VI Southern-Summer School on Mathematical Biology

Mathematical Theory of Biological Invasions

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Overall goals

- To give you an overview of the subject: what it is all about. To consider several real-world examples and instructive case-studies
- To introduce you to the array of mathematical approaches used to study biological invasions
- Starting from simple examples and basic modeling tools, to bring you to the frontiers in this field

Interdisciplinary Applied Mathematics 44

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Jonathan R. Potts

The Mathematics Behind Biological Invasions

MPE

Springer

Outline of the course

- Introduction & a glance at field data
- Overview of mathematical tools
- Diffusion-reaction systems
    - Single-species system: traveling waves, the problem of critical domain, effects of environmental heterogeneity
    - Predator-prey system and the problem of biological control: traveling waves and pattern formation
    - Beyond the traveling waves: patchy invasion
- Lattice models
- Kernel-based models (integro-difference equations): fat-tailed kernels, “superspread”, pattern formation
- Extensions, discussion, conclusions

Chapter I

Introduction and examples

General

Biological invasion begins when a new, “alien” or exotic species is brought into a given ecosystem.

Ecology is a science that studies species living in their natural environment. It focuses on the species interaction between themselves and with the abiotic factors. Ecology aims to understand the principles and mechanisms of population’s spatiotemporal organization and to identify factors that may affect species abundance.

Mathematical ecology is application of the tools and techniques of mathematics to ecological problems.

Why biological invasion?

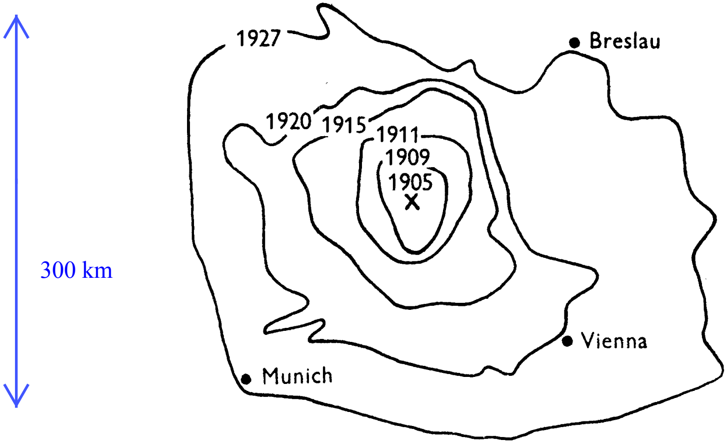
The term biological invasion is a common name for a variety of phenomena related to introduction and spatial spread of alien or exotic species, i.e., species that have not been present in a given ecosystem until they are brought in.

Consequences of species invasion:

1. A new species often becomes a pest and that can result in huge economic losses. For instance, economic loss from the invasion of insect pests in the USA for the period from 1906 to 1991 is estimated to be $ 92 billion (U.S. Office of Technology Assessment, 1993).

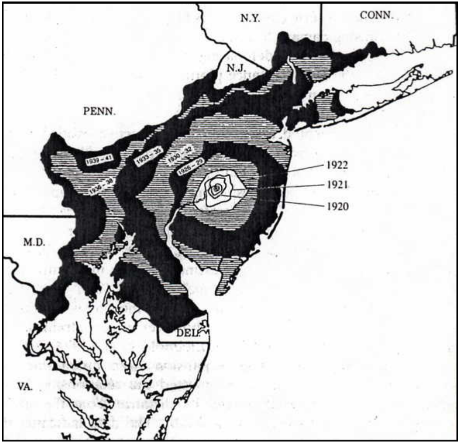
2. Severe damage to biodiversity.

A glance at the data I: muskrat in Europe

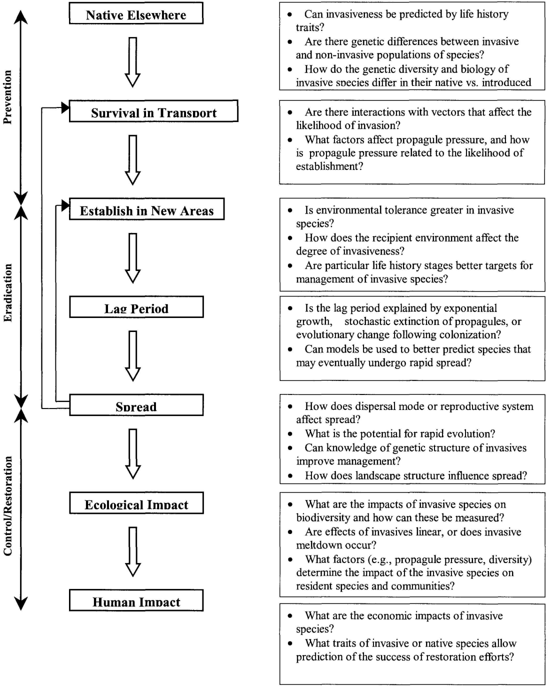


(Skellam, 1951)

A glance at the data II: Japanese beetle in the USA



(United States Bureau of Entomology and Plant Quarantine, 1941)



Prevention

Eradication

Control/Restoration

Native Elsewhere

- Can invasiveness be predicted by life history traits?
- Are there genetic differences between invasive and non-invasive populations of species?
- How do the genetic diversity and biology of invasive species differ in their native vs. introduced

Survival in Transport

- Are there interactions with vectors that affect the likelihood of invasion?
- What factors affect propagule pressure, and how is propagule pressure related to the likelihood of establishment?

Establish in New Areas

- Is environmental tolerance greater in invasive species?
- How does the recipient environment affect the degree of invasiveness?
- Are particular life history stages better targets for management of invasive species?

Lag Period

- Is the lag period explained by exponential growth, stochastic extinction of propagules, or evolutionary change following colonization?
- Can models be used to better predict species that may eventually undergo rapid spread?

Spread

- How does dispersal mode or reproductive system affect spread?
- What is the potential for rapid evolution?
- Can knowledge of genetic structure of invasives improve management?
- How does landscape structure influence spread?

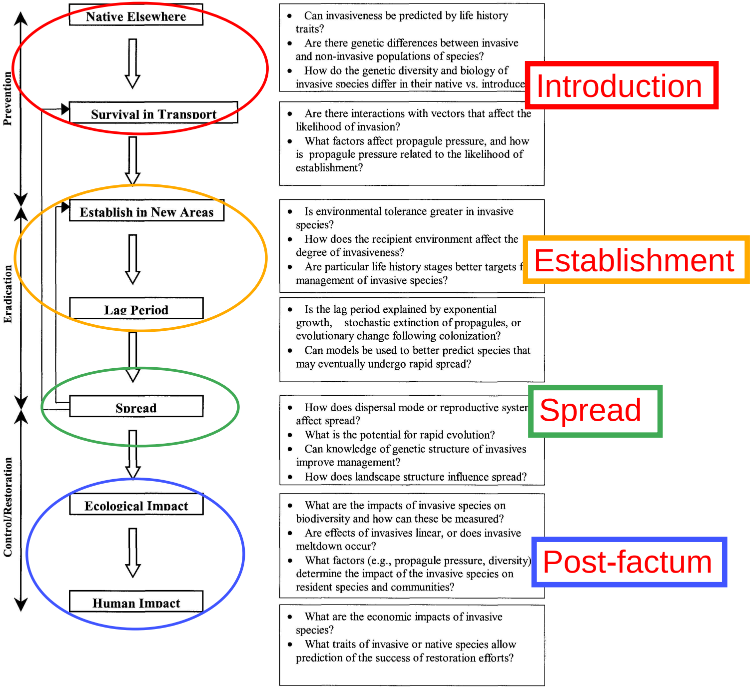
Ecological Impact

- What are the impacts of invasive species on biodiversity and how can these be measured?
- Are effects of invasives linear, or does invasive meltdown occur?
- What factors (e.g., propagule pressure, diversity) determine the impact of the invasive species on resident species and communities?

Human Impact

- What are the economic impacts of invasive species?
- What traits of invasive or native species allow prediction of the success of restoration efforts?

(Sakai et al., 2001)



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Post-factum

Human Impact

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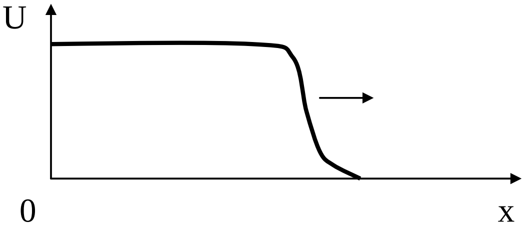
The stage of geographical spread

Spread of the introduced species over space:



(U is the population density)

Fisher, 1937: existence of the traveling population front

Kolmogorov, Petrovskii & Piskunov (KPP), 1937:
convergence of the initial condition to the traveling front

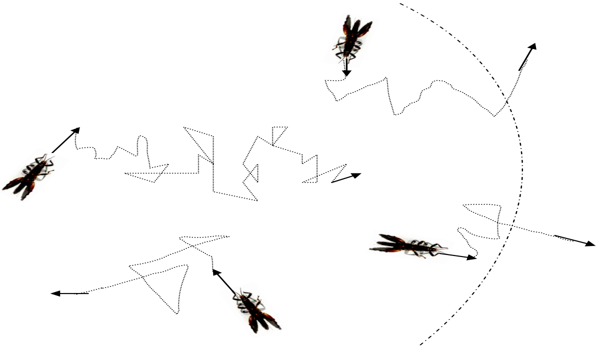
Chapter II

Overview of mathematical tools

Overview of mathematical tools

- Individual-based or mean-field?

