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# Stochastic and deterministic approaches for populations with age and trait-structure

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## Abstract

Understanding how stochastic and non-linear deterministic processes interact is a major challenge in population dynamics theory. After a short review, we introduce a stochastic individual-centered particle model to describe the evolution in continuous time of a population with (continuous) age and trait structures. The individuals reproduce asexually, age, interact and die. In a large population limit, the random process converges to the solution of a Gurtin-McCamy type PDE. We show that the random model has a long time behavior that differs from its deterministic limit. However, the results on the limiting PDE and large deviation techniques *à la* Freidlin-Wentzell provide estimates of the extinction time and a better understanding of the long time behavior of the stochastic process. This has applications in the theory of Adaptive Dynamics. In a last section, we present on simulations three biological issues dealing with the consequences of size plasticity when taking growth into account, with growth-reproduction trade-offs and with periodic behavior.

Nous illustrons ici certaines interactions entre processus probabilistes et déterministes en dynamique des populations. Après une courte revue, nous commençons par introduire un modèle particulaire stochastique individu-centré pour décrire l'évolution en temps continu d'une population structurée en âge (continu) et en trait. Les individus se reproduisent de façon asexuée, vieillissent, interagissent et meurent. Dans une limite de grande population, notre processus aléatoire converge vers la solution d'une EDP du type Gurtin-McCamy. Nous montrons que le comportement en temps long du processus aléatoire diffère de celui de sa limite déterministe. Cependant, les deux types de modèles sont complémentaires : les résultats sur l'EDP limite et des techniques de grandes déviations *à la* Freidlin-Wentzell, nous fournissent des estimées du temps d'extinction et une description précise du comportement en temps grand de notre processus aléatoire, avec des applications à la théorie des Dynamiques Adaptatives. Dans une dernière section, nous présentons sur des simulations trois problèmes biologiques liés aux conséquences de plasticité de la taille suite à la prise en compte de la croissance, aux choix de stratégies d'histoire de vie et aux apparitions de phénomènes périodiques.

**Keywords:** Population dynamics, age-structure, individual-centered model, large population scaling, extinction, reproduction-growth trade-off.

**AMS code:** 60J80, 60K35, 92D15, 92D25, 92D40, 35-99.

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This paper is a proceeding of the CANUM 2008 conference, where a mini-symposium entitled *Hybrid methods* was organized by Tony Lelièvre and Madalina Deaconu. In this work, we are interested in the modelling of populations with age and trait structures. In particular (and this was the purpose of the mini-symposium *Hybrid methods*) we wish to emphasize the interplay between stochastic and deterministic descriptions.

Structured populations are populations in which the individuals differ according to variables that characterize their survival and reproduction abilities. *Traits* are morphological, physiological or behavioral

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variables that are hereditarily transmitted from a parent to its descendants unless a mutation happens. Other types of variables are *ages*, which are increasing functions of time, *sex* or *spatial location*. Here we focus on population with trait and age structures.

Age variables sum up individuals past histories and it is natural to take several ages into account to model the present dynamics. Examples are the *physical age* (the time since birth), the *biological age* (the intrinsic physiological stage that can grow nonlinearly in time), the age or stage of an illness, time since maturation... To take age-structure into account allows to enrich the modelling of individuals' life histories. For example, the salmon *Oncorhynchus gorbuscha* breeds at about 2 years-old, after returning to native freshwater streams. To study such species, it is important to take life stages into account. Moreover, age and trait-structures evolve jointly, since the age of expression of a trait and the life-history implied by a trait modify its fixation into the population, as well as future evolution.

We start with a short review of the literature for stochastic and deterministic modelling of populations with age and trait-structures in Section 1. In Section 1.3, the links between these descriptions is established: from a stochastic individual-centered model, we recover the PDEs of Demography *via* a large population limit. Section 1.4 proposes some illustrations of how deterministic and stochastic approaches complement each other. The PDEs bring us information to study the measure-valued stochastic differential equations (SDEs) that are introduced. The latter in turn provides results that can not be observed in large populations. An application to the study of extinction time is presented. Using these results, a second application (obtained in [65]) in the Adaptive Dynamics theory for Evolution is developed in Section 1.5. This example highlights the importance of probabilistic modelling of point events. We address some interesting biological applications through simulations in Section 2.

## 1 Populations with continuous age (and trait) structure: a brief review

Here, we restrict our attention to the literature dealing with continuous age and time population models (for discrete-time models with age or stage classes, the interested reader can refer to [13, 18, 81] for instance).

### 1.1 Deterministic models

Population models with continuous age and time that generalize the equations of Malthus [59] and Verhulst's well-known *logistic equation* [84] have often been written as PDEs (see *e.g.* [18, 43, 72, 81, 86] for introductory presentations).

PDE models for populations structured by a scalar age have been introduced by Sharpe and Lotka [77], Lotka [58], McKendrick [62] and Von Foerster [34]:  $\forall t \geq 0, \forall a \geq 0$ ,

$$\frac{\partial n}{\partial t}(a, t) + \frac{\partial n}{\partial a}(a, t) = -d(a)n(a, t), \quad n(0, t) = \int_0^{+\infty} b(a)n(a, t)da, \quad n(a, 0) = n_0(a), \quad (1)$$

where  $d$ ,  $b$  and  $n_0$  are nonnegative continuous functions (death and birth rates, initial age distribution) with  $b$  bounded and  $n_0$  integrable. Equation (1) is known as McKendrick-Von Foerster PDE. It is a transport PDE that describes the aging phenomenon, with death terms and births on the boundary  $a = 0$ . A drawback is that phenomena that model regulations in the size of the population or environmental limitations are not taken into account (no interaction terms).

The first nonlinear models for populations with age structure have been introduced by Gurtin and MacCamy [39]. The rates  $b(a)$  and  $d(a)$  of (1) are replaced by functions  $b(a, N_t)$  and  $d(a, N_t)$  of the scalar age  $a \in \mathbb{R}_+$  and of the size  $N_t = \int_0^{+\infty} n(a, t)da \in \mathbb{R}_+$  of the population at time  $t$ . The nonlinearity involves the unknown solution and introduces a *feed-back* term that allows to control the population size. A particular case is when

$$d(a, N_t) = d(a) + \eta N_t \quad (2)$$

where  $d(a)$  is the natural death rate at age  $a$  and where  $\eta N_t$  is the logistic competition term. The stationary solutions, their global stabilities and estimates of the rates of decay are studied by Marcati [60]. Stability conditions for a more general class of birth and death rates have been obtained in [32, 31]. The logistic competition term assumes that the competitors exert the same interactions. Busenberg and

Iannelli [9] study the case where the death rate takes the form  $d(a) + F(t, N_t, S_1(t), \dots, S_m(t))$  where  $\forall i \in [1, m]$ ,  $S_i(t) = \int_0^{+\infty} \gamma_i(a)n(a, t)da$ ,  $F$  being continuous in  $t$  and Lipschitz continuous with respect to the other variables, and the  $\gamma_i$  being positive continuous bounded functions that describe the pressure exerted by an individual depending on its age. However the competition term remains non-local (and thus finite-dimensional).

Webb [86] proposed PDEs with local interactions in the coefficients with rates of the form  $b(a, n(\cdot, t))$  and  $d(a, n(\cdot, t))$ , where  $n(\cdot, t)$  belongs to the Banach space  $L^1(\mathbb{R}_+, \mathbb{R}_+)$  of integrable functions w.r.t.  $a \in \mathbb{R}_+$ . The case of multitype populations was also considered. Local interactions mean that the competition terms are of the form  $\int_0^{+\infty} U(a, \alpha)n(\alpha, t)d\alpha$  where  $U(a, \alpha)$  is the interaction of an individual of age  $\alpha$  on an individual of age  $a$ .

More recently, entropy methods have extended to equations that are not conservation laws the notion of relative entropy for conservative equations. They have been developed by Perthame and coauthors [68, 69, 72, 73] with the aim of providing new proofs of existence of solutions, long time behavior or attraction to periodic forcing.

There are many examples in the literature where additional structures other than age-based have been taken into account. The population can be divided into a finite number of classes: see [86] for a survey on multi-type models, including prey-predator or epidemiological models (*e.g.* [10, 44]). In epidemic models, the class of susceptible, infectious or removed individuals are considered, leading to different behavior in the propagation of the infectious illness. From the modelling point of view, taking age-structure into account is important as, for example, the time since the primal infection matters.

To our knowledge, populations with age structure and spatial diffusions have been first studied by Langlais [55, 56, 57] and Busenberg and Iannelli [8].

Structure variables with values in a non-finite state-space other than position have been considered for instance by Rotenberg [76] for instance. He considered the maturation velocity  $x \in \mathcal{X} = ]0, 1]$  as a trait that can change at birth and during the life of an individual. For an individual born at time  $c \in \mathbb{R}$  and with traits  $x_i \in ]0, 1]$  on  $[t_i, t_{i+1}[$  ( $i \in \mathbb{N}$ ,  $t_0 = c$  and  $(t_i)_{i \in \mathbb{N}}$  are times of trait change in  $[c, +\infty[$ ), the biological age at  $t > c$  is  $a = \sum_{i \in \mathbb{N}} x_i(t_{i+1} \wedge t - t_i \wedge t)$ . Here, the biological age  $a$  differs from the physical age  $t - c$  as soon as  $\exists i \in \mathbb{N}$ ,  $t_i < t$  and  $x_i \neq 1$ . A nonlinear version of this model has been studied by Mischler *et al.* [69].

## 1.2 Stochastic models

Dealing with stochastic models, generalization of the Galton-Watson process [38] have been studied by Bellman and Harris [3, 40], and then Athreya and Ney ([1] Chapter IV). They consider non Markovian processes, called age-structured branching processes, in which the lifespan of an individual does not follow an exponential law. Upon death, a particle is replaced by a random number of daughter particles, with a reproduction law that does not depend on the age of the mother, nor on the state of the population.

