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Steady-state analysis of structured population models

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Abstract

Our systematic formulation of nonlinear population models is based on the notion of the environmental condition. The defining property of the environmental condition is that individuals are independent of one another (and hence equations are linear) when this condition is prescribed (in principle as an arbitrary function of time, but when focussing on steady states we shall restrict to constant functions). The steady-state problem has two components: (i) the environmental condition should be such that the existing populations do neither grow nor decline; (ii) a feedback consistency condition relating the environmental condition to the community/population size and composition should hold. In this paper we develop, justify and analyse basic formalism under the assumption that individuals can be born in only finitely many possible states and that the environmental condition is fully characterized by finitely many numbers. The theory is illustrated by many examples. In addition to various simple toy models introduced for explanation purposes, these include a detailed elaboration of a cannibalism model and a general treatment of how genetic and physiological structure should be combined in a single model.

Keywords: Population dynamics; Physiological structure; Nonlinear; Feedback via the environment; Deterministic at population level; Cannibalism; Finitely many states at birth; Population genetics; Adaptive dynamics; Competitive exclusion

1. Introduction

1.1. Aim of the paper

The aim of this paper is to provide a technical framework for analysing the existence (as well as dependence on parameters) of steady states for very large classes of population models, including models for interacting physiologically structured populations. In particular, we show that the steady-state problem can be brought into the form

$$\begin{cases} b = L(I)b, \\ I = G(I)b, \end{cases} \tag{1.1}$$

where

(i) b is a vector of *birth rates* (each component b_j of b is the steady rate at which individuals are born with the state at birth numbered j).

(ii) I is a vector describing the *environmental conditions* as far as they are influenced by interaction. The defining property is that individuals are independent of one another when I is given (in general as a function of time; in this paper we restrict to constant I).

(iii) $L(I)$ is the *next-generation matrix*. The (i, j)-element of $L(I)$ is the expected number of offspring with birth state i born to an individual that itself was born with state j, given steady environmental conditions as specified by I.

(iv) $G(I)$ is the *feedback matrix*. The (i, j)-element of $G(I)$ gives the lifetime contribution to the ith component I_i of I of an individual born with state j, given steady environmental conditions as specified by I.

Following up on earlier work (Diekmann et al., 2001; Kirkilionis et al., 2001) we include an operational description of how to derive $L(I)$ and $G(I)$ from more basic modelling ingredients, such as maturation-, death-, and birth-rates. Moreover, we develop

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constructive methods for analysing the solution structure of problem (1.1), exploiting the fact that it is linear in b.

A key feature of (1.1) is that we consider b and I as elements of, respectively, $\mathbf{R}^k$ and $\mathbf{R}^n$, that is, as finite-dimensional variables. The motivation is twofold:

- many models have this form,
- even if they do not, a computational approach requires an approximation which involves only finitely many dimensions (Claessen and de Roos, 2002).

Yet in Section 3.1 we discuss briefly a more general formulation in terms of birth rates which, in the way they specify the state-at-birth, are measures. We show when and how this more general problem reduces to (1.1).

As explained by Diekmann et al. (2001) and illustrated by examples below, identifying the so-called environmental interaction variable (or, alternatively, input) I is a helpful illuminating step in the systematic formulation of structured population models. Usually, the components of I are biologically interpretable and easily (in principle at least) measurable quantities, like food availability and predation pressure. The matrix $L(I)$ then captures how population growth or decline depends on the environmental conditions. The second model ingredient, $G(I)$, captures how, in turn, the environmental conditions are determined by the population size and composition. It closes the feedback loop that we cut by introducing I. To some extent it is helpful to think about this closing of the feedback loop as a two step procedure: first an *output* is computed which then is fed back as input via a *feedback map*. The contributions to the output of the individuals can simply be added since, given the input, individuals are independent (so "output" is in terms of *linear* functionals). In the initial stage of the (cyclic!) modelling process, such a distinction between input and output is often helpful. Once the final model structure has emerged, one can dispense of output and focus on input, as we shall do in this paper. (A minor point is that outputs are naturally equal to zero in the absence of a population, whereas, biologically, inputs need not necessarily have this property; yet (1.1) embodies that with a tailor made choice of input it too will be zero in the absence of a population. Readers who find this paragraph fuzzy are asked to have a look at Example 1.2 in Section 1.3, where, at first, the input consists of food density and the availability of mates while eventually it consists of densities of, respectively, juveniles and adults.)

Clearly $L(I)$ is a positive matrix. When we consider only one species the matrix $L(I)$ will be, as a rule, irreducible and so it has a well-defined dominant eigenvalue, the basic reproduction ratio $R_0(I)$ (Diekmann et al., 1990), and a corresponding positive eigenvector which is unique up to a multiplicative factor c. The first equation of (1.1) then amounts, for $b\neq 0$, to the scalar equation $R_0(I)=1$ and in this sense (1.1) is a system of $(n+1)$ equations in as many unknowns, namely the n components of I and the scalar c. In the multi-species case, however, $L(I)$ is reducible (in fact to a block-diagonal form) and there are more than one positive eigenvalue with corresponding positive eigenvectors. Then the first equation of (1.1) amounts to as many conditions on I as there are species, a fact that immediately leads to a version of the principle of competitive exclusion, see Section 2.2.

Traditionally, structured population models have been formulated as partial differential equations specified in terms of vital rates, consumption rates, etc. (Calsina and Saldaña, 1995, 1997; Gurtin and MacCamy, 1974; Metz and Diekmann, 1986; Tucker and Zimmermann, 1988; Webb, 1985). The derivation of $L(I)$ and $G(I)$ from such basic modelling ingredients may involve a substantial amount of work. Building on our earlier papers (Diekmann et al., 1998, 2001) we shall both explain the general methodology and present several examples. We emphasize that this work pays off: once the problem has been brought into the form (1.1) the analysis is rather simple and many conclusions can be drawn. Computational procedures to derive $L(I)$ and $G(I)$ are implemented in the computer package *BASE* and so is a numerical continuation method to solve (1.1) (Kirkilionis et al., 2001).

1.2. Structure of the paper

In the next and final subsection of this introduction the basic idea is illustrated by two very simple examples. For these examples the methodology is, in fact, a bit of an overkill. Yet they may serve to catalyse understanding by illustrating two key features: bookkeeping in generation perspective and feedback via environmental variables. As a bonus we find in Section 3.3 that a rather complex size-structured predator–prey model exhibits exactly the same steady-state solution structure as the simple variant studied in Section 1.3.

Section 2 is devoted to the analysis of system (1.1). It starts out by showing how a branch of positive solutions bifurcates from the trivial solution when a parameter passes a critical value (and how one can compute whether the branch extends to sub- or supercritical parameter values). Next, it explains how the number of species is reflected in the structure of L and G. And finally it is demonstrated how the explicit introduction of I serves as an ideal starting point for analysing a model in the spirit of adaptive dynamics, that is, with an aim to understand how natural selection has shaped life history.

Section 3 deals with the derivation of system (1.1) when the starting point is a model of a physiologically structured population. Section 3.1 describes the class of models we consider (and discusses size-structured predators as an illustrative example), while in Section 3.2 the corresponding steady state problem is formulated. This formulation reduces to (1.1) whenever there are only finitely many states-at-birth possible. In Section 3.3 the example of a size-structured predator is elaborated. It is found that, due to the use of I and the generation perspective, the insights derived by analysing the unstructured variant in Section 1.3 carry over immediately.

Section 4 presents two case studies. The first centres around cannibalism in a size-structured population. We motivate the choice of I as well as various other aspects of the model formulation. Next, we demonstrate how extremely simple the computation of the direction of bifurcation is, after the preparatory work involved in writing the steady-state problem in the form (1.1). In the spirit of earlier work by van den Bosch et al. (1988) we derive ecological understanding by giving a careful interpretation, in terms of energy loss and gain at the individual level, of the criterion for subcritical bifurcation. Under additional assumptions we even derive the global bifurcation diagram.

The second case study of Section 4 concerns the intertwining of genetic and physiological structure. The key point is to show how ecologically meaningful forms of density dependence can, with hardly any strain, be incorporated in genetic models (we restrict the presentation to the one-locus two-alleles diploid situation). While at work we expose some of the knacks of dealing with the first equation of (1.1) and, subsequently, with the equations for allele frequencies.

In the short final Section 5 we reiterate our main conclusions and list some open problems that we intend to address in the near future.

This paper is admittedly rather long. Yet, we think, the information density is about right. Having it all in one paper, rather than distributing it over two or three, is efficient: There is no need (neither for the writers nor for the readers) to repeat motivating introductions and conclusions. For the apprehensive reader, who fears to have to devote too much time, we stress the independence of various parts: the Sections 2, 3, 4.1 and 4.2 can be read and understood independently of one another (but Section 4.1 does employ notation introduced in Section 3; in fact, by showing the framework in action, Section 4.1 serves to reinforce the understanding of Sections 2.1 and 3).

1.3. The basic idea illustrated by two simple examples

We start out by considering the Rosenzweig–MacArthur prey–predator model.

Example 1.1. We assume that the dynamics of the prey population density S and the predator population density P is governed by the differential equations

$$\frac{dS}{dt} = \lambda S - \mu S - \nu S^2 - \frac{\alpha SP}{1+\alpha hS}, \tag{1.2}$$

$$\frac{dP}{dt} = \frac{\beta SP}{1+\alpha hS} - \gamma P. \tag{1.3}$$

The first step in the analysis is to rewrite the system in a form in which all interaction is via a variable I:

$$\frac{dS}{dt} = \left(\lambda - \mu - \nu I_1 - \frac{\alpha I_2}{1+\alpha h I_1}\right) S. \tag{1.4}$$

$$\frac{dP}{dt} = \left(\frac{\beta I_1}{1+\alpha h I_1} - \gamma\right) P \tag{1.5}$$

with

$$I_1 = S, \tag{1.6}$$

$$I_2 = P. \tag{1.7}$$

We then have

$$L(I) = \begin{pmatrix} L_{11}(I) & 0 \\ 0 & L_{22}(I) \end{pmatrix} \tag{1.8}$$

with

$$L_{11}(I) = \frac{\lambda}{\mu + \nu I_1 + \frac{\alpha I_2}{1+\alpha h I_1}} \tag{1.9}$$

and

$$L_{22}(I) = \frac{\beta I_1}{\gamma(1+\alpha h I_1)}. \tag{1.10}$$

The derivation is as follows. Predators experience a constant probability γ per unit of time of dying, so they live on average for $1/\gamma$ units of time. They produce offspring at a rate $\beta I_1/(1+\alpha h I_1)$. The quantity $L_{22}(I)$ is the product of these two factors. The expression for $L_{11}(I)$ is obtained in exactly the same way. We shall assume that $\beta > \alpha\gamma h$, that is, that the predator population does grow under the best possible conditions ($I_1 \to \infty$).

Clearly $L_{22}(I) = 1$ is equivalent to

$$I_1 = \frac{\gamma}{\beta - \alpha\gamma h} \tag{1.11}$$

and $L_{11}(I) = 1$ is equivalent to

$$I_2 = (1+\alpha h I_1)\frac{\lambda - \mu - \nu I_1}{\alpha}. \tag{1.12}$$

The first equation of (1.1) tells us that

- either $L_{11}(I) = 1$ or $S = 0$

and

- either $L_{22}(I) = 1$ or $P = 0$.

Clearly, if $S=0$, then $I_1=0$ so $L_{22}(I)=0$ and therefore $P=0$ as well. If, on the other hand, $P=0$, then $I_2=0$ so $L_{11}=\frac{\lambda}{\mu+\nu I_1}$ and then $L_{11}(I)=1$ amounts to $S=I_1=\frac{\lambda-\mu}{\nu}$.

Combining the information gathered above we conclude that, apart from the trivial solution $(S, P)=(0, 0)$, we have the solutions

$$(S,P)=\left(\frac{\lambda-\mu}{\nu},0\right) \tag{1.13}$$

and

$$(S,P)=\left(\frac{\gamma}{\beta-\alpha\gamma h},\left(1+\alpha h\frac{\gamma}{\beta-\alpha\gamma h}\right)\frac{1}{\alpha}\left(\lambda-\mu-\nu\frac{\gamma}{\beta-\alpha\gamma h}\right)\right), \tag{1.14}$$

which, of course, need to be positive in order to make biological sense. Note that we did not use the second equation in (1.1). Also note that the two solutions (1.13) and (1.14) coincide precisely when

$$L_{22}(I)=1\Leftrightarrow I=\begin{pmatrix}\frac{\lambda-\mu}{\nu}\\0\end{pmatrix}. \tag{1.15}$$

The biological interpretation is as follows. Whether or not the predator can 'invade' successfully the environment as set and formed by the prey is determined by the sign of $L_{22}(I)$–1, with $I=\begin{pmatrix}\frac{\lambda-\mu}{\nu}\\0\end{pmatrix}$ (recall that $L_{22}(I)$ is the expected number of offspring produced by a predator in the environment specified by I). A change in the solution structure should therefore occur when this sign switches.

A more mathematical reformulation is in terms of bifurcations. Consider, for instance, λ as a parameter. Then the two solutions correspond to branches in a bifurcation diagram. If we follow the branch with $P=0$, we notice a stability switch at the parameter value $\lambda=\lambda_c=\mu+\nu\gamma/(\beta-\alpha\gamma h)$ which is such that $L_{22}(I_c)=1$ for $I_c=\begin{pmatrix}\frac{\lambda_c-\mu}{\nu}\\0\end{pmatrix}$. At $\lambda=\lambda_c$ a transcritical bifurcation and an exchange of stability take place (see Fig. 1).

In Section 3.3 we show that a much more complicated prey–predator model than the one considered here, viz., a model in which the predator is size-structured, has exactly the same solution structure. The key features are

- L_{22} depends only on I_1 and in a monotone manner;
- given I_1, L_{11} depends monotonically on I_2.

Of course, we do not obtain explicit expressions for the steady states in the more complicated situation.

As a second introductory example we consider a population with structure, but a very simple structure with only two possible states. Biologically, the example is motivated by the dynamics of insect populations (Nisbet and Gurney, 1983).

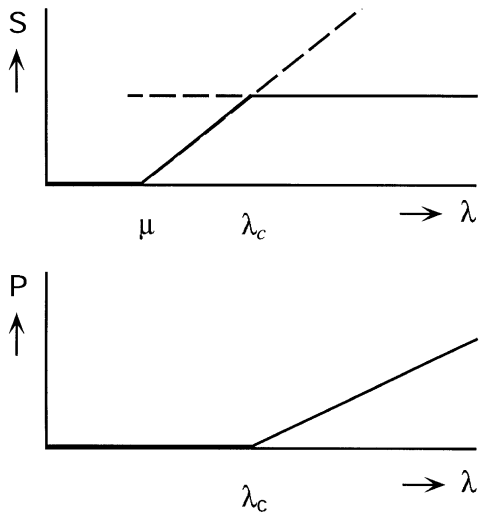

Fig. 1. Bifurcation diagram of the prey-predator system of Example 1.1.

Example 1.2. Consider a structured single-species model in which the individuals can be in either of two states: juvenile and adult. Juveniles are recruited to the adult state at a per capita rate ρ and adults give birth to juveniles at a per capita rate β. Juveniles and adults are subject to mortality given by the per capita death rates μ_J and μ_A respectively.

We shall assume that the death rates μ_J and μ_A are given constant parameters. On the other hand, the birth rate and the recruitment rate depend on the environmental condition (input) and thus incorporate interactions among individuals. We assume that adults and juveniles interact only with individuals of the same state. Juveniles compete for food and adults need mates to reproduce. This is modelled by assuming that ρ depends on food density and β on the availability of mates. To obtain expressions for ρ and β in terms of the environmental input we must specify how food is produced and consumed and model how availability of mates depends on the adult density. During this process we also find the most convenient choice of input variables.

We assume chemostat dynamics of food production and removal and a linear functional response for food consumption. This means that

$$\frac{dS}{dt}=D(S_0-S)-YSJ, \tag{1.16}$$

where S is the food density, S_0 is the constant food density in an external reservoir, D is the dilution rate, Y is the consumption rate proportionality constant, and J is the juvenile density. We now invoke a time-scale argument by assuming that the production and consumption of food happen at a much faster time-scale than the other population dynamical processes, i.e.,

maturation, reproduction and death. Formally, this is achieved by replacing D and Y in (1.16) by D/ε and Y/ε, respectively, and letting $\varepsilon \to 0$. This results in the so-called quasi-steady-state approximation

$$S = \frac{1}{1+qJ}, \tag{1.17}$$

where we have scaled S_0 to 1 and introduced the parameter $q = Y/D$. We assume that the rate of recruitment to the adult state is directly proportional to the food density thus arriving at

$$\rho = \phi S = \phi \frac{1}{1+qJ} \tag{1.18}$$

for some positive real number ϕ.

There are several possibilities to model mechanistically the availability M of mates as a function of adult density A (Gyllenberg et al., 1999; Heesterbeek and Metz, 1993). Here we choose the following:

$$M = \frac{1+\alpha A}{1+\alpha+\alpha A}. \tag{1.19}$$

We call the parameter α the *strength of the Allee effect*. If $\alpha = 0$, then M reduces to the constant 1, that is, the availability of mates does not depend on adult density or, in other words, there is no Allee effect. In the limiting case $\alpha = \infty$ one has

$$M = \frac{A}{1+A}. \tag{1.20}$$

This means that at low adult densities (effectively at $A = 0$) there are no mates available. We call this a full Allee effect.

