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Diffusive and Nondiffusive Population Models

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Diffusive and nondiffusive population models

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1 Introduction

The modeling of populations is of great importance in ecology and economy, for instance, to describe predator-prey and competition interactions, to predict the dynamics of cell divisions and infectious diseases, and to manage renewable resources (harvesting). Population models describe the change of the number of species due to birth, death, and movement from position to position (in space) or from stage to stage (age, size, etc.). In this short survey, we review some mathematical results for *deterministic* and *continuous* population models. We concentrate on the following model classes:

- spatially homogeneous population models;
- spatially inhomogeneous population models;
- age- and size-structured population models; and
- time-delayed population models.

The evolution of spatially homogeneous populations may be modeled by *ordinary differential equations*, for instance, by the logistic-growth model. The interaction of competing populations can be described by a system of coupled equations, one of which is the famous Lotka-Volterra system, introduced in Section 2. Important questions, beside the wellposedness of the corresponding problems, include the stability of steady states and the biological consequences.

In a spatially heterogeneous setting, the population number varies in space and may diffuse in the environment. This gives the class of *reaction-diffusion equations* and their systems. Turing found that the stationary solution to a diffusion system may become unstable even if the steady state of the corresponding system without diffusion is stable. Thus, the stability analysis is much more involved than in the spatially homogeneous case. Roughly speaking, in the long-time limit, one may have extinction or coexistence of the species (see Section 3 for details).

The solutions of the diffusive Lotka-Volterra competition model do not show pattern formation. Hence, this model is not able to describe segregation phenomena. In Section 4, we review several *cross-diffusion models* which allow for inhomogeneous steady states. Roughly speaking, such stationary solutions exist if cross-diffusion is large compared to diffusion. The existence analysis of cross-diffusion systems is complicated due to the strong nonlinear coupling and since the diffusion matrices may be neither symmetric nor positive definite. Recently, some analytical tools have been developed to prove the existence of global-in-time weak solutions. These tools are explained in detail since they reveal interesting connections between the symmetrization of the diffusion matrix and the existence of an entropy (Lyapunov functional). Section 4 is the key section of this survey.

When the individuals of a population are not identical but can be distinguished by their age, size, etc., we need to introduce *structured population models*. In Section 5, we introduce some age-structured and size-structured balance equations of hyperbolic type. Following [121], results on the existence and the long-time behavior of the solutions are presented.

The change of a population may be delayed due to maturation or regeneration time, for instance. In Section 6 we consider *time-delayed population models*, following partially [56]. If the time delay is not discrete but distributed, we arrive to nonlocal equations in which the term with the retarded variable is replaced by a convolution in time.

The field of population modeling has become so large that this survey can review only a small part of the published modeling and mathematical topics. Many model classes and important issues will not be discussed. For instance, we ignore difference and matrix equations, stochastic approaches, and models including mutations, maturation structures, metapopulations, and demographic or biomedical applications. For details about these topics, we refer to the monographs [15, 38, 73, 100, 113, 114, 117, 121].

2 Initial-value population models

First, we consider the population dynamics of a single species without interactions in a homogeneous environment. Let $u(t)$ be the population number at time $t \geq 0$. Its rate of change is given by the difference of the birth and death rates. Assuming that these rates are proportional to the population number, we obtain the differential equation $du/dt = au$, first suggested by Malthus [101] in the 18th century, where a , which is typically a positive number, is the effective growth rate of the population. Its solution models unlimited exponential growth. The capacity of the environment (limited food supply or other environmental resources) can be taken into account by introducing a self-limiting term:

$$\frac{du}{dt} = u(a - bu), \quad t > 0, \quad u(0) = u_0, \quad (1)$$

where $b > 0$ is a measure of the environment capacity. This equation, proposed by Verhulst [143] in the 19th century, is called the *logistic-growth model*. Its solution $u(t)$ converges to the so-called carrying capacity limit a/b as $t \rightarrow \infty$ (if $u(0) > 0$), which is a stable steady state.

Next, let us consider the population of two species $u(t)$ and $v(t)$. When they are not interacting, its evolution is described in the logistic-growth approach by the equations

$$\frac{du}{dt} = u(a_1 - b_1u), \quad \frac{dv}{dt} = v(a_2 - c_2v), \quad t > 0.$$

The coefficients $b_1 \geq 0$ and $c_2 \geq 0$ are called the intra-specific competition constants. In this situation, the populations are evolving independently from each other. When the species are interacting, we add competition terms proportional to the population numbers:

$$\frac{du}{dt} = u(a_1 - b_1u - c_1v), \quad \frac{dv}{dt} = v(a_2 - b_2u - c_2v), \quad t > 0, \quad (2)$$

where the new coefficients c_1 and b_2 model inter-specific competition or benefit, depending on their sign. We distinguish three types of interactions:

- *Predator-prey model*: $c_1 > 0$, $b_2 < 0$. This choice decreases the (effective) growth rate of the species u and increases the growth rate for v . Since the growth rate for v becomes larger when the population number u is large, v represents a predator species and u the prey. Clearly, taking $c_1 < 0$ and $b_2 > 0$ changes the roles of prey and predator.
- *Competition model*: $c_1 > 0$, $b_2 > 0$. The interaction terms are nonpositive, thus decreasing the growth rates of the species. This means that both species are competing for the (food or environmental) resources.
- *Mutualistic (or symbiotic) model*: $c_1 < 0$, $b_2 < 0$. When the two species benefit from the interactions, the growth rates are enhanced. In this situation, the interaction terms are taken nonnegative and the constants c_1 and b_2 are negative.

A particular predator-prey model is obtained when the intra-specific competition vanishes, $b_1 = c_2 = 0$:

$$\frac{du}{dt} = u(a_1 - c_1v), \quad \frac{dv}{dt} = -v(\alpha - \beta u), \quad t > 0,$$

where we have set $\alpha := -a_2 > 0$ and $\beta := -b_2 > 0$. The sign assumption on a_2 means that the predators will become extinct in the absence of the prey, since in this situation, $dv/dt = -\alpha v$. This system is usually called the *Lotka-Volterra model*, proposed by Volterra [144] and independently by Lotka to describe a chemical reaction [94] in the first half of the 20th century. It has the remarkable property of possessing a first integral,

$$\beta u + c_1 v - \log(u^\alpha v^{\alpha_1}) = \text{const.},$$

showing that the system admits positive oscillating solutions if $u(0) > 0$, $v(0) > 0$ [114, Chap. 3.1]. The predator-prey model with limited growth (i.e. (2) with $a_2 < 0$ and $b_2 > 0$) allows for two scenarios. Depending on the choice of the parameters and the initial data, the predator population becomes extinct and the prey population approaches its carrying capacity limit, or there is coexistence of both species, i.e., $(u(t), v(t))$ converges to the asymptotically stable steady state

$$s^* = \left(\frac{a_1 c_2 - a_2 c_1}{b_1 c_2 - b_2 c_1}, \frac{b_1 a_2 - b_2 a_1}{b_1 c_2 - b_2 c_1} \right) \quad (3)$$

as $t \rightarrow \infty$. Notice that our sign assumption on b_2 implies that $b_1 c_2 - b_2 c_1 > 0$. Similar results are valid for the competition model [145, Chap. 2].

In the mutualistic model, one distinguishes between the *weak mutualistic case* $b_1 c_2 > b_2 c_1$, in which the self-limitation, expressed by b_1 and c_2 , dominates the mutualistic interaction, expressed by b_2 and c_1 , and the *strong mutualistic case*, in which mutualism dominates self-limitation. In the former case, there is generally stable coexistence, whereas in the latter case, there are three scenarios: either at least one of the species become extinct, or the solution $(u(t), v(t))$ converges to the steady state (3) as $t \rightarrow \infty$, or $(u(t), v(t))$ blows up in finite time [96].

