

# Evolution with Positive Feedback between Phenotype and Inheritance

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## Abstract

TODO

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## Model

### 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).

### Definitions

- $N$ : constant population size.
- $\phi_i$ : phenotype of individual  $i$ ,  $1 \leq i \leq N$ ,  $\phi_i \in \{A, B\}$ .
- $\epsilon_t$ : 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,  $\phi_i \neq \epsilon_t$ .
- $\omega_i$ : 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.
- $\pi_i$ : phenotype probability, the probability that individual  $i$  becomes phenotype  $A$ ,  $1 \leq i \leq N$ .
- $\Pi$ : set of phenotype probabilities in the population,  $\Pi = \{\pi_i\}_{1 \leq i \leq N}$
- $\eta$ : phenotypic inheritance rate,  $0 \leq \eta \leq 1$ .

### 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,  $\omega_i$ . Therefore, reproduction is modeled by a multinomial distribution. Therefore, reproduction includes the effects of natural selection and random genetic drift.

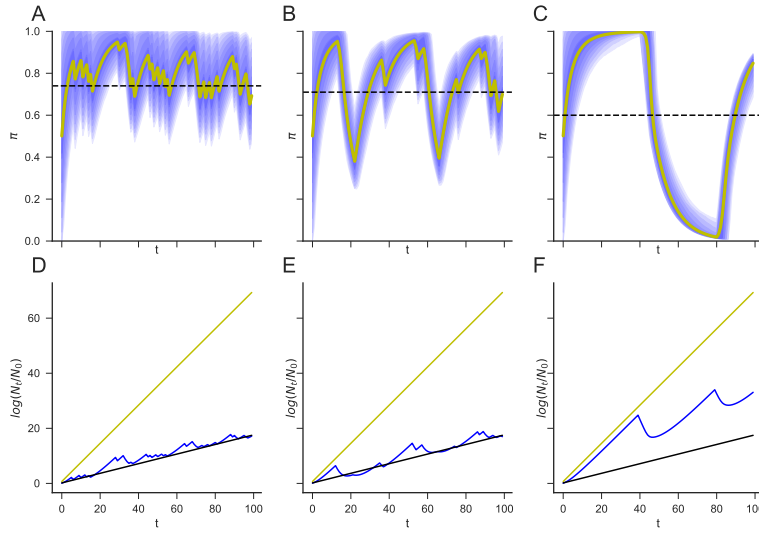


Figure 1: Reproduction of Figure 2 from Xue and Leibler (2016). **A-C**: the average  $\pi$  in the population over time and the distribution in blue; **D-F**: the effective population growth rate. **A,D**: the environment is randomly chosen at each generation such that  $P(A)=0.7$  and  $P(B)=0.3$ ; **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,  $\eta=0.1$ ,  $W=2$ ,  $w=0.2$ .

## 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  $i$ :

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

## 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.

## Note

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

## Iteration

At each generation  $t$ ,  $\Pi$  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  $\epsilon_t$  is independent of the iteration on  $Pi$ .

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  $i$ ,  $\Pi$  includes exactly  $b_i$  copies of  $(\pi_i \cdot (1 - \eta) + \eta \cdot 1_{\phi_i=A})$ .

## Note

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

## 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.

## 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):

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

Where  $\omega_A$  and  $\omega_B$  are the fitness of phenotypes  $A$  and  $B$  in the current generation (depending on  $\epsilon_t$ ).

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:

$$x' = x \frac{x(1 - \eta)(\omega_A - \omega_B) + \eta\omega_A + (1 - \eta)\omega_B}{x(\omega_A - \omega_B) + \omega_B} \quad (3)$$

## Results

### Constant environment

We start with a constant environment  $\epsilon_t = A \forall t$ , such that  $\omega_A = W > w = \omega_B$ .

**Proposition for  $\eta = 0$** 

If  $\eta = 0$  then any  $x \in [0, 1]$  solves  $x' = x$ .

**Proof**

Set  $x' = x, \eta = 0$  in Eq. 3:

$$x = x \frac{x(\omega_A - \omega_B) + \omega_B}{x(\omega_A - \omega_B) + \omega_B}$$

First,  $x = 0$  solves this equality. Otherwise, for  $x > 0$ :

$$\Leftrightarrow x(\omega_A - \omega_B) + \omega_B = x(\omega_A - \omega_B) + \omega_B$$

which is an identity ■.

