Steady states of a selection-mutation model for an age structured population*

Àngel Calsina and Josep M. Palmada

Abstract

We introduce a selection-mutation model for a density of populations with respect to physiological age and maturation age, where the latter is considered as an evolutionary trait on which the vital rates depend, subject to selection by competition, and to mutation modelled by a convolution-like operator in the birth term. We prove well-posedness of the initial value problem and the existence of non-trivial steady states under suitable hypotheses which give uniqueness when the interaction variable is one-dimensional.

1 Introduction

One of the most active topics in Mathematical Biology is structured population dynamics which consists in models for populations where individual differences are taken into account giving rise to densities with respect to internal physiological variables, usually age and size. Indeed, we could go back to Euler ([14], 1760), the linear model by Sharpe, Lotka and McKendrick in [31] (1911) and in [25] (1926), and the non linear of Gurtin and MacCamy in [17] (1974) as pioneers in this subject, and more recently, at a risk of being much partial and incomplete, see for example [26], [32], [19], [8], [21] and [23]). Likely, but with a more particular meaning of the structuring variable, recently many other papers have appeared, see e.g. [27], [1] where it stands for the content of a certain group of proteins, and [18] and [15], where it is the pathogen load bore by infected individuals.

Nevertheless, sometimes the structuring variables are phenotypic continuous variables (genetically fixed and generally submitted to hereditary mutations) like for example the maturation age, the degree of virulence of a certain virus, or its latency period, or the time an individual invests in searching and processing a certain resource to the detriment of another one, etc. (see, among much others, [3], [4], [5], [6], [10], [16] and [28]). Of course, the mathematical setting of the first type of models and the other one are quite different due to the underlying biological meaning of the structuring variable. Indeed, physiological variables change

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along the life course of individuals, i.e., individuals *travel* through the physiological space, usually continuous, and this gives rise to mathematical models based in transport equations, whereas phenotypic variables do not change at all along life and they are transmitted from progenitors to offspring, sometimes with mutations occurring mainly during the *birth* process (understood in a wide sense). So individuals diffuse (by mutation) in the phenotypical space, giving rise to models where diffusion operators (like in [3], [16] and [28]) or integral (convolution-like) operators are used ([4], [5], [6] and [28]).

In the present paper we are interested in modeling the evolution of life histories, in particular, in modeling the evolution of the maturation age. We treat the latter as a phenotypic variable in the sense of the preceding paragraph, submitted to mutation and selection, that is, as an evolutionary trait. So we consider a model of population dynamics continuously structured by age and by an evolutionary variable (the age at maturity). We assume two kinds of individuals, young (infertile) and adult (reproductive), and that the transition from one group to the other occurs when the age at maturity is reached. This maturation age is in principle different from one individual to another, it is genetically fixed for any individual and it suffers hereditary mutation (modelled by an integral operator). We need an age structure superposed to the simpler two groups age structure considered in [4] and [5] for similar purposes because we are interested in a deterministic evolutionary trait taking a definite value for any individual and thus we have to take into account the age of that individual. The difference and main novelty of this model compared to other selection-mutation models is that, for a fixed value of the evolutionary trait and ignoring the mutation kernel (the so called purely selection or ecological model), we still face a dynamical system in infinite dimension: a problem of age structured population dynamics.

The structure of the paper is as follows. In the next section we introduce the model with some assumptions on the parameters. In Section 3 we present and briefly discuss two alternative formulations of the initial value problem. In Section 4 we prove the existence of nontrivial stationary solutions under suitable conditions. And in the final section we briefly interpret these conditions from the biological point of view.

2 Description of the evolutionary model

We consider the following model for the dynamics of a population with age structure, which consists of individuals with different values of an evolutionary variable, genetically determined and denoted by l, namely, the maturation age.

More precisely, we think of two kinds of individuals: young (and non fertile) and adult (and reproductive), and the transition from the first to the second group occurs at a given age l, in general different for any individual, and fixed at birth:

$$
\begin{cases}
\dfrac{\partial u}{\partial t}(l,a,t) + \dfrac{\partial u}{\partial a}(l,a,t) = -m(E[u(t)],l,a)u(l,a,t) \\[2ex]
u(l,0,t) = \displaystyle\int_0^{+\infty} \int_{\hat{l}}^{+\infty} \beta(l,\hat{l})\ b(E[u(t)],\hat{l},a)\ u(\hat{l},a,t)\ da\ d\hat{l} \\[2ex]
u(l,a,0) = u_0(l,a).
\end{cases}
\tag{1}
$$

Here $u(l,a,t)$ is the density of population of individuals of physiological age a and maturation age l at time t (young if $a < l$, and adult otherwise). E is a continuous linear function from the state space $X = L^1((0,\infty)^2)^+$ to (the positive cone of) a (in principle finite) N-dimensional space Y and summarizes the interaction between individuals through competition. We will assume that $E[u] \neq 0 \in Y$ whenever u is non negative and different from 0. Usually E is a total weighted population (in which case N would be 1), or for instance, it can have two components ($N = 2$) if the total population of young individuals $P(t) = \int_0^{+\infty} \int_0^l u(l,a,t)\ da\ dl$ and the total population of adult individuals $Q(t) = \int_0^{+\infty} \int_l^{+\infty} u(l,a,t)\ da\ dl$ are considered separately. A case of dimension larger than two would arise, for instance, if moreover, the biomass of adults was considered in E, as given by $\int_0^{+\infty} \int_l^{+\infty} w(l)u(l,a,t)\ da\ dl$, assuming that adults don't grow and have a size determined by their maturation age. On the other hand, we would have an infinite dimensional environment if, for instance, there was a hierarchical interaction of the type $E[u](a) = \int_0^{\infty} \int_a^{\infty} u(l,\alpha,t)\ d\alpha dl$, i.e., if the environment sensed by individuals of age a depended on (and only on) the whole individuals which are older than them.

