Probability meets Biology III

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Rates of sweeps and clicks

Anton Wakolbinger and Felix Hermann

Goethe-Universität Frankfurt am Main, Institut für Mathematik

based on joint work with
András Tóbiás, Florin Boenkost, Renato Soares dos Santos,
Adrián González Casanova, Charline Smadi and Jan Lukas Igelbrink

Moran model with recurrent mutations

either all beneficial, leading to successive

take-overs of new (fitter) types:

“selective **sweeps**” (Part I)

or all deleterious, leading to successive

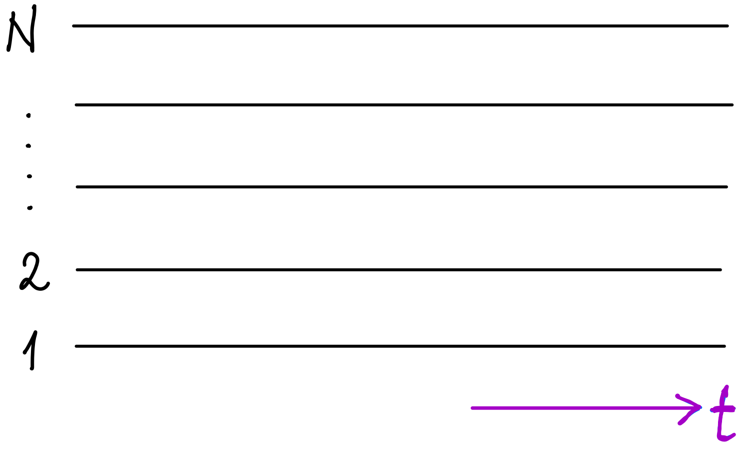
disappearances of the currently fittest class:

“**clicks** of the ratchet” (Part II)

Graphical representation

Lines are numbered by $i = 1, \ldots, N$.

At any time t, each line carries one individual (i, t).



N ... population size: constant over time t

Graphical representation

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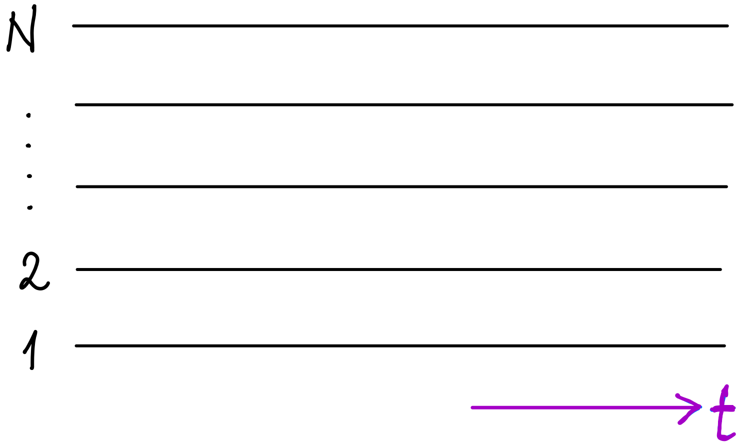
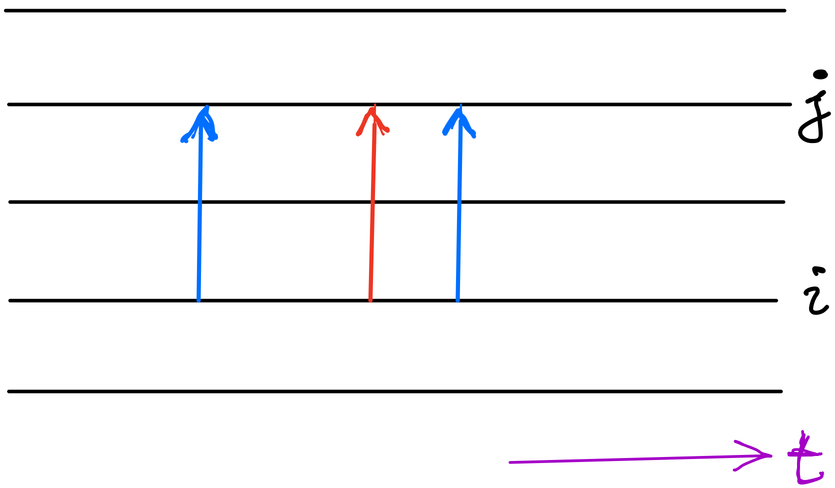
At any time t, each line carries one individual (i, t).



Each individual (i, t) has a fitness level $f(i, t) \in \mathbb{R}$

Neutral arrows are shot from i to j at rate $\frac{1}{N}$.

Selective arrows are shot from i to j at rate $\varphi_N \frac{1}{N}\big(f(i,t) - f(j,t)\big)^+$.



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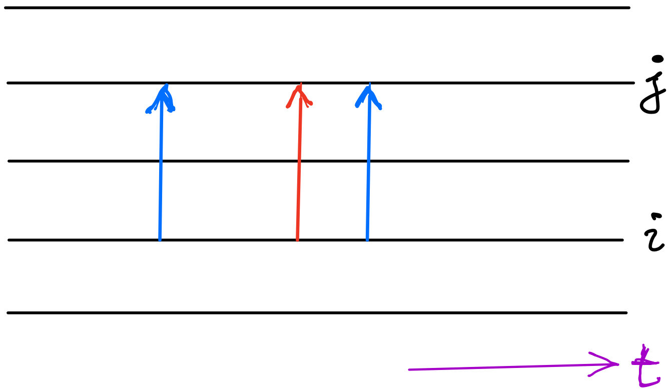

Thus selective arrows from i to j only are at work

while the fitness level of j is not larger than that of i.

At the time t of an arrow from i to j,

(i, t) splits into $\{(i, j), (j, t)\}$.

and the fitness level f is updated as

$$f(j, t) := f(i, t-).$$

Neutral arrows are shot from i to j at rate $\frac{1}{N}$.

Selective arrows are shot from i to j

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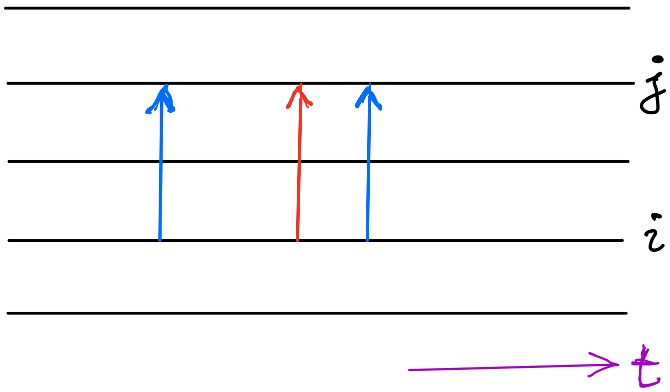


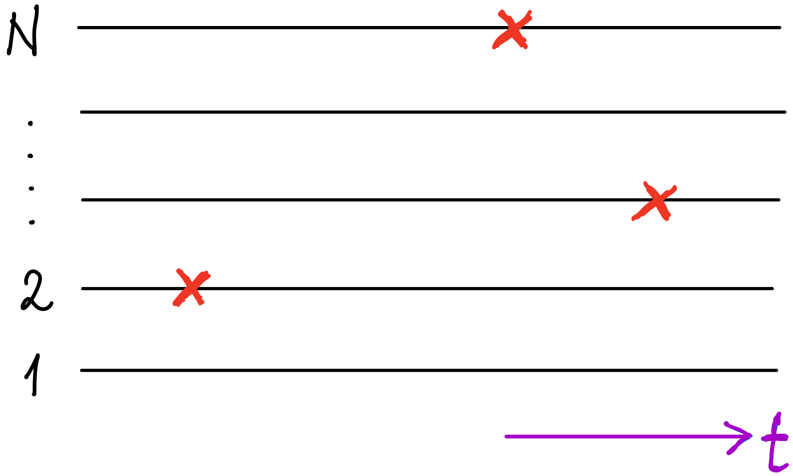
Thus individual lineages split or die

at a rate of order 1 (*"ecological timescale"*.

Mutations come at rate $\mathfrak{m}_N$ per line,

i.e. as independent Poisson processes with intensity $\mathfrak{m}_N\, dt$

for all $i = 1, \ldots, N$



When (i, t) experiences a mutation, its fitness level jumps:

$$f(i,t) = f(i,t-) + A(i,t)$$

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$$f(i, t) = f(i, t-) + A(i, t)$$

The $A(i, t)$ will be

- in part I: ≥ 0, independent and identically distributed
- in part II: all equal to -1.

Tracing back the ancestral lineage of (i, t) leads to

$\mathfrak{A}_0(i, t)$:= the ancestor of (i, t) at time 0

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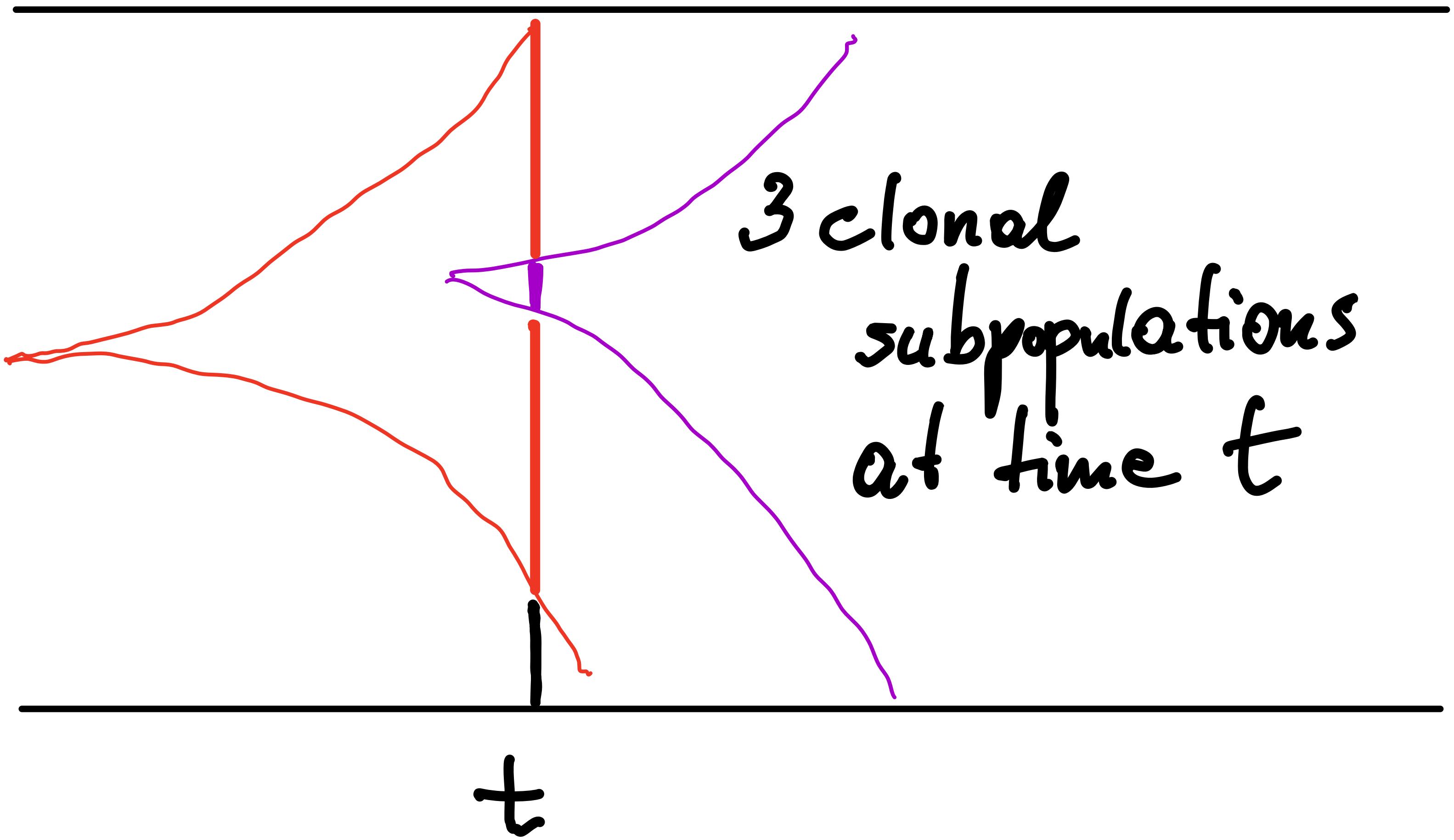
$\mathfrak{A}_0(i,t)$:= the ancestor of (i,t) at time 0

In this way, the fitness level $f(i,t)$ becomes
$f(\mathfrak{A}_0(i,t))$ plus the sum of the fitness increments
along the ancestral lineage of (i,t) back to time 0,
where each fitness increment is caused by a mutation event.

