Integrodifference equations in spatial ecology

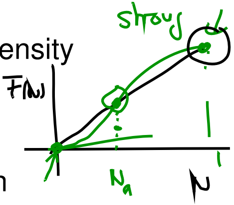
Lecture 8: Spread with Allee effect

Frithjof Lutscher

Allee effect

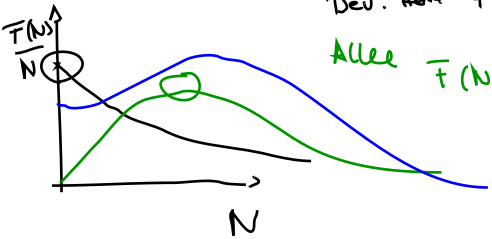
$N_{t+1} = F(N_t)$

- per-capita growth rate maximal at intermediate density
- strong vs weak
- examples
- mathematical difficulty: bistability, no linearization

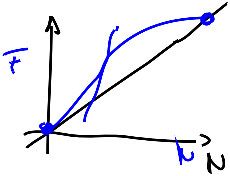


Dev. Holt $F(N) = \frac{RN}{1+(R-1)N}$

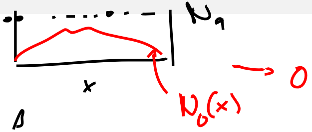
Allee $F(N) = \frac{RN^2}{1+(R-1)N^2}$



$F(N) > N$



Spread with Allee effect



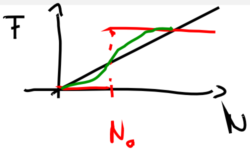
- Speed of spread?
- Spread or not?
- Traveling waves?
- Recall the steady-state result with Allee effect?

Idea: If $\sigma^2 \ll 1$ then we get persistence in the IDE on bd domain if $F(1)=1$ is stable for non-spatial model

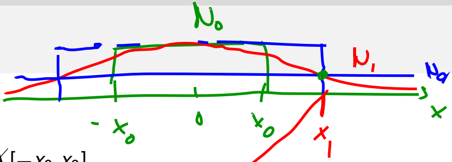
Answer: No

A caricature Allee function (Kot et al 1996)

$$F(N) = \begin{cases} 0, & N < N_a, \\ 1, & N \geq N_a, \end{cases}$$



Calculating spatial extent I



$$N_0(x) = \chi_{[-x_0,x_0]}$$

$$F(N_0) = N_0$$

$$N_1(x) = \int_{-\infty}^{\infty} K(x-y)F(N_0(y))\,dy = \int_{-\infty}^{\infty} K(x-y)\,\chi_{[-x_0,x_0]}\,dy$$

$$= \int_{-x_0}^{x_0} K(x-y)\,dy = \int_{x-x_0}^{x+x_0} K(z)\,dz$$

$z = x-y$

$y = -x_0$ $\quad z = x+x_0$

$$\int_{x_1-x_0}^{x_1+x_0} K(z)\,dz = N_a$$

$$F(N_1(x)) = \chi_{[-x_1,x_1]} \Rightarrow x_1 \text{ is determined by}$$

Calculating spatial extent II

$$\boxed{\int_{\underbrace{x_{t+1}-x_t}_{=0}}^{\overbrace{x_{t+1}+x_t}^{=2x_0}} K(y)dy = N_a}$$

This is a 1-D iteration

Case 1: $x_1 < x_0$ in general $x_{t+1} < x_t$

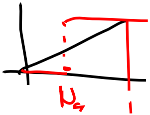
Case 2: $x_1 > x_0$ in general $x_{t+1} > x_t$

threshold initial size:

$x_{t+1} = x_t = x_c$

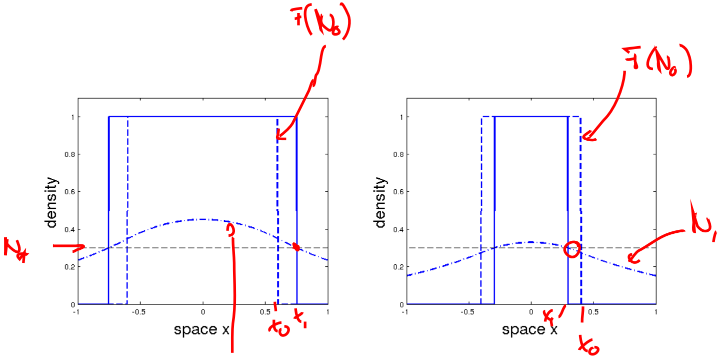
Critical initial size

$$\boxed{\underbrace{\int_0^{2x_c} K(y)dy}_{<\frac{1}{2}} = N_a}$$



Requires $\underbrace{N_a < 1/2}$.

