7.5.3 The dual representation of the Fleming-Viot process

The Fleming-Viot process has state space $\mathcal{P}(E)$. We assume that the mutation process has semigroup S_t with generator A and there exists an algebra of functions $D_0(E)$ dense in $C(E)$ and $S_t : D_0(E) \to D_0(E)$.

We can then consider the extension of the mutation process to E^n, $n \geq 1$ corresponding to n i.i.d. copies of the basic mutation process and with generator $A^{(n)} = \sum_{i=1}^n A_i$ where A_i denotes the action of A on the ith variable.

Let

(7.46) $E_2 := \{(f,n) : f \in (D_0(E))^n \cap,\ n \in \mathbb{N}\}$.

Define $F : \mathcal{P}(E) \times E_2 \to \mathbb{R}$ by

(7.47) $$F(\mu,(f,n)) = \int_{E^n} f_n(x_1,\dots,x_n)\mu(dx_1)\dots\mu(dx_n.$$

Now consider the Fleming-Viot process with generator:

(7.48)
$$GF(\mu,(f,n)) = \int_E \left(A\frac{\partial F(\mu,(f,n))}{\partial\mu(x)}\right)\mu(dx) + \frac{\gamma}{2}\int_E\int_E \frac{\partial^2 F(\mu,(f,n))}{\partial\mu(x)\partial\mu(y)}Q(\mu;dx,dy)$$

and note that for for each $\mu \in \mathcal{P}(E)$ this coincides with

(7.49) $$HF(\mu,(f,n)) = F(\mu,(A^{(n)}f,n)) + \frac{\gamma}{2}\sum_{j=1}^n\sum_{k\neq j}[F(\mu,(\widetilde{\Theta}_{jk}f,n) - F(\mu,(f,n)))]$$

where $\widetilde{\Theta}_{jk} : (D_0(E))^n \to (D_0(E))^{n-1}$ is defined by (7.44).

Then H is the generator of a càdlàg process with values in E_2 and law $\{Q_f : f \in E_2\}$ which evolves as follows:

- $Y(t)$ jumps from $(D_0(E)^n, n)$ to $(D_0(E)^{n-1}, n-1)$ at rate $\frac{1}{2}\gamma n(n-1)$
- at the time of a jump, f is replaced by $\widetilde{\Theta}_{jk}f$
- between jumps, $Y(t)$ is deterministic on $D_0(E)^n$ and evolves according to the semigroup (S_t^n) with generator $A^{(n)}$.

Theorem 7.15 *(a) Let $(\{X(t)\}_{t\geq 0}, \{P_\mu : \mu \in \mathcal{P}(E)\})$ be a solution to the Fleming-Viot martingale problem and the process $(\{Y(t)\}_{t\geq 0}, \{Q_{(f,n)} : (f,n) \in E_2\}$ be defined as above. Then*

(a) these processes are dual, that is,

(7.50) $P_\mu(F(X(t),(f,n))) = Q_f(F(\mu,Y(t)))$, $\quad (f,n) \in E_2$.

(b) The martingale problem is well-posed and the Fleming-Viot process is a strong Markov process.

Proof. In this case for $(f,n) \in E_2$ $\mu \in \mathcal{P}(E)$,

(7.51) $GF(\mu,(f,n)) = HF(\mu,(f,n))$

and the uniqueness follows from Theorem (7.9). (b) follows by the Stroock-Varadhan Theorem. ■

7.5.4 The Kingman coalescent

Consider the special case with no mutation, that is, $A \equiv 0$. Then we can represent the dual process $Y(t)$ with $Y(0) = (f,n)$ as follows.

