Integrodifference equations in spatial ecology

Lecture 12: The shape of spatial spread

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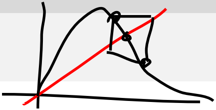
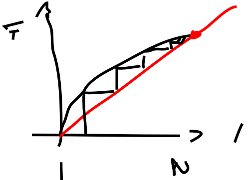
Wave profiles

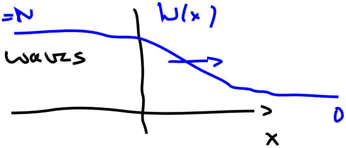


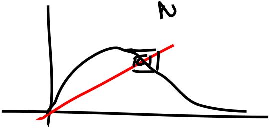
1. existence of monotone TW for monotone growth functions
2. shape?
3. non-monotone TW for non-monotone growth functions
4. shape?
5. what if the positive steady state is unstable? $N_t(x) = W(x-ct)$



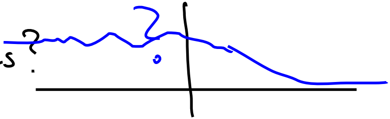
K is exp bounded $\Rightarrow$ $\exists$ Travelling waves

$F(N)=N$



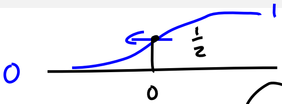


$\Rightarrow$ Travelling waves?



The TW equation

$\boxed{N_{t+1}(x) = N_t(x \pm c)}$



$K(x) = \frac{a}{2} e^{-a|x|}$

$$N(x + c) = \int_{-\infty}^{\infty} K(x - y)F(N(y))dy.$$

$F(1) = 1$

profile travels left: $c > 0$

boundary conditions $N(-\infty) = 0$, $N(\infty) = 1$

uniqueness: $N(0) = 1/2$

2^{nd} order, diff. eq.

Use Laplace kernel only:

$$\boxed{N''(x + c) = a^2[N(x + c) - F(N(x))]}$$

"delay"

Asymptotic expansion: rescaling

$$N''(x+c) = a^2[N(x+c) - F(N(x))]$$

Set new variable $\boxed{z = x/c}$ and write $\tilde{N}(x/c) = N(x)$. Then

$$\frac{dN}{dx} = \frac{d\tilde{N}}{dz} \cdot \frac{dz}{dx} = \frac{d\tilde{N}}{dz} \cdot \frac{1}{c}$$

$$\frac{1}{c^2}\tilde{N}''(z+1) = a^2\left(\tilde{N}(z+1) - F(\tilde{N}(z))\right)$$

$$\frac{1}{a^2c^2} = \varepsilon \text{ small}$$

$$\varepsilon \tilde{N}''(z+1) = \tilde{N}(z+1) - F(\tilde{N}(z))$$

write N again

Asymptotic expansion

$F(N^{(0)} + \varepsilon N^{(1)} + \dots) = F(N^{(0)}) + F'(N^{0}) \cdot \varepsilon N^{(1)} + \dots$

$$\epsilon N''(z+1) + F(N(z)) - N(z+1) = 0$$

Expand

$$N(z) = \overset{\varepsilon^0}{N^{(0)}(z)} + \overset{\varepsilon^1}{\epsilon N^{(1)}(z)} + \overset{\varepsilon^2}{\epsilon^2 N^{(2)}(z)} + \dots$$

Substitute

$$\varepsilon\left(N^{(0)''}(z+1) + \varepsilon N^{(1)''}(z+1) + \dots\right) + F\left(N^{(0)} + \varepsilon N^{(1)} + \varepsilon^2 N^{(2)} + \dots\right) - \left(N^{(0)} + \varepsilon N^{(1)} + \varepsilon^2 N^{(2)} \dots\right) = 0$$

Sort by powers of ε:

ε^0: $F(N^{(0)}(z)) - N^{(0)}(z+1) = 0$

ε^1: $N^{(0)''}(z+1) + F'(N^{(0)}(z))N^{(1)}(z) - N^{(1)}(z+1) = 0$

The zero-order equation

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

$$\boxed{N^{(0)}(z+1) = F(N^{(0)}(z))}$$

discrete

We get the non-spatial equation back!
We can solve with Beverton-Holt dynamics.

