WF diffusions with randomized fitness and alternative paths to neutrality.

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1 Preliminaries on diffusions on $[0,1]$

1.1 Kolmogorov backward and forward

$$dx_t \overset{Itô}{=} f(x_t)\, dt + g(x_t)\, dw_t,\ x_0 = x \in (0,1)\,. \tag{1}$$

$$G = f(x)\,\partial_x + \frac{1}{2} g^2(x)\,\partial_x^2 \text{ and } G^*(\cdot) = -\partial_y (f(y)\cdot) + \frac{1}{2}\partial_y^2 \left(g^2(y)\cdot\right)$$

$$u := u(x,t) = \mathbf{E}\psi\left(x_{t\wedge\tau_x}\right) \text{ and } p := p(x;t,y)$$

$$\partial_t u = G(u)\,;\ u(x,0) = \psi(x) \text{ and } \partial_t p = G^*(p)\,,\ p(x;0,y) = \delta_y(x)\,. \tag{2}$$

In u, $t\wedge\tau_x := \inf(t,\tau_x)$ where $\tau_x = \tau_{x,0}\wedge\tau_{x,1} < \infty$ or ∞. $g(0) = g(1) = 0$.

1.2 Natural coordinate, scale and speed measure

$$\begin{aligned} \varphi'(y) &= e^{-2\int^{y}\frac{f(z)}{g^{2}(z)}dz} > 0 \\ \varphi(x) &= \int^{x} e^{-2\int_{y_0}^{y}\frac{f(z)}{g^{2}(z)}dz} dy. \end{aligned}$$

φ harmonic kills f of $\{x_t\}$: $G(\varphi) = 0$. Speed density: $m(x) = 1/(g^2\varphi')(x)$: $G^*(m) = 0$.

Examples (population genetics). Reversibility of x_t w.r. to m.

- $f(x) = 0$ and $g^2(x) = x(1-x)$. Neutral WF model .
- $u_1, u_2 > 0$, $f(x) = u_1 - (u_1 + u_2)x$ and $g^2(x) = x(1-x)$.
- $\sigma \in \mathbf{R}$, logistic drift $f(x) = \sigma x(1-x)$ and $g^2(x) = x(1-x)$.
- $f(x) = \sigma x(1-x) + u_1 - (u_1 + u_2)x$ and $g^2(x) = x(1-x)$.

1.3 Transition probability density

Boundaries abs. $\rho_t(x) := \int_0^1 p(x; t, y)\, dy$: $\rho_t(x) = \mathbf{P}(\tau_x > t)$.

$$\partial_t \rho_t(x) = G(\rho_t(x)), \text{ with } \rho_0(x) = \mathbf{1}_{(0,1)}(x).$$

Normalize: $q(x; t, y) := p(x; t, y)/\rho_t(x)$

$$\partial_t q = -\partial_t \rho_t(x)/\rho_t(x) \cdot q + G^*(q), \; q(x; 0, y) = \delta_y(x).$$

Creation of mass process: birth rate $b_t(x) := -\partial_t \rho_t(x) / \rho_t(x) > 0$ create mass to compensate loss of mass of $\{x_t\}$ at boundaries. $b_t(x)$ depends on x and t, not on y. $\exists$ positive eigenvalues $(\lambda_k)_{k\geq 1}$

$$-G^*(v_k) = \lambda_k v_k \text{ and } -G(y_k) = \lambda_k u_k.$$

$$p(x;t,y) = \sum_{k\geq 1} e^{-\lambda_k t} \frac{u_k(x) v_k(y)}{\int_0^1 u_k(x) v_k(x) dx} \text{ (spectral exp.)}$$

$\lambda_1 > \lambda_0 = 0$ smallest non-null eigenvalue: $b_t(x) \underset{t\to\infty}{\to} \lambda_1$.

YAGLOM limit of $[\{x_t\}$ conditioned on $\tau_x > t]$

$$q(x;t,y) \underset{t\to\infty}{\to} q_\infty(y) = v_1(y), \tag{3}$$

Example. *Neutral WF, $\lambda_1 = 1$ with $v_1 \equiv 1$. Yaglom limit uniform.*

1.4 Feller classification of boundaries

Boundaries $\partial I := \{0,1\}$ are of 2 types: accessible or inaccessible. Accessible boundaries are either regular or exit (absorbing) boundaries, whereas inaccessible boundaries are either entrance (reflecting) or natural boundaries.

1.5 Additive functionals along sample paths

Boundaries absorbing (exit). Process transient.

$$\alpha(x) = \mathbf{E}\left(\int_0^{\tau_x} c(x_s)\, ds + d(x_{\tau_x})\right), \tag{4}$$

c and d non-negative. $\alpha(x) > 0$ on $(0,1)$ (superharmonic) solves Dirichlet:

$$-G(\alpha) = c \text{ if } x \in \overset{\circ}{I} \text{ and } \alpha = d \text{ if } x \in \partial I.$$

Examples.

1. $c = 0$ and $d(\circ) = \mathbf{1}(\circ = 1)$.

$$\alpha =: \alpha_1(x) = \mathbf{P}(\tau_{x,1} < \tau_{x,0}) = \frac{\varphi(x) - \varphi(0)}{\varphi(1) - \varphi(0)}.$$

$\alpha_1(x) : G(\alpha_1) = 0$, with BC $\alpha_1(0) = 0$ and $\alpha_1(1) = 1$.

$$\alpha_0(x) = \mathbf{P}(\tau_{x,0} < \tau_{x,1}) = 1 - \alpha_1(x).$$

2. $\alpha =: \mathfrak{g}(x,y) = \mathbf{E}\left(\lim_{\varepsilon \to 0} \frac{1}{2\varepsilon} \int_0^{\tau_x} \mathbf{1}_{(y-\varepsilon, y+\varepsilon)}(x_s)\, ds\right) = \int_0^{\infty} p(x; s, y)\, ds$ Green function,

$$-G(\mathfrak{g}) = \delta_y(x) \text{ if } x \in \overset{\circ}{I} \text{ and } \mathfrak{g} = 0 \text{ if } x \in \partial I.$$

$\mathfrak{g}$ = expected local time at y, starting from x (sojourn time dens. at y).

$$\mathfrak{g}(x,y) = 2\alpha_0(x)\,m(y)\,(\varphi(y)-\varphi(0)) \text{ if } 0 \leq y \leq x$$

$$\mathfrak{g}(x,y) = 2\alpha_1(x)\,m(y)\,(\varphi(1)-\varphi(y)) \text{ if } x < y \leq 1 \tag{5}$$

Green kernel inverts $-G$

$$\alpha(x) = \int_{\overset{\circ}{I}} \mathfrak{g}(x,y)\,c(y)\,dy \text{ if } x \in \overset{\circ}{I} \text{ and } \alpha = d \text{ if } x \in \partial I.$$

$$\mathbf{3}.\ \alpha_\lambda(x) = \mathbf{E}\left(\int_0^{\tau_x} e^{-\lambda s} c(x_s)\,ds + d(x_{\tau_x})\right),$$

$\alpha_\lambda(x) \geq 0$ solves Dynkin problem:

$$(\lambda I - G)(\alpha_\lambda) = c \text{ if } x \in \overset{\circ}{I} \text{ and } \alpha_\lambda = d \text{ if } x \in \partial I$$

involving the resolvent operator $(\lambda I - G)^{-1}$ on c.
If $c(x) = \delta_y(x)$, $d = 0$, then,

$$\alpha_\lambda =: \mathfrak{g}_\lambda(x,y) = \mathbf{E}\left(\int_0^{\tau_x} e^{-\lambda s}\delta_y(x_s)\,ds\right) = \int_0^\infty e^{-\lambda s} p(x;s,y)\,ds$$

$\lambda-$potential function, solution to:

$$(\lambda I - G)(\mathfrak{g}_\lambda) = \delta_y(x) \text{ if } x \in \overset{\circ}{I} \text{ and } \mathfrak{g}_\lambda = 0 \text{ if } x \in \partial I.$$

$\mathfrak{g}_\lambda$ temporal Laplace transform of the tpd p from x to y at t, $\mathfrak{g}_0 = \mathfrak{g}$.

$$\alpha_{\lambda}(x) = \int_{\overset{\circ}{I}} \mathfrak{g}_{\lambda}(x,y)\, c(y)\, dy \text{ if } x \in \overset{\circ}{I} \text{ and } \alpha_{\lambda} = d \text{ if } x \in \partial I.$$

LST of law of $\tau_{x,y}$ [first-passage time to y starting from x]

$$\mathbf{E}\left(e^{-\lambda \tau_{x,y}}\right) = \mathfrak{g}_{\lambda}(x,y) / \mathfrak{g}_{\lambda}(y,y). \tag{6}$$

1.6 Transformation of sample paths (Doob transform)

$$\{\overline{x}_t\} \text{ df } \rightarrow \overline{p}(x;t,y) = \frac{\alpha(y)}{\alpha(x)} p(x;t,y). \tag{7}$$

Sample paths $x \rightarrow y$ of $\{x_t\}$ with $\alpha(y)/\alpha(x)$ large favored.

$$\overline{G}^{*}(\overline{p}) = \alpha(y)\, G^{*}(\overline{p}/\alpha(y) \text{ and } \overline{G}(\cdot) = \frac{1}{\alpha(x)} G(\alpha(x)\cdot).$$

$\widetilde{G}(\cdot) := \frac{\alpha'}{\alpha} g^2 \partial_x(\cdot) + G(\cdot)$, $[\widetilde{f}(x) := f(x) + \frac{\alpha'}{\alpha} g^2(x)]$

$$\overline{G}(\cdot) = \frac{1}{\alpha} G(\alpha)\cdot + \widetilde{G}(\cdot) = -\frac{c}{\alpha}\cdot + \widetilde{G}(\cdot) \tag{8}$$

$$d\widetilde{x}_t = \widetilde{f}(\widetilde{x}_t)\, dt + g(\widetilde{x}_t)\, dw_t,\ \widetilde{x}_0 = x \in (0,1), \tag{9}$$

possibly killed at rate $d = \frac{c}{\alpha}$ as soon as $c \neq 0$.

Whenever $\{\widetilde{x}_t\}$ killed $\Rightarrow$ enters into coffin state $\{\partial\}$.

$\widetilde{\tau}_x$ abs. time at the boundaries of $\{\widetilde{x}_t\}$ started at x, with $\widetilde{\tau}_x = \infty$ if boundaries inaccessible to new process $\widetilde{x}_t$. $\widetilde{\tau}_{x,\partial}$ killing time in I of $\{\widetilde{x}_t\}$ started at x (the hitting time of ∂), with $\widetilde{\tau}_{x,\partial} = \infty$ if $c = 0$. Then $\overline{\tau}_x := \widetilde{\tau}_x \wedge \widetilde{\tau}_{x,\partial}$ novel stopping time of $\{\widetilde{x}_t\}$.

SDE for $\{\widetilde{x}_t\}$, together with its global stopping time $\overline{\tau}_x$ characterize $\{\overline{x}_t\}$.

