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▶ **To cite this version:**

Sylvie Méléard, Viet Chi Tran. Age-structured Trait Substitution Sequence Process and Canonical Equation. 2007. hal-00181811v1

HAL Id: hal-00181811

https://hal.science/hal-00181811v1

Preprint submitted on 24 Oct 2007 (v1), last revised 25 Oct 2007 (v2)

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Age-structured Trait Substitution Sequence Process and Canonical Equation

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October 24, 2007

Abstract

We are interested in a stochastic model of trait and age-structured population undergoing mutation and selection. We start with a continuous time, discrete individual-centered population process. Taking the large population and rare mutations limits under a well-chosen time-scale separation condition, we obtain a jump process that generalizes the Trait Substitution Sequence process describing Adaptive Dynamics for populations without age structure. Under the additional assumption of small mutations, we derive an age-dependent ordinary differential equation that extends the Canonical Equation. These evolutionary approximations have never been introduced to our knowledge. They are based on ecological phenomena represented by PDEs that generalize the Gurtin-McCamy equation in Demography. Another particularity is that they involve a fitness function, describing the probability of invasion of the resident population by the mutant one, that can not always be computed explicitly. Examples illustrate how adding an age-structure enrich the modelling of structured population by including life history features such as senescence. In the cases considered, we establish the evolutionary approximations and study their long time behavior and the nature of their evolutionary singularities when computation is tractable. Numerical procedures and simulations are carried.

Keywords: Age-structure, adaptive dynamics, mutation-selection, Trait Substitution Sequence, time scale separation, Canonical Equation, interacting particle systems.
AMS Subject Classification: 92D15, 60J80, 60K35, 60F99.

1 Introduction

Structured populations are populations in which individuals differ according to variables that affect their reproductive or survival capacities. These variables can be phenotypic, genotypic or behaviorial *traits* that are assumed to be hereditarily transmitted from a parent to its descendants unless a mutation occurs. They can also be *position*, *sex* or *age*. In this article, we are interested in modelling the adaptive evolution of trait and age-structured populations, describing the ability of a population to generate and select trait diversity at an individual level and through the expression of the individual ages and traits. Individual-centered models allow us to give a realistic description of these phenomena and to obtain macroscopic equations, at a large population scale.

As emphasized by Charlesworth [7], it is important to take age structure into account. Most populations consist in sets of individuals born over a range of past times, with behaviors that depend on their ages. As mentioned in [7], there exist for many species a juvenile and an adult periods. The first period is devoted to maturation and growth, and the individual starts reproducing only during the second period. See the *Tribolium* population (cf. [19]) as an

illustration. For many species, and mammals in particular, fecundity and survival functions are decreasing with age (cf. [32]). Some other species exhibit long postponement of reproduction. The pink salmon *Oncorhynchus Gorbuscha* breeds at about 2 years old, which is approximatively its life expectation (cf. [7, 22]), and the cicada *Magicicada* reproduces and dies at 13-17 years old ([7]) for instance.

Adding an age-structure allows us to study life history traits, such as age at maturity, or to consider senescence phenomena, which describe the fixation of deleterious genes or the decrease of reproductive and survival capacities in the course of life. Many questions concerning these age-structured populations can be raised. How does the age influence the trait evolution? For a given trait, how does the probability of fixation or elimination by natural selection depend on its age of expression? How does the age-structure of a population influence the selective pressure exerted on individuals? Which age distributions will appear at equilibrium for a given trait?

In this paper, our main interest is to generalize to age-structured populations the recent theory of *Adaptive Dynamics*. First models of Adaptive Dynamics have been introduced by Hofbauer and Sigmund [20], Metz *et al.* [26], Dieckmann and Law [10] and rigorous microscopic derivations have been obtained by Champagnat [3, 4], Champagnat *et al.* [6, 5]. In these models, the population is only structured by the trait of interest.

We start with the description of a discrete stochastic individual-centered model of population structured by trait and age. We consider approximations of the microscopic process under a large population asymptotic and obtain in the limit a deterministic partial differential equation (PDE) involving trait and age, that generalizes classical demographic PDEs (see McKendrick [24], Von Foerster [14], Gurtin and McCamy [17], Webb [38], Murray [28], Charlesworth [7], Thieme [35]). This gives us information on the long time behavior of the population. We are then able to characterize rare mutation rates for which it is possible, under an additional assumption of non-coexistence in the long term of two different traits, to separate the time scale of ecology describing the demographic variations in the population and the time scale of evolution linked to the occurrence of mutations. The latter hypothesis generalizes the "Invasion implies Fixation" assumption of the Adaptive Dynamics theory. We prove in this case that the microscopic process converges to the so-called *Age-structured Trait Substitution Sequence Process* that jumps from a monomorphic equilibrium (where all the individuals carry the same trait) to another. This process extends to populations with age-structure the *Trait Substitution Sequence* (TSS) introduced by Metz *et al.* [26]. A difficulty in our case lies in the fact that the fitness function describing the invasion of a mutant trait in the resident population and which appears in the generator of the TSS process can not be computed explicitly. Taking the limit of the TSS when the mutation steps tend to zero gives us an age-dependent ordinary differential equation (ODE), generalizing the *Canonical Equation* proposed by Dieckmann and Law [10]. We show that an explicit expression for the fitness gradient appearing in the ODE is available despite of the implicit definition of the fitness function for the TSS. To our knowledge, the equations that we establish have not been introduced in the biological literature yet and are more general than the ones previously proposed by Dieckmann *et al.* [9], Ernande *et al.* [13], Metz [25], Parvinen *et al.* [30].

Our results point out that in the adaptive dynamics limit, the age-structured TSS and Canonical Equation involve averaged functions in age. The age-structure does not mainly affect the qualitative behavior of the population but plays a role in the trade-offs determining the Evolutionary Stable Strategies (ESS). With age-structure, we gain in realism and refine the results by including effects due to life histories and age-dependent behaviors.

Sections 2 to 3 are devoted to the presentation of the three models of interest: the microscopic model, the TSS model, and the Canonical Equation. Then, we state the limit theorems linking these models (Theorems 3.1 and 4.1). Several examples are considered. in Section 5, we begin

with a logistic model with senescence in the birth rate and size dependence in the competition term. The long time behaviors of the TSS process and of the solution of the Canonical Equation are studied. We highlight differences with the case without age-structure. In our model, senescence acts as a penalization term that favors fast reproduction to growth. We then consider a model belonging to a class that we call *age-logistic*. Computation becomes rapidly complicated. In Section 6 we investigate an example where the competition kernel is nonlocal, asymmetric in trait (cf. Kisdi [23]) and decreasing in the age of the competitors. The explicit expression of the fitness gradient allows us to compute the ESS value and to show that coexistence is possible. The existence of an "evolutionary branching" is suggested by numerical simulations.

2 Microscopic model

We start with a stochastic microscopic model of age and trait structured asexual population describing the dynamics at the individual level. We take into account births, either clonal or with mutation and death, natural or due to the competition with other individuals. A large population limit is studied. We provide by this way a microscopic justification of PDEs generalizing models introduced in Demography ([7, 24, 28, 35, 38]). This gives us a better understanding of the large time behavior of the microscopic process and allows us to define the rare mutations asymptotics leading to Adaptive Dynamics limits. To our knowledge, there are only a few models dealing with trait and age-structured populations, all deterministic (Rotenberg [34], Mischler *et al.* [27]) and the stochastic models taking age into account do not consider trait evolution, see Kendall [21], Athreya and Ney [1], Doney [12], Oelschläger [29], Tran [37]. We generalize all these models by introducing a dependence between trait and age at the individual level and by taking into account mutation and competition between individuals, which yields nonlinearity in the limiting phenomena.

2.1 Microscopic description

Individuals are characterized by a trait x belonging to a compact set $\mathcal{X}$ of $\mathbb{R}^d$ and by their physical age $a \in \mathbb{R}_+$. We set $\widetilde{\mathcal{X}} := \mathcal{X} \times \mathbb{R}_+$. The population is discrete and described by the point measure

$$Z_t(dx, da) = \sum_{i=1}^{\langle Z_t, 1\rangle} \delta_{(x_i(t), a_i(t))}. \tag{2.1}$$

Each individual is represented by a Dirac mass on its trait and age, and $\langle Z_t, 1\rangle$ is the population size at time t. We denote by $\mathcal{M}_F(\widetilde{\mathcal{X}})$ the set of finite measures on $\widetilde{\mathcal{X}}$. For $Z \in \mathcal{M}_F(\widetilde{\mathcal{X}})$ and for a real-valued bounded measurable function f, we define $\langle Z, f\rangle = \int_{\widetilde{\mathcal{X}}} f dZ$.
An individual with trait $x \in \mathcal{X}$ and age $a \in \mathbb{R}_+$ in the population described by Z gives birth to a new individual with rate $b(x, a)$. With probability $p \in [0, 1]$ the new individual is a mutant of age 0 and trait $x + h$, where h is drawn from a probability distribution $k(x, h)\, dh$ with support on $\mathcal{X} - \{x\} = \{y - x \,|\, y \in \mathcal{X}\}$ (so that $x + h \in \mathcal{X}$). With probability $1 - p \in [0, 1]$, the new individual is clonal, with age 0 and trait x. The individual dies with rate $d(x, a) + ZU(x, a)$ where $d(x, a)$ is the natural death rate and $ZU(x, a) = \int_{\widetilde{\mathcal{X}}} U((x, a), (y, \alpha))Z(dy, d\alpha)$. Here, U is a real-valued kernel describing the interaction exerted by an individual with trait y and age α on an individual with trait x and age a. During their life, individuals age with velocity 1, so that the age at time $t \in \mathbb{R}_+$ of an individual born at time $c \leq t$ is $a = t - c$. (Notice that the birth date c varies from an individual to another).
Let us now describe the generator of the $\mathcal{M}_F(\widetilde{\mathcal{X}})$-valued Markov process Z. This generator L sums the aging phenomenon and the ecological dynamics of the population. Let $\mathcal{C}_b^{0,1}(\widetilde{\mathcal{X}}, \mathbb{R})$ be the space of continuous bounded real-valued functions on $\widetilde{\mathcal{X}}$ with bounded continuous derivatives

with respect to the age variable. As developed in Dawson [8] Theorem 3.2.6, the set of cylindrical functions defined for each $\mu \in \mathcal{M}_F(\widetilde{\mathcal{X}})$ by $F_f(\mu) = F(\langle \mu, f \rangle)$, with $F \in C_b^1(\mathbb{R})$ and $f \in C_b^{0,1}(\widetilde{\mathcal{X}})$, generates the set of bounded measurable functions on $\mathcal{M}_F(\widetilde{\mathcal{X}})$. For such function,

$$\begin{aligned} LF_f(\mu) &= \langle \mu, \partial_a f(.) \rangle F_f'(\mu) \\ &+ \int_{\widetilde{\mathcal{X}}} \big[(d(x,a) + \mu U(x,a))(F_f(\mu - \delta_{(x,a)}) - F_f(\mu)) + b(x,a)(1-p)(F_f(\mu + \delta_{(x,0)}) - F_f(\mu)) \\ &\qquad + b(x,a)p \int_{\mathbb{R}^d} (F_f(\mu + \delta_{(x+h,0)}) - F_f(\mu)) k(x,h) dh \Big] \mu(dx, da). \quad (2.2) \end{aligned}$$

In the sequel, we make the following assumption.

Assumption 2.1. *The functions b, d and U are assumed to be of class $\mathcal{C}^1$ and $x \mapsto k(x,h)$ is Lipschitz continuous, uniformly in h. We suppose that there exist strictly positive constants $\bar{b}$, $\underline{d}$, $\bar{d}$, $\bar{U}$, $\underline{U}$ such that $\forall (x,a) \in \widetilde{\mathcal{X}}$, $\forall (y,\alpha) \in \widetilde{\mathcal{X}}$,*

$$0 \leq b(x,a) \leq \bar{b}, \quad \underline{d} \leq d(x,a) \leq \bar{d}, \quad \underline{U} \leq U((x,a),(y,\alpha)) \leq \bar{U}, \quad \int_{\mathbb{R}^d} (\sup_x k(x,h)) dh < +\infty.$$

Under Assumption 2.1, the process Z can be obtained as the unique strong solution of a stochastic differential equation driven by a multivariate Poisson point measure corresponding to the dynamics described above (we can adapt Fournier Méléard [15] and Tran [37] concerning respectively trait-structured and age-structured cases).

Let us mention different forms for the birth rate that can be found in the literature. The period devoted to reproduction is very different from one specie to another. For some species, there is no reproduction in the first growth period (as juvenile or larva states, cf. Henson [19]). The parameters of interest are the maturity age a_M and the constant birth rate b_1, which are the heritable traits. The birth rate for an individual with traits (a_M, b_1) and age a can be $b(a_M, b_1, a) = b_1 \mathbf{1}_{\{a \geq a_M\}}$.
Many other species reproduce early in life, and the reproduction function is decreasing with age. The heritable traits submitted to mutation are then the initial reproduction rate b_1 and the senescence parameter b_2. As in (cf. Webb [38] p.39 Ex. 2.1), the birth rate of an individual with traits (b_1, b_2) and age a can be $b(b_1, b_2, a) = b_1 e^{-b_2 a}$.
Conversely, for other species ([38] p.41 Ex. 2.2), reproduction happens at the end of life and the birth rate of an individual with age a can be modelled as $b(b_1, b_2, a) = b_1(1 - e^{-b_2 a})$. The individual trait will be (b_1, b_2), with b_1 the reproduction rate at maturation and b_2 the maturation parameter.

The competition kernel U describes the competition intensity between two individuals and can depend on their respective ages and traits. The simplest case is the (density dependent) *logistic* one, for which $U((x,a),(y,\alpha)) = \eta(x,a)$. The interaction exerted on an individual is then proportional to the total number of individuals in the population, and thus nonlocal. Another interesting case is when $U((x,a),(y,\alpha)) = \eta(x,a)U(x,y)$. Then interaction is nonlocal in age and local in the trait space. Such population will be called *age-logistic*.

In Sections 5 and 6, we develop examples of asexual age and size-structured populations. We first consider a logistic population with senescence in the birth rate. Computation can be developed in details. We compare it with the corresponding model without senescence and with a model with age-logistic interaction. In the last model, we investigate a case for which the competition kernel is local in trait and age.

In these examples, the trait space is the size space $[0,4]$ and the size trait is heritable except when a mutation occurs. With probability $p \in]0,1[$, the descendant of an individual with trait x is a mutant with trait $x+h$. Mutation amplitude h is distributed on $[-x, 4-x]$ following the centered law $k(x,h)dh$, so that $x+h$ remains in $[0,4]$. With probability $1-p$, the descendant is clonal.

