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An agile modeling framework for population dynamics

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Abstract

In this work, we present an agile modeling framework for structured population dynamics, leading to automated generation of population models' equations. The structure of a population, *i.e.* its separation in strata, according to one or many criteria (such as sex, income, health, geographic area or species if dealing with animal populations), represents a major issue for the precision and richness of population dynamics simulations. The intensity of some phenomena and mechanisms is highly dependent on the involved subpopulation characteristics. This modeling framework can be seen as an extension of the classical McKendrick-von Foerster equation, which embeds the population structure. It allows showing, under appropriate hypothesis, an existence and local uniqueness result for the solution of a transport equation. A modeler has been implemented, to generate models that respect the desired structure hypotheses. We illustrate its abilities on an age-structured predator-prey model, subject to migratory dynamics and to an epidemic, based on a SIRD model.

Keywords: population dynamics, McKendrick equation, structured population models, predator-prey model, model generation, bifurcations

2020 MSC: 92D25, 92-10, 35Q49, 34K20, 92D30, 65P30

Introduction

Modeling and simulating population is a major issue in our modern societies. Forecasting population movements, changes in composition, health evolutions represents a key feature for governments, public institutions or private insurances. In this work, we aim to provide a unified framework for population dynamics modeling and simulation. As age is an important feature, we generalize the classical McKendrick-von Foerster equation, in order to take into account various phenomena in a multi-structured population, such as exchanges between compartments. These are defined as subpopulations sharing common traits. We will rely on this framework to present a modeler, *i.e.* a software able to generate simulable models in a high-level model description language like Modelica. Our goal is to be able to model and simulate any structured population problem. For example, studying the dynamics of a structured Lotka-Volterra model, including aging,

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migration and an epidemic, would be a satisfying objective.

Since the end of the 18th century, modeling a population with discrete or differential equations has been well known and has proved its efficiency in a first approach (Malthus, 1798). But to get a precise simulation, heterogeneity needs to be taken into account, which leads to structured models of population. Such models describe a population as a set of subpopulations, defined with one or several traits (sex or gender, size, age, geographic area...). These traits which may influence natality, growth or mortality rates, as well as interactions between individuals within a compartment or between compartments. The study of structured population aims at analyzing how those traits affect the model dynamics (Magal and Ruan, 2008). Structured population models are highly used in biological mathematics, including the study of cells growth (Arino, 1995) or epidemic dynamics (Mollison, 1995). To model heterogeneity and provide insights on differences between individual, stage-structured models have been developed, sometimes within a non-deterministic point of view (Tuljapurkar et al., 2009). Related works deal with life expectancy through stage and age-structured models (Steiner et al., 2012). Structured populations may also be studied from the genetic point of view (Kumagai and Uyenoyama, 2015; Uyenoyama et al., 2019), but this is not the approach retained in this work.

The McKendrick-von Foerster equation (Murray, 2002) is one of the most fundamental equations of population dynamics. This transport equation describes the evolution in time of an age-structured population, with births, aging and death. This model appeared for the first time in the context of epidemiology (McKendrick, 1925; Kermack and McKendrick, 1927), but its thorough analysis was achieved in a later step (Feller, 1941; Bellman and Cooke, 1963), thanks to methods related to Volterra integral equations and Laplace transformation.

More recently, the introduction of non-linear models breathed new life into age-structured populations study. In Gurtin and Maccamy (1974), using non-linear integral Volterra equations, authors showed the existence, uniqueness and convergence to an equilibrium of solutions to a non-linear Sharpe-Lotka-McKendrick model. This work paved the way to breakthroughs on non-linear models, as much on theoretical developments as on biological applications (see Iannelli (1995) for an exhaustive approach). The growing mathematical complexity of non-linearities in age-structured models led to developments of new tools and methods, such as linear and non-linear operator semigroups in Banach spaces, with a functional analysis approach (Diekmann and Getto, 2005).

Structured population models has been studied in a cumulative formulation (O. Diekmann et al., 1994), which consists in considering various mechanisms (aging, reproduction, death, migration...) separately and adding their contributions, leveraging the superposition principle on linear differential equations. In a such approach, population dynamics can be studied at both individual and population level (i -level and p -level, respectively) (O. Diekmann et al., 1998). At the i -level, a probabilistic point of view prevails, as equations such as the Chapman-Volmgorov involve the probability to reach a state in a given subset of the states space, for an individual at a given state, at a given time. At the p -level, a book-keeping operates to aggregate changes at the i -level.

The renewal of the population, due to reproduction and deaths, is expressed through integral equations that can be related, if one considers age as a transport variable, to McKendrick-like equations.

The branching processes field introduced the terminology of kernel (Jagers, 1989, 1991) to describe an elementary operator which rules a phenomenon's dynamic (*e.g.* the reproduction kernel).

In their works, O. Diekmann, M. Gyllenberg, J.A.J. Metz and H.R. Thieme a strong formal and theoretical framework, enabling to derive mathematical properties from population models (see O. Diekmann et al. (1994, 1998, 2001, 2003)), was built. In this paper, our goal is different and consists in building a formal framework to enable a consistent numerical implementation.

The McKendrick-von Foerster equation is still used in both epidemiology and demography studies (Keyfitz and Keyfitz, 1997). For further reading on transport equations and application to structured population modeling, one should consult (Perthame, 2007).

At Dassault Systèmes, we have been interested in population dynamics simulation for many years. We used an algebraic differential equation (DAE) formalism, representing subpopulations as compartments, relying on the Modelica language (Fritzson and Engelson, 1998), a high-level model description language, and a Modelica solver such as Dymola (D. Brück et al., 2002). Our objective is to develop a population model and simulation that could be adapted and tuned to stakeholder's hypotheses and needs, for instance in terms of structuration, granularity, scale, or scope of the simulation. Unfortunately, editing manually huge Modelica models, in order to change its structuration and behaviour laws, is time-consuming, painful and presents an important error risk. There was a need for a tool able to take as input comprehensive population structuration and demographic phenomena description, and to provide as output an executable file which will then be given to the solver for simulation.

To support such generality, this tool needed a unified framework – a metamodel – able to take into account any population structure and describe any demographic phenomenon. The McKendrick-von Foerster equation turned out to be a remarkable complete metamodel for this objective. It can be instantiated with a DAE model, that is what we did, but also within other paradigms, such as Monte-Carlo or multi-agent simulations.

This article is divided in three sections. In the first section, we present a modeling framework for structured populations, based on an extension of the McKendrick-von Foerster equation. In the second section, we present a model generator developed and implemented to generate structured population models based on the previous formalism. In the last section, we apply this formalism and this model generator to a structured Lotka-Volterra model, and briefly discuss numerical results.

1. Modeling framework

1.1. Extension of McKendrick formalism

1.1.1. The McKendrick-von Foerster equation

The McKendrick-von Foerster equation is a transport equation, highly used in biological and ecological mathematics. It models the evolution in time of an age-structured population undergoing natality and mortality. The specificity of this equation compared to a usual transport equation lies in its boundary condition: the births depend on the whole population. The original McKendrick-von Foerster equation (McKendrick, 1925) is stated as follows:

$$\begin{cases} \partial_t \phi(t, a) + \partial_a \phi(t, a) + \mu(a)\phi(t, a) = 0 & \forall (t, a) \in \mathbb{R}_+^* \times \mathbb{R}_+^*, & (1a) \\ \phi(t, 0) = \int_0^{+\infty} b(a)\phi(t, a) da & \forall t \in \mathbb{R}_+^*, & (1b) \\ \phi(0, a) = \phi_0(a) & \forall a \in \mathbb{R}_+^*, & (1c) \end{cases}$$

where ϕ is the population density, depending on the time t and the age a , μ is the mortality rate, depending on a , b the birth rate, also depending on a . It is generally assumed that b has compact support in \mathbb{R}_+^* , which ensures that $\phi(t, 0)$ can be computed from $\phi(t, a)$ for a in $[a_{\min}, a_{\max}]$ with $0 < a_{\min} < a_{\max}$. (1a)-(1c) can be solved in a closed form thanks to the method of characteristics (see Murray (2002)).

1.1.2. Generalization in a multi-structured context

We aim to generalize this equation in a unified formalism to deal with structured populations, with any structure one can imagine (any number of traits, any number of values of these traits, continuous or discrete traits...). In this way, we consider the following generalized McKendrick equation:

$$\begin{cases} \partial_t \phi(t, a, x) + \partial_a \phi(t, a, x) + K(t, \phi(t), a, x) = 0 & \forall (t, a) \in I \times \mathbb{R}_+, \text{ for a.e. } x \in \mathbb{D}, & (2a) \\ \phi(t, 0, x) = \int_0^{+\infty} \int_{\mathbb{D}} b(t, \phi(t), a, x, y)\phi(t, a, y) dy da & \forall t \in I, \text{ for a.e. } x \in \mathbb{D}, & (2b) \\ \phi(0, a, x) = \phi_0(a, x) & \forall a \in \mathbb{R}_+, \text{ for a.e. } x \in \mathbb{D}, & (2c) \end{cases}$$

where:

- x belongs to a set \mathbb{D} called the *hyperparameters* set; typically, one could have $\mathbb{D} = \prod_{i=1}^N \mathbb{D}_i$ where N is the number of traits¹ and \mathbb{D}_i the set of values of the i^{th} trait.
- I is an interval of \mathbb{R} , of the form $[0, T]$ or $[0, +\infty[$,
- $K : I \times L^1(\mathbb{R}_+ \times \mathbb{D}) \times \mathbb{R}_+ \times \mathbb{D} \rightarrow \mathbb{R}$ is a **global operator**, defined for a.e. (a, x) in $\mathbb{R}_+ \times \mathbb{D}$,

¹excepted age, which is considered separately because it is the transport trait

- $b : I \times L^1(\mathbb{R}_+ \times \mathbb{D}) \times \mathbb{R}_+ \times \mathbb{D} \times \mathbb{D} \rightarrow \mathbb{R}_+$ is the **natality rate function**, also defined for a.e. (a, x) in $\mathbb{R}_+ \times \mathbb{D}$. $b(t, g, a, x, y)$ represents the natality rate at time t , for a population distribution at instant t defined by g , for parents with age a and hyperparameter x giving birth to children with hyperparameter y ,
- ϕ_0 is the **initial population**, belonging to $L^1(\mathbb{R}_+ \times \mathbb{D})$,
- ϕ is the **population**, considered at least in $L^1(I \times \mathbb{R}_+ \times \mathbb{D})$. We will later give a precise meaning of the partial derivatives in (2a)

In (2b) we assume that the natality rate for a parent with (a, x) characteristics giving birth to a newborn with y characteristics may depend on the whole population $\phi(t)$. For example, taking into account resources or influence between different compartments. This is a first step of complexity compared to the original McKendrick boundary condition (1b). But we also assume that this natality rate only depends on the population $\phi(t)$ at instant t , and not on the population evolution history $(\phi(s))_{s \in [0, t]}$. This hypothesis is done for the sake of simplicity and does not seem to be limitative from a modeling point of view, since the natality rate is at first order influenced by real-time factors, such as the economic development, access to education, status of women in society, access to healthcare, and so on. This consideration also applies to global operator K , which may include mortality, geographic migration, evolution of the income level, etc.

