A variant of the Wright-Fisher diffusion model coming from the theory of matrix-valued spherical functions

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Outline

1. The Wright-Fisher model
   - The original problem
   - The diffusion approximation
   - Spectral methods
2. A variant of the Wright-Fisher model
   - The coefficients of the hybrid process
   - Probabilistic interpretation
   - Spectral methods

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The Wright-Fisher model

The Wright-Fisher model considers a gene population of constant size M composed of two types A and B. Call $\#A = i$.

The next generation is determined by M independent binomial trials: each trial results in A or B with probabilities

$$p_i = \frac{i}{M}, \quad q_i = 1 - p_i = 1 - \frac{i}{M}$$

Therefore we generate a discrete-time Markov chain $\{X(n)\}$ where

$$X(n) = \{\#A \text{ in the } n\text{-th generation}\}$$

with state space $\mathcal{S} = \{0, 1, \ldots, M\}$ and transition probability matrix

$$\Pr\{X(n+1) = j | X(n) = i\} = \binom{M}{j} p_i^j q_i^{M-j}$$

A more realistic model takes account of mutation pressures

$$A \xrightarrow{a} B, \quad B \xrightarrow{b} A, \quad a, b > 0$$

We have the same transition probability matrix but now

$$p_i = \frac{i}{M}(1-a) + \left(1 - \frac{i}{M}\right) b, \quad q_i = 1 - p_i$$

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EXAMPLE $M = 15$

$A=$● brown eyes, $B=$● blue eyes

$X(0) = 8$

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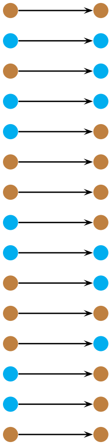

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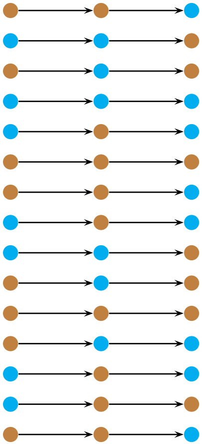

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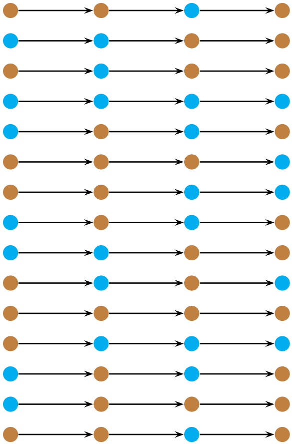

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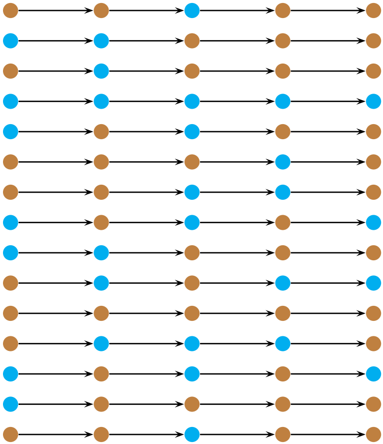

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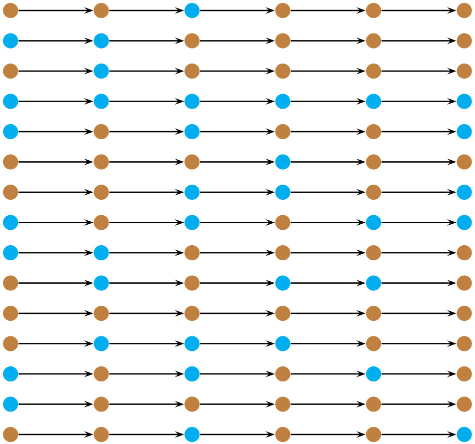

