

Dynamics of hierarchical models in discrete-time

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(Received 8 September 2003; In final form 3 March 2004)

We derive and analyze a general class of difference equation models for the dynamics of hierarchically organized populations. Different forms of intra-specific competition give rise to different types of nonlinearities. For our models, we prove that contest competition results asymptotically in only equilibrium dynamics. Scramble competition, on the other hand, can result in more complex asymptotic dynamics. We study both the case when the limiting resource is a constant and when it is dynamically modeled. We prove, in all cases, that the population persists if the inherent net reproductive number of the population is greater than one.

Keywords: Discrete-time model; Intra-specific competition; Inherent net reproductive number; Uniform persistence

1. Introduction

Intra-specific competition is an important intrinsic mechanism that regulates the growth of biological populations. Often, competition among individuals is based on some kind of physical or behavioral hierarchy of individuals within the population. For a population in which there is a hierarchical ranking among individuals, there are two commonly distinguished forms of intra-specific competition: contest and scramble. Contest competition occurs when no individual in a class of lower rank can affect the birth or death rate of any individual of higher rank. Scramble competition, on the other hand, occurs when every individual can affect the vital rates of any other individual in the population [13]. See Begon *et al.* [2] for more biological discussion about these two types of competition.

Several authors have developed and studied models of intra-specific competition based on competition hierarchies. A model based on chronological age and the McKendrick (partial differential) equation is due to Cushing [5]. In a subsequent paper, Cushing [6] derived and analyzed a hierarchical model in which intra-specific competition is based on the body size of individuals. These studies conclude that contest competition results in higher population equilibrium levels than does scramble competition and that the contest equilibrium is more resilient. In a later study, Henson and Cushing [10] use a comparison

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criterion based on the total amount of limiting resource available to the population to show that the concavity of the nonlinear, resource uptake rate is important in deciding the outcome of the comparison.

Many biological populations are accurately modeled using discrete structuring classes and discrete time [4,7]. Jang and Cushing [12] investigate a discrete version of the (partial differential equation) model studied by Henson and Cushing [10]. In [17], Xu studies a discrete analogue of the model examined by Cushing in [5]. In the absence of structuring, Ricker and Beverton-Holt equations are frequently used to describe scramble and contest competition for single species discrete-time population models, respectively [14].

By ignoring differences among individuals in each species and assuming local population dynamics are topologically conjugate to either Ricker or Beverton-Holt equations, Best *et al.* [3] investigated discrete-time competitive metapopulation models of a single patch in which there is an hierarchy among competing species. Explicit conditions were derived for the coexistence of all species and for the dominance of top species in the hierarchy [3]. Multiple patches with dispersal between patches were also discussed in [3]. Yakubu studied single species discrete-time models with two age classes in which there is no competition between two classes and only individuals in the adult class can reproduce [18]. Yakubu showed that in the absence of Allee effect, the model supports only single attractor when competition between juveniles is pure contest and multiple attractors are supported under scramble competition. However, both contest and scramble competition can generate multiple attractors when Allee effect is incorporated into the model [18].

Our models presented here are in different spirit than those studied by Best *et al.* [3] and Yakubu [18]. In particular, a single species is considered and the population is classified into several different classes based on either age, size, or stage. Individuals in any class are capable of reproducing and transition between classes is assumed to be arbitrary during one time unit. Intra-specific competition occurs between individuals in different classes. Specifically, the modeling methodology of Henson and Cushing [10] and Cushing [5–7] is followed. However, unlike in [12] for which equations are derived and investigated separately for two forms of intra-specific competition, the contest and scramble competitions in the present study are connected by means of a homotopy class of equations. In one extreme of the equations we have, pure contest competition and pure scramble competition is represented by the other end of the equations. We will give a more complete analysis of this model than [17] in the case when the resource is constant. In the case when the resource is dynamically modeled, we will study a new and more general model than that studied in [17] and [12].

The manuscript is organized as follows. In the following section we derive a general class of hierarchical competition models and show how they can be reduced to one dimensional equation for total population size. In section 3, we study the asymptotic dynamics of this one dimensional equation and compare the two forms of competition when resource level is a constant. In section 4, we consider the case when the resource varies dynamically. The final section contains a summary.

2. A general hierarchical model

The model we consider is based on a hierarchical matrix model of Xu and Cushing [7,17]. In this model all individuals in a population are categorized into a finite number m of classes,

$m \geq 2$. Any suitable feature of the individuals can serve for the classification scheme (e.g. age, size, life cycle stage, genetic composition, etc.). Let $x_i(t) \geq 0$ denote the density of individuals in class i , $1 \leq i \leq m$, at time $t = 0, 1, 2, \dots$, and let $x_t = \text{col}(x_i(t))_{i=1}^m$ be the column vector consisting of these densities, i.e. the class distribution vector at time t . The dynamics of the class distribution vector is given by the matrix equation

$$x_{t+1} = (\mathbf{T} + \mathbf{F})x_t. \quad (2.1)$$

In this equation, the entries in the $m \times m$ matrix \mathbf{T} (the ‘transition’ matrix) are the fractions of (surviving) individuals who move from one class to another. The entries in the matrix \mathbf{F} (the ‘fertility’ matrix) are the class specific, per capita numbers of (class specific, surviving) newborns per unit time. In general, the model allows for transitions among any two classes and births from any class individual into any class. In specific applications, of course, some transitions and birth classes might be ruled out and hence result in zero entries in the matrices.

The hierarchical model of Xu and Cushing assumes that the class specific entries in the transition and fertility matrices are functions of a hierarchy based on rank associated with the classes. Specifically,

$$\mathbf{T} = (\tau_{ij}\sigma_j), \quad \mathbf{F} = (\varphi_{ij}\beta_j) \quad (2.2)$$

where σ_j is the probability that an individual of class j will survive one unit of time and β_j is the number of surviving offspring from an individual in class j . The numbers τ_{ij} and φ_{ij} are the fractions of the surviving j -class individuals and newborns that lie in class i , respectively, after one unit of time. The fractions τ_{ij} and φ_{ij} are assumed constant in time (and hence density independent) whereas σ_j and β_j are density dependent functions related to the class rank as follows. Let y_i denote the total number (or density) of individuals of rank less than i , i.e.

$$y_i = \begin{cases} 0 & i = 1 \\ \sum_{j=1}^{i-1} x_j & 2 \leq i \leq m + 1. \end{cases} \quad (2.3)$$

In particular, $y_{m+1} = P = \sum_{i=1}^m x_i$ is the total population size. The hierarchical model utilizes functions

$$\sigma \in C^0(\mathbb{R}_+, [0, 1]), \quad \beta \in C^0(\mathbb{R}_+, \mathbb{R}_+)$$

that provide submodels for the quantities σ_j and β_j in the matrix model. 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 . The per capita birth rate of the individual is $\beta(z, P)$. In the hierarchical model of Xu and Cushing

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

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

If $\sigma(z, P)$ and $\beta(z, P)$ are functions of P alone then the (nonlinear) density dependence in the model is a function of total population size and not of hierarchical rank. If these functions

do not depend on P , then the density dependence is class rank dependent alone. In general, the model allows for a mixture of both extremes.

Rather amazingly, from the complicated m -dimensional models (2.1)–(2.4), one can derive a one dimensional model for total population size, namely,

$$P_{t+1} = \bar{s}(P_t) + \bar{b}(P_t), \quad (2.5)$$

where

$$\bar{s}(P) = \int_0^P \sigma(z, P) dz, \quad \bar{b}(P) = \int_0^P \beta(z, P) dz.$$

Our study of scramble and contest competition, in the following section, is based on this equation.