Example 1: The individuals reproduce at rate

$$b(x,a) = x(4-x)e^{-a}. \tag{2.3}$$

Dependence in x explains as follows: if the individual is small, it has not enough energy to reproduce with high rate. If it is large, descendants' size will also be large by hereditary transmission, and more energy is required to produce such descendants than smaller ones. The term e^{-a} expresses a senescence phenomenon and the reproduction rate is decreasing with age. The logistic death rate of an individual with trait x is given whatever its age by

$$d(x, \langle Z, 1\rangle) = \frac{1}{4} + 0.001 \cdot (4-x)\langle Z, 1\rangle. \tag{2.4}$$

The term $1/4$ is the natural death rate and the logistic term has intensity $0.001(4-x)$, meaning that big individuals are less sensitive to competition. The trait maximizing the birth rate is $x = 2$. Since the logistic competition favors individuals with size close to 4, we can expect that the optimal traits, taking birth and death rates into account, are lying in the interval [2,4].
In Section 5, computation will allow us to obtain the value of the trait equilibrium (evolutionary stable strategy) in which the population will stabilize in the evolution time scale. We will compare this model with the similar one with $b(x) = x(4-x)$, (a size-structured population without age structure) and will show that the senescence phenomenon appears as a penalization factor, reducing the equilibrium trait value. We also compare the first model with the one in which the logistic interaction term $0.001(4-x)\langle Z, 1\rangle$ is replaced by

$$a \int_{\widetilde{\mathcal{X}}} U(x,y) Z(dy, d\alpha), \qquad \text{where} \qquad U(x,y) = C\left(1 - \frac{1}{1+\nu \exp\left(-k(x-y)\right)}\right) \tag{2.5}$$

is Kisdi's asymmetric competition function [23] ($C = 0.002$, $\nu = 1.2$ and $k = 4$). Its sigmoïd shape models the fact that the competition on an individual is mainly exerted by larger ones. We see how intricate computation can be.

Example 2: We investigate a model where the competition kernel is a function of the traits and ages of the competitors. An individual with trait x and age a reproduces at rate $b(x) = x(4-x)$. There is no natural death and the action exerted by a competitor of trait y and age α is described by the interaction function $\eta(a)\,(1+e^{-\alpha})\,U(x,y)$ of *separable multiplicative form*, with U defined in (2.5). The term $1+e^{-\alpha}$ is a senescence parameter diminishing the interaction intensity with the competitor's age. When η is a constant function, we recover models studied by [2, 31] with a deterministic approach. In Section 6, we investigate the case $\eta(a) = a$.

Simulations using an individual-based algorithm are given in Figure 1 (c). They present the trait-support of the point measure Z defined in (2.1) for the three examples previously described. We remark a qualitative difference between cases (a) and (b) and case (c). In the two first plots, the trait-support is very dense. Conversely, in Figure 1 (c), the population separates into smaller groups once it has reached a certain trait value which seems to be approximatively 3.2. This phenomenon is known as *branching* in the biological literature.

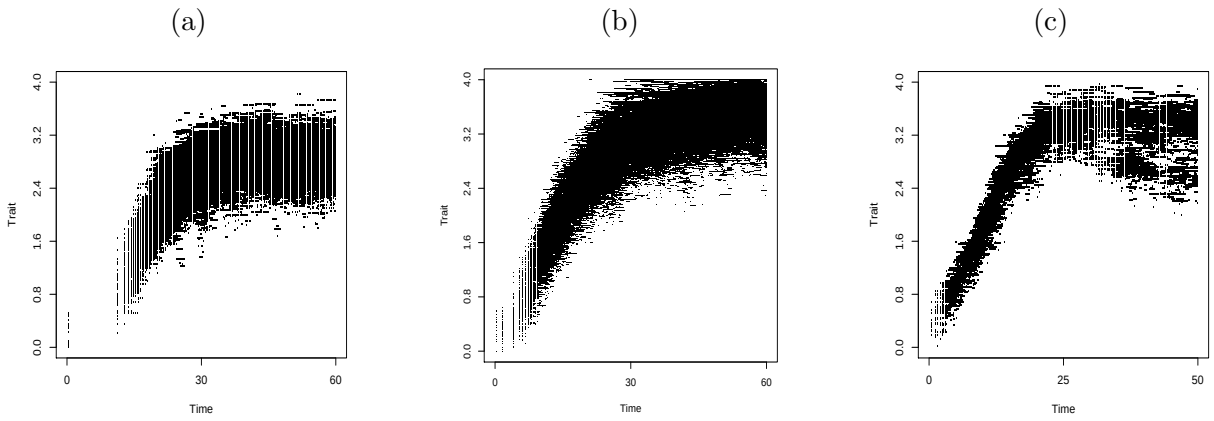

Figure 1: *Simulation of the microscopic process, using an individual-based algorithm: the traits in the population are represented in function of time. We start with* $n = 2000$ *individuals. The initial traits are drawn uniformly between 0 and 1.3, and the ages are drawn in an exponential distribution of parameter 2. For the mutations,* $p = 0.13$ *and* k *is the gaussian law with mean* 0 *and variance* 0.15*, conditioned to stay in* $[0, 4]$*. (a): Logistic population with age structure (2.3, 2.4). (b): Logistic population without age structure and (2.4). (c): Age-structured population with nonlocal interaction kernel (Example 2).*

2.2 Large population and rare mutation renormalizations

We are interested in studying approximations of the age-trait dynamics presented in Section 2.1 under a large initial population and rare mutation assumption.

The processes of interest are the renormalized population processes $(Z^n)_{n\in\mathbb{N}^*}$ given by:

$$\forall n \in \mathbb{N}^*,\ \forall t \in \mathbb{R}_+,\ Z_t^n(dx, da) = \frac{1}{n} \sum_{i=1}^{n\langle Z_t^n, 1\rangle} \delta_{(x_i(t), a_i(t))}. \tag{2.6}$$

The assumptions are as follows.

Assumption 2.2. *(i)* $\exists \varepsilon > 0, \quad \sup_{n\in\mathbb{N}^*} \mathbb{E}\left(\langle Z_0^n, 1\rangle^{2+\varepsilon}\right) < +\infty$.
(ii) The sequence Z_0^n *converges in law in* $\mathcal{M}_F(\widetilde{\mathcal{X}})$ *to a finite measure* ξ_0.
(iii) The ecological parameters stay unchanged, except the interaction kernel $U_n = \frac{U}{n}$*. This hypothesis corresponds heuristically to the expression of a resource constraint. The death rate of an individual* (x, a) *of* Z_t^n *is thus equal to* $d(x, a) + Z_t^n U(x, a)$.
(iv) The mutation probability is given by $u_n p$*, with* $u_n,\ p \in [0, 1]$ *and* u_n *is assumed to decrease to* 0 *when* $n \to +\infty$.

Adapting tightness-compactness results in Fournier and Méléard [15], one can prove that the sequence $(Z^n)_{n\in\mathbb{N}^*}$ converges to a deterministic limit when $n \to +\infty$. More precisely:

Proposition 2.3. *(cf. Tran [36] (Section 3.2)) Under Assumptions 2.1 and 2.2, the sequence* $(Z^n)_{n\in\mathbb{N}^*}$ *converges in* $\mathbb{D}(\mathbb{R}_+, \mathcal{M}_F(\widetilde{\mathcal{X}}))$ *to a deterministic continuous process* $\xi \in \mathcal{C}(\mathbb{R}_+, \mathcal{M}_F(\widetilde{\mathcal{X}}))$ *characterized as the unique solution of the evolution equation:* $\forall f \in \mathcal{C}_b^{0,1}(\widetilde{\mathcal{X}}, \mathbb{R}),\ \forall t \in \mathbb{R}_+$,

$$\langle \xi_t, f\rangle = \langle \xi_0, f\rangle + \int_0^t \int_{\widetilde{\mathcal{X}}} \left[\partial_a f(x, a) + f(x, 0)b(x, a) - f(x, a)(d(x, a) + \xi_s U(x, a))\right] \xi_s(dx, da)\, ds, \tag{2.7}$$

Let us roughly give the main ideas of the proof. Since every individual is weighted by $1/n$, the size of population jumps converges to zero, and the limiting values of $(Z^n)_{n\in\mathbb{N}^*}$ are continuous processes. Moreover, for $f \in \mathcal{C}_b^{0,1}(\widetilde{\mathcal{X}},\mathbb{R})$, $\langle Z_t^n, f\rangle$ writes as the sum of a finite variation term and a random term whose square is of order $1/n$. The random part disappears when $n \to +\infty$ and the limit is deterministic. In the finite variation part, mutations also disappear in the limit, since $(u_n)_{n\in\mathbb{N}^*}$ tend to 0, leading to (2.7). No diversity appears since there is no mutation. Uniqueness of the solution of (2.7) implies uniqueness of the limiting value of $(Z^n)_{n\in\mathbb{N}^*}$.

In cases where the support of the trait-marginal of ξ_0 is a singleton $\{x_0\}$, respectively a pair $\{x_0, y\}$, the population remains monomorphic, respectively dimorphic. Equation (2.7) is then parameterized by these values and relations between (2.7) and classical partial differential equations have been studied by Tran ([37] Propositions 3.4 and 3.6).

Proposition 2.4. *(i) Assume that $\xi_0(dx,da) = \delta_{x_0}(dx)m_0(x_0,a)da$. Then for every $t \geq 0$, $\xi_t(dx,da) = \delta_{x_0}(dx)m(x_0,a,t)da$ and the function $m(x_0,a,t)$ is the unique weak function solution of the partial differential equation parameterized by x_0:*

$$\frac{\partial m}{\partial t}(x_0,a,t)+\frac{\partial m}{\partial a}(x_0,a,t) = -\left(d(x_0,a) + \int_{\mathbb{R}_+} U((x_0,a),(x_0,\alpha))m(x_0,\alpha,t)d\alpha\right) m(x_0,a,t),$$
$$m(x_0,0,t) = \int_0^{+\infty} b(x_0,a)m(x_0,a,t)da, \quad m(x_0,a,0) = m_0(x_0,a). \tag{2.8}$$

(ii) Assume that $\xi_0(dx,da) = \delta_{x_0}(dx)m_0(x_0,a)da + \delta_y(dx)m_0(y,a)da$. Then for every $t \geq 0$,

$$\xi_t(dx,da) = \delta_{x_0}(dx)m(x_0,a,t)da + \delta_y(dx)m(y,a,t)da$$

where $(m(x_0,a,t), m(y,a,t))$ is the unique weak solution of

$$\frac{\partial m}{\partial t}(x_0,a,t) + \frac{\partial m}{\partial a}(x_0,a,t) =$$
$$-\left(d(x_0,a) + \int_{\mathbb{R}_+} (U((x_0,a),(x_0,\alpha))m(x_0,\alpha,t) + U((x_0,a),(y,\alpha))m(y,\alpha,t))\, d\alpha\right) m(x_0,a,t),$$
$$\frac{\partial m}{\partial t}(y,a,t) + \frac{\partial m}{\partial a}(y,a,t) =$$
$$-\left(d(y,a) + \int_{\mathbb{R}_+} (U((y,a),(x_0,\alpha))m(x_0,\alpha,t) + U((y,a),(y,\alpha))m(y,\alpha,t))\, d\alpha\right) m(y,a,t),$$
$$m(x_0,0,t) = \int_0^{+\infty} b(x_0,a)m(x_0,a,t)da, \quad m(y,0,t) = \int_0^{+\infty} b(y,a)m(y,a,t)da,$$
$$m(x_0,a,0) = m_0(x_0,a), \quad m(y,a,0) = m_0(y,a). \tag{2.9}$$

Equation (2.8) generalizes Demography equations, as McKendrick-Von Foerster or Gurtin-McCamy Equations (see [24, 14, 17]).

In the sequel, we will make the following assumptions concerning the long time behavior of the solutions of (2.8) and (2.9).

Assumption 2.5. *Let $x_0 \in \mathcal{X}$ and $m_0(x_0,a)da \in \mathcal{M}_F(\mathbb{R}_+)$. The solution of (2.8) admits a unique nontrivial stable stationary solution $\widehat{m}(x_0,a)$ such that $m(x_0,a,t)da$ converges for the weak convergence topology in $\mathcal{M}_F(\mathbb{R}_+)$ to $\widehat{m}(x_0,a)da$ when $t \to +\infty$. We will denote by*

$$\widehat{M}_{x_0} = \int_0^{+\infty} \widehat{m}(x_0,a)da \tag{2.10}$$

the mass of the stationary age measure and by $\widehat{\xi}_{x_0}$ the space-time stationary measure $\widehat{\xi}_{x_0}(dx,da) = \delta_{x_0}(dx)\widehat{m}(x_0,a)da$.

Under Assumption 2.5, $\widehat{m}(x_0, a)$ is solution of

$$\frac{\partial \widehat{m}}{\partial a}(x_0, a) = -\widehat{d}(x_0, a, x_0)\widehat{m}(x_0, a), \quad \widehat{d}(x_0, a, x_0) := d(x_0, a) + \int_{R_+} U((x_0, a), (x_0, \alpha))\widehat{m}(x_0, \alpha)d\alpha, \tag{2.11}$$

with the boundary condition:

$$\widehat{m}(x_0, 0) = \int_0^{+\infty} b(x_0, a)\widehat{m}(x_0, a)da. \tag{2.12}$$

Solutions to (2.11) have the form

$$\widehat{m}(x_0, a) = \widehat{m}(x_0, 0) \exp\left(-\int_0^a \widehat{d}(x_0, \alpha, x_0)d\alpha\right). \tag{2.13}$$

From (2.13) and (2.12), we obtain the following balance condition

$$\int_0^{+\infty} b(x_0, a)e^{-\int_0^{+\infty} \widehat{d}(x_0,\alpha,x_0)d\alpha}da = 1. \tag{2.14}$$

A necessary condition to get Assumption 2.5 is then that

$$R_0(x_0) := \int_0^{+\infty} b(x_0, a)e^{-\int_0^a d(x_0,\alpha)d\alpha}da > 1. \tag{2.15}$$

The term $R_0(x_0)$, called net reproduction rate, is the integral in age of the birth rate weighted by the survival probability in absence of competition. It's the well known threshold between sub and super-criticality in age-structured models (see [1, 12, 17, 38]). If the birth and death rates $b(x)$ and $d(x)$ do not depend on age, $R_0(x) = b(x)/d(x) > 1$ if and only if $b(x) > d(x)$, which is the standard super-criticality condition.

With the notation of Section 2.1, in the age-logistic case and for a monomorphic population with trait x_0, the death rate in (2.8) equals $d(x_0, a) + \eta(x_0, a)U(x_0, x_0)\int_{\mathbb{R}_+} m(x_0, \alpha, t)d\alpha$. Equation (2.8) is then a Gurtin-McCamy equation parameterized by x_0 and Condition (2.15) is also sufficient to obtain Assumption 2.5 as proved in Webb [38], Section 5.4.

