Adaptive evolution : a population approach

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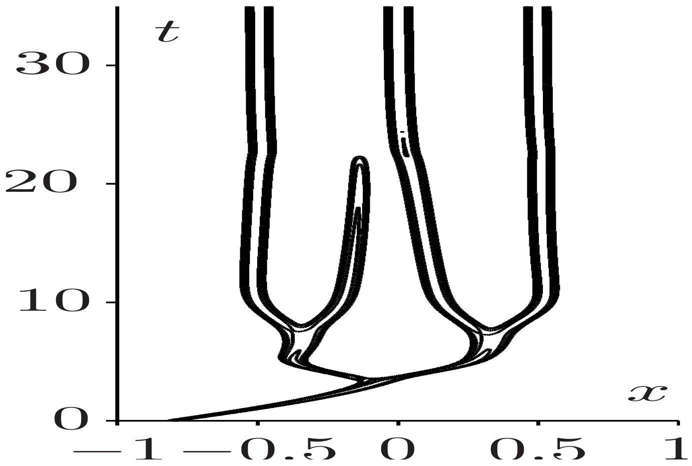
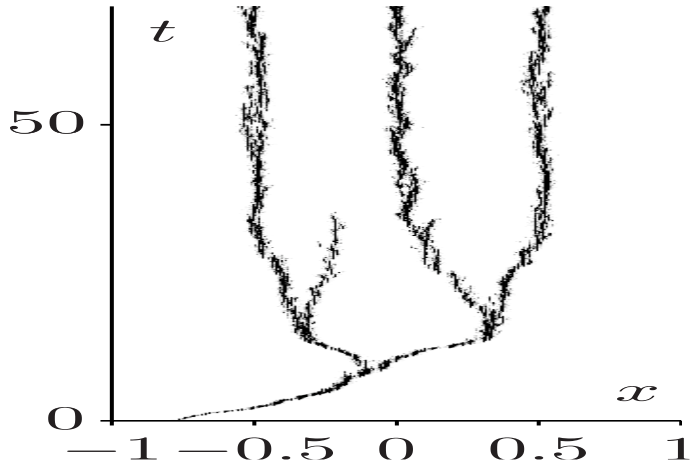




OUTLINE OF THE LECTURE

DIRECT COMPETITION AND POLYMORPHIC CONCENTRATIONS

I. Direct competition

II. Turing instability

II. Lyapunov functional

Direct competition

Other models are typically direct competiton

$$\frac{\partial}{\partial t} n(x,t) = n(x,t) \underbrace{\left[r(x) - \int C(x,y) n(t,y) dy \right]}_{:= R\left(x, [n(t)]\right)},$$

$r(x) =$ basic growth rate (non-necessarily positive)

$C(x,y) \geq 0$ competition kernel, non symmetric

Can model : Competition is higher when traits are closer, x competes again y only if $x \gg y$,...

See Gyllenberg and Meszena, Desvillettes, Jabin, Raoul, and Champagnat, Méléard

Direct competition

$$\frac{\partial}{\partial t}n(x,t) = n(x,t)\underbrace{\left[r(x) - \int C(x,y)n(t,y)dy\right]}_{:=R\left(x,[n(t)]\right)},$$

Examples

1. $C(x,y) = d(x)\psi(y)$ then

$$R\left(x,[n(t)]\right) = r(x) - d(x)I(t), \qquad I(t) = \int \psi(x)n(x,t)dx$$

2. $C(x,y) = \sum d_i(x)\psi_i(y)$ then

$$R\left(x,[n(t)]\right) = r(x) - \sum d_i(x)I_i(t), \qquad I_i(t) = \int \psi(x)n(x,t)dx$$

