Evolution of a quantitative trait in a metapopulation setting: Propagation of chaos meets adaptive dynamics

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Joint work with Amaury Lambert, Hélène Leman and Hélène Morlon

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Biological motivation

Understanding the drivers of biodiversity

Study the link between Ecology and Evolution:

▷ Quantitative trait distributed in a population ;

▷ Mechanisms : ◦ Heredity ◦ Mutations (Rares et small) ◦ Selection ◦ Migration (Rares)

Hofbauer & Sigmund (1990); Marrow et al. (1992); Metz et al. (1992)

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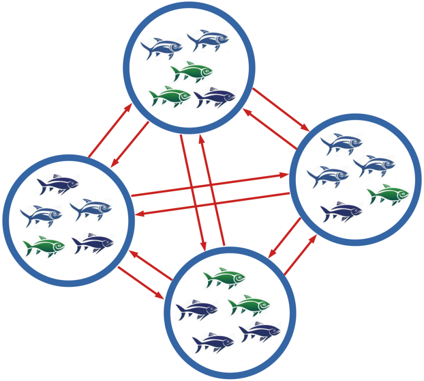
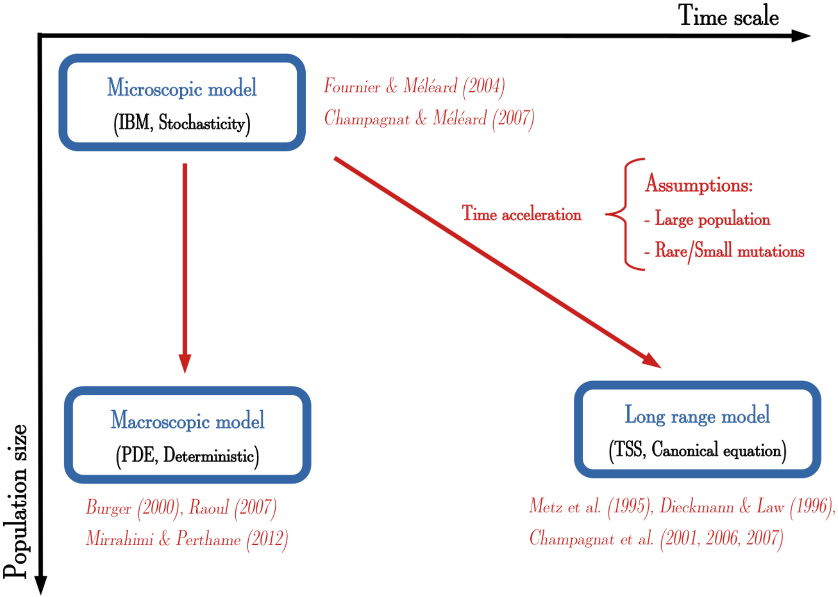


- **Mean-field setting:** complete graph, homogeneity.
- **Large metapopulation.**

How does spatial dispersion influence evolution at the local scale ?

Several scales



The model

Description

- ▷ K patches $(\ell = 1, ..., K)$ · N individuals per patch · The trait $x \in \mathbb{R}$
- ▷ Mutation at rate $\gamma\theta(x)$, i.e $x \xrightarrow{\text{becomes}} y \sim m_\varepsilon(x, \mathrm{d}y)$
- ▷ Local re-sampling: y replaces x at rate $c(x, y)$
- ▷ Non local re-sampling: y in ℓ' replaces x in ℓ at rate $\dfrac{\gamma\lambda(x, y)}{K}$

$\gamma \to 0$ (Rare mutations and migrations) · $K \to +\infty$ (Large metapopulation) · $\varepsilon \to 0$ (Small mutations)

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Càd-làg measure valued stochastic process defined by

$$\nu_t^{\gamma,\varepsilon,K}(\mathrm{d}r, \mathrm{d}x) = \frac{1}{K}\sum_{\ell=1}^{K} \underbrace{\frac{1}{N}\sum_{i=(\ell-1)N+1}^{\ell N} \delta_{(\frac{\ell}{K}, x_t^i)}(\mathrm{d}r, \mathrm{d}x)}_{\substack{\text{Trait distribution} \\ \text{in the } \ell-\text{th patch}}}, \forall t \geq 0. \tag{1}$$

$\gamma \to 0$ (Rare mutations and migrations) · $K \to +\infty$ (Large metapopulation) · $\varepsilon \to 0$ (Small mutations)