In the individual-based modelling (IBM), each individual is described and modelled explicitly (e.g. as given by certain rules):



Overview of mathematical tools

- Individual-based or mean-field?

In the mean-field approach, ecosystem's state is described by an array of its state variables:

$$\Omega = \{U_1(\mathbf{r},t),\ \dots,\ U_N(\mathbf{r},t),\ \alpha_1(\mathbf{r},t),\ \dots,\ \alpha_M(\mathbf{r},t)\}\ .$$

Typically, U_i is the population density of the ith species, and $\alpha_1,\ \dots,\ \alpha_M$ are 'parameters' (e.g. the growth rates).

Depending on the spatial scale, some of the components may be better described as discrete.

Mathematical tools: **nonspatial systems**

How to account for different reproduction systems?

Time-continuous systems (overlapping generations):

$$\frac{dU_i(t)}{dt} = f_i(U_1, \ldots, U_n), \quad i = 1, \ldots, N \; .$$

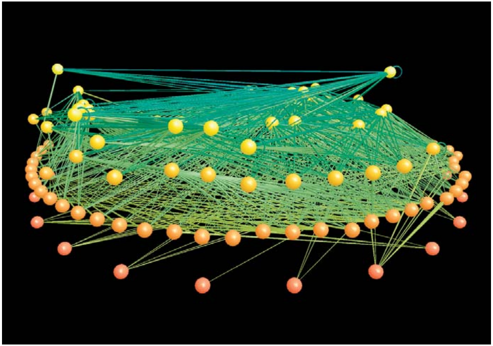
where N is the number of species included into the model.

Time-discrete systems (non-overlapping generations):

$$U_i(t+T) = f_i(U_1(t), \ldots, U_N(t)), \quad i = 1, \ldots, N \; ,$$

What are the values of N reasonable for modeling?

Ecological communities usually consist of many species linked together into a complicated food web:



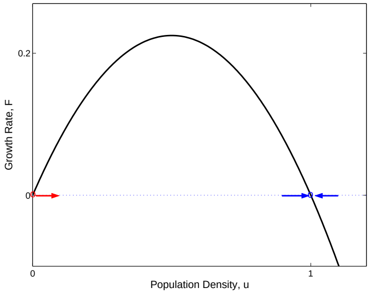
(Lake food web, from Pascual 2005)

Remarkably, however, many important insights can be made based on simple few-species models.

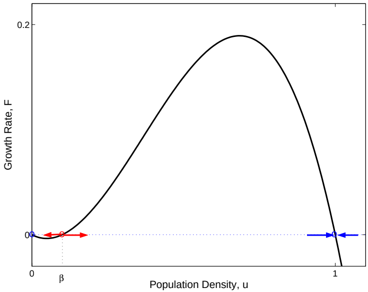
Example 1: single-species system

$$\frac{dU(T)}{dT} = f(U)$$

Logistic growth



Strong Allee effect



$$f(U) = \alpha U(K - U)$$

$$f(U) = \gamma U(U - \beta)(K - U)$$

Example 2: predator-prey system

$$\begin{aligned} \frac{dU(T)}{dT} &= P(U) - E(U,V) , \\ \frac{dV(T)}{dT} &= \kappa E(U,V) - \mu(V) , \end{aligned}$$

where U and V are prey and predator densities.

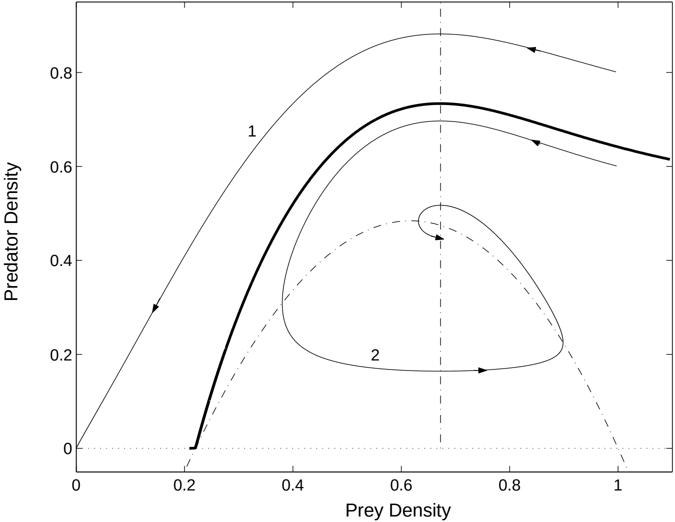
Prey growth rate P can be logistic or with the Allee effect.

Predation E can also have different properties, for instance:

$$E(U,V) = A\frac{UV}{U+H} \qquad \text{or} \qquad E(U,V) = A\frac{U^2V}{U^2+H^2} ,$$

that is, Holling type II and Holling type III, respectively.

Predator-prey system can have complicated properties!



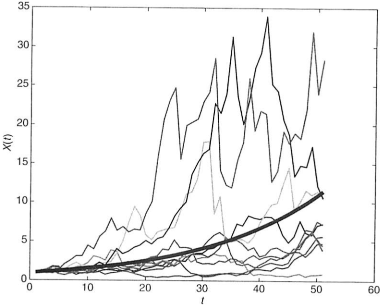
Deterministic or stochastic?

The impact of stochastisity can be described as a noise applied to the 'deterministic skeleton,' for instance:

$$\frac{dU(t)}{dt} = f(U) + \xi(t)U \, .$$

where $U(t)$ is the population size and ξ is a random variable.

How the system will behave?



A fundamental result (**Central Limit Theorem**):

the relative magnitude of the fluctuations decreases as the number of individuals increases!

> “Large scale random phenomena
> in their collective action create
> strict, non random regularity.”
>
> (Gnedenko & Kolmogorov, 1954)

- Population dynamics is intrinsically stochastic, but that does not necessarily mean that the model must be stochastic.

- I will mostly focus on deterministic models

Mathematical tools: **spatial systems**

Time-discrete and space-continuous, IDEs:

$$U_i(x, t+T) = \int_{-\infty}^{\infty} K(x-\xi) f_i(U_1(\xi, t), \ldots, U_n(\xi, t)) d\xi \ .$$

Time- and space-continuous, “**diffusion-reaction**” PDEs:

$$\frac{\partial U_i(\mathbf{r}, t)}{\partial t} = D_i \nabla^2 U_i(\mathbf{r}, t) + f_i(U_1, \ldots, U_n) \ .$$

Time- and space-discrete: Coupled Maps Lattices.

Dynamical systems' approach to invasion

Native community before invasion:

$$\frac{dU_i(t)}{dt} = f_i(U_1, \ldots, U_n), \quad i = 1, \ldots, N \, . \qquad (1)$$

As a result of invasion, a new species U_{n+1} is added:

$$\frac{dU_i(t)}{dt} = f_i(U_1, \ldots, U_n, U_{n+1}), \quad i = 1, \ldots, N, (N+1) \, . \qquad (2)$$

Invasion will be successful if the system (2) allows for the existence of an attractor such as $U_{n+1}(T) > 0$, for instance, a stable steady state:

$$(\bar{U}_1, \bar{U}_2, \ldots, \bar{U}_n, \bar{U}_{n+1}) \quad \text{with} \quad \bar{U}_{n+1} > 0 \, .$$

Questions to be asked (and answered)

- How likely the new species will establish in the new environment?
- Will it start spreading and, if yes, how soon after the introduction? – How large can be the gap?
- What are the rate and pattern of spread?
- What are the mechanisms of spread?
- Can we control the rate of spread?
- Can we eradicate the invading species?

Chapter III

PDE models of biological invasion:
Single-species system

How can we build a model?

