The bd-model of ageing: from individual-based dynamics to evolutive differential inclusions

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Abstract
Ageing’s sensitivity to natural selection has long been discussed because of its apparent negative effect on individual’s fitness. Thanks to the recently described (Smurf) 2-phase model of ageing we were allowed to propose a fresh angle for modeling the evolution of ageing. Indeed, by coupling a dramatic loss of fertility with a high-risk of impending death - amongst other multiple so-called hallmarks of ageing - the Smurf phenotype allowed us to consider ageing as a couples of sharp transitions. The bd model we describe here is a simple life-history trait model where each asexual and haploid individual is described by its fertility period $x_b$ and survival period $x_d$. We show that, thanks to the Lansing effect, $x_b$ and $x_d$ converge during evolution to configurations $x_b - x_d \approx 0$. This guarantees that a certain proportion of the population maintains the Lansing effect which in turn, confers higher evolvability to individuals.

To do so, we build an individual-based stochastic model which describes the age and trait distribution dynamics of such a finite population. Then we rigorously derive the adaptive dynamics models, which describe the trait dynamics at the evolution-ary time-scale. First, we extend the Trait substitution sequence with age structure to take into account the Lansing effect. Finally, we study the limiting behaviour of this jump process when mutations are small. We show that the limiting behaviour is described by a differential inclusion whose solutions $x(t) = (x_b(t), x_d(t))$ reach in finite time the diagonal $\{x_b = x_d\}$ and then stay on it. This differential inclusion is a natural way to extend the canonical equation of adaptive dynamics in order to take into account the lack of regularity of the invasion fitness function on the diagonal $\{x_b = x_d\}$.

1 Introduction
Ageing is commonly defined as an age-dependant increase of the probability to die after the maturation phase (Kirkwood and Austad [20]). It affects a broad range of organisms in various ways ranging from negligible senescence to fast post-reproductive death (reviewed in [19]). In the recent years, a new 2-phases model
of ageing proposed by Tricoire and Rera [42] described the ageing process not as being continuous but as made of at least 2 consecutive phases separated by a dramatic transition. This transition, dubbed “Smurf transition”, was first described in drosophila ([35], [36]). In short, this transition occurs in every individuals prior to death and is marked by a series of associated phenotypes encompassing high-risk of impending death, increased intestinal permeability, loss of energy stores, reduced fertility (c.f [37]). It was later shown to be evolutionarily conserved in *Caenorhabditis elegans* and *Danio rerio* (c.f [10]). Such broad evolutionary conservation of a physiological marker of physiological age raises the question of an active selection of the underlying mechanisms throughout evolution. Since the beginning of ageing studies, the question of its ability to appear through evolution has been raised. In fact, since the Darwinian theory of evolution stipulates that species arise and develop thanks to the natural selection of small, inherited variations that increase the individual’s ability to compete, survive, and reproduce (c.f [11]), many suggested that ageing - and more precisely senescence - could not be actively and directly selected thanks to evolution (c.f [14]). One of the first to publicly address the question of the evolution of ageing was August Weismann who proposed in 1881 that the life expectancy was programmed by “the needs of the species” (c.f [45]). Numerous theoretical works have been developed about ageing for the past 60 years in order to recenter the selection of an ageing process on the individuals more than the population. Here we will focus our attention on the capability of a trait such as ageing to be selected through evolution.

The concept of evolvability comes from the EvoDevo community. It “is an abstract, robust, dispositional property of populations, which captures the joint causal influence of their internal features upon the outcomes of evolution” (c.f [3]). In other terms, it is “the capacity to generate heritable selectable phenotypic variation” (c.f [22]). It is an interesting concept as it allows for a character that has no direct effect on fitness to be under strong selection simply for its ability to birth the genetic-phenotypic variation that is the support of evolution.

If the only fitness - as an individual reproductive success or its average contribution to the gene pool of the next generation - were at play in the evolution process, the best adapted individuals would have infinite fertility as well as longevity. Nevertheless, this situation is never observed mainly because organisms adapted to constant variations of environmental conditions and physical limitations of resources availability. Thus, an active form mechanism for the elimination of these fitness-excessive individuals would represent a selective advantage in an environment where scarcity is the rule. The Lansing effect is a good candidate for such a mechanism. It is the effect through which the “progeny of old parents do not live as long as those of young parents” in rotifers (c.f [24], [25]). More recently, it has been shown that older drosophila females and in some extent males tend to produce shorter lived offspring (c.f [33]), zebra finch males give birth to offspring with shorter telomere lengths and reduced lifespans (c.f [31]) and finally in humans, “Older father’s children have lower evolutionary fitness across four centuries and in four populations” (c.f [2]).

In the present article, we decided to approach the problem of ageing selection and evolution by using an extremely simplified version of a living organism. It is a haploid and asexual organism carrying only two “genes”, $x_b$ that defines the duration of its ability to reproduce and $x_d$ that defines the duration of its ability to maintain its integrity - stay alive (see Figure 1). We will further discuss the properties of this simple model in the next part. Although quite simple, it allows the modeling
of all types of observed ageing modes from negligible senescence to sudden post-
reproductive death through post-reproductive “menopause-like” survival.
The main result of the present article is that a pro-senescence program can be se-
lected through Darwinian mechanisms thanks to the Lansing effect. Indeed, our
main mathematical result (see Theorem 4.17) shows that evolution drives the trait
\( (x_b, x_d) \) towards configurations \( x_b = x_d \). It means that the individuals can enjoy
all their reproductive capacity, and then are quickly removed from the population.
Moreover, this theorem shows that after reaching the configurations \( x_b = x_d \),
the traits \( x_b \) and \( x_d \) continue to increase with decreasing speed, while maintaining
\( x_b = x_d \). This decrease in the speed of evolution is a consequence of the fitness gra-
dients being decreasing functions of the traits (see Remark 4.4) and is related to the
well-known fact that the strength of selection decreases with age (c.f. [17], [27], [18]).
We built an individual based stochastic model inspired by Tran [41]. It describes an
asexual and haploid population with a continuous age and a continuous life-history
trait structure. In this model, the life-history trait of every individual is thus a
couple of positive numbers \( (x_b, x_d) \in \mathbb{R}^2_+ \). An individual with trait \( (x_b, x_d) \) repro-
duces at rate one as long as it is younger than \( x_b \) and cannot die as long as it is
younger than \( x_d \) (see Figure 1). This model leads to three typical configurations

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{figure1.png}
\caption{Life-history associated with the trait \( x = (x_b, x_d) \).}
\end{figure}

(see Figure 2). From one generation to the next, variation is generated by genetic

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{figure2.png}
\caption{Three typical configurations of the model. (a) ‘Too young to die’: it corresponds to
configurations \( (x_b, x_d) \) which satisfies \( x_d < x_b \); (b) ‘Now useless’: it corresponds to configurations
\( (x_b, x_d) \) which satisfy \( x_b = x_d \); (c) ‘Menopause’: it corresponds to configurations \( (x_b, x_d) \) which
satisfies \( x_d > x_b \).}
\end{figure}

mutations. In addition, natural selection occurs through mortality due to compe-
tition for resources thanks to a logistic equation defining the maximum load of the
medium. Finally, we model the epigenetic effect of senescence through the Lansing
Effect. It introduces a source of phenotypic variation at a much faster time-scale.
than genetic mutations. In that aim, we assume that an individual that reproduces after age $x_d$ transmits to his descendant a shorter life expectancy (see Section 2 for details). Therefore, only individuals with trait $x_d < x_b$ are affected (see Figure 2 (c)). That creates an adaptive trade-off which impacts the phenotypic evolution of the population.

The purpose of this paper is to study the long-term evolution of the trait $x = (x_b, x_d)$ and to determine whether it concentrates on $x_b - x_d = 0$. To do so, we are inspired by the theory of adaptive dynamics [30, 29, 12]. Adaptive dynamics theory studies the phenotypic eco-evolution of large populations under the assumption that genetic mutations are rare and have small effects. A central tool in that theory is the concept of invasion fitness. The invasion fitness is a function $1 - z(y, x)$ formally defined as the probability that an individual with trait $y$ survives in a resident population with trait $x$. In section 4, we prove that the invasion fitness satisfies the simple relation $1 - z(y, x) = \max(\lambda(y) - \lambda(x), 0)$ where $\lambda(x)$ is the Malthusian parameter, describing the adaptive value associated with the trait $x$ (see Section 3.1 for the definition). This allows us to introduce the Trait Substitution Sequence process (TSS) which is a pure jump process describing the successive invasions of successful mutants in monomorphic populations at the demographic equilibrium. The TSS has been heuristically introduced in [29, 12] for population structured in traits. In [6], it has been rigorously derived from an individual based model and generalised in [28], to age-structured populations. Our case differs from [28] by mainly two reasons: the additional Lansing effect and the specific form of the mutation kernel which is not absolutely continuous with respect to Lebesgue measure on $\mathbb{R}^2$ (as assumed in [6, 28]). In the usual case, the TSS is approximated by the solution of the Canonical equation of adaptive dynamics when the size of mutation is small and in a longer time-scale (cf. [5, 8, 28]). This limiting theorem requires the Lipschitz regularity of the fitness gradient. In our case this assumption is not satisfied. Nonetheless, we prove that the limiting behaviour of the TSS when mutation are small is captured by a differential inclusion, using an approach developed in [15].

A differential inclusion is an extension of ordinary differential equation to set-valued time-derivatives, which extends Cauchy-Lipschitz theory to non regular gradient cases. In our case, the gradient is smooth except on the diagonal $\{x_b = x_d\}$. Therefore, we prove that the solutions are well-defined until they attain the diagonal (in finite time). Then they stay on this line and evolve with different speeds. The drift of the differential inclusion depends on the derivatives of the Malthusian parameter with respect to the trait variable. These derivatives are expressed as functions of the stable age distribution and reproductive value as in [18, 4] (see Remark 4.4).

In section 2, we present the individual based model. Thanks to simulations, we show what was suggested by observations. The trait distribution of the population stabilises on the diagonal $x_b - x_d = 0$.

In Section 3, we study the deterministic approximations of the stochastic dynamics under the assumption of large population and rare mutations. These approximations are non-linear systems of partial differential equations similar to the Gurtin-McCamy Equation [16]. We study their long-time behaviour and give some results of convergence to the stationary states.

In section 4, we state and prove the main mathematical results of this paper concerning the approximation by the TSS and the canonical inclusion of adaptive dynamics. (Theorem 4.13 and Theorem 4.17).
2 A stochastic model for the evolution of life-history traits

At each time \( t \geq 0 \), the population is described by a point measure on \((\mathbb{R}_+^*)^2 \times \mathbb{R}_+\)

\[
Z^K_t(dx, da) = \frac{1}{K} \sum_{i=1}^{N^K_t} \delta(x^i(t), a^i(t))(dx, da)
\]

(1)

where \( N^K_t = K\langle Z^K_t, 1 \rangle \) is the population size, \( K \) is the order of the population size and weights each individual, \( x^i(t) = (x^i_b(t), x^i_a(t)) \in (\mathbb{R}_+^*)^2 \) is the trait of the individual \( i \) and \( a^i(t) \in \mathbb{R}_+ \) is its age. The dynamics is defined as a piecewise deterministic Markov process which jumps as follows:

- An individual \((x, a) \in (\mathbb{R}_+^*)^2 \times \mathbb{R}_+\) reproduces at rate \( 1_{a \leq x_b} \). The trait of the newborn \( y = (y_b, y_d) \) is determined by the following two-steps mechanism (see Figure 3 below for an illustration):
  - Step 1: If \( a \leq x_d \), the offspring inherits the trait \( x = (x_b, x_d) \).
    - Lansing Effect: if \( a > x_d \), we assume that the offspring carries the trait \((x_b, 0)\). Let us denote by \( \tilde{x} \) the trait defined as \( \tilde{x} = x \) if \( a \leq x_d \) and \( \tilde{x} = (x_b, 0) \) if \( a > x_d \). Let us observe that \( x_b \) stays unchanged and that only individuals with configurations \( x_d < x_b \) are concerned by the second type \((x_b, 0)\) (see Figure 2(c)).
  - Step 2: Genetic mutations. A mutation appears instantaneously on each trait \( x_b \) and \( \tilde{x}_d \) independently with probability \( p_K \in [0, 1] \). If the trait \( x_b \) mutates, the trait \( y_b \) of the newborn is \( y_b = x_b + h_b \) where \( h_b \in \mathbb{R} \) is chosen according to the probability measure \( k(x_b, h_b)dh_b \); if the trait \( \tilde{x}_d \) mutates, the trait \( y_d = \tilde{x}_d + h_d \) where \( h_d \in \mathbb{R} \) is chosen according to \( k(\tilde{x}_d, h_d)dh_d \), where the mutational kernel \( k \) is defined for all \( u \in \mathbb{R}_+ \) and \( v \in \mathbb{R} \) by

\[
k(u, v) = \frac{1_{[\max(0, u-1), u+1]}(u + v)e^{-\frac{u^2}{2\sigma^2}}}{\int_{\mathbb{R}} 1_{[\max(0, u-1), u+1]}(u + z)e^{-\frac{z^2}{2\sigma^2}}dz}
\]

(2)

where \( \sigma^2 > 0 \). Note that for \( u > 1 \),

\[
k(u, v) = k(v) = \frac{1_{[-1,1]}(v)e^{-\frac{v^2}{2\sigma^2}}}{\int_{\mathbb{R}} 1_{[-1,1]}(z)e^{-\frac{z^2}{2\sigma^2}}dz}.
\]

(3)

- An individual with trait \((x, a)\) has a death rate \( 1_{a > x_d} + \eta N^K_t \), with \( \eta > 0 \), meaning that each individual is submitted to the same competition pressure \( \eta \) from any individual in the population and whatever the value of its trait.
- Between jumps, individuals age at speed one: an individual with age \( a \) at time \( t \) has an age \( a + s \) at time \( t + s \).

