Effects of clonality on evolutionary lag and rescue

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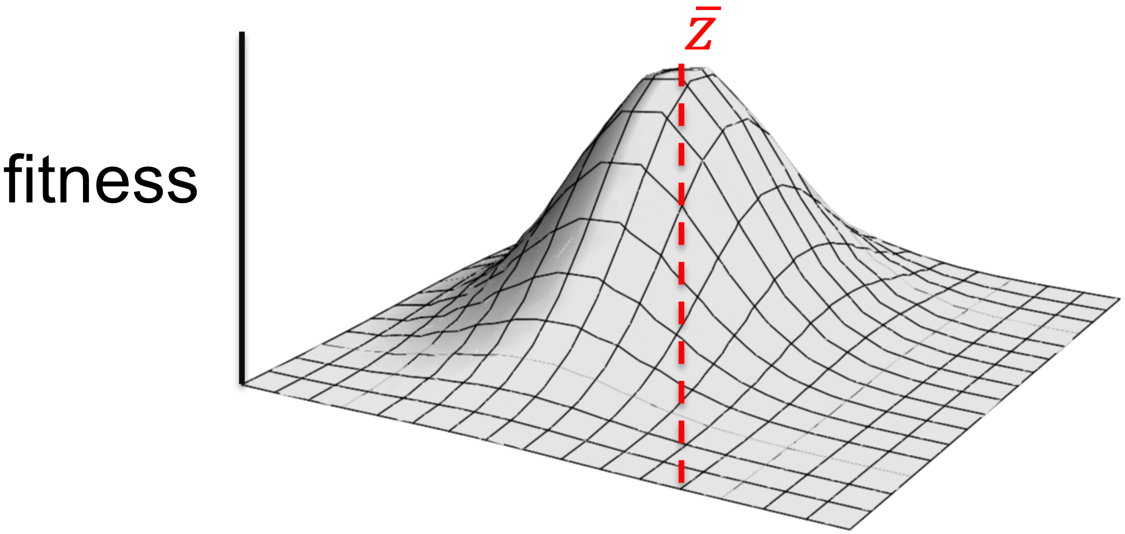
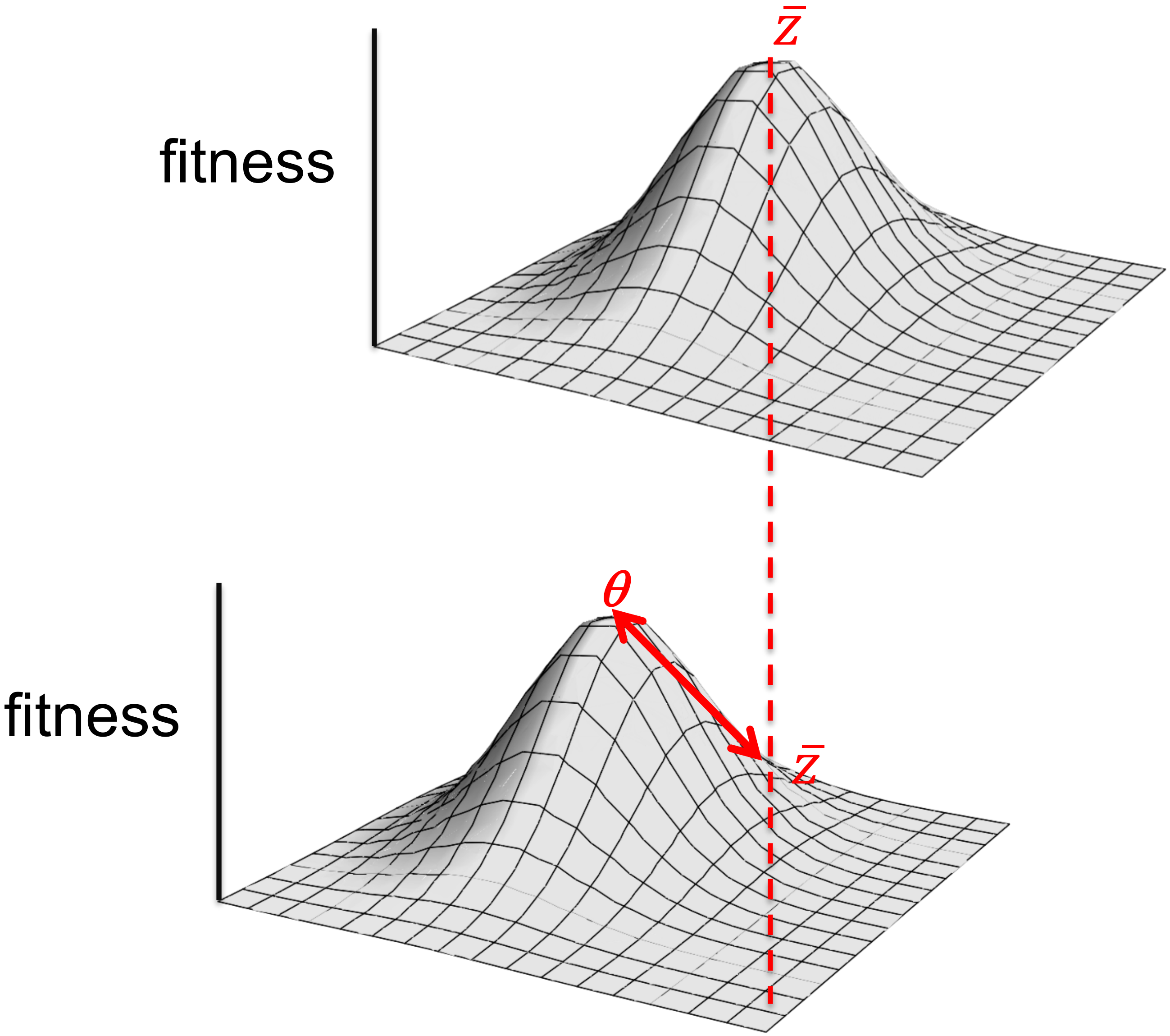
tracking environmental change



tracking environmental change

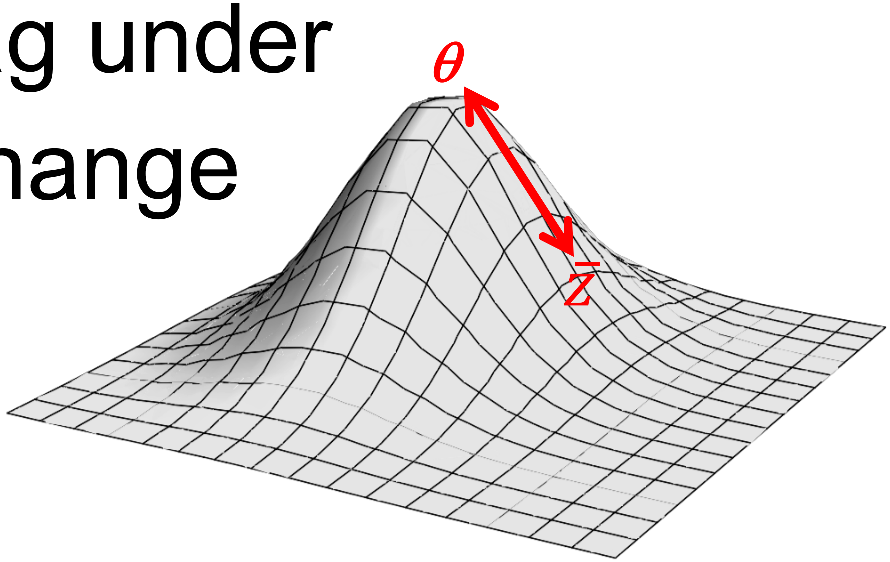


evolutionary lag

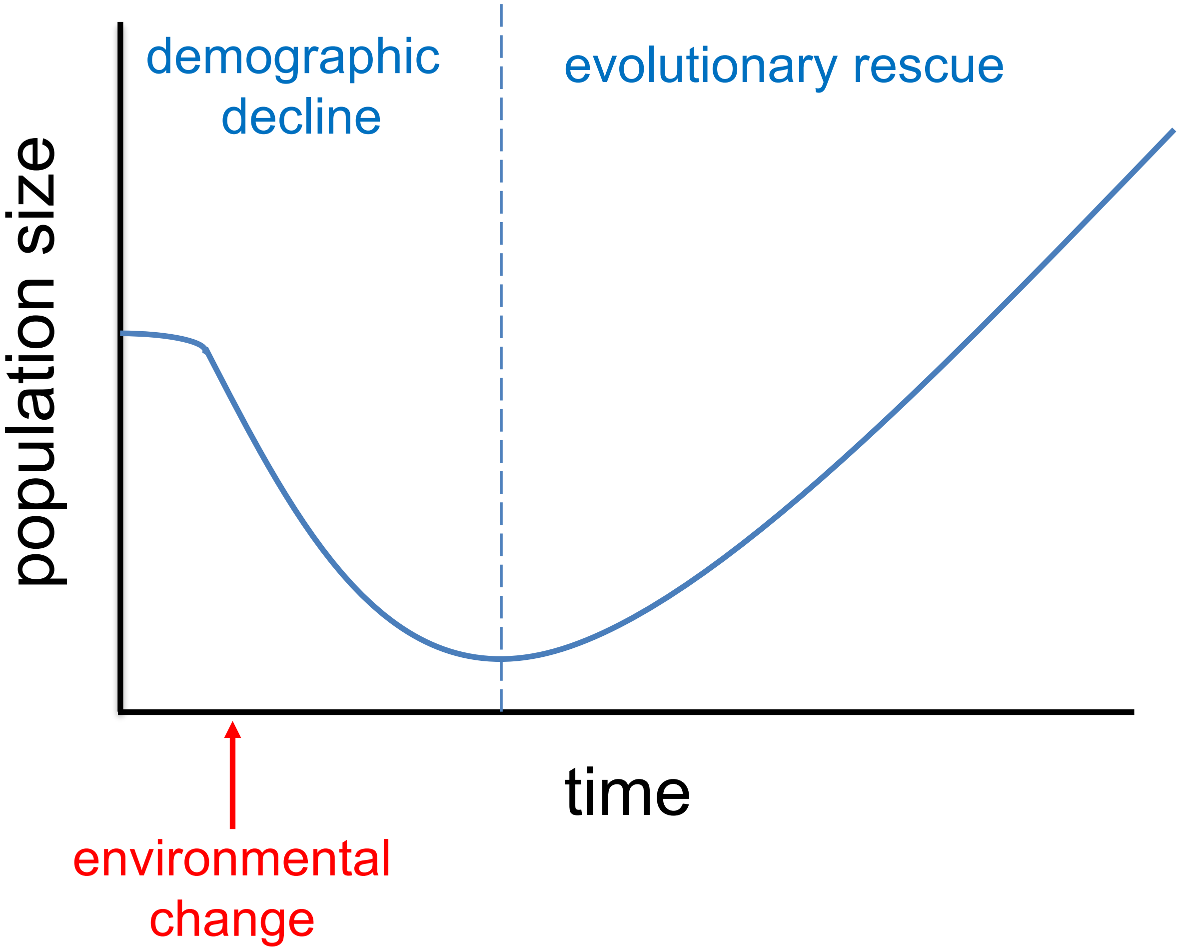
- evolutionary lag (or lag load)
  - difference between phenotypic trait mean and its optimum

$$L_\theta = \frac{(\bar{z} - \theta)^2}{2\sigma_w^2}$$ Maynard Smith (1976)

