Evolution of species' range and niche in changing environments

Jitka Polechová

SMTPB at ICERM, 5.6.2026

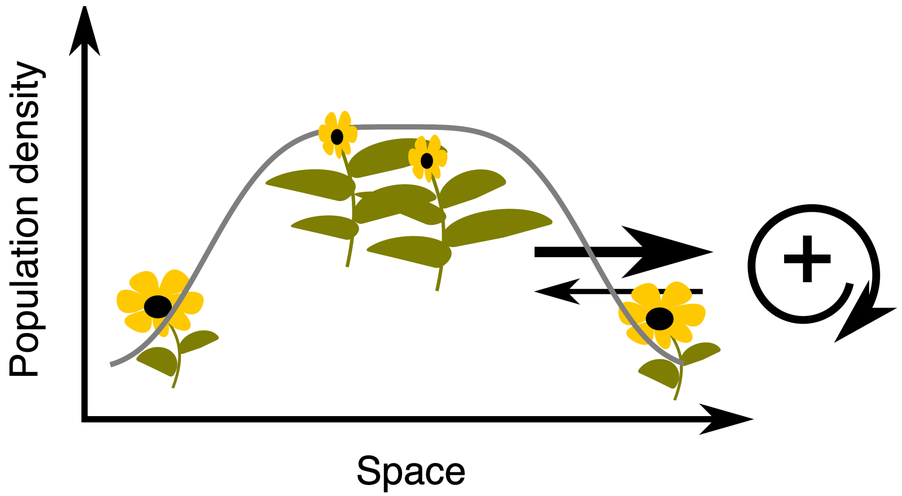
What determines a species' range?

Species' range is determined by a narrow phase of conditions [its ecological niche].

[J. Grinnell (1917): The Niche-Relationships of the California Thrasher. The Auk, 34(4).]

Joseph Grinnell

Limits of adaptation, species' niche and range



"swamping gene flow"

(migrational meltdown)

→ **stable range margin**

?

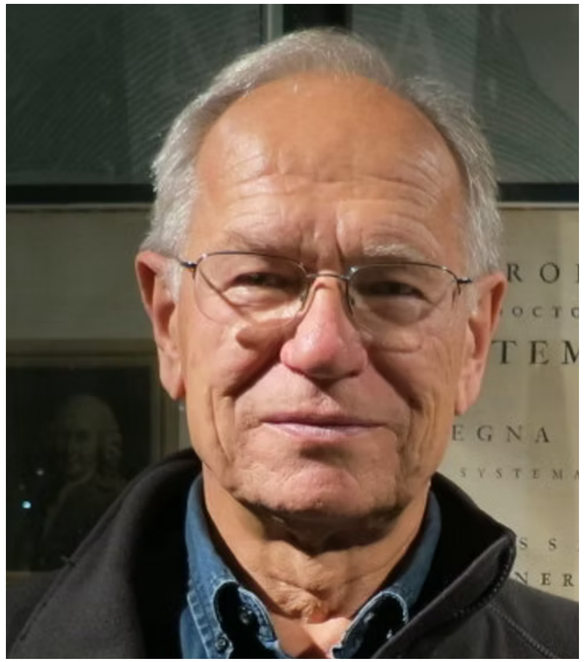
[J.B.S. Haldane (1957): The relation between density regulation and natural selection.]

J.B.S. Haldane (and Aldous Huxley)

Limits of adaptation, species' niche and range

Insufficient genetic variability and the swamping effects of gene flow are inadequate explanations of limits to natural selection.

[J. Antonovics (1976): The nature of limits to natural selection.]



THE NATURE OF LIMITS TO NATURAL SELECTION[1]

JANIS ANTONOVICS[2]

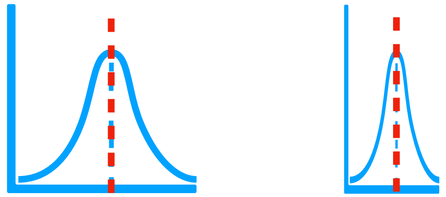
ABSTRACT

Insufficient genetic variability and the swamping effects of gene flow are inadequate explanations of limits to natural selection. Comparison of evolutionary responses in different populations subjected to similar selective forces, comparison of rare and widespread species, and comparison of marginal and central populations are all neglected research areas that bear on the nature of limits to natural selection.

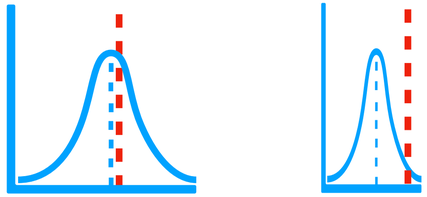
Genetic variance V_G evolves with mutation, selection, dispersal and genetic drift.

↑ genetic variance V_G

$\Longrightarrow$ ↑ standing (variance) load



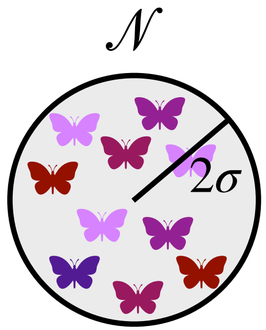
$\Longrightarrow$ ↑ adaptability $\frac{\partial \bar{z}}{\partial t} = V_G \frac{\partial \bar{r}}{\partial \bar{z}}$: ↓ lag load



genetic variance increases with dispersal

↑ dispersal $\Longrightarrow$ ↑ neighbourhood size $\mathcal{N}$ $\Longrightarrow$ ↓ genetic drift

$\mathcal{N} \sim 4\pi N\sigma^2$ .. *Wright (1943): "size of a single panmictic population that would give the same probability of identity-by-descent in the previous generation"*



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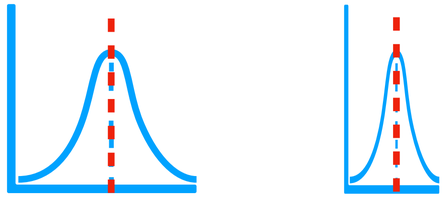

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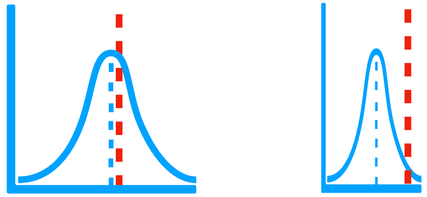
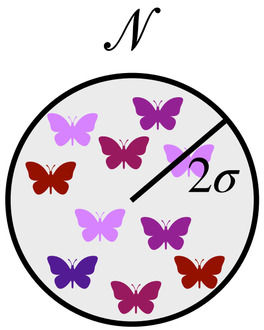
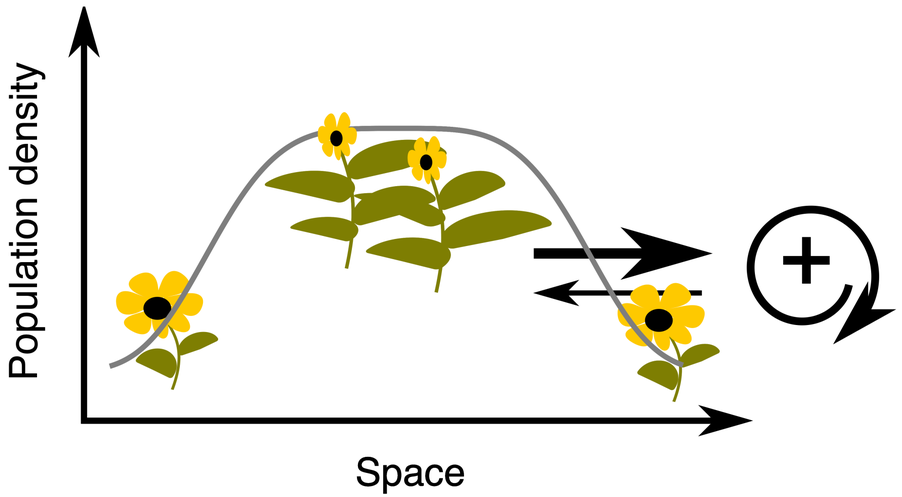


genetic variance increases with dispersal

↑ dispersal $\Longrightarrow$ ↑ neighbourhood size $\mathcal{N}$ $\Longrightarrow$ ↓ *genetic drift*

$\mathcal{N} \sim 4\pi N\sigma^2$ .. *number of individuals within one generation's dispersal range*



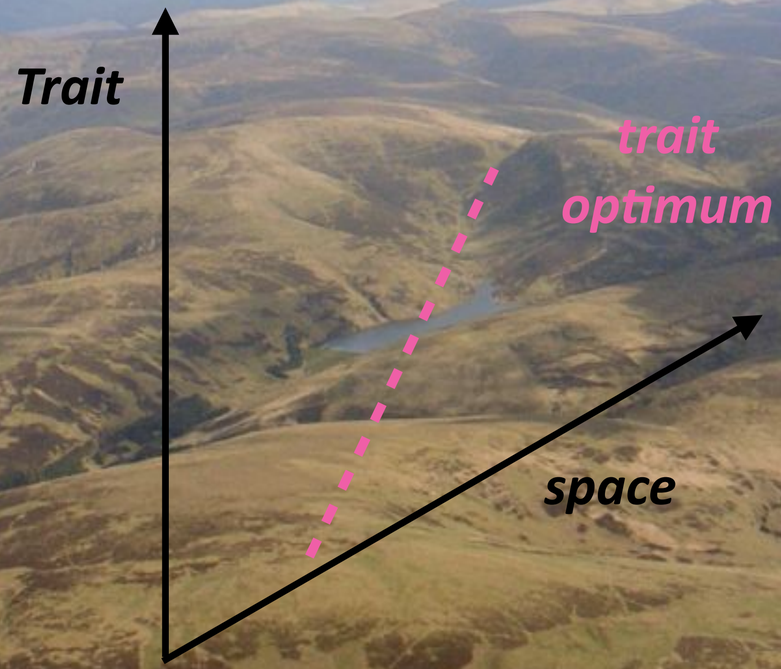


Evolution ↔ **Ecology**

- Adaptation
- Evolution of genetic variance
- Genetic drift

- Population dynamics

- **Species’ range limits: model outline**



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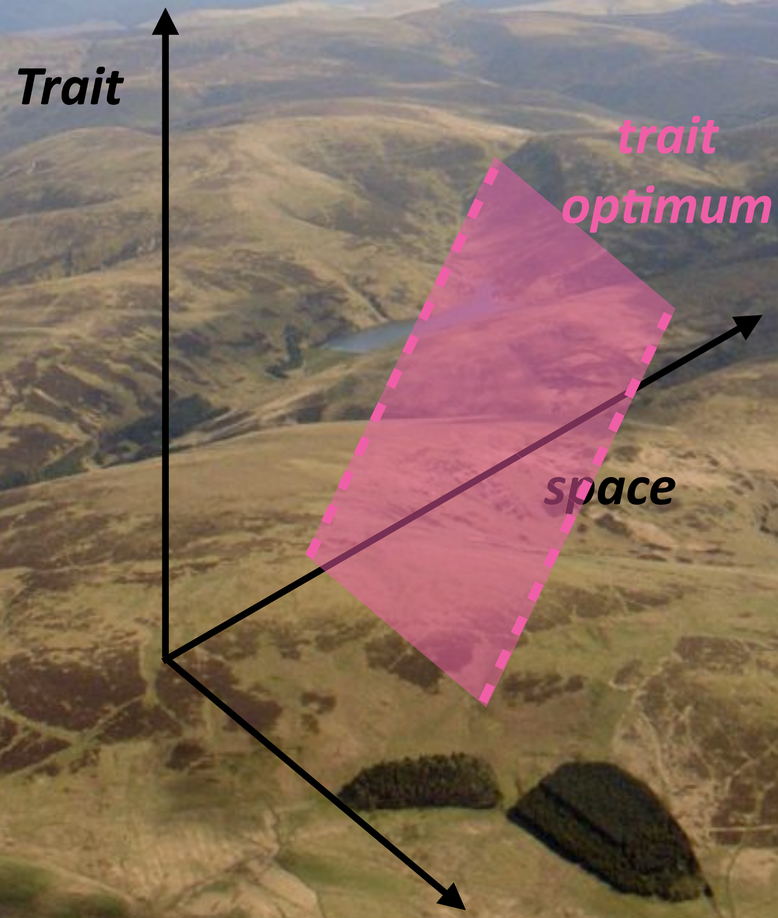