Those individuals in the offspring of a mutant individual $\mathcal{I}$

that have not yet acquired an additional mutation
along their ancestral lineage back to $\mathcal{I}$

form a so-called **clonal subpopulation**.


3 clonal subpopulations at time t
t

Part I

Beneficial mutations

The story:

The clonal subpopulations (CSP‘s) compete for taking over,
with the fitter ones having an advantage.

As soon as a new CSP is born,
it first has to fight against the neutral fluctuations.

Assume that at the birth time of a (mutant) CSP
almost the entire population consists of its *parent CSP*.

Then, given the mutant's fitness increment $A = a$,
as long as the mutant CSP is small, each of its individuals

- is hit (and thus killed) by arrows at rate $\sim \mathtt{1}$
- shoots arrows (and thus splits) at rate $\sim \mathtt{1} + \varphi_N a$.

Then, initially the mutant CSP behaves like
a branching process with supercriticality $a\varphi_N$.

The probability that this CSP is not killed by the initial fluctuations
is (asymptotically as $N \to \infty$) equivalent to
the survival probability $\frac{a\varphi_N}{1+a\varphi_N}$.

A critical size from which survival happens
with high probability (as $N \to \infty$) is $c_N := \frac{\log N}{\varphi_N}$.

After the mutant CSP has reached the critical size c_N,

(say this happens at time t_N),

its size $Y(t)$ has exponential growth rate $a\varphi_N$,

as long as it competes essentially only agains its “parent CSP”.

$$Y(t) \approx c_N \, e^{a\varphi_N \cdot (t - t_N)}, \quad t \geq t_N$$

as long as Y is way below N.

Speed up time by the factor $\frac{\log N}{\varphi_N}$,

assume $t_N \approx t_0 \frac{\log N}{\varphi_N}$

$$Y\left(t \cdot \frac{\log N}{\varphi_N}\right) \approx c_N \, N^{a \cdot (t - t_0)}, \quad t \geq t_0.$$

$$(*) \qquad Y\left(t \cdot \frac{\log N}{\varphi_N}\right) \approx c_N\, N^{a\cdot(t-t_0)}, \quad t \geq t_0.$$

Define the *logarithmic CSP size* $H^N(t) := \log_N Y\left(t \cdot \frac{\log N}{\varphi_N}\right)$:

Then $(*)$ becomes

$$\boxed{H^N(t) \approx \log_N c_N + a(t - t_0), \quad t \geq t_0.}$$

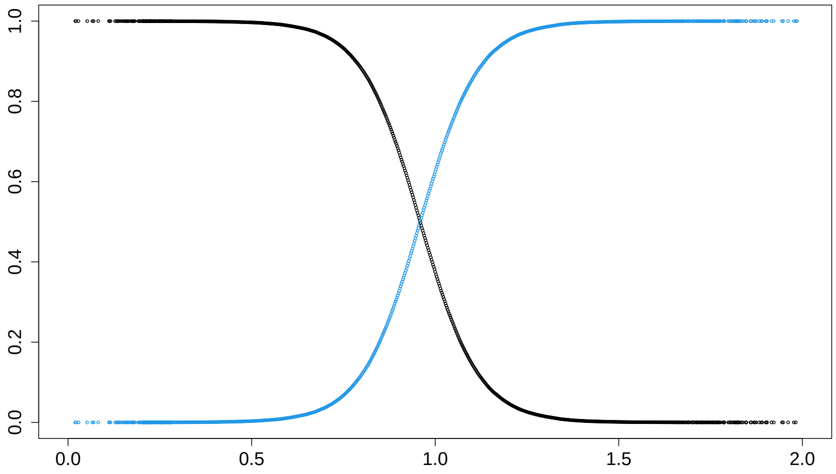
Before reaching height 1,

H^N increases (approximately) linearly with slope a,

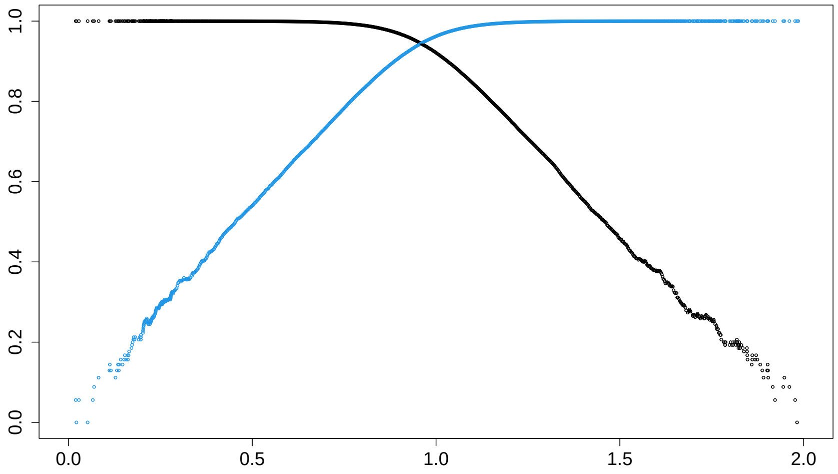
as long as the mutant CSP has to compete only with its parent CSP.

Simulation, $N = 250\,000$, $\varphi_N = 1$, $a = 1$

relative sizes of CSP's



logarithmic sizes



The arrival process of contending CSP’s

We say that a mutant CSP has established itself as a contender as soon as it has reached the critical size c_N.

Assume that mutant CSP’s in their early phase have to compete essentially only against their parent CSP. Then the probability that a mutant CSP becomes a contender, given its fitness increment was a, is

$$\approx \frac{a\varphi_N}{1+a\varphi_N}$$

The arrival intensity of contending CSP's

With $\gamma(da) := \mathbf{P}(A \in da), \;\; a \geq 0$,

the arrival intensity of contending CSP's is

$$\approx N\mathfrak{m}_N \, dt \, \gamma(da) \tfrac{a\varphi_N}{1+a\varphi_N}$$

With time speeded up by the factor $\frac{\log N}{\varphi_N}$,

i.e. passing to the Gerrish-Lenski timescale, this becomes

$$N \log N \, \mathfrak{m}_N \, dt \, \gamma(da) \tfrac{a}{1+a\varphi_N}$$

$$N \log N \, \mathfrak{m}_N \, dt \, \gamma(da) \tfrac{a}{1+a\varphi_N}$$

With the individual mutation rate chosen as

$\mathfrak{m}_N = \frac{\lambda}{N \log N}$ (for some constant $\lambda > 0$)

we get

$$\lambda \, dt \, \gamma(da) \tfrac{a}{1+a\varphi_N}$$

as the arrival intensity of contending CSP's

on the Gerrish-Lenski timescale.

Strong selection: $\varphi_N \equiv 1$

$$\mathfrak{m}_N = \frac{\lambda}{N \log N}$$

time speeded up by factor $\log N$

$$\gamma(da) := \mathbf{P}(A \in da).$$

The arrival intensity of contending CSP’s is

$$\approx \lambda\, dt\, \gamma(da) \tfrac{a}{1+a}$$

Assume that at time 0

all of the N individuals have fitness level zero:

$$f(i, 0) = 0, \quad i = 1, \ldots, N.$$

Theorem 1 (Scaling of clonal interference, strong selection)

(HGSTW25 Thm 1)

Let, on the Gerrish-Lenski time scale, (T_j^N, A_j^N) be the arrival times and fitness increments of the *contending CSP's*, i.e. those mutant CSP that ever reach size $c_N = \log N$

Then, as $N \to \infty$,

(a) $$(T_j^N, A_j^N) \xrightarrow{d} (T_j, A_j) =: \Pi^*,$$

a Poisson process with intensity $\lambda \, dt \, \gamma(da) \frac{a}{1+a}$.

(where the convergence is "local in time", or equivalently, is for all finite prefixes of the infinite sequence (T_j^N, A_j^N))

Theorem 1 (Scaling of clonal interference, strong selection)

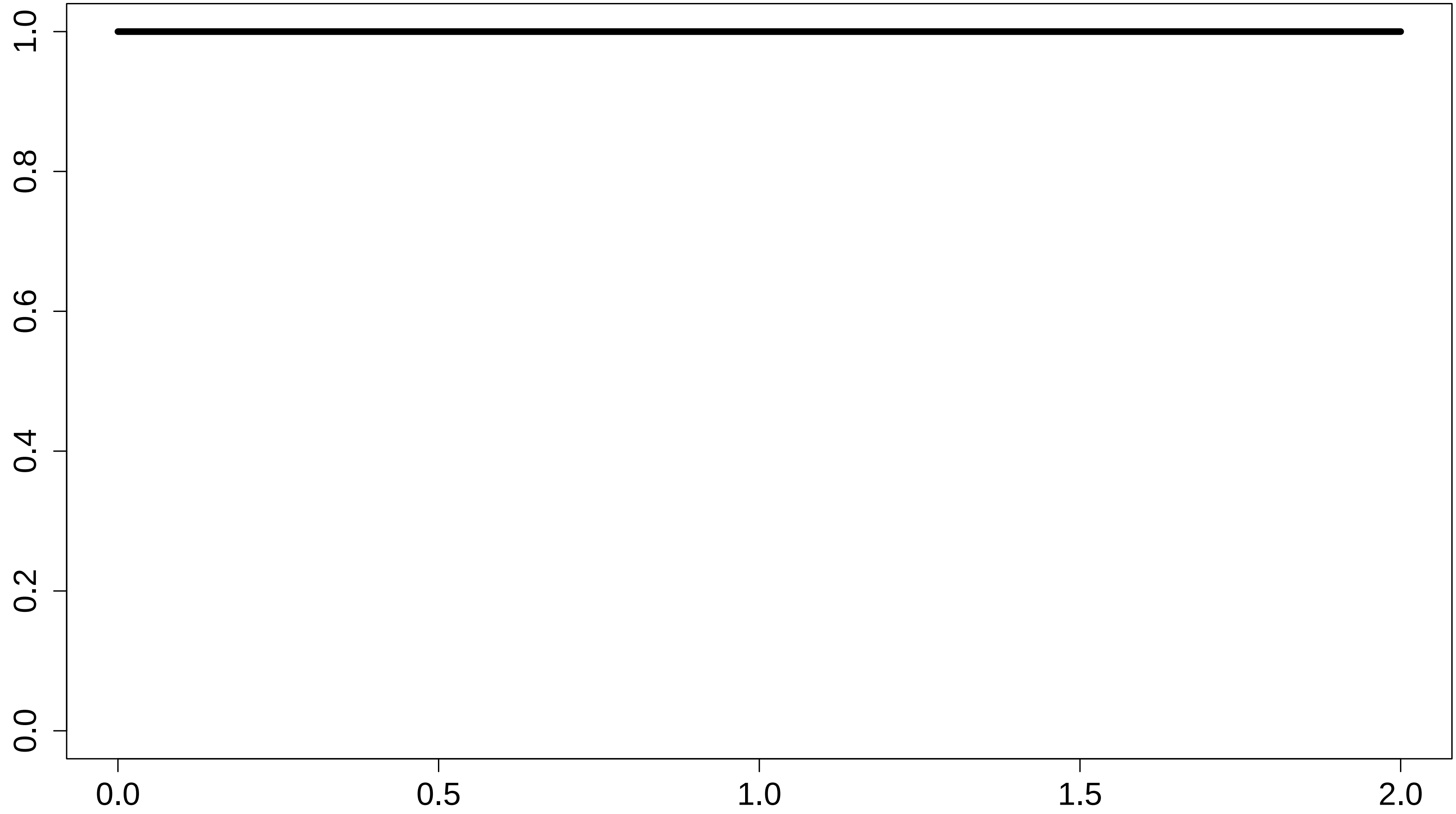
(HGSTW25 Thm 1)