Illustration of expansion and retreat



$N_1 = k * F(N_0)$

Spatial extent and Laplace kernel

Defining eq. $$\boxed{\int_{x_{t+1}-x_t}^{x_{t+1}+x_t} \frac{a}{2} e^{-a|y|} dy = N_a}$$

Critical extent

$$\int_0^{2x_c} \frac{a}{2} e^{-ay} dy = -\frac{1}{2} e^{-ay} \Big|_0^{2x_c} = \frac{1}{2}\left(1 - e^{-2ax_c}\right) = N_a$$

$$1 - e^{-2ax_c} = 2N_a$$

$$1 - 2N_a = e^{-2ax_c}$$

$$-2ax_c = \ln(1-2N_a)$$

$$\boxed{x_c = \frac{-1}{2a} \ln(1-2N_a)}$$

$N_a < \frac{1}{2}$

Iterations for $\boxed{x_{t+1} > x_t}$

$$\int_{x_{t+1}-x_t}^{x_{t+1}+x_t} \frac{a}{2} e^{-ay}\,dy = N_a \qquad \text{solve for } x_t$$

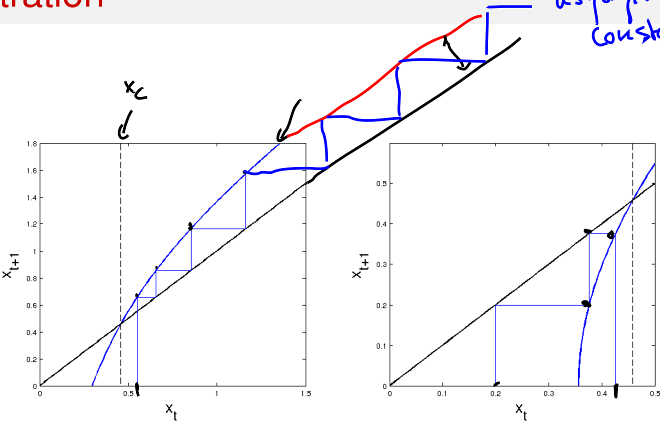
$$= -\frac{1}{2} e^{-ay}\Big|_{x_{t+1}-x_t}^{x_{t+1}+x_t} = -\frac{1}{2}\left(e^{-a(x_{t+1}+x_t)} - e^{-a(x_{t+1}-x_t)}\right)$$

$$= +\frac{1}{2} e^{-a(x_{t+1})}\left(e^{+ax_t} - e^{-ax_t}\right) = + e^{-ax_{t+1}} \sinh(ax_t)$$

$$e^{-ax_{t+1}} \sinh(ax_t) = N_a \quad \Rightarrow \quad \boxed{x_{t+1} = \frac{1}{a} \ln\left(\frac{\sinh(ax_t)}{N_a}\right)}$$

Illustration

asymptotic constant speed



$$\boxed{x_{t+1} = \frac{1}{a}\ln\left(\frac{\sinh(ax_t)}{N_a}\right)}$$

$\sinh(ax_t) \simeq \frac{1}{2} e^{ax_t}$ for x_t large

$$x_{t+1} \simeq \frac{1}{a}\ln\left(\frac{e^{ax_t}}{2N_a}\right) \simeq x_t - \frac{\ln(2N_a)}{a}$$

$N_a < \frac{1}{2}$

The asymptotic spreading speed

TW:

$N_0 = \chi(-\infty, 0]$

$F(N) \sim \chi(-\infty, c)$

$x_{t+1} - x_t = c$

$x_{t+1} + x_t \to \infty$ as $t \to \infty$

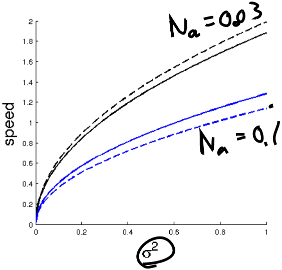
$$\int_{x_{t+1}-x_t}^{x_{t+1}+x_t} K\,dy = N_a$$

