# Diffusion processes and coalescent trees

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#### The frequency of a mutation

The relative frequency  $\{X(t), t \geq 0\}$  of genes of type a in a population of two types a and A is modelled by a diffusion process with generator

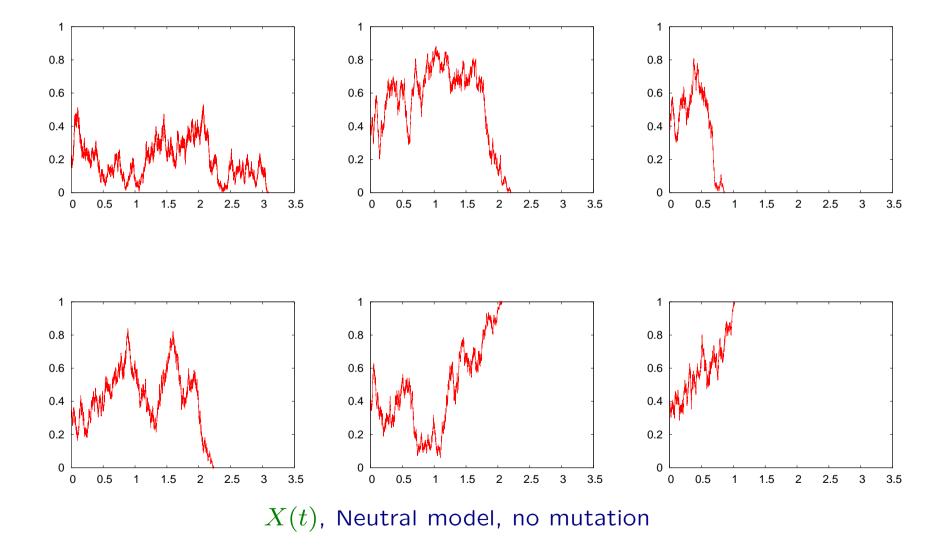
$$L = \frac{1}{2}x(1-x)\frac{\partial^2}{\partial x^2}$$

Simplest model with no mutation or selection.

Denote 
$$\Delta X(t) = X(t + \Delta t) - X(t)$$

$$E(\Delta X(t) \mid X(t) = x) = 0\Delta t + o(\Delta t)$$
 
$$\operatorname{Var}(\Delta X(t) \mid X(t) = x) = x(1-x)\Delta t + o(\Delta t)$$

Kimura (1955), Bochner (1954) in a different context.



Wright-Fisher model N genes, Types a,A. Fixed population size of N genes. Offspring in a generation choose their parents at random with replacement from the prior generation and inherit their type.

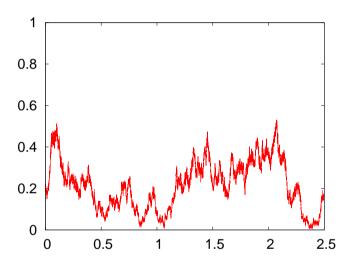
 $X^N(\tau), \tau=0,1,\ldots$  is the relative frequency of a genes in generation  $\tau$ .

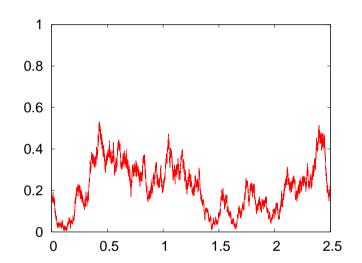
$$E(\Delta X^N(\tau) \mid X^N(\tau) = x) = 0$$
 
$$\operatorname{Var}(\Delta X^N(\tau) \mid X^N(\tau) = x) = x(1-x) \cdot \frac{1}{N}$$

Higher moments of  $\Delta X^N(\tau)$  are of order smaller than  $\frac{1}{N}$ .

