Filtering and models in population biology

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- Abstract

with Peter Donnelly, Eliane Rodrigues, Giovanna Nappo, Sabrina Guettes

Stochastic equations in random environments

Consider stochastic equations of the form

$$X(t) = X(0) + \int_0^t \sigma(X(s), Z(s))dW(s) + \int_0^t b(X(s), Z(s))ds, \qquad (1)$$

where W is a standard Brownian motion independent of $X(0)$ and Z, or

$$X(t) = X(0) + \sum_k Y_k(\int_0^t \lambda_k(X(s), Z(s))ds)\zeta_k, \qquad (2)$$

where $\zeta_k \in \mathbb{Z}^d$ and the Y_k are independent unit Poisson processes that are independent of $X(0)$ and Z.

Thinking of Z as determining the "environment" in which X evolves, in (1), X is a *diffusion process in a random environment*, and in (2), X is a *Markov chain in a random environment*.

Martingale problems with random environments

If f is C^2 with compact support, $a(x,z)=\sigma(x,z)\sigma(x,z)^T$, and

$$Af(x,z)=\frac{1}{2}\sum_{i,j}a_{ij}(x,z)\partial_{x_i}\partial_{x_j}f(x)+\sum_i b_i(x,z)\partial_{x_i}f(x), \qquad (3)$$

then for (1), by Itô's formula

$$f(X(t))-f(X(0))-\int_0^t Af(X(s),Z(s))ds=\int_0^t \nabla f(X(s))^T\sigma(X(s),Z(s))dW(s)$$

is a martingale. or more precisely, for g bounded and appropriately measurable,

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

is a martingale with respect to the filtration $\mathcal{F}_t=\mathcal{F}_t^X\vee\sigma(Z)$.

Martingale problem for Markov chain in a random environment

Similarly, setting

$$Af(x,z)=\sum_k \lambda_k(x,z)(f(x+\zeta_k)-f(x)), \qquad (4)$$

if X satisfies (2), then

$$g(Z)f(X(t))-g(Z)f(X(0))-\int_0^t g(Z)Af(X(s),Z(s))ds$$
$$=\sum_k \int_0^t g(Z)(f(X(s-)+\zeta_k)-f(X(s-)))$$
$$d\widetilde{Y}_k(\int_0^s \lambda_k(X(r-),Z(r-))dr),$$

where $\widetilde{Y}_k(u)=Y_k(u)-u$, is a martingale.

Martingale problem in a random environment

Let E and S be complete, separable metric spaces,

$$A \subset \overline{C}(E) \times B([0,\infty) \times E \times S),$$

and $\mu_0 \in \mathcal{P}(E \times S)$. Then a progressive E-valued process X and an S-valued random variable Z give a solution of the martingale problem for (A, μ_0) if $(X(0), Z)$ has distribution μ_0 and there exists a filtration $\{\mathcal{F}_t\}$ such that for each $f \in \mathcal{D}(A)$ and $g \in B(S)$

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

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

Equivalence

Theorem 1 *If A is of the form (3) (resp. (4)), then any solution of the martingale problem that does not explode in finite time can be obtained as a solution of the corresponding stochastic equation.*

Proof. The diffusion case follows essentially by the same arguments as in the nonrandom environment setting. See Stroock and Varadhan (1972). Most examples of the jump case will follow by a result of Meyer (1971). In some cases, it may be helpful to apply results in Kurtz (2011). □

A martingale lemma

Let $\{\mathcal{F}_t\}$ and $\{\mathcal{G}_t\}$ be filtrations with $\mathcal{G}_t \subset \mathcal{F}_t$.

Lemma 2 *Suppose U and V are $\{\mathcal{F}_t\}$-adapted and*

$$U(t) - \int_0^t V(s)ds$$

is an $\{\mathcal{F}_t\}$-martingale. Then

$$E[U(t)|\mathcal{G}_t] - \int_0^t E[V(s)|\mathcal{G}_s]ds$$

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

Proof. The lemma follows by the definition and properties of conditional expectations. □

Filtered martingale problems

Let (X,Z) be a solution of the martingale problem for (A,μ_0) with respect to a filtration $\{\mathcal{F}_t\}$, and let $\{\mathcal{G}_t\}$ be a filtration with $\mathcal{G}_t \subset \mathcal{F}_t$. Let π_t be the conditional distribution of $(X(t),Z)$ given $\mathcal{G}_t$. Then for $f \in \mathcal{D}(A)$ and $g \in B(S)$,

$$\pi_t(gf) - \pi_0(gf) - \int_0^t \pi_s(gAf)ds$$

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

Converse

Theorem 3 *Suppose that* $\{\tilde{\pi}_t, t \geq 0\}$ *is a progressive,* $\mathcal{P}(E \times S)$*-valued process adapted to a filtration* $\{\tilde{\mathcal{G}}_t\}$ *such that for each* $f \in \mathcal{D}(A)$ *and* $g \in B(S)$,

$$\tilde{\pi}_t(gf) - \tilde{\pi}_0(gf) - \int_0^t \tilde{\pi}_s(gAf)ds$$

is a $\{\tilde{\mathcal{G}}_t\}$*-martingale. Then for* $\mu_0 = E[\tilde{\pi}_0]$*, there exists a solution* (X, Z) *of the martingale problem for* (A, μ_0) *and a filtration* $\{\mathcal{G}_t\}$ *such that the* $\mathcal{P}(E \times S)$*-valued process given by the conditional distributions* π_t *of* $(X(t), Z)$ *given* $\mathcal{G}_t$ *has the same finite dimensional distributions as* $\{\tilde{\pi}_t, t \geq 0\}$.

