Sex as information processing

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"Sex is a way of asynchronous evolution rather than a way of reproduction." — V. Geodakyan

Sex & evolution: two problems

(1) Why sex? and not asexual reproduction?

Benefit of recombination?

Many hypotheses, including:
- varying selective pressures (red-queen hypothesis)
- genetic constraints (Muller's ratchet)

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(2) Why two sexes (dioecy)? and not hermaphroditism (monoecy)?

Two-fold cost of males: half of a dioecious population (males) is not bearing children

A factor 2 per generation = major growth reduction!

Main hypothesis: ‣ sexual selection

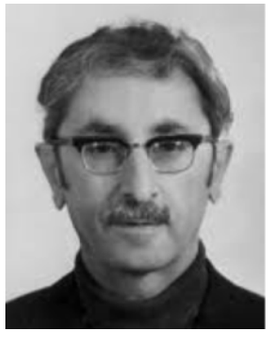
Alternative hypothesis: adaptation to varying environments

Sexual dimorphism for optimal information processing

V. A. Geodakyan, Prob. Pered. Inf.1 ,105 (1965).

"Any system adapting to a variable environment divides into two conjugated subsystems, specialized according to conservative and operative trends of evolution"

http://www.geodakian.com



Vigen Geodakyan

Sexual dimorphism as optimal information processing

Dilemma of adaptation by natural selection:
efficient long-term adaptation $\Longrightarrow$ strong selection $\Longrightarrow$ short-term growth reduction

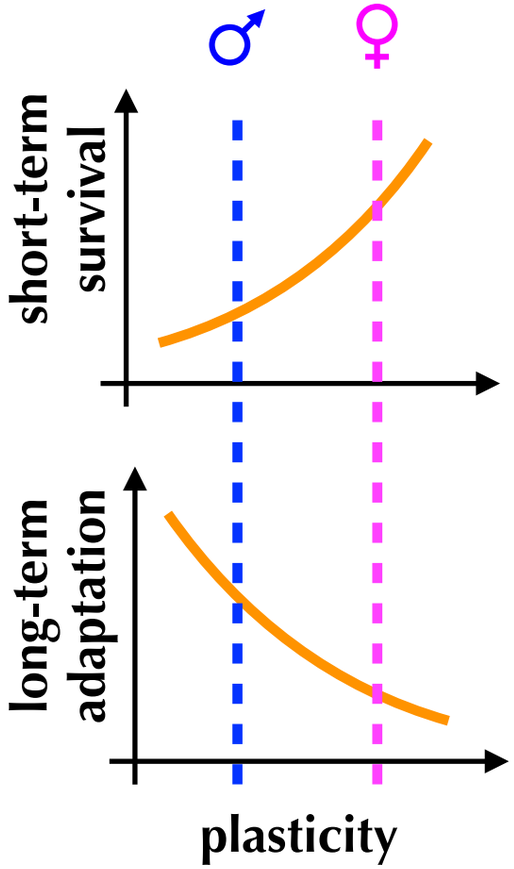
One parameter: phenotypic plasticity = ability to produce a phenotype regardless of genetic or environmental changes.

Geodakyan's theory:
(i) fecundity depends primarily on females
(ii) females are more plastic

Females guarantee short-term growth, males permit long-term adaptation.

Few males survive but transmit their adapted genes to many offsprings born from the many surviving females.

Empirical support for female plasticity (Darwin, The Descent of Man)
"… males [are] more liable to vary than the females—as I concluded they were—after a long study of domesticated animals."



Can the adaptive benefit of dioecy compensate for its two-fold cost?

Modeling development, selection & heredity

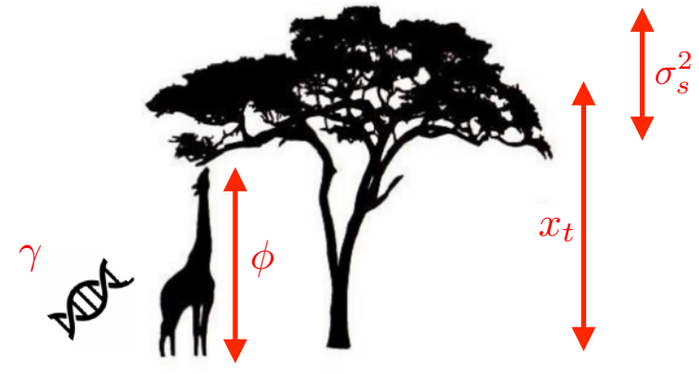
Continuous traits (quantitative genetics)