**Proposition for  $W = w$** 

If  $W = w$  then any  $x \in [0, 1]$  solves  $x' = x$ .

**Proof**

Set  $W = w > 0, x' = x \neq 0$  in Eq. 3:

$$\begin{aligned} x &= x\eta W + (1 - \eta)WW \Leftrightarrow \\ &1 = 1\eta + (1 - \eta)1 \Leftrightarrow \\ &1 = 1 \end{aligned}$$

■

**Proposition for general case**

If  $\eta > 0$  and  $\omega_A > \omega_B$ , then  $x^* = 1$  is the only solution for  $x' = x$ .

**Proof**

First, we check that  $x^* = 1$  solves  $x' = x$ . Set  $x = 1$  in Eq. 3:

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

Next, we check that  $x = 0$  doesn't solve  $x' = x$  by setting  $x = 0$  in Eq. 3:

$$x' = \frac{\eta\omega_A + (1-\eta)\omega_B}{\omega_B} > 0$$

since both the denominator and the numerator are positive.

Next, we check that any  $0 < x < 1$  doesn't solve  $x' = x$ . Set  $x' = x$  in Eq. 2 and substituting  $\bar{\omega} = x\omega_A + (1-x)\omega_B$ :

$$\begin{aligned} x &= x \cdot \frac{\omega_A}{\bar{\omega}} \cdot ((1-\eta)x + \eta) + (1-x) \cdot \frac{\omega_B}{\bar{\omega}} \cdot (1-\eta)x \Leftrightarrow \\ \bar{\omega} &= \omega_A \cdot ((1-\eta)x + \eta) + (1-x) \cdot \omega_B \cdot (1-\eta) \Leftrightarrow \\ x\omega_A + (1-x)\omega_B &= (1-\eta)x\omega_A + \eta\omega_A + (1-\eta)(1-x)\omega_B \Leftrightarrow \\ \eta(x\omega_A + (1-x)\omega_B) &= \eta\omega_A \Leftrightarrow \\ x\omega_A + (1-x)\omega_B &= \omega_A \Leftrightarrow \\ (1-x)\omega_A &= (1-x)\omega_B \Leftrightarrow \\ x &= 1 \end{aligned}$$

■

## Periodic environment

We concentrate on periodic environments in which both environments occur exactly the same number of generations in each “period”. A simple example is  $A1B1=ABABABAB\dots$ , in which the environment switches every generation every generation from  $A$  to  $B$  and vice versa, or  $A2B1=AABAABAAB\dots$  in which the every two  $\_A\_$ s are followed by a single  $B$ . In general,  $AkBl$  denotes an environmental regime in which the period is of length  $k+l$  and composed of exactly  $k$   $\_A\_$ s and  $l$   $\_B\_$ s.

We simulated evolution in such environments, and Fig. 2 shows the evolution of the distribution of  $\pi$  in a population evolving in three such environmental regimes.

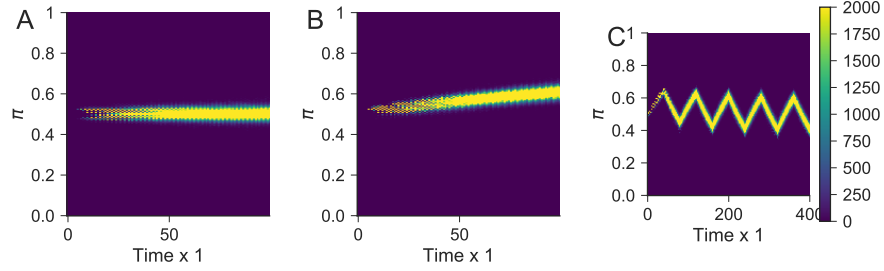


Figure 2: Distribution of  $\pi$  in populations evolving in periodic environments. (A) A1B1, (B) A2B1, (C) A40B40. Parameters:  $N=100,000$ ,  $\eta=0.01$ ,  $W=1$ ,  $w=0.1$ .

