Supporting Information S2
for
When three traits make a line: Evolution of phenotypic plasticity and genetic assimilation through linear reaction norms in stochastic environments

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Mathematical analysis and comparisons with simulation results

1 Introduction

In order to explain the simulation results we here analyze the three-trait linear reaction norm model mathematically. We assume that the traits are uncorrelated with both U and Θ. In Section 2 we derive the conditional phenotypic variance $V_y(u) = var(y|U = u)$, and find the environmental cue $u = u_0$ where $V_y(u)$ is minimized (eq. (5) in the main text). We also find the unconditional phenotypic variance $V_y = E\left[V_y(U)\right]$. In Section 3 we consider the constant environment (ce) case with $\sigma_U^2 = \sigma_\Theta^2 = 0$, i.e. with $u = \mu_U$ and $\theta = \mu_\Theta$, and develop expressions for the equilibrium mean traits $\bar{z}_a^{*ce}$, $\bar{z}_b^{*ce}$ and $\bar{z}_c^{*ce}$ as well as for the equilibrium value u_0^{*ce}. We also show that these theoretical expressions are supported by simulation results. In Section 4 we formulate two conjectures regarding equilibrium properties in the stochastic case with $\sigma_U^2 \neq 0$, $\sigma_\Theta^2 \neq 0$ and $\sigma_{U\Theta} \neq 0$, from which follows the important equilibrium result $u_0^* = \mu_U$. In Section 5 we make the approximation that the phenotypic distribution is normal, such that the selection gradient and the equilibrium mean traits as well as u_0^* can be found analytically. The results support the conjectures in Section 4. In Section 6 we finally consider the influence from the fluctuations in the stationary mean trait values (as seen in the simulation results, Figure 2 in the paper) caused by the excitation sequences u_t and θ_t, which we assume to be normal and white, and again we compare theory with simulation results.

2 Minimization of the conditional and unconditional phenotypic variances

Our three-trait reaction norm model of the individual plastic phenotype y as function of u is according to eq. (3) in the main text

$$y(u) = z_a + z_b\left(u - z_c\right) \tag{S2-1}$$

We assume a large population where the traits z_a, z_b and z_c are normally distributed with phenotypic variances P_{aa}, P_{bb} and P_{cc}, and covariances P_{ab}, P_{ac} and P_{bc}. Since we are here only interested in the equilibrium case, we omit the time index and write the mean reaction norm as

$$\bar{y}(u) = \bar{z}_a + \bar{z}_b (u - \bar{z}_c) - P_{bc} \tag{S2-2}$$

From this follows the conditional variance of $y(u)$, which using the notation $V_y(u) = var(y|U = u)$ and with $E[(z_a - \bar{z}_a)(z_b - \bar{z}_b)(z_c - \bar{z}_c)] = E\left[(z_b - \bar{z}_b)^2 (z_c - \bar{z}_c)\right] = E\left[(z_b - \bar{z}_b)(z_c - \bar{z}_c)^2\right] = 0$ (Isserlis 1918) is

$$\begin{aligned} V_y(u) &= E\left[(z_a + z_b (u - z_c) - \bar{z}_a - \bar{z}_b (u - \bar{z}_c) - P_{bc})^2\right] \\ &= E\left[(z_a - \bar{z}_a + (z_b - \bar{z}_b + \bar{z}_b)(u - (z_c - \bar{z}_c) - \bar{z}_c) - \bar{z}_b (u - \bar{z}_c) - P_{bc})^2\right] \\ &= E\left[(z_a - \bar{z}_a + (z_b - \bar{z}_b)(u - \bar{z}_c) - (z_b - \bar{z}_b)(z_c - \bar{z}_c) - \bar{z}_b (z_c - \bar{z}_c) - P_{bc})^2\right] \\ &= P_{aa} + 2(P_{ab} - \bar{z}_b P_{bc})(u - \bar{z}_c) - 2\bar{z}_b P_{ac} + P_{bb}(u - \bar{z}_c)^2 + P_{bb}P_{cc} + \bar{z}_b^2 P_{cc} + 2P_{bc}^2 \end{aligned} \tag{S2-3}$$

We will need eq. (S2-3) also in the approximative analysis in Section 5 below. From eq. (S2-3) follows the value u_0 of u that minimizes $V_y(u)$. Setting

$$\frac{\partial V_y(u)}{\partial u} = 2(P_{ab} - \bar{z}_b P_{bc}) + 2P_{bb}(u - \bar{z}_c) = 0 \tag{S2-4}$$

we find

$$u_0 = \bar{z}_c + \frac{\bar{z}_b P_{bc} - P_{ab}}{P_{bb}} \tag{S2-5}$$

This is the same result as in eq. (5) in the main text, and we will soon find the expression for u_0 at equilibrium.

Since U is independent of $\bar{z}_b$ and $\bar{z}_c$ the unconditional phenotypic variance V_y follows from eq. (S2-3) as

$$\begin{aligned} V_y &= E[V_y(U)] = E\left[\begin{array}{c} P_{aa} + 2(P_{ab} - \bar{z}_b P_{bc})(U - \bar{z}_c) - 2\bar{z}_b P_{ac} \\ +P_{bb}(U - \bar{z}_c)^2 + P_{bb}P_{cc} + \bar{z}_b^2 P_{cc} + 2P_{bc}^2 \end{array}\right] \\ &= P_{aa} + 2(P_{ab} - \bar{z}_b P_{bc})(\mu_U - \bar{z}_c) - 2\bar{z}_b P_{ac} \\ &\quad + P_{bb}\sigma_U^2 + P_{bb}(\mu_U - \bar{z}_c)^2 + P_{bb}P_{cc} + \bar{z}_b^2 P_{cc} + 2P_{bc}^2 \end{aligned} \tag{S2-6}$$

and V_y is thus minimized by setting

$$\frac{\partial V_y}{\partial \bar{z}_b} = -2P_{bc}(\mu_U - \bar{z}_c) - 2P_{ac} + 2\bar{z}_b P_{cc} = 0 \tag{S2-7}$$

and

$$\frac{\partial V_y}{\partial \bar{z}_c} = -2(P_{ab} - \bar{z}_b P_{bc}) - 2P_{bb}(\mu_U - \bar{z}_c) = 0 \tag{S2-8}$$

3 Equilibrium results in a constant environment

From eqs. (8) and (9) in the main text follows the mean fitness

$$\bar{W}(u,\theta) = \int_{-\infty}^{\infty} p(y(u)) W(u,\theta)\, dy = W_{\max} \int_{-\infty}^{\infty} p(y(u)) \exp\left(-\frac{(y(u) - \theta)^2}{2\omega^2}\right) dy \tag{S2-9}$$

and the general problem is now to find the equilibrium mean traits that maximize $E[\ln(\bar{W}(u,\theta))]$. Owing to the product $z_b z_c$ in eq. (S2-1) the plastic phenotype $y(u)$ is not normally distributed, and solving eq. (S2-9) is therefore difficult if at all possible (international Maple experts have not been able to solve the alternative triple integral over z_a, z_b and z_c). However, in a constant environment with $\sigma_U^2 = \sigma_\Theta^2 = 0$, i.e. with $u = \mu_U$ and $\theta = \mu_\Theta$, maximum $E[\ln(\bar{W}(\mu_U, \mu_\Theta))]$ is found for the mean traits that maximize $\bar{W}(\mu_U, \mu_\Theta)$, i.e. for the mean traits that at the same time minimize the unconditional phenotypic variance and give a mean phenotype $\bar{y}(\mu_U)$ that maximize fitness. From eqs. (S2-7) and (S2-8) thus follow the equilibrium results in a constant environment

$$\bar{z}_b^{*ce} = \frac{P_{bb}P_{ac} - P_{ab}P_{bc}}{P_{bb}P_{cc} - P_{bc}^2} \quad \text{(S2-10)}$$

and

$$\bar{z}_c^{*ce} = \mu_U - \frac{\bar{z}_b^{*ce}P_{bc} - P_{ab}}{P_{bb}} \quad \text{(S2-11)}$$

