Introduction
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Microscopic model
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Large popu scalings
ooooooooooooo

Large population scalings of stochastic population dynamics in ecology and evolution

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Workshop/School on Stochastic PDEs, Mean Field Games and Biology, L'Aquila, 6–8 Sept. 2017

Darwinian evolution

Three main ingredients:

- Heredity: transmissions of individual characteristics from a generation to the next one.
- Mutation: cause of the variability in individual characteristics.
- Selection: consequence of interactions between individuals and their environment, including the rest of the population (ecology).

Introduction
○○●○○○○

Microscopic model
○○○○○○○○○○○

Large popu scalings
○○○○○○○○○○○○○

Adaptive dynamics/Ecology

Adaptive dynamics (AD)

Adaptive dynamics (Hofbauer and Sigmund 1990, Marrow et al. 1992, Metz et al. 1992):

- describe the evolution of a population by putting emphasis on the ecological interactions
  ⤳ density-dependent selection modelled in detail
- heredity (in a first approach) is simplified as much as possible: asexual (clonal) reproduction

- individual-based

- stochastic

- interactions are modelled in a realistic way

- population size can fluctuate

Introduction
○●○○○○

Microscopic model
○○○○○○○○○○

Large popu scalings
○○○○○○○○○○○○○

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- describe the evolution of a population by putting emphasis on the ecological interactions
  ⤳ density-dependent selection modelled in detail

- heredity (in a first approach) is simplified as much as possible:
  asexual (clonal) reproduction

Grounded on models that are

- individual-based

- stochastic

- interactions are modelled in a realistic way

- population size can fluctuate

Introduction
○○●○○○

Adaptive dynamics/Ecology

Microscopic model
○○○○○○○○○○

Large popu scalings
○○○○○○○○○○○○

Biological motivations

Evolutionary time-scale is not always slow w.r.t. ecological time-scale

- evolution of resistance in pathogens
- genetic adaptation to harvesting
- experimental evolution in microorganisms

⤳ Makes sense to study the interplay between ecology and evolution in models

Introduction
○○●○○○
Adaptive dynamics/Ecology

Microscopic model
○○○○○○○○○○

Large popu scalings
○○○○○○○○○○○○

Biological motivations

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Implications in biodiversity management

- rapid evolutions usually involve human pressure
- adaptive evolution does not necessarily "rescue" populations
- how can management and restoration practice account for/use the evolutionary process?

Introduction
○○○●○○

Microscopic model
○○○○○○○○○○○

Large popu scalings
○○○○○○○○○○○○○○

Adaptive dynamics/Ecology

Adaptive dynamics scales

The theory of adaptive dynamics (Metz et al., 1996, Dieckman and Law, 1996) proposes simple models approaching the evolution under several assumptions:

- Large populations
- Rare mutations
- Small mutation steps

Introduction
OOOOO●O
Adaptive dynamics/Ecology

Microscopic model
OOOOOOOOOO

Large popu scalings
OOOOOOOOOOOO

Ecological models of dispersal

The models of adaptive dynamics can also have a spatial interpretation

- mutations can be seen as spatial dispersion, or other motions (Bolker, Pacala, 1997, Champagnat, Méléard, 2007)
- classical ecological question: links between local interaction and spatial dispersion
- invasion, survival, extinction
- competition between species
- similar scalings can be considered (spatial scaling, dispersal probability/range, time...)

Introduction
○○○○○●

Microscopic model
○○○○○○○○○○

Large popu scalings
○○○○○○○○○○○○

Outline of the lectures

Outline of the lectures

1. Description of the stochastic individual-based ecological model; first properties
2. Several large population scalings ⤳ recover classical or original macroscopic models under various biological assumptions and scales, including superprocesses
3. Basic properties of the class of SPDE obtained this way
4. Properties of local extinction and persistence of these SPDE
5. The case of age-dependent evolutionary dynamics

Introduction
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Microscopic model
●○○○○○○○○○○

Large popu scalings
○○○○○○○○○○○○○

The model

Microscopic model

A general birth-and-death measure-valued process with competition and mutation (already studied in Bolker and Pacala 1997, Dieckmann and Law 2000, Fournier and Méléard 2004,...)

