Annual Review (*Inst. Nat. Sci., Nagoya City Univ.*), *Vol. 2, 13-23 (1997)*

A genealogical problem of a stepping stone Fleming-Viot process

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Key words and phrases: Fleming-Viot process, stepping stone model, infinite-sites-model, genealogy, Kingman's coalescent process

Abstract

A measure valued diffusion is discussed which describes the infinite-sites-model with stepping stone structure. The average probability that there exist s segregating sites in randomly chosen two genes at the stationary state is written in terms of the coalescent time of the dual process.

1. Introduction

Let E be the space defined by

$$E=[0,1]^{Z_+}=\{x=(x_0,x_1,\cdots,x_n,\cdots)\ ;\ x_n\in[0,1] \quad \text{for all } n\in Z_+\},$$

and S be a countable (or finite) set, where Z_+ denotes the non-negative integers. $P(E)$ stands for the Borel probability measures on E with the topology of weak covergence, and $\widetilde{P}$ is defined by

$$\widetilde{P}=\{\widetilde{\mu}\equiv(\mu_k)_{k\in S}\ ;\ \mu_k\in P(E),\ k\in S\},$$

with the product topology.

We consider a $\widetilde{P}$ -valued diffusion process characterized by a positive constant θ and constants $m_{k_1k_2}, k_1, k_2\in S$. S is called the set of colonies, and the constant $(1/2)\ \theta$ and the matrix $\{m_{k_1k_2}\}$ are called the mutation rate and the migration rates respectively. The generator of the diffusion is written in terms of random sampling, mutation and migration. The precise definition of the diffusion is given in Section 2. Our diffusion is known to have a unique stationary distribution[5], denoted by $\widetilde{Q}(d\widetilde{\mu})$ which is a probability measure on $\widetilde{P}$.

Define A_s, for $s\in Z_+$, by

$$A_s=\{(x,y)\in E^2\ ;\ x=(x_0,x_1,\cdots)\in E \text{ and } y=(y_0,y_1,\cdots)\in E$$

satisfy

(i) $x_0, x_1, \cdots$ are distinct, and $y_0, y_1, \cdots$ are distinct,

and

(ii) there exist l and m$\in Z_+$ such that

(a) $l+m=s$,

(b) $x_l=y_m$,

(c) $x_0,\cdots,x_{l-1},y_0,\cdots,y_{m-1}$ are distinct,

(d) $x_{l+j}=y_{m+j}$ for all $j\in Z_+$ }.

Here, in the condition (c) of (ii), the set $\{x_0, \cdots, x_{l-1}\}$ is regarded as empty if $l=0$, and the set $\{y_0, \cdots, y_{m-1}\}$ is considered in the same way for $m=0$.
We consider a Markov chain $\{k(t)\}$ with state space $S \cup S^2 \cup S^3 \cup \cdots$. The definition of $\{k(t)\}$ is given in Section 2. The coalescent time T of the Markov chain is the first passage time to the set S. I_{A_S} denotes the indicator function of A_S.

Our main result is stated as follows:

$$(1.1) \qquad \int <1_{A_S}, \mu_{k_1} \times \mu_{k_2}> \widetilde{Q}(d\widetilde{\mu}) = E_{(k_1,k_2)}[\, e^{\theta T} \frac{(\theta T)^s}{s!}; T<\infty \,],\ (k_1,k_2) \in S^2,$$

where $<1_{A_s}, \mu_{k_1} \times \mu_{k_2}>$ is the integral of 1_{A_s} with respect to the product measure $\mu_{k_1} \times \mu_{k_2}$. This statement appears in Corollary 5.1.

An element $x \in E$ is called a type of genes, and $x_0, x_1, \cdots, x_n, \cdots$ are called sites where mutations have occurred in the lines of descent of the gene. x_0 is the site at which the most recent mutation have occurred. $A_s \subset E^2$ is the set of pairs of types which have s segregating sites. For $(x,y) \in A_s$, there exist l and m $\in Z_+$ appeared in the definition A_s. Here, $(x_l, x_{l+1}, x_{l+2}, \cdots) = (y_m, y_{m+1}, y_{m+2}, \cdots)$ is called a common ancestor of x and y. $<1_{A_s}, \mu_{k_1} \times \mu_{k_2}>$ stands for the probability with respect to $\widetilde{\mu}$ that the pair of types chosen from colonies k_1 and k_2 independently has s segregating sites. The left-hand side of (1,1) is the average (with respect to $\widetilde{Q}(d\widetilde{\mu})$) quantity of $<1_{A_s}, \mu_{k_1} \times \mu_{k_2}>$. The right-hand side is determined by the Markov chain $\{k(t)\}$.

