Modeling evolutionary branching by a nonlocal Fisher equation

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Motivation

Systems Biology and Cellular Modeling: biologists, computer scientists, mathematicians.

Olivier Gandrillon, cellular differentiation, hematopoiesis.
Hematopoiesis
Instructive model vs Darwinian point of view
Cellular darwinism

Signaling pathways specific recognition vs
Cell population effects non specific recognition competition for signals
Individually based simulations (cellular automata).

Population of elements recognizing signals (resources).
Recognition → duplication,
no recognition → death.

Recognizers characterized by a morphological trait.
Trait quantified by a real number.
Trait determines which signal is recognized.
Trait transmitted to offsprings (with slight variations).
Gandrillon → Sergei Atamas’ work (medical doctor):

6 Non specific (degenerate) recognition:

→ competition for the signals between similar recognizers.
Typical result of the simulations:

Evolutionary branching.
Mathematical model

“Nonlocal Fisher equation”:

\[ \partial_t f(t, x) = a f(t, x) \left( K - C(f)(t, x) \right) + d \Delta_x f(t, x), \]

- \( f \): population density, \( x \in \Omega \): morphological trait (\( \Omega \) morphological space).
- \( a f(t, x) \left( K - C(f)(t, x) \right) \): logistic term, ecological interactions.
- \( d \Delta_x f(t, x) \): diffusion term, evolutive phenomena.
Mathematical model

Logistic term, \( af(t, x) \left( K - C(f)(t, x) \right) \):

\( a \): malthusian parameter,
\( K \): carrying capacity of the environment (resources),
\( C(f)(t, v) = \int_{\Omega} \Phi(x - x') f(t, x') dx' \): degenerate competition, convolution with the competition kernel \( \Phi \):

\[
\begin{array}{c}
1/(2b) \\
\phi(X)
\end{array}
\]

\[
\begin{array}{c}
-b \\
0 \\
b
\end{array}
\]
Mathematical model

Diffusive term, $d \Delta_x f(t, x)$:

Spreading of the population in the morphospace, due to the slight modifications from generation to generation (mutations).

Ecological parameters: $a, b, K$.

Evolutive parameter: $d$.

Expect $d$ to be small with respect to $a, b, K$. 
Linear stability analysis

Homogeneous equilibrium $f \equiv K$ unstable if $\frac{d}{aKb^2}$ is small enough:

\[
\frac{d}{(aKb^2)}
\]

Stability condition depends on the actual form of $\Phi$, but general feature:

$\hat{\Phi} > 0 \rightarrow$ stabilizing effect, $\hat{\Phi} < 0 \rightarrow$ pattern forming effect.

Modeling evolutionary branching by a nonlocal Fisher equation – p. 8
Linear stability analysis

Instability:

Morphological trait

Time
Linear stability analysis

Similar to Turing structures but

- Not a competition between an activator and an inhibitor, only one population.
- Instability arises even in the absence of diffusion.
Evolutionary branching

Initially monomorphic population:

→ similar to Atamas’ results.
Evolutionary branching

Is it more important to know the history of a species or its place in its ecosystem? (And for cells?)

Who is best fitted? Adaptive dynamics: the fitness evolves due to the ecological interactions.
Evolutionary branching

How to introduce a new plant in an ecosystem?

Darwin (Origin of species): it must be different enough from the indigenous plants.
(See the plants successfully naturalised in the United States).
Divergence of characters

Darwin’s principle of divergence:

[...] the more diversified these descendants become, the better will be their chance in succeeding in the battle of life.

Thus the small differences distinguishing varieties of the same species, will steadily tend to increase till they come equal to the greater differences between species [...] 

(Origin of species).
Divergence of characters
Divergence of characters
Separation of time scales
Separation of time scales
Separation of time scales

Concentration phenomenon:
when the ecological and evolutive scales become more separated, the peaks become higher and more narrow.

Saltatory evolution:
When the scales are well separated, new lineages seem to appear without intermediate morphologies.
Asymmetric competition
Concentration points

With Benoit Perthame:

\[ \partial_t f_\varepsilon(t, x) = \frac{1}{\varepsilon} f_\varepsilon(t, x) \left( K - (\Phi \ast f_\varepsilon)(t, x) \right) + \varepsilon \Delta_x f_\varepsilon(t, x), \]

What is in the kernel of \( f \mapsto f \left( K - \Phi \ast f \right) \)?

