# The $\boldsymbol{\Lambda}$-Fleming-Viot process and a connection with Wright-Fisher diffusion

Bob Griffiths

University of Oxford

A $d$-dimensional $\Lambda$-Fleming-Viot process $\{\boldsymbol{X}(t)\}_{t\geq 0}$ representing frequencies of $d$ types of individuals in a population has a generator described by

$$\mathcal{L}g(\boldsymbol{x}) = \int_0^1 \sum_{i=1}^{d} x_i \Big( g(\boldsymbol{x}(1-y) + y\boldsymbol{e}_i) - g(\boldsymbol{x}) \Big) \frac{F(dy)}{y^2}.$$

The population is partitioned at events of change by choosing type $i \in [d]$ to reproduce with probability $x_i$, then rescaling the population with additional offspring $y$ of type $i$ to be $\boldsymbol{x}(1-y)+y\boldsymbol{e}_i$ at rate $y^{-2}F(dy)$.

## Examples

Eldon and Wakeley (2006). A model where $F$ has a single point of increase in $(0,1]$ with a possible atom at 0.

A natural class that arises from discrete models is when $F$ has a Beta$(\alpha,\beta)$ density, particularly a Beta$(2-\alpha,\alpha)$ density coming from a discrete model where the offspring distribution tails are asymptotic to a power law of index $\alpha$. Birkner, Blath, Capaldo, Etheridge, Möhle, Schweinsberg, Wakolbinger (2005) give a connection to stable processes.

Birkner and Blath (2009) describe the $\Lambda$-Fleming-Viot process and discrete models whose limit gives rise to it.

If $F$ has a single atom at $0$, then $\{\boldsymbol{X}_t\}_{t\geq 0}$ is the $d$-dimensional Wright-Fisher diffusion process with generator

$$\mathcal{L} = \frac{1}{2}\sum_{i,j=1}^{d} x_i(\delta_{ij} - x_j)\frac{\partial^2}{\partial x_i \partial x_j}$$

$X_1(t)$ is a one-dimensional Wright-Fisher diffusion process with generator

$$\mathcal{L} = \frac{1}{2}x(1-x)\frac{\partial^2}{\partial x^2}$$

The $\Lambda$-coalescent process is a random tree process back in time which has multiple merger rates for a specific $k$ lineages coalescing while $n$ edges in the tree of

$$\lambda_{nk} = \int_0^1 x^k (1-x)^{n-k} \frac{F(dx)}{x^2},\ k \geq 2$$

After coalescence there are $n-k+1$ edges in the tree.

This process was introduced by Pitman (1999), Sagitov (1999) and has been extensively studied. Berestycki (2009); recent results in the $\Lambda$-coalescent.

There is a connection between continuous state branching processes and the $\Lambda$-coalescent. The connection is through the Laplace exponent

$$\psi(q) = \int_0^1 \Big(e^{-qy} - 1 + qy\Big) y^{-2} F(dy)$$

Bertoin and Le Gall (2006) showed that the $\Lambda$-coalescent comes down from infinity under the same condition that the continuous state branching process becomes extinct in finite time, that is when

$$\int_1^\infty \frac{dq}{\psi(q)} < \infty$$

## Some papers on the $\Lambda$-coalescent


Berestycki (2009) Recent progress in coalescent theory.

Berestycki, Berestycki, and Limic (2012) Asymptotic sampling formulae for $\Lambda$-coalescents.

Berestycki, Berestycki, and Limic (2012) A small-time coupling between $\Lambda$-coalescents and branching processes.

Bertoin and Le Gall (2003) Stochastic flows associated to coalescent processes.

Bertoin and Le Gall (2006) J. Bertoin and J.-F. Le Gall (2006). Stochastic flows associated to coalescent processes III: Limit theorems.

Birkner, Blath, Capaldo, Etheridge, Möhle, Schweinsberg, Wakolbinger, (2005) Alpha-stable branching and Beta-coalescents.

Birkner and Blath (2009) Measure-Valued diffusions, general coalescents and population genetic inference.

