Maternal effects and environmental change

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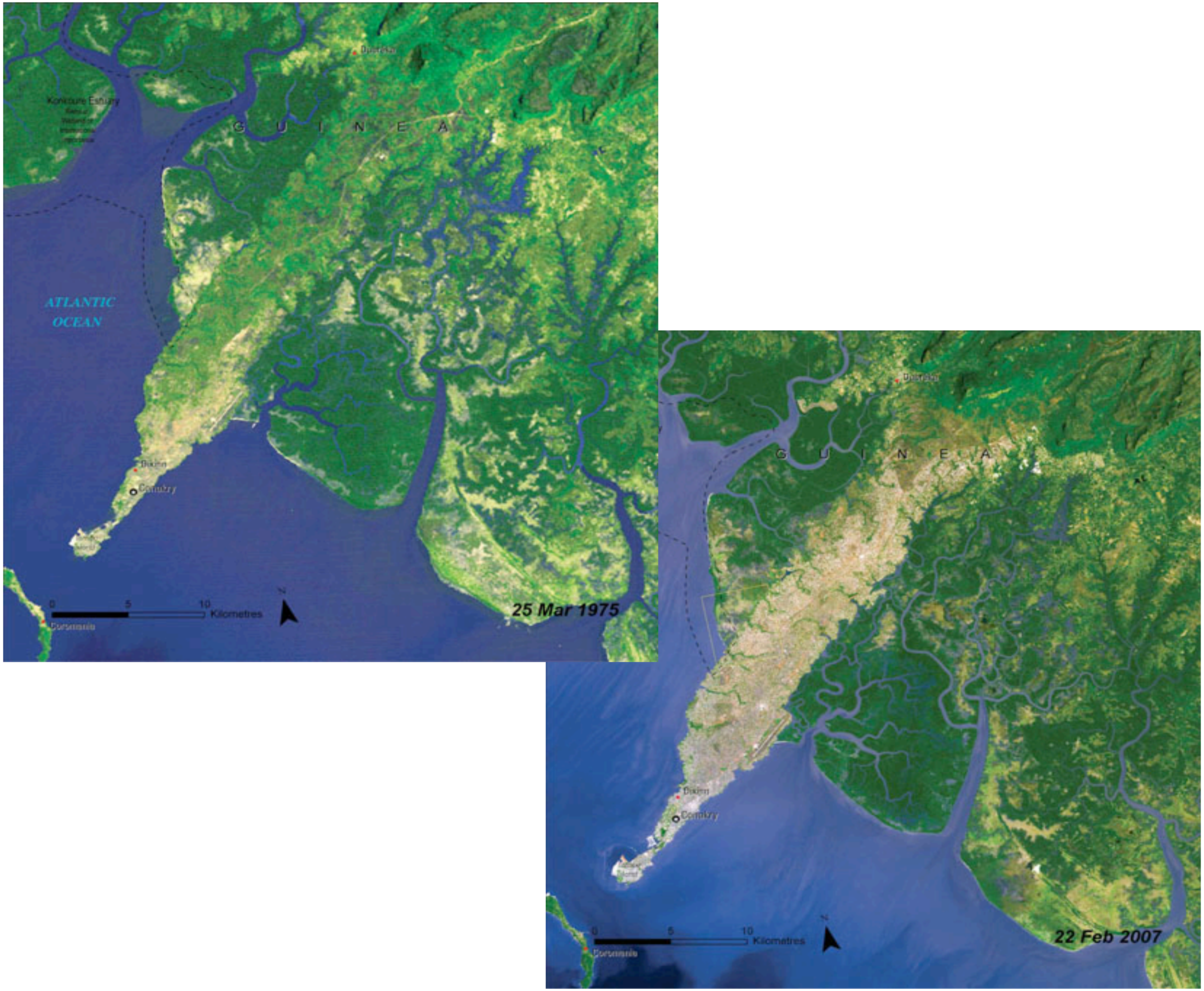
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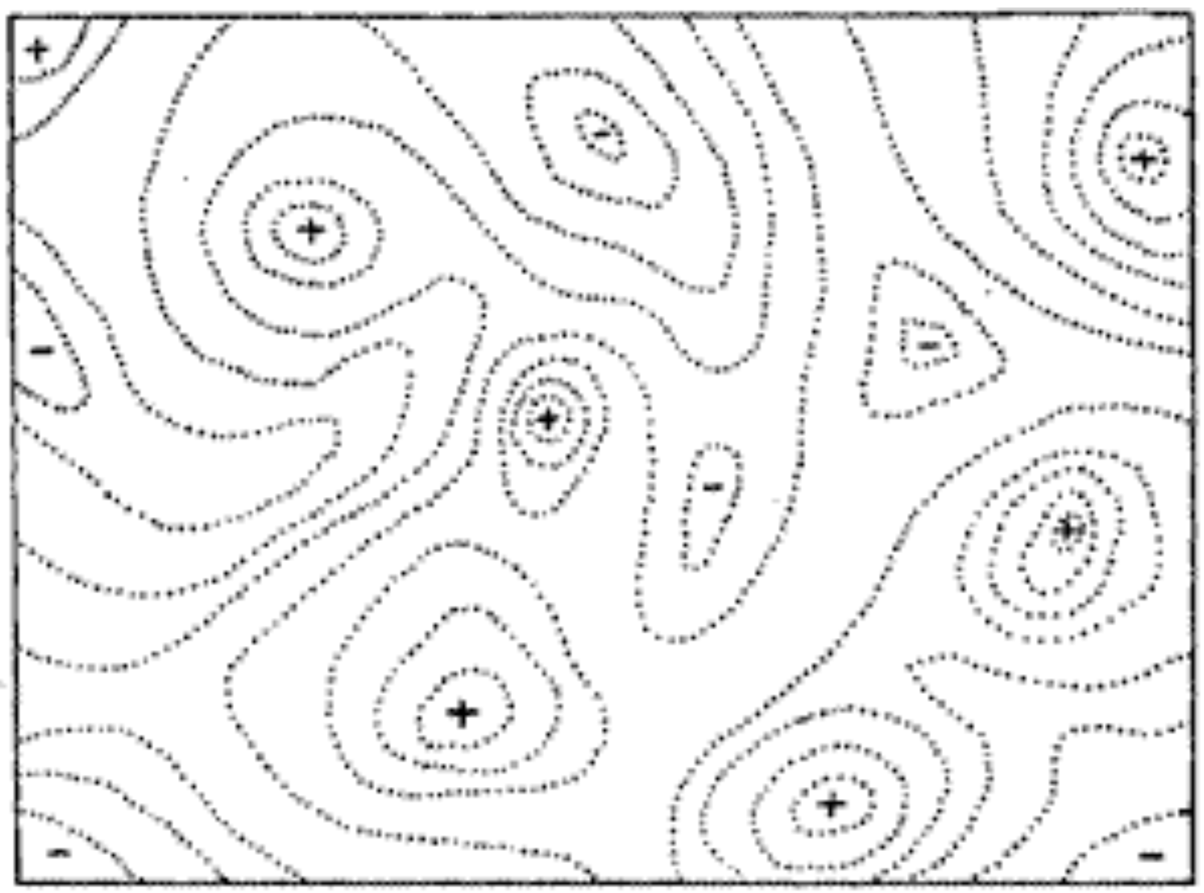
Facilitating adaptation



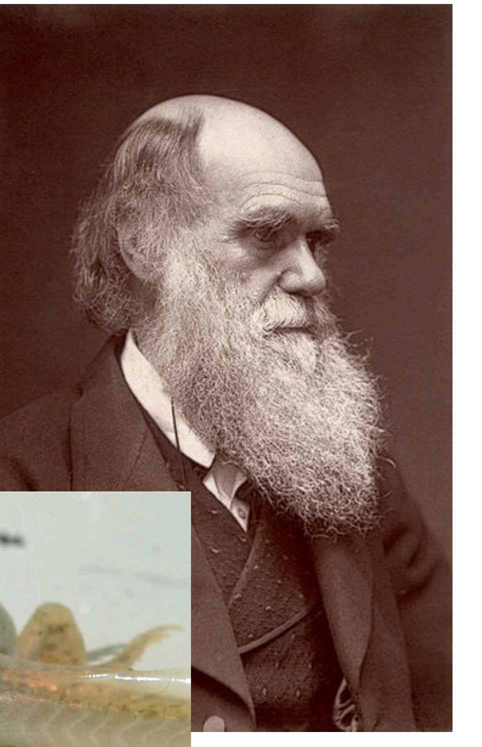
In the real world, the adaptive landscape fluctuates like a “choppy sea”.

What do organisms adapt?

- Phenotype: the set of observable characteristics of an organism resulting from the interaction of its genes with other factors, such as the environment

How do organisms adapt?

- Natural selection on the genes
- Developmental plasticity (within a generation)
- Maternal effects: the influence of the phenotype (e.g. body size) of the mother on her offspring independent of the inherited genes

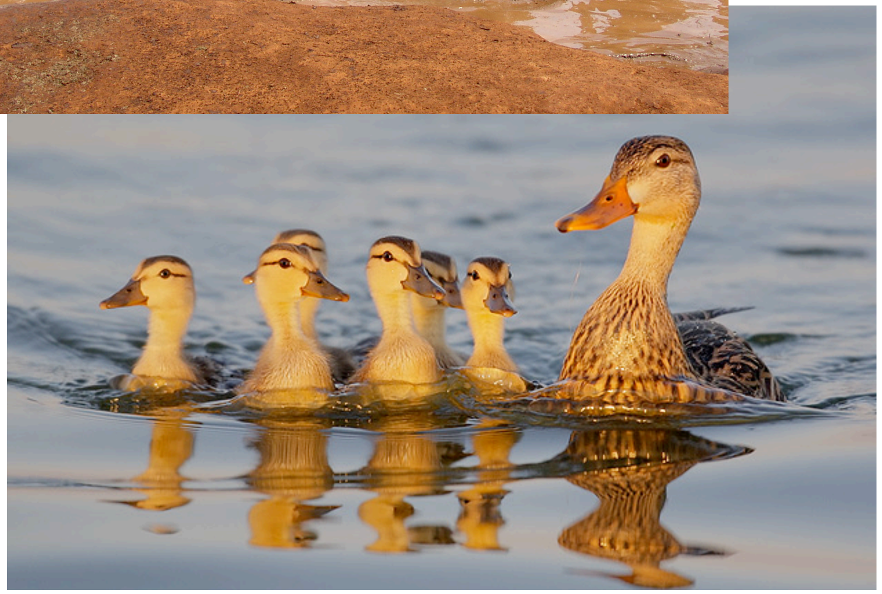


Why are maternal effects important?

- They may...
  - Be implicated in human obesity
  - Boost the initial colonisation ability of plants
  - Increase early survival in insects
  - Expand potential for evolution in vertebrates
  - Provide a flexible way of maximising fitness in a changing environment

Bypassing genetic constraints

- Maternal effects are "epigenetic influences of parental phenotypes on offspring"
  - Badyaev (2009) *Phil. Trans. Roy. Soc. B* 364:1125–1141 doi: 10.1098/rstb.2008.0285.
- Enable rapid fine-tuning of the phenotype in response to a changing environment.



Questions

- Do maternal effects influence the rate of adaptation to environmental change?
- Can maternal effects be adaptive?



If a rapid response to environmental upheaval is a critical coping mechanism in evolutionary biology, then **why do estimates of maternal inheritance frequently suggest it** does not accelerate but **retards adaptation?**

A quantitative genetic model

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Add fixed maternal effects to Lande's (2009) reaction norm that describes the dependence of offspring phenotype on genes and the environment

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Adult phenotype of an individual subject to selection at time (=generation) t

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Additive genetic effect

Slope of the plastic response to the environment

Environment during critical period of juvenile development

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Slope of the maternal effect

Adult phenotype after selection in generation *t*-1

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Independent residual component of phenotypic variation

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Gaussian population mean fitness around an optimal phenotype that is a linear function of the environment

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Width of fitness function

Phenotypic variance

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Mutation-selection balance: fixed genetic variances G_{aa} & G_{bb}

Phenotypic variance minimised in the reference environment $\varepsilon=0$

Natural selection

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Unit step change at time t=0

Amplitude of change

Gaussian stationary autocorrelated random process, mean zero, variance σ_ξ^2 and autocorrelation ρ_τ over a time interval τ

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Expected values averaged over environmental noise

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Consider a noisy step change in environment

