PHASE-SPACE ANALYSIS OF LARGE ODE SYSTEMS USING A LOW-DIMENSIONAL CONSERVATION LAW

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Abstract. Simultaneous deterministic and weakly stochastic dynamics of multiple populations described by a large system of ODE’s is considered in the phase space of population sizes and ODE’s parameters. We show that many practically interesting problems can be formulated as a low-dimensional phase-space conservation law and solved either explicitly or with simple iterative methods. In particular, we consider: non-interacting populations with unbounded and logistic growth, populations with randomized and biased migration, populations competing for a resource, coexisting species, and populations with phase-space interactions. The method provides an alternative to Monte Carlo simulations and may be useful in the fast analysis of biological data and/or removal of deterministic trends.

1. Introduction. Many natural phenomena can be described as a large number of simultaneously developing ‘populations’. The various coexisting species is the most obvious case. However, even a single plant consists of many cells that in turn contain significant numbers of mitochondria – small organelles capable of multiplying on their own. Thus, considering the mitochondria of a single cell to be the elementary population, one can view each individual plant as a population of populations, or a multi-population. On another level, viewing a single plant as an elementary population of cells, a field of plants is a population of populations, etc. (see, e.g., Merchant et al. 1960; Carrie et al. 2012).

Although, classical population dynamics is a very well developed subject (see, e.g., Shonwinkler and Herod 2009; Begon et al. 2006; Newman et al. 2014), its main concern has traditionally been the growth of a single or at most of a few populations simultaneously. The question of dynamics of dispersing populations has led to the development of the metapopulation theory (e.g., Levin 1969; Eriksson et al. 2014) that treats populations with spatially disjoint habitats as a single metapopulation, and reduces the mathematical description to a single ODE. Alternatively, it is sometimes advantageous to consider the space-time dynamics of all members of all populations simultaneously, perhaps, subdividing them in a few species as well. This leads to spatially-resolved PDE models, such as the Fischer equation (Fischer 1930), that have produced many valuable insights over the years (see, e.g., Edelstein-Keshet 2005).

Mathematically, all problems under consideration in this paper represent large systems of coupled ODE’s. We resort to the phase-space analysis for the following reasons. Firstly, studying multiple populations with large systems of ODE’s or spatially-resolved PDE’s does not always provide explicit answers to the pertaining questions. For example, in agriculture and ecology (e.g., Hautala and Hakojärvi 2011; Lin et al. 2013; Xu et al. 2014; Velazquez et al. 2014), where the growth of an individual plant or species is typically described by a logistic or a reaction-type ODE, the actual question of interest or the measured data is often the histogram/distribution of plant or population sizes. Such a distribution is then typically obtained with a Monte-Carlo simulation, where the individual ODE’s are solved over a set of points in the range of their parameters. It is a well-known fact that the choice of these points (sampling) may significantly influence the quality of the prediction of the corresponding distribution function. Secondly, although the phase-space formulation results in a
PDE rather than ODE, we show that many practically interesting systems of ODE’s feature special types of coupling corresponding to low-dimensional phase-space problems, where the solution is simple to obtain.

To avoid further confusion we mention that the term ‘dimension’ refers here to the dimension of the underlying manifold (number of phase-space variables) not the dimension of the phase space itself. Formally, the phase space is infinite-dimensional in our formulation, since the state of the system at any given time is represented by a continuous function of phase-space variables, not just one point as with the usual dynamical systems described by a few ODE’s, such as the predator-prey system (see, e.g., Edelstein-Keshet 2005).

To predict the time evolution of the distribution function we employ the phase-space conservation law, where the mathematical form of the phase-space current is determined by the dynamic equations (coupled or uncoupled ODE’s) of individual populations. This approach is a systematic extension of the Lifshitz-Slyozov-Wagner method from materials science (Lifshitz and Slyozov 1961; Wagner 1961; Kampman and Wagner 1991; Myhr and Grong 2000; Collet and Goudon 2000; Laurencot 2002). Conceptually it may be viewed as a version of the Fokker-Planck equation tuned, in our case, to the specific needs of the multi-population dynamics. The present approach is also similar in spirit to the Liouville equation of Hamiltonian mechanics, except that the population dynamics is not necessarily Hamiltonian. The closest analogue in the field of population dynamics is, probably, the state-space method discussed in (Newman et al. 2014).

In the next section we present the general formulation of the problem and elucidate the meaning and the intended purpose of our multi-population distribution functions. Next, we illustrate the benefits and limitations of the proposed framework on seven population models relevant to plant biology, ecology, and migration studies. We focus on problems that have either completely explicit solutions or can be solved with a simple iterative algorithm. In particular, we consider populations with unlimited (exponential) growth, populations whose growth is limited by the carrying capacity of the medium (logistic equation), populations/species competing for resources (e.g. oxygen, food, etc.), populations with migrating members, and populations whose rate of growth depends on the distribution function. The mathematical analysis of the resulting PDE’s is mostly available in the literature, apart from the case of the coexisting species, which is studied in some details in the corresponding section.

2. General formulation. Let the growth of $P$ populations be governed by the following system of ODE’s:

\[
\frac{dn_i}{dt} = f_i(n_1,\ldots,n_P,\alpha_1,\ldots,\alpha_k,t); \quad i = 1,\ldots,P,
\]

\[
\frac{d\alpha_j}{dt} = g_j(t), \quad j = 1,\ldots,k,
\]

(2.1)

where $f_i$ and $g_j$ are differentiable functions of the indicated variables, and the variables $\alpha_j$, $j = 1,\ldots,k$, represent the various dynamical parameters of the ODE’s, such as the rates of birth and death.

In general, the phase-space formulation of this problem is even more difficult than the original system of ODE’s. For example, if all rate functions $f_i$ were, indeed, different, then the associated phase-space manifold is $(P+k)$-dimensional, i.e., the size of each population requires a separate coordinate. Hence, from the practical point of view, the phase-space analysis of large ODE systems only makes sense if the number
of dimensions of the phase-space manifold is much smaller than \( P \). The possibility of such a low-dimensional phase-space formulation depends on the type of the rate functions \( f_i \). Here we shall limit ourselves to a specific \((k+1)\)-dimensional manifold, which in turn limits the class of admissible dynamic systems.

Our goal is the distribution function \( u(n, \alpha_1, \ldots, \alpha_k, t) : \mathbb{R}^{k+2} \to \mathbb{R} \) with the following properties:

\[
\int \cdots \int u(n, \alpha_1, \ldots, \alpha_k, t) \, dn \, d\alpha_1 \ldots d\alpha_k = P, \tag{2.2}
\]

\[
\int \cdots \int nu(n, \alpha_1, \ldots, \alpha_k, t) \, dn \, d\alpha_1 \ldots d\alpha_k = \sum_{i=1}^{P} n_i(t) = N(t), \tag{2.3}
\]

\[
u(n, \alpha_1, \ldots, \alpha_k, 0) = u_0(n, \alpha_1, \ldots, \alpha_k), \tag{2.4}\]

where \( u_0 \) is the given initial distribution of the populations over the \((k+1)\)-dimensional phase space \( \Omega \).

The conservation of the total number of populations means that the time-evolution of the distribution function \( u \) is governed by the generalized continuity equation:

\[
\frac{\partial u}{\partial t} + \frac{\partial J_n}{\partial n} + \sum_{j=1}^{k} \frac{\partial J_{\alpha_j}}{\partial \alpha_j} = 0, \tag{2.5}
\]

where the phase-space current density \( J \) has the form

\[
J = \langle J_n, J_{\alpha_1}, \ldots, J_{\alpha_k} \rangle = \langle uv_n, uv_{\alpha_1}, \ldots, uv_{\alpha_k} \rangle. \tag{2.6}
\]

Since, e.g., \( v_n = dn/dt \), by definition, the phase-space ‘velocities’ are to be deduced from the corresponding ODE’s:

\[
v_n = \tilde{f}(n, \alpha_1, \ldots, \alpha_k, t),
\]

\[
v_{\alpha_j} = g_j(t), \quad j = 1, \ldots, k. \tag{2.7}
\]

where \( \tilde{f} \) is the phase-space representation of the functions \( f_i \). The success of this \((k+1)\)-dimensional approach depends on the existence of a one-to-one correspondence between \( f_i \) and \( \tilde{f} \), i.e., one should be able to express \( f_i \) purely in terms of the chosen set of phase-space coordinates \( \{n, \alpha_1, \ldots, \alpha_k\} \) and time \( t \). Below we describe several types of such \( f_i \)’s.