In section 2, we give a precise statement of our problem and the main result (Theorem 2.4). Section 3 is devoted to the key,Theorem 3.1, for the proof of Theorem 2.4. In Section 4, we give the proof of Theorem 2.4. A corollary of Theorem 2.4 is given in Section 5. In Section 6, two examples are given,where the set S is assumed to be the d-dimensional lattice Z^d.

2. Preliminaries

Define E^m, $m \in N$, by the set

$$E^m = E \times E \times \cdots \times E \text{ (m-fold)}$$

with the product topology, where N denotes the set of natural numbers. $C(E^m)$ denotes the space of continuous functions on E^m, and $B(E^m)$ stands for the space of bounded Borel measurable function on E^m. Here, for each $m \in N$, we introduce the operators ϕ_{ij}, $1 \le i < j \le m$, $\phi_{ij}: B(E^m) \to B(E^{m-1})$ and $L_i, 1 \le i \le m$, $: B(E^m) \to B(E^m)$, are given by

$$(\phi_{ij} f)(x_1, \cdots x_{m-1}) = f(x_1, \cdots, x_{j-1}, x_i, x_j, \cdots, x_{m-1})$$

and

$$(L_i f)(x_1, \cdots, x_m) = \frac{1}{2}\theta \int_0^1 \{f(x_1, \cdots, x_{j-1}, (u, x_i), x_m) - f(x_1, \cdots, x_m)\} du,$$

for $f \in B(E^m)$, where $x_i \in E$ $(i=1,2,\cdots,m)$, and where $(u,x) = (u, x_0, x_1, \cdots) \in E$ for $x = (x_0, x_1, \cdots) \in E$.

Throughout this paper, the constant θ is assumed to be positive. For $f \in B(E^m)$ and $k = (k_1, k_2, \cdots, k_m) \in S^m$, we put

$$\phi_{f,k}(\widetilde{\mu}) = <f, \widetilde{\mu_k}>,$$

where $\widetilde{\mu} = (\mu_k)_{k \in S} \in \widetilde{P}$ and $\widetilde{\mu_k}$ is the product measure $\mu_{k_1} \times \mu_{k_2} \times \cdots \times \mu_{k_m}$. Now, we are in position to define the generator G of our $\widetilde{P}$-valued diffusion process. Define G for $f \in B(E^m)$ by

$$(G\phi_{f,k})(\widetilde{\mu}) = \sum_{i=1}^{m} <L_i f, \widetilde{\mu_k}> + \sum_{k' \in S} \sum_{i=1}^{m} m_{k' k_i} <f, \widetilde{\mu_{\gamma_i(k')k}}> + \sum_{\substack{1 \le i < j \le m \\ k_i = k_j}} (<\phi_{ij} f, \widetilde{\mu_{\beta_j k}}> - <f, \widetilde{\mu_k}>),$$

where $\beta_j k = (k_1, \cdots, k_{j-1}, k_{j+1}, \cdots, k_m) \in S^{m-1}$ for $j \ge 2$, and $\gamma_i(k')k = (k_1, \cdots, k_{i-1}, k', k_{i+1}, \cdots, k_m) \in S^m$ for $1 \le i \le m$.

We assume in this paper that the coefficients $m_{k_1k_2}, k_1, k_2 \in S$, satisfy

$$m_{k_1k_2} \geq 0 \text{ for } k_1 \neq k_2$$

and

$$sup_k |m_{kk}| < +\infty \quad \text{with } m_{kk} \equiv -\Sigma_{k' \neq k} m_{k'k}.$$

Define $A \subset C(\widetilde{P}) \times C(\widetilde{P})$ by

$$A = \{(\phi_{f,k}, G\phi_{f,k}) ; m \in N, k \in S^m, f \in C(E^m)\}.$$

$C([0, \infty), \widetilde{P})$ denotes the space of continuous functions $\omega : [0, \infty) \to \widetilde{P}$ with the topology of uniform convergence on compact subsets of $[0, \infty)$. The coordinate process $\widetilde{\mu}(t) = \{\mu_k(t)\}_{k \in S}; t \geq 0\}$ on $\Omega = C([0, \infty), \widetilde{P})$ is defined by

$$\widetilde{\mu}(t)(\omega) = \omega(t), \omega \in \Omega,$$

and we set the σ -fields

$$F = \sigma(\widetilde{\mu}(s); s \geq 0) \text{ and } F_t = \sigma(\widetilde{\mu}(s); 0 \leq s \leq t) \quad \text{for } t \geq 0.$$

Define the martingale problem as follows.

Definition 2.1. For $\widetilde{\mu}^0 \in \widetilde{P}$, a probability measure $\boldsymbol{P}$ on $(C[0, \infty), \widetilde{P}), F)$ is called a solution of the $C([0, \infty), \widetilde{P})$ martingale problem for $(A, \widetilde{\mu}^0)$ if $\boldsymbol{P}(\widetilde{\mu}(0) = \widetilde{\mu}^0) = 1$, and if

$$\phi_{f,k}(\widetilde{\mu}(t)) - \int_0^t (G\phi_{f,k})(\widetilde{\mu}(s)) ds,$$

is a $(\boldsymbol{P}, \{F_t\})$-martingale for all $(\phi_{f,k}, G\phi_{f,k}) \in A$.