The dynamics of Lotka-Volterra systems with more than two species is more involved. For instance, chaos has been observed in models with four competing species (see [142] and the references therein).

3 Reaction-diffusion population models

In the previous section, we have considered populations which are spatially homogeneous. However, in a spatially heterogeneous environment, the population density will depend on space. Assuming that populations tend to move to regions with smaller number density, it is reasonable to include diffusive terms in the evolution equations, which may be justified as limiting expressions of a Brownian motion [117]. Then a single-species population density $u(x, t)$ evolves in the bounded domain $\Omega \subset \mathbb{R}^n$ according to

$$u_t - d\Delta u = u f(x, u), \quad x \in \Omega, \quad t > 0, \quad u(\cdot, 0) = u_0, \quad (4)$$

supplemented with some boundary conditions, where u_t abbreviates the time derivative $\partial u / \partial t$. Often, homogeneous Neumann boundary conditions $\nabla u \cdot \nu = 0$ on $\partial\Omega$ are taken, where ν is the exterior unit normal on $\partial\Omega$. These conditions signify that the number of individuals is fixed in the domain (no migration occurs). Also homogeneous Dirichlet boundary conditions $u = 0$ on $\partial\Omega$ can be used, expressing a very hostile environment at the boundary. The coefficient $d > 0$ is the diffusion constant, and $f(x, u)$ is the growth rate per capita, depending on the population and the heterogeneous environment. A

typical example is the logistic-growth function $f(x, u) = a(x) - b(x)u$; then (4) is called the *Fisher-Kolmogorov-Petrovsky-Piskunov equation*, introduced by Fisher [44] and studied by Kolmogorov et al. [78]. Reaction-diffusion models of type (4) have been also considered in physics, chemistry, ecology etc.; see the monographs of Okubo and Levin [117] and Murray [113].

The function $f(x, u) = a(x) - b(x)u$ is decreasing in u (if $b(x) > 0$). Some population ecologists argue that the growth rate f may not be decreasing in u for all $u \geq 0$, but it may achieve a maximum at an intermediate density. This so-called *Allee effect* [3] may be caused by, for instance, shortage of mates at low density, lack of effective pollination, or predator saturation [131]. Whereas in the logistic growth case (with $a(x) > 0$) there exists a unique nonnegative steady state (positive for slow diffusion and zero for fast diffusion; see [19]), there may be two steady states when an Allee effect is present [131]. Matano [102] and Casten and Holland [20] showed that any stable steady state to (4) (with homogeneous Neumann boundary conditions) is constant if the domain Ω is convex.

The situation becomes much more complex when we consider systems of equations,

$$u_t - \Delta(Du) = g(x, u), \quad x \in \Omega, \quad t > 0, \quad u(\cdot, 0) = u_0, \quad (5)$$

where $u \in \mathbb{R}^m$ is a vector-valued function, $D = \text{diag}(d_1, \dots, d_m)$ is a diagonal matrix with constant coefficients d_i , and $g = (g_i) : \Omega \times \mathbb{R}^m \rightarrow \mathbb{R}^m$ ($m > 1$). Turing found in his seminal work [141] that different diffusion rates d_i in a parabolic system, modeling the interaction of two chemical substances, may lead to inhomogeneous distributions of the reactants, which allows one to model a pattern structure. Moreover, even if the steady state of the differential equation without diffusion is stable, the corresponding steady state of the diffusion system may become unstable and bifurcations may occur. This phenomenon is generally called *diffusion-driven instability*.

Similar to the scalar case, Kishimoto and Weinberger [76] proved that, in a convex domain, the system (5) with homogeneous Neumann boundary conditions has no stable nonconstant steady state if $\partial g_i / \partial u_j > 0$ for all $i \neq j$ (cooperation-diffusion system); the same conclusion holds for $m = 2$ if $\partial g_i / \partial u_j < 0$ for $i \neq j$ (competition-diffusion system). On the other hand, in nonconvex domains, stable nonconstant steady states may exist, see the works [66, 67, 103] for certain dumbbell-shaped domains. For more references, we refer to [40].

One may ask if a diffusion-driven instability also occurs in Lotka-Volterra diffusion systems. For this, following Lou and Ni [97], we discuss the competition model

$$u_t - d_1 \Delta u = u(a_1 - b_1 u - c_1 v), \quad v_t - d_2 \Delta v = v(a_2 - b_2 u - c_2 v), \quad (6)$$

for $x \in \Omega$ and $t > 0$, with initial and homogeneous Neumann boundary conditions. The coefficients a_i, b_i, c_i, d_i ($i = 1, 2$) are positive. This model

may be supplemented by adding a given common environmental potential ϕ , modeling territories in which the environmental conditions are more or less favorable. In this situation, the equation for u has to be replaced by

$$u_t - \operatorname{div}(d_1 \nabla u - e_1 u \nabla \phi) = u(a_1 - b_1 u - c_1 v),$$

and similar for the equation for v .

It is known that the initial-boundary value problem from (6) has a unique nonnegative smooth solution, see, e.g., [149] for systems with m equations and general semilinearities. The long-time behavior depends on the values of the reaction coefficients, and there are, in contrast to the Lotka-Volterra differential equations (2), three situations. Set $A = a_1/a_2$, $B = b_1/b_2$, $C = c_1/c_2$. Then [97]

- *Extinction:* $A > \max\{B, C\}$ or $A < \min\{B, C\}$. The solution $(u(t), v(t))$ converges to $(a_1/b_1, 0)$ or $(0, a_2/c_2)$, respectively, uniformly as $t \rightarrow \infty$. Thus, one species dominates and the other species becomes extinct.
- *Weak competition:* $B > A > C$. The solution $(u(t), v(t))$ converges to the steady state s^* , defined in (3), uniformly as $t \rightarrow \infty$. This means that both species coexist.
- *Strong competition:* $B < A < C$. The steady states $(a_1/b_1, 0)$ and $(0, a_2/c_2)$ are locally stable, but s^* is unstable. If the domain is convex, no stable positive steady state exists.

In particular, in the weak competition case, the steady state s^* is globally asymptotically stable regardless of the values of the diffusion coefficients d_1 and d_2 . In fact, there exists a Lyapunov functional which allows for a long-time asymptotic analysis [89, 126]. Therefore, no nonconstant steady state exists for any d_1 and d_2 , and there is no pattern structure. For the Volterra model with diffusion, for any number of interacting populations, Murray [112] has shown that the effect of uniform diffusion is to damp all spatial variations. General reaction rates and the stability of constant steady states have been considered by Conway and Smoller [27]. The situation changes when cross-diffusion terms are present in (6), modeling the population pressures created by the competitors; see Section 4 for details.

The asymptotic behavior of solutions to reaction-diffusion systems similar to (6) has been studied in several papers. For instance, the existence of traveling wave solutions in one-dimensional diffusive Lotka-Volterra predator-prey models with a logistic growth condition was shown by Dunbar [37]. More recently, traveling waves for a reaction-diffusion system with one diffusion term omitted were analyzed by Ai and Huang [1].