The first type corresponds to the uncoupled system of ODE’s and a uniform (independent of index \( i \)) rate function:

\[
f_i(n_1, \ldots, n_P, \alpha_1, \ldots, \alpha_k, t) = f(n, \alpha_1, \ldots, \alpha_k, t). \tag{2.8}
\]

For example, the polynomial rate functions

\[
f_i = \alpha_i + \beta_i n_i + \gamma_i n_i^2 + \ldots, \tag{2.9}
\]

correspond to the phase-space velocity

\[
v_n = \tilde{f}(n, \alpha, \beta, \gamma, \ldots, t) = \alpha + \beta n + \gamma n^2 + \ldots. \tag{2.10}
\]

Such uncoupled systems result in linear low-dimensional phase-space Cauchy problems that can be solved completely explicitly.
The second type of $f_i$ is also uniform and features a uniform coupling of the form:

$$f_i(n_1, \ldots, n_P, \alpha_1, \ldots, \alpha_k, t) = f(n_i, N(t), \alpha_1, \ldots, \alpha_k, t),$$  \hspace{1cm} (2.11)

where $N(t)$ is given by [2.3]. For example, if the coupling has the form

$$f_i = \alpha_i \sum_j n_j = \alpha_i N(t),$$  \hspace{1cm} (2.12)

then the corresponding phase-space velocity is

$$v_n = \tilde{f}(\alpha, t) = \alpha \int \int n u(n, \alpha, t) \, dn \, d\alpha.$$  \hspace{1cm} (2.13)

The resulting weakly nonlinear low-dimensional phase-space problems can be solved with simple iterative methods.

However, the important general case, where the coupling has the form:

$$f_i = \sum_j \alpha_{ij} n_j,$$  \hspace{1cm} (2.14)

would require a separate phase-space coordinate for each population and is, therefore, impractical.

A further generalization of [2.11] that admits an explicit phase-space representation has the form

$$f_i(n_1, \ldots, n_P, \alpha_1, \ldots, \alpha_k, t) = f(n_i, F[u], \alpha_1, \ldots, \alpha_k, t),$$  \hspace{1cm} (2.15)

where $F[u]$ is a functional of the distribution function $u$. Below we consider one such problem that leads to the Burgers equation in the phase space.

We conclude this section with a few words about the interpretation of the proposed phase-space picture. Since the population dynamics considered here is mainly deterministic, the functions $u_0$ and $u$ are not probability density functions, although, upon suitable normalization, they can be interpreted as such for a randomly selected population.

The relation of the distribution function $u$ to the populations whose dynamics is governed by (2.1) is similar to the relation between the data, their histogram, and the corresponding probability density function. It is even more similar to the continuous description of discrete natural phenomena common in the classical macroscopic theories of mechanics, fluid motion, and electromagnetism.

It is well-known that one has to be careful when choosing the appropriate bin size for a histogram. Take it too small and the histogram breaks down into a meaningless collection of separated bars each containing only one data point, i.e., each having height equal to one. Similarly, in macroscopic continuum physics the basic assumption is the so-called elementary volume, which while being relatively small contains a sufficient number of particles, so that the concept of number density makes sense. Generally, the continuum hypothesis and the corresponding equations are not considered to be valid at scales smaller than the elementary volume.

The intended purpose and the desired property of the distribution function $u$ is that it approximates the number $\delta P$ of populations with their parameters within a subregion $\delta \Omega$ of the phase space, i.e.,

$$\delta P(\delta \Omega, t) \approx \int \cdots \int_{\delta \Omega} u(n, \alpha_1, \ldots, \alpha_k) \, d\Omega.$$  \hspace{1cm} (2.16)
For this interpretation to be valid (i.e., reasonably precise) the region \( \delta \Omega \) must be sufficiently large. Obviously, the interpretation is exact, if \( \delta \Omega \) coincides with the whole of \( \Omega \). The acceptable lower bound on \( \delta \Omega \), in general, will depend on both the number of populations \( P \) and the smoothness/extent of the distribution \( u \).

In what follows we apply our approach to a series of models of increasing complexity. We restrict ourselves to the so-called autonomous case, where the dynamic parameters \( \alpha_j \) are constant in time. On the one hand, extension to the non-autonomous case of time-dependent \( \alpha_j \)'s is trivial. On the other hand, the practical aspects of problems requiring such an extension deserve a detailed investigation, which is beyond the scope of the present paper. an \( n \)-dimensional

3. Examples of problems with low-dimensional conservation laws.

3.1. Populations with unlimited growth. Let a very large number of populations be growing in accordance with the following equations:

\[
\frac{d n_i}{dt} = \alpha_i n_i, \quad n_i(0) > 0, \quad i = 1, 2, \ldots P,
\]  

(3.1)

where \( \alpha_i > 0 \) are the growth constants. The variable \( n_i \) will be referred to as the size of the \( i \)-th population, but, in practice, it may denote many different things. For example, it can be the length, volume, or the biomass of a plant. It can also be a continuous approximation of the number of animals within a habitat, or the number of cells in a plant, or the number of mitochondria in a cell. The units of time are also completely arbitrary here.

As was explained in the previous section, instead of solving all these ODE’s we consider the time evolution of the distribution function \( u(n, \alpha, t) \), whose integral over the size variable \( n \) and the growth constant variable \( \alpha \) represents the total number of populations, which is conserved:

\[
\int_0^\infty \int_0^\infty u(n, \alpha, t) \, dn \, d\alpha = P.
\]  

(3.2)

Integrating the distribution over \( \alpha \) only,

\[
\int_0^\infty u(n, \alpha, t) \, d\alpha = \rho(n, t),
\]  

(3.3)

one obtains a continuous approximation of the distribution of populations over their sizes at time \( t \).

We assume that the sufficiently smooth continuous approximation of the initial distribution \( u(n, \alpha, 0) = u_0(n, \alpha) \) is given. The latter is interpreted as a two-dimensional distribution of populations over their initial sizes \( n_0 \) and their growth constants \( \alpha \).

In the present case the phase-space current has at most two components

\[
J = \langle uv_n, uv_\alpha \rangle,
\]  

(3.4)

and the corresponding ‘velocities’ are easily deduced from the dynamic equation (3.1) as: \( v_n = \alpha n \) and \( v_\alpha = 0 \). Since \( J \) has only one nonzero component, the continuity equation (2.5) reduces to the following Cauchy problem:

\[
\frac{\partial u}{\partial t} + \alpha n \frac{\partial u}{\partial n} + \alpha u = 0, \quad u(n, \alpha, 0) = u_0(n, \alpha).
\]  

(3.5)
The solution of this problem, obtained with the method of characteristics, is

$$u(n, \alpha, t) = e^{-\alpha t} u_0(ne^{-\alpha t}, \alpha).$$

(3.6)

An example of the time evolution of $u(n, \alpha, t)$ is shown in Fig. 3.1, where the initial distribution $u_0(n, \alpha)$ is a Gaussian centered at $n_c = 15$ and $\alpha_c = 20$, which was set to zero for $\alpha, n < 0$ (see the top-left image). The size distributions of populations $\rho(n, t)$ (bottom row of Fig. 3.1) were obtained by numerical integration over $\alpha$ and demonstrate a progressively fattening tail due to the rapidly growing populations corresponding to the upper part of $u(n, \alpha, t)$, i.e., larger growth rate constants $\alpha$. An interesting feature in the evolution of $u(n, \alpha, t)$ that becomes more pronounced at larger $t$’s, is the gradual downwards shift of the maximum of $u(n, \alpha, t)$ with time. This is due to the fact that the populations with smaller $\alpha$’s tend to grow more evenly (synchronously) even if their initial $n$’s are different, whereas, populations with larger $\alpha$’s and slightly different initial $n$’s rapidly grow apart.

