

# To adapt and persist in a changing environment

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## Introduction

- Habitats are undergoing unprecedented rates of fragmentation and change
- Isolated populations respond to a changing environment by altering both traits and abundance<sup>1</sup>
- Very few models incorporate the responses of both traits and abundances<sup>2</sup>
- By including both we capture the nature of the race: hurry up and adapt before you go extinct<sup>3</sup>

## Evolutionary rescue

- Maladapted populations will rapidly decline to extinction if they do not evolve
- Populations which evolve fast enough to prevent extinction are ‘rescued’ by evolution<sup>2</sup>

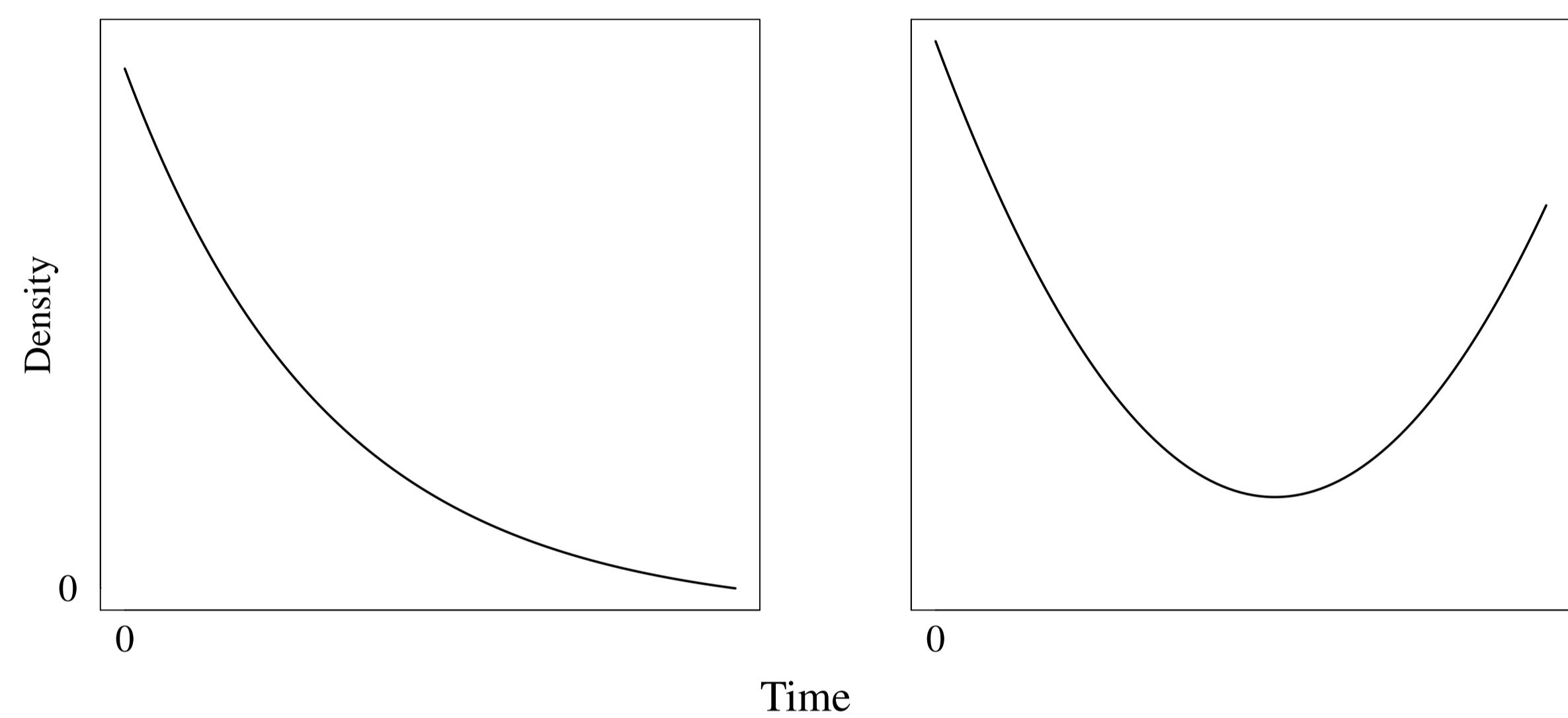


Figure 1. A change in environment at time 0 causes abundances to decline. Extinction occurs if adapted individuals do not increase fast enough (left panel). If, however, adapted individuals are able to propagate fast enough, the population can persist (right panel)<sup>4</sup>.

- Evolutionary rescue may be important with global climate change
- E.g., with ever-earlier springs, can birds adjust their date of egg-laying fast enough to persist?<sup>5</sup>

