Historical processes and their diffusion limits for modelling populations with past dependence

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Motivation

★ Structured populations: individuals are characterized by variables that affect their reproducing and survival capacities. Here: trait $x \in \mathcal{X} \subset \mathbb{R}^d$ that is inherited from a parent to its offspring.

★ Continuous time birth-death processes, stochastic evolution based on individual dynamics with past dependence and competition.

★ **Purpose here: Modelling of genealogies and ancestral paths**
Ex: Application to the modelling of social interactions based on kin relations (cooperative breeding).

The biological assumptions

★ Large population,

★ Fixed amount of resources: small individuals with density dependence,

★ Fast births and deaths: allometric demographies (lifetimes and gestation lengths are proportional to individual biomass),

however the demographic balance is preserved.

★ Asexual reproduction,

★ Small mutation steps: mutant offspring look like their parent.

Births and ancestral lineages

★ Trait at birth:

- With probability $1-p$, the trait of the parent x is inherited.
- With probability p, there is a mutation. The new trait is $x+h$ where $h \rightsquigarrow \pi^n(h)dh$, π^n being a Gaussian kernel with expectation 0 and variance $(\sigma^2/n)\mathrm{Id}$.

We define:

$$K^n(dh) = p\ \pi^n(h)dh + (1-p)\ \delta_0(dh).$$

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We define:

$$K^n(dh) = p\ \pi^n(h)dh + (1-p)\ \delta_0(dh).$$

★ We consider the ancestral path or lineage:

$$y_t = \text{trait of the ancestor living at time } t$$

$y \in \mathbb{D}_{\mathbb{R}^d} = \mathbb{D}(\mathbb{R}_+, \mathbb{R}^d)$ embedded with the Skohorod topology.

Notation: y_t, $y^t = y_{.\wedge t}$, $(y|s|w)$

Particle system

★ Recall: $y \in \mathbb{D}_{\mathbb{R}^d} = \mathbb{D}(\mathbb{R}_+, \mathbb{R}^d)$

Notation: y_t, $y^t = y_{.\wedge t}$, $(y|s|w)$

★ Population:

$$X_t^n(dy) = \frac{1}{n} \sum_{i=1}^{N_t^n} \delta_{y^i_{.\wedge t}}(dy)$$

in $\mathcal{M}(\mathbb{D}_{\mathbb{R}^d})$ embedded with the weak convergence topology. Thus $X^n \in \mathbb{D}(\mathbb{R}_+, \mathcal{M}_F(\mathbb{D}_{\mathbb{R}^d}))$, embedded with the Skorohod topology.

Related works

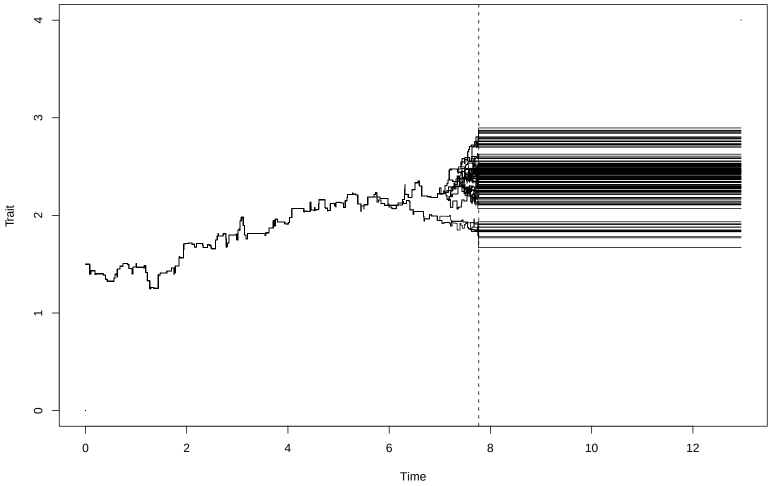
★ Historical Processes: Dawson-Perkins (1991), Perkins (1995), Etheridge (2000)

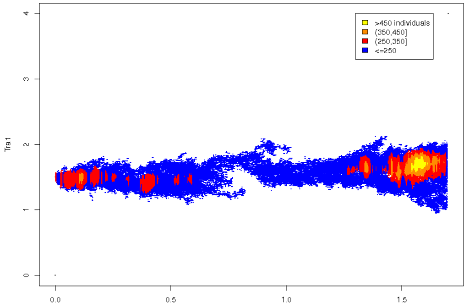
★ Coalescent: Berestycki N. (book: 2009), Schweinsberg (2000), Möhle Sagitov (2001)

