

## A REVERSIBILITY PROBLEM FOR FLEMING-VIOT PROCESSES

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*Abstract:*

*Fleming-Viot processes incorporating mutation and selection are considered. It is well-known that if the mutation factor is of uniform type, the process has a reversible stationary distribution, and it has been an open problem to characterize the class of the processes that have reversible stationary distributions. This paper proves that if a Fleming-Viot process has a reversible stationary distribution, then the associated mutation operator is of uniform type.*

### 1 Problem and Result

Fleming-Viot processes form a class of probability measure-valued diffusion processes, which are derived as a continuum limit from Markov chain models in population genetics. The processes have attracted not only probabilists but also mathematical population genetists since they are very reasonable models to analyze the geneological structure. (cf. [1], [3]). In particular, if the mutation factor is of uniform type, namely the distribution of mutants

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is independent of their parent's genotype, then the Fleming-Viot processes have reversible stationary distributions, that makes the genealogical analysis extremely tractable. However it has been an open problem whether there exists another class of mutation operators such that the associated Fleming-Viot processes have reversible stationary distributions.

In the present paper we shall solve this problem. Our result is that if a Fleming-Viot process has a reversible stationary distribution, then the mutation operator is of uniform type.

Let us begin with description of the Fleming-Viot processes. Let  $E$  be a locally compact separable space. We denote by  $B(E)$  the set of all bounded Borel measurable functions on  $E$ , and by  $C_\infty(E)$  the Banach space of bounded continuous functions vanishing at infinity if  $E$  is non-compact, which is equipped with the supremum norm  $\|\cdot\|_\infty$ . We denote by  $C_0(E)$  the set of continuous functions with compact support, and by  $C_0^+(E)$  the set of nonnegative functions in  $C_0(E)$ . Let  $M_1(E)$  be the space of Borel probability measures on  $E$  endowed with the topology of weak convergence. For  $\mu \in M_1(E)$ , we denote by  $\mu^{\otimes n} \in M_1(E^n)$  the  $n$ -fold product of  $\mu$ . We also use the notation  $\mu(f) := \int_E f d\mu$  for  $f \in B(E)$  and  $\mu \in M_1(E)$ .

Let  $(A, \mathcal{D}(A))$  be the generator of a conservative Markovian Feller semigroup  $T_t$  acting on  $C_\infty(E)$ , which governs a mutational evolution, and let  $\sigma = (\sigma(x, y))$  be a symmetric bounded Borel measurable function on  $E \times E$ , which is interpreted as a selective density. For given  $(A, \mathcal{D}(A))$  and  $\sigma$  let us consider the following operator  $(\mathcal{L}, \mathcal{D}(\mathcal{L}))$ :

$$\begin{aligned} \mathcal{L}\phi(\mu) &= \frac{1}{2} \int_E \int_E (\mu(dx)\delta_x(dy) - \mu(dx)\mu(dy)) \frac{\delta^2\phi(\mu)}{\delta\mu(x)\delta\mu(y)} \\ &+ \int_E \mu(dx) A \left( \frac{\delta\phi(\mu)}{\delta\mu(\cdot)} \right) (x) + \int_E \int_E \mu(dx)\mu(dy) (\sigma(x, y) - \mu^{\otimes 2}(\sigma)) \frac{\delta\phi(\mu)}{\delta\mu(x)} \end{aligned}$$

where  $\delta\phi(\mu)/\delta\mu(x) = \lim_{r \rightarrow 0^+} r^{-1} \{\phi(\mu + r\delta_x) - \phi(\mu)\}$ , and we take  $\mathcal{D}(\mathcal{L})$  to be the set of all  $\phi \in C(M_1(E))$  of the form

$$\phi(\mu) = F(\mu(f_1), \dots, \mu(f_k)),$$

where  $k \geq 1$ ,  $f_1, \dots, f_k \in \mathcal{D}(A)$ , and  $F \in C^2(\mathbf{R}^k)$ .

Let  $\Omega$  be the space of continuous paths from  $[0, \infty)$  to  $M_1(E)$  with the coordinate process denoted by  $\{X_t : t \geq 0\}$ . We furnish  $\Omega$  with the compact uniform topology. Let  $(\mathcal{F}, \mathcal{F}_t)_{t \geq 0}$  be the natural  $\sigma$ -algebras on  $\Omega$  generated by  $\{X_t : t \geq 0\}$ . It is known that for every  $\mu \in M_1(E)$  there is a unique probability measure  $\mathbf{Q}_\mu$  on  $\Omega$  such that for every  $\phi \in \mathcal{D}(\mathcal{L})$

$$\phi(X_t) - \phi(\mu) - \int_0^t \mathcal{L}\phi(X_s) ds$$

is a  $\mathbf{Q}_\mu$ -martingale starting at 0. Then  $(\Omega, (\mathcal{F}_t)_{t \geq 0}, \mathbf{Q}_\mu, X_t)$  defines a diffusion process in  $M_1(E)$ , which is called a *Fleming-Viot process incorporating mutation and selection*. Hereafter we simply write  $(X_t, \mathbf{Q}_\mu)$  for the Fleming-Viot process  $(\Omega, (\mathcal{F}_t)_{t \geq 0}, \mathbf{Q}_\mu, X_t)$ .