3. Convolution kernels

$$C(x,y) = K(x-y).$$

Direct competition

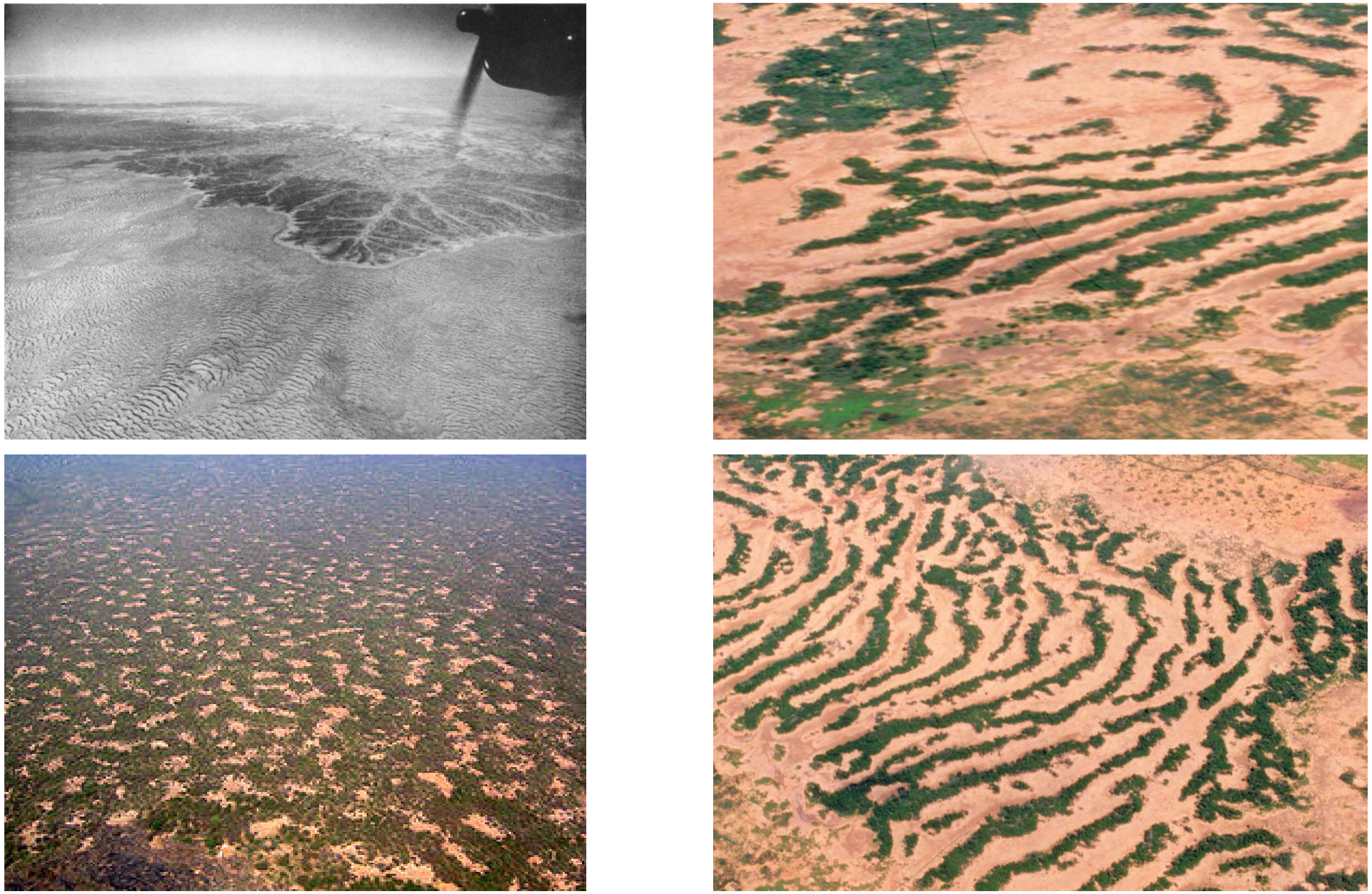
$$\frac{\partial}{\partial t} n(x,t) = n(x,t) \underbrace{\left[r(x) - \int C(x,y) n(t,y) dy \right]}_{:= R\left(x,[n(t)]\right)},$$

Examples

4. Fisher/KPP equation

$$C(x,y) = K(x-y) = \delta(x-y).$$

This explains why the model is used in ecology for access to long range resources



(i) Gapped Bush in Niger ; Nicolas Barbier'Survey over W regional park,
(ii) Tigger Bush ; from papers of Lefever, Barbier, Couteron, Deblauwe, Lejeune.

Direct competition

After rescaling

$$\varepsilon \frac{\partial}{\partial t} n_\varepsilon(x,t) = n_\varepsilon(x,t)\Big[r(x) - \int C(x,y) n_\varepsilon(y,t)dy\Big],$$

Question : Give general conditions on $C(x,y)$ ensuring that

$$n_\varepsilon(x,t) \underset{\varepsilon \to 0}{\longrightarrow} \sum \varrho_i(t) \delta\Big(x - \bar{x}_i(t)\Big)$$

Direct competition

$$\varepsilon \frac{\partial}{\partial t} n_\varepsilon(x,t) = n_\varepsilon(x,t)\Big[r(x) - \int C(x,y) n_\varepsilon(t,y) dy\Big],$$

