Mutation-Selection Dynamics and Error Threshold in an Evolutionary Model for Turing Machines

joint work with G. Feverati, LAPTH, Annecy, France

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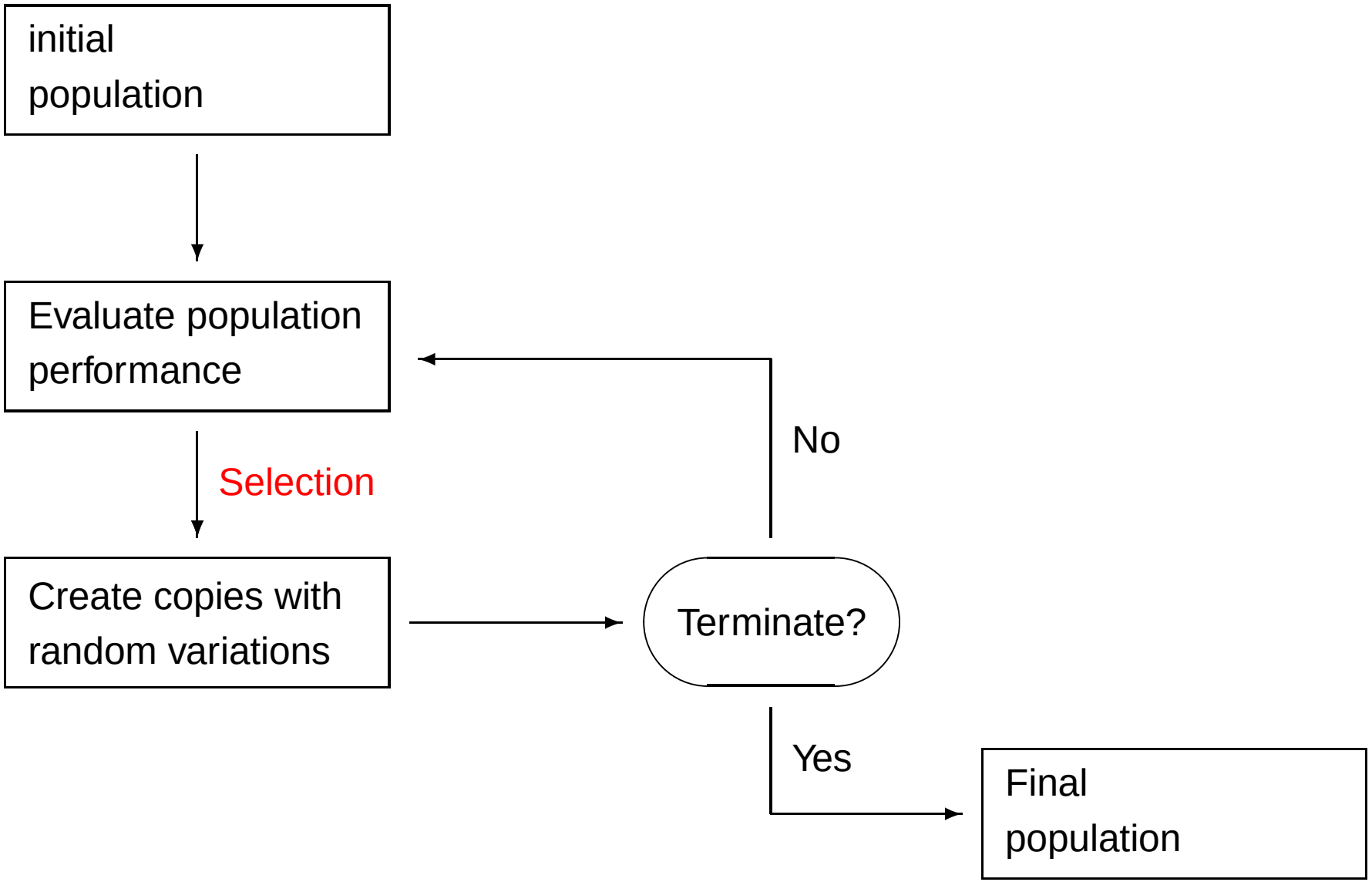
Selection: the average number of copies (with mutation) of an algorithm at the next generation is an increasing function of its performance.

Performance $\begin{cases} \text{Evaluation of the output vs a goal output} \\ \text{Evaluation of the procedure (i.e. time consumption)} \end{cases}$

Flowchart


initial
population
Evaluate population
performance
Selection
Create copies with
random variations
Terminate?
No
Yes
Final
population

Why?

- Maynard-Smith: “...we badly need a comparative biology. So far, we have been able to study only one evolving system and we cannot wait for interstellar flight to provide us with a second. If we want to discover generalizations about evolving systems, we will have to look at artificial ones.”

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- Long term evolutionary experiments (even if in a strongly simplified setting):
  - Very fast (50000 generations for 300 TMs last half a day/processor in our model)
  - Unexpensive
  - repeatable
  - Complete control on the experimental apparatus (full reductionistic approach)

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Organisms$=$Algorithms

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We think that coupling computer simulations with population genetic models is a good strategy to understand the causes underlying the observed phenomena and determine their eventual biological relevance.

Our model

- We use Turing machines (TMs) to encode the algorithms
- Mutation procedure: point mutation and code size increase
- Performance evaluation: comparison between the output tape and a goal tape
- Selection procedure:asexual reproduction determined by tournament selection of size 2 without replacement

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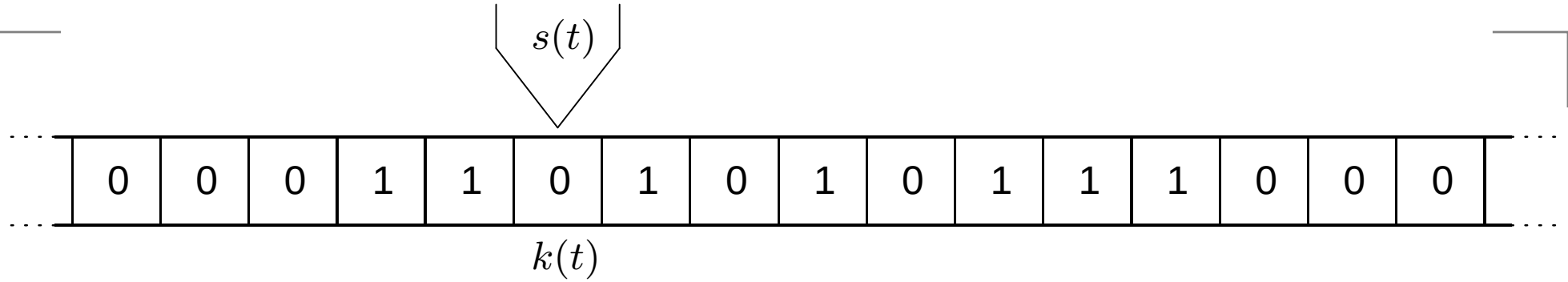