The assumptions of births at the parent's death and of independence between the reproduction law and the age of the parent are biologically restrictive. Kendall [52], Crump and Mode [20, 21], Jagers [46, 47], Doney [27], study birth and death processes in which a particle can give birth at several random times during its life, with rates that may depend on its age. More recently Lambert [54] uses contour processes to study the properties of splitting trees which are formed by individuals with independent and identically distributed (*i.i.d.*) lifespans and who give birth at the same constant rate during their lives. His results give a new interpretation of the link between branching processes and Lévy processes [37, 74].

In the two types of models introduced above, particles alive at the same time are independent, which is also a biologically restrictive assumption. Wang [85], Solomon [78] have considered birth and death processes in which the lifespans of individuals are independent, but where the birth rate and reproduction law of each particle depend on the state of the population. Oelschläger [70], Jagers [46], Jagers Klebaner [50] study models in which both the birth and death rates include interactions, but these rates remain bounded. In [50, 46], the interactions vanish in the limit, so that the authors recover the population-independent behaviors. These models hence exclude logistic-type interactions. Such interactions are included in the models considered by [83].

When the individuals interact, the key *branching property* does not hold, and classical approaches based on generating or Laplace functions (*e.g.* [1]) do not apply. The behavior of the stochastic processes is then difficult to study. However, in a large population limit, a law of large number can be established [85, 78, 70, 83], under which we obtain a limiting deterministic process that can be identified as a weak

solution of a PDE that generalizes the McKendrick-Von Foerster equation (1). We present such results in Section 1.3. Once this link between PDEs and stochastic processes has been evaluated, results for PDEs may provide interesting results for the stochastic process, even if the behaviors of the stochastic model and of its corresponding deterministic limit differ (see Sections 1.4 and 1.5).

Multitype populations with age-structure have been considered by many authors (*e.g.* Athreya and Ney [1], Chap. V.10). A stochastic model of epidemics with age structure has been considered for instance in [19]. Stochastic models of populations with age and trait-structures have been addressed by Jagers [48, 49] and Méléard and Tran [65] for instance. In [65], the mutation rate which is responsible for generating the trait diversity is decreased so that the mutations become more and more rare. A separation of the time scales of mutations and demography (births and deaths) is obtained with applications to the evolutionary theory of Adaptive Dynamics (see Section 1.5).

Finally, let us mention that other large-population scalings have made the object of abundant research. Superprocess limits of age-structured branching processes obtained by rescaling the lifespan and mass of the particles, by increasing their number and by modifications of the birth rate or reproduction law have been studied by Dynkin [29], Kaj et Sagitov [51]. For age-structured birth and death processes, this has been investigated by Dawson *et al.* [22], Bose and Kaj [5, 6].

### 1.3 From stochastic individual-centered modelling of age-structured populations to deterministic PDEs

#### 1.3.1 A microscopic model

We study a stochastic model that takes into account trait and age dependence in the birth and death rates together with interactions between individuals. We introduce a microscopic process that generalizes the approach of Fournier and Méléard [35], Champagnat *et al.* [17, 16], for which the dynamics is specified at the level of individuals. When the population is large, we establish a macroscopic approximation of the process, which describes the evolution at the scale of the population (individual paths are lost). These results are taken from [83].

More precisely, in the individual centered model that is studied, the population is discrete and represented at time  $t \geq 0$  by a point measure

$$Z_t = \sum_{i=1}^{N_t} \delta_{(x_i(t), a_i(t))}, \quad (3)$$

where each individual is described by a Dirac mass  $(x, a) \in \tilde{\mathcal{X}} := \mathcal{X} \times \mathbb{R}_+$ ,  $\mathcal{X} \subset \mathbb{R}^d$  being the trait space and  $\mathbb{R}_+$  the age space. We denote by  $N_t$  the number of individuals alive at time  $t$ . For a function  $f$ , we denote by  $\langle Z_t, f \rangle$  the integral  $\int_{\tilde{\mathcal{X}}} f(x, a) Z_t(dx, da) = \sum_{i=1}^{N_t} f(x_i(t), a_i(t))$ . An individual of trait  $x$  and age  $a$  in a population  $Z \in \mathcal{M}_P(\tilde{\mathcal{X}})$  reproduces asexually, ages and dies. When reproduction occurs, the trait is transmitted hereditarily to descendants unless a mutation occurs. The mechanism is as follows:

- Birth rate is  $b(x, a) \in \mathbb{R}_+$ . With probability  $p \in [0, 1]$ , the new individual is a mutant with trait  $x + h$  where  $h$  is chosen in the probability distribution  $k(x, a, h)P(dh)$  (that depends on the characteristics of the parent) where  $P(dx)$  is a  $\sigma$ -finite reference measure on  $\mathcal{X}$  (the Lebesgue measure or the uniform measure when  $\mathcal{X}$  is bounded for instance),
- Death rate is  $d(x, a, ZU(x, a)) \in \mathbb{R}_+$ . It depends on the trait and age of the individual but also on the measure  $Z$  describing the whole population. The function  $U : \tilde{\mathcal{X}}^2 \mapsto \mathbb{R}^m$  is an interaction kernel: each component of  $U((x, a), (y, \alpha))$  describes a different interaction of  $(y, \alpha)$  on  $(x, a)$ , and  $ZU(x, a) = \int_{\tilde{\mathcal{X}}} U((x, a), (y, \alpha)) Z(dy, d\alpha)$ .
- Aging velocity is here 1.

**Assumption (H1)** The birth rate  $b(x, a)$  is assumed continuous and bounded by a positive constant  $\bar{b}$ . The function  $k(x, a, h)$  is assumed to be bounded by a positive constant  $\bar{k}$ . The death rate is assumed continuous in  $(x, a)$ , Lipschitz continuous in the interaction term and such that it is lower bounded by a

strictly positive constant and upper bounded by  $\bar{d}(1 + \langle Z, 1 \rangle)$  with  $\bar{d} > 0$ .

More general models are considered in [82, 83], where vectorial ages with nonlinear aging velocities are considered for instance.

Following [35, 17, 16, 83], we describe the evolution of  $(Z_t)_{t \in \mathbb{R}_+}$  by a SDE driven by a Poisson point process. The mathematical difficulty lies in the fact that the birth and death rates depend on age which varies continuously with time.

Let  $Z_0 \in \mathcal{M}_P(\tilde{\mathcal{X}})$  be a random variable (r.v.) such that  $\mathbb{E}(\langle Z_0, 1 \rangle) < +\infty$ , and let  $Q(ds, di, d\theta, dx')$  be a Poisson point measure (P.P.M.) on  $\mathbb{R}_+ \times \mathcal{E} := \mathbb{R}_+ \times \mathbb{N}^* \times \mathbb{R}_+ \times \mathcal{X}$  with intensity  $q(ds, di, d\theta, dx') := ds \otimes n(di) \otimes d\theta \otimes P(dx')$  and independent of  $Z_0$  (For P.P.Ms, the reader can for instance refer to [45] Chapter I).

Let us denote by  $X_i(t)$  and  $A_i(t)$  the trait and age of the  $i^{\text{th}}$  particle at time  $t$ , the particles being ranked in the lexicographical order on  $\mathbb{R}^d \times \mathbb{R}_+$  (see [35, 83] for a rigorous notation).

$$\begin{aligned} Z_t = & \sum_{i=1}^{N_0} \delta_{(X_i(0), A_i(0)+t)} + \int_0^t \int_{\mathcal{E}} \mathbf{1}_{\{i \leq N_{s-}\}} \left[ \delta_{(X_i(s-), t-s)} \mathbf{1}_{\{0 \leq \theta < m_1(s, Z_{s-}, i, x')\}} \right. \\ & + \delta_{(x', t-s)} \mathbf{1}_{\{m_1(s, Z_{s-}, i, x') \leq \theta < m_2(s, Z_{s-}, i, x')\}} \\ & \left. - \delta_{(X_i(s-), A_i(s-)+t-s)} \mathbf{1}_{\{m_2(s, Z_{s-}, i, x') \leq \theta < m_3(s, Z_{s-}, i, x')\}} \right] Q(ds, di, d\theta, dx'), \end{aligned} \quad (4)$$

where:

$$\begin{aligned} m_1(s, Z_{s-}, i, x') &= (1-p)b(X_i(s-), A_i(s-))k(X_i(s-), A_i(s-), x') \\ m_2(s, Z_{s-}, i, x') &= m_1(s, Z_{s-}, i, x') + pb(X_i(s-), A_i(s-))k(X_i(s-), A_i(s-), x') \\ m_3(s, Z_{s-}, i, x') &= m_2(s, Z_{s-}, i, x') + d(X_i(s-), A_i(s-), Z_{s-}U(X_i(s-), A_i(s-)))k(X_i(s-), A_i(s-), x'). \end{aligned}$$

The interpretation is as follows. To describe the population at a given time  $t$ , we start with the individuals present at  $t = 0$ . Then we add all the ones that were born between 0 and  $t$  and finally we delete the points corresponding to individuals who died between 0 and  $t$ . The individuals of the initial condition are expected at time  $t$  with an age that is increased by  $t$  (first term of (4)). When a birth takes place at time  $s$ , we add in the measure describing the population at time  $t$  a point at age  $t - s$  (the age expected for this newborn individual, second and third term of (4)). When an individual of age  $a$  dies at time  $s$ , in the measure describing the population at time  $t$  we suppress a point at age  $a + t - s$  (the age this individual would have had if it had survived). As the rates vary with time, we use a P.P.M. with a rate that upper-bounds the age-dependent rates and use an acceptance-rejection procedure (the indicators in  $\theta$ ) to obtain exactly the rates that we need.

We emphasize that exact simulation of this SDE can be done easily (see Section 2) and correspond to the algorithms used by many biologists who run simulations of individual-based population models.