We assume that the death rate m is a bounded function (below by a positive constant μ), which is strictly increasing (due to competition for resources) and Lipschitzian with respect to its N first variables (if Y is an infinite dimensional Banach lattice then we would assume that $m(w_1,l,a) < m(w_2,l,a)$ whenever $w_1 \leq w_2$ and $w_1 \neq w_2$). In fact, the hypothesis that $m(\lambda_1 w,l,a) < m(\lambda_2 w,l,a)$ for any $\lambda_1 > \lambda_2 \geq 0$, $(l,a) \in \mathbb{R}_+^2$ is enough to prove the results of the paper. For instance, a particular form of the death rate can be written if the young individuals and the adults have separated mortalities m_1 and m_2 which only depend on $P(t)$ and $Q(t)$ respectively (for instance because the two age groups feed on different resources) and are relatively insensitive to age (as it is usual in many animal populations):

$$
m(P,Q,l,a) = \begin{cases} m_1(P) & a < l \\ m_2(Q) & a > l. \end{cases}
\tag{2}
$$

$b(E,l,a)$ is the birth function or fertility of individuals with age a and maturation age l if the environment or interaction variable takes the value E, which we will assume to be bounded above by a constant b_0. Analogously to what we assume on the mortality rate, to take into account the competition for resources, we may think that b is strictly decreasing with respect to its N first variables (with analogous meaning as above in the infinite dimensional case), but assuming, as above, that it is strictly decreasing along rays of the first variable suffices. We will assume that young individuals do not reproduce and so that b vanishes for $a < l$ and that adults always have a positive fertility, i.e. $b > 0$ for $a > l$. On the other hand, from the biological meaning, we can assume that young individuals increase their size with age, whereas they give up growing when they reach the age $a = l$ and become adult. As in most cases size is a main indicator of the reproductive capacity, it is then natural to assume that the function $b(E, l, a)$ is increasing with respect to $l < a$, i.e. a delayed age at maturity will imply a larger fertility.

On the other hand, if the life expectancy of the adult individuals is very small, we could even assume that b only depends on l and E: $b(E, l, a) = b(E, l)$ (for $a > l$ of course), but in general, we rather think that b decreases with age, at least for large values of a.

For instance we can take a function b like the following:

$$b(E, l, a) = \begin{cases} 0 & a < l \\ b_1(a)b_2(l)b_3(E) & a \geq l, \end{cases} \tag{3}$$

where $b_1(a)$ is a constant until a certain critical age and from there on, it decreases and tends to 0, and $b_2(l)$ is a strictly increasing function, bounded and such that $b_2(0) = 0$. Finally $b_3(E)$ is a decreasing function (in an analogous sense as m), vanishing as $\|E\|$ goes to infinity to take into account the effect in the birth rate of the competition for resources. Notice that the dependence of the birth rate b on the maturation age l is essential for the biological meaning of the model, whereas it is dispensable in the case of the death rate m.

For technical reasons, we will assume uniform continuity of m and b in the sense that for any $\epsilon > 0$ there is $\delta > 0$ such that

$$|b(w_1, l, a) - b(w_2, l, a)| < \epsilon \tag{4}$$

and

$$|m(w_1, l, a) - m(w_2, l, a)| < \epsilon \tag{5}$$

for all l and a if $\|w_1 - w_2\| < \delta$.

The first equation in (1) gives the temporal evolution of $u(l, a, t)$: age changes with time at *speed* 1, and the mortality affects $u(l, a, t)$ by the negative term $m(E, l, a)u(l, a, t)$.

The second equation (or boundary condition) gives the influx of newborns. One first considers the density number of offspring per time unit of individuals of type $\hat{l}$, i.e., the integral with respect to age of the fertility rate $b(E, \hat{l}, a)$ times the density of adults with maturation age $\hat{l}$ and physiological age a at time t: $\int_{\hat{l}}^{+\infty} b(E[u], \hat{l}, a)u(\hat{l}, a, t)\, da$. This term is multiplied by a probability density $\beta(l, \hat{l})$ modelling the mutation or erroneous replication of the evolutionary trait in such a way that $\int_{l_1}^{l_2} \beta(l, \hat{l})\ dl$ is the probability that the offspring of an individual with age at maturity $\hat{l}$ has maturation age $l \in (l_1, l_2)$. Since $\beta(l, \hat{l})$ is a density function, $\int_0^{+\infty} \beta(l, \hat{l})\ dl = 1$ holds for all $\hat{l}$. And finally, we integrate with respect to the type $\hat{l}$.

We are mostly interested in densities such that the expected value of $(l - \hat{l})^2$, $\int_0^{\infty} (l - \hat{l})^2\ \beta(l, \hat{l})\ dl$, is small, being the interpretation that we assume that large mutations are very improbable. In most cases the function $\beta(l, \hat{l})$ will be concentrated along the diagonal $l\hat{l}$, i. e., adults with maturation age close to $\hat{l}$ will have a larger probability of having offspring with maturation age close to $\hat{l}$.

The leitmotiv of the model (1) is twofold. On the one hand, there is a trade-off between a moderately large value of the maturation age l, taking advantage of a larger fertility b and the inconvenience that less individuals will reach adultness, and a smaller value of l, which can compensate a low fertility by a larger number of individuals promoting to adult. On the other hand, we address the classical balance between the selection forcing toward a definite intermediate value of l (as it can be expected from the preceding comments) and the mutation tending to preserve a large amount of different values of l. So, one should expect stationary solutions as densities (of equilibrium) more or less concentrated around optimal values in some sense of l. The works [4] and [5] address a similar model, even though there, as there is no age structure apart from the distinction between young and adults, the age at maturity has to be interpreted as an average value and the length of the juvenile period as an exponentially distributed random variable instead of a deterministic value as in the present paper.
Finally, the third equation is an initial condition.

