# Appendix A: Obtaining an expression for average fitness under unconstrained population growth.

The aim is to simplify Eq. 14 in the main text. The expanded form of that expression is:

$$F = \frac{\int\limits_E \left( \sum_{j=1}^{K} \sum_{r=0}^{2} \beta_{r,j} x_j^r \right) \exp\left( \sum_{k=1}^{K} \sum_{r=0}^{2} \gamma_{r,k} x_k^r \right) \sum_{l=1}^{L} \psi_l \exp\left( -\frac{1}{2} \sum_{k=1}^{K} \left( \frac{x_k - \mu_{l,k}}{\sigma_k} \right)^2 \right) d\mathbf{x}}{\int\limits_E \exp\left( \sum_{k=1}^{K} \sum_{r=0}^{2} \gamma_{r,k} x_k^r \right) \sum_{l=1}^{L} \psi_l \exp\left( -\frac{1}{2} \sum_{k=1}^{K} \left( \frac{x_k - \mu_{l,k}}{\sigma_k} \right)^2 \right) d\mathbf{x}} \quad \text{A.1}$$

Rearranging the integrals and sums gives,

$$F = \frac{\sum_{l=1}^{L} \psi_l \int\limits_E \left( \sum_{j=1}^{K} \sum_{r=0}^{2} \beta_{r,j} x_j^r \right) \exp\left( \sum_{k=1}^{K} \sum_{r=0}^{2} \gamma_{r,k} x_k^r - \frac{1}{2} \sum_{k=1}^{K} \left( \frac{x_k - \mu_{l,k}}{\sigma_k} \right)^2 \right) d\mathbf{x}}{\sum_{l=1}^{L} \psi_l \int\limits_E \exp\left( \sum_{k=1}^{K} \sum_{r=0}^{2} \gamma_{r,k} x_k^r - \frac{1}{2} \sum_{k=1}^{K} \left( \frac{x_k - \mu_{l,k}}{\sigma_k} \right)^2 \right) d\mathbf{x}} \quad \text{A.2}$$

We focus first on the integral in the denominator. For each dimension ($j$) in $E$-space, this can be written as

$$\int\limits_{E_{(-j)}} \exp\left( \sum_{\substack{k=1 \\ k \neq j}}^{K} \sum_{r=0}^{2} \gamma_{r,k} x_k^r - \frac{1}{2} \sum_{\substack{k=1 \\ k \neq j}}^{K} \left( \frac{x_k - \mu_{l,k}}{\sigma_k} \right)^2 \right) \int\limits_j \exp\left( \gamma_{0,j} + \gamma_{1,j} x_j + \gamma_{2,j} x_j^2 - \frac{1}{2} \left( \frac{x_j - \mu_{l,j}}{\sigma_j} \right)^2 \right) dx_j \, d\mathbf{x}_{(-j)} \quad \text{A.3}$$

Where the subscript (-$j$) denotes vectors without the $j^{\text{th}}$ element and multiple integrals without the $j^{\text{th}}$ dimension. Focusing on the one-dimensional inner integral in this latest expression:

$$\int_j \exp\left\{\left(\gamma_{0,j} - \frac{\mu_{l,j}^2}{2\sigma_j^2}\right) + \left(\gamma_{1,j} + \frac{\mu_{l,j}}{\sigma_j^2}\right)x_j + \left(\gamma_{2,j} - \frac{1}{2\sigma_j^2}\right)x_j^2\right\}dx_j =$$

$$\exp\left(\gamma_{0,j} - \frac{\mu_{l,j}^2}{2\sigma_j^2}\right)\int_j \exp\left\{\left(\gamma_{1,j} + \frac{\mu_{l,j}}{\sigma_j^2}\right)x_j + \left(\gamma_{2,j} - \frac{1}{2\sigma_j^2}\right)x_j^2\right\}dx_j \qquad \text{A.4}$$

The infinite integral in this last expression belongs to the class of Gaussian integrals (Owen 1980). The particular closed form of interest here is provided by the general formula:

$$\int_{-\infty}^{\infty} \exp\left(-\frac{1}{2}ax^2 + Jx\right)dx = \left(\frac{2\pi}{a}\right)^{\frac{1}{2}} \exp\left(\frac{J^2}{2a}\right) \qquad \text{A.5}$$