1.1.3. Kernel and pointwise operators

As a global operator K , we may consider two subtypes of operators that will be useful for population dynamic modeling: pointwise and kernel operators. The term of *kernel* can be linked to the terminology of Jagers (1989, 1991) and the field of branching processes.

Pointwise operators. A **pointwise operator** describes an incoming or outgoing flow proportional to a subpopulation, whose intensity may vary depending on the characteristics of the subpopulation but also on the global population at time t .

We define it as a mapping $K : I \times L^1(\mathbb{R}_+ \times \mathbb{D}) \times \mathbb{R}_+ \times \mathbb{D} \rightarrow \mathbb{R}$, defined only for a.e. (a, x) in $\mathbb{R}_+ \times \mathbb{D}$, so that for any (t, g) in $I \times L^1(\mathbb{R}_+ \times \mathbb{D})$ and for a.e. (a, x) in $\mathbb{R}_+ \times \mathbb{D}$,

$$K(t, g, a, x) = \mu(t, g, a, x)g(a, x),$$

where $\mu : I \times L^1(\mathbb{R}_+ \times \mathbb{D}) \times \mathbb{R}_+ \times \mathbb{D} \rightarrow \mathbb{R}$ is a **rate** on $\mathbb{R}_+ \times \mathbb{D}$ *i.e.* a mapping defined only for almost every (a, x) in $\mathbb{R}_+ \times \mathbb{D}$; $\mu(t, g, a, x)$ represents the intensity of an incoming or outgoing flow within the (a, x) compartment.

Kernel operators. A **kernel operator** quantifies precisely the transfer flow to a given compartment from other ones. It is defined as a mapping $K : I \times L^1(\mathbb{R}_+ \times \mathbb{D}) \times \mathbb{R}_+ \times \mathbb{D} \rightarrow \mathbb{R}$, defined only for a.e. (a, x) in $\mathbb{R}_+ \times \mathbb{D}$, so that for any (t, g) in $I \times L^1(\mathbb{R}_+ \times \mathbb{D})$ and for a.e. (a, x) in $\mathbb{R}_+ \times \mathbb{D}$,

$$K(t, g, a, x) = \int_{\mathbb{D}} \kappa(t, g, a, x, y) g(a, y) dy,$$

where κ is a **kernel** on $\mathbb{R}_+ \times \mathbb{D}$, *i.e.* a mapping $\kappa : I \times L^1(\mathbb{R}_+ \times \mathbb{D}) \times \mathbb{R}_+ \times \mathbb{D} \times \mathbb{D} \rightarrow \mathbb{R}$ defined only for almost every (a, x, y) in $\mathbb{R}_+ \times \mathbb{D} \times \mathbb{D}$; $\kappa(t, g, a, x, y)$ represents the intensity of an exchange flow² from the (a, y) to the (a, x) state in a population distribution g , at time t . It is assumed that a kernel may model a change of hyperparameter y to x , but does not affect age, which evolves only through the transport term.

1.1.4. Scope of the extended McKendrick formalism

From the two elementary types of operators, it is interesting noting that one can build conservative operators representing an exchange between compartments. Let k be a rate of transfer, defined on $I \times L^1(\mathbb{R}_+ \times \mathbb{D}) \times \mathbb{R}_+ \times \mathbb{D} \times \mathbb{D}$, defined only for almost every $(a, x, y) \in \mathbb{R}_+ \times \mathbb{D} \times \mathbb{D}$. We build the following operator:

$$K(t, g, a, x) = \int_{\mathbb{D}} (k(t, g, a, x, y)g(a, y) - k(t, g, a, y, x)g(a, x)) dy$$

We may see this exchange operator as a combination of a kernel operator with kernel k and a pointwise operator with rate $(t, g, a, x) \mapsto \int_{\mathbb{D}} k(t, g, a, y, x) dy$. As we have

$$\int_{\mathbb{D}} K(t, g, a, x) dx = 0,$$

we recognize a conservative property of such operator; for example, conservation of the total population considering migrations between territories.

There exists a variety of models that can be embedded in the extended McKendrick formalism. Being able to build conservative exchange operators paves the way to model a wide range of behaviours. For example, as we will develop below, the predator-prey model and the Lotka-Volterra equations can be rewritten in this framework, same as epidemic compartmental models (SIR, SIRD, and all their variations...). Modeling economic evolutions in a population, or information propagation, would also be possible within our formalism.

1.2. Existence and local uniqueness

1.2.1. Fixed point formulation

We firstly reformulate (2a)-(2c) with $L^1(\mathbb{D})$ objects, to get closer to (1a)-(1c) formulation:

$$\begin{cases} \partial_t \phi(t, a) + \partial_a \phi(t, a) + K(t, \phi(t), a) = 0 & \forall (t, a) \in I \times \mathbb{R}_+, & (3a) \\ \phi(t, 0) = \int_0^{+\infty} \int_{\mathbb{D}} b(t, \phi(t), a, \cdot, y) \phi(t, a, y) dy da & \forall t \in I, & (3b) \\ \phi(0, a) = \phi_0(a) & \forall a \in \mathbb{R}_+. & (3c) \end{cases}$$

To give a precise meaning to the $\partial_t + \partial_a$ transport operator, even if ϕ is not smooth, we reformulate (3a)-(3c) into a fixed point formulation which will not involve such partial

²see the convention on the order of origin y and destination x hyperparameters

derivative operator, and will be equivalent to (3a)-(3c) if ϕ is smooth enough. This reformulation is based on the characteristics methods (Murray, 2002). We define a mapping f by

$$f : (t, a) \mapsto \phi(t, a + t).$$

for any real a , not necessarily positive, and t in the time interval $[0, T]$. This a will be called **pseudo-age**, as $a + t$ is the real age considered and must be positive. We denote by $\phi(t)$ the mapping $a \mapsto \phi(t, a)$ for any age a . We then have $\phi(t) = f(t, \cdot - t)$ and (3a) rewrites, for fixed real pseudo-age a ,

$$d_t f(t, a) = -K(t, f(t, \cdot - t), a + t).$$

Integrating this equation, distinguishing cases $a > 0$ and $-t \leq a \leq 0$ and taking into account initial and boundary conditions leads to the following integral formulation, for all $t \in [0, T]$ and for a.e. $a \in [-t, +\infty[$,

$$f(t, a) = \begin{cases} \phi_0(a) - \int_0^t K(s, f(s, \cdot - s), a + s) ds & \text{if } a > 0, \\ \int_{|a|}^{+\infty} \int_{\mathbb{D}} b(|a|, f(|a|, \cdot - |a|), \tau, \cdot, y) \left(\phi_0(\tau - |a|, y) - \int_0^{|a|} K(s, f(s, \cdot - s), \tau - |a| + s, y) ds \right) dy d\tau \\ \quad - \int_{|a|}^t K(s, f(s, \cdot - s), a + s) ds & \text{if } -t \leq a \leq 0. \end{cases} \quad (4)$$

This formulation requires less regularity than (3a)-(3c) to be studied, and then may allow less regular solutions. One could think that such integral formulation is making a mountain out of a molehill, as we could study regular solutions of (3a)-(3c), but there is nothing of the sort. It is well known that in a transport problem, the regularity of the initial condition is usually reported to the global solution. In population dynamics, we may imagine violent phenomena such as demographic shocks, wars, pandemics, baby-booms, etc. Such events may be modeled as non-regular initial conditions. This justifies the study of a non-regular formulation of the extended McKendrick equation.

1.2.2. Functional framework

To study (4), we introduce, for a time limit $T > 0$, the following time-pseudo-age space:

$$U_T = \{(t, a) \in [0, T] \times \mathbb{R}, a + t \geq 0\}.$$

We will look for solutions of (4) that will be measurable on U_T , defined everywhere in time³, $L^1(\mathbb{D})$ valued, for which the norm defined by:

$$\|f\|_{\infty, L^1} = \sup_{t \in [0, T]} \int_{-t}^{+\infty} \|f(t, a)\|_{L^1} da$$

³a function f defined on U_T will be said defined everywhere in time if it is defined almost everywhere on U_T , with for any t in $[0, T]$, $f(t, \cdot) : [-t, +\infty[\rightarrow L^1(\mathbb{D})$ is well-defined.

is finite. We will denote $L^{\infty,1}(U_T)$ the Banach space of such functions f with $\|f\|_{\infty,L^1} < +\infty$.

We also define a specific norm on $\mathbb{D} \times \mathbb{D}$:

Definition 1 ($\|\cdot\|_{L^1,L^\infty}$ norm). *Let u be a function defined almost everywhere on $\mathbb{D} \times \mathbb{D}$. We will denote by $\|u\|_{L^1,L^\infty}$ the (potentially infinite) quantity:*

$$\|u\|_{L^1,L^\infty} = \sup_{y \in \mathbb{D}} \operatorname{ess} \int_{\mathbb{D}} |u(x,y)| \, dx = \|y \mapsto \|u(\cdot,y)\|_{L^1}\|_{L^\infty}.$$

We will denote by $(L^1 \times L^\infty)(\mathbb{D} \times \mathbb{D})$ the space of functions u defined almost everywhere on $\mathbb{D} \times \mathbb{D}$ such as $\|u\|_{L^1,L^\infty} < +\infty$.

