

# How much does evolution delay doom?

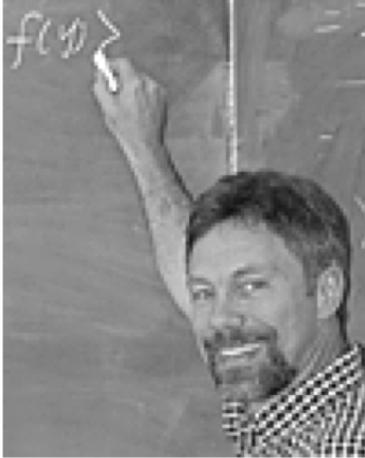
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11 February 2020

# Collaborators



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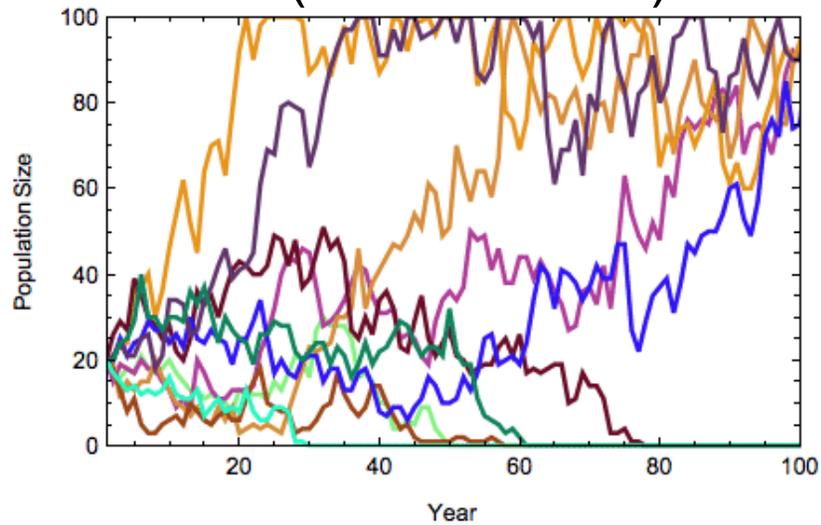
## References

- Gomulkiewicz, Krone, & Remien. 2017. *Evolutionary Applications* 10:471-484.
- Bull, Krone, & Remien. 2019. *PeerJ* 7:e7921 <http://doi.org/10.7717/peerj.7921>

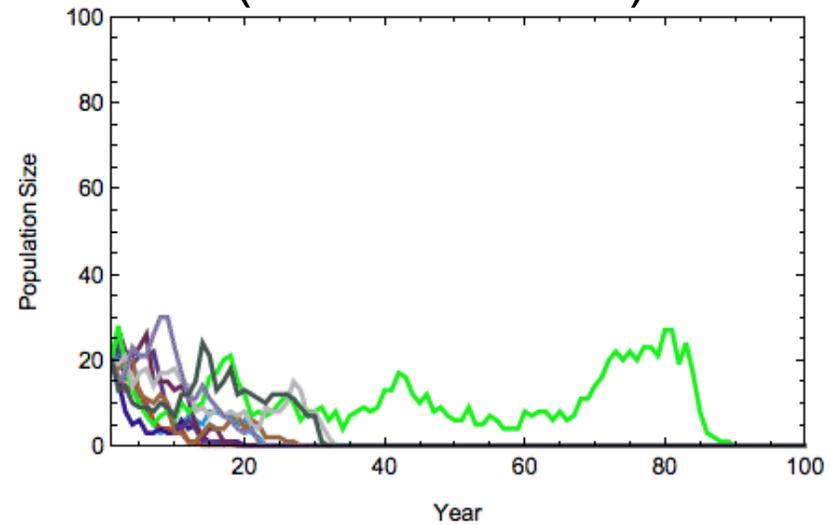
# Rescue vs Doom

$$X_{t+1} = (1 + r)X_t + \text{noise}$$

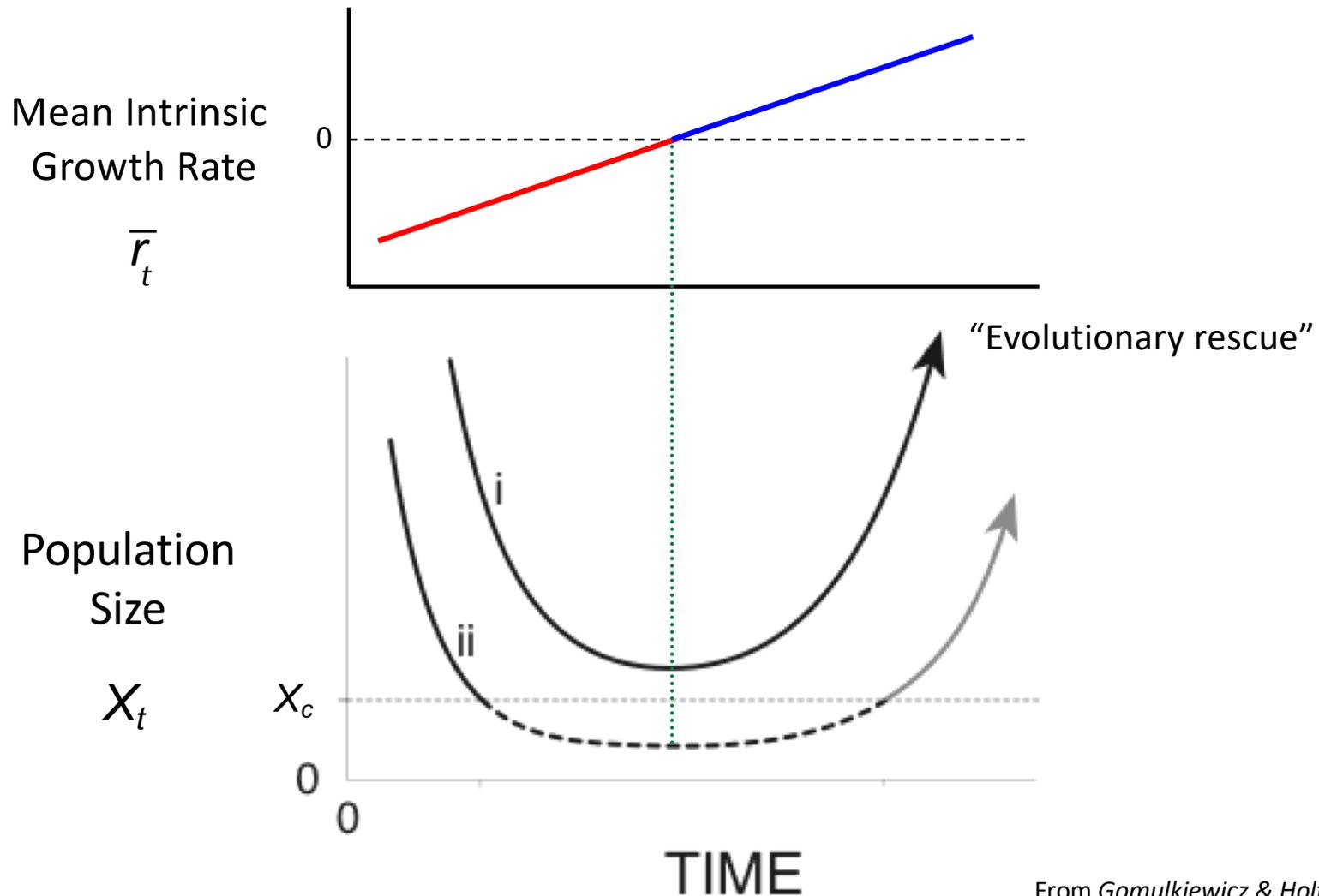
$r > 0$   
(births > deaths)



