Exchangeable representations of measure-valued population processes II

Neutral models: Model I

$N(t)$ denotes the population size at time t.

$N_b(t)$ the number of births up to time t.

$N_d(t)$ the number of deaths, so

$$N(t) = N(0) + N_b(t) - N_d(t) \ .$$

For simplicity, assume that N_b and N_d do not have simultaneous jumps.

At a birth event, the parent is selected at random.

At a death event, the individuals that are eliminated from the population are selected at random, that is, if there are k deaths, the $\binom{N(t-)}{k}$ possible subsets of the population immediately prior to the death event are equally likely to be eliminated.

Types/locations

At each time t, each individual in the population has a *type* or *location* in a space E; at a birth event, the *offspring* are given the same type as the parent and in between birth and death events, the types evolve as independent, E-valued Markov processes corresponding to a specified generator B.

Therefore, the population at time t can be described by a vector

$$(Y_1(t), \ldots, Y_{N(t)}) \in E^{N(t)}$$

in which we order the population by decreasing age or, since age and hence the above order do not play a role in the birth and death events, by the empirical measure

$$Z^I(t) = \sum_{i=1}^{N(t)} \delta_{Y_i(t)} \ .$$

Neutral models: Model II (ordered model)

The population size is defined as in Model I, and in between birth and death events, the types or locations of the individuals evolve as independent Markov processes with generator B.

At a death event, the individuals removed are the individuals with the highest indices in $(X_1(t), \ldots, X_{N(t-)}(t))$.

At a birth event occuring at time t in which there are k offspring, $k+1$ indices, $i_1 < \cdots < i_{k+1}$, are selected at random from $\{1, \ldots N(t)\}$.

Since $N(t) - N(t-) = k$, $i_1 \leq N(t-)$ and i_1 will be the index of some individual in the population immediately before the birth event. That individual will be the parent. After the birth event, the parent and the k offspring will be indexed by $i_1, \ldots, i_{k+1}$. The remaining $N(t) - (k+1)$ indiviuals are reindexed by $\{1, \ldots, N(t)\} - \{i_1, \ldots, i_{k+1}\}$ maintaining their previous order.

Equivalence of the models

Theorem 1 *[2] Suppose that the initial population vectors* $(Y_1(0), \ldots, Y_{N(0)}(0))$ *in Model I and* $(X_1(0), \ldots, X_{N(0)}(0))$ *in Model II have the same exchangeable distribution and define*

$$Z^{II}(t) = \sum_{i=1}^{N(t)} \delta_{X_i(t)} , \quad Z^{I}(t) = \sum_{i=1}^{N(t)} \delta_{Y_i(t)}$$

Then Z^{II} *has the same distribution as* Z^I *and for each* $t > 0$*,* $(X_1(t), \ldots, X_{N(t)}(t))$ *is exchangeable.*

Infinite population limit

Let $P^n(t) = \frac{N^n(t)}{n} = P^n(0) + \frac{N_b^n(t)}{n} - \frac{N_d^n(t)}{n}$, and assume P^n converges.

Let $N_{12}^n(t)$ denote the number of birth events up to time t that involve the levels 1 and 2. Then (X_1^n, X_2^n) converges in distribution provided the counting process N_{12}^n converges in distribution.

If there is a birth event at time t with k offspring, then, conditioning on N^n and N_b^n for all time (not just up to time t), the probability that levels 1 and 2 are involved is just

$$\frac{\binom{N^n(t)-2}{k-1}}{\binom{N^n(t)}{k+1}} = \frac{k(k+1)}{N^n(t)(N^n(t)-1)} .$$

Martingale properties

Set $U^n(t) = \frac{[N_b^n]_t + N_b^n(t)}{n^2}$, and let $\{t_m\}$ be the jump times of N_b^n and $k_m = N_b^n(t_m) - N_b^n(t_m-)$. Then

$$\begin{aligned} & N_{12}^n(t) - \sum_{\{m: t_m \le t, k_m > 0\}} \frac{k_m(k_m+1)}{N^n(t_m)(N^n(t_m)-1)} \\ & \quad = N_{12}^n(t) - \int_0^t \frac{1}{P^n(s)(P^n(s)-\frac{1}{n})} dU^n(s) \end{aligned} \tag{1}$$

is a martingale.