Measure time in units of N generations, so  $\delta t = \frac{1}{N}$ , then

$$\{X^N([Nt]), t \ge 0\} \Longrightarrow \{X(t), t \ge 0\}$$





Reversibility of  $\boldsymbol{X}(t)$ 

#### Transition density in the neutral model

$$f(p, x; t) = x^{-1}(1 - x)^{-1} \sum_{i=2}^{\infty} e^{-\frac{1}{2}i(i-1)t} P_i(p) P_i(x)$$

where  $\{P_i(\cdot)\}$  are scaled Gegenbauer polynomials, orthogonal on

$$m(x) = x^{-1}(1-x)^{-1}$$

Reversibility before hitting 0 or 1

$$m(x)f(x,p;t) = m(p)f(p,x;t)$$

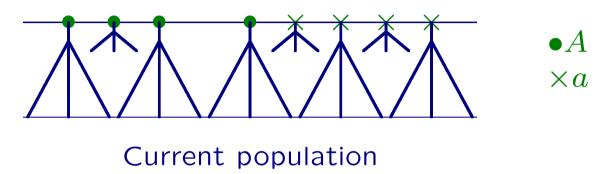
#### Genealogical form of the transition density

$$f(p, x; t) = \sum_{\ell=1}^{\infty} q_{\ell}(t) \sum_{k=1}^{\ell} {\ell \choose k} p^{k} (1-p)^{\ell-k} \times \frac{\Gamma(\ell)}{\Gamma(k)\Gamma(\ell-k)} x^{k-1} (1-x)^{\ell-k-1}$$

where  $\{q_\ell(t)\}$  are transition probabilities of a death process (coalescent process)  $\{A(t),\ t\geq 0\}$  with death rates  $\mu_k={k\choose 2}$  and  $A(0)=\infty.$ 

G (1980), Ethier and G (1993).

Time t back,  $A(t) = \ell$  ancestors



The relative frequency of family sizes in the  $\ell$  lines is Dirichlet  $(1,1,\ldots,1)$ .

Line types are chosen from a,A independently with probability p,1-p.

If k of the l lines are of type a, then the density of a is

$$\frac{\Gamma(\ell)}{\Gamma(k)\Gamma(\ell-k)} x^{k-1} (1-x)^{\ell-k-1}$$

#### Two-allele models with mutation

Wright-Fisher model with genes of type a, A Mutation  $a \to A$  with probability u per gene per generation Mutation  $A \to a$  with probability v per gene per generation

Diffusion process  $\{X(t), t \geq 0\}$  for the relative frequency of a genes at time t.

Generator

$$L = \frac{1}{2}x(1-x)\frac{\partial^2}{\partial x^2} + \frac{1}{2}(-\alpha x + \beta(1-x))\frac{\partial}{\partial x}$$

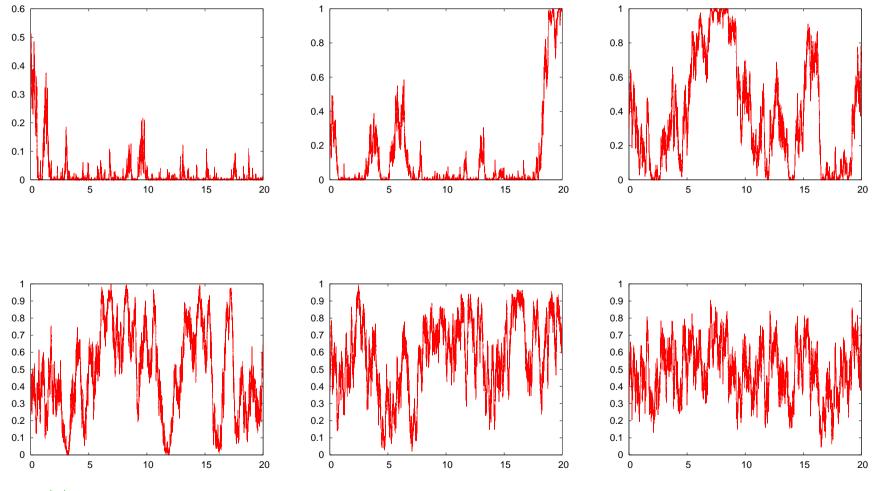
where  $\alpha = 2Nu$ ,  $\beta = 2Nv$ .