$r < 0$   
(births < deaths)



# Can the Doomed be Rescued by Evolution?





## The probability of evolutionary rescue: towards a quantitative comparison between theory and evolution experiments

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Guillaume Martin<sup>1,2</sup>, Robin Aguilée<sup>1,2</sup>, Johan Ramsayer<sup>1,2</sup>, Oliver Kaltz<sup>1,2</sup>  
and Ophélie Ronce<sup>1,2</sup>

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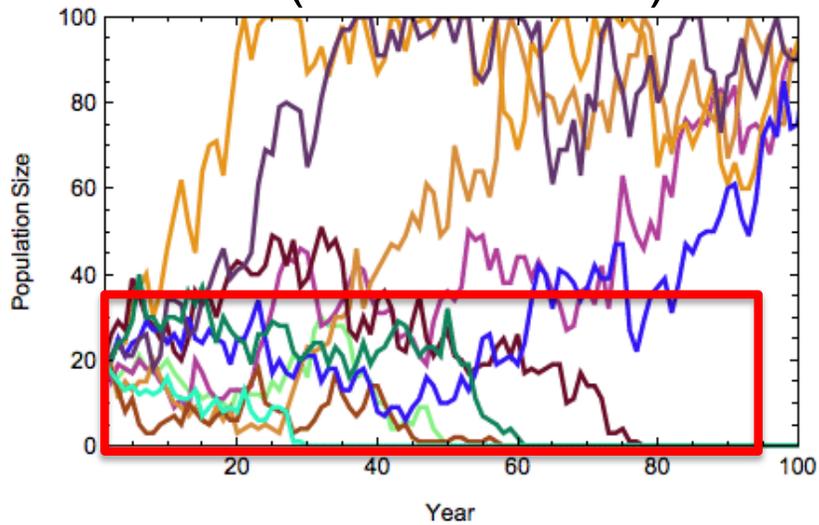
<sup>1</sup>Université Montpellier 2, and <sup>2</sup>CNRS, IRD Institut des Sciences de l'Évolution, CC 065, Place Eugène Bataillon, 34095 Montpellier Cedex 05, France

*“Measuring the probability of rescue is not that straightforward. First, **one must choose the time period over which populations can be said to be either doomed or rescued.**”(2013)*

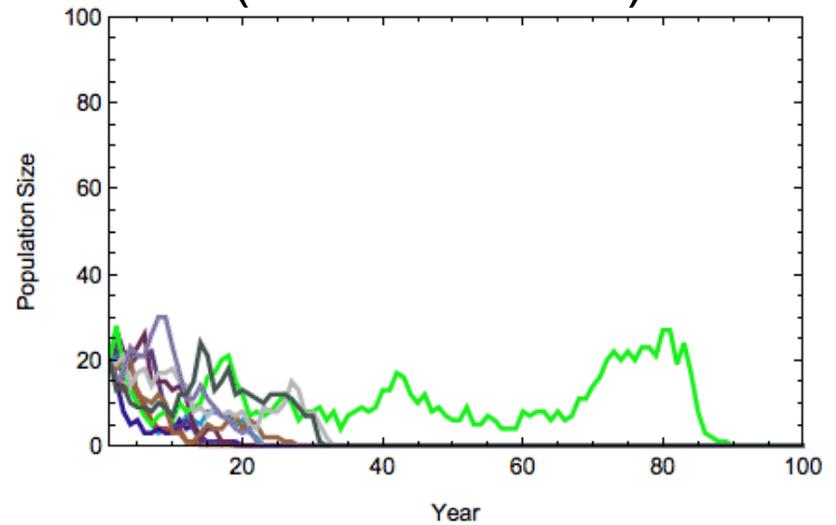
# Time to Doom

$$X_{t+1} = (1 + r)X_t + \text{noise}$$

$r > 0$   
(births > deaths)



$r < 0$   
(births < deaths)



# Questions

1. What is the distribution of time to extinction for evolving populations?
2. How does this distribution depend on genetic diversity and abundances?
3. How does adaptive evolution affect the longevity of populations headed to extinction?