3 Initial value problem

There are several possible formulations of the initial value problem for systems like (1). The classical one, along the lines of G. Webb book [32] (see also [19]), initiated by the seminal paper [17], consists in the natural option of taking as state space the space of population densities $u(l, a)$, say $X = L^1((0, \infty)^2)$, and it reduces the problem to find a continuous curve on $[0, T]$ (for some positive T) with values in X, such that coincides with the initial condition for $t = 0$ and it is a unique fixed point of a contractive map $\mathcal{F}$.
The contraction $\mathcal{F}$ is constructed as follows. First consider the "birth map" giving the density number (with respect to the type $\hat{l}$ of the father) of offspring per time unit

$$B : X \times Y = L^1(\mathbb{R}_+{}^2) \times Y \longrightarrow L^1(\mathbb{R}_+)$$

defined as $B(u, w)(\hat{l}) = \int_{\hat{l}}^{\infty} b(w, \hat{l}, a) u(\hat{l}, a) da$, and secondly, the "mutation operator",

$$K : v \in L^1(\mathbb{R}_+) \longrightarrow \int_0^\infty \beta(l,\hat{l})v(\hat{l})d\hat{l} \in L^1(\mathbb{R}_+),$$

which transforms the latter into a density with respect to the type l of the offspring.
Now let us consider the inflow of newborns (at age 0) $\mathcal{B}$ and the "environment" (interaction variable) $\mathcal{E}$ as continuous curves belonging to the spaces $\mathcal{C}([0,T],L^1(\mathbb{R}_+))$ and $\mathcal{C}([0,T],Y)$ respectively. Once determined $\mathcal{B}$ and $\mathcal{E}$, the corresponding population density u is given by

$$U(\mathcal{B},\mathcal{E})(t)(l,a) := u(l,a,t) = \begin{cases} u_0(l,a-t)e^{-\int_0^t m(\mathcal{E}(s),l,a-t+s)ds} & \text{if } a > t, \\ \mathcal{B}(t-a)(l)e^{-\int_{t-a}^t m(\mathcal{E}(s),l,s-t+a)ds} & \text{if } a < t. \end{cases} \tag{6}$$

Here U maps $\mathcal{C}([0,T],L^1(\mathbb{R}_+)\times Y)$ to $\mathcal{C}([0,T],X)$.
Also, just for convenience, define Id_i as the operator mapping the pair (x_1,x_2) to the coordinate x_i (and $Id(x)=x$).
Then one defines, on a closed subset of the space $\mathcal{C}([0,T],X)$ of the form

$$\mathcal{M} = \{u \in \mathcal{C}([0,T],X) : u(0)=u_0, \|u\| \le 2\|u_0\| \ \},$$

the map

$$\mathcal{F} = U \circ (\widetilde{K} \circ \widetilde{B}, \widetilde{Id_2}) \circ (\widetilde{Id}, \widetilde{E}),$$

where the notation $\tilde{f}$ stands for the (Nemytskii) operator induced between the spaces of (continuous) curves on the (arbitrary) spaces S_1 and S_2 respectively by a function f mapping S_1 in S_2 as $\tilde{f}(c) = f \circ c$ and the natural identification of the spaces $\mathcal{C}([0,T],S_1\times S_2)$ and $\mathcal{C}([0,T],S_1)\times\mathcal{C}([0,T],S_2)$ has been made when needed.
Notice that all the functions appearing in $\mathcal{F}$ are bounded linear (more precisely, the dependence of U on its first argument is affine) with norms independent of T, except for the dependence of B on its second argument (i.e., the dependence of b on the interaction variable) and the dependence of U also in its second argument (i.e., the dependence of m on the interaction variable).
That $\mathcal{F}$ leaves invariant $\mathcal{M}$ and it is a contraction follows by a standard argument from assuming that b and m are locally Lipschitzian continuous functions of their first argument, i.e., that for any $r>0$ there exist positive constants L_b and L_m such that if $\|w_1\| < r$ and $\|w_2\| < r$ then:

$$|b(w_1,l,a) - b(w_2,l,a)| < L_b\|w_1 - w_2\| \tag{7}$$

and

$$|m(w_1,l,a) - m(w_2,l,a)| < L_m\|w_1 - w_2\| \tag{8}$$

for all l and a.
Indeed, (7) and (8) imply that U is a Lipschitzian continuous function and that its Lipschitz constant is proportional to T. For instance,

$$
\begin{aligned}
&\|U(\mathcal{B}_1(t),\mathcal{E}(t))-U(\mathcal{B}_2(t),\mathcal{E}(t))\|_X \leq \\
&\int_0^\infty\int_0^t |\mathcal{B}_1(t-a)(l)-\mathcal{B}_2(t-a)(l)|dadl = \\
&\int_0^t \parallel \mathcal{B}_1(s)-\mathcal{B}_1(s) \parallel_{L^1(\mathbb{R}_+)} ds \leq \\
&t\sup_{s\in[0,T]}\|\mathcal{B}_1(s)-\mathcal{B}_2(s)\|_{L^1(\mathbb{R}_+)} \leq T\|\mathcal{B}_1-\mathcal{B}_2\|,
\end{aligned}
$$

and

$$
\begin{aligned}
&\|U(\mathcal{B}(t),\mathcal{E}_1(t))-U(\mathcal{B}(t),\mathcal{E}_2(t))\|_X \leq \\
&\int_0^\infty\int_0^t \mathcal{B}(t-a)(l)\int_{t-a}^t L_m \parallel \mathcal{E}_1(s)-\mathcal{E}_2(s)\parallel dsdadl + \\
&\int_0^\infty\int_t^\infty u_0(l,a-t)\int_0^t L_m \parallel \mathcal{E}_1(s)-\mathcal{E}_2(s)\parallel dsdadl \leq \\
&tL_m\sup_{s\in[0,t]}\parallel \mathcal{E}_1(s)-\mathcal{E}_2(s)\parallel (t\sup_{s\in[0,t]}\|\mathcal{B}(s)\|+\|u_0\|) \leq \\
&TL_m(T\|\mathcal{B}\|+\|u_0\|)\|\mathcal{E}_1-\mathcal{E}_2\|,
\end{aligned}
$$

where we used (6) and (8) and the inequality $|e^{-x}-e^{-y}|\leq|x-y|$ for $x\geq 0$ and $y\geq 0$. Obviously, the Lipschitz constant of the composed function $\mathcal{F}$ can be made as small as required to make $\mathcal{F}$ a contraction by taking T small enough.
Now we can state the following

Theorem 3.1. *Under (7) and (8), for any $u_0\in X$ there exists $T>0$ and a unique $u\in\mathcal{M}$ such that solves the equation*

$$
u(t)(l,a)=\begin{cases} u_0(l,a-t)e^{-\int_0^t m(E[u(s)],l,a-t+s)ds} & \text{if } a>t,\\ \mathcal{B}(t-a)(l)e^{-\int_{t-a}^t m(E[u(s)],l,s-t+a)ds} & \text{if } a<t,\end{cases} \tag{9}
$$

where

$$
\mathcal{B}(t)(l)=\int_0^{+\infty}\int_{\hat{l}}^{+\infty}\beta(l,\hat{l})\ b(E[u(t)],\hat{l},a)\ u(\hat{l},a,t)\ da\ d\hat{l}. \tag{10}
$$