Suppose $\widetilde{x}_t$ absorbed at $\{0,1\}$. For $\{\overline{x}_t\}$, evaluate [$\widetilde{c}$ and $\widetilde{d}$ both ≥ 0]

$$\widetilde{\alpha}(x) := \widetilde{\mathbf{E}}^x \left(\int_0^{\overline{\tau}(x)} \widetilde{c}(\widetilde{x}_s)\, ds + \widetilde{d}\left(\widetilde{x}_{\overline{\tau}(x)}\right) \right)$$

$$-\overline{G}(\widetilde{\alpha}) = \widetilde{c} \text{ if } x \in \overset{\circ}{I} \text{ and } \widetilde{\alpha} = \widetilde{d} \text{ if } x \in \partial I.$$

$$\text{It is: } \widetilde{\alpha}(x) = \frac{1}{\alpha(x)} \int_{\overset{\circ}{I}} \mathfrak{g}(x,y)\, \alpha(y)\, \widetilde{c}(y)\, dy,\ x \in \overset{\circ}{I} .$$

Normalizing and conditioning. $\overline{\rho}_t(x) := \int_{\overset{\circ}{I}} \overline{p}(x;t,y)\, dy = \widetilde{\mathbf{P}}(\overline{\tau}_x > t)$ solves

$$\partial_t \overline{\rho}_t(x) = \overline{G}(\overline{\rho}_t(x)) = -d(x)\, \overline{\rho}_t(x) + \widetilde{G}(\overline{\rho}_t(x)),\ \overline{\rho}_0(x) = \mathbf{1}_{(0,1)}(x) . \quad (10)$$

Normalize. $\overline{q}(x;t,y) := \overline{p}(x;t,y) / \overline{\rho}_t(x)$, $\overline{q}(x;0,y) = \delta_y(x)$,

$$\partial_t \overline{q} = -\partial_t \overline{\rho}_t(x) / \overline{\rho}_t(x) \cdot \overline{q} + \overline{G}^*(\overline{q}) = \left(\overline{b}_t(x) - d(y)\right) \cdot \overline{q} + \widetilde{G}^*(\overline{q}).$$

$$\overline{b}_t(x) \to \lambda_1 \;\Rightarrow\; \overline{q}(x;t,y) \underset{t\to\infty}{\to} \overline{q}_\infty(y), \tag{11}$$

$$-\widetilde{G}^*(\overline{q}_\infty) = (\lambda_1 - d(y)) \cdot \overline{q}_\infty, \text{ or } -\overline{G}^*(\overline{q}_\infty) = \lambda_1 \cdot \overline{q}_\infty.$$

$$\overline{q}_\infty(y) = \alpha(y) v_1(y) \Big/ \int_0^1 \alpha(y) v_1(y)\, dy. \tag{12}$$

$\overline{q}_\infty = \alpha v_1/\text{norm}$ Yaglom limit law of $(\overline{x}_t; t \geq 0)$ conditioned on the event $\overline{\tau}_x > t$.

Examples: (i) Take α : $-G(\alpha) = 0$ if $x \in \overset{\circ}{I}$ with BCs $\alpha(0) = 0$ and $\alpha(1) = 1 \Rightarrow c = 0 : \widetilde{\tau}_{x,\partial} = \infty$ so $\overline{\tau}_x := \widetilde{\tau}_x$. $\overline{G} = \widetilde{G}$. $\{\widetilde{x}_t\}$ is $\{x_t\}$ conditioned on exit at $x = 1$. Boundary 1 exit ; 0 entrance.

$$\alpha =: \alpha_1(x) = \frac{\varphi(x) - \varphi(0)}{\varphi(1) - \varphi(0)}$$

$$\text{drift}: \; \widetilde{f}(x) = f(x) + \frac{g^2(x)\, \alpha_1'(x)}{\alpha_1(x)}$$

$\widetilde{\alpha}(x) := \widetilde{\mathbf{E}}(\widetilde{\tau}_x)$ solves $-\widetilde{G}(\widetilde{\alpha}) = 1 \to \widetilde{\alpha}(x) = \frac{1}{\alpha_1(x)} \int_{\overset{\circ}{I}} \mathfrak{g}(x,y)\, \alpha_1(y)\, dy$

(ii) $\alpha : -G(\alpha) = \delta_y(x)$ if $x \in \overset{\circ}{I}$, BC $\alpha(0) = \alpha(1) = 0$: Selects $\{x_t\}$ sample paths with **large sojourn time density** at y

$$\begin{aligned}\widetilde{f}(x) &= f(x) + g^2(x)\frac{\alpha_0'(x)}{\alpha_0(x)} \text{ if } y \leq x \\ &= f(x) + g^2(x)\frac{\alpha_1'(x)}{\alpha_1(x)} \text{ if } x < y\end{aligned}$$

$\{\widetilde{x}_t\}$ is $\{x_t\}$ conditioned on exit at $\circ = 1$ if $x < y$ and $\{x_t\}$ conditioned on exit at $\circ = 0$ if $x > y$. Stopping time $\widetilde{\tau}_y(x)$ of $\{\widetilde{x}_t\}$ occurs at rate $\delta_y(x)/\mathfrak{g}(x,y)$. Killing time when process at y for the last time.

(iii) λ_1 smallest eigenvalue $\neq 0$ of G. $\alpha = u_1 : -G(u_1) = \lambda_1 u_1$

$$\overline{G}(\cdot) = \frac{1}{\alpha}G(\alpha)\cdot + \widetilde{G}(\cdot) = -\lambda_1 \cdot + \widetilde{G}(\cdot),$$

kill sample paths of $\{\widetilde{x}_t\}$ governed by $\widetilde{G}$ at **constant death rate** $d = \lambda_1$.

$$\overline{p}(x;t,y) = \frac{u_1(y)}{u_1(x)}p(x;t,y).$$

$\widetilde{p}(x;t,y) = e^{\lambda_1 t}\overline{p}(x;t,y)$: tpd of $\{\widetilde{x}_t\}$ governed by $\widetilde{G}$: $\{x_t\}$ conditioned on **never** hitting boundaries $\{0,1\}$ ($Q-$process of $\{x_t\}$).

$$\widetilde{p}(x;t,y) \sim e^{\lambda_1 t}\frac{u_1(y)}{u_1(x)}e^{-\lambda_1 t}\frac{u_1(x)\,v_1(y)}{\int_0^1 u_1(y)\,v_1(y)\,dy} = \frac{u_1(y)\,v_1(y)}{\int_0^1 u_1(y)\,v_1(y)\,dy}. \tag{13}$$

Limit law of $Q-$process $\{\widetilde{x}_t\}$ is norm. product of u_1 and v_1.

SUPER-H, SUB-H or none:

(i) $\alpha \geq 0$ s.t $-G(\alpha) = c \geq 0$ ($\alpha \geq 0 \Leftrightarrow \alpha > 0$ in I, possibly with $\alpha(0)$ or $\alpha(1)$ equal 0). α super-harmonic (or excessive) function for $G-$process.

Rate $\lambda(x) := -\frac{c}{\alpha}(c) =: -d(x)$ satisfies $\lambda(x) \leq 0$: ONLY killing at rate $d(x)$.

(ii) $\alpha \geq 0$ s.t. $-G(\alpha) = c \leq 0$. α sub-harmonic function for $G-$process.

BD at rate $\lambda(x) =: b(x)$: $\widetilde{G}-$diffusing mother particle lives Exp(1) random time. When mother dies $\rightarrow M(x)$ particles ($M(x) \overset{d}{=} 1 + \Delta(\lambda(x))$, $\Delta(\lambda(x))$ geometric RV on $\{0, 1, 2, ...\}$ mean $\lambda(x)$. $M(x) \geq 1$ independent daughter $\widetilde{G}-$particles start afresh. If $\lambda(x) =: b(x)$ bounded above

$$\lambda(x) = \lambda^* (\mu(x) - 1) = \lambda^* p_2(x),$$

where $\lambda^* = \sup_{x \in [0,1]} \lambda(x)$ and $1 \leq \mu(x) \leq 2$. $M(x) \in \{1, 2\}$ (binary BD rate λ_*).

EXAMPLE: G is neutralWF, $\alpha = \exp(\sigma x) \Rightarrow \widetilde{G}$ WF with selection (transient), ONLY branching at rate $\lambda(x) = b(x) = G(\alpha)/\alpha = \sigma^2 x(1-x)/2$.

(iii) α s.t. $-G(\alpha)$ has no specific sign $\rightarrow$ killing and branching. $\lambda(x) = b(x) - d(x)$ $b(x)$ and $d(x)$ are birth (branching) and death (killing) components of $\lambda(x)$.

• $\lambda(x)$ bounded below $\lambda_* = -\inf_{x\in[0,1]} \lambda(x) > 0$.

$$\lambda(x) = \lambda_* (\mu(x) - 1),$$

where $\mu(x) \geq 0$. Branching occurs at rate λ_*. $M(x)$ particles (where $M(x) \overset{d}{=} \Delta(\mu(x))$ and $\Delta(\mu(x))$ is a geom. distributed random variable on $\{0, 1, 2, ...\}$.

• $\lambda = G(\alpha)/\alpha$ bounded above and below.

$$\lambda(x) = \lambda^* (\mu(x) - 1) = \lambda^* (p_2(x) - p_0(x)),$$

where $\lambda^* = \sup_{x\in[0,1]} |\lambda(x)|$ and $0 \leq \mu(x) \leq 2$. $M(x) \in \{0, 2\}$(binary branching).

• α super-harm for $G \Rightarrow \beta = 1/\alpha \geq 0$ is sub-harm for $\widetilde{G}$. Results from

$$\beta^{-1}\widetilde{G}(\beta) = -\alpha^{-1}G(\alpha) \text{ thus } -G(\alpha) \geq 0 \Rightarrow -\widetilde{G}(\beta) \leq 0.$$

2 The Wright-Fisher and Moran examples

Neutral WF: Cannings reproduction law. 1st-generation random offspring #s $\boldsymbol{\nu}_N := (\nu_N(1), ..., \nu_N(N))$

$$\mathbf{P}(\boldsymbol{\nu}_N = \mathbf{k}_N) = \frac{N! \cdot N^{-N}}{\prod_{n=1}^{N} k_n!}, \quad |\mathbf{k}_N| = N. \tag{14}$$

Condition N independent Poisson r.v.s on summing to N. Same if conditioned Compound Poisson (ID).

$N_r(n)$: offspring # of n individuals at generation $r \in \mathbf{N}_0$ corresponding to (say) allele A_1. MC:

$$\mathbf{P}\left(N_{r+1}(n) = k' \mid N_r(n) = k\right) = \binom{N}{k'} \left(\frac{k}{N}\right)^{k'} \left(1 - \frac{k}{N}\right)^{N-k'}.$$

$n = [Nx]$ with $x \in (0,1)$. Dynamics of scaled process $x_t := N_{[Nt]}(n)/N$, $t \in \mathbf{R}_+$

$$dx_t = \sqrt{x_t(1 - x_t)} dw_t, \; x_0 = x. \tag{15}$$

Time measured in units of N. If Moran $\boldsymbol{\nu}_N$:=random perm$(2, 0, 1, .., 1)$ time scale N^2.

