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The stationary distributions of Fleming-Viot processes with selection

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1 Introduction of Fleming-Viot processes with selection

Let us denote the operator L of the infinitesimal generator in $C(R^K)$ by the following:

$$L=\frac{1}{2}\sum_{i,j=1}^{K}x_i(\delta_{ij}-x_j)\frac{\partial^2}{\partial x_i\partial x_j}+\sum_{i=1}^{K}b_j(x)\frac{\partial}{\partial x_j}$$

where $b_i(x)=\sum_{j=1}^{K}q_{ij}x_j+x_i(\sum_{j=1}^{K}\sigma_{ij}x_j-\sum_{k,l=1}^{K}\sigma_{kl}x_kx_l))$, $q_{ij}\geq 0$ for $i\neq j$ and $\sum_j q_{ij}=0$ and $\sigma_{ij}=\sigma_{ji}$. This defines the infinitesimal generator of a Markov process on $\Delta_K=\{x=(x_1,\cdots,x_K):x_1\geq 0,\cdots,x_K\geq 0,x_1+\cdots+x_K=1\}$, this process is called the Wright-Fisher diffusion model with selection according to Ethier and Kurtz [4]. Here x_i is a gene frequency of type i, q_{ij} is mutation intensity of $i\rightarrow j$, and σ_{ij} is selection intensity of (i,j)-type. Put $u(x)=exp(\frac{1}{2}\sum_{i,j=1}^{K}\sigma_{ij}x_ix_j)$, and denote by L_0 an operator L in the case of $\sigma=0$ then

$$L_0(f(x)u(x))=\frac{1}{2}\sum_{i,j}x_i(\delta_{ij}-x_j)f_{x_ix_j}u+\sum_{i,j}x_i(\delta_{ij}-x_j)f_{x_i}\sum_{l=1}^{K}\sigma_{il}x_lu$$

$$+\frac{1}{2}\sum_{i,j}x_i(\delta_{ij}-x_j)fu_{x_ix_j}+\sum_{i}[\sum_{j}q_{ij}x_j]f_{x_i}u+\sum_{i}[\sum_{j}q_{ij}x_j]fu_{x_i}=uLf+fL_0u$$

In the haploid case $\sigma_{ij}=h_i+h_j$. This operator can be generalized according to Ethier and Kurtz [4].

2 Ergodic theorems of Fleming-Viot processes with selection

Let E be a locally compact separable metric space and $\mathcal{P}(E)$ be the space of all probability measures on E. For $\mu \in \mathcal{P}(E)$ let us denote $\langle f, \mu \rangle = \int_E f d\mu$. For any $f_1, \cdots, f_m \in \mathcal{D}(A)$ and $F \in C^2(R^m)$ let $\varphi(\mu) = F(\langle f_1, \mu \rangle, \cdots, \langle f_m, \mu \rangle) = F(\langle \mathbf{f}, \mu \rangle)$ and let us denote

$$
\begin{aligned}
(1)\mathcal{L}\varphi(\mu) &= \frac{1}{2}\sum_{i,j=1}^{m}(\langle f_i f_j, \mu\rangle - \langle f_i, \mu\rangle\langle f_j, \mu\rangle)F_{z_i z_j}(\langle \mathbf{f}, \mu\rangle) \\
&+ \sum_{i=1}^{m}\{\langle Af_i, \mu\rangle + \langle (f_i \circ \pi)\sigma, \mu^2\rangle - \langle f_i, \mu\rangle\langle \sigma, \mu^2\rangle\}F_{z_i}(\langle \mathbf{f}, \mu\rangle).
\end{aligned}
$$