**Proposition 1.1.** *For every given Poisson point measure  $Q$  on  $\mathbb{R}_+ \times \mathcal{E}$  with intensity measure  $q$ , and every initial condition  $Z_0$  such that  $\mathbb{E}(\langle Z_0, 1 \rangle) < +\infty$ , there exists a unique strong solution to SDE (4) in  $\mathbb{D}(\mathbb{R}_+, \mathcal{M}_P(\tilde{\mathcal{X}}))$ . The solution is a Markov process with infinitesimal generator given for all  $f \in \mathcal{C}^{0,1}(\tilde{\mathcal{X}}, \mathbb{R})$ ,  $F \in \mathcal{C}^1(\mathbb{R}, \mathbb{R})$ , and  $Z \in \mathcal{M}_P(\tilde{\mathcal{X}})$  by*

$$\begin{aligned} LF_f(Z) = & \int_{\tilde{\mathcal{X}}} [\partial_a f(x, a) F'(\langle Z, f \rangle) + (F_f(Z + \delta_{(x,0)}) - F_f(Z)) b(x, a)(1 - p(x, a)) \\ & + \int_{\mathcal{X}} (F_f(Z + \delta_{(x',0)}) - F_f(Z)) b(x, a)p(x, a)k(x, a, x')P(dx') \\ & + (F_f(Z - \delta_{(x,a)}) - F_f(Z)) d(x, a, ZU(x, a))] Z(dx, da), \end{aligned} \quad (5)$$

with  $F_f(Z) = F(\langle Z, f \rangle)$ .

The proof of this result is given in Propositions 2.2.5, 2.2.6 and Theorem 2.2.8 of [82]. It is based on moment estimates and uses the algorithmic construction of (4) which will be detailed in Section 2. The behaviour of the solution is far more difficult to study. For this reason, and also in order to link the SDE (4) with the PDEs that are classically introduced in Demography (see Section 1.1), we consider a large

population limit that consists in letting the size of the initial population grow to infinity proportionally to an integer parameter  $n$  while individuals and interaction intensities are assigned a weight  $1/n$ . Under proper assumptions on the initial condition, the sequence of rescaled processes  $(Z^n)_{n \in \mathbb{N}}$  converges in the limit to the solution of a deterministic equation that we will identify as weak solution of a PDE that generalizes the ones introduced in Section 1.1.

### 1.3.2 Large population limit

The large population renormalization that we consider is inspired by the work of Fournier and Méléard [35]. Full details and proofs can be found in [83, 82]. We will consider a sequence  $(Z_t^n, t \in \mathbb{R}_+)_{n \in \mathbb{N}^*}$  satisfying SDEs as in (4) but with the following recalings:

- We let the size of the initial population tend to infinity proportionally to the parameter  $n \in \mathbb{N}^*$  and renormalize the weights of the individuals by  $1/n$ :

**Assumption (H2):** The sequence  $(Z_0^n)_{n \in \mathbb{N}^*} = (\frac{1}{n} \sum_{i=1}^{N_t^n} \delta_{(X_i(0), A_i(0))})$  converges in probability to the finite measure  $\xi_0 \in \mathcal{M}_F(\tilde{\mathcal{X}})$  for the weak convergence topology.

- In addition, we also rescale the interactions between individuals by  $1/n$  so that the interaction term  $ZU(x, a) = \sum_{i=1}^{N_t^n} U((x, a), (x_i, a_i))$  is replaced by  $\frac{1}{n} \sum_{i=1}^{N_t^n} U((x, a), (x_i, a_i)) = Z^n U(x, a)$ .

This rescaling can be understood as a constraint in resources: if we increase the size of the population, we have to decrease the biomass of the individuals to keep the system alive. If the individuals are smaller, their interactions will be decreased proportionally to their weights.

**Proposition 1.2.** (i) *If  $\sup_{n \in \mathbb{N}^*} \mathbb{E}(\langle Z_0^n, 1 \rangle^2) < +\infty$ , then for every  $f \in \mathcal{C}^{1,1,0}(\mathbb{R}_+ \times \tilde{\mathcal{X}}, \mathbb{R})$  the process*

$$M_t^{n,f} = \langle Z_t^n, f(\cdot, \cdot, t) \rangle - \langle Z_0^n, f(\cdot, \cdot, 0) \rangle - \int_0^t \int_{\tilde{\mathcal{X}}} [\partial_a f(x, a, s) + \partial_s f(x, a, s) + f(x, 0, s)b(x, a)(1 - p(x, a)) \\ + \int_{\mathcal{X}} f(x', 0, s)b(x, a)p(x, a)k(x, a, x')dx' - f(x, a, s)d(x, a, Z_s^n U(x, a))] Z_s^n(dx, da) ds, \quad (6)$$

*is a square integrable martingale with the following quadratic variation process:*

$$\langle M^{n,f} \rangle_t = \frac{1}{n} \int_0^t \int_{\tilde{\mathcal{X}}} \left[ f^2(x, 0, s)b(x, a)(1 - p(x, a)) + \int_{\mathcal{X}} f^2(x', 0, s)b(x, a)p(x, a)k(x, a, x')dx' \right. \\ \left. + f^2(x, a, s)d(x, a, Z_s^n U(x, a)) \right] Z_s^n(dx, da) ds. \quad (7)$$

(ii) *If  $\exists \eta > 0$ ,  $\sup_{n \in \mathbb{N}^*} \mathbb{E}(\langle Z_0^n, 1 \rangle^{2+\eta}) < +\infty$ , then the sequence  $(Z^n)_{n \in \mathbb{N}^*}$  converges in distribution in  $\mathbb{D}(\mathbb{R}_+, \mathcal{M}_F(\tilde{\mathcal{X}}))$  to the unique solution  $\xi \in \mathcal{C}(\mathbb{R}_+, \mathcal{M}_F(\tilde{\mathcal{X}}))$  of the following equation:  $\forall f : (s, x, a) \mapsto f_s(x, a) \in \mathcal{C}^{1,0,1}(\mathbb{R}_+ \times \tilde{\mathcal{X}}, \mathbb{R})$ ,*

$$\langle \xi_t, f(\cdot, \cdot, t) \rangle = \langle \xi_0, f(\cdot, \cdot, 0) \rangle + \int_0^t \int_{\tilde{\mathcal{X}}} [\partial_a f(x, a, s) + \partial_s f(x, a, s) + f(x, 0, s)b(x, a)(1 - p(x, a)) \\ + \int_{\mathcal{X}} f(x', 0, s)b(x, a)p(x, a)K(x, a, dx') - f(x, a, s)d(x, a, \xi_s U(x, a))] \xi_s(dx, da) ds, \quad (8)$$

This result is proved by a tightness-uniqueness argument (see [35, 83]). Point (i) is obtained by stochastic calculus for jump process. Heuristically, since the quadratic variation is in  $1/n$ , it vanishes as  $n \rightarrow +\infty$ . Moreover, when births or deaths occur, we add or delete individuals of weight  $1/n$  (the process has a jump of order  $1/n$ ). This explains why we obtain in the limit a continuous deterministic process.

The link of (8) with PDEs is specified in the next proposition, which is proved in [83] (Propositions 3.6 and 3.7).

**Assumption (H3):**  $\xi_0$  admits a density  $n_0(x, a)$  with respect to  $P(dx) \otimes da$  on  $\tilde{\mathcal{X}}$ .

**Proposition 1.3.** *The measures  $\xi_t \in \mathcal{M}_F(\tilde{\mathcal{X}})$ , for  $t \in \mathbb{R}_+$ , admit densities  $n(x, a, t)$  with respect to  $P(dx) \otimes da$  on  $\tilde{\mathcal{X}}$  and the family of these densities  $(n(\cdot, \cdot, t))_{t \in \mathbb{R}_+}$  is a weak solution of:*

$$\begin{aligned} \frac{\partial n}{\partial t}(x, a, t) &= -\partial_a n(x, a, t) - d \left( x, a, \int_{\tilde{\mathcal{X}}} U((x, a), (y, \alpha)) n(y, \alpha, t) P(dy) d\alpha \right) n(x, a, t) \\ n(x, 0, t) &= \int_{\mathbb{R}_+} n(x, a, t) b(x, a) (1 - p(x, a)) da + \int_{\tilde{\mathcal{X}}} b(x', a) p(x', a) k(x', a, x) n(x', a, t) P(dx') da \\ n(x, a, 0) &= n_0(x, a). \end{aligned} \quad (9)$$

These equations generalize the McKendrick-Von Foerster's PDEs. They describe ecological dynamics at the scale of the population (individual trajectories are lost). The densities  $n(x, a, t)$ , when they exist, correspond to the *number density*, that describes the trait and age distributions of a "continuum" of individuals. An interesting point is that the equation (8) does not always admit function solutions (see [83]).

### 1.3.3 Central limit theorem

In large populations, the microscopic process  $Z^n$  can be approximated by the solution of PDE (9) that generalizes classical PDEs of Demography for populations in continuous time and structured by a scalar age. In order to construct confidence intervals or to assess the quality of the approximation, it is useful to study the fluctuation process,

$$\forall t \in [0, T], \forall n \in \mathbb{N}^*, \quad \eta_t^n(dx, da) = \sqrt{n} (Z_t^n(dx, da) - \xi_t(dx, da)). \quad (10)$$

For  $n \in \mathbb{N}^*$ ,  $\eta^n$  is a process of  $\mathbb{D}([0, T], \mathcal{M}_S(\tilde{\mathcal{X}}))$ . Since the space  $\mathcal{M}_S(\tilde{\mathcal{X}})$  of signed measures on  $\tilde{\mathcal{X}}$  can not be meterized when embedded with the topology of weak convergence, we follow the works of Métivier [66] and Méléard [64], and consider  $\eta^n$  as a distribution-valued process.

