Survival of the fittest: asymptotic competitive exclusion in structured population and community models

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Abstract. McKendrick-von Foerster physiologically structured partial differential equation models are used to investigate asymptotic competitive exclusion, a nongenetic "survival of the fittest" for ecological morphs which are closed under reproduction. We consider both the age structured and the individual-based age-size structured settings, and allow birth, death, and individual growth rates to be time and density dependent in the general cases. Results suggest a good measure of "ecotypic fitness" is the product βL of the birth rate function β and survivorship function L. Density dependence in mortality that uniformly affects the different morphs does not modify the characteristic behavior.*

1. Introduction

Suppose n ecotypes of a species, or perhaps n species, are competing for a common resource. Assume the ecotypes are closed under reproduction in that offspring always belong to the same ecotype as the parent. The Competitive Exclusion Principle asserts that these ecotypes cannot coexist (e.g. Hallam [4]). Many models have been analyzed to illustrate this principle and its exceptions.

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For example, Hsu et al [8] use equilibria/stability arguments to get competitive exclusion (except for one structurally unstable case) in a chemostat. In other classical competition models, cases of persistence can be demonstrated using the concept of *invasibility* (Hallam [4]). If one species is at a globally stable equilibrium in the absence of the other, the absent species can *invade* if and only if it has a positive growth rate at the equilibrium. Coexistence occurs when each species can invade the other and both are given positive initial densities.

The complexity of some models may preclude analysis of equilibria and invasibility criteria. We investigate competitive exclusion as a nongenetic, non-invasive version of "survival of the fittest" using structured partial differential equation models and find sufficient conditions for the asymptotic domination of the system by the "fittest" ecological morph. Our results suggest a good measure of ecotypic fitness to be βL, the product of the birth rate function β and the survivorship function L.

Let the ith ecotype be modelled with an individual-based age-size structured model of McKendrick-von Foerster type for $i = 1, 2, \ldots, n$:

$$\frac{\partial \rho_i}{\partial t} + \frac{\partial \rho_i}{\partial a} + \sum_{j=1}^{q} \frac{\partial}{\partial m_j}(\rho_i g_{ij}) = -\mu_i \rho_i$$

$$\rho_i(t, 0, \vec{m}_0) = \int_\Omega \int_0^\infty \beta_i(t, a, \vec{m}, P(t))\rho_i(t, a, \vec{m}) da\, d\vec{m} \tag{1}$$

$$\rho_i(0, a, \vec{m}) = \hat{\rho}_i(a, \vec{m})$$

$$P(t) = F(\rho_1(t, \cdot, \cdot), \rho_2(t, \cdot, \cdot), \ldots, \rho_n(t, \cdot, \cdot)).$$

$\rho_i(t, a, \vec{m})$ is the density at time t, age a, and mass vector $\vec{m} = (m_1, m_2, \ldots m_q)$ of the ith ecotype in numbers per unit age per unit mass per unit volume, $dm_j/ds = g_{ij}(t, a, \vec{m}, P(t))$ is the growth rate along a characteristic curve parametrized by s of the jth physiological variable in an individual organism of ecotype i, $\mu_i(t, a, \vec{m}, P(t))$ is the per capita mortality rate, $\beta_i(t, a, \vec{m}, P(t))$ is the birth rate, $\hat{\rho}_i(a, \vec{m})$ is the initial distribution as a function of age and mass, and $P(t)$ is some time-dependent measure of the population or community. $P(t) = \sum_{k=1}^n \int_\Omega \int_0^\infty \rho_k(t, a, \vec{m}) da\, d\vec{m}$, for example, gives the total number of individuals in the population at time t. All functions, including solutions, are assumed to be continuously differentiable and nonnegative on the appropriate nonnegative real cones.

For a derivation of Equation (1) when $q = 1$, see Sinko and Streifer [11]. The equation for $q > 1$ was apparently first employed by Auslander et al [1]. Existence and uniqueness of solutions will not be addressed in this paper; existence proofs for some cases can be found in Li [10] and Tucker and Zimmerman [12].

The ecotypes (or species) are coupled together through density-dependent effects by the possible dependence of birth, growth, and/or mortality rates on

$P(t)$. The common resource for which the ecotypes compete may be food, or some other resource such as space. Hallam et al [5],[6] have applied such a model to *Daphnia* and rainbow trout metapopulations.

We demonstrate the competitive exclusion principle in an asymptotic sense by establishing conditions under which

$$\lim_{t \to \infty} \frac{P_{Ti}(t)}{P_{Tj}(t)} = \lim_{t \to \infty} \frac{\int_\Omega \int_0^\infty \rho_i(t, a, \vec{m}) da\, d\vec{m}}{\int_\Omega \int_0^\infty \rho_j(t, a, \vec{m}) da\, d\vec{m}} = \infty, \tag{2}$$

where $P_{Ti}(t)$ and $P_{Tj}(t)$ are the total numbers of individuals of ecotype i and j, respectively (we will henceforth say "ecotype i dominates ecotype j"). We assume all n ecotypes are initially established and examine the asymptotic composition of the system by determining relative asymptotic behavior of ecotype pairs. If solutions are bounded, all slower growing ecotypes are forced to extinction. Of course, ecotype i may dominate ecotype j while both go to extinction. If solutions are not bounded, Equation (2) simply describes the relative asymptotic composition of the pair; both ecotypes might in fact be growing.

In Section 2 we first consider the linear age structured model and then progress to various cases of time and density dependence in the birth and death rates. In Section 3 we derive analogous results for the age-size structured model.

2. The age structured model

The age structured model consists of n partial differential equations of the form

$$\frac{\partial \rho_i}{\partial t} + \frac{\partial \rho_i}{\partial a} = -\mu_i(t, a, P(t))\rho_i$$

$$\rho_i(t, 0) = \int_0^A \beta_i(t, a, P(t))\rho_i(t, a) da \tag{3}$$

$$\rho_i(0, a) = \hat{\rho}_i(a),$$

$i = 1, 2, \ldots, n$. Here $P(t) = F(\rho_1(t, \cdot), \rho_2(t, \cdot), \ldots, \rho_n(t, \cdot))$ couples the ecotypes in birth and mortality rates, and A is assumed to be the maximum age attainable by an individual of any ecotype.