- greater evolutionary lag under rapid environmental change

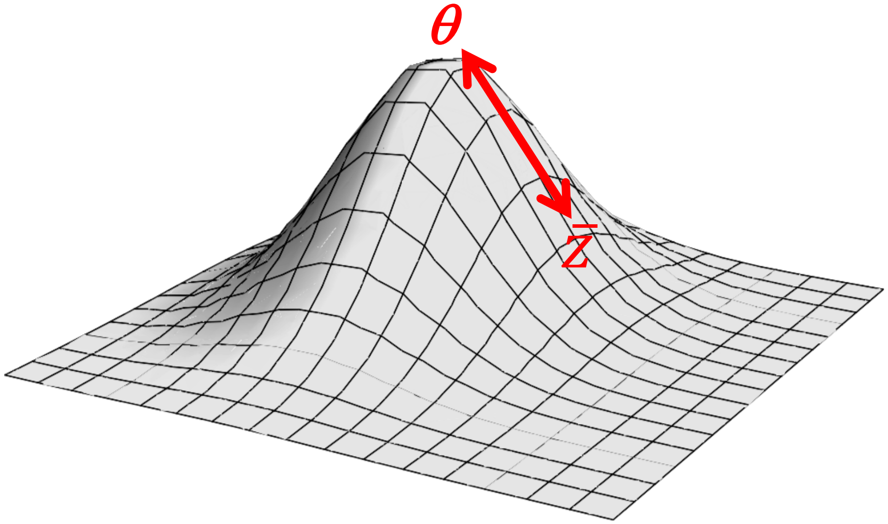


evolutionary rescue



life history and environmental change

- how do stage structure and clonal reproduction affect a population’s ability to track change?



stage structure and clonality

image by Forest & Kim Starr.

image by Nadiatalent

image from Oxford Scientific

image from NOAA website

Combining phenotypic evolution and stage-structured life histories

- evolution in stage-structured populations

  Barfield et al. (2011)

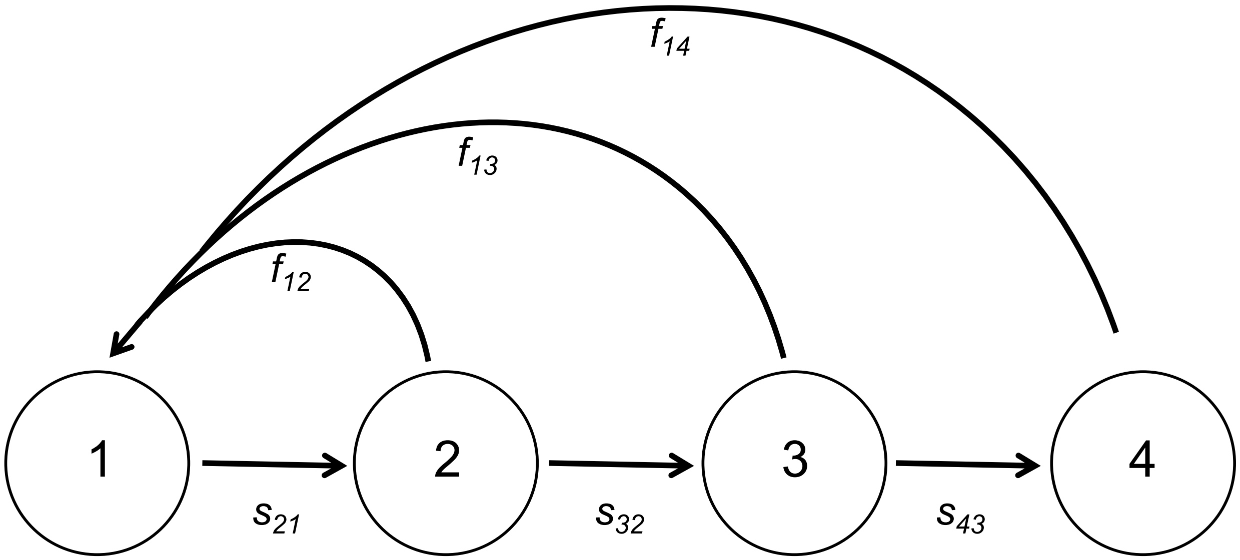
  - multivariate phenotypic trait

$$\mathbf{z} = (z_1, z_2, \cdots, z_n)^T$$

$$\mathbf{z} = \mathbf{g} + \mathbf{e}$$

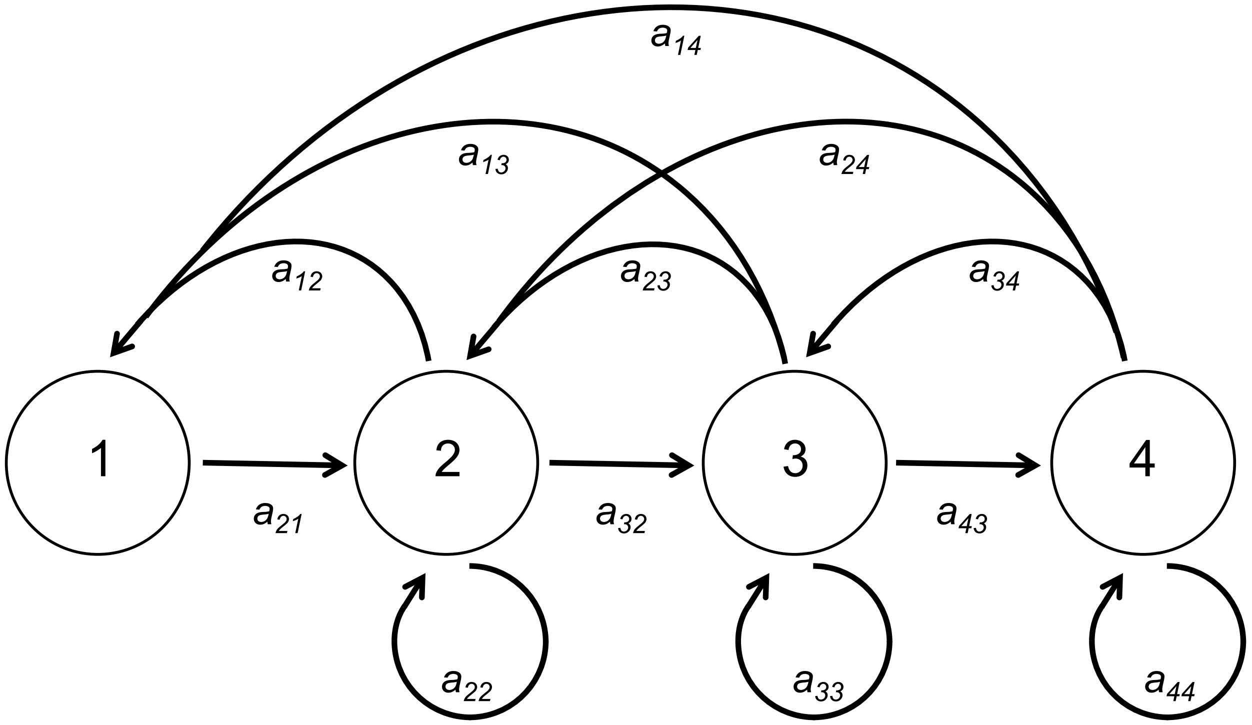
  - N_i = number of individuals for each stage i
  - $p_i(\mathbf{g}, \mathbf{z})$ = joint probability density function (PDF) for $\mathbf{g}$ and $\mathbf{z}$ of stage i