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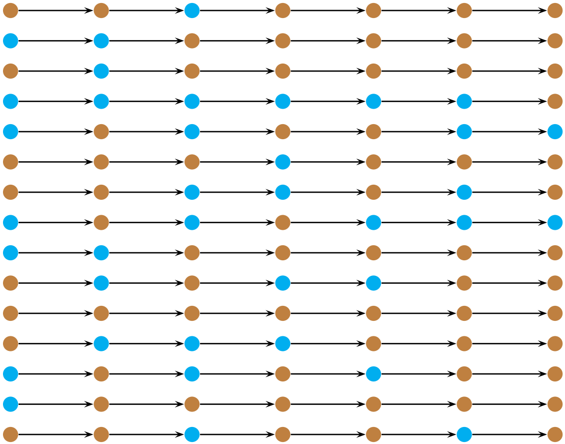

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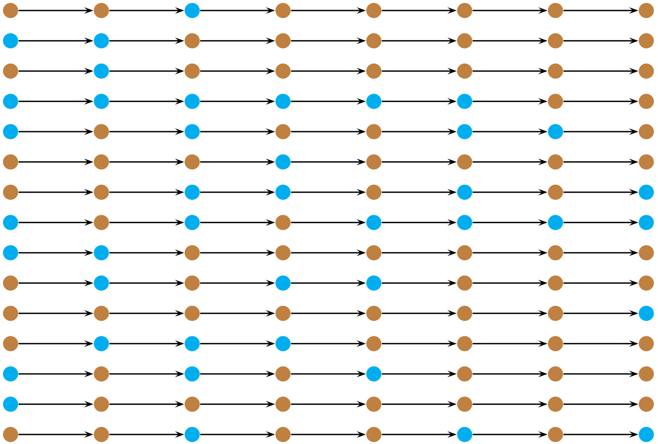

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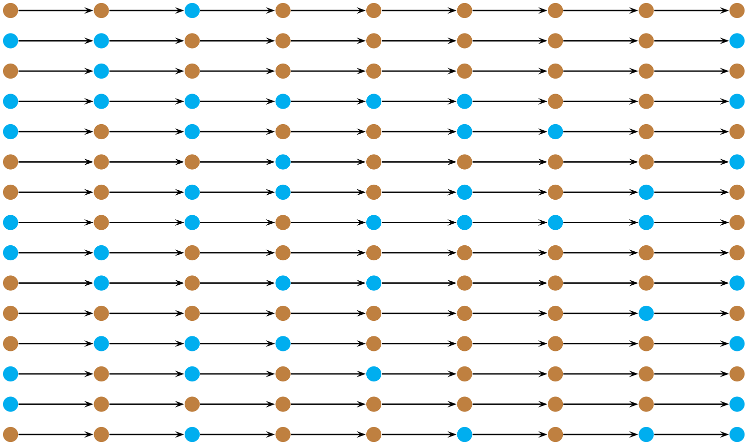

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The diffusion approximation

Consider the process

$$Y(t) = \lim_{M\to\infty} Y_M(t) = \lim_{M\to\infty} \frac{X([Mt])}{M}$$

If we call $h = 1/M$ and $x = i/M$, we have that

$$\tau(x) = \lim_{h\to 0^+} \frac{1}{h} E\left[Y_M(t+h) - Y_M(t) | Y_M(t) = x\right] = -\gamma_1 x + (1-x)\gamma_2$$

$$\sigma^2(x) = \lim_{h\to 0^+} \frac{1}{h} E\left[(Y_M(t+h) - Y_M(t))^2 | Y_M(t) = x\right] = x(1-x)$$

where $\gamma_1 = aM$ and $\gamma_2 = bM$ are the intensities of mutation.

