A GENERALIZED STEPPING STONE MODEL WITH Ξ-RESAMPLING MECHANISM

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Abstract. In this paper we formulate a generalized stepping stone model with Ξ-resampling mechanism to describe the evolution of relative frequencies for different types of alleles in a population with migration between two colonies. For a Ξ-coalescent and a jump type mutation generator $A$, such a probability-measure-valued Markov process is dual to the $(Ξ, A)$-coalescent process with geographical labels and migration. The existence of the generalized stepping stone model is directly established from a moment duality by verifying a multidimensional Hausdorff moment problem, and its probability law is also uniquely determined by the moment duality. Further, we characterize the stationary distribution for this model and show that the model is not reversible when the mutation operator is of uniform type.

1. Introduction

In population genetics a stepping stone model is a probability-measure-valued stochastic process describing the evolution of relative frequencies for different types of alleles in a population with geographical structure. The stepping stone model was first proposed by Kimura (1953) to investigate local differentiations in a geographically structured population. Since then this model has been extensively studied by both biologists and mathematicians. Most of the early studies were carried out for discrete time models. Shiga (1980a,b) defined the continuous time model as an infinite dimensional diffusion process, and characterized the stationary states and ergodic behaviors of the model with two alleles, and Shiga (1982) considered the continuous time model with multi alleles. However, such work only involves migration rates as geographical factors and does not involve selection and recombination. Later, Shiga and Uchiyama (1986) discussed the stepping stone model involving mutation and selection, and investigated the stationary states and stability. Handa (1990) formulated the stepping stone model involving mutation and selection, and investigated the stationary states and stability. Kermany et al. (2008) derived expressions for joint stationary moments of a two-island diffusion model and represented the sampling formula in terms of the joint moments. More recent work on stepping stone model can be found in Feng et al. (2011) where the stepping stone model is characterized as a system of interacting Fleming-Viot processes and its irreversibility was discussed.

The classical Fleming-Viot process, introduced in Fleming and Viot (1973), is regarded as a particular stepping stone model with one colony. It is well known that when the classical Fleming-Viot process only involves mutation and resampling, its moment dual is a function-valued Markov process governed by Kingman’s coalescent and mutation semigroup. As the development of coalescent theory in recent years, various coalescent processes have been introduced to generalize the classical Kingman’s coalescent. We refer to Pitman (1999) and Sagitov (1999) for introductions on $Λ$-coalescent,
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and Sagitov (2003) and Schweinsberg (2000) for Ξ-coalescent. It comes natural to study the generalized Fleming-Viot process whose dual evolves in the same way as the classical Fleming-Viot dual but with Kingman’s coalescent replaced by more general coalescent. Related studies on the generalized Fleming-Viot processes can be found in Birkner et al. (2009), Donnelly and Kurtz (1999) and Li et al. (2013).

Notohara (1990) extended Kingman’s coalescent to geographically structured population model with migration among colonies and proved that the extended coalescent model is the dual process of the classical stepping stone model. Handa (1990) defined the dual process of classical stepping stone model with migration and selection directly as a function-valued Markov process involving Kingman’s coalescent. It is then interesting to know whether there exists a generalized stepping stone model whose dual is also a function-valued Markov process evolving in the same way as the dual of the classical stepping stone model but with Kingman’s coalescent replaced by a more general coalescent, namely, the generalized stepping stone model with Ξ-resampling mechanism.

In this paper, we consider such a generalized stepping stone model with Ξ-resampling mechanism. Intuitively, there is a large population of individuals in each of the two colonies. Each population undergoes reproduction that is described by a Ξ-coalescent with simultaneous multiple collisions, i.e. there are prolific individuals that can simultaneously give birth to children of large amounts comparable to the total population. At the same time, each individual is subject to independent mutation described by an operator $A$ and migration to the other colony at a certain rate.

The Fleming-Viot models and stepping stone models often arise as scaling limits of the empirical measures of the associated particle systems, and the uniqueness is often justified by the duality. In the paper we adopt an alternative approach to show the existence of such a model which is similar to that in Evans (1997), where it is shown that any system of coalescing Borel right processes gives rise to a Feller semigroup, serving as the transition kernel whose existence is established based on the solution to the multidimensional Hausdorff moment problem. Our aim in this paper is to show that, subject to duality, a function-valued Markov process with Ξ-resampling mechanism, mutation generator $A$, geographical labels and migration, gives rise to a Feller semigroup, which determines a probability-measure-valued stochastic process. Compared with Evans (1997), the novelty of our work is that our coalescing processes have the more general reproduction mechanism involving simultaneous multiple reproduction, mutation and migration. In addition, we characterize the stationary distribution of this generalized stepping stone model with Ξ-resampling mechanism. We show that it has a unique invariant measure if the mutation process allows a unique invariant measure.

The reversibility of a population genetic model is an important issue for statistical inference. Li et al. (1999) proved that if a Fleming-Viot process has a reversible stationary distribution, then the associated mutation operator has to be of uniform type. It was also shown in Li et al. (1999) that the classical Fleming-Viot process with mutation operator of uniform type is reversible. Feng et al. (2011) proved the irreversibility for an interacting Fleming-Viot processes with mutation, selection and recombination. The reversibility for the generalized Ξ-Fleming-Viot process was investigated in Li et al. (2013), where the authors proved that the Ξ-Fleming-Viot process is not reversible except for the degenerate case of classical Fleming-Viot process with mutation operator of uniform type. In this paper we also consider the reversibility for the generalized stepping stone model with Ξ-resampling mechanism. By assuming that the mutation operator is of uniform type, we show that the process is not reversible.

This paper is arranged as follows. In Section 2 we extend the simultaneous multiple Ξ-coalescent to a geographically structured model with mutation and migration, i.e. the (Ξ, $A$)-coalescent process with geographical labels and migration, which serves as the dual process and is described by a continuous time function-valued Markov process. In Section 3, we formulate the generalized stepping stone model with Ξ-resampling mechanism and prove our main theorem by verifying a multidimensional Hausdorff moment
problem. Moreover, we discuss the stationary distribution and irreversibility for the
generalized stepping stone model with \( \Xi \)-resampling mechanism in Section 11 and Section 5,
respectively.

2. (\( \Xi \), \( A \))-COALESCENT PROCESS WITH GEOGRAPHICAL LABELS AND MIGRATION

In this section we first give a short review on \( \Xi \)-coalescent, and then introduce the
\( \Xi \)-coalescent with geographical labels and migration. Moreover, by adding the mutation
operator, we construct a function-valued Markov process, which is defined as the (\( \Xi \), \( A \))-
coalescent process with geographical labels and migration ((\( \Xi \), \( A \)) -CGM process for short).

2.1. \( \Xi \)-coalescent. Put \( [n] := \{1, \ldots, n\} \), \( [n]_0 := \{0, 1, \ldots, n\} \), \( [\infty] := \{1, 2, \ldots\} \)
and \( [\infty]_0 := \{0, 1, 2, \ldots\} \). A partition of \( D \subseteq [\infty] \) is a countable collection
\( \pi = \{\pi_i, i = 1, 2, \ldots\} \) of disjoint blocks such that \( \cup_i \pi_i = D \) and \( \min \pi_i < \min \pi_j \)
for \( i < j \). \( |\pi| \) denotes the cardinality of \( \pi \). Let \( \mathcal{P}_D \) be the collection of partitions for
\( D \subseteq [\infty] \). In particular, we write \( 1^D \) for the singleton partition for \( D \). For example, \( 1^{[n]} := \{\{1\}, \ldots, \{n\}\} \).

Given a partition \( \pi \in \mathcal{P}_D \) with \( |\pi| = n \) and \( \pi' \in \mathcal{P}_{[k]} \) with \( n \leq k \), the coagulation of \( \pi \)
by \( \pi' \), denoted by \( \text{Coag}(\pi, \pi') \), is defined as the following partition of \( D \),

\[
\text{Coag}(\pi, \pi') := \pi'' := \left\{ \begin{array}{ll}
\pi''_j := \cup_{i \in \pi'_j} \pi_i, & j = 1, \ldots, |\pi'| \end{array} \right.
\]

Given a partition \( \pi \) with \( |\pi| = n \) and a sequence of positive integers \( s, k_1, \ldots, k_r \) such that
\( k_i \geq 2, i = 1, \ldots, r \) and \( n = s + \sum_{i=1}^r k_i \), we say a partition \( \pi'' \) is obtained by a
\( (n; k_1, \ldots, k_r, s) \)-collision of \( \pi \) if \( \pi'' = \text{Coag}(\pi, \pi') \) for some partition \( \pi' \) such that
\[
\{\pi''_i : i = 1, \ldots, |\pi'|\} = \{k_1, \ldots, k_r, k_{r+1}, \ldots, k_{r+s}\},
\]
where \( k_{r+1} = \cdots = k_{r+s} = 1 \); i.e. \( \pi'' \) is obtained by merging the \( n \) blocks of \( \pi \) into \( r+s \)
blocks in which \( s \) blocks remain unchanged and the other \( r \) blocks contain \( k_1, \ldots, k_r \)
blocks from \( \pi \), respectively.

The \( \Xi \)-coalescent is a \( \mathcal{P}_{[\infty]} \)-valued Markov process \( \Pi_{[\infty]} = (\Pi_{[\infty]}(t))_{t \geq 0} \) starting from
partition \( \Pi_{[\infty]}(0) \in \mathcal{P}_{[\infty]} \) such that for any \( D \subset [\infty] \), its restriction to \( D \), \( \Pi_D = (\Pi_D(t))_{t \geq 0} \) is a Markov chain and given that \( \Pi_D(t) \) has \( n \) blocks, each \( (n; k_1, \ldots, k_r; s) \)-
collision occurs at rate \( \lambda_{n:k_1,\ldots:k_r;s} \) with
\[
\lambda_{n:k_1,\ldots:k_r;s} := \int_{\Delta} \sum_{\ell=0}^s \sum_{i_1 \neq \cdots \neq i_{r+\ell}} \sum_{j=1}^s \sum_{x} \frac{s!}{x_{i_1} \cdots x_{i_r} x_{i_{r+1}} \cdots x_{i_{r+\ell}}} \left( 1 - \sum_{j=1}^\infty x_j \right)^{s-\ell} \Xi(dx) \sum_{j=1}^\infty x_j \gamma,
\]
where \( \Xi \) is a finite measure on the infinite simplex
\[
\Delta := \left\{ x = (x_1, x_2, \ldots) : x_1 \geq x_2 \geq \cdots \geq 0, \sum_{i=1}^\infty x_i \leq 1 \right\}.
\]

Note that there exists at least one \( \pi' \in \mathcal{P}_{[n]} \) which induces the \( (n; k_1, \ldots, k_r; s) \)-collision.
For simplicity we write \( \lambda_{\pi'} := \lambda_{n:k_1,\ldots:k_r;s} \) and \( \lambda_n := \sum_{\pi' \in \mathcal{P}_{[n]} \setminus \{[n]\}} \lambda_{\pi'} \).