The following two propositions are essentially due to K. Handa[5]. By Theorem 3.2 and 3.7 of his paper, we have the next proposition.

Proposition 2.2.

For any $\widetilde{\mu}^0 \in \widetilde{P}$, there exists a unique solution $\boldsymbol{P}$ of the $C([0, \infty), \widetilde{P})$ martingale problem for $(A, \widetilde{\mu}^0)$. That is, the $C([0, \infty), \widetilde{P})$ martingale problem is well posed.

The definition of the martingale problem in [5] is slightly different from ours. In [5], the class of functions f in the definition of the set A is restricted to the family of continuous functions on $\boldsymbol{E}$ which can be represented in the form

(2.1) $\quad f(x) = f_1(x) \cdots f_m(x), \; f_i \in C(\boldsymbol{E}).$

However, it is obvious that Proposition 2.2 is obtained from Theorem 3.2 ans 3.7 in [5], because any $f \in C(\boldsymbol{E}^m)$ can be approximated uniformly by a sequence of finite linear combinations of functions having form(2.1).

We set

$$Pf(x) = \int_0^1 f((u, x)) du$$

and

$$(\widetilde{L}f)(x) = \frac{1}{2}\theta(P - I)f, \quad \text{for } f \in B(\boldsymbol{E}) \equiv B(\boldsymbol{E}^1),$$

where I is the identity operator. Obviously, $\widetilde{L}$ is the infinitesimal generator of a Feller semigroup $T_t \equiv e^{\widetilde{L}t}$ on $C(\boldsymbol{E}) = C(\boldsymbol{E}^1)$.

Define $C_m(E)$ by

$C_m(E)=\{f\in C(E); f(x)=f(x')$ if $x_0=x'_0, \cdots, x_m=x'_m$ for $x=(x_0,x_1,\cdots)$ and $x'=(x'_0,x'_1,\cdots)$ in $E\}$, $m\in Z_+$.

Let λ be the Lebesgue measure on $[0,1]$, and λ^∞ is the product measure $\lambda\times\lambda\times\cdots$ on E. For $f\in B(E)$, $<f>$ denotes $\int_E f(x)\lambda^\infty(dx)$. For any $f\in C_m(E)$,

$$T_t f=e^{-\frac{1}{2}\theta t}\sum_{k=0}^{\infty}\frac{\left(\frac{1}{2}\theta t\right)^k}{k!}P^k f=e^{-\frac{1}{2}\theta t}\sum_{k=0}^{m}\frac{\left(\frac{1}{2}\theta t\right)^k}{k!}(P^k f-<f>)+<f>\to<f>$$

uniformly on E, as $t\to+\infty$.

Since $\cup_{m=0}^{+\infty}C_m(E)$ is dense in $C(E)$, the assumption of Theorem 5.1 in [5] is satisfied. Hence, we obtain the next proposition. Here, $P(\widetilde{P})$ denotes the set of Borel probability measures on $\widetilde{P}$.

Proposition 2.3. The measure valued diffusion process $\{\widetilde{\mu}(t); t\geq 0\}$ corresponding to the solution of the $C([0,+\infty),\widetilde{P})$ martingale problem for A is ergodic in a weak sense. Namely, there exists a uniquely stationary distribution $\widetilde{Q}\in P(\widetilde{P})$, and

$$\lim_{t\to+\infty}E_{\mu_0}^{P}[<f,\widetilde{\mu}(t)_k>]=\int_{\widetilde{P}}<f,\widetilde{\mu_k}>\widetilde{Q}(d\widetilde{\mu})$$

holds for any $(f,k)\in\bigcup_{m=1}^{+\infty}(C(E^m)\times S^m)$.

Let $K=\{k(t); t\geq 0\}$ be a Markov chain on the state space $S^*=\cup_{n=0}^{\infty}S^m$, whose generator is of the form

$$Lh(k)=\sum_{j=2}^{|k|}\#\{i; 1\leq i<j, k_i=k_j\}\{h(\beta_j k)-h(k)\}+\sum_{i=1}^{|k|}\sum_{k'\neq k_i}\{m_{k'k_i}(h(\gamma_i(k')k-h(k))\},\ k\in S^*,$$

for any bounded function $h: S^*\to R$, where k_i is the ith component of k and $|k|$ is a positive constant m such that $k\in S^m$. For $k\in S^m$, $\lambda(k)$ denotes the transition rate from k.