simple age-structured life history graph

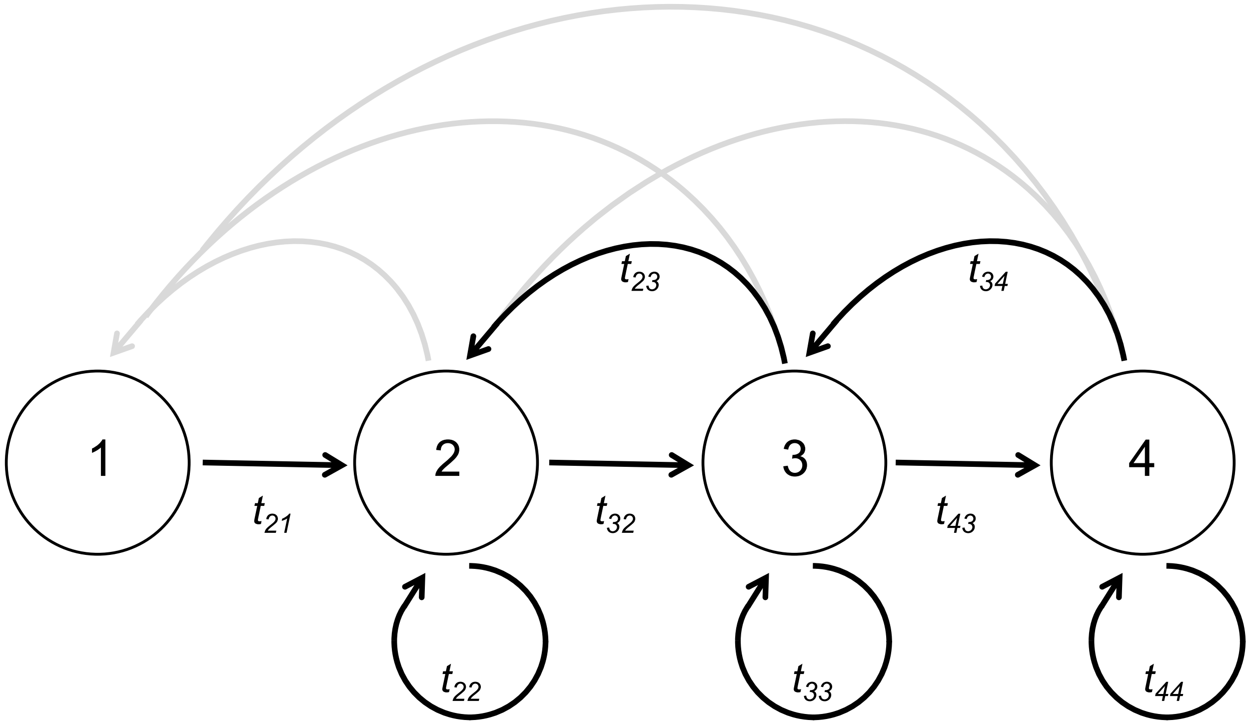


$$\boldsymbol{N}' = \mathbf{A}\,\boldsymbol{N} \qquad \mathbf{A} = \begin{bmatrix} 0 & f_{12} & f_{13} & f_{14} \\ s_{21} & 0 & 0 & 0 \\ 0 & s_{32} & 0 & 0 \\ 0 & 0 & s_{43} & 0 \end{bmatrix} \quad \boldsymbol{N} = \begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \end{bmatrix}$$

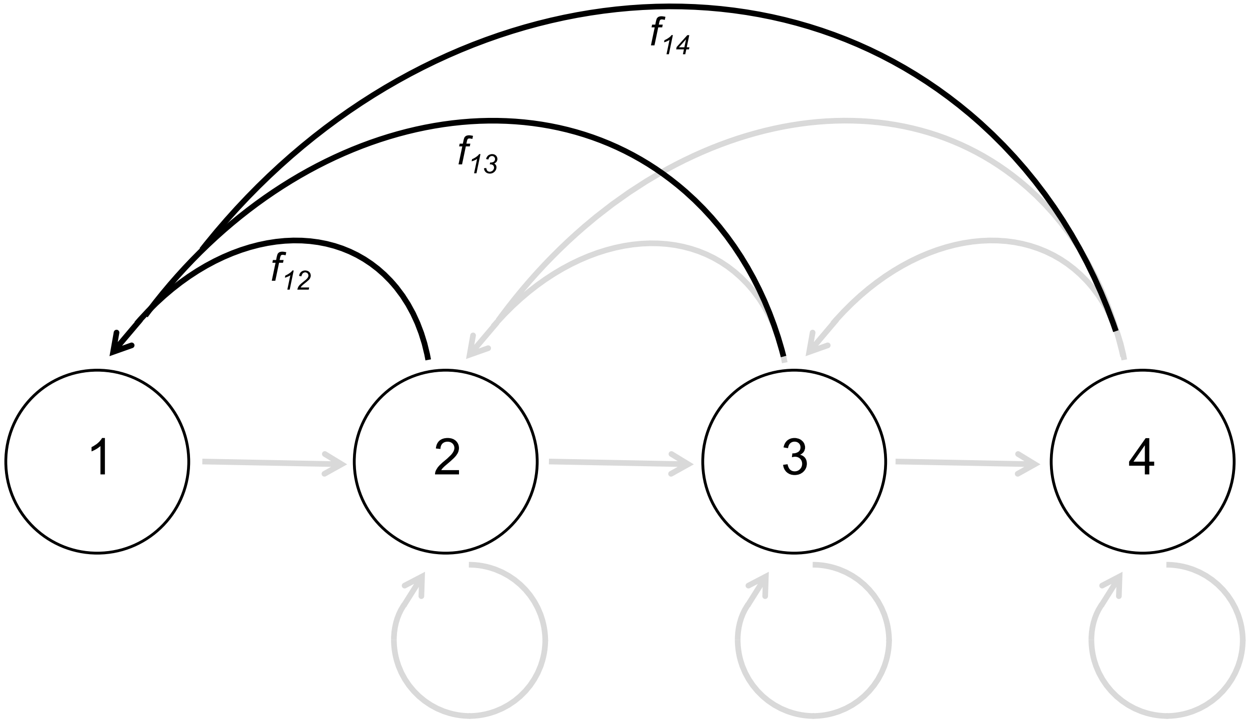
stage-structured life history graph



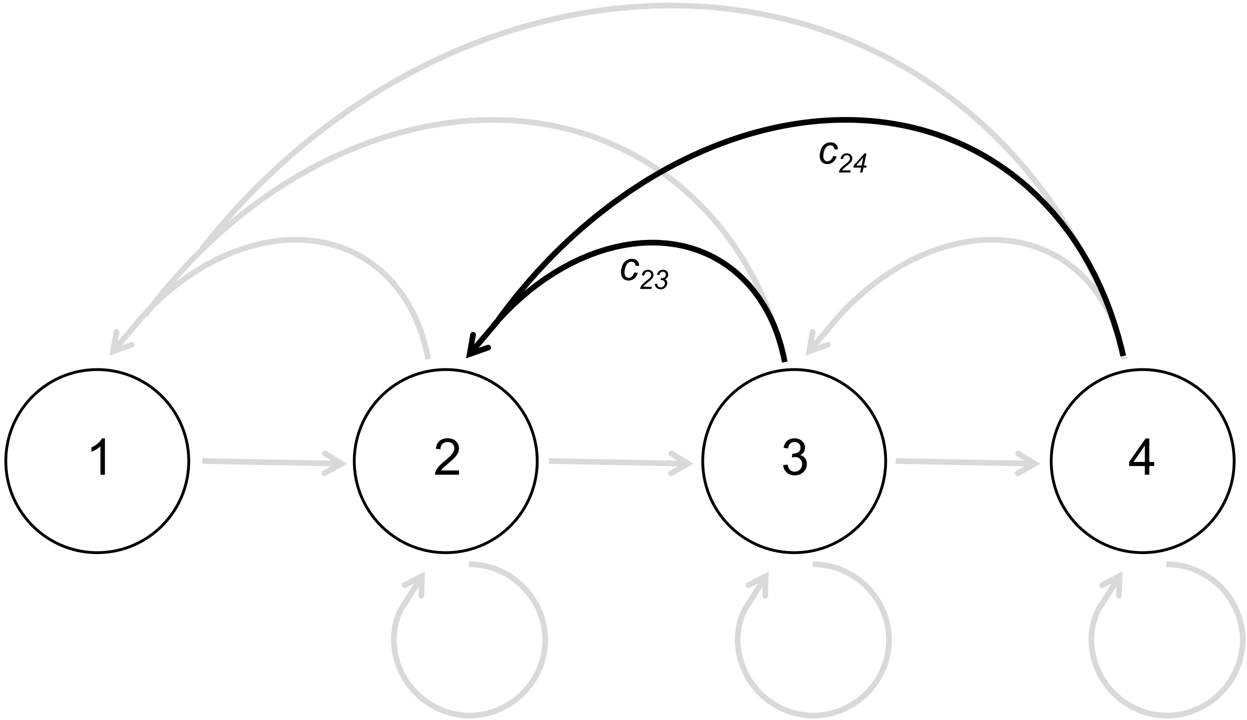
transitions



sexual reproduction



clonal reproduction



Explicitly considering clonal reproduction

- three types of movements

$$N_i' = \sum_j N_j \bar{a}_{ij} = \sum_j N_j \left(\bar{t}_{ij} + \bar{f}_{ij} + \bar{c}_{ij}\right)$$

$$= \sum_j N_j \bar{t}_{ij} + \sum_j N_j \bar{f}_{ij} + \sum_j N_j \bar{c}_{ij} = T_i' + F_i' + C_i'$$

t_{ij} = transition from stage j to stage i

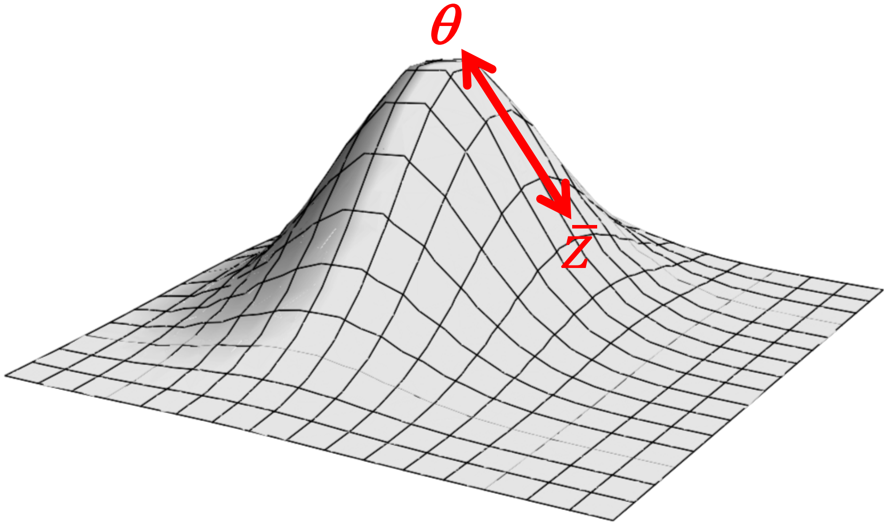
f_{ij} = sexual reproduction from stage j to stage i