Here, it remains to find the expression for $\bar{z}_a^{*ce}$. In Appendix S2-A we show that a constant environment with $u = \mu_U$ and $P_{ab} = P_{bc} = 0$ gives a symmetric probability density function $p(y)$. The corresponding values $\bar{z}_b^{*ce} = P_{ac}/P_{cc}$ and $\bar{z}_c^{*ce} = \mu_U$ according to eqs. (S2-10) and (S2-11) will then maximize $\bar{W}(\mu_U, \mu_\Theta)$ (and hence $E[\ln(\bar{W})]$ in this case) if and only if at the same time the equilibrium mean phenotype is $\bar{y}^*(\mu_U) = \mu_\Theta$, such that the individual phenotypic values are symmetrically distributed around the plastic phenotype that gives maximum fitness. When $p(y)$ is skewed we must expect that maximum $\bar{W}(\mu_U, \mu_\Theta)$ is found for $\bar{y}^*(\mu_U) = \mu_\Theta + \Delta_{\bar{y}^*}$, where $\Delta_{\bar{y}^*}$ depends on the degree of skewness and the width ω of the fitness function, as shown in Figure S2-1 for two very different values of ω. Note that the peak of the fitness function for small values of ω will tend to coincide with the peak of the probability density function, while large values of ω give small values of $\Delta_{\bar{y}^*}$. From eqs. (S2-2) and (S2-11) thus follows

$$\bar{z}_a^{*ce} = \mu_\Theta + \Delta_{\bar{y}^*} - \bar{z}_b^{*ce}\frac{\bar{z}_b^{*ce}P_{bc} - P_{ab}}{P_{bb}} + P_{bc} \quad \text{(S2-12)}$$

Remark 1 *The P matrix in Supporting Figure S1 gives a highly skewed phenotypic distribution (Supporting Figure S2 and Figure S2-1 below). In a constant environment with* $\mu_U = 6$ *and* $\mu_\Theta = 12$*, the means of the means over the last 5000 generations (*$n = 1000$ *independent simulations) were* $\widehat{E[\bar{z}_{a,t}]} = 11.472219$ *(SE* $= 0.000007$*),* $\widehat{E[\bar{z}_{b,t}]} = -0.166756$ *(SE* $= 0.000007$*) and* $\widehat{E[\bar{z}_{c,t}]} = 6.333212$ *(SE* $= 0.000013$*), and the mean standard deviations among generations were* $\widehat{SD(\bar{z}_{a,t})} = 0.0011776$ *(SE* $= 0.0000027$*),* $\widehat{SD(\bar{z}_{b,t})} = 0.0014573$ *(SE* $= 0.0000026$*) and* $\widehat{SD(\bar{z}_{c,t})} = 0.0029082$ *(SE* $= 0.0000052$*). The value of* $\widehat{E[\bar{z}_{b,t}]}$ *should according to eq. (S2-10) be compared to* $\bar{z}_b^{*ce} = -0.166666$*, and the deviation is thus* 6% *of the standard deviation among generations. According to equation (S2-11) with* $\widehat{E[\bar{z}_{b,t}]}$ *inserted,* $\widehat{E[\bar{z}_{c,t}]}$ *should be compared to* $\bar{z}_c^{*ce} = 6.333224$*, and the deviation is thus* 0.4% *of the standard deviation among generations. The value of* $\widehat{E[\bar{z}_{a,t}]}$ *should according eq. (S2-12) with* $\widehat{E[\bar{z}_{b,t}]}$ *inserted be compared to* $\bar{z}_a^{*ce} - \Delta_{\bar{y}^*} = 11.444416$*, from which follows* $\widehat{\Delta_{\bar{y}^*}} = 0.028$ *(as used in Figure S2-1).*

From eqs. (S2-5) and (S2-11) follows the equilibrium result in the constant environment case

$$u_0^{*ce} = \mu_U \quad \text{(S2-13)}$$

Remark 2 *The same P matrix as in Remark 1 above gave in the same constant environment the means of the means over the last 5000 generations (*$n = 1000$ *independent simulations)* $\widehat{E[u_{0,t}]} = 5.999973$ *(SE* $= 0.000014$*), and the mean standard deviation among generations* $\widehat{SD(u_{0,t})} = 0.0041173$ *(SE* $= 0.0000067$*). This should according to eq. (S2-13) be compared to* $u_0^{*ce} = 6$*, and the deviation is thus* 0.7% *of the standard deviation among generations.*

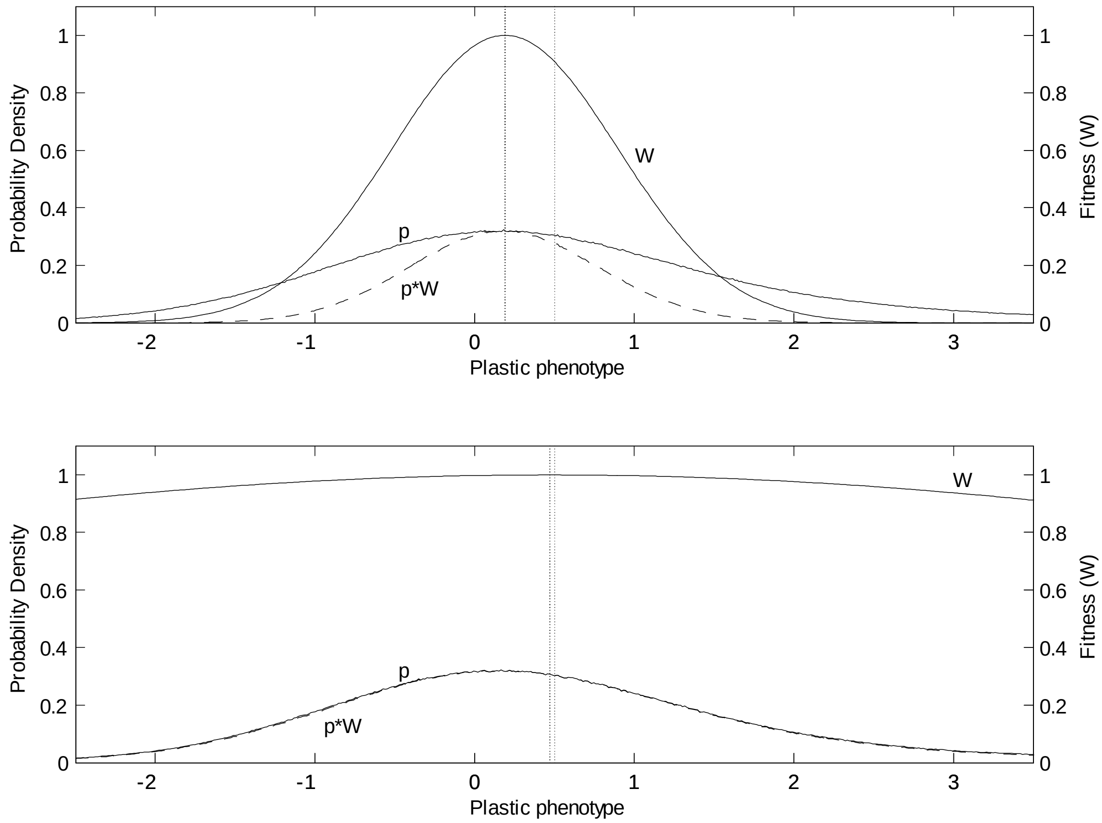

Figure S2-1 The probability density function $p(y(\mu_U))$, computed for a population with 10^7 individuals and $\mu_U = 0$, given the phenotypic variance-covariance matrix $P = \begin{bmatrix} 1 & 0.25 & -0.5 \\ 0.25 & 0.5 & -0.5 \\ -0.5 & -0.5 & 2 \end{bmatrix}$ and $\bar{z}_a^{*ce} + \bar{z}_b^{*ce}(\mu_U - \bar{z}_c^{*ce}) = 0$ (marked 'p' in both panels). According to eq. (S2-2) this gives $\bar{y}^*(\mu_U) = -P_{bc} = 0.5$ (right dotted vertical lines in both panels). The fitness functions $W(y(\mu_U), \mu_\Theta)$ with $W_{\max} = 1$ are shown for $\omega^2 = 0.5$ (upper panel, marked 'W') and $\omega^2 = 50$ (lower panel, marked 'W'). The fitness functions have their peaks at $\mu_\Theta = \bar{y}^*(\mu_U) - \Delta_{\bar{y}^*}$, with $\Delta_{\bar{y}^*} = 0.31$ (upper panel) and $\Delta_{\bar{y}^*} = 0.028$ (lower panel), respectively (left dotted vertical lines in both panels). These values of $\Delta_{\bar{y}^*}$ maximize the areas under the plots of $p(y(\mu_U))W(y(\mu_U), \mu_\Theta)$ (dashed lines marked 'p*W' in both panels), as found by numerical integration (see also Remark 1 above).