For $r > 0$ and f_0 in $L^{\infty,1}(U_T)$, we will denote by $\overline{B}(f_0, r)$ the closed ball with center f_0 and radius r in the space $L^{\infty,1}(U_T)$ endowed with $\|\cdot\|_{\infty,L^1}$ norm.

1.2.3. Assumptions on K and b

We will assume the following properties on the global operator K and the natality rate b .

Assumptions on the global operator K . We assume that:

- (a) K is **integrable** on \mathbb{R}_+ , in the sense that

$$\forall (t, g) \in I \times L^1(\mathbb{R}_+ \times \mathbb{D}), \quad K(t, g) \in L^1(\mathbb{R}_+ \times \mathbb{D}). \quad (5)$$

- (b) K is **locally semi-lipschitz**, in the sense that for any t_0 in I and g_0 in $L^1(\mathbb{R}_+ \times \mathbb{D})$ there exists V_0 a neighborhood of (t_0, g_0) inside $I \times L^1(\mathbb{R}_+ \times \mathbb{D})$, and $c_0 \geq 0$, such that for any (t, g_1) and (t, g_2) in V_0 ,

$$\|K(t, g_1) - K(t, g_2)\|_{L^1} \leq c_0 \|g_1 - g_2\|_{L^1}. \quad (6)$$

- (c) K is **bounded on every compact**, in the sense that for any compact subset V of $L^1(\mathbb{R}_+ \times \mathbb{D})$, there exists $M_{K,V} \geq 0$, such that for any (t, g) in V

$$\|K(t, g)\|_{L^1} \leq M_{K,V}. \quad (7)$$

Assumptions on the natality rate b . We assume that:

- (a) b is L^1, L^∞ -**integrable**, in the sense that

$$\forall (t, g, a) \in I \times L^1(\mathbb{R}_+ \times \mathbb{D}) \times \mathbb{R}_+, \quad b(t, g, a) \in (L^1 \times L^\infty)(\mathbb{D} \times \mathbb{D}) \quad (8)$$

- (b) b has **uniform compact support** in age a . More precisely, there exists $0 < a_{\min} < a_{\max}$ such that for any t in I and f in $L^1(\mathbb{R}_+, L^1(\mathbb{D}))$, the support of $b(t, f)$ is included in $[a_{\min}, a_{\max}]$.

(c) b is **essentially uniformly L^1, L^∞ -bounded**, in the sense that for any t in I and g in $L^1(\mathbb{R}_+ \times \mathbb{D})$,

$$b(t, g) \in L^\infty(\mathbb{R}_+, (L^1 \times L^\infty)(\mathbb{D} \times \mathbb{D})), \quad (9)$$

where $\|b(t, g)\|_{L^\infty} = \sup_{a \in \mathbb{R}_+} \text{ess} \|b(t, g, a)\|_{L^1, L^\infty}$.

(d) b is **locally semi-lipschitz**, in the sense that for any t_0 in I and g_0 in $L^1(\mathbb{R}_+ \times \mathbb{D})$, there exists V_1 a neighborhood of (t_0, g_0) inside $I \times L^1(\mathbb{R}_+ \times \mathbb{D})$, there exists $c_1 \geq 0$, such that for any $(t, g_1), (t, g_2)$ in V_1 ,

$$\|b(t, g_1) - b(t, g_2)\|_{L^\infty} \leq c_1 \|g_1 - g_2\|_{L^1}. \quad (10)$$

(e) b is **uniformly L^∞ -bounded**, in the sense that there exists $B > 0$ such that

$$\forall (t, g) \in I \times L^1(\mathbb{R}_+ \times \mathbb{D}), \text{ for a.e. } a \in \mathbb{R}_+, \quad \|b(t, g, a)\|_{L^\infty} \leq B. \quad (11)$$

1.2.4. Existence and local uniqueness

Under the previous assumptions, we prove the following result.

Theorem 1 (Existence and local uniqueness for extended McKendrick equation with integral formulation). *Let ϕ_0 be an initial condition in $(L^1 \cap L^\infty)(\mathbb{R}_+, L^1(\mathbb{D}))$, K a global operator satisfying assumptions (5)-(7), and b a natality rate function satisfying (8)-(11). There exists $T > 0$ and $r > 0$ such that if we define f_0 on U_T by $f_0(t, a) = \phi_0(a+t)$, then f_0 is in $L^{\infty,1}(U_T)$ and there exists a unique f in $\bar{B}(f_0, r)$ solution of (4).*

Proof sketch. The proof is inspired by the proof of Cauchy-Lipschitz theorem (see Teschl (2012, p.47)), using the Banach fixed-point theorem (see Agarwal et al. (2018)). We denote by $F(f)$ the mapping between (t, a) and the right member of (4). We define F for f on a closed ball $\bar{B}(f_0, r)$ centered on f_0 , with radius r judiciously chosen later, using hypotheses on K and b locally semi-Lipschitz character. We firstly prove that F is well-defined and that $F(f)$ is in $\bar{B}(f_0, r)$ for f in $\bar{B}(f_0, r)$.

For the well-definition, we show that

$$\int_{-t}^{+\infty} \|F(f)(t, a)\|_{L^1} da \leq (BT + 1) \left(\|\phi_0\|_{L^1} + (c_0 \|f - f_0\|_{\infty, L^1} + M_0) T \right)$$

where T is chosen small enough, c_0 is given by (6) on a neighborhood of $(0, \phi_0)$ and M_0 is given by (7) on $[0, r_0] \times \{\phi_0\}$, where r_0 is the radius of an open ball centered on $(0, \phi_0)$ included in a such neighborhood.

To show the stability of $\bar{B}(f_0, r)$ by F , we firstly show that

$$\|F(f) - f_0\|_{\infty, L^1} \leq \frac{T(B\|\phi_0\|_{L^1} + \|\phi_0\|_{L^\infty}) + T(c_0 r + M_0) + \varepsilon_0}{1 - BT}$$

where ε_0 is chosen as $\frac{r_0}{4}$. We suppose that r and T are chosen such that

$$\frac{(B\|\phi_0\|_{L^1} + \|\phi_0\|_{L^\infty} + M_0)T + \varepsilon_0}{1 - (B + c_0)T} \leq r,$$

which gives

$$\|F(f) - f_0\|_{\infty, L^1} \leq r.$$

Thus, $\overline{B}(f_0, r)$ is stable by F .

We then show that F is contractant on $\overline{B}(f_0, r)$. More precisely, we show that for f and g in $\overline{B}(f_0, r)$,

$$\|F(f) - F(g)\|_{\infty, L^1} \leq \left((c_0 + c_1 \|\phi_0\|_{L^1})T + (Bc_0 + c_1(c_0r + M_0)) \frac{T^2}{2} \right) \|f - g\|_{\infty, L^1},$$

where c_1 is given by (10) on a neighborhood of $(0, \phi_0)$. We suppose that r and T are chosen such that

$$(c_0 + c_1 \|\phi_0\|_{L^1})T + (Bc_0 + c_1(c_0r + M_0)) \frac{T^2}{2} < 1.$$

Thus, $\overline{B}(f_0, r)$ is stable by F and F is contractant on $\overline{B}(f_0, r)$. Applying the fixed-point Banach theorem, there exists a unique fixed-point of F in $\overline{B}(f_0, r)$, which is solution of (4) for t in $[0, T]$ and almost everywhere in a . \square

2. Model generator

2.1. Motivation

When studying structured population dynamics, our goal was to take into account population structuration to reach a more precise model. For example, because of cultural reasons, the mortality rate may vary according to the geographical area considered, other things being equal. When modeling an epidemic, factors such as age, gender, cultural framework or educational level influence the probability to be infected. It is still possible to model populations and interactions as homogenous blocs, but the results would be rough, and the conclusions would not be applicable. This justifies the interest for structured population models.

Building and simulating a model is usually made of several steps. The modeling itself consists in specifying a set of choices on formalism, hypothesis scopes which states are defined in our model, and how the individual parameters influence transitions between these states. This abstract model is then transcribed into a formal model, for example a set of UML diagrams, which may itself give an executable model written in a modeling or programming language.

A modeling language such as Modelica (Fritzson and Engelson, 1998) enables users to describe a model as a list of algebraic-differential equations, without the need to go through translation and simulation steps, where the model description is transformed into numerical results through the execution of powerful solvers. Thus, users do not need to handle discretization and integration of the ordinary differential equations, approximate resolutions of algebraics equations, and all the numerical issues that such topics arise. The only input required by the solver is the model description.

However, writing a model description for large population models, with lots of structuration criteria and values, is less easy than meets the eye. Avoiding errors (syntax,

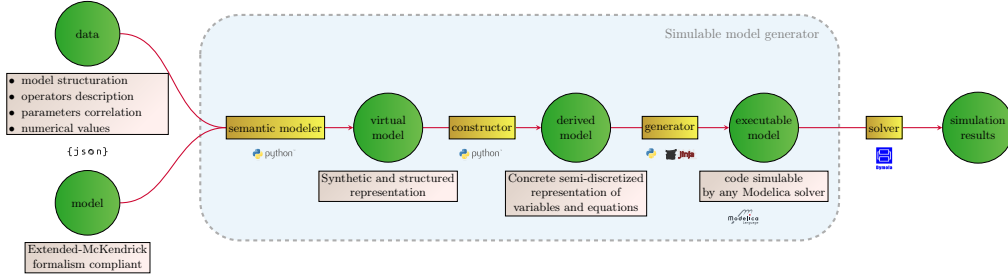


Figure 1: Model generator’s working principle

consistency between equations, model completeness) is tricky. Enhancing a model description which is already written is painful, time-consuming, and this work is not easily reusable when one wants to multiply modifications.

Here the need of a model generating tool arises. This tool must be able to take as input a textual and comprehensive description of a population dynamics model. It will use it to generate model description written in the Modelica language. Then, to change the structuration hypothesis, for instance, one only has to change the textual input and give it to the generator, which will rewrite the whole model description corresponding to the new modeling choices.