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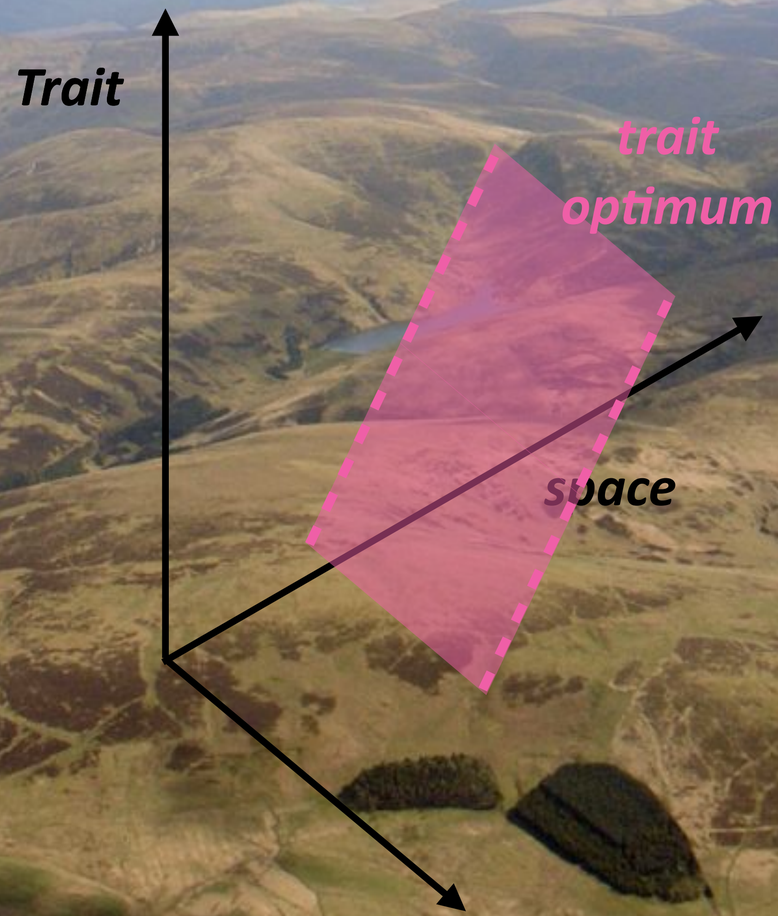


Eco ↔ **Evo** coupling

Population dynamics and evolution are coupled via mean fitness $\bar{\mathbf{r}}$

$q_i = 1 - p_i$

both trait mean $\bar{\mathbf{z}} = \sum \alpha_i p_i$ and genetic variance $V_G \approx \sum \alpha_i^2 p_i q_i$ evolve

Coupling:

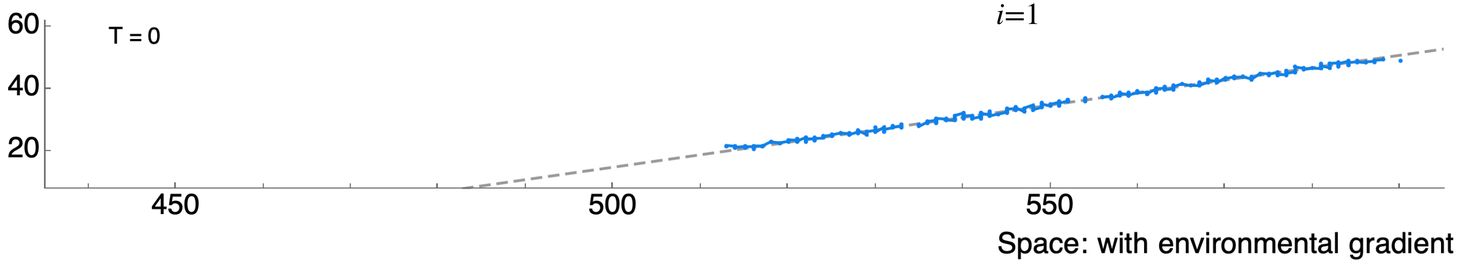
$$\bar{r} = r_m(1 - N/K) - (\bar{z} - \theta)^2/(2V_s) - V_G/(2V_s)$$

standing (variance) load

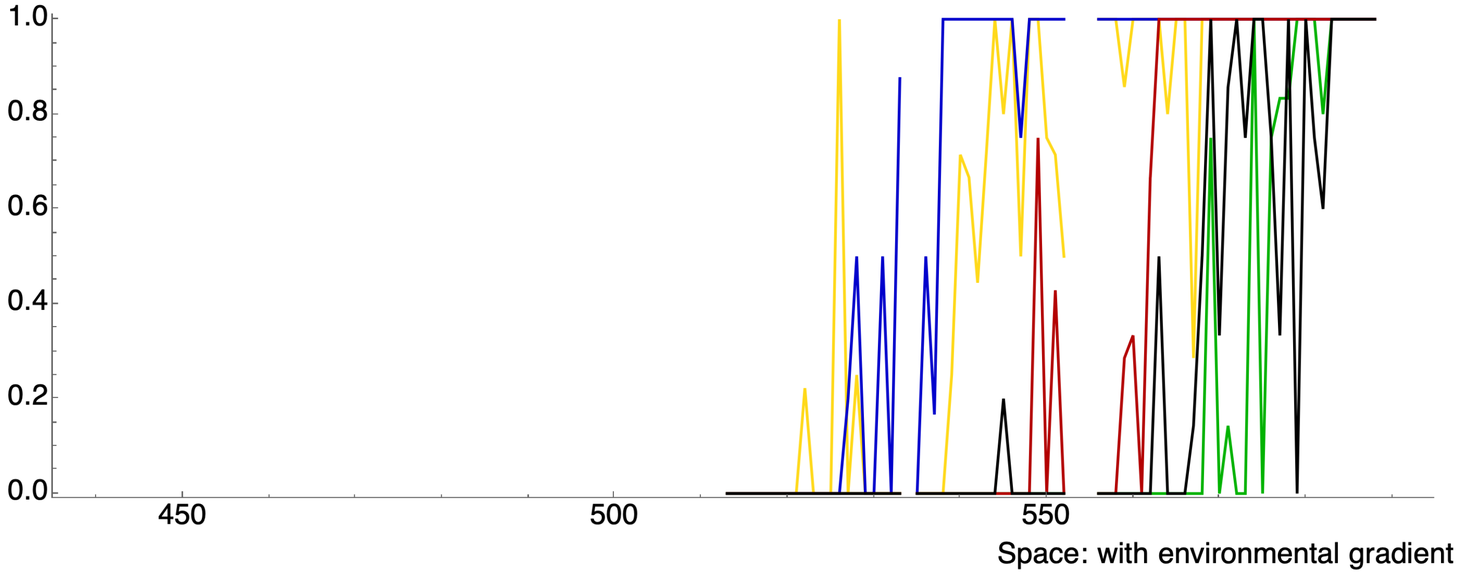
stabilising selection V_s around moving optimum $\theta = b\,x - k\,t$

Evolution: population genetic model

Trait: transect $\bar{z} = \sum_{i=1}^{loci} \alpha_i p_i$



Allele frequencies p_i – clines



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Population dynamics and evolution are coupled via mean fitness $\bar{\mathbf{r}}$

both trait mean $\bar{\mathbf{z}} = \sum \alpha_i p_i$ and genetic variance $V_G \approx \sum \alpha_i^2 p_i q_i$ evolve

via change in allele frequencies p_i due to dispersal, selection, mutation and stochasticity

Evolution:

$$\frac{\partial p_i}{\partial t} = \frac{\sigma^2}{2}\left(\frac{\partial^2 p_i}{\partial x^2} + \frac{\partial^2 p_i}{\partial y^2}\right) + \sigma^2\left(\frac{\partial p_i}{\partial x}\frac{\partial \ln(N)}{\partial x} + \frac{\partial p_i}{\partial y}\frac{\partial \ln(N)}{\partial y}\right) + p_i q_i \frac{\partial \bar{r}}{\partial p_i}$$
$$-\mu(p_i - q_i) + \sqrt{\frac{p_i q_i}{N}}\ W_\epsilon(x, y, t)$$

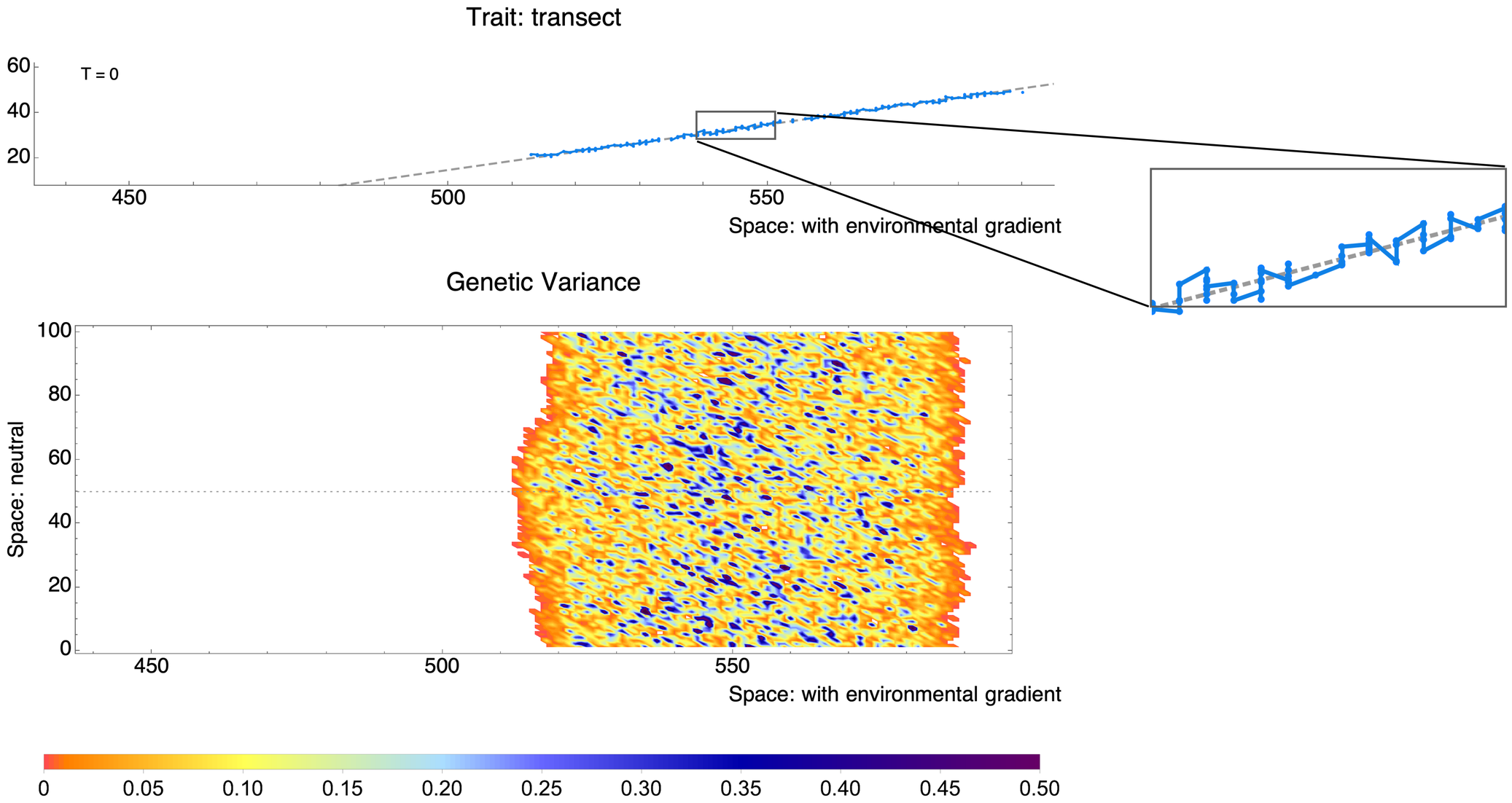
Ecology:

$$\frac{\partial N}{\partial t} = \frac{\sigma^2}{2}\left(\frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2}\right) + \bar{r}N + \sqrt{N}\ W_\xi$$

