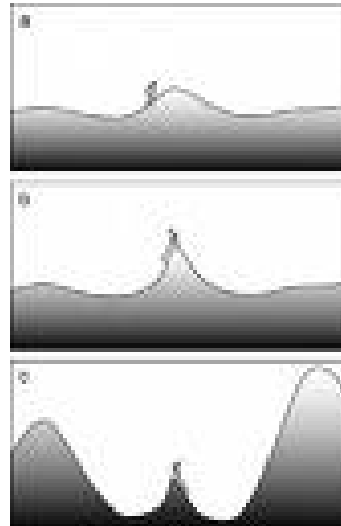


SHIFTING FITNESS LANDSCAPES – GENERAL SELECTION SCHEMES

Towards more Ecology



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1. Frequency-dependent selection

2. Approximation – adaptive dynamics

3. Selection response in structured populations

RECAP FIXED FITNESS LANDSCAPES

Breeder's equation

$$\Delta\boldsymbol{\mu}_z = \mathbf{G}\mathbf{P}^{-1}\left(\boldsymbol{\mu}_z^* - \boldsymbol{\mu}_z\right) = \mathbf{G}\boldsymbol{\beta}$$

Fitness gradient if the phenotype distribution of \mathbf{z} is MVN

$$\begin{aligned}\nabla_{\boldsymbol{\mu}_z} \ln(\overline{W}(\mathbf{z})) &= \nabla_{\boldsymbol{\mu}_z} \int d\mathbf{z} f(\mathbf{z}, \boldsymbol{\mu}_z) \frac{W(\mathbf{z})}{\overline{W}(\mathbf{z})} \\ &= \int d\mathbf{z} w(\mathbf{z}) f(\mathbf{z}) \mathbf{P}^{-1}(\mathbf{z} - \boldsymbol{\mu}_z) \\ &= \mathbf{P}^{-1} \left(\int d\mathbf{z} w(\mathbf{z}) f(\mathbf{z}) \mathbf{z} - \boldsymbol{\mu}_z \int d\mathbf{z} w(\mathbf{z}) f(\mathbf{z}) \right) \\ &= \mathbf{P}^{-1}(\boldsymbol{\mu}_z^* - \boldsymbol{\mu}_z) = \mathbf{P}^{-1}\mathbf{s} = \boldsymbol{\beta}\end{aligned}$$

1. FREQUENCY DEPENDENT SELECTION

Fitness $W(\mathbf{z}, \boldsymbol{\mu}_z)$ depends on population average

Mean fitness $\overline{W}(\mathbf{z}, \boldsymbol{\mu}_z) = \int d\mathbf{z} f(\mathbf{z}, \boldsymbol{\mu}_z) W(\mathbf{z}, \boldsymbol{\mu}_z)$

Another way of writing the selection gradient

$$\begin{aligned} \boldsymbol{\beta} &= \mathbf{P}^{-1} \left(\int d\mathbf{z} f(\mathbf{z}) w(\mathbf{z}) \mathbf{z} - \boldsymbol{\mu}_z \int d\mathbf{z} f(\mathbf{z}) w(\mathbf{z}) \right) \\ &= \mathbf{P}^{-1} \text{Cov}(\mathbf{z}, w(\mathbf{z})) \end{aligned}$$