Theorem Assume L^1 control on n_ε, n_ε^0 is monomorphic and

$$r(\cdot) \text{ concave,} \qquad\qquad C(\cdot, y) \text{ convex } \forall y,$$

then (after extraction)

$$n_\varepsilon(x,t) \underset{\varepsilon \to 0}{\longrightarrow} \bar{\varrho}(t)\delta(x - \bar{x}(t)),$$

Proof (Follow the strong theory) Assume

$$n_\varepsilon^0 := \exp\Big(\frac{\varphi_\varepsilon^0}{\varepsilon}\Big), \qquad \varphi_\varepsilon^0 \text{ concave.}$$

Direct competition

$$n_\varepsilon(x,t) := \exp\left(\frac{\varphi_\varepsilon(x,t)}{\varepsilon}\right),$$

$$\frac{\partial}{\partial t}\varphi_\varepsilon(x,t) = r(x) - \int C(x,y)n_\varepsilon(t,y)dy$$

therefore, $\varphi_\varepsilon(x,t)$ is concave, Lipschitz

$$\varphi_\varepsilon(x,t) \underset{\varepsilon\to 0}{\longrightarrow} \varphi(x,t),$$

and the maximum point of $\varphi(x,t)$ gives us

$$n_\varepsilon(x,t) \underset{\varepsilon\to 0}{\longrightarrow} \bar{\varrho}(t)\delta(x-\bar{x}(t))$$

Direct competition

The constrained H.-J. eq. holds

$$\begin{cases} \frac{\partial}{\partial t}\varphi(x,t) = r(x) - \bar{\varrho}(t)C(x,\bar{x}(t)) \quad \Big(+ |\nabla\varphi^2 \Big) \\ \\ \max_x \varphi(x,t) = 0 = \varphi(\bar{x}(t),t) \end{cases}$$

Apparent contradiction : two multipliers $\bar{\varrho}(t)$, $\bar{x}(t)$.

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Apparent contradiction : two multipliers $\bar{\varrho}(t)$, $\bar{x}(t)$.

But

$$r(\bar{x}(t)) - \bar{\varrho}(t)C(\bar{x}(t),\bar{x}(t)) = 0$$

which is still not enough because $\bar{x}(t) \in \mathbb{R}^d$

Convolution kernels

Is this concentration effect generic ?

Consider the Gaussian convolution case

$$\frac{\partial}{\partial t} n(x,t) = n(x,t)\Big[r(x) - K * n(x,t)\Big], \qquad x \in \mathbb{R}$$

$$r(x) = \frac{1}{\sqrt{\sigma_1}} e^{-\frac{|x|^2}{2\sigma_1}}, \qquad K(x) = \frac{1}{\sqrt{\sigma_2}} e^{-\frac{|x|^2}{2\sigma_2}}$$

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• $\sigma_1 > \sigma_2$, then a STEADY STATE solution is

$$n(x) = \frac{1}{\sqrt{\sigma}} e^{-\frac{|x|^2}{2\sigma}}, \qquad \sigma = \sigma_1 - \sigma_2$$

• $\sigma_1 \leq \sigma_2$, then STEADY STATE solutions are Dirac masses.

Convolution kernels

A simpler case

$$\frac{d}{dt}n(x,t) - \varepsilon\Delta n = \frac{1}{\varepsilon}n(x,t)\Big[1 - K * n(x,t)\Big],$$

$$K(z) \quad \text{a probabilty}$$

Then (from Auger, Genieys, Volpert)

- If $\widehat{K} \geq 0$, then $n(x) = 1$ is a linearly stable steady state

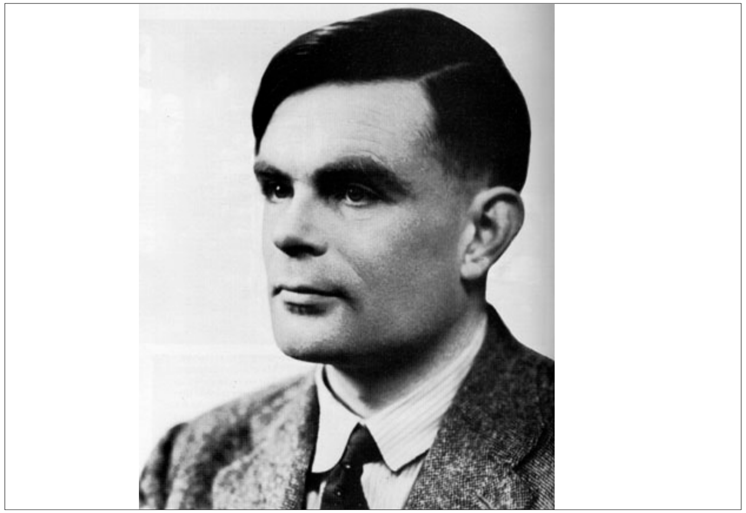
- If $\widehat{K}(\xi_0) < 0$, then $n(x) = 1$ and ε is small, then it is linearly unstable

These are Turing instabilities (only bounded unstable modes)

Direct competition

For $K = \delta$ the system is Fisher/KPP and STABLE. Convolution is regularizing. The outcome is UNSTABLE !