We assume that the per capita birth rate is directly proportional (with proportionality constant θ) to the availability of mates:

$$\beta = \theta M = \theta \frac{1+\alpha A}{1+\alpha+\alpha A}. \tag{1.21}$$

We now observe from (1.18) and (1.21) that the model fits exactly into our framework if we choose $I = (I_1, I_2) = (J, A)$ as input. We then have

$$\rho = \rho(I_1) = \phi \frac{1}{1+qI_1}, \tag{1.22}$$

$$\beta = \beta(I_2) = \theta \frac{1+\alpha I_2}{1+\alpha+\alpha I_2}. \tag{1.23}$$

For constant input $I = (I_1, I_2)$ both ρ and β are constant and one can easily compute the number $L(I)$ which, by definition, is the expected number of offspring born to an individual during its entire life. To be able to reproduce, an individual must first reach the adult state. This happens with probability $\rho/(\rho+\mu_J)$. Once an adult, the individual will have an exponentially distributed (with expectation $1/\mu_A$) remaining lifetime and will produce β offspring per unit of time. We therefore conclude that

$$L(I) = \frac{\rho(I_1)}{\rho(I_1)+\mu_J} \frac{\beta(I_2)}{\mu_A}. \tag{1.24}$$

The first equilibrium condition in (1.1) now reads: Either $b = 0$ or b is arbitrary and

$$L(I) = 1. \tag{1.25}$$

In view of (1.24), condition (1.25) is one equation in two unknowns and we see that, in contrast to the preceding example, we cannot solve for the nontrivial steady state without the other equilibrium conditions.

We now derive the second equilibrium condition $I = G(I)b$ in such a way that it illustrates the more general approach that we are going to develop in Section 3.1. Consider a newborn individual. The probability that it is still alive and in the juvenile state at age a is

$$e^{-(\rho+\mu_J)a}. \tag{1.26}$$

Its lifetime contribution to $I_1 = J$ is obtained by integrating (1.26) over all ages:

$$\int_0^\infty e^{-(\rho+\mu_J)a}\, da = \frac{1}{\rho+\mu_J}. \tag{1.27}$$

As already noted when deriving (1.24), the lifetime contribution to I_2, the density of adults, is

$$\frac{\rho}{(\rho+\mu_J)\mu_A}. \tag{1.28}$$

We have thus arrived at the equations

$$I_1 = \frac{1}{\rho(I_1)+\mu_J} b, \tag{1.29}$$

$$I_2 = \frac{\rho(I_1)}{(\rho(I_1)+\mu_J)\mu_A} b, \tag{1.30}$$

or, in short, $I = G(I)b$, supplementing (1.25).

The expected number of offspring born to an individual in the virgin environment is

$$L(0) = \frac{\phi}{\phi+\mu_J} \frac{\theta}{(1+\alpha)\mu_A}. \tag{1.31}$$

If $L(0) > 1$, then a small population will initially grow, whereas if $L(0) < 1$ it will go extinct. Note, in particular, that if $\alpha = \infty$, then $L(0) = 0$. In words, if there is a full Allee effect, then invasion is impossible: the trivial solution is (locally) stable.

Combining (1.29) and (1.30) one finds

$$I_2 = \frac{\rho(I_1)}{\mu_A} I_1. \tag{1.32}$$

Substituting (1.32) and (1.18) into (1.25) one obtains the equation

$$L(I_1) = \frac{\phi}{\phi+\mu_J(1+qI_1)} \frac{\theta}{\mu_A} \frac{\mu_A(1+qI_1)+\alpha\phi I_1}{\mu_A(1+qI_1)(1+\alpha)+\alpha\phi I_1} = 1 \tag{1.33}$$

in the single unknown I_1. Once $J=I_1$ has been solved from (1.33), the steady adult density $A=I_2$ is obtained from (1.32).

Next, we consider bifurcation from the trivial solution. In Section 2.1 we describe in general terms both local and global bifurcations much in the spirit of this example.

We consider θ as the bifurcation parameter and write $L(I_1, \theta)$ instead of $L(I_1)$. Note that $L(0, \theta)$ is linear in θ. From this fact we infer that there exists a unique $\theta=\theta_c$ such that

$$L(0,\theta_c) = 1 \tag{1.34}$$

unless $\alpha=\infty$ in which case (as noted above) $L(0, \theta)=0$ for all θ. Solving (1.33) for θ at $I_1=0$ one finds

$$\theta_c = \frac{\mu_A}{\phi}(1+\alpha)(\phi+\mu_J). \tag{1.35}$$

If $\alpha<\infty$, then a branch of nontrivial equilibria (a curve in the (θ, I_1)-plane the points of which satisfy Eq. (1.33)) bifurcates from the point $(I_1,\theta)=(0, \theta_c)$.

Eq. (1.33) can be solved for the parameter θ as a function of I_1:

$$\theta = \frac{\mu_A}{\phi}(\phi+\mu_J(1+qI_1))\frac{\mu_A(1+qI_1)(1+\alpha)+\alpha\phi I_1}{\mu_A(1+qI_1)+\alpha\phi I_1}. \tag{1.36}$$

From this expression we see that as I_1 tends to infinity the curve will approach an asymptote which is a straight line with positive slope. To determine the direction of bifurcation at $(0, \theta_c)$ for $0\leqslant\alpha<\infty$ we differentiate θ with respect to I_1 and evaluate at $I_1=0$. The result is

$$\frac{d\theta}{dI_1}\Big|_{I_1=0} = \left(\frac{1}{\phi}(1+\alpha)\mu_A\mu_J q - \alpha^2(\phi+\mu_J)\right). \tag{1.37}$$

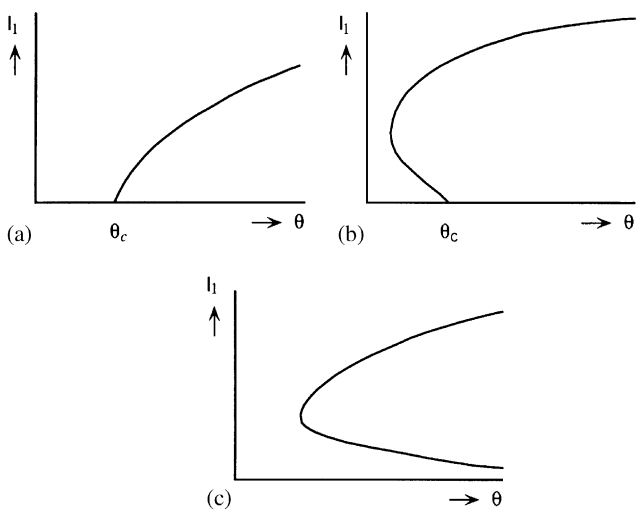

Fig. 2. Bifurcation diagrams of the model treated in Example 1.2 for different strengths of the Allee-effect. (a): supercritical bifurcation when the Allee-effect is weak $(0\leqslant\alpha<\bar{\alpha})$, (b): subcritical bifurcation when the Allee-effect is strong $(\bar{\alpha}<\alpha<\infty)$, (c): full Allee-effect $(\alpha=\infty)$ gives nonintersecting branches.

The right-hand side of (1.37) is quadratic in α and therefore we conclude that there is a critical value $\bar{\alpha}$ of the strength of the Allee-effect such that for a weak (or no) Allee-effect $(0\leqslant\alpha<\bar{\alpha})$ there is a supercritical bifurcation (Fig. 2(a)) but for a strong Allee-effect $(\bar{\alpha}<\alpha<\infty)$ there is a *subcritical* bifurcation (Fig. 2(b)). In the case of a full Allee-effect $(\alpha=\infty)$ the branch of nontrivial equilibria does not intersect the branch of trivial solutions (Fig. 2(c)).

2. General methodology

In this section we implement the basic idea presented in the previous section and study the steady-state problem in a systematic way.

2.1. Bifurcation from the trivial solution at a simple eigenvalue

Consider a population model which distinguishes k possible birth states and for which the environmental condition has n components. Assume that the $k\times k$ next-generation matrix L and the $n\times k$ feedback matrix G are continuously differentiable functions of the environmental condition I and a real parameter θ.

The steady-state problem

$$\begin{cases} b = L(I,\theta)b, \\ I = G(I,\theta)b \end{cases} \tag{2.1}$$

has the branch $(b, I, \theta)=(0, 0, \theta)$ of trivial solutions. Our aim is to deduce necessary and sufficient conditions for the bifurcation of a branch of non-trivial solutions. Along a branch of nontrivial solutions $L(I, \theta)$ necessarily has eigenvalue one. So only those θ for which $L(0, \theta)$ has eigenvalue one are candidates for bifurcation from the trivial branch.

The interpretation requires that $L(I,\theta)$ is a nonnegative matrix and that b is a nonnegative eigenvector. In the multi-species case $L(I, \theta)$ is decomposable into block diagonal form (see Section 2.2 for details) and accordingly there are, in general, several positive eigenvalues with corresponding nonnegative eigenvectors. As a rule, each of the diagonal blocks is irreducible or even primitive. Recall that a $k\times k$ matrix L is irreducible if and only if for each $(i, j)\in\{1,2, \ldots k\}^2$ there exists an integer p such that the (i, j)-element of L^p is strictly positive. L is primitive if and only if there exists a p such that all the elements of L^p are strictly positive. The biological interpretation of irreducibility is that every individual (independent of its state-at-birth) will sooner or later with positive probability get descendants (not necessarily children as grandchildren, great-grandchildren, etc., should be included) of all possible birth states. The stronger primitivity condition excludes cycling at

the generation level: from some generation onwards, each generation of a clan will with positive probability contain individuals of any possible state-at-birth, independently of the state at which the ancestor was born.

According to the Perron–Frobenius theorem an irreducible nonnegative square matrix L has a unique positive eigenvalue R which is dominant (all other eigenvalues have absolute value less than or equal to R) and algebraically simple. If L is primitive, then R is strictly dominant (the other eigenvalues have absolute value strictly less than R). In our case the eigenvalues of $L(0, \theta)$ are functions of the parameter θ and it is not expected that two or more of them (corresponding to different diagonal blocks, or species) are equal to one for the same value of θ. Hence the following theorem covers the generic situation.

Theorem 2.1. *Assume that 1 is a simple eigenvalue of* $L(0, \theta)$ *for* $\theta=\theta_c$ *with associated eigenvector* ${}^1b$ *and adjoint eigenvector* ${}^1b^*$, *normalized, say, such that* $|{}^1b|=1$ *and* $\langle {}^1b^*, {}^1b\rangle = 1$. *Assume that*

$$\left\langle {}^1b^*, \frac{\partial L}{\partial \theta}(0,\theta_c)\,{}^1b \right\rangle \neq 0. \tag{2.2}$$

Then (2.1) *admits a branch of nontrivial solutions*

$$\begin{aligned} b &= \varepsilon\,{}^1b + o(\varepsilon),\\ I &= \varepsilon G(0,\theta_c)\,{}^1b + o(\varepsilon),\\ \theta &= \theta_c - \varepsilon \frac{\left\langle {}^1b^*, \left(\frac{\partial L}{\partial I}(0,\theta_c) G(0,\theta_c)\,{}^1b\right){}^1b\right\rangle}{\left\langle {}^1b^*, \frac{\partial L}{\partial \theta}(0,\theta_c)\,{}^1b\right\rangle} + o(\varepsilon), \end{aligned} \tag{2.3}$$

parametrized by ε *(with* ε *varying in a neighbourhood of zero; but only solutions for* $\varepsilon>0$ *make biological sense!). For* (b, I, θ) *in a neighbourhood of* $(0, 0, \theta_c)$, *these and the trivial solutions are the only solutions of* (2.1).

For a more general result, requiring slightly stronger assumptions, see Crandall and Rabinowitz (1971, Theorem 1.7; Chow and Hale 1982, Theorem 5.1, Section 5.5); Smoller (1994, Theorem 13.5). But because it is instructive to see how the special structure of (2.1) makes some technical aspects a bit easier we present the main part of the proof in the present notation and setting in Appendix A. Here in the main text we give only a heuristic sketch based on Taylor expansions. The approach is to substitute the Taylor expansions

$$b = \varepsilon\,{}^1b + \cdots, \tag{2.4}$$

$$I = \varepsilon\,{}^1I + \cdots, \tag{2.5}$$

$$\theta = \theta_c + \varepsilon\,{}^1\theta + \cdots \tag{2.6}$$

into (2.1) (or, rather, the Taylor expanded version of (2.1)) and then to collect terms of the same order to determine ${}^1b$, ${}^1I$, ${}^1\theta$, … . From the first equation of (2.1) one immediately obtains

$$L(0,\theta_c)\,{}^1b = {}^1b \tag{2.7}$$

or, in words, that ${}^1b$ should be an eigenvector corresponding to the eigenvalue 1 of $L(0, \theta_c)$. We may normalize ${}^1b$ any way we want and this corresponds just to a rescaling of ε. The second equation of (2.1) gives

$${}^1I = G(0,\theta_c)\,{}^1b, \tag{2.8}$$

that is, an explicit formula for ${}^1I$ in terms of ${}^1b$. Continuing in the first equation to the next order we find

$${}^2b = L(0,\theta_c)\,{}^2b + \frac{\partial L}{\partial I}(0,\theta_c)\,{}^1I\,{}^1b + \frac{\partial L}{\partial \theta}(0,\theta_c)\,{}^1\theta\,{}^1b \tag{2.9}$$

which can be solved for ${}^2b$ if and only if we choose ${}^1\theta$ such that the sum of the last two terms belongs to the range of $Id-L(0, \theta_c)$. The solvability condition is found by pairing Eq. (2.9) with ${}^1b^*$ and reads

$${}^1\theta = -\frac{\left\langle {}^1b^*, \frac{\partial L}{\partial I}(0,\theta_c)\,{}^1I\,{}^1b\right\rangle}{\left\langle {}^1b^*, \frac{\partial L}{\partial \theta}(0,\theta_c)\,{}^1b\right\rangle}. \tag{2.10}$$

Note that (2.10) is a formula for the *direction of bifurcation*, that is, one can read off whether the biologically meaningful solutions with $\varepsilon>0$ exist for $\theta>\theta_c$ or for $\theta<\theta_c$.

Theorem 2.1 is a local result. It tells us that a branch of nontrivial nonnegative solutions ('nonnegative' meaning that $b\in\mathbf{R}^k_+ = \{b\in\mathbf{R}^k : b_i\geqslant 0, i=1,2,\ldots,k\}$ and hence the solutions make biological sense) exists near $(b, I, \theta) = (0, 0, \theta_c)$ and it gives some information about the initial shape of this branch. The goal, of course, is to be able to follow the branch away from the neighbourhood of $(0, 0, \theta_c)$.

A practical method is numerical continuation. We refer to Kuznetsov (1998, Section 10.2.1) for an exposition of the general methodological issues and to Kirkilionis et al. (2001) for an elaboration in the context of structured population models.

A theoretical result of great importance is Rabinowitz' global bifurcation theorem (Rabinowitz, 1971; Chow and Hale, 1982, Section 5.8; Smoller, 1994, Section 13C). Essentially, this result states that either the branch extends to infinity in $\mathbf{R}^k_+\times\mathbf{R}^n\times\mathbf{R}$ or it meets another bifurcation point $(0, 0, \tilde{\theta}_c)$. The application of this result to structured population problems was pioneered by Cushing (1985); see also the very readable exposition in Cushing (1998, Sections 1.2.3 and 2.2.2).

In Appendix A we present a version of the global bifurcation theorem which directly applies to (2.1).

2.2. Multi-species models

As already noted in Example 1.1, our general framework incorporates multi-species models. The model describes p species if the next-generation matrix L is of the block diagonal form

$$L = \begin{pmatrix} L_1 & & 0 \\ & L_2 & \\ & & \ddots \\ 0 & & \\ & & L_p \end{pmatrix}, \tag{2.11}$$

where each block is a square matrix that cannot be further decomposed into diagonal blocks. (Here one has to be careful; the birth states may be in the 'wrong' order, so that the matrix or submatrix is not in block diagonal form at the start of the analysis, but then a reordering of the birth states will bring it into such a form.)

Let $b=(b_1\ b_2\cdot\cdots\ b_p)^T$ be a decomposition of b according to the block structure of L. The component b_j is then the vector of birth rates of the j th species. The feedback matrix G takes the form

$$G = (G_1\ G_2\cdots G_p), \tag{2.12}$$

where the submatrix G_j has the same number of columns as L_j for all $j=1, 2,\ldots, p$. G_j is the lifetime contribution to I by an individual of the jth species.

The interaction between the populations is incorporated in the choice of I and the dependence of L and G on I (which, as we show in Section 3.1, is derived from the dependence of more basic modelling ingredients on I). The special structure of L and G implies that the steady-state condition (2.1) takes the form

$$\begin{aligned} b_1 &= L_1(I,\theta)b_1,\\ b_2 &= L_2(I,\theta)b_2,\\ &\vdots\\ b_p &= L_p(I,\theta)b_p,\\ I &= G_1(I,\theta)b_1 + G_2(I,\theta)b_2 + \cdots + G_p(I,\theta)b_p. \end{aligned} \tag{2.13}$$

The key point is that the first p components of (2.13) are coupled only by I.

Clearly, system (2.13) may have solutions in which one or more, say k, of the species are missing. Without loss of generality, we may assume that at least the last species is among the missing ones. Whether or not this missing species starts to grow when introduced in small numbers can be decided (at least from the deterministic point of view, which ignores the effects of demographic stochasticity) at once:

> If the dominant eigenvalue of the positive matrix $L_p(I,\theta)$ (where I is determined by the $(p-k)$-species equilibrium) exceeds one, then the pth species will start to grow when introduced, whereas if this eigenvalue is less than one it will not.

Remark 2.2. The dominant eigenvalue of $L_p(I,\theta)$ is often called the *transversal* eigenvalue and if it exceeds one we say that the missing species can *invade successfully*. Hofbauer and Sigmund (1988) call a steady-state *saturated* if either there are no missing species or none of the missing species can invade successfully. They showed that certain systems have, under certain conditions, at least one saturated steady state. One could imagine that this result can be extended to our framework. To find the right formulation (in particular, natural and not too restrictive assumptions) and a proof constitutes a challenging problem which, so we hope, is taken up by at least one of our readers.