The method of characteristics for systems of quasi-linear partial differential equations with the same principle part (Courant and Hilbert [2]) yields the

system

$$\frac{dt}{ds} = 1$$

$$\frac{da}{ds} = 1 \tag{4}$$

$$\frac{d\rho_i}{ds} = -\mu_i(t, a, P(t))\rho_i(t, a),$$

and integration of Equations (4) gives

$$\rho_i(t, a) = \begin{cases} \rho_i(t - a, 0)e^{-\int_0^a \mu_i(t-a+\alpha, \alpha, P(t-a+\alpha))d\alpha} & \text{if } t \geq a \\ \rho_i(0, a - t)e^{-\int_{a-t}^a \mu_i(t-a+\alpha, \alpha, P(t-a+\alpha))d\alpha} & \text{if } t < a. \end{cases}$$

The survivorship $L_i(t, a, P) = e^{-\int_0^a \mu_i(t-a+\alpha, \alpha, P(t-a+\alpha))d\alpha}$ is the probability that an organism born at time $t - a$ survives until age a. $M_i(t, a, P) = e^{-\int_{a-t}^a \mu_i(t-a+\alpha, \alpha, P(t-a+\alpha))d\alpha}$ is the probability that an organism survives until age a, given its survival at age $a - t$ and time 0.

Case 1: $\beta_i = \beta_i(a)$ *and* $\mu_i = \mu_i(a)$

In this case, the equations are linear and uncoupled. The asymptotic behavior is well known (see Frauenthal [3]):

$$\lim_{t \to \infty} \rho_i(t, a)e^{-\lambda_i t} = C_i(a) > 0.$$

The eigenvalue λ_i is the unique real root of the characteristic equation $\Delta_i(\lambda) = 1$, where

$$\Delta_i(\lambda) = \int_0^A e^{-\lambda a}\beta_i(a)L_i(a)da,$$

and

$$L_i(a) = e^{-\int_0^a \mu_i(\alpha)d\alpha}.$$

Theorem 1. *If* $\beta_1(a)L_1(a) \geq \beta_2(a)L_2(a)$ *for all* $a \in [0, A]$ *with the strict inequality holding for at least one a in* $[0, A]$, *then ecotype* 1 *dominates ecotype* 2.

Proof. For all $\lambda \in \mathbb{R}$ and $a \in [0, A]$, $e^{-\lambda a}\beta_1(a)L_1(a) \geq e^{-\lambda a}\beta_2(a)L_2(a)$ with the strict inequality holding for at least one $a \in [0, A]$. Thus,

$$\Delta_1(\lambda) = \int_0^A e^{-\lambda a}\beta_1(a)L_1(a)da > \int_0^A e^{-\lambda a}\beta_2(a)L_2(a)da = \Delta_2(\lambda)$$

for all $\lambda \in \mathbb{R}$. Let λ_i be the unique real root of the characteristic equation $\Delta_i(\lambda) = 1$. Because each Δ_i is monotonically decreasing in λ, $\lambda_1 > \lambda_2$.

Since $C_i(a)$ is a continuous function of a, $\rho_i(t, a)e^{-\lambda_i t} \to C_i(a)$ uniformly in a on $[0, A]$. Thus,

$$\lim_{t \to \infty} \frac{P_{T1}(t)e^{-\lambda_1 t}}{P_{T2}(t)e^{-\lambda_2 t}} = \lim_{t \to \infty} \frac{\int_0^A \rho_1(t, a)e^{-\lambda_1 t}\, da}{\int_0^A \rho_2(t, a)e^{-\lambda_2 t}\, da}$$

$$= \frac{\int_0^A C_1(a)\, da}{\int_0^A C_2(a)\, da} > 0,$$

and so

$$\lim_{t \to \infty} \frac{P_{T1}(t)}{P_{T2}(t)} = \infty.$$

In particular, $\frac{P_{T1}(t)}{P_{T2}(t)}$ is asymptotic to $e^{(\lambda_1 - \lambda_2)t}$.   □

Lemma. *Let $f \in C(\mathbb{R})$, $x \in C^1(\mathbb{R})$, and x be positive and nonincreasing. If $\int_a^t f(s)\, ds > 0$ for all $t > a$, then $\int_a^t x(s)f(s)\, ds > 0$ for all $t > a$.*

Proof. Integration by parts yields

$$\int_a^t x(s)f(s)\, ds = x(t) \int_a^t f(s)\, ds - \int_a^t x'(s) \int_a^s f(u)\, du\, ds,$$

and thus $\int_a^t x(s)f(s)\, ds \geq x(t) \int_a^t f(s)\, ds > 0$.   □

Theorem 1 compares the fitness of ecotype 1 and ecotype 2 at every age. It is natural to hope that some measure of average fitness will instead suffice. The following theorem weakens the fitness hypothesis of Theorem 1, but does so at the cost of an extra hypothesis.

Theorem 2. *If $\lambda_1 \geq 0$ and $\int_0^a \beta_1(\alpha)L_1(\alpha)\, d\alpha > \int_0^a \beta_2(\alpha)L_2(\alpha)\, d\alpha$ for all $a \in (0, A]$, then ecotype 1 dominates ecotype 2.*

Proof. If $\lambda_2 < 0$ the conclusion is obvious, so we may suppose $\lambda_2 \geq 0$. For $\lambda \geq 0$, $x(\alpha) = e^{-\lambda \alpha}$ is a positive, nonincreasing function in C^1. For all $a \in (0, A]$, $\int_0^a [\beta_1(\alpha)L_1(\alpha) - \beta_2(\alpha)L_2(\alpha)]\, d\alpha > 0$, and so by the lemma, $\int_0^a e^{-\lambda \alpha}[\beta_1(\alpha)L_1(\alpha) - \beta_2(\alpha)L_2(\alpha)]\, d\alpha > 0$ for all $a \in (0, A]$. In particular, $\int_0^A e^{-\lambda \alpha}\beta_1(\alpha)L_1(\alpha)\, d\alpha > \int_0^A e^{-\lambda \alpha}\beta_2(\alpha)L_2(\alpha)\, d\alpha$ for all $\lambda \geq 0$, and so $\lambda_1 > \lambda_2$. The conclusion follows as in the proof of Theorem 1.   □

Thus, ecotype 1 dominates if it is not declining and its net reproduction up to age a exceeds that of ecotype 2 at every age.

