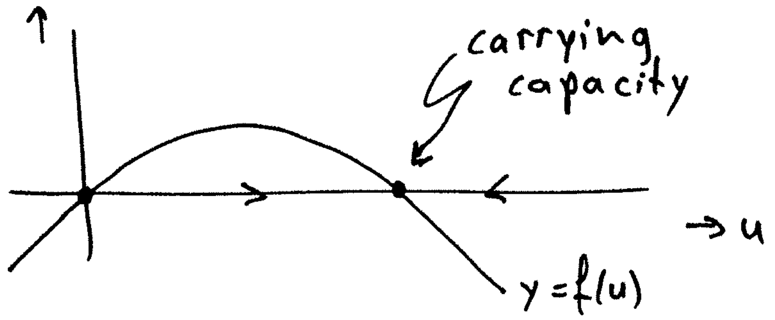
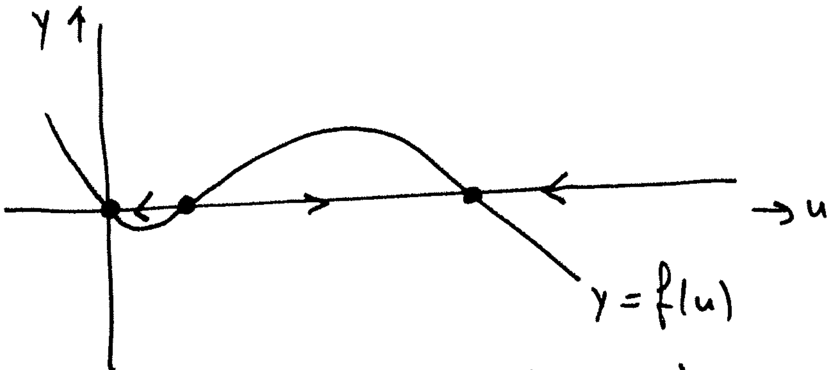
Spatial Ecology

single species

$\dot{u} = f(u)$



Allee effect
$\Downarrow$
bistability
$\Downarrow$



introduction must exceed threshold to be successful

Note: ODE model ignores development / maturation of individual

PSPM (physiologically structured population models) do incorporate maturation by first introducing the notion of i-state; at the p-level these models lead to delay equations

Also note: ODE ignores demographic stochasticity

Question: how fast does a newly introduced species grow to carrying capacity?

Answer: there exists a well defined asymptotic speed of propagation, aka 'spreading speed' c_0

Moral: caricatures are useful!

Consider $\frac{\partial u}{\partial t} = D \Delta u + r u$ $\quad D>0$, $r>0$, $x \in \mathbb{R}^2$

In fact, consider the fundamental solution

$$u(t,x) = \frac{1}{4\pi D t} e^{rt - \frac{|x|^2}{4Dt}}$$

note $\lim_{t\to\infty} u = \infty$, $\lim_{|x|\to\infty} u = 0$

Claim For any $\varepsilon > 0$

$$\lim_{t\to\infty} \sup\{u(t,x) : |x| \geq (\sqrt{4Dr} + \varepsilon)t\} = 0$$

$$\lim_{t\to\infty} \min\{u(t,x) : |x| \leq (\sqrt{4Dr} - \varepsilon)t\} = \infty$$

Conclusion The region in which the species has achieved a substantial density expands with rate $c_0 = 2\sqrt{Dr}$ (known as the Fisher speed or KPP speed)

Is this conclusion robust? Yes!

- nonlinear $\frac{\partial u}{\partial t} = D \Delta u + f(u)$

with $f(u) = u g(u)$ and $g(0) = r$ and $g(u) < g(0)$ for $u > 0$

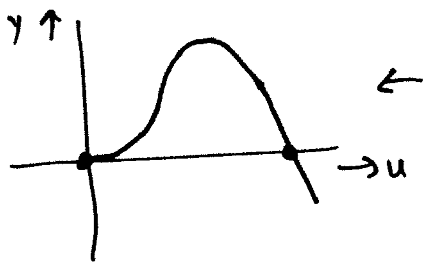
replace ∞ by the carrying capacity

use the $\boxed{\text{maximum principle, super- and subsolutions}}$

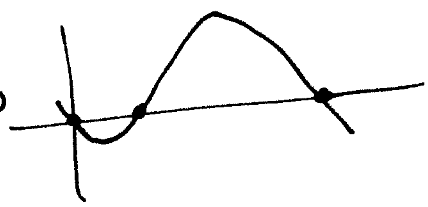
- finite domain $\Rightarrow$ intermediate asymptotics conclusion holds after peculiarities of initial condition are no longer important and boundary has no impact yet, so for times such that $c_0 t \ll$ domain size

<u>Mathematical curiosity</u>: what if

$g(u) < g(0)$ for $u > 0$ does not hold?