★ Tree-valued processes: Greven Pfaffelhuber Winter (2009,2010)

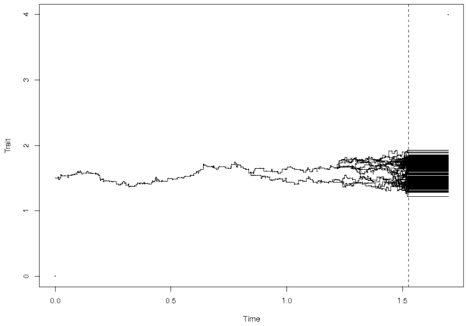
★ Superprocess renormalization: Dynkin (1991), Dawson (1991).

An example of evolving genealogies





>450 individuals
(350,450]
(250,350]
<=250
Trait
0
1
2
3
4
0.0
0.5
1.0
1.5



Trait
0
1
2
3
4
0.0
0.5
1.0
1.5
Time

Birth and death rates: examples

★ Allometric birth and death rates:

$$nr(t, y) + b(t, y)$$
$$nr(t, y) + d(t, y, X_t^n)$$

★ **Birth rate:** $n\, r(t, y) + b(t, y)$ with

$$b(t, y) = B\Big(\int_{[0,t)} y_{t-s} \nu_b(ds) \Big)$$

- $\nu_b(ds) = \delta_0(ds)$
- $\nu_b(ds) = e^{-\alpha s} ds$

★ **Death rate:** $n\, r(t, y) + d(t, y, X)$ with

$$d(t, y, X) = d_0(t, y) + \int_0^t \int_{\mathbb{D}} U(t, y, y') X_{t-s}(dy') \nu_d(ds)$$

Examples

★ **Dieckmann-Doebeli:** $r(t,y) = 1$ and

$$b(t,y) = \exp\left(-\frac{(y_t-2)^2}{2\sigma_b^2}\right), \quad d(t,y,X) = \int_{\mathbb{D}} \exp\left(-\frac{(y_t-y'_t)^2}{2\sigma_U^2}\right) X(dy')$$

★ **Adler**'s fattened goats:

$$U(t,y,y') = K_\varepsilon(y_t - y'_t),$$
$$d(t,y,X) = \int_0^t \int_{\mathbb{D}_{\mathbb{R}^d}} K_\varepsilon\left(y_t - y'_s\right) X_s(dy') e^{-\alpha(t-s)} ds.$$

Evolution equation

★ $\sup_{n\in\mathbb{N}^*}\mathbb{E}\big(\langle X_0^n,1\rangle^3\big) < +\infty, \Rightarrow \sup_{n\in\mathbb{N}^*}\mathbb{E}\big(\sup_{t\in[0,T]}\langle X_t^n,1\rangle^3\big) < +\infty.$

★ For bounded test functions φ of $y\in\mathbb{D}_{\mathbb{R}^d}$:

$$M_t^{n,\varphi} = \langle X_t^n,\varphi\rangle - \langle X_0^n,\varphi\rangle - \int_0^t\int_{\mathbb{D}_{\mathbb{R}^d}} X_s^n(dy)\,ds\Big[nr(s,y)\int_{\mathbb{R}^d}\big(\varphi(y|s|y_s+h)-\varphi(y)\big)K^n(y_s,dh) + b(s,y)\int_{\mathbb{R}^d}\varphi(y|s|y_s+h)K^n(y_s,dh) - d(s,y,(X^n)^s)\varphi(y)\Big]$$

is a square integrable martingale starting from 0 with quadratic variation:

$$\langle M^{n,\varphi}\rangle_t = \frac{1}{n}\int_0^t\int_{\mathbb{D}_{\mathbb{R}^d}} X_s^n(dy)\,ds\Big[\big(nr(s,y)+b(s,y)\big)\int_{\mathbb{R}^d}\varphi^2(y|s|y_s+h)K^n(y_s,dh) + \big(nr(s,y)+d(s,y,(X^n)^s)\big)\varphi^2(y)\Big].$$

Test functions

★ Dawson, Dynkin, Perkins use the following class of test functions:

$$\varphi(y) = \prod_{j=1}^{m} g_j(y_{t_j})$$

for $m \in \mathbb{N}^*$, $0 \leq t_1 < \cdots < t_m$ and $\forall j \in [\![1, m]\!]$, $g_j \in \mathcal{C}_b^2(\mathbb{R}^d, \mathbb{R})$.
However these functions are not necessarily continuous for discontinuous y's.

