

# Phenotypic Diversity, Population Growth, and Information in Fluctuating Environments

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## Abstract

The following paper is aimed to study the model of population growth proposed in the titled paper. Here you can find some theoretical description of the model, the repetition of the numerical experiment shown in the paper and a simulation of a population according to the proposed model.

## 1 Theoretical part

### 1.1 Introduction

In regularly varying environments organisms mostly adapt their behaviour by adjusting to the daily light cycles, however, due to fluctuations in chemical composition, local temperature or something else the environment can be changing irregularly. This case is defined as fluctuating environment and we are going to study the behaviour of the organisms in such situations.

In fluctuating environments organisms adapt by switching their phenotype or behavior and there are different ways to do it. For example, in genetically clonal populations, phenotypic diversity is generated by stochastic phenotype-switching mechanisms. The most common example of such randomization of phenotype which can be found in literature is *bet-hedging*. [1] This helps to explain the existence of reservoirs of ungerminated seeds in the soil. Actually this strategy helps for annual plants to *hedge their bets* in case of a drought as drought can lead to death of the population if the whole population of seeds germinate.

In this paper we will use a computation model which can produce two types of phenotype switching: Responsive switching (R), occurring as a direct response to an outside cue detected by a sensing mechanism, and spontaneous stochastic switching (S), occurring without any direct sensing of the environment.

The idea is to find the answers to three following questions: When to use each type of switching? What determines switching rates? How does information about switching environments affects survival?

## 1.2 Population - environment model

Let's determine and describe the way to get closer to fluctuating environment (pic. 5). The main property that we have here is a continuous-time stochastic process  $\varepsilon(t)$  which is determining the environment at each moment of time. However, we have some limitations for this variable which are located in the duration of times  $T_i$  where we assume that our environment remains stable (each duration should be long enough to achieve the equilibrium in our system)

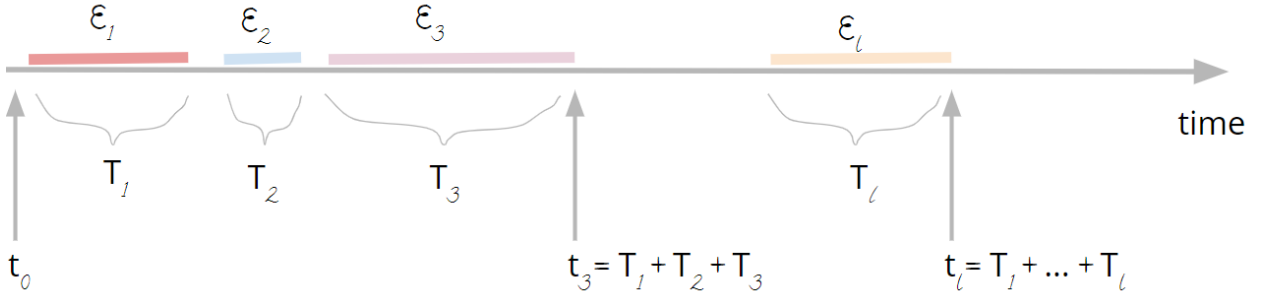


Figure 1: Change of environments through time.  $\varepsilon_i$  - environment,  $T_i$  - corresponding duration of the environment.

So to initialize the model we need to pick a finite number  $\mathbf{n}$  of environment types and designate each of them with unique index in range  $[1 : \mathbf{n}]$ . This simultaneously makes our population to have also  $\mathbf{n}$  different phenotypes.

1. The average duration of environment  $\mathbf{i}$  is  $\tau_i$  (we also define  $\tau = \text{average}_i \tau_i$ ).
2. The occurrence probability of environment  $\mathbf{i}$  is  $p_i$ .
3. The probability that environment  $\mathbf{i}$  follows environment  $\mathbf{j}$  is  $b_{ij}$  ( $b_{ii} = 0$ )
4. Phenotype  $\mathbf{i}$  grows(decays if negative) with rate  $f_i^{(k)}$  in environment  $\mathbf{k}$
5. The phenotype with the largest growth rate in environment  $\mathbf{k}$
6. Individuals may switch phenotype at any time with  $H_{ij}^{(k)}$  as a switching rate from phenotype  $\mathbf{j}$  to phenotype  $\mathbf{i}$  in the environment  $\mathbf{k}$
7. Population vector  $\mathbf{x}(t)$  shows number of individuals with phenotype  $\mathbf{i}$  at time  $t$  at its  $i$ th coordinate.