2.2. \( \Xi \)-coalescent with geographical labels and migration. Let \( S := \{\mathbb{1}, 2\} \) be
the labels of colonies. \( S^n := S \times \cdots \times S \) is the Cartesian product. Write \( |\eta| \) for the
dimension of \( \eta = (\eta_1, \ldots, \eta_n) \in S^n \). Then \( |\eta| = n \). Let \( |\eta|_1 := \#\{i | \eta_i = 1, i = 1, \ldots, n\} \)
and \( |\eta|_2 := \#\{i | \eta_i = 2, i = 1, \ldots, n\} \).

Given a partition \( \pi = \{\pi_1, \pi_2, \ldots, \pi_n\} \) of \( D \subseteq [\infty] \) with cardinality \( n \) and label
\( \eta = (\eta_1, \eta_2, \ldots, \eta_n) \in S^n \), we define a \( \eta \)-labeled partition \( \pi \) as
\[
\pi^\eta = \{\pi_{\eta_1}^\eta, \pi_{\eta_2}^\eta, \ldots, \pi_{\eta_n}^\eta\},
\]
where \( \pi_{\eta_i}^\eta \) denotes a \( \eta_i \)-labeled block. Write \( \mathbb{L}(\pi^\eta) := \eta \) and \( \mathbb{L}(\pi_{\eta_i}^\eta) := \eta_i \).
The Ξ-coalescent with geographical labels and migration is defined as a pure jump stochastic process taking values in the collection of labeled partitions where the coalescence events or the migration events may happen, and the coalescence can only take place among blocks with the same label. Given a η-labeled-partition πη, denote by πη,1 the collection of blocks from πη with label 1 and by πη,2 the collection of blocks in πη with label 2, respectively, where in each collection the blocks are ordered by their least elements. Thus, πη = πη,1 ∪ πη,2. Consequently, |η|1 = |πη,1| and |η|2 = |πη,2|. For any π ∈ P[k] with k ≥ |η|1, put

\[ \text{Coag}^1(\pi^n, \pi') := \text{Coag}(\pi^n,1, \pi') \cup \pi^n,2 \]

where Coag(πη,1, π') is the coagulation of πη,1 by π', which is obtained in the same way as \([1]\) but keeps the labels unchanged. Similarly, define Coag^2(πη,1, π') for any π' ∈ P[k] with k ≥ |η|2. There are also possible migrations between coalescence times. At rate u, one of the blocks with label 2 is randomly sampled with its label replaced by label 1. Conversely, at rate v, one of the blocks with label 1 is randomly sampled with its label replaced by label 2.

2.3. \((\Xi,A)\)-coalescent process with geographical labels and migration. Let a compact Polish space \(E\) be the state space. The distribution of types in each colony is described by a probability measure on \(E\). We assume that the \(\sigma\)-algebra \(\mathcal{E}\) on \(E\) is separable. Denote by

\[ B(E) = \{\text{real-valued bounded measurable functions on } E\} \]

and

\[ C(E) = \{\text{real-valued continuous functions on } E\}. \]

Let \(E^n\) be the \(n\)-fold product of \(E\). Define \(M_1(E)\) as the collection of probability measures on \(E\). \(M_1(E \times E)\) is the collection of probability measures on \(E \times E\). \(B(E^n)\) and \(C(E^n)\) are defined similarly for \(E^n\).

To describe the mechanism of mutation we consider a jump-type Feller generator

\[ Af(x) = \frac{\theta}{2} \int_E (f(y) - f(x)) q(x, dy) \]

where \(f(x) \in B(E), \theta > 0\) is a constant, and \(q(x, dy)\) is a transition function on \(E \times E\). Let \((T_t)_{t \geq 0}\) be the Feller semigroup associated to \(A\).

Denote by \(A^{(n)}\) the linear operator on \(B(E^n)\) that generates the Feller semigroup \(((T_t^{(n)})_{t \geq 0})\) corresponding to \(n\) independent copies of the processes associated to \((T_t)_{t \geq 0}\).

Given \(\eta = (\eta_1, \ldots, \eta_n) \in S^n, \mu = (\mu_1, \mu_2) \in M_1(E \times E)\) and \(f \in B(E^n)\), denote

\[ G_{f,\eta}(\mu) := \mathcal{G}_\mu(f, \eta) := \langle \mu_\eta, f \rangle \]

\[ = \int_E \cdots \int_E f(x_1, \ldots, x_n) \mu_{\eta_1}(dx_1) \cdots \mu_{\eta_n}(dx_n). \]

In particular, for \(f(x_1, \ldots, x_n) := \prod_{i=1}^n f_i(x_i)\) with \(f_i \in B(E), i = 1, \ldots, n\), we have

\[ A^{(n)} f(x_1, \ldots, x_n) = \sum_{i=1}^n A f_i(x_i) \prod_{j \neq i} f_j(x_j) \]

and

\[ \mathcal{G}_{f,\eta}(\mu) = \mathcal{G}_\mu(f, \eta) = \langle \mu_\eta, f \rangle = \prod_{i=1}^n \langle \mu_{\eta_i}, f_i \rangle \]

\[ = \prod_{\{i|\eta_i = 1\}} \langle \mu_1, f_i \rangle \prod_{\{i|\eta_i = 2\}} \langle \mu_2, f_i \rangle \]

\[ = \langle \mu_1^{\otimes |\eta_1|}, f^1(x_{i_1}, \ldots, x_{i_{|\eta_1|}}) \rangle \langle \mu_2^{\otimes |\eta_2|}, f^2(x_{j_1}, \ldots, x_{j_{|\eta_2|}}) \rangle \]

\[ (2) \]
where
\[ f^1(x_{i_1}, \ldots, x_{i|\ell|_1}) := \otimes \{i|\eta_i = 1, i = 1, \ldots, n\} f_i(x_i) \]
and
\[ f^2(x_{j_1}, \ldots, x_{j|\ell|_2}) := \otimes \{i|\eta_i = 2, i = 1, \ldots, n\} f_i(x_i). \]

In the following we construct a \( \bigcup_{m=1}^{\infty} (B(E^m) \times \mathcal{S}^m) \)-valued Markov process \((Y(t), \eta(t))_{t \geq 0}\) on some probability space \((\Omega, \mathcal{F}, \mathbb{P})\) serving as the dual process. For simplicity We use \( \mathbb{P}(\cdot) \) to represent both the probability measure and the associated expectation.

Process \((\eta(t))_{t \geq 0}\) is a Markov chain taking values in \( \bigcup_{m=1}^{\infty} \mathcal{S}^m \), which can be defined iteratively to keep track of the coalescence and migration events of the \( \Xi \)-coalescent with geographical labels and migration. Given an initial value \( \eta(0) = \eta \in \bigcup_{m=1}^{\infty} \mathcal{S}^m \), we associate \( \eta \) with a labeled singleton partition \( \{1|\eta_i\}_{\eta_i} := \{\{1\}_{\eta_i}, \ldots, \{\eta_i\}_{\eta_i}\} \), which is regarded as the initial value of the \( \Xi \)-coalescent with geographical labels and migration. The value of \((\eta(t))_{t \geq 0}\) does not change until either the next coalescence or the next migration event first arrives. Depending on whether the arrival event is a coalescence or a migration, define

\[
\begin{align*}
\beta^1_{\pi'}(\eta) := & \mathbb{L} \left( \text{Coag}^2 \left( \{1|\eta_i\}_{\eta_i}, \pi' \right) \right) \quad \text{for any } \pi' \in \mathcal{P}_{\|\eta_i\|_1} \setminus \{1|\eta_i\_1\}, \\
\beta^2_{\pi'}(\eta) := & \mathbb{L} \left( \text{Coag}^2 \left( \{1|\eta_i\}_{\eta_i}, \pi' \right) \right) \quad \text{for any } \pi' \in \mathcal{P}_{\|\eta_i\|_2} \setminus \{1|\eta_i\_2\}, \\
\gamma_i(\xi)(\eta) := & (\eta_1, \ldots, \eta_i-1, \xi, \eta_i+1, \ldots, \eta|\eta|) \quad \text{for } \xi \in \mathcal{S}, 1 \leq i \leq |\eta|,
\end{align*}
\]

where the operators \( \beta^1_{\pi'} \) and \( \beta^2_{\pi'} \) are related to coalescence and \( \gamma_i(\xi) \) is associated with migration. Consequently, the jump process \((\eta(t))_{t \geq 0}\) has a generator \( \mathcal{L} \) of the form

\[
\mathcal{L} h(\eta) = \sum_{\pi' \in \mathcal{P}_{\|\eta_i\|_1} \setminus \{1|\eta_i\_1\}} \lambda_{\pi'} \left( h \left( \beta^1_{\pi'}(\eta) \right) - h(\eta) \right) \\
+ \sum_{\pi' \in \mathcal{P}_{\|\eta_i\|_2} \setminus \{1|\eta_i\_2\}} \lambda_{\pi'} \left( h \left( \beta^2_{\pi'}(\eta) \right) - h(\eta) \right) \\
+ \sum_{i=1}^{n} u \left( h(\gamma_i(\eta)) - h(\eta) \right) + \sum_{i=1}^{n} v \left( h(\gamma_i(\eta)) - h(\eta) \right)
\]

where \( h \in B \left( \bigcup_{m=1}^{\infty} \mathcal{S}^m \right) \), the collection of bounded functions on \( \bigcup_{m=1}^{\infty} \mathcal{S}^m \). Once \((\eta(t))_{t \geq 0}\) jumps to a new state, we restart the iteration.

For any \( \{i_1, i_2, \ldots, i_m\} \subseteq [n] \) with cardinality \( m \) and any \( \pi \in \mathcal{P}_{[m]} \), set

\[
\pi' := \text{Coag}(\{\{i_1\}, \{i_2\}, \ldots, \{i_m\}, \pi) = \{\pi'_\ell, \ell = 1, 2, \ldots, |\pi'|\}. \]

A map \( \Phi_\pi \) from \( B(E^m) \) to \( B(E^{|\pi'|}) \) is defined as

\[
\Phi_\pi g(x_{i_1}, \ldots, x_{i_m}) = g(x_{i_1}, x_{i_2}, \ldots, x_{i_m})
\]

where \( g \in B(E^m) \) and \( \hat{i}_j = \min\{\pi'_\ell, i_j \in \pi'_\ell\} \) with \( j = 1, \ldots, m \). For example, let \( \pi = \{1, 2\}, \{3, 4\} \) and

\[
\pi' := \text{Coag}(\{\{1\}, \{3\}, \{7\}, \{9\}, \pi) = \{\{1, 3\}, \{7, 9\}\}. \]

Then \( \Phi_\pi \) is a map from \( B(E^3) \) to \( B(E^2) \) such that

\[
\Phi_\pi g(x_1, x_3, x_7, x_9) = g(x_1, x_1, x_7, x_7).
\]

