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GLOBAL DYNAMICS AND OPTIMAL LIFE HISTORY OF A STRUCTURED POPULATION MODEL*

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Abstract. The first part of this paper is devoted to a complete description of the dynamics of a continuously structured population model coupled with a dynamical resource. In the model, it is assumed that the energy each individual obtains from the resource is channeled between growth and reproduction in a proportion that depends on the individual's size. In the second part, an optimal allocation of this energy is obtained that turns out to be a convergence-stable ESS and is described by what is called a "bang-bang" strategy.

Key words. structured population dynamics, evolutionarily stable strategies, life history, optimization

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1. Introduction.

One of the most useful features of structured population modeling is that it allows one not only to study the dynamics of populations, but also to analyze evolutionary aspects of the life histories of such populations. This is so because the ingredients of a structured population model, the vital rates (growth, death, and reproduction rates), define the life history of an individual since they are functions of age and/or other internal variables structuring the population. In other words, giving the vital rates is equivalent to describing the life history of an organism.

However, not any choice of such rates is suitable. Life history models assume some constraints among these rates (the energy available to an individual is finite) and an evolutionary process, driven by natural selection, to establish in the population an optimal life history. Finding this optimum constitutes the *general life history problem* (see [26]) and it can be formulated more precisely in terms of the following question (see [2]): "How should an organism optimally allocate its resources to growth, survival, and reproduction?" One way of formalizing this partition of the total resource amount among vital rates is to introduce the notion of *reproductive effort*—percent allocation of resources to reproduction—and the models dealing with it are known as "reproductive effort models."

A concept that links both topics, population dynamics and life history theory, is the *evolutionarily stable strategy* (ESS), introduced by Maynard Smith and Price in 1973 in the context of game theory (see [14]) and its (dynamical) generalization, the *evolutionarily stable attractor* (ESA).

The idea behind the classical concept of ESS is to assume a homogeneous population with respect to an evolutionary trait in a steady state (see [1], [12], [18]). Once the latter is achieved, a small amount of individuals with a different value of the evolutionary trait (*mutants* or *invaders*) are introduced. "Small" means that the

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number of mutants/invaders do not change the environmental conditions (levels of resources, etc.) imposed by the population of *residents*. Afterwards, if the population of mutants/invaders spreads under such conditions, i.e., if the mutant/invader growth rate is positive (the resident growth rate is zero because of the equilibrium condition), then it will be a displacement of the evolutionary trait from the resident's strategy (or trait value) to the mutant/invader's strategy. When no choice of the mutant/invader strategy is able to displace the resident strategy, it is said that the latter is an ESS with respect to this trait. Therefore, the concept of ESS makes it possible to deal with the evolution of life histories as a problem in maximizing (intrinsic) growth rates.

Nevertheless, the (ecological) dynamics do not always drive a population towards an equilibrium level; instead, there are periodic, quasi-periodic, or even chaotic oscillations as asymptotic behaviors. Therefore, the criterion of (initial) success of a mutant type has to be measured in a different way. For instance, it has been suggested as a criterion the largest Lyapunov exponent of a sequence of transition matrices when the dynamics of the resident population tends to a generic attractor (see [10], [17]). On the other hand, the generalization of the idea of evolutionary stability of an equilibrium to include such generic attractors has motivated the notion of ESA (see [22]).

Another aspect that also is neglected in the definition of ESS is that the growth of the population of mutants/invaders—when it occurs— will change the initial environmental conditions determined by the resident population. Under such conditions, the above comparison of growth rates is no longer valid and mutual invasibilities are possible—for instance, when the environmental conditions imposed by the initially successful mutant allow the resident to grow faster than the former. A situation like that is nicely illustrated in [8], where a two-population discrete time model showing mutual invasibilty is considered. This fact introduces *invasibility* as one of the aspects related to the *stability* of an ESS. Furthermore, it is well known that an ESS may be an attractor or a repeller of the adaptive dynamics (see [5], [9], [27]). Therefore, a stability analysis from the evolutionary point of view has been made in order to classify the ESSes. (See [11] and [16] for a mathematical framework of the modern theory of ESSes.)

The first structured population models that have been studied from an evolutionary point of view are those describing age-dependent dynamics in discrete time, i.e., matrix models. Aspects of life history such as the age of reproductive maturity or the more general notion of *reproductive function* (see [4]), that gives the reproductive effort as a function of age, are studied by means of the Euler–Lotka equation (see, for instance, [24] and [25], and [4, Chapter 5] for continuous time models) and, more recently, by means of the optimal control theory (see [26]) and numerical optimization approaches (see [2]).

Lately, the study of the evolution of life histories also contemplates size-dependent populations. For instance, in [1] a discretely size- structured population model in continuous time is considered with the growth rate at each size stage being the trait to be optimized. This particular aspect of life history, growth, does not appear in age-dependent population models because one considers age and not size as the important factor in determining the physiological state of an individual. However, this model does not belong to the class of reproductive effort models because no partition of resources among growth, maintenance, and reproduction is considered. However, it is the first reference (as far as we know) where an optimization of the growth rate is made and where the role of growth rates in the survival of organisms is emphasized.

In this paper we present a model of a size-dependent population with a dynamical resource, and we analyze it from both dynamical and evolutionary points of view.

This model is a generalization of the one considered in [3, Example 2], in the sense of including a general allocation function (see below), a dynamical resource and two sorts of individuals: the nongrowing and the growing ones. In its turn, the model of the example is a modified version of the one presented in [6], also with a dynamical resource, which is based on a model for the growth dynamics of simple ectothermic filter-feeding species, such as *Daphnia* and many zooplankton species (see [15, Part A, Chapter I, section 3]).

A basic assumption in all of the previous models and the present one is that individual resource uptake rate depends only on resource density. A second basic assumption of the model is that the energy uptake coming from the resource ingestion is channeled between growth (in a proportion $k(x)$) and reproduction (in a proportion $(1-k(x))$) in such a way that this partition of resources in growing individuals, i.e., the reproductive effort, depends on their size x. Maintenance requirements are neglected. In [3], [6], and [15], this fraction of channeled energy is considered a (given) constant ($k(x) \equiv \kappa$) and, therefore, to be independent of size.

The aim of the paper is twofold: first, to study the dynamics of a family of models characterized by different choices of the *energy allocation function* $k(x)$ and, second, to find an evolutionarily stable strategy among the previous choices of $k(x)$. The set of the possible strategies $k(x)$ is called *trait space* which, in our case, is infinite-dimensional. Notice that $(1-k(x))$ corresponds to the notion of *reproductive function* we mentioned above. With respect to the optimization of $k(x)$, we would like to emphasize that, first, we do not assume any sort of asymptotic behavior for the population dynamics in order to obtain results about the ESS as in other works; instead, all the asymptotic behaviors are established, as well as the conditions under which they are possible. Second, while most of the results on ESS are obtained assuming that the resident population is stationary, here the existence and the value of an ESS are obtained under any regime of the resident population. Third, the evolutionary trait is not a scalar parameter of the model (e.g., a maturation size) but a *function* of the individual size.

Section 2 gives a description of the model we study: a nonlinear first-order PDE for the (structured) population of growing consumers, an ODE for the (unstructured) population of nongrowing consumers, and an ODE for the (unstructured) resource. In order to find an optimal $k(x)$, the set of possible allocation functions is defined. This set and the consequences that different choices of $k(x)$ have on the model are also discussed. For example, the existence of nongrowing individuals in the population of consumers does not always make sense since, assuming there is a maximum size l, growing individuals can never achieve this size when $k(l) = 0$ and $|k'(l)| < \infty$, i.e., they grow during all of their life.