Let us now introduce assumptions describing the "invasion implies fixation" principle, for the age-dependent system defined by (2.9). Assertion (ii) impedes the co-existence of the two traits x_0 and y in the long time.

Assumption 2.6. *(i) Let $x_0, y \in \mathcal{X}$ with $R_0(x_0) > 1$. One of the following assumptions holds:*

$$\textit{Either: } \int_{\mathbb{R}_+} b(x_0, a)e^{-\int_0^a \widehat{d}(x_0,\alpha,y)d\alpha}da > 1 \textit{ and } \int_{\mathbb{R}_+} b(y, a)e^{-\int_0^a \widehat{d}(y,\alpha,x_0)d\alpha}da < 1 \tag{2.16}$$

$$\textit{Or: } \int_{\mathbb{R}_+} b(x_0, a)e^{-\int_0^a \widehat{d}(x_0,\alpha,y)d\alpha}da < 1 \textit{ and } \int_{\mathbb{R}_+} b(y, a)e^{-\int_0^a \widehat{d}(y,\alpha,x_0)d\alpha}da > 1, \tag{2.17}$$

where

$$\widehat{d}(x, a, y) := d(x, a) + \int_0^{+\infty} U((x, a), (y, \alpha))\widehat{m}(y, \alpha)d\alpha \tag{2.18}$$

is the death rate of an individual (x, a) in the population at equilibrium $\widehat{\xi}_y$.

(ii) The solution of (2.7) with the dimorphic initial condition $\xi_0(dx, da) = \delta_{x_0}(dx)m_0(x_0, a)da + \delta_y(dx)m_0(y, a)da$ converges as $t \to \infty$ to $\widehat{\xi}_{x_0}$ if (2.16) is satisfied and to $\widehat{\xi}_y$ if (2.17) is satisfied (for the weak convergence topology in $\mathcal{M}_F(\widetilde{\mathcal{X}})$).

For a logistic dimorphic population with traits x_0 and y ($R_0(x_0) > 1$), Assumption 2.6 is fulfilled as soon as $U(x_0,x_0)U(y,y) - U(x_0,y)U(y,x_0) \leq 0$ and one of the following assertion is satisfied:

$$\begin{aligned} U(x_0,x_0)\widehat{M}_{x_0} - U(x_0,y)\widehat{M}_y < 0 \quad &\text{and} \quad U(y,y)\widehat{M}_y - U(y,x_0)\widehat{M}_{x_0} > 0, \\ \text{or } U(x_0,x_0)\widehat{M}_{x_0} - U(x_0,y)\widehat{M}_y > 0 \quad &\text{and} \quad U(y,y)\widehat{M}_y - U(y,x_0)\widehat{M}_{x_0} < 0. \end{aligned}$$

(Let us recall that $\widehat{M}_{x_0}$ has been defined in (2.10)).

3 Age Structured Trait Substitution Sequence Process

In order to obtain the Adaptive Dynamics limit, we consider here the same mutation scale as in the work of Champagnat [4] without age-structure. We assume that

$$\forall\, V > 0, \quad \exp(-Vn) = o(u_n) \quad \text{and } u_n = o\left(\frac{1}{n\log n}\right). \tag{3.1}$$

This scaling is here again the right one to derive from the microscopic process a jump process generalizing the Trait Substitution Sequence (see Metz *et al.* [26], Champagnat [4]) for age-structured populations. It is obtained from a fine study of the different time steps in the invasion process of the resident population by a mutant one. This study has been done by Champagnat in [4] and adapted to include age structure in Tran's thesis [36]. Let us roughly recall the main ideas justifying (3.1). They are summarized in Figure 2. If no mutation occurs, then with a probability that tends to 1 when $n \to +\infty$, a monomorphic population with initial size n enters a given neighborhood of its equilibrium after a sufficiently large time that does not depend on n. By large deviation results, the microscopic process stays in this neighborhood during an exponential time e^{nV}. Mutation time is of order $1/(nu_n)$, and an invasion period is proved to be of order $\log n$. Thus the condition $u_n = o(1/(n\log n))$ in (3.1) implies that the mutations are sufficiently rare so that the population has returned to its monomorphic equilibrium when the next mutation occurs. The condition $\exp(-Vn) = o(u_n)$ tells us that the mutations occur sufficiently often so that a mutant appears before a rare event drives the resident population far from its equilibrium. Hence, if we change time and consider $(Z^n_{\cdot/(nu_n)})_{n\in\mathbb{N}^*}$ at the mutation time scale, we will obtain in the limit, when $n \to +\infty$, a process where the transition periods have disappeared and where only the sequence of equilibrium states remains. Under our hypotheses preventing the trait co-existence, the latter have a singleton trait-support and then reduce to age-measures. Therefore, the limiting process jumps from an age-measure to another, each of these parameterized by a trait. This provides a generalization of the TSS proposed by Metz *et al.* [26]. The result is stated in Theorem 3.1 and proved in Appendix A.

Theorem 3.1. *Let us consider (Z^n) defined by (2.6) with a monomorphic trait support $\{X_0\}$ and satisfying Assumptions 2.1, 2.2 with $\xi_0(dx,da) = \delta_{X_0}(dx)m_0(X_0,a)da$. Assume moreover that $(u_n)_{n\in\mathbb{N}}$ satisfies (3.1) and that Assumptions 2.5 and 2.6 are satisfied for each $x_0, y \in \mathcal{X}$ with $R_0(x_0) > 1$. Then, for every $t \in \mathbb{R}_+$, the sequence $(Z^n_{t/(nu_n)})_{n\in\mathbb{N}^*}$ converges in law in $\mathcal{M}_F(\widetilde{\mathcal{X}})$ to the measure Z_t defined by*

$$Z_t(dx,da) = \delta_{X_t}(dx)\widehat{m}\,(X_t,a)\,da, \tag{3.2}$$

where X is a Markov jump process of generator defined for $\phi \in \mathcal{B}_b(\mathcal{X},\mathbb{R})$, $x \in \mathcal{X}$ by

$$L\phi(x) = \int_{\mathbb{R}^d}\left[(\phi(x+h)-\phi(x))\,p\left(\int_{\mathbb{R}_+} b(x,a)\widehat{m}(x,a)da\right)(1-z_0(x+h,x))\right]k(x,h)dh, \tag{3.3}$$

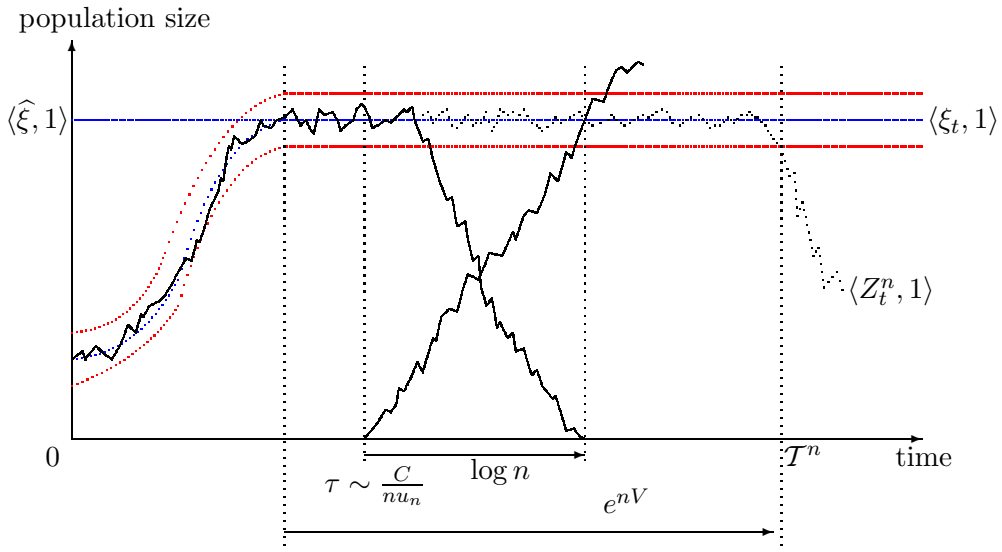

Figure 2: *Large time behaviour of the microscopic process Z^n and of its deterministic approximation ξ. On compact time intervals and for sufficiently large n, the behaviour of Z^n follows the one of its approximation ξ. On a large time scale, if no mutation occurs, Z^n leaves the neighborhood of the stationary equilibrium of ξ at $\mathcal{T}^n$ after an exponentially long period and drives the population to extinction. However, before it gets extinct, the population can be invaded by a mutant in a time scale of order $1/nu_n$. Under the "Invasion implies fixation" Assumption 2.6, if the mutant population does not die, it replaces the resident population after a transition period of order* $\log n$.

where $z_0(y,x)$ is the smallest solution in $[0,1]$ of:

$$z = \int_0^{+\infty} e^{(z-1)\int_0^a b(y,u)du} \widehat{d}(y,a,x) e^{-\int_0^a \widehat{d}(y,u,x)du} da. \tag{3.4}$$

The death rate $\widehat{d}(y,a,x)$ has been defined in (2.18).

Corollary 3.2. *The sequence $(Z^n_{\cdot/(nu_n)})_{n\in\mathbb{N}^*}$ converges to Z in $\mathbb{D}(\mathbb{R}_+, \mathcal{M}_F(\widetilde{\mathcal{X}}))$ in the sense of finite-dimensional distributions.*

The process X is called *Age Structured Trait Substitution Sequence Process.*

We have already given the main ideas of Theorem 3.1's proof. Let us comment on the different terms of the generator (3.3).
1. The term $p\,k(x,h)\int_0^{+\infty} b(x,a)\widehat{m}(x,a)da$ is the rate at which the monomorphic population of trait x, in its equilibrium, generates a mutant of trait $x+h$. This term equals $pb(x)\widehat{M}_x k(x,h)$ in the absence of age-structure.
2. The term $(1-z_0(x+h,x))$ is called *fitness* of the mutant trait $x+h$ in the population of trait x and is the probability that the mutant descendants invade the resident population. In most cases, this probability $z_0(x+h,x)$ can not be computed explicitly conversely to the case without age-structure. Nevertheless, its implicit definition given in Equation (3.4) makes possible its numerical computation as developed in the examples of Sections 5 and 6.
Let us now focus on the way we establish the equation defining the fitness function $z_0(y,x_0)$ where $x_0 \in \mathcal{X}$ is the resident trait and y the mutant trait. When the mutant y appears in the monomorphic resident population with trait x_0, we can neglect in a first approximation the mutant population and the deviations of the resident population from its equilibrium. The mutant population is then compared to a linear age-structured birth and death process with

parameters $b(y,a)$ and $\widehat{d}(y,a,x_0)$. For this process, the extinction probability is the smallest solution $z_0(y,x_0)$ in $[0,1]$ of (3.4). Next proposition proved in Appendix A identifies $z_0(y,x_0)$ as the extinction probability of the real mutant progeny in large population.

Proposition 3.3. *Consider the process Z^n as in Theorem 3.1 and starting from $Z_0^n(dx,da) = \delta_{x_0}(dx)q_0^n(x_0,da) + \frac{1}{n}\delta_{(y,0)}(dx,da)$, where $\delta_{x_0}(dx)q_0^n(x_0,da)$ is a point measure weighted by $1/n$ with support in $\{x_0\}\times\mathbb{R}_+$ and converging to $\widehat{\xi}_{x_0}$ in $\mathcal{M}_F(\widetilde{\mathcal{X}})$. We denote by $\mathbb{P}^n_{x_0,q_0^n,y}$ its law. Let τ be the first time at which a mutation occurs, θ the first time of return to a monomorphic population and V the survival trait at time θ. Then, under the assumptions of Theorem 3.1,*
i) $\lim_{n\to+\infty}\mathbb{P}^n_{x_0,q_0^n,y}(\theta<\tau,\, V=y) = 1-z_0(y,x_0)$,
ii) $\lim_{n\to+\infty}\mathbb{P}^n_{x_0,q_0^n,y}(\theta<\tau,\, V=x_0) = z_0(y,x_0)$, *where $z_0(y,x)$ is the extinction probability of a linear age-structured birth and death process with parameters $b(y,a)$ and $\widehat{d}(y,a,x_0)$.*

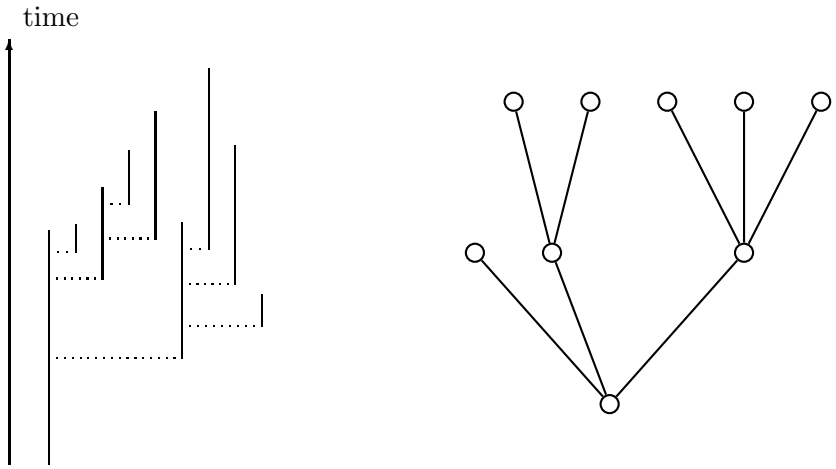

Figure 3: *An age-structured process in continuous time and its discrete time generation-tree.*

A proof of (3.4) is adapted from Doney [12]. Noticing that the extinction of the mutant progeny for the linear age-structured birth and death process is equivalent to the extinction of the discrete-time Galton-Watson process corresponding to the underlying generation process (see Figure 3), $z_0(y,x_0)$ is characterized as the smallest fixed point on $[0,1]$ of the generating function of the number of children and satisfies:

$$z = G(z) = \int_0^{+\infty} e^{(z-1)\int_0^a b(y,u)du}\widehat{d}(y,a,x_0)e^{-\int_0^a \widehat{d}(y,u,x_0)du}da \tag{3.5}$$

$$= 1 + \int_0^{+\infty}(z-1)b(y,a)e^{(z-1)\int_0^a b(y,u)du - \int_0^a \widehat{d}(y,u,x_0)du}da, \tag{3.6}$$

Equation (3.6) is obtained from (3.5) by integration by parts.

A main issue is to know whether extinction happens almost surely or not.