It is convenient to describe the process  $(X_t)$  by the following stochastic equation associated with a martingale measure introduced in [8]: For  $f \in \mathcal{D}(A)$

$$X_t(f) - X_0(f) = \int_0^t \{X_s(Af) + X_s^{\otimes 2}(\sigma f \otimes 1) - X_s^{\otimes 2}(\sigma)X_s(f)\} ds + \int_0^t \int_E f(x) M(dsdx) \quad (1.1)$$

where  $\sigma \cdot f \otimes 1(x, y) = \sigma(x, y)f(x)$ , and  $M(dsdx)$  is a martingale measure such that

$$M_t(f) = \int_0^t \int_E f(x) M(dsdx)$$

is a continuous martingale with quadratic variation process

$$\langle M(f) \rangle_t = \int_0^t (X_s(f^2) - X_s(f)^2) ds. \tag{1.2}$$

Then it holds that for every  $f \in C_\infty(E)$

$$\begin{aligned} X_t(f) &= X_0(T_t f) + \int_0^t \{X_s^{\otimes 2}(\sigma \cdot (T_{t-s} f) \otimes 1) \\ &\quad - X_s^{\otimes 2}(\sigma) X_s(T_{t-s} f)\} ds + \int_0^t \int_E T_{t-s} f(x) M(ds dx). \end{aligned} \tag{1.3}$$

Now we give two examples.

**Example 1.1** Let  $E = \mathbf{R}^d$ ,  $A = \Delta$  (Laplacian on  $\mathbf{R}^d$ ) and  $\sigma = 0$ . Then the associated Fleming-Viot process is a limit process of the step-wise mutation model of Ohta-Kimura [7]. In this case there exists no stationary distribution, instead the process exhibits a wandering phenomenon (c.f. [2]). If we start the step-wise mutation model with periodic boundary condition, then the limit process is a Fleming-Viot process associated with  $E = \mathbf{T}^d$  ( $d$ -dimensional torus),  $A$  is the Laplacian on  $\mathbf{T}^d$  and  $\sigma = 0$ . In this case there is a unique stationary distribution, but it has not been known whether the stationary distribution is reversible or not.

**Example 1.2** Let  $A$  be the following jump-type generator;

$$Af(x) = \frac{\theta}{2} \int_E (f(y) - f(x)) P(x, dy),$$

where  $\theta > 0$  is a constant and  $P(x, dy)$  is a stochastic kernel on  $E \times E$ . This class of Fleming-Viot processes are investigated by Ethier and Kurtz ([3]) for sample path properties and ergodic behaviors. In particular, if  $P(x, dy) = \nu(dy)$  is independent of  $x \in E$ , that is

$$Af(x) = \frac{\theta}{2} \int_E (f(y) - f(x)) \nu(dy), \tag{1.4}$$

the mutation operator is called of uniform type, which is the case having been well-studied from geneological view point. An advantage of the uniform mutation is that the associated Fleming-Viot process has a reversible stationary distribution which is identified with Poisson-Dirichlet distribution (c.f. [3]).

It is known that in the non-selective case;  $\sigma = 0$ , the Fleming-Viot process is ergodic if and only if the mutation semigroup is ergodic. In the selective case, i.e.  $\sigma \neq 0$ , it might be expected that the same conclusion holds, but it has not yet been proved completely.

In the present paper we consider a reversibility problem for Fleming-Viot processes incorporating mutation and selection, that is to characterize the mutation operator  $(A, \mathcal{D}(A))$  with which the associated Fleming-Viot process has a reversible stationary distribution.

Now we state our main theorem.

**Theorem 1.1** Suppose that  $T_t$  is irreducible, i.e. for every  $x \in E$  and  $f \in C_0^+(E)$  with  $f \neq 0$

$$T_t f(x) > 0 \quad \text{for some } t > 0.$$

If the Fleming-Viot process  $(X_t, \mathbf{Q}_\mu)$  with the mutation operator  $(A, \mathcal{D}(A))$  and the selective density  $\sigma$  has a reversible stationary distribution  $\mathcal{Q}$ , then  $(A, \mathcal{D}(A))$  is of the form (1.4) with  $\nu(f) = \int_{M_1(E)} \mu(f) \mathcal{Q}(d\mu)$ .

We remark that the above irreducibility assumption seems to be natural. Because, if there exists a unique stationary distribution, it can be reduced to this case by restricting the basic space  $E$  to a smaller one. On the other hand, if there are more than two stationary distributions, the basic space  $E$  splits into several disjoint subsets, and on each subset the mutation operator will be of uniform type.

Our method of the proof is based on moment calculations. Assuming that  $\sigma = 0$ , we first show by second moment calculations that the barycenter of the reversible stationary distribution  $\mathcal{Q}$  is a reversible distribution for the mutation semigroup  $T_t$ , with which a regular Dirichlet space is associated. Then combining the Beurling-Deny formula for the Dirichlet form with third moment calculations we obtain the theorem in the non-selective case, which is discussed in the next section. Section 3 is devoted to the proof in the selective case, which is carried out by reducing it to the non-selective case by making use of a transformation of the probability law  $\mathcal{Q}_\mu$ .