- each individual is characterized by a phenotypic trait x (individual size, age at maturity,...) in a closed subset $\mathcal{X}$ of $\mathbb{R}^k$

- a population of $N(t)$ individuals holding traits $x_1, \ldots, x_{N(t)} \in \mathcal{X}$

  is represented by $\nu_t = \sum_{i=1}^{N(t)} \delta_{x_i}$

- state space: $\mathcal{M} = \left\{ \sum_{i=1}^{n} \delta_{x_i} : n \geq 0, x_i \in \mathcal{X} \right\}$

Introduction
oooooo

Microscopic model
o●oooooooooo

Large popu scalings
oooooooooooooo

The model

Transitions

- as in the pure multitype branching process:
  - each individual with trait x gives birth at rate $b(x)$ to a single individual of trait x
  - each individual of trait x dies at rate $d(x)$

- in addition,
  each individual of trait y picks any given individual of trait x at rate $\alpha(x, y)$ and then kills him
  $\rightsquigarrow$ an individual with trait x dies at rate

$$d(x) + \sum_{i=1}^{N_t} \alpha(x, x_i) = d(x) + \int_{\mathcal{X}} \alpha(x, y)\nu_t(dy)$$

- at each birth from an individual with type x
  - $\mu(x)$ mutation probability
  - $x + h$ mutant trait, where $h \sim m(x, dh)$

Introduction
○○○○○○

Microscopic model
○●○○○○○○○○○

Large popu scalings
○○○○○○○○○○○○○

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Introduction
○○○○○○

Microscopic model
○●○○○○○○○○○

Large popu scalings
○○○○○○○○○○○○○

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Generator

$\rightsquigarrow$ Markov jump process $(\nu_t, t \geq 0)$ on $\mathcal{M}$ with generator

$$L\phi(\nu) = \int_{\mathcal{X}} [\phi(\nu + \delta_x) - \phi(\nu)](1 - \mu(x))b(x)\nu(dx)$$
$$+ \int_{\mathcal{X}} \int_{\mathbb{R}^d} [\phi(\nu + \delta_{x+h}) - \phi(\nu)]\mu(x)b(x)m(x,h)dh\,\nu(dx)$$
$$+ \int_{\mathcal{X}} [\phi(\nu - \delta_x) - \phi(\nu)] \left(d(x) + \int_{\mathcal{X}} \alpha(x,y)\nu(dy) \right) \nu(dx)$$

Biological comments

- Logistic interaction = competition
  Easy generalization to more general interactions (Champagnat, Ferrière, Méléard, 2008)
    - birth rate $b(x, U * \nu_t(x))$
    - death rate $d(x, V * \nu_t(x))$

  Example:
  $b(x, U * \nu_t(x)) = b(x) + U * \nu_t(x),\ d(x, U * \nu_t(x)) = d(x) + V * \nu_t(x)$
  $U \geq V$ corresponds to mutualistic interaction

- Multispecific (prey-predator, host-parasite, ressource exploitation, mutulistic community,...) generalization

Introduction
000000
Microscopic model
0000●000000
Large popu scalings
00000000000
First properties

Assumptions

(A1) $0 \leq \alpha(\cdot,\cdot) \leq \bar{\alpha} < +\infty$

(A1) $0 \leq b(\cdot) \leq \bar{b} < +\infty$

(A1) $0 \leq d(\cdot) \leq \bar{d} < +\infty$

(A2) $m(x, dh)$ has a density $m(x, h)$ w.r.t. the Lebesgue measure such that $m(x, h) \leq m(h)$ with $\int m(h) dh < +\infty$