When we follow a solution for which the pth species is missing it may happen that while the parameter θ is varied the dominant eigenvalue of $L(I,\theta)$ passes the value one. Under appropriate nondegeneracy conditions a local bifurcation result like Theorem 2.1 holds, asserting the existence and uniqueness of a branch of solutions with one more species. (We did not manage to produce a useful general formula for the direction of the bifurcation.) Likewise there is an analogue of Theorem A.1.

If the parameter pertains only to the first $p-1$ species (recall that the prey carrying capacity figured as a bifurcation parameter in the analysis of the prey–predator model of Example 1.1), both L_p and G_p are independent of θ, which simplifies some aspects of the analysis (note that in such a case the bifurcation of the second species is via the parameter dependence of the I-variable at steady state). Another simplifying feature is that L_p may depend only on some components of I (e.g., predator reproduction being determined completely by the scalar prey density with the effect that the latter is fixed by the requirement of a steady predator population), which leads to a further decoupling of (2.13). Such special features should always be exploited when analysing (2.13). The extent of their importance makes it impossible (at least as far as we can see now) to say anything general and useful about (2.13).

We conclude with a remark on the principle of competitive exclusion. The usual formulation of this principle states that if q species compete for n resources and if $n<q$, then, if a steady state is attained, at least $q-n$ of the species will be extinct. The block-diagonal form (2.11) of the next-generation matrix tells us that in order to obtain a steady community with q coexisting species, q eigenvalues of $L(I)$ should be equal to one. As we have $n=\dim I$ degrees of freedom to achieve this, this is generically impossible when $\dim I<q$. Within our

framework we can therefore formulate the principle of competitive exclusion as follows:

> The dimension of the environmental interaction variable is an upper bound for the number of species that generically can coexist at steady state.

We point out that whether or not the components of I can be interpreted as resources is completely irrelevant.

2.3. Adaptive dynamics

The theory of adaptive dynamics, as initiated by Metz et al. (1992) and developed by Metz et al. (1996), Dieckmann and Law (1996), Geritz et al. (1997, 1998) and others, explicitly relates evolution by natural selection to population dynamics. A basic question in this theory is whether a rare mutant phenotype can invade an environment set by a resident population. Here, as in the rest of the paper, we restrict our attention to steady environments.

The phenotype (or *strategy*) is characterized by an element θ of a set $\mathscr{S}$ (the *strategy space*). By this we mean that the next-generation matrix L and the feedback matrix G depend not only on the input I but also on the strategy $\theta\in\mathscr{S}: L(I,\theta)$, $G=G(I,\theta)$.

We assume clonal reproduction, in particular, the strategy θ is faithfully inherited by the offspring from the parent. As a consequence, a *dimorphic* population (that is, a population consisting of individuals of two different phenotypes) can be interpreted in the terminology of Section 2.2 as a two-species community with all interactions incorporated in the dependence on I and the feedback to I. The question of whether a rare mutant phenotype can invade a resident population is therefore a special case of the question whether a missing species starts to spread when introduced in small quantities.

So consider a monomorphic resident population playing strategy $\theta^{\mathrm{res}}\in\mathscr{S}$. The input I^{res} at steady state is implicitly defined by

$$\begin{cases} b^{\mathrm{res}} = L(I^{\mathrm{res}},\theta^{\mathrm{res}})b^{\mathrm{res}}, \\ I^{\mathrm{res}} = G(I^{\mathrm{res}},\theta^{\mathrm{res}})b^{\mathrm{res}}. \end{cases} \tag{2.14}$$

Exactly as in Section 2.2 we find that

> A mutant phenotype θ^{mut} invades successfully if and only if $R_0(I^{\mathrm{res}},\theta^{\mathrm{mut}})$, that is, the dominant eigenvalue of $L(I^{\mathrm{res}},\theta^{\mathrm{mut}})$, is greater than one.

We therefore call $R_0(I^{\mathrm{res}},\theta^{\mathrm{mut}})$ the *invasion fitness* of a rare mutant phenotype θ^{mut} into the environment I^{res} set by the resident.

We now specialize to the case of a one-dimensional strategy space $\mathscr{S}\subset\mathbf{R}$. The *selection gradient* at $(I^{\mathrm{res}},\theta^{\mathrm{res}})$ is defined by

$$\frac{\partial}{\partial\theta^{\mathrm{mut}}} R_0(I^{\mathrm{res}},\theta^{\mathrm{mut}})\big|_{\theta^{\mathrm{mut}}=\theta^{\mathrm{res}}}. \tag{2.15}$$

Note that, in general, we have to specify both the strategy θ^{res} and the environment I^{res} because there may exist several population steady states corresponding to the same strategy. If, for example, the selection gradient is positive then the fitness of a mutant phenotype with θ^{mut} slightly larger than θ^{res} is greater than one and accordingly such a mutant can invade. The importance of the selection gradient stems from the fact that mutational steps occurring in nature are usually small.

It is not possible to determine what happens after invasion using only the steady-state analysis of this paper; for that the full dynamical system must be considered. In many cases the invader will oust the resident and become the new resident and in such cases the selection gradient determines the "direction of evolution". Therefore, away from singular points at which the selection gradient vanishes, we can provide the branches of stable steady states in a bifurcation diagram with an arrow indicating the direction in which the life-history parameter under selection will change in the course of evolution. On the other hand, Mylius and Diekmann (2001) gave an example in which invasion caused the resident to switch to another attractor with the consequence that the initially successful invader was outcompeted in the end. Geritz et al. (2002) formulated conditions that exclude such attractor-switching.

At a saddle-node bifurcation the branch of steady states ceases to exist when the bifurcation parameter is varied in one direction. If the selection gradient points in that direction, then selection will lead to an abrupt evolutionary change (attractor-switching). It may happen that the new attractor is the trivial steady state corresponding to extinction (this is the case for instance if the trivial steady state is the only attractor on the side of the bifurcation point where the previous attractor does not exist). This scenario in which selection drives a population to extinction was coined "evolutionary suicide" by Ferrière (2000) and was investigated in detail by Gyllenberg and Parvinen (2001) and Gyllenberg et al. (2002).

3. On general structured population models

In this section we derive the steady-state equations (1.1) from the basic individual-based ingredients. We start at the most general level in which both b and I are not necessarily finite dimensional. We consider the full dynamics first before getting to the steady-state problem. By specializing to the finite-dimensional case we finally recover (1.1). For the sake of concreteness we intersperse the abstract developments with some representative examples.

3.1. Derivation of population models from basic ingredients at the individual level

When modelling structured populations one starts by describing individual behaviour such as development (e.g. growth), survival and reproduction. To make this description mathematically precise one has to choose an *individual state space* (*i*-state space, that is, the set of all admissible *i*-states) and give rules for how the individual development, survival and reproduction depend on the *i*-state and the environmental condition. We denote the *i*-state space by Ω.

The *population state* (*p*-state) is a measure m on Ω with the interpretation that $m(\omega)$ equals the number of individuals with *i*-state in the (measurable) subset ω of Ω. If the number of *i*-states is finite, say k, such a measure is fully determined by a k-vector, the components of which give the number of individuals in the different *i*-states.

The structured population problem consists of constructing a dynamical system describing the time evolution of the *p*-state from model assumptions about individual behaviour. This exercise was performed by Diekmann et al. (1998, 2001). Here we summarize this work only for as far as it is needed for the present paper.

In linear population models the environmental condition, or input, is assumed to be a given function I defined on the time-interval $[0, \ell(I))$ of length $\ell(I)$ and taking on values in a set Z. The model is then defined through two families u_I and Λ_I of kernels with the input I as parameter, which have the following interpretations:

- $u_I(x, \omega)$ is the probability that, given the input I, an individual which has *i*-state $x \in \Omega$ at a certain time, is still alive $\ell(I)$ time units later and then has *i*-state in the (measurable) subset ω of Ω.
- $\Lambda_I(x, \omega)$ is the expected number of offspring, with state-at-birth in the set ω, produced by an individual, with *i*-state $x \in \Omega$ at a certain time, within the time interval of length $\ell(I)$ following that time, given the input I.

Examples of how to construct such kernels are given at the end of this section and in Sections 3.3, 4.1 and 4.2. In all these examples the construction involves the solution of an ODE describing deterministic *i*-state movement in Ω as well as ODEs describing survival (or, rather, the lack thereof) and reproduction. However, the general formalism accommodates just as easily models in which *i*-state development is stochastic and is specified, for instance, in terms of a diffusion process so that one has to solve parabolic PDEs in order to calculate the model ingredients u_I and Λ_I (see Diekmann et al., 1998, Section 8.3). Starting from a consistent specification of individual behaviour, for instance in terms of ODEs or PDEs, one will obtain kernels u_I and Λ_I, which, apart from being positive, satisfy a number of consistency and monotonicity conditions. These were discussed at some length by Diekmann et al. (1998, 2001) and are for the convenience of the reader summarized in Appendix B. In an axiomatic approach these conditions are taken as the starting point when defining structured population models. This then leads to the following definition.

Definition 3.1. A *linear structured population model* consists of a couple (u_I, Λ_I) of parametrized families of positive kernels satisfying the consistency and monotonicity conditions **C** and **M** of Appendix B.

Diekmann et al. (1998, 2001) showed that, for a given linear structured population model, one can construct a pair (u_I^c, Λ_I^c) with the same interpretation as (u_I, Λ_I), but now not for direct offspring, but for the whole *clan*, that is, all children, grand-children, great-grand-children, etc., descending from a single ancestor. They then showed that

$$T_I m^0 = u_I^c \times m^0 \tag{3.1}$$

defines a semigroup $\{T_I\}_{I \in \mathscr{B}(Z)}$ of linear operators on (a subspace of) the space $M(\Omega)$ of measures on Ω, mapping the initial population state m^0 to the state at time $\ell(I)$, thus solving the corresponding linear structured population problem with input. The $\times$-product appearing in (3.1) is defined in Appendix B. It can be viewed as an analogue of ordinary matrix multiplication. Indeed, at the end of Section 3.2 we show that in the case of finitely many states at birth this is more than an analogue: with the right choice of coordinates $\Lambda_I \times$ is represented by $L(I)$.

Whereas in linear structured population models the environment is assumed to be fully under experimental control, we make exactly the opposite assumption for nonlinear models:

Definition 3.2. A *nonlinear (autonomous) structured population model* is a linear model together with a feedback law that describes how the current value of the input depends on the current *p*-state.

A nonlinear model in this sense may very well be a model of the interaction of *several* populations, as indeed the example below in this section shows.

To make Definition 3.2 operational one needs an additional piece of notation (see also Appendix B):

> for $t < \ell(I)$, $\rho(t)I$ is the same as I but restricted to the interval $[0, t)$.

With this notation we can, with the use of (3.1), write the *p*-state at time t, given that the *p*-state at time 0 is m^0,

as $u^c_{\rho(t)I} \times m^0$. This prepares the way for the following definition.

Definition 3.3. The *pure mass action* feedback law is given by

$$I(t) = \gamma \times u^c_{\rho(t)I} \times m^0, \tag{3.2}$$

where γ is a (bounded measurable) function from Ω to Z, the set of environmental conditions.

We believe in pure mass action feedback laws as the basic mechanistic modelling ingredient. However, often such laws feed through to the population level through a number of mechanisms acting on faster time scales. Although, in principle, we could explicitly account for these mechanisms in the population model itself, this would greatly enlarge the *i*-state space and, in addition, lead to a model unamenable to analysis and numerics. Therefore we prefer to incorporate such mechanisms using time-scale arguments. They yield instantaneous feedback loops inside the ordinary mass action ones. This motivates the following definition. We first introduce some notation. Let $Z = Z_1 \times Z_2$ and let $\gamma_1 : \Omega \to Z_1$ and $\gamma_2 : Z_1 \times \Omega \to Z_2$ be bounded measurable functions. The value of γ_2 at $(z, x) \in Z_1 \times \Omega$ is written as $\gamma_2(z)\ (x)$.

Definition 3.4. The *generalized mass action law with two time-scale levels* is given by

$$I_1(t) = \gamma_1 \times u^c_{\rho(t)I} \times m^0, \tag{3.3}$$

$$I_2(t) = \gamma_2(I_1(t)) \times u^c_{\rho(t)I} \times m^0. \tag{3.4}$$

We close the description of our basic framework by a few examples.

Example 3.5. Consider a population structured by age a and size w feeding on an unstructured substrate, the density of which is denoted by S. In the absence of the population the substrate grows logistically with intrinsic growth rate r and carrying capacity K. We assume a size specific attack rate $\alpha(w)$ and a Holling type II functional response. The balance law for the substrate then takes the form

$$\frac{dS(t)}{dt} = rS(t)\left(1 - \frac{S(t)}{K}\right) - \frac{S(t)}{1 + S(t)} \int_{\mathbf{R}^2_+} \alpha(w) n(t, da \times dw), \tag{3.5}$$

where the measure $n(t, \cdot)$ on $\mathbf{R}^2_+$ is the age–size distribution at time t (we hope that the readers are not scared by the notation, which might be unfamiliar; the integral is over all age–size combinations and the (weight) function α depends only on size). Here we have assumed that the size specific handling time decreases with increasing attack rate in such a way that the coefficient of $S(t)$ in the denominator in the latter term on the right-hand side of (3.5) can be scaled to 1, the idea being that the growth of the animal entails a scaling up of all its food gathering and processing apparatus. We shall interpret the former term on the right-hand side of (3.5) as a pure birth term and the latter as a death term, thus assuming that death of substrate individuals is due to predation only.

The individual growth rate $g(w, S)$ and the rate $\beta(w, S)$ of giving birth depend on the size w and the current value of the substrate concentration. The assumption of Holling type II functional response should, of course, be reflected in the analytic expression of $g(w, S)$, but since this is irrelevant for our purposes we do not write this out explicitly. We assume that all individuals suffer a sudden death upon reaching age $a^\dagger$. In the age-interval $[0, a^\dagger)$ there is a constant background mortality μ. All newborns are assumed to have the same size w_b.

To translate the above model description into a nonlinear population model in the sense of Definition 3.2 we first choose the *i*-state space as the union of $\Omega_1 = [0, a^\dagger) \times [w_b, \infty)$ and a one point set $\Omega_2 = \{s\}$. Here s should not be considered as a number but simply as an arbitrarily chosen symbol. We thus have

$$\Omega = ([0, a^\dagger) \times [w_b, \infty)) \bigcup \{s\}. \tag{3.6}$$

An *i*-state $x = (a, w) \in \Omega_1$ characterizes an individual of age a and size w, whereas the *i*-state $x = s$ refers to an individual of the substrate population. The fact that Ω_2 is a one point set reflects the fact that the substrate is unstructured: all substrate individuals are identical.

The population state at time t is the measure

$$m(t, \cdot) = n(t, \cdot) + S(t)\delta_s, \tag{3.7}$$

where, as usual, δ denotes the unit mass (Dirac measure) concentrated at the point indicated by the subscript.

To cut the feedback loop to make the model linear we define the inputs

$$I_1(t) = S(t), \tag{3.8}$$

$$I_2(t) = \int_{\Omega_1} \alpha(w) n(t, da \times dw). \tag{3.9}$$

The feedback is then of the pure mass action type (3.2) with

$$I = \begin{pmatrix} I_1 \\ I_2 \end{pmatrix}, \quad \gamma = \begin{pmatrix} \gamma_1 \\ \gamma_2 \end{pmatrix}$$

and

$$\gamma_1(x) = \begin{cases} 0 & \text{if } x \in \Omega_1 \\ 1 & \text{if } x = s \end{cases},$$

$$\gamma_2(x) = \gamma_2((a,w)) = \begin{cases} \alpha(w) & \text{if } x \in \Omega_1, \\ 0 & \text{if } x = s. \end{cases}$$

The *i*-state $x=(a, w)$ of an individual with initial state $(a_0, w_0) \in \Omega_1$ is given by the solutions of the initial value problem

$$\frac{dw(t)}{dt} = g(w(t), I_1(t)), \quad w(0) = w_0, \tag{3.10}$$

$$\frac{da}{dt} = 1, \quad a(0) = a_0. \tag{3.11}$$

Denote the solution of (3.10) at time $\ell(I)$ by $X_{I_1}(w_0)$. The probability that the individual is still alive at time $\ell(I)$ is

$$\mathscr{F}_{I_1}(a_0) = \begin{cases} e^{-\mu\ell(I)} & \text{if } \ell(I) < a^\dagger - a_0, \\ 0 & \text{if } \ell(I) \geqslant a^\dagger - a_0. \end{cases} \tag{3.12}$$

We therefore get

$$u_I(x,\cdot) = u_{I_1}((a,w),\cdot) = \mathscr{F}_{I_1}(a)\delta_{(a+\ell(I), X_{I_1}(w))}, \quad x = (a,w) \in \Omega_1. \tag{3.13}$$

For $x=s$ we have

$$u_I(s,\cdot) = e^{-\int_0^{\ell(I)} \frac{I_2(\tau)}{1+I_1(\tau)} d\sigma} \delta_s. \tag{3.14}$$

The reproduction kernel is obtained by multiplying the probability that an individual is still alive at time τ by the rate at which it produces offspring at time τ and integrating with respect to τ over the length of the input. We thus get

$$\Lambda_I(x,\cdot) = \Lambda_{I_1}((a,w),\cdot) = \int_{[0,\ell(I))} \beta\big(X_{\rho(\tau)I_1}(x), I_1(\tau)\big)\ \mathscr{F}_{\rho(\tau)I_1}(a)\, d\tau\, \delta_{(0,w_b)}, \quad x = (a,w) \in \Omega_1 \tag{3.15}$$

and

$$\Lambda_I(s,\cdot) = \int_{[0,\ell(I))} r\left(1 - \frac{I_1(\tau)}{K}\right) e^{-\int_0^\tau \frac{I_2(\sigma)}{1+I_1(\sigma)} d\sigma} d\tau\, \delta_s. \tag{3.16}$$

Example 3.6. This example is the same as Example 3.5 but with chemostat dynamics instead of logistic growth of the substrate. In other words, the balance equation (3.5) is replaced by

$$\frac{dS(t)}{dt} = D(S_0 - S(t)) - \frac{S(t)}{1+S(t)} \int_{\mathbf{R}_+^2} \alpha(w) n(t, da \times dw), \tag{3.17}$$

where S_0 is the constant concentration of substrate in an external reservoir from which substrate is fed to the reactor tank at the dilution rate D. Substrate is removed at the same rate D and so are individuals of the age–size structured population.