The growth equation is formulated with an equation:

$$\frac{d}{dt} \mathbf{x}(t) = A_{\varepsilon(t)} \mathbf{x}(t), \quad (1)$$

where the matrix  $A_{\varepsilon(t)}$  is one of  $\mathbf{n}$  matrices  $A_k$  depending on  $\varepsilon(t)$ . It can be written as

$$A_k = H^{(k)} \times (-I) + \text{diag } f^{(k)} = \begin{pmatrix} f_1^{(k)} - H_{11}^{(k)} & H_{12}^{(k)} & \dots & H_{1n}^{(k)} \\ H_{21}^{(k)} & f_1^{(k)} - H_{12}^{(k)} & \dots & H_{2n}^{(k)} \\ \vdots & \vdots & \ddots & \vdots \\ H_{n1}^{(k)} & H_{n2}^{(k)} & \dots & f_1^{(k)} - H_{nn}^{(k)} \end{pmatrix} \quad (2)$$

### 1.3 Types of phenotype switching

We can affect on initial conditions by choosing appropriate switching rates ( $H_{ij}^{(k)}$ ). So different choices of this parameter can form our cases of R (responsive switching) and S (stochastic switching)

For stochastic switching, switching rates are independent of the environment  $k$ ; therefore, for all values  $k$

$$H_{ij}^{(k)} = H_{ij} \quad (3)$$

For responsive switching, the sensing mechanism allows switching rates to depend strongly on  $k$ . In the extreme case, all phenotypes switch with the same rate  $H_m$  to phenotype  $k$  in environment  $k$ , so

$$\begin{aligned} H_{ij}^{(k)} &= H_m \text{ for all } j \neq k \\ H_{ij}^{(k)} &= 0 \text{ for all } i \neq k \end{aligned} \quad (4)$$

We can see that when environment  $j$  changes to  $i$ , there is a delay time,  $T_{ij}^*$ , in which  $\mathbf{x}(t)$

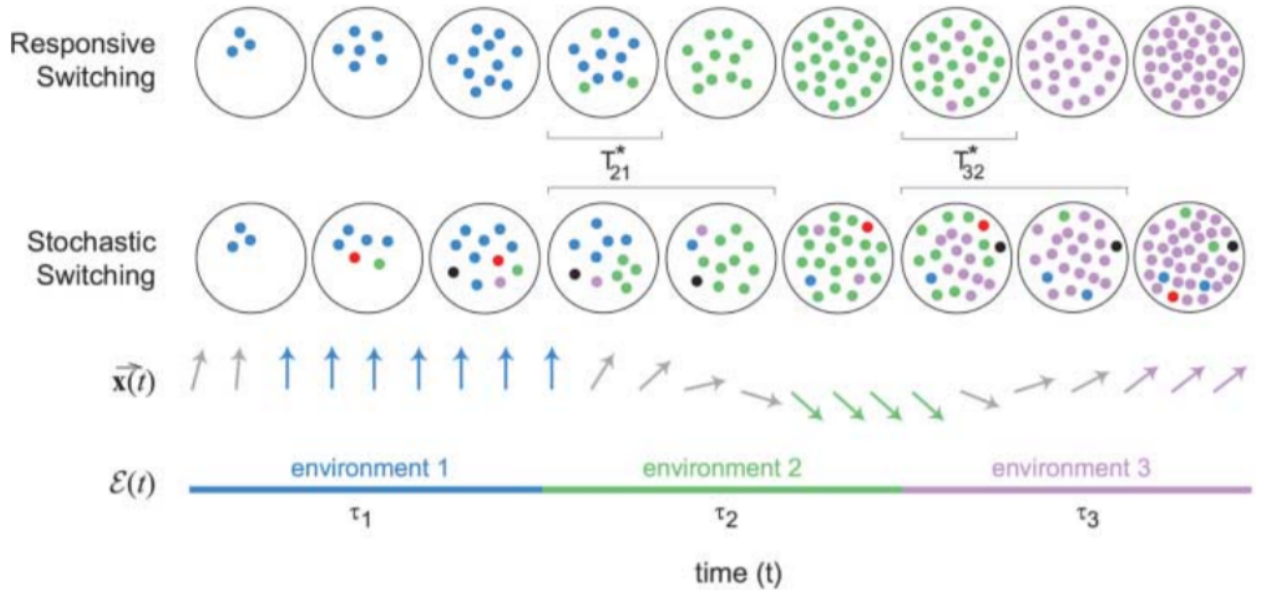


Figure 2: Visualisation of phenotypic switching [2]

rotates (shown in gray pic. 2) before the population attains its new composition. In responsive switching, individuals switch directly to the fastest-growing phenotype. In stochastic switching, subpopulations exist in different phenotypes; when the environment changes, the fastest-growing

subpopulation brings about a change in population composition.