We now define process \((Y(t))_{t \geq 0}\), a \( \bigcup_{m=1}^{\infty} B(E^m) \)-valued process with initial value \( Y(0) \in B(E^{(0)}) \). Divide the time interval into subintervals according to the jumping times of \((\eta(t))_{t \geq 0}\). Let \( \tau_n, n = 1, 2, \ldots \) be the consecutive jumping times with \( \tau_0 = 0 \). \((Y(t))_{t \geq 0}\) can be defined recursively as follows. For \( n = 0, 1, 2, \ldots \), define

\[
Y(t) = T_{[\tau_n, \tau_n+1)}^{(\eta(\tau_n))} Y(\tau_n) \quad \text{for any } t \in [\tau_n, \tau_{n+1}).
\]
Given $\eta(\tau_{n+1}-)$, $Y(\tau_{n+1}-)$ can be expressed as the product of $Y^1(\tau_{n+1}-)$ and $Y^2(\tau_{n+1}-)$ as in (2). At time $\tau_{n+1}$, we have

$$
P \left( Y(\tau_{n+1}) = (\Phi_2 Y^2(\tau_{n+1}-)) \otimes Y^2(\tau_{n+1}-) \mid (\eta(t))_{t \geq 0} \right)
$$

$$
= \frac{\lambda_\sigma}{\lambda_{\eta(\tau_{n+1})_1} + \lambda_{\eta(\tau_{n+1})_2}} \Pi \left\{ \{\eta(\tau_{n+1})_1 < \eta(\tau_{n+1})_2, \pi \in \mathcal{P}[\eta(\tau_{n+1})_1] \} \} \Pi[\eta(\tau_{n+1})]_1 \{\eta(\tau_{n+1})_2 \} \}
$$

and

$$
P(Y(\tau_{n+1}) = Y(\tau_{n+1}) \mid (\eta(t))_{t \geq 0}) = \Pi(\eta(\tau_{n+1}) = \eta(\tau_{n+1}^-))
$$

where $\Pi_\omega$ denotes the indicator function of an event $\omega$. The first two cases are due to the coalescence within colony 1 and colony 2, respectively, and the last case is due to the migration between the two colonies.

**Definition 2.1.** The $\bigcup_{m=1}^{\infty} (B(E^m) \times \mathbb{S}^m)$-valued Markov process $(Y(t), \eta(t))_{t \geq 0}$ is called the $(\Xi, A)$-CGM process.

**Proposition 2.2.** Given $\eta(0) = \eta$ and $Y(0) = \prod_{i=1}^{[n]} f_i(x_i)$, the generator of the $(\Xi, A)$-CGM process $(Y(t), \eta(t))_{t \geq 0}$ is of the form

$$
\mathcal{L} G_\mu(f, \eta) = \sum_{i=1}^{[n]} \left( \langle \mu_{\eta_i}, A f_i \rangle \prod_{j \neq i, j=1, \ldots, [n]} \langle \mu_{\eta_j}, f_j \rangle \right)
$$

$$
+ \sum_{\pi \in \mathcal{P}[\eta_1] \setminus \{\eta_1\}} \lambda_\pi \left( \langle \mu_1^{\circ}[\pi], \Phi \Phi, f \rangle - \langle \mu_1^{\circ}[\pi], f^1 \rangle \right) \left( \langle \mu_2^{\circ}[\pi], f^2 \rangle - \langle \mu_2^{\circ}[\pi], f^1 \rangle \right)
$$

$$
+ \sum_{\pi \in \mathcal{P}[\eta_2] \setminus \{\eta_2\}} \lambda_\pi \left( \langle \mu_2^{\circ}[\pi], \Phi \Phi, f \rangle - \langle \mu_2^{\circ}[\pi], f^2 \rangle \right) \left( \langle \mu_1^{\circ}[\pi], f^1 \rangle - \langle \mu_1^{\circ}[\pi], f^2 \rangle \right)
$$

$$
+ \sum_{\{i|\eta_i=2,j=1,\ldots,[n]\}} u(\langle \mu_1, f_i \rangle - \langle \mu_2, f_i \rangle) \prod_{j \neq i, j=1, \ldots, [n]} \langle \mu_{\eta_j}, f_j \rangle
$$

$$
+ \sum_{\{i|\eta_i=1,j=1,\ldots,[n]\}} v(\langle \mu_2, f_i \rangle - \langle \mu_3, f_i \rangle) \prod_{j \neq i, j=1, \ldots, [n]} \langle \mu_{\eta_j}, f_j \rangle.
$$

**Proof.** The result is easily obtained from the construction of the $(\Xi, A)$-CGM process. \qed

**Proposition 2.3.** Given $\eta = (\underbrace{1, \ldots, 1}_n, \underbrace{2, \ldots, 2}_m)$ for any $n, m \in [\infty]$ and $f_i, g_j \in B(E)$ with $i \in [n]$ and $j \in [m]$, we have

$$
\mathcal{L} G_\mu \left( \prod_{i=1}^{n} f_i(x_i) \prod_{j=1}^{m} g_j(y_j), \eta \right) = \mathcal{L} G_\mu \left( \prod_{i=1}^{n} f_i \left( x_{\sigma_1(i)} \right) \prod_{j=1}^{m} g_j \left( y_{\sigma_2(j)} \right), \eta \right)
$$

where $\sigma_1$ and $\sigma_2$ are independent permutations on $[n]$ and $[m]$, respectively.

**Proof.** It follows from Proposition 2.2. \qed
3. Generalized stepping stone model with Ξ-resampling mechanism

In this section we formulate the generalized stepping stone model to describe the gene frequency for a population genetic model with two colonies. It is the generalization of classical stepping stone model but with Kingman’s coalescent replaced by simultaneous multiple Ξ-coalescent.

In this model the evolution of type frequency over time is caused by three factors: reproduction determined by simultaneous multiple resampling mechanism ($\Xi$–coalescent) and mutation (operator $A$) in each colony, as well as migration between the two colonies (with rate $u$ from colony 2 to colony 1 and rate $v$ in the reverse direction).

3.1. The main result. Denote by $\langle C (M_1 (E \times E)) \rangle$ the Banach space of continuous functions on $M_1 (E \times E)$ with $\| \cdot \| = \sup_{\mu \in M_1 (E \times E)} |F (\mu)|$. In order to formulate a $M_1 (E \times E)$-valued Markov process $(\mu (t))_{t \geq 0}$, we first introduce some appropriate subspace of $C (M_1 (E \times E))$. Define $C_p (M_1 (E \times E))$ as the linear span of monomials of the form

$$F_{f, \eta, n} (\mu) = \int_E \cdots \int_E f (x_1, \ldots, x_n) \prod_{i=1}^n \mu_{\eta_i} (dx_i)$$

with $n \in [\infty]$, $f (x_1, \ldots, x_n) = f_1 (x_1) f_2 (x_2) \cdots f_n (x_n) \in (C (E))^n$ and $\eta = (\eta_1, \ldots, \eta_n) \in \mathbb{S}^n$. It follows from the Stone-Weierstrass Theorem that $C_p (M_1 (E \times E))$ is dense in $C (M_1 (E \times E))$.

Let $C_{b,p} (M_1 (E \times E))$ be the collection of those $F_{f, \eta, n} (\mu)$ with $n \in [\infty]$, $f \in B (E^n)$ and $\eta = (\eta_1, \ldots, \eta_n) \in \mathbb{S}^n$. Clearly, $C_{b,p} (M_1 (E \times E)) \supseteq C_p (M_1 (E \times E))$.

**Theorem 3.1.** Given a mutation generator $A$, migration rates $u > 0$, $v > 0$ and a $\Xi$-coalescent, there exists a unique, Feller semigroup $(Q_t)_{t \geq 0}$ on $C (M_1 (E \times E))$ such that for any $F_{f, \eta, n} \in C_{b,p} (M_1 (E \times E))$ and $\mu \in M_1 (E \times E)$, we have

$$Q_t F_{f, \eta, n} (\mu) = \int_{M_1 (E \times E)} F_{f, \eta, n} (v) Q_t (\mu, dv)$$

$$= \mathbb{P} (f, \eta) \left[ (\mu_{\eta(t)}, Y (t)) = \mathbb{P} (f, \eta) \mathbb{P} (Y (t), \eta (t), \eta (t)) (\mu),
$$

where $(Y (t), \eta (t))_{t \geq 0}$ is the $\cup_{n=1}^\infty (B (E^n) \times \mathbb{S}^m)$-valued $(\Xi, A)$-CGM process with initial value $(Y (0), \eta (0)) = (f, \eta)$. Consequently, there is a $M_1 (E \times E)$-valued Markov process $(\mu (t))_{t \geq 0}$ on some complete probability space $(\Omega^*, \mathcal{F}^*, \mathbb{Q})$ with transition semigroup $(Q_t)_{t \geq 0}$.

We defer the proof to Section 3.3.

**Definition 3.2.** The $M_1 (E \times E)$-valued Markov process

$$(\mu (t))_{t \geq 0} := (\mu_3 (t), \mu_2 (t))_{t \geq 0}$$

defined above is called the generalized stepping stone model with $\Xi$-resampling mechanism.

3.2. Preliminary results. In this section we first construct a countable semiring on the state space $E \times E$. Then we show a property on disjoint sets in the semiring. In addition, we introduce the multidimensional Hausdorff moment problem.

**Proposition 3.3.** Given a separable $\sigma$-algebra $\mathcal{E}$ on $E$, there exists a countable collection of sets $\mathcal{D}$ such that $\mathcal{D}$ is a semiring with

$$E \in \mathcal{D}, \sigma (\mathcal{D}) = \mathcal{E}$$

and

$$\mathcal{D} = \mathcal{D}_0 \cup \mathcal{D}_1 \cup \cdots \cup \mathcal{D}_n \cup \cdots$$

where $\mathcal{D}_n$ is a finite partition of $E$ and $\mathcal{D}_{n+1}$ is finer than $\mathcal{D}_n$ for $n = 0, 1, 2, \ldots$
Proof. Since the $\sigma$-algebra $E$ is separable, there exists a countable collection of sets $B = \{B_1, B_2, \ldots\}$ that generates $E$. Set

$$D_0 := \{E, \emptyset\};$$
$$D_1 := \{B_1, B_1^c\};$$
$$D_2 := \{B_1 \cap B_2, B_1 \cap B_2^c, B_1^c \cap B_2, B_1^c \cap B_2^c\};$$
$$\ldots$$
$$D_n := \{A_1 \cap A_2 \cap \cdots \cap A_n | A_i \in \{B_i, B_i^c\}, i = 1, \ldots, n\};$$
$$\ldots$$
$$D := D_0 \cup D_1 \cup \cdots \cup D_n \cup \cdots$$

where $B^c$ is the complement of $B$. Each $D_n$ is a partition of $E$ and the larger subindex implies the finer partition. It is easy to show that $D$ is a semiring by verifying (i) $\emptyset \in D$; (ii) $\forall D_1, D_2 \in D$, $D_1 \cap D_2, D_1 \setminus D_2$ and $D_2 \setminus D_1$ can be represented as disjoint unions of sets in $D$. \hfill \Box

Write $D \times D := \{(C_i \times D_j) | C_i \in D, D_j \in D\}$. Then $D \times D$ is a countable semiring on $E \times E$ with $E \times E \in D \times D$ and $\sigma (D \times D) = \sigma (E \times E)$.