Sums of Dirac masses?
Concentration points

With Benoit Perthame:

\[ \partial_t f_\varepsilon(t, x) = \frac{1}{\varepsilon} f_\varepsilon(t, x) \left( K - (\Phi * f_\varepsilon)(t, x) \right) + \varepsilon \Delta_x f_\varepsilon(t, x), \]

What is in the kernel of \( f \mapsto f \left( K - \Phi * f \right) \)?

\( f \equiv K : \)
Concentration points

With Benoit Perthame:

\[
\partial_t f_\varepsilon(t, x) = \frac{1}{\varepsilon} f_\varepsilon(t, x) \left( K - (\Phi \ast f_\varepsilon)(t, x) \right) + \varepsilon \Delta_x f_\varepsilon(t, x),
\]

What is in the kernel of \( f \mapsto f(K - \Phi \ast f) \)?

\[
f = \sum_{i=1}^{I} \rho_i(t) \delta(x - x_i(t)):
\]
Concentration points

With Benoît Perthame:

\[ \partial_t f_\varepsilon(t, x) = \frac{1}{\varepsilon} f_\varepsilon(t, x) \left( K - (\Phi * f_\varepsilon)(t, x) \right) + \varepsilon \Delta_x f_\varepsilon(t, x), \]

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What is in the kernel of \( f \mapsto f \left( K - \Phi \ast f \right) \)?

\[ f = \sum_{i=1}^{I} u(x - x_i(t)). \]
Concentration points

With Benoît Perthame:

\[ \partial_t f_\varepsilon(t, x) = \frac{1}{\varepsilon} f_\varepsilon(t, x) \left( K - (\Phi * f_\varepsilon)(t, x) \right) + \varepsilon \Delta_x f_\varepsilon(t, x), \]

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\[ \partial_t f_\epsilon(t, x) = \frac{1}{\epsilon} f_\epsilon(t, x) \left( K - (\Phi * f_\epsilon)(t, x) \right) + \epsilon \Delta_x f_\epsilon(t, x), \]

What is in the kernel of \( f \mapsto f \left( K - \Phi * f \right) \)?

No condition on \( \Phi \) and the initial data to obtain Dirac masses.

Condition on \( I \):
\[ \frac{1}{2b} < I < \frac{1}{b}. \]
Concentration points

Change of variable \( f_\varepsilon(t, x) = \exp\left(\frac{\phi_\varepsilon(t, x)}{\varepsilon}\right) \),

(exemple: \( f_\varepsilon(t, x) = \exp(-|x|^2/\varepsilon) \)).

\( \phi_\varepsilon \rightarrow \phi \), solution of a Hamilton-Jacobi equation:

\[
\partial_t \phi(t, x) = |\nabla_x \phi|^2 + r(t, x),
\]

\( r \): invasion exponent, \( (\nabla_x r \) selection gradient, Dieckmann).

Populated places: \( f > 0 \Leftrightarrow \phi = 0 \).
Concentration points

Change of variable $f_\varepsilon(t, x) = \exp \left( \frac{\varphi_\varepsilon(t, x)}{\varepsilon} \right)$,

(exemple: $f_\varepsilon(t, x) = \exp(-|x|^2/\varepsilon)$).

$\varphi_\varepsilon \to \varphi$, solution of a Hamilton-Jacobi equation:

$$\partial_t \varphi(t, x) = |\nabla_x \varphi|^2 + r(t, x),$$

$r$: invasion exponent, ($\nabla_x r$ selection gradient, Dieckmann).

If sum of Dirac masses located at $x_i$, $\varphi(t, x_i(t)) = 0$ for all $t$.

$\rightarrow$ equation for $\dot{x}_i$, motion of the peaks.
Adaptive dynamics: feedback of the population on the fitness. Link evolution-ecology.

Evolutionary cycles, evolution towards extinction, evolutionary branching...

Sylvie Méléard (probabilities), Laurent Desvillettes (PDEs), Odo Diekmann (ODEs), Benoît Perthame (Hamilton-Jacobi).

Cellular darwinism. Bipotent hematopoietic cells?
Thank you for your attention!