Proposition 3.4. *Let $x_0, y \in \mathcal{X}$.*
(i) If

$$\int_0^{+\infty} b(y,a)e^{-\int_0^a \widehat{d}(y,u,x_0)du}da > 1, \tag{3.7}$$

then $z_0(y,x_0) < 1$ and defines a $\mathcal{C}^1$ function in both variables.
(ii) Else, $z_0(y,x_0) = 1$.
(iii) Finally, when $y = x_0$, $z_0(x_0,x_0) = 1$.

Of course, $z = 1$ is an obvious solution of (3.6). Each other solution is a zero of F where

$$F(z,y,x) = \int_0^{+\infty} b(y,a) e^{(z-1)\int_0^a b(y,u)du - \int_0^a \widehat{d}(y,u,x_0)du} da - 1. \tag{3.8}$$

The proof is therefore an immediate consequence of the following lemma.

Lemma 3.5. *For each pair of traits x, y, the equation $F(z,y,x) = 0$ admits a unique solution $z = g(y,x)$ on $\mathbb{R}_+$ of class C^1 in both variables and such that $g(x,x) = 1$.*

Proof. The function F is of class $\mathcal{C}^1$ with a positive partial derivative with respect to z. It is thus strictly increasing in z. Since $\int_0^{+\infty} b(y,a) e^{-\int_0^a b(y,u)du} da = e^{-\int_0^{+\infty} b(y,u)du} - 1 < 0$, then $F(0,y,x) < 0$. Moreover $\lim_{z\to+\infty} F(z,y,x) = +\infty$. We deduce that for every $x, y \in \mathcal{X}$, there is a unique solution $z = g(y,x)$ on $\mathbb{R}_+$ to $F(z,y,x) = 0$ which is equal to 1 if and only if $\int_0^{+\infty} b(y,a) e^{-\int_0^a \widehat{d}(y,u,x_0)du} da = 1$. This condition is true for $y = x_0$ by (2.14). Using the Implicit Function Theorem we obtain moreover that g is of class $\mathcal{C}^1$. ■

In both cases, we can notice that:

$$z_0(y,x_0) = g(y,x_0) \wedge 1 \text{ and } 1 - z_0(y,x_0) = [1 - g(y,x_0)]_+ , \tag{3.9}$$

where $[.]_+$ denotes the positive part.

Remark 3.6. For a population without age-structure Equation (3.5) can be solved explicitly and we recover the infinitesimal generator introduced by Metz et *al.* [26] with:

$$1 - z_0(y,x_0) = \left[\frac{b(y) - d(y) - U(y,x_0)\widehat{M}_{x_0}}{b(y)} \right]_+ . \tag{3.10}$$

4 Canonical Equation for an Age-structured population

We are interested in the limit of the *Age-structured Trait Substitution Sequence Process* when the mutation step tends to zero. Generalizing the approach of Dieckmann and Law [10] and Champagnat [3] in the case without age, we consider, for $\varepsilon > 0$, the infinitesimal generator L^ε defined for every $\phi \in \mathcal{B}_b(\mathcal{X}, \mathbb{R})$ and $x \in \mathcal{X}$ by:

$$L^\varepsilon \phi(x) = \frac{1}{\varepsilon^2} \int_{\mathbb{R}^d} (\phi(x + \varepsilon h) - \phi(x))\, p \int_{\mathbb{R}_+} b(x,a) \widehat{m}(x,a) da (1 - z_0(x + \varepsilon h, x)) k(x,h) dh. \tag{4.1}$$

When $\varepsilon \to 0$, the sequence of such renormalized TSS-processes converges to the solution of an ODE that generalizes the Canonical Equation introduced by Diekmann and Law [10]:

Theorem 4.1. *Under Assumptions 2.1, 2.5, 2.6, the sequence $(X^\varepsilon)_{\varepsilon>0}$ converges in probability, for the Skorohod topology on $\mathbb{D}(\mathbb{R}_+, \mathcal{X})$ to the solution of the following ODE:*

$$\frac{dx}{dt} = p \int_{\mathbb{R}_+} b(x,a) \widehat{m}(x,a) da \int_{\mathbb{R}^d} h\, D_h^1 z_0(x,x)\, k(x,h) dh, \tag{4.2}$$

where $\dfrac{dx}{dt} = \lim_{h\to 0} \dfrac{|x(t+h) - x(t)|}{h}$, *and* $D_h^1 z_0(x,x) := \lim_{\substack{\varepsilon \to 0 \\ \varepsilon > 0}} \dfrac{z_0(x,x) - z_0(x+\varepsilon h, x)}{\varepsilon}$.

The Proof of Theorem 4.1, based on a tightness-uniqueness argument, can be adapted from Theorem 1 in Champagnat [3].

Let us remark that $D_h^1 z_0(x,x)$ is nonnegative since $z_0(x+\varepsilon h, x) \in [0,1]$ and $z_0(x,x) = 1$ by Proposition 3.4. Using (3.9), one gets

$$D_h^1 z_0(x,x) = \left[\lim_{\substack{\varepsilon \to 0 \\ \varepsilon > 0}} \frac{1 - g(x+\varepsilon h, x)}{\varepsilon} \right]_+ . \tag{4.3}$$

Hence, as in the classical case, the evolution follows the directions where the fitness gradient $D_h^1 z_0(x,x)$ is positive, and along which the extinction probability $y \mapsto z_0(y,x)$ is a decreasing function.
Although z_0 is implicitly defined, an explicit expression of $D_h^1 z_0(x,x)$ can be established.

Proposition 4.2. *Let us consider the scalar case $d = 1$ for sake of simplicity. Under Assumptions 2.1, 2.5, 2.6, for $h > 0$, $D_1^h z_0(x,x) = h[-\partial_1 g(x,x)]_-$ and for $h < 0$, $D_1^h z_0(x,x) = h[-\partial_1 g(x,x)]_+$, with g defined in Lemma 3.5, and*

$$\begin{aligned} \partial_1 g(x,x) = -\int_{\mathbb{R}_+} \left(\partial_1 b(x,a) - b(x,a) \int_0^a \left(\partial_1 d(x,\alpha) + \int_{\mathbb{R}_+} \partial_1 U((x,\alpha),(x,u)) \widehat{m}(x,u) du \right) d\alpha \right) \\ \times e^{-\int_0^a \widehat{d}(x,\alpha,x) d\alpha} da \times \left(\int_0^{+\infty} b(x,a) \left(\int_0^a b(x,\alpha) d\alpha \right) e^{-\int_0^a \widehat{d}(x,\alpha,x) d\alpha} da \right)^{-1} . \end{aligned} \tag{4.4}$$

Proof. We replace y by $x+\varepsilon$ in (3.8) and consider the expansion with respect to ε, using:

$$\begin{aligned} &b(x+\varepsilon, a) = b(x,a) + \varepsilon \partial_1 b(x,a) + o(\varepsilon), \\ &d(x+\varepsilon, a) = d(x,a) + \varepsilon \partial_1 d(x,a) + o(\varepsilon), \\ &U((x+\varepsilon, a),(x,\alpha)) = U((x,a),(x,\alpha)) + \varepsilon \partial_1 U((x,a),(x,\alpha)) + o(\varepsilon), \\ &g(x+\varepsilon, x) = 1 + \varepsilon \partial_1 g(x,x) + o(\varepsilon). \end{aligned}$$

Identifying the terms of order ε, we obtain (4.4). ■

Remark 4.3. (i) When $\partial_1 g(x,x) > 0$, $D_1^1 z_0(x,x) = 0$ and $D_{-1}^1 z_0(x,x) = \partial_1 g(x,x)$. When $\partial_1 g(x,x) < 0$, $D_1^1 z_0(x,x) = -\partial_1 g(x,x)$ and $D_{-1}^1 z_0(x,x) = 0$.
(ii) In the scalar case without age-structure, (4.4) allows us to recover the expression of the classical fitness gradient:

$$\begin{aligned} D_1^1 z_0(x,x) &= \left[\frac{b'(x)(d(x) + U(x,x)\widehat{M}_x) - b(x)(\partial_1 d(x) + \partial_2 U(x,x)\widehat{M}_x)}{b(x)^2} \right]_+ \\ &= \left[\partial_y \left(\frac{b(y) - (d(y) + U(y,x)\widehat{M}_x)}{b(y)} \right) \Big|_{y=x} \right]_+ . \end{aligned}$$

5 Example 1

We now present several examples for which we specify the adaptive dynamics approximations and study their behavior. We used **R** for simulations which illustrate our purpose, and MAPLE for formal calculus, when computation becomes too technical.

5.1 A logistic age and size-structured population

We develop in this section a simple example highlighting the difficulties that appear when considering a trait and age-structured population and for which computations can be carried explicitly. The birth and death rates that are used have been specified and explained in (2.3) and (2.4). Compared with models with only trait structure, the specificity here lies in the introduction of a senescence term. The latter, even if it is simple, introduces a notion of *life history* that will have an effect on the traits selected through evolution.

5.1.1 Monomorphic equilibrium in large populations

The large population approximation is given by Proposition 2.4:

$$\begin{aligned}\frac{\partial m}{\partial t}(x,a,t)+\frac{\partial m}{\partial a}(x,a,t) &= -\left(\frac{1}{4}+0.001(4-x)\int_{\mathbb{R}_+} m(x,\alpha,t)d\alpha\right)m(x,a,t)\\ m(x,0,t) &= \int_0^{+\infty} x(4-x)e^{-a}m(x,a,t)da. \end{aligned} \tag{5.1}$$

From (2.15), there exists a non trivial stationary solution if and only if:

$$\begin{aligned}R_0(x)=\int_0^{+\infty} x(4-x)e^{-5a/4}da>1 \;&\Leftrightarrow \frac{4x(4-x)}{5}>1\\ &\Leftrightarrow x\in\left]2-\frac{\sqrt{11}}{2},2+\frac{\sqrt{11}}{2}\right[\approx]0.35,3.65[. \end{aligned}\tag{5.2}$$

Under (5.2), Assumption 2.5 is satisfied.

Proposition 5.1. *If (5.2) is satisfied, then (5.1) admits a unique nontrivial stationary solution*

$$\widehat{m}(x,a)=\frac{(x(4-x)-5/4)\,(x(4-x)-1)}{0.001(4-x)}\exp\left(-(x(4-x)-1)a\right). \tag{5.3}$$

Proof. Any stationary solution is of the form $\widehat{m}(x,a)=\widehat{m}(x,0)\exp\left(-(1/4+0.001(4-x)\widehat{M}_x)a\right)$ by (2.13). Plugging this expression into (2.12) gives

$$\widehat{m}(x,0)=\widehat{m}(x,0)\int_0^{+\infty} x(4-x)e^{-\left(\frac{5}{4}+0.001(4-x)\widehat{M}_x\right)a}da=\widehat{m}(x,0)\frac{x(4-x)}{\frac{5}{4}+0.001(4-x)\widehat{M}_x}. \tag{5.4}$$

Since we are looking for a nontrivial solution, $\widehat{m}(x,0)\neq 0$ and necessarily:

$$\widehat{M}_x=\frac{x(4-x)-5/4}{0.001(4-x)}. \tag{5.5}$$

The definition of $\widehat{M}_x$ implies $\widehat{M}_x=\widehat{m}(x,0)/(1/4+0.001(4-x)\widehat{M}_x)$ which gives $\widehat{m}(x,0)$. ■

5.1.2 Invasibility

With our choice of competition kernel, Assumptions 2.6 are satisfied. Let us consider the invasion phenomena. An explicit expression can not be obtained for $z_0(y,x)$, but we can compute it numerically (see Figure 4), which allows us to simulate the paths of the TSS process (see Figure 5). Even if $z_0(y,x)$ remains implicit, the study of the domain of invasibility, that consists in pairs (x,y) of traits y with positive fitness in a resident population of trait x, can be carried explicitly. It brings information on the long time behavior of the Age structured TSS process.

Proposition 5.2. *Let $x \in [0,4]$ satisfy (5.2). The mutant traits y which can invade the monomorphic resident population with trait x belong to $]\min(x, f(x)), \max(x, f(x))[$, where:*

$$f(x) := 4 - \frac{5/4}{4-x}. \tag{5.6}$$

Proof. From Proposition 3.4, we know that $z_0(y,x) < 1$ (*i.e.* the invasion of the resident population by the mutant one is possible) if and only if $\int_0^{+\infty} b(y,a)e^{-d(y,\widehat{M}_x)a}da > 1$. Since

$$\int_0^{+\infty} b(y,a)e^{-d(y,\widehat{M}_x)a}da = \int_0^{+\infty} b(y,a)e^{-d(y,\widehat{M}_y)a+\left(d(y,\widehat{M}_y)-d(y,\widehat{M}_x)\right)a}da, \tag{5.7}$$

and

$$\int_0^{+\infty} b(y,a)e^{-d(y,\widehat{M}_y)}da = 1$$

by the balance condition (2.14), Equation (5.7) is satisfied if and only if $d(y,\widehat{M}_y) - d(y,\widehat{M}_x) > 0$. This is equivalent to:

$$\begin{aligned}
\widehat{M}_y - \widehat{M}_x > 0 \Leftrightarrow & \frac{x(4-x)-5/4}{0.001(4-x)} < \frac{y(4-y)-5/4}{0.001(4-y)} \\
\Leftrightarrow & x(4-x)(4-y) - \frac{5}{4}(4-y) < y(4-x)(4-y) - \frac{5}{4}(4-x) \\
\Leftrightarrow & (x-y)(4-x)(4-y) - \frac{5}{4}(4-y-4+x) < 0 \\
\Leftrightarrow & (x-y)\left[(4-x)(4-y) - \frac{5}{4}\right] < 0.
\end{aligned} \tag{5.8}$$

Case 1: if $x > y$ (5.8) becomes:

$$(4-x)(4-y) < \frac{5}{4} \Leftrightarrow y > 4 - \frac{5/4}{(4-x)},$$

and hence $f(x) < y < x$, with f defined in (5.6).
Case 2: if $x < y$, we obtain with similar computation that $x < y < f(x)$. ■

Corollary 5.3. *Let $x_0 \in [0,4]$ be an initial condition that satisfies (5.2). The TSS process $(X_t)_{t\in\mathbb{R}_+}$ starting from x_0 converges almost surely to the unique fixed point x^* of f on $[0,4]$ when $t \to +\infty$.*

Proof. The function f is a decreasing concave function satisfying

$$\forall x \in [0,4[,\ f\circ f(x) = 4 - \frac{5/4}{4-\left(4-\frac{5/4}{4-x}\right)} = 4 - \frac{5/4}{\frac{5/4}{4-x}} = x.$$