3.2. Populations with logistic growth. Let the dynamics of populations be governed by the logistic equations

$$\frac{dn_i}{dt} = \gamma_i n_i(k_i - n_i), \quad n_i(0) > 0, \quad i = 1, 2, \ldots,$$

(3.7)

where $\gamma_i \geq 0$ is a rate constant, and $k_i > 0$ is a constant determining the maximum sustainable population. The distribution function $u(n, \gamma, k, t)$ over the three-dimensional $(n, \gamma, k)$ phase space satisfies the following Cauchy problem:

$$\frac{\partial u}{\partial t} + \gamma n(k - n) \frac{\partial u}{\partial n} + \gamma(k - 2n)u = 0, \quad u(n, \gamma, k, 0) = u_0(n, \gamma, k).$$

(3.8)

Here too the solution can be obtained with the method of characteristics. Since it is more involved than in the previous case, we shall provide the intermediate steps. The
characteristic equations of (3.8) are
\[
\begin{align*}
\frac{dt}{ds} &= 1, \\
\frac{dn}{ds} &= \gamma n(k-n), \\
\frac{du}{ds} &= -\gamma(k-2n)u.
\end{align*}
\] (3.9)

This leads to the following relations:
\[
C_0 = \frac{n}{|k-n|} e^{-\gamma kt}, \quad u = \frac{C_1}{n|k-n|}.
\] (3.10)

We shall restrict ourselves to the segment \(0 \leq n < k\), so that \(|k-n| = k-n\). The general form of the solution to (3.8) in this case is
\[
u = \frac{f(p)}{n(k-n)}, \quad p = \frac{n}{k-n} e^{-\gamma kt}.
\] (3.11)

The function \(f(p)\) should be chosen in such a way that the initial condition is satisfied. To this end we introduce two smooth functions of \(p\) that at \(t=0\) behave as follows:
\[
\begin{align*}
\frac{kp}{p+1} \bigg|_{t=0} &= n, \\
\frac{k^2p}{(p+1)^2} \bigg|_{t=0} &= n(k-n).
\end{align*}
\] (3.12)

The initial condition from (3.8) is satisfied if these functions are used as
\[
\begin{align*}
\frac{k^2p}{n(k-n)(p+1)^2} u_0 \left( \frac{kp}{p+1}, \gamma, k \right) \bigg|_{t=0} &= u_0(n, \gamma, k).
\end{align*}
\] (3.13)

Thus, the solution of the Cauchy problem (3.8) on the strip \(0 \leq n < k\) is
\[
u(n, \gamma, k, t) = \frac{k^2e^{-\gamma kt}}{(ne^{-\gamma kt}+k-n)^2} u_0 \left( \frac{kne^{-\gamma kt}}{ne^{-\gamma kt}+k-n}, \gamma, k \right),
\] (3.14)

and for \(n = k\), we obviously have \(u(k, \gamma, k, t) = u_0(k, \gamma, k)\).

An example of the time evolution of \(u(n, \gamma, k, t)\) for a fixed \(k = 80\) is shown in Fig. 3.2 where the initial distribution \(u_0(n, \gamma, 80)\) (top left) is the same Gaussian as in the example of Fig. 3.1. As \(t\) grows the corresponding size distributions \(\rho(n, t)\) (bottom row) tend to a distribution localized at the right boundary \(n = k\). This time the maximum of the distribution \(u(n, \gamma, k, t)\) shifts upwards (eventually), meaning that for larger \(t\)’s the populations with larger growth rates \(\gamma\) will dominate, as they will rapidly accumulate around the maximum attainable size.

### 3.3. Populations competing for a finite resource

Consider populations competing for a finite resource \(c\) that controls their growth rate. As an example one can think of a batch of seeds germinating in a sealed container. Seeds need oxygen to germinate and there is only a finite amount of it in a sealed container (Bewley et al. 2013, van Duijn and Koenig 2001, van Asbrouck and Taridno 2009, Budko et al. 2013). Hence, there will be some sort of passive competition for this oxygen among the seeds, but none of the seeds can actually ‘win’, as all oxygen will be depleted at the end anyway, and all the seeds will suffocate (stop their growth). Although this fate is inevitable, the questions about the time evolution of the distribution of seed sizes and the corresponding oxygen consumption curve have some practical interest to them, since the initial stages in the growth of the seed are indicative of the plant vitality.
Fig. 3.2. **Logistic growth with fixed $k = 80$.** Top row – snapshots of $u(n, \gamma, k, t)$ at $t = 0.0, 0.001$, and $0.002$; Bottom row – corresponding numerically integrated $\rho(n, t)$ showing the distribution of populations over their sizes.

We further assume that the control substance is absorbed equally well by all members of all populations (with the same reaction rate coefficient $\gamma$). However, the overall rate of consumption of $c$ is proportional to the concentration of $c$ (or partial pressure, if the control substance is a gas). Populations convert $c$ into energy and biomass and grow. The growth of a population slows down and eventually stops if the supply of $c$ drops to some minimal value $c_{\text{min}}$, which is here taken to be zero for simplicity. The following coupled system of reaction-type equations describes this situation:

\[
\frac{dc}{dt} = -\gamma c \sum_i n_i, \quad c(0) = c_0, \gamma > 0,
\]

\[
\frac{dn_i}{dt} = \beta_i n_i c, \quad n_i(0), \beta_i > 0, \quad i = 1, 2, \ldots \tag{3.15}
\]

Integrating the first equation and substituting the result in the second equation we arrive at:

\[
\frac{dn_i}{dt} = \beta_i n_i c_0 e^{-\gamma \tilde{N}(t)}, \quad i = 1, 2, \ldots \tag{3.16}
\]

where

\[
\tilde{N}(t) = \int_0^t \sum_i n_i \, dt'.
\]

The integrand above is the total size $N(t)$ of all populations that can be expressed via the phase-space distribution as

\[
N(t) = \int_0^\infty \int_0^\infty n u(n, \beta, t) \, dn \, d\beta.
\]
Hence, eq. (3.17) can be rewritten in terms of the distribution as well

\[ \tilde{N}(t) = \int_0^t N(t') dt' = \int_0^\infty \int_0^\infty nu(n, \beta, t') dn d\beta dt' \]  

(3.19)

Thus, the phase-space dynamics of the distribution function will be governed by the weakly nonlinear equation:

\[ \frac{\partial u}{\partial t} + c_0 \beta ne^{-\gamma \tilde{N}(t)} \frac{\partial u}{\partial n} + c_0 \beta ue^{-\gamma \tilde{N}(t)} = 0, \quad u(n, \beta, 0) = u_0(n, \beta), \]  

(3.20)

The questions of existence and uniqueness of solutions to a slightly more general problem of this type have been discussed by Collet and Goudon (2000). Mathematically, the present problem is not as challenging, since for all \( n \) and \( \beta \) the velocity of the phase-space flow is positive and goes to zero exponentially in time, meaning that \( \partial u/\partial t \) approaches zero as \( t \to \infty \).