For more details about the model and the derivation of the equation (2.5) see [7].

3. Scramble and contest models

In a model of pure scramble competition, the model components $\sigma(z, P)$ and $\beta(z, P)$ are functions of P alone. In a model of pure contest competition they are functions of $P - z$. We study models in which both types of competitive interactions are present and σ and β are functions of a linear combination of z and P . Specifically, assume

$$\sigma(z, P) = \alpha_0 s(rz + (1 - r)(P - z))$$

$$\beta(z, P) = \beta_0 b(rz + (1 - r)(P - z))$$

where r is a real number between 0 (contest competition) and 1/2 (scramble competition). The functions s and b satisfy the conditions

$$(H1) \quad b \in C^2(\mathbb{R}_+, \mathbb{R}_+), \quad b(0) = 1, \quad b' < 0, \quad b'' > 0, \quad \lim_{z \rightarrow \infty} b(z) = 0.$$

$$(H2) \quad s \in C^2(\mathbb{R}_+, [0, 1]), \quad s(0) = 1, \quad s' < 0, \quad s'' > 0, \quad \lim_{z \rightarrow \infty} s(z) \geq 0.$$

Note that if $r < 1/2$ then σ and β are increasing functions of z (for fixed population size P). Thus, an individual of higher rank (higher class membership) has an increased survivorship and birth rate.

The quantities $\beta_0 > 0$ and $0 < \alpha_0 < 1$ are the ‘inherent’ birth rate and survival probability of per unit time in the absence of competitive interactions and

$$n = \beta_0 (1 + \alpha_0 + \alpha_0^2 + \dots) = \frac{\beta_0}{1 - \alpha_0}$$

is the ‘inherent net reproductive number’, i.e. the expected number of offspring per individual over its life time [7] (in the absence of intra-specific competition). It has been shown in many discrete and continuous hierarchical models that the dynamics of the total population size depend on n . This parameter will play an important role in our analysis.

Under assumptions (H1) and (H2) we can rewrite the equation (2.5) for P as follows. Let $w = rz + (1 - r)(P - z)$ and write

$$\int_0^P \beta(z, P) dz = \frac{\beta_0}{1 - 2r} \int_{rP}^{(1-r)P} b(w) dw$$

if $r \neq 1/2$ and

$$\int_0^P \beta(z, P) dz = \beta_0 b\left(\frac{P}{2}\right) P$$

if $r = 1/2$. Similar calculations can be performed for $\int_0^P \sigma(z, P) dz$. Letting $\delta(z) = \beta_0 b(z) + \alpha_0 s(z)$, equation (2.5) becomes

$$P_{t+1} = \begin{cases} \frac{1}{1-2r} \int_{rP_t}^{(1-r)P_t} \delta(z) dz, & 0 \leq r < 1/2 \\ \delta\left(\frac{P_t}{2}\right) P_t, & r = 1/2. \end{cases}$$

We rewrite this equation as

$$\begin{aligned} P_{t+1} &= F(r, P_t) P_t \triangleq f(r, P_t) \\ P_0 &\geq 0, \end{aligned} \tag{3.6}$$

where

$$F(r, P) = \begin{cases} \frac{1}{(1-2r)P} \int_{rP}^{(1-r)P} \delta(z) dz, & 0 \leq r < 1/2 \\ \delta\left(\frac{P}{2}\right), & r = 1/2. \end{cases} \tag{3.7}$$

Equation (3.6) is a family of difference equations with parameter r , $0 \leq r \leq 1/2$. Note $f(r, P)$ is a C^2 -function on $[0, 1/2] \times [0, \infty)$ and a C^3 -function on $[0, 1/2) \times [0, \infty)$.

Equation (3.6) has a trivial steady state $P = 0$ for all r . A positive steady state $P^* > 0$ must satisfy $F(r, P) = 1$. Our first goal is to show that under the given assumptions there exists a unique positive steady state for $n > 1$. Note that $\lim_{P \rightarrow 0^+} F(r, P) = \delta(0)$ for $0 \leq r \leq 1/2$, and for $0 \leq r < 1/2$, that

$$\frac{\partial F}{\partial P} = \frac{(1-r)P\delta((1-r)P) - rP\delta(rP) - \int_{rP}^{(1-r)P} \delta(z) dz}{(1-2r)P^2}.$$

Since

$$\int_{rP}^{(1-r)P} \delta(z) dz = \delta(z^*)[(1-r)P - rP]$$

for some $z^* \in (rP, (1-r)P)$ and

$$\delta(z^*)[(1-r)P - rP] > \delta((1-r)P)(1-r)P - \delta(rP)rP,$$

we have

$$\frac{\partial F}{\partial P} < 0, \quad 0 \leq r < \frac{1}{2}.$$

If $r = 1/2$, then

$$\frac{\partial F}{\partial P} = \frac{1}{2} \delta'\left(\frac{P}{2}\right) < 0.$$

We have shown that

$$\frac{\partial F}{\partial P} < 0, \quad 0 \leq r \leq \frac{1}{2}, \quad P \geq 0.$$

Moreover,

$$\lim_{r \rightarrow 1/2^-} \frac{\partial F}{\partial P} = \frac{1}{2} \delta' \left(\frac{P}{2} \right) = \frac{\partial F}{\partial P} \Big|_{(r,P)=(1/2,P)}$$

and $\partial F / \partial P$ is continuous for $0 \leq r \leq 1/2$, $P \geq 0$.

On the other hand if $0 \leq r < 1/2$, it follows from the Mean Value Theorem that

$$\begin{aligned} \lim_{P \rightarrow \infty} F(r, P) &= \lim_{P \rightarrow \infty} \delta(z^*), \quad z^* \in (rP, (1-r)P) \\ &= \lim_{z \rightarrow \infty} \delta(z) \\ &= \lim_{P \rightarrow \infty} F \left(\frac{1}{2}, P \right). \end{aligned}$$

Thus

$$\lim_{P \rightarrow \infty} F(r, P) = \lim_{P \rightarrow \infty} \delta(P) < 1, \quad 0 \leq r \leq \frac{1}{2}.$$

Since $F(r, P)$ is a decreasing function of P and $F(r, 0) = \delta(0)$, we conclude that equation (3.6) has a positive steady state $P^*(r)$ if and only if $\delta(0) > 1$ (i.e. $n > 1$) and that this steady state is unique.

THEOREM 3.1 *The dynamics of equation (3.6) are summarized below.*

- (a) If $n < 1$, then solutions P_t of equation (3.6) satisfy $\lim_{t \rightarrow \infty} P_t = 0$ for $0 \leq r \leq 1/2$.
- (b) If $n > 1$ and $r = 0$, then solutions P_t of equation (3.6) with $P_0 > 0$ converge to $P^*(0)$.
- (c) If $n > 1$ and $0 < r \leq 1/2$, then solutions of equation (3.6) are bounded. Moreover, $P^*(r)$ is locally asymptotically stable if $\delta'(0)P^*(r) > -1/r$.

Proof Clearly $P_t = 0$ for $t \geq 0$ if $P_0 = 0$, and $P_t > 0$ for $t > 0$ if $P_0 > 0$. We may assume $P_0 > 0$.

(a) There exists $z^* \in (rP_t, (1-r)P_t)$ such that

$$P_{t+1} = \begin{cases} \delta(z^*)P_t, & 0 \leq r < \frac{1}{2} \\ \delta\left(\frac{P_t}{2}\right)P_t, & r = \frac{1}{2}. \end{cases}$$

Thus $P_{t+1} < \delta(0)P_t$ for $t \geq 0$ as $\delta' < 0$. Hence $\lim_{t \rightarrow \infty} P_t = 0$ when $n < 1$.