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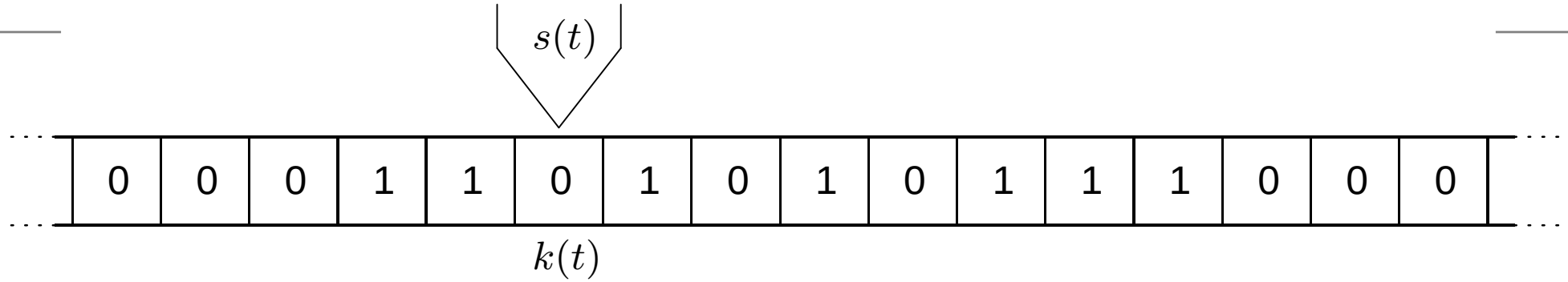

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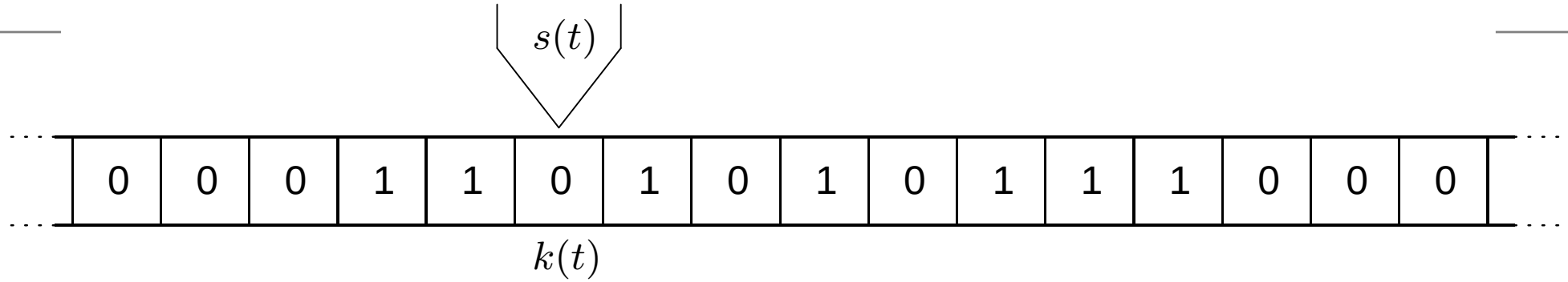

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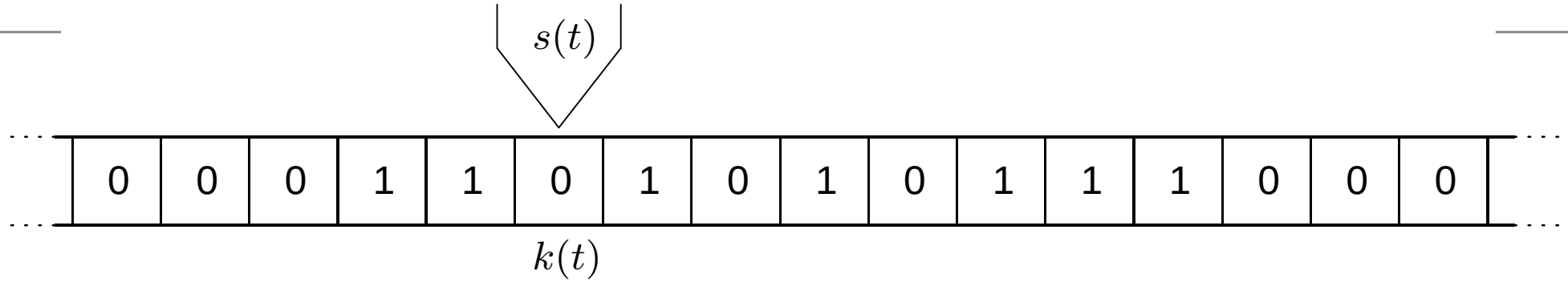

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The internal state $s(t)$, on the basis of the symbol stored inside the $k(t)$ cell, specifies three actions for the head to perform:

- write: writes a new symbol on the $k(t)$ cell, ($T(t) \mapsto T(t+1)$)
- move: moves right or left ($k(t) \mapsto k(t+1)$),
- call: changes its internal state ($s(t) \mapsto s(t+1)$)

The call to the special state H causes the machine to halt. The tape $T(0)$ is the input tape and the tape $T(\bar{t})$ after the halt state has been called is the output tape.

Example

The following machine performs the sum of two numbers, in the example: $3 + 2$.

read \ state	$\mathbf{1}$	$\mathbf{2}$	$\mathbf{3}$
0	1 – Right – $\mathbf{2}$	0 – Left – $\mathbf{3}$	_ – _ – _
1	1 – Right – $\mathbf{1}$	1 – Right – $\mathbf{2}$	0 – _ – **Halt**

1

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Initial population

We begin with a population of 300 1-state TM of the following form:

	1
0	0-R/L-Halt
1	1-R/L-Halt

and let them evolve for 50000 generations (termination condition).

Mutation procedure

Mutation is composed of two steps:

- State increasing: with a probability p_i the TM passes from N to N+1 states by the addition of the further state:

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- 0 or 1 for the “write” entries;
- Right, Left for the “move” entries;
- The Halt state or an integer from $\mathbf{1}$ to the number of states $\mathbf{N}$ of the machine for the “call” entries.

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- The two TM are eliminated from the old population and placed in the new population. And the process restart until exhaustion of the old population

Example

Goal tape: prime numbers

	1	2	3	4	5	6	7	8
0	1-R-4	1-R-5	1-R-6	1-R-3	1-R-7	0-R-2	1-L-7	0-R-8
1	1-R-3	1-L-2	0-L-3	0-L-5	0-L-4	1-L-1	0-L-H	0-R-2

1

0 0 0 0 0 0 0 0 . . .

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Blue=Coding Triplets, Total states$= 8$, Coding triplets$= 8$, Non-coding triplets$= 8$.