That is,

$$\lambda(k)=\#\{(i,j); 1\leq i<j\leq|k|,\ k_i=k_j\}+\sum_{i=1}^{|k|}\sum_{k'\neq k_i}m_{k'k_i}.$$

Define T by $T=inf\{t\geq 0; |k(t)|\leq 1\}$.

The Markov chain $\{k(t);\geq 0\}$ is a generalized Kingman's coalescent process, and the stopping time T is called the coalescent time of the Markov chain. For any $l,m\in Z_+$, define $A_{(l,m)}$ by

$A_{(l,m)}=\{(x,y)\in E^2; x=(x_0,x,\cdots)\in E$ and $y=(y_0,y_1,\cdots)\in E$ satisfy

1. $x_0,x_1,\cdots$ are distinct and $y_0,y_1,\cdots$ are distinct,
2. $x_l=y_m$ and $x_0,x_1,\cdots x_{l-1},y_0,y_1,\cdots y_{m-1}$ are distinct,
3. $x_{l+j}=y_{m+j}$ for all $j\in Z_+\}$.

Now, we can state our main result.

Theorem 2.4. The equality

$$\int<1_{A(l,m)},\mu_{k_1}\times\mu_{k_2}>\widetilde{Q}(d\widetilde{\mu})=E_k[e^{-\theta T}\frac{\left(\frac{1}{2}\theta T\right)^{(l+m)}}{l!m!};T<+\infty],\tag{2.2}$$

holds for any $k=(k_1,k_2)\in S^2$, where $1_{A(l,m)}$ denotes the indicator function of the set $A(l,m)$.

The integrand of the left-hand side is the probability with respect to a random distribution $\widetilde{\mu}$ that the pair of x and y chosen independently from colonies k_1 and k_2 belongs to the set $A(l,m)$. The left-hand side is the expectation of the above probability with respect to the measure $\widetilde{Q}(d\widetilde{\mu})$ on $\widetilde{P}$ which is the stationary distribution of the measure-valued diffusion $\{\widetilde{\mu}(t)\}_t \geq 0$. The integrand of the right -hand side is a functional of the Markov chain $\{k(t)\}_{t\geq 0}$, and the right-hand side is the expectation of the functional with respect to the measure P_k of the Markov chain.

3. Dual process of the measure valued diffusion process

First, define random operators $\{\Gamma_n\}_{n\geq 1}$ for $l \in N$. Let $\{\tau_n\}_{n\geq 0}$ be the sequence of jump times of the Markov chain $\{k(t)\}_{t\geq 0}$, where $\tau_0=0$. $\{\Gamma_n\}_{n\geq 0}$ denotes a sequence of random operators which are conditionally independent given $K=\{k(t)\,;t\geq 0\}$ and satisfy

$$P[\Gamma_n=\phi_{ij}\,|K]=\#\{l\,;1\leq l<j,\ k_l(\tau_n-)=k_j(\tau_n-)\}^{-1}\times \mathbf{1}_{\{k(\tau_n)=\beta_j k(\tau_n-),\ \text{and}\ k_i(\tau_n-)=k_j(\tau_n-)\}} \quad \text{for } 1\leq u<j,$$

and

$$P[\Gamma_n=identity|K]=\mathbf{1}_{\{|k(\tau_n)|=|k(\tau_n-)|\}}.$$

Here, $\mathbf{1}_\Lambda$ denotes the indicator function of an event Λ.

Since the operator $\sum_{i=1}^{l} L_i$, $l\in N$, is bounded on the both spaces $C(E^l)$ and $B(E^l)$, the family of operators $\{T_l(t)\}_{t\geq 0}$ given by $T_l(t)=exp\{t\sum_{i=1}^{l} L_i\}$ is a Feller semigroup on $C(E^l)$, and a strongly continuous semigroup on $B(E^l)$. We set $M(t)=|k(t)|$. Let us define a $\bigcup_{m=1}^{\infty} B(E^m)$-valued process $\{Y(t)\,;t\geq 0\}$ by

$$Y(0)\in B(E^{M(0)}),$$

$$Y(t)=T_{M(\tau_n)}(t-\tau_n)\,Y(\tau_n) \qquad \text{for } t\in[\tau_n,\tau_n),$$

and

$$Y(\tau_{n+1})=\Gamma_{n+1}T_{M(\tau_n)}(\tau_{n+1}-\tau_n)\,Y(\tau_n)$$

for $n\in Z_+$.

Let P be the solution of the martingale problem $(A,\widetilde{\mu}^0)$, and $\{\widetilde{\mu}(t)\,;t\geq 0\}$ be the coordinate process on $\Omega=C([0,\infty),\widetilde{P})$. The process $\{Y(t),\,K(t)\,;t\geq 0\}$ is called the dual process of the measure valued diffusion process $(\{\widetilde{\mu}(t)\,;t\geq 0\},P)$. Now, we are in position to give a key statemant to prove Theorem 2.5.