(b) If $n > 1$, then a unique positive steady state $P^*(r)$ exists for equation (3.6). When $r = 0$,

$$f(0, P) = \int_0^P \delta(z) dz \quad \text{and} \quad \frac{\partial f(0, P)}{\partial P} = \delta(P) > 0.$$

Since $\partial F/\partial P < 0$,

$$(P - P^*(0))(f(0, P) - P) = (P - P^*(0))(F(0, P) - 1)P < 0$$

for $0 < P \neq P^*(0)$. Thus if $0 < P < P^*(0)$, then $P_0 < P_1 < P^*(0)$ and (by induction) $\{P_t\}_{t=0}^{\infty}$ is an increasing sequence of real numbers which is bounded above by $P^*(0)$. Thus $\{P_t\}$ converges to a positive steady state by the continuity of $f(0, P)$. We conclude that $\lim_{t \rightarrow \infty} P_t = P^*(0)$. Similarly if $P_0 > P^*(0)$, then $\{P_t\}_{t=0}^{\infty}$ is a decreasing sequence which is bounded below by $P^*(0)$. Thus one can conclude that $\lim_{t \rightarrow \infty} P_t = P^*(0)$ if $P_0 > P^*(0)$, and the proof of (b) is complete.

(c) We first prove that solutions of equation (3.6) are bounded. A calculation yields

$$\frac{\partial f}{\partial r} = \begin{cases} (1-2r)^{-2} \{ -(1-2r)P[\delta((1-r)P) + \delta(rP)] + 2 \int_{rP}^{(1-r)P} \delta(z) dz \}, & 0 \leq r < \frac{1}{2} \\ 0, & r = \frac{1}{2}, \end{cases}$$

and

$$\lim_{r \rightarrow 1/2^-} \frac{\partial f(r, P)}{\partial r} = 0 = \frac{\partial f(r, P)}{\partial r} \Big|_{r=1/2}.$$

Since $\delta' < 0$ and $\delta'' > 0$, it is straightforward to show that

$$2 \int_{rP}^{(1-r)P} \delta(z) dz < (1-2r)P[\delta((1-r)P) + \delta(rP)].$$

It follows that

$$\frac{\partial f}{\partial r} \begin{cases} < 0, & r \in [0, \frac{1}{2}), & P > 0 \\ = 0, & r = \frac{1}{2}, & P \geq 0. \end{cases}$$

Therefore, $P_{t+1} = f(r, P_t) \leq f(0, P_t)$ for $t \geq 0$. Since $(\partial f(0, P)/\partial P) > 0$ for $P \geq 0$ and positive solutions of equation (3.6) converge to $P^*(0)$ when $n > 1$ and $r = 0$, we immediately conclude that solutions of equation (3.6) satisfy $\limsup_{t \rightarrow \infty} P_t \leq P^*(0)$ for any r with $0 < r \leq 1/2$.

We next derive a sufficient condition for the local stability of the positive steady state $P^*(r)$. For simplicity we denote $P^*(r)$ by P^* . Observe that

$$\frac{\partial f}{\partial P} \Big|_{(r, P)=(r, P^*)} = \begin{cases} \frac{1}{1-2r} \{ (1-r)\delta((1-r)P^*) - r\delta(rP^*) \}, & 0 \leq r < \frac{1}{2} \\ \frac{1}{2} \delta'(\frac{P^*}{2}) P^* + 1, & r = \frac{1}{2}, \end{cases}$$

where

$$\frac{(1-r)\delta((1-r)P^*) - r\delta(rP^*)}{1-2r} < \delta((1-r)P^*) < 1$$

and thus

$$\left. \frac{\partial f}{\partial P} \right|_{(r,P)=(r,P^*)} < 1, \quad 0 \leq r \leq \frac{1}{2}.$$

When $0 < r < 1/2$,

$$\frac{(1-r)\delta((1-r)P^*) - r\delta(rP^*)}{1-2r} > r\delta'(z^*)P^* > r\delta'(0)P^*$$

for some $z^* \in (rP^*, (1-r)P^*)$. Thus

$$\left. \frac{\partial f}{\partial P} \right|_{(r,P)=(r,P^*)} > -1$$

if $\delta'(0)P^* > -1/r$.

If $r = 1/2$, then since

$$\left. \frac{\partial f}{\partial P} \right|_{(r,P)=(1/2,P^*)} > \frac{1}{2} \delta' \left(\frac{1}{2} P^* \right) P^*,$$

$P^*(1/2)$ is locally asymptotically stable if $\delta'(0)P^* > -2$. □

Our result in Theorem 3.1 is more complete than that in [17]. In particular, we showed the trivial steady state 0 is globally asymptotically stable when $n < 1$, and when $n > 1$ and $r = 0$, we showed the positive steady state is globally asymptotically stable. We also verified that solutions of the equation are bounded when $n > 1$.

We remark that $P^*(r)$ is locally asymptotically stable when $r > 0$ is sufficiently small since $P^*(0)$ is locally asymptotically stable and $f(r, P)$ is smooth. On the other hand, since $P^*(r)$ is continuous, letting $r \rightarrow 0^+$ in $\delta'(0)P^*(r) > -1/r$, the inequality becomes $\delta'(0)P^*(0) > -\infty$ which is trivially true. Consequently the condition (c) in Theorem 3.1 implies that $P^*(0)$ is locally asymptotically stable.

Recall that $\partial f / \partial P|_{(r,P^*)} < 1$ for $0 < r \leq 1/2$. Therefore, $P^*(r)$ will lose its stability only when $\partial f / \partial P|_{(r,P^*)} > -1$ is violated. It is strongly suspected that a period doubling bifurcation will occur as r increases. An example illustrates this observation. Let $\beta_0 = 20$, $\alpha_0 = 0.7$, $b(z) = e^{-z}$ and $s(z) = e^{-2z}$. Then the total population size equation (3.6) becomes

$$P_{t+1} = \begin{cases} \frac{1}{1-2r} \int_{rP_t}^{(1-r)P_t} (20e^{-z} + 0.7e^{-2z}) dz, & 0 \leq r < 1/2 \\ (20e^{-P_t/2} + 0.7e^{-P_t})P_t, & r = 1/2 \end{cases} \tag{3.8}$$

The bifurcation diagram in figure 1 shows a period doubling cascade to chaos as r increases.

We next turn to a comparison of two forms of intra-specific competition. We first compare equilibrium sizes. Our analysis presented here is the same as that of Xu [17]. Since $F(r, P^*(r)) = 1$ for $0 \leq r \leq 1/2$, we have

$$\frac{\partial F}{\partial r} + \frac{\partial F}{\partial P} \frac{dP^*}{dr} = 0$$