## 2 The non-selective case

In this section we assume  $\sigma = 0$ . Let  $\mathcal{Q}$  be a stationary distribution of the Fleming-Viot process  $(X_t, \mathcal{Q}_\mu)$ . For  $\mathcal{Q}$  we define the moment measures  $m_n$  on the product space  $E^n = E \times \cdots \times E$  by

$$m_n = \int_{M_1(E)} \mu^{\otimes n} \mathcal{Q}(d\mu), \quad n = 1, 2, \dots, \quad (2.1)$$

and simply write  $m = m_1$ . From (1.3) with  $\sigma = 0$  it is easy to see that  $m$  is a stationary distribution of  $T_t$ .

Recall that  $m \in M_1(E)$  is  $T_t$ -reversible if and only if it holds that

$$m(fT_tg) = m(gT_tf) \quad (f, g \in C_\infty(E)). \quad (2.2)$$

**Lemma 2.1** *The probability measure  $m$  is  $T_t$ -reversible if and only if*

$$m_2(f \otimes T_tg) = m_2(g \otimes T_tf), \quad t \geq 0, f, g \in C_\infty(E), \quad (2.3)$$

where  $f \otimes g(x, y) = f(x)g(y)$ . In particular, if  $\mathcal{Q}$  is a reversible stationary distribution of  $(X_t, \mathcal{Q}_\mu)$ , then  $m$  is  $T_t$ -reversible.

*Proof.* Applying (1.3) to  $f \in C_\infty(E)$  and  $T_rg \in C_\infty(E)$ , we have

$$X_t(f) = X_0(T_tf) + \int_0^t \int_E T_{t-s}f(x)M(dsdx),$$

and

$$X_t(T_rg) = X_0(T_{t+r}g) + \int_0^t \int_E T_{t+r-s}g(x)M(dsdx).$$

Using the independence of  $X_0$  and  $M(dsdx)$  and (1.2) to compute  $m_2(f \otimes T_rg) = E(X_t(f)X_t(T_rg))$  we have

$$m_2(f \otimes T_rg) - m_2(T_tf \otimes T_{t+r}g) = \int_0^t m(T_sfT_{s+r}g)ds - \int_0^t m_2(T_sf \otimes T_{s+r}g)ds. \quad (2.4)$$

Suppose that (2.3) holds. Then (2.4) implies

$$\int_0^t m(T_s f T_{s+r} g) ds = \int_0^t m(T_{s+r} f T_s g) ds, \quad (2.5)$$

which yields (2.2). Thus  $m$  is  $T_t$ -reversible.

Conversely, if  $m$  is  $T_t$ -reversible, then (2.2) holds. Let

$$h(r, t) = m_2(T_{t+r} f \otimes T_t g) - m_2(T_{t+r} g \otimes T_t f).$$

By (2.4) and (2.5) it satisfies

$$h(r, 0) = h(r, t) - \int_0^t h(r, s) ds,$$

which yields  $h(r, t) = 0$  for all  $r, t \geq 0$ . In particular,  $h(t, 0) = 0$  is the conclusion (2.3). Finally if  $\mathcal{Q}$  is a reversible distribution of  $(X_t, \mathbf{Q}_\mu)$ , denoting by  $\mathbf{Q}$  the associated stationary Markovian probability measure on  $\Omega$  with initial distribution  $\mathcal{Q}$ , it holds

$$\mathbf{Q}\{X_0(f)X_t(g)\} = \mathbf{Q}\{X_0(g)X_t(f)\},$$

which yields (2.3) because of

$$\mathbf{Q}\{X_0(f)X_t(g)\} = \mathbf{Q}\{X_0(f)X_0(T_t g)\} = m_2(f \otimes T_t g).$$

Hence  $m$  is  $T_t$ -reversible.  $\square$

In the sequel of this section, we assume  $\mathcal{Q}$  is a reversible stationary distribution of  $(X_t, \mathbf{Q}_\mu)$ , hence by Lemma 2.1  $m$  is  $T_t$ -reversible. Let  $L^2(E; m)$  be the Hilbert space of real-valued  $m$ -square-integrable functions on  $E$  with the inner product  $(f, g)_m := m(fg)$ . Then  $T_t$  can be extended as a symmetric contraction semigroup acting on  $L^2(E; m)$ . We denote its generator by  $(\bar{A}, \mathcal{D}(\bar{A}))$ , which is a self-adjoint and non-positive definite operator on  $L^2(E; m)$ . Let

$$\mathcal{D}[\mathcal{E}] = \mathcal{D}(\sqrt{-\bar{A}}),$$

and for  $f, g \in \mathcal{D}(\sqrt{-\bar{A}})$  let

$$\mathcal{E}(f, g) = (\sqrt{-\bar{A}}f, \sqrt{-\bar{A}}g)_m \quad \text{and} \quad \mathcal{E}_\alpha(f, g) = \mathcal{E}(f, g) + \alpha(f, g)_m \quad (\alpha > 0).$$

Then  $(\mathcal{D}[\mathcal{E}], \mathcal{E}_\alpha)$  is a Hilbert space, and  $(\mathcal{D}[\mathcal{E}], \mathcal{E})$  defines an  $L^2$ -Dirichlet space (cf. [6]). Moreover it holds that

**Lemma 2.2**  $(\mathcal{D}[\mathcal{E}], \mathcal{E})$  is a regular Dirichlet space, that is,

$$C_0(E) \cap \mathcal{D}[\mathcal{E}] \text{ is dense both in } C_0(E) \text{ and in } (\mathcal{D}[\mathcal{E}], \mathcal{E}_\alpha).$$

*Proof.* Denote by  $G_\lambda$  ( $\lambda > 0$ ) the resolvent operators of  $(A, \mathcal{D}(A))$ . The Feller property of  $T_t$  implies  $G_\alpha[C_\infty(E)] \subset C_\infty(E)$ , from which the desired regularity follows. (See [6], Lemma 1.4.2.)  $\square$

For a regular Dirichlet space, it is known that the Dirichlet form has the following expression (cf. [5]).

