Centrum voor Wiskunde en Informatica

REPORT*RAPPORT*

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M.A. Kirkilionis, O. Diekmann, B. Lisser, M. Nool, A.M. de Roos, B.P. Sommeijer

Modelling, Analysis and Simulation (MAS)

MAS-R9714 May 31, 1997

Report MAS-R9714
ISSN 1386-3703

CWI
P.O. Box 94079
1090 GB Amsterdam
The Netherlands

Numerical Continuation of Equilibria of Physiologically Structured Population Models. I. Theory

Markus Kirkilionis*†, Odo Diekmann†,
Bert Lisser*, Margreet Nool*,
André M. de Roos‡, Ben Sommeijer*

* *CWI,*
P.O. Box 94079, 1090 GB Amsterdam, The Netherlands
† *RUU (University of Utrecht),*
Faculty of Mathematics, P.O Box 80010, 3508 TA Utrecht, The Netherlands
‡ *UvA (University of Amsterdam),*
Faculty of Biology, Kruislaan 320, 1098 SM Amsterdam, The Netherlands

ABSTRACT

The paper introduces a new numerical method for continuation of equilibria of models describing physiologically structured populations. To describe such populations, we use integral equations coupled with each other via interaction (or feedback) variables. Additionally we allow interaction with unstructured populations, described by ordinary differential equations. The interaction variables are chosen such that if they are given functions of time, each of the resulting decoupled equations becomes linear. Our numerical procedure to approximate an equilibrium will use heavily this special form of the underlying equations. We also establish a method for local stability analysis of equilibria in dependence on parameters.

1991 Mathematics Subject Classification: 45G15, 45L10, 65C20, 65J99, 65R20, 92D25
Keywords and Phrases: Physiologically structured population models, numerical continuation of equilibria.
Note: The research by Markus Kirkilionis was supported by the NWO programs "NLS-Populatiedynamica" and "MPR-Dynamische Biologische Systemen". Partially, this work was carried out at CWI under project MAS2.6 (Modelling of processes in biology and chemistry).

1. Introduction.

Numerical methods for continuation and bifurcation analysis of maps and ODEs gave a number of new insights in the qualitative behaviour of these classes of dynamical systems. Moreover, they enabled the detailed analysis of concrete cases arising in applications (see for example Kuznetsov [11] for a general introduction to finite-dimensional bifurcation analysis and a number of numerical examples. Especially section 10.8 gives an overview to the relevant literature and available software). The underlying aim of this paper is to obtain similar methods for a special class of deterministic infinite dimensional dynamical systems describing physiologically structured populations (which in the following will be refered to as PSPMs). Relevant introductions to this type of equations can be found in Metz & Diekmann [13] (general PSPMs) and Webb [18] (age-structured PSPMs). However, our approach will not be based on partial differential equations, together with integral boundary conditions (as being used in the above cited references), but uses a related integral equation formulation (see Diekmann et al. [2], and also the discussion).

Naturally, the study of equilibria (and their stability) of PSPMs is the first thing to try. We will describe a quite natural method to calculate a finite dimensional approximation of the equilibrium equation for fixed parameter values. Standard methods can then be used for numerical continuation of an isolated equilibrium with respect to one free parameter. Using a (formal) linearization at the equilibrium, we are able to calculate stability boundaries in the plane spanned by two free parameters.

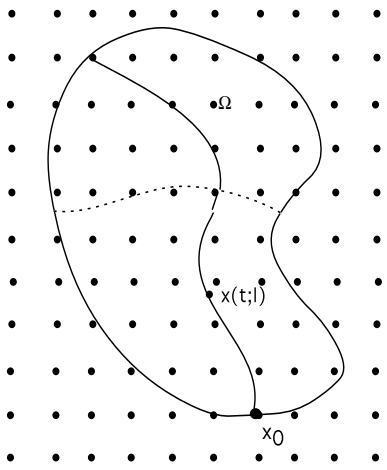

Fig. 1. *Characteristic (solid line) in the i-state space* Ω. *Each individual has the same state-at-birth* x_0. *The dotted line separates* Ω *in subregions for which we will assume that all quantities describing individual behaviour, like growth etc., are continuous. A regular grid discretizing* Ω *can be seen in the background. It is used for comparison of our method with a fixed-grid discretization. Arrows indicate the direction in which an individual is moving in the i-state space* Ω *while getting older.*

An important restriction we will make is that only one state-at-birth for newborns is possible, a well-known situation from the theory of age-structured populations where every newborn necessarily has exactly age zero. Examples of such models and their detailed numerical analysis will be given in a second paper ([8]), together with a description of implementational aspects of the numerical algorithms. The extension to models with a continuum of possible states-at-birth is postponed to later work. (This will involve approximation by finitely many states-at-birth.)

To illustrate how our numerical method will work, it is interesting to compare it with already existing methods for time-integration of equations describing a PSPM (see Goudriaan [4], Ito et al. [6], Kappel & Zhang [7], Kostova [10], Milner & Rabbiolo [12], de Roos [14] and [15], Sulsky [16] and [17]). All these methods deal with a differential formulation which approximates the shifts of the population density. The most straightforward method can be applied if individuals are classified by age. In this case the individual state space Ω, the space of all possible states of an individual, equals the positive half-line of real numbers. An Eulerian method with a fixed, a-priori given grid (i.e. the grid is constructed without using partial knowledge of the solution) can be used, see for example Sulsky [16]. There are essentially two problems with this approach that arise if one looks at generalizations: If the individual state space remains one-dimensional, but the variable x structuring the individuals (here always called the i-state) is an entity like size, mass etc, one has to define a 'growth'-rate describing the speed with which the i-states change. In general, the growth-rate will be a nonlinear function. If the i-state becomes multidimensional (say of dimension $s \geq 1$) and there is just one fixed state-at-birth x_0, each individual still follows a curve during its lifetime, given by

$$\begin{aligned} &\frac{dx}{da} = g(t+a, a, x) \quad \text{with age} \quad a \in \mathbb{R}_+, x \in \mathbb{R}^s \\ &x(t,0) = x_0, \end{aligned} \tag{1.1}$$

where t is the time of birth of the individual and g the "growth" rate. This equation will be non-autonomous, because growth is depending on environmental conditions as well. Any fixed grid

discretizing Ω will not be appropriate, because $x(t,a)$ is not known a-priori. Moreover it is very costly from a numerical point of view to have discretization points all over Ω, see Fig.1. A better solution can be a moving grid method. But even then discretization points outside the current characteristic (i.e. the curve $a \mapsto x(t-a,a)$ with x the solution of Eq. (1.1)) are not needed. We therefore will introduce a method which will only discretize the characteristic itself, thus avoiding a discretization of the whole i-state space Ω. Such an approach was followed by de Roos [14]. Similar schemes using integration along characteristics have been published in Ito et al. [6] and Sulsky [17], both for less general classes of equations, but with 'full' discretization, i.e. also the time is discretized, whereas in [14] the PSPM is approximated by sets of ODEs. We will employ a similar approximation by ODEs in the context of numerical continuation.

For continuation, we have to constructively define a finite-dimensional map $G : \mathbb{R}^n \to \mathbb{R}^n$, where an equilibrium is characterized by $y^* \in \mathbb{R}^n$ satisfying $G(y^*) = 0$. This condition will comprise the requirement that at equilibrium each individual exactly replaces itself and, in addition, that input from the environment must equal output to the environment. The nonlinear mapping G itself is assembled by quantities obtained from integrating Eq. (1.1) along with equations describing cumulative birth and output to the environment. This provides an efficient approximation of the state space Ω where no discretization outside a characteristics are needed.

The organization of the paper is as follows: We first present a general population model in several steps (section 3). While looking at a single structured population, all building blocks for describing an individual are listed. By book-keeping arguments we derive the integral equations describing the system on the population level. As already mentioned, the lines along which we will formulate the model are very close to the ones presented in Diekmann et al. [2]. The section on model formulation ends with the construction of a general n-species model, where some of the populations might be unstructured and can therefore be described by ODEs. Building the final food-web is a matter of coupling one population building blocks via the interaction function relating input to output variables. These concepts are introduced sections 2 and 3. The next step, in section 4, is to formulate conditions any equilibrium of this general model has to satisfy. Important for our purposes is an infinite-dimensional representation which arises quite naturally after an easy reformulation of the equilibrium conditions. The final finite-dimensional approximation then uses this reformulation, with the only difference that indivduals which have reached a certain maximal approximating age are neglected. Section 5 introduces the characteristic equation derived from a formal linearization of the equilibrium. Again we discuss briefly a finite-dimensional approximation for our numerical purposes. The following section 6 introduces numerical continuation, where we use the approximations from sections 4 and 5 to follow equilibria and stability boundaries as, respectively, one or two parameters are varied. We give a discussion of possible extensions of the method in section 7.