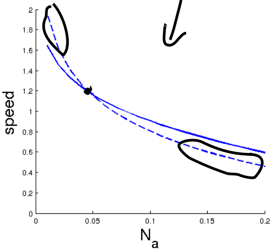
$$\boxed{\int_0^{c^*} K(z)dz = \frac{1}{2} - N_a}$$

Explicit, <u>finite</u> for ~~many~~ all kernels, including Cauchy (but!)

$$\int_c^{\infty} K\,dy = N_a$$

$$\int_\infty^{c} K\,dy = -N_a$$



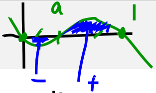


$$\int_0^{\infty} K\,dy = \frac{1}{2}$$

Gauss (solid) vs Laplace (dashed)

$$N_a \simeq \int_c^{\infty} K\,dy = \int_c^{0} K\,dy + \boxed{\int_0^{\infty} K\,dy} = \int_c^{0} K\,dy + \frac{1}{2}$$

Direction of the wave



The reaction-diffusion case with bistable nonlinearity

Nagumo

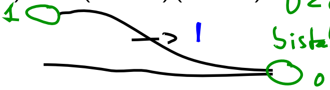
random growth

$u(t,x)$ $\qquad \frac{\partial u}{\partial t}$

$$u_t = Du_{xx} + f(u), \qquad f(u) = u(1-u)(u-a)$$

$0 < a < 1$

bistability



TW: $U(x-ct) = u(x,t) = U(z)$

$$-cU' = DU'' + f(U) \rightarrow DU'' + cU' + f(U) = 0$$

multiply by U' $\qquad DU''U' + cU'^2 + f(U)U' = 0$

integrate: $\displaystyle D\int_{-\infty}^{\infty} U''U'\,dz + c\underbrace{\int_{-\infty}^{\infty} U'^2\,dz}_{>0} + \int_{-\infty}^{\infty} f(U)U'\,dz = 0$

$\displaystyle \frac{(U')^2}{2}\Big|_{-\infty}^{\infty} = 0$

$\displaystyle = \int_1^0 f(u)\,du$

$\mathrm{sign}(c) = \mathrm{sign}\int f(u)\,du$

$\Rightarrow c = \dfrac{\int_0^1 f(u)\,du}{\int U'^2\,dz}$

The integrodifference case - visual

$N_{t+1}(x) = \int_{-\infty}^{\infty} k(x-y)\, F(N_t(y))\, dy$

Allee

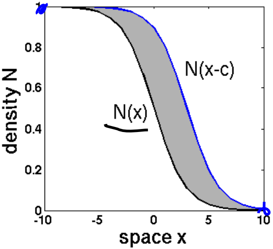
strong

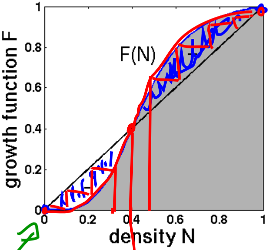
for $\tilde{u} = \delta(u)$

$\int_0^1 f(u)\, du$

N(x-c)

here: $N_{t+1} = F(N_t)$





N_a

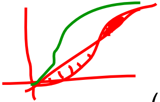
$$\int_0^1 (F(N) - N)\, dN$$

1 = grey + white $= \int_0^1 F(N)\, dN + \int_0^1 F^{-1}(y)\, dy$

The theorem (Wang et al 2002)

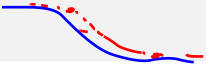
Kot, Neubert

Consider the IDE $N_{t+1}(x) = (K * F(N_t))(x)$ with monotone growth function F and steady states $N = 1$ and $N = 0$. Assume that there is a monotone decreasing travelling front with with speed c and profile $N(x)$, connecting the two states.
Furthermore, assume that F and N are real analytic functions, that derivatives of any order of N vanish as $x \to \pm\infty$ and that the derivatives $d^i F(N(x))/dx^i$ are bounded uniformly in i.
Then we have the following relation for the sign of the speed of the travelling front:



$$\boxed{\mathrm{sign}(c) = \mathrm{sign}\left(\int_0^1 [F(N) - N]dN\right).} \quad (1)$$

Sketch of the proof



If N is decreasing then $c > 0 \iff N(x) < N(x-c) \ \forall x$

$$\frac{d}{dx}F(N(x)) = \underbrace{\frac{dF}{dN}}_{>0}\cdot\underbrace{\frac{dN}{dx}}_{<0} < 0 \qquad \iff (N(x)-N(x-c))\frac{dF(N(x))}{dx} > 0 \quad \forall x$$