Figure 3 summarizes the trait dynamics described above.
Figure 3: Picture of the reproduction and mutation mechanism. (a): the individual reproduces before age $x_d$, there is no Lansing Effect. (b): the individual reproduces after age $x_d$, the Lansing Effect acts.

Figure 4: Simulation of the individual based model (see the script in Appendix A.4). (a): Dynamics of the trait $x_b$ as a function of time. (b): Dynamics of the trait $x_d$ as a function of time. (c): Dynamics of $x_b - x_d$ as a function of time. (d): Population size as a function of time. Parameters: $N_0^K = 10000$ individuals with trait $(1.2, 1.6)$, $\eta = 0.0005$, $p = 0.05$, $\sigma = 0.05$. 
Numerical simulation. The pictures in Figure 4 represent a simulation of the trait marginals dynamics of the process $Z^K_t(dx, da)$. We consider a monomorphic initial population with trait $x = (1.2, 1.6)$ and $N^K_0 = 10000$. We consider a competition rate $\eta = 0.0005$, a probability of mutation $p_K = 0.05$ and a variance of mutations $\sigma = 0.05$.

At time $t = 0$, the population is monomorphic with trait $(x_b, x_d) = (1.2, 1.6)$. We observe that before that the trait $x_b$ reaches the value of 1.5, the trait $x_d$ doesn’t evolve, there is no selection pressure on it. When $x_b$ reaches $x_d \simeq 1.6$, the traits $x_b$ and $x_d$ continue to increase by maintaining $x_b \simeq x_d$.

3 Monomorphic and bimorphic deterministic dynamics

In this section, we study a deterministic approximation of the process $Z^K$ when $K$ goes to infinity. We also assume that $p_K$ goes to zero: it means that almost no mutation occurs on a time interval $[0, T]$. Nonetheless, some phenotypic variation is created by Lansing Effect. Since our model is density-dependent, the deterministic approximation is a system of classical non-linear partial differential equations similar as the Gurtin MacCamy Equation [16]. In the monomorphic case, we show that the dynamics converges to the unique non-trivial equilibrium. In the bimorphic case, we show the convergence to a monomorphic equilibrium. Note that a monomorphic population with trait $x$ is composed of two subpopulations with traits $(x_b, x_d)$ and $(x_b, 0)$.

Notation 3.1. We define $I = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}$.

3.1 Monomorphic dynamics

Let $x = (x_b, x_d) \in \mathbb{R}_+^2$ be a phenotypic trait. We consider a monomorphic initial sequence $(Z^K_0)_K$ such that $Z^K_0$ converges as $K \to \infty$ to the measure $\delta_x n_x(0, a) da$ which describes a monomorphic population with trait $x$. Then, as in [41], we can prove that the sequence of processes $(Z^K)_K$ converges in probability on any finite time interval to the weak solution $(n_x(t, .), t \geq 0) = ((n^1_x(t, .), n^2_x(t, .)), t \geq 0) \in C(\mathbb{R}_+, L^1(\mathbb{R}_+)^2)$ of the following system of partial differential equations

$$\begin{cases} \partial_t n_x(t, a) + \partial_a n_x(t, a) = - (D_x(a) + \eta \|n_x(t, .)\|_1) n_x(t, a) \\ n_x(t, 0) = \int_{\mathbb{R}_+} B_x(a) n_x(t, a) da \end{cases}$$ (4)

where the densities $n^1_x(t, .)$ and $n^2_x(t, .)$ describe the population distributions with trait $(x_b, x_d)$ and $(x_b, 0)$ respectively;

$$\|n_x(t, .)\|_1 = \sum_{i \in \{1, 2\}} \int_{\mathbb{R}_+} |n^i_x(t, a)| da$$

is the total population size and

$$B_x(a) = \begin{pmatrix} 1_{a \leq x_b} & 0 \\ 1_{x_d < a \leq x_b} & 1 \end{pmatrix}, \quad D_x(a) = \begin{pmatrix} 1_{a > x_d} & 0 \\ 0 & 1 \end{pmatrix}$$ (5)
are the birth and death interactions. Equation (4) can be interpreted as a selection-mutation equation with discrete trait space and age structure. We refer to [44] for the well-posedness theory of $L^1(\mathbb{R}_+)^2$ solutions of Equation (4).

We introduce the set of viable traits

$$\mathcal{V} = \{ x = (x_b, x_d) \in (\mathbb{R}_+^2) : x_b \wedge x_d > 1 \}. \quad (6)$$

We show that for any trait $x \in \mathcal{V}$, there exists a unique non-trivial and globally stable stationary state of (4).

**Proposition 3.2.** Assume that $x \in \mathcal{V}$. There exists a unique non-trivial stationary solution $n_x \in L^1(\mathbb{R}_+)^2$ to Equation (4). Moreover, any $L^1(\mathbb{R}_+)^2$ non negative solution $n_x(t, \cdot)$ of (4) such that $n_x^1(t, \cdot) \neq 0$ converges to $n_x$ in $L^1(\mathbb{R}_+)^2$ as $t \to \infty$.

**Remark 3.3.** In Proposition 3.6 below, we will give a more explicit expression for the stationary state $n_x$.

The proof of Proposition 3.2 is based on the study of the associated linear dynamics. We introduce the linear operator

$$A : D(A) \subset L^1(\mathbb{R}_+)^2 \quad \to \quad L^1(\mathbb{R}_+)^2$$

$$u \quad \mapsto \quad -u' - D_x(a)u$$

where $D(A) = \{ u \in L^1(\mathbb{R}_+)^2 : u \text{ abs. cont., } u' \in L^1(\mathbb{R}_+)^2, \ u(0) = \int_{\mathbb{R}_+} B_x(\alpha) u(\alpha) \, d\alpha \}$. It is well known that $A$ is the infinitesimal generator of a strongly continuous semigroup of linear operators [44, Proposition 3.7] which describes the solutions of the linear system of McKendrick Von- Foerster Equation

$$\begin{cases}
\dot{v}_x(t, a) + \delta_a v_x(t, a) = -D_x(a) v_x(t, a) \\
v_x(t, 0) = \int_{\mathbb{R}_+} B_x(\alpha) v_x(t, \alpha) \, d\alpha.
\end{cases} \quad (8)$$

In [9], a similar linear model is studied. The "entropy method" introduced in [32] allows the authors to prove the convergence of the normalised solutions to some stable distribution in some weighted $L^1$-space. We need stronger convergence in order to study the long-time behaviour of the masses of the solutions of (4). Since the birth matrix $B_x$ is not irreducible and the parameters $B_x$ and $D_x$ are not smooth, we cannot apply Theorems 4.9 and 4.11 in [44]. Nonetheless, we easily extend them to our reducible and non-smooth setting.

We define the Malthusian parameter $\lambda(x)$ associated with some trait $x$ as the unique solution of the equation

$$\int_0^{x_b \wedge x_d} e^{-\lambda(x) a} \, da = 1. \quad (9)$$

Proposition 3.4 justifies this definition and shows that $\lambda(x)$ is the asymptotic growth rate of the dynamics defined by (8). Its proof is postponed to Appendix.

Let us define for all $z \in \mathbb{C}$ the $2 \times 2$ matrix

$$F(z) = \int_{\mathbb{R}_+} B_x(a) \exp \left( -\int_0^a (D_x(\alpha) + zI) \, d\alpha \right) \, da. \quad (10)$$

(Note that it is well-defined since $B_x$ has compact support).
Proposition 3.4. Assume that \( x \in \mathcal{V} \). Then the linear operator \( A \) admits a unique couple of simple principal eigenelements \( (\lambda(x), N_x) \in \mathbb{R}^*_+ \times D(A) \) where the stable age distribution \( N_x \) satisfies

\[
N_x^1(a) = e^{-(\lambda(x)a+(a-x_d)v_0)}, \quad N_x^2(a) = \frac{[F(\lambda(x))]_{21}}{1-[F(\lambda(x))]_{22}} e^{-(1+\lambda(x))a}.
\]

Moreover, for any non-negative solution \( v_x(t,a) \) of \([3]\) in \( L^1(\mathbb{R}_+)^2 \), there exists a positive constant \( c(v_x(0,\cdot)) \) such that \( e^{-\lambda(x)t}v_x(t,\cdot) \rightarrow c(v_x(0,\cdot))N_x \) in \( L^1(\mathbb{R}_+)^2 \) as \( t \rightarrow +\infty \).

Let us now give a lemma which will be used to study the long-time behaviour of the masses of the solutions of \([4]\) and whose proof is postponed to Appendix.

Lemma 3.5. Let \((m_{11}, m_{12}, m_{22}) \in \mathbb{R}^*_+ \times \mathbb{R}^*_+ \times \mathbb{R}^*_+\). Let \( \mathcal{D}_{11}(t), \mathcal{D}_{12}(t), \mathcal{D}_{22}(t) \) be continuous functions from \( \mathbb{R}_+ \) to \( \mathbb{R} \) which tend to zero as \( t \rightarrow \infty \). Let us denote

\[
M = \begin{pmatrix} m_{11} & 0 \\ m_{21} & m_{22} \end{pmatrix}, \quad \mathcal{D}(t) = \begin{pmatrix} \mathcal{D}_{11}(t) & 0 \\ \mathcal{D}_{21}(t) & \mathcal{D}_{22}(t) \end{pmatrix}.
\]

Then any solution \((z(t), t \geq 0)\) of the equation

\[
\frac{dz(t)}{dt} = (M + \mathcal{D}(t))z(t) - \eta \|z(t)\|_1 z(t)
\]

started at \((z(0), z(0)) \in \mathbb{R}^*_+ \times \mathbb{R}_+ \) converges to a vector \( \mathbf{z} \) which satisfies

\[
\mathbf{z}_1 = \frac{m_{11}}{\eta} \left( 1 + \frac{m_{21}}{m_{11}-m_{22}} \right), \quad \mathbf{z}_2 = m_{21} - m_{22} \mathbf{z}_1.
\]

We conclude this section by proving Proposition 3.2.