4 Equilibrium results in a stochastic environment

We will derive eqs. (S2-11) and (S2-12) also in the approximative stochastic analysis in Section 5 below (although with $\bar{z}_b^* \neq \bar{z}_b^{*ce}$ and $\Delta_{\bar{y}^*} = 0$), and since these results are also supported by simulation results as summarized in Section 6, we formulate the following conjectures regarding the stochastic case with σ_U^2, σ_Θ^2 and $\sigma_{U\Theta}$ different from zero:

Conjecture 1 *The variances σ_U^2 and σ_Θ^2, and the covariance $\sigma_{U\Theta}$, affect the equilibrium mean traits $\bar{z}_a^*$ and $\bar{z}_c^*$ only through the equilibrium mean slope $\bar{z}_b^*$. With $P_{ab} = P_{bc} = 0$ they have no effect on $\bar{z}_a^*$ and $\bar{z}_c^*$.*

Note that the equilibrium slope $\bar{z}_b^*$ in the stochastic case will be a function of σ_U^2, σ_Θ^2 and $\sigma_{U\Theta}$, such that $E\left[\ln(\bar{W})\right]$ according to eq. (S2-9) is maximized. This slope will be equal to the slope that minimizes V_y only in the special case when $\sigma_U^2 = \sigma_\Theta^2 = 0$ (eq. S2-10).

Conjecture 2 *Given the equilibrium slope $\bar{z}_b^*$ that maximizes $E\left[\ln(\bar{W})\right]$, directional and stabilizing selection will minimize the unconditional phenotypic variance (S2-6), such that the equilibrium values of $\bar{z}_c$ and $\bar{z}_a$ are given by the generalized versions of eqs. (S2-11) and (S2-12), i.e.*

$$\bar{z}_c^* = \mu_U - \frac{\bar{z}_b^* P_{bc} - P_{ab}}{P_{bb}} \tag{S2-14}$$

and

$$\bar{z}_a^* = \mu_\Theta + \Delta_{\bar{y}^*} - \bar{z}_b^* \frac{\bar{z}_b^* P_{bc} - P_{ab}}{P_{bb}} + P_{bc} \tag{S2-15}$$

where $E[\Delta_{\bar{y}^*}] = 0$ when $P_{ab} = P_{bc} = 0$, such that $p(y(U))$ is symmetric (Appendix S2-A).

Note that eq. (S2-14) follows directly from eq. (S2-8), i.e. $\bar{z}_c^*$ would minimize the unconditional variance V_y if $\bar{z}_b$ were chosen according to eq. (S2-10). In a stochastic environment, however, this would not minimize $E[\ln(\bar{W})]$, and $\bar{z}_b^*$ must therefore be a function of σ_U^2, σ_Θ^2 and $\sigma_{U\Theta}$.

From eqs. (S2-5) and (S2-14) follows the same equilibrium result as in the constant environment case above, i.e.

$$u_0^* = \mu_U \tag{S2-16}$$

which also is found from the simulations (Fig. 2 in the main text).

Remark 3 *Simulation results for $\bar{z}_c^*$, $\bar{z}_a^*$ and u_0^* given σ_U^2, σ_Θ^2 and $\sigma_{U\Theta}$ different from zero are summarized in Section 6, where the influence of the excitation noise on the equilibrium mean trait values is discussed.*

5 Approximative analysis

The aim is here to find theoretical but approximate expressions for the mean traits $\bar{z}_a$, $\bar{z}_b$ and $\bar{z}_c$ at equilibrium, under the assumption of a normal phenotypic distribution. In order to do that we first solve eq. (S2-9), and find the selection gradient $\boldsymbol{\beta}$ as a function of the environmental cue u. We then find expressions for the equilibrium mean traits by considering u and the phenotypic expression θ that maximize fitness as normal random variables, and setting the expected gradient $E[\boldsymbol{\beta}]= \mathbf{0}$. Finally we show that setting $E[\boldsymbol{\beta}]= \mathbf{0}$ also maximizes the expectation $E\left[\ln(\bar{W})\right]$, where $\bar{W}$ is the population mean fitness.

Due to the product $z_b z_c$ in eq. (S2-1) the plastic phenotype $y(u)$ is not normal, and as mentioned above this makes it difficult to find the population mean fitness $\bar{W}$ from eq. (9) in the main text (eq. (S2-9) above), if at all possible. In order to find an approximative solution we therefore assume that P_{bb} is small, such that the phenotype distribution $p\left(y(u)\right)$ is approximately normal, while still assuming $P_{bb} > 0$ (Fig. S2-2). Finally, we assume that the fitness W is a Gaussian function with 'width' ω.

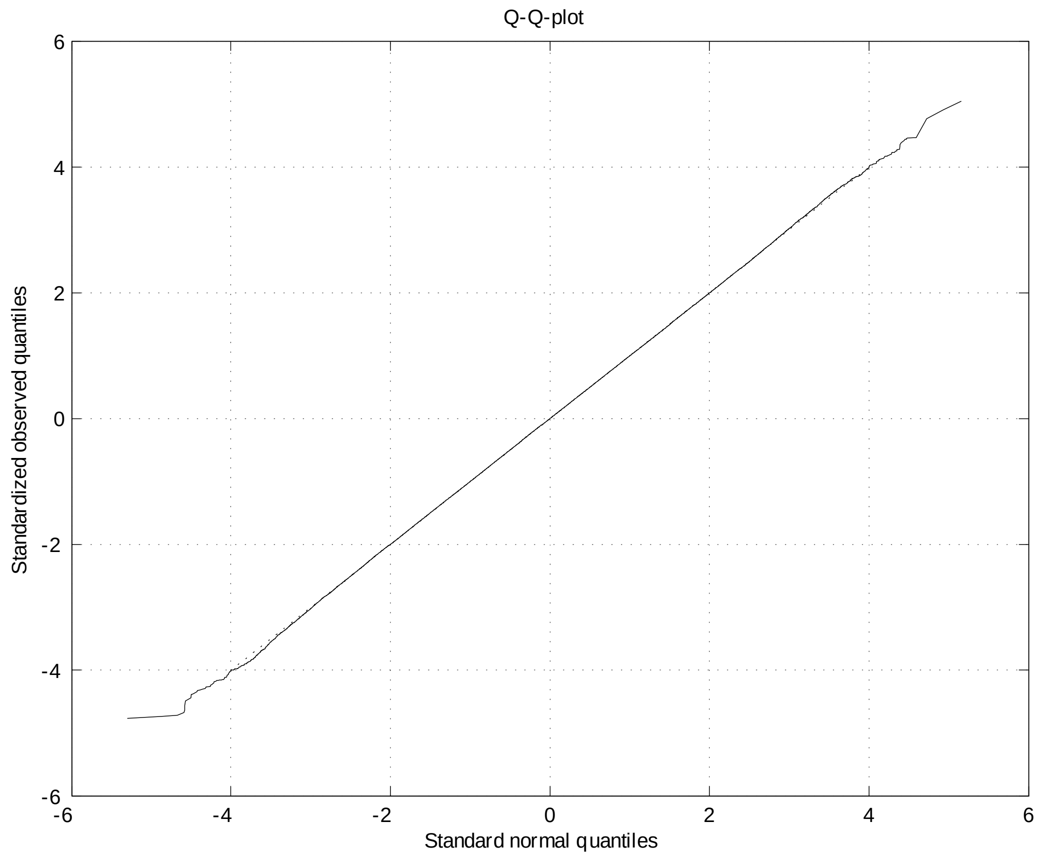

Figure S2-2. Typical Q-Q-plot for the plastic phenotype $y(u)$ computed for a population with 10^6 individuals with use of our main parameter values (given in Figure 2 in the main text), $\bar{z}_a = \bar{z}_c = 0$ and $\bar{z}_b = 0.3528$ (the mean stationary value in Figure 2 in the main text), and the environmental cue $u = 0$.