Introduction
○○○○○○

Microscopic model
○○○○●○○○○○

Large popu scalings
○○○○○○○○○○○○○

First properties

Assumptions

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(A2) $m(x, dh)$ has a density $m(x, h)$ w.r.t. the Lebesgue measure such that $m(x, h) \leq m(h)$ with $\int m(h)dh < +\infty$

$\rightsquigarrow$ Total jump rate less than $\langle \nu_t, 1 \rangle (\bar{b} + \bar{d} + \bar{\alpha}(\langle \nu_t, 1 \rangle - 1))$

Introduction
000000
First properties

Microscopic model
0000000000

Large popu scalings
0000000000000

Construction as a SDE driven by Poisson point measures

Given independent PPM M_1, M_3 (resp. M_2) on $\mathbb{R}_+ \times \mathbb{N} \times \mathbb{R}_+$ (resp. $\mathbb{R}_+ \times \mathbb{N} \times \mathbb{R}^d \times \mathbb{R}_+$) with intensity $ds(\sum_{k \geq 1} \delta_k(di))d\theta$ (resp. $ds(\sum_{k \geq 1} \delta_k(di))\bar{m}(h)dh\, d\theta$),

$$
\begin{aligned}
\nu_t = \nu_0 &+ \int_0^t \int_{\mathbb{N}} \int_0^\infty \delta_{H_{s-}^i} \mathbb{1}_{i \leq \langle \nu_{s-}, 1 \rangle} \mathbb{1}_{\theta \leq b(1-\mu)(H_{s-}^i)} M_1(ds, di, d\theta) \\
&+ \int_0^t \int_{\mathbb{N}} \int_{\mathbb{R}^d} \int_0^\infty \delta_{x+h} \mathbb{1}_{i \leq \langle \nu_{s-}, 1 \rangle} \mathbb{1}_{\theta \leq b\mu(H_{s-}^i)m(H_{s-}^i,h)/\bar{m}(H_{s-}^i)} M_2(ds, di, dh, d\theta) \\
&- \int_0^t \int_{\mathbb{N}} \int_0^\infty \delta_{H_{s-}^i} \mathbb{1}_{i \leq \langle \nu_{s-}, 1 \rangle} \mathbb{1}_{\theta \leq d(H_{s-}^i) + \int \alpha(H_{s-}^i, y)\nu_{s-}(dy)} M_3(ds, di, d\theta),
\end{aligned}
$$

where H_t^i is the i-th atom in ν_t (for some arbitrary order).

Introduction
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Microscopic model
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Large popu scalings
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First properties

Martingale properties (Fournier, Méléard, 2004)

- Bounded birth rate: for $p \geq 1$,
  $\mathbf{E}[\langle \nu_0, \mathbf{1} \rangle^p] < +\infty \Rightarrow \mathbf{E}[\sup_{t \leq T} \langle \nu_t, \mathbf{1} \rangle^p] < +\infty$

- for ϕ with appropriate growth, $\phi(\nu_t) - \phi(\nu_0) - \int_0^t L\phi(\nu_s)\,ds$ is
  a càdlàg martingale

- In particular, for $\phi(\nu) = \langle \nu, f \rangle$, assuming $\mathbf{E}[\langle \nu_0, \mathbf{1} \rangle^2] < +\infty$

$$\langle \nu_t, f \rangle = \langle \nu_0, f \rangle + M_t^f$$
$$+ \int_0^t \int_{\mathcal{X}} \Big\{ \big[(1 - \mu(x))b(x) - d(x) - \int \alpha(x, y)(\nu_s(dy) - \delta_x(dy)) \big] f(x)$$
$$+ b(x)\mu(x) \int f(x + z)M(x, z)\,dz \Big\} \nu_s(dx)\,ds,$$

with

$$\langle M^f \rangle_t = \int_0^t \int_{\mathcal{X}} \Big\{ \big[(1 - \mu(x))b(x) - d(x) - \int \alpha(x, y)(\nu_s(dy) - \delta_x(dy)) \big] f^2(x)$$
$$+ b(x)\mu(x) \int f^2(x + z)M(x, z)\,dz \Big\} \nu_s(dx)\,ds.$$

