

Quantitative natural selection

Pierre Bernhard

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1 Fisher's fundamental theorem of evolution

1.1 The fundamental theorem

In a population, a given locus may host one of n alleles: A_1, A_2, \dots, A_n . The frequency *at birth time* of the pair (A_i, A_i) is P_{ii} , and, because the pairs (A_i, A_j) and (A_j, A_i) are undistinguishable, their frequency is $2P_{ij}$. Obviously, $\sum P_{ij} = 1$.

The pair (A_i, A_j) causes a *viability* w_{ij} , which measures the probability that an individual with this pair of alleles reach the age of reproduction. (Alternatively: a measure of the number of his progeny). The mean fitness and variance of the population at birth are

$$\bar{w} = \sum_{ij} P_{ij} w_{ij}, \quad \text{and} \quad \sigma^2 = \sum_{ij} (w_{ij} - \bar{w})^2 P_{ij}.$$

The frequency of the pair (A_i, A_j) at the age of reproduction is

$$P'_{ij} = \frac{w_{ij}}{\bar{w}} P_{ij}.$$

This is also the frequency in the next generation. The new mean fitness is

$$\bar{w}' = \sum_{ij} P'_{ij} w_{ij} = \sum_{ij} \frac{w_{ij}^2}{\bar{w}} P_{ij},$$

and the variation of mean fitness is therefore

$$\Delta \bar{w} = \frac{1}{\bar{w}} \left(\sum_{ij} w_{ij}^2 P_{ij} - \bar{w}^2 \right) = \frac{1}{\bar{w}} \sum_{ij} (w_{ij}^2 - \bar{w}^2) P_{ij}.$$

This can also be written as

$$\Delta \bar{w} = \frac{1}{\bar{w}} \left(\sum_{ij} (w_{ij} - \bar{w})^2 P_{ij} + 2 \sum_{ij} w_{ij} \bar{w} P_{ij} - 2\bar{w}^2 \right).$$

The last two terms cancel, to leave

$$\Delta \bar{w} = \frac{1}{\bar{w}} \sum_{ij} (w_{ij} - \bar{w})^2 P_{ij} = \frac{\sigma^2}{\bar{w}}. \quad (1)$$

1.2 Further remarks

1. In the above calculation, whose result is known as Fisher's fundamental theorem of evolution, the fact that we deal with *pairs* of alleles and double indices (ij) plays no role.
2. In that respect, one considers the frequencies of isolated alleles as

$$p_i = \sum_j P_{ij},$$

and *random mating* translates into the equality $P_{ij} = p_i p_j$, which is *not* satisfied under preferred mating. The increase in p_i during one generation is

$$\delta_i := p'_i - p_i = \frac{1}{\bar{w}} \sum_j P_{ij} (w_{ij} - \bar{w}).$$

3. One defines the marginal viability effect of allele i as α_i defined as the solution of the following "least squares" optimisation problem (see [1])

$$\min_{\alpha} \sum_{ij} P_{ij} (w_{ij} - \bar{w} - \alpha_i - \alpha_j)^2,$$

which is given in terms of the matrix $P = (P_{ij})$, its diagonal D and the vector δ of marginal increases by (caution: $\delta \bar{w}$ is just the product of the vector δ and the scalar \bar{w}) $\alpha = (P + D)^{-1} \delta \bar{w}$.

4. The variation of the genetic viability variance may also be evaluated, as

$$\begin{aligned} \Delta \sigma^2 &:= \sigma'^2 - \sigma^2 = \sum_{ij} P_{ij} \frac{w_{ij}}{\bar{w}} \left(w_{ij} - \bar{w} - \frac{\sigma^2}{\bar{w}} \right) - \sum_{ij} P_{ij} (w_{ij} - \bar{w}) \\ &= \sum_{ij} P_{ij} \left(\frac{w_{ij}}{\bar{w}} - 1 \right) (w_{ij} - \bar{w})^2 - 2 \frac{\sigma^2}{\bar{w}} \sum_{ij} P_{ij} \frac{w_{ij}}{\bar{w}} (w_{ij} - \bar{w}) + \frac{\sigma^4}{\bar{w}^2} \\ &= \frac{1}{\bar{w}} \sum_{ij} P_{ij} (w_{ij} - \bar{w})^3 - 2 \frac{\sigma^2}{\bar{w}^2} \sum_{ij} P_{ij} (w_{ij} - \bar{w})^2 \\ &\quad - 2 \frac{\sigma^2}{\bar{w}^2} \sum_{ij} P_{ij} \bar{w} (w_{ij} - \bar{w}) + \frac{\sigma^4}{\bar{w}^2} \\ &= \frac{1}{\bar{w}} \sum_{ij} P_{ij} (w_{ij} - \bar{w})^3 - \frac{\sigma^4}{\bar{w}^2} \\ &= \frac{1}{\bar{w}} \sum_{ij} P_{ij} (w_{ij} - \bar{w})^3 - (\Delta \bar{w})^2. \end{aligned} \tag{2}$$

