

Spatial ecology via reaction-diffusion equations, by R. S. Cantrell and C. Cosner,
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This book is largely about reaction-diffusion systems such as

$$(1) \quad \begin{aligned} \frac{\partial u_i}{\partial t} &= d_i \nabla^2 u_i + u_i f_i(x, u), & x \in \Omega \\ 0 &= \alpha_i(x) \frac{\partial u_i}{\partial n} + \beta_i(x) u_i, & x \in \partial\Omega \\ u_i(x, 0) &= u_i^0(x), & x \in \Omega \end{aligned}$$

and what the analysis of such equations can say about spatial ecology. Here, $u_i(t, x)$ denotes the spatial density of some diffusing population at time t , u_i^0 denotes its initial density, and f_i denotes the specific growth rate of the i -th population, which may depend on location and on the densities of the other n populations at that location. For reasons discussed extensively in the book under review and mentioned briefly below, equilibrium solutions of (1), namely solutions of

$$(2) \quad \begin{aligned} 0 &= d_i \nabla^2 u_i + u_i f_i(x, u), & \Omega \\ 0 &= \alpha_i(x) \frac{\partial u_i}{\partial n} + \beta_i(x) u_i, & x \in \partial\Omega \end{aligned}$$

play a major role in the theory and applications.

The authors identify the principal advances in mathematical knowledge that have led to increased understanding of the dynamics of reaction-diffusion systems in general and to their application to ecology in particular. These include advances in bifurcation theory; the formulation of reaction-diffusion systems as dynamical systems; and, more generally, the adoption of the dynamical systems viewpoint in the study of evolution equations; the development of a theory of persistence, also called permanence, for dynamical systems models in population biology; and finally to the development of the theory of monotone systems.

Most readers will know that bifurcation theory has revolutionized the study of dynamics, but its early development focused primarily on steady states and how they change with model parameters. The equilibrium problem (2) takes the mathematical form of determining the structure of the set of solutions of $F(u, \lambda) = 0$ where λ denotes a parameter such as the size of the domain, carrying capacity, intrinsic growth rates, etc. The problem becomes particularly interesting near solutions (u_0, λ_0) where the hypotheses of the Implicit Function Theorem break down. From a biological perspective, this occurs when u_0 represents some proper subcommunity equilibrium of the full community and at a value of the parameter where this state changes stability type from stable to unstable due to potential invasion of the subcommunity by a “missing population”. It is this older theory, due to Crandall and Rabinowitz [4], which is useful in the present context, and the most striking results are the dependence of steady state solutions on the size of the habitat patch Ω .

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The formulation of reaction-diffusion systems as dynamical systems generating a semiflow on a suitable Banach space and the adoption of the dynamical systems viewpoint in the study of evolutionary PDEs—more precisely, the focus on the long-time behavior of solutions, and on stability, recurrence properties, and global attractors—is now standard following the work of Henry [7], Hale [5], Ladyzhenskaya [16], and many others. The system (1) induces a semi-dynamical system on the cone K of nonnegative functions in a Banach function space X (either $C^0(\overline{\Omega})^n$ or $C^1(\overline{\Omega})^n$ depending on boundary conditions): a map $\pi : K \times [0, \infty) \rightarrow K$ where $\pi(u^0, t)$ gives the state of the system at time t which starts ($t = 0$) at state u^0 . In (1), $u(\bullet, t) = \pi(t, u^0)$. The map π is continuous and satisfies the semigroup property $\pi(t, \pi(s, u^0)) = \pi(t + s, u^0)$ for $t, s \geq 0$ and $u^0 \in K$. The orbit of $u^0 \in K$ is $O(u^0) := \{\pi(u^0, t) : t \geq 0\}$, and its omega limit set, given by $\omega(u^0) = \{y \in K : \pi(u^0, t_n) \rightarrow y, t_n \nearrow \infty\}$, captures the asymptotic behavior of $O(u^0)$. If $O(u^0)$ has compact closure in K , then $\omega(u^0) \neq \emptyset$ is compact, connected, invariant ($\pi(\omega(u^0), t) = \omega(u^0)$), and $\text{Dist}(\pi(u^0, t), \omega(u^0)) \rightarrow 0$ as $t \rightarrow \infty$. An equilibrium e is a point of K such that $O(e) = \{e\}$. For (1), these are just the solutions of (2). The set of all equilibria for π is denoted by E . For scalar equations ($n = 1$) of the form (1), describing a single population, there is (when certain conditions are met) a Liapunov function V on K such that $t \rightarrow V(\pi(u^0, t))$ is nonincreasing and therefore $\omega(u^0) \subset E$ by the LaSalle Invariance Principle. This explains the importance of (2) for the dynamics of single populations.

