Quantitative Genetics & Phenotypic plasticity

Selection responses

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I will ignore models with explicit costs of plasticity

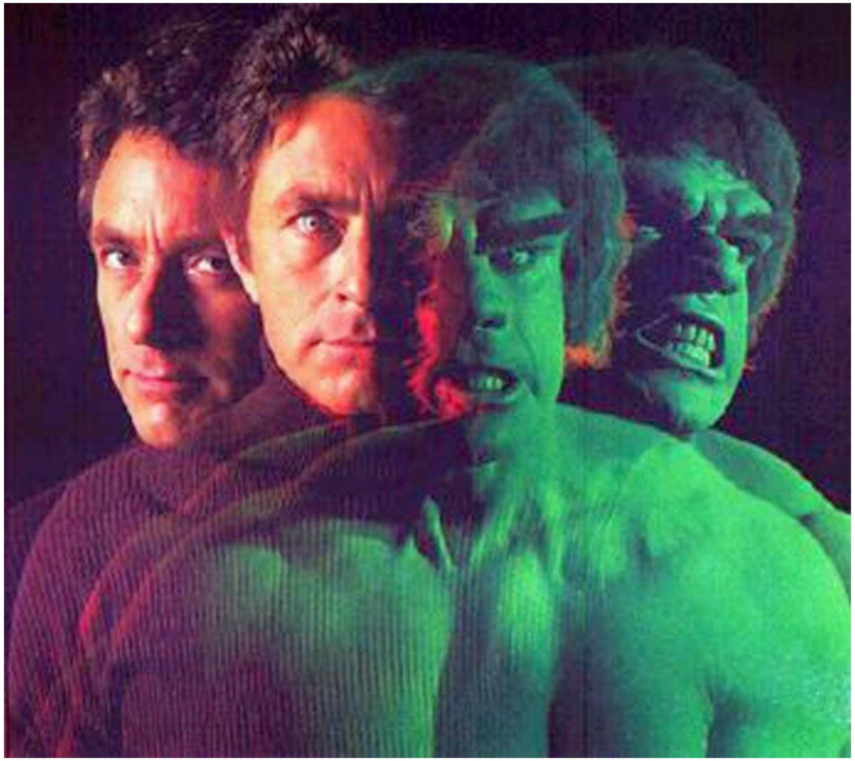
[personal opinion] They either require

(strange) fiddling with fitness

An explicit causal mechanistic model of responding to the environment

Plasticity: phenotypic variation a single genotype can generate depending on environmental input

A general ability to "fix" things, to adjust phenotype to environmental state rapidly



Our work horse

The breeder's equation for selection response

$\boldsymbol{R} = \boldsymbol{G}\,\boldsymbol{\beta}$

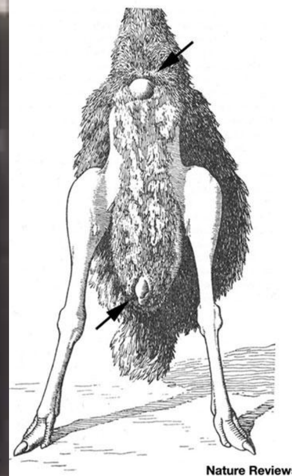
Used to track the average trait value in a population

Plasticity:

- An intercept and slope parameter which are seen as a genotypically determined property of an individual

- Separate traits per environmental state

- Function-valued traits



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Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation

R. LANDE

Phenotype reaction norm

$$z_t = a_t + b_t \varepsilon_{t-\tau} + e_t$$

τ : lag selection - observation

$$\bar{z}_t = \bar{a}_t + \bar{b}_t \varepsilon_{t-\tau}$$

Phenotypic variance components

$${\sigma_z}^2 = G_{aa} + 2G_{ab}\varepsilon_{t-\tau} + G_{bb}\left(\varepsilon_{t-\tau}\right)^2 + {\sigma_e}^2$$

Optimum for selection $$\theta_t = A + B\varepsilon_t$$

ε_t autocorrelated with zero expectation

stationary autocorrelated process $\varepsilon_t = \xi_t$ with mean $\bar{\xi}_t = 0$, variance σ_ξ^2 and autocorrelation ρ_τ over time interval τ. For simplicity, the width of the fitness function

$$W(\varepsilon_t, z_t) = W_{\max}(\varepsilon_t)\exp\left\{-\frac{(z_t - \theta_t)^2}{2\omega^2}\right\}. \qquad (2b)$$