**Lemma 2.3** [Beurling-Deny formula] For  $f, g \in \mathcal{D}[\mathcal{E}] \cap C_0(E)$ ,

$$\mathcal{E}(f, g) = \mathcal{E}_c(f, g) + \int_{E \times E \setminus \Delta} (f(y) - f(x))(g(y) - g(x))J(dx, dy), \quad (2.6)$$

where  $\mathcal{E}_c$  is the diffusion part which satisfies the local property;

$$\mathcal{E}_c(f, g) = 0 \quad \text{if } f, g \in \mathcal{D}[\mathcal{E}] \cap C_0(E) \text{ and } \text{supp}(f) \cap \text{supp}(g) = \emptyset,$$

and  $J$  is the jumping measure, which is a symmetric Radon measure on the product space  $E \times E$  off the diagonal  $\Delta$ .

**Lemma 2.4**

$$m_2(dx, dy) = \frac{1}{2}m(dx)G_{1/2}(x, dy), \quad x, y \in E. \quad (2.7)$$

*Proof.* From (2.4) with  $r = 0$  it follows that

$$m_2(f \otimes g) = e^{-t}m_2(T_t f \otimes T_t g) + \int_0^t e^{-s}m(T_s f T_s g)ds, \quad t \geq 0.$$

Letting  $t \rightarrow \infty$  and using  $T_t$ -symmetry of  $m$  we get

$$m_2(f \otimes g) = \int_0^\infty e^{-s}(T_s f, T_s g)_m ds = \int_0^\infty e^{-s}(f, T_{2s}g)_m ds = \frac{1}{2}(f, G_{1/2}g)_m,$$

which yields the desired conclusion.  $\square$

**Lemma 2.5** For  $f \in \mathcal{D}(A)$  and  $g, h \in C_\infty(E)$

$$m_3((I - A)f \otimes g \otimes h) = \frac{1}{2}m_2((fg) \otimes h + (fh) \otimes g). \quad (2.8)$$

*Proof.* We first assume  $f, g, h \in \mathcal{D}(A)$ . Let  $(X_t, \mathbf{Q})$  be the reversible stationary Markov process with initial distribution  $\mathbf{Q}$ . Note that by Itô's formula

$$\begin{aligned} X_t^{\otimes 2}(f \otimes g) - X_0^{\otimes 2}(f \otimes g) &= \int_0^t \{X_s^{\otimes 2}(Af \otimes g + f \otimes Ag) + X_s(fg) - X_s^{\otimes 2}(f \otimes g)\}ds \\ &\quad + \text{martingale}. \end{aligned} \quad (2.9)$$

Now use the reversibility of  $(X_t, \mathbf{Q})$  to get

$$\mathbf{Q}\{(X_t^{\otimes 2}(f \otimes g) - X_0^{\otimes 2}(f \otimes g))X_0(h)\} = \mathbf{Q}\{X_0^{\otimes 2}(f \otimes g)(X_t(h) - X_0(h))\},$$

from which together with (2.9) it follows that

$$\mathbf{Q}\{X_0^{\otimes 2}(f \otimes g)X_0(T_t h - h)\} = \int_0^t \mathbf{Q}\{(X_s^{\otimes 2}(Af \otimes g + f \otimes Ag - f \otimes g) + X_s(fg))X_0(h)\}ds.$$

Then dividing the equality by  $t > 0$  and letting  $t \rightarrow 0$  we get

$$m_3(f \otimes g \otimes Ah) = m_3(Af \otimes g \otimes h + f \otimes Ag \otimes h - f \otimes g \otimes h) + m_2((fg) \otimes h).$$

Interchanging  $g$  and  $h$ ,

$$m_3(f \otimes Ag \otimes h) = m_3(Af \otimes g \otimes h + f \otimes g \otimes Ah - f \otimes g \otimes h) + m_2((fh) \otimes g).$$

A combination of the last two equations gives the desired result for  $f, g, h \in \mathcal{D}(A)$ . The extension to  $g, h \in C_\infty(E)$  is trivial.  $\square$

**Lemma 2.6** *If  $f, g \in \mathcal{D}[\mathcal{E}] \cap C_\infty(E)$  and  $h \in C_\infty(E)$ , then  $fG_{1/2}h, gG_{1/2}h \in \mathcal{D}[\mathcal{E}]$  and*

$$\mathcal{E}(g, fG_{1/2}h) + \frac{1}{2}m(fhG_{1/2}g) = \mathcal{E}(f, gG_{1/2}h) + \frac{1}{2}m(ghG_{1/2}f). \quad (2.10)$$