What we need is to keep the balance of mass:

$$\left(\begin{array}{c} \textit{Change in the} \\ \textit{population density} \end{array} \right) = \left(\begin{array}{c} \textit{Local} \\ \textit{growth} \end{array} \right) + \textit{Dispersal}$$

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Translate it to the mathematical language:

$$\frac{\partial U(X,T)}{\partial T} = f(U) + D\frac{\partial^2 U}{\partial X^2},$$

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Translate it to the mathematical language:

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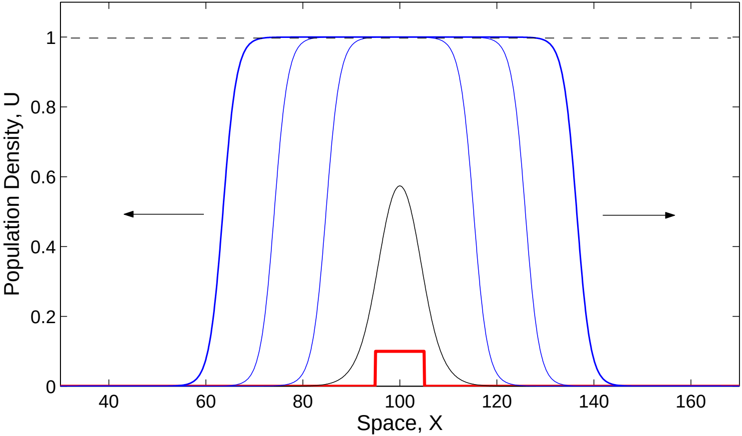
Biological invasion is accounted for by finite initial conditions:

$$\begin{aligned} u(x,0) &= \Phi(x) \geq 0 \quad \text{for} \quad x_1 \leq x \leq x_2, \\ u(x,0) &= 0 \ \text{ for } \ x < x_1 \ \text{ and } \ x > x_2 \geq x_1. \end{aligned}$$

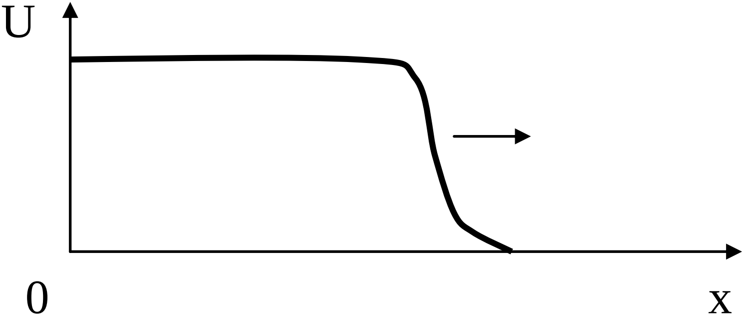
The corresponding conditions at infinity: $U(X \to \pm\infty, t) = 0$.

Consider the evolution of the initial conditions.

Easy to do using computer simulations:



The solution eventually converges to a travelling front:



Single-species model

$$\frac{\partial U(X,T)}{\partial T} = D\frac{\partial^2 U}{\partial X^2} + f(U), \tag{3}$$

where $f(0) = f(K) = 0$ and $f(U) \geq 0$ for $0 < U < K$,

with corresponding conditions at infinity:

$$U(X \to -\infty, t) = K, \qquad U(X \to \infty, t) = 0.$$

Single-species model

$$\frac{\partial U(X,T)}{\partial T} = D\frac{\partial^2 U}{\partial X^2} + f(U), \tag{4}$$

where $f(0) = f(K) = 0$ and $f(U) \geq 0$ for $0 < U < K$,

with corresponding conditions at infinity:

$$U(X \to -\infty, t) = K, \qquad U(X \to \infty, t) = 0.$$

Traveling wave solution – change of variables:

$$U(x,t) = \phi(\xi) \quad \text{where} \quad \xi = x - ct$$

where c is the speed of the wave.

The shape of the front does not change with time!

Using the chain rule,

$$\frac{d}{dx} = \frac{d}{d\xi}, \qquad \frac{d^2}{dx^2} = \frac{d^2}{d\xi^2}, \qquad \frac{d}{dt} = -c\frac{d}{d\xi},$$

the partial differential equation (4) turns into an ODE:

$$D\frac{d^2\phi(\xi)}{d\xi^2} + c\frac{d\phi(\xi)}{d\xi} + f(\phi) = 0, \tag{5}$$

where

$$\phi(\xi \to -\infty) = K, \qquad \phi(\xi \to \infty) = 0.$$

What is the direction of the front propagation:

invasion or retreat?

We multiply Eq. (5) by $\frac{d\phi}{d\xi}$ and integrate it over the whole line:

$$D\int_{-\infty}^{\infty}\frac{d^2\phi}{d\xi^2}\left(\frac{d\phi}{d\xi}\right)d\xi+c\int_{-\infty}^{\infty}\left(\frac{d\phi}{d\xi}\right)^2 d\xi+\int_{-\infty}^{\infty}f(\phi)\left(\frac{d\phi}{d\xi}\right)d\xi=0.$$

Note that

$$\int_{-\infty}^{\infty}\frac{d^2\phi}{d\xi^2}\left(\frac{d\phi}{d\xi}\right)d\xi=\frac{1}{2}\int_{-\infty}^{\infty}\frac{d}{d\xi}\left(\frac{d\phi}{d\xi}\right)^2=\frac{1}{2}\left(\frac{d\phi}{d\xi}\right)^2\Bigg|_{-\infty}^{\infty}=0,$$

and

$$\int_{-\infty}^{\infty}f(\phi)\left(\frac{d\phi}{d\xi}\right)d\xi=\int_{K}^{0}f(\phi)d\phi=-\int_{0}^{K}f(\phi)d\phi\,.$$

We therefore obtain:

$$c \int_{-\infty}^{\infty} \left(\frac{d\phi}{d\xi} \right)^2 d\xi = \int_0^K f(\phi) d\phi \ \equiv \ M.$$

Note that

$$\int_{-\infty}^{\infty} \left(\frac{d\phi}{d\xi} \right)^2 d\xi > 0.$$

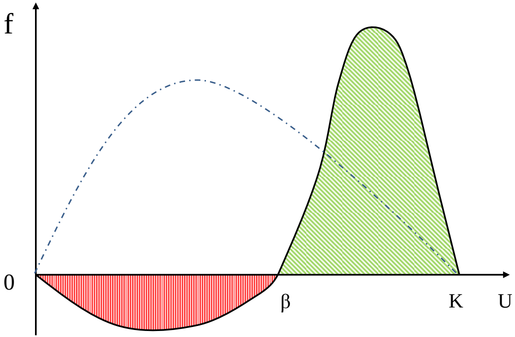
Therefore,

$$c \ \sim \ M, \qquad \text{sign}(c) = \text{sign}(M) \ .$$

Direction of front propagation is defined by the sign of M.

In case of logistic growth invasion is always successful: the front propagates from the area where the species is abundant, $U = K$, towards the area where the species is absent, $U = 0$.

However, in case of the strong Allee effect, it is not necessarily so:



M>0: invasion success, species spread

M<0: invasion failure, species retreat

What can we tell about the value of c?

Consider the solution far in front of the front, i.e. where ϕ is small; then,

$$f(\phi) \approx \alpha\phi$$

and Eqn. (5) becomes linear:

$$D\frac{d^2\phi(\xi)}{d\xi^2} + c\frac{d\phi(\xi)}{d\xi} + \alpha\phi = 0, \tag{6}$$

and its general solution is known:

$$\phi(\xi) = C_1 e^{\lambda_1 \xi} + C_2 e^{\lambda_2 \xi},$$

where $\lambda_{1,2}$ are the solutions of the characteristic equation:

$$D\lambda^2 + c\lambda + \alpha = 0,$$

so that

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

We are only interested in solutions that are nonnegative, which means that the solution cannot oscillate around zero, which means that $\lambda_{1,2}$ cannot be complex.

Thus, we obtain $c^2 - 4\alpha D \geq 0$, so that

$$c \geq c_{min} = 2\sqrt{\alpha D}.$$

There are no slow waves!

It only works if $\alpha > 0$, i.e. when there is **no** strong Allee effect!

The actual value of the speed depends on the initial condition. For ecologically meaningful compact initial conditions, $c = c_{min}$.

In case of the Allee effect, things are different.

For a general $f(u)$, the wave speed is not known.

Consider a specific but meaningful case:

$$f(u) = \gamma U(U-\beta)(K-U),$$

so that Eq. (5) for the traveling wave takes the form:

$$D\frac{d^2\phi(\xi)}{d\xi^2} + c\frac{d\phi(\xi)}{d\xi} + \gamma\phi(\phi-\beta)(K-\phi) = 0. \qquad (7)$$

If we look for a monotone front, then $\frac{d\phi}{d\xi} = \psi(\phi)$,
where ψ is a certain (unknown) function.

Consider the following ansatz:

$$\frac{d\phi}{d\xi} \overset{1}{=} \psi(\phi) \overset{2}{=} a\phi(\phi - K) \ ,$$

and substitute it into Eq. (7), taking into account that

$$\frac{d^2\phi(\xi)}{d\xi^2} = \frac{d}{d\xi}\left(\frac{d\phi}{d\xi}\right) = \frac{d\phi}{d\phi} \cdot \frac{d\psi(\phi)}{d\xi} = \frac{d\phi}{d\xi} \cdot \frac{d\psi(\phi)}{d\phi} = \psi \frac{d\psi(\phi)}{d\phi}.$$

Equation (7) then turns into

$$Da^2\phi(\phi - K)(2\phi - K) + ca\phi(\phi - K) + \gamma\phi(\phi - \beta)(K - \phi) = 0,$$

or, after obvious simplifications,

$$(2Da^2 - \gamma)\phi + (ca - KDa^2 + \gamma\beta) = 0. \qquad (8)$$

Equation (8) holds for any ϕ, which is only possible if

$$2Da^2 - \gamma = 0 \qquad \text{and} \qquad ca - KDa^2 + \gamma\beta = 0,$$

from which we obtain $a = \sqrt{\gamma/(2D)}$ and the speed:

$$c = \left(\frac{D\gamma}{2}\right)^{1/2} (K - 2\beta).$$

We therefore observe that $c > 0$ (invasion) for $\beta < \frac{1}{2}K$, but $c < 0$ (retreat) for $\beta > \frac{1}{2}K$.