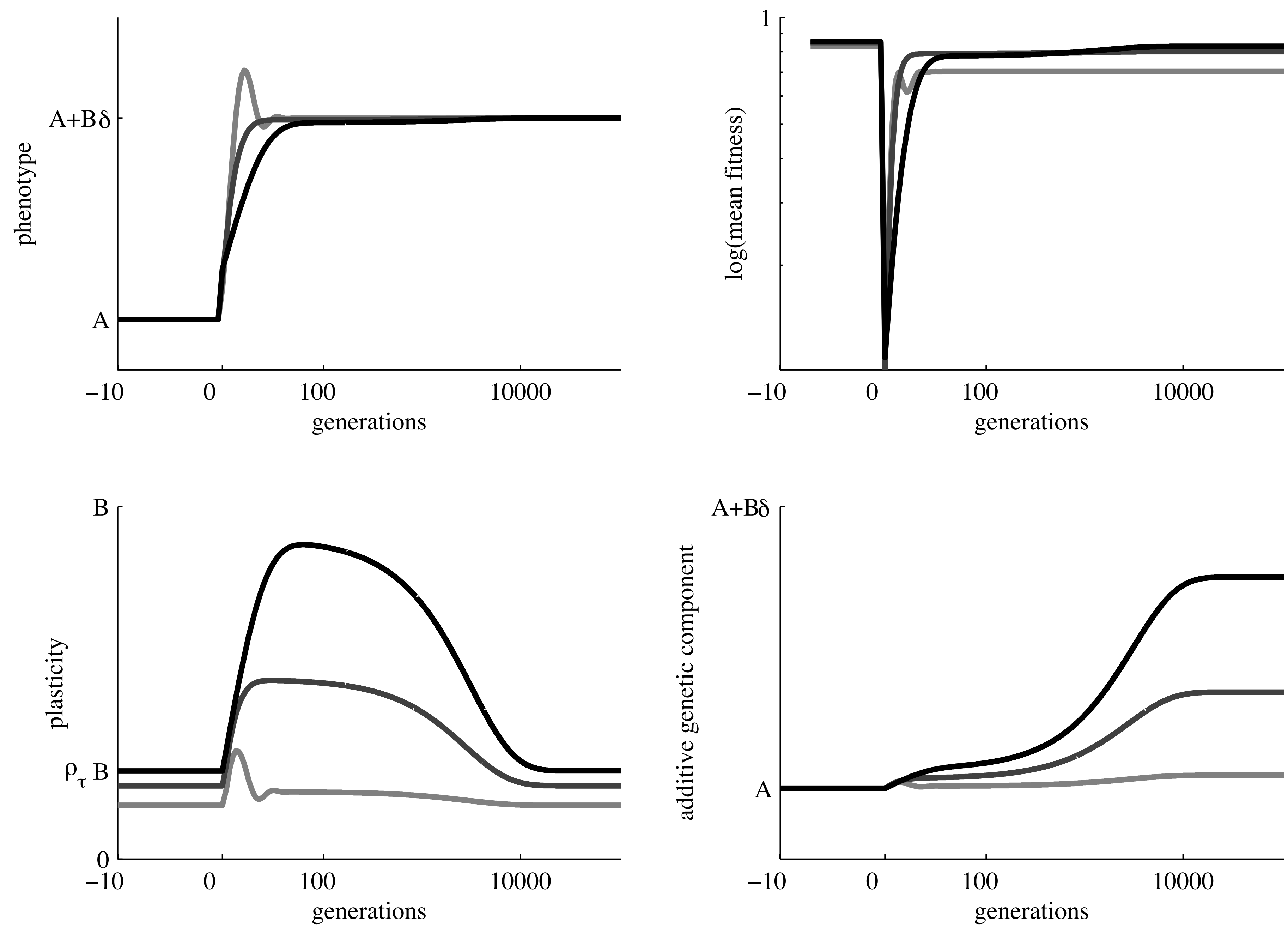
$$\varepsilon_t = U_t\delta + \xi_t$$

Expected values averaged over environmental noise

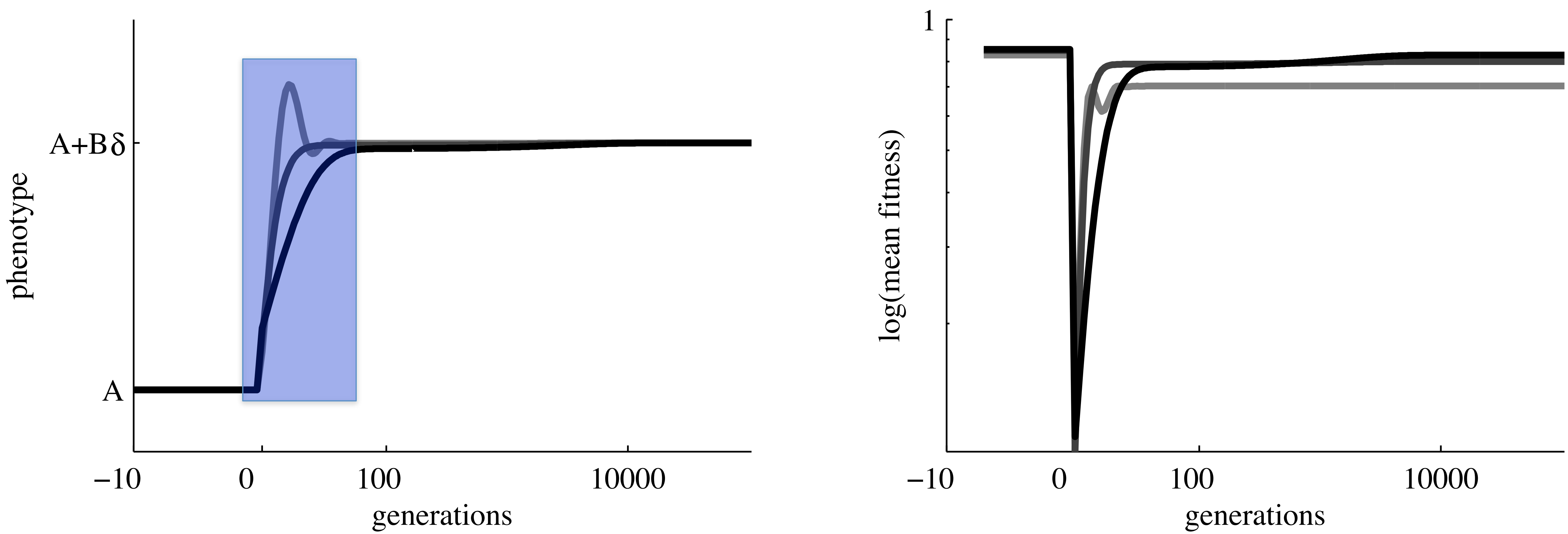
$$E(\Delta\bar{a}) \approx -\gamma_e G_{aa}(1+m)\{\bar{a}_t - A + (\delta U_{t-\tau}\bar{b}_t - \delta U_t B) + mE(\bar{z}^*_{t-1})\},$$

$$E(\Delta\bar{b}) \approx -\gamma_e G_{bb}((\delta U_{t-\tau} + m\delta U_{t-\tau-1})\{\bar{a}_t - A + (\delta U_{t-\tau}\bar{b}_t - \delta U_t B) + mE(\bar{z}^*_{t-1})\}$$
$$+ \{\bar{b}_t(1+m^2) - \rho_\tau B\}\sigma^2_\xi),$$

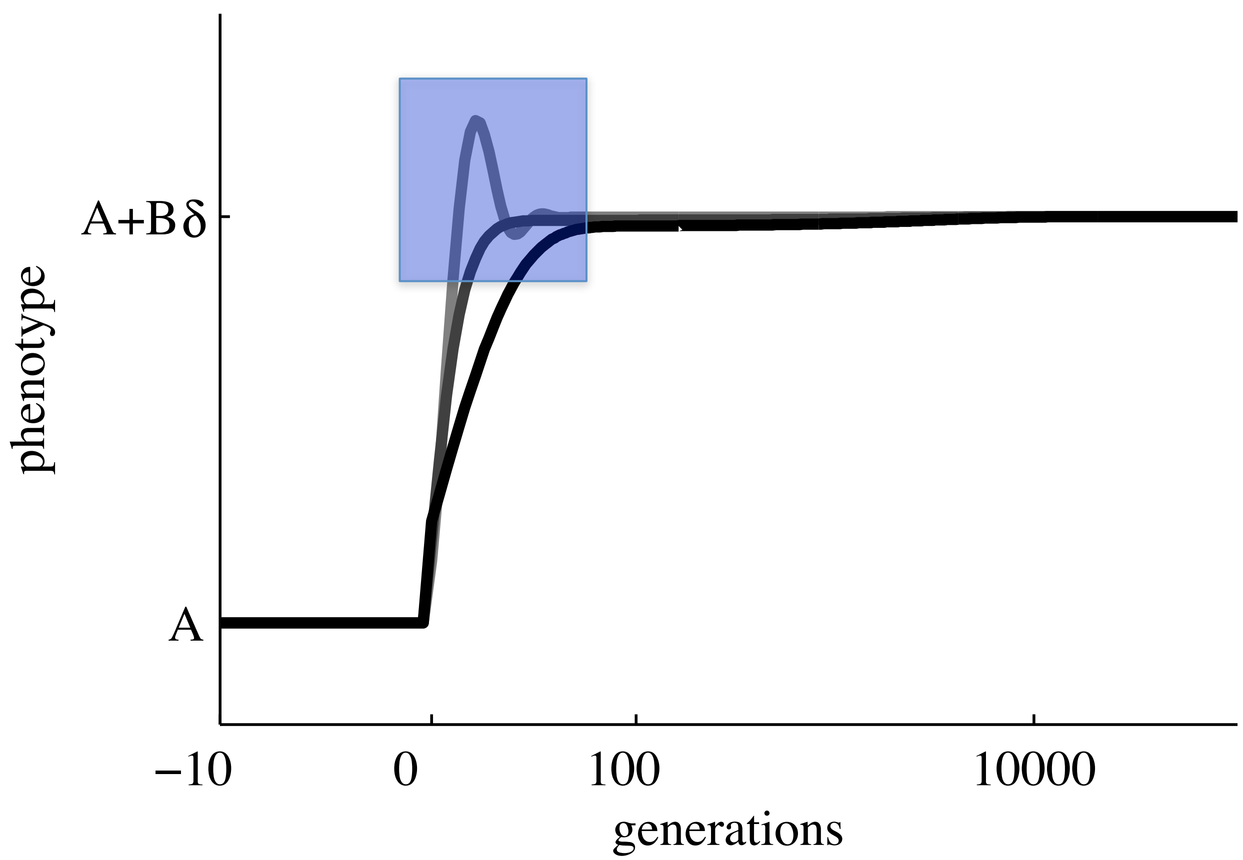
Positive maternal effects speed adaptation to rapid environmental change (or it pays to copy mum)

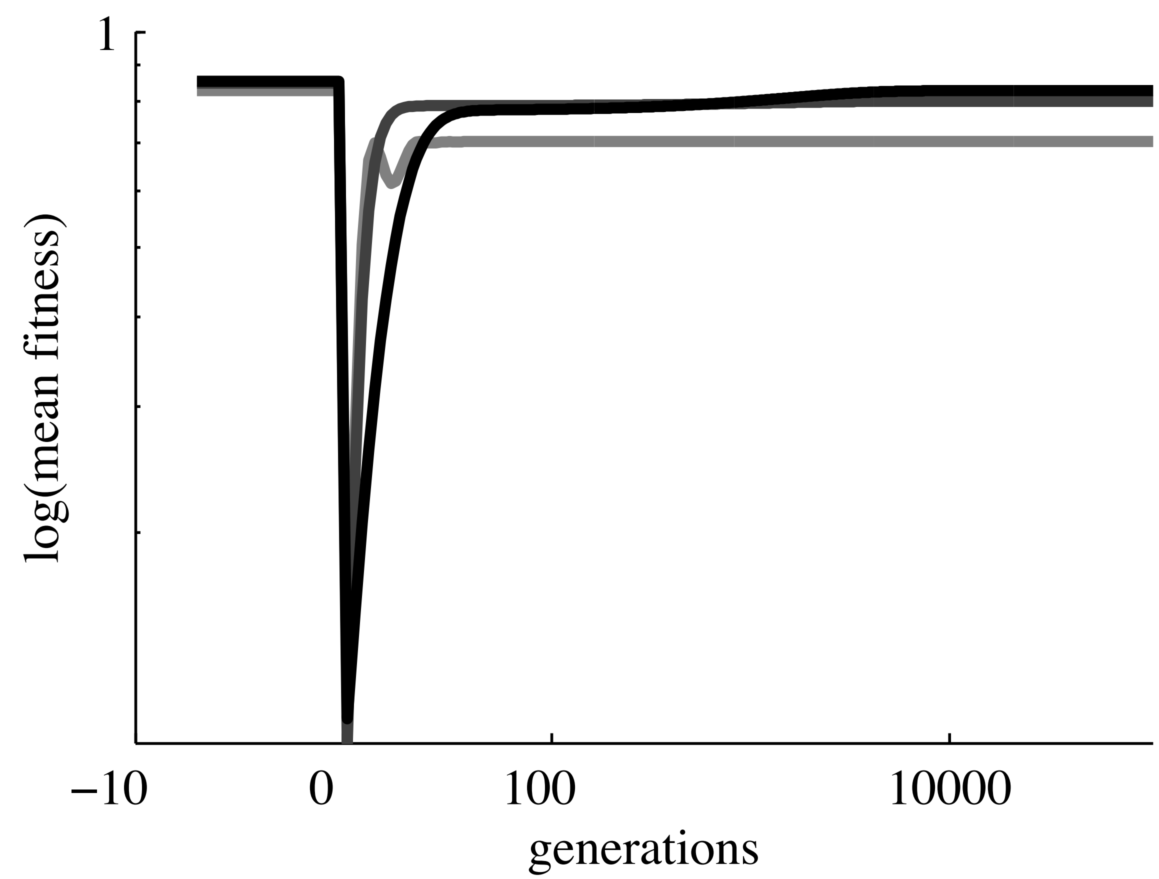


Expected evolution in the absence of maternal effects (m=0, black) and with moderate (m=0.45, dark grey) and larger (m=0.8) positive maternal effects