## A Wright-Fisher generator connection

### Theorem

Let $\mathcal{L}$ be the $\Lambda$-Fleming-Viot generator, $V$ be a uniform random variable on $[0,1]$, $U$ a random variable on $[0,1]$ with density $2u$, $0 < u < 1$ and $W = YU$, where $Y$ has distribution $F$ and $V, U, Y$ are independent. Denote the second derivatives of a function $g(\boldsymbol{x})$ by $g_{ij}(\boldsymbol{x})$.

Then

$$\mathcal{L}g(\boldsymbol{x}) = \frac{1}{2}\sum_{i,j=1}^{d} x_i(\delta_{ij} - x_j)\mathbb{E}\Big[g_{ij}\Big(\boldsymbol{x}(1-W) + WV\boldsymbol{e}_i\Big)\Big]$$

where expectation $\mathbb{E}$ is taken over $V, W$.

Wright-Fisher generator

$$\mathcal{L}g(\boldsymbol{x}) = \frac{1}{2}\sum_{i,j=1}^{d} x_i(\delta_{ij} - x_j)g_{ij}\Big(\boldsymbol{x}\Big)$$

$\Lambda$-Fleming-Viot generator

$$\mathcal{L}g(\boldsymbol{x}) = \frac{1}{2}\sum_{i,j=1}^{d} x_i(\delta_{ij} - x_j)\mathbb{E}\Big[g_{ij}\Big(\boldsymbol{x}(1-W) + WV\boldsymbol{e}_i\Big)\Big]$$

## Method of proof

$$\mathcal{L}g(\boldsymbol{x}) = \int_0^1 \sum_{i=1}^{d} x_i \Big( g(\boldsymbol{x}(1-y) + y\boldsymbol{e}_i) - g(\boldsymbol{x}) \Big) \frac{F(dy)}{y^2}$$

$$\mathcal{L}g(\boldsymbol{x}) = \frac{1}{2} \sum_{i,j=1}^{d} x_i(\delta_{ij} - x_j) \mathbb{E}\Big[ g_{ij}\Big( \boldsymbol{x}(1-W) + WV\boldsymbol{e}_i \Big) \Big]$$

Show that the generators have the same answer acting on

$$g(\boldsymbol{x}) = \exp\Big\{ \sum_{i=1}^{d} \eta_i x_i \Big\},\ \boldsymbol{\eta} \in \mathbb{R}^d$$

## 1-dimensional generator

Wright-Fisher diffusion generator

$$\mathcal{L}g(x) = \frac{1}{2}x(1-x)g''\Big(x\Big)$$

$\Lambda$-Fleming-Viot process generator

$$\mathcal{L}g(x) = \frac{1}{2}x(1-x)\mathbb{E}\Big[g''\Big(x(1-W)+WV\Big)\Big]$$

or

$$\mathcal{L}g(x) = \frac{1}{2}x(1-x)\mathbb{E}\left[\frac{g'\Big(x(1-W)+W\Big)-g'\Big(x(1-W)\Big)}{W}\right]$$

The Laplace transform of $W$ is related to the Laplace exponent by

$$\mathbb{E}\left[e^{-\eta W}\right] = 2\int_0^1 \frac{e^{-\eta y} - 1 + \eta y}{(y\eta)^2} F(dy)$$

$W = UY$ is continuous in $(0,1)$ with a possible atom at $0$.

$$P(W = 0) = P(Y = 0)$$

## Adding mutation

The generator has an additional term added of

$$\frac{\theta}{2}\sum_{i=1}^{d}\Big(\sum_{j=1}^{d}p_{ji}x_j - x_i\Big)\frac{\partial}{\partial x_i}$$

If mutation is parent independent $\theta p_{ij} = \theta_j$, not depending on $i$, and the additional term is

$$\frac{1}{2}\sum_{i=1}^{d}\Big(\sum_{j=1}^{d}\theta_j x_j - \theta x_i\Big)\frac{\partial}{\partial x_i}$$

## Eigenstructure of the $\Lambda$-Fleming-Viot process

Theorem

Let $\{\lambda_{\boldsymbol{n}}\}$, $\{P_{\boldsymbol{n}}(\boldsymbol{x})\}$ be the eigenvalues and eigenvectors of $\mathcal{L}$, the generator which includes mutation, satisfying

$$\mathcal{L}P_{\boldsymbol{n}}(\boldsymbol{x}) = -\lambda_{\boldsymbol{n}}P_{\boldsymbol{n}}(\boldsymbol{x})$$

Denote the $d-1$ eigenvalues of the mutation matrix $P$ which have modulus less than 1 by $\{\phi_k\}_{k=1}^{d-1}$.