$$N^{(0)}(z) = \frac{R^z \cdot N_0}{(R^z - 1)N_0 + 1}$$

here $N_0 = \frac{1}{2}$

$$N^{(0)}(z) = \frac{R^z}{1 + R^z}$$

continuous

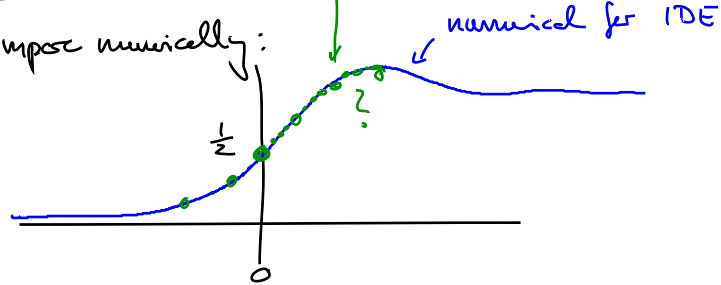
Extensions and caution

1) $k(x) = \begin{cases} a\, e^{-ax} & x > 0 \\ 0 & x < 0 \end{cases}$

2) $N^{(0)}(z+1) = F(N^{(0)}(z))$ $\qquad N^{0}(0) = \frac{1}{2}$

continuous vs discrete. $\qquad$ {0,1)

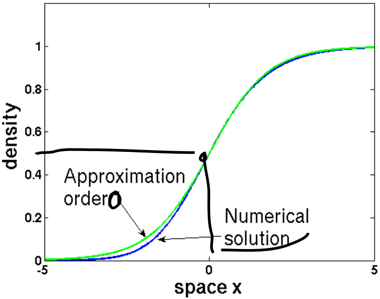
3) Compute numerically:

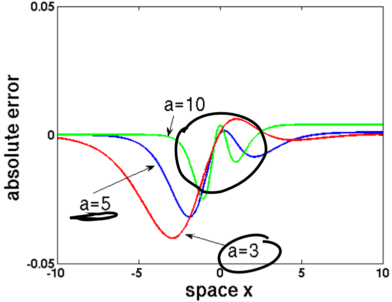


Illustration

$N_{t+1}(x) = \int K(x-y) F(N_t(y))\,dy$ $\qquad$ $\frac{a}{2} e^{-a|x|}$ $\qquad$ $a = \sqrt{\frac{2}{\sigma^2}}$

→ calculate c

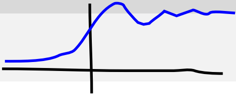




No need to solve the $N^{(1)}$ eq.

Kot 1992

Traveling waves in the 'phase plane'



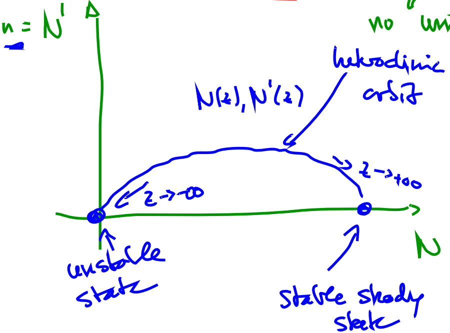
Start with

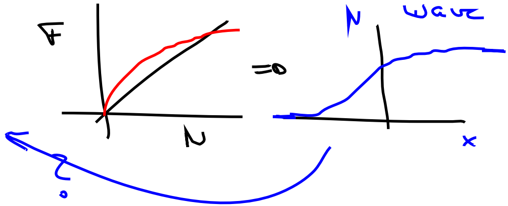
$$\boxed{N''(\overset{y}{x+c}) = a^2[N(\overset{y}{x+c}) - F(N(\overset{y-c}{x}))]}$$

and use $y = x + c$ to get

$$N'(y) = n(y), \qquad n'(y) = a^2[N(y) - F(N(y-c))]$$

no "uniqueness" in the phase plane.





Recall Ricker: $F(N) = Ne^{r(1-N)}$. State $N = 1$ is stable for $0 < r < 2$.

Plotting the phase plane

$F(N) = N e^{r(1-N)}$

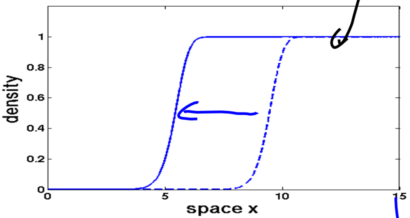
$N=1$ is steady state.