The following diffusive mutualistic model was considered by Lou, Nagilaki, and Ni [96]:

$$u_t - d_1 \Delta u = u(a_1 - b_1 u + c_1 v), \quad v_t - d_2 \Delta v = v(a_2 + b_2 u - c_2 v)$$

in $\Omega \times (0, \infty)$ with initial and homogeneous Neumann boundary conditions and $a_i, b_i, c_i > 0$. Compared to (6), the signs of the interaction terms are reversed,

expressing mutualistic interactions. Lou, Nagilaki, and Ni prove the interesting result that, in the strong mutualistic case (see Section 2), the population of the species may blow up in finite time, although one or both species with exactly the same initial data would die out if *no* diffusion effects are taken into account. The mathematical reason is that diffusion first averages u and v , possibly increasing the densities, and, after some time, the reaction terms dominate and may force the solution to blow up. As the diffusion initiates the blowup process at the first stage, this phenomenon is called *diffusion-induced blowup*.

A related effect is *diffusion-induced extinction*. Iida et al. [65] have studied the diffusive Lotka-Volterra model in the strong competition case. In the absence of diffusion, if one species is initially superior to the other one, the superior species wipes out the other species. On the other hand, allowing for diffusion (with the same diffusion rates), Iida et al. proved that the superior species may become extinct. If the diffusion rates are different, the situation is more complicated, and we refer to [116] for details.

Finally, we remark that systems with more than two equations have been considered too. For instance, the coexistence of competing species in a reaction-diffusion system with one predator and two competing prey is analyzed in [70], and the existence and stability of stationary and periodic solutions to a reaction-diffusion system consisting of m species is proved in [39].

4 Cross-diffusion population models

The diffusive Lotka-Volterra competition model has no nonconstant steady state for all possible diffusion rates, thus excluding biologically reasonable pattern structures. Inhomogeneous steady states may be obtained by taking into account cross-diffusion terms instead of just adding pure diffusion to the population models. In this section, cross-diffusion models are analyzed in detail.

First, let us consider cross-diffusion systems with constant diffusion rates,

$$u_t - (d_1 \Delta u + d_2 \Delta v) = uf(x, u, v), \quad v_t - (d_3 \Delta u + d_4 \Delta v) = vg(x, u, v)$$

in $\Omega \times (0, \infty)$ with initial and homogeneous Neumann boundary conditions. Clearly, a necessary condition to have – at least local – existence of solutions is that the diffusion matrix

$$\begin{pmatrix} d_1 & d_2 \\ d_3 & d_4 \end{pmatrix}$$

is positive definite (see, e.g., [7]). The above system shows indeed diffusion-driven instabilities. Farkas [41] has proved that the one-dimensional stationary model undergoes a Turing bifurcation at a certain size of the interval under suitable conditions on the coefficients of the system. This means that a larger

domain may lead to a heterogeneous distribution of the steady states even if the conditions are homogeneous everywhere. We also refer to [62, 80] for results in this direction. The stability and cross-diffusion-driven instability of constant stationary solutions was studied by Flavin and Rionero [45]. Also wavelike solutions are possible in such cross-diffusion systems. For instance, Kopell and Howard [79] have proved the existence of plane-wave solutions of the type $(u, v)(x, t) = (U, V)(k \cdot x - \omega t)$, and they have analyzed the stability and instability of the waves. Summarizing, we may say that diffusion tends to suppress pattern formation, whereas cross-diffusion seems to help creating pattern under suitable conditions.

Generally, we expect that the cross-diffusion rate of one species is not constant but depends on the population density of the other species and vice versa. Therefore, we replace the linear term by a nonlinear one involving the product of both populations. This leads to the following system, first suggested by Shigesada, Kawasaki, and Teramoto [132]:

$$u_t - \Delta((d_1 + \alpha_{11}u + \alpha_{12}v)u) = u(a_1 - b_1u - c_1v), \quad (7)$$

$$v_t - \Delta((d_2 + \alpha_{21}u + \alpha_{22}v)v) = v(a_2 - b_2u - c_2v), \quad (8)$$

$$\nabla u \cdot \nu = \nabla v \cdot \nu = 0 \quad \text{on } \partial\Omega, \quad t > 0, \quad u(\cdot, t) = u_0, \quad v(\cdot, t) = v_0 \quad \text{in } \Omega, \quad (9)$$

where $\Omega \subset \mathbb{R}^n$ is a bounded domain. The diffusion coefficients d_i and α_{ij} as well as the reaction coefficients a_i , b_i , and c_i are assumed to be constant (and nonnegative). The expressions $\alpha_{12}\Delta(uv)$ and $\alpha_{21}\Delta(uv)$ are the nonlinear cross-diffusion terms, and $\alpha_{11}\Delta(u^2)$ and $\alpha_{22}\Delta(v^2)$ describe the self-diffusion of the species. The basic idea is that the primary cause of dispersal is migration to avoid crowding instead of just random motion (modeled by diffusion). In the following, we review some mathematical properties of the above cross-diffusion system.

Stability. Mathematicians started to pay attention to the model (7)-(8) from the 1980s on, first examining mainly stability issues. One of the first papers is due to Mimura and Kawasaki [109], who have shown, neglecting self-diffusion and assuming reaction coefficients such that $b_1 = b_2$, $c_1 = c_2$, and $c_1/b_1 > a_1/a_2 > b_1/c_1$, that the stationary one-dimensional system has spatial patterns exhibiting segregation. Matano and Mimura [103] showed that, if the diffusion coefficients d_1 and d_2 are sufficiently large, *bounded* stationary solutions must be constant. A segregation result in a triangular diffusion system (i.e. $\alpha_{21} = 0$) is shown by Mimura [108].

An important paper on the interplay between diffusion and cross-diffusion was published by Lou and Ni [97], and in the following, we will describe their results (also see the review [115]). We consider the weak competition case $B > A > C$ (see Section 3), since in this case, the system (7)-(9) without cross-diffusion has no nonconstant steady states. It holds:

- Let $B > A > (B + C)/2$ and d_2 belonging to a proper range. Then, if $\alpha_{21} \geq 0$ is fixed and α_{12} is sufficiently large, there exists a nonconstant steady state.

- Let $B > A > C$. If one of the diffusion constants d_1 or d_2 is sufficiently large (compared to the cross-diffusion coefficients α_{12} and α_{21}), the constant vector s^* , defined in (3), is the only positive steady state.

This means that there are nonconstant steady states if cross-diffusion is sufficiently large, and large diffusion coefficients tend to eliminate any pattern. In the strong competition case $B < A < C$, the situation is more complicated but cross-diffusion has similar effects in helping to create pattern formation; see [97] for details.

The existence of positive steady states for coefficients (a_1, a_2) lying in a certain region was shown by Ruan [127], generalizing results by Mimura [108] and Li and Logan [90]. See also [25] for the same issue. Hopf bifurcations of coexistence steady states have been analyzed by Kuto [83]. The existence and nonexistence of coexistence steady states of the mutualistic model was analyzed by Pao [118], later generalized by Delgado et al. [32]. In recent years, several works were considered with *three-species* cross-diffusion systems providing sufficient conditions for the existence of nonconstant positive steady states, see [24, 52, 95, 128, 129].

Partial existence theory. First, we report the mathematical difficulties in the analysis of the time-dependent system (7)-(9). Its diffusion matrix

$$A = \begin{pmatrix} d_1 + 2\alpha_{11}u + \alpha_{12}v & \alpha_{12}u \\ \alpha_{21}v & d_2 + 2\alpha_{22}v + \alpha_{21}u \end{pmatrix} \quad (10)$$

is neither symmetric nor in general positive definite such that even the local existence of solutions is far from being trivial. Moreover, there exists generally no maximum principle for parabolic systems, which would allow one to derive bounds on the solutions. Finally, it is not clear how to prove the nonnegativity or positivity of the population densities, which is desirable from a biological point of view. It is therefore not surprising that the first existence results in the literature were concerned with special cases, and partial results were obtained only: local-in-time existence, and global-in-time existence for small cross-diffusion constants or for triangular diffusion matrices ($\alpha_{21} = 0$).