The eigenvalues of $\mathcal{L}$ are

$$\lambda_{\boldsymbol{n}} = \frac{1}{2}n(n-1)\mathbb{E}\Big[(1-W)^{n-2}\Big] + \frac{\theta}{2}\sum_{k=1}^{d-1}(1-\phi_k)n_k$$

## Polynomial Eigenvectors

Denote the $d-1$ eigenvalues of $P$ which have modulus less than 1 by $\{\phi_k\}_{k=1}^{d-1}$ corresponding to eigenvectors which are rows of a $d-1 \times d$ matrix $R$ satisfying

$$\sum_{i=1}^{d} r_{ki} p_{ji} = \phi_k r_{kj},\ k = 1, \ldots, d-1.$$

Define a $d-1$ dimensional vector $\boldsymbol{\xi} = R\boldsymbol{x}$.

The polynomials $P_{\boldsymbol{n}}(\boldsymbol{x})$ are polynomials in the $d-1$ terms in $\boldsymbol{\xi} = (\xi_1, \ldots, \xi_{d-1})$ whose only leading term of degree $n$ is

$$\prod_{j=1}^{d-1} \xi_j^{n_j}$$

In the parent independent model of mutation

$$\lambda_{\boldsymbol{n}} = \lambda_n = \frac{1}{2}n\left\{(n-1)\mathbb{E}\Big[(1-W)^{n-2}\Big] + \theta\right\}$$

repeated $\binom{n+d-2}{n}$ times with non-unique polynomial eigenfunctions within the same degree $n$.

The non-unit eigenvalues of the mutation matrix with identical rows are zero.

Wright-Fisher diffusion, general mutation structure.

$$\lambda_{\boldsymbol{n}} = \frac{1}{2}n(n-1) + \frac{\theta}{2}\sum_{k=1}^{d-1}(1-\phi_k)n_k$$

## $\Lambda$-coalescent eigenvalues and rates

$$\frac{1}{2}n(n-1)\mathbb{E}\Big[(1-W)^{n-2}\Big] = \sum_{k=2}^{\infty}\binom{n}{k}\lambda_{nk}$$

which is the total jump rate away from $n$ individuals.

These are the eigenvalues in the $\Lambda$-coalescent tree.

The individual rates can be expressed as

$$\binom{n}{k}\lambda_{nk} = \binom{n}{k}\int_0^1 y^k(1-y)^{n-k}\frac{F(dy)}{y^2}$$
$$= \frac{n}{2}\mathbb{E}\left[\frac{P_k(n,W)-P_{k-1}(n,W)}{W^2}\right],$$

where

$$P_k(n,w) = \binom{n-1}{k-1}(1-w)^{n-k}w^k$$

is a negative binomial probability of a waiting time of $n$ trials to obtain $k$ successes, where the success probability is $w$.

Two types

The generator is specified by

$$\mathcal{L}g(x) = \frac{1}{2}x(1-x)\mathbb{E}\Big[g''\Big(x(1-W)+WV\Big)\Big] + \frac{1}{2}(\theta_1 - \theta x)g'(x)$$

The eigenvalues are

$$\lambda_n = \frac{1}{2}n\left\{(n-1)\mathbb{E}\Big[(1-W)^{n-2}\Big] + \theta\right\}$$

and the eigenvectors are polynomials satisfying

$$\mathcal{L}P_n(x) = -\lambda_n P_n(x),\ n \geq 1.$$

## Polynomial eigenvectors

$$\frac{1}{2}x(1-x)\mathbb{E}\left[\frac{P_n'\Big(x(1-W)+W\Big) - P_n'\Big(x(1-W)\Big)}{W}\right]$$

$$+\frac{1}{2}(\theta_1 - \theta x)P_n'(x)$$

$$= \frac{1}{2}n\left[(n-1)\mathbb{E}\Big[(1-W)^{n-2}\Big] + \theta\right]P_n(x)$$

The monic polynomial $P_n(x)$ is uniquely defined by recursion of its coefficients.