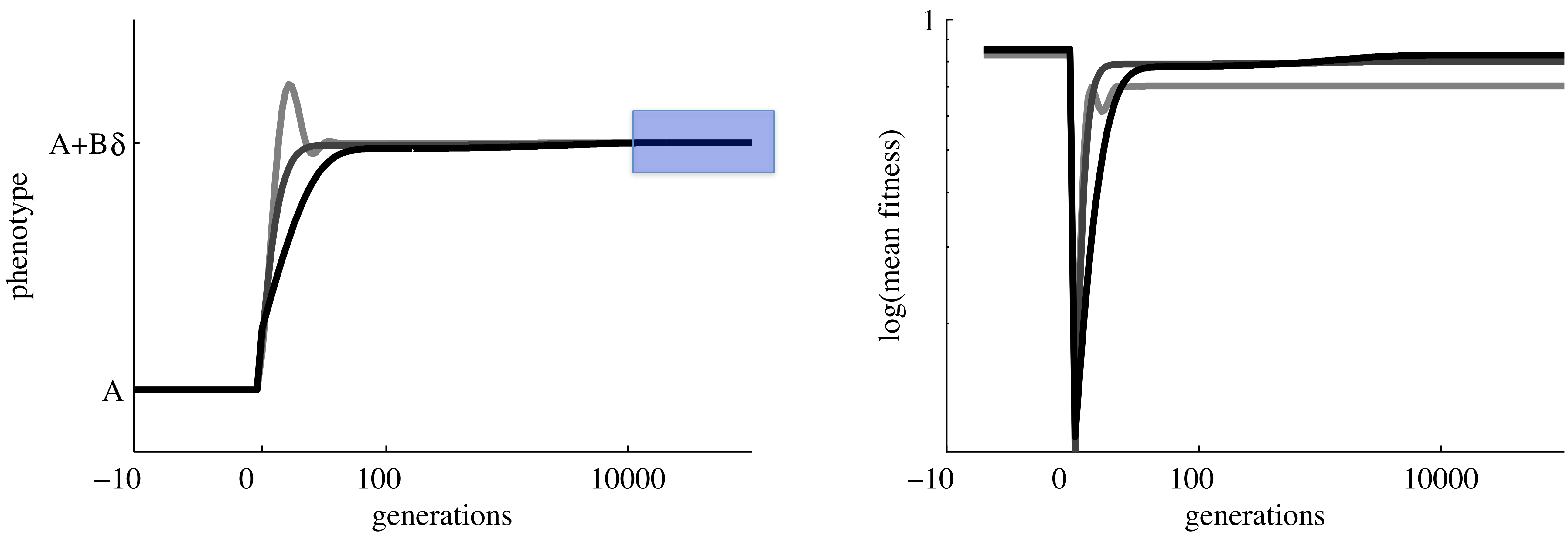


m>0 speeds up adaptation
to new environment

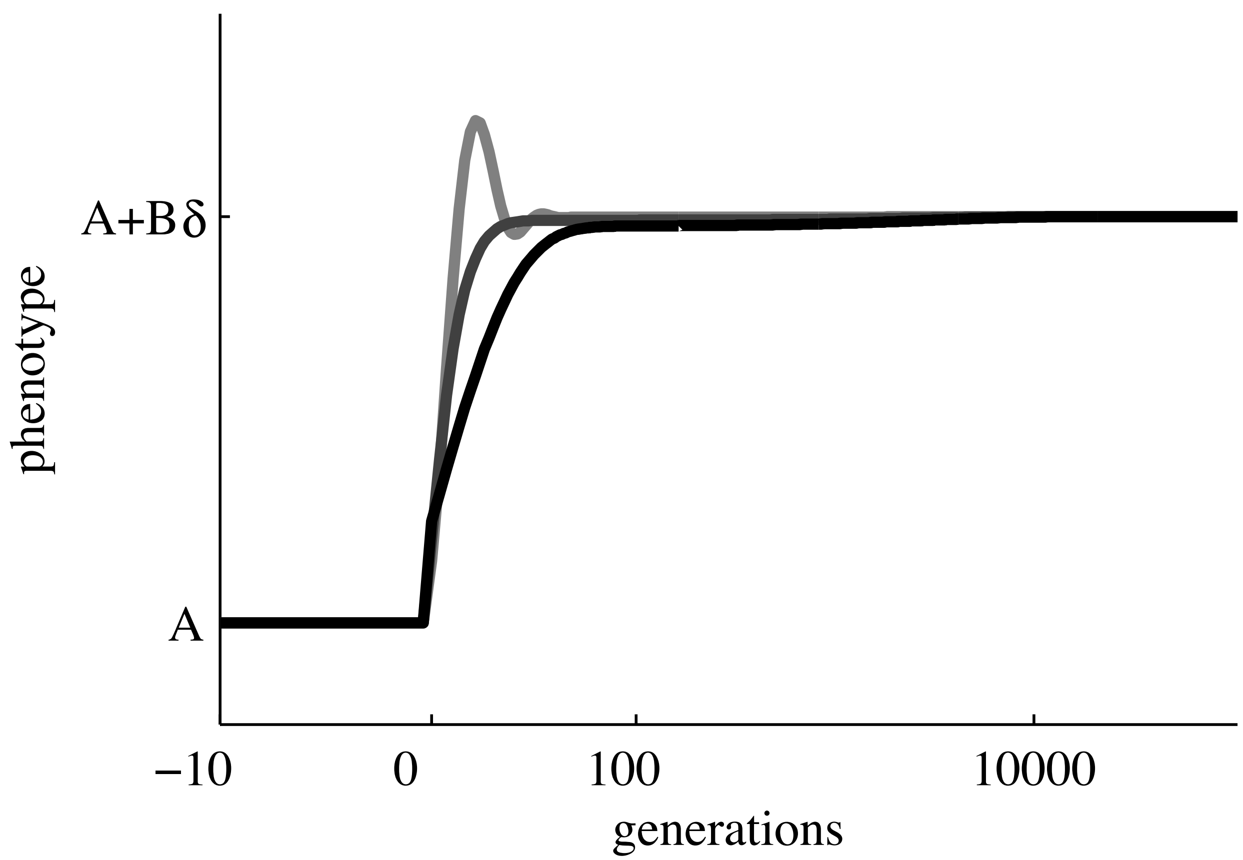


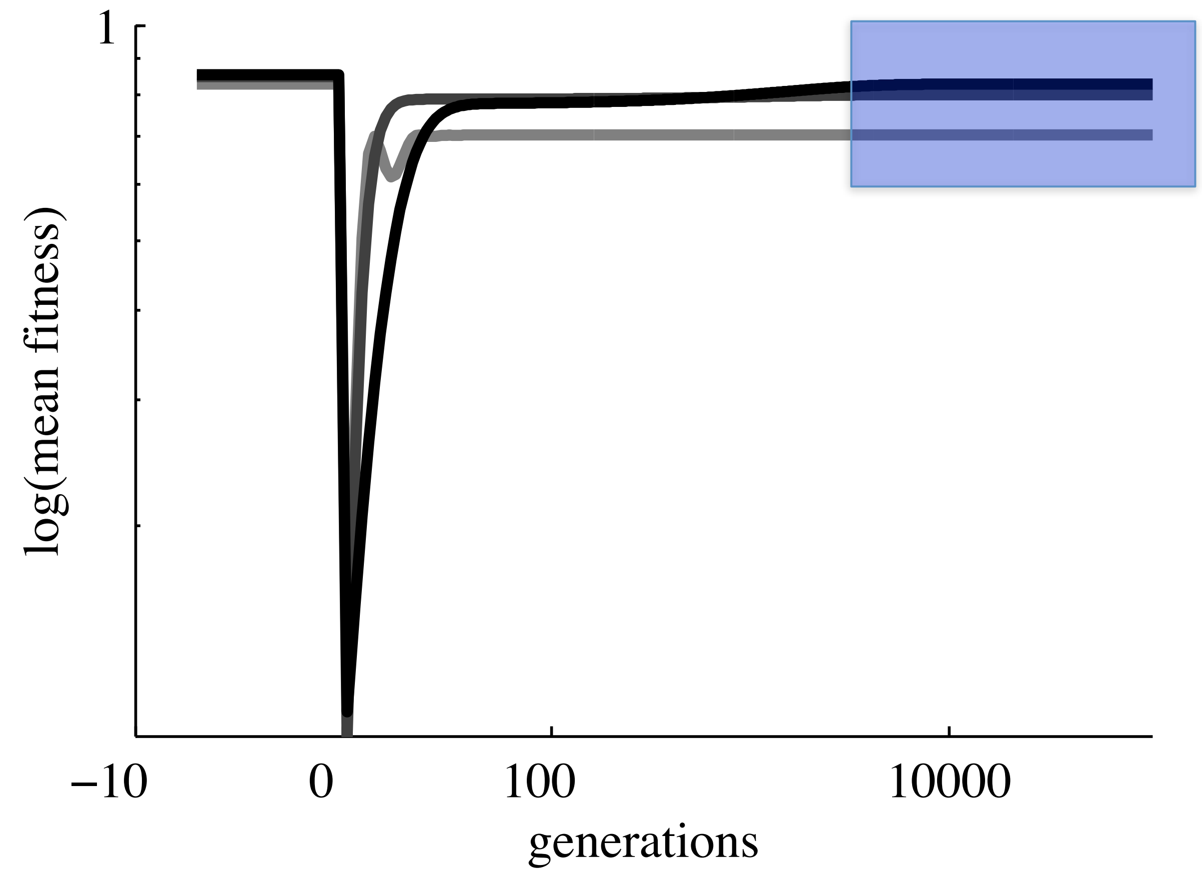


m>0 can provoke oscillations
in the phenotypic dynamics

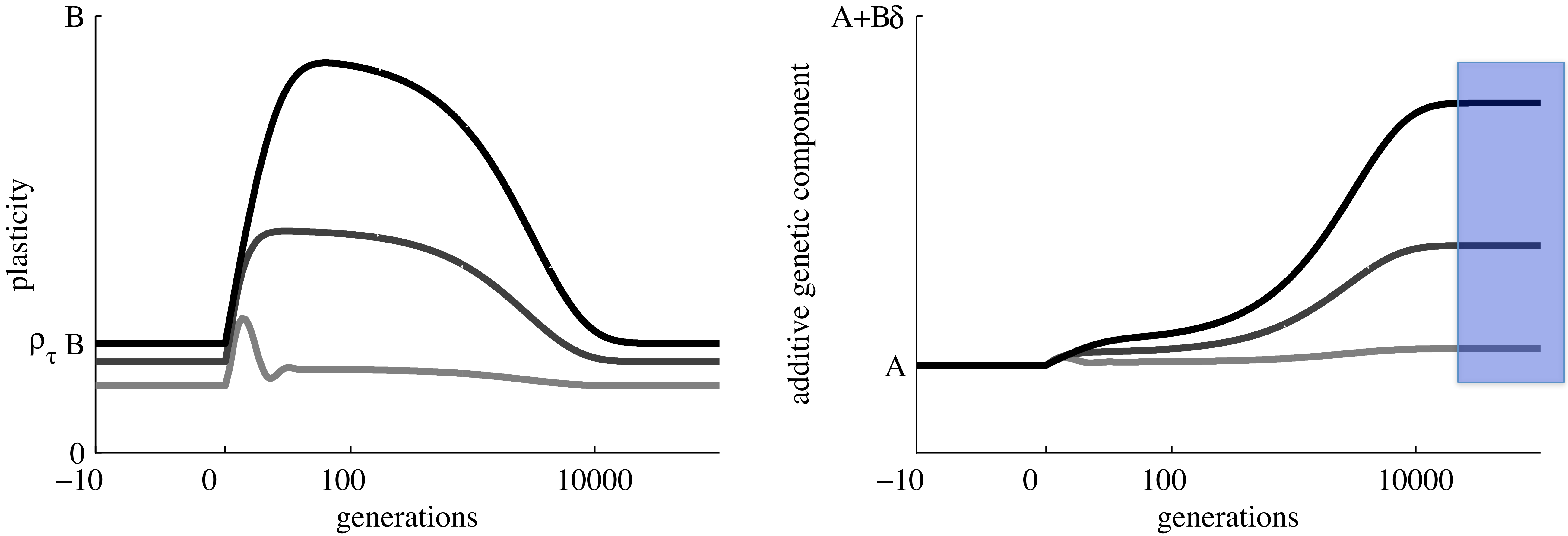


No difference to expected equilibrium phenotypes

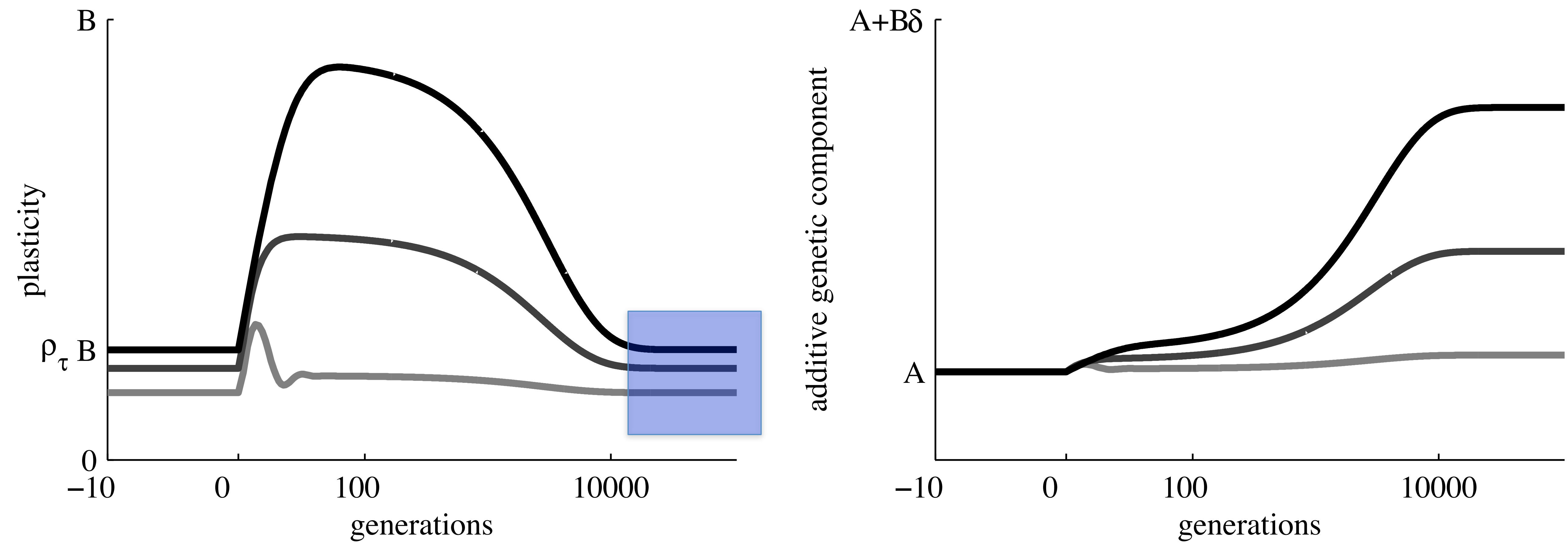




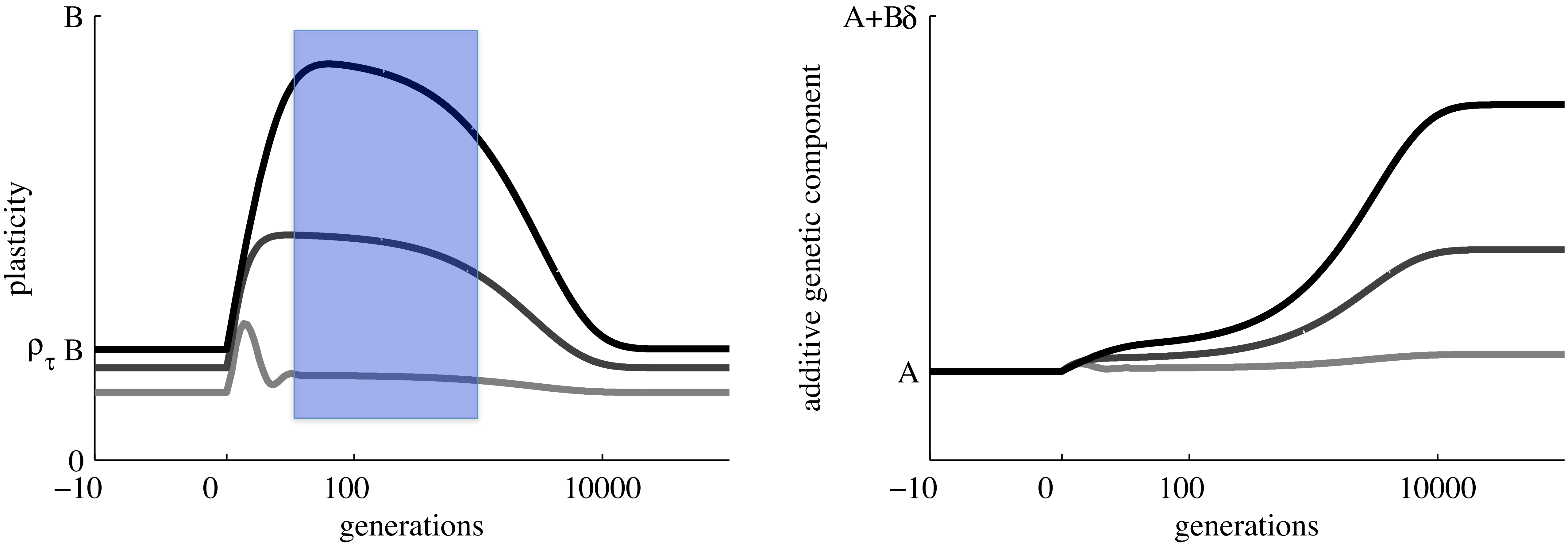
m>0 reduces fitness at equilibrium



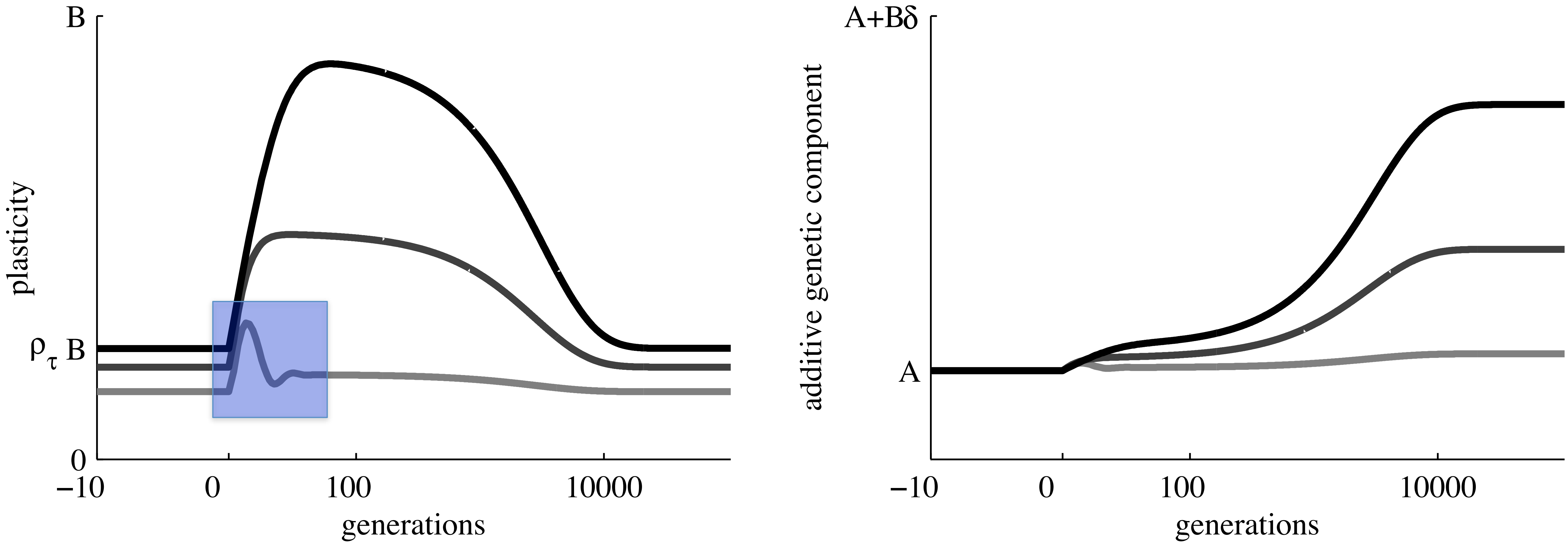
m>0 lowers expected equilibrium additive genetic component



m>0 reduces expected equilibrium plasticity



m>0 reduces transient peak in plasticity



Phenotypic oscillations driven by phenotypic plasticity

So why is m often negative?

So why is *m* often negative?

- Empirical estimates of maternal effect coefficients are often negative
  - Most thorough evidence comes from red squirrels: $m = -0.3, -0.29$ and -0.27 to -0.21 (Humphries and Boutin, 2000; McAdam and Boutin, 2003, 2004)

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To understand this consider a stable stochastic environment without a step change:

$$\varepsilon_t = \delta + \xi_t$$

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- We can show that the expected phenotypic variance at equilibrium is given by

