Population models as partial observations of genealogical models

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Kurtz and Rodrigues (2011); Etheridge and Kurtz (2018)

How to specify a Markov model

An E-valued process is *Markov* wrt $\{\mathcal{F}_t\}$ if

$$E[f(X(t+s))|\mathcal{F}_t] = E[f(X(t+s))|X(t)], \quad f \in B(E)$$

"Infinitesimal changes of distribution"

$$E[f(X(t+\Delta t))|\mathcal{F}_t] \approx f(X(t)) + Af(X(t))\Delta t$$

or

$$E[f(X(t+\Delta t)) - f(X(t)) - Af(X(t))\Delta t|\mathcal{F}_t] \approx 0$$

which suggests

$$E[f(X(t+r)) - f(X(t)) - \int_t^{t+r} Af(X(s))ds|\mathcal{F}_t] = 0$$

$$f(X(t)) - f(X(0)) - \int_0^t Af(X(s))ds \quad \text{a martingale}$$

Examples of generators

Poisson process ($E = \{0, 1, 2 \ldots\}$, $\mathcal{D}(A) = B(E)$)

$$Af(k) = \lambda(f(k+1) - f(k))$$

Pure jump process (E arbitrary)

$$Af(x) = \lambda(x) \int_E (f(y) - f(x))\mu(x, dy)$$

Diffusion process ($E = \mathbb{R}^d$, $\mathcal{D}(A) = C_c^2(\mathbb{R}^d)$)

$$Af(x) = \frac{1}{2} \sum_{i,j} a_{ij}(x) \frac{\partial^2}{\partial x_i \partial x_j} f(x) + \sum_i b_i(x) \frac{\partial}{\partial x_i} f(x)$$

ODE $\dot{X} = F(X)$ ($E = \mathbb{R}^d$, $\mathcal{D}(A) - C_c^1(\mathbb{R}^d)$)

$$Af(x) = F(x) \cdot \nabla f(x)$$

The martingale problem for A

X is a solution for the martingale problem for (A, ν_0), $\nu_0 \in \mathcal{P}(E)$, if $PX(0)^{-1} = \nu_0$ and there exists a filtration $\{\mathcal{F}_t\}$ such that

$$f(X(t)) - f(X(0)) - \int_0^t Af(X(s))ds$$

is an $\{\mathcal{F}_t\}$-martingale for all $f \in \mathcal{D}(A)$.

Theorem 1 *If any two solutions of the martingale problem for A satisfying $PX_1(0)^{-1} = PX_2(0)^{-1}$ also satisfy $PX_1(t)^{-1} = PX_2(t)^{-1}$ for all $t \geq 0$, then the f.d.d. of a solution X are uniquely determined by $PX(0)^{-1}$*

If X is a solution of the MGP for A and $Y_a(t) = X(a+t)$, then Y_a is a solution of the MGP for A.

Theorem 2 *If the conclusion of the above theorem holds, then any solution of the martingale problem for A is a Markov process.*

First fundamental theorem of filtering

Theorem 3 *(first pointed out to me by Giorgio Koch)*

Let X be a solution of the martingale problem for A with filtration $\{\mathcal{F}_t\}$, that is, for each $f \in \mathcal{D}(A)$,

$$M_f(t) = f(X(t)) - f(X(0)) - \int_0^t Af(X(s))ds$$

is a $\{\mathcal{F}_t\}$-martingale, and let $\{\mathcal{G}_t\}$ be a filtration with $\mathcal{G}_t \subset \mathcal{F}_t$.

Define $\pi_t(C) = P\{X(t) \in C|\mathcal{G}_t\}$, so $E[f(X(t))|\mathcal{G}_t] = \pi_t f$. Then

$$M_f^{\mathcal{G}}(t) = \pi_t f - \pi_0 f - \int_0^t \pi_s Af ds$$

is a $\{\mathcal{G}_t\}$-martingale.

Second fundamental theorem of filtering

Theorem 4 *Kurtz and Nappo (2011)*

Under appropriate technical conditions on A, if $\{\pi_t\}$ is a cadlag $\mathcal{P}(E)$-valued stochastic process adapted to a filtration $\{\mathcal{G}_t\}$ and for each $f \in \mathcal{D}(A) \subset C_b(E)$

$$M_f^{\mathcal{G}}(t) = \pi_t f - \pi_0 f - \int_0^t \pi_s A f ds$$

is a $\{\mathcal{G}_t\}$-martingale, then there exists a filtration $\{\widetilde{\mathcal{F}}_t\}$ a process X adapted to $\{\widetilde{\mathcal{F}}_t\}$, and a filtration $\{\widetilde{\mathcal{G}}_t\}$ with $\widetilde{\mathcal{G}}_t \subset \widetilde{\mathcal{F}}_t$ such that for each $f \in \mathcal{D}(A)$

$$M_f(t) = f(X(t)) - f(X(0)) - \int_0^t Af(X(s))ds$$

is a $\{\widetilde{\mathcal{F}}_t\}$-martingale and $\widetilde{\pi}_t(C) = P\{X(t) \in C|\widetilde{\mathcal{G}}_t\}$, $C \in \mathcal{B}(E)$, $t \geq 0$, defines a $\mathcal{P}(E)$-valued process that has the same finite dimensional distributions as $\{\pi_t, t \geq 0\}$.