The theory of persistence or permanence is, in my view, one of the truly significant ideas that mathematicians have recently contributed to theoretical population biology and to dynamics itself. Although we may be unable to determine the asymptotic behavior of high dimensional (more than two) models of multiple interacting biological populations, might it still be possible to answer the fundamental question of which populations survive in the long run without fully understanding the asymptotic behavior of every solution? This is the key question.

The extinction subset of our state space K consists of those points on the boundary of the cone ∂K where $u_i \equiv 0$ for some i , i.e., states where one or more populations are absent. The interior of K represents nonextinction states for which every population is present (everywhere), even if some are present only at very low densities. Points of ∂K not in the extinction set immediately enter the interior of K due to the nice effects of diffusion. Therefore, from a mathematical point of view, we want to decide if there is a compact invariant set A , situated a positive distance from ∂K , which attracts all states u^0 belonging to the interior of K : $\omega(u^0) \subset A$. This would provide reasonable assurance that all populations persist indefinitely provided they are initially present.

The authors (with V. Hutson) champion the stronger notion of ecological permanence for systems of PDEs such as (1) [3]. For Dirichlet boundary conditions (other boundary conditions may be more easily handled), this means that there exist smooth functions $e_i(x) > 0$ in Ω , vanishing on $\partial\Omega$ but with negative exterior normal derivative there, and positive numbers m, M such that for each initial data u^0 with $u_i^0 > 0$ in Ω for all i , there is a $t_0 > 0$ such that

$$(3) \quad me_i(x) \leq u_i(x, t) \leq M, \quad x \in \Omega, \quad t > t_0$$

for all i . It should be stressed that m, M are independent of the initial data, but t_0 may depend on it. Typically, e_i is the positive, unit-norm principal eigenvector of

$\nabla^2 u = \lambda u$ with Dirichlet boundary conditions on Ω . Ecological permanence follows from the existence of a compact attractor and permanence.

However, it may be that we are primarily interested in the survival of only a subcommunity of the full community. In that case, it's more appropriate to decompose our state space K into a disjoint union $X_1 \cup X_2$ such that X_1 represents extinction of one or more populations of the subcommunity of interest and X_2 represents the survival of all populations of the subcommunity. It is clearly mathematically important that X_2 be positively invariant ($\pi(X_2, t) \subset X_2$) so as to rule out extinction in finite time, but this is usually biologically trivial. The mathematical problem is the same: we want to show the existence of a compact attractor in X_2 , a positive distance from X_1 , which attracts all states in X_2 . We then say that the subcommunity is permanent or persists. Biologically, permanence of a subcommunity has the interpretation that if all member populations are initially present, then the dynamics is such that the set of ultimate states of the system is bounded away from extinction of the subcommunity. The fundamental idea of permanence has had an impact in theoretical population dynamics: it's now part of the language of the field. It is easy to imagine the underlying mathematical problem arising in dynamical systems models in other fields. For example, in cancer modelling does the cancer persist? In a model of HIV infection within a host, does the virus persist?

All this sounds nice, but we must be able to establish persistence in some way without a complete understanding of system dynamics since we cannot hope to have this knowledge for systems with an even moderate number of interacting populations. That this might be possible is suggested by the obvious necessary condition for permanence: namely that the stable manifold $W^s(I) = \{u \in K : \pi(u, t) \rightarrow I\}$ of each invariant set I (e.g., equilibrium, periodic orbit, etc.) belonging to the extinction set X_1 must not contain a point of X_2 : $W^s(I) \cap X_2 = \emptyset$, for then there would exist some nonextinction state whose ultimate state would be the extinction state I . If this condition were sufficient, it would mean that it essentially suffices to understand the behavior of $\pi|_{X_1}$; we need only find the I in X_1 . Presumably X_1 is a lower dimensional space, so we may be able to answer this question.

Unfortunately, this necessary condition for permanence is not sufficient. A striking counterexample is given by the symmetric three species Lotka-Volterra competition system of ODEs studied by May and Leonard [19], where species one beats species two in head-to-head competition, species three beats species one, and species two beats species three. Aside from an unstable coexistence state involving all three populations and its one-dimensional stable manifold, all other nonextinction states approach a heteroclinic cycle consisting of the three single-population equilibria $((1, 0, 0), (0, 1, 0), (0, 0, 1))$ and connecting orbits on the boundary of $K = \mathbb{R}_+^3$. Permanence fails due to an attracting heteroclinic cycle despite the fact that $W^s(I) \cap X_2 = \emptyset$ for each single-population equilibria I .