# Adaptive Evolution & Time to Extinction

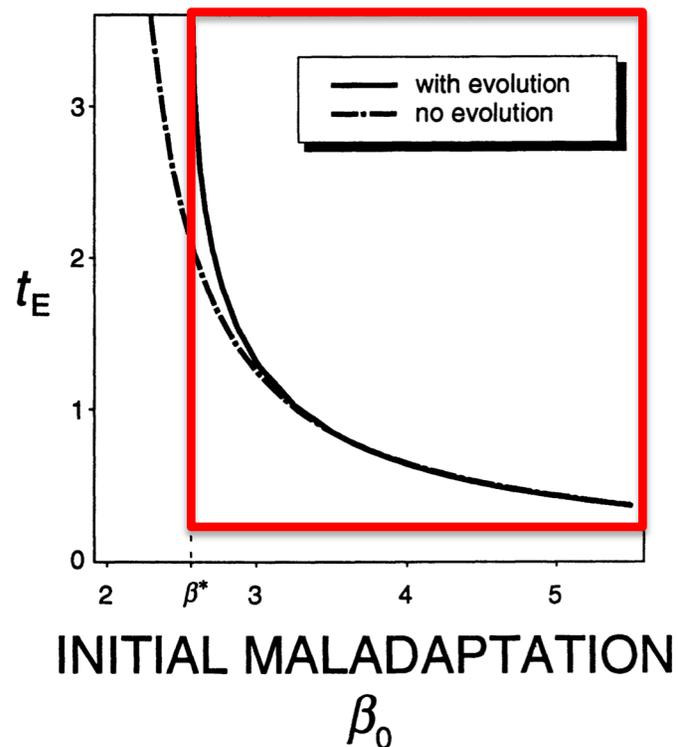
*Evolution*, 49(1), 1995, pp. 201–207

## WHEN DOES EVOLUTION BY NATURAL SELECTION PREVENT EXTINCTION?

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## Basic Model of Demography & Evolution

- ▶  $G$  clones
- ▶  $X_i(t) \geq 0$  is **density** of clone  $i$  at time  $t$  ( $i = 1, \dots, G$ )
- ▶ Each  $X_i$  an independent *continuous branching* diffusion
- ▶ Genotype  $i$  characterized by **intrinsic growth rate**  $r_i$  & **reproductive variance**  $v_i$
- ▶ Genotype dynamics described by *stochastic differential equation* and initial condition