The method of characteristics yields the following implicit solution:

\[ u(n, \beta, t) = e^{-\beta \xi(t)} u_0(ne^{-\beta \xi(t)}, \beta), \]  

(3.21)

where

\[ \xi(t) = \int_0^t c(\tau) d\tau, \]  

(3.22)

\[ c(\tau) = c_0 e^{-\gamma \tilde{N}(\tau)}. \]  

(3.23)

We seek to approximate \( u(n, \beta, t) \) via an explicit time-stepping scheme. Let \( u_k(n, \beta) = u(n, \beta, t_k), \tilde{N}_k = \tilde{N}(t_k), c_k = c(t_k), \xi_k = \xi(t_k) \), and \( t_{k+1} = t_k + \Delta t \). Choosing a sufficiently small \( \Delta t \) we compute:

**Algorithm 1**

- Given: \( \xi_0 = 0, c_0 > 0, u_0(n, \beta), \tilde{N}_0 = 0 \), and a sufficiently large \( \Omega \).
- For \( k = 0, 1, 2, \ldots \), while \( c_k \geq 0 \), do:
  
  \[ \xi_{k+1} = \xi_k + c_k \Delta t, \]

  \[ u_{k+1}(n, \beta) = e^{-\beta \xi_{k+1}} u_0(ne^{-\beta \xi_{k+1}}, \beta), \]

  \[ \tilde{N}_{k+1} = \int_{\Omega} nu_{k+1}(n, \beta) dn d\beta, \]

  \[ \hat{N}_{k+1} = \tilde{N}_k + N_{k+1} \Delta t \]

  \[ c_{k+1} = c_0 \exp(-\gamma \hat{N}_{k+1}) \]

An example of the time evolution of \( u(n, \beta, t) \) and the corresponding consumption of the resource \( c(t) \) computed with the Algorithm 1 \((c_0 = 1 \) and \( \gamma = 0.005) \) is shown in Fig. 3.3. Due to the mathematical equivalence of the two solutions, the states (snapshots) of \( u(n, \beta, t) \) given by (3.21) are exactly equal to the states \( u(n, \alpha, t) \) of the unmitigated exponential growth given by (3.6), provided \( \alpha = \beta \). However, the evolution of \( u(n, \beta, t) \) proceeds at a different rate and asymptotically slows down to a halt as \( c(t) \to 0 \). In fact, it takes more than twice as much time to reach the same state as the last one of Fig. 3.1. The accuracy of the Algorithm 1 can be eventually improved using the predictor-corrector technique.
3.4. Coexistence of competing species. In the previous section all populations eventually stop growing (suffocate), since the resource $c$ is asymptotically exhausted for $t \to \infty$. Here we assume that the resource is not only consumed, but is also generated at a given fixed rate $\alpha$, i.e.,

\[
\frac{dc}{dt} = \alpha - \gamma c \sum_i n_i, \quad c(0) = c_0, \gamma > 0,
\]

\[
\frac{dn_i}{dt} = \beta_i n_i(c - \kappa), \quad n_i(0), \beta_i, \kappa > 0, \quad i = 1, 2, \ldots
\]  

(3.24)

where $\kappa$ denotes the level of resource below which populations begin to decline (alternative interpretation is that for $c < \kappa$ the death rate becomes greater than the birth rate). Different $\beta$’s – reaction rates of species on the changes in the availability of resource (on the changes in the environment) – could be viewed as different survival strategies. This problem is intrinsically interesting, because it may result in the so-called equilibrium state, where species with different survival strategies coexist without exhausting the resource.

The analogue of the eq. (3.16) can be obtained by integrating the first equation as

\[
c(t) = c_0 e^{-\gamma \tilde{N}(t)} + \alpha e^{-\gamma \tilde{N}(t)} \int_0^t e^{\gamma \tilde{N}(t')} \, dt',
\]

(3.25)

and substituting this result into the second equation of (3.24). Note that $\tilde{N}$ is still given by (3.17) and (3.19). Keeping in mind that $c(t)$ is given by (3.25), we write the phase-space problem as

\[
\frac{\partial u}{\partial t} + (c - \kappa) n \frac{\partial u}{\partial n} + (c - \kappa) \beta u = 0, \quad u(n, \beta, 0) = u_0(n, \beta),
\]

(3.26)
Mathematically this problem is more challenging than the one of the previous section, since the phase-space velocity \((c-\kappa)\beta n\) may change its sign, albeit for all \(n\) and \(\beta\) at the same time. Moreover, one cannot immediately conclude that this velocity will tend to some well-defined limit as \(t \to \infty\).

The following Lemma 3.1 establishes the necessary condition for an instantaneous steady-state at time \(t\), which we define as \(u(n, \beta, t)\), such that \(\partial u/\partial t = 0\) at \(t\). This is the moment when the phase-space velocity becomes zero everywhere in \(\Omega\).

**Lemma 3.1.** A function \(\tilde{u}(n, \beta, t) \neq 0\), integrable on \(\Omega = \{(n, \beta) | 0 \leq n < \infty, 0 \leq \beta < \infty\}\) for any \(t \geq 0\), is a steady-state solution of the problem (3.26) at time \(t\) if and only if this function yields \(c(t) = \kappa\) with \(c(t)\) given by (3.25), (3.19).

**Proof.** The if part is obvious. To prove the rest, assume that there exists a steady-state solution \(\tilde{u}(n, \beta, t) \neq 0\) integrable on \([0, \infty) \times [0, \infty)\) for \(c(t) \neq \kappa\). Hence, it must satisfy the following linear equation:

\[
\frac{n}{\partial} \tilde{u} + \tilde{u} = 0, \tag{3.27}
\]

i.e., it should have the form \(\tilde{u} = C/n\), where \(C \neq 0\) is a constant. Such functions, however, are not integrable on \([0, \infty) \times [0, \infty)\), and we arrive at a contradiction. \(\Box\)

A steady state defined as above is, in general, not stable. Indeed, although \(\partial u/\partial t = 0\) whenever \(c(t) = \kappa\), the resource function \(c(t)\) may continue to change in time, thus deviating away from its steady-state level \(\kappa\), which, according to Lemma 1, will necessarily ‘restart’ the evolution of \(u\). The time derivative of \(c(t)\) is found from (3.25) to be \(c' = \alpha - \gamma cN\) and, understandably, coincides with the resource equation in (3.24). In a steady state we have \(c'(t) = \alpha - \gamma \kappa N(t)\), which may be non-zero. To prevent \(u\) from leaving the steady state, one needs \(c'(t) = 0\) as well, i.e., \(N(t) = \alpha / (\gamma \kappa)\).

**Definition 3.2.** A function \(u(n, \beta, t)\) represents an equilibrium state if it simultaneously satisfies the following conditions:

\[
c(t) = \kappa, \tag{3.28}
\]

\[
N(t) = \frac{\alpha}{\gamma \kappa}, \tag{3.29}
\]

where \(c(t)\) and \(N(t)\) depend on \(u\) as in (3.25) and (3.18).

We shall assume the existence and uniqueness of the solution \(u(n, \beta, t)\) to the problem (3.25)–(3.26) for any \(t \geq 0\). It should be possible to arrive at the corresponding proof along the lines of Collet and Goudon (2000) who considered very similar problems. Here we focus on the stability of the equilibrium state.

**Theorem 3.3.** Let \(\alpha, \gamma, \kappa > 0\), and let \(u(n, \beta, t)\) be a solution of (3.26) on \(\Omega = \{(n, \beta) | 0 \leq n < \infty, 0 \leq \beta < \infty\}\) for any \(t \geq 0\), corresponding to the initial state \(u_0(n, \beta)\), such that \(u_0(n, \beta) = 0\) for \(\beta > B\). Further, let

\[
\lim_{n \to \infty} n^2 u(n, \beta, t) = 0, \quad \beta \in [0, B], \quad t \geq 0. \tag{3.30}
\]

Then, the equilibrium state is asymptotically stable.

