$$\begin{aligned}
NE_\mu[F(X_1^N)-F(\mu)] &= \sum_{1\le i<j\le n} \left(\langle f_i f_j, \mu P_N\rangle - \langle f_i,\mu P_N\rangle\langle f_j,\mu P_N\rangle\right)\prod_{\ell:\ell\neq i,j}\langle f_\ell,\mu P_N\rangle \\
&+\sum_{i=1}^n \langle Af_i,\mu\rangle \prod_{j:j<i}\langle f_j,\mu\rangle\prod_{j:j>i}\langle f_j,\mu P_N\rangle + O(N^{-1}) \\
&= GF(\mu)+o(1)
\end{aligned}$$

uniformly in μ.

The completes the verification of condition (6.7). ■

6.4 The Infinitely Many Alleles Model

This is a special case of the Fleming-Viot process which has played a crucial role in modern population biology. It has type space $E=[0,1]$ and *type-independent* mutation operator with mutation source $\nu_0 \in \mathcal{P}([0,1])$

$$\begin{aligned}
Af(x) &= \theta\left(\int p(x,dy)f(y)-f(x)\right) \\
&= \theta\left(\int f(y)\nu_0(dy)-f(x)\right).
\end{aligned}$$

Since A is a bounded operator we can take indicator functions of intervals in $D(A)$. If we have a partition $[0,1]=\cup_{j=1}^K B_j$ where the B_j are intervals, consider the set $D(G)$ of functions

(6.10) $F(\mu)=\langle f_1,\mu\rangle \ldots \langle f_n,\mu\rangle$

with $n \ge 1$ and where the functions $f_1,\ldots,f_n$ are finite linear combinations of indicator functions of the intervals $\{A_j\}$. Then the function $GF(\mu)$ can be written in the same form and we can prove that the Δ_{K-1}-valued process $\{p_t(A_1),\ldots,p_t(A_K)\}$ is a version of the $K-$*allele* process with generator

(6.11) $$G^K f(p) = \frac{1}{2}\sum_{i,j=1}^{K-1} p_i(\delta_{ij}-p_j)\frac{\partial^2 f(p)}{\partial p_i \partial p_j} + \theta\sum_{i=1}^{K-1}(\nu_0(A_i)-p_i)\frac{\partial f(p)}{\partial p_i}.$$

We will next give an explicit construction of this process that allows us to derive a number of interesting properties of this important model.

6.4.1 Projective Limit Construction of the Infinitely Many Alleles Model

Let $\mu,\nu_0 \in \mathcal{P}(E)$, $\mathcal{C}=C_{[0,\infty)}([0,\infty))$. Let U denote the collection of finite partitions $u=(A_1^u,\ldots,A_{|u|}^u)$ of E into measurable subsets in $\mathcal{B}(E)$ and $|u|$ denotes the number of sets in the partition u. We place a partial ordering on U as follows:

$$v \succ u$$

if v is a refinement of u. We can also identify partitions with the finite algebras of subsets of E they generate. Given a partition we define the probability measure, P_u on $\mathcal{C}^u$ as the law of the Wright-Fisher diffusion with generator

$$\begin{aligned} G^{(K)}f(p) &= \frac{1}{2}\sum_{i,j=1}^{K-1} p_i(\delta_{ij}-p_j)\frac{\partial^2 f(p)}{\partial p_i \partial p_j} \\ &+ \frac{1}{2}\sum_{i=1}^{K-1}\theta(\nu_i - p_i)\frac{\partial f(p)}{\partial p_i} \\ \nu_i &:= \nu_0(A_j) \end{aligned}$$

and initial measure μ, that is, the law of $(p_t(A_1^u), \dots, p_t(A_{|u|}^u)$ (and the additive extension of this to the algebra generated by u).

Remark 6.6 *Recall that the associated Markov transition function is determined by the joint moments as follows.*

Since the family of functions $p_1^{k_1}\dots, p_{K-1}^{k_{K-1}}$ *belong to* $D(G^{(K)})$ *we can apply* $G^{(K)}$ *and obtain the following system of equations for the joint moments:*

(6.12) $m_{k_1,\dots,k_{K-1}}(t) := E[p_1^{k_1}(t)\dots p_{K-1}^{k_{K-1}}(t)],$

$$\begin{aligned} \frac{\partial}{\partial t} m_{k_1,\dots,k_{K-1}}(t) &= \frac{1}{2}\sum_i k_i(k_i-1) m_{k_1,.,k_i-1,..k_{K-1}}(t) \\ &- \frac{1}{2}\sum_{i\neq j} k_i k_j m_{k_1,\dots k_K}(t) \\ &+ \frac{\theta}{2}\sum_{i=1}^{K-1} \nu_i k_i m_{k_1,.k_j-1,.,k_i+1,..k_K}(t) \\ &- \frac{\theta}{2}\sum_{i=1}^{K-1} k_i m_{k_1,\dots k_{K-1}}(t) \end{aligned}$$