Section 3 deals with the mathematical analysis of the model. It starts with results on the linear semigroup associated to the model equations (Theorem 1) that will be needed for the analysis of the dynamics of the full problem and also for the study of the adaptive dynamics. Afterwards, the existence and uniqueness of (global) solutions to the full problem and, moreover, their asymptotic behaviors, are established by means of a reduction to an asymptotically autonomous system of ODEs. As a result we conclude that solutions are bounded and, more precisely, that they tend to an equilibrium point or to a periodic orbit. This boundedness of trajectories is used in section 4 to elucidate the adaptive dynamics arising when different strategies, represented by different choices of $k(x)$, are played among members of the consumer population.

Finally, section 4 begins with the study of the dynamics of the trait substitution in populations where n arbitrary strategies $k^i(x)$ $(i = 1, \ldots, n)$ are simultaneously adopted by their members (a polymorphic population composition). A consequence of this study is the existence, under certain hypotheses, of a limit for the sequence of trait substitutions which is obtained when an arbitrary set of $n-1$ strategies is successively added to a resident one. We call this sequential process *trait substitution dynamics*, and its limit, when it exists, defines a *convergence-stable ESS*. Mathematically, an ESS corresponds to a strategy—a choice of $k(x)$—that maximizes the dominant eigenvalue of the generator of the linear semigroup. The section ends with the calculation of the optimal allocation function, which turns out to be the investment of all the energy uptake to growth until a certain size is reached and, then, after growth has stopped, the investing of all of it in reproduction, i.e., the ESS is a "bang-bang" strategy.

2. Description of the model.

2.1. The initial value problem. Let $u(x,t)\,dx$ be the number of growing individuals of the consumer population at time t with a size between x and $x+dx$, $v(t)$ the number of nongrowing individuals in that population at time t, and $r(t)$ the level of resources available to the consumers at time t.

Now, let us build the model assuming the following hypotheses:

a. the individual growth rate of a growing consumer is proportional to the resource uptake rate, $f(r)$, times the allocation function, $k(x)$;
b. there exists a maximum size $l \le \infty$ for the growing individuals;
c. the reproduction rate, β, is proportional to $f(r)$ times $(1 - k(x))$, the reproductive function, times $b(x)$, the intrinsic reproduction rate of a growing individual of size x. For a nongrowing individual, β is simply $f(r)\,b(l)$;
d. the death rate, m, of the consumers depends only on the resource level; hence it is assumed to be the same for growing and nongrowing individuals;
e. the resource without any consumer has logistic-like dynamics.

Then the equations governing the dynamics of the consumer-resource system are

$$\text{(2.1)} \qquad \begin{cases} u_t + (V_0 f(r)\,k(x)\,u)_x = -m(r)\,u, \quad x \in [0,l),\ t > 0, \\[2ex] v' + m(r)\,v = \lim\limits_{x\to l^-} V_0\,f(r)\,k(x)\,u(x,t), \quad t > 0, \\[2ex] r' = g(r)\,r - f(r)\,L(u,v), \quad t > 0, \end{cases}$$

plus the boundary condition (linear in u after the cancellation of the common factor $f(r)$):

$$\text{(2.2)} \qquad V_0\,k(0)\,u(0,t) = \int_0^l (1-k(x))\,b(x)\,u(x,t)\,dx + b(l)\,v(t), \qquad t > 0,$$

where $V_0 > 0$ is the proportionality constant between energy uptake per unit of time and growth that, without loss of generality, will be taken as 1. Finally, L denotes a linear functional of u and v. For instance, one can consider the functional

$$L(u,v)(t) = \int_0^l \rho(x)\,u(x,t)\,dx + \sigma\,v(t)$$

with $\rho(x)$ and σ being consumption measures of a growing individual of size x and a nongrowing individual, respectively.

The initial value problem (IVP) is given by equations (2.1)–(2.2) plus an initial condition (u_0, v_0, r_0) with $u_0(x) \ge 0$, $v_0 \ge 0$ and $r_0 > 0$.

2.2. Hypotheses of the model: Choices of the allocation function $k(x)$. Since our aim is to find an allocation function that optimizes the growth rate of the consumer population in an evolutionary sense (see section 4), we cannot reject a priori any candidate $k(x)$ satisfying the natural condition of an allocation function, namely, $0 \leq k(x) \leq 1$ $\forall x \in [0,l]$, plus some regularity conditions needed in the proof of the existence and uniqueness of solution to the IVP (2.1)–(2.2).

This purpose of being as general as possible leads us to deal with a *family* of systems (2.1), each one characterized by $k(x)$, in such a way that, for some members of the family, $(2.1)_2$ can be meaningless from a biological point of view. However, this approach allows us to give a unified treatment to the search of an optimum allocation function inside this family.

To see that, it is important to realize that the election of $k(x)$ strongly determines the dynamics of the system. Recall that the characteristic system associated with $(2.1)_1$ is

$$\frac{dx(t)}{dt} = f(r(t))\,k(x(t)),$$

where $x(t)$ is the characteristic curve in the plane (t,x). Thus, the time spent by a growing consumer to reach the maximum size l satisfies, for any initial condition (u_0, v_0, r_0) with $u_0(x) \geq 0$, $v_0 \geq 0$ and $r_0 > 0$, the inequality

$$t \geq \frac{1}{f_\infty} \int_0^l \frac{dx}{k(x)},$$

where it is used $f(r) \leq f_\infty$. It is clear that whenever the previous integral diverges, $t = \infty$. For instance, this is so if $l = \infty$. When l is finite, this implies that there is no flow of growing consumers through the boundary $x = l$, i.e., to the stage of nongrowing consumers. In this case, the equation for the nongrowing individuals has a mathematical meaning because of the possible existence of a positive initial condition but, from a biological point of view, can be superfluous. Conversely, if $k(x)$ tends to zero "abruptly" as $x \to l$ or if $k(l) > 0$, a (finite) size l will be achieved in finite time because f is a function bounded from below by a strictly positive constant for any $r_0 > 0$, and then all the equations of the model become relevant.

From now on we will assume the following hypotheses on the functions appearing in the model:

(H1) Let b, $k \in W^{1,\infty}(0,l)$, $l \leq \infty$, with $0 < k(x) \leq 1$ $\forall x \in [0,l)$, $b(x) \geq 0$ and $\lim_{x\to l^-} b(x) = b(l) > 0$. Moreover, if $l = \infty$ then $\limsup_{x\to\infty} k(x) < 1$.

(H2) $f(r)$ is a $\mathcal{C}^1$-function globally bounded from above by f_∞ with $f(0) = 0$ and $f(r) > 0$ for every $r > 0$.

(H3) g and m are $\mathcal{C}^1(0,\infty)$, g is positive for small r and negative for large r, m is bounded from below by a positive constant.

Remark. A particular case of the regularity requirement of (H1) is b and k in $\mathcal{C}^1([0,l])$.

DEFINITION 1. *We understand by a* (*local*) *solution of the IVP* (2.1)–(2.2) *any vector of functions* (u,v,r) *belonging to* $\mathcal{C}^1([0,T]; L^1_+(0,l) \times \mathbf{R}^+ \times \mathbf{R}^+)$ *with* $(u(t), v(t)) \in D := \{(f,g) \in L^1_+(0,l) \times \mathbf{R}^+ : kf \in W^{1,1}(0,l),\ k(0)\,f(0) = \int_0^l (1 - k(x))\,b(x)\,f(x)\,dx + b(l)g\}$ *and satisfying* (2.1) *in a strong sense.*

3. Ecological dynamics of the model.

3.1. The linear semigroup. In order to have a complete description of the dynamics of the IVP given by (2.1)–(2.2) plus an initial condition (u_0, v_0, r_0) with $u_0(x) \geq 0$, $v_0 \geq 0$ and $r_0 > 0$, it will be useful to know the behavior of the linear semigroup associated with that IVP when no dependence of the consumer equations on the resource level is considered. From a biological point of view, this would correspond to a situation with a maximum availability of resources for any consumer population. Such a situation sometimes has been called a "virgin environment" to denote the best possible environment (see [18]). In our model this means $f(r) = f_\infty$, which can be taken as 1.

