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Kyoto University
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 $b_i(x) = \sum_{j=1}^{K} q_{ij} x_j + x_i(\sum_{j=1}^{K} \sigma_{ij} x_j - \sum_{k,l=1}^{K} \sigma_{kl} x_k x_l)$, $q_{ij} \geq 0$ 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 $\sigma_{ij}$ is selection intensity of $(i,j)$-type. Put $u(x) = exp\left(\frac{1}{2} \sum_{i,j=1}^{K} \sigma_{ij} x_i x_j\right)$, and denote by $L_0$ an operator $L$ in the case of $\sigma = 0$ then

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

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

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 $F \in C^2(\mathbb{R}^m)$ let $\varphi(\mu) = F(\langle f_1, \mu \rangle, \cdots, \langle f_m, \mu \rangle) = F(\langle f, \mu \rangle)$ and let us denote

\[
(1) \mathcal{L} \varphi(\mu) = \frac{1}{2} \sum_{i,j=1}^{m} (\langle f_i f_j, \mu \rangle - \langle f_i, \mu \rangle \langle f_j, \mu \rangle) F_{z_i z_j}(\langle f, \mu \rangle)
\]

\[
+ \sum_{i=1}^{m} \{ \langle A f_i, \mu \rangle + \langle f_i \circ \pi \sigma, \mu^2 \rangle - \langle f_i, \mu \rangle \langle \sigma, \mu^2 \rangle \} F_{z_i}(\langle f, \mu \rangle).
\]

Here $E$ is the space of genetic types and $A$ is a mutation operator in $\hat{C}(E) (\equiv$ the space of bounded continuous functions on $E$) which is the generator for a Feller semigroup $\{T(t)\}$ on $\hat{C}(E) (\equiv$ the space of continuous functions vanishing at infinity), $\mu^k$ is the $n$-fold product of $\mu$, 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 $\sigma(x, y) = h(x) + h(y)$:

\[
(2) \mathcal{L} \varphi(\mu) = \frac{1}{2} \sum_{i,j=1}^{m} (\langle f_i f_j, \mu \rangle - \langle f_i, \mu \rangle \langle f_j, \mu \rangle) F_{z_i z_j}(\langle f, \mu \rangle)
\]

\[
+ \sum_{i=1}^{m} \{ \langle A f_i, \mu \rangle + \langle f_i h, \mu \rangle - \langle f_i, \mu \rangle \langle h, \mu \rangle \} F_{z_i}(\langle f, \mu \rangle).
\]

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 $\pi$ 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
\[ \lim_{t \to \infty} \| T(t) - \langle \cdot, \pi \rangle \| = 0. \]
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 \( \overline{C}(E^2) \).

**Theorem 1.** ([6]) Assume \( (A1) \): \( \sigma \in D(A^{(2)}), \ A^{(2)} \sigma \in \overline{C}(E^2) \), and let
\[ D(\mathcal{L}_\sigma) = \{ \varphi \in C(\mathcal{P}(E)) : e^g \varphi \in D(\mathcal{L}_0) \}. \]
Then there exists a semigroup \( \{ T(t) \} \) corresponding to \( (\mathcal{L}_\sigma, D(\mathcal{L}_\sigma)) \) and
\[ T(t)\varphi(\mu) = e^{-g(\mu)}E_\mu[\exp\{g(\mu_t) - \int_0^t \psi(\mu_s)ds\}\varphi(\mu_t)] \]
holds.

**Theorem 2.** ([6]) Assume \( (A1) \) and that \( (A2) \): \( \{ T_0(t) \} \) is ergodic and that for some positive constants \( M \) and \( \lambda_0 \) and a stationary distribution \( \Pi_0 \)
\[ \| T_0(t)\varphi - \langle \varphi, \Pi_0 \rangle \| \leq Me^{-\lambda_0 t}\| \varphi \|. \]
Then there exists a stationary distribution \( \Pi \) such that for any \( \epsilon > 0 \) there exist constants \( M_1 = M_1(\epsilon), \delta = \delta(\epsilon) > 0 \) satisfying that
\[ \| T(t)\varphi - \langle \varphi, \Pi \rangle \| \leq M_1e^{-(\lambda_0 - \epsilon)t}\| \varphi \|. \]
if \( \| \psi \| \leq \delta \).

**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 $\{T_0(t)\}$ satisfies that

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

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

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

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 $\lambda_0$ and a stationary distribution $\nu_0$ such that for any $f \in \overline{C}(E)$

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

Then there exists a stationary distribution $\Pi_0$ such that for any $\epsilon > 0$ there exist constants $M = M(\epsilon), \lambda_1 = \lambda_1(\epsilon) > 0$ satisfying that

$$\|T_0(t)\varphi - \langle \varphi, \Pi_0 \rangle 1\| \leq Me^{-\lambda_1 t} \|\varphi\|.$$ 

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 $\overline{C}(E^k)$ 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 $S = \sum_{k=1}^{\infty} \overline{C}(E^k)$ be a space of direct sum of Banach spaces and define a Markov process on $S$ with the generator

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

$$= \sum_{1 \leq i < j \leq k} (F(\Phi_{ij}^{(k)}f) - F(f)) + \lim_{t \to 0} \frac{F(T(t)f) - F(f)}{t}$$

where $\Phi_{ij}^{(k)}$ are the transition operators of $T_k(t)$.
for $f \in \overline{C}(E^k)$ where
\[
(\Phi_{ij}^{(k)} f)(x_1, \ldots, x_{k-1}) = f(x_1, \ldots, x_{j-1}, x_i, x_j, \ldots, x_{k-1})
\]
for $k \geq 2$ and $1 \leq i < j \leq k$ and $f \in \overline{C}(E^k)$.