2. The modelling of a food web with the help of interaction variables.

An important aspect of the modelling phase is the specification of nonlinear feedback mechanisms in a model of interacting species. Such feedbacks occur because all relevant model ingredients describing a single individual, like death- and growth-rates etc., will in general depend on the abundance, behaviour etc. of other individuals.

When modelling interactions, we follow a three-step procedure. First we introduce names for variables like 'predation pressure' (i.e., probability per unit of time to fall victim to a predator), 'food availability' (amount of food available for an individual per unit area (or volume)). We do this for all quantities that influence the life history of individuals. As a result, individuals are independent of each other when these quantities are given functions of time. We will call such quantities *input variables* and denote them by $I = I(t)$. They describe the environment which each individual of each population experiences in the model. In this paper we restrict our attention to the case in which there are only finitely many input variables and assume $I(t) \in \mathbb{R}^k$. This means especially that I cannot depend explicitely on the i-state of individuals (it may depend on the i-states indirectly via the integral contribution of all individuals of a population.)

The second step consists of specifying the *output variables*. The individuals react to the input I. By summing up all contributions from individuals the corresponding output $O = O(t) \in \mathbb{R}^k$ will be produced. For example, in the case of cannibalism, the predation pressure on small individuals depends on the abundance of large individuals. While calculating the output contributions, we make the following destinction: Populations are modelled as being either structured or unstructured. We will give a more detailed discussion of how to construct a submodel for a physiologically structured population in the next section. An unstructured population is simply one where all individuals are identical, and in a deterministic time-continuous setting such a population is described by an ODE. The state of a population at time $t \in \mathbb{R}_+$ will be denoted by $m(t)$, where

$$m(t) \in \begin{cases} M_+(\Omega) & : \quad \text{if the population is structured,} \\ \mathbb{R}_+ & : \quad \text{if the population is unstructured.} \end{cases}$$

Here Ω is the i-state space of the structured population (see next section) and $M_+(\Omega)$ is the cone of positive measures on Ω. We can compute the number of individuals in the population at time t from the state m: Either $m(t)$ itself is giving this information directly (in the unstructured case) or the number of individuals is equal to $\int_\Omega m(t)(dx)$ (in the structured case). Let there be n populations with state m_j, $1 \le j \le n$. We need to determine how each population contributes to each of the components of O. Let Γ_{ij} be the recipe to compute the contribution of population j to the i-th component of the output variable O. We assume Γ_{ij} are linear functionals mapping from the population state space into $\mathbb{R}$, i.e.

$$\Gamma_{ij} : M_+(\Omega_j) \to \mathbb{R}$$

In the case that Ω_j contains just a single point, which is the case for unstructured populations, we use the convention that $M_+(\Omega_j) = \mathbb{R}_+$. ($\Omega_j$ is now the i-state space of the population with index j). These functionals are defined by

$$\Gamma_{ij} m_j = \begin{cases} \int\limits_{\Omega_j} \gamma_{ij}(x) m_j(dx) & : \quad \text{if the population is structured,} \\ \gamma_{ij} m_j & : \quad \text{if the population is unstructured.} \end{cases}$$

The quantities γ_{ij} are the individual output contributions. The output variable is now assembled according to the rule

$$O = \Gamma m,$$

where $\Gamma = (\Gamma_{ij})_{\substack{1 \le i \le k \\ 1 \le j \le n}}$ is the matrix of population output contributions and $m = (m_1, \ldots, m_n)$. In other words, each component of O is obtained by summing up the contributions from all populations.

The final step 3 in our scheme is now relating output (of all populations) to input (to all populations). Because the individual output contributions γ_{ij} may themselves depend on I, i.e. $\gamma_{ij} = \gamma_{ij}(I)$, this leads to the consistency relation

$$I = O = \Gamma(I) m.$$

We will use this relationship later to formulate equilibrium conditions for solutions of our model. We do not distinguish between the two symbols I and O in the following and use only the symbol I when constructing the feedback relationships among and inside populations. The vector I is now called the *interaction* variable.

3. A GENERAL n SPECIES POPULATION MODEL.

Populations can or cannot show structure, in the sense that understanding their growth or decline requires knowledge of individual differences. We like to include both possibilities. First a model for

a single structured population is introduced. An unstructured population is thereafter treated as a special case, by making the simplifying assumption that all individuals are identical.

There are a lot of different mechanisms that can be included in a model of a physiologically structured population. Individual developpment (movement in Ω) can be either stochastic or deterministic, birth of individuals can be modelled as a discrete event or taking place continuously, newborns may start with the same state at birth or there may be a distribution over the individual state space already at birth, growth rates may change discontinuously when individuals reach a certain stage etc. The setting we will introduce for each structured population in this paper can be seen as a straightforward generalisation of the classical deterministic age-structured linear model (see Webb [18], section 1.2) as given by an integral equation derived after integration along characteristics. Our generalisation becomes nonlinear by introducing the interaction variable I, just in the same manner as the Gurtin-MacCamy model (see Gurtin and MacCamy [3], also [18]) is nonlinear by letting all individual rates depend on total population size. Additionally we extend the model such that individuals 'live' in a general i-state space Ω of dimension $s \geq 1$. However, we keep the assumption that every newborn has the same state-at-birth. As already mentioned, at the same time this formulation can be interpreted as a special case of the linear PSPM formulated in Diekmann et al. [2], see the discussion at the end of the paper.

3.1 A single structured population

The modelling of a single structured population, as presented here, requires five steps. We give first a brief overview of the modelling procedure in its natural ordering and then go into detail. For simplicity we will not give an index to the population under consideration as long as we consider one species only. The five steps are the following:

Step 1: The choice of structuring variables. We denote the resulting vector by x and call it the **individual state** or, shorter, the **i-state** (vector). After having made this choice, x_0, the **state-at-birth** has to be specified. The space of possible i-states will be denoted by $\Omega \subset \mathbb{R}^s$, $s \geq 1$. This set is also called the **i-state-space**.

Step 2: To characterize an individual further, four different types of functions have to be provided by the modeller: First the **individual growth rate** $g(x, I)$, secondly the **individual interaction** or **feedback contributions** $\gamma_i(x, I)$ to each component I_i of the interaction vector I, thirdly the **individual offspring production rate** $\beta(x, I)$, and in the fourth place the **individual death rate** $\mu(x, I)$.

Step 3: After step 2 it will be possible to derive the following two quantities under the assumption that the interaction vector I is given as a function of time: First we can compute $x(t, a; I)$, the **i-state** of an individual of age a, born at time t, given the course of I in the time interval $[t, t+a)$. Secondly we can compute the **individual survival probability**, denoted by $\mathcal{F}(t, a; I)$.

Step 4: All functions described in step 2 might be discontinuous. A typical example is that the individual's life history contains different life stages, where growth and birth rates etc. differ drastically. We have to know (for the biological interpretation, but also for numerical purposes) at what age of an individual such discontinuities occur. To do so, we require that the modeller is providing for each discontinuity a *(discontinuity) detection functional* $d_j(x, I)$, $1 \leq j \leq n_d$, which exactly switches sign when the discontinuity occurs.

Step 5: This step leads us to the population level. By integrating over all contributions of the living individuals we can derive the **population birth rate** $b(t)$ and compute the **population feedback contributions** $\Gamma_i(I)$, $1 \leq i \leq k$.

By $\Phi(v)$ we will in the following always denote the index set of the components of a (column-)vector v. The vector v will also be written in the form $v = (v_i)_{i \in \Phi(v)}$.

3.2 First step: The choice of structuring variables.
The choice of the structuring variables for the **i-state** x must be done in such a way that the distinction between individuals suits the purpose of the model. It is also important to note that at the same time these quantities should preferably be either directly or indirectly measurable in experiments. Most commonly x has components which are identified as age, size, weight, energy content etc., but possible choices include also non-physiological quantities like a rank in a social hierachy.

Next the **state-at-birth** x_0 has to be specified. Because we assume a single identical state-at-birth for all newborn individuals, we must exclude at the moment that newborns exhibit a high variation in x. Sometimes the choice of x_0 is easy after the choice of the structuring variables has been made: For a purely age-structured model the state-at-birth will always be zero. For other situations the identification of x_0 is less obvious.

We always assume that the **i-state-space** $\Omega \subset \mathbb{R}^m$. Note that at this stage we are not able to compute what the possible i-states are. We must first give a recipe in the following steps how to compute them.