Let's remark that f has a unique fixed point in $[0,4]$ given by

$$x^* := 4 - \frac{\sqrt{5}}{2} \approx 2.88. \tag{5.9}$$

If $x < y < f(x)$, then $x = f\circ f(x) < f(y) < f(x)$, and if $x > y > f(x)$ then $x = f \circ f(x) > f(y) > f(x)$. Thus, the new interval of invasible traits $[\min(y, f(y)), \max(y, f(y))] \subsetneq [\min(x, f(x)), \max(x, f(x))]$.
Hence the sequence $[\min(X_t, f(X_t)), \max(X_t, f(X_t))]$ is almost surely a strictly decreasing sequence for the inclusion and it converges to x^*. Since a monomorphic population with trait x^* cannot be invaded, x^* is an Evolutionary Stable Strategy (ESS) in the sense developed by Diekmann [11], Metz *et al.* [26] and Geritz *et al.* [16]. ■

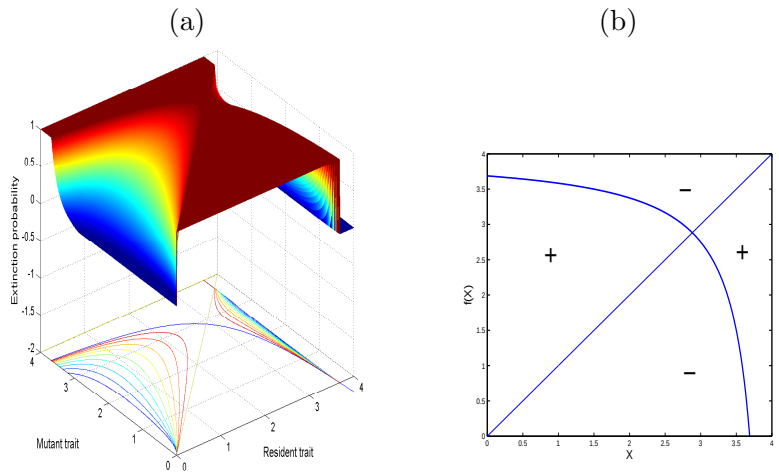

Figure 4: *(a): Probability of extinction as a function of the resident and mutant traits. For every possible values of resident and mutant traits on a grid in* $[0,4]$*, we have computed the solution of (3.5) numerically. (b): Graph of function* f *defined in (5.6). It gives the regions of the left figure where* $z_0(y,x)=1$ *and* $z_0(y,x)<1$*. This graph is called Pairwise Invasibility Plot (PIP).*

5.1.3 Simulations of the Age-structured TSS

The *Age-structured TSS* Z defined by (3.2) is a measure-valued process jumping from an equilibrium measure to another. Each equilibrium measure is characterized by a trait x and by the density $\widehat{m}(x,a)$ defined in (5.3). Simulations are given in Figure 5 below.

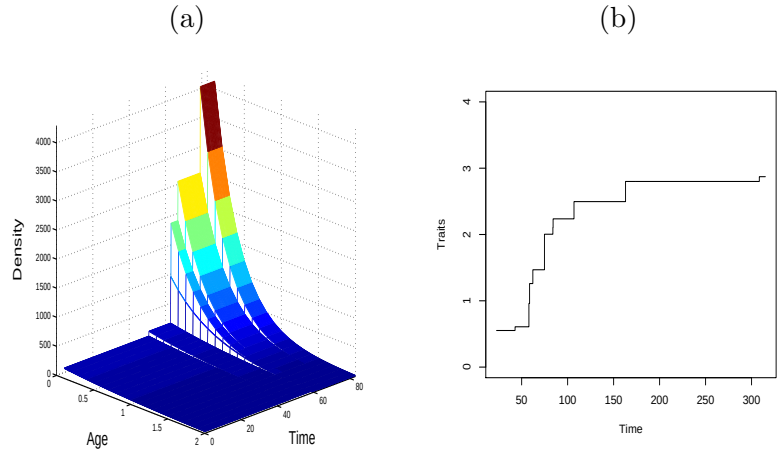

Figure 5: *Age-structured Trait Substitution Sequence process: the measure-valued process jumps from one equilibrium age-distribution to another one. (a): Each strip describes an equilibrium* $\widehat{m}(x,a)$ *as age-function. These equilibria are given in (5.3). (b): the trait-valued process* X *describing the trait jumps.*

On the Figure 5, the initial resident trait is $x_0 = 0.552$ and the size of the population at its equilibrium is $\widehat{M}_{x_0} \approx 189.47$. In the beginning, successful invasions favours increasing traits and $\widehat{M}_x$ increases too, as well as the jump rate. For instance, after 4 successful invasions, the trait is approximatively $x = 2$ and $\widehat{M}_2 = 1375$. When the trait approaches $x^* \approx 2.88$, the interval of possible invading traits decreases and the extinction probability of possible successful mutants tends to one making invasions rare.

5.1.4 Age-structured Canonical Equation

When the mutation step decreases to zero and time accelerates as in Section 4, the evolution is described by the age-structured Canonical Equation (4.2).

Proposition 5.4. *The fitness gradient $D_1^1 z_0(x,x)$ is obtained from (4.3) with:*

$$\partial_1 g(x,x) = \frac{(4x^2-32x+59)(x^2-4x-1)}{4x^2(x-4)^3} \tag{5.10}$$

and the Canonical Equation has the following explicit form:

$$\frac{dx}{dt} = p\left([\partial_1 g(x,x)]_- \int_{\mathbb{R}_+} h^2 k(x,h)dh - [\partial_1 g(x,x)]_+ \int_{\mathbb{R}_-} h^2 k(x,h)dh \right) \times \frac{(-x^2+4x-5/4)(-x^2+4x-1)}{0.001(4-x)} =: \varphi(x). \tag{5.11}$$

Proof. The fitness $z_0(x+\varepsilon,x)$ is the smallest solution in $[0,1]$ of Equation (3.6), which writes

$$z-1 = (z-1)\int_0^{+\infty} (x+\varepsilon)(4-x-\varepsilon) e^{(z-1)(x+\varepsilon)(4-x-\varepsilon)(1-e^{-a}) - \left(\frac{5}{4}+(4-x-\varepsilon)\frac{x(4-x)-5/4}{4-x}\right)a} da. \tag{5.12}$$

For the case where

$$\begin{aligned} 1 &\geq \int_0^{+\infty} b(x+\varepsilon,a) e^{-d(x+\varepsilon,x)a} da = \int_0^{+\infty} (x+\varepsilon)(4-x-\varepsilon) e^{-\left(\frac{5}{4}+(4-x-\varepsilon)\frac{x(4-x)-5/4}{4-x}\right)a} da \\ &= \frac{(x+\varepsilon)(4-x-\varepsilon)}{\frac{5}{4}+(4-x-\varepsilon)\frac{x(4-x)-5/4}{4-x}}, \end{aligned}$$

the unique solution is $z_0(x+\varepsilon,x)=1$. Else, (5.12) admits a solution in $[0,1[$. Writing that $g(x+\varepsilon,x)-1 = \varepsilon\partial_1 g(x,x) + o(\varepsilon)$ (since $g(x,x)=1$), and expanding the integrand of (5.12) with respect to ε gives:

$$\begin{aligned} 1 =& 1 + \int_0^{+\infty} \Big\{ \Big[e^{-x(4-x)a} \left(\partial_1 g(x,x) x^2 (4-x)^2 (1-e^{-a}) \right. \\ &- \left. \left(\frac{5}{4} - x(4-x) \right) xa + 4 - 2x \right) \Big] \varepsilon + o(\varepsilon) \Big\} da \\ =& 1 + \left[\frac{1}{4} \frac{\partial_1 g(x,x) \left(4x^5 - 48x^4 + 192x^3 - 256x^2\right) + 48x^3 - 183x^2 + 204x - 4x^4 + 59}{x(x-4)^2(x^2-4x-1)} \right] \varepsilon + o(\varepsilon). \end{aligned}$$

The bracket vanishes for $\partial_1 g(x,x)$ given in (5.10). From

$$\begin{aligned} \int_{\mathbb{R}} h D_h^1 z_0(x,x) k(x,h) dh &= \int_{\mathbb{R}_+} h^2 D_1^1 z_0(x,x) k(x,h) dh + \int_{\mathbb{R}_-} h|h| D_{-1}^1 z_0(x,x) k(x,h) dh \\ &= \int_{\mathbb{R}_+} h^2 \left[-\partial_1 g(x,x) \right]_+ k(x,h) dh - \int_{\mathbb{R}_-} h^2 \left[\partial_1 g(x,x) \right]_+ k(x,h) dh, \end{aligned}$$

we obtain (5.11). ∎

The graph of $x \to \partial_1 g(x,x)$ is drawn in Figure 6 (b). We can verify that the fitness gradient vanishes at $x^* \approx 2.88$. For $x < x^*$ the fitness gradient is positive, implying that the size tends to increase to x^*. Similarly, for $x > x^*$, the fitness gradient is negative and evolution reduces the size to x^*.

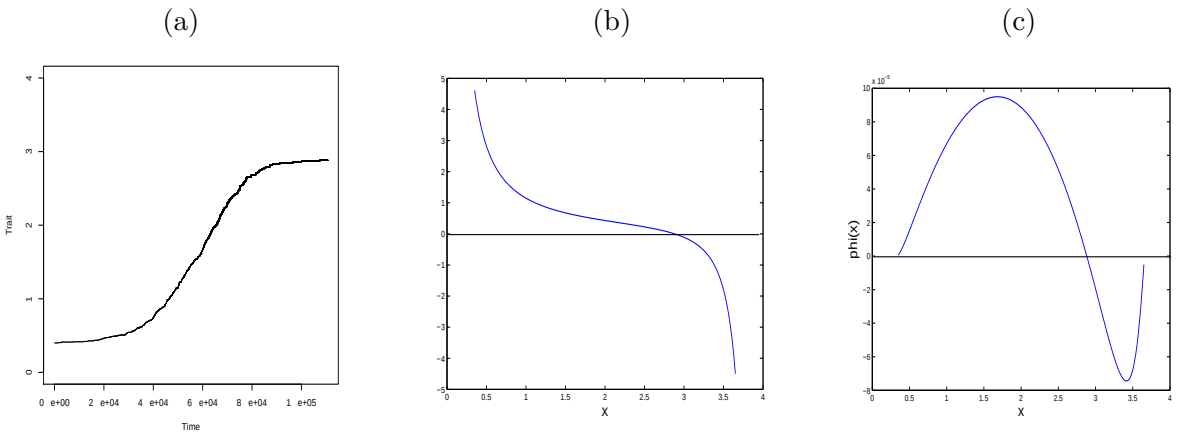

Figure 6: *(a): The Age-structured Canonical Equation, obtained from the Trait Substitution Sequence process in the limit of small mutation. (b): Graph of the function* $x \mapsto -\partial_1 g(x,x)$ *defined in (5.10). (c): The function* φ *defined in (5.11).*

5.2 Comparison with a penalized logistic population without age-structure

We compare the previous example with a logistic population, whithout age-structure, where the birth rate is $b(x) = x(4-x)$ (senescence is absent) and the death rate is $d(x,M) = 1/4 + 0.001(4-x)M$. The large population approximation corresponds to the logistic equation

$$\frac{dm}{dt}(x,t) = \left(x(4-x) - \frac{1}{4}\right) m(x,t) - 0.001(4-x)m^2(x,t), \quad m(x,0) = m_0(x),$$

which admits the following unique solution in $\mathcal{C}^1(\mathbb{R}_+, \mathbb{R}_+)$:

$$m(x,t) = \frac{\left(x(4-x) - \frac{1}{4}\right) m_0(x) e^{(x(4-x)-1/4)t}}{\left(x(4-x) - \frac{1}{4}\right) + 0.001(4-x)m_0(x)e^{(x(4-x)-1/4)t}} \overset{t\to+\infty}{\to} \widehat{m}(x) := \frac{\left[x(4-x) - \frac{1}{4}\right]_+}{0.001(4-x)}. \tag{5.13}$$

The infinitesimal generator of the TSS process takes here the following explicit form:

$$L\phi(x) = \int_{\mathbb{R}} (\phi(x+h) - \phi(x))\, px \frac{[x(4-x) - 1/4]_+}{0.001} \left[\left(1 - \frac{1}{4(4-x)(4-x-h)}\right) \frac{h}{x+h}\right]_+ k(x,h)dh$$

and the Canonical Equation becomes:

$$\frac{dx}{dt} = \int_{\mathbb{R}} \frac{px}{0.001} \left[x(4-x) - \frac{1}{4}\right]_+ \left[\frac{1}{x} - \frac{1}{4x(4-x)^2}\right]_+ h^2 k(x,h)dh.$$

A mutant y can invade the monomorphic resident population of trait x at equilibrium if

$$\frac{y(4-y) - \frac{1}{4} - (4-y)\frac{x(4-x)-1/4}{4-x}}{y(4-y)} > 0 \Leftrightarrow (y-x)(4-y)(4-x) - \frac{1}{4}(y-x) > 0$$
$$\Leftrightarrow y \in \,]\min(x, f_2(x)), \max(x, f_2(x))[$$

where $f_2(x) = 4 - (1/4)/(4-x)$. The same conclusion as in Section 5.1.2 holds. The trait $x^* = 7/2$ is an ESS to which the TSS and the Canonical Equation converge.

Let us comment on these results. First, we point out that the ESS is larger in absence of senescence. In this case, the size $\widehat{M}_x$ (5.13) of the population at equilibrium for a given trait x is

larger since the birth rate does not decrease with age. The stronger competition then favors large sizes in the trade-off between growth and reproduction. Another reason for this difference is that senescence more or less reduces the reproduction period to the beginning of life. Without senescence, the individual has more flexibility in its reproduction strategy. It may choose a size that ensures him a longer life and that allows him to give birth at more spaced intervals.

Let us also notice that the model with senescence is similar to a *penalized* version of the logistic model of this section, with a stronger natural death rate

$$b(x) = x(4-x), \quad d(x, \langle Z, 1\rangle) = \frac{5}{4} + 0.001(4-x)\langle Z, 1\rangle,$$

in the sense that these models lead to the same equilibrium sizes $\widehat{M}_x$ (5.5) and ESS x^* (5.9).

5.3 Age-logistic population interacting through the Kisdi interaction kernel

We replace the logistic death rate by an age-logistic death rate where individuals interact through Kisdi's interaction kernel (2.5). In this example, computation becomes rapidly intricated.