The stationary distribution of the diffusion process is Beta

$$\phi(x; \alpha, \beta) = B(\alpha, \beta)^{-1} x^{\alpha - 1} (1 - x)^{\beta - 1}, \ 0 < x < 1$$

satisfying the forward equation

$$\frac{1}{2} \frac{\partial^2}{\partial x^2} \Big\{ x(1-x)\phi(x;\alpha,\beta) \Big\} - \frac{\partial}{\partial x} \Big\{ \mu(x)\phi(x;\alpha,\beta) \Big\} = 0$$



X(t) , Neutral model, with mutation,  $\alpha=\beta=0.01, 0.1, 0.5, 1.0, 2.0, 5.0$ 

# Wright-Fisher diffusion process with d types

 $X(t)=(X_1(t)\dots,X_d(t))$  are gene frequencies of d types, labelled  $1,2,\dots,d$  at time  $t\geq 0$ .  $|X(t)|=X_1(t)+\dots+X_d(t)=1.$  Mutations  $i\to j$  occur at rate  $\frac{1}{2}\epsilon_j$ ,  $i,j=1,\dots d$ .

#### Backwards generator

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

Stationary distribution is Dirichlet

$$\mathcal{D}(x,\epsilon) = \frac{\Gamma(|\epsilon|)}{\Gamma(\epsilon_1)\cdots\Gamma(\epsilon_d)} x_1^{\epsilon_1-1}\cdots x_d^{\epsilon_d-1}$$

for 
$$x_1, \dots x_d > 0$$
 and  $|x| = \sum_1^d x_i = 1$ 

Transition density  $(x \rightarrow y \text{ in time } t)$  is

$$f(x,y;t) = \mathcal{D}(y,\epsilon) \Big\{ 1 + \sum_{\{n;n \in \mathbb{Z}_+^{d-1}, |n| > 0\}} \rho_{|n|}(t) Q_n^{\circ}(x) Q_n^{\circ}(y) \Big\}$$

Eigenfunctions  $Q_n^{\circ}(x)$  are orthonormal polynomials on the Dirichelt distribution.

Eigenvalues are  $\rho_{|n|}(t)=\exp\{-\frac{1}{2}|n|(|n|+|\epsilon|-1)t\}$  repeated  $\binom{|n|+d-2}{|n|}$  times corresponding to eigenvectors  $Q_n^{\circ}(x)$ , G (1979). Karlin and McGregor (1975) - Moran model version whose stationary distribution is the Dirichlet-Multinomial. Polynomials are Hahn multivariable analogues explicitly constructed.

#### Backward generator

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

#### Forward generator

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

### Eigenfunction equations

$$\mathcal{L}Q_n^{\circ}(x) = -\frac{1}{2}|n|(|n|+|\epsilon|-1)Q_n^{\circ}(x)$$

$$\widetilde{\mathcal{L}}\mathcal{D}(x,\epsilon)Q_n^{\circ}(x) = -\frac{1}{2}|n|(|n|+|\epsilon|-1)\mathcal{D}(x,\epsilon)Q_n^{\circ}(x)$$

#### Mutant families in an infinite-leaf coalescent tree

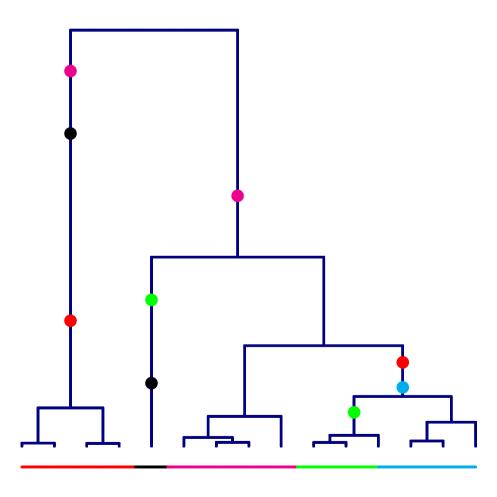
Mixture distribution arising from the coalescent

$$f(x, y; t) = \sum_{|l|=0}^{\infty} q_{|l|}^{|\epsilon|}(t) \sum_{\{l:|l| \text{ fixed}\}} {|l| \choose l} \prod_{1}^{d} x_i^{l_i} \mathcal{D}(y, \epsilon + l)$$