Markov branching process

Let

$$Cf(n) = \lambda n(f(n+1) - f(n) + \mu n(f(n-1) - f(n)), \quad n \in \mathbb{N},$$

that is, C is the generator for a Markov branching process N, where $N(t)$ is the size of the population at time t.

Intuitively, C models a population in which each new particle has a parent and hence an ancestral line leading back to an individual alive at time zero, but the ancestral line cannot be recovered from observations of N.

There should be a another model Z, say with generator A, such that for $\pi_t(D) = P\{Z(t) \in D | \mathcal{F}_t^N\}$,

$$\pi_t f - \pi_0 f - \int_0^t \pi_s A f ds$$

is a $\{\mathcal{F}_t^N\}$-martingale.

Feller diffusion approximation

Let

$$C_\lambda f(n) = \lambda a n(f(n+1) - f(n)) + (\lambda a - b)n(f(n-1) - f(n)).$$

For $x \in E_\lambda = \{\frac{n}{\lambda} : n \in \mathbb{N}\}$ and $f(n) = h(x)$,

$$\begin{aligned} C_\lambda h(x) &= \lambda^2 a x(h(x+\frac{1}{\lambda}) - h(x)) + (\lambda^2 a - \lambda b)x(h(x-\frac{1}{\lambda}) - h(x)) \\ &\to a x h''(x) + b x h'(x) = C_\infty h(x) \end{aligned}$$

There are lots of choices for A_λ, but we want one that models the genealogy in a way that converges to the genealogy for C_∞.

Lookdown construction

Kurtz and Rodrigues (2011)

Let $E_\lambda = \cup_n [0,\lambda]^n$ and

$$\mathcal{D}(A_\lambda) = \{f(u,n) = \prod_{i=1}^{n} g(u_i) : 0 \le g \le 1, g \in C^1[0,\lambda], g(\lambda) = 1, g'(\lambda) = 0\},$$

For parameters $a > 0$ and $b \in \mathbb{R}$ satisfying $\lambda a - b > 0$, define

$$A_\lambda f(u,n) = f(u,n) \sum_{i=1}^{n} 2a \int_{u_i}^{\lambda} [g(v) - 1]\, dv + f(u,n) \sum_{i=1}^{n} \left(a u_i^2 - b u_i\right) \frac{g'(u_i)}{g(u_i)}. \tag{1}$$

Properties of the process

$f(u,n) = \prod_{i=1}^{n} g(u_i)$

$$f(u,n) \sum_{i=1}^{n} 2a \int_{u_i}^{\lambda} [g(v) - 1] \, dv$$
$$= f(u,n) \sum_{i=1}^{n} 2a(\lambda - u_i) \frac{1}{\lambda - u_i} \int_{u_i}^{\lambda} [g(v) - 1] \, dv$$

A particle with level $U_i(t)$ gives birth at rate $2a(\lambda - U_i(t))$ to a particle whose initial level is uniformly distributed between $U_i(t)$ and λ.

Particle levels satisfy

$$\dot{U}_i(t) = aU_i^2(t) - bU_i(t).$$

Critical levels

$$\dot{u} = au^2 - bu$$

If $0 < b < a\lambda$, then $u_c = \frac{b}{a}$.

If the lowest initial level is below u_c, then the population lives forever. If the lowest initial level is above u_c, then the population dies out.

A calculation

Let $\alpha_\lambda(n, du)$ be the joint distribution of n iid uniform $[0, \lambda]$ random variables. $\widehat{f}(n) = \int f(u,n)\alpha_\lambda(n,du) = e^{-\beta_g n}$, $e^{-\beta_g} = \frac{1}{\lambda}\int_0^\lambda g(u)du$

Calculate $\int A_\lambda f(u,n)\alpha_\lambda(n,du)$ by noting

$$\lambda^{-1}2a\int_0^\lambda g(z)\int_z^\lambda (g(v)-1)dv = a\lambda e^{-2\beta_g} - 2a\lambda^{-1}\int_0^\lambda g(z)(\lambda - z)dz$$

and

$$\begin{aligned}\lambda^{-1}\int_0^\lambda (az^2 - bz)g'(z)dz &= -\lambda^{-1}\int_0^\lambda (2az-b)(g(z)-1)dz \\ &= -2a\lambda^{-1}\int_0^\lambda zg(z)dz + a\lambda + b(e^{-\beta_g}-1).\end{aligned}$$