3.3 Second step: The description of an individual's movement in Ω.
The four functions listed below are assumed to determine completely the dynamical behaviour of every individual of the population. The requirements on their smoothness will depend on the type of numerical algorithm we apply, most dominantly on the nonlinear iteration scheme used to calculate successive approximations of equilibria. We therefore do not determine their smoothness here explicitly:

individual growth rate: We assume that the development of individuals is purely deterministic. The function $g(x, I)$, the individual growth rate, describes how an individual moves in the i-state space Ω, that is, we postulate that for an individual $\frac{dx}{dt} = g(x, I)$ holds. Thus 'growth' is meant in a rather general sense. It can mean growth in length or size but also the production or loss of energy reserves etc.

individual interaction or feedback contributions: Let the quantity $\gamma_i(x, I)$ be the per capita contribution to a component I_i of the interaction variable I, $1 \leq i \leq k$, given the individual has state x and given the vector of interaction variables is I. The function $\gamma_i(x, I)$ will be called the **individual's i-th interaction contribution**.

individual birth rate: The individual birth rate $\beta(x, I)$ is the rate at which an individual with state x produces offspring with state-at-birth x_0, given the vector of interaction variables is I.

individual death rate: The quantity $\mu(x, I)$ is the **individual death rate** (i.e. the probability per unit of time of dying), given the individual has state x and given the vector of interaction variables is I.

Regularity and other assumptions on these functions are of two kinds: First, these assumptions have to be made from a modelling point of view. Very often jump discontinuities are introduced to describe (idealized) biological events. This is discussed in step 4 seperately, because the numerical treatment of such discontinuities requires some extra effort. Other assumptions will ensure nonnegative numbers of individuals at each time point, etc. Such a set of assumptions must be stated for each specific model, but we at least assume $\beta \geq 0$ on Ω for any feasible given $I(t)$. A similar positivity requirement for μ will be given in the next step after introducing the survival probability $\mathcal{F}$.

On the other hand, the model should be mathematically tractable. We do not discuss the necessary assumptions to have well-posedness in this context. A requirement needed for numerical reasons is that each of the functions g, γ_i, β, and μ is twice piecewise continuously differentiable with respect to its arguments.

3.4 Third step: Computation of the individual state and of the survival probability.
This step consists of a recipe how to compute two important quantites related to the structure- (age-, size-) distribution of the population from functions provided in step 2. Let $x(t,a)$ denote the **i-state** at age a of an individual which was born at time t with state-at-birth x_0. Then

$$\begin{aligned} &\frac{\partial}{\partial a}x(t,a) = g(x(t,a), I(t+a)), \\ &x(t,0) = x_0, \end{aligned} \tag{3.1}$$

describes the change of the i-state x when the individual gets older. Likewise the **survival probability** $\mathcal{F}(t,a)$ satisfies

$$\begin{aligned} &\frac{\partial}{\partial a}\mathcal{F}(t,a) = -\mu(x(t,a), I(t+a))\mathcal{F}(t,a), \\ &\mathcal{F}(t,0) = 1. \end{aligned} \tag{3.2}$$

This quantity is by definition the probability that an individual which was born at time t with state-at-birth x_0 survives at least until time $t+a$. For our numerical approximation of equilibria, it will be essential that we require $\mu \geq 0$ on Ω for any feasible given $I(t)$, such that $\lim_{a\to\infty} \mathcal{F}(t,a) = 0$. This can be achieved by different assumptions; it suffices for example that $\frac{\partial}{\partial a}\mathcal{F}(t,a) < 0$ for $a > a^* > 0$, i.e. the survival probability must only be strictly monotonically decreasing for old enough ages of the individuals.

We can now give interpretations to the following two quantities: First

$$\gamma_i(x(t-a,a), I(t))\mathcal{F}(t-a,a)$$

is the expected contribution at time t to the interaction I_i, $1 \leq i \leq k$, of an individual born at time $t-a$. Such an individual contributes

$$\beta(x(t-a,a), I(t))\mathcal{F}(t-a,a)$$

to the rate at which individuals are born at time t.

3.5 Fourth step: The individual's sudden changes in behaviour: Detection of discontinuities.
As outlined above, the functions g, γ_i, β and μ are in general only piecewise continuously differentiable. We can solve Eq. (3.1) and Eq. (3.2) uniquely on subintervals of the age axis $\mathbb{R}_+$. This is how we will interpret the meaning of a solution of these ODEs in the following, without further mentioning it: Solve the ODE until a discontinuity occurs, determine the values of the unknowns at the end of that interval, and restart the integration process with the updated values of the right hand side and with the updated values of the unknowns from the end of the previous age interval. In order to be able to detect discontinuities, we make the following assumption: There are continuous functionals $d_j : \Omega \times \mathbb{R}^k \to \mathbb{R}$, $d_j = d_j(x, I)$, $1 \leq j \leq n_d$, such that for given I the $(m-1)$-manifolds implicitly defined by $d_j(x, I(t^*)) = 0$ partition Ω at each instant of time t^* in regions where the functions g, γ_i, β and μ are smooth, see also Fig 1. Moreover, the separation of Ω is such that characteristics (i.e. the solutions of Eq. (3.1), see below) cross the manifolds always transversally. More precisely we assume that for an individual born at time t, and given I, there is locally in time at most one point in time, say $t + a^*$ such that

$$\begin{aligned} &d_j(x(t, a^* - \epsilon), I(t + a^* - \epsilon)) < 0, \\ &d_j(x(t, a^* + \epsilon), I(t + a^* + \epsilon)) > 0, \end{aligned} \tag{3.3}$$

for all $\epsilon > 0$ whenever there is a discontinuity in g, γ_i, β or μ. This transversality condition will in practise be checked numerically.

The reason why we allow jumps in the different rates β, g, μ and γ_i with respect to the state x is: First, as already noted, they allow to model things like sudden stage changes with completely different growth-, reproduction-, etc. behaviour, occuring for example in insects or crustaceans. Secondly, jumps are often used to simplify models by reducing the number of necessary model parameters.

3.6 Fifth step: The population level.
Now we have to integrate over all individual contributions to handle the population level. Given the individual states, what becomes a state for the whole population? We already introduced in section 2 a measure $m(t) \in M_+(\Omega)$ describing the distribution of individuals in Ω at time t. Additionally, to monitore the population state, we have to sum individual contributions to calculate the population feedback contributions to the ith component of I, $1 \leq i \leq k$, which was denoted by $\Gamma_i(I(t))m(t)$.

Instead of taking m directly as a representation of population state, we rather will work with the (population) birth rate

$$b(t) = \text{ rate of birth of individuals at time } t.$$

This means we censor the population by keeping track of new individuals entering the population. Because we can calculate the survival probability $\mathcal{F}(t,a)$ and the movement in state space $x(t,a)$ for each of these individuals from the time on when they were born, the information given by $b(t)$, as a function of time, enables us to compute m. To elaborate this point, we introduce a new measure $\tilde{m} = \tilde{m}(t,a)(\omega)$ which we define as the number per unit of time of individuals at time t with age a having their state in $\omega \subset \Omega$. Then

$$\tilde{m}(t,a)(\omega) = \mathcal{X}_\omega(x(t-a,a))\mathcal{F}(t-a,a)b(t-a). \tag{3.4}$$

Here $\mathcal{X}_\omega$ is the characteristic function:

$$\mathcal{X}_\omega(x) = \begin{cases} 1 & : \quad x \in \omega \\ 0 & : \quad x \notin \omega. \end{cases}$$

In words Eq. (3.4) is telling us that at time t an individual of age a can only have a state $x \in \omega$ if it has been born at time $t-a$ (with state x_0) and survived a time units. From this we immediately obtain an expression to reformulate m in terms of $\mathcal{F}$ and b:

$$m(t)(\omega) = \int_0^\infty \tilde{m}(t,a)(\omega)\, da = \int_0^\infty \mathcal{X}_\omega(x(t-a,a))\mathcal{F}(t-a,a)b(t-a)\, da.$$

Using this reformulation of m, or, alternatively, directly using the new formulation, we can derive the following expressions for $b(t)$ and $\Gamma_i(I(t))m(t)$ (given in their translation invariant form, i.e. without consideration of initial conditions):

$$\begin{aligned} b(t) &= \int_0^\infty \beta(x(t-a,a),I(t))\mathcal{F}(t-a,a)b(t-a)\, da, \\ \Gamma_i(I(t))m(t) &= \int_0^\infty \gamma_i(x(t-a,a),I(t))\mathcal{F}(t-a,a)b(t-a)\, da, \end{aligned} \tag{3.5}$$

with $1 \leq i \leq k$. We have suppressed in the notation of Eq.(3.5) the dependence on parameters, which will only become important later when we consider continuation. All components of I are, so far, assumed to be sufficiently smooth given functions of time.