### A1B1 regime

When the environment changes every generation, we can write the following recursion, which sets  $\omega_A = W, \omega_B = w$  in Eq. 3 to determine  $x'$  and then sets  $\omega_A = w, \omega_B = W$  to determine  $x''$ :

$$\begin{aligned} x' &= x \frac{x(1-\eta)(W-w) + \eta W + (1-\eta)w}{x(W-w) + w} \\ x'' &= x' \frac{x(1-\eta)(w-W) + \eta w + (1-\eta)W}{x'(w-W) + W} \end{aligned} \quad (4)$$

We are looking for solutions for  $x'' = x$ , which evaluates to a quartic polynomial. Two solutions are  $x = 0, 1$  (assign to Eq. 7 to check), but there are two more potential solutions such that

$$\begin{aligned} x'' - x &= x(1-x)G(x) = 0 \\ G(x) &= Ax^2 + Bx + C \end{aligned}$$

Using SymPy, a Python library for symbolic mathematics, a free alternative to Wolfram Mathematica™ (Team 2014), we find all four solution of  $x'' - x = 0$ :

$$G(x) = x^2 - \frac{W(1-\eta) - w(3-\eta)}{(2-\eta)(W-w)}x - \frac{w}{(2-\eta)(W-w)} \quad (5)$$

To find the roots of  $G(x)$ , recall that  $W > w \geq 0, 1 \geq \eta \geq 0$ , so

$$G(0) = \frac{-w}{(2-\eta)(W-w)} < 0$$



and

$$G(1) = 1 - \frac{W(1-\eta) - w(3-\eta)}{(2-\eta)(W-w)} - \frac{w}{(2-\eta)(W-w)} = \frac{W}{(2-\eta)(W-w)} > 0$$

and  $\lim_{x \rightarrow \pm\infty} G(x) = +\infty$ .

Therefore, one root of  $G(x)$  is negative and one,  $\tilde{x}$ , is positive and below 1. Let  $\delta = \frac{-B - \sqrt{B^2 - 4AC}}{2A} - \frac{-B + \sqrt{B^2 - 4AC}}{2A}$  (where  $A, B, C$  are the coefficients of  $G(x)$ , defined in Eq. 5). Then,  $\delta = \frac{\sqrt{(W+w)^2 - \eta(2-\eta)(W-w)^2}}{(2-\eta)(W-w)}$ . Because  $\eta(2-\eta)$  is maximized at 1,

$$(W+w)^2 - \eta(2-\eta)(W-w)^2 > (W+w)^2 - (W-w)^2 = 4Ww > 0$$

so  $\delta > 0$ . Therefore, the positive root is:

$$\tilde{x} = \frac{-B - \sqrt{B^2 - 4AC}}{2A} \quad (6)$$

Fig. 3 shows  $\tilde{x}$  (dashed green) compared with  $x$  from iteration of Eq. 7 (blue) and with the population mean  $\pi$  ( $\bar{\pi}$ ) in Wright-Fisher simulations (orange) for several combinations of  $\eta, W, w$ . All iterations started with  $\bar{\pi} = 0.5$ ; in the WF simulations, population size  $N$  is 100,000, the initial population is drawn from  $N(0.5, 0.05)$ , and the results are based on 50 simulations per parameter set. Note that the x-axis shows every other generation\* (end of each period). The analytic approximation is good when selection is extreme ( $w = 0$ ), but overestimates  $\bar{\pi}$  when selection is not extreme ( $w = 0.1$ ). In both cases the initial population distribution did not affect the results (as long as it wasn't trivial, *i.e.*  $\pi = 0$ , see Fig. 5).

## A2B1 regime

In the *A2B1* regime (every two generations in the *A* environment are followed by a generation in environment *B*), an analytic approximation is not possible, as solving  $x''' - x = 0$  requires solving a polynomial of degree 6. However, iterating the relevant recurrence equation:

$$\begin{aligned} x' &= x \frac{x(1-\eta)(W-w) + \eta W + (1-\eta)w}{x(W-w) + w} \\ x'' &= x' \frac{x'(1-\eta)(W-w) + \eta W + (1-\eta)w}{x'(W-w) + w} \\ x''' &= x'' \frac{x''(1-\eta)(w-W) + \eta w + (1-\eta)W}{x''(w-W) + W} \end{aligned} \quad (7)$$