2 Quantitative genetics and the breeder's equation

(Pierre Bernhard, January, 22, 2013)

2.1 Introduction

We consider a population Ω of a given species. Each individual is characterized by a phenotype (collection of traits) $z \in \mathbb{R}^n$. However, the value of each trait may be partitioned as a mean value ζ , which depends on the genotype of the individual, and an environmental variability ε , a random variable with zero mean, density $\pi(\cdot)$, independent from the distribution of ζ . Our set of hypotheses is therefore: $z, \zeta, \varepsilon \in \mathbb{R}^n$, and

$$\begin{aligned} z &= \zeta + \varepsilon, \\ \mathbb{E}\varepsilon &= \int_{\mathbb{R}^n} \varepsilon \pi(\varepsilon) d\varepsilon = 0 \quad \implies \quad \bar{z} := \mathbb{E}z = \mathbb{E}\zeta =: \bar{\zeta}, \\ \mathbb{E} \begin{pmatrix} \zeta - \bar{\zeta} \\ \varepsilon \end{pmatrix} \begin{pmatrix} (\zeta - \bar{\zeta})^t & \varepsilon^t \end{pmatrix} &= \begin{pmatrix} G & 0 \\ 0 & E \end{pmatrix}, \end{aligned}$$

hence also

$$P := \mathbb{E}(z - \bar{z})(z - \bar{z})^t = G + E.$$

(G stands for Genetic, E for Environmental, and P for Population. Notations borrowed from [2].)

The (misleading ?) notation $\mathbb{E}\zeta$ refers to the mean *over the population* Ω . The total “weight” of Ω is N . There is a difficulty here in the fact that, to simplify the notation, we shall often do *as if* Ω were a continuum. Therefore we call “weight” of the population what should be the number of individuals if it were finite.

The “weight” of individuals with traits in a given subdomain of \mathbb{R}^n is a measure over \mathbb{R}^n . We assume that it has a density $n(z)$, and that there is a corresponding density $\nu(\zeta)$ of the genotype-induced mean traits. (We shall call ζ the genotype, in short.)

We shall assume with little loss of generality that π , n and ν have compact support. All integrals will be over \mathbb{R}^n or $\mathbb{R} \times \mathbb{R}^n$ as needed. Hence

$$N = \int \nu(\zeta) d\zeta, \quad \bar{z} = \bar{\zeta} = \frac{1}{N} \int \zeta \nu(\zeta) d\zeta.$$

We shall consider the change in these variables from generation k to generation $k + 1$, adding a subscript k or $k + 1$ as needed to the quantities that change with them. We assume that the *fitness* of the individuals is related to z by a function $F(z)$ which measures the excess of births over deaths per capita among individuals with phenotype z .

2.2 Traits mean value

2.2.1 Asexual reproduction

In this simple model, “likes beget likes”, i.e. the offspring have the same genotype as their parent. As a result, we get the following simple hereditary mechanism:

$$\nu_{k+1}(\zeta) = \int (1 + F(\zeta + \varepsilon)) \nu_k(\zeta) \pi(\varepsilon) d\varepsilon, \quad (3)$$

and

$$N_{k+1} = \iint (1 + F(\zeta + \varepsilon)) \nu_k(\zeta) \pi(\varepsilon) d\varepsilon d\zeta$$

