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Reversibility of Interacting Fleming–Viot Processes with Mutation, Selection, and Recombination

Shui Feng, Byron Schmuland, Jean Vaillancourt, and Xiaowen Zhou

Abstract. Reversibility of the Fleming–Viot process with mutation, selection, and recombination is well understood. In this paper, we study the reversibility of a system of Fleming–Viot processes that live on a countable number of colonies interacting with each other through migrations between the colonies. It is shown that reversibility fails when both migration and mutation are non-trivial.

1 Introduction

The Fleming–Viot process is a probability-measure-valued Markov process describing the evolution of the distribution of allelic types in a large population. It arises most naturally in population genetics as the limit in distribution of certain sequences of Markov chains undergoing mutation, natural selection, recombination, and random genetic drift.

Reversibility plays an important role in statistical inference in the neutral theory of population genetics. When reversibility holds, techniques used for future predictions can then be used to understand the starting distribution that leads to the present state. Several models, such as the Wright–Fisher Markov chain and the finite alleles Wright–Fisher diffusion, are reversible. The reversibility of the Fleming–Viot process with parent independent mutation was obtained in [3, 14]. On the other hand, reversibility is a very restrictive property. The results in [8, 10–12] show that the Fleming–Viot process is reversible only if the mutation, natural selection, and recombination have special forms.

The interacting Fleming–Viot process studied in this paper is a countable collection of Fleming–Viot processes that interact through geographical migration. It is the diffusion approximation to the stepping-stone model involving infinitely many alleles. Without migration, our system would simply be a collection of independent Fleming–Viot processes. The migration can be viewed as an external force acting upon the independent system of the Fleming–Viot processes. Since the internal reversible forces such as mutation and selection are constantly corrected by the external migration force, it is natural to expect the loss of reversibility in the interacting Fleming–Viot process due to competition between local forces and migration.

The long-time behavior of the interacting Fleming–Viot process is well known. In the absence of mutation, selection, and recombination, a complete characteriza-

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tion of stationary distributions were obtained in [13] for the two allele case and in [1] for the general case in terms of migration. In [15] (two allele) and [2] (general), the structures of the stationary distributions were investigated for models involving mutation, selection, and recombination. The recent work in [9], where a two island model was considered, shows the difficulty of obtaining the explicit expression of the nonreversible stationary distributions. In this paper we study the reversibility of the general Fleming–Viot process and investigate the interrelation between mutation, selection and recombination, and migration. Under very general hypotheses, we show that the interacting Fleming–Viot process with mutation, selection, recombination, and migration is irreversible. Our results cover all models in [1, 2, 13, 15].

2 Model

Let I be a countable index set where each element $\xi \in I$ labels a colony. The different genetic types of individuals in the population will be modelled by a compact metric space E. Let $M_1(E)$ denote the space of Borel probability measures on E, and let $M(E)$ be the space of finite signed Borel measures on E. We let $B(E)$ denote the space of bounded measurable functions on E, and $C(E)$ the space of continuous functions on E. For any μ in $M(E)$ and g in $B(E)$, we use the notation $\langle \mu, g\rangle = \int_E g(x)\,\mu(dx)$. Let

$$B(E)^I := \{\mathbf{f} = (f_\xi)_{\xi\in I} : f_\xi \in B(E)\}$$
$$M(E)^I := \{X = (X_\xi)_{\xi\in I} : X_\xi \in M(E)\}.$$

For X in $M(E)^I$ and $\mathbf{f}$ in $B(E)^I$, we write $\langle X, \mathbf{f}\rangle := \sum_{\xi\in I}\langle X_\xi, f_\xi\rangle$ whenever the sum converges. The state space for our process will be $M_1(E)^I \subseteq M(E)^I$.

For every ξ, ξ' in I, let $a(\xi, \xi')$ denote the migration probability from colony ξ to colony ξ'. We assume

$$a(\xi,\xi) = 0, \sum_{\xi'\in I} a(\xi,\xi') = 1. \tag{2.1}$$

Define the mutation operator $(A, \mathcal{D}(A))$ to be the generator of a conservative Feller semigroup (P_t) on $C(E)$. We assume that the domain $\mathcal{D}(A)$ of A is dense in $C(E)$.

The sets $C(E)^I$ and $\mathcal{D}(A)^I$ denote subsets of $B(E)^I$, where the coordinate functions are in $C(E)$ and $\mathcal{D}(A)$, respectively. Set

$$B(E)^I_0 := \{\mathbf{f} \in B(E)^I : f_\xi \equiv 0 \text{ for all } \xi \text{ outside a finite subset of } I\},$$

and define $C(E)^I_0$ and $\mathcal{D}(A)^I_0$ similarly.

For any symmetric bounded measurable function V on E^2, we define the selection operator $S\colon M_1(E) \to M(E)$ by

$$S(\mu)(du) := \left(\int_E V(u,v)\mu(dv) - \int_E\int_E V(v,w)\mu(dv)\mu(dw)\right)\mu(du).$$

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When two types u, v undergo recombination, the distribution of the resulting type is distributed according to the probability kernel $\eta(u, v; dw)$ so that $\eta(u, v; A)$ is bounded measurable with respect to (u, v) for any measurable subset A of E. The recombination operator $R\colon M_1(E) \to M(E)$ is given by

$$R(\mu)(du) := \int_E \int_E \eta(v, w; du)\mu(dv)\mu(dw) - \mu(du).$$

Let $\tilde{\mathcal{A}}$ be the algebra of functions on $M_1(E)^I$ given by the collection of linear combinations of functions of the form

$$F(X) := \prod_{i=1}^{m} \langle X_{\xi_i}, f_i \rangle, \tag{2.2}$$

where $m \geq 1$, $f_i \in B(E)$ for $1 \leq i \leq m$, and $(\xi_1, \dots, \xi_m) \in I^m$. Similarly, let $\mathcal{A}$ be the sub-algebra of $\tilde{\mathcal{A}}$, given by linear combinations of functions of the form (2.2) with $f_i \in \mathcal{D}(A)$ for $1 \leq i \leq m$. Note that both $\tilde{\mathcal{A}}$ and $\mathcal{A}$ are measure determining on $M_1(E)^I$.

For $F : M_1(E)^I \to \mathbb{R}$ we define partial derivatives as follows, whenever the limit exists:

$$\frac{\delta F(X)}{\delta X_\xi(u)} := \lim_{\varepsilon \downarrow 0} \frac{F(X^\varepsilon(\xi, u)) - F(X)}{\varepsilon} \quad \text{for } u \in E,\ \xi \in I,$$

with

$$(X^\varepsilon(\xi, u))_{\xi'} := \begin{cases} X_{\xi'} & \text{if } \xi' \neq \xi, \\ X_\xi + \varepsilon \delta_u & \text{if } \xi' = \xi. \end{cases}$$

This definition requires us to extend the domain of F infinitesimally from $M_1(E)^I$ to $M(E)^I$. For F in $\tilde{\mathcal{A}}$, this is done via (2.2).

For any u in E, let δ_u denote the Dirac measure with unit mass at u. For non-negative numbers s, r, ρ, the generator $\mathcal{L}_{s,r,\rho}$ of the interacting Fleming–Viot process incorporating migration, mutation, selection, and recombination is defined for $F \in \mathcal{A}$ by

$$\mathcal{L}_{s,r,\rho} F(X) := \mathcal{L}_{s,r} F(X) + \mathcal{L}_\rho F(X),$$

where

$$\mathcal{L}_\rho F(X) := \rho \sum_{\xi, \xi' \in I} a(\xi, \xi') \Big\langle X_{\xi'} - X_\xi, \frac{\delta F}{\delta X_\xi(\,\cdot\,)} \Big\rangle,$$

$$\begin{aligned} \mathcal{L}_{s,r} F(X) := \sum_{\xi \in I} \Big\langle X_\xi, A \frac{\delta F}{\delta X_\xi(\,\cdot\,)} \Big\rangle + s \sum_{\xi \in I} \Big\langle S(X_\xi), \frac{\delta F}{\delta X_\xi(\,\cdot\,)} \Big\rangle + r \sum_{\xi \in I} \Big\langle R(X_\xi), \frac{\delta F}{\delta X_\xi(\,\cdot\,)} \Big\rangle \\ + \frac{1}{2} \sum_{\xi \in I} \int_E \int_E \frac{\delta^2 F}{\delta X_\xi(u) \delta X_\xi(v)} Q_{X_\xi}(du, dv), \end{aligned}$$