A model generating tool could be helpful when choosing discretization schemes for the numerical simulation of the model. Indeed, if we decide to use only an ODE or DAE formulation for the model, we have to apply to (2a)-(2c) a semi-discretization for the age partial derivative. For example, with an upwind finite difference scheme, it would write:

$$d_t \phi_i(t, z) + \frac{\phi_i(t, z) - \phi_{i-1}(t, z)}{\Delta a} + K(t, \phi_i(t), a_i, z) = 0$$

with i the number of the age class considered. But the choice of scheme can be seen as arbitrary, and one could want to change the age discretization scheme without having to rewrite the whole model. A tool that separates the model and the input data from the numerical scheme could offer a such feature.

2.2. Methods

Our model generator’s working principle is illustrated in Figure 1. The program is written in the Python language.

An example model. To illustrate how the generator enables to create a Modelica model from simple user input, let us take a dummy example of a population, age-discretized in five age groups, living in a territory divided in three zones A , B , C . People are born, get old and die of old age only. The natality rate can depend on age, but not on zone. They may change the zone during their life, through migration whose intensity depends on age and on attractivity of each zone, which can be arbitrarily fixed for illustration purpose. For example, the graph represented on Figure 2 represents the connectivity between zones A , B and C in our dummy model. The numerical parameters for the intensity of these flows are chosen arbitrarily and vary with the age class.

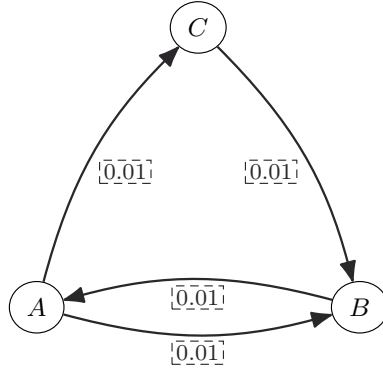


Figure 2: Chosen migration dynamics for the dummy model. The indicated numerical values are nominal values which vary according to age.

```
{
  "zone": ["A", "B", "C"]
}
```

Listing (1) Population structuration file, except age (JSON)

```
{
  "population": {
    "max": 100,
    "steps": 5
  }
}
```

Listing (2) Age structuration file (JSON)

Figure 3: Structuration input files for the dummy model. The value of "max" in "population" means that the age of an individual is truncated at 100 years.

2.2.1. Input data

We write as input a textual description of the model, embedding the model structuration, the description of various operators used in the model, the correlation between various parameters (for example, there is a correlation of many traits between parents and their newborn, such as geographic area, income level, etc.), and the numerical values such as natality or mortality rates, initial distribution of traits in the population.

This information is gathered in a set of JSON files, to facilitate the treatment by the generator.

Population structuration. As illustrated on Figure 3, we write in a first file (Listing 1) the structuration of population as a set of criteria and values⁴. The age structure will be written in a second file (Listing 2), because age plays a particular role in the equations derived from the McKendrick extended model. One may also consider many population components, with no exchange between them (such as in a predator-prey model). Then the structuration of each population component will be written in separate files.

⁴In the dummy model, there is only one criterion (zone) with three values (A , B and C).

Evolution operators. The input data files also include the description of operators, *i.e.* what is hidden behind the global operator evolution K . For example, in our dummy model, we have mortality as a pointwise operator, migration as an exchange operator, a combination of a kernel and of a pointwise operator, and natality which also has a special role in our metamodel. As shown in Listing 3, we store the names of such phenomena in front of keys describing the type of operator. These key names ("pointwise", "exchange", "boundary") refer to various operator classes implemented in the model generator. The values refer to the specific operator names given in the model.

```
{
  "pointwise": "mortality",
  "exchange" : "migration",
  "boundary" : "natality"
}
```

Listing 3: Operator description file for the dummy model

An exchange operator, such as migration, needs to be given a connectivity graph to know which values are connected to each other. We store this information in a separate JSON file (Listing 4). The convention adopted is that keys represent destination compartments, and the associated values or lists of values represent origin compartments where the population flow may come from.

```
{
  "trait" : "zone",
  "graph" : {
    "A": ["B"],
    "B": ["A", "C"],
    "C": ["A"]
  }
}
```

Listing 4: Connectivity graph file for migrations in the dummy model, immediately derived from the graph on Figure 2

Behavior laws for non-linear operators. A population dynamics model is usually way more complex than our dummy model. Some relationships between subpopulations may be non-linear. For example, in an epidemic model, the amount of newly infected people depends on the product between sensible and infected people. Such relationships are written in a separate file, in a mathematical textual input using natural symbols, or functions defined in another file. Such files are parsed to capture the non-linear relationships and then translate it in the executable code.

Numerical parameters. Finally, we need to feed our model generator with the numerical values of structured parameters. For example, with our age and zone structured model, we need a natality values file with the natality rate of each age group, in each geographic zone (Listing 5). The amount of values needed may explode when the number of structuration criteria increases, thus one may use a script to generate such values as a

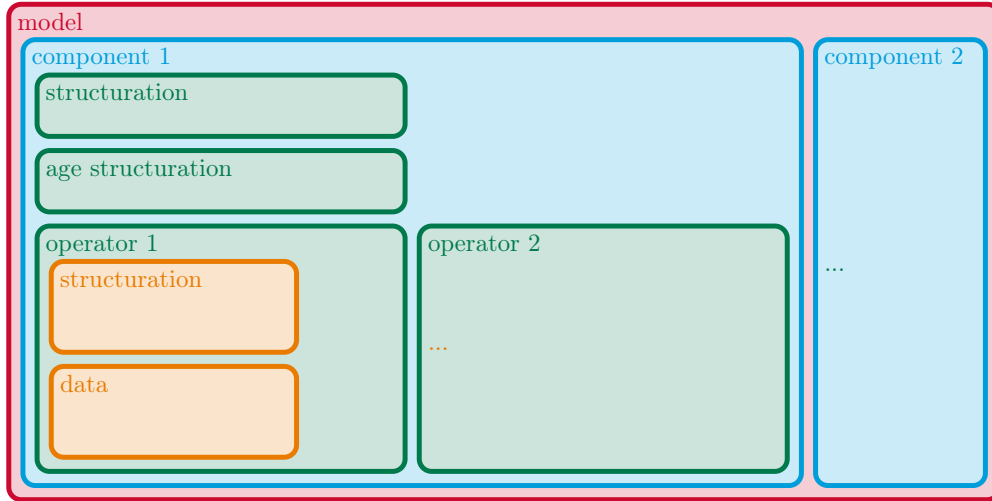


Figure 4: Structure of a virtual model

combination of statistical data on a population. The initial condition is also given with a such format.

```
[
  {"A": 0.004, "B": 0.004, "C": 0.004},
  {"A": 0.077, "B": 0.077, "C": 0.077},
  {"A": 0.003, "B": 0.003, "C": 0.003},
  ...
]
```

Listing 5: Numerical values of natality (excerpt)

2.2.2. From input data to virtual model: the semantic modeler

The first step in our model generator is to take the input data and put it together within a single Python object. This virtual model (see Figure 4) will have a treelike structure, composed of one or several components which represent separated populations, which may interact but without exchanging people.

Each component includes operators as instances of the operator class of the same name. Each operator including structuration information, behaviour laws or diagrams if necessary and numerical values. The choices of a strongly typed implementation and an oriented-object development were guided by the will to provide semantics on input data. For example, to call an **appropriate** generation method for each type of operator (pointwise, kernel, natality), in terms of equation generations, we needed to develop specific methods for each type. The virtual model given to the constructor embeds this meaning to ensure that every piece of the input data will be treated correctly.

```

<model.operator.pointwiseOperator.LinearAgePointwiseOperator>
name: mortality
structuration: zone : ['A', 'B', 'C']
ageStructuration: max : 100, steps : 5
data: mortality_data

```

Listing 6: A mortality operator in the virtual model

The Listing 6 shows how a mortality operator is represented in the virtual model. In the dummy model, the mortality operator is a linear age-structured pointwise operator. Non-linear operators have also been implemented. The structuration for all criteria except age is represented in the `structuration` attribute. For some operators, such as exchange operators, user will need to specify the criteria susceptible to change between source and destination, and the unchanged ones. The `ageStructuration` attribute carries information about the maximal age considered (here, 100 years old) and the number of age groups considered (5 in our example). The `data` attribute refers to an instance of the `Data` class, in which the mortality rates are available. This instance is built from numerical parameters given as input data.

A virtual model can have as many operators as necessary, each operator describing only one phenomenon undergone by the population. The tree-like structure enables to always have, for the children nodes of an operator, all the information necessary to provide the next steps of the simulable model generation.

2.2.3. From virtual to derived model: the constructor

The second step is to transform our virtual model into a concrete representation of our variables and equations. This step prepares the generation of Modelica code, as it reproduces in an object-oriented programming context the structure and the objects of Modelica: a list of variable declarations, and a list of equations involving the declared variables.

The primitive objects are typed to reproduce Modelica's typing. The structure of the derived model's equation is strongly linked to the extended McKendrick formalism.

In Figure 5-Figure 6, we show parts of the derived model we get from our dummy model. The list of the variables involved in the model is stored as reference (Listing 7) The `population` variable is implemented as a multi-dimensionnal array, in order to handle multi-structuration. Listing 8 corresponds to the main loop of the age semi-discretization :

$$d_t \phi_i(t, z) + \frac{\phi_i(t, z) - \phi_{i-1}(t, z)}{\Delta a} + K(t, \phi_i(t), a_i, z) = 0 \quad (12)$$

where z is the zone considered, and i the number of age group. This age semi-discretization has been performed through an upwind finite difference method, but any other numeric scheme could be used here. There is a strong isomorphism between (12) and Listing 8, knowing that Δa is here represented by the parameter `dAge`, in a context of uniform subdivision of the age interval.

K will be the sum of K_μ and K_z operators, respectively standing for mortality and migration flows.