## 1.4 Lyapunov exponent

To compare the two types of switching, the so-called Lyapunov exponent  $\Lambda$  is calculated. It is the asymptotic growth rate of total population size given by equation

$$\Lambda = \lim_{t \rightarrow \infty} \frac{1}{t} \log N(t) \quad (5)$$

$\Lambda$  depends on both the organism (growth rates of its phenotypes and switching rates) and the changing environment so this is actually a nice way of describing populations grown, however, it is difficult to compute. The authors of the title paper show how this equation can be re-written according to our model (see the supplementary material to [2]). Here you can find the equation

$$r\Lambda = \lim_{L \rightarrow \infty} \frac{1}{L} \sum_{i=1}^a \sum_{k=1}^L T_i^{(n)} \lambda_1(A_i) + \frac{1}{L} \sum_{i,j=1}^n p_{ij} b_{ij} L \log q_{ij} = \sum_{i=1}^n p_i \tau_i \lambda_1(A_i) + \sum_{i,j=1}^{\infty} p_{ij} b_{ij} \log q_{ij}. \quad (6)$$

The further analysis of this equations turns us to the specific cases of responsive and stochastic switching. For responsive switching

$$\tau\Lambda_R = \sum_{i=1}^n p_i \tau_i f_i^{(i)} - c\tau - \sum_{i,j=1}^n p_j b_{ij} \log(1 + \Delta_{ji}^R/H_m). \quad (7)$$

$$[\text{long-term growth}] = [\text{fastest growth}] - [\text{sensing cost}] - [\text{delay-time cost}]$$

For stochastic switching

$$\tau\Lambda_S = \sum_{i=1}^n p_i \tau_i f_i^{(i)} - \sum_{i=1}^n p_i \tau_i H_{ii} - \sum_{i,j=1}^n p_j b_{ij} \log(1 + \Delta_{ij}^S/H_{ij}) + \dots \quad (8)$$

$$[\text{long-term growth}] = [\text{fastest growth}] - [\text{diversity cost}] - [\text{delay-time cost}]$$

Where  $\Delta_{ij} \equiv f_j^{(j)} - f_i^{(j)}$ ,  $\Delta_{ij}^R \equiv \Delta_{ij}$ , and  $1/\Delta_{ij}^S \equiv 1/\Delta_{ij} + 1/\Delta_{ji}$ .

## 2 Experiment

### 2.1 Repetition of the experiment of the authors

The idea is to show that the long-term growth rate will depend only on the mean durations of the environments  $\tau_i$  and on the pairwise correlations between them  $b_{ij}$  and will not depend on other characteristics of the environmental fluctuations.

So the authors have taken two matrices

$$A_1 = \begin{pmatrix} 2 & 0.05 \\ 10^{-6} & -0.05 \end{pmatrix} \quad A_2 = \begin{pmatrix} -7 & 0.05 \\ 10^{-6} & -0.05 \end{pmatrix}. \quad (9)$$

Here the environment 1 had a duration denoted by a random variable  $T_k^{(1)}$  with different distributions: uniform (from 0 to  $2\tau_1$ ), exponential (rate  $1/\tau_1$ ), delta distribution (constant  $\tau_1$ ). The environment 2 had a constant duration of 20 hours. The Lyapunov exponent is then derived by formula<sup>1</sup>

$$\tau\Lambda = \log(\text{Tr}G)/2L, \quad \text{where } G = \prod_{k=1}^L \left( e^{20 A_2} e^{T_k^{(1)} A_2} \right) \quad (10)$$

The fact is that is that we expect (equations 1 and 5 from SA to [2]) the exponent to become