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★ For a real $\mathcal{C}_b^2$-function g on $\mathbb{R}_+ \times \mathbb{R}^d$ and a real $\mathcal{C}_b^2$-function G on $\mathbb{R}$, we define the continuous function G_g as

$$G_g(y) = G\Big(\int_0^T g(s, y_s) ds \Big).$$

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★ **Lemma:** Let φ be a test function of the 1st form. Then, there exists a sequence of test functions of the second form $(\varphi_q)_{q\in\mathbb{N}^*}$ such that for every $y \in \mathbb{D}_{\mathbb{R}^d}$ and every $t \in \mathbb{R}_+$ at which y is continuous,

$$\lim_{q\to+\infty} \varphi_q(y) = \varphi(y).$$

(choose $G(x) = e^x$ and $g_q(s, y_s) = \sum_{j=1}^{m} \log g_j(y_s)k^q(t_j - s)$)

Superprocess limit

★**Prop 1:** The sequence $(X^n)_{n\in\mathbb{N}^*}$ converges in law in $\mathbb{D}(\mathbb{R}_+,\mathcal{M}_F(\mathbb{D}_{\mathbb{R}^d}))$ to the superprocess $\bar{X}\in\mathcal{C}(\mathbb{R}_+,\mathcal{M}_F(\mathbb{D}_{\mathbb{R}^d}))$ characterized as follows, for test functions φ of $y\in\mathbb{D}_{\mathbb{R}^d}$:

$$M_t^{\varphi}=\langle\bar{X}_t,\varphi\rangle-\langle\bar{X}_0,\varphi\rangle-\int_0^t\int_{\mathbb{D}_{\mathbb{R}^d}}\Big(p\,r(s,y)\frac{\sigma^2}{2}\;D^2\varphi_{G,g}(s,y)+\Big[b(s,y)-d\big(s,y,\bar{X}_s\big)\Big]\varphi(y)\Big)\bar{X}_s(dy)\,ds$$

is a square integrable martingale where:

$$D^2\varphi_{G,g}(t,y)=G'\Big(\int_0^T g(s,y_s)ds\Big)\int_t^T\Delta_x g(s,y_t)ds+G''\Big(\int_0^T g(s,y_s)ds\Big)\sum_{i=1}^d\Big(\int_t^T\partial_{x_i}g(s,y_t)ds\Big)^2.$$

with quadratic variation:

$$\langle M^{\varphi_{G,g}}\rangle_t=\int_0^t\int_{\mathbb{D}_{\mathbb{R}^d}}2\,r(s,y)\sigma^2\varphi_{G,g}^2(y)\bar{X}_s(dy)\,ds.$$

Martingale problem for the tests functions of Dawson

★ For the Laplacian Δ of $\mathbb{R}^d$, a path $y \in \mathbb{D}_{\mathbb{R}^d}$, a time $t > 0$ and a test function φ of the product form:

$$\widetilde{\Delta}\varphi(t,y) = \sum_{k=0}^{m-1} \mathbf{1}_{[t_k,t_{k+1}[}(t)\Big(\prod_{j=1}^{k} g_j(y_{t_j})\Delta\big(\prod_{j=k+1}^{m} g_j\big)(y_t)\Big)$$

with $t_0 = 0$ and $t_{m+1} = t$.

★ **Prop 2:** The solutions of the MP of Prop 1 satisfy the MP:

$$M_t^{\varphi} = \langle \bar{X}_t, \varphi\rangle - \langle \bar{X}_0, \varphi\rangle - \int_0^t \int_{\mathbb{D}_{\mathbb{R}^d}} \Big(pr(s,y)\frac{\sigma^2}{2}\widetilde{\Delta}\varphi(s,y) + \Big[b(s,y) - d\big(s,y,\bar{X}_s\big)\Big]\varphi(y)\Big)\bar{X}_s(dy)\,ds,$$

the bracket being as in Prop 1.

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the bracket being as in Prop 1.

★ **Idea of the proof of the Prop 1:**
Tightness of the sequence (X^n).
Uniqueness of the solution of the MP of Prop 2.