(b) The logarithmic CSP sizes (H_j^N) of the contending CSP's
converge, as $N \to \infty$, in distribution
(with respect to uniform convergence on bounded time intervals)

to a system of piecewise linear interacting trajectories (H_j)
with random initial condition Π^*,

and *determinstic dynamics* (given $\Pi^* = (t_j, a_j)$) as follows:

Illustration of PIT dynamics



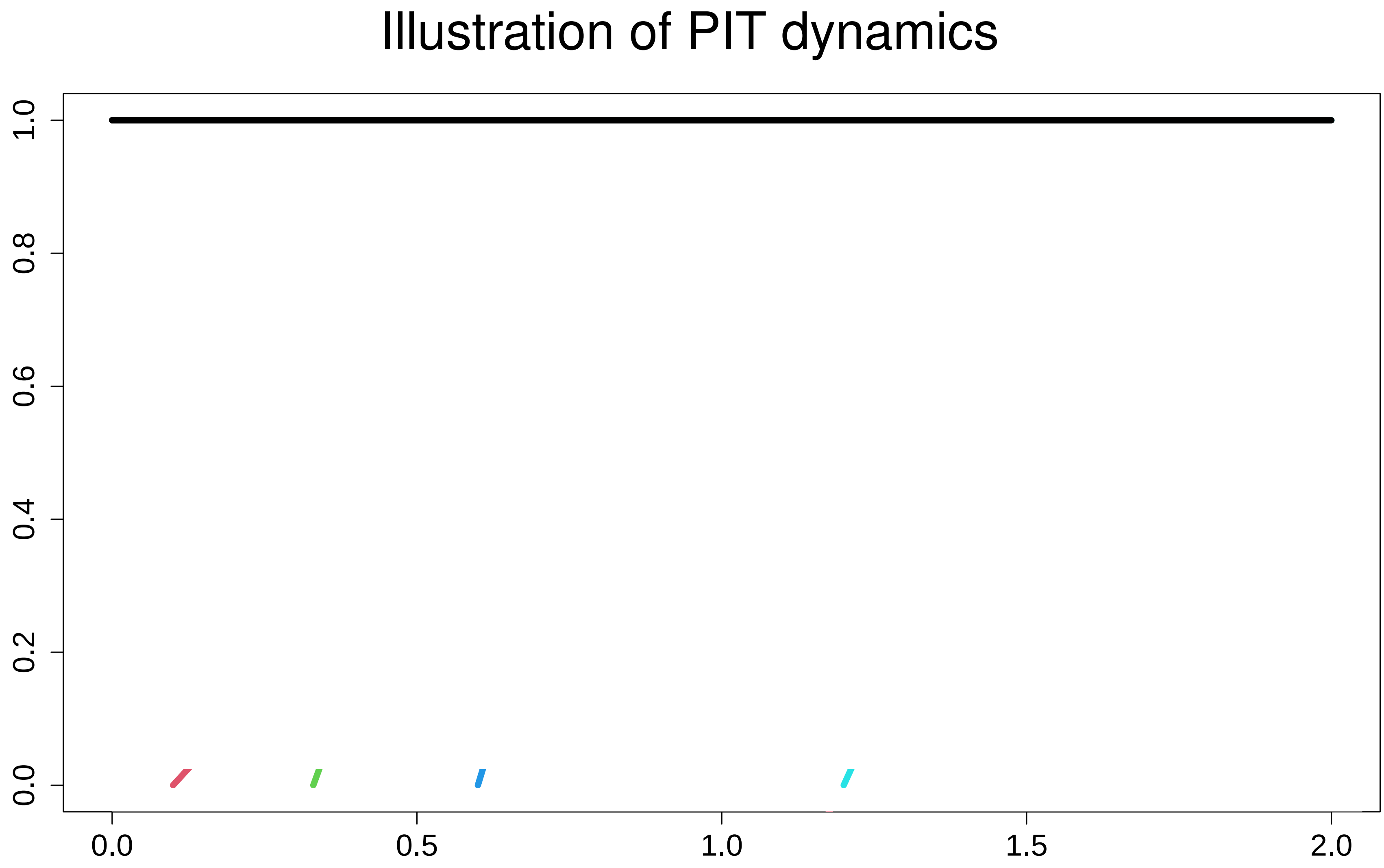


Illustration of PIT dynamics
1.0
0.8
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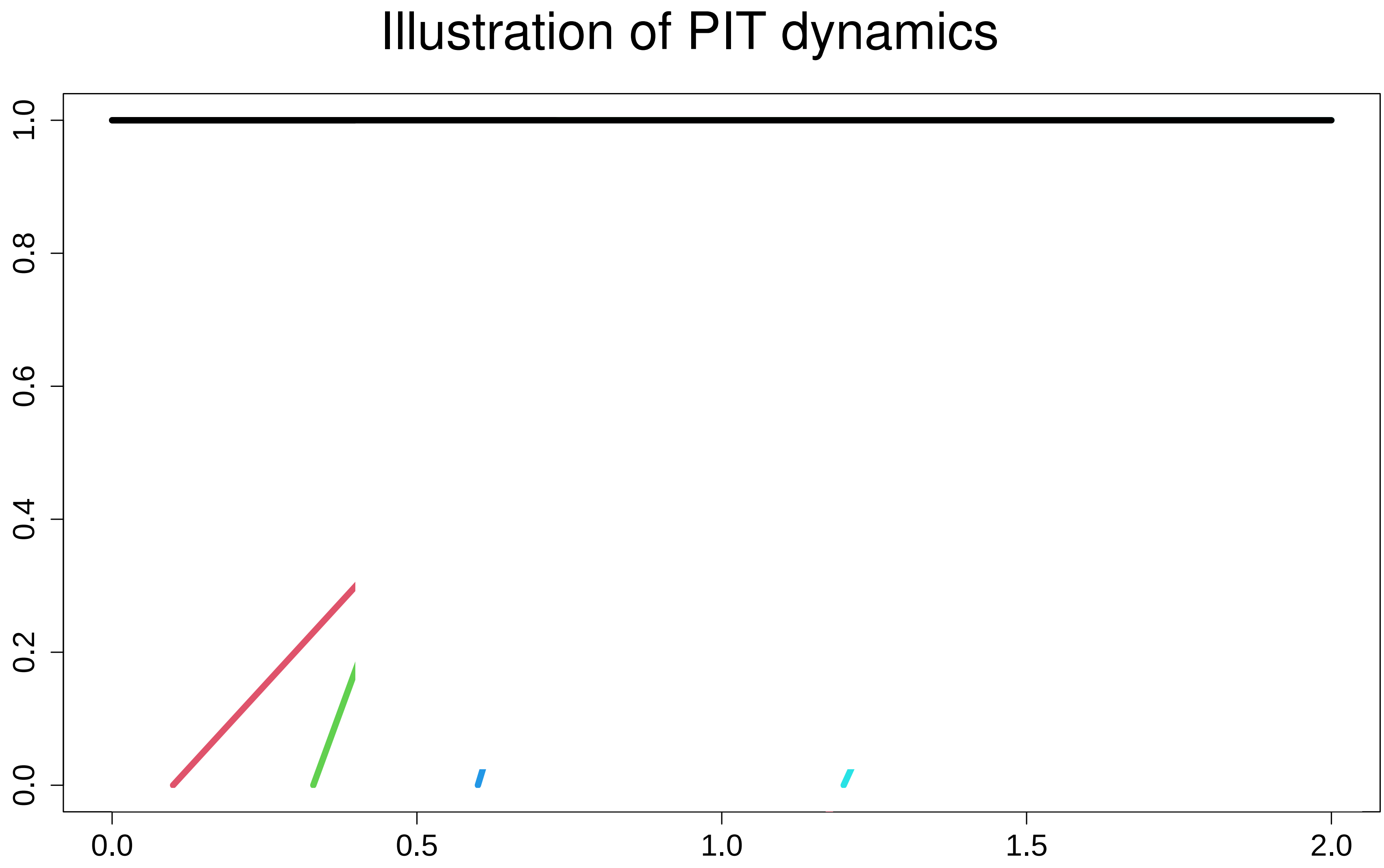
0.4
0.2
0.0
0.0
0.5
1.0
1.5
2.0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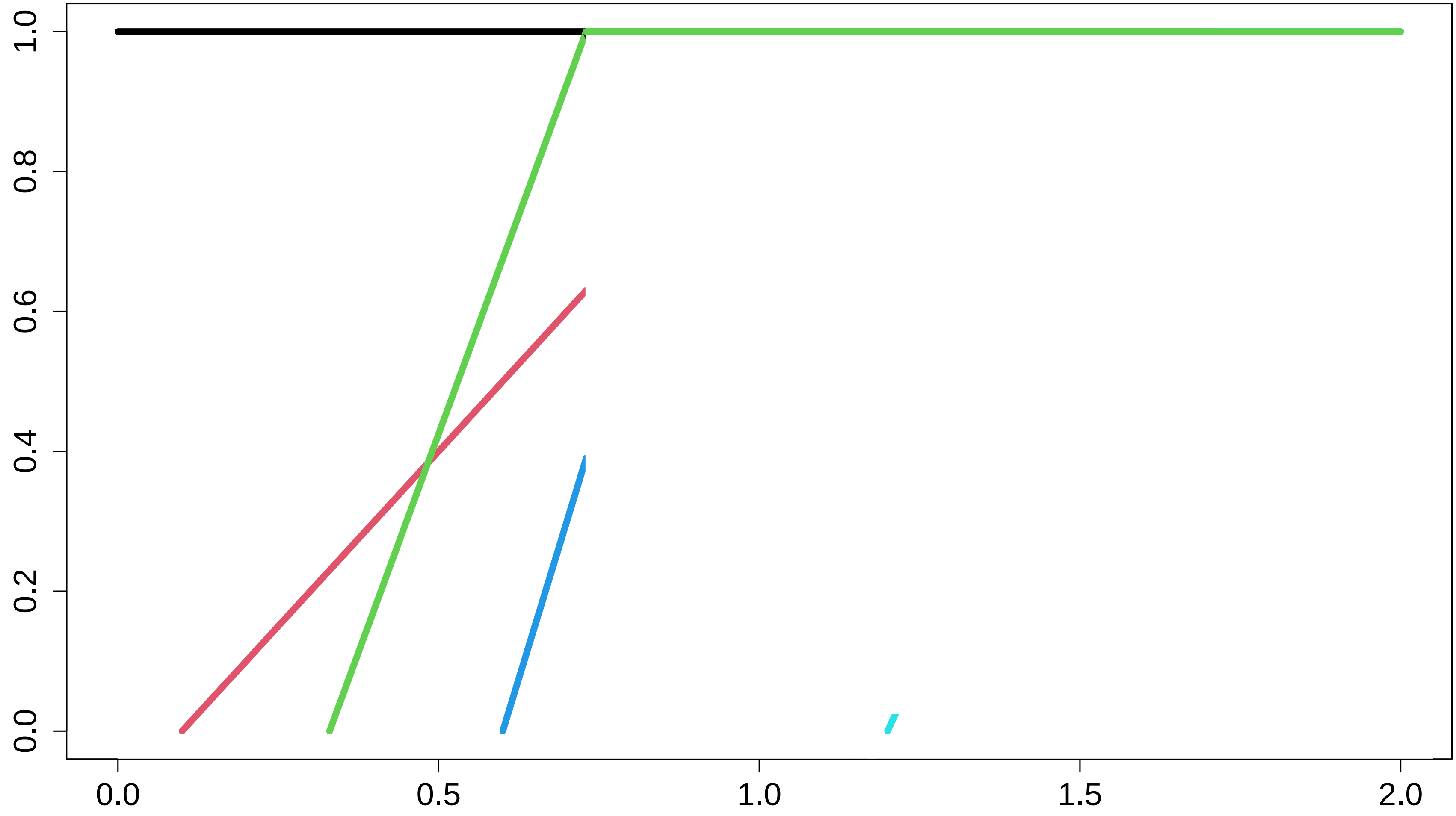