Therefore $Y(t)$ is a continuous-time diffusion process with *state space* $\mathcal{S} = [0,1]$, *drift* $\tau(x)$ and *diffusion* coefficient $\sigma^2(x)$.
$Y(t) = Y_t$ evolves according to the stochastic differential equation

$$dY_t = \tau(Y_t) + \sigma(Y_t)dB_t$$

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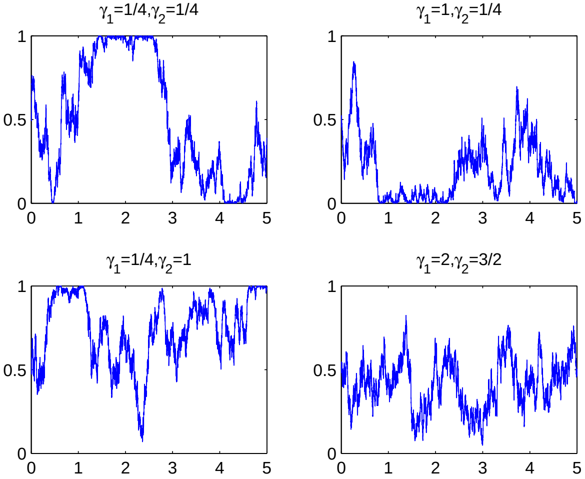
Boundary behavior

The boundaries $1, 0$ are absorbing if $0 < \gamma_1, \gamma_2 < 1/2$ and reflecting if $\gamma_1, \gamma_2 \geq 1/2$.



Spectral methods

Write $\gamma_1 = \frac{1+\beta}{2}$ and $\gamma_2 = \frac{1+\alpha}{2}$.
The infinitesimal operator $\mathcal{A}$ of the process Y_t is

$$\mathcal{A} = x(1-x)\frac{d^2}{dx^2} + (1+\alpha - x(\alpha+\beta+2))\frac{d}{dx}, \quad \alpha, \beta > -1$$

The orthonormal Jacobi polynomials $P_n^{\alpha,\beta}(x)$ (orthogonal w.r.t $\omega(x) = x^\alpha(1-x)^\beta$) are eigenfunctions of $\mathcal{A}$, i.e.

$$\mathcal{A}P_n^{\alpha,\beta}(x) = \lambda_n P_n^{\alpha,\beta}(x), \quad \lambda_n = -n(n+\alpha+\beta+1)$$

We have two important properties:

Spectral representation of the probability density

$$p(t;x,y) = \sum_{n=0}^{\infty} e^{\lambda_n t} P_n^{\alpha,\beta}(x) P_n^{\alpha,\beta}(y) y^\alpha (1-y)^\beta$$

Invariant distribution $(\alpha, \beta \geq 0)$

$$\psi(y) = \lim_{t\to\infty} p(t;x,y) = \frac{\Gamma(\alpha+1)\Gamma(\beta+1)}{\Gamma(\alpha+\beta+2)} y^\alpha (1-y)^\beta$$

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THE COEFFICIENTS OF THE HYBRID PROCESS

We consider now a *hybrid process* of the form

$$\{(Y_t, R_t) : t \in [0, +\infty)\}$$

where $Y_t \in [0, 1]$ is a Wright-Fisher type diffusion process and $R_t \in \{1, 2, \ldots, N\}$ is a continuous-time Markov chain representing N different phases for which the coefficients of the process Y_t may change. These processes are also known as diffusions with Markovian switching.

Our process evolves according to the stochastic differential equation

$$dY_t = \tau_{R_t}(Y_t) + \sigma_{R_t}(Y_t)dB_t$$

$$\tau_i(x) = \alpha + 1 + N - i - x(\alpha + \beta + 2 + N - i), \quad \sigma_i^2(x) = 2x(1 - x)$$

Observe that the intensities of mutations depend on the phase so

$$A \xrightarrow{\frac{\beta+1}{2}} B \quad \text{and} \quad B \xrightarrow{\frac{\alpha+N-i+1}{2}} A, \quad i = 1, 2, \ldots, N$$

- At phase N we recover the original Wright-Fisher model.
- $B \to A$ grows as we get closer to the first phases.