Example 1. At first glance, one might conjecture that if $R_{10} = \int_0^A \beta_1(a)L_1(a)da$ $> \int_0^A \beta_2(a)L_2(a)da = R_{20}$, that is, if the net reproduction over a lifetime of ecotype 1 exceeds that of ecotype 2, then ecotype 1 must dominate ecotype 2. The following counterexample uses step functions; continuous functions can be chosen close enough to the step functions to supply the same result.

Let $\mu_1 \equiv \mu_2 \equiv 0$ (so $L_1 \equiv L_2 \equiv 1$), and consider the β_i's defined as

$$\beta_1(a) = \begin{cases} 4.5 & 3 \le a \le 4 \\ 0 & \text{otherwise} \end{cases}, \quad \beta_2(a) = \begin{cases} 1 & 0 \le a \le 4 \\ 0 & \text{otherwise} \end{cases}.$$

Then $R_{10} = 4.5 > 4 = R_{20}$, $\lambda_1 \simeq 0.44$, and $\lambda_2 \simeq 1$. This shows that small numbers of births early in life may compound faster than a large peak of births later on.

Note, however, that if $\lambda_1 = 0$ and $R_{10} > R_{20}$, then $\lambda_2 < 0$, so ecotype 1 dominates ecotype 2. From an invasibility perspective, $\lambda_2 < 0$ implies ecotype 2 cannot invade if the initial distributions of the ecotypes are assumed to be the stable age distributions $C_i(a)$. Otherwise, transient dynamics might allow ecotype 2 to invade even though its dominant eigenvalue is negative.

Example 2. This example illustrates that the condition $\int_0^a \beta_1(\alpha)L_1(\alpha)d\alpha > \int_0^a \beta_2(\alpha)L_2(\alpha)d\alpha$ for all $a \in (0, A]$ does not in general guarantee $\lambda_1 > \lambda_2$. Let the β_i's be defined as

$$\beta_1(a) = \begin{cases} 1 & 0 \le a \le 4 \\ 0 & \text{otherwise} \end{cases}, \quad \beta_2(a) = \begin{cases} 6 & 1 \le a \le 2 \\ 0 & \text{otherwise} \end{cases},$$

and let $\mu_1 \equiv \mu_2 \equiv 2$, so that $L_1(a) = L_2(a) = e^{-2a}$. Then $\int_0^a \beta_1(\alpha)L_1(\alpha)d\alpha > \int_0^a \beta_2(\alpha)L_2(\alpha)d\alpha$ for all $a \in (0, \infty)$, and yet $\lambda_1 \simeq -1 < -0.7 \simeq \lambda_2$.

In summary, ecotype 1 dominates when any one of the following is true:
1. $\beta_1(a)L_1(a) \ge \beta_2(a)L_2(a)$ for all $a \in [0, A]$, with the strict inequality holding for at least one $a \in [0, A]$;
2. $\lambda_1 \ge 0$ and $\int_0^a \beta_1(\alpha)L_1(\alpha)d\alpha > \int_0^a \beta_2(\alpha)L_2(\alpha)d\alpha$ for all $a \in (0, A]$;
3. $\lambda_1 = 0$ and $\int_0^A \beta_1(\alpha)L_1(\alpha)d\alpha > \int_0^A \beta_2(\alpha)L_2(\alpha)d\alpha$.

Case 2: $\beta_i = \beta_i(a)$, and $\mu_i = \sigma_i(a) + \nu(t, P(t))$

In this case we will see that time and density dependent mortality assessed uniformly across ecotypes does not influence the outcome of competition. The following lemma, which is used to prove Theorem 3, may be found in Karev [9].

Lemma. $\rho_i(t, a) = q_i(t, a)u(t)$ *is the solution to*

$$\frac{\partial \rho_i}{\partial t} + \frac{\partial \rho_i}{\partial a} = -(\sigma_i(a) + \nu(t, P(t)))\rho_i$$

$$\rho_i(t, 0) = \int_0^A \beta_i(a)\rho_i(t, a)da \tag{5}$$

$$\rho_i(0, a) = \hat{\rho}_i(a),$$

where $q_i(t, a)$ is the solution to

$$\frac{\partial q_i}{\partial t} + \frac{\partial q_i}{\partial a} = -\sigma_i(a)q_i$$

$$q_i(t, 0) = \int_0^A \beta_i(a)q_i(t, a)da \tag{6}$$

$$q_i(0, a) = \hat{\rho}_i(a)$$

and $u(t)$ is the solution to

$$\frac{du}{dt} = -u(t)\nu(t, Q(t))$$

$$u(0) = 1 \tag{7}$$

$$Q(t) = F(u(t)q_1(t, \cdot), u(t)q_2(t, \cdot), \ldots, u(t)q_n(t, \cdot)). \qquad \square$$

Theorem 3. *Suppose $\mu_i = \sigma_i(a) + \nu(t, P(t))$ for $i = 1, 2$. Let ρ_i and q_i be the solutions to Equations (5) and (6), respectively. Then*

$$\lim_{t \to \infty} \frac{\int_0^A \rho_1(t, a)da}{\int_0^A \rho_2(t, a)da} = \lim_{t \to \infty} \frac{\int_0^A q_1(t, a)da}{\int_0^A q_2(t, a)da}. \qquad \square$$

Let ρ_i be the solution to Equation (5), and

$$L_i(t, a, P) = \exp\left\{-\int_0^a [\sigma_i(\alpha) + \nu(t - a + \alpha, P(t - a + \alpha))]d\alpha\right\}.$$

Theorem 4. *If $\beta_1(a)L_1(t, a, P) \geq \beta_2(a)L_2(t, a, P)$ for all $t \in [0, \infty)$ and $a \in [0, A]$ with the strict inequality holding for at least one pair (t, a), then ecotype 1 dominates ecotype 2.*

Proof. For all $a \in [0, A]$, $\beta_1(a)e^{-\int_0^a \sigma_1(\alpha)d\alpha} \geq \beta_2(a)e^{-\int_0^a \sigma_2(\alpha)d\alpha}$ with the strict inequality holding for at least one $a \in [0, A]$. By Theorems 1 and 3, ecotype 1 dominates ecotype 2. $\qquad \square$

Even though the survivorships $L_i(t, a, P)$ depend on the solutions to the partial differential equations, Theorem 4 demonstrates that $\beta_i L_i$, which could be measured empirically, is still the appropriate measure of ecotypic fitness.

