Large population and rare mutations asymptotics for a spatially structured population

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Aim : to understand the sensibility to heterogeneously distributed resources and the interplay between spatial dynamics and evolutionary changes.

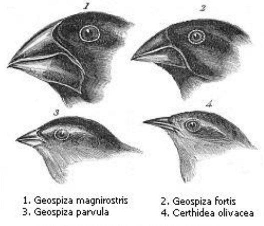

Figure: Finches from Galapagos Archipelago

Model description

For any time $t \geq 0$, the individual i is characterized by:

- its **phenotypic trait**, $U_t^i \in \mathcal{U}$, compact subset of $\mathbb{R}^q$,
- its **location**, X_t^i, that belongs to $\mathcal{X}$, open, bounded and convex subset of $\mathbb{R}^d$.

Definition

The total population is represented at any time t by the finite measure:

$$\nu_t^K = \frac{1}{K} \sum_{i=1}^{N_t} \delta_{(X_t^i, U_t^i)}$$

where

- N_t is the number of individuals at time t,
- K is a scaling parameter.

Migration

Any individual with phenotypic trait u moves according to a diffusion driven by the following stochastic differential equation normally reflected at the boundary of $\mathcal{X}$:

$$\boxed{dX_t = \sqrt{2m^u} Id \cdot dB_t - n(X_t) dl_t}$$

where

- l is an adapted continuous, non-decreasing process with $l_0 = 0$,
- B is a d dimensional brownian motion.

Birth and death dynamics

An individual with location $x \in \mathcal{X}$ and trait $u \in \mathcal{U}$:

- gives **birth** to a new individual at rate

$$\boxed{b^u(x)},$$

  - with probability $\boxed{1 - q_K \cdot p}$, the offspring is a **clone**,
  - with probability $\boxed{q_K \cdot p}$, the offspring is a **mutant**.

- dies because of **natural death** at rate

$$\boxed{d^u(x)}.$$

- dies because of **competition** at rate

$$\boxed{\frac{1}{K} \sum_{i=1}^{N_t} c^{u,u^i}(x^i)}.$$

Assumptions

Two scalings :

- **Large population** asymptotic: $\boxed{K \to +\infty}$.
- **Rare mutations** asymptotic: $\boxed{q_K \to 0}$.

First asymptotic

Assume that

$$\nu_0^K \underset{K\to+\infty}{\Rightarrow} \xi_0 \text{ with } \xi_0(dx,dw) = \xi_0^u(dx)\delta_u(dw) + \xi_0^v(dx)\delta_v(dw),$$

Theorem (Champagnat, Méléard (2007))

$$(\nu_t^K)_{t\in[0,T]} \underset{K\to+\infty}{\Rightarrow} (\xi_t)_{t\in[0,T]}$$

such that

$$\xi_t(dx,dw) = \xi_t^u(dx)\delta_u(dw) + \xi_t^v(dx)\delta_v(dw),$$

and ξ *is the weak solution to :*

$$\partial_t \xi_t = m^w \Delta_x \xi_t + \left(b^w(x) - d^w(x) - \int_{\mathcal{X}\times\mathcal{U}} c^{ww'}(y)\xi_t(dy,dw') \right)\xi_t, \quad (1)$$

with Neumann boundary condition.

Long time behavior of Equation (1)

Theorem (L.,Mirrahimi,Méléard)

For any initial condition in $L^2(\mathcal{X})$*, the solution to* (1) *converges in* $L^\infty(\mathcal{X})$ *towards a stationary state,*

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For any initial condition in $L^2(\mathcal{X})$, the solution to (1) converges in $L^\infty(\mathcal{X})$ towards a stationary state,

and we can explicit two parameters :

- $\boxed{f_{v\to u}}$: invasion fitness of an individual v in a u-population
- $\boxed{f_{u\to v}}$: invasion fitness of an individual u in a v-population

which describe the stability of the stationary states :

1) the null state $(0,0)$: unstable,
2) the monomorphic state $(\bar{\xi}^u, 0)$: stable iff $f_{v\to u} < 0$,
3) the monomorphic state $(0, \bar{\xi}^v)$: stable iff $f_{u\to v} < 0$,
4) and a state with coexistence which exists and is stable iff $f_{v\to u} > 0$ and $f_{u\to v} > 0$.

Exit time of a neighborhood of the equilibrium

The initial population is dimorphic such that

$$\boxed{\nu_0^{K,u} \approx \bar{\xi}^u \text{ et } \nu_0^{K,v} = \frac{\delta_{x_0}}{K}}.$$

Question:

How long does the **stochastic process** stay close to the equilibrium $\bar{\xi}^u$?