With MVN phenotype distribution

$$\begin{aligned}
\nabla_{\mu_z} \ln(\overline{W}(\mathbf{z}, \boldsymbol{\mu}_z)) &= \overline{W}^{-1} \nabla_{\mu_z} \overline{W}(\mathbf{z}, \boldsymbol{\mu}_z) \\
&= \nabla_{\mu_z} \int d\mathbf{z} f(\mathbf{z}, \boldsymbol{\mu}_z) w(\mathbf{z}, \boldsymbol{\mu}_z) \\
&= \int d\mathbf{z} w(\mathbf{z}, \boldsymbol{\mu}_z) \nabla_{\mu_z} f(\mathbf{z}, \boldsymbol{\mu}_z) + \int d\mathbf{z} f(\mathbf{z}, \boldsymbol{\mu}_z) \nabla_{\mu_z} w(\mathbf{z}, \boldsymbol{\mu}_z) \\
&= \mathbf{P}^{-1} \int d\mathbf{z} f(\mathbf{z}) \mathbf{z} w(\mathbf{z}, \boldsymbol{\mu}_z) - \mathbf{P}^{-1} \boldsymbol{\mu}_z + \int d\mathbf{z} f(\mathbf{z}, \boldsymbol{\mu}_z) \nabla_{\mu_z} w(\mathbf{z}, \boldsymbol{\mu}_z) \\
&= \mathbf{P}^{-1} (\boldsymbol{\mu}_z^* - \boldsymbol{\mu}_z) + \overline{W}^{-1} \int d\mathbf{z} f(\mathbf{z}, \boldsymbol{\mu}_z) \nabla_{\mu_z} [W(\mathbf{z}, \boldsymbol{\mu}_z)]
\end{aligned}$$

The frequency-dependent breeder's equation becomes

$$\begin{aligned}\Delta\boldsymbol{\mu}_z &= \mathbf{G}\mathbf{P}^{-1}(\boldsymbol{\mu}_z^* - \boldsymbol{\mu}_z) \\ &= \mathbf{G}\left(\nabla_{\boldsymbol{\mu}_z} \ln(\bar{W}(z, \boldsymbol{\mu}_z)) - \bar{W}^{-1} \int dz f(z, \boldsymbol{\mu}_z) \nabla_{\boldsymbol{\mu}_z} [W(z, \boldsymbol{\mu}_z)]\right)\end{aligned}$$

→ Evolution does not climb to a top of the mean fitness landscape
(Day and Taylor 1996)

2. ESS APPROXIMATIONS adaptive dynamics

goal: get an equation for the selection gradient that depends on the phenotypic mean only.

$$\begin{aligned}\Delta\mu_z &= \mathbf{GP}^{-1}(\mu_z^* - \mu_z) \\ &= \mathbf{GP}^{-1}\overline{W}(\mathbf{z}, \mu_z)^{-1} \int d\mathbf{z} f(\mathbf{z}, \mu_z)(\mathbf{z} - \mu_z)W(\mathbf{z}, \mu_z)\end{aligned}$$

What we can expand, is the fitness of an individual:

$$W(\mathbf{z}, \mu_z) = W(\mu_z, \mu_z) + (\mathbf{z} - \mu_z)^T D_1 W(\mu_z, \mu_z) + \frac{1}{2}(\mathbf{z} - \mu_z)^T D_{11} W(\mu_z, \mu_z)(\mathbf{z} - \mu_z) + h.o.t$$

ESS APPROXIMATIONS
adaptive dynamics

Inserting this expansion yields

$$\Delta\boldsymbol{\mu}_z = \mathbf{GP}^{-1}\overline{W}(\mathbf{z}, \boldsymbol{\mu}_z)^{-1} \left(\begin{array}{l} \int dz f(\mathbf{z}, \boldsymbol{\mu}_z)(\mathbf{z} - \boldsymbol{\mu}_z)W(\boldsymbol{\mu}_z, \boldsymbol{\mu}_z) \\ + \int dz f(\mathbf{z}, \boldsymbol{\mu}_z)(\mathbf{z} - \boldsymbol{\mu}_z)(\mathbf{z} - \boldsymbol{\mu}_z)^T D_1 W(\boldsymbol{\mu}_z, \boldsymbol{\mu}_z) \\ + \frac{1}{2} \int dz f(\mathbf{z}, \boldsymbol{\mu}_z)(\mathbf{z} - \boldsymbol{\mu}_z)(\mathbf{z} - \boldsymbol{\mu}_z)^T D_{11} W(\boldsymbol{\mu}_z, \boldsymbol{\mu}_z)(\mathbf{z} - \boldsymbol{\mu}_z) \\ + h.o.t. \end{array} \right)$$

With symmetric probability distributions f (of phenotypes), the integrals over odd powers of $\mathbf{z} - \boldsymbol{\mu}_z$ will vanish.

