Growth, competition, and cooperation in spatial population genetics

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Competition

growth of a colony of two neutral E.Coli strains

Hallatscheck and Nelson (2007)
Competition in the ocean

growth of a colony of two neutral E.Coli strains

plankton bloom in the Barents sea

Hallatscheck and Nelson (2007)
Tel et al. (2005)
Invasion of a neutral variant of green crab along the eastern north american coast
Transport of larvae from currents (rather than fitness) determines invasion

Pringle et al. (2011)
Phytoplankton types

At the beginning of the bloom (end of August), 3 mo ahead of the days previously analyzed. At this initial date, PHYSAT-reprocessed satellite images show no pattern of prevalence, the whole region being dominated by picophytoplankton and nanoeukariotes (Fig. 2A). We labeled with different colors three regions of subpolar and one of subtropical origin, as displayed in Fig. 2B, and we advected forward in time for 3 mo the points within these circles (Fig. 2D). We estimated the initial position of these patches by a back-trajectory analysis (Fig. S8). The comparison of Fig. 2D and F shows a striking similarity between the ecological landscape from PHYSAT analysis (Fig. 2F) and the physical landscape of passive tracers numerically advected with altimetry-derived velocities (Fig. 2D). Water patches sustaining the same dominant type, even if spread far apart in the basin late in November, appear to have the same origin and advection history. Therefore, patches associated to the same type share their climatological prebloom characteristics. They also come in contact with the same environmental conditions (like nutrient enrichment at the shelf break; ref. 22) along their common pathway. These observations indicate horizontal stirring as a viable mechanism for restructuring the ocean surface in fluid dynamical niches, i.e., in water patches of contrasted physicochemical characteristics, capable of sustaining the emergence of different dominant types.

The role of the mesoscale surface turbulence can be pinpointed by repeating the advection experiment with only the large-scale component of the geostrophic currents, obtained by averaging the geostrophic velocities in space and time (respectively, 200 km and 3 mo) (Fig. 2C). In this case, the lack of mesoscale turbulence removed systematically interpatch intrusion filaments, reducing for each patch the extent and number of contacts between planktonic types.

The position and boundaries of the patches of dominant types evolve in the course of time. A direct observation of the temporal evolution of individual patches from PHYSAT data is not possible due to cloud episodes. Models have shown that planktonic fronts can be controlled by both physical forcing (23) and by the ecological dynamics of invasion/substitution processes (24). In our analysis, the borders of the observed patches compared well to the fronts generated by the horizontal stirring and separating water masses of different origin.

In order to analyze the temporal evolution of the plankton patches, we turned to the dynamics associated to the stirring process. In general, stirring creates filaments that are stretched in progressively thinner structures and are eventually dispersed by small-scale turbulence. Stirring intensity and the location of filaments it induces can be estimated by computing the largest finite-size Lyapunov exponent (FSLE) from the geostrophic velocities. An FSLE map (Fig. 2E) is obtained by measuring the backward-in-time divergence of particle trajectories initialized nearby. Highest FSLE values are found along the boundaries that separate water masses coming from regions far apart and match remarkably well the ecological boundaries of dominant types.
Logistic growth

\[ \frac{dc}{dt} = ac - bc^2 \]

- exponential growth at small density
- saturation at higher density (finite resources)

interpretation: growth of a population
OR spread in a population of an advantageous mutation

from J. Maynard Smith, “Evolutionary Genetics”, 1998
Fisher equation

\[ \partial_t c = D \partial_x^2 c + sc(1 - c) \]

Spread of a population (or advantageous mutation) in space

Fisher (1937)
Fisher equation

$$\partial_t c = D \partial_x^2 c + sc(1 - c)$$

Spread of a population (or advantageous mutation) in space

Basic result: propagating front of velocity

$$v = \sqrt{2Ds}$$

Fisher (1937)
Stochasticity and the stepping stone model

continuum limit: stochastic Fisher equation

\[ \frac{\partial_t c}{c} = D \frac{\partial^2_x c}{c} + \mu c(1 - c) + \sqrt{2c(1 - c)/N} \xi \]

where:
- \( c(x,t) \) = fraction of one of the two species
- \( \mu \) = selective advantage
- \( N \) = local population size
- \( D \) = diffusion constant

Kimura et al (1964)
Two different fixation mechanisms

stochastic Fisher equation

$$\partial_t c = D \partial_x^2 c + \mu c(1 - c) + \sqrt{2c(1 - c)/N} \xi$$

\[\mu \gg 1/N\]

Fisher wave, speed = \(\sqrt{2D\mu}\)

\[\mu = 0\]

Stochastic fixation
Overshooting the carrying capacity

forces affecting the density of individuals

\[ \partial_t c = -\partial_x [v(x)c] + D \partial_x^2 c + \mu c(1 - c) + \sqrt{2c(1 - c)/N} \xi \]

Problem: c>1 leads to imaginary noise

- clustering of finite-size particles
- inertial effects
- gyrotaxis (swimming)

Upwelling - large nutrients concentration

Downwelling - low nutrients concentration

other effects:

- clustering of finite-size particles
- inertial effects
- gyrotaxis (swimming)

Thursday, January 31, 2013
- individuals are advected and diffuse in space (Lagrangian description)
- reaction are implemented like in stochastic chemical kinetics
Eqs. for the densities

equations for the densities of A and B particles, $c_A(x, t)$ and $c_B(x, t)$

\[
\begin{align*}
\partial_t c_A(x, t) &= -\partial_x [v(x, t)c_A] + D\nabla^2 c_A + c_A(\mu_A - \lambda_{A A}c_A - \lambda_{A B}c_B) + \sigma_A \xi(x, t) \\
\partial_t c_B(x, t) &= -\partial_x [v(x, t)c_A] + D\nabla^2 c_B + c_B(\mu_B - \lambda_{B A}c_A - \lambda_{B B}c_B) + \sigma_B \xi'(x, t)
\end{align*}
\]

\[\sigma_i^2 = \frac{\mu_i c_i(1 + \lambda_{i A}c_A + \lambda_{i B}c_B)}{N}\] noise is well defined also when $c>1$
Example: neutral, no flow