Non-neutral cases

$$\mathbf{P}\left(N_{r+1}(n) = k' \mid N_r(n) = k\right) = \binom{N}{k'} \left(p_N\left(\frac{k}{N}\right)\right)^{k'} \left(1 - p_N\left(\frac{k}{N}\right)\right)^{N-k'}$$

$$\text{where } p_N(x) : x \in (0,1) \to (0,1)$$

state-dependent prob. ($\neq$ identity x) : Diffusion approximation in terms of $x_t := N_{[Nt]}(n)/N$, $t \in \mathbf{R}_+$ under suitable conditions.

- $p_N(x) = (1 - \pi_{2,N})\, x + \pi_{1,N}\,(1 - x)$

$(\pi_{1,N}, \pi_{2,N})$ small (N-dependent) mutation prob. from A_2 to A_1 (respectively A_1 to A_2) $(N \cdot \pi_{1,N}, N \cdot \pi_{2,N}) \underset{N\to\infty}{\to} (u_1, u_2) \to$ WF model with mutations.

- $p_N(x) = \dfrac{(1 + s_{1,N})\, x}{1 + s_{1,N} x + s_{2,N}\,(1 - x)}$

where $s_{i,N} > 0 : \ N \cdot s_{i,N} \underset{N\to\infty}{\to} \sigma_i > 0$, $i = 1, 2, \to$ WF model with selective drift $\sigma x\,(1 - x)$, $\sigma := \sigma_1 - \sigma_2$.

3 The WF-Karlin model: randomized fitness

3.1 Karlin model: small population case

Disorder is the simplest possible: replace constant selection intensities $(s_{1,N}, s_{2,N})$ at each generation r by the random iid sequence $\left(s_{1,N}^{(r)}, s_{2,N}^{(r)}\right)_{r\geq 1}$. Conditions (C)

$$N \cdot \mathbf{E}\left(s_{i,N}\right) \underset{N\to\infty}{\to} \sigma_i > 0, i = 1, 2$$

$$N \cdot \mathbf{E}\left(s_{i,N}^2\right) \underset{N\to\infty}{\to} \mu_i > 0, i = 1, 2$$

$$N \cdot \mathbf{E}\left(s_{1,N} s_{2,N}\right) \underset{N\to\infty}{\to} \mu_{1,2}.$$

all moment terms higher than $2 : o\left(1/N\right)$.

Diffusion approximation of $x_t := N_{[Nt]}\left(n\right)/N$, $t \in \mathbf{R}_+$

$$f\left(x\right) = x\left(1-x\right)\left[\eta - \rho x\right] \text{ and } g\left(x\right) = \sqrt{x\left(1-x\right) + \rho x^2\left(1-x\right)^2} \qquad (16)$$

(C) $\Rightarrow$

$$\begin{aligned} \eta &= \sigma_1 - \sigma_2 + \mu_2 - \mu_{1,2} = \lim_{N\to\infty} N\mathbf{E}\left(\left(1-s_{2,N}\right)\left(s_{1,N} - s_{2,N}\right)\right) \\ \rho &= \mu_1 + \mu_2 - 2\mu_{1,2} = \lim_{N\to\infty} N\mathbf{E}\left(\left(s_{1,N} - s_{2,N}\right)^2\right) > 0. \end{aligned}$$

$$\text{Drift also} : f\left(x\right) = x\left(1-x\right)\left[\gamma + \rho\left(\frac{1}{2} - x\right)\right] \qquad (17)$$

$\gamma = \gamma_1 - \gamma_2$, with $\gamma_i = \sigma_i - \mu_i/2$, $i = 1, 2$.

- f has 2 contributions: one involving γ, the other one ρ. Latter one introduces a stabilizing **drift towards** $1/2$.

- $g^2\left(x\right)$ has 2 contributions: binomial sampling and within generation selection variance. If ρ is not large compared to 1 (small population size case) both terms contribute equally likely. Selective advantage of allele A_1 over allele $A_2 : \gamma_1 > \gamma_2$.

$\gamma_i = \sigma_i - \mu_i/2 \Rightarrow$ involve 2nd-order moment of the $s_{i,N}$, not only means σ_i.

Additive functionals. $\varphi'(y) = e^{-\int^y \frac{2f(x)}{g^2(x)}dx}$.

$$r = \sqrt{1+4/\rho} > 1 \text{ and } r_i = \frac{1 \mp \sqrt{1+4/\rho}}{2}, i = 1, 2.$$

Normalized scale function (Boundaries exit). Process small population size transient

$$\alpha_1(x) = \frac{\varphi(x) - \varphi(0)}{\varphi(1) - \varphi(0)} = \frac{1}{Z}\int_0^x (y - r_1)^{-1-\frac{2\gamma}{\rho r}} (1 - y - r_1)^{-1+\frac{2\gamma}{\rho r}} dy,$$

$$\text{speed dens.: } m(x) = \frac{(x - r_1)^{\frac{2\gamma}{\rho r}} (1 - x - r_1)^{-\frac{2\gamma}{\rho r}}}{\rho x (1 - x)}. \tag{18}$$

$$\mathbf{E}(\tau_x) = 2\alpha_1(x)\int_x^1 m(y)[\varphi(1) - \varphi(y)]\, dy + 2\alpha_0(x)\int_0^x m(y)[\varphi(y) - \varphi(0)]\, dy$$

Symmetric case. suppose $s_{1,N} \stackrel{d}{=} s_{2,N} \Rightarrow \sigma_1 = \sigma_2$, $\mu_1 = \mu_2$ and

$$\eta = \mu_2 - \mu_{1,2} \text{ and } \rho = 2\left(\mu_2 - \mu_{1,2}\right).$$

Thus $\gamma = 0$ and

$$f(x) = \rho x(1 - x)\left(\frac{1}{2} - x\right) \text{ and } g^2(x) = x(1 - x) + \rho x^2 (1 - x)^2$$

Expected time to absorption:

$$\mathbf{E}(\tau_x) = 2\int_0^x \frac{\log((1-y)/y)}{1+\rho y(1-y)} dy \tag{19}$$

$\forall x$, $\mathbf{E}(\tau_x) \searrow \rho$: *fluctuations in differential selection intensities tend to decrease the expected fixation time (despite presence of the competing drift toward* 1/2*).*

3.2 The large population case $\rho \gg 1$

$$\text{DIFF with } g(x) = \sqrt{\rho}x(1-x) \;;\; f(x) = x(1-x)\left[\gamma + \rho\left(\frac{1}{2} - x\right)\right]. \tag{20}$$

Drop binomial sampling contribution to variance term $g^2(x)$ in (16) (small under the large population case assumption). Change of variable $y_t = \int_0^{x_t} \frac{dx}{x(1-x)} = \log\left(\frac{x_t}{1-x_t}\right)$ + Itô calculus

$$dy_t = \gamma dt + \sqrt{\rho} dw_t, \text{ Gaussian} \tag{21}$$

$$p(x;t,y) = \frac{1}{\sqrt{2\pi\rho t}} \frac{1}{y(1-y)} e^{-\frac{1}{2\rho t}\left(\log\left(\frac{y(1-x)}{(1-y)x}\right) - \gamma t\right)^2}. \tag{22}$$

$\gamma > 0$ (< 0): mass of law of x_t accumulates near $y = 1$ ($y = 0$).

$\gamma = 0$, law of x_t forms 2 symmetric peaks about both $y = 1$ and $y = 0$ as $t \uparrow$, but without reaching boundaries.

Both boundaries are natural ($-G$ and $-G^*$ of Karlin diffusion no longer have a discrete spectrum). From (22), $\forall \varepsilon > 0$

$$\begin{aligned} \mathbf{P}\left(x_t \in (1-\varepsilon, 1) \mid x_0 = x\right) \underset{t\to\infty}{\to} 1 \text{ if } \gamma &> 0 \\ \mathbf{P}\left(x_t \in (0, \varepsilon) \mid x_0 = x\right) \underset{t\to\infty}{\to} 1 \text{ if } \gamma &< 0 \\ \mathbf{P}\left(x_t \in (1-\varepsilon, 1) \mid x_0 = x\right) \underset{t\to\infty}{\to} 1/2 \text{ if } \gamma &= 0 \\ \mathbf{P}\left(x_t \in (0, \varepsilon) \mid x_0 = x\right) \underset{t\to\infty}{\to} 1/2 \text{ if } \gamma &= 0 \end{aligned}$$

At boundaries, quasi-fixation (or quasi-extinction) occurs. The limits do not depend on initial condition x.

Randomly varying selection: quasi-fixation of allele A_1 possessing selective advantage $\gamma_1 > \gamma_2$ over A_2 ($\gamma > 0$) occurs with prob. 1, regardless what its initial frequency is and no matter on how large fluctuations in selection intensities really are.

$p(x;t,y)$ increasingly concentrates near $\circ = 1$ stochast. locally stable [KL].

If $\gamma = 0$ (no selective advantage), quasi-abs. at both endpoints of I occurs equally likely, whatever x.

$$\text{speed d. Karlin: } m(x) = \frac{1}{(g^2\varphi')(x)} = x^{\frac{2\gamma}{\rho}-1}(1-x)^{-\frac{2\gamma}{\rho}-1}. \tag{23}$$

The symmetric (NEUTRAL) case. $\gamma = 0$. $\{x_t\}$ oscillate back and forth between the boundaries, i.o.: substantial amount of time spent in their neighborhood. Process $0-$recurrent. (20) is:

$$dx_t = \rho x_t(1-x_t)\left(\frac{1}{2}-x_t\right)dt + \sqrt{\rho}x_t(1-x_t)\,dw_t \tag{24}$$

with stabilizing drift toward 1/2.

Let $\varepsilon > 0$ small. Let $x \in I_\varepsilon = [\varepsilon, 1-\varepsilon]$. Boundaries inaccessible, so work on I_ε rather than on I and force $\{\varepsilon, 1-\varepsilon\}$ abs. Let $\tau_{x,I_\varepsilon} = \tau_{x,\varepsilon} \wedge \tau_{x,1-\varepsilon}$ first exit time of I_ε.

PBS: *Estimate* $\mathbf{P}(\tau_{x,1-\varepsilon} < \tau_{x,\varepsilon})$ *as* $\varepsilon \to 0$, *together with* $\mathbf{E}(\tau_{x,I_\varepsilon})$.

$$\mathbf{P}(\tau_{x,1-\varepsilon} < \tau_{x,\varepsilon}) = \alpha_\varepsilon(x) = \frac{1}{2}\left(1 - \frac{\log\left(\frac{x}{1-x}\right)}{\log\left(\frac{\varepsilon}{1-\varepsilon}\right)}\right). \tag{25}$$

Independently of ρ:

• If $x < \frac{1}{2}$, $\mathbf{P}\left(\tau_{x,1-\varepsilon} < \tau_{x,\varepsilon}\right) \underset{\varepsilon\to 0}{\sim} \frac{1}{2}\left(1 - \frac{\log\left(\frac{1-x}{x}\right)}{-\log\varepsilon}\right)$ slightly less than 1/2 correcting term of order $-1/\log\varepsilon$. If $\varepsilon = 1/(2N)$ and $x = 1/N$, quasi-fix. prob. at $1-\varepsilon$ of mutant is:

$$\frac{1}{2}\left(1 - \frac{\log\left(\frac{1}{N}\right)}{\log\left(\frac{2}{N}\right)}\right) \sim \frac{1}{\log N}. \tag{26}$$

• If $x > \frac{1}{2}$, $\mathbf{P}\left(\tau_{x,1-\varepsilon} < \tau_{x,\varepsilon}\right) \underset{\varepsilon\to 0}{\sim} \frac{1}{2}\left(1 + \frac{\log\left(\frac{x}{1-x}\right)}{-\log\varepsilon}\right)$ slightly greater than 1/2.