weak Allee $\leftarrow$ strong Allee $\rightarrow$



$\Uparrow$ we have to adapt the definition of c_0

$\Downarrow$

minimal speed for which <u>travelling wave</u> exists

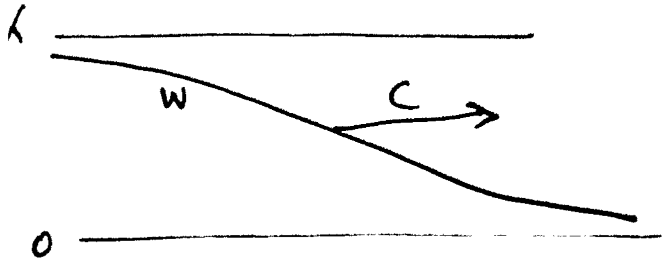
$\Uparrow$ here too adopt def. c_0 but in addition there are conditions on the initial condition

$\Downarrow$

$\exists !$ wave speed c_0

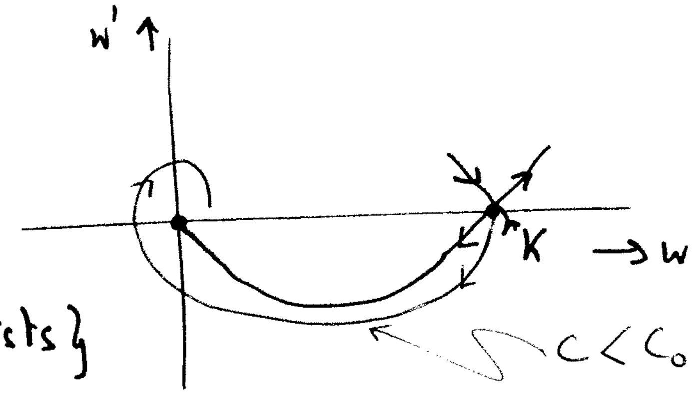
$$u(t,x) = w(x \pm ct)$$

profile: w; speed: c; direction: $\pm$ (does not matter, since we have <u>isotropy</u>)



$\xi := x \cdot \nu - ct \qquad Dw'' + cw' + f(w) = 0$

$\boxed{\text{phase plane analysis}}$



$c_0 = \min\{c : \text{tr.w.sol.}^n \text{ with speed } c \text{ exists}\}$

when $c_0 = 2\sqrt{Dg(0)}$ we say waves are <u>pulled</u>
when $c_0 > 2\sqrt{Dg(0)}$ we say waves are <u>pushed</u>

minimal wave speed is <u>true</u> speed of expansion:
$\boxed{\text{Aronson \& Weinberger 1975}}$: $u(0,\cdot)$ with <u>compact</u> support

$$\liminf_{t\to\infty} \min\{u(t,x) : |x| \leq ct\} \geq K \quad \text{if } c < c_0$$

$$\limsup_{t\to\infty} \sup\{u(t,x) : |x| \geq ct\} = 0 \quad \text{if } c > c_0$$

So waves with speed $c > c_0$ do <u>not</u> have much physical relevance (but characterizing initial data that do converge to these is quite a mathematical challenge, see Bramson, Uchiyama as well as modern work on branching Brownian motion)

Extensions

rivers : the drift paradox
moving climate
spatial heterogeneity
time periodicity
human digestive track ?

← robustness

Alternative equations : e.g. for plant disease transmitted by dispersing fungal spores

$$b(t,x) = \int_0^\infty \int_\Omega b(t-a, \xi)\, \underbrace{A(a, x, \xi)}_{|x-\xi| \text{ if homogeneous and isotropic}}\, d\xi\, da$$

$b(t,x)$ ↑ p-birth rate; a ↑ age

Hybrid models reproduction as a yearly event

(while consumption, predation, transmission of infection, dispersion, i.e., movement in space, occur in continuous time)

Nonlinear epidemic outbreak equation:

$$y(t,x) = \int_0^\infty \int_{\mathbb{R}^2} \left[1 - e^{-y(t-\tau,\xi)}\right] A(\tau, x-\xi)\, d\xi\, d\tau$$

Bounded Domains

We need to impose boundary conditions

no-flux : $-\nu \cdot \nabla u\big|_{\partial\Omega} = 0$

allows for "flat" (= spatially homogeneous) solutions

big monster at the boundary : zero Dirichlet $u\big|_{\partial\Omega} = 0$

in that case $g(0) > 0$ does not by itself guarantee persistence : for $|\Omega|$ too small extinction may occur

$\Rightarrow$ minimal critical patch size

Heterogeneity

$$\frac{\partial u}{\partial t} = D\Delta u + \beta(x)u - \mu(x)u \qquad u\big|_{\partial\Omega} = 0$$

Thm Let Ω be a bounded domain of class $C^{2,\alpha}$ and L an elliptic operator with coefficients of class $C^{0,\alpha}(\bar{\Omega})$, where $0<\alpha<1$. There exists a unique eigenvalue λ_1 of $-L$ characterized by the existence of a corresponding eigenfunction ϕ_1 (so $L\phi_1 + \lambda_1\phi_1 = 0$, $\phi_1 \not\equiv 0$, $\phi_1\big|_{\partial\Omega} = 0$) such that $\phi_1 \geq 0$ in Ω and $\frac{\partial\phi_1}{\partial\nu} < 0$ on $\partial\Omega$. Furthermore, λ_1 is simple and any other eigenvalue λ of $-L$ satisfies

$$\lambda_1 \leq \operatorname{Re} \lambda$$

with equality iff $\lambda_1 = \lambda$.