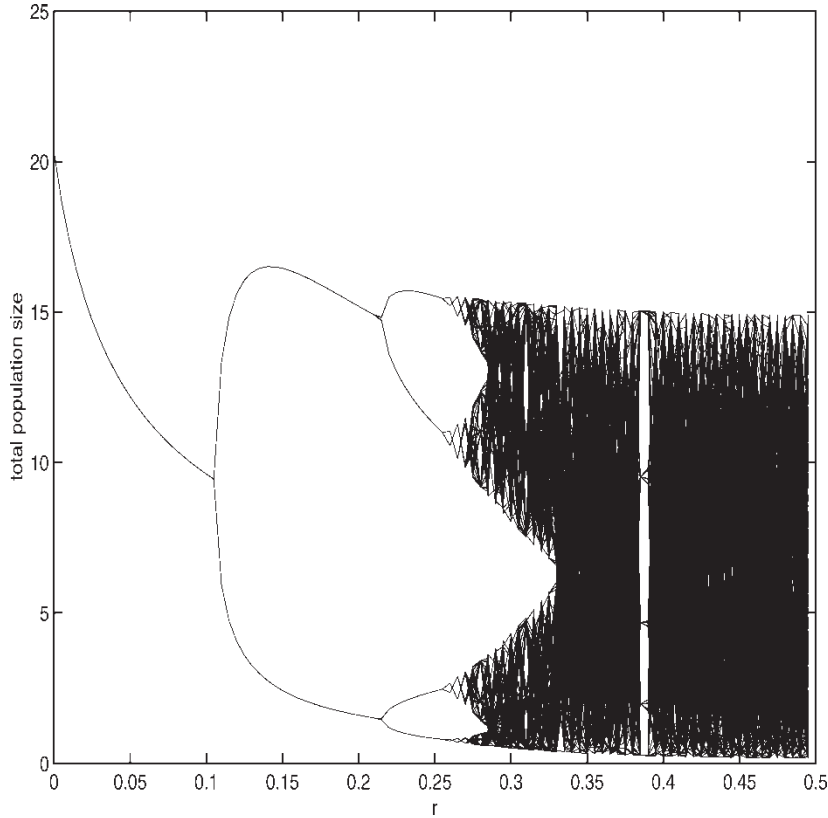


Figure 1. Bifurcation diagram for equation (3.8) using r as a bifurcation parameter. Numerical simulations suggest that the positive steady state is globally asymptotically stable when $r > 0$ is very small and the equation undergoes period doubling route bifurcations to chaos.

and thus

$$\frac{dP^*}{dr} = -\frac{\partial F/\partial r}{\partial F/\partial P}.$$

Recall that $\partial F/\partial P < 0$ for $0 \leq r \leq 1/2$ and $P \geq 0$. We proceed to calculate $\partial F/\partial r$. Since $F = f/P$, it follows from $\partial f/\partial r$ that

$$\frac{\partial F}{\partial r} = \begin{cases} \frac{1}{(1-2r)^2 P} \{ -(1-2r)P[\delta((1-r)P) + \delta(rP)] + 2 \int_r^{(1-r)P} \delta(z) dz \}, & 0 \leq r < \frac{1}{2} \\ 0, & r = \frac{1}{2}. \end{cases}$$

Hence, for $0 \leq r < 1/2$, we have $\partial F/\partial r < 0$, and when $r = 1/2$, $\partial F/\partial r = 0$. Moreover, $\lim_{r \rightarrow 1/2^-} \partial F/\partial r = 0$ for $P \geq 0$, and $\lim_{P \rightarrow 0^+} \partial F/\partial r = 0$ for $0 \leq r \leq 1/2$. Hence $\partial F/\partial r$ is continuous for $0 \leq r \leq 1/2$, $P \geq 0$. Thus $dP^*/dr < 0$ for $0 \leq r < 1/2$. Since dP^*/dr is continuous on $[0, 1/2]$, we have $P^*(0) > P^*(1/2)$, i.e. contest competition has a larger equilibrium size than scramble competition. We summarize our discussion into the following.

THEOREM 3.2 *Let $n > 1$ and $P^*(r)$ denote the positive steady state of equation (3.8). Then $P^*(0) > P^*(1/2)$.*

We next compare equilibrium resilience, a measure of how fast a population will return to its equilibrium if the population is perturbed from its equilibrium P^* . For hyperbolic equilibria it follows from the linearization theory that whether a small perturbation will die out or not depends on

$$\lambda(r) \doteq \left. \frac{\partial f(r, P)}{\partial P} \right|_{P=P^*}.$$

The smaller the magnitude of $\lambda(r)$, the more resilient is the steady state. Notice both P^* and λ are functions of r , and $P^*(r) = 0$ and $\lambda(r) = 1$ for $0 \leq r \leq 1/2$ when $n = 1$. Thus, for $n > 1$ and sufficiently close to 1, $\lambda(r) > 0$ on the interval $0 \leq r \leq 1/2$.

The following theorem demonstrates that a scramble competition leads to a more resilient population than contest competition. (See [17].)

THEOREM 3.3 *Let $n = 1 + \varepsilon$, where $\varepsilon > 0$ is sufficiently small. Then for $0 \leq r \leq 1/2$,*

$$\lambda(r) = 1 - (1 - \alpha_0)\varepsilon + \left(\frac{\delta'(0)}{6} P_1^2 q(r) \right) \varepsilon^2 + O(\varepsilon^3)$$

where $q(r) = r^2 - r + 1$ and $P_1 = -2(1 - \alpha_0)\delta'(0)$.

Proof Since when $n = 1$, $P^*(r) = 0$ and $\lambda(r) = 1$, second order Taylor expansions for P^* and λ around $P^* = 0$ and $\lambda = 1$ are respectively given by

$$P^* = 0 + P_1\varepsilon + \frac{1}{2}P_2\varepsilon^2 + O(\varepsilon^3) \quad \lambda = 1 + \lambda_1\varepsilon + \frac{1}{2}\lambda_2\varepsilon^2 + O(\varepsilon^3),$$

where $P_i, \lambda_i, i = 1, 2$ will be determined below. Since P^* satisfies $F(r, P) = 1$, we have (for $0 \leq r < 1/2$)

$$\int_{rP^*}^{(1-r)P^*} \delta(z) dz = (1 - 2r)P^*.$$

Therefore,

$$\int_{rP^*}^{(1-r)P^*} \left(\delta(0) + \delta'(0)z + \frac{\delta''(0)}{2}z^2 \right) dz = (1 - 2r)P^*$$

and

$$\delta(0) + \frac{\delta'(0)}{2}P^* + \frac{\delta''(0)}{6}P^{*2}(1 - r + r^2) = 1.$$

Let $q(r) \doteq r^2 - r + 1$ and use the expansion for P^* above to obtain

$$\delta(0) - 1 + \frac{\delta'(0)}{2}P_1\varepsilon + \frac{\delta'(0)}{4}P_2\varepsilon^2 + \frac{\delta''(0)}{6}q(r)P_1^2\varepsilon^2 + O(\varepsilon^3) = 0.$$

On the other hand, since $n = 1 + \varepsilon$ and $\delta(0) = \alpha_0 + \beta_0$, we have $\delta(0) - 1 = (1 - \alpha_0)\varepsilon$ and this equation becomes

$$\left(1 - \alpha_0 + \frac{\delta'(0)}{2}P_1 \right) \varepsilon + \frac{\delta'(0)}{4}P_2\varepsilon^2 + \frac{\delta''(0)}{6}P_1^2q(r)\varepsilon^2 + O(\varepsilon^3) = 0.$$

Hence,

$$P_1 = \frac{-2(1 - \alpha_0)}{\delta'(0)}, \quad P_2 = \frac{-8\delta''(0)(1 - \alpha_0)^2}{3[\delta'(0)]^3} q(r).$$

We now use P_1 and P_2 to find λ_1 and λ_2 . For $0 \leq r < 1/2$,

$$\begin{aligned} \lambda(r) &= \frac{1}{1 - 2r} [(1 - r)\delta((1 - r)P^*) - r\delta(rP^*)] \\ &= 1 + (1 - \alpha_0)\varepsilon + \delta'(0) \left(P_1\varepsilon + \frac{P_2}{2}\varepsilon^2 \right) + \frac{\delta''(0)}{2} q(r) \left(P_1\varepsilon + \frac{P_2}{2}\varepsilon^2 \right)^2. \end{aligned}$$

Thus, $1 - \alpha_0 + \delta'(0)P_1 = \lambda_1$ and

$$\frac{\delta'(0)}{2} P_2 + \frac{\delta''(0)}{2} q(r) P_1^2 = \frac{1}{2} \lambda_2.$$

Consequently,

$$\lambda_1 = -(1 - \alpha_0), \quad \lambda_2 = \frac{1}{3} \delta''(0) q(r) P_1^2$$

and

$$\lambda(r) = 1 - (1 - \alpha_0)\varepsilon + \left(\frac{\delta''(0)}{6} P_1^2 q(r) \right) \varepsilon^2 + O(\varepsilon^3)$$

for $0 \leq r < 1/2$.

