Let Markov chains evolve along genealogies

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Discrete time genealogy and Markov chains

We consider a population of individuals with a trait described by

- a genealogical tree $\mathbb{T}$ in discrete time (fixed or random)
- a trait for each individual, whose dynamic is given by (Markovian) transition kernels, with possible dependence on the number of offsprings and on the generation (time inhomogeneity).

Limit theorems for large populations. We assume *here* that the number of individuals in generation n goes to ∞ as $n \to \infty$.

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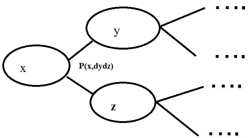
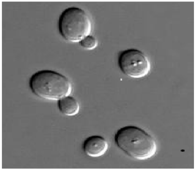
Motivation 1 : random transmission in cell division

One generation= cell division time. $k \in \{0, 1, 2\}$.
Trait = number of parasites, plasmids, mitochondrias, external DNA ... ; age, growth rate, damages ... of the cell.





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- Kimmel's branching models. (Binomial repartition of plasmids or parasites in the two daughter cells)
- Bifurcating autoregressive process for cellular aging ($X_{n+1} = a_n X_n + b_n$).

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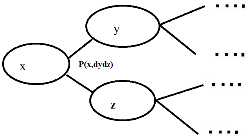

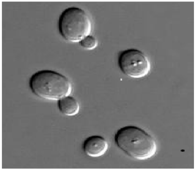

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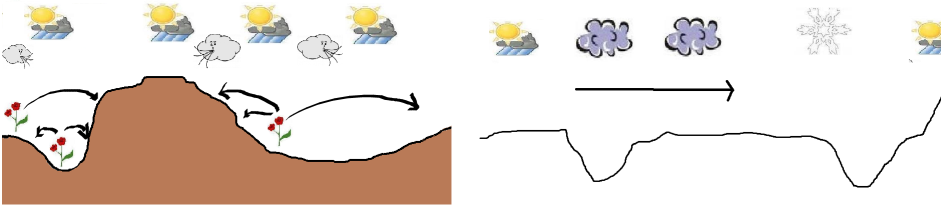

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Invasion dynamics and effect of time and space non-homogeneity.

Evolution with time non-homogeneity.

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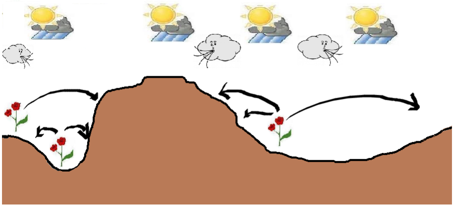

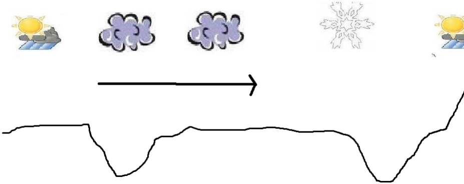

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Evolution with time non-homogeneity.

- Markov chain along binary or Galton-Watson tree (Athreya Khang 98, Guyon 05, Delmas Marsalle and al ...)
- Multitype branching processes (well known with finite number of types ; pioneering works of Moy, Seneta, Vere Jones, Kesten for infinite number of types).
- Branching random walks when P is additive (Biggins), with possibly random environment (see e.g. works of Comets, Gantert Müller, Yoshida.)

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Markov chain along genealogies

The model is specified by $P_n^{(k)}(x, dx_1 \cdots dx_k)$: if $u \in \mathbb{T}$ belongs to the generation n and has k offsprings, then

$$\mathbb{P}\Big(X(u1) \in dx_1 \cdots X(uk) \in dx_k \;\Big|\; (X(v) : |v| \leq n)\Big) = P_n^{(k)}(X(u), dx_1 \cdots dx_k).$$

Question :
What is the proportion of individuals with some given trait, i.e. the asymptotic behavior of $X_n(A)/X_n(\mathcal{X})$?

Early separation of the genealogies

Proposition

Let $A \in B_{\mathcal{X}}$. We assume that

(i) $N_n \to \infty$ *as* $n \to \infty$;

(ii) $\limsup_{n\to\infty} \mathbb{P}(|U_n \wedge V_n| \geq K) \to 0$ *as* $K \to \infty$, *where* U_n, V_n *are uniformly and independently chosen in generation* n ;

(iii) *there exists* $\mu_n(A)$ *such that for all* $u \in \mathbb{T}$ *and* $x \in \mathcal{X}$,

$$\lim_{n\to\infty} \mathbb{P}\left(X(U_n^{(u)}) \in A \middle| X(u) = x\right) - \mu_n(A) = 0,$$

where $U_n^{(u)}$ *is uniformly chosen in generation* n.