The constant R_0 is the same as in (5.2). Equation (2.11) defining $\widehat{m}(x,a)$ becomes here

$$\frac{\partial \widehat{m}}{\partial a}(x,a) = \left(\frac{1}{4} + \frac{C\nu a}{1+\nu}\widehat{M}_x\right)\widehat{m}(x,a). \tag{5.14}$$

As we have seen before, this type of equation is called age-logistic since the death rate in monomorphic populations is proportional to the size of the population. Plugging the solutions of (5.14) into the boundary equation of (2.12) gives for a non trivial equilibrium:

$$1 = \int_0^{+\infty} x(4-x)e^{-\frac{5}{4}a - \frac{1}{2}a^2\frac{C\nu\widehat{M}_x}{1+\nu}}\,da = x(4-x)e^{\frac{25(1+\nu)}{32C\nu\widehat{M}_x}}\sqrt{\frac{2\pi(1+\nu)}{C\nu\widehat{M}_x}}\left(1-\Phi\left(\frac{5}{4}\sqrt{\frac{1+\nu}{C\nu\widehat{M}_x}}\right)\right) \tag{5.15}$$

where Φ is the distribution function of the standard Gaussian law. Since the integral term defines a continuous and strictly decreasing function of $\widehat{M}_x$, there exists for the traits satisfying (5.2) a unique solution $\widehat{M}_x$ to (5.15). There is however no explicit expression, and we use numerical computation to obtain the approximation presented in Figure 7.

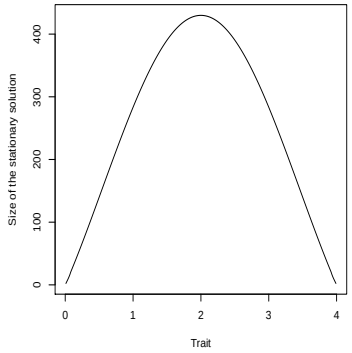

Figure 7: *A numerical resolution of Equation (5.15), giving for each trait x an approximation of the size $\widehat{M}_x$.*

Once $\widehat{M}_x$ has been computed, it is possible to obtain an approximation of the unique solution of (5.14), (5.15) given as a function of $\widehat{M}_x$ by:

$$\widehat{m}(x,a) = \frac{\widehat{M}_x\sqrt{C\nu\widehat{M}_x}}{e^{\frac{1+\nu}{32C\nu\widehat{M}_x}}\sqrt{2\pi(1+\nu)}\left(1-\Phi\left(\frac{1}{4}\sqrt{\frac{1+\nu}{C\nu\widehat{M}_x}}\right)\right)}\exp\left(-\frac{a}{4}-\frac{C\nu\widehat{M}_x}{2(1+\nu)}a^2\right). \tag{5.16}$$

To simulate approximations of the Age-structured TSS-jump process, we have to compute the fitness $z_0(y,x)$ of a mutant y in the monomorphic resident population of trait x. This can be obtained by solving numerically an equation in which the term $\widehat{M}_x$ is replaced by its numerical approximation $\widetilde{M}_x$:

$$1 = y(4-y)\int_0^{+\infty}\exp\left(-\frac{5}{4}a+(z-1)y(4-y)(1-e^{-a})-\frac{U(y,x)\widetilde{M}_x}{2}a^2\right)da. \tag{5.17}$$

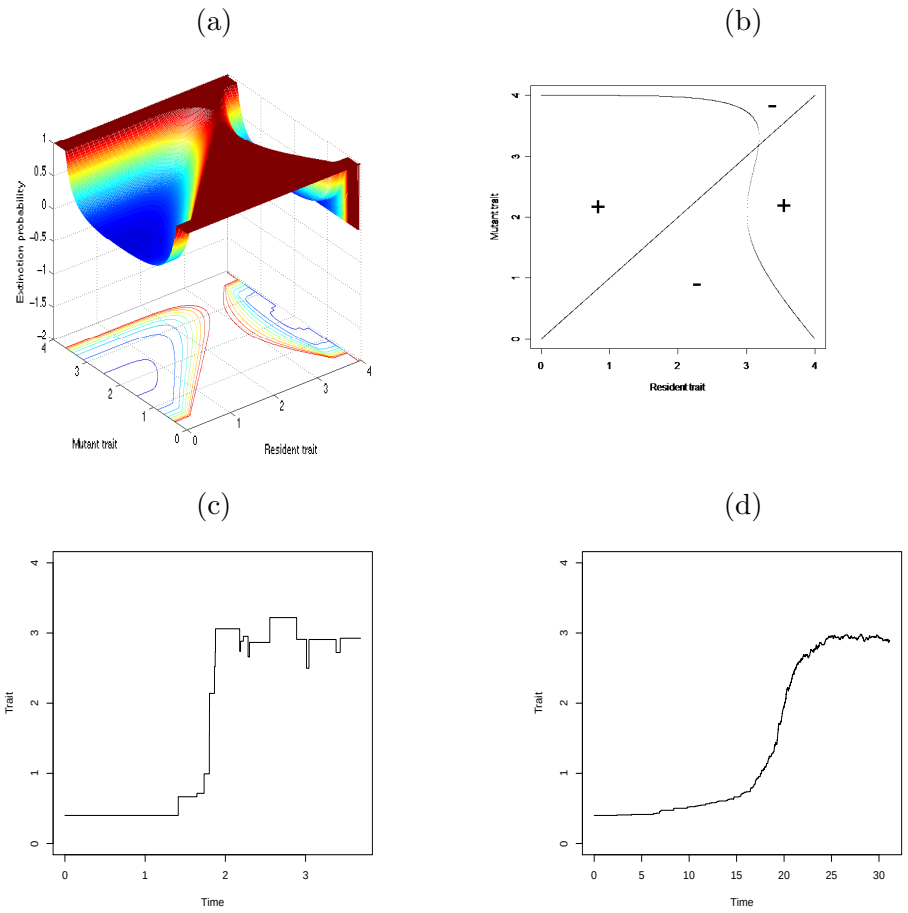

Figure 8: *(a): Probability of extinction as a function of the resident and mutant traits. (b): Associated PIP. The domain of invasibility is delimited by the first bissector and by a curve that is not the graph of a function any more. (c): Simulations of an Age-structured TSS path. (d): Approximation of the Age-structured Canonical Equation obtained in the limit of the TSS when mutations are small.*

Conversely to the example corresponding to the rates (2.3), (2.4), the TSS process does not seem to converge in long time here. The twisted curve in the PIP (Figure 8) shows indeed that we are in a case of *mutual invasibility* (see [11, 26, 16]).

6 Example 2

In this last example, we investigate a model where the death rate has the separable multiplicative form commented in Section 2.1

$$d(x,a,Z)=\int_{[0,4]\times\mathbb{R}_+} a(1+e^{-\alpha})U(x,y)Z(dy,d\alpha), \tag{6.1}$$

U being the Kisdi kernel defined in (2.5). The birth rate is here $b(x)=x(4-x)$. Here, it will be possible to carry an investigation of the branching phenomenon that is observed.

6.1 Monomorphic equilibrium in large population

In this example, the partial differential equation defined in Proposition 2.4 is given by

$$\frac{\partial m}{\partial t}(x,a,t)+\frac{\partial m}{\partial a}(x,a,t)=-am(x,a,t)\int_0^{+\infty}(1+e^{-\alpha})U(x,x)m(x,\alpha,t)d\alpha, \tag{6.2}$$

$$m(x,0,t)=\int_0^{+\infty}x(4-x)m(x,a,t)da. \tag{6.3}$$

Proposition 6.1. *Equations (6.2)-(6.3) admit a unique nontrivial stationary solution:*

$$\widehat{m}(x,a)=\frac{\pi x^3(4-x)^3(1+\nu)}{2C\nu\left[1+2e^{\frac{1}{\pi x^2(4-x)^2}}\left(1-\Phi\left(\frac{2}{\pi x^2(4-x)^2}\right)\right)\right]}\exp\left(-\frac{\pi x^2(4-x)^2a^2}{4}\right), \tag{6.4}$$

where Φ is the distribution function of the standard gaussian law.

Proof. (2.13) becomes here

$$\widehat{m}(x,a)=\widehat{m}(x,0)e^{-\int_0^a\alpha d\alpha\widehat{E}(x)}=\widehat{m}(x,0)e^{\frac{-a^2}{2}\widehat{E}(x)},\quad \widehat{E}(x)=\int_0^{+\infty}(1+e^{-\alpha})U(x,x)\widehat{m}(x,\alpha)d\alpha. \tag{6.5}$$

Plugging (6.5) in (6.3), we obtain

$$1=\int_0^{+\infty}x(4-x)e^{-\frac{\widehat{E}(x)a^2}{2}}da\Leftrightarrow\quad 1=\frac{x(4-x)}{2}\sqrt{\frac{2\pi}{\widehat{E}(x)}}\quad\Leftrightarrow\quad\widehat{E}(x)=\frac{\pi x^2(4-x)^2}{2}. \tag{6.6}$$

Finally, from (6.5)

$$\widehat{m}(x,0)=\frac{\widehat{E}(x)}{\int_0^{+\infty}(1+e^{-\alpha})U(x,x)e^{-\frac{\widehat{E}(x)\alpha^2}{2}}d\alpha}=\frac{\widehat{E}(x)^{3/2}(1+\nu)}{C\nu\sqrt{2\pi}\left[\frac{1}{2}+e^{\frac{1}{2\widehat{E}(x)}}\left(1-\Phi\left(\frac{1}{\widehat{E}(x)}\right)\right)\right]}. \tag{6.7}$$

We deduce the announced result from (6.5), (6.6) and (6.7). ■

In Appendix B, we show that the nontrivial equilibrium (6.4) is asymptotically stable.

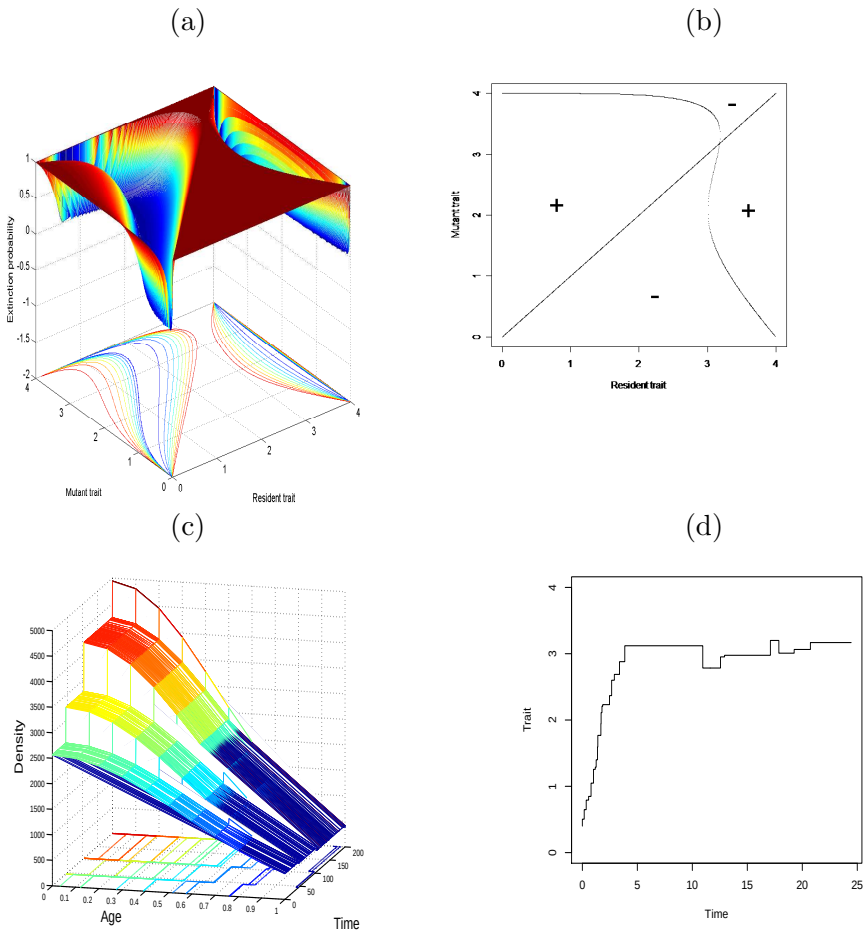

Figure 9: *(a): Extinction probability as function of the resident and mutant traits. (b): PIP showing the regions of possible invasion, obtained by solving (6.11). (c): Simulation of the Age-structured TSS process. (d): we show the successive equilibrium age distributions, and right, the sequence of corresponding traits.*

6.2 Invasibility

Invasion of the resident population of trait x at equilibrium by a mutant of trait y is possible if and only if

$$\int_0^{+\infty} y(4-y)e^{-\frac{a^2\widehat{E}(y,x)}{2}}da > 1, \qquad \text{where } \widehat{E}(y,x) = \int_0^{+\infty}(1+e^{-\alpha})U(y,x)\widehat{m}(x,\alpha)d\alpha. \tag{6.8}$$

The balance equation (2.14) is

$$1 = \int_0^{+\infty} y(4-y)e^{-\frac{\widehat{E}(y)a^2}{2}}da, \tag{6.9}$$

and hence, the probability of extinction $z_0(y,x)$ is strictly less than 1 if and only if:

$$\widehat{E}(y,x) < \widehat{E}(y) \tag{6.10}$$

Since $\widehat{E}(y,x) = \widehat{E}(x)\frac{(1+\nu)e^{-k(y-x)}}{1+\nu e^{-k(y-x)}}$, (6.10) becomes:

$$x^2(4-x)^2\frac{(1+\nu)e^{-k(y-x)}}{1+\nu e^{-k(y-x)}} < y^2(4-y)^2. \tag{6.11}$$

This inequality can be solved numerically and the PIP is given in Figure 9 (b).

In the case where invasion is possible, the fitness of the mutant of trait y in the resident population of trait x is the smallest solution in $[0,1]$ of (3.8) which in this example becomes

$$\begin{aligned} 1 =& \int_0^{+\infty} y(4-y) e^{(z-1)y(4-y)a - \widehat{E}(y,x)a^2/2} da \\ =& \frac{\sqrt{2\pi} y(4-y)}{\sqrt{\widehat{E}(y,x)}} \exp\left(\frac{(z-1)^2 y^2 (4-y)^2}{2\widehat{E}(y,x)}\right) \left(1 - \Phi\left(-\frac{(z-1)y(4-y)}{\sqrt{\widehat{E}(y,x)}}\right)\right). \end{aligned} \tag{6.12}$$

The solution of (6.12) cannot be obtained explicitly, but can be computed numerically for every x and y in $[0,4]$ as obtained in Figure 9.

Conversely to Example 1, the TSS process does not converge to a limit, even if it seems to stay in the neighborhood of the evolutionary singularity $x^* \approx 3.2$. Moreover, looking at the underlying microscopic process (Figure 1), we can observe splitting of the population into smaller groups once the neighborhood of this point has been reached. To understand this fact, let us study more carefully the directional derivatives of the solution of (6.12).