For a multi-index  $k \in \mathbb{N}^{d+1}$ , we denote by  $D^k f$  the derivative  $\partial^{|k|} f / \partial x_1^{k_1} \dots \partial x_d^{k_d} \partial a$ . The Banach space  $C^{\beta, \gamma}$  is the space of functions  $f$  of class  $C^\beta$  such that for  $k$  such that  $|k| \leq \beta$ ,  $\lim D^k f(x, a) / (1 + a^\gamma) = 0$  when  $a \rightarrow +\infty$  or when  $x \rightarrow \partial \mathcal{X}$ , embedded with the norm  $\|f\|_{C^{\beta, \gamma}} = \sum_{|k| \leq \beta} \sup_{(x, a) \in \tilde{\mathcal{X}}} |D^k f(x, a)| / (1 + a^\gamma)$ . The Hilbert space  $W_0^{j, \alpha}$  is the closure of  $C_K^\infty$  with respect to the norm  $\|f\|_{W_0^{\beta, \gamma}}^2 = \int_{\tilde{\mathcal{X}}} \sum_{|k| \leq \beta} |D^k f(x, a)|^2 / (1 + a^{2\gamma}) da$ . We denote by  $C^{-\beta, \gamma}$  and  $W_0^{-\beta, \gamma}$  their dual spaces.

We are going to consider the following embeddings. Let  $D = [(d+1)/2] + 1$ ,

$$C^{3D+1, 0} \hookrightarrow W_0^{3D+1, D} \hookrightarrow_{H.S.} W_0^{2D+1, 2D} \hookrightarrow C^{D+1, 2D} \hookrightarrow C^{D, 2D} \hookrightarrow W_0^{D, 3D} \hookrightarrow C^{0, 3D+1} \quad (11)$$

the second embedding being Hilbert-Schmidt.

**Assumption (H4):** We assume that Assumptions (H1), (H2) and (H3) are satisfied and that:

- The sequence  $(\eta_0^n)_{n \in \mathbb{N}^*}$  converges in  $W_0^{-D, 3D}$  to  $\eta_0$  and  $\sup_{n \in \mathbb{N}^*} \mathbb{E}(\|\eta_0^n\|_{W_0^{-D, 3D}}^2) < +\infty$
- $\sup_{n \in \mathbb{N}^*} \mathbb{E}((\int_{\tilde{\mathcal{X}}} |a|^{6D} Z_0^n(dx, da))^2) < +\infty$
- Assumption (H3) is satisfied and the functions  $(x, a) \mapsto b(x, a)$ ,  $(x, a) \mapsto k(x, a, x')$ ,  $(x, a) \mapsto U((x', \alpha), (x, a))$  and  $(x, a) \mapsto U((x, a), (x', \alpha))$  (for almost every  $(x', \alpha) \in \tilde{\mathcal{X}}$ ) belong to  $C^{3D+1, 0}$ .
- The death rate  $(x, a, u) \mapsto d(x, a, u)$  is such that for all  $u$ , it belongs to  $C^{3D+2, 0}$  with a norm bounded by a polynomial in  $u$ . We assume that its derivative with respect to  $u$  is Lipschitz continuous.

**Proposition 1.4.** *Let  $T > 0$ . Under Assumptions (H4), the sequence  $(\eta^n)_{n \in \mathbb{N}^*}$  converges in distribution in  $\mathbb{D}([0, T], W_0^{-3D+1, D})$  to the unique continuous solution of:  $\forall t \in [0, T], \forall f \in W_0^{3D+1, D}$ ,*

$$\begin{aligned} \langle \eta_t, f \rangle &= \langle \eta_0, f \rangle + W_t(f) + \int_0^t \int_{\tilde{\mathcal{X}}} \left[ \partial_a f(x, a) + b(x, a) ((1-p)f(x, 0) + p \int_{\mathcal{X}} f(x', 0) K(x, a, dx')) \right. \\ &\quad \left. - d(x, a, \xi_s U(x, a)) f(x, a) - \int_{\tilde{\mathcal{X}}} f(y, \alpha) d_u(y, \alpha, \xi_s U(y, \alpha)) U((y, \alpha), (x, a)) \xi_s(dy, d\alpha) \right] \eta_s(dx, da) ds \end{aligned} \quad (12)$$



where  $(W_t(f))_{t \in \mathbb{R}_+}$  is a continuous centered square-integrable Gaussian process with quadratic variation:

$$\langle W(f) \rangle_t = \int_0^t \int_{\tilde{\mathcal{X}}} \left[ b(x, a) \left( (1-p) f^2(x, a) + p \int_{\mathcal{X}} f^2(x', 0) K(x, a, dx') \right) + f^2(x, a) d(x, a, \xi_s U(x, a)) \right] \xi_s(dx, da) ds. \quad (13)$$

The tightness is proved in the space  $W_0^{-3D+1, D}$  using a tightness criteria for Hilbert-valued processes that is stated in [64] (Lemma C), and which necessitates the Hilbert-Schmidt embedding  $W_0^{3D+1, D} \hookrightarrow_{H.S.} W_0^{2D+1, 2D}$ . The spaces  $C^{-(D+1), 2D}$  and  $C^{-D, 2D}$  are the spaces in which the estimates of the norm of the finite variation part of the process are established (see Section 4.4.2 of [82]). We need these two spaces since  $\partial_a$  maps  $C^{D+1, 2D}$  into  $C^{D, 2D}$ . The norm of the martingale part is controlled in  $W_0^{-D, 3D}$ . Finally, uniqueness of the limiting value is proved thanks to the embedding  $W_0^{-3D+1, D} \hookrightarrow C^{-3D+1, 0}$ .

## 1.4 Extinction in logistic age-structured population

Extinction is one of the recurrent and important issue when studying the ecology of a population. Here, the conclusions given by the deterministic and the stochastic models differ, but we will see that they still provide complementary information.

For the sake of simplicity, we consider here a logistic age-structured population (without trait-structure). An individual of age  $a$  in a population of size  $N$  gives birth with rate  $b(a)$  and dies with the rate  $d(a) + \eta N$  given in (2). From Proposition 1.3, under the large population renormalization of Section 1.3.2, the sequence  $(Z^n)_{n \in \mathbb{N}^*}$  converges to the unique weak solution of the Gurtin McCamy PDE with the death rate (2). Let us recall some known facts about this PDE. We denote by  $\Pi(a_1, a_2) = \exp\left(\int_{a_1}^{a_2} \delta(\alpha) d\alpha\right)$  the probability of survival from age  $a_1$  to age  $a_2$  in absence of competition.

**Proposition 1.5.** (i) *The following renewal equation:  $\forall t \in \mathbb{R}_+$*

$$B(t) = \int_0^t g(a) B(t-a) da + B_0(t) \quad (14)$$

with

$$g(a) = b(a) \Pi(0, a) \mathbb{1}_{a \geq 0} \text{ and } B_0(t) = \mathbb{1}_{t \geq 0} \int_0^{+\infty} b(a+t) \frac{n_0(a)}{N_0} \Pi(a, a+t) da,$$

where  $N_0 = \int_0^{+\infty} n_0(a) da$  admits a unique bounded solution on compact sets of  $\mathbb{R}_+$  given by:

$$B(t) = B_0 * U(t), \quad \text{where } u(t) = \sum_{n=0}^{+\infty} g^{*n}(t). \quad (15)$$

(ii) *There exists a unique classical solution of class  $\mathcal{C}^1$  to the Gurtin-McCamy equation with death rate (2). It is given by:  $\forall a \in \mathbb{R}_+, \forall t \in \mathbb{R}_+$*

$$n(a, t) = \frac{N_0 v(a, t)}{1 + N_0 \int_0^t \int_0^{+\infty} v(\alpha, s) d\alpha ds} \quad \text{with } v(a, t) = \begin{cases} n_0(a-t) \Pi(a-t, a) / N_0 & \text{if } a \geq t \\ B(t-a) \Pi(a, 0) & \text{if } a < t \end{cases} \quad (16)$$

Point (i) is obtained by following [33] (Chap. XI) and [1] (Chap. IV.4). For Point (ii) see [86] (Section 5.4).

Since the family  $(n(a, t) da)_{t \in \mathbb{R}_+}$  defines a weak solution of the Gurtin-McCamy PDE in this case, we obtain as a corollary of Propositions 1.3 and 1.5:

**Corollary 1.1.** *In the case of logistic age-structured population, we have for the limiting process  $\xi$  of the sequence  $(Z^n)_{n \in \mathbb{N}^*}$ :  $\forall t \in \mathbb{R}_+, \xi_t(da) = n(a, t) da$  where  $n(a, t)$  is explicitly given in (16).*

Thanks to the results known for the PDE, an explicit expression and regularities of the density of  $\xi$  are obtained directly.

As explained in Section 1, the long time behavior of the Gurtin-McCamy PDE is well known. In particular:

**Proposition 1.6.** (see [60, 86]) Under the assumption  $R_0 := \int_0^{+\infty} b(a)\Pi(0, a)da > 1$ , which expresses the renewal of the generations in absence of competition, there exists a unique nontrivial asymptotically exponentially stable steady state given by:

$$\hat{n}(a) = \frac{\lambda_1 e^{\lambda_1 a} \Pi(0, a)}{\eta \int_0^{+\infty} e^{-\lambda_1 \alpha} \Pi(0, \alpha) d\alpha} \quad \text{where } \lambda_1 \text{ satisfies } 1 = \int_0^{+\infty} e^{-\lambda_1 a} b(a) \Pi(0, a) da. \quad (17)$$

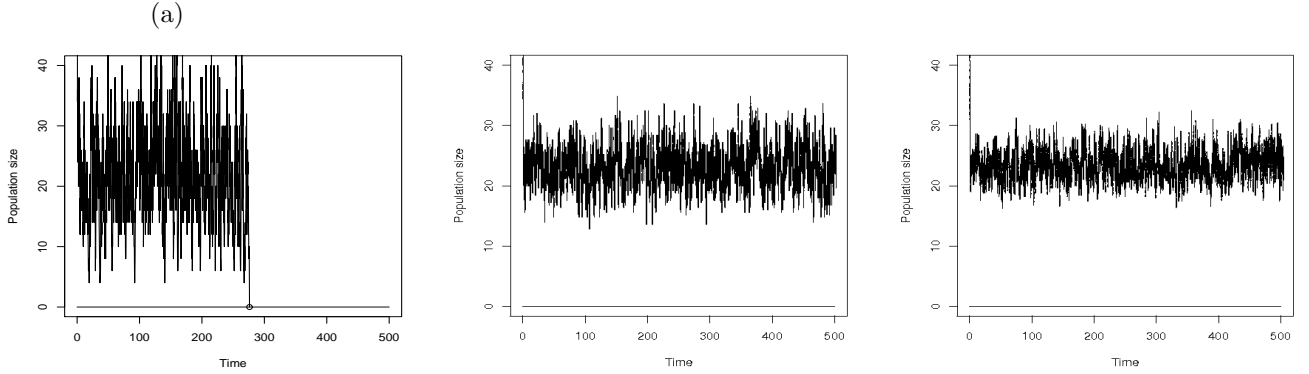


Figure 1: Simulated size of a logistic age-structured population. The model is given by (4) rescaled with  $n = 1, 5$  and 10 (from left to right).