## Box 1. the Math

The rate of evolution for an asexual population is  $\frac{ds}{dt} = \frac{\mu\sigma_\mu^2}{2} p(\bar{s}, s_{opt})g(\bar{s}, s_{opt})$ , where  $\bar{s}$  is the average trait value,  $s_{opt}$  is the optimal trait value,  $\frac{\mu\sigma_\mu^2}{2}$  is the supply rate of beneficial mutations,  $p(\bar{s}, s_{opt})$  is the population abundance, and  $g(\bar{s}, s_{opt})$  is the strength of selection<sup>6</sup>.

Assuming mutations are rare we calculate  $p$  and  $g$ , giving

$$\frac{ds}{dt} = \frac{-\mu\sigma_\mu^2 KR(\bar{s} - s_{opt})e^{-(\bar{s}-s_{opt})^2/2\sigma_k^2}}{2\sigma_k^2}.$$

And we see that the evolution halts  $\frac{ds}{dt} = 0$  when the population is perfectly adapted  $\bar{s} = s_{opt}$  or infinitely mal-adapted (extinct)  $\bar{s} - s_{opt} = \pm\infty$ .

We can now find the trait value  $\bar{s}^*$  at which the population experiences its maximum rate of evolution by setting  $\frac{\partial}{\partial s} \frac{ds}{dt} = 0$ , which gives  $\bar{s}^* = s_{opt} \pm \sigma_k$ . In other words, when the population’s trait value  $\bar{s}$  lags the optimum  $s_{opt}$  by  $\sigma_k$  the rate of evolution is maximal, and we can compute this maximum,

$$\frac{ds}{dt} \Big|_{max} = \frac{\pm\mu\sigma_\mu^2 KR}{\sigma_k\sqrt{e/2}}.$$