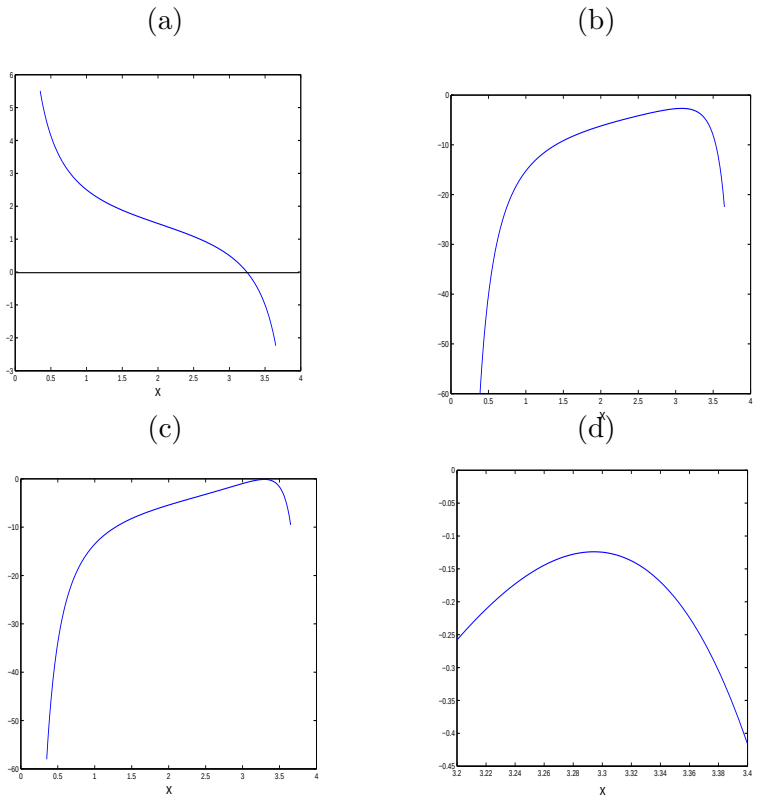

Figure 10: *(a): Graph of $x \mapsto \partial_1 g(x,x)$ defined in (6.13). (b): Graph of $x \to \partial^2_{22} g(x,x)$. (c), (d): graphs of $x \to \partial^2_{11} g(x,x)$ on $(0,4)$ and on $[3.2, 3.4]$.*

Proposition 6.2. *Recall that g has been defined in Lemma 3.5. Then, for all $x \in (0,4)$,*

$$\partial_1 g(x,x) = \frac{1.4(x+1.4)(x-3.2)}{x(4-x)} \tag{6.13}$$
$$\partial^2_{11} g(x,x) = -\frac{5.8(x^2+1.8x+1.1)(x^2-6.6x+10.9)}{x^2(4-x)^2}$$
$$\partial^2_{22} g(x,x) = -\frac{5.8(x^2+1.8x+1.5)(x^2-6.6x+11.1)}{x^2(4-x)^2}.$$

Proof. In order to obtain these derivatives, we replace as previously y by $y+\varepsilon_y$ and x by $x+\varepsilon_x$ in (6.12), expand the right hand side in series with MAPLE in ε_x and ε_y and identify the terms according to their order. ■

We remark that the function $x \to \partial_1 g(x,x)$ vanishes on the unique point $x^* = 3.2$ of the interval $[0,4]$, which confirms the simulations. $\partial^2_{11} g(x,x)$ remains negative on $[0,4]$ and the function $y \mapsto g(y,x) - 1$ is hence locally concave at the neighborhood of (x,x), for each $x \in (0,4)$. In particular, x^* corresponds to a local minimum of the fitness function. Moreover, we can check that $\partial^2_{22} g(x^*,x^*) \approx -2.9 < \partial^2_{11} g(x^*,x^*) \approx -0.3$ which entails that x^* is a *branching point* in the terminology of [11, 26, 16]. These results can also be read on the PIP (Figure 9 (b)) which shows that the population can still be invaded once it has reached the neighborhood of the evolutionary singularity x^*.

7 Conclusion

In this work, we have considered a population structured by traits and by a continuous age, varying with time. The ecology is approximated by a partial differential equation in both trait and age. Based on a measure-valued process approach and generalizing [4, 6], we have obtained new approximations extending the Trait Substitution Sequence and the Canonical Equation of Adaptive Dynamics to trait and age-structured populations. To our knowledge, these equations have not been proposed so far in the biological literature. Our approach emphasizes that the object of interest here is the whole age-distribution of the monomorphic population at equilibrium, and not only the equilibrium trait.

Adding an age structure to trait structured population models opens the way to new problems dealing with life history feature. In the examples, we have seen that age-structure does not seem to change the qualitative behavior of the evolutionary approximation but refines the computation of the evolutionary stable state. As in the case without age-structure, the choice of the competition kernel has a strong influence on the patterns that can be observed on the microscopic simulations, and on the nature of the evolutionary singularities.

Acknowledgments

The authors thank Nicolas Champagnat, Régis Ferrière and Pierre Collet for many fruitful discussions.

A Proof of Theorem 3.1 and of Proposition 3.3

The skeleton of the proof of Theorem 3.1 is similar to the one in Champagnat [4] for populations without age-structure, but with additional difficulties. In [4], the distance between a population and its equilibrium is obtained by comparisons of the trait values and of the sizes. Here, age-distributions have to be taken into account. We need to compare the measure Z^n_t with the

stationary solution of (2.8). Thus, we consider the space of finite measures $\mathcal{M}_F(\widetilde{\mathcal{X}})$ which we embed with the weak convergence topology, induced by the Dudley metric (see Rachev [33] p79):

$$\forall \mu,\, \nu \in \mathcal{M}_F(\widetilde{\mathcal{X}}),\, D(\mu,\nu) = \sup_{\substack{f \text{ 1-Lip} \\ \|f\|_\infty \leq 1}} |\langle \mu, f\rangle - \langle \nu, f\rangle|\,.$$

To prove Theorem 3.1, we establish that $\forall t \in \mathbb{R}_+$, $\forall \Gamma \subset \mathcal{X}$ mesurable, $\forall \varepsilon > 0$

$$\lim_{n\to+\infty} \mathbb{P}\left(Z^n_{t/nu_n} \text{ is monomorphic of trait } y \in \Gamma,\, D(Z^n_{t/nu_n}, \widehat{\xi}_y) < \varepsilon\right) = \mathbb{P}_{x_0}\left(X_t \in \Gamma\right), \quad \text{(A.1)}$$

where $(X_t)_{t\in\mathbb{R}_+}$ has been defined in Theorem 3.1. We use the exponential deviations and estimates of times of exit of domains established in [37] one the one hand, and comparisons with linear age-structured birth and death processes on the other hand. This last point is detailed through the main steps of the proof of Proposition 3.3 in the sequel. For a complete proof, we refer to [36] (Chapter 6).
Let $\varepsilon > 0$ and let us introduce the following stopping times:

$$\begin{aligned}
R^n_\varepsilon &= \inf\left\{t \geq 0 \;\mid\; D\left(1_{\{x_0\}}(x) Z^n_t(dx,da), \widehat{\xi}_{x_0}(dx,da)\right) \geq \varepsilon\right\} \\
S^n_\varepsilon &= \inf\left\{t \geq 0 \;\mid\; \int_{\widetilde{\mathcal{X}}} 1_{\{y\}}(x) Z^n_t(dx,da) \geq \varepsilon\right\} \\
S^n_0 &= \inf\left\{t \geq 0 \;\mid\; \int_{\widetilde{\mathcal{X}}} 1_{\{y\}}(x) Z^n_t(dx,da) = 0\right\}.
\end{aligned}$$

Recall that the time of first mutation τ and the time of return to a monomorphic state θ have been defined in Proposition 3.3. By large deviations results, and by comparison results, we can prove that (see [36], Section 6.2.4)

$$\exists \rho > 0,\, \exists n_0 \in \mathbb{N}^*,\, \forall n \geq n_0,\, \mathbb{P}^n_{x_0,q^n_0,y}\left(\frac{\rho}{nu_n} < \tau \wedge R^n_\varepsilon\right) \geq 1 - 2\varepsilon. \quad \text{(A.2)}$$

On the period $[0, \tau \wedge R^n_\varepsilon \wedge S^n_\varepsilon \wedge S^n_0]$, the mutant population is of mass smaller than ε and evolves in a resident population that is closed to $\widehat{\xi}_{x_0}$. The extinction probability $z_0(y,x)$ that appears in Theorem 3.1 comes from comparison of the mutant population process with the following linear birth and death age-structured (non-renormalized) processes: for sufficiently large $n \in \mathbb{N}^*$ (such that $1 - u_n p > 1 - \varepsilon$), $\forall t \in [0, \tau \wedge R^n_\varepsilon \wedge S^n_\varepsilon]$, $\forall f \in \mathcal{B}_b(\mathbb{R}_+, \mathbb{R}_+)$,

$$\frac{1}{n}\langle Z^{1,\varepsilon}_t, f\rangle \leq \int_{\widetilde{\mathcal{X}}} 1_{\{y\}}(x) f(a) Z^n_t(dx,da) \leq \frac{1}{n}\langle Z^{2,\varepsilon}_t, f\rangle,$$

where:

1. $(Z^{1,\varepsilon}_t)_{t\in\mathbb{R}_+}$ is the birth and death process with birth rate $b_1(a) = (1-\varepsilon)b(y,a)$ and death rate $d_1(a) = d(y,a) + \int_{\mathbb{R}_+} U((y,a),(x_0,\alpha))\widehat{m}(x_0,\alpha)d\alpha + \bar{U}\varepsilon$,

2. $(Z^{2,\varepsilon}_t)_{t\in\mathbb{R}_+}$ is the birth and death process with birth rate $b_2(a) = b(y,a)$ and death rate $d_2(a) = d(y,a) + \int_{\mathbb{R}_+} U((y,a),(x_0,\alpha))\widehat{m}(x_0,\alpha)d\alpha - \bar{U}\varepsilon$.

Let us define for $i \in \{1,2\}$:

$$S^i_{\varepsilon n} = \inf\left\{t \geq 0 \;\mid\; \langle Z^{i,\varepsilon}_t, 1\rangle \geq \varepsilon n\right\}, \qquad S^i_0 = \inf\left\{t \geq 0 \;\mid\; \langle Z^{i,\varepsilon}_t, 1\rangle = 0\right\}.$$

The probabilities that these processes reach the level εn before getting extinct are given by the following lemma, proved at the end of the section:

Lemma A.1. *Let $\varepsilon > 0$, and let $i \in \{1,2\}$. Let us consider the linear birth and death age-structured process $(Z_t^{i,\varepsilon})_{t\in\mathbb{R}_+}$ introduced above and starting from $Z_0^{i,\varepsilon}(da) = \delta_0(da)$. Let $(t_n)_{n\in\mathbb{N}^*}$ be a positive real sequence such that $\lim_{n\to+\infty} t_n/\log n = +\infty$.*

1. *If $\int_0^{+\infty} b_i(a)e^{-\int_0^a d_i(\alpha)d\alpha}da \leq 1$:*

$$\lim_{n\to+\infty} \mathbb{P}\left(S_0^i \leq t_n \wedge S_{\varepsilon n}^i\right) = 1 \tag{A.3}$$

2. *If $\int_0^{+\infty} b_i(a)e^{-\int_0^a d_i(\alpha)d\alpha}da > 1$:*

$$\lim_{n\to+\infty} \mathbb{P}\left(S_0^i \leq t_n \wedge S_{\varepsilon n}^i\right) = z_0^i(y,x_0) \tag{A.4}$$

$$\lim_{n\to+\infty} \mathbb{P}\left(S_{\varepsilon n}^i \leq t_n \leq S_0^i\right) = 1 - z_0^i(y,x_0), \tag{A.5}$$

where $z_0^i(y,x_0)$ is the smallest solution in $[0,1]$ of the equation analogous to (3.5), where the birth and death rates are replaced by $b_i(a)$ and $d_i(a)$. □

The probability that the mutant population gets extinct before having reached the mass ε, before the occurrence of a new mutation, and before the resident population deviates from its equilibrium is then lower bounded by:

$$\begin{aligned}\mathbb{P}^n_{x_0,q_0^n,y}\left(S_0^n < \tau \wedge R_\varepsilon^n \wedge S_\varepsilon^n\right) &\geq \mathbb{P}^n_{x_0,q_0^n,y}\left(S_0^n < \frac{\rho}{nu_n} \wedge S_\varepsilon^n,\ \ \frac{\rho}{nu_n} < \tau \wedge R_\varepsilon^n\right)\\ &\geq \mathbb{P}^n_{x_0,q_0^n,y}\left(S_0^2 < \frac{\rho}{nu_n} \wedge S_{\varepsilon n}^2,\ \ \frac{\rho}{nu_n} < \tau \wedge R_\varepsilon^n\right) \geq z_0(y,x_0) - C\varepsilon,\end{aligned} \tag{A.6}$$

by (A.2), by Lemma A.1 and by showing that when $\varepsilon \to 0$, $z_0^i(y,x) \to z_0(y,x)$. The continuity of the extinction probability when the birth and death rates are perturbed by ε is obtained thanks to the implicit function theorem (see Lemma 6.2.5 of [36]). Similarly, the probability that the mutant population reaches the mass ε before extinction, before the occurrence of another mutant or before the deviation of the resident population to its equilibrium is lower bounded by:

$$\begin{aligned}\mathbb{P}^n_{x_0,q_0^n,y}\left(S_\varepsilon^n < \tau \wedge R_\varepsilon^n \wedge S_0^n\right) &\geq \mathbb{P}^n_{x_0,q_0^n,x_0}\left(S_\varepsilon^n < \frac{\rho}{nu_n} \wedge S_0^n,\ \ \frac{\rho}{nu_n} < \tau \wedge R_\varepsilon^n\right)\\ &\geq \mathbb{P}^n_{x_0,q_0^n,x_0}\left(S_{\varepsilon n}^1 < \frac{\rho}{nu_n} \wedge S_0^1,\ \frac{\rho}{nu_n} < \tau \wedge R_\varepsilon^n\right) \geq 1 - z_0(y,x_0) - C\varepsilon.\end{aligned} \tag{A.7}$$

If $z_0(y,x_0) = 1$, we obtain by (A.6) that:

$$\mathbb{P}^n_{x_0,q_0^n,y}\left(S_0^n < \tau \wedge R_\varepsilon^n \wedge S_\varepsilon^n\right) = \mathbb{P}^n_{x_0,q_0^n,y}\left(\theta < \tau \wedge R_\varepsilon^n,\, V_0 = x_0,\, D(Z_\theta^n, \widehat{\xi}_{V_0}) < \varepsilon\right) \geq 1 - C\varepsilon. \tag{A.8}$$

Since this is valid for every $\varepsilon > 0$, Proposition 3.3 is proved in this case. If $z_0(y,x_0) \in]0,1[$, we show by following the proof of Lemma 3 in [4] that once the mutant population has reached the mass ε, it replaces the resident population with probability one. Indeed, the microscopic process in this case follows its deterministic *dimorphic* approximation. Since $z_0(y,x_0) < 1$, we necessarily have (Proposition 3.4):

$$\int_{\mathbb{R}_+} b(y,a)\exp\left(-\int_0^a \widehat{d}(y,\alpha,x_0)d\alpha\right)da > 1, \quad \text{and} \tag{A.9}$$

by the assumption of non coexistence in the long term of two traits (Ass. 2.6):

$$\int_0^{+\infty} b(x_0,a)\exp\left(-\int_0^a \widehat{d}(x_0,\alpha,y)d\alpha\right)da < 1. \tag{A.10}$$

Then, the deterministic approximation ξ converges to $\delta_y(dx)\widehat{m}(y,a)da$. Its neighborhood is reached by the microscopic process in finite time with a probability that tends to 1 when $n \to +\infty$. When this happens, we can approximate the dynamics of the resident population by comparing it with a linear birth and death age-structured process with birth rate $b(x_0,a)$ and death rate $\widehat{d}(x_0,a,y)$ as we did for the mutant population after its introduction in the system. Because of (A.10), these linear branching processes can be chosen sub-critical and we can then show that the resident population gets extinct with a probability that tends to 1 when $n \to +\infty$. This gives us that:

$$\lim_{n\to+\infty} \mathbb{P}^n_{x_0,q_0^n,y}\left(\theta \leq \tau,\ V = y\right) \geq 1 - z_0(y,x_0) - C\varepsilon.$$

Since (A.6) gave us that:

$$\lim_{n\to+\infty} \mathbb{P}^n_{x_0,q_0^n,y}\left(\theta \leq \tau,\ V = x_0\right) \geq z_0(y,x_0) - C\varepsilon,$$

and since $\mathbb{P}^n_{x_0,q_0^n,y}\left(\theta \leq \tau,\ V = x_0\right) + \mathbb{P}^n_{x_0,q_0^n,y}\left(\theta \leq \tau,\ V = y\right) = 1$, Proposition 3.3 is proved.