$$E(\sigma_z^2) = \frac{(2+m)(G_{aa} + \delta^2 G_{bb})}{(2-m)(1-m^2)} + \frac{\sigma_e^2 + G_{bb}\sigma_\xi^2}{1-m^2}$$

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The covariance between the genetic and maternal phenotypic components of the offspring phenotype means that the variance is minimised at slightly negative *m* expected population mean fitness

variation penalty

adaptation

$$E(\bar{W}) \approx \frac{1}{\sqrt{1 + E(\sigma_z^2)/\omega^2}} \times \exp\left\{-\frac{\gamma_e}{2}(\bar{a}_t - A + U_{t-\tau}\bar{b}_t - U_t B + m\bar{z}^*_{t-1})^2\right\}$$

$$\times \exp\left\{-\frac{\gamma_e \sigma_\xi^2}{2}(\bar{b}_t^2(1+m^2) + B^2 - 2\bar{b}_t B \rho_\tau)\right\}$$

trend/deterministic

mismatched plasticity

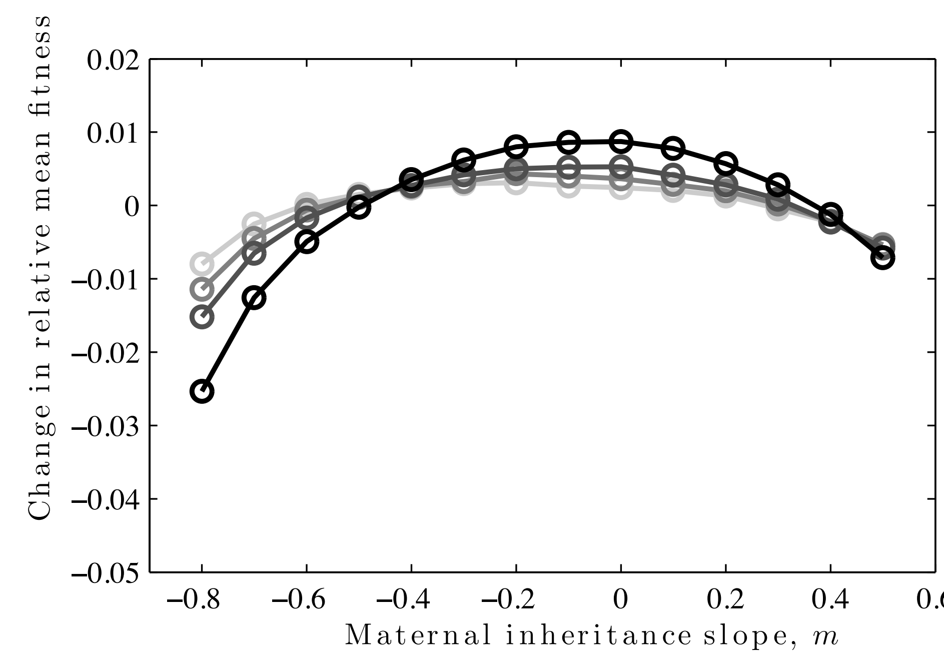
$$\varepsilon_{\mathrm{t}} = U_t + \xi_t$$

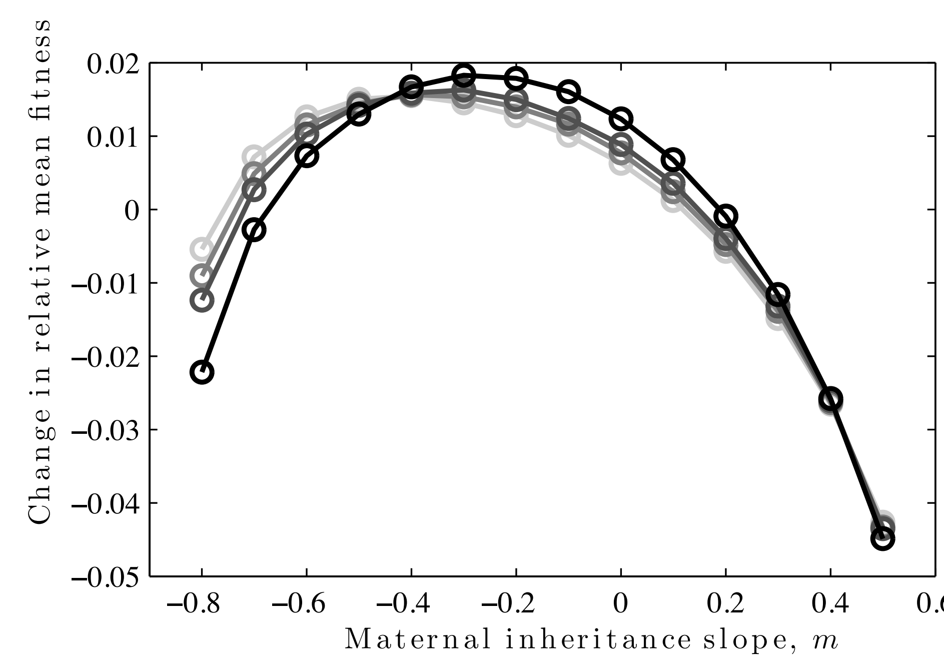
fluctuations

Components of population mean fitness

Stable environments favour negative *m*

Relative fitness curves





Stable environments favour negative *m*

If your environment is relatively stable, best not to copy mum too much

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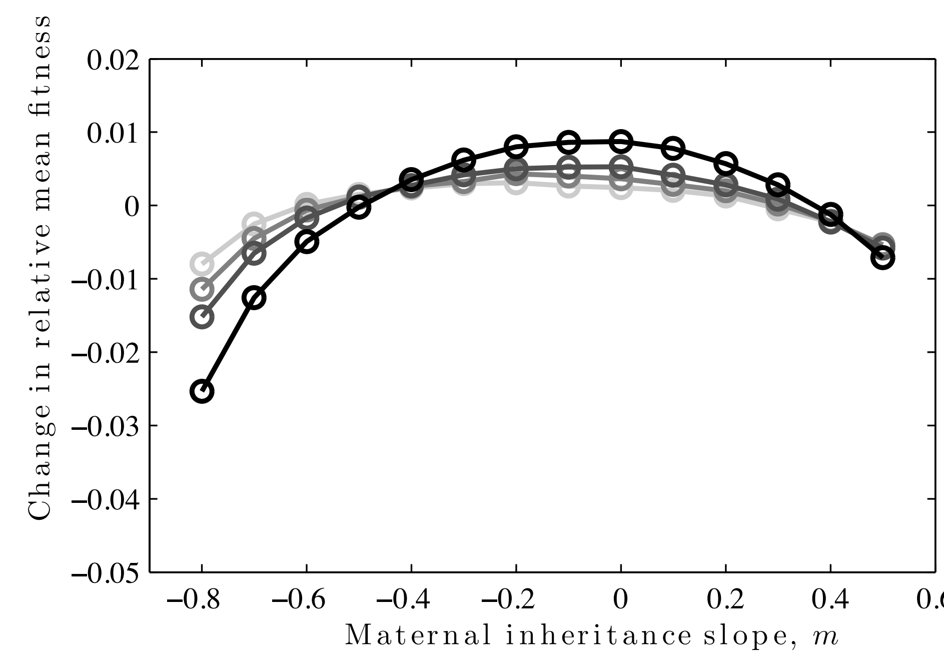