## Questions

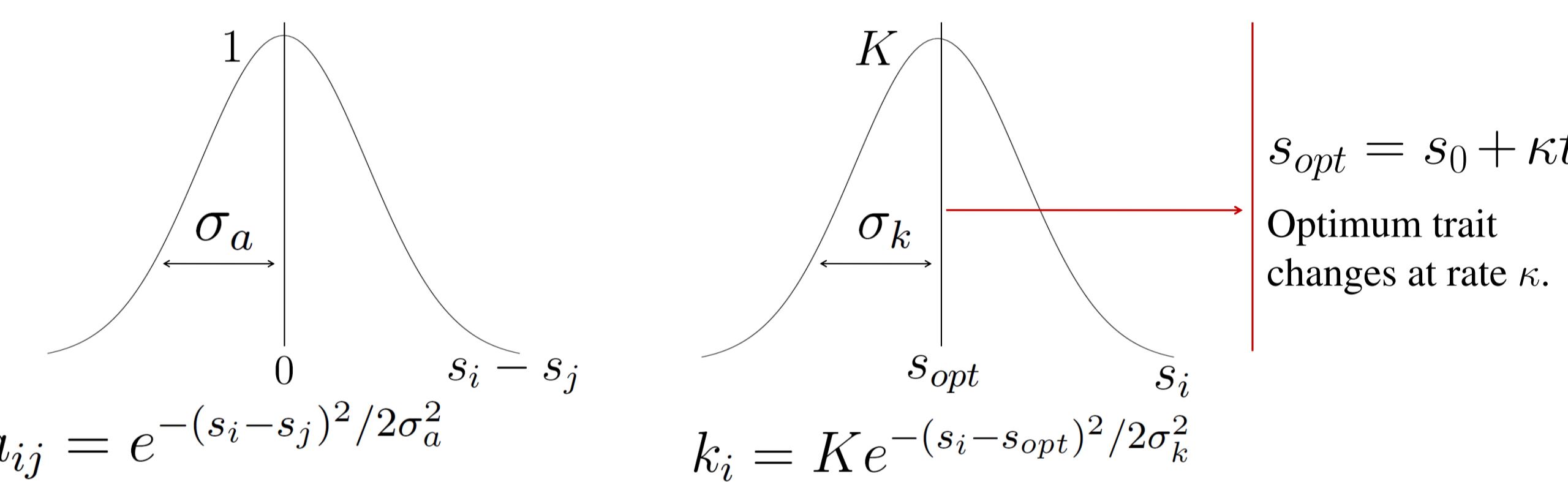
- What is the maximum rate of environmental change a population can withstand?
- Which aspects of a population does this maximum rate depend on?

## Model

- We model the evolution and abundance of a population as the environment changes gradually
- Abundance  $p_i$  of phenotype  $i$  grows logistically and experiences Lotka-Volterra competition:

$$\frac{dp_i}{dt} = p_i R \left(1 - \frac{1}{k_i} \sum_{j=1}^P a_{ij} p_j\right)$$

- One quantitative trait  $s_i$  determines fitness, through competition  $a_{ij}$  and carrying capacity  $k_i$ :



Trait-dependent competition  $a_{ij}$ ; similar values compete strongest.

Trait-dependent carrying capacity  $k_i$ ; maximum at optimal trait value  $s_{opt}$ .

## Analysis

$$\frac{d\bar{s}}{dt} \Big|_{max} = \frac{\pm\mu\sigma_\mu^2 KR}{\sigma_k\sqrt{e/2}}$$

- To persist, a population must evolve as fast as the environment changes<sup>7</sup>:  $\frac{d\bar{s}}{dt}|_{max} \geq \kappa$
- Maximum rate of evolution increases with:
  - mutation rate  $\mu$
  - mutational variance  $\sigma_\mu^2$
  - population size (carrying capacity)  $K$
  - reproductive rate  $R$
  - strength of stabilizing selection  $\frac{1}{\sigma_k}$