Then
$$\frac{X_n(A)}{X_n(\mathcal{X})} - \mu_n(A) \stackrel{n\to\infty}{\longrightarrow} 0 \qquad \text{in } L^2.$$

Examples for (i-ii) : supercritical branching processes.

Non late separation of the genealogies

Proposition

Let $A \in B_{\mathcal{X}}$. We assume that

(i) $N_n \to \infty$ *as* $n \to \infty$;

(ii) $\limsup_{n\to\infty} \mathbb{P}(|U_n \wedge V_n| \geq n - K) \to 0$ *as* $K \to \infty$, *where* U_n, V_n *are uniformly and independently chosen in generation* n ;

(iii) *there exists* $\mu_n(A)$ *such that*

$$\lim_{n\to\infty} \sup_{u\in\mathbb{T}, x\in\mathcal{X}} \left|\mathbb{P}\left(X(U_n^{(u)}) \in A \middle| X(u) = x\right) - \mu_n(A)\right| = 0,$$

where $U_n^{(u)}$ *is an individual uniformly chosen in generation* n.

Then
$$\frac{X_n(A)}{X_n(\mathcal{X})} - \mu_n(A) \to 0 \qquad \text{in } L^2.$$

Example for (ii) : bounded number of offsprings.

Two examples where (*iii*)[ergodic assumptions] can be obtained easily as the ergodicity of an auxiliary Markov chain.

- when the transitions $P^{(k)}$ do not depend on the number of offsprings ;
- when the genealogical tree $\mathbb{T}$ is a branching process.

What about branching Markov chains ? (non neutral framework, multitype branching processes, with possibly infinite number of types).

The individuals reproduce independently and each individual with trait $x \in \mathcal{X}$ in environment $\mathbf{e}$

- the reproduction law is $N(x, \mathbf{e})$
- the traits of the k offsprings are given by

$$P^{(k)}(x, \mathbf{e}, dx_1 \ldots dx_k) \qquad (k \geq 1)$$

- the offsprings live in environment $T\mathbf{e}$.

The auxiliary chain

We consider the transition kernel

$$Q_k(x,\mathbf{e},dy) = \mathbb{E}_{\delta_x,\mathbf{e}}(Z_1(dy))\frac{\mathbb{E}_{\delta_y,T\mathbf{e}}(Z_{k-1}(\mathcal{X}))}{\mathbb{E}_{\delta_x,\mathbf{e}}(Z_k(\mathcal{X}))}$$

and the trait $X_i(u)$ of the ancestor of u in generation i.

Lemma

For all $n \in \mathbb{N}, x \in \mathcal{X}$ and $F \in \mathcal{B}(\mathcal{X}^{n+1})$ non-negative, we have

$$\mathbb{E}_{\mathbf{e},\delta_x}\left(\sum_{|u|=n} F(X_0(u),\ldots,X_n(u))\right) = \mathbb{E}_{\mathbf{e},\delta_x}(Z_n(\mathcal{X}))\mathbb{E}_{\mathbf{e},x}(F(Y_0^{(n)},\ldots,Y_n^{(n)})),$$

where $(Y_i^{(n)} : i=0,\ldots,n)$ is a non-homogeneous Markov chain with kernels $(Q_{n-i}(.,T^i\mathbf{e},.) : i=0,\ldots,n-1)$.

In particular $\mathbb{E}_{\mathbf{e},\delta_x}\left(\sum_{|u|=n} f(Z(u))\right) = \mathbb{E}_{\mathbf{e},\delta_x}(Z_n(\mathcal{X}))\mathbb{E}_{\mathbf{e},x}(f(Y_n^{(n)}))$.

