

Adaptive dynamics in an infinite dimensional setting

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Introduction

The theory of evolution by means of natural selection was discovered independently by two scientists, Charles Darwin and Alfred Russell Wallace who, in 1858 made it public in a joint paper presented to the Linnean Society of London [16]. This paper was the precursor of Darwin's book "The origin of species" (1859), one of the most important and controversial books ever written.

The theory of evolution is based on two fundamental principles:

- Mutation, that is, "mistakes" in the replication of the genetic material carrying hereditary characteristics.
- Natural selection that states that, in a population, the characteristics better adapted to the environment are the ones that persist as a consequence of differential reproduction. In other words, individuals with "better" characteristics are more likely to have more offspring, and therefore, the frequency of this "better" characteristics increases in the next generation.

An important weakness in this theory was the lack of explanation on how characteristics were inherited. At the beginning of the twentieth century the role of chromosomes was elucidated and the problem was solved in the first half of the twentieth century by making a synthesis between the theory of evolution (of Darwin and Wallace) and the genetic laws discovered by Mendel (who was a contemporary of Darwin and Wallace, but whose work remained unknown for many years). This project, whose founders were Fisher, Haldane and Wright has been called "The Modern Synthesis" and it combines Mendelian genetics, mathematics and evolutionary theory into a set of ideas called population genetics.

In population genetics evolution is viewed as a change in the genetic composition of a population, therefore evolution can be considered in quantitative terms, that is, mathematics.

On the other hand, mathematical ecology was initiated by the works of Lotka and Volterra ([34], [60]) and quantitative aspects of natural selection such as

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prey-predator interactions, competition and competitive exclusion were clarified.

Ever since, many mathematical models have been applied to study evolutionary dynamics (see [46]).

One of the most used mathematical approaches to quantitative evolutionary theory is phenotypic evolution analysis, that is, to assume that reproduction is clonal avoiding then the complications of sexual reproduction and of the (complicated) genotype-phenotype map.

The first phenotypic evolution models are based in evolutionary game theory, which, in Maynard-Smith's words ([38]), is "a way of thinking about evolution at the phenotype level when the fitnesses of particular phenotypes depend on their frequencies in the population " (the so-called frequency-dependent selection).

In this framework, the starting point is the concept of an *Evolutionarily Stable Strategy* (ESS), introduced by Maynard Smith and Price in the context of game theory (see [39]).

In a few words, a strategy x (i.e. a value of a phenotypic characteristic or an "evolutionary trait") is an ESS if a clonal population of individuals with strategy x (called *resident* population) cannot be invaded by another small clonal population of individuals with a different strategy y (called *mutant* population), that is, a small mutant population goes to extinction in the environmental conditions determined by the (large) resident population.

In this respect, an ESS is (by definition) stable against the invasion of mutants but it is not necessarily an evolutionary attractor. This means that an ESS is not necessarily a limiting value of a sequence of strategies driven by natural selection.

Therefore, a stability analysis from the evolutionary point of view should be made.

A general theory of adaptive dynamics has been developed by Metz et al. ([40]), G6rritz et al. ([23]) in which a generalization of the concept of ESS is made. Adaptive dynamics consists essentially in the sequence of evolutionary traits defined by sequential substitutions of resident populations by invading ones.

The framework for adaptive dynamics usually makes the following assumptions:

1. Individuals reproduce asexually.
2. Reproduction is clonal, i.e. offspring are identical to the parent.
3. Only one-dimensional strategies are considered.

4. There is a unique attractor (which is an equilibrium solution) for the resident population dynamics.
5. The resident population has reached its attractor before a new mutant appears.
6. Phenotypic mutations are small and random.
7. The mutant population is initially small.
8. A resident population successfully invaded by a mutant population eventually becomes extinct, i.e., substituted by the mutant one.

Hypothesis 7 is needed in order that the mutant population does not change the steady state condition of the resident population.

Let us note that hypotheses 4 and 5 say that we are assuming that the resident population is in a steady state (a non trivial equilibrium point) or in a more complicated attractor such as a limit cycle, or even worse! [51] and then we introduce a small mutant population. Thus two different time scales are considered, one of convergence to the attractor (ecological time scale) and another of introduction of the mutant population (evolutionary time scale). Let us note as well that, even though in Nature it is possible to have individuals of many different strategies at the same time, only competition between two strategies (mutant and invader) is usually considered at the same time, and also that the mutation is not included intrinsically in the model, but added once the system has reached the steady state (the attractor).

As an attempt to try to overcome some of these difficulties, some selection-mutation models considering densities with respect to the evolutionary variable were introduced (see [10], [11]). In these models, the mutation process is represented by a diffusion term, so it becomes part of the deterministic population dynamics.

However, it is not the first time that selection-mutation models are used to describe evolutionary dynamics. In population genetics, selection-mutation models have already been considered in order to include the possibility of a continuum of possible alleles (see [5]).

In [10] three different reaction-diffusion equations models are considered. The first one represents a one parameter family competing for a limited amount of resources, the second one is a model for competing families feeding on more than one resource and the third one is a prey predator model.

In [11] a version for the densities with respect to the evolutionary variable of

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the prey predator model of Lawlor and Maynard-Smith is studied (the finite dimensional model of L-M consists of a system of three ordinary differential equations modeling a single consumer exploiting two different resources where the evolutionary variables are the probability of capturing and consuming each resource item per unit time, that may either represent the efficiency of prey capture or the amount of time spent searching different habitats, see [32]).

In all cases it was proved that when the mutation rate is small, the equilibria of these systems for the densities with respect to the evolutionary variable tend to concentrate at the ESS values of the respective evolutionary variables of the ecological models obtained when there is no mutation and all individuals have the same value of the evolutionary variable.

More recently, in [1], [35], [36], [54] selection-mutation models for densities of individuals with respect to an evolutionary variable were also considered although they are studied in the sense of asymptotic behavior of solutions and not in the sense of convergence of equilibrium solutions of the selection-mutation models to the ESS values of the pure selection models obtained when there is no mutation.

In [1] the authors study a logistic model for the density of individuals with respect to a two dimensional evolutionary variable (the growth and mortality parameters). This model only takes into account selection, mutation is not considered. They prove that the solution of the model tends to concentrate at the value that maximizes the fitness (in this case the growth to mortality ratio) in the parameter space.

In [35] a model incorporating mutation, selection and recombination is investigated. They prove, under the hypothesis of small recombination, existence of a unique globally asymptotically stable non trivial equilibrium. In this paper, as in [10] and [11] mutation is modelled by means of a Laplacian operator. A similar model of phenotype evolution is treated in [36], being the difference that, in [36], mutation is modelled by means of an integral operator with a piece-wise constant kernel, and, moreover, that they make the (strong) assumption that there is not natural selection. For this model it is proved that each solution converges (in the weak star topology) to a Radon measure.

Finally, in [54] the authors present a general selection-mutation model of evolution on a one-dimensional continuous fitness space that includes two ways of modeling mutation: with a diffusion operator and with an integral operator with a mutation kernel. They present an application of this models to recent experimental studies of “in vitro” viral evolution.

The purpose of this thesis is, as in [10] and [11] to study the behaviour of the equilibria of some models for the density of individuals with respect to an evolutionary variable and its relation with the evolutionarily stable strategies of the underlying ecological models but for equations different than the ones studied there.

The main difference in the equations will be in the way of modeling the mutation. In [10], [11], mutation was modeled by means of a Laplacian operator that lead to partial differential equations, whereas in all models in this thesis mutation will be represented by an integral operator with a mutation kernel that will represent the probability of mutation and that will lead to integro-differential systems.

This is also an important feature in this thesis, that the models that we study will not be single equations but systems of equations. This will make things technically more complicated, especially when dealing with eigenvalue problems and stability of steady states.

As a starting point, in Chapter 1 we consider the following system for a population with two age groups (juvenile and adult)

$$\begin{cases} u'(t) &= b(x)v(t) - m_1(u(t))u(t) - xu(t), \\ v'(t) &= xu(t) - m_2(v(t))v(t), \end{cases} \quad (1)$$

with population numbers $u(t)$ and $v(t)$ respectively and where the average age at maturity $T := \frac{1}{x}$ is the (phenotypic, genetically fixed) evolutionary variable, b is the fertility rate (assumed increasing with respect to the age at maturity T) and m_i are the respective mortality rates (also assumed increasing). This model was suggested by Mylius and Diekmann in [42] (see the appendices of that paper). The convenience of having a simple problem for the ecological/dynamical problem lead us to suppress the age-structure in the juvenile group. This transforms an age-structured population dynamics system into a two dimensional ordinary differential system but forces to make the hypothesis that the length of the juvenile period is an exponentially distributed random variable with expected value T . This slightly changes the meaning of the evolutionary variable with respect to that of [42].

Section 1.2 is devoted to the presentation of the model as well as of some assumptions related to the monotonicity of the mortality rates with respect to the population numbers and to the concavity of the fertility rate with respect to the maturation age. This latter, less justified from the biological point of view, is useful to simplify and unify the mathematical treatment.

In Section 1.3 we give a complete description of the asymptotic behaviour of the solutions of the model depending on the values of the parameter and

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an interpretation of the results in terms of the expected number of offspring of an individual in its lifespan, R_0 . Theorem 1.3.6 states that in “natural” biological hypotheses, there is an interval of values of the maturation age for which there is a non trivial equilibrium attracting all the solutions but the zero one. Moreover, zero is a global attractor when the parameter does not belong to this interval. The non trivial equilibrium is born from the zero equilibrium at the extremes of the interval, suggesting that there is at least an ESS value of the maturation age in the interior of it. This conjecture is proved in Theorem 1.4.3, already in Section 1.4, and uniqueness of the ESS is proved in Theorem 1.4.4.

In Section 1.5 a study of the ESS of the model from the evolutionary dynamics point of view is undertaken. In particular Proposition 1.5.4 shows that the ESS is convergence-stable in the sense of [23], i.e. a resident population with a value of the evolutive variable close to the ESS can be invaded by mutants whose value of the evolutive variable is closer to the ESS.

Finally in Proposition 1.5.5 we give a rather general result about evolutionary dynamics. It states that when the environment is one-dimensional and the fitness function is strictly monotonous with respect to it, the ESS is always convergence stable.

In Chapter 2 we study the following integrodifferential equations model for the distribution of individuals with respect to the age at maturity which is obtained by considering densities of the individuals with respect to the age at maturity in System (1)

$$\begin{cases} u_t(x, t) &= \int_0^\infty b(y)\beta_\varepsilon(x, y)v(y, t)dy - m_1\left(\int_0^\infty u(y, t)dy\right)u - xu(x, t), \\ v_t(x, t) &= xu(x, t) - m_2\left(\int_0^\infty v(y, t)dy\right)v(x, t), \end{cases} \quad (2)$$

where $u(x, t)$ and $v(x, t)$ are the density of young and adult individuals (respectively) at time t with respect to the trait $x := \frac{1}{T}$ and $\beta_\varepsilon(x, y)$ is a continuous kernel representing the density of probability that the trait of the offspring of an individual with trait y is x and ε denotes the (maximum) size of the mutation (we will assume $\text{supp}\beta_\varepsilon(x, \cdot) \subset [x - \varepsilon, x + \varepsilon]$).

Section 2.2 is devoted to the formulation of the model and its assumptions. In Section 2.3 we study, using the standard theory for semilinear equations, the existence and uniqueness of global positive solutions of the initial value problem for model (2), as well as continuous dependence with respect to initial conditions.

In Section 2.4 we prove, under some conditions on the variables constitut-

ing the model, the existence of a stationary solution of (2). We do it by proving the existence of a unique positive eigenfunction corresponding to the (dominant) eigenvalue zero of a certain linear operator in the Banach lattice $L^1(0, \infty)$ and afterwards solving a fixed point problem. The proofs for the results on the eigenvalue problem are extensively based on the theory of positive semigroups and the infinite dimensional version in Banach lattices of the Perron Frobenius theorem (see [14], [24], [45], [55]) (since the positive cone of $L^1(0, \infty)$ has empty interior, the results by Krein and Rutman that generalize to a class of positive operators the results by Perron and Frobenius in the theory of matrices cannot be used).

The fixed point problem is solved using Bolzano's theorem and the results about perturbation of the spectrum of a closed operator of [31].

Finally, in Section 2.5 we show that, when the size of the mutation tends to zero, the stationary solutions of System (2) tend to concentrate at a Dirac mass at the ESS value of System (1). Moreover, we show that the total population at equilibrium of System (2) tends to the equilibrium of System (1) for the value of ESS of the parameter.

In Chapter 3 we study a (rather) general class of selection mutation models given by the nonlinear equation

$$\vec{u}_t = A_\varepsilon(F(\vec{u}))\vec{u} = B_\varepsilon(x, F(\vec{u}))\vec{u} + \varepsilon T\vec{u} \quad (3)$$

in the space $L^1(I, \mathbb{R}^n)$, where x represents an evolutionary variable, B_ε is a matrix valued multiplication operator, T is a bounded operator and F is a function from $L^1(I, \mathbb{R}^n)$ to a m -dimensional space. We assume that, when the mutation rate (given by ε) tends to zero, this model becomes an ecological (finite dimensional) model of the form

$$\vec{v}_t = B_0(x, G(x, \vec{v}))\vec{v}. \quad (4)$$

In Section 3.3 we consider the linear operator obtained by fixing the nonlinear part ($F(\vec{u}) = E$) in (3), $A_\varepsilon(E)$. Under some hypotheses, including the existence of a dominant eigenvalue λ_ε of $A_\varepsilon(E)$ with a corresponding (positive) eigenfunction, the existence of a dominant eigenvalue $\mu_0(x)$ of $B_0(x, E)$, the existence of a value x_0 where $\mu_0(x)$ attains its maximum and finally the existence of an ESS value of (4) we prove convergence of the dominant eigenvalue of $A_\varepsilon(E)$, λ_ε , to the maximum value (with respect to x) of the dominant eigenvalue of $B_0(x, E)$, $\mu_0(x_0)$, as well as convergence of the family of eigenfunctions corresponding to the eigenvalue λ_ε (in the weak star topology) to a Dirac mass concentrated at x_0 .

From a biological point of view, the dominant eigenvalue λ_ε can be interpreted as the growth rate of the population with evolutionary variable x

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modeled by (3) when the environment is given by E .

In Section 3.4 we apply the results of Section 3.3 to the nonlinear problem (3) to obtain convergence of the equilibria of System (3) (of which we assume existence) to a Dirac mass at the ESS value of System (4). Moreover we obtain that the integral of the equilibria of System (3) tend to the equilibria of System (4) for the value of ESS of the parameter x .

In Chapter 4 we study two examples of models where the results of Chapter 3 can be applied.

In Section 4.2 we consider the following maturation age model

$$\begin{cases} u_t(x, t) &= (1 - \varepsilon)b(x)v(x, t) + \varepsilon \int_0^\infty b(y)\gamma(x, y)v(y, t)dy \\ &- m_1 \left(\int_0^\infty u(y, t)dy \right) u(x, t) - xu(x, t), \\ v_t(x, t) &= xu(x, t) - m_2 \left(\int_0^\infty v(y, t)dy \right) v(x, t). \end{cases} \quad (5)$$

This model is another version for the densities of individuals with respect to the maturation age of System (1) and differs from (2) in the meaning of the parameter ε , being in (5) the probability of mutation, whereas in (2) it was the size of (maximum) mutation (the probability of mutation was one).

We prove, for ε small enough, existence of a family of equilibrium solutions of (5) by formulating an eigenvalue problem (in this case in the Banach lattice $L^1(0, \infty) \times L^1(0, \infty)$) and afterwards solving a fixed point problem.

The results on the eigenvalue problem are based, as in Chapter 2, on the theory of positive semigroups and the infinite dimensional version in Banach lattices of the Perron Frobenius theorem. However, the treatment of the problem, even though it is based in the same theory, will be different than in Chapter 2 because in Chapter 3 we formulate it in the Banach lattice $L^1(0, \infty) \times L^1(0, \infty)$ (instead of in $L^1(0, \infty)$).

Since System (5) can be written as (3), an application of the results of Sections 3.3 and 3.4 gives that the family of equilibrium solutions of (5) tend to concentrate, when the probability of mutation tends to zero, at the ESS value of System (1). Moreover, the total population at equilibrium of System (5) tends to the equilibrium of System (1) for the value of ESS of the parameter. Sections 4.3 and 4.4 are devoted to the application of the convergence results of Chapter 3 to a predator prey model. We start by introducing the following finite dimensional predator prey model

$$\begin{cases} f'(t) = \left(a - \mu f(t) - \frac{\beta(x)u(t)}{1 + \beta(x)hf(t)} \right) f(t), \\ u'(t) = \left(\alpha \frac{\beta(x)f(t)}{1 + \beta(x)hf(t)} - d(x) \right) u(t), \end{cases} \quad (6)$$

for the number of prey $f(t)$ and the number of predators $u(t)$, where the parameter x denotes the index of activity of the predator population and it is the evolutionary variable, $\beta(x)$ is the searching efficiency, $d(x)$ the mortality rate of the predator population (both assumed increasing), a and μ the intrinsic growth rate and the competition coefficient of the prey population respectively and α the energy conversion factor that prey consumption gives to the predator.

In this model the *functional response*, that is, the rate of prey consumption per predator and how it is influenced by prey density, is modeled by a Holling type II functional response, that is, the attack rate of predators increases at a decreasing rate with prey because of fixed prey handling and consumption times.

Under reasonable hypotheses we show the existence of values of the parameter x for which System (6) has an asymptotically stable interior equilibrium and also the existence of a unique value of ESS that moreover, since the environment is one dimensional, is convergence stable.

Finally, in Section 4.4 we consider the infinite dimensional predator prey model

$$\begin{cases} f'(t) = \left(a - \mu f(t) - \int_0^\infty \frac{\beta(x)u(x,t)}{1 + \beta(x)hf(t)} dx \right) f(t), \\ \frac{\partial u(x,t)}{\partial t} = (1 - \varepsilon) \frac{\alpha\beta(x)f(t)u(x,t)}{1 + \beta(x)hf(t)} + \varepsilon \int_0^\infty \gamma(x,y) \frac{\alpha\beta(y)f(t)u(y,t)}{1 + \beta(y)hf(t)} dy \\ \quad - d(x)u(x,t), \end{cases} \quad (7)$$

in the Banach lattice $\mathbb{R} \times L^1(0, \infty)$ (only the predator evolves).

Since the operator given by the second equation in (7) can be written as (3), we obtain, for ε small enough (and once we prove that all the hypotheses of Chapter 3 hold), existence of a family of equilibria of System (7) that tend to concentrate at the ESS value of System (6).

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Chapter 5 is devoted to the study of the spectrum of the linearized operator at a positive equilibrium \vec{z}_ε of a nonlinear equation of the form

$$\vec{z}_t = A_\varepsilon(F(\vec{z}))\vec{z} \quad (8)$$

in order to study linear stability of the equilibrium solution \vec{z}_ε .

The models studied in Chapter 2 and 4 are all of the form (8).

In the same way as in Chapter 3 (although the equation (8) is more general than the one studied there) we assume that, when the mutation rate (given by ε) tends to zero, (8) becomes a finite dimensional ecological model of the form (4) for which existence of an ESS value \hat{x} of the parameter x is assumed. Convergence results will be used in order to establish a relation between the spectrum of the linearized operator of (8) at \vec{z}_ε and the spectrum of the linearized operator of (4) at the equilibrium $\vec{v}_{\hat{x}}$ (for the value of ESS of the parameter).

Finally, in the appendix we do some computations in order to apply the results of Chapter 5 to the maturation age and the predator prey model of Chapter 4.

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Introduction

Preliminaries

In the literature of evolutionary dynamics, the classical method used to locate an ESS is to maximize a fitness measure (for example in the paper by Lawlor and Maynard Smith, [32], the growth rate for the evolving population with respect to the evolutionary variable is maximized).

However, as the choice of this fitness measure depends on the way density dependence acts on the population (see for example, [43], [47]), the way to proceed is to start by studying a general invasion problem instead of by choosing a fitness measure .

We will do it by undertaking a mathematical formulation of the ESS concept rather general but appropriate to the models that we are going to study.

Let us assume that we have a system that describes the ecological dynamics of a resident population

$$\vec{u}_t = A(\vec{u}, x)\vec{u} \quad (9)$$

where \vec{u} denotes the resident population ($\vec{u}(t)$ belongs to a Banach space X), x is a one dimensional parameter denoting the strategy of the population and $A(\vec{u}, x)$ is a linear operator in X (generating a positive semigroup).

We assume that this system has a unique attractor which is a hyperbolic non trivial equilibrium point. Let us denote it by \vec{u}_r . A small mutant population, \vec{u}^i , with strategy y is introduced and this leads to the following system for the couple of populations

$$\begin{cases} \vec{u}_t = A(\vec{u}, \vec{u}^i, x)\vec{u}, \\ \vec{u}_t^i = A(\vec{u}, \vec{u}^i, y)\vec{u}^i. \end{cases} \quad (10)$$

where $A(\vec{u}, \vec{u}^i, x)$ is a linear operator in X .

Moreover, for all \vec{u} and x , $A(\vec{u}, 0, x) = A(\vec{u}, x)$ holds.

Definition 0.0.1 *We say that the value x of the evolutionary variable is a global ESS if the equilibrium point $(\vec{u}_r, 0)$ is asymptotically stable for System (10) for any $y \neq x$ where \vec{u}_r is the unique attractor for System (9). When*

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only small differences between the strategies of the resident and the mutant are allowed we call x a local ESS.

Fitness was defined by Metz et al. ([41]) as the long-term exponential growth rate of a phenotype in a given environment.

Definition 0.0.2 *In the mathematical formulation we use, we define **fitness** of the mutant y invading a resident x by*

$$\Lambda(\vec{u}_r, y) = \begin{array}{l} \text{dominant eigenvalue} \\ \text{of the operator } A(\vec{u}_r, y) \end{array}$$

Definition 0.0.3 [19], [45]

- A real eigenvalue λ_0 of a matrix A is called **dominant** if $\text{Re}\lambda < \lambda_0$ for all $\lambda \neq \lambda_0$ where λ is an eigenvalue of A .
- If A is a linear operator defined in an infinite dimensional vector space, a real eigenvalue λ_0 is called **dominant** provided that $\text{Re}\lambda < \lambda_0$ for every $\lambda \in \sigma(A)$ and it is called **strictly dominant** if for some $\delta > 0$ one has $\text{Re}\lambda \leq \lambda_0 - \delta$ for every λ belonging to the spectrum of A , $\lambda \neq \lambda_0$.
- If A is a linear operator in a Banach space we define the **spectral bound** $s(A)$ as

$$s(A) := \sup\{\text{Re}\lambda \quad : \quad \lambda \in \sigma(A)\}.$$

In the infinite dimensional context, the existence of a dominant eigenvalue of the generator of a positive semigroup is not guaranteed in general (this needs some additional hypotheses related to the irreducibility of the semigroup (see [45])).

On the other hand, if $X = \mathbb{R}^n$ there are results that guarantee the existence of a dominant eigenvalue of a matrix $A = (\alpha_{ij})_{n \times n}$.

If $A > 0$ (i.e. $\alpha_{ij} > 0$ for all i, j) it was discovered by Perron [49] that the spectral radius, $r(A)$, (where $r(A) := \max\{|\lambda| \text{ s.t. } \lambda \in \sigma(A)\}$) is a simple eigenvalue of A with a strictly positive eigenvector.

If $A \geq 0$ (i.e. $\alpha_{ij} \geq 0$ for all i, j) it can only be concluded that $r(A)$ is an eigenvalue of A with positive eigenvector (i.e. some of the components may be zero)(for a proof, see for example [29]).

Later on, Frobenius proved in [21], [22] that for a matrix $A \geq 0$ that is irreducible, $r(A)$ is a simple eigenvalue with strictly positive eigenvector.

Definition 0.0.4 An $n \times n$ matrix P is called a **permutation matrix** if, for some permutation π of $\{1, 2, \dots, n\}$, we have $Pe_i = e_{\pi(i)}$ where $e_i = (\delta_{ij})$.

In other words, a matrix P is called a permutation matrix if exactly one entry in each row and column is equal to 1, and all other entries are 0.

Definition 0.0.5 [64] A square matrix $A \in M_n(\mathbb{R})$ is called **reducible** if there exists a subspace

$$J_M := \{(\xi_1, \dots, \xi_n) : \xi_i = 0 \text{ for } i \in M\} \subset \mathbb{R}^n$$

for some $\emptyset \neq M \subsetneq \{1, \dots, n\}$ which is invariant under A . If A is not reducible it is called **irreducible**.

Remark 0.0.6 The vector subspaces of the form J_M , where M is any subset of $\{1, \dots, n\}$ are the (order) ideals of \mathbb{R}^n (see [55]).

This definition leads to the following characterization for irreducible matrices.

Lemma 0.0.7 [29], [64]

A square matrix A is **irreducible** if there exists no permutation matrix such that

$$P^{-1}AP = \begin{pmatrix} A_1 & 0 \\ B & A_2 \end{pmatrix}$$

where A_i is a square matrix of order m_i ($1 \leq m_i < n$), or equivalently, if there exists no order ideal invariant under A except $\{0\}$ and \mathbb{R}^n .

Since we will not only deal with positive matrices, we are going to give some results that ensure the existence of a dominant eigenvalue of a matrix A (not necessarily positive).

The following result characterizes the generator of a positive semigroup in \mathbb{R}^n .

Theorem 0.0.8 [64]

A matrix $A = (\alpha_{ij})_{n \times n} \in M_n(\mathbb{C})$ generates a positive semigroup (i.e., $e^{tA} \geq 0$) if and only if it is real and $\alpha_{ij} \geq 0$ whenever $i \neq j$.

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Proof: Let us suppose that $(\alpha_{ij}) \geq 0$ when $i \neq j$. Then there exists $\lambda \in \mathbb{R}$ such that $B := A + \lambda I \geq 0$ (i.e. all coefficients of B are non negative). Therefore

$$e^{tA} = e^{-\lambda t} e^{tB} \geq 0 \quad \forall t \geq 0.$$

Let us now assume that A generates a positive semigroup. Let us denote by $\{e_i\}_{i=1..n}$ the canonical basis of \mathbb{R}^n . We have, for $i \neq j$

$$\begin{aligned} a_{ij} &= \langle Ae_j, e_i \rangle \\ &= \langle \lim_{t \rightarrow 0} \frac{1}{t} (e^{tA} e_j - e_j), e_i \rangle \\ &= \lim_{t \rightarrow 0} \frac{1}{t} (\langle e^{tA} e_j, e_i \rangle - \langle e_j, e_i \rangle) \\ &= \lim_{t \rightarrow 0} \frac{1}{t} \langle e^{tA} e_j, e_i \rangle \geq 0 \end{aligned}$$

□

The next theorem states the existence of a dominant eigenvalue of the generator of a positive semigroup in \mathbb{R}^n .

Theorem 0.0.9 [64] *If a matrix A generates a positive semigroup $(e^{tA})_{t \geq 0}$, then $s(A)$ is a strictly dominant eigenvalue.*

Proof: Applying Perron's theorem (that says that the spectral radius $r(T)$ of a matrix T such that $T \geq 0$ is an eigenvalue of T with positive eigenvector, see [49]) to the matrix $A + \lambda I$ (defined in the proof of Theorem 0.0.8) we obtain that $r(A + \lambda I) = s(A + \lambda I)$ is an eigenvalue of the matrix $A + \lambda I$. The definition of spectral bound implies that $s(A + \lambda I)$ is a strictly dominant eigenvalue of $A + \lambda I$ and therefore $s(A)$ is a strictly dominant eigenvalue of A . □

Theorem 0.0.10 *In the hypotheses of Theorem 0.0.9, if moreover the matrix A is irreducible, then $s(A)$ is a simple eigenvalue and the eigenvector corresponding to $s(A)$ is strictly positive.*

Proof: It is immediate applying Frobenius theorem to the matrix $A + \lambda I$ defined in the proof of Theorem 0.0.8. □

Remark 0.0.11 *In order to see why the irreducibility is important, let us briefly prove the strict positivity of the eigenvector corresponding to $s(A)$ given by Theorem 0.0.10.*

Applying Perron's theorem to the matrix $A + \lambda I$ defined in the proof of Theorem 0.0.8, we obtain that $s(A + \lambda I)$ is an eigenvalue of A with corresponding positive eigenvector. Let us denote it by \vec{v} . That is, we have

$$(A + \lambda I)\vec{v} = s(A + \lambda I)\vec{v} = (s(A) + \lambda I)\vec{v}.$$

So, \vec{v} is an eigenvector of A corresponding to the eigenvalue $s(A)$. By definition, \vec{v} is invariant under A .

The irreducibility of A implies that \vec{v} is not only positive but strictly positive (because the only order ideals invariant under A are $\{0\}$ and \mathbb{R}^n).

Let us go back to the mathematical formulation of the ESS.

As the hyperbolic non trivial equilibrium point of (9), \vec{u}_r , is completely determined by x , we can write $\lambda(x, y) := \Lambda(\vec{u}_r(x), y)$ and think of the fitness as a function $\lambda : \mathbb{R}_+^2 \mapsto \mathbb{R}$. Note that $\lambda(x, x) = 0$ for any x (because it is the dominant eigenvalue of the operator $A(\vec{u}_r, x)$).

The following result means that all the mutants trying to invade a resident population with evolutionarily stable strategy \hat{x} have negative fitness (and so do not succeed).

Theorem 0.0.12 *A value of the evolutive variable \hat{x} is a global (local) ESS if the condition*

$$\lambda(\hat{x}, y) < \lambda(\hat{x}, \hat{x}) \quad \forall y \neq \hat{x} \quad (\text{for all } y \text{ sufficiently close to } \hat{x}) \quad (11)$$

holds.

A value of the evolutive variable \hat{x} is not a global (local) ESS if the opposite strict inequality holds for some y (arbitrarily close to \hat{x}).

Proof: The linear part of System (10) at the equilibrium $(\vec{u}_r, 0)$ is

$$\begin{pmatrix} v \\ u^i \end{pmatrix}_t = \begin{pmatrix} A(\vec{u}_r, 0, x) + A_{\vec{u}}(\vec{u}_r, 0, x)\vec{u}_r & A_{\vec{u}^i}(\vec{u}_r, 0, x)\vec{u}_r \\ 0 & A(\vec{u}_r, 0, y) \end{pmatrix} \begin{pmatrix} v \\ u^i \end{pmatrix}$$

The set of eigenvalues of this matrix is the union of those of the operator $A(\vec{u}_r, x) + A_{\vec{u}}(\vec{u}_r, x)\vec{u}_r$, all of them having negative real part because this operator is the linear part of the equation (9) at the (hyperbolic) asymptotically

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stable equilibrium \vec{u}_r , and those of $A(\vec{u}_r, y)$. The statement follows from the definition of $\lambda(x, y)$. \square

The principal significance of the theorem is that it states that a (local) global ESS is a (local) maximum in the direction of the second variable of the fitness function $\lambda(x, y)$. So we have proved the following theorem

Theorem 0.0.13 *A value \hat{x} of the evolutive variable is a local ESS if (\hat{x}, \hat{x}) is a critical point of the fitness of the mutant population, which is a strict maximum in the direction of the second variable.*

Adaptive dynamics models the interaction between the resident and the mutant. It is described as a substitution sequence of strategies: If the mutant growth rate is positive, then the mutant population can spread and a displacement of the evolutive variable value can occur. If the mutant growth rate is negative then the mutant population dies out.

The analysis of the adaptive dynamics, when the space of strategies is one-dimensional, can be made by plotting the sign of the fitness, $\lambda(x, y)$, and that of its second derivatives. The sign plots of the fitness function are called **Pairwise invasibility plots** (see figures at the end of this chapter). They were first used by Van Tienderen and De Jong in [59].

On the main diagonal $y = x$, $\lambda(x, y)$ vanishes by definition because it is the fitness of the resident population at demographic equilibrium, i.e. a 0 eigenvalue of the matrix A .

The coordinate of a point of intersection of the diagonal with another curve on which $\lambda(x, y)$ is zero is called a **singular strategy**.

So, from the mathematical point of view, a singular strategy is a critical point (i.e., a zero of the gradient vector) of the function $\lambda(x, y)$ lying on the straight line $y = x$ (which is a zero level curve). More precisely, it is a saddle point of $\lambda(x, y)$ which is assumed to be non-degenerate.

Notice that a singular strategy \hat{x} is a global ESS if and only if $\lambda(\hat{x}, y) < 0$ for $y \neq \hat{x}$ and that it is a local ESS if $\lambda_{yy}(\hat{x}, \hat{x}) < 0$.

On the other hand, a singular strategy x_* is called **convergence-stable** (see [13], [23]) if a resident population with strategy x close to x_* can be invaded by mutants whose strategy y is still closer to x_* . That means that x_* is an attractor for the evolutionary dynamics.

In terms of the fitness function $\lambda(x, y)$, this can be formulated by saying that there is an $\varepsilon > 0$ such that $|y - x| < |x_* - x| < \varepsilon$ implies $\lambda(x, y) > 0$ i.e., $\lambda(x, y)$ is positive above the diagonal $y = x$ and to the left (and close to) x_* and below the diagonal and to the right (and close to) x_* (see figures at the end of this Chapter). Equivalently, $(x_* - x)\lambda_y(x, x) > 0$ if $0 < |x_* - x| < \varepsilon$,

i.e., $\lambda_y(x, x)$ is decreasing in a neighborhood of x_* . A sufficient condition for this is $D_{(1,1)}D_{(0,1)}\lambda(x_*, x_*) = \lambda_{yx}(x_*, x_*) + \lambda_{yy}(x_*, x_*) < 0$.

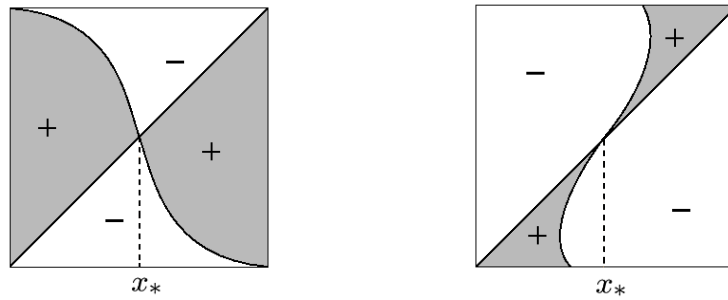
Combining this inequality with

$$D_{(1,1)}D_{(1,1)}\lambda(x_*, x_*) = \lambda_{xx}(x_*, x_*) + 2\lambda_{xy}(x_*, x_*) + \lambda_{yy}(x_*, x_*) = 0$$

(as $\lambda(x, x) = 0$ for all x), one obtains a sufficient condition in order that a singular strategy x_* is convergence-stable, namely $\lambda_{xx}(x_*, x_*) > \lambda_{yy}(x_*, x_*)$ (see [23].)

A singular strategy that is both an ESS and convergence stable is called a **continuously stable strategy** or CSS (see [20], [23]).

Continuously stable strategies represent the final outcome of the evolutionary process.



Continuously stable strategy ESS that is not convergence stable

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Chapter 1

A finite-dimensional model for the adaptive dynamics of the maturation age

1.1 Introduction

In this chapter we study a time continuous model with two groups of age. Juveniles (non fertile individuals) are assumed to be born with a birth rate depending on their mean maturation age T . The same parameter T plays the role of transition rate from the juvenile stage to the adult one. The death rates of both juveniles and adults are density depending only on the respective population numbers. This corresponds to assuming that the two groups of age feed on different resources. We assume that the birth rate is an increasing function of the maturation age, so establishing a balance between the need to grow and consequently to remain as a juvenile a long period in order to increase the fertility when becoming an adult, and the increased risk of dying before maturity when this is delayed.

Our interest is the study of the maturation age from the evolutionary point of view. The same idea has been succesfully used to illustrate several properties of the so-called evolutionarily stable strategies, as for instance in [18] (inspired in the paper by Kaitala and Getz [30]) in a discrete time and discrete evolutionary variable model and in [17] and [28] in an age-dependent model (see also [7]).

1.2 The model

We consider a biological population distributed into two groups of age: juveniles and adults.

Let $u(t)$ denote the number of individuals of the young population at time t and $v(t)$ the number of individuals of the adult population at time t .

The type of an individual is given by the expected value of the length of its juvenile period T .

After becoming an adult every individual produces offspring at a constant rate which depends on T . We denote it by $b(T)$.

The mortality rates are density-dependent in such a way that there is not competition for the resources between juveniles and adults.

Let us build up the model making the following assumptions :

- (a) The maturation age is exponentially distributed with mean T so that the transition rate from juveniles to adults is $\frac{1}{T}u(t)$.

Let us note that the exponential distribution is the only possible probability distribution of the maturation age that gives a transition rate term independent of the age distribution of individuals and so it is the only one allowing an unstructured (with respect to age) model.

- (b) The mortality rate of the young population, $m_1(u)$, is a smooth, strictly increasing and bounded function such that $m_1(0) > 0$.

- (c) The mortality rate of the adult population, $m_2(v)$, is a smooth, increasing and bounded function such that $m_2(0) > 0$.

- (d) The fertility, $b(T)$, is a smooth, strictly increasing and bounded function with strictly negative second derivative. It satisfies $b(0) = 0$ and there exists T_0 such that $b(T_0) > m_2(0)$.

Then the following system of ordinary differential equations constitutes the model

$$\begin{cases} u'(t) = b(T)v(t) - m_1(u(t))u(t) - \frac{1}{T}u(t), \\ v'(t) = \frac{1}{T}u(t) - m_2(v(t))v(t), \end{cases} \quad (1.1)$$

where $'$ indicates time derivatives and $u(t) \geq 0$ and $v(t) \geq 0$ (because it does not make sense to consider negative population numbers).

Remark 1.2.1 *The hypotheses on the fertility and mortality functions are “natural” biological hypotheses that will guarantee existence of a unique non trivial equilibrium point and of a unique evolutionarily stable strategy value of the age at maturity of System 1.1.*

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A complete description of the asymptotic behaviour of the (positive) solutions of System (1.1) depending on the value of the parameter T is possible by means of the theorem that we will formulate at the end of this section based on the following technical results.

Lemma 1.3.1 *Let f_1 and f_2 be positive, continuous and increasing functions defined on $[0, \infty)$. Suppose that one of them is strictly increasing. Then there exists a unique non trivial solution of the system*

$$\begin{cases} v = f_1(u)u, \\ u = f_2(v)v. \end{cases}$$

if and only if the following conditions hold

$$\begin{aligned} f_1(0)f_2(0) &< 1, \\ \lim_{u \rightarrow \infty} f_1(u) \lim_{u \rightarrow \infty} f_2(u) &> 1. \end{aligned}$$

Proof: A couple (u, v) is a nontrivial solution of the system if and only if

$$F(u) := f_2(f_1(u)u)f_1(u) = 1 \quad \text{and} \quad v = f_1(u)u.$$

F is a continuous and strictly increasing function and

$$F(0) = f_2(0)f_1(0) < 1$$

and

$$\lim_{u \rightarrow \infty} F(u) = \lim_{u \rightarrow \infty} f_2(u) \lim_{u \rightarrow \infty} f_1(u) > 1$$

are necessary and sufficient conditions for the existence of a (unique) $u > 0$ satisfying $F(u) = 1$. \square

Lemma 1.3.2 *System (1.1) has a unique non trivial equilibrium point if and only if the parameter T satisfies*

$$m_1(0) < \frac{1}{T} \left(\frac{b(T)}{m_2(0)} - 1 \right) =: f(T), \tag{1.2}$$

$$M_1 > \frac{1}{T} \left(\frac{b(T)}{M_2} - 1 \right) =: g(T), \tag{1.3}$$

where

$$M_1 := \lim_{u \rightarrow \infty} m_1(u), \quad M_2 := \lim_{u \rightarrow \infty} m_2(u).$$

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Proof: The equilibria are the solutions of the system

$$\begin{aligned} v &= \frac{1}{b(T)} \left(m_1(u) + \frac{1}{T} \right) u &:= f_1(u)u, \\ u &= Tm_2(v)v &:= f_2(v)v. \end{aligned}$$

The statement readily follows from Lemma 1.3.1. \square

Lemma 1.3.3 *Let $h : [0, \infty) \rightarrow \mathbb{R}$ be a C^2 function satisfying : $h'(T) > 0$, $h''(T) < 0$, $h(0) < 0$, $h(T)$ bounded and $h(T_*) > 0$ for some T_* . Then $\frac{h(T)}{T}$ has a unique critical point which is a maximum.*

Proof: Existence follows easily applying the Weierstrass theorem and using that $\frac{h(T)}{T} > 0$ for all $T > T_*$ and $\lim_{T \rightarrow \infty} \frac{h(T)}{T} = 0$.

On the other hand, as the derivative of the function $\frac{h(T)}{T}$ is positive when $h(T) \leq 0$, a critical point is only possible when $h(T) > 0$. Furthermore, a critical point is a zero of the function $\frac{h(T)}{h'(T)} - T$ which is strictly increasing when $h(T) > 0$. This gives uniqueness. \square

Corollary 1.3.4 *The function $f(T)$ defined in Lemma 1.3.2 has a unique critical point which is a maximum.*

Proof: We can write $f(T) = \frac{h(T)}{T}$ where $h(T) := \frac{b(T)}{m_2(0)} - 1$. It is straightforward to see that $f(T)$ satisfies the hypotheses of Lemma 1.3.3. \square

Corollary 1.3.5 *Let us assume that there exists T_* such that $b(T_*) > M_2$. Then the function $g(T)$ defined in Lemma 1.3.2 has a unique critical point which is a maximum. Otherwise, $g(T)$ satisfies*

$$\sup_{T \in (0, \infty)} g(T) = 0.$$

Proof: Applying Lemma 1.3.3. \square

Theorem 1.3.6 Let $f(T) := \frac{1}{T} \left(\frac{b(T)}{m_2(0)} - 1 \right)$ and $g(T) := \frac{1}{T} \left(\frac{b(T)}{M_2} - 1 \right)$, where $M_1 := \lim_{u \rightarrow \infty} m_1(u)$, $M_2 := \lim_{u \rightarrow \infty} m_2(u)$.
If the conditions

$$m_1(0) < \max_{T \in (0, \infty)} f(T) \tag{1.4}$$

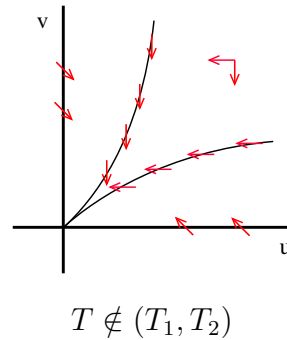
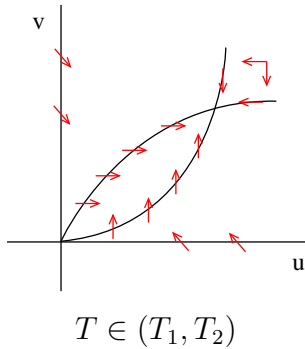
$$M_1 > \sup_{T \in (0, \infty)} g(T) \tag{1.5}$$

hold, then there exists an interval (T_1, T_2) such that if the parameter T belongs to (T_1, T_2) , System (1.1) has a unique non trivial equilibrium point which is a global attractor (except for the zero solution) and otherwise $\vec{0}$ is a global attractor of (1.1). Moreover the non trivial equilibrium describes a curve in the open first quadrant parametrized by $T \in (T_1, T_2)$ and tending to the origin of coordinates when T tends to the extreme points of the interval.

Proof: When the hypotheses are satisfied, by Corollaries 1.3.4 and 1.3.5, there exist $T_1 < T_2$ such that $f(T_1) = f(T_2) = m_1(0)$ and so, for any $T \in (T_1, T_2)$ the hypotheses of Lemma 1.3.2 hold. This gives existence and uniqueness of the non trivial equilibrium point.

On the other hand, if $T \notin (T_1, T_2)$ from Lemma 1.3.2 it follows that there is not non trivial equilibrium.

In both cases, any rectangle with two of their sides lying on the coordinate axes and with a vertex in the region of the first quadrant where the two components of the vectorial field are negative is positively invariant. These rectangles do not contain periodic orbits due to the direction of the vectorial field on the isocline lines (see figures below). The statement about asymptotic behaviour follows from the Bendixson-Poincaré theorem.



□

The main statement of the theorem is that, under suitable hypotheses, a non trivial equilibrium attracts any positive solution whenever the age at

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maturity belongs to some interval and that the population die out otherwise. This is a convenient scenario in order to deal with the evolutionary aspects of the age at maturity.

Nevertheless, this is not the only possible situation. Indeed, the concept of ESS and, more in general, the evolutionary dynamics, have been studied in ecological systems with attractors not reduced to an equilibrium, but containing periodic orbits or even more complicated objects (see [51],[43]).

Interpretation of the results

The results of the former theorem can be interpreted using the concept of the expected number of offspring of an individual in its lifespan, R_0 . Let us compute R_0 for our model.

Let N be the random variable of the number of offspring in the lifespan of an individual, let Z be a random variable taking the value 1 if a young individual taken at random reaches maturity and the value 0 otherwise, let N_a be the random variable of the number of offspring in the lifespan of an adult individual and, finally, let t be the random variable of the lifetime of an individual after becoming adult (exponentially distributed with expected value $\frac{1}{m_2}$).

Notice that $Z = 1$ is the event that an exponentially distributed variable X with expected value $\frac{1}{m_1}$ takes a value larger than another independent exponentially distributed random variable T , with expected value T .

So,

$$\begin{aligned} P(Z = 1) &= P(X > Y) = \int_0^\infty \int_y^\infty m_1 e^{-m_1 x} \frac{e^{-\frac{y}{T}}}{T} dx dy \\ &= \frac{1}{T} \frac{1}{\frac{1}{T} + m_1} = \frac{1}{1 + T m_1}. \end{aligned}$$

Now, using the concept of conditional expectation and the equality

$$E(E(Y|X)) = EY,$$

we can write, as $N = 0$ if $Z = 0$,

$$\begin{aligned} EN &= E(E(N|Z)) = E(N|Z = 1)P(Z = 1) + E(N|Z = 0)P(Z = 0) \\ &= (EN_a)P(Z = 1). \end{aligned}$$

On the other hand, as $b(T)$ is the number of births per adult individual and unit of time, the expected value of N_a conditioned to a lifetime as adult t is

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$b(T)t$. So,

$$R_0 = EN = E(E(N_a|t))P(Z = 1) = b(T)E(t)P(Z = 1) = b(T)\frac{1}{m_2}\frac{1}{1 + Tm_1},$$

or equivalently

$$R_0 = \frac{b(T)}{m_2(v)}\frac{\frac{1}{T}}{\frac{1}{T} + m_1(u)},$$

for fixed u and v .

- If condition (1.4) of Theorem 1.3.6 is not satisfied, i.e. if $R_0 < 1$ for any value of T in ideal conditions (zero population numbers), then condition (1.5) holds automatically and for all T , $\vec{0}$ is a global attractor of the system.
- If condition (1.4) of Theorem 1.3.6 is satisfied but condition (1.5) does not hold, i.e. if $R_0 > 1$ for some T in starvation conditions (infinite population numbers) then there exist two disjoint intervals (T_1, T_3) , (T_4, T_2) with $T_1 < T_3 < T_4 < T_2$ such that if $T \in (0, T_1] \cup [T_2, \infty)$ then $\vec{0}$ is a global attractor, if $T \in (T_1, T_3) \cup (T_4, T_2)$ then there is a unique non trivial equilibrium which is a global attractor (except for the zero solution) and, finally, if $T \in [T_3, T_4]$ then all the trajectories of the system but the zero one are unbounded.

Nevertheless, notice that this last situation has few biological significance because it requires small mortality rates for large populations compared to fertility.

1.4 Existence and Uniqueness of the ESS

In this section, existence and uniqueness of an evolutionarily stable strategy for System (1.1) is proved by means of the mathematical formulation introduced at the Preliminaries.

System (1.1) can be written in the form

$$\begin{pmatrix} u \\ v \end{pmatrix}' = \mathbf{A} \begin{pmatrix} u \\ v \end{pmatrix} \quad (1.6)$$

where

$$\mathbf{A} = \begin{pmatrix} -m_1(u(t)) - x & \hat{b}(x) \\ x & -m_2(v(t)) \end{pmatrix} \quad (1.7)$$

1.4. Existence and Uniqueness of the ESS

where $x = \frac{1}{T}$ and $\hat{b}(x) = b(\frac{1}{x}) = b(T)$.

As the matrix modeling the dynamics of the mutant population when the environmental conditions are the equilibrium of the resident population (denoted by (u_r, v_r)),

$$\mathbf{A}(\vec{u}_r, y) = \begin{pmatrix} -m_1(u_r) - y & \hat{b}(y) \\ y & -m_2(v_r) \end{pmatrix}, \quad (1.8)$$

has a dominant eigenvalue (by Theorems 0.0.8 and 0.0.9 in Preliminaries), the fitness function is well defined in our model. It will be used in order to calculate the conditions of ESS.

We begin with a result that gives sufficient conditions such that a value of the evolutionary variable is an ESS.

Proposition 1.4.1 *Let \hat{x} be a positive value of the evolutionary variable.*

Let $F(\lambda, x, y)$ the characteristic polynomial of the matrix (1.8).

A sufficient condition for \hat{x} being a local ESS of System (1.1) is that it satisfies

$$\begin{cases} F_y(0, \hat{x}, \hat{x}) = 0, \\ F_{yy}(0, \hat{x}, \hat{x}) > 0. \end{cases} \quad (1.9)$$

Proof: It suffices to show that the conditions (1.9) and the following conditions

$$\begin{cases} \lambda_y(\hat{x}, \hat{x}) = 0, \\ \lambda_{yy}(\hat{x}, \hat{x}) < 0. \end{cases} \quad (1.10)$$

(which imply the sufficient conditions of ESS given by theorem (0.0.13) in the Preliminaries) are equivalent and this follows easily taking implicit derivatives of the equation $F(\lambda, x, y) = 0$ with respect to y , evaluating at (\hat{x}, \hat{x}) and noticing that $F_\lambda(0, \hat{x}, \hat{x}) > 0$. \square

A direct application of Proposition 1.4.1 gives

Theorem 1.4.2 *In the hypotheses of Theorem 1.3.6, let $\hat{x} \in (\frac{1}{T_2}, \frac{1}{T_1})$ satisfying*

$$\begin{cases} (x\hat{b}(x))' |_{\hat{x}} = m_2(\tilde{v}(\hat{x})), \\ (x\hat{b}(x))'' |_{\hat{x}} < 0, \end{cases}$$

1.4. Existence and Uniqueness of the ESS

where $\tilde{v}(\hat{x})$ is the second component of the non trivial equilibrium of System (1.6), (1.7) with parameter \hat{x} .

Then \hat{x} is a local ESS of System (1.1).

Theorem 1.4.3 (existence of the ESS)

In the hypotheses of Theorem 1.3.6, there exists at least one local ESS of System (1.6), (1.7), which belongs to the interval $(\frac{1}{T_2}, \frac{1}{T_1})$.