Averaging over the phenotype distribution $p(z_t)$ yields the mean fitness

$$\begin{aligned}\bar{W}(\varepsilon_t, \bar{z}_t) &= \int p(z_t)W(\varepsilon_t, z_t)\mathrm{d}z_t \\ &= W_{\max}(\varepsilon_t)\sqrt{\gamma\omega^2}\exp\left\{-\frac{\gamma}{2}(\bar{z}_t - \theta_t)^2\right\}\end{aligned} \qquad (2c)$$

$$\gamma = 1/(\sigma_z{}^2 + \omega^2)$$

notation from previous part $\Delta \boldsymbol{b} = \boldsymbol{G_b} \boldsymbol{\beta_b}$

$$\Delta \begin{pmatrix} \bar{a} \\ \bar{b} \end{pmatrix} = \begin{pmatrix} G_{aa} & G_{ab} \\ G_{ba} & G_{bb} \end{pmatrix} \boldsymbol{\beta} \tag{3a}$$

is the product of the additive genetic variance-covariance matrix for a and b and the selection gradient, β, which can be derived by substituting eqns (1b,c, 2a) into eqn (2c) and differentiating (Lande, 1979; Gavrilets & Scheiner, 1993a,b; de Jong, 1995, 1999)

$$\boldsymbol{\beta} = \begin{pmatrix} \partial/\partial\bar{a} \\ \partial/\partial\bar{b} \end{pmatrix} \ln \bar{W} = -\gamma \begin{pmatrix} \bar{a} - A + \bar{b}\varepsilon_{t-\tau} - B\varepsilon_t \\ (\bar{a} - A + \bar{b}\varepsilon_{t-\tau} - B\varepsilon_t)\varepsilon_{t-\tau} \end{pmatrix}. \tag{3b}$$

$\boldsymbol{\beta}$ is this derivative of mean fitness when phenotypes are MVN

MEAN FITNESS - WHICH MEAN?

The expected selection gradient, given $\bar{a}$ and $\bar{b}$, is

$$E(\boldsymbol{\beta}) = -\gamma \begin{pmatrix} \bar{a} - A \\ (\bar{b} - \rho_\tau B)\sigma_\xi^2 \end{pmatrix}. \quad (3c)$$

Gavrilets & Scheiner (1993a) and de Jong & Gavrilets (2000) previously analysed this model for spatial rather than temporal environmental variation, and assumed (for simplicity) that $G_{ab} = 0$ in the reference environment. Supposing that the population has adapted to the background environmental stochasticity, before the change in average environment the expected mean reaction norm parameters are

$$E(\bar{a}_0) = A, \quad E(\bar{b}_0) = \rho_\tau B \quad (3d)$$

The average intercept becomes *A;* the average plasticity becomes *B* discounted by the autocorrelation in the environment across time period τ