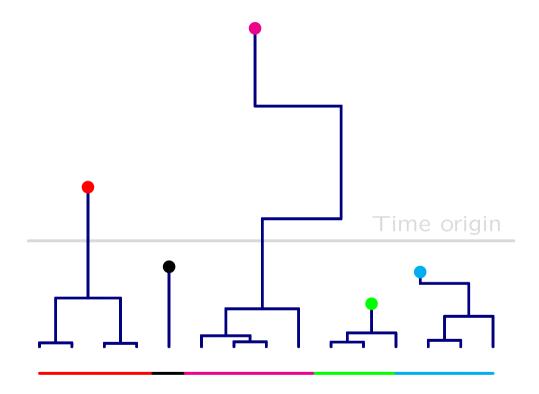
 $q_{|l|}^{|\epsilon|}(t)$  is the distribution of  $L^{|\epsilon|}(t)$ , the number of non-mutant founder lineages at time t back.  $L^{|\epsilon|}(t)$  is a death process back in time, starting from infinity, where lineages are reduced by coalescence or mutation from  $k \to k-1$  at rate  $k(k-1)/2+k|\epsilon|/2$ . Families are either from founder lineages or new mutations, giving the Dirichlet mixture.

f(x, y; t) and the eigenfunction form are identical.

Infinite-leaf coalescent tree with mutations, type j with probability  $\epsilon_j/|\epsilon|$ 



Forest of non-mutant ancestral lineages, to defining mutations



Ancestral lineages are lost back in time by coalescence or mutation at rates intering 0 and intering 0 while intering 0 non-mutant lineages.

#### Dirichlet family sizes

$$\sum_{\{l:|l| \text{ fixed}\}} {|l| \choose l} \prod_{1}^{d} x_i^{l_i} \mathcal{D}(y, \epsilon + l)$$

### Eigenfunction expansion

$$f(x, y; t) = \mathcal{D}(y, \epsilon) \left\{ 1 + \sum_{1}^{\infty} \rho_{|n|}(t) Q_{|n|}(x, y) \right\}$$

#### n-Kernel polynomials

$$Q_{|n|}(x,y) = \sum_{\{n;|n| \text{ fixed }\}} Q_n^{\circ}(x)Q_n^{\circ}(y)$$

invariant under which orthogonal polynomial set is used.

$$Q_{|n|}(x,y) = (|\epsilon| + 2|n| - 1) \sum_{m=0}^{n} (-1)^{|n|-m} \frac{(|\epsilon| + m)_{(|n|-1)}}{m!(|n| - m)!} \xi_m$$

where 
$$\xi_m = \sum_{|l|=m} {m \choose l} \frac{|\epsilon|_{(m)}}{\prod_1^d \epsilon_{i(l_i)}} \prod_1^d (x_i y_i)^{l_i}$$

#### Two forms of the density

$$f(x,y;t) = \mathcal{D}(y,\epsilon) \left\{ 1 + \sum_{1}^{\infty} \rho_{|n|}(t) Q_{|n|}(x,y) \right\}$$

 $ho_{|n|}(t)$  are eigenvalues.

$$f(x, y; t) = \sum_{|l|=0}^{\infty} q_{|l|}^{|\epsilon|}(t) \sum_{\{l:|l| \text{ fixed}\}} {|l| \choose l} \prod_{1}^{d} x_i^{l_i} \mathcal{D}(y, \epsilon + l)$$

 $q_{|l|}^{|\epsilon|}(t)$  are death process transition probabilities. Fleming-Viot Dirichlet process version in Ethier & G (1993).

#### Poisson Dirichlet random measure

$$\mu = \sum_{i=1}^{\infty} x_i \delta_{\xi_i}$$

where  $\{x_i\}$  is  $PD(\theta)$  and independent of  $\{\xi_j\}$  which are *i.i.d.*  $\nu_0 \in \mathcal{P}(S)$ , with S a compact metric space.