The case when $r = 1/2$ is more straightforward. Since P^* satisfies $\delta(P/2) = 1$, using the expansions we have

$$(1 - \alpha_0)\varepsilon + \frac{\delta'(0)}{2} P_1\varepsilon + \frac{\delta'(0)}{4} P_2\varepsilon^2 + \frac{\delta''(0)}{8} P_1^2\varepsilon^2 + O(\varepsilon^3) = 0.$$

As a result,

$$P_1 = \frac{-2(1 - \alpha_0)}{\delta'(0)} \quad \delta'(0)P_2 = -\frac{2}{3} q\left(\frac{1}{2}\right) \delta''(0) P_1^2.$$

On the other hand,

$$\begin{aligned} \lambda(1/2) &= 1 + \frac{1}{2} \delta' \left(\frac{P^*}{2} \right) P^* \\ &= 1 + \frac{1}{2} \delta'(0) P^* + \frac{1}{4} \delta''(0) P^{*2} \\ &= 1 + \frac{1}{2} \delta'(0) P_1\varepsilon + \left(\frac{1}{4} \delta'(0) P_2 + \frac{1}{4} \delta''(0) P_1^2 \right) \varepsilon^2. \end{aligned}$$

Therefore,

$$\lambda_1 = -(1 - \alpha_0), \quad \lambda_2 = \frac{1}{3} \delta''(0) q\left(\frac{1}{2}\right) P_1^2$$

and the proof is complete. \square

Since $q'(r) = 2r - 1 < 0$, we see that $\lambda(0) > \lambda(1/2) > 0$ for $n > 1$ sufficiently close to 1. Therefore, when $n > 1$ is sufficiently close to 1, scramble competition is more resilient than contest competition. This conclusion is different from that found in the continuous time models studied in [5,6].

4. An hierarchical model with a dynamic resource

Suppose the intra-specific competition is for a (limiting) resource. In this section, we consider a hierarchical model that includes the dynamics of the resource. We will focus on the case when the resource uptake rate of an individual effects its fertility rate, but not its death rate. Thus, in equation (3.6) we have

$$\sigma(z, P) = \alpha_0, \quad 0 < \alpha_0 < 1.$$

We model the per capita birth rate of the population $\beta(z, P)$ as follows. Let R_t denote the resource abundance at time t . We assume $\beta(z, P)$, is a function of the resource uptake rate for individuals of rank z . In the absence of competition, the resource uptake rate is a function of R that satisfies the following conditions [16]:

$$(H3) \quad u \in C^1(R_+, R_+), \quad u(0) = 0, \quad \text{and} \quad 0 < u'(x) \leq u'(0) \quad \text{for} \quad x \geq 0.$$

With intra-specific competition, the consumption rate of an individual of rank z during one unit of time is decreased by a fraction c which depends on the rank z . Specifically, this consumption rate is

$$u(R_t)c(rz + (1 - r)(P_t - z)),$$

where the competition coefficient c , as a function of its argument, satisfies

$$(H4) \quad c \in C^2(R_+, [0, 1]), \quad c(0) = 1, \quad c' < 0, \quad c'' > 0 \quad \text{and} \quad \lim_{z \rightarrow \infty} c(z) = 0.$$

Under these assumptions, we have

$$\beta(z, P) = \beta_0 u(R_t) c(rz + (1 - r)(P_t - z))$$

where $\beta_0 > 0$ is the birth rate per unit resource per individual. In equation (3.6) we substitute

$$\int_0^{P_t} \beta_0 u(R_t) c(rz + (1 - r)(P_t - z)) dz = \beta_0 u(R_t) B(r, P_t)$$

where

$$B(r, P) \triangleq \int_0^P c(rz + (1 - r)(P - z)) dz.$$

A calculation shows

$$B(r, P) = \begin{cases} \frac{1}{1-2r} \int_{rP}^{(1-r)P} c(z) dz, & 0 \leq r < 1/2 \\ c(\frac{1}{2}P)P, & r = 1/2. \end{cases}$$

For future reference, observe that there exists $z^* \in (rP, (1 - r)P)$ such that $B(r, P) = Pc(z^*)$. Hence

$$B(r, P) \leq P, \quad P \geq 0, \quad 0 \leq r \leq 1/2.$$

Equation (3.6) yields the difference equation

$$P_{t+1} = \beta_0 u(R_t) B(r, P_t) + \alpha_0 P_t,$$

for the dynamics of the total population size P_t . What remains for the specification of the model is an equation for the dynamics of the resource R_t .

To model R_t we assume in the absence of the population the resource is governed by the ‘chemostat’ law $R_{t+1} = (1 - k_0)R_t + k_0R^0$, where $0 < k_0 < 1$ denotes the resource washout and renewal rate, and $R^0 > 0$ is the steady state of the resource. In the presence of the population, we assume consumption occurs first, followed by washout. Since the resource consumed by the total population P is given by $u(R)B(r, P)$, the resource equation becomes

$$R_{t+1} = (1 - k_0)[R_t - u(R_t)B(r, P_t)] + k_0R^0.$$

In summary, the dynamics of the population and the resource are governed by the system.

$$\begin{aligned} P_{t+1} &= \beta_0 u(R_t) B(r, P_t) + \alpha_0 P_t \\ R_{t+1} &= (1 - k_0)[R_t - u(R_t)B(r, P_t)] + k_0R^0, R_0 \geq 0. \end{aligned} \tag{4.9}$$

Note that solutions of the system (4.9) might not remain nonnegative. This is because the resource consumed by the population $u(R_t)B(r, P_t)$ during a unit of time might exceed the available resource level R_t . To deal with this biological constraint, Xu used the positive part of the expression $R_t - u(R_t)B(r, P_t)$ [17].

Following [12], we instead impose the following constraints [15,16].

(H5) There exists a $W > \beta_0 R^0$ and an $\eta \in (0, 1 - k_0)$ such that $u'(0)W \leq \eta$.

Let

$$\Delta = \{(P, R) \in R_+^2 : (1 - k_0)P + \beta_0 R \leq W\}.$$

We show that solutions starting in Δ remain in Δ for all future time, provided $\alpha_0 + k_0 \leq 1$.

PROPOSITION 4.1 *Let $\alpha_0 + k_0 \leq 1$. Then Δ is positively invariant for system (4.9) for $0 \leq r \leq 1/2$.*

Proof Let $(P_0, R_0) \in \Delta$ be given arbitrarily. It is enough (by induction) to show that $(P_1, R_1) \in \Delta$. Clearly $P_1 \geq 0$. If $R_0 > 0$, then our assumptions imply

$$\frac{u(R_0)B(r, P_0)}{R_0} \leq u'(0)B(r, P_0) \leq u'(0)P_0 \leq \frac{\eta}{1 - k_0} < 1,$$

and thus $R_1 > k_0R^0$. The case when $R_0 = 0$ is trivial. Furthermore,

$$\begin{aligned} (1 - k_0)P_1 + \beta_0 R_1 &= (1 - k_0)\alpha_0 P_0 + (1 - k_0)\beta_0 R_0 + \beta_0 k_0 R^0 \\ &\leq (1 - k_0)W + (1 - k_0)P_0(\alpha_0 + k_0 - 1) + \beta_0 k_0 R^0 \\ &\leq W \end{aligned}$$

as $\alpha_0 + k_0 \leq 1$. Therefore Δ is positively invariant for system (4.9). \square

We now know that solutions of equation (4.9) remain nonnegative and bounded. We proceed to discuss asymptotic dynamics. The system (4.9) may be regarded as a parameterized family of difference equations, with parameter $r, 0 \leq r \leq 1/2$. Since

$B(r, 0) = 0$ for $0 \leq r \leq 1/2$, the system always has the trivial steady state $E_0 = (0, R^0)$. Since in the absence of the population the resource level always stabilizes at R^0 ,

$$n \doteq \frac{\beta_0 u(R^0)}{1 - \alpha_0}$$

is the inherent net reproductive number.