Let $\bar{F}_k = (1/N_k) \int F(\zeta + \varepsilon) \nu_k(\zeta) \pi(\varepsilon) d\zeta d\varepsilon$ denote the average fitness of the generation k . We get

$$N_{k+1} = (1 + \bar{F}_k) N_k.$$

We aim to compute \bar{z}_{k+1} . We have

$$\begin{aligned} \bar{z}_{k+1} &= \frac{1}{N_{k+1}} \int \zeta \nu_{k+1}(\zeta) d\zeta = \frac{1}{N_{k+1}} \iint \zeta (1 + F(\zeta + \varepsilon)) \nu_k(\zeta) \pi(\varepsilon) d\varepsilon d\zeta \\ &= \frac{1}{N_{k+1}} \iint \zeta (1 + \bar{F}_k) \nu_k(\zeta) \pi(\varepsilon) d\varepsilon d\zeta + \\ &\quad \frac{1}{N_{k+1}} \iint \zeta (F(\zeta + \varepsilon) - \bar{F}_k) \nu_k(\zeta) \pi(\varepsilon) d\varepsilon d\zeta \\ &= \bar{z}_k + \frac{1}{(1 + \bar{F}_k) N_k} \iint (\zeta - \bar{\zeta}_k) (F(\zeta + \varepsilon) - \bar{F}_k) \nu_k(\zeta) \pi(\varepsilon) d\varepsilon d\zeta. \end{aligned}$$

The last equation uses the fact that

$$\frac{1}{N_k} \iint \bar{\zeta}_k (F(\zeta + \varepsilon) - \bar{F}_k) \nu_k(\zeta) \pi(\varepsilon) d\varepsilon d\zeta = 0.$$

Let

$$\gamma_k = \frac{1}{N_k} \iint (\zeta - \bar{\zeta}_k) (F(\zeta + \varepsilon) - \bar{F}_k) \nu_k(\zeta) \pi(\varepsilon) d\varepsilon d\zeta \quad (4)$$

denote the covariance between the additive genetic variation and fitness in the population.

We obtain the fundamental theorem:

Theorem 1 *The variation in mean phenotype value in one generation is proportional to the covariance between additive genetic variation and fitness in the population:*

$$\bar{z}_{k+1} = \bar{z}_k + \frac{\gamma_k}{1 + \bar{F}_k}. \quad (5)$$

Affine approximation Assume that the variations in z are actually sufficiently small so that in the range considered, F is well approximated by its first order linear approximation

$$F(z) = \alpha + \langle \beta, z \rangle. \quad (6)$$

The vector β plays the role of ∇F or *selection gradient*. It follows that $\bar{F} = \alpha + \langle \beta, \bar{z} \rangle$. Hence, the variation in \bar{z} is

$$\begin{aligned} \bar{z}_{k+1} - \bar{z}_k &= \frac{1}{N_k(1 + \bar{F}_k)} \iint (\zeta - \bar{\zeta}_k)(\zeta + \varepsilon - \bar{\zeta}_k)^t \beta \nu_k(\zeta) \pi(\varepsilon) \, d\varepsilon \, d\zeta \\ &= \frac{1}{1 + \bar{F}_k} G_k \beta + \frac{1}{(1 + \bar{F}_k) N_k} \int \left[\int (\zeta - \bar{\zeta}_k) \nu_k(\zeta) \, d\zeta \right] \varepsilon^t \beta \pi(\varepsilon) \, d\varepsilon. \end{aligned}$$

The last integral is null (it is the product of two null terms), and we obtain the *main equation of natural selection*:

$$\bar{z}_{k+1} - \bar{z}_k = \frac{1}{1 + \bar{F}_k} G_k \beta. \quad (7)$$

However, the selection gradient β is not directly measurable. What is measurable is the covariance S between traits and fitness. Let therefore

$$S_k := \int (z - \bar{z}_k)(F(z) - \bar{F}_k) n_k(z) \, dz,$$

with the same affine approximation of F , this gives

$$S_k = P_k \beta,$$

so that with the main equation (7), we get the *breeder's equation*:

$$\bar{z}_{k+1} - \bar{z}_k = \frac{1}{1 + \bar{F}_k} G_k P_k^{-1} S_k. \quad (8)$$

2.2.2 Sexual reproduction

We provide a vastly simplified model of sexual reproduction. Say, for now, that we are interested in a male character, typically a male “display” such as considered in sexual selection. Let now $n(z)$ and $\nu(\zeta)$ be densities of males. We assume that the genotypes of the offspring of a given male are distributed around the parent's genotype, the difference being a random variable η with zero mean, and density $\rho(\cdot)$. Hence, the offspring of every male with genotype ζ are of the form $\zeta + \eta$, with

$$\int \eta \rho(\eta) \, d\eta = 0.$$

Let $\mu_{k+1}(\zeta)$ be the measure density of the offspring of all males with genotype ζ in population k , i.e.