## Stationary distribution $\psi(x)$

$$\int_0^1 \mathcal{L}g(x)\psi(x)dx = 0$$

$$\sigma^2(x) = x(1-x), \;\; \mu(x) = \theta_1 - \theta x$$

$$k(x) = \mathbb{E}\Big[(1-W)^{-2} g\Big(x(1-W) + VW\Big)\Big]$$

## An equation for the stationary distribution

$$0 = \int_0^1 \Big[k(x)\frac{1}{2}\frac{d^2}{dx^2}\big[\sigma^2(x)\psi(x)\big] - g(x)\frac{d}{dx}\big[\mu(x)\psi(x)\big]\Big]dx$$
$$+ k(x)\frac{d}{dx}\big[\frac{1}{2}\sigma^2(x)\psi(x)\big]\Big|_0^1 + g(x)\mu(x)\psi(x)\Big|_0^1$$

In a diffusion process $k(x) = g(x)$ and the boundary terms vanish. Then there is a solution found by solving

$$\frac{1}{2}\frac{d^2}{dx^2}\Big[\sigma^2(x)\psi(x)\Big] - \frac{d}{dx}\Big[\mu(x)\psi(x)\Big] = 0$$

however $k(x) \neq g(x)$ so we do not have an equation like this.

## Green's function, $\gamma(x)$

Solve, for a given function $g(x)$

$$\mathcal{L}\gamma(x) = -g(x),\;\; \gamma(0) = \gamma(1) = 0.$$

Then

$$\gamma(x) = \int_0^1 G(x,\xi)g(\xi)d\xi$$

A non-linear equation, equivalent to

$$\frac{1}{2}x(1-x)\mathbb{E}\Big[\gamma''(x(1-W)+VW)\Big] = -g(x)$$

## Green's function solution

Define

$$k(x) = \mathbb{E}\Big[(1-W)^{-2}\gamma\Big(x(1-W)+VW\Big)\Big]$$

then

$$k''(x) = -2\frac{g(x)}{x(1-x)}$$

with a solution

$$\begin{aligned} k(x) &= k(0)(1-x) + k(1)x \\ &\quad + (1-x)\int_0^x \frac{2g(\eta)}{(1-\eta)}d\eta + x\int_x^1 \frac{2g(\eta)}{\eta}d\eta \end{aligned}$$

## Mean time to absorption

If $g(x) = 1$, $x \in (0,1)$ then $\gamma(x)$ is the mean time to absorption at 0 or 1 when $X(0) = x$.

$$\begin{aligned} k(x) &= k(0)(1-x) + k(1)x \\ &\quad + (1-x)\int_0^x \frac{2}{(1-\eta)}d\eta + x\int_x^1 \frac{2}{\eta}d\eta \end{aligned}$$

There is a non-linear equation to solve of

$$k(x) = k(0)(1-x) + k(1)x - 2(1-x)\log(1-x) - 2x\log x$$

where

$$k(x) = \mathbb{E}\Big[(1-W)^{-2}\gamma\Big(x(1-W) + VW\Big)\Big]$$

## Stationary distribution, $\Lambda$-Fleming process with mutation

Let $Z$ be a random variable with the size-biassed distribution of $X$, $Z_*$ a size-biassed $Z$ random variable and $Z^*$ a size-biassed random variable with respect to $1 - Z$.

Let $B$ be Bernoulli random variable, independent of the other random variables in the following equation such that

$$P(B = 1) = \frac{\theta - \theta_1}{\theta(\theta_1 + 1)}$$

## An interesting distributional identity

$$VZ_* =^{\mathcal{D}} \Big(1 - B\Big)VZ + B\Big(Z^*(1 - W) + WV\Big)$$

## The frequency spectrum in the infinitely-many-alleles model

Take a limit from a $d$-allele model with $\theta_i = \theta/d$, $i \in [d]$. The limit is a point process $\{X_i\}_{i=1}^{\infty}$. The 1-dimensional frequency spectrum $h(x)$ is a non-negative measure such that for suitable functions $k$ on [0,1] in the stationary distribution

$$\mathbb{E}\Big[\sum_{i=1}^{\infty} k(X_i)\Big] = \int_0^1 k(x)h(x)dx.$$

Symmetry in the $d$-allele model shows that

$$\int_0^1 k(x)h(x)dx = \lim_{d\to\infty} d\mathbb{E}\Big[k(X_1)\Big].$$

The classical Wright-Fisher diffusion gives rise to the Poisson-Dirichlet process with a frequency spectrum of