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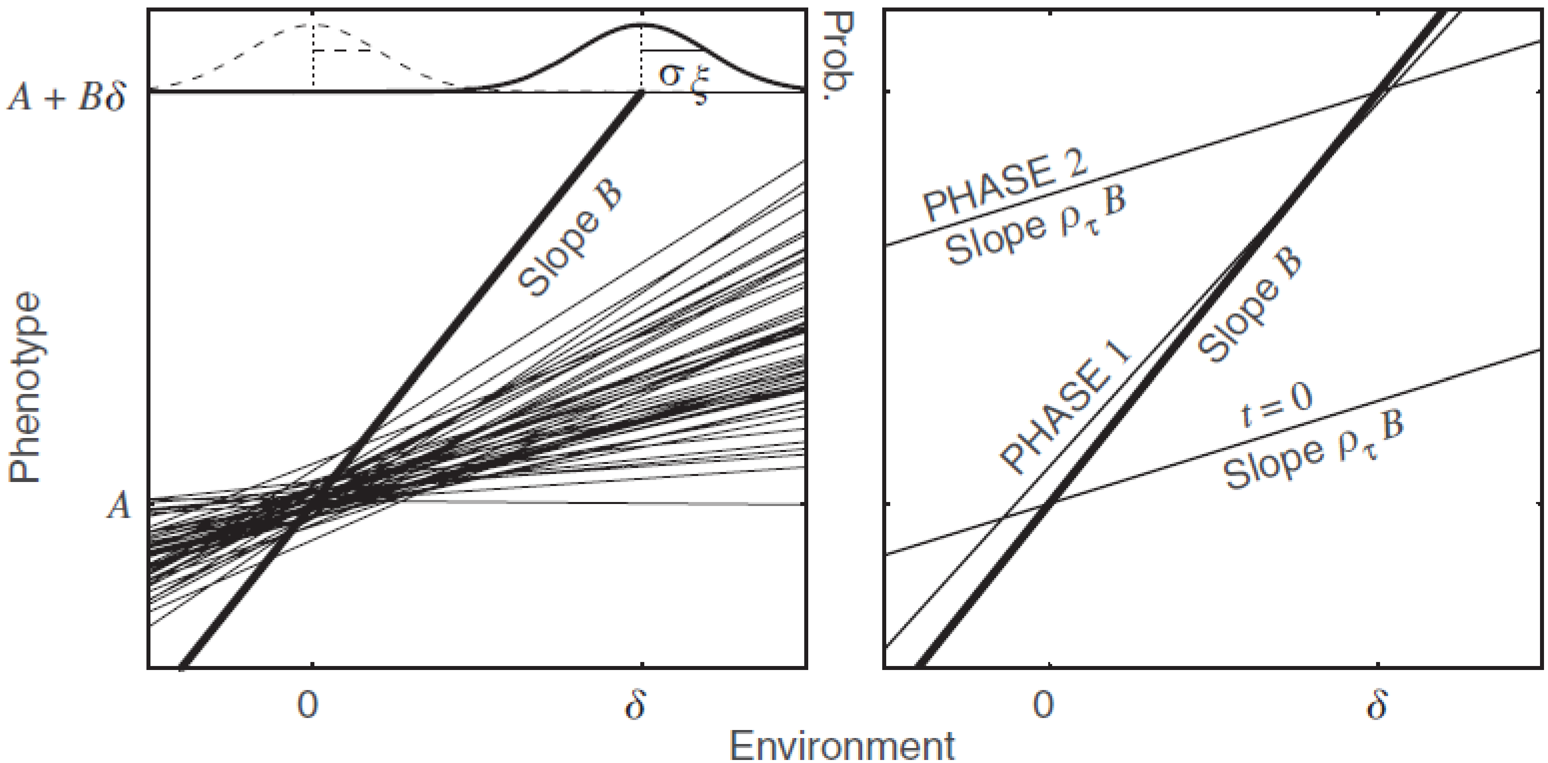

A + Bδ
A
Phenotype
Prob.
σ ξ
Slope B
0
δ
Environment
PHASE 2
Slope ρτ B
PHASE 1
Slope B
t = 0
Slope ρτ B

a sudden environmental change occurs, at time t = 0.

Let the environment be composed of two parts,

$$\varepsilon_t = U_t \delta + \xi_t. \tag{4}$$

The unit step function U_t (which changes from 0 to 1 at $t = 0$) governs the sudden change in average environment by amount δ at time 0. Background environmental stochasticity ξ_t constitutes a stationary autocorrelated process described above. This model is illustrated in Fig. 1 (upper left panel).

After the sudden change in average environment (for t ≥ 0), the expected selection gradient, given $\bar{a}$ and $\bar{b}$, is

$$E(\boldsymbol{\beta}) = -\gamma\left[\begin{pmatrix} 1 & \delta \\ \delta & \delta^2 \end{pmatrix}\begin{pmatrix} \bar{a} - A \\ \bar{b} - B \end{pmatrix} + \begin{pmatrix} 0 \\ (\bar{b} - \rho_\tau B)\sigma_\xi^2 \end{pmatrix}\right]. \tag{5a}$$

From eqns (3a) and (5a,b) the expected evolution of the mean reaction norm parameters for $t \geq 0$ obeys

$$\Delta\begin{pmatrix} E(\bar{a}) \\ E(\bar{b}) \end{pmatrix} = -\gamma\begin{pmatrix} G_{aa} & G_{aa}\delta \\ G_{bb}\delta & G_{bb}(\delta^2 + \sigma_\xi^2) \end{pmatrix}\begin{pmatrix} E(\bar{a}) - E(\bar{a}_\infty) \\ E(\bar{b}) - E(\bar{b}_\infty) \end{pmatrix}. \tag{6a}$$