$$\phi = \gamma + \zeta$$

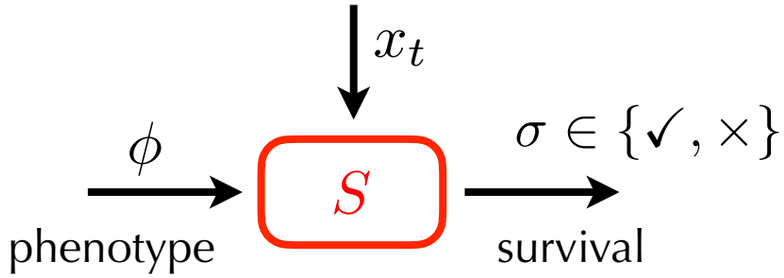
$$\zeta \sim \mathcal{N}(\sigma_D^2)$$

$$\mathbb{P}(\phi|\gamma) = \frac{1}{\sqrt{2\pi\sigma_D^2}} e^{-(\phi-\gamma)^2/(2\sigma_D^2)}$$

developmental variance



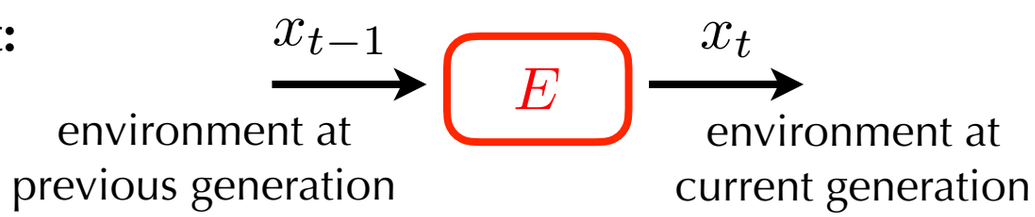
Selection:



$$\mathbb{P}[\sigma = ✓|\phi, x_t] = e^{-(\phi-x_t)^2/(2\sigma_s^2)}$$

stringency of selection

Environment:

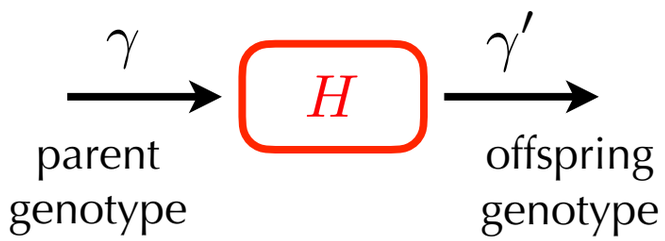


$$\mathbb{P}(x_t|x_{t-1}) = \frac{1}{\sqrt{2\pi\sigma_E^2}} e^{-(x_t - a x_{t-1})^2/(2\sigma_E^2)}$$

temporal correlations

variance of fluctuations

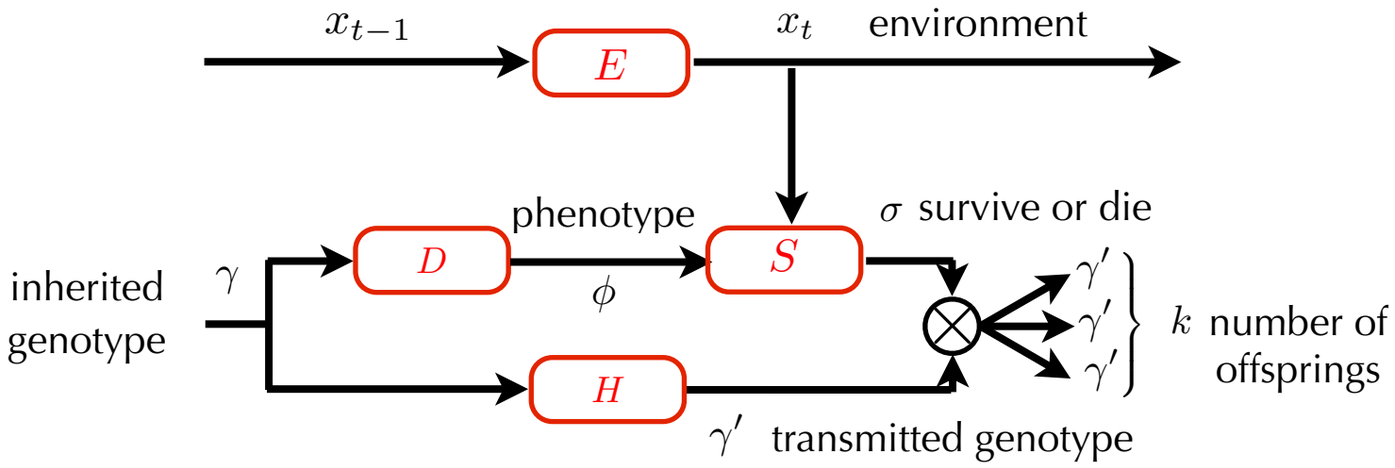
Heredity (asexual case):