Proof of Proposition 3.2. We prove the first assertion. Let \( x \in \mathcal{V} \) and let \( \lambda(x) \) be the principal eigenvalue of \( A \) given by Proposition 3.4. Let \( \pi_x \) be the (unique) principal eigenvector of \( A \) which satisfies \( \eta \|\pi_x\|_1 = \lambda(x) \). It is obvious that \( \pi_x \) is a non-trivial stationary state of \([4]\). Reciprocally, let \( \pi \) be a stationary state of \([4]\). Then we have necessarily \( \lambda(x) = \eta \|\pi\|_1 \) and that \( \pi \) is an eigenvector of \( A \) associated with the eigenvalue \( \lambda(x) \) that allows us to conclude. We now study the long-time behaviour of the solutions. Let us define

\[
v_x(t,a) = \exp \left( \eta \int_0^t \|n_x(s,\cdot)\|_1 ds \right) n_x(t,a).
\]

It is straightforward to prove that \( v_x \) is a solution of the linear equation \([8]\). By Proposition 3.4 we have \( e^{-\lambda(x)t}v_x(t,\cdot) \rightarrow c(v_x(0,\cdot))N_x \) in \( L^1(\mathbb{R}_+)^2 \) as \( t \rightarrow \infty \). We deduce that for \( i \in \{1,2\} \) and denoting \( \rho_x^i(t) = \|n_x^i(t,\cdot)\|_1 \),

\[
\frac{n_x^i(t,\cdot)}{\rho_x^i(t)} = \frac{e^{-\lambda(x)t}v_x^i(t,\cdot)}{\int_{\mathbb{R}_+} e^{-\lambda(x)t}v_x^i(t,\alpha) d\alpha} \rightarrow \frac{N_x^i}{\int_{\mathbb{R}_+} N_x^i(\alpha) d\alpha}
\]

in \( L^1(\mathbb{R}_+)^2 \) as \( t \rightarrow +\infty \). We now study the behaviour of the masses \( \rho_x(t) \). By deriving under the integral, we obtain that for \( i \in \{1,2\} \)

\[
\frac{d\rho_x^i(t)}{dt} = \sum_{j=1}^2 \int_{\mathbb{R}_+} \left[ [B_x(\alpha)]_{ij} - [D_x(\alpha)]_{ij} \right] n_x^j(t,\alpha) d\alpha - \eta \rho_x^i(t) \rho_x(t)^1
\]

\[
= \sum_{j=1}^2 \rho_x^j(t) \int_{\mathbb{R}_+} \left[ [B_x(\alpha)]_{ij} - [D_x(\alpha)]_{ij} \right] \frac{n_x^j(t,\alpha)}{\rho_x^j(t)} d\alpha - \eta \rho_x^i(t) \rho_x(t)^1.
\]
Hence we obtain by (13) that
\[
\frac{d\rho_x(t)}{dt} = (A + A(t))\rho_x(t) - \eta\|\rho_x(t)\|_1 \rho_x(t)
\]
where \(A = (a_{ij})\) and for \((i, j) \in \{1, 2\}^2\),
\[
a_{ij} = \int_{\mathbb{R}_+} \left[ (B_x(\alpha))_{ij} - [D_x(\alpha)]_{ij} \right] \frac{N^2_j(\alpha)}{N_x} d\alpha,
\]
and \(A(t)\) is a continuous function decreasing to zero as \(t\) tends to infinity. Since \(a_{11} = \lambda(x) > 0, a_{21} \geq 0, a_{12} = 0\) and \(a_{22} < 0\), Lemma 3.5 allows us to conclude that \(\rho_x(t)\) converges to \(\bar{\rho}_x\), which is defined as the unique solution of the equation
\[
A\bar{\rho}_x - \eta\|\bar{\rho}_x\|_1 \bar{\rho}_x = 0.
\]
We easily solve this system and we obtain that \(\bar{\rho}_x\) satisfies
\[
\bar{\rho}_x^1 = \frac{\lambda(x)}{\eta} 1 + \frac{a_{21}}{\lambda(x) - a_{22}} , \quad \bar{\rho}_x^2 = \frac{a_{21}}{\lambda(x) - a_{22}} \bar{\rho}_x^1.
\]
We conclude this section by writing more explicit formulas for the stationary state \(\bar{\rho}_x\).

**Proposition 3.6.** Let \(x \in \mathcal{V}\) then we have
\[
\bar{\rho}_x^1(a) = \frac{\lambda(x)}{\eta} 1 + \frac{a_{21}}{\lambda(x) - a_{22}} N^1_x(\alpha) d\alpha, \quad \bar{\rho}_x^2(a) = \frac{a_{21}}{\lambda(x) - a_{22}} \bar{\rho}_x^1(a)
\]
where
\[
\bar{\rho}_x^1 = \frac{\lambda(x)}{\eta} 1 + \frac{a_{21}}{\lambda(x) - a_{22}}, \quad \bar{\rho}_x^2 = \frac{a_{21}}{\lambda(x) - a_{22}} \bar{\rho}_x^1,
\]
\(N_x\) is defined in Proposition 3.4 and \(a_{ij}\) are defined in (14).

**Proof.** It is a direct consequence of (13) and (15). \(\Box\)

**Biological interpretation 3.7.** Equation (4) describes the dynamics of a large monomorphic population with trait \(x\). Proposition 3.3 shows that the age distribution of the population stabilizes around the equilibrium \(\bar{\rho}_x = (\bar{\rho}_x^1, \bar{\rho}_x^2)\). The equilibria \(\bar{\rho}_x^1\) and \(\bar{\rho}_x^2\) describe the age equilibria of the population with trait \((x_b, x_d)\) and \((x_b, 0)\) respectively. We observe that if \(x_b < x_d\), then \(a_{21} = 0 = \bar{\rho}_x^2\) and Proposition 3.6 leads to the equilibrium \(\bar{\rho}_x = (\bar{\rho}_x^1, 0)\).

### 3.2 Bimorphic dynamics

Let \(x = (x_b, x_d)\) and \(y = (y_b, y_d)\) be two viable traits. We consider a bimorphic initial sequence \((z^K_0)_K\) weakly converging to \(\delta_x n_x(0, a) da + \delta_y n_y(0, a) da\) as \(K\) tends to infinity. Using similar arguments as in [11], we can prove that the sequence of processes \((z^K_0)_K\) converges in probability, on any finite time interval, to the solution \(((n_x(t, .), n_y(t, .)), t \geq 0) \in L^1(\mathbb{R}_+)^4\) of the following system of non-linear partial differential equations

\[
\begin{aligned}
\partial_t n_x(t, a) + \partial_a n_x(t, a) &= -(D_x(a) + \eta(\|n_x(t, .)\|_1 + \|n_y(t, .)\|_1)) n_x(t, a) \\
n_x(t, 0) &= \int_{\mathbb{R}_+} B_x(a) n_x(t, a) da \\
\partial_t n_y(t, a) + \partial_a n_y(t, a) &= -(D_y(a) + \eta(\|n_x(t, .)\|_1 + \|n_y(t, .)\|_1)) n_y(t, a) \\
n_y(t, 0) &= \int_{\mathbb{R}_+} B_y(a) n_y(t, a) da.
\end{aligned}
\]

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Equations (16) describe the dynamics of two monomorphic populations with traits \( x \) and \( y \) interacting by competition. We prove the following proposition.

**Proposition 3.8.** Let \( x, y \in \mathcal{V} \) such that \( x_b \wedge x_d < y_b \wedge y_d \). Then any \( L^1(\mathbb{R}_+)^4 \)-solution \( (n_x(t,\cdot),n_y(t,\cdot)) \) of (16) satisfying \( n^1_y(t,\cdot) \neq 0 \) converges to \((0,\pi_y)\) in \( L^1(\mathbb{R}_+)^4 \) as \( t \to \infty \).

**Proof.** Let \( x, y \in \mathcal{V} \) such that \( x_b \wedge x_d < y_b \wedge y_d \). Then by (10), we have that \( \lambda(x) < \lambda(y) \). For \( u \in \{x,y\} \) we define

\[
v_u(t,a) = \exp \left( \eta \int_0^t (\|n_x(s,\cdot)\|_1 + \|n_y(s,\cdot)\|_1)ds \right) n_u(t,a).
\]

The functions \( v_x \) and \( v_y \) are solutions of the linear systems (8). We deduce from Proposition 3.4 that \( e^{-\lambda(\cdot)t}v_u(t,\cdot) \to c(v_u(0,\cdot))N_u \) in \( L^1(\mathbb{R}_+)\) as \( t \to +\infty \), for a positive constant \( c(v_u(0,\cdot)) \). Hence, we obtain that \( e^{-\lambda(y)t}\int_{\mathbb{R}_+} v^1_x(t,\alpha)d\alpha \) converges to a positive limit. Since \( \lambda(y) > \lambda(x) \) it comes that \( e^{-\lambda(y)t}\int_{\mathbb{R}_+} v^1_x(t,\alpha)d\alpha \) converges to 0 as \( t \to +\infty \). We deduce that

\[
\frac{\rho^1_x(t)}{\rho^2_x(t)} = \frac{e^{-\lambda(y)t}\int_{\mathbb{R}_+} v^1_x(t,\alpha)d\alpha}{e^{-\lambda(x)t}\int_{\mathbb{R}_+} v^1_x(t,\alpha)d\alpha} \to +\infty.
\]

Since \( \rho^1_x(t) \) is bounded we deduce that \( \rho^1_x(t) \to 0 \) and similarly that \( \rho^2_x(t) \to 0 \). Then the population with trait \( x \) becomes extinct. Using similar arguments as in the previous proof we obtain that \( n_y(t,\cdot) \to \pi_y \) in \( L^1(\mathbb{R}_+)^2 \) which allows us to conclude. \( \square \)

**Biological interpretation 3.9.** Equation (16) describes a competition dynamics between two large monomorphic populations with trait \( x \) and \( y \). Proposition 3.8 shows that if \( x_b \wedge x_d < y_b \wedge y_d \), then the population with trait \( y \) invades and becomes fixed while the population with trait \( x \) becomes extinct. That gives us an invasion-implies-fixation criterion.

4 Adaptive dynamics analysis

In this section, we study the model that we introduced in Section 2 under the different scaling of the adaptive dynamics. We generalise the Trait substitution sequence with age structure (cf. [28]) to take into account the Lansing Effect. Then we study the behaviour of the TSS on a large time-scale when mutations are small. We show that the limiting behaviour of the TSS is described by a differential inclusion which generalises the canonical equation of adaptive dynamics (cf. [12], [5], [8]) to non regular fitness functions. We first state some properties of the demographic parameters and introduce the invasion fitness function.

4.1 Malthusian parameter and invasion fitness

Let us introduce the following sets: \( U_1 = \{x \in \mathcal{V} : x_b < x_d\} \), \( U_2 = \{x \in \mathcal{V} : x_d < x_b\} \) and \( \mathcal{H} = \{x \in \mathcal{V} : x_b = x_d\} \).
4.1.1 Malthusian parameter

We now give some properties of the Malthusian parameter \( \lambda \) defined in (9).

Proposition 4.1. (i) For all \( x \in \mathcal{V} \), \( 0 \leq \lambda(x) < 1 \).

(ii) The map \( x \in \mathcal{V} \mapsto \lambda(x) \) is continuous. It is differentiable on \( U_1 \cup U_2 \) and satisfies

\[
\forall x \in U_1, \quad \nabla \lambda(x) = \begin{pmatrix} e^{-\lambda(x)x_b} & 0 \\ \frac{e^{-\lambda(x)x_d}}{G(x)} & 0 \end{pmatrix} \tag{17}
\]

where \( G(x) = \int_{0}^{x_b \land x_d} ae^{-\lambda(x)a} da \).

(iii) We have \( \sup_{x \in U_1 \cup U_2} \| \nabla \lambda(x) \| < +\infty \). Moreover, for all \( i \in \{1, 2\} \), the fitness gradient \( \nabla \lambda \) is Lipschitz on \( U_i \).

Remark 4.2. Note that the Malthusian parameter \( \lambda(x) \) is not differentiable on the diagonal \( \mathcal{H} \), which can be easily obtained by computing left and right partial derivatives on \( \mathcal{H} \).

Notation 4.3. For all \( h \in \mathbb{R} \) we define \( (h)_1 = \begin{pmatrix} h \\ 0 \end{pmatrix} \) and \( (h)_2 = \begin{pmatrix} 0 \\ h \end{pmatrix} \).

Proof. (i) Since \( x_b \land x_d > 1 \) we obtain from the definition (9) that \( \lambda(x) > 0 \). Assume that \( \lambda(x) \geq 1 \). Then we obtain that \( 1 = \int_{0}^{x_b \land x_d} e^{-\lambda(x)a} da \leq 1 - e^{-x_b \land x_d} \) which is absurd.

(ii) We prove the continuity. Let \( x \in \mathcal{V} \) and let \( (x_n) \) be a sequence of \( \mathcal{V} \) such that \( x^n \to x \). By (i), \( \lambda \) is bounded and we can extract a subsequence (still denoted \( (x^n)_n \)) by simplicity such that \( \lambda(x^n) \to \lambda^* \). We deduce that \( 1 = \int_{0}^{x_b \land x_d} e^{-\lambda(x^n)a} da \to \int_{0}^{x_b \land x_d} e^{-\lambda^*a} da = 1 \) which allows us to conclude. Differentiability properties are a direct consequence of the Implicit Function Theorem. For each \( i \in \{1, 2\} \) we apply implicit function Theorem to the map

\[
(\lambda, x) \in \mathbb{R} \times U_i \mapsto \int_{0}^{x_b \land x_d} e^{-\lambda a} da - 1.
\]
We deduce that \( \lambda \) is differentiable over \( U_1 \cup U_2 \) and that
\[
\forall i \in \{1, 2\}, \quad \forall x \in U_i, \quad \nabla \lambda (x) = \left( \frac{e^{-\lambda(x)(x_b \wedge x_d)}}{G(x)} \right)_i.
\]

(iii) It is straightforward to check that for all \( x \in \mathcal{V} \),
\[
e^{-\lambda(x)(x_b \wedge x_d)} \leq \frac{1}{\int_0^1 ae^{-a} da}
\]
which allows us to obtain that \( \sup_{x \in \mathcal{V}} \| \nabla \lambda (x) \| < +\infty \). Moreover, the gradient \( \nabla \lambda \) is obviously differentiable on \( U_i \). Since \( G \) is bounded below by \( \int_0^1 ae^{-a} da \), we deduce that \( \nabla \lambda \) has bounded derivatives on \( U_i \) and that \( \nabla \lambda \) is Lipschitz on \( U_i \). \( \square \)

**Remark 4.4.** Formulae (17) describe the sensitivity of the Malthusian parameter to small variations of the trait \( x \) as well as the strength of selection at ages \( x_b \) and \( x_d \) for a population with Lansing effect. The quantity \( G(x) \) can be interpreted as the mean generation time associated with the trait \( x \). Moreover (17) and Proposition 3.4 yield
\[
\forall i \in \{1, 2\}, \quad \forall x \in U_i, \quad \nabla \lambda (x) = \left( \frac{\alpha^i_1(x_b \wedge x_d)}{G(x)} \right)_i
\]

where \( \alpha^i_1 \) is the stable age distribution. In [4], Caswell obtains similar formulae for derivatives of the Malthusian parameter with respect to some little perturbations on the intensity of birth or death at some given age while our formulae are obtained considering a small perturbation on the duration of the reproduction phase (not on the intensity).

