

VI Southern-Summer School on Mathematical Biology

Mathematical Theory of Biological Invasions

Part II

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<http://www.math.le.ac.uk/PEOPLE/sp237>

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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
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fat-tailed kernels, “superspread”, pattern formation
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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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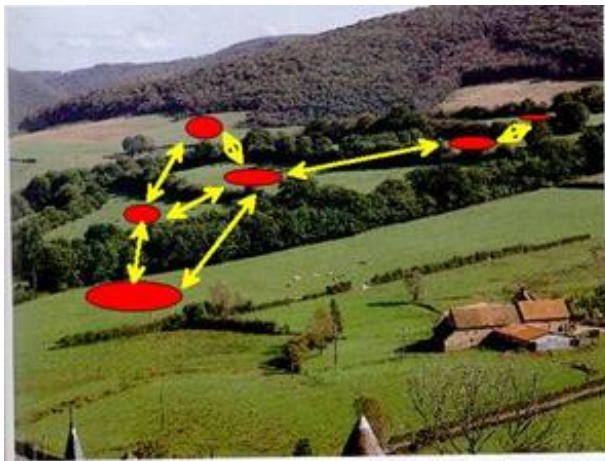
- Is the patchy spread an artifact of the diffusion-reaction system?
- **Concerns:** Time-discrete framework may be more appropriate, at least in some cases (e.g. for species with clearly different **life stages**)

How essential is the choice of the model?

Specific questions:

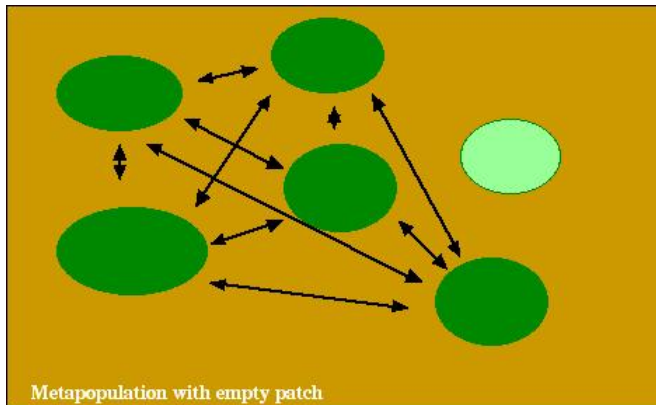
- Is the patchy spread an artifact of the diffusion-reaction system?
- **Concerns:** Time-discrete framework may be more appropriate, at least in some cases (e.g. for species with clearly different **life stages**)
- In order to take into account also the environment heterogeneity, we now consider a 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:



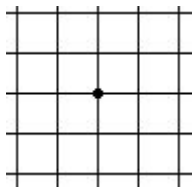
(by Victoria Sork, UCLA)

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 $k = 1, \dots, M$ and $n = 1, \dots, N$.

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:

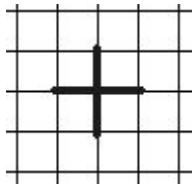
$$N'_{x,y,t} = (1 - \mu)N_{x,y,t} + \sum_{(a,b) \in V_{x,y}} \frac{\mu}{4} N_{a,b,t},$$

where μ 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

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

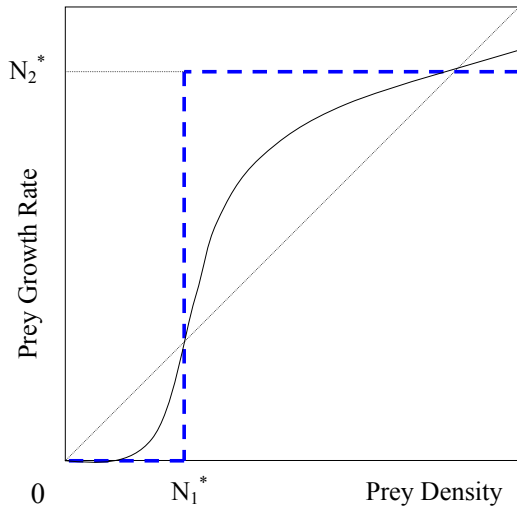
This function $f(N)$ has two steady states, N_1^* and N_2^* .