Expected exit time of I_ε

$$\mathbf{E}\left(\tau_{x,I_\varepsilon}\right) \underset{\varepsilon\to 0}{\sim} \frac{1}{\rho}\left[\log\left(\varepsilon\right)\right]^2.$$

Quantifies how inaccessible natural boundaries are. $\mathbf{E}\left(\tau_{x,I_\varepsilon}\right) \searrow \rho$.

• Empirical average of heterozygosity. Expect it should be close to 0, $\{x_t\}$ spending substantial amount of time near boundaries.

$$\text{speed dens.: } m\left(x\right) = \frac{1}{\rho x\left(1-x\right)}.$$

Ergodic Chacon-Ornstein ratio theorem for $0-$recurrent processes

$$\frac{t^{-1}\int_0^t 2x_s\left(1-x_s\right)1_{x_s\in(\varepsilon,1-\varepsilon)}ds}{t^{-1}\int_0^t 1_{x_s\in(\varepsilon,1-\varepsilon)}ds}\underset{t\to\infty}{\to}\frac{2\int_\varepsilon^{1-\varepsilon}dx}{\int_\varepsilon^{1-\varepsilon}\frac{1}{x(1-x)}dx}\underset{\varepsilon\to 0}{\sim}\frac{1}{-\log\left(\varepsilon\right)} \tag{27}$$

tends to 0 when $\varepsilon\to 0$, independently of ρ.

Ratio: conditional empirical average of $\{x_t\}-$heterozygosity given remains inside $(\varepsilon,1-\varepsilon)$. Process spends most of the time close to 0 and 1 where heterozygosity vanishes $\Rightarrow$ empirical average of heterozygosity$\to 0$ as $\varepsilon\to 0$.

• Particle spends substantial amount of time near boundaries: time to move from ε to $1-\varepsilon$ large. (22) with $x<y$ and $\gamma=0$.

Green potential function neutral Kimura model:

$$\mathfrak{g}_\lambda\left(x,y\right)=\int_0^\infty e^{-\lambda t}p\left(x;t,y\right)dt.$$

$\tau_{x,y}<\infty$ a.s.: first time $\{x_t\}$ hits y starting from x

$$\mathbf{E}\left(e^{-\lambda\tau_{x,y}}\right)=\frac{\mathfrak{g}_\lambda\left(x,y\right)}{\mathfrak{g}_\lambda\left(y,y\right)}=e^{-\sqrt{2\delta_2\lambda}} \tag{28}$$

$\Rightarrow\tau_{x,y}\overset{d}{=}bS_{1/2}$, $S_{1/2}$ stable law, $b\overset{scale}{=}2\delta_2=\frac{2}{\rho}\left[\log\left(\frac{y(1-x)}{x(1-y)}\right)\right]^2$.

• $x = \varepsilon$ and $y = 1 - \varepsilon$, scale parameter is

$$b = \frac{2^3}{\rho}\left[\log\left(\frac{1-\varepsilon}{\varepsilon}\right)\right]^2 \underset{\varepsilon\to 0}{\sim} \frac{2^3}{\rho}\left[\log\left(1/\varepsilon\right)\right]^2 \to \infty.$$

Takes a long time to move from ε to $1 - \varepsilon$ and back, but move occurs with prob. 1.

$$\frac{\rho}{2^3\left[\log\left(1/\varepsilon\right)\right]^2}\tau_{\varepsilon,1-\varepsilon} \underset{\varepsilon\to 0}{\overset{d}{\to}} S_{1/2}.$$

$$\text{Also } \frac{\rho}{2^5\varepsilon^2}\tau_{\frac{1}{2}\pm\varepsilon,\frac{1}{2}} \underset{\varepsilon\to 0}{\overset{d}{\to}} S_{1/2}.$$

telling how small first return time to $x = 1/2$ is.

4 A related model due to Kimura

Consider Itô-Karlin diffusion model

$$f\left(x\right) = x\left(1-x\right)\left[\gamma + \rho\left(\frac{1}{2} - x\right)\right] \text{ and } g\left(x\right) = \sqrt{\rho}x\left(1-x\right).$$

$$dx_t \overset{Strato}{=} \left[f\left(x_t\right) - \frac{1}{2}gg'\left(x_t\right)\right]dt + g\left(x_t\right)\circ dw_t,\ x_0 = x \tag{29}$$

$\int_0^t g\left(x_s\right)\circ dw_s$ Stratonovitch integral. Stratonovitch form of Itô-Karlin

$$dx_t \overset{Strato}{=} \gamma x_t\left(1-x_t\right)dt + \sqrt{\rho}x_t\left(1-x_t\right)\circ dw_t,\ x_0 = x. \tag{30}$$

$$\text{Kimura: } dx_t \overset{It\hat{o}}{=} \gamma x_t (1 - x_t)\, dt + \sqrt{\rho} x_t (1 - x_t)\, dw_t, \; x_0 = x. \tag{31}$$

Why? Continuous-time deterministic evolution equation for A_1 gene frequency driven by fitness σ:

$$dx_t = \sigma x_t (1 - x_t)\, dt.$$

Selection differential σdt random → modelled by some $d\widetilde{w}_t$ with $\mathbf{E}(d\widetilde{w}_t) = \gamma dt$ and $\sigma^2 (d\widetilde{w}_t) = \rho dt$. Then we get (31).

Kimura model (31) $\neq$ its Karlin counterpart defined in (20).

4.1 The symmetric case (Kimura martingale of neutrality)

$\gamma = 0$. (31) is Kimura martingale $dx_t = \sqrt{\rho} x_t (1 - x_t)\, dw_t$.

Again 2 natural boundaries; process 0−recurrent. For driftless Kimura model, solution to KFE [Kimura]

$$\widetilde{p}(x; t, y) = \frac{1}{\sqrt{2\pi\rho t}} \frac{(x(1-x))^{1/2}}{(y(1-y))^{3/2}} e^{-\left(\frac{\rho t}{8} + \frac{1}{2\rho t}\left[\log\left(\frac{y(1-x)}{x(1-y)}\right)\right]^2\right)}. \tag{32}$$

Density (32) converges more rapidly than its Karlin version (22) to quasi-abs. states $\{0, 1\}$. Based on (32), [Kimura and Tuckwell]

$$\mathbf{P}\left(x_t \in (0,\varepsilon) \mid x_0 = x\right) \underset{t\to\infty}{\to} 1-x$$
$$\mathbf{P}\left(x_t \in (1-\varepsilon,1) \mid x_0 = x\right) \underset{t\to\infty}{\to} x$$

with limiting quantities depending on the initial condition.

Scale of Kimura diffusion $\varphi(x) = x$. Speed measure density is $m(x) = \frac{1}{\rho x^2(1-x)^2}$.

PBS: *Let* $\tau_{x,I_\varepsilon} = \tau_{x,\varepsilon} \wedge \tau_{x,1-\varepsilon}$ *first exit time of* I_ε*. Estimate prob.* $\mathbf{P}\left(\tau_{x,1-\varepsilon} < \tau_{x,\varepsilon}\right)$ *as* $\varepsilon \to 0$*, together with* $\mathbf{E}\left(\tau_{x,I_\varepsilon}\right)$*, for Kimura martingale.*

Scale function $\alpha_\varepsilon(x) = \frac{\varphi(x)-\varphi(\varepsilon)}{\varphi(1-\varepsilon)-\varphi(\varepsilon)}$ (with $\varphi(x) = x$), satisfying $\alpha_\varepsilon(\varepsilon) = 0$ and $\alpha_\varepsilon(1-\varepsilon) = 1$, gives

$$\mathbf{P}\left(\tau_{x,1-\varepsilon} < \tau_{x,\varepsilon}\right) = \alpha_\varepsilon(x) = \frac{x-\varepsilon}{1-2\varepsilon}, \tag{33}$$

independently of ρ.

Result very $\neq$ from the Karlin one close to $1/2$: origin of this difference $\to$ attracting drift to $1/2$ in Karlin model (24), not present in Kimura martingale.

• $\alpha(x) = \mathbf{E}\left(\tau_{x,I_\varepsilon}\right)$ expected exit time of I_ε. Solves $-G\alpha(x) = 1$ where $G = \frac{\rho}{2}x^2(1-x)^2\partial_x^2$ and $\alpha(\varepsilon) = \alpha(1-\varepsilon) = 0$.

$$\alpha(x) = \mathbf{E}(\tau_{x,I_\varepsilon}) = \frac{2}{\rho}(h(\varepsilon) - h(x)) \tag{34}$$

$$h(x) = 2x\log x + 2(1-x)\log(1-x) - \log(x(1-x)). \tag{35}$$

Expected time diverges like $-\frac{2}{\rho}\log(\varepsilon)$, smaller than $\frac{1}{\rho}[\log(\varepsilon)]^2$ obtained previously for Karlin . *Kimura model hits the boundaries of I_ε in a shorter time.* $\mathbf{E}(\tau_{x,I_\varepsilon})$ *again a decreasing function of* ρ.

• Empirical average measure of heterozygosity for the Kimura martingale x_t as in (31) with $\gamma = 0$. Speed measure is here

$$m(x) = \frac{1}{\rho x^2 (1-x)^2}.$$

By ergodic Chacon-Ornstein ratio theorem

$$\frac{t^{-1}\int_0^t 2x_s(1-x_s)\,1_{x_s\in(\varepsilon,1-\varepsilon)}ds}{t^{-1}\int_0^t 1_{x_s\in(\varepsilon,1-\varepsilon)}ds} \underset{t\to\infty}{\to} \frac{2\int_\varepsilon^{1-\varepsilon}\frac{1}{x(1-x)}dx}{\int_\varepsilon^{1-\varepsilon}\frac{1}{x^2(1-x)^2}dx} \underset{\varepsilon\to 0}{\sim} -2\varepsilon\log\varepsilon \tag{36}$$

which $\to 0$ as $\varepsilon \to 0$, but much faster than in (27). *Kimura martingale spends much more time close to boundaries than Karlin process.*

4.2 Non-symmetric Kimura model with a drift

Consider the full Kimura model (31) with $\gamma \neq 0$.

Natural boundaries. $\{0, 1\}$ always natural boundaries for the Kimura model with drift.