5.1 Basic equations

Under the assumption of an approximately normal $p(y(u))$ we find the population mean fitness from eq. (S2-9),

$$\begin{aligned}\bar{W}(u,\theta) &= \int_{-\infty}^{\infty} p(y(u))W(u,\theta)\,dy \approx W_{\max}\frac{1}{\sqrt{2\pi V_y(u)}}\int_{-\infty}^{\infty}\exp\left(-\frac{(y(u)-\bar{y})^2}{2V_y(u)}-\frac{(y(u)-\theta)^2}{2\omega^2}\right)dy \\ &= W_{\max}\sqrt{\frac{\omega^2}{\omega^2+V_y(u)}}\exp\left(-\frac{(\bar{y}(u)-\theta)^2}{2\left(\omega^2+V_y(u)\right)}\right) \qquad \text{(S2-17)}\end{aligned}$$

were u and θ are realizations of the random variables U and Θ, and where the solution of the integral follows from the known result $\int_{-\infty}^{\infty}\exp(-\left(ax^2+bx+c\right))dx$ $=\sqrt{\frac{\pi}{a}}\exp(\frac{b^2}{4a}-c)$ (Rottmann 1991), see also http://www.math10.com/en/university-math/definite-integrals/definite-integrals.html or http://en.wikipedia.org/wiki/List_of_definite_integrals #Definite_integrals_involving_exponential_functions). From eq. (S2-17) we thus find

$$\ln\bar{W} \approx \ln W_{\max} + \frac{1}{2}\ln\omega^2 - \frac{1}{2}\ln\left(\omega^2+V_y(u)\right) - \frac{(\bar{y}(u)-\theta)^2}{2\left(\omega^2+V_y(u)\right)} \qquad \text{(S2-18)}$$

In addition to $V_y(u)$ from eq. (S2-3) we here need to develop

$$(\bar{y}(u)-\theta)^2 = (\bar{z}_a + \bar{z}_b(u-\mu_U) + \bar{z}_b(\mu_U - \bar{z}_c) - P_{bc} - (\theta-\mu_\Theta) - \mu_\Theta)^2 \tag{S2-19}$$

From eq. (S2-18) follow the gradient components

$$\beta_a = \frac{\partial}{\partial \bar{z}_a}\ln \bar{W} = -\frac{\bar{y}(u)-\theta}{\omega^2 + V_y(u)} = -\frac{\bar{z}_a + \bar{z}_b(u-\bar{z}_c) - P_{bc} - \theta}{\omega^2 + V_y(u)} \tag{S2-20}$$

$$\begin{aligned}\beta_b \quad = \quad & \frac{\partial}{\partial \bar{z}_b}\ln \bar{W} = -\frac{1}{\omega^2 + V_y(u)}\left(-P_{bc}(u-\bar{z}_c) - P_{ac} + \bar{z}_b P_{cc}\right) - (u-\bar{z}_c)\frac{\bar{y}(u)-\theta}{\omega^2 + V_y(u)} \\ & + \frac{(\bar{y}(u)-\theta)^2}{(\omega^2 + V_y(u))^2}\left(-P_{bc}(u-\bar{z}_c) - P_{ac} + \bar{z}_b P_{cc}\right)\end{aligned} \tag{S2-21}$$

and

$$\begin{aligned}\beta_c \quad = \quad & \frac{\partial}{\partial \bar{z}_c}\ln \bar{W} = \frac{1}{\omega^2 + V_y(u)}\left(P_{ab} - \bar{z}_b P_{bc} + P_{bb}(u-\bar{z}_c)\right) + \bar{z}_b\frac{\bar{y}(u)-\theta}{\omega^2 + V_y(u)} \\ & - \frac{(\bar{y}(u)-\theta)^2}{(\omega^2 + V_y(u))^2}\left(P_{ab} - \bar{z}_b P_{bc} + P_{bb}(u-\bar{z}_c)\right) \\ = \quad & \frac{1}{\omega^2 + V_y(u)}\left(P_{ab} - \bar{z}_b P_{bc} + P_{bb}(u-\bar{z}_c)\right) - \bar{z}_b\beta_a - \frac{(\bar{y}(u)-\theta)^2}{(\omega^2 + V_y(u))^2}\left(P_{ab} - \bar{z}_b P_{bc} + P_{bb}(u-\bar{z}_c)\right)\end{aligned} \tag{S2-22}$$

The goal is now to find the equilibrium values of $\bar{z}_a$, $\bar{z}_b$ and $\bar{z}_c$, and we start with the simple constant environment case.

5.2 Equilibrium mean traits in a constant environment

In a constant environment we have $\sigma_U^2 = 0$ and $\sigma_\Theta^2 = 0$, i.e. $u = \mu_U$ and $\theta = \mu_\Theta$, and thus no fluctuations in the mean traits. Then both $V_y(u)$ (eq. S2-3) and $(\bar{y}(u)-\theta)^2$ (eq. S2-19) will be deterministic, and when $\boldsymbol{\beta} = \begin{bmatrix} \beta_b & \beta_b & \beta_c \end{bmatrix}^T \rightarrow \mathbf{0}^T$, i.e. when the selection comes to an end, eqs. (S2-20) to (S2-22) give the constant environment equilibrium expressions

$$\bar{z}_c^{*ce} = \mu_U - \frac{\bar{z}_b^{*ce} P_{bc} - P_{ab}}{P_{bb}} \tag{S2-23}$$

$$\bar{z}_a^{*ce} = P_{bc} - \bar{z}_b^{*ce}(\mu_U - \bar{z}_c^{*ce}) + \mu_\Theta = \mu_\Theta - \bar{z}_b^{*ce}\frac{\bar{z}_b^{*ce} P_{bc} - P_{ab}}{P_{bb}} + P_{bc} \tag{S2-24}$$

and

$$\bar{z}_b^{*ce} = \frac{P_{bb}P_{ac} - P_{ab}P_{bc}}{P_{bb}P_{cc} - P_{bc}^2} \tag{S2-25}$$

Note that these expressions are the same as in Appendix C, where we maximized $E[\ln(W)]$ for a random individual, only that we here assume $\sigma_U^2 = \sigma_\Theta^2 = \sigma_{U\Theta} = 0$. Also note that the expressions for the mean traits are the same as in eqs. (S2-10) to (S2-12) above, which we found by at the same time minimizing the total phenotypic variance V_y and setting $\bar{y}^* = \mu_\Theta + \Delta_{\bar{y}^*}$ (although here $\Delta_{\bar{y}^*} = 0$ because $p(y)$ is symmetric).

5.3 Equilibrium mean traits in a stochastic environment

In the stationary stochastic case the selection will never come to an end, and the problem is then to find the equilibrium solutions, i.e. the expressions for $\bar{z}_a^*$, $\bar{z}_b^*$ and $\bar{z}_c^*$ that give the expected gradient components $E[\beta_a] = E[\beta_b] = E[\beta_c] = 0$. We will first show that the eqs. (S2-23) and (S2-24) are valid also in this case (although $\bar{z}_b^* \neq \bar{z}_b^{*ce}$), and we will then find the slope $\bar{z}_b^*$ that gives $E[\beta_b] = 0$.

We must here regard both the environmental cue and the phenotypic expression that maximize fitness as random variables U and Θ, which makes $V_y(u)$ in eq. (S2-3) stochastic also in a large population. The mean traits are also stochastic, since they according to eqs. (6) to (8) in the main text are driven by the realizations u_t and θ_t in previous generations. The assumption that they are uncorrelated with U and Θ, thus implies that u_t and θ_t are white sequences. Setting $U - \bar{z}_c = U - \mu_U + \mu_U - \bar{z}_c$ eq. (S2-3) gives

$$\begin{aligned} V_y(U) &= P_{aa} + 2\left(P_{ab} - \bar{z}_b P_{bc}\right)\left(U - \mu_U + \mu_U - \bar{z}_c\right) - 2\bar{z}_b P_{ac} + P_{bb}\left(U - \mu_U\right)^2 \\ &\quad + 2P_{bb}\left(U - \mu_U\right)\left(\mu_U - \bar{z}_c\right) + P_{bb}\left(\mu_U - \bar{z}_c\right)^2 + P_{bb}P_{cc} + \bar{z}_b^2 P_{cc} + 2P_{bc}^2 \end{aligned} \qquad \text{(S2-26)}$$

The solution of $E[\boldsymbol{\beta}] = 0$ will involve $E\left[\ln\left(\omega^2 + V_y(U)\right)\right]$ and $E\left[1/\left(\omega^2 + V_y(U)\right)\right]$, and in order to find the solution we write

$$\omega^2 + V_y(U) = D\left(1 + \frac{S}{D}\right) = D\left(1 + x\right) \qquad \text{(S2-27)}$$

where D is the deterministic part of $\omega^2 + V_y(U)$, i.e. from eq. (S2-26)

$$\begin{aligned} D &= \omega^2 + P_{aa} + 2\left(P_{ab} - \bar{z}_b P_{bc}\right)\left(\mu_U - \bar{z}_c\right) - 2\bar{z}_b P_{ac} + P_{bb}\left(\mu_U - \bar{z}_c\right)^2 \\ &\quad + P_{bb}P_{cc} + 2P_{bc}^2 + \bar{z}_b^2 P_{cc} \end{aligned} \qquad \text{(S2-28)}$$

while S is the stochastic part of $\omega^2 + V_y(U)$, i.e. from eq. (S2-26) and using $\bar{z}_c' = \bar{z}_c + \frac{\bar{z}_b P_{bc} - P_{ab}}{P_{bb}}$

$$x = \frac{P_{bb}}{D}\left(\left(U - \mu_U\right)^2 + 2\left(\mu_U - \bar{z}_c'\right)\left(U - \mu_U\right)\right) \qquad \text{(S2-29)}$$