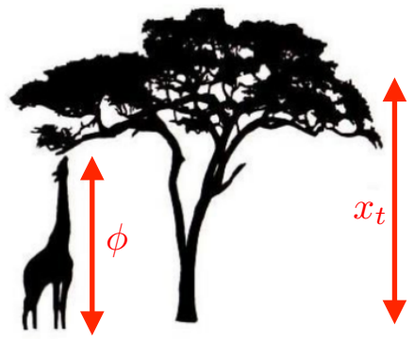


$$\mathbb{P}(\gamma'|\gamma) = \frac{1}{\sqrt{2\pi\sigma_H^2}} e^{-(\gamma'-\gamma)^2/(2\sigma_H^2)}$$

mutational variance

Optimal information processing: asexual case



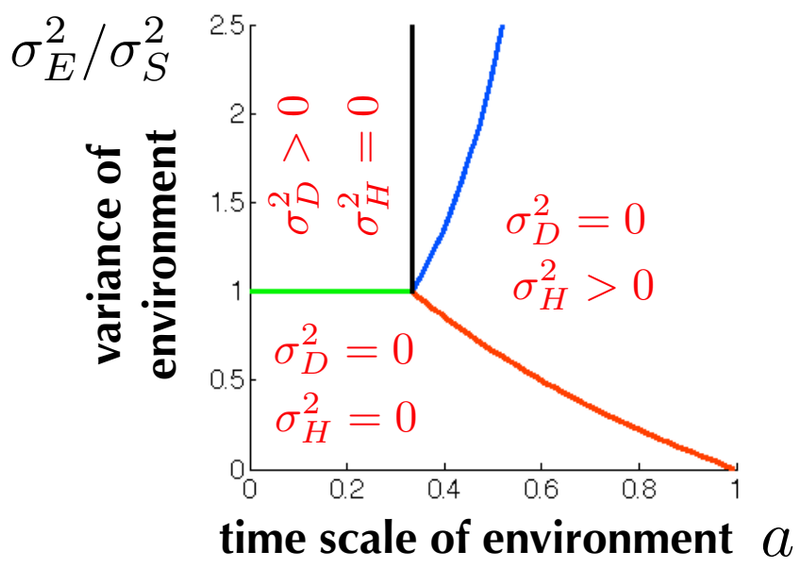


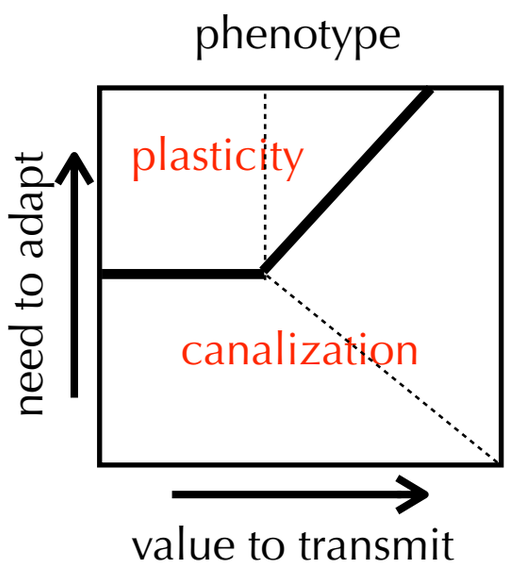
Population dynamics: $M_t(\gamma) = \int d\phi S(\checkmark|\phi, x_t) D(\phi|\gamma) N_t(\gamma)$ = # mature individuals at *t*

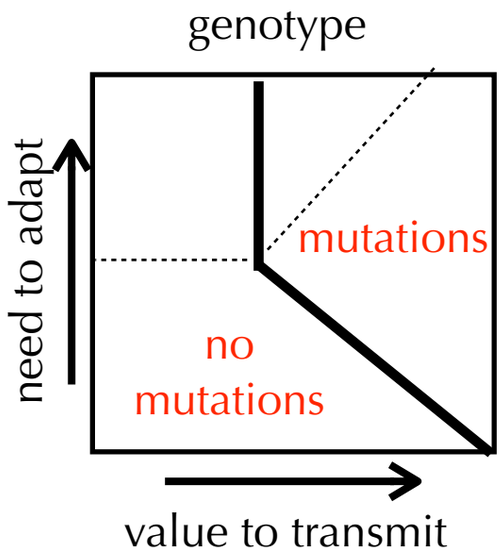
$N_{t+1}(\gamma') = k \int d\gamma H(\gamma'|\gamma) M_t(\gamma)$ = # newly born individuals at *t+1*