The equation in Listing 9 refers to the description of a mortality operator equation, as a pointwise operator:

$$K_\mu(t, \phi(t), a_i, z) = \mu(t, a_i, z) \phi_i(t, z)$$


```

variables :
population, populationOperator, mortality, natality, migration
parameters: dPopulationAge

```

Listing (7) List of variables of the derived model

```

+
|-- Real der(population[populationAge]) = Real[zone] zeros(3)
|-- /
| | |-- -
| | | |-- Real[zone] population[populationAge]
| | | `-- Real[zone] population[populationAge-1]
| | | `-- parameter Real dpopulationAge = 20.0
|-- Real[zone] populationOperator[populationAge]

```

Listing (8) Derived equation from McKendrick equation semi-discretization

Figure 5: Variables and main equation for the derived dummy model

The equation in Listing 10 refers to the description of a natality operator equation, with a sum over all age components represented by `+_age`. The natality variable on the left-hand side is used for the equation of the youngest age group :

$$\phi(t, 0, z) = \sum_{i=1}^N b(t, a_i, z) \phi_i(t, z).$$

Finally, the equation in Listing 11 refers to the description of a migration operator equation. The `oldZone` attributes corresponds to the origin zone, and the `zone` one refers to the destination. The list of terms considered in such equation is given by the connectivity graph (Listing 4), to avoid writing unexisting flows between compartments. A such equation would be written as:

$$\begin{aligned} K_z(t, \phi(t), a_i, z = A) = & -\kappa_z(t, a_i, B \rightarrow A) \phi_i(t, z = B) \\ & + \kappa_z(t, a_i, A \rightarrow B) \phi_i(t, z = A) \\ & + \kappa_z(t, a_i, A \rightarrow C) \phi_i(t, z = A) \end{aligned}$$

The sign of terms in the right-hand side corresponds to whether the term in an incoming or outgoing migration flow.

2.2.4. From derived model to executable model: the generator

The last step consists in generating a Modelica code simulable by any Modelica solver such as OpenModelica (P. Fritzson et al., 2020) or Dymola (D. Brück et al., 2002). To do so, we used a templating approach using the Python library Jinja2 (Ronacher, 2014) to convert the derived model into a Modelica code file. The power of the templating approach is to iterate inside the template while rendering it, to write each equation needed, and keep the derived model synthetic. The Figure 7 shows an excerpt from a Jinja template used to generate a part of the model, and the corresponding generated model.

```

Real mortality[age][zone=A] = .*
    |-- parameter Real mortality[age][zone=A]
    `-- Real population[age][zone=A]

```

Listing (9)

```

Real natality[zone=A] = +_age
    |-- *
    |-- parameter Real natality[age][zone=A]
    `-- Real population[age][zone=A]

```

Listing (10)

```

variables :
population, populationKernel, dpopulationAge, mortality, natality, migration
statements :
+
    = Real[zone] zeros(3)
|-- +
|   |-- Real der(population[populationAge])
|   |-- /
|   |   |-- -
|   |   |   |-- Real[zone] population[populationAge]
|   |   |   |-- Real[zone] population[populationAge-1]
|   |   |   |-- parameter Real dpopulationAge = 20.0
|   |   |-- parameter Real dpopulationAge = 20.0
|   |-- Real[zone] populationKernel[populationAge]
...
Real mortality[populationAge][zone=A] = .*
    |-- parameter Real mortality[populationAge][zone=A]
    `-- Real population[populationAge][zone=A]
...
Real natality[zone=A] = +_populationAge
    |-- *
    |-- parameter Real natality[populationAge][zone=A]
    `-- Real population[populationAge][zone=A]
...
Real migration[populationAge][zone=A] = +
    |-- Real -migration[populationAge][zone=A, oldZone=B]
    |-- .*population[populationAge][zone=B]
    |-- .*
    |-- parameter Real migration[populationAge][
zone=B, oldZone=A]
    |-- `-- Real population[populationAge][zone=A]
    |-- .*
    |-- parameter Real migration[populationAge][
zone=C, oldZone=A]
    |-- `-- Real population[populationAge][zone=A]

```

Listing (11)

Figure 6: Equations describing operators of mortality, natality and migration for the dummy model (excerpts)

```

equation
{% for component in rep.components %}

    // {{component.name}}

    // McKendrick equation and evolution operator decomposition
    {% for statement in component.statements %}
    {{statement.to_modelica()}} ;
    {% endfor %}

    // {{component.name}} kernels

    {% for kernel in component.kernels %}
    // {{kernel.name}}
        {% for equation in kernel.statements %}
        {{equation.to_modelica()}} ;
        {% endfor %}
    {% endfor %}

{% endblock %}

```

Listing 12: Excerpt from the Jinja template

```

equation
// population
// McKendrick equation and evolution operator decomposition
der(population[1]) + (population[1]-natality)/dAge + populationKernel[1] = zeros(3) ;
for age in 2:4 loop
    der(population[age]) + (population[age]-population[age-1])/dAge + populationKernel[
age] = zeros(3) ;
end for ;
der(population[5])-population[4]/dAge + populationKernel[5] = zeros(3) ;
populationKernel = mortality + migration ;
// population kernels
// mortality
mortality[1:5, 1] = mortality1[1:5].*population[1:5, 1] ;
mortality[1:5, 2] = mortality2[1:5].*population[1:5, 2] ;
mortality[1:5, 3] = mortality3[1:5].*population[1:5, 3] ;
// natality
natality[1] = sum((natality1[age]*population[age, 1]) for age in 1:5) ;
natality[2] = sum((natality2[age]*population[age, 2]) for age in 1:5) ;
natality[3] = sum((natality3[age]*population[age, 3]) for age in 1:5) ;
// migration
migration[1:5, 1] = (-migration12[1:5].*population[1:5, 2]) + migration21[1:5].*
population[1:5, 1] + migration31[1:5].*population[1:5, 1] ;
migration[1:5, 2] = migration12[1:5].*population[1:5, 2] - migration21[1:5].*population
[1:5, 1] - migration23[1:5].*population[1:5, 3] ;
migration[1:5, 3] = migration23[1:5].*population[1:5, 3] - migration31[1:5].*population
[1:5, 1] ;

```

Listing 13: Modelica code generated rendering the template

Figure 7: From Jinja template to generated Modelica code

2.3. Summary

We developed and implemented a model generator to handle generation of executable models conforming to our extended-McKendrick formalism. These models are written using the Modelica language, from synthetic inputs that can be manually written using the JSON language, respecting a set of rules that have been documented. We tackled the issue of writing structured models, with a number of variables and equations that may explode as the structuration is refined and gets more and more complex. Our model generator handles ODE and PDE formalisms, and generates as output models written in Modelica, but its structure is robust enough to consider developments with other formalisms and other modeling or programming languages.

For now, the input data interface is not very user-friendly. JSON files have many advantages – they are light, parsing libraries already exist in almost every programming language, and the standard is complete enough to store any type of data we would need. This format of input data is acceptable for research uses, as it enables a synthetic representation of a population dynamic model. But is not suitable for various modeling purposes, which need a simpler and more ergonomic interface to indicate the structure of the model and equations. For this reason, we plan to implement a UML/SysML interface between the user and the model generator input. This interface should be user-friendly, for example with drag-and-dropping boxes to represent the steps of a population process (for example in education, economics or health fields).

3. Application to a structured Lotka-Volterra model

3.1. Introduction and model description

The Lotka-Volterra model has been widely studied by mathematicians (Wangersky, 1978). Its goal is to model a predator-prey dynamics within an ecosystem, where there may be a competition for resources and an asymmetric role played by preys and predators. This model is well known by the mathematical community. For this reason, we found interesting taking it as a toy model to show how our modeling framework may apply and what interesting results can emerge from the introduction of structuration thanks to the extended McKendrick formalism.

3.1.1. The original Lotka-Volterra model

To begin with, let us recall the original Lotka-Volterra equations:

$$\begin{cases} d_t X(t) &= \alpha X(t) - \beta Y(t)X(t) \\ d_t Y(t) &= \delta X(t)Y(t) - \gamma Y(t) \end{cases} \quad (13)$$

where X (resp. Y) is the number of preys (resp. predators), α is the prey natality rate, only due to intrinsic reproduction, β is the prey mortality rate, due to predation, δ is the predator natality rate, due to predation, and γ is the predator mortality rate, only from natural origin.

For the sake of completeness, we remind the classical shapes of time-evolution and phase portrait for the usual predator-prey model (Figure 8).

3.1.2. Structuration of prey and predator populations

To illustrate our modeling framework and the model generator's abilities, we decide to give to our populations of preys and predators a structuration according to many criteria.

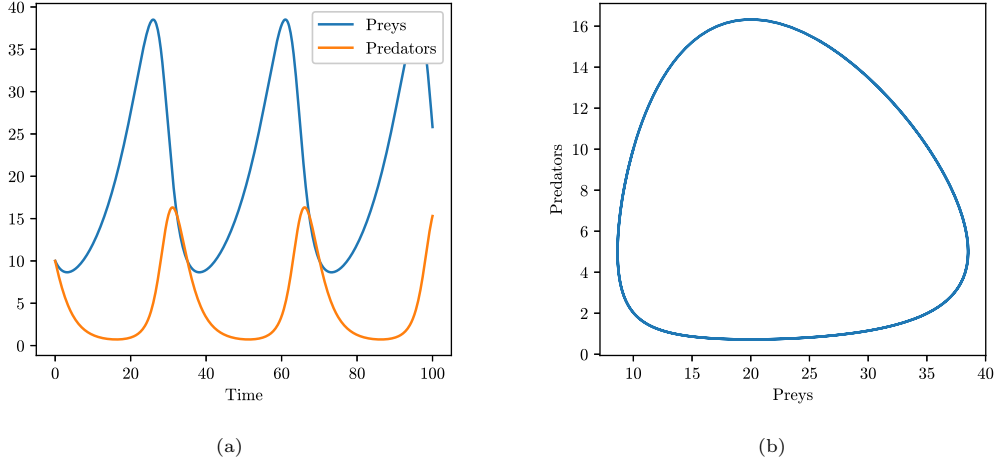


Figure 8: Time evolution (a) and phase portrait (b) of the classic predator-prey model

Species structuration. We will separate preys and predators in **components** (see Figure 4), as they will not necessarily have the same structuration and no population exchange will happen between these populations. The prey (resp. predator) component will be denoted by ϕ_X (resp. ϕ_Y).

Age structuration. Both populations will be age structured, to take into account the aging process. The time derivatives in (13) will be replaced by transport operator $\partial_t + \partial_a$.