Case 3: $\beta_i = \beta_i(a)$ and $\mu_i = \mu_i(t, a)$; or $\beta_i = \beta_i(t, a)$ and $\mu_i = \mu_i(a)$

Theorem 5 (Induction on closed, bounded-below subsets of $\mathbb{R}$). (Henson and Hallam [7]). *Let Q be a proposition and "$Q(t)$" mean "$Q(t)$ is true." Suppose $K \subset \mathbb{R}$ is closed and bounded below in $\mathbb{R}$, the truth set $S = \{t \in \mathbb{R} | Q(t)\}$ is open in $\mathbb{R}$, and for all $t \in K$, we have $Q(t)$ whenever $Q(x)$ for all $x \in K$ such that $x < t$. Then*

$$\forall t \in K (Q(t)). \qquad \square$$

Let $L_i(t, a) = e^{-\int_0^a \mu_i(t-a+\alpha, \alpha) d\alpha}$ for $t \geq a$ and $M_i(t, a) = e^{-\int_{a-t}^a \mu_i(t-a+\alpha, \alpha) d\alpha}$ for $t < a$, $i = 1, 2$.

Theorem 6. *If there exists $k > 1$ such that*
1) $\beta_1(a)L_1(t, a) \geq k^a \beta_2(a)L_2(t, a) > 0$ *for all* $a \in [0, A]$ *and* $t \in [a, \infty)$;
2) $\hat{\rho}_1(a - \alpha)\beta_1(a)M_1(\alpha, a) \geq k^a \hat{\rho}_2(a - \alpha)\beta_2(a)M_2(\alpha, a)$ *for all* $a \in [0, A]$ *and* $\alpha \in [0, a]$; *and*
3) $\hat{\rho}_1(0) > \hat{\rho}_2(0)$;
then ecotype 1 dominates ecotype 2.

Proof. Continuously extend $\rho_1(t, 0)$ and $\rho_2(t, 0)$ to all of $\mathbb{R}$ by defining $\rho_i(t, 0) = \rho_i(0, 0)$ for $t < 0$. Then the truth set $\{t \in \mathbb{R} | \rho_1(t, 0) > k^t \rho_2(t, 0)\}$ is open in $\mathbb{R}$. Let $T \in [0, \infty)$. If $T = 0$, then $\rho_1(T, 0) > k^T \rho_2(T, 0)$ by assumption 3.

Otherwise, assume $\rho_1(t, 0) > k^t \rho_2(t, 0)$ for all $t \in [0, T)$. We will show $\rho_1(T, 0) > k^T \rho_2(T, 0)$, and then apply Theorem 5.

If $T \leq A$,

$$\rho_1(T, 0) = \int_0^A \beta_1(a)\rho_1(T, a) da$$

$$= \int_0^T \beta_1(a)\rho_1(T - a, 0)L_1(T, a) da$$

$$+ \int_T^A \beta_1(a)\hat{\rho}_1(a - T)M_1(T, a) da$$

$$> \int_0^T \beta_2(a)k^{T-a}\rho_2(T - a, 0)k^a L_2(T, a) da$$

$$+ \int_T^A \beta_2(a)k^T \hat{\rho}_2(a - T)M_2(T, a) da$$

$$= k^T \int_0^T \beta_2(a)\rho_2(T,a)da + k^T \int_T^A \beta_2(a)\rho_2(T,a)da$$

$$= k^T \rho_2(T,0).$$

(If $T > A$, it is not necessary to split the renewal integral into two integrals.) Thus, $\rho_1(t,0) > k^t\rho_2(t,0)$ for all $t \in [0,\infty)$; and for each $a \in [0,A]$,

$$\lim_{t\to\infty} \frac{\rho_1(t,a)}{\rho_2(t,a)} = \lim_{t\to\infty} \frac{\rho_1(t-a,0)L_1(t,a)}{\rho_2(t-a,0)L_2(t,a)}$$

$$\geq \lim_{t\to\infty} k^{t-a}k^a\frac{\beta_2(a)}{\beta_1(a)}$$

$$= \infty.$$

Since the β_i's are positive and continuous, $\frac{\beta_2(a)}{\beta_1(a)}$ attains a positive minimum value on $[0,A]$, so the limits converge uniformly in a. Thus,

$$\lim_{t\to\infty} \frac{P_{T1}(t)}{P_{T2}(t)} = \lim_{t\to\infty} \frac{\int_0^A \rho_1(t,a)da}{\int_0^A \rho_2(t,a)da} = \infty. \qquad \Box$$

Now suppose $\beta_i = \beta_i(t,a)$ and $\mu_i = \mu_i(a)$. The analogous theorem does not require the β_i's to be positive:

Theorem 7. *If there exists $k > 1$ such that*
1) $\beta_1(t,a)L_1(a) \geq k^a\beta_2(t,a)L_2(a)$ *for all $a \in [0,A]$ and $t \in [a,\infty)$;*
2) $\hat{\rho}_1(a-\alpha)\beta_1(\alpha,a)M_1(a) \geq k^\alpha\hat{\rho}_2(a-\alpha)\beta_2(\alpha,a)M_2(a)$ *for all $a \in [0,A]$ and $\alpha \in [0,a]$; and*
3) $\hat{\rho}_1(0) > \hat{\rho}_2(0)$;
then ecotype 1 dominates ecotype 2.