Stationary distribution of the random measure

$$\Pi_{\theta,\nu_0}(\cdot) = P(\mu \in \cdot)$$

Fleming-Viot process with type space S, and mutation operator

$$(Af)(x) = \frac{\theta}{2} \int_{S} (f(\xi) - f(x)) \nu_0(d\xi)$$

The Fleming-Viot process with type space S and mutation operator A has transition function  $P(t,\mu,d\nu)$  for given  $\mu\in\mathcal{P}(S)$ 

$$P(t, \mu, .) = q_0^{\theta}(t) \Pi_{\theta, \nu_0}(\cdot) + \sum_{n=1}^{\infty} q_n^{\theta}(t) \int_{S^n} \mu^n (dy_1 \times \cdots \times dy_n) \Pi_{n+\theta, (n+\theta)^{-1}\{n\eta_n(y_1, ..., y_n) + \theta\nu_0\}}(\cdot)$$

where  $\eta_n(y_1,\ldots,y_n)$  as the empirical measure of points  $y_1,\ldots,y_n\in S$ ,

$$\eta_n(y_1, \dots, y_n) = n^{-1}(\delta_{y_1} + \dots + \delta_{y_n})$$

Characterization of Markov processes with Beta stationary distributions and polynomial eigenfunctions

#### Characterization of distributions with polynomial eigenfunctions

$$B(\alpha,\beta)^{-1}y^{\alpha-1}(1-y)^{\beta-1} \times \left\{ 1 + \sum_{n=1}^{\infty} \omega_n h_n R_n^{(\alpha,\beta)}(x) R_n^{(\alpha,\beta)}(y) \right\}, \ 0 < x, y < 1$$

is a probability distribution for a sequence of constants  $\{\omega_n\}$  if and only if  $\{\omega_n\}$  is a positive definite sequence.

 $\{R_n^{(\alpha,\beta)}(x)\}$  are Jacobi polynomials on the Beta distribution with  $R_n^{(\alpha,\beta)}(1)=1.$  Scaling by  $\sqrt{h_n}$  makes them orthonormal.

Bochner (1954) A bounded sequence  $\{c_n\}$  is positive definite if

$$\sum a_n h_n R_n^{(\alpha,\beta)}(x) \ge 0, \ \sum |a_n| h_n < \infty$$

implies that

$$\sum a_n c_n h_n R_n^{(\alpha,\beta)}(x) \ge 0$$

Gasper (1972) Let  $\alpha < \beta$ . If either  $1/2 \le \alpha$  or  $\alpha + \beta \ge 2$ , then a sequence  $\rho_n$  is positive definite if and only if

$$\rho_n = \mathbb{E}[R_n^{(\alpha,\beta)}(Z)]$$

for some random variable Z in [0,1].

Bochner (1954): A family of bounded sequences  $\{c_n(t)\}$ ,  $0 \le t < \infty$  is called a homogeneous stochastic process if

- (i)  $\{c_n(t)\}$  is positive definite for each t
- (ii)  $c_n(t)$  is continuous in t
- (iii)  $c_n(0) = c_0(t) = 1$
- (iv)  $c_n(t+s) = c_n(t)c_n(s)$

Gasper (1972): Under the conditions on  $\alpha$  and  $\beta$ , it is N & S that  $c_n(t) = e^{-d_n t}$  with

$$d_n = \sigma n(n + \alpha + \beta - 1) + \int_0^{1-} \frac{1 - R_n^{(\alpha, \beta)}(z)}{1 - z} d\nu(z)$$

where  $\sigma \geq 0$  and  $\nu$  is a finite measure on [0,1). Sequences  $\{c_n(t)\}$  characterize eigenvalues of transition probability functions with polynomials as eigenfunctions.

Subordinated Diffusion Process Let  $\{X(t)\}$  be the two allele Wright-Fisher diffusion process with eigenvalues  $e^{-\frac{1}{2}n(n+\theta-1)t}$ , where  $\theta=\alpha+\beta$ 

Let  $\{Z(t)\}$  be a Lévy process with Laplace transform

$$\mathbb{E}[\exp(-\phi Z(t))] = \exp\left\{-t \int_0^\infty \frac{1 - e^{-y\phi}}{y} G(dy)\right\}$$

where  $\int_1^\infty \frac{1}{y} G(dy) < \infty$ .

