$ attracts to x_0. If it lies below $y=x$, then every point of $[0,x_0)$ attracts to 0.

If $M>x_0$, then either $f(x)<m$ for some $x\in(x_0,M)$ or $f(x)>m$ for all $x\in[m,M]$. For the former case, there exists $x^*\in(x_0,x)$ such that $f(x^*)=m$ and thus $f^2(x^*)=M$. But since $f^2(M)<M$ (or else f has M as a periodic 2 point), f^2 must have a fixed point between x^* and M which leads to a contradiction. For the latter case, $f[m,M]\subset[m,M]$ and so that $I=\bigcap_{n\geqslant 1}f^n[m,M]$ contains x_0. Thus $I=\{x_0\}$ by Lemma A.1 and hence x_0 attracts points in $[m,M]$.

Let $x\in(0,m)$. Then $f(x)>x$ and so there exists an integer N such that $f^n(x)\in[m,M]$ for all $n\geqslant N$ for otherwise $\{f^n(x)\}$ would increase to a positive fixed point for f which is less than x_0. This shows that $\omega(x)\subset\{0,x_0\}$ for all $x\geqslant 0$. □

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