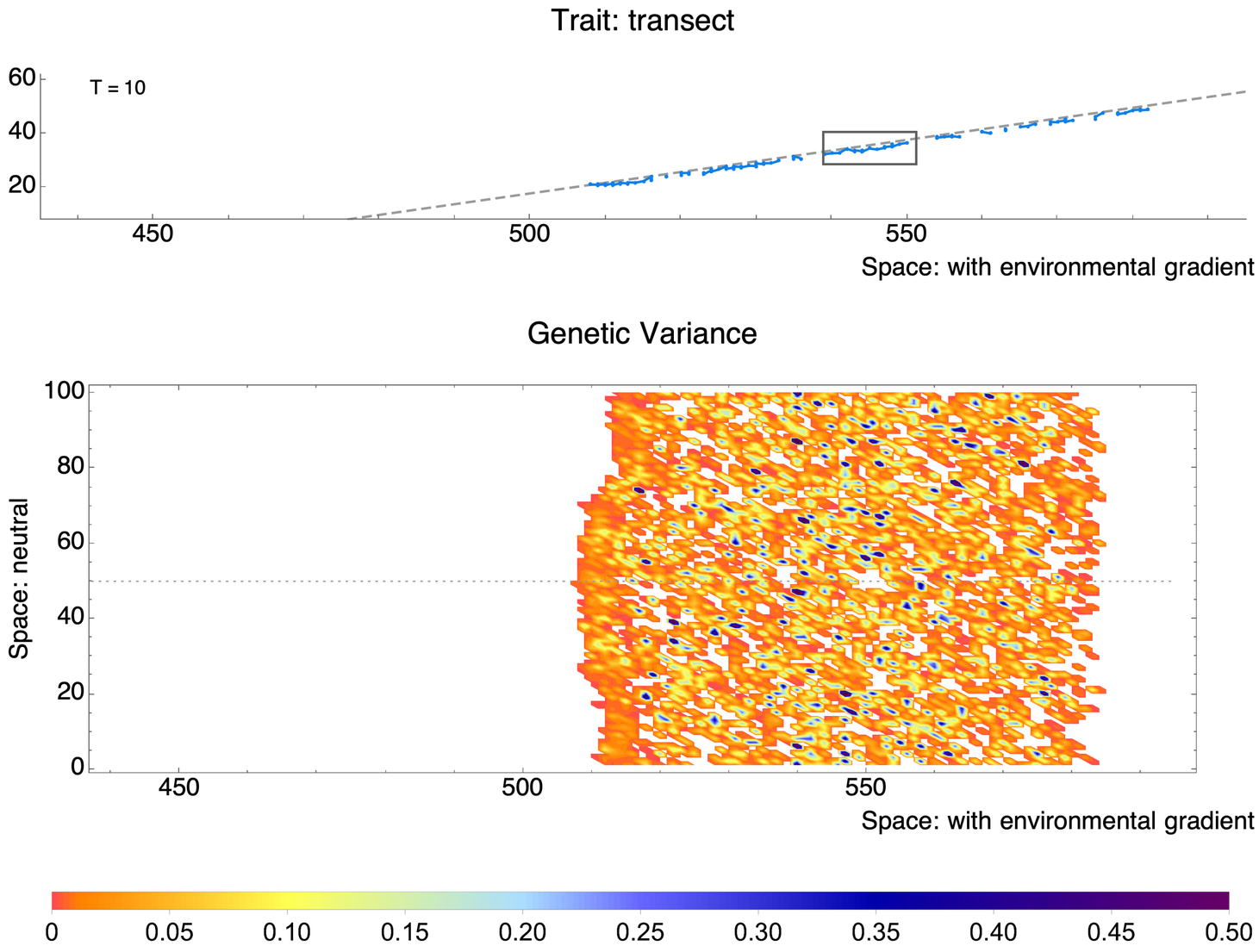
Coupling:

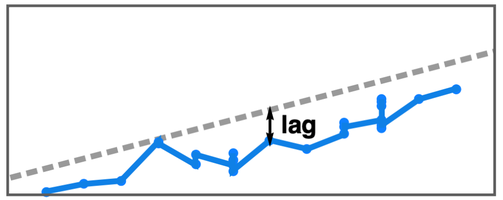
$$\bar{r} = r_m(1 - N/K) - (\bar{z} - \theta)^2/(2V_s) - V_G/(2V_s)$$

Evolution of species' range: IBM



Evolution of species' range in changing environments





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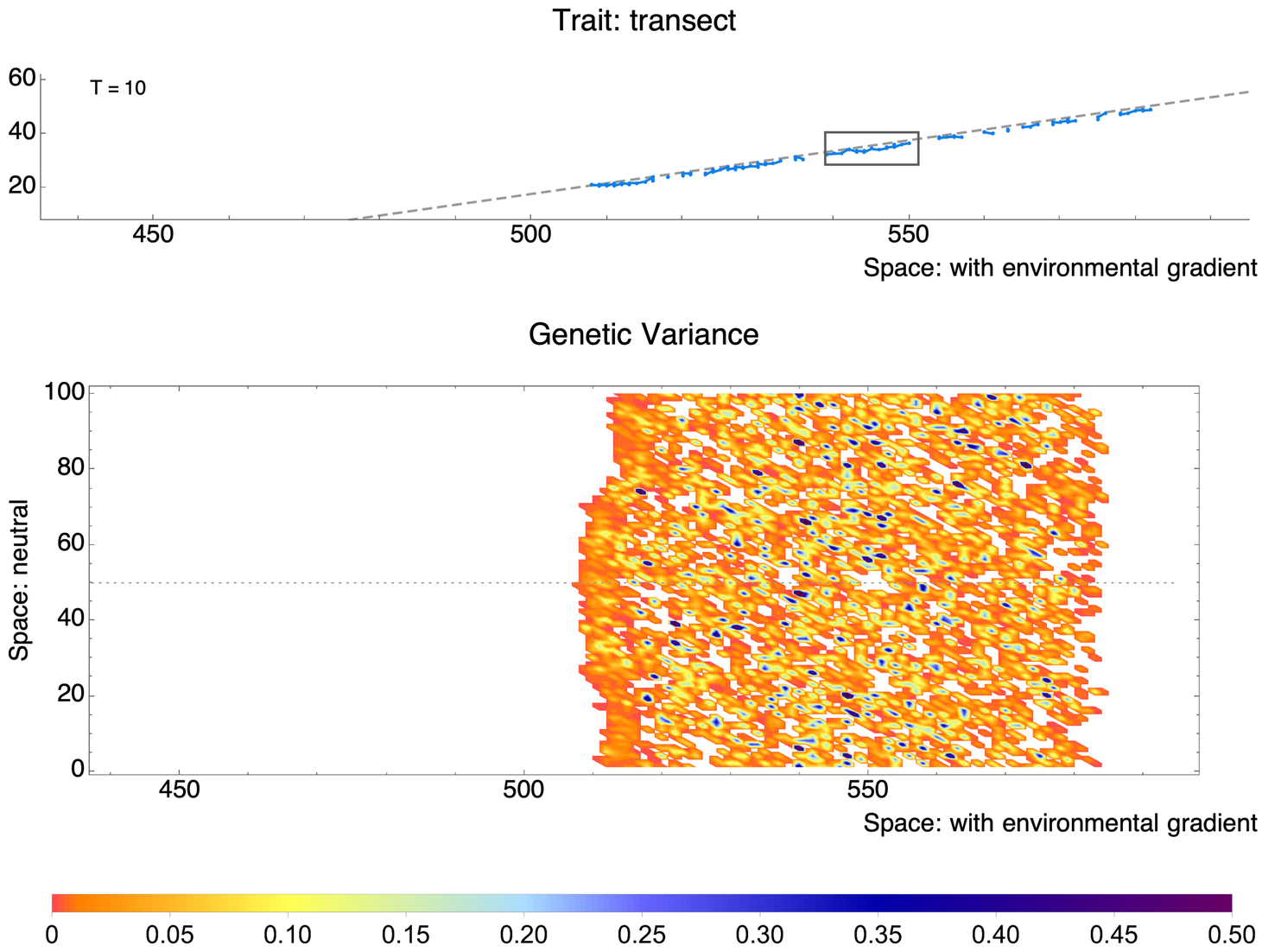
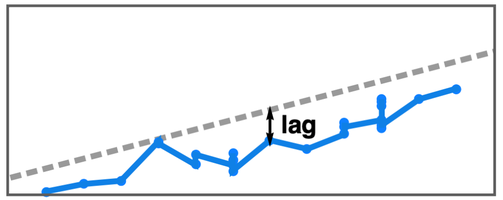
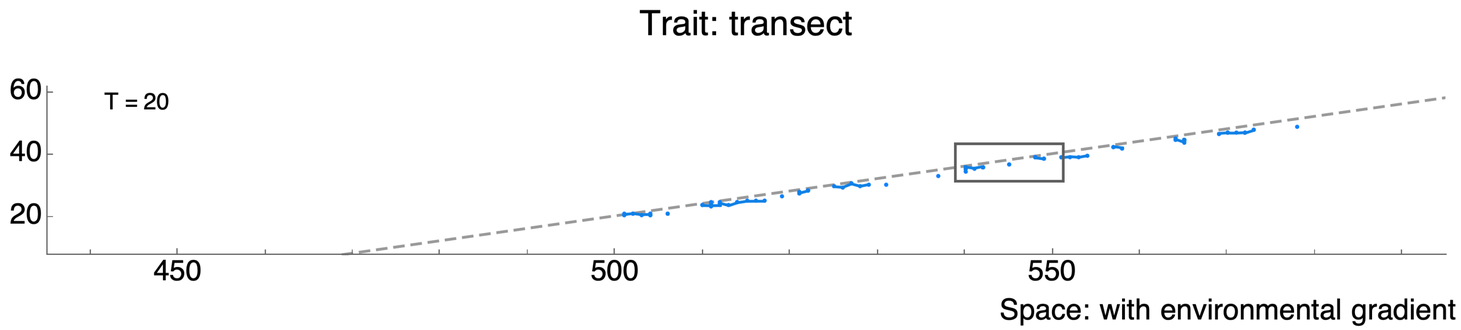
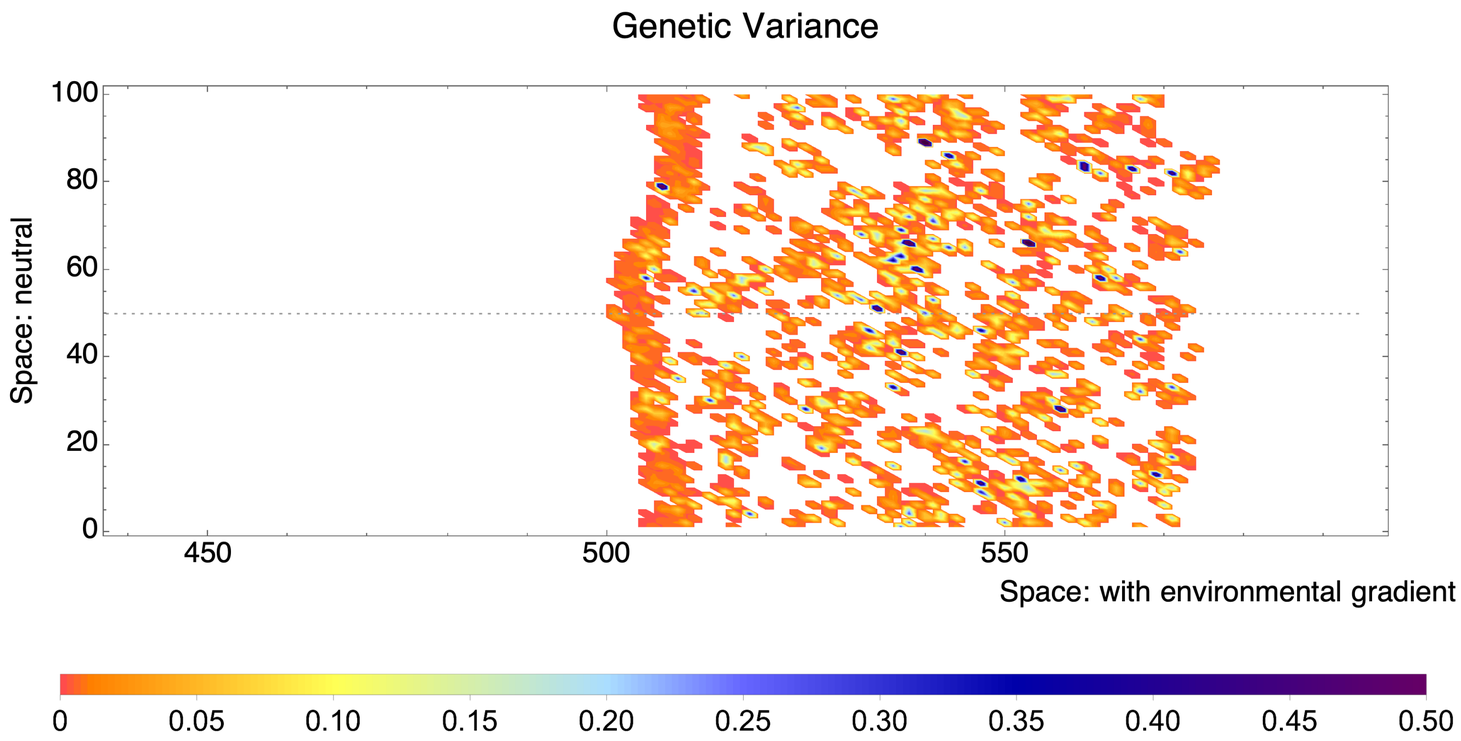