Proposition 3.4. Let $C_1 \times D_1$ and $C_2 \times D_2$ be two nonempty disjoint sets in $D \times D$ with their union $(C_1 \times D_1) \cup (C_2 \times D_2) \in D \times D$. Then we have either $C_1 \cap C_2 = \emptyset$, $D_1 = D_2$ or $D_1 \cap D_2 = \emptyset$, $C_1 = C_2$.

Proof. Since $(C_1 \times D_1) \cup (C_2 \times D_2) \in D \times D$, there exist $C, D \in D$ such that $C \times D = (C_1 \times D_1) \cup (C_2 \times D_2)$. $(C_1 \times D_1) \cap (C_2 \times D_2) = \emptyset$ implies that either $C_1 \cap C_2 = \emptyset$ or $D_1 \cap D_2 = \emptyset$.

If $C_1 \cap C_2 = \emptyset$, then $C = C_1 \cup C_2$ by projection. There are four possible relations between $D_1$ and $D_2$: $D_1 \cap D_2 = \emptyset$; $D_1 \subset D_2$; $D_2 \subset D_1$; $D_1 = D_2$. By considering the four cases respectively, we exclude the possibility of the first three cases and conclude that $D_1 = D_2$. Alternatively, we have $C_1 = C_2$ if $D_1 \cap D_2 = \emptyset$. \hfill \Box

The next lemma presents necessary and sufficient conditions for solutions of multidimensional Hausdorff moment problem, which will be applied in the proof of our main result.

Lemma 3.5 (cf. Proposition 4.6.11 in [Berg et al., 1984]). Given a positive integer $k$, for a function $\psi : \mathbb{[}\infty\mathbb{]}^k_0 \rightarrow \mathbb{R}$, the following conditions are equivalent:

(i) $\psi$ is completely monotone;

(ii) $\sum_{0 \leq p \leq n} (-1)^p \binom{n}{p} \psi (m + p) \geq 0$ for all $n, m \in \mathbb{[}\infty\mathbb{]}^k_0$

where $\leq$ denotes the usual coordinatewise partial order on $\mathbb{[}\infty\mathbb{]}^k_0$, $n = (n_1, \ldots, n_k)$, $m = (m_1, \ldots, m_k)$, $p = (p_1, \ldots, p_k)$, $\|p\| := p_1 + \cdots + p_k$ and

$$\binom{n}{p} := \prod_{i=1}^k \binom{n_i}{p_i};$$

(iii) There exists $\mu \in M_+ ([0, 1]^k)$ such that

$$\psi (n) = \int_{[0, 1]^k} x^n d\mu (x), \; n \in \mathbb{[}\infty\mathbb{]}^k_0$$

where $M_+ (X)$ is the collection of Radon measures on $X$. 

Stepping stone model
3.3. Proof of Theorem 3.1

In what follows we proceed to prove Theorem 3.1. For any $t > 0$ and $\mu \in M_1(E \times E)$, we first define a nonnegative set function on the semiring by verifying a multidimensional Hausdorff moment problem. Then by the Carathéodory measure extension theorem, the set function is uniquely extended to a probability measure $V_{\mu,t}$ on $\sigma(D \times D)$. Further, the transition semigroup $Q_t$ is defined as the distribution of $V_{\mu,t}$, which determines a probability-measure-valued stochastic process.

Proof. In order to show that for each $\mu \in M_1(E \times E)$ and $t \geq 0$, there exists a probability measure $Q_t(\mu, \cdot)$ on $(M_1(E \times E))$ satisfying (3), it suffices to show that on some complete probability space $(\Omega^*, \mathcal{F}^*, \mathbb{P})$ there is a $M_1(E \times E)$-valued random variable $V_{\mu,t}$ such that for any $\mathbb{F}_{t,n} \in C_{b,p}(M_1(E \times E))$, we have

$$\mathbb{Q} \mathbb{F}_{t,n}(V_{\mu,t}) = \mathbb{P}(\{\mu(t), Y(t)\})$$

because we can then define $Q_t(\mu, \cdot)$ as the distribution of $V_{\mu,t}$. We break the proof into four steps.

(i) Existence of set function $V_{\mu,t}$ on the semiring $D \times D$. For any $k, \ell \in [\omega]$ with $k + \ell > 0$, let $n_1 = (n_{11}, \ldots, n_{1k}) \in [\omega]^k_0$, $n_2 = (n_{21}, \ldots, n_{2\ell}) \in [\omega]^\ell_0$. Consequently $\| n_1 \| = n_{11} + \cdots + n_{1k}$ and $\| n_2 \| = n_{21} + \cdots + n_{2\ell}$.

Let $(Y_{n_1,n_2}(t), \eta_{n_1,n_2}(t))_{t \geq 0}$ be the $(\Xi, A)$-CGM process with initial values $Y_{n_1,n_2}(0) = \otimes_{i=1}^k \| C_i \| \otimes_{i=1}^\ell \| D_i \|$ and $\eta_{n_1,n_2}(0) = \{1, \ldots, 1, 2, \ldots, 2\}$.

From the construction of the $(\Xi, A)$-CGM process, we know that $Y_{n_1,n_2}(t)$ is always a product of one variable functions for any $t \geq 0$. The number of variables in $Y_{n_1,n_2}(t)$ equals to the dimension of $\eta_{n_1,n_2}(t)$. Without loss of generality, we assume that

$$Y_{n_1,n_2}(t) = g_1(x_1) g_2(x_2) \cdots g_{|\eta_{n_1,n_2}(t)|} (x_{|\eta_{n_1,n_2}(t)|}).$$

Following (2) we write

$$Y^1_{n_1}(t) := \otimes_{i=1}^{|\eta_{n_1,n_2}(t)|} \mathbb{1}_{i=1,\ldots,|\eta_{n_1,n_2}(t)|} g_i(x_i)$$

and

$$Y^2_{n_2}(t) := \otimes_{i=2,\ldots,|\eta_{n_1,n_2}(t)|} \mathbb{1}_{i=1,\ldots,|\eta_{n_1,n_2}(t)|} g_i(x_i).$$

For simplicity, write

$$\alpha^1_{n_1}(t) := |\eta_{n_1,n_2}(t)|_1$$

and

$$\alpha^2_{n_2}(t) := |\eta_{n_1,n_2}(t)|_2.$$

Define

$$F(n_1, n_2) := \mathbb{P}\left[ \langle \mu_{n_1,n_2}(t), Y_{n_1,n_2}(t) \rangle \right]$$

and

$$\mu^1 \otimes \alpha^1_{n_1}(t), Y^1_{n_1}(t) \rangle \langle \mu^2 \otimes \alpha^2_{n_2}(t), Y^2_{n_2}(t) \rangle.$$ (5)

By Lemma 3.3. we need to verify

$$\sum_{0 \leq p \leq r} \sum_{0 \leq q \leq h} (-1)^{|p| + |q|} \binom{r}{p} \binom{h}{q} F(n_1 + p, n_2 + q) \geq 0$$

for any $r = (r_1, \ldots, r_k) \in [\omega]^k_0$ and $h = (h_1, \ldots, h_\ell) \in [\omega]^\ell_0$, $p = (p_1, \ldots, p_k)$ with $p_i \leq r_i$ and $q = (q_1, \ldots, q_\ell)$ with $q_i \leq h_i$. For $r$ and $h$ write

$$G_r := \{ c = c_1 \times \cdots \times c_k : c_i \subset [r_i]_0, 1 \leq i \leq k \}$$

and

$$G_h := \{ \tilde{c} = \tilde{c}_1 \times \cdots \times \tilde{c}_\ell : \tilde{c}_i \subset [h_i]_0, 1 \leq i \leq \ell \}.$$
Then
\[
\sum_{0 \leq p \leq r} \sum_{0 \leq q \leq h} \binom{r}{p} \binom{h}{q} (-1)^{|p|+|q|} F(n_1 + p, n_2 + q)
= \sum_{0 \leq p \leq r} \sum_{0 \leq q \leq h} \binom{r}{p} \binom{h}{q} (-1)^{|p|+|q|} P \left[ \left( \mu_{n_1+p,n_2+q}(t), Y_{n_1+p,n_2+q}(t) \right) \right]
= \sum_{0 \leq p \leq r} \sum_{0 \leq q \leq h} \binom{r}{p} \binom{h}{q} (-1)^{|p|+|q|} P \left[ \left( \mu_1^1 \alpha_{n_1+p}^1(t), Y_{n_1+p}^1(t) \right), \left( \mu_2^2 \alpha_{n_2+q}^2(t), Y_{n_2+q}^2(t) \right) \right]
\]
with initial values
\[
Y_{n_1+p}^1(0) = \otimes_{i=1}^k \mathbb{I}_{C_i}^{n_{1i}+p_i}, \quad Y_{n_2+q}^2(0) = \otimes_{i=1}^l \mathbb{I}_{D_i}^{n_{2i}+q_i},
\]
and
\[
\alpha_{n_1+p}^1(0) = \|n_1\| + |p|, \quad \alpha_{n_2+q}^2(0) = \|n_2\| + |q|.
\]
Put \( \mathbf{c} = (|c_1|, \ldots, |c_k|) \in [\infty]^k \) with \( \|\mathbf{c}\| = |c_1| + \cdots + |c_k| \), and \( \tilde{\mathbf{c}} = (|\tilde{c}_1|, \ldots, |\tilde{c}_l|) \in [\infty]^l \) with \( \|\tilde{\mathbf{c}}\| = |\tilde{c}_1| + \cdots + |\tilde{c}_l| \). It follows that
\[
\sum_{0 \leq p \leq r} \sum_{0 \leq q \leq h} \binom{r}{p} \binom{h}{q} (-1)^{|p|+|q|} F(n_1 + p, n_2 + q)
= \sum_{0 \leq p \leq r} \sum_{0 \leq q \leq h} \sum_{\mathbf{c} \in \mathcal{E}_r} \sum_{\tilde{\mathbf{c}} \in \mathcal{E}_h} \binom{r}{p} \binom{h}{q} (-1)^{|p|+|q|}
\times P \left[ \left( \mu_1^2 \alpha_{n_1+e}^2(t), Y_{n_1+e}^1(t) \right), \left( \mu_2^1 \alpha_{n_2+\tilde{c}}^1(t), Y_{n_2+\tilde{c}}^2(t) \right) \right]
= \sum_{\mathbf{c} \in \mathcal{E}_r} \sum_{\tilde{\mathbf{c}} \in \mathcal{E}_h} (-1)^{|\mathbf{c}|+|\tilde{\mathbf{c}}|} P \left[ \left( \mu_1^2 \alpha_{n_1+e_1}^2(t), Y_{n_1+\mathbf{c}}^1(t) \right), \left( \mu_2^1 \alpha_{n_2+\tilde{c}}^1(t), Y_{n_2+\tilde{c}}^2(t) \right) \right]
\]
with initial values
\[
Y_{n_1+\mathbf{c}}^1(0) = \otimes_{i=1}^k \left( \mathbb{I}_{C_i}^{n_{1i}+r_i} \right), \quad Y_{n_2+\tilde{c}}^2(0) = \otimes_{i=1}^l \left( \mathbb{I}_{D_i}^{n_{2i}+h_i} \right),
\]
where
\[
h_{ij} := \begin{cases} 
\mathbb{I}_{C_i} & \text{if } j - n_{1i} \in c_i, \\
\mathbb{I} & \text{if } j - n_{1i} \notin c_i,
\end{cases}
\]
and
\[
g_{ij} := \begin{cases} 
\mathbb{I}_{D_i} & \text{if } j - n_{2i} \in \tilde{c}_i, \\
\mathbb{I} & \text{if } j - n_{2i} \notin \tilde{c}_i,
\end{cases}
\]
and \( \alpha_{n_1+\mathbf{c}}^1(0) = \|n_1\| + |\mathbf{c}|, \quad \alpha_{n_2+\tilde{c}}^2(0) = \|n_2\| + |\tilde{\mathbf{c}}| \). Therefore,
\[
\sum_{0 \leq p \leq r} \sum_{0 \leq q \leq h} \binom{r}{p} \binom{h}{q} (-1)^{|p|+|q|} F(n_1 + p, n_2 + q)
= P \left[ \left( \mu_1^1 \alpha_{n_1+r}^1(t), Y_{n_1+r}^1(t) \right), \left( \mu_2^2 \alpha_{n_2+h}^2(t), Y_{n_2+h}^2(t) \right) \right]
\geq 0
\]
with initial values
\[
Y_{n_1+r}^1(0) = \otimes_{i=1}^k \left( \mathbb{I}_{C_i}^{n_{1i}+r_i} \right), \quad Y_{n_2+h}^2(0) = \otimes_{i=1}^l \left( \mathbb{I}_{D_i}^{n_{2i}+h_i} \right),
\]
and \( \alpha_{n_1+r}^1(0) = \|n_1\| + |r|, \quad \alpha_{n_2+h}^2(0) = \|n_2\| + |h| \).
Consequently, for any \( n_1 \in [\infty]^k_0 \) and \( n_2 \in [\infty]^\ell_0 \) with \( k + \ell > 0 \), there exist \([0,1]\)-valued random variables \( W_1, \ldots, W_k \) and \( Z_1, \ldots, Z_\ell \) on some complete probability space \((\Omega^*, \mathcal{F}^*, \mathbb{Q})\) such that