$$dX_i = r_i X_i dt + \sqrt{v_i X_i} dW_i$$

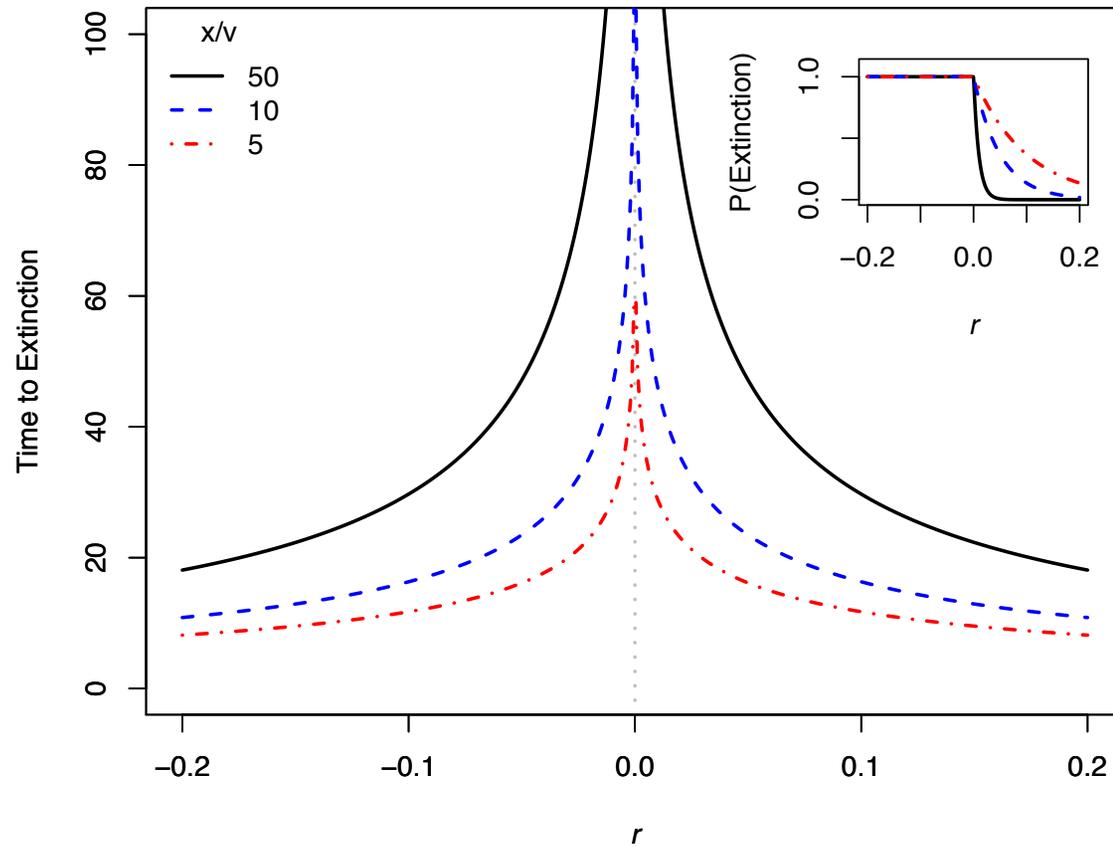
$$X_i(0) = x_i$$

## Genetically Uniform Populations

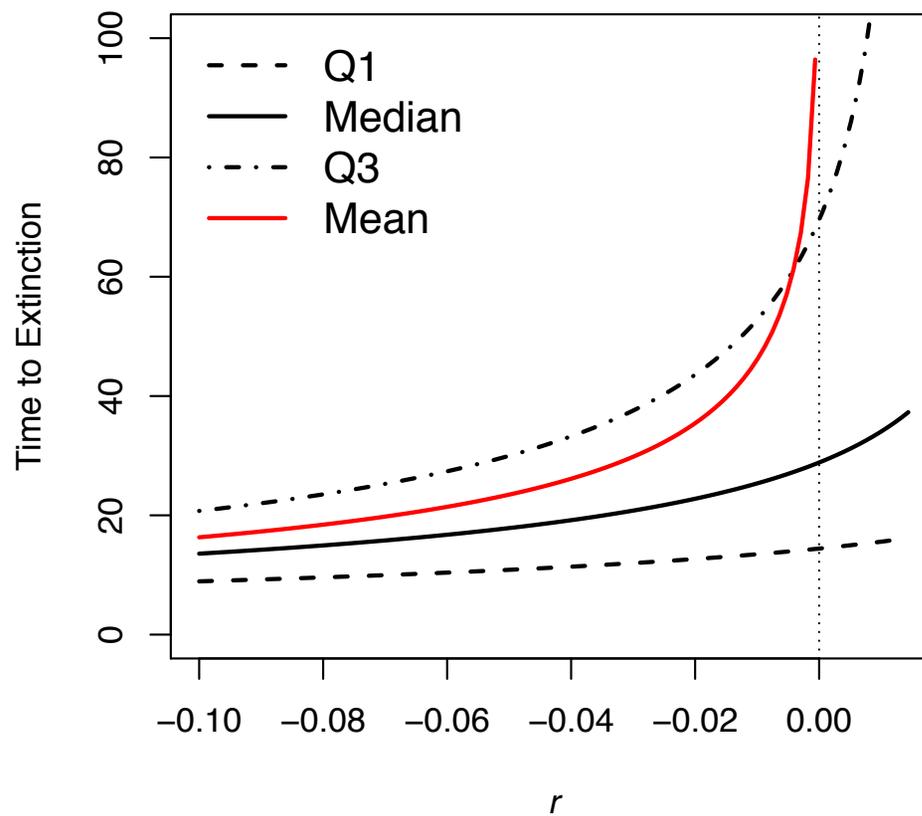
- ▶ Population monomorphic for genotype with growth & variance parameters  $g = (r, v)$
- ▶ Dynamics:  $dX = rXdt + \sqrt{vX}dW$
- ▶ Initial density  $X(0) = x$
- ▶ P(extinct at time  $t$ ) =  $[f(t; g)]^x$
- ▶ *Genotypic Risk Function:*

$$\ln f(t; g) = \begin{cases} -2r / [v(1 - e^{-rt})] & \text{if } r \neq 0 \\ -2/(vt) & \text{if } r = 0. \end{cases}$$

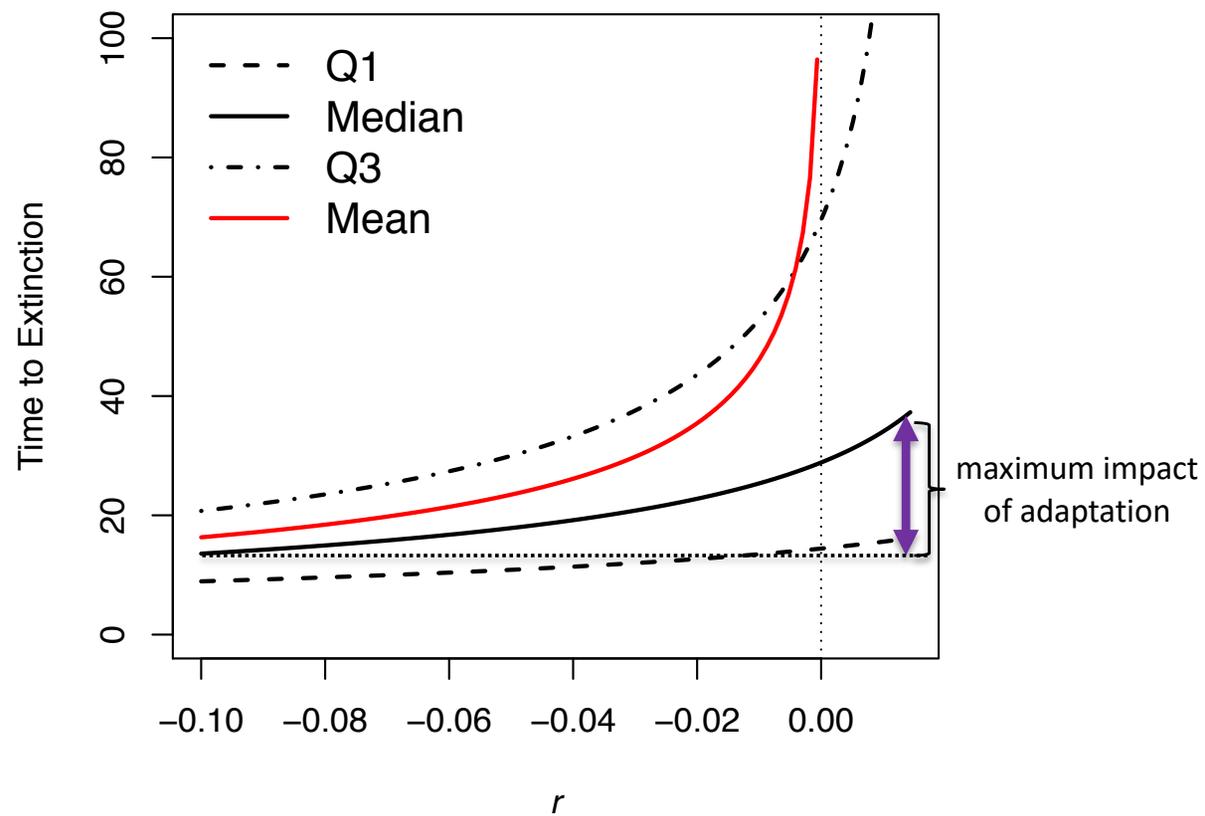
# Conditional Mean Time to Extinction: No Evolution