$F'(1) = 1-r$

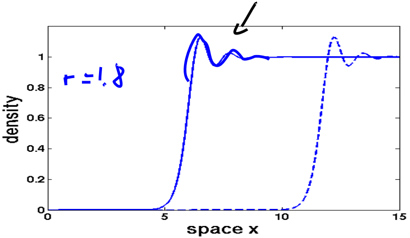
$\Rightarrow$ 1 is stable if $0<r<2$

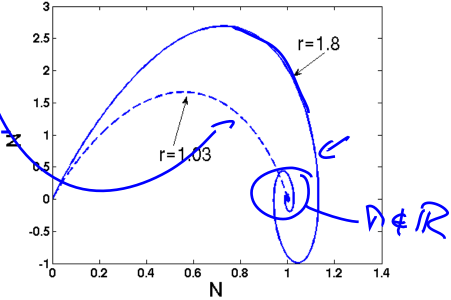
$\Rightarrow$ $F'(1)$ is increasing if $r<1$

monotone

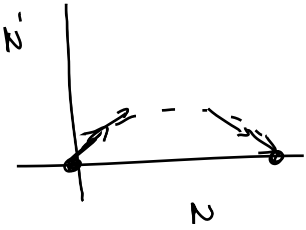


Ricker, $r=1.03$





Requirements for heteroclinic connections



1) Need steady states $(N^*, 0)$

2) Stability:

(0,0) has to have 1-dim unstable mfd.

(1,0) has to have 1-dim stable mfd

For steady state: $N' = 0$ and $F(N) = N$

Steady-state analysis

Linearize

$$N''(y) \approx a^2[N(y) - F'(N^*)N(y-c))]$$

Ansatz: $N(y) = e^{\mu y}$

$$\mu^2 e^{\mu y} \simeq a^2\left[e^{\mu y} - F'(N^*)e^{\mu(y-c)}\right]$$

$$\frac{\mu^2}{a^2} = 1 - F'(N^*)e^{-\mu c}$$

$c\mu = \lambda$

$\mu = \frac{\lambda}{c}$

$$\frac{\lambda^2}{a^2c^2} = 1 - F'(N^*)e^{-\lambda}$$

and find

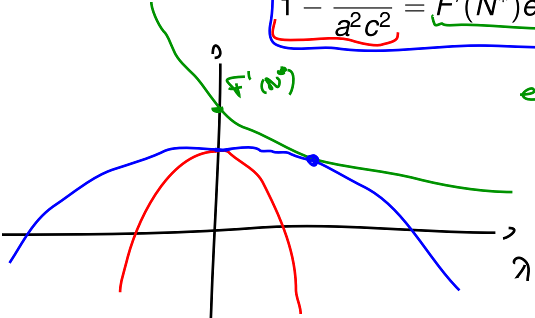
RHS

LHS

$$1 - \frac{\lambda^2}{a^2c^2} = F'(N^*)e^{-\lambda}$$

Case 1: $F'(N^*) > 1$ e.g. $N^* = 0$

$$1 - \frac{\lambda^2}{a^2c^2} = F'(N^*)e^{-\lambda} \quad (*)$$



e.g. make c larger:

$\Rightarrow$ there is a positive λ if c is large enough.

How large must c be? Tangency condition: $(*)$

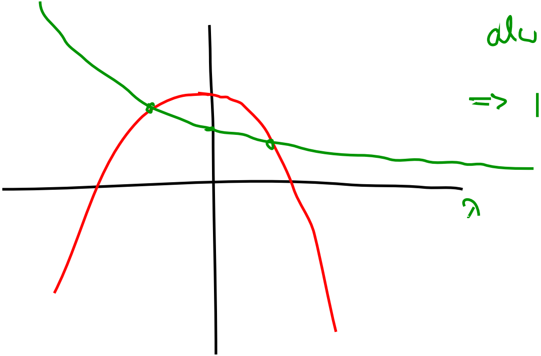
and $\quad + \frac{2\lambda}{a^2c^2} = + F'(N^*)e^{-\lambda} \quad (**)$