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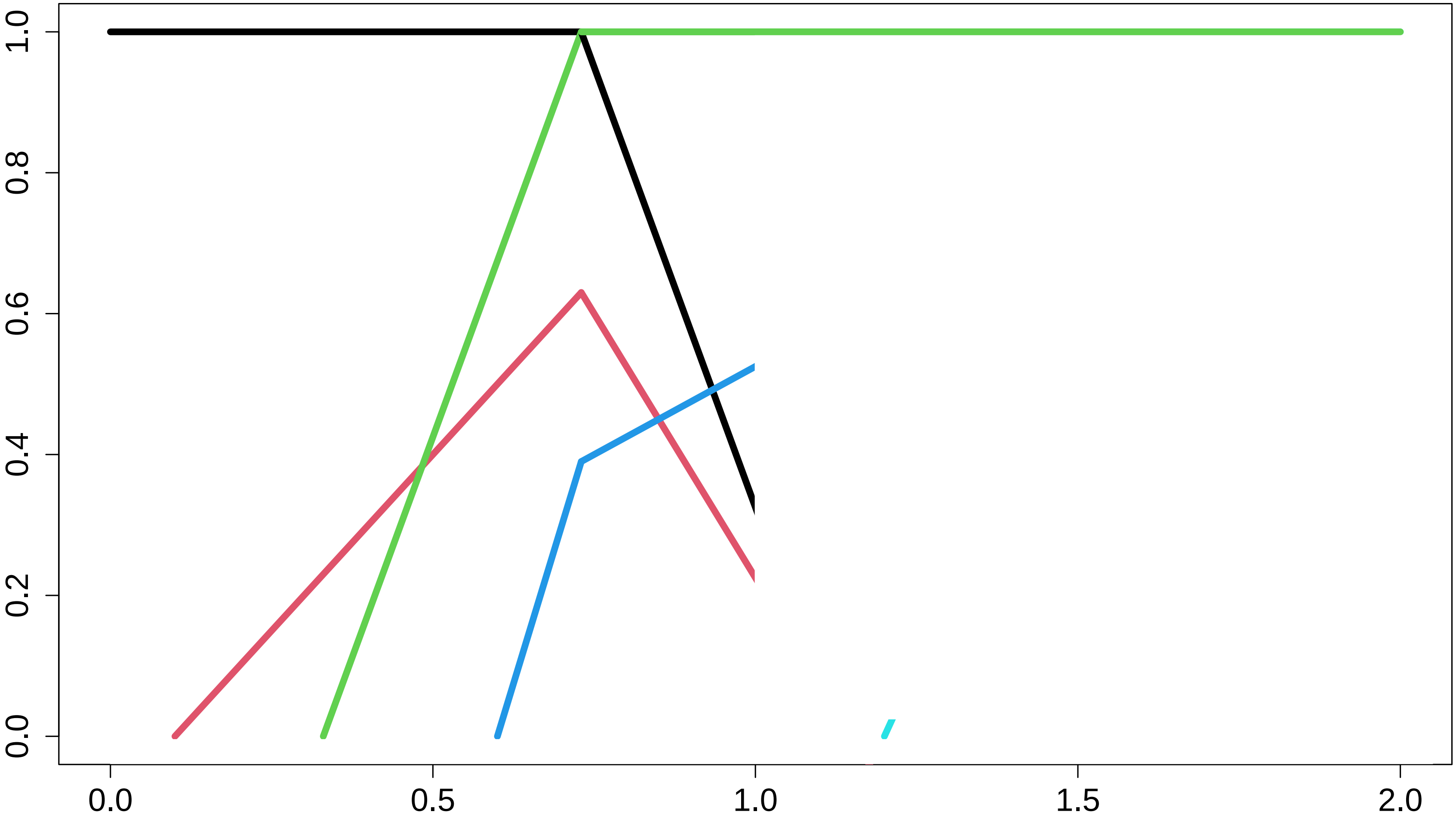

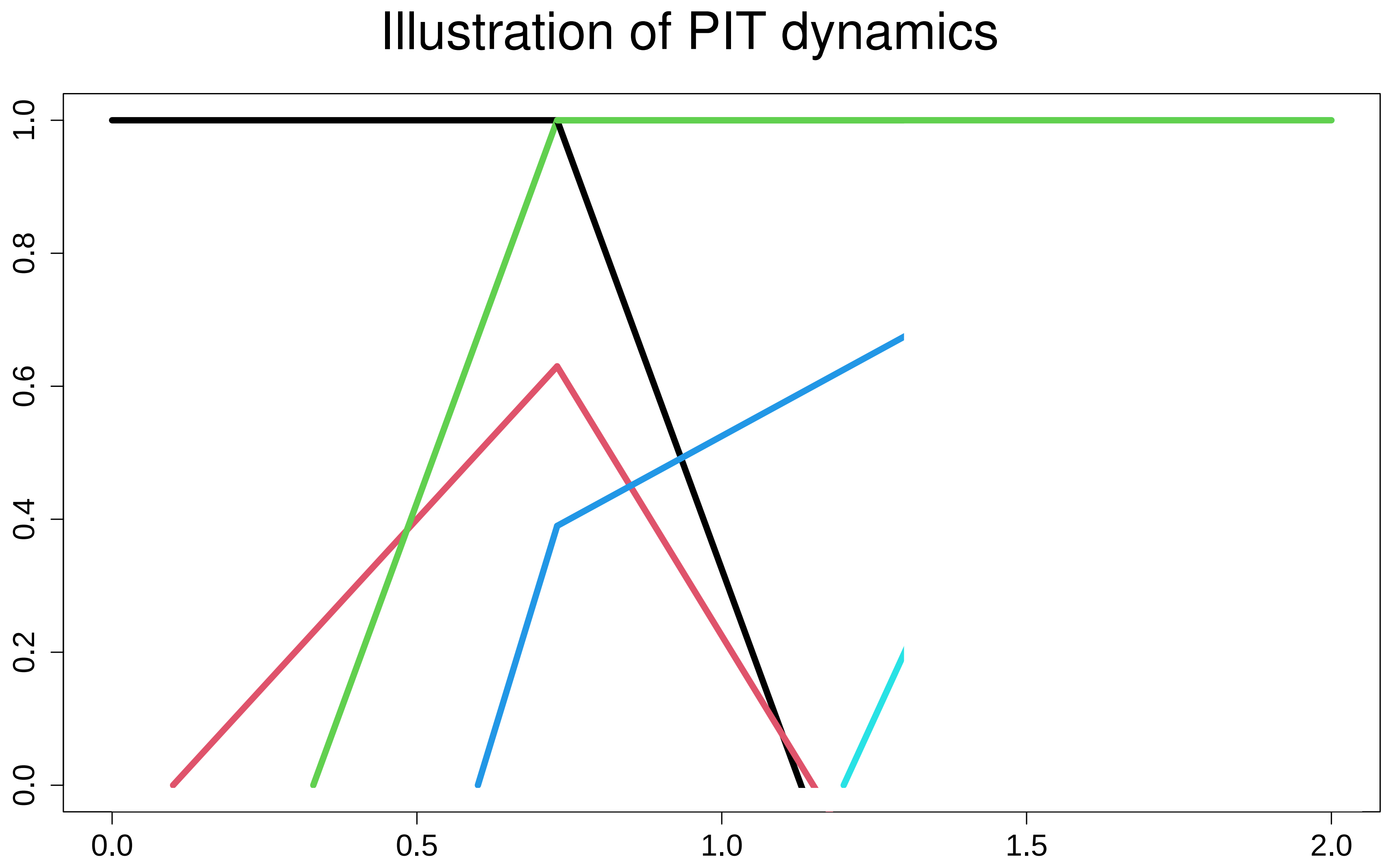
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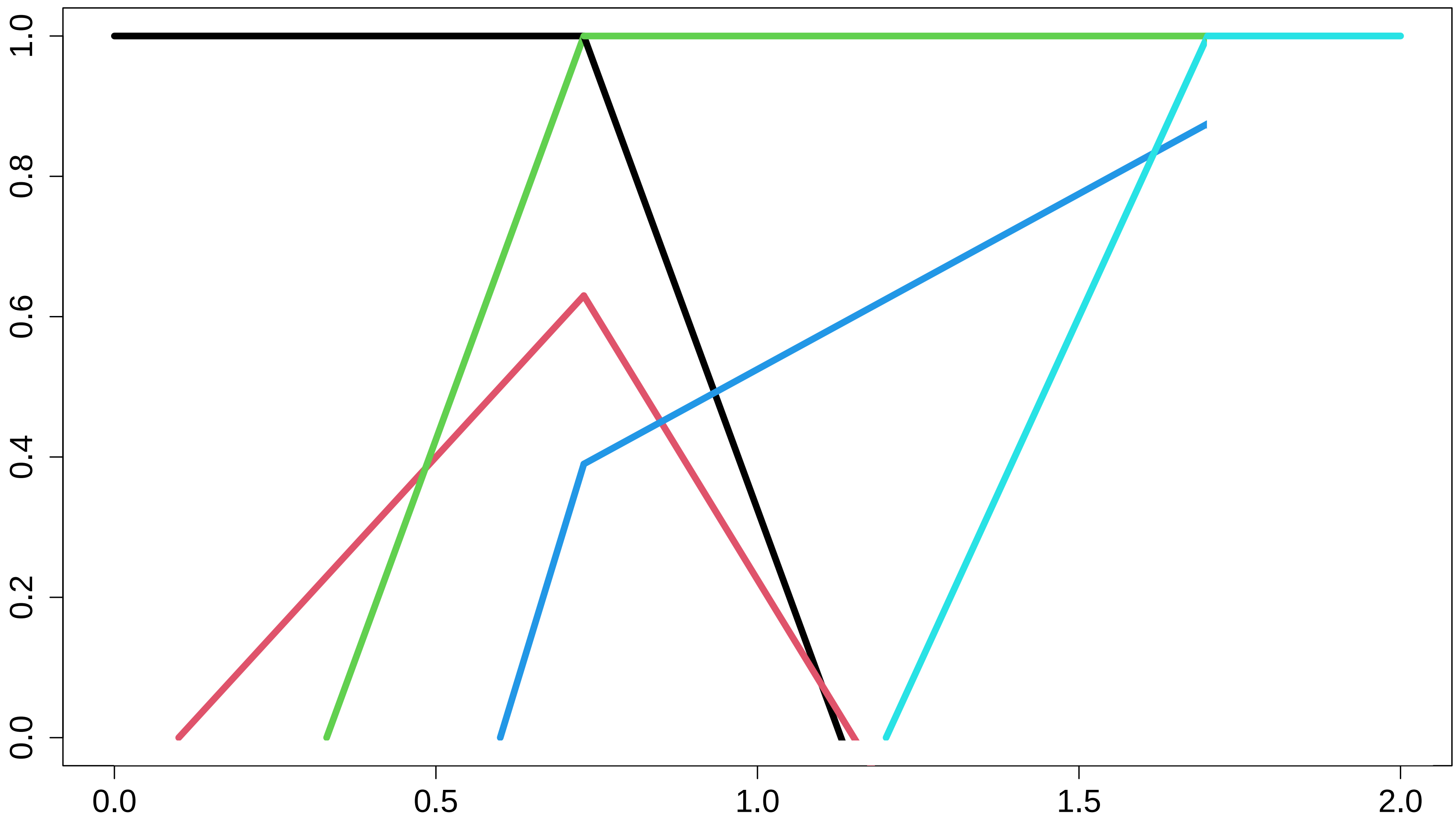