Long-term: $N_t = \int d\gamma N_t(\gamma) \sim e^{\Lambda t}$ $\Lambda =$ population growth rate (fitness) Rivoire & Leibler PNAS 2014

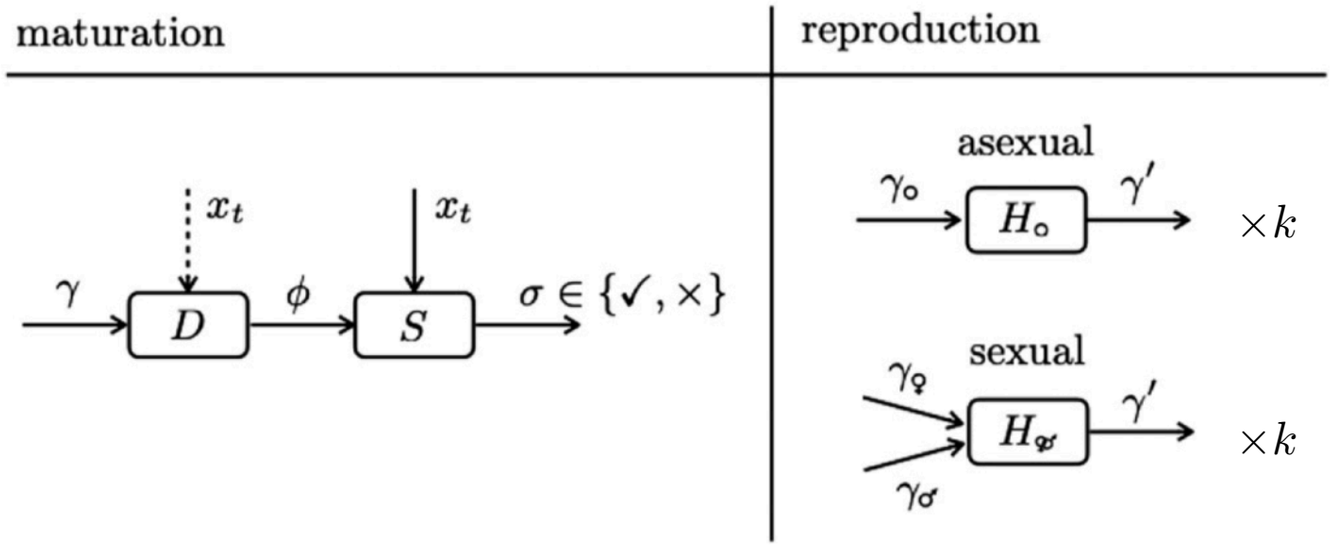
Optimal information processing: what D, H optimize Λ for given E, S ?







Extension to sexual reproduction



$\gamma =$ genotype

$\phi =$ phenotype

$x_t =$ environment

$\sigma =$ survival (binary)

$k =$ number of offsprings

Asexual

$$M_t(\gamma) = \int d\phi\, S(\checkmark|\phi) D_\circ(\phi|\gamma, x_t) N_t(\gamma), \quad = \#\text{ mature individuals at } t$$

$$N_{t+1}(\gamma') = k_\circ \int d\gamma\, H_\circ(\gamma'|\gamma) M_t(\gamma), \quad = \#\text{ newly born individuals at } t{+}1$$

Sexual (two sexes)

$$M_{\bullet,t}(\gamma) = \frac{1}{2} \int d\phi\, S(\checkmark|\phi, x_t) D_\bullet(\phi|\gamma) N_t(\gamma) \quad (\bullet = ♀, ♂),$$

$$N_{t+1}(\gamma') = k_{♂♀} \int d\gamma_♀ d\gamma_♂\, H_{♂♀}(\gamma'|\gamma_♀, \gamma_♂) \frac{M_{♂,t}(\gamma_♂)}{M_{♂,t}} M_{♀,t}(\gamma_♀)$$

two-fold cost

asymmetry ♀ / ♂

fecondity depends primarily on females

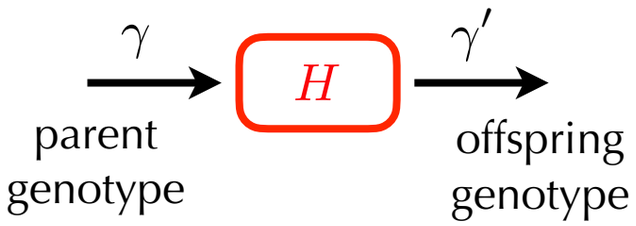
Sexual (hermaphroditic)

$$M_t(\gamma) = \int d\phi\, S(\checkmark|\phi, x_t) D_☿(\phi|\gamma) N_t(\gamma),$$

$$N_{t+1}(\gamma') = k_☿ \int d\gamma_♀ d\gamma_♂\, H_{♂♀}(\gamma'|\gamma_♀, \gamma_♂) \frac{M_t(\gamma_♂)}{M_t} M_t(\gamma_♀)$$