**Proof.** To analyze the stability of equilibrium we need another direct relation between \(c(t)\) and \(N(t)\) in addition to (3.25), preferably, less complicated than the
PDE (3.26). For this purpose we rewrite the time derivative of $N(t)$ as:

$$
N' = \int\int_{\Omega} n \frac{\partial u}{\partial t} d\Omega = - (c - \kappa) \int\int_{\Omega} \beta n \frac{\partial}{\partial n} (nu) d\Omega = - (c - \kappa) \int^{\nu}_{0} \frac{\partial}{\partial n} (n^2 u(n, \beta, t)) dn + (c - \kappa) \int_{\Omega} nu d\Omega
$$

(3.31)

where we have employed the Mean Value Theorem with $\beta, \beta_c \in [0, B]$. Hence, using (3.30) we arrive at the coupled quasi-linear system:

$$
c' = \alpha - \gamma c N,
N' = (c - \kappa) \beta c N,
$$

(3.32)

with the equilibrium (3.28)–(3.29) as its critical point. The Jacobian at equilibrium is given by:

$$
\begin{bmatrix}
-\alpha/\kappa & -\gamma \\
\alpha \beta c / (\gamma \kappa) & 0
\end{bmatrix},
$$

(3.33)

and its eigenvalues are:

$$
\lambda_{1,2} = -\frac{\alpha}{2\kappa} \pm \sqrt{\frac{\alpha(\alpha - 4\beta c \kappa^2)}{2\kappa}}.
$$

(3.34)

The real part of the eigenvalues is negative for all $\alpha, \kappa, \beta_c > 0$. Since, in equilibrium both $\partial u/\partial t = 0$ and $c' = 0$, stability of equilibrium for $c(t)$ and $N(t)$ implies stability of equilibrium for $u(n, \beta, t)$. 

Thus, we have established that, as soon as the distribution $u(n, \beta, t)$ evolves into a state, for which the scalars $c(t)$ and $N(t)$ are close enough to their equilibrium values (3.28)–(3.29), the system (3.25)–(3.26) will converge to the equilibrium. The possibility of complex eigenvalues for $\alpha < 4B\kappa^2$ shows that $c$ and $N$ may spiral towards the equilibrium point, i.e., oscillate in time. The condition (3.30) of the Theorem 3.3, albeit natural (it means the absence of infinitely large populations at any given $t \geq 0$), is not really necessary. Everything depends on how close the system is to its equilibrium state at $t = 0$. It is sufficient that the convergence to equilibrium happens faster in time than the blow up of potentially unbounded populations.

To investigate the behavior of the distribution function for coexisting species we employ the formal implicit solution of (3.26), which has the same form as (3.21) with

$$
\xi(t) = \int_{0}^{t} (c(t') - \kappa) dt',
$$

(3.35)

where $c(t)$ is given by (3.25). The analogue of the Algorithm 1 in the present case may be formulated as follows:

**Algorithm 2**

- Given: $\xi_0 = 0, c_0 > 0, u_0(n, \beta), N_0 = 0, R_0 = 0$, and a sufficiently large $\Omega$. 

Fig. 3.4. Coexistence of competing species. Top: quasi-equilibrium distributions \( u(n, \beta, t) \) achieved starting with the same initial distribution as in Fig. 3.3 for environments with different resource generation rates (left: \( \alpha = 20 \), right: \( \alpha = 50 \)). The distributions are shown at \( t = 0.84 \) and \( t = 0.392 \), respectively. Bottom-left: amount of the available resource \( c(t) \) as a function of time. Bottom-right: the time evolution of the total size of all populations \( N(t) \).

- For \( k = 0, 1, 2, \ldots \), while \( |c_k - \kappa| > 0 \) and \( |N_k - \alpha/(\gamma \kappa)| > 0 \), do:
  
  \[
  \xi_{k+1} = \xi_k + \Delta t(c_k - \kappa),
  \]
  
  \[
  u_{k+1}(n, \beta) = e^{-\beta \xi_{k+1}} u_0 (ne^{-\beta \xi_{k+1}}, \beta),
  \]
  
  \[
  N_{k+1} = \int \int_{\Omega} n u_{k+1}(n, \beta) \, dn \, d\beta,
  \]
  
  \[
  \tilde{N}_{k+1} = \tilde{N}_k + \Delta t \tilde{N}_{k+1}
  \]
  
  \[
  R_{k+1} = R_k + \Delta t \exp \left( \gamma \tilde{N}_{k+1} \right)
  \]
  
  \[
  c_{k+1} = (c_0 + \alpha R_{k+1}) \exp \left( -\gamma \tilde{N}_{k+1} \right)
  \]

As a measure of approach to equilibrium we use the differences \( |c_k - \kappa| \) and \( |N_k - \alpha/(\gamma \kappa)| \).

Figure 3.4 illustrates two cases of the evolution of the distribution function \( u(n, \beta, t) \) for competing species with the parameters of the problem set as \( c_0 = 1.0, \gamma = 0.01, \kappa = 0.9, \Delta t = 0.001, \) and the same initial distribution as in Figure 3.3.

As expected, in all our numerical experiments the distribution functions (virtually) stop changing as soon as the resource and the total size approach their equilibrium values. For example, the two images in the top of Figure 3.4 and the solid and dashed curves in the bottom plots show the stabilization of the distribution in environments with different resource generation rates: \( \alpha = 20 \) corresponds to the top-left image and solid curves, \( \alpha = 50 \) corresponds to the top-right image and dashed curves. As predicted, after a few oscillations the resource and the total size tend to stabilize. Although, the total size converges to \( N = \alpha/(\gamma \kappa) \) at a much slower rate than the resource converges to \( c = \kappa \).
Fig. 3.5. Dependence of the quasi-equilibrium for coexisting species on the initial state. Top row: initial distributions \( w_0(n, \beta) \) with centers at \( n_c = 15, \ n_c = 30, \) and \( n_c = 50. \) Middle row: quasi-equilibrium distributions obtained from the above initial distributions. Bottom row: amount of the available resource \( c(t) \) and the total size of all populations \( N(t) \) as functions of time.

Although the evolution towards equilibrium appears to be a stable process, the equilibrium state itself is not unique (even with fixed parameters \( c_0, \gamma, \alpha, \) and \( \kappa) \) and strongly depends on the initial state \( u_0. \) Figure 3.5 illustrates this phenomenon for \( c_0 = 1, \gamma = 0.01, \alpha = 50, \) and \( \kappa = 0.9, \) and three different initial states (Gaussian distributions with their centers at \( \beta_c = 20, \) and \( n_c = 15, 30, \) and \( 50, \) respectively). The resource \( c \) and the total size of populations \( N \) approach the same values in all three cases. However, the quasi-equilibrium distributions are very different.

In general, however, a stable coexistence of species whose survival strategies span a continuum of possibilities is not possible (Gyllenberg and Meszéna 2005). This result can be confirmed in the present formulation as well if one allows for different carrying capacities. Namely, consider a generalized version of the problem \[3.24\]:

\[
\frac{dc}{dt} = \alpha - \sum_i \gamma_i n_i, \quad c(0) = c_0, \quad \gamma_i > 0, \quad i = 1, 2, \ldots,
\]

\[
\frac{dn_i}{dt} = \beta_i n_i(c - \kappa_i), \quad n_i(0), \beta_i, \kappa_i > 0, \quad i = 1, 2, \ldots,
\]

where the rate of resource consumption \( \gamma_i \) as well as the lowest growth-sustaining level of resource \( \kappa_i \) depend on the species. Multiplying the second equation in \[3.36\] with \( \gamma_i \) and introducing the new size variable \( m_i = \gamma_i n_i \) we arrive at the following problem:

\[
\frac{dc}{dt} = \alpha - \sum_i m_i, \quad c(0) = c_0, \]

\[
\frac{dm_i}{dt} = \beta_i m_i(c - \kappa_i), \quad m_i(0), \beta_i, \kappa_i > 0, \quad i = 1, 2, \ldots,
\]

\[3.37\]
which has almost the same form as (3.24), except for the species-dependent $\kappa_i$. The corresponding distribution function $u(m, \beta, \kappa, t)$ satisfies the same phase-space equations (3.25)–(3.26) with $n$ replaced by $m$, $\gamma = 1$, and with $N(t)$, $\tilde{N}(t)$ replaced by $M(t)$, $\tilde{M}(t)$, where the latter are defined as:

$$M(t) = \int \int \int_{\Omega} mu(m, \beta, \kappa, t) d\Omega, \quad \tilde{M}(t) = \int_0^t M(t') dt'.$$  

(3.38)

Obviously, Lemma 3.1 prohibits any equilibrium for this problem, since there does not exist a single value of the resource $c(t)$ that would satisfy the necessary condition $c(t) = \kappa$ over a whole range of $\kappa$'s. Thus, the distribution function will keep changing in time.