Proof. As in the proof of Theorem 6, $\rho_1(t,0) > k^t\rho_2(t,0)$ for all $t \in [0,\infty)$. Thus,

$$\lim_{t\to\infty} \frac{\rho_1(t,a)}{\rho_2(t,a)} = \lim_{t\to\infty} \frac{\rho_1(t-a,0)L_1(a)}{\rho_2(t-a,0)L_2(a)} \geq \lim_{t\to\infty} k^{t-a}\frac{L_1(a)}{L_2(a)} = \infty,$$

and so the conclusion follows by a uniform convergence argument. $\qquad \Box$

Theorems 6 and 7 can be used to compare the asymptotic behavior of nonlinear models to that of linear ones if the proper inequalities hold. If the theorems are applied to two linear models, there is a relationship between k and the dominant eigenvalues:

$$\frac{C_1(a)}{C_2(a)} = \lim_{t \to \infty} \frac{\rho_1(t,a)e^{-\lambda_1 t}}{\rho_2(t,a)e^{-\lambda_2 t}} \geq \lim_{t \to \infty} (ke^{\lambda_2 - \lambda_1})^t \frac{\beta_2(a)}{\beta_1(a)},$$

so $\lambda_2 + \ln k \leq \lambda_1$.

Case 4: $\beta_i = \beta_i(t,a,P(t))$, and $\mu_i = \mu_i(t,a,P(t))$

In this case, birth and mortality rates are functions of the total population measure P. Notice the survivorships $L_i(t,a,P)$ and $M_i(t,a,P)$ depend not only on $P(t)$, but on the segments $P([t-a,t])$ in the case of L_i, and $P([0,t])$ in the case of M_i. Although βL is still the measure of fitness and the proofs proceed as in the previous two theorems, we avoid stating assumptions that depend on the solution, and in so doing we destroy the trade-off between birth rate and survivorship.

Theorem 8. *If there exists $k > 1$ such that*
1) $\beta_1(t,a,p) \geq k^a \beta_2(t,a,p)$ *for all* $t, p \in [0, \infty)$ *and* $a \in [0, A]$;
2) $\mu_1(t,a,p) \leq \mu_2(t,a,p)$ *for all* $t, p \in [0, \infty)$ *and* $a \in [0, A]$;
3) $\hat{\rho}_1(a-\alpha) \geq k^{a-\alpha} \hat{\rho}_2(a-\alpha)$ *for all* $a \in [0, A]$ *and* $\alpha \in [0, a]$ *with the strict inequality holding for* $a = \alpha$;
then ecotype 1 dominates ecotype 2.

Proof. By 2), $L_1(t,a,P) \geq L_2(t,a,P)$ for all $a \in [0, A]$ and $t \in [a, \infty)$, and $M_1(t,a,P) \geq M_2(t,a,P)$ for all $a \in [0, A]$ and $t \in [0, a]$. Thus, by 1) and 3), $\beta_1(t,a,P(t))L_1(t,a,P) \geq k^a \beta_2(t,a,P(t))L_2(t,a,P)$ for all $a \in [0, A]$ and $t \in [a, \infty)$; and $\hat{\rho}_1(a-\alpha)\beta_1(\alpha,a,P(\alpha))M_1(\alpha,a,P) \geq k^a \hat{\rho}_2(a-\alpha)\beta_2(\alpha,a,P(\alpha))M_2(\alpha,a,P)$ for all $a \in [0, A]$ and $\alpha \in [0, a]$. Also, $\hat{\rho}_1(0) > \hat{\rho}_2(0)$ by 3).

By the same argument as in the proof of Theorem 6, $\rho_1(t,0) > k^t \rho_2(t,0)$ for all $t \in [0, \infty)$. Then for each $a \in [0, A]$,

$$\lim_{t \to \infty} \frac{\rho_1(t,a)}{\rho_2(t,a)} = \lim_{t \to \infty} \frac{\rho_1(t-a,0)L_1(t,a,P)}{\rho_2(t-a,0)L_2(t,a,P)}$$

$$\geq \lim_{t \to \infty} k^{t-a}$$

$$= \infty.$$

The last (and hence first) limit is uniform in a on $[0, A]$, so

$$\lim_{t \to \infty} \frac{P_{T1}(t)}{P_{T2}(t)} = \lim_{t \to \infty} \frac{\int_0^A \rho_1(t, a)da}{\int_0^A \rho_2(t, a)da} = \infty. \qquad \square$$

3. The age-size structured model

We now present analogues of the main results of Section 2 using an age-size structured model with one mass variable:

$$\frac{\partial \rho_i}{\partial t} + \frac{\partial \rho_i}{\partial a} + \frac{\partial}{\partial m}(\rho_i g_i) = -\mu_i(t, a, m, P(t))\rho_i$$

$$\rho_i(t, 0, m_0) = \int_0^M \int_0^A \beta_i(t, a, m, m_0, P(t))\rho_i(t, a, m)da\, dm \qquad (8)$$

$$\rho_i(0, a, m) = \hat{\rho}_i(a, m)$$

$$P(t) = F(\rho_1(t, \cdot, \cdot), ..., \rho_n(t, \cdot, \cdot)),$$

where $g_i = g_i(t, a, m, P(t))$.

In Equation (1), all newborns were assumed to have the same birth size $\vec{m}_0$. If mass increases monotonically with age, such a model is equivalent to an age structured model. Even if mass and age are not one-to-one, mass can be parametrized by age and time, and so all the results of Section 2 still hold with a few modifications. In Equation (8), however, newborn size m_0 can take on any value in the mass range $[0, M]$. We will assume an organism of age a and mass m gives birth to newborns within this continuous range of sizes. $\beta_i(t, a, m, m_0, P(t))$ will denote the rate at time t at which an organism of age a and mass m gives birth to newborns of size m_0. We also assume that given an organism of age a and mass m at time t, its unique size $m_0(t, a, m)$ at birth can be determined (characteristic curves do not intersect). If an organism born at time $t - a$ has birth size m_0, its unique mass $m(t - a, a, m_0)$ at age a and time t is determined.