Since this system of linear equations is closed, there exists a unique solution which characterizes the K*-allele Wright-Fisher diffusion.*

In a similar way we can apply this to the function corresponding to the coalescence of two partition elements

$$\begin{aligned} f(p) &= \tilde{f}(\tilde{p}) \\ \tilde{p} &= (\tilde{p}_1, \dots, \tilde{p}_{K-1}) \\ &= (p_1, \dots, p_{\ell-1}, p_{\ell+1}, \dots, p_{k-1}, p_{k+1}, \dots, p_{K-1}, (p_\ell + p_k)) \end{aligned}$$

$$
\begin{aligned}
G^{(K)}f(p) &= \frac{1}{2}\sum_{i,j=1}^{K-2}\tilde{p}_i(\delta_{ij}-\tilde{p}_j)\frac{\partial^2 f(\tilde{p})}{\partial\tilde{p}_i\partial\tilde{p}_j} \\
&+ \frac{\theta}{2}\sum_{i=1}^{K-2}(\widetilde{\nu}_i-\widetilde{p}_i)\frac{\partial\tilde{f}(\tilde{p})}{\partial\tilde{p}_i} \\
&= G^{(K-1)}\tilde{f}(\tilde{p})
\end{aligned}
$$

In other words we have consistency under coalescence of the partition elements. Because of uniqueness this implies that the process $\tilde{p}(t) = (\tilde{p}_1(t),\dots,\tilde{p}_{K-1}(t))$ coincides with the $(K-1)-$allele Wright-Fisher diffusion.

We denote the canonical projections $\pi_u : \mathcal{C}^{\mathcal{B}(E)} \to \mathcal{C}^u$ and $\pi_{uv} : \mathcal{C}^v \to \mathcal{C}^u$ if $v \succ u$ such that

$\pi_u = \pi_{uv}\pi_v,\ v \succ u.$

The family $\{P_u\}_{u\in U}$ forms a projective system of probability laws, that is for every pair, (u,v), $v \succ u$, $\{P_u\}$ then satisfies

(6.13) $\pi_{uv}(P_v) = P_u, \qquad P_u(B) = P_v(\pi_{uv}^{-1}(B)).$

Therefore, by Theorem 17.6 (in Appendix I) there exists a projective limit measure, that is, a probability measure P_∞ on $\mathcal{C}^{\mathcal{B}([0,1])}$ such that for any $u \in U$, $\pi_u P_\infty = P_u$.

For fixed t (or any finite set of times) we can identify the projective limit,

(6.14) $\{\tilde{p}_t(A) : A \in \mathcal{B}([0,1])\}$

with an element of $\mathcal{X}([0,1])$, the space of all finitely additive, non-negative, mass one measures on $[0,1]$, equipped with the projective limit topology, i.e., the weakest topology such that for all Borel subset B of $[0,1]$, $\mu(B)$ is continuous in μ. Under this topology, $\mathcal{X}([0,1])$ is Hausdorff. The σ-algebra $\mathcal{B}$ of the space $\mathcal{X}([0,1])$ is the smallest σ-algebra such that for all Borel subset B of $[0,1]$, $\mu(B)$ is a measurable function of μ.

For fixed $t \in [0,\infty)$, $\tilde{p}_t(\cdot)$ is a.s. a finitely additive measure, that is, a member of $\mathcal{X}[0,1]$ and satisfies the conditions of Theorem 17.8 in the Appendices (conditions 1,2 follow immediately from the construction, 3 follows since for any $A \in \mathcal{B}([0,1])$ $E(p_t(A)) \le \max(\mu(A),\nu_0(A))$ and (4) is automatic since all measures are bounded by 1). Therefore for fixed t this determines a unique countably additive version $p_t(\cdot)$, that is, a random countable additive measure $p_t \in \mathcal{P}([0,1])$ a.s. Similarly, taking two times t_1, t_2 we obtain a the joint distribution of a pair (p_{t_1}, p_{t_2}) of random probability measures. We can then verify that $t \to \int f(x)p_t(dx)$ is a.s. continuous for a countable convergence determining class of functions so that there is an a.s. continuous version with respect to the topology of weak convergence.