Even if simulations may lead us to the false impression that the long time behavior of the stochastic processes is the same as for their deterministic limit, the situation is much more complicated. We show that the stochastic process gets extinct almost surely, but after having spent an exponentially long time in the neighborhood of the stationary solution  $\hat{\xi}(da) = \hat{n}(a)da$  (17) of its deterministic approximation. Here, deterministic and stochastic models give different conclusions, but the results for the limiting PDE make it possible to understand the behavior of the stochastic processes.

First of all, on compact time intervals, the stochastic process belongs with large probability to a tube centered on the deterministic limit:

$$\forall \varepsilon > 0, \forall T > 0, \lim_{n \rightarrow +\infty} \mathbb{P} \left( \rho(Z_{t_\varepsilon}^n, \hat{\xi}) > \varepsilon \right) = 0, \quad (18)$$

where  $\rho$  is for instance the Dudley metric which metrizes the topology of weak convergence on  $\mathcal{M}_F(\tilde{\mathcal{X}})$  (see [75] p79). Heuristically, stochastic and deterministic processes have the same behavior on compact time intervals. In particular, since the deterministic process enters a given  $\varepsilon$ -neighborhood of its nontrivial stationary solution  $\hat{\xi}$  after a sufficiently large time that does not depend on  $n$ , the stochastic process enters an  $2\varepsilon$ -neighborhood with a probability that tends to 1 when  $n$  grows to infinity. However, when  $T \rightarrow +\infty$ , the long time behavior differ.

**Proposition 1.7.** For fixed  $n$ , one has almost sure extinction:

$$\mathbb{P}(\exists t \in \mathbb{R}_+, \langle Z_t^n, 1 \rangle = 0) = 1. \quad (19)$$

Because of the logistic competition, the population stays finite with a size that is controlled and can not grow to infinity (see Proposition 5.6 [83]). The stochastic process finally quits the neighborhood of  $\hat{\xi}$  to drive the population to extinction. We can thus wonder how long the stochastic process stays in the neighborhood of  $\hat{\xi}$ .

An estimate of the time  $\mathcal{T}^n$  that the stochastic process spends in the neighborhood of  $\hat{\xi}$  can be established by large deviation results *à la* Freidlin and Ventzell [36, 23] and generalized to our measure-valued setting (see Section 5.2 [83]).

**Proposition 1.8.**  $\exists \bar{V} > 0, \underline{V} > 0, \forall \delta > 0$ ,

$$\lim_{n \rightarrow +\infty} \mathbb{P}(e^{n(\underline{V}-\delta)} < \mathcal{T}^n < e^{n(\bar{V}+\delta)}) = 1 \quad (20)$$

Of course, when  $n \rightarrow +\infty$ ,  $\mathcal{T}^n$  also tends to infinity in probability and extinction eventually disappears in the limit. As a corollary, for every sequence  $(t_n)_{n \in \mathbb{N}^*}$  such that  $\lim_{n \rightarrow +\infty} t_n e^{-n(\underline{V}-\delta)} = 0$  and  $\lim_{n \rightarrow +\infty} t_n = +\infty$ ,

$$\lim_{n \rightarrow +\infty} \mathbb{P}(\rho(Z_{t_n}^n, \hat{\xi}) > \varepsilon) = 0. \quad (21)$$

Equation (20) is interesting in itself to understand the persistence time of a stochastic finite population but is also useful to separate timescales in models of Adaptive Dynamics, which we now present.

## 1.5 Application to the Adaptive Dynamics theory of Evolution

In the theory of Evolution, mutations are responsible for generating trait diversity in the population while natural selection acting through interactions and competitions determines the traits that are getting fixed. Important questions in evolutionary biology require to include age structure in population models, as was emphasized by Charlesworth [18], Medawar [63] or Stearns [79]. The selective pressure and fixation probability of a trait may be functions of the age at which this trait is expressed, as well as of the age-structure of the population. Reciprocally, the traits that are getting fixed can modify the age-structure of the population.

The frame of Adaptive Dynamics are large population asymptotics and *rare mutations*. They describe the evolution of traits in the population when it is possible to separate the time scales of ecology (birth and death events) and evolution (generation of new traits). For populations with only trait structure, these models have been introduced and studied by Hofbauer and Sigmund [42], Marrow *et al.* [61], Dieckmann and Law [25], Metz *et al.* [67, 28] and Champagnat *et al.* [15, 17, 16].

These studies have been generalized to population with age and trait-structured by Méléard and Tran [65], where equations of Adaptive Dynamics are derived from microscopic models by following [15] and where several examples are studied and illustrated with numerical simulations. When mutations are sufficiently rare, natural selection wipes out the weakest competitors so that the resident population at the next mutation is monomorphic and in a stationary state. The estimates of extinction time provided in Section 1.4 tell us that the mutation should not be *too* rare if we wish to neglect the fact that the population could get extinct before the occurrence of a new mutant. Neglecting the transition periods, it is possible to describe evolution as a jump process by considering only the successive monomorphic equilibria (trait value and corresponding stationary age-structure). If there exists a unique nontrivial stable stationary solution  $\hat{\xi}_x(da) = \hat{n}(x, a)da$ , then it is sufficient to consider the trait-value process that jumps from one equilibrium trait to another. This process, called *trait substitution sequence process for age-structured populations* (TSSPASP), introduced and analyzed in [65], can be described as follows:

- in a monomorphic population of trait  $x$  at equilibrium, mutants are generated with rate

$$p \int_{\mathbb{R}_+} b(x, a) \hat{n}(x, a) da = p \hat{n}(x, 0) = \frac{p \hat{N}_x}{\mathbb{E}(T_x)}$$

where  $\hat{N}_x = \int_0^{+\infty} \hat{n}(x, a) da$  is the size of the population at equilibrium and  $\mathbb{E}(T_x) = \int_0^{+\infty} \exp(-\int_0^a d(x, \alpha, \hat{\xi}_x U(x, \alpha))) d\alpha$  is the expected individual lifespan.

- The probability that the resulting mutant population with trait  $x'$  replaces the resident population with trait  $x$  can not be always explicitly calculated when we deal with populations that are age-structured. However, it can be numerically computed.

Here, the theory of random point processes is necessary to model these events that occur at discrete random times. Evolution models have also been considered from a deterministic point of view, but with different renormalizations that do not describe the same *rare* mutations [26, 12].

When we additionally assume that mutation steps are small, the TSSPASP can be approximated by the solution of an ordinary differential equation that generalizes the *canonical equation* of [25, 14].

Recently, models of population with age structure have been involved in adaptive dynamics studies dealing with functional traits (*e.g.* [30], [24], [71]). The traits  $x(a)$  are then functions of age such as the growth curve, the flowering intensity, the birth or death curves... In [24] or [71], the birth and death rates are functions of the functional trait, but not of age (they take for instance the averaged form  $b(x) = B(\int_0^{+\infty} x(a) da)$ , where  $B \in \mathcal{C}_b(\mathbb{R}, \mathbb{R}_+)$ ).

## 2 Age and trait structures: a large variety of situations (the simulation point of view)

We now present several examples of interesting biological questions involving populations with age and trait structures. Mechanisms are described at the individual level, and we are interested in the resulting macroscopic dynamics. The more realistic and complex the model is, and the more difficult it is to carry the theoretical study to the end. Simulations allow us to go forward in the understanding and in the study of these problems.

### 2.1 Simulation algorithm

Following the algorithms proposed by Fournier and Méléard [35], it is possible to simulate in the exact law of the process  $Z$  (4) without approximation scheme nor grid. The main difficulty comes from the fact that the rates depend on age that changes continuously in time. We use for this acceptance-reject procedures.

Let  $Z_0 \in \mathcal{M}_P(\tilde{\mathcal{X}})$  be an initial condition. We simulate by recursion a succession of birth and death events that modify the size of the population. Let us set  $T_0 = 0$  for the event number 0. Assume that we have already simulated  $k$  events ( $k \in \mathbb{N}$ ), and that the last of these events has occurred at time  $T_k$ . The size of the population  $N_{T_k} = \langle Z_{T_k}, 1 \rangle$  at time  $T_k$  is finite and the global jump rate is upper bounded by  $\bar{b}N_{T_k} + \bar{d}(1 + N_{T_k})N_{T_k}$ , which is finite. To obtain  $T_{k+1}$  for the  $k + 1^{\text{th}}$  event, we simulate candidate events from time  $T_k$ . The latter are given by a sequence  $(\tau_{k,\ell})_{\ell \in \mathbb{N}}$  of possible event times following a Poisson point process with intensity  $\bar{b}N_{T_k} + \bar{d}(1 + N_{T_k})N_{T_k}$ . The first of these times which is accepted by the procedure defines  $T_{k+1}$ .