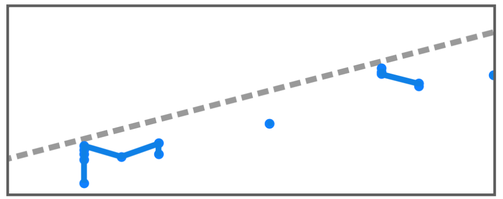


↑ demographic cost

● Evolution of species' range in changing environments







↑ demographic cost

⇓

↑ genetic drift

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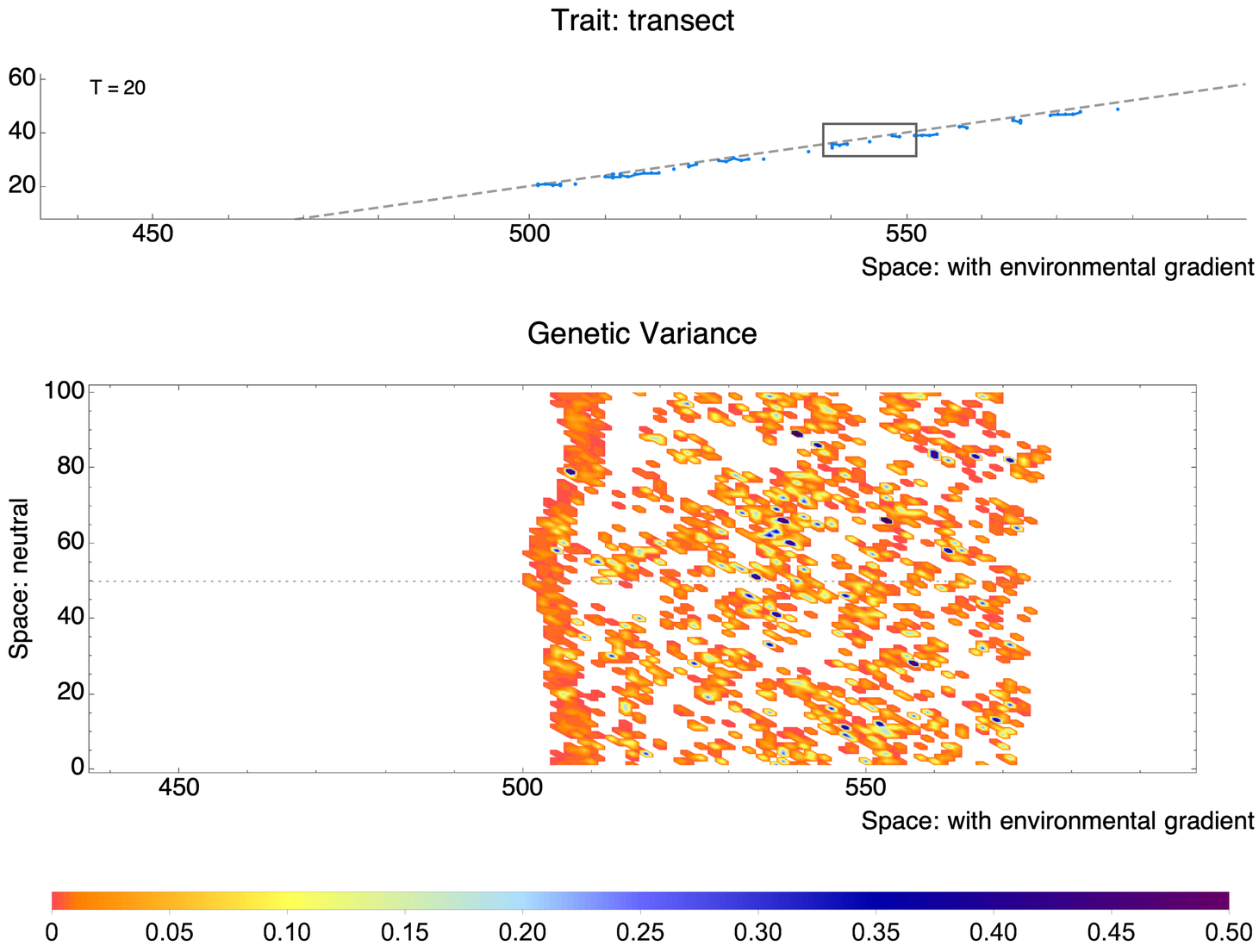

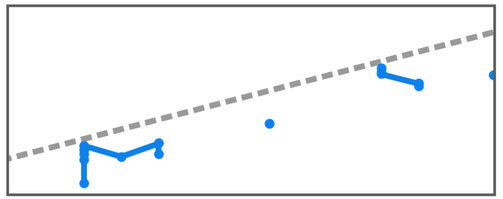

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↑ genetic drift

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↓ genetic variance

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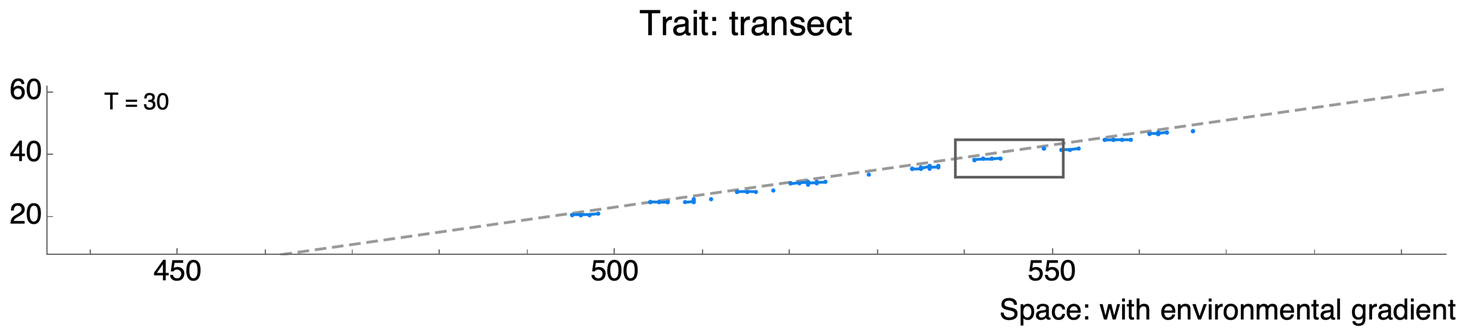