Proof. See Kurtz and Nappo (2011). (The result is a direct descendent of Kurtz and Ocone (1988).) □

Branching processes in random environments

Let $E = \cup_n [0,r]^n$.

For $0 \le \varphi \le 1$, $\varphi(r) = 1$, let $f(u,n) = \prod_{i=1}^n \varphi(u_i)$. For $Z = \{(a(t), b(t)), t \ge 0\}$ satisfying $a(t) > 0$ and $-\infty < b(t) \le ra(t)$, define

$$\begin{aligned} A_r f(t, Z, u, n) &= f(u,n) \sum_{i=1}^n 2a(t) \int_{u_i}^r (\varphi(v) - 1) dv \\ &\quad + f(u,n) \sum_{i=1}^n (a(t) u_i^2 - b(t) u_i) \frac{\varphi'(u_i)}{\varphi(u_i)}. \end{aligned}$$

In other words, particle levels satisfy

$$\dot{U}_i(t) = a(t) U_i^2(t) - b(t) U_i(t),$$

and a particle with level z gives birth at rate $2a(t)(r - z)$ to a particle whose initial level is uniformly distributed between z and r.

Let $N(t) = \#\{i : U_i(t) < r\}$ and let $\alpha_r(n, du)$ be the joint distribution of n iid uniform $[0,r]$ random variables.

A calculation

$\widehat{f}(n) = \int f(u,n)\alpha_r(n,du) = e^{-\lambda_\varphi n}$, $e^{-\lambda_\varphi} = \frac{1}{r}\int_0^r \varphi(u)du$

To calculate $C\widehat{f}(t,Z,n) = \int A_r f(t,Z,u,n)\alpha_r(n,du)$, observe that

$$r^{-1}2a(t)\int_0^r \varphi(z)\int_z^r (\varphi(v)-1)dv = a(t)re^{-2\lambda_\varphi} - 2a(t)r^{-1}\int_0^r \varphi(z)(r-z)dz$$

and

$$\begin{aligned} r^{-1}\int_0^r (a(t)z^2 - b(t)z)\varphi'(z)dz &= -r^{-1}\int_0^r (2a(t)z - b(t))(\varphi(z)-1)dz \\ &= -2a(t)r^{-1}\int_0^r z\varphi(z)dz + a(t)r + b(t)(e^{-\lambda_\varphi}-1). \end{aligned}$$

Then

$$\begin{aligned} C\widehat{f}(t,n) &= ne^{-\lambda_\varphi(n-1)}\left(a(t)re^{-2\lambda_\varphi} - 2a(t)re^{-\lambda_\varphi} + a(t)r + b(t)(e^{-\lambda_\varphi}-1)\right) \\ &= a(t)rn(\widehat{f}(n+1) - \widehat{f}(n)) + (a(t)r - b(t))n(\widehat{f}(n-1) - \widehat{f}(n)). \end{aligned}$$

Conclusion

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

$$C\widehat{f}(t,n,Z) = a(t)rn(\widehat{f}(n+1) - \widehat{f}(n)) + (a(t)r - b(t))n(\widehat{f}(n-1) - \widehat{f}(n)),$$

that is, $\widetilde{N}$ is a branching process in a random environment with birth rate $a(t)r$ and death rate $(a(t)r - b(t))$.

Then, taking $\widetilde{\pi}_t(du, dz) \in \mathcal{P}(E \times S)$ to be $\alpha_r(\widetilde{N}(t), du)\delta_Z(dz)$,

$$C\widehat{f}(t, \widetilde{N}(t), Z) = \widetilde{\pi}_t A_r(t, \widetilde{N}(t), Z),$$

and by Theorem 3, there exists a solution $(U_1(t), \ldots, U_{N(t)}(t), N(t), Z)$ of the martingale problem for A_r such that (N, Z) has the same distribution as $(\widetilde{N}, Z)$.

See Kurtz and Rodrigues (2011).