So, to begin the study of the dynamics of the model, we are interested in the properties of the semigroup associated with the solutions of the following linear IVP:

$$\begin{cases} u_t + (k(x)\,u)_x + \lambda\, u = 0, \quad x \in [0,l),\ t > 0, \\ v' + \lambda\, v = \lim\limits_{x \to l^-} k(x)\,u(x,t), \quad t > 0, \\ k(0)\,u(0,t) = \int_0^l \beta(s)\,u(s,t)\,ds + b\,v(t), \quad t > 0, \\ u(x,0) = u_0(x),\ v(0) = v_0. \end{cases} \tag{3.1}$$

For this purpose it is convenient to consider the operator

$$A_\lambda \begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} -(k\,u)' - \lambda\, u \\ k(l)\,u(l) - \lambda\, v \end{pmatrix} \tag{3.2}$$

with domain

$$D = \left\{ (u,v) \in X : ku \in W^{1,1}(0,l);\ k(0)\,u(0) = \int_0^l \beta(s)\,u(s)\,ds + b\,v \right\} \tag{3.3}$$

dense in $X := L^1(0,l) \times \mathbf{R}$, and the characteristic equation corresponding to 0 being an eigenvalue of A_λ, namely,

$$\mathcal{F}(\lambda) = \int_0^l \frac{\beta(x)}{k(x)} e^{-\lambda a(x)} dx + b\frac{e^{-\lambda a(l)}}{\lambda} = 1, \tag{3.4}$$

where $a(x) = \int_0^x ds/k(s)$. The following theorem gives the properties we will need about A_λ and about the semigroup $T_\lambda(t)$ generated by this operator in the analysis of the full problem (see appendix for a proof of the theorem and properties of T_λ).

THEOREM 1. *Let us assume $\beta \in L^\infty(0,l)$, $(k\beta') \in L^\infty(0,l)$, and $\liminf_{x \to l^-} \beta(x) > 0$ if $a(l) = \infty$, or $b > 0$ if $a(l) < \infty$. Moreover, let λ^* be the only positive solution of the characteristic equation* (3.4). *Then 0 is a strictly dominant eigenvalue of A_{λ^*} with algebraic multiplicity 1 and*

$$\hat{U} := \left(\frac{e^{-\lambda^* a(x)}}{k(x)}, \frac{e^{-\lambda^* a(l)}}{\lambda^*} \right)$$

is the corresponding eigenvector.

Furthermore, there exist constants $\delta > 0$ and $M \geq 1$, and a continuous linear form α in $X = L^1(0,l) \times \mathbf{R}$ such that, $\forall\ U \in X$ and $t \geq 0$,

$$||T_{\lambda^*}(t)U - \alpha(U)\hat{U}|| \leq M\, e^{-\delta t}||U||.$$

Finally, $\alpha(U) > 0$ whenever U belongs to the positive cone $X^+ - \{0\}$.

3.2. The full problem. Once we know the behavior of the linear semigroup associated with the IVP, in particular the existence of a strictly dominant eigenvalue of its infinitesimal generator, we are concerned with the behavior of the full model. The key point is the expression of the solution corresponding to the consumer population as a product of two functions; namely, the solution of the previous linear problem times a scalar function which is a solution of a system of ODEs and which *modulates* the growth of the linear part. That is, $U(t) = \varphi(t)\, T(t)\, U_0$. This special form of the solution is possible because the death rate m depends only on the resource level.

More precisely, this subsection is devoted to the mathematical treatment of the nonlinear system

$$\begin{cases} u_t + \left(f(r)\, k(x)\, u\right)_x = -m(r)\, u, \quad x \in [0,l),\ t > 0, \\ v' + m(r)\, v = \lim\limits_{x \to l^-} f(r)\, k(x)\, u(x,t), \quad t > 0, \\ r' = g(r)\, r - f(r)\, L(u,v), \quad t > 0, \end{cases} \tag{3.5}$$

plus the boundary condition for u :

$$k(0)\, u(0,t) = \int_0^l (1 - k(s))\, b(s)\, u(s,t)\, ds + b(l)\, v(t), \qquad t > 0.$$

In section 3.3 we prove the existence and uniqueness of a global solution of the IVP for this system. Furthermore, we completely describe the dynamics. Under suitable hypotheses we prove that there exists a unique coexistence equilibrium (with nonvanishing resource and consumer populations) which is a global attractor for the solutions corresponding to nonzero initial conditions with resource and consumer populations.

Let us write system (3.5) in the following abstract form:

$$\begin{cases} U_t - f(r)\, A\, U + m(r)\, U = 0, \\ r' - g(r)\, r + f(r)\, L\, U = 0. \end{cases} \tag{3.6}$$

Here $U(t) := (u(t), v(t))$ belongs to the Banach space $X = L^1(0,l) \times \mathbf{R}$, $l \leq \infty$, $r(t)$ is a real number, A is a linear operator in X with domain (dense in X) given by (3.3) with $\beta(s) = (1 - k(s))\, b(s)$ and $b = b(l)$, and it is defined by

$$A \begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} -(k\, u)' \\ k(l)\, u(l) \end{pmatrix}; \tag{3.7}$$

f, m, and g are smooth functions, m is positive $\forall\, r \geq 0$, f is positive $\forall\, r > 0$, and L is a positive continuous linear form in X.

3.3. The semilinear equations: Reduction to an SODE. To solve the IVP $U(0) = U_0,\ r(0) = r_0$ for system (3.6), we first obtain a solution $(\varphi(t)\, T(t)\, U_0,\, r(t))$ of the auxiliary system

$$\begin{cases} U_t - A_{\lambda^*}\, U = h_2(r)\, U, \\ r' = h_1(r) - L\, U, \\ U(0) = U_0,\ r(0) = r_0, \end{cases} \tag{3.8}$$

where $T(t) = T_{\lambda^*}(t)$ is the C_0-semigroup generated by the linear operator $A_{\lambda^*} = A - \lambda^* I$, λ^* is the dominant eigenvalue of A, and $r(t)$ and $\varphi(t)$ are the solutions of the system of ordinary differential equations

$$\begin{cases} r' = h_1(r) - \varphi\, L\, T(t)\, U_0, \\ \varphi' = h_2(r)\, \varphi, \\ r(0) = r_0, \;\; \varphi(0) = 1. \end{cases} \tag{3.9}$$

Here we assume that h_1 and h_2 are smooth real functions, that h_1 is positive for small r and negative for large r, that U_0 belongs to the positive cone X^+ of X and it is not zero, and that $r_0 > 0$. It is easy to prove that (3.9) has a unique global (for $t > 0$) solution which is positive. Moreover, $r(t)$ is trivially bounded for $t \geq 0$.

When U_0 belongs to the domain of A_{λ^*}, one checks directly that $(\varphi(t)\, T(t)\, U_0,\, r(t))$ is a (strong) solution of (3.8) and uniqueness follows from the standard theory of semilinear equations (see, for instance, [20]).

Now we obtain a solution of the IVP of system (3.6). First notice that $f(r(t))$ is a positive bounded function of $t \in [0, \infty)$.

THEOREM 2. *Let $h_1(r) = g(r)\, r / f(r), h_2(r) = \lambda^* - m(r)/f(r)$, and let $\tilde{r}(t)$ be the first component of the solution of system* (3.9) *for a U_0 in $X^+ \cap D(A)$ and $r_0 > 0$. Let $G(\tau) = \int_0^\tau ds / f(\tilde{r}(s))$ for $\tau \geq 0$. Then the IVP for system* (3.6) *has a unique solution $\forall t \geq 0$ which is positive and given by*

$$U(t) = \tilde{U}(G^{-1}(t)), \qquad r(t) = \tilde{r}(G^{-1}(t)),$$

where $\tilde{U}$ is the first component of the solution of system (3.8).