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$$
\begin{aligned}
p_{\mathsf{i}} \quad \in \quad & \{9.26 \cdot 10^{-5}\,; 1.66 \cdot 10^{-4}\,; 3.00 \cdot 10^{-4}\,; 5.40 \cdot 10^{-4}\,; 9.72 \cdot 10^{-4}\,; 1.75 \cdot 10^{-3}\,; \\
& 3.14 \cdot 10^{-3}\,; 5.68 \cdot 10^{-3}\,; 1.02 \cdot 10^{-2}\,; 1.85 \cdot 10^{-2}\,; 3.33 \cdot 10^{-2}; 6.00 \cdot 10^{-2}\,; \\
& 1.08 \cdot 10^{-1}\,; 1.95 \cdot 10^{-1}\,; 3.51 \cdot 10^{-1}\,; 6.33 \cdot 10^{-1}\,; 1.14\} \ . \\
p_{\mathsf{m}} \quad \in \quad & \{4.91 \cdot 10^{-5}\,; 8.10 \cdot 10^{-5}\,; 1.34 \cdot 10^{-4}\,; 2.21 \cdot 10^{-4}\,; 3.64 \cdot 10^{-4}\,; 6.01 \cdot 10^{-4}\,; \\
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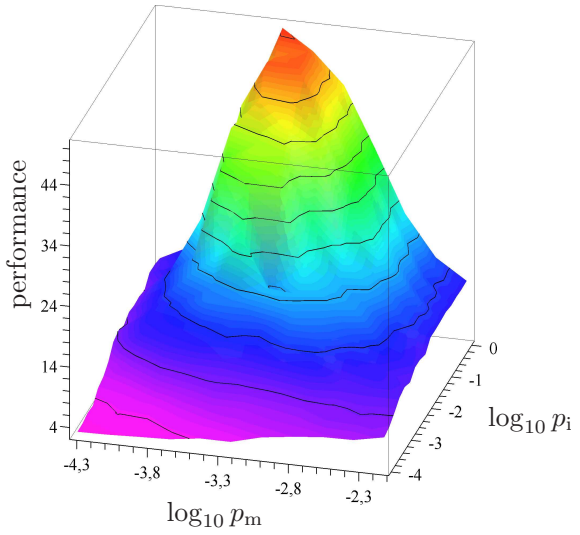
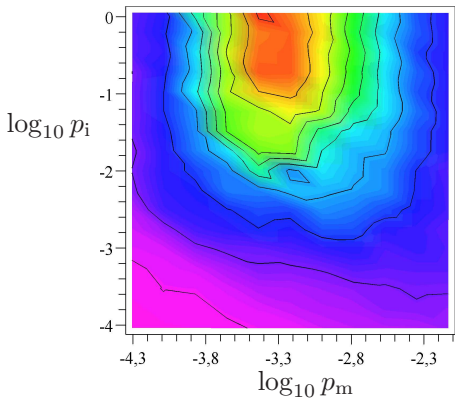
- For any pair p_m, p_i we performed 20 simulations of 50000 generations varying the seed of the random number generator

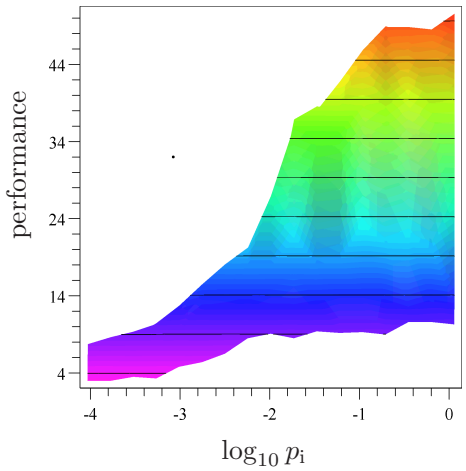
Results



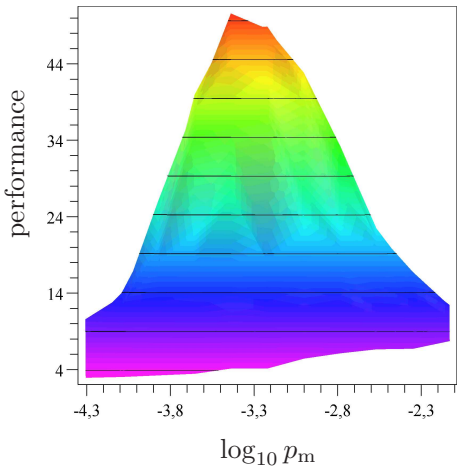
(a)



(b)



(c)

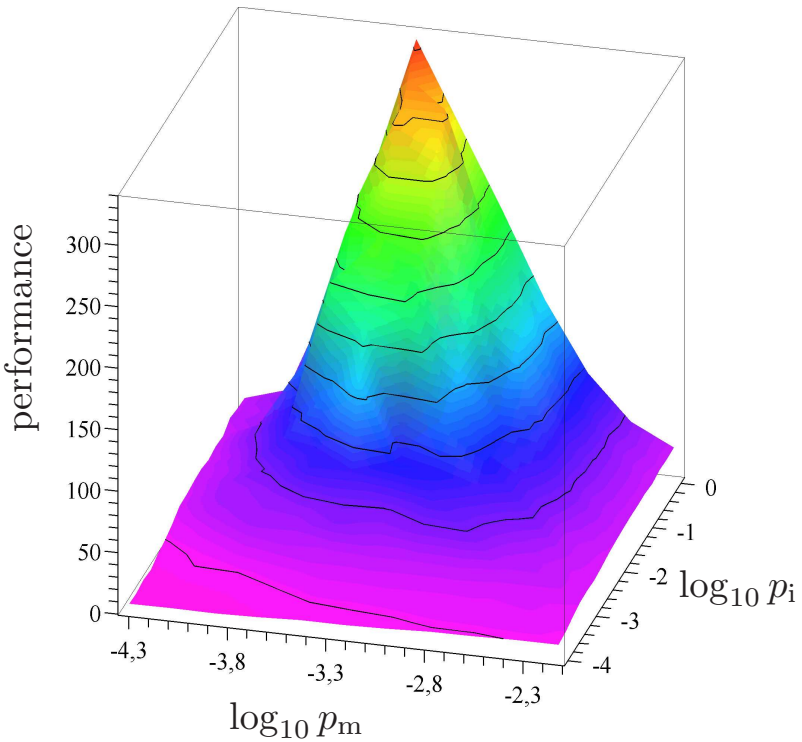


(d)

Best performance value in the population at the last generation.