Proof: We only need to show that the conditions given by Theorem 1.4.2 hold for some \hat{x} in $(\frac{1}{T_2}, \frac{1}{T_1})$.

The equation

$$(x\hat{b}(x))'_{|\hat{x}} = m_2(\tilde{v}(\hat{x}))$$

can be written in terms of T in the form

$$(b(T) - Tb'(T))_{|\hat{T}} = m_2(v(T))_{|\hat{T}}$$

where $\hat{T} = \frac{1}{\hat{x}}$ and $v(T) := \tilde{v}(\frac{1}{T})$.

Let $G(T) = b(T) - Tb'(T) - m_2(v(T))$ be defined for $T \in [T_1, T_2]$ by extending v continuously at the extreme points of the interval.

Notice that then $v(T_1) = v(T_2) = 0$. Therefore,

$$\begin{aligned} G(T_1) &= b(T_1) - T_1b'(T_1) - m_2(0), \\ G(T_2) &= b(T_2) - T_2b'(T_2) - m_2(0). \end{aligned}$$

We conclude from Corollary 1.3.4 and Theorem 1.3.6 that

$$\begin{aligned} f'(T_1) &= \frac{-b(T_1) + m_2(0) + T_1b'(T_1)}{T_1^2m_2(0)} > 0, \\ f'(T_2) &= \frac{-b(T_2) + m_2(0) + T_2b'(T_2)}{T_2^2m_2(0)} < 0. \end{aligned}$$

Hence that

$$\begin{aligned} G(T_1) &< 0, \\ G(T_2) &> 0 \end{aligned}$$

and finally that there exists at least a $\hat{T} \in (T_1, T_2)$ such that $G(\hat{T}) = 0$.

What is left to show is that the condition

$$(x\hat{b}(x))''_{|\hat{x}} < 0 \quad \text{where} \quad \hat{x} = \frac{1}{\hat{T}} \tag{1.11}$$

1.4. Existence and Uniqueness of the ESS

holds.

An easy computation shows that

$$(x\hat{b}(x))'' = T^3b''(T).$$

The function $T^3b''(T)$ is negative for any T . Then condition (1.11) holds for any x , in particular for \hat{x} . This completes the proof. \square

Theorem 1.4.4 (*uniqueness of the ESS*)

In the hypotheses of Theorem 1.4.3 the ESS is unique.

Proof:

The equations of the equilibrium and the condition of ESS yield the system

$$\begin{cases} \hat{b}(x)v - (m_1(u) + x)u = 0, \\ xu - m_2(v)v = 0, \\ (x\hat{b}(x))' = m_2(v), \end{cases} \quad (1.12)$$

for (positive) unknown u , v and x .

A solution of (1.12) (u, v, x) also satisfies the system

$$\begin{cases} \frac{u}{v} - \frac{m_2(v)}{x} = 0, \\ (x\hat{b}(x))' = m_2(v), \\ \frac{x\hat{b}(x)}{m_1(u) + x} = (x\hat{b}(x))'. \end{cases} \quad (1.13)$$

The two last equations allow to write x and v as functions of u (x_u and $v(u)$) as follows.

Notice that for any fixed $u > 0$, the function $x \rightarrow \frac{x\hat{b}(x)}{m_1(u) + x}$ has a unique critical point x_u , which is a maximum and satisfies (it is the only solution of)

$$\frac{x_u\hat{b}(x_u)}{(x\hat{b}(x))'(x_u)}. \quad (1.14)$$

Indeed, this condition is equivalent to that the first derivative vanishes, whereas the second derivative evaluated at any critical point x_u equals

1.5. A sketch on evolutionary dynamics

$\frac{(x\hat{b}(x))''}{m_1(u) + x_u}$ and, hence, it is negative, implying the two first statements.

Therefore, using the two last equations in (1.13) we have

$$v(u) = m_2^{-1} \left(\max_x \frac{x\hat{b}(x)}{m_1(u) + x} \right). \quad (1.15)$$

Moreover, x_u and $v(u)$ are increasing and decreasing functions respectively and this can be seen as follows. First, x_u satisfies the relation

$$(x\hat{b}(x))' = \max_x \frac{x\hat{b}(x)}{m_1(u) + x},$$

and the assertion about the monotony of x_u follows because the left hand side is a decreasing function of x (remember that $(x\hat{b}(x))'' < 0$) and the right hand side is a decreasing function of u .

Second, (1.15) directly gives that $v(u)$ is decreasing.

So, a solution (u, v, x) of (1.13) is necessarily of the form $(u, v(u), x_u)$ where (due to the first equation) u is a zero of the function

$$F(u) := \frac{u}{v(u)} - \frac{m_2(v(u))}{x_u}.$$

Uniqueness follows from the fact that F is a strictly increasing function. \square

1.5 A sketch on evolutionary dynamics

Let us return to the notation of the Preliminaries, let us assume that the model system (9) is two dimensional and that the equilibrium population of the resident \vec{u}_r depends on the evolutionary variable in the form $\vec{u}_r(x) = (u(x), v(x))$. The fitness of a mutant with evolutionary variable y invading a resident population x is now $\lambda(x, y) = \Lambda(u(x), v(x), y)$ (recall Definition 0.0.2).

Using the implicit function theorem and the definition of singular strategy some results about the derivatives of the equilibrium populations with respect to the evolutionary variable evaluated at a singular strategy are obtained. The first of them does not refer specifically to System 1.6, 1.7 and it is in some sense, a generalization of Result 3 [42] (see also the paragraph preceding Proposition 1.5.5).

On the other hand, they will be used to prove that an ESS of System 1.6, 1.7 is always convergence-stable (see Proposition 1.5.4).

1.5. A sketch on evolutionary dynamics

Lemma 1.5.1 *Let x_* be a singular strategy. Let us assume that $\Lambda_u(u(x_*), v(x_*), x_*)$ and $\Lambda_v(u(x_*), v(x_*), x_*)$ have the same sign. Then $u'(x_*)$ and $v'(x_*)$ have different signs or both vanish.*

Proof: As $\Lambda(u(x), v(x), x) = \lambda(x, x) = 0$ for all x , we have

$$\Lambda_u(u(x), v(x), x)u'(x) + \Lambda_v(u(x), v(x), x)v'(x) + \Lambda_y(u(x), v(x), x) = 0.$$

Using the fact that in a singular point $\Lambda_y(u(x_*), v(x_*), x_*) = \lambda_y(x_*, x_*) = 0$ we obtain

$$\Lambda_u(u(x_*), v(x_*), x_*)u'(x_*) + \Lambda_v(u(x_*), v(x_*), x_*)v'(x_*) = 0 \quad (1.16)$$

The last equation gives the statement. \square

Lemma 1.5.2 *Let $(u(x), v(x))$, $x \in (\frac{1}{T_2}, \frac{1}{T_1})$ be the curve of non trivial equilibria of System 1.6, 1.7. The following claims hold*

- a) $v'(x) > 0$ if x is such that $u'(x) = 0$.
- b) $u'(x) < 0$ if x is such that $v'(x) = 0$.

Proof: The proof is straightforward taking the derivative with respect to x of the second equilibrium equation in 1.6, i.e.,

$$xu(x) - m_2(v(x))v(x) = 0.$$

\square

Lemma 1.5.3 *Under the hypotheses of Lemma 1.5.1, if \hat{x} is an ESS of System 1.6, 1.7, then $u'(\hat{x}) < 0$ and $v'(\hat{x}) > 0$.*

Proof: By Lemma 1.5.1 and Lemma 1.5.2 $u'(\hat{x})$ and $v'(\hat{x})$ have different sign (they cannot vanish).

Let us assume that $u'(\hat{x}) > 0$ and $v'(\hat{x}) < 0$. Let $x_0 = \sup\{x \in [\frac{1}{T_2}, \hat{x}) : u'(x)v'(x) = 0\}$. Notice that x_0 exists by continuity since $u'(\frac{1}{T_2})v'(\frac{1}{T_2}) \geq 0$ and $u'(\hat{x})v'(\hat{x}) < 0$.

We distinguish two cases :

- a) $x_0 = \frac{1}{T_2}$.

This implies $v'(x) < 0$ for all $x > \frac{1}{T_2}$ and hence $v(x) < 0$ a contradiction.

- b) $x_0 \neq \frac{1}{T_2}$.

If $u'(x_0) = 0$, then $v'(x_0) > 0$ by Lemma 1.5.2. As by hypothesis $v'(\hat{x}) < 0$ there must exist $\tilde{x} \in (x_0, \hat{x})$ such that $v'(\tilde{x}) = 0$. This is a contradiction with the fact that x_0 is the supremum. If $v'(x_0) = 0$ an analogous argument leads to a contradiction too.

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□

Proposition 1.5.4 *Under the hypotheses of Theorem 1.4.3, the ESS \hat{x} is convergence-stable.*

Proof: Taking implicit derivatives twice of the characteristic equation of the matrix (1.8), $F(\lambda, x, y) = 0$, and evaluating at (\hat{x}, \hat{x}) we get the following equalities

$$\begin{cases} \lambda_{yy}(\hat{x}, \hat{x}) = \frac{-F_{yy}(0, \hat{x}, \hat{x})}{F_\lambda(0, \hat{x}, \hat{x})}, \\ \lambda_{xx}(\hat{x}, \hat{x}) = \frac{-F_{xx}(0, \hat{x}, \hat{x})}{F_\lambda(0, \hat{x}, \hat{x})}. \end{cases} \quad (1.17)$$

As $F_\lambda(0, \hat{x}, \hat{x}) = m_2(v(\hat{x})) + m_1(u(\hat{x})) + \hat{x} > 0$, the sign of $\lambda_{yy}(\hat{x}, \hat{x})$ and that of $\lambda_{xx}(\hat{x}, \hat{x})$ only depend on those of $F_{yy}(0, \hat{x}, \hat{x})$ and $F_{xx}(0, \hat{x}, \hat{x})$ respectively. As the equilibrium condition implies

$$m_1(u(x))m_2(v(x)) + xm_2(v(x)) - \hat{b}(x)x = 0,$$

and we have

$$F(0, x, y) = m_1(u(x))m_2(v(x)) + ym_2(v(x)) - \hat{b}(y)y,$$

we obtain

$$F(0, x, y) = x\hat{b}(x) - y\hat{b}(y) + (y - x)m_2(v(x)).$$

So,

$$F_{xx}(0, \hat{x}, \hat{x}) = (x\hat{b}(x))''|_{\hat{x}} - 2\frac{d}{dx}(m_2(v(x)))|_{\hat{x}},$$

$$F_{yy}(0, \hat{x}, \hat{x}) = -(x\hat{b}(x))''|_{\hat{x}},$$

These equalities imply that the condition $\lambda_{xx}(\hat{x}, \hat{x}) > \lambda_{yy}(\hat{x}, \hat{x})$ (sufficient for convergence-stability) is equivalent to $(x\hat{b}(x))''|_{\hat{x}} < \frac{d}{dx}(m_2(v(x)))|_{\hat{x}}$.

Since $(x\hat{b}(x))'' < 0$ for any x (see the proof of Theorem 1.4.3) and $m_2'(v) \geq 0$, the last inequality holds whenever $v'(\hat{x}) > 0$.

Let us consider the function $\Lambda(u, v, y)$ implicitly defined by the characteristic equation $\det(\mathbf{A}(\vec{u}, y) - \Lambda I) = \Lambda^2 + (m_2(v) + m_1(u) + y)\Lambda + (m_1(u) + y)m_2(v) - \hat{b}(y)y = 0$ where \mathbf{A} is defined in 1.8 and $\vec{u} = (u, v)$. Using the implicit function theorem and the equality $\Lambda(u(\hat{x}), v(\hat{x}), \hat{x}) = \lambda(\hat{x}, \hat{x}) = 0$ we obtain

$$\Lambda_u(u(\hat{x}), v(\hat{x}), \hat{x}) = \frac{-m_2(v(\hat{x}))m_1'(u(\hat{x}))}{m_2(v(\hat{x})) + y + m_1(u(\hat{x}))},$$

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$$\Lambda_v(u(\hat{x}), v(\hat{x}), \hat{x}) = \frac{-(m_1(u(\hat{x})) + y)m_2'(v(\hat{x}))}{m_2(v(\hat{x})) + y + m_1(u(\hat{x}))}.$$

Let us note that the monotonies of m_1 and m_2 imply $\Lambda_u(u(\hat{x}), v(\hat{x}), \hat{x}) < 0$ and $\Lambda_v(u(\hat{x}), v(\hat{x}), \hat{x}) \leq 0$.

If the last inequality is strict, Lemma 1.5.3 implies $v'(\hat{x}) > 0$. Otherwise, $u'(\hat{x}) = 0$ by 1.16 and $v'(\hat{x}) > 0$ again by Lemma 1.5.2. \square

In the literature of evolutionary dynamics (see [42],[17]), it is usual to substitute in Equation (9) in the Preliminaries the linear operator $A(\vec{u}, x)$ by $A(E(\vec{u}), x)$ where E is a function from the state space to a (lower) dimensional space. $E(\vec{u})$ is called the environment determined by a population \vec{u} because it summarizes the feedback of the population numbers on the population growth rate.

In the model dealt with in this chapter, the function E is simply the identity and so does not reduce the dimension of the state space, which is two dimensional. Nevertheless this is not always the case. Indeed, one can even find papers where one-dimensional environments are associated to infinite dimensional state spaces (see [12]). The one-dimensional environment makes some things easier. In particular, there is an interesting characterization of the ESS when the environment is one-dimensional and the fitness function $\Lambda(E, x)$, i.e. the dominant eigenvalue of the matrix $A(E, x)$, is increasing (decreasing) with respect to E . Namely, a value of the evolutionary variable \hat{x} is an ESS if and only if it is a point of minimum (maximum) of the function $E(x) := E(\vec{u}(x))$ where $\vec{u}(x)$ is the equilibrium of Equation (3.8)(see [17] and Result 3 in [42]).

In this context we give a general result about evolutionary stability.

Proposition 1.5.5 *Assume that the environment is one-dimensional and that the fitness function is strictly monotonous with respect to E . Let \hat{x} be an ESS such that the critical point (\hat{x}, \hat{x}) of the fitness is non-degenerate. Then \hat{x} is convergence-stable.*

Proof: Let us recall that $\lambda(x, y) = \Lambda(E(x), y)$ is the fitness of the mutant y invading a resident x .

We first prove that the curve where the fitness vanishes (which, together with the diagonal determines the ESS value) is symmetrical with respect to the diagonal.

Assuming $\lambda(x, y) = \Lambda(E(x), y) = 0$, we claim that $\lambda(y, x) = \Lambda(E(y), x) = 0$ too.

Indeed, as $\lambda(y, y) = \Lambda(E(y), y) = 0$, using the monotony of the fitness with respect to E , it follows that $E(x) = E(y)$. This gives $\lambda(y, x) = \Lambda(E(y), x) =$

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$$\Lambda(E(x), x) = \lambda(x, x) = 0.$$

The symmetry of the zero level curves, the non degeneracy condition and the fact that \hat{x} is an ESS give that for x close to \hat{x} , $|y - \hat{x}| < |x - \hat{x}|$ implies that y can invade x , i.e. $\lambda(x, y) > 0$. \square

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Chapter 2

An infinite-dimensional model for the adaptive dynamics of the maturation age

2.1 Introduction

In this chapter we study an integro-differential equations model for the distribution of individuals with respect to the age at maturity which is obtained by considering densities of the individuals with respect to the evolutionary variable in the ordinary differential equations model of Chapter 1.

In the model described in this chapter the mutation is already included and it is given by an integral operator that models non-clonal newborn output.

Existence and uniqueness of positive global solutions of the initial value problem is studied using the standard theory of semilinear evolution equations (see [48]).

It will be shown that, under some conditions on the variables constituting the model, there exists a steady state and that, when the mutation rate tends to zero, the steady state becomes concentrated at the ESS value of the ordinary differential equations model for the age at maturity described in Chapter 1.

2.2 Description of the model

We consider a population distributed into two groups of age: juveniles and adults. Let $u(x, t)$ and $v(x, t)$ be the density of young and adult individuals (respectively) at time t with respect to the trait $x = \frac{1}{T}$ where T is the expected value of the length of the juvenile period of an individual.

We suppose that the maturation age is an exponentially distributed random

2.2. Description of the model

variable so that the per capita transition rate from juveniles with trait x to adults is x (independently of the age distribution of the population). The inflow of newborns will be given by the integral operator $\int_0^\infty \hat{b}(y)\beta_\varepsilon(x, y)v(y, t)dy$ where $\hat{b}(y)$ is the trait specific fertility of the adult population and $\beta_\varepsilon(x, y)$ is the density of probability that the trait of the offspring of an individual with trait y is x .

The mortality rates depend on the total population of each age group. So, we are assuming that there is no competition for the resources between juveniles and adults.

The model leads to the following integro-differential system

$$\begin{cases} u_t(x, t) &= \int_0^\infty \hat{b}(y)\beta_\varepsilon(x, y)v(y, t)dy - m_1\left(\int_0^\infty u(y, t)dy\right)u(x, t) - xu(x, t), \\ v_t(x, t) &= xu(x, t) - m_2\left(\int_0^\infty v(y, t)dy\right)v(x, t). \end{cases} \quad (2.1)$$

Let us make the following hypotheses on the functions appearing in the model:

- The mortality rates, m_i , are smooth, strictly increasing and bounded functions such that $m_i(0) > 0$.
- The fertility function $b(T)$ satisfies the same assumptions as in Chapter 1, that is, it is a smooth (in $[0, \infty)$), strictly increasing and bounded function with strictly negative second derivative and such that $b(0) = 0$. As a consequence, $\hat{b}(x) := b(\frac{1}{x})$ has “similar” properties, in particular $x\hat{b}(x)$ is bounded in $[0, \infty)$ and $(x\hat{b}(x))'' = \frac{1}{x^3}b''(\frac{1}{x}) < 0$ for $x > 0$. From now on we will use the simpler notation $b(x)$ for $\hat{b}(x)$.
- β_ε is a strictly positive globally lipschitzian function that by definition, satisfies $\int_0^\infty \beta_\varepsilon(x, y)dx = 1$ (the probability of having offspring of whatever strategy is one) and such that the improper integral converges uniformly with respect to y on bounded intervals.

Let us also formulate some assumptions that we will need throughout the chapter:

- (H1) For all $\varepsilon > 0$ there exists $\delta > 0$ such that for all $y \geq 0$, $\text{supp}\beta_\varepsilon(\cdot, y)$ contains the interval $(\max(0, y - \delta), y + \delta)$,
- (H2) $\text{supp}\beta_\varepsilon(x, \cdot) \subset [x - \varepsilon, x + \varepsilon]$ for $\varepsilon > 0$ sufficiently small,
- (H3) $\lim_{\varepsilon \rightarrow 0} \int_{x-\varepsilon}^{x+\varepsilon} \beta_\varepsilon(x, y)dy = 1$,

$$(H4) \quad \lim_{\varepsilon \rightarrow 0} \frac{\int_{x-\varepsilon}^{x+\varepsilon} (y-x)\beta_\varepsilon(x,y)dy}{\min\left(\int_x^{x+\varepsilon} (y-x)^2\beta_\varepsilon(x,y)dy, \int_{x-\varepsilon}^x (y-x)^2\beta_\varepsilon(x,y)dy\right)} = 0.$$

Let us note that, the fact that $\int_0^\infty \beta_\varepsilon(x,y)dx = 1$ and hypothesis (H2) imply that, for any continuous function with compact support f ,

$$\int_0^\infty f(x)\beta_\varepsilon(x,y)dx \xrightarrow{\varepsilon \rightarrow 0} f(y).$$

Let us also note that hypotheses (H3) and (H4) would be implied by assuming symmetry of β_ε , although we do not explicitly ask for it. That is, if we would assume that $\beta_\varepsilon(x,y)$ is symmetrical and moreover that $\int_0^\infty x\beta_\varepsilon(x,y)dx = y$ then we would have $\int_0^\infty \beta_\varepsilon(x,y)dy = 1$ and $\int_0^\infty (y-x)\beta_\varepsilon(x,y)dy = 0$.

2.3 Existence and Uniqueness of positive solutions of the Initial Value Problem

The semilinear form of System (2.1) allows us to apply some results that can be found in [48] in order to study the initial value problem.

2.3.1 Previous Results

System (2.1) can be written in the following way

$$\begin{pmatrix} u \\ v \end{pmatrix}_t = A \begin{pmatrix} u \\ v \end{pmatrix} + K \begin{pmatrix} u \\ v \end{pmatrix} + f(u(t), v(t)),$$

where

$$A = \begin{pmatrix} -x & 0 \\ x & 0 \end{pmatrix}, \quad K = \begin{pmatrix} 0 & \int_0^\infty b(y)\beta_\varepsilon(x,y) \cdot dy \\ 0 & 0 \end{pmatrix}.$$

$A + K$ is an operator defined in the Banach space

$$X = L^1(0, \infty) \times L^1(0, \infty)$$

and the non-linear part of the system is

$$\begin{aligned} f : L^1(0, \infty) \times L^1(0, \infty) &\longrightarrow L^1(0, \infty) \times L^1(0, \infty) \\ (u(t), v(t)) &\longmapsto \left(-m_1(\int_0^\infty u(x,t)dx)u, -m_2(\int_0^\infty v(x,t)dx)v \right). \end{aligned}$$

2.3.1. Previous Results

Remark 2.3.1 In Chapter 1 we defined the mortality rates m_1 and m_2 only for positive values. In order to have the nonlinear part defined for all functions of the space $X = L^1(0, \infty) \times L^1(0, \infty)$ we extend the functions m_1 and m_2 in a Lipschitz (and bounded) way for negative values of the arguments.

Therefore our initial value problem is

$$\begin{cases} \left(\begin{array}{c} u \\ v \end{array} \right)_t = A \begin{pmatrix} u \\ v \end{pmatrix} + K \begin{pmatrix} u \\ v \end{pmatrix} + f(u(t), v(t)), \\ (u(0), v(0)) = (u_0, v_0). \end{cases} \quad (2.2)$$

Theorem 2.3.2 The operator $A + K$ is the infinitesimal generator of an analytic semigroup with domain

$$D(A+K) = D(A) = \{u \in L^1(0, \infty) \text{ such that } xu \in L^1(0, \infty)\} \times L^1(0, \infty).$$

Proof: The semigroup generated by the operator A defined by

$$A \begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} -xu \\ xu \end{pmatrix}$$

can be computed explicitly and is the following analytic semigroup

$$T(t) \begin{pmatrix} u_0(x) \\ v_0(x) \end{pmatrix} = \begin{pmatrix} u_0(x)e^{-xt} \\ v_0(x) + (1 - e^{-xt})u_0(x) \end{pmatrix}.$$

As the perturbation by a bounded operator of the generator of an analytic semigroup is the generator of an analytic semigroup (see [48]) we obtain that $A + K$ generates an analytic semigroup. \square

Theorem 2.3.3 The analytic semigroup $(S(t))_{t \geq 0}$ generated by the operator $A + K$ is positive.

Proof: The positivity of a semigroup can be characterized in terms of its resolvent operator (see [14] p.161). Hence, $R(\lambda, A)$ is positive for all $\lambda > \omega(A)$. Since K is a bounded operator we have

$$R(\lambda, A + K) = \sum_{k=0}^{\infty} R(\lambda, A)(KR(\lambda, A))^k \quad \text{for } \lambda > \omega(A) + |K|,$$

(where $|\cdot|$ stands for some norm equivalent to $\|\cdot\|$ (the norm of X), see [48]), which is positive. \square

2.3.2 Local Existence and Uniqueness

Definition 2.3.4 A function $z := (u, v) : [0, T) \rightarrow X$ is a (classical) solution of (2.2) on $[0, T)$ if z is continuous on $[0, T)$, continuously differentiable on $(0, T)$, $z(t) \in D(A + K) = D(A)$ for $0 < t < \infty$ and (2.2) is satisfied on $[0, T)$.

If (2.2) has a (classical) solution, $z(t)$, then (see Section 4.2 in [48]) it satisfies the integral equation

$$z(t) = S(t)z_0 + \int_0^t S(t-s)f(z(s))ds \quad (2.3)$$

where $S(t)$ is the semigroup generated by $A + K$, i.e., $S(t) = e^{(A+K)t}$ and f is the nonlinear part of the initial value problem (2.2).

It is therefore natural to define

Definition 2.3.5 A continuous solution z of the integral equation (2.3) is called a mild solution of the initial value problem (2.2).

The following result ensures the existence and uniqueness of mild solutions of the initial value problem (2.2).

Theorem 2.3.6 For all initial condition $(u_0, v_0) \in L^1(0, \infty) \times L^1(0, \infty)$ there exists $0 < t_{\max} < \infty$ such that the initial value problem has a unique mild solution $(u(t), v(t))$ in a maximal interval of existence $[0, t_{\max})$.

Moreover if $t_{\max} < \infty$, then $\lim_{t \rightarrow t_{\max}} \|(u(t), v(t))\| = \infty$.

Proof: It suffices to show that f is locally Lipschitzian. This implies the statement of the theorem (see [48] p. 185).

As m_1 and m_2 are C^1 functions, it is easy to check that f is locally Lipschitz. Indeed, if we consider $z_1(t) = (u_1(t), v_1(t))$, $z_2(t) = (u_2(t), v_2(t))$ two elements of a ball of radius R of $L^1(0, \infty) \times L^1(0, \infty)$ and we call

$$P_1 := \int_0^\infty u_1(x, t)dx, \quad Q_1 := \int_0^\infty v_1(x, t)dx,$$

$$P_2 := \int_0^\infty u_2(x, t)dx, \quad Q_2 := \int_0^\infty v_2(x, t)dx,$$

2.3.3. Continuous dependence on initial conditions

we have

$$\begin{aligned}
& \|f(u_1(t), v_1(t)) - f(u_2(t), v_2(t))\|_{L^1(0,\infty) \times L^1(0,\infty)} = \\
& \| -m_1(P_1)u_1 + m_1(P_2)u_2 \|_{L^1(0,\infty)} + \| -m_2(Q_1)v_1 + m_2(Q_2)v_2 \|_{L^1(0,\infty)} = \\
& \| -m_1(P_1)u_1 + m_1(P_1)u_2 - m_1(P_1)u_2 + m_1(P_2)u_2 \|_{L^1(0,\infty)} + \\
& \| -m_2(Q_1)v_1 + m_2(Q_1)v_2 - m_2(Q_1)v_2 + m_2(Q_2)v_2 \|_{L^1(0,\infty)} = \\
& \|m_1(P_1)(u_2 - u_1) + u_2(m_1(P_2) - m_1(P_1))\|_{L^1(0,\infty)} + \\
& \|m_2(Q_1)(v_2 - v_1) + v_2(m_2(Q_2) - m_2(Q_1))\|_{L^1(0,\infty)} \leq \\
& |m_1(P_1)| \|u_2 - u_1\|_{L^1(0,\infty)} + M_1 R |P_2 - P_1| + \\
& |m_2(Q_1)| \|v_2 - v_1\|_{L^1(0,\infty)} + M_2 R |Q_2 - Q_1| \leq \\
& (|m_1(P_1)| + M_1 R) \|u_2 - u_1\|_{L^1(0,\infty)} + (|m_2(Q_1)| + M_2 R) \|v_2 - v_1\|_{L^1(0,\infty)} \leq \\
& D (\|u_2 - u_1\|_{L^1(0,\infty)} + \|v_2 - v_1\|_{L^1(0,\infty)}) = D \|z_2(t) - z_1(t)\|_{L^1(0,\infty) \times L^1(0,\infty)},
\end{aligned}$$

where M_1 i M_2 are the lipschitz constants of the mortality rates and

$$D := \max(|m_1(P_1)| + M_1 R, |m_2(Q_1)| + M_2 R).$$

□

2.3.3 Continuous dependence on initial conditions

In this subsection we show that two local solutions corresponding to initial conditions that are close in the norm of the space $L^1(0, \infty) \times L^1(0, \infty)$ remain close to each other.

Proposition 2.3.7 *Let $z(t)$ and $\tilde{z}(t)$ be two local solutions of the initial value problem (2.2) corresponding to initial conditions z_0 and \tilde{z}_0 respectively. Then the following inequality*

$$\|z(t) - \tilde{z}(t)\|_{L^1(0,\infty) \times L^1(0,\infty)} \leq C e^{(CL+a)t} \|z_0 - \tilde{z}_0\|_{L^1(0,\infty) \times L^1(0,\infty)}$$

holds for all $\tau < \min(t_{\max}(z_0), t_{\max}(\tilde{z}_0))$ where C and a are the constants given by the (semigroup) inequality $\|e^{(A+K)t}\| \leq C e^{at}$ and L is the Lipschitz

2.3.4. Global Existence of solutions

constant of the function f in a bounded set that contains the sets $\{z(s) : s \in [0, \tau]\}$ and $\{\tilde{z}(s) : s \in [0, \tau]\}$.

Proof: By definition of mild solution, $z(t)$ and $\tilde{z}(t)$ satisfy

$$\begin{aligned} z(t) &= e^{(A+K)t} z_0 + \int_0^t e^{(A+K)(t-s)} f(z(s)) ds, \\ \tilde{z}(t) &= e^{(A+K)t} \tilde{z}_0 + \int_0^t e^{(A+K)(t-s)} f(\tilde{z}(s)) ds. \end{aligned}$$

Using the equalities we obtain

$$\begin{aligned} \|z(t) - \tilde{z}(t)\|_{L^1(0,\infty) \times L^1(0,\infty)} &\leq C e^{at} \|z_0 - \tilde{z}_0\|_{L^1(0,\infty) \times L^1(0,\infty)} \\ &\quad + e^{at} \int_0^t C L e^{-as} \|z(s) - \tilde{z}(s)\|_{L^1(0,\infty) \times L^1(0,\infty)} ds, \end{aligned}$$

and finally, by Gronwall's inequality

$$\|z(t) - \tilde{z}(t)\|_{L^1(0,\infty) \times L^1(0,\infty)} \leq C e^{(CL+a)t} \|z_0 - \tilde{z}_0\|_{L^1(0,\infty) \times L^1(0,\infty)}.$$

□

2.3.4 Global Existence of solutions

Theorem 2.3.8 *For all initial condition $z_0 = (u_0, v_0) \in L^1(0, \infty) \times L^1(0, \infty)$ there exists a unique mild solution of (2.2), $z(t)$, defined in $[0, \infty)$.*

Proof: Let us assume $t_{\max} < \infty$. By Theorem 1.4 p.184 in [48] we only need to show that

$$\limsup_{t \rightarrow t_{\max}} \|z(t)\| < \infty.$$

Using the equality of the last proof we have

$$\begin{aligned} \|z(t)\|_{L^1(0,\infty) \times L^1(0,\infty)} &\leq C e^{at} \|z_0\|_{L^1(0,\infty) \times L^1(0,\infty)} \\ &\quad + M C e^{at} \int_0^t e^{-as} \|z\|_{L^1(0,\infty) \times L^1(0,\infty)} ds, \end{aligned}$$

where M is the bound of the mortality rates.

And, using Gronwall's inequality we can conclude that

$$\|z(t)\|_{L^1(0,\infty) \times L^1(0,\infty)} \leq C \|z_0\|_{L^1(0,\infty) \times L^1(0,\infty)} e^{(MC+a)t}.$$

Therefore

$$\limsup_{t \rightarrow t_{\max}} \|z(t)\| < \infty$$

2.3.5. Positivity of solutions

which proves the theorem. \square

The smoothness of the mortality functions m_1 and m_2 imply that mild solutions of the initial value problem (2.2) with initial conditions (u_0, v_0) belonging to the domain $A + K$ are classical solutions of (2.2) (by the regularity Theorem in p. 187 in [48]).

2.3.5 Positivity of solutions

The positivity of solutions is needed in order that the problem makes biological sense.

Let us begin by showing the positivity of local solutions of the initial value problem (2.2).

Theorem 2.3.9 *Every local solution of (2.2) with positive initial condition $z_0 = (u_0, v_0)$ is positive.*

Proof: Let λ be a constant bigger than the maximum of the bounds of the functions m_1 and m_2 .

If we add and subtract $\lambda \begin{pmatrix} u \\ v \end{pmatrix}$ to the initial value problem (2.2) we get

$$\begin{cases} \begin{pmatrix} u \\ v \end{pmatrix}_t = (A + K - \lambda I) \begin{pmatrix} u \\ v \end{pmatrix} + f(u(t), v(t)) + \lambda \begin{pmatrix} u(t) \\ v(t) \end{pmatrix}, \\ (u(0), v(0)) = (u_0, v_0). \end{cases} \quad (2.4)$$

The mild solutions of this problem, and therefore also those of problem (2.2) are limit of a recurrent sequence in $[0, t_{\max})$, $(z_n)_{n \geq 0}$, given by the formula

$$z_{n+1}(t) = \tilde{S}(t)z_0 + \int_0^t \tilde{S}(t-s)(f(z_n(s)) + \lambda z_n(s))ds,$$

where $\tilde{S}(t)$ is the semigroup generated by the operator $A + K - \lambda I$, that is, $\tilde{S}(t) = e^{-\lambda t}S(t)$.

As z_0 is positive, the semigroup $\tilde{S}(t)$ is positive and λ is bigger than the bound of m_1 and m_2 , we obtain that z_1 is positive.

By induction over n we have that $(z_n)_{n \geq 0}$ is positive.

Since the cone of the positive functions of X is closed, we obtain that $z(t)$ is positive. \square

The positivity of local solutions will be used to show positivity of global solutions.

Theorem 2.3.10 *Every global solution of (2.2), $z(t)$, with positive initial condition $z_0 = (u_0, v_0)$ is positive.*

Proof: Let us denote by C the cone of the positive functions in $L^1(0, \infty) \times L^1(0, \infty)$.

Let us consider the set $I = \{t \geq 0 : z(s) \geq 0 \quad \forall s \leq t\}$. By Theorem 2.3.9 I is not empty.

The proof is completed by showing that I is closed and open.

We first prove that I is closed :

Let $T = \sup\{t \in I\}$. Assume that $T \notin I$. This means that $z(T)$ belongs to the complement set of C , which is an open set.

As $z(t)$ is continuous, there exists $t' < T$ such that $z(t')$ belongs to the complement set of C too. Therefore T is not the supremum which is a contradiction.

It remains to prove that I is open :

We only need to show that, if $\tau \in I$ then $t \in [\tau, \tau + \varepsilon] \in I$ (because by definition of I , $t \in [0, \tau] \subset I$)

If $\tau \in I$, $z(\tau) \in C$. By the above theorem, there exists $\varepsilon > 0$ such that $t \in [\tau, \tau + \varepsilon] \in I$ and this completes the proof. \square

2.4 Stationary Solutions

From now on, we will use the following notation

$$\int_0^\infty u(y, t) dy := P(t) = \text{Total population of young individuals at time } t,$$

$$\int_0^\infty v(y, t) dy := Q(t) = \text{Total population of adult individuals at time } t.$$

The equilibria of System (2.1) will be given by solutions of the equations

$$\begin{cases} \int_0^\infty b(y)\beta_\varepsilon(x, y)v(y)dy - m_1(P)u(x) - xu(x) = 0, \\ xu(x) - m_2(Q)v(x) = 0. \end{cases} \quad (2.5)$$

Isolating $v(x)$ in the second equation and substituting it in the first one we obtain

$$\frac{1}{m_2(Q)} \int_0^\infty b(y)\beta_\varepsilon(x, y)yu(y)dy - xu(x) = m_1(P)u(x). \quad (2.6)$$

For simplicity in the notation from now on we will denote $\mu := m_2(Q)$.

So, in order to find non trivial stationary solutions it is necessary to find (positive) eigenfunctions $u_\mu(x)$ corresponding to an eigenvalue, λ_μ , satisfying

$$\lambda_\mu = m_1(P) \quad (2.7)$$

2.4.1. The eigenvalue problem

of the operator B_μ defined in $L^1(0, \infty)$ in the following way

$$B_\mu u := K_\mu u + Au, \quad (2.8)$$

where

$$\begin{aligned} (Au)(x) &= -xu(x), \\ (K_\mu u)(x) &= \int_0^\infty \frac{y}{\mu} b(y) \beta_\varepsilon(x, y) u(y) dy. \end{aligned} \quad (2.9)$$

As we are looking for a positive eigenfunction we can assume that it has norm 1, that is, $\int_0^\infty u_\mu(x) dx = 1$.

Let us consider the eigenfunction $\tilde{u}_\mu(x) = c_\mu u_\mu(x)$ where c_μ satisfies $\lambda_\mu = m_1(c_\mu)$.

On the other hand, substituting $\tilde{u}_\mu(x)$ in the second equation in (2.5) gives $v(x) = \frac{xc_\mu}{\mu} u_\mu(x)$.

Integrating, we have $Q = \frac{c_\mu}{\mu} \int_0^\infty xu_\mu(x) dx$ and, finally

$$m_2\left(\frac{c_\mu}{\mu} \int_0^\infty xu_\mu(x) dx\right) = \mu.$$

Any solution μ of the last equation gives a stationary solution of (2.1), $(c_\mu u_\mu(x), \frac{c_\mu}{\mu} xu_\mu(x))$, provided that λ_μ belongs to the set of values of m_1 .

And conversely, any non trivial solution of (2.5) is of the form $(c_\mu u_\mu(x), \frac{c_\mu}{\mu} xu_\mu(x))$ for a fixed point of the function

$$\mu \rightarrow m_2\left(\frac{c_\mu}{\mu} \int_0^\infty xu_\mu(x) dx\right).$$

2.4.1 The eigenvalue problem

The aim of this section is to show the existence of a dominant eigenvalue of the operator B_μ . Even though we are working in $L^1(0, \infty)$, most of the results we will formulate in this section hold, more in general, for an arbitrary Banach lattice X (that is, a Banach space X with an ordering \leq such that any two elements f, g in X have a supremum and such that if $|f| \leq |g|$ then $\|f\| \leq \|g\|$, where $|f| = \sup(f, -f)$, the absolute value of f).

Let us start by giving some definitions that can be found in [14], [24], [45] and [55].

Definition 2.4.1 [24] *The boundary spectrum, $\sigma_b(A)$, of a generator A is the intersection of the spectrum with the line $\{\lambda \in \mathbb{C} : \operatorname{Re}\lambda = s(A)\}$.*

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Definition 2.4.2 [45] *A linear subspace J of a Banach lattice X is called **ideal** if $u \in J$ and $|v| \leq u$ implies $v \in J$.*

Definition 2.4.3 [45] *An element u in the positive cone of a Banach lattice X having the property that the closed ideal generated by u is all of X is called a **quasi-interior point** of X^+ .*

Definition 2.4.4 [14], [55] *Let X be a Banach lattice. Given a positive linear operator T from X into itself, the closed ideal J in X is called **T -invariant** if $T(J) \subset J$.*

*The operator T is called **irreducible** if $\{0\}$ and X are the only T -invariant closed ideals.*

Equivalently, T is irreducible if there exists $m \in \mathbb{N}$ such that $\langle T^m f, g \rangle > 0$ whenever $0 < f \in X$, $0 < g \in X'$ (where $f > 0$ means $f \geq 0$ and $f \neq 0$).

*Furthermore, T is called **strongly irreducible** if Tu is a quasi-interior point for all $0 < u \in X$. A strongly irreducible operator is irreducible.*

Definition 2.4.5 [45] *A semigroup $T(t)$ with generator A is called **irreducible** if the linear operators $T(t)$ are irreducible for all $t \geq 0$.*

The importance of the following theorem is that it ensures the existence of a strictly dominant eigenvalue for certain perturbations of the generator of a positive semigroup.

Theorem 2.4.6 [24] *Suppose that A is the generator of a positive semigroup and that K is a positive bounded linear operator on a Banach lattice X . If $KR(\lambda_0, A)$ is compact for some $\lambda_0 \in \rho(A)$ and if $s(A + K) > s(A)$ then $\sigma_b(A + K)$ is a finite union of "subgroups" (i.e. $\sigma_b(A + K) = \bigcup_{k=1}^n \{s(A + K) + i\alpha_k \mathbb{Z}\}$ ($\alpha_k \in \mathbb{R}$)) and consists only of poles of finite algebraic multiplicity. Moreover if K is irreducible then $s(A + K)$ is a strictly dominant eigenvalue of algebraic multiplicity one and the semigroup generated by $B := A + K$ is irreducible.*

It is trivial to prove that K_μ (defined in (2.9)) is a positive bounded operator (remember that, by hypothesis $yb(y)$ is a bounded function) and that A (also defined in (2.9)) generates a positive semigroup (see the proof of Theorem 2.3.2).

Next, we give some results that we need in order to prove that $B_\mu (= A + K_\mu)$ satisfies all the assumptions of Theorem 2.4.6.

The first one is a standard compactness criterion in L^p spaces.

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Proposition 2.4.7 [4]

Let $\Omega \subset \mathbb{R}^n$ be an open set and let F be a bounded subset in $L^p(\Omega)$ with $1 \leq p < \infty$.

Let us assume that

1. For all $\varepsilon > 0$ for all $\omega \subset\subset \Omega$ and $\tau_h f(x) := f(x+h)$ there exists $\delta > 0$, $\delta < \text{dist}(\omega, \partial\Omega)$ such that

$$\|\tau_h f - f\|_{L^p(\omega)} < \varepsilon$$

for all $h \in \mathbb{R}^n$ with $|h| < \delta$ and for all $f \in F$.

2. For all $\varepsilon > 0$ there exists $\omega \subset\subset \Omega$ such that

$$\|f\|_{L^p(\Omega \setminus \omega)} < \varepsilon \quad \text{for all } f \in F.$$

Then F is a precompact set in $L^p(\Omega)$.

An application of Proposition 2.4.7 gives

Proposition 2.4.8 Let A and K_μ be the operators defined by (2.9). Let $R(\lambda, A)$ be the resolvent operator of A . Then the operator $K_\mu R(1, A)$ is compact.

Proof:

The resolvent operator of A can be computed explicitly

$$R(\lambda, A)f(x) = \frac{f(x)}{x + \lambda} \quad \text{for } \lambda \in \rho(A).$$

Let us consider the unit ball B of L^1 .

We will show that

$$\begin{aligned} F &= \{K_\mu R(1, A)f \quad : \quad f \in B\} \\ &= \left\{ \int_0^\infty \frac{y}{\mu} b(y) \beta_\varepsilon(x, y) \frac{f(y)}{y+1} dy \quad : \quad f \in B \right\} \end{aligned}$$

is precompact .

Let us note that F is bounded. Indeed,

$$\begin{aligned} \|F\|_{L^1} &= \sup_{f \in F} \int_0^\infty \left| \int_0^\infty \frac{y}{\mu} b(y) \beta_\varepsilon(x, y) \left(\frac{f(y)}{y+1} \right) dy \right| dx \\ &\leq \sup_{f \in F} \int_0^\infty \frac{yb(y)}{\mu(y+1)} |f(y)| \int_0^\infty \beta_\varepsilon(x, y) dx dy \\ &\leq \frac{b(0)}{\mu}. \end{aligned}$$

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We have, assuming that $\omega = (0, l)$, for all $g = K_\mu R(\lambda, A)f \in F$, $l > 0$, $h > 0$,

$$\begin{aligned}
\|\tau_h g - g\|_{L^1(\omega)} &= \int_\omega |(\tau_h g - g)(x)| dx \\
&= \int_0^l \left(\left| \int_0^\infty \frac{y}{\mu} b(y) \left(\frac{f(y)}{y+1} \right) (\beta_\varepsilon(x+h, y) - \beta_\varepsilon(x, y)) dy \right| \right) dx \\
&\leq \frac{1}{\mu} \int_0^\infty \left(\frac{y b(y)}{y+1} |f(y)| \int_0^l |\beta_\varepsilon(x+h, y) - \beta_\varepsilon(x, y)| dx \right) dy \\
&\leq \frac{1}{\mu} \int_0^\infty \frac{y b(y)}{y+1} |f(y)| \int_0^l L h dx dy \\
&\leq \frac{b(0)}{\mu} L h l < \varepsilon \quad \text{if } h < \frac{\mu \varepsilon}{b(0) L l},
\end{aligned}$$

where we have used that $b(y) \leq b(0)$ and that $\beta_\varepsilon(x, y)$ is a globally lipschitzian function.

We also have

$$\begin{aligned}
\|g\|_{L^1((0, \infty) \setminus \omega)} &= \int_l^\infty \left| \int_0^\infty \frac{y}{\mu} b(y) \beta_\varepsilon(x, y) \left(\frac{f(y)}{y+1} \right) dy \right| dx \\
&= \frac{1}{\mu} \int_0^\infty \frac{y}{y+1} b(y) |f(y)| \int_l^\infty \beta_\varepsilon(x, y) dx dy \\
&\leq \frac{1}{\mu} \sup_{y \in (0, \infty)} \left(b(y) \int_l^\infty \beta_\varepsilon(x, y) dx \right) < \varepsilon,
\end{aligned}$$

where the last inequality is due to the following results on β_ε and b

1. $\forall M \quad \forall \varepsilon > 0 \quad \forall \delta > 0 \quad \exists L > 0$ such that if $y < M$ then

$$\int_L^\infty \beta_\varepsilon(x, y) dx < \delta,$$

- 2.

$$\lim_{y \rightarrow \infty} b(y) = 0.$$

Indeed, given ε , let M_ε be such that

$$b(y) < \mu \varepsilon \quad \text{if } y \geq M_\varepsilon,$$

2.4.1. The eigenvalue problem

and, for this M_ε let L be such that if $y < M_\varepsilon$

$$\int_L^\infty \beta_\varepsilon(x, y) dx < \frac{\varepsilon \mu}{b(0)}.$$

Then, if $l > L$ we have

$$\frac{b(y)}{\mu} \int_l^\infty \beta_\varepsilon(x, y) dx < \varepsilon \quad \text{if } y < M_\varepsilon,$$

$$\frac{b(y)}{\mu} \int_l^\infty \beta_\varepsilon(x, y) dx \leq \frac{1}{\mu} \mu \varepsilon = \varepsilon \quad \text{if } y \geq M_\varepsilon.$$

By Proposition 2.4.7 F is a precompact set, i.e., $K_\mu R(1, A)$ is a compact operator.

□

In order to be able to apply Theorem 2.4.6 to the operator $B_\mu := A + K_\mu$ we have to prove the irreducibility of the operator K_μ . It is the statement of the following result.

Proposition 2.4.9 *Let us assume that (H1) holds. Then the operator K_μ defined in (2.9) is irreducible.*

Proof: We have to show that, given $u \in L^1$, $u > 0$ and $\phi \in (L^1)' = L^\infty$, $\phi > 0$, there exists $m \in \mathbb{N}$ such that

$$\langle K_\mu^m u, \phi \rangle > 0.$$

Let us consider $m = 1$. We have

$$\begin{aligned} \langle K_\mu u, \phi \rangle &= \int_0^\infty K_\mu u(x) \phi(x) dx \\ &= \int_0^\infty \int_0^\infty \frac{y}{\mu} b(y) \beta_\varepsilon(x, y) u(y) dy \phi(x) dx \geq 0. \end{aligned}$$

It might happen that the support of $\beta_\varepsilon(\cdot, y)$ has empty intersection with the support of $\phi(x)u(y)$ and then

$$\langle K_\mu u, \phi \rangle = 0.$$

By hypothesis for all ε there exists $\delta > 0$ such that for all $y \geq 0$, $\text{supp} \beta_\varepsilon(\cdot, y)$ contains the interval $(\max(0, y - \delta), y + \delta)$.

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For $m = 2$,

$$\begin{aligned}
 K_\mu^2 u(x) &= K_\mu(K_\mu(u(x))) \\
 &= K_\mu\left(\int_0^\infty \frac{y}{\mu} b(y) \beta_\varepsilon(x, y) u(y) dy\right) \\
 &= \int_0^\infty \frac{z}{\mu} b(z) \beta_\varepsilon(x, z) \int_0^\infty \frac{y}{\mu} b(y) \beta_\varepsilon(z, y) u(y) dy dz \\
 &= \int_0^\infty \frac{y}{\mu} b(y) \left(\int_0^\infty \frac{z}{\mu} b(z) \beta_\varepsilon(x, z) \beta_\varepsilon(z, y) dz\right) u(y) dy.
 \end{aligned}$$

If we denote

$$\int_0^\infty \frac{z}{\mu} b(z) \beta_\varepsilon(x, z) \beta_\varepsilon(z, y) dz := \tilde{\beta}_\varepsilon(x, y),$$

we have

$$K_\mu^2 u(x) = \int_0^\infty \frac{y}{\mu} b(y) \tilde{\beta}_\varepsilon(x, y) u(y) dy,$$

where $\tilde{\beta}_\varepsilon(x, y)$ satisfies that for all $y \geq 0$, $\text{supp } \tilde{\beta}_\varepsilon(\cdot, y)$ contains the interval $(\max(0, y - 2\delta), y + 2\delta)$.

This is so because $\tilde{\beta}_\varepsilon(x, y)$ is strictly positive whenever there exists a z such that $|x - z| < \delta$ and $|z - y| < \delta$, i.e., whenever $|x - y| < 2\delta$.

Thus, for m big enough we will have

$$\langle K^m u(x), \phi(x) \rangle > 0.$$

□

The former proposition implies the next result

Theorem 2.4.10 *Let us assume that (H1) holds. Then, the semigroup generated by the operator B_μ is positive and irreducible.*

Proof: Since K_μ is a bounded positive operator and A generates a positive semigroup, $A + K_\mu$ is the generator of a positive semigroup.

Irreducibility follows from Proposition 2.4.9 and the fact that the perturbation by a bounded (positive) irreducible operator of the generator of a positive semigroup generates an irreducible semigroup (see [45] p. 307). □

The only hypothesis of Theorem 2.4.6 that we still have to prove is that $s(A + K_\mu) > s(A)$ which, in general, is difficult to verify. In order to show it, let us first formulate two results.

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Proposition 2.4.11 *Let us assume that (H2), (H3) and (H4) hold. Then for all $l < 1$ there exists $\varepsilon > 0$ such that for all $[c, d] \subset (0, \infty)$ there exists a positive function u with $\text{supp } u \subset [c, d]$ satisfying*

$$\int_0^\infty \beta_\varepsilon(x, y)u(y) dy \geq lu(x).$$

Proof: Let us consider $u(x)$ a positive smooth function with $\text{supp } u \subset [c, d]$ and such that u'' is increasing in $[c, c']$, and decreasing in $[d', d]$, for c' and d' satisfying $c < c' - \varepsilon$ and $d' - \varepsilon < d$. Notice that this is only possible if $\varepsilon < \frac{d - c}{2}$ restricting already the size of ε . We also assume that u is strictly positive in $[c' - \varepsilon, d' + \varepsilon]$. The former hypotheses imply the following inequalities that we will use in the proof

$$u(x) \geq k_0, \quad |u'(x)| \leq k_1 \quad u''(x) \geq -k_2$$

for some $k_0 > 0$, $k_1 \geq 0$, $k_2 \geq 0$ in $[c' - \varepsilon, d' + \varepsilon]$.