We retain the following approximate expression:

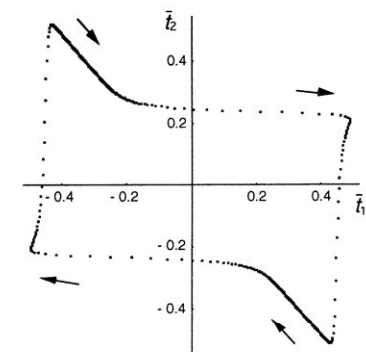
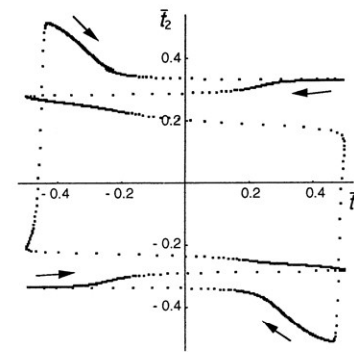
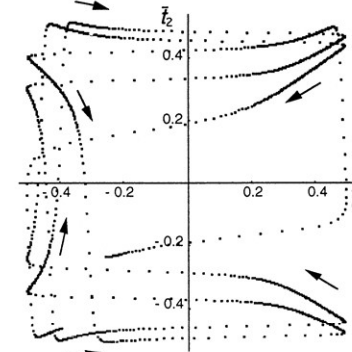
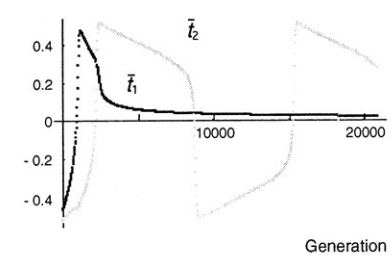
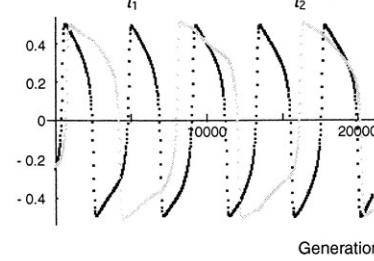
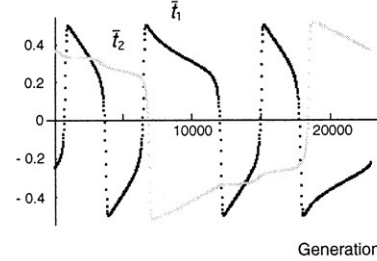
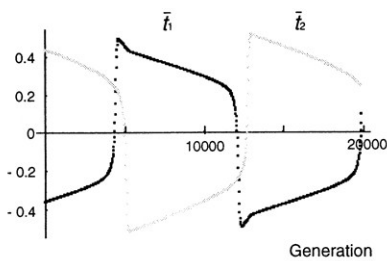
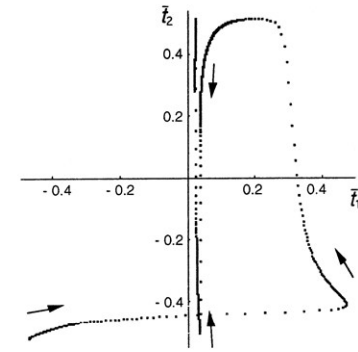
$$\begin{aligned}
 \Delta\boldsymbol{\mu}_z &= \mathbf{GP}^{-1}\overline{W}(\mathbf{z}, \boldsymbol{\mu}_z)^{-1} \left(\int d\mathbf{z} f(\mathbf{z}, \boldsymbol{\mu}_z) (\mathbf{z} - \boldsymbol{\mu}_z) (\mathbf{z} - \boldsymbol{\mu}_z)^T D_1 W(\boldsymbol{\mu}_z, \boldsymbol{\mu}_z) + h.o.t. \right) \\
 &= \mathbf{GP}^{-1}\overline{W}(\mathbf{z}, \boldsymbol{\mu}_z)^{-1} \left(\mathbf{P} D_1 W(\boldsymbol{\mu}_z, \boldsymbol{\mu}_z) + h.o.t. \right) \\
 &\cong \mathbf{G}\overline{W}(\mathbf{z}, \boldsymbol{\mu}_z)^{-1} D_1 W(\boldsymbol{\mu}_z, \boldsymbol{\mu}_z)
 \end{aligned}$$

This approximation holds good as long as selection is not too weak (Abrams 1993).