Suppose the system consists of 2 ecotypes. Because in general the ecotypic individual growth rates g_1, g_2 are distinct, the mass variable m (a function of age and time) is different in each ecotype. We will denote them by m_1 and m_2, respectively. In particular, we can no longer directly use the method of characteristics, for the principle parts

$$\frac{\partial \rho_i}{\partial t} + \frac{\partial \rho_i}{\partial a} + g_i \frac{\partial \rho_i}{\partial m_i}$$

of the equations are not the same. Hence, we extend each three dimensional distribution into a four dimensional distribution

$$\frac{\partial \rho_i}{\partial t} + \frac{\partial \rho_i}{\partial a} + \frac{\partial}{\partial m_1}(\rho_i g_1) + \frac{\partial}{\partial m_2}(\rho_i g_2) = -\mu_i(t, a, m_i, P(t))\rho_i$$

$$\rho_i(t, 0, m_{10}, m_{20}) =$$

$$\int_0^M \int_0^M \int_0^A \tilde{\beta}_i(t, a, m_i, m_{10}, m_{20}, P(t))\rho_i(t, a, m_1, m_2)da\,dm_1\,dm_2 \qquad (9)$$

$$\rho_i(0, a, m_1, m_2) = \hat{\rho}_i(a, m_1, m_2)$$

$$P(t) = \bar{F}(\rho_1(t, \cdot, \cdot, \cdot), \rho_2(t, \cdot, \cdot, \cdot)),$$

where $g_i = g_i(t, a, m_i, P(t))$, so the density of each ecotype is expressed per unit mass of the other ecotype.

Model (9) can be reduced to the original model because $q_i(t, a, m_i) = \int_0^M \rho_i(t, a, m_1, m_2)dm_j$, $j \neq i$, is the solution to Equation (8) under the following assumptions:

1. $\hat{q}_i(a, m_i) = \int_0^M \hat{\rho}_i(a, m_1, m_2)dm_j$, $i \neq j$;
2. $F(\int_0^M \rho_1(t, \cdot, \cdot, m_2)dm_2, \int_0^M \rho_2(t, \cdot, m_1, \cdot)dm_1) = \bar{F}(\rho_1(t, \cdot, \cdot, \cdot), \rho_2(t, \cdot, \cdot, \cdot))$;
3. $g_j = 0$ whenever $m_j = M$ or $m_j = 0$; and
4. $\tilde{\beta}_i(t, a, m_i, m_{10}, m_{20}, P(t))$, the rate at which newborns of ecotype i are started on the characteristic curve that has initial mass values of m_{10} and m_{20}, is given by

$$\tilde{\beta}_i = \beta_i(t, a, m_i, m_{i0}, P(t))D_i(m_{j0}), \quad i \neq j, \quad \text{with} \quad \int_0^M D_i(m_{j0})dm_{j0} = 1.$$

Each equation can be written with the same principle part:

$$\frac{\partial \rho_i}{\partial t} + \frac{\partial \rho_i}{\partial a} + g_1\frac{\partial \rho_i}{\partial m_1} + g_2\frac{\partial \rho_i}{\partial m_2} = -(\mu_i + \frac{\partial g_1}{\partial m_1} + \frac{\partial g_2}{\partial m_2})\rho_i. \qquad (10)$$

The extra "mortality" terms on the right hand side are "elastic" terms for the distribution in the m_1 and m_2 directions, caused by changes in the population density due to the nonlinear growth of mass in time. The equations for the characteristic curves are now

$$\frac{dt}{ds} = 1 \qquad (11)$$

$$\frac{da}{ds} = 1$$

$$\frac{dm_1}{ds} = g_1(t, a, m_1, P(t))$$

$$\frac{dm_2}{ds} = g_2(t, a, m_2, P(t))$$

$$\frac{d\rho_1}{ds} = -(\mu_1 + \frac{\partial g_1}{\partial m_1} + \frac{\partial g_2}{\partial m_2})\rho_1$$

$$\frac{d\rho_2}{ds} = -(\mu_2 + \frac{\partial g_1}{\partial m_1} + \frac{\partial g_2}{\partial m_2})\rho_2.$$

Along characteristics, t, a, m_1, and m_2 progress together according to the first four ordinary differential equations and their initial conditions. Whenever a point (t, a, m_1, m_2) is specified, unique birth sizes $m_{10} = m_{10}(t, a, m_1)$ and $m_{20} = m_{20}(t, a, m_2)$ are determined; and whenever an age a and time t and birth sizes m_{10} and m_{20} of an organism born at time $t - a$ are specified, unique sizes $m_1 = m_1(t - a, a, m_{10})$ and $m_2 = m_2(t - a, a, m_{20})$ at age a and time t are determined.

Integration of Equations (11) yields

$$\rho_i(t, a, m_1, m_2) =$$

$$\begin{cases} \rho_i(t - a, 0, m_{10}, m_{20})L_i(t, a, m_i, P)J(t, a, m_1, m_2, P), \\ \qquad \text{for } t \geq a \\ \rho_i(0, a - t, \tilde{m}_1(a - t), \tilde{m}_2(a - t))M_i(t, a, m_i, P)K(t, a, m_1, m_2, P), \\ \qquad \text{for } t < a \end{cases}$$

where

$$J(t, a, m_1, m_2, P) = e^{-\int_0^a (\frac{\partial g_1}{\partial m_1} + \frac{\partial g_2}{\partial m_2})(t-a+\alpha, \alpha, m_1(t-a, \alpha, m_{10}), m_2(t-a, \alpha, m_{20}), P(t-a+\alpha))d\alpha}$$

$$K(t, a, m_1, m_2, P) = e^{-\int_{a-t}^a (\frac{\partial g_1}{\partial m_1} + \frac{\partial g_2}{\partial m_2})(t-a+\alpha, m_1(t-a+\alpha, m_{10}), m_2(t-a, \alpha, m_{20}), P(t-a+\alpha))d\alpha}$$

$$L_i(t, a, m_i, P) = e^{-\int_0^a \mu_i(t-a+\alpha, \alpha, m_i(t-a, \alpha, m_{i0}), P(t-a+\alpha))d\alpha}$$

$$M_i(t, a, m_i, P) = e^{-\int_{a-t}^a \mu_i(t-a+\alpha, \alpha, m_i(t-a, \alpha, m_{i0}), P(t-a+\alpha))d\alpha}$$

$$m_{i0} = m_{i0}(t, a, m_i),$$

and $\tilde{m}_{i0}(a - t)$ is the mass at age $a - t$ and time 0 in the initial distribution of an organism which has mass m_i at age a and time t.