The chemostat model can easily be put into our framework in the following way. We consider the substrate particles to be structured by their location: the state r means that the particle resides in the external reservoir and the state s that it resides in the reactor tank and can be consumed by the individuals of the age–size structured population. To keep the concentration in the reservoir constant we assume that r-particles leaving the reservoir are immediately replaced, that is, we assume a per particle reproduction rate D.

The expressions for $u_I(x,\cdot)$ and $\Lambda_I(x,\cdot)$ remain the same as in Example 3.5 with the only difference that washout is now an additional cause of removal and μ has to be replaced by $\mu + D$. For the substrate particles we get

$$u_I(r,\cdot) = e^{-D\ell(I)}\delta_r + \int_{[0,\ell(I))} De^{-D\tau} e^{-\int_\tau^{\ell(I)} \left(D + \frac{I_2(\sigma)}{1+I_1(\sigma)}\right) d\sigma} d\tau\, \delta_s, \tag{3.18}$$

$$u_I(s,\cdot) = e^{-\int_0^{\ell(I)} \left(D + \frac{I_2(\tau)}{1+I_1(\tau)}\right) d\tau} \delta_s \tag{3.19}$$

and

$$\Lambda_I(r,\cdot) = \left(1 - e^{-D\ell(I)}\right)\delta_r, \tag{3.20}$$

$$\Lambda_I(s,\cdot) = 0. \tag{3.21}$$

The nonlinear models in these examples all have the special feature of having a finite number of birth states. As a matter of fact a large fraction (the majority, we think) of relevant population models has this property, which facilitates the analysis of the model considerably. In the sequel, we shall pay special attention to models with a finite number of possible birth states.

3.2. Characterization of steady states

Consider a structured population model defined by the two families of kernels u_I and Λ_I and either a pure mass action feedback law (Definition 3.3), defined by a function γ, or a generalized mass action feedback law with two time-scale levels (Definition 3.4), defined by γ_1 and $\gamma_2(I_1)$.

To have a steady population state requires first of all that the environmental condition is constant. In this section we shall consider only constant inputs defined on $[0, \infty)$. Even though it is abuse of notation, we shall denote such inputs just by I (that is, we abstain from

adding any warning index, hoping that the present notification is enough warning).

We assume finite life expectancy:

$$-\int_0^\infty a u_{\rho(da)I}(x,\Omega) = \int_0^\infty u_{\rho(a)I}(x,\Omega)\,da < \infty \quad \text{for all } x\in\Omega. \tag{3.22}$$

Note that $u_{\rho(a)I}(x, \Omega)$ is the survival probability as a function of the individual state x and the length a of the time interval considered. Hence it is a decreasing function of a and the Stieltjes integral at the left-hand side is indeed the life expectancy; the equality is obtained by partial integration.

In a growing or declining population under constant conditions the (invariant) distribution with respect to state-at-birth may be quite different when we sample from one generation or when we sample at some moment in time. However, as we will show below, these two distributions are the same for a steady population. This idea underlies the results (and proofs) below, so it is helpful to have it in mind.

The invariant (stable) birth-state-distribution b can be computed by solving the eigenvalue problem

$$\Lambda_I \times b = R_0(I)b \tag{3.23}$$

and if we are looking for a steady population we should require $R_0(I)=1$. Our first result tells us how to obtain the steady population distribution from b by using $u_{\rho(\sigma)I}$.

The key idea is that, under constant conditions, individuals are fully characterized by the combination of their state-at-birth and their age. Very often the subset $\Omega_b\subset\Omega$ of possible states-at-birth is much smaller than Ω itself (e.g., in the case of age-structured populations we have $\Omega=[0,\ \infty)$ but $\Omega_b=\{0\}$). As it is wise to take advantage of this fact we use Ω_b explicitly in the formulation.

Lemma 3.7. *Assume I and b are such that*

$$\Lambda_I \times b = b. \tag{3.24}$$

Define

$$m = \int_0^\infty u_{\rho(a)I} \times b\,da, \tag{3.25}$$

that is,

$$m(\omega) = \int_0^\infty \int_{\Omega_b} u_{\rho(a)I}(\xi,\omega)b(\xi)\,d\xi\,da$$

for measurable subsets ω of Ω. Then

$$u^c_{\rho(t)I} \times m = m \ \text{ forall } \ t\geqslant 0, \tag{3.26}$$

or, in words, m is a steady population state.

Can we also go in the other direction, i.e. start from a population steady state and then compute the distribution of state-at-birth b which satisfies (3.24)? The answer is "yes".

Lemma 3.8. *Assume I and m are such that* (3.26) *holds. Then b defined by*

$$b = \frac{1}{t}(\Lambda^c_{\rho(t)I} \times m) \tag{3.27}$$

does not depend on t and satisfies (3.24). *Moreover, m can be expressed in terms of b by* (3.25).

The two lemmas are proved in Appendix B. Together they motivate the following definition and provide a proof of the following theorem.

Definition 3.9. The steady-state problem for a nonlinear structured population model consists of finding a measure b on Ω_b fit and a constant input I such that

$$b = L(I)b, \tag{3.28}$$

$$I = G(I)b, \tag{3.29}$$

where

$$L(I)b = \Lambda_I \times b \tag{3.30}$$

and

$$G(I)b = \int_0^\infty (\gamma \times u_{\rho(a)I} \times b)\,da \tag{3.31}$$

in the pure mass action case and

$$G(I)b = G\begin{pmatrix} I_1 \\ I_2 \end{pmatrix} = \begin{pmatrix} \int_0^\infty (\gamma_1 \times u_{\rho(a)I} \times b)\,da \\ \int_0^\infty (\gamma_2(I_1) \times u_{\rho(a)I} \times b)\,da \end{pmatrix} \tag{3.32}$$

in the two-level generalized mass action case.

Theorem 3.10. *The measure m on Ω is a steady population state if and only if it is of the form* (3.25) *with (b, I) a solution of the steady state problem of Definition* 3.9.

Remark 3.11. The results of this section are, essentially, already contained in Theorem 6.1 of (Diekmann et al., 1998). But we have given new formulations and proofs since here the feedback part is included (so now it should be clear how the result applies to nonlinear problems) and, therefore, the notation is somewhat different.

We close this section by showing how to rewrite (3.24) and (3.31) or (3.32) in the form (1.1) when there are only finitely many possible birth states. So assume the kernel Λ_I allows the representation

$$\Lambda_I(x,\omega) = \sum_{i=1}^k l_{Ii}(x)\delta_{x_i}(\omega) \tag{3.33}$$

which, biologically, means that birth states are restricted to the finite set $\Omega_b=\{x_1,\ldots,x_\kappa\}\subset\Omega$ and that an individual with state x will, under constant environmental conditions as specified by I, on average produce $l_{Ii}(x)$ offspring with state-at-birth x_i in its entire (remaining) life.

Let $M_b\subset M(\Omega)$ denote the linear subspace of $M(\Omega)$ spanned by $\{\delta_{x_1},\ldots,\delta_{x_k}\}$. Then, since

$$\begin{aligned}(\Lambda_1\times b)(\omega) &= \int_\Omega \Lambda_I(\xi,\omega)b(d\xi)\\ &= \int_\Omega \sum_{i=1}^k l_{I_i}(\xi)\delta_{x_i}(\omega)b(d\xi)\\ &= \sum_{i=1}^k \int_\Omega l_{I_i}(\xi)b(d\xi)\delta_{x_i}(\omega),\end{aligned}\tag{3.34}$$

we see that the linear operator $\Lambda_I\times$ maps $M(\Omega)$ into M_b. So when looking for eigenvectors we can restrict to M_b. When

$$b=\sum_{i=1}^k c_i\delta_{x_i},\tag{3.35}$$

we find

$$\Lambda_I\times b=\sum_{i=1}^k\left(\sum_{j=1}^k (L(I))_{ij}c_{ij}\right)\delta_{x_i},\tag{3.36}$$

where

$$(L(I))_{ij}:=l_{Ii}(x_j).\tag{3.37}$$

In words, the restriction of $\Lambda_I\times$ to M_b is, with respect to the basis $\{\delta_{x_1},\ldots,\delta_{x_k}\}$ represented by the matrix $L(I)$. Thus the eigenvalue problem $\Lambda_I\times b=b$ leads to the first equation of (1.1), where b in (1.1) is the vector with the coefficients c_i from (3.35) as its components.

When we evaluate (3.31) for b belonging to M_b, i.e. b of the form (3.35), we find

$$I=\sum_{j=1}^k\int_0^\infty\int_\Omega \gamma(\xi)u_{\rho(a)I}(x_j,d\xi)\,da c_j.\tag{3.38}$$

So if both I and $\gamma(x)$ are n-vectors then we write

$$I=G(I)c,\tag{3.39}$$

where the $n\times k$-matrix $G(I)$ has elements

$$(G(I))_{ij}=\int_0^\infty\int_\Omega \gamma_i(\xi)u_{\rho(a)I}(x_j,d\xi)\,da.\tag{3.40}$$

In the two-level generalized mass action case we also arrive at (3.39), but we need to work a bit harder to define $G(I)$. Let n_1 be the dimension of the vectors I_1 and $\gamma_1(x)$ and put $n_2=n-n_1$. Define the $n_1\times k$-matrix $G_1(I)$ by

$$(G_1(I))_{ij}=\int_0^\infty\int_\Omega \gamma_{1,i}(\xi)u_{\rho(a)I}(x_j,d\xi)\,da\tag{3.41}$$

and, for given I_1, the $n_2\times k$-matrix $G_2(I)$ by

$$(G_2(I))_{ij}=\int_0^\infty\int_\Omega \gamma_{2,i}(I_1,\xi)u_{\rho(a)I}(x_j,d\xi)\,da.\tag{3.42}$$

Then

$$G(I)=\begin{pmatrix}G_1(I)\\ G_2(I)\end{pmatrix}.\tag{3.43}$$

3.3. Example: size-structured predator

In order to illustrate the general results/methodology with a concrete example, we return to the size-structured predator feeding on an unstructured prey as introduced in Example 3.5.

Since there is only one predator-state-at-birth, the matrix $L(I)$ is 2×2. Since we have two species, it is diagonal. Let us number the prey 1 and the predator 2. Recall from the beginning of this section that I is now a *constant* function defined for all time. So from (3.16) we get at once that

$$L_{11}(I)=r\left(1-\frac{I_1}{K}\right)\frac{1+I_1}{I_2}\tag{3.44}$$

and by combining (3.15) and (3.12) we obtain

$$L_{22}(I)=\int_0^{a^\dagger}\beta(W(\tau,I_1),I_1)e^{-\mu\tau}\,d\tau,\tag{3.45}$$

where we have put

$$W(\tau,I_1)=X_{\rho(\tau)I_1}(w_b)\tag{3.46}$$

or, in other "words", W is the solution of the initial value problem

$$\frac{dW}{da}=g(W,I_1),\quad W(0)=w_b.\tag{3.47}$$

Next, let us specify $G(I)$. Since I is two dimensional, this is a 2×2-matrix as well. Since I_1 refers to the first species only and I_2 to the second only, it also is diagonal. The definition of γ_1, (3.14) and (3.31) yield

$$G_{11}(I)=\frac{1+I_1}{I_2}.\tag{3.48}$$

The definition of γ_2, (3.13) and (3.31) yield

$$G_{22}(I)=\int_0^{a^\dagger}\alpha(W(\tau,I_1))e^{-\mu\tau}\,d\tau.\tag{3.49}$$

Concerning the steady-state problem (1.1), there is now a complete analogy between the present situation and the unstructured predator–prey steady-state analysis from the introduction (a minor difference being that we would for the prey calculate first the steady birth rate and only then the steady population density (rather than using the shortcut $S=I_1$) if we follow the "standard" procedure). Provided we make natural monotonicity assumptions concerning $g(w,I_1)$, $\beta(w,I_1)$ and $\alpha(w)$, all

results for the unstructured model have their counterpart for the structured model.

A natural further specification of g and β would be

$$g(w,I_1)=\theta\kappa(w)\alpha(w)\frac{I_1}{1+I_1}-\zeta w,$$
$$\beta(w,I_1)=\eta(1-\kappa(w))\alpha(w)\frac{I_1}{1+I_1}, \tag{3.50}$$

where κ is the allocation rule for how ingested energy is partitioned between, on the one hand, growth and maintenance and, on the other hand, reproduction (see Kooijman, 2000; Thieme, 1988), θ and η are conversion factors, and ζ is proportional to the amount of energy that, per unit of time and size, is needed for maintenance (these quantities reappear in Section 4.1). Assumptions on these quantities should guarantee that g is bounded away from zero and that larger individuals have (not necessarily strictly) larger reproduction rate β.

4. Two case studies

To show how the general theory of Sections 2 and 3 can be put to use we work out in some detail two concrete examples. In each of the two cases conclusions are reached which are of independent biological interest.

4.1. A single-species model involving cannibalistic behaviour

This subsection is inspired by the work of van den Bosch et al. (1988). It introduces several new aspects

- we consider a size-structured, rather than an age-structured, population;
- we incorporate a Holling type II functional response;
- we extend and correct the biological interpretation of the formula for the direction of bifurcation.

Given the simplifying assumptions we shall make, the first of these hardly makes a difference (but our methodology extends to situations where the size-structure does matter).

So consider a size-structured population. Assume that individuals of size x ingest energy at a rate

$$\frac{E(x)C(x)Z(x)+\int e(y)c(x,y)m(dy)}{1+H(x)C(x)Z(x)+\int h(x,\xi)c(x,\xi)m(d\xi)},$$

where Z is the food density, m is the measure describing the population composition and the characters e, c and h, as well as the corresponding capitals, refer to, respectively, energy content, attack rate and handling time (see also Diekmann et al. (2001) for a slightly more informative description). Consistency then requires that individuals of size y experience a probability per unit of time

$$\int\frac{c(\xi,y)}{1+H(\xi)C(\xi)Z(\xi)+\int h(\xi,\eta)c(\xi,\eta)m(d\eta)}\,m(d\xi)$$

of falling victim to intraspecific predation. To fit the model into our framework we make the separability assumptions

$$c(x,y)=\psi(x)\phi(y),$$
$$h(x,y)=h_1(x)h_2(y).$$

So ψ describes the size-specific degree of cannibalistic activity and ϕ the size-specific vulnerability to cannibalistic predation. The size of predator and prey have an independent influence on handling time described by, respectively, h_1 and h_2. These assumptions allow us to define two environmental interaction variables in terms of linear functionals:

$$I_1=\int e(y)\phi(y)m(dy),$$

$$I_2=\int h_2(y)\phi(y)m(dy),$$

and a third one in terms of an I_2-dependent linear functional:

$$I_3=\int\frac{\psi(\xi)}{1+H(\xi)C(\xi)Z(\xi)+I_2h_1(\xi)\psi(\xi)}\,m(d\xi)$$

(note that in Diekmann et al. (2001) indices 2 and 3 were interchanged). The energy ingestion rate then reads

$$\frac{E(x)C(x)Z(x)+I_1\psi(x)}{1+H(x)C(x)Z(x)+I_2h_1(x)\psi(x)}$$

and the intraspecific predation death rate

$$I_3\phi(y).$$

We assume that all individuals are born with size x_b and that they grow with rate

$$g(x,I)=\kappa(x)\frac{E(x)C(x)Z(x)+I_1\psi(x)}{1+H(x)C(x)Z(x)+I_2h_1(x)\psi(x)}-\zeta x.$$

Here the size-specific allocation rule κ describes how much of the ingested energy goes to growth and maintenance and how much to reproduction. The parameter ζ is the amount of energy per unit of time and size that is required to cover maintenance.

Individuals of size x have probability

$$\mu(x,I)=\mu_0(x)+I_3\phi(x)$$

per unit of time of dying (so μ_0 is the size-specific noncannibalistic predation pressure) and probability

$$\beta(x,I)=\eta(1-\kappa(x))\frac{E(x)C(x)Z(x)+I_1\psi(x)}{1+H(x)C(x)Z(x)+I_2h_1(x)\psi(x)}$$

per unit of time of giving birth, where η denotes the conversion factor for the transformation of available energy into offspring.