3.5. Randomized migration. Let a single metapopulation be nonuniformly distributed over some spatial domain at time $t = 0$. The whole habitat may be divided either naturally or virtually into a large number of elementary cells (sub-habitats) and a question can be posed about the distribution of cell populations over their size at time $t$. The growth of these elementary cell populations could be described by one of the models from the preceding sections with growth parameters varying from cell to cell. If all individual members stay within their original cells or the whole metapopulation uniformly translates in space the phase-space methods developed earlier and the resulting distribution functions, obviously, apply without change.

Allowing for the migration of individuals between the cells usually requires a PDE-based space-time dynamic law (e.g. Fischer equation). Such a law cannot be directly incorporated into the phase-space current, since a low-dimensional phase-space approach completely neglects the spatial ordering of the cells. Nevertheless, certain types of migration mechanisms can be described by ODE systems with low-dimensional phase spaces.

Consider a stationary metapopulation, where the total number of individuals and the total number of sub-habitats (that play the role of populations in this case) do not change. Suppose that all individuals from time to time (with frequency $\beta$) decide to emigrate from its native population so that each population is subject to the emigration rate $\beta n_i$, proportional to its size. Depending on the choice strategy of migrants as far as their new population is concerned one arrives at different ODE systems.

For example, let each emigrant choose a new population (habitat) completely at random. If viewed spatially, this is, obviously, a variant of super-diffusion with a random step size, which is a non-trivial problem if one considers it directly in space and time. On a sufficiently large time scale, there will be the steady immigration rate $\gamma$ in all populations (since the total emigration rate is constant). The emigration and immigration coefficients $\beta$ and $\gamma$ must be balanced to guarantee the steady state of the metapopulation:

$$\frac{d}{dt} \sum_{i=1}^{P} n_i = \sum_{i=1}^{P} (\gamma - \beta n_i) = 0.$$  

(3.39)

Let $\sum_i n_i = N = \text{const}$, then $\gamma = \beta \bar{n}$, where $\bar{n} = N/P$, and $P$ is the number of
habitats. The dynamic law becomes

\[ \frac{dn_i}{dt} = \beta (\pi - n_i), \quad i = 1, 2, \ldots P. \] (3.40)

Notice that \( \pi = N/P \) is the total number of individuals divided by the number of habitats, which would be exactly the size of populations in all habitats if all individuals were evenly spread throughout. From (3.40) it follows that a population stops changing once it reaches this equilibrium size \( \pi \).

The distribution function \( u(n, t) \) is then found by solving the following Cauchy problem:

\[ \frac{\partial u}{\partial t} + \beta (\pi - n) \frac{\partial u}{\partial n} - \beta u = 0, \quad u(n, 0) = u_0(n), \] (3.41)

and is given by

\[ u(n, t) = \begin{cases} 
    e^{\beta t} u_0 (\pi - (n - \pi) e^{\beta t}), & n < \pi, \\
    e^{\beta t} u_0 (\pi), & n = \pi, \\
    e^{\beta t} u_0 (\pi + (n - \pi) e^{\beta t}), & n > \pi.
\end{cases} \] (3.42)

The middle branch of this solution shows that the number (density) of populations with \( n = \pi \) growth exponentially with time. As can be seen in Fig. 3.6 the upper and lower branches of the solution (3.42) represent the initial distribution that shrinks, respectively, from the left and from the right, towards \( \pi \). This behaviour is indicative of a mollifier of the Dirac delta function centred at \( \pi \), which, indeed, is the limit of \( u(n, t) \) as \( t \to \infty \), since all populations will eventually have the same size \( \pi \). An interesting feature of (3.42) is the preservation of the main features of the initial \( u_0(n) \) over time, albeit in a scaled (shrank) form, e.g., the double peaked shape shown in Fig. 3.6.
3.6. Biased migration. Consider populations with potentially unlimited growth and constant emigration frequency. Let the choice of the new population by the migrants be biased towards populations with higher growth rates. The ODE describing this situation is:

\[
\frac{dn_i}{dt} = \alpha_i n_i - \beta n_i + \gamma \alpha_i, \quad i = 1, \ldots, P,
\]  

(3.43)

where \(\alpha_i\) is the growth coefficient, \(\beta\) is the emigration frequency, and \(\gamma\) is the immigration coefficient. Since migration does not change the total number of individuals (only the growth does), the following balance equation should be satisfied at all times:

\[
\beta \sum_{i=1}^{P} n_i = \gamma \sum_{i=1}^{P} \alpha_i,
\]  

(3.44)

reducing equation (3.43) to

\[
\frac{dn_i}{dt} = (\alpha_i - \beta) n_i + \alpha_i \beta \sum_{j=1}^{P} n_j, \quad i, j = 1, \ldots, P.
\]  

(3.45)

The corresponding nonzero component of the phase-space current is

\[
J_n = (\alpha - \beta)nu + \alpha \beta Ru,
\]  

(3.46)

where

\[
R = \frac{N}{A},
\]

\[
N = \int \int nu(n, \alpha, t) \, d\alpha \, dn, \quad A = \int \int \alpha u(n, \alpha, t) \, d\alpha \, dn,
\]  

(3.47)

and, since the \(\alpha\)-component of the phase-space current is zero, \(A\) will stay constant in time. Thus, we arrive at the following weakly nonlinear continuity equation for the distribution \(u(n, \alpha, t)\):

\[
\frac{\partial u}{\partial t} + (\alpha \beta R + (\alpha - \beta)u) \frac{\partial u}{\partial n} + (\alpha - \beta)u = 0, \quad u(n, \alpha, 0) = u_0(n, \alpha).
\]  

(3.48)

Assuming that \(R(t)\) is a given function of time we use the method of characteristics to obtain the implicit solution of this problem as

\[
u(n, \alpha, t) = e^{-(\alpha - \beta)t} u_0 \left( ne^{-(\alpha - \beta)t} - \alpha \beta \xi(\alpha, t), \alpha \right),
\]

\[
\xi(\alpha, t) = \int_0^t R(t') e^{-(\alpha - \beta)t'} \, dt'. 
\]  

(3.49)

However, \(R(t)\) and, hence, \(\xi(\alpha, t)\) are functions of \(u\) as well, see eq. (3.47). Thus, we employ an iterative algorithm similar to the Algorithms 1 and 2.

**Algorithm 3**

- Given: \(\xi_0(\alpha) = 0, u_0(n, \beta), N_0, R_0,\) and a sufficiently large \(\Omega\).
Fig. 3.7. Time evolution of the distribution function $u(n, \alpha, t)$ for populations with biased migration, see eq. (3.49). Top row – snapshots at $t = 0.0, 0.018,$ and $0.034$; Bottom row – corresponding numerically integrated $\rho(n,t)$ showing the distribution of populations over their sizes.