combined $\Rightarrow$ see chapter 5

Case 2: $0 \leq F'(N^*) < 1$

e.g. $N^* = 1$ is stable
and F is monotone
e.g. Ricker $0 < r < 1$

$$1 - \frac{\lambda^2}{a^2 c^2} = \underline{F'(N^*) e^{-\lambda}}$$

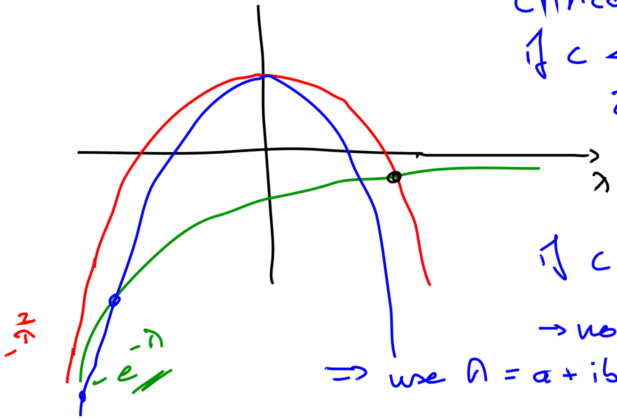


always $\lambda \in \mathbb{R}$, $\lambda < 0$

$\Rightarrow$ 1-d stable mfd.

Case 3: $F'(N^*) < 0$ e.g. Ricker $1 < r < 2$

$$1 - \frac{\lambda^2}{a^2 c^2} = \underline{F'(N^*)}e^{-\lambda}$$



critical c

if c < critical c:

2 intersections

⇒ stable wave.

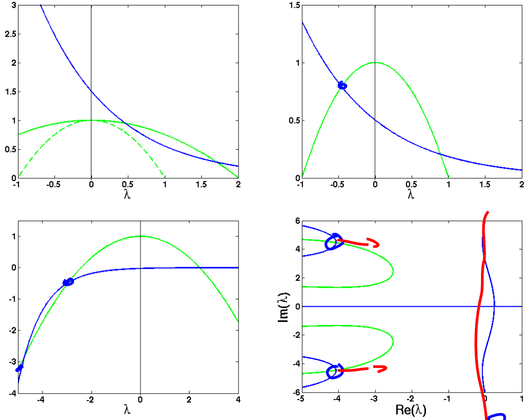
if c > crit. c

→ no negative real roots

⇒ use $\lambda = a + ib$

Illustration

case 1 case 2



case 3 a) Case 3 b

increase r

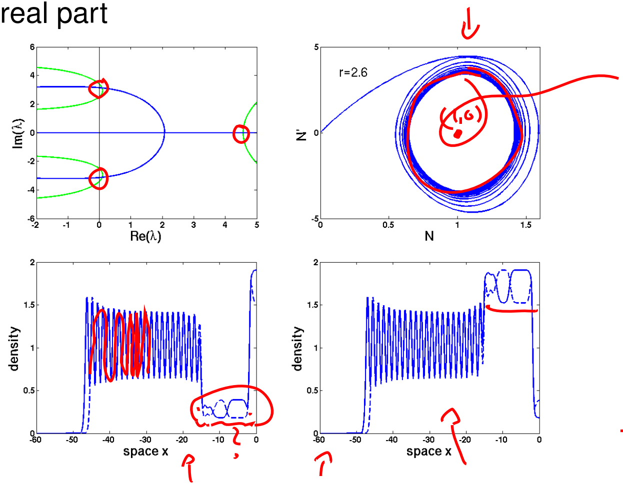
Re λ < 0 ⇒ stable mfd.

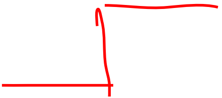
"decaying oscillations"

⇑ on stable mfd.

A Hopf bifurcation?