and

$$Q_\mu(du,dv) := \mu(du)\delta_u(dv) - \mu(du)\mu(dv).$$

For $X \in M_1(E)^I$ and $\mathbf{f} \in \mathcal{D}(A)_0^I$, define

$$\langle b_\xi(X), f_\xi\rangle := \langle X_\xi, Af_\xi\rangle + \rho \sum_{\xi' \in I} a(\xi,\xi')\langle X_{\xi'} - X_\xi, f_\xi\rangle + \langle sS(X_\xi) + rR(X_\xi), f_\xi\rangle,$$

and let $\langle b(X), \mathbf{f}\rangle := \sum_{\xi \in I}\langle b_\xi(X), f_\xi\rangle$. The generator $\mathcal{L}_{s,r,\rho}$ can then be written as

$$\mathcal{L}_{s,r,\rho}F(X) = \Big\langle b(X), \frac{\delta F}{\delta X}\Big\rangle + \frac{1}{2}\sum_{\xi\in I}\int_E\int_E \frac{\delta^2 F}{\delta X_\xi(u)\delta X_\xi(v)}\, Q_{X_\xi}(du,dv), \tag{2.3}$$

where $\frac{\delta F}{\delta X} = \left(\frac{\delta F}{\delta X_\xi}\right)_{\xi\in I}$.

Theorem 2.1 *For each X in $M_1(E)^I$, the martingale problem associated with generator $(\mathcal{L}_{s,r,\rho}, \mathcal{A})$ starting at X is well-posed.*

Proof The case of $\rho = 0$, and the case of $A = 0, s = r = 0$ can be found respectively in [5] and [1]. The case of $r = 0$ was obtained in [7]. The general case was studied in [2], where the index set I is either the finite dimensional lattice or the hierarchical group, and the type space is the set of integers.

Even though the index set and state space in our model are more general, the proofs are similar to those used in [7] and [2]. For completeness, we sketch a proof below.

Following [6], define the following system of Wright–Fisher type Markov chains. For each colony ξ in I, consider a population of N individuals with types in the space E. The population evolves under the influence of mutation, selection, recombination, migration, and genetic drift. Future generations are formed as follows: each individual chooses a pair in the current generation as parents. The probability that a particular pair is chosen is weighted by the fitness (described by $V(x,y)$) of the pair. After the parents are selected, a recombination of the parent types occurs. The type created through recombination will change again, first through migration and then mutation. Existence for the martingale problem follows from the tightness of the empirical processes of approximating systems of Markov chains.

Uniqueness follows from the existence of a dual process. For any $m \geq 1$, let $B(E^m)$ be the set of all bounded measurable functions on E^m. Set

$$\mathcal{J} := \bigcup_{m=1}^{\infty}(B(E^m) \times I^m).$$

For each solution $X(t) = (X_\xi(t))$ to the martingale problem associated with $\mathcal{L}_{s,r,\rho}$, the law of $X(t)$ is determined by

$$F((f,\pi),X(t)) = E_{X(0)}\Big(\int_E \cdots \int_E f(u_1,\dots,u_m)X_{\xi_1}(t)(du_1)\cdots X_{\xi_m}(t)(du_m)\Big)$$

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for all (f,π) in $B(E^m)\times I^m$, $m\geq 1$.

For $F(X)=\prod_{i=1}^m\langle X_{\xi_i},f_i\rangle$ in $\mathcal{A}$, direct calculations give

$$(2.4)\ \mathcal{L}_{s,r,\rho}F(X)=\sum_{i=1}^m\Big\{\langle X_{\xi_i},Af_i\rangle+\langle sS(X_{\xi_i})+rR(X_{\xi_i}),f_i\rangle \\ +\rho\sum_{\xi'\in I}a(\xi_i,\xi')\langle X_{\xi'}-X_{\xi_i},f_i\rangle\Big\}\prod_{j\neq i}\langle X_{\xi_j},f_j\rangle \\ +\sum_{1\leq i<k\leq m,\xi_i=\xi_k}(\langle X_{\xi_i},f_if_k\rangle-\langle X_{\xi_i},f_i\rangle\langle X_{\xi_k},f_k\rangle)\prod_{j\neq i,k}\langle X_{\xi_j},f_j\rangle.$$

Define for $\pi=(\xi_1,\dots,\xi_m)$ in I^m, $m\geq 1$ and $f(u_1,\dots,u_m)=\prod_{i=1}^m f_i(u_i)$

$$X_\pi(du_1,\dots,du_m):=\prod_{i=1}^m X_{\xi_i}(du_i),$$
$$\tilde{\pi}^i:=(\xi_1,\dots,\xi_m,\xi_i),\ i=1,\dots,m,$$
$$\tilde{\pi}^{ii}:=(\xi_1,\dots,\xi_m,\xi_i,\xi_i),\ i=1,\dots,m,$$
$$\hat{\pi}^j:=(\xi_1,\dots,\xi_{j-1},\xi_{j+1},\dots,\xi_m),\ j=2,\dots,m,$$
$$\pi^{i,\xi}:=(\xi_1,\dots,\xi_{i-1},\xi,\xi_{i+1},\dots,\xi_m),$$

and

$$A^mf(u_1,\dots,u_m):=\sum_{i=1}^m Af_i(u_i)\prod_{j\neq i}f_j(u_j),$$
$$H_{im}f(u_1,\dots,u_m,u_{m+1},u_{m+2}):=(V(u_i,u_{m+1})-V(u_{m+1},u_{m+2}))f(u_1,\dots,u_m),$$
$$K_if(u_1,\dots,u_m,u_{m+1}):=\int_E f(u_1,\dots,\nu,u_{i+1},\dots,u_m)\eta(u_i,u_{m+1};d\nu) \\ -f(u_1,\dots,u_m).$$

Then (2.4) can be written as

$$\mathcal{L}_{s,r,\rho}F(X)=\langle X_\pi,A^mf\rangle \\ +\sum_{i=1}^m\Big\{s\langle X_{\tilde{\pi}^{ii}},H_{im}f\rangle+r\langle X_{\tilde{\pi}^i},K_if\rangle+\rho\sum_{\xi'\in I}a(\xi_i,\xi')\langle X_{\pi^{i,\xi'}}-X_\pi,f\rangle\Big\} \\ +\sum_{1\leq i<k\leq m,\xi_i=\xi_k}(\langle X_{\hat{\pi}^k},\Phi_{ik}f\rangle-\langle X_\pi,f\rangle),$$

where $\Phi_{ik}f$ is the function in $B(E^{m-1})$ that is obtained from f by replacing u_k with u_i and relabeling the variables.

The dual process (f_t,π_t) is an $\mathcal{J}$-valued process, starting from $(f_0,\pi_0)=(f,\pi)$, that involves the following transitions:

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- Coordinates of π_t are independent continuous time Markov chains on I with transition rate $(\rho a(\xi,\xi'))_{\xi,\xi'\in I}$.
- Any two coordinates of π_t that are the same will coalesce into one element at the same site with rate one.
- At rate s a coordinate of π_t will create two copies of itself so that the size $|\pi_t|$ of π_t is increased by two.
- At rate r a coordinate of π_t will create a copy of itself so that the size of π_t is increased by one.
- f_0 is in $C(E^{|\pi_0|})$; between transitions of π_t, f_t follows a deterministic path determined by the semigroup associated with $|\pi_t|$ independent copies of A-motion.
- At the time of coalescence, the corresponding variables in f_t are set equal, which results in a jump from space $C(E^{|\pi_{t-}|})$ to space $C(E^{|\pi_{t-}|-1})$.
- If two new coordinates are created when the current number of variables is m, then we have

$$f(u_1,\dots,u_m) \to (V(u_i,u_{m+1}) - V(u_{m+1},u_{m+2}))f(u_1,\dots,u_m).$$

- If one new coordinate is created when the current number of variables is m, then we have

$$f(u_1,\dots,u_m) \to \int_E f(u_1,\dots,u_{i-1},\nu,u_{i+1}\dots,u_m)\eta(u_i,u_{m+1};d\nu).$$

The uniqueness now follows from the following duality relation

$$E_{X(0)}\big[\langle X_\pi(t), f\rangle\big] = E_{(f,\pi)}\big[\langle X_{\pi_t}(0), f_t\rangle\, e^{s\int_0^t |\pi_u|du}\big]. \qquad \blacksquare$$

3 Quasi-Invariance and the Cocycle Identity

In this section we prove the main result of the paper relating the reversibility of probability measures on $M_1(E)$ with their quasi-invariance. These results generalize those proved by Handa for the single site Fleming–Viot process. In the sections that follow, we will show that reversibility is a very restrictive condition that only applies to very special cases of the Fleming–Viot model.