Here E is the space of genetic types and A is a mutation operator in $\bar{C}(E)$($\equiv$ the space of bounded continuous functions on E) which is the generator for a Feller semigruop $\{T(t)\}$ on $\hat{C}(E)$($\equiv$ the space of continuous functions vanishing at infinity) , μ^k is the n-fold product of μ , and $\sigma = \sigma(x, y)$ is a bounded symmetric function on $E \times E$ which is selection parameters for types $x, y \in E$. According to [4], this operator defines a generator corresponding to a Markov process on $\mathcal{P}(E)$ in the sense that the $C_{\mathcal{P}(E)}[0, \infty)$ martingale problem for $\mathcal{L}$ is well posed. This process is called the Fleming-Viot process. We consider another formula with $\sigma(x, y) = h(x) + h(y)$:

$$
\begin{aligned}
(2) \qquad \mathcal{L}\varphi(\mu) &= \frac{1}{2}\sum_{i,j=1}^{m}(\langle f_i f_j, \mu\rangle - \langle f_i, \mu\rangle\langle f_j, \mu\rangle)F_{z_i z_j}(\langle \mathbf{f}, \mu\rangle) \\
&+\sum_{i=1}^{m}\{\langle Af_i, \mu\rangle + \langle f_i h, \mu\rangle - \langle f_i, \mu\rangle\langle h, \mu\rangle\}F_{z_i}(\langle \mathbf{f}, \mu\rangle).
\end{aligned}
$$

Here we consider of the haploid case and that $h = h(x)$ is a selection intensity for type $x \in E$. The maximal coupling argument is applied to the mutation process in Donnelly and Kurtz [1] and there it follows that strong ergodicity of the mutation process guarantees strong ergodicity of the Fleming-Viot process. Here the mutation process is strongly ergodic with stationary distribution π is defined by that

$$\lim_{t\to\infty} \|T^*(t)\nu - \pi\| = 0.$$

We consider the uniform convergence of the Fleming-Viot processes under the condition of uniform convergence of the mutation semigroup in the sense

$$\lim_{t \to \infty} \|T(t) - \langle \cdot, \pi \rangle 1\| = 0.$$

We consider the case of (1) and assume $B = 0$. Denote $\mathcal{L}$ of (1) by $\mathcal{L}_\sigma$. Then we have

Lemma 1.([6]) *Let $g(\mu) = \frac{1}{2}\langle \sigma, \mu^2 \rangle$. Then we have for $\varphi \in C(\mathcal{P}(E))$*

$$\mathcal{L}_\sigma \varphi = e^{-g}(\mathcal{L}_0 - \psi)(e^g \varphi),$$

where $\psi(\mu) = \frac{1}{2}(\langle \sigma^{(2)}, \mu^3 \rangle - \langle \sigma, \mu^2 \rangle^2 + \langle A^{(2)}\sigma, \mu^2 \rangle + \langle \Phi_{12}^{(2)}\sigma, \mu \rangle - \langle \sigma, \mu^2 \rangle)$ and $\sigma^{(2)}(x, y, z) = \sigma(x, y)\sigma(y, z)$, and $\Phi_{12}^{(2)}\sigma(x) = \sigma(x, x)$ and $A^{(2)}$ is an infinitesimal generator of the semigroup $T(t) \otimes T(t)$ in $\bar{C}(E^2)$.
Theorem 1.([6]) *Assume (A1): $\sigma \in \mathcal{D}(A^{(2)})$, $A^{(2)}\sigma \in \bar{C}(E^2)$, and let*

$$\mathcal{D}(\mathcal{L}_\sigma) = \{\varphi \in C(\mathcal{P}(E)) : e^g \varphi \in \mathcal{D}(\mathcal{L}_0)\}.$$

Then there exists a semigroup $\{\mathcal{T}(t)\}$ corresponding to $(\mathcal{L}_\sigma, \mathcal{D}(\mathcal{L}_\sigma))$ and

$$\mathcal{T}(t)\varphi(\mu) = e^{-g(\mu)} E_\mu[\exp\{g(\mu_t) - \int_0^t \psi(\mu_s)ds\}\varphi(\mu_t)]$$

holds.
Theorem 2.([6]) *Assume (A1) and that (A2): $\{\mathcal{T}_0(t)\}$ is ergodic and that for some positive constants M* and λ_0 *and a stationary distribution* Π_0

$$\|\mathcal{T}_0(t)\varphi - \langle \varphi, \Pi_0 \rangle 1\| \le M e^{-\lambda_0 t}\|\varphi\|.$$