0. We set  $\tau_{k,0} := T_k$ ,  $N_{\tau_k} := N_{T_k}$  and  $\ell := 0$ .
1. We simulate independent exponential variables  $\varepsilon_{k,\ell}$  with parameter 1 and define  $\tau_{k,\ell+1} = \tau_{k,\ell} + \varepsilon_{k,\ell}/[\bar{b}N_{T_k} + \bar{d}(1 + N_{T_k})N_{T_k}]$ .
2. On the interval  $[\tau_{k,\ell}, \tau_{k,\ell+1}[$ , only aging takes place. For  $i \in \llbracket 1, N_{T_k} \rrbracket$ , the age of individual  $i$  becomes  $A_i(\tau_{k,\ell}) + \tau_{k,\ell+1} - \tau_{k,\ell}$  at time  $\tau_{k,\ell+1}$ .
3. We simulate an integer valued r.v.  $I_{k,\ell}$  uniformly distributed on  $\llbracket 1, N_{T_k} \rrbracket$ , and define the following quantities in  $[0, 1]$ :

$$\begin{aligned} \tilde{m}_1(\tau_{k,\ell+1}, Z_{\tau_{k,\ell+1}-}, I_{k,\ell}) &= \frac{(1-p)b(X_{I_{k,\ell}}(\tau_{k,\ell+1}-), A_{I_{k,\ell}}(\tau_{k,\ell+1}-))}{\bar{b} + \bar{d}(1 + N_{T_k})} \\ \tilde{m}_2(\tau_{k,\ell+1}, Z_{\tau_{k,\ell+1}-}, I_{k,\ell}) &= \tilde{m}_1(\tau_{k,\ell+1}, Z_{\tau_{k,\ell+1}-}, I_{k,\ell}) + \frac{pb(X_{I_{k,\ell}}(\tau_{k,\ell+1}-), A_{I_{k,\ell}}(\tau_{k,\ell+1}-))}{\bar{b} + \bar{d}(1 + N_{T_k})} \\ \tilde{m}_3(\tau_{k,\ell+1}, Z_{\tau_{k,\ell+1}-}, I_{k,\ell}) &= \tilde{m}_2(\tau_{k,\ell+1}, Z_{\tau_{k,\ell+1}-}, I_{k,\ell}) \\ &+ \frac{d(X_{I_{k,\ell}}(\tau_{k,\ell+1}-), A_{I_{k,\ell}}(\tau_{k,\ell+1}-), Z_{\tau_{k,\ell+1}-}, U(X_{I_{k,\ell}}(\tau_{k,\ell+1}-), A_{I_{k,\ell}}(\tau_{k,\ell+1}-)))}{\bar{b} + \bar{d}(1 + N_{T_k})} \end{aligned}$$

4. We simulate a r.v.  $\Theta_{k,\ell}$  with uniform law on  $[0, 1]$ 
  - (a) If  $0 \leq \Theta_{k,\ell} < \tilde{m}_1(\tau_{k,\ell+1}, Z_{\tau_{k,\ell+1}-}, I_{k,\ell})$ , then the  $k + 1^{\text{th}}$  event occurs: Individu  $I_{k,\ell}$  gives birth to a clone with age  $0 \in \mathbb{R}_+$  and one defines  $T_{k+1} = \tau_{k,\ell+1}$ .
  - (b) If  $\tilde{m}_1(\tau_{k,\ell+1}, Z_{\tau_{k,\ell+1}-}, I_{k,\ell}) \leq \Theta_{k,\ell} < \tilde{m}_2(\tau_{k,\ell+1}, Z_{\tau_{k,\ell+1}-}, I_{k,\ell})$ , then Individu  $I_{k,\ell}$  gives birth to a mutant with trait  $x'$  where  $x'$  follows  $k(X_{I_{k,\ell}}(\tau_{k,\ell+1}-), A_{I_{k,\ell}}(\tau_{k,\ell+1}-), x')P(dx')$  and age  $0 \in \mathbb{R}_+$ . One defines  $T_{k+1} = \tau_{k,\ell+1}$ .
  - (c) If  $\tilde{m}_2(\tau_{k,\ell+1}, Z_{\tau_{k,\ell+1}-}, I_{k,\ell}) \leq \Theta_{k,\ell} < \tilde{m}_3(\tau_{k,\ell+1}, Z_{\tau_{k,\ell+1}-}, I_{k,\ell})$ , then Individu  $I_{k,\ell}$  dies and one defines  $T_{k+1} = \tau_{k,\ell+1}$ .
  - (d) If  $\tilde{m}_3(\tau_{k,\ell+1}, Z_{\tau_{k,\ell+1}-}, I_{k,\ell}) \leq \Theta_{k,\ell}$  then nothing happens. We reiterate the algorithm from 1. with  $N_{\tau_{k,\ell+1}} = N_{T_k}$  and  $\ell + 1$  in place of  $\ell$  until we obtain the  $k + 1^{\text{th}}$  event.

**Remark 2.1.** *To each individual are associated three clocks corresponding respectively to birth (with or without mutation) and death events. The event that occurs corresponds to the minimum of these three durations, on the set of whole individuals.*

## 2.2 Examples

Simulations on particular cases are now presented. For each example, simulations have been run several time ; only one particular simulation is presented for each example as an illustration. The programs have been written with the **R** freeware <sup>(2)</sup> and MATLAB.

### 2.2.1 Example 1: Size-dependent competition in an age-structured population

In this example, we are interested in a population with size-dependent competition, and ask how the evolution of body size changes when we take the growth of individuals into account.

Individuals are characterized by their body size at birth  $x_0 \in [0, 4]$  which is the trait that is submitted to hereditary transmission and mutations, and by the physical age  $a \in [0, 2]$ , with aging velocity 1. Body size  $x$  is an increasing function of age:

$$x = x_0 + g a, \quad (22)$$

where  $g$  is the growth rate, which is assumed fixed and identical for all individuals.

An individual of trait  $x_0 \in [0, 4]$  and age  $a \in [0, 2]$  gives birth at rate:

$$b(x_0) = 4 - x_0. \quad (23)$$

This is a simple expression of the standard trade-off between fecundity and offspring size (*e.g.* Stearns [79]). With probability  $p = 0.03$  a mutation occurs and affects  $x_0$ . The new trait is  $x'_0 = \min(\max(0, x_0 + y_{x_0}), 4)$ , where  $y_{x_0}$  is a Gaussian r.v. with expectation 0 and variance 0.01. With probability  $1 - p$ , the offspring is a clone of its parent with the same trait  $x_0$ .

The death rate of an individual with trait  $x_0 \in [0, 4]$  and age  $a \in [0, 2]$  living in a population  $Z \in \mathcal{M}_P([0, 4] \times [0, 2])$  is given by:

$$d(x_0, a, Z) = \int_{\tilde{x}} U(x_0 + g a - x'_0 - g \alpha) Z(dx'_0, d\alpha), \quad (24)$$

$$\text{where } U(x - y) = \frac{2}{300} \left( 1 - \frac{1}{1 + 1.2 \exp(-4(x - y))} \right) \in \left[ 0, \frac{2}{300} \right] \quad (25)$$

is the asymmetric competition kernel introduced by Kisdi [53] that favors larger individuals. The important point is that the sizes  $x$  on which the selection operates are not constant when  $g \neq 0$ , they vary with the age of the individual. Even in a monomorphic population, sizes vary across individuals and the competition exerted on individuals is not uniform.

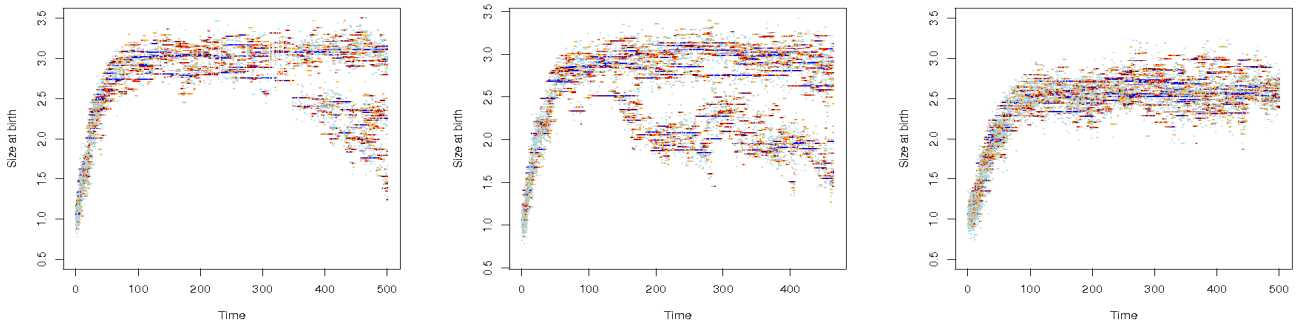


Figure 2: *Trait dynamics (size at birth) in an age-structured population with size-dependent competition. See Example 1 in main text for details. From left to right: (a)  $g = 0$ , (b)  $g = 0.3$ , (c)  $g = 1$*

In the simulations of Figure 2, we choose  $g = 0$ ,  $g = 0.3$  and  $g = 1$ . The population at time  $t = 0$  is monomorphic with trait  $x_0 = 1,06$ , and its size is  $N_0 = 900$  individuals. The initial age distribution is uniform on  $[0, 2]$ , and sizes are computed using (22). For each  $t$  the support of the measure  $\sum_{i=1}^{N_t} \delta_{(x_0)_i}$  is represented.

<sup>2</sup><http://www.r-project.org/>

For  $g = 0$  (constant size during life), we observe a branching phenomenon at the neighborhood of  $t = 300$ . For  $g = 0.3$ , the population separates in two subpopulations ( $x_0 \simeq 2.7$  and  $x_0 \simeq 2$ ) around  $t = 100$ . For  $g = 1$ , this "branching" phenomenon is not observed anymore. When  $g$  takes small values ( $g = 0.3$ ), differences between sizes at birth are lessened since growth acts as a mixing factor: adult individuals with smaller  $x_0$  can compete equally with juvenile individuals with a larger  $x_0$ . Thanks to this, branching may appear more rapidly (at  $t = 100$ ). However, when  $g$  is large, this phenomenon hands over to increased competition as individuals with a bigger size at birth are much more competitive than juveniles individuals with small  $x_0$ . This domination prevents the development of the lower branches observed in Fig. 2(a) and 2(b).