When $\gamma \neq 0$, no known solution of KBE for tpd associated to (31). For Kimura model with drift, [Tuckwell]

$$\mathbf{P}\left(x_t \in (0, \varepsilon) \mid x_0 = x\right) \underset{t\to\infty}{\to}$$

$$\left(1 \text{ if } \gamma < -\rho/2;\ \tfrac{1-x}{2} \text{ if } \gamma = -\rho/2;\ 1 - x \text{ if } \rho/2 > \gamma > -\rho/2 \text{ and } 0 \text{ if } \gamma > \rho/2\right)$$

and

$$\mathbf{P}\left(x_t \in (1-\varepsilon, 1) \mid x_0 = x\right) \underset{t\to\infty}{\to}$$
$$\left(1 \text{ if } \gamma > \rho/2;\ \tfrac{x}{2} \text{ if } \gamma = \rho/2;\ x \text{ if } \rho/2 > \gamma > -\rho/2 \text{ and } 0 \text{ if } \gamma < -\rho/2\right),$$

Nonneutral Kimura model: $\exists$ *a non-null prob. that an allele gets quasi-fixed (quasi-extinct) even if its selective differential* γ *is negative (positive), depending on the initial allele frequency. This differential simply needs to be larger (smaller) than* $-\rho/2$ *(respectively* $\rho/2$*).*

From Karlin to Kimura using appropriate Doob transform.

$$\text{Karlin}: \ f(x) = x(1-x)\left[\gamma + \rho\left(\frac{1}{2} - x\right)\right]; \ g(x) = \sqrt{\rho}x(1-x).$$

Let $\alpha(x) = g(x)^{-1/2} = \rho^{-1/4}(x(1-x))^{-1/2}$. $G = f\partial_x + \frac{1}{2}g^2\partial_x^2$

$$G\alpha = \frac{1}{2}f\frac{g'}{g} - \frac{3}{8}g'^2 + \frac{1}{4}gg''.$$

Transformed version of Karlin model (20) using $\alpha(x)$.

$$G \to \overline{G}(\cdot) = \alpha^{-1}G(\alpha\cdot) = \widetilde{G}(\cdot) + \frac{G\alpha}{\alpha}\cdot$$

$$\text{drift } f \to \widetilde{f}(x) = f(x) + \frac{\alpha'(x)}{\alpha(x)}g^2(x) = f(x) - \frac{1}{2}gg'(x) = \gamma x(1-x),$$

switching from Karlin model (20) to Kimura one. Affine creating-annihilating paths rate function

$$\lambda(x) = \frac{G\alpha}{\alpha}(x) = -\frac{1}{2}\left(\gamma - \frac{\rho}{4}\right) + \gamma x. \tag{37}$$

Rate λ bounded above and below. $\lambda(x) = \lambda_*(\mu(x) - 1)$ with

$$\lambda_* = \frac{\rho}{8} + \frac{|\gamma|}{2} > 0 \ ; \ \mu(x) = 2 - \frac{2|\gamma|}{|\gamma| + \frac{\rho}{4}}\left(1 - x^{\mathbf{1}(\gamma\geq 0)}(1-x)^{\mathbf{1}(\gamma<0)}\right)$$

Transformed process is BD: a diffusing Kimura Eve particle (started in x) lives a random exponential time with constant rate λ_*. When Eve dies, gives birth to a spatially dependent random # $M(x)$ of particles (with mean $\mu(x)$). If $M(x) \neq 0$, $M(x)$ independent daughter particles start afresh where Eve died; move along a Kimura diffusion and reproduce, independently and so on... If $M(x) = 0$, process stops in 1st generation. BD with binary scission

$$M(x) = 0 \text{ w.p. } p_0 = 1 - \mu(x)/2$$

$$M(x) = 1 \text{ w.p. } p_1 = 0$$

$$M(x) = 2 \text{ w.p. } p_2 = \mu(x)/2,$$

with $p_2(x) \geq p_0(x)$ for all x iff $|\gamma| \leq \rho/4$.

Modifying Karlin model x_t using $\alpha(x) = g(x)^{-1/2}$, the law $p(x;t,y)$ of x_t is transformed into

$$\overline{p}(x;t,y) = \frac{\alpha(y)}{\alpha(x)} p(x;t,y),$$

explicitly known because so is p from (22). Branching rate also

$$\lambda(y) = \lambda_* \left(p_2(y) - p_0(y)\right).$$

Not a positively regular BD [Asmussen-Hering], leading to global population growth.

SUPPOSE it is: $\overline{\rho}_t(x) := \int_{\overset{\circ}{I}} \overline{p}(x; t, y)\, dy$ would be global expected # $\mathbf{E}(N_t(x))$ of Kimura particles alive at t in $\overset{\circ}{I}$

$$\partial_t \overline{\rho}_t(x) = \overline{G}(\overline{\rho}_t(x)) = \lambda(x)\, \overline{\rho}_t(x) + \widetilde{G}(\overline{\rho}_t(x)),\ \overline{\rho}_0(x) = \mathbf{1}_{(0,1)}(x).$$

We have

$$\overline{\rho}_t(x) = x e^{t(\gamma/2+\rho/8)} + (1-x)\, e^{-t(\gamma/2-\rho/8)},\ \text{so}$$

$$-\frac{1}{t} \log \overline{\rho}_t(x) \underset{t\to\infty}{\to} \lambda_1 := -\left(\frac{|\gamma|}{2} + \frac{\rho}{8}\right) = -\lambda_* < 0.$$

Suggests $-\lambda_1$ could be global Malthus exponential rate of growth of the global expected # of particles within the whole system.

IF TRUE: Conditional prob. presence density $\overline{q}(x;t,y) := \overline{p}(x;t,y)/\overline{\rho}_t(x)$,

$$\partial_t \overline{q} = -\partial_t \overline{\rho}_t(x)/\overline{\rho}_t(x) \cdot \overline{q} + \overline{G}^*(\overline{q}) = \left(\overline{d}_t(x) + \lambda(y)\right) \cdot \overline{q} + \widetilde{G}^*(\overline{q}).$$

$\overline{d}_t(x) = -\partial_t \overline{\rho}_t(x)/\overline{\rho}_t(x) < 0$ rate at which mass removed to compensate creation of mass of BD process $\left(\left(\widetilde{x}_t^{(n)}\right)_{n=1}^{N_t(x)} ;\ t \geq 0\right)$ arising from splitting:

$$\overline{q}(x;t,y) = \frac{\mathbf{E}\left(\sum_{n=1}^{N_t(x)} \widetilde{p}^{(n)}(x;t,y)\right)}{\mathbf{E}(N_t(x))}$$

$p^{(n)}(x;t,y)$: density at (t,y) of nth alive particle in system, descending from Eve started at x. $\overline{q}(x;t,y)$ would be average presence density at (t,y) of branching system of Kimura particles.

Would have $\overline{d}_t(x) \to \lambda_1$ where λ_1 should be largest negative eigenvalue of $-G$. λ_1 would be effective generalized principal eigenvalue?

$$\partial_t \overline{q} = 0 \;\Rightarrow\; \overline{q}\,(x;t,y) \underset{t\to\infty}{\to} \overline{q}_\infty\,(y)\,, \text{ where}$$

$$-\widetilde{G}^*(\overline{q}_\infty) = (\lambda_1 + \lambda\,(y)) \cdot \overline{q}_\infty, \text{ or} - \overline{G}^*\,(\overline{q}_\infty) = \lambda_1 \cdot \overline{q}_\infty.$$

$$\text{product form} : \overline{q}_\infty\,(y) = \alpha\,(y)\, v_1\,(y) \,/ \int_0^1 \alpha\,(y)\, v_1\,(y)\, dy, \tag{38}$$

would v_1 be the eigenfunction of $-G^*$ associated to $\lambda_1 < 0$.
Similarly, should exist $\overline{\phi}_\infty\,(x)$ s.t. $-\overline{G}\left(\overline{\phi}_\infty\right) = \lambda_1 \overline{\phi}_\infty$ with $\overline{\phi}_\infty\,(x) = u_1\,(x)\,/\alpha\,(x)$ with u_1 eigenfunction of $-G$ associated to $\lambda_1 < 0$.

IF TRUE (Asmussen-Hering): $e^{\lambda_1 t} \sum_{n=1}^{N_t(x)} \overline{\phi}_\infty \left(\widetilde{x}_t^{(n)}\right)$ would be martingale converging a.s. to nondegenerate r.v. $W\,(x)$ s.t. $\mathbf{E}\,(W\,(x)) = \overline{\phi}_\infty\,(x)$. For any a.e. continuous bounded measurable function ψ on I

$$e^{\lambda_1 t} \sum_{n=1}^{N_t(x)} \psi \left(\widetilde{x}_t^{(n)}\right) \underset{t\to\infty}{\overset{a.s.}{\to}} W\,(x)\, \frac{\int_{(0,1)} \psi\,(x) \cdot \overline{q}_\infty\,(x)\, dx}{\int_{(0,1)} \overline{q}_\infty\,(x)\, dx}.$$

$$\text{In particular, } e^{\lambda_1 t} N_t\,(x) \underset{t\to\infty}{\overset{a.s.}{\to}} W\,(x)\,,$$

telling how fast global expected # of particles would grow within I.

This global picture does **NOT** hold: no positive $(u_1(x); v_1(y)) : -G(u_1) = \lambda_1 u_1$ and $-G^*(v_1) = \lambda_1 v_1$ for $\lambda_1 = -\left(\frac{|\gamma|}{2} + \frac{\rho}{8}\right)$.

Eigenvectors exist but for some $\lambda_c > \lambda_1$. So criticality of $\overline{G}(\cdot) + \lambda_1 \cdot$ not valid : global AH approach fails. Rather criticality of $\overline{G}(\cdot) + \lambda_c \cdot$ Focus on a local approach. Introduce

$$\lambda_c = -\frac{\rho}{8}\left(1 - 4\left(\frac{\gamma}{\rho}\right)^2\right) > \lambda_1 = -\frac{\rho}{8}\left(1 + 4\frac{|\gamma|}{\rho}\right), \tag{39}$$

with $\lambda_c < 0$ iff $|\gamma| < \rho/2$.

$\overline{G}(\cdot) + \lambda_c \cdot$ and $\overline{G}^*(\cdot) + \lambda_c \cdot$ are critical with ground states $\overline{\phi}_\infty(x) > 0$ and $\overline{q}_\infty(y) > 0 \Rightarrow \lambda_c$ IS effective generalized principal eigenvalue.

$$\overline{\phi}_\infty(x) = x^{-\frac{\gamma}{\rho}}(1-x)^{\frac{\gamma}{\rho}} \tag{40}$$

$$\overline{q}_\infty(y) = y^{\frac{\gamma}{\rho}-2}(1-y)^{-\frac{\gamma}{\rho}-2} \tag{41}$$

$$\int_{(0,1)} \overline{\phi}_\infty(x)\,\overline{q}_\infty(x)\,dx = \int_{(0,1)} x^{-2}(1-x)^{-2}\,dx = \infty.$$

Product criticality property does not hold (growth property under concern is only local): take B a Borel subset of $\overset{\circ}{I}$ with closure $\overline{B} \subset \overset{\circ}{I}$ [suitable choice of B could typically be the interior of I_{ε}].