Theorem 3.1. Let (f,k) be any element of the set $\bigcup_{m=1}^{\infty}(B(E^m)\times S^m)$. Then, the equality

$$E^P[<f,\widetilde{\mu}(t)_k>]=E_{(f,k)}[Y(t),\widetilde{\mu}^0_{k(t)}>] \tag{3.1}$$

holds for any $t\geq 0$

This is a modified statement of Theorem 3.5 in [5]. He has established the relation (3.1) for any (f,k) of $\bigcup_{m=1}^{+\infty}(C(E^m)\times S^m)$. Note that the continuity of f is not assumed in Theorem 3.1.

Since the proof is almost the same as that of Theorem 3.5 in [5], we will give only the outline of our proof in the rest of this section.

First, we note the following. We can construct the $\widetilde{P}$-valued process $\{\widetilde{\mu}(t)\,;t\geq 0\}$ whose distribution is P and the dual process $\{(Y(t),k(t))\,;t\geq 0\}$ starting from (f,k) on the same probability space so that these two processes are mutually independent. Fix $t \in (0, \infty)$, and set

$$F(s)=E[< Y(s), \widetilde{\mu}(t-s)_{k(s)} >] \quad \text{for } 0 \leq s \leq t$$

Then (3.1) is equivalent to the identity $F(0)=F(t)$.

We set

$$I(h)=E[< Y(s+h), \widetilde{\mu}(t-s-h)_{k(s+h)} >],$$

then, the next lemma can be proved by the same way as the proof of Proposition 4.1 in [5].

Lemma 3.2. If

(3.2) $\quad |I(h)-I(0)| \leq O(h^2)$

holds as $h \downarrow 0$ uniformly in $s \in [0, t)$, then (3.1) is valid.

Set

(3.3) $\quad I(h)=I_1(h)+I_2(h)+I_3(h)+R(h)$

where

(3.4) $\quad I_1(h)=E[< T_{M(s)}(h) Y(s), \widetilde{\mu}(t-s-h)_{k(s)} >],$

$$I_2(h)=E[\sum_{1 \leq i < j \leq M(s)} \int_0^h (< T_{M(s)-1}(h-r) \phi_{ij} T_{M(s)}(r) Y(s), \widetilde{\mu}(t-s-h)_{\beta_j k(s)} >$$

$$- < T_{M(s)}(h) Y(s), \widetilde{\mu}(t-s-h)_{k(s)} >) dr],$$

$$I_3(h)=E[\sum_{i=1}^{M(s)} \sum_{k' \in S} m_{k' k_i(s)} < T_{M(s)}(h) T(s) Y(s) \widetilde{\mu}(t-s-h)_{\gamma_i(k') k(s)} >] \times h,$$

$$R(h)=I(h)-(I_1(h)+I_2(h)+I_3(h)).$$

The inequality,

(3.5) $\quad |R(h)| \leq O(h^2) \quad$ uniformly in s as $h \downarrow 0$,

can be verified by the same argument as that of Proposition 4.2 in [5].

Here, we give a remark on the solution $\boldsymbol{P}$ of the martingale problem for $(A, \widetilde{\mu}^0)$ which is stated in Proposition 2.2.

Proposition 3.3. Let $|\boldsymbol{k}|=m$ and $f \in B(\boldsymbol{E}^m)$.

$$M_{f,k}(t) \equiv \phi_{f,k}(\widetilde{\mu}(t)) - \int_0^t (G\phi_{f,k})(\widetilde{\mu}(s)) ds$$

is a $(\boldsymbol{P}, \{F_t\})$-martingale whose sample paths belong to $C([0, \infty); R)$ almost surely.

Proof. We can easily show that

$$D_1^m = \{f \in B(\boldsymbol{E}^m) ; M_{f,k}(t) \text{ is a } (P, \{F_t\})\text{-martingale}\}$$

is closed with respect to the bounded pointwise convergence. Since D_1^m includes $C(\boldsymbol{E}^m)$, we see that $D_1^m = B(\boldsymbol{E}^m)$.

Next, $X(t) \equiv \phi_{f,k}(\widetilde{\mu}(t))$ is shown to satisfy that

$$X(t)^l - \int_0^t \{l(l-1) U(s) X(s)^{l-2} + l V(s) X(s)^{l-1}\} ds$$

is a $(\boldsymbol{P}, \{F_t\})$-martingale for each $l \in N$,

where $U(s)$ and $V(s)$ are $\{F_s\}$-adapted bounded processes not depending on l. Therefore, we see that

$$E^P[|X(t)-X(s)|^4] \leq c|t-s|^2, \quad 0 \leq s \leq t < +\infty,$$

which implies the continuity of paths of $M_{f,k}(t)$.