A.1 Proof of Lemma A.1

For the linear birth and death processes, there is no accumulation of birth and death events and

$$\lim_{n\to+\infty} t_n \wedge S^i_{\varepsilon n} = +\infty,\ \mathbb{P}-p.s.$$

By dominated convergence, the left hand side of (A.3) and (A.4) converges to $\mathbb{P}\left(S_0^i < +\infty\right)$, which solves an equation similar to (3.5). The result is then obtained from Proposition 3.4. Let us now consider (A.5):

$$\mathbb{P}\left(S^i_{\varepsilon n} \leq t_n \leq S_0^i\right) = \mathbb{P}\left(S^i_{\varepsilon n} \leq t_n \text{ and } S_0^i = +\infty\right) + \mathbb{P}\left(S^i_{\varepsilon n} \leq t_n \leq S_0^i < +\infty\right). \tag{A.11}$$

The second term of (A.11) is upper-bounded by $\mathbb{P}\left(t_n \leq S_0^i < +\infty\right)$, which tends to 0 when $n \to +\infty$ by the choice of t_n. Let us now turn to the first term. Under the assumptions of Point 2, there exists a unique $\lambda > 0$ such that:

$$\int_0^{+\infty} b_i(a) e^{-\lambda a - \int_0^a d_i(\alpha)d\alpha} da = 1.$$

Let Y_1 and W be the number of children and lifelength of an individual with birth rate $b_i(a)$ and death rate $d_i(a)$. From the sufficient conditions of Doney [12], when $t \to +\infty$, $(e^{-\lambda t}\langle Z_t^{i,\varepsilon}, 1\rangle)_{t\in\mathbb{R}_+}$ converges almost surely and in mean square to a strictly positive random variable on $\{S_0^i = +\infty\}$ if $\mathbb{E}(Y_1^2) < +\infty$ and $\mathbb{E}\left(\left(\int_0^W e^{-\lambda a} b_i(a)da\right)\log\left(\int_0^W e^{-\lambda a} b_i(a)da\right)\right) < +\infty$. Recall Assumptions 2.1, and let $\varepsilon > 0$ be sufficiently small so that d_2 remains bounded below by $\underline{d} > 0$. Since the density of W is $d_i(w)\exp(\int_0^w d_i(\alpha)d\alpha)$ and since conditionally to W, Y_1 is a Poisson random variable with parameter $\int_0^W b_i(a)da$, we have

$$\mathbb{E}\left(Y_1^2\right) = \int_0^{+\infty}\left(\int_0^w b_i(a)da\right) d_i(w) e^{-\int_0^w d_i(a)da} dw \leq \bar{b}(\bar{d} + \varepsilon\bar{U} + \bar{U}\widehat{M}_x)\int_0^{+\infty} w e^{-\underline{d}w} dw < +\infty.$$

The function $x \in \mathbb{R}^* \mapsto x\log(|x|)$ tends to 0 when $x \to 0$. On $\mathbb{R}_+$, this function first decreases from 0 to $-e^{-1}$ and then increases. Thus:

$$\begin{aligned} -\frac{1}{e} \leq \mathbb{E}\left(\left(\int_0^W e^{-\lambda a} b_i(a)da\right)\log\left(\int_0^W e^{-\lambda a} b_i(a)da\right)\right) &\leq \mathbb{E}\left(\max(0, \bar{b}W\log(\bar{b}W))\right) \\ &\leq \bar{b}(\bar{d} + \varepsilon\bar{U} + \bar{U}\widehat{M}_x)\int_0^{+\infty} w\left|\ln(\bar{b}w)\right| e^{-\underline{d}w} dw < +\infty. \end{aligned}$$

Doney's sufficient conditions are then satisfied. On $\{S_0^i = +\infty\}$ we thus have

$$\lim_{t\to+\infty} \frac{\log\langle Z_t^{i,\varepsilon}, 1\rangle}{t} = \lambda > 0. \tag{A.12}$$

Let us consider $n > 1/\varepsilon$, so that $\log(\varepsilon n) > 0$. Since $\lim_{n\to+\infty} S_{\varepsilon n}^i = +\infty$ almost surely, we have by (A.12) that almost surely on $\{S_0^i = +\infty\}$

$$\lim_{n\to+\infty} \frac{\log \varepsilon n}{S_{\varepsilon n}^i} \geq \lim_{n\to+\infty} \frac{\log\langle Z_{S_{\varepsilon n}^i -}, 1\rangle}{S_{\varepsilon n}^i} = \lambda > 0. \tag{A.13}$$

Then:

$$\begin{aligned}\lim_{n\to+\infty} \mathbb{P}\left(S_{\varepsilon n}^i \leq t_n, \quad S_0^i = +\infty\right) = \lim_{n\to+\infty} \mathbb{P}\left(\frac{S_{\varepsilon n}^i}{\log(\varepsilon n)} \leq \frac{t_n}{\log(\varepsilon n)}, \quad S_0^i = +\infty\right)\\ = \mathbb{P}\left(S_0^i = +\infty\right) = 1 - z_0^i(y, x),\end{aligned} \tag{A.14}$$

as by choice of t_n, $\lim_{n\to+\infty} t_n/(\log \varepsilon n) = +\infty$.

B Stability of the nontrivial equilibrium in Example 2

Let us prove that the nontrivial equilibrium (6.4) of Equations (6.2)-(6.3) is asymptotically stable. In view of Theorem 4.12 in Webb [38] (p207), it is sufficient to study the eigenvalues of the operator B associated to the linearization of these equations in the neighborhood of this equilibrium. This leads us to study existence of non trivial solutions for the following equations:

$$\frac{du}{da}(a) = -\left(a\widehat{E}(x) + \lambda\right) u(a) - a\widehat{m}(x, a)E(x), \tag{B.1}$$

$$u(0) = \int_0^{+\infty} x(4 - x)u(a)da, \tag{B.2}$$

$$E(x) = \int_0^{+\infty} U(x, x)(1 + e^{-\alpha})u(\alpha)d\alpha. \tag{B.3}$$

Equation (B.1) implies that:

$$u(a) = e^{-\widehat{E}(x)\frac{a^2}{2} - \lambda a}\left(u(0) - \widehat{m}(x, 0)E(x)\int_0^a \alpha e^{\lambda\alpha}d\alpha\right). \tag{B.4}$$

Plugging this in Equation (B.2):

$$u(0) = \int_0^{+\infty} x(4 - x)e^{-\frac{\widehat{E}(x)a^2}{2} - \lambda a}\left(u(0) - \widehat{m}(x, 0)E(x)\int_0^a \alpha e^{\lambda\alpha}d\alpha\right)da. \tag{B.5}$$

If $\lambda = 0$, then (B.5) and the balance condition (6.9) lead us to:

$$0 = \widehat{m}(x, 0)E(x)x(4 - x)\int_0^{+\infty} \frac{a^2}{2}e^{-\frac{\widehat{E}(x)a^2}{2}}da,$$

which is never satisfied, since the right hand side is strictly positive. Hence $\lambda = 0$ is not an eigenvalue of B.
If $\lambda \neq 0$, (B.5) gives

$$u(0) = -\frac{\widehat{m}(x, 0)E(x)\int_0^{+\infty} e^{-\frac{\widehat{E}(x)a^2}{2}}\left(e^{-\lambda a} + \lambda a - 1\right)da}{\lambda^2\int_0^{+\infty} e^{-\frac{\widehat{E}(x)a^2}{2}}\left(1 - e^{-\lambda a}\right)da}. \tag{B.6}$$

If $\lambda > 0$, then (B.6) has a sign opposite to $E(x)$ and we deduce from (B.4) that so has $u(a)$. This contradicts (B.3) unless both members of the equation are zero. This is excluded since u is an eigenfunction and hence is not constant equal to zero. Hence there is no eigenvalue on the nonnegative real axis.
Let us now consider $\lambda = \lambda_1 + i\lambda_2$ with $\lambda_1 > 0$. Since $\int_0^{+\infty} a e^{-\widehat{E}(x)a^2/2} da = 1/\widehat{E}(x)$,

$$u(0) = \frac{\widehat{m}(x,0)E(x)}{\lambda^2}\left(1 - \frac{\lambda}{\widehat{E}(x)\int_0^{+\infty} e^{-\frac{\widehat{E}(x)a^2}{2}}(1-e^{-\lambda a})\,da}\right),$$

and hence (B.4) becomes

$$u(a) = e^{-\widehat{E}(x)\frac{a^2}{2}}\frac{\widehat{m}(x,0)E(x)}{\lambda}\left(-a + \frac{1}{\lambda} - \frac{e^{-\lambda a}}{\widehat{E}(x)\int_0^{+\infty} e^{-\frac{\widehat{E}(x)\alpha^2}{2}}(1-e^{-\lambda\alpha})\,d\alpha}\right). \tag{B.7}$$

Using (B.7) in (B.3)

$$0 = \int_0^{+\infty} \frac{C\nu}{1+\nu}\widehat{m}(x,0)(1+e^{-a})e^{-\frac{\widehat{E}(x)a^2}{2}} \times \left(-a + \frac{1}{\lambda} - \frac{e^{-\lambda a}}{\widehat{E}(x)\int_0^{+\infty} e^{-\frac{\widehat{E}(x)\alpha^2}{2}}(1-e^{-\lambda\alpha})\,d\alpha}\right) da - \lambda =: \Lambda(\lambda, x). \tag{B.8}$$

We wish to check that for any given x in $[0,4]$, the complex function $\lambda \mapsto \Lambda(\lambda, x)$ does not

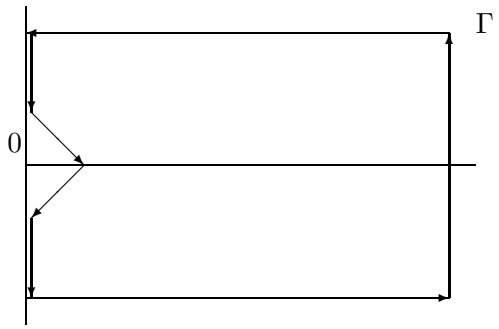

Figure 11: The Jordan curves used to study the zeros of $\lambda \mapsto \Lambda(\lambda, x)$

have roots in the half plane $\mathcal{P}^+$ of complex numbers with nonnegative real part. Let $x \in [0,4]$ be fixed. When $|\lambda| \to +\infty$, the integral in (B.8) converges to a finite value. Hence, the roots of $\Lambda(\lambda, x)$ in $\mathcal{P}^+$, if they exist, belong necessarily to a compact set. In order to show that there are no roots on compact sets of $\mathcal{P}^+$, we use the argument principle (see Henrici [18], Section 4.10). The function $\lambda \mapsto \Lambda(\lambda, x)$ is analytic on $\mathcal{P}^+ \setminus \{0\}$. Let $\Gamma : \tau \in [0,1] \mapsto \Gamma(\tau)$ be a positively oriented Jordan curve of $\mathcal{P}^+ \setminus \{0\}$. Assume that there are J zeros $(z_j)_{j\in[\![1,J]\!]}$ with multiplicities $(m_j)_{j\in[\![1,J]\!]}$ contained in Γ. Then

$$\sum_{j=1}^{J} m_j = \frac{1}{2\pi i}\int_\Gamma \frac{\Lambda'(\lambda,x)}{\Lambda(\lambda,x)}d\lambda = \frac{1}{2\pi i}\int_{\Lambda(\Gamma,x)} \frac{1}{w}dw = n(\Lambda(\Gamma,x),0) \tag{B.9}$$

$$\text{where } n(\Lambda(\Gamma,x),0) := \frac{[\arg(\lambda)]_{\Lambda(\Gamma,x)}}{2\pi} = \frac{\phi(1)-\phi(0)}{2\pi}, \tag{B.10}$$

where $\phi(\tau)$ is a continuous version of the argument of $\Lambda(\Gamma(\tau), x)$. Our purpose is to show that for chosen Jordan curves in $\mathcal{P}^+ \setminus \{0\}$, the right member of (B.10) is zero. This will entail that no zeros are contained in the chosen curves. We consider the Jordan curves drawn in Figure 11. Since the computations can not been carried explicitly, we compute numerically $n(\Lambda(\Gamma, x), 0)$ by following the algorithm proposed by Henrici ([18], end of Section 4.6). We then let x vary along a grid between 0 and 4. The numerical results tell us that the variation of the argument $(\phi(1)-\phi(0))/(2\pi)$ remains zero for every $x \in [0, 4]$. We have thus checked numerically that there is no complex solution λ of (B.8) with nonnegative real part, and the nontrivial equilibrium (6.4) is asymptotically stable.

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