Where, in our case,

$$a = \frac{1}{\sigma_j^2} - 2\gamma_{2,j} \quad \text{and} \quad J = \gamma_{1,j} + \frac{\mu_{l,j}}{\sigma_j^2} \qquad \text{A.6}$$

Applying this to eq. A.4 gives

$$\left(\frac{2\pi\sigma_j^2}{1-2\gamma_{2,j}\sigma_j^2}\right)^{\frac{1}{2}} \exp\left(\gamma_{0,j} - \frac{\mu_{l,j}^2}{2\sigma_j^2} + \frac{\left(\gamma_{1,j}\sigma_j^2 + \mu_{l,j}\right)^2}{2\sigma_j^2(1-2\gamma_{2,j}\sigma_j^2)}\right) \qquad \text{A.7}$$

By peeling off all the one-dimensional integrals in eq. A.3 in this way (i.e. using eqs A.4-A.7) we get an integral-free expression for the denominator of eq. A.2

$$\sum_{l=1}^{L}\psi_l \prod_{j=1}^{K}\left(\frac{2\pi\sigma_j^2}{1-2\gamma_{2,j}\sigma_j^2}\right)^{\frac{1}{2}} \exp\left(\gamma_{0,j} - \frac{\mu_{l,j}^2}{2\sigma_j^2} + \frac{\left(\gamma_{1,j}\sigma_j^2 + \mu_{l,j}\right)^2}{2\sigma_j^2(1-2\gamma_{2,j}\sigma_j^2)}\right) \qquad \text{A.8}$$

We now return to the numerator of eq. A.2

$$\sum_{l=1}^{L}\psi_l \sum_{j=1}^{K}\sum_{r=0}^{2} \int_E \beta_{r,j}x_j^r \exp\left(\sum_{k=1}^{K}\sum_{r=0}^{2}\gamma_{r,k}x_k^r - \frac{1}{2}\sum_{k=1}^{K}\left(\frac{x_k - \mu_{l,k}}{\sigma_k}\right)^2\right)d\mathbf{x} \qquad \text{A.9}$$

For given values of $j$ and $r$ in the outer sums, the inner integral can be written

$$\left\{ \int_{E_{(-j)}} \exp\left( \sum_{\substack{k=1\\k\neq j}}^{K} \sum_{r=0}^{2} \gamma_{r,k} x_k^r - \frac{1}{2} \sum_{\substack{k=1\\k\neq j}}^{K} \left( \frac{x_k - \mu_{l,k}}{\sigma_k} \right)^2 \right) d\mathbf{x}_{(-j)} \right\} \times \left\{ \beta_{r,j} \int_j x_j^r \exp\left( \gamma_{0,j} + \gamma_{1,j} x_j + \gamma_{2,j} x_j^2 - \frac{1}{2} \left( \frac{x_j - \mu_{l,j}}{\sigma_j} \right)^2 \right) dx_j \right\} \qquad \text{A.10}$$

The first part of this product is provided by applying eq. A.7 to get

$$\prod_{\substack{k=1\\k\neq j}}^{K} \left( \frac{2\pi\sigma_k^2}{1-2\gamma_{2,k}\sigma_k^2} \right)^{\frac{1}{2}} \exp\left( \gamma_{0,k} - \frac{\mu_{l,k}^2}{2\sigma_k^2} + \frac{\left(\gamma_{1,k}\sigma_k^2 + \mu_{l,k}\right)^2}{2\sigma_k^2(1-2\gamma_{2,k}\sigma_k^2)} \right) \qquad \text{A.11}$$

The second component of the product in eq. A.10 is another Gaussian integral.

$$\beta_{r,j} \exp\left( \gamma_{0,j} - \frac{1}{2} \frac{\mu_{l,j}^2}{\sigma_j^2} \right) \int_j x_j^r \exp\left( \left( \gamma_{1,j} + \frac{\mu_{l,j}}{\sigma_j^2} \right) x_j + \left( \gamma_{2,j} - \frac{x_j^2}{2\sigma_j^2} \right) x_j^2 \right) dx_j \qquad \text{A.12}$$

