VI Southern-Summer School on Mathematical Biology

Mathematical Theory of Biological Invasions

Part II

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Plan 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
Plan of the course – Part II

- Lattice models
- **Kernel-based models** (integro-difference equations): fat-tailed kernels, “superspread”, pattern formation
- Extensions, discussion, conclusions
Chapter V

Lattice models of biological invasion
How essential is the choice of the model?

Specific questions:

- Is the patchy spread an artifact of the diffusion-reaction system?
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Concerns: Time-discrete framework may be more appropriate, at least in some cases (e.g. for species with clearly different life stages)
How essential is the choice of the model?

Specific questions:

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- **Concerns**: Time-discrete framework may be more appropriate, at least in some cases (e.g. for species with clearly different life stages)

- In order to take into account also the environment heterogeneity, we now consider a system that is discrete both in space and time
Ecological example: metapopulation

(by Katrin Körner & Florian Jeltsch, University of Potsdam)
In a more formal way:

Metapopulation with empty patch

(by Victoria Sork, UCLA)

A possible mathematical framework: discrete space, continuous time (Keitt et al., 2001)
Coupled Map Lattice: single species

Continuous space \((x, y)\) changes into a discrete ‘lattice’ \((x_m, y_n)\) where \(k = 1, \ldots, M\) and \(n = 1, \ldots, N\).

Population numbers are defined only in the lattice nodes:

Each discrete step from \(t\) to \(t + 1\) consists of distinctly different dispersal stage and the ‘reaction’ stage.
The dispersal stage includes emigration and immigration:

\[ N'_{x,y,t} = (1 - \mu)N_{x,y,t} + \sum_{(a,b) \in V_{x,y}} \frac{\mu}{4} N_{a,b,t}, \]

where \( \mu \) is the population fraction that emigrates from the site.

The choice of \( V_{x,y} \) can be different, for instance

\[ V_{x,y} = \{(x-1, y), (x+1, y), (x, y-1), (x, y+1)\}, \]

which corresponds to a certain ‘dispersal stencil’:
The reaction stage is \( N_{x,y,t+1} = f(N'_{x,y,t}) \).

We assume that the population growth is hampered by the strong Allee effect.

In particular, we consider

\[
N_{t+1} = f(N_t) = \frac{\alpha (N_t)^2}{1 + \beta^2 (N_t)^2}.
\]

This function \( f(N) \) has two steady states, \( N^*_1 \) and \( N^*_2 \).

We also consider its approximation with a simpler function:

\[
f(N) \approx \tilde{f}(N) = N^*_2 H(N - N^*_1)
\]

where \( H(z) \) is the Heaviside step function.
Population growth in discrete time

![Diagram showing the relationship between prey density and prey growth rate.]
Consider a single-site species introduction:

Questions to be answered:

- Under what conditions this introduction will lead to successful establishment (and, possibly, spread)?
- What can be the rate of spread?
- What can be the pattern of spread?
Establishment

The species will persist at the site $p$ of initial introduction iff its size after dispersal does not fall below the Allee threshold:

$$N_p' = (1 - \mu)N_2^* > N_1^*,$$

that is, for

$$\mu < 1 - \kappa \quad \text{where} \quad \kappa = N_1^*/N_2^*. \quad (1)$$

The spread into a neighboring site $q$ will be successful iff the density after dispersal exceeds the Allee threshold:

$$N_q' = \frac{\mu}{4}N_2^* > N_1^*,$$

that is, for

$$\mu > 4\kappa. \quad (2)$$

Conditions for establishment and spread are now not the same!
Domain I - establishment & spread, Domain III - establishment without spread (invasion pinning), Domain II - spread with pattern formation in the wake, Domain IV - extinction

(Mistro, Rodrigues & Petrovskii, 2012)
For the step-like growth function, the rate of spread is exactly 1 (one site per generation).

The shape of the envelope is an artefact of the dispersal stencil.
But with a little bit of environmental heterogeneity...