Set

(3.6) $$R_t(f,k;u)=\sum_{\substack{1\le i<j\le m\\ k_i=k_j}}(<\phi_{ij}T_m(u)f,\tilde{\mu}(t-u)_{\beta_j k}>-<T_m(u)f,\tilde{\mu}(t-u)_k>)$$
$$+\sum_{i=1}^{m}\sum_{k'\in S}m_{k'k_i}<T_m(u)f,\tilde{\mu}(t-u)\gamma_{i(k')k}>$$

for $f\in B(E^m)$, $k=(k_1,\cdots,k_m)\in S^m$ and $0\le u\le t$.

Lemma 3.4. For each $s\in[0,t]$,

(3.7) $|R_t(f,k;u)|\le 2\lambda(k)\|f\|$,

and

(3.8) $E^P[<f,\tilde{\mu}(t)_k>]=E^P[<T_m(s)f,\tilde{\mu}(t-s)_k>]+E^P[\int_0^s R_t(f,k;u)du]$

holds, where P is the solution of the martingale problem for $(A,\tilde{\mu}^0)$.

Proof. (3.7) follows from (3.6) immediately. Making use of Lemma 4.3.4 of Ethier and Kurtz[1] and Proposition 3.3, we can see that

(3.9) $Z(s)\equiv<T_m(t-s)f,\tilde{\mu}(s)_k>-\int_0^s R_t(f,k;t-u)du$

is a $(P,\{F_t\})$-martingale for $s\in[0,t]$. Hence,

$$E^P[Z(t)]=E^P[Z(t-s)],$$

which is equivalent to (3.8).

As a consequence of Lemma 3.4, we have

$$I(0)=E[<Y(s),\tilde{\mu}(t-s)_{k(s)}>]$$
$$=E[E[<Y(s),\tilde{\mu}(t-s)_{k(s)}>|K]]$$
$$=E[<T_{M(s)}(h)Y(s),\tilde{\mu}(t-s-h)_{k(s)}>]+E[\int_0^h R_{t-s}(Y(s),k(s);r)dr]$$
$$=I_1^*(h)+I_2^*(h)+I_3^*(h),$$

where

$$I_1^*(h)=I_1(h)=E[T_{M(s)}(h)Y(s),\tilde{\mu}(t-s-h)_{k(s)}>],$$
$$I_2^*(h)=E[\sum_{\substack{1\le i<j\le M(s)\\ k_i(s)=k_j(s)}}\int_0^h(<\phi_{ij}T_{M(s)}(r)Y(s),\tilde{\mu}(t-s-r)_{\beta_j k_{(s)}}>-T_{M(s)}(r)Y(s),\tilde{\mu}(t-s-r)_{k_{(s)}}>)dr],$$

and

$$I_3^*(h)=E[\sum_{i=1}^{M(s)}\sum_{k'\in S}m_{k'k_i(s)}\int_0^h<T_{M(s)}(r)Y(s),\tilde{\mu}(t-s-r)_{\gamma_i(k')k_{(s)}}>dr]$$

In order to get (3.2), it is sufficient to prove that

(3.10) $|I_i(h)-I_i^*(h)|\le O(h^2)\quad(i=2,3)$,

holds uniformly in s as $h\downarrow 0$.

Observing that the equalities

(3.11) $$E[<\phi_{ij}T_{M(s)}(r)Y(s),\tilde{\mu}(t-s-r)_{\beta_j k_{(s)}}>]$$
$$=E[<T_{M(s)-1}(h-r)\phi_{ij}T_{M(s)}(r)Y(s),\tilde{\mu}(t-s-h)_{\beta_j k_{(s)}}>]$$
$$+E[\int_0^{h-r}R_{t-s-r}(\phi_{ij}T_{M(s)}(r)Y(s),\beta_j k(s),u)du]$$
$$=E[<T_{M(s)-1}(h-r)\phi_{ij}T_{M(s)}(r)Y(s),\tilde{\mu}(t-s-h)_{\beta_j k_{(s)}}>]+O(h-r),$$

and

(3.12) $E[<T_{M(s)}(r)Y(s),\tilde{\mu}(t-s-r)_{k_{(s)}}>]=E[<T_{M(s)}(h)Y(s),\tilde{\mu}(t-s-r)_{k_{(s)}}>]$

$$+E\left[\int_0^{h-r} R_{t-s-r}(T_{M(s)}(r)\,Y(s),k(s),u)du\right]$$
$$=E[< T_{M(s)}(h)\,Y(s),\tilde{\mu}(t-s-r)_{k(s)}>]+O(h-r)$$

follow from Lemma 3.4, we see

$$|I_2(h)-I_2^{\cdot}(h)|\leq\int_0^h O(h-r)dr=O(h^2),$$

uniformly in s as $h\downarrow 0$. Similarly, we can see that

$$|I_3(h)-I_3^{\cdot}(h)|\leq O(h^2)$$

uniformly in s as $h\downarrow 0$. Therefore, we obtain Theorem 3.1.