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The transition of phases

The continuous-time process R_t (depending also on the position Y_t) evolves according to a birth-and-death process whose infinitesimal operator is given by an $N \times N$ tridiagonal matrix $\mathbf{Q}(x)$ where

$$\mathbf{Q}_{i,i-1}(x) = \frac{1}{1-x}(N-i)(i+\beta-k), \quad \mathbf{Q}_{i,i+1}(x) = \frac{x}{1-x}(i-1)(N-i+k)$$

$$\mathbf{Q}_{i,i}(x) = -(\mathbf{Q}_{i,i-1}(x) + \mathbf{Q}_{i,i+1}(x)), \quad 0 < k < \beta + 1$$

$\mathbf{Q}(x)$ only depends on β and a new parameter k.

For example: $N = 3$ phases, $\beta = 1, k = 3/2$:

$$\mathbf{Q}(x) = \begin{pmatrix} -\frac{1}{1-x} & \frac{1}{1-x} & 0 \\ \frac{5x}{2(1-x)} & \frac{-3-5x}{2(1-x)} & \frac{3}{2(1-x)} \\ 0 & \frac{3x}{1-x} & -\frac{3x}{1-x} \end{pmatrix}, \quad x \in (0,1)$$

The transition of phases

The continuous-time process R_t (depending also on the position Y_t) evolves according to a birth-and-death process whose infinitesimal operator is given by an $N \times N$ tridiagonal matrix $\mathbf{Q}(x)$ where

$$\mathbf{Q}_{i,i-1}(x) = \frac{1}{1-x}(N-i)(i+\beta-k), \quad \mathbf{Q}_{i,i+1}(x) = \frac{x}{1-x}(i-1)(N-i+k)$$

$$\mathbf{Q}_{i,i}(x) = -(\mathbf{Q}_{i,i-1}(x) + \mathbf{Q}_{i,i+1}(x)), \quad 0 < k < \beta + 1$$

$\mathbf{Q}(x)$ only depends on β and a new parameter k.

For example: $N = 3$ phases, $\beta = 1, k = 3/2$:

$$\mathbf{Q}(x) = \begin{pmatrix} -\dfrac{1}{1-x} & \dfrac{1}{1-x} & 0 \\ \dfrac{5x}{2(1-x)} & \dfrac{-3-5x}{2(1-x)} & \dfrac{3}{2(1-x)} \\ 0 & \dfrac{3x}{1-x} & -\dfrac{3x}{1-x} \end{pmatrix}, \quad x \in (0,1)$$

Stochastic representation

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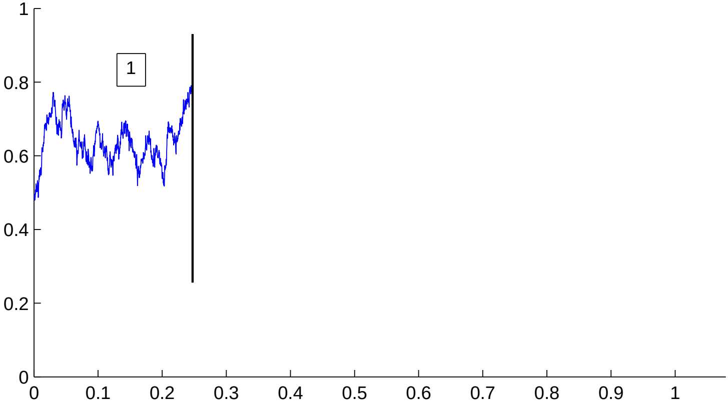
Phase 1: $\sigma^2(x) = 2x(1-x), \tau_1(x) = 3 - 5x, \mathbf{Q}_{1,1}(x) = -\frac{1}{1-x}$



Stochastic representation

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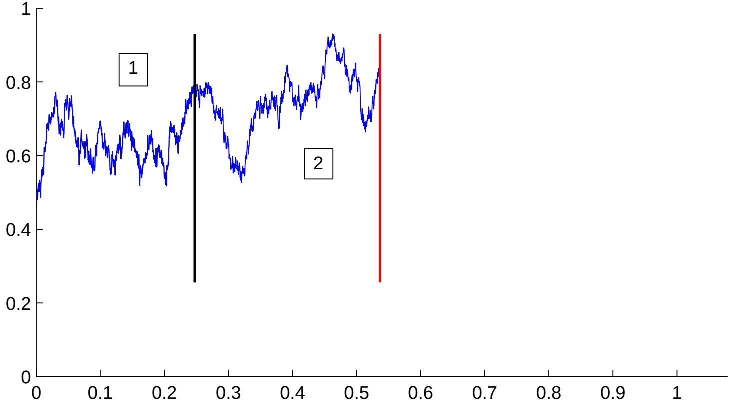
Phase 2: $\sigma^2(x) = 2x(1-x), \tau_2(x) = 2 - 4x, \mathbf{Q}_{2,2}(x) = \frac{-3-5x}{2(1-x)}$