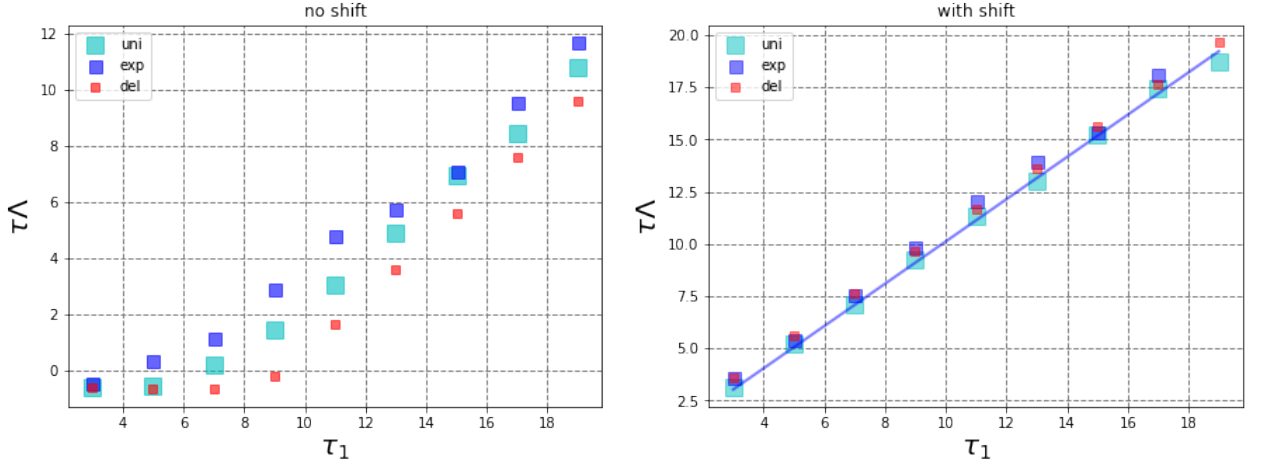


Figure 3: Repetition of the author's experiments. The dependence of Lyapunov exponent  $\tau\Lambda$  from the average length of the environment 1. Different rectangles refer to different distributions of the durations of environments 1. The line on the right graph has the slope from the equation 6

independent of the exact distribution if  $T_k^{(1)}$  is always larger than some cutoff value (here it is 10 hours and it changes the formula for  $G = \prod_{k=1}^L \left( e^{20 A_2} e^{T_k^{(1)} A_2} \right)$ ). And we can see that in right side of the figure 3 all distributions align on a straight. Here the straight is derived from the equation 6. Which actually shows the applicability of this formula.

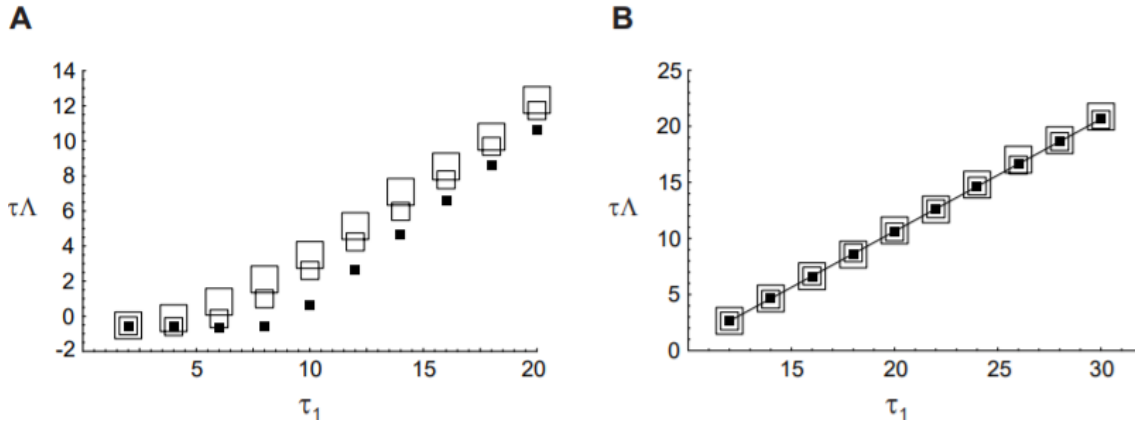


Figure 4: The initial graph from the original article

<sup>1</sup>The only difference to the initial conditions in this repetition is that here  $L = 10$ , however, in the original paper it was  $L = 100$ , which is due to lack of computing resources for such large computations. However is haven't greatly affect the result

## 2.2 Modelling

Using the initial conditions from the equations 3 and 4 we can model the population this some random initial conditions. The repository with code is placed in [GitHub](#).