*Proof.* The former fact is found in [6], Lemma 1.4.2. If  $f \in \mathcal{D}(A)$  and  $g, h \in C_0(E)$ , Lemmas 2.4 and 2.5 imply

$$m_3((I - A)f \otimes g \otimes h) = \frac{1}{4}m(fgG_{1/2}h) + \frac{1}{4}m(fhG_{1/2}g).$$

Moreover, if  $g \in \mathcal{D}(A)$ , inserting  $(I - A)g$  in place of  $g$  in the above equation we get

$$\begin{aligned} & m_3((I - A)f \otimes (I - A)g \otimes h) \\ &= \frac{1}{4}m(f(I - A)gG_{1/2}h) + \frac{1}{4}m(fhG_{1/2}(I - A)g) \\ &= \frac{1}{4}m(fgG_{1/2}h) + \frac{1}{4}\mathcal{E}(g, fG_{1/2}h) + \frac{1}{8}m(fhG_{1/2}g) + \frac{1}{4}m(fhg). \end{aligned}$$

Then the desired equality follows from the symmetry between  $f$  and  $g$ . It is trivial to extend for  $f, g \in \mathcal{D}[\mathcal{E}] \cap C_\infty(E)$ .  $\square$

**Lemma 2.7** *The jumping measure  $J(dx, dy)$  of (2.6) is everywhere dense in  $E \times E \setminus \Delta$ , that is,*

$$J(U \times V) > 0 \quad \text{for every disjoint non-empty open sets } U, V \subset E.$$

*Proof.* Suppose that the conclusion fails. Then there are two non-empty open sets  $U$  and  $V$  such that  $U \cap V = \emptyset$  and  $J(U \times V) = J(V \times U) = 0$ . Now take non-zero functions  $f, g \in \mathcal{D}(\mathcal{E}) \cap C_0^+(E)$  and  $h \in C_0^+(E)$ ,  $\text{supp}(f) \subset U$  and  $\text{supp}(g) \subset V$ . Then by the local property of  $\mathcal{E}_c$  we have  $\mathcal{E}_c(f, gG_{1/2}h) = \mathcal{E}_c(g, fG_{1/2}h) = 0$ . Hence

$$\begin{aligned} \mathcal{E}(f, gG_{1/2}h) &= \int_E \int_E (f(y) - f(x))(g(y)G_{1/2}h(y) - g(x)G_{1/2}h(x))J(dx, dy) \\ &= - \int_E \int_E (f(x)g(y)G_{1/2}h(y) + f(y)g(x)G_{1/2}h(x))J(dx, dy) \\ &= 0. \end{aligned}$$

Here we have used the symmetry of  $J$  for the last equality. Similarly  $\mathcal{E}(g, fG_{1/2}h) = 0$  holds. Accordingly by Lemma 2.6 we have

$$m(hfG_{1/2}g) = m(hgG_{1/2}f), \quad h \in \mathcal{D}(A). \quad (2.11)$$

Note that the irreducibility of  $T_t$  implies that  $m$  is everywhere dense in  $E$  and  $G_\lambda f(x) > 0$  ( $x \in E$ ) for  $f \in C_0^+(E)$  with  $f \neq 0$ , so that from (2.11) and the Feller property of  $G_\lambda$  it follows that

$$f(x)G_{1/2}g(x) = g(x)G_{1/2}f(x) \quad (x \in E), \quad (2.12)$$

which yields a contradiction, because  $G_{1/2}f(x) > 0$ ,  $G_{1/2}g(x) > 0$  for every  $x \in E$ , and  $f$  and  $g$  have disjoint supports. Thus the proof is completed.  $\square$

*Proof of Theorem 1.1 in the non-selective case.* We claim that for  $f, g, h \in C_0(E)$  with mutually disjoint supports, it holds

$$\int_E \int_E f(x)g(y) (G_{1/2}h(y) - G_{1/2}h(x)) J(dx, dy) = 0. \quad (2.13)$$

It suffices to show it for  $f, g \in \mathcal{D}[\mathcal{E}] \cap C_0(E)$  since it follows from the regularity of the Dirichlet space that for every  $f \in C_0^+(E)$  there exists  $\{f_n\} \subset \mathcal{D}[\mathcal{E}] \cap C_0^+(E)$  such that

$$\lim_{n \rightarrow \infty} \|f_n - f\|_\infty = 0 \quad \text{and} \quad \text{supp}(f_n) \subset \text{supp}(f) \quad (n \geq 1).$$

Noting that

$$\mathcal{E}_c(g, fG_{1/2}h) = \mathcal{E}_c(f, gG_{1/2}h) = 0 \quad \text{and} \quad fh(x) = gh(x) = 0 \quad (x \in E),$$

by Lemma 2.6 we have

$$\begin{aligned} & \int_E \int_E (g(x) - g(y)) (f(x)G_{1/2}h(y) - f(y)G_{1/2}h(y)) J(dx, dy) \\ &= \int_E \int_E (f(x) - f(y)) (g(x)G_{1/2}h(y) - g(y)G_{1/2}h(y)) J(dx, dy), \end{aligned}$$

hence it holds that

$$\begin{aligned} & \int_E \int_E (f(x)g(y)G_{1/2}h(y) + f(y)g(x)G_{1/2}h(x)) J(dx, dy) \\ &= \int_E \int_E (g(x)f(y)G_{1/2}h(y) + g(y)f(x)G_{1/2}h(x)) J(dx, dy), \end{aligned}$$

which yields (2.13) due to the symmetry of  $J$ .