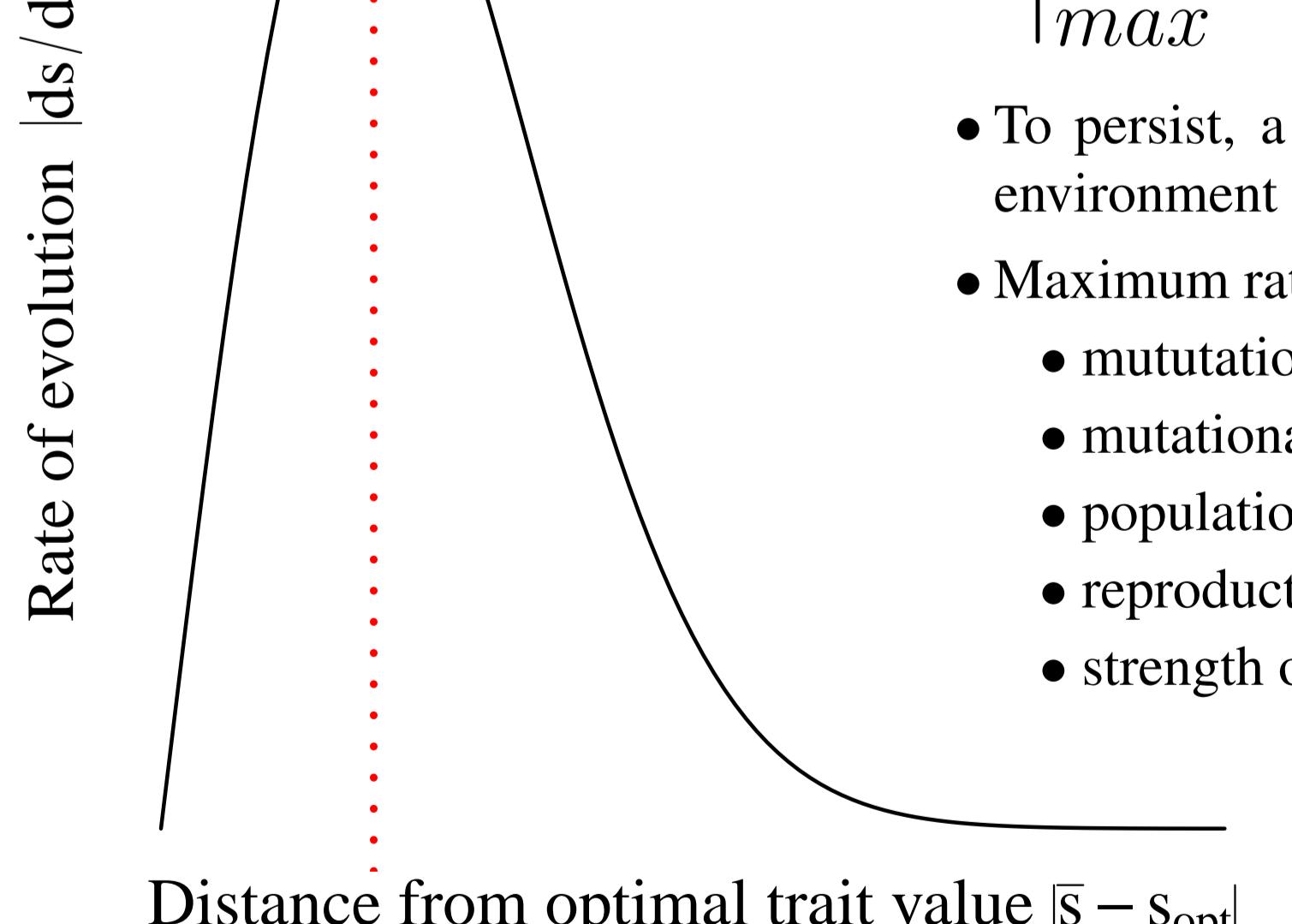


Figure 2. The rate of evolution  $\frac{ds}{dt}$  as a function of the distance from the optimal  $|\bar{s} - s_{opt}|$ . It is maximal  $\frac{ds}{dt}|_{max}$  at an intermediate distance. See Box 1 for details.