Note that, since $f(U)$ is a cubic polynomial, this is equivalent to $M > 0$ and $M < 0$, respectively.

Note that, considering the ansatz as the ODE for $\phi(\xi)$,

$$\frac{d\phi}{d\xi} = a\phi(\phi - K) \ ,$$

we can easily obtain the exact solution of the problem:

$$U(x - ct) = \phi(\xi) = \frac{K}{1 + A \exp(aK\xi)}$$

where A is an arbitrary constant depending on the initial position of the front.

Thus, ansatz is a powerful method to find a special solution of the problem.

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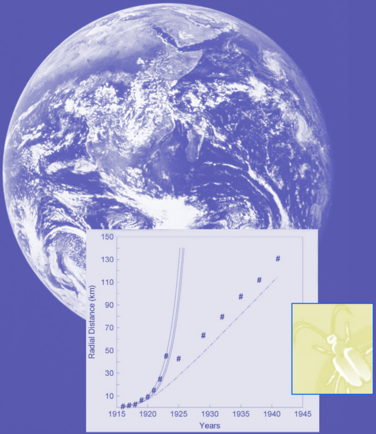
EXACTLY SOLVABLE MODELS OF BIOLOGICAL INVASION



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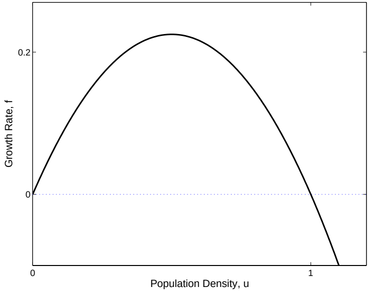
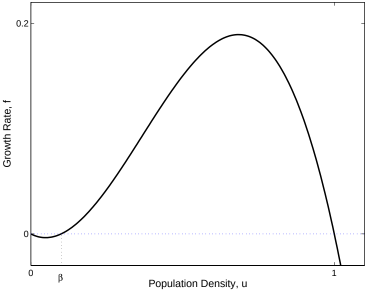
Single-species invasion – a brief summary

$$\frac{\partial U(X,T)}{\partial T} = D\frac{\partial^2 U}{\partial X^2} + f(U)$$



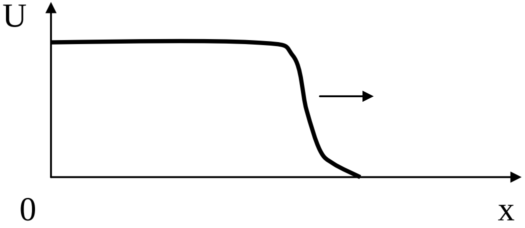
Logistic growth



Strong Allee effect

Single-species invasion – a brief summary

Spread of the introduced species over space:



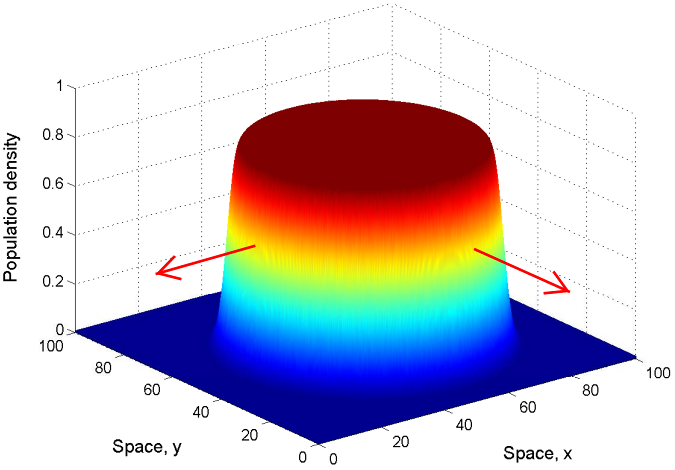
$$c \;=\; 2\sqrt{Df'(0)}$$

Logistic growth

$$c \sim \int_0^K f(U)dU$$

Strong Allee effect

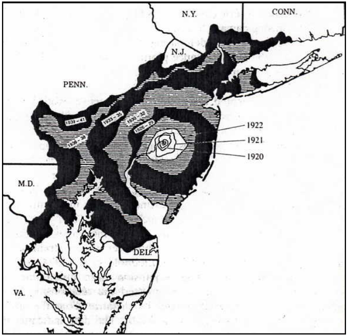
Single-species invasion in a 2D space

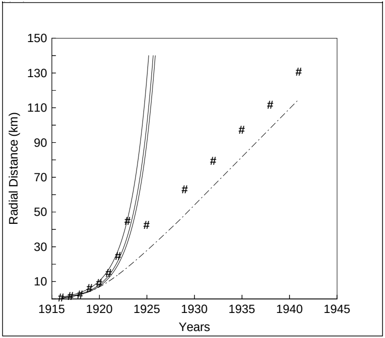


Example of historical data

In many cases, this simple model works very well.

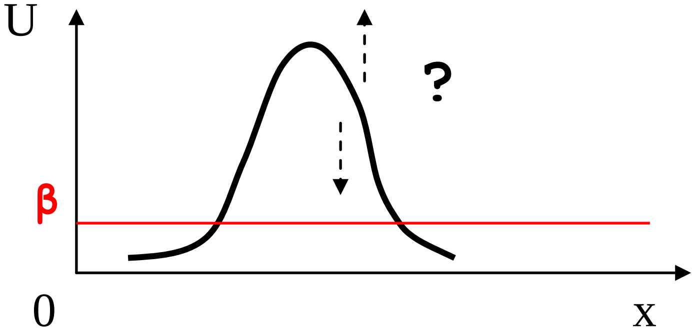
Invasion of Japanese beetle in the United States:





(Petrovskii & Shigesada, 2001)

Stage of species establishment

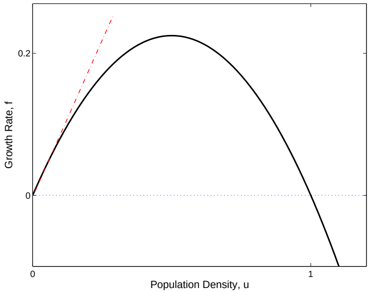


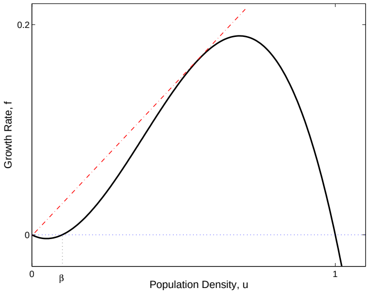
The species will only survive if its maximum density remains above a certain critical threshold β.

A Very Simple Model

$$\frac{\partial U(X,T)}{\partial T} = D\frac{\partial^2 U}{\partial X^2} + \alpha U \tag{9}$$

$$(-\infty < X < \infty, \quad T > 0)$$





Solution of Eq. (9) therefore gives an upper bound for the solution of the corresponding nonlinear equation.

(by virtue of the comparison principle)

A Very Simple Model

Consider the following initial condition

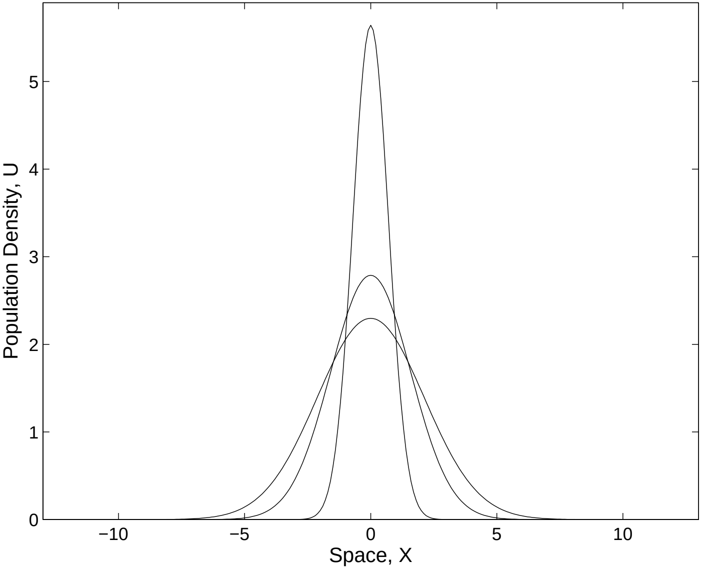
$$U(X,0) = \frac{G}{\sqrt{4\pi\delta^2}} \exp\left(-\frac{X^2}{4\delta^2}\right),$$