We also consider its **approximation** with a simpler function:

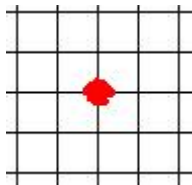
$$f(N) \approx \tilde{f}(N) = N_2^* H(N - N_1^*)$$

where $H(z)$ is the Heaviside **step function**.

Population growth in discrete time



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:

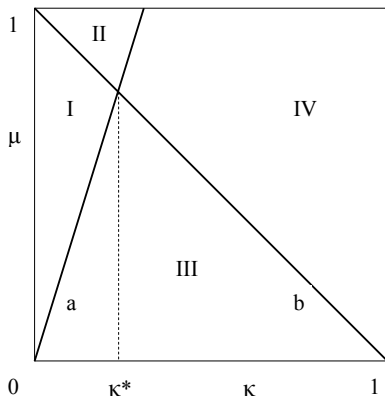
$$N'_q = \frac{\mu}{4}N_2^* > N_1^*,$$

that is, **for**

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

Conditions for establishment and spread are now not the same!

Extinction-invasion diagram

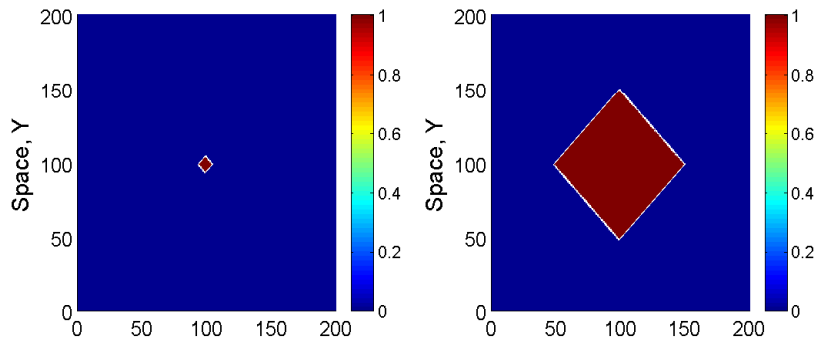


Domain I - **establishment & spread**, Domain III - establishment without spread (**invasion pinning**), Domain II - spread with **pattern formation** in the wake, Domain IV - **extinction**

(Mistro, Rodrigues & Petrovskii, 2012)

Spread

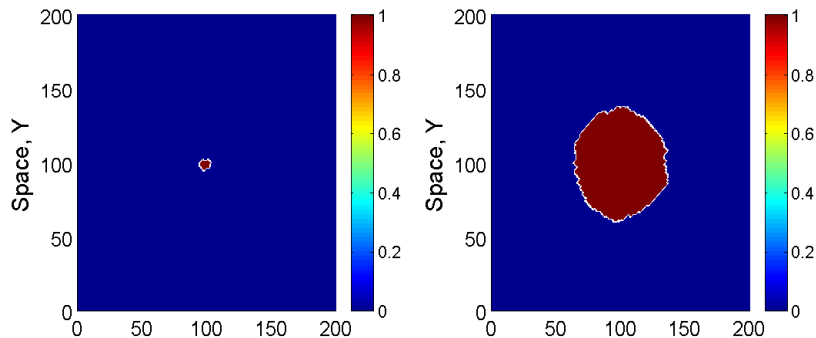
For the step-like growth function, the rate of spread is exactly 1 (one site per generation).



The shape of the envelope is an artefact of the dispersal stencil.

Spread

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

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

$$P_{x,y,t+1} = g \left(N'_{x,y,t}, P'_{x,y,t} \right) .$$

Predator-prey on a lattice

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

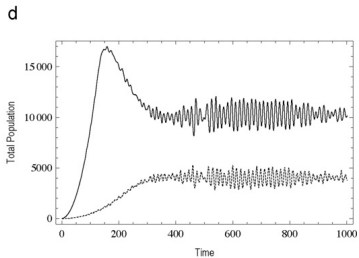
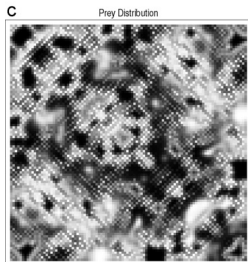
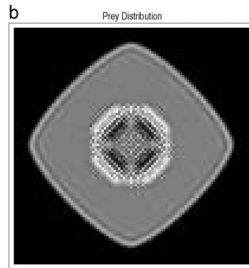
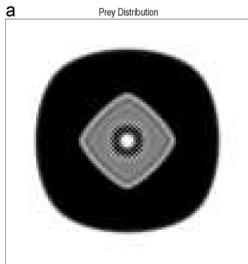
$$P_{x,y,t+1} = N_{x,y,t} P_{x,y,t}.$$