Tightness criterion

Prop: from [Dawson-Perkins, (Ethier-Kurtz)] $(X^n)_{n\in\mathbb{N}^*}$ is tight in $\mathbb{D}(\mathbb{R}_+, \mathcal{M}_F(\mathbb{D}_{\mathbb{R}^d}))$ if:

(i) $\forall T > 0$, $\forall \varepsilon > 0$, $\exists K \subset \mathbb{D}_{\mathbb{R}^d}$ compact,

$$\sup_{n\in\mathbb{N}^*} \mathbb{P}\left(\exists t \in [0, T], X_t^n(K_T^c) > \varepsilon\right) \le \varepsilon,$$

where

$$K_T = \left\{y^t, y^{t-} \mid y \in K, \, t \in [0, T]\right\} \subset \mathbb{D}_{\mathbb{R}^d}. \tag{1}$$

(ii) $\forall \varphi \in \mathcal{C}_b(\mathbb{D}_{\mathbb{R}^d}, \mathbb{R}_+)$, the family $(\langle X_.^n, \varphi\rangle)_{n\in\mathbb{N}^*}$ is tight in $\mathbb{D}_{\mathbb{R}_+}$.

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(ii) $\forall \varphi \in \mathcal{C}_b(\mathbb{D}_{\mathbb{R}^d}, \mathbb{R}_+)$, the family $(\langle X^n_\cdot, \varphi\rangle)_{n\in\mathbb{N}^*}$ is tight in $\mathbb{D}_{\mathbb{R}_+}$.

★ Let us define $S^n_\varepsilon = \inf\{t \geq 0,\; X^n_t(K^c_T) > \varepsilon\}$.

$$\mathbb{P}(S^n_\varepsilon < T) = \mathbb{P}\left(S^n_\varepsilon < T,\; X^n_T((K^T)^c) > \frac{\varepsilon}{2}\right) + \mathbb{P}\left(S^n_\varepsilon < T,\; X^n_T((K^T)^c) \leq \frac{\varepsilon}{2}\right)$$

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$$\leq \frac{2}{\varepsilon}\mathbb{E}\big(X^n_T((K^T)^c)\big) + \mathbb{P}(S^n_\varepsilon < T)(1-\eta)$$

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(ii) $\forall \varphi \in \mathcal{C}_b(\mathbb{D}_{\mathbb{R}^d}, \mathbb{R}_+)$, the family $(\langle X^n_., \varphi\rangle)_{n\in\mathbb{N}^*}$ is tight in $\mathbb{D}_{\mathbb{R}_+}$.

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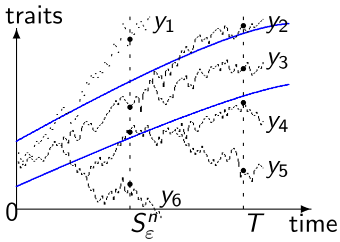
$$\leq \frac{2}{\varepsilon}\mathbb{E}\big(X^n_T((K^T)^c)\big) + \mathbb{P}(S^n_\varepsilon < T)(1-\eta)$$

Then:

$$\mathbb{P}(S^n_\varepsilon < T) \leq \frac{2\mathbb{E}\big(X^n_T((K^T)^c)\big)}{\varepsilon\eta}.$$

Upperbound of $\mathbb{P}\Big(S^n_\varepsilon < T,\ X^n_T((K^T)^c) \leq \frac{\varepsilon}{2}\Big)$



★ The mass of particles started at S^n_ε and corresponding to trajectories $y^{S^n_\varepsilon} \notin K^{S^n_\varepsilon}$ is approximated by:

$$\mathcal{Y}_t = \mathcal{Y}_0 + \int_0^t (\bar{b} - \underline{d})\mathcal{Y}_s ds + \int_0^t \sqrt{\rho(s)\mathcal{Y}_s} dB_s$$

where $2\underline{r} \leq \rho(s) \leq 2\bar{r}$ is defined by the limit of the quadratic variation.

★ $\mathbb{P}_\varepsilon(\inf_{s\in[0,T]} \mathcal{Y}_s > \varepsilon/2) > 0$.

Uniqueness

★ By Dawson-Girsanov's theorem, we can find a probability measure $\mathbb{Q}$ on $\mathcal{C}([0,T],\mathcal{M}_F(\mathbb{D}_{\mathbb{R}^d}))$ under which:

$$\widetilde{M}_t^{\varphi} = \langle \bar{X}_t, \varphi\rangle - \langle \bar{X}_0, \varphi\rangle - \int_0^t \int_{\mathbb{D}_{\mathbb{R}^d}} \frac{pr(s,y)\sigma^2}{2} \widetilde{\Delta}\varphi(s,y)\bar{X}_s(dy)\, ds$$

is a martingale with the same bracket as above.