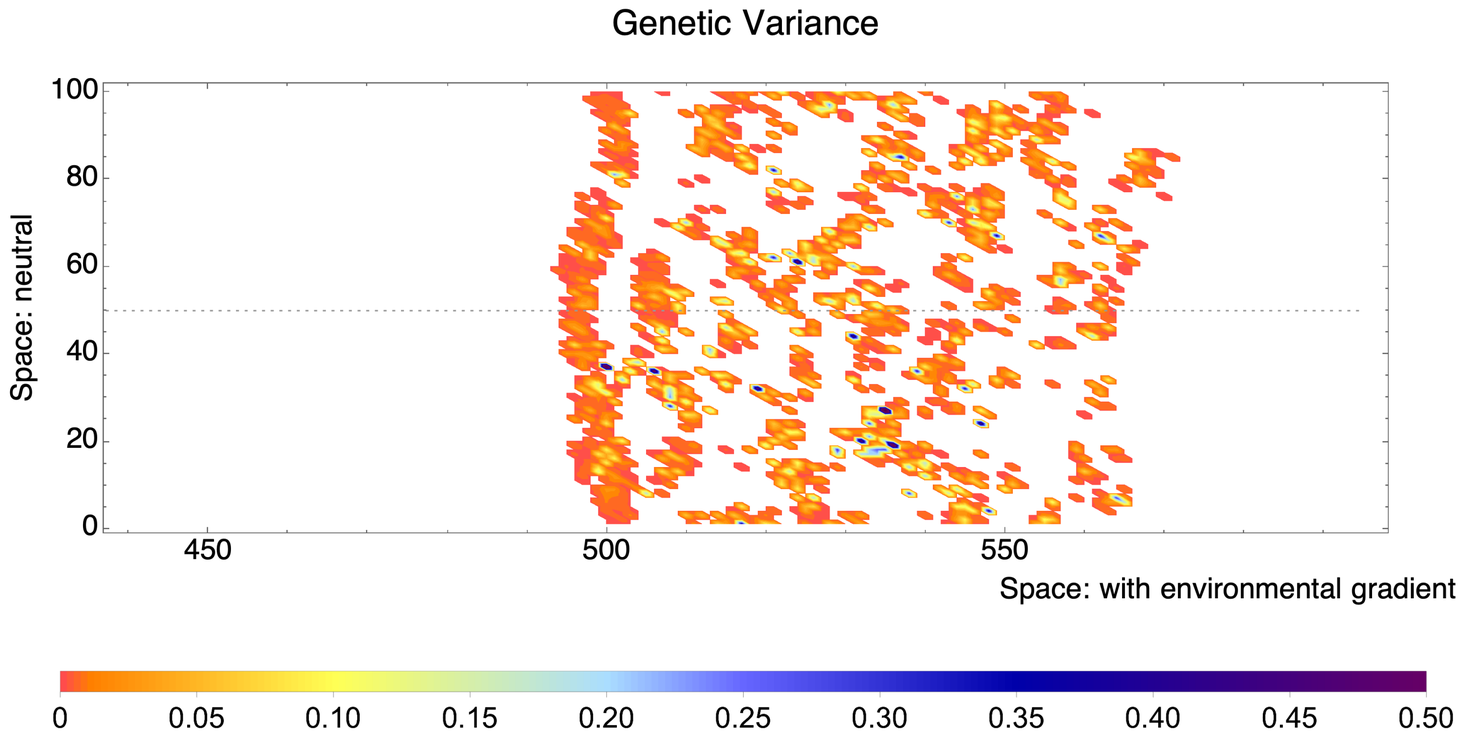

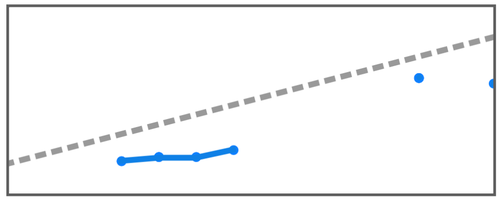

↑ demographic cost

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↑ genetic drift

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↓ genetic variance

⇓

↓ adaptation

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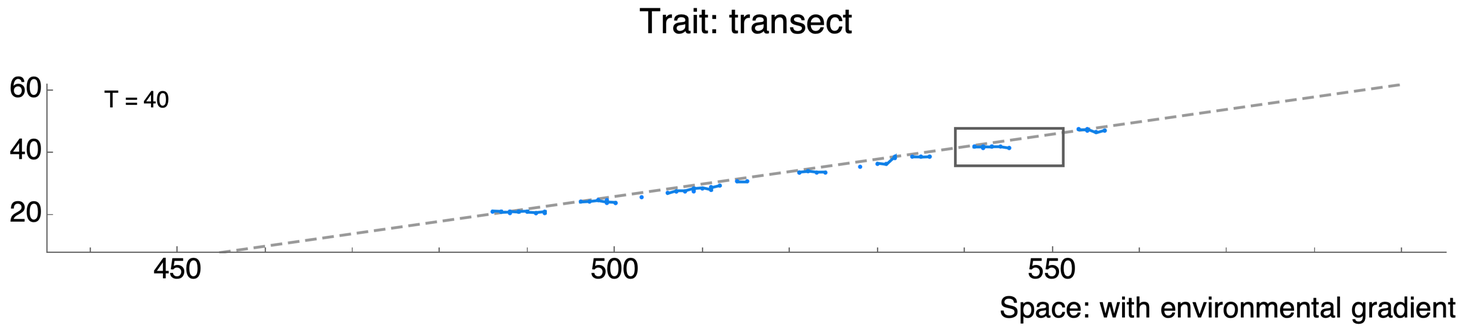