Markov property

Proposition

The stochastic process $(\nu_t^{\gamma,\varepsilon,K})_{t\geq 0}$ is a $\mathcal{M}_1([0,1]\times\mathbb{R})-$valued Markov process with infinitesimal generator given for $\phi\in\mathcal{C}_b(\mathcal{M}_1([0,1]\times\mathbb{R}))$ by

$$\begin{aligned}
&\mathcal{L}^{\gamma,\varepsilon,K}\phi(\nu)\\
&\quad= NK\gamma\int\theta(x)\nu(\mathrm{d}r,\mathrm{d}x)\int m_\varepsilon(x,\mathrm{d}y)\left[-\phi(\nu)+\phi\left(\nu-\frac{\delta_{(r,x)}}{NK}+\frac{\delta_{(r,y)}}{NK}\right)\right]\\
&\quad+NK\int\nu(\mathrm{d}r,\mathrm{d}x)\left(NK\int c(x,y)1_{r=r'}\nu(\mathrm{d}r',\mathrm{d}y)\right)\left[-\phi(\nu)+\phi\left(\nu-\frac{\delta_{(r,x)}}{NK}+\frac{\delta_{(r,y)}}{NK}\right)\right]\\
&\quad+N^2K\gamma\int\nu(\mathrm{d}r,\mathrm{d}x)\left(\int\lambda(x,y)1_{r\neq r'}\nu(\mathrm{d}r',\mathrm{d}y)\right)\left[-\phi(\nu)+\phi\left(\nu-\frac{\delta_{(r,x)}}{NK}+\frac{\delta_{(r,y)}}{NK}\right)\right]
\end{aligned}$$

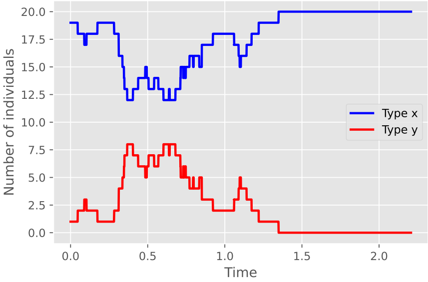
i.e

$$\phi(\nu_t^{\gamma,\varepsilon,K})-\phi(\nu_0^{\gamma,\varepsilon,K})-\int_0^t\mathcal{L}^{\gamma,\varepsilon,K}\phi(\nu_s^{\gamma,\varepsilon,K})\mathrm{d}s,\forall t\geq 0$$

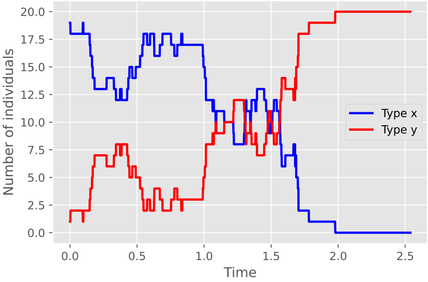
is a real-valued Martingale.

Invasion in an isolated patch ($\gamma = 0$)

Initial condition $\delta_y + (N-1)\delta_x$ with $x \neq y$



Invasion failed...



Invasion succeeded !

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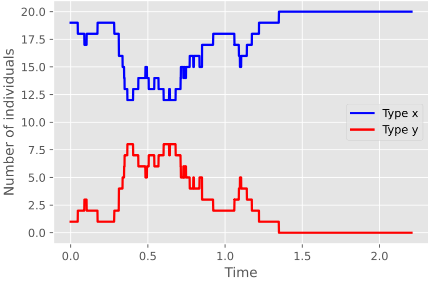

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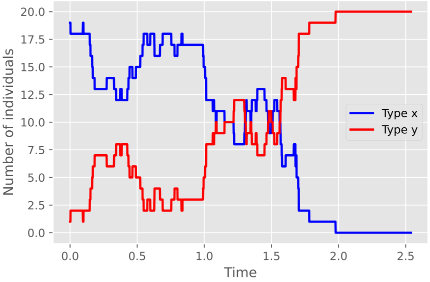
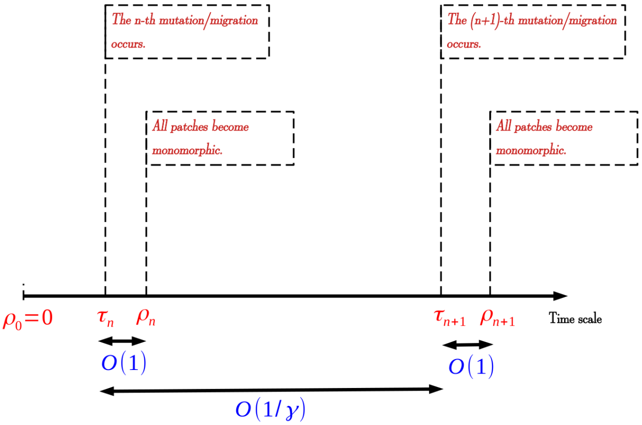