Averaged generator

Then for $\widehat{f}(n) = \int f(u,n)\alpha_\lambda(n,du) = e^{-\beta_g n}$, $e^{-\beta_g} = \frac{1}{\lambda}\int_0^\lambda g(u)du$,

$$\begin{aligned}
\int A_\lambda f(u,n)\alpha_\lambda(n,du) \\
&= ne^{-\beta_g(n-1)}\left(\lambda a e^{-2\beta_g} - 2\lambda a e^{-\beta_g} + \lambda a + b(e^{-\beta_g}-1)\right) \\
&= \lambda a n(\widehat{f}(n+1) - \widehat{f}(n)) + (\lambda a - b)n(\widehat{f}(n-1) - \widehat{f}(n)) \\
&= C_\lambda \widehat{f}(n)
\end{aligned}$$

Conclusion

Let $\widetilde{N}$ be a solution of the martingale problem for

$$C_\lambda \widehat{f}(n) = a\lambda n(\widehat{f}(n+1) - \widehat{f}(n)) + (a\lambda - b)n(\widehat{f}(n-1) - \widehat{f}(n)),$$

that is, $\widetilde{N}$ is a branching process with birth rate λa and death rate $(\lambda a - b)$.

Then, taking $\widetilde{\pi}_t(du) \in \mathcal{P}(E)$ to be $\alpha_\lambda(\widetilde{N}(t), du)$,

$$C_\lambda \widehat{f}(\widetilde{N}(t)) = \widetilde{\pi}_t A_\lambda f,$$

and

$$\widetilde{\pi}_t f - \widetilde{\pi}_0 f - \int_0^t \widetilde{\pi}_s A_\lambda f,$$

is a $\{\mathcal{F}_t^{\widetilde{N}}\}$-martingale. By Theorem 4, a solution $(U_1(t), \ldots, U_{N(t)}(t), N(t))$ of the martingale problem for A_λ exists such that N has the same distribution as $\widetilde{N}$ and the conditional distribution of $(U_1(t), \ldots, U_{N(t)}(t))$ given $\mathcal{F}_t^N$ is $\alpha_\lambda(N(t), du)$.

The large population limit

Take $\lambda \to \infty$, so let $E_\lambda = \cup_n [0,\lambda]^n \to E_\infty = \cup_{n=0}^\infty [0,\infty)^n$ and

$$\mathcal{D}(A_\infty) = \{f(u) = \prod_i g(u_i) : 0 \le g \le 1, g \in C^1[0,\infty), g(v) = 1, v \ge v_g\},$$

$$\begin{aligned} & A_\lambda f(u,n) \\ & \quad = f(u,n) \sum_{i=1}^n 2a \int_{u_i}^\lambda [g(v)-1]\, dv \\ & \qquad + f(u,n) \sum_{i=1}^n (a u_i^2 - b u_i) \frac{g'(u_i)}{g(u_i)}. \\ \to \; & A_\infty f(u) \\ & \quad = f(u) \sum_i 2a \int_{u_i}^\infty [g(v)-1]\, dv \\ & \qquad + f(u) \sum_i (a u_i^2 - b u_i) \frac{g'(u_i)}{g(u_i)}. \end{aligned} \tag{2}$$

Particle representation of Feller diffusion

If $n\lambda^{-1} \to x$, then $\alpha_\lambda(n, du) \to \alpha(x, du)$, where $\alpha(x, du)$ is the distribution of a Poisson process on $[0, \infty)$ with intensity x.

$$\widehat{f}(x) = \alpha f(x) = \int f(u)\alpha(x, du) = e^{-x\int_0^\infty (1-g(z))dz} = e^{-x\beta_g}$$

and

$$\begin{aligned} \alpha A f(x) &= e^{-x\beta_g}\Big(2ax\int_0^\infty g(z)\int_z^\infty (g(v)-1)dvdz \\ &\qquad + x\int_0^\infty (az^2 - bz)g'(z)dz\Big) \\ &= e^{-x\beta_g}(ax\beta_g^2 - bx\beta_g) \\ &= ax\widehat{f}''(y) + bx\widehat{f}'(y) \end{aligned}$$

Application of filtering theorem

Let $\{U_i(0)\}$ be a conditionally Poisson process on $[0,\infty)$ with (conditional) intensity $X(0)$. Then, $\{U_i(t)\}$ is conditionally Poisson with intensity $X(t)$,

$$X(t) = \lim_{r\to\infty} \frac{1}{r}\#\{i : U_i(t) \le r\},$$

and X is a Feller diffusion with generator $C_\infty f(x) = axf''(y) + bxf'(y)$

$$E[\{U_i(t)\} \in D | \mathcal{F}_t^X] = \pi_t(D) = \alpha(X(t), D)$$

Markov branching processes: Models with type and locations

Individuals have types/locations in E. η is a counting measure on $E \times [0, \lambda]$ or a set of points in $E \times [0, \lambda]$

$$\eta = \sum \delta_{(x,u)}$$

B is a generator of a Markov process in E.