By the Taylor formula and the hypotheses on β_ε we have

$$\begin{aligned} \int_0^\infty \beta_\varepsilon(x, y)u(y)dy &= \int_{x-\varepsilon}^{x+\varepsilon} \beta_\varepsilon(x, y)u(y)dy \\ &= u(x) \int_{x-\varepsilon}^{x+\varepsilon} \beta_\varepsilon(x, y)dy + u'(x) \int_{x-\varepsilon}^{x+\varepsilon} (y-x)\beta_\varepsilon(x, y)dy \\ &\quad + \frac{1}{2} \int_{x-\varepsilon}^{x+\varepsilon} u''(\xi(y))(y-x)^2\beta_\varepsilon(x, y)dy, \end{aligned} \tag{2.10}$$

where $x - \varepsilon < \xi(y) < x + \varepsilon$.

Let us consider three cases:

a) $x \in [c', d']$.

Then $u'(x) \geq -\frac{k_1}{k_0}u(x)$ and $u''(x) \geq \frac{k_2}{k_0}u(x)$ and (2.10) yields

$$\begin{aligned} \int_0^\infty \beta_\varepsilon(x, y)u(y)dy &\geq u(x) \int_{x-\varepsilon}^{x+\varepsilon} \beta_\varepsilon(x, y)dy \\ &\quad - \left(\frac{k_1}{k_0} \int_{x-\varepsilon}^{x+\varepsilon} (y-x)\beta_\varepsilon(x, y)dy \right. \\ &\quad \left. + \frac{k_2}{k_0} \frac{1}{2} \int_{x-\varepsilon}^{x+\varepsilon} (y-x)^2\beta_\varepsilon(x, y)dy \right) u(x) \end{aligned}$$

which implies the statement of the Proposition (using that $\lim_{\varepsilon \rightarrow 0} \int_{x-\varepsilon}^{x+\varepsilon} \beta_\varepsilon(x, y)dy = 1$, $\lim_{\varepsilon \rightarrow 0} \int_{x-\varepsilon}^{x+\varepsilon} (y-x)\beta_\varepsilon(x, y)dy = 0$ and $\lim_{\varepsilon \rightarrow 0} \int_{x-\varepsilon}^{x+\varepsilon} (y-x)^2\beta_\varepsilon(x, y)dy = 0$).

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b) $x \in [c, c']$.

Then, since $u''(x)$ is increasing we have $u''(\xi) > u''(x)$ if $y > x$ and therefore

$$\frac{1}{2} \int_{x-\varepsilon}^{x+\varepsilon} u''(\xi(y))(y-x)^2 \beta_\varepsilon(x, y) dy \geq \frac{u''(x)}{2} \int_x^{x+\varepsilon} (y-x)^2 \beta_\varepsilon(x, y) dy$$

where we have used also that $\int_{x-\varepsilon}^x u''(\xi(y))(y-x)^2 \beta_\varepsilon(x, y) \geq 0$.

Moreover, using that $u''(x)$ is increasing we have

$$u'(x) = \int_c^x u''(s) ds \leq u''(x)(x-c).$$

Then (2.10) yields

$$\begin{aligned} \int_0^\infty \beta_\varepsilon(x, y) u(y) dy &\geq u(x) \int_{x-\varepsilon}^{x+\varepsilon} \beta_\varepsilon(x, y) dy \\ &+ \left(-u''(x)(x-c) \int_{x-\varepsilon}^{x+\varepsilon} (y-x) \beta_\varepsilon(x, y) dy \right. \\ &\left. + \frac{u''(x)}{2} \int_x^{x+\varepsilon} (y-x)^2 \beta_\varepsilon(x, y) dy \right) u(x) \end{aligned}$$

which implies the statement of the Proposition (using (H3) and (H4)).

c) $x \in [d', d]$.

It follows from the same argument as in b).

□

Corollary 2.4.12 *Let us assume that (H2), (H3) and (H4) hold. Let $f(x)$ and $g(x)$ be functions such that $f(x) > 0$ in $(0, \infty)$. If $f(x) - g(x) > M$ in $[c, d] \subset (0, \infty)$ then there exists a positive function $v(x)$ with $\text{supp } v \subset [c, d]$ such that*

$$\int_0^\infty \beta_\varepsilon(x, y) f(y) v(y) dy - g(x) v(x) \geq M v(x).$$

Proof: By Proposition 2.4.11 we have that, for all $l < 1$ there exists $\varepsilon > 0$ such that there exists u with $\text{supp } u \subset [c, d]$ satisfying

$$\int_0^\infty \beta_\varepsilon(x, y) u(y) dy \geq l u(x).$$

Taking $v(x) = \frac{u(x)}{f(x)}$ we have

$$\int_0^\infty \beta_\varepsilon(x, y) f(y) v(y) dy \geq l f(x) v(x).$$

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Then

$$\begin{aligned} \int_0^\infty \beta_\varepsilon(x, y) f(y) v(y) dy - g(x) v(x) &\geq (lf(x) - g(x))v(x) \\ &\geq Mv(x) \end{aligned}$$

for l such that $1 - l$ is small enough, that is, when ε is small enough. \square

We can now formulate the theorem that ensures the existence of a dominant eigenvalue of the operator B_μ (defined in (2.8) and (2.9)) under some hypotheses on the functions appearing in the model.

In order to prove it we will use the inequality

$$s(A) \geq \sup\{\mu \in \mathbb{R} : Af \geq \mu f \text{ for some } 0 < f \in D(A)\} \quad (2.11)$$

(where recall that $f > 0$ means $f \geq 0$ and $f \neq 0$) formulated in [45] for the spectral bound of the generator, A , of a strongly continuous positive semigroup in $C(K)$, the space of all real-valued continuous functions on a compact space K .

The proof given in [45] is also valid for the generator of an analytic positive semigroup in a Banach lattice and for the generator of an eventually compact semigroup in a Banach lattice (a semigroup $(T(t))_{t \geq 0}$ is called eventually compact if there exists $t_0 > 0$ such that $T(t_0)$ is compact (and hence $T(t)$ is compact for all $t \geq t_0$)), being the clue that, in all cases the growth bound of the semigroup coincides with the spectral bound $s(A)$.

If the Banach lattice is either L^1 or L^2 and A is the generator of a positive C_0 -semigroup, then also the growth bound of the semigroup coincides with the spectral bound (in these particular cases only positivity of the semigroup is needed, see [14], [45]) and therefore (2.11) is valid.

More recently, in [62] and [63], Weis has proved the general case, that is, that for a positive semigroup $T(t)$ on L^p , $1 \leq p < \infty$, with generator A , the growth bound of $T(t)$ equals the spectral bound of A .

Theorem 2.4.13 *Let us assume that (H1), (H2), (H3) and (H4) hold and that there exists $\delta > 0$ and an interval $[c, d]$ such that the inequality*

$$\frac{xb(x)}{\mu} - x > (1 + \delta)m_1(0) \quad \forall x \in [c, d] \quad (2.12)$$

holds. Let B_μ be the operator defined in (2.8) and (2.9). Then, for ε small enough, $s(B_\mu)$ is a strictly dominant eigenvalue with algebraic multiplicity 1 of the operator B_μ and moreover, $s(B_\mu) > m_1(0)$.

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Proof: We are going to apply Theorem 2.4.6 to show that $s(A + K_\mu)$ is a dominant eigenvalue with algebraic multiplicity 1 of the operator $B_\mu = A + K_\mu$ (where A and K_μ are defined in (2.9)).

In order to see that $A + K_\mu$ satisfies the hypotheses of the theorem it only remains to prove that $s(A + K_\mu) > s(A) = 0$.

Moreover, as the dominant eigenvalue has to be in the image of m_1 (see (2.7)) we have to prove $s(A + K_\mu) > m_1(0) > 0$.

Using the characterization (2.11) for the spectral bound of the generator of a positive semigroup

$$s(A + K_\mu) \geq \sup\{\lambda \in \mathbb{R} : (A + K_\mu)u \geq \lambda u \quad \text{for some } 0 < v \in D(A + K_\mu)\},$$

we are reduced to find a non vanishing $v(x) \geq 0$ such that the inequality

$$\int_0^\infty \frac{y}{\mu} b(y) \beta_\varepsilon(x, y) v(y) dy \geq ((1 + \delta)m_1(0) + x)v(x), \quad (2.13)$$

or, equivalently,

$$\int_0^\infty \frac{y}{\mu} b(y) \beta_\varepsilon(x, y) v(y) dy - xv(x) \geq (1 + \delta)m_1(0)v(x) \quad (2.14)$$

holds $\forall x \geq 0$.

This follows immediately from Proposition 2.4.11 and Corollary 2.4.12 (with $f(x) = \frac{yb(y)}{\mu}$ and $g(x) = x$).

So there exists $\varepsilon_0 = \varepsilon_0(\mu)$ such that the statement of the theorem holds when $\varepsilon < \varepsilon_0(\mu)$. \square

In order to give a result about the eigenfunction corresponding to the eigenvalue $s(B_\mu)$ we will apply the following theorems

Theorem 2.4.14 [14] *Let $(T(t))_{t \geq 0}$ be a positive irreducible C_0 semigroup generated by the operator A and $s(A) > -\infty$ a pole of the resolvent $R(\lambda, A)$ on a Banach lattice X . Then $s(A)$ is a first-order pole with geometric multiplicity one. Moreover there exists a quasi-interior point x_0 of X^+ such that $Ax_0 = s(A)x_0$ and a strictly positive point x_0^* of $(X^+)^*$ such that $A^*x_0^* = s(A)x_0^*$, (where A^* denotes the adjoint operator of A).*

Theorem 2.4.15 [45] *Suppose T is an irreducible semigroup on the Banach lattice X and let A be its generator. Assume that $s(A) = 0$ and that there exists a positive linear form $\psi \in D(A')$ with $A'\psi \leq 0$. If $P\sigma(A) \cap i\mathbb{R}$ is non-empty, then 0 is the only eigenvalue of A admitting a positive eigenvector.*

The following theorem is a consequence of Theorems 2.4.14 and 2.4.15.

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Theorem 2.4.16 *Let $(T(t))_{t \geq 0}$ be a positive irreducible C_0 semigroup generated by the operator A and $s(A) > -\infty$ a pole of the resolvent $R(\lambda, A)$ on a Banach lattice X . Then $s(A)$ is a first-order pole with geometric multiplicity one and there exists a quasi-interior point x_0 of X^+ such that $Ax_0 = s(A)x_0$. Moreover $s(A)$ is the only eigenvalue of A admitting a positive eigenvector.*

The existence and uniqueness of a strictly positive eigenfunction corresponding to the eigenvalue $s(B_\mu)$ is guaranteed by the following theorem

Theorem 2.4.17 *Under the hypothesis of Theorem 2.4.13 there exists a strictly positive eigenfunction $u_\mu(x)$ corresponding to the eigenvalue $s(B_\mu)$ of the operator B_μ . Moreover, $s(B_\mu)$ is the only eigenvalue of B_μ admitting a positive eigenfunction.*

Proof: By Theorem 2.4.10 we have that the semigroup generated by B_μ is irreducible.

If λ is an eigenvalue with finite algebraic multiplicity of an operator then λ is a pole of the resolvent of this operator.

In this situation, Theorem 2.4.14 gives the existence of a strictly positive eigenfunction of the operator B_μ (a L^1 - function which is positive almost everywhere).

The uniqueness is obtained applying Theorem 2.4.16. □

So far we have proved that the spectral bound, $s(B_\mu)$, of the operator B_μ is a dominant eigenvalue with corresponding strictly positive eigenfunction $u_\mu(x)$. But, in order to have stationary solutions we also needed the dominant eigenvalue of the operator B_μ to be in the image of m_1 . By Theorem 2.4.13 we know that $s(B_\mu) > m_1(0)$.

The next theorem gives an upper bound for the spectral bound that we will use to derive sufficient hypotheses in order that the inequality $s(B_\mu) < m_1(\infty)$ holds.

Proposition 2.4.18 *Let $s(B_\mu)$ be the spectral bound of the operator B_μ (defined in (2.8) and (2.9)). Then $s(B_\mu) \leq M_\mu := \max\left(\frac{xb(x)}{\mu} - x\right)$.*

Proof: We can write the operator B_μ in the following way

$$B_\mu u = T f_\mu(x)u(x) + g(x)u(x)$$

where $f_\mu(x)u(x) = \frac{1}{\mu}xb(x)u(x)$, $g(x)u(x) = -xu(x)$,
 $Tv(x) = \int_0^\infty \beta_\varepsilon(x, y)v(y)dy$.

2.4.1. The eigenvalue problem

We have $\|T\| = 1$. This implies $\operatorname{Re}\sigma(T) \leq 1$ because the spectrum of a bounded operator B is a subset of the closed disk $|\xi| \leq \|B\|$ (see [31] p. 176). Therefore $s(T) \leq 1$.

This implies that for all $\delta > 0$ and for all $v \gg 0$, $v \in D(T)$ the measure of the set $\{x : Tv(x) \leq (1 + \delta)v(x)\}$ is strictly positive, because otherwise applying the characterization for the spectral bound (2.11) we would obtain $S(T) > 1$, a contradiction.

So, taking $u \gg 0$ (that means u strictly positive almost everywhere), $u \in D(B_\mu)$ we have that for any $\delta > 0$ there exists x such that

$$\begin{aligned} B_\mu u(x) &= Tf_\mu(x)u(x) + g(x)u(x) \\ &\leq (1 + \delta)f_\mu(x)u(x) + g(x)u(x) \\ &\leq \left(M_\mu + \delta\left(\max_x \frac{xb(x)}{\mu}\right)\right)u(x) \quad \forall \delta. \end{aligned}$$

This gives, using (2.11) again,

$$s(B_\mu) \leq M_\mu + \delta\left(\max_x \frac{xb(x)}{\mu}\right) \quad \forall \delta.$$

Therefore $s(B_\mu) \leq M_\mu$. □

Remark 2.4.19 *Observe that the former theorem is valid for all $\varepsilon > 0$.*

Corollary 2.4.20 *Let $s(B_\mu)$ be the spectral bound of the operator B_μ defined in (2.8) and (2.9). If the inequality*

$$\max\left(\frac{xb(x)}{\mu} - x\right) < m_1(\infty),$$

holds, then $s(B_\mu) < m_1(\infty)$.

Proof: It is straightforward by Proposition 2.4.18. □

From the former theorems and the strict monotony and continuity of m_1 we can conclude that, in the hypotheses of Theorem 2.4.13 and Corollary 2.4.20, that is, for $\mu \in \left(\sup \frac{yb(y)}{m_1(\infty) + y}, \sup \frac{yb(y)}{m_1(0) + y}\right)$ and ε small enough, there exists a unique c_μ such that $m_1(c_\mu) = s(B_\mu)$.

Hence, for each $\mu \in \left(\sup \frac{yb(y)}{m_1(\infty) + y}, \sup \frac{yb(y)}{m_1(0) + y}\right)$ we have a unique $\tilde{u}_\mu(x) = c_\mu u_\mu(x)$ satisfying

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$$\frac{1}{\mu} \int_0^\infty b(y) \beta_\varepsilon(x, y) y \tilde{u}_\mu(y) dy - x \tilde{u}_\mu(x) = m_1(P) \tilde{u}_\mu(x).$$

In order to obtain stationary solutions we still have to find out μ . If we integrate and apply m_2 in the second equation of (2.5) we obtain

$$\mu = m_2 \left(\frac{c_\mu \int_0^\infty x u_\mu(x) dx}{\mu} \right).$$

Summarizing, we may define

$$F_\varepsilon(\mu) := m_2 \left(\frac{c_\mu \int_0^\infty x u_\mu(x) dx}{\mu} \right) \quad (2.15)$$

for $\mu \in \left(\sup \frac{yb(y)}{m_1(\infty)+y}, \sup \frac{yb(y)}{m_1(0)+y} \right)$ and ε in intervals of the form $(0, \varepsilon_0(\mu))$ with $\varepsilon_0(\mu) > 0$ given by Theorem 2.4.13. Then we will have that the eigenfunction \tilde{u}_μ will be the first component of an stationary solution if and only if μ is a fixed point of the function $F_\varepsilon(\mu)$.

2.4.2 The fixed point problem

In this section we will show that (in some cases) the function $F_\varepsilon(\mu)$ has (at least) one fixed point, and therefore we will have (at least) one stationary solution of (2.1).

We will start formulating some results of [31] and [15] that we will use in order to prove continuity of $F_\varepsilon(\mu)$.

Definition 2.4.21 [31] *Let us consider the set $C(X, Y)$ of all closed operators from the Banach space X to the Banach space Y .*

If $T, S \in C(X, Y)$, their graphs $G(T), G(S)$ are closed linear manifolds in the product space $X \times Y$. Let us call

$$\delta(T, S) = \delta(G(T), G(S)),$$

where $\delta(M, N) = \sup_{u \in S_M} \text{dist}(u, N)$, where $S_M = \text{unit sphere of } M$.

Finally, $\hat{\delta}(T, S) = \hat{\delta}(G(T), G(S)) = \max[\delta(T, S), \delta(S, T)]$.

Theorem 2.4.22 [31] *Let $T \in C(X, Y)$ and $S = T + A \in C(X, Y)$ such that $A \in B(X, Y)$. Then*

$$\hat{\delta}(S, T) \leq \|A\|.$$

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Theorem 2.4.23 [31] *Let $T \in C(X)$ and let $\sigma(T)$ be separated into two parts $\sigma'(T)$, $\sigma''(T)$ by a closed curve Γ . Let $X = M'(T) \oplus M''(T)$ be the associated decomposition of X . Then there exists a $\delta > 0$, depending on T and Γ , with the following properties: any $S \in C(X)$ with $\hat{\delta}(S, T) < \delta$ has spectrum $\sigma(S)$ likewise separated by Γ into two parts $\sigma'(S)$, $\sigma''(S)$. In the associated decomposition $X = M'(S) \oplus M''(S)$, $M'(S)$, $M''(S)$ are respectively isomorphic with $M'(T)$ and $M''(T)$. In particular $\dim M'(S) = \dim M'(T)$, $\dim M''(S) = \dim M''(T)$ and both $\sigma'(S)$ and $\sigma''(S)$ are nonempty if this is true for T .*

The decomposition $X = M'(S) \oplus M''(S)$ is continuous in S in the sense that the projection $P[S]$ of X onto $M'(S)$ along $M''(S)$ tends to $P[T]$ in norm as $\hat{\delta}(S, T) \rightarrow 0$.

Lemma 2.4.24 [15] *Let $T_0 \in B(X, Y)$ and assume that $r_0 \in \mathbb{R}$ is a simple eigenvalue of T_0 . Then there exists a value $\delta > 0$ such that whenever $T \in B(X, Y)$ and $\|T - T_0\| < \delta$, there is a unique $r(T) \in \mathbb{R}$ satisfying $|r(T) - r_0| < \delta$ for which $T - r(T)$ is singular.*

The map $T \rightarrow r(T)$ is analytic and $r(T)$ is a simple eigenvalue of T . Finally, if $\text{Ker}(T_0 - r_0) = \text{span}\{x_0\}$ and Z is a complement of $\text{span}\{x_0\}$ in X , there is a unique null vector $x(T)$ of $T - r(T)$ satisfying $x(T) - x_0 \in Z$.

The map $T \rightarrow x(T)$ is also analytic.

Proposition 2.4.25 *The function $F_\varepsilon(\mu)$ defined by (2.15) is continuous.*

Proof: If we prove that both c_μ and $\int_0^\infty xu_\mu(x)dx$ are continuous with respect to μ , the assertion of the theorem follows.

We have $c_\mu = m_1^{-1}(s(B_\mu))$. Hence, we only need to show that the dominant eigenvalue $s(B_\mu)$ of the operator B_μ is continuous with respect to μ .

Let us define the operators T and S in the following way

$$Tu := B_{\mu_1}u = \frac{1}{\mu_1} \int_0^\infty b(y)\beta_\varepsilon(x, y)yu(y)dy - xu(x),$$

$$Su := B_{\mu_2}u = \frac{1}{\mu_2} \int_0^\infty b(y)\beta_\varepsilon(x, y)yu(y)dy - xu(x).$$

S can be written as $S = T + A$ where A is the bounded operator

$$Au = \left(\frac{1}{\mu_2} - \frac{1}{\mu_1} \right) \int_0^\infty b(y)\beta_\varepsilon(x, y)yu(y)dy.$$

Let us consider Γ_1 a closed curve containing $m_1(\infty)$ and $s(T)$ (= dominant eigenvalue of T) and such that $s(T)$ is the unique element of $\sigma(T)$ inside Γ_1 .

2.4.2. The fixed point problem

By Theorem 2.4.23 there exists $\delta_1 > 0$ such that any operator $\tilde{T} \in C(X)$ satisfying $\tilde{\delta}(\tilde{T}, T) < \delta_1$ has only one eigenvalue inside of Γ_1 .

Choosing μ_2 sufficiently close to μ_1 , by Theorem 2.4.22 we have that $\tilde{\delta}(S, T) \leq \|A\| < \delta_1$. Therefore there exists a unique eigenvalue of S inside Γ_1 . This eigenvalue is dominant because of the restriction $s(B_\mu) < m_1(\infty)$.

The proof of the continuity of $s(B_\mu)$ is completed by showing that the distance between $s(S)$ and $s(T)$ is small.

Indeed, for all $\delta_\varepsilon > 0$ such that $\delta_\varepsilon < \delta_1$ there exists $\gamma > 0$ such that if $|\mu_1 - \mu_2| < \gamma$, then $\tilde{\delta}(S, T) < \delta_\varepsilon$. The curve corresponding to δ_ε , namely Γ_ε , is contained in Γ_1 and has radius ε . By Theorem 2.4.23 there is one eigenvalue of S contained in Γ_ε and it has to be $s(S)$ because otherwise we would have two eigenvalues of S inside of Γ_1 .

It remains to prove that $\int_0^\infty xu_\mu(x)dx$ is continuous with respect to μ . We will apply Lemma 2.4.24 to the operators $T_0 = B_{\mu_1}$ and $T = B_\mu$ with $\mu \neq \mu_1$. We consider $T_0, T \in B(X, Y)$ where $Y = L^1(0, \infty)$ and $X = \{x \in L^1(0, \infty) : xu \in L^1(0, \infty)\}$ (Banach space with the norm $\|u\|_X = \int_0^\infty |u(x)| + \int_0^\infty |xu(x)|$).

For μ_2 close enough to μ_1 , $\|T - T_0\| < \delta$ and by Lemma 2.4.24 the application that associates to each operator the eigenfunction corresponding to the eigenvalue $s(T)$ is analytic and hence continuous. \square

Theorem 2.4.26 *Let (H1),(H2),(H3) and (H4) hold. If moreover*

$$m_2(0) > \sup\left(\frac{yb(y)}{m_1(\infty) + y}\right) \quad (2.16)$$

and

$$m_2(\infty) < \sup\left(\frac{yb(y)}{m_1(0) + y}\right), \quad (2.17)$$

then, for ε small enough we have a stationary solution $(u_\varepsilon, v_\varepsilon)$ of System (2.1).

Proof: Let us take $\mu_1 = m_2(0)$ and $\mu_2 = m_2(\infty)$. Notice that under the conditions (2.16) and (2.17) $F_\varepsilon(\mu)$ is defined on the interval $[\mu_1, \mu_2]$ for any ε small enough. By the monotonicity of m_2 we have

$$F_\varepsilon(\mu_1) = m_2\left(\frac{c_{\mu_1} \int xu_{\mu_1}(x)dx}{\mu_1}\right) > m_2(0) = \mu_1,$$

$$F_\varepsilon(\mu_2) = m_2\left(\frac{c_{\mu_2} \int xu_{\mu_2}(x)dx}{\mu_2}\right) < m_2(\infty) = \mu_2.$$

By Bolzano's theorem we obtain that there exists $\mu_* \in (\mu_1, \mu_2)$ such that $F(\mu_*) = \mu_*$. \square

Remark 2.4.27 Assuming $m_1(\infty)$ sufficiently big, condition (2.16) holds automatically. Then, in case that condition (2.17) does not hold, denoting $\mu_3 = \sup\left(\frac{yb(y)}{m_1(0) + y}\right)$ we will have that the inequality

$$\frac{F_\varepsilon(\mu_3)}{\mu_3} < 1$$

implies the existence of at least one stationary solution.

2.5 Small Mutation

In this section we would like to study the steady states of System (2.1) that, recall, is

$$\begin{cases} u_t(x, t) = \int_0^\infty b(y)\beta_\varepsilon(x, y)v(y, t)dy - m_1\left(\int_0^\infty u(y, t)dy\right)u(x, t) - xu(x, t), \\ v_t(x, t) = xu(x, t) - m_2\left(\int_0^\infty v(y, t)dy\right)v(x, t), \end{cases}$$

when the size of the mutation, ε , is very small.

We have proved, under some conditions on the functions appearing in the model and for ε small enough, the existence of a steady state of System (2.1), namely $(u_\varepsilon(x), v_\varepsilon(x))$, where $u_\varepsilon(x) = c_{\varepsilon, \mu_\varepsilon} u_{\varepsilon, \mu_\varepsilon}(x)$, $u_{\varepsilon, \mu_\varepsilon}(x)$ is the normalized eigenfunction of eigenvalue $m_1(c_{\varepsilon, \mu_\varepsilon}) = s(B_{\varepsilon, \mu_\varepsilon})$ of the operator $B_{\varepsilon, \mu_\varepsilon}$, and μ_ε is a solution of the fixed point problem

$$\mu = m_2\left(\frac{c_{\varepsilon, \mu} \int_0^\infty xu_{\varepsilon, \mu}(x)dx}{\mu}\right) =: F_\varepsilon(\mu).$$

Let us start by giving some results about the dominant eigenvalue of the operator $B_{\varepsilon, \mu}$ defined (as B_μ) in (2.8).

Let us recall that $M_\mu := \max\left(\frac{xb(x)}{\mu} - x\right)$. Notice that, as $(xb(x))'' < 0$, there is only one point x_μ such that $\frac{x_\mu b(x_\mu)}{\mu} - x_\mu = M_\mu$.

Proposition 2.5.1 *Let us assume that the hypotheses of Proposition 2.4.11 hold. Then*

$$s(B_{\varepsilon, \mu}) \xrightarrow{\varepsilon \rightarrow 0} M_\mu.$$

Proof: By Proposition 2.4.18 we only have to show that for all $\delta > 0$ $s(B_{\varepsilon, \mu}) \geq M_\mu - \delta$ when ε is small enough. Let us consider the same decomposition of $B_{\varepsilon, \mu}$ as in the proof of Proposition 2.4.18, that is

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$$B_{\varepsilon,\mu}u = T_\varepsilon f_\mu(x)u(x) + g(x)u(x),$$

where $f_\mu(x)u(x) = \frac{1}{\mu}xb(x)u(x)$, $g(x)u(x) = -xu(x)$ and $(T_\varepsilon u)(x) = \int_0^\infty \beta_\varepsilon(x,y)u(y)dy$.

Let us fix $\delta > 0$ and let γ be such that if $|x - x_{0,\mu}| < \gamma$ (where, recall, x_μ satisfies $\frac{x_\mu b(x_\mu)}{\mu} - x_\mu = M_\mu$) then

$$|f_\mu(x) - f_\mu(x_\mu)| < \frac{\delta}{4},$$

$$|g(x) - g(x_\mu)| < \frac{\delta}{4}.$$

Note that the last inequality is equivalent to assume $\gamma < \frac{\delta}{4}$ because $g(x) = x$. Let us consider a smooth function $u(x) > 0$ with $\text{supp} u \subset [x_\mu - \gamma, x_\mu + \gamma]$. Let us denote $v_\mu(x) := f_\mu(x)u(x)$. Let us assume for the present that $T_\varepsilon v_\mu(x) \geq v_\mu(x) - \hat{\delta}v_\mu(x)$ for some $\hat{\delta}$. Then

$$\begin{aligned} B_{\varepsilon,\mu}u(x) &= T_\varepsilon f_\mu(x)u(x) + g(x)u(x) \\ &\geq f_\mu(x)u(x) - \hat{\delta}f_\mu(x)u(x) + g(x)u(x) \\ &\geq f_\mu(x)u(x) - \hat{\delta}(\max f_\mu)u(x) + g(x)u(x) \\ &\geq (f_\mu(x_\mu) - \frac{\delta}{4})u(x) - \hat{\delta}(\max f_\mu)u(x) + (g(x_\mu) - \frac{\delta}{4})u(x) \\ &= M_\mu u(x) - (\frac{\delta}{4} + \frac{\delta}{4} + \hat{\delta}(\max f_\mu))u(x) \\ &\geq (M_\mu - \delta)u(x), \end{aligned}$$

where the last inequality holds if and only if

$$\hat{\delta} \leq \frac{\delta}{2(\max f_\mu)}. \quad (2.18)$$

What is left to show is

$$T_\varepsilon v_\mu(x) \geq v_\mu(x) - \hat{\delta}v_\mu(x), \quad \text{where } \hat{\delta} \text{ satisfies (2.18).}$$

By Proposition 2.4.11 we only have to choose ε small enough such that (2.18) holds.

□

The former proposition yields information about the convergence of the spectral bound (which is a dominant eigenvalue under the hypotheses of Theorem 2.4.13) of the operators $B_{\varepsilon,\mu}$ when ε tends to zero.

We are also interested in the convergence of the corresponding eigenfunction. But first, we formulate some results that we will use in the forthcoming.

Theorem 2.5.2 [53](Banach-Alaoglu) *Let X be a topological vector space and X' its dual space. The set $B_{X'} = \{f \in X' : \|f\| \leq 1\}$ is compact in the weak star topology.*

The theorem says that denoting by X' the dual space of X then $\varphi_n \in X'$ bounded has a subsequence φ_{n_k} for which there exists $\varphi_0 \in X'$ such that

$$\varphi_{n_k} \xrightarrow{\varepsilon \rightarrow 0} \varphi_0$$

in the weak star topology, that is, for all $u \in X$,

$$\langle u, \varphi_{n_k} \rangle \xrightarrow{\varepsilon \rightarrow 0} \langle u, \varphi_0 \rangle.$$

Proposition 2.5.3 [4] *Let φ_n be a sequence of X' . If $\varphi_n \rightarrow \varphi$ in the weak star topology and if $f_n \rightarrow f$ strongly in X then $\langle f_n, \varphi_n \rangle \rightarrow \langle f, \varphi \rangle$.*

If we consider the space of the continuous functions with compact support on the interval $(0, \infty)$, $C_c(0, \infty)$, its dual space is the space of Radon measures on $(0, \infty)$. Let us denote it by M .

$L^1(0, \infty)$ can be identified with a closed subspace of M by the isometry $T : L^1(0, \infty) \rightarrow M$ defined by

$$\langle Tf, u \rangle_{M, C_c} = \int_0^\infty fu,$$

(see [4] for more details).

By the Banach-Alaoglu theorem, for every sequence ε_n going to zero, the sequence $u_{\varepsilon_n, \mu}(x) \in L^1(0, \infty) \subset M$ of normalized eigenfunctions corresponding to the eigenvalues $s(B_{\varepsilon_n, \mu})$ has a subsequence $u_{\varepsilon_{n_k}, \mu}(x)$ that converges in the weak star topology to a measure $u_{0, \mu}(x)$. The following result gives us this limit explicitly.

Proposition 2.5.4 *Let us assume that the hypotheses of Theorem 2.4.13 hold. If the limit $u_{0, \mu}(x)$ of the subsequence $u_{\varepsilon_{n_k}, \mu}(x)$ is not zero, then it is an eigenfunction of the multiplication operator $\frac{xb(x)}{\mu} - x$ corresponding to the eigenvalue M_μ .*

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Proof:

The subsequence $u_{\varepsilon_{n_k}, \mu}(x)$ satisfies

$$B_{\varepsilon_{n_k}, \mu} u_{\varepsilon_{n_k}, \mu}(x) = s(B_{\varepsilon_{n_k}, \mu}) u_{\varepsilon_{n_k}, \mu}(x).$$

Taking $f \in C_c(0, \infty)$,

$$\langle f, B_{\varepsilon_{n_k}, \mu} u_{\varepsilon_{n_k}, \mu} \rangle = s(B_{\varepsilon_{n_k}, \mu}) \langle f, u_{\varepsilon_{n_k}, \mu} \rangle.$$

By the Banach-Alaouglu theorem and Proposition 2.5.1,

$$s(B_{\varepsilon_{n_k}, \mu}) \langle f, u_{\varepsilon_{n_k}, \mu} \rangle \xrightarrow{\varepsilon \rightarrow 0} M_\mu \langle f, u_{0, \mu} \rangle.$$

And to end with,

$$\begin{aligned} \langle f, B_{\varepsilon_{n_k}, \mu} u_{\varepsilon_{n_k}, \mu} \rangle &= \frac{1}{\mu} \int_0^\infty f(x) \int_0^\infty b(y) \beta_{\varepsilon_{n_k}}(x, y) y u_{\varepsilon_{n_k}, \mu}(y) dy dx \\ &\quad - \int_0^\infty f(x) x u_{\varepsilon_{n_k}, \mu}(x) dx \xrightarrow{\varepsilon \rightarrow 0} \\ &\quad \frac{1}{\mu} \int_0^\infty y b(y) f(y) u_{0, \mu}(y) dy - \int_0^\infty f(x) x u_{0, \mu}(x) dx = \\ &= \langle f, \left(\frac{x b(x)}{\mu} - x \right) u_{0, \mu} \rangle \end{aligned}$$

where we have used that

$$\int_0^\infty f(x) \beta_\varepsilon(x, y) dx \xrightarrow{\varepsilon \rightarrow 0} f(y) \quad (\text{uniformly})$$

and Proposition 2.5.3. □

A multiplication operator, B , induced on $C_c(0, \infty)$ by some continuous function $q : (0, \infty) \rightarrow \mathbb{R}$ is defined by $Bf := qf$.

The spectrum of B is the closed range of q , that is, $\sigma(B) := \overline{\{q(x) : x \in (0, \infty)\}}$, (see, for instance, [19] for more details on multiplication operators).

The definition of B can be generalized to an operator on M by

$$\langle f, B\varphi \rangle = \langle fB, \varphi \rangle$$

for any $f \in C_c(0, \infty)$ and $\varphi \in M$.

Any real number in the image set of q , $q(x)$, is an eigenvalue of B with corresponding eigenvector the Dirac measure concentrated at the point x , δ_x .

Moreover, any eigenvector of B is of the preceding form. Finally, $\sigma(B)$ coincides with the point spectrum of B if and only if $\{q(x) : x \in (0, \infty)\}$ is a closed set.

So what we have proved in Proposition 2.5.4 is that there is a subsequence of $u_{\varepsilon_n, \mu}(x)$ with limit $a\delta_{x_\mu}$ for some $a \geq 0$. Now we are going to prove that $u_{\varepsilon, \mu}(x)$ has limit and it is δ_{x_μ} . For this, we will use three results, the first one concerning the convergence, when ε goes to zero, of the integral of $u_{\varepsilon, \mu}(x)$ and $xu_{\varepsilon, \mu}(x)$ outside a certain bounded interval and the other two, more general, about some properties of a family of functions that converge (in the weak star topology) to a Dirac measure.

Proposition 2.5.5 *Let us assume that the hypotheses of Theorem 2.4.13 hold. Let $u_{\varepsilon, \mu}(x)$ be the family of eigenfunctions of eigenvalue $s(B_{\varepsilon, \mu})$ of the operator $B_{\varepsilon, \mu}$. There exists a bounded interval K containing x_μ such that*

$$\int_{K^c} u_{\varepsilon, \mu}(x) dx \xrightarrow{\varepsilon \rightarrow 0} 0,$$

$$\int_{K^c} xu_{\varepsilon, \mu}(x) dx \xrightarrow{\varepsilon \rightarrow 0} 0,$$

uniformly with respect to μ on intervals $[a, b]$ with $a > 0$.

Proof: By Proposition 2.5.1 $s(B_{\varepsilon, \mu}) \xrightarrow{\varepsilon \rightarrow 0} M_\mu$. Therefore, as x_μ is a strict (and unique) maximum point, for any bounded interval K containing x_μ there exists ε_0 such that for $\varepsilon < \varepsilon_0$

$$s(B_{\varepsilon, \mu}) > \frac{xb(x)}{\mu} - x \quad \text{if } x \in K^c. \quad (2.19)$$

Furthermore, there exists $C_K > 0$ such that $\left(s(B_{\varepsilon, \mu}) + x - \frac{xb(x)}{\mu}\right) > C_K$ whenever $x \in K^c$ and $\varepsilon < \varepsilon_0$. If we integrate over K^c the equality

$$0 = (B_{\varepsilon, \mu} - s(B_{\varepsilon, \mu}))u_{\varepsilon, \mu}(x)$$

we obtain

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$$\begin{aligned}
0 &= \int_{K^c} \left(\int_0^\infty \frac{y}{\mu} b(y) \beta_\varepsilon(x, y) u_{\varepsilon, \mu}(y) dy - x u_{\varepsilon, \mu}(x) - s(B_{\varepsilon, \mu}) u_{\varepsilon, \mu}(x) \right) dx \\
&= \int_{K^c} \left(\int_K \frac{y}{\mu} b(y) \beta_\varepsilon(x, y) u_{\varepsilon, \mu}(y) dy + \int_{K^c} \frac{y}{\mu} b(y) \beta_\varepsilon(x, y) u_{\varepsilon, \mu}(y) dy \right) dx \\
&+ \int_{K^c} (-x - s(B_{\varepsilon, \mu})) u_{\varepsilon, \mu}(x) dx \\
&= \int_K \left(\frac{y}{\mu} b(y) u_{\varepsilon, \mu}(y) \int_{K^c} \beta_\varepsilon(x, y) dx \right) dy \\
&+ \int_{K^c} \left(\frac{y}{\mu} b(y) u_{\varepsilon, \mu}(y) \int_{K^c} \beta_\varepsilon(x, y) dx \right) dy + \int_{K^c} (-x - s(B_{\varepsilon, \mu})) u_{\varepsilon, \mu}(x) dx \\
&\leq \int_K \left(\frac{y}{\mu} b(y) u_{\varepsilon, \mu}(y) \int_{K^c} \beta_\varepsilon(x, y) dx \right) dy \\
&+ \int_{K^c} \left(\frac{xb(x)}{\mu} - x - s(B_{\varepsilon, \mu}) \right) u_{\varepsilon, \mu}(x) dx
\end{aligned}$$

where we have used Fubini's theorem and that $\int_{K^c} \beta_\varepsilon(x, y) dx \leq 1$. By (2.19) and the former inequality we have that, for ε small enough

$$\begin{aligned}
C_K \int_{K^c} u_{\varepsilon, \mu}(x) dx &\leq \int_{K^c} \left(-\frac{xb(x)}{\mu} + x + s(B_{\varepsilon, \mu}) \right) u_{\varepsilon, \mu}(x) dx \\
&\leq \int_K \left(\frac{y}{\mu} b(y) u_{\varepsilon, \mu}(y) \int_{K^c} \beta_\varepsilon(x, y) dx \right) dy
\end{aligned}$$

for some $C_K > 0$.

As

$$\int_K \left(\frac{y}{\mu} b(y) u_{\varepsilon, \mu}(y) \int_{K^c} \beta_\varepsilon(x, y) dx \right) dy \xrightarrow{\varepsilon \rightarrow 0} 0,$$

we obtain

$$\int_{K^c} u_{\varepsilon, \mu}(x) dx \xrightarrow{\varepsilon \rightarrow 0} 0.$$

In the same way, we obtain, for ε small enough

$$\begin{aligned}
\tilde{C}_K \int_{K^c} x u_{\varepsilon, \mu}(x) dx &\leq \int_{K^c} \left(-\frac{b(x)}{\mu} + 1 + \frac{s(B_{\varepsilon, \mu})}{x} \right) x u_{\varepsilon, \mu}(x) dx \\
&\leq \int_K \left(\frac{y}{\mu} b(y) u_{\varepsilon, \mu}(y) \int_{K^c} \beta_\varepsilon(x, y) dx \right) dy
\end{aligned}$$

for some $\tilde{C}_K > 0$ (such that $s(B_{\varepsilon, \mu}) - \tilde{C}_K x \geq \frac{xb(x)}{\mu} - x$ if $x \in K^c$), and thus

$$\int_{K^c} x u_{\varepsilon, \mu}(x) dx \xrightarrow{\varepsilon \rightarrow 0} 0.$$

□

Lemma 2.5.6 *Let us assume that we have a sequence of normalized positive functions $u_{\varepsilon_n}(x)$ such that $u_{\varepsilon_n}(x) \xrightarrow{\varepsilon \rightarrow 0} a \delta_{x_0}$ in the weak star topology and such that there exists a bounded interval K containing x_0 and such that $\int_{K^c} u_{\varepsilon_n}(x) dx \xrightarrow{\varepsilon \rightarrow 0} 0$. Then $a = 1$.*

Proof: Let us choose f a positive continuous function with compact support such that $f(x) = 1$ for all $x \in K$ and $f(x) < 1$ for $x \in K^c$. Then we can write

$$\int_0^\infty f(x) u_{\varepsilon_n}(x) dx = \int_K u_{\varepsilon_n}(x) dx + \int_{K^c} f(x) u_{\varepsilon_n}(x) dx.$$

As $u_{\varepsilon_n}(x) \xrightarrow{\varepsilon \rightarrow 0} a \delta_{x_0}$ in the weak star topology, the left hand side tends to a when ε goes to zero.

As $\int_{K^c} u_{\varepsilon_n}(x) f(x) dx < \int_{K^c} u_{\varepsilon_n}(x) dx$ and $\int_{K^c} u_{\varepsilon_n} \xrightarrow{\varepsilon \rightarrow 0} 0$ we have that

$$\int_K u_{\varepsilon_n}(x) dx \xrightarrow{\varepsilon \rightarrow 0} a.$$

Finally as, by hypothesis, $\int_0^\infty u_{\varepsilon_n}(x) dx = 1$ we have

$$1 = \int_0^\infty u_{\varepsilon_n}(x) dx = \int_K u_{\varepsilon_n}(x) dx + \int_{K^c} u_{\varepsilon_n}(x) dx \xrightarrow{\varepsilon \rightarrow 0} a,$$

and hence $a = 1$.

□

Lemma 2.5.7 *Let us assume that we have a sequence of positive functions $u_{\varepsilon_n}(x)$ such that $u_{\varepsilon_n}(x) \xrightarrow{\varepsilon \rightarrow 0} \delta_{x_0}$ in the weak star topology and such that there exists a bounded interval K_1 containing x_0 and such that $\int_{K_1^c} u_{\varepsilon_n}(x) dx \xrightarrow{\varepsilon \rightarrow 0} 0$. Then for all bounded interval K containing x_0 in its interior we have*

$$\int_{K^c} u_{\varepsilon_n}(x) dx \xrightarrow{\varepsilon \rightarrow 0} 0.$$

Proof:

It is obvious if $K_1 \subseteq K$.

Let us choose $K \subset K_1$. Let f be a continuous function with compact support

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such that $f(x) = 1$ for all $x \in K_1 \setminus K$, $f(x_0) = 0$ and $f(x) < 1$ otherwise. Then,

$$\langle f, u_{\varepsilon_n} \rangle = \int_0^\infty f(x)u_{\varepsilon_n}(x)dx \xrightarrow{\varepsilon \rightarrow 0} f(x_0) = 0.$$

As f and u_{ε_n} are positive

$$\int_0^\infty f(x)u_{\varepsilon_n}(x)dx \geq \int_{K_1 \setminus K} f(x)u_{\varepsilon_n}(x)dx = \int_{K_1 \setminus K} u_{\varepsilon_n}(x)dx.$$

Therefore

$$\int_{K_1 \setminus K} u_{\varepsilon_n}(x)dx \xrightarrow{\varepsilon \rightarrow 0} 0.$$

And thus,

$$\int_{K^c} u_{\varepsilon_n}(x)dx = \int_{K_1^c} u_{\varepsilon_n}(x)dx + \int_{K_1 \setminus K} u_{\varepsilon_n}(x)dx \xrightarrow{\varepsilon \rightarrow 0} 0$$

and the proof is complete. □

Theorem 2.5.8 *Let us assume that the hypotheses of Theorem 2.4.13 hold. The family of eigenfunctions $u_{\varepsilon,\mu}(x)$ corresponding to the eigenvalues $s(B_{\varepsilon,\mu})$ satisfies*

$$u_{\varepsilon,\mu}(x) \xrightarrow{\varepsilon \rightarrow 0} u_{0,\mu}(x) = \delta_{x_\mu}$$

in the weak star topology.

Proof: As $\|u_{\varepsilon,\mu}\| = 1$ by the Banach-Alaouglu theorem any sequence $u_{\varepsilon_n,\mu}(x)$ with $\varepsilon_n \rightarrow 0$ has a subsequence that converges. By Propositions 2.5.4 and 2.5.5 and Lemma 2.5.6 the limit is the same for any of these subsequences. This gives the statement. □

So far we have proved the following convergences for the dominant eigenvalues $s(B_{\varepsilon,\mu}) = m_1(c_{\varepsilon,\mu})$ and the corresponding normalized eigenfunctions, $u_{\varepsilon,\mu}(x)$, of the family of operators $B_{\varepsilon,\mu}$

$$s(B_{\varepsilon,\mu}) \xrightarrow{\varepsilon \rightarrow 0} M_\mu,$$

$$u_{\varepsilon,\mu}(x) \xrightarrow{\varepsilon \rightarrow 0} \delta_{x_\mu},$$

(the second convergence in the weak star topology).

Let us remind that the steady states of System (2.1) are given by $c_{\varepsilon,\mu}u_{\varepsilon,\mu}(x)$ where $\mu = \mu_\varepsilon$ is a solution of the fixed point problem $\mu = F_\varepsilon(\mu)$ ($F_\varepsilon(\mu)$ defined in (2.15)).

Under the hypotheses of Theorem 2.4.26 we know that the fixed point, μ_ε , exists. However, later on in this section we will see that, for ε small enough, μ_ε exists under weaker conditions than the ones in Theorem 2.4.26.

Now we will give some results about the convergence of the sequences $c_{\varepsilon,\mu}$ and μ_ε which will allow us to give the final result about the convergence of the steady states of System (2.1) when ε tends to zero.

Proposition 2.5.9 *Let us assume that the hypotheses of Theorem 2.4.13 and Corollary 2.4.20 hold. Then*

$$c_{\varepsilon,\mu} \xrightarrow{\varepsilon \rightarrow 0} u(x_\mu)$$

uniformly with respect to μ where $u(x_\mu)$ is the first component of the equilibrium of the system

$$\begin{cases} u' &= b(x)v(x) - m_1(u)u - xu, \\ v' &= xu - \mu v \end{cases} \quad (2.20)$$

for $x = x_\mu$, the value that satisfies $(xb(x))'|_{x_\mu} = \mu$.

Remark 2.5.10 *The value x satisfying $(xb(x))'|_{x_\mu} = \mu$ coincides with the value satisfying $(\frac{xb(x)}{\mu} - x) = M_\mu = \max(\frac{xb(x)}{\mu} - x)$.*

Proof: The continuity of m_1 and Proposition 2.5.1 give

$$c_{\varepsilon,\mu} = m_1^{-1}(s(B_{\varepsilon,\mu})) \xrightarrow{\varepsilon \rightarrow 0} m_1^{-1}(M_\mu).$$

The maximum of the function $(\frac{xb(x)}{\mu} - x)$ is attained at the value that satisfies $(xb(x))'|_{x_\mu} = \mu$.

The non trivial equilibrium of System (2.20) is given by the only solution $u(x)$ of

$$\begin{vmatrix} -m_1(u(x)) - x & b(x) \\ x & \mu \end{vmatrix} = 0.$$

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That is $u(x) = m_1^{-1}\left(\frac{xb(x)}{\mu} - x\right)$.

Therefore $m_1^{-1}(M_\mu) = u(x_\mu)$. □

In order to give the result about the convergence of the sequence μ_ε we need the following proposition.

Proposition 2.5.11 *Let us assume that the hypotheses of Theorem 2.4.13 hold. Let $u_{\varepsilon,\mu}(x)$ be the sequence of normalized eigenfunctions corresponding to the eigenvalues $s(B_{\varepsilon,\mu})$ of the operator $B_{\varepsilon,\mu}$. Then*

$$xu_{\varepsilon,\mu}(x) \xrightarrow{\varepsilon \rightarrow 0} x_\mu \delta_{x_\mu}$$

in the weak star topology.

Moreover

$$\int_0^\infty xu_{\varepsilon,\mu}(x) dx \xrightarrow{\varepsilon \rightarrow 0} x_\mu.$$

Proof: By Theorem 2.5.8 we have that

$$\forall g \in C_c \quad \int_0^\infty g(x)u_{\varepsilon,\mu}(x) dx \xrightarrow{\varepsilon \rightarrow 0} g(x_\mu).$$

Therefore, if we call $g(x) := xf(x)$ we have that

$$\begin{aligned} \forall f \in C_c \quad \int_0^\infty f(x)xu_{\varepsilon,\mu}(x) dx &= \int_0^\infty g(x)u_{\varepsilon,\mu}(x) dx \\ &\xrightarrow{\varepsilon \rightarrow 0} g(x_\mu) = x_\mu f(x_\mu). \end{aligned}$$

This proves the first part of the theorem.

Since we have just proved that

$$xu_{\varepsilon,\mu}(x) \xrightarrow{\varepsilon \rightarrow 0} x_\mu \delta_{x_\mu}$$

in the weak star topology and moreover, by Proposition 2.5.5 we have that there exists a bounded interval such that $\int_{K^c} xu_{\varepsilon,\mu}(x) dx \xrightarrow{\varepsilon \rightarrow 0} 0$ then in the same manner as in the proof of Lemma 2.5.6 we can say that

$$\int_0^\infty xu_{\varepsilon,\mu}(x) dx \xrightarrow{\varepsilon \rightarrow 0} x_\mu. \quad \square$$

Let us now define

$$F_0(\mu) := m_2\left(\frac{u(x_\mu)x_\mu}{\mu}\right) \quad (2.21)$$

for $\mu \in \left(\sup \frac{yb(y)}{m_1(\infty)+y}, \sup \frac{yb(y)}{m_1(0)+y} \right)$ where $u(x_\mu)$ has been defined in Proposition 2.5.9 as the first component of the equilibrium of the system

$$\begin{cases} u' &= b(x)v(x) - m_1(u)u - xu, \\ v' &= xu - \mu v, \end{cases}$$

for $x = x_\mu$, the value that satisfies $(xb(x))'|_{x_\mu} = \mu$. Notice that the condition on μ implies the existence of $u(x_\mu)$ and hence that of $F_0(\mu)$.

Let \hat{x} be an ESS of System (1.6), (1.7) (as in Theorem 1.4.2) and let us call $\mu_0 = m_2(v(\hat{x}))$. Then $x_{\mu_0} = \hat{x}$ and $F_0(\mu_0) = m_2\left(\frac{u(x_{\mu_0})x_{\mu_0}}{\mu_0}\right) = m_2\left(\frac{u(\hat{x})\hat{x}}{m_2(v(\hat{x}))}\right) = m_2(v(\hat{x})) = \mu_0$.