Introduction
000000
First properties
Microscopic model
0000000●00
Large popu scalings
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Proof of the moments bound

Introducing $\tau_n = \inf\{t \geq 0 : \langle \nu_t, 1 \rangle \geq n\}$, using
$(x+1)^p - x^p \leq C_p(1 + x^{p-1})$ and

$$\sup_{s \leq t \wedge \tau_n} \langle \nu_s, 1 \rangle^p \leq \langle \nu_0, 1 \rangle^p + \int_0^{t \wedge \tau_n} \int_{\mathbb{N}} \int_{\mathbb{R}^d} \int_0^\infty [(\langle \nu_{s-}, 1 \rangle + 1)^p - \langle \nu_{s-}, 1 \rangle^p]$$
$$\mathbb{1}_{i \leq \langle \nu_{s-}, 1 \rangle} \mathbb{1}_{\theta \leq \bar{b}} M_2(ds, di, dh, d\theta)$$
$$+ \text{ similar term for } M_1,$$

taking expectation, we deduce that

$$\mathbb{E} \sup_{s \leq t \wedge \tau_n} \langle \nu_s, 1 \rangle^p \leq C_p + C_p \mathbb{E} \int_0^t (1 + \langle \nu_{s \wedge \tau_n}, 1 \rangle^p) ds$$

and the result follows from Gronwall.

Example

Parameters from Kisdi (1999)

$$\mathcal{X} = [0,4] \quad d(x) \equiv 0 \quad \mu(x) \equiv \mu$$
$$m(x,h)dh = \mathcal{N}(0,\sigma^2)$$
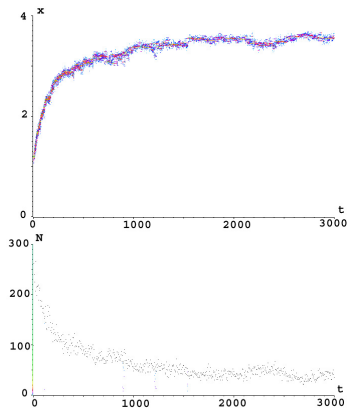$$\text{(conditioned on } x + h \in \mathcal{X})$$
$$b(x) = 4 - x \quad \alpha(x,y) = \alpha(x-y) \quad \text{with}$$
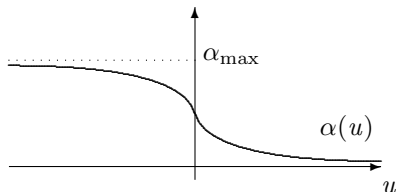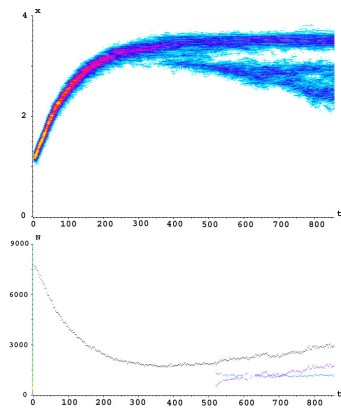

Asymetric competition

- arm-race competition
- evolution of the cell size at division

Simulations

$$\mu = 0.1 \quad \sigma = 0.03$$
$$\alpha_{\max} = 0.02$$

$$\mu = 0.1 \quad \sigma = 0.03$$
$$\alpha_{\max} = 0.001$$

Introduction
○○○○○○

Microscopic model
○○○○○○○○○○

Large popu scalings
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Preliminaries

Large population scalings (C., Ferrière, Méléard, 2008)

Parameter K: b_K, d_K, μ_K, M_K and $\alpha_K(x, y) = \dfrac{\alpha(x, y)}{K}$

Biological interpretations: K scales the amount of ressources available (carrying capacity, or "system size"), or the size of individuals (w.r.t. their competitive pressure).