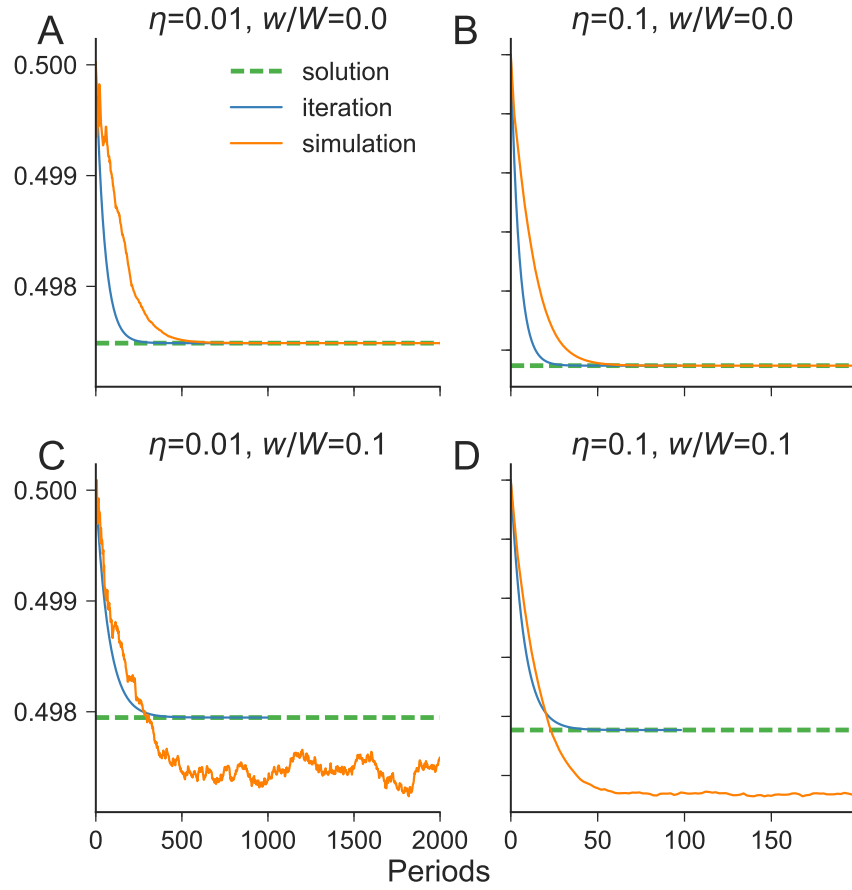


Figure 3: Population mean  $\pi$  in environment regime  $A1B1$ .  $N=100,000$ .

provides similar results: the equilibrium value is in good fit with Wright-Fisher simulations for extreme selection ( $w = 0$ ) but over estimates the equilibrium otherwise (Fig. 4).