Since in Theorems 1.4.3 and 1.4.4 it has been proved that, under the hypotheses of Theorem 1.3.6, there exists a unique ESS of System (1.1), we have that there exists a unique fixed point μ_0 of $F_0(\mu)$.

Furthermore, $F_0(\mu)$ is a monotonous function.

Lemma 2.5.12 *The function $F_0(\mu)$ (defined in (2.21)) is strictly decreasing.*

Proof: x_μ satisfies $(xb(x))'(x_\mu) = \mu$. Taking the derivative with respect to μ we obtain that

$$\frac{dx}{d\mu} = \frac{1}{(xb(x))''} < 0,$$

that is, x_μ is strictly decreasing with respect to μ .

Furthermore, as $u(x_\mu) = m_1^{-1}(M_\mu)$ where $M_\mu = \max\left(\frac{xb(x)}{\mu} - x\right)$ and m_1 is an increasing function, we have that $u(x_\mu)$ is strictly decreasing and the proof is complete. \square

The next, technical result about convergence of a family of functions will be used to prove the convergence of the sequence μ_ε to μ_0 (the fixed point of $F_0(\mu)$).

Lemma 2.5.13 *Let f_ε be a family of continuous real functions that converge pointwise to f_0 .*

Let us assume that either $(x - x_0)f_0(x) > 0$ or $(x - x_0)f_0(x) < 0$ for $0 < |x - x_0| < \gamma$ for some $\gamma > 0$.

Then for all $\eta \leq \gamma$ there exists ε_0 such that for $\varepsilon < \varepsilon_0$, f_ε has at least one zero x_ε such that $|x_\varepsilon - x_0| < \eta$.

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Proof: As $f_0(x_0 - \eta) < 0$ and $f_0(x_0 + \eta) > 0$ (for instance), by the pointwise convergence of f_ε to f_0 we obtain that there exists ε_0 such that if $\varepsilon < \varepsilon_0$, then $f_\varepsilon(x_0 - \eta)f_\varepsilon(x_0 + \eta) < 0$, and by continuity, there exists x_ε satisfying $f_\varepsilon(x_\varepsilon) = 0$ and $|x_\varepsilon - x_0| < \eta$. \square

Proposition 2.5.14 *Let us assume that the hypotheses of Theorem 2.4.13 and Corollary 2.4.20 hold. Let $F_\varepsilon(\mu) = m_2\left(\frac{c_{\varepsilon,\mu} \int_0^\infty x u_{\varepsilon,\mu}(x) dx}{\mu}\right)$ (already defined in (2.15)) and $F_0(\mu)$ defined by (2.21). Then, there exists a sequence of fixed points of $F_\varepsilon(\mu)$, denoted by μ_ε satisfying*

$$\mu_\varepsilon \xrightarrow{\varepsilon \rightarrow 0} \mu_0$$

where μ_0 is the fixed point of $F_0(\mu)$.

Proof: By Propositions 2.5.9 and 2.5.11 we have that

$$F_\varepsilon(\mu) \xrightarrow{\varepsilon \rightarrow 0} F_0(\mu).$$

Let us define $G_0(\mu) := F_0(\mu) - \mu$.

We have seen that there exists μ_0 satisfying $G_0(\mu_0) = 0$. Moreover, by Lemma 2.5.12, $G_0(\mu)$ is a strictly decreasing function.

Therefore, applying Lemma 2.5.13 we obtain that there exists a sequence of zeros of the functions $G_\varepsilon(\mu) := F_\varepsilon(\mu) - \mu$ that converge to the zero of $G_0(\mu)$ and this proves the proposition. \square

Let us recall that $x_{\mu_0} := \hat{x}$ and that \hat{x} satisfies $(xb(x))' |_{\hat{x}} = \mu_0$, where μ_0 is the solution of the fixed point problem $F_0(\mu) = \mu$ i.e. \hat{x} is the ESS value of the ordinary differential equations model studied in Chapter 1.

Finally, we are able to give the result that tells us how the steady states of system (2.1) behave when the size of the mutation tends to zero.

Theorem 2.5.15 *Let us assume that the hypotheses of Theorem 2.4.26 hold. Let $(u(\hat{x}), v(\hat{x}))$ be the steady state of System (1.1) when $x = \hat{x}$. The sequence of equilibrium solutions of System (2.1) given by Theorem 2.4.26, $(u_\varepsilon(x), v_\varepsilon(x))$, satisfies*

$$(u_\varepsilon(x), v_\varepsilon(x)) \xrightarrow{\varepsilon \rightarrow 0} (u(\hat{x})\delta_{\hat{x}}, v(\hat{x})\delta_{\hat{x}})$$

in the weak star topology.

Moreover, for any bounded interval K of $(0, \infty)$ containing \hat{x} in its interior,

$$\int_{K^c} u_\varepsilon(x) dx \xrightarrow{\varepsilon \rightarrow 0} 0$$

$$\int_{K^c} v_\varepsilon(x) dx \xrightarrow{\varepsilon \rightarrow 0} 0.$$

Proof:

For any $f \in C_c$ we have

$$\langle f, B_{\varepsilon, \mu_\varepsilon} u_\varepsilon - m_1(c_{\varepsilon, \mu_\varepsilon}) u_\varepsilon \rangle = 0,$$

or, equivalently, (as $u_\varepsilon(x) = c_{\varepsilon, \mu_\varepsilon} u_{\varepsilon, \mu_\varepsilon}(x)$),

$$\langle f, B_{\varepsilon, \mu_\varepsilon} u_{\varepsilon, \mu_\varepsilon} - m_1(c_{\varepsilon, \mu_\varepsilon}) u_{\varepsilon, \mu_\varepsilon} \rangle = 0. \quad (2.22)$$

Since $u_{\varepsilon, \mu_\varepsilon}(x)$ is a normalized family, the Banach Alaoglu theorem gives

$$u_{\varepsilon, \mu_\varepsilon}(x) \xrightarrow{\varepsilon \rightarrow 0} u_0(x) \quad (2.23)$$

in the weak star topology, for some measure $u_0(x)$ (in principle for a subsequence of any sequence $\varepsilon_n \rightarrow 0$). We omit the notation ε_{n_k} .

Using Proposition 2.5.14 we obtain that for any $f \in C_c$

$$B_{\varepsilon, \mu_\varepsilon} f \xrightarrow{\varepsilon \rightarrow 0} \left(\frac{xb(x)}{\mu_0} - x \right) f \quad \text{uniformly, i.e.,}$$

in the supremum norm.

Therefore by Proposition 2.5.3 and (2.23),

$$\langle f, B_{\varepsilon, \mu_\varepsilon} u_{\varepsilon, \mu_\varepsilon} \rangle \xrightarrow{\varepsilon \rightarrow 0} \langle f, \left(\frac{xb(x)}{\mu_0} - x \right) u_0 \rangle$$

Moreover

$$c_{\varepsilon, \mu_\varepsilon} \xrightarrow{\varepsilon \rightarrow 0} u(\hat{x}). \quad (2.24)$$

Indeed,

$$\begin{aligned} |c_{\varepsilon, \mu_\varepsilon} - u(\hat{x})| &\leq |c_{\varepsilon, \mu_\varepsilon} - u(x_{\mu_\varepsilon})| + |u(x_{\mu_\varepsilon}) - u(x_{\mu_0})| \\ &= |c_{\varepsilon, \mu_\varepsilon} - u(x_{\mu_\varepsilon})| + |m_1^{-1}(M_{\mu_\varepsilon}) - m_1^{-1}(M_{\mu_0})| \\ &< \delta \quad \text{if } \varepsilon < \varepsilon_0 \end{aligned}$$

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by Proposition 2.5.9 (the first term), and because M_μ is continuous with respect to μ , and m_1^{-1} is also continuous (the second term).

Using again Proposition 2.5.3 and (2.23),

$$\langle f, m_1(c_{\varepsilon, \mu_\varepsilon})u_{\varepsilon, \mu_\varepsilon} \rangle \xrightarrow{\varepsilon \rightarrow 0} \langle f, m_1(u(\hat{x}))u_0 \rangle = \langle f, M_{\mu_0}u_0 \rangle.$$

Therefore we have

$$\langle f, B_{\varepsilon, \mu_\varepsilon}u_{\varepsilon, \mu_\varepsilon} - m_1(c_{\varepsilon, \mu_\varepsilon})u_{\varepsilon, \mu_\varepsilon} \rangle \xrightarrow{\varepsilon \rightarrow 0} \langle f, \left(\frac{xb(x)}{\mu_0} - x - M_{\mu_0}\right)u_0 \rangle.$$

So, equation (2.22) yields that u_0 is an eigenfunction of eigenvalue M_{μ_0} of the multiplication operator $\frac{xb(x)}{\mu_0} - x$, that is, $u_0 = a\delta_{\hat{x}}$.

Since by Proposition 2.5.5 there exists a bounded interval K containing \hat{x} such that $\int_{K^c} u_{\varepsilon, \mu_\varepsilon}(x)dx \xrightarrow{\varepsilon \rightarrow 0} 0$, then, applying Lemma 2.5.6 we obtain $a = 1$, that is $u_0(x) = \delta_{\hat{x}}$. As above, the uniqueness of the weak star limit implies (2.23). This, together with (2.24), implies

$$u_\varepsilon(x) = c_{\varepsilon, \mu_\varepsilon}u_{\varepsilon, \mu_\varepsilon}(x) \xrightarrow{\varepsilon \rightarrow 0} u(\hat{x})\delta_{\hat{x}},$$

in the weak star topology.

Finally, in the same way as in the proof of Proposition 2.5.11

$$v_\varepsilon(x) = \frac{xu_\varepsilon(x)}{\mu_\varepsilon} \xrightarrow{\varepsilon \rightarrow 0} \frac{\hat{x}u(\hat{x})\delta_{\hat{x}}}{\mu_0} = v(\hat{x})\delta_{\hat{x}},$$

(in the weak star topology) and the first statement is proved.

By Proposition 2.5.5 and using that $\mu_\varepsilon \xrightarrow{\varepsilon \rightarrow 0} \mu_0$ and $c_{\varepsilon, \mu_\varepsilon} \xrightarrow{\varepsilon \rightarrow 0} u(\hat{x})$ we have the existence of a bounded interval K containing \hat{x} such that

$$\int_{K^c} u_\varepsilon(x)dx \xrightarrow{\varepsilon \rightarrow 0} 0,$$

$$\int_{K^c} v_\varepsilon(x)dx = \int_{K^c} \frac{xu_\varepsilon(x)}{\mu_\varepsilon}dx \xrightarrow{\varepsilon \rightarrow 0} 0.$$

Lemma 2.5.7 gives the second statement. \square

Summarizing, under reasonable hypotheses, we have proved the existence of a family of equilibrium solutions $(u_\varepsilon(x), v_\varepsilon(x))$ of System (2.1) that, when the size of the mutation (ε) tends to zero, tend to concentrate at the ESS value \hat{x} of the finite dimensional age at maturity model (1.1). Moreover, the total population at equilibrium of System (2.1) (the integral of $(u_\varepsilon(x), v_\varepsilon(x))$) tends to the equilibrium of (1.1) for the value \hat{x} of the parameter.

Chapter 3

Small mutation rate and evolutionarily stable strategies in some (abstract quasilinear) equations

3.1 Introduction

We start this chapter by formulating another integro-differential equations model for the distribution of individuals with respect to the age at maturity that is obtained by considering densities of the individuals with respect to the evolutionary variable in the ordinary differential equations model for the age at maturity of Chapter 1.

The difference between the model in Chapter 2 and the one in this chapter is that in Chapter 2 ε was a parameter measuring the mutation size because we were assuming that a mutation, perhaps very small, occurred in every reproduction whereas in the model described in this chapter, ε will stand for the probability of mutation.

More in general, in Sections 3.3 and 3.4 we study a (rather) general class of selection-mutation infinite dimensional models that include the age at maturity model presented in Section 3.2. When the mutation rate tends to zero this models become “ecological” models, that is, ordinary differential equations models where all individuals have the same type.

It will be shown, under some conditions on the variables constituting the infinite dimensional models, the existence of a steady state converging, when the probability of mutation tends to zero, to a Dirac mass at the point of ESS of the ordinary differential equations models obtained when the mutation

3.2. Description of a model for the maturation age

tends to zero.

3.2 Description of a model for the maturation age

The model equations are:

$$\begin{cases} u_t(x, t) = (1 - \varepsilon)b(x)v(x, t) + \varepsilon \int_0^\infty b(y)\gamma(x, y)v(y, t)dy \\ \quad \quad \quad - m_1 \left(\int_0^\infty u(y, t)dy \right) u(x, t) - xu(x, t), \\ v_t(x, t) = xu(x, t) - m_2 \left(\int_0^\infty v(y, t)dy \right) v(x, t). \end{cases} \quad (3.1)$$

We assume the same hypotheses as in Chapter 2 for the functions appearing in the model. The main difference in the equations (between the model in Chapter 2 and the one here) is in the inflow of newborns term, that, in System (3.1) is given by $(1 - \varepsilon)b(x)v(x, t) + \varepsilon \int_0^\infty b(y)\gamma(x, y)v(y, t)dy$, where $(1 - \varepsilon)b(x)v(x, t)$ represents the inflow of clonal newborns and $\varepsilon \int_0^\infty b(y)\gamma(x, y)v(y, t)dy$ represents the inflow of nonclonal newborns, where $b(y)$ is the trait specific fertility of the adult population and $\gamma(x, y)$ is the density of probability that the trait of the mutant offspring of an individual with trait y is x . So ε stands for the probability of mutation.

γ is a strictly positive globally lipschitzian function that satisfies $\int_0^\infty \gamma(x, y)dx = 1$ (in a non clonal reproduction, the probability of having offspring of whatever strategy is one) and such that the improper integral converges uniformly with respect to y on bounded intervals.

We can rewrite model (3.1) in the following way (that will be useful in the next sections)

$$\begin{aligned} \begin{pmatrix} u_t \\ v_t \end{pmatrix} &= A_{\varepsilon, P, Q} \begin{pmatrix} u \\ v \end{pmatrix} = B_{\varepsilon, P, Q} \begin{pmatrix} u \\ v \end{pmatrix} + \varepsilon T \begin{pmatrix} u \\ v \end{pmatrix} \\ &= \begin{pmatrix} -m_1(P) - x & (1 - \varepsilon)b(x) \\ x & -m_2(Q) \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix} \\ &\quad + \varepsilon \begin{pmatrix} 0 & \int_0^\infty b(y)\gamma(x, y) \cdot dy \\ 0 & 0 \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix} \end{aligned} \quad (3.2)$$

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where $P := \int_0^\infty u(x, t)dx$, $Q := \int_0^\infty v(x, t)dx$ (total population of young and adult individuals, respectively, at time t).

3.3 The eigenvalue problem for a general class of operators

As in Chapter 2 our aim is to study the equilibria of System (3.1) when the probability of mutation, ε , is very small (in this case meaning that, in every reproduction, the probability of mutation is very small). We will do this by studying an eigenvalue problem. However, we will not only study the eigenvalue problem for the operators defined in (3.2) but for a more general class of operators to which the operators defined in (3.2) belong and that we define next.

That is, in this section we are going to study the behavior when $\varepsilon \in (0, 1)$ goes to zero of the (dominant) eigenvalue of a linear operator of the form

$$A_\varepsilon = B_\varepsilon + \varepsilon T \tag{3.3}$$

in the space X of L^1 \mathbb{R}^n -valued functions defined on an interval, I , of \mathbb{R} (bounded or not), endowed with the natural Banach lattice structure.

Let us now formulate the hypotheses on this operators:

From now on we will assume that for any $\varepsilon \geq 0$, A_ε is the generator of a positive C_0 semigroup.

Moreover, for any $\varepsilon > 0$, we assume that the spectral bound $s(A_\varepsilon)$ is a dominant eigenvalue λ_ε of algebraic multiplicity 1 of the operator A_ε with corresponding strictly positive eigenfunction $\vec{u}_\varepsilon(x)$. This holds, for example (see [14] pag 209) if A_ε is the generator of a positive analytic irreducible semigroup and $s(A_\varepsilon) > -\infty$ is a pole of the resolvent $R(\lambda, A_\varepsilon)$.

For any $\varepsilon \geq 0$, B_ε is a matrix valued multiplication operator, that is, when we fix a value x we obtain a matrix, that we will denote by $B_\varepsilon(x)$.

Let us assume that the operator $B_\varepsilon - B_0$ is bounded and such that $\|B_\varepsilon - B_0\| \xrightarrow{\varepsilon \rightarrow 0} 0$. The elements of the matrix $B_\varepsilon(x)$ depend smoothly on x . Moreover the off-diagonal ones are non-negative and $B_\varepsilon(x)$ is an irreducible matrix. So, by Theorems 0.0.8, 0.0.9 and 0.0.10 in the Preliminaries, $B_\varepsilon(x)$ has a strictly dominant eigenvalue with a corresponding strictly positive eigenvector.

For $\varepsilon \geq 0$, let us denote by $\mu_\varepsilon(x)$ the dominant eigenvalue of the matrix $B_\varepsilon(x)$.

3.3. The eigenvalue problem for a general class of operators

Let us remind that the spectrum of a matrix valued multiplication operator M_α where $\alpha : I \longrightarrow M(n)$, ($M(n)$ is the space of all complex $n \times n$ matrices) is given as $\sigma(M_\alpha) = \overline{\cup_{x \in I} \sigma(\alpha(x))}$ (see [45]).

Let us define $\mu_\varepsilon := \sup \operatorname{Re} \sigma(B_\varepsilon) = \sup_x \mu_\varepsilon(x)$.

Let us assume that for any $\varepsilon \geq 0$ there exists x_ε such that $\mu_\varepsilon = \mu_\varepsilon(x_\varepsilon) = \max_x \mu_\varepsilon(x)$.

Let us assume that the maximum value of $\mu_0(x)$ is attained at a unique x_0 .

Finally, we assume that T is a positive bounded operator.

In Chapter 4 we will prove that (fixed the nonlinearities) System (3.1) satisfies all the preceding hypotheses and therefore we will be able to apply all the results that we will obtain for the operators (3.3). There are more examples of models that can be written using the operators (3.3). That was the reason to study the eigenvalue problem in a more general way and not only for System (3.1). In Chapter 4 we will give another example.

We begin with a result about the dominant eigenvalue λ_ε of the operator A_ε .

In order to prove it we will use the inequality (2.11) of Chapter 2, that recall, is

$$s(A) \geq \sup\{\mu \in \mathbb{R} \quad : \quad Af \geq \mu f \quad \text{for some} \quad 0 < f \in D(A)\} \quad (3.4)$$

(where $f > 0$ means $f \geq 0$ and $f \neq 0$) and A is the generator of a strongly continuous positive semigroup.

Since we are working in the Banach lattice $L^1(I, \mathbb{R}^n)$, the spectral bound of the generator of a positive semigroup and the growth bound of the semigroup coincide and therefore we can use (3.4) (see Chapter 2 for more details).

Proposition 3.3.1 *Let λ_ε and $\mu_0(x)$ be the dominant eigenvalues of the operator A_ε and the matrix $B_0(x)$ respectively. Then*

$$\lambda_\varepsilon \xrightarrow{\varepsilon \rightarrow 0} \mu_0(x_0)$$

where x_0 is the (unique) point where the maximum value of $\mu_0(x)$ is attained.

Proof: We begin by showing that for all $\delta > 0$ there exists ε_0 such that for any $\varepsilon < \varepsilon_0$,

$$s(A_\varepsilon) = \lambda_\varepsilon \geq \mu_0(x_0) - \delta.$$

The continuity hypotheses on $B_\varepsilon(x)$ imply that there exists $\eta > 0$ and $\varepsilon_0 > 0$ such that $\mu_\varepsilon(x) \geq \mu_0(x_0) - \delta$ whenever $x \in J := [x_0 - \eta, x_0 + \eta]$ and $\varepsilon < \varepsilon_0$.

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For any x and $\varepsilon \geq 0$, let $\vec{v}_{x,\varepsilon}$ be the (unique except for a scalar factor) positive eigenvector corresponding to the eigenvalue $\mu_\varepsilon(x)$, that is

$$B_\varepsilon(x)\vec{v}_{x,\varepsilon} = \mu_\varepsilon(x)\vec{v}_{x,\varepsilon}.$$

We are going to apply (3.4) to the function

$$\vec{v}_\varepsilon(x) = \vec{v}_{x,\varepsilon}\chi_J(x)$$

which belongs to $D(A_\varepsilon)$. Notice that this latter coincides with $D(B_\varepsilon)$ (because εT is a bounded operator) and that any bounded measurable function with compact support belongs to the domain of the multiplication operator.

We have

$$(B_\varepsilon\vec{v}_\varepsilon)(x) = \chi_J(x)B_\varepsilon(x)\vec{v}_{x,\varepsilon} \geq \chi_J(x)(\mu_0(x_0) - \delta)\vec{v}_{x,\varepsilon} = (\mu_0(x_0) - \delta)\vec{v}_\varepsilon(x).$$

As εT is a positive operator, we get

$$\begin{aligned} A_\varepsilon\vec{v}_\varepsilon(x) &= B_\varepsilon\vec{v}_\varepsilon(x) + \varepsilon T\vec{v}_\varepsilon(x) \\ &\geq (\mu_0(x_0) - \delta)\vec{v}_\varepsilon(x), \end{aligned}$$

and by (3.4),

$$\lambda_\varepsilon = s(A_\varepsilon) \geq \mu_0(x_0) - \delta.$$

Now we will show that for all $\delta > 0$ there exists ε_0 such that for any $\varepsilon < \varepsilon_0$

$$\lambda_\varepsilon \leq \mu_0(x_0) + \delta.$$

In order to prove it we will use a result about perturbation of the spectrum of a closed operator of [31] that says that if T is a closed operator and $S = T + A$ where A is a bounded operator then

$$\Gamma \subset \rho(S) \quad \text{if} \quad \|A\| < \min_{\xi \in \Gamma} \|R(\xi, T)\|^{-1},$$

where $\rho(S)$ is the resolvent set of S , $R(\xi, T)$ is the resolvent operator of T and Γ is a closed subset of the resolvent set of T such that $\|R(\xi, T)\|^{-1}$ has positive minimum.

The operator A_ε can be written as $A_\varepsilon = B_0 + \varepsilon T + B_\varepsilon - B_0$. Since by hypothesis B_0 is the generator of a positive semigroup, namely $T_0(t)$,

3.3. The eigenvalue problem for a general class of operators

we have that the resolvent operator of B_0 equals the Laplace transform of the semigroup:

$$R(\xi, B_0) = \int_0^\infty e^{-\xi t} T_0(t) dt$$

for $\operatorname{Re}(\xi) > \omega(T_0)$ (the growth bound of the semigroup, that, since we are working in $L^1(I, \mathbb{R}^n)$ coincides with the spectral bound of the generator).

Therefore, if $\operatorname{Re}(\xi) > s(B_0) = \mu_0(x_0)$ we have

$$\|R(\xi, B_0)\| \leq \frac{C}{\operatorname{Re}\xi - \mu_0(x_0)}$$

(where C is such that $\|T_0(t)\| \leq C e^{\omega(T_0)t}$).

If we consider $\Gamma_\delta = (\mu_0(x_0) + \delta, +\infty)$ with $\delta > 0$ then

$$\min_{\xi \in \Gamma_\delta} \frac{1}{\|R(\xi, T)\|} \geq \min_{\xi \in \Gamma_\delta} \frac{\xi - \mu_0(x_0)}{C} = \frac{\delta}{C}.$$

Finally, since by hypothesis $\|B_\varepsilon - B_0\| \xrightarrow{\varepsilon \rightarrow 0} 0$, taking ε small enough, we have $\|\varepsilon T + B_\varepsilon - B_0\| < \frac{\delta}{C}$ and therefore $\lambda_\varepsilon < \mu_0(x_0) + \delta$. \square

In the second part of the proof of the previous proposition we have showed that, for all $\delta > 0$ there exists ε small enough such that $\lambda_\varepsilon \leq \mu_0(x_0) + \delta$. It is possible to show that $\lambda_\varepsilon \leq \mu_0(x_0)$ for all $\varepsilon \in (0, 1)$, under the following additional hypothesis:

(H) The operator A_ε can be written as

$$A_\varepsilon = B_\varepsilon + \varepsilon T = C + (1 - \varepsilon)S + \varepsilon T$$

where S is a positive bounded operator such that for all $\vec{u} \in X^+$ there exists a set of positive measure such that $S\vec{u}(x) \geq T\vec{u}(x)$, i.e., S and T are such that $T - S$ is not positive.

Under assumption (H), taking $\vec{u}_\varepsilon(x)$ the positive eigenfunction corresponding to the eigenvalue λ_ε , we have, for x in a set of positive measure,

$$\begin{aligned} \lambda_\varepsilon \vec{u}_\varepsilon(x) = A_\varepsilon \vec{u}_\varepsilon(x) &= B_\varepsilon(x) \vec{u}_\varepsilon(x) + \varepsilon T \vec{u}_\varepsilon(x) \\ &= C \vec{u}_\varepsilon(x) + (1 - \varepsilon) S \vec{u}_\varepsilon(x) + \varepsilon T \vec{u}_\varepsilon(x) \\ &\leq C \vec{u}_\varepsilon(x) + S \vec{u}_\varepsilon(x) \\ &= B_0(x) \vec{u}_\varepsilon(x). \end{aligned}$$

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So, applying (3.4) to the operator $B_0(x)$ there exists a set of x of positive measure such that $\lambda_\varepsilon \leq \mu_0(x)$ and therefore $\lambda_\varepsilon \leq \mu_0(x_0)$ (for all $\varepsilon \in (0, 1)$). Let us note that, in model (3.2), the hypothesis (H) holds automatically and moreover, that it has a natural biological interpretation.

Indeed, $B_{\varepsilon,P,Q}$ can be written as

$$\begin{aligned} B_{\varepsilon,P,Q} &= C_{P,Q} + (1 - \varepsilon)S \\ &= \begin{pmatrix} -m_1(P) - x & 0 \\ x & -m_2(Q) \end{pmatrix} + (1 - \varepsilon) \begin{pmatrix} 0 & b(x) \\ 0 & 0 \end{pmatrix}. \end{aligned}$$

Let us prove that for all $\vec{u} \in L^1 \times L^1$ there exists a set of positive measure such that $S\vec{u} \geq T\vec{u}$ where

$$S = \begin{pmatrix} 0 & b(x) \\ 0 & 0 \end{pmatrix} \quad \text{and} \quad T = \begin{pmatrix} 0 & \int_0^\infty b(y)\gamma(x,y) \cdot dy \\ 0 & 0 \end{pmatrix}.$$

Indeed, otherwise, for almost every x ,

$$\int_0^\infty b(y)\gamma(x,y)v(y)dy - b(x)v(x) > 0.$$

Integrating the left hand side with respect to x and using $\int_0^\infty \gamma(x,y)dx = 1$ we obtain

$$\int_0^\infty \left(\int_0^\infty b(y)\gamma(x,y)v(y)dy - b(x)v(x) \right) dx = 0, \quad (3.5)$$

a contradiction. So, in model (3.2) hypothesis (H) holds.

Let us note that, in model (3.2), the total number of newborns is given by $\int_0^\infty \left((1 - \varepsilon)b(x)v(x) + \varepsilon \int_0^\infty b(y)\gamma(x,y)v(y)dy \right) dx$.

Assuming that (3.5) holds, we obtain

$$\begin{aligned} &\int_0^\infty \left((1 - \varepsilon)b(x)v(x) + \varepsilon \int_0^\infty b(y)\gamma(x,y)v(y)dy \right) dx = \\ &= \int_0^\infty b(x)v(x)dx + \varepsilon \left(\int_0^\infty (b(x)v(x) - \int_0^\infty b(y)\gamma(x,y)v(y)dy) dx \right) = \\ &= \int_0^\infty b(x)v(x)dx. \end{aligned}$$

Therefore equality (3.5) biologically means that the total number of newborns does not change because of the mutation.

3.3. The eigenvalue problem for a general class of operators

Once we have studied the dominant eigenvalue of the operators A_ε defined in (3.3), we are going to analyze how the corresponding eigenfunction behaves when ε tends to zero.

It is convenient to choose the eigenfunctions $\vec{u}_\varepsilon(x)$ corresponding to λ_ε satisfying

$$\|\vec{u}_\varepsilon(x)\| = 1.$$

Proposition 3.3.2 *Let M be the space of measures of Radon, the dual space of the normed space of continuous functions with compact support $C_c(I, \mathbb{R}^n)$. For every sequence ε_n going to zero, the sequence $\vec{u}_{\varepsilon_n}(x) \in L^1(I, \mathbb{R}^n) \subset M$ of normalized eigenfunctions corresponding to the eigenvalues λ_{ε_n} of the operator A_{ε_n} (defined in (3.3)) has a subsequence $\vec{u}_{\varepsilon_{n_k}}(x)$ satisfying*

$$\vec{u}_{\varepsilon_{n_k}}(x) \xrightarrow{\varepsilon \rightarrow 0} \vec{u}_0(x)$$

in the weak star topology, for some measure $\vec{u}_0(x)$, i.e., for any $\vec{f} \in C_c(I, \mathbb{R}^n)$,
 $\langle \vec{f}, \vec{u}_{\varepsilon_{n_k}} \rangle \xrightarrow{\varepsilon \rightarrow 0} \langle \vec{f}, \vec{u}_0 \rangle$.

Proof: It is just an application of the Banach Alaoglu theorem. □

Let B be a matrix valued multiplication operator on $C_c(I, \mathbb{R}^n)$. In the same way as in Chapter 2, we can generalize this definition to a matrix valued operator on M by

$$\langle \vec{f}, B\varphi \rangle = \langle \vec{f}^t B, \varphi \rangle,$$

(where t denotes transpose) for any $\vec{f} \in C_c(I, \mathbb{R}^n)$ and $\varphi \in M$.

Then $\sigma(B) = \cup_{x \in I} \sigma(B(x))$. More precisely, a complex number is an eigenvalue of $B(x)$ with corresponding eigenvector \vec{u}_x if and only if it is an eigenvalue of B with corresponding eigenfunction $\vec{u}_x \delta_x$. Moreover, $\sigma(B)$ coincides with the point spectrum of B if and only if $\cup_{x \in I} \sigma(B(x))$ is a closed set.

Proposition 3.3.3 *If the limit $\vec{u}_0(x)$ of the subsequence $\vec{u}_{\varepsilon_{n_k}}(x)$ is not $\vec{0}$, then it is an eigenfunction of the multiplication operator B_0 corresponding to the eigenvalue $\mu_0(x_0)$.*

Proof: Let us assume that the weak star limit does not vanish.

The subsequence $\vec{u}_{\varepsilon_{n_k}}(x)$ satisfies

$$B_{\varepsilon_{n_k}}(x) \vec{u}_{\varepsilon_{n_k}}(x) + \varepsilon_{n_k} T \vec{u}_{\varepsilon_{n_k}}(x) = \lambda_{\varepsilon_{n_k}} \vec{u}_{\varepsilon_{n_k}}(x).$$

Taking $\vec{f} \in C_c$ we have

3.3. The eigenvalue problem for a general class of operators

$$\langle \vec{f}^t B_{\varepsilon_{n_k}}, \vec{u}_{\varepsilon_{n_k}} \rangle + \varepsilon_{n_k} \langle \vec{f}, T \vec{u}_{\varepsilon_{n_k}} \rangle = \lambda_{\varepsilon_{n_k}} \langle \vec{f}, \vec{u}_{\varepsilon_{n_k}} \rangle. \quad (3.6)$$

As $\vec{f}^t B_{\varepsilon_{n_k}}$ is a sequence of continuous functions with compact support, it converges (uniformly) to $\vec{f}^t B_0$. Then by Proposition 3.3.2 and Proposition 2.5.3 in Chapter 2,

$$\langle \vec{f}^t B_{\varepsilon_{n_k}}, \vec{u}_{\varepsilon_{n_k}} \rangle \longrightarrow \langle \vec{f}^t B_0, \vec{u}_0 \rangle.$$

As T is a bounded operator,

$$\varepsilon_{n_k} \langle \vec{f}, T \vec{u}_{\varepsilon_{n_k}} \rangle \longrightarrow 0,$$

and by Proposition 3.3.1 and Proposition 3.3.2,

$$\lambda_{\varepsilon_{n_k}} \langle \vec{f}, \vec{u}_{\varepsilon_{n_k}} \rangle \longrightarrow \mu_0(x_0) \langle \vec{f}, \vec{u}_0 \rangle.$$

Then, equation (3.6) yields

$$\langle \vec{f}^t B_0, \vec{u}_0 \rangle = \mu_0(x_0) \langle \vec{f}, \vec{u}_0 \rangle.$$

That is, \vec{u}_0 is an eigenfunction corresponding to the eigenvalue $\mu_0(x_0)$ of the multiplication operator B_0 . \square

So, we have proved that there is a subsequence of $\vec{u}_{\varepsilon_n}(x)$ with limit $a \vec{v}_{x_0,0} \delta_{x_0}$ for some $a \geq 0$, where $\vec{v}_{x_0,0}$ is the normalized eigenvector corresponding to the eigenvalue $\mu_0(x_0)$ of the matrix $B_0(x_0)$ (where $\mu_0(x_0) = \max_x \mu_0(x)$).

Notice that, in principle, a may depend on the subsequence.

Now we are going to prove that, under an additional hypothesis, $\vec{u}_\varepsilon(x)$ has limit and this is $\vec{v}_{x_0,0} \delta_{x_0}$.

Theorem 3.3.4 *Let $\mu_0(x)$ be the dominant eigenvalue of the operator $B_0(x)$. Let x_0 be the (unique) point where the maximum value of $\mu_0(x)$ is attained. Let us assume that for $i = 1..n$, there exists a bounded interval K containing x_0 such that*

$$\int_{K^c} u_\varepsilon^i(x) dx \xrightarrow{\varepsilon \rightarrow 0} 0,$$

where u_ε^i is the i -component of the eigenfunction \vec{u}_ε corresponding to the eigenvalue λ_ε of the operator A_ε .

Then the family of eigenfunctions \vec{u}_ε corresponding to the eigenvalues λ_ε satisfy

$$\vec{u}_\varepsilon \xrightarrow{\varepsilon \rightarrow 0} \vec{u}_0 = \vec{v}_{x_0,0} \delta_{x_0}.$$

in the weak star topology.

Moreover

$$\int_0^\infty u_\varepsilon^i(x) dx \xrightarrow{\varepsilon \rightarrow 0} v_{x_0,0}^i$$

for $i = 1, \dots, n$.

3.4. Equilibria of some (abstract quasilinear) equations

Proof: As $\|\vec{u}_\varepsilon(x)\| = 1$, by the Banach-Alaouglu Theorem any sequence $\vec{u}_{\varepsilon_n}(x)$ with $\varepsilon_n \rightarrow 0$ has a subsequence that converges. By Proposition 3.3.3 the limit is of the form $av_{x_0,0}\delta_{x_0}$ for any of these subsequences. So,

$$\int_0^\infty u_{\varepsilon_{n_k}}^i(x)f(x)dx \longrightarrow av_{x_0,0}^i f(x_0) \quad \text{for all } f \in C_c(I, \mathbb{R}). \quad (3.7)$$

We choose f a positive continuous function with compact support such that $f(x) = 1$ for all $x \in K$ and $f(x) < 1$ for $x \in K^c$. Then we can write

$$\int_0^\infty u_{\varepsilon_{n_k}}^i(x)f(x)dx = \int_K u_{\varepsilon_{n_k}}^i(x)f(x)dx + \int_{K^c} u_{\varepsilon_{n_k}}^i(x)f(x)dx.$$

By (3.7) the left hand side goes to $av_{x_0,0}^i$.

As

$$0 < \int_{K^c} u_{\varepsilon_{n_k}}^i(x)f(x)dx < \int_{K^c} u_{\varepsilon_{n_k}}^i(x)dx$$

and $\int_{K^c} u_{\varepsilon_{n_k}}^i dx \longrightarrow 0$, we have that

$$\int_K u_{\varepsilon_{n_k}}^i(x)dx \longrightarrow av_{x_0,0}^i.$$

Therefore

$$\int_0^\infty u_{\varepsilon_{n_k}}^i(x)dx \longrightarrow av_{x_0,0}^i.$$

Since by hypothesis $\sum_{i=1}^n \int_0^\infty u_\varepsilon^i(x)dx = \sum_{i=1}^n v_{x_0,0}^i = 1$, it follows that $a = 1$. Therefore the w^* -limit is the same for any subsequence. This gives the first statement and hence the second. \square

3.4 Equilibria of some (abstract quasilinear) equations

Let us consider the nonlinear equation

$$\vec{u}_t = A_\varepsilon(F(\vec{u}))\vec{u} = B_\varepsilon(x, F(\vec{u}))\vec{u} + \varepsilon T\vec{u} \quad (3.8)$$

where F is a (linear and continuous) function from the state space $X = L^1(I, \mathbb{R}^n)$ to a m -dimensional space. For fixed $E = F(\vec{u})$ we assume all the hypotheses of Section 3.3 on $A_\varepsilon(E)$. In particular, that $A_\varepsilon(E)$ has a dominant eigenvalue $\lambda_\varepsilon(E)(= s(A_\varepsilon(E)))$ with a normalized (positive) eigenvector $\vec{u}_{\varepsilon,E}(x)$. Moreover we assume that $\vec{u}_{\varepsilon,E}(x)$ is the only positive eigenvector of $A_\varepsilon(E)$ and that the elements of $B_\varepsilon(x, E)$ depend smoothly on E .

3.4. Equilibria of some (abstract quasilinear) equations

Remark 3.4.1 *Let us note that in model (3.1), F is given by*

$$\begin{aligned} F : L^1([0, \infty), \mathbb{R}^{2+}) &\longrightarrow \mathbb{R}^{2+} \\ (u, v) &\longrightarrow (P, Q). \end{aligned}$$

Formally speaking, as long as one does not have an existence and uniqueness theorem for the initial value problem, $\vec{u}(x) \in X$ is a positive equilibrium of (3.8) if and only if there exist $c > 0$ and $E \in \mathbb{R}^m$ such that $\vec{u}(x) = c\vec{u}_{\varepsilon, E}(x)$ and c and E satisfy

$$\begin{cases} \lambda_{\varepsilon}(E) = s(A_{\varepsilon}(E)) = 0, \\ F(c\vec{u}_{\varepsilon, E}) - E = 0. \end{cases} \quad (3.9)$$

Let us assume that for every (sufficiently small) $\varepsilon > 0$ there exists a solution $(c_{\varepsilon}, E_{\varepsilon})$ of (3.9) (and therefore an equilibrium solution $\vec{u}_{\varepsilon}(x)$ of (3.8)).

On the other hand, let us consider the n -dimensional ordinary differential equations system

$$\vec{v}_t = B_0(x, G(x, \vec{v}))\vec{v} \quad (3.10)$$

where for fixed x , G is a (linear) function from \mathbb{R}^n to \mathbb{R}^m , $x \in I$ is a real parameter and $B_0(x, E)$ is a $n \times n$ matrix. As above, for fixed $G(x, \vec{v})$ we assume the hypotheses of the previous section. In particular that $B_0(x, E)$ has a dominant eigenvalue $\mu_0(x, E)$ with a normalized (positive) eigenvector $\vec{v}_{x, E}$.

F and G are related as follows:

F is a linear and continuous function from $L^1(I, \mathbb{R}^n)$ to \mathbb{R}^m , that is, each component F_i , $i = 1..m$, belongs to the dual space of $L^1(I, \mathbb{R}^n)$ and therefore, it is of the form

$$\begin{aligned} F_i : L^1(I, \mathbb{R}^n) &\longrightarrow \mathbb{R} \\ \vec{u}(x) = (u_1(x), \dots, u_n(x)) &\longrightarrow \sum_{i=1}^n \int_I a_i(x) u_i(x), \end{aligned}$$

where $(a_1(x), \dots, a_n(x)) \in (L^{\infty})^n$.

Then

$$\begin{aligned} F : L^1(I, \mathbb{R}^n) &\longrightarrow \mathbb{R}^m \\ \vec{u}(x) &\longrightarrow \left(\sum_{i=1}^n \int_I a_{i1}(x) u_i(x), \dots, \sum_{i=1}^n \int_I a_{im}(x) u_i(x) \right), \end{aligned}$$

where, for fixed j , ($j = 1, \dots, m$), $(a_{1j}(x), \dots, a_{nj}(x)) \in (L^{\infty})^n$.

3.4. Equilibria of some (abstract quasilinear) equations

Let us denote $(\sum_{i=1}^n \int_I a_{i1}(x)u_i(x), \dots, \sum_{i=1}^n \int_I a_{im}(x)u_i(x)) := \int_I a(x)u(x)$, where $a(x) = (a_{ij}(x))$ is a $n \times m$ matrix.

Since, formally, for fixed E , $A_\varepsilon(E) \xrightarrow{\varepsilon \rightarrow 0} A_0(E) = B_0(x, E)$ it is natural to ask

$$G(x, \vec{v}) = F(\vec{v}\delta_x)$$

to hold, obtaining then the following relation between F and G :

Given $F : M^n \rightarrow \mathbb{R}^m$ (note that, as we want F to be defined in the space of Radon measures, we will also ask a_{ij} to be continuous (for fixed i and j)), then for $\vec{v} \in \mathbb{R}^n$

$$G(x, \vec{v}) = F(\vec{v}\delta_x) = \int_I a(x)\vec{v}\delta_x dx = a(x)\vec{v}.$$

Given $G : I \times \mathbb{R}^n \rightarrow \mathbb{R}^m$ then for $\vec{v} \in L^1(I, \mathbb{R}^n)$

$$F(\vec{v}) = \int_I G(x, \vec{v}(x))dx = \int_I a(x)\vec{v}(x)dx.$$

Remark 3.4.2 In the case of model (3.1) B_0 is given by

$$B_0 \begin{pmatrix} v_1 \\ v_2 \end{pmatrix} = \begin{pmatrix} -m_1(v_1) - x & b(x) \\ x & -m_2(v_2) \end{pmatrix} \begin{pmatrix} v_1 \\ v_2 \end{pmatrix}$$

where $\vec{v} = (v_1, v_2)$.

In this case

$$G : \mathbb{R}^2 \rightarrow \mathbb{R}^2$$

$$(v_1, v_2) \rightarrow (v_1, v_2).$$

Notice that, for any x , $\vec{v} \in \mathbb{R}^n$ is a positive equilibrium of (3.10) if and only if there exist $c > 0$ and $E \in \mathbb{R}^m$ such that $\vec{v} = c\vec{v}_{x,E}$ and c and E satisfy

$$\begin{cases} \mu_0(x, E) = 0, \\ G(x, c\vec{v}_{x,E}) - E = 0. \end{cases} \quad (3.11)$$

For any $E \geq 0$ we assume that the function $x \rightarrow \mu_0(x, E)$ attains its maximum value in a point x_E .

Let us now assume that there exists a solution (c_0, E_0) of

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$$\begin{cases} \mu_0(x_E, E) = 0, \\ G(x_E, c\vec{v}_{x_E, E}) - E = 0. \end{cases} \quad (3.12)$$

So, we have an equilibrium solution of (3.10) for $x = x_{E_0} := \hat{x}$, namely $\vec{v}_{\hat{x}} := c_0 \vec{v}_{x_{E_0}, E_0}$.

Furthermore, \hat{x} is a value of ESS of System (3.10) because it satisfies $\mu_0(x, E_0) \leq \mu_0(\hat{x}, E_0) = 0$ (a definition and discussion of ESS in the context of System (3.10) has been done in the Preliminaries).

Let us assume that $(c_\varepsilon, E_\varepsilon) \xrightarrow{\varepsilon \rightarrow 0} (c_0, E_0)$. Notice that this can be expected due to Proposition 3.3.1 which gives the convergence of the first equation of (3.9) to the first one of (3.12) when ε tends to 0 and to Theorem 3.3.4 that, in some cases, implies that $F(c\vec{u}_{\varepsilon, E}) \xrightarrow{\varepsilon \rightarrow 0} G(x_E, c\vec{v}_{x_E, E})$.

Then, for a continuous function with compact support $\vec{f}(x)$ we have that $\vec{f}^t(x)B_\varepsilon(x, E_\varepsilon) \xrightarrow{\varepsilon \rightarrow 0} \vec{f}^t(x)B_0(x, E_0)$ uniformly (i.e., in the supremum norm).

Using the same argument as in Proposition 3.3.3 and Theorem 3.3.4 we obtain that the family of normalized eigenvectors $\vec{u}_{\varepsilon, E_\varepsilon}$ converge in the weak star topology to the measure $a\vec{v}_{x_{E_0}, E_0} \delta_{x_{E_0}}$, where $\vec{v}_{x_{E_0}, E_0}$ is the normalized eigenvector of eigenvalue 0 of the operator $B(\hat{x}, E_0)$.

Indeed, by the Banach Alaouglu theorem there is a subsequence $\vec{u}_{\varepsilon_{n_k}, E_{\varepsilon_{n_k}}}(x)$ of the normalized equilibrium solutions that converges to a measure $\vec{u}_0(x)$.

Moreover it satisfies

$$B_{\varepsilon_{n_k}}(x, E_{\varepsilon_{n_k}})\vec{u}_{\varepsilon_{n_k}, E_{\varepsilon_{n_k}}}(x) + \varepsilon_{n_k} T\vec{u}_{\varepsilon_{n_k}, E_{\varepsilon_{n_k}}}(x) = \lambda_{\varepsilon_{n_k}} \vec{u}_{\varepsilon_{n_k}, E_{\varepsilon_{n_k}}}(x) = 0.$$

Taking $\vec{f} \in C_c$ we have

$$\langle \vec{f}^t B_{\varepsilon_{n_k}}(x, E_{\varepsilon_{n_k}}), \vec{u}_{\varepsilon_{n_k}, E_{\varepsilon_{n_k}}} \rangle + \varepsilon_{n_k} \langle \vec{f}, T\vec{u}_{\varepsilon_{n_k}, E_{\varepsilon_{n_k}}} \rangle = \lambda_{\varepsilon_{n_k}} \langle \vec{f}, \vec{u}_{\varepsilon_{n_k}, E_{\varepsilon_{n_k}}} \rangle = 0 \quad (3.13)$$

By Proposition 2.5.3, using that

$$\vec{f}^t B_{\varepsilon_{n_k}}(x, E_{\varepsilon_{n_k}}) \longrightarrow \vec{f}^t B_0(x, E_0)$$

and

$$\vec{u}_{\varepsilon_{n_k}, E_{\varepsilon_{n_k}}} \longrightarrow \vec{u}_0$$

(in the weak star topology) it follows that

$$\langle \vec{f}^t B_{\varepsilon_{n_k}}(x, E_{\varepsilon_{n_k}}), \vec{u}_{\varepsilon_{n_k}, E_{\varepsilon_{n_k}}} \rangle \longrightarrow \langle \vec{f}^t B_0(x, E_0), \vec{u}_0 \rangle.$$

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Therefore, when ε tends to 0, equation (3.13) yields

$$\langle \vec{f}^t B_0(x, E_0), \vec{u}_0 \rangle = 0$$

i.e. \vec{u}_0 is either 0 or it is an eigenfunction of eigenvalue 0 of the operator $B_0(x, E_0)$, that is, $\vec{u}_0 = a\vec{v}_{x_{E_0}, E_0} \delta_{x_{E_0}}$ for $a \geq 0$.

Moreover, if we assume that for $i = 1..n$, there exists a bounded interval K containing \hat{x} such that

$$\int_{K^c} u_{\varepsilon, E_\varepsilon}^i(x) dx \xrightarrow{\varepsilon \rightarrow 0} 0,$$

then by the same argument as in the proof of Theorem 3.3.4 we obtain that $a = 1$ and therefore the following

Theorem 3.4.3 *The family of equilibrium solutions $\vec{u}_\varepsilon(x)$ of System (3.8) satisfies*

$$\vec{u}_\varepsilon(x) \xrightarrow{\varepsilon \rightarrow 0} \vec{v}_{\hat{x}} \delta_{\hat{x}}$$

in the weak star topology. Moreover, $\int_0^\infty u_\varepsilon^i(x) dx \xrightarrow{\varepsilon \rightarrow 0} v_{\hat{x}}^i$.

Summarizing, under reasonable hypotheses, System (3.8) has a family of equilibria \vec{u}_ε that tend to concentrate at the ESS, \hat{x} , of the finite dimensional “limit” system (3.10) when ε tends to 0. Moreover, the integral of \vec{u}_ε (the total population at equilibrium) tends to the equilibrium of (3.10) for the value \hat{x} of the parameter.

Chapter 4

Two examples: age at maturity model and prey predator model

4.1 Introduction

This chapter is devoted to the application of the convergence results obtained in Chapter 3 for the equilibria of some abstract (quasilinear) equations to two models. The first one is the age at maturity model that we started Chapter 3 with, for which we obtain that, when the probability of mutation tends to zero, the steady states converge to a Dirac mass at the point of ESS of the ordinary differential equations maturation age model in Chapter 1 .

A predator prey model is also studied, as another example of the class of models for which the convergence results of Chapter 3 hold.

4.2 A model for the maturation age

Let us recall the maturation age model of Chapter 3

$$\begin{cases} u_t(x, t) = (1 - \varepsilon)b(x)v(x, t) + \varepsilon \int_0^\infty b(y)\gamma(x, y)v(y, t)dy \\ \quad - m_1 \left(\int_0^\infty u(y, t)dy \right) u(x, t) - xu(x, t), \\ v_t(x, t) = xu(x, t) - m_2 \left(\int_0^\infty v(y, t)dy \right) v(x, t). \end{cases} \quad (4.1)$$

In order to apply the results of Chapter 3 we write it in the following way

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$$\begin{aligned}
 \begin{pmatrix} u_t \\ v_t \end{pmatrix} &= A_{\varepsilon, P, Q} \begin{pmatrix} u \\ v \end{pmatrix} = B_{\varepsilon, P, Q} \begin{pmatrix} u \\ v \end{pmatrix} + \varepsilon T \begin{pmatrix} u \\ v \end{pmatrix} \\
 &= \begin{pmatrix} -m_1(P) - x & (1 - \varepsilon)b(x) \\ x & -m_2(Q) \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix} \\
 &\quad + \varepsilon \begin{pmatrix} 0 & \int_0^\infty b(y)\gamma(x, y) \cdot dy \\ 0 & 0 \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix}
 \end{aligned} \tag{4.2}$$

where $P := \int_0^\infty u(x, t)dx$, $Q := \int_0^\infty v(x, t)dx$ (total population of young and adult individuals, respectively, at time t).

4.2.1 Existence and Uniqueness of positive solutions of the Initial Value Problem

Existence and uniqueness of positive global solutions of the initial value problem follow, as in Chapter 2, from a standard application of the theory of semilinear evolution equations.