This process $\{Y(t)\}$ is a dual process to the Fleming-Viot process as a sense of the followings. If $Y(t) \in \overline{C}(E^k)$, put $N(t) = k$, then $(N(t), Y(t))$ satisfies that
\[
E_\mu[(f, \mu^N_t)] = E[(Y(t), \mu^N_t)]
\]
where $Y(0) = f$.

Proof of Theorem 4. Let $\tau = \inf \{t > 0; N(t) = 1\}$, then from the above theorem
\[
(3) \quad E_\mu[(f, \mu^N_t)] = E[(Y(t), \mu^N_t); \tau \leq t] + E[(Y(t), \mu^N_t); \tau > t].
\]
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 $\tau_0$ the hitting time at 1 of the death process started from an entrance boundary at $\infty$, 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
\[
|E[(Y(t), \mu^N_t); \tau > t] - E[(Y(\tau), \mu); \tau > t]| \leq 6e^{-t}\|f\|
\]
and by the condition (C)
\[
|E[(Y(t), \mu^N_t); \tau \leq t] - E[(Y(\tau), \nu_0); \tau \leq t]| = |E[(T(t-\tau)Y(\tau), \mu) - (Y(\tau), \nu_0); \tau \leq t]|
\leq M_0 E[e^{-\lambda_0(t-\tau)}]\|f\| \leq M_0 e^{-\lambda_1 t} E e^{-\lambda_1 \tau} \|f\|.
\]
Therefore by (4) we have
\[
|E_\mu[(f, \mu^k_t)] - E[(Y(\tau), \nu_0)]| \leq M_1 e^{-\lambda_1 t}\|f\|
\]
with $M_1 = 6 + M_0$. Because $\bigcup \{\varphi(\mu) = (f, \mu^k) : f \in \overline{C}(E^k)\}$ 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 $\Pi$ 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 $P_0 = \langle \cdot, \Pi_0 \rangle 1, Q = \psi x, V = e^{g} x, \mathcal{R}_\lambda = (\lambda - \mathcal{L}_0)^{-1}$, $\mathcal{R}^*_\lambda$ 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 $\Pi$ is a distribution on $S$. Assume $B$ is a bounded operator on $L = \overline{C}(S)$ with $1 - B$ is invertible and $\langle (1 - B)^{-1}1, \Pi_0 \rangle \neq 0$. Let $P_0 = \langle \cdot, \Pi_0 \rangle$ and $U = P_0 + B$. If $U$ has an eigenvalue $1$ with eigenfunction $\varphi_0$, then we have that $\varphi_0 = (1 - B)^{-1}1$ and

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

let

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

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 $\varphi_0$ 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
\[ \|P_0 - P_1\| \leq \|B\|(1 - \|\psi\|)^{-2} + (1 - \|B\|)^{-1}. \]
Therefore the inequality holds.

Q.E.D.

**Lemma 3.** Under the assumption of Theorem 2, we have that
\[ \|(\lambda - \bar{L}_0)^{-1} - (\lambda - \mathcal{L}_0)^{-1}\| \leq \lambda^{-2}(1 - \lambda^{-1}\|\psi\|)^{-1}\|\psi\|, \]
\[ \|\lambda(\lambda - \bar{L}_0)^{-1} - P_0\| \leq M\lambda/(\lambda + \lambda_0) + \lambda^{-1}(1 - \lambda^{-1}\|\psi\|)^{-1}\|\psi\|. \]

Proof. By the assumption of Theorem 2
\[ \|\lambda\mathcal{R}_\lambda - P_0\| \leq M\lambda/(\lambda + \lambda_0). \]
By
\[ \bar{L}_0 = \mathcal{L}_0 - \psi \]
we have
\[ \bar{R}_\lambda = [1 + \mathcal{R}_\lambda Q]^{-1}\mathcal{R}_\lambda. \]
The inequality is obtained by
\[ \lambda\bar{R}_\lambda - P_0 = -\lambda[1 + \mathcal{R}_\lambda Q]^{-1}\mathcal{R}_\lambda Q\mathcal{R}_\lambda - \lambda\mathcal{R}_\lambda + P_0. \]
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
\[ \|\psi\| \leq \delta \]
\[ \|\lambda\bar{R}_\lambda - P_0\| < 1/2 \]
is satisfied. Put \( B = \lambda\bar{R}_\lambda - P_0 \). Then \( \|B\| \leq 1/2 \). By Lemma 2. we have
\[ \bar{R}_\lambda P_1 = P_1\bar{R}_\lambda = \lambda^{-1}P_1 \]
with some projection \( P_1 = \langle \cdot, \Pi_1 \rangle \varphi_0 \) and \( \Pi_1 = c(1 - B^*)^{-1}\Pi_0 \). By Lemma 3 \( \Pi_1 \) is eigenfunction of \( \lambda\bar{R}_\lambda \) 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.
References