The following proposition recalls a simple link between the Malthusian parameter and the stationary state of the monomorphic partial differential equation (4).

**Proposition 4.5.**

(i) For all \( x \in \mathcal{V} \), we have \( \lambda (x) = \eta \| \pi_x \|_1 \).

(ii) The map \( x \in \mathcal{V} \mapsto \pi_x(0) \) is continuous and bounded.

**Proof.** (i) has been proved at the beginning of the proof of Proposition 3.2.

(ii) By (i) we have
\[
\lambda (x) = \eta \left( \pi^1_x(0) u_1(x) + \pi^2_x(0) u_2(x) \right)
\]
where
\[
u_1(x) = \int_0^{+\infty} \exp \left( - \int_0^a 1_{\alpha > x_d} d\alpha - \lambda(x) a \right) d\alpha \quad ; \quad u_2(x) = \int_0^{+\infty} \exp \left( -(1 + \lambda(x)) a \right) d\alpha.
\]

Moreover \( \pi_x(0) \) is a solution of
\[
\pi_x(0) = F(\lambda(x)) \pi_x(0)
\]
where \( F \) is defined in [10]. From (19) and (20) we obtain by simple computation that
\[
(\pi^1_x(0) = \frac{\lambda(x)}{u_1(x) + u_2(x)} \left[ \frac{F(\lambda(x))}{1 - \| F(\lambda(x)) \|_2} \right])_1
\]
which is a continuous function of \( x \). Boundedness is obvious arguing that \( \pi^1_x(0) \leq \| \pi_x \|_1 \). \( \square \
4.1.2 Invasion fitness

We extend the definition of the invasion fitness for age-structured populations introduced in [28] Section 3 to take into account the Lansing effect.

**Definition 4.6.** For all $y \in \mathbb{R}^*_+$ and $x \in \mathcal{V}$, the invasion fitness $1 - z(y, x)$ is defined as the survival probability of a bi-type age structured branching process with birth rates and death rates defined in (5), respectively equal to

$$B_y(a) \quad \text{and} \quad D_y(a) + \eta \left\| \pi_x \right\| I.$$

The next proposition gives a precise and precious relation between the invasion fitness and the Malthusian parameter.

**Proposition 4.7.** Let $y \in \mathbb{R}^*_+$ and $x \in \mathcal{V}$, then the invasion fitness satisfies

$$1 - z(y, x) = \max(\lambda(y) - \lambda(x), 0). \quad (21)$$

**Proof.** Let $Z_t(da) = (Z^1_t(da), Z^2_t(da))$ be an age-structured branching process with birth rates $B_y(a)$ and death rates $D_y(a) + \eta \left\| \pi_x \right\| I = D_y(a) + \lambda(x)I$. The process $Z_t$ becomes extinct if and only if the process $Z^1_t$ becomes extinct. Indeed, if $Z^1_0 = 0$, the process $Z^2_t$ evolves as a sub-critical branching process. The process $Z^1_t$ is an age structured branching process with birth rates and death rates respectively

$$[B_y(a)]_{11} = \mathbb{1}_{a \leq y_h \wedge y_d} \quad \text{and} \quad [D_y(a)]_{11} + \lambda(x) = \mathbb{1}_{a > y_d} + \lambda(x).$$

We deduce that $z(y, x)$ equals the smallest solution of the equation $z = F(z)$ where

$$F(z) = \int_{\mathbb{R}_+} e^{(z-1) \int_0^{y_h \wedge y_d} \lambda(a) da} \left( [D_y(a)]_{11} + \lambda(x) \right) e^{- \int_0^{y_d} \lambda(a) da} \left( [B_y(a)]_{11} \right) da$$

$$= \int_0^{y_h \wedge y_d} \lambda(x) e^{(z-1-\lambda(x))a} da + e^{(z-1)(y_h \wedge y_d)} \int_{y_h \wedge y_d}^{y_d} \lambda(x) e^{-\lambda(x)a} da$$

$$= 1 - e^{(z-1-\lambda(x))(y_h \wedge y_d)} + (z - 1) \int_0^{y_h \wedge y_d} e^{(z-1-\lambda(x))a} da$$

$$+ e^{(z-1)(y_h \wedge y_d)} e^{-\lambda(x)(y_h \wedge y_d)} - e^{-\lambda(x)y_d} + e^{(z-1)(y_h \wedge y_d)} + e^{(z-1)(y_h \wedge y_d)} e^{-\lambda(x)y_d}$$

$$= 1 + (z - 1) \int_0^{y_h \wedge y_d} e^{(z-1-\lambda(x))a} da.$$

We have obtained that the equation $z = F(z)$ is equivalent to

$$z - 1 = (z - 1) \int_0^{y_h \wedge y_d} e^{(z-1-\lambda(x))a} da. \quad (22)$$

If $\lambda(y) > \lambda(x)$, Equation (22) admits two solutions $z = 1$ and $z = \lambda(x) - \lambda(y) + 1 < 1$. If $\lambda(y) < \lambda(x)$, Equation (22) admits a unique solution $z = 1$. That allows us to conclude the proof.

**Remark 4.8.** It is interesting to note that in our model, the invasion fitness (which is a concept from adaptive dynamics theory) and the Malthusian parameter are connected thanks to a simple relation.
The following proposition characterises the set of traits \( y \) which can invade some given trait \( x \).

**Proposition 4.9.** For all \( x \in \mathcal{V}, \, y \in \mathbb{R}^2_+ \),

\[
1 - z(y, x) > 0 \iff \lambda(y) > \lambda(x) \iff x_b \land x_d < y_b \land y_d.
\]

**Proof.** The first equivalence is obvious seeing Proposition 4.7.

By definition of the Malthusian parameter, for all \( u \in \{x, y\} \) we have

\[
\int_0^{u_b \land u_d} e^{-\lambda(u)_a} da = 1.
\]

From this definition, we easily deduce the following equivalences:

\[
\max(\lambda(y) - \lambda(x), 0) > 0 \iff \lambda(y) > \lambda(x) > 0
\]

\[
\iff \int_{x_b \land x_d}^{y_b \land y_d} e^{-\lambda(y)_a} da < 1
\]

\[
\iff x_b \land x_d < y_b \land y_d,
\]

which conclude the proof. \( \square \)

### 4.2 Trait Substitution Sequence with age structure

We first generalise the definition of the Trait Substitution Sequence (TSS) with age structure defined in [28] to take into account the Lansing Effect.

**Definition 4.10.** We define the measure valued process \( (T_t(dx, da), t \geq 0) \) by

\[
T_t(dx, da) = \delta_{X(t)}(dx)\pi^1_{X(t)}(a)da + \delta_{(X_b(t), 0)}(dx)\pi^2_{X(t)}(a)da
\]

where \( (X(t), t \geq 0) = ((X_b(t), X_d(t)), t \geq 0) \) is defined as the pure jump Markov process on \( \mathcal{V} \) with infinitesimal generator \( L \) defined for all measurable and bounded function \( \varphi : \mathcal{V} \to \mathbb{R} \) and \( x \in \mathcal{V} \) by

\[
L\varphi(x) = \int_{(\mathbb{R}_+)^2} (\varphi(x + h) - \varphi(x))(\lambda(x + h) - \lambda(x)) \pi^1_{X(t)}(0) \mu(dh) \tag{23}
\]

where

\[
\mu(dh) = \frac{k(h_b)dh_b \otimes \delta_0(dh_d) + \delta_0(dh_b) \otimes k(h_d)dh_d}{2},
\]

\( k \) being defined in [3].

The process \( X \) will be called the Trait Substitution Sequence.

**Remark 4.11.** The process \( (T_t, t \geq 0) \) describes the evolution of the phenotypic structure of the population at the mutational time-scale. At each time, and because of the Lansing effect, the population is composed of two sub-populations at each time \( t \): the first one corresponds to viable individuals with trait \( X(t) = (X_b(t), X_d(t)) \in \mathcal{V} \) whose age distribution is given by \( \pi^1_{X(t)}(a)da \); and the second one is composed of individuals generated by the Lansing effect, with trait \( (X_b(t), 0) \) and age distribution \( \pi^2_{X(t)}(a)da \).
Remark 4.12. Figure 6 describes the behaviour of the process \((X(t), t \geq 0)\). Any trait \(x \in \mathcal{H}\) is an absorbing state for the process \(X\). Indeed, by Proposition 4.9, for all \(\varphi : \mathcal{V} \to \mathbb{R}\) measurable and bounded, for all \(x \in \mathcal{H}\), \(L\varphi(x) = 0\).

By definition of the measure \(\mu(\text{d}h)\) the process evolves horizontally or vertically (which means that the two traits \(x_b\) and \(x_d\) do not mutate simultaneously). By Proposition 4.9, we deduce easily that the process evolves from the left to the right on \(U_1\) and from bottom to top on \(U_2\).

Since the jump rates are continuous and tend to zero on \(\mathcal{H}\), the process slows down as it approaches \(\mathcal{H}\).

Figure 6: (a): This picture represents a trajectory of the TSS process. (b): This picture represents the drift associated with the TSS process.

We now explain the heuristics, rigorously proved in [28], which allow to obtain the TSS from the individual-based model defined in Section 2.1. The main ideas have been introduced in [6], for a population without age-structure. They are based on the time-scale separation assumption on mutation probability \(p_K\): as \(K \to +\infty\)

\[
\forall V > 0, \quad \exp(-KV) = o(p_K), \quad p_K = o\left(\frac{1}{K \log(K)}\right),
\]

which allows to separate the effect of the natural selection and the appearance of new mutants. Let \(x \in \mathcal{V}\) and consider a sequence \((Z^K_0)_K\) converging to \(\delta_x n^1_x(0,a)\text{d}a\) as \(K \to +\infty\).

1) Monomorphic approximation. For large \(K\), the process \(Z^K_t\) stays close to the measure \(\delta_x n^1_x(t,.)+\delta_{(x_b,0)} n^2_x(t,.\) where \(n_x(t,. = (n^1_x(t,.), n^2_x(t,.))\) satisfies the partial differential equation (4). By Proposition 3.2, the dynamics \(n_x(t,.\) converges to \(\pi_x = (\pi^1_x, \pi^2_x)\) as \(t\) tends to infinity and hence reaches a given neighbourhood of \(\pi_x\) in finite time. By using large deviation results [41], we obtain with probability tending to one as \(K\) tends to infinity that the process \(Z^K_t\) stays in this neighbourhood of \(\delta_x \pi^1_x+\delta_{(x_b,0)}\pi^2_x\) during a time \(e^{CK}\) for some \(C > 0\). The left-hand side in Assumption (24) ensures that the next mutation appears before the process leaves this neighbourhood.

2) Appearance of a mutant. We deduce that the monomorphic population with trait \(x\) creates a mutant with trait:
equilibrium

If the mutant population becomes extinct, the resident population stays close to its equilibrium that allows to obtain the left hand side of (23).

Moreover (25) and (26) imply that

\[ \lambda(x_b, x_d) > \lambda(x) \iff h_b > 0 \quad \text{and} \quad x \in U_1. \tag{25} \]

With probability 1/2, \( y = (x_b, x_d + h_d) \) and can survive if and only if

\[ \lambda(x_b, x_d + h_d) > \lambda(x) \iff h_d > 0 \quad \text{and} \quad x \in U_2. \tag{26} \]

Case (iii) (Lansing effect). The mutant has the trait \( y = (x_b, h_d) \) or \( y = (x_b + h_b, 0) \). By (3), we have \( y \wedge y_d < 1 \) which implies that \( \lambda(y) < 0 \) and then \( \max(\lambda(y) - \lambda(x), 0) = 0 \). In this case, the mutant population becomes extinct.

We deduce that the mutant can only survive (with positive probability) in case (i). The birth rate of such a mutant (on the time-scale \( t/2p_K(1 - p_K) \)) is given by the intensity measure on \( \mathbb{R} \)

\[ \pi_1^1(0)\mu(dh) \]

that leads to the right hand side in (23). The probability that such a mutant survives and reaches a size of order \( K \) equals

\[ \max(\lambda(y) - \lambda(x), 0). \]

Moreover (25) and (26) imply that

\[ \max(\lambda(x + h) - \lambda(x), 0)\mu(dh) = (\lambda(x + h) - \lambda(x))\mathbf{1}_{\mathbb{R}^+}(h)\mu(dh) \]

that allows to obtain the left hand side of (23).