## Simulations

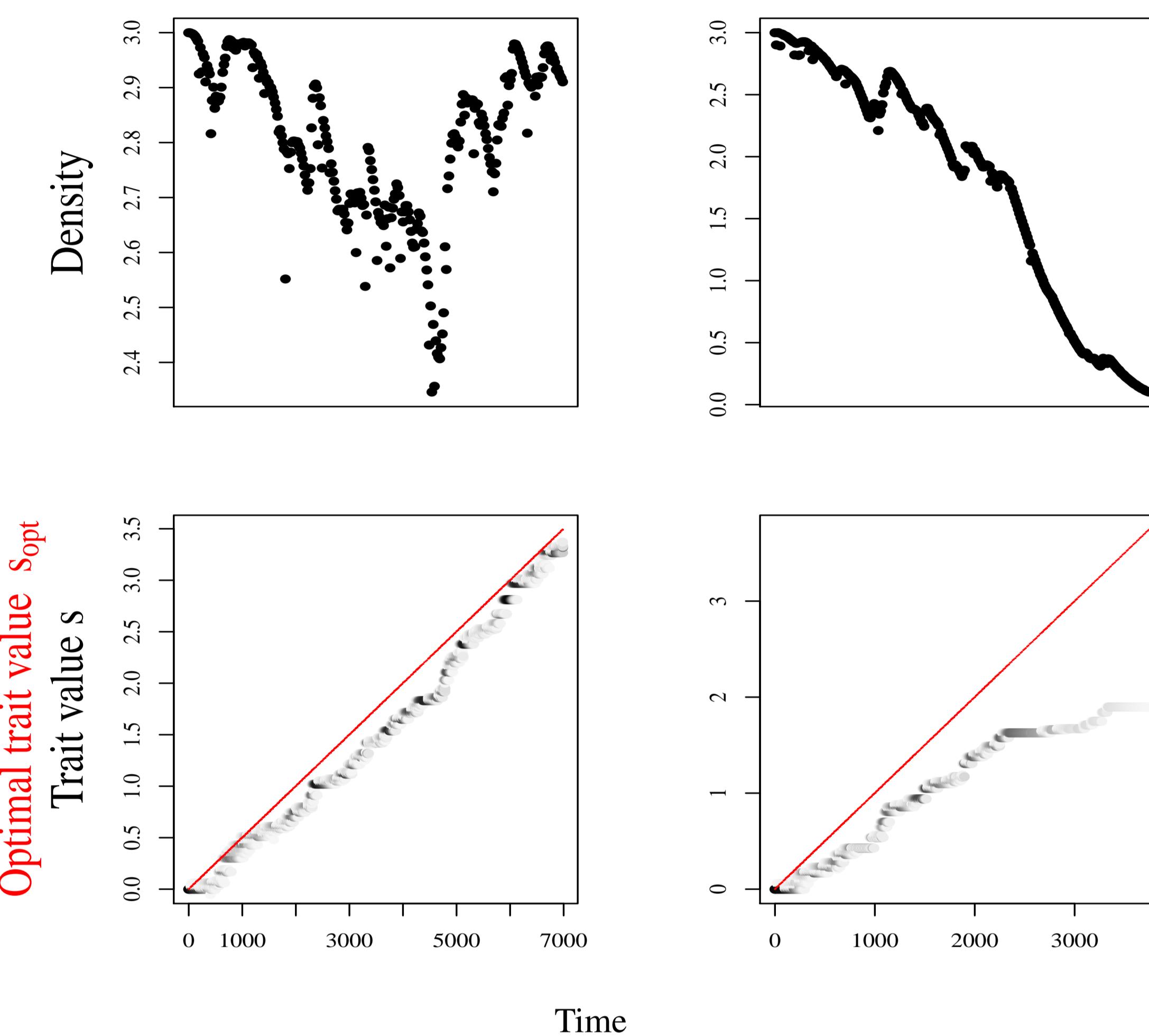


Figure 3. Individual-based simulations corroborate findings: when the maximum rate of evolution is greater than the rate of change in the optimal populations persist ( $\frac{d\bar{s}}{dt}|_{max} > \kappa$ ; left panel), otherwise populations go extinct ( $\frac{d\bar{s}}{dt}|_{max} < \kappa$ ; right panel). Abundance in bottom panel indicated by greyscale; black abundant and white extinct.

## Conclusions

- We have formulated an expression for the maximum rate a population can evolve
- In the long-run, a population must evolve as fast as the environment changes, or go extinct<sup>7</sup>
- Conservation efforts should therefore take the above variables into account when assessing risk

## Directions

- Compare maximum rate of evolution with quantitative genetic models<sup>8,9,7,10</sup>
- Test predictions with experiment: expose yeast to increasing salt concentrations<sup>2</sup>
- Examine extinction risk when the environment changes abruptly

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