3.7 Simplifications in the case of an unstructured population.
Now we briefly treat the case that a given species is unstructured. This can be interpreted as meaning that the individual's state space consists of just one possible state, i.e $\Omega = \{x^*\}$, a space of dimension zero. This implies that all individuals have the same state at every instant of time. With this assumption, the equations describing the population dynamics can be considerably simplified. We will not give any derivation, but immediately formulate the result in the more common form of ordinary differential equations. However, we keep the assumption that these equations become nonlinear only by feedback via the interaction variables:

$$\begin{aligned} \frac{\partial}{\partial t} m(t) &= [\beta(I(t)) - \mu(I(t))]m(t), \\ I_i(t) &= \gamma_i(I(t))m(t) \end{aligned} \tag{3.6}$$

Because we will only be interested in equilibria of Eq. (3.6), no initial conditions are provided.

3.8 The n-species model.
After the consideration of a single species, we now consider the interaction of n such species. In order to do so, we label the ingredients describing a particular species with an index j, $1 \leq j \leq n$. First we label the individual state spaces. Assume $\Omega_j = \{x_j^*\}$ for $j \in \Phi_u$. Here $\Phi_u \subset \{1, \ldots, n\}$ is the set of indices labeling the unstructured populations. Let $\Phi_s \stackrel{\text{def}}{=} \{1, \ldots, n\} \setminus \Phi_u$ be the set of indices labeling structured populations. We have $\Omega_j \subset \mathbb{R}^{\nu_j}$, $\nu_j \in \mathbb{N}$, $j \in \Phi_s$. After labelling likewise all other population ingredients, the result is:

$$\begin{aligned} &\frac{\partial}{\partial t} m_j(t) = [\beta_j(I(t)) - \mu_j(I(t))]m_j(t) \quad \text{for} \quad j \in \Phi_u, \\ &b_j(t) = \int_0^\infty \beta_j(x_j(t-a,a), I(t)) \mathcal{F}_j(t-a,a) b_j(t-a)\, da \quad \text{for} \quad j \in \Phi_s, \\ &I_i(t) = \sum_{j=1}^{n} \Gamma_{ij}(I(t)) m_j(t) \quad \text{for} \quad 1 \leq i \leq k. \end{aligned} \tag{3.7}$$

The quantities $\Gamma_{ij}(I(t))m_j(t)$ are defined by

$$\Gamma_{ij}(I(t))m_j(t) = \begin{cases} \gamma_{ij}(I(t))m_j(t) & : \quad j \in \Phi_u \\ \int_0^\infty \gamma_{ij}(x_j(t-a,a), I(t)) \mathcal{F}_j(t-a,a) b_j(t-a)\, da & : \quad j \in \Phi_s. \end{cases}$$

Moreover, the quantities x_j and $\mathcal{F}_j$ for $j \in \Phi_s$ have to be calculated according to Eq. (3.1) and Eq. (3.2), so by solving

$$\begin{aligned} &\frac{\partial}{\partial a} x_j(t,a) = g_j(x_j(t,a), I(t+a)), \\ &x_j(t,0) = x_{j,0}, \end{aligned} \tag{3.8}$$

and

$$\begin{aligned} &\frac{\partial}{\partial a} \mathcal{F}_j(t,a) = -\mu_j(x_j(t,a), I(t+a)) \mathcal{F}_j(t,a), \\ &\mathcal{F}_j(t,0) = 1. \end{aligned} \tag{3.9}$$

To avoid indices, we will use in the following a more compact notation for equations like (3.7), (3.8) and (3.9). We use the following conventions: For two vectors $v^1 = (v_1^1, \ldots, v_{n_1}^1)^T$ and $v^2 =$

$(v_1^2, \ldots, v_{n1}^2)^T$ we set $v^1 v^2 = (v_1^1 v_1^2, \ldots, v_{n_1}^1 v_{n1}^2)^T$. In case M is a $(n_2 \times n_1)$-matrix, Mv^1 is the usual matrix-vector product. First we rewrite Eq. (3.7) as

$$\begin{aligned} &\frac{\partial}{\partial t} m_u(t) = [\beta_u(I(t)) - \mu_u(I(t))] m_u(t), \\ &b(t) = \int_0^\infty \beta_s(x(t-a,a), I(t)) \mathcal{F}(t-a,a) b(t-a)\, da, \\ &I = \Gamma(I(t)) m(t), \end{aligned} \tag{3.10}$$

with

$$\begin{aligned} &m_u \stackrel{\text{def}}{=} (m_j)_{j \in \Phi_u}, \\ &\beta_u(I(t)) \stackrel{\text{def}}{=} (\beta_j(I(t)))_{j \in \Phi_u}, \\ &\mu_u(I(t)) \stackrel{\text{def}}{=} (\mu_j(I(t)))_{j \in \Phi_u}, \\ &b \stackrel{\text{def}}{=} (b_j)_{j \in \Phi_s}, \\ &\beta_s(x(t-a,a), I(t)) \stackrel{\text{def}}{=} (\beta_j(x_j(t-a,a), I(t)))_{j \in \Phi_s}, \\ &\mathcal{F} \stackrel{\text{def}}{=} (\mathcal{F}_j)_{j \in \Phi_s}. \end{aligned} \tag{3.11}$$

We always assume that indices are sorted in such a way that we can write

$$\Gamma(I) m = \gamma_u(I) m_u + \Gamma_s(I) m_s. \tag{3.12}$$

Again, Eq. (3.10) has to be supplemented by the analogues of Eqs. (3.8) and (3.9):

$$\begin{aligned} &\frac{\partial}{\partial a} x(t,a) = g_s(x(t,a), I(t+a)), \\ &x(t,0) = x_0, \end{aligned} \tag{3.13}$$

and

$$\begin{aligned} &\frac{\partial}{\partial a} \mathcal{F}(t,a) = -\mu_s(x(t,a), I(t+a)) \mathcal{F}(t,a), \\ &\mathcal{F}(t,0) = \mathbf{1}. \end{aligned} \tag{3.14}$$

The different vectors occuring in (3.13) and (3.14) are given by $x = (x_j)_{j \in \Phi_s}$, and $\mathbf{1} = (1, \ldots, 1)^t$ (the 1s are repeated $dim(\Phi_s)$ times). Moreover, the above notation in (3.12), (3.13) and (3.14) for the different vector- respectively matrix-valued functions describing growth, feedback and death, uses the following definitions:

$$\begin{aligned} &\gamma_s(x(t-a,a), I(t)) \stackrel{\text{def}}{=} (\gamma_{ij}(x_j(t-a,a), I(t)))_{\substack{1 \le i \le k \\ j \in \Phi_s}}, \\ &\gamma_u(I(t)) \stackrel{\text{def}}{=} (\gamma_{ij}(I(t)))_{\substack{1 \le i \le k \\ j \in \Phi_u}}, \\ &g_s(x(t,a), I(t+a)) \stackrel{\text{def}}{=} (g_j(x_j(t,a), I(t+a)))_{j \in \Phi_s}, \\ &\mu_s(x(t,a), I(t+a)) \stackrel{\text{def}}{=} (\mu_j(x_j(t,a), I(t+a)))_{j \in \Phi_s}. \end{aligned} \tag{3.15}$$

We will use analogous definitions like (3.11) and (3.15) in the time-independent case without ex-

plicitly stating them again.

4. Equilibria.

By an equilibrium of problem (3.10) we mean a vector $y = (\overline{m_u}, \overline{b}, \overline{I})$, where $\overline{m_u}$, $\overline{b}$ and $\overline{I}$ are time independent and satisfy the system of equations

$$\begin{aligned} 0 &= \beta_u(\overline{I}) - \mu_u(\overline{I}), \\ \overline{b} &= \overline{b} \int_0^\infty \beta_s(\bar{x}(a), \overline{I}) \overline{\mathcal{F}}(a)\, da, \\ \overline{I} &= \Gamma(\overline{I}) \bar{m}. \end{aligned} \tag{4.1}$$

Again we can decompose the expression $\Gamma(\overline{I})m$ and write $\Gamma(\overline{I})m = \Gamma_u(\overline{I})\overline{m_u} + \Gamma_s(\overline{I})\bar{m}_s$, with $\bar{m}_s = \left(\overline{b}\int_o^\infty \overline{\mathcal{F}}_j(a)\, da\right)_{j\in\Phi_s}$. Because we have taken the population birth rates b as the states of structured populations, we rewrite the action of the functional $\Gamma_s(\overline{I})$ on m_s as a matrix product $\Theta^s(\overline{I})\overline{b}$, where $\Theta^s(\overline{I})$ is defined as

$$\Theta^s(\overline{I}) = \int_0^\infty \gamma_s(\bar{x}(a), \overline{I}) \overline{\mathcal{F}}(a)\, da.$$