If the mutant population becomes extinct, the resident population stays close to its equilibrium \( \pi_x \).

If the mutant population survives, then it reaches a size of order \( K \) with a probability that tends to one and the population dynamics is approximated by the solution \((n_x(t, .), n_y(t, .))\) of the bimorphic system of partial differential equations (16). In

\[ \text{(i) } y = (x_b + h_b, x_d) \quad \text{or} \quad y = (x_b, x_d + h_d) \text{ at a rate approximatively equal to } 2Kp_K(1 - p_K)\pi_1^1(0); \]

\[ \text{(ii) } y = (x_b + h_b, x_d + h_d) \text{ at a rate approximatively equal to } Kp_K^2\pi_1^1(0); \]

\[ \text{(iii) } y = (x_b, h_d) \quad \text{or} \quad y = (x_b + h_b, 0) \text{ at rate approximatively equal to } 2Kp_K(1 - p_K)\pi_1^1(0); \]

\[ \text{(iv) } y = (x_b + h_b, h_d) \text{ at rate approximatively equal to } Kp_K^2\pi_1^1(0). \]

where the variables \( h_b \) and \( h_d \) are chosen independently with distribution \( k \).

Since \( p_K^2 = o(p_K(1 - p_K)) \), the cases (ii) and (iv) cannot be observed on the mutation time-scale \( t/2K(1 - p_K) \).

3) Effect of the natural selection. In cases (i) and (iii), the mutant population dynamics is approximated by a bi-type age structured branching process with birth rates \( \mathbf{B}_y \) and death rates \( \mathbf{D}_y + \eta\|\pi_x\|_1\mathbf{1} \). By Proposition 4.7, the mutant population survives with probability

\[ \max(\lambda(y) - \lambda(x), 0). \]

Let us detail the two different cases.

- Case (i). With probability 1/2, the trait of the mutant is \( y = (x_b + h_b, x_d) \). By Proposition 4.7, we deduce that the mutant can survive if and only if

\[ \lambda(x_b + h_b, x_d) > \lambda(x) \iff h_b > 0 \quad \text{and} \quad x \in U_1. \]

- Case (iii) (Lansing effect). The mutant has the trait \( y = (x_b, h_d) \) or \( y = (x_b + h_b, 0) \). By (3), we have \( y \wedge y_d < 1 \) which implies that \( \lambda(y) < 0 \) and then \( \max(\lambda(y) - \lambda(x), 0) = 0 \). In this case, the mutant population becomes extinct.

We deduce that the mutant can only survive (with positive probability) in case (i). The birth rate of such a mutant (on the time-scale \( t/2p_K(1 - p_K) \)) is given by the intensity measure on \( \mathbb{R} \)

\[ \pi_1^1(0)\mu(dh) \]

that leads to the right hand side in (23). The probability that such a mutant survives and reaches a size of order \( K \) equals

\[ \max(\lambda(y) - \lambda(x), 0). \]

Moreover (25) and (26) imply that

\[ \max(\lambda(x + h) - \lambda(x), 0)\mu(dh) = (\lambda(x + h) - \lambda(x))\mathbf{1}_{\mathbb{R}^+}(h)\mu(dh) \]

that allows to obtain the left hand side of (23).
this case we have necessarily $\lambda(y) > \lambda(x)$. By Proposition 3.8, the deterministic dynamics $(n_x(t, .), n_y(t, .))$ reaches a neighbourhood of $(0, \pi_y)$. By using branching processes approximations and arguments introduced in [6], we can deduce that the resident population with trait $x$ becomes extinct. One can prove as in [6] that this competition phase has a duration of order $\log(K)$.

The right hand side of Assumption (24) ensures that the three steps of invasion are completed before the next mutation occurs. The Markov property allows to reiterate the same reasoning for the next mutation occurrence. In summary, the following theorem holds.

**Theorem 4.13.** The following convergence holds in the sense of finite dimensional marginals:

$$
\left( \frac{Z^K_{\lambda \pi_y}}{\lambda \pi_y(1 - \lambda \pi_y)}, t \geq 0 \right) \longrightarrow (T_t, t \geq 0), \quad \text{as } K \to \infty,
$$

where the process $T$ is defined in Definition 4.10.

### 4.3 A canonical inclusion for adaptive dynamics

In this section, we assume in addition that mutations are small. We study the behaviour of the process $X$ defined in (23) when the mutation size scale equals $\epsilon > 0$ and the time is rescaled by $1/\epsilon^2$. To this aim, we define the rescaled trait substitution sequence process $X^\epsilon$ and study the limiting behaviour of the process $X^\epsilon$ as $\epsilon \to 0$. In the usual cases (smooth fitness functions) the canonical equation introduced by Dieckmann-Law can be derived as limit of $X^\epsilon$ as $\epsilon \to 0$ (cf. [8]). As observed in Section 4.1, the fitness function $\lambda(x)$ does not satisfy these regularity assumptions. To overpass this difficulty, we use the approach developed in [15] based on differential inclusions. We prove in Theorem 4.17 that the set of limit points of the family $X^\epsilon$ is characterised as the set of solutions of a differential inclusion.

**Definition 4.14.** The rescaled TSS process $(X^\epsilon(t), t \geq 0)$ is defined as a pure jump Markov process with infinitesimal generator $L^\epsilon$ defined for all measurable and bounded function $\varphi : V \to \mathbb{R}$ and $x \in V$ by

$$
L^\epsilon \varphi(x) = \frac{1}{\epsilon^2} \int_{(\mathbb{R}_+)^2} \left( \varphi(x + \epsilon h) - \varphi(x) \right) \left( \lambda(x + \epsilon h) - \lambda(x) \right) \pi \mathbb{1}(0) \mu(dh) \quad (27)
$$

**Remark 4.15.** The process $X^\epsilon$ shows a dynamics similar to the process $X$. The jump rates are of order $1/\epsilon$ and the jump sizes are of order $\epsilon$.

We first introduce the set-valued map $F : V \to \mathcal{P}(\mathbb{R}_+^2)$ defined for any $x \in V$ by

$$
\forall i \in \{1, 2\}, \quad \forall x \in U_i, \quad F(x) = (f(x, 1))_i
$$

$$
\forall x \in \mathcal{H}, \quad F(x) = \left\{ \frac{1}{2} \left( \begin{array}{c} f(x, u) \\ f(x, u) \end{array} \right), u \in [0, 1] \right\}, \quad (28)
$$

where for all $(x, u) \in V \times [0, 1],

$$
f(x, u) = \left( \int_0^u h^2 k(h) dh + \int_1^1 h u k(h) dh \right) e^{-\lambda(x)(x_k \wedge x_a)} \frac{\pi \mathbb{1}(0)}{G(x)} \frac{2}{2}; \quad (29)
$$

and $G$ is defined in Proposition 4.1.
This set-valued map $F$ somehow generalises the classical fitness gradient. It is represented by a picture in Figure 7. Let us explain the ideas leading to this function. Let us consider a compact subset $K$ of $U_i$. Since the Malthusian parameter $\lambda$ is differentiable on $U_i$, the following approximation holds: for all $h \in \mathbb{R}_+$, uniformly for $x \in K$, we have

$$\lambda(x + \epsilon(h)_i) - \lambda(x) \approx \epsilon(h)_i \nabla \lambda(x),$$

(30)

which leads to the definition of $F$ on $U_i$. We analyse the case $x \in \mathcal{H}$ for which the approximation (30) is not true. Indeed, let $x \in \mathcal{H}$ and let $u \in [0, 1]$ and let us consider a sequence $x^\epsilon = x - \epsilon(u)_i$, we have

$$\lambda(x^\epsilon + \epsilon(h)_i) - \lambda(x^\epsilon) = \lambda(x + \epsilon(h - u)_i) - \lambda(x - \epsilon(u)_i)$$

(31)

Assume $h < u$, since $\lambda$ is differentiable on $U_i$ we obtain when $\epsilon$ tends to 0 that

$$\lambda(x^\epsilon + \epsilon(h)_i) - \lambda(x^\epsilon) \approx \epsilon(h - u)_i \nabla \lambda(x) + \epsilon(u)_i \nabla \lambda(x) \approx \epsilon(h)_i \nabla \lambda(x),$$

where $\nabla \lambda(x)$ is defined as the limit of $\nabla \lambda(y), y \rightarrow x, y \in U_i$. That leads to the first integral in (29). If $h > u$, we obtain that $\lambda(x + \epsilon(h - u)_i) - \lambda(x) = 0$ and

$$\lambda(x^\epsilon + \epsilon(h)_i) - \lambda(x^\epsilon) \approx \epsilon(u)_i \nabla \lambda(x) \leq \epsilon(h)_i \nabla \lambda(x),$$

which leads to the second integral in (29). The inequality above means that when the process evolves near the diagonal $\mathcal{H}$ the adaptation slows down.

**Figure 7: Representation of the set-valued map $F$.**

We now introduce the differential inclusion associated with $F$ that generalises the classical canonical equation for adaptive dynamics. For any $T > 0$ and $x^0 \in \mathcal{V}$, we denote by $\mathcal{S}_F(T, x^0)$ the set of solutions of the differential inclusion

\[
\begin{cases}
\frac{dx(t)}{dt} \in F(x(t)), & t \in [0, T] \\
x(0) = x^0.
\end{cases}
\]
Remark 4.16. A solution of the differential inclusion (31) is an absolutely continuous function $x : [0, T] \to \mathcal{V}$ which satisfies, for almost all $t \in [0, T]$,
$$\frac{dx(t)}{dt} \in F(x(t)).$$

The following theorem characterises the limit of the process $X^\epsilon$ as the solution of the differential inclusion (31).

**Theorem 4.17.** Let $x^0 \in \mathcal{V}$. Assume that $X^\epsilon(0) \to x^0$ in probability as $\epsilon \to 0$. For all $T, \delta > 0$,
$$\lim_{\epsilon \to 0} \mathbb{P} \left( \inf_{x \in S_F(T, x^0)} \sup_{t \in [0, T]} |X^\epsilon(t) - x(t)| > \delta \right) = 0.$$

**Remark 4.18.** Theorem 4.17 justifies our complete study. Let $(x(t), t \in [0, T])$ be a solution of (31). On each $U_i$, it satisfies
$$\frac{dx(t)}{dt} = (f(x(t), 1))_i, \quad x(t) \in U_i.$$

The map $x \in U_i \mapsto (f(x, 1))_i$ is Lipschitz and bounded below by a positive constant. Hence, unicity holds on $U_i$ for (31) and any solution reaches in finite time the diagonal $H$. On $H$, the solution satisfies
$$\frac{dx(t)}{dt} \in F(x(t)), \quad x(t) \in H.$$

Since for all $x \in H$, $F(x) \subset H$, we deduce that any solution stays in $H$. 

Figure 8 illustrates Theorem 4.17. We represent some trajectories of the process $(X^\epsilon(t), t \geq 0)$ started at $X^\epsilon(0) = (2, 1.5)$ for $\epsilon = 0.001$.

![Figure 8](image-url)

- (a): We represent $X_\delta(t)$ as a function of $X_\delta(t)$. (b): $(X_\delta(t), t \geq 0)$. (c): $(X_\delta(t), t \geq 0)$.

We observe on (b) and (c) that before reaching the diagonal $H$ the dynamics is unique. On $H$, the process evolves with speed in $F(x)$ for $x \in H$.

The proof of Theorem 4.17 is based on [15, Theorem 1] recalled in Appendix. We start by writing the process $X^\epsilon$ as a time-changed Markov chain. We first re-write
Lemma 4.19. Let \( \tau = \sup_{x \in V} \pi_x^1(0) \). Let \( (Y^\epsilon(k), k \geq 0) \) be a Markov chain with jump law
\[
\tilde{k}^\epsilon(x, dh) = \frac{\pi_x^1(0)}{\tau} k^\epsilon(x, dh) + \left( 1 - \frac{\pi_x^1(0)}{\tau} \right) \delta_0(dh)
\]
and \( \Lambda^\epsilon \) be a Poisson process with intensity \( \tau/\epsilon \). Then the processes \( X^\epsilon \) and \( Y^\epsilon(\Lambda^\epsilon) \) have the same law.