The best performance is averaged on the twenty different seeds and plotted as a function of the states-increase rate p_{i} and of the mutation rate p_{m}

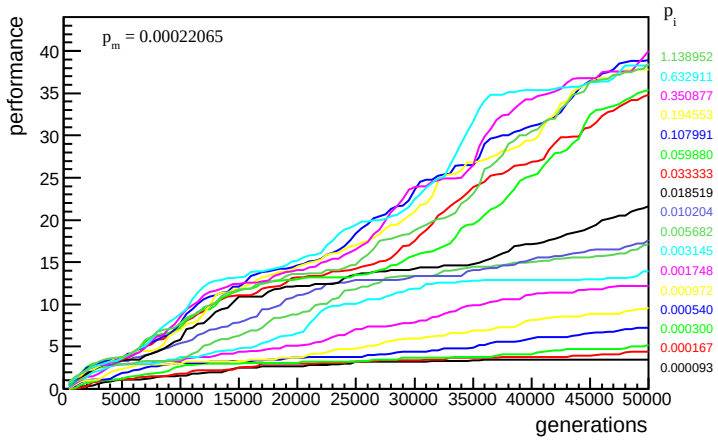
Coding Triplets



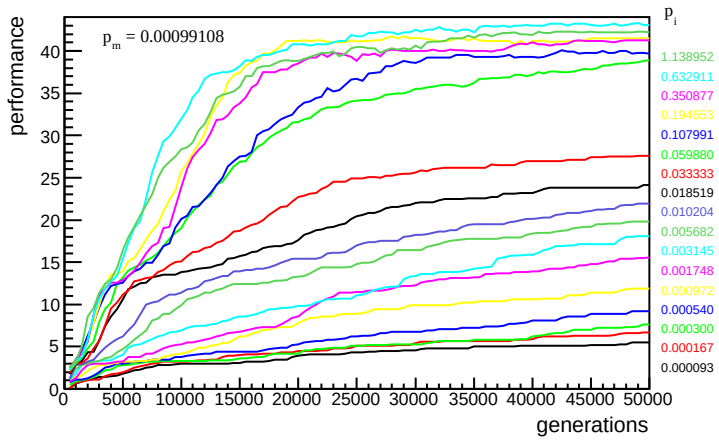
Number of coding triplets in the population at the last generation averaged on the best machines and on the seeds.

There is a positive correlation between the performance and the number of coding triplets ($r = 0.95$).

Accumulation of coding triplets happens in a gradual way, so that it is slower for low values of p_{m}; high values of p_{m} limit the number of coding triplets.



(a)



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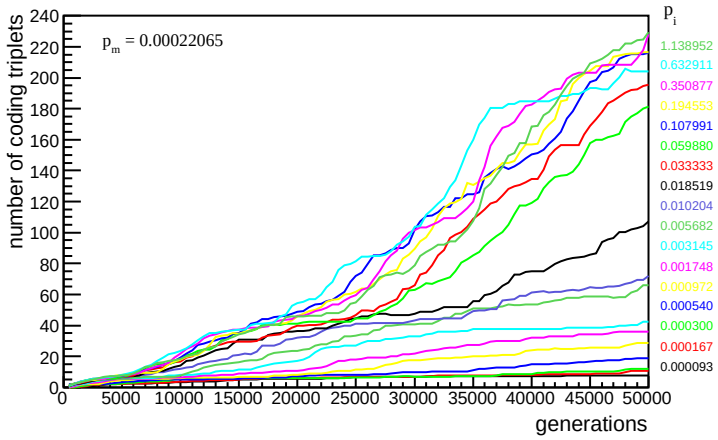

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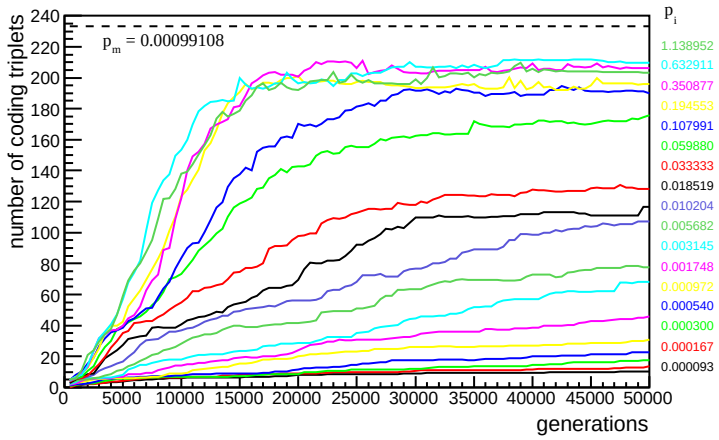

(d)

Data along the generations. Data are sampled every 100 generations and averaged on the seeds.

TMs increase their performance by increasing their number of coding triplets.

Error threshold

Given a mutation probability, what is the maximum amount of coding triplets?

How near do the TMs come to this maximum amount?

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The selection mechanism used in the Eigen model is different from our, so that we need a different mathematical model.

Deterministic model

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With this mechanism, the probabilities of producing $2, 1$ or 0 offsprings for an individual belonging to the $i-$th performance class are, respectively

$$
\begin{aligned}
P_2 &= f\frac{\sum_{j<i} n_j}{N-1} \\
P_1 &= \frac{1}{N-1}\left((1-f)\sum_{j<i} n_j + n_i - 1 + (1-f)\sum_{j>i} n_j\right) \\
P_0 &= \frac{f}{N-1}\sum_{j>i} n_j
\end{aligned}
$$

It follows that the expected number n_i' of individuals in the ith performance class after selection is given by:

$$n_i' = n_i \left[1 + \frac{f}{N-1} \left(\sum_{j<i} n_j - \sum_{j>i} n_j \right) \right]$$

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Let Q_i be the probability of neutral or no mutation and g_{ij} the probability to pass from class j to class i because of mutation ($g_{ii} = 0$), then the number of individuals inside the $i-$th class after the mutation step will be:

$$n_i'' = n_i' Q_i + \sum_{j=1}^{M} (1 - Q_j) n_j' g_{ij}$$

Let s be the best occupied performance class at a given time $n_s > 0$, $n_i = 0,\ i > s$ and let us suppose that $g_{ij} \ll 1$ if $i > j$, then

$$n_s'' \simeq n_s Q_s \left[1 + \frac{f}{N-1} \left(\sum_{j<s} n_j \right) \right] = n_s Q_s \left[1 + \frac{f}{N-1} \left(N - n_s \right) \right]$$

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Imposing the existence of a stable equilibrium larger than zero $n_s'' = n_s > 0$, we get

$$Q_s > \frac{1}{1 + f\frac{N}{N-1}} = \frac{1}{1+f} + O\left(\frac{1}{N}\right) \doteq \bar{Q}$$