We assume that for some $\varepsilon > 0$ and for all $x \geqslant x_b$

$$\kappa(x)\frac{E(x)C(x)Z(x)}{1+H(x)C(x)Z(x)} - \zeta x \geqslant \varepsilon$$

(this guarantees that the individual growth rate is bounded away from zero). The solution of the initial value problem

$$\frac{dx}{da} = g(x, I), \quad x(0) = x_b$$

is denoted by $X(a, I)$. It yields the size of an individual of age a, given constant environmental conditions I. The survival probability $\mathscr{F}(a, I)$ is obtained by solving

$$\frac{d\mathscr{F}}{da} = -(\mu_0(X(a,I)) + I_3\phi(X(a,I)))\mathscr{F}, \qquad \mathscr{F}(0,I) = 1.$$

The expected number of offspring $\tilde{L}(a, I)$ produced before reaching age a is likewise obtained as the solution of an initial value problem:

$$\frac{d\tilde{L}}{da} = \beta(X(a,I),I)\mathscr{F}(a,I), \quad \tilde{L}(0,I) = 0. \tag{4.1}$$

We define

$$L(I) = \tilde{L}(\infty, I).$$

Since the births are concentrated in the single point x_b we have (with still unknown scalar c)

$$(u_{\rho(a)I} \times b)(\omega) = cu_{\rho(a)I}(x_b, \omega) = c\mathscr{F}(a,I)\delta_{X(a,I)}(\omega)$$

and so the steady p-state measure is, according to (3.25), given by

$$\begin{aligned} m(\omega) &= \int_0^\infty (u_{\rho(a)I} \times b)(\omega)\, da \\ &= c\int_0^\infty \mathscr{F}(a,I)\delta_{X(a,I)}(\omega)\, da \\ &= c\int_\omega \mathscr{F}(\alpha(\xi),I)\frac{1}{g(\xi,I)}\, d\xi, \end{aligned} \tag{4.2}$$

where $a = \alpha(\xi, I)$ is the inverse of $\xi = X(a, I)$ whence $\frac{d\xi}{da} = g(\xi, I)$. So m is absolutely continuous with density

$$c\mathscr{F}(\alpha(x,I),I)\frac{1}{g(x,I)}$$

and consequently,

$$I_1 = c\int_{x_b}^\infty e(y)\phi(y)\mathscr{F}(\alpha(y,I),I)\frac{1}{g(y,I)}\, dy, \tag{4.3}$$

$$I_2 = c\int_{x_b}^\infty h_2(y)\phi(y)\mathscr{F}(\alpha(y,I),I)\frac{1}{g(y,I)}\, dy, \tag{4.4}$$

$$\begin{aligned} I_3 = c\int_{x_b}^\infty & \frac{\psi(y)}{1+H(y)C(y)Z(y)+I_2h_1(y)\psi(y)} \\ & \mathscr{F}(\alpha(y,I),I)\frac{1}{g(y,I)}\, dy. \end{aligned} \tag{4.5}$$

To any nontrivial steady state there correspond I_1, I_2, I_3 and c such that (4.3)–(4.5) as well as the equation $L(I) = 1$ hold. And, vice versa, one can constructively define a nontrivial steady state by (4.2) whenever one has found such a quadruple (I_1, I_2, I_3, c).

Now specialize to the following situation:

(i) ϕ has as its support the interval $[x_v, x_w]$, which we shall call the vulnerability window;
(ii) individuals become adults when passing size $x_A > x_w$, the main characteristics of adults being that they (and only they) reproduce and practise cannibalism.

Define

$$g_0(x) = \kappa(x)\frac{E(x)C(x)Z(x)}{1+H(x)C(x)Z(x)} - \zeta x$$

and let $X_0(a)$ be the solution of the initial value problem

$$\frac{dx}{da} = g_0(x), \quad x(0) = x_b,$$

then

$$X(a,I) = X_0(a)$$

for $a \leqslant a_A$ where a_A is the age at which individuals become adult, so mathematically a_A is defined by the equation

$$X_0(a_A) = x_A.$$

The probability that a newborn individual survives long enough to become an adult is given by

$$\begin{aligned} \mathscr{F}(a_A,I) &= \exp\left(-\int_0^{a_A}(\mu_0(X_0(a)) + I_3\phi(X_0(a))\, da\right) \\ &= \exp\left(-\int_{x_b}^{x_A}\frac{\mu_0(\xi)}{g_0(\xi)}d\xi - I_3\int_{x_v}^{x_w}\frac{\phi(\xi)}{g_0(\xi)}d\xi\right) \end{aligned}$$

which we rewrite in the form

$$\mathscr{F}(a_A,I) = e^{-I_3\bar{\phi}}\mathscr{F}_0(x_A),$$

where

$$\bar{\phi} := \int_{x_v}^{x_w}\frac{\phi(\xi)}{g_0(\xi)}d\xi, \tag{4.6}$$

$$\mathscr{F}_0(x) := \exp\left(-\int_{x_b}^{x}\frac{\mu_0(\xi)}{g_0(\xi)}d\xi\right). \tag{4.7}$$

As yet another simplification we now introduce the assumption that all adults are the same, i.e., their size is irrelevant. This assumption allows us to choose ψ and h_1 to be identically equal to one and to write for $x > x_A$

$$\beta(x,I) = \eta(1-\kappa)\frac{ECZ+I_1}{1+HCZ+I_2},$$

where we omit the arguments of κ, E, C, H and Z since, by assumption, these functions are constant for $x > x_A$. Note in particular that from now on the symbol Z denotes the density of 'standard' adult food.

We now have

$$L(I) = \eta(1-\kappa)\frac{ECZ+I_1}{1+HCZ+I_2}\mathscr{F}(a_A,I)\frac{1}{\mu_A},$$

where μ_A is the death rate of adults, so $\frac{1}{\mu_A}$ is the expected duration of the adult stage for individuals that survive the juvenile stage (indeed, when β equals zero for $x<x_A$ and is constant for $x>x_A$, we obtain, upon integration of (4.1), exactly this expression for $L(I)$).

After we made these simplifying assumptions we can write the steady-state equations in the form

$$\eta(1-\kappa)\frac{ECZ+I_1}{1+HCZ+I_2}\mathscr{F}_0(x_A)\frac{1}{\mu_A}e^{-I_3\bar{\phi}}=1,$$

$$I_1=c\int_{x_v}^{x_w}e(y)\phi(y)\mathscr{F}_0(y)\frac{1}{g_0(y)}e^{-I_3\int_{x_v}^{y}\frac{\phi(\xi)}{g_0(\xi)}}dy,$$

$$I_2=c\int_{x_v}^{x_w}h_2(y)\phi(y)\mathscr{F}_0(y)\frac{1}{g_0(y)}e^{-I_3\int_{x_v}^{y}\frac{\phi(\xi)}{g_0(\xi)}d\xi}dy,$$

$$I_3=c\frac{1}{1+HCZ+I_2}\mathscr{F}_0(x_A)\frac{1}{\mu_A}e^{-I_3\bar{\phi}}.$$

These equations are for nontrivial steady states and we shall now look for a bifurcation from the trivial steady state, while considering the adult food level Z as the bifurcation parameter. Since

$$R_0=L(0)=\eta(1-\kappa)\frac{ECZ}{1+HCZ}\mathscr{F}_0(x_A)\frac{1}{\mu_A},$$

there exists a food level Z_c at which $R_0=1$ provided

$$\eta(1-\kappa)\frac{E}{H}\mathscr{F}_0(x_A)\frac{1}{\mu_A}>1 \tag{4.8}$$

(note that the left-hand side equals the limit of R_0 for $Z\uparrow\infty$ and that R_0 is monotonically increasing in Z). Let us assume that (4.8) holds. Then $(Z, c, I)=(Z_c, 0, 0)$ is a solution of the steady-state problem, with Z considered as an additional "unknown". By the implicit function theorem we can use c to parametrize locally the one-dimensional branch of solutions through this point. Clearly

$$I_i=ck_i+o(c)\quad\text{as}\quad c\to 0,$$

where

$$k_1=\int_{x_v}^{x_w}e(y)\phi(y)\mathscr{F}_0(y)\frac{1}{g_0(y)}dy,$$

$$k_2=\int_{x_v}^{x_w}h_2(y)\phi(y)\mathscr{F}_0(y)\frac{1}{g_0(y)}dy,$$

$$k_3=\frac{1}{1+HCZ_c}\mathscr{F}_0(x_A)\frac{1}{\mu_A}.$$

We put

$$Z=Z_c+cK+o(c)$$

and try to determine K (note that the bifurcation is supercritical if $K>0$ and subcritical if $K<0$, where supercritical means that the biologically meaningful half of the branch, i.e., the positive half, exists for parameter values for which $R_0>1$ while subcritical means it exists for parameter values for which $R_0<1$; beware that this is a local property and that the branch may turn when we follow it away from the bifurcation point). Writing the equation $L(I)=1$ in the form

$$1+HCZ+I_2=\eta(1-\kappa)(ECZ+I_1)\mathscr{F}_0(x_A)\frac{1}{\mu_A}e^{-I_3\bar{\phi}}$$

and substituting the expansions for I_i and Z we find, upon equating first order coefficients:

$$HCK+k_2=\eta(1-\kappa)(ECK+k_1)\mathscr{F}_0(x_A)\frac{1}{\mu_A}-\eta(1-\kappa)ECZ_c\mathscr{F}_0(x_A)\frac{1}{\mu_A}\bar{\phi}k_3$$

which we solve for K to obtain

$$K=\frac{1}{HC-\eta(1-\kappa)EC\mathscr{F}_0(x_A)\frac{1}{\mu_A}}\times\left(\eta(1-\kappa)k_1\mathscr{F}_0(x_A)\frac{1}{\mu_A}-\eta(1-\kappa)ECZ_c\mathscr{F}_0(x_A)\frac{1}{\mu_A}\bar{\phi}k_3-k_2\right).$$

Since $\eta(1-\kappa)EC\mathscr{F}_0(x_A)\frac{1}{\mu_A}=\frac{1+HCZ_c}{Z_c}=HC+\frac{1}{Z_c}$ the first factor is negative. If we multiply the second factor by $\frac{ECZ_c}{1+HCZ_c}\eta(1-\kappa)$, divide by $\bar{\phi}$ and use the defining identities for k_3 and Z_c we obtain the quantity

$$\eta(1-\kappa)\frac{k_1}{\bar{\phi}}-\eta(1-\kappa)\frac{ECZ_c}{1+HCZ_c}\frac{k_2}{\bar{\phi}}-1 \tag{4.9}$$

which admits, as we now explain, a clear biological interpretation.

Consider a newborn individual. In the absence of cannibalism it will reach adulthood with probability $\mathscr{F}_0(x_A)$. One effect of cannibalism is that this survival probability is reduced by a certain factor, say P. Another effect is that the subpopulation of adults gains extra energy, say an expected amount $\Phi(x_A)$ per newborn individual. A fraction $1-\kappa$ of this energy is channelled to reproduction. To deduce how much offspring can be made from this we have to multiply by the conversion factor η. So define

$$q=\eta(1-\kappa)\Phi(x_A) \tag{4.10}$$

If we take into account one "recycle" opportunity, we then must count one newborn individual as $1+q$. But if we also take into account the second recycle opportunity we must count $1+q+q^2$. And so on. Summing up the resulting geometric series we conclude that one newborn individual must be counted as

$$\frac{1}{1-q}$$

when $0<q<1$ (and as infinity when $q\geqslant 1$).

The combined negative and positive effect is now expressed by the product

$$\frac{P}{1-q}.$$

When this product exceeds one, cannibalism is a positive feedback mechanism and we expect a backward (that is, subcritical) bifurcation. If the product (4.11) is less than one, cannibalism is a negative feedback mechanism and we expect a forward (supercritical) bifurcation when Z is varied.

It remains to compute P and $\Phi(x_A)$. We do so by following a newborn individual in the time window needed to grow from x_b to x_A, but instead of time we use size as the bookkeeping variable. For the survival probability we have the differential equation

$$\frac{d\mathscr{F}}{dx} = -\frac{\mu_0(x)+I_3\phi(x)}{g_0(x)}\mathscr{F}, \quad \mathscr{F}(x_b)=1.$$

So the cannibalism induced survival reduction factor P is given by

$$P = \exp\left(-I_3\int_{x_b}^{x_A}\frac{\phi(\xi)}{g_0(\xi)}\,d\xi\right) = e^{-I_3\bar{\phi}}.$$

If we ignore the loss of time (or digestion capacity or whatever may be the underlying mechanism for the functional response) then the expected amount of extra energy for adults would increase from $\Phi(x_b)=0$ according to the differential equation

$$\frac{d\Phi}{dx} = I_3 e(x)\frac{\phi(x)}{g_0(x)}\mathscr{F}(x).$$

However, from the energy gain $e(x)$ we should subtract the expected energy $h_2(x)\frac{ECZ}{1+HCZ}$ that is lost by spending time or digestion capacity to the cannibalized juvenile. So the correct formula is

$$\frac{d\Phi}{dx} = I_3\left(e(x)-h_2(x)\frac{ECZ}{1+HCZ}\right)\frac{\phi(x)}{g_0(x)}\mathscr{F}(x), \quad \Phi(x_b)=0$$

and we find

$$\Phi(x_A) = I_3\int_{x_v}^{x_w}\left(e(y)-h_2(y)\frac{ECZ}{1+HCZ}\right)\frac{\phi(x)}{g_0(x)}\mathscr{F}(y)\,dy.$$

We now focus on the neighbourhood of the bifurcation point by taking $Z-Z_c$ small and simultaneously we focus on first-order effects of cannibalism by taking I_1, I_2 and I_3 small. Then

$$P = 1 - I_3\bar{\phi} + \text{h.o.t.}$$

and, since $\mathscr{F}(x) = \mathscr{F}_0(x) + \text{h.o.t.}$,

$$\Phi(x_A) = I_3\left(k_1 - \frac{ECZ_c}{1+HCZ_c}k_2\right) + \text{h.o.t.},$$

whence the inequality $\frac{P}{1-q}>1$ reduces to

$$\eta(1-\kappa)\left(k_1 - \frac{ECZ_c}{1+HCZ_c}k_2\right) > \bar{\phi}$$

in the limit.

Now recall (4.9) and its relation to the sign of K. There are two differences with the presentation of van den Bosch et al. (1988). Firstly, since we incorporate a functional response, we have to subtract from the energy gain $e(x)$ the energy lost by spending time and/or digestion capacity on the cannibalized young. Secondly, we interpret $\bar{\phi}$ more carefully in terms of the reduction in the survival probability due to cannibalism.

In the setting of van den Bosch et al. (1988) h_2 and therefore k_2 are zero and the quantity $k_1/\bar{\phi}$ is interpreted as the energy gain per cannibalized young. The latter quantity, however, equals $k_1/\int_{x_v}^{x_w}\frac{\phi(\xi)}{g_0(\xi)}\mathscr{F}_0(\xi)\,d\xi$ in the limit (so the survival probability $\mathscr{F}_0$ has to be taken into account). The difference relates to the "possibility" of death due to other (than cannibalism) mechanisms *after* falling victim to cannibalism: those juvenile individuals that are eaten by adults, but would not have grown up to reach adulthood anyhow, provide extra energy but do not contribute to the loss in numbers! They come, so to speak, for free.

What can be said about the global behaviour of the branch of steady states bifurcating at $Z=Z_c$? When we make the reasonable assumption that handling time is proportional to energy content, we may take $h_2(y)=\theta e(y)$ to obtain $I_2=\theta I_1$ (this is in particular reasonable when "handling" amounts to "digestion" and the two types of food have a rather similar chemical composition).

The steady-state problem now reads

$$\eta(1-\kappa)\frac{ECZ+I_1}{1+HCZ+\theta I_1}\,e^{-I_3\bar{\phi}}\frac{\mathscr{F}_0(x_A)}{\mu_A} = 1, \tag{4.12}$$

$$I_1 = c\int_{x_v}^{x_w} e(y)\mathscr{F}_0(y)\frac{\phi(y)}{g_0(y)}\,e^{-I_3\int_{x_v}^{y}\frac{\phi(\xi)}{g_0(\xi)}\,d\xi}\,dy, \tag{4.13}$$

$$I_3 = c\frac{1}{1+HCZ+\theta I_1}\frac{\mathscr{F}_0(x_A)}{\mu_A}e^{-I_3\bar{\phi}}. \tag{4.14}$$

Combining (4.12) and (4.14) we find

$$I_3 = \frac{c}{\eta(1-\kappa)}\frac{1}{ECZ+I_1}$$

and, solving for c and putting the result into (4.13), we obtain

$$I_1 = \eta(1-\kappa)(ECZ+I_1)Q(I_3), \tag{4.15}$$

where, by definition,

$$Q(I_3) = I_3\int_{x_v}^{x_w} e(y)\mathscr{F}_0(y)\frac{\phi(y)}{g_0(y)}e^{-I_3\int_{x_v}^{y}\frac{\phi(\xi)}{g_0(\xi)}\,d\xi}. \tag{4.16}$$

Solving (4.15) for I_1, we find

$$I_1 \frac{\eta(1-\kappa)ECZQ(I_3)}{1-\eta(1-\kappa)Q(I_3)}. \tag{4.17}$$

Inserting (4.17) into (4.12) we get one equation in one unknown, I_3, with one parameter, Z. It is not possible to solve for I_3 in terms of Z, but the other way round it does work and one obtains

$$Z = \left(\eta(1-\kappa)EC\left(1+\frac{Q(I_3)}{1-\eta(1-\kappa)Q(I_3)}\right)\frac{\mathscr{F}_0(x_A)}{\mu_A}e^{-\bar{\phi}I_3} - \frac{\theta\eta(1-\kappa)ECQ(I_3)}{1-\eta(1-\kappa)Q(I_3)} - HC\right)^{-1}. \tag{4.18}$$

The graph of this function provides us with the global bifurcation diagram in the (Z, I_3)-plane, but of course one needs to evaluate $Q(I_3)$ to plot the graph.