c_{ij} = clonal reproduction from stage j to stage i

phenotypic evolution

z = phenotypic trait

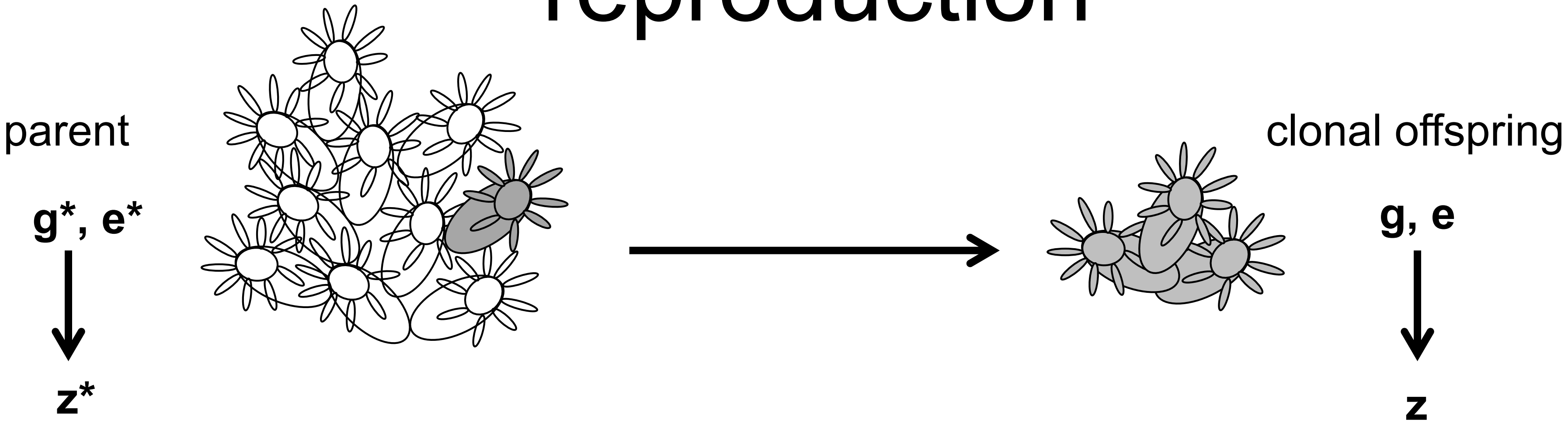
z = g + e



g = additive genetic factor

e = non-additive genetic
+ random environmental factor

Two key aspects of clonal reproduction



parent

$\mathbf{g}^*, \mathbf{e}^*$

$\downarrow$

$\mathbf{z}^*$

clonal offspring

$\mathbf{g}, \mathbf{e}$

$\downarrow$

$\mathbf{z}$

- somatic mutation
  - can be incorporated clonally into next generation
  - mapping parental genotype $\mathbf{g}^*$ to offspring genotype $\mathbf{g}$

- environmental component of phenotype, $\mathbf{e}$
  - non-additive genetic variance + environmental deviation
  - mapping $\mathbf{z} = \mathbf{g} + \mathbf{e}$ for clonal offspring
  - correlation between $\mathbf{e}$ and $\mathbf{e}^*$ (ρ, association parameter)

ρ = association between **e** in parent and clonal offspring

ρ close to 0

Joerg Hauke/Getty Images

ρ close to 1

© Steffen Clauss

Discrete time model

- change in population size

$$N_i' = \sum_j N_j \bar{t}_{ij} + \sum_j N_j \bar{f}_{ij} + \sum_j N_j \bar{c}_{ij} = T_i' + F_i' + C_i'$$

- change in joint probability density function (PDFs) of genotype and phenotype

$$p_i'(\mathbf{g},\mathbf{z}) = \theta_i(\mathbf{g},\mathbf{z})\frac{T_i'}{N_i'} + \phi_{\boldsymbol{i}}(\mathbf{g},\mathbf{z})\frac{F_i'}{N_i'} + \kappa_i(\mathbf{g},\mathbf{z})\frac{C_i'}{N_i'}$$

Discrete time model

- change in population size

$$N_i' = \sum_j N_j \bar{t}_{ij} + \sum_j N_j \bar{f}_{ij} + \sum_j N_j \bar{c}_{ij} = T_i' + F_i' + C_i'$$

- change in joint probability density function (PDFs) of genotype and phenotype

$$p_i'(\mathbf{g}, \mathbf{z}) = \theta_i(\mathbf{g}, \mathbf{z}) \frac{T_i'}{N_i'} + \phi_{\boldsymbol{i}}(\mathbf{g}, \mathbf{z}) \frac{F_i'}{N_i'} + \boxed{\kappa_i(\mathbf{g}, \mathbf{z})} \frac{C_i'}{N_i'}$$

Clonal offspring joint PDF

$$\kappa_i\,(\boldsymbol{g},\boldsymbol{z}) = \frac{1}{C'_i}\sum_j N_j \int\int S_{ij}(\boldsymbol{g},\boldsymbol{z}|\boldsymbol{g}^*,\boldsymbol{z}^*)\; c_{ij}(\boldsymbol{z}^*)\; p_j(\boldsymbol{g}^*,\boldsymbol{z}^*)\; d\boldsymbol{g}^*\, d\boldsymbol{z}^*$$

$S_{ij}(\boldsymbol{g},\boldsymbol{z}|\boldsymbol{g}^*,\boldsymbol{z}^*) =$ joint PDF of stage *i* clonal offspring with genotype **g** and phenotype **z** given parent genotype **g*** and phenotype **z*** for stage *j* parents

$$S_{ij}(\boldsymbol{g},\boldsymbol{z}|\boldsymbol{g}^*,\boldsymbol{z}^*) = S_{ij}(\boldsymbol{g}|\boldsymbol{g}^*,\boldsymbol{z}^*)S_{ij}(\boldsymbol{z}|\boldsymbol{g},\boldsymbol{g}^*,\boldsymbol{z}^*)$$

$$= S_{ij}(\boldsymbol{g}|\boldsymbol{g}^*)S_{ij}(\boldsymbol{z}|\boldsymbol{g},\boldsymbol{g}^*,\boldsymbol{z}^*)$$

Determining genotype – including somatic mutation

- clonal offspring genotype from parental genotype

$$\boldsymbol{g} = \boldsymbol{m} + \boldsymbol{g}^*$$

$$\boldsymbol{g} - \boldsymbol{g}^* = \boldsymbol{m}$$

- PDF of genotype for clonal offspring

$$S_{ij}(\boldsymbol{g}|\boldsymbol{g}^*) = \frac{1}{\sqrt{(2\pi)^m \det(\mathbf{V}_{\mathrm{M,ij}})}} exp\left[-\frac{1}{2}(\boldsymbol{g} - \boldsymbol{g}^*)^T \mathbf{V}_{\mathrm{M,ij}}^{-1}(\boldsymbol{g} - \boldsymbol{g}^*)\right]$$

if $n = 2,$ $\quad \mathbf{V}_{\mathrm{M}} = \begin{bmatrix} \sigma^2(m_1) & Cov(m_1, m_2) \\ Cov(m_1, m_2) & \sigma^2(m_2) \end{bmatrix}$

Determining phenotype

- mapping phenotype

$$\mathbf{z} = \mathbf{g} + \mathbf{e}$$
$$\mathbf{z} - \mathbf{g} = \mathbf{e}$$

- vector of association parameters, ρ_{ij}
  - give association between **e** for a stage *i* clonal offspring and **e*** for its stage *j* parent
- for a particular variable of the multivariate trait, z_k

$$e_k = \rho_k e_k^* + \sqrt{(1 - {\rho_k}^2)V_{E,k}}\,\zeta$$

Determining phenotype

- PDF of phenotype for clonal offspring

$$S_{ij}(\boldsymbol{z}|\boldsymbol{g},\boldsymbol{g}^*,\boldsymbol{z}^*) = \frac{1}{\sqrt{(2\pi)^m \det\left(\mathbf{V}_{\mathrm{ER,ij}}\right)}}$$

$$\times\, exp\left[-\frac{1}{2}[(\boldsymbol{z}-\boldsymbol{g})-\mathbf{R}(\boldsymbol{z}^*-\boldsymbol{g}^*)]^{\mathbf{T}}\mathbf{V}_{\mathrm{ER,ij}}^{-1}[(\boldsymbol{z}-\boldsymbol{g})-\mathbf{R}(\boldsymbol{z}^*-\boldsymbol{g}^*)]\right]$$

$$\mathbf{R} = \begin{bmatrix} \rho_1 & 0 & \cdots & 0 \\ 0 & \rho_2 & \cdots & 0 \\ \vdots & & \ddots & \vdots \\ 0 & \cdots & \cdots & \rho_m \end{bmatrix}$$

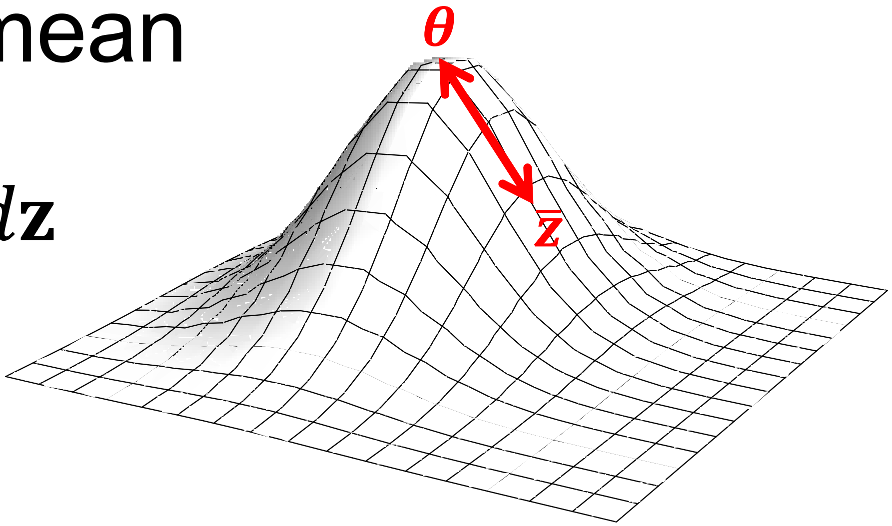
Recursions for genotypic and phenotypic means

- change in genotypic mean

$$\bar{\mathbf{g}}_i' = \iint \mathbf{g}\ p_i'(\mathbf{g},\mathbf{z})\ d\mathbf{g}d\mathbf{z}$$