Then we are led to study the Markov chain \( (Y^\epsilon(k), k \geq 0) \). We first define the drift of the Markov chain \( Y^\epsilon \) by
\[
g_\epsilon(x) = \mathbb{E} [Y^\epsilon(1) - Y^\epsilon(0)|Y^\epsilon(0) = x].
\]
A simple calculation gives us
\[
\forall i \in \{1, 2\}, \forall x \in U_i, \quad g_\epsilon(x) = \frac{\epsilon \pi_x^1(0)}{2\tau} \int_{\mathbb{R}_+} \frac{\lambda(x + \epsilon(h) i) - \lambda(x)}{\epsilon} k(h)(h) dh
\]
\[
\forall x \in \mathcal{H}, \quad g_\epsilon(x) = 0.
\]
Then, we write the Markov chain \( Y^\epsilon \) as a stochastic approximation algorithm
\[
Y^\epsilon(k + 1) = Y^\epsilon(k) + \frac{\epsilon}{\tau} U^\epsilon(k) + g^\epsilon(Y^\epsilon(k))
\]
where \( U^\epsilon \) is a martingale difference sequence. Assumptions of Theorem A.2 are clearly satisfied. In order to apply it, we compute the following set-valued map
\[
\forall x \in \mathcal{V}, \quad H(x) = \text{conv} \left\{ \text{acc}_{\epsilon \rightarrow 0} \frac{\tau g_\epsilon(x^\epsilon)}{\epsilon} : x^\epsilon \rightarrow x \right\}
\]
where \( \text{conv}(A) \) denotes the smallest convex set which contains \( A \) and \( \text{acc}_{\epsilon \rightarrow 0} \tau g_\epsilon(x^\epsilon)/\epsilon \) is the set of accumulation points of the sequence \( \tau g_\epsilon(x^\epsilon)/\epsilon \) as \( \epsilon \) tends to zero.

Lemma 4.20. The set-valued map \( H \) satisfies
\[
\forall i \in \{1, 2\}, \forall x \in U_i, \quad H(x) = \{(f(x, 1))\}
\]
\[
\forall x \in \mathcal{H}, \quad H(x) = \left\{ \alpha \begin{pmatrix} f(x, u) \\ 0 \end{pmatrix} + (1 - \alpha) \begin{pmatrix} 0 \\ f(x, v) \end{pmatrix} : (u, v, \alpha) \in [0, 1]^3 \right\}
\]
where
\[
f(x, u) = \frac{e^{-\lambda(x)(x_h \wedge x_d)}}{G(x)} \frac{\pi_x^1(0)}{2} \left( \int_0^u h^2 k(h) dh + \int_0^1 uhk(h) dh \right).
\]
Proof. Let \( i \in \{1, 2\} \). Let \( K \) be a compact subset of \( U_i \). Let \( \delta > 0 \). We fix \( \epsilon_0 > 0 \) such that for all \( x \in K \), \( \epsilon < \epsilon_0 \) and \( h \in [0,1] \), we have \( x + \epsilon(h)_i \in U_i \). The map \( \lambda \) is differentiable on \( U_i \). Hence, for all \((x, \epsilon, h) \in K \times [0, \epsilon_0] \times [0,1] \), there exists \( \theta \in [x, x + \epsilon(h)_i] \) such that

\[
\lambda(x + \epsilon(h)_i) - \lambda(x) = \epsilon(h)_i, \nabla \lambda(\theta).
\]

Let \( x \in K \), we have

\[
\left\| \frac{\tau g'(x)}{\epsilon} - (f(x,1))_i \right\| = \frac{\pi^1_x(0)}{2} \left| \int_{\mathbb{R}^+} \left[ \nabla \lambda(\theta) \right]_i \ h^2 k(h)dh - \left[ \nabla \lambda(x) \right]_i \int_{\mathbb{R}^+} h^2 k(h)dh \right|
\]

\[
\leq \sup_{x \in \mathbb{E}} \frac{\pi^1_x(0)}{2} \int_{\mathbb{R}^+} \left| \nabla \lambda(\theta) \right|_i - \left[ \nabla \lambda(x) \right]_i \ h^2 k(h)dh.
\]

By Proposition 4.1, the map \( \nabla \lambda \) is Lipschitz on \( U_i \) with some Lipschitz constant \( C \). We deduce that

\[
\left\| \frac{\tau g'(x)}{\epsilon} - (f(x,1))_i \right\| \leq \epsilon \sup_{x \in \mathbb{E}} \frac{\pi^1_x(0)}{2} C \int_{\mathbb{R}^+} h^2 k(h)dh.
\]

We obtain that \( \tau g'/\epsilon \) converges uniformly on all compact subsets of \( U_i \) and we conclude that for all \( x \in U_i \), \( H(x) = (f(x,1))_i \).

Let \( x \in \mathcal{H} \). We first show that

\[
\left\{ \text{acc}_{\epsilon \to 0} \frac{\tau g(x^\epsilon)}{\epsilon} : x^\epsilon \to x \right\} = \bigcup_{i \in \{1,2\}} \{(f(x,u))_i : u \in [0,1]\}.
\]  

(32)

We prove the inclusion from right to left. Let \( i \in \{1,2\} \), let \( u \in [0,1] \), we define the sequence \( x^\epsilon = x - \epsilon(u)_i \). We have

\[
\frac{\tau g'(x^\epsilon)}{\epsilon} = \left( \int_{\mathbb{R}^+} \frac{\lambda(x - \epsilon(u)_i + \epsilon(h)_i) - \lambda(x - \epsilon(u)_i)}{\epsilon} k(h)_i dh \right) \frac{\pi^1_x(0)}{2}
\]

\[
= \left( \int_0^u \frac{\lambda(x - \epsilon(u)_i + \epsilon(h)_i) - \lambda(x - \epsilon(u)_i)}{\epsilon} k(h)_i dh \right) \frac{\pi^1_x(0)}{2}
\]

\[
+ \left( \int_u^1 \frac{\lambda(x - \epsilon(u)_i + \epsilon(h)_i) - \lambda(x - \epsilon(u)_i)}{\epsilon} k(h)_i dh \right) \frac{\pi^1_x(0)}{2}.
\]

For all \( h \in [0,u] \), we have \([x - \epsilon(u)_i, x - \epsilon(u)_i - \epsilon] \subset U_i \). So we can find \( \theta \in [x - \epsilon(u)_i, x - \epsilon(u)_i - \epsilon] \) such that \( \lambda(x - \epsilon(u)_i) - \lambda(x - \epsilon(u)_i)_i(\epsilon) = \epsilon(h)_i, \nabla \lambda(\theta) \). By Proposition 4.1 (ii), we deduce that

\[
\int_0^u \frac{\lambda(x - \epsilon(u)_i + \epsilon(h)_i) - \lambda(x - \epsilon(u)_i)}{\epsilon} k(h)_i dh \to e^{\frac{-\lambda(x)(x, x)_d}{G(x)}} \int_0^u (h^2)_i k(h)dh
\]

as \( \epsilon \) tends to zero. For all \( h \in [u,1] \) we have \( \lambda(x + \epsilon(h)_i) = \lambda(x) \). We deduce similarly that

\[
\int_u^1 \frac{\lambda(x - \epsilon(u)_i + \epsilon(h)_i) - \lambda(x - \epsilon(u)_i)}{\epsilon} k(h)_i dh \to e^{\frac{-\lambda(x)(x, x)_d}{G(x)}} \int_u^1 (h)_i k(h)dh
\]

as \( \epsilon \) tends to zero. We conclude the proof of the first inclusion arguing that \( \pi^1_x(0) \to \pi^1_{x'}(0) \) as \( \epsilon \) tends to zero.

We prove the inclusion from left to right. Let \( x \in \mathcal{V} \). If \( x \in \mathcal{H} \) then we have

\[
g'(x) = 0.
\]

(33)
If \( x \in U_i \), for some \( i \in \{1, 2\} \), then we have

\[
\frac{\tau g^\epsilon(x)}{\epsilon} = \frac{\pi^1_x(0)}{2} \int_0^1 \lambda(x + \epsilon(h)x) - \lambda(x) \frac{k(h)h}{\epsilon} dh
\]

Moreover for all \( \epsilon, h \) there exists \( \theta \in [x, x + \epsilon(h)x] \) such that \( \lambda(x + \epsilon(h)x) - \lambda(x) \leq \frac{\partial \lambda(\theta)}{\partial x_i} \epsilon(h). \) We deduce that

\[
\left[ \frac{\tau g^\epsilon(x)}{\epsilon} \right]_i \leq \frac{\pi^1_x(0)}{2} \int_0^1 \frac{\partial \lambda(\theta)}{\partial x_i} \epsilon(h) dh
\]

From (33) and (34), we deduce easily the second inclusion in (32). We conclude that

\[
\text{conv} \left\{ \text{acc}_{\epsilon \to 0} \frac{\tau g_\epsilon(x^\epsilon)}{\epsilon} : x^\epsilon \to x \right\} = \text{conv} \left\{ \cup_{i \in \{1, 2\}} \{(f(x, u))_i : u \in [0, 1]\} \right\} = H(x).
\]

In Lemma 4.22, we prove that differential inclusions associated with \( H \) and \( F \) have identical solutions. Before, we give a technical lemma.

**Lemma 4.21.** Let \( x \in \mathcal{H} \). Let \( (u, v, \alpha) \in [0, 1]^3 \) and let

\[
m = \alpha \begin{pmatrix} f(x, u) \\ 0 \end{pmatrix} + (1 - \alpha) \begin{pmatrix} 0 \\ f(x, v) \end{pmatrix} \in H(x).
\]

Assume that \( m \notin F(x) \). Then we have \( \alpha f(x, u) \neq (1 - \alpha) f(x, v) \).

**Proof.** We prove the lemma by contradiction. Assume that \( \alpha f(x, u) = (1 - \alpha) f(x, v) \). Then we obtain that

\[
m = \frac{1}{2} \begin{pmatrix} 2f(x, u)f(x, v) + f(x, v) \\ 2f(x, u)f(x, v) \end{pmatrix}
\]

We assume without loss of generality that \( f(x, u) \leq f(x, v) \). Then we obtain that

\[
0 \leq \frac{2f(x, u)f(x, v)}{f(x, u) + f(x, v)} \leq f(x, v). \]

Finally we remark that the map \( s \mapsto f(x, s) \) is a bijection from \([0, 1]\) to \([0, f(x, 1)]\). Hence there exists \( w \in [0, 1] \) such that \( f(x, w) = \frac{2f(x, u)f(x, v)}{f(x, u) + f(x, v)} \) that allows us to obtain the contradiction.

**Lemma 4.22.** Any solution of

\[
\begin{cases}
\frac{dx(t)}{dt} \in F(x(t)), & t \in [0, T] \\
x(0) = x^0.
\end{cases}
\]

is a solution of

\[
\begin{cases}
\frac{dx(t)}{dt} \in H(x(t)), & t \in [0, T] \\
x(0) = x^0.
\end{cases}
\]

and conversely.

**Proof.** For all \( x \in \mathcal{V} \), we have \( F(x) \subseteq H(x) \). We deduce that if \( (x(t), t \in [0, T]) \) is a solution of (35) then it is a solution of (36). Assume conversely that there exists a solution \( (x(t), t \in [0, T]) \) of (36) which is not a solution of (35). We deduce that
there exists \( t_0 \in [0, T] \) such that \( x \) is differentiable at \( t_0 \), \( dx(t_0)/dt \in H(x(t_0)) \) and \( dx(t_0)/dt \notin F(x(t_0)) \). Then we have \( x(t_0) \in \mathcal{H} \) and \( dx(t_0)/dt \notin F(x(t_0)) \).

We now deduce the contradiction. By Lemma 4.21, we obtain that \( \frac{dx(t_0)}{dt} \neq \frac{dx_d(t_0)}{dt} \). Without loss of generality, we may assume that \( \frac{dx_h(t_0)}{dt} < \frac{dx_d(t_0)}{dt} \). Since \( x_h(t_0) = x_d(t_0) \), there exists an interval \([t_0, t_1]\) such that for all \( s \in [t_0, t_1] \), \( x(s) \in U_1 \). Assume that for all \( s \in [t_0, t_1] \) such that \( x \) is differentiable at \( s \), we have

\[
\frac{dx_d(s)}{dt} = 0. \tag{37}
\]

The solution \( x \) of the differential inclusion (36) is absolutely continuous. Hence for all \( s \in [t_0, t_1] \), \( x_d(s) = x_d(t_0) = x_h(t_0) \). Since \( x(s) \in U_1 \), we obtain that \( x_h(s) = x_d(t_0) \). It is absurd since \( x_h \) is non-decreasing and hence it contradicts (37). So, there exists \( s_0 \in [t_0, t_1] \) such that \( x(s_0) \in U_1 \), \( x \) is differentiable at \( s_0 \) and satisfies \( \frac{dx_h(s_0)}{dt} > 0 \). However, \( x \) is a solution of (36) that leads to the final contradiction.

We now give the proof of Theorem 4.17. It is a direct consequence of [15, Theorem 1] recalled in Appendix A.3.