$$X_t^K = \frac{1}{K} \sum_{i=1}^{I(t)} \delta_{x_t^i} = \frac{\nu_t^K}{K}$$

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$$L \ \phi(\nu) = \int_{\mathcal{X}} [\phi(\nu + \delta_x) - \phi(\nu)](1 - \mu \ (x))b \ (x)\nu(dx)$$

$$+ \int_{\mathcal{X}} \int_{\mathbb{R}^d} [\phi(\nu + \delta_{x+z}) - \phi(\nu)]\mu \ (x)b \ (x)M \ (x,z)dz\nu(dx)$$

$$+ \int_{\mathcal{X}} [\phi(\nu - \delta_x) - \phi(\nu)] \left(d \ (x) + \int_{\mathcal{X}} \alpha(x,y)\nu(dy) \right) \nu(dx)$$

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$$X_t^K = \frac{1}{K} \sum_{i=1}^{I(t)} \delta_{x_t^i} = \frac{\nu_t^K}{K}$$

$$L^K \phi(\nu) = \int_{\mathcal{X}} [\phi(\nu + \delta_x) - \phi(\nu)](1 - \mu_K(x)) b_K(x) \nu(dx)$$

$$+ \int_{\mathcal{X}} \int_{\mathbb{R}^d} [\phi(\nu + \delta_{x+z}) - \phi(\nu)] \mu_K(x) b_K(x) M_K(x, z) dz \nu(dx)$$

$$+ \int_{\mathcal{X}} [\phi(\nu - \delta_x) - \phi(\nu)] \left(d_K(x) + \int_{\mathcal{X}} \alpha(x, y) \nu(dy) \right) \nu(dx)$$

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$$L^K \phi(X) = \int_{\mathcal{X}} [\phi(X + \frac{\delta_x}{K}) - \phi(X)](1 - \mu_K(x))b_K(x)\nu(dx)$$

$$+ \int_{\mathcal{X}} \int_{\mathbb{R}^d} [\phi(X + \frac{\delta_{x+z}}{K}) - \phi(X)]\mu_K(x)b_K(x)M_K(x, z)dz\nu(dx)$$

$$+ \int_{\mathcal{X}} [\phi(X - \frac{\delta_x}{K}) - \phi(X)] \left(d_K(x) + \int_{\mathcal{X}} \frac{\alpha(x, y)}{K}\nu(dy) \right) \nu(dx)$$

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$$L^K \phi(X) = \int_{\mathcal{X}} [\phi(X + \frac{\delta_x}{K}) - \phi(X)](1 - \mu_K(x)) b_K(x) K X(dx)$$

$$+ \int_{\mathcal{X}} \int_{\mathbb{R}^d} [\phi(X + \frac{\delta_{x+z}}{K}) - \phi(X)] \mu_K(x) b_K(x) M_K(x,z) dz \, K X(dx)$$

$$+ \int_{\mathcal{X}} [\phi(X - \frac{\delta_x}{K}) - \phi(X)] \left(d_K(x) + \int_{\mathcal{X}} \frac{\alpha(x,y)}{K} K X(dy) \right) K X(dx)$$

Simplest large population limit

$b_K = b$, $d_K = d$, $\mu_K = \mu$, $M_K = M$.

Only the competitive kernel is modified: limit of large population size.

Theorem

Assume that $X_0^K \Rightarrow \xi_0$, $\sup_K \mathbf{E}[\langle X_0^K, \mathbf{1} \rangle^3] < +\infty$
and smooth parameters.

Then $X^K \Rightarrow \xi \in \mathcal{C}([0, T], M_F(\mathcal{X}))$ deterministic, where

$$\langle \xi_t, f \rangle = \langle \xi_0, f \rangle$$
$$+ \int_0^t \int_{\mathcal{X}} \Big\{ \big[(1 - \mu(x)) b(x) - d(x) - \int_{\mathcal{X}} \alpha(x, y) \xi_s(dy) \big] f(x)$$
$$+ b(x) \mu(x) \int f(x + z) M(x, z) dz \Big\} \xi_s(dx) ds. \qquad (1)$$

Kimura's equation for "continuum of alleles", extended to
density-dependent selection.