4. Proof of Theorem 2.4

Define P_1 and P_2 by

(4.1) $$(P_1f)(x_0,x_1,\cdots;y_0,y_1,\cdots)=\int_0^1 f(u,x_0,x_1,\cdots;y_0,y_1,\cdots)du$$

and

$$(P_2f)(x_0,x_1,\cdots;y_0,y_1,\cdots)=\int_0^1 f(x_0,x_1,\cdots;u,y_0,y_1,\cdots)du$$

for any $f\in B(\boldsymbol{E}^2)$. Then, we see

$$\sum_{i=1}^{2}L_i=\frac{1}{2}\theta(P_1+P_2-2I),$$

and

$$T_2(t)=\exp\{\frac{1}{2}\theta t(P_1+P_2-2I)\}$$
$$=e^{-\theta t}\times\sum_{k=0}^{\infty}\frac{(\theta t/2)^k}{k!}(P_1+P_2)^k.$$

Note that P_1 and P_2 are commutative. Put $Y(0)=\mathbf{1}_{A(l,m)}$. Obviously, $Y(t)=T_2(t)\,Y(0)$ for $t<T$. Here, we need the following lemma.

Lemma 4.1.

(1) $(P_1^lP_2^m)\mathbf{1}_{A(l,m)}=\mathbf{1}_D$, where D is the diagonal set of $\boldsymbol{E}^2$,

(2) $(P_1^{n_1}P_2^{n_2})\mathbf{1}_{A(l,m)}=0$, if $n_1>l$ or $n_2>m$,

(3) $\phi_{12}(P_1^{n_1}P_2^{n_2})\mathbf{1}_{A(l,m)}=0$, if $(n_1,n_2)\neq(l,m)$.

The proof of Lemma 4.1 is omitted, since it is easily shown. Using (2) in Lemma 4.1, we have

$$T_2(t)\,Y(0)=T_2(t)\mathbf{1}_{A(l,m)}=e^{-\theta t}\sum_{k=0}^{l+m}\frac{(\theta t/2)^k}{k!}(P_1+P_2)^k\mathbf{1}_{A(l,m)}.$$

By (1) and (3) in Lemma 4.1, we see that

$$Y(T)=\phi_{12}T_2(T)\,Y(0)$$
$$=e^{-\theta T}\frac{(\theta T/2)^{l+m}}{l!m!},\qquad \text{if } T<+\infty.$$

Observing that $Y(t)$ is equal to the constant for $t\geq T$, we get

$$\lim_{t\to+\infty}< Y(t),\tilde{\mu}^{\,0}_{k(t)}>=e^{-\theta T}\frac{(\theta T/2)^{l+m}}{l!m!}\quad \text{a.s.,}\quad \text{for } T<\infty.$$

Since the equality

$$\lim_{t\to+\infty}< T_2(t)\,Y(0)=0$$

holds uniformly in E^2, we see that

$$\lim_{t\to\infty} < Y(t), \tilde{\mu}^0_{k(t)} > = 0 \text{ a.s,, } \quad \text{for } T=+\infty.$$

Hence, we get

$$(4.2) \qquad \lim_{t\to+\infty} E_{<1_{A(l,m)},k>}[< Y(t), \tilde{\mu}^0_{k(t)} >] = E_{(1_{A(l,m)},k)}[e^{-\theta T}\frac{(\theta T/2)^{l+m}}{l!m!}; T<+\infty]$$

$$= E_k[e^{-\theta T}\frac{(\theta T/2)^{l+m}}{l!m!}; T<+\infty].$$

The last equality follows from the fact that T is a functional of the Markov chain $\{k(t)\}$. Using (3.1) and (4.2), we see that

$$(4.3) \qquad \lim_{t\to+\infty} E^P[<1_{A(l,m)}, \mu_{k_1}(t)\times\mu_{k_2}(t)>] = E_k[e^{-\theta T}\frac{(\theta T/2)^{l+m}}{l!m!}; T<+\infty].$$

It is clear that (4.3) implies

$$\int <1_{A(l,m)}, \mu_{k_1}\times\mu_{k_2}> \tilde{Q}(d\tilde{\mu}) = E_k[e^{-\theta T}\frac{(\theta T/2)^{l+m}}{l!m!}; T<+\infty].$$

Thus, the proof of Theorem 2.4 is complete.

5. Corollary

Recall that

$$A_s = \bigcup_{l+m=s,\, l,m\in Z_+} A(l,m), s\in Z_+.$$

A_s stands for the set of pairs $(x,y)\in E^2$, which have s segregating sites. Let $A_\infty = \bigcup_{s=0}^{\infty} A_s$.

A_∞ means the set of pairs $(x,y)\in E^2$, which have an common ancestor. Then, we obtain the next statement.