A straightforward calculation shows that a positive steady state (P^*, R^*) must satisfy the equation

$$g(P) \doteq u \left(R^0 - \frac{(1 - \alpha_0)(1 - k_0)}{k_0 \beta_0} P \right) \frac{B(r, P)}{P} = \frac{u(R^0)}{n}. \quad (4.10)$$

Let $g(P)$ denote the left hand side of equation (4.10) and

$$\hat{P} \doteq \frac{k_0 \beta_0 R^0}{(1 - \alpha_0)(1 - k_0)}.$$

Then $g(0) = u(R^0)$, $g(\hat{P}) = 0$ and

$$g'(P) = -u'(x) \frac{(1 - \alpha_0)(1 - k_0) B(r, P)}{k_0 \beta_0 P} + u(x) \frac{P \frac{\partial B}{\partial P} - B(r, P)}{P^2},$$

where

$$x \doteq R^0 - \frac{(1 - \alpha_0)(1 - k_0)}{k_0 \beta_0} P.$$

Note that

$$P \frac{\partial B}{\partial P} - B(r, P) = \begin{cases} \frac{1}{1-2r} \{ (1-r)Pc((1-r)P) - rPc(rP) - \int_{rP}^{(1-r)P} c(z)dz \}, & 0 \leq r < 1/2 \\ \frac{1}{2} c'(\frac{P}{2}) P^2, & r = 1/2 \end{cases}$$

and as a result we can conclude that

$$P \frac{\partial B}{\partial P} - B(r, P) < 0, \quad P > 0, \quad 0 \leq r \leq 1/2.$$

Hence $g'(P) < 0$ for $P \geq 0$ and a positive solution $P^*(r)$ of equation (4.10) exists if and only if $n > 1$. Consequently, a positive steady state $E_1 = (P^*(r), R^*(r))$ exists for system (4.9) if and only if $n > 1$, where

$$R^*(r) = R^0 - \frac{(1 - \alpha_0)(1 - k_0)}{k_0 \beta_0} P^*(r) < R^0.$$

This positive steady state is unique (when it exists). A calculation shows $E_1 \in \Delta$. Indeed,

$$(1 - k_0)P^*(r) + \beta_0 R^*(r) = (1 - k_0)P^*(r) \left(1 - \frac{1 - \alpha_0}{k_0} \right) + \beta_0 R^0 \leq \beta_0 R^0 \leq W$$

as $\alpha_0 + k_0 \leq 1$. Thus, E_1 is feasible if $n > 1$.

The Jacobian matrix of the system (4.9) is

$$J = \begin{pmatrix} \alpha_0 + \beta_0 u(R) \frac{\partial B}{\partial P} & \beta_0 u'(R) B(r, P) \\ -(1 - k_0) u(R) \frac{\partial B}{\partial P} & (1 - k_0) [1 - u'(R) B(r, P)] \end{pmatrix},$$

where $\partial B / \partial P$ is evaluated at (r, P) . In particular, since

$$\left. \frac{\partial B}{\partial P} \right|_{P=0} = 1, \quad 0 \leq r \leq 1/2,$$

the Jacobian matrix at $E_0 = (0, R^0)$ is

$$J(E_0) = \begin{pmatrix} \alpha_0 + \beta_0 u(R^0) & 0 \\ -(1 - k_0) u(R^0) & 1 - k_0 \end{pmatrix}.$$

Therefore, E_0 is locally asymptotically stable if $n < 1$, and is unstable if $n > 1$.

In the following, we show that when the inherent net reproductive number n is less than one, the population will inevitably become extinct.

THEOREM 4.2 *Let $\alpha_0 + k_0 \leq 1$. If $n < 1$, then E_0 is globally asymptotically stable for system (4.9) for $0 \leq r \leq 1/2$.*

Proof Since

$$R_{t+1} \leq (1 - k_0) R_t + k_0 R^0$$

for $t \geq 0$, we have $\limsup_{t \rightarrow \infty} R_t \leq R^0$. Hence, for any $\varepsilon > 0$ there exists $t_0 > 0$ such that $R_t \leq R^0 + \varepsilon$ for $t \geq t_0$. We choose $\varepsilon > 0$ such that

$$\frac{\beta_0 u(R^0 + \varepsilon)}{1 - \alpha_0} < 1.$$

As a result,

$$P_{t+1} \leq \beta_0 u(R_t) P_t + \alpha_0 P_t \leq [\alpha_0 + \beta_0 u(R^0 + \varepsilon)] P_t$$

for $t \geq t_0$. Thus, $\lim_{t \rightarrow \infty} P_t = 0$.

It remains to show that $\liminf_{t \rightarrow \infty} R_t \geq R^0$. Notice that for any $\delta > 0$ there exists $t_1 > t_0$ such that $R_t \leq R^0 + \delta$ and $P_t \leq \delta$ for $t \geq t_1$. We choose $\delta > 0$ such that

$$k_0 R^0 - (1 - k_0) u(R^0 + \delta) \delta > 0.$$

Hence,

$$R_{t+1} \geq (1 - k_0) [R_t - u(R_t) P_t] + k_0 R^0 \geq (1 - k_0) [R_t - u(R^0 + \delta) \delta] + k_0 R^0$$

for $t \geq t_1$. Let

$$\hat{x} = k_0 R^0 - (1 - k_0) u(R^0 + \delta) \delta$$

and consider the equation $x_{t+1} = (1 - k_0)x_t + \hat{x}$ for $t \geq t_1$ with $x_{t_1} = R_{t_1}$. Since $\lim_{t \rightarrow \infty} x_t = \hat{x}/k_0$, we have

$$\liminf_{t \rightarrow \infty} R_t \geq R^0 - \frac{1 - k_0}{k_0} u(R^0 + \delta) \delta.$$

Letting $\delta \rightarrow 0^+$, we see that $\liminf_{t \rightarrow \infty} R_t \geq R^0$ and the proof is complete. \square

When $n > 1$, a unique positive steady state (P^*, R^*) exists and its local stability is determined by the Jacobian matrix

$$J(E_1) = \begin{pmatrix} \alpha_0 + \beta_0 u(R^*) \frac{\partial B}{\partial P} & \beta_0 u'(R^*) B(r, P^*) \\ -(1 - k_0) u(R^*) \frac{\partial B}{\partial P} & (1 - k_0) [1 - u'(R^*) B(r, P^*)] \end{pmatrix},$$

where $\partial B / \partial P$ is evaluated at (r, P^*) . When $r = 0$, $\partial B / \partial P = c(P) > 0$ for $P \geq 0$ and in particular

$$\left. \frac{\partial B}{\partial P} \right|_{(r, P) = (0, P^*)} > 0. \quad (4.11)$$

In the following Proposition, we show that (P^*, R^*) is locally asymptotically stable for system (4.9) when $r = 0$.