One of the first results on the existence of transient solutions was achieved by Kim [74]. He proved the local existence of nonnegative solutions to the one-dimensional cross-diffusion system without self-diffusion. If all diffusion coefficients are set equal to one, he obtained the global existence of solutions. The reason for the last result is easy to see: Taking the difference of the equations

$$\begin{aligned} u_t - \Delta(u + uv) &= u(a_1 - b_1u - c_1v), \\ v_t - \Delta(v + uv) &= v(a_2 - b_2u - c_2v), \end{aligned}$$

the difference $w := u - v$ solves

$$w_t - \Delta w = u(a_1 - b_1u - c_1v) - v(a_2 - b_2u - c_2v).$$

Thus, for given u and v , the function w is a solution to the linear heat equation and can be easily controlled by the right-hand side. Kim derived $H^2(\Omega)$ estimates for u , v , and w , which enabled him to extend the local solution for any time. Another result is due to Deuring [34]. For sufficiently small cross-diffusion parameters α_{12} and α_{21} (or equivalently, sufficiently small initial data) and vanishing self-diffusion coefficients $\alpha_{11} = \alpha_{22} = 0$, he proved the global existence of solutions to (7)-(9).

Several papers are concerned with the global existence of solutions in the special case $\alpha_{21} = 0$. Then the diffusion matrix is triangular and the equation (8) for the second species is only weakly coupled through the reaction terms, considerably facilitating the analysis. We mention some works in this direction: Pozio and Tesi [123] have assumed rather restrictive conditions on the reaction terms for their global existence results. The conditions have been weakened later by Yamada [153]. Redlinger [125] has neglected self-diffusion but he has chosen general reaction terms of the form $uf(u, v)$ and $vg(u, v)$; Yang [154, 155] generalized his results. Lou, Ni, and Wu [98] examined the case of one and two space dimensions and included self-diffusion in the equation for v . The system in any space dimension was treated by Choi, Lui, and Yamada [26] under the hypotheses that the cross-diffusion in the equation for u is sufficiently small and that there is no self-diffusion in the equation for v . This work was generalized by Van Tuoc [140], assuming that the cross-diffusion parameter of one species is smaller than the self-diffusion coefficient of the other species.

Considerable progress was made by Amann [6]. He derived sufficient conditions for the solutions to general quasilinear parabolic systems to exist globally in time. The question if a given (local) solution exists globally is reduced to the problem of finding a priori estimates in the space $W^{k,p}(\Omega)$. More precisely, if the local solution is bounded in $W^{1,p}(\Omega)$ uniformly in $(0, T)$, where $T > 0$ is the maximal time of existence and $p > n$ (n being the space dimension), or if one can control the L^∞ and Hölder norms, then the solution exists globally. These results have been applied to triangular cross-diffusion systems, see the works by Amann [6] and later by Le [84].

Full diffusion matrices were considered in [92, 147, 151]. Li and Zhao [92] proved the global existence of solutions under some restrictions on the (cross) diffusion coefficients, whereas Wen and Fu [147] achieved related results for systems with m species. Yagi [151] studied the two-dimensional problem without self-diffusion and showed a global existence result under the conditions

$$0 < \alpha_{12} < 8\alpha_{11}, \quad 0 < \alpha_{21} < 8\alpha_{22}, \quad \alpha_{12} = \alpha_{21}.$$

This hypothesis is easily understood by observing that in this case, the diffusion matrix A in (10) is positive definite,

$$z^\top A z \geq \min\{d_1, d_2\}|z|^2 \quad \text{for all } z \in \mathbb{R}^2.$$

If the above condition does not hold, there are choices of the parameters such that A is not positive definite.

Finally, we mention the work [47] by Fu, Gao, and Cui, who have proved the global existence of classical solutions to a three-species cross-diffusion model with two competitors and one mutualist.

Global existence theory. Remarkably, the positive definiteness of A is *not* necessary to obtain global existence of solutions to (7)-(9). The first global existence result for the *one-dimensional* cross-diffusion system without any restriction on the diffusion coefficients (except positivity) was achieved by Galiano et al. [49]. Their result is based on two observations which are described in the following.

First, there exists a transformation of variables which symmetrizes the problem. This transformation reads as

$$u = e^{w_1}/\alpha_{21}, \quad v = e^{w_2}/\alpha_{12}.$$

Then system (7)-(8) transforms into

$$\frac{\partial}{\partial t} \begin{pmatrix} e^{w_1} \\ e^{w_2} \end{pmatrix} - \operatorname{div}(B(w)\nabla w) = f(w),$$

where

$$w = \begin{pmatrix} w_1 \\ w_2 \end{pmatrix}, \quad f(w) = \begin{pmatrix} e^{w_1}(a_1 - b_1 e^{w_1}/\alpha_{21} - c_1 e^{w_2}/\alpha_{12}) \\ e^{w_2}(a_2 - b_2 e^{w_1}/\alpha_{21} - c_2 e^{w_2}/\alpha_{12}) \end{pmatrix}.$$

The new diffusion matrix

$$B(w) = \begin{pmatrix} (d_1 + 2\alpha_{11}\alpha_{21}^{-1}e^{w_1} + e^{w_2})e^{w_1} & e^{w_1+w_2} \\ e^{w_1+w_2} & (d_2 + 2\alpha_{22}\alpha_{12}^{-1}e^{w_2} + e^{w_1})e^{w_2} \end{pmatrix},$$

is symmetric and positive definite,

$$\det B(w) \geq d_1 e^{w_1} + d_2 e^{w_2},$$

i.e., the operator $\operatorname{div}(B(w)\nabla w)$ is elliptic for all positive d_i and nonnegative α_{ij} (but not uniformly in w). Another advantage of the above transformation is that if L^∞ bounds for w_i are available, the functions u_i are automatically positive. This idea circumvents the maximum principle which cannot be applied to the present problem. We remark that exponential changes of unknowns have been used in other models to prove the existence of nonnegative or positive solutions to elliptic or parabolic systems and to higher-order equations, see [50, 61, 68, 69].

The second idea is that the cross-diffusion system admits a priori estimates via the functional

$$E_1(t) = \int_{\Omega} \left(\frac{u}{\alpha_{12}}(\log u - 1) + \frac{v}{\alpha_{21}}(\log v - 1) \right) dx. \quad (11)$$

Due to the similarity to the physical entropy, we call this functional an *entropy*. It satisfies the so-called entropy inequality

$$\begin{aligned} \frac{dE_1}{dt} + 2 \int_{\Omega} \left(\frac{2d_1}{\alpha_{12}} |\nabla \sqrt{u}|^2 + \frac{\alpha_{11}}{\alpha_{12}} |\nabla u|^2 + \frac{2d_2}{\alpha_{21}} |\nabla \sqrt{v}|^2 + \frac{\alpha_{22}}{\alpha_{21}} |\nabla v|^2 \right. \\ \left. + 2|\nabla \sqrt{uv}|^2 \right) dx \leq C_1, \end{aligned} \quad (12)$$

where $C_1 > 0$ is a constant depending only on the reaction parameters. This provides, for positive self-diffusion parameters, $H^1(\Omega)$ estimates for u and v .

It is not a coincidence that the symmetrizable system (7)-(8) possesses an entropy functional; see below for a discussion of the relation between symmetry and entropy.