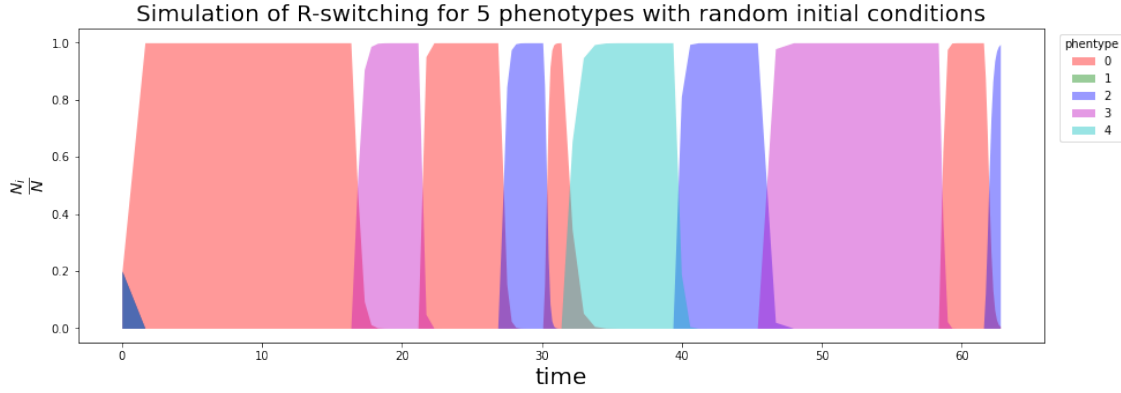


Figure 5: Simulation of responsive switching for population with 5 different environment types with random initial conditions with applied limitations on matrix H from equations 4

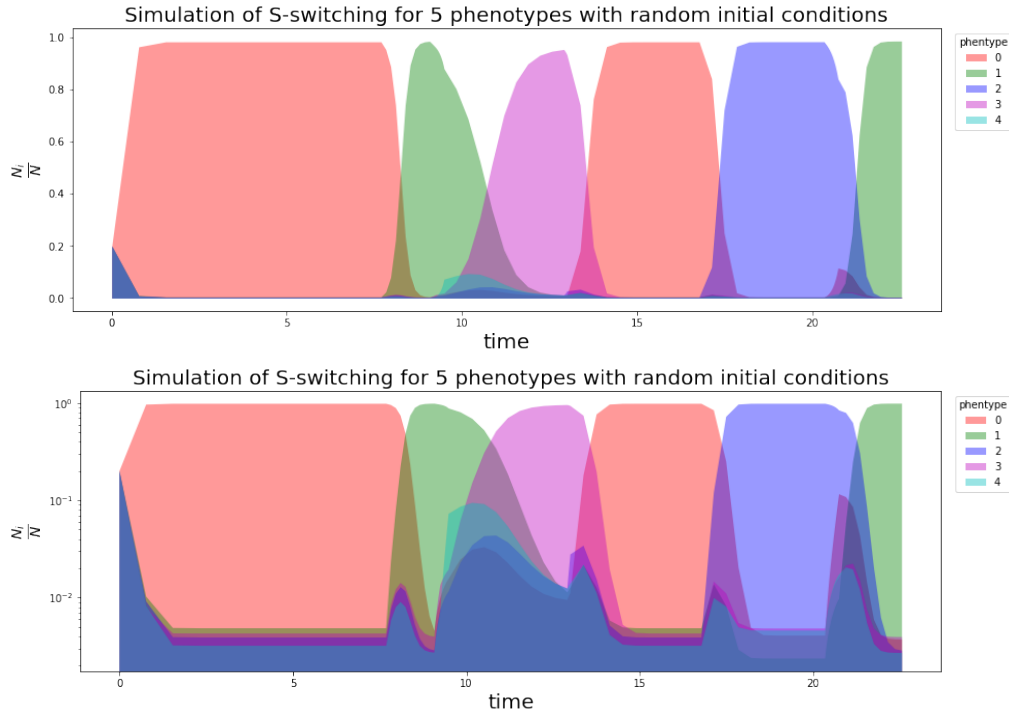


Figure 6: Simulation of stochastic switching for population with 5 different environment types with random initial conditions with applied limitations on matrix H from equations 3. The upper plot it in linear scale, the lower is in log scale

On the plots we can observe how the population is changing in time. We can note that all phenotypes coexist in each current environment and the population is able to reach equilibrium at each change of environment. The *coexistence* is more vividly reflected in the case of stochastic switching which converges actually with the fundamental idea under this process. The interesting

characteristic of R-switching are delay times  $T_i^*$  that we were discussing in the theoretical part also can be observed in this graphs in a slow growth of the population of the best phenotype after each switching of the environment. Also this feature can be observed in the S case.