$\mathcal{D}(A_\lambda)$ is the collection of $f(\eta)$ of the form $f(\eta) = \prod_{(x,u)\in\eta} g(x, u)$ where

$$0 \le g \le 1, g \in C^1[0, \lambda], g(\lambda) = 1, g'(\lambda) = 0, g(\cdot, u) \in \mathcal{D}(B).$$

Generator with type/location

For $f \in \mathcal{D}(A_\lambda)$,

$$A_\lambda f(u) \tag{3}$$

$$= f(\eta) \sum_{(x,u)} \frac{Bg(x,u)}{g(x,u)} \tag{4}$$

$$+ f(\eta) \sum_{(x,u)\in\eta} 2a(x) \int_u^\lambda [g(x,v) - 1] \, dv$$

$$+ f(\eta) \sum_{(x,u)\in\eta} \left(a(x)u^2 - b(x)u\right) \frac{g'(x,u)}{g(x,u)}.$$

Averaged generator

$$\overline{\eta} = \sum_{(x,u)\in\eta} \delta_x \qquad\qquad \overline{g}(x) = \frac{1}{\lambda}\int_0^\lambda g(x,u)du$$

$\alpha(\overline{\eta}, d\eta)$ is the distribution under which the levels are iid uniform.

For $f(\eta) = \prod_{(x,u)\in\eta} g(x,u)$, $\overline{f}(\overline{\eta}) \equiv \alpha f(\overline{\eta}) = \prod_{x\in\overline{\eta}} \overline{g}(x)$ and

$$\begin{aligned} \alpha A_\lambda f(\overline{\eta}) &= \alpha f(\overline{\eta})\Big(\sum_{x\in\overline{\eta}} \frac{B\overline{g}(x)}{\overline{g}(x)} + \lambda a(x)(\overline{g}(x) - 1) \\ &\qquad + (\lambda a(x) - b(x))(\frac{1}{\overline{g}(x)} - 1)\Big) \end{aligned}$$

Primary goal: High density limits

We want infinite population limits in which the limiting model is countably infinite and we can identify individuals and their relationships to other individuals, for example, their genealogies.

Population models

Modeling finite or infinite populations in which each individual has a location and/or type in E.

Individuals may move and/or mutate (change type).

Must specify how individuals die and how they give birth, and change type.

Assign each individual to a "level" so that observations of X up to time t give no information about the levels at time t.

Assign levels so that in the pre-limiting model, the levels are iid uniform on $[0, \lambda]$.

Elements in the domain

State of the process $\eta = \sum \delta_{(x,u)}$, a locally finite counting measure on $E \times [0, \lambda]$, and $\overline{\eta} = \sum \delta_x$.

$$f(\eta) = \prod_{(x,u)\in\eta} g(x, u)$$

$0 \le g \le 1$, $g(x, u) = 1$, $u > \lambda$ or $x \ne K_g$ plus regularity as needed

$$\overline{g}(x) = \lambda^{-1} \int_0^\lambda g(x, u)du$$

so

$$E[f(\eta_t)|\mathcal{F}_t^{\overline{\eta}}] = \prod_{x\in\overline{\eta}_t} \overline{g}(x)$$

High density limits

A high-density limit corresponds to $\lambda \to \infty$ while $\lambda^{-1}\overline{\eta}_t^\lambda(C) \to \Xi(t,C)$.

If $g(x,u) = 1$ for $u \geq u_g$ and, perhaps, $x \notin K_g$, then assuming $\eta_t^\lambda \Rightarrow \eta_t$ in the vague, or perhaps weak, topology,

$$\prod_{(x,u)\in\eta_t^\lambda} g(x,u) \to \prod_{(x,u)\in\eta_t} g(x,u).$$

Since the original levels were iid uniform $[0,\lambda]$, the limiting η_t must be conditionally Poisson with Cox measure $\Xi(t)$. In particular

$$E[\prod_{(x,u)\in\eta_t} g(x,u)|\mathcal{F}_t^\Xi] = e^{-\int_E \int_0^\infty (1-g(x,u))du\Xi(t,dx)}.$$

Modeling multiple death events

For each $(x,u) \in \eta$, multiply the u by $\rho > 1$ and kill off all particles with $\rho u \geq \lambda$.