Henceforth we specify $D_1(m_{20}) = D_2(m_{10}) = \frac{1}{M}$ so that

$$\tilde{\beta}_i(t, a, m_i, m_{10}, m_{20}, P(t)) = \beta_i(t, a, m_i, m_{i0}, P(t))\frac{1}{M}.$$

Case 1: $\beta_i = \beta_i(a, m_i, m_{i0}) = \beta_i'(a, m_i)b_i(m_{i0})$, $\int_0^M b_i(m_{i0})dm_{i0} = 1$, $\mu_i = \mu_i(a, m_i)$, and $g_i = g_i(a, m_i)$

In this case the asymptotic behavior is known to be

$$\lim_{t \to \infty} \rho_i(t, a, m_1, m_2)e^{-\lambda_i t} = C_i(a, m_1, m_2) > 0,$$

where λ_i is the unique real root of the equation $\Delta_i(\lambda) = 1$, and

$$\Delta_i(\lambda) = \int_0^M \int_0^M \int_0^A e^{-\lambda a} \beta_i'(a, m_i)b_i(m_{i0}(a, m_i))$$

$$D_i(m_{j0}(a, m_j))L_i(a, m_i)J(a, m_1, m_2)da\, dm_1\, dm_2$$

(Webb [13]; Karev [9]).

Theorem 9. *If* $\beta_1'(a, m_1)b_1(m_{10}(a, m_1))L_1(a, m_1) \geq \beta_2'(a, m_2)b_2(m_{20}(a, m_2))$ $L_2(a, m_2)$ *for all* $a \in [0, A]$ *and* $m_1, m_2 \in [0, M]$ *with the strict inequality holding for at least one triple* (a, m_1, m_2), *then ecotype 1 dominates ecotype 2.*

Proof. $\Delta_1(\lambda) > \Delta_2(\lambda)$ for all $\lambda \in \mathbb{R}$, and so $\lambda_1 > \lambda_2$. The conclusion follows as in the proof of Theorem 1. □

Case 2: $\beta_i = \beta_i(a, m_i, m_{i0}) = \beta_i'(a, m_i)b_i(m_{i0})$, $\int_0^M b_i(m_{i0})dm_{i0} = 1$, $\mu_i = \sigma_i(a, m_i) + \nu(t, P(t))$, and $g_i = g_i(a, m_i)$

Again, mortality assessed uniformly across ecotypes does not change the outcome of competition. The theorems and proofs in this case are analogous to those in Case 2, Section 2.

Henceforth $\tilde{\beta}_i$ need not be separable in the m_{i0} variable as it was in Cases 1 and 2.

Case 3: $\beta_i = \beta_i(a, m_i, m_{i0})$, $\mu_i(t, a, m_i)$, and $g_i = g_i(t, a, m_i, P(t))$

Theorem 10. *If there exists* $k > 1$ *such that*
1) $\beta_1(a, m_1, m_{10})L_1(t, a, m_1) \geq k^a \beta_2(a, m_2, m_{20})L_2(t, a, m_2) > 0$ *for all* $a \in [0, A]$, $m_1, m_{10}, m_2, m_{20} \in [0, M]$, *and* $t \in [a, \infty)$;
2) $\hat{\rho}_1(a - \alpha, \tilde{m}_1, \tilde{m}_2)\beta_1(a, m_1, m_{10})M_1(\alpha, a, m_1) \geq$ $k^\alpha \hat{\rho}_2(a - \alpha, \tilde{m}_1, \tilde{m}_2)\beta_2(a, m_2, m_{20})M_2(\alpha, a, m_2)$ *for all* $a \in [0, A]$, $m_1, m_{10}, m_2, m_{20} \in [0, M]$, *and* $\alpha \in [0, a]$, *where* $\tilde{m}_i = \tilde{m}_i(a - \alpha)$ *is the mass at age* $a - \alpha$ *and time 0 of an organism having age* a *and mass* m_i *at time* α; *and*

3) $\hat{\rho}_1(0, m_{10}, m_{20}) > \hat{\rho}_2(0, m_{10}, m_{20})$ for all $m_{10}, m_{20} \in [0, M]$;
then ecotype 1 dominates ecotype 2.

Proof. Let

$$S = \{t \in \mathbb{R} \mid \forall m_{10}, m_{20} \in [0, M](\rho_1(t, 0, m_{10}, m_{20}) > k^t \rho_2(t, 0, m_{10}, m_{20})\}$$

be the truth set. We will show $[0, \infty) \subseteq S$ using Theorem 5.

First we must show S is open in $\mathbb{R}$. By 3), $0 \in S$, so S is nonempty. Let $\tau \in S$ and define $f(t, m_{10}, m_{20}) = \rho_1(t, 0, m_{10}, m_{20}) - k^t \rho_2(t, 0, m_{10}, m_{20})$. Let $c = \min_{x, y \in [0, M]}\{f(\tau, x, y)\}$. $f(t, m_{10}, m_{20})$ is uniformly continuous on the compact rectangle $B = [0, 2\tau] \times [0, M] \times [0, M]$, so there is $\delta > 0$ such that for any two points (t, m_{10}, m_{20}), $(t', m'_{10}, m'_{20}) \in B$, $|f(t, m_{10}, m_{20}) - f(t', m'_{10}, m'_{20})| < \frac{c}{2}$ whenever $\|(t, m_{10}, m_{20}) - (t', m'_{10}, m'_{20})\| < \delta$. Thus, $|\tau - t| < \delta$ implies $|f(\tau, m_{10}, m_{20}) - f(t, m_{10}, m_{20})| < \frac{c}{2}$ for all $m_{10}, m_{20} \in [0, M]$, and so $f(t, m_{10}, m_{20}) > 0$ for all $m_{10}, m_{20} \in [0, M]$. Hence, $t \in S$ whenever $|\tau - t| < \delta$.