### 2.2.2 Example 2: A population structured into two age-classes

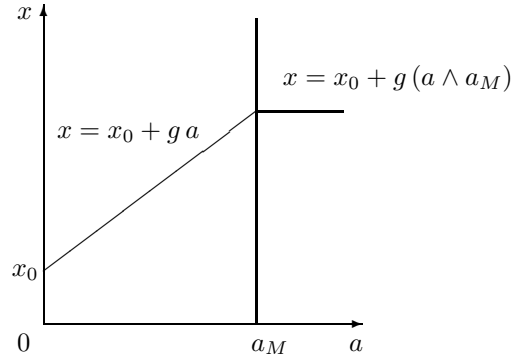
As in Example 1, we consider an age- and trait-structured population where the traits are the size at birth  $x_0 \in [0, 4]$ , the growth rate  $g \in [0, 2]$ , and the age at maturity  $a_M \in [0, 2]$ . The scalar age  $a \in [0, 2]$  (with aging velocity 1) still corresponds to the physical age.

The age at maturity  $a_M$  separates the life history of individuals into two periods: a growth period and a reproduction period. Calsina and Cuadrado [11] also study a population that is structured into two age classes, juveniles and adults. Assuming that the length of the juvenile period is exponentially distributed, they describe population dynamics by a system of two ODEs. They then study the age at maturity from the evolutionary point of view by considering whether a small mutant population can invade the resident population, leading to stability problems of stationary solutions. Ernande *et al.* [30] consider a similar problem: their population is divided into age-classes, and the age at maturity is plastic and determined by a functional reaction norm that is hereditarily transmitted and subject to mutation.

In our model, the size of an individual with trait  $(x_0, g, a_M)$  and age  $a$  is given by:

$$x(a, x_0, g, a_M) = x_0 + g(a \wedge a_M). \quad (26)$$

Before maturity, individuals do not reproduce and invest all their resources into growth. Once the age  $a_M$  has been reached, adult individuals have constant size and begin to reproduce.



The birth rate of an individual with traits  $(x_0, g, a_M) \in [0, 4] \times [0, 2] \times [0, 2]$  is 0 for juvenile individuals and it is a decreasing function of  $x_0$  for adults:

$$b(x_0, a_M, a) = (4 - x_0) \mathbf{1}_{a \geq a_M}. \quad (27)$$

The traits  $x_0$ ,  $g$  and  $a_M$  are hereditarily transmitted and mutations can occur at birth with probability  $p = 0,03$ . Mutated traits are chosen according to:

$$x'_0 = \min(\max(0, x_0 + y_{x_0}), 4) \quad g' = \min(\max(0, g + y_g), 2), \quad a'_M = \min(\max(0, a_M + y_{a_M}), 2),$$

where  $y_{x_0}$ ,  $y_g$  and  $y_{a_M}$  are Gaussian independent r.v. with 0 expectation and variance 0.01.

The death rate of an individual with traits  $(x_0, g, a_M) \in [0, 4] \times [0, 2] \times [0, 2]$  and age  $a \in [0, 2]$  in the population  $Z \in \mathcal{M}_P([0, 4] \times [0, 2] \times [0, 2] \times [0, 2])$  is given by:

$$d(x_0, g, a_M, a, Z) = \begin{cases} d_0 \times g + 10^{-5} \int_{\tilde{\mathcal{X}}} U(x_0 + g a - x'_0 - g'(a' \wedge a'_M)) Z(dx'_0, dg', da'_M, da') & \text{if } a \leq a_M, \\ \int_{\tilde{\mathcal{X}}} U(x_0 + g a_M - x'_0 - g'(a' \wedge a'_M)) Z(dx'_0, dg', da'_M, da') & \text{if } a_M < a \leq 2, \\ +\infty & \text{if } a > 2, \end{cases}$$

where  $U$  is the kernel introduced in (25) and where  $d_0 \geq 0$  measures the hostility of the environment: individuals with high growth rates  $g$  need more resources and incur a survival cost of foraging, hence the density-independent component  $d_0 g$  of their death rate is all the higher that  $d_0$  is important.

As for Example 1, we chose for the initial state is a monomorphic population ( $x_0 = 1.06$ ,  $g = 0.74$  and  $a_M = 0.20$ ) with  $N_0 = 900$  individuals whose ages are uniformly drawn in  $[0, 2]$ .

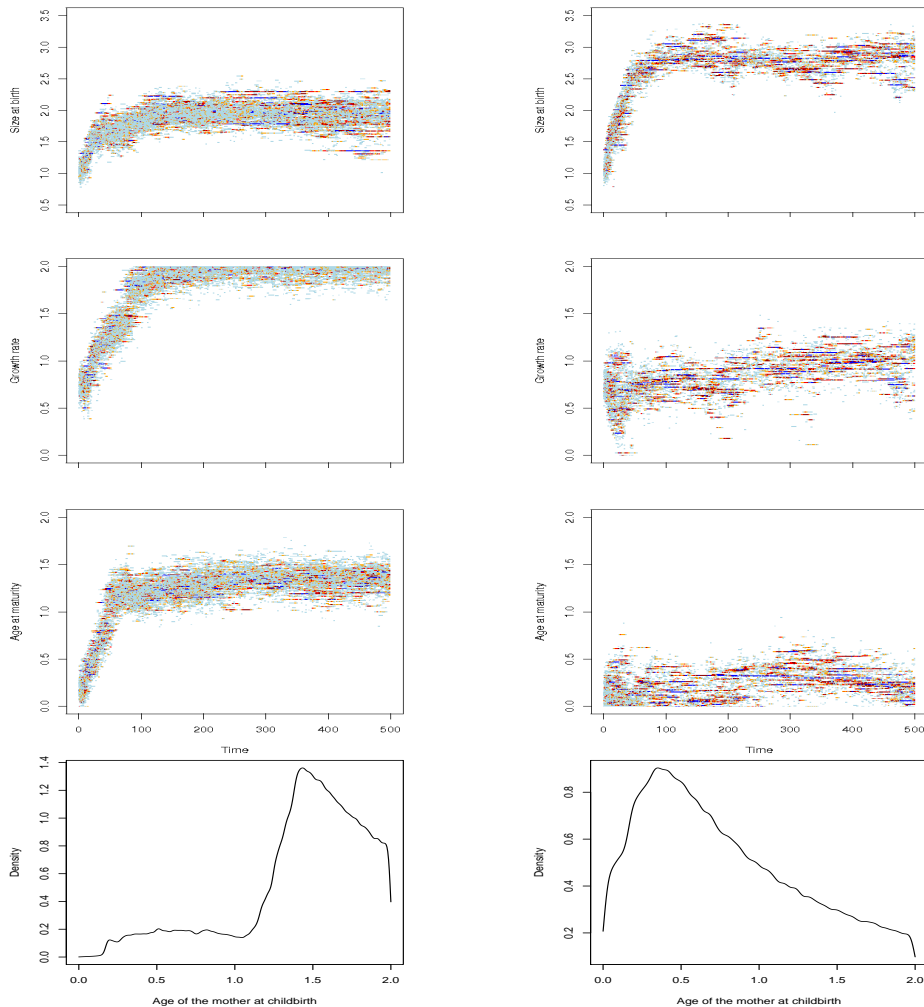


Figure 3: *Dynamics of three co-evolving traits: size at birth, growth rate, age at maturity (rows 1-3), and population structure; distribution of maternal ages at birth (row 4). See Exemple 2 in main text for details.  $d_0 = 3.3 \cdot 10^{-3}$  (left),  $d_0 = 0.5$  (right).*

We first choose  $d_0 = 3.3 \cdot 10^{-3}$ , and then  $d_0 = 0.5$ . Fig. 3 shows that changing  $d_0$  results in two very different dynamics. When  $d_0$  is small, individuals with higher growth rates do not pay much of a cost. The population stabilizes numerically around a state with high growth rate and late maturation. When  $d_0$  is large, a state with moderate growth rate and very early maturation appears.

In Figure 3 (a),  $d_0 = 3.3 \cdot 10^{-3}$  is very small. Individuals with high growth rate  $g$  are little penalized during the juvenile period ( $\forall g \in [0, 2], 0 \leq d_0 g \leq 6.6 \cdot 10^{-3}$ ). Since the death rate during the juvenile period is small (of the order of  $10^{-2}$  for a population of 1000 individuals) compared with the death rate during the adult period (of the order of the unit), and since the competition favors large individuals (the terms  $U(x_0 + ga_M - x)$  describing the competition exerted by an individual with size  $x$  on an adult with size  $x_0 + ga_M$  is minimized when  $x_0 + ga_M$  is large), there is a strong selective advantage to large individuals having high growth rate ( $g \simeq 2$ ) and long growth period ( $a_M \simeq 1.3$ ). We see that it is the competitiveness of an individual in its adult period that is decisive.

When  $d_0 = 0.5$  (Figure 3 (b)), we observe that the growth rate decreases towards 1 and maturity is reached early in life ( $a_M \simeq 0.3$ ). To understand the changes when  $d_0$  increases, let us introduce the probability that an individual of traits  $(x_0, g, a_M)$  born at  $t = c$  survives until age at maturity  $a_M$  in a population  $(Z_t)_{t \in \mathbb{R}_+}$ :

$$\Pi(x_0, g, a_M) = \mathbb{E} \left[ \exp \left( - \int_c^{c+a_M} d(x_0, g, a_M, a, Z_a) da \right) \right]. \quad (28)$$

When the population size is bounded by  $N$ , the probability  $\Pi(x_0, g, a_M)$  can be upper and lower bounded:

$$\exp\left(-a_M\left(d_0g + N \cdot 10^{-5} \frac{2}{300}\right)\right) \leq \Pi(x_0, g, a_M) \leq \exp(-d_0ga_M). \quad (29)$$

In the simulations, we observe that the size of the population remains bounded and that it stabilizes around an "equilibrium" value (600 for  $d_0 = 3.3 \cdot 10^{-3}$  and 200 for  $d_0 = 0.5$ , see Fig. 4). The "equilibrium" traits obtained in the two simulations of Figure 3 are  $(x_0, g, a_M) = (1.8, 2, 1.3)$  and  $(x_0, g, a_M) = (2.6, 0.8, 0.3)$ . The strategy that is observed can hence be naturally explained. For  $d_0 = 0.5$  and  $N = 600$ , we hence obtain  $0.27251 \leq \Pi(1.8, 2, 1.3) \leq 0.27254$ , instead of  $\Pi(1.8, 2, 1.3) \simeq 0.99$  when  $d_0 = 3.3 \cdot 10^{-3}$ , whereas  $0.88690 \leq \Pi(2.6, 0.8, 0.3) \leq 0.88692$ . For  $d_0 = 0.5$ , the traits  $(x_0, g, a_M) = (2.6, 0.8, 0.3)$  are more competitive. They correspond to individual who have a higher probability to reach maturity and reproduce, even if these individuals are likely to be exposed to higher competition pressure than individuals with trait  $(x_0, g, a_M) = (1.8, 2, 1.3)$ .