Modeling heredity

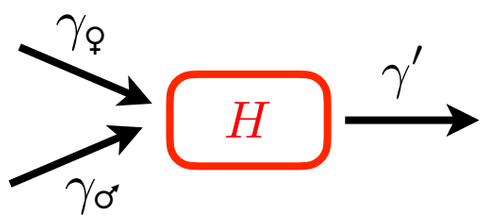
Heredity (asexual):



$$\gamma' = \gamma + \mu, \qquad \mu \sim \mathcal{N}(\sigma_M^2)$$

mutational variance

Heredity (sexual):



$$\gamma' = \frac{\gamma_♂ + \gamma_♀}{2} + \mu, \qquad \mu \sim \mathcal{N}(\sigma_M^2 + \sigma_R^2)$$

mutational variance — **segregation variance**

cf. infinitesimal model: $\gamma = \frac{1}{M}\sum_{i=1}^{M} a_i$ ← contribution from allele i

Optimal information processing?

Given environmental fluctuations a, σ_E^2 and the possibility to optimize $\sigma_M^2, \sigma_R^2, \sigma_D^2$
what is most advantageous, i.e., what mode of reproduction maximizes long-term growth Λ ?

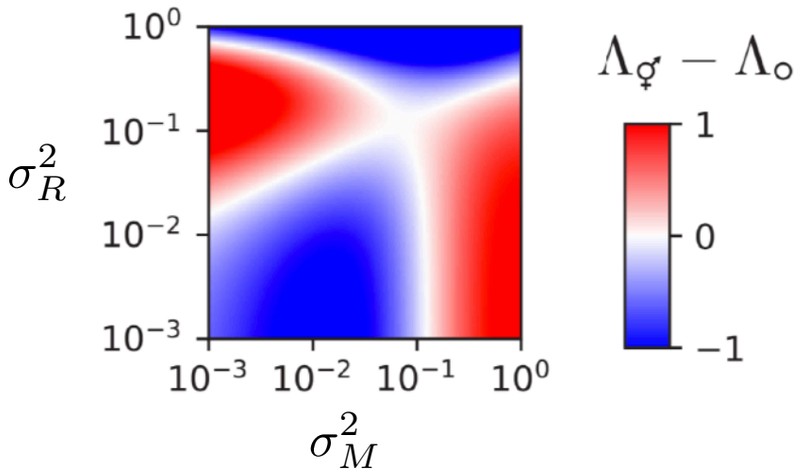
Zadorin & Rivoire, PRE 2021

Optimal reproduction given genetic constraints

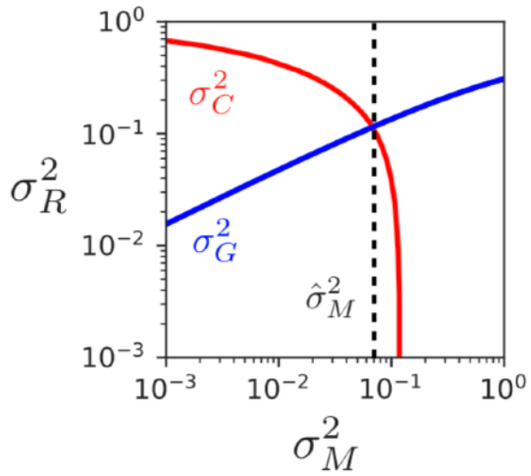
Optimizing over σ_M^2, σ_R^2 **: sex is never beneficial** — possibly adaptive only given genetic constraints