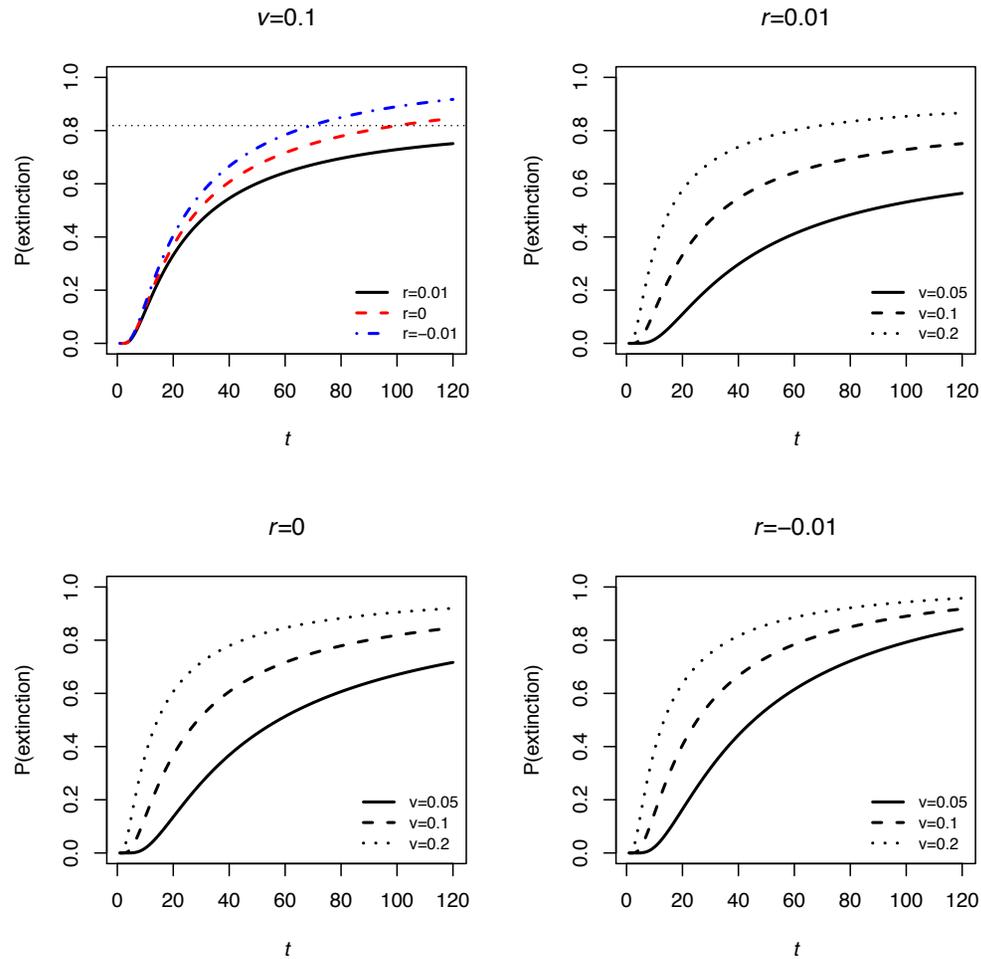
# Extinction Time Percentiles: No Evolution



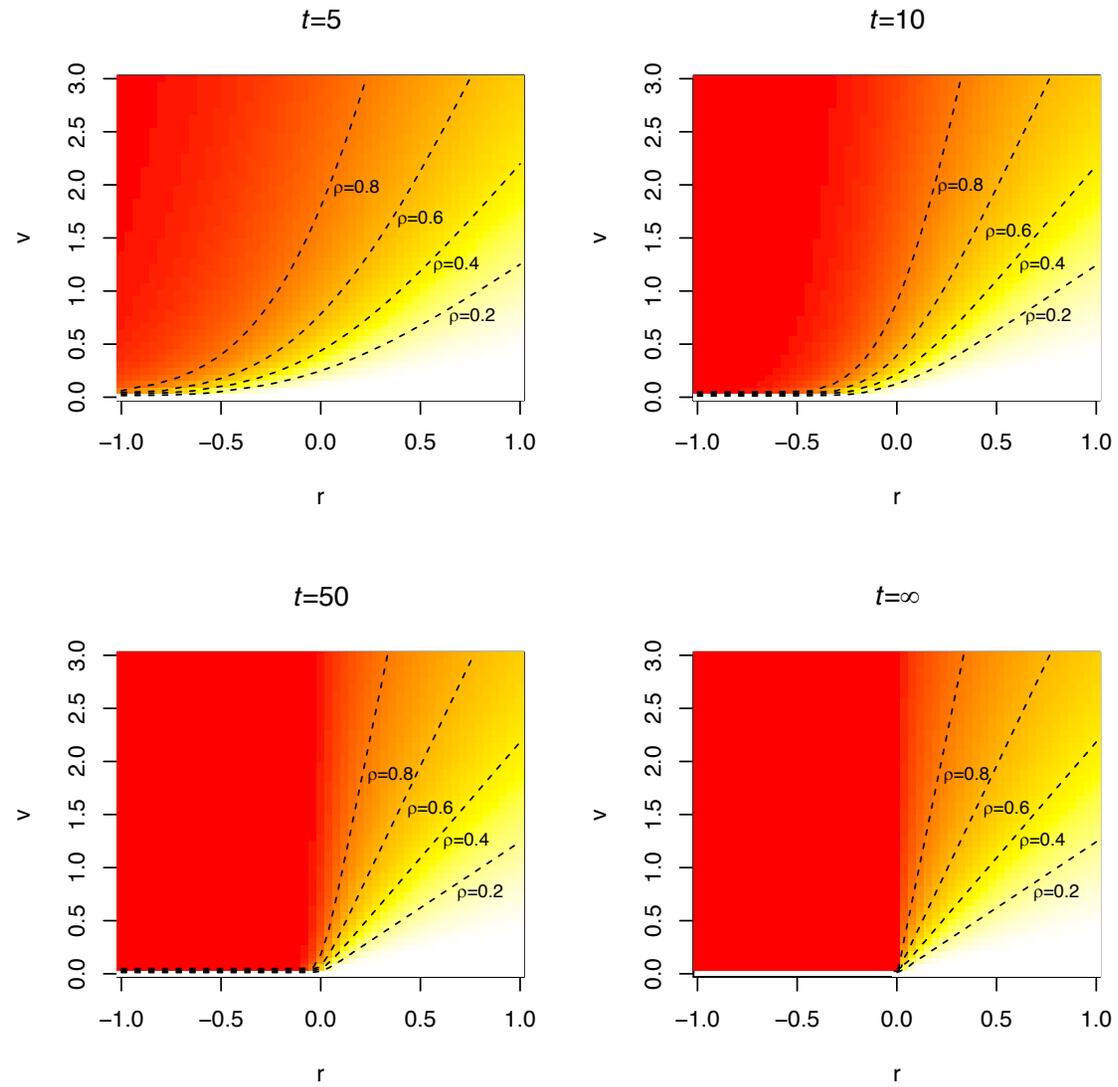
# Extinction Time Percentiles: No Evolution