Proof. From (H2) and (H3) it follows that h_1 and h_2 satisfy the hypotheses mentioned above. Since G is a monotonously increasing smooth function mapping $[0, \infty)$ onto $[0, \infty)$, then G^{-1} is well defined, differentiable with derivative $(G^{-1})'(t) = f(\tilde{r}(G^{-1}(t)))$ and $G^{-1}(0) = 0$. Now, the statement follows by direct checking. □

3.4. Asymptotic behavior. The special form of the solutions of the full problem allows a study of their asymptotic behavior by means of a study of the asymptotically autonomous two-dimensional system (3.9). First notice that (H1) implies that $\beta(x) = (1 - k(x))\, b(x)$ and $b = b(l)$ satisfy the hypotheses of Theorem 1. So the nonautonomous term in (3.9), $T(t)U_0$, tends to a positive multiple of the eigenvector $\hat{U}$ of the operator A corresponding to the eigenvalue λ^* because U_0 belongs to $X^+ - \{0\}$. Let us assume that $\hat{U}$ is normalized in such a way that $L\,\hat{U} = 1$. Now let us set $\lim_{t\to\infty} T(t)U_0 = \alpha\hat{U}$, where α is a positive real number (see section 3.1).

So the limit system of (3.9) is

$$\begin{cases} r' = h_1(r) - \alpha\varphi, \\ \varphi' = h_2(r)\, \varphi, \end{cases}$$

which can be reduced to the case $\alpha = 1$ by taking $\psi(t) = \alpha\varphi(t)$, that is,

$$\begin{cases} r' = h_1(r) - \psi, \\ \psi' = h_2(r)\, \psi. \end{cases} \tag{3.10}$$

LEMMA 1. *Let h_1 be positive in $[0, r_c)$ and negative for $r > r_c$. Let h_2 be negative for $r < r_e$ and positive for $r > r_e$ and assume $r_e < r_c$. Moreover, let us assume that $\lim_{r\to 0^+} h_2(r) = -\infty$. Then*

a. *for any $a > r_c$, the trapezium T_a of vertexes $(0,0)$, $(a,0)$, (r_e, ψ_a), and $(0, \psi_a)$, and the pentagon P_a of vertexes $(0,0)$, $(r_c, 0)$, (r_c, ψ_c), (r_e, ψ_a), and $(0, \psi_a)$, where ψ_a is any number larger than $(a - r_e)\max_{r\in[r_e,a]}(h_2(r) + h_1(r)/(a - r))$, and $\psi_c := \psi_a(a - r_c)/(a - r_e)$, are positively invariant regions for system (3.10).*

b. *The ω-limit set of any solution of system (3.10) with initial condition in the open first quadrant is the equilibrium point $(r_e, h_1(r_e))$ or a periodic orbit $(r_p(t), \psi_p(t))$ surrounding it counterclockwise and contained in $\bigcap_{a>r_c} P_a$.*

Proof. a. As the open first quadrant is invariant and the vectorial field points inward at points of the form (r_c, ψ) and at points of the form (r, ψ_a) for $r < r_e$, it suffices to show that the scalar product of the vectorial field in a point (r, ψ) of the segment joining the points $(a, 0)$ and (r_e, ψ_a) and the exterior unitary normal vector (n_1, n_2) to the same segment at the same point is nonpositive. As $\psi = \psi_a(a-r)/(a-r_e)$ and $n_2/n_1 = (a - r_e)/\psi_a$, we have

$$(h_1(r) - \psi, h_2(r)\psi) \cdot (n_1, n_2) = \frac{a - r}{a - r_e} n_1 \left[(a - r_e)\left(h_2(r) + \frac{h_1(r)}{a - r}\right) - \psi_a\right] \le 0$$

$\forall\, r \in (r_e, a)$.

b. Statement a implies that any solution is bounded for positive time because any initial condition belongs to some T_a. Now b follows from the Poincaré–Bendixson theorem. ◻

LEMMA 2. *Let us assume the hypotheses of Lemma 1. Then if $U_0 \in X^+ - \{0\}$, the solution of problem (3.9) is bounded.*

Proof. As in the previous lemma, we can construct positively invariant trapeziums like T_a, now taking

$$\psi_a \ge \frac{a - r_e}{\inf_{t\ge 0}\{L\,T(t)\,U_0\}} \max_{r\in[r_e,a]} \left(h_2(r) + \frac{h_1(r)}{a - r}\right)$$

for any $a > r_c$. Notice that the denominator is strictly positive because $L\,T(t)\,U_0$ tends to a positive number α (see Theorem 1). ◻

From this lemma we have the following

COROLLARY 1. *Let us assume that the periodic orbits of system (3.10) are isolated. Then for any $r_0 > 0$, the solution of problem (3.9) tends to the point $(r_e, h_1(r_e)/\alpha)$ or to a periodic orbit $(r_p(t), \psi_p(t)/\alpha)$.*

Proof. A well-known result (see [13] and [28]) ensures that the ω-limit set of a forward-bounded solution of an asymptotically autonomous two-dimensional system is connected and is either an equilibrium or the union of periodic orbits of the limit system. So, the statement follows from Lemma 1 and the relationship between systems (3.9) and (3.10). ◻

THEOREM 3. *Let us assume the hypotheses of Lemma 1 and Corollary 1. Then the solution of system (3.8) for $U_0 \in X^+ - \{0\}$ and $r_0 > 0$ tends to the equilibrium point $(h_1(r_e)\hat{U}, r_e)$ or to a periodic orbit $(\psi_p(t)\hat{U}, r_p(t))$.*

Proof. It follows immediately from the previous corollary, recalling that the solution of (3.8) is written $(\varphi(t)\,T(t)\,U_0, r(t))$ and that $\lim_{t\to\infty} T(t)\,U_0 = \alpha\hat{U}$. ◻

THEOREM 4. *Let λ^* be the dominant eigenvalue of the operator A and $\hat{U}$ the associated eigenvector such that $L\,\hat{U} = 1$. Let us assume that $m(r)/f(r) > \lambda^*$ for*

$0 < r < r_e$ and $m(r)/f(r) < \lambda^*$ for $r > r_e$, that $g(r) > 0$ for $0 \le r < r_c$ and $g(r) < 0$ for $r > r_c$, and, finally, that $r_e < r_c$. Finally, let us assume that the periodic orbits of system (3.10) with $h_1(r) = r\,g(r)/f(r)$ and $h_2(r) = \lambda^* - m(r)/f(r)$ are isolated. Then, for any initial condition $U_0 \in X^+ \cap D(A)$, $U_0 \neq 0$, $r_0 > 0$, the solution of system (3.6) tends to the unique coexistence equilibrium $(\frac{g(r_e)\,r_e}{f(r_e)}\hat{U},\, r_e)$ or to a periodic solution $(\psi_p(t)\,\hat{U},\, r_p(t))$, where the pair of functions $(r_p(t), \psi_p(t))$ is a limit cycle of system (3.10) with $h_1(r) = r\,g(r)/f(r)$ and $h_2(r) = \lambda^* - m(r)/f(r)$.

Proof. Notice that $h_1(r) = r\,g(r)/f(r)$ and $h_2(r) = \lambda^* - m(r)/f(r)$ satisfy the hypotheses of Lemma 1. As $\lim_{t\to\infty} G^{-1}(t) = \infty$, the solution of system (3.6), given by Theorem 2, has the same asymptotic behavior as the solution of system (3.8), which is specified in Theorem 3. □

Remark. The case $r_c < r_e$ leads to the extinction of the consumer because the resource level needed for its persistence is larger than the carrying capacity r_c for the resource.