Territory structuration and migrations. We suppose that the land where our preys and predators are living is divided into four zones, numbered from 1 to 4. We do arbitrary hypotheses on connectivity between zones and numerical parameters representing the proportion of each zone population which will move to another zone – see Figure 9. The values indicate a nominal exchange rate, which is then linearly modulated according to the age and eventually the health status of individuals.

Epidemic structuration. For illustration purpose, we decide to assume that the prey population is affected by an epidemic, according to a SIRD model (Kermack and McKendrick, 1927). Susceptible (S) individuals, once infected, move to the compartment of infected (I) individuals, which may recover (R) from their disease or die (D). This simple model does not take into account reinfection (no transition from R to S or I) nor other mortality factors than the infection, such as natural mortality due to aging. The equations of this model are given by (14). The compartments are illustrated on Figure 10.

$$\begin{cases} d_t S &= -kIS \\ d_t I &= kIS - (\lambda + \nu)I \\ d_t R &= \lambda I \\ d_t D &= \nu I \end{cases} \quad (14)$$

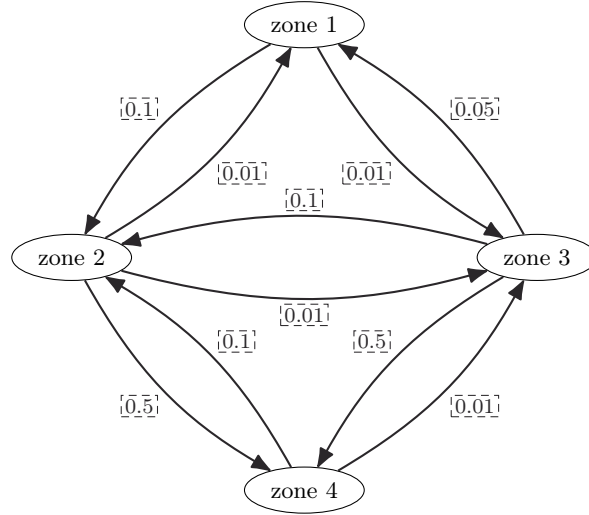


Figure 9: Chosen migration dynamics for the structured Lotka-Volterra model

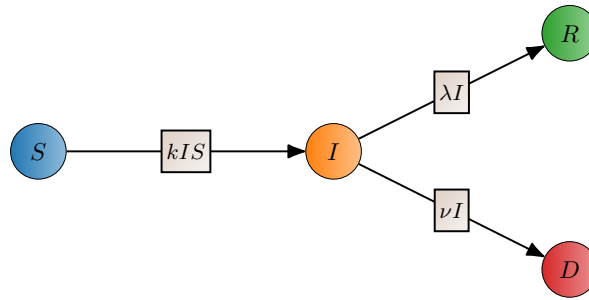


Figure 10: SIRD epidemic model

k represents the infectivity rate, λ the recovering rate, and ν the letality rate.

The goal is to include each of these structuration criteria and the behaviour laws governing these phenomena, as they are, for now, isolated from each other, within a unique population dynamics model, to describe a structured predator-prey model. The modeling framework developed around the extended McKendrick formalism will tackle this issue.

3.2. Rewriting the problem to conform to the extended McKendrick framework

3.2.1. Extended-McKendrick equations

As explained above, the population variable ϕ will be split into two separated components ϕ_X and ϕ_Y . What follows will still conform to the McKendrick formulation (3a)-(3b), as we may consider ϕ as a couple (ϕ_X, ϕ_Y) and study both equations separately. The hyperparameters set will be, for preys, $\mathbb{D}_X = \llbracket 1, 4 \rrbracket \times \{S, I, R, D\}$, and for

predators, $\mathbb{D}_Y = \llbracket 1, 4 \rrbracket$. As \mathbb{D}_X and \mathbb{D}_Y are finite sets, the integrals $\int_{\mathbb{D}} dx$ will be replaced by discrete summations on elements of \mathbb{D}_X or \mathbb{D}_Y , for example $\sum_{z=1}^4 \sum_{s \in \{S, I, R, D\}}$ for preys. We assumed that an individual whose parents were in zone z at birth is born in zone z . We get the following equations:

$$\begin{cases} \partial_t \phi_X(t, a, z, s) + \partial_a \phi_X(t, a, z, s) + K_X(t, \phi(t), a, z, s) = 0 & \forall (t, a, (z, s)) \in I \times \mathbb{R}_+ \times \mathbb{D}_X, & (15a) \\ \phi_X(t, 0, z, s) = \int_0^{+\infty} \sum_{\bar{s} \in \{S, I, R, D\}} b_X(t, \phi(t), a, z, s) \phi_X(t, a, z, s) da & \forall (t, (z, s)) \in I \times \mathbb{D}_X, & (15b) \\ \phi_X(0, a, z, s) = \phi_{0, X}(a, z, s) & \forall (a, (z, s)) \in \mathbb{R}_+ \times \mathbb{D}_X. & (15c) \end{cases}$$

$$\begin{cases} \partial_t \phi_Y(t, a, z) + \partial_a \phi_Y(t, a, z) + K_Y(t, \phi(t), a, z) = 0 & \forall (t, z) \in I \times \mathbb{R}_+ \times \mathbb{D}_Y, & (16a) \\ \phi_Y(t, 0, z) = \int_0^{+\infty} b_Y(t, \phi(t), a, z) \phi_Y(t, a, z) da & \forall (t, z) \in I \times \mathbb{D}_Y, & (16b) \\ \phi_Y(0, a, z) = \phi_{0, Y}(a, z) & \forall (a, z) \in \mathbb{R}_+ \times \mathbb{D}_Y. & (16c) \end{cases}$$

3.2.2. Global operators

For each species, we decompose the global operators K_X and K_Y as a sum of operators corresponding to each phenomenon, except for natality which is handled in the boundary condition. For preys, we take into account a $K_{X,m}$ operator for migrations, a $K_{X,\mu}$ operator for mortality, and a $K_{X,s}$ operator for epidemic. For predators, we only take into account a $K_{Y,m}$ operator for migrations and a $K_{Y,\mu}$ operator for mortality.

$$\begin{cases} K_X &= K_{X,m} + K_{X,\mu} + K_{X,s}, \\ K_Y &= K_{Y,m} + K_{Y,\mu}. \end{cases}$$

Migration. Let us denote by m_{ij} the migration flow intensity from zone i to zone j , as introduced in Figure 9. The migration operator can be written as

$$K_{X,m}(t, \phi(t), a, i, s) = \sum_{j=1}^4 (m_{ij} \phi_X(t, a, i, s) - m_{ji} \phi_X(t, a, j, s))$$

for preys and similarly as

$$K_{Y,m}(t, \phi(t), a, i) = \sum_{j=1}^4 (m_{ij} \phi_Y(t, a, i) - m_{ji} \phi_Y(t, a, j))$$

for predators. We observe that each operator does not depend on the other species, and that age and health are supposed not to change when an individual migrates, as this change can be considered as instant. Such exchange operators can be rewritten as the sum of a kernel and of a pointwise operator. For example, for predators, we may write

$$K_{Y,m}(t, \phi(t), a, i) = \left(\sum_{j=1}^4 m_{ij} \right) \phi_Y(t, a, i) - \sum_{j=1}^4 m_{ji} \phi_Y(t, a, j)$$

where $\sum_{j=1}^4 m_{ij}$ is the rate of the pointwise operator representing the emigration flow from zone i , and m_{ji} is the value of the (discrete) kernel of the kernel operator representing the immigration flow from zone j to zone i .

Mortality. The mortality operators $K_{X,\mu}$ and $K_{Y,\mu}$ will typically be defined as pointwise operators, according to the following expressions issued from mortality terms in (13):

$$K_{X,\mu}(t, \phi(t), a, z, s) = \left(\int_0^{+\infty} \beta(\tilde{a}, z) \phi_Y(t, \tilde{a}, z) d\tilde{a} \right) \phi_X(t, a, z, s),$$

$$K_{Y,\mu}(t, \phi(t), a, z) = \gamma(a, z) \phi_Y(a, z).$$

The non-dependance of β and γ on t is purely a modeling choice.

Epidemic status evolution. The SIRD equations are rewritten in the McKendrick formalism, using pointwise and kernel operators, resulting in a sum on health statuses.

The sign is reversed in (17a)-(17d) because the global operator K_X is on the left side of the extended McKendrick equation (15a).

$$\left\{ \begin{array}{l} K_{X,s}(t, \phi(t), a, z, S) = \left(\int_0^{+\infty} k(a, \tilde{a}) \phi_X(t, \tilde{a}, z, I) d\tilde{a} \right) \phi_X(t, a, z, S) \quad (17a) \\ K_{X,s}(t, \phi(t), a, z, I) = - \left(\int_0^{+\infty} k(a, \tilde{a}) \phi_X(t, \tilde{a}, z, I) d\tilde{a} \right) \phi_X(t, a, z, S) + (\lambda(a) + \nu(a)) \phi_X(t, a, z, I) \quad (17b) \\ K_{X,s}(t, \phi(t), a, z, R) = -\lambda(a) \phi_X(t, a, z, I) \quad (17c) \\ K_{X,s}(t, \phi(t), a, z, D) = -\nu(a) \phi_X(t, a, z, I) \quad (17d) \end{array} \right.$$

In (17a) the flow of susceptible people is represented as a pointwise operator, with a rate expressed as a continuous sum over ages of infected people a susceptible individual could meet. $k(a, \tilde{a})$ is the infectiosity between infected people at age \tilde{a} and susceptible people at age a . In (17b) the flow of infected people is the sum of a two terms. The first one is a kernel operator representing the incoming infection flow due to contacts between susceptible and infected people, same as in (17a) but with opposite sign. The second one is a pointwise operator representing the outgoing flows of infected people who recover, with recovery rate $\lambda(a)$, or die, with letality $\nu(a)$. The equations (17c) and (17d) are kernel operators for incoming flows of recovered or died infected people.