If the u are independent and uniformly distributed on $[0,\lambda]$ and independent of the x, and $\rho u < \lambda$, then $u' = \rho u$ is uniformly distributed on $[0,\lambda]$ and independent of the x.

$$P\{\rho u \geq \lambda\} = P\{u > \lambda \rho^{-1}\} = 1 - \rho^{-1} = \frac{\rho - 1}{\rho}$$

Let $0 \leq g(x,u) \leq 1$ and $g(x,u) = 1$ for $u \geq \lambda$. Set $\overline{g}(x) = \lambda^{-1}\int_0^\lambda g(x,u)du$. Then setting $p(x) = \rho(x)^{-1}(\rho(x) - 1)$

$$\begin{aligned} \lambda^{-1}\int_0^\lambda g(x,\rho(x)u)du &= \lambda^{-1}\rho(x)^{-1}\int_0^{\rho(x)\lambda} g(x,v)dv \\ &= \rho(x)^{-1}\overline{g}(x) + \rho(x)^{-1}(\rho(x) - 1) \end{aligned}$$

$$E[\prod_{(x,u)\in\eta_{t-}} g(x,\rho(x)u))|\overline{\eta}_{t-}] = \prod_{x\in\overline{\eta}_{t-}} (\overline{g}(x)(1 - p(x)) + p(x))$$

Thinning

$f(\eta) = \prod_{(x,u)\in\eta} g(x,u)$

$$A_{th}f(\eta) = \beta(\overline{\eta}) \int_{\mathbb{U}} (\prod_{(x,u)\in\eta} g(x, u\rho(x,z)) - f(\eta))\mu(\overline{\eta}, dz),$$

for some $\rho(x,z) \geq 1$. Let $p(x,z) = \frac{\rho(x,z)-1}{\rho(x,z)}$. Then

$$\alpha A_{th}f(\overline{\eta}) = \beta(\overline{\eta}) \int_{\mathbb{U}} (\prod_{x\in\overline{\eta}}((1-p(x,z))\overline{g}(x) + p(x,z)) - \alpha f(\overline{\eta}))\mu(\overline{\eta}, dz),$$

When a thinning event of type z occurs individuals are independently eliminated with (type-dependent) probability $p(x,z)$.

High density limit

For the high density limit, assume

$$\lambda^{-1}\overline{\eta} \to \Xi \text{ implies } \beta_\lambda(\overline{\eta}) \to \beta(\Xi).$$

Then

$$A_{th}f(\eta) = \beta(\Xi)\int_{\mathbb{U}}(\prod_{(x,u)\in\eta} g(x, u\rho(x,z)) - f(\eta))\mu(\Xi, dz),$$

and the projected operator becomes

$$\alpha A_{th}f(\Xi) = \beta(\Xi)\int_{\mathbb{U}}(e^{-\int_E \frac{1}{\rho(x,z)}h(x)\Xi(dx)} - \alpha f(\Xi))\mu(\Xi, dz),$$

where $h(x) = \int_0^\infty (1 - g(x,u))du$ and $\alpha f(\Xi) = e^{-\int_E h(x)\Xi(dx)}$.

Modeling individual deaths

For $d_0(x) \geq 0$,

$$A_{pd}f(\eta) = f(\eta) \sum_{(x,u)\in\eta} d_0(x)u\frac{\partial_u g(x,u)}{g(x,u)}.$$

which says the levels satisfy $\dot{u} = d_0(x)u$

$$\alpha A_{pd}f(\overline{\eta}) = \alpha f(\overline{\eta}) \sum_{x\in\overline{\eta}} \frac{1}{\overline{g}(x)} \lambda^{-1} \int_0^\lambda d_0(x)u\partial_u g(x,u)du\,.$$

Since

$$\lambda^{-1}\int_0^\lambda u\partial_u g(x,u)du = \lambda^{-1}u(g(x,u)-1)\big|_0^\lambda - \lambda^{-1}\int_0^\lambda (g(x,u)-1)du = 1-\overline{g}(x),$$

$$\alpha A_{pd}f(\overline{\eta}) = \alpha f(\overline{\eta}) \sum_{x\in\overline{\eta}} d_0(x)(\frac{1}{\overline{g}(x)} - 1), \qquad (5)$$

which is the generator of a pure death process.