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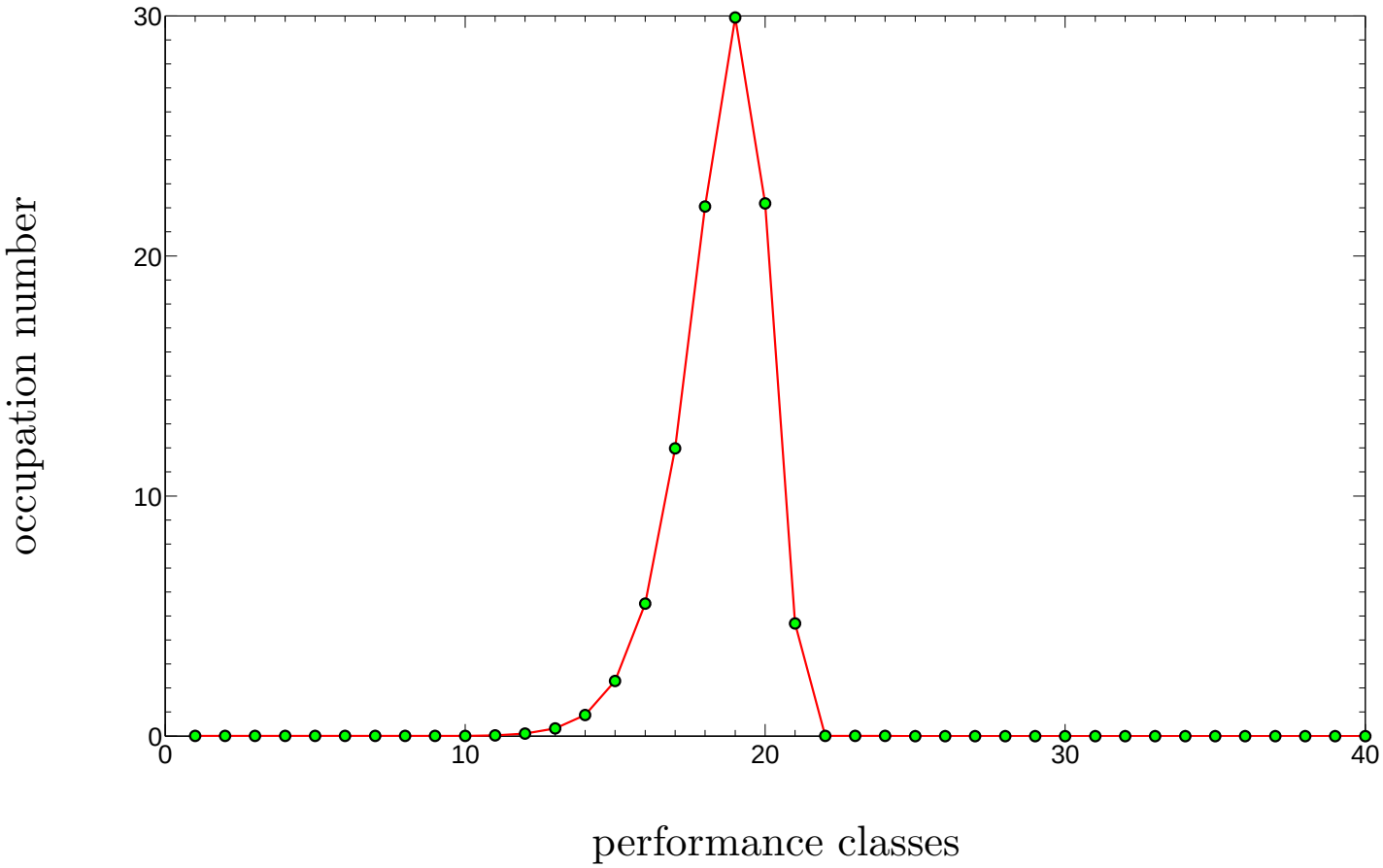
For example, if $M = 40$, $N = 100$, $f = 10^{-3}$,

$$g_{ij} = (1 - 10^{-6})(\delta_{i,1}\delta_{j,1} + \delta_{j,i+1}) + 10^{-6}(\delta_{i,40}\delta_{j,40} + \delta_{j,i-1}),$$

$$Q_i = (1 - 10^{-5})^{\sqrt{i^3}}, \qquad i = 1, \ldots, 40,$$

the last occupied class will be the $21-$st.

Numerical simulation



It can be shown that under these mutation-selection mechanisms, after an infinite number of generations, the population reaches the error threshold or the maximum performance class.

If we assume that almost all mutations inside a coding triplet are deleterious, then the fidelity rate of a TM with N_c coding triplets is:

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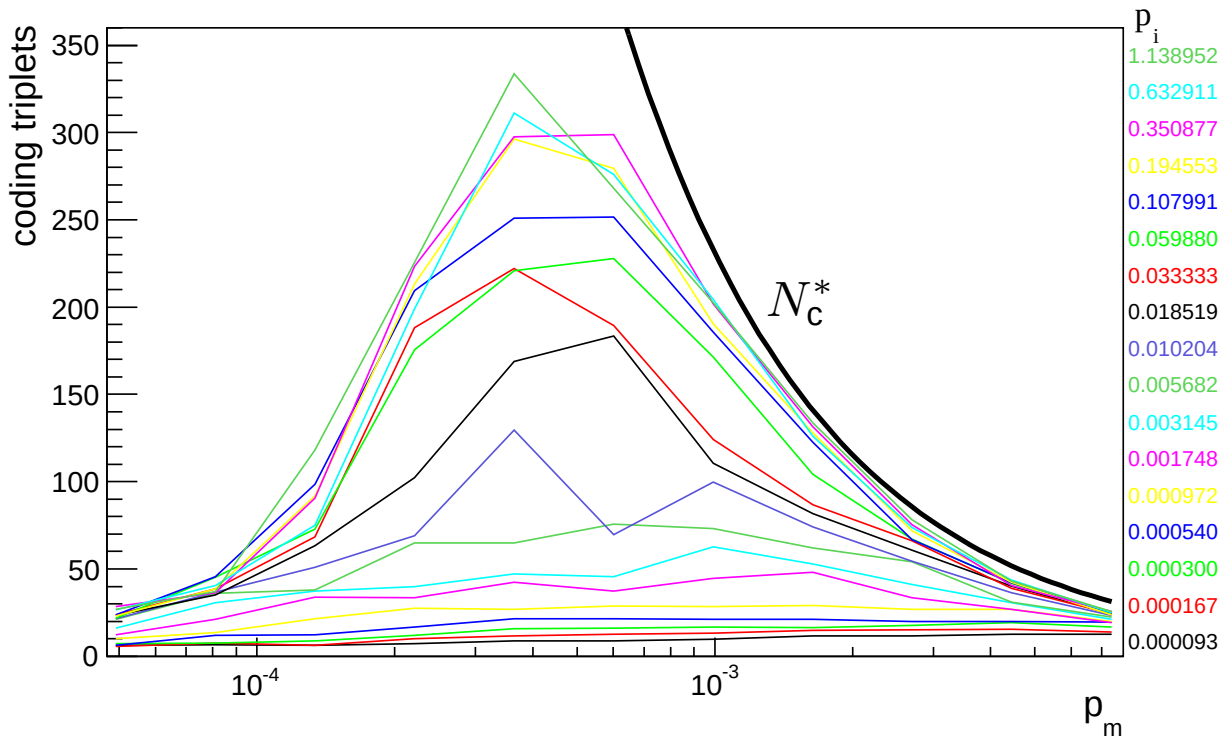
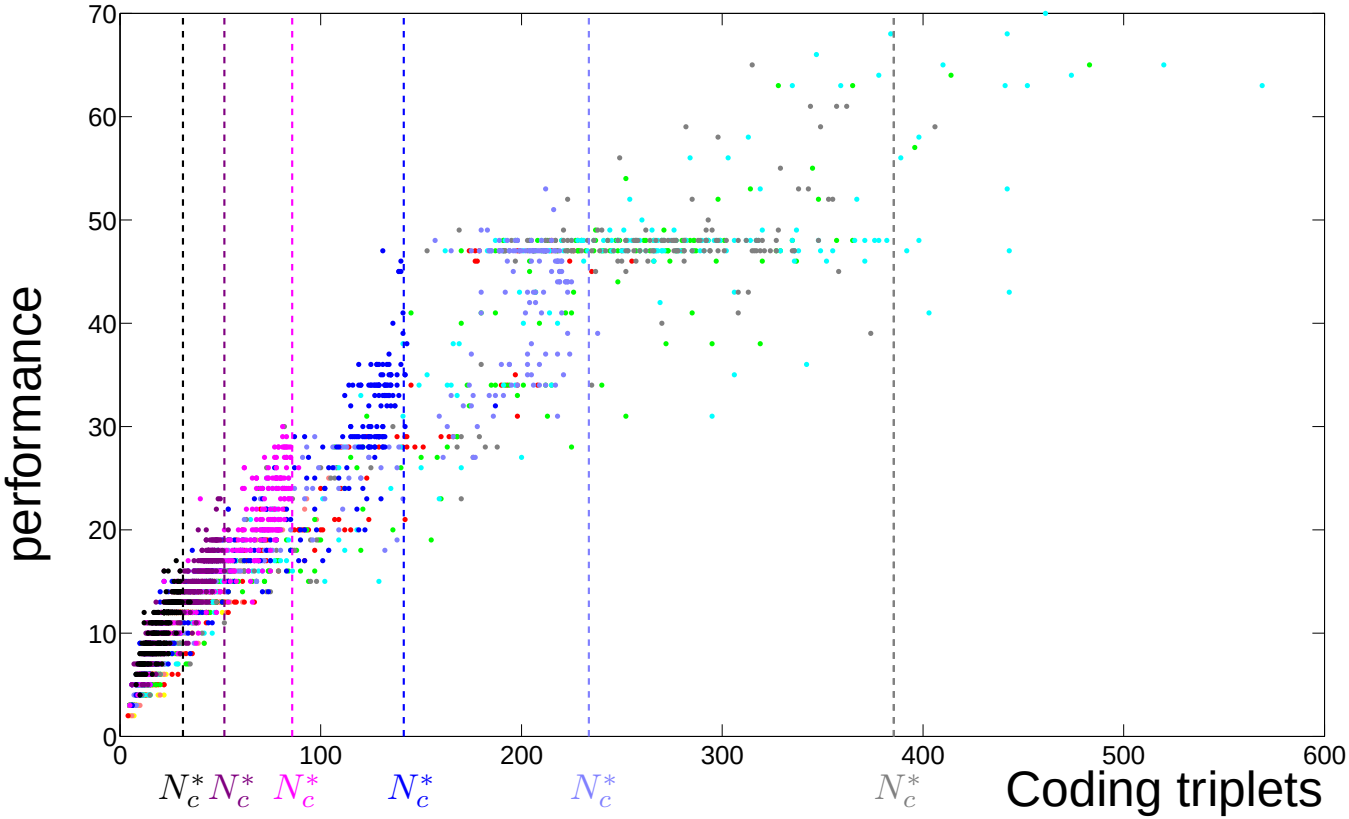
So, the maximum number of coding triplets is