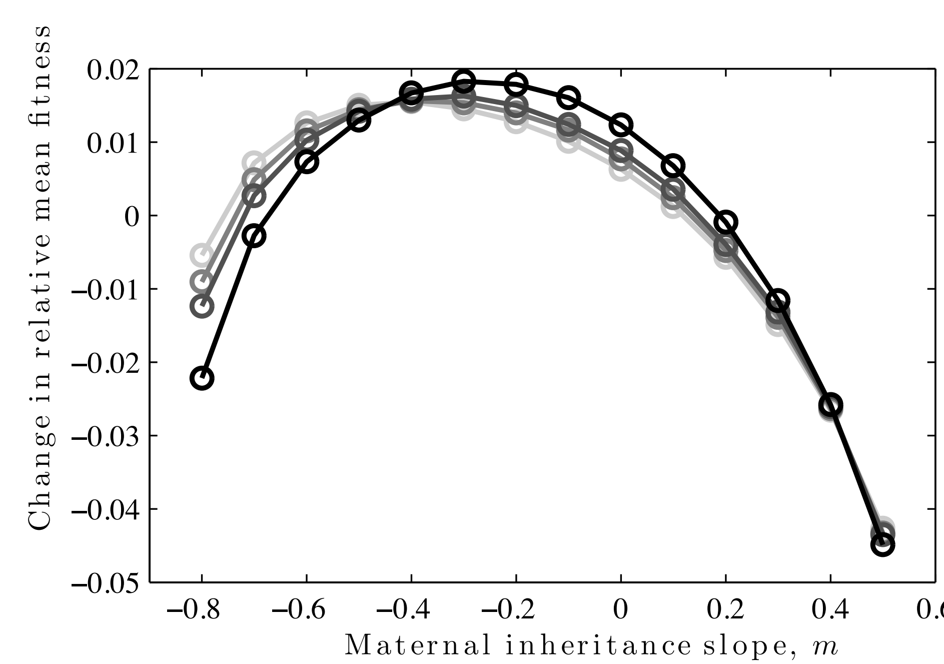

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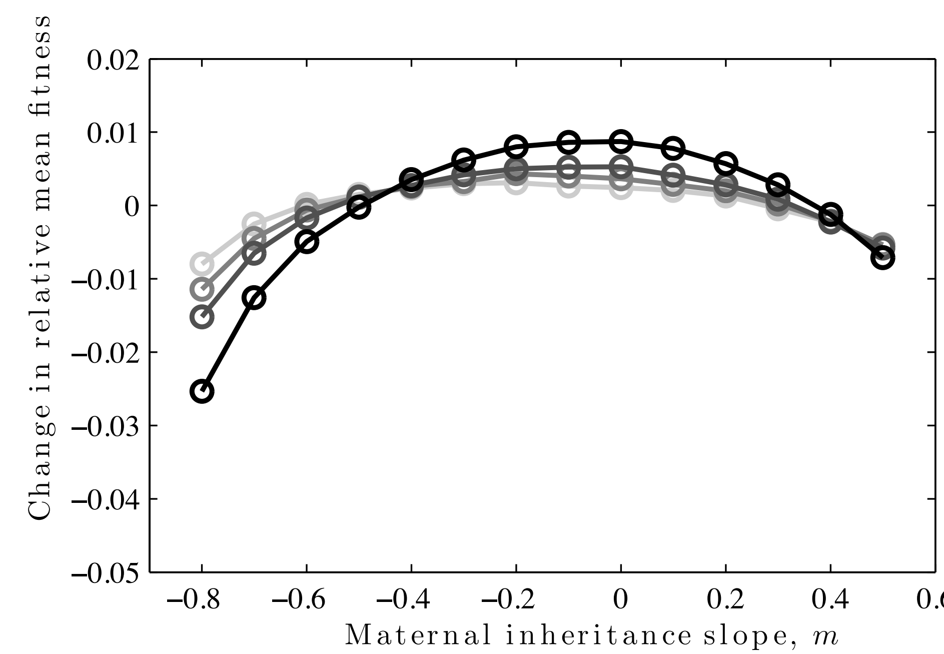

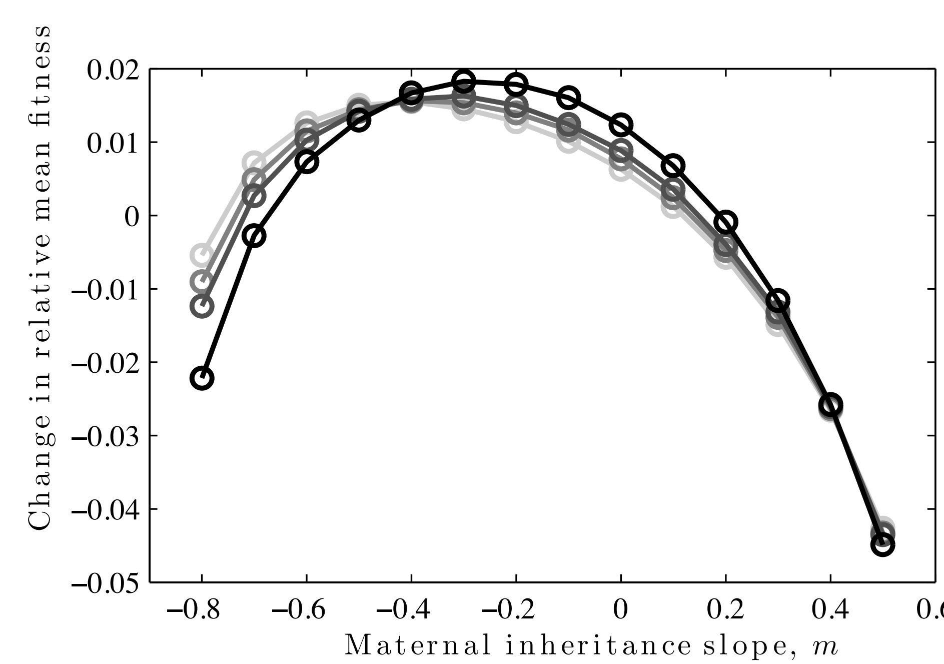

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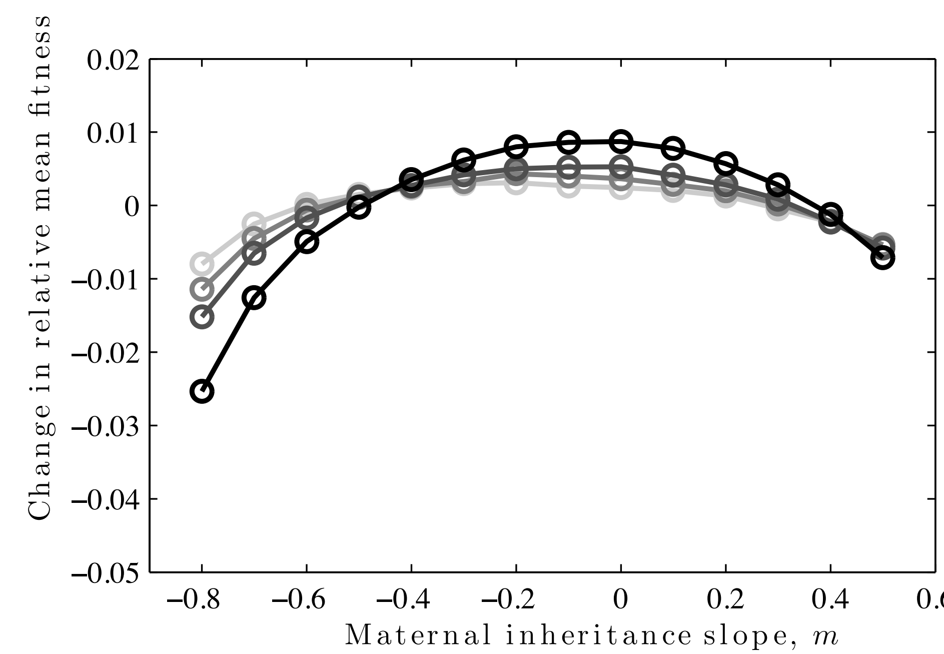

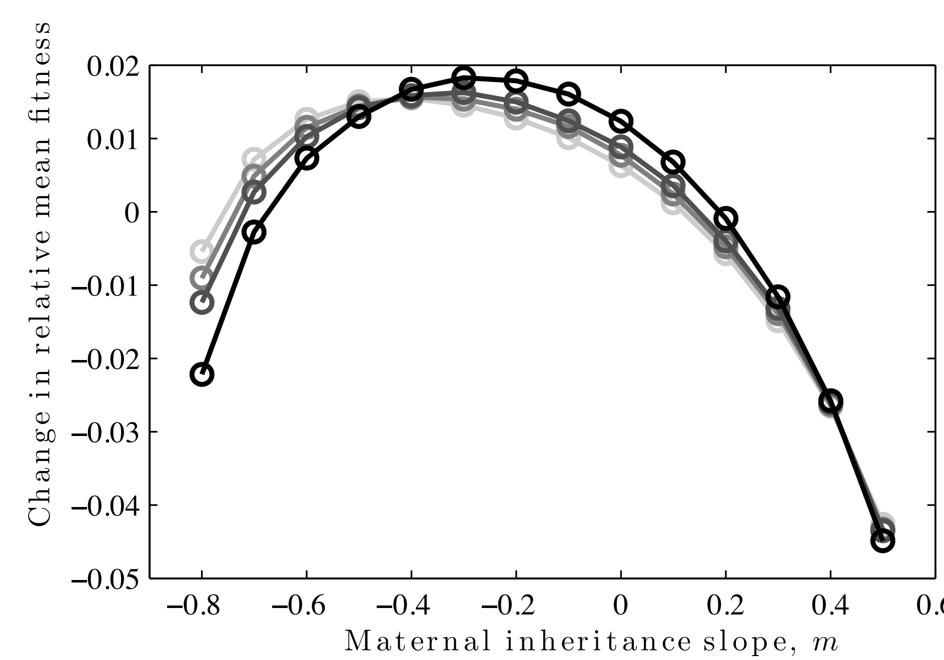

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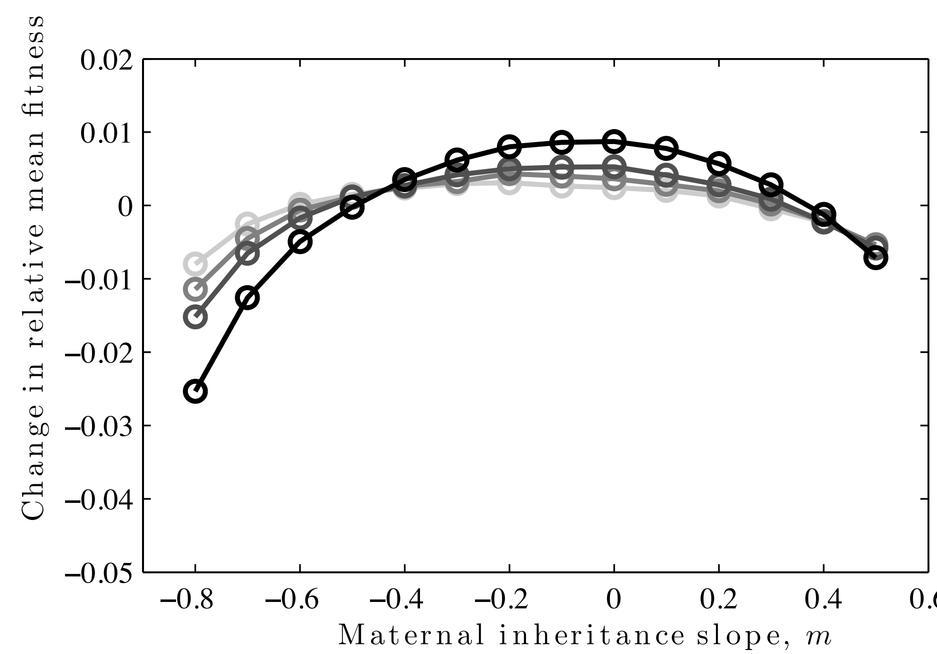
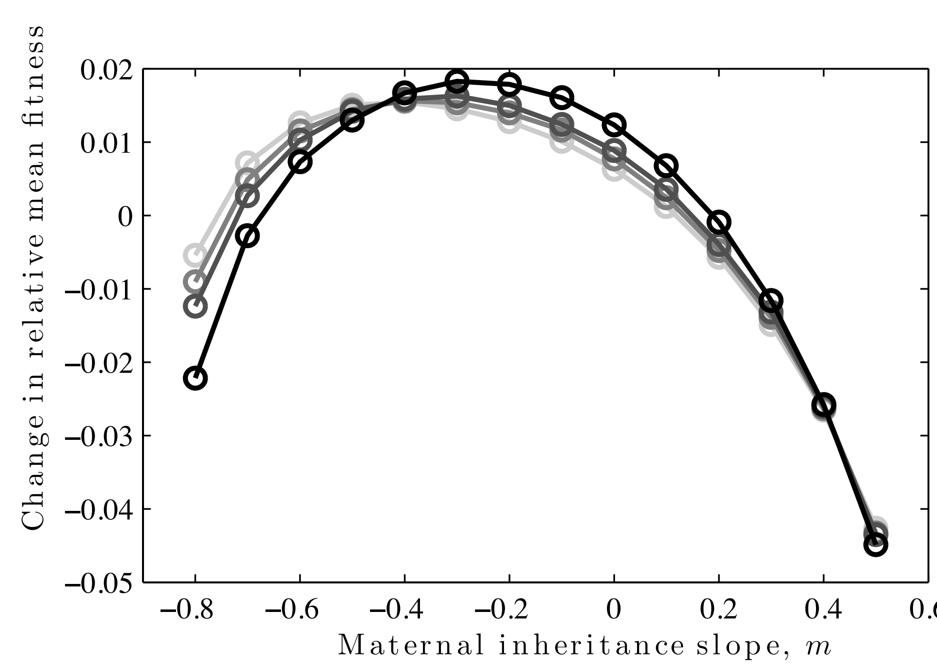
- As environmental predictability increases, optimal m moves closer to zero and fitness costs of expressing suboptimal m increase: black = greater environmental autocorrelation

Relative fitness curves





- *m*>0 accelerates adaptation to a novel environment.
- *m*<0 maximises fitness in relatively stable environments.
  - Hoyle, R.B. & Ezard, T.H.G. (2012) The benefits of maternal effects in novel and in stable environments. *J. R. Soc. Interface*, **9**:2403-2413, doi: 10.1098/rsif.2012.0183
- *m*>0 optimal if environmental change is predictable across generations (and there is time to adapt)
  - T.H.G. Ezard, R. Prizak and R.B. Hoyle [2014] The fitness implications of adaptation via phenotypic plasticity and maternal effects. *Funct. Ecol.*, **28**:693-701, doi:10.1111/1365-2435.12207.
- Evolved maternal effects speed up the response to sudden environmental change, improve fitness when environmental change is predictable, and may facilitate the evolution of phenotypic plasticity
  - B. Kuijper and R.B. Hoyle [2014] An evolutionary model of maternal effects.