4. Evolutionarily stable energy allocation. Once we know the dynamics of the population for a given energy allocation function $k(x)$, we turn our interest to evolutionary aspects of the model. More precisely, we want to know what choice of $k(x)$ defines an evolutionarily stable life history. Notice that we are not seeking an optimal value of a scalar parameter (*trait*) that characterizes the life history as usual in this sort of analysis, but trying to find an optimal *function* $k(x)$ of the body size that defines, at each size, the proportion of energy invested in growth.

Moreover, for this optimization we will not restrict ourselves to any assumption on the dynamics of the resident population except for the boundedness of trajectories of the resident population, a property previously proved in Lemma 2. This is in contrast to what it is usually done in defining the environment experienced by the population of mutants/invaders.

4.1. ESS and trait substitution dynamics. An ESS is an *unbeatable* strategy in the sense that, if the resident adopts it, any invasion of individuals (*mutants* or *invaders*) adopting another strategy will not succeed. In our case a strategy is a choice of $k(x)$, the energy allocation function, and its ESS value will be called the ES energy allocation.

In this definition of ESS it is usually implicitly assumed that the number of mutants/invaders is low with respect to the number of residents and, moreover, that mutant/invader strategy differs but slightly from the resident strategy. The first assumption implies that the environmental conditions (for instance, the resource level) experienced by the mutants/invaders can be taken as known functions of time which are given by the solutions of the equations governing the resident-resource dynamics. This fact implies that the equation for the dynamics (spread) of the initial mutant/invader population becomes linear (see [12], [18]). In other words, an ESS so obtained is an equilibrium point of the adaptive dynamics (AD) under perturbations by small mutant/invader populations. However, such an ESS does not necessarily have to be an attractor of the AD. Instead, it can be a repeller of the AD (see [5], [8], [9], [11], [17], [18]).

In order to avoid this misleading terminology, some authors have renamed the singular points of the AD as *evolutionarily singular strategies* (see [7] and [11]), a choice that maintains the acronym ESS, or as evolutionarily unbeatable strategies (see [17], [18]). From now on, to keep notation as simple as possible, we will follow the first option and denote the singular points (strategies) of the AD by ESS.

The assumption that mutant strategies are close to the resident one in the *trait or strategy space* seems suitable from a point of view of occurrence of mutants, but it is restrictive when invasions are considered: there is no need to restrict invaders to only slightly different strategies. The ESSes obtained under this assumption are called *local* ESSes (see the previous references).

On the other hand, since the energy allocation function constitutes an infinite-dimensional trait, one has to be precise with the meaning of the word "attractivity" and, in particular, with the notions of *neighborhood* in the definition of a local ESS and *convergence* to an ESS in the AD. Both concepts are straightforward when a scalar-valued trait (or a finite number of them) is considered, but they become more sophisticated when one deals with an infinite-dimensional trait space.

We say that an ESS is *globally stable* if a resident population adopting it outcompetes *any* initial number of mutants/invaders playing $n-1$ alternative strategies ($n \geq 2$) that have been taken arbitrarily from the trait space. Hence, a globally stable ESS cannot be invaded (even if initially rare itself) by any other strategy because the definition of global stability is made regardless of the initial number of individuals playing the strategies. (This notion of global stability is analogous to the one used in the theory of dynamical systems.) On the other hand, if one restricts this definition of ESS to $n-1$ *nearby* alternative strategies, then the ESS is only *local*. In this case, the noninvasibility of the (local) ESS is only guaranteed for those strategies that are close to it.

Now, let us consider the sequence of trait (or strategy) substitutions which is obtained when, repeatedly, an *arbitrary* set of $n-1$ strategies ($n \geq 2$) is added to a resident population with any numbers of individuals playing each of the strategies. This (sequential) replacement of a current trait or strategy is called a *trait substitution sequence* and its limit, when it exists, corresponds to a globally *convergence-stable* ESS (see [5], [11]). Notice that, in general, (a measure of) fitness can be maximized by different strategies which are not necessarily close to each other; consequently, the convergence of the trait substitution sequence is not always possible.

In our case, thanks to the special form of the solutions, the ES energy allocation can be specified and its stability determined. In order to see this, we will consider a population consisting of n subpopulations, the members of which adopt strategies $k^i(x)$ with $i = 1, \dots, n$, respectively.

The system of equations governing the dynamics of this polymorphic population, together with a dynamical resource, is the natural generalization of (3.6) given by

$$\text{(4.1)} \qquad \begin{cases} U_t^i - f(r) A^{k^i} U^i = -m(r)\, U^i, \;\; i = 1, \dots, n, \\[2ex] r' - g(r)\, r + f(r) \displaystyle\sum_{i=1}^{n} L\, U^i = 0, \quad t > 0, \end{cases}$$

where $k^i(x)$ is the energy allocation function of the i-strategy, A^{k^i} is the operator given by (3.7) for each k^i, and U^i is the density of consumers adopting this strategy.

Rescaling time by means of the function $\tau = G^{-1}(t) = \int_0^t f(r(s))\, ds$, as in Theorem 2, we can rewrite the previous system as

$$\text{(4.2)} \qquad \begin{cases} U_\tau^i - A^{k^i} U^i = -\frac{m(r)}{f(r)}\, U^i, \;\; i = 1, \dots, n, \\[2ex] r' - \dfrac{g(r)}{f(r)}\, r + \displaystyle\sum_{i=1}^{n} L\, U^i = 0, \quad \tau > 0, \end{cases}$$

where $\tau = G^{-1}(t)$ tends to infinity as t tends to infinity (see Theorem 4). From now on, let us denote τ by t.

Now, given a set of strategies $\{k^i(x)\}$, denote by $\tilde\lambda$ the maximum of the set $\Lambda = \{\lambda_i : \lambda_i \text{ is the dominant eigenvalue of } A^{k^i},\ i = 1, \ldots, n\}$. Recall that, for any strategy $k^i(x)$, the existence of a dominant eigenvalue is guaranteed by Theorem 1.

Adding and substracting $\tilde\lambda U^i$ to the equation for the i-consumer, and introducing the form of the solutions $U^i(t) = \varphi^i(t)\, T^{k^i}_{\tilde\lambda}(t)\, U_0$, where, for any λ, we call $T^{k^i}_\lambda(t)$ the semigroup generated by $A^{k^i} - \lambda I$, it follows that the functions φ^i, $i = 1, 2, \ldots, n$ satisfy a system of equations analogous to (3.9), namely,

$$
\text{(4.3)} \qquad \begin{cases} r' = \dfrac{g(r)}{f(r)} r - \displaystyle\sum_{i=1}^{n} \varphi^i\, L\, T^{k^i}_{\tilde\lambda}(t)\, U_0, \\[2ex] \varphi^{i'} = \left(\tilde\lambda - \dfrac{m(r)}{f(r)}\right) \varphi^i, \quad i = 1, \ldots, n, \end{cases}
$$

with initial condition $r(0) = r_0,\ \varphi^i(0) = 1,\ i = 1, \ldots, n$.

However, since all the equations for the φ^i are the same and so is their initial condition ($\varphi^i(0) = 1$), all the functions $\varphi^i = \varphi$ for $i = 1, \ldots, n$ by the uniqueness of solution. Hence, system (4.3) is equivalent to

$$
\text{(4.4)} \qquad \begin{cases} r' = \dfrac{g(r)}{f(r)} r - \varphi \displaystyle\sum_{i=1}^{n} L\, T^{k^i}_{\tilde\lambda}(t)\, U_0, \\[2ex] \varphi' = \left(\tilde\lambda - \dfrac{m(r)}{f(r)}\right) \varphi, \end{cases}
$$

with initial condition $r(0) = r_0$ and $\varphi(0) = 1$.