Moreover, $u(0)(l,a)=u_0(l,a)$, $u(t)(l,0)=\mathcal{B}(t)(l)$ if $t>0$ and, if $t\neq a$,

$$
\lim_{h\to 0^+}\frac{1}{h}(u(t+h)(l,a+h)-u(t)(l,a)) = -m(E[u(t)],l,a)u(t)(l,a). \tag{11}
$$

Proof. The first claim has already been proven (for u being the fixed point of $\mathcal{F}$). That u satisfies the initial and boundary condition is trivial. To prove the last claim whether $a>t$ as if $a<t$, notice that

$$
\frac{u(t+h)(l,a+h)-u(t)(l,a)}{h} = u(t)(l,a)\frac{e^{-\int_t^{t+h} m(E[u(s)],l,a-t+s)ds}-1}{h} \longrightarrow_{h\to 0}
$$

$$-m(E[u(t)], l, a)u(t)(l, a).$$

□

Remark 3.1. *(11) is a slightly weak form of the partial differential equation in (1) expressing conservation of mass except because of mortality.*

Remark 3.2. *The solution is positive whenever $u_0 \in X^+$ because $\mathcal{F}$ is a positive operator since then U is positive, whereas the other operators involved in the definition of $\mathcal{F}$ are positive too.*

Another more recent approach to the formulation of the initial value problem for systems including (1), which directly adopts as state variables flux and interaction variables (more precisely, their *histories* on a time interval $[-h, 0]$, in our case, $h := \infty$) instead of the usual space of population densities with respect to structuring variables is the one developed by O. Diekmann and its collaborators (see [12]). Potentially slightly more restrictive than the previous one with respect to initial conditions ([13] Introduction), it has the important advantage that it admits the semilinear formulation of the delay equations (see [9]) which, can be traced back to the work by J. Hale (in the case of delay differential equations) and has been developed in several papers in the last years, allowing a direct proof of the so called linear stability principle (see [11], [12], [13]).
Following the lines of [12], Sect. 5, we take as state variables the flux of newborns $\mathcal{B}(t)$ and, instead of the obvious choice $\mathcal{E}(t)$, a new interaction variable, namely the death rate, related to the previous one by

$$\mathcal{I}(t)(l, a) = m(\mathcal{E}(t), l, a).$$

The state space is now a L^1 space of functions of the time variable (weighted in order that it contains constant functions, i.e., steady states), $L^1_\rho((-\infty, 0], Z)$, of the integrable functions with respect to the measure $e^{\rho\theta}d\theta$ (for some $\rho > 0$), with values in the Banach space Z which is defined as $Z = L^1(\mathbb{R}_+) \times \mathcal{C}(\mathbb{R}^2_+)$. The problem is formulated as a delay equation of the form

$$\begin{cases} x(t) = F(x_t), t > 0, \\ x_0(\theta) = \varphi(\theta), \theta \in (-\infty, 0]. \end{cases} \tag{12}$$

In our case $x(t) := (\mathcal{B}(t), \mathcal{I}(t))$ with the usual meaning $x_t(\theta) = x(t+\theta), \theta \in (-\infty, 0]$ and F is defined on $L^1_\rho((-\infty, 0], Z)$ with values in Z as follows. First consider an operator U_0, similar to the operator U of the previous paragraphs, giving as above, the population density u; defined on $L^1_\rho((-\infty, 0], Z)$ and with values in $X = L^1(0, \infty)^2$:

$$U_0(\mathcal{B}, \mathcal{I})(l, a) := u(l, a) = \mathcal{B}(-a)(l)e^{-\int_{-a}^{0} \mathcal{I}(s)(l, s+a)ds}. \tag{13}$$

Secondly, consider the function M defined on Y with values in $\mathcal{C}(\mathbb{R}^2_+)$ as $M(w) = m(w, \cdot, \cdot)$.

Finally write $F := (K \circ B, M \circ Id_2) \circ (Id, E) \circ U_0$.
The interpretation of the initial value problem in the form of the renewal equation

$$\begin{cases} (\mathcal{B}(t), \mathcal{I}(t)) = F(\mathcal{B}_t, \mathcal{I}_t), t > 0, \\ (\mathcal{B}_0(\theta), \mathcal{I}_0(\theta)) = \varphi(\theta), \theta \in (-\infty, 0] \end{cases} \tag{14}$$

is clear. Indeed, for any $t > 0$, the right hand side of the first equation starts with the *histories* of the flux and the interaction variable, $\mathcal{B}_t$ and $\mathcal{I}_t$; it computes, by means of the operator U_0, the corresponding population density u (with respect to type l and age a) multiplying the flux density of newborns at time $t-a$ by the survival probability until age a of individuals of type l born at time $t-a$, after it computes the value of the "environment" $E[u]$ for this density, and finally it computes the flux density of newborns $\mathcal{B}$ at time t using the birth operator B and the mutation operator K, and the value of the interaction variable $\mathcal{I}$ (also at time t) just computing $M(E[u])$.
The only nonlinear ingredients of F are the dependence of U_0 on $\mathcal{I}$ which is very easy to prove that is Lipchitzian; the dependence of B on w, Lipchitzian if we assume the global version of hypothesis (7):

$$\|B(u, w_1) - B(u, w_2)\|_{L^1(\mathbb{R}_+)} \leq L_b \|u\|_X \|w_1 - w_2\|_Y;$$