Definition 3.1 A probability measure Π on $M_1(E)$ is reversible with respect to the Fleming–Viot operator $(\mathcal{L}_{s,r,\rho},\mathcal{A})$ if for $\Phi,\Psi\in\mathcal{A}$,

$$\int \mathcal{L}_{s,r,\rho}\Phi(X)\Psi(X)\,\Pi(dX) = \int \mathcal{L}_{s,r,\rho}\Psi(X)\Phi(X)\,\Pi(dX).$$

For each $\mathbf{f}$ in $C(E)^I$, define a map $S_{\mathbf{f}} : M_1(E)^I \to M_1(E)^I$ by $S_{\mathbf{f}}(X) = (X_\xi^{f_\xi})_{\xi\in I}$, where

$$X_\xi^{f_\xi}(dv) := \frac{e^{f_\xi(v)}X_\xi(dv)}{\langle X_\xi, e^{f_\xi}\rangle}.$$

It follows from the definition that $S_{\mathbf{f}}(S_{\mathbf{g}}) = S_{\mathbf{f}+\mathbf{g}}$ for any $\mathbf{f},\mathbf{g}$ in $C(E)^I$. For any $\mathbf{f}$ in $C(E)^I$ and probability measure Π on $M_1(E)^I$, set $\Pi^{\mathbf{f}}(\cdot) := \Pi(S_{\mathbf{f}}(\cdot))$.

The probability Π is called *quasi-invariant* for $\mathcal{D}(A)_0^I$ if for any $\mathbf{f} \in \mathcal{D}(A)_0^I$, the measures $\Pi^{\mathbf{f}}$ and Π are mutually absolutely continuous with

$$\frac{d\Pi^{\mathbf{f}}}{d\Pi}(X) = \exp\{\Lambda(\mathbf{f}, X)\},$$

where $\Lambda : \mathcal{D}(A)_0^I \times M_1(E)^I \mapsto \mathbb{R}$ is called the *cocycle* associated with Π.

A direct result of the quasi-invariance is the following *cocycle identity*: for any $\mathbf{f}, \mathbf{g} \in \mathcal{D}(A)_0^I$, for Π almost all X,

$$\Lambda(\mathbf{f} + \mathbf{g}, X) = \Lambda(\mathbf{f}, S_{\mathbf{g}}(X)) + \Lambda(\mathbf{g}, X). \tag{3.1}$$

The *carré du champ* associated with the operator $\mathcal{L}_{s,r,\rho}$ is defined by

$$\Gamma(\Phi, \Psi) = \tfrac{1}{2}\big(\mathcal{L}_{s,r,\rho}(\Phi\Psi) - \Phi\mathcal{L}_{s,r,\rho}(\Psi) - \mathcal{L}_{s,r,\rho}(\Phi)\Psi\big), \quad \Phi, \Psi \in \mathcal{A}. \tag{3.2}$$

For any two functions f, g in $B(E)$, set $(f \otimes g)(u, v) := f(u)g(v)$. By an argument similar to that used in the proof of [8, Lemma 3.1], we obtain the following result.

Lemma 3.2 *For $\Phi, \Psi \in \mathcal{A}$ and $X \in M_1(E)^I$,*

$$\Gamma(\Phi, \Psi)(X) = \frac{1}{2}\sum_{\xi \in I}\Big\langle Q_{X_\xi}, \frac{\delta\Phi(X)}{\delta X_\xi} \otimes \frac{\delta\Psi(X)}{\delta X_\xi}\Big\rangle, \tag{3.3}$$

and for $\Phi, \Psi_1, \Psi_2 \in \mathcal{A}$,

$$\Gamma(\Phi\Psi_1, \Psi_2) + \Gamma(\Phi\Psi_2, \Psi_1) - \Gamma(\Phi, \Psi_1\Psi_2) = 2\Phi\Gamma(\Psi_1, \Psi_2). \tag{3.4}$$

Lemma 3.3 *The probability measure Π is reversible with respect to $\mathcal{L}_{s,r,\rho}$ if and only if*

$$-\frac{1}{2}\int\Big\langle Q_{X_\xi}, \frac{\delta\Phi(X)}{\delta X_\xi} \otimes f_\xi\Big\rangle \Pi(dX) = \int \Phi(X)\langle b_\xi(X), f_\xi\rangle \Pi(dX) \tag{3.5}$$

for any $\Phi \in \mathcal{A}$, $\xi \in I$, and $f_\xi \in \mathcal{D}(A)$.

Proof Assume that Π is reversible with respect to $\mathcal{L}_{s,r,\rho}$. For a fixed ξ in I, let $\Psi(X) = \langle X_\xi, f_\xi\rangle$. It follows from (2.3) that $\mathcal{L}_{s,r,\rho}\Psi(X) = \langle b_\xi(X), f_\xi\rangle$. This, combined with Lemma 3.2 and reversibility, implies (3.5).

Next we assume that (3.5) holds. First we show, by induction on n, that for any $n \geq 1$

$$\int \Phi(X)\mathcal{L}_{s,r,\rho}\Psi^{(n)}(X)\,\Pi(dX) = -\int \Gamma(\Phi, \Psi^{(n)})(X)\,\Pi(dX), \tag{3.6}$$

for any $\Phi \in \mathcal{A}$, $f_i \in \mathcal{D}(A)$, $\xi_i \in I$, $i = 1, \dots, n$, and

$$\Psi^{(n)}(X) := \prod_{i=1}^{n} \Psi_i(X) := \prod_{i=1}^{n} \langle X_{\xi_i}, f_i\rangle.$$

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The case of $n = 1$ follows from (3.3) and (3.5). Assume that (3.6) holds for $n \leq k$. It follows from (3.2) and (3.4) that

$$\begin{aligned}\Phi\mathcal{L}_{s,r,\rho}(\Psi^{(k+1)}) &= \Phi[2\Gamma(\Psi^{(k)}, \Psi_{k+1}) + \Psi_{k+1}\mathcal{L}_{s,r,\rho}(\Psi^{(k)}) + \Psi^{(k)}\mathcal{L}_{s,r,\rho}\Psi_{k+1}] \\ &= \Gamma(\Phi\Psi^{(k)}, \Psi_{k+1}) + \Phi\Psi^{(k)}\mathcal{L}_{s,r,\rho}\Psi_{k+1} \\ &\quad + \Gamma(\Phi\Psi_{k+1}, \Psi^{(k)}) + \Phi\Psi_{k+1}\mathcal{L}_{s,r,\rho}(\Psi^{(k)}) - \Gamma(\Phi, \Psi^{(k+1)})\end{aligned}$$

which implies that

$$\int \Phi(X)\mathcal{L}_{s,r,\rho}(\Psi^{(k+1)})(X)\Pi(dX) = -\int \Gamma(\Phi, \Psi^{(k+1)})(X)\Pi(dX).$$

It follows from (3.6) that for any Φ, Ψ in $\mathcal{A}$,

$$\int \Phi(X)\mathcal{L}_{s,r,\rho}\Psi(X)\Pi(dX) = -\int \Gamma(\Psi, \Phi)(X)\Pi(dX);$$

and by symmetry,

$$\int \Psi(X)\mathcal{L}_{s,r,\rho}\Phi(X)\Pi(dX) = \int \Phi(X)\mathcal{L}_{s,r,\rho}\Psi(X)\Pi(dX).$$