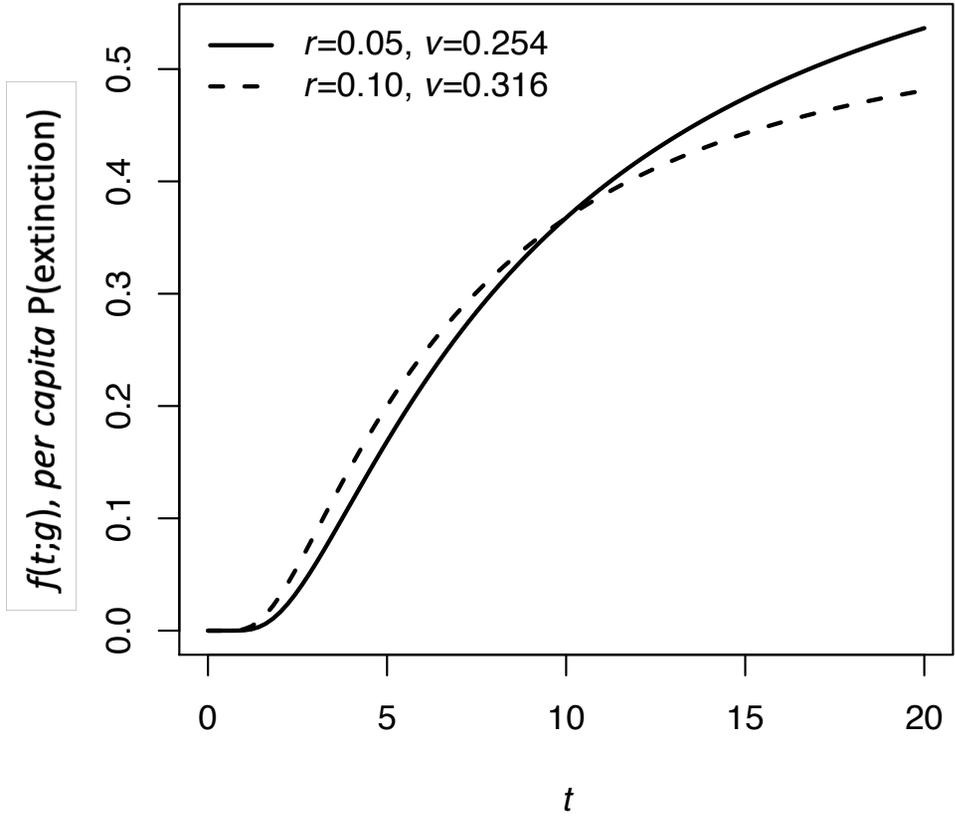
# Genotypic Risk Functions, $f(t;g)$



# “Maladaptive” Landscapes



# Genotypic Risks over Time



## Polymorphic Populations

- ▶ Genotypes:  $g_i = (r_i, v_i)$
- ▶ Initial densities:  $X_i(0) = x_i$
- ▶ Genotypic risk functions:

$$\ln f(t; g_i) = \begin{cases} -2r_i / [v_i (1 - e^{-r_i t})] & \text{if } r_i \neq 0 \\ -2 / (v_i t) & \text{if } r_i = 0. \end{cases}$$

- ▶  $P(\text{extinct at time } t) = \prod_{i=1}^G [f(t; g_i)]^{x_i}$

# Three Types of Change

*Polymorphic analysis key result:* abundance, genetic diversity, vital rates have distinct effects

## 1. Genetic Diversity

- change diversity without changing *total* abundance or individual vital rates
- e.g., mutation