\[
\text{Q} \left[ \prod_{i=1}^{k} W_i^{n_{1,i}} \prod_{j=1}^{\ell} Z_j^{n_{2,j}} \right] = F(n_1, n_2),
\]

where for convenience, we use \( \text{Q}(\cdot) \) to denote both the probability measure and the associated expectation. Let \( V_{\mu,t} \) be a set function on the semiring \( D \times D \) satisfying

\[
\{ V_{\mu,t}(C_i \times D_j) \}_{i,j=1,2,\ldots} = \{ W_i \times Z_j \}_{i,j=1,2,\ldots}
\]

with \( C_i \times D_j \in D \times D \) for any \( i, j = 1, 2, \ldots \). Choosing \( Y_{(1),(1)}(0) = \mathbb{I}_0 \otimes \mathbb{I}_0 \) and \( Y_{(1),(4)}(0) = \mathbb{I}_E \otimes \mathbb{I}_E \) in \([3]\), we obtain \( V_{\mu,t}(\emptyset \times \emptyset) = 0 \) and \( V_{\mu,t}(E \times E) = 1 \), respectively.

(ii) Existence of transition distribution \( Q_t \) for any \( t \geq 0 \). We first show that \( V_{\mu,t} \) is finitely additive. By Proposition \([3,4]\) the finitely additive property holds if

\[
\text{Q} [V_{\mu,t}((C_1 \cup C_2) \times D) - V_{\mu,t}(C_1 \times D) - V_{\mu,t}(C_2 \times D)]^2 = 0
\]

for any \( C_1 \times D, C_2 \times D, (C_1 \cup C_2) \times D \in D \times D \) with \( C_1 \cap C_2 = \emptyset \) and

\[
\text{Q} [V_{\mu,t}(C \times (D_1 \cup D_2)) - V_{\mu,t}(C \times D_1) - V_{\mu,t}(C \times D_2)]^2 = 0
\]

for any \( C \times D_1, C \times D_2, C \times (D_1 \cup D_2) \in D \times D \) with \( D_1 \cap D_2 = \emptyset \).

Put \( \eta = \{1, 1, 2, 2\} \) and

\[
\begin{align*}
Y_1(0) &= (f_1(x_1) + f_2(x_1))(f_1(x_2) + f_2(x_2))g_1(y_1)g_2(y_2), \\
Y_2(0) &= f_1(x_1)f_1(x_2)g_1(y_1)g_2(y_2), \\
Y_3(0) &= f_2(x_1)f_2(x_2)g_1(y_1)g_2(y_2), \\
Y_4(0) &= -2(f_1(x_1) + f_2(x_1))f_1(x_2)g_1(y_1)g_2(y_2), \\
Y_5(0) &= -2(f_1(x_1) + f_2(x_1))f_2(x_2)g_1(y_1)g_2(y_2), \\
Y_6(0) &= 2f_1(x_1)f_2(x_2)g_1(y_1)g_2(y_2),
\end{align*}
\]

where \( f_1, f_2, g_1, g_2 \in B(E) \). Let \((Y_i(t), \eta_i(t))_{t \geq 0}\) be the \((\Xi, A)\)-CGM process with initial value \((Y_i(0), \eta)\) for \( i = 1, \ldots, 6 \). Using a coupling argument, without loss of generality, we assume that they are driven by the same coalescent and migration events. Consequently, \( \eta_1(t) = \cdots = \eta_6(t) := \eta(t) \) for any \( t \geq 0 \). After cancelations due to different signs, the superposition of those six processes becomes exactly the same as two processes with initial values

\[
(f_1(x_1)f_2(x_2)g_1(y_1)g_2(y_2), \eta)
\]

and

\[
(-f_2(x_1)f_1(x_2)g_1(y_1)g_2(y_2), \eta)
\]

respectively. By Propositions \([22] \) and \([23] \) we know

\[
\sum_{i=1}^{6} \mathcal{L} \mathbb{E}_{\mu} (Y_i(t), \eta(t)) = 0 \text{ for any } t \geq 0.
\]

Note that

\[
\begin{align*}
&\left[ V_{\mu,t}((C_1 \cup C_2) \times D) - V_{\mu,t}(C_1 \times D) - V_{\mu,t}(C_2 \times D) \right]^2 \\
= &V_{\mu,t}^2((C_1 \cup C_2) \times D) + V_{\mu,t}^2(C_1 \times D) + V_{\mu,t}^2(C_2 \times D) \\
- &2V_{\mu,t}((C_1 \cup C_2) \times D) \times V_{\mu,t}(C_1 \times D) \\
- &2V_{\mu,t}((C_1 \cup C_2) \times D) \times V_{\mu,t}(C_2 \times D) \\
+ &2V_{\mu,t}(C_1 \times D) \times V_{\mu,t}(C_2 \times D).
\end{align*}
\]
Choose \( f_1 (\cdot) = \mathbb{1}_{C_1} (\cdot) \), \( f_2 (\cdot) = \mathbb{1}_{C_2} (\cdot) \), \( g_1 (\cdot) = \mathbb{1}_{D_1} (\cdot) \) and \( g_2 (\cdot) = \mathbb{1}_{D_2} (\cdot) \). It follows from (9) and (10) that
\[
Q [V_{\mu,t} ((C_1 \cup C_2) \times D) - V_{\mu,t} (C_1 \times D) - V_{\mu,t} (C_2 \times D)]^2 = \sum_{i=1}^{6} \mathbb{P} ([\mu_{\eta(t)}, Y_i (t)]) .
\]

Since \( f \) is the distribution of \( V \), we have
\[
\mathbb{P} ([\mu_{\eta(t)}, Y_i (t)]) = \mathbb{P} \mathcal{G}_\mu (Y_i (t), \eta (t)) = \mathbb{P} \mathcal{G}_\mu (Y_i (0), \eta) + \mathbb{P} \int_0^t \mathcal{L} \mathcal{G}_\mu (Y_i (s), \eta (s)) \, ds ,
\]
we have
\[
\mathbb{P} \sum_{i=1}^{6} ([\mu_{\eta(t)}, Y_i (t)]) = \sum_{i=1}^{6} \mathbb{P} \mathcal{G}_\mu (Y_i (0), \eta) + \mathbb{P} \int_0^t \mathcal{L} \mathcal{G}_\mu (Y_i (s), \eta (s)) \, ds .
\]
By (10), we have
\[
\mathbb{P} \sum_{i=1}^{6} ([\mu_{\eta(t)}, Y_i (t)]) = \sum_{i=1}^{6} \mathbb{P} \mathcal{G}_\mu (Y_i (0), \eta) = 0 .
\]

Consequently, identity (7) holds. Identity (8) can be proved in a similar way.

We now show that \( V_{\mu,t} \) has the sub-countably additive property. Let \( C \times D \in \mathcal{D} \times \mathcal{D} \), \( C_i \times D_i \in \mathcal{D} \times \mathcal{D} \), \( i \geq 1 \) and \( C \times D \subseteq \bigcup_{i=1}^{\infty} C_i \times D_i \). Note that
\[
\mathbb{I}_{C \times D} (x, y) \leq \sum_{i=1}^{\infty} \mathbb{I}_{C_i \times D_i} (x, y) .
\]
By (9), we can easily get
\[
V_{\mu,t} (C \times D) \leq \sum_{i=1}^{\infty} V_{\mu,t} (C_i \times D_i) .
\]

Note that a nonnegative set function on a semiring is countably additive if and only if it is finitely additive and sub-countably additive; see e.g. Proposition 1.1.4 of Yan (2004). Thus, \( V_{\mu,t} \) is countably additive. Applying the Carathéodory measure extension theorem, \( V_{\mu,t} \) can be uniquely extended to a random probability measure on \( \sigma(\mathcal{D} \times \mathcal{D}) \).

Let \( Q_t (\mu, \cdot) \) be the distribution of \( V_{\mu,t} \). Consequently, \( Q_t (\mu, \cdot) \) induces a transition distribution.

(iii) Uniqueness of transition distribution \( Q_t \) for any \( t \geq 0 \). Since \( Q_t (\mu, \cdot) \) is defined as the distribution of \( V_{\mu,t} \), we have
\[
Q [\mathbb{F} (V_{\mu,t})] = \int_{M_1 (E \times E)} \mathbb{F} (v) Q_t (\mu, dv)
\]
for any \( \mathbb{F} \in C (M_1 (E \times E)) \).

In particular, for any \( \mathbb{F}_{f,\eta,n} \in C_{b,p} (M_1 (E \times E)) \) we apply the monotone class theorem to show that the integration on the RHS of (LU) can be represented by moments of the dual \((\Xi, A)\)-CGM process.