Given σ_M^2, σ_R^2**: four regimes**

$a = 0.75, \sigma_E^2 = 1$



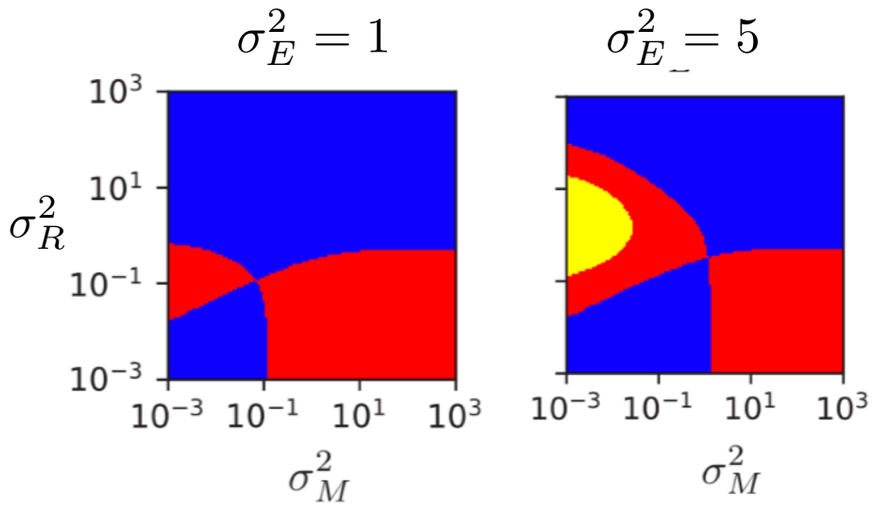
Interpretation in terms of genetic variance = variance of the trait γ in the population



$\sigma_R^2 > \sigma_G^2$ sex increases genetic variance

$\sigma_R^2 < \sigma_C^2$ an increased genetic variance is beneficial

Genetic & environmental constraints under which the two-fold cost of males is overcome:



sex is advantageous ($\Lambda_♂ > \Lambda_o$)

two-fold advantage ($\Lambda_♂ > \Lambda_o \Leftrightarrow \Lambda_♀ > \Lambda_o - \ln 2$)

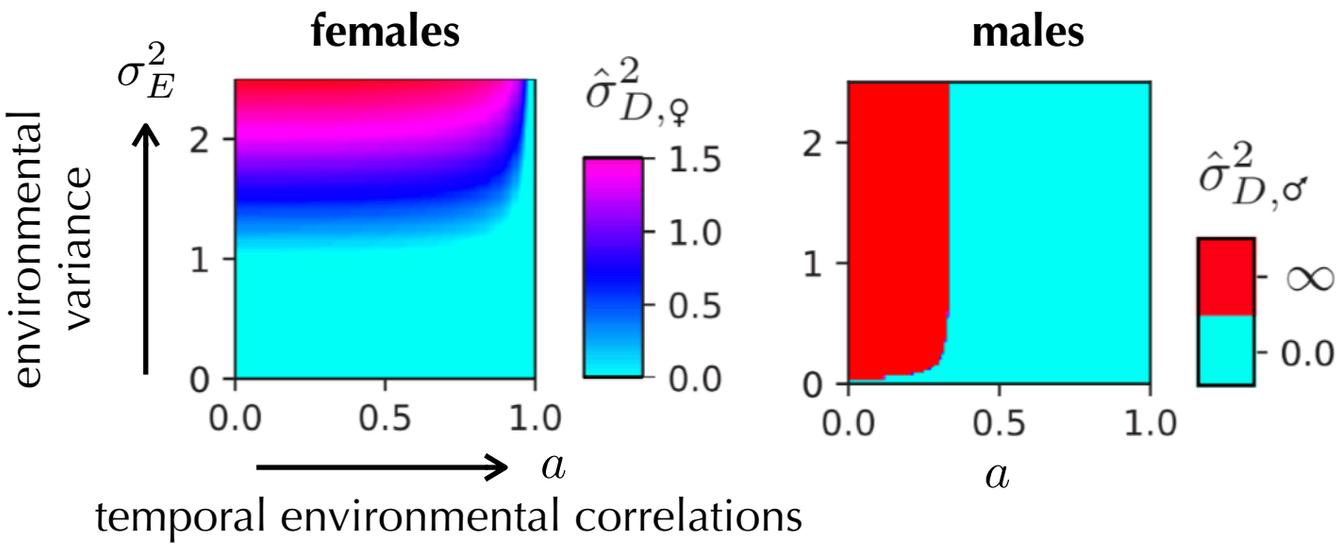
Requires: large environmental fluctuations σ_E^2
small mutational variance σ_M^2
intermediate segregation variance σ_R^2