(7.52) $Y(t) = (f_t, n_t)$

where $n_t \leq n$ and there is a map

(7.53) $\pi_t : \{1,\dots,n\} \to \{1,\dots,n_t\}$

and $f_t \in C(E^{n_t})$ given by

(7.54) $f_t(y_1,\dots,y_{n_t}) = f(x_1,\dots,x_n) \quad \text{with } x_i = y_{\pi_t(i)},\ i = 1,\dots,n.$

In other words π_t is a process with values in the set of partitions of $\{1,\dots,n\}$ and n_t is a pure death process with deaths rate $\gamma \begin{pmatrix} k \\ 2 \end{pmatrix}$ where $n_t = k$. This partition-valued process is the *Kingman coalescent* [392] and plays an important role in population genetics.

10.4 Neutral Stepping Stone Models

10.4.1 The two type stepping stone model

The neutral two type stepping stone model on a countable abelian group S with migration kernel $p(\cdot)$ is given by the system

$$\begin{aligned} dX_t(x) &= \sum_{y\in S_1} p_{y-x}(X_t(y) - X_t(x)dt \\ &\quad + \sqrt{2X_t(x)(1-X_t(x))}dW_t(x) \end{aligned}$$
$$x_0(x) \in [0,1],\ x \in S$$

This process can be embedded in the infinitely many types stepping stone model which we now consider.

10.4.2 The infinitely many types stepping stone model

Consider a collection (finite or countable) of subpopulations (demes), indexed by S. The subpopulation at $\xi \in S$ at time t is described by a probability distribution $X_\xi(t)$ over a space $E = [0,1]$ of possible types (alleles). In other words, $X_\xi(t) \in \mathcal{P}(E)$, the set of probability measures on E so that the state space is

$$(10.13)\quad (\mathcal{P}([0,1]))^S.$$

Within each subpopulation there is mutation, selection and finite population sampling. Mutation is assumed produce a new type chosen by sampling from a fixed source distribution $\theta \in \mathcal{P}(E)$. Selection is prescribed by a fitness function $V(x)$ in the haploid case or by $V(x,y) = V(y,x)$ in the diploid case. Migration from site ξ to site ξ' is assumed to occur via a symmetric random walk with rates $q_{\xi,\xi'} = p(\xi - \xi')$. Finally Fleming-Viot continuous sampling is assumed to take place within each subpopulation. It is a basic property of this model that for any $t > 0$, $X_\xi(t)$ is a purely atomic random measure (with countably many atoms) and therefore can be represented in the form

$$X_\xi(t) = \sum_{k\in I} m_{\xi,k}(t)\delta_{y_k}$$

where $m_{\xi,k}(t) \geq 0$ denotes the proportion of the population in subpopulation ξ of type $y_k \in E$ at time t. Note that in this model two individuals are related if and only if they are of the same type.

We denote the vector $\{\mu_\xi\}_{\xi\in S}$ by $\bar{\mu}$. The generator is then given by

(10.14)

$$\begin{aligned} GF(\bar{\mu}) &= c\cdot\sum_{\xi\in S}\int_{[0,1]}\frac{\partial F(\bar{\mu})}{\partial\mu_\xi(u)}(\theta(du)-\mu_\xi(du)) \\ &\quad+\sum q_{\xi,\xi'}\int_{[0,1]}\frac{\partial F(\bar{\mu})}{\partial\mu_\xi(u)}(\mu_{\xi'}(du)-\mu_\xi(du)) \\ &\quad+\frac{\gamma}{2}\sum\int_{[0,1]}\int_{[0,1]}\frac{\partial^2 F(\bar{\mu})}{\partial\mu_\xi(u)\partial\mu_\xi(v)}Q_{\mu_\xi}(du,dv) \end{aligned}$$

$$X_{0,\xi}=\nu\ \forall\,\xi,\quad Q_\mu(du,dv)=\mu(du)\delta_u(dv)-\mu(du)\mu(dv).$$

The first term corresponds to mutation with source distribution θ, the second to spatial migration and the last to continuous resampling. The resampling rate coefficient γ is inversely proportional to the effective population size of a deme.

This existence and uniqueness of this system of interacting Fleming-Viot processes was established by Vaillancourt [586] and Handa [306].