We will examine the cases $r=0, r=1, r=2$ separately, each time leading to an expression for the entire product in eq. A.10

*Case* $r=0$ *:* In this case, the integral of eq. A.12 falls back to the form of eq.A.5, it has the closed form solution in eq. A.7 and the entire product in eq. A.10 takes the form

$$\sum_{j=1}^{K} \beta_{0,j} \left\{ \prod_{k=1}^{K} \left( \frac{2\pi\sigma_k^2}{1-2\gamma_{2,k}\sigma_k^2} \right)^{\frac{1}{2}} \exp\left( \gamma_{0,k} - \frac{\mu_{l,k}^2}{2\sigma_k^2} + \frac{\left(\gamma_{1,k}\sigma_k^2 + \mu_{l,k}\right)^2}{2\sigma_k^2(1-2\gamma_{2,k}\sigma_k^2)} \right) \right\} \qquad \text{A.13}$$

Case $r=1$: In this case we need to use the Gaussian closed-form

$$\int_{-\infty}^{\infty} x \exp\left( -\frac{1}{2} a x^2 + Jx \right) dx = \left( \frac{2\pi}{a} \right)^{\frac{1}{2}} \frac{J}{a} \exp\left( \frac{J^2}{2a} \right) \qquad \text{A.14}$$

For $J$ and $a$as specified in eq. A.6 . Applying this to eq. A.12gives

$$\beta_{1,j}\left(\frac{2\pi\sigma_j^2}{\left(1-2\gamma_{2,j}\sigma_j^2\right)}\right)^{\frac{1}{2}}\frac{\left(\gamma_{1,j}\sigma_j^2+\mu_{l,j}\right)}{\left(1-2\gamma_{2,j}\sigma_j^2\right)}\exp\left(\gamma_{0,j}-\frac{1}{2}\frac{\mu_{l,j}^2}{\sigma_j^2}+\frac{\left(\gamma_{1,j}\sigma_j^2+\mu_{l,j}\right)^2}{2\sigma_j^2(1-2\gamma_{2,j}\sigma_j^2)}\right) \qquad \text{A.15}$$

And the entire product in eq. A.10 takes the form

$$\sum_{j=1}^{K}\beta_{1,j}\frac{\left(\gamma_{1,j}\sigma_j^2+\mu_{l,j}\right)}{\left(1-2\gamma_{2,j}\sigma_j^2\right)}\left\{\prod_{k=1}^{K}\left(\frac{2\pi\sigma_k^2}{1-2\gamma_{2,k}\sigma_k^2}\right)^{\frac{1}{2}}\exp\left(\gamma_{0,k}-\frac{\mu_{l,k}^2}{2\sigma_k^2}+\frac{\left(\gamma_{1,k}\sigma_k^2+\mu_{l,k}\right)^2}{2\sigma_k^2(1-2\gamma_{2,k}\sigma_j^2)}\right)\right\} \qquad \text{A.16}$$

Case $r=2$: In this case we need to use the Gaussian closed-form

$$\int_{-\infty}^{\infty}x^2\exp\left(-\frac{1}{2}ax^2+Jx\right)dx=\left(\frac{2\pi}{a}\right)^{\frac{1}{2}}\frac{1}{a}\left(1+\frac{J^2}{a}\right)\exp\left(\frac{J^2}{2a}\right) \qquad \text{A.17}$$

For $J$ and $a$ as specified in eq. A.6. Applying this to eq. A.12 gives

$$\beta_{2,j}\left(\frac{2\pi\sigma_j^2}{\left(1-2\gamma_{2,j}\sigma_j^2\right)}\right)^{\frac{1}{2}}\frac{\sigma_j^2}{\left(1-2\gamma_{2,j}\sigma_j^2\right)}\left(1+\frac{\left(\gamma_{1,j}\sigma_j^2+\mu_{l,j}\right)^2}{\sigma_j^2\left(1-2\gamma_{2,j}\sigma_j^2\right)}\right)\exp\left(\gamma_{0,j}-\frac{1}{2}\frac{\mu_{l,j}^2}{\sigma_j^2}+\frac{\left(\gamma_{1,j}\sigma_j^2+\mu_{l,j}\right)^2}{2\sigma_j^2(1-2\gamma_{2,j}\sigma_j^2)}\right)$$