System (4.1) can be written in the following way

$$\begin{pmatrix} u \\ v \end{pmatrix}_t = A \begin{pmatrix} u \\ v \end{pmatrix} + K \begin{pmatrix} u \\ v \end{pmatrix} + f(u(t), v(t)),$$

where

$$A = \begin{pmatrix} -x & 0 \\ x & 0 \end{pmatrix} \quad K = \begin{pmatrix} 0 & (1 - \varepsilon)b(x) + \varepsilon \int_0^\infty b(y)\gamma(x, y) \cdot dy \\ 0 & 0 \end{pmatrix}$$

and

$$\begin{aligned}
 f : L^1(0, \infty) \times L^1(0, \infty) &\longrightarrow L^1(0, \infty) \times L^1(0, \infty) \\
 (u(t), v(t)) &\longmapsto \left(-m_1(\int_0^\infty u(x, t)dx)u, -m_2(\int_0^\infty v(x, t)dx)v \right)
 \end{aligned}$$

In the same way as in Section 2.2 in Chapter 2 we obtain existence and uniqueness of positive global solutions of the initial value problem for System (4.1).

4.2.2 The eigenvalue problem

In this subsection we will prove the existence of a dominant eigenvalue $\lambda_\varepsilon(P, Q)$ of $A_{\varepsilon, P, Q}$ (defined in (4.2) as the linear operator that we obtain when we fix the nonlinearities in System (4.1)) and of a corresponding strictly positive eigenfunction.

In this model it is not possible to apply, as in Chapter 2, Theorem 2.4.6 in order to obtain the existence of a simple strictly dominant eigenvalue of $A_{\varepsilon, P, Q}$ because it is not possible to decompose the operator $A_{\varepsilon, P, Q}$ in the sum of two operators (denoted in Theorem 2.4.6 by A and K) satisfying all the hypotheses of Theorem 2.4.6.

Let us first recall some results about spectral properties of positive linear operators on ordered Banach spaces (see [45], [55], [24]).

Definition 4.2.1 [45] [55] *A positive semigroup $(T(t))$ on a Banach lattice X with generator A is called **irreducible** if there is no closed ideal which is invariant for every operator $T(t)$ except $\{0\}$ and X .*

Equivalent conditions are:

- Given $f \in X$, $g \in X'$, both positive and non-zero, then $\langle T(t_0)f, g \rangle > 0$ for some $t_0 \geq 0$.
- For some (every) $\lambda > s(A)$, $R(\lambda, A)f$ is a quasi-interior point of X^+ (i.e., the minimal ideal containing it is the whole X) whenever $f > 0$ (where $R(\lambda, A)$ denotes the resolvent operator of A).

Theorem 4.2.2 [45] *Let $T(t)$ be an irreducible semigroup on a Banach lattice and let A be its generator.*

If $s(A)$ is a pole of the resolvent then there exists $\alpha \geq 0$ such that the boundary spectrum (see Definition 2.4.1) $\sigma_b(A) = s(A) + i\alpha\mathbb{Z}$. Moreover, $\sigma_b(A)$ contains only algebraically simple poles.

The following abstract theorem is a consequence of the previous one. We will use it to prove (in Theorem 4.2.15) the existence of a simple strictly dominant eigenvalue of $A_{\varepsilon, P, Q}$.

Theorem 4.2.3 *Let us assume that A is the generator of a positive analytic irreducible semigroup on a Banach lattice and that $s(A)$ is a pole of $R(\lambda, A)$, the resolvent operator of A .*

Then $s(A)$ is a strictly dominant eigenvalue of algebraic multiplicity one.

Proof: By Theorem 4.2.2 the boundary spectrum of a generator of an irreducible semigroup such that $s(A)$ is a pole, $\sigma_b(A)$, is $\sigma_b(A) = s(A) + i\alpha\mathbb{Z}$

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with $\alpha \geq 0$ and contains only algebraically simple poles (i.e. algebraically simple eigenvalues).

As the semigroup generated by A is analytic, it is sectorial, and therefore $s(A)$ is the unique spectral value having maximal real part, that is, it is a strictly dominant eigenvalue. \square

Next, we will prove (immediately after Proposition 4.2.4, in Proposition 4.2.11 and in Proposition 4.2.14) that $A_{\varepsilon,P,Q}$ satisfies the hypotheses of Theorem 4.2.3.

Proposition 4.2.4 *The operator $B_{\varepsilon,P,Q}$ given in model (4.2) is the infinitesimal generator of an analytic semigroup with domain*

$$D(B_{\varepsilon,P,Q}) = \{u \in L^1(0, \infty) \text{ such that } xu \in L^1(0, \infty)\} \times L^1(0, \infty).$$

Moreover, the semigroup generated by $B_{\varepsilon,P,Q}$ is positive.

Proof: The semigroup generated by the operator L defined in $D(B_{\varepsilon,P,Q})$ by

$$L \begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} -xu \\ xu \end{pmatrix}$$

can be computed explicitly and it is the following analytic semigroup

$$S(t) \begin{pmatrix} u_0(x) \\ v_0(x) \end{pmatrix} = \begin{pmatrix} u_0(x)e^{-xt} \\ v_0(x) + (1 - e^{-xt})u_0(x) \end{pmatrix}.$$

As the perturbation by a bounded operator of the generator of an analytic semigroup is the generator of an analytic semigroup (see [48]) we obtain that $B_{\varepsilon,P,Q}$ generates an analytic semigroup.

The positivity of the semigroup generated by the multiplication operator $B_{\varepsilon,P,Q}$ follows from the non-negativity of the off-diagonal elements of $B_{\varepsilon,P,Q}$ (see Theorem 0.0.8 in Preliminaries). \square

Since the perturbation by a bounded positive operator of the generator of an analytic semigroup is the generator of a positive analytic semigroup we obtain that $A_{\varepsilon,P,Q}$ generates a positive analytic semigroup.

In order to prove that $s(A_{\varepsilon,P,Q})$ is a pole of finite algebraic multiplicity of the resolvent operator $R(\lambda, A_{\varepsilon,P,Q})$ we will apply Theorem 2.4.6. Let us prove that $A_{\varepsilon,P,Q}$ satisfies the hypotheses of Theorem 2.4.6 needed in order to obtain that $s(A_{\varepsilon,P,Q})$ is a pole of finite algebraic multiplicity of $R(\lambda, A_{\varepsilon,P,Q})$.

Proposition 4.2.5 *Let $B_{\varepsilon,P,Q}$ and T be the operators defined in (4.2) and let $R(\lambda, B_{\varepsilon,P,Q})$ be the resolvent operator of $B_{\varepsilon,P,Q}$. The operator $TR(\lambda, B_{\varepsilon,P,Q})$ is compact.*

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Proof: As $R(\lambda, B_{\varepsilon, P, Q})$ is a bounded operator, we only have to see that T is compact.

Let us consider the unit ball B of L^1 . We will show that

$$F = \left\{ \int_0^\infty \gamma(x, y) b(y) f(y) dy \quad : \quad f \in B \right\}$$

is a precompact set .

Let us note that F is bounded since

$$\begin{aligned} \|F\| &= \sup_{f \in B} \int_0^\infty \left| \int_0^\infty \gamma(x, y) b(y) f(y) dy \right| dx \\ &\leq b(0) \sup_{f \in B} \int_0^\infty |f(y)| \int_0^\infty \gamma(x, y) dx dy \\ &\leq b(0). \end{aligned}$$

We have, for $v \in F$, $l > 0$, $h > 0$ and $\tau_h v(x) := v(x + h)$,

$$\begin{aligned} \|\tau_h v - v\|_{L^1(0, l)} &\leq \int_0^\infty b(y) |f(y)| \int_0^l |\gamma(x + h, y) - \gamma(x, y)| dx dy \\ &\leq b(0) \int_0^\infty |f(y)| \int_0^l L h dx dy \\ &\leq b(0) L h l < \varepsilon \quad \text{if } h < \frac{\varepsilon}{b(0)L}, \end{aligned}$$

where we have used that $b(y) \leq b(0)$ and that γ is lipschitzian .

We also have, for l sufficiently large,

$$\begin{aligned} \|v\|_{L^1(l, \infty)} &= \int_l^\infty \left| \int_0^\infty \gamma(x, y) b(y) f(y) dy \right| dx \\ &\leq \int_0^\infty b(y) \int_l^\infty \gamma(x, y) dx |f(y)| dy \\ &\leq \sup_{y \in (0, \infty)} \left(b(y) \int_l^\infty \gamma(x, y) dx \right) < \varepsilon, \end{aligned}$$

where the last inequality is due to the following hypotheses (see Section 3.1)

1. $\forall K \quad \forall \varepsilon > 0 \quad \exists L > 0$ such that if $y < K$ then

$$\int_L^\infty \gamma(x, y) dx < \varepsilon$$

- 2.

$$\lim_{y \rightarrow \infty} b(y) = 0.$$

4.2.2. The eigenvalue problem

Indeed, given ε , let K_ε be such that

$$b(y) < \varepsilon \quad \text{if } y \geq K_\varepsilon$$

and, for this K_ε let L be such that if $y < K_\varepsilon$

$$\int_L^\infty \gamma(x, y) dx < \frac{\varepsilon}{b(0)}.$$

Then, if $l > L$ we have

$$b(y) \int_l^\infty \gamma(x, y) dx \leq b(0) \frac{\varepsilon}{b(0)} = \varepsilon \quad \text{if } y < K_\varepsilon,$$

$$b(y) \int_l^\infty \gamma(x, y) dx \leq \varepsilon \quad \text{if } y \geq K_\varepsilon.$$

By the standard compactness criterion in L^p -spaces stated in Chapter 2 (see Proposition 2.4.7) F is precompact, and so $TR(\lambda, B_{\varepsilon, P, Q})$ is compact. \square

Now we proceed to state Lemma 4.2.6 which will be used in the proof of Proposition 4.2.10 that is needed to prove Proposition 4.2.11.

In accordance with the notation of Section 3.3, $\mu_\varepsilon(P, Q, x)$ will stand for the dominant eigenvalue of the matrix

$$\begin{pmatrix} -m_1(P) - x & (1 - \varepsilon)b(x) \\ x & -m_2(Q) \end{pmatrix}. \quad (4.3)$$

From now on we will assume that for all $\varepsilon \geq 0$, P and Q are such that

$$m_2(Q) < m_1(P) + (1 - \varepsilon)b(0). \quad (4.4)$$

Now, we proceed to prove that condition (4.4) is necessary and sufficient in order that the function $\mu_\varepsilon(P, Q, x)$ has a maximum point and moreover that this maximum point $x(P, Q)$, say, is always unique.

Lemma 4.2.6 *Let $\mu_\varepsilon(P, Q, x)$ be the dominant eigenvalue of the matrix (4.3). The function $\mu_\varepsilon(P, Q, x)$ has a unique (strict) maximum point $x(P, Q)$ if and only if hypothesis (4.4) holds.*

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Proof: The characteristic polynomial of the matrix (4.3) is

$$p(\varepsilon, x, \lambda) := \lambda^2 + (x + m_1(P) + m_2(Q))\lambda + (x + m_1(P))m_2(Q) - (1 - \varepsilon)xb(x).$$

Taking derivatives twice (with respect to x) of the equation $p(\varepsilon, x, \lambda) = 0$ we obtain

$$(2\lambda'(x) + 2)\lambda'(x) + (2\lambda(x) + x + m_1(P) + m_2(Q))\lambda''(x) - (1 - \varepsilon)(xb(x))'' = 0.$$

At a critical point \tilde{x} , $\lambda'(\tilde{x}) = 0$ and the former equation yields

$$\lambda''(\tilde{x}) = \frac{(1 - \varepsilon)(xb(x))''|_{\tilde{x}}}{2\lambda(\tilde{x}) + \tilde{x} + m_1(P) + m_2(Q)}.$$

As $(xb(x))''|_{\tilde{x}} < 0$ (see (1.11) and hypotheses of Section 1.2) and $2\lambda(\tilde{x}) + \tilde{x} + m_1(P) + m_2(Q) > 0$ we obtain that $\lambda''(\tilde{x}) < 0$, that is, any critical point is a maximum, which implies that the continuous function $\lambda(x)$ has, at most, one critical point.

On the other hand, since

$$\lambda(0) = -\min(m_1(P), m_2(Q)) \geq \lim_{x \rightarrow \infty} \lambda(x) = -m_2(Q),$$

we can conclude that $\lambda(x)$ will have a maximum point if and only if $\lambda'(0) > 0$. Taking derivatives once of the equation $F(x, \lambda) = 0$ gives, if $m_1(P) \neq m_2(Q)$,

$$\begin{aligned} \lambda'(x)|_{x=0} &= \frac{-\lambda(0) - m_2(Q) + (1 - \varepsilon)(xb(x))'|_{x=0}}{2\lambda(0) + m_1(P) + m_2(Q)} \\ &= \frac{\min(m_1(P), m_2(Q)) - m_2(Q) + (1 - \varepsilon)b(0)}{|m_1(P) - m_2(Q)|}. \end{aligned}$$

Therefore, if $m_1(P) > m_2(Q)$ then

$$\lambda'(x)|_{x=0} = \frac{(1 - \varepsilon)b(0)}{m_1(P) - m_2(Q)} > 0$$

and if $m_2(Q) - (1 - \varepsilon)b(0) < m_1(P) < m_2(Q)$ then

$$\lambda'(x)|_{x=0} = -1 + \frac{(1 - \varepsilon)b(0)}{m_2(Q) - m_1(P)} > 0.$$

Finally, the case $m_1(P) = m_2(Q)$ gives $\lim_{x \rightarrow 0^+} \lambda'(x) = +\infty$ and the statement is proved. \square

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Let us remind that we wanted to see that $A_{\varepsilon,P,Q}$ (defined in (4.2)) satisfies the conditions of Theorem 4.2.3. We have already seen that $A_{\varepsilon,P,Q}$ generates a positive analytic semigroup.

We would like to apply Theorem 2.4.6 to ensure that $s(A_{\varepsilon,P,Q})$ is a pole of finite algebraic multiplicity of the resolvent operator $R(\lambda, A_{\varepsilon,P,Q})$.

Let us note that the only hypothesis of Theorem 2.4.6 (of the hypotheses that are necessary to obtain that $s(A_{\varepsilon,P,Q})$ is a pole of finite algebraic multiplicity of $R(\lambda, A_{\varepsilon,P,Q})$) that we have not proved yet is the inequality $s(A_{\varepsilon,P,Q}) > s(B_{\varepsilon,P,Q})$.

In order to do it let us first write down some results from [58].

Definition 4.2.7 [58] *A linear closed operator B on an ordered Banach space X with closed convex cone X_+ is called **resolvent positive** if the resolvent set of B , $\rho(B)$, contains a ray (ω, ∞) such that $R(\lambda, B)$ is a positive operator for all $\lambda > \omega$.*

Definition 4.2.8 [58] *Let $A = B + C$ where B is a resolvent positive operator and let $C : D(A) \rightarrow X$ be a linear operator such that the operators*

$$F(\lambda) = CR(\lambda, B)$$

*are positive for λ in a ray $(\alpha, \infty) \subseteq \rho(B)$. Then C is called a **positive perturbator** of B .*

Theorem 4.2.9 [58] *Let X be an ordered Banach space with normal and generating cone X_+ and $A = B + C$ be a positive perturbation of B . Let $\text{spr}F(\lambda)$ denote the spectral radius of $F(\lambda)$. Then $\text{spr}F(\lambda)$ is a decreasing convex function of λ and exactly one of the following three cases holds:*

- i) $\text{spr}F(\lambda) \geq 1$ for all $\lambda > s(B)$. Then A is not resolvent positive.*
- ii) $\text{spr}F(\lambda) < 1$ for all $\lambda > s(B)$. Then A is resolvent positive and $s(A) = s(B)$.*
- iii) There exists $\lambda_2 > \lambda_1 > s(B)$ such that*

$$\text{spr}F(\lambda_2) < 1 \leq \text{spr}F(\lambda_1).$$

Then A is resolvent positive and $s(B) < s(A) < \infty$. Further the spectral radius of $F(\lambda)$ is a decreasing, log-convex function of $\lambda > s(B)$ and $s(A)$ is characterized by

$$\text{spr}F(s(A)) = 1, \quad 1 \in \sigma(F(s(A))).$$

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Proposition 4.2.10 *Let $A_{\varepsilon,P,Q}$ and $B_{\varepsilon,P,Q}$ the operators defined in (4.2). Then $s(A_{\varepsilon,P,Q}) > s(B_{\varepsilon,P,Q})$.*

Proof: First notice that $B_{\varepsilon,P,Q}$ is resolvent positive because it generates a positive (analytic) semigroup (Proposition 4.2.4). As T is a positive bounded operator we have that $A_{\varepsilon,P,Q} := B_{\varepsilon,P,Q} + \varepsilon T$ is the generator of a positive (analytic) semigroup. Since the resolvent of an operator A is expressed by the semigroup, $T(t)$, generated by A , by

$$R(\lambda, A) = \int_0^{\infty} e^{\lambda t} T(t) dt$$

for $\lambda > \omega(A)$ (see [45]) we obtain that $R(\lambda, A_{\varepsilon,P,Q})$ is a positive operator for $\lambda > \omega(A_{\varepsilon,P,Q}) (= s(A_{\varepsilon,P,Q}))$.

Hence, case *i*) of Theorem 4.2.9 is discarded and so there exists λ_2 such that $\text{spr} F(\lambda_2) < 1$, where $F(\lambda) := \varepsilon TR(\lambda, B_{\varepsilon,P,Q})$.

Therefore we only have to prove that there exists $\lambda > s(B_{\varepsilon,P,Q})$ such that the spectral radius of the operator $F(\lambda)$ is bigger than or equal to 1.

Since by Proposition 4.2.5 the operator $TR(\lambda, B_{\varepsilon,P,Q})$ is compact, its spectrum $\sigma(TR(\lambda, B_{\varepsilon,P,Q}))$ is not empty. Then $s(TR(\lambda, B_{\varepsilon,P,Q})) \in \sigma(TR(\lambda, B_{\varepsilon,P,Q}))$ (because the spectral bound of the generator of a positive semigroup on a Banach lattice belongs to the spectrum of the generator unless it is empty, (see [45] p. 292).

We are reduced to prove that $s(\varepsilon TR(\lambda_1, B_{\varepsilon,P,Q})) \geq 1$ for some $\lambda_1 > s(B_{\varepsilon,P,Q})$ (because it implies $\text{spr}(F(\lambda)) \geq 1$).

Computing explicitly $TR(\lambda, B_{\varepsilon,P,Q})$ we obtain

$$\begin{aligned} TR(\lambda, B_{\varepsilon,P,Q}) \begin{pmatrix} f \\ g \end{pmatrix} &= \\ &= \begin{pmatrix} \varepsilon \int_0^{\infty} \gamma(x, y) b(y) \left(\frac{yf(y)}{(\lambda + m_1(P) + y)(\lambda + m_2(Q)) - (1 - \varepsilon)yb(y)} \right. \\ \left. + \frac{(\lambda + m_1(P) + y)g(y)}{(\lambda + m_1(P) + y)(\lambda + m_2(Q)) - (1 - \varepsilon)yb(y)} \right) dy \\ 0 \end{pmatrix} \end{aligned}$$

Applying the characterization (3.4) yields that it suffices to prove that there exists $f(x) > 0$, $(f(x), 0) \in D(B_{\varepsilon,P,Q})$ such that

$$\int_0^{\infty} \frac{\varepsilon y b(y)}{p(\varepsilon, \lambda_1, y)} \gamma(x, y) f(y) dy \geq f(x) \quad (4.5)$$

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where $p(\varepsilon, \lambda, y) := (\lambda + m_1(P) + y)(\lambda + m_2(Q)) - (1 - \varepsilon)yb(y)$.
 Let us choose $f(x) := \chi_{[\hat{x}-\delta, \hat{x}+\delta]}$, δ to be chosen and \hat{x} satisfying

$$\begin{cases} p(\varepsilon, s(B_{\varepsilon, P, Q}), \hat{x}) = 0, \\ \frac{\partial}{\partial y} p(\varepsilon, \lambda, y) |_{(\varepsilon, s(B_{\varepsilon, P, Q}), \hat{x})} = 0. \end{cases}$$

The existence of this \hat{x} is guaranteed by the fact that the function $x \rightarrow \mu_\varepsilon(P, Q, x)$ has a strictly positive maximum point (see Lemma 4.2.6).

Substituting $f(x)$ in (4.5) yields

$$\int_{\hat{x}-\delta}^{\hat{x}+\delta} \frac{\varepsilon y b(y)}{p(\varepsilon, \lambda_1, y)} \gamma(x, y) dy \geq 1 \quad \text{for } x \in [\hat{x} - \delta, \hat{x} + \delta].$$

As $\gamma(x, y)$ is a strictly positive continuous function, there exists a constant K such that $\gamma(x, y) > K > 0$ for $(x, y) \in [\hat{x} - \delta, \hat{x} + \delta]^2$ and any $\delta > 0$ (such that $\delta < \hat{x}$).

Therefore,

$$\begin{aligned} \int_{\hat{x}-\delta}^{\hat{x}+\delta} \frac{\varepsilon y b(y)}{p(\varepsilon, \lambda_1, y)} \gamma(x, y) dy &\geq \int_{\hat{x}-\delta}^{\hat{x}+\delta} \frac{\varepsilon y b(y)}{p(\varepsilon, \lambda_1, y)} K dy \\ &\geq 2\delta \varepsilon K \min_{y \in [\hat{x}-\delta, \hat{x}+\delta]} \frac{y b(y)}{p(\varepsilon, \lambda_1, y)}. \end{aligned}$$

So, the inequality (4.5) is implied by

$$2\delta \varepsilon K \min_{y \in [\hat{x}-\delta, \hat{x}+\delta]} \frac{y b(y)}{p(\varepsilon, \lambda_1, y)} \geq 1. \quad (4.6)$$

If, for every fixed ε , we develop by the Taylor formula $p(\varepsilon, \lambda_1, y)$ (as a function of the two last variables) at the point $(s(B_{\varepsilon, P, Q}), \hat{x})$ we have, for any $y \in [\hat{x} - \delta, \hat{x} + \delta]$ and for some z such that $|z - \hat{x}| < |z - y|$,

$$\begin{aligned} p(\varepsilon, \lambda_1, y) &= k_1(\lambda_1 - s(B_{\varepsilon, P, Q})) + (\lambda_1 - s(B_{\varepsilon, P, Q}))^2 \\ &\quad - \frac{(1-\varepsilon)}{2} (y b(y))''(z)(y - \hat{x})^2 + (\lambda_1 - s(B_{\varepsilon, P, Q}))(y - \hat{x}) \\ &\leq (k_1 + \delta)(\lambda_1 - s(B_{\varepsilon, P, Q})) + k_2 \delta^2 + (\lambda_1 - s(B_{\varepsilon, P, Q}))^2 \end{aligned}$$

where k_1, k_2 are constants.

So choosing $\delta \sim (\lambda_1 - s(B_{\varepsilon, P, Q}))^{\frac{1}{2}}$ for λ_1 close enough to (and bigger than) $s(B_{\varepsilon, P, Q})$ the inequality (4.6) holds. □

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Proposition 4.2.11 *Let $A_{\varepsilon,P,Q}$ be the operator defined by (4.2). Then $s(A_{\varepsilon,P,Q})$ is a pole of finite algebraic multiplicity of $R(\lambda, A_{\varepsilon,P,Q})$.*

Proof: By Propositions 4.2.4, 4.2.5, 4.2.10 and the first part of Theorem 2.4.6 in Chapter 2. □

So far, we have proved that $A_{\varepsilon,P,Q}$ generates a positive analytic semigroup and that $s(A_{\varepsilon,P,Q})$ is a pole of finite algebraic multiplicity of the resolvent operator of $A_{\varepsilon,P,Q}$.

If we prove that the semigroup generated by the operator $A_{\varepsilon,P,Q}$ is irreducible, then, by Theorem 4.2.3 we obtain the existence of a simple strictly dominant eigenvalue of the operator $A_{\varepsilon,P,Q}$.

To prove the irreducibility we will first formulate a result that ensures the irreducibility, under some hypotheses, of a certain perturbation of a generator of a positive semigroup.

The perturbation by a bounded operator of the generator of a semigroup generates a semigroup ([48], [45]...). The perturbation by an unbounded operator of the generator of a semigroup does not always generate a semigroup. However, there are some cases, under some additional hypotheses, when it does, like, for instance, in the following result of Voigt, that we will use next.

Lemma 4.2.12 [61] *Let E be a real AL-space. Let A be the generator of a positive C_0 semigroup on E . Let $B : D(A) \rightarrow E$ be a positive operator and assume that there exists $\lambda > s(A)$ such that $\|B(\lambda - A)^{-1}\| < 1$. Then $A + B$ is the generator of a positive semigroup.*

An AL-space (abstract L-space) is an L-normed Banach lattice, where an L-norm is a lattice norm $x \mapsto \|x\|$ on a vector lattice, E , that satisfies the axiom

$$\|x + y\| = \|x\| + \|y\| \quad (x, y \in E_+ \quad (\text{the positive cone}))$$

(see [55]).

The former result of Voigt works only when the space is an AL-space. Otherwise there are counterexamples given by Arendt in [3].

Let us now formulate the result about the irreducibility of a certain perturbation of a generator of a positive semigroup.

Theorem 4.2.13 *Let B be the generator of a positive semigroup in an AL-space X . Let $K : D(B) \rightarrow X$ be a positive operator and assume that there exists $\lambda_0 > s(B)$ such that $\|KR(\lambda_0, B)\| < 1$ (where $R(\lambda, B)$ is the resolvent operator of B) and that the operator $KR(\lambda_0, B)$ is irreducible. Then $B + K$ is the generator of a positive irreducible semigroup.*

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Proof: The fact that $B + K$ generates a positive semigroup follows from Lemma 4.2.12.

Let us consider arbitrary $f \in X$, $\phi \in X^*$ (dual space of X) such that $f > 0$, $\phi > 0$. As $R(\lambda_0, B)$ is positive, $R(\lambda_0, B)^*$ is also positive and its kernel reduces to $\{0\}$. So $R(\lambda_0, B)^*\phi > 0$ and since by hypothesis $KR(\lambda_0, B)$ is irreducible, there exists m such that

$$0 < \langle (KR(\lambda_0, B))^m f, R(\lambda_0, B)^*\phi \rangle = \langle R(\lambda_0, B)(KR(\lambda_0, B))^m f, \phi \rangle.$$

As $\|KR(\lambda_0, B)\| < 1$ we can write

$$\begin{aligned} R(\lambda_0, B + K) &= R(\lambda_0, B)(I - KR(\lambda_0, B))^{-1} \\ &= R(\lambda_0, B) \sum_{n=0}^{\infty} (KR(\lambda_0, B))^n. \end{aligned}$$

So, $\langle R(\lambda_0, B + K)f, \phi \rangle = \sum_{n=0}^{\infty} \langle R(KR)^n f, \phi \rangle > 0$, i.e., $R(\lambda_0, B + K)f$ is a quasi-interior point of $(L^1)^+$ and therefore, the semigroup generated by $B + K$ is irreducible. □

Proposition 4.2.14 *The semigroup generated by the operator $A_{\varepsilon, P, Q}$ (defined in (4.2)) is irreducible.*

Proof:

In order to prove the result we have to consider a different decomposition of $A_{\varepsilon, P, Q}$, namely,

$$\begin{aligned} A_{\varepsilon, P, Q} &:= \tilde{B}_{\varepsilon, P, Q} + \tilde{T}_{\varepsilon} = \begin{pmatrix} -m_1(P) - x & (1 - \varepsilon)b(x) \\ 0 & -m_2(Q) \end{pmatrix} \\ &+ \begin{pmatrix} 0 & \varepsilon \int_0^{\infty} b(y)\gamma(x, y) \cdot \\ x & 0 \end{pmatrix}. \end{aligned}$$

The resolvent operator of $\tilde{B}_{\varepsilon, P, Q}$ can be computed explicitly

$$R(\lambda, \tilde{B}_{\varepsilon, P, Q}) = \begin{pmatrix} \frac{1}{(\lambda + m_1(P) + x)} & \frac{(1 - \varepsilon)b(x)}{(\lambda + m_1(P) + x)(\lambda + m_2(Q))} \\ 0 & \frac{1}{(\lambda + m_2(Q))} \end{pmatrix}.$$

4.2.2. The eigenvalue problem

It is easy to check that for λ_0 big enough $\|\tilde{T}_\varepsilon R(\lambda_0, \tilde{B}_{\varepsilon, P, Q})\| < 1$.

Let us show that the operator $\tilde{T}_\varepsilon R(\lambda_0, \tilde{B}_{\varepsilon, P, Q})$ is irreducible.

Let us consider a closed ideal \tilde{J} of the Banach lattice $X = L^1(0, \infty) \times L^1(0, \infty)$. We will assume that $\tilde{T}_\varepsilon R(\lambda_0, \tilde{B}_{\varepsilon, P, Q})\tilde{J} \subset \tilde{J}$ and we would like to prove that then, either $\tilde{J} = \{0\}$ or $\tilde{J} = X$.

Obviously $\tilde{T}_\varepsilon R(\lambda_0, \tilde{B}_{\varepsilon, P, Q})\tilde{J} \subset \tilde{J} \Rightarrow \tilde{T}_\varepsilon R(\lambda_0, \tilde{B}_{\varepsilon, P, Q})(\tilde{J} \cap X^+) \subset \tilde{J}$.

On the other hand, if we assume that $\tilde{T}_\varepsilon R(\lambda_0, \tilde{B}_{\varepsilon, P, Q})(\tilde{J} \cap X^+) \subset \tilde{J}$, as for all $u \in \tilde{J}$ we have the decomposition $u = u^+ - u^-$, with $u^+, u^- \in \tilde{J} \cap X^+$ (where $u^+ = \sup(u, 0)$, $u^- = \sup(-u, 0)$, the positive and negative part, respectively), then

$$\tilde{T}_\varepsilon R(\lambda_0, \tilde{B}_{\varepsilon, P, Q})u = \tilde{T}_\varepsilon R(\lambda_0, \tilde{B}_{\varepsilon, P, Q})u^+ - \tilde{T}_\varepsilon R(\lambda_0, \tilde{B}_{\varepsilon, P, Q})u^- \in \tilde{J},$$

that is,

$$\tilde{T}_\varepsilon R(\lambda_0, \tilde{B}_{\varepsilon, P, Q})(\tilde{J} \cap X^+) \subset \tilde{J} \Rightarrow \tilde{T}_\varepsilon R(\lambda_0, \tilde{B}_{\varepsilon, P, Q})\tilde{J} \subset \tilde{J}.$$

Therefore

$$\tilde{T}_\varepsilon R(\lambda_0, \tilde{B}_{\varepsilon, P, Q})\tilde{J} \subset \tilde{J} \Leftrightarrow \tilde{T}_\varepsilon R(\lambda_0, \tilde{B}_{\varepsilon, P, Q})(\tilde{J} \cap X^+) \subset \tilde{J}. \quad (4.7)$$

In the Banach lattice $L^1(0, \infty)$ each subset S of $(0, \infty)$ determines a closed ideal

$$J_S := \{f \in L^1(0, \infty) \text{ s.t. } f|_S = 0 \text{ a.e.}\},$$

and conversely, every closed ideal has this form (see [55], III, §1).

Then

$$\begin{aligned} \tilde{J} &= J_{S_1} \times J_{S_2} = \{f \in L^1(0, \infty) \text{ s.t. } f|_{S_1} = 0 \text{ a.e.}\} \\ &\quad \times \{f \in L^1(0, \infty) \text{ s.t. } f|_{S_2} = 0 \text{ a.e.}\} \end{aligned}$$

for some subsets S_1 and S_2 of $(0, \infty)$.

Let us assume that for arbitrary $\begin{pmatrix} u \\ v \end{pmatrix} \in \tilde{J} \cap X^+$ necessarily

$$\tilde{T}_\varepsilon R(\lambda_0, \tilde{B}_{\varepsilon, P, Q}) \begin{pmatrix} u \\ v \end{pmatrix} \in \tilde{J}. \quad (4.8)$$

If we prove that then, either $\tilde{J} = \{0\}$ or $\tilde{J} = X$ then by (4.7) we will obtain that $\tilde{T}_\varepsilon R(\lambda_0, \tilde{B}_{\varepsilon, P, Q})$ is irreducible.

So, by assumption (4.8) we have

$$\int_0^\infty b(y)\gamma(x, y)v(y)dy = 0 \text{ for almost every } x \in S_1, \quad (4.9)$$

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and

$$\left[\frac{xu(x)}{(\lambda_0 + m_1(P) + x)} + \frac{x(1 - \varepsilon)b(x)v(x)}{(\lambda_0 + m_1(P) + x)(\lambda_0 + m_2(Q))} \right]_{|_{S_2}} = 0 \quad \text{a.e..} \quad (4.10)$$

Since $v(x) \in J_{S_2}$, we have $\left[\frac{x(1 - \varepsilon)b(x)v(x)}{(\lambda_0 + m_1(P) + x)(\lambda_0 + m_2(Q))} \right]_{|_{S_2}} = 0$ a.e. and then (4.10) yields

$$\left[\frac{xu(x)}{(\lambda_0 + m_1(P) + x)} \right]_{|_{S_2}} = 0 \quad \text{a.e..} \quad (4.11)$$

i.e. $u(x) = 0$ almost everywhere in S_2 . That is, we have that for all $u \in J_{S_1} \cap (L^1)^+$ (so, it satisfies $u_{|_{S_1}} = 0$ a.e.) also $u_{|_{S_2}} = 0$ a.e. holds. This implies

$$S_2 \subseteq S_1. \quad (4.12)$$

Moreover, since, $v(y) \geq 0$, then (4.9) implies that either S_1 has zero measure or $v(x) = 0$ a.e. in $(0, \infty)$ and so $S_2 = (0, \infty)$. Then, by (4.12) we have that either S_1 and S_2 have both measure zero or $S_1 = S_2 = (0, \infty)$, and therefore either $\tilde{J} = X$ or $\tilde{J} = \{0\}$, that is, $\tilde{T}_\varepsilon R(\lambda_0, \tilde{B}_{\varepsilon, P, Q})$ is irreducible.

Finally, by Theorem 4.2.13 we obtain that the semigroup generated by the operator $A_{\varepsilon, P, Q}$ is irreducible. □

We can now give the theorem that ensures the existence of a simple strictly dominant eigenvalue of the operator $A_{\varepsilon, P, Q}$ defined in (4.2).

Theorem 4.2.15 *The spectral bound of the operator $A_{\varepsilon, P, Q}$, $s(A_{\varepsilon, P, Q})$, is a strictly dominant eigenvalue of algebraic multiplicity one and its corresponding eigenfunction is strictly positive.*

Proof: Since $A_{\varepsilon, P, Q}$ is the generator of a positive analytic semigroup, the first statement is given by Proposition 4.2.11, Proposition 4.2.14 and Theorem 4.2.3.

By Theorem 2.4.14 in Chapter 2 we obtain existence of an eigenfunction of $s(A_{\varepsilon, P, Q})$ which is a quasi interior point of the positive cone of $L^1(0, \infty) \times L^1(0, \infty)$, that is, a strictly positive function almost everywhere. □

Theorem 4.2.16 *The dominant eigenvalue $s(A_{\varepsilon, P, Q})$ of the operator $A_{\varepsilon, P, Q}$ is the only eigenvalue of $A_{\varepsilon, P, Q}$ such that the corresponding eigenfunction is positive.*

Proof: Applying Theorem 2.4.16. □

4.2.3 Steady states

In this subsection we will show the existence, under reasonable hypotheses, of a family of equilibrium solutions of System (4.1). Moreover we will show that, when the probability of mutation (ε) tends to zero, the equilibrium solution tends to concentrate at the ESS value of the maturation age model (1.1). We will apply the results of Sections 3.3 and 3.4.

For $\varepsilon \in (0, 1)$ and positive P and Q let $s(A_{\varepsilon,P,Q}) = \lambda_{\varepsilon}(P, Q)$ be the dominant eigenvalue of the linear operator $A_{\varepsilon,P,Q}$ and let $\vec{u}_{\varepsilon,P,Q}(x) = (u_{\varepsilon,P,Q}^1(x), u_{\varepsilon,P,Q}^2(x))$ be the corresponding normalized positive eigenvector. Then the equilibria of System (4.2) will be given by $(P+Q)\vec{u}_{\varepsilon,P,Q}(x)$ where P and Q are the solutions of

$$\begin{cases} \lambda_{\varepsilon}(P, Q) = 0, \\ \Psi_{\varepsilon}(P, Q) = 0, \end{cases} \quad (4.13)$$

where

$$\Psi_{\varepsilon}(P, Q) := \frac{\int_0^{\infty} u_{\varepsilon,P,Q}^1(x) dx}{\int_0^{\infty} u_{\varepsilon,P,Q}^2(x) dx} - \frac{P}{Q}.$$

For $\varepsilon = 0$ we can consider System (4.2) as the following system in \mathbb{R}^2

$$\begin{pmatrix} u_t \\ v_t \end{pmatrix} = B_{0,P,Q}(x) \begin{pmatrix} u \\ v \end{pmatrix} := \begin{pmatrix} -m_1(P) - x & b(x) \\ x & -m_2(Q) \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix} \quad (4.14)$$

For positive P , Q and x let $\mu_0(P, Q, x)$ be the dominant eigenvalue of the matrix $B_{0,P,Q}(x)$ and let $\vec{u}_{0,P,Q}(x) = (u_{0,P,Q}^1(x), u_{0,P,Q}^2(x))$ be the corresponding normalized positive eigenvector.

Let us define $\tilde{\mu}_0(P, Q) := \max_x \mu_0(P, Q, x) = \mu_0(P, Q, x(P, Q))$ and $\vec{u}_{0,P,Q} := \vec{u}_{0,P,Q}(x(P, Q))$.

The equilibria of the following system

$$\begin{pmatrix} u_t \\ v_t \end{pmatrix} = B_{0,P,Q}(x(P, Q)) \begin{pmatrix} u \\ v \end{pmatrix}$$

will be given by $(P + Q)\vec{u}_{0,P,Q}$ where P and Q are the solutions of

$$\begin{cases} \tilde{\mu}_0(P, Q) = 0, \\ \Psi_0(P, Q) = 0, \end{cases} \quad (4.15)$$

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where $\Psi_0(P, Q) = \frac{u_{0,P,Q}^1(x(P, Q))}{u_{0,P,Q}^2(x(P, Q))} - \frac{P}{Q}$.

Let us give some lemmas that we will need in order to prove the existence (for $\varepsilon > 0$) of steady states of System (4.2) and to describe their behavior when ε goes to zero.

Let us recall the definition of strongly irreducible operator.

Definition 4.2.17 *Let X be a Banach lattice. A positive bounded linear operator B is **strongly irreducible** ($B \gg 0$) if Bf is a quasi-interior point for all $f \in X^+$, $f \neq 0$.*

Remark 4.2.18 *A strongly irreducible positive operator is called strictly positive in [2].*

Proposition 4.2.19 [2] *Let A_1, A_2 be resolvent positive operators with dense domain such that*

$$0 \ll R(\lambda, A_1) \leq R(\lambda, A_2) \quad \text{for } \lambda > \max \{s(A_1), s(A_2)\}.$$

Assume that

- a) $A_1 \neq A_2$ and
- b) $s(A_i)$ is a pole of the resolvent of A_i , $i = 1, 2$.

Then $s(A_1) < s(A_2)$.

Lemma 4.2.20 *The dominant eigenvalue of the operator $A_{\varepsilon,P,Q}$ (defined in (4.2)), $\lambda_\varepsilon(P, Q)$, is a continuous strictly decreasing function with respect to P and Q .*

Proof:

Let us first prove the continuity of λ_ε with respect to P .
 Let us consider P_1, P_2 such that $|P_1 - P_2| < \delta$.
 We can write $A_{\varepsilon,P_1,Q} = A_{\varepsilon,P_2,Q} + L$ where

$$L = \begin{pmatrix} m_1(P_2) - m_1(P_1) & 0 \\ 0 & 0 \end{pmatrix}$$

Using Theorem 2.4.22 in Chapter 2 we have

$$\tilde{\delta}(A_{\varepsilon,P_1,Q}, A_{\varepsilon,P_2,Q}) \leq \|L\|$$

and applying the results of continuity of a finite system of eigenvalues (see [31] pag 213) we get the continuity of λ_ε with respect to P .

The same reasoning applies to prove the continuity with respect to Q .

We proceed now to show that $\lambda_\varepsilon(P, Q)$ is decreasing with respect to P . Let $P_1 < P_2$. Since m_1 is a strictly increasing function we have for all $\vec{v}(x) > 0$,

$$A_{\varepsilon, P_1, Q} \vec{v}(x) \geq A_{\varepsilon, P_2, Q} \vec{v}(x) \quad (4.16)$$

and $A_{\varepsilon, P_1, Q} \neq A_{\varepsilon, P_2, Q}$.

Since, for any closed linear operators A and B ,

$$R(\lambda, A) - R(\lambda, B) = R(\lambda, A)(A - B)R(\lambda, B)$$

holds whenever $D(A) = D(B)$ and $\lambda > \max(s(A), s(B))$, inequality (4.16) implies $R(\lambda, A_{\varepsilon, P_1, Q}) \geq R(\lambda, A_{\varepsilon, P_2, Q})$.

As by Proposition 4.2.14 the semigroup generated by $A_{\varepsilon, P_2, Q}$ is irreducible (and therefore its resolvent is strongly irreducible) and by Proposition 4.2.11, $s(A_{\varepsilon, P_2, Q})$ is a pole of the resolvent of $A_{\varepsilon, P_2, Q}$, Proposition 4.2.19 implies $\lambda_\varepsilon(P_1, Q) > \lambda_\varepsilon(P_2, Q)$.

Obviously, the same proof applies for the dependence of λ_ε on Q .

□

The following is a somehow parallel result to the previous one for the $\varepsilon = 0$ finite dimensional associated problem (4.14).

Lemma 4.2.21 *Let $\mu_0(P, Q, x)$ be the dominant eigenvalue of the matrix $B_{0, P, Q}(x)$ defined in (4.14). Let $\tilde{\mu}_0(P, Q) = \max_x \mu_0(P, Q, x)$. Then $\tilde{\mu}_0(P, Q)$ is a continuous, strictly decreasing function of P and Q .*

Proof: Computing explicitly $\mu_0(P, Q, x)$ we have

$$\mu_0(P, Q, x) = \frac{1}{2} \left(-(m_1(P) + x + m_2(Q)) + \sqrt{(m_1(P) + x - m_2(Q))^2 + 4xb(x)} \right)$$

which is a continuous function of P and Q .

Since the maximum of $\mu_0(P, Q, x)$ with respect to x is unique, $\tilde{\mu}_0(P, Q)$ is a continuous function of P and Q .

In order to check the monotonicity we compute the partial derivatives of $\tilde{\mu}_0(P, Q)$ with respect to P and Q that are

$$\frac{\partial \tilde{\mu}_0(P, Q)}{\partial P} = \frac{\partial \mu_0}{\partial P}, \quad \frac{\partial \tilde{\mu}_0(P, Q)}{\partial Q} = \frac{\partial \mu_0}{\partial Q},$$

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where we have used that $\frac{\partial \mu_0(P, Q, x(P, Q))}{\partial x} = 0$.

If we denote by $F(P, Q, \mu_0, x)$ the characteristic polynomial of $B_{0,P,Q}(x)$, taking implicit derivatives of the equation $F(P, Q, \mu_0, x) = 0$ with respect to P and Q we obtain

$$\frac{\partial \mu_0}{\partial P} = \frac{-m'_1(P)(\mu_0(P, Q, x) + m_2(Q))}{2\mu_0(P, Q, x) + x + m_1(P) + m_2(Q)},$$

$$\frac{\partial \mu_0}{\partial Q} = \frac{-m'_2(Q)(\mu_0(P, Q, x) + x + m_1(P))}{2\mu_0(P, Q, x) + x + m_1(P) + m_2(Q)}.$$

Since $\mu_0(P, Q, x) + m_2(Q) > 0$, $\mu_0(P, Q, x) + x + m_1(P) > 0$, $2\mu_0(P, Q, x) + x + m_1(P) + m_2(Q) > 0$ and the mortality rates are increasing functions we conclude that $\frac{\partial \tilde{\mu}_0}{\partial P} < 0$ and $\frac{\partial \tilde{\mu}_0}{\partial Q} < 0$. □

We proceed with the study of the solutions of System (4.2) when ε goes to zero.

In order to be able to apply the results of Section 3.3 we need the following lemmas.

Proposition 4.2.22 *Let $\vec{u}_{\varepsilon,P,Q}(x)$ be the (normalized positive) eigenfunction corresponding to the dominant eigenvalue $\lambda_\varepsilon(P, Q)$ of the operator $A_{\varepsilon,P,Q}$ given by (4.2). Let $\mu_0(P, Q, x)$ be the dominant eigenvalue of the matrix $B_{0,P,Q}(x)$ defined in (4.14) and let $x(P, Q)$ be the point where the maximum of $\mu_0(P, Q, x)$ is attained.*

There exists a bounded interval of $(0, \infty)$, K , with $x(P, Q) \in K$ and such that

$$\int_{K^c} u_{\varepsilon,P,Q}^i(x) dx \xrightarrow{\varepsilon \rightarrow 0} 0 \quad i = 1, 2,$$

uniformly with respect to P and Q on compact sets.

Proof:

By Proposition 3.3.1 we have $\lambda_\varepsilon(P, Q) \xrightarrow{\varepsilon \rightarrow 0} \mu_0(P, Q, x(P, Q)) \geq \mu_0(P, Q, x)$ for all x .

Let us take an open interval K containing $x(P, Q)$ and ε_0 such that for $0 \leq \varepsilon \leq \varepsilon_0$ and $x \in K^c$,

$$\lambda_\varepsilon(P, Q) > \mu_0(P, Q, x) = \sup\{\mu \in \mathbb{R} : B_0(P, Q, x)\vec{v} \geq \mu\vec{v}$$

$$\text{for some } 0 < \vec{v} \in \mathbb{R}^2\}.$$

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Here we understand $\lambda_0(P, Q) = \mu_0(P, Q, x(P, Q))$.

Then for $\varepsilon < \varepsilon_0$ and for all $x \in K^c$, there exists $i \in \{1, 2\}$ such that

$$(B_0(P, Q, x)u_{\varepsilon, P, Q}(x))^i - \lambda_\varepsilon(P, Q)u_{\varepsilon, P, Q}^i(x) < 0. \quad (4.17)$$

As for $i = 2$ we have

$$(B_0(P, Q, x)u_{\varepsilon, P, Q}(x))^2 = (A_{\varepsilon, P, Q}u_{\varepsilon, P, Q}(x))^2 = \lambda_\varepsilon(P, Q)u_{\varepsilon, P, Q}^2(x) \quad (4.18)$$

the inequality (4.17) must hold for $i = 1$.

So, for $x \in K^c$, using (4.17) and (4.18),

$$\begin{aligned} 0 &= ((A_{\varepsilon, P, Q} - \lambda_\varepsilon(P, Q)I)u_{\varepsilon, P, Q}(x))^1 \\ &= (B_{\varepsilon, P, Q}(x)u_{\varepsilon, P, Q}(x))^1 - \lambda_\varepsilon(P, Q)u_{\varepsilon, P, Q}^1(x) + \varepsilon(Tu_{\varepsilon, P, Q}(x))^1 \\ &\leq (B_0(P, Q, x)u_{\varepsilon, P, Q}(x))^1 - \lambda_\varepsilon(P, Q)u_{\varepsilon, P, Q}^1(x) + \varepsilon(Tu_{\varepsilon, P, Q}(x))^1 \\ &= \left(-m_1(P) - x + \frac{xb(x)}{\lambda_\varepsilon(P, Q) + m_2(Q)} - \lambda_{\varepsilon, P, Q}\right)u_{\varepsilon, P, Q}^1(x) \\ &\quad + \varepsilon \int_0^\infty b(y)\gamma(x, y)u_{\varepsilon, P, Q}^2(y)dy \end{aligned} \quad (4.19)$$

where we have used (4.18), (that is $(B_0(P, Q, x)u_{\varepsilon, P, Q}(x))^2 = \lambda_\varepsilon(P, Q)u_{\varepsilon, P, Q}^2(x)$,

i.e., $u_{\varepsilon, P, Q}^2(x) = \frac{xu_{\varepsilon, P, Q}^1(x)}{\lambda_\varepsilon(P, Q) + m_2(Q)}$) and the inequality

$$((B_{\varepsilon, P, Q}(x)u_{\varepsilon, P, Q}(x))^1 \leq (B_0(P, Q, x)u_{\varepsilon, P, Q}(x))^1.$$

Since

$$\lim_{x \rightarrow +\infty} \left(-m_1(P) - x + \frac{xb(x)}{\lambda_\varepsilon(P, Q) + m_2(Q)} - \lambda_\varepsilon(P, Q)\right) = -\infty$$

and

$$\lim_{x \rightarrow 0} \left(-m_1(P) - x + \frac{xb(x)}{\lambda_\varepsilon(P, Q) + m_2(Q)} - \lambda_\varepsilon(P, Q)\right) = -m_1(P) - \lambda_\varepsilon(P, Q) < 0$$

(because $\lambda_\varepsilon(P, Q) = s(A_{\varepsilon, P, Q}) > s(B_{\varepsilon, P, Q}) \geq \mu_\varepsilon(P, Q, x) > -\min(m_1(P), m_2(Q))$ see the proof of Lemma 4.2.6), both limits uniformly with respect to ε , P and Q (on compact sets), and using (4.17), the Weierstrass theorem and the continuity of $\lambda_\varepsilon(P, Q)$ with respect to ε , P , Q , we obtain that

$$-m_1(P) - x + \frac{xb(x)}{\lambda_\varepsilon(P, Q) + m_2(Q)} - \lambda_\varepsilon(P, Q) \leq -C$$

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for a constant $C > 0$ independent of $\varepsilon \in [0, \varepsilon_0)$ and P, Q in a compact set contained in the region defined by hypothesis (4.4).