Then  $\{X(Z(t))\}$  has polynomial eigenvectors and eigenvalues

$$c_n(t) = \exp\left\{-t \int_0^\infty \frac{1 - e^{-yn(n+\theta-1)/2}}{y} G(dy)\right\}$$

Markov Process  $\{\widetilde{X}(t)\}$  with transition density

$$B(\alpha,\beta)^{-1}y^{\alpha-1}(1-y)^{\beta-1} \times \left\{ 1 + \sum_{n=1}^{\infty} e^{-nt} h_n R_n^{(\alpha,\beta)}(x) R_n^{(\alpha,\beta)}(y) \right\}, \ 0 < x, y < 1$$

Poisson kernel in orthogonal polynomial theory

$$1 + \sum_{n=1}^{\infty} r^n h_n R_n^{(\alpha,\beta)}(x) R_n^{(\alpha,\beta)}(y), \ 0 < x, y < 1, |r| < 1$$

 $\widetilde{X}(t) = X(Z(t)),$  where  $\{Z(t)\}$  is a Lévy process with Laplace transform

$$\exp\left\{-t\left[\sqrt{2\lambda + (\theta - 1)^2/4} - \sqrt{(\theta - 1)^2/4}\right]\right\}, \ \theta \ge 1$$

Z(t) is a tilted positive stable process with index  $rac{1}{2}$  and density

$$\frac{t}{2\pi z^3}e^{-\frac{1}{2}\frac{t}{\sqrt{z}}}\cdot e^{-\frac{1}{8}(\theta-1)^2z+\frac{1}{2}|(\theta-1)|t}, \ z>0$$

Z(t) is a Lévy process with Laplace transform

$$\exp\left\{-\frac{t}{\sqrt{2\pi}} \int_0^\infty \frac{e^{-x(\theta-1)^2/8}}{x^{3/2}} (1 - e^{-x\lambda}) \, dx\right\}$$

The eigenvalues of  $\widetilde{X}(t)$  are, for  $\theta \geq 1$ ,

$$\mathbb{E}\Big[\exp\Big\{-\frac{1}{2}n(n+\theta-1)Z(t)\Big\}\Big] = \exp\{-nt\}$$

 $\widetilde{X}(t)$  has a generator  $\widetilde{L}$  satisfying

$$-\tilde{L} = \sqrt{2(-L) + (\theta - 1)^2/4} - \sqrt{(\theta - 1)^2/4}$$

A series expansion with positive coefficients of L is

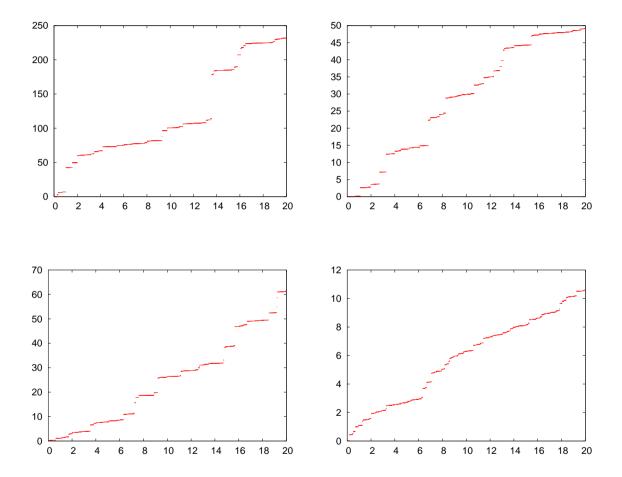
$$\widetilde{L} = \sqrt{c} \sum_{k=1}^{\infty} \frac{2^k}{k!} \left(\frac{1}{2}\right)_{(k-1)} \left(\frac{L}{c}\right)^k$$

where  $c = (\theta - 1)^2/4$ .