Corollary 5.1. The equalities

$$(5.1) \qquad \int <1_{A_s}, \mu_{k_1}\times\mu_{k_2}> \tilde{Q}(d\tilde{\mu}) = E_{(k_1,k_2)}[e^{-\theta T}\frac{(\theta T)^s}{s!}; T<+\infty]$$

$$(5.2) \qquad \int <1_{A_\infty}, \mu_{k_1}\times\mu_{k_2}> \tilde{Q}(d\tilde{\mu}) = P_{(k_1,k_2)}[T<+\infty],$$

$$(5.3) \qquad \int <1_{A_0}, \mu_{k_1}\times\mu_{k_2}> \tilde{Q}(d\tilde{\mu}) = E_{(k_1,k_2)}[e^{-\theta T}; T<+\infty],$$

and

$$(5.4) \qquad \int \sum_{s=0}^{\infty} s <1_{A_s}, \mu_{k_1}\times\mu_{k_2}> \tilde{Q}(d\tilde{\mu}) = \theta E_{(k_1,k_2)}[T; T<+\infty]$$

hold for any $(k_1, k_2)\in S^2$.

Proof. We can obtain (5.1) by summing up the both sides of (2,2) for l and m satisfying $l+m=s$. (5.2) follows from (5.1) through the summation for s. (5.3) is included in (5.1). We obtain (5.4) by summing up for s after multiplying the both sides of (5.1) by s. The proof is complete.

The left-hand side of (5.1),(5.2) and (5.3) stands for the average probability that the types of two genes randomly chosen from colonies k_1 andk_2 have s segragating sites(have an common ancestor and are idetical respectively). That of (5.4) means the averaged number of segregating sites in a sample of two genes chosen in the same way as above.

6. Examples

This section is devoted to two examples.

Example 1. We consider the case that the set S of colonies is the d dimensional lattice Z^d. Assume on the migration rates $\{m_{k_1k_2}\}_{k_1,k_2\in Z^d}$ that $m_{k_1k_2}$ depends only on k_2-k_1, and that $m_{k_1k_2}>0$ if and only if $k_2-k_1=\pm\varepsilon_i$ for some $i\in\{1,2,\cdots,d\}$, where $\varepsilon_i=(\delta_{i0},\delta_{i1},\cdots,\delta_{id})$.
Put

$$m_k=m_{0k} \text{ for } k\neq 0, \text{ and } m_0==+\sum_{k\neq 0} m_k.$$

Define a Markov chain $\{k(t)\}$ with state space $Z^d\cup\Delta$, where Δ is an extra point. The transition from $k\in Z^d$ is as follows. The distribution of the holding time τ at the initial state $k\in Z^d(k\neq 0)$ is the exponential distribution with parameter $2m_0$. The distribution of $k(\tau)$ is given by

$$P(k(\tau)=k\pm\varepsilon_i)=(m_{e_i}+m_{-e_i})/2m_0 \quad (i=1,2,\cdots,d).$$

The distribution of the holding time τ at the state 0 is the exponential distribution with parameter $(1+2m_0)$, and the distribution $k(\tau)$ is given by

$$P(k(\tau)=\Delta)=1/(1+2m_0)$$

and

$$P(k(\tau)=\pm\varepsilon_i)=(m_{e_i}+m_{-e_i})/(1+2m_0) \quad (i=1,\cdots,d)$$

Δ is assumed to be a trap. Define T' by $T'=inf\{t\geq 0:k(t)\in\Delta\}$. Then, we can easily see that the distribution T' with initial state $k_2-k_1\in Z^d$ is the same as that of T with initial state $(k_1,k_2)\in Z^d\times Z^d$. Hence, we see that

$$P_{k_2-k_1}(T'<+\infty)=P_{(k_1,k_2)} \quad (T<+\infty).$$

Therefore, we obtain that $P_{(k_1,k_2)}(T<+\infty)=1$ if and only if $d\leq 2$.

Example 2. Assume that $S=Z^1$. The migration rate is assumed to have the same form as in Example 1. Namely,

$$m_{k_1k_2}=\begin{cases} p & \text{if } k_2=k_1+1 \\ q & \text{if } k_2=k_1-1 \\ 0 & \text{if otherwise,} \end{cases}$$

where $p>0$, $q>0$, $p+q=1$, and $m_0=p+q$.

In this case, we can get the explicit form of the Laplace transform of the distribution of T.
That is,

$$E_{(k_1,k_2)}[e^{-\lambda T}]=a(\lambda)b(\lambda)^{\ell}, \quad l=|k_1-k_2|\in Z_+,$$

where

$$a(\lambda)=\frac{1}{1+\sqrt{\lambda^2+4m_0\lambda}},$$

$$b(\lambda)=\frac{1}{2m_0}(\lambda+2m_0-\sqrt{\lambda^2+4m_0\lambda}).$$

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