We call λ_1 the $\boxed{\text{principal eigenvalue}}$ and a corresponding positive eigenfunction is called principal eigenfunction

<u>Proof</u> Krein–Rutman (= ∞-dim Perron–Frobenius)

In order to apply this theorem, we need to know the

$$\boxed{\text{sign of } \lambda_1} \leftarrow \text{Cantrell \& Cosner}$$

Digression on Perron–Frobenius in population context:

$$\dot{x} = (\underset{\substack{\uparrow \\ \text{reproduction/} \\ \text{transmission}}}{T} + \Sigma) x$$

Σ: change-of-state

$T \geq 0$ $\quad \Sigma$ is POD (positive-off-diagonal)

Note $\quad -\Sigma^{-1} = \int_0^\infty e^{a\Sigma} \, da$, so $(-\Sigma^{-1})_{ij}$ is expected time an individual now in state j will spend in state i during the rest of its life (note that $\Sigma^{-1} \geq 0$)

$(-T\Sigma^{-1})_{ij}$ = expected # offspring produced by newborn individual with state j

offspring with state-at-birth i;

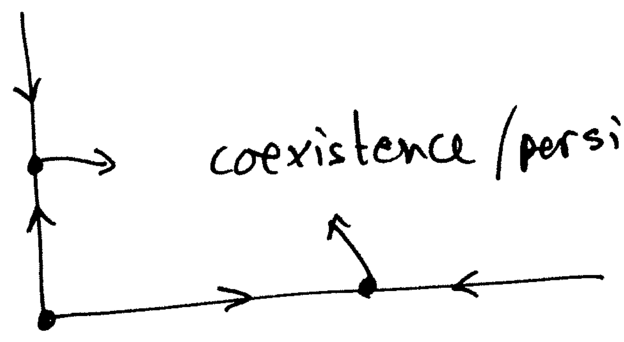
So $-T\Sigma^{-1}$ is the next-generation matrix
Its dominant eigenvalue is called
the basic reproduction number R_0

$$\boxed{\operatorname{sign}(R_0 - 1) = -\operatorname{sign} \lambda_1} \quad \leftarrow \text{Thieme}$$

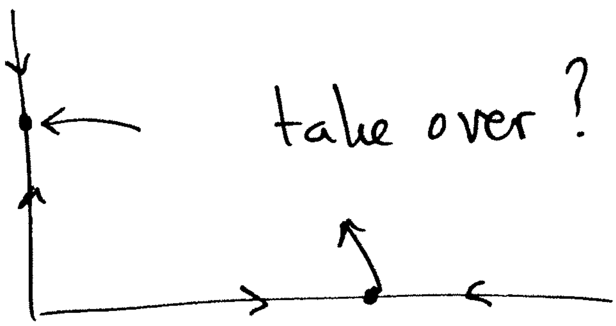
In spatial models, state-at-birth is <u>position</u> where individual is born.

Critical question: do movement and reproduction indeed take place at the same <u>time scale</u>?

<u>Multi-species</u>



coexistence/persistence/permanence



take over? Adaptive Dynamics!

e.g. evolution of dispersal strategy
Yuan Lou (among others)

Patterns

for scalar equations and convex domains and zero-flux b.c. NO stable patterns!
(diffusion equilibriates)

Turing: for systems of equations "flat" steady states may destabilize when diffusion coefficients are sufficiently unequal
(short range activation & long range inhibition)

Miscellaneous

Max Rietkerk: arid ecosystem do patterns provide early warning for catastrophic collaps?

i.) local correlation of
genetic relatedness
infection status
has strong impact on, respectively, evolution and disease dynamics

Solutions of diffusion equations are everywhere positive, which may lead to artefacts

Alternative representations of space:
lattices
networks

A bit related: do prey-predator cycles synchronize or are local cycles out of phase?
(same question for infectious disease oscillations)

ii) communication by way of chemical signals
e.g. quorum sensing of bacteria
plants attract natural ennemies of herbivores
by way of pheromones

iii) animal grouping : schools, herds, flocks, swarms

Projects

1. Maximum Principle, principal eigenvalue
   super- & sub-solutions
   Chapter 2 of "Reaction-diffusion equations and propagation phenomena" by H. Berestycki & F. Hamel
2. Fisher/KPP travelling waves via ODE (or PDE?)
3. Aronson & Weinberger: the asymptotic speed of propagation
4. integro-difference equations
5. Volterra integral equations with "non-local in space" effects: the spread of infectious disease
6. flowing rivers / moving climate
7. $\operatorname{sign}(R_0 - 1) = -\operatorname{sign} \lambda_1$
8. Turing instability