and the function M, which is also Lipchitzian also assuming the global version of hypothesis (8). Then, Theorems 3.2 and 2.5 in [12] give a unique solution of (14) for any initial condition $\varphi \in L^1_\rho((-\infty, 0], Z)$. Additionally, if F is also continuously differentiable, ([12], Theorem 2.6) ensures that the linearized stability principle holds.
On the other hand, given $\varphi \in L^1_\rho((-\infty, 0], Z)$, and defining $u_0 = U_0(\varphi)$, it can be easily checked that the solution $(\mathcal{B}, \mathcal{I})$ of the delay problem (14) leads to a density $u(t) := U_0(\mathcal{B}_t, \mathcal{I}_t)$ which fulfills (9)-(11). Also note that for any $u_0 \in X$ we can find a $\varphi \in L^1_\rho((-\infty, 0], Z)$ such that $u_0 = U_0(\varphi)$. Indeed, simply define $\mathcal{B}(\theta)(l) = u_0(l, -\theta)$, thus $\mathcal{B} \in L^1_\rho((-\infty, 0], L^1(\mathbb{R}_+))$, and take $\varphi = (\mathcal{B}, 0)$. Obviously φ cannot be a solution of the renewal equation $(\mathcal{B}(t), \mathcal{I}(t)) = F(\mathcal{B}_t, \mathcal{I}_t)$ for any negative t since the second component of F takes values in the range of m and so it is strictly positive whereas $\mathcal{I}(t) = 0$.

4 Steady states

A nontrivial stationary solution of (1) is, for some value $w_e \in Y^+$ of the *environmental variable*, of the form

$$u_e(l, a) = c(l) e^{-M(w_e, l, a)}, \tag{15}$$

where $M(w, l, a) = \int_0^a m(w, l, s)\, ds$ (hence $e^{-M(w,l,a)}$ is the survival probability until age a of individuals of type l when the environmental conditions are given by a -fixed- w), the boundary condition (at birth) or density rate of newborns of type l, $c(l)$, must fulfill

$$c(l) = u_e(l,0) = \int_0^{+\infty} \int_{\hat{l}}^{+\infty} \beta(l,\hat{l}) b(w_e,\hat{l},a)\ c(\hat{l}) e^{-M(w_e,\hat{l},a)}\ da\ \ d\hat{l},$$

and finally, $E[u_e] = w_e$ must hold (i.e., the "environmental condition" determined by the stationary population density u_e must coincide with the a priori postulated value w_e, closing the feedback loop). That is, if we define, for $w \in Y^+$, the positive integral operator on L^1

$$K_w(C)(l) = \int_0^{+\infty} \beta(l,\hat{l}) \int_{\hat{l}}^{+\infty} b(w,\hat{l},a)\ e^{-M(w,\hat{l},a)}\ da C(\hat{l})\ d\hat{l} \tag{16}$$

then w_e is such that the spectral radius $r(w_e)$ of K_{w_e} is equal to 1 (indeed it is a simple eigenvalue) and $c = \alpha C_{w_e}$, for some $\alpha > 0$, where C_{w_e} is *the* normalized positive eigenvector corresponding to this eigenvalue (we see below that under the hypotheses, only the right most eigenvalue has positive eigenvectors).

We shall call

$$R(w,l) = \int_l^{+\infty} b(w,l,a)\ e^{-M(w,l,a)}\ da$$

and thus, (16) reads

$$K_w(C)(l) = \int_0^{+\infty} \beta(l,\hat{l}) R(w,\hat{l}) C(\hat{l})\ d\hat{l} = \int_0^{+\infty} k_w(l,\hat{l}) C(\hat{l})\ d\hat{l},$$

where $k_w(l,\hat{l}) = \beta(l,\hat{l}) R(w,\hat{l})$.

Notice that we have the obvious bound $R(w,l) \le \sup_{a \ge l} b(0,l,a) \frac{e^{-\mu l}}{\mu} \le b_0 \frac{e^{-\mu l}}{\mu}$.

To ensure existence and uniqueness of a (normalized) positive eigenfunction of the operator K_w we will use the following theorem (which is contained in Theorem 6.6 in [30], Chap. V], except for the uniqueness of the eigenvalue having a positive eigenvector which follows from the proof of the same theorem and Theorem 2.2 of [24])

Theorem 4.1. *Let $E = L^p(\mathcal{X})$, where $1 \le p \le +\infty$ and $\mathcal{X}$ is a metric space. Let us assume that $T \in \mathcal{L}(E)$ is an integral operator given by a measurable kernel $k \ge 0$ fulfilling*

1. *Some power of T is compact.*
2. *For any $S \subset \mathcal{X}$ such that S and $\mathcal{X} \setminus S$ have positive measure, the following holds*
$$\int_{\mathcal{X} \setminus S} \int_S k(s,t)\ ds\ dt > 0.$$

Then the spectral radius of T, $r(T)$, is strictly positive and it is an isolated simple eigenvalue of T, the only one with a corresponding positive a.e. eigenfunction. Moreover, if $k > 0$ a.e., then any eigenvalue λ of T different from $r(T)$ has modulus $|\lambda| < r(T)$.

Remark 4.1. *The second hypothesis of the Theorem 4.1 is a characterization of the irreducible integral operators defined by a positive kernel (see Chapter V of [30]).*

We will assume from now on the following hypotheses on the kernel of the operator K_w:

(H1) $\int_0^{+\infty} ess \sup_{\hat{l}\in(0,\infty)} |k_w(l,\hat{l})|\, dl < \infty$, where $k_w(l,\hat{l})$ is the kernel of the operator K_w.

(H2) The support of the function $\beta(l,\hat{l})$ contains a strip around the diagonal of the plane $l\hat{l}$, i.e., there exists $h > 0$ such that the support of β contains the set $\cup_{l\in(0,\infty)}([\max\{0, l-h\}, l+h] \times \{l\})$.

Remark 4.2. *Hypothesis (H1) is equivalent to saying that the operator K_w is of Hille-Tamarkin type (see [20]). It holds if β is sufficiently concentrated along the diagonal (i.e. if large mutations are very improbable) and $R(w,l)$ is sufficiently small for large values of l (which is always true under the hypotheses we are assuming). For instance, let us assume that there exist a positive constant C such that $\beta(l,\hat{l}) \le \frac{C}{1+(l-\hat{l})^2}$. We will then have, for l large enough,*

$$\sup_{\hat{l}\in(0,\infty)} \beta(l,\hat{l})R(w,\hat{l}) \le C\frac{b_0}{\mu} \max_{0\le\hat{l}\le l} \frac{e^{-\mu\hat{l}}}{1+(l-\hat{l})^2} = C\frac{b_0}{\mu}e^{-\mu l} \max_{0\le z\le l} \frac{e^{\mu z}}{1+z^2} = \frac{Cb_0/\mu}{1+l^2}$$

since the function $\frac{e^{\mu z}}{1+z^2}$ attains its maximum at the right end of the interval for l large enough. On the other hand, (H1) also holds if for instance, $\beta(l,\hat{l}) \le \beta_0(l)$ for some integrable function $\beta_0(l)$.