As r increases, there are complex conjugate eigenvalues with positive real part



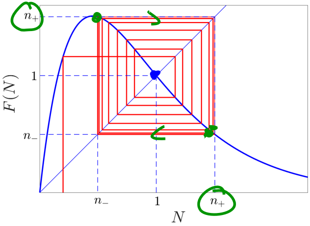


Two cycles A. Bourgeois

$F(n_+) = n_-$, $F(n_-) = n_+$

Back to non-spatial Ricker:

$F(F(n_+)) = n_+$

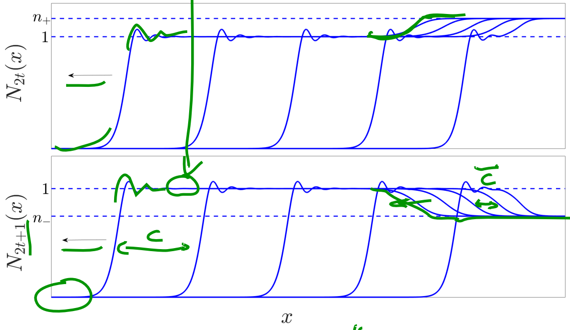


$G = F \circ F$

Simulations with two-cycles

F has stable 2-cycle (n_+, n_-)

observer



"travelling 2-cycle"

$c > \bar{c}$

$\Downarrow$

plateau at $N=1$ grows

dynamical stabilization

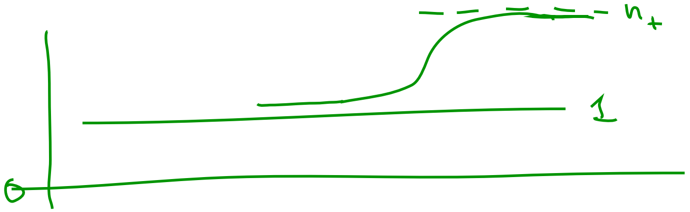
Kot 1989

The second-iterate operator

$$\tilde{Q}[N] = Q \circ Q[N] = \int K(x-y)F\left(\int K(y-z)F(N(z))dz\right)dy$$

Has fixed points 0, 1, n_-, n_+. (const. functions)

generalized spreading speed



A theorem

Assume that K is continuous and that its moment-generating function is bounded for at least one nonzero value. Let F be a growth function that satisfies the following conditions:

i) F is bounded and continuously differentiable;

ii) F has exactly one stable two-cycle, i.e. there exist $n_\pm$ such that $0 < n_- < 1 < n_+$, and $F(n_-) = n_+$ and $F(n_+) = n_-$, and all non-negative initial conditions converge to this two-cycle under the map $N_{t+1} = F(N_t)$;

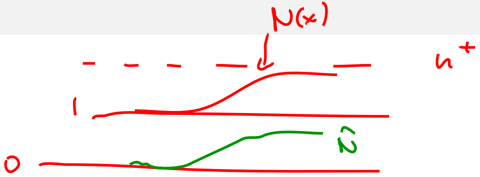
iii) $N = 1$ is the only fixed point of F on the interval $[n_-, n_+]$;

iv) $F'(1) < -1$;

v) F is non-increasing on the interval $[n_-, n_+]$.

Then, there exists a spreading speed $c^*_{(1,n_+)}$ for the operator $\widetilde{Q}$ from 1 to n^+. Furthermore, for every $c \geq c^*_{(1,n_+)}$, there exists a monotone traveling wave $W(x - ct)$ with $W(-\infty) = n_+$ and $W(\infty) = 0$.

Key idea



Shift the functions:

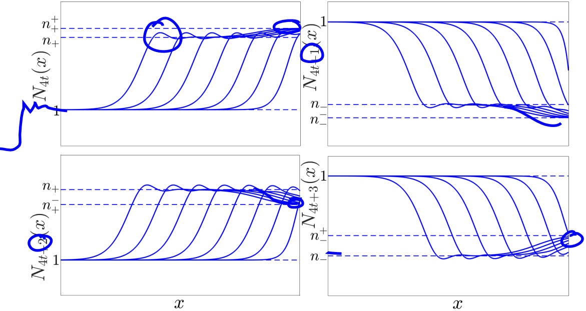
If $N(x) \in [1, n_+]$, define $\widehat{N}(x) = N(x) - 1 \in [0, n_+ - 1]$ and

$$\widehat{Q}[\widehat{N}](x) = Q \circ Q[N](x) - 1 = Q \circ Q[\widehat{N} + 1](x) - 1.$$

$[0, n_+ - 1]$

Then $\widehat{Q}$ satisfies the assumptions of the spread speed theorem.

A four-cycle



Summary: travelling waves

1. asymptotics
2. linear stability analysis when 1 is stable for F.
3. iterate operators and generalized spreading speeds when 1 is unstable.