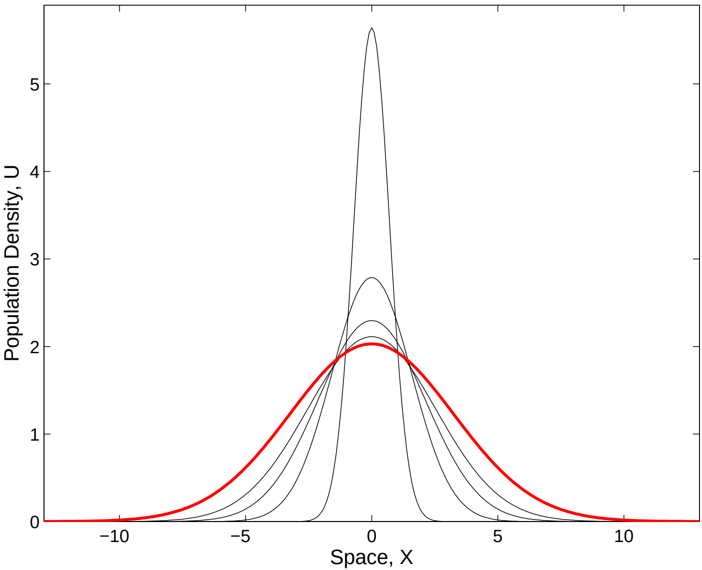
where G is the total initial population size, δ is the width and $U_0 = G(4\pi\delta^2)^{-1/2}$ is the height of the distribution.

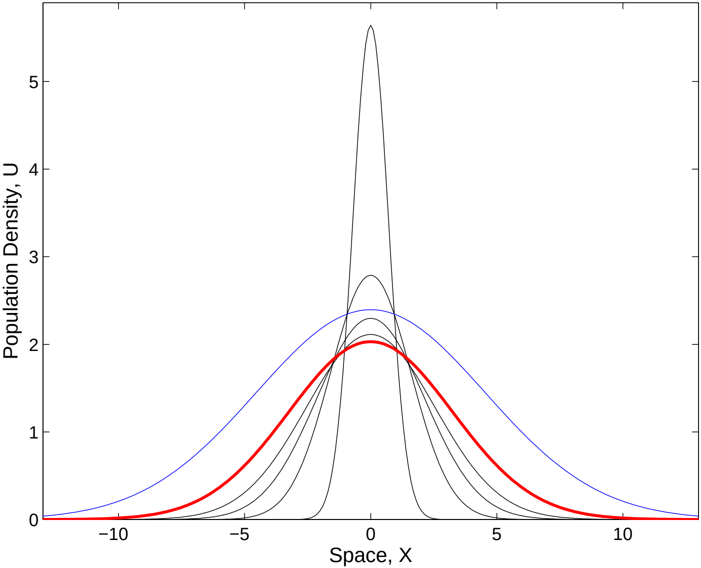
It is readily seen that the corresponding solution of the linearized diffusion-reaction equation (9) is

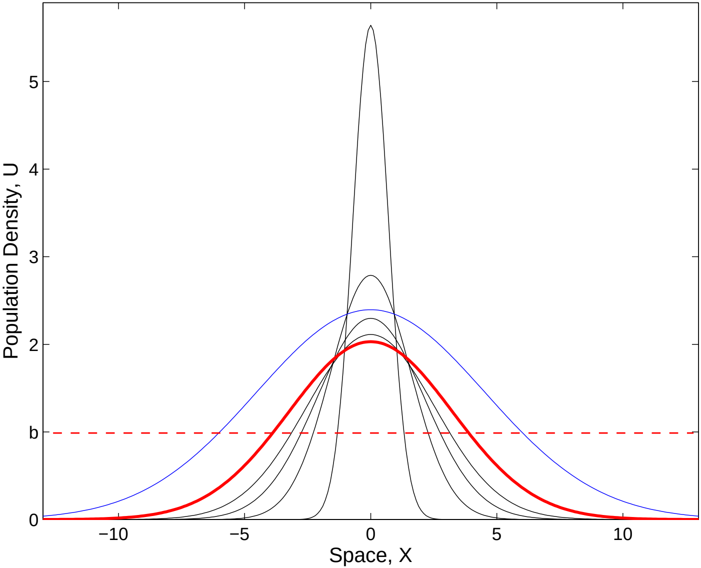
$$U(X,T) = \frac{G}{\sqrt{4\pi(\delta^2 + DT)}} \exp\left(-\frac{X^2}{4(\delta^2 + DT)} + \alpha T\right).$$

What are the properties of this solution?


Population Density, U
5
4
3
2
1
0
−10
−5
0
5
10
Space, X


Population Density, U
Space, X
0
1
2
3
4
5
−10
−5
0
5
10


Population Density, U
0
1
2
3
4
5
−10
−5
0
5
10
Space, X


Population Density, U
5
4
3
2
b
0
−10
−5
0
5
10
Space, X

Obviously, the solution has its maximum $U_m(T)$ at $X = 0$:

$$U_m(T) = \frac{G \exp(\alpha T)}{\sqrt{4\pi(\delta^2 + DT)}} \ ,$$

which reaches its minimum at a certain $T_* \geq 0$:

$$U_* = \min_T U_m(T) = U_m(T_*) \ .$$

Therefore, all we need to do is to compare U_* with the extinction threshold β.

It is readily seen that

$$T_* = \frac{1}{2\alpha} - \frac{\delta^2}{D} \ .$$

Correspondingly, we obtain:

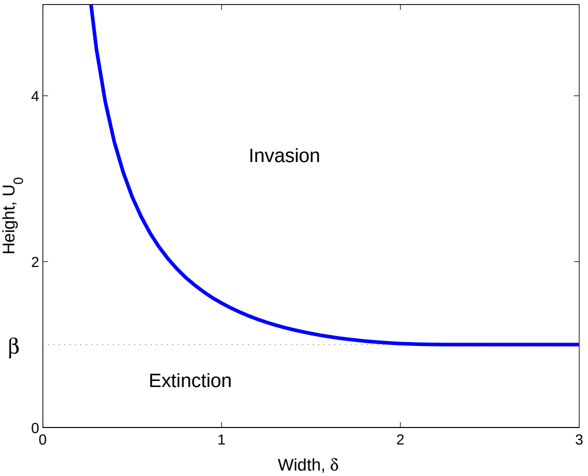
$$\begin{aligned} U_* &= U_m(T_*) \quad \text{for} \quad \delta < \delta_* = \sqrt{\frac{D}{2\alpha}} \ , \\ U_* &= U_0 \quad \text{for} \quad \delta \geq \delta_* \ , \end{aligned}$$

where

$$U_m(T_*) = G\sqrt{\frac{\alpha}{2\pi D}} \exp\left(\frac{1}{2} - \frac{\alpha\delta^2}{D}\right) .$$

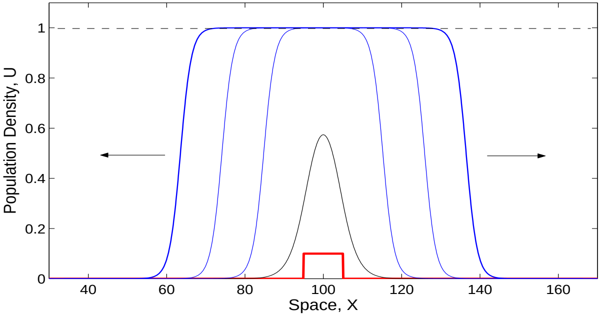
Equating $U_* = \beta$, we obtain the critical relation between the height and width of the initial distribution!

Extinction-invasion diagram



More realistic models gives the curve of the same shape.

A supercritical initial condition will develop into a traveling wave:



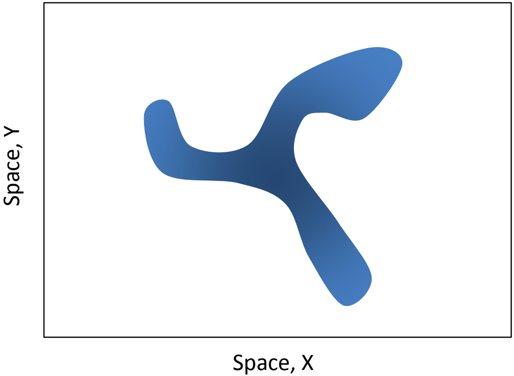
For a subcritical initial condition, strictly speaking, extinction only can happen in case of the strong Allee effect.

Theorem (Aronson): In case of logistic growth, any compact positive initial condition will converge to the traveling wave.

In case of the logistic growth, the threshold is not the inherent property of the model: cf. “practical stability concept”

Challenges

The situation is much less clear in the 2D case:



The outcome of the species introduction can strongly depend on the shape of the originally invaded area!