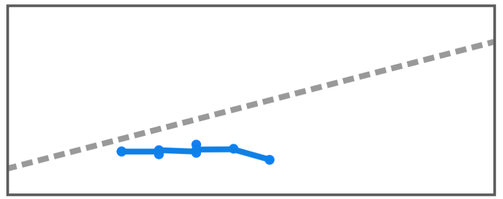

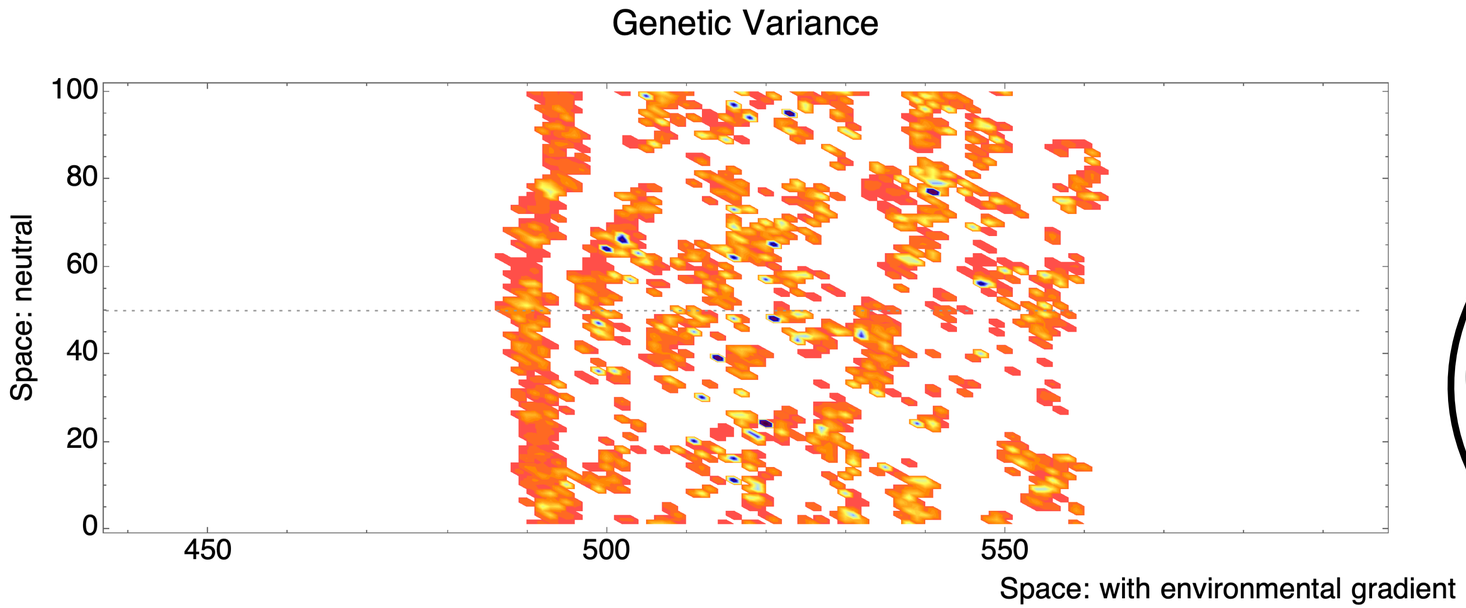

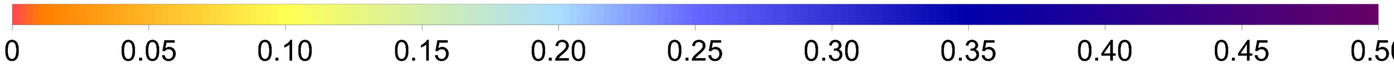

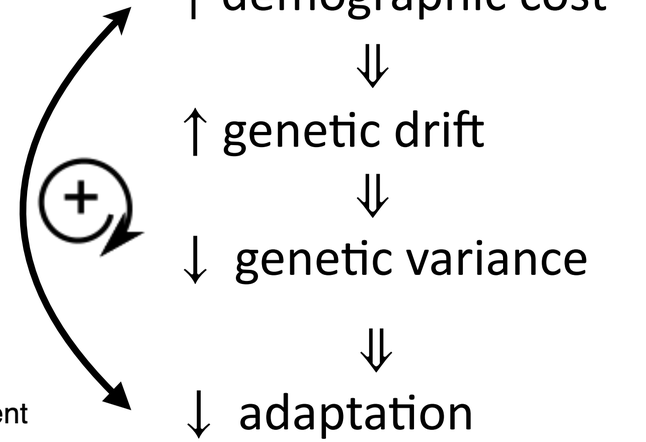

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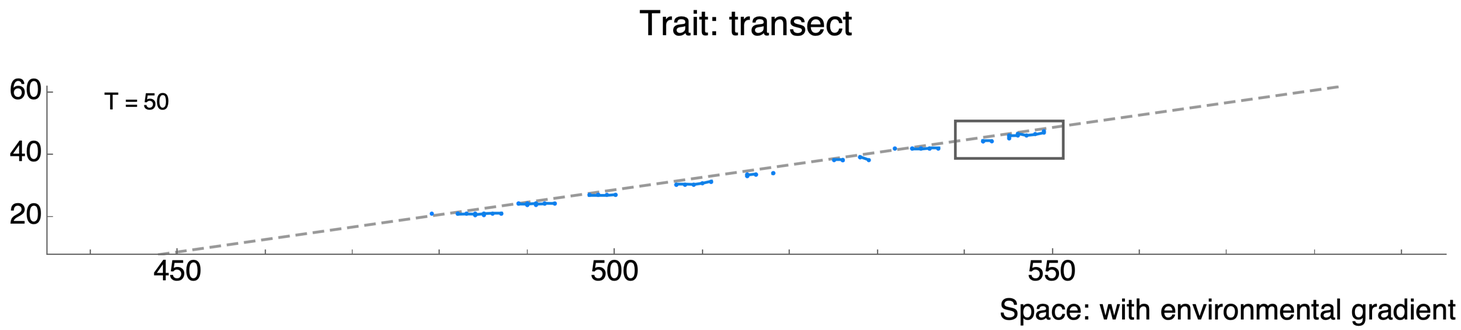
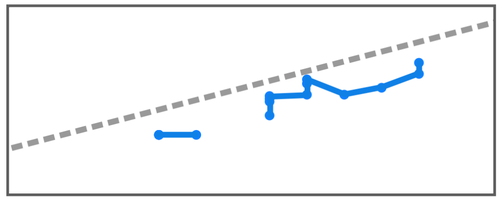
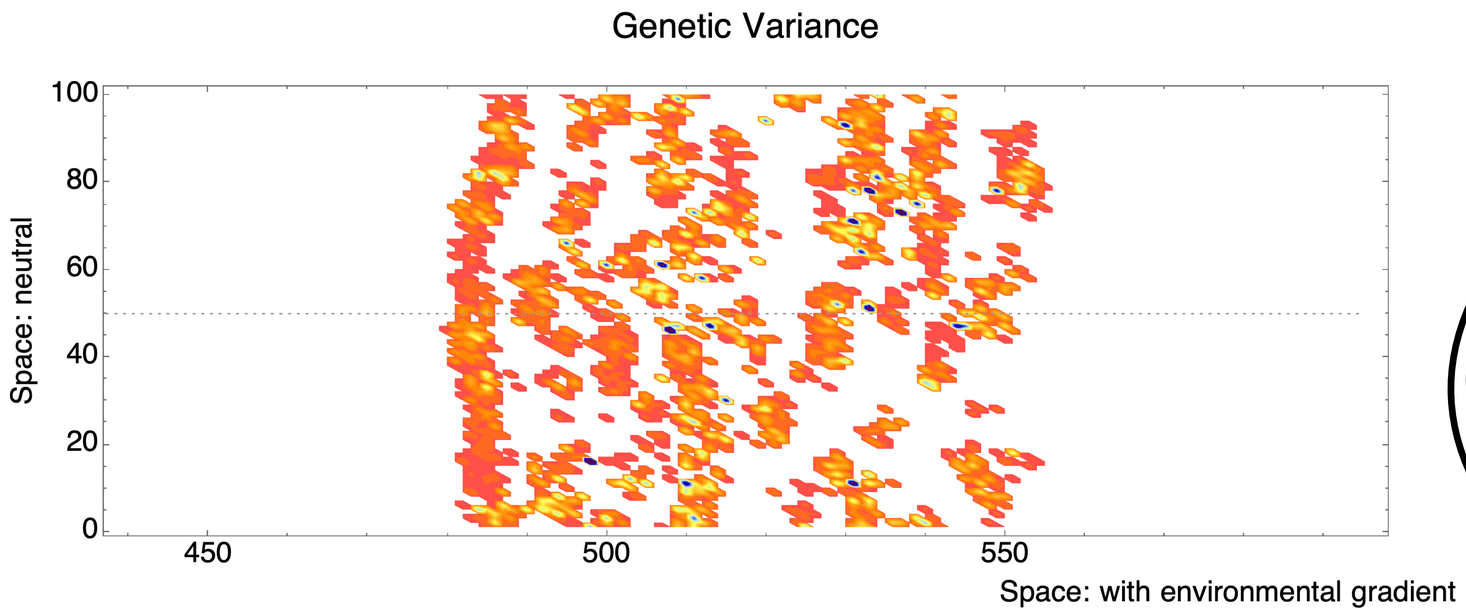
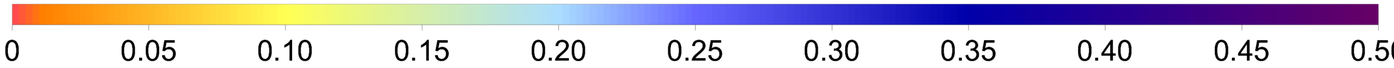
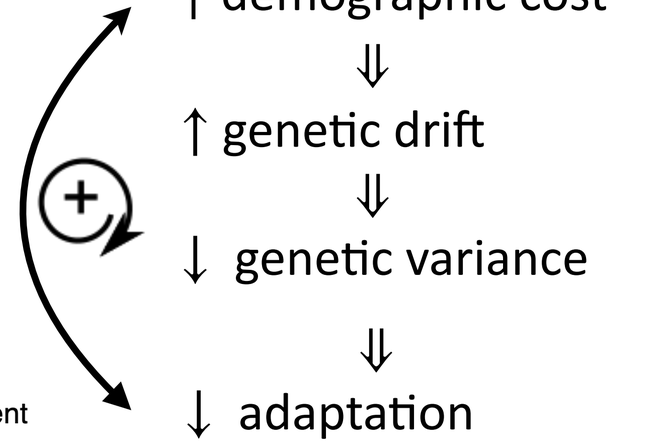






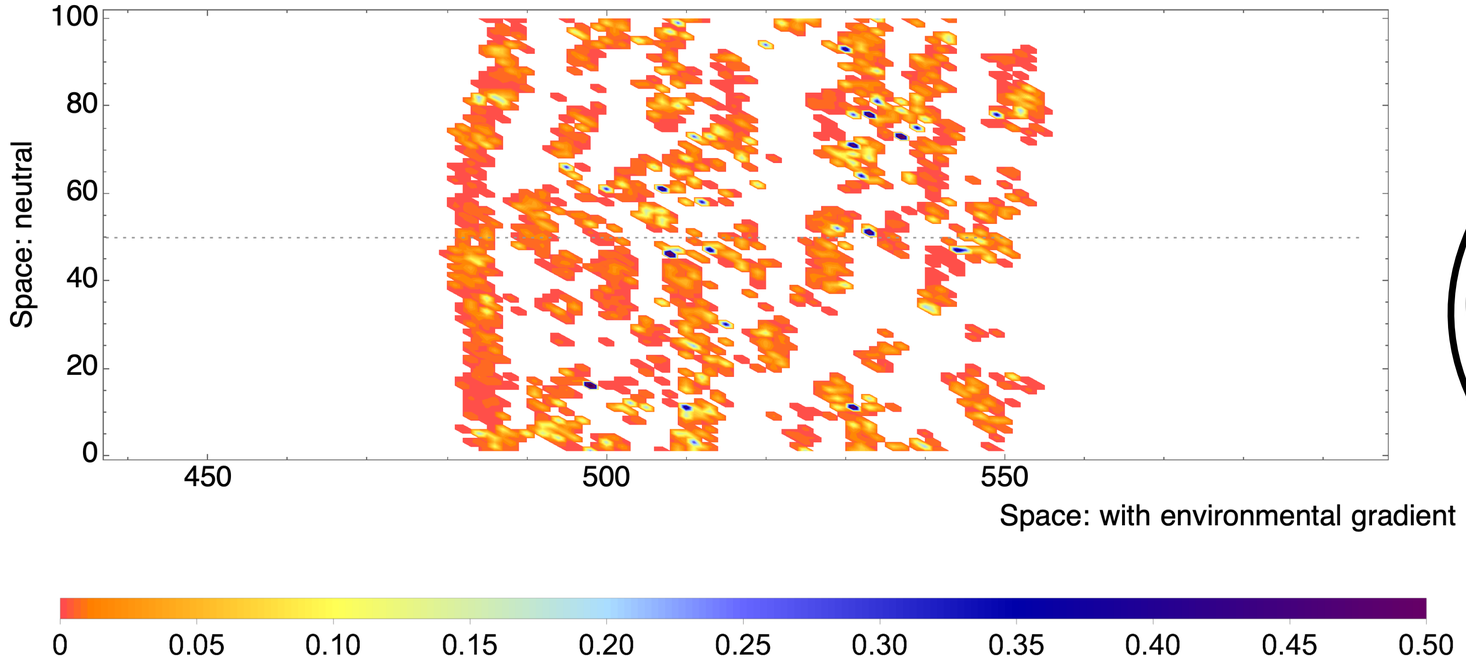


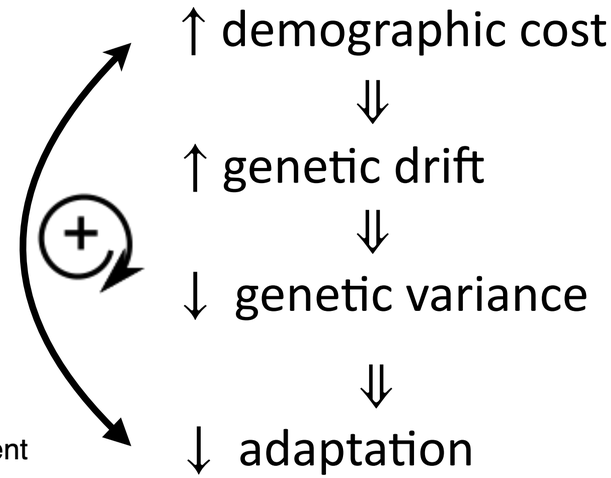


- **Evolution of species' range in changing environments**

➡ species' ranges can fragment abruptly

due to eco ↔ evo feedback





- **Evolution of species' range in changing environments**

➡ **species' ranges can fragment abruptly**

due to eco ↔ evo feedback (from IBM)

➡ **dimensionless parameters**

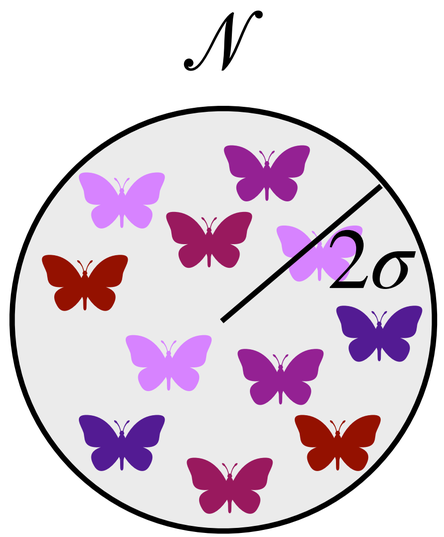
(from SPDE formalization)

Five dimensionless parameters

- $\mathbf{B} = \dfrac{b\sigma}{r^*\sqrt{2V_S}}$ effective environmental gradient

  loss of fitness due to dispersal to a different environment

- $\mathbf{k}^* = \dfrac{k}{\sqrt{r^{*3}V_S}}$ effective rate of temporal change



- $\mathcal{N} = 4\pi N\sigma^2$ neighbourhood size

- s/r^* strength of selection $s \equiv \alpha^2/(2V_s)$
  relative to the rate of return to equilibrium population size

- μ/r^* scaled mutation rate $r^* \to r_m - V_G/(2V_s)$

Three dimensionless parameters

that matter for the equilibrium

- $\mathbf{B} = \dfrac{b\sigma}{r^*\sqrt{2V_S}}$ effective environmental gradient

  loss of fitness due to dispersal to a different environment

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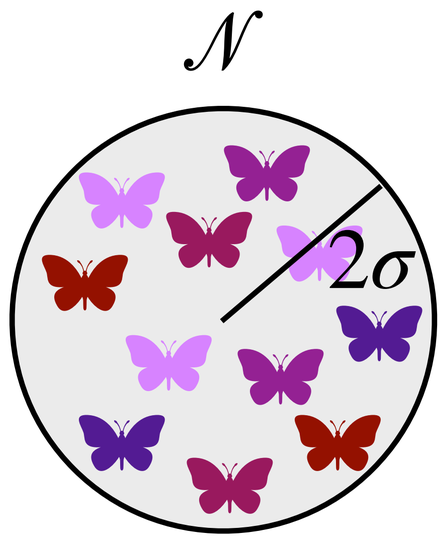


s/r^* strength of selection $s \equiv \alpha^2/(2V_s)$
relative to the rate of return to equilibrium population size