The vectors $\bar{x} = (\bar{x}_j)_{j\in\Phi_s}$ and $\overline{\mathcal{F}} = \left(\overline{\mathcal{F}}_j\right)_{j\in\Phi_s}$ must satisfy the equations

$$\begin{aligned} &\frac{\partial}{\partial a}\bar{x}(a) = g_s(\bar{x}(a), \overline{I}), \\ &\bar{x}(0) = x_0, \end{aligned} \tag{4.2}$$

and

$$\begin{aligned} &\frac{\partial}{\partial a}\overline{\mathcal{F}}(a) = -\mu_s(\bar{x}(a), \overline{I})\overline{\mathcal{F}}(a), \\ &\overline{\mathcal{F}}(0) = \mathbf{1}. \end{aligned} \tag{4.3}$$

We now make a simple, but for our later numerical treatment, essential transformation of these equations defining an equilibrium. By setting $R_0^s(\overline{I}) \stackrel{\text{def}}{=} \int_0^\infty \beta_s(\bar{x}(a), \overline{I})\overline{\mathcal{F}}(a)da$ and by letting $R_0^u = \left(R_{0,j}(\overline{I})\right)_{j\in\Phi_u}$, with $R_{0,j}(\overline{I}) \stackrel{\text{def}}{=} \frac{\beta_j(\overline{I})}{\mu_j(\overline{I})}$, we can reformulate the problem as follows:

$$\begin{aligned} R_0^u(\overline{I}) - \mathbf{1} &= 0, \\ R_0^s(\overline{I}) - \mathbf{1} &= 0, \\ \overline{I} - \gamma_u(\overline{I})\overline{m_u} - \Theta^s(\overline{I})\overline{b} &= 0, \end{aligned} \tag{4.4}$$

where $R_0^s(\overline{I}) \stackrel{\text{def}}{=} r_0^s(\infty)$ and $\Theta^s(\overline{I}) \stackrel{\text{def}}{=} \theta^s(\infty)$ are computed according to the scheme

$$\begin{aligned} &\frac{\partial}{\partial a} r_0^s(a) = \beta_s(\bar{x}(a), \overline{I})\overline{\mathcal{F}}(a), \\ &\frac{\partial}{\partial a} \theta^s(a) = \gamma_s(\bar{x}(a), \overline{I})\overline{\mathcal{F}}(a), \end{aligned} \tag{4.5}$$

with initial conditions

$$r_0^s(0) = 0, \qquad \theta^s(0) = 0. \tag{4.6}$$

Clearly, system (4.5) has to be solved together with systems (4.2) and (4.3) in paralell. Note that Eq. (4.4) is already of the form

$$G(y) = 0,$$

with the obvious specifications of the different components of y and G. The dimension of both y and G is $n + k$ (where n is the number of species and k is the dimension of the (environmental) interaction vector I), i.e. we have the same number of equations and unknowns. The quantities R_0^u and R_0^s are called the *basic reproduction ratios* in the population dynamics literature, see for example Heesterbeek[5].

4.1 Numerical approximation of an equilibrium

How can we numerically (approximately) find an equilibrium, i.e. find $\overline{m_u}, \overline{b}$ and $\overline{I}$ such that they satisfy Eq.(4.4)? First of all Eq.(4.5), together with (4.2) and (4.3) has to be solved for infinite ages of the individuals for each population $j \in \Phi_s$, something which is not possible numerically. We define implicitly quantities $a_{j,\epsilon}$ by $\overline{\mathcal{F}}_j(a_{j,\epsilon}) = \epsilon$. Such quantities exist for each $\epsilon \in (0,1)$, because $\overline{\mathcal{F}}_j(a) \in (0,1]$ for $a \in \mathbb{R}^+$ and $\overline{\mathcal{F}}_j(a) \to 0$ monotonically as $a \to \infty$. This holds because we assumed all death rates are bounded away from zero for large ages. Clearly ϵ is a quantity which enters considerations of numerical accuracy, and the approximation should become better if ϵ becomes smaller. Define $a_\epsilon \stackrel{\text{def}}{=} \max_{j\in\Phi_s} a_{j,\epsilon}$. In our numerical approximation, we will replace R_0^s and Θ^s in Eq. (4.4) by $R_0^{s,\epsilon}$ and $\Theta^{s,\epsilon}$, where $R_0^{s,\epsilon} = (r_{0,j}(a_\epsilon))_{j\in\Phi_s}$ and $\Theta^{s,\epsilon} = (\theta_{ij}(a_\epsilon))_{\substack{1\le i\le k \\ j\in\Phi_s}}$. To express this in the notation, we write $G_\epsilon(y) = 0$ instead of $G(y) = 0$. Usually one solves a nonlinear equation, like $G_\epsilon(y) = 0$, numerically by an iteration method, for example and most prominently by Newton's method. We will do the same, but we have to make additional computations whenever for a given value y^* the values of $G_\epsilon(y^*)$ are evaluated. The following algorithm and all forthcoming ones are formulated in a pseudo-code format (adapted from Allgower and Georg[1]). In the algorithm below we follow the strategy to first (explicitly or iteratively) compute the i-states where discontinuities occur. This is done with the help of the discontinuity functionals d_{ij}, $1 \le i \le n$ and $1 \le j \le n_{d_i}$ (with n_{d_i} being the number of discontinuity functionals needed to describe population i), and can be done if a fixed value of $\overline{I}$ is given. Alternatively, in the case the knowledge of the ages at which a discontinuity occurs is not needed as output, one can use a numerical method which allows to integrate over the discontinuities. In any case, because the determination of these 'stop ages' requires computational efforts, one should use specific knowledge of the model under investigation to simplify the calculations.

We now describe two algorithms: The first one describes the computation of the value of G_ϵ for a given value of $y \in \mathbb{R}^p$, with $p = n + k$ (and also given parameter values, which only becomes important later). The second algorithm will describe how to approximate a solution of $G_\epsilon(y) = 0$ by Newtons-method.

Algorithm 1: (Computation of $G_\epsilon(y)$) *comment:*

input

begin

$a_\epsilon > 0$; *age at which integration stops*

$\delta > 0$; *perturbation used for numerical differentiation*

$y = (\overline{m_u}, \overline{b}, \overline{I})$; *given value of y*

end;

compute (iteratively or explicitly) for each d_{ij} the i-states x_{ij} such that

$d_{ij}(x_{ij}, \overline{I}) = 0$ *computation of i-states where discontinuities occur*

a:=0; *start age*

repeat *integration along characteristic*

integrate system (4.2), (4.3), (4.5) in parallel from age a on;

system (4.2), (4.3), (4.5) becomes autonomous for a given value of $\overline{I}$

stop integration at an age a_{ij} if $\bar{x}(a_{ij}) = x_{ij}$;

store $\overline{x}(a_{ij})$, $\overline{\mathcal{F}}(a_{ij})$, $r_0^s(a_{ij})$, $\theta^s(a_{ij})$ and a_{ij};

$a := a_{ij}$;

until $a = a_\epsilon$; *final approximation age is reached*

assemble $G_\epsilon(y)$;

G_ϵ is defined by replacing R_0^s and Θ^s in the left hand side of (4.4) by $r_0^s(a_\epsilon)$ and $\theta^s(a_\epsilon)$

evaluate $G_\epsilon(y)$;

We can now use algorithm 1 to approximate a root of G, which we will denote by y_ϵ. By using algorithm 1, we will at the same time iteratively approximate G by G_ϵ.

Algorithm 2: (Find y_ϵ approximately solving $G(y) = 0$) *comment:*

input

begin

$a_\epsilon > 0$; *age at which integration stops*

$\delta > 0$; *perturbation used for numerical differentiation*

$\epsilon_G > 0$; *numerical accuracy constant*

$\epsilon_y > 0$; *numerical accuracy constant*

$y^{(0)} = (\overline{m_u}^{(0)}, \overline{b}^{(0)}, \overline{I}^{(0)})$; *starting point, the initial guess*

end;

$k := 0$; *iteration index*

repeat *iteration loop*

$k := k + 1$;

compute $G_\epsilon^{(k-1)} := G_\epsilon(\overline{m_u}^{(k-1)}, \overline{b}^{(k-1)}, \overline{I}^{(k-1)})$ by algorithm 1;

compute $\frac{d}{dy} G_\epsilon^{(k-1)}(y^{(k-1)})$; *step involves numerical differentiation*

integration along characteristic has to be repeated

with perturbed values $\overline{m_u}^{(k-1)} + \delta$ etc.

to compute difference quotients

solve $\frac{d}{dy}G_\epsilon^{(k-1)}(y^{(k-1)})\eta^{(k-1)} = -G_\epsilon^{(k-1)}(y^{(k-1)})$;