Now the shape of the envelope looks much more realistic!
Coupled Maps Lattice: predator-prey system

Now we have, for the dispersal stage

\[ N'_{x,y,t} = (1 - \mu_N)N_{x,y,t} + \sum_{(a,b)\in V_{x,y}} \frac{\mu N}{4} N_{a,b,t} , \]

\[ P'_{x,y,t} = (1 - \mu_P)P_{x,y,t} + \sum_{(a,b)\in V_{x,y}} \frac{\mu P}{4} P_{a,b,t} , \]

and for the reaction stage

\[ N_{x,y,t+1} = f \left( N'_{x,y,t}, P'_{x,y,t} \right) , \]

\[ P_{x,y,t+1} = g \left( N'_{x,y,t}, P'_{x,y,t} \right) . \]
Specifically, we choose the reaction term as follows

\[ N_{x,y,t+1} = \frac{r (N_{x,y,t})^2}{1 + b (N_{x,y,t})^2} \cdot \exp(-P_{x,y,t}), \]

and

\[ P_{x,y,t+1} = N_{x,y,t} P_{x,y,t}. \]

(in dimensionless variables) where \( N \) is prey and \( P \) is predator.

This system shows a very complicated dynamical behavior including traveling waves, regular spatial patterns and spatiotemporal chaos.

(Mistro, Rodrigues & Petrovskii, 2012)
Coupled Map Lattice: simulations

Once the rings are, eventually, pushed to the domain boundary (Fig. 8e, f), both species go extinct. Since the domain boundary is impenetrable (due to the no-flux condition) and the prey pulse is followed by the pulse of predators, there is no way to escape, so that finally all prey population is consumed which, in its turn, leads to the extinction of their specialist predator. The corresponding total population size over time is shown in Fig. 12a.

A completely different regime of species spread is shown in Fig. 9 (obtained for $m_N = 0.5$ and $m_P = 0.8$). In this case, no continuous traveling front is formed and the spread takes place through formation and movement of separate patches of high population density. Correspondingly, we will call this regime the "patchy invasion" (cf. Petrovskii et al., 2002a, 2005b; Morozov et al., 2006). The patch dynamics follows a complicated scenario: the patches can move, split, merge and split again, eventually...

Fig. 7. Spatial distribution of prey for $r = 4.5$, $b = 2$, $m_N = 0.9$, $m_P = 0.002$ in time-step (a) $t = 100$, (b) $t = 200$ and (c) $t = 2000$. (d) Total population size of prey (solid curve) and predator (dashed curve).
Coupled Map Lattice: simulations

**Figure 11:** Spatial distribution of prey in different time steps: (a) $t = 25$, (b) $t = 35$, (c) $t = 50$, (d) $t = 100$, (e) $t = 200$ and (f) $t = 235$ for $r = 4.2$, $b = 0.7$, $\mu_N = 0.5$ and $\mu_P = 0.8$.

We consider the following non-symmetric initial condition, which we will call Initial Condition II: prey population is found inside the rectangle $48 \leq x \leq 53$ and $47 \leq y \leq 55$ at its equilibrium value $N^*$, while predator is initially present inside the rectangle $48 \leq x \leq 51$ and $47 \leq y \leq 50$ at $P^*$. For three different combinations of the dynamical parameters, namely $r = 6.2$ and $b = 1.5$, $r = 4.2$ and $b = 0.7$, and $r = 2.5$ and $b = 0.5$, we analyzed the invasion pattern for different dispersal parameter values.

The structure of the dispersal rate parameters regarding different scenarios of invasion obtained are illustrated in Fig. 15. We observed extinction of both species, travelling bands (Figure 16), patchy invasion (Fig. 17), transitional patterns of invasion (Fig. 18) and wave fronts with chaos in the wake of invasion (Fig. 19) were obtained. Symbols in Fig. 15 have the same meaning as before; circles stand for travelling bands. The corresponding total prey and predator populations are illustrated in Figure (20).

Extinction occurs by the same mechanisms as for Initial Condition I and, for the sake of brevity, we omit the illustrations of this case.

This patchy invasion occurs in the parameter range where the nonspatial system goes extinct.
Coupled Map Lattice: simulations

Figure 21: Spatial distribution of prey in different time steps: (a) $t = 50$, (b) $t = 100$, (c) $t = 150$, (d) $t = 200$, (e) $t = 250$ and (f) $t = 300$ for $r = 4.2$, $b = 0.7$, $\mu_N = 0.3$ and $\mu_P = 0.5$.

Asymmetrical, coincident and non-coincident prey and predator initial conditions.

Regarding biocontrol: Looking at the local dynamics, we would say that the predator controls the prey (pest) in region C and can control in region F, depending on its initial density. When space is added, we observed coexistence, in region C, for a relatively broad region of the dispersal rates (see Fig. (19)). Predators lead the prey population to extinction for dispersal rates indicated by filled diamonds in Fig. (19)). On the other hand, when the species persist, the mean prey density is dramatically smaller than it would be without predator.