Invasion succeeded !

$$\alpha(y,x) := \mathbb{P}_{\delta_y+(N-1)\delta_x}(\text{Type } y \text{ invades the patch}) = \frac{1}{1+\sum_{k=1}^{N-1}\left(\frac{c(y,x)}{c(x,y)}\right)^k} \quad (2)$$

Rare mutations/migrations regime (Heuristics)

Scaling parameters: K fixed · ε fixed · $\gamma \ll 1$ (Rare mutations/migrations)



We set for any $\ell = 1, \dots, K$

$$S_t^{\ell,\gamma} = \sum_{n=0}^{\infty} V_n^{\ell,\gamma} \mathbb{1}_{\rho_n \leq t < \rho_{n+1}}, \, t \geq 0.$$

A mean-field network of TSS (I)

Scaling parameters: K fixed · ε fixed · $\gamma \ll 1$ (Rare mutations/migrations)

Proposition (adapted from Champagnat & Lambert 2007)

As $\gamma \to 0$,

$$\left(S^{1,\gamma}_{\cdot/\gamma}, \ldots, S^{K,\gamma}_{\cdot/\gamma}\right)_{\gamma>0} \Longrightarrow \left(X^{1,K}, \ldots, X^{K,K}\right) \tag{3}$$

in law in $\mathbb{D}([0,T], \mathbb{R}^K)$, Markovian pure jump process with transitions

$$(x^1, \ldots, x^K) \xrightarrow{\text{becomes}} (x^1, \ldots, x^{\ell-1}, y^\ell, x^{\ell+1}, \ldots, x^K),\ 1 \leq \ell \leq K \tag{4}$$

at rate

$$\alpha(y^\ell, x^\ell)\left(N\theta(x^\ell)m_\varepsilon(x^\ell, \mathrm{d}y^\ell) + \frac{N^2}{K}\sum_{\ell'=1}^{K}\lambda(x^\ell, y^\ell)\delta_{x^{\ell'}}(\mathrm{d}y^\ell)\right). \tag{5}$$

A mean-field network of TSS (II)

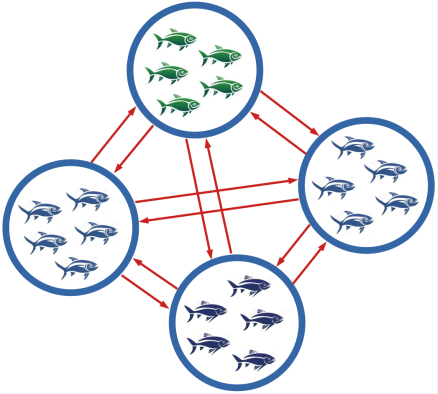
Scaling parameters: K fixed · ε fixed · $\gamma \ll 1$ (Rare mutations/migrations)

Corollary

$\left\{\left(\nu^{\gamma,\varepsilon,K}_{t/\gamma}\right)_{t\geq 0}, \gamma > 0\right\} \xrightarrow[\gamma\to 0]{\mathcal{L}} (\nu^{\varepsilon,K}_t)_{t\geq 0}$ in the sense of finite dimensional distributions, where

$$\nu^{\varepsilon,K}_t(\mathrm{d}r, \mathrm{d}x) = \frac{1}{K}\sum_{\ell=1}^{K} \delta_{\left(\frac{\ell}{K}, X^{\ell,K}_t\right)}(\mathrm{d}r, \mathrm{d}x), \forall t \geq 0.$$

- **Monomorphic patches.**
- **Mean-field network of TSS** (Gyllenberg et al. (1997)).



Mean-field network of TSS $\Longleftrightarrow$ Giant Moran model

The limit process $(X^{1,K}, ..., X^{K,K})$ can be seen as a new Moran model where:

INDIVIDUALS:

Monomorphic patches

TRAITS:

Dominant trait in the patches

MUTATION KERNEL:

Mutation & Fixation in the patch

RESAMPLING RATE:

Migration & Fixation in the patch

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K individuals

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Dominant trait in the patches

$X_t^{\ell,K} \in \mathbb{R}$ for patch ℓ at time $t \geq 0$

MUTATION KERNEL:

Mutation & Fixation in the patch

$N\theta(x)\alpha(y,x)m_\varepsilon(x, \mathrm{d}y)$

RESAMPLING RATE:

Migration & Fixation in the patch

$N^2 \frac{\lambda(x,y)}{K}\alpha(y,x)$

Propagation of chaos

Scaling parameters: $K \gg 1$ (Large metapopulation) · ε fixed

Theorem (Lambert, Leman, Morlon, T., 2025+)

Assume i.i.d patches at time $t = 0$ with common law $\mu_0(\mathrm{d}x)$.
As $K \to +\infty$, finite families of $(X^{1,K}, ..., X^{K,K})$ with fixed size converge in law in the Skorohod space toward i.i.d copies of the pure jump process $(X_t^\varepsilon)_{t\geq 0}$ with inhomogeneous transitions

$$x \xrightarrow{\text{becomes}} y \text{ at rate } \alpha(y,x)\left(N\theta(x)m_\varepsilon(x,\mathrm{d}y) + N^2\lambda(x,y)\mu_{t-}^\varepsilon(\mathrm{d}y)\right) \tag{6}$$

where $\mu_t^\varepsilon(\mathrm{d}y) = \mathcal{L}(X_t^\varepsilon | X_0^\varepsilon \sim \mu_0)(\mathrm{d}y)$ for any $t \geq 0$.

Continent-Island model of population evolution (see Statkin (1977); Bürger & Akerman (2011))

⇝ McKean-Vlasov equation for $(X_t^\varepsilon)_{t\geq 0}$

⇝ Nonlinear PDE for $(\mu_t^\varepsilon)_{t\geq 0}$.

Small mutations regime

We start from the limit process $(X_t^\varepsilon)_{t\geq 0}$

Scaling parameters: $\varepsilon \ll 1$ (Small mutations)

Mutation steps

Recall that $y \sim m_\varepsilon(x, \mathrm{d}y)$ is equivalent to $y = x + \varepsilon z$ with $z \sim \Sigma(x, \mathrm{d}z)$ centered.

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The transitions of $(X_t^\varepsilon)_{t\geq 0}$ can be rewritten

$$x \xrightarrow{\text{becomes}} \begin{cases} x + \varepsilon z & \text{at rate } N\theta(x)\alpha(x+\varepsilon z, x)\Sigma(x, \mathrm{d}z) \\ y & \text{at rate } N^2\lambda(x,y)\alpha(y,x)\mu_{t-}^\varepsilon(\mathrm{d}y) \end{cases}$$

Mutations are frequent but with small effects.

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Mutations are frequent but with small effects.

▷ Either **migrations are fast** and then the strong spatial selection will dominate,

▷ Or **migrations are slow enough** and we describe the joint effects of mutations and migrations under weak spatial selection.

Small mutations regime: No slowdown in migrations

- ▷ Pure migration metapopulation model in the limit $\varepsilon \to 0$.
- ▷ Spatial invasion fitness $G(y,x) = \lambda(x,y)\alpha(y,x) - \lambda(y,x)\alpha(x,y)$.

Proposition (Finite trait space)

Assume that the initial traits are $x_1, ..., x_n \in \mathbb{R}$, then $\mu_t(\mathrm{d}x) = \sum_{k=1}^{n} w_k(t)\delta_{x_k}(\mathrm{d}x)$ such that

$$\frac{\mathrm{d}w_k(t)}{\mathrm{d}t} = N^2 w_k(t) \sum_{k'=1}^{n} G(x_k, x_{k'}) w_{k'}(t), \forall t \geq 0. \tag{7}$$

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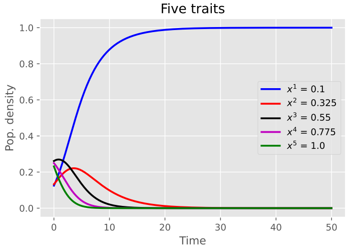
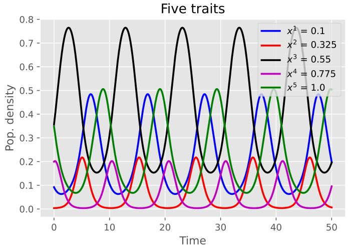


There is an optimal trait $G(x_{opt}, x) > 0$



No optimal trait !

Small mutations regime: Slowing down migrations

Scaling parameters: $\varepsilon \ll 1$ (Small mutations) · Migration rate: $\varepsilon^2 \lambda(x, y)$

The transitions of $(X_t^\varepsilon)_{t \geq 0}$ can be rewritten

$$x \xrightarrow{\text{becomes}} \begin{cases} x + \varepsilon z & \text{at rate } N\theta(x)\alpha(x+\varepsilon z, x)\Sigma(x, \mathrm{d}z) \\ y & \text{at rate } N^2 \varepsilon^2 \lambda(x, y)\alpha(y, x)\mu_{t-}^\varepsilon(\mathrm{d}y) \end{cases}$$

▷ Small (resp. large) modifications are frequent (resp. rare):
Use the time rescaling $t \mapsto t/\varepsilon^2$.