Basic assumption: $(P^n, U^n) \Rightarrow (P, U)$. If $P > 0$, then

$$\int_0^t \frac{1}{P^n(s)(P^n(s) - \frac{1}{n})} dU^n(s) \Rightarrow H(t) = \int_0^t \frac{1}{P(s)^2} dU(s)$$

and N_{12} converges to the unique counting process with

$$N_{12}(t) - H(t)$$

a martingale. (Note that the discontinuities of H are bounded by 1.)

Convergence of lookdown processes

In general, fix a level l, and let $K \subset \{1, \ldots, l\}$. $|K|$ will denote the cardinality of the set. Let $\eta_m \subset \{1, \ldots, N^n(t_m)\}$ be the subset of indices selected at the birth time t_m, and define

$$N_K^n(t) = |\{m : t_m \le t, \eta_m \cap \{1, \ldots, l\} = K\}| \,.$$

Then

$$N_K^n(t) - \sum_{\{m: t_m \le t, k_m + 1 \ge |K|\}} \frac{\binom{N^n(t_m) - l}{k_m + 1 - |K|}}{\binom{N^n(t_m)}{k_m + 1}} \tag{2}$$

is a martingale. Let $H_K^n(t)$ denote the sum in (2), and let U_c denote the continuous part of U.

Convergence of lookdown processes

If $|K| = 2$, it follows that $H_K^n(t)$ converges to

$$\int_0^t \frac{1}{P(s)^2} dU_c(s) + \sum_{s \leq t} \frac{\Delta U(s)}{P(s)^2} \left(1 - \frac{\sqrt{\Delta U(s)}}{P(s)}\right)^{l-2},$$

where $\Delta U(s) = U(s) - U(s-)$.

If $|K| > 2$, then the sum converges in distribution to

$$\sum_{s \leq t} \left(\frac{\sqrt{\Delta U(s)}}{P(s)}\right)^{|K|} \left(1 - \frac{\sqrt{\Delta U(s)}}{P(s)}\right)^{l-|K|}.$$

In particular, if U is continuous and $|K| > 2$, then $N_K^n \Rightarrow 0$, that is, in the limit, only two levels are involved in any birth event.

Birth and death processes

Consider birth and death processes satisfying

$$
\begin{aligned}
N_b^n(t) &= V_1(n^2 \int_0^t \lambda_n(P^n(s))ds) \\
N_d^n(t) &= V_2(n^2 \int_0^t \mu_n(P^n(s))ds) \\
P^n(t) &= \frac{N^n(t)}{n} = P^n(0) + \frac{1}{n} N_b^n(t) - \frac{1}{n} N_d^n(t) \; .
\end{aligned}
$$

If $P^n(0) \Rightarrow P(0)$, $\lambda_n(\cdot) \to \lambda(\cdot)$, and $n(\lambda_n(\cdot) - \mu_n(\cdot)) \to b(\cdot)$ uniformly on compact sets, then P^n converges to a solution of

$$
P(t) = P(0) + W_1(\int_0^t \lambda(P(s))ds) - W_2(\int_0^t \lambda(P(s))ds) + \int_0^t b(P(s))ds \; . \tag{3}
$$

If $\lambda_n(p) = \lambda_n p$ and $\mu_n(p) = \mu_n p$, then P is a continuous state branching process.

Limiting lookdown rate

$$U_n = \frac{2N_b^n(\cdot)}{n^2} \Rightarrow \int_0^{\cdot} 2\lambda(P(s))ds \ ,$$

provided the solution of (3) does not blow-up in finite time. In this case, P is a diffusion with generator

$$Gf(z) = \lambda(z)f''(z) + b(z)f'(z)$$

(see [4], Theorem 6.5.4) and

$$H^n_{\{i,j\}}(t) = \int_0^t \frac{2}{N^n(s)(N^n(s)-1)} dN_b^n(s) \Rightarrow \int_0^t \frac{2\lambda(P(s))}{P(s)^2} ds$$

Conditioning the branching model

Etheridge and March (1991) [3]:

Theorem 2 *The neutral Dawson-Watanabe process conditioned to have total mass identically 1 for all $t \geq 0$ is a Fleming-Viot process.*