$$N_{\mathsf{c}}^{*} = -\frac{\ln(2)}{3\ln(1 - p_{\mathsf{m}})}$$



Plot of the number of coding triplets for the best machine in the population. The number of coding triplets after 50000 generations, averaged on the seeds, is shown as a function of p_{m}, for all the values of p_{i}. The black thick line on the right represents the critical number of coding triplets.



p_{m} : $4.91 \cdot 10^{-5}$, $8.10 \cdot 10^{-5}$, $1.34 \cdot 10^{-4}$, $2.21 \cdot 10^{-4}$, $3.64 \cdot 10^{-4}$, $6.01 \cdot 10^{-4}$, $9.91 \cdot 10^{-4}$, $1.64 \cdot 10^{-3}$, $2.70 \cdot 10^{-3}$, $4.44 \cdot 10^{-3}$, $7.35 \cdot 10^{-3}$

Performance versus the number of coding triplets. The performance is shown for the best performant TMs at generation 50000 for the 3740 runs of our simulations.

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We will consider the evolution in the number n_s of the best individuals only.
For the selection step we have:

$$P_{rip}(n_s \to n'_s) = \begin{cases} 0 & \text{if } n'_s < n_s \text{ or } n'_s > \min(2n_s, N) \\ 0 & \text{if } n'_s \text{ odd} \\ 2^{(n'_s - n_s)} \begin{pmatrix} \frac{N}{2} \\ \frac{2n_s - n'_s}{2} \end{pmatrix} \begin{pmatrix} \frac{N - 2n_s + n'_s}{2} \\ n'_s - n_s \end{pmatrix} \Big/ \begin{pmatrix} N \\ n_s \end{pmatrix} & \text{otherwise.} \end{cases}$$

The mutation step

We use the two simplifying assumptions that we already used for the deterministic model, namely:

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We have:

$$P_{mut}(n_s' \to n_s'' = n_s' - k) = \left(\begin{array}{c} n_s' \\ k \end{array} \right) P^k (1-P)^{n_s'-k},$$

where P is the probability that an individual in the best performance class will undergo at least one mutation into a coding triplet

$$P = 1 - (1 - p_{\mathsf{m}})^{3N_{\mathsf{c}}}.$$

The Markov matrix

In our case the state of the system is labelled by the number n_s of individuals into the best performance class and the entries of M will be given by

$$M_{n_s+1,n_s''+1} = \sum_{n_s'=0}^{N} P_{rip}(n_s \to n_s') P_{mut}(n_s' \to n_s''), \qquad n_s, n_s'' = 0, \ldots, N$$