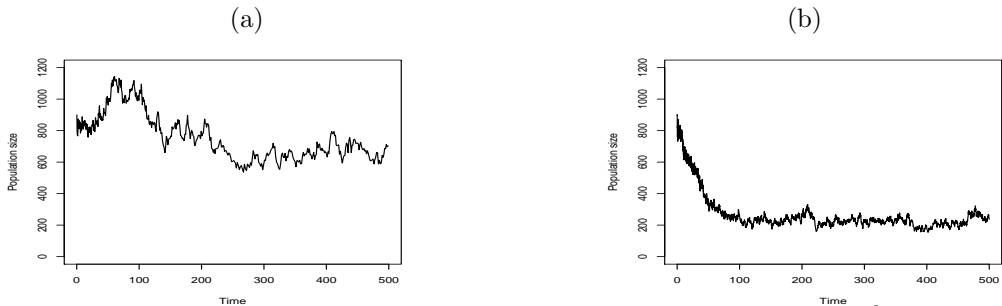


Figure 4: *Population size dynamics. See text for details. (a)  $d_0 = 3.3 \cdot 10^{-3}$ , (b)  $d_0 = 0.5$*

In the case of a favorable environment with abundant resources ( $d_0$  is small), the growth period has a small cost and a long growth phase ( $a_M$  large) allows individuals to reach a *mortality refuge*: *i.e.* a state where they escape the effects of strong competition pressure. When  $d_0$  increases, the mortality refuge becomes inaccessible: long period of initial growth result in low probabilities of survival to the reproduction period. An alternative life profile appears, with early reproduction (small  $a_M$ ) and small individuals. Similar phenomena have been discovered and discussed in Taborsky *et al.* [80].

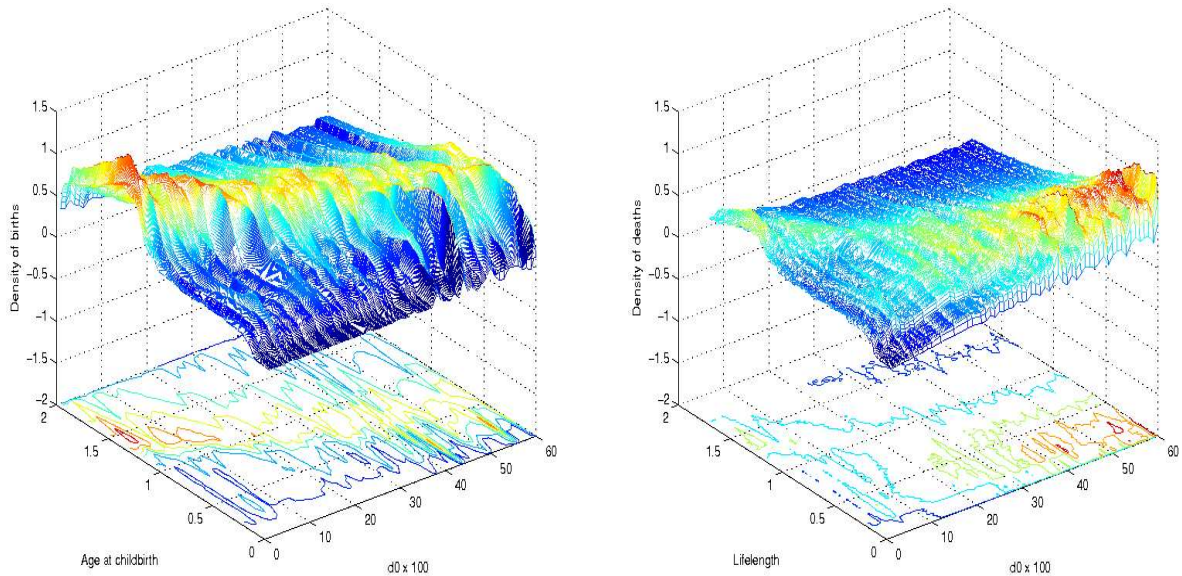


Figure 5: *Long term density of maternal ages at birth (a) and lifespans (b) with respect to the mortality cost of growth,  $d_0$ . See main text for details.*

We now investigate in more detail the transition from the column (a) of Fig. 3 to column (b). In Fig.



5 we let  $d_0$  vary between 0.01 and 0.6. In Figure 5 (a), we have plotted for each value of  $d_0$  the kernel density estimator of the age of mothers at birth times. In Fig. 5 (b), we have done the same for lifespans.

It can be observed that when  $d_0$  increases from 0.01 (favorable environment) to 0.6 (hostile environment), lifespans and ages at reproduction decrease continuously from 1.5 to 0.5. Contrarily to the results of [80], the surfaces that are represented in Fig. 5 do not show abrupt discontinuities. This can be understood as a consequence of the survival probability (28) (and hence the lifespan density) being a continuous function of  $d_0$ .

### 2.2.3 Example 3: competition between age classes

Here, we consider a monomorphic population for which  $(x_0, g, a_M) = (0, 0.90, 3.72)$ ,  $x_0$  being the size at birth,  $g$  the individual growth rate,  $a_M$  the age at maturity. The population is structured by physical age  $a$  and by size:  $\forall a \in [0, 10]$ ,

$$x(x_0, g, a_M, a) = x_0 + g \times a 1_{a \leq a_M} + (g \times a_M + 0.95 g \times (a - a_M)) 1_{a > a_M}. \quad (30)$$

The birth rate is proportional to the size  $x$ :

$$b(x_0, g, a_M, a) = 2x(x_0, g, a_M, a) 1_{a > a_M}. \quad (31)$$

The death rate of an individual  $(x_0, g, a_M)$  with age  $a$  in a population of size  $N$ :

$$d(x_0, g, a_M, a, N) = \begin{cases} 3, 3 \cdot 10^{-3} g N & \text{if } a \leq a_M \\ 1, 6 \cdot 10^{-2} a N & \text{if } a_M < a \leq 10 \\ +\infty & \text{if } a > 10. \end{cases} \quad (32)$$

We assume that growth continues after  $a_M$ , but individuals have to face a trade-off between reproduction and growth. Individuals are subject to logistic competition, with coefficients depending of whether  $a \leq a_M$  or  $a > a_M$ .

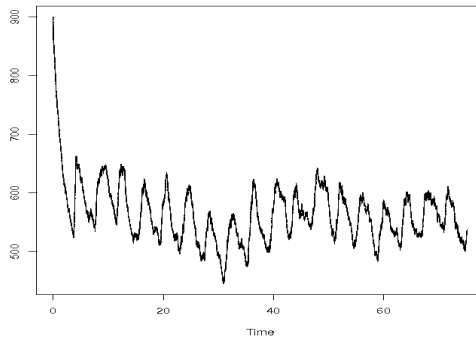


Figure 6: *Sustained oscillations of population size. The population is initiated as monomorphic, with 900 individuals and traits  $(x_0, g, a_M) = (0, 0.90, 3.72)$ . There is no mutation. Competition is size-dependent. Size, birth rate and death rate are given by Eqs. (30)-(32).*

Simulations (Fig. 6) show that the size of the population undergoes sustained oscillations probably driven by deterministic nonlinearities rather than stochastic noise. This phenomenon has been studied for instance by Thieme [81] Chapter 11, Mischler *et al.* [69] or Henson [41] for ODE and PDE models.

Heuristically, the adult population crashes when the size of the population becomes larger than a certain threshold which occurs when the juvenile population becomes too large. The deficit in adults entails a deficit in births resulting subsequently in a small juvenile class. This juvenile class experience less competition during its growth phase, and competition is less severe also in the resulting adult class. As a consequence, the birth rate rises, and the cycle is repeated.

## 3 Conclusion

We have shown here that the PDEs that are used in age-structured population modelling and Demography can be seen as large-populations limits of stochastic particle processes. The latter are often used by

biologists as they allow to describe the population dynamics at the level of individuals and are easy to simulate. We have seen in Section 1.4 that both approaches complement each other. Some phenomena that exist only in finite or random populations, such as almost sure extinction in finite exponentially long time, may disappear in the large population limit. However the study of the deterministic approximation provides useful information about the random process, for example estimates of the time to extinction.

Another benefit from random particle models, that has been elaborated in [19, 4] is that the stochastic process approach suits the formalism of statistical methods which involve sets of individual data. This makes it possible to use the battery of statistical methods which deal with problems that may not always be treated with deterministic methods (such as missing or noisy data). The convergence and fluctuations of Propositions 1.3 and 1.4 would then provide consistence and asymptotic normality for the estimators. Calibrating the parameters of a PDE thanks to its underlying microscopic interpretation provides an alternative to deterministic approaches (*e.g.* [2, 7]).

Introducing age structure is important to take life histories into account. We have seen that age and trait-structures evolve jointly. In some examples, age-structure acts like a refinement (see the examples developed in [65] for instance). In other cases, when the traits imply trade-offs in life-histories strategies for instance, age structure becomes a key ingredient of the model. This makes the mathematical development of age and trait-structured population theory utterly valuable.

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