Proof of Theorem 4.17. Let \( T > 0 \) be fixed. By Lemma 4.22 and Theorem A.2, we deduce that for all \( \delta > 0 \) we have

\[
\lim_{\epsilon \to 0} P \left( \inf_{x \in S_F(T, x^0)} \sup_{t \in [0, T]} |Y^\epsilon([t\tau/\epsilon]) - x(t)| > \delta \right) = 0. \tag{38}
\]

We conclude by using similar arguments as in the proof of [15, Theorem 4]. Since \( \Lambda^\epsilon \) is a Poisson process with parameter \( \tau/\epsilon \), we obtain that for all \( \delta > 0 \),

\[
P \left( \sup_{t \in T} |\Lambda^\epsilon(t) - t\tau/\epsilon| \geq \frac{\tau \delta}{\epsilon} \right) \leq \frac{T \epsilon}{\tau \delta}. \tag{39}
\]
We have \[P \left( \inf_{x \in S_F(T, x^0)} \sup_{t \leq T} |X^\epsilon(t) - x(t)| > \delta \right) \]
\[= P \left( \inf_{x \in S_F(T, x^0)} \sup_{t \leq T} |Y^\epsilon(\Lambda^\epsilon(t)) - x(t)| > \delta \right) \]
\[\leq P \left( \inf_{x \in S_F(T, x^0)} \sup_{t \leq T} \left\{ \left| Y^\epsilon(\Lambda^\epsilon(t)) - x \left( \frac{\epsilon \Lambda^\epsilon(t)}{\tau} \right) \right| + \left| x \left( \frac{\epsilon \Lambda^\epsilon(t)}{\tau} \right) - x(t) \right| \right\} > \delta \right). \]

(40)

Let \( x \in S_F(T, x^0) \) be a solution of the differential inclusion \([81]\). For almost all \( t \in [0, T] \), we have \( \frac{dx(t)}{dt} \in F(x(t)) \). Since \( \sup_{x \in S} \sup \{F(x)\} < +\infty \), we deduce that there exists \( C_T > 0 \) such that for all \( y \in S_F(T, x^0) \), for all \( s, t \in [0, T] \), \( |y(t) - y(s)| \leq C_T |t - s| \). We deduce that (40) is less than
\[P \left( \inf_{x \in S_F(T, x^0)} \sup_{t \leq T} \left\{ \left| \frac{\epsilon \Lambda^\epsilon(t)}{\tau} \right| \right\} + C_T \sup_{t \leq T} \left| \frac{\epsilon \Lambda^\epsilon(t)}{\tau} - t \right| > \delta \right) \]
\[\leq P \left( \inf_{x \in S_F(T, x^0)} \sup_{t \leq T} \left| \frac{\epsilon \Lambda^\epsilon(t)}{\tau} \right| > \delta \right) + \left| \frac{\epsilon \Lambda^\epsilon(t)}{\tau} - t \right| > \delta \]
and we conclude by using \([38]\) and \([39]\). \(\square\)

### 5 Discussion

In the present article, we studied the genotypic/phenotypic evolution of a population with a trait structure describing a simple class of life-histories. We built a stochastic individual-based model in a framework that is continuous for time, age and trait. The trait is a pair of parameters \((x_h, x_d)\) characterising the age at end-of-reproduction \(x_h\) and the age at transition to a non-zero mortality risk \(x_d\). The model sees two origins of phenotypic variation. First, the genetic mutations that are supposed to be rare and do modify the traits symmetrically - equal probability to increase or decrease the face value of the parameter. Second, we model the Lansing effect which can be considered as an epigenetic mutation affecting the progeny of an “old” individual. It is acting on a much faster time-scale - one generation - than genetic mutations and has only a negative effect on the life expectancy of the progeny. We must admit that we have chosen here to model the Lansing effect by an extremely strong effect on the descendant. Indeed, it acts at each generation and degrades dramatically the life-expectancy of the descendant. Although, it would be interesting to later study more generally and realistically the impact of epigenetic modifications on the genetic evolution, we chose this strong effect here to accelerate evolution. Some aspects of this question have been studied in \([23]\). It is based on the fact that epigenetic modifications are more frequent than genetic mutations \([38]\).

We think it would be interesting to develop adaptive dynamics theory using this new framework. Nevertheless, multiple experimental data do support the existence of a Lansing effect in a broad range of organisms.

We studied the long term evolution of the trait using adaptive dynamics theory and wrote the TSS process associated to the microscopic model. The main mathematical result of the present work concerns the behaviour of the TSS when mutations are small. We show in Theorem \([4.17]\) that the behaviour of the TSS towards the limit is characterised by a differential inclusion whose solutions are not unique on the diagonal \( \mathcal{H} = \{ x_h = x_d \} \). This differential inclusion allows to generalize the
canonical equation in order to consider the non-smooth fitness gradient. The proof is based on [15]. Thanks to this approach, we show that the evolution of our model, whatever its initial configuration, leads to the apparition and maintenance of configurations \((x_b, x_d)\) satisfying \(x_b - x_d = 0\).

To our knowledge, differential inclusions have never been used before in the adaptive dynamics theory. In [5], [8], [28], the fitness gradient is assumed to be a Lipschitz function, which ensures the uniqueness of the solutions. Our approach seems to be very useful for generalizing the canonical equation to situations where the fitness gradient is neither Lipschitz nor continuous.

The drift associated with the differential inclusion depends on the fitness gradient which satisfies (see Proposition 4.1)

\[ \nabla \lambda(x) = \left( \frac{e^{-\lambda(x)(x_b, x_d)}}{G(x)} \right)_i \]

where \(\lambda(x)\) is the Malthusian parameter and \(G(x)\) the mean generation time associated with the trait \(x\). Hence the fitness gradient \(\nabla \lambda(x)\) describes the evolution’s speed of the trait \(x\). It can be related to the seminal work of Hamilton [18] on the moulding of senescence. In this article, Hamilton states that senescence is inevitable because the strength of selection decreases with age. To show it, he defines the strength of selection at some given age \(a_0\) as the sensitivity of the Malthusian parameter with respect to some little perturbation on the birth or death intensities at age \(a_0\). He concluded arguing that these quantities decrease to zero as \(a_0\) tends to infinity. Similarly, formula (41) describes the sensitivity of the Malthusian parameter with respect to some perturbation on the duration of the reproduction or the survival phase at ages \(x_b\) and \(x_d\). Then, they can be interpreted as the strength of selection at ages \(x_b\) and \(x_d\) and describe the speed of evolution of the traits \(x_b\) and \(x_d\) in the canonical inclusion (31).

The present article studies a case of bd-model with a strong Lansing effect and constant competition applied to asexual and haploid individuals in order to validate mathematically the favored convergence of \(x_b\) and \(x_d\) observed in the numerical exploration. Further characterisation of this model is in progress, in order to better understand the influence of its different parameters on the evolution of \((x_b, x_d)\).

To conclude, our initial motivation for developing the bd-model was an attempt to understand whether a phenomenon leading to a dramatic decrease of an individual’s fitness could be selected through evolution with simple and no explicitly constraining trade-offs. Indeed, in the past years, Rera and collaborators have identified and characterized a dramatic transition preceding death in drosophila (see [35], [36]) as well as other organisms (see [37], [10]). We show here that, in conditions of uniform competition - i.e. environmental limitation equally affecting all genotypes - a mechanism coupling the end of reproductive capabilities and organismal homeostasis can and will be selected thanks to evolution. Thus, at least these two characteristics of senescent organisms can directly be selected through evolution. In regards to the biological interpretation of our model, our thesis is that individuals with a senescence mechanism associated with the Lansing effect tend to produce more genetic variants - i.e. individuals - than those without senescence. Hence, these individuals could show a higher evolvability. This question is investigated in a on going work. This result is reminiscent of [43] that proposed a new selective mechanism for post-reproductive life span. It relies on the hypothesis that it can evolve as an insurance
against indeterminacy; a longer life expectancy reducing the risk of dying by chance before the cessation of reproductive activity. Here, the maintenance of individuals with Lansing effect is the counterpart of individuals with post-reproductive survival in our model where we observe a convergence of $x_b$ and $x_d$. As discussed in [21], one of August Weismann’s concepts that persisted without changes throughout his life is a conviction that “life is endowed with a fixed duration, not because it is contrary to its nature to be unlimited, but because unlimited existence of individuals would be a luxury without any corresponding advantage” (see [46]). To our knowledge, broadly evolutionarily conserved manifestation of such a mechanism has been described in vivo in the past years as the Smurf phenotype.

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A Appendix

A.1 Proof of Proposition 3.4

Proof. The proof is based on classical arguments of spectral theory for strongly continuous semi-groups. Let us denote by $(P_t)_{t \geq 0}$ the semi-group on $L^1(\mathbb{R}_+)^2$ associated with the infinitesimal generator $(A, D(A))$. Let us denote by $\sigma(A)$ and $\sigma_e(A)$ the spectrum and the essential spectrum of the operator $A$ respectively. Let us denote by $\alpha [P_t]$ the measure of non-compactness of $P_t$ (see [44, Definition 4.14 p 165]), and define $w_1(A) := \lim_{t \to \infty} t^{-1} \log(\alpha [P_t])$. We show that there exists $\omega > 0$ such that

$$\max \left( \frac{w_1(A)}{z \in \sigma(A) \setminus \sigma_e(A)} \right) < \omega < \lambda(x).$$  \hspace{1cm} (42)

By using arguments similar to [34, Section 1], we obtain that for all $t$ large enough

$$\alpha [P_t] \leq e^{-t}.$$  

and that

$$w_1(A) := \lim_{t \to \infty} t^{-1} \log(\alpha [P_t]) \leq -1.$$  

By [34] Proposition 4.13 p 170, we obtain that $\sigma_e(A) \subset \{ z \in \mathbb{C} : \mathcal{R}(z) \leq -1 \}$. Let $z \in \sigma(A) \setminus \sigma_e(A)$. Then there exists a non-zero $u \in L^1(\mathbb{R}_+, \mathbb{C})^2$ such that

$$\begin{cases} -u'(a) - D_x(a)u = zu(a) \\ u(0) = \int_{\mathbb{R}_+} B_x(a)u(a)da. \end{cases}$$  \hspace{1cm} (43)

By solving the first equation in (43) and by injecting the result in the second equation, we obtain that $u(0)$ satisfies

$$u(0) = \mathbf{F}(z)u(0)$$  \hspace{1cm} (44)
where

\[
F(z) = \int_{\mathbb{R}^+} B_x(a) \exp \left( - \int_0^a (D_x(\alpha) + zI) \, d\alpha \right) \, da. \tag{45}
\]

Equation (44) admits a non-trivial solution \( u(0) \) if and only if \( \det[F(z) - I] = 0 \). Since the matrix \( F(z) \) is triangular we have

\[
\det[F(z) - I] = (|F(z)|_{11} - 1)(|F(z)|_{22} - 1) \tag{46}
\]

where \( |F(z)|_{11} = \int_0^{\beta x} e^{-\alpha} \, d\alpha \) and \( |F(z)|_{22} = \int_0^{\beta x} e^{-(1+z)\alpha} \, d\alpha \). We deduce that the Malthusian parameter \( \lambda(x) \) is the largest real solution of \( \det[F(z) - I] = 0 \). By using similar analytical arguments as in the proof of [44, Theorem 4.10], we deduce that there exists only finitely many \( z \in \mathbb{C} \) such that \( \Re e(z) > 0 \) and \( \det[F(z) - I] = 0 \) which allows us to conclude for (42). We prove that \( \lambda(x) \) is a simple eigenvalue of \( A \) by showing that \( \lambda(x) \) is a simple zero of the equation \( \det[F(z) - I] = 0 \). Indeed we have

\[
\frac{d\det[F(\lambda(x))] - I}{d\lambda} = \frac{d|F(\lambda(x))|_{11}}{d\lambda} (|F(\lambda(x))|_{22} - 1) > 0.
\]

Let \( N_x \) be a principal eigenvector associated with the eigenvalue \( \lambda(x) \). By (43), we have

\[
N^2_2(a) = N^2_2(0) e^{-(a-x_a)\wedge 0 - \lambda(x)a}, \quad N^2_2(a) = N^2_2(0) e^{-(1+\lambda(x))a}
\]

and Equation (44) gives that

\[
N^2_2(0) = \frac{|F(\lambda(x))|_{21}}{1 - |F(\lambda(x))|_{22}} N^1_2(0).
\]

We conclude for the convergence by using arguments similar to proof of [44, Theorem 4.9 p187].