Let N_{ij}, $i < j$, be the counting process that counts lookdowns from j to i. Then

$$N_{ij}(t) = Y_{ij}\left(\int_0^t \frac{2\lambda(P(s))}{P(s)^2} ds\right).$$

Conditioning on $P \equiv 1$ is the same as replacing N_{ij} by

$$N_{ij}(t) = Y_{ij}(2\lambda(1)t).$$

Type distribution at the extinction time

Let $\tau = \inf\{t : P(t) = 0\}$. If P is a continuous state branching process, then

$$\int_0^\tau \frac{1}{P(s)} ds = \infty$$

Tribe (1992) [8]

$$\lim_{t \to \tau-} Z(t) = \delta_{\xi_0}, \qquad \xi_0 = X_1(\tau)$$

Theorem 3 *Let τ be an $\{\mathcal{F}_t^P\}$-stopping time. Suppose*

$$\int_0^\tau \frac{\lambda(P(s))}{P(s)^2} ds = \infty$$

on $\{\tau < \infty\}$. Then on $\{\tau < \infty\}$,

$$\lim_{t \to \tau-} Z(t) = \delta_{X_1(\tau-)} .$$

Conditioning on nonextincition

Assuming $Gf(v) = avf''(v) - bvf'(v)$ $(b \geq 0)$, conditioning P on nonextinction (cf. Evans and Perkins (1990) [6]) is equivalent to replacing P with a process $\hat{P}$ with generator

$$\hat{G}f(v) = avf''(v) + (2a - bv)f'(v). \tag{4}$$

If $\hat{P}(0) > 0$, then $\hat{P}$ never hits zero, but

$$\int_0^\infty \frac{c}{\hat{P}(s)} ds = \infty.$$

It follows that eventually all particles trace their ancestory back to the bottom-level particle. In particular, the bottom-level particle in our construction is the "immortal particle" of Evans (1993) [5].

Discrete generation models

Fixed population size n

L_i^k number of offspring for the ith individual in the kth generation

$\{(L_1^k, \ldots, L_n^k), k \geq 1\}$ independent and identically distributed

For fixed k, $\{L_i^k\}$ is exchangeable and $\sum_{i=1}^n L_i^k = n$.

n generations per unit time

Select $\{D_i^k\}$ randomly uniformly over all partitions of $\{1, \ldots, n\}$ such that $|D_i^k| = L_i^k$. Let $\xi_i^k = \min D_i^k$ ($\xi_i^k = \infty$) if $L_i^k = 0$) and let $\xi_{(1)}^k < \xi_{(2)}^k < \cdots$ be the corresponding order statistics. Let $X_i(k)$ be the parent for all $l \in D_j^k$ if $\xi_j^k = \xi_{(i)}^k$.

Lookdown rate

How often do the particles at levels $\alpha < \beta$ have the same parent?

$$P\{\alpha,\beta\in D_i^k,\ \text{some } i\} = E[\sum_{i=1}^{n}\frac{L_i^k}{n}\frac{(L_i^k-1)}{n-1}] = \frac{1}{n-1}E[L_1^k(L_1^k-1)]$$

$$P\{\alpha,\beta,\gamma\in D_i^k,\ \text{some } i\} = \frac{E[L_1^k(L_1^k-1)(L_1^k-2)]}{(n-1)(n-2)}$$

$$\begin{aligned} P\{\alpha,\beta\in D_i^k,\gamma,\delta\in D_j^k \text{ some } i\neq j\} &= E[\sum_{i\neq j}\frac{L_i^k}{n}\frac{(L_i^k-1)}{n-1}\frac{L_j^k}{n-2}\frac{(L_j^k-1)}{n-3}] \\ &= \frac{E[L_1^k(L_1^k-1)L_2^k(L_2^k-1)]}{(n-2)(n-3)} \end{aligned}$$

Infinite population limit

The distribution of L_1^k may depend on n. If $\{(L_1^{k,n})^2\}$ is uniformly integrable and $\lim_{n\to\infty} E[L_1^{k,n}(L_1^{k,n}-1)] = \lambda$, then assuming n generations per unit time, the process converges to the Fleming-Viot process with lookdown rate λ

$$Af(x) = \sum_{i=1}^m B_i f(x) + \lambda \sum_{1\le i<j\le m} (f(\theta_{ij}(x)) - f(x))$$

$$\mathbb{A}F(\mu) \equiv \sum_{i=1}^m \langle B_i f, \mu^m\rangle + \lambda \sum_{1\le i<j\le m} (\langle \Phi_{ij} f, \mu^{m-1}\rangle - \langle f, \mu^m\rangle)$$