μ/r^* scaled mutation rate

$r^* \to r_m - V_G/(2V_s)$

Two dimensionless parameters

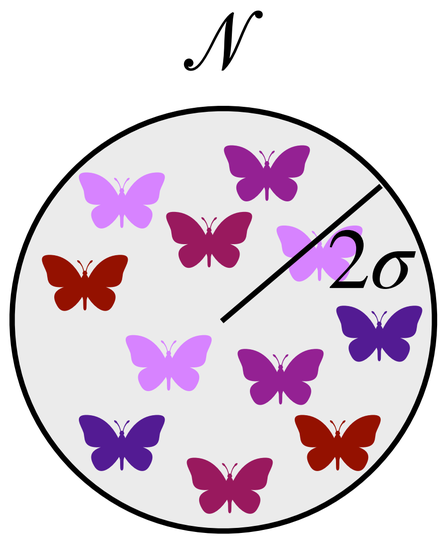
in the absence of temporal change

- $\mathbf{B} = \dfrac{b\sigma}{r^*\sqrt{2V_S}}$ effective environmental gradient

  loss of fitness due to dispersal to a different environment

- $\mathbf{k}^* = \dfrac{k}{\sqrt{r^{*3}V_S}}$ effective rate of temporal change

- $\mathcal{N} = 4\pi N\sigma^2$ neighbourhood size



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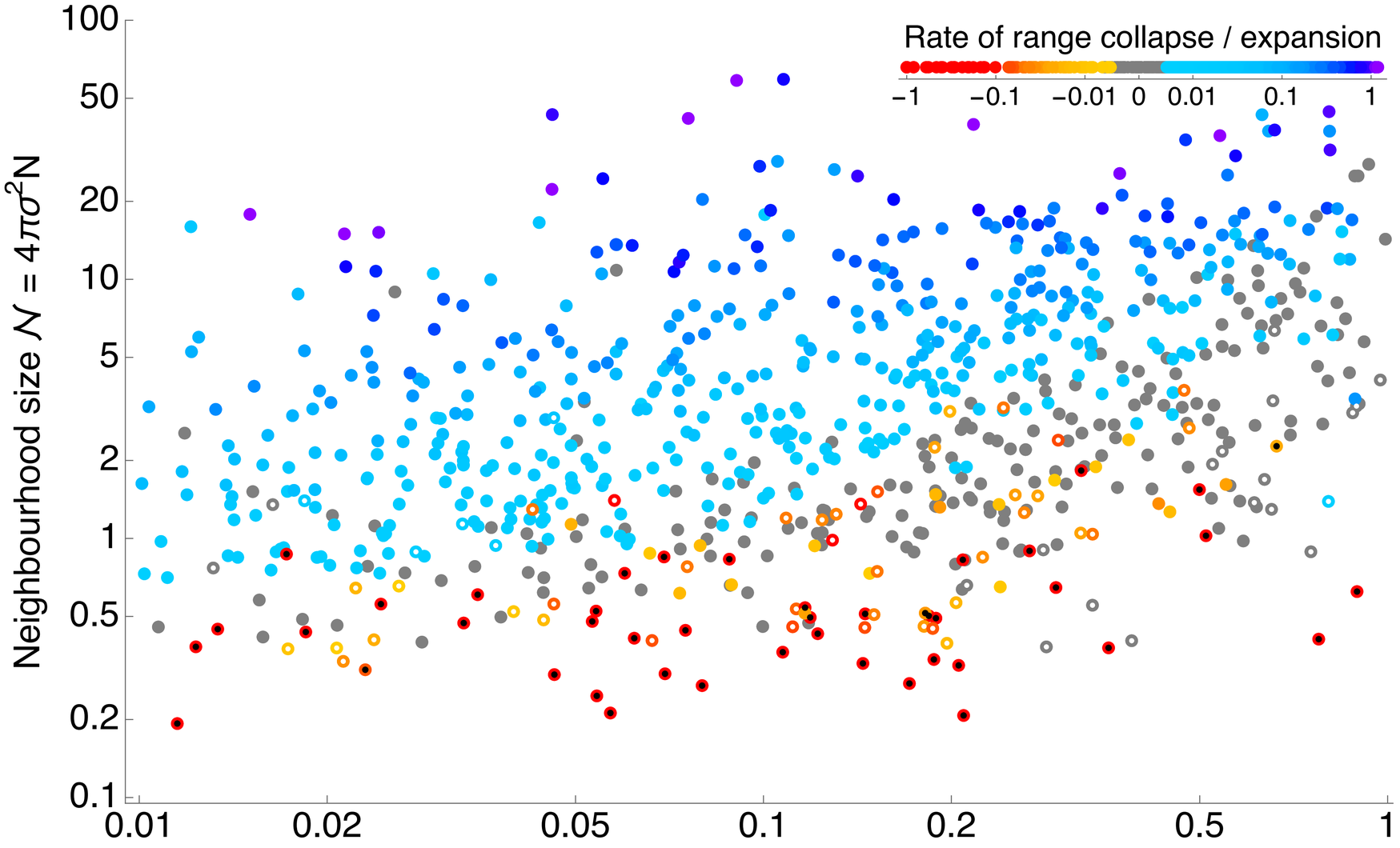
μ/r^* scaled mutation rate

$r^* \to r_m - V_G/(2V_s)$

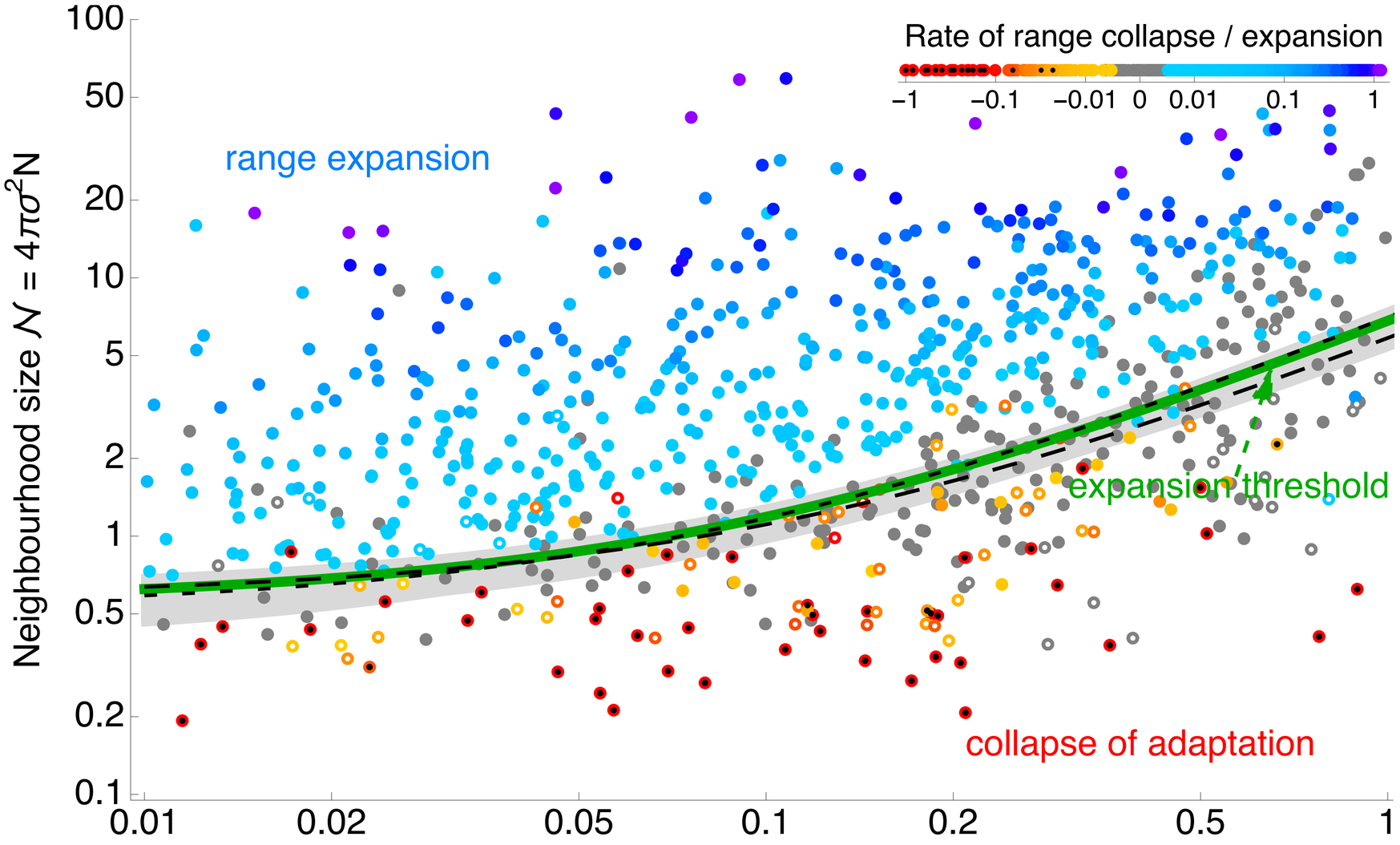
Expansion threshold with no temporal change



Polechová (2018), PLoS Biology

Expansion threshold with no temporal change

Species' range expands if genetic drift $1/\mathcal{N}$ is weak relative to spatial gradient B