This is very counter-intuitive. Diffusion/convolution destablizes



Direct competition

With mutations

$$\begin{cases} \frac{\partial n(x,t)}{\partial t} - \varepsilon \Delta n(x,t) = \frac{n(x,t)}{\varepsilon}\Big(1 - K_b \star n(t)\Big), \\ \\ K_b(x) = \frac{1}{b^d}\, K(\frac{x}{b}). \end{cases}$$

As usual in reaction diffusion,
If $b \to 0$, ε *fixed*, (short range inhibitor, long range activitor), we recover Fisher front propagation,
If $\varepsilon \to 0$, b *fixed*, we recover Turing pattern formation... and Dirac concentrations which can be analyzed as before.

Convolution kernels

$$\frac{d}{dt}n(x,t) - \varepsilon \Delta n = \frac{1}{\varepsilon} n(x,t)\Big[1 - K * n(x,t)\Big], \qquad \int K(z)dz = 1,$$

- If $\widehat{K} \geq 0$, then $n(x) = 1$ is a linearly stable steady state
- If $\widehat{K}(\xi_0) < 0$, then $n(x) = 1$ and ε is linearly unstable

Proof the linearized equation is

$$\frac{d}{dt}n(x,t) - \varepsilon \Delta n = -\frac{1}{\varepsilon} K * n(x,t),$$

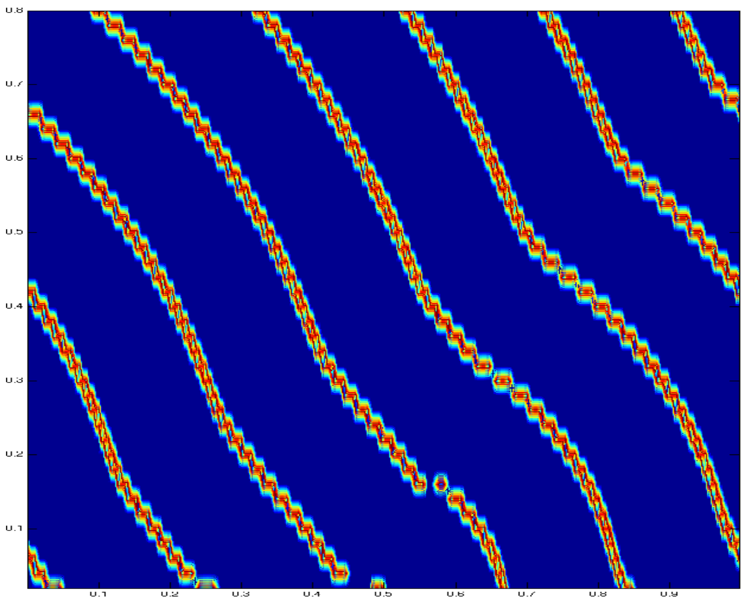
Try to find an eigenmode $n = e^{\lambda t}\widehat{n}(\xi)e^{i\xi . x}$

$$\lambda \widehat{n}(\xi) + \varepsilon \xi^2 \widehat{n}(\xi) = -\frac{1}{\varepsilon}\widehat{K}(\xi)\widehat{n}(\xi),$$