Taylor series expansions of the last two terms in eq. (S2-18) give

$$\ln \bar{W} \approx \ln W_{\max} + \frac{1}{2}\ln\omega^2 - \frac{1}{2}\ln D + \frac{1}{2}\sum_{i=1}^{\infty}\frac{1}{i}\left(-1\right)^i x^i - \frac{\left(\bar{y}(u) - \theta\right)^2}{2}\left(\frac{1}{D} + \frac{1}{D}\sum_{i=1}^{\infty}\left(-1\right)^i x^i\right) \qquad \text{(S2-30)}$$

where by use of the binomial formula and corresponding constants d_j

$$\begin{aligned} x^i &= \frac{P_{bb}^i}{D^i}\left(U - \mu_U\right)^i \sum_{j=0}^{i}\binom{i}{j}\left(U - \mu_U\right)^{i-j} 2^j \left(\mu_U - \bar{z}_c'\right)^j \\ &= \frac{P_{bb}^i}{D^i}\left(\left(U - \mu_U\right)^{2i} + \sum_{j=1}^{i} d_j \left(U - \mu_U\right)^{2i-j}\left(\mu_U - \bar{z}_c'\right)^j\right) \end{aligned} \qquad \text{(S2-31)}$$

We are now ready to establish the components in the expected selection gradient, and find the mean traits $\bar{z}_a^*$, $\bar{z}_b^*$ and $\bar{z}_c^*$ that give the equilibrium solution in a stochastic environment. Writing $U - \bar{z}_c = U - \mu_U + \mu_U - \bar{z}_c$ and $\Theta = \Theta - \mu_\Theta + \mu_\Theta$, and using $E\left[\left(U - \mu_U\right)^{2i+1}\right] = E\left[\left(\Theta - \mu_\Theta\right)\left(U - \mu_U\right)^{2i}\right] = 0$

(Isserlis 1918), eq. (S2-30) first gives

$$\begin{aligned} E[\beta_a] &= E\left[\frac{\partial}{\partial \bar{z}_a}\ln \bar{W}\right] = -E\left(\bar{y}(U)-\Theta\right)\left(\frac{1}{D}+\frac{1}{D}\sum_{i=1}^{\infty}(-1)^i x^i\right) \\ &= -E\left[\left(\bar{y}(U)-\Theta\right)\frac{1}{D}\right] - \frac{1}{D}\sum_{i=1}^{\infty}(-1)^i E\left[\left(\bar{y}(U)-\Theta\right)x^i\right] \\ &= -\frac{1}{D}\left(\bar{z}_a+\bar{z}_b(\mu_U-\bar{z}_c)-P_{bc}-\mu_\Theta\right) \\ &\quad -\sum_{i=1}^{\infty}(-1)^i\frac{P_{bb}^i}{D^{i+1}}\left(\bar{z}_a+\bar{z}_b\left(\mu_U-\bar{z}_c\right)-P_{bc}-\mu_\Theta\right)E\left[\left(U-\mu_U\right)^{2i}\right] \\ &\quad -\sum_{i=1}^{\infty}(-1)^i\frac{P_{bb}^i}{D^{i+1}}\sum_{j=1}^{i}d_j E\left[\left(\bar{y}(U)-\Theta\right)\left(U-\mu_U\right)^{2i-j}\right]\left(\mu_U-\bar{z}_c'\right)^j \end{aligned} \tag{S2-32}$$

From this follows that $E\left[\beta_a\right]=0$ when $\bar{z}_c'=\mu_U$ and $\bar{z}_a=\mu_\Theta+P_{bc}-\bar{z}_b^*\frac{\bar{z}_b^*P_{bc}-P_{ab}}{P_{bb}}$, i.e. the same solution as in the constant environment case above (although $\bar{z}_b^*\neq\bar{z}_b^{*ce}$), but other solutions could possibly exist.

Next, it follows from eq. (S2-30) that

$$\begin{aligned} E\beta_c &= E\left[\frac{\partial}{\partial \bar{z}_c}\ln\bar{W}\right] = \frac{1}{D}\left(-\left(P_{ab}-\bar{z}_bP_{bc}\right)+P_{bb}\left(\mu_U-\bar{z}_c\right)\right)+\frac{1}{2}\sum_{i=1}^{\infty}\frac{1}{i}(-1)^i E\left[\frac{\partial}{\partial\bar{z}_c}x^i\right] \\ &\quad +\bar{z}_bE\left[\beta_a\right]-E\left[\frac{\left(\bar{y}(U)-\Theta\right)^2}{2}\frac{\partial}{\partial\bar{z}_c}\left(\frac{1}{D}+\frac{1}{D}\sum_{i=1}^{\infty}(-1)^i x^i\right)\right] \end{aligned} \tag{S2-33}$$

When we insert x^i from eq. (S2-31) and develop this with $E[\beta_a]=0$, we find

$$\begin{aligned} E\left[\beta_c\right] &= \frac{1}{D}\left(-\left(P_{ab}-\bar{z}_bP_{bc}\right)+P_{bb}\left(\mu_U-\bar{z}_c\right)\right) \\ &\quad +\frac{1}{2}\sum_{i=1}^{\infty}\frac{1}{i}(-1)^i\begin{pmatrix} -2\frac{P_{bb}^i}{D^{i+1}}E\left[\left(U-\mu_U\right)^{2i}\right]P_{bb}\left(\mu_U-\bar{z}_c'\right) \\ -2\frac{P_{bb}^i}{D^{i+1}}\sum_{j=1}^i d_jE\left[\left(U-\mu_U\right)^{2i-j}\right]P_{bb}\left(\mu_U-\bar{z}_c'\right)\left(\mu_U-\bar{z}_c'\right)^j \\ -j\frac{P_{bb}^i}{D^i}\sum_{j=1}^i d_jE\left[\left(U-\mu_U\right)^{2i-j}\right]\left(\mu_U-\bar{z}_c'\right)^{j-1}\end{pmatrix} \\ &\quad +E\left[\left(\bar{y}(U)-\Theta\right)^2\right]\frac{1}{D^2}\left(-\left(P_{ab}-\bar{z}_bP_{bc}\right)+P_{bb}\left(\mu_U-\bar{z}_c\right)\right) \\ &\quad -\frac{1}{2}\sum_{i=1}^{\infty}(-1)^iE\left[\left(\bar{y}-\Theta\right)^2\begin{pmatrix} -2\frac{P_{bb}^i}{D^{i+1}}\left(U-\mu_U\right)^{2i}P_{bb}\left(\mu_U-\bar{z}_c'\right) \\ -2\frac{P_{bb}^i}{D^{i+2}}\sum_{j=1}^i d_j\left(U-\mu_U\right)^{2i-j}P_{bb}\left(\mu_U-\bar{z}_c'\right)\left(\mu_U-\bar{z}_c'\right)^j \\ -j\frac{P_{bb}^i}{D^{i+1}}\sum_{j=1}^i d_j\left(U-\mu_U\right)^{2i-j}\left(\mu_U-\bar{z}_c'\right)^{j-1}\end{pmatrix}\right] \end{aligned} \tag{S2-34}$$

Here, all terms have a factor $(\mu_U-\bar{z}_c')$, except the two sums over i with factors $(\mu_U-\bar{z}_c')^{j-1}$ that disappear for $j=1$. In the first of these sums all terms have the factor $E\left[\left(U-\mu_U\right)^{2i-1}\right]\left(\mu_U-\bar{z}_c'\right)^{1-1}=E\left[\left(U-\mu_U\right)^{2i-1}\right]=0$ (Isserlis 1918). The terms of the other sum have a factor that based on eq. (S2-19) is

$$\begin{aligned} & E\left[\left(\bar{y}(u)-\Theta\right)^2\left(U-\mu_U\right)^{2i-1}\right] \\ = \;& 2\left(\bar{z}_a-P_{bc}+\bar{z}_b(\mu_U-\bar{z}_c)-\mu_\Theta\right)\begin{pmatrix}\bar{z}_bE\left[\left(U-\mu_U\right)^{2i}\right] \\ -E\left[\left(\Theta-\mu_\Theta\right)\left(U-\mu_U\right)^{2i-1}\right]\end{pmatrix} \end{aligned} \tag{S2-35}$$