The expected dynamics can be solved using eigenvalues, λ, and eigenvectors, $\mathbf{v}$, of the matrix (Searle, 1966),

$$\begin{pmatrix} E(\bar{a}_t) - E(\bar{a}_\infty) \\ E(\bar{b}_t) - E(\bar{b}_\infty) \end{pmatrix} = c_1\mathbf{v_1}(1+\lambda_1)^t + c_2\mathbf{v_2}(1+\lambda_2)^t \tag{6b}$$

When adaptation to the new environment is completed,

$$E(\bar{a}_\infty) = A + (1-\rho_\tau)B\delta, \quad E(\bar{b}_\infty) = \rho_\tau B. \tag{5b}$$

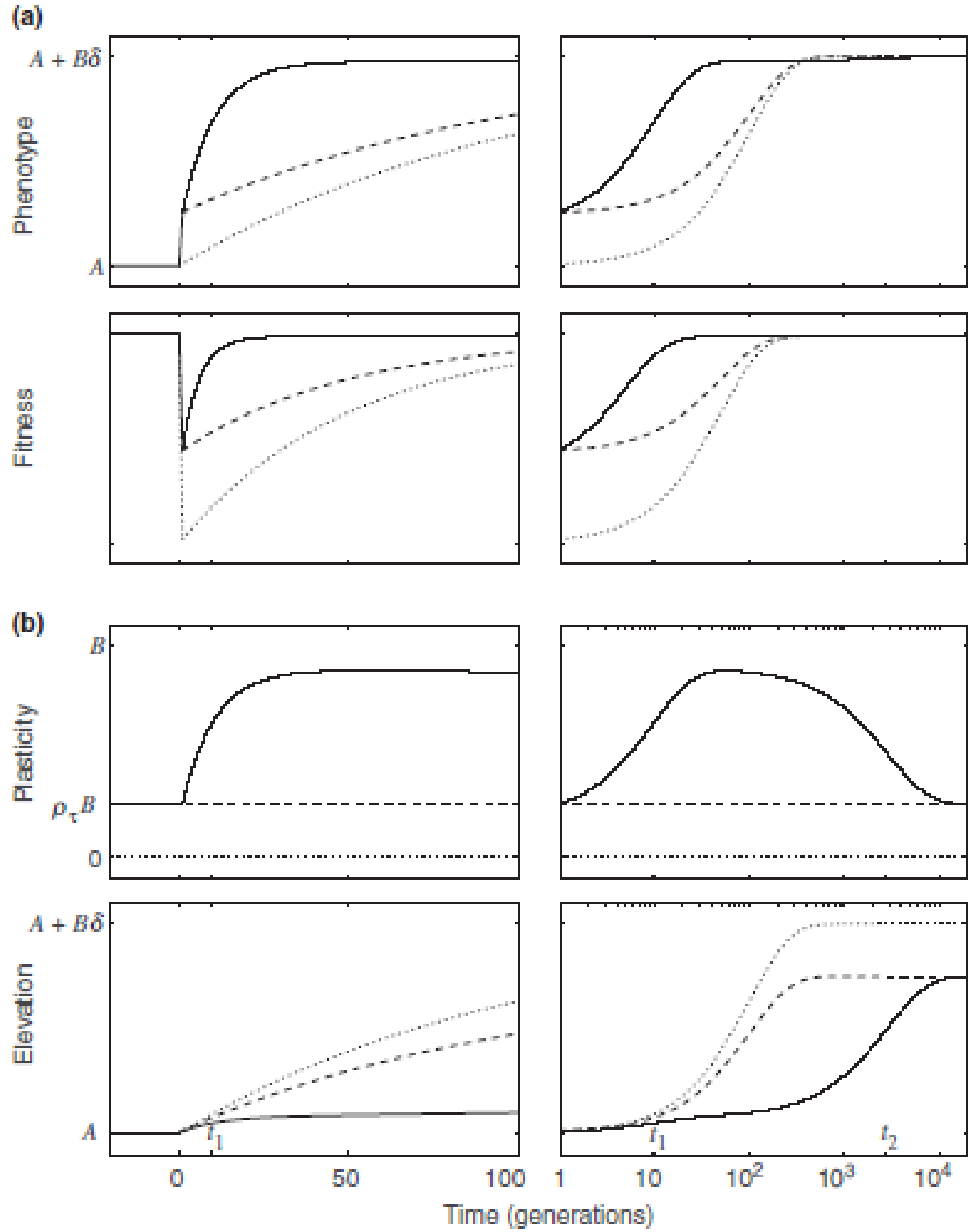


Fig. 2 Dynamics of (a) the expected mean phenotype $E(\bar{z}_t)$ and log mean fitness in the average environment $\ln \bar{W}$, with (b) expected mean reaction norm slope (plasticity) $E(\bar{b}_t)$ and elevation in the reference environment $E(\bar{a}_t)$, following a sudden extraordinary change in average environment. Solid lines: Two-phase adaptation with evolution of plasticity occur on time scales t_1 and t_2. Dashed lines: Adaptation with constant partially adaptive plasticity followed by natural selection (Baldwin effect). Dotted lines: Adaptation by natural selection alone with no plasticity. Left panels depict short-term dynamics including PHASE 1. Right panels illustrate long-term dynamics including PHASE 2 with time plotted logarithmically.