Theorem 4.2. *Under hypotheses (H1) and (H2) the spectral radius $r(w)$ of K_w is a strictly positive isolated simple eigenvalue of the operator K_w and it is the only eigenvalue with a corresponding normalized positive a.e. eigenfunction $C_w(l)$.*

Proof. We will see that we are under the hypotheses of Theorem 4.1, the first one of which follows immediately from the fact that the square of a Hille-Tamarkin operator from $L^1(0,\infty)$ to $L^1(0,\infty)$ is compact (see Theorem 11.9 of [20]).

To prove the second one is sufficient to show that for any set $S \subset \mathbb{R}^+$ such that S and S^c have both positive measure, the set $(S\times S^c)\cap supp(\beta)$ has positive measure too. Let us first assume that for any interval I we have $meas(I\cap S)\cdot meas(I\cap S^c) > 0$. Then we take I with length less than h (given by (H2)) and hence $(I\cap S)\times(I\cap S^c)$ is contained in $supp(\beta)$ and has positive measure. Otherwise, we take an interval $I = [a,b]$ such that $meas(I\cap S) > 0$ and $meas(I\cap S^c) = 0$, maximal in the sense that, for any interval J, $J \supset I$ implies $meas(J\cap S^c) > 0$. Now, using (H2), we consider the interval $\tilde{I} = [\max\{b-\frac{h}{2}, 0\}, b+\frac{h}{2}]$ if $b < \infty$, or $\tilde{I} = [\max\{a-\frac{h}{2}, 0\}, a+\frac{h}{2}]$ if $b = \infty$, which fulfils that $meas(\tilde{I}\cap S)\cdot meas(\tilde{I}\cap S^c) > 0$ and $(\tilde{I}\cap S)\times(\tilde{I}\cap S^c) \subset (S\times S^c)\cap supp(\beta)$. $\square$

Theorem 4.3. *Under hypotheses (H1) and (H2) the spectral radius $r(w)$ of K_w is a continuous function. Moreover, the function $\lambda \in [0,\infty) \to r(\lambda w)$ is strictly decreasing for any $w > 0$. Furthermore, the function that maps w to the eigenfunction $C_w(l)$, given by the previous theorem, is also continuous.*

Proof. In order to prove that $r(w)$ is continuous we use a result included in Chapter 4, § 3.5, of [22], which gives the continuity with respect to parameters of isolated eigenvalues, whenever the dependence of the operator with respect to the parameters is norm continuous. This holds since

$$\begin{aligned}
\|K_w - K_{w'}\| &= \sup_{\|c\|\le 1} \int_0^\infty |(K_w - K_{w'})c(l)|\, dl \\
&\le \sup_{\|c\|\le 1} \int_0^\infty \int_0^\infty \beta(l,\hat{l})|R(w,\hat{l}) - R(w',\hat{l})||c(\hat{l})| d\hat{l}\, dl \\
&= \sup_{\|c\|\le 1} \int_0^\infty |R(w,\hat{l}) - R(w',\hat{l})||c(\hat{l})| d\hat{l},
\end{aligned}$$

and, using (4) i (5), and that the function m is bounded below by $\mu > 0$, we have that for any $\epsilon > 0$

$$\begin{aligned}
|R(w,\hat{l}) - R(w',\hat{l})| &\le \int_{\hat{l}}^\infty |b(w,\hat{l},a) - b(w',\hat{l},a)| e^{-M(w,\hat{l},a)} da \\
&+ \int_{\hat{l}}^\infty b(w',\hat{l},a)|e^{-M(w,\hat{l},a)} - e^{-M(w',\hat{l},a)}| da \\
&\le \frac{\epsilon}{\mu} + \sup b \int_{\hat{l}}^\infty e^{-\mu a} |e^{\mu a - \int_0^a m(w,\hat{l},s)ds} - e^{\mu a - \int_0^a m(w',\hat{l},s)ds}| da \\
&\le \frac{\epsilon}{\mu} + \sup b \int_{\hat{l}}^\infty e^{-\mu a} \left| \int_0^a (m(w,\hat{l},s) - m(w',\hat{l},s)) ds \right| da \\
&\le \epsilon \left(\frac{1}{\mu} + \frac{\sup b}{\mu^2} \right),
\end{aligned}$$

if $\|w - w'\| < \delta$.

We shall now prove the strict monotonicity of the spectral radius. First we recall from the previous theorem that $r(w)$ is a strictly positive eigenvalue of the operator K_w with a corresponding positive a.e. eigenfunction.

On the other hand from the proof of Theorem 4.1 in [30] it follows that $r(w)$ is a pole of the resolvent. Now, Theorem 2.2 of [24] (proved in [29]), states that if the spectral radius of an irreducible (called non-supporting in the cited papers) bounded operator satisfies this property, then it is also an eigenvalue of the adjoint operator K_w^* with a unique strictly positive eigenfunctional.

To end with, we take $0 \le \lambda_1 < \lambda_2$. By the hypotheses on strict monotony of the functions $b(w,l,a)$ and $m(w,l,a)$, we have that $K_{\lambda_1 w} \ge K_{\lambda_2 w}$ and $K_{\lambda_1 w} \ne K_{\lambda_2 w}$.

Hence, we are under the hypotheses of Theorem 4.3 of [24] and so

$$r(\lambda_1 w) > r(\lambda_2 w).$$

Finally, the continuity of the eigenfunction $C_w(l)$ is guaranteed by Lemma 1.3 of [7].