## 2. Vital Rates

- changes in environment that enhance or impair survival & reproduction

## 3. Abundance

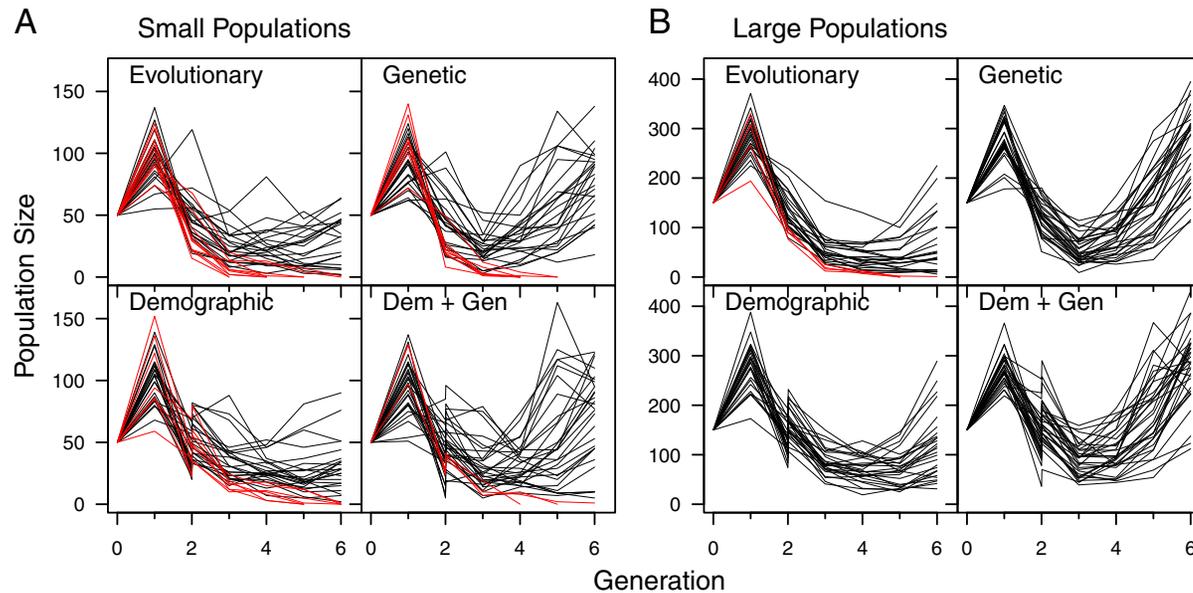
- supplementation
- removal

# Three types of rescue can avert extinction in a changing environment

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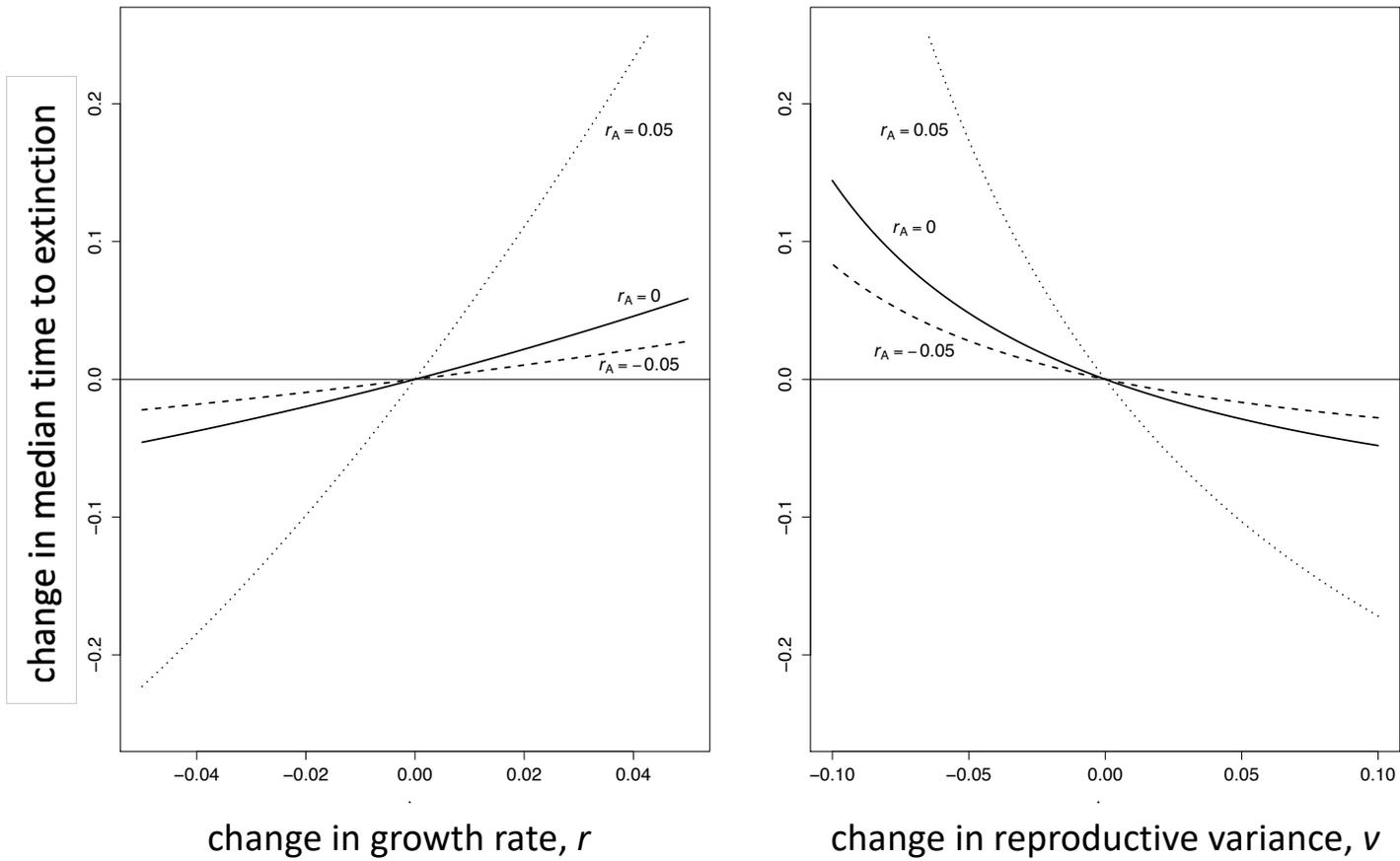
Edited by James H. Brown, University of New Mexico, Albuquerque, NM, and approved July 7, 2015 (received for review March 8, 2015)