Therefore, Π is reversible with respect to $\mathcal{L}_{s,r,\rho}$. ■

Lemma 3.4 *Suppose* $\mathbf{f} \in C(E)^I$ *and put* $X_t := S_{-t\mathbf{f}}X$ *for* $X \in M_1(E)^I$ *and* $t \in \mathbb{R}$. *For every* $\Phi \in \tilde{\mathcal{A}}$ *we have*

$$\frac{d}{dt}\Phi(X_t) = -\sum_{\xi\in I}\Big\langle Q_{X_\xi}, f_\xi \otimes \frac{\delta\Phi(X_t)}{\delta X_\xi}\Big\rangle. \tag{3.7}$$

Proof Since both sides of the equation are linear, it suffices to prove the result for functions of the form $\Phi(X) = \prod_{i=1}^m \langle X_{\xi_i}, g_i\rangle$, where m a positive integer, $(\xi_i)_{1\leq i\leq m}$ in I, and $g_i \in B(E)$. But both sides of the equation are also derivations in Φ, so it suffices to take $m = 1$. But in this case, (3.7) follows from an easy calculation or [8, Lemma 3.3]. ■

For $\mathbf{f} \in \mathcal{D}(A)_0^I$ and $X \in M_1(E)^I$, we let

$$\Lambda(\mathbf{f}, X) := 2\int_0^1 \langle b(S_{s\mathbf{f}}X), \mathbf{f}\rangle\, ds. \tag{3.8}$$

Lemma 3.5 *Suppose* $\mathbf{f} \in \mathcal{D}(A)_0^I$, *and put* $X_t = S_{-t\mathbf{f}}X$ *for* $X \in M_1(E)^I$ *and* $t \in \mathbb{R}$. *Then we can write*

$$\Lambda(t\mathbf{f}, X_t) = 2\int_0^t \langle b(X_s), \mathbf{f}\rangle\, ds.$$

Proof

$$\begin{aligned}\Lambda(t\mathbf{f}, X_t) &= 2\int_0^1 \langle b(S_{st\mathbf{f}}X_t), t\mathbf{f}\rangle\, ds = 2t\int_0^1 \langle b(S_{-(1-s)t\mathbf{f}}X), \mathbf{f}\rangle\, ds \\ &= 2t\int_0^1 \langle b(S_{-st\mathbf{f}}X), \mathbf{f}\rangle\, ds = 2\int_0^t \langle b(S_{-s\mathbf{f}}X), \mathbf{f}\rangle\, ds. \qquad \blacksquare\end{aligned}$$

The following lemma proves formula (3.7) for certain functions $F \notin \tilde{\mathcal{A}}$.

Lemma 3.6 *Suppose $\mathbf{f} \in C(E)_0^I$, and put $X_t = S_{-t\mathbf{f}}X$ for $X \in M_1(E)^I$ and $t \in \mathbb{R}$. For $h \in C(E)$ and the sequence $c(\xi)$ satisfying $\sum_{\xi\in I} |c(\xi)| < \infty$, define $F : M_1(E)^I \to \mathbb{R}$ by*

$$F(X) := \Big\langle \sum_{\xi\in I} c(\xi)X_\xi, h\Big\rangle.$$

Then

$$\frac{d}{dt}F(X_t) = -\sum_{\xi\in I}\Big\langle Q_{X_\xi},\ f_\xi \otimes \frac{\delta F(X_t)}{\delta X_\xi}\Big\rangle. \tag{3.9}$$

Proof Let I_0 be a finite subset of I such that $f_\xi = 0$ for $\xi \notin I_0$. Define

$$F_0(X) := \Big\langle \sum_{\xi\in I_0} c(\xi)X_\xi, h\Big\rangle.$$

Clearly $F_0 \in \tilde{\mathcal{A}}$. Also, $(X_t)_\xi = X_\xi$ for $\xi \notin I_0$, so those terms have a zero time derivative. Therefore, $\frac{d}{dt}F(X_t) = \frac{d}{dt}F_0(X_t)$. It follows from direct calculation that

$$\frac{\delta F_0(X_t)}{\delta X_\xi} = \begin{cases} \frac{\delta F(X_t)}{\delta X_\xi} & \text{if } \xi \in I_0, \\ 0 & \text{if } \xi \notin I_0. \end{cases}$$

Since $f_\xi \equiv 0$ for $\xi \notin I_0$, this gives

$$\begin{aligned}\sum_{\xi\in I}\Big\langle Q_{X_\xi},\ f_\xi \otimes \frac{\delta F(X_t)}{\delta X_\xi}\Big\rangle &= \sum_{\xi\in I_0}\Big\langle Q_{X_\xi},\ f_\xi \otimes \frac{\delta F(X_t)}{\delta X_\xi}\Big\rangle \\ &= \sum_{\xi\in I_0}\Big\langle Q_{X_\xi},\ f_\xi \otimes \frac{\delta F_0(X_t)}{\delta X_\xi}\Big\rangle \\ &= \sum_{\xi\in I}\Big\langle Q_{X_\xi},\ f_\xi \otimes \frac{\delta F_0(X_t)}{\delta X_\xi}\Big\rangle,\end{aligned}$$

which, combined with Lemma 3.4, implies the result. ■

Remark By taking the bounded pointwise limit, it can be shown that (3.9) holds for $F(\mu) = \langle b(\mu), \mathbf{f}\rangle$ for any $\mathbf{f}$ in $C(E)^I$. More details are found in Part 1 of the Appendix.

Theorem 3.7 *If the probability measure Π in $M_1(M_1(E)^I)$ is reversible with respect to $\mathcal{L}_{s,r,\rho}$, then Π is quasi-invariant for $\mathcal{D}(A)_0^I$ with cocycle $\Lambda(\mathbf{f}, X)$ given by* (3.8).

Proof Assume that $\Pi \in M_1(M_1(E)^I)$ is reversible with respect to $\mathcal{L}_{s,r,\rho}$, and fix $\mathbf{f} \in \mathcal{D}(A)_0^I$. We must show that

$$\int F(X)\,(S_{\mathbf{f}}\Pi)(dX) = \int F(S_{-\mathbf{f}}X)\,\Pi(dX) = \int F(X)e^{\Lambda(\mathbf{f},X)}\,\Pi(dX)$$

for sufficiently many functions $F : M_1(E)^I \to \mathbb{R}$. Since $\exp(-\Lambda(\mathbf{f}, X))$ is strictly positive and $\mathcal{A}$ is measure determining, it suffices to prove that for any $\Phi \in \mathcal{A}$

$$\int \Phi(S_{-\mathbf{f}}X)e^{-\Lambda(\mathbf{f},S_{-\mathbf{f}}X)}\,\Pi(dX) = \int \Phi(X)\,\Pi(dX).$$

In what follows we shall show that

$$Z(t) := \int \Phi(S_{-t\mathbf{f}}X)e^{-\Lambda(t\mathbf{f},S_{-t\mathbf{f}}X)}\,\Pi(dX)$$

is a constant function of $t \in \mathbb{R}$. Setting

$$\tilde{\Phi}_t(X) := \Phi(X_t)e^{-\Lambda(t\mathbf{f},X_t)} = \Phi(S_{-t\mathbf{f}}X)e^{-\Lambda(t\mathbf{f},S_{-t\mathbf{f}}X)},$$

and noting that $\Lambda(t\mathbf{f}, X_t) = 2\int_0^t \langle b(X_s), \mathbf{f}\rangle\, ds$, we have

$$\frac{\delta\tilde{\Phi}_t(X)}{\delta X_\xi}(u) = \frac{\delta\Phi(X_t)}{\delta X_\xi}(u)e^{-\Lambda(t\mathbf{f},X_t)} - 2\tilde{\Phi}_t(X)\int_0^t \frac{\delta\langle b(X_s), \mathbf{f}\rangle}{\delta X_\xi}(u)\,ds. \tag{3.10}$$