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

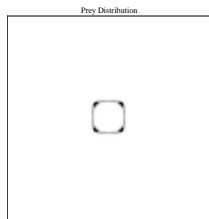
This system shows a very complicated dynamical behavior including traveling waves, regular spatial patterns and spatiotemporal chaos.

(Mistro, Rodrigues & Petrovskii, 2012)

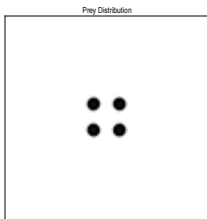
Coupled Map Lattice: simulations



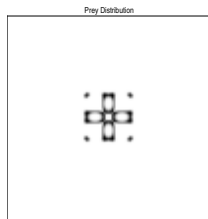
Coupled Map Lattice: simulations



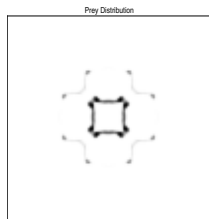
(a)



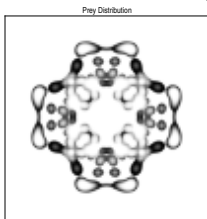
(b)



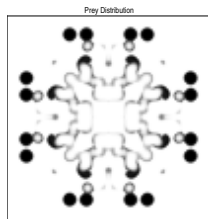
(c)



(d)



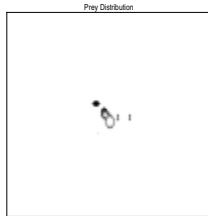
(e)



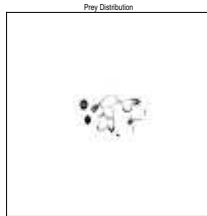
(f)

This patchy invasion occurs in the parameter range where the nonspatial system goes extinct

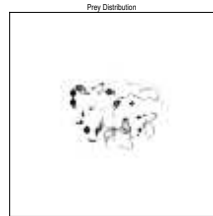
Coupled Map Lattice: simulations



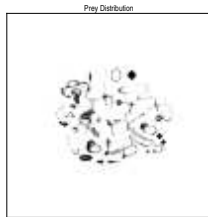
(a)



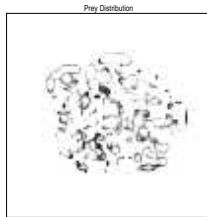
(b)



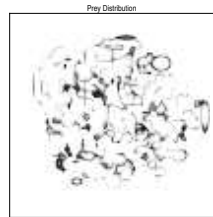
(c)



(d)

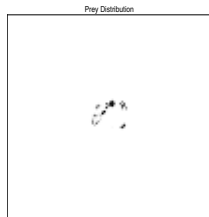


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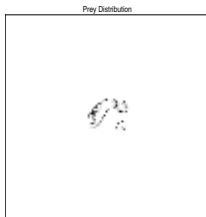


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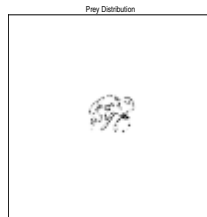
Coupled Map Lattice: simulations



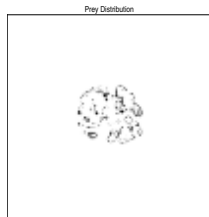
(a)



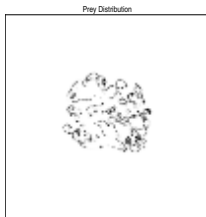
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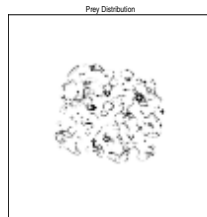
(c)



(d)



(e)



(f)

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
settling down

laid eggs,
larvae etc.

adult moth,
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**, $k(x, y) \rightarrow k(x - y)$.