□

$R(w,l)$ can be interpreted as the expected number of offspring (of any type) of an individual of type l along its lifespan if the environmental conditions are given by a fixed w. So it is not surprising that we have the following

Lemma 4.1. *If $R(w,l) \leq 1$ for all l then $r(w) \leq 1$ holds.*

Proof. To prove this lemma is sufficient to show that $\|K_w\| \leq 1$:

$$\|K_w\, C\| = \int_0^\infty |\int_0^\infty \beta(l,\hat{l})R(w,\hat{l})C(\hat{l})\, d\hat{l}|\, dl \leq \int_0^\infty \int_0^\infty \beta(l,\hat{l})R(w,\hat{l})|C(\hat{l})|\, d\hat{l}\, dl \leq$$

$$\sup_l R(w,l) \int_0^\infty \int_0^\infty \beta(l,\hat{l})|C(\hat{l})|\, d\hat{l}\, dl \leq \int_0^\infty \int_0^\infty \beta(l,\hat{l}) dl |C(\hat{l})|\, d\hat{l}\ = \|C\|.$$

□

Theorem 4.4. *If $R_0(l) := R(0,l) \leq 1$ for all l then there is no nontrivial stationary solution.*

Proof. First recall that $E[u_e] = 0$ implies that $u_e = 0$. By Lemma 4.1 $r(0)$ is less than or equal to 1. Since r is strictly decreasing with respect to any component of w (Theorem 4.3), then there is no positive u_e such that $r(u_e) = 1$.

□

Remark 4.3. *There is no stationary solution if* $\sup_a b(0,l,a) \leq \inf m_a(0,l,a)$ *for all l since this obviously implies* $\sup R_0(l) \leq 1$.

Certainly, that $R_0(l)$ takes values larger than 1 for some l, i.e., the fact that in *ideal conditions* ($w = 0$) there are individuals whose expected number of offspring is larger than 1, is not a sufficient condition for existence of non trivial stationary solutions, since one has to take into account the possible harmful effect of mutations. For instance let us consider an extremely unrealistic but still meaningful case, the so-called *house of cards* model for the mutation kernel (see [2]), which lies in that the type of the offspring is independent of the type of the progenitor, i.e. $\beta(l,\hat{l}) = \beta(l)$, where β is a density of probability (strictly positive in order that (H2) holds). Then the range of the operator K_w reduces to the set of scalar multiples of the function β and its spectrum to the set $\{0, \int_0^\infty R(w,\hat{l})\beta(\hat{l})\, d\hat{l}\}$ and so its spectral radius is

$$r(w) = \int_0^\infty R(w,\hat{l})\beta(\hat{l})\, d\hat{l}.$$

It is obvious that $r(0) = \int_0^\infty R_0(\hat{l})\beta(\hat{l})\; d\hat{l}$ may be less than 1 even in the case that $R_0(l)$ takes values larger than 1 for some l.

From now on, we are interested in giving sufficient conditions of existence of non-trivial steady states, related to the function $R_0(l)$ taking values larger than 1 supplemented by appropriate hypotheses on the mutation kernel β.

For any closed interval $I \subset (0, \infty)$, let us define the set

$$\mathcal{I} = \{\varphi \in C^0(0, \infty) : \text{supp}(\varphi) \subset I, \varphi(x) > 0 \; if \; x \in I^\circ\}$$

and the number

$$\beta_I = \sup_{\mathcal{I}} \inf_{l \in I} \frac{\int_0^\infty \beta(l, \hat{l})\varphi(\hat{l})\; d\hat{l}}{\varphi(l)}.$$

Remark 4.4. *Notice that $\beta_I \leq 1$, since otherwise a function $\varphi \in \mathcal{I}$ would exist such that $\varphi(l) < \int_0^\infty \beta(l, \hat{l})\varphi(\hat{l})\; d\hat{l}$ for all $l \in I$. Integrating the inequality on I and interchanging the integration order, we would find a contradiction:*

$$\int_0^\infty \varphi(l)dl = \int_I \varphi(l)dl < \int_I \int_0^\infty \beta(l, \hat{l})\varphi(\hat{l})\; d\hat{l}\; dl \leq$$

$$\int_0^\infty \int_0^\infty \beta(l, \hat{l})\varphi(\hat{l})\; d\hat{l}\; dl = \int_0^\infty \varphi(\hat{l})d\hat{l}$$

Proposition 4.1. *Let us assume that there exists an interval $I \subset (0, \infty)$ such that $\beta_I \inf_{l \in I} R(w, l) > 1$. Then the spectral radius $r(w)$ of the linear operator K_w is larger than 1.*

Proof. Due to the definition of β_I, for any $\epsilon > 0$ there exists a positive continuous function ψ with support in I such that for all $l \in I^\circ$,

$$\frac{\int_0^\infty \beta(l, \hat{l})\psi(\hat{l})\; d\hat{l}}{\psi(l)} \geq \beta_I - \epsilon.$$

From the hypothesis there exists $\delta > 0$ such that $\beta_I > \dfrac{1 + \delta}{\inf_{l \in I} R(w, l)}$. Taking $\epsilon = \beta_I - \dfrac{1 + \delta}{\inf_{l \in I} R(w, l)} > 0$ we have

$$(K_w\psi)(l) = \int_0^\infty \beta(l, \hat{l})R(w, \hat{l})\psi(\hat{l})\; d\hat{l} \geq \inf_{l \in I} R(w, l) \int_0^\infty \beta(l, \hat{l})\psi(\hat{l})\; d\hat{l} \geq$$

$$(\beta_I - \varepsilon) \inf_{l \in I} R(w, l)\psi(l) \geq (1 + \delta)\psi(l)$$

for all l, and it follows that $r(w) > 1$. □

Remark 4.5. *Lower bounds on β_I obviously depend on the function $\beta(x,y)$ and in particular, in how* concentrated *around the diagonal $\beta(x,y)$ is.*

To gain intuition we can think, for instance, of $\beta(l,\hat{l}) = \beta^t(l,\hat{l})$ as given by the integral kernel of the solution $u(l,t)$, for some fixed φ and t of the initial and boundary value problem for the heat equation

$$u_t = u_{ll}, l \in (0,\infty); u_l(0,t) = 0, u(l,0) = \varphi(l).$$

That is, $u(l,t) = \int_0^\infty \beta^t(l,\hat{l})\varphi(\hat{l})\ d\hat{l}$. Notice that $\beta^t(l,\hat{l})$ satisfies the hypotheses on the function β.