★ Pathwise existence and uniqueness for the SDE in $\mathbb{R}^d$:

$$Y_t = Y_0 + \int_0^t \sqrt{\sigma^2 pr(s, Y^s)}dB_s.$$

$W_t = Y_.^t$ and $S_{s,t}\varphi(y) = \mathbb{E}^{\mathbb{Q}}\big(\varphi(W_t)\,|\,W_s = y^s\big)$.

★ We have that

$$\mathbb{E}^{\mathbb{Q}}\big(\exp(-\langle \bar{X}_t,\varphi\rangle)\,|\,\bar{X}_s = \delta_{y^s}\big) = e^{-V_{s,t}\varphi(y)}$$

where $V_{s,t}\varphi(y)$ is the unique solution of:

$$V_{s,t}\varphi(y) = S_{s,t}\varphi(y) - \int_s^t \frac{p\sigma^2}{2} S_{s,u}\Big(r(u,.)\big(V_{u,t}\varphi(.)\big)^2\Big)(y)du.$$

Lineages' distributions

★ Perkins' representation:
Under $\mathbb{Q}$, we have in distribution:

$$Y_t(y) = Y_0(y) + \int_0^t \sqrt{\sigma^2 pr(s, Y^s(y))} dy_s$$

$$\bar{X}_0, \qquad \langle \bar{X}_t, \varphi \rangle = \int_{\mathbb{D}_{\mathbb{R}^d}} \varphi(Y(y)^t) H_t(dy)$$

where $(H_t(dy))_{t \in \mathbb{R}_+}$ is under $\mathbb{Q}$ a historical Brownian superprocess.

Lineages' distributions: case of constant r and $b-d$'s

★ $\langle \mu_t, \varphi \rangle = \langle \bar{X}_t, \varphi \rangle / \langle \bar{X}_t, 1 \rangle$. When r and $b-d$ are constant:

$$\langle \mathbb{E}(\mu_t), \varphi \rangle = \langle \mathbb{E}(\mu_0), \varphi \rangle + \int_0^t \langle \mathbb{E}(\mu_s), pr\sigma^2 \widetilde{\Delta} \varphi(s,.) \rangle \, ds.$$

$b-d=0$: historical super Brownian motion (Dawson Perkins 91).

★ For the historical super Brownian motion, we have a very precise description of the probabilistic structure of the genealogies.

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$b-d=0$: historical super Brownian motion (Dawson Perkins 91).

★ For the historical super Brownian motion, we have a very precise description of the probabilistic structure of the genealogies.
★ Let $\phi(\mu) = \langle \mu \otimes \mu, \varphi \rangle = \int_{\mathbb{D}_{\mathbb{R}^d}} \int_{\mathbb{D}_{\mathbb{R}^d}} \varphi(t, y, z) \mu_t(dy) \mu_t(dz)$ and $\widetilde{\Delta}^{(2)} \varphi(y, z) = \widetilde{\Delta}(y \mapsto \varphi(y, z)) + \widetilde{\Delta}(z \mapsto \varphi(y, z))$. We recover Fleming-Viot generator:

$$\begin{aligned} L^{FV} \phi(X) = & \frac{pr\sigma^2}{2} \Big\langle \frac{X}{\langle X, 1 \rangle} \otimes \frac{X}{\langle X, 1 \rangle}, \widetilde{\Delta}^{(2)} \varphi \Big\rangle \\ & + \frac{2r\sigma^2}{\langle X, 1 \rangle} \Big(\int_{\mathbb{D}_{\mathbb{R}^d}} \varphi(y, y) \frac{X(dy)}{\langle X, 1 \rangle} - \Big\langle \frac{X}{\langle X, 1 \rangle} \otimes \frac{X}{\langle X, 1 \rangle}, \varphi \Big\rangle \Big) \end{aligned}$$

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Adler's fattening goats

$$r(t,y)=1, \qquad b(t,y)=b,$$

$$\text{and } d(t,y,X)=\int_0^t\int_{\mathbb{R}^d}\frac{K_\varepsilon\big(y'(s)-y(t)\big)}{K}X_s(dy',dc')\,e^{-\alpha(t-s)}ds$$