Sexual dimorphism as an adaptive trait

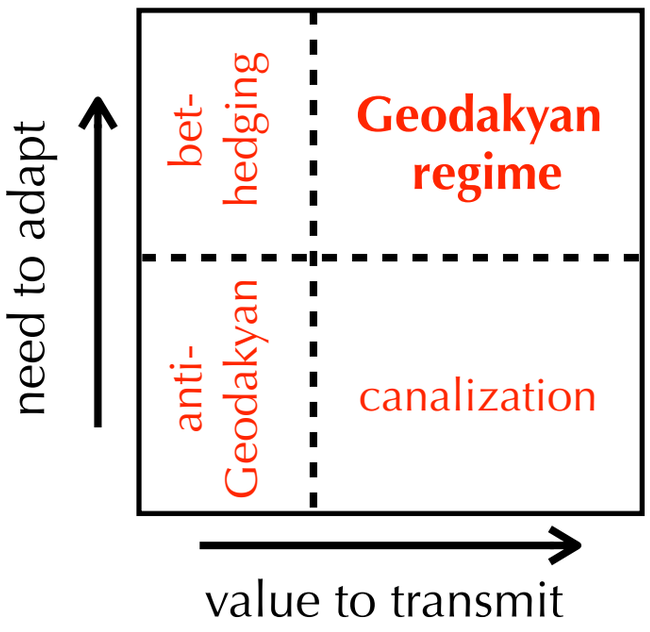
$$\phi = \gamma + \zeta \qquad \zeta \sim \mathcal{N}(\sigma^2_D)$$

$$\sigma^2_{D,♀} \neq \sigma^2_{D,♂} \quad ?$$

Optimal developmental variance for each sex?

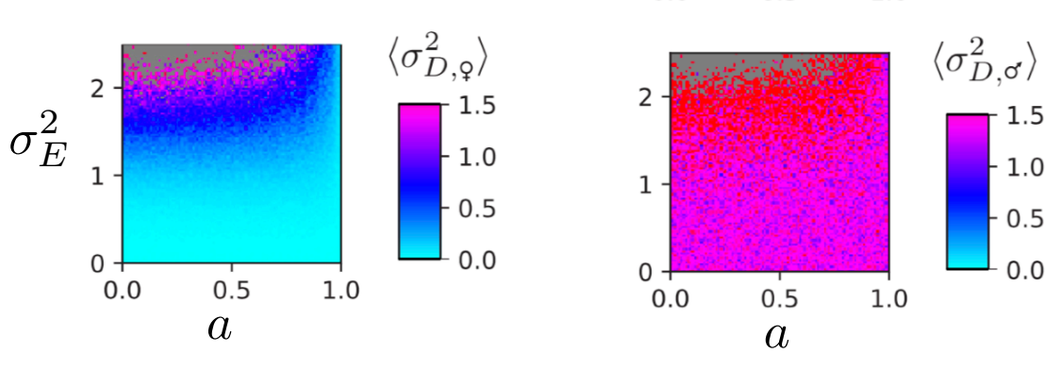


Interpretation:



But what is optimal does not necessarily evolve!

Simulations where developmental variances evolve:



Weak selection on male developmental variance

Can sexual dimorphism overcome the two-fold cost?

No — but…

More favorable constraints

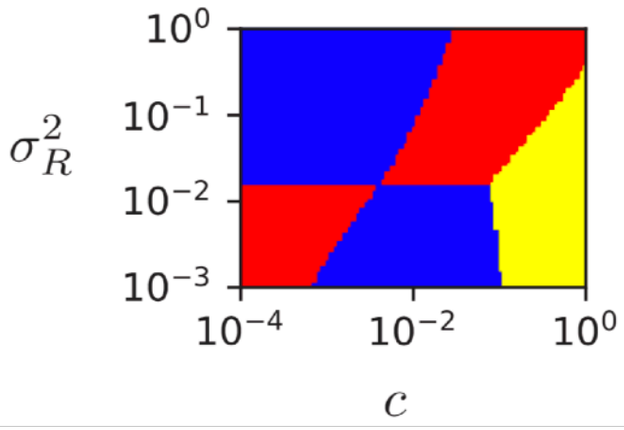
So far $x_t = ax_{t-1} + b, \qquad b \sim \mathcal{N}(\sigma_E^2)$ (auto-regressive process)

Consider instead a **steadily changing environment** $x_t = ct$

Favorable condition for sexual over asexual reproduction (Charlesworth 1993)

Two sexes (dioecy) can be more favorable than hermaphroditism (monoecy) for c large enough:

With $\sigma_M^2 = 10^{-3}$



Largest growth rate:

- asexual
- hermaphroditism
- two sexes

But: huge cost on males, sustainable only for large enough populations

Equivalent genetic constraint: **mutational bias**

$$x_{t-1} \longrightarrow \boxed{E} \longrightarrow x_t = x_{t-1} + c \quad \Leftrightarrow \quad \gamma \longrightarrow \boxed{H} \longrightarrow \gamma' = \gamma - c$$

environment at previous generation — environment at current generation

parent genotype — offspring genotype

More relevant constraint? (Vanhoenacker, Sandell, Roze 2018)