Modeling births

$$
\begin{aligned}
A_{cb}f(\eta) &= f(\eta)\sum_{(x,u)\in\eta} r(x)\Big[\frac{2}{\lambda}\int_u^\lambda (g(x,v)-1)dv + G_1^\lambda(u)\frac{\partial_u g(x,u)}{g(x,u)}\Big] \\
&= f(\eta)\sum_{(x,u)\in\eta}\Big[\frac{2r(x)(\lambda-u)}{\lambda}\frac{1}{\lambda-u}\int_u^\lambda (g(x,v)-1)dv \\
&\qquad + r(x)G_1^\lambda(u)\frac{\partial_u g(x,u)}{g(x,u)}\Big]
\end{aligned}
$$

For each $x \in \overline{\eta}$, write $\overline{\eta}_x$ for $\overline{\eta}\backslash x$. Then

$$
\begin{aligned}
\alpha A_{cb}f(\eta) = \sum_{x\in\overline{\eta}} r(x)f(\overline{\eta}_x)\Big[&\frac{1}{\lambda}\int_0^\lambda g(x,u)\frac{2}{\lambda}\int_u^\lambda (g(x,v)-1)dvdu \\
&+\frac{1}{\lambda}\int_0^\lambda G_1^\lambda(u)\partial_u g(x,u)du\Big]
\end{aligned}
$$

Calculations

$$\frac{2}{\lambda^2}\int_0^\lambda g(x,u)\int_u^\lambda g(x,v)dvdu = \left(\frac{1}{\lambda}\int_0^\lambda g(x,u)du\right)^2.$$

$$\frac{1}{\lambda}\int_0^\lambda \left(G_1^\lambda(u)\partial_u g(x,u) - \frac{2(\lambda-u)}{\lambda}g(x,u)\right)du. \tag{6}$$

Take

$$G_1^\lambda(u) = \lambda^{-1}(\lambda-u)^2 - (\lambda-u) = \lambda^{-1}u^2 - u$$

Then integrating by parts, (6) reduces to $-\frac{1}{\lambda}\int_0^\lambda g(x,u)du$ and

$$\alpha A_{cb} f(\overline{\eta}) = \alpha f(\overline{\eta}) \sum_{x\in\overline{\eta}} r(x)(\overline{g}(x) - 1).$$

A branching process

Kurtz and Rodrigues (2011)

$$\begin{aligned} Af(\eta) &= f(\eta) \sum_{(x,u)\in\eta} r(x) \Big[\frac{2}{\lambda}\int_u^\lambda (g(x,v)-1)dv + G_1^\lambda(u)\frac{\partial_u g(x,u)}{g(x,u)}\Big] \\ &\quad + f(\eta)\sum_{(x,u)} f(\eta) d_0(x) u \frac{\partial_u g(x,u)}{g(x,u)} \\ &= f(\eta)\sum_{(x,u)\in\eta} \Big[\frac{2r(x)}{\lambda}\int_u^\lambda (g(x,v)-1)dv \\ &\qquad + (r(x)G_1^\lambda(u) + d_0(x)u)\frac{\partial_u g(x,u)}{g(x,u)}\Big] \end{aligned}$$

and

$$\alpha A f(\overline{\eta}) = \alpha f(\overline{\eta}) \sum_{x\in\overline{\eta}} (r(x)\left[\overline{g}(x) - 1\right] + d_0(x)(\frac{1}{\overline{g}(x)} - 1))$$

Discrete birth events

The event is determined by

- The number of new particles k.
- The choice of parent with relative chance $r(x)$.
- The placement of the offspring determined by a transition function $q(x, dy)$ from E to E^k.

Mechanism for lookdown construction

The race to become parent

k points are chosen independently and uniformly on $[0, \lambda]$. These will be the levels of the offspring of the event. v^* denotes the lowest of the chosen levels.

For $(x, u) \in \eta$ with $u > v^*$ and $r(x) > 0$, let τ_x be defined by

$$e^{-r(x)\tau_x} = \frac{\lambda - u}{\lambda - v^*}.$$

$\frac{\lambda-u}{\lambda-v^*}$ is uniform $[0, 1]$, so τ_x is exponential with parameter $r(x)$.

For $(x, u) \in \eta$ satisfying $u < v^*$ and $r(x) > 0$, let τ_x be defined by

$$e^{-r(x)\tau_x} = \frac{u}{v^*}$$

Again, τ_x is exponentially distributed with parameter $r(x)$.

Probability of being the parent

The τ_x are independent. Let (x^*, u^*) be the point in η with $\tau_{x^*} = \min_{(x,u)\in\eta} \tau_x$. Then

$$P\{x^* = x'\} = \frac{r(x')}{\int r(x)\overline{\eta}(dx)}, \quad x' \in \overline{\eta}.$$

The new configuration

Assign types $(y_1, \ldots, y_k)$ with joint distribution $q(x^*, dy)$ uniformly at random to the k new levels and transforming the old levels so that

$$\begin{aligned}\gamma_{k,r,q}\eta = \{(x, \lambda - (\lambda - u)e^{r(x)\tau_{x^*}}) : (x,u) \in \eta, \tau_x > \tau_{x^*}, u > v^*\} \\ \cup\{(x, ue^{r(x)\tau_{x^*}}) : (x,u) \in \eta, \tau_x > \tau_x^*, u < v^*\} \\ \cup\{(y_i, v_i), i = 1, \ldots, k\}.\end{aligned}$$

Notice that the parent has been removed from the population and that if $r(x) = 0$, the point (x, u) is unchanged.