- change in phenotypic mean

$$\bar{\mathbf{z}}_i' = \iint \mathbf{z}\ p_i'(\mathbf{g},\mathbf{z})\ d\mathbf{g}d\mathbf{z}$$



recursions for phenotypic and genotypic means

$$\begin{aligned}\bar{\boldsymbol{z}}_{\boldsymbol{i}}' = \sum\nolimits_{\boldsymbol{j}} \Big[& \big(d_{ij}^{t} + \mathbf{R} d_{ij}^{c}\big)\bar{\boldsymbol{z}}_j + \big(d_{ij}^{f} + (\mathbf{I} - \mathbf{R}) d_{ij}^{c}\big)\bar{\boldsymbol{g}}_j \\ & + \frac{d_{ij}}{\bar{a}_{ij}}\Big(\boldsymbol{P}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j}\bar{t}_{ij} + \boldsymbol{G}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j}\bar{f}_{ij} + \mathbf{R}\,\boldsymbol{P}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j}\bar{c}_{ij} + (\mathbf{I} - \mathbf{R})\boldsymbol{G}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j}\bar{c}_{ij}\Big)\Big]\end{aligned}$$

$$\bar{\boldsymbol{g}}_i' = \sum_j d_{ij}\ \bar{\boldsymbol{g}}_j + \sum\nolimits_j d_{ij}\, \boldsymbol{G}_j\, \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j}\ \mathbf{ln}\, \bar{\boldsymbol{a}}_{\boldsymbol{ij}}$$

$\boldsymbol{P}_j$ = phenotypic covariance matrix

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$\bar{a}_{ij} = \bar{t}_{ij} + \bar{f}_{ij} + \bar{c}_{ij}$

$d_{ij} = \bar{a}_{ij} N_j / N_{\boldsymbol{i}}'$

$d_{ij}^{t} = \bar{t}_{ij} N_j / N_{\boldsymbol{i}}'$, $d_{ij}^{f} = \bar{f}_{ij} N_j / N_{\boldsymbol{i}}'$, $d_{ij}^{c} = \bar{c}_{ij} N_j / N_{\boldsymbol{i}}'$

$\boldsymbol{\nabla}_{\bar{\mathbf{z}}_j} = (\partial/\partial\, \bar{z}_1\,, \partial/\partial\, \bar{z}_2\,, \cdots, \partial/\partial\, \bar{z}_m)^{\mathrm{T}}$

$$\mathbf{R} = \begin{bmatrix} \rho_1 & 0 & \cdots & 0 \\ 0 & \rho_2 & & 0 \\ \vdots & & \ddots & \vdots \\ 0 & \cdots & \cdots & \rho_m \end{bmatrix}$$

recursions for phenotypic and genotypic means

$$\bar{\boldsymbol{z}}'_{\boldsymbol{i}} = \sum_{\boldsymbol{j}} \Bigg[\left(d^t_{ij} + \boxed{\mathbf{R} d^c_{ij}} \right) \bar{\boldsymbol{z}}_j + \left(d^f_{ij} + (\mathbf{I} - \mathbf{R}) d^c_{ij} \right) \bar{\boldsymbol{g}}_j$$

$$+ \frac{d_{ij}}{\bar{a}_{ij}} \left(\boldsymbol{P}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j} \bar{t}_{ij} + \boldsymbol{G}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j} \bar{f}_{ij} + \boxed{\mathbf{R}\, \boldsymbol{P}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j} \bar{c}_{ij}} + (\mathbf{I} - \mathbf{R}) \boldsymbol{G}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j} \bar{c}_{ij} \right) \Bigg]$$

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$$\mathbf{R} = \begin{bmatrix} \rho_1 & 0 & \cdots & 0 \\ 0 & \rho_2 & & 0 \\ \vdots & & \ddots & \vdots \\ 0 & \cdots & \cdots & \rho_m \end{bmatrix}$$

recursions for phenotypic and genotypic means

$$\bar{\boldsymbol{z}}'_{\boldsymbol{i}} = \sum\nolimits_{\boldsymbol{j}} \Big[\boxed{\big(d^{t}_{ij}} + \boxed{\mathbf{R} d^{c}_{ij}\big)\bar{\boldsymbol{z}}_j} + \big(d^{f}_{ij} + (\mathbf{I} - \mathbf{R}) d^{c}_{ij}\big)\bar{\boldsymbol{g}}_j$$

$$+ \frac{d_{ij}}{\bar{a}_{ij}} \Big(\boxed{\boldsymbol{P}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j} \bar{t}_{ij}} + \boldsymbol{G}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j} \bar{f}_{ij} + \boxed{\mathbf{R}\, \boldsymbol{P}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j} \bar{c}_{ij}} + (\mathbf{I} - \mathbf{R}) \boldsymbol{G}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j} \bar{c}_{ij} \Big) \Big]$$

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recursions for phenotypic and genotypic means

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$$\left. + \frac{d_{ij}}{\bar{a}_{ij}} \Big(\boldsymbol{P}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j} \bar{t}_{ij} + \boldsymbol{G}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j} \bar{f}_{ij} + \mathbf{R}\, \boldsymbol{P}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j} \bar{c}_{ij} + \boxed{(\mathbf{I} - \mathbf{R}) \boldsymbol{G}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j} \bar{c}_{ij})} \right]$$

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recursions for phenotypic and genotypic means

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$$+ \frac{d_{ij}}{\bar a_{ij}}\Big(\boldsymbol P_j \boldsymbol\nabla_{\bar{\mathbf z}_j}\bar t_{ij} + \boxed{\boldsymbol G_j \boldsymbol\nabla_{\bar{\mathbf z}_j}\bar f_{ij}} + \mathbf{R}\,\boldsymbol P_j \boldsymbol\nabla_{\bar{\mathbf z}_j}\bar c_{ij} + \boxed{(\mathbf{I} - \mathbf{R})\boldsymbol G_j \boldsymbol\nabla_{\bar{\mathbf z}_j}\bar c_{ij}\Big)}\Big]$$

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$$\mathbf{R} = \begin{bmatrix} \rho_1 & 0 & \cdots & 0 \\ 0 & \rho_2 & & 0 \\ \vdots & & \ddots & \vdots \\ 0 & \cdots & \cdots & \rho_m \end{bmatrix}$$

recursions for phenotypic and genotypic means

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recursions for phenotypic and genotypic means

$$\bar{\boldsymbol{z}}'_{\boldsymbol{i}} = \sum_{\boldsymbol{j}} \Big[\big(d^{t}_{ij} + \mathbf{R}\, d^{c}_{ij}\big)\bar{\boldsymbol{z}}_j + \big(d^{f}_{ij} + (\mathbf{I}-\mathbf{R})\, d^{c}_{ij}\big)\bar{\boldsymbol{g}}_j$$

$$+ \frac{d_{ij}}{\bar{a}_{ij}}\Big(\boldsymbol{P}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j}\bar{t}_{ij} + \boldsymbol{G}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j}\bar{f}_{ij} + \mathbf{R}\,\boldsymbol{P}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j}\bar{c}_{ij} + (\mathbf{I}-\mathbf{R})\boldsymbol{G}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j}\bar{c}_{ij}\Big)\Big]$$

$$\bar{\boldsymbol{g}}'_i = \sum_j d_{ij}\,\bar{\boldsymbol{g}}_j + \boxed{\sum_j d_{ij}\,\boldsymbol{G}_j\,\boldsymbol{\nabla}_{\bar{\mathbf{z}}_j}\,\ln \bar{\boldsymbol{a}}_{\boldsymbol{ij}}}$$

$\boldsymbol{P}_j$ = phenotypic covariance matrix

$\boldsymbol{G}_j$ = additive genetic covariance matrix

$\bar{a}_{ij} = \bar{t}_{ij} + \bar{f}_{ij} + \bar{c}_{ij}$

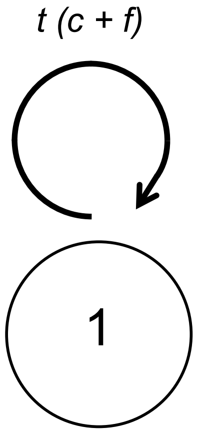
$d_{ij} = \bar{a}_{ij} N_j / N'_{\boldsymbol{i}}$

$d^{t}_{ij} = \bar{t}_{ij} N_j / N'_{\boldsymbol{i}},\ d^{f}_{ij} = \bar{f}_{ij} N_j / N'_{\boldsymbol{i}},\ d^{c}_{ij} = \bar{c}_{ij} N_j / N'_{\boldsymbol{i}}$

$$\boldsymbol{\nabla}_{\bar{\mathbf{z}}_j} = (\partial/\partial\,\bar{z}_1, \partial/\partial\,\bar{z}_2, \cdots, \partial/\partial\,\bar{z}_m)^{\mathrm{T}}$$

$$\mathbf{R} = \begin{bmatrix} \rho_1 & 0 & \cdots & 0 \\ 0 & \rho_2 & & 0 \\ \vdots & & \ddots & \vdots \\ 0 & \cdots & \cdots & \rho_m \end{bmatrix}$$

Simple life history



clonal and sexual reproduction

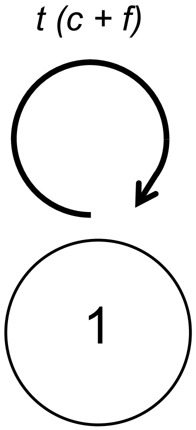
selection on survival probability $t = \exp\left[-\frac{(\bar{z}_1 - \theta)^2}{(2\omega^2)}\right]$

amount of clonal reproduction $r_c = c/(f + c)$

$$\Delta\bar{z} = (1 - r_c\rho)(\bar{g} - \bar{z}) + \{r_c\rho P + (1 - r_c\rho)G\}\frac{\theta - \bar{z}}{\omega^2}$$