- coarsening dynamics, fixation time is determined by diffusion

\[ D = 2 \times 10^{-4}, \mu = 1 \]

neutral dynamics:

\[
\begin{align*}
\partial_t c_A(x, t) &= D \nabla^2 c_A + \mu c_A (1 - c_A - c_B) + \sigma_A \xi(x, t) \\
\partial_t c_B(x, t) &= D \nabla^2 c_B + \mu c_B (1 - c_A - c_B) + \sigma_B \xi'(x, t)
\end{align*}
\]
Selective advantage

Species A reproduces faster (by a factor s)

\[
\begin{align*}
\partial_t c_A(x, t) & = D \nabla^2 c_A + \mu c_A (1 + s - c_A - c_B) + \sigma_A \xi(x, t) \\
\partial_t c_B(x, t) & = D \nabla^2 c_B + \mu c_B (1 - c_A - c_B) + \sigma_B \xi'(x, t)
\end{align*}
\]

The stochastic Fisher equation is recovered for the relative fraction \( f = c_A/(c_A + c_B) \) - quantitative agreement in absence of flows

Fixation probability

\[
p_{fix} = 1 - \exp \left[ -s N \int dx \ f(x, t = 0) \right]
\]

(independent of spatial diffusion)

SP, Benzi, Perlekar, Jensen, Toschi, Nelson (2013)
**Mutualism**

- reduced competition between alleles

\[
\frac{d}{dt} c_A = \mu c_A (1 - c_A - c_B) + \epsilon_A c_A c_B + \text{noise}
\]

\[
\frac{d}{dt} c_B = \mu c_B (1 - c_A - c_B) + \epsilon_B c_A c_B + \text{noise}
\]

mean field: exponentially long fixation times

\[
t^* \sim \exp \left[ \frac{N \min(\epsilon_A^2, \epsilon_B^2)}{2\mu \epsilon_A + \epsilon_B} \right].
\]
\[ \begin{align*}
\partial_t c_A(x, t) &= D \nabla^2 c_A + \mu c_A (1 - c_A - c_B) + \epsilon_A c_A c_B + \sigma_A \xi(x, t) \\
\partial_t c_B(x, t) &= D \nabla^2 c_B + \mu c_B (1 - c_A - c_B) + \epsilon_B c_A c_B + \sigma_B \xi'(x, t)
\end{align*} \]

\hspace{1cm}

\begin{align*}
\epsilon_A = \epsilon_B = 0.7
\end{align*}

**Mutualism - 1d**
\[
\begin{align*}
\partial_t c_A(x, t) &= D \nabla^2 c_A + \mu c_A (1 - c_A - c_B) + \epsilon_A c_A c_B + \sigma_A \xi(x, t) \\
\partial_t c_B(x, t) &= D \nabla^2 c_B + \mu c_B (1 - c_A - c_B) + \epsilon_B c_A c_B + \sigma_B \xi'(x, t)
\end{align*}
\]
Flows: linear velocity field

\[ v(x) = -k x \]

\[ k = 0.075, D = 2 \times 10^{-4}, \mu = 1 \]

coexistence of neutral species
Dynamics of boundaries

even number of boundaries, fast fixation

odd number of boundaries, demixing

-> bimodal fixation time distribution
Linear flow + reproductive advantage

Neutral

Red reproduces 30% faster

balance between flow and Fisher wave $\delta x = k^{-1} \sqrt{2D_s}$
Sine wave

\[ v(x) = k \sin(x) \]

\[ k = 10^{-2}, \quad D = 2 \times 10^{-4}, \quad \mu = 1 \]

always very short fixation time (never odd number of boundaries)
Fixation time

Theory:

if boundary collapse exponentially, then:

\[ \tau_f = \tau_0 + \frac{c}{k} \]

k = average gradient close to the sink
Fixation time

Theory:

\[ u(x) = -k(x-x_0) \]

if boundary collapse exponentially, then:

\[ \tau_f = \tau_0 + \frac{c}{k} \]

\[ k = \text{average gradient close to the sink} \]

Turbulence

\[ V(x) \sim \sin(x) \]

Fixation is much faster than in neutral theory
2D dynamics

density of interfaces scales as:

\[ \frac{1}{\sqrt{t}} \quad 1D \]
\[ \frac{1}{\log(t)} \quad 2D \]

-> fixation is a very slow process
dramatic reduction in number of particles (effective carrying capacity) and fixation times also with small compressibility
2D + compressible flow

2D “slice” of 3D Navier-Stokes.
Diffusion determines an advantage

- when two species expand into open space, advantage can be estimated by looking at the difference of Fisher wave speeds

- what happens if they are mixed?
neutral

red diffuses 5% faster
## Theory

### Equation for the Relative Fraction $f = c_A/(c_A + c_B)$

$$\partial_t f = \nabla^2 f + \delta D (1 - f) \nabla^2 f + \sqrt{\frac{2 \mu f (1 - f)}{N}} \xi$$

### Scaling in $N$ from Perturbation Theory

$$\langle f(t) \rangle \approx N \delta D g[t/(DN^2), D]$$
Conclusions

- flows can radically change the outcome of competition

- relaxing the assumption of constant total density leads to interesting effects also in the absence of flows