Clearly, the above computation can be made rigorous only if u and v are nonnegative (or even positive) functions. For this, we need to show L^∞ bounds for w_i , which cannot be deduced from the above entropy estimate. The idea of [49] was to employ another “entropy” functional,

$$E(t) = E_1(t) + \gamma E_2(t), \quad E_2(t) = \int_{\Omega} \left(\frac{1}{\alpha_{12}} (u - \log u) + \frac{1}{\alpha_{21}} (v - \log v) \right) dx,$$

where $\gamma = 4 \min\{d_1/\alpha_{12}, d_2/\alpha_{21}\}$. Indeed, employing Young’s inequality, we arrive to

$$\begin{aligned} \frac{dE_2}{dt} \leq - \int_{\Omega} \left(\frac{d_1}{\alpha_{12}} |\nabla \log u|^2 + \frac{d_2}{\alpha_{21}} |\nabla \log v|^2 + 8 \frac{\alpha_{11}}{\alpha_{12}} |\nabla \sqrt{u}|^2 \right. \\ \left. + 8 \frac{\alpha_{22}}{\alpha_{21}} |\nabla \sqrt{v}|^2 \right) dx + \int_{\Omega} (|\nabla \sqrt{u}|^2 + |\nabla \sqrt{v}|^2) dx \\ + \int_{\Omega} (-a_1 - a_2 + (b_1 + b_2)u + (c_1 + c_2)v) dx. \end{aligned}$$

The second integral can be estimated by the corresponding terms in E_1 , and the last integral is controlled by the reactions terms coming from dE_1/dt . After some manipulations we arrive to

$$\frac{dE}{dt} + \int_{\Omega} \left(\frac{\gamma d_1}{\alpha_{12}} |\nabla \log u|^2 + \frac{\gamma d_2}{\alpha_{21}} |\nabla \log v|^2 \right) dx \leq C_2,$$

where $C_2 > 0$ depends again only on the reaction constants. This estimate gives a bound for $\log u$ and $\log v$ in $L^2(0, T; H^1(\Omega))$. Up to now, the arguments are valid in any space dimension n . Now, we need the assumption $n = 1$. Indeed, in this case, the space $H^1(\Omega)$ embeddes continuously into $L^\infty(\Omega)$, thus showing that $u = e^{w_1}$ and $v = e^{w_2}$ are positive.

Unfortunately, there are no L^∞ bounds for w_i in time. Therefore, Galiano et al. [49] have discretized the cross-diffusion system in time (by the backward Euler scheme), obtaining a sequence of elliptic equations, which are solved recursively in time. Since time is discrete, the semidiscrete population densities are strictly positive. The above a priori estimates are sufficient to pass to the limit $\tau \rightarrow 0$ of the time discretization parameter τ , using Aubin compactness results for the sequence of semi-discrete solutions $\exp(w_1^{(\tau)})$ and $\exp(w_2^{(\tau)})$.

Since the compactness holds for $\exp(w_i^{(\tau)})$ and not for $w_i^{(\tau)}$, we lose the boundedness of $\log u$ and $\log v$ and thus the strict positivity of u and v in the limit $\tau \rightarrow 0$, but still obtaining the nonnegativity of u and v as limits of sequences of positive functions.

The assumption of one space dimension to define the exponentials e^{w_i} is crucial in the above argument. In order to deal with multi-dimensional problems, Chen et al. [21] have used another idea. They have discretized the cross-diffusion term $\Delta(uv) = \operatorname{div}(uv \log(uv))$ by the finite differences

$$D^{-h}(\chi_h uv D^h(\log(uv))),$$

with D^{-h} being an approximation of the divergence, D^h an approximation of the gradient, and χ_h the characteristic function of $\{x \in \Omega : \operatorname{dist}(x, \partial\Omega) > h\}$. This discretization is inspired from [77], in which a cross-diffusion problem from semiconductor theory was studied. The approximate problem possesses an entropy inequality similar to (12) but with the term $|\nabla \sqrt{uv}|^2$ replaced by $\chi_h uv |D^h \log(uv)|^2$. In order to avoid problems arising from the logarithm, u and v are replaced by $u^+ + \eta$ and $v^+ + \eta$, respectively, where $u^+ = \max\{0, u\}$ is the positive part of u and $\eta > 0$ is a parameter. The nonnegativity of the approximate solutions is proved by taking the negative part $(u^-, v^-) = (\min\{0, u\}, \min\{0, v\})$ as a test function in the weak formulation of the system, yielding an estimate of the type

$$\|u^-(\cdot, t)\|_{L^2(\Omega)} + \|v^-(\cdot, t)\|_{L^2(\Omega)} \leq \frac{C}{|\log \eta|} \quad \text{uniformly in } t > 0.$$

In the limit $\eta \rightarrow 0$ this gives $u^- = v^- = 0$ in $\Omega \times (0, \infty)$ and hence the nonnegativity of the population densities. Further approximations are necessary: The system is discretized in time by the backward Euler scheme, and the diffusion coefficients in $B(w)$ are approximated by bounded functions. Then the discrete entropy estimates allow for the limit of vanishing approximation parameters.

In [21], the self-diffusion coefficients need to be positive in order to deduce $H^1(\Omega)$ bounds for u and v . This condition has been weakened later in [22] by allowing for vanishing self-diffusion, $\alpha_{11} = \alpha_{22} = 0$. Then there are no $H^1(\Omega)$ bounds for u (and v) which are needed for the Aubin compactness argument. This problem is solved by exploiting the bounds on \sqrt{u} . Indeed, by the Gagliardo-Nirenberg inequality, u is bounded in $L^{4/3}(0, T; W^{1,4/3}(\Omega))$. Together with an $L^1(0, T; (H^s(\Omega))^*)$ bound for u_t , where $(H^s(\Omega))^*$ denotes the dual space of $H^s(\Omega)$, one can apply the Aubin lemma [137]. However, there remains a problem: The $L^1(0, T; (H^s(\Omega))^*)$ bound for u_t does not imply weak compactness in the context of L^p spaces since L^1 is not reflexive. This problem is overcome by using a weak compactness result in L^1 due to Yoshida (see Lemma 6 in [22]).

We mention that the approximation procedure in [22], compared to [21], has been simplified. Indeed, instead of discretizing the cross-diffusion terms,

a Galerkin approximation, together with a semi-discretization in time, is performed. In order to deal with a possible degeneracy of the diffusion matrix, the elliptic regularizations $\varepsilon\Delta w_1$ and $\varepsilon\Delta w_2$ are added. Thus, there are three instead of four approximation levels needed in [21]: the dimension of the Galerkin space, the time-discrete parameter, and the regularization parameter $\varepsilon > 0$.

Another (simpler) regularization was suggested by Barrett and Blowey [10]. They have derived entropy-type estimates by using an approximate entropy functional E_ε , which is quadratic for very small and very large population densities, together with a truncation of the diffusion coefficients to ensure uniform ellipticity. This approximation gives

$$\|u^-(\cdot, t)\|_{L^2(\Omega)} + \|v^-(\cdot, t)\|_{L^2(\Omega)} \leq C\sqrt{\varepsilon},$$

and hence $u, v \geq 0$ in the limit $\varepsilon \rightarrow 0$.

The above procedures fail in the whole-space case $\Omega = \mathbb{R}^n$. Indeed, it is natural to assume that the solutions (u, v) decay to zero as $|x| \rightarrow \infty$ which implies that $\log u(x, t) = \infty$ and $\log v(x, t) = \infty$ at infinity. But then the partial integrations needed to derive the entropy estimates have to be justified. This difficulty was overcome by Dreher [36] by introducing a modified entropy which compares the solution (u, v) against an exponentially decaying weight function. Dreher also used a semi-discretization in time but a higher-order elliptic regularization with the operator Δ^4 .