$$\mu_{k+1}(\zeta) = \int (1 + F(\zeta + \varepsilon)) \nu_k(\zeta) \pi(\varepsilon) d\varepsilon.$$

Our simplified model of sexual reproduction yields

$$\nu_{k+1}(\zeta) = \int \mu_{k+1}(\zeta - \eta) \rho(\eta) d\eta.$$

Hence,

$$\nu_{k+1}(\zeta) = \iint (1 + F(\zeta - \eta + \varepsilon)) \nu_k(\zeta - \eta) \pi(\varepsilon) \rho(\eta) d\varepsilon d\eta, \quad (9)$$

and

$$\bar{z}_{k+1}(\zeta) = \frac{1}{(1 + \bar{F}_k) N_k} \iiint \zeta (1 + F(\zeta - \eta + \varepsilon)) \nu_k(\zeta - \eta) \pi(\varepsilon) \rho(\eta) d\varepsilon d\eta d\zeta.$$

Hence

$$\begin{aligned} \bar{z}_{k+1}(\zeta) &= \\ &= \frac{1}{(1 + \bar{F}_k) N_k} \iiint (\zeta - \eta) (1 + F(\zeta - \eta + \varepsilon)) \nu_k(\zeta - \eta) \pi(\varepsilon) \rho(\eta) d\varepsilon d\eta d\zeta \\ &+ \frac{1}{(1 + \bar{F}_k) N_k} \iiint \eta (1 + F(\zeta - \eta + \varepsilon)) \nu_k(\zeta - \eta) \pi(\varepsilon) \rho(\eta) d\varepsilon d\eta d\zeta. \end{aligned}$$

Using Fubini's theorem, we integrate first in ζ as the inner integral, then in ε , and finally in η as the outer integral. Let $\theta = \zeta - \eta$. We get

$$\begin{aligned} \bar{z}_{k+1}(\zeta) &= \frac{1}{(1 + \bar{F}_k) N_k} \int \left[\iint \theta (1 + F(\theta + \varepsilon)) \nu_k(\theta) \pi(\varepsilon) d\theta d\varepsilon \right] \rho(\eta) d\eta \\ &+ \frac{1}{(1 + \bar{F}_k) N_k} \int \eta \left[\iint (1 + F(\theta + \varepsilon)) \nu_k(\theta) \pi(\varepsilon) d\zeta d\varepsilon \right] \rho(\eta) d\eta. \end{aligned}$$

In the first line, the inner double integral is exactly the same as for the asexual reproduction, and is independent from η , it is therefore multiplied by $\int \rho(\eta) d\eta = 1$. In the second line, the inner double integral is again independent from η . It is therefore just multiplied by $\int \eta \rho(\eta) d\eta = 0$ by hypothesis.

Therefore, for this highly simplified model of sexual reproduction, we recover the same theorem and equations (7), (8), as in our model of asexual reproduction.

2.3 Genetic covariance

In [2], the authors question whether the genetic covariance matrix G changes from generation to generation, and, based upon statistical laboratory experiments, concludes that indeed, it does. We propose here a investigation of that question based upon our model.

2.3.1 Asexual reproduction

We start again from equation (3), and get

$$G_{k+1} = \frac{1}{(1 + \bar{F}_k)N_k} \iint (\zeta - \bar{\zeta}_{k+1})(\zeta - \bar{\zeta}_{k+1})^t (1 + \bar{F}_k(\zeta + \varepsilon)) \nu_k(\zeta) \pi(\varepsilon) d\varepsilon d\zeta.$$

Replacing as previously $1 + F$ by $(1 + \bar{F}_k) + (F - \bar{F}_k)$ and using (5), we get

$$G_{k+1} = A + B$$

with

$$\begin{aligned} A &= \frac{1}{N_k} \iint \left(\zeta - \bar{\zeta}_k - \frac{\gamma_k}{1 + \bar{F}_k}\right) \left(\zeta - \bar{\zeta}_k - \frac{\gamma_k}{1 + \bar{F}_k}\right)^t \nu_k(\zeta) \pi(\varepsilon) d\varepsilon d\zeta \\ B &= \frac{1}{(1 + \bar{F}_k)N_k} \iint \left(\zeta - \bar{\zeta}_k - \frac{\gamma_k}{1 + \bar{F}_k}\right) \left(\zeta - \bar{\zeta}_k - \frac{\gamma_k}{1 + \bar{F}_k}\right)^t (F(\zeta + \varepsilon) - \bar{F}_k) \\ &\quad \nu_k(\zeta) \pi(\varepsilon) d\varepsilon d\zeta. \end{aligned}$$