Then there exists a stationary distribution Π *such that for any* $\epsilon > 0$ *there exist constants $M_1 = M_1(\epsilon), \delta = \delta(\epsilon) > 0$ satisfying that*

$$\|\mathcal{T}(t)\varphi - \langle \varphi, \Pi \rangle 1\| \le M_1 e^{-(\lambda_0 - \epsilon)t}\|\varphi\|.$$

if $\|\psi\| \le \delta$.
Theorem 3. (Ethier and Griffiths [2], Ethier and Kurtz [4], Shiga [7], Tavaré [8]) *Let A be an operator as*

$$Af(x) = \frac{\theta}{2}\int_E (f(\xi) - f(x))\nu(d\xi),$$

Then there exists a stationary distribution $\Pi_{\theta,\nu}$ *such that the transition probability* $P(t,\mu,\cdot)$ *of the semigroup* $\{\mathcal{T}_0(t)\}$ *satisfies that*

$$\|P(t,\mu,\cdot)-\Pi_{\theta,\nu}\|_{var} \le 1-d_0(t),$$

where $\|\cdot\|_{var}$ *is total variation and* $d_0(t)$ *satisfies that*

$$e^{-\lambda_1 t} \le 1-d_0(t) \le (1+\theta)e^{-\lambda_1 t}$$

where $\lambda_1 = \frac{\theta}{2}$.

We will show an example with the assumption of Theorem 2 including the case of the mutation operator in Theorem 3. Let us consider the Fleming-Viot process defined by the generator of the form (1) with $B=0$ and $\sigma=0$. In [4] the ergodic theorem has been proved in the sense of weak convergence under the condition that the mutation operator is ergodic in the sense of weakly convergence. We have that

Theorem 4. *Assume that* $\{T(t)\}$ *is ergodic and that* (C):
for some positive constants M_0 *and* λ_0 *and a stationary distribution* ν_0 *such that for any* $f \in \bar{C}(E)$

$$\|T(t)f-\langle f,\nu_0\rangle 1\| \le M_0 e^{-\lambda_0 t}\|f\|.$$

Then there exists a stationary distribution Π_0 *such that for any* $\epsilon > 0$ *there exist constants* $M = M(\epsilon), \lambda_1 = \lambda_1(\epsilon) > 0$ *satisfying that*

$$\|\mathcal{T}_0(t)\varphi - \langle \varphi, \Pi_0\rangle 1\| \le Me^{-\lambda_1 t}\|\varphi\|.$$

where $\lambda_1 = \min(1-\epsilon, \lambda_0)$.
For the proof the next Theorem will be used. For any k define a semigroup $\{T_k(t)\}$ on $\bar{C}(E^k)$ with the generator $A^{(k)}$ by $T_k(t) = T(t)\otimes\cdots\otimes T(t)$ (k fold direct product of $T(t)$), then we have

Theorem 5(Ethier and Kurtz[4]). *Let* $S = \sum_{k=1}^{\infty} \bar{C}(E^k)$ *be a space of direct sum of Banach spaces and define a Markov process on* S *with the generator*

$$\hat{\mathcal{L}}F(f) = \sum_{1\le i<j\le k} (F(\Phi_{ij}^{(k)}f)-F(f)) + \lim_{t\to 0}\frac{F(T_k(t)f)-F(f)}{t}$$

for $f \in \bar{C}(E^k)$ *where*

$$(\Phi_{ij}^{(k)} f)(x_1, \cdots, x_{k-1}) = f(x_1, \cdots, x_{j-1}, x_i, x_j, \cdots, x_{k-1})$$

for $k \geq 2$ *and* $1 \leq i < j \leq k$ *and* $f \in \bar{C}(E^k)$.