If we expand mean fitness as well (Iwasa et al. 1991):

$$\Delta\boldsymbol{\mu}_z \cong \mathbf{G}\nabla_{\mathbf{z}} \ln W(\boldsymbol{\mu}_z, \boldsymbol{\mu}_z)$$

....Hey ! That looks simple!

(a) $\theta=0.05$ (b) $\theta=0.2$ (c) $\theta=0.8$ (d) $\theta=1.2$ 

Coevolution of two preferences for separate male ornaments as a function of epistasis in the joint cost of choice θ . Phase-space of the mean male ornaments (\bar{t}_1 and \bar{t}_2) every 20 generations; second as \bar{t}_1 (black) and \bar{t}_2 (gray) values through time.

Iwasa, Y. and A. Pomiankowski, 1995. Continual change in mate preferences. *Nature* 377:420-422.

STABILITY ANALYSIS

Use this approximation to define a dynamics system with discrete time steps

$$\mu_{z,t+1} = \mu_{z,t} + \Delta\mu_{z,t}$$

We can investigate the (convergence) stability of an equilibrium μ_z^{CS}

$$\begin{aligned}(\mu_{z,t+1} - \mu_z^{\text{CS}}) &= \frac{\partial}{\partial \mu_{z,t}} (\mu_{z,t} + \Delta\mu_{z,t}) \Big|_{\mu_{z,t} = \mu_z^{\text{CS}}} (\mu_{z,t} - \mu_z^{\text{CS}}) \\ &= 1 + \frac{\partial}{\partial \mu_{z,t}} \Delta\mu_{z,t} \Big|_{\mu_{z,t} = \mu_z^{\text{CS}}} (\mu_{z,t} - \mu_z^{\text{CS}}) \\ &= \left(1 + \frac{\partial}{\partial \mu_{z,t}} \Delta\mu^{\text{CS}} \right) (\mu_{z,t} - \mu_z^{\text{CS}})\end{aligned}$$

HESSIAN- INVASIBILITY

What about invasibility of μ^{CS}_z by new mutants?

$$\mathbf{H}_{ij}(\mu^{\text{CS}}_z) = \left(D_{11} W(\mu^{\text{CS}}_z, \mu^{\text{CS}}_z) \right)_{ij} = \frac{\partial^2}{\partial z_i \partial z_j} W(z, \mu^{\text{CS}}_z) \Bigg|_{z=\mu^{\text{CS}}_z}$$

When the Hessian \mathbf{H} , evaluated at a point μ^{CS}_z , is positive definite, then μ^{CS}_z is a local minimum

with \mathbf{H} negative definite, μ^{CS}_z is a local maximum

When some eigenvalues of \mathbf{H} are negative and some positive, the hessian \mathbf{H} corresponds to a saddle at μ^{CS}_z

DIRECTIONAL EVOLUTIONARY DYNAMICS

'Continuous' time (e.g. Day and Taylor 2003)

$$\frac{d\boldsymbol{\mu}_z}{dt} = \text{cov}(z, w(\boldsymbol{\mu}_z, \boldsymbol{\mu}_z))$$

If the derivative of w does not change much over the distribution of z

$$\frac{d\boldsymbol{\mu}_z}{dt} = \mathbf{G}(\boldsymbol{\mu}_z) \nabla_z w(\boldsymbol{\mu}_z, \boldsymbol{\mu}_z)$$

The points in trait space which are equilibria of this dynamic are often written as

$$\boldsymbol{\mu}^*$$

Where the z is now omitted too...