Remark 6.7 *We can carry out the same construction assuming that for each $u \in U$ the Wright-Fisher diffusion starts with the stationary Dirichlet measure and obtain by the projective limit a probability measure on $\mathcal{P}(E)$ which for any partition has the associated Dirichlet distribution.*

6.5 The Jirina Branching Process

In 1964 Jirina [355] gave the first construction of a measure-valued branching process. The state space is the space of finite measures on $[0,1]$, $M_f([0,1])$. $\nu_0 \in M_1([0,1])$. We will construct a version of this process with immigration by a projective limit construction.

Given a partition $(A_1,\dots,A_K)$ of $[0,1]$ let $\{X_t(A_i) : t \geq 0,\ i = 1,\dots,K\}$ satisfy the SDE (Feller CSB plus immigration):

$$\begin{aligned} dX_t(A_i) &= c(\nu_0(A_i) - X_t(A_i))dt + \sqrt{2\gamma X_t(A_i)}dW_t^{A_i} \\ X_0(A_i) &= \mu(A_i) \end{aligned} \tag{6.15}$$

where ν_0 is in $\mathcal{P}([0,1])$ and for each i, $W_t^{A_i}$ is a standard Brownian motion and for $i \neq j$ $W_t^{A_i}$ and $W_t^{A_j}$ are independent.

We can then verify that the processes $X_t(A_i) : i = 1,\dots,K$ are independent and as $t \to \infty$, $X_t(A_i)$ converges in distribution to a stationary measure $X_\infty(A_i)$ with density which satisfies

$$f_i(x) = \frac{1}{Z} x^{\theta_i - 1} e^{-\theta x},\ x > 0$$

where $\theta = \frac{c}{\gamma}$, $\theta_i = \theta\nu_0(A_i)$.

This can be represented by $X_\infty(A) = \theta^{-1}G(\theta\nu_0(A))$ where $\theta = \frac{c}{\gamma}$ and

$$\begin{aligned} &\mathcal{L}\{(X_\infty(A_1),\dots,X_\infty(A_K))\} = \\ &\mathcal{L}\{\frac{1}{\theta}[G(\theta_1), G(\theta_1+\theta_2) - G(\theta_1),\dots,G(\theta) - G(\theta - \theta_K)]\} \end{aligned}$$

where $G(s)$ is the *Moran subordinator* - see subsection 6.6.1 below.

For $u = (A_1^u,\dots,A_{|u|}^u) \in U$ (defined as in the last subsection) let $\{P_u = \mathcal{L}(\{(X_t(A_1),\dots,X_t(A_{|u|}) : t \geq 0,\ A \in u\})\}$. Then the collection $\{P_u\}_{u\in U}$ forms a projective system and as in the previous section there exists a projective limit measure P_∞ on $(C_{[0,\infty)}([0,\infty)))^{\mathcal{B}([0,1])}$. Moreover for fixed $t \in [0,\infty)$, $X_t(\cdot)$ is a.s. a finitely additive measure that is regular (on a countable generating subset of $\mathcal{B}([0,1])$) we obtain a unique countably additive version (recall Theorem 17.8). Thus, $\{X_t(\cdot) : t \geq 0\}$ is a measure-valued process and again we can obtain an a.s. continuous $M_F([0,1])$-valued version. This $M_F([0,1])$-valued process is called the *Jirina process.*

Corollary 6.8 *The stationary measure for the Jirina process is given by the random measure*

$$(6.16)\quad X_\infty(A) = \frac{1}{\theta}\int_0^1 1_A(x)dG(\theta s), \quad A \in \mathcal{B}([0,1])$$

where $G(\cdot)$ is the Moran gamma subordinator.

6.6 Invariant Measures of the IMA and Jirina Processes

6.6.1 The Moran (Gamma) Subordinator

We begin by recalling the the *Gamma distribution* with parameter $\alpha > 0$ given by the density function

$$g_\alpha(u) = u^{\alpha-1}e^{-u}/\Gamma(\alpha)$$

and Laplace transform of g_α is

$$\int_0^\infty g_\alpha(y)e^{-\lambda y}dy = \frac{1}{(1+\lambda)^\alpha},\ \lambda > -1,$$

The Moran subordinator $\{G(\alpha) : \alpha \geq 0\}$ is an increasing process with stationary independent increments $G(\alpha_2) - G(\alpha_1),\ \alpha_1 < \alpha_2$ given by $g_{\alpha_2-\alpha_1}$.