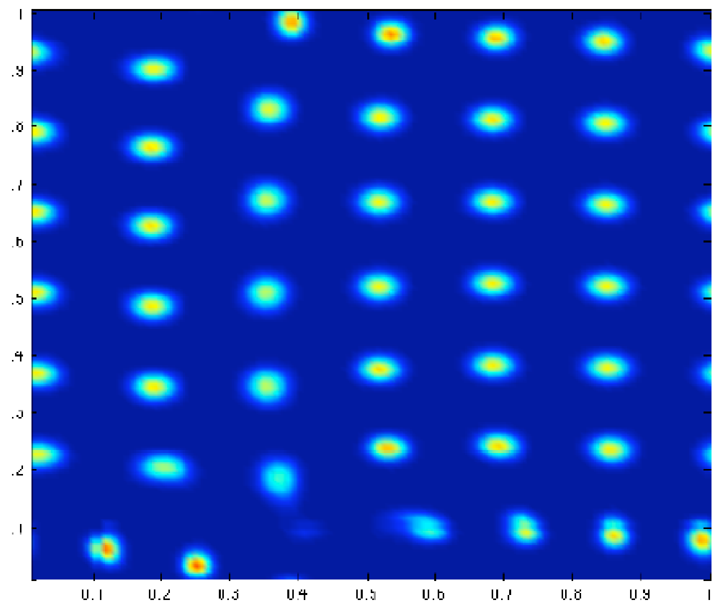
$$\lambda = -\varepsilon \xi^2 - \frac{1}{\varepsilon}\widehat{K}(\xi)$$