We use the Wasserstein distance between two measures :

$$\mathcal{W}(\nu, \mu) = \sup_{f \in Lip, \|f\|_{Lip} \leq 1} \left| \int f d\nu - \int f d\mu \right|.$$

Exit time of a neighborhood of the equilibrium

There exist γ', ϵ, $V > 0$ such that:

$$\text{if } \mathcal{W}(\nu_0^{K,u}, \bar{\xi}^u) < \gamma' \text{ and } \nu_0^{K,v} \in B_{\mathcal{W}}(0, \epsilon)$$

Theorem

$$\mathbb{P}_{\nu_0^K}\Bigg(\underbrace{T_\gamma^{K,u}}_{\substack{\textit{first time}\\ \textit{such that}\\ \mathcal{W}(\nu_t^{K,u},\bar{\xi}^u)>\gamma}} > e^{KV} \wedge \underbrace{T_\epsilon^{K,v}}_{\substack{\textit{first time}\\ \textit{such that}\\ \nu_t^{K,v}\in B_{\mathcal{W}}(0,\epsilon)}} \wedge \underbrace{S_1}_{\substack{\textit{first}\\ \textit{mutation}\\ \textit{time}}} \Bigg) \underset{K\to+\infty}{\longrightarrow} 1.$$

Invasion time of a mutant

When a mutant with trait v appears, the mutant population can be approximated by a branching diffusion :

- move according to a diffusion with coefficient m^v,
- birth rate $b^v(x)$,
- death rate $d^v(x) + \int_{\mathcal{X}} c^{v,u}(y)\bar{\xi}^u(dy)$,
- the first mutant appears at the location $x_0 \in \mathcal{X}$.

Questions:

- ▷ What characterizes the survival probability of the diffusion process?
- ▷ How long does it take for its size to be non-negligible compared to a parameter K which tends to $+\infty$?

Invasion time of a mutant

Let T_0 be the extinction time,
let $T_{K\epsilon}$ be the first time when the population reaches the size $K\epsilon$.

Theorem

$$\mathbb{P}_{x_0}(T_{K\epsilon} < T_0) \underset{K \to +\infty}{\longrightarrow} \phi(x_0)$$

$$\mathbb{P}_{x_0}(T_{K\epsilon} < t_K) \underset{K \to +\infty}{\longrightarrow} \phi(x_0), \ \textit{with } t_K \gg \log(K),$$

where

- ▷ **1^{st} case** *($f_{v \to u} < 0$):* $\phi \equiv 0$,
- ▷ **2^{nd} case** *($f_{v \to u} > 0$): ϕ is the unique positive solution to the following elliptic equation with Neumann boundary condition* $0 = m^v \Delta_x \phi + (b^v - d^v - \int_{\mathcal{X}} c^{vu} \bar{\xi}^u)\phi - b^v \phi^2$.

Convergence to a spatially structured TSS

Assumptions :

- **Large population** asymptotic: $\boxed{K \to +\infty}$.
- **Rare mutations** asymptotic: $\boxed{q_K \to 0}$.

  The mathematical link between K and q_K:

$$\boxed{\log(K) \ll \frac{1}{Kq_K} \ll e^{KV}}, \text{ for any } V > 0.$$

- **"Invasion-Implies-Fixation"**: two different traits cannot coexist for a long time scale.

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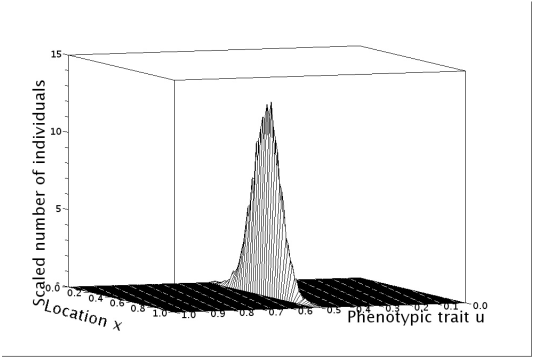
- **"Invasion-Implies-Fixation"**: two different traits cannot coexist for a long time scale.

Aim : change the time scale $t \mapsto \frac{t}{Kq_K}$.

Simulations



Convergence to a spatially structured TSS

Theorem

$$\boxed{(\nu^K_{t/Kq_K})_{t\in[0,T]} \underset{t\to+\infty}{\longrightarrow} (\Lambda_t)_{t\in[0,T]}}$$

(in the sense of the finite dimensional distributions)

$(\Lambda_t)_{t\geq 0}$ is a jump process on $\{\bar{\xi}^w\delta_w, w\in\mathcal{U}\}\subset M_F(\mathcal{X}\times\mathcal{U})$, it jumps from the state u to the state v with infinitesimal rate

$$\int_{\mathcal{X}} p^u(x)b^u(x) \underbrace{\phi^{uv}(x)} \underbrace{\theta(x,u,v)} \bar{\xi}^u(dx)dv$$

Invasion probability mutation kernel

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Thank you.