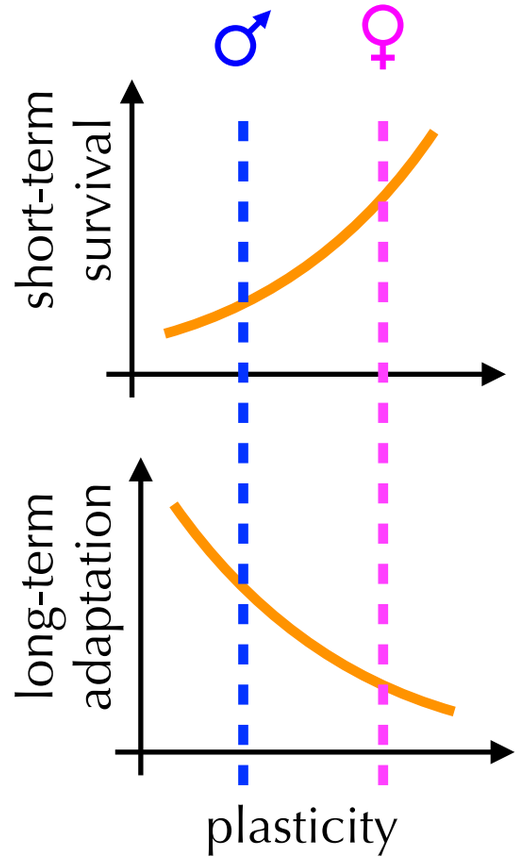
Should not oppose genetic constraints & varying selective pressures

Sex as information processing

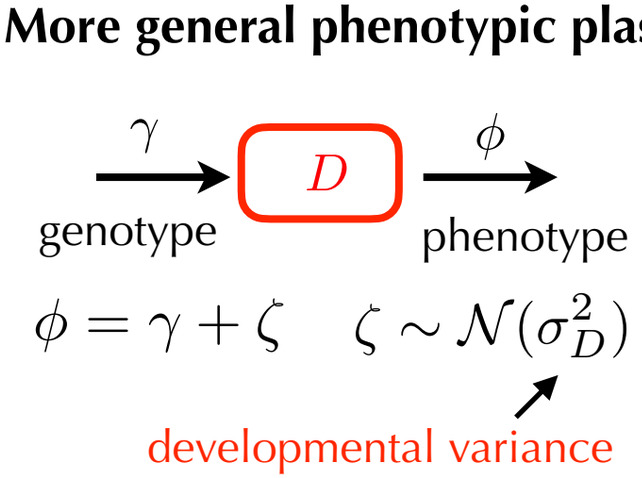
Dilemma: efficient long-term adaptation $\Longrightarrow$ strong selection $\Longrightarrow$ short-term growth reduction

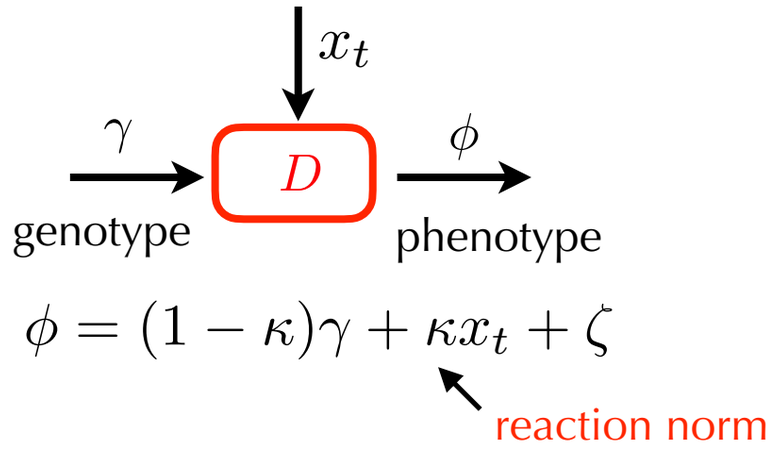
Solution with two sexes: selection on males, growth through females which are more plastic

Results from mathematical model: sexual dimorphism can be favored and overcome the two-fold cost of males but only under specific genetic and environmental constraints



More general phenotypic plasticity:

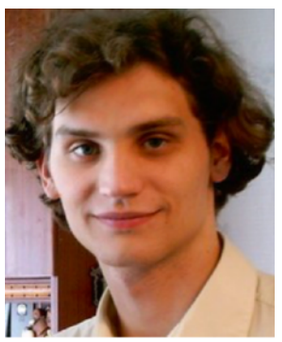




Beyond $\kappa = 0$, still analytically solvable, but

How to account for the cost of plasticity? (without cost, $\kappa = 1$ is a trivial optimum)

- What relevant constraints?
- What available data?
- Relation to other principles, e.g. division of labor transmission/utilisation?



Anton Zadorin

Ref: Zadorin & Rivoire, PRE 2021 — arXiv:2102.05459