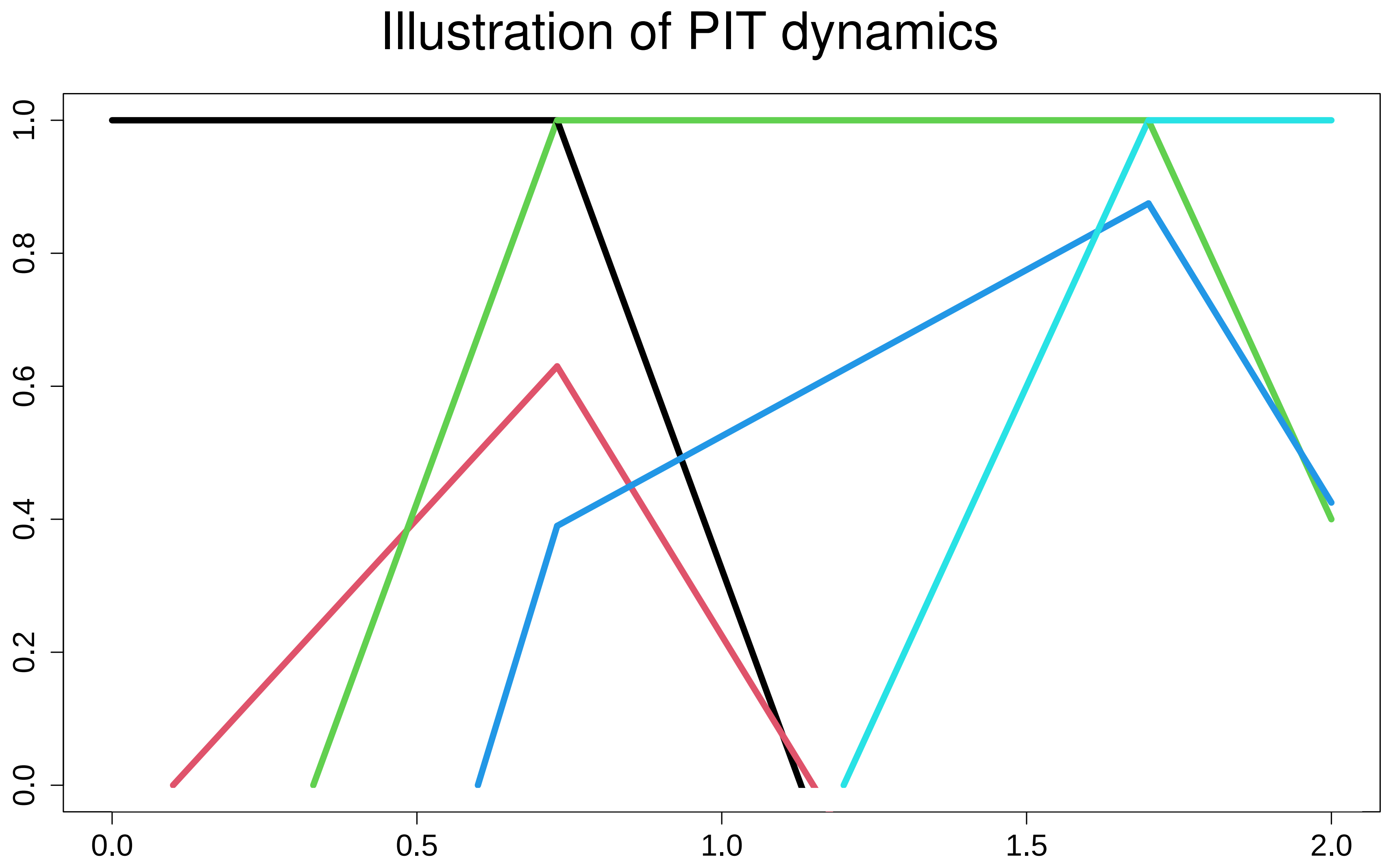

Illustration of PIT dynamics
0.0
0.2
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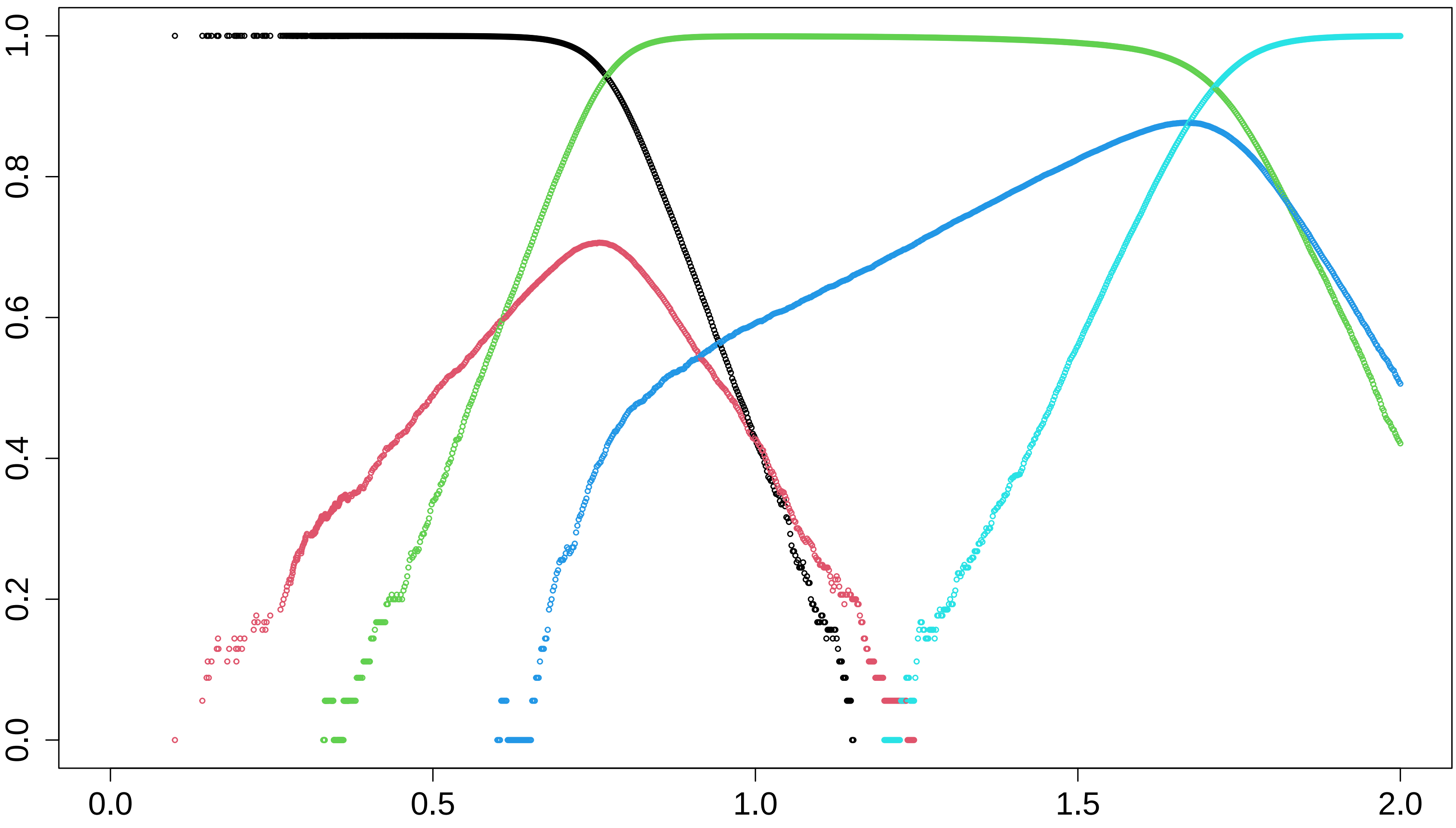
1.0
0.0
0.5
1.0
1.5
2.0

Comparison to simulation ($N = 250\,000$)



When randomized over the initial condition Π^* we speak of
the *Poissonian system of interacting trajectories*, or PIT(λ, γ).

The trajectories in the PIT correspond to
the contending CSP's in the limit as $N \to \infty$.

A trajectory H_j is called *resident* at time t if $H_j(t) = 1$.

The j-th trajectory in the PIT is born
from a resident parent, say the $p(j)$-th trajectory in the PIT,
and thus has fitness level

$$F_j := F_{p(j)} + A_j.$$

Iterating this back to $j = 0$ specifies (recursively)
the random sequence $(F_j)_{j\in\mathbb{N}_0}$.

In the N-th system, denote by F_j^N
the fitness level of the j-th contending CSP.
(This is well-defined via the ancestral lineages
in the graphical representation of the Moran system.)

Theorem 1 (Scaling of clonal interference, strong selection)

(HGSTW25 Thm 1)

c) For all $n \in \mathbb{N}$,

$$(T_j^N, F_j^N)_{1 \le j \le n} \xrightarrow{d} (T_j, F_j)_{1 \le j \le n}.$$

Theorem 2 (Speed of adaptation in the PIT)

(HGSTW25 Thm 2)

$$\lim_{j\to\infty} \frac{F_j}{T_j} =: \overline{v} \quad \text{exists almost surely,}$$

$\overline{v}$ is nonrandom, and $\overline{v} < \lambda \int a\gamma(da)$
if $\int a\gamma(da) < \infty$.

Problem 1.

a) Does $\lim_{j\to\infty} \frac{F_j^N}{T_j^N} =: \overline{v}^N$ exists almost surely for all N?

b) If so, is it true that $\overline{v}^N \to \overline{v}$ as $N \to \infty$?

In other words: Does the speed of adaptation in the PIT capture the asymptotics of the speed of adaptation in the finite systems as $N \to \infty$?

Moderate selection: $\frac{1}{N} \ll \varphi_N \ll 1$

Specifically: $-\log_N \varphi_N \to b \in [0,1)$

i.e. φ_N is logarithmically equivalent to N^{-b}.

Assume that

- initially all individuals have fitness level 0,
- a single mutation happens in the population (w.l.o.g. at time 0)
- this mutation has fitness increment a, and
- the mutant's offspring reaches the critical size $c_N = \frac{\log N}{\varphi_N}$.

Let $Y^N_{\mathsf{res}}(t)$ and $Y^N_{\mathsf{mut}}(t)$ be

the resident and the mutant CSP size at (ecological) time t,

and $H^N_i(t) := \log_N Y^N_i\left(t\,\frac{\log N}{\varphi_N}\right), \;\; i \in \{\mathsf{res}, \mathsf{mut}\}$,

the resident's and mutant's logarithmic CSP sizes

at the Gerrish-Lenski time t.