$$\Delta\bar{g} = G\,\frac{\theta - \bar{z}}{\omega^2}$$

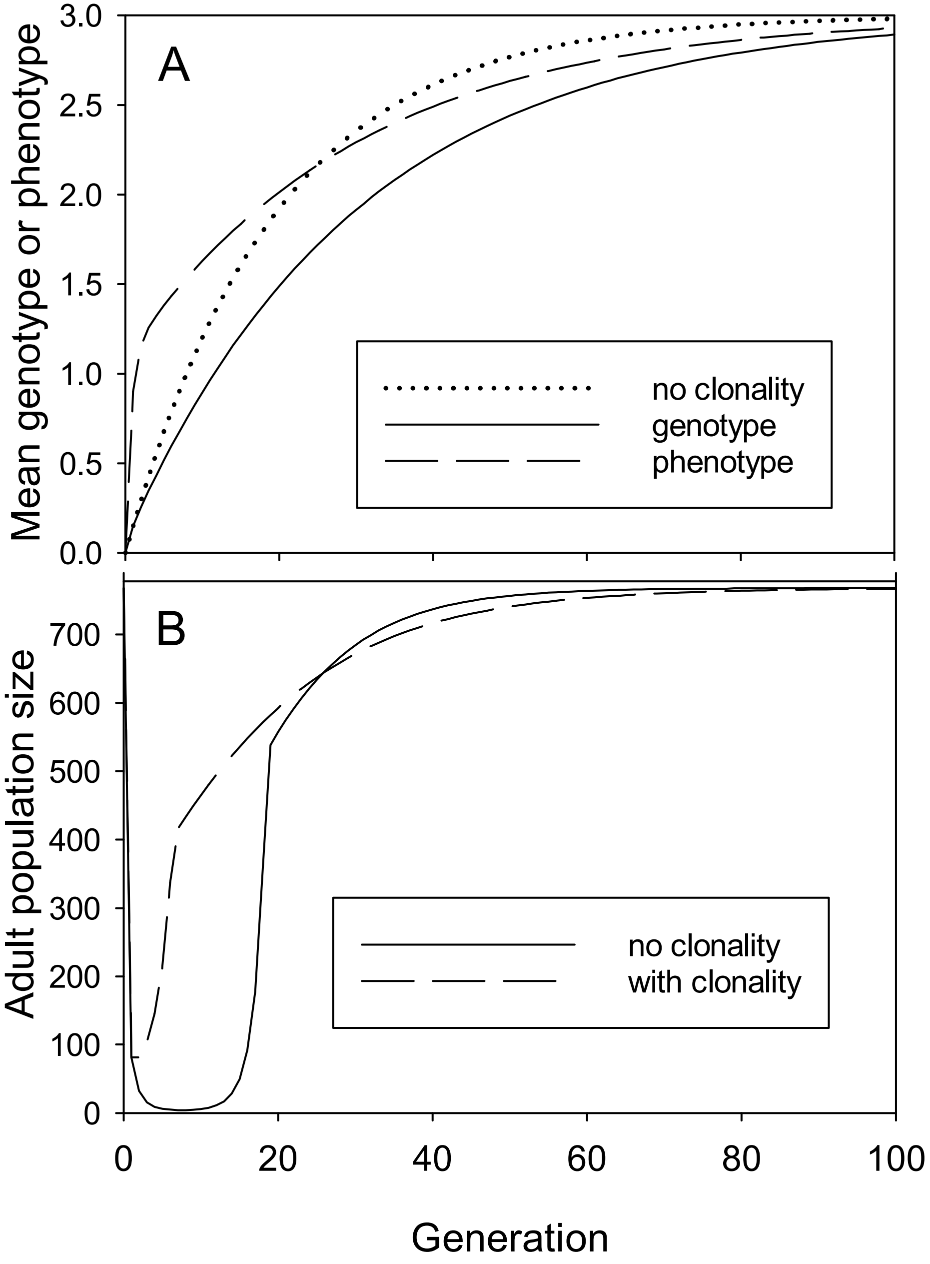
analytical results – effect of clonality



no clonality ($r_c\,\rho = 0$)

vs.

with clonality ($r_c\,\rho = 0.5$)



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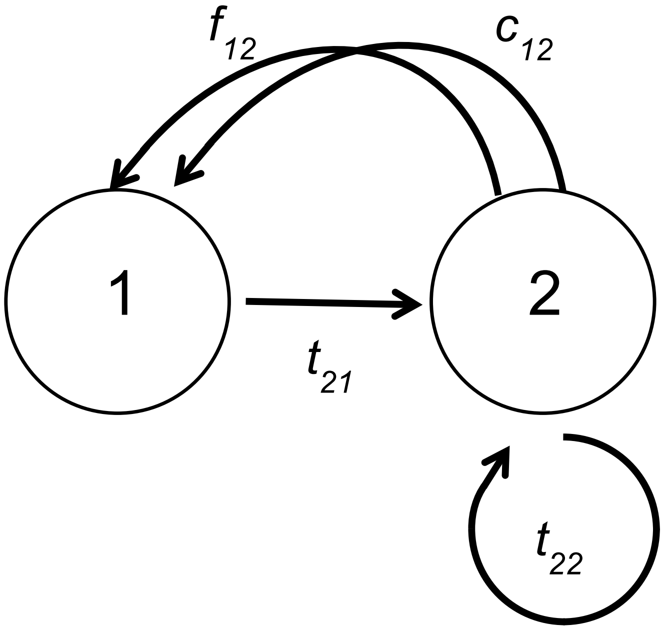
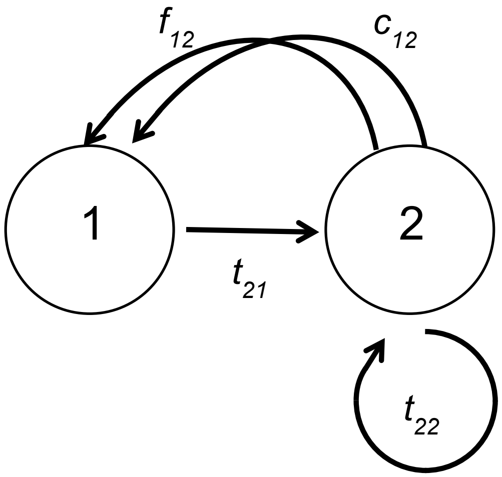
Life history with stage structure



$$\begin{pmatrix} N_1 \\ N_2 \end{pmatrix}' = \begin{pmatrix} 0 & c_{12} + f_{12} \\ t_{21} & t_{22} \end{pmatrix} \begin{pmatrix} N_1 \\ N_2 \end{pmatrix}$$

Life history with stage structure



selection on juvenile survival

$$\bar{t}_{21} = t_{\max}\exp\left[-\frac{(\bar{z}_1-\theta)^2}{(2\omega^2)}\right]$$

$$r_c = c_{12}/(c_{12}+f_{12})$$

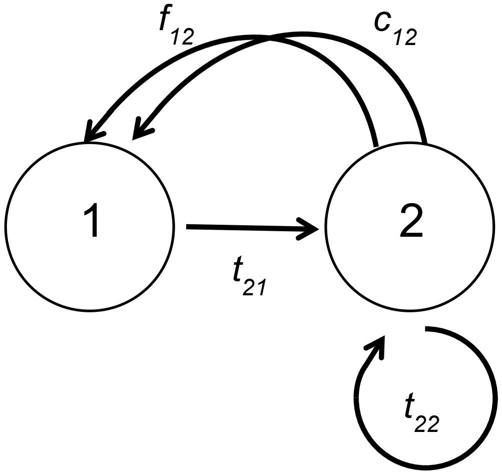
$$\bar{z}_1' = r_c\rho(\bar{z}_2-\bar{g}_2)+\bar{g}_2$$

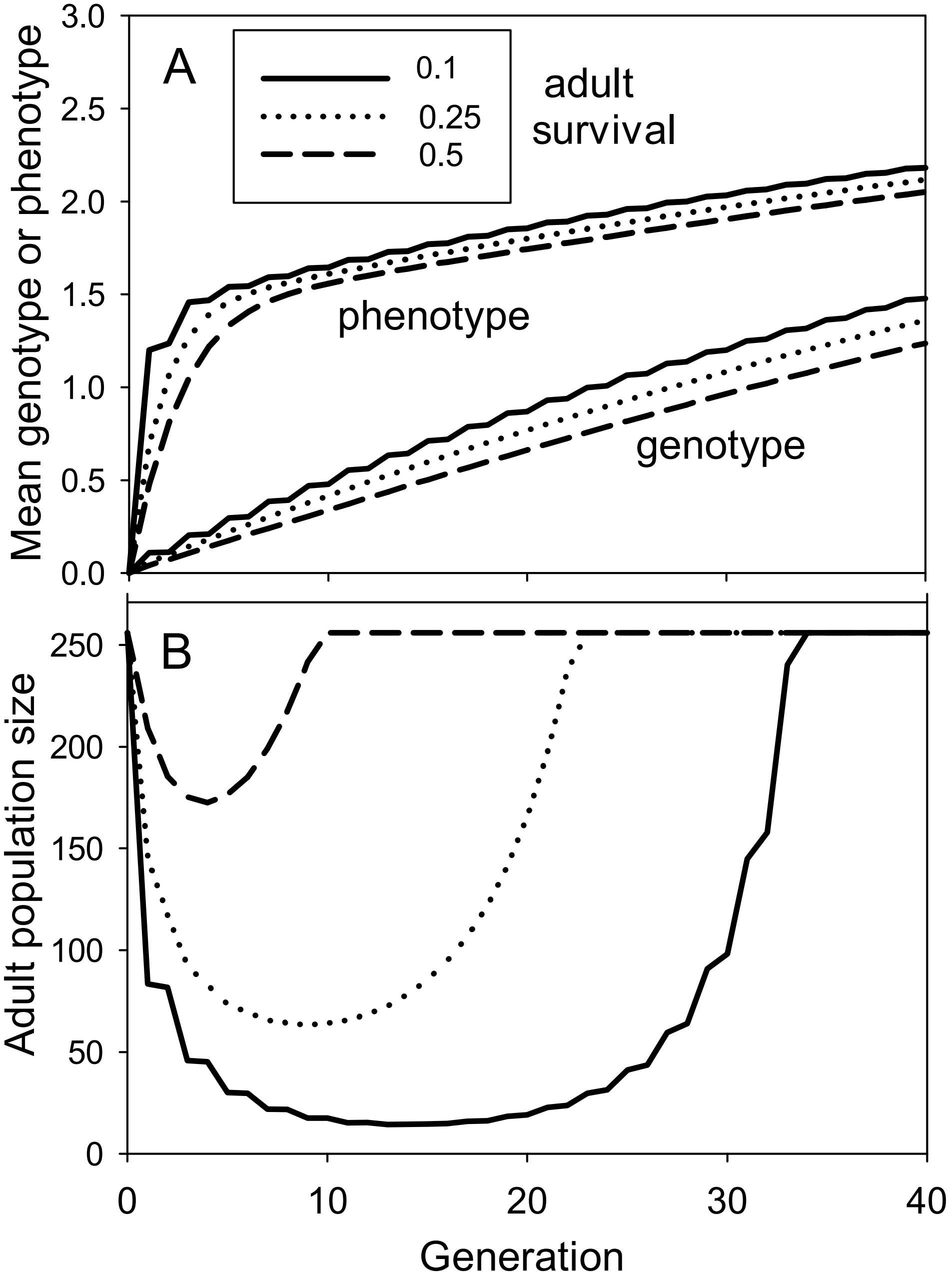
$$\bar{z}_2' = \bar{z}_2 + \frac{N_1}{\bar{t}_{21}N_1+\bar{t}_{22}N_2}\bar{t}_{21}\left[(\bar{z}_1-\bar{z}_2)+P_1\left(\frac{\theta-\bar{z}_1}{\omega^2}\right)\right]$$