$N_t(x, B) = \sum_{n=1}^{N_t(x)} \mathbf{1}_B\left(\widetilde{x}_t^{(n)}\right)$ local # of Kimura particles within B at t given Eve at x. $\overline{\phi}_{\infty}^{B}(x)$ and $\overline{q}_{\infty}^{B}(y)$ denote eigen-states with multiplicative constants adjusted s.t. : $\int_B \overline{\phi}_{\infty}^{B}(x) \cdot \overline{q}_{\infty}^{B}(x)\, dx = \int_B \overline{q}_{\infty}^{B}(x)\, dx = 1$. Local version of Asmussen-Hering result:

Local supercriticality (growth). If $\lambda_c < 0$ ($|\gamma| < \rho/2$):

$\forall B$, $e^{\lambda_c t} \sum_{n=1}^{N_t(x)} \overline{\phi}_{\infty}^{B}\left(\widetilde{x}_t^{(n)}\right) \mathbf{1}_B\left(\widetilde{x}_t^{(n)}\right)$ martingale converging a.s. to a nondegenerate r.v. $W_B(x)$ s.t. $\mathbf{E}(W_B(x)) = \overline{\phi}_{\infty}^{B}(x)$ (Englander-Kyprianou, p. 84).

For any a.e. continuous bounded measurable function ψ on I,

$$e^{\lambda_c t} \sum_{n=1}^{N_t(x)} \psi\left(\widetilde{x}_t^{(n)}\right) \mathbf{1}_B\left(\widetilde{x}_t^{(n)}\right) \underset{t\to\infty}{\overset{a.s.}{\to}} W_B(x) \frac{\int_B \psi(x) \cdot \overline{q}_{\infty}^{B}(x)\, dx}{\int_B \overline{q}_{\infty}^{B}(x)\, dx}. \tag{42}$$

$$\text{In particular } (\psi \equiv 1),\ e^{\lambda_c t} N_t(x, B) \underset{t\to\infty}{\overset{a.s.}{\to}} W_B(x), \tag{43}$$

clarifies how fast expected # of particles grows locally within B.

$-\lambda_c > 0$: **local** Malthus growth parameter of $N_t(x, B)$. Conventional wisdom: smaller than the global one $-\lambda_c < -\lambda_1$.

Local subcriticality (extinction). If $\lambda_c > 0$ ($|\gamma| > \rho/2$):

(i)

$$\forall B: \ \mathbf{P}(N_t(x, B) = 0) \underset{t\to\infty}{\to} 1, \text{ unif. in } x. \tag{44}$$

(ii) $x \in B$. $\exists$ a constant $\gamma_B > 0$ s.t.:

$$e^{\lambda_c t}\left[1 - \mathbf{P}(N_t(x, B) = 0)\right] \underset{t\to\infty}{\to} \gamma_B \overline{\phi}_\infty^B(x), \text{ unif. in } x. \tag{45}$$

(iii) $\forall\ \psi$ bounded measurable function on I :

$$\mathbf{E}\left[\sum_{n=1}^{N_t(x)} \psi\left(\widetilde{x}_t^{(n)}\right) \mathbf{1}_B\left(\widetilde{x}_t^{(n)}\right) \mid N_t(x, B) > 0\right] \underset{t\to\infty}{\to} \gamma_B^{-1} \int_B \psi(y)\, \overline{q}_\infty^B(y)\, dy. \tag{46}$$

From (i) : $|\gamma| > \rho/2 \Rightarrow$ process ultimately extinct with prob. 1, locally for each B. *Subcritical regime: drift is so strong (+ affinity of Kimura particles for the boundaries so large) that it pushes all the particles very close to either boundaries, all ending up eventually outside* B.

From (ii) : $1 - \mathbf{P}(N_t(x,B) = 0) = \mathbf{P}(N_t(x,B) > 0) = \mathbf{P}(T(x,B) > t)$, $T(x,B)$ local extinction time in B of the particle system descending from Eve started at $x \in B$. The # $-\lambda_c < 0$ is the usual local Malthus decay parameter. From (ii), $\overline{\phi}_{\infty}^{B}(x)$ *reproductive value in demography.*

(iii) with $\psi \equiv 1$ reads $\mathbf{E}[N_t(x,B) \mid N_t(x,B) > 0] \underset{t\to\infty}{\to} \gamma_B^{-1}$ interprets γ_B.

If $\lambda_c = 0$ or $|\gamma| = \rho/2$ local criticality: process gets ultimately locally extinct with prob. 1 but at a smaller-$1/t$ speed than in subcritical regime.

5 Extreme reproduction events.

Extended Moran model (very productive guy). EMM is Cannings model with reproduction law $\boldsymbol{\nu}$ (Moehle, H.):

DEF: $M_N > 1$ RV in $\{2, \ldots, N\}$ + offspring vector $\boldsymbol{\mu} := (\mu_1, \ldots, \mu_N)$ via $\mu_n := 1$ for $n \in \{1, \ldots, N - M_N\}$, $\mu_n := 0$ for $n \in \{N - M_N + 1, \ldots, N - 1\}$, and $\mu_N := M_N$. μ_n is # descendants at 0 of n-th individual. ($M_N \equiv 2$: standard Moran model).

$$\boldsymbol{\nu} = (\nu_1, \ldots, \nu_N) = \text{Random Perm. of } \boldsymbol{\mu}.$$

• **Forward in time:** N_t = # of descendants of n out of N individuals at t forward in time. N_t ($N_0 = n$), discrete-time MC on $\{0, \ldots, N\}$ and abs. barriers $\{0, N\}$ with $P_{i,j}^{(N)} := \mathbf{P}\left(N_{t+1} = j \mid N_t = i\right)$ [Moehle, H.]: hypergeo.

$$\begin{aligned}
P_{i,j}^{(N)} &= \frac{1}{\binom{N}{i}} \mathbf{E}\left[\binom{N - M_N}{j}\binom{M_N - 1}{i - j}\right] \text{ if } j < i \\
P_{i,j}^{(N)} &= \frac{1}{\binom{N}{i}} \mathbf{E}\left[\binom{N - M_N}{i} + \binom{N - M_N}{N - i}\right] \text{ if } j = i \qquad (47) \\
P_{i,j}^{(N)} &= \frac{1}{\binom{N}{i}} \mathbf{E}\left[\binom{N - M_N}{N - j}\binom{M_N - 1}{j - i}\right] \text{ if } j > i.
\end{aligned}$$

• **Backward in time:** $n-$sub-sample of size n from $[N]$ at $t=0$. Identify 2 individuals from $[n]$ if share a CA one generation backward in time $\rightarrow$ Ancestral backward process. $\widehat{x}_t^{(N)} = \widehat{x}_t^{(N)}(n)$ counts # of ancestors at $t \in \mathbb{N}$, backward in time, $\widehat{x}_0^{(N)} = n \leq N$. DT Markov chain on $\{0, ..., N\}$

$$\mathbf{P}\left(\widehat{x}_{t+1}^{(N)} = j \mid \widehat{x}_t^{(N)} = i\right) =: \widehat{P}_{i,j}^{(N)} = \frac{i!}{j!} \sum_{\substack{i_1,..,i_j \in \mathbb{N}_+ \\ i_1+...+i_j=i}} \frac{\widehat{P}_{i,j}^{(N)}(\mathbf{i}_j)}{i_1!...i_j!}.$$

$\boldsymbol{\nu}$ EMM, for $i, j \in \{1, \ldots, N\}$, (Moehle, H.) $\Rightarrow$

$$\begin{aligned}
\widehat{P}_{i,j}^{(N)} &= \frac{\mathbf{E}\left[\binom{N-M_N}{j-1}\binom{M_N}{i-j+1}\right]}{\binom{N}{i}} \text{ if } j < i \\
\widehat{P}_{i,j}^{(N)} &= \frac{\mathbf{E}\left[\binom{N-M_N}{i} + M_N\binom{N-M_N}{i-1}\right]}{\binom{N}{i}} \text{ if } j = i \\
\widehat{P}_{i,j}^{(N)} &= 0 \text{ if } j > i.
\end{aligned} \tag{48}$$

Coalescence probability $c_N := \widehat{P}_{2,1}^{(N)} = \mathbf{E}\left[(M_N)_2\right]/(N(N-1))$ and $d_N := \widehat{P}_{3,1}^{(N)}$ prob that 3 individuals chosen at random share a CA. For scaling limits, important: ($c_N \rightarrow 0$ or not) ($\frac{d_N}{c_N} \rightarrow 0$ or not) [Sagitov, Moehle].

(i) (occasional extreme events): $M_N/N \overset{d}{\to} 0$ (as $N \to \infty$) or

(ii) (systematic extreme events): $M_N/N \overset{d}{\to} U$ (as $N \to \infty$) U non-degenerate $[0,1]$ $-$valued RV $\mathbf{E}(U) > 0$. SCALING LIMITS $(N \to \infty)$?.

(i) If

$$\phi(k) := \lim_{N\to\infty} \frac{\mathbf{E}\left[(M_N)_k\right]}{N^{k-2}\mathbf{E}\left[(M_N)_2\right]} \text{ exist } \forall k \in \{2,3,...\} \Rightarrow \tag{49}$$

EMM in domain of attraction of CT $\Lambda-$coalescent: Λ prob. measure on $[0,1]$ with moments: $\int_0^1 u^{k-2}\Lambda(du) = \phi(k)$. All continuous-time $\Lambda-$coalescents can be produced in this way (Moehle, H.).

$c_N \to 0$ and $x_\tau = N_{[\tau/c_N]}(\lfloor Nx \rfloor)/N$ with $x_0 = x$ and $\tau \in \mathbb{R}_+$, CT Markov process with state-space $[0,1]$.

$$\text{KBE: } \psi \in C^2([0,1]) \to G(\psi)(x) = \frac{\Lambda(\{0\})}{2} x(1-x)\partial_x^2\psi(x) +$$

$$\int_{[0,1]\setminus\{0\}} \left[x\psi(x+(1-x)u) + (1-x)\psi(x(1-u)) - \psi(x)\right] \frac{1}{u^2}\Lambda(du),$$

pure jump process if Λ has no atom at $\{0\}$.

$$u(x,t) = \mathbf{E}_x\psi(x_t) \text{ obeying } \partial_t u = G(u);\; u(x,0) = \psi(x).$$

$$x_\tau - x_0 = \int_0^\tau \sqrt{\Lambda(\{0\})\, x_s\,(1-x_s)}dw_s + \tag{50}$$

$$\int_{(0,\tau]\times(0,1]\times[0,1]} \left(1_{v\le x_{s\_}}\, u\left(1-x_{s_-}\right) - 1_{v>x_{s\_}}\, u x_{s_-}\right) N\left(ds\times du\times dv\right),$$

N Poisson measure on $[0,\infty)\times(0,1]\times[0,1]$ with intensity $ds\times\frac{1}{u^2}\Lambda(du)\times dv$, $\perp w_t$. If $\Lambda(0)\neq 0 \Rightarrow$ Wright-Fisher diffusion has to be included. Clock-time τ in units of $N_e = c_N^{-1}$.

Eldon and Wakeley model. Let $\gamma > 0$. M_N mixture model

$$M_N = 2 \text{ with probability } 1 - N^{-\gamma} \text{ (Moran model)}$$

$$M_N = 2 + \lfloor (N-2)\, V\rfloor \text{ with probability } N^{-\gamma}$$

V r.v. on $[0,1]$. $c_N \to 0$.

- $\gamma > 2$: Attraction basin of Kingman coalescent ($\frac{d_N}{c_N} \to 0$).
- $\gamma \le 2$: Attraction basin of $\Lambda-$coalescent ($\frac{d_N}{c_N} \nrightarrow 0$).