$$h(x) = \theta x^{-1}(1-x)^{\theta-1},\ 0 < x < 1.$$

## $\Lambda$ Fleming-Viot frequency spectrum

Let $Z$ have a density

$$f(z) = zh(z),\ 0 < z < 1$$

Interesting identity

$$VZ_* =^{\mathcal{D}} Z^*(1-W) + WV$$

where $Z_*$ is size-biassed with respect to $Z$, and $Z^*$ is size-biassing with respect to $1-Z$.
The constant $\theta$ appears in the identity through scaling in the size-biassed distributions.

Limit distribution of excess life in a renewal process

$$P(VZ_* > \eta) = \int_\eta^1 \frac{P(Z > z)}{\mathbb{E}[Z]} dz$$

## Typed dual $\Lambda$-coalescent

The $\Lambda$-Fleming-Viot process is dual to the system of coalescing lineages $\{L(t)\}_{t\geq 0}$ which takes values in $\mathbb{Z}_+^d$ and for which the transition rates are, for $i,j \in [d]$ and $l \geq 2$,

$$\begin{aligned} q_\Lambda(\xi, \xi - e_i(l-1)) &= \int_{[0,1]} \binom{|\xi|}{l} y^l (1-y)^{|\xi|-l} \frac{F(dy)}{y^2} \\ &\qquad \times \frac{\xi_i + 1 - l}{|\xi| + 1 - l} \frac{\mathcal{M}(\xi - e_i(l-1))}{\mathcal{M}(\xi)} \\ q_\Lambda(\xi, \xi + e_i - e_j) &= \mu_{ij}(\xi_i + 1 - \delta_{ij}) \frac{\mathcal{M}(\xi + e_i - e_j)}{\mathcal{M}(\xi)} \end{aligned}$$

The process is constructed as a moment dual from the generator.

## A different dual process

Define a sequence of monic polynomials $\{g_n(x)\}$ by the generator equation

$$\begin{aligned} & \frac{1}{2}x(1-x)\mathbb{E}g_n''(x(1-W)+VW) + \frac{1}{2}(\theta_1 - \theta x)g_n'(x) \\ = & \binom{n}{2}\mathbb{E}(1-W)^{n-2}[g_{n-1}(x) - g_n(x)] + n\frac{1}{2}[\theta_1 g_{n-1}(x) - \theta g_n(x)] \end{aligned}$$

The defining equation mimics the Wright-Fisher diffusion acting on test functions $g_n(x) = x^n$

$$\begin{aligned} & \frac{1}{2}x(1-x)\frac{d^2}{dx^2}x^n + \frac{1}{2}(\theta_1 - \theta x)\frac{d}{dx}x^n \\ = & \binom{n}{2}(x^{n-1} - x^n) + \frac{1}{2}n(\theta_1 x^{n-1} - \theta x^n) \end{aligned}$$

## Jacobi polynomial analogues

The eigenfunctions are polynomials $\{P_n(x)\}$ satisfying

$$\mathcal{L}P_n(x) = \lambda_n P_n(x)$$

$$P_n(x) = g_n(x) + \sum_{r=0}^{n-1} c_{nr} g_r(x)$$

The coefficients are

$$c_{nr} = \frac{\lambda^{\circ}_{r+1} \cdots \lambda^{\circ}_{n}}{(\lambda_r - \lambda_n) \cdots (\lambda_{n-1} - \lambda_n)}$$

where
$$\begin{aligned} \lambda_n &= \frac{n}{2}\Big[(n-1)\mathbb{E}(1-W)^{n-2} + \theta\Big] \\ \lambda^{\circ}_n &= \frac{n}{2}\Big[(n-1)\mathbb{E}(1-W)^{n-2} + \theta_1\Big] \end{aligned}$$

In the stationary distribution

$$\mathbb{E}\Big[g_n(X)\Big] = \omega_n$$

where $\omega_n$ is a Beta moment analog

$$\omega_n = \frac{\prod_{j=1}^{n}\Big((j-1)\mathbb{E}(1-W)^{j-2} + \theta_1\Big)}{\prod_{j=1}^{n}\Big((j-1)\mathbb{E}(1-W)^{j-2} + \theta\Big)}$$