It follows that

$$\begin{aligned}
&\sum_{\xi\in I}\Big\langle Q_{X_\xi},\ f_\xi \otimes \frac{\delta\tilde{\Phi}_t(X)}{\delta X_\xi}\Big\rangle \\
&= \sum_{\xi\in I}\Big\langle Q_{X_\xi},\ f_\xi \otimes \frac{\delta\Phi(X_t)}{\delta X_\xi}\Big\rangle e^{-\Lambda(t\mathbf{f},X_t)} - 2\tilde{\Phi}_t(X)\int_0^t \sum_{\xi\in I}\Big\langle Q_{X_\xi},\ f_\xi \otimes \frac{\delta\langle b(X_s), \mathbf{f}\rangle}{\delta X_\xi}\Big\rangle\,ds \\
&= -\frac{d}{dt}\Phi(X_t)\,e^{-\Lambda(t\mathbf{f},X_t)} + 2\tilde{\Phi}_t(X)\int_0^t \frac{d}{ds}\big\langle\, b(X_s), \mathbf{f}\big\rangle\,ds \\
&= -\frac{d}{dt}\Phi(X_t)\,e^{-\Lambda(t\mathbf{f},X_t)} + 2\tilde{\Phi}_t(X)\big(\langle b(X_t), \mathbf{f}\rangle - \langle b(X), \mathbf{f}\rangle\big),
\end{aligned}$$

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where Lemma 3.4, Lemma 3.6, and the remark after Lemma 3.6 are used for obtaining the second equality. Therefore,

$$\begin{aligned}
Z'(t) &= \int \Big(\frac{d}{dt}\Phi(X_t)\, e^{-\Lambda(t\mathbf{f},X_t)} + \Phi(X_t)\frac{d}{dt}e^{-\Lambda(t\mathbf{f},X_t)}\Big)\,\Pi(dX) \\
&= \int \Big(-\sum_{\xi\in I}\Big\langle Q_{X_\xi},\ f_\xi \otimes \frac{\delta\tilde{\Phi}_t(X)}{\delta X_\xi}\Big\rangle + 2\tilde{\Phi}_t(X)\big(\langle b(X_t),\mathbf{f}\rangle - \langle b(X),\mathbf{f}\rangle\big) \\
&\qquad\qquad - 2\tilde{\Phi}_t(X)\langle b(X_t),\mathbf{f}\rangle\Big)\,\Pi(dX) \\
&= -\int \sum_{\xi\in I}\Big\langle Q_{X_\xi},\ f_\xi \otimes \frac{\delta\tilde{\Phi}_t(X)}{\delta X_\xi}\Big\rangle\,\Pi(dX) - 2\int \tilde{\Phi}_t(X)\langle b(X),\mathbf{f}\rangle\,\Pi(dX).
\end{aligned}$$

By reversibility and Lemma 3.3,

$$\int \sum_{\xi\in I}\Big\langle Q_{X_\xi},\ f_\xi \otimes \frac{\Phi(X)}{\delta X_\xi}\Big\rangle\,\Pi(dX) + 2\int \langle b(X),\mathbf{f}\rangle\Phi(X)\,\Pi(dX) = 0, \tag{3.11}$$

for $\Phi \in \mathcal{A}$. In the Appendix, we introduce a space of functions $\mathcal{H}$ that contains $\mathcal{A}$, and show that $\tilde{\Phi}_t(X) \in \mathcal{H}$ and (3.11) holds for all Φ in $\mathcal{H}$. These imply that $Z'(t) = 0$. Therefore, $Z(1) = Z(0)$ and the theorem follows from

$$\int \Phi(S_{-\mathbf{f}}X)e^{-\Lambda(\mathbf{f},S_{-\mathbf{f}}X)}\,\Pi(dX) = Z(1) = Z(0) = \int \Phi(X)\Pi(dX). \qquad \blacksquare$$

Theorem 3.8 *If the probability measure Π in $M_1(M_1(E)^I)$ is quasi-invariant for $\mathcal{D}(A)_0^I$ with cocycle given by* (3.8)*, then Π is reversible with respect to $\mathcal{L}_{s,r,\rho}$.*

Proof Suppose that Π is quasi-invariant with cocycle given by (3.8). Then for any $\xi \in I$ and $\mathbf{f}$ in $C(E)^I$ such that $f_\xi \in \mathcal{D}(A)$ and $f_{\xi'} = 0$ for $\xi' \neq \xi$, the function

$$Z(t) = \int \Phi(S_{-t\mathbf{f}}X)e^{-\Lambda(t\mathbf{f},S_{-t\mathbf{f}}X)}\,\Pi(dX)$$

is constant in $t \in \mathbb{R}$. Noting that

$$0 = Z'(0) = -\int \sum_{\xi\in I}\Big\langle Q_{X_\xi}, f_\xi \otimes \frac{\delta\Phi(X)}{\delta X_\xi}\Big\rangle\,\Pi(dX) - 2\int \Phi(X)\langle b(X),\mathbf{f}\rangle\,\Pi(dX),$$

and f_ξ is arbitrary in $\mathcal{D}(A)$, the theorem follows from Lemma 3.3. $\blacksquare$

4 Consequences of the Cocycle Identity

It follows from the cocycle identity (3.1) that for any X in $M_1(E)^I$ and any $\mathbf{f},\mathbf{g} \in \mathcal{D}(A)_0^I$,

$$\Lambda\big(\mathbf{f}, S_{\mathbf{g}}(X)\big) - \Lambda(\mathbf{f},X) = \Lambda\big(\mathbf{g}, S_{\mathbf{f}}(X)\big) - \Lambda(\mathbf{g},X). \tag{4.1}$$

For any two distinct ξ_1, ξ_2 in I, and f, g in $\mathcal{D}(A)$, let $\mathbf{f} = (f_\xi)$ and $\mathbf{g} = (g_\xi)$ be such that $f_{\xi_1} = f$, $f_\xi = 0$ for $\xi \neq \xi_1$, and $g_{\xi_2} = g$, $g_\xi = 0$ for $\xi \neq \xi_2$. By direct calculation,

$$\begin{aligned}\Lambda(\mathbf{f}, X) &= 2\int_0^1 \Big\{ \langle S_{u\mathbf{f}}(X)_{\xi_1}, Af\rangle + s\Big\langle S(S_{u\mathbf{f}}(X)_{\xi_1}), f\Big\rangle \\ &\quad + r\Big\langle R(S_{u\mathbf{f}}(X)_{\xi_1}), f\Big\rangle + \rho\sum_{\xi'} a(\xi_1,\xi')\Big\langle S_{u\mathbf{f}}(X)_{\xi'} - S_{u\mathbf{f}}(X)_{\xi_1}, f\Big\rangle \Big\}\, du \\ &= 2\int_0^1 \Big\{ \langle X^{uf}_{\xi_1}, Af\rangle + s\langle S(X^{uf}_{\xi_1}), f\rangle \\ &\quad + r\Big\langle R(X^{uf}_{\xi_1}), f\Big\rangle + \rho\sum_{\xi'\neq\xi_1} a(\xi_1,\xi')\langle X_{\xi'} - X^{uf}_{\xi_1}, f\rangle\Big\}\, du,\end{aligned}$$

and

$$\begin{aligned}\Lambda(\mathbf{f}, S_{\mathbf{g}}(X)) &= 2\int_0^1 \Big\{ \Big\langle S_{u\mathbf{f}+\mathbf{g}}(X)_{\xi_1}, Af\Big\rangle + s\Big\langle S(S_{u\mathbf{f}+\mathbf{g}}(X)_{\xi_1}), f\Big\rangle \\ &\quad + r\Big\langle R(S_{u\mathbf{f}} + \mathbf{g}(X)_{\xi_1}), f\Big\rangle \\ &\quad + \rho\sum_{\xi'} a(\xi_1,\xi')\Big\langle S_{u\mathbf{f}+\mathbf{g}}(X)_{\xi'} - S_{u\mathbf{f}+\mathbf{g}}(X)_{\xi_1}, f\Big\rangle\Big\}\, du \\ &= 2\int_0^1 \Big\{ \langle X^{uf}_{\xi_1}, Af\rangle + s\langle S(X^{uf}_{\xi_1}), f\rangle + r\langle R(X^{uf}_{\xi_1}), f\rangle \\ &\quad + \rho\sum_{\xi'\neq\xi_1,\xi_2} a(\xi_1,\xi')\langle X_{\xi'} - X^{uf}_{\xi_1}, f\rangle + \rho a(\xi_1,\xi_2)\langle X^g_{\xi_2} - X^{uf}_{\xi_1}, f\rangle\Big\}\, du,\end{aligned}$$

which leads to

$$\Lambda\big(\mathbf{f}, S_{\mathbf{g}}(X)\big) - \Lambda(\mathbf{f}, X) = 2\rho a(\xi_1,\xi_2)\langle X^g_{\xi_2} - X_{\xi_2}, f\rangle. \tag{4.2}$$

Together, (4.1) and (4.2) imply that for $\rho > 0$

$$a(\xi_1,\xi_2)\langle X^g_{\xi_2} - X_{\xi_2}, f\rangle = a(\xi_2,\xi_1)\langle X^f_{\xi_1} - X_{\xi_1}, g\rangle. \tag{4.3}$$

Let Δ be the set of Dirac measures on E, and

$$\hat{I} := \{\xi \in I : \text{there exists } \ \eta \in I, \text{ such that } a(\eta,\xi) > 0\}.$$

It follows from (2.1) that the set $\hat{I}$ is not empty.