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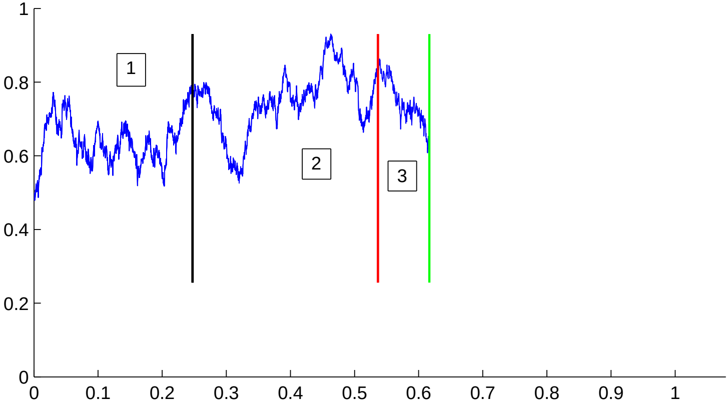

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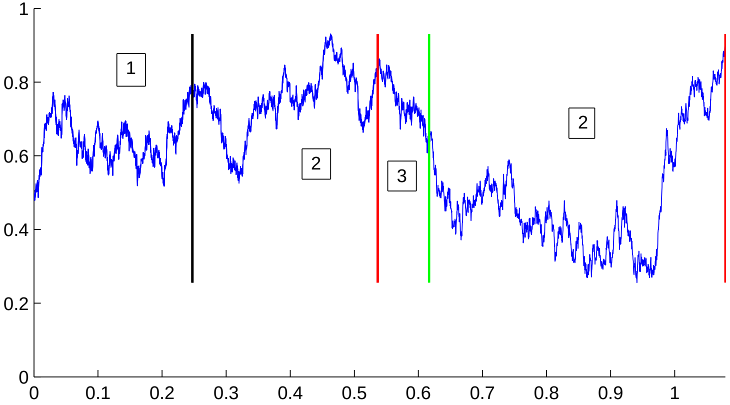
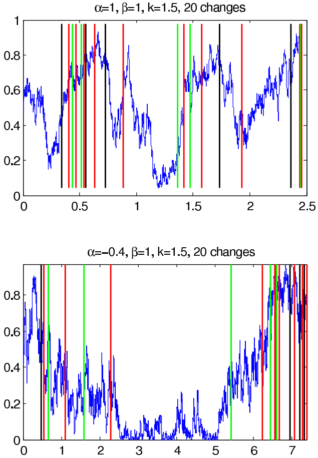


Boundary behavior

The boundary 0 (or 1) is *reflecting* if $\alpha \geq 0$ (or $\beta \geq 0$) and *absorbing* if $-1 < \alpha < 0$ AND phase N (or $-1 < \beta < 0$).



Waiting times and tendency

Waiting times

We have to take a look to the *diagonal entries* of $\mathbf{Q}(x)$:

$$\mathbf{Q}_{ii}(x) = -\frac{1}{1-x}\left[(N-i)(i+\beta-k) + x(i-1)(N-i+k)\right]$$

- If $x \to 1^- \Rightarrow$ all phases are *instantaneous*.
- If $x \to 0^+$ or $k \to 0^+ \Rightarrow$ phase N is *absorbing*.
- If $k \to \beta + 1 \Rightarrow$ phase 1 is *absorbing*.