Therefore, inequality (4.19) implies

$$0 \leq -C u_{\varepsilon, P, Q}^1(x) + \varepsilon \int_0^\infty b(y) \gamma(x, y) u_{\varepsilon, P, Q}^2(y) dy.$$

Integrating with respect to x in K^c the last inequality we get

$$-C \int_{K^c} u_{\varepsilon, P, Q}^1(x) dx + \varepsilon \int_{K^c} \int_0^\infty b(y) \gamma(x, y) u_{\varepsilon, P, Q}^2(y) dy dx \geq 0.$$

As $\int_{K^c} \gamma(x, y) dx \leq 1$, $b(y) \leq b(0)$ and $\int_0^\infty u_{\varepsilon, P, Q}^2(y) dy \leq 1$, then

$$\int_{K^c} \int_0^\infty b(y) \gamma(x, y) u_{\varepsilon, P, Q}^2(y) dy dx \leq b(0).$$

So $-C \int_{K^c} u_{\varepsilon, P, Q}^1(x) dx + \varepsilon b(0) \geq 0$ and thus

$$\int_{K^c} u_{\varepsilon, P, Q}^1(x) dx \xrightarrow{\varepsilon \rightarrow 0} 0.$$

For the second component applying the equality (4.18) in (4.19) (in this case that $u_{\varepsilon, P, Q}^1(x) = \frac{\lambda_{\varepsilon, P, Q} + m_2(Q)}{x} u_{\varepsilon, P, Q}^2(x)$) we get

$$\begin{aligned} 0 &\leq \left(\frac{(-m_1(P) - x)}{x} (\lambda_\varepsilon(P, Q) + m_2(Q)) + b(x) - \frac{\lambda_\varepsilon(P, Q) (\lambda_\varepsilon(P, Q) + m_2(Q))}{x} \right) u_{\varepsilon, P, Q}^2(x) \\ &+ \int_0^\infty b(y) \gamma(x, y) u_{\varepsilon, P, Q}^2(y) dy. \end{aligned} \tag{4.20}$$

Using again (4.17), the Weierstrass theorem, the continuity of $\lambda_\varepsilon(P, Q)$ with respect to ε, P, Q , and the fact that

$$\lim_{x \rightarrow +\infty} \left((\lambda_\varepsilon(P, Q) + m_2(Q)) \left(\frac{-m_1(P) - \lambda_\varepsilon(P, Q)}{x} - 1 \right) + b(x) \right) < 0,$$

$$\lim_{x \rightarrow 0} \left((\lambda_\varepsilon(P, Q) + m_2(Q)) \left(\frac{-m_1(P) - \lambda_\varepsilon(P, Q)}{x} - 1 \right) + b(x) \right) = -\infty,$$

(where again we have used that $\lambda_\varepsilon(P, Q) = s(A_{\varepsilon, P, Q}) > s(B_{\varepsilon, P, Q}) \geq \mu_\varepsilon(P, Q, x) > -\min(m_1(P), m_2(Q))$),

we obtain that

$$\left(\frac{-m_1(P) - x}{x} (\lambda_\varepsilon(P, Q) + m_2(Q)) + b(x) - \frac{\lambda_\varepsilon(P, Q)(\lambda_\varepsilon(P, Q) + m_2(Q))}{x} \right) \leq -C$$

for a constant $C > 0$ independent of $\varepsilon \in [0, \varepsilon_0)$ and P, Q in a compact set contained in the region defined by hypothesis (4.4).

By the same argument as for the first component we obtain the convergence. \square

The following result gives the existence of stationary solutions of System (4.2).

Theorem 4.2.23 *Let us assume that the conditions*

$$\begin{aligned} m_2(0) &< \max_x \left(\frac{xb(x)}{m_1(0)+x} \right) \\ m_2(\infty) &> \max_x \left(\frac{xb(x)}{m_1(\infty)+x} \right) \end{aligned} \tag{4.21}$$

hold. Then, for ε small enough there exists a solution $(P_\varepsilon, Q_\varepsilon)$ of (4.13) and therefore a nontrivial equilibrium of System (4.2) (of the form $(P_\varepsilon + Q_\varepsilon)\vec{u}_{\varepsilon, P_\varepsilon, Q_\varepsilon}(x)$).

Moreover, it satisfies

$$P_\varepsilon \xrightarrow{\varepsilon \rightarrow 0} P_0,$$

$$Q_\varepsilon \xrightarrow{\varepsilon \rightarrow 0} Q_0,$$

where (P_0, Q_0) is the solution of (4.15).

Proof: We have seen in Lemma 4.2.20 and Lemma 4.2.21 that the functions $\lambda_\varepsilon(P, Q)$ and $\tilde{\mu}_0(P, Q)$ are strictly decreasing with respect to P and Q .

Then, their zero level curves define functions $Q = g_\varepsilon(P)$ and $Q = g_0(P)$.

From the continuity of g_ε, g_0 and Proposition 3.3.1 we can say that

$$g_\varepsilon(P) \xrightarrow{\varepsilon \rightarrow 0} g_0(P).$$

The solution set of System (4.13) is the intersection of the zero level curve of $\Psi_\varepsilon(P, Q)$ with the graph of the function $g_\varepsilon(P)$ and the solution set of System (4.15) is the intersection of the zero level curve of $\Psi_0(P, Q)$ with the graph of the function $g_0(P)$.

4.2.3. Steady states

The statement of the proposition will be proved showing that a family of zeros of the function

$$\Phi_\varepsilon(P) := \frac{\int_0^\infty u_{\varepsilon,P,g_\varepsilon(P)}^1(x)dx}{\int_0^\infty u_{\varepsilon,P,g_\varepsilon(P)}^2(x)dx} - \frac{P}{g_\varepsilon(P)}$$

tend, when ε goes to zero, to the zero of the function

$$\Phi_0(P) := \frac{u_{0,P,g_0(P)}^1(x(P, g_0(P)))}{u_{0,P,g_0(P)}^2(x(P, g_0(P)))} - \frac{P}{g_0(P)}.$$

By Theorem 3.3.4

$$\int_0^\infty u_{\varepsilon,P,Q}^1(x)dx \xrightarrow{\varepsilon \rightarrow 0} u_{0,P,Q}^1(x(P, Q))$$

$$\int_0^\infty u_{\varepsilon,P,Q}^2(x)dx \xrightarrow{\varepsilon \rightarrow 0} u_{0,P,Q}^2(x(P, Q))$$

So $\Phi_\varepsilon(P) \xrightarrow{\varepsilon \rightarrow 0} \Phi_0(P)$.

Then by Lemma 2.5.13 in Chapter 2 it only remains to show that $\Phi_0(P)$ changes sign and that the zero is isolated.

In Chapter 1 it was shown that there exists \hat{P} such that $\Phi_0(\hat{P}) = 0$ because it corresponds to a solution (\hat{x}, P_0, Q_0) (where $\hat{x} = x(P_0, Q_0)$) of (4.15) which, recall, is the following system

$$\begin{cases} \tilde{\mu}_0(P, Q) = 0, \\ \Psi_0(P, Q) = 0, \end{cases}$$

that is, an equilibrium solution of the system

$$\begin{pmatrix} u_t \\ v_t \end{pmatrix} = \begin{pmatrix} -m_1(P) - x & b(x) \\ x & -m_2(Q) \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix}$$

for an evolutionarily stable parameter value \hat{x} .

We will finish the proof showing that $\Phi_0(P)$ is a strictly decreasing function.

An explicit computation of the eigenvector gives

$$\Phi_0(P) = \frac{m_2(g_0(P))}{x(P, g_0(P))} - \frac{P}{g_0(P)}.$$

4.2.3. Steady states

Since $g_0(P)$ is a strictly decreasing function we only have to show that $x(P, g_0(P))$ is a strictly increasing function.

Taking implicit derivatives with respect to x of the equation $F(P, Q, \mu_0, x) = 0$ (where, as in the proof of Lemma 4.2.21 $F(P, Q, \mu_0, x)$ denotes the characteristic polynomial of $B_{0,P,Q}(x)$) we obtain that

$$\frac{\partial x}{\partial P} = \frac{\frac{\partial \mu_0}{\partial P}}{(xb(x))''} \quad \text{and} \quad \frac{\partial x}{\partial Q} = \frac{\frac{\partial \mu_0}{\partial Q} + m'_2(Q)}{(xb(x))''}.$$

From the explicit computation of $\frac{\partial \mu_0}{\partial P}$ and $\frac{\partial \mu_0}{\partial Q}$ in the proof of Lemma 4.2.21 and the fact that $(xb(x))'' < 0$ we conclude that $\frac{\partial x}{\partial P} > 0$ and $\frac{\partial x}{\partial Q} < 0$, and from this we obtain that

$$\frac{\partial x(P, g_0(P))}{\partial P} = \frac{\partial x}{\partial P} + \frac{\partial x}{\partial Q} g'_0(P) > 0,$$

and the proof is complete. □

Theorem 4.2.24 *Let $\mu_0(P, Q, x)$ be the dominant eigenvalue of the matrix $B_{0,P,Q}(x)$ defined in (4.14) and let $\vec{u}_{0,P,Q}(x)$ be the corresponding normalized positive eigenvector. Let $x(P, Q)$ be the point where the maximum of $\mu_0(P, Q, x)$ is attained. Let (P_0, Q_0) be the solution of (4.15). Let us denote by $\{\vec{u}_\varepsilon(x)\}_{\varepsilon \geq 0}$ the family $\{(P_\varepsilon + Q_\varepsilon)\vec{u}_{\varepsilon,P_\varepsilon,Q_\varepsilon}(x)\}_{\varepsilon \geq 0}$ of stationary solutions given by Theorem 4.2.23. Let us denote by \hat{x} the value $x(P_0, Q_0)$.*

Then

$$\vec{u}_\varepsilon(x) \xrightarrow{\varepsilon \rightarrow 0} (P_0 + Q_0)\vec{u}_{0,P_0,Q_0}(\hat{x})\delta_{\hat{x}}$$

in the weak star topology.

Moreover, for any bounded interval of $(0, \infty)$, K , containing \hat{x} ,

$$\int_{K^c} u_{\varepsilon,P_\varepsilon,Q_\varepsilon}^i(x) dx \xrightarrow{\varepsilon \rightarrow 0} 0 \quad i = 1, 2.$$

Proof: Let us note that in Chapter 3 $P_\varepsilon + Q_\varepsilon$ and that $P_0 + Q_0$ are called c_ε and c_0 respectively. By Proposition 4.2.22 we have the existence of a bounded interval K satisfying that $\int_{K^c} u_{\varepsilon,P_\varepsilon,Q_\varepsilon}^i(x) dx \xrightarrow{\varepsilon \rightarrow 0} 0 \quad i = 1, 2$.

Since we are in the hypotheses of Sections 3.3 and 3.4, Theorem 3.4.3 gives the convergence of \vec{u}_ε .

By Lemma 2.5.7, the second part of the statement follows. □

Summarizing, under reasonable hypotheses, we have proved (as for the model in Chapter 2) the existence of a family of equilibrium solutions $\vec{u}_\varepsilon(x)$

4.3. Finite dimensional predator prey model

of System (2.1) that, when the probability of the mutation (ε) tends to zero, tend to concentrate at the ESS value \hat{x} of the finite dimensional age at maturity model (1.1). Moreover, the total population at equilibrium of System (2.1) (the integral of $\vec{u}_\varepsilon(x)$) tends to the equilibrium of (1.1) for the value \hat{x} of the parameter.

4.3 Finite dimensional predator prey model

4.3.1 Introduction

The rest of the chapter will be devoted to the application of the convergence results for the equilibria of some (abstract quasilinear) equations obtained in Section 3.4 to a predator prey model.

We consider a general predator prey Rosenzweig-MacArthur model consisting on two ordinary differential equations depending on a parameter x (that will be considered an evolutionary variable) and such that the so called “functional response” (defined by Solomon in [57] in terms of the relationship between the number of prey consumed per unit of time per predator and the prey density) will be given by a Holling’s type 2 functional response (see [26], [52], [37]).

We will find necessary conditions to guarantee existence and uniqueness of a globally asymptotically stable non trivial equilibrium and also necessary conditions to guarantee existence and uniqueness of a convergence stable evolutionarily stable strategy value of the phenotypic variable.

4.3.2 Description of the model

Let $f(t)$ denote the number of individuals of a prey population at time t and $u(t)$ the number of individuals of a predator population at time t , feeding on the former.

Let us assume that in absence of predators, the prey population follows a logistic growth law, i.e.,

$$f' = af - \mu f^2,$$

where a is the intrinsic growth rate of the prey and μ the competition coefficient among preys.

The parameter x will denote the “index of activity of the predator population during daytime”. We assume that the searching efficiency of the predator will depend on the parameter x in an increasing way. It will be denoted by $\beta(x)$.

We also assume that the mortality rate of the predator population will depend on the parameter x in an increasing way due to a bigger risk of being captured by another predator when the index of activity is bigger. It will be denoted by $d(x)$.

Predation rate is simulated using the Holling's "disc equation" of functional response, i.e., the expected number of prey consumed by a predator during a hunting session is given by

$$f_p = \frac{\beta(x)ft}{1 + \beta(x)hf} \quad (4.22)$$

where h is the time spent handling individual prey.

This comes from the following argument : the number of prey consumed by a predator during a hunting session depends on the searching efficiency, the time spent searching (we denote it by s) and the number of prey, i.e.,

$$f_p = \beta(x)sf. \quad (4.23)$$

As the total time t is the searching time plus the handling time times the prey consumed,

$$t = s + hf_p, \quad (4.24)$$

isolating s in (4.24) and substituting it in (4.23) we obtain (4.22).

Therefore, the rate of prey consumption by all predators per unit time is

$$\frac{f_p u}{t} = \frac{\beta(x)fu}{1 + \beta(x)hf}.$$

Finally, let us denote by α the energy that the prey consumption gives to the predator.

The following system of ordinary differential equations models the population

$$\begin{cases} f'(t) = (a - \mu f(t) - \frac{\beta(x)u(t)}{1 + \beta(x)hf(t)})f(t), \\ u'(t) = (\alpha \frac{\beta(x)f(t)}{1 + \beta(x)hf(t)} - d(x))u(t), \end{cases} \quad (4.25)$$

where $\beta(x)$ and $d(x)$ are increasing bounded functions of x , satisfying $\beta(0) = 0$ and $d(0) = d > 0$ whereas a, μ, h and x are positive numbers.

4.3.3 Ecological Dynamics

In this section we are going to study the equilibria of System (4.25) and its stability.

4.3.3. Ecological Dynamics

EQUILIBRIA

In case of zero predator population ($u = 0$) we obtain two equilibria that are $(0, 0)$ and $(\frac{a}{\mu}, 0)$.

In case of non zero predator population, from the second equation of (4.25) we obtain that the equality

$$\alpha \frac{\beta(x)f}{1 + \beta(x)hf} = d(x)$$

must hold. Isolating f we obtain the first component of the third equilibrium point which is

$$f(x) = \frac{d(x)}{\beta(x)(\alpha - d(x)h)}. \quad (4.26)$$

As f denotes the prey population, we are only interested in positive equilibria. Let us note that (4.26) is positive if and only if

$$\alpha > d(x)h. \quad (4.27)$$

Substituting f in the first equation of (4.25) (and assuming $f \neq 0$ because otherwise we would obtain the trivial equilibrium again) we derive the second component of the third equilibrium point which is

$$u = \frac{\alpha(a\beta(x)(\alpha - d(x)h) - \mu d(x))}{\beta(x)^2(\alpha - d(x)h)^2}. \quad (4.28)$$

Let us note that u is positive if and only if $a\beta(x)(\alpha - d(x)h) - \mu d(x) > 0$, that is,

$$\alpha > \frac{a\beta(x)d(x)h + \mu d(x)}{a\beta(x)}, \quad (4.29)$$

or, equivalently,

$$\mu < \frac{a\beta(x)(\alpha - d(x)h)}{d(x)}. \quad (4.30)$$

Remark 4.3.1 Hypothesis (4.29) includes the hypothesis $\alpha > d(x)h$ because

$$\frac{a\beta(x)d(x)h + \mu d(x)}{a\beta(x)} \geq d(x)h.$$

Remark 4.3.2 A necessary condition in order that there exists x satisfying (4.27) is $d(0) < \frac{\alpha}{h}$.

A sufficient condition in order that there exists x satisfying (4.29) is

$$\frac{\mu}{a}d(\infty) < \beta(\infty)(\alpha - d(\infty)h) \quad (4.31)$$

where $\beta(\infty) := \lim_{x \rightarrow \infty} \beta(x)$.

Note that (4.31) is equivalent to $d(\infty) < \frac{\alpha}{\frac{\mu}{a\beta(\infty)} + h}$ so it implies $d(0) < \frac{\alpha}{h}$.

Therefore we have obtained, three equilibrium points of System (4.25), namely,

$$(f_1, u_1) = (0, 0),$$

$$(f_2, u_2) = \left(\frac{a}{\mu}, 0\right),$$

$$(f_3, u_3) = \left(\frac{d(x)}{\beta(x)(\alpha - d(x)h)}, \frac{\alpha(a\beta(x)(\alpha - d(x)h) - \mu d(x))}{\beta(x)^2(\alpha - d(x)h)^2}\right).$$

LOCAL STABILITY

The differential matrix of System (4.25) is

$$D = \begin{pmatrix} a - 2\mu f - \frac{\beta(x)u}{(1 + \beta(x)hf)^2} & -\frac{\beta(x)f}{1 + \beta(x)hf} \\ \frac{\alpha\beta(x)u}{(1 + \beta(x)hf)^2} & \frac{\alpha\beta(x)f}{1 + \beta(x)hf} - d(x) \end{pmatrix}.$$

The matrix D evaluated at the equilibrium point $(f_1, u_1) = (0, 0)$ has eigenvalues $\lambda_1 = a$ and $\lambda_2 = -d(x)$. Therefore the trivial equilibrium point is unstable.

4.3.3. Ecological Dynamics

The matrix D evaluated at the equilibrium point $(f_2, u_2) = (\frac{a}{\mu}, 0)$ is

$$\begin{pmatrix} -a & -\frac{\beta(x)\frac{a}{\mu}}{1 + \beta(x)h\frac{a}{\mu}} \\ 0 & \frac{\alpha\beta(x)\frac{a}{\mu}}{1 + \beta(x)h\frac{a}{\mu}} - d(x) \end{pmatrix}.$$

Let us note that under the hypothesis (4.29) (of existence of a positive interior equilibrium point (f_3, u_3)), the eigenvalue $\lambda_2 = \frac{\alpha\beta(x)\frac{a}{\mu}}{1 + \beta(x)h\frac{a}{\mu}} - d(x)$ of the

former matrix is strictly positive and therefore we can conclude that the equilibrium point (f_2, u_2) is unstable under the condition of existence of a positive interior equilibrium point. Moreover, (f_2, u_2) is asymptotically stable whenever (f_3, u_3) is not positive.

Finally, computing the determinant of the differential matrix evaluated at the point (f_3, u_3) we obtain (using that $\frac{\alpha\beta(x)f_3}{1 + \beta(x)hf_3} - d(x) = 0$),

$$\det(D|_{(f_3, u_3)}) = \left(\frac{\beta(x)f_3}{1 + \beta(x)hf_3}\right) \left(\frac{\alpha\beta(x)u_3}{(1 + \beta(x)hf_3)^2}\right) > 0.$$

Computing the trace of the differential matrix evaluated at the equilibrium point (f_3, u_3) (using that $\frac{\alpha\beta(x)f_3}{1 + \beta(x)hf_3} - d(x) = 0$ and $\frac{\beta(x)u_3}{1 + \beta(x)hf_3} = a - \mu f_3$) we obtain

$$\begin{aligned} \text{trace}(D|_{(f_3, u_3)}) &= a - 2\mu f_3 - \frac{\beta(x)u_3}{(1 + \beta(x)hf_3)^2} \\ &= \frac{a(\beta(x)hf_3) - \mu f_3(1 + 2\beta(x)hf_3)}{1 + \beta(x)hf_3}. \end{aligned}$$

It can be easily proved that under the condition

$$\mu > \frac{a\beta(x)h(\alpha - d(x)h)}{\alpha + d(x)h}$$

the trace is strictly negative and then (f_3, u_3) is locally stable. Therefore, we have proved the following

Theorem 4.3.3 *Let $x \in (0, \infty)$ satisfying*

$$\frac{a\beta(x)h(\alpha - d(x)h)}{\alpha + d(x)h} < \mu < \frac{a\beta(x)(\alpha - d(x)h)}{d(x)}.$$

Then System (4.25) has a positive interior locally stable equilibrium point.

GLOBAL STABILITY

In order to prove global stability of the interior equilibrium point (f_3, u_3) we will use the same argument as in Lemma 2 in [44].

Lemma 4.3.4 *Let us assume $ah\beta(x) \leq \mu < a\beta(x)\frac{\alpha - d(x)h}{d(x)}$ holds for some $x \in (0, \infty)$. Then the equilibrium point (f_3, u_3) is globally asymptotically stable in the open first quadrant.*

Remark 4.3.5 *Let us note that if $\mu \geq ah\beta(x)$ then $\mu > \frac{a\beta(x)h(\alpha - d(x)h)}{\alpha + d(x)h}$ (condition for the local stability of the positive interior equilibrium) holds automatically.*

Proof: Let us consider the function

$$H(f, u) := \frac{1 + \beta(x)hf}{\beta(x)uf}.$$

Obviously if $f > 0$ and $u > 0$, $H(f, u) > 0$.

If we denote by

$$G_1(f, u) := \left(a - \mu f - \frac{\beta(x)u}{1 + \beta(x)hf}\right)f,$$

$$G_2(f, u) = \left(\alpha \frac{\beta(x)f}{1 + \beta(x)hf} - d(x)\right)u,$$

we have that

$$\frac{\partial}{\partial f}(G_1H) + \frac{\partial}{\partial u}(G_2H) = \frac{a\beta(x)h - \mu - 2\mu\beta(x)hf}{\beta(x)u}.$$

Under the hypothesis $\mu \geq ah\beta(x)$ we have that $\frac{\partial}{\partial f}(G_1H) + \frac{\partial}{\partial u}(G_2H) < 0$ and by the Bendixson-Dulac criterion we will not have periodic orbits in the first quadrant. This proves the lemma. \square

4.3.4. Adaptive Dynamics

4.3.4 Adaptive Dynamics

Let us remark that in model (4.25) the environment reduces to the prey population number f and hence, it is one-dimensional. This allows us to compute the evolutionarily stable strategy in a different way than the one we used in Chapter 1 (see [42]) because when the environment is one-dimensional the following result can be used

Proposition 4.3.6 [42] *Let φ be the function that gives, for every resident population with evolutionary trait x , the environment f_x for which it is in ecological equilibrium, i.e. $\varphi(x) = f_x$, and $\lambda(x, y) := \lambda(f_x, y)$ the fitness of the mutant population.*

If the environment is one-dimensional and $f \rightarrow \lambda(f, y)$ is decreasing (increasing), then \hat{x} is an ESS if and only if the function φ has a maximum (minimum) in $x = \hat{x}$.

Let us note that in model (4.25) only the predator evolves. The fitness of the mutant is given by

$$\lambda(f_x, y) = \frac{\alpha\beta(y)f_x}{1 + \beta(y)hf_x} - d(y).$$

This function is increasing with respect to f_x . Indeed,

$$\frac{\partial\lambda(f_x, y)}{\partial f_x} = \frac{\alpha\beta(y)}{(1 + \beta(y)hf_x)^2} > 0.$$

By Proposition 4.3.6 in order to find ESS we have to find minima of the function $x \rightarrow f_x$, i.e.,

$$f(x) = \frac{d(x)}{\beta(x)(\alpha - d(x)h)}.$$

From now on let us assume that the functions involved in the model are such that, for fixed f , the function

$$x \rightarrow \lambda(f, x) = \frac{\alpha\beta(x)f}{1 + \beta(x)hf} - d(x)$$

has a unique critical point which is an absolute maximum that will be denoted by $x(f)$ and moreover that there exists \hat{f} such that

$$\lambda(x(\hat{f}), \hat{f}) = 0. \tag{4.32}$$

Let us denote $x(\hat{f}) := \hat{x}$ (and note that $\hat{f} = f(\hat{x})$).

This hypotheses imply that the function $f(x)$ has a unique absolute minimum, and therefore, that the predator-prey system has a unique evolutionarily stable strategy value.

Indeed, taking derivatives with respect to x in the equation $\lambda(x, f(x)) = 0$ we obtain the equality

$$\lambda_x(x, f(x)) + \lambda_f(x, f(x))f'(x) = 0. \quad (4.33)$$

Using that $\lambda_x(\hat{x}, \hat{f}) = 0$ and that λ is strictly increasing with respect to f we have that $f'(\hat{x}) = 0$.

Taking derivatives with respect to x in (4.33) and evaluating at \hat{x} we obtain that $f''(\hat{x}) > 0$, that is, \hat{x} is a local minimum point of f .

Finally, to show that \hat{x} is an absolute minimum point of f , let us assume that there exists $x_1 \neq \hat{x}$ such that $f(x_1) \leq f(\hat{x})$, then

$$\lambda(x_1, f(\hat{x})) \geq \lambda(x_1, f(x_1)) = 0 = \lambda(\hat{x}, f(\hat{x}))$$

which contradicts the fact that \hat{x} is the absolute maximum of $\lambda(x, \hat{f})$.

Summarizing, we have proved the following

Theorem 4.3.7 *Let us consider the values of x such that*

$$\frac{a\beta(x)h(\alpha - d(x)h)}{\alpha + d(x)h} < \mu < \frac{a\beta(x)(\alpha - d(x)h)}{d(x)}$$

(condition for existence of a locally stable positive equilibrium). Let us assume that, for fixed f , the function

$$x \rightarrow \lambda(f, x) = \frac{\alpha\beta(x)f}{1 + \beta(x)hf} - d(x)$$

has a unique critical point which is an absolute maximum that will be denoted by $x(f)$ and moreover that there exists \hat{f} such that

$$\lambda(x(\hat{f}), \hat{f}) = 0. \quad (4.34)$$

Then $x(\hat{f}) := \hat{x}$ is an ESS of (4.25). Moreover, the ESS is unique.

Remark 4.3.8 *Let us note that the ESS, \hat{x} , is convergence stable because we are in the hypotheses of Proposition 1.5.5 in Chapter 1.*

4.4 Infinite Dimensional Predator Prey Model

4.4.1 Introduction

In this section we formulate an integrodifferential equations model by considering densities of the predators with respect to the evolutionary variable in the ordinary differential equations predator prey model (4.25). We will apply the results of Section 3.4. to the infinite dimensional predator prey model obtaining convergence (when the probability of mutation tends to zero) of the steady states to a Dirac mass concentrated at the ESS value of the ordinary differential equations predator prey model (4.25).

4.4.2 Description of the model

The model equations are:

$$\left\{ \begin{array}{l} f'(t) = (a - \mu f(t) - \int_0^\infty \frac{\beta(x)u(x,t)}{1 + \beta(x)hf(t)} dx) f(t), \\ \frac{\partial u(x,t)}{\partial t} = (1 - \varepsilon) \frac{\alpha\beta(x)f(t)u(x,t)}{1 + \beta(x)hf(t)} + \varepsilon \int_0^\infty \gamma(x,y) \frac{\alpha\beta(y)f(t)u(y,t)}{1 + \beta(y)hf(t)} dy \\ -d(x)u(x,t), \end{array} \right. \quad (4.35)$$

where $u(x,t)$ denotes the density of predator individuals at time t with respect to the trait x that denotes, as in Section 4.3, the index of activity of the predators during daytime.

$\beta(x)$ and $d(x)$ are, as in Section 4.3 increasing bounded functions of $x \in [0, \infty)$ satisfying $\beta(0) = 0$ and $d(0) = d > 0$ and a , μ and h are fixed positive numbers.

Finally, $\gamma(x,y)$ is the density of probability that the trait of the mutant offspring of a predator with trait y is x . The parameter ε stands for the probability of mutation. As in the maturation age model in this chapter, γ is a strictly positive globally lipschitzian function that satisfies $\int_0^\infty \gamma(x,y)dx = 1$ and the improper integral converges uniformly with respect to y on bounded intervals.

4.4.3 Existence and Uniqueness of solutions of the initial value problem

The model (4.35) can be written as

$$\begin{pmatrix} f \\ u \end{pmatrix}' = g \begin{pmatrix} f \\ u \end{pmatrix} \quad (4.36)$$

where

$$g : \mathbb{R} \times L^1(0, \infty) \longrightarrow \mathbb{R} \times L^1(0, \infty)$$

$$(f, u) \longmapsto \begin{pmatrix} (a - \mu f - \int_0^\infty \frac{\beta(x)u(x)}{1 + \beta(x)hf} dx) f \\ (1 - \varepsilon) \frac{\alpha\beta(x)fu(x)}{1 + \beta(x)hf} \\ + \varepsilon \int_0^\infty \gamma(x, y) \frac{\alpha\beta(y)fu(y)}{1 + \beta(y)hf} dy - d(x)u(x) \end{pmatrix}.$$

Our initial value problem is

$$\begin{cases} \begin{pmatrix} f \\ u \end{pmatrix}' = g \begin{pmatrix} f \\ u \end{pmatrix} \\ (f(t_0), u(t_0)) = (f_0, u_0). \end{cases} \quad (4.37)$$

Local existence and uniqueness. Continuous dependence on initial conditions

As g is bounded and Lipschitz in the region $|f - f_0| \leq \delta_1$, $\|u - u_0\| \leq \delta_2$ for some δ_1, δ_2 small enough, Picard's theorem gives us existence and uniqueness of local solutions $(f(t), u(t))$ for $|t - t_0| < t_{\max}(f_0, u_0)$ of the initial value problem (4.37).

Moreover, if $t_{\max}(f_0, u_0) < \infty$ then $\lim_{t \rightarrow \infty} \|(f(t), u(t))\| = \infty$.

Unlike in the previous models, in this one we can use Picard's theorem to obtain existence and uniqueness of local solutions of the initial value problem.

The fact that g is a locally Lipschitzian function also implies that, given $z(t) := (f(t), u(t))$ and $\tilde{z}(t) := (\tilde{f}(t), \tilde{u}(t))$ two solutions of (4.36) with initial conditions $z_0 := (f_0, u_0)$ and $\tilde{z}_0 := (\tilde{f}_0, \tilde{u}_0)$ respectively, the inequality

$$\|z(t) - \tilde{z}(t)\|_{\mathbb{R} \times L^1(0, \infty)} \leq \|z_0 - \tilde{z}_0\|_{\mathbb{R} \times L^1(0, \infty)} e^{L|t-t_0|} \quad (4.38)$$

4.4.3. Existence and uniqueness...

(where L is the Lipschitz constant of g) holds for all $|t - t_0| < \min(t_{\max}(z_0), t_{\max}(\tilde{z}_0))$.

Inequality (4.38) is proved using the integral equation formulation of the Initial Value Problem (i.e. $z(t) = z_0 + \int_{t_0}^t g(z(s), s)ds$) and Gronwall's inequality (for more details see, for instance, [25]).

From (4.38) we obtain continuous dependence on initial conditions of the Initial Value Problem.

Positivity of solutions and global existence

Let us consider $z_1(t) := (f_1(t), u_1(t))$ a local solution of the initial value problem (4.37), with $t_0 = 0$, $f_0 > 0$, $u_0 > 0$. We claim that $f_1(t)$ is positive. Indeed, if we consider $T = \inf\{t : f_1(t) = 0\}$ then $(f_1(t), u_1(t))$ is a solution of the initial value problem

$$\left\{ \begin{array}{l} f'(t) = (a - \mu f(t) - \int_0^\infty \frac{\beta(x)u(x,t)}{1 + \beta(x)hf(t)} dx) f(t), \\ \frac{\partial u(x,t)}{\partial t} = (1 - \varepsilon) \frac{\alpha\beta(x)f(t)u(x,t)}{1 + \beta(x)hf(t)} + \varepsilon \int_0^\infty \gamma(x,y) \frac{\alpha\beta(y)f(t)u(y,t)}{1 + \beta(y)hf(t)} dy \\ \quad - d(x)u(x,t), \\ (f(T), u(T)) = (0, u_1(T)). \end{array} \right. \quad (4.39)$$

As $z_2(t) := (f_2(t), u_2(t))$ where $f_2(t) \equiv 0$ and $u_2(t) = u_1(T)e^{-d(x)(t-T)}$ is also a solution of (4.39) it contradicts the uniqueness of local solution of the initial value problem (4.39) (note that $f_1(t)$ is not identically 0 because $f_1(0) = f_0 > 0$).

From the first equation

$$f'(t) = (a - \mu f(t) - \int_0^\infty \frac{\beta(x)u(x,t)}{1 + \beta(x)hf(t)} dx) f(t),$$

we can see that if $\frac{a}{\mu} < f(t)$ then $f'(t) < 0$. Therefore $f(t)$ is bounded above in $[0, t_{\max}]$ (and we have just seen that it is bounded below by 0).

So we have that, if $f_0 > 0$, the first component of the local solution of the Initial Value Problem (4.37) is positive, and moreover, that the first component of a solution of (4.37) is bounded for positive t .

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In order to prove the positivity of u , let us note that the equation

$$\begin{aligned} \frac{\partial u(x, t)}{\partial t} &= (1 - \varepsilon) \frac{\alpha\beta(x)f(t)u(x, t)}{1 + \beta(x)hf(t)} + \varepsilon \int_0^\infty \gamma(x, y) \frac{\alpha\beta(y)f(t)u(y, t)}{1 + \beta(y)hf(t)} dy \\ &\quad - d(x)u(x, t), \end{aligned}$$

can be written as

$$u_t = Au + B(t)u, \tag{4.40}$$

where

$$Au := -d(x)u,$$

$$B(t)u := (1 - \varepsilon) \frac{\alpha\beta(x)f(t)u(x)}{1 + \beta(x)hf(t)} + \varepsilon \int_0^\infty \gamma(x, y) \frac{\alpha\beta(y)f(t)u(y)}{1 + \beta(y)hf(t)} dy.$$

A local solution of the initial value problem

$$\begin{cases} u_t = Au + B(t)u, \\ u(0) = u_0. \end{cases} \tag{4.41}$$

satisfies the integral equation

$$u(t) = e^{tA}u_0 + \int_0^t e^{(t-s)A}B(s)u(s)ds \tag{4.42}$$

(see [48]) where e^{tA} is the positive semigroup generated by the operator A (that satisfies $\|e^{tA}\| \leq Me^{wt}$).

Since we have just proved that $f(t)$ is positive and bounded, $B(t)$ is a positive and bounded linear operator (for all t). Therefore, if u_0 is positive, by (4.42) $u(t)$ is positive.

So far we have proved existence and uniqueness of positive local solutions of the initial value problem (4.37). In order to obtain global existence of solutions of the initial value problem (4.37) we only have to prove that, if $t_{\max} < \infty$,

$$\lim_{t \rightarrow t_{\max}} \|z(t)\| < \infty$$

where $z(t)$ is a local solution of the initial value problem (4.37) defined in $(0, t_{\max})$.

4.4.4. Equilibria and small mutation rate

We have already showed that the first component of a positive solution $f(t)$ satisfies $\limsup_{t \rightarrow \infty} f(t) < \infty$.

From (4.42) we have that

$$\|u(t)\| \leq M e^{wt} \|u_0\| + B M e^{wt} \int_0^t e^{-ws} \|u(s)\| ds,$$

(where $\sup_{0, t_{\max}} \|B(t)\| = B < \infty$) that is,

$$\|u(t)\| e^{-wt} \leq M \|u_0\| + B M \int_0^t e^{-ws} \|u(s)\| ds.$$

By Gronwall's inequality

$$\|u(t)\| e^{-wt} \leq M \|u_0\| e^{MBt},$$

that is,

$$\|u(t)\| \leq M \|u_0\| e^{(MB+w)t}.$$

Therefore $\limsup_{t \rightarrow t_{\max}} \|z(t)\| < \infty$ if $t_{\max} < \infty$, what implies that the solutions are defined in $[0, \infty)$.

In order to prove that every global solution is positive, the same argument used in Theorem 2.3.10 in Chapter 2 works.

4.4.4 Equilibria and small mutation rate

In this section we will show, using the results of Sections 3.3 and 3.4, the existence of a family of equilibrium solutions of the predator prey model (4.35) converging, when the probability of mutation tends to zero, to a Dirac measure at the ESS value of the finite dimensional predator prey model (4.25).

The (nontrivial) equilibria of (4.35) will be given by the solutions of

$$\begin{aligned} 0 &= a - \mu f - \int_0^\infty \frac{\beta(x)u(x)}{1 + \beta(x)hf} dx, \\ 0 &= (1 - \varepsilon) \frac{\alpha\beta(x)fu(x)}{1 + \beta(x)hf} + \varepsilon \int_0^\infty \gamma(x, y) \frac{\alpha\beta(y)fu(y)}{1 + \beta(y)hf} dy - d(x)u(x) \\ &:= A_{\varepsilon, fu}. \end{aligned} \tag{4.43}$$

4.4.4. Equilibria and small mutation rate

First we will study the eigenvalue problem for the operator $A_{\varepsilon,f}$. We will show that it has a strictly dominant eigenvalue (we will denote it by $\lambda_\varepsilon(f)$) with a corresponding strictly positive normalized eigenfunction $\varphi_{\varepsilon,f}$. The first component of the steady state, f_ε , will then be given by the solution of the equation $\lambda_\varepsilon(f) = 0$ and the second component by $u_\varepsilon := c\varphi_{\varepsilon,f_\varepsilon}$ where c is given by

$$c = \frac{a - \mu f_\varepsilon}{\int_0^\infty \frac{\beta(x)\varphi_{\varepsilon,f_\varepsilon}(x)}{1 + \beta(x)hf_\varepsilon} dx}.$$

The eigenvalue problem

As in Chapter 2 we would like to apply Theorem 2.4.6 to the operator $A_{\varepsilon,f}$ to prove that the spectral bound $s(A_{\varepsilon,f})$ is a strictly dominant eigenvalue. So, we are going to show that $A_{\varepsilon,f}$ satisfies the hypotheses of Theorem 2.4.6. In order to do it we consider $A_{\varepsilon,f}$ as the sum of the two following operators

$$\begin{aligned} (B_{\varepsilon,f}u)(x) &= -d(x)u(x) + (1 - \varepsilon)\frac{\alpha\beta(x)fu(x)}{1 + \beta(x)hf}, \\ (K_{\varepsilon,f}u)(x) &= \varepsilon \int_0^\infty \gamma(x,y)\frac{\alpha\beta(y)fu(y)}{1 + \beta(y)hf} dy. \end{aligned} \tag{4.44}$$

Let us note that, as the function $-d(x) + (1 - \varepsilon)\frac{\alpha\beta(x)f}{1 + \beta(x)hf}$ is bounded, the multiplication operator $B_{\varepsilon,f}$ generates a positive analytic semigroup.

Proposition 4.4.1 *Let $B_{\varepsilon,f}$ and $K_{\varepsilon,f}$ be the operators defined in (4.44). Let $R(\lambda, B_{\varepsilon,f})$ be the resolvent operator of $B_{\varepsilon,f}$. The operator $K_{\varepsilon,f}R(\lambda, B_{\varepsilon,f})$ is compact.*

Proof: As $R(\lambda, B_{\varepsilon,f})$ is a bounded operator it suffices to show that $K_{\varepsilon,f}$ is a compact operator.

This follows by the same method as in the proof of Proposition 4.2.5 (with $\frac{\alpha\beta(y)f}{1 + \beta(y)hf}$ instead of $b(y)$). □

Proposition 4.4.2 *Let $B_{\varepsilon,f}$ and $K_{\varepsilon,f}$ be the operators defined in (4.44). Let $s(B_{\varepsilon,f} + K_{\varepsilon,f})$ be the spectral bound of the operator $B_{\varepsilon,f} + K_{\varepsilon,f}$ and $s(B_{\varepsilon,f})$ the spectral bound of the operator $B_{\varepsilon,f}$. Then $s(B_{\varepsilon,f} + K_{\varepsilon,f}) > s(B_{\varepsilon,f})$.*

4.4.4. Equilibria and small mutation rate

Proof: As in the proof of Proposition 4.2.10 it is enough to show that $s(K_{\varepsilon,f}R(\lambda_1, B_{\varepsilon,f})) \geq 1$ for some $\lambda_1 > s(B_{\varepsilon,f})$.

An explicit computation gives that $(K_{\varepsilon,f}R(\lambda_1, B_{\varepsilon,f})g)(x)$ equals

$$\varepsilon \int_0^\infty \gamma(x, y) \frac{\alpha\beta(y)f}{1 + \beta(y)hf} \frac{g(y)}{\lambda_1 - (1 - \varepsilon)\left(\frac{\alpha\beta(y)f}{1 + \beta(y)hf}\right) + d(y)} dy.$$

Denoting by $p(\varepsilon, \lambda, y) := \lambda - (1 - \varepsilon)\left(\frac{\alpha\beta(y)f}{1 + \beta(y)hf}\right) + d(y)$ we would like to see that there exists $g > 0$ such that

$$(K_{\varepsilon,f}R(\lambda_1, B_{\varepsilon,f})g)(x) = \varepsilon \int_0^\infty \gamma(x, y) \frac{\alpha\beta(y)f}{1 + \beta(y)hf} \frac{g(y)}{p(\varepsilon, \lambda_1, y)} dy \geq g(x)$$

for some $\lambda_1 > s(B_{\varepsilon,f})$.

In the same way as in the proof of Proposition 4.2.10, choosing $g(x) := \chi_{[\hat{x}-\delta, \hat{x}+\delta]}$, δ to be chosen and \hat{x} satisfying

$$\begin{cases} p(\varepsilon, s(B_{\varepsilon,f}), \hat{x}) = 0, \\ \frac{\partial}{\partial y} p(\varepsilon, \lambda, y) |_{(\varepsilon, s(B_{\varepsilon,f}), \hat{x})} = 0, \end{cases}$$

and using the Taylor's formula we obtain (choosing δ small enough), in the same way as in the proof of Proposition 4.2.5, the result. \square

Proposition 4.4.3 *The operator $K_{\varepsilon,f}$ (defined in (4.44)) is irreducible.*

Proof: In the Banach lattice $L^1(0, \infty) \times L^1(0, \infty)$ the quasi-interior points coincide with the functions strictly positive almost everywhere (see [45] p.238). It is obvious that $K_{\varepsilon,f}g$ is a quasi-interior point whenever $g > 0$ (recall that $g > 0$ means $g \geq 0$ and $g \neq 0$). \square

We can now apply Theorem 2.4.6 to the operator $A_{\varepsilon,f}$.

Theorem 4.4.4 *Let $B_{\varepsilon,f}$ and $K_{\varepsilon,f}$ be the operators defined in (4.44). Let $s(B_{\varepsilon,f} + K_{\varepsilon,f})$ be the spectral bound of the operator $B_{\varepsilon,f} + K_{\varepsilon,f}$.*

Then $s(B_{\varepsilon,f} + K_{\varepsilon,f})$ is a strictly dominant eigenvalue of algebraic multiplicity one of the operator $B_{\varepsilon,f} + K_{\varepsilon,f}$.

Moreover the semigroup generated by $B_{\varepsilon,f} + K_{\varepsilon,f}$ is irreducible.

Proof: The operator $B_{\varepsilon,f}$ generates a positive semigroup. $K_{\varepsilon,f}$ is a positive bounded linear operator. Propositions 4.4.1, 4.4.2 and 4.4.3 yield that $K_{\varepsilon,f}R(\lambda, B_{\varepsilon,f})$ is compact, $s(B_{\varepsilon,f} + K_{\varepsilon,f}) > s(B_{\varepsilon,f})$ and $K_{\varepsilon,f}$ is irreducible,

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respectively. Therefore, a direct application of Theorem 2.4.6 in Chapter 2 gives the result. \square

As we mentioned before, in the forthcoming we will denote the dominant eigenvalue of the operator $A_{\varepsilon,f}$ by $\lambda_\varepsilon(f)$.

Theorem 4.4.5 *Let $A_{\varepsilon,f} = B_{\varepsilon,f} + K_{\varepsilon,f}$ be the operator defined in (4.43). There is a unique positive eigenfunction of $A_{\varepsilon,f}$ corresponding to the eigenvalue $\lambda_\varepsilon(f)$ and it is strictly positive.*

Moreover, $\lambda_\varepsilon(f)$ is the only eigenvalue of $A_{\varepsilon,f}$ admitting a positive eigenfunction.

Proof: Applying Theorem 2.4.16 in Chapter 2. \square

We will denote by $\varphi_{\varepsilon,f}$ the family of normalized eigenfunctions corresponding to the eigenvalue $\lambda_\varepsilon(f)$.

Our aim is to apply the results of Sections 3.3 and 3.4 to System (4.25) in order to prove the existence of steady states and to study their behavior when the probability of mutation (ε) is very small.

We are going to prove that System (4.25) satisfies the hypotheses of Section 3.3 in order to be able to use the convergence results obtained there.

In the notation of Section 3.3 we have

$$A_\varepsilon = B_\varepsilon + \varepsilon T \quad \text{where, in this case}$$

$$B_\varepsilon u(x) := -d(x)u(x) + (1 - \varepsilon) \frac{\alpha\beta(x)fu(x)}{1 + \beta(x)hf},$$

$$(Tu)(x) := \int_0^\infty \gamma(x, y) \frac{\alpha\beta(y)fu(y)}{1 + \beta(x)hf} dy.$$

Let us see that we are in the hypotheses of Section 3.3.

- A_ε generates a positive semigroup.
 A_ε is obtained by adding a bounded positive perturbation to the operator B_ε . We have just proved that B_ε generates an analytic and positive semigroup. Therefore A_ε generates an analytic and positive semigroup.
- $s(A_\varepsilon)$ is a dominant eigenvalue of algebraic multiplicity 1 of A_ε with corresponding strictly positive eigenfunction.
This statement has been proved in Theorems 4.4.4 and 4.4.5.
- B_ε is a matrix valued multiplication operator.
In our case $B_\varepsilon = (1 - \varepsilon) \frac{\alpha\beta(x)f}{1 + \beta(x)hf} - d(x)$ that is a one-dimensional multiplication operator.

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- There exists x_ε such that $\mu_\varepsilon(x_\varepsilon) = \max_x \mu_\varepsilon(x)$.

This is equivalent to say that the function $(1 - \varepsilon) \frac{\alpha\beta(x)f}{1 + \beta(x)hf} - d(x)$ has a maximum. This holds by the hypothesis made in Section 4.3.4.

- There exists a unique x_0 such that $\mu_0(x_0) = \max_x \mu_0(x)$.

This is equivalent to say that the function $\frac{\alpha\beta(x)f}{1 + \beta(x)hf} - d(x)$ has a unique maximum point. This holds by the hypothesis made in Section 4.3.4.

- T is a positive bounded operator.

Obvious.

Let us remark that, for this model, also the hypothesis (H) stated in section 3.3 holds. That is, B_ε can be written as $C + (1 - \varepsilon)S$ where

$$\begin{aligned} C &= -d(x) \\ S &= \frac{\alpha\beta(x)f}{1 + \beta(x)hf} \end{aligned}$$

and for all $u \in X^+$ there exists a set of positive measure such that $Su(x) \geq (Tu)(x)$.

Indeed, let us assume that $Su(x) \geq (Tu)(x)$ does not hold. Then for almost all x

$$\frac{\alpha\beta(x)fu(x)}{1 + \beta(x)hf} < \int_0^\infty \gamma(x, y) \frac{\alpha\beta(y)fu(y)}{1 + \beta(y)hf} dy,$$

that is,

$$\int_0^\infty \gamma(x, y) \frac{\alpha\beta(y)fu(y)}{1 + \beta(y)hf} dy - \frac{\alpha\beta(x)fu(x)}{1 + \beta(x)hf} > 0, \quad \text{a.e.}$$

But integrating with respect to x and using that $\int_0^\infty \gamma(x, y) dy = 1$ we obtain

$$\int_0^\infty \int_0^\infty \gamma(x, y) \frac{\alpha\beta(y)fu(y)}{1 + \beta(y)hf} dy - \frac{\alpha\beta(x)fu(x)}{1 + \beta(x)hf} dx = 0$$

a contradiction.

Since we are in the hypotheses of Sections 3.3 and 3.4 let us apply the results obtained there.

Proposition 4.4.6 *Let $A_{\varepsilon, f}$ be the operator defined in (4.43). Let $\lambda_\varepsilon(f)$ be the strictly dominant eigenvalue of $A_{\varepsilon, f}$. Then*

$$\lambda_\varepsilon(f) \xrightarrow{\varepsilon \rightarrow 0} \max_x \left(\frac{\alpha\beta(x)f}{1 + \beta(x)hf} - d(x) \right) := \mu_0(f).$$

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Proof: By Proposition 3.3.1. □

Let us denote by $x(f)$ the point where $\mu_0(f)$ is attained.

Proposition 4.4.7 *For every sequence ε_n going to zero, the sequence $\varphi_{\varepsilon_n, f} \in L^1(0, \infty) \subset M$ (the space of measures of Radon) of normalized eigenfunctions corresponding to the eigenvalues $\lambda_{\varepsilon_n}(f)$ of the operator $A_{\varepsilon_n, f}$ has a subsequence $\varphi_{\varepsilon_{n_k}, f}$ satisfying*

$$\varphi_{\varepsilon_{n_k}, f} \xrightarrow{\varepsilon \rightarrow 0} a\delta_{x(f)}$$

in the weak star topology.

Proof: By Propositions 3.3.2 and 3.3.3, the sequence has a limit that either is zero or it is an eigenfunction of the multiplication operator $\frac{\alpha\beta(x)f}{1 + \beta(x)hf} - d(x)$ of eigenvalue $\mu_0(f)$ (that recall, is the maximum value of the function $\left(\frac{\alpha\beta(x)f}{1 + \beta(x)hf} - d(x)\right)$). This proves the proposition. □

If we prove that there exists a bounded interval K containing the point $x(f)$ such that $\int_{K^c} \varphi_{\varepsilon, f}(x)dx \xrightarrow{\varepsilon \rightarrow 0} 0$ then we have that $a = 1$ in Proposition 4.4.7 (see Lemma 2.5.6 in Chapter 2).

Proposition 4.4.8 *There exists a bounded interval K containing the point $x(f)$ such that*

$$\int_{K^c} \varphi_{\varepsilon, f}(x)dx \xrightarrow{\varepsilon \rightarrow 0} 0$$

uniformly with respect to f , where $\varphi_{\varepsilon, f}$ is the normalized eigenfunction corresponding to the (dominant) eigenvalue $\lambda_{\varepsilon}(f)$ of the operator $A_{\varepsilon, f}$.

Proof: By Proposition 4.4.6 we have

$$\lambda_{\varepsilon}(f) \xrightarrow{\varepsilon \rightarrow 0} \max_x \left(\frac{\alpha\beta(x)f}{1 + \beta(x)hf} - d(x) \right) = \mu_0(f).$$

Therefore, for any K containing $x(f)$ there exists ε_0 such that for $\varepsilon < \varepsilon_0$

$$\lambda_{\varepsilon}(f) > \left(\frac{\alpha\beta(x)f}{1 + \beta(x)hf} - d(x) \right) \quad \text{if } x \in K^c.$$

Integrating over K^c the equality $0 = (A_{\varepsilon, f} - \lambda_{\varepsilon}(f))\varphi_{\varepsilon, f}$ the same argument used in Proposition 2.5.5 in Chapter 2 yields

$$\int_{K^c} \varphi_{\varepsilon, f}(x)dx \xrightarrow{\varepsilon \rightarrow 0} 0.$$

□

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Theorem 4.4.9 *The family of eigenfunctions $\varphi_{\varepsilon,f}$ corresponding to the (dominant) eigenvalue $\lambda_\varepsilon(f)$ of the operators $A_{\varepsilon,f}$ satisfy*

$$\varphi_{\varepsilon,f} \xrightarrow{\varepsilon \rightarrow 0} \delta_{x(f)}$$

in the weak star topology.