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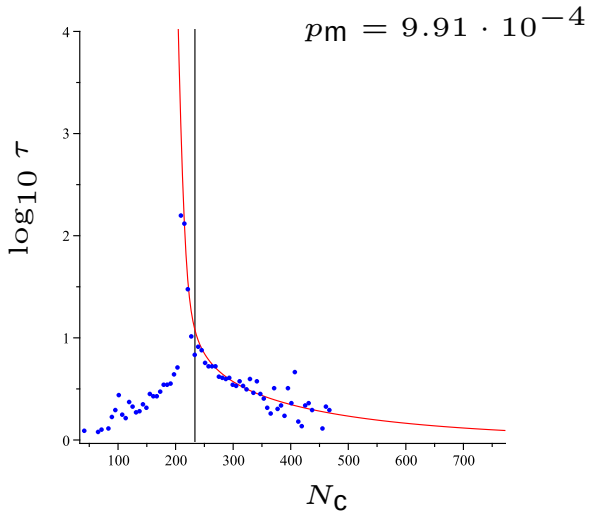
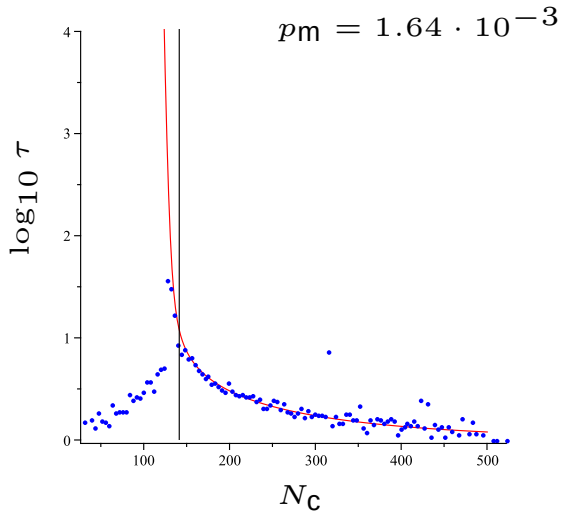
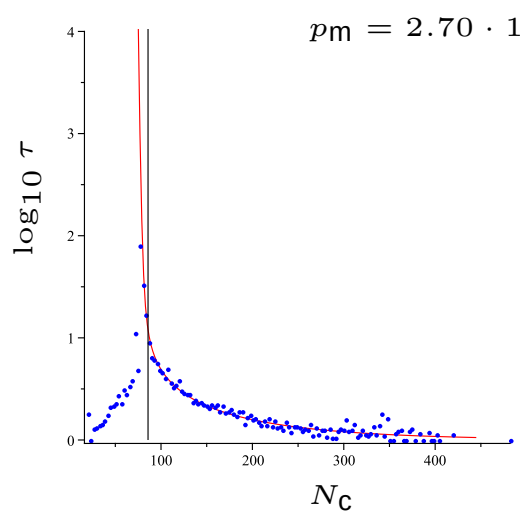
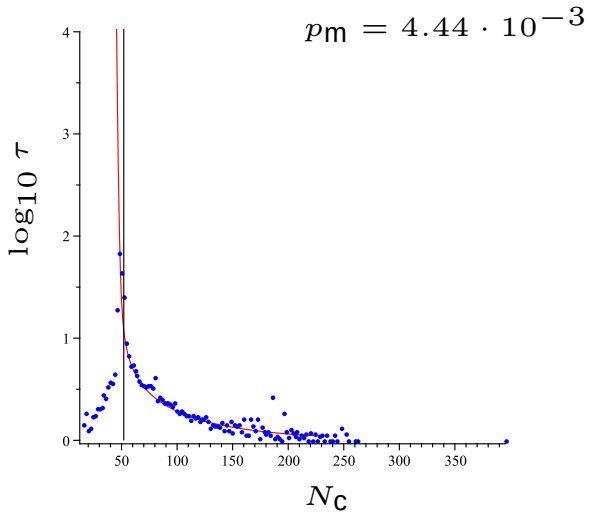
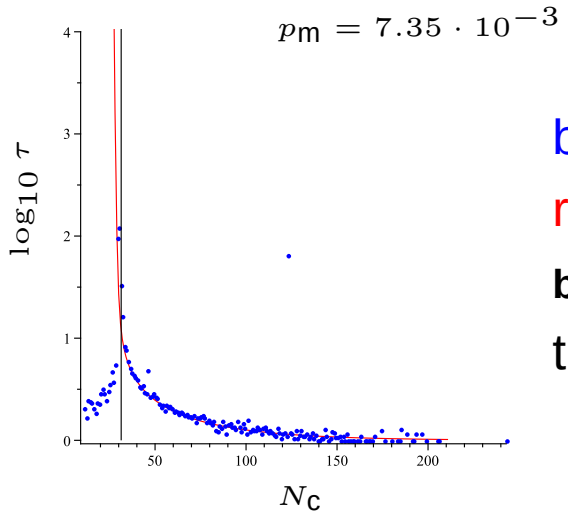
This equation assumes an infinite number of generations.