The questions which we wish to investigate are

- the distribution in a given subpopulation, that is what is the joint distribution of the $\{m_{\xi,k}\}$
- the spatial distribution of relatives
- how are these affected by the migration geometry.

10.4.3 The Dual Process Representation

Given $n\in\mathbb{N}$ consider the collection

(10.15)

$$\begin{aligned} \Pi_n &= \{\bar{\eta}:=(\eta,\pi)\}:\ \text{where} \\ &\quad \pi \text{ is a partition of } \{1,\dots,n\},\ \text{that is,} \\ &\quad \pi:\{1,\dots,n\}\to\{1,\dots,|\pi|\}\text{ with }|\pi|\le n, \\ &\quad \eta:\{1,\dots,|\pi|\}\to S. \end{aligned}$$

Now consider the family of functions in $C((\mathcal{P}([0,1]))^S\times\Pi)$ of the form

$$F_f(\bar{\mu},\bar{\eta}):=\int_{[0,1]}\dots\int_{[0,1]}f(u_{\pi(1)},\dots,u_{\pi(n)})\mu_{\eta_1}(du_1)\dots\mu_{\eta_{|\pi|}}(du_{|\pi|}) \tag{10.16}$$

with $f\in C([0,1]^n)$.

We now consider a continuous time Markov chain, $\bar{\eta}_t=(\eta_t,\pi_t)$, with state space Π_n and jump rates:

- the partition elements perform continuous time symmetric random walks on S with rates $q_{\xi,\xi'}$ and in addition a partition element can jump to $\{\infty\}$ with rate c (once a partition element reaches ∞ it remains there without change of further coalescence).
- each pair of partition elements during the period they reside at an element of S (but not $\{\infty\}$) coalesce at rate γ to the partition element equal to the union of the two partition elements.

Let H denote the generator of $\bar{\eta}$. Then for a function of the form (10.16)

(10.17) $HF_f(\bar{\mu}, \bar{\eta}) = GF_f(\bar{\mu}, \bar{\eta})$.

We then obtain the dual relationship

(10.18) $E(F_f(X_t, (\eta, \pi))) = E(F_f(X_0, (\eta_t, \pi_t)))$

and this proves that the infinitely many types stepping stone martingale problem is well-posed.

Remark 10.23 *Given the dual we can construct a* spatially structured coalescent *that describes the ancestral structure of a sample of a finite number of individuals located at the same or different sites.*

Note that this is essentially equivalent to the coalescent geographically structured populations introduced by developed by Notohara (1990) [488] and Takahata (1991) [577].

Remark 10.24 *Note that as $\gamma \to \infty$ the dual converges to the dual of the voter model and we can regard the voter model as the limit as $\gamma \to \infty$ of the interacting Fisher-Wright diffusions.*

10.4.4 Spatial homogeneity and the local-fixation coexistence dichotomy

Theorem 10.25 *(Dawson-Greven-Vaillancourt (1995) [142], Theorem 0.1)*

Let S be a countable abelian group and consider the infinitely many types stepping stone model with now mutation ($c = 0$). Assume that the initial random field is spatially stationary and ergodic and has mean measure $\int(\int g(u)x_\xi(0))\mu(dx) = \int g(u)\theta(du), \quad \theta \in \mathcal{P}[0,1]$.

(a) If $q_{\xi,\xi'}$ is a symmetric transient r.w. on S, then the stepping stone process converges in distribution to a nontrivial invariant random measure ν_θ which has single site mean measure θ. ν_θ is ergodic, in particular

(10.19) $E(\langle x_\xi, f\rangle \langle x_\zeta, f\rangle) \to \langle \mu, f\rangle^2$ *as* $d(\xi,\zeta) \to \infty, \quad \forall\, f \in L_\infty([0,1])$.

(b) In (a) the equilibrium state decomposes into countably many coexisting infinite families.