Maternal effects and environmental change

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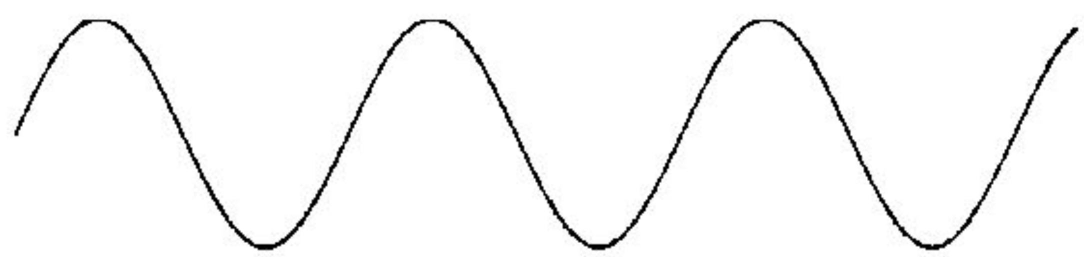
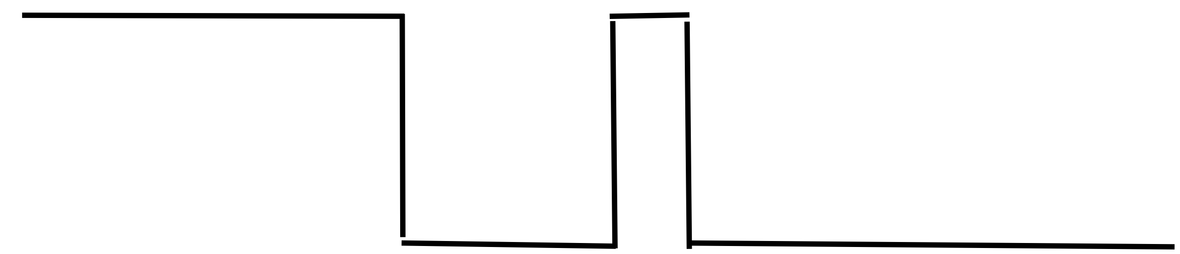
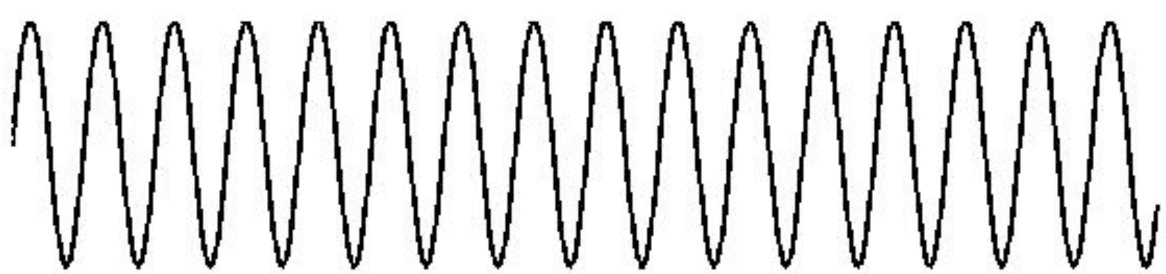
Slow sinusoidal



Slow stochastic flipping



Fast sinusoidal



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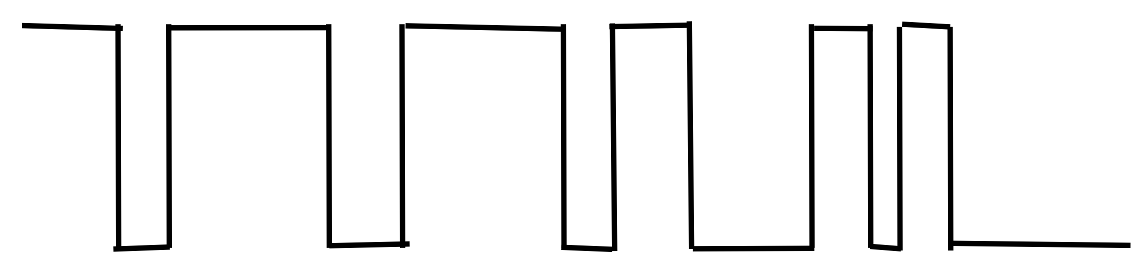
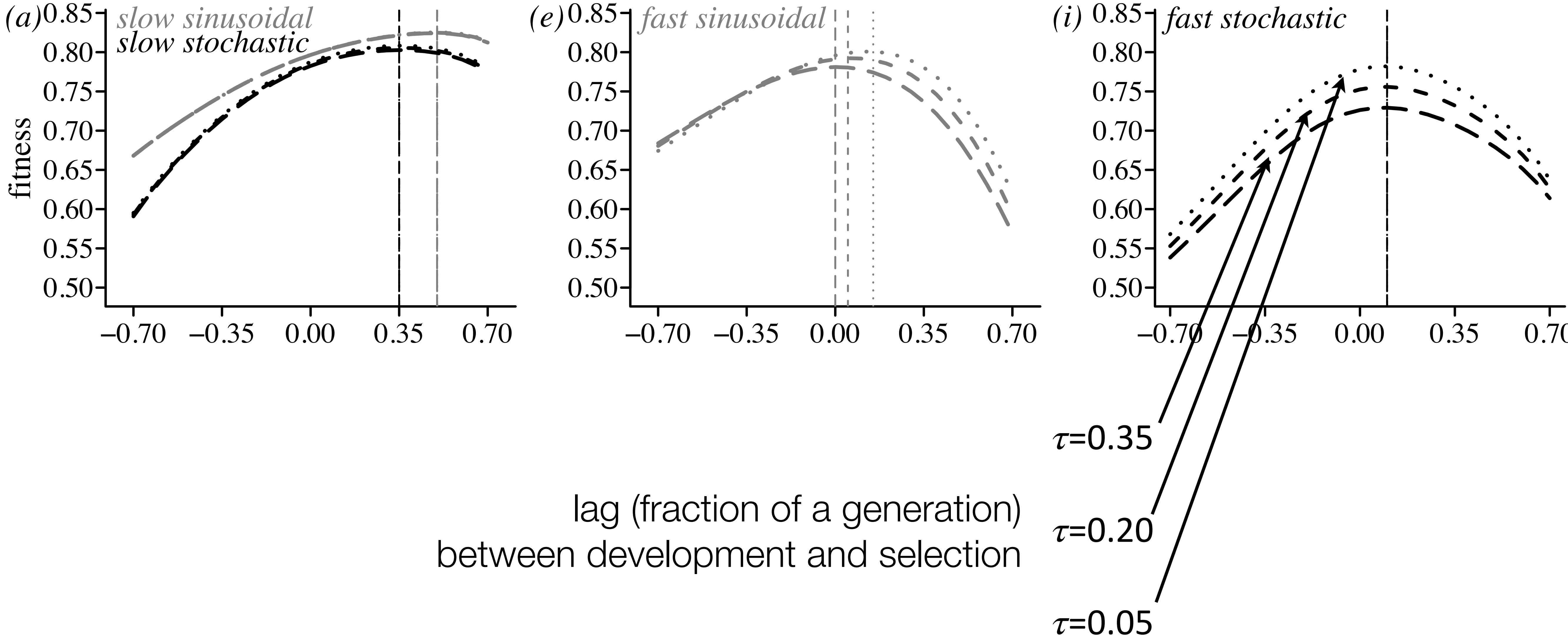
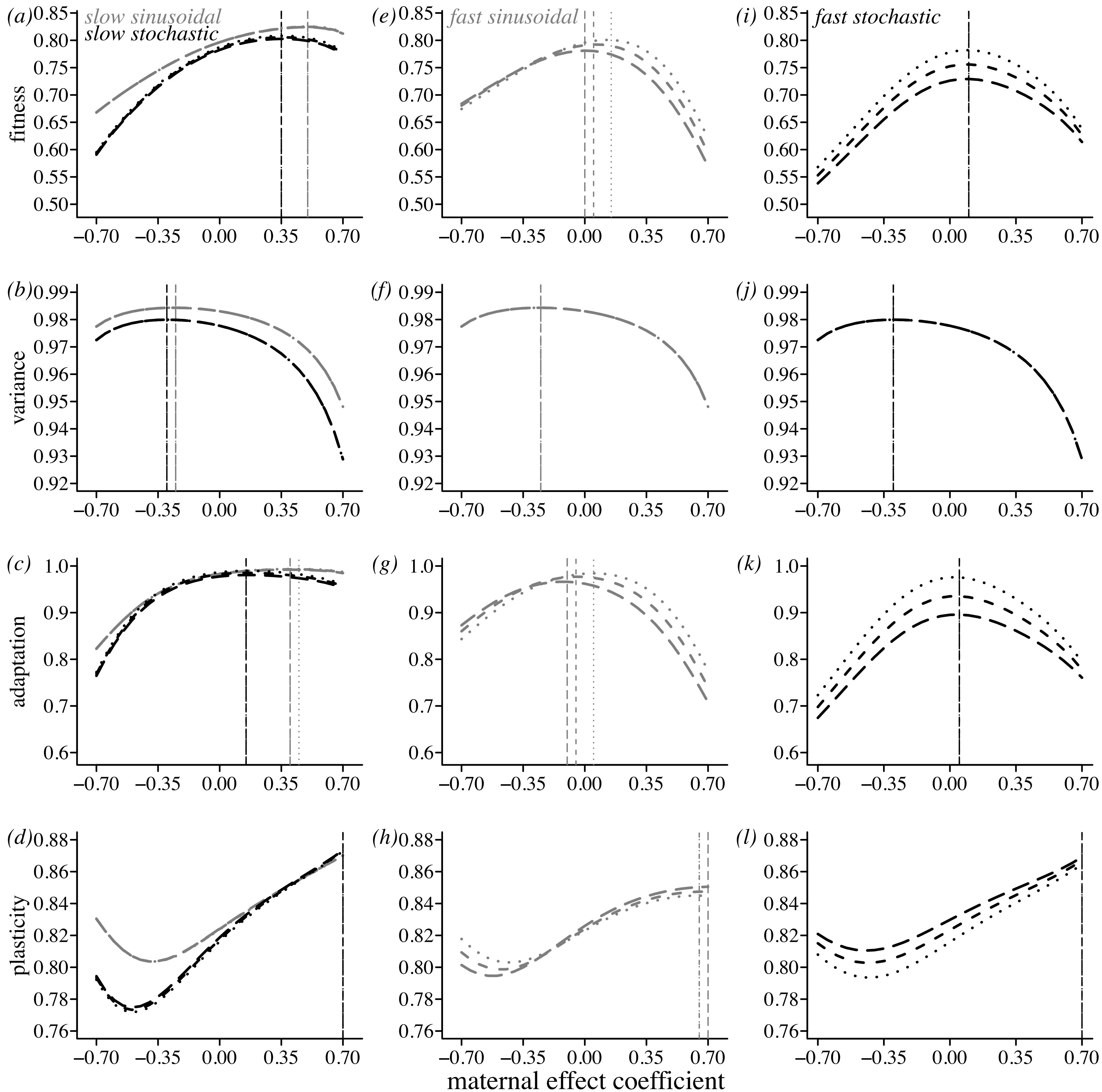


Predictable vs unpredictable
environmental change

m>>0, no lag effect *m≈0, larger for shorter τ* *m≈0, lag changes max fitness only*



m > 0 favoured where environment is more predictable
(and you can adapt fast enough)



fitness

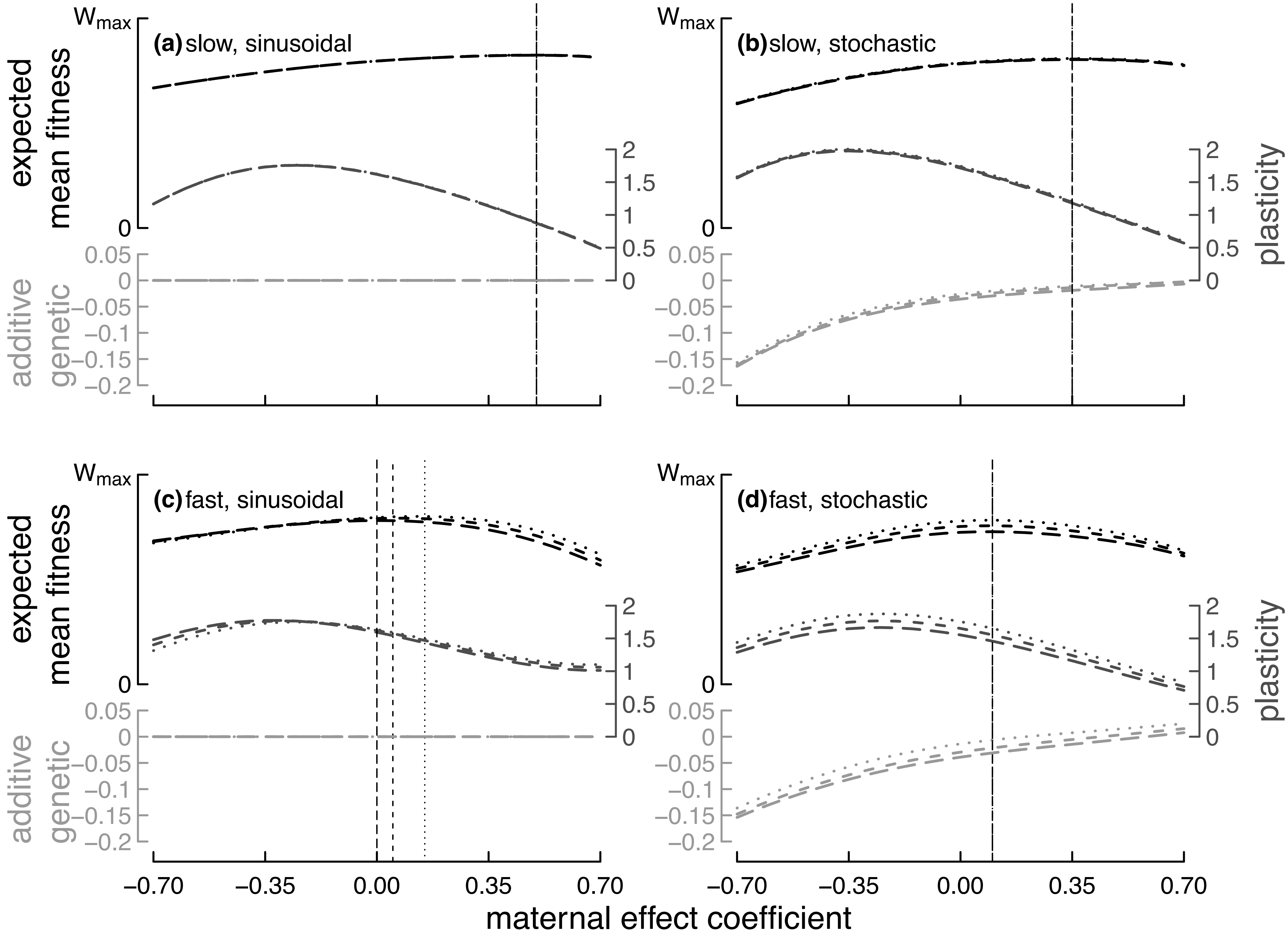
variation
penalty

adaptation
(dominates)