Via and Lande 1985: plasticity effects and simple scenarios of population structure

Soft Selection.—With q_i defined as the proportion of individuals entering the *i*th habitat ($\sum q_i = 1$), $\bar{z}_i$ as the mean value of the character state expressed in the *i*th environment, P_{ii}^{-1} as the reciprocal of the phenotypic variance in the *i*th environment, and s_i as the difference between the mean phenotype before and after selection in the *i*th environment, the dynamical equation for soft selection in two environments is:

$$\begin{pmatrix} \Delta\bar{z}_1 \\ \Delta\bar{z}_2 \end{pmatrix} = \begin{pmatrix} G_{11} & G_{12} \\ G_{21} & G_{22} \end{pmatrix} \begin{pmatrix} q_1 P_{11}^{-1} s_1 \\ q_2 P_{22}^{-1} s_2 \end{pmatrix}. \quad (1)$$

$$\begin{pmatrix} \Delta\bar{z}_1 \\ \Delta\bar{z}_2 \end{pmatrix} = \begin{pmatrix} G_{11} & G_{12} \\ G_{21} & G_{22} \end{pmatrix} \cdot \begin{pmatrix} \nabla_1 \\ \nabla_2 \end{pmatrix} \ln[\overline{W}_1^{\,q} \overline{W}_2^{\,(1-q)}]. \quad (5)$$

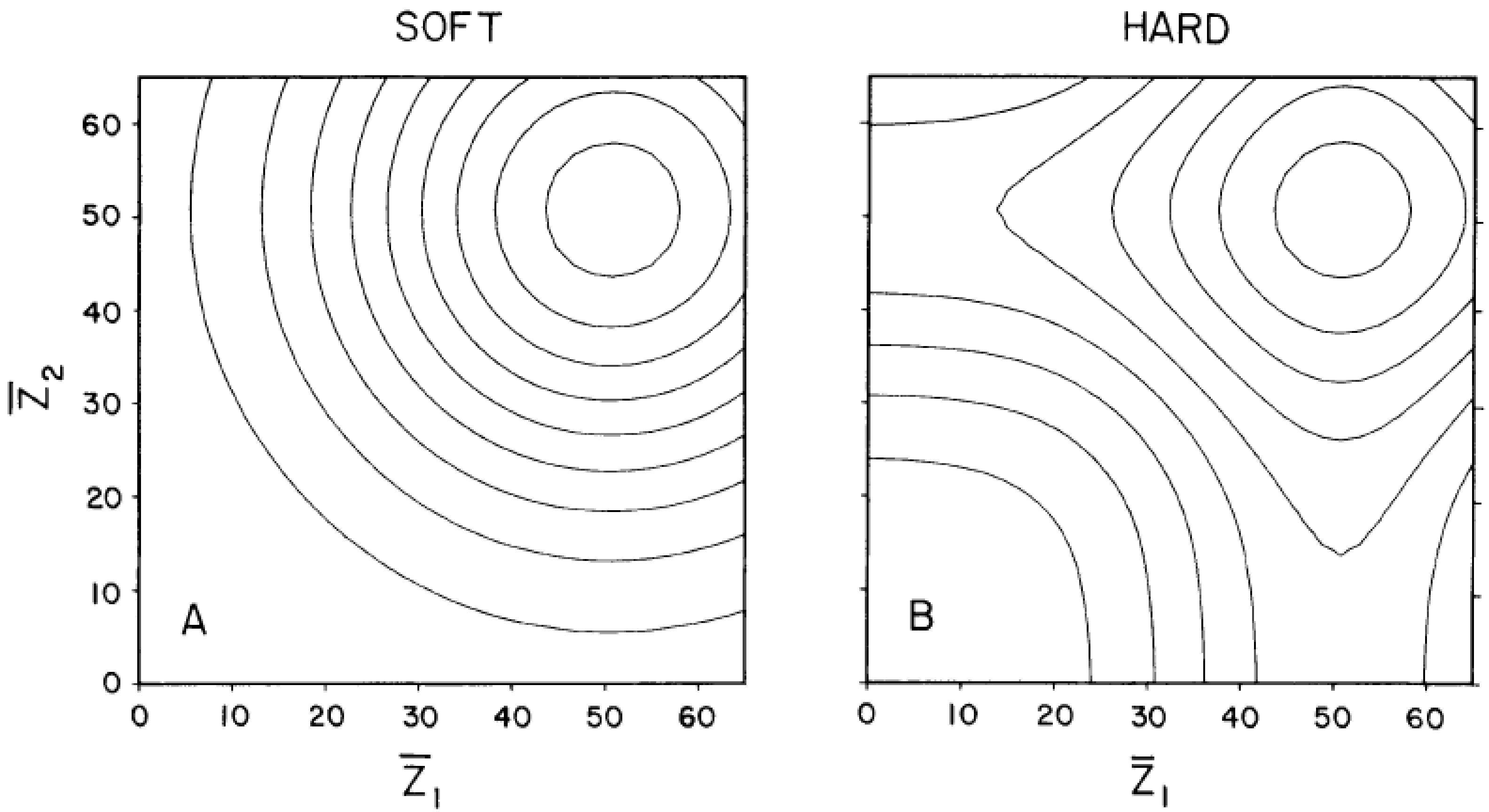
The function $\overline{W} = \overline{W}_1^{\,q} \overline{W}_2^{\,(1-q)}$ gives the joint mean fitness under soft selection as the weighted geometric mean of the mean fitnesses in the two environments, defin-