We therefore obtain the following equation:

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

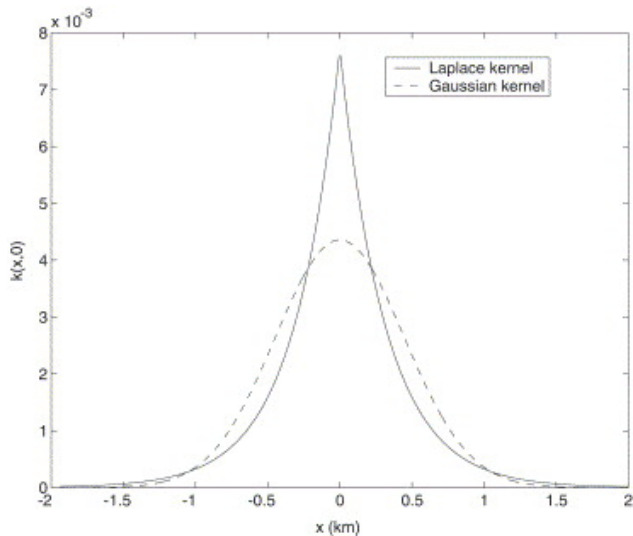
where $k(z)$ is also called the **dispersal kernel**.

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**:

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

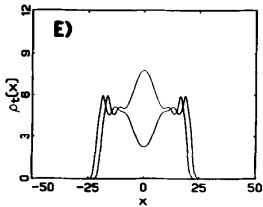
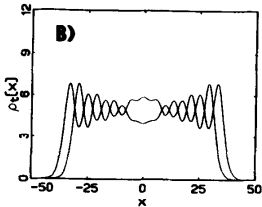
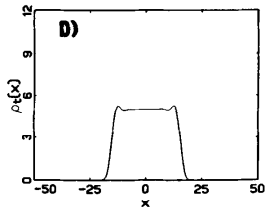
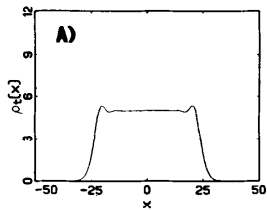
(Kot et al. 1996), that is:

- 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:



Questions arising

What can be the **effect of other species**?

How it may change the pattern of spread?

Consider a **predator-prey** system:

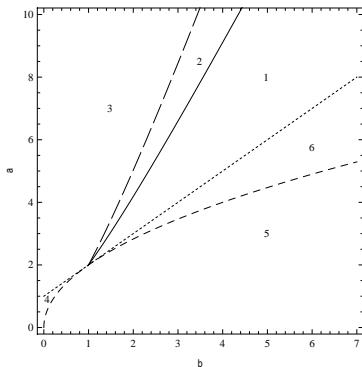
$$u_{t+1}(\mathbf{r}) = \int_{\Omega} k^{(u)}(|\mathbf{r} - \mathbf{r}'|) f(u_t(\mathbf{r}'), v_t(\mathbf{r}')) d\mathbf{r}',$$

$$v_{t+1}(\mathbf{r}) = \int_{\Omega} k^{(v)}(|\mathbf{r} - \mathbf{r}'|) g(u_t(\mathbf{r}'), v_t(\mathbf{r}')) d\mathbf{r}',$$

Local demography: predator-prey system

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

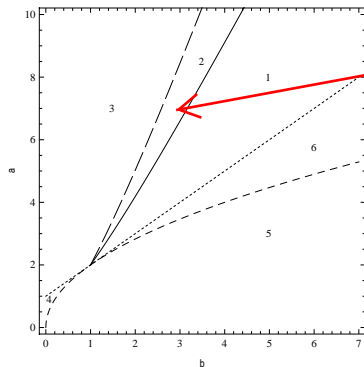
$$v_{t+1}(\mathbf{r}) = u_t(\mathbf{r})v_t(\mathbf{r}).$$