Heterogeneous environment

$$\frac{\partial U(X,T)}{\partial T} = D(X)\frac{\partial^2 U}{\partial X^2} + f(U,X),$$

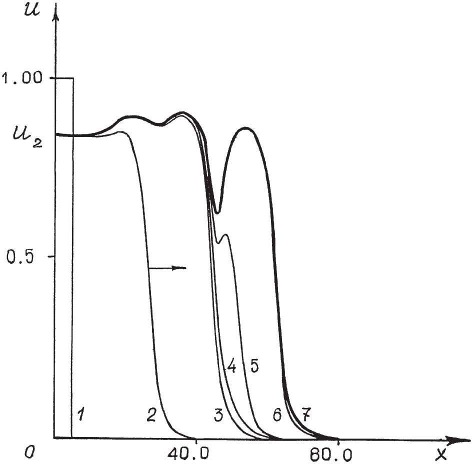
i.e. parameters are now functions of the position in space.

Definition of the traveling wave now becomes less obvious, such as a "non-stationary traveling wave," $U(X,T) = \phi(\xi, T)$.

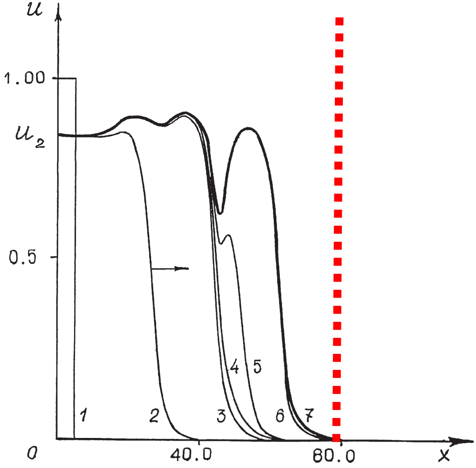
Population distribution behind the front will become heterogeneous, too:

$$U(X,T) \to \tilde{U}(X) \quad \text{where} \quad D(X)\frac{\partial^2 \tilde{U}}{\partial X^2} + f(\tilde{U},X) = 0.$$

Heterogeneous environment: a sketch



Heterogeneous environment: a sketch



Is there a possibility of wave blocking?

Heterogeneous environment

Example I: Logistic growth

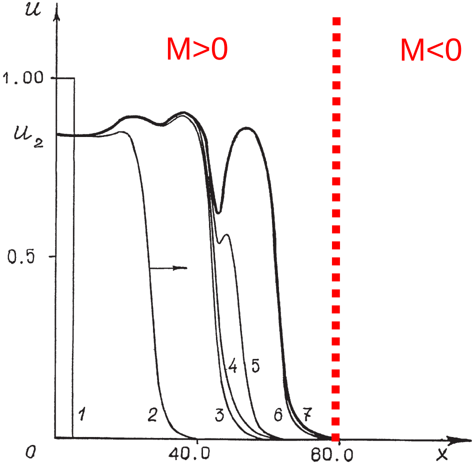
$$f(U,X) = \alpha(X)U\left(1 - \frac{U}{K(X)}\right) .$$

No wave blocking is possible.

Example II: the strong Allee effect

$$f(U,X) = \alpha(X)U\left(\beta - U\right)\left(1 - \frac{U}{K(X)}\right) .$$

Idea: wave blocking can occur if $M(X) < 0$ in front of the traveling front


u
1.00
u_2
0.5
0
40.0
80.0
x
1
2
3
4
5
6
7
M>0
M<0

A single-hump heterogeneity

Consider $K(X) = const$ and $\alpha(X) = \alpha_0[1 + \psi(X)]$,

$$f(U, X) = -\alpha_0[1 + \psi(X)]U + \alpha_2 U^2 - \alpha_3 U^3 \ ,$$

where $\psi(X)$ is positive only in a compact domain:

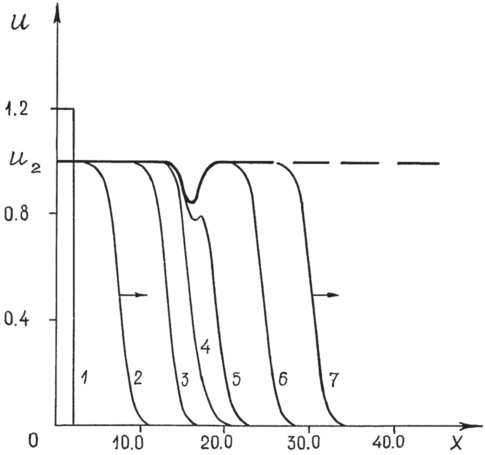
$$\begin{aligned} &\psi(X) > 0 \quad \text{for} \quad X_1 < X < X_2 \ , \\ &\psi(X) \equiv 0 \quad \text{for} \quad X < X_1 \ \text{ or } \ X > X_2 . \end{aligned}$$

Heterogeneity leads to a backward shift Δ in the front position.

Theorem. Consider $\epsilon = \max \psi(X) \ll 1$. Then $\Delta = \frac{B}{2M} + o(\epsilon)$ where

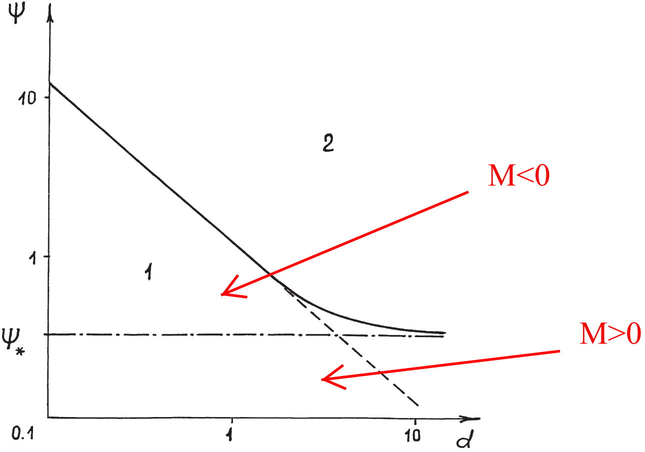
$$M = \int_0^K f(U)dU \quad \text{and} \quad B = \int_{X_1}^{X_2} \psi(X)dX \ .$$

A single-hump heterogeneity



What if the hump is not small, i.e. $\epsilon \sim 1$ or larger?

The stop-go diagram:



Domain 1 for wave propagation, Domain 2 for wave blocking

This property is used in practice (e.g. control of gypsy moth spread)

Chapter IV

PDE models of biological invasion:
Multi-species system

Impact of other species

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  (Even in a homogeneous environment: pattern formation!)

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Impact of other species

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  (Even in a homogeneous environment: pattern formation!)

- Being motivated by the problem of biological control, we will mostly focus on two-species systems such as predator-prey and host-pathogen.

- Biological control is a strategy in invasive species management when natural factors are used in order to slow down or to block the species spread and/or to lead to its eradication

Factors that may affect the pattern of spread

- Heterogeneity of environment
- Human-assisted dispersal (aka “stratified diffusion”)
- Predation?
- Impact of pathogens?
- . . . ?

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- Human-assisted dispersal (aka “stratified diffusion”)
- Predation?
- Impact of pathogens?
- … ?

Mathematical model

A predator-prey / host-pathogen system:

$$\frac{\partial U(\mathbf{R},T)}{\partial T} = D_1 \nabla^2 U(\mathbf{R},T) + f(U)U - r(U)V \ ,$$

$$\frac{\partial V(\mathbf{R},T)}{\partial T} = D_2 \nabla^2 V(\mathbf{R},T) + \kappa r(U)V - MV$$

Mathematical model

A predator-prey / host-pathogen system:

$$\frac{\partial U(\mathbf{R},T)}{\partial T} = D_1 \nabla^2 U(\mathbf{R},T) + f(U)U - r(U)V \ ,$$
$$\frac{\partial V(\mathbf{R},T)}{\partial T} = D_2 \nabla^2 V(\mathbf{R},T) + \kappa r(U)V - MV$$

We consider

- Allee effect for prey/host: $f(U) = \alpha(U - U_0)(K - U)$
- $r(U) = \eta \frac{U}{H+U}$ in case of predation
- $r(U) = \eta U$ in case of pathogens

Mathematical model (contd.)

In dimensionless variables:

$$\begin{aligned}\frac{\partial u(\mathbf{r},t)}{\partial t} &= \nabla^2 u(\mathbf{r},t) + \gamma u(u-\beta)(1-u) - \frac{uv}{1+\Lambda u}\ , \\ \frac{\partial v(\mathbf{r},t)}{\partial t} &= \epsilon \nabla^2 v(\mathbf{r},t) + \frac{uv}{1+\Lambda u} - mv\ .\end{aligned}$$

For $\Lambda = 0$, these equations coincide with an SI model of a host-pathogen system.

1D case

Analytical results

The generic pattern of species spread is considered to be the traveling front

Question: can predation block or reverse the front?

Yes is the answer.