$y^{(k)} := y^{(k-1)} + \eta^{(k-1)}$; *new approximation to equilibrium*

until

$$\frac{\left\|\eta^{(k)} - \eta^{(k-1)}\right\|}{1 + \left\|\eta^{(k)} - \eta^{(k-1)}\right\|} < \epsilon_y \text{ and } \frac{\left\|G_\epsilon^{(k-1)}(y^{(k)})\right\|}{1 + \left\|G_\epsilon^{(k-1)}(y^{(k)})\right\|} < \epsilon_G;$$

$G_\epsilon := G_\epsilon^{(k-1)}$ and $y_\epsilon = y^{(k)}$; *new approximation accepted*

5. Linearization at the equilibrium.
Now we like to determine numerically when there are solutions of Eq. (4.4) starting close to the equilibrium $y = (\overline{m_u}, \overline{b}, \overline{I})$ which, to first approximation, neither grow away nor decline to the equilibrium, i.e. we look at the critical case for linearized stability of this equilibrium. For this purpose we denote by $\mathcal{Y}(t) = (\mathcal{M}(t), \mathcal{B}(t), \mathcal{I}(t))$ the perturbations from the equilibrium $y = (\overline{m_u}, \overline{b}, \overline{I})$. Here we use analogously to previous conventions the following vector notations: $\mathcal{M} = (\mathcal{M}_j)_{j\in\Phi_u}$, $\mathcal{B} = (\mathcal{B}_j)_{j\in\Phi_s}$, $\mathcal{I} = (\mathcal{I}_j)_{1\le i\le k}$. The (formal) linearization that determines $\mathcal{Y}(t)$ consists of the following set of equations (5.1) - (5.3):

$$\frac{\partial}{\partial t}\mathcal{M}(t) = [\beta_u(\overline{I}) - \mu_u(\overline{I})]\mathcal{M}(t) + \frac{\partial}{\partial I}[\beta_u(\overline{I})\overline{m_u} - \mu_u(\overline{I})\overline{m_u}]\mathcal{I}(t) \tag{5.1}$$

$$\begin{aligned}\mathcal{B}(t) = \int_0^\infty \Big\{ &\beta_s(\bar{x}(a), \overline{I})\overline{\mathcal{F}}(a)\mathcal{B}(t-a) + \frac{\partial}{\partial x}\beta_s(\bar{x}(a), \overline{I})\xi(t-a, a)\overline{\mathcal{F}}(a)\overline{b} \\ &+ \frac{\partial}{\partial I}\beta_s(\overline{x}(a), \overline{I})\mathcal{I}(t)\overline{\mathcal{F}}(a)\overline{b} + \beta_s(\overline{x}(a), \overline{I})f(t-a, a)\overline{b}\Big\}\, da.\end{aligned} \tag{5.2}$$

Here $\frac{\partial}{\partial x}\beta_s(\bar{x}(a), \overline{I}) \stackrel{\text{def}}{=} \left(\frac{\partial}{\partial x_j}\beta_j(\overline{x}_j(a), \overline{I})\right)_{j\in\Phi_s}$ and $\frac{\partial}{\partial I}\beta_s(\overline{x}(a), \overline{I})$ is the matrix $\left(\frac{\partial}{\partial I_i}\beta_j(\overline{x}_j(a), \overline{I})\right)_{\substack{1\le i\le k \\ j\in\Phi_s}}$. Other derivatives occuring in the following are defined analogously and we omit the componentwise formulation.

Components of the vector functions $\xi = (\xi_j)_{j\in\Phi_s}$ and $f = (f_j)_{j\in\Phi_s}$ are computed from respectively Eq. (5.4) and (5.5) below. Finally, the linearisation of the interaction variable I at the equilibrium y is given by

$$\begin{aligned}\mathcal{I}(t) = &\gamma_u(\overline{I})\mathcal{M}(t) + \frac{\partial}{\partial I}\gamma_u(\overline{I})\overline{m_u}\mathcal{I}(t) \\ &+ \int_0^\infty \Big\{\gamma_s(\bar{x}(a), \overline{I})\overline{\mathcal{F}}(a)\mathcal{B}(t-a) + \frac{\partial}{\partial x}\gamma_s(\overline{x}(a), \overline{I})\xi(t-a, a)\overline{\mathcal{F}}(a)\overline{b} \\ &+ \frac{\partial}{\partial I}\gamma_s(\bar{x}(a), \overline{I})\mathcal{I}(t)\overline{\mathcal{F}}(a)\overline{b} + \gamma_s(\overline{x}(a), \overline{I})f(t-a, a)\overline{b}\Big\}\, da.\end{aligned} \tag{5.3}$$

The quantities ξ_j and f_j are calculated from the following equation

$$\begin{aligned} &\frac{\partial}{\partial a}\xi(t,a) = \frac{\partial}{\partial x}g_s(\overline{x}(a),\overline{I})\xi(t,a) + \frac{\partial}{\partial I}g_s(\overline{x}(a),\overline{I})\mathcal{I}(t+a), \\ &\xi(t,0) = 0, \end{aligned} \tag{5.4}$$

and

$$\begin{aligned} \frac{\partial}{\partial a}f(t,a) = &-\mu_s(\overline{x}(a),\overline{I})f(t,a) - \frac{\partial}{\partial x}\mu_s(\overline{x}(a),\overline{I})\xi(t,a)\overline{\mathcal{F}}(a) \\ &- \frac{\partial}{\partial I}\mu_s(\overline{x}(a),\overline{I})\mathcal{I}(t+a)\overline{\mathcal{F}}(a), \\ f(t,0) = 0. & \end{aligned} \tag{5.5}$$

5.1 Characteristic equation

We like to derive next, again formally, a characteristic equation determining by the position of its roots relative to the imaginary axis the local asymptotic stability of an equilibrium. To do this, we replace in Eqs. (5.1)-(5.5) $\mathcal{M}$, $\mathcal{B}$, $\mathcal{I}$, ξ and f by the trial solutions

$$\begin{aligned} \mathcal{M}(t) &= e^{\lambda t}\overline{\mathcal{M}} \\ \mathcal{B}(t+a) &= e^{\lambda(t+a)}\overline{\mathcal{B}} \\ \mathcal{I}(t+a) &= e^{\lambda(t+a)}\overline{\mathcal{I}} \\ \xi(t,a) &= e^{\lambda t}\overline{\xi}(a;\lambda)\overline{\mathcal{I}} \\ f(t,a) &= e^{\lambda t}\overline{f}(a;\lambda)\overline{\mathcal{I}}, \end{aligned}$$

where λ is a complex number. This leads to the following algebraic problem for $\overline{\mathcal{Y}} = (\overline{\mathcal{M}}, \overline{\mathcal{B}}, \overline{\mathcal{I}})$:

$$\overline{\mathcal{Y}} = M(\lambda)\overline{\mathcal{Y}}.$$

The matrix M has the form

$$M(\lambda) = \begin{pmatrix} M_{m_u,m_u}(\lambda) & 0 & M_{m_u,I}(\lambda) \\ 0 & M_{b,b}(\lambda) & M_{b,I}(\lambda) \\ M_{I,m_u}(\lambda) & M_{I,b}(\lambda) & M_{I,I}(\lambda) \end{pmatrix}$$

The different entries of M are given by

$$M_{m_u,m_u}(\lambda) \stackrel{\text{def}}{=} \frac{1}{\lambda}[\beta_u(\overline{I}) - \mu_u(\overline{I})],$$

$$M_{m_u,I}(\lambda) \stackrel{\text{def}}{=} \frac{1}{\lambda}\frac{\partial}{\partial I}[\beta_u(\overline{I})\overline{m_u} - \mu_u(\overline{I})\overline{m_u}],$$

$$M_{b,b}(\lambda) \stackrel{\text{def}}{=} \int_0^\infty \beta_s(\bar{x}(a),\overline{I})\overline{\mathcal{F}}(a)e^{-\lambda a}\,da$$

$$M_{b,I}(\lambda) \stackrel{\text{def}}{=} \int_0^\infty \left\{ \frac{\partial}{\partial x}\beta_s(\bar{x}(a),\overline{I})\overline{\xi}(a;\lambda)e^{-\lambda a}\overline{\mathcal{F}}(a)\overline{b} \right.$$
$$\left. + \frac{\partial}{\partial I}\beta_s(\bar{x}(a),\overline{I})\overline{\mathcal{F}}(a)\overline{b} + \beta_s(\bar{x}(a),\overline{I})e^{-\lambda a}\overline{f}(a;\lambda)\overline{b} \right\}\, da.$$

$$M_{I,m_u}(\lambda) \stackrel{\text{def}}{=} \gamma_u(\overline{I})$$

$$M_{I,b}(\lambda) \stackrel{\text{def}}{=} \int_0^\infty \gamma_s(\overline{x}(a),\overline{I})\overline{\mathcal{F}}(a)e^{-\lambda a}\, da$$

$$M_{I,I}(\lambda) \stackrel{\text{def}}{=} \frac{\partial}{\partial I}\gamma_u(\overline{I})\overline{m_u}$$
$$+ \int_0^\infty \left\{ \frac{\partial}{\partial x}\gamma_s(\bar{x}(a),\overline{I})\overline{\xi}(a;\lambda)e^{-\lambda a}\overline{\mathcal{F}}(a)\overline{b} \right.$$
$$\left. + \frac{\partial}{\partial I}\gamma_s(\bar{x}(a),\overline{I})\overline{\mathcal{F}}(a)\overline{b} + \gamma_s(\overline{x}(a),\overline{I})e^{-\lambda a}\overline{f}(a;\lambda)\overline{b} \right\}\, da.$$