Proof: As $\|\varphi_{\varepsilon,f}\| = 1$ by the Banach Alaouglu Theorem any sequence $\varphi_{\varepsilon_n,f}$ with $\varepsilon_n \rightarrow 0$ has a subsequence that converges. By Propositions 4.4.7 and 4.4.8 the limit is $\delta_{x(f)}$ for all of them. This completes the proof. \square

The (first components of the) steady states are given by the solutions of $\lambda_\varepsilon(f) = 0$. We are going to give a result about the monotonicity of the function $\lambda_\varepsilon(f)$ that will give us uniqueness of the steady state (for every ε).

Lemma 4.4.10 *Let $\lambda_\varepsilon(f)$ be the (strictly dominant) eigenvalue of the operator $A_{\varepsilon,f}$. The function $\lambda_\varepsilon(f)$ is strictly increasing with respect to f .*

Proof: Let $f_1 > f_2$. Let us take $u > 0$. Since the function $\frac{f}{1 + \beta(x)hf}$ is strictly increasing with respect to f we have

$$A_{\varepsilon,f_1}u > A_{\varepsilon,f_2}u \quad \text{and} \quad A_{\varepsilon,f_1} \neq A_{\varepsilon,f_2}. \quad (4.45)$$

Since, for any closed linear operators A and B ,

$$R(\lambda, A) - R(\lambda, B) = R(\lambda, A)(A - B)R(\lambda, B)$$

whenever $D(A) = D(B)$ and $\lambda > \max(s(A), s(B))$, inequality (4.45) and the fact that A_{ε,f_1} and A_{ε,f_2} are resolvent positive imply $R(\lambda, A_{\varepsilon,f_1}) \geq R(\lambda, A_{\varepsilon,f_2})$. As by Theorem 4.4.4 the semigroup generated by A_{ε,f_i} is irreducible and $s(A_{\varepsilon,f_i})$ is a pole of the resolvent of A_{ε,f_i} , Proposition 4.2.19 implies $\lambda_\varepsilon(f_1) > \lambda_\varepsilon(f_2)$. \square

We will now formulate two results that, for ε small enough and, under the hypotheses of existence of a locally stable positive equilibrium corresponding to the (unique) ESS value of the finite dimensional predator prey model (4.25), give us existence of a steady state of the infinite dimensional predator prey system (4.35).

Moreover, we will show that, when ε tends to zero, the steady states tend to concentrate at the mentioned ESS value.

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Theorem 4.4.11 *Let $\lambda_\varepsilon(f)$ be the (strictly dominant) eigenvalue of the operator $A_{\varepsilon,f}$. Under the hypotheses of Theorem 4.3.7 and for ε small enough there exists a unique solution f_ε of $\lambda_\varepsilon(f) = 0$ (and therefore a unique interior equilibrium of System (4.35)). Moreover it satisfies*

$$f_\varepsilon \xrightarrow{\varepsilon \rightarrow 0} \hat{f}$$

where \hat{f} is the solution of $\max_x \left(\frac{\alpha\beta(x)f}{1 + \beta(x)hf} - d(x) \right) = 0$.

Proof: By Proposition 4.4.6 and Lemma 2.5.13. □

Theorem 4.4.12 *Let us consider the family $(f_\varepsilon, u_\varepsilon)$ of stationary solutions of (4.35). Let us denote by \hat{x} the value $x(\hat{f})$. Then*

$$u_\varepsilon \xrightarrow{\varepsilon \rightarrow 0} \hat{u}\delta_{\hat{x}}$$

in the weak star topology and

$$f_\varepsilon \xrightarrow{\varepsilon \rightarrow 0} \hat{f}$$

where (\hat{f}, \hat{u}) is the solution of the finite dimensional predator prey model (4.25) when $x = \hat{x}$.

Moreover for any bounded interval of $(0, \infty)$, K , containing \hat{x}

$$\int_{K^c} u_\varepsilon \xrightarrow{\varepsilon \rightarrow 0} 0.$$

Proof: We are reduced to proving the result for the second component $\vec{u}_\varepsilon = c_\varepsilon \varphi_{\varepsilon, f_\varepsilon}$ of the steady state because Theorem 4.4.11 gives the result for the first component.

By the Banach Alaoglu Theorem we obtain, with the same argument used to prove Theorem 3.4.3, that

$$\varphi_{\varepsilon, f_\varepsilon} \xrightarrow{\varepsilon \rightarrow 0} b\delta_{\hat{x}} \quad \text{for } b \geq 0.$$

Moreover, by Proposition 4.4.8 there exists K such that

$$\int_{K^c} \varphi_{\varepsilon, f_\varepsilon}(x) dx \xrightarrow{\varepsilon \rightarrow 0} 0$$

which implies that $b = 1$.

Finally,

$$c_\varepsilon = \frac{a - \mu f_\varepsilon}{\int_0^\infty \frac{\beta(x)\varphi_{\varepsilon, f_\varepsilon}(x)}{1 + \beta(x)hf_\varepsilon} dx} \xrightarrow{\varepsilon \rightarrow 0} \frac{a\mu\hat{f}}{\frac{\beta(\hat{x})}{1 + \beta(\hat{x})h\hat{f}}} = \hat{u}.$$

By Lemma 2.5.7 we obtain the last statement of the theorem. □

4.4.4. Equilibria and small mutation rate

Chapter 5

Towards a stability theory

5.1 Stability of equilibria of some (abstract quasilinear) equations

Let us consider a nonlinear equation of the form

$$\vec{z}_t = A_\varepsilon(F(\vec{z}))\vec{z} \quad (5.1)$$

in the space X of L^1 \mathbb{R}^n -valued functions defined on an interval I , of \mathbb{R} (bounded or not), endowed with the natural Banach lattice structure.

F is a function from the state space X to a m - dimensional space, which we assume linear and continuous.

For fixed $E = F(\vec{z})$, let us assume that $A_\varepsilon(E)$ is the generator of an analytic positive semigroup on X .

Let us assume that for every (sufficiently small) $\varepsilon > 0$ there exists a positive equilibrium solution \vec{z}_ε of (5.1).

Our aim is to give some results related to the stability of the equilibrium solution.

Assuming that (5.1) has semilinear structure, we can apply the results about stability by the linear approximation of [27] or [48], that is, if the spectrum of the linearization of (5.1) at the equilibrium point \vec{z}_ε lies in $\{\text{Re}\lambda < \beta\}$ for some $\beta < 0$ then \vec{z}_ε is uniformly asymptotically stable in X .

Moreover we assume that $A_\varepsilon(E)$ can be written as the sum of a constant (independent of E) operator and a bounded linear operator depending smoothly on E . By abuse of notation, $DA_\varepsilon(E)$ will denote the differential of this bounded operator.

Let us compute the linearization of (5.1) at the equilibrium point \vec{z}_ε .

Taking a perturbation of \vec{z}_ε , namely $\vec{z} = \vec{z}_\varepsilon + \vec{v}$ we have

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$$\vec{v}_t = A_\varepsilon(F(\vec{z}_\varepsilon) + F(\vec{v}))(\vec{z}_\varepsilon + \vec{v}),$$

where we have used that $(\vec{z}_\varepsilon)_t = 0$ and that F is linear.

If we denote $F(\vec{z}_\varepsilon) := E_\varepsilon$ and we develop by the Taylor formula we have

$$\begin{aligned} \vec{v}_t &= A_\varepsilon(F(\vec{z}_\varepsilon) + F(\vec{v}))(\vec{z}_\varepsilon + \vec{v}) \\ &= \left(A_\varepsilon(E_\varepsilon) + DA_\varepsilon(E_\varepsilon)F(\vec{v}) + \dots \right) (\vec{z}_\varepsilon + \vec{v}). \end{aligned}$$

Taking only the linear terms and using that $A_\varepsilon(E_\varepsilon)\vec{z}_\varepsilon = 0$ we obtain

$$\begin{aligned} \vec{v}_t &= A_\varepsilon(E_\varepsilon)\vec{v} + DA_\varepsilon(E_\varepsilon)F(\vec{v})\vec{z}_\varepsilon \\ &:= \tilde{A}_\varepsilon\vec{v} + S_\varepsilon\vec{v}. \end{aligned} \tag{5.2}$$

S_ε is an operator with finite dimensional range.

Indeed, recall that $F : X \longrightarrow \mathbb{R}^m$. Then, if $\vec{v} \in X$, we have $F(\vec{v}) = \sum_{i=1}^m f_i(\vec{v})e_i$, where $f_i \in X'$ and $\{e_i\}_{i=1}^m$ is a basis of \mathbb{R}^m . Then,

$$S_\varepsilon\vec{v} = DA_\varepsilon(E_\varepsilon)F(\vec{v})\vec{z}_\varepsilon = \sum_{i=1}^m f_i(\vec{v})DA_\varepsilon(E_\varepsilon)e_i\vec{z}_\varepsilon \in \langle DA_\varepsilon(E_\varepsilon)e_i\vec{z}_\varepsilon \rangle_{i=1}^m.$$

That is, $\{DA_\varepsilon(E_\varepsilon)e_i\vec{z}_\varepsilon\}_{i=1}^m$ is a generator system of the range of S_ε and therefore the dimension of the range of S_ε is smaller than or equal to m .

Let us give some definitions that we will use in the forthcoming.

Definition 5.1.1 [31] *Let A and T be operators with the same domain space X (but not necessarily with the same range space) such that $D(A) \subset D(T)$ and*

$$\|Tu\| \leq a\|u\| + b\|Au\|, \quad u \in D(A),$$

where a, b are nonnegative constants. Then we shall say that T is relatively bounded with respect to A or simply A -bounded.

T is A -degenerate if T is A -bounded and the range of T is finite dimensional.

Definition 5.1.2 [31] *Let A be a closed operator in a Banach space X and T an operator in X relatively degenerate with respect to A . For any ξ belonging to the resolvent set of A , $T(A - \xi)^{-1}$ is a degenerate bounded operator and*

$$\omega(\xi) = \det(I + T(A - \xi)^{-1})$$

is defined and it is called the Weinstein-Aronszajn determinant (of the first kind) associated with A and T .

$\omega(\xi)$ is a meromorphic function of ξ in any domain of the complex plane consisting of points of the resolvent set of A and of isolated eigenvalues of A with finite (algebraic) multiplicities (see [31]).

We would like to study the spectrum of the operator $\tilde{A}_\varepsilon + S_\varepsilon$ (defined in (5.2)), that is, we would like to study the problem

$$\tilde{A}_\varepsilon \vec{v} + S_\varepsilon \vec{v} - \lambda I \vec{v} = \vec{f},$$

(where $\vec{f} \in X$), or, equivalently,

$$(\tilde{A}_\varepsilon - \lambda I) \vec{v} = -S_\varepsilon \vec{v} + \vec{f}.$$

Let us assume that $\lambda \notin \sigma(\tilde{A}_\varepsilon)$, then

$$\vec{v} = -(\tilde{A}_\varepsilon - \lambda I)^{-1} S_\varepsilon \vec{v} + (\tilde{A}_\varepsilon - \lambda I)^{-1} \vec{f}.$$

Applying S_ε to both sides we obtain,

$$S_\varepsilon \vec{v} = -S_\varepsilon (\tilde{A}_\varepsilon - \lambda I)^{-1} S_\varepsilon \vec{v} + S_\varepsilon (\tilde{A}_\varepsilon - \lambda I)^{-1} \vec{f},$$

or, equivalently,

$$(I + S_\varepsilon (\tilde{A}_\varepsilon - \lambda I)^{-1}) S_\varepsilon \vec{v} = S_\varepsilon (\tilde{A}_\varepsilon - \lambda I)^{-1} \vec{f}.$$

This problem has a unique solution, $S_\varepsilon \vec{v}$, if and only if

$$\det(I + S_\varepsilon (\tilde{A}_\varepsilon - \lambda I)^{-1}) \neq 0.$$

That is, the problem has a solution for the values of λ ($\lambda \notin \sigma(\tilde{A}_\varepsilon)$) such that the Weinstein-Aronszajn determinant associated with \tilde{A}_ε and S_ε does not vanish.

Remark 5.1.3 *The former determinant is defined as*

$$\det(I + S_\varepsilon (\tilde{A}_\varepsilon - \lambda I)^{-1}) = \det\left((I + S_\varepsilon (\tilde{A}_\varepsilon - \lambda I)^{-1})|_{R(S_\varepsilon)}\right).$$

where $R(S_\varepsilon)$ denotes the range of the operator S_ε , (see [31] for the definition of the determinant of a degenerate operator).

Summarizing, we have obtained that

$$\sigma(\tilde{A}_\varepsilon + S_\varepsilon) \subset \sigma(\tilde{A}_\varepsilon) \cup \{\lambda \quad : \quad \det(I + S_\varepsilon (\tilde{A}_\varepsilon - \lambda I)^{-1}) = 0\}. \quad (5.3)$$

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From now on, we will denote

$$\omega_\varepsilon(\lambda) := \det(I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1}). \quad (5.4)$$

Since we are interested in infinite dimensional selection-mutation models that converge to pure selection “ecological” models, we will assume, as in Section 3.4 in Chapter 3 that, for fixed E

$$A_\varepsilon(E) \xrightarrow{\varepsilon \rightarrow 0} A_0(E) \quad \text{formally,}$$

where $A_0(E)$ is a multiplication operator, that is,

$$(A_0(E)\vec{u})(x) := B_0(x, E)\vec{u}(x),$$

where $B_0(x, E)$ is a $n \times n$ matrix which depends smoothly on x and E . Let us consider the n -dimensional ordinary differential equations system

$$\vec{v}_t = B_0(x, G(x, \vec{v}))\vec{v}, \quad (5.5)$$

with x playing the role of a parameter and where G and F are related in the same way as in Section 3.4 in Chapter 3.

Let us assume that \vec{v}_x is an equilibrium of (5.5) and let us linearize (5.5) at the equilibrium point \vec{v}_x .

Taking $\vec{v} = \vec{v}_x + \vec{w}$ and recalling that $G(x, \vec{v})$ is assumed to be linear with respect to \vec{v} we have

$$\begin{aligned} \vec{w}' &= B_0(x, G(x, \vec{v}_x + \vec{w}))(\vec{v}_x + \vec{w}) \\ &= B_0(x, G(x, \vec{v}_x) + G(x, \vec{w}))(\vec{v}_x + \vec{w}). \end{aligned}$$

Let \hat{x} denote a value of ESS of System (5.5), (see section 3.4). When $x = \hat{x}$ the former equation yields

$$\vec{w}' = B_0(\hat{x}, G(\hat{x}, \vec{v}_{\hat{x}}) + G(\hat{x}, \vec{w}))(\vec{v}_{\hat{x}} + \vec{w}).$$

Denoting $G(\hat{x}, \vec{v}_{\hat{x}}) := E_0$ (as in Section 3.4 in Chapter 3) and developing by the Taylor formula,

$$\vec{w}' = \left(B_0(\hat{x}, E_0) + \frac{\partial B_0}{\partial G}(\hat{x}, E_0)G(\hat{x}, \vec{w}) + \dots \right) (\vec{v}_{\hat{x}} + \vec{w}).$$

Taking only the linear terms and using that $B_0(\hat{x}, E_0)\vec{v}_{\hat{x}} = 0$ we have

$$\begin{aligned}\vec{w}' &= B_0(\hat{x}, E_0)\vec{w} + \left(\frac{\partial B_0}{\partial G}(\hat{x}, E_0)G(\vec{w})\right)\vec{v}_{\hat{x}} \\ &:= \tilde{B}_0\vec{w} + T_0\vec{w}.\end{aligned}$$

In the same way as we did for System (5.1), we can define

$$\omega_0(\lambda) := \det(I + T_0(\tilde{B}_0 - \lambda I)^{-1}). \quad (5.6)$$

where $\omega_0(\lambda)$ is holomorphic for $\lambda \notin \sigma(\tilde{B}_0)$. In particular, if 0 is a dominant eigenvalue of \tilde{B}_0 then $\omega_0(\lambda)$ is holomorphic for λ such that $\operatorname{Re} \lambda \geq 0$, $\lambda \neq 0$. As we assume that the equilibrium point $\vec{v}_{\hat{x}}$ is hyperbolic and asymptotically stable, $\omega_0(\lambda)$ does not vanish for λ such that $\operatorname{Re} \lambda \geq 0$.

Our aim is to show that, under some hypotheses including ε small enough, if $\omega_0(\lambda)$ does not vanish for λ such that $\operatorname{Re} \lambda \geq 0$, $\omega_\varepsilon(\lambda)$ has the same property. In order to do it, we will first formulate some results.

Definition 5.1.4 [33] *For any closed path γ , its winding number with respect to a point α is*

$$\omega(\gamma, \alpha) = \frac{1}{2\pi i} \int_{\gamma} \frac{1}{z - \alpha} dz$$

provided the path does not pass through α .

Definition 5.1.5 [33] *Let U be an open set. We say that a closed path γ in U is homologous to 0 in U if*

$$\int_{\gamma} \frac{1}{z - \alpha} dz = 0$$

for every point α not in U .

Definition 5.1.6 [33] *Let γ be a closed path. We say that γ has an interior if $\omega(\gamma, \alpha) = 0$ or 1 for every complex number α which does not lie on γ . Then the set of points α such that $\omega(\gamma, \alpha) = 1$ will be called the interior of γ .*

Theorem 5.1.7 (Rouché) [33] *Let γ be a closed path homologous to 0 in U and assume that γ has an interior.*

Let f, g be analytic on U , and such that

$$|f(z) - g(z)| < |f(z)|$$

for z on γ . Then, f and g have the same number of zeros in the interior of γ .

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Theorem 5.1.8 [45] *Let A be a densely defined operator on a Banach space X and $\alpha \in (0, \frac{\pi}{2}]$. Then A is the generator of a bounded analytic semigroup of angle α if and only if*

$$S(\alpha + \frac{\pi}{2}) \subset \rho(A)$$

and for every $\alpha_1 \in (0, \alpha)$ there exists a constant M such that

$$\|R(\lambda, A)\| \leq \frac{M}{|\lambda|} \quad \lambda \in S(\alpha_1 + \frac{\pi}{2}),$$

(where $S(\alpha) = \{re^{i\theta} : r > 0, \theta \in (-\alpha, \alpha)\}$).

Theorem 5.1.9 *Let \vec{z}_ε be a positive equilibrium solution of the nonlinear equation*

$$\vec{z}_t = A_\varepsilon(F(\vec{z}))\vec{z}$$

where F is a linear function from the state space X to a m -dimensional space and such that, for fixed $E = F(\vec{z})$, $A_\varepsilon(E)$ is the generator of a bounded analytic positive semigroup on X .

Let $\tilde{A}_\varepsilon + S_\varepsilon$ be, as in (5.2), the linearized operator at the equilibrium \vec{z}_ε and let $\omega_\varepsilon(\lambda)$ and $\omega_0(\lambda)$ be defined as in (5.4) and (5.6) respectively.

Let us denote by $D := \{\lambda \in \mathbb{C} \quad \text{s.t.} \quad \text{Re}\lambda \geq 0, \lambda \neq 0\}$.

Let us assume that $\omega_\varepsilon(\lambda)$ and $\omega_0(\lambda)$ are holomorphic functions for all $\lambda \in D$.

Let C_ε be a constant such that $\|R(\lambda, \tilde{A}_\varepsilon)\| \leq \frac{C_\varepsilon}{|\lambda|}$ for $\lambda \in D$. Let us assume that $\limsup_{\varepsilon \rightarrow 0} \|S_\varepsilon\|C_\varepsilon$ is bounded.

Moreover, let us assume that $\omega_0(\lambda)$ does not vanish for $\lambda \in D$ and that

$$\omega_\varepsilon(\lambda) \xrightarrow{\varepsilon \rightarrow 0} \omega_0(\lambda)$$

uniformly on λ in compact sets contained in D .

Then, for all $L_1 > 0$ there exists ε small enough such that $\omega_\varepsilon(\lambda)$ does not vanish for $\lambda \in \{\lambda \in \mathbb{C} \quad \text{s.t.} \quad \text{Re}\lambda \geq 0, |\lambda| \geq L_1\}$.

Remark 5.1.10 *If 0 is a strictly dominant algebraically simple eigenvalue of \tilde{A}_ε then the semigroup generated by \tilde{A}_ε is bounded (see for instance Theorem 3.1 p. 329 in [19]).*

Remark 5.1.11 *The hypothesis saying that $\omega_\varepsilon(\lambda)$ is holomorphic for all $\lambda \in D$ (that is, for λ such that $\text{Re}\lambda \geq 0, \lambda \neq 0$) is guaranteed by assuming that 0 is a dominant eigenvalue of the operator \tilde{A}_ε and, in the same way, the hypothesis that $\omega_0(\lambda)$ is holomorphic for all $\lambda \in D$ is guaranteed by assuming that 0 is a dominant eigenvalue of the operator \tilde{B}_0 .*

Remark 5.1.12 *If the operator \tilde{A}_ε can be written as $\tilde{A}_\varepsilon = A + B_\varepsilon$ where A generates an bounded analytic semigroup (then there exists a constant C such that $R(\lambda, A) \leq \frac{C}{|\lambda|}$) and B_ε is a bounded operator such that $\limsup_{\varepsilon \rightarrow 0} \|B_\varepsilon\|$ is bounded, then C_ε is bounded.*

Indeed, since $R(\lambda, \tilde{A}_\varepsilon) = R(\lambda, A)(I + B_\varepsilon R(\lambda, A))^{-1}$ we have

$$\|R(\lambda, \tilde{A}_\varepsilon)\| \leq \frac{\|R(\lambda, A)\|}{1 - \|B_\varepsilon\| \|R(\lambda, A)\|} \leq \frac{2C}{|\lambda|}$$

if $|\lambda| > 2C\|B_\varepsilon\|$ (see [48], [14]).

Proof: Let us denote by $L_2 := \sup_\varepsilon \|S_\varepsilon\|C_\varepsilon$ (by hypothesis this supremum is bounded). Let us consider the compact set

$$K := \{\lambda : \operatorname{Re}\lambda \geq 0, 0 < L_1 \leq |\lambda| \leq L_2\}$$

for some $L_1 > 0$.

Let us denote by $I := \inf_K |\omega_0(\lambda)|$.

As $\omega_\varepsilon(\lambda) \xrightarrow{\varepsilon \rightarrow 0} \omega_0(\lambda)$ we have that, for ε small enough,

$$|\omega_0(\lambda) - \omega_\varepsilon(\lambda)| < I \leq |\omega_0(\lambda)| \quad \text{if } \lambda \in K.$$

Hence, Rouché's theorem implies that there exists ε_0 such that for $\varepsilon < \varepsilon_0$

$$\omega_\varepsilon(\lambda) \neq 0 \quad \text{for } \lambda \in K.$$

Let us assume now that $\lambda \notin K$.

Since \tilde{A}_ε is the infinitesimal generator of a bounded analytic semigroup, it satisfies

$$\|R(\lambda, \tilde{A}_\varepsilon)\| \leq \frac{C_\varepsilon}{|\lambda|}$$

for λ such that $\operatorname{Re}\lambda \geq 0$, $|\lambda| > L_2$ and C_ε a constant.

Therefore

$$\|S_\varepsilon R(\lambda, \tilde{A}_\varepsilon)\| \leq \|S_\varepsilon\| \frac{C_\varepsilon}{|\lambda|}.$$

Thus, for $|\lambda| > L_2$ we have $\|S_\varepsilon R(\lambda, \tilde{A}_\varepsilon)\| < \frac{1}{2}$ and this implies that

$$\|S_\varepsilon R(\lambda, \tilde{A}_\varepsilon)|_{R(S_\varepsilon)}\| < \frac{1}{2}. \tag{5.7}$$

If $P(\mu)$ denotes the characteristic polynomial of $S_\varepsilon R(\lambda, \tilde{A}_\varepsilon)|_{R(S_\varepsilon)}$, by (5.7) we have that if μ_i is a zero of $P(\mu)$, it satisfies $|\mu_i| < \frac{1}{2}$ (because the spectrum

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of a bounded operator is contained in a ball of radius equal to the norm of the operator).

Since

$$\det((I + S_\varepsilon R(\lambda, \tilde{A}_\varepsilon))|_{R(S_\varepsilon)}) = P(-1) = (-1)^n \prod_{i=1}^n (-1 - \mu_i),$$

we obtain that

$$|\det((I + S_\varepsilon R(\lambda, \tilde{A}_\varepsilon))|_{R(S_\varepsilon)})| > \frac{1}{2^n} > 0 \quad \text{if } |\lambda| > L_2.$$

□

The former theorem, together with the characterization of the spectrum of the operator $\tilde{A}_\varepsilon + S_\varepsilon$ given by (5.3) allow us to give a (partial) result about the stability of the equilibrium solution \vec{z}_ε of System (5.1)

Theorem 5.1.13 *Let \vec{z}_ε be a positive equilibrium solution of the nonlinear equation*

$$\vec{z}_t = A_\varepsilon(F(\vec{z}))\vec{z}$$

where F is a function from the state space X to a m -dimensional space and such that, for fixed $E = F(\vec{z})$, $A_\varepsilon(E)$ is the generator of a bounded analytic semigroup on X .

Let us assume that 0 is an isolated eigenvalue of $\tilde{A}_\varepsilon = A_\varepsilon(F(\vec{z}_\varepsilon))$.

Let $\tilde{A}_\varepsilon + S_\varepsilon$ be, as in (5.2), the linearized operator at the equilibrium \vec{z}_ε . Let $\omega_\varepsilon(\lambda)$ and $\omega_0(\lambda)$ be defined as in (5.4) and (5.6) respectively. Under the hypotheses of Theorem 5.1.9, if, moreover there exists $L_1 > 0$ such that for ε small $\{\lambda \in \mathbb{C} \text{ s.t. } \operatorname{Re}\lambda \geq 0, |\lambda| < L_1\} \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$ then, for ε small enough, the equilibrium solution \vec{z}_ε is uniformly asymptotically stable.

Proof: We have seen that

$$\sigma(\tilde{A}_\varepsilon + S_\varepsilon) \subset \sigma(\tilde{A}_\varepsilon) \cup \{\lambda \text{ s.t. } \omega_\varepsilon(\lambda) := \det(I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1}) = 0\}.$$

By Theorem 5.1.9, for ε sufficiently small, the equation $\omega_\varepsilon(\lambda) = 0$ does not have a solution for $\lambda \in \{\lambda \in \mathbb{C} \text{ s.t. } \operatorname{Re}\lambda \geq 0, L_1 \leq |\lambda|\}$.

Moreover, by hypothesis $\{\lambda \in \mathbb{C} \text{ s.t. } \operatorname{Re}\lambda \geq 0, |\lambda| < L_1\} \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$.

On the other hand, also by hypothesis, $\omega_\varepsilon(\lambda)$ is holomorphic for all $\lambda \in D = \{\lambda \in \mathbb{C} \text{ s.t. } \operatorname{Re}\lambda \geq 0, \lambda \neq 0\}$, equivalently, $\tilde{A}_\varepsilon (= A_\varepsilon(F(\vec{z}_\varepsilon)))$ has 0 as a dominant eigenvalue.

Therefore $\sigma(\tilde{A}_\varepsilon + S_\varepsilon) \subset \{\lambda \text{ s.t. } \operatorname{Re}\lambda < 0\}$ and this proves the theorem. □

We have just seen that, under the hypotheses of Theorem 5.1.9, whenever we can exclude a set $\{\lambda \in \mathbb{C} \text{ s.t. } \operatorname{Re}\lambda \geq 0, |\lambda| < L_1\}$ (for some $L_1 > 0$) from the spectrum of the linearized operator $\tilde{A}_\varepsilon + S_\varepsilon$, then, for ε small enough the equilibrium solution \vec{z}_ε is uniformly asymptotically stable.

Let us remark that, in case that the hypothesis stated in Theorem 5.1.9 saying that $\omega_\varepsilon(\lambda)$ is holomorphic for all λ such that $\operatorname{Re} \lambda \geq 0, \lambda \neq 0$ does not hold, anyway we can use the same method to prove stability of the equilibrium \vec{z}_ε but we might have values with positive real part in the spectrum of \tilde{A}_ε that we will have to prove that do not belong to the spectrum of the linearized operator $\tilde{A}_\varepsilon + S_\varepsilon$ in order to obtain stability of \vec{z}_ε .

CASE F ONE DIMENSIONAL

In the particular case that the function F is one dimensional, it is possible to give conditions to exclude a set $\{\lambda \in \mathbb{C} \text{ s.t. } \operatorname{Re}\lambda \geq 0, |\lambda| < L_1\}$ (for some $L_1 > 0$) from the spectrum of the linearized operator $\tilde{A}_\varepsilon + S_\varepsilon$. Let us start by giving conditions to exclude 0 from the spectrum of $\tilde{A}_\varepsilon + S_\varepsilon$. We will use the first Weinstein-Aronszajn formula that we define next.

The first Weinstein-Aronszajn formula (see [31]) is

$$\tilde{\nu}(\lambda; S) = \tilde{\nu}(\lambda; T) + \nu(\lambda; \omega),$$

where T is a closed operator in a Banach space X , $S = T + A$ where A is an operator in X relatively degenerate with respect to T , $\omega(\lambda) = \det(I + A(T - \lambda)^{-1})$ and

$$\tilde{\nu}(\lambda; T) = \begin{cases} 0 & \text{if } \lambda \in \rho(T), \\ \dim(\operatorname{range} P) & \text{if } \lambda \text{ is an isolated point of } \sigma(T), \\ +\infty & \text{in all other cases,} \end{cases}$$

where P is the projection associated with the isolated point of $\sigma(T)$, and

$$\nu(\lambda; \omega) = \begin{cases} k & \text{if } \lambda \text{ is a zero of } \omega \text{ of order } k, \\ -k & \text{if } \lambda \text{ is a pole of } \omega \text{ of order } k, \\ 0 & \text{for other } \lambda \in \Delta, \end{cases}$$

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where Δ is the domain of the complex plane where ω is defined.

Theorem 5.1.14 *Let \vec{z}_ε be a positive equilibrium solution of the nonlinear equation*

$$\vec{z}_t = A_\varepsilon(F(\vec{z}))\vec{z}$$

where F is a function from the state space X to a one-dimensional space and such that, for fixed $E = F(\vec{z})$, $A_\varepsilon(E)$ is the generator of a bounded analytic semigroup on X . Let E_ε denote $F(\vec{z}_\varepsilon)$.

Let $\tilde{A}_\varepsilon + S_\varepsilon$ be, as in (5.2), the linearized operator at the equilibrium \vec{z}_ε . Let $\omega_\varepsilon(\lambda)$ and $\omega_0(\lambda)$ be defined as in (5.4) and (5.6) respectively.

Let us assume that 0 is an isolated eigenvalue of $\tilde{A}_\varepsilon = A_\varepsilon(F(\vec{z}_\varepsilon))$ with algebraic multiplicity 1. If $\vec{\xi}_\varepsilon := DA_\varepsilon(E_\varepsilon)\vec{z}_\varepsilon \notin \text{Range}(\tilde{A}_\varepsilon)$ and $F(\vec{z}_\varepsilon) \neq 0$ then $0 \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$.

Proof:

By hypothesis, 0 is an isolated dominant eigenvalue of \tilde{A}_ε with algebraic multiplicity one. Therefore $\tilde{\nu}(0, \tilde{A}_\varepsilon) = 1$.

So, applying the first Weinstein-Aronszajn formula, to say that 0 belongs to the resolvent set of $\tilde{A}_\varepsilon + S_\varepsilon$ is equivalent to say that 0 is a pole of $\omega_\varepsilon(\lambda)$ of order 1.

Since F is one dimensional, the range of S_ε is at most one dimensional and it is generated by $\vec{\xi}_\varepsilon$.

Moreover, as 0 is an isolated dominant eigenvalue of algebraic multiplicity one of \tilde{A}_ε , it is a simple pole of $R(\lambda, \tilde{A}_\varepsilon)$, and then, by the Laurent series at $\lambda = 0$ we have

$$\begin{aligned} (I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1})\vec{\xi}_\varepsilon &= \vec{\xi}_\varepsilon \\ + S_\varepsilon \left(\frac{1}{\lambda} P_\varepsilon \vec{\xi}_\varepsilon + \sum_{n=0}^{\infty} \frac{1}{2\pi i} \lambda^n \int_{\Gamma} -\frac{(\tilde{A}_\varepsilon - \lambda I)^{-1} \vec{\xi}_\varepsilon}{\lambda^{n+1}} d\lambda \right) \\ &= \vec{\xi}_\varepsilon + \frac{\beta_\varepsilon}{\lambda} S_\varepsilon \vec{z}_\varepsilon + S_\varepsilon \sum_{n=0}^{\infty} \frac{1}{2\pi i} \lambda^n \int_{\Gamma} -\frac{(\tilde{A}_\varepsilon - \lambda I)^{-1} \vec{\xi}_\varepsilon}{\lambda^{n+1}} d\lambda, \end{aligned}$$

where Γ is a positively-oriented small circle enclosing $\lambda = 0$ but excluding other eigenvalues of \tilde{A}_ε , P_ε is the spectral projection corresponding to the spectral set $\{0\}$ and $S_\varepsilon P_\varepsilon \vec{\xi}_\varepsilon = S_\varepsilon \beta_\varepsilon \vec{z}_\varepsilon = \beta_\varepsilon S_\varepsilon \vec{z}_\varepsilon$.

$\omega_\varepsilon(\lambda)$ will have a pole of first order (and therefore $0 \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$) if $\beta_\varepsilon \neq 0$ and $S_\varepsilon \vec{z}_\varepsilon \neq 0$.

Since $X = \langle \vec{z}_\varepsilon \rangle \oplus \text{Range}(\tilde{A}_\varepsilon)$, $\beta_\varepsilon \neq 0$ is equivalent to say that $\vec{\xi}_\varepsilon \notin \text{Range}(\tilde{A}_\varepsilon)$.

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Finally, $S_\varepsilon \vec{z}_\varepsilon = DA_\varepsilon(E_\varepsilon)F(\vec{z}_\varepsilon)\vec{z}_\varepsilon = F(\vec{z}_\varepsilon)\vec{\xi}_\varepsilon \neq 0$ because $\vec{\xi}_\varepsilon \neq 0$ (we have assumed $\vec{\xi}_\varepsilon \notin \text{Range}(\tilde{A}_\varepsilon)$) and, also by hypotheses $F(\vec{z}_\varepsilon) \neq 0$. \square

Remark 5.1.15 *Let us note that to ask the two following hypotheses*

$$\vec{\xi}_\varepsilon := DA_\varepsilon(E_\varepsilon)\vec{z}_\varepsilon \notin \text{Range}(\tilde{A}_\varepsilon) \quad \text{and} \quad F(\vec{z}_\varepsilon) \neq 0$$

to hold is equivalent to ask $F(P_\varepsilon DA_\varepsilon(E_\varepsilon)\vec{z}_\varepsilon) \neq 0$ to hold.

Let us now give conditions to exclude the set $\{\lambda \in \mathbb{C} \text{ s.t. } \text{Re}\lambda \geq 0, |\lambda| < L_1, \lambda \neq 0\}$, for some $L_1 > 0$ from the spectrum of the operator $\tilde{A}_\varepsilon + S_\varepsilon$, for ε small.

Theorem 5.1.16 *Let \vec{z}_ε be a positive equilibrium solution of the nonlinear equation*

$$\vec{z}_t = A_\varepsilon(F(\vec{z}))\vec{z}$$

where F is a function from the state space X to a one-dimensional space and such that, for fixed $E = F(\vec{z})$, $A_\varepsilon(E)$ is the generator of a bounded analytic semigroup on X .

Let $\tilde{A}_\varepsilon + S_\varepsilon$ be, as in (5.2), the linearized operator at the equilibrium \vec{z}_ε . Let $\omega_\varepsilon(\lambda)$ and $\omega_0(\lambda)$ be defined as in (5.4) and (5.6) respectively.

Let us assume that 0 is an isolated eigenvalue of $\tilde{A}_\varepsilon = A_\varepsilon(F(\vec{z}_\varepsilon))$ with algebraic multiplicity 1. Let P_ε be the projection corresponding to the eigenvalue 0 of \tilde{A}_ε . Let us assume that $F(P_\varepsilon DA_\varepsilon(E_\varepsilon)\vec{z}_\varepsilon) \neq 0$.

If $|F((\tilde{A}_\varepsilon - \lambda I)^{-1}(I - P_\varepsilon)DA_\varepsilon(E_\varepsilon)\vec{z}_\varepsilon)|$ is bounded for ε small enough and λ close to zero (with $\text{Re}\lambda \geq 0$) then there exists $L_1 > 0$ such that for ε small enough $\omega_\varepsilon(\lambda)$ does not vanish in the set $\{\lambda \in \mathbb{C} \text{ s.t. } \text{Re}\lambda \geq 0, |\lambda| < L_1, \lambda \neq 0\}$.

Proof: Since F is one dimensional, if $v \in X$ we have $F(v) \in \mathbb{R}$ and therefore

$$S_\varepsilon v = DA_\varepsilon(E_\varepsilon)F(v)\vec{z}_\varepsilon = F(v)DA_\varepsilon(E_\varepsilon)\vec{z}_\varepsilon = F(v)\vec{\xi}_\varepsilon.$$

Then

$$\begin{aligned} (I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1})\vec{\xi}_\varepsilon &= \vec{\xi}_\varepsilon + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1}\vec{\xi}_\varepsilon \\ &= \vec{\xi}_\varepsilon + F\left((\tilde{A}_\varepsilon - \lambda I)^{-1}\vec{\xi}_\varepsilon\right)\vec{\xi}_\varepsilon \\ &= \vec{\xi}_\varepsilon + F\left(\frac{P_\varepsilon\vec{\xi}_\varepsilon}{\lambda} + (\tilde{A}_\varepsilon - \lambda I)^{-1}(I - P_\varepsilon)\vec{\xi}_\varepsilon\right)\vec{\xi}_\varepsilon \\ &= \vec{\xi}_\varepsilon + \frac{1}{\lambda}F(P_\varepsilon\vec{\xi}_\varepsilon)\vec{\xi}_\varepsilon + F((\tilde{A}_\varepsilon - \lambda I)^{-1}(I - P_\varepsilon)\vec{\xi}_\varepsilon)\vec{\xi}_\varepsilon \end{aligned}$$

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Therefore, if $|F((\tilde{A}_\varepsilon - \lambda I)^{-1}(I - P_\varepsilon)DA_\varepsilon(E_\varepsilon)\vec{z}_\varepsilon)|$ is bounded for ε small enough and λ close to zero (with $\operatorname{Re}\lambda \geq 0$), $\omega_\varepsilon(\lambda) \neq 0$ for ε small and λ close to zero (with $\operatorname{Re}\lambda \geq 0$).

□

Finally, let us formulate the theorem summarizing all the conditions that we enunciated so far in order to obtain stability of the equilibrium \vec{z}_ε in the case of one dimensional environment.

Theorem 5.1.17 *Let \vec{z}_ε be a positive equilibrium solution of the nonlinear equation*

$$\vec{z}_t = A_\varepsilon(F(\vec{z}))\vec{z}$$

where F is a function from the state space X to a one-dimensional space and such that, for fixed $E = F(\vec{z})$, $A_\varepsilon(E)$ is the generator of a bounded analytic semigroup on X . Let E_ε denote $F(\vec{z}_\varepsilon)$.

Let $\tilde{A}_\varepsilon + S_\varepsilon$ be, as in (5.2), the linearized operator at the equilibrium \vec{z}_ε . Let $\omega_\varepsilon(\lambda)$ and $\omega_0(\lambda)$ be defined as in (5.4) and (5.6) respectively.

Let us assume that 0 is an isolated eigenvalue of $\tilde{A}_\varepsilon = A_\varepsilon(F(\vec{z}_\varepsilon))$ with algebraic multiplicity 1. Let P_ε be the projection corresponding to the (dominant) eigenvalue 0 of \tilde{A}_ε . Let us assume that $F(P_\varepsilon DA_\varepsilon(E_\varepsilon)\vec{z}_\varepsilon) \neq 0$ and that $|F((\tilde{A}_\varepsilon - \lambda I)^{-1}(I - P_\varepsilon)DA_\varepsilon(E_\varepsilon)\vec{z}_\varepsilon)|$ is bounded for ε small enough and λ close to zero (with $\operatorname{Re}\lambda \geq 0$). Then, under the hypotheses of Theorem 5.1.9 and for ε small enough, the equilibrium solution \vec{z}_ε is uniformly asymptotically stable.

Proof: An application of Theorems 5.1.13, 5.1.14 and 5.1.16. □

The last two hypotheses ($F(P_\varepsilon DA_\varepsilon(E_\varepsilon)\vec{z}_\varepsilon) \neq 0$ and $|F((\tilde{A}_\varepsilon - \lambda I)^{-1}(I - P_\varepsilon)DA_\varepsilon(E_\varepsilon)\vec{z}_\varepsilon)|$ bounded for ε small enough and λ close to zero (with $\operatorname{Re}\lambda \geq 0$)) hold automatically (assuming $F(\vec{z}_\varepsilon) \neq 0$) if $DA_\varepsilon(E_\varepsilon)$ is a scalar multiple of the identity operator.

This is the situation if equation (5.1) is of the form

$$\vec{z}_t = (A_\varepsilon - m(F(\vec{z}))I)\vec{z}$$

where $m : \mathbb{R} \rightarrow \mathbb{R}^+$.

This particular kind of nonlinearity has extensively been used in models in population dynamics ([5],[7], [8], [9]) where sometimes it is called uniform increase of mortality.

Appendix

In this appendix some computations are done in order to apply some of the stability results of Chapter 5 to the models studied in Chapter 4.

A.1 Prey Predator

Let us recall the prey predator model studied in Chapter 4

$$\left\{ \begin{array}{l} f'(t) = (a - \mu f(t) - \int_0^\infty \frac{\beta(x)u(x,t)}{1 + \beta(x)hf(t)} dx) f(t), \\ \frac{\partial u(x,t)}{\partial t} = (1 - \varepsilon) \frac{\alpha\beta(x)f(t)u(x,t)}{1 + \beta(x)hf(t)} + \varepsilon \int_0^\infty \gamma(x,y) \frac{\alpha\beta(y)f(t)u(y,t)}{1 + \beta(y)hf(t)} dy \\ -d(x)u(x,t). \end{array} \right. \quad (\text{A.8})$$

In Chapter 4 we proved, under the hypotheses of Theorem 4.3.7 and for ε small enough, the existence of an interior equilibrium $(f_\varepsilon, u_\varepsilon)$ of System (A.8).

In this appendix we are going to apply the results of Chapter 5 to study the stability of $(f_\varepsilon, u_\varepsilon)$.

Writing the prey predator model (A.8) in the form $\vec{z}'_t = A_\varepsilon(F(\vec{z}))\vec{z}$ we see that, in this case

$$\begin{aligned} F &: \mathbb{R} \times L^1(0, \infty) \longrightarrow \mathbb{R} \\ (f, u) &\longrightarrow f \end{aligned}$$

and

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$$A_\varepsilon(f) = \begin{pmatrix} a - \mu f & - \int_0^\infty \frac{\beta(x)f}{1+\beta(x)hf} \cdot dx \\ 0 & -d(x) + (1 - \varepsilon)\alpha \frac{\beta(x)f}{1+\beta(x)hf} + \\ & \varepsilon \int_0^\infty \alpha\gamma(x, y) \frac{\beta(y)f}{1+\beta(y)hf} \cdot dy \end{pmatrix}.$$

Note that in Chapter 5 we considered the state space X of L^1 - \mathbb{R}^n valued functions defined on an interval I of \mathbb{R} .

In the prey predator model (A.8) the state space is $X = \mathbb{R} \times L^1(0, \infty)$. Nevertheless, all the results stated in Chapter 5 are also true if the state space is $X = \mathbb{R} \times L^1(0, \infty)$.

Let us denote by

$$T_\varepsilon(f) := -d(x) + (1 - \varepsilon)\alpha \frac{\beta(x)f}{1 + \beta(x)hf} + \varepsilon \int_0^\infty \alpha\gamma(x, y) \frac{\beta(y)f}{1 + \beta(y)hf} \cdot dy,$$

(note that the same operator was denoted in Chapter 4 by $A_{\varepsilon, f}$ but we change the notation here because we have already used $A_\varepsilon(f)$ in this chapter to denote a different operator).

The linearized system for the prey predator model (A.8) at the equilibrium $(f_\varepsilon, u_\varepsilon)$ (considering $f(t) = f_\varepsilon + \bar{f}$, $u(x, t) = u_\varepsilon + \bar{u}(x, t)$, using that $(f_\varepsilon, u_\varepsilon)$ is a steady state, eliminating higher order terms and using Taylor's formula) is

$$\begin{aligned} \bar{f}' &= a\bar{f} - 2\mu\bar{f}f_\varepsilon - \int_0^\infty \frac{\beta(x)u_\varepsilon\bar{f}}{(1 + \beta(x)hf_\varepsilon)^2} dx - \int_0^\infty \frac{\beta(x)f_\varepsilon\bar{u}}{(1 + \beta(x)hf_\varepsilon)} dx, \\ \frac{\partial \bar{u}}{\partial t} &= -d(x)\bar{u} + (1 - \varepsilon)\alpha \left(\frac{\beta(x)u_\varepsilon\bar{f}}{(1 + \beta(x)hf_\varepsilon)^2} + \frac{\beta(x)f_\varepsilon\bar{u}}{(1 + \beta(x)hf_\varepsilon)} \right) \\ &\quad + \varepsilon \int_0^\infty \alpha\gamma(x, y) \left(\frac{\beta(y)u_\varepsilon\bar{f}}{(1 + \beta(y)hf_\varepsilon)^2} + \frac{\beta(y)f_\varepsilon\bar{u}}{(1 + \beta(y)hf_\varepsilon)} \right) dy, \end{aligned} \tag{A.9}$$

that is, in this case, the operators \tilde{A}_ε and S_ε defined in Chapter 5 are

$$\tilde{A}_\varepsilon = \begin{pmatrix} a - \mu f_\varepsilon & - \int_0^\infty \frac{\beta(x)f_\varepsilon}{(1+\beta(x)hf_\varepsilon)} \cdot dx \\ 0 & -d(x) + (1 - \varepsilon)\alpha \frac{\beta(x)f_\varepsilon}{1+\beta(x)hf_\varepsilon} \\ & + \varepsilon \int_0^\infty \alpha\gamma(x, y) \frac{\beta(y)f_\varepsilon}{1+\beta(y)hf_\varepsilon} \cdot dy \end{pmatrix} \tag{A.10}$$

and

$$S_\varepsilon = \begin{pmatrix} -\mu f_\varepsilon - \int_0^\infty \frac{\beta(x)u_\varepsilon(x)}{(1 + \beta(x)hf_\varepsilon)^2} dx & 0 \\ (1 - \varepsilon)\alpha \frac{\beta(x)u_\varepsilon(x)}{(1 + \beta(x)hf_\varepsilon)^2} + \varepsilon \int_0^\infty \alpha\gamma(x, y) \frac{\beta(y)u_\varepsilon(y)}{1 + \beta(y)hf_\varepsilon} dy & 0 \end{pmatrix}. \quad (\text{A.11})$$

Let us note that

$$\sigma(\tilde{A}_\varepsilon) = \sigma(A_\varepsilon(f_\varepsilon)) = \{a - \mu f_\varepsilon\} \cup \sigma(T_\varepsilon(f_\varepsilon)).$$

In Chapter 4 we proved that zero is the dominant eigenvalue of $T_\varepsilon(f_\varepsilon)$. Since $a - \mu f_\varepsilon > 0$, the hypothesis of Theorem 5.1.9 saying that $\omega_\varepsilon(\lambda) = \det(I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1})$ is holomorphic for all λ such that $\text{Re } \lambda \geq 0$, $\lambda \neq 0$ (or equivalently, that 0 is the dominant eigenvalue of \tilde{A}_ε) does not hold. However, let us note that this hypothesis was only used because if it holds then, $\sigma(\tilde{A}_\varepsilon)$ does not contain values with positive real part and since

$$\sigma(\tilde{A}_\varepsilon + S_\varepsilon) \subset \sigma(\tilde{A}_\varepsilon) \cup \{\lambda \text{ s.t. } \det(I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1}) = 0\},$$

we only had to show that $\det(I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1}) \neq 0$ for λ such that $\text{Re } \lambda \geq 0$, $\lambda \neq 0$ and that $0 \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$.

From now on, let us denote

$$D_\varepsilon := \{\lambda \in \mathbb{C} \text{ s.t. } \text{Re } \lambda \geq 0, \lambda \neq 0, \lambda \neq a - \mu f_\varepsilon\}.$$

In the prey predator model (A.8), in order to obtain stability of $(f_\varepsilon, u_\varepsilon)$ we will have to show that $\omega_\varepsilon(\lambda) := \det(I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1}) \neq 0$ for $\lambda \in D_\varepsilon$, that $0 \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$ and moreover, that $a - \mu f_\varepsilon \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$.

Let us recall the finite dimensional prey predator model of Chapter 4 at the ESS value

$$\begin{cases} f' = \left(a - \mu f - \frac{\beta(\hat{x})u}{1 + \beta(\hat{x})hf}\right)f, \\ u' = \left(\alpha \frac{\beta(\hat{x})f}{1 + \beta(\hat{x})hf} - d(\hat{x})\right)u. \end{cases} \quad (\text{A.12})$$

Linearizing at the equilibrium point (\hat{f}, \hat{u}) and eliminating higher order terms we obtain the linear system

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$$\begin{aligned}
\begin{pmatrix} \bar{f} \\ \bar{u} \end{pmatrix}' &= \begin{pmatrix} a - \mu\hat{f} & -\frac{\beta(\hat{x})\hat{f}}{1 + \beta(\hat{x})h\hat{f}} \\ 0 & 0 \end{pmatrix} \begin{pmatrix} \bar{f} \\ \bar{u} \end{pmatrix} \\
&+ \begin{pmatrix} -\mu\hat{f} - \frac{\beta(\hat{x})\hat{u}}{(1 + \beta(\hat{x})h\hat{f})^2} & 0 \\ \frac{\alpha\beta(\hat{x})\hat{u}}{(1 + \beta(\hat{x})h\hat{f})^2} & 0 \end{pmatrix} \begin{pmatrix} \bar{f} \\ \bar{u} \end{pmatrix} \\
&=: \tilde{B}_0 \begin{pmatrix} \bar{f} \\ \bar{u} \end{pmatrix} + T_0 \begin{pmatrix} \bar{f} \\ \bar{u} \end{pmatrix}.
\end{aligned}$$

Let us define $\omega_0(\lambda) := \det(I + T_0(\tilde{B}_0 - \lambda I)^{-1})$ for $\lambda \notin \sigma(\tilde{B}_0)$ (i.e. for λ such that $\lambda \neq 0$ and $\lambda \neq a - \mu\hat{f}$).