Relation between symmetry and entropy. Above, we have shown that the cross-diffusion system (7)-(8) can be “symmetrized”, by a change of variables, and that it possesses an entropy functional. This is not a coincidence. In fact, it is well known from the theory of hyperbolic conservation laws that the existence of a symmetric formulation is equivalent to the existence of an entropy functional [72]. This equivalence was reconsidered for parabolic systems by Degond et al. [30] and exploited for the mathematical analysis of energy-transport systems in nonequilibrium thermodynamics [29].

Consider the system

$$u_t - \operatorname{div}(A(u)\nabla u) = f(x, u) \text{ in } \Omega, \quad t > 0, \quad u(\cdot, 0) = u_0 \geq 0 \text{ in } \Omega, \quad (13)$$

supplemented with homogeneous Neumann boundary conditions. The same results hold for Dirichlet and mixed Dirichlet-Neumann boundary conditions [29]. The vector $\operatorname{div}(A(u)\nabla u)$ is defined by its components $\sum_j \operatorname{div}(A_{ij}(u)\nabla u_j)$. The diffusion matrix $A(u) \in \mathbb{R}^{m \times m}$ may be *neither* symmetric *nor* positive definite. Systems (13) have been studied by Alt and Luckhaus [5] but only for positive definite matrices $A(u)$ and for solutions u which may change sign. The case of indefinite diffusion matrices can be mathematically treated if there exists a change of unknowns $u = b(w)$ with $b : \mathbb{R}^m \rightarrow \mathbb{R}^m$ such that

$$B(w) := A(b(w))b'(w) \text{ is symmetric and positive definite.}$$

To ensure that (13) is of parabolic type, we assume further that the function b is monotone and a gradient, i.e., $(b(w_1) - b(w_2)) \cdot (w_1 - w_2) \geq 0$ for all w_1, w_2 ,

$w_2 \in \mathbb{R}^m$ and there exists a function $\chi : \mathbb{R}^m \rightarrow \mathbb{R}$ such that $\chi' = b$. Then (13) can be reformulated as

$$(b(w))_t - \operatorname{div}(B(w)\nabla w) = f(x, b(w)).$$

We claim that this system admits some a priori estimates if the reaction term f can be controlled. Define the *entropy*

$$E(t) = \int_{\Omega} (b(w) \cdot w - \chi(w)) dx.$$

Then, after a formal computation,

$$\frac{dE}{dt} + \int_{\Omega} (\nabla w)^\top B(w) (\nabla w) dx = \int_{\Omega} f(x, b(w)) \cdot w dx.$$

Since $B(w)$ is positive definite, by assumption, the integral on the left-hand side is nonnegative. If the right-hand side can be controlled, this equation provides an a priori estimate for w . When $-f$ is monotone in the sense of $f(x, b(w)) \cdot w \leq 0$, E is even a Lyapunov functional.

In the population cross-diffusion system (7)-(8), we have $b(w) = (e^{w_1}, e^{w_2})$ which is a gradient since $\chi(w) = e^{w_1} + e^{w_2}$ satisfies $\chi' = b$. (Here, we assumed that $\alpha_{12} = \alpha_{21} = 1$, which can be achieved by a rescaling [49].) The entropy becomes

$$\begin{aligned} E &= \int_{\Omega} (e^{w_1}(w_1 - 1) + e^{w_2}(w_2 - 1)) dx \\ &= \int_{\Omega} (u_1(\log u_1 - 1) + u_2(\log u_2 - 1)) dx, \end{aligned}$$

which is of the form (11). The advantage of the special transformation $u = b(w) = (e^{w_1}, e^{w_2})$ is that it gives automatically nonnegative or even positive solutions u . These ideas have been employed in the analysis of systems from various applications, such as thermodynamics [29, 31], semiconductor theory [23], and granular materials [50].

Regularity theory and long-time behavior of solutions. Since Hölder continuity of bounded weak solutions plays an important role in showing the global existence of solutions in the framework of Amann, several authors proved the Hölder regularity of solutions under suitable assumptions. For the triangular system, Le [84] proved that if the L^∞ norm of v and the L^n norm of u (n being the space dimension) can be controlled in the sense of [84], then their Hölder norms are also controlled. Furthermore, if the control is possible for every solution, there exists a global attractor with finite Hausdorff dimension. The Hölder continuity results have been generalized by Le in [85, 86] to include more general diffusion coefficients.

Shim derived uniform L^∞ bounds for the solutions under additional conditions on the diffusion constants in the one-dimensional setting, and he showed

the convergence to the steady states as $t \rightarrow \infty$ [133, 134, 135, 136]. The existence of an exponential attractor (i.e., a compact, finite-dimensional, positively invariant set which attracts any bounded set at an exponential rate) was shown by Yagi [152]. Kuiper and Dung [82] proved the existence of a global attractor for cross-diffusion systems with general diffusion functions. For further results in this direction, we refer to the works [87, 88] of Le and coworkers.

The long-time behavior of solutions is connected with the existence of constant or nonconstant steady states, as reviewed above. Lou and Ni [97] discussed the question if nonconstant steady states in the weak competition case still exist if *both* cross-diffusion constants are strong but qualitatively similar. (The answer is yes if only *one* of the cross-diffusion parameters is sufficiently large.) A partial answer is given by Chen et al. [22] by studying the long-time behavior of the solutions. More precisely, they showed that for vanishing intra-specific competitions $b_2 = c_1 = 0$, which is a special case of weak competition, only constant steady states exist no matter how strong the cross-diffusion coefficients are.

The argument is as follows. Define the *relative entropy*

$$E_R(t) = \int_{\Omega} \left(\frac{u}{\alpha_{12}} \phi\left(\frac{u}{u^*}\right) + \frac{v}{\alpha_{21}} \phi\left(\frac{v}{v^*}\right) \right) dx,$$

where $\phi(s) = s(\log s - 1) + 1$ for $s \geq 0$ and $(u^*, v^*) = (a_1/b_1, a_2/c_2)$ are homogeneous steady states. Then a computation shows that for all $t \geq s > 0$, since $b_2 = c_1 = 0$,

$$\begin{aligned} & \frac{dE_R}{dt} + C \int_{\Omega} (|\nabla \sqrt{u}|^2 + |\nabla \sqrt{v}|^2) dx \\ & \leq - \int_{\Omega} (b_1 u(u - u^*)(\log u - \log u^*) + c_2 v(v - v^*)(\log v - \log v^*)) dx \leq 0, \end{aligned}$$

where $C > 0$ depends on the diffusion coefficients. Now, if (u, v) is a stationary solution to the cross-diffusion system, clearly $dE_R/dt = 0$ and

$$\|\nabla \sqrt{u}\|_{L^2(\Omega)}^2 + \|\nabla \sqrt{v}\|_{L^2(\Omega)}^2 \leq 0.$$

Thus, u and v are constant in Ω . Since they satisfy the stationary equations, we conclude that $u(a_1 - b_1 u) = v(a_2 - c_2 v) = 0$ in Ω . Hence, either $u = 0$ or $u = a_1/b_1$ and either $v = 0$ or $v = a_2/c_2$. In both cases, (u, v) is a constant stationary solution.