Thus
$$0 < \int_{-\infty}^{\infty}(N(x)-N(x-c))\frac{dF}{dx}\,dx \overset{\text{lemma}}{=} \int_{-\infty}^{\infty}(N-F(N))\frac{dF}{dx}\,dx$$

$y = F(N(x))$

$\Downarrow$

$F^{-1}(y) = N$

$$\int_1^0 [F^{-1}(y) - y]\,dy = \int_0^1 (y - \underbrace{F^{-1}(y)}_{T})\,dy$$

$$\boxed{\int_0^1 (F(N)-N)\,dN > 0}$$

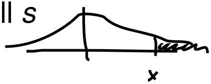
$$\| $$

$$= \underbrace{\int_0^1 y\,dy} + \int_0^1 F(N)\,dN - 1 = -\int_0^1 N\,dN + 1 + \int_0^1 F\,dN - 1$$

General theory (Lui 1983)

Consider the IDE $N_{t+1}(x) = (K * F(N_t))(x)$ where

i) K continuous, symmetric; $M(s)$ exists for all s

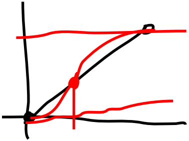


ii) $\int_x^\infty K(y)dy \leq CK(x)$ for large x.

iii) F is $\mathcal{C}^1$ and $F(0) = 0 = F(1) - 1 = F(N_a) - N_a$.

iv) $F'(N) \leq F'(N_a)$ for $N \in [0, 1]$.

v) $F'(0)N \leq F(N) \leq F'(1)(N - 1) + 1$ for $N \in [0, 1]$.



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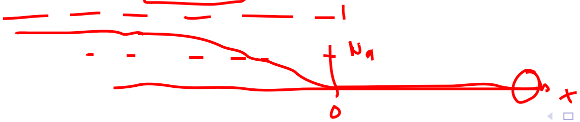
1. There exists an asymptotic spreading speed c^* is the following sense. If $N_0(x) = 0$ for $x > 0$ and $N_0(x) > N_a$ as $x \to -\infty$, then

$$\limsup_{t\to\infty} \max_{x>(c^*+\epsilon)t} N_t(x) = 0 \quad \text{and} \quad \liminf_{t\to\infty} \min_{x<(c^*-\epsilon)t} N_t(x) = 1.$$



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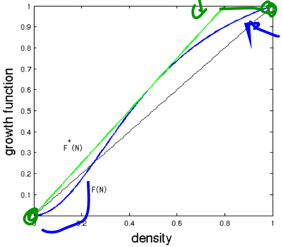
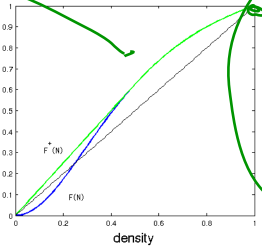
2. A monotone travelling wave can exist for at most one speed.
3. There exists a speed $c^* \in \mathbb{R}$ and a family of monotone travelling waves with speed c^*.

A bound for the spreading speed

Use the monostable theory to bound the spreading speed in the bistable case

$$c^* \leq \max_{s>0} \frac{1}{s} \ln \left(\max_{N>0} \frac{F(N)}{N} M(s) \right).$$



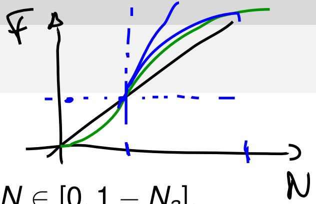


green(x) ≥ blue(x)

$Q^g \geq Q^b$

speed Q^g ≥ speed Q^b

Another traveling wave



Assume F is as in Lui's theorem. Define

$$G(N) = F(N + N_a) - N_a, \quad N \in [0, 1 - N_a].$$

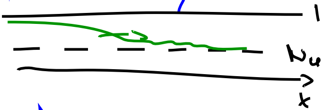
Then G is a monotable function and the IDE

$$N_{t+1}(x) = (K * G(N_t))(x)$$

has a linearly determined spreading speed and monotone traveling waves.

$G(0) = 0$, $G(1-N_a) = 1 - N_a$. G is monotone,

$G(N) \le G'(0) \cdot N$



$\Rightarrow$ There are TW for Q^G from 0 to $1 - N_a$

$\Rightarrow$ " " for Q^F from N_a to 1