Uniformity of levels

For $(x,u) \in \eta$, $(x,u) \neq (x^*,u^*)$, let $h_r^\lambda(x,u,\eta,v^*)$ denote the new level, that is,

$$\begin{aligned} h_r^\lambda(x,u,\eta,v^*) &= \mathbf{1}_{\{u>v^*\}}(\lambda - (\lambda-u)e^{r(x)\tau_{x^*}}) + \mathbf{1}_{\{u<v^*\}} u e^{r(x)\tau_{x^*}} \\ &= \mathbf{1}_{\{u>v^*\}}(u e^{r(x)\tau_{x^*}} - \lambda(e^{r(x)\tau_{x^*}} - 1)) + \mathbf{1}_{\{u<v^*\}} u e^{r(x)\tau_{x^*}}, \end{aligned}$$

and

$$f(\gamma_{k,r,q}\eta) = \prod_{(x,u)\in\eta, u\neq u^*} g(x, h_r^\lambda(x,u,\eta,v^*)) \prod g(y_i,v_i).$$

Lemma 5 *Conditional on* $\{(y_i,v_i)\}$ *and* $\overline{\eta}$, $\{h_r^\lambda(x,u,\eta,v^*) : (x,u)\in\eta, u\neq u^*\}$ *are independent and uniformly distributed on* $[0,\lambda]$.

Limit as λ goes to ∞

Suppose $\lambda \to \infty$, $\lambda^{-1}\overline{\eta} \to \Xi$, and $\lambda^{-1}k \to \zeta$. Then, in the limit:

The new levels in a birth event form a Poisson process with intensity ζ.

v^* will be exponentially distributed with parameter ζ.

$u^* > v^*$ and $\tau_{x^*}^{\lambda} \to 0$.

For $u > u^*$, $h_r^{\lambda}(x, u, \eta, v^*) \to u - (u^* - v^*)\frac{r(x)}{r(x^*)}$.

Event based models

cf. Berestycki, Etheridge, and Hutzenthaler (2009) Etheridge (2000); Barton, Etheridge, and Véber (2010); Véber and Wakolbinger (2015)

A discrete event birth generator will be of the form

$$A_{db}f(\eta) = \int_{\mathbb{U}} (H_z(g,\eta) - f(\eta))\mu(dz),$$

where

$$\begin{aligned} H_z(g,\eta) &= \lambda^{-k(z)} \int_{[0,\lambda]^{k(z)}} \prod_{(x,u)\in\eta, u\neq u^*(\eta,v^*)} g(x, h^{\lambda}_{r(\cdot,z)}(x,u,\eta,v^*)) \\ &\quad \times \prod_{i=1}^{k(z)} \int_E g(y_i,v_i) q(x^*(\eta,v^*),z,dy_i) dv_1 \ldots dv_{k(z)}. \end{aligned}$$

μ may be σ-finite and has the interpretation that there exists a Poisson random measure ξ with mean measure $\mu \times \ell$ on $\mathbb{U} \times [0,\infty)$, and if $(z,t) \in \xi$, then at time t,

$$E[f(\eta_t)|\eta_{t-}] = H_z(g,\eta_{t-}).$$

Birth event followed by thinning

$$A_{db,th}f(\eta) = \int_{\mathbb{U}} (H_z(g,\eta) - f(\eta))\mu(dz),$$

where

$$H_z(g,\eta) = \lambda^{-k(z)} \int_{[0,\lambda]^{k(z)}} \prod_{(x,u)\in\eta, u\neq u^*(\eta,v^*)} g(x, \rho(x,z)h^{\lambda}_{r(\cdot,z)}(x,u,\eta,v^*))$$
$$\times \int \prod_{i=1}^{k(z)} \int_E g(y_i, \rho(y_i,z)v_i)q(x^*(\eta,v^*), z, dy_i)dv_1 \ldots dv_{k(z)}$$

Note that (x^*, u^*) is a function of η and v^*, and if and event z occurs at time t, then

$$\eta_t = \sum_{(x,u)\in\eta_{t-}, u\neq u^*} \mathbf{1}_{\{\rho(x,z)h^{\lambda}_{r(\cdot,z)}(x,u,\eta_{t-},v^*)<\lambda\}} \delta_{(x,\rho(x,z)h^{\lambda}_{r(\cdot,z)}(x,u,\eta_{t-},v^*))}$$
$$+ \sum_{i=1}^{k(z)} \mathbf{1}_{\{\rho(y_i,z)v_i<\lambda\}} \delta_{(y_i,\rho(y_i,z)v_i)}$$