As in Lemma 2, the solution (r, φ) of system (4.4) with the previous initial condition is bounded, since $\sum_{i=1}^{n} L\, T^{k^i}_{\tilde\lambda}(t)\, U_0$ is bounded from below by a positive number. This is true because there is at least one i such that $\lambda_i = \tilde\lambda$ and so $L\, T^{k^i}_{\tilde\lambda}(t)\, U_0$ tends to a positive limit by Theorem 1.

Then, using again the expression for the solution to the full problem in terms of the semigroup $T^{k^j}_{\tilde\lambda}(t)$, namely, $U^j(t) = \varphi^j(t)\, T^{k^j}_{\tilde\lambda}(t)\, U_0$, we have that all the densities of the consumers adopting a strategy k^j with $\lambda_j < \tilde\lambda$ tend exponentially to zero because $T^{k^j}_{\tilde\lambda}(t) U_0 = e^{(\lambda_j - \tilde\lambda)t} T^{k^j}_{\lambda_j}(t) U_0$ tends to zero when time goes to infinity (see Theorem 1) and, moreover, that $\varphi^j(t)$ is bounded. So, recalling the previous definitions on stability of an ESS, we have proved the following.

THEOREM 5. a.) *Trait substitution: Given n different consumer strategies $k^i(x)$ and any initial polymorphic population adopting them, if $\lambda_i < \tilde\lambda := \max_i\{\lambda_i\}$ then the consumer (sub)populations with strategy $k^i(x)$ tend to zero as time tends to infinity whereas the (sub)populations adopting strategies with $\lambda_i = \tilde\lambda$ persist for any positive time.*

b.) *Convergence of the trait substitution sequences: If the dominant eigenvalue of A^k is maximized by a unique strategy $\hat k(x)$, then this strategy is the limit of any trait substitution sequence, i.e., a globally convergence-stable strategy. Moreover, $\hat k(x)$ is a globally stable ESS since it outcompetes all the other possible strategies for any initial number of consumers adopting each of them.*

Remarks. i.) If A^k has a strictly dominant eigenvalue λ and r is constant, then the operator $f(r)A^k + m(r)I$ associated to the full problem has also a strictly dominant eigenvalue, μ. In fact, for any r, μ attains its maximum value at the same strategy k as does λ, which is independent of r. Hence, the criterion of maximizing the dominant eigenvalue of A^k coincides with the classical ESS criterion of maximizing fitness by means of maximizing the per capita rate of increase of the consumer population at an ecological equilibrium (see [12]).

ii.) According to [9] and [11], an ESS that is both (globally) stable and (globally) convergence-stable is called a (globally) *continuously stable strategy* (CSS). So $\hat{k}(x)$ is a globally CSS.

4.2. The characteristic equation. The results of the previous section lead us to the eigenvalue problem associated to the linear system

$$\begin{cases} -(k\,u)' = \lambda u, \\ k(l)\,u(l) = \lambda v, \end{cases} \tag{4.5}$$

plus the boundary condition for u

$$k(0)\,u(0) = \int_0^l (1 - k(s))\,b(s)\,u(s)\,ds + b(l)\,v.$$

Notice that if there is no flow at the boundary $x = l$, then $k(l)\,u(l) = 0$ and the second component of the eigenvector (u, v) is equal to 0. Even so, we will obtain the characteristic equation for the general case assuming that terms containing v must be zero in the particular case of nonflow at the boundary.

With $Q(x) = k(x)\,u(x)$ the first equation of (4.5) becomes $Q'(x) = \frac{-\lambda Q(x)}{k(x)}$ and, hence,

$$Q(x) = Q(0)\,e^{-\lambda \int_0^x \frac{ds}{k(s)}} = Q(0)\,e^{-\lambda a(x)}, \qquad x \le l,$$

where we have denoted $a(x) = \int_0^x \frac{ds}{k(s)}$ as in section 3. Introducing $Q(x)$ in the boundary condition and using that $v = Q(l)/\lambda$, we have the characteristic equation for λ

$$\int_0^l (1 - k(s))\frac{b(s)}{k(s)}e^{-\lambda a(s)}ds + \frac{1}{\lambda}b(l)e^{-\lambda a(l)} = 1. \tag{4.6}$$

Integrating by parts and using that $Q(x)/k(x) = -Q'(x)/\lambda$, we obtain the following expression of the characteristic equation

$$\frac{b(0)}{\lambda} + \frac{1}{\lambda}\int_0^l \frac{d}{dx}\left(b(x)e^{-\lambda x}\right)(\varphi(x))^{\lambda}\,dx = 1,$$

where $\varphi(x) := e^{-a(x)+x}$ and so satisfies $\varphi(0) = 1$, $\varphi(x) > 0$ if $x < l$, and $\varphi'(x) \le 0$ because $k(x) \le 1$.

Now let us define the function $\tilde{\varphi}(x)$ as $\varphi(x)$ if $x \le l$ and as 0 otherwise. From now on and to simplify the notation, we will denote φ this new function.

Then we write the characteristic equation as

$$\mathcal{F}(\lambda, \varphi) := \frac{b(0)}{\lambda} + \frac{1}{\lambda}\int_0^\infty \frac{d}{dx}\left(b(x)e^{-\lambda x}\right)\varphi^{\lambda}(x)dx = 1 \tag{4.7}$$

or, equivalently,

$$\mathcal{G}(\lambda, \phi) := \frac{b(0)}{\lambda} + \frac{1}{\lambda}\int_0^\infty (b'(x) - \lambda b(x))\, \phi(x)\, dx = 1, \tag{4.8}$$

where $\phi(x) = e^{-\lambda x}\varphi^\lambda(x) (= e^{-\lambda a(x)}$ if $x < l)$.

4.3. Optimization of $\boldsymbol{\lambda(k)}$. Notice that, in the characteristic equation, λ and $k(x)$ (or $\varphi(x)$, or $\phi(x)$) are unknown. In view of Theorem 5, the goal of this subsection is to find a function $k(x)$ on $[0, l]$ strictly positive and bounded from above by 1 that maximizes λ among those satisfying (4.7) or (4.8). The next lemma and procedure will simplify this search.

We say that a function φ defined on $[0, \infty)$ is *admissible* if it is decreasing with, at most, one point of discontinuity (at $x = l$), and satisfies $\varphi(0) = 1$ and $\varphi(x) \geq 0$ $\forall\, x$. Then, since $\frac{\partial}{\partial\lambda}\mathcal{F}(\lambda, \varphi) < 0$ (see (4.6)), $\mathcal{F}(0, \varphi) = \infty$, and $\mathcal{F}(\infty, \varphi) = 0$, the next lemma immediately follows.

Lemma 3. *The characteristic equation $\mathcal{F}(\lambda, \varphi) = 1$ defines λ as an implicit function of φ, $\lambda = \lambda(\varphi)$, for any admissible φ.*

Now we have the following procedure: To maximize λ in the characteristic equation $\mathcal{F}(\lambda, \varphi) = 1$, we find, for any given λ, a function φ_λ that strictly maximizes $\mathcal{F}(\lambda, \varphi)$, and then we obtain the value of $\lambda = \hat{\lambda}$ such that $\mathcal{F}(\hat{\lambda}, \varphi_{\hat{\lambda}}) = 1$.

In order to see that $\lambda(\varphi) < \hat{\lambda}$ for $\varphi \neq \varphi_{\hat{\lambda}}$, notice that

$$\mathcal{F}(\hat{\lambda}, \varphi) < \mathcal{F}(\hat{\lambda}, \varphi_{\hat{\lambda}}) = 1 = \mathcal{F}(\lambda(\varphi), \varphi),$$

which implies $\lambda(\varphi) < \hat{\lambda}$ because $\mathcal{F}$ is a decreasing function of λ.