In region A, the predator can control the prey invasion, depending on the area where the predator is initially released. When both species are released only in the central site, the range of the prey dispersal rate for which the invasion is successful is smaller than that without the predator. (This simulation is not shown in the text). However, if the prey range is initially larger than the predator, the control of the prey is not observed.
Coupled Map Lattice: simulations

Figure 16: Spatial distribution of prey in different time steps: (a) $t = 25$, (b) $t = 35$, (c) $t = 50$, (d) $t = 100$, (e) $t = 150$ and (f) $t = 200$ for $r = 2.5$, $b = 0.5$, $\mu_N = 0.6$ and $\mu_P = 0.1$.

Figure 17: Spatial distribution of prey in different time steps: (a) $t = 25$, (b) $t = 35$, (c) $t = 50$, (d) $t = 100$, (e) $t = 150$ and (f) $t = 200$ for $r = 4.2$, $b = 0.7$, $\mu_N = 0.2$ and $\mu_P = 0.2$. 
Chapter VI

Kernel-based (integral-difference) models of biological invasion
Kernel-based models

Consider an insect population, e.g. moth, in a continuous space but with separated growth and dispersal stages:

\[ U_t(x) \rightarrow \tilde{U}_t = f(U_t(x)) \rightarrow \mathcal{L}(\tilde{U}) = U_{t+1}(x) \]

- adult moth laid eggs, adult moth,
- settling down larvae etc. new generation

where \( \mathcal{L} \) is a spatial operator describing dispersal.

For simplicity, we consider dispersal at the infinite space.

Let \( k(x, y) \) is the probability distribution that a moth released at \( x \) will lay eggs at the position \( y \), then

\[ U_{t+1}(x) = \int_{-\infty}^{\infty} k(x, y)\tilde{U}_t(y)dy \]
Kernel-based models

Assume that space is homogeneous, \( k(x, y) \to k(x - y) \).

We therefore obtain the following equation:

\[
U_{t+1}(x) = \int_{-\infty}^{\infty} k(x - y) f(U_t(y)) \, dy,
\]

where \( k(z) \) is also called the dispersal kernel.

Questions:

- How much different the kernel-based framework is from diffusion-reaction equations?
- If it is different, what can be the rate of spread?

The answer depends on the properties of the dispersal kernel.
Examples of dispersal kernel
Intuitively, the faster the rate of decay of $k(z)$ at large $z$, the lower the rate of spread.

The properties of the kernel can be quantified by the behavior of its moments. (e.g. see Kot et al., 1996)

The moment of the $n$th order:

$$m_n = \int_{-\infty}^{\infty} z^n k(z) dz, \quad m_0 = 1, \quad m_1 = \langle z \rangle .$$

For almost any $k(z)$, $m_n$ is an increasing function of $n$.

However, a lot depends on how fast is the rate of increase.
Case 1. All moments exist and the asymptotical rate of increase of $m_n$ is not faster than the factorial of $n$, i.e. at most

$$m_n \sim n!$$

which means that $k(z)$ is exponentially bounded.

In this case, the kernel-based equation with compact initial conditions describes a traveling front propagating with a constant speed (Lui 1983; Kot 1992)

The kernel-based model appears to be equivalent to the diffusion-reaction equation

(Petrovskii & Li, 2006, Section 2.2; Lewis et al., 2016, Section 2.4)
Case 2. For a $k(z)$ with a fatter tail (rate of decay lower than exponential), the model has solutions of a new type: accelerating traveling waves.

The difference between the corresponding kernels can be expressed in terms of the moment-generating function:

$$M(s) = \int_{-\infty}^{\infty} e^{sz} k(z) dz$$

(Kot et al. 1996), that is:

- Constant-speed traveling waves if $M(s)$ exists
- Accelerating traveling waves if $M(s)$ does not exist (the integral diverges for any $s \neq 0$)

Accelerating waves do not exist if the population growth is dumped by the strong Allee effect.
Patterns in the wake

Interestingly, pattern formation in the wake of the traveling front appears possible even in a single-species kernel-based model:

(Andersen, 1991)
Questions arising

What can be the effect of other species?

How it may change the pattern of spread?