Introduction
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Microscopic model
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Large popu scalings
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First limit

Remark

- If $\xi_0(dx) = u_0(x)dx$, then $\xi_t(dx) = u(t,x)dx$, $\forall t > 0$ and $u(t,x)$ is weak solution to

$$\partial_t u = [(1 - \mu(x))b(x) - d(x) - \int \alpha(x,y)u(t,y)dy]u(t,x)$$
$$+ \int \mu(y)b(y)M(y, x-y)u(t,y)dy$$

Introduction
000000

Microscopic model
0000000000

Large popu scalings
0000000000000

First limit

Sketch of the proof (1)

- Martingale problem

$$\langle \nu_t, f \rangle = \langle \nu_0, f \rangle + M_t^f$$
$$+ \int_0^t \int_{\mathcal{X}} \left\{ \left[(1 - \mu(x))b(x) - d(x) - \int_{\mathcal{X}} \alpha(x, y) \nu_s(dy) \right] f(x) \right.$$
$$\left. + b(x)\mu(x) \int f(x + z) M(x, z) dz \right\} \nu_s(dx) ds,$$

Introduction
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Microscopic model
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Large popu scalings
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First limit

Sketch of the proof (1)

- Martingale problem

$$
\langle X_t^K, f \rangle = \langle X_0^K, f \rangle + M_t^{f,K}
$$
$$
+ \int_0^t \int_{\mathcal{X}} \Big\{ \big[(1 - \mu(x)) b(x) - d(x) - \int_{\mathcal{X}} \alpha(x, y) X_s^K(dy) \big] f(x)
$$
$$
+ b(x) \mu(x) \int f(x + z) M(x, z) dz \Big\} X_s^K(dx) ds,
$$

Introduction
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Microscopic model
○○○○○○○○○○

Large popu scalings
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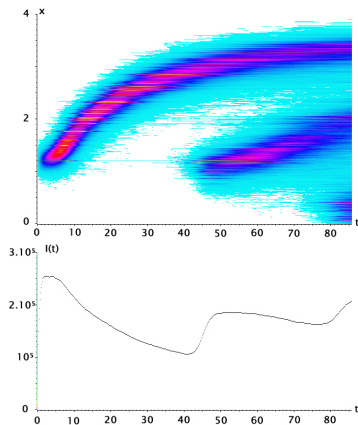$$\left. + b(x)\mu(x) \int f(x + z) M(x, z) dz \right\} X_s^K(dx) ds,$$

with

$$\langle M^{f,K} \rangle_t$$
$$= \frac{1}{K^2} \int_0^t \int_{\mathcal{X}} \left\{ \left[(1 - \mu(x))b(x) - d(x) - \int_{\mathcal{X}} \alpha(x, y) X_s^K(dy) \right] f^2(x) \right.$$
$$\left. + b(x)\mu(x) \int f^2(x + z) M(x, z) dz \right\} K X_s^K(dx) ds.$$

Idea of the proof (2)

- Since $\sup_K \mathbf{E}[\sup_{t \geq T} \langle X_t^K, \mathbf{1} \rangle^3] < +\infty$,
  $\langle X^K, f \rangle$ is tight (Aldous-Rebolledo criterion) $\rightsquigarrow X^K$ is tight
  (Roelly, 1986)

- $\sup_{t \leq T} \sup_{\|f\|_\infty \leq 1} |\langle X_t^K, f \rangle - \langle X_{t-}^K, f \rangle| \leq 1/K$

  $\rightsquigarrow$ continuity of the limit process

- Since $\langle M^{f,K} \rangle \leq \dfrac{C}{K}$, any accumulation point is deterministic and
  must satisfy (1)