The matrices $\overline{\xi}(a;\lambda) = \left(\overline{\xi}_{ij}(a;\lambda)\right)_{\substack{1\le i\le k \\ j\in\Phi_s}}$ and $\overline{f}(a;\lambda) = \left(\overline{f}_{ij}(a;\lambda)\right)_{\substack{1\le i\le k \\ j\in\Phi_s}}$ have to be computed from

$$\begin{aligned} &\frac{\partial}{\partial a}\overline{\xi}(a;\lambda) = \frac{\partial}{\partial x}g_s(\overline{x}(a),\overline{I})\overline{\xi}(a;\lambda) + \frac{\partial}{\partial I}g_s(\overline{x}(a),\overline{I})e^{\lambda a} \\ &\overline{\xi}(0;\lambda) = 0, \end{aligned} \tag{5.6}$$

and

$$\begin{aligned} \frac{\partial}{\partial a}\overline{f}(a;\lambda) &= -\mu_s(\overline{x}(a),\overline{I})\overline{f}(a;\lambda) - \frac{\partial}{\partial x}\mu_s(\overline{x}(a),\overline{I})\overline{\xi}(a;\lambda)\overline{\mathcal{F}}(a) \\ &\quad - \frac{\partial}{\partial I}\mu_s(\overline{x}(a),\overline{I})e^{\lambda a}\overline{\mathcal{F}}(a), \\ \overline{f}(0;\lambda) &= 0. \end{aligned} \tag{5.7}$$

The characteristic equation $F(y,\lambda)$ is now defined by

$$F(y,\lambda) \stackrel{\text{def}}{=} 0,$$

where $F(y,\lambda) \stackrel{\text{def}}{=} \det(M(\lambda) - Id)$.

5.2 Finite-dimensional approximation of the characteristic equation

Analogously to the approximation G_ϵ of G, we will define an approximation F_ϵ of F in the following way: Let $M_\epsilon(\lambda) \stackrel{\text{def}}{=} M(a_\epsilon;y,\lambda)$, with

$$M(a;y,\lambda) \stackrel{\text{def}}{=} \begin{pmatrix} M_{m_u,m_u}(\overline{I},\lambda) & 0 & \Phi_1(\overline{I},\lambda)\overline{m_u} \\ 0 & \Psi_1(a;\overline{I},\lambda) & \Psi_2(a;\overline{I},\lambda)\overline{b} \\ M_{I,m_u}(\overline{I},\lambda) & \Psi_3(a;\overline{I},\lambda) & \Phi_2(\overline{I})\overline{m_u} + \Psi_4(a;\overline{I},\lambda)\overline{b} \end{pmatrix}$$

Here we singled out expressions which are only dependent on $\overline{I}$, λ, and eventually, on a. Also the explicit dependence on $\overline{I}$ has been included in the notation of entries of M. The reason is that, like the role of $\overline{I}$ played in algorithm 1, we will construct a system of ODE used to assemble F_ϵ, which becomes autonomous if the pair $(\overline{I}, \lambda)$ is known. The Φ's are obviously defined by

$$\begin{aligned}\Phi_1(\overline{I},\lambda) &\stackrel{\text{def}}{=} \frac{1}{\lambda}\frac{\partial}{\partial \overline{I}}[\beta_u(\overline{I}) - \mu_u(\overline{I})],\\ \Phi_2(\overline{I}) &\stackrel{\text{def}}{=} \frac{\partial}{\partial I}\gamma_u(\overline{I}),\end{aligned}$$

and, instead of using integral representations, we decide again to calculate the age-dependent submatrices Ψ_1, Ψ_2, Ψ_3, and Ψ_4 by solving the following system of ODEs:

$$\begin{aligned}\frac{\partial}{\partial a}\psi_1(a;\overline{I},\lambda) &= \beta_s(\bar{x}(a),\overline{I})\overline{\mathcal{F}}(a)e^{-\lambda a},\\ \frac{\partial}{\partial a}\psi_2(a;\overline{I},\lambda) &= \frac{\partial}{\partial x}\beta_s(\bar{x}(a),\overline{I})\overline{\xi}(a;\lambda)e^{-\lambda a}\overline{\mathcal{F}}(a)\\ &\quad + \frac{\partial}{\partial I}\beta_s(\bar{x}(a),\overline{I})\overline{\mathcal{F}}(a) + \beta_s(\bar{x}(a),\overline{I})e^{-\lambda a}\overline{f}(a;\lambda),\\ \frac{\partial}{\partial a}\psi_3(a;\overline{I},\lambda) &= \gamma_s(\overline{x}(a),\overline{I})\overline{\mathcal{F}}(a)e^{-\lambda a},\\ \frac{\partial}{\partial a}\psi_4(a;\overline{I},\lambda) &= \frac{\partial}{\partial x}\gamma_s(\bar{x}(a),\overline{I})\overline{\xi}(a;\lambda)e^{-\lambda a}\overline{\mathcal{F}}(a)\\ &\quad + \frac{\partial}{\partial I}\gamma_s(\bar{x}(a),\overline{I})\overline{\mathcal{F}}(a) + \gamma_s(\overline{x}(a),\overline{I})e^{-\lambda a}\overline{f}(a;\lambda),\end{aligned} \tag{5.8}$$

with initial conditions

$$\begin{aligned}\psi_1(0) &= 0,\\ \psi_2(0) &= 0,\\ \psi_3(0) &= 0,\\ \psi_4(0) &= 0.\end{aligned} \tag{5.9}$$

The finite dimensional approximation M_ϵ of M is obtained by first solving Eq. (5.8) only up to a finite time a_ϵ. Then the quantities Ψ_i, in M must be replaced by $\psi_i(a_\epsilon;\overline{I},\lambda)$, $i = 1,2,3,4$.

6. Continuation of equilibria

We are now able to use the results we have established so far to describe continuation techniques and the construction of bifurcation diagrams. Bifurcation diagrams show in general characteristic properties of equilibria (and other invariant sets) of dynamical systems under parameter variation, like their number, position and stability. We will describe how to compute such diagrams for the general n-species model. To do so, the dependence of the model equation on parameters must be introduced.

The red line this chapter follows is quite common in numerical continuation theory where an infinite-dimensional model is analysed: First a finite-dimensional approximation of the mapping defining the invariant set has to be found. This was the theme of the previous sections. The second step is now discussed in this section: The resulting finite-dimensional mappings can be analysed by finite-dimensional numerical continuation methods. Most frequently so-called predictor-corrector (PC-) methods are used. Because they are quite standard (see Allgower and Georg[1]), we only give a brief introduction to explain them in our context.

6.1 One parameter continuation.
Let $\alpha \in \mathbf{IR}$ denote a parameter occuring in some or all functions constituting Eq. (3.10), for which we like to study equilibrium behaviour under its variation. This means we fix all other parameters occuring in Eq. (3.10), and thus make the parameter space of our problem one dimensional. The parameter α is also called the free parameter. As ususal in the theory of continuation, we write Eq. (4.4) in the form

$$G(y, \alpha) = 0 \ , \ G : \mathbf{IR}^{p+1} \to \mathbf{IR}^{p}. \tag{6.1}$$

Here $p = n + k$ is the dimension of system (4.4). Eq. (6.1) generically implicitly defines a curve $y(s)$ (parametrized by s) in $p+1$-dimensional space. We like to compute this curve and describe briefly the usual predictor-corrector method for following such curves numerically, together with some remarks concerning our special situation. We will use the finite dimensional approximation G_ϵ of G. The following is a typical predictor-corrector method, adapted from Allgower and Georg[1] (page 48) which uses a tangent prediction and a Newton-like corrector. Note that algorithm 1 is heavily used by algorithm 3: Whenever, for a fixed value of (y, α), the value of $G_\epsilon(y, \alpha)$ must be evaluated, algorithm 1 is used. The corrector part of algorithm 3 is a variant of algorithm 2, having a redefined Newton step, accounting for the fact that the derivative $G'(y, \alpha)$ is a non-square matrix:

Algorithm 3: (Continuation of equilibria with one free parameter)

input

begin

u such that $G_\epsilon(u) = 0$; — *start point on curve, with* $u \stackrel{\text{def}}{=} (y, \alpha)$

$h > 0$; — *steplength with which curve is traversed*

end;

repeat — *predictor loop*

calculate $G'_\epsilon(u)$ numerically; — G'_ϵ *is the derivative of* G_ϵ *at* u, *a* $p \times (p+1)$*-matrix; numerical differentiation involved, like in the computation of* $\frac{d}{dy} G_\epsilon(y)$ *in algorithm 2*

compute tangent $t(u)$;

set $v = u + t(u) * h$; — *predictor step*

repeat — *corrector loop*

$v := u - G'_\epsilon(u)^+ G_\epsilon(u)$; — *Newton step*

Moore-Penrose inverse used: $A^+ \stackrel{\text{def}}{=} A^*(AA^*)^{-1}$, *with* A *being a* $p \times (p+1)$*-matrix*

$u := v$;

measure quality of correction; — *like contraction rate, distance from curve etc.*

until convergence or quality too bad;

check if step was accepted;

if step was not accepted, reduce stepsize h;

if step was accepted, $u := v$;

until traversing is stopped;

6.2 Two parameter continuation.
In the case of 2 free parameters, our specific aim is to compute *stability boundaries* of equilibria, projected in two-parameter space. Define $w = (\overline{m_u}, \overline{b}, \overline{I}, i\omega, \alpha^1, \alpha^2)$ and $H = (G, F)$, where α^1 and α^2 are now the two free parameters. We can abreviate the equation

$$G(y, \alpha^1, \alpha^2) = 0$$
$$F(y, i\omega, \alpha^1, \alpha^2) = 0$$

by simply writing $H(w) = 0$. The approximation of H by (G_ϵ, F_ϵ) is denoted by H_ϵ. It follows that $H_\epsilon : \mathbb{R}^{p+3} \to \mathbb{R}^{p+2}$. We can again use the continuation algorithm 2 to approximate the stability boundaries, defined by the condition $H(w) = 0$. But in this case we must replace algorithm 1 in algorithm 3 by an analogous algorithm dealing with the computation of $H_\epsilon(w)$, with w being given.

Algorithm 4: (Computation of $H_\epsilon(w)$) *comment:*

input

begin
$a_\epsilon > 0$; *approximating age*
$w^{(0)} = (\overline{m_u}^{(0)}, \overline{b}^{(0)}, \overline{I}^{(0)}, i\omega^{(0)}, \alpha^{1(0)}, \alpha^{2(0)})$; *initial guess*
end;

compute ages at which discontinuities occur *see algorithm 1*

a:=0; *start age*

repeat *integration along characteristic*

integrate system (4.2), (4.3), (4.5) with given $\overline{I}$ and in
parallel system (5.6), (5.7),(5.8) with given $\overline{I}$ and λ from age a on
stop eventually at discontinuities; *see algorithm 1*

until $a = a_\epsilon$;

define $R_0^s = r_0^s(a_\epsilon)$ and $\Theta^s = \theta^s(a_\epsilon)$;

define $\Psi_i = \psi(a_\epsilon, \overline{I}, i\omega)$, $i = 1, 2, 3, 4$;

assemble with these quantities $H_\epsilon(w)$;

evaluate $H_\epsilon(w)$;

Secondly, G_ϵ in algorithm 3 has obviously to be replaced by H_ϵ everywhere. The projections of the stability boundaries into the (α^1, α^2)-plane divide generically the plane into subregions with parameter constellations for which a given equilibrium is either locally asymptotically stable or unstable.

Remark: A problem of algorithms 2 and 3 is to find a first point on the respective curves. This is discussed in Kirkilionis et al. [8] while considering some continuation strategies.

7. Discussion.

The aim of this paper is twofold. It contains a framework for formulating PSPMs and also establishes a method how to investigate PSPMs by means of numerical continuation techniques. We discuss both aspects in the following.

7.1 Relation to other modeling approaches

The important step in the model formulation was the introduction of environmental interaction variables. These describe either internal feedback (like cannibalism) or external feedback (like a prey-predator relationship). Their introduction allows a separation of two phases in modeling, first the formulations of individual and population behaviour with given interaction variables (making the models linear) and then combining the submodels via the interaction variables (which makes them in general nonlinear). We think that in practice the formulation of feedback mechanisms and the formulation of submodels cannot be really separated, but it may be an iterative, hopefully convergent procedure.

What is the relationship with other formulations of PSPMs? As already noted in the begining of section 3, our formulation can be interpreted as a generalisation of the age-structured model formulated by Webb [18] in its integral form after integration along characteristics. In Diekmann et al.[2], a linear model for a PSPM has been proposed, together with some analysis concerning the existence of solutions and their stability under constant environmental conditions. It is also possible to transform our setting into this framework, and we describe this transformation briefly, and only on the individual level for comparison. The approach in Diekmann et al.[2] uses two essential ingredients: First the *reproduction kernel* Λ given by

$$\Lambda(t,y)(A) = \begin{array}{l}\text{the expected number of children, with relative birth}\\ \text{coordinates in } A, \text{ of an individual which at time } t \text{ has state } y.\end{array}$$

In the case $A = [0,s) \times \omega$, with ω a measurable subset of the i-state space Ω, $\Lambda(t,y)(A)$ is the expected number of offsprings produced in the time intervall $[t, t+s)$ with state-at-birth in Ω. The word 'relative' means that time is measured from t on.

The second ingredient is the *development and survival probability* u given by

$$u(t,y;s)(\omega) = \begin{array}{l}\text{probability that an individual which has state } y \text{ at time } t\\ \text{is alive } s \text{ time units later and then has a state in } \omega.\end{array}$$

The relationships with our model based on the rates β, μ and g are as follows. We again skip species indices because we are looking at a single population and make the following assumptions and definitions:

(a) The environmental interaction variable I in the linear autonomous case must be constant. We denote by $\overline{I}$ this constant value.

(b) The model we considered in this paper deals with relative time, the time-at-birth from which on each individual is traced. We now denote the time-at-birth by t' instead of t. Let $t \geq t'$ such that $x(t', t-t') = y$, where $x(t',a)$, $a = t - t' > 0$, is computed from Eq. (3.1).

Then, for $A = [0,s) \times \omega$,

$$\Lambda(t,y)(A) \stackrel{\text{def}}{=} \delta_{x_0} \int_0^s \beta(x(t', (t+\sigma)-t'), \overline{I}) \mathcal{F}(t', (t+\sigma)-t')\, d\sigma,$$

and

$$u(t,y;s)(\omega) \stackrel{\text{def}}{=} \delta_{x(t', (t+s)-t')} \mathcal{F}(t', (t+s)-t').$$

The symbol δ_x denotes the Dirac measure at $x \in \Omega$.

7.2 Numerical continuation
In this paper we presented a technique to follow equilibria of PSPMs while varying one (free) parameter and also to compute their stability boundaries in two-parameter space (two free parameters). The following questions naturally arise and must be answered in the future:

- How can we detect branching points, i.e. points where the parametrized curve we follow is intersecting other branches? Can we compute branching points accurately, given the fact that G is a finite-dimensional approximation of an infinite-dimensional problem? For practical purposes we must also be able to switch branches at these points. This will be discussed in Kirkilionis et al. [8].

- There are two generic codim 1 bifurcations, the fold- and the Hopf-bifurcation. Usually one traces them along a curve of equilibria $x(s)$ (s being the parametrization) satisfying $G(x(s), \alpha(s)) = 0$ by looking at sign-switches of the functionals

$$\Psi_{fold} = \det\left(\frac{\partial G(x,\alpha)}{\partial x}\right)$$

  which detects fold-points, and

$$\Psi_{Hopf} = \det\left(2\frac{\partial G(x,\alpha)}{\partial x} \odot I\right),$$

  detecting Hopf-points, where '$\odot$' is the so-called 'bialternate' product, see Kuznetsov [11]. After detection, one has to check certain nondegeneracy conditions to be sure that a bifurcation actually occurs. The question is now if a similar way of tracing bifurcation points is possible in our context?

7.3 Final remarks
We have so far not provided a rigid convergence proof and error estimates. But in Kirkilionis et al. [8] we will treat some examples and test the numerical stability of the algorithm we proposed. Also some details of the numerical implementation are provided there, see also Kirkilionis [9]. Finally, we express our hope that in the future numerical approaches, like the one presented here, will enhance our understanding of phenomena resulting from individual differences in populations.

Acknowledgement: We like to thank Hans Metz, Mats Gyllenberg and Horst Thieme for inspiration and advise.

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