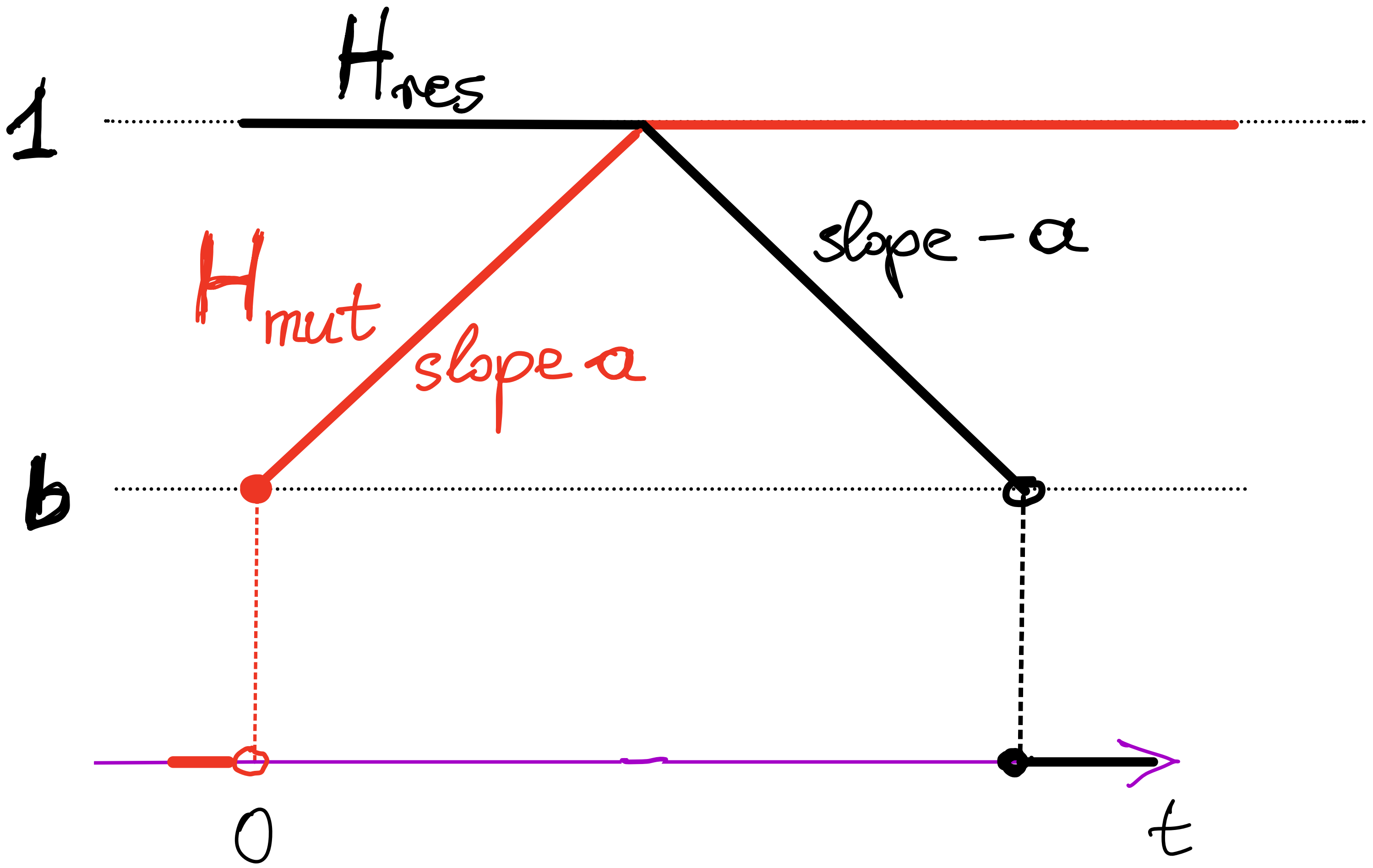
Theorem 3 (Logarithmic scaling of selective sweep curves)

(“House Theorem”, BHTW26)

Given the above described event,

the sequence $(H^N_{\mathsf{res}}, H^N_{\mathsf{mut}})$ converges in probability

to the “house” $(H_{\mathsf{res}}, H_{\mathsf{mut}})$ given by


H_{res}
1
H_{mut}
slope a
slope $-a$
b
0
t

The convergence in the House Theorem
refers to Skorokhod's M1-topology.
It is uniform in the roof,
and gives a control on the fluctuations on the way
up the western and down the eastern wall of the house.

Problem 2.

Work for a marriage of

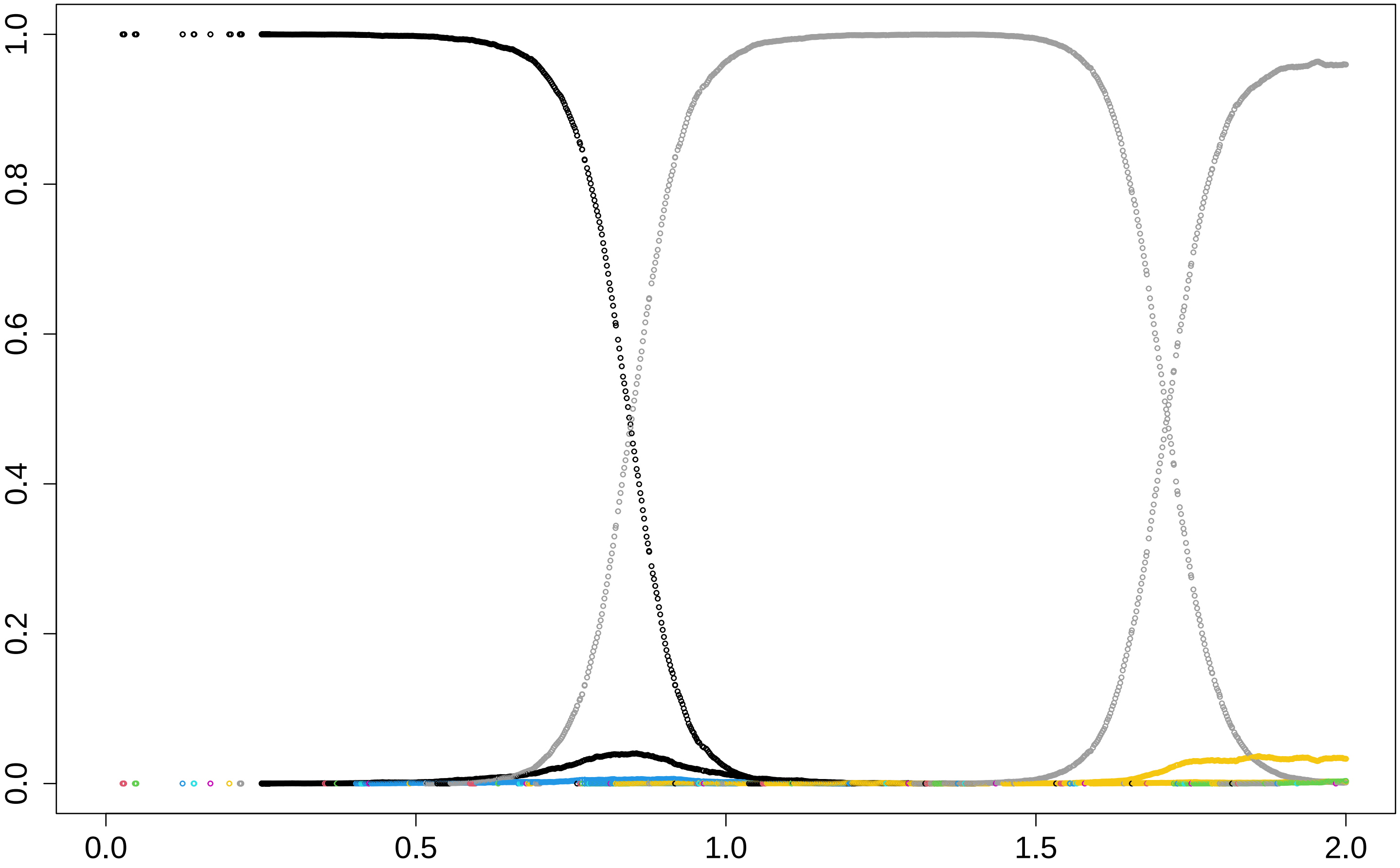
Theorem 1 (Convergence to the PIT under strong selection)

and Theorem 3 (Convergence to the House)

which (hopefully) gives a convergence to the b-PIT

under moderate ($\asymp N^{-b}$) selection.

Simulation, $N = 250\,000$, $A \sim \text{unif}\{1, 2\}$, $b = 0.3$



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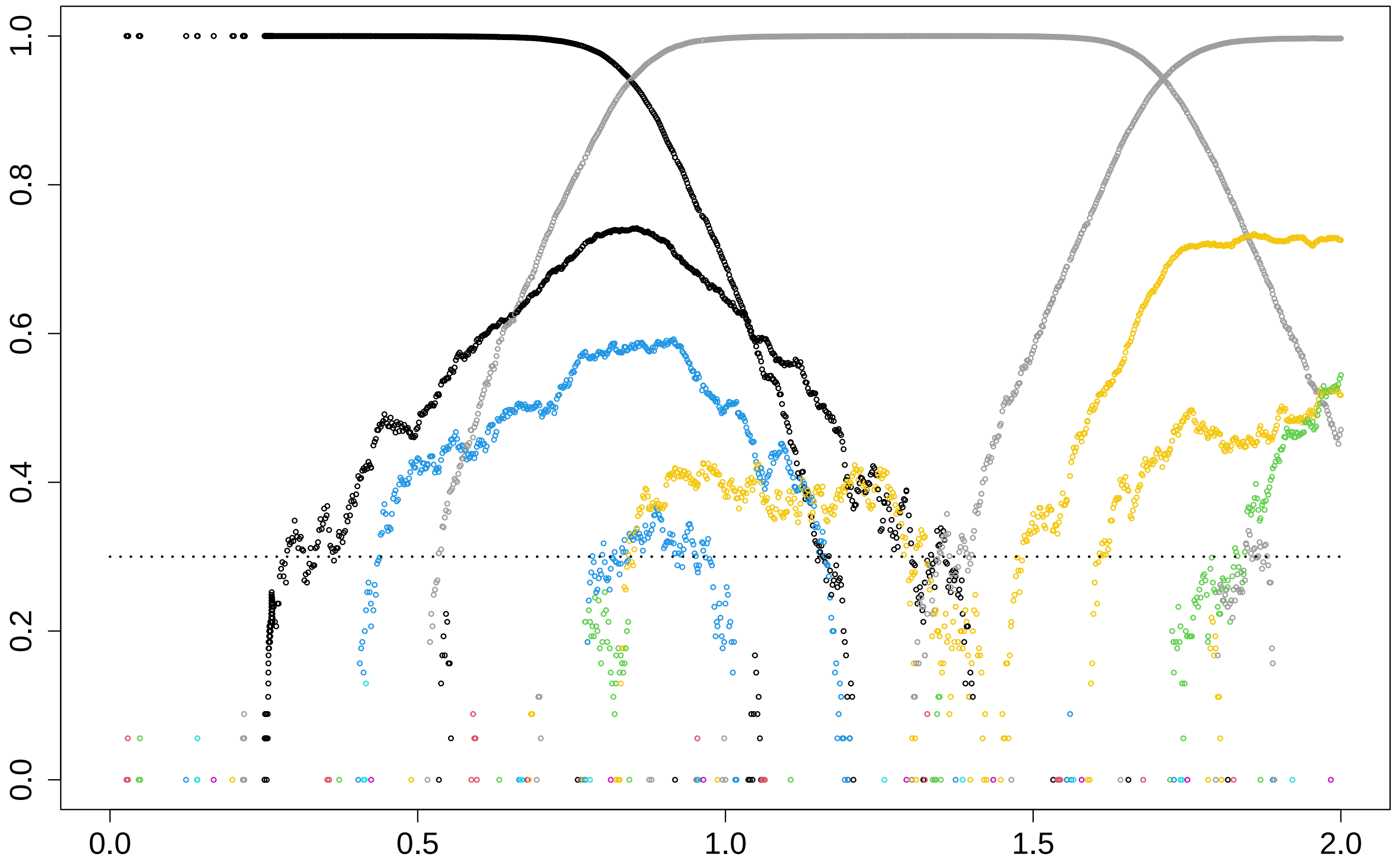