Given \( n > 0 \) and \( \eta \in \mathbb{S}^n \), \( \overbrace{\mathcal{D} \times \cdots \times \mathcal{D}}^n \) is a \( \pi \)-system on \( E^n \). Let \( \mathcal{H} \) be the collection of functions \( f \in B (E^n) \) satisfying
\[
\int_{M_1 (E \times E)} \mathbb{F}_{f,\eta,n} (v) Q_t (\mu, dv) = \mathbb{P}_{(f, \eta)} ([\mu_{\eta(t)}, Y(t)]) ,
\]
where \( (Y(t), \eta(t))_{t \geq 0} \) is the \( \bigcup_{n=1}^{\infty} (B (E^n) \times \mathbb{S}^n) \)-valued \((\Xi, A)\)-CGM process with initial value \((f, \eta) \in B (E^n) \times \mathbb{S}^n \).

It follows from (10) that
\[
\otimes_{i=1}^{k} \mathbb{I}_{C_i} \otimes_{j=1}^{\ell} \mathbb{I}_{D_j} \in \mathcal{H}
\]
where \( n_{11} + \cdots + n_{1k} = |\eta|_1 \) and \( n_{21} + \cdots + n_{2\ell} = |\eta|_2 \). By the linearity of expectation and integration we also have \( ah + bg \in \mathcal{H} \) for any \( h, g \in \mathcal{H} \) and \( a, b \in \mathbb{R} \). It is obvious that \( I_{F_n} \in \mathcal{H} \). If \( h_m \in \mathcal{H}, m \geq 1, 0 \leq h_m \uparrow h \) and \( h \) is finite, let \( (Y_m(s), \eta(s))_{s \leq t} \) be the associated dual processes with initial values \((h_m, \eta)\) and \((h, \eta)\), respectively. Observing that \( Y_m(t) \uparrow Y(t) \) as \( m \to \infty \), then by the dominated convergence theorem,

\[
\int_{M_1(E \times E)} F_{h,\eta,n}(v) Q_t(\mu, dv)
= \mathbb{Q}[F_{h,\eta,n}(V_{\mu,t})]
= \lim_{m \to \infty} \mathbb{Q}[F_{h_m,\eta,n}(V_{\mu,t})]
= \lim_{m \to \infty} \int_{M_1(E \times E)} F_{h_m,\eta,n}(v) Q_t(\mu, dv)
= \lim_{m \to \infty} \mathbb{P}(h_m, \eta) \left[ (\mu_{q(t)}, Y_m(t)) \right]
= \mathbb{P}(h, \eta) \left[ (\mu_{q(t)}, Y(t)) \right],
\]

and we have \( h \in \mathcal{H} \). By [6] we know that \( I_B \in \mathcal{H} \) for any \( B \in \bigotimes_{n=1}^n \mathcal{D} \). Applying the monotone class theorem, \( \mathcal{H} \) contains all of the \( \sigma(\mathcal{D} \times \cdots \times \mathcal{D}) \)-measurable real-valued functions and the RHS of (11) holds for any \( f \in B(E^n) \). That is to say, the moment dual equation

\[
Q \mathbb{F}_{f,\eta,n}(V_{\mu,t}) = \mathbb{P}(f, \eta) \left[ (\mu_{q(t)}, Y(t)) \right] = \mathbb{P}F_{Y(t),\eta(t),|\eta(t)|}(\mu)
\]

is always true for any \( \mathbb{F}_{f,\eta,n} \in C_{b,p}(M_1(E \times E)) \).

The moments of \( Q_t \) can be obtained by choosing some particular forms of \( \mathbb{F}_{f,\eta,n} \). It is shown in Lemma 2.4.1 of [Dawson 1991] that a random probability measure is uniquely determined by its moment measures of all orders. Hence, we obtain the uniqueness of \( Q_t \) for any \( t > 0 \).

(iv) **Semigroup property and Feller property of the transition distribution \((Q_t)_{t \geq 0}\).** For any \( \mathbb{F} \in C(M_1(E \times E)) \), there exists a sequence \( \{\mathbb{F}_k, k \geq 1\} \subseteq C_p(M_1(E \times E)) \) such that

\[
\lim_{k \to \infty} \sup_{\mu \in M_1(E \times E)} |\mathbb{F}_k(\mu) - \mathbb{F}(\mu)| = 0.
\]

Then for any \( t \geq 0 \) and \( \mu \in M_1(E \times E) \), we have

\[
|Q_t \mathbb{F}(\mu) - Q_t \mathbb{F}_k(\mu)| \to 0 \text{ as } k \to \infty
\]

and consequently,

\[
Q_t \mathbb{F}(\mu) = \lim_{k \to \infty} Q_t \mathbb{F}_k(\mu).
\]

By the Markov property of the dual process \((Y(s), \eta(s))_{s \geq 0}\), for any \( \mathbb{F}_{f,\eta,n} \in C_p(M_1(E \times E)) \) and \( \mu \in M_1(E \times E) \),

\[
Q_s Q_t \mathbb{F}_{f,\eta,n}(\mu) = \mathbb{P}(f, \eta) \left[ Q_s \mathbb{F}Y(t),\eta(t),|\eta(t)|)(\mu) \right]
= \mathbb{P}(f, \eta) \left[ \mathbb{F}Y(s+t),\eta(s+t),|\eta(s+t)|)(\mu) \right]
= Q_{s+t} \mathbb{F}_{f,\eta,n}(\mu).
\]

Consequently, for any \( \mathbb{F} \in C(M_1(E \times E)) \),

\[
Q_s Q_t \mathbb{F}(\mu) = \lim_{k \to \infty} Q_s Q_t \mathbb{F}_k(\mu)
= \lim_{k \to \infty} Q_{s+t} \mathbb{F}_k(\mu)
= Q_{s+t} \mathbb{F}(\mu).
\]

The semigroup property then follows.
Given $\mathbb{F}_{f,n} \in C_p(M_1(E \times E))$ and $\eta$, we can express $f$ as $f = f^1 \otimes f^2 = \otimes_{i=1}^{\eta_1} f^{1,i} \otimes_{j=1}^{\eta_2} f^{2,j}$. Let $\tau_1$ be the first jump time of $Y(t)$ which is exponential with parameter $\lambda = |\eta|_2 u + |\eta|_3 v + \lambda_{|\eta|_2} + \lambda_{|\eta|_1}$. Consequently, we have

$$Q_t \mathbb{F}_{f,n}(\mu) = \mathbb{P}(f,\eta) \left[ \langle \mu_{\eta(t)}, Y(t) \rangle \right]$$

and initial value $\mu = (\mu_1, \mu_2)$. Let $\mu_{|\eta|_1}$ and $\mu_{|\eta|_2}$ be the functions of $\mu_1$ and $\mu_2$ respectively, and consider $\frac{d}{dt} \mu_{|\eta|_1}$ and $\frac{d}{dt} \mu_{|\eta|_2}$, which are of the form $\otimes_{i=1}^{\eta_1} f^{1,i}$ and $\otimes_{j=1}^{\eta_2} f^{2,j}$, respectively. 

By the construction of the dual $(\Xi, A)$-CGM process, the probability of $\{ \tau_1 < t \}$ (that is either coalescence or migration has occurred by time $t$) converges to 0 as $t \to 0$. Thus, we have

$$\lim_{t \to 0} |Q_t \mathbb{F}_{f,n}(\mu) - \mathbb{F}_{f,n}(\mu)| = 0.$$ 

For any $\mathbb{F} \in C(M_1(E \times E))$, reapplying the approximate sequence $\{ \mathbb{F}_k, k \geq 1 \} \subseteq C_p(M_1(E \times E))$, we have

$$\lim_{k \to \infty} |Q_t \mathbb{F}(\mu) - \mathbb{F}(\mu)| = 0.$$

So, $Q_t$ is strongly continuous.

Note that

$$\| Q_t \mathbb{F} \| := \sup_{\mu} |Q_t \mathbb{F}(\mu)|$$

$$= \sup_{\mu} \left| \int_{M_1(E \times E)} \mathbb{F}(\nu) Q_t(\mu, d\nu) \right|$$

$$\leq \| \mathbb{F} \|.$$

Consequently, $Q_t$ is a contraction operator.

Further, for any $\mathbb{F} \in C(M_1(E \times E))$, since

$$Q_t \mathbb{F}(\mu) = \lim_{k \to \infty} Q_t \mathbb{F}_k(\mu),$$

we know that $Q_t \mathbb{F}(\mu)$ is a limit point of a sequence belonging to $C_p(M_1(E \times E))$. Thus, $Q_t \mathbb{F}(\mu) \in C(M_1(E \times E)) = C_p(M_1(E \times E)).$

In summary, $(Q_t)_{t \geq 0}$ is a strongly continuous semigroup of positive contraction operator on $C(M_1(E \times E))$, and consequently, $(Q_t)_{t \geq 0}$ is a Feller semigroup.

By Proposition 1.6 on Page 161 of Ethier and Kurtz (1986), the semigroup $(Q_t)_{t \geq 0}$ and initial value $\mu$ uniquely determine the finite dimensional distribution of $(\mu(t))_{t \geq 0}$.

Let $\mathbb{L}^*$ be the generator of the generalized stepping stone model with $\Xi$-resampling mechanism $(\mu(t))_{t \geq 0} = (\mu_1(t), \mu_2(t))_{t \geq 0}$ such that

$$\mathbb{L}^* \mathbb{F}_{f,n} (\mu) = \lim_{t \to 0^+} \frac{Q_t \mathbb{F}_{f,n} (\mu) - \mathbb{F}_{f,n} (\mu)}{t}$$

where $\mathbb{F}_{f,n} \in C_{b,p}(M_1(E \times E))$ with $f \in B(E^n)$ and $\eta \in \mathbb{S}^n$.

**Corollary 3.6.** Given $\mathbb{F}_{f,n} \in C_{b,p}(M_1(E \times E))$ with $f(x_1, \ldots, x_n) = \prod_{i=1}^{n} f_i(x_i)$, the generator $\mathbb{L}^*$ is of the form

$$\mathbb{L}^* \mathbb{F}_{f,n} (\mu) = \mathbb{L} \mathbb{G}_\mu(f, \eta)$$

where $\mathbb{L}$ is given by (3).
For any \( \delta > K \) and hence, note that
\[
\begin{align*}
\text{tight in} & \quad \text{stone model. As} \quad (T_t)_{t \geq 0} \\
& \quad \text{proof is an adaption of their proofs.}
\end{align*}
\]

Thus, the family \( \nu \in \text{resampling mechanism} \) for any \( \Theta \)
\[
\begin{align*}
\text{mutation operator} & \quad \text{Mutation operator}
\end{align*}
\]

4. Stationary distribution of the generalized stepping stone model

In this section we discuss the limit stationary distribution under the following assumption.

**Assumption (I)** The mutation operator \( A \) generates an irreducible semigroup \( (T_t)_{t \geq 0} \) and \( \tilde{\pi} \) is the unique invariant measure in \( M_1(E) \) such that \( T_t^{*} \nu \to \tilde{\pi} \) weakly for any \( \nu \in M_1(E) \) as \( t \to \infty \), where \( T_t^{*} \) is the adjoint for \( T_t \).