When we set $E[\beta_a] = E(\beta_c) = 0$ we thus find that

$$E[\beta_a] = C_A(\bar{z}_a - P_{bc} + \bar{z}_b(\mu_U - \bar{z}_c) - \mu_\Theta) + S_A(\mu_U - \bar{z}'_c) = 0 \tag{S2-36}$$

and

$$E[\beta_c] = C_C(\bar{z}_a - P_{bc} + \bar{z}_b(\mu_U - \bar{z}_c) - \mu_\Theta) + S_C(\mu_U - \bar{z}'_c) = 0 \tag{S2-37}$$

where C_A and C_C are different constants, while S_A and S_C are different sums of terms with factors $(\mu_U - \bar{z}'_c)$ of various orders. From this follows that $\bar{z}_a - P_{bc} + \bar{z}_b(\mu_U - \bar{z}_c) - \mu_\Theta = 0$ and $\mu_U - \bar{z}'_c = 0$ is the only solution, and since $\bar{z}'_c = \bar{z}_c + \frac{\bar{z}_b P_{bc} - P_{ab}}{P_{bb}}$ the equilibrium mean trait values are thus

$$\bar{z}_a^* = \mu_\Theta - \bar{z}_b^* \frac{\bar{z}_b^* P_{bc} - P_{ab}}{P_{bb}} + P_{bc} \tag{S2-38}$$

and

$$\bar{z}_c^* = \mu_U - \frac{\bar{z}_b^* P_{bc} - P_{ab}}{P_{bb}} \tag{S2-39}$$

This is the same solution as in the constant environment case above (eqs. S2-24 and S2-23), only that $\bar{z}_b^*$ is different from $\bar{z}_b^{*ce}$. We thus find that $\bar{z}_a$ and $\bar{z}_c$ at equilibrium are affected by σ_Θ^2 and σ_U^2 only through the equilibrium value $\bar{z}_b^*$, which supports Conjecture 1 above. Note that eqs. (S2-38) and (S2-39) support Conjecture 2 above, although we here have $\Delta_{\bar{y}^*} = 0$ because $p(y)$ is symmetric. Also note that we find the same solutions as when maximizing $E[\ln(W)]$ for a random individual (Appendix C), only that $\bar{z}_b^*$ is different, as we will see below.

Finally, we will find an approximate expression for the equilibrium slope $\bar{z}_b^*$, and for simplicity of presentation we here set $P_{ab} = P_{bc} = 0$, such that $\bar{z}_a^* = \mu_\Theta$ and $\bar{z}_c^* = \mu_U$. Inserting $\bar{z}_a = \mu_\Theta$ and $\bar{z}_c = \mu_U$ into eq. (S2-30), where we also set the first sum to $-x$ (the first term) and the second sum to zero, we find

$$\begin{aligned} E[\beta_b] &\approx E\frac{\partial}{\partial \bar{z}_b}\left(\ln W_{\max} + \frac{1}{2}\ln\omega^2 - \frac{1}{2}\ln D - \frac{1}{2}\frac{P_{bb}}{D}\left((u-\mu_U)^2\right) - \frac{1}{2}\frac{(\bar{z}_b(U-\mu_U) - (\Theta-\mu_\Theta))^2}{D}\right) \\ &= -\frac{-P_{ac} + \bar{z}_b P_{cc}}{D} + \frac{P_{bb}}{D^2}(-P_{ac} + \bar{z}_b P_{cc})\sigma_U^2 \\ &\quad - \frac{\left(\bar{z}_b\sigma_U^2 - \sigma_{U\Theta}\right)D - \left(\bar{z}_b^2\sigma_U^2 - 2\bar{z}_b\sigma_{U\Theta} + \sigma_\Theta^2\right)(-P_{ac} + \bar{z}_b P_{cc})}{D^2} \end{aligned} \tag{S2-40}$$

When $E[\beta_b] = 0$ we thus find

$$\bar{z}_b^* \approx \frac{\sigma_{U\Theta} + P_{ac}}{\sigma_U^2 + P_{cc}} + \frac{\left(\sigma_\Theta^2 + \bar{z}_b^{*2}\sigma_U^2 - 2\bar{z}_b^*\sigma_{U\Theta} + P_{bb}\sigma_U^2\right)(-P_{ac} + \bar{z}_b^* P_{cc})}{(\omega^2 + P_{aa} - 2\bar{z}_b^* P_{ac} + P_{bb}P_{cc} + \bar{z}_b^{*2}P_{cc})(\sigma_U^2 + P_{cc})} \tag{S2-41}$$

from which $\bar{z}_b^*$ can be determined numerically.

Remark 4 *Note that $\sigma_\Theta^2 \to 0$ and $\sigma_U^2 \to 0$ (and thus $\sigma_{U\Theta} \to 0$) results in $\bar{z}_b^* = P_{ac}/P_{cc}$, as found in the constant environment case above (eq. (S2-25) with $P_{ab} = P_{bc} = 0$), and that $\bar{z}_b^*$ gradually changes when σ_Θ^2 and σ_U^2 increase from zero.*

Remark 5 *With our main simulation values (Fig. 2 in the main text) the second term in eq. (S2-41) is positive, and less than 10% of the first term. If we also used the next terms in the two sums in eq. (S2-30), we would get an additional negative term in eq. (S2-41), but due to the factor $P_{bb}/D \approx 0.0001$ that term would be only 0.5% of the first term.*

With parameter values as in our main simulations the last term in eq. (S2-41) is small, and a more approximate result is therefore

$$\bar{z}_b^* \approx \frac{\sigma_{U\Theta} + P_{ac}}{\sigma_U^2 + P_{cc}} \tag{S2-42}$$

i.e. the same as we found when maximizing $E[\ln(W)]$ for a random individual (Appendix C, with $P_{ab} = P_{bc} = 0$).

For the 2-traits model (where $P_{ac} = P_{cc} = 0$) the equilibrium slope result becomes

$$\bar{z}_b^* = \frac{\sigma_{U\Theta}}{\sigma_U^2} \tag{S2-43}$$

as also found from the result in Appendix C.

5.4 Maximization of $E\left[\ln(\bar{W})\right]$

Note that the mean trait values that give $E[\boldsymbol{\beta}] = E\left[\frac{\partial}{\partial \bar{\mathbf{z}}} \ln \bar{W}\right] = 0$, will also be found by setting $\frac{\partial}{\partial \bar{\mathbf{z}}} E\left[\ln \bar{W}\right] = 0$, i.e. by maximizing $E\left[\ln \bar{W}\right]$. This is so because $\ln(\bar{W})$ is a discrete random variable, such that the sum rule of differentiation applies, i.e. we have

$$\frac{\partial}{\partial \bar{\mathbf{z}}} E\left[\ln(\bar{W})\right] = \frac{\partial}{\partial \bar{\mathbf{z}}}\left[\lim_{N \to \infty} \frac{1}{N}\sum_{n=1}^{N} \ln(\bar{W}_n)\right] = \lim_{N \to \infty} \frac{1}{N}\sum_{n=1}^{N} \frac{\partial}{\partial \bar{\mathbf{z}}}\left[\ln(\bar{W}_n)\right] = E\left[\frac{\partial}{\partial \bar{\mathbf{z}}} \ln(\bar{W})\right] \tag{S2-44}$$

6 Approximate expected mean traits at stationarity

The expected mean traits at stationarity are affected by the fluctuations in the mean trait values caused by the white excitation sequences u_t and θ_t. In order to find the effect of this we set $\bar{z}_{a,t} = E[\bar{z}_{a,t}] + v_{a,t}$, $\bar{z}_{b,t} = E[\bar{z}_{b,t}] + v_{b,t}$ and $\bar{z}_{c,t} = E[\bar{z}_{c,t}] + v_{c,t}$, where $E[\bar{z}_{a,t}] = \lim_{N\to\infty} \frac{1}{N}\sum_{t=1}^{N} \bar{z}_{a,t}$ etc., and where $E[v_{a,t}] = E[v_{b,t}] = E[v_{c,t}] = 0$. Since new values of the mean traits are formed according to the difference eq. (6) in the main text, the fluctuation components $v_{a,t}$, $v_{b,t}$ and $v_{c,t}$ are correlated only with previous values of u_t and θ_t, and since u_t and θ_t are white we therefore know that expectations like $E[v_{a,t}(u_t - \mu_U)]$ and $E[v_{a,t}(\theta_t - \mu_\Theta)]$ will be zero (chapter 6, Åström and Wittenmark 1990). For the mean traits $\bar{z}_{a,t}$ and $\bar{z}_{c,t}$ the analysis of the fluctuation effect based on the series expansions in eq. (S2-30) is complicated, and it involves expectations like $E\left[v_{a,t}^2\right]$, $E[v_{a,t}v_{c,t}]$ and $E\left[v_{c,t}^2\right]$ for which we can find numerical values only from our simulations. Under the assumption of a normal phenotypic distribution, eqs. (S2-38) and (S2-39) are exact when there is no excitation (i.e. for $\sigma_U^2 = 0$ and $\sigma_\Theta^2 = 0$), in which case they are replaced by eqs. (S2-24) and (S2-23). When σ_U^2 and σ_Θ^2 increase from zero, the mean traits will gradually be corrupted by noise, and eqs. (S2-38) and (S2-39) will then be replaced by approximations that may become gradually poorer,

$$E[\bar{z}_{a,t}] \approx \mu_\Theta + P_{bc} - E[\bar{z}_{b,t}]\frac{E[\bar{z}_{b,t}]P_{bc} - P_{ab}}{P_{bb}} \tag{S2-45}$$

and

$$E[\bar{z}_{c,t}] \approx \mu_U - \frac{E[\bar{z}_{b,t}]P_{bc} - P_{ab}}{P_{bb}} \tag{S2-46}$$