Numerical approximation. There are only few papers concerned with the numerical discretization of the cross-diffusion system (7)-(8). The one-dimensional stationary problem was numerically solved in [48] using semi-implicit finite differences. The numerical experiments confirm that segregation of the species occurs for sufficiently large cross-diffusion parameters. As mentioned above, a semi-discretization in time was proposed in [49], and the

convergence of the semi-discrete solutions to a continuous one was proved. Barrett and Blowey [10] presented a convergence proof for a fully discrete finite-element approximation. Very recently, Gambino et al. [51] have discretized the one-dimensional problem by a particle approximation in space and an operator-splitting method in time together with an Alternating Direction Implicit (ADI) scheme.

5 Structured population models

The population models in the previous sections are based on the assumption that all individuals of a certain species are identical. However, populations typically consist of individuals which can be distinguished by various variables such as age, size, gender, etc. In this section we review some models which include an age or size structure, following [119, 121]. Other structured models can be found in [28, 100, 106].

Age-structured models. A model in which the vital rates depend on the age variable was first given by Sharpe and Lotka [130], known as the Lotka-McKendrick or McKendrick-von Foerster equation [46, 105]. Let $u(a, t)$ be the age density of a single-species population, where $a \geq 0$ is the age and $t \geq 0$ the time. Denote by $b(a)$ and $\mu(a)$ the birth and death rate, respectively, of the species of age a . Then the change $du = u_t dt + u_a da$ of the population of age a in a small increment of time dt equals $-\mu(a)u dt$ [113, Sec. 1.7]. Here, $u_t = \partial u / \partial t$ and $u_a = \partial u / \partial a$. The birth rate $b(a)$ only contributes to $u(0, t)$ since species are born at age $a = 0$. Dividing the equation for du by dt and noting that $da/dt = 1$ since a is the chronological age, $u(a, t)$ satisfies the following hyperbolic equation with a nonlocal boundary condition:

$$u_t + u_a + \mu(a)u = 0, \quad t > 0, \quad u(a, 0) = u_0(a), \quad a \geq 0, \quad (14)$$

$$u(0, t) = \int_0^\infty b(a)u(a, t)da, \quad t > 0. \quad (15)$$

This equation is sometimes referred to as the *renewal equation* since it describes how a population is renewed [59]. When we assume that the life span is finite, $a \in [0, a_+]$ with $a_+ < \infty$, this problem can be formulated as a Volterra equation of second kind (for the variable $B(t) := u(0, t)$), which is called the renewal or Lotka equation [64]. Using this formulation, it can be shown [64, 146] that the solution of the renewal equation has the asymptotic behavior $B(t) = B_0 \exp(\lambda t)(1 + o(t))$, where $B_0 \geq 0$, $\lambda \in \mathbb{R}$, and $o(t)$ tends to zero as $t \rightarrow \infty$. This means that the number of newborns changes exponentially with rate λ , at least for large time.

Mischler et al. [110] have proved the existence and long-time behavior of solutions to (14)-(15) without using a maximal life span condition (also see [121]). Their idea is to use a generalized relative entropy method. To illustrate this idea, we first observe that the death rate term can be eliminated via the

transformation $w(a, t) = e^{m(a)}u(a, t)$, where $m(a) = \int_0^a \mu(a)da$, since w solves the equation

$$w_t + w_a = 0, \quad a \geq 0, \quad t > 0.$$

Therefore, we may assume, without any loss of generality, that $\mu(a) = 0$. It is convenient to introduce the variable $v(a, t) = e^{-\lambda t}u(a, t)$, where (U, V, λ) with $U > 0$, $V \geq 0$, and $\lambda > 0$ are the first eigenlements of

$$\begin{aligned} U_a + \lambda U &= 0, \quad a \geq 0, \quad U(0) = \int_0^\infty B(a)U(a)da, \quad \int_0^\infty U(a)da = 1, \\ -V_a + \lambda V &= V(0)B(a), \quad a \geq 0, \quad \int_0^\infty U(a)V(a)da = 1. \end{aligned}$$

The function U is the eigenfunction associated with the operator in (15), with the first eigenvalue λ , and V is the eigenvector of the same eigenvalue associated with the adjoint operator. The factor $e^{-\lambda t}$ scales the population density in such a way that v stays bounded for all time. In other words, the population density grows exponentially with rate $\lambda > 0$, also called the Malthus parameter.

The following entropy inequality holds for all convex functions H satisfying $H(0) = 0$:

$$\int_0^\infty U(a)H\left(\frac{v(a, t)}{U(a)}\right)V(a)da \leq \int_0^\infty U(a)H\left(\frac{u_0(a)}{U(a)}\right)V(a)da, \quad t \geq 0.$$

This property allows one to show the long-time limit of $v(\cdot, t)$. The limit is expected to be proportional to the steady state U . In fact, if u_0 is bounded by U , up to a factor, it follows that [121, Sec. 3.6]

$$\lim_{t \rightarrow \infty} \int_0^\infty |v(a, t) - v_0 U(a)|V(a)da = 0,$$

where $v_0 = \int_0^\infty u_0 V da$. Exponential decay can be shown under a (restrictive) lower bound on the birth rate B [121, Sec. 3.7], and the decay rate depends on this lower bound.

To some extent, the Lotka-McKendrick model is an age-structured version of the Malthus model, introduced in Section 2. The drawback of both models is the unlimited exponential growth of the population. In the literature, many extensions and variants of the Lotka-McKendrick model have been proposed. Here, we mention some of them.

A simple model for a cell division cycle with a single phase is the following variant of the Lotka-McKendrick system [121, Sec. 3.9]:

$$u_t + u_a + \mu(a)u = 0, \quad t > 0, \quad u(0, t) = 2 \int_0^\infty \mu(a)u(a, t)da,$$

with the initial condition $u(\cdot, 0) = u_0$, where μ is the mitosis (cell division) rate. In this situation, a cell is withdrawn from the differential equation at age

a with the rate $\mu(a)$ and it creates two daughter cells at age $a = 0$ with the same rate. The (mathematical) advantage of this model is that its solutions decay exponentially fast to the steady state under the natural assumption that very young cells do not undergo mitosis (thus avoiding the restrictive assumption on B needed in the model (14)-(15)).

When the birth and death rates depend on certain variables (sizes) $s_1(t), \dots, s_m(t)$, which represent different ways of weighting the age distribution, we arrive at the system [119]

$$\begin{aligned} u_t + u_a + \mu(a, s_1, \dots, s_m)u &= 0, \quad a \geq 0, \\ u(0, t) &= \int_0^\infty b(a, s_1, \dots, s_m)u(a, t)da, \\ s_i(t) &= \int_0^\infty c_i(a)u(a, t)da, \quad i = 1, \dots, m, \quad t > 0, \end{aligned}$$

together with an initial condition for $u(\cdot, 0)$. For $i = 1$ and $c_1(a) = 1$, we obtain the *Gurtin-MacCamy model* introduced in [59]. The existence and uniqueness of solutions to this model is proved in [146] using a semigroup approach. A numerical analysis was performed in [139]. A special case is given by the logistic-growth model $i = 1$ with $\mu(a, s_1) = \mu_0(a)$. The age-specific fertility b is assumed to be nonnegative and decreasing with $b(a, \infty) = 0$. This means that the birth rate decreases when the weighted population average s_1 becomes larger.