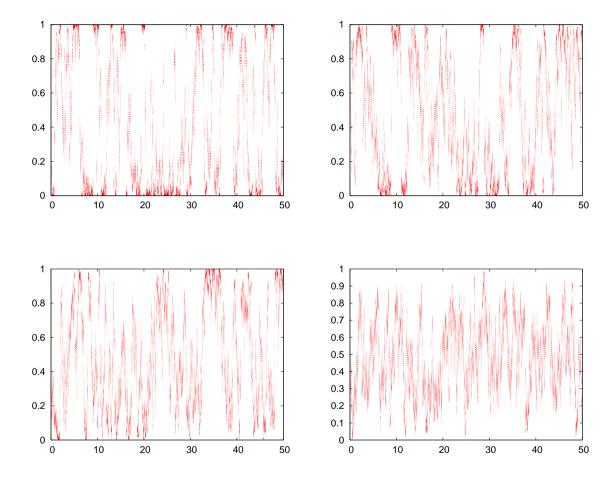
$$L = \frac{1}{2} \left( -\widetilde{L}^2 + (\theta - 1)\widetilde{L} \right)$$

# Eigenfunctions

$$\widetilde{L}R_n^{(\alpha,\beta)}(x) = -nR_n^{(\alpha,\beta)}(x)$$



Tilted Stable subordinator, index half (  $\theta=1.0, 1.5, 2.0, 5.0)$ 



Subordinated Wright-Fisher diffusion (  $\theta=1.0, 1.5, 2.0, 5.0)$ 

If  $\theta < 1$  then for  $n \ge 1$ ,

$$\mathbb{E}\Big[\exp\Big\{-\frac{1}{2}n(n+\theta-1)Z(t)\Big\}\Big] = \exp\{-nt\} \times \exp\{t(1-\theta)\}$$

Let  $\widetilde{f}(x,y;t)$  be the transition density of  $\widetilde{X}(t)$ , then the transition density with eigenvalues  $\exp\{-nt\}$ ,  $n\geq 0$  is

$$e^{-t(1-\theta)}\widetilde{f}(x,y;t) + (1-e^{-t(1-\theta)})B(\alpha,\beta)^{-1}y^{\alpha-1}(1-y)^{\beta-1}$$

Subordinated process  $X(\widehat{Z}(t))$  where  $\widehat{Z}(t)$  is a similar process to Z(t) but has an extra state  $\infty$ . Z(t) is killed by a jump to  $\infty$  at a rate  $(1-\theta)$ .

#### Subordinated genealogical form of the transition density

$$\sum_{\ell=1}^{\infty} q_{\ell}^{\theta}(t) \sum_{k=1}^{\ell} {\ell \choose k} p^{k} (1-p)^{\ell-k} B(\alpha+k, \beta+\ell-k)^{-1} x^{\alpha+k-1} (1-x)^{\beta+\ell-k-1}$$

where  $\{q_\ell^\theta(t)\}$  are transition probabilities of a death process  $\{A^\theta(t),\,t\geq 0\}$  with death rates  $\mu_k={k\choose 2}+\frac{k\theta}{2}$  and  $A^\theta(0)=\infty.$ 

Subordinated process X(t)=X(Z(t)) has a similar form for the transition density, with  $q_\ell^\theta(t)$  replaced by  $\mathbb{E}(q_l^\theta(Z(t)))$ , transition functions of the subordinated death process  $A^\theta(Z(t))$ .

# Subordinated death process $A^{ heta}(Z(t))$ example

Z(t) is a tilted positive stable process with index  $\frac{1}{2}$ .  $\widetilde{A}^{ heta}(t)=A^{ heta}(Z(t))$  is a Markov process with  $\widetilde{A}^{ heta}(0)=\infty$  and a pgf of

$$G_{\widetilde{A}^{\theta}(t)}(s) = \Big(\frac{1-4pqs}{1-4pq}\Big)^{-\frac{1}{2}} \times \Big(\frac{1-\sqrt{1-4pqs}}{2ps}\Big)^{\theta-1}, \; \theta \geq 0,$$
 where  $p = e^{-t}/(1+e^{-t})$  and  $q = 1/(1+e^{-t}).$ 

Random walk on  $\mathbb{Z}$  with transitions  $j \to j+1$  with probability p and  $j \to j-1$  with probability q=1-p and  $q \ge p$ .

Let the number of steps to hit  $-\theta$ , starting from 0 be  $2\xi + \theta$ .