Remark 6 *The simulation results in Figure 2 in the main text (with $P_{ab} = P_{ac} = P_{bc} = 0$) are based on a P matrix that gives a nearly normal phenotypic distribution (Figure S2-2). Computation of the mean of the means over the last 5000 generations ($n = 2000$ independent simulations) gave $\widehat{E[\bar{z}_{a,t}]} = 11.9989$ ($SE = 0.0012$) and $\widehat{E[\bar{z}_{c,t}]} = 5.9979$ ($SE = 0.0012$), which should be compared to the theoretical equilibrium values $\mu_\Theta = 12$ (eq. S2-38) and $\mu_U = 6$ (eq. S2-39). The deviations from the theoretical results are thus within $\pm 2SE$.*

Remark 7 *The mean of mean u_0 (eq. S2-5) over the last 5000 generations in Figure 2 in the main text ($n = 2000$ independent simulations) were $\widehat{E[\bar{z}_{c,t}]} = 5.9979$ ($SE = 0.0012$), which should be compared to $\mu_U = 6$. The deviation from the theoretical equilibrium result in eq. (S2-16) is thus within $\pm 2SE$.*

Remark 8 *The simulation results in Supporting Figure S1 are based on a P matrix that gives a far from normal phenotypic distribution (Supporting Figure S2). Means of the means over the last 5000 generations (*$n = 1000$ *independent simulations) were* $\widehat{E[\bar{z}_a]} = 11.8199$ *(*$SE = 0.0019$*) and* $\widehat{E[\bar{z}_c]} = 6.8253$ *(*$SE = 0.0014$*), and the mean standard deviations among generations were respectively* $\widehat{SD}(\bar{z}_a) = 0.2219$ *(*$SE = 0.0007$*) and* $\widehat{SD}(\bar{z}_c) = 0.3389$ *(*$SE = 0.0006$*). The corresponding slope result was* $\widehat{E[\bar{z}_b]} = 0.3487$ *(*$SE = 0.0007$*), and using this we obtain the theoretical values* $\bar{z}_a^* = 11.7960$ *(eq. S2-38) and* $\bar{z}_c^* = 6.8487$ *(eq. S2-39). Hence, the differences between the estimates from the simulations and the theoretical values are respectively* 11% *and* 7% *of the standard deviations among generations. If we according to eq. (S2-15) add* $\Delta_{\bar{y}^*} = 0.028$ *(as found in Remark 1) to the theoretical value of* $\bar{z}_a^*$*, we get* $\bar{z}_a^* = 11.8240$*, and the difference* $\widehat{E[\bar{z}_{a,t}]} - \bar{z}_a^*$ *is then reduced to* 2% *of the standard deviation among generations.*

Remark 9 *The mean of mean* u_0 *(equation S2-5) over the last* 5000 *generations of the* 1000 *independent simulations in Supporting Figure S1 were* $\widehat{E[u_0]} = 5.9765$ *(*$SE = 0.0012$*), and the mean standard deviation among generations were* $\widehat{SD}(u_0) = 0.4660$ *(*$SE = 0.0007$*). Hence, the difference from* $\mu_U = 6$ *is* 5% *of the standard deviation among generations.*

Our simulations with $P_{ab} = P_{bc} = 0$ also show that the effect of $v_{b,t}$ on $E[\bar{z}_{b,t}]$ is negligible, and with $P_{ab} = P_{bc} = 0$ we thus find

$$\begin{aligned} E\left[(y(u_t) - \theta_t)^2\right] &\approx E\left[\left(\begin{array}{c} E[\bar{z}_{a,t}] + v_{a,t} + E[\bar{z}_{b,t}](u_t - \mu_U) - E[\bar{z}_{b,t}]\left(E[\bar{z}_{c,t}] + v_{c,t} - \mu_U\right) \\ -(\theta_t - \mu_\Theta) - \mu_\Theta \end{array}\right)^2\right] \\ &= E[v_{a,t}^2] - 2E[\bar{z}_{b,t}]E\left[v_{a,t}v_{c,t}\right] + E[\bar{z}_{b,t}]\sigma_U^2 \\ &\quad -2E[\bar{z}_{b,t}]\sigma_{U\Theta} + E[\bar{z}_{b,t}^2]E[v_{c,t}^2] + \sigma_\Theta^2 \end{aligned} \quad \text{(S2-47)}$$

where we made use of $E[\bar{z}_{a,t}] - \mu_\Theta = 0$ and $E[\bar{z}_{c,t}] - \mu_U = 0$ (from eqs. (S2-45) and (S2-46)). Eq. (S2-30) with the first sum set to $-x$ (the first term) and the second sum set to zero then gives

$$\begin{aligned} E\left[\beta_{b,t}\right] &\approx -\frac{-P_{ac} + \bar{z}_{b,t}P_{cc}}{D} + \frac{P_{bb}}{D^2}\left(-P_{ac} + E[\bar{z}_{b,t}]P_{cc}\right)\sigma_U^2 \quad \text{(S2-48)} \\ &\quad -\frac{\left(\begin{array}{c} \left(-E\left[v_{a,t}v_{c,t}\right] + E\left[\bar{z}_{b,t}\right]\sigma_U^2 - \sigma_{U\Theta} + E\left[\bar{z}_{b,t}\right]E[v_{c,t}^2]\right)D \\ -\left(\begin{array}{c} E\left[v_{a,t}^2\right] - 2E[\bar{z}_{b,t}]E\left[v_{a,t}v_{c,t}\right] + E[\bar{z}_{b,t}]\sigma_U^2 \\ -2E\left[\bar{z}_{b,t}\right]\sigma_{U\Theta} + E\left[\bar{z}_{b,t}^2\right]E\left[v_{c,t}^2\right] + \sigma_\Theta^2 \end{array}\right)\left(-P_{ac} + E\left[\bar{z}_{b,t}\right]P_{cc}\right) \end{array}\right)}{D^2} \end{aligned}$$

Setting $E\left[\beta_{b,t}\right] = 0$ this gives

$$\begin{aligned} E\left[\bar{z}_{b,t}\right] &\approx \frac{\sigma_{U\Theta} + P_{ac} + E\left[v_{a,t}v_{c,t}\right]}{\sigma_U^2 + P_{cc} + E\left[v_{c,t}^2\right]} \\ &\quad + \frac{\left(\begin{array}{c} \sigma_\Theta^2 + E\left[v_{a,t}^2\right] + E\left[\bar{z}_{b,t}^2\right]\left(\sigma_U^2 + E[v_{c,t}^2]\right) \\ -2E\left[\bar{z}_{b,t}\right]\left(\sigma_{U\Theta} + E\left[v_{a,t}v_{c,t}\right]\right) + P_{bb}\sigma_U^2 \end{array}\right)\left(-P_{ac} + E\left[\bar{z}_{b,t}\right]P_{cc}\right)}{\left(\omega^2 + P_{aa} - 2E\left[\bar{z}_{b,t}\right]P_{ac} + P_{bb}P_{cc} + E\left[\bar{z}_{b,t}^2\right]P_{cc}\right)\left(\sigma_U^2 + P_{cc}\right)} \end{aligned} \quad \text{(S2-49)}$$

This is the result in eq. (S2-41), with additional noise variance and covariance terms. Analytical expressions for $E\left[v_{a,t}v_{c,t}\right]$, $E\left[v_{a,t}^2\right]$ and $E\left[v_{c,t}^2\right]$ are difficult to find, if at all possible, but numerical values can be found from our simulations.