Consider a predator-prey system:

\[ u_{t+1}(r) = \int_{\Omega} k^{(u)} (|r - r'|) f (u_t (r'), v_t (r')) \, dr', \]

\[ v_{t+1}(r) = \int_{\Omega} k^{(v)} (|r - r'|) g (u_t (r'), v_t (r')) \, dr', \]
Local demography: predator-prey system

\[ u_{t+1}(r) = \frac{r(u_t(r))^2}{1 + b(u_t(r))^2} \cdot \exp(-v_t(r)), \]

\[ v_{t+1}(r) = u_t(r)v_t(r). \]

(Mistro, Rodrigues & Petrovskii, 2012)
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(Mistro, Rodrigues & Petrovskii, 2012)
Dispersal kernel: the “reference case”

\[ k_G(|\mathbf{r} - \mathbf{r}'|) = \frac{1}{2\pi \alpha_i^2} \exp \left( -\frac{|\mathbf{r} - \mathbf{r}'|^2}{2\alpha_i^2} \right). \]

Dispersal with the Gaussian kernel is known to be equivalent (in some sense) to diffusion.

t=140  

t=200
Fat-tailed kernels in 1D

Long-distance asymptotics for the Gaussian kernel:

\[ k(x) \sim e^{-ax^2}. \]

Fat tailed kernel – power-law decay:

\[ k(x) \sim x^{-\mu} \quad (1 < \mu < 3) \]

In case \( \mu = 2 \), the stable distribution is available in a closed form known as Cauchy distribution:

\[ k_C(x) = \frac{\beta}{\pi(\beta^2 + x^2)} \sim x^{-2}. \]
Fat-tailed kernels in 2D

Long-distance asymptotics: \( k(r) \sim r^{-(\mu+1)} \) \((1 < \mu < 3)\)

Explicit form of the stable distribution is not available, hence extension onto the 2D case is ambiguous.

**Cauchy kernels** Type I:

\[
k_{C_I}(r, r') = \frac{\beta_i^2}{\pi (\beta_i + |r - r'|)^3} \sim |r - r'|^{-3},
\]

**Cauchy kernels** Type II:

\[
k_{C_{II}}(r, r') = \frac{\gamma_i}{2\pi (\gamma_i^2 + |r - r'|^2)^{3/2}} \sim |r - r'|^{-3}.
\]

(Rodrigues et al., 2015)
Fat-tailed kernels

Cauchy kernel has significantly different properties compared to the Gaussian kernel: the variance does not exist, \( < r^2 > = \infty \).

- The fact that \( < r^2 > = \infty \) is sometimes interpreted as the infinite correlation length
- Invasive species can spread with an accelerating speed
  (Kot et al. 1996)

Questions arising:
- Can patchy spread occur for the fat-tailed dispersal?
- How the rate of spread may differ between different kernels?
Simulations, kernel Type I

Figure 1: Snapshots of the prey spatial distribution at different moments $t$, (a) 20, (b) 100, (c) 140, and (d) 190, as obtained for the Cauchy kernel Type I and the asymmetrical initial conditions ($\ldots$ – $\ldots$). Parameters are $\beta_N = 0.0488$ and $\beta_P = 0.098$. 
Simulations, kernel Type II

Figure 2: Snapshots of the prey spatial distribution at different moments $t$, (a) 40, (b) 80, (c) 140 and (d) 200, as obtained for the Cauchy kernel Type II and the asymmetrical initial conditions ($\gamma_\text{N} - \gamma_\text{P}$). Parameters are $\gamma_\text{N} = 0.068$ and $\gamma_\text{P} = 0.1205$. 
How can we compare the results for different dispersal kernels, i.e. Gaussian, Cauchy Type I and Cauchy Type II?

Standard approach (equating the variances) does not work as the variance does not exist – "scale-free" process.
Conditions of equivalence

Consider radius $\epsilon$ within which the probability of finding an individual after dispersal is $1/2$:

$$P_\epsilon = \int\int_{|r| \leq \epsilon} d\mathbf{r} = \int_0^{2\pi} \int_0^\epsilon k_i(r, \theta) r dr d\theta = \frac{1}{2}.$$ 

For the Gaussian kernel, we obtain $\epsilon = \alpha \sqrt{2 \ln 2}$.

For Cauchy kernel Type I:

$$\beta = \epsilon (\sqrt{2} - 1) = \alpha (2 - \sqrt{2}) \sqrt{\ln 2} \approx 0.4877 \alpha.$$ 

For Cauchy kernel Type II:

$$\gamma = \frac{\epsilon}{\sqrt{3}} = \alpha \sqrt{\frac{2}{3} \ln 2} \approx 0.6798 \alpha.$$
Invasion rates are related by the above equivalence condition. There is no accelerated spread.

Invasion rates obtained for the Cauchy kernels are between 1-10 km/year, hence in excellent agreement with field data.

(Rodrigues et al., 2015)
This is **the end** of the course...
This is **the end** of the course...

But **certainly not** the end of the story


Good luck with your research!