Let us denote

$$D_0 := \{\lambda \in \mathbb{C} \text{ s.t. } \operatorname{Re} \lambda \geq 0, \lambda \neq 0, \lambda \neq a - \mu\hat{f}\}.$$

We proved in Chapter 4 that, under the hypotheses of Theorem 4.3.7, the equilibrium point (\hat{f}, \hat{u}) is hyperbolic and asymptotically stable, therefore

$$\omega_0(\lambda) = \det(I + T_0(\tilde{B}_0 - \lambda I)^{-1}) \neq 0$$

for $\lambda \in D_0$, that is,

$$\begin{aligned}
&1 + \left(-\mu\hat{f} - \frac{\beta(\hat{x})\hat{u}}{(1 + \beta(\hat{x})h\hat{f})^2} \right) \left(\frac{1}{(a - \mu\hat{f} - \lambda)} \right) \\
&+ \frac{\alpha\beta(\hat{x})\hat{u}}{(1 + \beta(\hat{x})h\hat{f})^2} \left(\frac{\frac{\beta(\hat{x})\hat{f}}{1 + \beta(\hat{x})h\hat{f}}}{(a - \mu\hat{f} - \lambda)(-\lambda)} \right) \neq 0
\end{aligned}$$

for $\lambda \in D_0$.

Remark A.1.1 *Note that the equation*

$$1 + \left(-\mu\hat{f} - \frac{\beta(\hat{x})\hat{u}}{(1 + \beta(\hat{x})h\hat{f})^2} \right) \left(\frac{1}{(a - \mu\hat{f} - \lambda)} \right) \\ + \frac{\alpha\beta(\hat{x})\hat{u}}{(1 + \beta(\hat{x})h\hat{f})^2} \left(\frac{\frac{\beta(\hat{x})\hat{f}}{1 + \beta(\hat{x})h\hat{f}}}{(a - \mu\hat{f} - \lambda)(-\lambda)} \right) = 0$$

is equivalent (for $\lambda \neq 0$, $\lambda \neq a - \mu\hat{f}$) to

$$(a - \mu\hat{f} - \lambda)(-\lambda) + (-\lambda) \left(-\mu\hat{f} - \frac{\beta(\hat{x})\hat{u}}{(1 + \beta(\hat{x})h\hat{f})^2} \right) \\ + \frac{\alpha\beta(\hat{x})\hat{u}}{(1 + \beta(\hat{x})h\hat{f})^2} \frac{\beta(\hat{x})\hat{f}}{1 + \beta(\hat{x})h\hat{f}} = 0,$$

that is,

$$\lambda^2 - \lambda \left(a - 2\mu\hat{f} - \frac{\beta(\hat{x})\hat{u}}{(1 + \beta(\hat{x})h\hat{f})^2} \right) \\ + \frac{\alpha\beta(\hat{x})\hat{u}}{(1 + \beta(\hat{x})h\hat{f})^2} \frac{\beta(\hat{x})\hat{f}}{1 + \beta(\hat{x})h\hat{f}} = 0. \tag{A.13}$$

In Chapter 4 we assumed (in order to have asymptotical stability of the non-trivial equilibrium) that the trace of the differential matrix of the prey predator system at the equilibrium point was negative, which led to the condition,

$$a - 2\mu\hat{f} - \frac{\beta(\hat{x})\hat{u}}{(1 + \beta(\hat{x})h\hat{f})^2} < 0. \tag{A.14}$$

Since $\frac{\alpha\beta(\hat{x})\hat{u}}{(1 + \beta(\hat{x})h\hat{f})^2} \frac{\beta(\hat{x})\hat{f}}{1 + \beta(\hat{x})h\hat{f}} > 0$ it is obvious that, under the hypothesis (A.14), the equation (A.13) does not have a solution for $\lambda \in D_0$.

Our aim is to apply Theorem 5.1.17 to the prey predator model (A.8). Therefore one of the hypotheses that we have to prove is that $\omega_\varepsilon(\lambda) \xrightarrow{\varepsilon \rightarrow 0} \omega_0(\lambda)$ uniformly on λ in compact sets contained in D_0 (it is one of the hypotheses of Theorem 5.1.9).

In order to show it, let us consider the following operators in $\mathbb{R} \times M$ (where M is the space of Radon measures),

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$$A_0 = \begin{pmatrix} a - \mu\hat{f} & -\int_0^\infty \frac{\beta(x)\hat{f}}{1 + \beta(x)h\hat{f}} \cdot dx \\ 0 & \frac{\alpha\beta(x)\hat{f}}{1 + \beta(x)h\hat{f}} - d(x) \end{pmatrix}, \quad (\text{A.15})$$

$$S_0 = \begin{pmatrix} -\mu\hat{f} - \frac{\beta(\hat{x})\hat{u}}{(1 + \beta(\hat{x})h\hat{f})^2} & 0 \\ \frac{\alpha\beta(x)\hat{u}\delta_{\hat{x}}}{(1 + \beta(x)h\hat{f})^2} & 0 \end{pmatrix}. \quad (\text{A.16})$$

We can define

$$g_0(\lambda) := \det(I + S_0(A_0 - \lambda I)^{-1})|_{R(S_0)}. \quad (\text{A.17})$$

The operator $(A_0 - \lambda I)^{-1}$ can be computed explicitly

$$(A_0 - \lambda I)^{-1} = \begin{pmatrix} \frac{1}{(a - \mu\hat{f} - \lambda)} & \frac{1}{(a - \mu\hat{f} - \lambda)} \int_0^\infty \frac{\beta(x)\hat{f}}{1 + \beta(x)h\hat{f}} \frac{1}{\frac{\alpha\beta(x)\hat{f}}{1 + \beta(x)h\hat{f}} - d(x) - \lambda} \cdot dx \\ 0 & \frac{1}{\frac{\alpha\beta(x)\hat{f}}{1 + \beta(x)h\hat{f}} - d(x) - \lambda} \end{pmatrix}.$$

The range of S_0 is one dimensional and generated by

$$\begin{pmatrix} -\mu\hat{f} - \frac{\beta(\hat{x})\hat{u}}{(1 + \beta(\hat{x})h\hat{f})^2} \\ \frac{\alpha\beta(x)\hat{u}\delta_{\hat{x}}}{(1 + \beta(x)h\hat{f})^2} \end{pmatrix}.$$

Therefore we can compute

$$\begin{aligned}
g_0(\lambda) &= 1 + \left(\frac{1}{(a - \mu\hat{f} - \lambda)} \right) \left(-\mu\hat{f} - \frac{\beta(\hat{x})\hat{u}}{(1 + \beta(\hat{x})h\hat{f})^2} \right) \\
&+ \frac{\alpha\beta(\hat{x})\hat{u}}{(1 + \beta(\hat{x})h\hat{f})^2} \left(\frac{\frac{\beta(\hat{x})\hat{f}}{1 + \beta(\hat{x})h\hat{f}}}{(a - \mu\hat{f} - \lambda) \left(\alpha \frac{\beta(\hat{x})\hat{f}}{1 + \beta(\hat{x})h\hat{f}} - d(\hat{x}) - \lambda \right)} \right) \\
&= 1 + \left(\frac{1}{(a - \mu\hat{f} - \lambda)} \right) \left(-\mu\hat{f} - \frac{\beta(\hat{x})\hat{u}}{(1 + \beta(\hat{x})h\hat{f})^2} \right) \\
&+ \frac{\alpha\beta(\hat{x})\hat{u}}{(1 + \beta(\hat{x})h\hat{f})^2} \left(\frac{\frac{\beta(\hat{x})\hat{f}}{1 + \beta(\hat{x})h\hat{f}}}{(a - \mu\hat{f} - \lambda)(-\lambda)} \right).
\end{aligned}$$

Let us note that $g_0(\lambda) = \omega_0(\lambda)$. This implies that, under the hypotheses of Theorem 4.3.7, $g_0(\lambda) \neq 0$ for $\lambda \in D_0$.

Proposition A.1.2 *Let $\omega_\varepsilon(\lambda) := \det(I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1})$ where \tilde{A}_ε and S_ε are defined by (A.10) and (A.11) respectively. Then*

$$\omega_\varepsilon(\lambda) \xrightarrow{\varepsilon \rightarrow 0} g_0(\lambda) (= \omega_0(\lambda))$$

uniformly on λ in compact sets contained in D_0

Proof: It is enough showing that

$$\left\| (S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1}) \Big|_{R(S_\varepsilon)} - (S_\varepsilon(A_0 - \lambda I)^{-1}) \Big|_{R(S_\varepsilon)} \right\| \xrightarrow{\varepsilon \rightarrow 0} 0 \quad (\text{A.18})$$

where A_0 is defined by (A.15), and that

$$\left\| (S_\varepsilon(A_0 - \lambda I)^{-1}) \Big|_{R(S_\varepsilon)} - (S_0(A_0 - \lambda I)^{-1}) \Big|_{R(S_0)} \right\| \xrightarrow{\varepsilon \rightarrow 0} 0. \quad (\text{A.19})$$

where S_0 is defined by (A.16).

Let us denote by $B_\varepsilon := \tilde{A}_\varepsilon - A_0$. Then

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$$B_\varepsilon = \begin{pmatrix} -\mu f_\varepsilon + \mu \hat{f} & -\int_0^\infty \frac{\beta(x) f_\varepsilon}{1 + \beta(x) h f_\varepsilon} \cdot dx \\ & +\int_0^\infty \frac{\beta(x) \hat{f}}{1 + \beta(x) h \hat{f}} \cdot dx \\ 0 & \frac{\alpha \beta(x) f_\varepsilon}{1 + \beta(x) h f_\varepsilon} - \frac{\alpha \beta(x) \hat{f}}{1 + \beta(x) h \hat{f}} \\ & -\varepsilon \frac{\alpha \beta(x) f_\varepsilon}{1 + \beta(x) h f_\varepsilon} + \varepsilon \int_0^\infty \alpha \gamma(x, y) \frac{\beta(y) f_\varepsilon}{1 + \beta(y) h f_\varepsilon} \cdot dy \end{pmatrix}$$

Then

$$\begin{aligned} (\tilde{A}_\varepsilon - \lambda I)^{-1} &= R(\lambda, \tilde{A}_\varepsilon) = R(\lambda, (A_0 + B_\varepsilon)) \\ &= R(\lambda, A_0)(I - B_\varepsilon R(\lambda, A_0))^{-1} \\ &= R(\lambda, A_0) \sum_{n=0}^{\infty} (B_\varepsilon R(\lambda, A_0))^n \end{aligned}$$

where in the last equality we have used that, as $\|B_\varepsilon\| \xrightarrow{\varepsilon \rightarrow 0} 0$, for ε small enough $\|B_\varepsilon R(\lambda, A_0)\| < 1$.

Hence, for ε small enough

$$\begin{aligned} \|(S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1}) - (S_\varepsilon(A_0 - \lambda I)^{-1})\| &= \\ \|S_\varepsilon R(\lambda, A_0) \sum_{i=0}^{\infty} (B_\varepsilon R(\lambda, A_0))^i - S_\varepsilon R(\lambda, A_0)\| &= \\ \|S_\varepsilon R(\lambda, A_0) \sum_{i=1}^{\infty} (B_\varepsilon R(\lambda, A_0))^i\| &\leq \\ \|S_\varepsilon\| \|R(\lambda, A_0)\| \frac{\|B_\varepsilon R(\lambda, A_0)\|}{1 - \|B_\varepsilon R(\lambda, A_0)\|} \end{aligned}$$

where in the last inequality we have used that

$$\left\| \sum_{i=1}^{\infty} (B_\varepsilon R(\lambda, A_0))^i \right\| \leq \sum_{i=1}^{\infty} \|B_\varepsilon R(\lambda, A_0)\|^i = \frac{\|B_\varepsilon R(\lambda, A_0)\|}{1 - \|B_\varepsilon R(\lambda, A_0)\|}.$$

As $R(\lambda, A_0)$ and S_ε are bounded operators and $\|B_\varepsilon\| \xrightarrow{\varepsilon \rightarrow 0} 0$ we obtain that

$$\|(S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1}) - (S_\varepsilon(A_0 - \lambda I)^{-1})\| \xrightarrow{\varepsilon \rightarrow 0} 0.$$

Therefore we have that

$$\|(S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1})|_{R(S_\varepsilon)} - (S_\varepsilon(A_0 - \lambda I)^{-1})|_{R(S_\varepsilon)}\| \xrightarrow{\varepsilon \rightarrow 0} 0.$$

In order to prove (A.19) let us compute $S_\varepsilon R(\lambda, A_0)$ in the basis of the range of S_ε which is

$$\left(\begin{array}{c} -\mu f_\varepsilon - \int_0^\infty \frac{\beta(x)u_\varepsilon}{(1 + \beta(x)hf_\varepsilon)^2} dx \\ (1 - \varepsilon)\alpha \frac{\beta(x)u_\varepsilon}{1 + \beta(x)hf_\varepsilon} + \varepsilon \int_0^\infty \alpha \gamma(x, y) \frac{\beta(y)u_\varepsilon}{1 + \beta(y)hf_\varepsilon} dy \end{array} \right).$$

Then

$$\begin{aligned} S_\varepsilon R(\lambda, A_0)|_{R(S_\varepsilon)} &= \frac{1}{(a - \mu f_\varepsilon - \lambda)} \left(-\mu f_\varepsilon - \int_0^\infty \frac{\beta(x)u_\varepsilon}{(1 + \beta(x)hf_\varepsilon)^2} dx \right) \\ &+ \frac{1}{(a - \mu f_\varepsilon - \lambda)} \int_0^\infty \frac{\beta(x)f}{1 + \beta(x)hf} \left(\frac{(1 - \varepsilon)\alpha \frac{\beta(x)u_\varepsilon}{(1 + \beta(x)hf_\varepsilon)^2} + \varepsilon \int_0^\infty \alpha \gamma(x, y) \frac{\beta(y)u_\varepsilon}{1 + \beta(y)hf_\varepsilon} dy}{\frac{\alpha \beta(x)f}{1 + \beta(x)hf} - d(x) - \lambda} \right) dx \end{aligned}$$

The convergence results obtained in Chapter 4 imply that

$$\begin{aligned} S_\varepsilon R(\lambda, A_0)|_{R(S_\varepsilon)} &\xrightarrow{\varepsilon \rightarrow 0} S_0 R(\lambda, A_0)|_{R(S_0)} \\ &= \left(\frac{1}{(a - \mu \hat{f} - \lambda)} \right) \left(-\mu \hat{f} - \frac{\beta(\hat{x})\hat{u}}{(1 + \beta(\hat{x})h\hat{f})^2} \right) \\ &+ \frac{\alpha \beta(\hat{x})\hat{u}}{(1 + \beta(\hat{x})h\hat{f})^2} \left(\frac{\frac{\beta(\hat{x})\hat{f}}{1 + \beta(\hat{x})h\hat{f}}}{(a - \mu \hat{f} - \lambda) \left(\alpha \frac{\beta(\hat{x})\hat{f}}{1 + \beta(\hat{x})h\hat{f}} - d(\hat{x}) - \lambda \right)} \right) \\ &= \left(\frac{1}{(a - \mu \hat{f} - \lambda)} \right) \left(-\mu \hat{f} - \frac{\beta(\hat{x})\hat{u}}{(1 + \beta(\hat{x})h\hat{f})^2} \right) \\ &+ \frac{\alpha \beta(\hat{x})\hat{u}}{(1 + \beta(\hat{x})h\hat{f})^2} \left(\frac{\beta(\hat{x})\hat{f}}{(a - \mu \hat{f} - \lambda)(-\lambda)} \right). \end{aligned}$$

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□

We have just proved that $\omega_\varepsilon(\lambda) \xrightarrow{\varepsilon \rightarrow 0} g_0(\lambda)(= \omega_0(\lambda))$ uniformly on λ in compact sets contained in D_0 . Since, under the hypotheses of Theorem 4.3.7, $g_0(\lambda)$ does not vanish in D_0 , using the same argument as in the proof of Theorem 5.1.9 we will be able to prove that, there exist $0 < L_1$ and $\delta > 0$ such that for ε small $\omega_\varepsilon(\lambda)$ does not vanish for $\lambda \in \{\lambda \in \mathbb{C} \text{ s.t. } \operatorname{Re} \lambda \geq 0, L_1 \leq |\lambda|\} \cap \{\lambda \in \mathbb{C} \text{ s.t. } |\lambda - (a - \mu \hat{f})| \geq \delta\}$. Now we will prove that for ε small $\omega_\varepsilon(a - \mu \hat{f}) \neq 0$. In order to show it we will use the following result.

Lemma A.1.3 *Let $f_0(\lambda)$ be a meromorphic function. Let λ_0 be a simple pole of f_0 . Let $f_\varepsilon(\lambda)$ be a family of meromorphic functions. Let us assume that for every ε small enough, λ_ε is a simple pole of f_ε . Moreover, let us assume that $\lambda_\varepsilon \xrightarrow{\varepsilon \rightarrow 0} \lambda_0$ and that*

$$f_\varepsilon(\lambda) \xrightarrow{\varepsilon \rightarrow 0} f_0(\lambda)$$

uniformly on compact sets that do not contain λ_0 .

Then $f_\varepsilon(\lambda_0) \neq 0$ for ε small enough.

Proof: If we develop f_0 by the Laurent series at λ_0 we can write

$$f_0(\lambda) = \frac{a_{-1}}{\lambda - \lambda_0} + h_0(\lambda)$$

where $h_0(\lambda)$ is an holomorphic function and $a_{-1} = \frac{1}{2\pi i} \int_C f_0(\xi) d\xi$ where C is a positively oriented small circle enclosing λ_0 but excluding other poles of f_0 .

In the same way

$$f_\varepsilon(\lambda) = \frac{(b_{-1})_\varepsilon}{\lambda - \lambda_\varepsilon} + h_\varepsilon(\lambda)$$

where $h_\varepsilon(\lambda)$ is an holomorphic function and $(b_{-1})_\varepsilon = \frac{1}{2\pi i} \int_C f_\varepsilon(\xi) d\xi$, and where we have used that, since $\lambda_\varepsilon \xrightarrow{\varepsilon \rightarrow 0} \lambda_0$, for ε small enough C also encloses λ_ε .

Therefore

$$\frac{(b_{-1})_\varepsilon}{\lambda - \lambda_\varepsilon} \xrightarrow{\varepsilon \rightarrow 0} \frac{a_{-1}}{\lambda - \lambda_0}$$

uniformly on compact sets that do not contain λ_0 .

This implies that $h_\varepsilon(\lambda) \xrightarrow{\varepsilon \rightarrow 0} h_0(\lambda)$ uniformly on compact sets that do not contain λ_0 . Since

$$h_\varepsilon(\lambda_0) = \frac{1}{2\pi i} \int_C \frac{h_\varepsilon(\xi)}{\xi - \lambda_0} d\xi \xrightarrow{\varepsilon \rightarrow 0} \frac{1}{2\pi i} \int_C \frac{h_0(\xi)}{\xi - \lambda_0} d\xi = h_0(\lambda_0),$$

we have that $h_\varepsilon(\lambda) \xrightarrow{\varepsilon \rightarrow 0} h_0(\lambda)$ uniformly on compact sets in \mathbb{C} . Then

$$(\lambda - \lambda_\varepsilon)f_\varepsilon(\lambda) = (b_{-1})_\varepsilon + (\lambda - \lambda_\varepsilon)h_\varepsilon(\lambda) \xrightarrow{\varepsilon \rightarrow 0} a_{-1} + (\lambda - \lambda_0)h_0(\lambda) = (\lambda - \lambda_0)f_0(\lambda)$$

uniformly on compact sets in \mathbb{C} . Applying Rouché's theorem we obtain that, for ε small enough, $(\lambda - \lambda_\varepsilon)f_\varepsilon(\lambda)$ does not vanish at λ_0 and therefore that $f_\varepsilon(\lambda_0) \neq 0$. □

Remark A.1.4 *In fact we have proved that, for ε small enough there exists $\delta > 0$ such that $\omega_\varepsilon(\lambda) \neq 0$ for λ such that $|\lambda - \lambda_0| < \delta$.*

Proposition A.1.5 *Let (\hat{f}, \hat{u}) be the equilibrium point of the ordinary differential equations prey predator model (A.12). Let $\omega_\varepsilon = \det(I + S_\varepsilon(\tilde{A}_\varepsilon \lambda I)^{-1})$ where \tilde{A}_ε and S_ε are the operators defined in (A.10) and (A.11) respectively. Then for ε small there exists $\delta > 0$ such that $\omega_\varepsilon(\lambda) \neq 0$ for λ such that $|\lambda - (a - \mu \hat{f})| < \delta$.*

Proof: An application of Lemma A.1.3 and Remark A.1.4. □

Theorem A.1.6 *Let $\omega_\varepsilon(\lambda) := \det(I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1})$ where \tilde{A}_ε and S_ε are defined by (A.10) and (A.11) respectively. Then, under the hypotheses of Theorem 4.3.7 for all $L_1 > 0$ there exists ε small enough such that $\omega_\varepsilon(\lambda)$ does not vanish for $\lambda \in \{\lambda \in \mathbb{C} \text{ s.t. } \operatorname{Re} \lambda \geq 0, L_1 \leq |\lambda|\}$.*

Proof: The operator \tilde{A}_ε generates a bounded analytic semigroup, therefore it satisfies $\|R(\lambda, \tilde{A}_\varepsilon)\| \leq \frac{C_\varepsilon}{|\lambda|}$. By remark 5.1.12 and the fact that $\|S_\varepsilon\|$ is bounded (with respect to ε) we obtain that $\sup_\varepsilon \|S_\varepsilon\|C_\varepsilon$ is bounded.

Theorem 5.1.9 gives that for ε small there exist $0 < L_1$ and $\delta > 0$ such that $\omega_\varepsilon(\lambda)$ does not vanish for $\lambda \in \{\lambda \in \mathbb{C} \text{ s.t. } \operatorname{Re} \lambda \geq 0, L_1 \leq |\lambda|\} \cap \{\lambda \in \mathbb{C} \text{ s.t. } |\lambda - (a - \mu \hat{f})| \geq \delta\} := D_1$. However, the result does not follow from a direct application of Theorem 5.1.9 because $\omega_\varepsilon(\lambda)$ is not defined for $a - \mu f_\varepsilon$ and $\omega_0(\lambda)$ is not defined for $a - \mu \hat{f}$. Nevertheless, since $a - \mu f_\varepsilon \xrightarrow{\varepsilon \rightarrow 0} a - \mu \hat{f}$, using the same argument as in the proof of Theorem 5.1.9 we obtain that for ε small $\omega_\varepsilon(\lambda)$ does not vanish for $\lambda \in D_1$.

By Proposition A.1.5 we obtain that, in fact, for ε small enough $\omega_\varepsilon(\lambda)$ does not vanish for $\lambda \in \{\lambda \in \mathbb{C} \text{ s.t. } \operatorname{Re} \lambda \geq 0, L_1 \leq |\lambda|\}$. □

Let us recall that, in order to prove stability of the equilibrium $(f_\varepsilon, u_\varepsilon)$ of the prey predator model (4.35) we have to show that $\omega_\varepsilon(\lambda) = \det(I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1}) \neq 0$ for $\lambda \in D_\varepsilon := \{\lambda \in \mathbb{C} \text{ s.t. } \operatorname{Re} \lambda \geq 0, \lambda \neq 0, \lambda \neq a - \mu f_\varepsilon\}$, that $0 \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$ and moreover, that $a - \mu f_\varepsilon \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$ (where recall

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$(\tilde{A}_\varepsilon + S_\varepsilon)$ is the linearization of (4.35) at $(f_\varepsilon, u_\varepsilon)$.

By Theorem A.1.6 what is left to show is that $0 \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$, that $a - \mu f_\varepsilon \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$ and that, for ε small, $\omega_\varepsilon(\lambda) \neq 0$ for $\lambda \in \{\lambda \in \mathbb{C} \text{ s.t. } \operatorname{Re}\lambda \geq 0, |\lambda| < L_1\}$ for some $L_1 > 0$.

Proposition A.1.7 *Let $\tilde{A}_\varepsilon, S_\varepsilon$ be the operators given by (A.10) and (A.11) respectively. Then $0 \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$.*

Proof: 0 is a simple eigenvalue of \tilde{A}_ε with corresponding eigenfunction $(f_\varepsilon, u_\varepsilon)$. By the Weinstein Aronszajn formula, if we show that 0 is a pole of order 1 of $\omega_\varepsilon(\lambda) = \det((I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1})|_{R(S_\varepsilon)})$, we will obtain that $0 \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$.

The range of S_ε is one dimensional and a basis is

$$DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} = \begin{pmatrix} -\mu f_\varepsilon - \int_0^\infty \frac{\beta(x)u_\varepsilon}{(1 + \beta(x)hf_\varepsilon)^2} dx \\ (1 - \varepsilon)\alpha \frac{\beta(x)f_\varepsilon}{1 + \beta(x)hu_\varepsilon} + \varepsilon \int_0^\infty \alpha\gamma(x, y) \frac{\beta(y)u_\varepsilon}{1 + \beta(y)hf_\varepsilon} dy \end{pmatrix}.$$

In the proof of Theorem 5.1.14 we showed that 0 is a pole of order 1 of ω_ε (and therefore $0 \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$) if and only if the following two conditions

$$DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} \notin \operatorname{Range}(\tilde{A}_\varepsilon). \quad (\text{A.20})$$

$$F \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} \neq 0. \quad (\text{A.21})$$

hold.

Since $F \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} = f_\varepsilon$, condition (A.21) holds.

Let us now show that (A.20) also holds.

Since $N(\tilde{A}_\varepsilon^*) = \operatorname{Range}(\tilde{A}_\varepsilon)^\perp$ (see [4]), where \tilde{A}_ε^* denotes the adjoint operator of \tilde{A}_ε , $N(\tilde{A}_\varepsilon^*)$ denotes the kernel of the operator \tilde{A}_ε^* and \perp denotes orthogonal (in the dual space sense), condition (A.20) is equivalent to

$$\left\langle \begin{pmatrix} f_\varepsilon^* \\ u_\varepsilon^* \end{pmatrix}, DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} \right\rangle \neq 0, \quad (\text{A.22})$$

where $\begin{pmatrix} f_\varepsilon^* \\ u_\varepsilon^* \end{pmatrix}$ is the eigenfunction of eigenvalue 0 of \tilde{A}_ε^* .

Condition (A.22) is

$$\begin{aligned} & -\mu f_\varepsilon f_\varepsilon^* - f_\varepsilon^* \int_0^\infty \frac{\beta(x)u_\varepsilon}{(1 + \beta(x)hf_\varepsilon)^2} + (1 - \varepsilon)\alpha \int_0^\infty \frac{\beta(x)u_\varepsilon u_\varepsilon^*}{(1 + \beta(x)hf_\varepsilon)^2} dx \\ & + \varepsilon \int_0^\infty u_\varepsilon^*(x) \int_0^\infty \alpha \gamma(x, y) \frac{\beta(y)u_\varepsilon(y)}{(1 + \beta(x)hf_\varepsilon)^2} dy dx \neq 0. \end{aligned}$$

Computing \tilde{A}_ε^* we obtain

$$\tilde{A}_\varepsilon^* = \begin{pmatrix} a - \mu f_\varepsilon & 0 \\ \frac{-\beta(x)f_\varepsilon}{1 + \beta(x)hf_\varepsilon} & -d(x) + (1 - \varepsilon)\alpha \frac{\beta(x)f_\varepsilon}{1 + \beta(x)hf_\varepsilon} \\ & + \varepsilon \alpha \frac{\beta(x)f_\varepsilon}{1 + \beta(x)hf_\varepsilon} \int_0^\infty \gamma(y, x) \cdot dy \end{pmatrix}.$$

Since $\tilde{A}_\varepsilon^* \begin{pmatrix} f_\varepsilon^* \\ u_\varepsilon^* \end{pmatrix} = 0$ we obtain that $f_\varepsilon^* = 0$ and u_ε^* satisfies

$$\begin{aligned} & \left(-d(x) + (1 - \varepsilon)\alpha \frac{\beta(x)f_\varepsilon}{1 + \beta(x)hf_\varepsilon} \right) u_\varepsilon^* \\ & + \varepsilon \alpha \frac{\beta(x)f_\varepsilon}{1 + \beta(x)hf_\varepsilon} \int_0^\infty \gamma(y, x) u_\varepsilon^*(y) dy = 0. \end{aligned}$$

The operator $-d(x) + (1 - \varepsilon)\alpha \frac{\beta(x)f_\varepsilon}{1 + \beta(x)hf_\varepsilon} + \varepsilon \alpha \frac{\beta(x)f_\varepsilon}{1 + \beta(x)hf_\varepsilon} \int_0^\infty \gamma(y, x) \cdot dy$ is the adjoint operator of

$$T_\varepsilon(f_\varepsilon) = -d(x) + (1 - \varepsilon)\alpha \frac{\beta(x)f_\varepsilon}{1 + \beta(x)hf_\varepsilon} + \varepsilon \int_0^\infty \alpha \gamma(x, y) \frac{\beta(y)f_\varepsilon}{1 + \beta(y)hf_\varepsilon} \cdot dy.$$

In Chapter 3 we proved that the operator $T_\varepsilon(f_\varepsilon)$ satisfies the hypothesis of Theorem 2.4.14. Applying this theorem we obtain that u_ε^* is strictly positive (and also that u_ε is strictly positive) and therefore

$$\begin{aligned} \left\langle \begin{pmatrix} f_\varepsilon^* \\ u_\varepsilon^* \end{pmatrix}, DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} \right\rangle &= (1 - \varepsilon)\alpha \int_0^\infty \frac{\beta(x)u_\varepsilon(x)u_\varepsilon^*(x)}{(1 + \beta(x)hf_\varepsilon)^2} dx \\ &+ \varepsilon \int_0^\infty u_\varepsilon^*(x) \int_0^\infty \alpha \gamma(x, y) \frac{\beta(y)u_\varepsilon(y)}{(1 + \beta(x)hf_\varepsilon)^2} dy dx > 0 \end{aligned}$$

and the proof is complete. □

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Proposition A.1.8 *Let $\tilde{A}_\varepsilon, S_\varepsilon$ be the operators given by (A.10) and (A.11) respectively. Then $a - \mu f_\varepsilon \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$.*

Proof: $a - \mu f_\varepsilon$ is a simple eigenvalue of \tilde{A}_ε with corresponding eigenfunction $\begin{pmatrix} 1 \\ 0 \end{pmatrix}$.

In the same way as in the proof of Proposition A.1.7, by the Weinstein-Aronszajn formulas, if we show that $a - \mu f_\varepsilon$ is a pole of order 1 of $\omega_\varepsilon(\lambda) = \det((I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1})|_{R(S_\varepsilon)})$ we will obtain that $a - \mu f_\varepsilon \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$.

Let us recall that the range of S_ε is $DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix}$.

In the same way as in the proof of Theorem 5.1.14, since $a - \mu f_\varepsilon$ is a simple pole of $R(\lambda, \tilde{A}_\varepsilon)$ by the Laurent series at $\lambda = a - \mu f_\varepsilon$ we have

$$\begin{aligned} & (I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1})DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} \\ &= DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} + S_\varepsilon \frac{1}{(\lambda - (a - \mu f_\varepsilon))} P_\varepsilon DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} \\ &+ S_\varepsilon \sum_{n=0}^{\infty} \frac{1}{2\pi i} (\lambda - (a - \mu f_\varepsilon))^n \int_\Gamma - \frac{(\tilde{A}_\varepsilon - \lambda I)^{-1} DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix}}{(\lambda - (a - \mu f_\varepsilon))^{n+1}} d\lambda, \end{aligned}$$

where Γ is a positively-oriented small circle enclosing $\lambda = a - \mu f_\varepsilon$ but excluding other eigenvalues of \tilde{A}_ε and P_ε is the spectral projection corresponding to the spectral set $\{a - \mu f_\varepsilon\}$.

$\omega_\varepsilon(\lambda)$ will have a pole of first order in $a - \mu f_\varepsilon$ if $S_\varepsilon P_\varepsilon DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} \neq 0$.

Since the eigenvector corresponding to the eigenvalue $a - \mu f_\varepsilon$ of the operator \tilde{A}_ε is of the form $\begin{pmatrix} 1 \\ 0 \end{pmatrix}$ we have

$$P_\varepsilon DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} = \begin{pmatrix} -\mu f_\varepsilon - \int_0^\infty \frac{\beta(x)u_\varepsilon}{(1 + \beta(x)hf_\varepsilon)^2} \\ 0 \end{pmatrix}.$$

Finally, since the equilibrium $(f_\varepsilon, u_\varepsilon)$ is strictly positive we have $S_\varepsilon P_\varepsilon DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} \neq 0$ and the proof is complete. \square

Summarizing, with all the results we proved so far for the prey predator model, by Theorem 5.1.17, showing that

$$|F((\tilde{A}_\varepsilon - \lambda I)^{-1}(I - P_\varepsilon)DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix})| \quad (\text{A.23})$$

(where P_ε is the spectral projection corresponding to the eigenvalue zero of the operator \tilde{A}_ε) is bounded for λ close to zero with $\text{Re}\lambda \geq 0$ and ε small, we would obtain that the equilibrium $(f_\varepsilon, u_\varepsilon)$ is uniformly asymptotically stable.

In this particular model we can compute

$$\begin{aligned} & F((\tilde{A}_\varepsilon - \lambda I)^{-1}DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix}) = \\ & \text{first component of } (\tilde{A}_\varepsilon - \lambda I)^{-1}DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} = \\ & \frac{1}{a - \mu f_\varepsilon - \lambda} \left(-\mu f_\varepsilon - \int_0^\infty \frac{\beta(x)u_\varepsilon(x)}{(1 + \beta(x)hf_\varepsilon)^2} dx \right) + \\ & \frac{1}{a - \mu f_\varepsilon - \lambda} \int_0^\infty \frac{\beta(x)f_\varepsilon}{1 + \beta(x)f_\varepsilon} R(\lambda, T_\varepsilon(f_\varepsilon)) \\ & \left((1 - \varepsilon)\alpha \frac{\beta(x)u_\varepsilon(x)}{(1 + \beta(x)hf_\varepsilon)^2} + \varepsilon \int_0^\infty \alpha\gamma(x, y) \frac{\beta(y)u_\varepsilon(y)}{1 + \beta(y)hf_\varepsilon} dy \right) dx \end{aligned}$$

Since 0 is a simple pole of $R(\lambda, T_\varepsilon(f_\varepsilon))$ we can write

$$R(\lambda, T_\varepsilon(f_\varepsilon)) = \frac{\tilde{P}_\varepsilon}{\lambda} + R(\lambda, T_\varepsilon(f_\varepsilon))(I - \tilde{P}_\varepsilon)$$

where \tilde{P}_ε is the projection corresponding to 0. So, in this case, to see that A.23 is bounded for λ close to zero with $\text{Re}\lambda \geq 0$ and ε small is equivalent to see that

$$\begin{aligned} & \frac{1}{a - \mu f_\varepsilon - \lambda} \int_0^\infty \frac{\beta(x)f_\varepsilon}{1 + \beta(x)f_\varepsilon} R(\lambda, T_\varepsilon(f_\varepsilon)) (I - \tilde{P}_\varepsilon) \\ & \left((1 - \varepsilon)\alpha \frac{\beta(x)u_\varepsilon(x)}{(1 + \beta(x)hf_\varepsilon)^2} + \varepsilon \int_0^\infty \alpha\gamma(x, y) \frac{\beta(y)u_\varepsilon(y)}{1 + \beta(y)hf_\varepsilon} dy \right) dx \end{aligned}$$

is bounded for λ close to zero with $\text{Re}\lambda \geq 0$ and ε small.

It is an open problem to prove this boundedness due to the undetermined limit of the form $\infty \cdot 0$ appearing in the first term. The resolvent operator tends to be singular at 0 when $\varepsilon \xrightarrow{\varepsilon \rightarrow 0} 0$ because $T_\varepsilon(f_\varepsilon)$ tends to a multiplication operator (with continuous spectrum), whereas the projection $I - \tilde{P}_\varepsilon$ acts on a vector which approaches $\langle \vec{u}_\varepsilon \rangle = \text{Ker}(I - \tilde{P}_\varepsilon)$.

A.2 Maturation age

Let us recall the maturation age model of Chapter 4

$$\begin{cases} u_t(x, t) = (1 - \varepsilon)b(x)v(x, t) + \varepsilon \int_0^\infty b(y)\gamma(x, y)v(y, t)dy \\ \quad - m_1 \left(\int_0^\infty u(y, t)dy \right) u(x, t) - xu(x, t), \\ v_t(x, t) = xu(x, t) - m_2 \left(\int_0^\infty v(y, t)dy \right) v(x, t). \end{cases} \quad (\text{A.24})$$

In Chapter 4 we proved, under the conditions of Theorem 1.3.6 and for ε small enough, the existence of a positive equilibrium, $(u_\varepsilon, v_\varepsilon)$, of (A.24).

In this case, since the environment is not one dimensional, Theorem 5.1.17 does not suffices to prove stability of $(u_\varepsilon, v_\varepsilon)$. However, let us show that the model satisfies the hypotheses of Theorem 5.1.9.

If we linearize around the equilibrium $(u_\varepsilon, v_\varepsilon)$, we obtain (using the Taylor formula and eliminating the higher order terms)

$$\begin{aligned} \begin{pmatrix} u \\ v \end{pmatrix}_t &= \begin{pmatrix} -x - m_1(P_\varepsilon) & (1 - \varepsilon)b(x)v(x, t) \\ & + \varepsilon \int_0^\infty b(y)\gamma(x, y) \cdot dy \\ x & -m_2(Q_\varepsilon) \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix} \\ &+ \begin{pmatrix} -m'_1(P_\varepsilon)u_\varepsilon \int_0^\infty \cdot & 0 \\ 0 & -m'_2(Q_\varepsilon)v_\varepsilon \int_0^\infty \cdot \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix} \quad (\text{A.25}) \\ &:= \tilde{A}_\varepsilon \begin{pmatrix} u \\ v \end{pmatrix} + S_\varepsilon \begin{pmatrix} u \\ v \end{pmatrix} \end{aligned}$$

We can define, in this case, in the same way as in Chapter 5,

$$\omega_\varepsilon(\lambda) := \det(I + (S_\varepsilon(\tilde{A}_\varepsilon - \lambda)^{-1})|_{R(S_\varepsilon)}).$$

Let us denote by $D := \{\lambda \in \mathbb{C} \text{ s.t. } \operatorname{Re} \lambda \geq 0, \lambda \neq 0\}$.

Since 0 is a strictly dominant eigenvalue of \tilde{A}_ε , $\omega_\varepsilon(\lambda)$ is holomorphic for all $\lambda \in D$.

Let us recall the finite dimensional model for the maturation age studied in Chapter 1 at the ESS value

$$\begin{cases} u' &= b(\hat{x})v(t) - m_1(u(t))u(t) - \hat{x}u(t), \\ v' &= \hat{x}u(t) - m_2(v(t))v(t). \end{cases} \quad (\text{A.26})$$

In Chapter 1 we proved, under the hypotheses of Theorem 1.3.6, the existence of a hyperbolic asymptotically stable equilibrium point $(u(\hat{x}), v(\hat{x}))$. Linearizing at the equilibrium point $(u(\hat{x}), v(\hat{x}))$ and eliminating higher order terms we obtain the linear system

$$\begin{aligned} \begin{pmatrix} w_1 \\ w_2 \end{pmatrix}' &= \begin{pmatrix} -m_1(u(\hat{x})) - \hat{x} & b(\hat{x}) \\ \hat{x} & -m_2(v(\hat{x})) \end{pmatrix} \begin{pmatrix} w_1 \\ w_2 \end{pmatrix} \\ &+ \begin{pmatrix} -m_1'(u(\hat{x}))u(\hat{x}) & 0 \\ 0 & -m_2'(v(\hat{x}))v(\hat{x}) \end{pmatrix} \begin{pmatrix} w_1 \\ w_2 \end{pmatrix} \\ &:= \tilde{B}_0 \begin{pmatrix} w_1 \\ w_2 \end{pmatrix} + T_0 \begin{pmatrix} w_1 \\ w_2 \end{pmatrix}. \end{aligned} \quad (\text{A.27})$$

Since the equilibrium point $(u(\hat{x}), v(\hat{x}))$ is hyperbolic and asymptotically stable, $\sigma(\tilde{B}_0 + T_0) \subset \{\lambda : \operatorname{Re}\lambda < 0\}$, therefore

$$\omega_0(\lambda) := \det(I + T_0(\tilde{B}_0 - \lambda I)^{-1}) \neq 0$$

for $\lambda \in D$, that is, the determinant

$$\det \begin{pmatrix} 1 + \frac{(m_2(v(\hat{x})) + \lambda)m_1'(u(\hat{x}))u(\hat{x}))}{f(\lambda)} & \frac{b(\hat{x})m_1'(u(\hat{x}))u(\hat{x})}{f(\lambda)} \\ \frac{\hat{x}m_2'(v(\hat{x}))v(\hat{x})}{f(\lambda)} & 1 + \frac{(\hat{x} + m_1(u(\hat{x}))m_2'(v(\hat{x}))v(\hat{x}))}{f(\lambda)} \end{pmatrix}$$

where $f(\lambda) := (\hat{x} + m_1(u(\hat{x})) + \lambda)(m_2(v(\hat{x})) + \lambda) - \hat{x}b(\hat{x})$, does not vanish for $\lambda \in D$.

Our aim is to apply Theorem 5.1.9 to $\omega_\varepsilon(\lambda)$.

In order to see that $\omega_\varepsilon(\lambda) \rightarrow \omega_0(\lambda)$ uniformly on compact sets in D , let us consider the multiplication operator

A.2. Maturation age

$$A_0 = \begin{pmatrix} -x - m_1(u(\hat{x})) & b(x) \\ x & -m_2(v(\hat{x})) \end{pmatrix} \quad (\text{A.28})$$

in $M \times M$, where M is the space of the measures of Radon, with domain

$$D(A_0) = \{(u, v) \in M \times M \quad : \quad \exists C_u \text{ such that } \langle xf, u \rangle \leq C_u \\ \text{if } \|f\|_\infty = 1\} := D_1 \times M.$$

Lemma A.2.1 *The operator A_0 defined in (A.28) is a closed operator.*

Proof: It is sufficient to show that the operator B defined in D_1 by

$$\langle f, Bu \rangle = \langle xf, u \rangle$$

is closed.

Let us consider a sequence $\{u_n\}_n$ with $u_n \in D_1$ and such that

$$u_n \xrightarrow{n \rightarrow \infty} u \quad (\in M), \quad (\text{A.29})$$

$$Bu_n \xrightarrow{n \rightarrow \infty} v \quad (\in M). \quad (\text{A.30})$$

We would like to prove that $u \in D_1$ and that $Bu = v$.

By (A.29) we have that

$$\sup_{g \in C_c, \|g\|_\infty = 1} |\langle g, u_n - u \rangle| = \|u_n - u\|_M \xrightarrow{n \rightarrow \infty} 0, \quad (\text{A.31})$$

where C_c denotes the space of continuous functions with compact support in $(0, \infty)$.

Let f be a continuous function with compact support. Then by (A.29)

$$\begin{aligned} |\langle xf, u_n \rangle - \langle xf, u \rangle| &= |\langle xf, u_n - u \rangle| \\ &= \max_x |xf| \left\langle \frac{xf}{\max_x |xf|}, u_n - u \right\rangle \xrightarrow{n \rightarrow \infty} 0. \end{aligned}$$

Therefore $\langle f, Bu_n \rangle = \langle xf, u_n \rangle \xrightarrow{n \rightarrow \infty} \langle xf, u \rangle$.

By (A.30) we have that

$$\sup_{g \in C_c, \|g\|_\infty = 1} |\langle g, Bu_n - v \rangle| = \|Bu_n - v\|_M \xrightarrow{n \rightarrow \infty} 0. \quad (\text{A.32})$$

Taking the same f as before, by (A.32) we obtain

$$|\langle f, Bu_n \rangle - \langle f, v \rangle| = \max_x |f| \left\langle \frac{f}{\max_x |f|}, Bu_n - v \right\rangle \xrightarrow{n \rightarrow \infty} 0.$$

That is, $\langle f, Bu_n \rangle \xrightarrow{n \rightarrow \infty} \langle f, v \rangle$.

As we also proved that $\langle f, Bu_n \rangle \xrightarrow{n \rightarrow \infty} \langle xf, u \rangle$, by uniqueness of the limit we have that $\langle xf, u \rangle = \langle f, v \rangle$. Then,

$$|\langle xf, u \rangle| = |\langle f, v \rangle| \leq \|v\|_M \|f\|_\infty,$$

that is, $u \in D_1$.

On the other hand,

$$\langle f, Bu \rangle = \langle xf, u \rangle = \langle f, v \rangle.$$

Therefore $Bu = v$. □

The resolvent operator of A_0 can be computed explicitly

$$(A_0 - \lambda I)^{-1} = \frac{1}{f(\lambda, x)} \begin{pmatrix} -m_2(v(\hat{x})) - \lambda & -b(x) \\ -x & -x - m_1(u(\hat{x})) - \lambda \end{pmatrix}$$

where $f(\lambda, x) := (x + m_1(u(\hat{x})) + \lambda)(m_2(v(\hat{x})) + \lambda) - xb(x)$.

Let us also consider the operator

$$S_0 = \begin{pmatrix} -m'_1(u(\hat{x}))u(\hat{x})\delta_{\hat{x}} \int_0^\infty \cdot(dx) & 0 \\ 0 & -m'_2(v(\hat{x}))v(\hat{x})\delta_{\hat{x}} \int_0^\infty \cdot(dx) \end{pmatrix}$$

(where we understand $\int_0^\infty \mu(dx) = \mu(0, \infty)$) in $M \times M$.

We define $h_0(\lambda) := \det((I + S_0(A_0 - \lambda I)^{-1})|_{R(S_0)})$. The function $h_0(\lambda)$ can be computed explicitly. If we consider the basis of the range of S_0

$$\langle (u(\hat{x})\delta_{\hat{x}}, 0), (0, v(\hat{x})\delta_{\hat{x}}),$$

then $h_0(\lambda)$ is

$$\det \begin{pmatrix} 1 + \frac{(m_2(v(\hat{x})) + \lambda)m'_1(u(\hat{x}))u(\hat{x})}{f(\lambda)} & \frac{b(\hat{x})m'_1(u(\hat{x}))u(\hat{x})}{f(\lambda)} \\ \frac{\hat{x}m'_2(v(\hat{x}))v(\hat{x})}{f(\lambda)} & 1 + \frac{(\hat{x} + m_1(u(\hat{x})))m'_2(v(\hat{x}))v(\hat{x})}{f(\lambda)} \end{pmatrix}$$

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where $f(\lambda) := (\hat{x} + m_1(u(\hat{x})) + \lambda)(m_2(v(\hat{x})) + \lambda) - \hat{x}b(\hat{x})$.
That is, $h_0(\lambda) = \omega_0(\lambda)$.

Theorem A.2.2 *Let $\omega_\varepsilon(\lambda) = \det(I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1})$ where \tilde{A}_ε and S_ε are defined in (A.25). Let us consider $D = \{\lambda \in \mathbb{C} \text{ such that } \operatorname{Re} \lambda \geq 0, \lambda \neq 0\}$. Then, under the hypothesis of Theorem 1.3.6 and if ε is small enough, $\omega_\varepsilon(\lambda)$ does not vanish for $\lambda \in D$.*

Proof: Let us consider $\omega_0(\lambda) = \det(I + T_0(\tilde{B}_0 - \lambda I)^{-1})$ where \tilde{B}_0 and T_0 are defined in (A.27). We have showed that $\omega_0(\lambda) \neq 0$ for $\lambda \in D$ (because the equilibrium point $(u(\hat{x}), v(\hat{x}))$ of (A.26) is hyperbolic and asymptotically stable).

By Theorem 5.1.9 we have to prove that $\omega_\varepsilon(\lambda) \xrightarrow{\varepsilon \rightarrow 0} \omega_0(\lambda)$ uniformly in λ on compact sets in D .

It suffices to show that

$$\|(S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1})_{|_{R(S_\varepsilon)}} - (S_0(A_0 - \lambda I)^{-1})_{|_{R(S_0)}}\| \xrightarrow{\varepsilon \rightarrow 0} 0.$$

Adding and subtracting $(S_\varepsilon(A_0 - \lambda I)^{-1})_{|_{R(S_\varepsilon)}}$ we have

$$\begin{aligned} & \|(S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1})_{|_{R(S_\varepsilon)}} - (S_0(A_0 - \lambda I)^{-1})_{|_{R(S_0)}}\| \leq \\ & \|(S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1})_{|_{R(S_\varepsilon)}} - (S_\varepsilon(A_0 - \lambda I)^{-1})_{|_{R(S_\varepsilon)}}\| + \\ & \|(S_\varepsilon(A_0 - \lambda I)^{-1})_{|_{R(S_\varepsilon)}} - (S_0(A_0 - \lambda I)^{-1})_{|_{R(S_0)}}\| \end{aligned}$$

We can write $\tilde{A}_\varepsilon = A_0 + B_\varepsilon$ where

$$B_\varepsilon = \begin{pmatrix} -m_1(P_\varepsilon) + m_1(P_0) & -\varepsilon b(x) + \varepsilon \int_0^\infty b(y)\gamma(x, y) \cdot dy \\ 0 & -m_2(Q_\varepsilon) + m_2(Q_0) \end{pmatrix}.$$

Since $\|B_\varepsilon\| \xrightarrow{\varepsilon \rightarrow 0} 0$, by the same argument as in the proof of Proposition A.1.2 we have that

$$\|(S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1})_{|_{R(S_\varepsilon)}} - (S_0(A_0 - \lambda I)^{-1})_{|_{R(S_0)}}\| \xrightarrow{\varepsilon \rightarrow 0} 0$$

holds.

We are reduced to proving

$$\|(S_\varepsilon(A_0 - \lambda I)^{-1})_{|_{R(S_\varepsilon)}} - (S_0(A_0 - \lambda I)^{-1})_{|_{R(S_0)}}\| \xrightarrow{\varepsilon \rightarrow 0} 0.$$

A.2. Maturation age

Computing $S_\varepsilon R(\lambda, A_0)$ in the basis $\langle (u_\varepsilon, 0), (0, v_\varepsilon) \rangle$ of the rank of S_ε we obtain that it is

$$\begin{pmatrix} -m'_1(P_\varepsilon) \int_0^\infty \frac{-m_2(v(\hat{x}))-\lambda}{f(\lambda,x)} u_\varepsilon(x) dx & -m'_1(P_\varepsilon) \int_0^\infty \frac{-b(x)}{f(\lambda,x)} v_\varepsilon(x) dx \\ -m'_2(Q_\varepsilon) \int_0^\infty \frac{-x}{f(\lambda,x)} u_\varepsilon(x) dx & -m'_2(Q_\varepsilon) \int_0^\infty \frac{-x-m_1(u(\hat{x}))-\lambda}{f(\lambda,x)} v_\varepsilon(x) dx \end{pmatrix}.$$

The convergence results of $(u_\varepsilon, v_\varepsilon)$ in Chapter 3 give the result. □

A.2. Maturation age

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