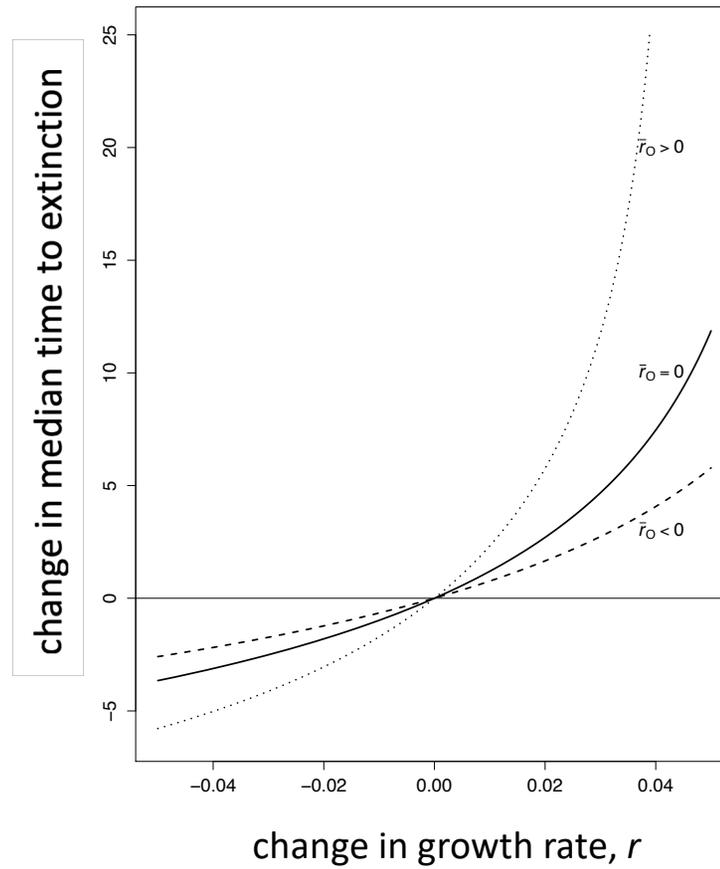
# 1. Change Genetic Diversity

- Genetically uniform “ancestral” population
  - density  $x$
  - growth parameters  $r$  and  $v$
- Substitution/Mutation
  - replace  $x^*$  individuals with mutant genotype
- Hufbauer et al. *Tribolium* experiments
  - ancestral  $r < 0$
  - “mutant”  $r^* > 0$
  - small populations:  $x^* = 1$
  - large populations:  $x^* = 3$

# Impact of Novel Mutation



## 2. Impact of Abrupt Environment Change



### 3. Impacts of Abundance Change

- *Supplementation*: add density  $y_i$  of genotype with growth parameters  $r_i$  and  $v_i$ ,  $i = 1, \dots, G$ 
  - Hufbauer et al.:
    - $r^* > 0$
    - $y^* = 1$  (small populations)
    - $y^* = 3$  (large populations)
  - Conservation/management goal: ensure  $\Pr(\text{extinction})$  no more than  $\phi$  at time  $\tau$
- *Removal*: remove density  $z_i$  of genotype with growth parameters  $r_i$  and  $v_i$ ,  $i = 1, \dots, G$ 
  - disease management goal: ensure  $\Pr(\text{eradicate})$  at least  $\phi$  at time  $\tau$

## Deliberate Supplementation or Removal

- ▶ Change densities and/or frequencies of genotypes to achieve management goals
  - ▶ Conservation:  $P(\text{extinct before time } \tau) \leq \phi$
  - ▶ Pest/Pathogen:  $P(\text{extinct before time } \tau) \geq \phi$
- ▶ “management gap”:  $S(\phi, \tau, \mathbf{x}) = \log \phi - \sum_{i=1}^G x_i \log f(\tau; g_i)$
- ▶ Additions  $(y_1, y_2, \dots, y_G)$  satisfy

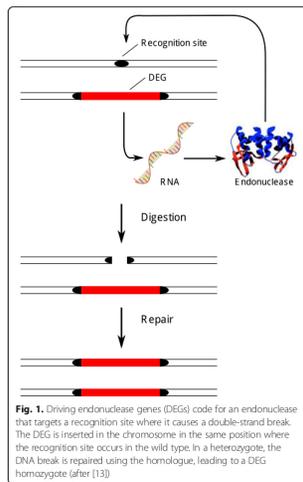
$$\sum_{i=1}^G y_i \log f(\tau; g_i) = S(\phi, \tau, \mathbf{x}) < 0$$

- ▶ Removals  $(z_1, z_2, \dots, z_G)$  satisfy

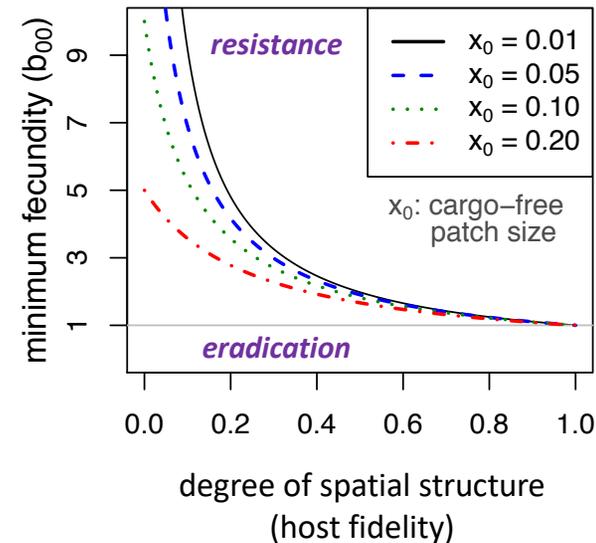
$$\sum_{i=1}^G z_i |\log f(\tau; g_i)| = S(\phi, \tau, \mathbf{x}) > 0$$

# Spatially-structured Gene Drives & Parasite “Doom”

## Drive Endonuclease Genes



Godfray et al. *BMC Biology* (2017) 15:81



- Engineered gene drive eradication effective in well-mixed systems
- Real world has spatial structure
- More opportunities for resistance, but cause for concern?
- Yes, perhaps more than expected
- Model and analysis details: Steve Krone’s Thursday presentation

## Summary of General Findings

- Process-based theoretical framework for predicting time to extinction of evolving populations
  - useful for basic and applied biology (human health, agriculture, conservation)
- Genetic abundances and diversity both affect persistence
  - impacts are distinct but cannot be cleanly separated
- Genotypic risk functions define “maladaptive” landscape
- Prediction: Impact of adaptive evolution on time to extinction is small
  - larger in demographically benign than in harsh conditions
- Spatial structure can undermine parasite eradication by gene drive cargo
  - use models to explore strategies that mitigate gene drive failure

# Merci

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