- For $k = 0, 1, 2, \ldots$, do:
  
  \[
  \xi_{k+1}(\alpha) = \xi_k(\alpha) + R_k e^{-(\alpha - \beta) t_k} \Delta t,
  \]
  
  \[
  u_{k+1}(n, \alpha) = e^{-(\alpha - \beta) t_{k+1}} u_0 \left( n e^{-(\alpha - \beta) t_{k+1}} - \alpha \beta \xi_{k+1}(\alpha), \alpha \right),
  \]
  
  \[
  R_{k+1} = \frac{1}{A} \iint_{\Omega} n u_{k+1}(n, \alpha) \, dn \, d\alpha,
  \]

A quick look at the implicit solution (3.49) reveals similarity with the case of exponential growth (3.5). Indeed, as expected, the two solutions are identical for $\beta = 0$, remain similar at low values of the emigration frequency, and become very different for larger values. One of the predictions of the metapopulation theory (Levin 1969; Eriksson et al. 2014) is that migration may prevent extinction. In the present case, as follows from (3.45), none of the populations can disappear as long as there is at least one nonzero population somewhere. Yet, it does not mean that all populations are always growing in size. In the early stages some populations may decrease. From (3.45) we deduce that the condition on the growth of a population is

\[
\frac{\alpha_i}{\sum_j \alpha_j} > \left( 1 - \frac{\alpha_i}{\beta} \right) \frac{n_i}{\sum_j n_j}, \quad \beta > 0.
\]  

(3.50)

Obviously, this condition is satisfied for all populations with $\alpha_i > \beta$. However, for a population with $\alpha_i < \beta$ it is easy to imagine a sufficiently large initial state $n_i(0)$ such that this condition is violated and the population size will decrease. Nevertheless, when such a decreasing $n_i$ becomes sufficiently small, the condition will become satisfied again and the population will resume its growth.

An example of the evolution of distribution function for populations with biased migration computed with the Algorithm 3 is shown in Fig. 3.7. The initial distribution
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(the leftmost image and plot) is a Gaussian centred at \( n_c = 20 \) and \( \alpha_c = 30 \). The emigration frequency is set at \( \beta = 50 \) in this simulation, which is higher than most of the growth coefficients \( \alpha \) in the initial distribution. The first striking conclusion is that despite the immigration bias we do not observe an explosive growth of some particular (chosen) populations at the expense of others. Apparently, any such growth is efficiently mitigated by a higher emigration rate.

The early-time transient decrease of some populations mentioned above (those with large initial \( n \)’s) causes the distribution function to contract slightly in the horizontal \( n \)-dimension, since the right side of the distribution moves to the left, while the left side moves to the right. This happens in the very early stages of the evolution (not shown). The same effect prevents the distribution from widening in the horizontal direction in the course of the evolution. In fact, as the Figure 3.7 shows, the distribution only keeps contracting.

Thus, the main consequence of the large emigration frequency \( \beta \) for the late-time evolution appears to be the uniformity of size for populations with equal \( \alpha \)’s and the uniformity of \( \alpha \)’s for populations of the same size. Also, for large \( t \)’s the populations show a very strong correlation (almost direct proportionality) between the population size and its growth coefficient \( \alpha \) (see the top-right image of Fig. 3.7).

3.7. Growth rates depending on the distribution function. The present approach is indispensable for dynamic models where the rate of growth of populations is a functional \( R(u, n) \) of both the size \( n \) of the local population and the distribution \( u \) of populations over the phase space. The phase-space current vector will have as many nonzero components as there are time varying parameters in \( R \). If all parameters, except \( n_i \), are time invariant, then the problem is described by the following equations:

$$\frac{dn_i}{dt} = R(u, n_i), \quad i = 1, 2, \ldots P, \quad (3.51)$$

$$\frac{\partial u}{\partial t} = -\frac{\partial}{\partial n} (uR(u, n)). \quad (3.52)$$

Obviously, it is now impossible to solve the dynamic equations (3.51) without first solving the phase-space problem (3.52).

Consider populations with unlimited growth discussed earlier. Suppose that one is able to influence the rate of growth of each population (e.g., by judicially watering and fertilizing each plant) proportionally to its current ‘weight’ in the phase space. Such a problem is described by the following equations:

$$\frac{dn_i}{dt} = \alpha_i n_i \int \int u(n, \alpha, t) \, dn \, d\alpha \approx \alpha_i n_i u(n_i, \alpha_i, t) \delta, \quad i = 1, 2, \ldots P, \quad (3.53)$$

$$\frac{\partial u}{\partial t} + 2\alpha \delta n \frac{\partial u}{\partial n} + \alpha \delta u^2 = 0, \quad u(n, \alpha, 0) = u_0(n, \alpha), \quad (3.54)$$

where \( \delta = 4\Delta \alpha \Delta n \), i.e., we use the mid-point approximation for the integral in (3.53). The resulting approximate phase-space problem (3.54) is a variant of the Burgers equation (see e.g. Smoller 1994) whose characteristic equations are:

$$\frac{dt}{ds} = 1, \quad \frac{dn}{ds} = 2\alpha \delta n, \quad \frac{du}{ds} = -\alpha \delta u^2, \quad (3.55)$$

or

$$dn = 2\alpha \delta n \, dt, \quad -\alpha \delta \, dt = \frac{du}{u^2}, \quad \frac{dn}{2n} = -\frac{du}{u}. \quad (3.56)$$
The solutions of the last two are:
\[ \alpha \delta t - \frac{1}{u} = C_2, \quad u \sqrt{n} = C_3, \]  
which allows rewriting and solving the first equation in (3.56) as
\[ \frac{dn}{\sqrt{n}} = 2\alpha \delta C_3 dt, \quad 2\sqrt{n}(1 - \alpha \delta tu) = C_1. \]  
Combining this result with the first equation in (3.57) we get
\[ u = \frac{1}{\alpha \delta t - f(p)}, \quad p = 2\sqrt{n}(1 - \alpha \delta tu). \]  
The initial condition requires that
\[ f(p)|_{t=0} = -\frac{1}{u_0(n, \alpha)}. \]  
Hence, we choose
\[ f(p) = -\frac{1}{u_0(p^2/4, \alpha)} = -\frac{1}{u_0(n(\alpha \delta tu - 1)^2, \alpha)}, \]  
and arrive at the following equation that implicitly defines the distribution \( u(n, \alpha, t) \):
\[ u = \frac{u_0(n(\alpha \delta tu - 1)^2, \alpha)}{\alpha \delta tu_0(n(\alpha \delta tu - 1)^2, \alpha) + 1}, \]  
or
\[ u = (1 - \alpha \delta tu) u_0(n(1 - \alpha \delta tu)^2, \alpha). \]  
These representations are only valid in the smooth regime, i.e., prior to the development of shock.

A fixed-point iterative algorithm that computes the distribution at a given time \( t \) may be formulated as follows (one can use any suitable norm for the computation of the current mismatch \( \epsilon_k \)):

**Algorithm 4**
- Given: \( u_0(n, \alpha), t, \) and \( \epsilon \).
- For \( k = 0, 1, 2, \ldots \), while \( \epsilon_k > \epsilon \), do:
  \[ u_{k+1}(n, \alpha) = \frac{u_0(n(\alpha \delta tu_k(n, \alpha) - 1)^2, \alpha)}{\alpha \delta tu_0(n(\alpha \delta tu_k(n, \alpha) - 1)^2, \alpha) + 1}, \]
  \[ \epsilon_k = \|u_{k+1}(n, \alpha) - u_k(n, \alpha)\|. \]

Figure 3.8 illustrates the application of this algorithm (with \( \epsilon = 10^{-4} \) and \( \delta = 0.1 \)). The initial distribution is the same as in the example of the previous section. As expected from the non-viscous Burgers equation the solution develops a shock (notice the almost vertical front in the plot at the bottom-right of Fig. 3.8). Even though we have used the distribution computed at the previous time instant as the initial guess for the next time instant, the convergence of the Algorithm 4 slows down as time grows. Around \( t = 0.1 \), as one approaches the shock in this example, the convergence
of the Algorithm 4 breaks down completely: initially the error \( \epsilon_k \) decreases, however, it never reaches the tolerance of \( \epsilon = 10^{-4} \) and even begins to increase as iterations continue.