It is possible to achieve a drastic simplification by a limiting procedure in which the vulnerability window is shrunk to a point x_v while the vulnerability ϕ itself is blown up such that the quantity $\bar{\phi}$ defined by (4.6) remains constant. By writing

$$Q(I_3) = \int_{x_v}^{x_w} e(y)\mathscr{F}_0(y)\left(-\frac{d}{dy}e^{-I_3\int_{x_v}^{y}\frac{\phi(\xi)}{g_0(\xi)}d\xi}\right)dy \tag{4.19}$$

and realizing that, in the limit, $\exp\left(-I_3\int_{x_v}^{y}\frac{\phi(\xi)}{g_0(\xi)}d\xi\right)$ jumps down from 1 to exp $(-\bar{\phi}I_3)$ when y passes x_v, one deduces that, in the limit

$$Q(I_3) = e(x_v)\mathscr{F}_0(x_v)\left(1-e^{-\bar{\phi}I_3}\right). \tag{4.20}$$

Consequently, we can now conclude from (4.15) that

$$\eta(1-\kappa)(ECZ+I_1)e^{-\bar{\phi}I_3} = \eta(1-\kappa)(ECZ+I_1) - \frac{I_1}{e(x_v)\mathscr{F}_0(x_v)}. \tag{4.21}$$

It follows that (4.12) is a *linear* relation between I_1 and Z which, after some rearranging reads

$$\left(\theta-\eta(1-\kappa)\frac{\mathscr{F}_0(x_A)}{\mu_A}+\frac{1}{e(x_v)\mathscr{F}_0(x_v)}\frac{\mathscr{F}(x_A)}{\mu_A}\right)I_1 = \left(\eta(1-\kappa)EC\frac{\mathscr{F}_0(x_A)}{\mu_A}-HC\right)Z-1.$$

We note the following:

(i) $I_1=0$ corresponds to $Z=Z_c$, as should be the case.

(ii) The linear relationship between I_1 and Z implies that the global bifurcation diagram in the (Z, I_1)-plane is completely determined by the local bifurcation diagram near $(Z, I_1)=(Z_c, 0)$ and that there are exactly two generic possibilities and one exceptional one, namely those depicted in Fig. 3.

(iii) In the case of the backward bifurcation it is possible for the species to 'live' on a combination of food for juveniles and cannibalism. There are indeed lakes in Scotland and Scandinavia in which the only fish are pike, so the small individuals, which eat zooplankton, extend the foraging possibilities of the big individuals.

(iv) The coefficient of Z is positive, since we assumed (4.8), which expresses the fact that the species can grow on standard food, provided it is available in a sufficient amount. Accordingly, the direction of bifurcation is completely determined by the sign of the coefficient of I_1.

(v) In the limit of vanishingly small vulnerability window we have

$$k_1 = e(x_v)\mathscr{F}_0(x_v)\bar{\phi},$$

$$k_2 = \theta e(x_v)\mathscr{F}_0(x_v)\bar{\phi}.$$

Combining this with the identity

$$\frac{ECZ_c}{1+HCZ_c} = \frac{\mu_A}{\mathscr{F}_0(x_A)}\frac{1}{\eta(1-\kappa)},$$

one can check that the condition for backward bifurcation derived earlier coincides exactly with the condition that the coefficient of I_1 has negative sign.

We conclude that in this caricatural situation there is a dichotomy:

- Either cannibalism is a positive feedback mechanism, the bifurcation is subcritical and the branch extends to $Z=0$. In this case, presumably, there is bistability: either the population goes extinct because it is too small or, if it exceeds a threshold, it grows beyond bound (essentially on juvenile food which in the model is kept at a constant level).
- Or cannibalism is a negative feedback mechanism, the bifurcation is supercritical and the branch extends to $Z=\infty$. In this case, presumably, the nontrivial steady states are stable for Z somewhat larger than Z_c but may lose the stability for larger values of Z by a Hopf bifurcation due to delayed negative feedback.

In general the branch may show wiggles (see van den Bosch et al., 1988, Figs. 2(a)–(c) and 4). The reason is that the gain or loss (whether we express this in terms of numbers or in terms of energy does not matter) criterion may have a different outcome for juveniles in the lower part of the vulnerability window compared to juveniles in the upper part of the vulnerability window. As cannibalism affects the steady size distribution and the criterion involves taking an average, the balance may turn different ways along the branch. In other words, in a mixed feedback situation a quantitative aspect has a decisive influence and the branch may show one or more turns.

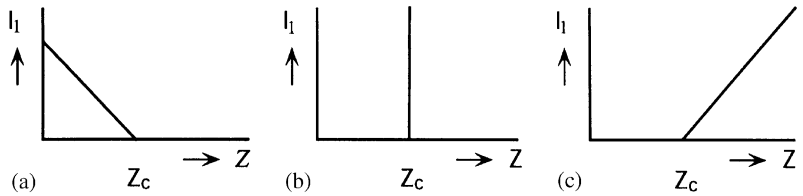

Fig. 3. Bifurcation diagram of the cannibalism model in the case of vanishingly small vulnerability window. (a) subcritical bifurcation, (b) vertical bifurcation (exceptional case), (c) supercritical bifurcation.

4.2. Population genetics with physiological structure

4.2.1. Model specification

In this subsection we show how any of the earlier models in this paper can be extended to incorporate genetic differences. To this end we distinguish newborns not only on the basis of their physiological state but also on the basis of their genotype, i.e., $\Omega_b = \Omega_{p,b} \times \Omega_g$, where $\Omega_{p,b}$ represents the physiological differences among newborns, and Ω_g the genetic ones. For exposition purposes we confine ourselves to a one-locus two-alleles diploid system, so that $\Omega_g = \{aa, aA, AA\}$. In addition we assume that $\Omega_{p,b}$ contains a single element only, i.e., everybody is born equal but for its genotype, so that we may write $\Omega_b = \Omega_g$. We do not claim originality as in essence our approach conforms to that of Charlesworth (1976, 1994) and Charlesworth and Charlesworth (1973). All our notation shows is how little effort is needed to deal meaningfully with more involved forms of density dependence. At the mathematical end our example brings out some of the technicalities of dealing with higher dimensional Ω_b.

The one special assumption that we make at the genetic end is that of random mating, or, equivalently, random union of gametes. This assumption allows us to write $I = \begin{pmatrix} I_g \\ I_e \end{pmatrix}$, where the ecological component of I, I_e, influences the production of newborns by females (and/or hermaphrodites) and of sperm, and/or the average male mating propensity, but not their genotype, and the genetic component, I_g, only affects the genotype of the newborns. The components of $I_g = \begin{pmatrix} I_a \\ I_A \end{pmatrix}$ can be interpreted as the effectively available sperm. Therefore, the average lifetime production of newborns by an $\mathscr{A}\mathscr{A}$ individual, to be denoted as $E_{\mathscr{A}\mathscr{A}}$ (E for eggs), $\mathscr{A}\mathscr{A} \in \{aa, aA, AA\}$, only depends on I_e. $E_{\mathscr{A}\mathscr{A}}$ incorporates the chance of a newborn $\mathscr{A}\mathscr{A}$ being a female, or becoming female somewhere during its lifetime, all in dependence on I_e. Thus, the model allows for any form of sex determination. As the genetic component of the state does not change over the lifetime of an individual, the calculation of each $E_{\mathscr{A}\mathscr{A}}$ proceeds in the same manner as in models without genetic differentiation, but for the fact that we also have to take account of an individual's sexual role. A similar statement applies to the lifetime sperm production, or male mating propensity, to be denoted as $S_{\mathscr{A}\mathscr{A}}$ (S for sperm). A straightforward application of Mendel's rules then gives

$$b = L(I)b \text{ with } b = \begin{pmatrix} b_{aa} \\ b_{aA} \\ b_{AA} \end{pmatrix} \text{ and}$$

$$L = \begin{pmatrix} E_{aa}p_a & \frac{1}{2}E_{aA}p_a & 0 \\ E_{aa}p_A & \frac{1}{2}E_{aA} & E_{AA}p_a \\ 0 & \frac{1}{2}E_{aA}p_A & E_{AA}p_A \end{pmatrix}, \tag{4.22}$$

with the $E_{\mathscr{A}\mathscr{A}}$ depending on I_e, and

$$p_a = \frac{I_a}{I_a + I_A}, \quad p_A = \frac{I_A}{I_a + I_A} \tag{4.23}$$

(the relative allele frequencies in sperm) together with

$$I_g = G_g(I_e)b, \quad \text{with } G_g = \begin{pmatrix} S_{aa} & \frac{1}{2}S_{aA} & 0 \\ 0 & \frac{1}{2}S_{aA} & S_{AA} \end{pmatrix}, \tag{4.24}$$

with the $S_{\mathscr{A}\mathscr{A}}$ depending on I_e, and

$$I_e = G_e(I_e)b. \tag{4.25}$$

4.2.2. Bringing the equations in more explicit and simpler form

The standard linear algebra approach to the eigenvalue problem

$$L(I)b = b \tag{4.26}$$

is to separate the solvability condition

$$\det(L(I) - Id) = 0 \tag{4.27}$$

on I from the (subsequent) computation of an eigenvector. In line with the population genetics tradition we follow a somewhat different approach here (analogues of which may very well have great advantages beyond the special genetic context). The characteristic features are:

(i) From the very beginning we look for a *normalized* eigenvector u (Note: the meaning of the symbol u in this section differs from that in Section 3). So we require

$$L(I)u = u \tag{4.28}$$

and

$$\langle 1, u \rangle := u_{aa} + u_{aA} + u_{AA} = 1, \tag{4.29}$$

so that the components of u are the *relative frequencies* of the genotypes at birth. The general solution of (4.26) is then given by

$$b = cu, \quad c \in \mathbf{R}. \tag{4.30}$$

(ii) We make an educated guess about the structure of u in terms of p_a and a second parameter q_a. The quantity q_a is the relative frequency of the allele a in eggs (just as p_a is the relative frequency of a in sperm). Thus we restore the symmetry of the two sexes, which was (temporarily) broken in the formulation (4.22)–(4.25).

Proposition 4.1. *The three-dimensional vector u satisfies* (4.28), (4.29) *if and only if*

$$u = \begin{pmatrix} p_a q_a \\ p_a q_A + p_A q_a \\ p_A q_A \end{pmatrix}, \tag{4.31}$$

where $q_A = 1-q_a$, $p_a = 1-P_a$, *and* p_a, q_a *and E satisfy*

$$q_a = \frac{E_{aa} p_a q_a + \frac{1}{2} E_{aA}(p_a q_a + p_A q_a)}{\bar{E}} \tag{4.32}$$

and

$$\bar{E} := E_{aa} p_a q_a + E_{aA}(p_a q_A + p_A q_a) + E_{AA} p_A q_A = 1. \tag{4.33}$$

Eq. (4.32) tells us that q_a is indeed the relative frequency of allele a in the eggs and (4.33) that the individuals in the population on average just replace themselves.

Proof. Assume $L(I)u = u$. In view of (4.22) we can write the first and the third equation of this system as

$$\begin{cases} u_{aa} &= p_a q_a, \\ u_{AA} &= p_A q_A, \end{cases} \tag{4.34}$$

provided

$$\begin{cases} q_a &= E_{aa} u_{aa} + \frac{1}{2} E_{aA} u_{aA}, \\ q_A &= \frac{1}{2} E_{aA} u_{aA} + E_{AA} u_{AA}. \end{cases} \tag{4.35}$$

If we add the three equations that together constitute $L(I)u = u$ we find that necessarily

$$q_a + q_A = 1. \tag{4.36}$$

Since

$$u_{aA} = 1 - u_{aa} - u_{AA} = 1 - p_a q_a - p_A q_A = p_a q_A + p_A q_a, \tag{4.37}$$

we have now verified (4.31), while simple substitutions establish that (4.36) is (4.33) in disguise, and that the first equation of (4.35) amounts to (4.32). The "only if" part has now been proved. Proving the "if" part proceeds by making the same steps in reverse order. For completeness we provide the details.

Let u be given by (4.31) with $q_A = 1-q_a$ and $p_A = 1-p_a$. Then (recall the last identity in (4.37)) normalization (4.29) holds. The first equation of $L(I)u = u$ is, apart from a factor p_a, exactly (4.32). Combining (4.32) and (4.33) we may write

$$q_A = 1 - q_a = \tfrac{1}{2} E_{aA} u_{aA} + E_{AA} u_{AA}$$

and from this it follows at once that the third equation of $L(I)u = u$ holds. Identity (4.33) can also be written as $\langle 1, Lu \rangle = \langle 1, u \rangle$, i.e., the equation obtained by summing the three equations holds. But then the second equation has to hold.

Remark 4.2. (i) Readers familiar with population genetics will recognize (4.33) as the condition that at ecological equilibrium the mean fitness $\bar{E}$ should equal one. The two Eqs. (4.32) and (4.33) are, essentially, the solvability condition (4.27) and the normalization condition (4.29).

(ii) Yet, another way of formulating the problem is: we want to solve the nonlinear system of equations

$$u = \frac{L(I)u}{\langle 1, L(I)u \rangle}$$

for u in the simplex $\{u : \langle 1, u \rangle = 1, u \geqslant 0\}$ which we parametrize with the unit square in $\mathbf{R}^2$ according to (4.31) (the simplex is covered twice by the unit square, corresponding to the symmetry of interchanging p and q). This way, however, misses the point that p_a in (4.31) is the same as p_a in the expression for $L(I)$ in (4.22). That is why we prefer to consider (4.31) an educated (by population genetics literature!) guess.

Corollary 4.3. *Problem* (4.22)–(4.25) *is equivalent to the system of equations*

$$p_a = \frac{S_{aa} p_a q_a + \frac{1}{2} S_{aA}(p_a q_A + p_A q_a)}{S_{aa} p_a q_a + S_{aA}(p_a q_A + p_A q_a) + S_{AA} p_A q_A}, \tag{4.38}$$

$$q_a = \frac{E_{aa} p_a q_a + \frac{1}{2} E_{aA}(p_a q_A + p_A q_a)}{E_{aa} p_a q_a + E_{aA}(p_a q_A + p_A q_a) + E_{AA} p_A q_A}, \tag{4.39}$$

$$E_{aa} p_a q_a + E_{aA}(p_a q_A + p_A q_a) + E_{AA} p_A q_A = 1, \tag{4.40}$$

$$I_e = c G_e(I_e) u \quad \text{with} \quad u = \begin{pmatrix} p_a q_a \\ p_a q_A + p_A q_a \\ p_A q_A \end{pmatrix} \tag{4.41}$$

in the unknowns p_a, q_a, c *and* I_e.

According to Eqs. (4.38) and (4.39), p_a and q_a are the relative frequency of the allele a in the sperm and in the eggs, respectively, Eq. (4.40) is the condition that the

population on average replaces itself and (4.41) gives the outcome of a random union of gametes.

Proof. Eq. (4.25) is, after substitution of (4.30) and (4.31) just copied as (4.41), while (4.32) and (4.33) are copied as (4.40) and (4.39). So it only remains to verify that (4.38) represents (4.23) and (4.24). Note that (4.24) is an explicit expression for the couple I_a and I_A in terms of S and $b=cu$. Eq. (4.38) is simply the first equation of (4.23) with this expression substituted and with u given by (4.31). Note that c drops out by the homogeneity of (4.23). As the second equation of (4.23) amounts to $p_A=1-p_a$ we are done. □

In the remaining subsections of 4.2 we focus our attention on (4.38)–(4.41). First, we consider special solutions, viz., those that correspond to the absence of one of the two alleles. Next, we consider special problems, i.e. we make additional assumptions concerning E and S (while keeping G_e general as our aim is to unravel the emerging genetic structure).

4.2.3. *Boundary equilibria and their stability*

As to be expected from the biological nature of the problem, (4.38) is satisfied if we put $p_a=q_a=1$ (and, likewise, if we put $p_a=g_a=0$ but, exploiting the symmetry of exchanging a and A, we shall restrict our attention to the first possibility without any loss of generality). Clearly both (4.40) and (4.39) are now satisfied as well provided

$$E_{aa}=1. \tag{4.42}$$

Together (4.41) and (4.42) constitute two equations in the unknowns c and I_e (whenever I_e is a scalar quantity these two equations decouple: (4.42) determines I_e and next c is determined from (4.41)).

Whether or not the allele A can invade successfully in the environment $I=\begin{pmatrix} I_g \\ I_e \end{pmatrix}$ as set by the homozygous aa population can be determined in a manner which is reminiscent of the "invasion" criteria of Section 2.3. The key difference is that now there are "hybrids", the heterozygotes. In fact these play the decisive role, as AA homozygotes are negligible in the linearization corresponding to the rareness of A. Indeed, ignoring second order effects, we deduce from (4.22) the iteration

$$b'_{aA}=\begin{pmatrix} E_{aa}p_A & \frac{1}{2}E_{aA} \end{pmatrix}\begin{pmatrix} c \\ b_{aA} \end{pmatrix}, \tag{4.43}$$

where the prime refers to the next generation. Similarly (4.23) and (4.24) yield

$$p_A=\frac{\frac{1}{2}S_{aA}b_{aA}}{S_{aa}c}. \tag{4.44}$$

So combining the two we arrive at the linear recursion

$$b'_{aA}=R_{0,A}(I)b_{aA} \tag{4.45}$$

with

$$R_{0,A}(I)=\frac{1}{2}\left(\frac{S_{aA}(I_e)}{S_{aa}(I_e)}+E_{aA}(I_e)\right), \tag{4.46}$$

the so-called invasion fitness of A. The quantity $R_{0,A}(I)$ should be compared to the classical Shaw–Mohler formula

$$F=\frac{1}{2}\left(\frac{S_{aA}}{S_{aa}}+\frac{E_{aA}}{E_{aa}}\right) \tag{4.47}$$

for the discrete-time invasion fitness F in a sex-differentiated population (Shaw and Mohler 1953; also see Charnov 1982); this formula made its first appearance in the population genetical literature in Parsons (1961). Due to our explicit accounting for density dependence we here have (4.42) as an additional condition. The conclusion is that A can invade successfully if $R_{0,A}>1$ while it will fail to invade when $R_{0,A}<1$, with I_e determined by the equilibrium of the single aa resident.