Martingale problem

E state space (a complete, separable metric space)

A generator (a linear operator with domain and range in $B(E)$

$\mu \in \mathcal{P}(E)$

X is a solution of the martingale problem for (A, μ) if and only if $\mu = PX(0)^{-1}$ and there exists a filtration $\{\mathcal{F}_t\}$ such that

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

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

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

Examples of generators

Standard Brownian motion ($E = \mathbb{R}^d$)

$$Af = \frac{1}{2}\Delta f, \quad \mathcal{D}(A) = C_c^2(\mathbb{R}^d)$$

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 ($E = \mathbb{R}^d$)

$$Af(x) = \frac{1}{2}\sum_{i,j} a_{ij}(x)\frac{\partial^2}{\partial x_i \partial x_j} f(x) + \sum_i b_i(x)\frac{\partial}{\partial x_i} f(x), \quad \mathcal{D}(A) = C_c^2(\mathbb{R}^d)$$

Uniqueness and the Markov property

Theorem 4 *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 5 *If the conclusion of the above theorem holds, then any solution of the martingale problem for A is a Markov process.*

If uniqueness holds, then A is called a *generator* for the Markov process.

Markov mappings[7]

Theorem 6 *$A \subset \bar{C}(E) \times \bar{C}(E)$ a pre-generator with bp-separable graph.*

$\mathcal{D}(A)$ closed under multiplication and separating.

$\gamma : E \to E_0$, Borel measurable.

α a transition function from E_0 into E satisfying $\alpha(y, \gamma^{-1}(y)) = 1$.

Define $C = \{(\int_E f(z)\alpha(\cdot, dz), \int_E Af(z)\alpha(\cdot, dz)) : f \in \mathcal{D}(A)\}$.

Let $\mu_0 \in \mathcal{P}(E_0)$, $\nu_0 = \int \alpha(y, \cdot)\mu_0(dy)$.

If $\tilde{Y}$ is a solution of the MGP for (C, μ_0), then there exists a solution Z of the MGP for (A, ν_0) such that $Y = \gamma \circ Z$ and $\tilde{Y}$ have the same distribution on $M_{E_0}[0, \infty)$.

$E[f(Z(t))|\mathcal{F}_t^Y] = \int f(z)\alpha(Y(t), dz)$ (at least for almost every t).

Moran models[1]

E "type space" (complete, separable metric space). A "population" of n individuals is represented by a point in E^n.

B generator for "mutation process"

$B^n f(x) = \sum_{i=1}^n B_i f(x)$ generator for Markov process in E^n given by n independent copies of the process corresponding to B. (B_i is the same as B operating on f as a function of x_i.)

Moran model with selection: Markov process in E^n

$$A_0^n f(x) = \sum_{i=1}^n B_i f(x) + \frac{1}{2(n-2)} \sum_{1 \le i \ne j \ne k \le n} (1 + \frac{2}{n}\sigma(x_i, x_j))(f(\hat{\theta}_{ik}(x)) - f(x))$$

$\hat{\theta}_{ik}(x)$ replaces the kth component of x by a copy of the ith

Frequency model

If $(X_1^0, \ldots, X_n^0)$ is a solution of the MGP for A_0^n, then for any permutation σ, $(X_{\sigma_1}^0, \ldots X_{\sigma_n}^0)$ is a solution of the MGP for A_0^n.

$$Z_0 = \frac{1}{n}\sum_{i=1}^n \delta_{X_i^0} = \gamma(X_1^0, \ldots, X_n^0) \in \mathcal{P}^n(E) = \{\frac{1}{n}\sum_{i=1}^n \delta_{x_i} : x \in E^n\}$$

For $f \in B(E^m)$ and $\mu \in \mathcal{P}^n(E)$

$$\langle f, \mu^{(m)} \rangle = \frac{1}{n \cdots (n-m+1)} \sum_{i_1 \neq \cdots \neq i_m} f(x_{i_1}, \ldots, x_{i_m}).$$

Martingale problem for frequency model

For $f \in B(E^n)$ and

$$F(\mu) = \langle f, \mu^{(n)} \rangle = \alpha f(\mu) \equiv \int f(x)\alpha(\mu, dx),$$

define

$$\mathbb{A}^n F(\mu) = \langle A_0^n f, \mu^{(n)} \rangle = \alpha A_0^n f.$$

Then Z_0 is a solution of the martingale problem for $\mathbb{A}^n$.

$$\langle f, Z_0^{(n)}(t) \rangle - \int_0^t \langle A_0^n f, Z_0^{(n)}(s) \rangle ds$$

is a $\{\mathcal{F}_t^{Z_0}\}$-martingale.