plasticity
mismatch

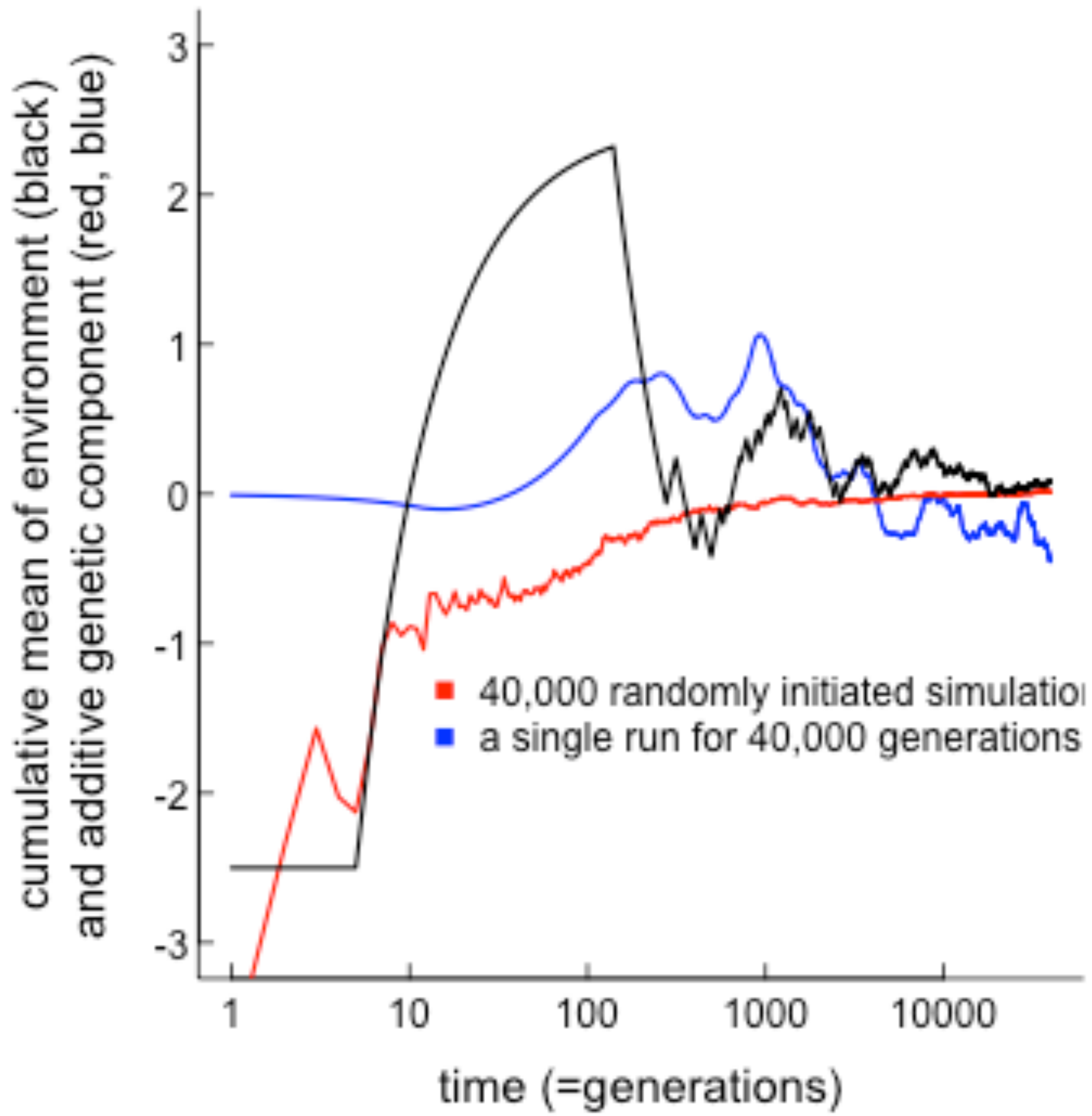
optimal phenotype far from peak plasticity

lower m in less predictable environments



Trade-off between within generation plasticity and transgenerational effects

E(a) varies with *m* owing to nonergodicity of evolutionary dynamics under stochastic forcing



Nonergodicity of evolutionary dynamics under stochastic forcing

- *m*>0 accelerates adaptation to a novel environment.
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  - Hoyle, R.B. & Ezard, T.H.G. (2012) The benefits of maternal effects in novel and in stable environments. *J. R. Soc. Interface*, **9**:2403-2413, doi: 10.1098/rsif.2012.0183

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Maternal effects and environmental change

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Evolving maternal effects

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Now let maternal effects vary across the population and be subject to selection:

$$z_t = a_t + b_t \epsilon_{t-\tau} + m_t z^*_{t-1} + e_t$$

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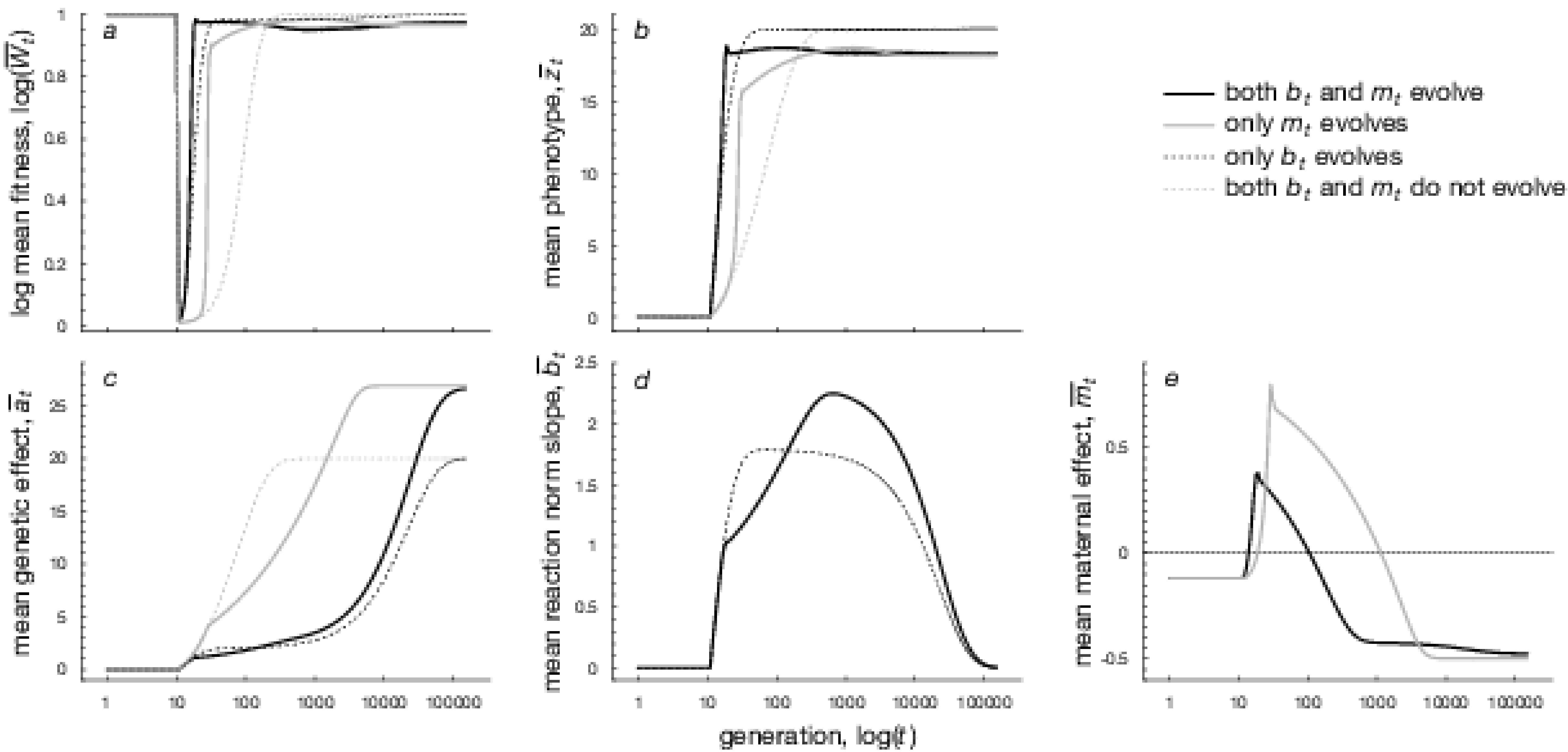
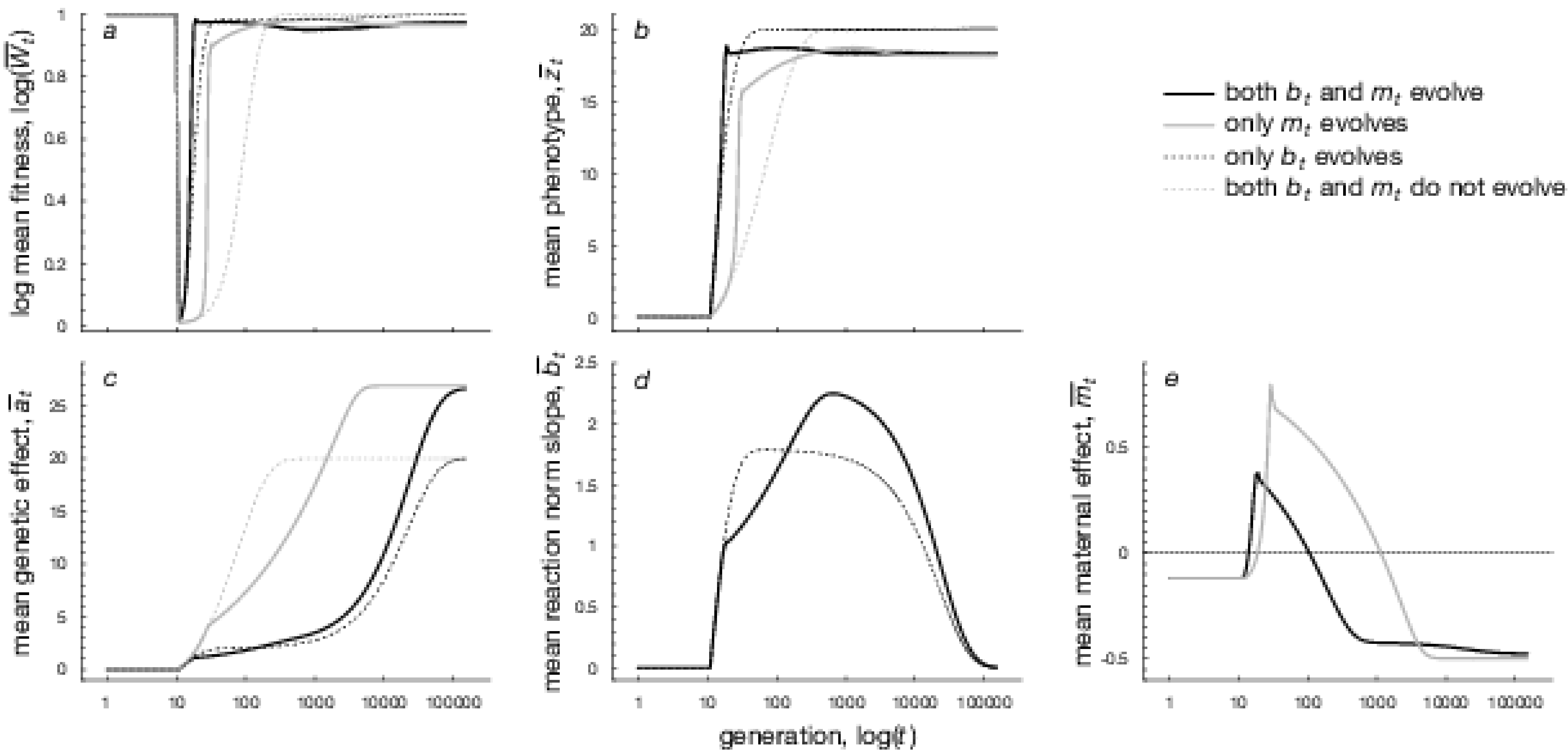
Details are technically messy, involving updates for z_t and its covariances and variance, but more or less tractable

Extraordinary new environment (unpredictable)



- maternal effect coefficient initially negative, evolves to be positive at environmental shift, and then back to negative at long times

Extraordinary new environment (unpredictable)



- fitness returns quicker if both plasticity and maternal effects present, but long-term fitness is better with plasticity only