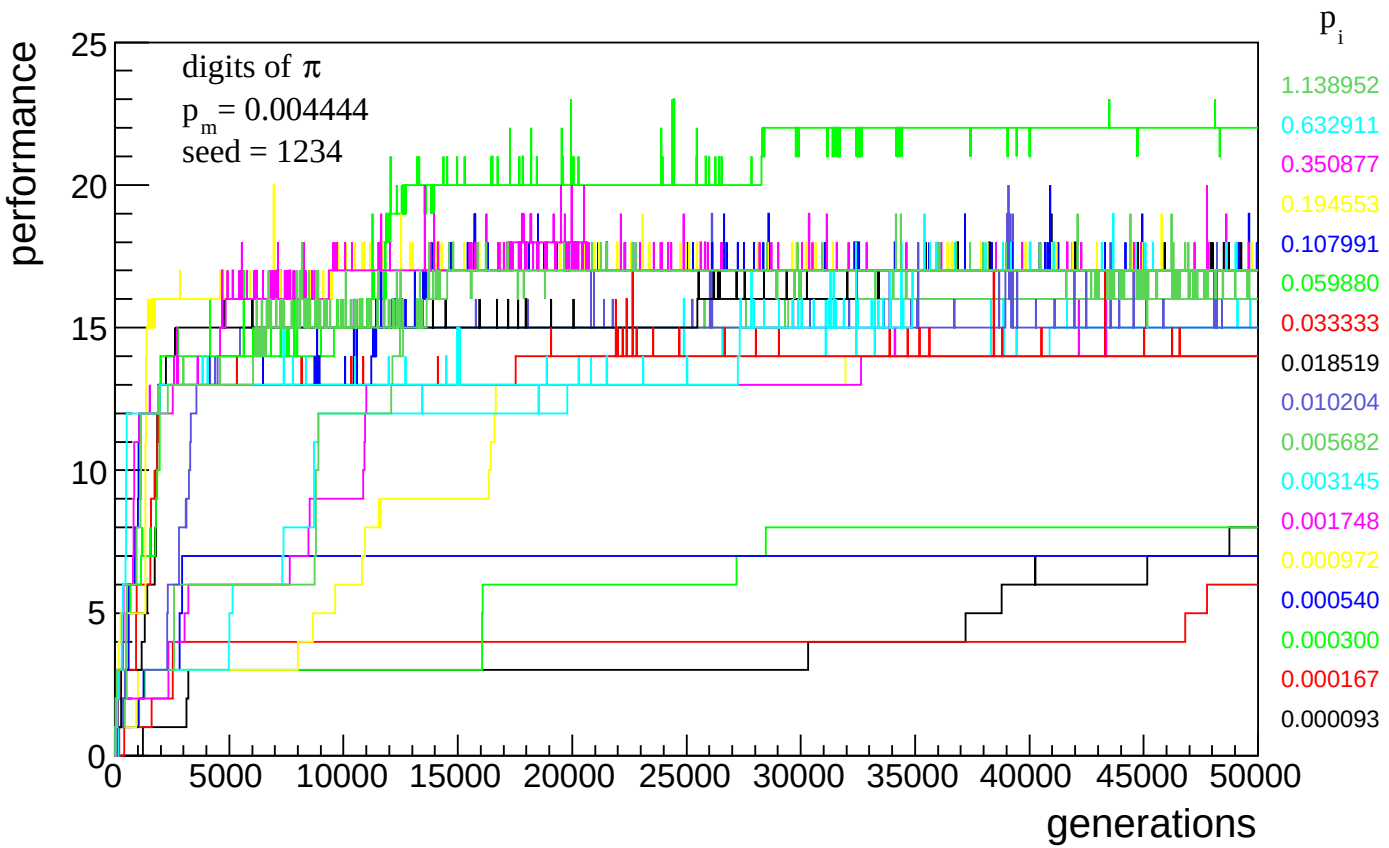


blue points: simulations data

red line: stochastic model

black line: deterministic error threshold

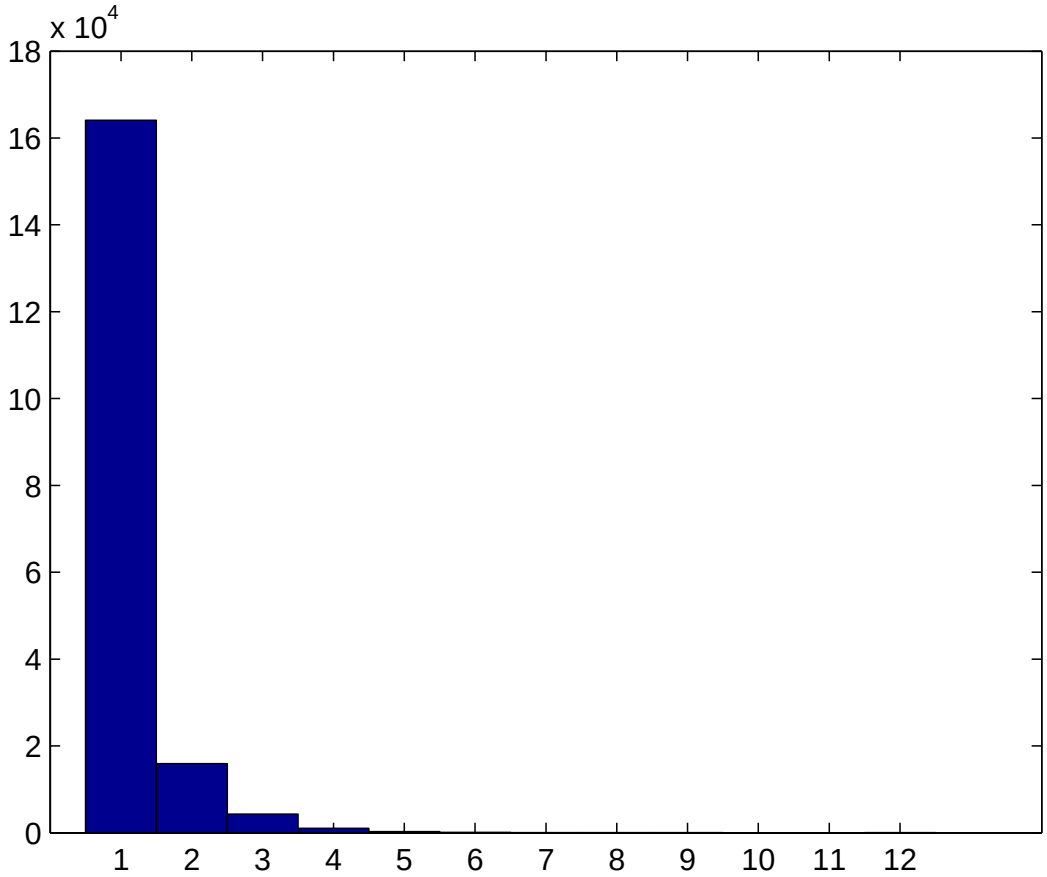
Life near the error threshold



For $p_{\mathrm{m}} = 0.0044$ and certain values of p_{i}, TMs reach the error threshold.

From there on, a typical oscillatory pattern emerges.

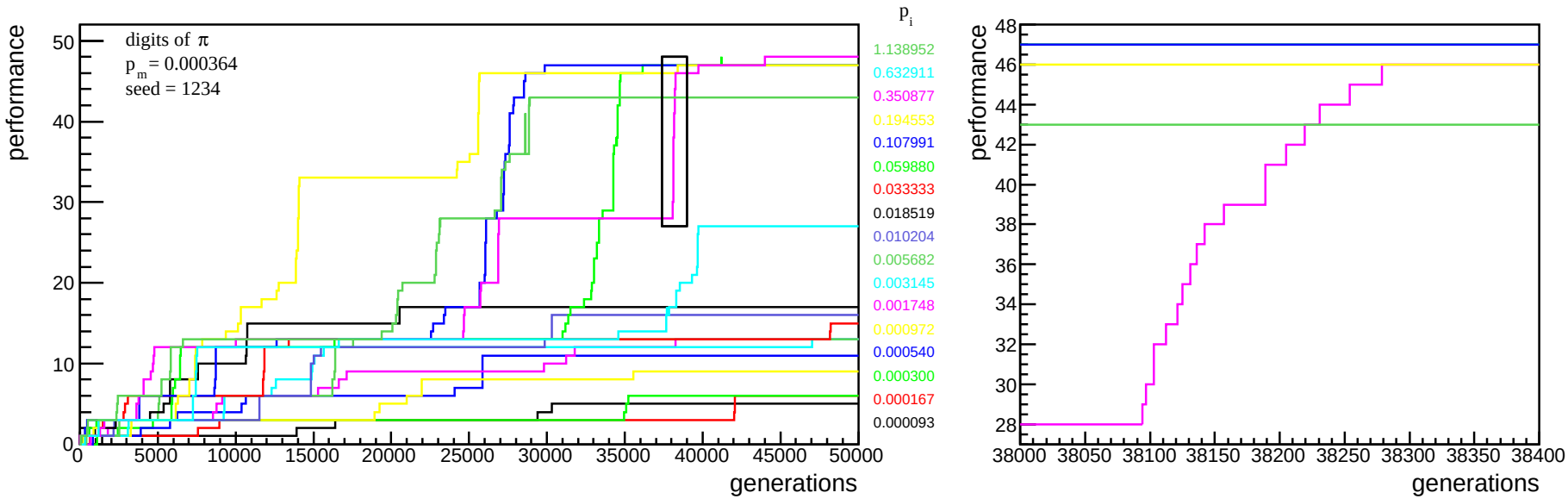
Performance jumps



This histogram shows the number of increases in the performance versus their amplitude.

Performance shows a gradualistic evolution.

Punctuated equilibria



We observe the presence of long stasis periods alternated by short periods of fast evolution.

The small black rectangle is zoomed on in the right part of the figure to show the actual jumps in the performance.

Conclusions

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The fact that this behaviour could be much more general than the present model only is suggested by the fact that it emerges also in a completely different evolutionary model (Knibbe et al 2007) that uses completely different algorithms coding, mutation and selection operators.

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