Lemma 4.1 *Suppose that Π is a reversible probability measure with respect to $\mathcal{L}_{s,r,\rho}$ with $\rho > 0$. Then for any $\xi \in \hat{I}$, X_ξ is a Dirac measure with Π probability one,* i.e,

$$\Pi\{X_\xi \in \Delta\} = 1. \tag{4.4}$$

Proof Let C be a countable dense subset of E. By definition, for each ξ in $\hat{I}$, there exists ξ' in I such that $a(\xi',\xi) > 0$. Assume that with positive Π probability, X_ξ is not a Dirac measure. For any two distinct elements c_1, c_2 in C, and any positive rational numbers r_1, r_2 satisfying $r_1 + r_2 < d(c_1, c_2)$, let

$$D(c_1, c_2; r_1, r_2) := \{X \in M_1(E)^I : X_\xi(B(c_1, r_1)) > 0, X_\xi(B(c_2, r_2)) > 0\},$$

where $B(c_i, r_i)$ denotes the open ball in E with center c_i and radius r_i. Clearly,

$$\bigcup_{c_1,c_2;r_1,r_2} D(c_1, c_2, r_1, r_2) = \{X \in M_1(E)^I : X_\xi \neq \delta_u, \forall u \in E\}.$$

Therefore, we can find rational numbers c_1, c_2, r_1, r_2 such that $\Pi\{D(c_1, c_2, r_1, r_2)\} > 0$. Choose a nonnegative continuous function f such that $f(x) = 0$ for $x \in B(c_1, r_1)$ and $f(x) > 0$ for $x \in B(c_2, r_2)$. For any $X \in D(c_1, c_2; r_1, r_2)$, observe that $\langle X_\xi, e^f\rangle > 1$. When the signed measure $X_\xi - X_\xi^f$ is restricted to set $B(c_1, r_1)$, we have

$$X_\xi - X_\xi^f = \left(1 - \langle X_\xi, e^f\rangle^{-1}\right) X_\xi,$$

which is a measure on $B(c_1, r_1)$ with strictly positive total mass. Let g be any continuous function such that $g(x) > 0$ for $x \in B(c_1, r_1)$ and $g(x) = 0$ for $x \notin B(c_1, r_1)$.

For any $h \in C(E)$ and any positive integer k, define

$$h^{(k)} := k \int_0^{\frac{1}{k}} P_s h ds.$$

Then $\|h^{(k)} - h\|_\infty \to 0$, $h^{(k)} \in \mathcal{D}(A)$ and $Ah^{(k)} = k(P_{1/k}h - h) \in C(E)$.

By dominated convergence theorem, we have

$$\lim_{k\to\infty} \langle X_\xi - X_\xi^{f^{(k)}}, ng^{(k)}\rangle = \langle X_\xi - X_\xi^f, ng\rangle = \langle X_\xi - X_\xi^f, ng 1_{B(c_1,r_1)}\rangle$$

and

$$\lim_{k\to\infty} \langle X_{\xi'} - X_{\xi'}^{ng^{(k)}}, f^{(k)}\rangle = \langle X_{\xi'} - X_{\xi'}^{ng}, f\rangle \leq \|f\|_\infty$$

for all n. Choosing $\xi' = \xi_2, \xi = \xi_1$, $f = f^{(k)}, g = ng^{(k)}$ in (4.3), and taking the limit in the order of $k \to \infty$ and $n \to \infty$, gives a contradiction. ■

Remark It follows from the above lemma that for each ξ in $\hat{I}$, there is a random variable x_ξ taking values in E such that $X_\xi = \delta_{x_\xi}$ almost surely under Π.

Lemma 4.2 *Suppose that $\rho > 0$ and Π is a reversible measure with respect to $\mathcal{L}_{s,r,\rho}$. For each ξ in I, let $I_\xi = \{\xi' \in I : a(\xi, \xi') > 0\}$. Then for $\xi \in \hat{I}$, we have $\Pi\{x_\xi = x_{\xi'}\} = 1$, for all $\xi' \in I_\xi$.*

Proof By Lemma 4.1, for Π almost all X, we have $X_{\xi'} = \delta_{x_{\xi'}}$ for any $\xi' \in I_\xi$. For $f, g \in \mathcal{D}(A)$, set $\Phi(X) = \langle X_\xi, f\rangle$ and $\Psi(X) = \langle X_\xi, g\rangle$. The reversibility, combined with Lemma 3.2, implies

$$-\int \Psi(X)\mathcal{L}_{s,r,\rho}\Phi(X)\Pi(dX) = \frac{1}{2}\int \langle Q_{X_\xi}, f \otimes g\rangle \Pi(dX) = 0, \tag{4.5}$$

since Q_{X_ξ} is the zero measure when X_ξ is a delta mass.

Then for any $f, g \in \mathcal{D}(A)$, equation (4.5) gives

$$\int g(x_\xi)\Big[\sum_{\xi'\neq\xi} \rho a(\xi,\xi')\big(f(x_{\xi'}) - f(x_\xi)\big) + Af(x_\xi) + \tilde{R}f(x_\xi)\Big]\ \Pi(dX) = 0, \tag{4.6}$$

where

$$\tilde{R}f(x) := r\Big[\int f(u)\eta(x,x;du) - f(x)\Big], \quad x \in E.$$

For any $c \in E$ and $0 < r < r'$, choose a sequence of continuous functions (f_m) on E such that $0 \le f_m \le 1$ and $f_m(x) = 1$ for $x \in \bar{B}(c,r')$ and f_m converges, pointwise, to $1_{\bar{B}(c,r')}$, where $\bar{B}(c,r')$ denotes the closed ball with center c and radius r'; also choose a sequence of continuous functions (g_n) on E such that $0 \le g_n \le 1$, $g_n(x) = 1$ for $x \in \bar{B}(c,r)$, g_n has its support in $\bar{B}(c,r')$, and g_n converges pointwise to $1_{\bar{B}(c,r)}$.

By the maximal principle for A, we have $Af_m^{(k)}(x) \le 0$ for $x \in \bar{B}(c,r')$, so that for m, n, k, k',

$$\int g_n^{(k')}(x_\xi)Af_m^{(k)}(x_\xi)\,\Pi(dX) \le 0. \tag{4.7}$$

Since $g_n^{(k')}$ converges pointwise to g_n as $k' \to \infty$ and $f_m^{(k)}$ converges pointwise to f_m as $k \to \infty$, taking limits in the order of $k' \to \infty$, $k \to \infty$, $m \to \infty$, and $n \to \infty$, we first have

$$\begin{aligned}\int g_n^{(k')}(x_\xi)\tilde{R}f_m^{(k)}(x_\xi)\,\Pi(dX)&\\ \to r\int 1_{\bar{B}(c,r)}(x_\xi)\Big(\eta(x_\xi,x_\xi;\bar{B}(c,r')) - 1_{\bar{B}(c,r')}(x_\xi)\Big)&\ \Pi(dX) \le 0,\end{aligned} \tag{4.8}$$

then combining (4.6), (4.7), and (4.8) we further have

$$\int 1_{\bar{B}(c,r)}(x_\xi)\sum_{\xi'\neq\xi} a(\xi,\xi')\Big(1_{\bar{B}(c,r')}(x_{\xi'}) - 1_{\bar{B}(c,r')}(x_\xi)\Big)\ \Pi(dX) \ge 0.$$

Letting $r' \to r+$ we have

$$\begin{aligned}&\int \sum_{\xi'\neq\xi} a(\xi,\xi')\Big[1_{\bar{B}(c,r)}(x_\xi)1_{\bar{B}(c,r)}(x_{\xi'}) - 1_{\bar{B}(c,r)}(x_\xi)\Big]\ \Pi(dX)\\ &= \int 1_{\bar{B}(c,r)}(x_\xi)\sum_{\xi'\neq\xi} a(\xi,\xi')\Big(1_{\bar{B}(c,r)}(x_{\xi'}) - 1_{\bar{B}(c,r)}(x_\xi)\Big)\ \Pi(dX) \ge 0.\end{aligned} \tag{4.9}$$

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Since

$$1_{\bar{B}(c,r)}(x_\xi)1_{\bar{B}(c,r)}(x_{\xi'}) - 1_{\bar{B}(c,r)}(x_\xi) \le 0,$$

it follows from (4.9) that for any $\xi' \in I_\xi$

$$1_{\bar{B}(c,r)}(x_\xi)1_{\bar{B}(c,r)}(x_{\xi'}) = 1_{\bar{B}(c,r)}(x_\xi),$$

Π almost everywhere. Because c and r are arbitrary and E is separable, we have $x_\xi = x_{\xi'}$ Π almost everywhere. ■

5 Reversibility

Let $\mathcal{L}$ denote the generator of the Fleming–Viot process with mutation, selection, and recombination.