This process $\{Y(t)\}$ *is a dual process to the Fleming-Viot process as a sense of the followings. If* $Y(t) \in \bar{C}(E^k)$ *, put* $N(t) = k$*, then* $(N(t), Y(t))$ *satisfies that*

$$E_\mu[\langle f, \mu_t^k \rangle] = E[\langle Y(t), \mu^{N(t)} \rangle]$$

where $Y(0) = f$.

Proof of Theorem 4. Let $\tau = \inf\{t > 0; N(t) = 1\}$, then from the above theorem

$$(3) \quad E_\mu[\langle f, \mu_t^k \rangle] = E[\langle Y(t), \mu^{N(t)} \rangle; \tau \leq t] + E[\langle Y(t), \mu^{N(t)} \rangle; \tau > t].$$

Here $N(t)$ is a death process, which jumps from k to $k-1$ with rate $k(k-1)/2$ for $k \geq 2$. Denote τ_0 the hitting time at 1 of the death process started from an entrance boundary at ∞, then $P(\tau > t) \leq P(\tau_0 > t) = 1 - d_1^0(t)$, and by [2] we have that $e^{-t} \leq 1 - d_1^0(t) \leq 3e^{-t}$. So we have

$$|E[\langle Y(t), \mu^{N(t)} \rangle; \tau > t] - E[\langle Y(\tau), \mu \rangle; \tau > t]| \leq 6e^{-t} \|f\|$$

and by the condition (C)

$$\begin{aligned} &|E[\langle Y(t), \mu^{N(t)} \rangle; \tau \leq t] - E[\langle Y(\tau), \nu_0 \rangle; \tau \leq t]| \\ &= |E[\langle T(t-\tau) Y(\tau), \mu \rangle - \langle Y(\tau), \nu_0 \rangle; \tau \leq t]| \\ (4) \qquad &\leq M_0 E[e^{-\lambda_0 (t-\tau)}] \|f\| \leq M_0 e^{-\lambda_1 t} E e^{-\lambda_1 \tau} \|f\|. \end{aligned}$$

Therefore by (4) we have

$$|E_\mu[\langle f, \mu_t^k \rangle] - E[\langle Y(\tau), \nu_0 \rangle]| \leq M_1 e^{-\lambda_1 t} \|f\|$$

with $M_1 = 6 + M_0$. Because $\bigcup_k \{\varphi(\mu) = \langle f, \mu^k \rangle : f \in \bar{C}(E^k)\}$ is dense in $C(\mathcal{P}(E))$ and by the Riesz' representation theorem the Theorem holds.Q.E.D.

3 The stationary distribution

On the stationary distributions of $\mathcal{L}_\sigma$, we have

Theorem 6. *Assume (A1) and (A2) with* $M \geq 1$. *Then under the assumption of Theorem 2 for any* $0 < \lambda < \lambda_0/(2M-1)$ *there exists* $\delta = \delta(\lambda) > 0$ *such that if* $\|\psi\| < \delta$,then the stationary distribution Π satisfies

$$\Pi = cV[1 + Q\mathcal{R}_\lambda^*][1 + Q\mathcal{R}_\lambda^* + P_0 + P_0^* Q\mathcal{R}_\lambda^* - \lambda\mathcal{R}_\lambda^*]^{-1}\Pi_0.$$

where $P_0 = \langle\cdot, \Pi_0\rangle 1, Q = \psi\times, V = e^g\times, \mathcal{R}_\lambda = (\lambda - \mathcal{L}_0)^{-1}$, $\mathcal{R}_\lambda^*$ *is the adjoint operator of* $\mathcal{R}_\lambda$ and c *is a suitable constant.*
For the proof the next Lemmas are used.