Obviously, the development of shock and the related breakdown of the Algorithm 4 does not mean that the populations stop growing. Rather, it is a result of the midpoint approximation of the integral in the equation (3.53) that reduces the problem to the Burgers equation with its well-known shock behavior. Keeping that in mind, we see that at least in the early stages of evolution there will emerge a sharp upper bound on the sizes of populations and many populations with the average growth factor will have that size.

4. Conclusions and possible applications. The phase-space approach presented above allows computing the evolution of the distribution function of simultaneously growing and interacting populations by solving a low-dimensional PDE. Although, such phase spaces impose substantial constraints on the types of interactions, many practical problems appear to satisfy these constraints. As the examples demonstrate, the main power of this approach is that, unlike typical Monte-Carlo simulations, it often provides rather explicit results that could be used as benchmark solutions.

In the case of precision agriculture (Hautala and Hakojärvi 2011), this method could be employed to predict and, perhaps, control the distribution of plant sizes at the time of harvest. To this end, models considered above can be easily extended to include deterministic (measured) time-varying growth coefficients and various environmental factors. Another straightforward extension could be the inclusion of the source term in the conservation law (2.5) reflecting the emergence of new populations, e.g., potato tubers.

The case of populations competing for limited resources could serve as a math-
ematical model for recovering the distribution of populations from the resource consumption curves. For example, in the analysis of seed quality it is common to monitor the oxygen consumption during the germination process (Bewley et al. 2013, van Duijn and Koenig 2001, van Asbroeck and Taridno 2009, Budko et al. 2013), with the main consumers of oxygen being the growing populations of mitochondria present in every seed. Our method provides the necessary link between the distribution of the seed parameters, including the initial number of active mitochondria, and the measured oxygen uptake curves for a batch of seeds germinating in a closed container.

On the theoretical level, our phase-space analysis, although different in form from the traditional approaches (Barabási and Meszéna 2009, Gyllenberg and Meszéna 2005), confirms the non-existence of a stable equilibrium for coexisting species featuring a continuum of survival strategies, if these strategies involve the range of carrying capacities. On the other hand, we show that an asymptotically stable equilibrium is possible, if the inter-species competition concerns other survival strategies, such as the rates of growth or resource consumption.

Low-dimensional conservation laws occur in migration studies as well. In particular, we have demonstrated that a completely randomized migration, corresponding to the case of spatial super diffusion, leads to an explicit phase-space solution resembling a time-dependent mollifier of the Dirac’s delta function. It is also possible to incorporate simple models of migration bias in this formulation, as long as these models do not involve any specific spatial ordering.

Finally, the phase-space coupling model considered in the last section may have potential applications in the analysis of dynamic systems, where the control is driven by the time-varying statistical data. For instance, in economics and social sciences, the decisions are often based on the perceived actions of the majority or minority.

It is easy to imagine that the vector phase-space dynamics featuring phase-space currents with several nonzero components is much more exciting. Such dynamics is expected if the growth coefficients or environmental factors are varying in time or with the classical predator-prey problem. The corresponding continuity equations, however, would have to be solved numerically (Leveque 2002).

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REFERENCES

[1] Barabási G and Meszéna G (2009) When the exception becomes the rule: The disappearance of limiting similarity in the Lotka-Volterra model. Journal of Theoretical Biology 258:89–94.
[2] Begon M, Townsend CR, and Harper JL (2006) Ecology: From Individuals to Ecosystems. Blackwell Publishing.
[3] Bewley JD, Bradford KJ, Hilhorst HWM, and Nonogaki H (2013) Seeds: Physiology of development, germination and dormancy. 3rd Edition, Springer, New York, Heidelberg, Dordrecht, London.
[4] Budko N, Corbetta A, van Duijn A, Hille S, Krehel O, Rottshäfer V, Wiegman L, and Zhelyazov D (2013) Oxygen transport and consumption in germinating seeds, Proceedings of the 90th European Study Group Mathematics With Industry, Leiden Jan. 28-Feb. 1: 5–30.
[5] Carrie C, Murcha MW, Giraud E, Ng S, Zhang MF, Narsai R, and Whelan J (2012) How do plants make mitochondria? Planta: An International Journal of Plant Biology, 10.1007/s00425-012-1762-3.
[6] Collet JF and Goudon T (2000) On solutions of the Lifshitz-Slyozov model. Nonlinearity 13:1239–1262.
[7] Edelstein-Keshet L (2005) Mathematical Models in Biology. SIAM.
[8] Eriksson A, Elias-Wolff F, Mehlig B, and Manica A (2014) The emergence of the rescue effect from explicit within- and between-patch dynamics in a metapopulation. Proc. R. Soc. B 281:20133127.
[9] Fisher RA (1930) The genetical theory of natural selection. Oxford University Press.
[10] Gyllenberg M and Meszéna G (2005) On the impossibility of coexistence of infinitely many strategies. J. Math. Biol. 50:133–160.
[11] Hautala M and Hakojiärvi M (2011) An analytical C3-crop growth model for precision farming. Precision Agric. 12:266–279.
[12] Kampman R and Wagner R (1991) Materials Science and Technology - A Comprehensive Treatment. Vol. 5, VCH, Weinheim, Germany.
[13] Laurencot P (2002) The Lifshitz-Slyozov-Wagner equation with conserved total volume. SIAM J. Math. Anal. 34(2):257–272.
[14] Leveque RJ (2002) Finite volume methods for hyperbolic problems. Cambridge University Press, Cambridge.
[15] Levin R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull. Entomol. Soc. Am. 15:237–240.
[16] Lifshitz IM and Slyozov VV (1961) The kinetics of precipitation from supersaturated solid solutions. J. Phys. Chem. Solids, 19:35–50.
[17] Lin Y, Berger U, Grimm V, Huth F, and Weiner J (2013) Plant Interactions Alter the Predictions of Metabolic Scaling Theory. PLoS ONE 8(2):e57612.
[18] Merchant DJ, Kuchler RB, and Munyo W (1960) Population dynamics in suspension cultures of an animal cell strain. Journal of Biochemical and Microbiological Technology and Engineering, II:253–266.
[19] Myhr OR and Grong Ø (2000) Modelling of non-isothermal transformations in alloys containing a particle distribution. Acta Materialia, Vol. 48(7):1605–1615.
[20] Newman K, Buckland ST, Morgan B, King R, Borchers DL, Cole D, Besbeas P, Gimenez O, and Thomas L (2014) Modelling Population Dynamics: Model Formulation, Fitting and Assessment using State-Space Methods. Series: Methods in Statistical Ecology, Springer Science+Business Media, New York.
[21] Shonkwiler RW and Herod J (2009) Mathematical Biology: An introduction with Maple and Matlab. 2nd Edition, Springer Dordrecht, Heidelberg, London, New York.
[22] Smoller J (1994) Shock waves and reaction-diffusion equations. Springer-Verlag, New York, Second Edition.
[23] van Asbruck J and Taridno P (2009) Using the single seed oxygen consumption measurement as a method of determination of different seed quality parameters for commercial tomato seed samples. Asian Journal of Food and Agro-Industry:S88–S95.
[24] van Duijn A and Koenig W (2001) Measuring metabolic rate changes. Patent EP1134583 (A1) WO0169243 (A1) US20040353775 (A1) CA2403253 (A1) DE60108480T.
[25] Velázquez J, Garrahan JP, and Eichhorn MP (2014) Spatial Complementarity and the Coexistence of Species. PLoS ONE 9(12):e114979.
[26] Wagner C (1961) Theorie der Alterung von Niederschlägen durch Umlösung (Ostwald-Reifung). Z. Elektrochem., 65:581–591.
[27] Xu L, Zhang F, Zhang K, Wang E, and Wang J (2014) The Potential and Flux Landscape Theory of Ecology. PLoS ONE 9(1):e86746.