(ii) $\widehat{P}_{i,1}^{(N)} \to \mathbf{E}\left(U^{i}\right) > 0$ EMM in domain of attraction of a DT $\Lambda-$coalescent with $\Lambda\left(du\right) = u^{2}\pi\left(du\right)$ and $\pi\left(du\right)$ law of U. $c_{N} \to c = \mathbf{E}\left(U^{2}\right) > 0$ and:

$$\left(\widehat{x}_{t}^{(N)},\ t \in \mathbb{N}\right) \overset{\mathcal{D}}{\to} \left(\widehat{x}_{t},\ t \in \mathbb{N}\right),$$

DT limiting $\Lambda-$coalescent

$$\widehat{P}_{i,j}^{\infty} = \binom{i}{j-1} \int_{0}^{1} u^{i-j+1} \left(1-u\right)^{j-1} \pi\left(du\right) \text{ if } 1 \leq j < i \tag{51}$$

$$\widehat{P}_{i,i}^{\infty} = \int_{0}^{1} \left(1-u\right)^{i-1} \left(1-u+iu\right) \pi\left(du\right) \text{ if } j = i. \tag{52}$$

Example: choice of π? π uniform on $[0,1] \Rightarrow$

$$\widehat{P}_{i,j}^{\infty} = \frac{1}{i+1} \text{if } 1 \leq j < i \text{ and } \widehat{P}_{i,i}^{\infty} = \frac{2}{i+1}. \diamond \tag{53}$$

Forward: x_{t} is MC (with state-space $[0,1]$) driven by $\left(U_{t}, V_{t}\right)_{t\geq 1}$ $\perp$:

$$x_{t+1} = x_{t} + U_{t+1}\left(1-x_{t}\right) 1\left(V_{t+1} \leq x_{t}\right) - U_{t+1} x_{t} 1\left(V_{t+1} > x_{t}\right);\ x_{0} = x. \tag{54}$$

6 Discrete-time coalescent and forward process.

$(U_t, V_t)_{t \geq 1}$ mutually $\perp$ sequences : $U_1 \overset{d}{\sim} \pi(du) = \frac{1}{u^2}\Lambda(du)$ and $V_1 \overset{d}{\sim}$ uniform on $[0,1]$. π AC density f no atom at $\{0\}$.

$$x_{t+1} = x_t + U_{t+1}(1 - x_t) 1 (V_{t+1} \leq x_t) - U_{t+1} x_t 1 (V_{t+1} > x_t) ; \; x_0 = x.$$

If at t, x_t close to say 1, $\exists$ big chance (x_t) that at $t+1$, it will even get closer to 1 by a small move, but $\exists$ always some small probability $1 - x_t$ that x_t moves back abruptly in the bulk (by a big move of amplitude $-U_{t+1}x_t$) : the whole process starts afresh.

• x_t martingale. The variance: $\sigma^2 (x_{t+1} \mid x_t = x) = \sigma^2 (U_{t+1}) (1 - x) x$.

• (if transient), x_t eventually hits boundaries $\{0, 1\}$ but not in finite time: $\tau_x = \tau_{x,0} \wedge \tau_{x,1}$ is ∞ with probability 1. Boundaries both abs. x_t eventually hit first the boundary $\{0\}$ (respectively $\{1\}$) with probability $1 - x$ (respectively x).

• $\psi \in C_0([0,1])$. With $t \geq 1$

$$u(x,t) = \mathbf{E}_x \psi(x_t) = \left(L^t \psi\right)(x), \; u(x,0) = \psi(x)$$

$$(L\psi)(x) = \mathbf{E}_x \psi(x_1) = \tag{55}$$

$$x \int_0^1 \psi(x + (1-x)u) f(u)\, du + (1-x) \int_0^1 \psi(x - xu) f(u)\, du.$$

- $\psi(x) = x^k$ monomial$\Rightarrow$ $(L\psi)(x)$ degree k polynomial

$$\left[x^k\right](L\psi)(x) = \mathbf{E}\left[(1-U)^{k-1}(1-U+kU)\right] = \widehat{P}_{k,k}^{\infty}$$

- $\psi(x) = a + bx$, $(L\psi)(x) = \psi(x)$, affine functions harmonic functions of L.

$$(L\psi)(x) = \frac{1-x}{x} \int_0^x f\left(\frac{x-y}{x}\right) \psi(y)\, dy + \frac{x}{1-x} \int_x^1 f\left(\frac{y-x}{1-x}\right) \psi(y)\, dy. \tag{56}$$

L integral Fredholm operator with kernel

$$K(x,y) = p(x;1,y) = \frac{1-x}{x} f\left(\frac{x-y}{x}\right) 1_{(0 \le y \le x)} + \frac{x}{1-x} f\left(\frac{y-x}{1-x}\right) 1_{(x < y \le 1)} \tag{57}$$

that is: $(L\psi)(x) = \int_0^1 K(x,y)\psi(y)\, dy$. L acts on Banach space $C_0([0,1])$, is bounded $\|L\|_{\infty} = 1 = \rho_S$.

• Forward adjoint generator L^* acts $\mathcal{M}_+([0,1])$

$$(L^*\mu)(y) = \int_0^y \frac{z}{1-z} f\left(\frac{y-z}{1-z}\right)\mu(dz) + \int_y^1 \frac{1-z}{z} f\left(\frac{z-y}{z}\right)\mu(dz). \quad (58)$$

L is not self-adjoint, nor normal.

• $\exists$ speed measure μ with density m satisfying $(L^*\mu)(y) = \mu$.

• x_t not reversible wr to speed measure $m(y)\,dy$:

$$m(x)\,p(x;1,y) \neq m(y)\,p(y;1,x).$$

• Only moves to the left: $l(x) = \mathbf{P}(... < x_2 < x_1 < x_0 = x)$ solves:

$$l(x) = \frac{1-x}{x}\int_0^x f\left(\frac{x-y}{x}\right) l(y)\,dy.$$

$l(x)$ should tend to 1 as $x \to 0$. Similar thing $r(x)$ (only moves to the right starting from x).

Would $l(x)$ and $r(x)$ be strictly positive $\Rightarrow x_t$ would be transient : $\forall y > x$ (resp. $\forall y < x$), $\exists$ prob$> l(x) > 0$ (resp. $> r(x) > 0$) that x_t with $x_0 = x$ never visits a neighborhood of y.

6.1 Special transient case ($\pi(du) = du$): FREDHOLM

$$(L\psi)(x) = \mathbf{E}_x\psi(x_1) = \frac{1-x}{x}\int_0^x \psi(y)\,dy + \frac{x}{1-x}\int_x^1 \psi(y)\,dy \tag{59}$$
$$= \int_0^1 K(x,y)\,\psi(y)\,dy$$

with $K(x,y) = \frac{1-x}{x}1_{(0\leq y\leq x)} + \frac{x}{1-x}1_{(x<y\leq 1)} = p(x;1,y)$.

K not TP, not bounded, not continuous on $[0,1]^2$, nor $\int_{[0,1]^2} K(x,y)^2\,dxdy < \infty$.

L not compact.

If particle originally at $x < 1/2$ ($x > 1/2$), p. dens of further move to the left (to the right) is $(1-x)/x$ (respectively $x/(1-x)$) with $(1-x)/x > x/(1-x)$ (respectively $x/(1-x) > (1-x)/x$) $\Rightarrow x_t$ is stoch. monotone.

$\exists$ Prob $l(x) = (1-x)e^{-x} > 0$ (resp. $r(x) = xe^{-(1-x)} > 0$) that particle always moves to the left (to the right) starting from x.

Spectral properties: $\lambda \in \mathbb{C}$. c bounded funct. $[0,1]$ satisfying $c(0) = c(1) = 0$. Look for continuous solutions α of: $(\lambda I - L)\alpha = c$ or, with $z = \lambda^{-1}$, of

$$(I - zL)\alpha = zc. \tag{60}$$

$|z| < 1$, α Liouville-Neumann converging power-series

$$\alpha(x) = \sum_{n \geq 0} z^{n+1} L^n(c)(x).$$

Integrate linear differential system
$A(x) = \int_0^x \alpha(y)\,dy \Rightarrow \alpha = A'$. $(I - zL)\alpha = zc$ is also the linear differential system

$$A'(x) - zA(x)\left(\frac{1}{x} - \frac{1}{1-x}\right) = z\left(c(x) + \frac{x}{1-x}A(1)\right) =: zf(x).$$

- $|z| < 1$.

$$\alpha(x) = zc(x) + z^2(1-2x)(x(1-x))^{z-1}\int_{1/2}^x (y(1-y))^{-z} c(y)\,dy, \tag{61}$$

an alternative representation to the Liouville-Neumann power-series. $\lambda = z^{-1} \Rightarrow$ the domain $\left|\lambda^{-1}\right| < 1$ complementary of the unit disk of $\mathbb{C}$ centered at 0. Such λs are regular points of L for which $(\lambda I - L)^{-1}$ exists, is bounded and is defined on the whole space $C_0([0,1])$.

- $\mathrm{Re}\,(z) \geq 1$ and $c \equiv 0$. $\exists$ Solutions (eigenstates):

$$\alpha\,(x) \propto (1-2x)\,(x\,(1-x))^{z-1}\,, \tag{62}$$

Closed disk of $\mathbb{C}$ centered at $(1/2,0)$ with radius $1/2$ (which is: $\mathrm{Re}\left(\lambda^{-1}\right) \geq 1$) = point spectrum of L. If λ belongs to complementary of the latter disk to the unit disk centered at 0 constitute the continuous spectrum where $(\lambda I - L)^{-1}$ exists but is not defined on the whole space $C_0\,([0,1])$: the operator $\lambda I - L$ is not surjective.

- Assume $z = 1$ and c not identically 0.

$$\begin{aligned} \alpha\,(x) &= (1-2x)\int_{1/2}^{x} (y\,(1-y))^{-1}\,c\,(y)\,dy + \\ &\quad A\,(1)\,(4x-1) + 4A\,(1/2)\,(1-2x) + c\,(x)\,, \end{aligned}$$

$A\,(1/2)$ and $A\,(1)$ determined from the imposed values $\alpha\,(0)$ and $\alpha\,(1)$ of α at the boundaries. $\alpha\,(x)$ solves: and so

$$-\,(L-I)\,\alpha = c \text{ if } x \in (0,1)\,;\; \alpha = d \text{ if } x \in \{0,1\} \tag{63}$$

$\Rightarrow \alpha\,(x) = \mathbf{E}_x\left[\sum_{t\geq 0} c\,(x_t) + d\,(x_\infty)\right].$

Examples:

(i) Let $\varepsilon > 0$, small and $I_\varepsilon = (\varepsilon, 1-\varepsilon)$. Let $c(y) = 1_{(y \in I_\varepsilon)}$ and $x \in I_\varepsilon$. $\alpha(x)$ expected time till x_t first exits out of the interval I_ε, starting from x within the interval. Putting $\alpha(\varepsilon) = \alpha(1-\varepsilon) = 0$ fixes the constants and we finally find

$$\alpha(x) = (1-2x)\log\frac{x}{1-x} - (1-2\varepsilon)\log\frac{\varepsilon}{1-\varepsilon} \sim -\log\varepsilon.$$

(ii) (Green function). $y_0 \in (0,1)$; $I_\delta(y_0) = [y_0 - \delta, y_0 + \delta]$, $x \notin I_\delta(y_0)$. Let $c(y) = 1_{(y \in I_\delta(y_0))}$. $\alpha(x) =: \alpha_{I_\delta(y_0)}(x)$ expected sojourn time spent by x_t in the interval $I_\delta(y_0)$, starting from x .

$$\alpha_{I_\delta(y_0)}(x) = \int_{I_\delta(y_0)} \mathfrak{g}(x,y)\, dy.$$

Green function:

$$\begin{aligned}
\mathfrak{g}(x, y_0) &= m(y_0)(1-x) \text{ if } y_0 < x \\
\mathfrak{g}(x, y_0) &= m(y_0)\, x \text{ if } y_0 > x.
\end{aligned}$$

Solution to (63) when $d(0) = d(1) = 0$: $\alpha(x) = \int_0^1 \mathfrak{g}(x,y)\, c(y)\, dy$.