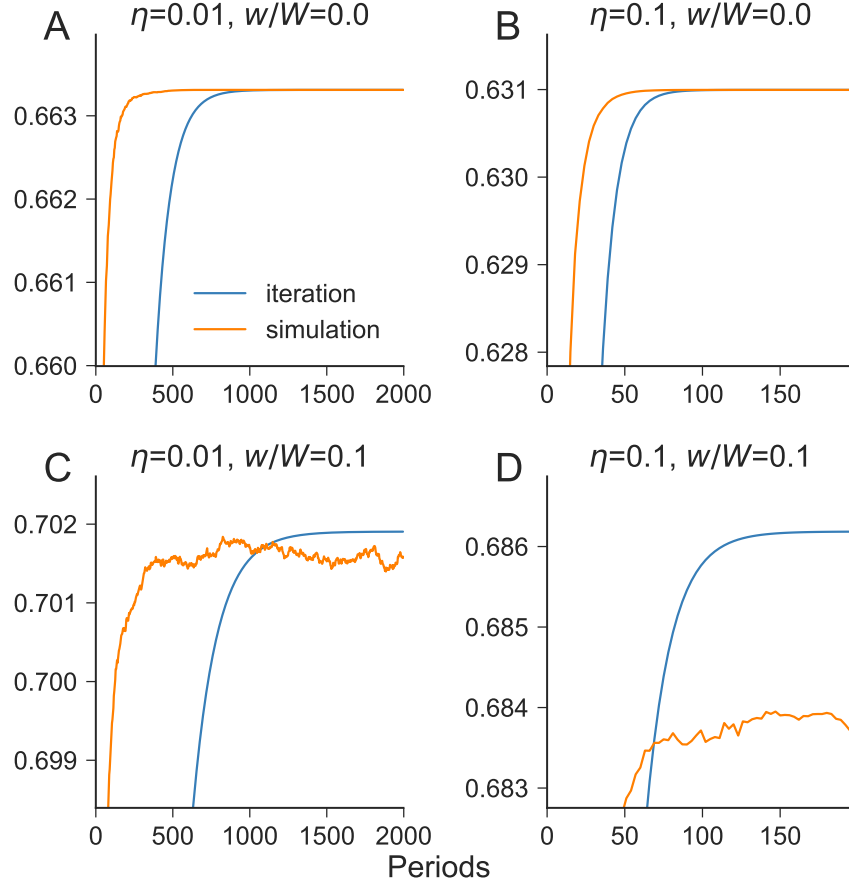


Figure 4: Population mean  $\pi$  in environment regime  $A2B1$ .  $N=100,000$ .

### Protected polymorphisms in $AkBl$ regime

What can we say about the more general case of  $k$  generations in environment  $A$  and  $l$  generations in  $B$ ? We examine the existence of a *protected polymorphism* (Prout 1968), which means that none of the phenotypes become extinct even when initially rare. Environments  $A$  and  $B$  select for  $\pi = 1$  and  $\pi = 0$ , respectively, and these are absorbing states: if all individuals are, for example,  $\pi = 0$ , then they are all of phenotype  $B$  and all offspring will be  $\pi = 0$ , too. Mathematically, we examine the stability of  $x = 0$  and  $x = 1$ ; if both are unstable,

then a protected polymorphism occurs. Intuitively, this will happen if neither environment occurs enough to fix its preferred state.

We rewrite Eq. 3 as  $x' = x \cdot f_A(x)$  in environment  $A$  and  $x' = x \cdot f_B(x)$  in environment  $B$ , where:

$$f_A(x) = \frac{x(1-\eta)(W-w) + \eta W + (1-\eta)w}{x(W-w) + w}$$

$$f_B(x) = \frac{x(1-\eta)(w-W) + \eta w + (1-\eta)W}{x(w-W) + W}$$

We concentrate on  $l \geq k$  and check if  $x = 0$  is stable, because (i) if  $x = 0$  is not stable when  $l \geq k$  then  $x = 1$  cannot be stable either, as selection is stronger, on the whole, towards 0; and (ii) checking the other case (stability of  $x = 1$  when  $k \geq l$ ) is symmetric, and can be done in the same way by writing a recurrence equation for the frequency  $y$  of phenotype  $B$  rather than  $A$  and studying the case of  $y = 0$ .

To check if  $x = 0$  is stable, we start with a value very close to 0 and check if after a period of  $k+l$  generations the population is closer or farther from 0 compared to where it started.

For  $x_0 = x(t=0) \sim 0$ , we can use a linear approximation of the form  $f_A(x_0) = f_A(0) + o(x_0)$  and  $f_B(x_0) = f_B(0) + o(x_0)$ , where:

$$f_A(0) = 1 + \eta\left(\frac{W-w}{w}\right)$$

$$f_B(0) = 1 + \eta\left(\frac{w-W}{W}\right)$$

For  $k$  generations in environment  $A$ , and  $l$  generations with environment  $B$ , in any given order, we can write:

$$x_{k+l} = x(t = k+l) \approx x_0 f_A^k(0) f_B^l(0) \Rightarrow$$

$$\frac{x_{k+l}}{x_0} \approx f_A^k(0) f_B^l(0)$$

so that if we start very close to zero ( $x_0 \sim 0$ ), the multiplicative change over the  $k+l$  generations can be approximated by  $f_A^k(0) f_B^l(0)$ .

If  $f_A^k(0) f_B^l(0) > 1$ , then  $x = 0$  is not stable; since  $x = 1$  is not stable either (due to  $l \geq k$ ), then we have a *protected polymorphism* somewhere ( $0 < x(t) < 1$  for any generation  $t$ ). In contrast, if  $f_A^k(0) f_B^l(0) < 1$ , then  $x = 0$  is stable and the *protected polymorphism* disappears.