A.2 Proof of Lemma 3.5

Proof. Equation [11] has the form \( du/dt = f(t, u) \) with \( f(t, u) \to g(u) \) as \( t \to \infty \). So (11) is called an asymptotically autonomous differential equation (see [26,39]) with the limit equation

\[
\frac{dy(t)}{dt} = My(t) - \eta \|y(t)\|_1 y(t). \tag{47}
\]

We first show that any solution \( y(t) \) of (47) started at \( y(0) \in \mathbb{R}_+^n \times \mathbb{R}_+ \) converges to a stationary state. In [11], the proof is given when \( M \) is irreducible. We give a slightly different proof. Let \( \pi \) be defined in [12]. It is straightforward to prove that \( \pi \) is the eigenvector of \( M \) associated with the simple eigenvalue \( m_{11} \), which satisfy the condition \( \|\pi\|_1 = m_{11}/n \). Since \( z(0) \in \mathbb{R}_+^n \times \mathbb{R}_+ \) there exists a positive constant \( c(z(0)) \) such that \( e^{-m_{11}t} e^{Mt} z(0) \to c(z(0)) \pi \) as \( t \to \infty \). We now write

\[
\frac{y_1(t)}{y_2(t)} = \left[ \frac{e^{-m_{11}t} e^{Mt} y(0)}{e^{-m_{11}t} e^{M2t} y(0)} \right]_1 \to \frac{\pi_1}{\pi_2}.
\]

We deduce that the \( \omega \)-limit set of any solution of (47) is a subset of \( \Delta = \{ z \in \mathbb{R}_+^2 : z_1 = \frac{\pi_1}{\pi_2} z_2 \} \). We conclude by proving that any solution starting from \( \Delta \) converges to
Let us consider such a solution (always denoted by \( y(t) \)). We have
\[
\frac{dy_1(t)}{dt} = y_1(t)(m_{11} - \eta \|y(t)\|_1),
\]
\[
\frac{dy_2(t)}{dt} = y_2(t)\left( m_{21} \frac{y_1(t)}{y_2(t)} + m_{22} - \eta \|y(t)\|_1 \right).
\]
Since the \( \omega \)-limit set is an invariant subset, we deduce that
\[
\frac{dy_2(t)}{dt} = y_2(t)(m_{11} - \eta \|y(t)\|_1),
\]
that \( \|y(t)\|_1 \to m_{11}/\eta \) and \( y(t) \to \pi \) as \( t \to \infty \). In order to conclude about the solutions of (11), we use [39, Theorem 1.2] arguing that \( \pi \) is an asymptotically stable equilibrium of (47) and that for any \( y(0) \in \mathbb{R}_+^n \), the \( \omega \)-limit set of any solution \( y(t) \) of (11) started at \( y(0) \) is not a subset of \( \{0\} \times \mathbb{R}_+ \). The first claim is easily proved by showing that the Jacobian matrix has negative eigenvalues. For the second claim, let us assume it is not satisfied. Then \( y_1(t) \to 0 \) as \( t \to \infty \). Let us show the contradiction. Let \( \epsilon \) be sufficiently small and \( t_0 \) such that for any \( t \geq t_0 \)
\[
0 < m_{11} - \epsilon \leq m_{11} + \mathcal{D}_{11}(t) \leq m_{11} + \epsilon \\
0 < m_{12} - \epsilon \leq m_{12} + \mathcal{D}_{12}(t) \leq m_{12} + \epsilon.
\]
We introduce
\[
P'(y_1, y_2) = y_1(m_{11} - \epsilon - \eta(y_1 + y_2)) \\
Q'(y_1, y_2) = y_2(m_{22} + \epsilon - \eta(y_1 + y_2)) + (m_{12} + \epsilon)y_1
\]
and
\[
\mathcal{A}' = \{ y \in \mathbb{R}_+^2 : y_1 + y_2 \leq m_{11} - \epsilon \} \\
\mathcal{B}' = \{ y \in \mathbb{R}_+^2 : y_2 \geq \frac{1}{2\eta} \left( m_{22} + \epsilon - \eta y_1 + \sqrt{(m_{22} + \epsilon - \eta y_1)^2 + 4\eta(m_{12} + \epsilon)y_1} \right) \}.
\]
We deduce that there exists \( t_1 \) such that for any \( t \geq t_1 \), \( \frac{dy_2(t)}{dt} < 0 \) on \( \mathcal{B}' \) and \( y_1(t) < \epsilon \). We deduce that there exists \( t_2 \) such that for all \( t \geq t_2 \), \( y_1(t) + y_2(t) \leq \frac{m_{11} - \epsilon}{\eta} \). So for all \( t \geq t_2 \), \( \frac{dy_1(t)}{dt} \geq 0 \) which is absurd. \( \square \)

### A.3 Differential inclusions

In this appendix, we recall the results of [15] which concern the approximation of Markov chains by differential inclusions.

Let \( \epsilon > 0 \) be a scale parameter. Let \( (Y^\epsilon(k), k \in \mathbb{N}) \) be a Markov chain with values in \( \mathbb{R}^d \). The drift of the Markov chain \( Y^\epsilon \) is defined by
\[
g^\epsilon(x) = \mathbb{E}[Y^\epsilon(k + 1) - Y^\epsilon(k)|Y^\epsilon(k) = x].
\]
Let \( (\gamma^\epsilon)_{\epsilon > 0} \) be such that \( \lim_{\epsilon \to 0} \gamma^\epsilon = 0 \) and let us denote
\[
f^\epsilon(x) = \frac{g^\epsilon(x)}{\gamma^\epsilon}.
\]
One can write the evolution of the Markov chain as a stochastic approximation algorithm with constant step size $\gamma$:

$$Y^\epsilon(k + 1) = Y^\epsilon(k) + \gamma \epsilon (f^\epsilon(Y^\epsilon(k)) + U^\epsilon(k + 1))$$

where $U^\epsilon$ is a martingale difference sequence with respect to the filtration associated with the process $Y^\epsilon$.

Let us define

$$F(x) = \operatorname{conv}\left(\{\text{acc}_{\epsilon \to 0} f^\epsilon(x^\epsilon) \text{ for all } x^\epsilon \text{ such that } \lim_{\epsilon \to 0} x^\epsilon = x\}\right)$$

where $\operatorname{conv}(A)$ denotes the convex hull of the set $A$ and $\text{acc}_{\epsilon \to 0} f^\epsilon(x^\epsilon)$ denotes the set of accumulation points of the sequence $f^\epsilon(x^\epsilon)$ as $\epsilon \to 0$. Let us denote by $\mathcal{S}_F(T, x^0)$ the set of solutions $(x(t), t \in [0, T])$ of the differential inclusion

$$\begin{cases}
\frac{dx(t)}{dt} \in F(x(t)), & t \in [0, T] \\
x(0) = x^0.
\end{cases} \quad (48)$$

Let us recall the definition of a solution of (48).

**Definition A.1.** A map $x : [0, T] \to \mathbb{R}^d$ is a solution of (48) if there exists a map $\varphi : [0, T] \to \mathbb{R}^d$ such that:

(i) For all $t \in [0, T]$, $x(t) = x^0 + \int_0^t \varphi(s)ds$,

(ii) For almost every $t \in [0, T]$, $\varphi(t) \in F(x(t))$.

In particular (i) is equivalent to saying that $x$ is absolutely continuous. (i) and (ii) imply that $x$ is differentiable at almost every $t \in [0, T]$ with $dx(t)/dt \in F(x(t))$.

We define the continuous process $Y^\epsilon(t)$ as the piecewise interpolation of $Y^\epsilon$ whose time has been accelerated by $1/\gamma^\epsilon$: for all $k \in \mathbb{N}$, $Y^\epsilon(k\gamma^\epsilon) = Y^\epsilon(k)$ and $Y^\epsilon$ is linear on $[k\gamma^\epsilon, (k + 1)\gamma^\epsilon]$. We have the following theorem proved in [15, Theorem 1].

**Theorem A.2.** Assume that:

- There exists a constant $c > 0$ such that for all $y \in \mathbb{R}^d$, $\|f^\epsilon(y)\| \leq c(1 + \|y\|)$.
- $U^\epsilon$ is a martingale difference sequence which is uniformly integrable.

If $Y^\epsilon(0)$ tends to $x^0$ in probability as $\epsilon$ tends to zero, then

$$\inf_{y \in \mathcal{S}_F(T, x^0)} \sup_{t \in [0, T]} \|Y^\epsilon(t) - x(t)\| \to 0$$

in probability as $\epsilon$ tends to zero.

### A.4 Numerical simulation

We give the Python script for the numerical simulations of the individual based model described in Section 2. The algorithm is based on a classical acceptance/reject method (see [10], [40]).
#parameters

competition = 0.0005  # intensity of competition
p_mut = 0.05  # probability of mutation
var_mut = 0.05  # variance of mutations
number_of_jumps = 1000000  # number of jumps
population_size = 10000  # initial population size

# traits in the initial population

trait = numpy. ones((population_size, 2))
for k in range(len(trait[:, 0])):
    trait[k, :] = [1.2, 1.6]

# initial matrix population: [x_b, x_d, living/dead, birth date, death date, id, id parent, parent senescent]

population_0 = numpy. zeros((len(trait[:, 0]), 8), order='C', dtype=numpy.float32)
population_0[:, 0:2] = trait
population_0[:, 2] = 1
population_0[:, 3:5] = 0
for l in range(len(population_0[:, 0])):
    population_0[l, 5] = l+1

# birth rates

def b(x, a):
    if a <= x[0]:
        u = 1
    else:
        u = 0.0
    return u

# death rates

def d(x, a):
    if a > x[1]:
        u = 1
    else:
        u = 0.0
    return u

# maximal jump intensity by individual (for the acceptance/reject method)
intmax = 2.0 + competition

# Lansing effect

def lansing_effect(x, u):
    if x[1] > 0:
        if u < x[1]:
            r = x
        else:
            r = [x[0], 0]
    else:
        r = x
    return r

# mutation kernel

def dm(x):

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g = random.gauss(0, var_mut)
while x + g < 0:
  g = random.gauss(0, var_mut)
return x + g

# functions for acceptation/reject method

def acceptation_rejet_clone(t, a, n):
    return b(t, a) * (1 - (p_mut * p_mut + 2 * p_mut * (1 - p_mut))) / (intmax * n)

def acceptation_rejet_mutant_1(t, a, n):
    return acceptation_rejet_clone(t, a, n) + (b(t, a) * p_mut * p_mut) / (intmax * n)

def acceptation_rejet_mutant_2(t, a, n):
    return acceptation_rejet_mutant_1(t, a, n) + (b(t, a) * p_mut * p_mut) / (intmax * n)

def acceptation_rejet_mort(t, a, n):
    return acceptation_rejet_mutant_2(t, a, n) + (d(t, a) + (n - 1) * intensite_competition) / (intmax * n)

# transition of the process: it is based on a classical acceptation/reject method

def transition(p, time):
    # initialisation for acceptation/reject method
    viv = p[(p[:, 2] == 1), :]
    n = len(viv[:, 0])  # population size
    jump_time = random.expovariate(1) / (intmax * n * n)  # jump time
    u = random.uniform(0, 1)  # uniform law on (0,1)
    ind = random.randint(0, n - 1)  # random sampling of one individual
    w = time - viv[ind, 3] + jump_time  # age of this individual

    # acceptation/reject method
    while u > acceptation_rejet_mort(viv[ind, :2], w, n):
        jump_time += (random.expovariate(1) / (intmax * n * n))
        u = random.uniform(0, 1)
        ind = random.randint(0, n - 1)
        w = time - viv[ind, 3] + jump_time

    # when accepted
    s = viv[ind, :]
    a1 = acceptation_rejet_clone(s[:2], w, n)
    a2 = acceptation_rejet_mutant_1(s[:2], w, n)
    a3 = acceptation_rejet_mutant_2(s[:2], w, n)

    a = 0
    if w > s[1]:
        a = 1

    # Lansing effect
    s[:2] = lansing_effect(s[:2], w)

    # if clonal birth
    if u <= a1:
        c1 = [1, time + jump_time, 0.0, p[-1, 5] + 1, s[5], a]
        p = numpy.vstack((p, numpy.append(numpy.array(s[:2]), numpy.array(c1)))))

    # if birth with mutation (1 trait)
    elif a1 < u <= a2:
        x1 = int(numpy.random.randint(1, 3, 1))
        z1 = [(dm(s[0]), s[1]), [s[0], dm(s[1])]]
        c2 = [1, time + jump_time, 0.0, p[-1, 5] + 1, s[5], a]

# end of the transition function

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p = numpy.vstack((p, numpy.append(numpy.array(z1[x1-1]), numpy.array(c2))))

# if birth with mutation (2 traits)
elif a2 < u <= a3:
c3 = [1, time + jump_time, 0.0, p[-1, 5]+1, s[5], a]
p = numpy.vstack((p, numpy.append(numpy.array([dm(s[0]), dm(s[1])]),
                   numpy.array(c3))))

# if death
else:
p[(p[:, 5] == s[5]), 2] = 0
p[(p[:, 5] == s[5]), 4] = time + jump_time

time += jump_time

return p, time

# for simulating one trajectory of the process of number_of_jumps jumps

def trajectoire(p):
    population_size = sum(p[:, 2])
    time = 0
    for cs in range(0, number_of_jumps):
        if population_size >= 1:
            x = transition(p, time)
p = x[0]
time = x[1]
    population_size = sum(p[:, 2])
    print cs
    else:
        break
    p[(p[:, 4] == 0), 4] = time
    return p, time

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