In order to model the spatial dispersal of population species, one may include diffusive terms leading to equations of the form

$$u_t + u_a + \mu(a)u = \operatorname{div}(d\nabla u), \quad x \in \Omega, \quad a \geq 0, \quad t > 0,$$

where $d > 0$ is a diffusion coefficient and (Dirichlet or Neumann) boundary conditions for x have to be imposed on $\partial\Omega$. The population density u depends on the spatial variable x , the age a , and time t . One of the first works in this direction is due to Gurtin [58]. Gurtin and MacCamy [60] presented age-structured models with random diffusion or directed diffusion to avoid crowding. Mathematical results are presented, for instance, by MacCamy [99] who studies nonlinear diffusion processes yielding porous-medium-type diffusion equations. Di Blasio [14] proved the existence and uniqueness of solutions to age-structured diffusion models, and Busenberg and Iannelli [18] analyzed a degenerated diffusion problem. A finite-difference scheme was proposed by Lopez and Trigiante [93]. Kim and Park [75] used finite differences in the characteristic age-time direction and finite elements in the spatial variable. A variable time step method was chosen by Ayati [8], and Pelovska [120] developed an accelerated explicit scheme.

Size-structured models. For some organisms, age is not the most relevant parameter, but rather the cell mass or its size. This leads to size-structured population models in the size parameter x . In the following, we review some

models from [121]. We distinguish between symmetric mitosis (two daughter cells of size x emerge from a mother cell of size $2x$) and asymmetric mitosis (the emerging daughter cells have different size). In the symmetric case, the population number $u(x, t)$ may evolve according to

$$u_t + u_x + b(x)u(x, t) = 4b(2x)u(2x, t), \quad u(0, t) = 0, \quad u(x, 0) = u_0(x), \quad (16)$$

where $x \geq 0$, $t > 0$, and b is the birth rate. The factor 4 can be understood by computing the change of the population number,

$$\begin{aligned} \frac{d}{dt} \int_0^\infty u(x, t) dx &= 4 \int_0^\infty b(2x)u(2x, t) dx - \int_0^\infty b(x)u(x, t) dx \\ &= \int_0^\infty b(x)u(x, t) dx, \end{aligned}$$

which increases with rate $b(x)$. Similar to the age-structured model (14)-(15), the mathematical analysis relies on a certain eigenvalue problem with the first eigenvalue λ (the Malthus parameter) and the corresponding eigenfunctions U , V of the stationary and dual problem, respectively. Perthame and Ryzhik [122] proved that for constant birth rate $b(x) = b_0$, it holds $\lambda = b_0$, $V = 1$, and

$$\left\| e^{-b_0 t} u(\cdot, t) - U \int_0^\infty u_0 dx \right\|_{L^1(0, \infty)} \leq C e^{-b_0 t}, \quad t \geq 0,$$

and the constant $C > 0$ depends on the initial datum u_0 . A similar result holds for nonconstant birth rates, see [122]. For a numerical solution, we refer to [35].

When the mitosis is asymmetric, we have to change the term on the right-hand side of (16):

$$u_t + u_x + b(x)u(x, t) = \int_x^\infty \beta(x, y)u(y, t) dy.$$

This models the division of a mother cell of size y into two daughter cells of sizes x and $x - y$ with rate $\beta(x, y)$. Under suitable assumptions on b , β , and u_0 , the exponential decay of (a rescaled version of) $u(x, t)$ to the steady state is proved by Michel et al. [107]. Furthermore, an equation in which the effects of cell division and aggregation are incorporated by coupling the coagulation-fragmentation equation with the Lotka-McKendrick model was analyzed by Banasiak and Lamb [9].

In the literature, also size-structured models with $(v(u)u)_x$ instead of u_x in (16) and different expressions on the right-hand side have been employed, interpreting $v(u)$ as a growth rate, for instance in [71] for optimal harvest modeling and in [42, 43] for linear stability and instability results of stationary solutions. For more models and references, we refer to the monographs of Metz and Dieckmann [106] and Cushing [28].

6 Time-delayed population models

The change in the population number of a species may not respond immediately to changes in its population or that of an interacting species, but rather after a certain time lag. Time delay in population dynamics models, for instance, the gestation or maturation time of a species or the time taken for food resources to regenerate. Hutchinson [63] postulated the equation

$$\frac{du}{dt} = u(t)(a - bu(t - T)), \quad t > 0, \quad u(0) = u_0, \quad (17)$$

where $a, b > 0$, which was analyzed by May in [104]. Without delay, $T = 0$, we recover the logistic-growth equation with the stable steady state $u = a/b$. In case of delay, $T > 0$, May discovered an interplay between the stabilizing resource limitation and the destabilizing time lag. More precisely, if $aT < \pi/2$, $u = a/b$ is still a stable steady state, which becomes unstable if $aT > \pi/2$. When the time lag is not constant, one may employ the distributed delay equation

$$\frac{du}{dt} = u(t) \left(a - \int_{-\infty}^t b(t-s)u(s)ds \right), \quad t > 0, \quad u(0) = u_0.$$

The model of May was generalized and applied to the modeling of Australian sheep-blowfly populations by Gurney et al. [57]. Diffusive versions can be found in [138, 148]. Time delay may be used to model immature and mature stages; see [2] for an example. For the analysis of a system of delayed equations, we refer to [4]. More references can be found in the monograph of Kuang [81].

Spatial structures have been also considered in delayed models. A simple diffusive extension of the Hutchinson equation (17) is given by

$$u_t - \Delta u = u(t)(a - bu(t - T)).$$

More elaborate models have been proposed by Gourley and Kuang [54]. Gourley et al. [56] argue that diffusion and time delays are not independent of each other, since individuals may be at different points in space at past times. Britton [16] has suggested a delay term which involves a weighted spatial averaging over the (infinite) domain in order to account for the drift of the individuals from all possible positions at previous times to the present position. The equation becomes

$$u_t - \Delta u = u(1 + \alpha u - (1 + \alpha)g * u), \quad x \in \mathbb{R}^n, \quad (18)$$

where g is a given function and $g * u$ is a convolution in the spatio-temporal variables. The term αu represents the advantageous local aggregation due to high mating probability, for instance; the convolution $-(1 + \alpha)g * u$ with $\alpha > -1$ models the intra-specific competition due to resource limitations in a neighborhood of the original position. When g is a delta distribution, we

recover the Fisher equation (see Section 3). The particular choice $g(x) = e^{-|y|}$ is the Green's function for an ordinary differential equation, and (18) can be reduced to a system of two local equations analyzed by Billingham [13]. General kernels were considered by Deng [33], establishing the existence, uniqueness, and long-time behavior of solutions. Furthermore, Gourley and Britton [53] studied the linear stability of a related predator-prey system. Equation (18) is an example of a parabolic equation with a functional term; general nonlocal parabolic problems were treated by Redlinger [124].

Population models in bounded domains have been proposed by Gourley and So [55]. The nonlinear stability of traveling wavefronts in a related single-species model was proved by Li, Mei, and Wong [91]. Xu and Zhao [150] showed the existence of a global attractor of a nonlocal reaction-diffusion model with time delay. A survey on nonlocal population models, induced by time delays, and more references can be found in [56].

An equation with a time lag in the spatial variable has been proposed recently by Berestycki et al. [11] in order to study the impact of climate change on the dynamics of an affected species:

$$u_t - \Delta u = uf(x - cte, u), \quad x \in \mathbb{R}^n, \quad t > 0,$$

where c is a constant and e is a unit vector. The space dependence of the growth rate f is affected by the time under the action $x - cte$, i.e., the zones with favorable climate change shift in the direction e with speed c . Heuristically, we expect that populations manage to persist by migrating in the direction e . Indeed, it is shown in [12] that traveling wave solutions of the type $u(x, t) = v(x - cte)$ exist if the climate shift is not too large (i.e., $c > 0$ is sufficiently small), otherwise there is extinction.

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