Next, noting that  $J$  is everywhere dense in  $E \times E \setminus \Delta$  by Lemma 2.7, (2.13) and the Feller property of  $G_\lambda$  imply that  $G_{1/2}h(x)$  is constant outside the support of  $h$ , so that for every compact subset  $K$ ,  $G_{1/2}(x, K)$  is constant in  $x \notin K$ . Accordingly for every compact set  $K$  there exists a constant  $c(K)$  such that

$$G_{1/2}(x, K) = c(K) \quad (x \notin K). \quad (2.14)$$

It is easy to see that  $c(K)$  can be extended to a Borel measure on  $E$  such that (2.14) holds for every Borel set. This observation implies that there exists a constant  $a \geq 0$  such that for every  $x \in E$

$$G_{1/2}(x, \cdot) = a\delta_x(\cdot) + c(\cdot).$$



Here note that  $0 < a < 2$  and  $a + c(E) = 2$ , which follow from the continuity, the irreducibility and the conservativity of  $T_t$ . Inserting this to the resolvent equation we obtain

$$\left(1 + \left(\lambda - \frac{1}{2}\right)a\right) G_\lambda(x, \cdot) = a\delta_x(\cdot) + \frac{1}{2\lambda}c(\cdot),$$

so that

$$Af(x) = \lim_{\lambda \rightarrow \infty} \lambda(\lambda G_\lambda f(x) - f(x)) = \frac{1}{2a} \int_E (f(y) - f(x))c(dy).$$

Thus  $(A, \mathcal{D}(A))$  is of the type of (1.4). Moreover, it is easy to see that  $c$  agrees with  $m$  up to a constant multiplication. Therefore the proof of Theorem 1.1 in the non-selective case is completed.  $\square$

### 3 The selective case

The Fleming-Viot process incorporating selection is obtained from the non-selective process by making use of Girsanov transformation. And if the selective density is of the form  $\sigma = f \otimes g + g \otimes f$  with  $f, g \in \mathcal{D}(A)$ , it is straightforward to show that the reversible stationary distribution of the selective model inherits the one of the non-selective model, so that the non-selective result is applicable. Furthermore, for a bounded measurable selective density  $\sigma$  it is possible to prove Theorem 1.1 by taking a suitable approximation.

In this section to emphasize the selective density  $\sigma$ , we denote by  $(X_t, \mathbf{Q}_\mu^\sigma)$  the associated Fleming-Viot process. Let  $M(dsdx)$  be the martingale measure defined by (1.1) and (1.2). We use the notation  $B_{sym}(E^2)$  for the set of symmetric and bounded measurable functions on  $E^2$ . For  $\varphi \in B_{sym}(E^2)$  we define the martingales

$$M_t^{(2)}(\varphi) := \int_0^t \int_E X_s(\varphi_x) M(dsdx)$$

with  $\varphi_x(y) = \varphi(x, y)$ , and

$$N_t^{(2)}(\varphi) := \exp \left\{ -M_t^{(2)}(\varphi) - \frac{1}{2} \langle M^{(2)}(\varphi) \rangle_t \right\}, \quad (3.1)$$

which is a positive martingale with mean one and

$$\langle M^{(2)}(\varphi) \rangle_t = \int_0^t \left( \int_E X_s(dx) X_s(\varphi_x)^2 - X_s^{\otimes 2}(\varphi)^2 \right) ds. \quad (3.2)$$

Let  $\mathbf{Q}_\mu^0$  be the probability measure on  $\Omega$  such that  $\mathbf{Q}_\mu^0(F) = \mathbf{Q}_\mu^\sigma \{ N_t^{(2)}(\sigma) 1_F \}$  for  $F \in \mathcal{F}_t$  and  $t \geq 0$ .

**Lemma 3.1** For  $f \in \mathcal{D}(A)$

$$M_t^0(f) := M_t(f) + \int_0^t (X_s^{\otimes 2}(\sigma \cdot f \otimes 1) - X_s^{\otimes 3}(\sigma \otimes f)) ds, \quad t \geq 0, \quad (3.3)$$

is a  $\mathbf{Q}_\mu^\sigma$ -martingale with quadratic variation process

$$\langle M^0(f) \rangle_t = \int_0^t (X_s(f^2) - X_s(f)^2) ds, \quad t \geq 0. \quad (3.4)$$

Accordingly,  $(X_t, \mathbf{Q}_\mu^0)$  defines a Fleming-Viot process with  $(A, \mathcal{D}(A))$  and  $\sigma = 0$ .