We easily get

$$A = G_k + \frac{\gamma_k \gamma_k^t}{(1 + \bar{F}_k)^2}.$$

Concerning B we have

$$\begin{aligned} B &= \frac{1}{(1 + \bar{F}_k)N_k} \iint (\zeta - \bar{\zeta}_k)(\zeta - \bar{\zeta}_k)^t (F(\zeta + \varepsilon) - \bar{F}_k) \nu_k(\zeta) \pi(\varepsilon) d\varepsilon d\zeta \\ &\quad - \left[\frac{1}{(1 + \bar{F}_k)N_k} \iint (\zeta - \bar{\zeta}_k)(F(\bar{\zeta} + \varepsilon) - \bar{F}_k) \nu_k(\zeta) \pi(\varepsilon) d\varepsilon d\zeta \right] \frac{\gamma_k^t}{1 + \bar{F}_k} \\ &\quad - \frac{\gamma_k}{1 + \bar{F}_k} \left[\frac{1}{(1 + \bar{F}_k)N_k} \iint (\zeta - \bar{\zeta}_k)^t (F(\bar{\zeta} + \varepsilon) - \bar{F}_k) \nu_k(\zeta) \pi(\varepsilon) d\varepsilon d\zeta \right] \\ &\quad + \frac{1}{(1 + \bar{F}_k)N_k} \frac{\gamma_k \gamma_k^t}{(1 + \bar{F}_k)^2} \iint (F(\bar{\zeta} + \varepsilon) - \bar{F}_k) \nu_k(\zeta) \pi(\varepsilon) d\varepsilon d\zeta. \end{aligned}$$

In this expression, the two bracketed integrals are transposed from each other, and are equal to $\gamma_k/(1 + \bar{F}_k)$, and the last line is null. The first line, on the other hand, involves a third moment statistics between ζ twice and fitness

$$T_k := \frac{1}{N_k} \iint (\zeta - \bar{\zeta}_k)(\zeta - \bar{\zeta}_k)^t (F(\zeta + \varepsilon) - \bar{F}_k) \nu_k(\zeta) \pi(\varepsilon) d\varepsilon d\zeta.$$

Hence

$$B = \frac{1}{1 + \bar{F}_k} T_k - 2 \frac{\gamma_k \gamma_k^t}{(1 + \bar{F}_k)^2},$$

and finally,

$$G_{k+1} = G_k - \frac{\gamma_k \gamma_k^t}{(1 + \bar{F}_k)^2} + \frac{1}{1 + \bar{F}_k} T_k. \quad (10)$$

or

$$G_{k+1} - G_k = \frac{1}{1 + \bar{F}_k} T_k - (\bar{z}_{k+1} - \bar{z}_k)(\bar{z}_{k+1} - \bar{z}_k)^t. \quad (11)$$

The second term in (10) is nonpositive definite. Hence, if the third moment T_k is small, natural selection tends to lower genetic diversity, as measured by its covariance matrix G .

Affine approximation If we use the affine approximation (6), we find (we must insert the term $F - \bar{F}_k = (\zeta + \varepsilon - \bar{\zeta}_k)^t \beta$ between the two $\zeta - \bar{\zeta}_k$ to have a correctly formed matrix product)

$$\begin{aligned} T_k &= \frac{1}{N_k} \iint (\zeta - \bar{\zeta}_k)(\zeta + \varepsilon - \bar{\zeta}_k)^t \beta (\zeta - \bar{\zeta}_k)^t \nu(\zeta) \pi(\varepsilon) d\varepsilon d\zeta \\ &= \frac{1}{N_k} \int (\zeta - \bar{\zeta}_k)(\zeta - \bar{\zeta}_k)^t \beta (\zeta - \bar{\zeta}_k)^t \nu(\zeta) d\zeta. \end{aligned}$$

As a matter of fact,

$$\iint (\zeta - \bar{\zeta}_k) \varepsilon^t \beta (\zeta - \bar{\zeta}_k)^t \nu(\zeta) \pi(\varepsilon) d\varepsilon d\zeta = 0$$

because each of its terms is of the form

$$\iint \phi(\zeta) \nu_k(\zeta) d\zeta \varepsilon_i \pi(\varepsilon) d\varepsilon = \int \phi(\zeta) \nu_k(\zeta) d\zeta \int \varepsilon_i \pi(\varepsilon) d\varepsilon = 0.$$