Law of large numbers (I)

Theorem

We assume that there exists a measure ν with finite first moment such that for all $x \in \mathcal{X}, k, l \geq 0$,

$$\mathbb{P}(N(x, T^k\mathbf{e}) \geq l) \leq \nu[l, \infty).$$

Assume also that there exists a sequence of probability measure μ_n such that

$$\sup_{\lambda \in \mathcal{M}_1(\mathcal{X})} \left| Q_{i,n}(\lambda, T^i\mathbf{e}, f \circ f_n) - \mu_n(f) \right| \longrightarrow 0,$$

uniformly for $n - i \to \infty$. Then,

$$\frac{f_n.Z_n(f)}{Z_n(\mathcal{X})} - \mu_n(f) \stackrel{n\to\infty}{\longrightarrow} 0$$

$\mathbb{P}_{\mathbf{e}}$ *a.s. on the event* $\left\{ \forall n,\ Z_n(\mathcal{X}) > 0;\ \liminf_{n\to\infty} Z_{n+1}(\mathcal{X})/Z_n(\mathcal{X}) > 1 \right\}.$

Law of large numbers (II)

Theorem

Let $\mathbf{e} \in E$, $x \in \mathcal{X}$ *and* $f \in \mathcal{B}(\mathcal{X})$ *bounded.*
Under some technical assumptions (bounded second moment and control on $(x, k) \to \mathbb{E}_{T^k\mathbf{e},\delta_x}(Z_n(\mathcal{X}))$) *and assuming that there exists a sequence of probability measures* μ_n *on* $\mathcal{X}$ *such that*

$$\sup_{i\in\mathbb{N}} \sum_{n\geq i} \sup_{\lambda\in\mathcal{M}_1} \left| Q_{i,n}(\lambda, T^i\mathbf{e}, f \circ f_n) - \mu_n(f) \right|^2 < \infty.$$

Then, $Z_n(\mathcal{X})/\mathbb{E}_{\mathbf{e}}(Z_n(\mathcal{X}))$ *is bounded in* $L^2_{\mathbf{e}}$ *and*

$$\frac{f_n.Z_n(f) - \mu_n(f)Z_n(\mathcal{X})}{\mathbb{E}_{\mathbf{e}}(Z_n(\mathcal{X}))} \xrightarrow{n\to\infty} 0 \qquad \mathbb{P}_{\mathbf{e}} \ a.s.$$

Applications

- Multitype branching process in varying / random environment
- Deriving the shape of the population from limit theorems for Random Walk in Random Environment
- A sufficient condition is given by [Doeblin type assumptions]

$$\mathbb{E}_{\mathbf{e},\delta_x}(Z_1(A)) \leq M(\mathbf{e})\mathbb{E}_{\mathbf{e},\delta_y}(Z_1(A)) \quad (x, y \in \mathcal{X}).$$

+control on $\mathbf{e} \to M(\mathbf{e})$.

- Using Lyapounov assumptions : *WIP*.

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Two more questions :

- How many individuals have some given (non common) trait ? (local densities and extremal traits)
- What is the growth rate of the population ? When does the population survives ?

Local densities and extremal individuals

Question : can we get

$$Z_n(A_n) \asymp \mathbb{E}_{\mathbf{e}}(Z_n(\mathcal{X}))\mathbb{P}(Y_n^{(n)} \in A_n)$$

from the many-to-one formula

$$\mathbb{E}_{\mathbf{e}}(Z_n(A_n)) = \mathbb{E}_{\mathbf{e}}(Z_n(\mathcal{X}))\mathbb{P}(Y_n^{(n)} \in A_n)$$

and the trajectory of $Y^{(n)}$ associated to the (large deviation event) A_n.

Problem : lower bound.

Solution : coupling by a branching process in varying environment in the first steps and LLN I for the rest of the time.

Application : under monotonicity and neutrality assumption, with a control of the trajectory of the auxiliary process.

Let X be the Markov chain with transition inherited from $P^{(k)}$.

Theorem

Assume that X satisfies a LDP with good rate function $I_{\mathbf{e}}$ in environment $\mathbf{e}$ and $\log m : \mathcal{X} \times E \to (-\infty, \infty)$ is continuous and bounded. Then, for every $x \in \mathcal{X}$,

$$\lim_{n\to\infty} \frac{1}{n} \log \mathbb{E}_{\mathbf{e},\delta_x}(Z_n(\mathcal{X})) = \sup_{\mu\in\mathcal{M}_1(\mathcal{X}\times E)} \left\{ \int_{\mathcal{X}\times E} \log(m(x,e))\mu(dxde) - I_{\mathbf{e}}(\mu) \right\}$$

and

$$M_{\mathbf{e}} := \left\{ \mu \in \mathcal{M}_1(\mathcal{X} \times E) : \int \log(m(x,e))\mu(dxde) - I_{\mathbf{e}}(\mu) = \varrho_{\mathbf{e}} \right\}$$

is compact and non empty.

Applications in fixed environment (via Sanov's theorem) and stationary ergodic random environment (via Seppäläinen LDP 95).