Definition 5.1 A generator A is said to be irreducible if for all x in E and any non-negative, non-zero measurable function $g \in C(E)$, there exists $t > 0$ such that $(P_t g)(x) > 0$, where P_t is the semigroup generated by A.

Theorem 5.2 *Assume that there is no migration, and the mutation generator A is irreducible. Let Π be the reversible measure for $\mathcal{L}_{s,r,0}$. Then for each ξ in I,*

$$\Pi\{X \in M_1(E)^I : supp(X_\xi) = E\} = 1.$$

A probability measure Π in $M_1(M_1(E)^I)$ is reversible with respect to $\mathcal{L}_{s,r,0}$ if and only if there are $\theta > 0$, μ in $M_1(E)$, and h in $C(E)$ such that, for any g in $C(E)$, the mutation generator A and recombination kernel $\eta(x, y; dz)$ satisfy

$$Ag(x) + r\Big[\int g(z)\eta(x, x; dz) - g(x)\Big] = \frac{\theta}{2}[\langle \mu, g\rangle - g(x)],$$

$$\eta(x, y; dz) = \frac{1}{2}\Big(\eta(x, x; dz) + \eta(y, y; dz)\Big) + (h(x) - h(y))(\delta_x(dz) - \delta_y(dz)).$$

Proof When there is no migration, the interacting system becomes a system of independent Fleming–Viot processes. The theorem is then a direct result of [8, Proposition 3.1 and Theorem 2.2]. ■

Theorem 5.3 *Assume that $\rho > 0$ and that E is not a one point space. If the mutation operator A is irreducible, then there is no reversible measure with respect to $\mathcal{L}_{s,r,\rho}$.*

Proof Let Π be reversible with respect to $\mathcal{L}_{s,r,\rho}$. For any ξ in $\hat{I}$, (4.4) shows that X_ξ is Π-almost surely a Dirac measure. Let Π_ξ be the projection of Π to colony ξ. It follows from Lemmas 3.3 and 4.2 that for any f, g in $C_b(R)$ and φ, ψ in $B(E)$,

$$\begin{aligned}\int_{M_1(E)} f(\langle \mu, \varphi\rangle)\mathcal{L}g(\langle \mu, \psi\rangle)\Pi_\xi(d\mu) &= \int_{M_1(E)^I} f(\langle X_\xi, \varphi\rangle)\mathcal{L}_{s,r,\rho}g(\langle X_\xi, \psi\rangle)\Pi(dX)\\ &= \int_{M_1(E)^I} g(\langle X_\xi, \varphi\rangle)\mathcal{L}_{s,r,\rho}f(\langle X_\xi, \psi\rangle)\Pi(dX)\\ &= \int_{M_1(E)} f(\langle \mu, \varphi\rangle)\mathcal{L}g(\langle \mu, \psi\rangle)\Pi_\xi(d\mu).\end{aligned}$$

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Thus Π_ξ is reversible with respect to $\mathcal{L}$ for each ξ in $\hat{I}$. Applying [8, Proposition 3.1] again it follows that X_ξ has full support Π-almost surely. This implies that E is a one point space. We thus reach a contradiction. ■

We now consider the case of zero mutation. For any $\xi, \xi' \in I$, write $\xi' \to \xi$ if either $a(\xi', \xi) > 0$ or there exists a finite sequence $\xi_i, i = 1, \dots, n$ such that $a(\xi', \xi_1) > 0, a(\xi_1, \xi_2) > 0, \dots, a(\xi_n, \xi) > 0$. Recall that Δ denotes the collection of Dirac measures on E. Set

$$\Delta_a := \{X \in M_1(E)^I : X_\xi = X_{\xi'} \in \Delta, \forall\, \xi, \xi' \in I \text{ with } \ \xi' \to \xi\}.$$

Theorem 5.4 *Suppose that $\rho > 0$ and for any ξ in I, there is ξ' such that $\xi' \to \xi$. If there is no mutation or recombination, then Π is reversible if and only if its support is in Δ_a.*

Proof The necessity follows from Lemmas 4.1 and 4.2. If the mutation and recombination are zero, then for any $X \in \Delta_a$ and any $F \in \mathcal{A}$, we have $\mathcal{L}_{s,0,\rho}F(X) = 0$, which gives the sufficiency. ■

6 Examples

In this section, we discuss the reversibility of several well-known examples.

Example 6.1 (Two Type Stepping-Stone Model). Let $I = \mathbb{Z}^d$ be the d dimensional lattice, and $E = \{0, 1\}$. Let x_i denote the the proportion of type 0 individuals on colony i in $\mathbb{Z}^d$. The generator of the system is $L_{s,0,\rho} = \sum_{i \in \mathbb{Z}^d} L_i$, where

$$L_i = \frac{1}{2} a_i(x) \frac{\partial^2}{\partial x_i^2} + b_i(x) \frac{\partial}{\partial x_i},$$

and

$$x = (x_i : i \in \mathbb{Z}^d), \qquad a_i(x) = x_i(1 - x_i),$$

$$b_i(x) = \sum_{j \in \mathbb{Z}^d} \rho\alpha(i, j)(x_j - x_i) + v - (u + v)x_i + s x_i(1 - x_i),$$

$$\rho \geq 0, \quad \alpha(i, j) = \frac{1}{2^d} 1_{|i-j|=1}, \quad u, v \geq 0.$$

Since $E = \{0, 1\}$, there is a one-to-one correspondence between elements in $M_1(E)$ and the points in $[0, 1]$. Thus the generator $L_{s,0,\rho}$ is an equivalent form of $\mathcal{L}_{s,0,\rho}$.

This is a special case of the models studied in [13, 15]. If $\rho = 0$, the system is reversible if and only if $u > 0, v > 0$. The reversible measure in this case is the infinite product of the reversible measure on each colony. If $\rho > 0$, the set $\hat{I}$ is $\mathbb{Z}^d$, and the projection to each colony of any reversible measure is a reversible measure in the colony. By Theorem 5.2, it is necessary that either $u > 0, v > 0$ or $u = v = 0$

in order to have a reversible measure for the system. If $u > 0, v > 0$, the mutation operator is irreducible, and by Theorem 5.3, the reversible measure does not exist. If $u = v = 0$, it follows from Theorem 5.4 that the reversible measures exist. For $d \geq 3$, the reversible measures are given by $\delta_{\mathbf{0}}$ and $\delta_{\mathbf{1}}$ with $\mathbf{0} = \{x_i = 0, i \in \mathbb{Z}^d\}$, $\mathbf{1} = \{x_i = 1, i \in \mathbb{Z}^d\}$. For $d = 1$ or 2, the reversible measures are convex combinations of $\delta_{\mathbf{0}}$ and $\delta_{\mathbf{1}}$.

