

Evolution with Positive Feedback between Phenotype and Inheritance

Yoav Ram^{*} Uri Liberman[†] Marcus W. Feldman[‡]

March 15, 2017 | v.0

Abstract

Lorem ipsum dolor sit amet, consectetur adipiscing elit. Fusce non ex metus. Etiam tempor nisl at lorem facilisis, vel malesuada est mollis. Pellentesque nunc lacus, porttitor in mollis quis, pellentesque quis sem. Nunc consequat, elit vel tincidunt tincidunt, urna arcu efficitur turpis, ac mollis turpis velit vitae libero. Aenean mauris lacus, blandit a nulla a, scelerisque lobortis dolor. Etiam viverra, nibh vehicula vehicula congue, nisl dui mattis risus, quis convallis massa nisi quis elit. Maecenas gravida nunc nec dignissim consequat. Fusce scelerisque magna ut odio ullamcorper dapibus. Vivamus et dignissim nunc.

1 Model

1.1 Wright-Fisher model

We model evolution of a constant, finite size population with non-overlapping generations using a Wright-Fisher model with natural selection, inheritance, and random genetic drift. This model is based on the simulation description in the final paragraph of the *Materials & Methods* section of Xue and Leibler (2016). Indeed, a simulation based on this model (<https://github.com/yoavram/Milpitas>) allowed us to reproduce Figure 2 of Xue and Leibler (2016) (Fig. 1).

1.1.1 Definitions

- N: constant population size.

^{*}Department of Biology, Stanford University, Stanford, CA 94305-5020, yoav@yoavram.com

[†]School of Mathematical Sciences, Tel Aviv University, Tel Aviv, Israel 69978, uril@tauex.tau.ac.il

[‡]Department of Biology, Stanford University, Stanford, CA 94305-5020, mfeldman@stanford.edu; Corresponding author

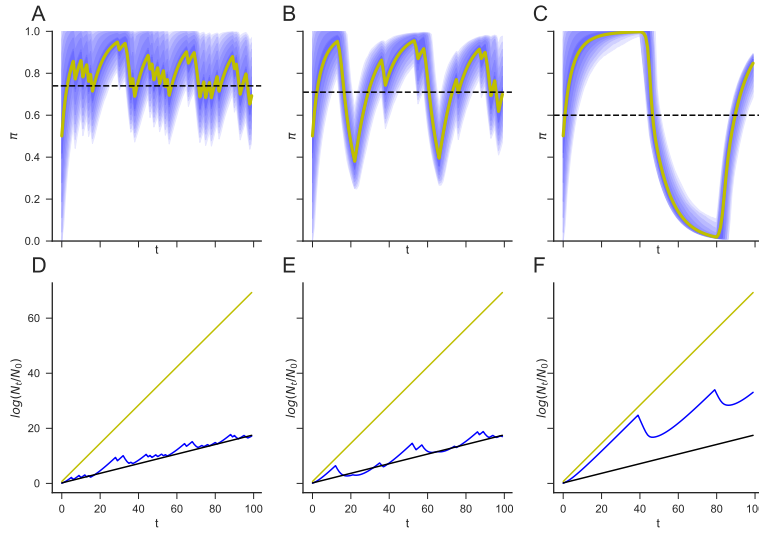


Figure 1: Reproduction of Figure 2 from Xue and Leibler (2016). **A-C**: the average π in the population over time and the distribution in blue; **D-F**: the effective population growth rate. **A,D**: the environment is randomly chosen at each generation such that $P(A)=0.7$ and $P(B)=0.3$; **B,E**: the environment flips between A and B, the duration of each is geometrically distributed with $p=1/10$ for A and $p=1/5$ for B; **C,F**: the environments flips every 40 generations. Parameters: $N=100,000$, # generations = 100, $\eta=0.1$, $W=2$, $w=0.2$.

- ϕ_i : phenotype of individual i , $1 \leq i \leq N$, $\phi_i \in \{A, B\}$.
- ϵ_t : the environment at generation t , $\epsilon_t \in \{A, B\}$.
- W : individual fitness when phenotype and environment match, $\phi_i = \epsilon_t$.
- w : individual fitness when phenotype and environment do not match, $\phi_i \neq \epsilon_t$.
- ω_i : fitness of individual i at time t , $\omega_i = W \cdot 1_{\phi_i = \epsilon_t} + w \cdot 1_{\phi_i \neq \epsilon_t}$.
- $\bar{\omega}$: population mean fitness.
- π_i : phenotype probability, the probability that individual i becomes phenotype A , $1 \leq i \leq N$.
- Π : set of phenotype probabilities in the population, $\Pi = \{\pi_i\}_{1 \leq i \leq N}$.
- η : phenotypic inheritance rate, $0 \leq \eta \leq 1$.