Lévy representation

Lemma 6.9

$$(6.17)\quad E\left(e^{-\lambda G(\alpha)}\right) = \exp\left(-\alpha\int_0^\infty (1-e^{-u\lambda})\frac{e^{-u}}{u}du\right).$$

Proof. Note that

$$\frac{\partial}{\partial\lambda}\int_0^\infty (1-e^{-\lambda z})z^{-1}e^{-z}dz = \int_0^\infty (e^{-\lambda z})e^{-z}dz = \frac{1}{1+\lambda}$$

$$\int_0^\infty (1-e^{-\lambda z})z^{-1}e^{-z}dz = \log(1+\lambda)$$

Hence we have the Lévy-Khinchin representation with Lévy measure $\frac{e^{-z}}{z},\ z > 0$

$$(6.18)\quad \frac{1}{(1+\lambda)^\alpha} = \exp\left\{-\alpha\int_0^\infty (1-e^{-\lambda z})z^{-1}e^{-z}dz\right\}.$$

■

Poisson representation

The *Poisson random field* with intensity measure μ is a random counting measure Π on a space S. $\Pi(A_i), \Pi(A_j)$ are independent if $i \neq j$ and $\Pi(A)$ is Poisson with parameter $\mu(A)$.

Theorem 6.10 *(Campbell's Theorem.) Let Π be a Poisson random field with intensity $\mu \in M(S)$ and $f : S \to \mathbb{R}$, $\Sigma = \sum_{x\in\Pi} f(x) = \int f(x)\Pi(dx)$ converges a.s. if and only if*

$$\int_S \min(|f(x)|, 1)\mu(dx) < \infty$$

and then

$$E(e^{s\int f(x)\Pi(dx)}) = \exp(\int (e^{sf(x)} - 1)\mu(dx)), \quad s \in R$$

provided the integral on the right exists.

Now consider the Poisson random measure on $[0, 1] \times (0, \infty)$

$$(6.19)\quad \Xi_\theta = \sum \delta_{\{x,u\}}$$

with intensity measure

$$\theta\nu_0(dx)\frac{e^{-u}}{u}du.$$

Let $\widetilde{X}_\infty(A) := \int_A \int_0^\infty u\Xi_\theta(dx, du)$. Then by Campbell's Theorem

$$(6.20)\quad \begin{aligned} E(e^{-\lambda\widetilde{X}_\infty(A)}) &= E(e^{-\lambda\int_A\int_0^\infty u\Xi_\theta(dx,du)}) \\ &= e^{-\theta\nu_0(A)\int(1-e^{-\lambda u})\frac{e^{-u}}{u}du}. \end{aligned}$$

Hence we can represent equilibrium of the Jirina process by the random measure with Poisson representation $\{X_\infty(A) : A \in \mathcal{B}([0, 1])\}$ by

$$(6.21)\quad X_\infty(A) = \theta^{-1}\int_A\int_0^\infty u\,\Xi_\theta(dx, du)$$

and this can be obtained as the projective limit of the finite systems.

If ν_0 is Lebesgue measure on $[0, 1]$ then have that the $\{X_\infty([0, s)\}_{0\leq s\leq 1} = \{G(s)\}_{0\leq s\leq 1}$ where $G(s)$ is the Moran subordinator with with increments $G(s_2)-G(s_1)$ having the Gamma $\theta(s_2 - s_1)$ distribution $\theta = \frac{c}{\gamma}$.

6.6.2 Representation of the Infinitely Many Alleles Equilibrium

Recall (Theorem 5.9) that the Dirichlet distribution Dirichlet$(\theta_1,\dots,\theta_n)$ has the joint density on relative to $(n-1)$-dimensional Lebesgue measure on Δ_{n-1} given by

$$f(p_1,\dots,p_{n-1}) = \frac{\Gamma(\theta_1+\dots+\theta_n)}{\Gamma(\theta_1)\dots\Gamma(\theta_n)}p_1^{\theta_1-1}p_2^{\theta_2-1}\dots p_n^{\theta_n-1}.$$

Recall that if the θ are large the measure concentrates away from the boundary whereas is the θ are small things concentrate near the boundary corresponding to highly disparate p with a few large p_j and the others small. For example if the θ_j are small but equal there is a high probability that at least one of the p_j is much greater than average; and which value or values of j have large p_j is a matter of chance.