Convolution kernels

These models can create TURING patterns



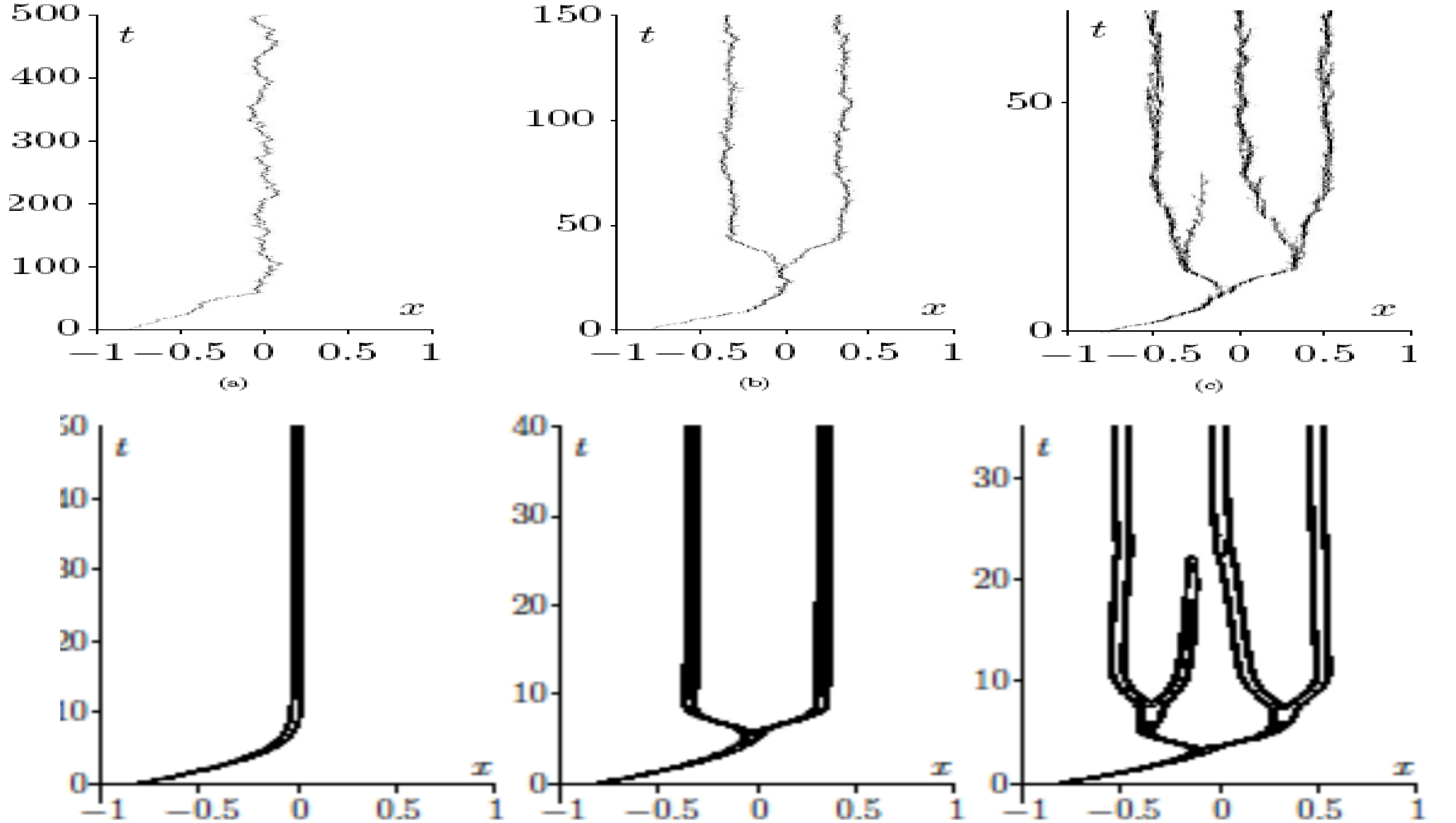
Asymmetric kernel

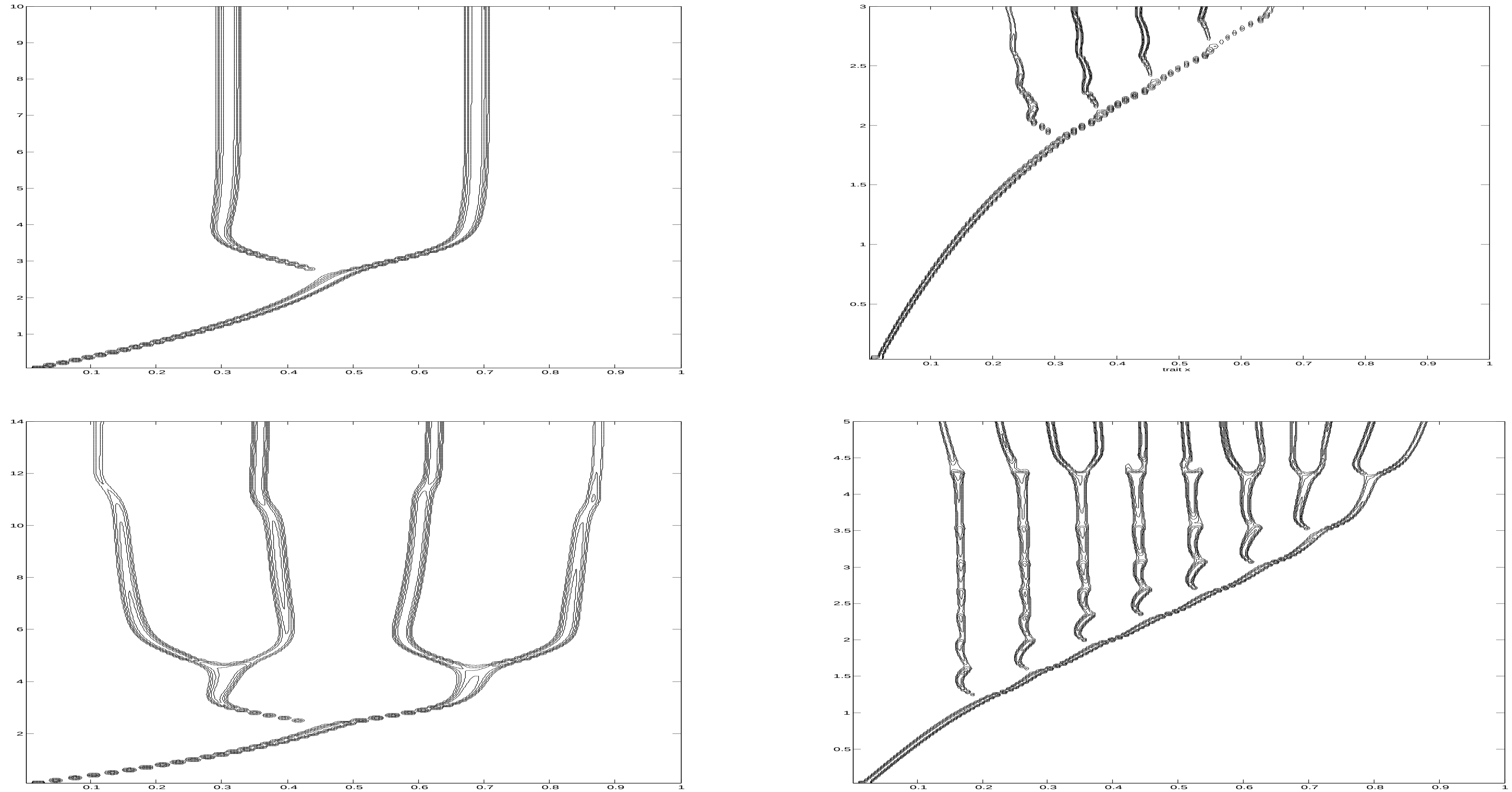


Nonlocal Fisher equation

. What is asymmetry ?