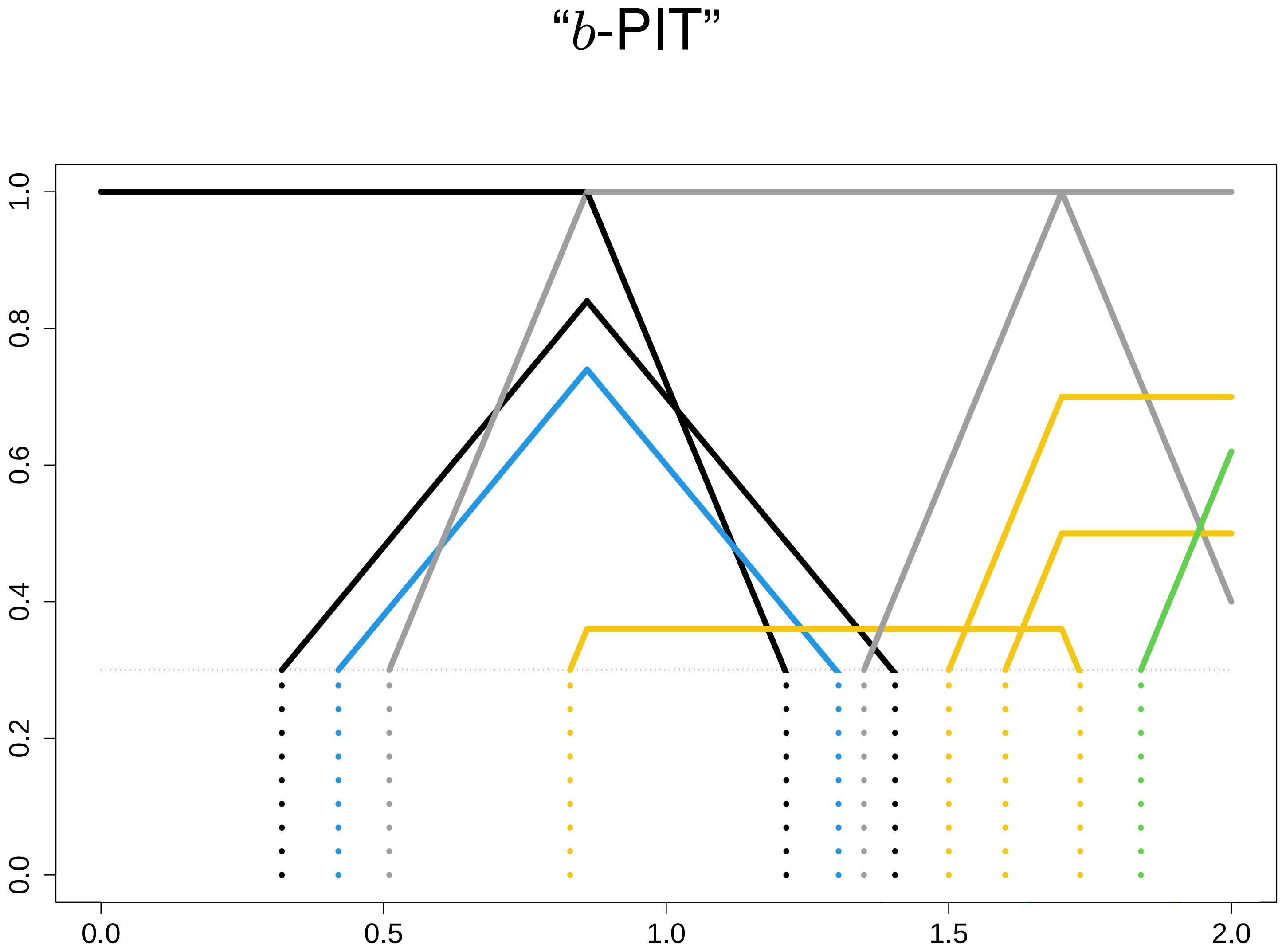
“b-PIT”
1.0
0.8
0.6
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0.2
0.0
0.0
0.5
1.0
1.5
2.0

Main references for Part I:

[HGSTW25]
Felix Hermann, Adrián González Casanova, Renato Soares dos Santos, András Tóbiás, and A.W.,
From clonal interference to Poissonian interacting trajectories,
Ann. Appl. Probab. 35 (2025), 2823-2865

[BHTW26]
Florin Boenkost, Felix Hermann, András Tóbiás and A.W.,
Logarithmic scaling of selective sweep curves: from tents to houses,
arxiv, May 2026

Part II

Deleterious mutations

$$A(i,t) \equiv -1$$

$$\kappa(i,t) := -f(i,t)$$

is the number of (deleterious) mutations carried

by (the ancestral lineage of) the individual (i,t)

(the individual’s *mutational load*)

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$$\kappa(i,t) := -f(i,t)$$

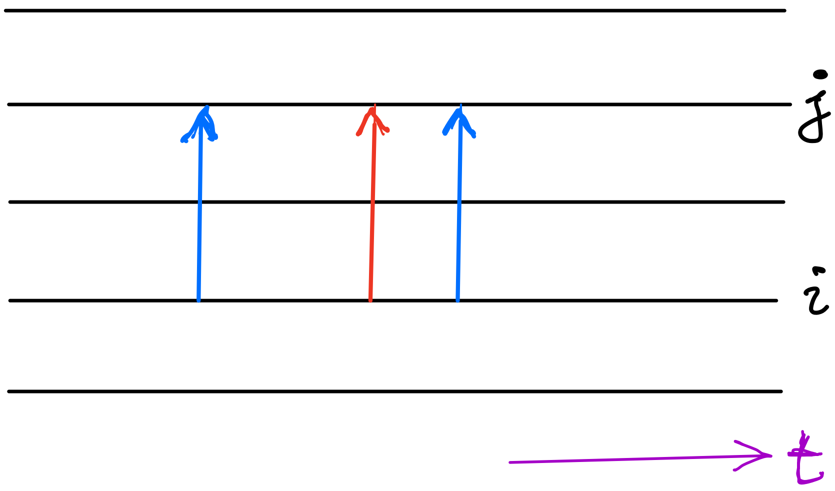
is the number of (deleterious) mutations carried by (the ancestral lineage of) the individual (i,t) (the individual's *mutational load*)

Assume $\kappa(i,0) \equiv 0$, and mutations come at rate $\mathfrak{m}_N$ per line.

Selective arrows are shot from i to j

at rate $s_N \frac{1}{N}\big(\kappa(j,t) - \kappa(i,t)\big)^+$.

Neutral arrows are shot from i to j at rate $\sim \frac{1}{2N}$.



For $\kappa \in \mathbb{N}_0$ and $t \geq 0$, let

$\mathfrak{N}_\kappa(t) :=$ the number of individuals at time t

with mutational load κ.

The net effect of selection

exerted upon an individual with mutational load κ is

to shoot a selective arrow a rate $s_N \sum\limits_{\kappa' > k} (\kappa' - \kappa)\frac{\mathfrak{N}_{\kappa'}}{N}$, and

to be hit by a selective arrow at rate $s_N \sum\limits_{\kappa' < \kappa} (\kappa - \kappa')\frac{\mathfrak{N}_{\kappa'}}{N}$

$$K^*(t) := \min\{\kappa(i,t) \mid i = 1, \ldots, N\},$$
$$Y_k(t) := \mathfrak{N}_{K^*(t)+k}(t).$$

Y_0, the size of the currently fittest class,

then performs a non-autonomous birth-and-death process

whose downward/upward jump rates from state n are

$$\delta_n := n\left(\tfrac{1}{2}\left(1 - \tfrac{n}{N}\right) + m_N\right)$$
$$\beta_n := n\left(\tfrac{1}{2}\left(1 - \tfrac{n}{N}\right) + s_N M\right)$$

with $M := \sum_{\ell > 0} \ell \, \frac{Y_\ell}{N}$

the first moment of the empirical frequency profile $(\frac{Y_k}{N})$

The net drift experienced by Y_k is (for $k > 0$):

$$(s(M-k)-m))Y_k + mY_{k-1}$$

With $\theta := m/s$, this net drift vanishes in $(\overline{Y}_k)$ if

$$(k+\theta-M)\overline{Y}_k = \theta\overline{Y}_{k-1}$$

Ansatz: $M = \theta$

$$k\overline{Y}_k = \theta\overline{Y}_{k-1}, \qquad k \geq 1,$$

is solved by the *Poisson profile* $(\frac{\overline{Y}_k}{N}) = (\overline{\pi}_k)$

with $\overline{\pi}_k^\theta := e^{-\theta}\frac{\theta^k}{k!}$

Etheridge, Pfaffelhuber , W. (2009): For $\pi(0) = (\pi_k(0))_{k \in \mathbb{N}_0}$

being arbitrary probability weights on $\mathbb{N}_0$ with $\pi(0) > 0$,

the solution $\pi(t)$ of the deterministic dynamical system

$$d\pi_k(t) = \Big(s\Big(\sum_{j=0}^{\infty}(j-k)\pi_j(t)\Big)\pi_k(t) + m(\pi_{k-1}(t) - \pi_k(t))\Big)dt$$

converges as $t \to \infty$ to the Poisson weights $(\overline{\pi}_k^{(\theta)})$.

A diffusion approximation to $(\frac{Y_k}{N})$ is given by the solution $(X_k(t))$

of a system of SDE's with drift of X_k as above,

plus a Fleming-Viot noise $\sum_{\ell \neq k} \sqrt{\frac{1}{N} X_k X_\ell}\, dW_{k\ell}$

For $X(0) := \overline{\pi}^{(\theta)}$, and Ns large, Heinzel, Pfaffelhuber, W. (arxiv, 2026), provide an explicit approximation (with controlled error) for functionals of $X(t)$.

Tournament selection:

For $\kappa \in \mathbb{N}_0$ and $t \geq 0$, let

$\mathfrak{N}_\kappa(t) :=$ the number of individuals at time t

with mutational load κ.

The net effect of selection

exerted upon an individual with mutational load κ is

to shoot a selective arrow a rate $s_N \sum_{\kappa' > \kappa} (\kappa' - \kappa) \frac{\mathfrak{N}_{\kappa'}}{N}$, and

to be hit by a selective arrow at rate $s_N \sum_{\kappa' < \kappa} (\kappa - \kappa') \frac{\mathfrak{N}_{\kappa'}}{N}$

$$K^*(t) := \min\{\kappa(i,t) \mid i = 1,\dots,N\},$$
$$Y_k(t) := \mathfrak{N}_{K^*(t)+k}(t).$$

Y_0, the size of the currently fittest class,

then performs a birth-and-death process

whose downward/upward jump rates from state n are

$$\delta_n := n\left(\frac{1}{2}\left(1 - \frac{n}{N}\right) + m_N\right)$$
$$\beta_n := n\left(\frac{1}{2}\left(1 - \frac{n}{N}\right) + s_N\widetilde{M}\right)$$

with $\widetilde{M} := \sum_{\ell>0} \ell\,\frac{Y_\ell}{N}$

the first moment of the empirical frequency profile $(\frac{Y_k}{N})$

$$K^*(t) := \min\{\kappa(i,t) \mid i = 1, \dots, N\},$$
$$Y_k(t) := \mathfrak{N}_{K^*(t)+k}(t).$$

Y_0, the size of the currently fittest class,

then performs a birth-and-death process

whose downward/upward jump rates from state n are

$$\delta_n := n\left(\tfrac{1}{2}\left(1 - \tfrac{n}{N}\right) + m_N\right)$$
$$\beta_n := n\left(\tfrac{1}{2}\left(1 - \tfrac{n}{N}\right) + s_N \widetilde{M}\right)$$

with $\widetilde{M} := \sum_{\ell>0} \ell \frac{Y_\ell}{N} = \frac{N-Y_0}{N} = 1 - \frac{Y_0}{N}$

the complement of the fittest class' frequency

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$$Y_k(t) := \mathfrak{N}_{K^*(t)+k}(t).$$

Y_0, the size of the currently fittest class,

then performs an autonomous birth-and-death process

whose downward/upward jump rates from state n are

$$\delta_n := n\left(\tfrac{1}{2}\left(1-\tfrac{n}{N}\right)+m_N\right)$$

$$\beta_n := n\left(\tfrac{1}{2}\left(1-\tfrac{n}{N}\right)+s_N(1-\tfrac{n}{N})\right)$$

Two important quantities:

$\mathfrak{a}_N := N\left(1 - \frac{m_N}{s_N}\right)$ .... the center of attraction

$\mathfrak{c}_N := \frac{1}{s_N - m_N}$ .... the critical size for quick extinction

Y_0 exhibits a metastable behaviour if (and only if)

$$(*) \quad \mathfrak{c}_N \ll \mathfrak{a}_N \quad \text{as} \quad N \to \infty.$$

This is particularly interesting if

- $\frac{1}{N} \ll m_N < s_N \ll 1$, and
- the mutation-selection ratio $\rho_N := \frac{m_N}{s_N}$ is close to 1.