$$\bar{g}_1' = \bar{g}_2$$

$$\bar{g}_2' = \bar{g}_2 + \frac{N_1}{\bar{t}_{21}N_1+\bar{t}_{22}N_2}\bar{t}_{21}\left[(\bar{g}_1-\bar{g}_2)+G_1\left(\frac{\theta-\bar{z}_1}{\omega^2}\right)\right]$$

analytical results – increased adult survival





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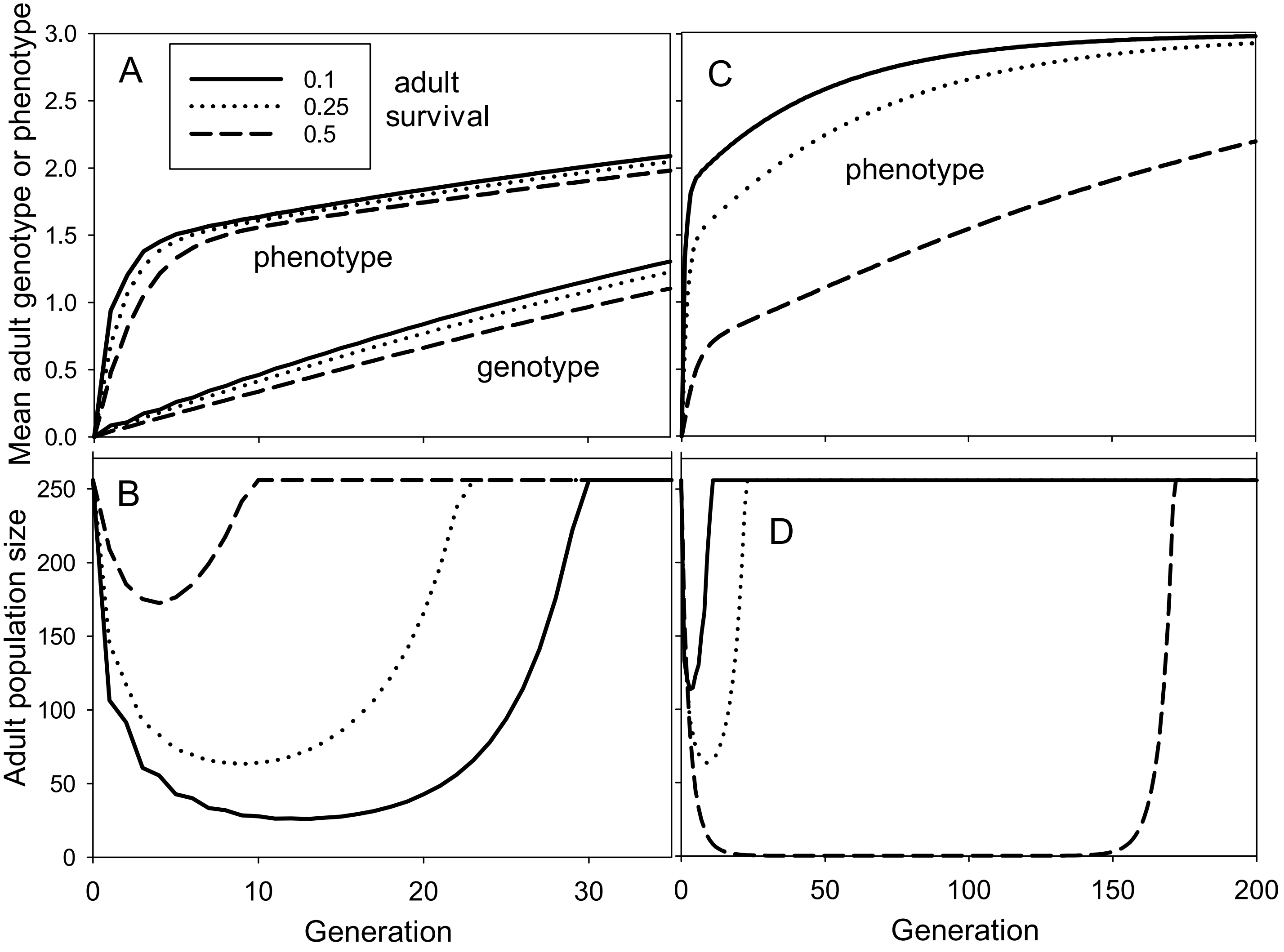
loss of demographic advantage of increased adult survival



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evolutionary lag in clonal organisms

- analytical results
  - clonality ($r_c \rho > 0$) and adult survival (stage structure) both slow approach to equilibrium phenotype
  - but both also reduce both extent and duration of population size decrease
    - demographic advantage

individual-based simulations

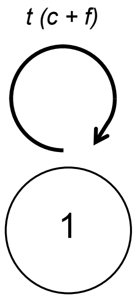
- single polygenic trait *z*
  - *n* = 10 loci, additive allelic effects
- **e** normally distributed, mean 0, variance 1
- $\mu_g = 100\mu_s$
- relative amounts of clonal reproduction, $r_c = c/(c + f)$
- association parameter, ρ
- change in optimum phenotype
  - one-step change
  - continuous, linear change

Burger & Lynch (1995), Holt et al. (2003)