Behind such equations, many modeling hypotheses have been done. For example, infectiosity, recovery rate and letality do not depend on time t , nor on geographic zone z . We observe that in kernel operators, kernel can be very sparse, because the incoming flow may come from a very restricted sample of compartments. In (17c)-(17d), the incoming flow comes only from the infected compartment of the same zone, resulting in a very sparse kernel.

3.2.3. Natality

Let us develop the natality rates behind b_X and b_Y in (15b) and (16b).

Prey natality rate. We suppose that the prey natality rate is constant over time, dependent on the age a of the parent, and independent of the global population state $\phi(t)$ and of the zone of birth z . It may depend on the epidemic status s , as infected individuals may be less fertile, and individuals who died from the epidemic cannot reproduce. There exists a mapping α such as

$$b_X(t, \phi(t), a, z, s) = \alpha(a, s)$$

Predator mortality rate. The formulation of the predator natality rate needs taking into account the non-linearity of the dependance on prey populations. We will then have

$$b_Y(t, \phi(t), a, z) = \int_0^{+\infty} \sum_{s \in \{S, I, R, D\}} \delta(a, \tilde{a}, z, s) \phi_X(t, \tilde{a}, z, s) d\tilde{a}. \quad (18)$$

(18) expresses the contribution of preys of any age \tilde{a} and epidemic status s , in the fixed and common zone z , to the natality rate of predator with age a . This is the typical case where the global population state $\phi(t)$ at instant t is necessary to compute the natality rate, through the prey population $\phi_X(t)$ specified in an age \tilde{a} and a hyperparameter (z, s) .

3.3. Numerical results

The following results aim to show the diversity of behaviours one can encounter in a structured population dynamics model, and the difficulty in forecasting a dynamic system's asymptotic behaviour. We base this statement on three numerical studies on structured Lotka-Volterra models. The first model consists in a set of 400 variables and equations, representing preys and predators with 20 age classes on each species, 4 zones, and 4 health statuses for preys. In the second model we removed the epidemic aspect, took 30 age classes and kept geographical structuration parameters same. The model results in 240 variables and equations. In the third model, we did not consider any structuration beyond the number of species, so that we only had 4 homogeneous species and then, 4 variables and equations.

These three examples illustrate how one may numerically grasp the notion of bifurcation in structured population models. Not only epidemic but also predation parameters, and even age discretization can generate bifurcations. Such bifurcations can be easily located and visualized using a model generator.

The models generated can be found as supplementary material (Online Resources 1, 2, 3).

3.3.1. When epidemic switches asymptotic behaviours

In the usual predator-prey model studied by Lotka and Volterra, solutions are known to be periodic (Lotka, 1925). Adding spatial structuration and migration between zones can change the type of asymptotic behaviour of the aggregated variables (the total amount of preys, and the total amount of predators) and present convergence to a fixed point. An epidemic could act as a perturbation of the system and preserve the fixed point convergence behaviour. Surprisingly, it has been observed through numerical investigations that for a precise parameter set of natality and mortality for preys and predators,

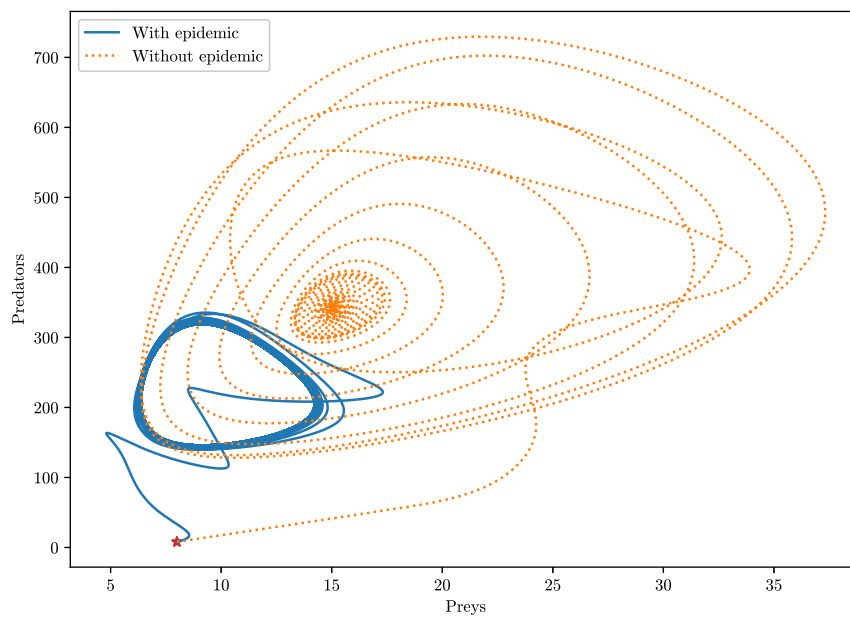


Figure 11: Predator-prey phase portrait. The presence of an epidemic has changed the asymptotic behavior from convergence to periodicity.

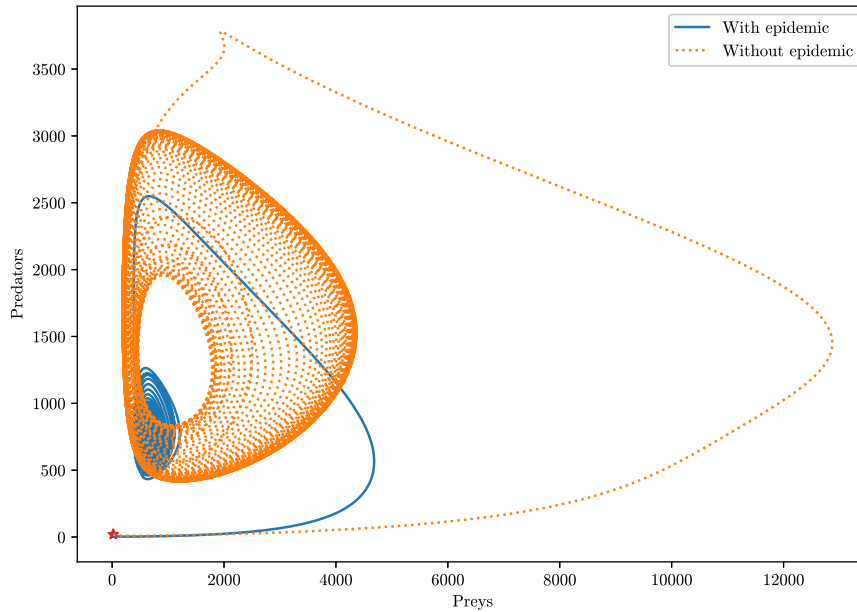


Figure 12: Predator-prey phase portrait. The presence of an epidemic has changed the asymptotic behavior from periodicity to convergence.

the presence of an epidemic could asymptotically make the system periodic again (see Figure 11).

For others demographic parameters, we observed that the populations, in a no-epidemic scenario, adopted a periodic trajectory, whereas the presence of an epidemic changed the behaviour to convergence to a fixed point (see Figure 12).

Two statements may be inferred from these examples, which are not isolated. Firstly, it is very difficult to forecast the future of a structured population. Many counter-intuitive phenomena can occur, and some parameters can have unexpected influence on the shapes of solutions. In our examples, we showed how demographic parameters affect both the asymptotic behaviour of the population without the epidemic and the influence of the epidemic on this behaviour. Secondly, the power of a model generator approach is enlightened, with the ability to build structured models over and over again until we find the appropriate structure and the appropriate parameters to study precise behaviours.

3.3.2. Simultaneous existence of stable cycles

Stability of fixed point and limit cycles is major in dynamic systems. It is well known that a dynamical system may have stable and unstable equilibrium points. The stability can be determined by studying the sign of real parts of the jacobian's eigenvalues at the equilibrium point. Equilibrium points partition the space of initial conditions into basins of attractions. Two stable equilibrium points may exist simultaneously, and the limit of

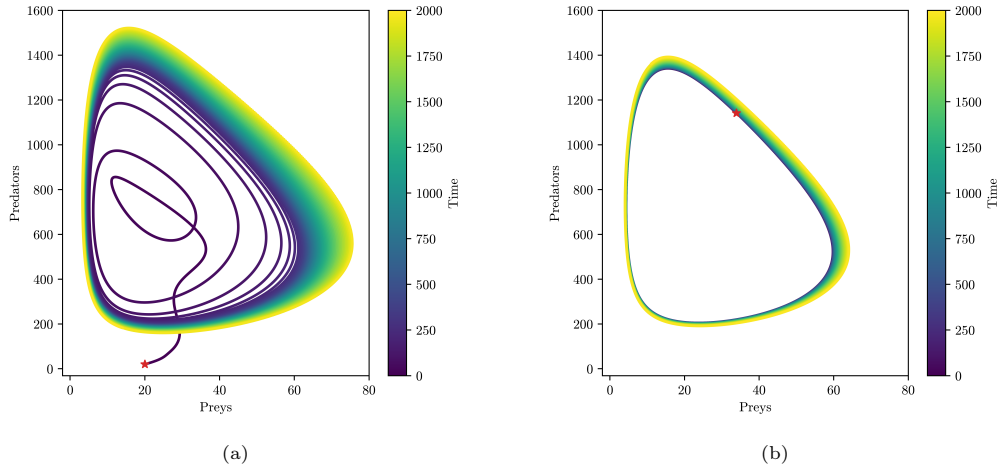


Figure 13: Phase portraits of predator-prey models with different initial conditions (a) and (b). The initial condition has been marked with a red star. The demographic parameters are unchanged between the two simulations.

the system will be determined according to which basin of attraction the initial condition belongs to.

We observed in our structured predator-prey models an interesting, similar phenomenon on stable cycles. The epidemic feature has been removed from the model for the sake of simplicity. The demographic parameters remained the same, and by changing the initial condition, we observed that the system winds around a different cycle Figure 13.

3.3.3. Time evolution by zone

Thanks to the model generator, one may plot a detailed evolution of populations over time, selecting one or many criteria. For example, in a prey-predator model without epidemic dynamic, for some choice of parameters and initial condition, we can visualize the evolution by species and by zone (see Figure 14). Both predation dynamic and territorial exchange influence the evolution of the populations. Such a structured model can provide insights about the detailed evolution and repartition of subpopulations, something that a homogeneous model could not achieve.