Then  $\xi$  has a pgf of

$$H(s) = \left(\frac{1 - \sqrt{1 - 4pqs}}{2ps}\right)^{\theta}$$

 $\widetilde{A}(t)+1$  has the same distribution as the size-biassed distribution of  $\xi,$  with pgf

$$G_{\widetilde{A}(t)} = \frac{sH'(s)}{H'(1)}$$

The probability distribution of  $\widetilde{A}^{ heta}(t)$  is

$${2j+\theta-1 \choose j} \left(\frac{z}{1+z}\right)^j \left(\frac{1}{1+z}\right)^{j+\theta} (1-z)$$

for j = 0, 1, ..., where  $z = e^{-t}$ .

The probability distribution of  $A^{\theta}(t)$  is

$$\sum_{k=j}^{\infty} \rho_k^{\theta}(t) (-1)^{k-j} \frac{(2k+\theta-1)(j+\theta)_{(k-1)}}{j!(k-j)!}$$

for  $j=0,1,\ldots$ , where  $\rho_k^{\theta}(t)=e^{-k(k+\theta-1)t/2}$ .

#### General characterization of eigenvalues

$$R_n^{(\alpha,\beta)}(x) = {}_{2}F_1(-n, n+\theta-1; \alpha; 1-y)$$

#### Eigenvalues

$$\int_{0}^{1-} \frac{1 - R_{n}^{(\alpha,\beta)}(y)}{1 - y} dG(y)$$

$$= -c \sum_{k=1}^{n} \frac{(-n)_{(k)}(n + \theta - 1)_{(k)} \mu_{k-1}}{\alpha_{(k)}} \frac{\mu_{k-1}}{k!}$$

$$= -c \sum_{k=1}^{n} \frac{\prod_{j=0}^{k-1} (-n(n + \theta - 1) + j(j + \theta - 1))}{\alpha_{k}} \frac{\mu_{k-1}}{k!}$$

where 
$$\int_0^{1-} (1-y)^k dG(y) = c\mu_k$$
.

The generator corresponding to a process with these eigenvalues is

$$\widehat{L} = c \sum_{k=1}^{\infty} \frac{\prod_{j=0}^{k-1} (2L + j(j+\theta - 1))}{\alpha_{(k)}} \frac{\mu_{k-1}}{k!}$$

This is a positive series in L.

Laguerre diffusion  $\{Y(t), t \geq 0\}$ Branching process with immigration

Generator

$$L = x \frac{\partial^2}{\partial x^2} + (-bx + c) \frac{\partial}{\partial x}, \ b = 1, c > 0$$

Transition functions, for x, y > 0

$$f(x,y;t) = \frac{y^{c-1}}{\Gamma(c)} e^{-y} \sum_{n=0}^{\infty} e^{-nt} L_n^{(c-1)}(x) L_n^{(c-1)}(y) \frac{n!}{c_{(n)}}$$

$$= \sum_{k=0}^{\infty} e^{-\mu x} \frac{(\mu x)^k}{k!} \frac{(1-r)^{-(c+k)}}{\Gamma(c+k)} y^{c+k-1} e^{-y/(1-r)}$$

where  $\{L_n^{(c-1)}(x)\}$  are Laguerre polynomials,  $r=e^{-t}$  and  $\mu=r/(1-r).$ 

Transition functions of a Markov process

$$\widetilde{f}(x,y;t) = \frac{y^{c-1}}{\Gamma(c)} e^{-y} \sum_{n=0}^{\infty} e^{-td_n} L_n^{(c-1)}(x) L_n^{(c-1)}(y) \frac{n!}{c_{(n)}}$$

are characterized by their eigenvalues having the representation

$$d_n = \int_0^1 \frac{1 - y^n}{1 - y} dG(y) = an + \int_0^{1 - y^n} \frac{1 - y^n}{1 - y} dG(y), \ a \ge 0$$

Sarmanov (1968), G (1969).

A Markov process with transition functions  $\widetilde{f}(x,y;t)$  has a characterization as a subordinated process

$$\widetilde{Y}(t) = Y(at + Z(t))$$

where  $\{Z(t), t \geq 0\}$  is a Lévy process with Laplace transform

$$\exp\left\{-\int_0^{1-} \frac{1 - e^{-\lambda(-\log y)}}{1 - y} dG(y)\right\}$$

$$\int_0^{1-} 1 \wedge (-\log y) \frac{1}{1-y} dG(y) < \infty \equiv \int_0^{1-} dG(y) < \infty$$

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