Example 6.2 This model, studied in [1], has zero mutation and zero recombination. Let I be either $\mathbb{Z}^d$ or the hierarchical group Ω_N. In addition to assumption (2.1), the migration rate satisfies

$$a(\xi,\xi') \in [0,1],\ a(\xi,\xi') = a(0,\xi-\xi'),$$

$$\sum_{\xi \in I} a(0,\xi) = 1,\ \sum_{n=0}^{\infty}\Big(a^n(0,\xi) + a^n(\xi,0)\Big) > 0,\ \text{for all } \xi,$$

where $a^n(\cdot\,,\cdot)$ denotes the n step transition function. Set $\hat{a}(\xi,\xi') = \frac{1}{2}[a(\xi,\xi') + a(\xi',\xi)]$.

It follows from [1, Theorem 0.1] that if the symmetrized kernel $\hat{a}$ is recurrent, the system clusters and the invariant distributions are given by $\int \delta_{(\delta_u)^I}\theta(du)$ for some probability measure θ in $M_1(E)$. By Theorems 5.3 and 5.4, these are also reversible measures. If $\hat{a}$ is transient, the system is stable and the set of reversible measures is given by $\{\delta_{(\delta_u)^I} : u \in E\}$.

7 Appendix

Definition Let S be a metric space. A sequence $\{h_n\} \subset B(S)$ is said to converge boundedly and pointwise to $h \in B(S)$ if $h_n(x) \to h(x)$ for all $x \in S$ and $\sup_n \|h_n\|_\infty < \infty$. We write $\text{bp} - \lim_{n\to\infty} h_n = h$.

Part 1. The space $\mathcal{H}$.

Define $\mathcal{H}$ to be the space of functions $F\colon M_1(E)^I \to \mathbb{R}$, so that the partial derivative $\delta F(X)/\delta X_\xi(u)$ exists for every X, ξ, and u, and (3.11) holds with Φ replaced by F.

Our first observation is that for any positive integer m, any $\mathbf{f} \in B(E^m)$, and any $(\xi_1,\dots,\xi_m) \in I^m$, the function $F_{\mathbf{f}}\colon M_1(E)^I \mapsto \mathbb{R}$ defined by $F_{\mathbf{f}}(X) := \langle \otimes_{i=1}^m X_{\xi_i}, \mathbf{f}\rangle$ belongs to $\mathcal{H}$. First consider the case of $\mathbf{f} = 1_{G_1\times\cdots\times G_m}$ for open sets $G_i \subset E, i = 1,\dots,m$. Since we can approximate the indicator function 1_{G_i} boundedly and pointwise by functions in $\mathcal{D}(A)$ that is dense in $C(E)$, it follows that one can find a sequence of functions $\mathbf{f}_n$ in $\mathcal{D}(A)^m$ such that $\text{bp} - \lim_{n\to\infty}\mathbf{f}_n = \mathbf{f}$. Since the bp-convergence of $\mathbf{f}_n$ to $\mathbf{f}$ implies the bp-convergence of the corresponding derivatives, we have that $\langle \otimes_{i=1}^m X_{\xi_i}, \mathbf{f}\rangle \in \mathcal{H}$. Then the observation follows from [4, Theorem 4.3, Appendices].

Using the above-mentioned observation and polynomial approximation we can further show that for any m_i, any $(\xi_{i1},\dots,\xi_{im_i}) \in I^{m_i}$, any $\mathbf{f}_i \in B(E^{m_i}), i = 1,\dots,n$, and any $\phi \in C^1(R^n)$, the function $F : M_1(E)^I \mapsto \mathbb{R}$ defined by

$$F(X) := \phi(\langle \otimes_{j=1}^{m_1} X_{\xi_{1j}}, \mathbf{f}_1\rangle, \dots, \langle \otimes_{j=1}^{m_n} X_{\xi_{nj}}, \mathbf{f}_n\rangle)$$

also belongs to $\mathcal{H}$.

Moreover, take $g = \otimes_{i=1}^m g_i$ with $g_i \in B(E)$ bounded below by $c > 0$, and $k \in B(E^m)$ and set $F(X) := F_k(X)/F_g(X)$. By polynomial approximation again we can show that $F \in \mathcal{H}$.

Part 2. Approximating $\tilde{\Phi}_t$.

Let $\mathbf{f} \in \mathcal{D}(A)_0^I$ such that outside the finite subset I_0 of I, $f_\xi \equiv 0$ and $X_s = S_{-s\mathbf{f}}X$. Then

$$\begin{aligned}
&\langle b(X_s), \mathbf{f}\rangle \\
&\quad = \sum_{\xi\in I_0} \langle X_\xi^{-sf_\xi}, Af_\xi\rangle + \rho \sum_{\xi\in I_0}\sum_{\xi'\in I} a(\xi,\xi')\langle X_{\xi'}^{-sf_{\xi'}} - X_\xi^{-sf_\xi}, f_\xi\rangle \\
&\qquad + s\sum_{\xi\in I_0}\Big(\int_E\int_E V(u,v) f_\xi(u) X_\xi^{-sf_\xi}(dv) X_\xi^{-sf_\xi}(du) - \langle X_\xi^{-sf_\xi}, f_\xi\rangle\langle {X_\xi^{-sf_\xi}}^{\otimes 2}, V\rangle\Big) \\
&\qquad + r\sum_{\xi\in I_0}\Big(\Big\langle {X_\xi^{-sf_\xi}}^{\otimes 2}, \int_E f_\xi(u)\eta(\,\cdot\,,\cdot\,;du)\Big\rangle - \langle X_\xi^{-sf_\xi}, f_\xi\rangle\Big).
\end{aligned}$$

Since $\sum_{\xi'\in I} a(\xi,\xi') < \infty$ and

$$\begin{aligned}
\sum_{\xi\in I_0}\sum_{\xi'\in I} & a(\xi,\xi')\langle X_{\xi'}^{-sf_{\xi'}}, f_\xi\rangle = \\
&\sum_{\xi\in I_0}\sum_{\xi'\in I_0} a(\xi,\xi')\langle X_{\xi'}^{-sf_{\xi'}}, f_\xi\rangle + \sum_{\xi\in I_0}\sum_{\xi'\notin I_0} a(\xi,\xi')\langle X_{\xi'}, f_\xi\rangle,
\end{aligned}$$

we have $\langle b(X_s), \mathbf{f}\rangle \in \mathcal{H}$ by Part 1.

Define $\Phi_t(X) := \Phi(X_t)$,

$$\Lambda_n(\mathbf{f}, X) := \frac{2t}{n}\sum_{i=1}^n \Big\langle b(X_{it/n}), \mathbf{f}\Big\rangle \quad \text{and} \quad \tilde{\Phi}_t^{(n)}(X) := \Phi(X_t) e^{-\Lambda_n(\mathbf{f},X)}.$$

Since both $\Phi(X_t) \in \mathcal{H}$ and $e^{-\Lambda_n(\mathbf{f},X)} \in \mathcal{H}$ by Part 1, then $\tilde{\Phi}_t^{(n)} \in \mathcal{H}$ and (3.11) holds with Φ replaced by $\tilde{\Phi}_t^{(n)}$.

Clearly, $\mathrm{bp}-\lim_{n\to\infty}\tilde{\Phi}_t^{(n)} = \tilde{\Phi}_t$. Similar to (3.10), we have

$$\frac{\delta\tilde{\Phi}_t^{(n)}(X)}{\delta X_\xi}(u) = \frac{\delta\Phi(X_t)}{\delta X_\xi}(u) e^{-\Lambda_n(\mathbf{f},X)} - 2\tilde{\Phi}_t^{(n)}(X)\frac{t}{n}\sum_{i=1}^n \frac{\delta\langle b(X_{it/n}), \mathbf{f}\rangle}{\delta X_\xi}(u).$$

Therefore,

$$\mathrm{bp}-\lim_{n\to\infty}\frac{\delta\tilde{\Phi}_t^{(n)}}{\delta X_\xi} = \frac{\delta\tilde{\Phi}_t}{\delta X_\xi}, \quad \forall\, \xi \in I,$$

and (3.11) holds for $\tilde{\Phi}_t$.

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Department of Mathematics and Statistics, McMaster University, Hamilton, ON
e-mail: shuifeng@mcmaster.ca

Mathematical and Statistical Sciences, University of Alberta, Edmonton, AB
e-mail: schmu@stat.ualberta.ca

Université du Québec en Outaouais, Gatineau, QC
e-mail: jean.vaillancourt@uqo.ca

Department of Mathematics and Statistics, Concordia University, Montreal, QC
e-mail: xzhou@mathstat.concordia.ca