Following we examine the protected polymorphism in several special and general cases.

$$W = w$$

In this case, fitness in both environments is equivalent, there is no selection, and therefore evolution is neutral. Indeed, we find that  $f_A(x) = f_B(x) \equiv 1$ , without an approximation.

$$\eta = 0$$

In this case, there is no feedback between phenotype and inheritance, and only drift generates genetic variance, and evolution is neutral. Indeed, we get  $f_A(x) = f_B(x) \equiv 1$ .

$$\eta = 1$$

In this case, development is not stochastic, and after one generation the model becomes a standard two-type genetic model. Only genetic drift generates genetic variance, but natural selection does play a role. Indeed, we get  $f_A^k(0)f_B^l(0) = \left(\frac{W}{w}\right)^{k-l}$ . Since  $W > w$ , we find that  $\frac{x_{k+l}}{x_0}$  is

$$\begin{cases} < 1 & , k < l \\ = 1 & , k = l \\ > 1 & , k > l \end{cases}$$

### **Proposition for $k = l$**

If  $k = l, W > w > 0, 1 > \eta > 0$ , then  $f_A^k(0)f_B^l(0) > 1$ .

### **Proof**

First,  $f_A^k(0)f_B^l(0) = (f_A(0)f_B(0))^k > 1$  iff  $f_A(0)f_B(0) > 1$ .

To show the latter,

$$f_A(0)f_B(0) =$$

$$\begin{aligned}
& (1 + \eta \frac{W-w}{w}) \cdot (1 + \eta \frac{w-W}{W}) = \\
& (1 - \eta + \eta \frac{W}{w}) \cdot (1 - \eta + \eta \frac{w}{W}) = \\
& (1 - \eta)^2 + \eta^2 + \eta(1 - \eta)(\frac{W}{w} + \frac{w}{W}) = \\
& 1 - 2\eta(1 - \eta) + \eta(1 - \eta)(\frac{W^2 + w^2}{Ww}) = \\
& 1 + \eta(1 - \eta) \frac{W^2 - 2Ww + w^2}{Ww} = \\
& 1 + \eta(1 - \eta) \frac{(W - w)^2}{Ww}
\end{aligned}$$

which, under the proposition conditions, is  $> 1$ . ■

**Proposition for  $l > k = 1$**

If  $l > 1 + (1 - \eta) \frac{W-w}{w}$  then  $f_A(0)f_B^l(0) < 1$ .

**Proof**

Set  $n = l - 1$ . Then,

$$\begin{aligned}
n > (1 - \eta) \frac{W-w}{w} & \Leftrightarrow \\
n\eta \frac{W-w}{W} & > \eta(1 - \eta) \frac{(W-w)^2}{Ww} \Leftrightarrow \\
1 - n\eta \frac{w-W}{W} & > 1 + \eta(1 - \eta) \frac{(W-w)^2}{Ww} \Leftrightarrow \\
1 & > \frac{1 + \eta(1 - \eta) \frac{(W-w)^2}{Ww}}{1 - n\eta \frac{w-W}{W}}
\end{aligned} \tag{8}$$

Now,  $W > w \Rightarrow 1 \geq \frac{W-w}{W} \geq 0$ , and together with  $1 \geq \eta \geq 0$  we get  $0 \geq \eta \frac{w-W}{W} \geq -1$ . These conditions allow us to use the following Bernoulli inequality (proof with induction):

$$(1 + x)^n \leq \frac{1}{1 - nx}, \quad \forall x \in [-1, 0], \forall n \in \mathbb{N}. \tag{9}$$

From the Bernoulli inequality we have:

$$\left(1 + \eta \frac{w-W}{W}\right)^n \leq \frac{1}{1 - n\eta \frac{w-W}{W}} \quad (10)$$

Taken together, Eq. 8 and Eq. 10 imply that:

$$\begin{aligned} f_A(0)f_B^{n+1}(0) &= \\ &= \left(1 + \eta \frac{W-w}{w}\right) \left(1 + \eta \frac{w-W}{W}\right) \left(1 + \eta \frac{w-W}{W}\right)^n = \\ &= \left(1 + \eta(1-\eta) \frac{(W-w)^2}{Ww}\right) \left(1 + \eta \frac{w-W}{W}\right)^n \leq \\ &= \frac{1 + \eta(1-\eta) \frac{(W-w)^2}{Ww}}{1 - n\eta \frac{w-W}{W}} < 1 \end{aligned}$$

■

**Proposition for general case:**  $l > k \geq 1$

If  $l > k \left(1 + (1-\eta) \frac{W-w}{w}\right)$ , then  $f_A^k(0)f_B^l(0) < 1$ .

**Proof**

First, assume  $\frac{l-k}{k} \in \mathbb{N}$  and set  $n = \frac{l-k}{k} \Rightarrow n > (1-\eta) \frac{W-w}{w}$ .