Proposition 6.11 *Let X_∞ denote the equilibrium random measure for the Jirina process and consider a partition $[0,1] = \cup_{i=1}^n A_i$ and define*

$$(6.22)\quad Y(A_i) := \frac{X_\infty(A_i)}{X_\infty([0,1])} = \frac{G(\theta|A_i|)}{G(\theta)}.$$

Then the family $(Y(A_1),\dots,Y(A_K))$ is ***independent*** *of $X_\infty([0,1])$ and has as distribution the Dirichlet$(\theta_1,\dots\theta_K)$ where $\theta_j = \theta\nu_0(A_j)$.*

Proof. Let Y be Gamma(θ) and $(P_1,\dots,P_K)$ Dirichlet $(\theta_1,\dots,\theta_K)$ with Y and $(P_1,\dots,P_K)$ independent, and define $(Y_1,\dots,Y_K)$ by

$$(6.23)\quad Y_i := YP_i.$$

We will verify that $(Y_1,\dots,Y_K)$ has the joint probability density function

$$(6.24)\quad g(y_1,\dots,y_K) = \prod_{i=1}^K u_i^{\theta_i-1}e^{-u_i}/\Gamma(\theta_i).$$

Consider the 1-1 transformation $(Y_1,Y_2,\dots,Y_K) \leftrightarrow (Y,P_2,\dots,P_K)$ with Jacobian

$$(6.25)\quad |J| = \left\{|\frac{\partial x_1,\dots,x_K}{\partial y_1,\dots,y_K}|,\ x_1 = y, x_2 = p_2,\dots,x_K = p_K\right\} = \frac{1}{y^{K-1}}.$$

By independence of Y and $(P_1,\dots,P_K)$, we obtain the joint density of $(Y_1,\dots,Y_K)$ as

$$\begin{aligned}
g(y_1,\dots,y_K) &= f(p_1,\dots,p_K|Y)f_Y(y)|J| \\
&= f(p_1,\dots,p_K)\frac{1}{\Gamma(\theta)}y^{\theta-1}e^{-y}\frac{1}{y^{K-1}} \\
&= \frac{\Gamma(\theta)}{\Gamma(\theta_1)\dots\Gamma(\theta_K)} \\
&\cdot\left(\frac{y_1}{\sum y_i}\right)^{\theta_1-1}\dots\left(\frac{y_K}{\sum y_i}\right)^{\theta_K-1}\frac{1}{\Gamma(\theta)}(\sum y_i)^{(\theta-1)}e^{-\sum y_i}.(\sum y_i)^{-(K-1)} \\
&= \prod_{i=1}^{K}\frac{1}{\Gamma(\theta_i)}y_i^{\theta_i-1}e^{-y_i}
\end{aligned}$$

Note that this coincides with the Dirichlet$(\theta_1,\dots,\theta_K)$ distribution. ■

Corollary 6.12 *The invariant measure of the infinitely many alleles model can be represented by the random probability measure*

(6.26) $$Y(A) = \frac{X_\infty(A)}{X_\infty([0,1])}, \quad ,A\in\mathcal{B}([0,1]).$$

where $X_\infty(\cdot)$ is the equilibrium of the above Jirina process and $Y(\cdot)$ and $X_\infty([0,1])$ are independent.

Reversibility

Recall that the Dirichlet distribution is a *reversible* stationary measure for the $K - type$ Wright-Fisher model with house of cards mutation (Theorem 5.9). From this and the projective limit construction it can be verified that $\mathcal{L}(Y(\cdot))$ is a reversible stationary measure for the infinitely many alleles process. Note that reversibility actually characterizes the IMA model among neutral Fleming-Viot processes with mutation, that is, any mutation mechanism other than the "type-independent" or "house of cards" mutation leads to a stationary measure that is not reversible (see Li-Shiga-Yau (1999) [431]).

6.6.3 The Poisson-Dirichlet Distribution

Without loss of generality we can assume that ν_0 is Lebesgue measure on $[0,1]$. This implies that the IMA equilibrium is given by a random probability measure which is pure atomic

(6.27) $$p_\infty = \sum_{i=1}^{\infty}a_i\delta_{x_i}, \quad \sum_{i=1}^{\infty}a_i = 1,\ x_i\in[0,1]$$

Supplementary EXERCISES FOR LECTURE 9

1. Consider two Feller CSB with immigration as in Equation 6.15 in the notes (with $W_t^{A_i}, W_t^{A_j}$ independent Brownian motions, $i \neq j$). Show that $Y_t := X_t(A_i) + X_t(A_j)$ is a Feller CSB with immigration.

2. Prove Campbell's Theorem.

3. Consider the Gamma subordinator $\{G(s) : s \geq 0\}$ and let $0 \leq a < b$.
(a) Prove that

$$P(G(b) - G(a) = 0) = 0$$

(b) Calcuate the probability that there is no jump in (a, b) larger than 1.