Ordered model

$$
\begin{aligned}
A^n f(x) &= \sum_{i=1}^{n} B_i f(x) + \sum_{1\le i<j\le n} (f(\theta_{ij}(x)) - f(x)) \\
&\quad + \frac{1}{n(n-2)} \sum_{1\le i\neq j\le n-1} \sum_{k=1}^{n} \sigma(x_i, x_j))(f(\hat{\theta}_{ik}(x)) - f(x))
\end{aligned}
$$

Compare with the unordered model

For $\mu \in \mathcal{P}^n(E)$, $f \in B(E^n)$, and $F(\mu) = \langle f, \mu^{(n)}\rangle$,

$$
\mathbb{A}^n F(\mu) = \langle A_0^n f, \mu^{(n)}\rangle = \langle A^n f, \mu^{(n)}\rangle = \alpha A_0^n f = \alpha A^n f
$$

Infinite population limit

Suppose $m < n$ and f depends only on $x_1, \ldots, x_m$.

$$
\begin{aligned}
A^n f(x) &= \sum_{i=1}^{m} B_i f(x) + \sum_{1\le i<j\le m} (f(\theta_{ij}(x)) - f(x)) \\
&\quad + \frac{1}{n(n-2)} \sum_{1\le i\ne j\le n-1} \sum_{k=1}^{m} \sigma(x_i, x_j))(f(\theta_{ik}(x)) - f(x))
\end{aligned}
$$

For $x \in E^\infty$ satisfying $\frac{1}{n}\sum_{i=1}^n \delta_{x_i} \to \mu \in \mathcal{P}(E)$,

$$
\begin{aligned}
A^n f(x) \to Af(x,\mu) &= \sum_{i=1}^{m} B_i f(x) + \sum_{1\le i<j\le m} (f(\theta_{ij}(x)) - f(x)) \\
&\quad + \int_{E\times E} \sum_{k=1}^{m} \sigma(y, z))(f(\theta_k(x|y)) - f(x))\mu(dy)\mu(dz)
\end{aligned}
$$

Measure-valued limit

$$\mathbb{A}^n F(\mu) \to \mathbb{A}F(\mu)$$

$$\equiv \sum_{i=1}^{m} \langle B_i f, \mu^m \rangle + \sum_{1 \le i < j \le m} (\langle \Phi_{ij} f, \mu^{m-1} \rangle - \langle f, \mu^m \rangle)$$

$$+ \sum_{1 \le k \le m} (\langle \sigma_k f, \mu^{m+1} \rangle - \langle \sigma f, \mu^{m+2} \rangle)$$

For $f \in B(E^m)$, $\Phi_{ij} f \in B(E^{m-1})$ is the function obtained by setting the ith and jth variables equal.

$\sigma_k f \in B(E^{m+1})$

$$\sigma(x_k, x_{m+1}) f(x_1, \ldots, x_m)$$

$\sigma f \in B(E^{m+2})$

$$\sigma(x_{m+1}, x_{m+2}) f(x_1, \ldots, x_m)$$

Fleming-Viot process

$X^n = (X_1^n, \ldots, X_n^n)$ solution of the MGP for A^n

$Z^n = \frac{1}{n}\sum_{i=1}^n \delta_{X_i}$ solution of the MGP for $\mathbb{A}^n$

$Z^n \Rightarrow Z$ solution of MGP for $\mathbb{A}$

$$F(Z(t)) - \int_0^t \mathbb{A}F(Z(s))ds$$

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

$X^n \Rightarrow X = (X_1, X_2, \ldots)$

$f(X_1(t), \ldots, X_m(t)) - \int_0^t Af(X_1(s), \ldots, X_m(s), Z(s))ds$

is a $\{\mathcal{F}_t^{X,Z}\}$-martingale.

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Abstract

Lookdown constructions for more general measure-valued processes will be given including neutral Dawson-Watanabe processes and processes with heavy-tailed offspring distributions. Examples of results on the measure-valued processes that can be derived easily from the lookdown constructions will be described.