Adaptive evolution : a population approach

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DIRECT COMPETITION AND POLYMORPHIC CONCENTRATIONS

I. Direct competition

II. Turing instability

II. Lyapunov functional
Direct competition

Other models are typically direct competition

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

\[
:= R\left( x, [n(t)] \right)
\]

\(r(x) = \) 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 with \(y\) only if \(x \gg y\),...

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

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

Examples

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

   \[ R(x,[n(t)]) = r(x) - d(x)I(t), \quad I(t) = \int \psi(x)n(x,t)dx \]

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

   \[ R(x,[n(t)]) = r(x) - \sum d_i(x)I_i(t), \quad I_i(t) = \int \psi(x)n(x,t)dx \]

3. Convolution kernels

   \[ C(x,y) = K(x - y). \]
Direct competition

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

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’s Survey over W regional park,
(ii) Tigger Bush; from papers of Lefever, Barbier, Couteron, Deblauwe, Lejeune.
Direct competition

After rescaling

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

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

$$n_\varepsilon(x, t) \xrightarrow[\varepsilon \to 0]{} \sum \varrho_i(t) \delta(x - \bar{x}_i(t))$$
Direct competition

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

**Theorem** Assume \( L^1 \) control on \( n_\varepsilon, n^0_\varepsilon \) is monomorphic and

\[ r(\cdot) \text{ concave}, \quad C(\cdot, y) \text{ convex } \forall y, \]

then (after extraction)

\[ n_\varepsilon(x, t) \xrightarrow{\varepsilon \to 0} \bar{g}(t) \delta(x - \bar{x}(t)), \]

**Proof** (Follow the strong theory) Assume

\[ n^0_\varepsilon := \exp \left( \frac{\varphi_\varepsilon^0}{\varepsilon} \right), \quad \varphi_\varepsilon^0 \text{ concave.} \]
Direct competition

\[ n_\epsilon(x, t) := \exp\left(\frac{\varphi_\epsilon(x, t)}{\epsilon}\right), \]

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

therefore, \( \varphi_\epsilon(x, t) \) is concave, Lipschitz

\[ \varphi_\epsilon(x, t) \xrightarrow{\epsilon \to 0} \varphi(x, t), \]

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

\[ n_\epsilon(x, t) \xrightarrow{\epsilon \to 0} \bar{\varrho}(t)\delta(x - \bar{x}(t)) \]
Direct competition

The constrained H.-J. eq. holds

\[
\begin{align*}
\frac{\partial}{\partial t} \varphi(x, t) &= r(x) - \bar{\varrho}(t) C(x, \bar{x}(t)) \quad (+ |\nabla \varphi|^2) \\
\max_x \varphi(x, t) &= 0 = \varphi(\bar{x}(t), t)
\end{align*}
\]

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

The constrained H.-J. eq. holds

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

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

\[ \frac{\partial}{\partial t} n(x, t) = n(x, t) \left[ r(x) - K \ast n(x, t) \right], \quad x \in \mathbb{R} \]

\[ r(x) = \frac{1}{\sqrt{\sigma_1}} e^{-\frac{|x|^2}{2\sigma_1}}, \quad K(x) = \frac{1}{\sqrt{\sigma_2}} e^{-\frac{|x|^2}{2\sigma_2}} \]
Convolution kernels

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

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

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

• \( \sigma_1 \leq \sigma_2 \), then STEADY STATE solutions are Dirac masses.
Convolution kernels

A simpler case

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

\[ K(z) \text{ a probability} \]

Then (from Auger, Genieys, Volpert)

- If \( \hat{K} \geq 0 \), then \( n(x) = 1 \) is a linearly stable steady state
- If \( \hat{K}(\xi_0) < 0 \), then \( n(x) = 1 \) and \( \varepsilon \) 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 destabilizes
Direct competition

With mutations

\[
\begin{aligned}
\frac{\partial n(x,t)}{\partial t} - \varepsilon \Delta n(x,t) &= \frac{n(x,t)}{\varepsilon} \left( 1 - K_b \ast n(t) \right), \\
K_b(x) &= \frac{1}{b^d} K\left( \frac{x}{b} \right).
\end{aligned}
\]

As usual in reaction diffusion,
If \( b \to 0 \), \( \varepsilon \) fixed, (short range inhibitor, long range activator), 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

\[ \frac{d}{dt} n(x, t) - \varepsilon \Delta n = \frac{1}{\varepsilon} n(x, t) \left[ 1 - K \ast n(x, t) \right], \quad \int K(z) dz = 1, \]

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

**Proof** the linearized equation is

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

Try to find an eigenmode \( n = e^{\lambda t} \hat{n}(\xi) e^{i\xi \cdot x} \)

\[ \lambda \hat{n}(\xi) + \varepsilon \xi^2 \hat{n}(\xi) = -\frac{1}{\varepsilon} \hat{K}(\xi) \hat{n}(\xi), \]

\[ \lambda = -\varepsilon \xi^2 - \frac{1}{\varepsilon} \hat{K}(\xi) \]
Convolution kernels

These models can create TURING patterns

Asymmetric kernel
What is asymmetry?