Let $T \in [0, \infty)$. If $T = 0$, then $T \in S$ by 3). Otherwise, assume $t \in S$ for all $t \in [0, T)$. Let $m_{10}, m_{20} \in [0, M]$. Then if $T \le A$,

$$\rho_1(T, 0, m_{10}, m_{20})$$

$$= \frac{1}{M} \int_0^M \int_0^M \int_0^A \beta_1(a, m_1, m_{10}) \rho_1(T, a, m_1, m_2) da\, dm_1\, dm_2$$

$$= \frac{1}{M} \int_0^M \int_0^M \int_0^T \beta_1(a, m_1, m_{10}) \rho_1(T - a, 0, \tilde{m}_{10}(T, a, m_1),$$

$$\tilde{m}_{20}(T, a, m_2)) \cdot L_1(T, a, m_1) J(T, a, m_1, m_2, P) da\, dm_1\, dm_2$$

$$+ \frac{1}{M} \int_0^M \int_0^M \int_T^A \beta_1(a, m_1, m_{10}) \hat{\rho}_1(a - T, \tilde{m}_1(a - T), \tilde{m}_2(a - T)) \cdot$$

$$M_1(T, a, m_1) K(T, a, m_1, m_2, P) da\, dm_1\, dm_2$$

$$> \frac{1}{M} \int_0^M \int_0^M \int_0^T k^a \beta_2(a, m_2, m_{20}) k^{T-a} \rho_2(T - a, 0, \tilde{m}_{10}(T, a, m_1),$$

$$\tilde{m}_{20}(T, a, m_2)) \cdot L_2(T, a, m_2) J(T, a, m_1, m_2, P) da\, dm_1\, dm_2$$

$$+ \frac{1}{M} k^T \int_0^M \int_0^M \int_T^A \beta_2(a, m_2, m_{20}) \hat{\rho}_2(a - T, \tilde{m}_1(a - T), \tilde{m}_2(a - T)) \cdot$$

$$M_2(T, a, m_2) K(T, a, m_1, m_2, P) da\, dm_1\, dm_2$$

$$= \frac{1}{M} k^T \int_0^M \int_0^M \int_0^A \beta_2(a, m_2, m_{20}) \rho_2(T, a, m_1, m_2) da\, dm_1\, dm_2$$

$$= k^T \rho_2(T, 0, m_{10}, m_{20}).$$

(If $T > A$, it is not necessary to split the renewal integral into two integrals.) Since m_{10} and m_{20} were arbitrary, $T \in S$. Thus,

$$\lim_{t \to \infty} \frac{\rho_1(t, a, m_1, m_2)}{\rho_2(t, a, m_1, m_2)}$$

$$= \lim_{t \to \infty} \frac{\rho_1(t - a, 0, m_{10}, m_{20}) L_1(t, a, m_1) J(t, a, m_1, m_2, P)}{\rho_2(t - a, 0, m_{10}, m_{20}) L_2(t, a, m_2) J(t, a, m_1, m_2, P)}$$

$$\geq \lim_{t \to \infty} k^t \frac{\beta_2(a, m_2, m_{20})}{\beta_1(a, m_1, m_{10})}$$

$$= \infty.$$

$\frac{\beta_2}{\beta_1}$ is positive and continuous on its compact domain and is hence bounded away from zero, making the above limits uniform in age and size. Thus,

$$\lim_{t \to \infty} \frac{P_{T1}(t)}{P_{T2}(t)} = \lim_{t \to \infty} \frac{\int_0^M \int_0^M \int_0^A \rho_1(t, a, m_1, m_2) \, da \, dm_1 \, dm_2}{\int_0^M \int_0^M \int_0^A \rho_2(t, a, m_1, m_2) \, da \, dm_1 \, dm_2} = \infty. \qquad \square$$

As before, the time dependency may be in the β_i instead of the μ_i, and in this event the β_i's can take on the value zero.

Case 4: $\beta_i = \beta_i(t, a, m_i, m_{i0}, P(t))$, $\mu_i = \mu_i(t, a, m_i, P(t))$, and
$g_i = g_i(t, a, m_i, P(t))$

The proof of the following theorem is directly analogous to that of Theorem 8.

Theorem 11. *If there exists $k > 1$ such that*
1) $\beta_1(t, a, m_1, m_{10}, p) \geq k^a \beta_2(t, a, m_2, m_{20}, p)$ *for all* $t, p \in [0, \infty)$, $a \in [0, A]$, *and* $m_1, m_{10}, m_2, m_{20} \in [0, M]$;
2) $\mu_1(t, a, m_1, p) \leq \mu_2(t, a, m_2, p)$ *for all* $t, p \in [0, \infty)$, $a \in [0, A]$, *and* $m_1, m_2 \in [0, M]$; *and*
3) $\hat{\rho}_1(a - \alpha, m_1, m_2) \geq k^{\alpha - a} \hat{\rho}_2(a - \alpha, m_1, m_2)$ *for all* $a \in [0, A]$, $\alpha \in [0, a]$, *and* $m_1, m_2 \in [0, M]$ *with the strict inequality holding for* $a = \alpha$; *then ecotype* 1 *dominates ecotype* 2. $\qquad \square$

The above results can be extended to an arbitrary finite number of state variables in the obvious way.

4. Conclusions

The notion of "survival of the fittest" tautologically identifies the survivors with the fittest types of individuals. The results in this paper suggest a measure of ecotypic or species fitness to be the product βL of the birth rate and survivorship

functions. This is basically true even when birth, growth, and mortality rates are time and density dependent and the asymptotic behavior of the solution is not known.

In general, determining relative asymptotic behavior between two ecotypes requires more than comparing "average" measures of fitness such as $R_0 = \int_\Omega \int_0^\infty \beta L da\, d\vec{m}$ (see examples 1 and 2). Small numbers of births early in life may compound more rapidly than a large birth spike later on. If, however, the fitness measure βL of one ecotype exceeds that of another at every set of state variables, then the first ecotype will be dominant. If solutions are bounded, a reasonable requirement for the density dependent cases, dominance in the first ecotype forces the other to extinction.

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