Limit theorem

Since $ra(t) \geq b(t)$ and

$$\dot{U}_i(t) = a(t)U_i^2(t) - b(t)U_i(t),$$

either $U_i(t)$ hits r in finite time or, noting that

$$\frac{d}{dt} e^{\int_0^t b(s)ds} U_i(t) = a(t) e^{\int_0^t b(s)ds} U_i(t)^2 \geq 0,$$

the limit

$$\eta_i = \lim_{t \to \infty} e^{\int_0^t b(s)ds} U_i(t)$$

exists for all i (possibly ∞) and

$$W = \lim_{t \to \infty} e^{-\int_0^t b(s)ds} N(t)$$

exists (possibly zero). If $\int_0^\infty a(t) e^{-\int_0^t b(s)ds} dt = \infty$, then $\eta_i = \infty$ for all i and $W = 0$. If $\int_0^\infty a(t) e^{-\int_0^t b(s)ds} dt < \infty$, then there is positive probability that $\eta_i < \infty$ for some i and $W > 0$. In particular, $\{W > 0\} = \{\inf \eta_i < \infty\}$ a.s.

Fleming-Viot processes

The neutral Fleming-Viot process with mutation operator B on E is the $\mathcal{P}(E)$-valued process with generator $\mathbb{A}$ with domain

$$\mathcal{D}(\mathbb{A}) = \{F(\mu) = \langle f, \mu^m \rangle : f \in \mathcal{D}(\sum_{i=1}^m B_i), m \geq 1\}$$

and

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

where for $f \in B(E^m)$, $\Phi_{ij} f$ is the function in $B(E^{m-1})$ obtained by setting $x_i = x_j$.

Lookdown construction

The lookdown construction for the neutral Fleming-Viot process given in Donnelly and Kurtz (1999) corresponds to the generator given by

$$f(x) = f(x_1, \ldots, x_m) \in \mathcal{D}(\sum_{i=1}^{m} B_i)$$

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

where $y = \theta_{ij}(x)$ is the element of E^∞ satisfying

$$\begin{aligned} y_k &= x_k, \quad k \le j-1 \\ y_j &= x_i \\ y_k &= x_{k-1}, \quad k > j \end{aligned}$$

that is $\theta_{ij}(x) = (x_1, \ldots, x_{j-1}, x_i, x_j, x_{j+1}, \ldots)$.

Application of Theorem 3

Observe that for $F(\mu) = \langle f, \mu^m \rangle$, $\mathbb{A}F(\mu) = \langle Af, \mu^m \rangle$, so if η is a solution of the martingale problem for $\mathbb{A}$ and we define $\tilde{\pi}_t = \prod_{i=1}^{\infty} \eta(t)$,

$$\begin{aligned}
\tilde{\pi}_t Af &= \langle Af, \eta(t)^m \rangle \\
&= \sum_{i=1}^{m} \langle B_i f, \eta(t)^m \rangle + \sum_{1 \leq i < j \leq m} (\langle \Phi_{ij} f, \eta(t)^{m-1} \rangle - \langle f, \eta(t)^m \rangle) \\
&= \mathbb{A}F(\eta(t))
\end{aligned}$$

and

$$\tilde{\pi}_t f - \tilde{\pi}_0 f - \int_0^t \tilde{\pi}_s Af ds$$

is a martingale. By Theorem 3, there is a solution X of the martingale problem for A and a filtration $\{\mathcal{G}_t\}$ such that $\{\pi_t, t \geq 0\}$, the conditional distributions of $X(t)$ given $\mathcal{G}_t$, has the same distribution as $\{\tilde{\pi}_t, t \geq 0\}$.

Sampling at multiple time points

For a fixed time t, by exchangeability, $X_1(t), \ldots, X_m(t)$ give a random sample of size m from π_t and the genealogy of the sample can be recovered from the lookdown construction. If the sampling occurs at multiple time points, then the original lookdown construction does not, at least immediately, give a simple representation of the sample.

For definiteness, assume that one member of the population is sample at the jump times of a Poisson process with parameter λ, and let $Y(t)$ be the type of the individual sampled most recently. Then (η, Y) will be Markov with generator

$$\begin{aligned}\mathbb{A}F(\mu, y) = \sum_{i=1}^{m}\langle B_i f(\cdot, y), \mu^m\rangle + \sum_{1\leq i<j\leq m}(\langle \Phi_{ij} f(\cdot, y), \mu^{m-1}\rangle - \langle f(\cdot, y), \mu^m\rangle) \\ +\lambda(\langle f, \mu^{m+1}\rangle - \langle f(\cdot, y), \mu^m\rangle\end{aligned}$$

A lookdown construction

Let

$$Af(x,y)=\sum_{i=1}^{m}B_i f(x,y)+\sum_{1\le i<j\le m}(f(\theta_{ij}(x),y)-f(x,y))$$
$$+\lambda(f(\kappa x,x_1)-f(x,y)),$$

where

$$\kappa x=(x_2,x_3,\ldots).$$

To verify the construction, again apply Theorem 3 with

$$\widetilde{\pi}_t=\prod_{i=1}^{\infty}\eta(t)\times\delta_{Y(t)}.$$

Again, the genealogy of the sample can be recovered from the lookdown construction.

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Abstract

Filtering and models in population biology

The simplest derivations of lookdown constructions for population models are based on filtering arguments. Some of the background of these methods will be discussed along with extensions to models in random environments and sampling at multiple time points.