Nonlocal Fisher equation
Motivation 1: population adaptive evolution
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 constrained H.-J. eq.

\[
\begin{cases}
\frac{\partial}{\partial t} \varphi(x, t) = 1 - \sum_i \varrho_i(t) K(x - \bar{x}_i(t)) + |\nabla \varphi|^2 \\
\max_x \varphi(x, t) = 0 = \varphi(\bar{x}(t), t) \\
\frac{d}{dt} \bar{x}_i(t) = \left(-D^2 \varphi\right)^{-1} \cdot \nabla K(x - \bar{x}_i(t)), \quad \text{at } x = \bar{x}_i(t)
\end{cases}
\]

therefore the speed is decided by the sign of \( \nabla K(0) \)
Convolution kernels

\[ \frac{d}{dt} n(x, t) - \varepsilon \Delta n = \frac{1}{\varepsilon} n(x, t) \left[ 1 - K \ast n(x, t) \right], \quad \int K(z)dz = 1, \]

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

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

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

Figure 2: Evolutionary branching. Periodic boundary conditions. Parameters are $a = 1$, $K = 1$, $b = 3$, $d = 0.05$, $L = 40$. Under the conditions of self-organization presented in section 3 an initially monomorphic population will undergo several successive branchings to become polymorphic. According to the numerical simulations, this polymorphic population is a stable asymptotic equilibrium. See figure 2 where the parameters are the same as in figure 1 except that the morphospace is larger ($L = 40$), and that initial conditions differ (the population is initially monomorphic). This monomorphic population first proliferates, but then it experiences an intense competition, which is favorable to its most different descendants:

(asymmetric branching, pulsating fronts)
Entropy

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

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

\[ := R(x,[n(t)]) \]

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

\[
R(x,[\bar{n}]) \leq 0, \quad R(x,[\bar{n}]) = 0 \quad \text{where} \quad \bar{n}(x) \neq 0,
\]

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

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

then the ESD $\bar{n}(x)$, 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**

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

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

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

**Remarks**

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

This condition is too restrictive!
**Entropy**

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

$$
\int C(x, y)n(x)n(y)dx\,dy \geq 0 \quad \forall n(x)
$$

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

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

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

$$
\frac{d}{dt}S(t) = -\int \int K(x-y)(n(x, t) - \bar{n}(x))(n(y, t) - \bar{n}(y))dx\,dy \leq 0
$$
Open questions

Caracterize \((r, C')\) that generate Dirac concentrations

Entropy method holds without mutation (diffusion)

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

\[
\begin{aligned}
\frac{\partial}{\partial t} \varphi(x, t) &= r(x) - \int C(x, y)n(y, t)dy \\
\max_x \varphi(x, t) &= 0.
\end{aligned}
\]
Related questions

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

\[
\begin{align*}
\frac{\partial}{\partial t} n_\varepsilon(x, t) &= n_\varepsilon(x, t) \left[ a_\varepsilon(x) + \frac{1}{\varepsilon} \int K(x, y) R_\varepsilon(y, t) \, dy \right], \\
\frac{\partial}{\partial t} R_\varepsilon(y, t) &= \frac{m(y)}{\varepsilon^2} \left[ R_{\text{in}}(y) - R_\varepsilon(y, t) \right] - \frac{1}{\varepsilon} R_\varepsilon(y, t) \int K(x, y) n_\varepsilon(x, t) \, dx,
\end{align*}
\]

has the limit

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

\[
c(x, x') = \int K(x, y) \frac{R_{\text{in}}(y)}{m(y)} K(x', y) \, dy.
\]

always satisfy the operator positivity/entropy dissipation condition
 Related questions

2. Fluctuating environment

\[ \varepsilon \frac{\partial}{\partial t} n_\varepsilon(x, t) - \varepsilon^2 \Delta n_\varepsilon = n_\varepsilon(x, t) R\left(x, \frac{t}{\varepsilon}, \varrho(t)\right) \]

Conclusion: fluctuations may increase the population size of the ESS
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