Moreover, T_k can be written as the contracted product of the third order statistics tensor of ζ . Let

$$H_k := \frac{1}{N_k} \int (\zeta - \bar{\zeta}_k) \otimes (\zeta - \bar{\zeta}_k) \otimes (\zeta - \bar{\zeta}_k) \pi(\varepsilon) d\zeta = \frac{1}{N_k} \int (\zeta - \bar{\zeta}_k)^{\otimes 3} \nu(\zeta) d\zeta,$$

we have

$$T_k = H_k \cdot \beta.$$

Using the evaluation of γ_k made above, we finally have

$$G_{k+1} = G_k - \frac{1}{(1 + \bar{F}_k)^2} G_k \beta \beta^t G_k + \frac{1}{1 + \bar{F}_k} H_k \cdot \beta.$$

2.3.2 Sexual reproduction

We now extend this analysis to our simple model of sexual reproduction, using (9).

We therefore have

$$G_{k+1} = \frac{1}{(1 + \bar{F}_k) N_k} \iiint (\zeta - \bar{\zeta}_k)(\zeta - \bar{\zeta}_k)^t (1 + F(\zeta - \eta + \varepsilon)) \nu_k(\zeta - \eta) \pi(\varepsilon) \rho(\eta) \, d\zeta \, d\varepsilon \, d\eta.$$

We rewrite this equation as

$$G_{k+1} = \frac{1}{(1 + \bar{F}_k) N_k} (A + B + B^t + C)$$

with

$$\begin{aligned} A &= \iiint (\zeta - \eta - \bar{\zeta}_{k+1})(\zeta - \eta - \bar{\zeta}_{k+1})^t (1 + F(\zeta - \eta + \varepsilon)) \nu_k(\zeta - \eta) \pi(\varepsilon) \, d\zeta \, d\varepsilon \rho(\eta) \, d\eta \\ B &= \int \eta \left[\iint (\zeta - \eta - \bar{\zeta}_{k+1})^t (1 + F(\zeta - \eta + \varepsilon)) \nu_k(\zeta - \eta) \pi(\varepsilon) \, d\varepsilon \, d\eta \right] \rho(\eta) \, d\eta \\ C &= \int \eta \eta^t \left[\iint (1 + F(\zeta - \eta + \varepsilon)) \nu_k(\zeta - \eta) \pi(\varepsilon) \, d\zeta \, d\varepsilon \right] \rho(\eta) \, d\eta. \end{aligned}$$

In each of these three terms, using Fubini's theorem, we integrate in η as the outer integral, and in the inner double integral, we make the change of variable $\zeta - \eta = \theta$. The three inner integrals are independant of η , therefore the integration in η amounts to a multiplication by 1 and can be ignored.

The term A coincides with the formula of the asexual reproduction case of the previous subsection. The inner double integral of the term B reads

$$\int (\theta - \bar{\zeta}_{k+1}) \nu_{k+1}(\theta) \, d\theta = 0,$$

and the double integral of the term C is just $1 + \bar{F}_k$. Let therefore the covariance matrix of η be

$$D := \mathbb{E} \eta \eta^t = \int \eta \eta^t \rho(\eta) \, d\eta,$$

we find

$$G_{k+1} = G_k - \frac{\gamma_k \gamma_k^t}{(1 + \bar{F})^2} + \frac{1}{1 + \bar{F}_k} (T_k + D). \quad (12)$$

or in the affine approximation

$$G_{k+1} = G_k - \frac{1}{(1 + \bar{F})^2} G_k \beta \beta^t G_k + \frac{1}{1 + \bar{F}_k} (H_k \cdot \beta + D).$$

2.4 Final remarks

- In the above model, let $1 + F = w$, and likewise $1 + \bar{F}_k = \bar{w}_k$, be the ratio of births to deaths and its mean in a population, and notice the striking similarity between equations (1) and (5) on the one hand, and (2) and (11) on the other hand.
- Comparison of equations (10) and (12) show that our overly simplified model suffices to show that sexual reproduction increases the genetic variance.

References

- [1] J. W. EWENS AND A. HASTINGS, *Aspects of optimality behavior in population genetics theory*, in *Evolution and biocomputation : computational models of evolution*, W. Banzhaf and F. H. Eeckman, eds., Springer, Berlin, 1995, pp. 7–17.
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