Another necessary condition for permanence, more or less built into the definition given above (but not in the usual definition of persistence), is that the system be dissipative in the sense that there exists a compact global attractor A for π . More precisely, A is compact, invariant and attracts bounded subsets of K . The necessity of some kind of dissipativity condition is clear from the well-known conservative Lotka-Volterra predator-prey model with a single positive neutrally stable steady state (a center) surrounded by periodic orbits of arbitrarily large size which approach arbitrarily close to the extinction set.

Despite the May-Leonard counterexample, the basic idea that one need only understand lower dimensional dynamics on the extinction sets to predict permanence prevailed. One approach to establishing permanence, after verifying the necessary condition $W^s(I) \cap X_2 = \emptyset$ holds for each invariant set I in the extinction set and that the system is dissipative, is to simply rule out potential cycles among the various invariant sets on the boundary since these are potential omega limit sets starting from nonextinction states. This is called the acyclicity approach to permanence. Clearly, it is a crude approach; far better would be to rule out only those cycles consisting of boundary states that attract nonextinction states, but determining easily checkable sufficient conditions for the latter is highly nontrivial (see [12]). It is simpler merely to rule out all cycles on the boundary. The acyclicity approach to permanence has been very successful in applications because boundary cycles are relatively rare. See Butler and Waltman [1], Butler, Freedman and Waltman [2], Hale and Waltman [6], Hutson and Schmitt [15], Thieme [26].

A second approach to permanence is to use a Lyapunov function. If one could find a function V that vanishes on the extinction set X_1 , is positive on X_2 , or perhaps only on a neighborhood of X_1 in X_2 , and that increases along orbits, then one should be able to establish that X_1 is a repeller and hence permanence. This works but is far too restrictive. If the dynamical system is dissipative, so that there is a compact global attractor, then it suffices to assume that K is compact. One really only need require that V be defined and positive on X_2 and that, roughly, $V(\pi(u, t))/V(u) > 1$ as $u \in X_2$ approaches a boundary invariant set I , uniformly in $t > 0$. This approach to permanence has also had its successes in applications. See Schuster, Sigmund, and Wolff [21], Hutson [14], Hutson and Schmitt [15]. However, it calls for intuition to select an appropriate Lyapunov function.

A good idea like permanence should be robust to perturbations in the dynamical system or equivalently to small changes in the reaction term f , boundary conditions, or any other parameters in the model. The basic formulation of permanence in terms of attractors suggests that it is robust. Schreiber [20] first established this for ODE models, and the general case was worked out in [11], [29].

From a practical point of view, the theory of permanence has allowed bi-mathematicians to make rigorous statements of importance to biologists about population models that include more populations than one would have thought possible to handle before. However, the required knowledge of the dynamics on the extinction set still sets bounds on our ability to handle large systems.

The theory of monotone dynamical systems, initiated by Hirsch [9] and Matano [18], has had a substantial impact in mathematical biology. Roughly, its focus is on semi-dynamical systems that preserve a partial order relation on the state space and the consequences of this order preservation on the asymptotic behavior of its solutions. The state space K is an order space: $u \leq v$ means $u(x) \leq v(x)$ for all $x \in \bar{\Omega}$. The semiflow π is order preserving, or monotone, if $u \leq v$ implies $\pi(u, t) \leq \pi(v, t)$, $t \geq 0$. Monotonicity alone is insufficient for there to be strong restrictions on asymptotic behavior of solutions. A stronger requirement, the so-called strong order preserving property (SOP), requires that monotonicity holds and if $u < v$ (i.e., $u \leq v$ and $u \neq v$), then there are neighborhoods U of u and V of v such that $\pi(u, t) < \pi(v, t)$ for all large t , and all $u \in U$ and $v \in V$. A state u is said to be quasiconvergent if $\omega(u) \subset E$ and to be convergent if $\omega(u) = \{e\}$ for some $e \in E$. Q denotes the set of all quasiconvergent points; C the set of all

convergent points. Assuming that every forward orbit has compact closure in K , an SOP semiflow has the following important property: Q is residual in K . With a bit more compactness (e.g., existence of a compact attractor) or if the order relation is particularly nice (e.g., compact invariant sets have supremum and infimum in K), one can show that Q contains an open and dense set. If the semiflow satisfies additional smoothness (say, C^1 in u with strongly positive and compact derivative), then C contains an open and dense set (Smith and Thieme [24], Smith [22], Hirsch and Smith [10]).