Remark 10 *Means of fluctuation variances and covariances over the last 5000 generations (*$n = 1000$ *independent simulations) in Figure 2 in the main text were* $\widehat{E\left[v_{a,t}^2\right]} = 0.0510$*,* $\widehat{E\left[v_{c,t}^2\right]} = 0.0938$ *and* $\widehat{E\left[v_{a,t}v_{c,t}\right]} = -0.0588$*.*

Remark 11 *The simulations in Figure 2 in the main text gave the mean of the means over the last 5000 generations (*$n = 2000$ *independent simulations)* $\widehat{E[\bar{z}_{b,t}]} = 0.3528$ *(SE* $= 0.0004$*), while eq. (S2-49) with use of the fluctuation variance and covariance values in Remark 10 gives* $E[\bar{z}_{b,t}] = 0.3539$*. The relative difference owing to the approximations made is thus 0.34%, and it would be even smaller with more terms from the Taylor series in eq. (S2-30) included.*

Remark 12 *If we completely ignore the fluctuation components* $v_{a,t}$ *etc., eq. (S2-49) gives* $E[\bar{z}_{b,t}] = 0.3695$*, i.e. a 5% relative difference from the simulation result. For this result we do not need the assumption that* u_t *and* θ_t *are white.*

Since the fluctuation contributions are small, we also here find the more approximate result

$$E[\bar{z}_b] \approx \frac{\sigma_{U\Theta} + P_{ac}}{\sigma_U^2 + P_{cc}} \tag{S2-50}$$

Remark 13 *From eq. (S2-50) we find* $E[\bar{z}_b] = 0.3333$*, i.e. a* -5.5% *relative difference from the simulation result.*

Appendix S2-A Symmetry of the phenotypic distribution

We will here study the symmetry of the equilibrium phenotypic distribution function when z_b is independent of both z_a and z_c, such that all expectations of the form $E[(z_a - \bar{z}_a)^m (z_c - \bar{z}_c)^n (z_b - \bar{z}_b)^p]$, where m, n and p are positive integers or zero, are equal to $E[(z_a - \bar{z}_a)^m (z_c - \bar{z}_c)^n] E[(z_b - \bar{z}_b)^p]$.

In a constant environment $P_{ab} = P_{bc} = 0$ gives $\bar{z}_c^{*ce} = \mu_U$ (eq. S2-11), such that $u = \mu_U$ gives $\bar{y}^*(\mu_U) = \bar{z}_a^{*ce}$ (eq. S2-2). For any positive integer n the binomial formula then gives the conditional odd-order central moments

$$\begin{aligned} E\left[(y(\mu_U) - \bar{y}^*(\mu_U))^{2n-1}\right] &= E\left[(z_a - \bar{z}_a^{*ce} + z_b(\bar{z}_c^{*ce} - z_c))^{2n-1}\right] \\ &= \sum_{k=0}^{2n-1} \binom{2n-1}{k} E\left[(z_a - \bar{z}_a^{*ce})^{2n-1-k} (\bar{z}_c^{*ce} - z_c)^k (z_b - \bar{z}_b^{*ce} + \bar{z}_b^{*ce})^k\right] \\ &= \sum_{k=0}^{2n-1} \binom{2n-1}{k} E[(z_a - \bar{z}_a^{*ce})^{2n-1-k} (\bar{z}_c^{*ce} - z_c)^k] E[(z_b - \bar{z}_b^{*ce} + \bar{z}_b^{*ce})^k] \end{aligned} \tag{S2-51}$$

Here $(z_a - \bar{z}_a^{*ce})^{2n-1-k} (\bar{z}_c^{*ce} - z_c)^k$ is the product of an odd number of normal variables, such that $E[(z_a - \bar{z}_a^{*ce})^{2n-1-k} (\bar{z}_c^{*ce} - z_c)^k] = 0$ (Isserlis 1918) and thus $E\left[(y(\mu_U) - \bar{y}^*(\mu_U))^{2n-1}\right] = 0$. All conditional odd-order central moments are thus zero, and $p(y(\mu_U))$ is therefore symmetric (Grimmett and Stirzaker 2009).

In a stochastic environment with $P_{ab} = P_{bc} = 0$ we still have $\bar{z}_c^* = \mu_U$ (eq. S2-14), but now $\bar{y}^*(u) = \bar{z}_a^* + \bar{z}_b^*(u - \mu_U)$ (eq. S2-2). The conditional odd-ordered central moments are thus

$$\begin{aligned} E\left[(y(u) - \bar{y}^*(u))^{2n-1}\right] &= E\left[(z_a - \bar{z}_a^* + z_b(u - z_c) - \bar{z}_b^*(u - \mu_U))^{2n-1}\right] \\ &= E\left[(z_a - \bar{z}_a^* + z_b(u - \mu_U + \bar{z}_c^* - z_c) - \bar{z}_b^*(u - \mu_U))^{2n-1}\right] \\ &= E\left[(z_a - \bar{z}_a^* + (z_b - \bar{z}_b^*)(u - \mu_U) + z_b(\bar{z}_c^* - z_c))^{2n-1}\right] \\ &= \sum_{k=0}^{2n-1} \binom{2n-1}{k} E\left[(z_a - \bar{z}_a^*)^{2n-1-k} ((z_b - \bar{z}_b^*)(u - \mu_U) + z_b(\bar{z}_c^* - z_c))^k\right] \\ &= \sum_{k=0}^{2n-1} \binom{2n-1}{k} \sum_{j=0}^{k} \binom{k}{j} \begin{pmatrix} E\left[(z_a - \bar{z}_a^*)^{2n-1-k} (\bar{z}_c^* - z_c)^j\right] \\ \times (u - \mu_U)^{k-j} E[(z_b - \bar{z}_b^*)^{k-j} z_b^j] \end{pmatrix} \end{aligned} \tag{S2-52}$$

Here, $E\left[\left(z_a-\bar{z}_a^*\right)^{2n-1-k}\left(\bar{z}_c^*-z_c\right)^j\right]=0$ only when $2n-1-k+j$ is an odd number, i.e. when $k-j$ is an even number. When $k-j$ is an odd number, $u=\mu_U+x$ gives $\left(u-\mu_U\right)^{k-j}=x^{k-j}$, while $u=\mu_U-x$ gives $\left(u-\mu_U\right)^{k-j}=-x^{k-j}$, such that

$$E\left[\left(y\left(u\right)-\bar{y}^*\left(u\right)\right)^{2n-1}\right]_{u=\mu_U+x}=-E\left[\left(y\left(u\right)-\bar{y}^*\left(u\right)\right)^{2n-1}\right]_{u=\mu_U-x} \tag{S2-53}$$

As a result $p(y(u))$ is skewed, but such that the mean centered distribution of $y(\mu_U-x)$ is a mirror of the mean centered distribution of $y(\mu_U+x)$ for all values of x. Hence, when U is symmetric, $y(U)$ will also be symmetric, even though $y(u)$ is symmetric only for $u=\mu_U$.

We can show this directly by use of the random variable U instead of u in the development of the odd-ordered central moments. From eq. (S2-2) and $\bar{z}_c^*=\mu_U$ then follows

$$\bar{y}^*=E[\bar{z}_a^*+\bar{z}_b^*(U-\bar{z}_c^*)]=\bar{z}_a^* \tag{S2-54}$$

such that the binomial formula gives the unconditional odd-ordered central moments

$$\begin{aligned}
E\left[\left(y-\bar{y}^*\right)^{2n-1}\right] &= E\left[\left(z_a+z_b\left(U-z_c\right)-\bar{z}_a^*\right)^{2n-1}\right]=E\left[\left(z_a-\bar{z}_a^*+z_b\left(U-\mu_U+\left(\bar{z}_c^*-z_c\right)\right)\right)^{2n-1}\right] \\
&= \sum_{k=0}^{2n-1}\binom{2n-1}{k}E\left[\left(z_a-\bar{z}_a^*\right)^{2n-1-k}\left(U-\mu_U+\left(\bar{z}_c^*-z_c\right)\right)^k z_b^k\right] \\
&= \sum_{k=0}^{2n-1}\binom{2n-1}{k}\sum_{j=0}^{k}\binom{k}{j}E[\left(z_a-\bar{z}_a^*\right)^{2n-1-k}\left(U-\mu_U\right)^{k-j}\left(\bar{z}_c^*-z_c\right)^j]E\left[z_b^k\right]
\end{aligned} \tag{S2-55}$$

This gives $E\left[\left(y-\bar{y}^*\right)^{2n-1}\right]=0$ because $E[\left(z_a-\bar{z}_a^*\right)^{2n-1-k}\left(U-\mu_U\right)^{k-j}\left(\bar{z}_c^*-z_c\right)^j]=0$ (Isserlis 1918), and the distribution $p(y(U))$ is therefore symmetric.

Note that we in Conjecture 2 (eq. S2-15) will find $\Delta_{\bar{y}^*}\neq 0$ for realizations $u\neq\mu_U$, but that the symmetry of $p(y(U))$ will give $E\left[\Delta_{\bar{y}^*}\right]=0$.

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