Remark 4.4. If Ω_b has more than one element, for example since kids inherit their social status from their mother (Leimar, 1996), the E_{AA} become matrices and we have to replace in (4.42) E_{aa} with its dominant eigenvalue. The invasion fitness $R_{0,A}$ then has to be calculated as the dominant eigenvalue of the matrix

$$\frac{1}{2}\left(\frac{S_{aA}}{S_{aa}}E_{aa}+E_{aA}\right).$$

4.2.4. *Separable density dependence*

Assume that both S and E depend on I_e by way of a scalar factor (i.e., I_e may determine the magnitude of S and of E, but not the relative proportions of the components of S and of E). Since the problem is homogeneous of degree zero in S, we may then as well consider S as a fixed (i.e., I_e independent) vector. Abusing notation we replace E by $\theta(I_e)E$ with the latter E considered as a fixed vector as well. This amounts to replacing $E_{\mathscr{A}\mathscr{A}}$ in (4.40), (4.39) by $\theta E_{\mathscr{A}\mathscr{A}}$ with $E_{\mathscr{A}\mathscr{A}}$ fixed and θ depending on I_e.

By homogeneity θ drops out in Eq. (4.39).

Together (4.38) and (4.39) constitute two equations in the two unknowns p_a and q_a. This forms the genetic half of the problem, which has to be analysed first (see Haldane, 1924, 1926; Owen, 1952; Parsons, 1961; Bodmer, 1965; Mandel, 1971, Appendix C). Once p_a and q_a are determined, it remains to solve (4.41) and

$$\theta(I_e)=\frac{1}{E_{aa}p_aq_a+E_{aA}(p_aq_A+p_Aq_a)+E_{AA}p_Aq_A} \tag{4.48}$$

which together constitute the ecological half of the problem, with c and I_e as the unknowns.

4.2.5. Sex determining alleles

When $E_{aA}=0$ we deduce from (4.40)–(4.39) that either $q_a=0$ or $E_{aa}p_a=1$. In the first case (4.40) requires $E_{AA}p_A=1$ and in the second case (4.40) requires that either $q_A=0$ or $E_{AA}p_A=1$. This gives three possibilities

(i) $q_a=0, E_{AA}p_A=1$,
(ii) $E_{aa}p_a=1=E_{AA}p_A$,
(iii) $q_A=0, E_{aa}p_a=1$

but we shall only study (i) and (ii) as (iii) differs only from (i) by the interchanging of a and A. In case (i) (4.38) boils down to

$$p_a=\frac{\frac{1}{2}S_{aA}p_a}{S_{aA}p_a+S_{AA}(1-p_a)} \tag{4.49}$$

which has the solutions $p_a=0$ and

$$p_a=\frac{\frac{1}{2}S_{aA}-S_{AA}}{S_{aA}-S_{AA}}, \tag{4.50}$$

the latter being feasible (i.e. satisfying $0<p_a<1$) if and only if $\frac{1}{2}S_{aA}>S_{AA}$ (so note that (4.50) is feasible if and only if the zero steady-state of the recursion defined by the right-hand side of (4.49) is unstable and that in that case the steady state defined by (4.50) is stable). After having solved the genetic half of the problem in this manner, it remains to solve the ecological half of (4.41) supplemented by

$$E_{AA}p_A=1 \tag{4.51}$$

for the unknowns I_e and c. Once I_e is determined, the formulas for p_a become explicit.

In the mammalian sex determination system males have an X- and a Y-chromosome, making $E_{XY}=0$. Females have two X-chromosomes, making $S_{XX}=0$. The lack of an X-chromosome is presumed to be lethal (Cavalli-Sforza and Bodmer, 1971), so $E_{YY}=S_{YY}=0$. With, for instance, $A=Y$ and $a=X$, we find from (4.50) that p_X is equal to $\frac{1}{2}$. The completely symmetrical mode of sex determination with the females as the heterozygote sex occurs in, for example, birds.

In the more general framework of this subsection one should interpret aA individuals as pure males (since $E_{aA}=0$) and AA individuals as hermaphrodites, The condition $\frac{1}{2}S_{aA}>S_{AA}$ then means that full males should be at least twice as fertile as hermaphrodites AA in their male role.

In case (ii) we have explicitly

$$p_a=E_{aa}^{-1}\ \&\ p_A=E_{AA}^{-1}, \tag{4.52}$$

which requires that

$$E_{aa}^{-1}+E_{AA}^{-1}=1. \tag{4.53}$$

Now I_e and c are determined by the couple of Eq. (4.41) and (4.53). It remains to determine q_a. This we do by substituting (4.52) into (4.38) and by subsequently solving the resulting linear equation for the unknown q_a. This yields (using (4.53) in the equivalent form $E_{aa}+E_{AA}=E_{aa}E_{AA}$)

$$q_a=\frac{S_{AA}+S_{aA}(\frac{1}{2}E_{AA}-1)}{S_{AA}+S_{aA}(\frac{1}{2}E_{AA}E_{aa}-2)+S_{aa}} \tag{4.54}$$

provided the expression at the right-hand side is above zero and below one.

From a mathematical point of view, what is special about $E_{aA}=0$ is that the matrix $L(I)$ specified in (4.22) is reducible and can have two independent eigenvectors corresponding to eigenvalue one.

4.2.6. The Hardy–Weinberg case

If we take account of the physiological intricacies of real life as stressed by our present framework, there appears to be little biological rationale for making the assumption that the vector S is proportional to the vector E, say with proportionality constant $\theta(I_e)$. Yet, because it exemplifies some features of the general problem in a relatively simple manner and because it dominates the population genetical literature, we shall consider this special so-called Hardy–Weinberg (HW) case in some detail. To achieve conformity with the notation used in population genetics we shall rename E as W.

When $S=\theta E$ the numerator at the right-hand side of (4.38) equals, in view of (4.39), θq_a, Whereas the denominator equals, in view of (4.40), θ. So $p_a=q_a$, as to be expected when male and female fertilities are essentially the same.

When in (4.38) we substitute $q_a=p_a$, divide out the roots $p_a=0$ and $p_a=1$ we obtain, after renaming S, the expression

$$p_a=\frac{W_{AA}-W_{aA}}{W_{aa}-2W_{aA}+W_{AA}} \tag{4.55}$$

provided the denominator is not zero (in the latter case there is no third solution or, in the still more special situation that $W_{aa}=W_{aA}=W_{AA}$, any p_a is a solution). The ecological half of the problem consists of solving the Eq. (4.41) and

$$\bar{W}(I_e)=W_{aa}p_a^2+2W_{aA}p_a(1-p_a)+W_{AA}(1-p_a)^2=1 \tag{4.56}$$

for the unknowns c and I_e. Only after I_e has been determined in this manner can one check whether (4.55) does indeed make sense, i.e. whether the right-hand side lies between 0 and 1 (which amounts to checking that either the heterozygote is superior, $W_{aA}>W_{aa}$, W_{AA} or inferior, $W_{aA}<W_{aa}$, W_{AA}).

In principle, we can also combine (4.41) with

$$W_{aa}(I_e)=W_{aA}(I_e)=W_{AA}(I_e)=1 \tag{4.57}$$

while considering, apart from c and I_e, also p_a as an unknown. As then there is one more equation than the number of unknowns, we should in general not expect to find a solution. However, there may be an a priori constraint on W, such as full dominance of A over a (i.e. $W_{aA}=W_{AA}$) and then there is a perfect match between equations and unknowns. So the possibility of satisfying (4.57) should not be dismissed too quickly.

4.2.7. The internal equilibria in the general case

It is, generically, possible to replace one equation of the duo (4.40) and (4.39) by an explicit expression for q_a in terms of p_a and E. To this end we write (4.40) as

$$\tfrac{1}{2}E_{aA}(p_aq_A+p_Aq_a)=\tfrac{1}{2}(1-E_{aa}p_aq_a-E_{AA}p_Aq_A)$$

and use this identity to write (4.39) as

$$\begin{aligned}q_a &= \tfrac{1}{2}(1+E_{aa}p_aq_a-E_{AA}p_Aq_A)\\ &= \tfrac{1}{2}(1-E_{AA}p_A)+\tfrac{1}{2}q_a(E_{aa}p_a+E_{AA}p_A).\end{aligned}$$

Provided

$$1-\tfrac{1}{2}E_{aa}p_a-\tfrac{1}{2}E_{AA}p_A\neq 0 \tag{4.58}$$

we then find

$$q_a=\frac{\tfrac{1}{2}(1-E_{AA}p_a)}{1-\tfrac{1}{2}E_{aa}p_a-\tfrac{1}{2}E_{AA}p_A}. \tag{4.59}$$

If we substitute this expression into (4.38) we get, after slight simplification,

$$p_a=\frac{S_{aa}p_a(1-E_{AA}p_A)+\tfrac{1}{2}S_{aA}[p_a(1-E_{aa}p_a)+p_A(1-E_{AA}p_A)]}{S_{aa}p_a(1-E_{AA}p_A)+S_{aA}[p_a(1-E_{aa}p_a)+p_A(1-E_{AA}p_A)]+S_{AA}p_A(1-E_{aa}p_a)}. \tag{4.60}$$

Considering S and E as given quantities (for the moment), this is a third degree equation in p_a.

Explicitly the coefficients of the polynomial are given by

$$\begin{aligned}p_a^3 &: S_{aa}E_{AA}-S_{aA}(E_{aa}+E_{AA})+S_{AA}E_{aa},\\ p_a^2 &: S_{aa}(1-2E_{AA})+\tfrac{1}{2}S_{aA}(5E_{AA}+E_{aa})-S_{AA}(1+E_{aa}),\\ p_a &: S_{aa}(E_{AA}-1)+S_{aA}(1-2E_{AA})+S_{AA},\\ 1 &: \tfrac{1}{2}S_{aA}(E_{AA}-1).\end{aligned}$$

If all of these coefficients vanish, we have a degenerate situation in which (4.60) holds for every $p_a\in[0,1]$. This is the case if and only if one of the following two conditions holds:

(i) $S_{aa}=S_{aA}=S_{AA}$ and $E_{aa}=E_{aA}=E_{AA}=1$,
(ii) $S_{aA}=0, S_{AA}=S_{aa}$ and $E_{aa}=E_{AA}=0$.

(If (i) holds we have $q_a=p_a$ whereas if (ii) holds we have $q_a=\tfrac{1}{2}$: strictly mathematically speaking there is a third condition, viz., $S_{aa}=S_{aA}=S_{AA}$ and E_{aa}, E_{AA} arbitrary, but this we dismiss as it would mean immediate extinction and, moreover, it would make many of the preceding quantities undefined, since denominators are zero in that case.) To these conditions we should add (4.40) and (4.39), but if (i) holds (4.40) is automatically true, so in both cases we have six equations and only three unknowns, viz., p_a, c and I_e. This clearly is an argument against giving the degenerate case any thought at all. However, in behavioural evolutionary ecology the ideal free distribution plays a prominent role and it is exactly based on equalizing fitnesses of the different strategies. So it may be that the evolutionary process itself brings the population precisely to an otherwise exceedingly nongeneric situation. It was this rather general consideration that encouraged us to exhibit the precise conditions, despite the fact that they lead to an overdetermined system.

In the nondegenerate case (4.60) has isolated solutions and up to three of them may lie in (0,1). We refer to the extensive population genetical literature, in particular Owen (1952) Bodmer (1965) and Mandel (1971). As the route taken in these references is rather different from the one described above, we give the connection in Appendix C.

4.2.8. Invasion of dimorphic equilibria by mutants

Evolution proceeds by the repeated appearance of new mutants which may or may not invade (see, for example, Hammerstein, 1996). In Section 4.2.3 we already discussed invasions in monomorphic populations. As a finale to our discussion of genetic models we here provide the tools for investigating the invasion of new alleles in a dimorphic population. We shall not write out the full three allele model, but immediately write down from first biological principles the appropriate linearized system, following the pattern that surfaced in Section 4.2.3.

Let

$$h=\begin{pmatrix}b_{a\alpha}\\ b_{A\alpha}\end{pmatrix}, \tag{4.61}$$

where α represents the new mutant allele. Whether α can invade or not can be determined from the iteration of

$$h'=\begin{pmatrix}E_{aa}p_\alpha & \tfrac{1}{2}E_{aA}p_\alpha & 0 & \tfrac{1}{2}E_{a\alpha}p_a & \tfrac{1}{2}E_{A\alpha}p_a\\ 0 & \tfrac{1}{2}E_{aA}p_\alpha & \tfrac{1}{2}E_{AA}p_\alpha & \tfrac{1}{2}E_{a\alpha}p_A & \tfrac{1}{2}E_{A\alpha}p_A\end{pmatrix}\begin{pmatrix}cu\\ h\end{pmatrix} \tag{4.62}$$

with

$$p_\alpha=\frac{S_{a\alpha}b_{a\alpha}+S_{A\alpha}b_{A\alpha}}{2c\bar{S}}, \tag{4.63}$$

where we suppress the dependence of $E_{\mathscr{A}\mathscr{A}}$ and $S_{\mathscr{A}\mathscr{A}}$ on I_e. Here I_e, $p_{\mathscr{A}}$, c, and u (and $q_{\mathscr{A}}$ occurring in (4.65)) are the quantities calculated in the previous subsections, while $\bar{S}$ is the analogue of $\bar{E}$ defined by (4.33), that is,

$$\bar{S} = S_{aa}u_{aa} + S_{aA}u_{aA} + S_{AA}u_{AA}. \tag{4.64}$$

By making use of (4.35) and the fact that $\bar{E}=1$, the pair of Eqs. (4.62) and (4.63) can be rewritten as

$h' = Mh$ with

$$M = \tfrac{1}{2}\left[\begin{pmatrix} q_a \\ q_A \end{pmatrix}\bar{S}^{-1}(S_{a\alpha}S_{A\alpha}) + \begin{pmatrix} p_a \\ p_A \end{pmatrix}(E_{a\alpha}E_{A\alpha})\right]. \tag{4.65}$$

So h grows, or declines, over the generations as a weighted sum of the relative male and female (remember that $\bar{E}=1$) contributions to the next generation. This is brought out even more poignantly in the Hardy–Weinberg case, where (4.65) reduces to

$$h' = \begin{pmatrix} p_a \\ p_A \end{pmatrix}(W_{a\alpha}W_{A\alpha})h, \tag{4.66}$$

so that h increases whenever $p_aW_{a\alpha}+p_AW_{A\alpha}>1$, and decreases when $p_aW_{a\alpha}+p_aW_{A\alpha}<1$. In the general case invasion occurs when the Perron–Frobenius eigenvalue of M, $R_{0,\alpha}(I_a, I_A; I_e)>1$ with I_a, I_A, and I_e determined by the two-allele resident equilibrium. This is the case if and only if

$$\mathrm{trace}(M) - |M| > 1, \tag{4.67}$$

while invasion cannot occur when the inequality is in the opposite direction.

5. Concluding remarks

Physiologically structured population models can encompass many mechanisms related to life history and interaction and that is, certainly, a strong point. Ideally then, they should be used to unravel the relationship between mechanisms at the individual level and phenomena at the population level (Metz and Diekmann, 1986; de Roos and Persson, 2001). When it comes to analysis, however, they have a tendency to be rather user unfriendly which is, for sure, a weak point.

Any step towards a general methodology for the formulation and analysis of structured population models may help to remedy this weak point. In this paper we have made such a step by showing that, under biologically not unreasonable conditions, the steady state problem can be reduced to the simple form (1.1), with the ingredients computable in terms of more basic ingredients by means of numerical integration of ordinary differential equations (Kirkilionis et al., 2001). We have provided tools for the analysis of (1.1) and illustrated the methodology by way of several examples.

A key feature is the systematic use of the interaction variable I characterizing the environmental conditions in which individuals have to lead their lives. We believe that the explicit use of I aids the model specification process. And once a model is formulated in terms of I, it is straightforward to superimpose the competition between variants of the same organism (recall Sections 2.3 and 4.2). Thus the formalism is tailor made for investigating the adaptive dynamics of life history traits.

There are, of course, still many open problems. How to determine whether or not a steady state is stable? How to "discretize" when the state-at-birth can take on values in a continuum and when the environmental condition is i-state specific? We intend to address such issues in future work.

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Appendix A. Additional material on bifurcation

In this appendix we prove the local bifurcation theorem (Theorem 2.1) and formulate a global bifurcation theorem.

Proof of Theorem 2.1. Because 1 is a *simple* eigenvalue of $L(0, \theta_c)$ we can decompose $\mathbf{R}^k$ as the direct sum

$$\mathbf{R}^k = \mathscr{N} \oplus \mathscr{R},$$

where $\mathscr{N} = \mathrm{span}\{{}^1b\}$ is the nullspace of $L(0, \theta_c)-Id$ and $\mathscr{R} = \{b | \langle {}^1b^*, b\rangle = 0\}$ is the range of $L(0, \theta_c)-Id$. Note that $\mathscr{R}$ is a $(k-1)$-dimensional linear subspace of $\mathbf{R}^k$.