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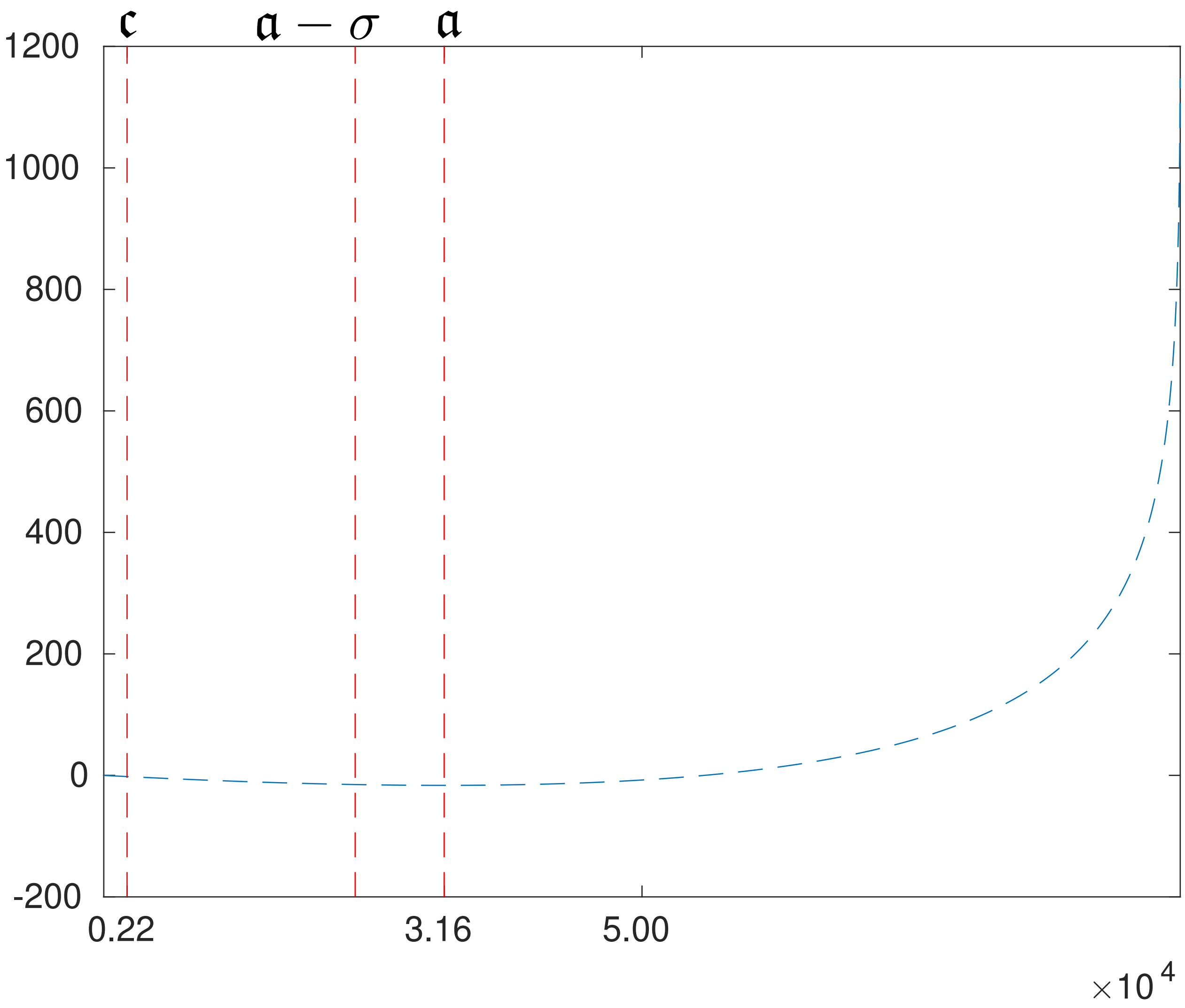
For example:

$$N = 10^5, \;\; m_N = N^{-0.6} = 0.001, \;\; \rho_N = 1 - N^{-0.1} = 0.68$$


$\mathfrak{c}$
$\mathfrak{a} - \sigma$
$\mathfrak{a}$
1200
1000
800
600
400
200
0
-200
0.22
3.16
5.00
$\times 10^4$

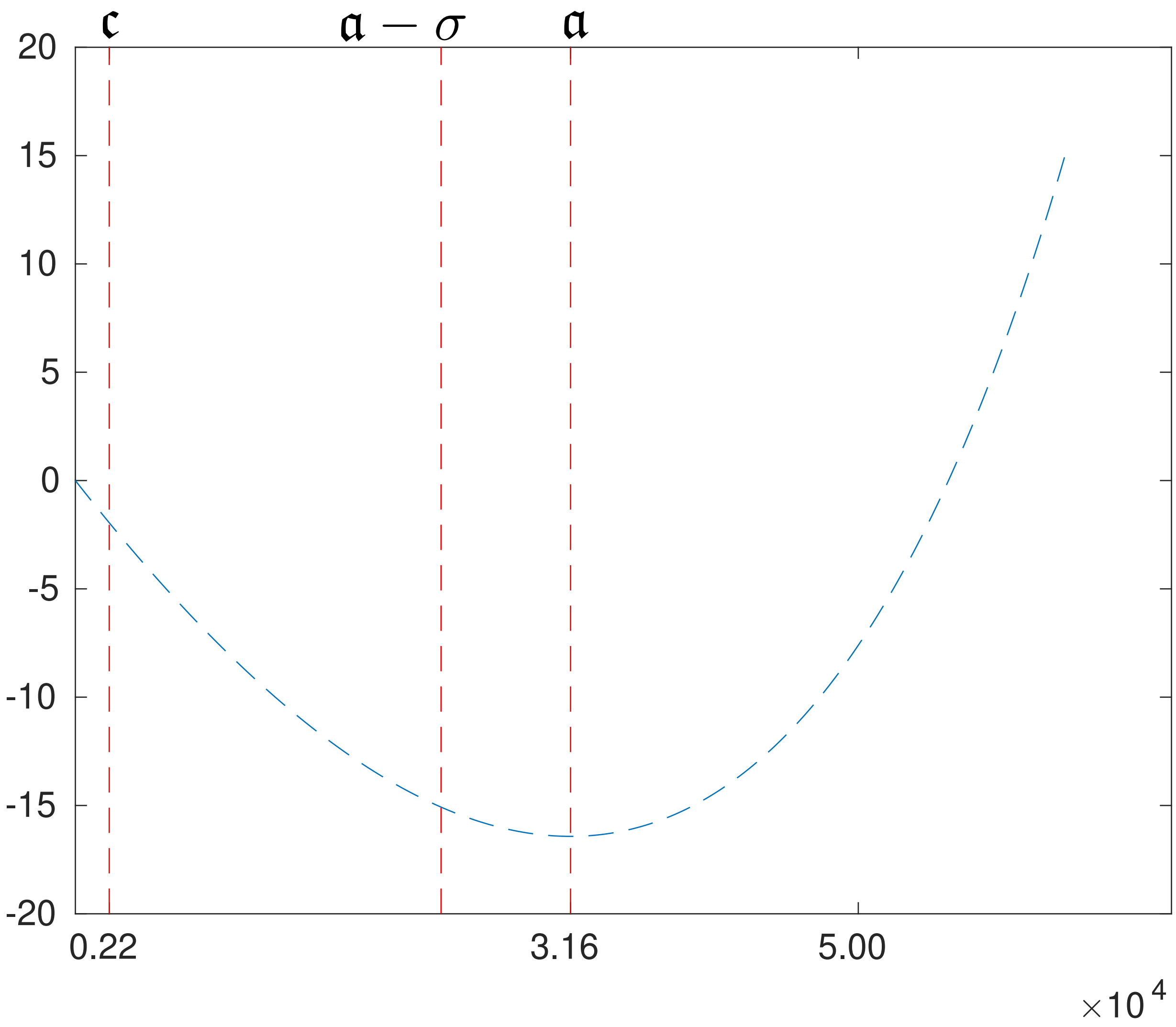
$$U(n) := \log \prod_{\ell=1}^{n} \frac{\delta_\ell}{\beta_\ell} = \sum_{\ell=1}^{n} \log \frac{\delta_\ell}{\beta_\ell}$$

$R = e^U$ is *harmonic* for Y_0

Zooming in at the center of attraction:

$$U^N(\mathfrak{a}_N + \sigma_N h) - U^N(\mathfrak{a}_N) \sim h^2 \quad \text{for all } h \in \mathbb{R},$$

where $\sigma_N := \sqrt{\rho_N \mathfrak{a}_N \mathfrak{c}_N}$



$\mathfrak{c}$
$\mathfrak{a} - \sigma$
$\mathfrak{a}$
20
15
10
5
0
-5
-10
-15
-20
0.22
3.16
5.00
$\times 10^4$

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where $\sigma_N := \sqrt{\rho_N \mathfrak{a}_N \mathfrak{c}_N}$

Proposition. With Y_0^N started in $\mathfrak{a}^N$,

$$\mathcal{H}_N := \left(\frac{1}{\sigma_N}\left(Y_0(\mathfrak{c}_N t) - \mathfrak{a}_N\right)\right)_{t \geq 0}$$

converges, as $N \to \infty$ in distribution

to a standard Ornstein-Uhlenbeck process $\mathcal{H}$:

$$d\mathcal{H} = -\mathcal{H}\, dt + d\mathcal{W}.$$

The depth of the potential turns out to be

$$-U_N(\mathfrak{a}_N) = 2\frac{\mathfrak{a}_N}{\mathfrak{c}_N}\eta(m_N, \rho_N) + o(1)$$

with $\eta(m, \rho)$ of order 1 (and explicitly given through a series)

Theorem (ISW25) The expected time between clicks of the tournament ratchet is asymptotically equivalent to

$$\boxed{\frac{1}{\rho_N a_N} \cdot \sqrt{\pi}\sigma_N \cdot \mathfrak{c}_N \exp\left(2\frac{\mathfrak{a}_N}{\mathfrak{c}_N}\eta(m_N, \rho_N)\right).}$$

This can be understood as

the expected holing time in states near $\mathfrak{a}$,

the duration of an excursion from (and back to) $\mathfrak{a}$,

the expected number of such excursions.

Problem 3

(maybe not for this week, but for the next months and beyond)

Does the ratchet with fitness proportionate selection show,
in a suitable parameter regime, a metastable behavior
that can be analysed in a way
similar as with the tournament ratchet?

Main references for Part II:

[IGSW24]
Jan Lukas Igelbrink, Adrián González Casanova, Charline Smadi, and A.W., ***Muller's ratchet in a near-critical regime: tournament versus fitness proportional selection***, Theor. Popul. Biol. 158, 121-138 (2024)

[ISW25]
Jan Lukas Igelbrink, Charline Smadi and A. Wakolbinger,
The tournament ratchet's clicktime process, and metastability in a Moran model, arxiv December 2025

[HPW26]
C. Heinzel, P. Pfaffelhuber and A. Wakolbinger,
A small noise approximation for Muller's Ratchet, arxiv June 2026.