*Proof.* It is sufficient to show that  $M_t^0(f)N_t^{(2)}(\sigma)$  is a  $\mathbf{Q}_\mu^\sigma$ -martingale, from which it follows that  $M_t^0(f)$  is a  $\mathbf{Q}_\mu^0$ -martingale, and (3.4) is trivial. By the definition of  $N_t^{(2)}(\sigma)$  we have  $dN_t^{(2)}(\sigma) = -N_t^{(2)}(\sigma)dM_t^{(2)}(\sigma)$ . It follows from (1.2) and (3.2)

$$d\langle M(f), N^{(2)}(\sigma) \rangle_t = -N_t^{(2)}(\sigma) (X_t^{\otimes 2}(\sigma \cdot f \otimes 1) - X_t^{\otimes 3}(\sigma \otimes f)) dt.$$

Thus, by (3.1), (3.3) and Itô's formula

$$d(M_t^0(f)N_t^{(2)}(\sigma)) = M_t^0(f)dN_t^{(2)}(\sigma) + N_t^{(2)}(\sigma)dM_t^0(f),$$

which is a  $\mathbf{Q}_\mu^\sigma$ -martingale.  $\square$

Now let  $\mathcal{Q}^\sigma$  be a stationary distribution of the Fleming-Viot process with mutation operator  $A$  and selective density  $\sigma$ , and let  $\mathbf{Q}^\sigma$  be the corresponding stationary Markovian measure on  $\Omega$ . We denote by  $m_n$ ,  $n = 1, 2, \dots$ , the moment measures of  $\mathcal{Q}^\sigma$  defined by (2.1).

**Lemma 3.2** *Suppose that  $\{\varphi, \varphi_n : n = 1, 2, \dots\} \subset B_{sym}(E^2)$  are uniformly bounded and that  $\varphi_n \rightarrow \varphi$  in  $L^2(E^2; m_2)$  as  $n \rightarrow \infty$ . Then for any  $t \geq 0$  it holds that*

$$X_t^{\otimes 2}(\varphi_n) \rightarrow X_t^{\otimes 2}(\varphi), \quad M_t^{(2)}(\varphi_n) \rightarrow M_t^{(2)}(\varphi), \quad \langle M^{(2)}(\varphi_n) \rangle_t \rightarrow \langle M^{(2)}(\varphi) \rangle_t$$

in  $L^2(\Omega; \mathbf{Q}^\sigma)$  as  $n \rightarrow \infty$ .

*Proof.* The first convergence follows from

$$\mathbf{Q}^\sigma \{ |X_t^{\otimes 2}(\varphi_n) - X_t^{\otimes 2}(\varphi)|^2 \} \leq \mathbf{Q}^\sigma \{ X_t^{\otimes 2}(|\varphi_n - \varphi|^2) \} = m_2(|\varphi_n - \varphi|^2).$$

The second one also follows from

$$\begin{aligned} \mathbf{Q}^\sigma \{ (M_t^{(2)}(\varphi_n) - M_t^{(2)}(\varphi))^2 \} &= \mathbf{Q}^\sigma \{ \langle M^{(2)}(\varphi_n - \varphi) \rangle_t \} \\ &\leq \int_0^t \mathbf{Q}^\sigma \left\{ \int_E X_s(dx) (X_s((\varphi_n)_x - \varphi_x))^2 \right\} ds \\ &\leq \int_0^t 2\mathbf{Q}^\sigma \{ X_s^{\otimes 2}(|\varphi_n - \varphi|^2) \} ds \\ &= 2t m_2(|\varphi_n - \varphi|^2). \end{aligned}$$

The last convergence can be easily shown using

$$|\langle M^{(2)}(\varphi_n) \rangle_t - \langle M^{(2)}(\varphi) \rangle_t| \leq 2(\|\varphi_n\|_\infty + \|\varphi\|_\infty) \int_0^t X_s^{\otimes 2}(|\varphi_n - \varphi|) ds.$$

Thus we can complete the proof of Lemma 3.2.  $\square$

**Lemma 3.3** *If  $\mathcal{Q}^\sigma$  is a reversible stationary distribution of the Fleming-Viot process with mutation operator  $(A, \mathcal{D}(A))$  and selective density  $\sigma$ , then*

$$\mathcal{Q}^0(d\mu) := \left( \int_{M_1(E)} \exp\{-\nu^{\otimes 2}(\sigma)\} \mathcal{Q}^\sigma(d\nu) \right)^{-1} \exp\{-\mu^{\otimes 2}(\sigma)\} \mathcal{Q}^\sigma(d\mu) \quad (3.5)$$

*is a reversible stationary distribution of the Fleming-Viot process with mutation operator  $(A, \mathcal{D}(A))$  and  $\sigma = 0$ .*

*Proof.* Let  $\mathbf{Q}^0$  be the probability measure on  $\Omega$  of the Fleming-Viot process associated with  $(A, \mathcal{D}(A))$  and  $\sigma = 0$  starting at the initial distribution  $\mathcal{Q}^0$ . In order to see that  $\mathcal{Q}^0$  is a reversible stationary distribution of  $(X_t, \mathbf{Q}^0)$  it suffices to show

$$\mathbf{Q}^0 \{F(X_0, X_t)\} = \mathbf{Q}^0 (F(X_t, X_0)) \quad (3.6)$$

for all  $t \geq 0$  and bounded continuous functions  $F$  on  $M_1(E)$ . By Lemma 3.1 (3.6) is reduced to showing

$$\mathbf{Q}^\sigma \left\{ \exp\{-X_0^{\otimes 2}(\varphi)\} F(X_t, X_0) N_t^{(2)}(\varphi) \right\} = \mathbf{Q}^\sigma \left\{ \exp\{-X_0^{\otimes 2}(\varphi)\} F(X_0, X_t) N_t^{(2)}(\varphi) \right\} \quad (3.7)$$

for all  $\varphi \in B_{sym}(E^2)$ , since (3.6) follows from (3.7) with  $\varphi = \sigma$ .