▷ In the mutation part, selection gradually drives the evolution in the direction of most adapted traits in the environment of the resident x.

Small mutations regime: Slowing down migrations (CEAD)

Scaling parameters: $\varepsilon \ll 1$ (Small mutations) · Migration rate: $\varepsilon^2\lambda(x,y)$

Theorem (Lambert, Leman, Morlon, T., 2025+)

As $\varepsilon \to 0$, $\left\{ \left(X^{\varepsilon}_{t/\varepsilon^2} \right)_{t\geq 0}, \varepsilon > 0 \right\}$ converges in law in the Skorohod space $\mathbb{D}([0,T],\mathbb{R})$ toward the unique process satisfying

$$\begin{cases} \mathrm{d}X_t = \dfrac{N-1}{2}\theta(X_t)\sigma^2(X_t)\partial_1 \mathrm{Fit}(X_t,X_t)\mathrm{d}t + \sqrt{\theta(X_t)\sigma^2(X_t)}\mathrm{d}B_t \\ + \text{ jump rate } N^2\lambda(X_{t-},y)\alpha(y,X_{t-})\mu_{t-}(\mathrm{d}y) \end{cases} \quad \text{(CEAD)}$$

where $\mu_t(\mathrm{d}y) = \mathcal{L}(X_t | X_0 \sim \mu_0)(\mathrm{d}y)$ for any $t \geq 0$.

$$\sigma^2(x) = \int_{\mathbb{R}} z^2 \Sigma(x,\mathrm{d}z) \text{ – variance of renormalized mutation steps}$$

$$\mathrm{Fit}(y,x) = \log\left(\frac{c(x,y)}{c(y,x)}\right) \text{ – relative fitness of trait } y \text{ compared to } x.$$

Structure of the McKean-Vlasov CEAD

$$
\begin{cases}
\mathrm{d}X_t = \underbrace{\frac{N-1}{2}\theta(X_t)\sigma^2(X_t)\partial_1 \mathrm{Fit}(X_t, X_t)\mathrm{d}t}_{\texttt{Selection}} + \underbrace{\sqrt{\theta(X_t)\sigma^2(X_t)}\mathrm{d}B_t}_{\texttt{Genetic drift}} \\
+ \text{ jump rate } \underbrace{N^2\lambda(X_{t-}, y)\alpha(y, X_{t-})\mu_{t-}(\mathrm{d}y)}_{\texttt{Immigration}}
\end{cases}
$$

where $\mu_t(\mathrm{d}y) = \mathcal{L}(X_t | X_0 \sim \mu_0)(\mathrm{d}y)$ for $t \geq 0$.

Conclusion

$$\text{IBM} \xrightarrow[\substack{\gamma\to 0 \\ \text{Rare mut./migr.}}]{\text{Time scale } t/\gamma} \begin{array}{c}\text{Mean-Field}\\ \text{Network}\\ \text{of TSS}\end{array} \xrightarrow[\substack{K\to+\infty \\ \text{Large metapop.}}]{\text{Prop. of chaos}} \begin{array}{c}\text{McKean}\\ -\\ \text{Vlasov}\\ \text{TSS}\end{array} \xrightarrow[\substack{\varepsilon\to 0 \\ \text{Small mut., Slow migr.}}]{\text{Time scale } t/\varepsilon^2} \begin{array}{c}\text{McKean}\\ -\\ \text{Vlasov}\\ \text{CEAD}\end{array}$$

Possible extensions to complete graphs structures and spatial heterogeneity.

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Possible extensions to complete graphs structures and spatial heterogeneity.

Ongoing perspectives

1. Extend those results to the case of unbounded migration rates.

   ▷ Non explosion and moment estimates of the solutions to the McKean-Vlasov equations.

2. Long time behavior of the McKean-Vlasov CEAD.

   ▷ Gaussian distributed solutions of the Ornstein-Uhlenbeck process with non-linear jumps and their asymptotics. (see Hansen (1997); Butler & King (2004))

Thank you for your attention.

[0]A. Lambert, H. Leman, H. Morlon and J. Tchouanti. Evolution of a trait distributed over a large fragmented population: Propagation of chaos meets adaptive dynamics.
Preprint https://hal.science/hal-04873740 (2025).