Local demography: predator-prey system

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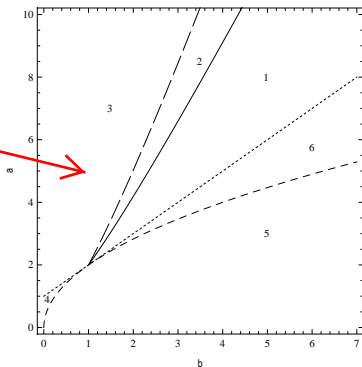
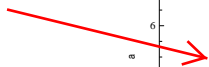
Limit cycle

Local demography: predator-prey system

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

$$v_{t+1}(\mathbf{r}) = u_t(\mathbf{r})v_t(\mathbf{r}).$$

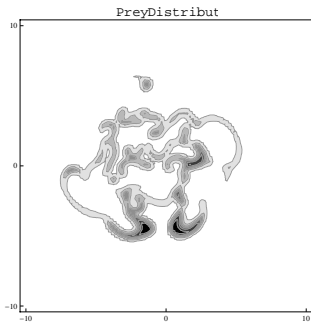
Extinction in the
nonspatial system



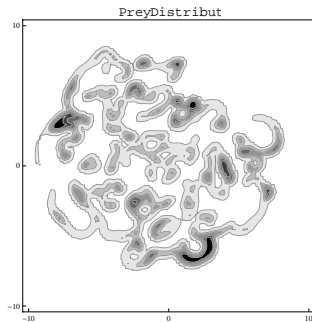
Dispersal kernel: the “reference case”

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

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: $k(\mathbf{r}) \sim r^{-(\mu+1)}$ ($1 < \mu < 3$)

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

Cauchy kernels Type I:

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

Cauchy kernels Type II:

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

(Rodrigues et al., 2015)

Fat-tailed kernels

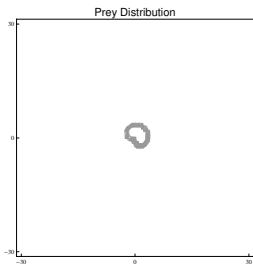
Cauchy kernel has significantly different properties compared to the Gaussian kernel: the **variance does not exist**, $\langle r^2 \rangle = \infty$.

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

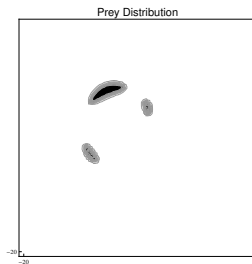
Questions arising:

- Can patchy spread **occur** for the fat-tailed dispersal?
- How the **rate of spread** may differ between different kernels?

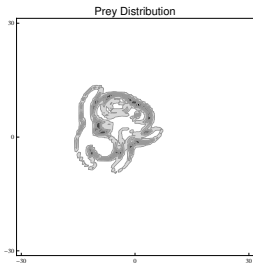
Simulations, kernel Type I



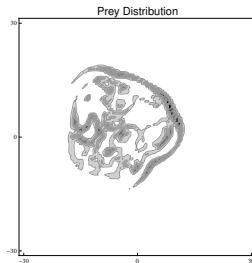
$t = 20$



$t = 100$

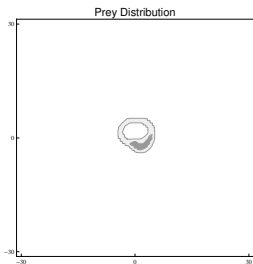


$t = 140$

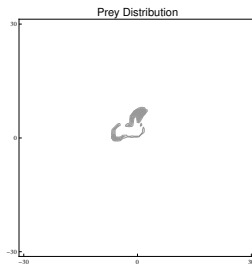


$t = 190$

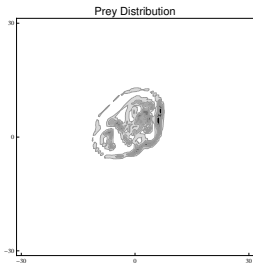
Simulations, kernel Type II



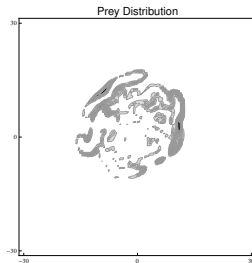
$t = 40$



$t = 80$



$t = 140$



$t = 200$

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 ϵ within which the probability of finding an individual after dispersal is $1/2$:

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

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

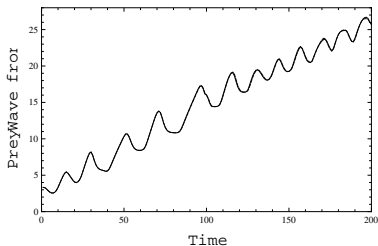
For Cauchy kernel Type I:

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

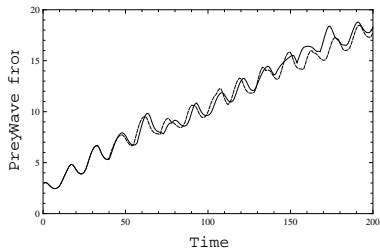
For Cauchy kernel Type II:

$$\gamma = \frac{\epsilon}{\sqrt{3}} = \alpha\sqrt{\frac{2}{3}\ln 2} \approx 0.6798\alpha.$$

Radius of invaded area vs time



Cauchy Type I



Cauchy Type II

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

Literature cited in the notes

Lewis, M.A., Petrovskii, S.V. & Potts, J. (2016) *The Mathematics Behind Biological Invasions*. Interdisciplinary Applied Mathematics, Vol. 44. Springer.

Petrovskii, S.V. & Li, B.-L. (2006) *Exactly Solvable Models of Biological Invasion*, Chapman & Hall / CRC Press. ([pdf is available on my website.](#))

Owen, M.R. & M.A. Lewis (2001). How predation can slow, stop or reverse a prey invasion. *Bull. Math. Biol.* **63**, 655-684.

Petrovskii, S.V., Malchow, H. & Li B.-L. (2005) An exact solution of a diffusive predator-prey system. *Proc. R. Soc.Lond. A* **461**, 1029-1053.

Sherratt, J.A., Lewis, M.A. & Fowler, A.C. (1995) Ecological chaos in the wake of invasion. *Proc. Natl. Acad. Sci. USA* **92**, 2524-2528.

Jankovic, M. & Petrovskii, S. (2013) Gypsy moth invasion in North America: A simulation study of the spatial pattern and the rate of spread. *Ecol. Compl.* **14**, 132-144.

Mistro, D.C., Rodrigues, L.A.D. & Petrovskii, S.V. (2012) Spatiotemporal complexity of biological invasion in a space- and time-discrete predator-prey system with the strong Allee effect. *Ecological Complexity* **9**, 16-32.

Rodrigues, L.A.D., Mistro, D.C., Cara, E.R., Petrovskaya, N. & Petrovskii, S.V. (2015) Patchy invasion of stage-structured alien species with short-distance and long-distance dispersal. *Bull. Math. Biol.* **77**, 1583-1619.

Kot, M., Lewis, M. A. & van der Driessche, P. (1996) Dispersal data and the spread of invading organisms. *Ecology* **77**, 2027-2042.

Other useful references

Shigesada, N. & Kawasaki, K. (1997) *Biological Invasions: Theory and Practice*. Oxford University Press.

Lewis, M.A. & Kareiva, P. (1993). Allee dynamics and the spread of invading organisms. *Theor. Popul. Biol.* **43**, 141-158.

Neubert, M.G., Kot, M. & Lewis, M.A. (1995) Dispersal and pattern formation in a discrete-time predator-prey model. *Theor. Pop. Biol.* **48**, 7-43.

Lui, R. (1983) Existence and stability of travelling wave solutions of a nonlinear integral operator. *J. Math. Biol.* **16**, 199-220.

Volpert, V. & Petrovskii, S.V. (2009) Reaction-diffusion waves in biology. *Physics of Life Reviews* **6**, 267-310.

Kot, M. (2001) *Elements of Mathematical Ecology*. Cambridge University Press.

Malchow, H., Petrovskii, S.V. & Venturino, E. (2008) *Spatiotemporal Patterns in Ecology and Epidemiology: Theory, Models, Simulations*. Chapman & Hall / CRC Press.

Keitt, T.H., Lewis, M.A., Holt R.D. (2001) Allee effects, invasion pinnings, and species' borders. *Am. Nat.* **157**, 203-216.

Good luck with your research!