Motivation 1 : population adaptive evolution




trait x

Convolution kernels

What is asymmetry ?

$$n(x,t) \approx \sum_i \varrho_i(t)\delta(x-\bar{x}_i(t))$$

The dynamics is described by the constrainded H.-J. eq.

$$\begin{cases} \frac{\partial}{\partial t}\varphi(x,t) = 1 - \sum_i \varrho_i(t) K(x-\bar{x}_i(t)) + |\nabla\varphi|^2 \\ \\ \max_x \varphi(x,t) = 0 = \varphi(\bar{x}(t),t) \end{cases}$$

$$\frac{d}{dt}\bar{x}_i(t)) = \Big(-D^2\varphi\Big)^{-1}.\nabla K(x-\bar{x}_i(t)), \qquad \text{at } x = \bar{x}_i(t)$$

therefore the speed is decided by the sign of

$$\nabla K(0)$$

Convolution kernels

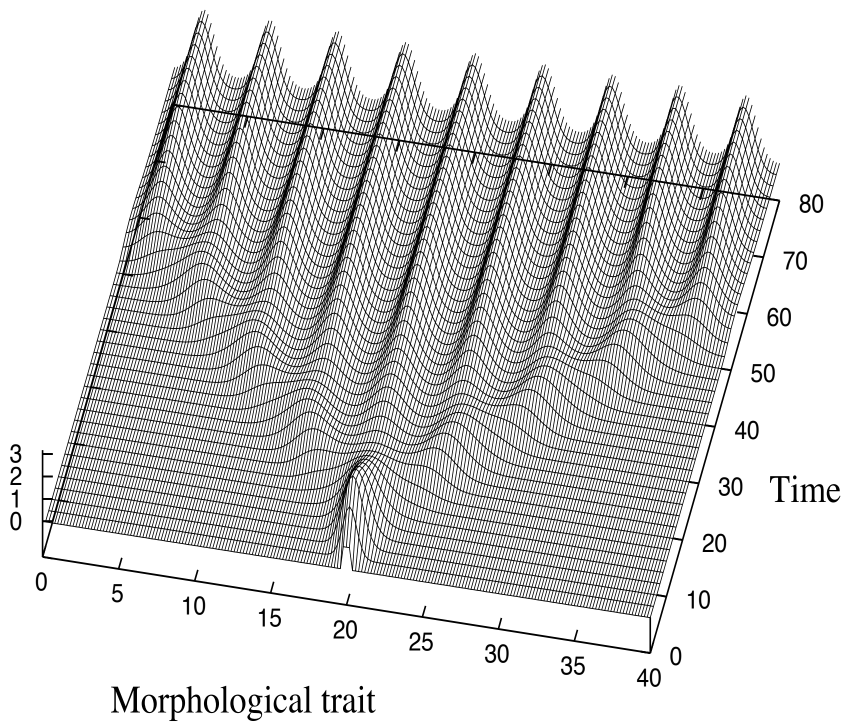
$$\frac{d}{dt}n(x,t) - \varepsilon \Delta n = \frac{1}{\varepsilon} n(x,t)\Big[1 - K * n(x,t)\Big], \qquad \int K(z)dz = 1,$$

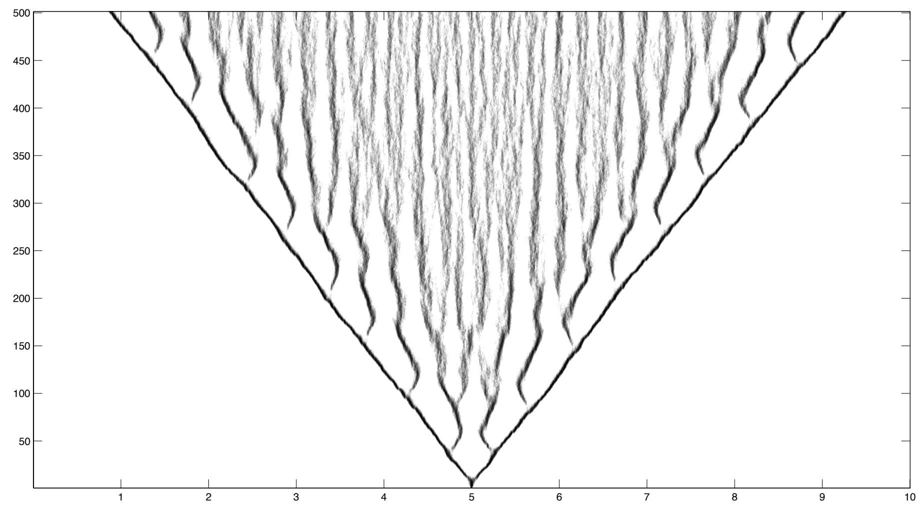
Fourier transform plays a role. Is there a nonlinear consequence ?