Let

$$h_n = \frac{g_n}{\omega_n}$$

so

$$\mathbb{E}\Big[h_n(X)\Big] = 1$$

Dual Generator

$$\mathcal{L}h_n = \lambda_n\Big[h_{n-1} - h_n\Big]$$

Dual equation

$$\mathbb{E}_{X(0)=x}\Big[h_n(X(t))\Big] = \mathbb{E}_{N(0)=n}\Big[h_{N(t)}(x)\Big]$$

where $\{N(t), t \geq 0\}$ is a death process with rates

$$\lambda_n = \frac{1}{2}n\Big((n-1)\mathbb{E}\Big[(1-W)^{n-2}\Big] + \theta\Big)$$

The process $\{N(t), t \geq 0\}$ comes down from infinity if and only if

$$\sum_{n=2}^{\infty} \lambda_n^{-1} < \infty$$

which implies the $\Lambda$-coalescent comes down from infinity.

The transition functions are then

$$P\Big(N(t) = j \mid N(0) = i\Big)$$
$$= \sum_{k=j}^{i} e^{-\lambda_k t}(-1)^{k-j} \frac{\prod_{\{l:j\leq l\leq k+1\}} \lambda_l}{\prod_{\{l:j\leq l\leq k+1,\, l\neq k\}}(\lambda_l - \lambda_k)}$$

$P\Big(N(t) = j \mid N(0) = \infty\Big)$ is well defined if $N(t)$ comes down from infinity.

In the Kingman coalescent the death rates are $n(n-1+\theta)/2$ and $N(t)$ describes the number of non-mutant lineages at time $t$ back in the population.

## Wright-Fisher diffusion. Fixation probability with selection. Two types.

Let $P(x)$ be the probability that the 1st type fixes, starting from an initial frequency of $x$. $P(x)$ is the solution of

$$\mathcal{L}^{\sigma} P(x) = \frac{1}{2} x(1-x) P''(x) - \sigma x(1-x) P'(x) = 0$$

with $P(0) = 0$, $P(1) = 1$. The solution of this differential equation is

$$P(x) = \frac{e^{2\sigma x} - 1}{e^{2\sigma} - 1}$$

## $\Lambda$-Fleming Viot process. Fixation probability with selection.

Let $P(x)$ be the probability that the 1st type fixes, starting from an initial frequency of $x$. $P(x)$ is the solution of

$$\mathcal{L}^\sigma P(x) = \frac{1}{2}x(1-x)\mathbb{E}\Big[P''(x(1-W)+WV)\Big]-\sigma x(1-x)P'(x) = 0$$

with $P(0) = 0$, $P(1) = 1$.

Der, Epstein and Plotkin (2011,2012). For some measures $F$ and $\sigma$ it is possible that $P(x) = 1$ or $0$ for all $x \in (0,1)$. If $\sigma > 0$, fixation is certain if

$$\sigma > -\int_0^1 \frac{\log(1-y)}{y^2}F(dy)$$

A computational solution for $P(x)$ when fixation or loss is not certain from $x \in (0,1)$.

Define a sequence of polynomials $\{h_n(x)\}_{n=0}^{\infty}$ for a choice of pre-specified constants $\{h_n(0)\}$ as solutions of

$$\mathbb{E}\left[\frac{h_n\Big(x(1-W)+W\Big)-h_n\Big(x(1-W)\Big)}{W}\right]=nh_{n-1}(x)$$

where the leading coefficient in $h_n(x)$ is

$$\frac{1}{\prod_{j=1}^{n-1}\mathbb{E}\Big[(1-W)^j\Big]}$$

## Polynomial solution for $P(x)$

$$P(x) = \left(e^{2\sigma} - 1\right)^{-1} \sum_{n=1}^{\infty} \frac{(2\sigma)^n}{n!} H_n(x),$$

where $\{H_n(x)\}$ are polynomials derived from

$$H_n(x) = \int_0^x n h_{n-1}(\xi) d\xi$$

and the constants $\{h_n(0)\}$ are chosen so that

$$\int_0^1 n h_{n-1}(\xi) d\xi = 1$$

The coefficients of $H_n(x)$ are well defined by a recurrence relationship with the coefficients of $H_{n-1}(x)$.