$\epsilon \ll 1$: Owen & Lewis (2001), singular perturbation analysis.

$\epsilon = 1$: Petrovskii et al. (2005), exact solution.

1D case (contd.)

However, the above analytical results were obtained in terms of traveling waves. This is a strong assumption.

Can the pattern of spread be different from the traveling front?

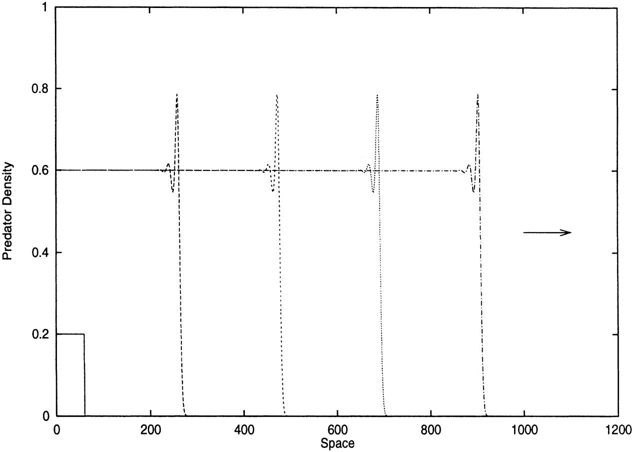
Simulations. Consider the following initial conditions:

$$u(x,0) = u_0 \quad \text{for} \ -\Delta_u < x < \Delta_u \ , \quad \text{otherwise} \ \ u(x,0) = 0 \ ,$$

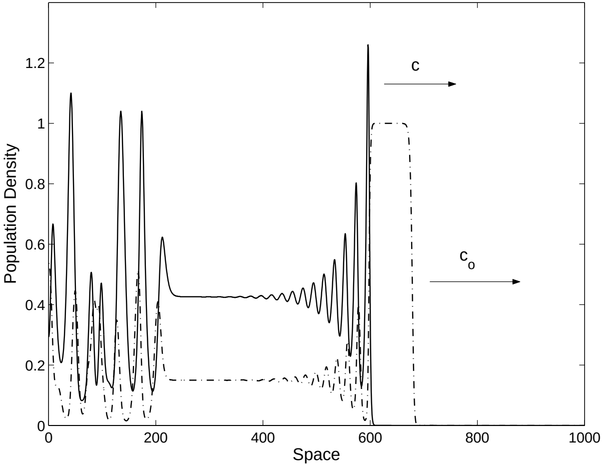
$$v(x,0) = v_0 \quad \text{for} \ -\Delta_v < x < \Delta_v \ , \quad \text{otherwise} \ \ v(x,0) = 0 \ ,$$

where $u_0, \ v_0$ are the initial population densities,
Δ_u and Δ_v give the radius of the initially invaded domain.

1D case (contd.)

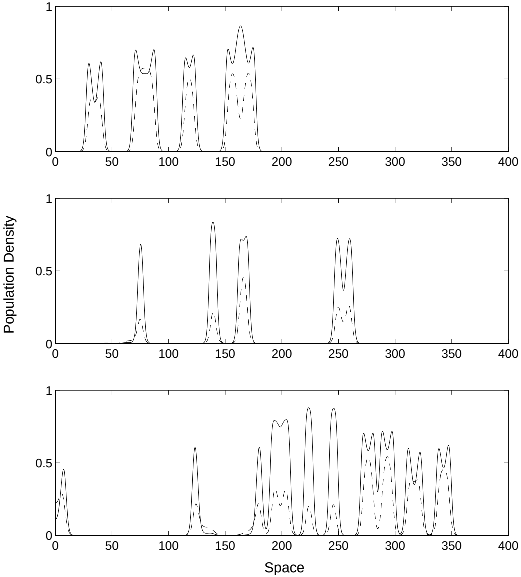


1D case (contd.)

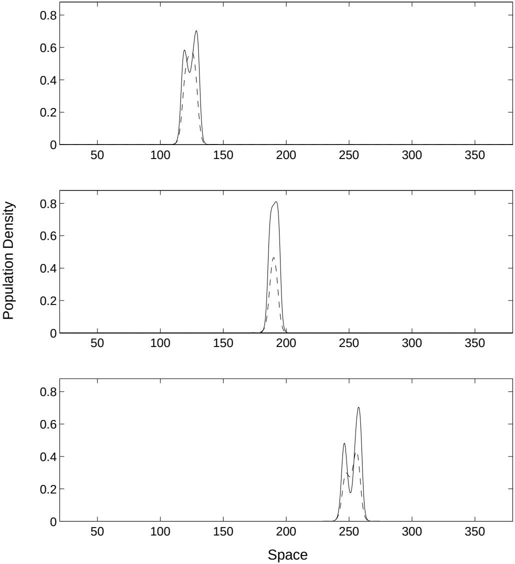


(Sherratt et al., 1995; Petrovskii & Malchow, 2000, 2002; Petrovskii et al., 2001)

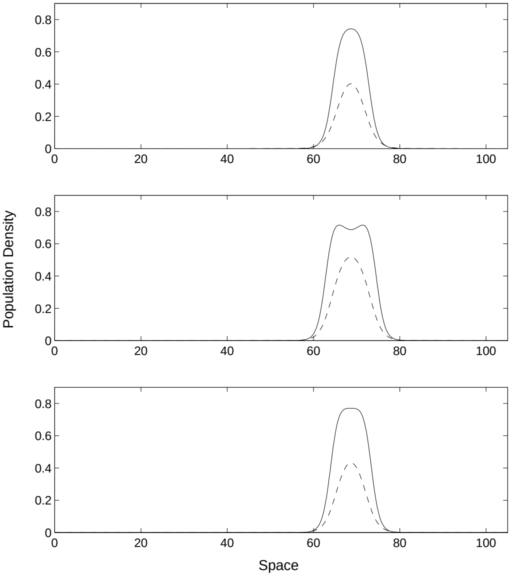
1D case (contd.)



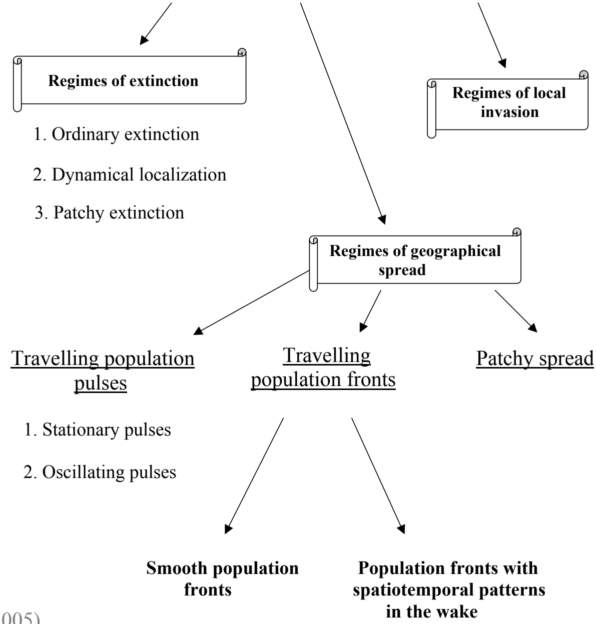
1D case (contd.)



1D case (contd.)



Regimes of biological invasion in a predator-prey system



Regimes of extinction

1. Ordinary extinction
2. Dynamical localization
3. Patchy extinction

Regimes of local invasion

Regimes of geographical spread

Travelling population pulses

1. Stationary pulses
2. Oscillating pulses

Travelling population fronts

Smooth population fronts

Population fronts with spatiotemporal patterns in the wake

Patchy spread

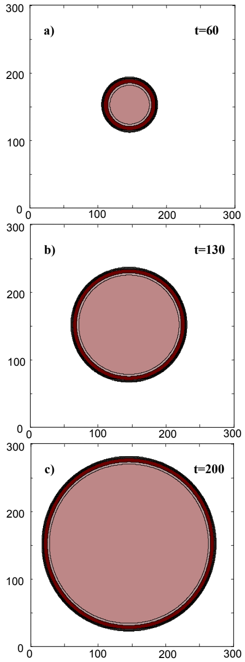
(Petrovskii et al., 2005)

2D case, simulations

The initial conditions:

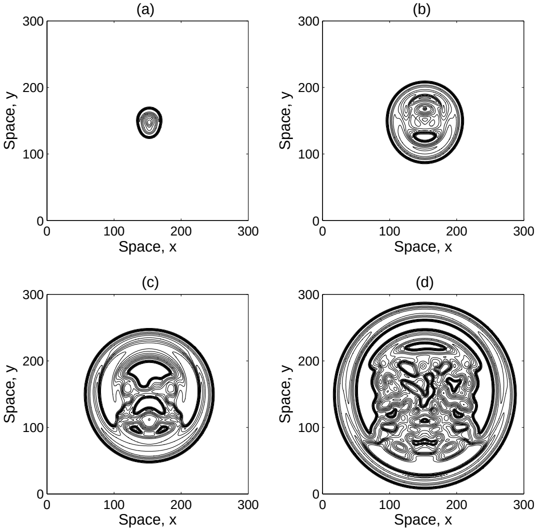
$$
\begin{aligned}
u(x, y, 0) &= u_0 \ \text{ for } \ x_{11} < x < x_{12}\ ,\ y_{11} < y < y_{12}\ , \\
u(x, y, 0) &= 0 \ \text{ otherwise,}
\end{aligned}
$$

$$
\begin{aligned}
v(x, y, 0) &= v_0 \ \text{ for } \ x_{21} < x < x_{22}\ ,\ y_{21} < y < y_{22}\ , \\
v(x, y, 0) &= 0 \ \text{ otherwise.}
\end{aligned}
$$


a)
t=60
b)
t=130
c)
t=200
0
100
200
300

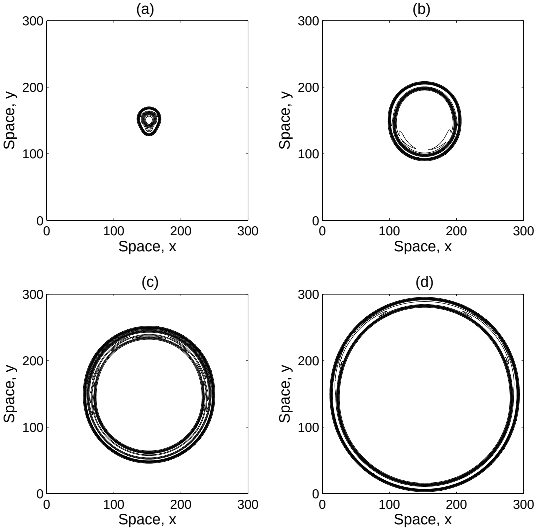
2D case (contd.)

Chaos in the wake

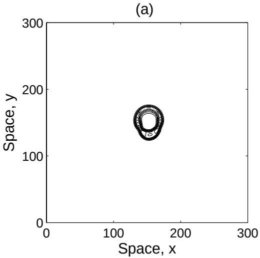


2D case (contd.)

Spread without invasion

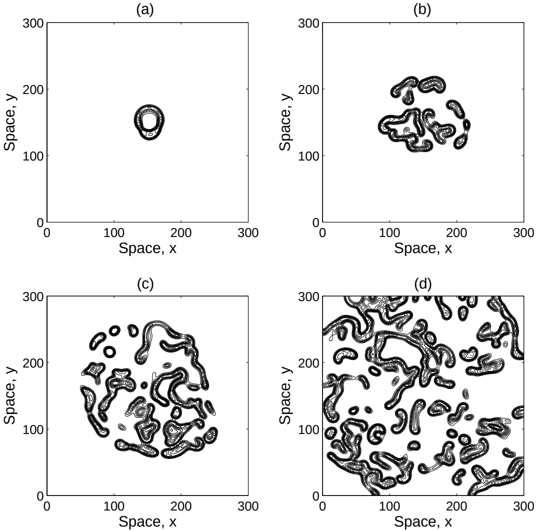


2D case (contd.)



2D case (contd.)

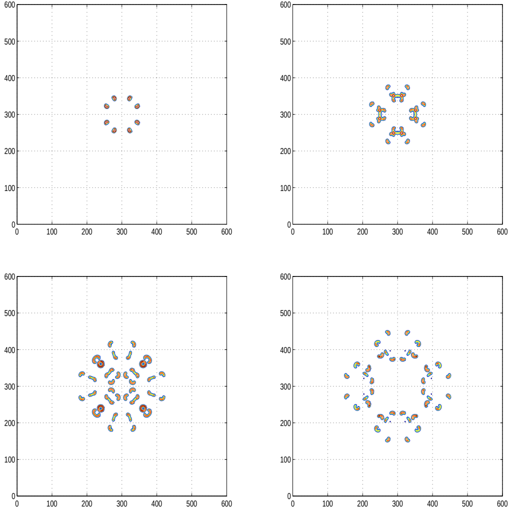
Patchy invasion



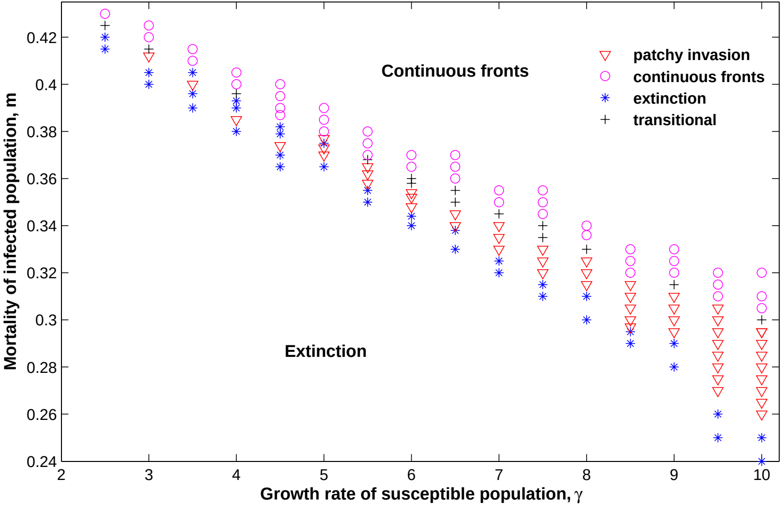
(Petrovskii et al., 2001)

2D case (contd.)

Patchy invasion
for symmetric initial conditions:

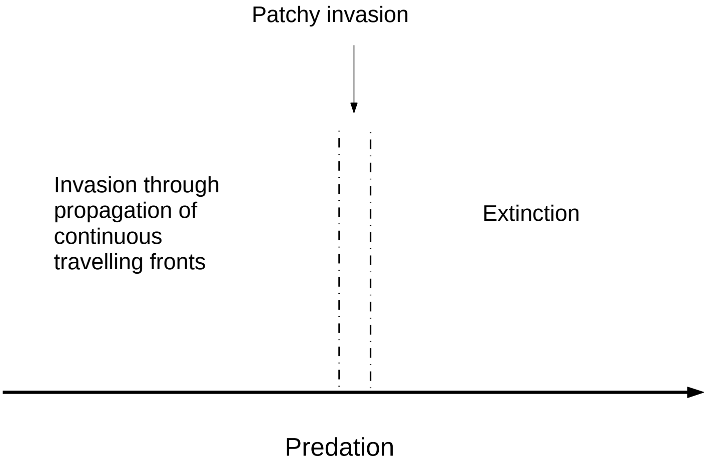


Summary of simulation results



(Jankovic & Petrovskii, 2013)

Invasion at the edge of extinction



Patchy invasion

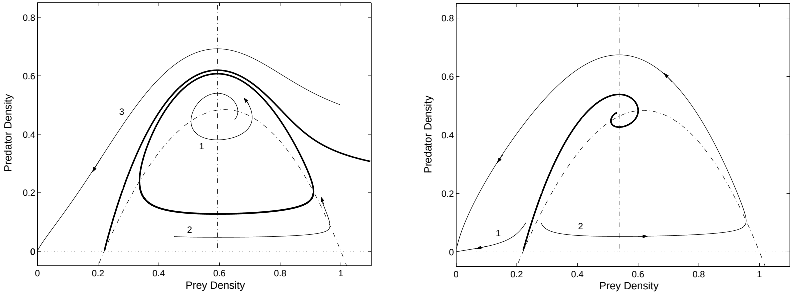
Invasion through
propagation of
continuous
travelling fronts

Extinction

Predation

Without space:

Predation/infection strength increases from left to right:

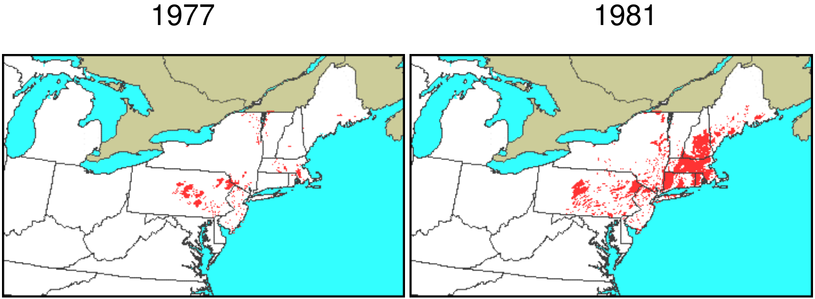


Limit cycle disappears through a heteroclinic bifurcation

Patchy spread occur when the nonspatial system is not viable!

(Malchow, Petrovskii & Venturino, 2008)

Theory against data: gypsy moth in the USA



1977

1981

The red spots show heavily infested areas

(from the US Forest Service, www.fs.fed.us/ne/morgantown)

The calculated rate of spread is between 0.36 and 3.3 km/year against the observed rate between 2 and 10 km/year

(Jankovic & Petrovskii, 2013)

The end of Part 1