1.1.2 Reproduction

For each offspring in the population of generation $t+1$ we choose a parent from the population of generation t and this choice depends on the parent relative fitness: the probability that individual i is the parent is relative to its fitness, ω_i . Therefore, reproduction is modeled by a multinomial distribution. Therefore, reproduction includes the effects of natural selection and random genetic drift.

1.1.3 Inheritance

The offspring inherits the phenotype probability of the parent with a modification – if the parent became A , then the offspring is even more likely to be A ; if the parent was B , then the offspring is less likely to be A . Specifically, for parent k and offspring i :

$$\pi_i = \pi_k \cdot (1 - \eta) + \eta \cdot 1_{\phi_k = A} \quad (1)$$

1.1.3.1 Note

The notation in Eq. 1 is different from Eq. 1 in Xue and Leibler (2016), as i denotes individual, rather than phenotype. But the process is the same.

1.1.3.2 Note

The expected difference between parent and offspring phenotype probability is $E[\pi_i - \pi_k | \pi_k] = 0$.

1.1.4 Iteration

At each generation t , Π is updated according to the following steps. Initial values can be determined (*i.e.*, $\forall i$, $\pi_i = 0.5$), or values can be drawn from an initial

distribution (*i.e.*, $\pi_i \sim TN(0.5, 0.05)$, TN is the truncated normal distribution). In addition, the sequence ϵ_t is independent of the iteration on P_i .

At each generation t :

1. **Development:** the phenotypes of all individuals are drawn from corresponding Bernoulli distributions depending on their phenotype probabilities: $P(\phi_i = A) = \pi_i$.
2. **Fitness:** the fitness of all individuals is set: $\omega_i = W \cdot 1_{\phi_i = \epsilon_t} + w \cdot 1_{\phi_i \neq \epsilon_t}$.
3. **Reproduction:** the number of offspring of each individual, b_i , is drawn from a multinomial distribution $MN(N, \{\frac{\omega_i}{\sum_i \omega_i}\}_{1 \leq i \leq N})$, such that

$$P(b_1 = x_1, \dots, b_N = x_N) = \frac{N!}{x_1! \cdot \dots \cdot x_N!} \cdot \left(\frac{\omega_1}{\sum_i \omega_i}\right)^{x_1} \cdot \dots \cdot \left(\frac{\omega_N}{\sum_i \omega_i}\right)^{x_N}$$

4. **Inheritance:** the set of phenotype probabilities of the offspring generation is updated using Eq. 1 such that for each i , Π includes exactly b_i copies of $(\pi_i \cdot (1 - \eta) + \eta \cdot 1_{\phi_i = A})$.

1.1.4.1 Note

Only development and reproduction are stochastic; natural selection and drift occur at the reproduction step.

1.1.4.2 Note

If $\eta = 0$, $\pi_i \in \{0, 1\}$, and $\epsilon_t \equiv A$, then we have a standard single locus bi-allelic selection-drift Wright-Fisher model.

1.2 Recurrence equation

We approximate the Wright-Fisher model using a recurrence equation. This approximation is most suitable when the population is composed of a single lineage – for example, when selection is extreme and there is a common ancestor.

Define x to be the probability that a random individual in the population is A . What is x' , the probability that a random offspring of that individual is A ?

Assuming an “infinite” population undergoing exponential growth, this depends on (i) if the parent was A or B , with probabilities x and $1-x$, (ii) on the relative contribution of A and B phenotypes to the next generation in terms of fitness, and (iii) on the probability that offspring of A or B phenotypes eventually become A , according to the inheritance process (Eq. 1):

$$x' = x \cdot \frac{\omega_A}{\bar{\omega}} \cdot ((1 - \eta)x + \eta) + (1 - x) \cdot \frac{\omega_B}{\bar{\omega}} \cdot (1 - \eta)x$$

Where ω_A and ω_B are the fitness of phenotypes A and B in the current generation (depending on ϵ_t).

When we write a similar recurrence for the probability that an individual is B ($(1-x)' = F(1-x)$) and sum the two equations, we find that $\bar{\omega} = x\omega_A + (1-x)\omega_B$ is the mean fitness.

This recurrence equation can be reorganized to:

$$x' = x \frac{x(1-\eta)(\omega_A - \omega_B) + \eta\omega_A + (1-\eta)\omega_B}{x(\omega_A - \omega_B) + \omega_B} \quad (2)$$

2 Results

To be continued...

References

Xue, B., and S. Leibler. 2016. Evolutionary learning of adaptation to varying environments through a transgenerational feedback. *Proceedings of the National Academy of Sciences* 201608756.