Lemma 2. *Let* S *be a locally compact space and* Π *is a distribution on* S. *Assume* B *is a bounded operator on* $L = \bar{C}(S)$ *with* $1 - B$ *is invertible and* $\langle(1-B)^{-2}1, \Pi_0\rangle \neq 0$. *Let* $P_0 = \langle\cdot, \Pi_0\rangle$ *and* $U = P_0 + B$. *If* U *has an eigenvalue 1 with eigenfunction* φ_0, *then we have that* $\varphi_0 = (1-B)^{-1}1$ *and*

$$\langle\varphi_0, \Pi_0\rangle = 1$$

let

(5) $$P_1 = \langle(1-B)^{-2}1, \Pi_0\rangle^{-1}\langle\cdot, (1-B^*)^{-1}\Pi_0\rangle(1-B)^{-1}1,$$

then

$$UP_1 = P_1 U = P_1,$$

and P_1 *is a projection. If in addition* $\|B\| \leq \frac{1}{2}$, *then the next relation holds*

$$\|U - P_1\| \leq 7\| B\|.$$

Proof. Because φ_0 is an eigenfunction, we have

$$\langle\varphi_0, \Pi_0\rangle 1 + B\varphi_0 = \varphi_0,$$

so that

$$\varphi_0 = \langle\varphi_0, \Pi_0\rangle(1-B)^{-1}1.$$

Obviously P_1 of (5) is a projection. Let $B_1 = U - P_1$, then

$$B_1 = P_0 - P_1 + B_0,$$

and we have

$$\|P_0 - P_1\| \leq \|B\|\{(1 - \|B\|)^{-2} + (1 - \|B\|)^{-1}\}.$$

Therefore the inequality holds. Q.E.D.

Lemma 3. *Under the assumption of Theorem 2. we have that*

$$\|(\lambda - \widetilde{\mathcal{L}}_0)^{-1} - (\lambda - \mathcal{L}_0)^{-1}\| \leq \lambda^{-2}(1 - \lambda^{-1}\|\psi\|)^{-1}\|\psi\|,$$

$$\|\lambda(\lambda - \widetilde{\mathcal{L}}_0)^{-1} - P_0\| \leq M\lambda/(\lambda + \lambda_0) + \lambda^{-1}(1 - \lambda^{-1}\|\psi\|)^{-1}\|\psi\|.$$

Proof. By the assumption of Theorem 2

$$\|\lambda\mathcal{R}_\lambda - P_0\| \leq M\lambda/(\lambda + \lambda_0).$$

By

$$\widetilde{\mathcal{L}}_0 = \mathcal{L}_0 - \psi$$

we have

$$\widetilde{\mathcal{R}}_\lambda = [1 + \mathcal{R}_\lambda Q]^{-1}\mathcal{R}_\lambda.$$

The inequality is obtained by

$$\lambda\widetilde{\mathcal{R}}_\lambda - P_0 = -\lambda[1 + \mathcal{R}_\lambda Q]^{-1}\mathcal{R}_\lambda Q\mathcal{R}_\lambda - \lambda\mathcal{R}_\lambda + P_0. \tag{6}$$

Q.E.D.

Proof of Theorem 6. By the assumption of the theorem we have for $0 < \lambda = \lambda_0/(M - 1)$ by Lemma 3 there exists $\delta = \delta(\lambda)$ such that for $\|\psi\| \leq \delta$

$$\|\lambda\widetilde{\mathcal{R}}_\lambda - P_0\| < 1/2$$

is satisfied. Put $B = \lambda\widetilde{\mathcal{R}}_\lambda - P_0$. Then $\|B\| \leq 1/2$. By Lemma 2. we have

$$\widetilde{\mathcal{R}}_\lambda P_1 = P_1\widetilde{\mathcal{R}}_\lambda = \lambda^{-1}P_1$$

with some projection $P_1 = \langle\cdot, \Pi_1\rangle\varphi_0$ and $\Pi_1 = c(1 - B^*)^{-1}\Pi_0$. By Lemma 3 Π_1 is eigenfunction of $\lambda\widetilde{\mathcal{R}}_\lambda^*$ corresponding to an eigenvalue 1 of multiplicity 1, so by Lemma 1 it is the stationary distribution multiplied by *constant* $\times\, e^{-g}$. Therefore the stationary distribution is in the form $cV(1 - B^*)^{-1}\Pi_0$. Q.E.D.

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