Under the previous procedure we obtain the following

Theorem 6. *Let us assume that the function b is such that, for any $\lambda > 0$, $b(x)e^{-\lambda x}$ has a unique maximum on $(0, \infty)$. Then, for any positive λ, the function φ that maximizes $\mathcal{F}$ is of the form $\chi_{[0,l]}$. The optimum values of l and λ, $\hat{l}$ and $\hat{\lambda}$, are the only solution of the system*

$$\text{i.) } \mathcal{F}(\lambda, \chi_{[0,l]}) = 1, \qquad \text{ii.) } \frac{\partial}{\partial l}\mathcal{F}(\lambda, \chi_{[0,l]}) = 0.$$

Moreover, this system in l, λ reads

$$\text{i}'\text{.) } b(l) = \lambda e^{\lambda l}, \qquad \text{ii}'\text{.) } b'(l) = \lambda b(l).$$

Proof. The hypothesis on b means that, for any $\lambda > 0$, $\frac{d}{dx}(b(x)e^{-\lambda x})$ changes sign once (from positive to negative) at a point, say, l_λ, which is a maximum point. The first statement, with $l = l_\lambda$, follows immediately from the definition of $\mathcal{F}$ and the bound $0 \leq \varphi(x) \leq 1$. Moreover, l_λ satisfies ii because this equation is the necessary condition for a maximum. Now, substituting φ by $\chi_{[0,l_\lambda]}$ in the definition of $\mathcal{F}$, we find

$$\mathcal{F}(\lambda, \chi_{[0,l_\lambda]}) = \frac{b(l_\lambda)}{\lambda}e^{-\lambda l_\lambda}.$$

So, the procedure described above gives that system i′–ii′ holds for the optimum values of λ and $l\,(= l_\lambda)$.

Finally, let us show that this system has one solution and only one. For $l \geq 0$, let $\lambda = f(l)$ be the function defined implicitly by equation i′ and, for $l > 0$, let $\lambda = g(l) = b'(l)/b(l)$ (the function defined by ii′). Notice that the hypothesis of the theorem implies that g is a decreasing function taking all the values in $(0, \infty)$. Simple computations give $f(0) = b(0)$ and $f'(l) = (g(l) - f(l))\, f(l)\, (1 + l f(l))^{-1}$ for $l > 0$. So, f is increasing if $f(l) < g(l)$. From this, the existence and uniqueness of solution of system i′–ii′ follows easily since one only has to solve $f(l) = g(l)$ uniquely. □

Remark. Under the hypothesis of the theorem, $\lim_{x\to 0^+}(b'(x)/b(x)) = \infty$. This is not too restrictive when $b(0) = 0$ but it is when $b(0) > 0$.

Relaxing the hypothesis on b introduced in the last theorem leads to some technical difficulties related to the optimization of the functional $\phi \to \mathcal{G}(\lambda, \phi)$ given by (4.8) for a given positive λ. This functional is a continuous affine function of ϕ defined in $L^1(0, \infty)$. The admissible ϕ belong to the set of monotonously decreasing functions taking the value 1 at zero and being smaller than or equal to $e^{-\lambda x}$. This set is contained in K, the closure in L^1 of the convex hull of the set E of the functions of the form $e^{-\lambda x}\chi_{[0,l]}(x)$, with $0 \leq l \leq \infty$. As E is compact in L^1, its closed convex hull is a compact set (see [23, Theorem 3.25, p. 76]). So the supremum of the affine function $\phi \to \mathcal{G}(\lambda, \phi)$ in K is attained, at least, at a point in E. The corresponding φ's are characteristic functions of intervals $[0, l]$, $0 \leq l \leq \infty$. Arguing as above, we arrive at the following theorem.

THEOREM 7. *For any positive λ, the functions φ maximizing $\mathcal{F}$ are of the form $\chi_{[0,l]}$. The optimum values of l and λ are either $\hat{l} = 0$ and $\hat{\lambda} = b(0)$ or a solution of the system* i′–ii′ *appearing in Theorem* 6 *having the maximum value of λ among the solutions of this system.*

From the definition of the function φ it follows immediately that the optimal allocation function defines a "bang-bang" strategy. More precisely, we have the following.

COROLLARY 2. a. *Under the hypothesis of Theorem* 6, *the optimal allocation function is $k(x) \equiv 1 \,\forall\, x \in [0, l]$ where $l > 0$ is the solution of the system* i′–ii′.

b. *Without this hypothesis, the optimal allocation function is again $k(x) \equiv 1 \,\forall\, x \in [0, l]$ but now either with $l = 0$ or l is a solution of the same system.*

Notice that, in the second case, $l = 0$ defines an extreme strategy, namely, to reproduce from the very beginning without any growth during the life span. Obviously, this could occur only if $b(0) > 0$.

5. Discussion. In the first part of the paper the dynamics of a structured population of consumers with a dynamical resource is studied. More precisely, we deal with a family of models "parametrized" by the energy allocation function $k(x)$, i.e., the (size-dependent) fraction of the energy uptake invested in growth. This allocation function, in fact, defines the life history of the consumers because it determines, together with the energy uptake, the values of the growth and reproduction rates. This uptake is assumed to be only dependent on the resource level, r.

Depending on the energy allocation function, the consumer population can consist of two sorts of members: growing and nongrowing individuals or only growing individuals. In the last case, the whole population is structured with respect to the size while, in the former, the nongrowing individuals are unstructured, all having size l. For these individuals $k = 0$, i.e., the reproductive function $1 - k$ is equal to 1. When l is finite, the form of $k(x)$ determines the existence of nongrowing individuals because, when $k(l) > 0$ (or when $k(x)$ tends "abruptly" to zero as x tends to l), there occurs a flow through the boundary $x = l$ to the class of nongrowing individuals.

The idea behind the first part of the paper is to provide a set of models with known dynamics that include as general $k(x)$ as possible. This is done in order to find an optimum of the allocation function $k(x)$ in this set, which is the aim of the second part of the paper. The optimal $k(x)$ maximizes the dominant eigenvalue of the operator A given by (3.7). This eigenvalue is a measure of the fitness of the given strategy $k(x)$ and it corresponds to the intrinsic growth rate of the population of consumers adopting this strategy in a virgin environment, i.e., regardless of the resource level.

The optimal life history of the consumers turns out to be the strategy of investing all the energy obtained from the resource into growth until certain size l is achieved. After that point all the energy is invested in reproduction. This result remains true under any environment given by the resident population and under any initial mutant/invader population, i.e., it defines a globally stable ESS. This situation differs from the one obtained in [8], where periodic solutions of a discrete-time model allow the coexistence of two different strategies, if there exists a correct synchronization of mutants/invaders with the resident oscillations, and under suitable choices of the parameter values. Moreover, under the hypothesis that guarantees the uniqueness of an ESS (see Theorem 6 and below), this ESS turns out to be globally convergence-stable and, therefore, a globally continuously stable strategy (because of its global stability).

It is worth noting that the optimal value of l is obtained from the optimization procedure and, depending on $b(x)$, this value can be even zero. In particular, the condition $b(0) > 0$ is obviously needed in this case (see Theorem 7 and Corollary 2). This situation ($l = 0$) corresponds to the extreme strategy of starting reproduction at the moment of birth without any growth during the lifespan. When this is not the case, there always exists an optimal maximum size for the growing individuals of the population.

Finally, a detailed analysis reveals that, when b does not satisfy the hypothesis of Theorem 6, several values of l can define local ESSes although only one of them turns out to be global (Theorem 7), except in the critical case that system i′–ii′ has solutions with different values of l but with the same value of λ. That is, only one strategy outcompetes *all* the others regardless of the initial polymorphic population composition and the initial number of consumers adopting them. The local ESSes would correspond to local maxima of the function $b(x)\, e^{-\lambda x}$ with $\lambda > 0$ being the root of the characteristic equation (4.7) and, so, for their existence it is required that $b'(x)/b(x)$ oscillates enough with size. The critical case with more than one global maximum gives rise to several (global) ESSes. In any case, the resulting ESSes are "bang-bang" strategies as described above.