Eigenpolynomials. $\psi(x) = x^k$ monomial of degree $k \geq 1$.

$$(L\psi)(x) = \frac{1}{k+1}\left(x + .. + x^{k-1} + 2x^k\right)$$

$\Rightarrow$ action of L on x^k does not change the degree of the polynomial image $\Rightarrow$ $\exists$ polynomials $u_k(x)$ of degree k such that, with $\lambda_k := 2/(k+1)$, $k \geq 1$

$$(\lambda_k I - L)\, u_k = 0.$$

These values of λ are particular (real and rational) values of the point spectrum of L [$\lambda_k = \widehat{P}^{\infty}_{k,k}$ coincide with the diagonal terms of $\widehat{P}^{\infty}$].

• k odd, $u_1(x) = x$ and

$$u_k(x) = (1-2x)\,(x(1-x))^{(k-1)/2}, \; k \geq 3. \tag{64}$$

with u_k anti-symmetric: $u_k(x) = -u_k(1-x)$.

• k even, u_ks symmetric: $u_k(x) = u_k(1-x)$, with

$$u_{2p}(x) = x(1-x)\sum_{q=1}^{p-1}\left(a_{q,p} + b_{q,p}\,(x(1-x))^q\right), \; p \geq 1 \tag{65}$$

for some sequences of real numbers $\left(a_{q,p}, b_{q,p}\right)_{q=1,..,p}$ which can be computed recursively by iterated Euclidean division of u_{2p} by $x(1-x)$.

For all $\psi \in C_0([0,1])$, decompose $\psi(x) = \sum_{l\geq 1} c_l u_l(x) \Rightarrow$

$$\left(L^t \psi\right)(x) = \mathbf{E}_x \psi(x_t) = \sum_{l\geq 1} \left(\frac{2}{l+1}\right)^t c_l \cdot u_l(x).$$

ADJOINT: $v_k(y) = (y(1-y))^{-(k+1)/2}$ eigenstates of L^* associated to λ_k : $(L^* v_k)(y) = \lambda_k v_k(y) . v_1(y) = (y(1-y))^{-1} = m(y)$, the speed measure density.

Examples:

(i) Dynamics of heterozygosity $\mathbf{E}_x(2x_t(1-x_t)) = 2\left(\frac{2}{3}\right)^t x(1-x)$, which tends to 0 exponentially fast as $t \to \infty$.

(ii) Variance of heterozygosity

$$\boldsymbol{\sigma}_x^2(2x_t(1-x_t)) = 4\mathbf{E}_x\left[u_4(x_t) + \frac{1}{8}u_2(x_t)\right] - 4\mathbf{E}_x[u_2(x_t)]^2$$

$$= 4x(1-x)\left[\frac{1}{8}\left(\frac{2}{3}\right)^t + \left(x(1-x) - \frac{1}{8}\right)\left(\frac{2}{5}\right)^t - x(1-x)\left(\frac{2}{3}\right)^{2t}\right].$$

Starts growing and then decays expon. to 0 at rate $2/3$ when $t \to \infty$. Intermediate time $t_* > 1$ at which they reach a maximum. $\diamond$

(iii) In particular also, if $\psi(x) = x^n$ and $x^n = \sum_{k=1}^{n} c_{k,n} u_k(x)$, then

$$\left(L^t \psi\right)(x) = \mathbf{E}_x\left(x_t^n\right) = \sum_{k=1}^{n} \left(\frac{2}{k+1}\right)^t c_{k,n} \cdot u_k(x).$$

useful with DUALITY

$$\mathbf{E}_x\left(x_t^n\right) = \mathbf{E}_n\left(x^{\widehat{x}_t}\right), \text{ for all } (n,t) \in \mathbb{N}_+, \ x \in [0,1], \tag{66}$$

we get the pgf $\mathbf{E}_n\left(x^{\widehat{x}_t}\right)$ of $\widehat{x}_t$ started at $\widehat{x}_0 = n$.

$$[x]\,\mathbf{E}_n\left(x^{\widehat{x}_t}\right) = [x]\,\mathbf{E}_x\left(x_t^n\right)$$

is the probability that $\widehat{x}_t = 1$ (starting from $\widehat{x}_0 = n$) or else that TMRCA T_n of $\widehat{x}_t$ is $\leq t$. More generally

$$\mathbf{P}_n\left(\widehat{x}_t = i\right) = \left[x^i\right] \mathbf{E}_x\left(x_t^n\right) = \sum_{k=1}^{n} \left(\frac{2}{k+1}\right)^t c_{k,n} \cdot \left[x^i\right] u_k(x).$$

Conditionnings. (i) Fixation (same with extinction)

$$p(x;1,y) \to \overline{p}_1(x;1,y) := \frac{y}{x} p(x;1,y)$$

is (54) conditioned on exit eventually at 1. New process $\widetilde{x}_t$.

$$\left(\overline{L}\psi\right)(x) = \mathbf{E}_x \psi\left(\widetilde{x}_1\right) = \frac{1-x}{x^2} \int_0^x y\psi(y)\, dy + \frac{1}{1-x} \int_x^1 y\psi(y)\, dy. \qquad (67)$$

$\left(\overline{L}1\right)(x) = 1$(no mass loss nor creation).

$$\mathbf{E}_x\left(\widetilde{x}_1\right) = \frac{1-x}{x^2} \int_0^x y^2 dy + \frac{1}{1-x} \int_x^1 y^2 dy = \frac{1}{3}(2x+1).$$

$\widetilde{x}_t$ has additional drift: $\mathbf{E}_x\left(\widetilde{x}_1\right) - x = \frac{1}{3}(1-x)$.

(ii) $Q-$process. $u_2 = x(1-x)$ eigenv. of L associated to $\lambda_2 = 2/3$. $\widetilde{x}_t$:

$$p(x;1,y) \to \overline{p}(x;1,y) := \lambda_2^{-1} \frac{y(1-y)}{x(1-x)} p(x;1,y).$$

$$\left(\overline{L}\psi\right)(x) = \mathbf{E}_x \psi\left(\widetilde{x}_1\right) = \frac{\lambda_2^{-1}}{x^2} \int_0^x y(1-y)\psi(y)\, dy + \frac{\lambda_2^{-1}}{(1-x)^2} \int_x^1 y(1-y)\psi(y)\, dy.$$

$\left(\overline{L}1\right)(x) = 1$, (no mass loss nor creation). x_t conditioned on never hitting $\{0,1\}$. $\widetilde{x}_t$ has additional stab. drift towards 1/2: $\frac{1}{4}\left(\frac{1}{2} - x\right)$. m of $\widetilde{x}_t$ obeys $\left(\overline{L}^* m\right)(y) = m(y)$ is: $m(y) \propto (y(1-y))^{-1/2} \to \widetilde{x}_t$ is $R+$.

Doob transforms. $\alpha \geq 0$ solves

$$-\left(L-I\right)\alpha = c,$$

for some c. If $c>0$ ($c<0$) on $(0,1)$, α is superharmonic (subharmonic). Harmonic if $c=0$. L backward gen. of x_t, define:

$$\left(\overline{L}\psi\right)(x) = \frac{1}{\alpha(x)} L\left(\alpha\psi\right)(x).$$

$\left(\overline{L}1\right)(x) - 1 = \frac{1}{\alpha(x)} L\left(\alpha\right)(x) - 1 = -c/\alpha =: \lambda(x) \Rightarrow$

$$\left(\overline{L}\psi\right)(x) = \left(\widetilde{L}\psi\right)(x) + \lambda(x)\cdot\psi$$

$$\left(\widetilde{L}\psi\right)(x) = \left(I - \left(\overline{L}1\right)(x)\right)\psi(x) + \left(\overline{L}\psi\right)(x) =$$

$$\psi(x) + \frac{1-x}{x\alpha(x)}\int_0^x \alpha(y)\left(\psi(y)-\psi(x)\right)dy + \frac{x}{(1-x)\alpha(x)}\int_x^1 \alpha(y)\left(\psi(y)-\psi(x)\right)dy$$

backward gen. of new stochastic process $\widetilde{x}_t$, noting $\left(\widetilde{L}1\right)(x) = 1$.

Depending on whether $\lambda>0$ ($\lambda<0$) on $(0,1)$ obtained when α is subharmonic (superharmonic), the multiplicative term $\psi \rightarrow \lambda(x)\cdot\psi$ accounts either for branching or for killing of $\widetilde{x}_t$. $\overline{L} = \widetilde{L}$ when $c=0$ (in the harmonic case).

Deviation from neutrality (drifts):

$$x_{t+1} = p(x_t) + U_{t+1}(1 - p(x_t))\, 1(V_{t+1} \le x_t) - U_{t+1} p(x_t)\, 1(V_{t+1} > x_t),$$

$x \to p(x)$ invertible $\uparrow [0,1] \to I \subseteq [0,1]$. x_t no longer a martingale:
$\mathbf{E}(x_{t+1} \mid x_t = x) = \frac{1}{2}(x + p(x))$. $\sigma^2_{x_t=x}(x_{t+1}) = \sigma^2(U_{t+1})\left[(1-x)x + (p(x)-x)^2\right]$.

$$f \equiv 1 \to (L^*\mu)(y) = \int_0^{p^{-1}(y)} \frac{z}{1-p(z)}\mu(dz) + \int_{p^{-1}(y)}^1 \frac{1-z}{p(z)}\mu(dz).$$

$$\text{speed d. obeys: } m'(y) = p^{-1}(y)' \left(\frac{p^{-1}(y)}{1-y} - \frac{1-p^{-1}(y)}{y}\right) m\left(p^{-1}(y)\right).$$

Small mutations: $p(x) = \pi_1(1-x) + (1-\pi_2)x$

$$m(y) \propto y^{\frac{\pi_2 - 1}{(1-\pi)^2}} (1-y)^{\frac{\pi_1 - 1}{(1-\pi)^2}}.$$

Both exponents $\alpha_i < -1$ m not integrable (x_t with mutations not ergodic).
Small selection: $p(x) = (1+s_1)x/(1+s_1x+s_2(1-x))$, $s = s_1 - s_2 > 0$.

$$m(y) \propto \frac{1}{y(1-y)}(1-y)^{-6s} e^{10sy}.$$

Biased to the right (A_1 is eventually favored) not integrable.