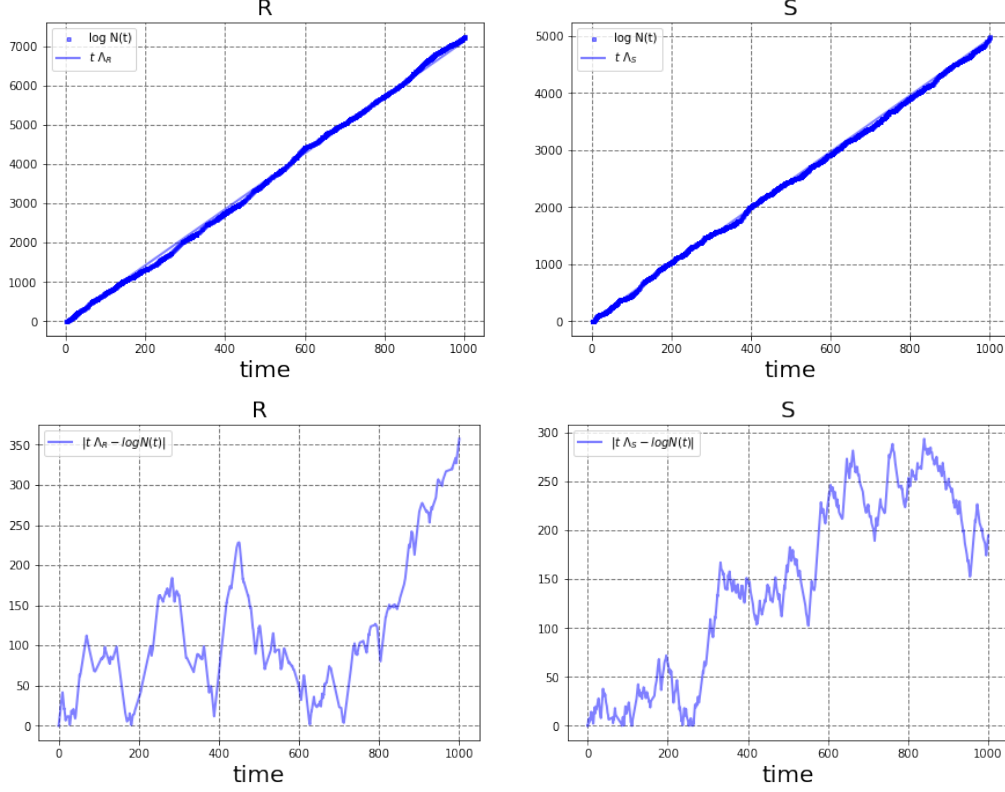


Figure 7: Simulation of population with different types of switching for 15 environments (and phenotypes) in comparison the Lyapunov exponent from equations 7, 8

Here we can see how the result of modelling is consistent with the formulas for Lyapunov exponent (equations 7, 8) There were 15 environments and prenotypes in each model. We can see that the numerical results are in nice accordance with theoretical estimation of Lyapunov exponent.

### 3 Conclusion

We tried to find out the way to describe phenotypic diversity in population growth with a numerical model. The implementation of this model accurately showed it accordance with estimation of Lyapunov exponent and singled out different physical fundamentals, staying at the core of the model. Also the repetition of the experiment was conducted with accurate accordance in the results.

\*References

- [1] (Wiki.org). URL: [https://en.wikipedia.org/wiki/Bet\\_hedging\\_\(biology\)](https://en.wikipedia.org/wiki/Bet_hedging_(biology)).

- [2] Edo Kussell, Stanislas Leibler. “Phenotypic Diversity, Population Growth, and Information in Fluctuating Environments”. *Science* **309** 5743 (2005), pp. 2075–2078. ISSN: 0036-8075. DOI: 10.1126/science.1114383. eprint: <https://science.sciencemag.org/content/309/5743/2075.full.pdf>. URL: <https://science.sciencemag.org/content/309/5743/2075>.