A.18

And the entire product in eq. A.10 takes the form

$$\sum_{j=1}^{K}\beta_{2,j}\frac{\sigma_j^2}{\left(1-2\gamma_{2,j}\sigma_j^2\right)}\left(1+\frac{\left(\gamma_{1,j}\sigma_j^2+\mu_{l,j}\right)^2}{\sigma_j^2\left(1-2\gamma_{2,j}\sigma_j^2\right)}\right)\left\{\prod_{k=1}^{K}\left(\frac{2\pi\sigma_k^2}{1-2\gamma_{2,k}\sigma_k^2}\right)^{\frac{1}{2}}\exp\left(\gamma_{0,k}-\frac{\mu_{l,k}^2}{2\sigma_k^2}+\frac{\left(\gamma_{1,k}\sigma_k^2+\mu_{l,k}\right)^2}{2\sigma_k^2(1-2\gamma_{2,k}\sigma_k^2)}\right)\right\} \text{A.19}$$

Using eqsA.13, A.16 and A.19 we can now write the closed-form expression for the numerator of eq. A.2

$$\sum_{l=1}^{L}\psi_l\Theta_l\sum_{j=1}^{K}\left\{\beta_{0,j}+\beta_{1,j}\frac{\left(\gamma_{1,j}\sigma_j^2+\mu_{l,j}\right)}{\left(1-2\gamma_{2,j}\sigma_j^2\right)}+\beta_{2,j}\frac{\sigma_j^2}{\left(1-2\gamma_{2,j}\sigma_j^2\right)}\left(1+\frac{\left(\gamma_{1,j}\sigma_j^2+\mu_{l,j}\right)^2}{\sigma_j^2\left(1-2\gamma_{2,j}\sigma_j^2\right)}\right)\right\} \qquad \text{A.20}$$

Where

$$\Theta_l = \prod_{k=1}^{K} \left( \frac{2\pi\sigma_k^2}{1-2\gamma_{2,k}\sigma_k^2} \right)^{\frac{1}{2}} \exp\left( \gamma_{0,k} - \frac{\mu_{l,k}^2}{2\sigma_k^2} + \frac{\left(\gamma_{1,k}\sigma_k^2 + \mu_{l,k}\right)^2}{2\sigma_k^2(1-2\gamma_{2,k}\sigma_k^2)} \right) \qquad \text{A.21}$$

We will not simplify these expressions further because they are most flexibly usable in this form. Collecting the above results together gives the following integral-free expressions for the exponential growth model

$$\frac{N_{t+1}}{N_t} = \exp\left( \frac{F_1}{F_2} \right) \qquad \text{A.22}$$

Where,

$$F_1 = \sum_{l=1}^{L} \left[ \psi_l \Theta_l \sum_{k=1}^{K} \left\{ \beta_{0,k} + \beta_{1,k} \frac{\left(\gamma_{1,k}\sigma_k^2 + \mu_{l,k}\right)}{\left(1-2\gamma_{2,k}\sigma_k^2\right)} + \beta_{2,k} \frac{\sigma_k^2}{\left(1-2\gamma_{2,k}\sigma_k^2\right)} \left( 1 + \frac{\left(\gamma_{1,k}\sigma_k^2 + \mu_{l,k}\right)^2}{\sigma_k^2\left(1-2\gamma_{2,k}\sigma_k^2\right)} \right) \right\} \right]$$

$$F_2 = \sum_{l=1}^{L} \psi_l \Theta_l \qquad \text{A.23}$$

$$\Theta_l = \prod_{k=1}^{K} \left( \frac{2\pi\sigma_k^2}{1-2\gamma_{2,k}\sigma_k^2} \right)^{\frac{1}{2}} \exp\left( \gamma_{0,k} - \frac{\mu_{l,k}^2}{2\sigma_k^2} + \frac{\left(\gamma_{1,k}\sigma_k^2 + \mu_{l,k}\right)^2}{2\sigma_k^2(1-2\gamma_{2,k}\sigma_k^2)} \right)$$