Via and Lande 1985: plasticity effects and simple scenarios of population structure

Hard Selection.—The dynamical equation for phenotypic evolution under hard selection can be expressed in a form which differs from (1) only by the weighting function: the contribution of each environment to the total population is now the product of its frequency, q, and the relative mean fitness ($\overline{W}_i/\overline{W}$) of individuals selected there, where, as shown below, $\overline{W} = q\overline{W}_1 + (1-q)\overline{W}_2$. For the two environment case,

$$\begin{pmatrix}\Delta\bar{z}_1\\ \Delta\bar{z}_2\end{pmatrix} = \begin{pmatrix}G_{11} & G_{12}\\ G_{21} & G_{22}\end{pmatrix}\begin{pmatrix}[q\overline{W}_1/\overline{W}]P_{11}^{-1}s_1\\ [(1-q)\overline{W}_2/\overline{W}]P_{22}^{-1}s_2\end{pmatrix} = \begin{pmatrix}G_{11} & G_{12}\\ G_{21} & G_{22}\end{pmatrix}\begin{pmatrix}[q\overline{W}_1/\overline{W}]\nabla_1\ln\overline{W}_1\\ [(1-q)\overline{W}_2/\overline{W}]\nabla_2\ln\overline{W}_2\end{pmatrix}$$

$$\begin{pmatrix}\Delta\bar{z}_1\\ \Delta\bar{z}_2\end{pmatrix} = \begin{pmatrix}G_{11} & G_{12}\\ G_{21} & G_{22}\end{pmatrix}\cdot\begin{pmatrix}\nabla_1\\ \nabla_2\end{pmatrix}\ln[q\overline{W}_1 + (1-q)\overline{W}_2]. \quad (11)$$


SOFT
HARD
60
50
40
30
20
10
0
$\bar{Z}_2$
A
B
0
10
20
30
40
50
60
$\bar{Z}_1$
$\bar{Z}_1$

$$\Delta \boldsymbol{b} = \boldsymbol{G}_{\boldsymbol{b}} \boldsymbol{E}^{\mathrm{T}} \boldsymbol{\beta}_{\boldsymbol{g}}$$

Selection response: transform to reaction norm parameters

Selection response: first equations for response in detail, then an average fitness rolls out
then translate into selection pressures on the "machine"