Appendix.

A.1. Properties of the semigroup $T(t)$. First, the operator A_λ given by (3.2) and (3.3) is the generator of the semigroup $T(t)$, which turns out to be positive contractions when λ is big enough. To see this one may use the Phillips theorem (see [21] or [19, Theorem 1.2, p. 249]). For convenience we will write $T = (T_1, T_2)$.

Now, integrating (3.1) along characteristics, one can show that the following representation holds, at least if $(u,\, v) \in D$, for the first component, T_1, of the semigroup:

$$T_1(t)\,(u,v)(x) = \begin{cases} B(t-a(x))\,\frac{e^{-\lambda a(x)}}{k(x)} & \text{if} \quad a(x) \le t, \\ k(x_0)\,u(x_0)\,\frac{e^{-\lambda t}}{k(x)} & \text{if} \quad a(x) > t, \end{cases} \tag{A.1}$$

where $B(\tau) := \int_0^l \beta(s) T_1(\tau)(u,v)(s)\, ds + b\, T_2(\tau)(u,v)$, $a(x) := \int_0^x ds/k(s)$, and $x_0 = x_0(x,t)$ is such that $\int_{x_0}^x ds/k(s) = t$.

Notice that $a(l) = \infty$ and $(u, v) \in D$ imply $k(l)T_1(t)(u, v)(l) = 0$. This is so because u and $(ku)'$ belonging to $L^1(0, l)$ implies that $(ku) \circ a^{-1}$ belongs to $W^{1,1}(0, a(l))$ and the functions in this Sobolev space are continuous and tend to 0 at infinity (if $a(l) = \infty$). This fact means that in this case there is no flow across the right boundary; i.e., no individual becomes a nongrowing adult, and the second component of the operator A_λ reduces to $-\lambda v$.

Second, $T(t)$ is quasi-compact under certain hypotheses on β and k (see theorem below). We recall that an operator $T(t)$ is said to be *quasi-compact* when $T(t)$ approaches a compact operator as $t \to \infty$ (see [19, Definition 2.7, p. 214]). In particular, if a semigroup $T(t)$ can be expressed as the sum of a compact operator $V(t)$ and of an operator $W(t)$ such that $||W(t)|| \leq e^{-\mu t}$ for a positive μ and for all positive time, then $T(t)$ is quasi-compact (see [29],[30]). This property will be needed to guarantee the negativity of the essential growth bound of $T(t)$ (see [19, Proposition 2.8, p. 214]) and, hence, the existence of a strictly dominant eigenvalue of the infinitesimal generator A_λ of $T(t)$. More precisely, we have

THEOREM A.1. *Let us assume $\beta \in L^\infty(0, l)$ and $k\beta' \in L^\infty(0, l)$. Then the semigroup generated by A_λ for any $\lambda > 0$ is quasi-compact.*

Proof. We consider two separate cases. First, in the case $a(l) = \infty$, the birth function $B(\tau) =< T(\tau)(u, v), (\beta, b) >$ is uniformly bounded for initial conditions (u, v) in a bounded set of X and $\tau \in [0, T]$, and its derivative can be written, for $(u, v) \in D$, as

$$B'(\tau) = \langle T(\tau)(u, v), A_\lambda^*(\beta, b)\rangle,$$

where A_λ^* is the adjoint operator of A_λ, with the domain being the pairs (α, a) in X^* such that $k\alpha' \in L^\infty$.

In the case $a(l) < \infty$, the birth function $B(\tau)$ can be written in the form

$$B(\tau) = \langle T(\tau)(u, v), \tilde{\beta}\rangle + (b - \beta(l))T_2(\tau)(u, v) \tag{A.2}$$

where $\tilde{\beta} = (\beta, \beta(l))$ belongs to the domain of the adjoint operator A_λ^*, namely,

$$D^* = \{(\alpha, a) \in X^* : \, k\alpha' \in L^\infty, \, \alpha(l) = a\}.$$

(Notice the difference between D^* and the domain of the adjoint operator in the case $a(l) = \infty$.) Thus, $B(\tau)$ turns out also to be uniformly bounded for initial conditions (u, v) in a bounded set of X and $\tau \in [0, T]$. Moreover, if $(u, v) \in D$, then $B(\tau)$ is also differentiable and its derivative is

$$B'(\tau) = \langle A_\lambda T(\tau)(u, v), \tilde{\beta}\rangle + (b - \beta(l))[k(l)T_1(\tau)(u, v)(l) - \lambda T_2(\tau)(u, v)].$$

Using (A.1), this derivative can be written for $\tau > a(l)$ as

$$B'(\tau) = \langle T(\tau)(u, v), A_\lambda^*\tilde{\beta}\rangle + (b - \beta(l)) \left[B(\tau - a(l))e^{-\lambda a(l)} - \lambda T_2(\tau)(u, v)\right].$$

So, in both cases, $B'(\tau)$ is uniformly bounded for initial conditions (u, v) in a bounded set of X and belonging to D and $\tau \in [0, T]$.

From this and using (A.1) again, it is easy to show the compactness of the operators $\chi_{[0,a^{-1}(t)]}T_1(t)$ for any $t > 0$ if $a(l) = \infty$, and $T_1(t)$ for $t > 2a(l)$ if $a(l) < \infty$.

Finally, the statement of the theorem follows from the fact that $||\chi_{[a^{-1}(t),l]}T_1(t)||_X = e^{-\lambda t}||u||_{L^1} \to 0$ as $t \to \infty$. □

A.2. Proof of Theorem 1. First, it is clear that $\mathcal{F}(\lambda)$ given by (3.4) is a monotonously decreasing function of $\lambda > 0$, tending to 0 when $\lambda \to \infty$ and, assuming $\liminf_{x\to l^-} \beta(x) > 0$ if $a(l) = \infty$ or $b > 0$ if $a(l) < \infty$, tending to ∞ when $\lambda \to 0$. Thus, the existence of a unique positive solution of (3.4) is guaranteed.

Second, an easy computation shows that 0 is an eigenvalue of A_{λ^*} with corresponding eigenvector $\hat{U}$. Moreover, A_{λ^*} has no positive (real) eigenvalues because these would imply the existence of real solutions of equation (3.4) greater that λ^*.

Now, as $T_{\lambda^*}(t)$ is quasi-compact, its essential growth bound is negative (see [19, Proposition 2.8, p. 214]) and so, Corollary 3.16, p. 318 in location cited implies that the spectral bound of A_λ is a strictly dominant eigenvalue. Hence, 0 is the strictly dominant eigenvalue.

When $T_{\lambda^*}(t)$ is irreducible (this is so if and only if $a(l) < \infty$) then 0 is a first order pole of the resolvent (see [19, Corollary 3.16, p. 318]) and, so, it is algebraically simple (see [19, Proposition 3.5, p. 310]). If $a(l) = \infty$ the latter is also true. Indeed, $A_{\lambda^*}U = \hat{U}$ implies that the second component of U is 0 (as the second component of $\hat{U}$ is). This would imply that 0 is an eigenvalue of, at least, algebraic multiplicity two of the generator of the semigroup $\tilde{T}(t)$ in L^1 given by the first component of $T_{\lambda^*}(t)$ restricted to initial conditions of the form $(u, 0)$, which is clearly irreducible. This would contradict Proposition 3.5, p. 310, in [19].

The remaining statements follow easily from the proof of Theorem 2.1, p. 343, in [19], and Remark 2.2.c following it. A direct computation of the resolvent of A_{λ^*} at 0 shows that $\alpha(U)\hat{U}$ is the residue of the resolvent, and the positiveness of the linear form $\alpha(U)$. $\square$

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