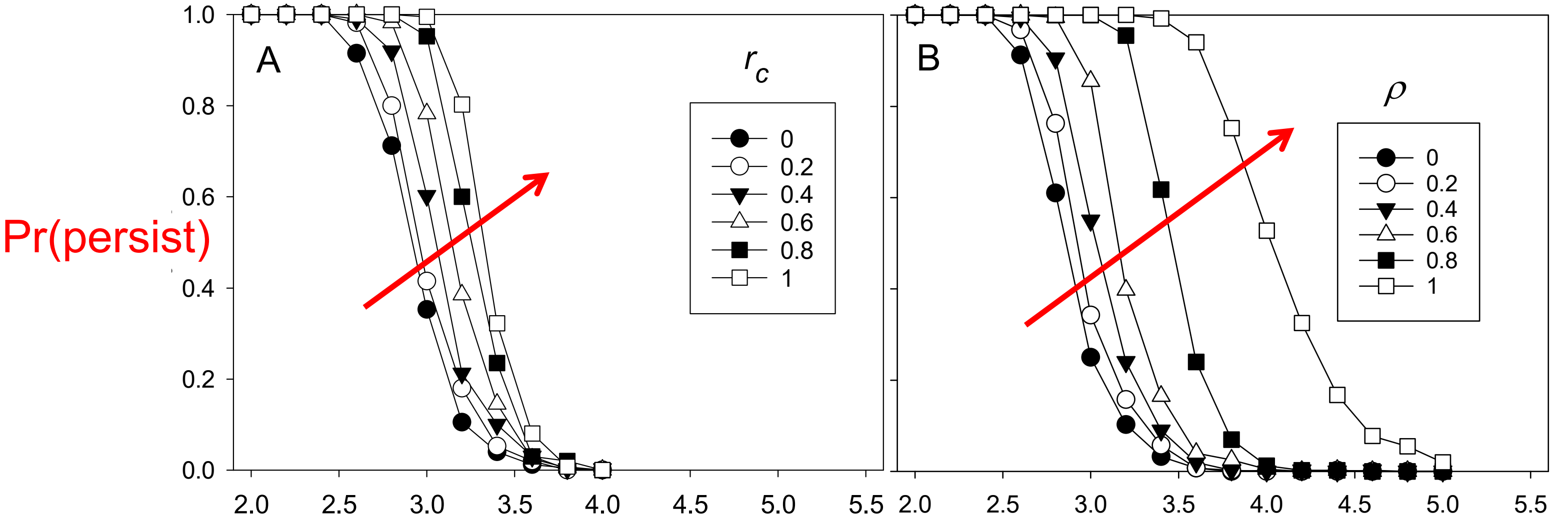
One-step change in optimal phenotype

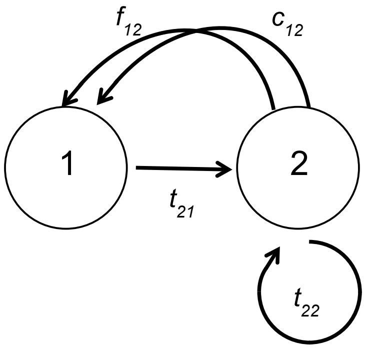
clonal reproduction r_c
ρ = 0.5

association parameter ρ
r_c = 0.5

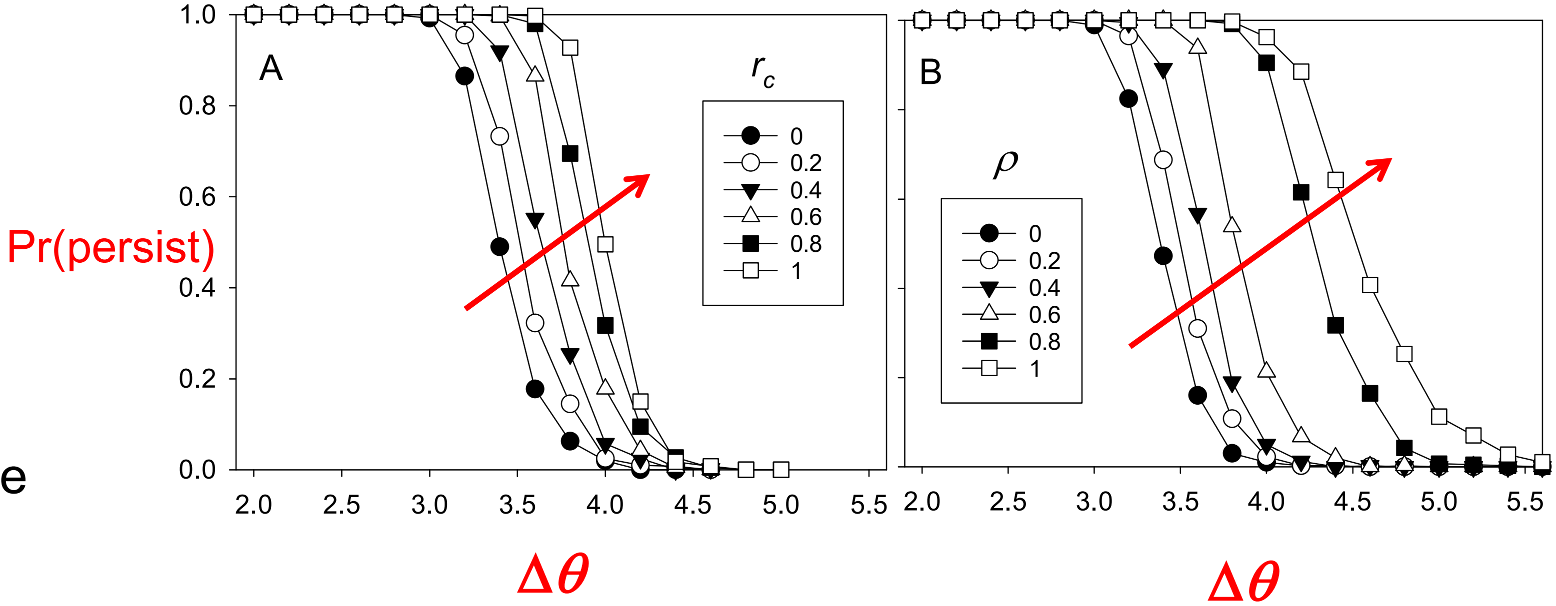


no stage structure



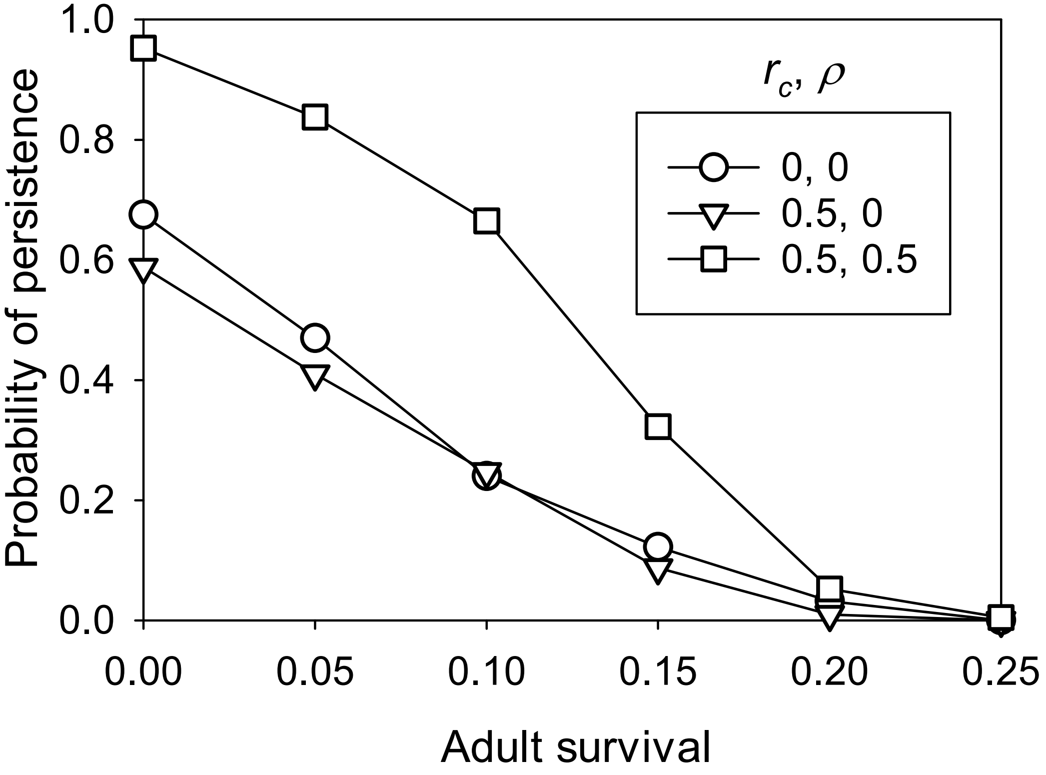


with stage structure



loss of demographic advantage of increased adult survival

decreased fecundity (*f*)
with increased adult survival (t_{22})



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one-step change in optimal phenotype

- greater population persistence with more clonal reproduction (r_c) and higher environmental component association (ρ)
  - standing genotypic variation

one-step change in optimal phenotype

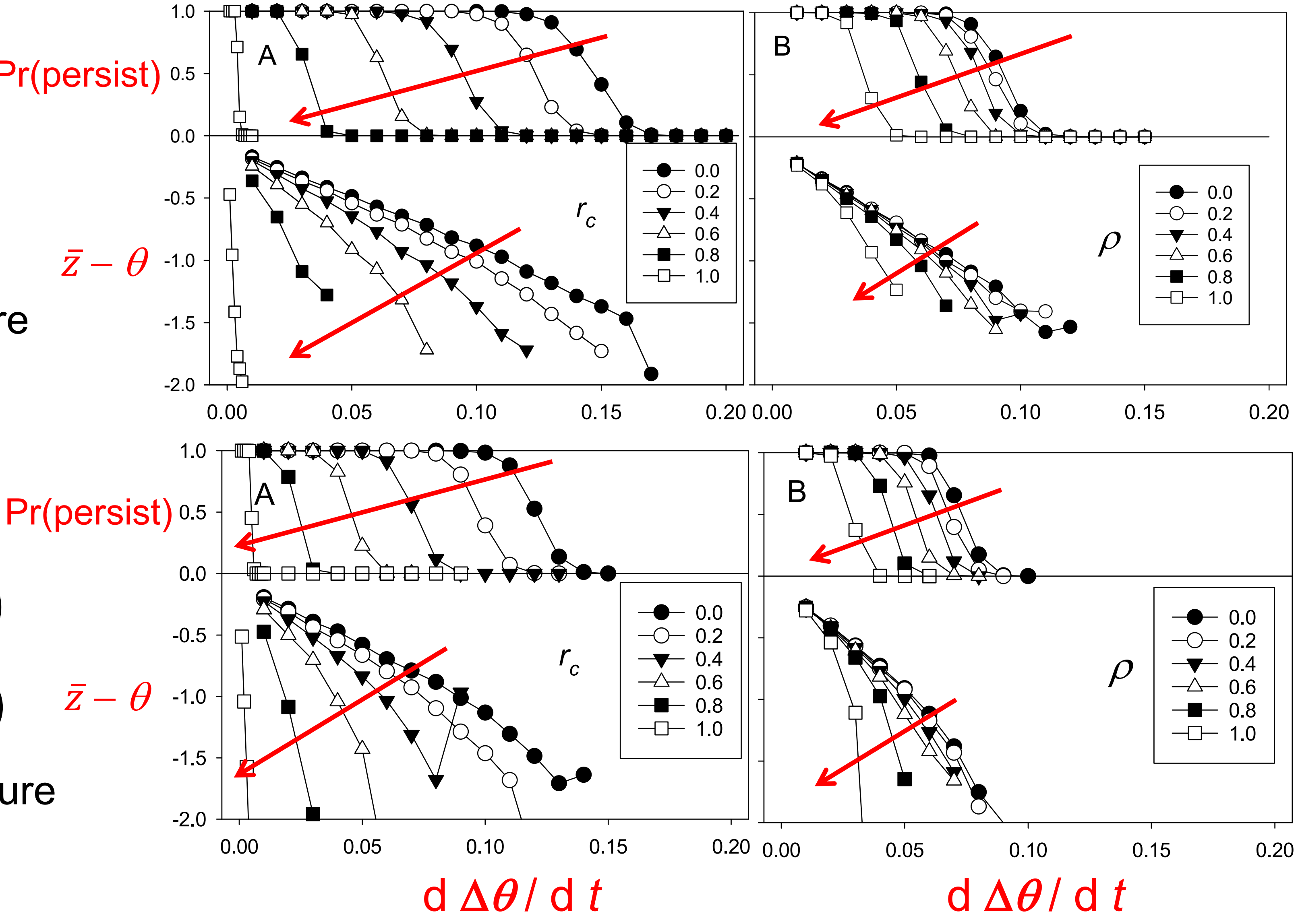
- greater population persistence with more clonal reproduction (r_c) and higher environmental component association (ρ)
  - standing genotypic variation

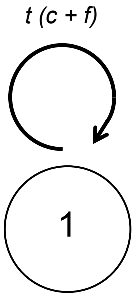
- stage structure increases probability of population persistence
  - demographic advantage

continuous change in optimal phenotype

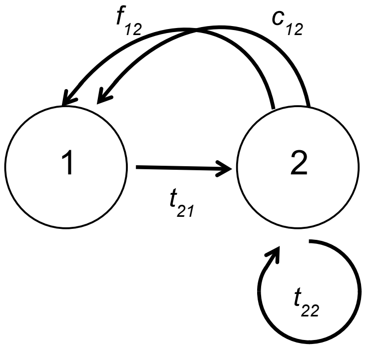
clonal reproduction r_c association parameter ρ

$\rho = 0.5$ $r_c = 0.5$





no stage structure



with stage structure

continuous, linear change in optimal phenotype

- decreased persistence and greater lag with more clonal reproduction, higher ρ
  - de novo genotypic variation

continuous, linear change in optimal phenotype

- decreased persistence and greater lag with more clonal reproduction, higher ρ
  - de novo genotypic variation

- stage structure decreases persistence and increases lag
  - increased generation time
  - decreased N_e of component of population experiencing phenotypic selection
  - maladaptive “gene flow through time”

evolutionary lag in clonal organisms

- how will clonal organisms respond under rapid environmental change?

evolutionary lag in clonal organisms

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- scale of change – whether population experiences that change as a single transition or not

evolutionary lag in clonal organisms

- how will clonal organisms respond under rapid environmental change?

- scale of change – whether population experiences that change as a single transition or not

- amount of phenotypic matching between organisms and their clonal offspring

evolutionary lag in clonal organisms

- how will clonal organisms respond under rapid environmental change?

- scale of change – whether population experiences that change as a single transition or not

- amount of phenotypic matching between organisms and their clonal offspring

- existence of stage structured life histories

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continuous change in optimal phenotype

varying relative amounts of sexual and clonal reproduction, r_c

"equal" sexual and clonal offspring

$\delta = 1,\ \rho = 0,\ \mu_g = \mu_s$