For reaction-diffusion systems, the well-known (strong) maximum principle implies the SOP property for scalar equations satisfying the usual boundary conditions. However, there is a strong restriction on the “reaction” vector field f for a system of reaction-diffusion equations to be SOP relative to the usual component-wise ordering. Namely, its Jacobian Df_u should be “cooperative”, $\frac{\partial f_i}{\partial u_j} \geq 0$ for $i \neq j$, and irreducible. Since cooperation is relatively rare in natural populations, this restriction would seem to limit the application of the theory of monotone systems. This, however, is only due to an unimaginative choice of partial orders. Consider, for example, two competing species A and B . One can increase the growth rate of species A by either decreasing the population of its competitor B or by increasing the number of its own kind. The same reasoning applies to the growth rate of B . Thus, if u and v denote the density of A and B respectively, then the natural partial order for two-species competition is $(u, v) \leq (u', v')$ if and only if $u \leq u'$ and $v \geq v'$. What about three species competition between competing species A, B, C ? Decreasing the population of C now has a mixed effect on species A . Besides having the same beneficial effect noted above, it has a deleterious effect on A due to its positive effect on A 's competitor, B ! A friend of an enemy is an enemy. Consequently, there is no natural order relation for three-species competition or, for that matter, for competition involving more than two competitors.

So we see that for two-species competition, there is a natural partial order relation, and sufficient conditions for the semiflow π defined by (1) to be SOP with respect to this order relation is that $\frac{\partial f_i}{\partial u_j} < 0$ for $i \neq j$. This is precisely the mathematical expression of competition. Consequently, we need only study the equilibria determined by (2) and their stability properties to understand the dynamics for two-species competition.

The reader may be familiar with the Lotka-Volterra ODE competition model whose phase plane is now a standard figure in nearly all elementary ecology texts. There are four possible outcomes: (1) competitive exclusion whereby species A goes extinct regardless of the initial data; (2) species B goes extinct regardless of the initial data; (3) a coexistence equilibrium attracts all initial data for which both populations are present; and (4) bistability: a (saddle-type) coexistence equilibrium exists but is unstable, its stable manifold separating the basins of attraction of the two attracting, single-population equilibria. That this simple Lotka-Volterra paradigm of two-species competition holds for many two-species competition models regardless of whether they arise from ODEs, PDEs, delay differential, or difference equations is biologically plausible but quite remarkable. Lazer and Hess [8] were the first to take an abstract approach to competition by supposing it to be governed by a semiflow π on a product space $K_1^+ \times K_2^+$, where K_i^+ is the positive cone in the ordered Banach space X_i , which is monotone relative to the natural competition ordering on $X_1 \times X_2$. The goal is to show that the only dynamical outcomes are

the Lotka-Volterra alternatives. This has been partially successful (simple examples show it cannot always be true) and has been refined by a number of authors [13], [23], [25], [27], [17].

Most of the ideas described above are contained in this book, which is built around the results of the authors' remarkable research collaboration on spatial models in ecology over nearly twenty years. This work is both mathematically rigorous and biologically insightful. There is a very nice review of the gamut of spatial models from meta-populations to interacting particle systems in addition to reaction-diffusion systems. Starting with this overview of spatial models and a well-motivated exposition of the mathematical background for reaction-diffusion systems, single-population models are taken up, first in linear models and later in nonlinear ones, including the logistic equation and consideration of Allee effects. It is remarkable what one can learn from linear models but even more important is that all stability considerations boil down to the principle eigenvalue of an elliptic eigenvalue problem which inevitably depends on a myriad of biologically important parameters. Discovering monotonicity properties of this eigenvalue with respect to variation of these parameters is crucial for biological insight; much of the analysis in this book revolves around these calculations. Later chapters treat multiple populations, Lotka-Volterra competition between two competitors occupying a good portion of this. Permanence theory is extensively treated and applied to spatial models. The reader will learn about critical patch size for maintenance of a single population, how spatial segregation may facilitate coexistence of populations, how habitat shape effects the outcome of competition, and the effects of boundary conditions and "edge effects" on populations. A strength of this book is its mathematical depth and the fact that the treatment is relatively self-contained.

No books are completely free of glitches, yet this one has remarkably few. There is an oversight in Theorem 4.3 (Acyclicity Test for Persistence) in the sense that the set $\omega(S)$ is incorrectly identified in the text leading up to the statement of the result. It should be the union of the omega limit sets of all points of S rather than the omega limit set of S as a set, as defined in Chapter 1. The former is usually a finite set, while the latter is typically infinite. For the May-Leonard example, the omega limit set of S , as defined in Chapter 1, consists of the intersection of the unstable manifold of the trivial equilibrium and the boundary of the positive orthant, a union of three two-dimensional triangular sets, while the correct interpretation of $\omega(S)$, as noted in the author's discussion below Theorem 4.3, consists of the 4 boundary equilibria.

In summary, this book will be useful to graduate students and researchers who wish to learn the mathematical techniques required in the study of reaction-diffusion systems and their applications to spatial models of population biology.

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