**Theorem 4.1.** Under Assumption (I), the generalized stepping stone model with \( \Xi \)-resampling mechanism \( \{\mu(t) \}_{t \geq 0} \) has a unique stationary distribution \( \Pi \in M_1(M_1(E \times E)) \) such that
\[
\int_{M_1(E \times E)} \langle \mu, f \rangle \Pi(d\mu) = \langle \tilde{\pi}, f \rangle,
\]
for any \( \xi \in S \) and \( f \in B(E) \).

**Proof.** The result of the current theorem for the \( \Xi \)-Fleming-Viot process and the classical stepping stone model was proved in Li et al. (2013) and Handa (1990), respectively. Our proof is an adaption of their proofs.

We first show the existence of a stationary distribution for the generalized stepping stone model. As \( (T_t^{*}, T_t^{*}) \mu \to (\tilde{\pi}, \tilde{\pi}) \), the family \( \{(T_t^{*}, T_t^{*}) \mu : t \geq 0 \} \) is pre-compact, and hence, tight in \( M_1(E \times E) \). Thus, for any \( \epsilon > 0 \), there exists a compact subset \( K_\epsilon \) of \( E \times E \) such that \( (T_t^{*}, T_t^{*}) \mu(K_\epsilon^c) < \epsilon \) for all \( t \geq 0 \). Let
\[
K_\epsilon = \{ \mu \in M_1(E \times E) : \mu(K_{ek^{1/2-k}}^c) \leq k^{-1}, \quad \forall \; k \geq 1 \}
\]

For any \( \delta > 0 \), choose \( k \geq 1 \) be such that \( k^{-1} < \delta \). Then for all \( \mu \in K_\epsilon \), we have
\[
\mu(K_{ek^{1/2-k}}^c) \leq k^{-1} < \delta,
\]
and hence, \( K_\epsilon \) is tight in \( M_1(E \times E) \). Then \( K_\epsilon \) is a pre-compact subset of \( M_1(E \times E) \). Note that
\[
\begin{align*}
t^{-1} \int_{0}^{t} \mathbb{Q} [\mu^{-1}(s)] ds(K_\epsilon^c) & := t^{-1} \int_{0}^{t} \mathbb{Q} [\mu(s) \in K_\epsilon^c] ds \\
& = t^{-1} \int_{0}^{t} \mathbb{Q} (\exists \; k \geq 1, \; \mu(s) (K_{ek^{1/2-k}}^c) > k^{-1}) ds \\
& \leq t^{-1} \int_{0}^{t} \sum_{k=1}^{\infty} k \mathbb{Q} \mu(s) (K_{ek^{1/2-k}}^c) ds \\
& = t^{-1} \int_{0}^{t} \sum_{k=1}^{\infty} k (T_s^{*}, T_s^{*}) \mu(K_{ek^{1/2-k}}^c) ds \\
& \leq t^{-1} \int_{0}^{t} \sum_{k=1}^{\infty} k e k^{-1/2-k} ds = \epsilon.
\end{align*}
\]

Thus, the family \( \{t^{-1} \int_{0}^{t} \mathbb{Q}[\mu^{-1}(s)]ds : t \geq 0 \} \) is tight, and hence, pre-compact in \( M_1(M_1(E \times E)) \). Let \( \Pi \) be a limit point. Then there exists a sequence \( (t_n) \) such
that $t_n \uparrow \infty$ and
\[
\lim_{n \to \infty} t_n^{-1} \int_0^{t_n} Q[\mu^{-1}(s)] ds = \Pi.
\]

For any $r \geq 0$,
\[
\Pi[\mu^{-1}(r)] = \lim_{n \to \infty} t_n^{-1} \int_0^{t_n} Q[\mu^{-1}(s)] \circ [\mu^{-1}(r)] ds
\]
\[
= \lim_{n \to \infty} t_n^{-1} \int_{t_n}^{t_n+r} Q[\mu^{-1}(s)] ds
\]
\[
= \Pi.
\]

Namely, $\Pi$ is an invariant measure of the stochastic process $(\mu(t))_{t \geq 0}$.

Recall the moment dual equation
\[
Q\mathbb{E}_{f,\eta,n}(V_{\mu,t}) = \mathbb{P}_{(f,\eta)}\left[\langle \mu_{\eta(t)}, Y(t) \rangle\right]
\]
where $\mathbb{F}_{f,\eta,n} \in C_b(p(M_1(E \times E)))$ with $(f, \eta) \in B(E^n) \times \mathbb{S}^n$. To prove the uniqueness, it suffices to show that the LHS of (16) converges as $t \to \infty$ and the limit does not depend on $\mu$.

By the construction of the dual $(\Xi, A)$-CGM process, we know that $|\eta(t)|$ is non-increasing with respect to $t$ and $\lim_{t \to \infty} |\eta(t)| = 1$. Denote by $\tau = \inf\{t \geq 0 : |\eta(t)| = 1\}$. Note that $\tau < \infty$ a.s. and $(Y(t), \eta(t)) \in B(E) \times \mathbb{S}$ for any $t \geq \tau$. We have
\[
\int_{M_1(E \times E)} \langle \mu_\tau, f \rangle \Pi(d\mu)
\]
\[
= \lim_{t \to \infty} \int_{M_1(E \times E)} \mathbb{P}_{(f,\eta)}(\mu_{\eta(t)}, Y(t)) \Pi(d\mu)
\]
\[
= \lim_{t \to \infty} \int_{M_1(E \times E)} \mathbb{P}_{(f,\eta)} \left[\langle \mu_{\eta(t)}, Y(t) \rangle \mathbb{1}_{\tau \leq t}\right] \Pi(d\mu)
\]
\[
= \lim_{t \to \infty} \int_{M_1(E \times E)} \mathbb{P}_{(f,\eta)} \left[\langle \mu_{\eta(t+\tau)}, Y(t+\tau) \rangle \mathbb{1}_{\tau \leq t}\right] \Pi(d\mu)
\]
\[
= \lim_{t \to \infty} \int_{M_1(E \times E)} \mathbb{P}_{(f,\eta)} \left[\langle T_t^{\tau} \mu_{\eta(t+\tau)}, Y(t+\tau) \rangle \right] \Pi(d\mu)
\]
\[
= \mathbb{P}_{(f,\eta)}(\tilde{\pi}, Y(\tau))
\]

Thus, (15) follows from (17) with $n = 1$. \hfill $\square$

5. Reversibility of the generalized stepping stone model

In this section we discuss the reversibility of the generalized stepping stone model $(\mu(t))_{t \geq 0}$. In view of the well-known results on probability-measure-valued stochastic process in the literature, we make the following assumption.

**Assumption (II)** The mutation operator $A$ is of the uniform type, i.e.
\[
Af(x) = \frac{\theta}{2} \int_E (f(y) - f(x)) \nu_0(dy)
\]
for some $\theta > 0$, $\nu_0 \in M_1(E)$ and $f \in B(E)$. 

The generalized stepping stone model with $\Xi$-resampling mechanism $(\mu(t))_{t \geq 0} = (\mu_1(t), \mu_2(t))_{t \geq 0}$ with stationary distribution $\Pi$ is reversible if for any non-negative integers $n, m, p$ and $q$, we have

$$
Q_{\Pi} \left( \left( \langle \mu_1(t)^{\otimes n}, f^1 \rangle, \langle \mu_2(t)^{\otimes m}, f^2 \rangle \right), \left( \langle \mu_1(t)^{\otimes p}, g^1 \rangle, \langle \mu_2(t)^{\otimes q}, g^2 \rangle \right) \right) =
Q_{\Pi} \left( \left( \langle \mu_1(t)^{\otimes p}, g^1 \rangle, \langle \mu_2(t)^{\otimes q}, g^2 \rangle \right), \left( \langle \mu_1(t)^{\otimes n}, f^1 \rangle, \langle \mu_2(t)^{\otimes m}, f^2 \rangle \right) \right),
$$

where $f^1 \in B(E^n)$, $f^2 \in B(E^m)$, $g^1 \in B(E^p)$, $g^2 \in B(E^q)$ and $\mathcal{L}$ is the generator defined in (17).

**Theorem 5.2.** Assuming $\theta > 0$, $u > 0$ and $v > 0$, the generalized stepping stone model with $\Xi$-resampling mechanism is not reversible.

**Proof.** The proof is based on computations of moments and joint moments of different orders. The software Maple is used to carry out symbolic calculations. We sketch the main steps and refer to Appendix for more details.

Let $E^*$ be any subset of $E$ with $\nu_0(E^*) = \alpha > 0$. We start with $(p, q) = (0, 0)$. By choosing different values of $n, m, f^1$ and $f^2$ in (18), expressions for the moments and joint moments

$$
Q[\mu_1(E^*)], Q[\mu_2(E^*)], Q[\mu_1(E^*)]\mu_2(E^*), Q[\mu_2(E^*)], Q[\mu_1^2(E^*)], Q[\mu_1^3(E^*)], Q[\mu_1^4(E^*)], Q[\mu_1^3(E^*)]\mu_2(E^*), Q[\mu_1^2(E^*)]\mu_2^2(E^*),
$$

are all available.

We then consider the case that $(p, q) \neq (0, 0)$. For $(n, m) = (1, 0), (p, q) = (0, 1)$ and $f^1 = g^2 = \mathbb{I}_{E^*}$, by (18) we have that the condition $u = v$ is necessary for the process being reversible. Further substituting

$$(n, m) = (2, 0), (p, q) = (0, 1) \text{ and } f^1 = \mathbb{I}_{E^* \times E^*}, g^2 = \mathbb{I}_{E^*},$$

in (18), we have that the condition $\alpha = 1/2$ is necessary for the process being reversible. Given $\alpha = 1/2$ and $v = u$, we choose

$$(n, m) = (1, 1), (p, q) = (2, 0), f^1 = f^2 = \mathbb{I}_{E^*}, g^3 = \mathbb{I}_{E^* \times E^*},$$

and

$$(n, m) = (2, 1), (p, q) = (1, 0), f^1 = \mathbb{I}_{E^* \times E^*}, f^2 = g^1 = \mathbb{I}_{E^*},$$

in (18), respectively. Note that the two equations can not hold at the same time and we reach a contradiction. Thus, the process is not reversible. \hfill \square

6. Appendix

In this section we carry out the calculations in the proof of Theorem 5.2 in detail. For simplicity of notation, we write

$$a_2 = \lambda_{2;2}, a_{21} = \lambda_{3;2}, a_3 = \lambda_{3;3}, a_{211} = \lambda_{4;2}, a_{22} = \lambda_{4;3}, a_{31} = \lambda_{4;3}, a_4 = \lambda_{4;4}.$$ 

Let $E^*$ be a subset of the type space $E$ with $\nu_0(E^*) = \alpha > 0$. For any positive integers $n$ and $m$, the joint moments are defined as

$$M_{n,m} = Q[\mu_1^n(E^*)\mu_2^m(E^*)].$$

We begin with the discussion for the first moments, i.e. $n + m = 1$. For $(n, m) = (1, 0), (p, q) = (0, 0)$ and $f^1 = \mathbb{I}_{E^*}$ in (18), we have

$$\left(\frac{\theta}{2} + v\right)M_{1,0} - vM_{0,1} = \frac{\theta\alpha}{2}. \tag{19}$$
For \((n, m) = (0, 1)\), \((p, q) = (0, 0)\) and \(f^2 = \mathbb{I}_{E^*}\) in \([18]\), we have
\[
(20) \quad -uM_{1,0} + \left(\frac{\theta}{2} + u\right) M_{0,1} = \frac{\theta \alpha}{2}.
\]
By \([19]\) and \([20]\) we have \(M_{1,0} = M_{0,1} = \alpha\).