Tendency

- If $k \to \beta + 1 \Rightarrow$ *Backward tendency*

  Meaning: The parameter k helps the population of A's to survive against the population of B's.

- If $k \to 0^+ \Rightarrow$ *Forward tendency*

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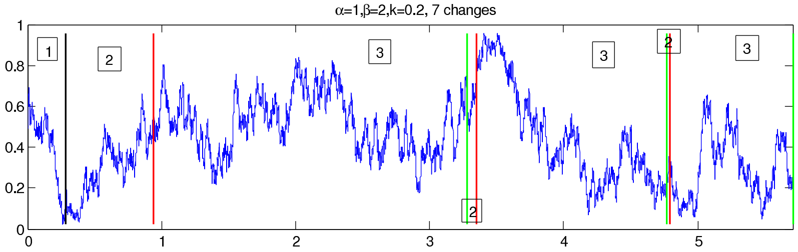
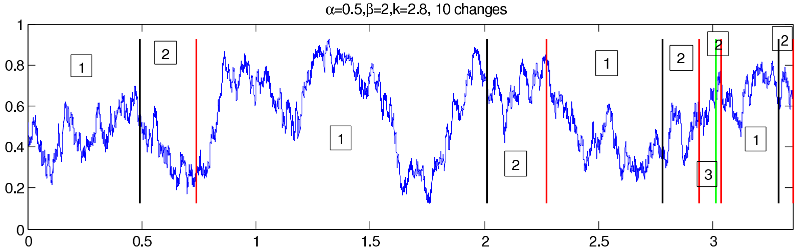
Example of tendency





SPECTRAL METHODS

The infinitesimal operator $\mathcal{A}$ is now matrix-valued

$$\mathcal{A} = \frac{1}{2}\mathbf{A}(x)\frac{d^2}{dx^2} + \mathbf{B}(x)\frac{d}{dx} + \mathbf{Q}(x)\frac{d^0}{dx^0}$$

$$\mathbf{A}(x) = 2x(1-x)\mathbf{I}, \quad \mathbf{B}_{ii}(x) = \tau_i(x)$$

We already know (Grünbaum-Pacharoni-Tirao, 2002) a family of matrix-valued orthonormal eigenfunctions $\Phi_n(x)$ of $\mathcal{A}$:

$$\mathcal{A}\Phi_n(x) = \Phi_n(x)\Gamma_n, \quad \Gamma_n \quad \text{diagonal}$$

They are called the matrix-valued spherical functions associated with the complex projective space.
The corresponding weight matrix $\mathbf{W}(x)$ is diagonal with entries

$$\mathbf{W}_{ii}(x) = x^{\alpha}(1-x)^{\beta}\binom{\beta-k+i-1}{i-1}\binom{N+k-i-1}{N-i}x^{N-i}$$

SPECTRAL REPRESENTATION OF THE PROBABILITY DENSITY

$$\mathbf{P}(t;x,y) = \sum_{n=0}^{\infty}\Phi_n(x)e^{\Gamma_n t}\Phi_n^*(y)\mathbf{W}(y)$$

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The invariant distribution $\boldsymbol{\psi}(y)$ ($\alpha, \beta \geq 0$) comes from the study of

$$\lim_{t \to \infty} \mathbf{P}(t; x, y)$$

This should be independent of the initial state and phase.
Therefore we should expect a row vector invariant distribution

$$\boldsymbol{\psi}(y) = (\psi_1(y), \psi_2(y), \ldots, \psi_N(y))$$

with $0 \leq \psi_j(y) \leq 1$ and

$$\sum_{j=1}^{N} \int_0^1 \psi_j(y) dy = 1$$

Explicit formula (MdI, 2012)

$$\Rightarrow \psi(y) = \left(\int_0^1 \mathbf{e}_N^T \mathbf{W}(x) \mathbf{e}_N dx \right)^{-1} \mathbf{e}_N^T \mathbf{W}(y)$$

where $\mathbf{e}^T = (1, 1, \ldots, 1)$. In particular

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Study of the invariant distribution