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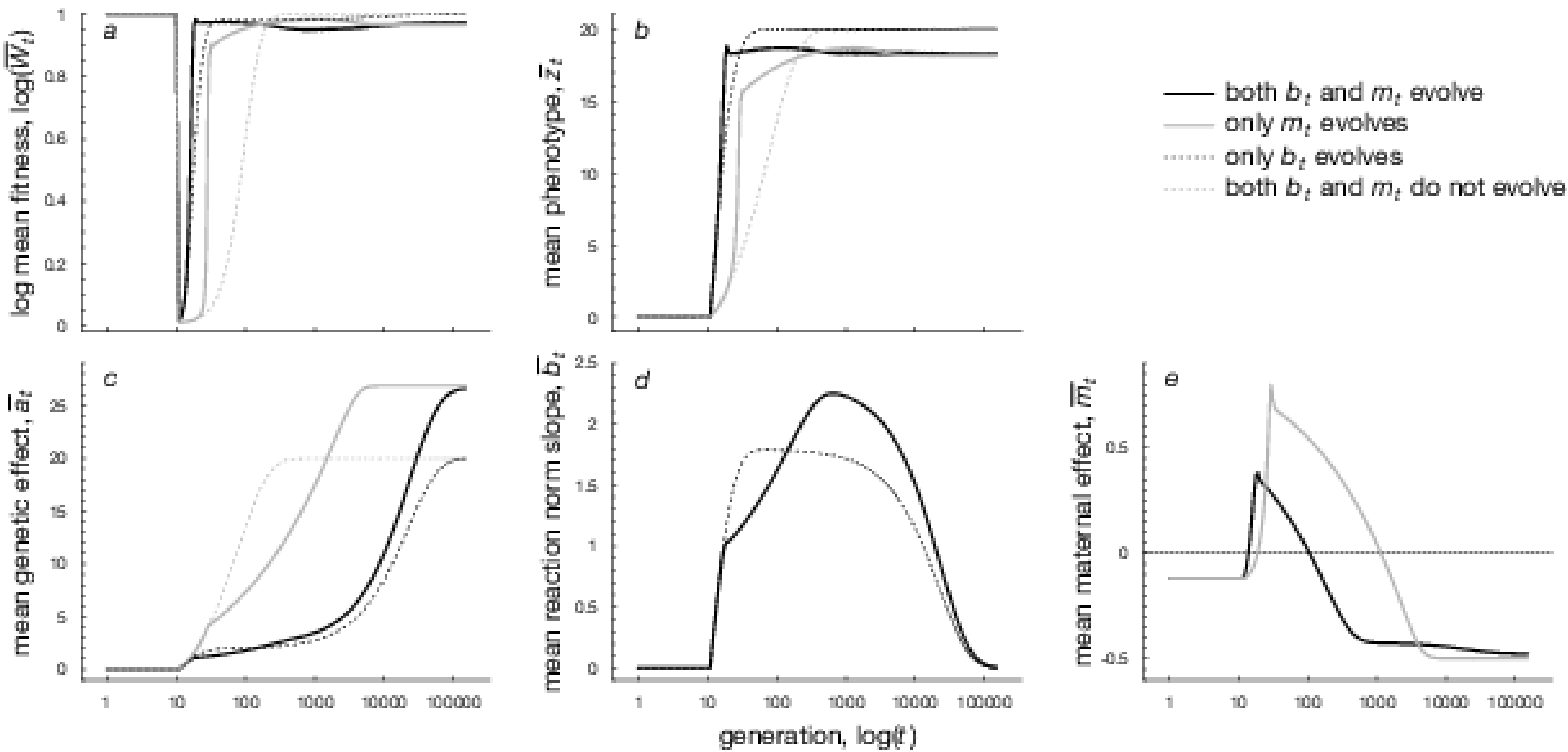
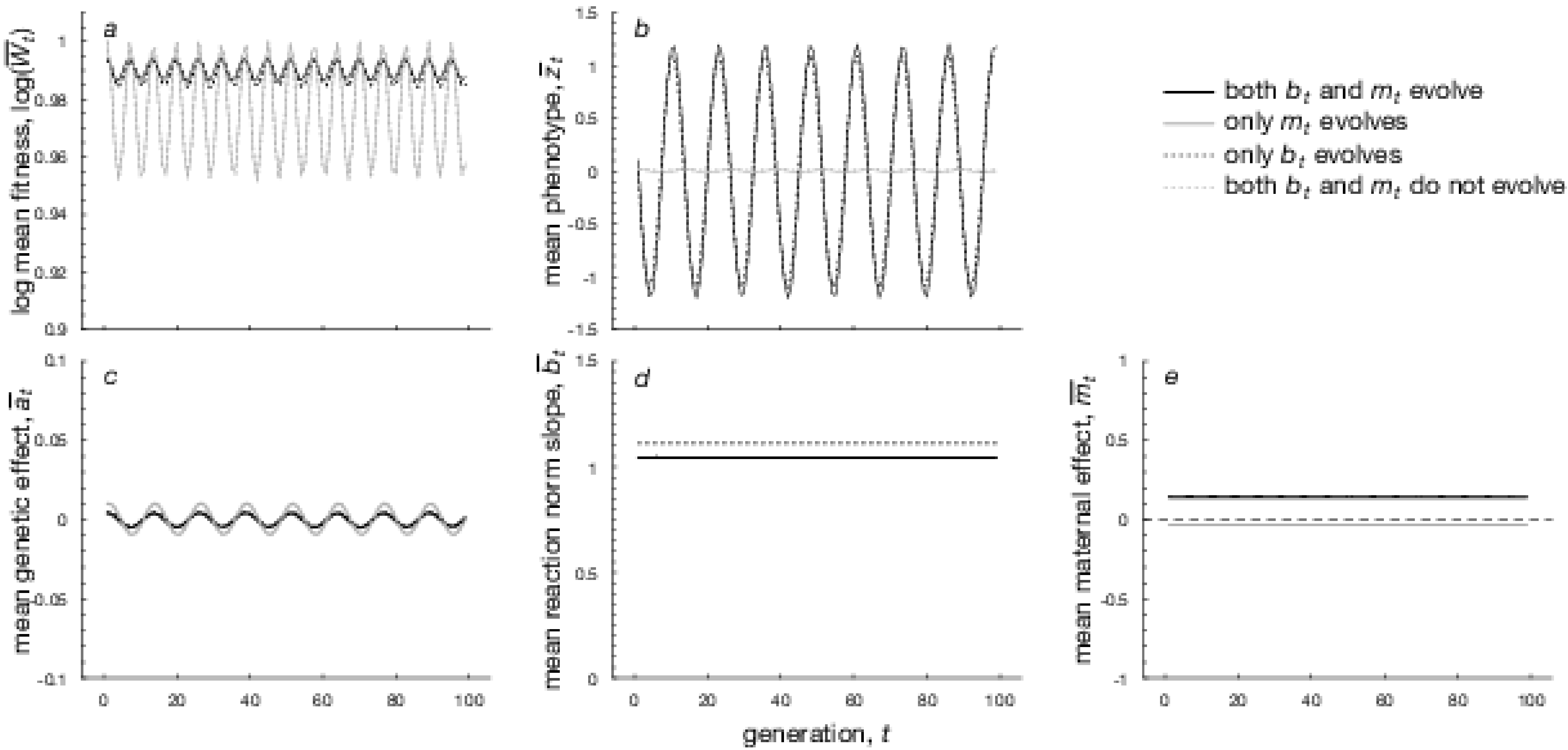


- plasticity evolves to larger values if maternal effects also present
- additive genetic component evolves to larger values if maternal effects present

Sinusoidal environment (predictable)



- maternal effects larger (and positive) when plasticity also present
- plasticity smaller when maternal effects present

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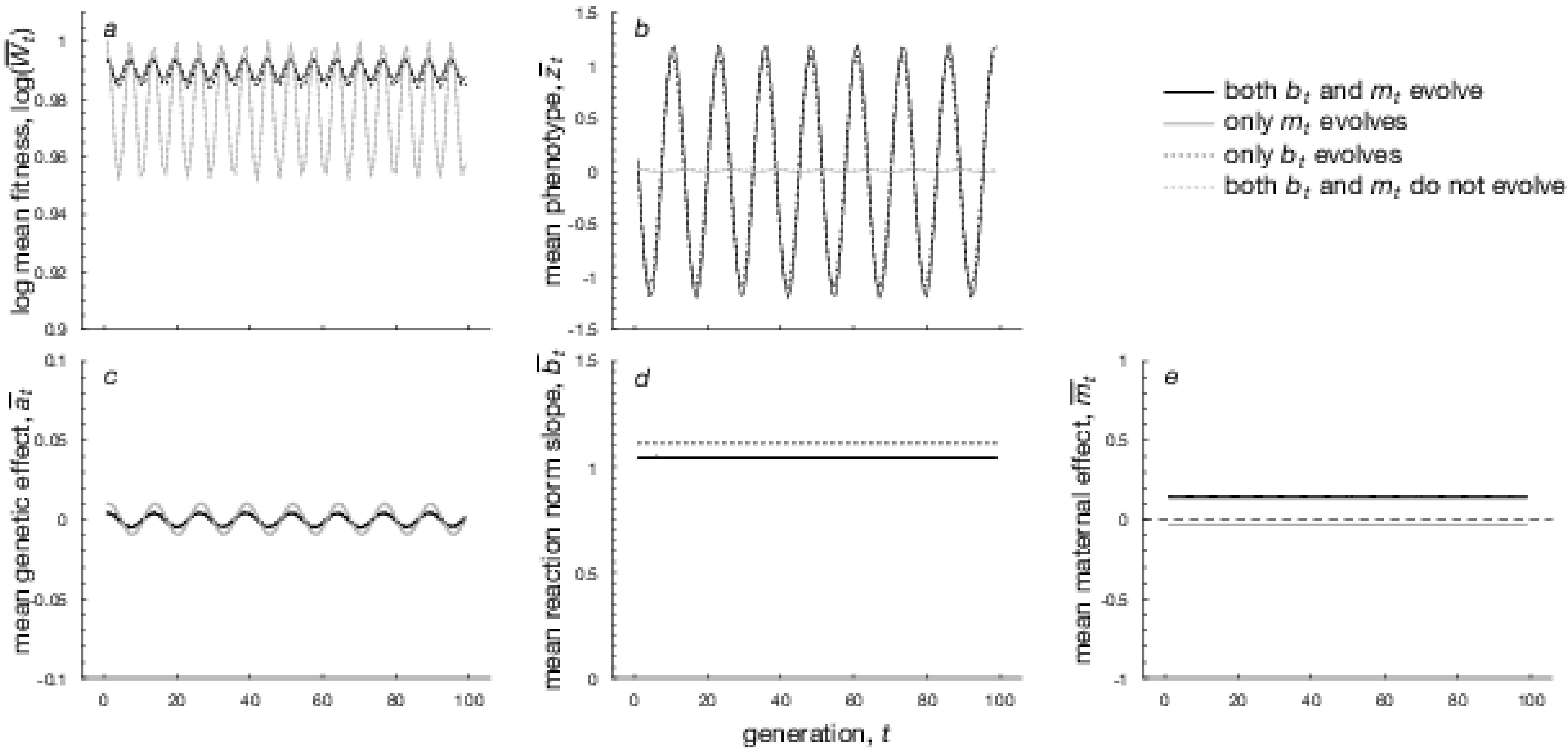
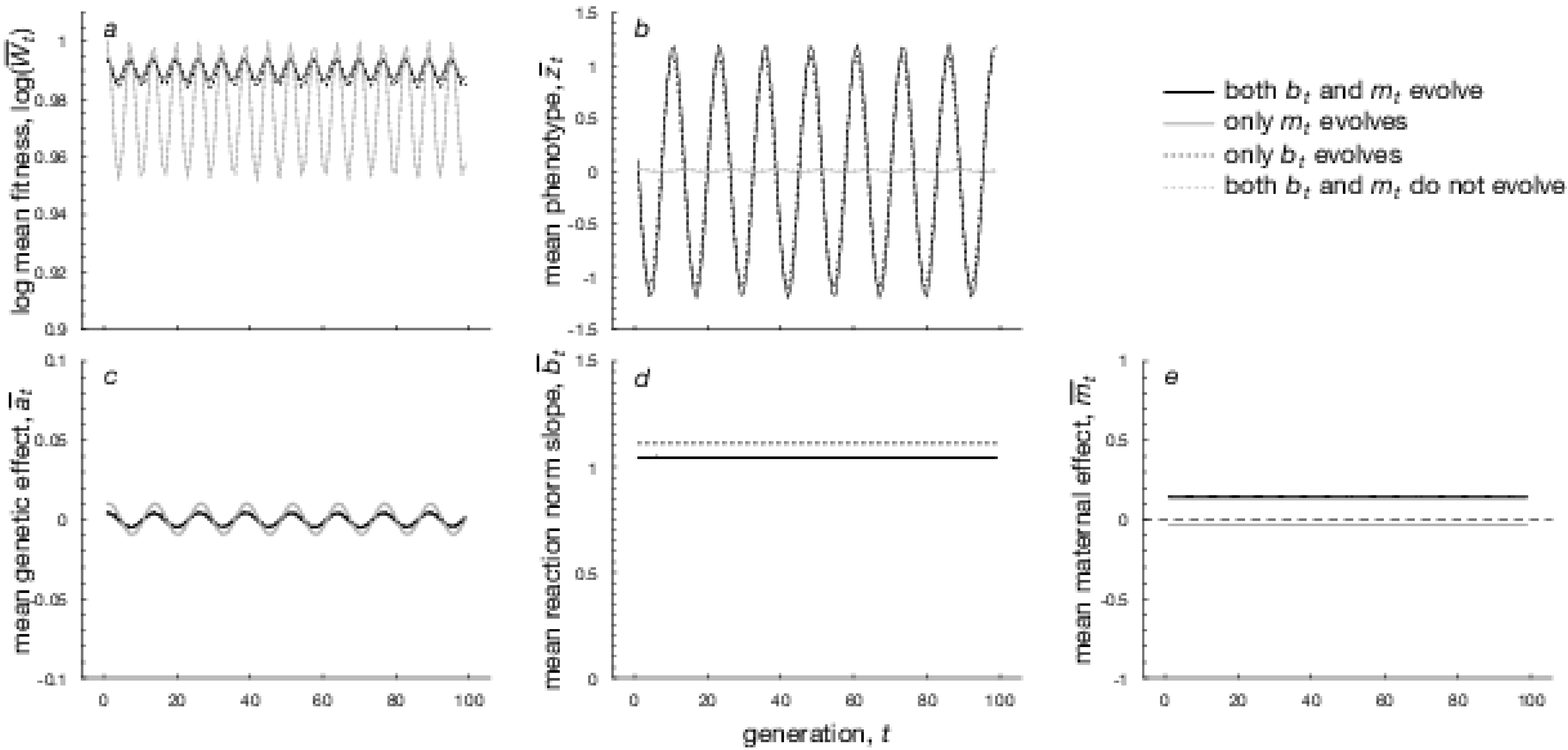


- additive genetic component smaller in presence of plasticity

Sinusoidal environment (predictable)



- mean fitness highest when both plasticity and maternal effects present

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Maternal effects evolve to be positive at environmental shift and then back to negative when the change is complete

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- Maternal effects evolve to be positive at environmental shift and then back to negative when the change is complete
- When change is predictable, then a mixture of maternal effects and phenotypic plasticity is optimal
- Maternal effects and phenotypic plasticity may each facilitate the evolution of the other

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