Theorem (Berestycki, Nadin, Perthame, Ryzhik) There are always generalized traveling waves solutions

- If $\widehat{K}(\xi) > 0$ then these are standard traveling waves
- For ε small they are non-monotonic
- When $\widehat{K}(\xi_0) < 0$ they can be unstable

Convolution kernels





(asymmetric branching, pulsating fronts)

Entropy

Fourier transform plays a role. Is there a nonlinear consequence ?

$$\frac{\partial}{\partial t} n(x,t) = n(x,t) \underbrace{\left[r(x) - \int C(x,y) n(t,y) dy \right]}_{:= R\big(x, [n(t)]\big)},$$

Definition An Evolutionary Stable Distribution (ESD) is a bounded measure $\bar{n}$ such that

$$R\Big(x, [\bar{n}]\Big) \leq 0, \qquad R\Big(x, [\bar{n}]\Big) = 0 \quad \textit{where} \quad \bar{n}(x) \neq 0,$$

This corresponds in the simpler case $\bar{n} = \bar{\varrho}_\infty \delta(x - \bar{x}_\infty)$ to

$$R(\bar{x}_\infty, \bar{\varrho}_\infty) = 0 = \max_x R(x, \bar{\varrho}_\infty)$$

Entropy

Theorem (P.-E. Jabin, G. Raoul) Assume $C(x,y)$ defines a positive operator

$$\int C(x,y)n(x)n(y)dxdy \geq 0 \qquad \forall n(x)$$

then the ESD $\overline{n}(x)$, if it exists, is unique and is attracting.

$$n(x,t) \underset{t\to\infty}{\longrightarrow} \bar{n}(x)$$

(with a positive initial data)

Entropy

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Remarks

- For $C(x,y) = K(x,y)$ this operator condition is $\widehat{K} > 0$
- For $C(x,y) = b(x)\psi(y)$ this operator condition is $b = \mu\psi$

This condition is too restrictive!

Entropy

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Proof. There is a convex entropy (smooth $\bar{n}$)

$$S(t) = -\int \overline{n}(x) \ln n(x,t)dx + \int n(x,t)dx.$$

$$\frac{d}{dt}S(t) = -\int\int K(x-y)\Big(n(x,t) - \overline{n}(x)\Big)\Big(n(y,t) - \overline{n}(y)\Big)dx\, dy$$

$$\leq 0$$

Open questions

Caracterize (r, C) that generate Dirac concentrations

Entropy method holds without mutation (diffusion)

How to connect operator positivity $\int C(x,y)n(x)n(y)dxdy \geq 0$ to the H.-J. eq.

$$\begin{cases} \frac{\partial}{\partial t}\varphi(x,t) = r(x) - \int C(x,y)n(y,t)dy \\ \\ \max_x \varphi(x,t) = 0. \end{cases}$$

Related questions

1. Direct competition is not usual. More usual are competitions for resources.

$$\begin{cases} \frac{\partial}{\partial t} n_\varepsilon(x,t) = n_\varepsilon(x,t)\Big[a_\varepsilon(x) + \frac{1}{\varepsilon}\int K(x,y)R_\varepsilon(y,t)dy\Big], \\ \frac{\partial}{\partial t} R_\varepsilon(y,t) = \frac{m(y)}{\varepsilon^2}\Big[R_{\mathrm{in}}(y) - R_\varepsilon(y,t)\Big] - \frac{1}{\varepsilon}R_\varepsilon(y,t)\int K(x,y)n_\varepsilon(x,t)dx, \end{cases}$$

has the limit

$$\frac{\partial}{\partial t} n(x,t) = n(x,t)\Big[a(x) - \int c(x,x')n(x',t)dx'\Big],$$

$$c(x,x') = \int K(x,y)\frac{R_{\mathrm{in}}(y)}{m(y)}K(x',y)dy.$$

always satisfy the operator positivity/entropy dissipation condition

Related questions

2. Fluctuating environment

$$\varepsilon \frac{\partial}{\partial t} n_\varepsilon(x,t) - \varepsilon^2 \Delta n_\varepsilon = n_\varepsilon(x,t) R\Big(x, \frac{t}{\varepsilon}, \varrho(t)\Big)$$

Conclusion : fluctuations may increase the population size of the ESS

Related questions

3. So far we have treated cases with homogeneous environment.

Next questions concern

- Interaction of space and trait
- How space can generate a non-proliferative advantage
- How space can create a continuum in traits