- Uniqueness of ξ (Gronwall lemma for the total variation distance
  between two solutions)

Introduction   Microscopic model   Large popu scalings
oooooo   oooooooooo   ooooo●ooooooo
First limit

Simulation

$$\mu = 0.1 \quad \sigma = 0.03$$
$$K = 100000$$

Introduction
○○○○○○

Microscopic model
○○○○○○○○○○

Large popu scalings
○○○○○○●○○○○○

Accelerated births and deaths

Large population limit with accelerated births and deaths

Here, the limit of large system size is combined with an acceleration of births and deaths $\mathcal{X} = \mathbb{R}^d$, $\alpha_K(x,y) = \alpha(x,y)/K$,

$$b_K(x) = K^\eta r(x) + b(x), \quad d_K(x) = K^\eta r(x) + d(x), \quad \eta \in (0,1].$$

Biological interpretation: fast births and deaths but slow demography

Introduction
○○○○○○

Microscopic model
○○○○○○○○○○

Large popu scalings
○○○○○○●○○○○○

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Biological interpretation: fast births and deaths but slow demography

$$\langle X_t^K, f \rangle = \langle X_0^K, f \rangle + M_t^{f,K}$$

$$+ \int_0^t \int_{\mathcal{X}} \left\{ \left[K^\eta r(x) + b(x) - K^\eta r(x) - d(x) - \int_{\mathcal{X}} \alpha(x, y) X_s^K(dy) \right] f(x) \right.$$

$$\left. + (K^\eta r(x) + b(x)) \mu_K(x) \int (f(x + z) - f(x)) M_K(x, z) dz \right\} X_s^K(dx) ds,$$

Introduction
○○○○○○
Microscopic model
○○○○○○○○○○
Large popu scalings
○○○○○○●○○○○○
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Biological interpretation: fast births and deaths but slow demography

$$\langle X_t^K, f \rangle = \langle X_0^K, f \rangle + M_t^{f,K}$$

$$+ \int_0^t \int_{\mathcal{X}} \left\{ \left[K^\eta r(x) + b(x) - K^\eta r(x) - d(x) - \int_{\mathcal{X}} \alpha(x,y) X_s^K(dy) \right] f(x) \right.$$

$$\left. + (K^\eta r(x) + b(x)) \mu_K(x) \int (f(x+z) - f(x)) M_K(x,z) dz \right\} X_s^K(dx) ds,$$

Since births are accelerated, the effect of mutation (either the mutation probability or the mutation amplitude) must be rescaled accordingly: $\mu_K = \mu$, $\quad M_K(x,z)dz \sim \mathcal{N}(0, \sigma^2(x)\mathrm{Id}/K^\eta)$.

$$\rightsquigarrow \quad \langle M^{K,f} \rangle_t \le C \frac{K^\eta}{K}.$$

Small mutation step

Case $\eta < 1$

- $X^K \Rightarrow \xi \in \mathcal{C}([0,T], M_F)$ where

$$\langle \xi_t, f \rangle = \langle \xi_0, f \rangle$$
$$+ \int_0^t \int_{\mathcal{X}} \Big\{ (b(x) - d(x) - \int_{\mathcal{X}} \alpha(x,y)\xi_s(dy))f(x)$$
$$+ \frac{1}{2} r(x)\mu(x)\sigma^2(x)\Delta f(x) \Big\} \xi_s(dx)\,ds.$$

⤳ Generalization of Fisher's models in ecology (Kimura's approximation for small mutation steps)

Introduction
oooooo

Microscopic model
oooooooooo

Large popu scalings
ooooooooo●oooo

Accelerated births and deaths

Case $\eta = 1$

$X^K \Rightarrow Z \in \mathcal{C}([0, T], M_F)$ where Z is defined by the 3 conditions:

- $\sup_{t \leq T} \mathbf{E}[\langle Z_t, \mathbf{1} \rangle^3] < \infty$

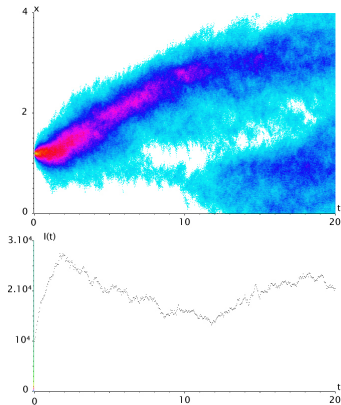- $\langle Z_t, f \rangle = \langle Z_0, f \rangle + \bar{M}_t^f$

$$+ \int_0^t \int_{\mathbb{R}^d} \left\{ (b(x) - d(x) - \int_{\mathcal{X}} \alpha(x, y) Z_s(dy)) f(x) \right.$$
$$\left. + \frac{1}{2} r(x) \mu(x) \sigma^2(x) \Delta f(x) \right\} Z_s(dx) ds$$

- $\langle \bar{M}^f \rangle_t = 2 \int_0^t \int_{\mathbb{R}^d} r(x) f^2(x) Z_s(dx) ds.$

$\rightsquigarrow$ Microscopic justification of superprocesses with density-dependent interaction, recently proposed and studied in population genetics (Etheridge 06)
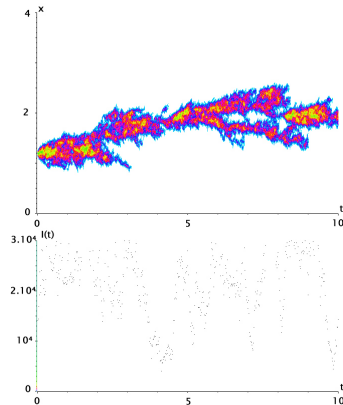
- birth and death stochasticity reflect on the demographic time-scale

- diversification vs extinction

Introduction
○○○○○○

Microscopic model
○○○○○○○○○○

Large popu scalings
○○○○○○○○○●○○

Accelerated births and deaths

Simulations

$$\mu = 0.3 \quad \sigma = 0.3$$
$$K = 10000 \quad \eta = 0.5$$

$$\mu = 0.3 \quad \sigma = 0.3$$
$$K = 10000 \quad \eta = 1$$

Introduction
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Microscopic model
0000000000

Large popu scalings
000000000000●0

Accelerated births and deaths

Simulations
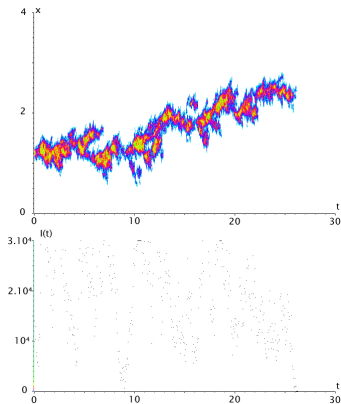
$$\mu = 0.3 \quad \sigma = 0.3$$
$$K = 10000 \quad \eta = 1$$
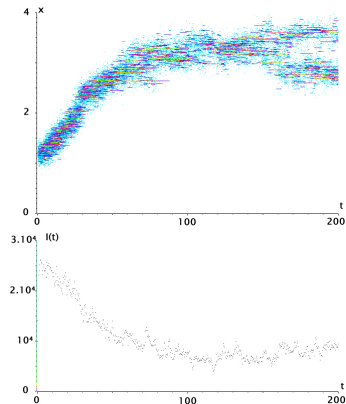
$$\mu = 0.1/K^\eta \quad \sigma = 0.1$$
$$K = 10000 \quad \eta = 0.5$$

Conclusion

- Mathematical justification of several (old and new) macroscopic evolutionary models
- Precising the biological assumptions and scales underlying each macroscopic model (large ressources, different scales for individual births and deaths and for demography,...)
- Unifying these models from the same microscopic model