3.3.4. Chaotic behaviour

Finally, we highlight a chaotic behaviour the predator-prey model may present if one gives it a few complexification. For example, we consider an ecosystem with no structuration, neither on age nor on geographic zones, but with two prey species (rabbits x_1 and squirrels x_2) and two predator species (foxes y_1 and wolves y_2) living together. The equations of a such system are the following :

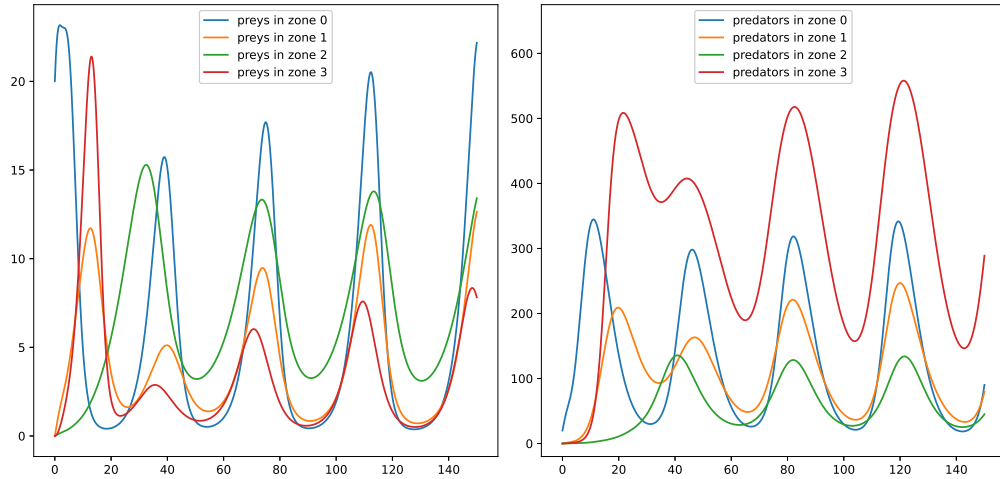


Figure 14: Time evolution by zone for rabbits and foxes in a prey-predator model

$$\begin{cases} d_t x_1(t) &= \alpha_1 x_1(t) - \beta_{11} x_1(t) y_1(t) - \beta_{12} x_1(t) y_2(t) \\ d_t x_2(t) &= \alpha_2 x_2(t) - \beta_{21} x_2(t) y_1(t) - \beta_{22} x_2(t) y_2(t) \\ d_t y_1(t) &= \delta_{11} x_1(t) y_1(t) + \delta_{12} x_2(t) y_1(t) - \gamma_1 y_1(t) \\ d_t y_2(t) &= \delta_{21} x_1(t) y_2(t) + \delta_{22} x_2(t) y_2(t) - \gamma_2 y_2(t) \end{cases}$$

where α_i , β_{ij} , δ_{ij} and γ_i , for $i, j = 1, 2$, are natality and mortality parameters, defined similarly as in the classic Lotka-Volterra model.

The appearance of chaos in such a simple model may be highlighted through the plot of a bifurcation diagram (Figure 15a). We let vary parameters in given ranges, and for each value, plotted intersection points of an orbit of (3.3.4) with a chosen hyperplane of \mathbb{R}^4 . One may distinguish parameter ranges of chaotic behavior, where intersection points (here their projection on the y_1 axis) spreaded on a large range of values, from periodic behavior, where intersection points form regular lines.

For $\lambda \approx 0.8$, we observe a phenomenon that needs explanations. Two periodic attractors coexist, and the initial condition switches from an attraction basin to the other. On Figure 15b, we plotted an example of a Poincaré map. The intersection points with the same hyperplane, for a chosen set of parameters, were plotted and colored by order of intersection. The various ramifications observed in this figure indicate a fractal nature that we can relate to usual chaotic systems (see Szemplińska-Stupnicka (2003)).

Discussion

The developed model generator is able to generate models conforming to a modeling framework introduced to systematically embed any population dynamics related problem with a stock-flow approach. The modularity of its implementation makes seamless changing the numerical scheme used to discretize our equations. As we mentioned in subsection 2.3, an objective would be to implement a user-friendlier interface to input

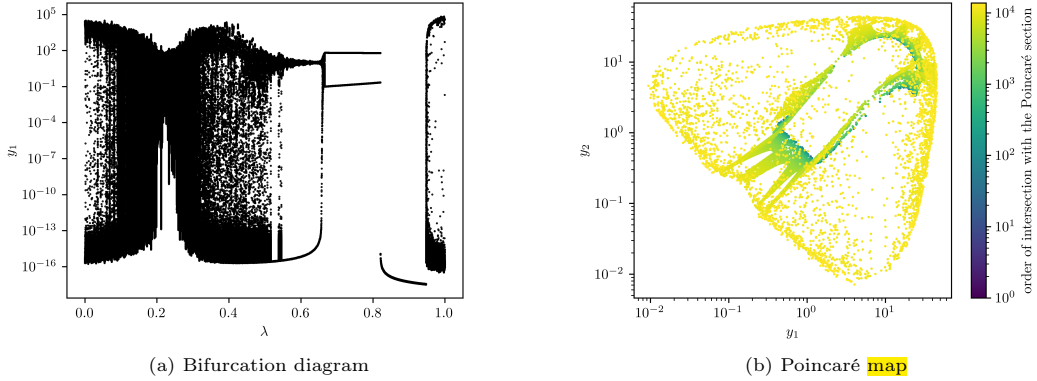


Figure 15: Illustration of chaos in a two preys-two predators system. The bifurcation diagram (Figure 15a) has been plotted with a λ parameter varying from 0 to 1 to explore a chosen line segment in the \mathbb{R}^{12} parameter space, between the following parameter values for $(\alpha_1, \alpha_2, \beta_{11}, \beta_{12}, \beta_{21}, \beta_{22}, \gamma_{11}, \gamma_{12}, \gamma_{21}, \gamma_{22})$: $(0.5, 0.533, 0.666, 0.03, 0.033, 0.066, 0.046, 0.023, 0.02, 0.046)$ and $(0.5, 0.483, 0.042, 0.045, 0.458, 0.042, 0.029, 0.041, 0.035, 0.029, 5.1, 5.1)$. The Poincaré section (Figure 15b) has been chosen for $\lambda \simeq 0.208$.

model descriptions into the generator, for example using the SysML modeling language. Using a model generator like the one presentend could be enlightening for convergence studies on age-structured models. One could generate models with a chosen number of age classes and observe the influence of this choice over the numerical results. It could also be used to put to the test numerical studies on age-structured models, to ensure the number of age classes do not influence the results.

Another limit is of technical nature. Simulating large models written in Modelica is tough. When tackling the issue of modeling a complete population, with many levels of structuration, one can easily reach the amount of 100 000 variables and equations to describe a such model. Generating it does not present any problem, but simulating it through Modelica solvers, as we tried with the one embedded in the Dymola software, may present crippling computation durations. This is a major obstacle to the calibration of these models, as calibration needs hundreds of simulation runs to converge to an optimal distribution of parameters.

Concerning the numerical results presented in subsection 3.3, the structured Lotka-Volterra model, which as been built, simulated and studied, is a toy model. It aims to demonstrate our model generator's abilities and how complex behaviours may emerge from a structured model. Our goal is not to forecast how prey and predator populations would evolve in an ecosystem if the structure was precisely taken into account. Thus, the model was not calibrated using field data, and many numerical values of parameters in it were chosen arbitrarily, for demonstration purposes. This toy model has been considered to illustrate our modeler abilities, and we may easily make it more complete and more complex by refining the modeling, taking into account new phenomena, etc. Again, this refinement would be helped by the large scope of our modeling framework.

The epidemiologic model could be refined, by differentiating predation coefficients for infected preys, or by integrating a transmission of the disease to predators. The goal with

Lotka-Volterra and SIRD models was to show how usual population dynamics models can be naturally embedded in our framework.

Future work

We plan several in-depth studies to carry on these works. As mentioned before, a SysML interface for the model generator input is planned for implementation; this will increase the efficiency in building new models and imagining new scenarios. We also plan to enhance the model generator to build and simulate models in various modeling paradigms, such as multi-agent system, stochastic simulation, and even build hybrid models mixing such paradigms on different scales.

Deepen the structured Lotka-Volterra model analysis could be of major interest, and deeply relatable with recent works (Lu et al., 2017; Bentout et al., 2022; Zhang and Liu, 2021), for example by studying and understanding the influence of an age structure on the modeling of predation between individuals. The stability study in a structured Lotka-Volterra model could be part of this analysis, to better understand the coexistence of stable cycles and the bifurcation phenomena observed when switching on and off the epidemic operator.

Conclusion

In this work, we developed an agile population modeling framework based on an extension of the well-known McKendrick equation, which tackles the introduction of structure in population models. This framework has proven to be sufficiently wide to embed complex structured models and many classical problems in population dynamics that can be easily coupled together (such as predator-prey and epidemiologic models). Here is the main interest of our approach. It can be relatively easily extended to other population or biological model, for example working on size structure in cell division models (see Perthame (2007); Michel (2006)).

We showed that the variety of phenomena usually considered can be reduced to two types of operators, called pointwise and kernel operators. The theorem of local existence and uniqueness is based on a fixed-point argument, inspired by the proof of Cauchy-Lipschitz theorem. We implemented a model generator in Python language, in order to generate various models easily and focus on the simulation results instead of writing the model code manually. We illustrated the power of this approach on a structured predator-prey model, with age structuration, territorial dynamics and an epidemic through an SIRD model. The introduction of structure in such model reveals a variety of behaviours, in terms of asymptotic behaviour, stability and appearance of chaos.

Supplementary information

We provide as supplementary materials the models generated to explore numerical behaviors on predator-prey structured models. These Modelica files contain the full description of these three models, including the numerical parameters used for demonstration purpose. More precisely, `supplementary_material_1.mo` refers to the model used in subsection 3.3.1, `supplementary_material_2.mo` refers to the model used in

subsubsection 3.3.2, and `supplementary_material_3.mo` refers to the model used in subsubsection 3.3.4.

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- The authors certify that they do not have any conflict of interest.
- The authors have no financial or non-financial interests to disclose.
- The authors provide their full consent for publication.
- Data and models availability: as supplementary material.

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