PROPOSITION 4.3 *Let $\alpha_0 + k_0 \leq 1$. If $n > 1$ and $r = 0$, then the steady state $E_1 = (P^*(0), R^*(0))$ of system (4.9) is locally asymptotically stable.*

Proof Let the corresponding Jacobian matrix be denoted by J . We apply the Jury conditions [1,8]. The eigenvalues λ of J satisfies $|\lambda| < 1$ if and only if

$$|\det J| < 1 \quad \text{and} \quad |\text{tr} J| < 1 + \det J.$$

By equation (4.11)

$$\begin{aligned} \det J &= (1 - k_0) \left[\alpha_0 + \beta_0 u(R^*) \frac{\partial B}{\partial P} - \alpha_0 u'(R^*) B(0, P^*) \right] \\ &\geq (1 - k_0) \left[\alpha_0 + \beta_0 u(R^*) \frac{\partial B}{\partial P} - \alpha_0 u'(0) P^* \right] \\ &\geq (1 - k_0) \left[\alpha_0 - \alpha_0 \frac{\eta}{1 - k_0} + \beta_0 u(R^*) \frac{\partial B}{\partial P} \right] \\ &> 0 \end{aligned}$$

since $0 < \eta < 1 - k_0$, where η is given in (H5). On the other hand,

$$\begin{aligned} \det J - 1 &= (1 - k_0) \left[\alpha_0 + \beta_0 u(R^*) \frac{\partial B}{\partial P} - \alpha_0 u'(R^*) B(0, P^*) \right] - 1 \\ &< (1 - k_0) \left[\alpha_0 + \beta_0 u(R^*) \frac{B(0, P^*)}{P^*} - \alpha_0 u'(R^*) B(0, P^*) - \frac{1}{1 - k_0} \right] \\ &= (1 - k_0) \left[1 - \alpha_0 u'(R^*) B(0, P^*) - \frac{1}{1 - k_0} \right] < 0. \end{aligned}$$

Thus $|\det J| < 1$.

Furthermore,

$$\begin{aligned}
\operatorname{tr} J + \det J + 1 &= \alpha_0 + (2 - k_0)\beta_0 u(R^*) \frac{\partial B}{\partial P} + (1 - k_0)(\alpha_0 + 1) \\
&\quad - (1 + \alpha_0)(1 - k_0)u'(R^*)B(0, P^*) + 1 \\
&> \alpha_0 + (2 - k_0)\beta_0 u(R^*) \frac{\partial B}{\partial P} + (1 - k_0)(\alpha_0 + 1) \\
&\quad - (1 + \alpha_0)(1 - k_0) + 1 \\
&= \alpha_0 + (2 - k_0)\beta_0 u(R^*) \frac{\partial B}{\partial P} + 1 > 0.
\end{aligned}$$

Also

$$\begin{aligned}
\operatorname{tr} J - 1 - \det J &= k_0 \left[\alpha_0 - 1 + \beta_0 u(R^*) \frac{\partial B}{\partial P} \right] \\
&\quad - (1 - k_0)(1 - \alpha_0)u'(R^*)B(0, P^*) \\
&< k_0 \left[\alpha_0 - 1 + \beta_0 u(R^*) \frac{B(0, P^*)}{P^*} \right] \\
&\quad - (1 - k_0)(1 - \alpha_0)u'(R^*)B(0, P^*) \\
&= -(1 - k_0)(1 - \alpha_0)u'(R^*)B(0, P^*) < 0.
\end{aligned}$$

We conclude from the Jury conditions that (P^*, R^*) is locally asymptotically stable. \square

It follows from Proposition 4.3 that $(P^*(r), R^*(r))$ is locally asymptotically stable for equation (4.9) when $r > 0$ is sufficiently small. Moreover, the computations given in the proof of Proposition 4.3 can be applied to any $(P^*(r), R^*(r))$ for which

$$\left. \frac{\partial B}{\partial P} \right|_{(r, P^*(r))} \geq 0.$$

Therefore, $(P^*(r), R^*(r))$ may lose its stability only when

$$\left. \frac{\partial B}{\partial P} \right|_{(r, P^*(r))} < 0.$$

We also note from the proof of Proposition 4.3 that the inequalities $\det J < 1$ and $\operatorname{tr} J - 1 - \det J < 0$ hold for any $r, 0 \leq r \leq 1/2$. Thus, (P^*, R^*) can be unstable only when either $\det J > -1$ or $\operatorname{tr} J + 1 + \det J > 0$ is violated. We illustrate this possibility by means of a numerical example.

Consider

$$u(R) = \frac{R}{1 + R}, \quad c(z) = e^{-z},$$

$R^0 = 1, k_0 = 0.3, \alpha_0 = 0.2$ and $\beta_0 = 150$. Then for $0 \leq r < 1/2$, system (4.9) has the following form

$$P_{t+1} = \frac{150R_t}{(1 + R_t)(1 - 2r)} \int_{rP_t}^{(1-r)P_t} e^{-z} dz + 0.3P_t$$

$$R_{t+1} = 0.7 \left[R_t - \frac{R_t}{(1 + R_t)(1 - 2r)} \int_{rP_t}^{(1-r)P_t} e^{-z} dz \right] + 0.3 \quad P_0, R_0 \geq 0. \quad (4.12)$$

Notice our chosen parameter values imply $n > 1$. Numerical simulations show that the positive steady state of equation (4.12) is unstable and there exists a periodic solution when $r = 0.2$. See figure 2.

Although we have not show that $(P^*(0), R^*(0))$ is globally asymptotically stable when $n > 1$, we can prove that the population does not go extinct when $n > 1$.