Looking for solutions of the form

$$\begin{aligned} b &= \varepsilon({}^1b + z), \\ I &= \varepsilon y, \end{aligned} \tag{A.1}$$

with z, y and θ depending on the free parameter ε, we can divide out a factor ε (thus eliminating the trivial solution) and rewrite (2.1) in the form

$$\begin{aligned} {}^1b + z - L(\varepsilon y, \theta)({}^1b + z) &= 0, \\ y - G(\varepsilon y, \theta)({}^1b + z) &= 0. \end{aligned} \tag{A.2}$$

Eq. (A.2) has the solution $(z, \theta, y, \varepsilon) = (0, \theta_c, G(0, \theta_c)\,{}^1b, 0)$. We want to use the implicit function theorem to solve the equation for (z, θ, y) as a function of ε, starting in the point $(0, \theta_c, G(0, \theta_c){}^1b, 0)$. The Jacobian matrix of partial derivatives with respect to (z, θ, y) evaluated at this point takes the form

$$\begin{pmatrix} Id - L(0,\theta_c)_{|\mathscr{R}} & -\frac{\partial L}{\partial \theta}(0,\theta_c){}^1b & 0 \\ -G(0,\theta_c) & -\frac{\partial G}{\partial \theta}(0,\theta_c){}^1b & Id \end{pmatrix}. \tag{A.3}$$

The linear map from $\mathscr{R} \times \mathbf{R} \times \mathbf{R}^n$ into $\mathbf{R}^k \times \mathbf{R}^n$ defined by matrix (A.3) is invertible if and only if the linear map

$$\left(Id - L(0,\theta_c) - \tfrac{\partial L}{\partial \theta}(0,\theta_c){}^1b\right)$$

is invertible (note the lower block triangular form and the Id in the right lower corner of (A.3)). So the question is whether we can solve, for any given $x \in \mathbf{R}^k$, the equation

$$z - L(0,\theta_c)z - \frac{\partial L}{\partial \theta}(0,\theta_c){}^1b\theta = x \tag{A.4}$$

for $z \in \mathscr{R}$ and $\theta \in \mathbf{R}$. Pairing Eq. (A.4) with ${}^1b^*$ we see that

$$-\left\langle {}^1b^*, \frac{\partial L}{\partial \theta}(0,\theta_c){}^1b \right\rangle \theta = \langle {}^1b^*, x \rangle \tag{A.5}$$

should hold. Provided $\langle 1b^*, \frac{\partial L}{\partial \theta}(0,\theta_c){}^1b \rangle \neq 0$, (A.5) holds if one chooses

$$\theta = -\frac{\langle {}^1b^*, x \rangle}{\langle {}^1b^*, \frac{\partial L}{\partial \theta}(0,\theta_c){}^1b \rangle}. \tag{A.6}$$

Because $Id - L(0,\theta_c)_{|\mathscr{R}}$ is an isomorphism, we can subsequently solve for z.

The implicit function theorem now yields the existence as well as the uniqueness of solutions of this particular form; a computation along the same lines gives the formula for the first order term in the expansion of θ.

To prove that all nontrivial solutions are of the form (A.1) with, in particular, $z(0) = 0$, requires an additional estimate, for which we refer to Crandall and Rabinowitz (1971). An essentially equivalent approach is to use the Lyapunov–Schmidt reduction method, as in Chow and Hale (1982). □

The standard form of the Rabinowitz theorem assumes that the steady-state equation can be written in the form

$$x = \theta L x + H(x, \theta) \tag{A.7}$$

with $H(x,\theta) = o(|x|)$ as $x \to 0$, uniformly for θ in bounded intervals. Here θ is the bifurcation parameter and x is the variable, so x corresponds to our (b, I). The steady-state equations (2.1) do not naturally fit into the form (A.7). In Section 2.2.2 of his book, Cushing (1998) uses the trick to write (translated into our notation) the second equation in (2.1) as $I = G(I;\theta)L(I,\theta)b$ in the case in which the parameter θ is a multiplicative factor in L, while it does not enter in G.

Nussbaum (1975, 1985) presents a version of the theorem which applies more easily. Translated to our special and relatively simple equation (2.1), the result can be formulated as follows.

Theorem A.1. *Let $J \subset \mathbf{R}$ be an open interval. Let*

$$\Gamma = \{\theta \in J : L(0,\theta) \quad \text{has} \quad \text{eigenvalue } 1\}$$

and assume that Γ is countable and has no accumulation points. Define $S \subset \mathbf{R}^k_+ \times \mathbf{R}^n \times J$ by

$$S = (\{(0,0)\} \times \Gamma) \bigcup \{(b, I, \theta) \in \mathbf{R}^k_+ \times \mathbf{R}^n \times J : (2.1) \text{ holds and } (b, I) \neq (0,0)\}.$$

Let $\theta_c \in \Gamma$ be such that 1 is a simple eigenvalue of $L(0, \theta_c)$. Let S_0 be the connected component of S which contains $(0, 0, \theta_c)$. Then either

(i) *S_0 is not compact*
or
(ii) *S_0 contains a point $(0, 0, \tilde{\theta}_c)$ with $\tilde{\theta}_c \in \Gamma$ and $\tilde{\theta}_c \neq \theta_c$.*

A frequently occurring situation is that one can rule out alternative (ii) in the above theorem for the very simple reason that Γ consists of only one point. Finally, S_0 may fail to be compact in different ways. For instance,

- the θ-component may approach the boundary of J if J is bounded or tend to $+\infty$ if J is only bounded from below (which is a rather common situation);
- the (b, I)-component may be unbounded;
- a combination of these two.

Appendix B. Terminology, definitions and basic results for structured population models

In this appendix we collect some terminology and notation from (Diekmann et al., 2001), which should be consulted for more details. We also provide proofs of the lemmas of Section 3.

As argued in the above-mentioned paper, it is advantageous to consider the environmental condition affecting individual behaviour as an input to the system.

An *input* is a function I defined on the time-interval $[0, \ell(I))$ of length $\ell(I)$. The input takes on values in a subset Z of a Banach space. The space of all admissible inputs is denoted by $\mathscr{B}(Z)$. The *concatenation* $I_2 \odot I_1$ of I_1 and I_2 is defined on the interval $[0, \ell(I_1)+\ell(I_2))$ by

$$(I_2 \odot I_1)(t) = \begin{cases} I_1(t) & \text{for} \quad 0 \leqslant t < \ell(I_1), \\ I_2(t-\ell(I_1)) & \text{for} \quad \ell(I_1) \leqslant t < \ell(I_1)+\ell(I_2). \end{cases}$$

For $0 \leqslant s \leqslant (I)$, $\rho(s)I$ is the *restriction* of I to the subinterval $[0, s)$, that is,

$$(\rho(s)I)(t) = I(t) \text{ for } 0 \leqslant t < s.$$

Let Ω be a measurable space with a countably generated σ-algebra Σ. A *kernel* k is a map from $\Omega \times \Sigma$ into $\mathbf{R}$ which is bounded and measurable with respect to the first variable and countably additive with respect to the second variable. (So for fixed $\omega \in \sum$ the function $x \mapsto k(x,\omega)$ is bounded and measurable, while for fixed $x \in \Omega$ the map $\omega \mapsto k(x,\omega)$ defines a finite signed measure on Ω.) We call a kernel *positive* if it assumes nonnegative values only.

The *product* $k^1 \times k^2$ of two kernels k^1 and k^2 is the kernel defined by

$$(k^1 \times k^2)(x,\omega) = \int_\Omega k^1(\xi,\omega) k^2(x, d\xi). \tag{B.1}$$

Likewise we define the *product* $f \times k$ of a bounded measurable function $f: \Omega \to Z$ and a kernel k as the function

$$(f \times k)(x) \int_\Omega f(\xi) k(x, d\xi). \tag{B.2}$$

The product of a kernel k and a measure m is defined analogously as the measure

$$(k \times m)(\omega) = \int_\Omega k(\xi,\omega) m(d\xi). \tag{B.3}$$

Finally, we agree that the product $f \times m$ of a function and a measure is

$$f \times m = \int_\Omega f(x) m(dx) \in Z. \tag{B.4}$$

The $\times$-product is associative in the following sense: If in the case of three objects f, k and m, say, both the products $(f \times k) \times m$ and $f \times (k \times m)$ are well defined, then they are equal. In this case we leave out the parentheses and write simply $f \times k \times m$.

We shall use inputs $I \in \mathscr{B}$ to parametrize kernels and functions. We then write k_I, f_I, etc.

The interpretation of the basic ingredients u_I and Λ_I of a structured population model (see Definition 3.1) requires that certain consistency and monotonicity conditions hold. We now formulate these conditions.

Consistency conditions **C**

(i) For every I_1 and I_2 in $\mathscr{B}(Z)$ the Chapman–Kolmogorov relation

$$u_{I_2 \odot I_1} = u_{I_2} \times u_{I_1}$$

holds

(ii) For every I_1 and I_2 in $\mathscr{B}(Z)$ one has consistency between individual development, survival and reproduction:

$$\Lambda_{I_2 \odot I_1} = \Lambda_{I_1} + \Lambda_{I_2} \times u_{I_1}.$$

Monotonicity conditions **M**

(i) For any $x \in \Omega$, $\omega \in \Sigma$, $I \in \mathscr{B}(Z)$ the function $\sigma \mapsto \Lambda_{\rho(\sigma)I}(x,\omega)$ is nondecreasing and

$$\lim_{\sigma \downarrow 0} \Lambda_{\rho(\sigma)I}(x,\omega) = 0.$$

(ii) For any $x \in \Omega$, $\omega \in \Sigma$, $I \in \mathscr{B}$ the function $\sigma \mapsto u_{\rho(\sigma)I}(x, \Omega)$ is nonincreasing and

$$\lim_{\sigma \downarrow 0} u_{\rho(\sigma)I}(x,\omega) = \delta_x(\omega).$$

In particular,

$$u_I(x, \Omega) \leqslant 1.$$

We close this appendix by proving the lemmas of Section 3.

Proof of Lemma 3.7. Assume for a moment that we can prove the identity

$$\Lambda^c_{\rho(t)I} \times m = tb \tag{B.5}$$

(which does state that an initial population state m gives rise to a steady population birth rate b). Then, using the definition

$$u^c_{\rho(t)I} = u_{\rho(t)I} + \int_{[0,t)} u_{\rho(t-\sigma)I} \times \Lambda^c_{\rho(d\sigma)I} \tag{B.6}$$

and the Chapman–Kolmogorov identity

$$u_{\rho(t)I} \times u_{\rho(\sigma)I} = u_{\rho(t+\sigma)I},$$

we can write

$$\begin{aligned} u^c_{\rho(t)I} \times m &= u_{\rho(t)I} \times m + \int_{[0,t)} u_{\rho(t-\sigma)I} \times d_\sigma(\sigma b) \\ &= u_{\rho(t)I} \times m + \int_{[0,t)} u_{\rho(s)I}\, ds \times b \\ &= \int_0^\infty u_{\rho(t+\sigma)I}\, d\sigma \times b + \int_{[0,t)} u_{\rho(s)I} ds \times b \\ &= \int_0^\infty u_{\rho(s)I}\, ds \times b. \\ &= m \end{aligned}$$

It remains to verify (B.5). We first compute $\Lambda_{\rho(t)I}\times m$, using definition (3.25) and the consistency relation

$$\Lambda_{\rho(t+\sigma)I}=\Lambda_{\rho(\sigma)I}+\Lambda_{\rho(t)I}\times u_{\rho(\sigma)I}$$

as follows:

$$\begin{aligned}\Lambda_{\rho(t)I}\times m&=\int_0^\infty \Lambda_{\rho(t)I}\times u_{\rho(\sigma)I}\times b\,d\sigma\\&=\int_0^\infty(\Lambda_{\rho(t+\sigma)I}-\Lambda_{\rho(\sigma)I})\times b\,d\sigma\\&=\int_0^\infty(\Lambda_{\rho(t+\sigma)I}-\Lambda_I)\times b\,d\sigma\\&\quad+\int_0^\infty(\Lambda_I-\Lambda_{\rho(\sigma)I})\times b\,d\sigma\\&=\int_{[t,\infty)}(\Lambda_{\rho(s)I}-\Lambda_I)\times b\,ds\\&\quad+\int_0^\infty(\Lambda_I-\Lambda_{\rho(\sigma)I})\times b\,d\sigma\\&=-\int_{[0,t)}(\Lambda_{\rho(s)I}-\Lambda_I)\times b\,ds\\&=tb-\int_{[0,t)}\Lambda_{\rho(s)I}\,ds\times b.\end{aligned}$$

Hence, using the renewal equation $\Lambda^c_{\rho(t)I}=\Lambda_{\rho(t)I}+\int_{[0,t)}\Lambda^c_{\rho(t-\sigma)I}\times\Lambda_{\rho(d\sigma)I}$, we obtain

$$\begin{aligned}\Lambda^c_{\rho(t)I}\times m&=\Lambda_{\rho(t)I}\times m+\int_{[0,t)}\Lambda^c_{\rho(t-\sigma)I}\times\Lambda_{\rho(d\sigma)I}\times m\\&=tb-\int_{[0,t)}\Lambda_{\rho(s)I}\,ds\times b\\&\quad+\int_{[0,t)}\Lambda^c_{\rho(\sigma)I}\times(b-\Lambda_{\rho(\sigma)I}\times b)\,d\sigma\\&=tb\int_{[0,t)}(\Lambda^c_{\rho(\sigma)I}-\Lambda_{\rho(s)I}\\&\quad-\Lambda^c_{\rho(t-s)I}\times\Lambda_{\rho(\sigma)I})\,ds\times b=tb\end{aligned}$$

where, to obtain the last identity, one has to integrate the renewal equation with respect to time (and then to change the order of integration in the double integral).

Proof of Lemma 3.8. From the consistency relation $\Lambda^c_{\rho(t+s)I}=\Lambda^c_{\rho(s)I}+\Lambda^c_{\rho(t)I}\times u^c_{\rho(s)I}$ and (3.26) we infer that $\Lambda^c_{\rho(t+s)I}\times m=\Lambda^c_{\rho(s)I}\times m+\Lambda^c_{\rho(t)I}\times m$

which is a functional equation of the form

$$f(t+s)=f(t)+f(s),t,s>0. \tag{B.7}$$

As is well known (and easily proven by first showing it by induction for rational numbers and then using the fact that real numbers can be approximated from both above and below by rational numbers) every additive function (i.e., a function f satisfying (B.7) on $\mathbf{R}_+$) is automatically linear (i.e., satisfies also $f(\lambda t)=\lambda f(t)$ for all $\lambda\geqslant 0$). Hence

$$f(t)=tf(1).$$

We conclude that the right-hand side of (3.27) is indeed independent of t.

To verify (3.24) we write

$$\begin{aligned}b&=\frac{1}{t}(\Lambda^c_{\rho(t)I}\times m)\\&=\frac{1}{t}\left(\Lambda_{\rho(t)I}\times m+\int_{[0,t)}(\Lambda_{\rho(t-\sigma)I}\times\Lambda^c_{\rho(d\sigma)I})\times m\right)\\&=\frac{1}{t}\left(\Lambda_{\rho(t)I}\times m+\int_{[0,t)}\Lambda_{\rho(t-\sigma)I}\times bd\sigma\right)=\frac{1}{t}\Lambda_{\rho(t)I}\times m\\&\quad+\frac{1}{t}\int_{[0,t)}\Lambda_{\rho(s)I}\,ds\times b.\end{aligned}$$

For $t\to\infty$ the first term at the final right-hand side goes to zero and the second converges to $\Lambda_I\times b$.

Finally, let us verify the "inversion" formula (3.25). We write

$$\begin{aligned}m&=u^c_{\rho(t)I}\times m=u_{\rho(t)I}\times m+\int_{[0,t)}u_{\rho(t-\sigma)I}\times\Lambda^c_{\rho(d\sigma)I}\times m\\&=u_{\rho(t)I}\times m+\int_{[0,t)}u_{\rho(t-\sigma)I}\times b\,d\sigma\\&=u_{\rho(t)I}\times m+\int_{[0,t)}u_{\rho(a)I}\times b\,da\end{aligned}$$

When $t\to\infty$ the first term goes to zero (finite life expectancy!) and so by taking this limit we arrive at (3.25).

Appendix C. Connecting the results from section 4.2.7 to the more standard ones from the population genetical literature

In this appendix we explain how to arrive, starting from the formulation and notation of this paper, at the third order polynomial studied by Owen (1952) Bodmer (1965) and Mandel (1971).

Define x and t by

$$x=\frac{q_a}{q_A},\quad t=\frac{p_aq_A}{p_Aq_a}, \tag{C.1}$$

then (4.38) can be rewritten as (Hint: write the analogue of (4.38) for p_A, then use both to deduce an expression for p_a/p_A, then multiply both sides by p_A/p_a)

$$1=\frac{S_{aa}x+\frac{1}{2}S_{aA}(1+t^{-1})}{S_{AA}+\frac{1}{2}S_{aA}x(1+t)} \tag{C.2}$$

and (4.39) as

$$1+\frac{E_{aa}xt+\frac{1}{2}E_{aA}(1+t)}{E_{AA}+\frac{1}{2}E_{aA}x(1+t)}. \tag{C.3}$$

Solving both equations for x in terms of t and requiring that the results coincide, we arrive at the equation

$$\frac{E_{aA}t-\tilde{E}_A}{E_{aA}t^{-1}-\tilde{E}_a}=\frac{S_{aA}t^{-1}-\tilde{S}_A}{S_{aA}-\tilde{S}_at^{-1}}, \tag{C.4}$$

where we have introduced the short hand notation

$$\begin{aligned}\tilde{E}_A&=2E_{AA}-E_{aA}, \quad \tilde{E}_a=2E_{aa}-E_{aA},\\ \tilde{S}_A&=2S_{AA}-S_{aA}, \quad \tilde{S}_a=2S_{aa}-S_{aA}.\end{aligned} \tag{C.5}$$

Finally, (C.4) can be transformed into a third degree equation for t:

$$\begin{aligned}&S_{aA}E_{aA}t^3-(\tilde{S}_aE_{aA}+\tilde{E}_AS_{aA}+\tilde{E}_a\tilde{S}_A)t^2\\&\quad+(\tilde{S}_AE_{aA}+\tilde{E}_aS_{aA}+\tilde{E}_A\tilde{S}_a)t-S_{aA}E_{aA}=0.\end{aligned} \tag{C.6}$$

If condition (i) of Section 4.2.7 holds this equation has a triple root $t=1$, but then the formulas for x underlying (C.4) have zero denominator and, in fact, for $t=1$ both (C.2) and (C.3) hold for arbitrary x. If condition (ii) of Section 4.2.7 holds then (C.6) is degenerate as well, i.e., any t is a solution. From (C.2) we now deduce $x=1$, i.e., $q_a=\frac{1}{2}$.

We conclude by referring once again to Owen (1952), Bodmer (1965) and Mandel (1971) for a detailed study of Eq. (C.6).

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