We first assume that  $\varphi = f \otimes g + g \otimes f$  for some  $f, g \in \mathcal{D}(A)$ , then by Itô's formula we have

$$\frac{1}{2} (X_t^{\otimes 2}(\varphi) - X_0^{\otimes 2}(\varphi)) = M_t^{(2)}(\varphi) + \int_0^t G(\varphi; X_s) ds, \quad (3.8)$$

where

$$\begin{aligned} G(\varphi; X_s) &= X_s(f) (X_s(Ag) + X_s^{\otimes 2}(\sigma \cdot g \otimes 1) - X_s^{\otimes 3}(\sigma \otimes g)) \\ &\quad + X_s(g) (X_s(Af) + X_s^{\otimes 2}(\sigma \cdot f \otimes 1) - X_s^{\otimes 3}(\sigma \otimes f)) \\ &\quad + (X_s(fg) - X_s(f)X_s(g)). \end{aligned}$$

We rewrite (3.2) by using a function  $H(\varphi, \mu)$  defined on  $M_1(E)$  as follows:

$$\langle M^{(2)}(\varphi) \rangle_t = \int_0^t H(\varphi, X_s) ds. \quad (3.9)$$

Then from (3.8) and (3.9) it follows that

$$\begin{aligned} &\mathbf{Q}^\sigma \left\{ \exp\{-X_0^{\otimes 2}(\varphi)\} F(X_t, X_0) N_t^{(2)}(\varphi) \right\} \\ &= \mathbf{Q}^\sigma \left\{ \exp\{-X_0^{\otimes 2}(\varphi) - M_t^{(2)}(\varphi) - \frac{1}{2} \langle M^{(2)}(\varphi) \rangle_t\} F(X_t, X_0) \right\} \\ &= \mathbf{Q}^\sigma \left\{ \exp \left\{ -\frac{1}{2} (X_0^{\otimes 2}(\varphi) + X_t^{\otimes 2}(\varphi)) + \int_0^t (G(\varphi; X_s) - H(\varphi; X_s)) ds \right\} F(X_t, X_0) \right\}. \end{aligned}$$

Then (3.7) follows by the reversibility of  $\mathbf{Q}^\sigma$ . Clearly, the linear span of  $\{f \otimes g + g \otimes f : f, g \in \mathcal{D}(A)\}$  is dense in  $C_{0, sym}(E^2)$  with the supremum norm. Moreover, it is easy to see that for an arbitrary  $\varphi \in B_{sym}(E^2)$ , there exists a uniformly bounded sequence  $\{\varphi_n\} \in C_{0, sym}(E^2)$

that converges to  $\varphi$  with the  $L^2(E^2; m_2)$ -norm. Therefore by Lemma 3.2, (3.7) holds for every  $\varphi \in B_{sym}(E^2)$ ,  $\square$

Now we can complete the proof of Theorem 1.1 in the selective case. Suppose that there exists a reversible stationary distribution  $\mathcal{Q}^\sigma$  of the Fleming-Viot process associated with  $(A, \mathcal{D}(A))$  and  $\sigma$ . Then by Lemma 3.3  $\mathcal{Q}^0$  defined by (3.5) is a reversible stationary distribution of the non-selective Fleming-Viot process  $(X_t, \mathcal{Q}^0)$ . Therefore, by the result of the non-selective case in the previous section, we conclude that  $(A, \mathcal{D}(A))$  is of the form (4), which complete the proof of Theorem 1.1 in the selective case.  $\square$

## References

- [1] Dawson, D.A., *Measure-valued Markov Processes*, Ecole d'Eté de Probabilités de Saint-Flour XXI-1991, Lecture Notes Math. **1541**, 1-260, Springer-Verlag, 1993.
- [2] Dawson, D.A. and Hochberg, K.J., *Wandering random measures in the Fleming-Viot model*, Ann. Probab. **10** (1982), 554-580.
- [3] Ethier, S.N. and Kurtz, T.G., *Fleming-Viot processes in population genetics*, SIAM J. Contr. Opt. **31** (1993), 345-386.
- [4] Fleming, W.H. and Viot, M., *Some measure-valued Markov processes in population genetics theory*, Indiana Univ. Math. J. **28** (1979), 817-843.
- [5] Fukushima, M., *Dirichlet Forms and Markov Processes*, North-Holland, 1980.
- [6] Fukushima, M., Oshima, Y., Takeda, M., *Dirichlet forms and symmetric Markov processes*, Walter de Gruyter, 1994.
- [7] Ohta, T. and Kimura, M., *A model of mutation appropriate to estimate the number of electrophoretically detectable alleles in a finite population*, Genet. Res. Camb. **22** (1973), 201-204.
- [8] Walsh, J.B., *An Introduction to Stochastic Partial Differential Equations*, Ecole d'Eté de Probabilités de Saint-Flour XIV-1984, Lect. Notes Math. **1180** (1986), Springer-Verlag.