Now, using the previous proposition,

$$f_A^k(0)f_B^l(0) = f_A^k(0)f_B^{(n+1)k}(0) = (f_A(0)f_B^{n+1}(0))^k < 1$$

because  $\forall y > 0, k > 0 \ y < 1 \Rightarrow y^k < 1$ .

Next, relax the assumption  $\frac{l-k}{k} \in \mathbb{N}$ ; set  $n = \lceil \frac{l-k}{k} \rceil > \frac{l-k}{k} > (1-\eta) \frac{W-w}{w}$ , then

$$f_A^k(0)f_B^l(0) < f_A^k(0)f_B^{(n+1)k}(0) = (f_A(0)f_B^{n+1}(0))^k < 1$$

and again, the previous proposition provides the last inequality. ■

**Proposition**

If  $l < k \left(1 + \frac{(1-\eta) \frac{W-w}{w}}{1 + \eta(1-\eta) \frac{(W-w)^2}{Ww}}\right)$  then  $f_A^k(0)f_B^l(0) > 1$ .

### **Proof**

Similar to previous proposition, but using a different Bernoulli inequality:

$$(1+x)^n \geq 1+nx, \quad \forall x > -1, \forall n \in \mathbb{R} \setminus (0,1).$$

■

### **Random environments**

TODO: - local stochastic stability - see Levikson & Karlin, 1970's; Liberman & Karlin, 1970's

## **Supporting figures**

- Fig. 5

## **References**

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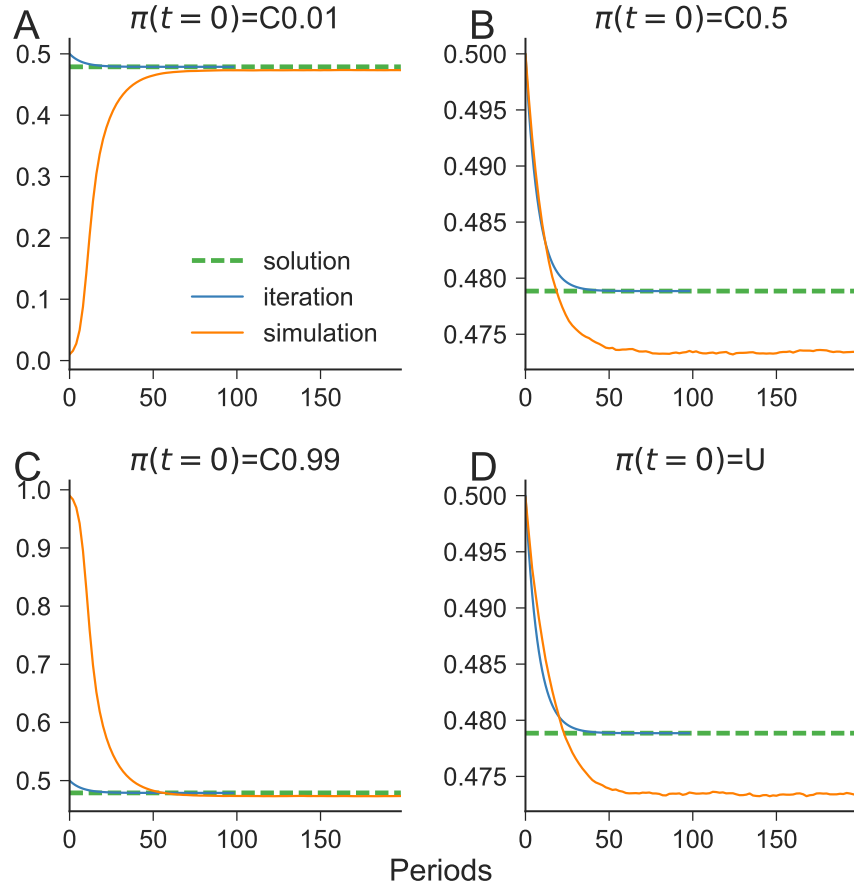


Figure 5: Population mean  $\pi$  in environment regime *A1B1*. Initial population distribution: (A)  $\pi_i=0.01$ ; (B)  $\pi_i=0.5$ ; (C)  $\pi_i=0.99$ ; (D)  $\pi_i \sim Uniform(0, 1)$ .  $N=100,000$ .