CONVERGENCE STABILITY OF CANDIDATE ESS'S

Expand the selection gradient $D_1 w$ around the singular point.
That gives, eventually,

$$D_1 w(\boldsymbol{\mu}^*, \boldsymbol{\mu}^*) \cong (\mathbf{H}(\boldsymbol{\mu}^*) + \mathbf{Q}(\boldsymbol{\mu}^*))(\boldsymbol{\mu} - \boldsymbol{\mu}^*) \cong \mathbf{J}(\boldsymbol{\mu}^*)(\boldsymbol{\mu} - \boldsymbol{\mu}^*)$$

$$\frac{d(\boldsymbol{\mu} - \boldsymbol{\mu}^*)}{dt} = \mathbf{G}(\boldsymbol{\mu}^*)\mathbf{J}(\boldsymbol{\mu}^*)(\boldsymbol{\mu} - \boldsymbol{\mu}^*)$$

Summarizing: the eigenvalues of \mathbf{H} determine INVASIBILITY,
the eigenvalues of \mathbf{J} will determine CONVERGENCE STABILITY.

3. POPULATION STRUCTURE



Southern Right Whale



Protea pudens

No density nor frequency-dependence

Lande (1982)

Weak selection and overlapping generations

Age structure

Approximation

Replace w by little r the intrinsic rate of growth

$$\frac{dz}{dt} = \mathbf{G}\nabla r$$

$$\int_0^{\infty} da e^{-ra} E[l_a(\mathbf{z})m_a(\mathbf{z})] = 1$$

Day and Taylor (1996)

Approximation + Frequency dependence

Lifetime reproductive output discounted for population growth

$$w(r, z, \mu) = \int_0^{\infty} da e^{-E[r]a} l_a(z, \mu) m_a(z, \mu)$$

$$\frac{dz}{dt} = \frac{dE[r]}{d\mu} - \bar{T}^{-1} \nabla E \left[\frac{dw}{d\mu} \right]$$

$$\bar{T} = \int_0^{\infty} da e^{-E[r]a} E[l_a(z, \mu) m_a(z, \mu)] a$$

These are still not 'general' population models
Selection has to be weak.

TRAIT VECTORS PER INDIVIDUAL STATE

Law (1991)

Different stages/ages where individuals can be in
 m traits, n stages

$$\mathbf{M}_t = \begin{pmatrix} \boldsymbol{\mu}_{1,t} \\ \vdots \\ \boldsymbol{\mu}_{n,t} \end{pmatrix}$$

and \mathbf{G} and \mathbf{P}_i which are $m \times m$ matrices

at birth the mean phenotypic values are equal to the mean genotypic values
Selection during life makes mean phenotypic and genotypic values different in
different stages.

Directional selection

update rules for mean trait vectors

G assumed constant and identical for all individual states
- a first assumption to relax

$$\mathbf{S}_t = \begin{pmatrix} \mu_{1,t}^* & -\mu_{1,t} \\ \vdots & \\ \mu_{n,t}^* & -\mu_{n,t} \end{pmatrix}$$

only non-zero elements for ages where traits are expressed.

Changes in genotypic values

$$\widehat{\mathbf{G}}_t \widehat{\mathbf{P}}_t^{-1} \mathbf{S}_t = \text{diag}(\mathbf{G}_t) \text{diag}(\mathbf{P}_{1,t}^{-1} \cdots \mathbf{P}_{n,t}^{-1}) \begin{pmatrix} \mu_{1,t}^* - \mu_{1,t} \\ \vdots \\ \mu_{n,t}^* - \mu_{n,t} \end{pmatrix}$$

Population dynamics

Transition matrix \mathbf{T}

T_{ij} probability that an individual in state i receives a gene from an individual in state j

$$\mathbf{M}_{t+1} = (\mathbf{T}_t \otimes \mathbf{I})(\mathbf{M}_t + \widehat{\mathbf{G}}_t \widehat{\mathbf{P}}_t^{-1} \mathbf{S}_t)$$

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