Then we consider the second moments, i.e. \(n + m = 2\).
For \((n, m) = (2, 0)\), \((p, q) = (0, 0)\) and \(f^1 = \mathbb{I}_{E^* \times E^*}\) in \([18]\), we have
\[
(21) \quad \left(\theta + 2v + a_2\right) M_{2,0} - 2vM_{1,1} = \theta \alpha^2 + a_2 \alpha.
\]
For \((n, m) = (0, 2)\), \((p, q) = (0, 0)\) and \(f^2 = \mathbb{I}_{E^* \times E^*}\) in \([18]\), we have
\[
(22) \quad -2uM_{1,1} + \left(\theta + 2u + a_2\right) M_{0,2} = \theta \alpha^2 + a_2 \alpha.
\]
For \((n, m) = (1, 1)\), \((p, q) = (0, 0)\) and \(f^1 = f^2 = \mathbb{I}_{E^*}\) in \([18]\), we have
\[
(23) \quad -uM_{2,0} + \left(\theta + v + u\right) M_{1,1} - vM_{0,2} = \theta \alpha^2.
\]
Equations \((21)-(23)\) constitutes a system of linear equations. Note that the coefficient matrix of \(M_{2,0}, M_{1,1}, M_{0,2}\) is invertible. Thus, the solution is unique. Substituting \((n, m) = (1, 0)\), \((p, q) = (0, 1)\) and \(f^1 = \mathbb{I}_{E^*}, g^2 = \mathbb{I}_{E^*}\) in \([18]\), we have the reversible equation
\[
(24) \quad (u - v) M_{1,1} - uM_{2,0} + vM_{0,2} = 0.
\]
Replacing the second moments, the numerator of \((21)\) equals to 0, i.e. \(\alpha \theta a_2 \left(\frac{\theta}{2} + u\right) \left(\theta + 2u + a_2 + 2v\right) (\alpha - 1) = 0\).

Thus, a necessary condition for this process being reversible is that \(u = v\).

Now we continue to consider the third moments, i.e. \(m + n = 3\).
For \((n, m) = (3, 0)\), \((p, q) = (0, 0)\) and \(f^1 = \mathbb{I}_{E^* \times E^* \times E^*}\) in \([18]\), we have
\[
(25) \quad \left(3a_{21} + a_3 + \frac{3}{2} \theta + 3v\right) M_{3,0} - 3vM_{2,1} = \left(3a_{21} + \frac{3}{2} \alpha \theta\right) M_{2,0} + a_3 \alpha.
\]
For \((n, m) = (2, 1)\), \((p, q) = (0, 0)\) and \(f^1 = \mathbb{I}_{E^* \times E^*}, f^2 = \mathbb{I}_{E^*}\) in \([18]\), we have
\[
(26) \quad -uM_{3,0} + \left(a_2 + \frac{3}{2} \theta + 2v + u\right) M_{2,1} - 2vM_{1,2} = \left(\alpha \theta + a_2\right) M_{1,1} + \frac{\theta \alpha}{2} M_{2,0}.
\]
For \((n, m) = (1, 2)\), \((p, q) = (0, 0)\) and \(f^1 = \mathbb{I}_{E^*}, f^2 = \mathbb{I}_{E^* \times E^*}\) in \([18]\), we have
\[
(27) \quad -2uM_{2,1} + \left(a_2 + \frac{3}{2} \theta + v + 2u\right) M_{1,2} - vM_{0,3} = \left(\alpha \theta + a_2\right) M_{1,1} + \frac{\theta \alpha}{2} M_{0,2}.
\]
For \((n, m) = (0, 3)\), \((p, q) = (0, 0)\) and \(f^1 = \mathbb{I}_{E^* \times E^* \times E^*}\) in \([18]\), we have
\[
(28) \quad -3uM_{1,2} + \left(3a_{21} + a_3 + \frac{3}{2} \theta + 3u\right) M_{0,3} = \left(3a_{21} + \frac{3}{2} \alpha \theta\right) M_{0,2} + a_3 \alpha.
\]
Equations \((25)-(28)\) constitutes a system of linear equations and the coefficient matrix for \(M_{3,0}, M_{2,1}, M_{1,2}, M_{0,3}\) is invertible. Thus, the system of equation has a unique solution. Substituting \((n, m) = (2, 0)\), \((p, q) = (0, 1)\) and \(f^1 = \mathbb{I}_{E^* \times E^*}, g^2 = \mathbb{I}_{E^*}\) in \([18]\), we have
\[
(29) \quad \left(\alpha \theta + a_2\right) M_{1,1} - \frac{\theta \alpha}{2} M_{2,0} - \left(2v + a_2 + \theta \frac{\alpha}{2} - u\right) M_{2,1} - uM_{3,0} + 2vM_{1,2} = 0.
\]
Note that \(a_2 = a_{21} + a_3\). Substituting the expressions for the moments, we have the numerator of \((29)\) equal to 0, i.e.
\[
4 \alpha \theta^2 u (\alpha - 1) \left(3a_{21}^2 + a_3^2 + 8a_3u + 2a_3\theta + 4a_3a_{21}\right) (-1 + 2 \alpha) = 0.
\]
So far we conclude that the process is not reversible except the case when there exists a subset \(E^* \subseteq E\) with \(\alpha = \nu_0 (E^*) = 1/2\).
For the case of $\alpha = 1/2$, we need higher moments to reach a contradiction. For $(n, m) = (4, 0)$, $(p, q) = (0, 0)$ and $f^1 = I_{E^* \times E^* \times E^*}$ in (18), we have

$$
(4v + 6a_{211} + 3a_{22} + 4a_{31} + a_4 + 2\theta) M_{4,0} - 4vM_{31}
$$

(30)

$$
= (2\theta + a + 6a_{211}) M_{3,0} + (3a_{22} + 4a_{31}) M_{2,0} + a_4 v.
$$

For $(n, m) = (3, 1)$, $(p, q) = (0, 0)$ and $f^1 = I_{E^* \times E^* \times E^*}$, $f^2 = I_{E^*}$ in (18), we have

$$
-um_{4,0} + (a_3 + 3a_{21} + 2\theta + 3v + u) M_{3,1} - 3vM_{2,2}
$$

(31)

$$
= \left(3a_{21} + 3\theta \alpha \right) M_{2,1} + a_3 M_{1,1} + \frac{\theta \alpha}{2} M_{3,0}.
$$

For $(n, m) = (2, 2)$, $(p, q) = (0, 0)$ and $f^1 = I_{E^* \times E^*}$, $f^2 = I_{E^* \times E^*}$ in (18), we have

$$
-2uM_{3,1} + (2a_2 + 2\theta + 2v + 2u) M_{2,2} - 2vM_{1,3}
$$

(32)

$$
= (\theta + a_2) M_{1,2} + (\theta + a_2) M_{2,1}.
$$

For $(n, m) = (1, 3)$, $(p, q) = (0, 0)$ and $f^1 = I_{E^*}$, $f^2 = I_{E^* \times E^* \times E^*}$ in (18), we have

$$
-3uM_{2,2} + (2\theta + v + 3u + 3a_{21} + a_3) M_{1,3} - vM_{0,4}
$$

(33)

$$
= \frac{\theta \alpha}{2} M_{0,3} + \left(3a_{21} + \frac{3\theta \alpha}{2}\right) M_{1,2} + a_3 M_{1,1}.
$$

For $(n, m) = (0, 4)$, $(p, q) = (0, 0)$ and $f^2 = I_{E^* \times E^* \times E^* \times E^*}$ in (18), we have

$$
-4uM_{1,3} + (6a_{211} + 3a_{22} + 4a_{31} + a_4 + 2\theta + 4u) M_{0,4}
$$

(34)

$$
= (2\theta + a_2) M_{0,3} + (3a_{22} + 4a_{31}) M_{0,2} + a_4 \alpha.
$$

We solve for $M_{4,0}$, $M_{3,1}$, $M_{2,2}$, $M_{1,3}$, $M_{0,4}$ uniquely from (30)-(34) which is also a system of linear equations with invertible coefficient matrix. Substituting $(n, m) = (1, 1)$, $(p, q) = (2, 0)$ and $f^1 = f^2 = I_{E^*}$, $g^1 = I_{E^* \times E^*}$, we have

$$
\frac{\theta \alpha}{2} M_{3,0} - \left(a_2 + \frac{\theta \alpha}{2}\right) M_{2,1} - vM_{2,2} + uM_{4,0} + (a_2 - u + v) M_{3,1} = 0.
$$

(35)

Substituting $(n, m) = (2, 1)$, $(p, q) = (1, 0)$ and $f^1 = I_{E^* \times E^*}$, $f^2 = g^1 = I_{E^*}$, we have

$$
\left(a_2 + \frac{\theta \alpha}{2}\right) M_{2,1} + \frac{\theta \alpha}{2} M_{3,0} - (\theta + v + u + a_2) M_{3,1} + vM_{2,2} + uM_{4,0} = 0.
$$

(36)

Substituting all the joint moments, the numerator of

$$
(35) - 2 \times (36) = 0
$$

is equivalent to

$$
(\theta + 4u) \theta u a_3 - 8a_4u - 4a_4a_3 - 4\theta a_4 + 8a_3^2 + 22a_3u + 11a_3\theta + 8a_21^2 + 16a_21a_3
$$

$$
+ 12a_{211}a_3 - 4a_4a_21 + 10a_21u + 5a_21\theta + 3a_{211}\theta + 6a_{211}u + 12a_{211}a_{211} = 0.
$$

(37)

The term in the second parentheses is always positive because

$$
-8a_4u + 22a_3u \geq 0, -4a_4a_3 + 8a_3^2 \geq 0, -4\theta a_4 + 11a_3\theta \geq 0
$$

and

$$
-4a_4a_{211} + 16a_{211}a_3 \geq 0.
$$

Since $u > 0$ and $\theta > 0$, a necessary condition for (37) is that $a_3 = 0$. By the consistent condition of coalescent rates

$$
\begin{align*}
a_2 &= a_21 + a_3; \\
a_3 &= a_31 + a_4; \\
a_{211} &= a_{211} + a_{22} + a_{31},
\end{align*}
$$

we have

$$
\begin{align*}
a_2 &= a_21 + a_3; \\
a_3 &= a_31 + a_4; \\
a_{211} &= a_{211} + a_{22} + a_{31},
\end{align*}
$$

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$a_3 = 0$ implies that $a_4 = a_{31} = a_{22} = 0$ and $a_2 = a_{21} = a_{211} =: a > 0$. Substituting these values into the numerator of (35), we get $4a^3 = 0$ which contradicts $a > 0$. Therefore, the process is not reversible.

A Maple note for all the calculations carried out in this paper is available upon request.

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