Now let us take φ supported in (an arbitrary interval) $I = [a,b] \subset (0,\infty)$. For $l \in I$, by the maximum principle, $u(l,t)$ is larger than or equal to the solution $u_0(l,t)$ of the heat equation with homogeneous Dirichlet boundary conditions on I and $\varphi \mid_I$ as initial condition. In particular, taking $\varphi(l) = \sin(\pi(\frac{l-a}{b-a}))\chi_{[a,b]}(l)$, we have

$$u_0(l,t) = e^{-(\frac{\pi}{b-a})^2 t}\sin(\pi(\frac{l-a}{b-a}))$$

for $l \in [a,b]$, and hence, $\int_0^\infty \beta^t(l,\hat{l})\varphi(\hat{l})\ d\hat{l} = u(l,t) \geq u_0(l,t) = e^{-(\frac{\pi}{b-a})^2 t}\varphi(l)$, also for $l \in I$. So, $(\beta^t)_I \geq e^{-(\frac{\pi}{b-a})^2 t}$. Certainly, $(\beta^t)_I$ is as close to 1 as we want taking t sufficiently small, i.e., when the kernel β is concentrated enough. On the other hand, the same is achieved for fixed β (i.e., for fixed t) if $b-a$ is large enough.

Now we can state the main theorem of this section

Theorem 4.5. *Under the hypotheses (H1) and (H2), let us assume that there exists an interval $I \subset (0,\infty)$ such that $\beta_I \inf_{l\in I} R_0(l) > 1$ and that there exist a positive number W such that $R(w,l) < 1$ for all l whenever $\|w\| \geq W$. Then there exists at least a nontrivial stationary solution of (1). Moreover, if $N = 1$, then it is unique.*

Proof. To prove existence of a stationary solution u_e we will rewrite the problem of finding $\alpha > 0$ and $w_e \in \mathbb{R}^N$ fulfilling the conditions at the beginning of the section, i.e. such that the spectral radius of K_{w_e} equals 1 and $E[u_e] = w_e$, as a fixed point problem in finite dimension. Let us begin by defining the continuous function $\widetilde{E}(w) = E[C_w(l)e^{-M(w,l,a)}]$ on $(\mathbb{R}^N)^+$ and with values in the same set (notice that here we use the continuity of the eigenfunction C_w with respect to the parameter w -see Theorem 4.3-). Let us also define the subset $\mathcal{R} = \{w \in (\mathbb{R}^N)^+ : r(w) = 1\}$. Since by (15)

$$E[u_e] = E[\alpha C_{w_e}(l)e^{-M(w_e,l,a)}] = \alpha E[C_{w_e}(l)e^{-M(w_e,l,a)}] = \alpha\widetilde{E}(w_e),$$

to find a stationary solution is equivalent to find $w_e \in \mathcal{R}$ such that there is $\alpha > 0$ such that $\alpha\widetilde{E}(w_e) = w_e$ that is, to find in $\mathcal{R}$ an eigenvector corresponding to a positive eigenvalue of the *nonlinear* operator $\widetilde{E} : (\mathbb{R}^N)^+ \to (\mathbb{R}^N)^+$.

Under the hypotheses, r is a continuous function (Theorem 4.3) such that $r(0) > 1$ (Proposition 4.1) and such that for all $w \in (\mathbb{R}^N)^+ \setminus \{0\}$, the function $\lambda \in (0,\infty) \to$

$r(\lambda w) \in (0, \infty)$ is strictly decreasing (Theorem 4.3) and $r(\lambda w) \leq 1$ holds when λ is large enough (Lemma 4.1). If $N = 1$, there is only one w_e such that $r(w_e) = 1$, i.e. $\mathcal{R} = \{w_e\}$. Then it suffices to take $\alpha = \frac{w_e}{\widetilde{E}(w_e)}$ and this gives existence and uniqueness in this case. Let us assume from now on that $N > 1$. We can define the continuous function

$$p := w \in (\mathbb{R}^N)^+ \setminus \{0\} \to p(w) \in (0, \infty)$$

such that $r(p(w)w) = 1$. That p is continuous can be seen as follows. Let us take any sequence w_n tending to w and let $p(w_{n_k})w_{n_k}$ be any convergent subsequence of $p(w_n)w_n$, whose limit must be of the form λw since w_{n_k} tends to w. Moreover, this implies $p(w_{n_k}) \to \lambda$ and so $p(w_n)w_n$ tends to λw and $r(\lambda w) = \lim r(p(w_n)w_n) = 1$. Since p is well defined (univalued), $\lambda = p(w)$ and hence $p(w_n) \to p(w)$.

Hence, the function P defined on $(\mathbb{R}^N)^+$ as $P(w) = p(w)w$ and taking values in $\mathcal{R}$ is also continuous. Now, $\mathcal{R}$ is homeomorphic to the intersection S_N^+ of the unit sphere of $\mathbb{R}^N$ with the closed cone $(\mathbb{R}^N)^+$ (P is indeed an homeomorphism from S_N^+ to $\mathcal{R}$) and so to the unit ball of $\mathbb{R}^{N-1}$. As $P \circ \widetilde{E}$ is a continuous function from the set $\mathcal{R}$ to itself, it has at least a fixed point w_e by the Brower theorem. Setting $\alpha = p(\widetilde{E}(w_e))$, we will have

$$\alpha \widetilde{E}(w_e) = p(\widetilde{E}(w_e))\widetilde{E}(w_e) = P(\widetilde{E}(w_e)) = w_e.$$

□

Remark 4.6. *The last hypothesis of the first claim of the theorem obviously holds if* $\sup_{a \geq l} b(w, l, a) < \inf_{a \geq 0} m(w, l, a)$ *for* w *large enough.*

5 Concluding remarks

Theorem 4.5 gives the existence of stationary solutions which are densities with respect to age and evolutionary trait, ensuring some phenotypic diversity as a consequence of the balance between mutation and selection. Very roughly speaking, the hypotheses of this theorem, amount to assume positive probability of small mutations, small probability of large mutations, and the existence of an interval of values of the evolutionary trait such that the basic reproduction number is larger than 1 and the mutation operator from theses values is small enough.

We leave for a future work the study of the stability of these equilibria and also the asymptotic profile when the mutation kernel tends to concentrate to a Dirac measure, as in [4] and [5].

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