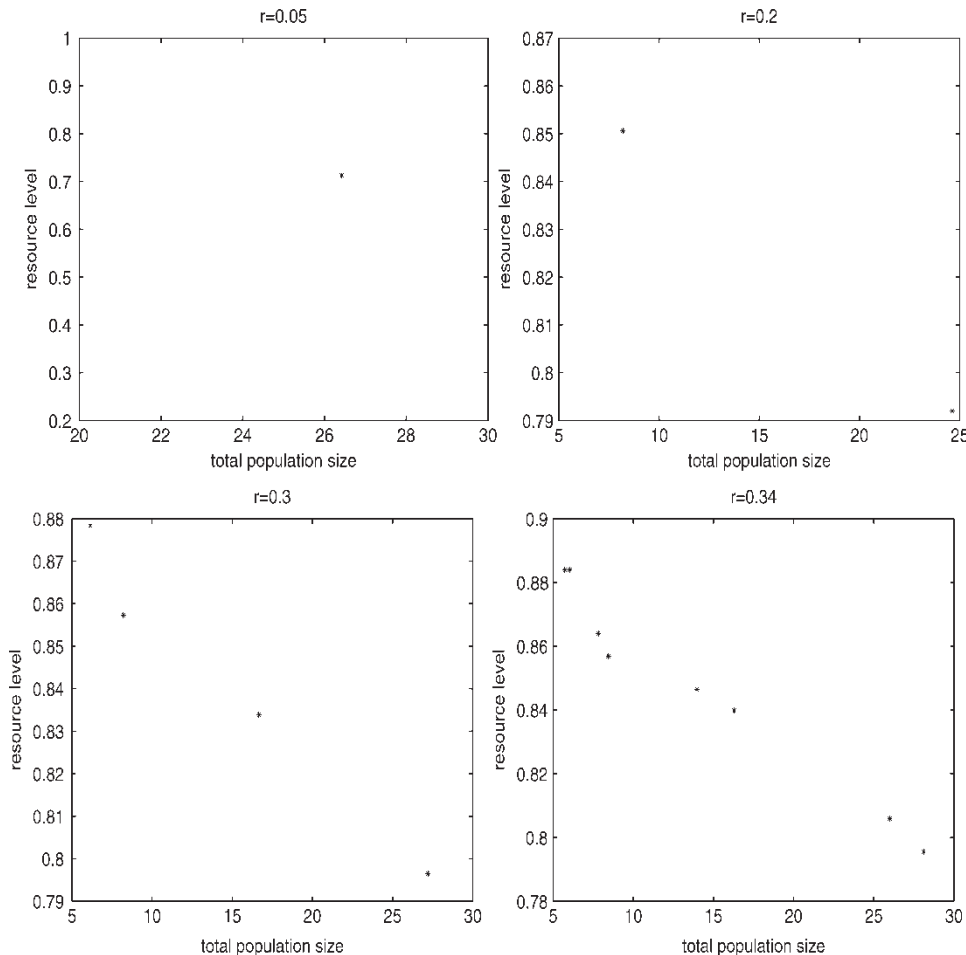


Figure 2. Using r as a bifurcation parameter, we present successive periodic-doubling bifurcations for equation (4.12). It is also shown numerically that the positive steady state is globally asymptotically stable when $r > 0$ is very small.

THEOREM 4.4 *Let $\alpha_0 + k_0 \leq 1$ and $n > 1$. Then for any fixed $r, 0 \leq r \leq 1/2$, system (4.9) is uniformly persistent, i.e. there exists $m > 0$ such that $\liminf_{t \rightarrow \infty} P_{t+1} \geq m$ and $\liminf_{t \rightarrow \infty} R_t \geq m$ for all solutions of equation (4.9) with $(P_0, R_0) \in \Delta$ and $P_0 > 0$.*

Proof Fix any $r, 0 \leq r \leq 1/2$. Since $R_{t+1} \geq k_0 R^0$ for $t \geq 0$, we have $\liminf_{t \rightarrow \infty} R_{t+1} \geq k_0 R^0 > 0$. Let $Y = \{(P, R) \in \Delta : P = 0\}$. Then $\Delta \setminus Y$ is positively invariant. It suffices to show uniform persistence with respect to Y . We apply Theorem 4.1 of Hofbauer and So [11]. Note that equation (4.9) has a global attractor X , since equation (4.9) is point dissipative and asymptotically smooth [9]. Let M be the maximal compact invariant set in Y . We need to verify that M is isolated in X and the stable manifold of M is contained in Y .

Clearly $M = \{E_0\} \subset X$. For $n > 1$, we choose $\varepsilon > 0$ such that

$$\alpha_0 + \beta_0 u(R^0 - \varepsilon) c((1-r)\varepsilon) > 1$$

for $0 \leq r \leq 1/2$. If $\{E_0\}$ were not isolated in X , then there would be a maximal invariant set K in $\overline{B(E_0, \varepsilon)} \cap X$ such that $K \neq \{E_0\}$. Let $P_0 = \sup\{P : (P, R) \in K\}$. Then there exists R_0 such that $(P_0, R_0) \in K$ and $0 < P_0 \leq \varepsilon$. As a result, we have

$$P_1 = [\beta_0 u(R_0) B(r, P_0) + \alpha_0 P_0] \geq [\alpha_0 + \beta_0 u(R^0 - \varepsilon) c((1-r)\varepsilon)] P_0 > P_0$$

for $0 \leq r \leq 1/2$, i.e. $(P_1, R_1) \notin K$ and K is not invariant, a contradiction. Therefore, $\{E_0\}$ must be isolated in X .

We next show that the stable manifold of E_0 lies in the R -axis. Suppose there exists $(P_0, R_0) \in \Delta$ with $P_0 > 0$ such that $\lim_{t \rightarrow \infty} P_t = 0$ and $\lim_{t \rightarrow \infty} R_t = R^0$. Let $\varepsilon > 0$ be chosen arbitrarily as above. Then there exists $t_0 > 0$ such that $R_t > R^0 - \varepsilon$ and $P_t < \varepsilon$ for $t \geq t_0$. Hence,

$$P_{t+1} > \left[\beta_0 u(R^0 - \varepsilon) c((1-r)\varepsilon) + \alpha_0 \right] P_t$$

for $t \geq t_0$ shows that $\lim_{t \rightarrow \infty} P_t = \bar{P} > 0$ exists, a contradiction. Therefore equation (4.9) is uniformly persistent if $n > 1$ \square .

Using an analysis similar to that of $\partial f / \partial r$ in the previous section, we can show that $\partial B / \partial r < 0$ for $0 \leq r < 1/2$, $P > 0$. Since $\partial B / \partial r$ is continuous, it follows from equation (4.10) that $P^*(r_1) > P^*(r_2)$ and consequently $R^*(r_1) < R^*(r_2)$ if $0 \leq r_1 \leq r_2 \leq 1/2$. Therefore, contest competition yields a larger equilibrium size.

THEOREM 4.5 *Let $\sigma_0 + k_0 \leq 1$ and $n > 1$. Then $0 \leq r_1 < r_2 \leq 1/2$ implies $P^*(r_1) > P^*(r_2)$ and $R^*(r_1) < R^*(r_2)$.*

5. Discussion

We investigated the relationship between two forms of intra-specific competition (scramble and contest) by means of a discrete time, discrete class structured model. The model is based on a hierarchy of classes that determines an individual's vital birth and death rates. The resulting high dimensional matrix model becomes tractable through a reduction in dimension that results in an uncoupled equation for the total population size. (For other hierarchical models of intra-specific competition see [3,5–7,10,12,17,18]) Using this model, we study two cases: when the limiting resource is constant and when it varies dynamically. In both cases we determine a quantity n (the inherent net reproductive rate) which determines the

survival of the population. If $n > 1$ the population goes asymptotically extinct. If $n < 1$ there is a positive steady state. We determined conditions under which this steady state is stable. In any case, we showed that contest competition results in a larger steady state. This result is consistent with the main conclusion of Lomnicki [13] that contest competition is more advantageous. However, we also showed (in the case of a constant resource) that the scramble steady state is more resilient.

The models derived in this study contain a parameter r used to connect two extreme forms of intra-specific competition. Consequently, mixed forms of intra-specific competition are also included in the models. For the constant resource model, both per capita birth rate and survival probability are functions of a linear combination of total population size and individual's rank. For the dynamic resource model, the per capita survival rate is assumed to be a constant while the per capita birth rate is a product of resource uptake rate and competition coefficient. In [12] the two forms of competition are characterized by means of two equations and analyses are performed separately. In particular, the per capita survival probability is assumed to be a constant for both the constant and dynamic resource models while the per capita birth rate depends on resource uptake function. It was demonstrated in [12] that population persistence also depends on the inherent net reproductive number. However, it was showed there that concavity of the resource uptake rate as a function of the resource availability is the deciding factor for comparison. Contest competition has a larger equilibrium size than scramble competition if the resource uptake rate is concave down and an opposite conclusion is reached if the resource uptake rate is concave up. The above competition outcome is reversed if equilibrium resilience is used as a mean of comparison.

We therefore conclude from these studies that which form of competition is more advantageous depends not only on how 'advantageous' is defined but also on sub-models proposed, and we suggest Lomnicki's tenet needs a more careful statement. (Also see [5–7,10,12,17].) Moreover, the question concerning the relationship of contest and scramble competition has not been addressed when the steady state is unstable and there is a non-equilibrium attractor.

Acknowledgements

The authors thank the referee for helpful suggestions on improving the manuscript. S. Jang thanks Bing Xu for a copy of her dissertation [17] and also thanks Aziz Yakubu for providing a copy of reference [18] electronically.

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