Projected model

$$\alpha A_{db,th} f(\overline{\eta}) = \int_{\mathbb{U}} \sum_{x^* \in \overline{\eta}} \frac{r(x^*, z)}{\int r(x,z)\overline{\eta}(dx)} (\overline{H}_z(g, \overline{\eta}, x^*) - \alpha f(\overline{\eta}))\mu(dz)$$

where, setting $p(x,z) = \frac{\rho(x,z)-1}{\rho(x,z)}$ and $\overline{\eta}_{x^*} = \overline{\eta} - \delta_{x^*}$,

$$\begin{aligned}\overline{H}_z(g, \eta, x^*) &= \lambda^{-k(z)} \int_{[0,\lambda]^{k(z)}} \prod_{x \in \overline{\eta}_{x^*}} ((1 - p(x,z))\overline{g}(x) + p(x,z)) \\ &\quad \times \prod_{i=1}^{k(z)} \int_E ((1 - p(y_i, z))\overline{g}(y_i) + p(y_i, z)) q(x^*, z, dy_i).\end{aligned}$$

High density limit

$\mu^\lambda(dz)$ governs the appearance of events of the form

$$(k(z), r(x,z), q(x,z,dy), \rho(x,z))$$

Assume

$$\int_{\mathbb{U}} h(\frac{k(z)}{\lambda})g(z)\mu(dz) \to \int_{\mathbb{U}}\int_0^\infty h(\zeta)\mu_\zeta(d\zeta,z)g(z)\mu(dz).$$

$$H_z(g,\eta) = \lambda^{-k(z)} \int_{[0,\lambda]^{k(z)}} \prod_{(x,u)\in\eta, u\neq u^*(\eta,v^*)} g(x, \rho(x,z) h^{\lambda}_{r(\cdot,z)}(x,u,\eta,v^*))$$

$$\times \int \prod_{i=1}^{k(z)} \int_E g(y_i, \rho(y_i,z)v_i) q(x^*, z, dy_i) dv_1 \ldots dv_{k(z)}$$

$$\to \int_0^\infty \int_0^\infty \Big[\zeta e^{-\zeta v^*} \prod_{(x,u)\in\eta, u\neq u^*(\eta,v^*)} g(x, \rho(x,z)(u - \mathbf{1}_{\{u>u^*\}}(u^*-v^*)\frac{r(x)}{r(x^*)}))$$

$$\times \int_E g(y, \rho(y,z)v^*) q(x^*, z, dy)$$

$$\times \exp\{-\zeta \int_E \int_{v^*}^\infty (1 - g(y,\rho(y,z)v) q(x^*, z, dy) dv)\} \Big] dv^* \mu_\zeta(d\zeta, z)$$

Projected generator

Therefore, $\alpha f(\Xi) = e^{-\int_E h(x)\Xi(dx)}$ and setting

$$p(x^*, \Xi) = \frac{r(x^*, z)}{\int_E r(x, z)\Xi(dx)}$$

$$\mathcal{H}_z(g, \Xi) = \int_0^\infty \int_0^\infty \Big[\exp\{-\int_E \frac{1}{\rho(x, z)} h(x)\Xi(dx)\} \\ \times \int_E p(x^*, \Xi) \exp\{-\zeta \int_E \frac{1}{\rho(y, z)} h(y) q(x^*, z, dy) dv)\} \Xi(dx^*) \Big] \mu_\zeta(d\zeta, z)$$

where $h(x) = \int_0^\infty (1 - g(x, u)) du$,

$$\alpha A^\infty_{bd,th} f(\Xi) = \int_{\mathbb{U}} (\mathcal{H}_z(g, \Xi) - \alpha f(\Xi)) \mu(dz)$$

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Abstract

Population models as partial observations of genealogical models

Classical models of biological populations, for example, Markov branching processes, typically model population size and possibly the distribution of types and/or locations of individuals in the population. The intuition behind these models usually includes ideas about the relationships among the individuals in the population that cannot be directly recovered from the model. This loss of information is even greater if one employs large populations approximations such as the diffusion approximations popular in population genetics. "Lookdown" constructions provide representations of population models in terms of countable systems of particles in which each particle has a "type" which may record both spatial location and genetic type and a "level" which incorporates the lookdown structure which captures the genealogy of the population. The original population model can then be viewed as the result of partial observation of the more com-

plex model. We will exploit ideas from filtering of Markov processes to make the idea of partial observation clear and to justify the lookdown construction.