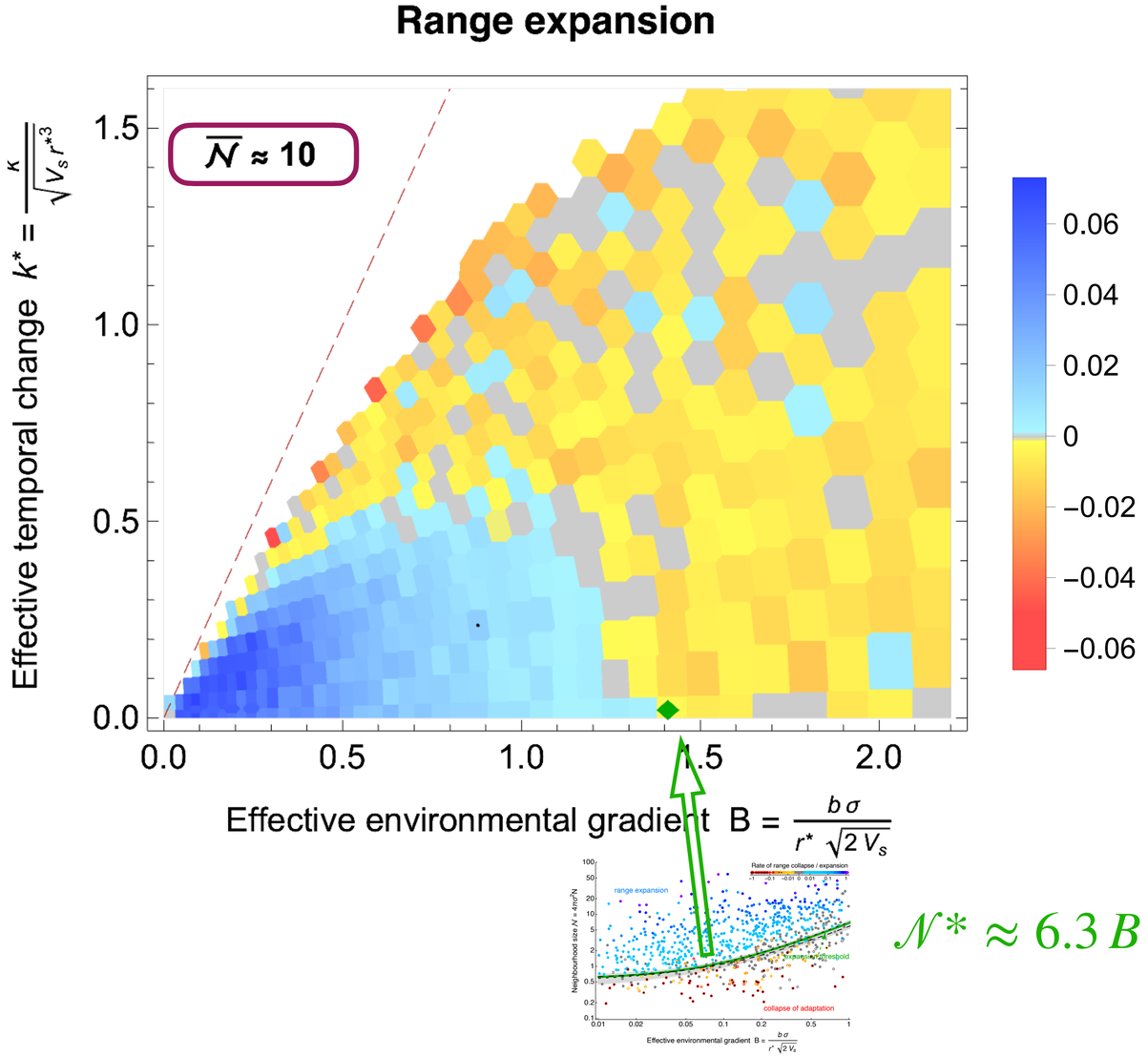


$\mathcal{N}^* \approx 6.3\,B + 0.56$

Effective environmental gradient $B = \dfrac{b\,\sigma}{r^*\sqrt{2\,V_s}}$

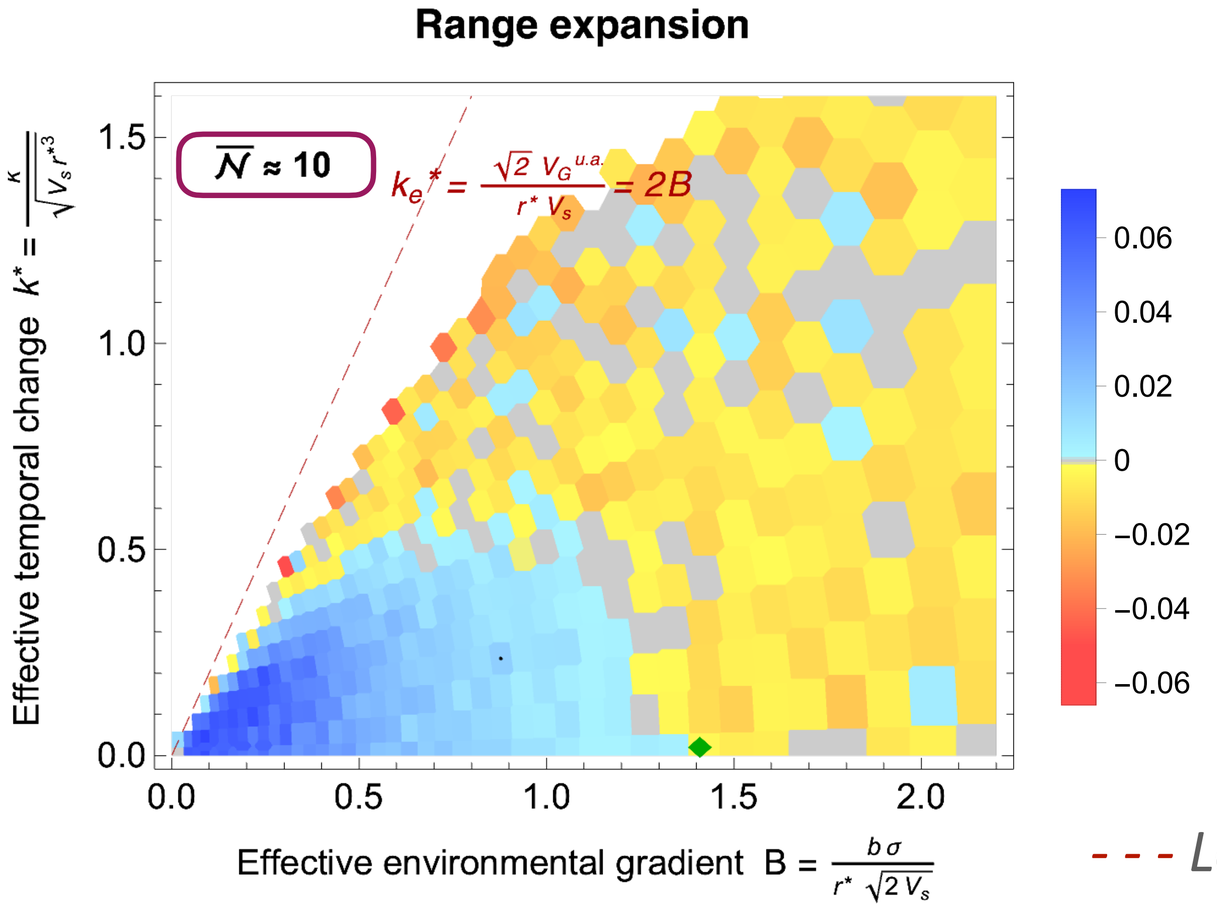
Polechová (2018), PLoS Biology

Expansion threshold with spatial gradient and temporal change



$$\mathcal{N}^* \approx 6.3\,B + 0.56$$

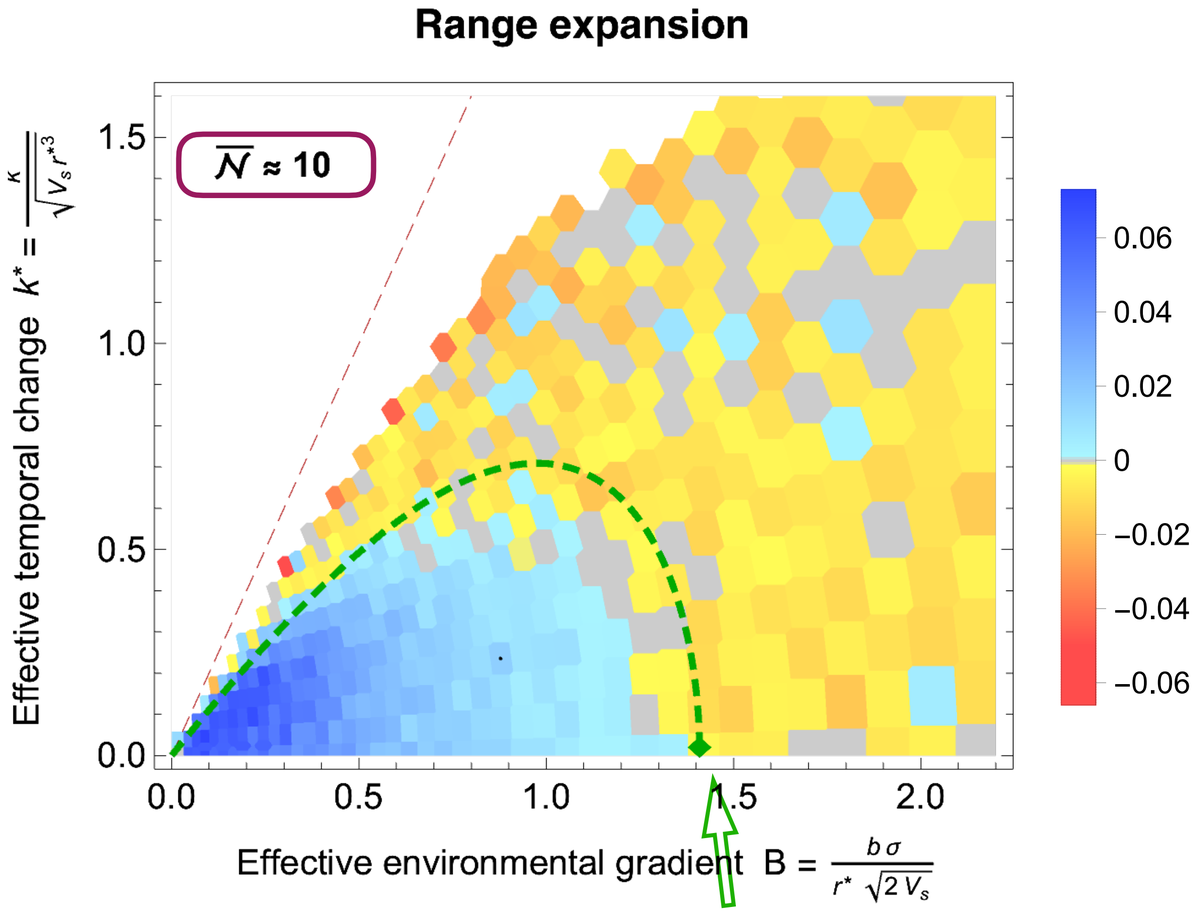
Expansion threshold with spatial gradient and temporal change



- - - Lande and Shannon (1996);

Barton (2001); Polechová, Barton and Marion (2009)

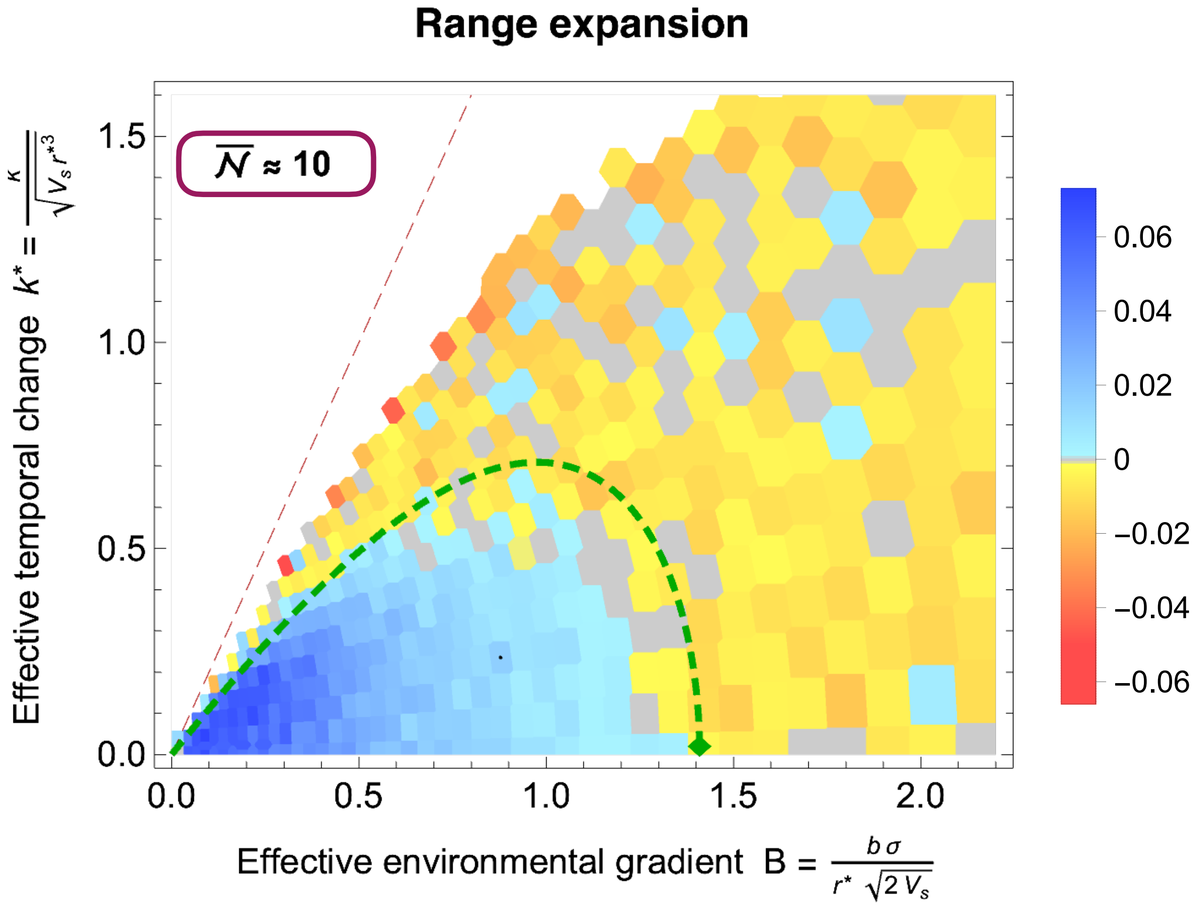
Expansion threshold with spatial gradient and temporal change



- - - expansion threshold corrected for lag load, assuming reduction of genetic variance due to genetic drift

Polechová (2026), PNAS

Expansion threshold with spatial gradient and temporal change

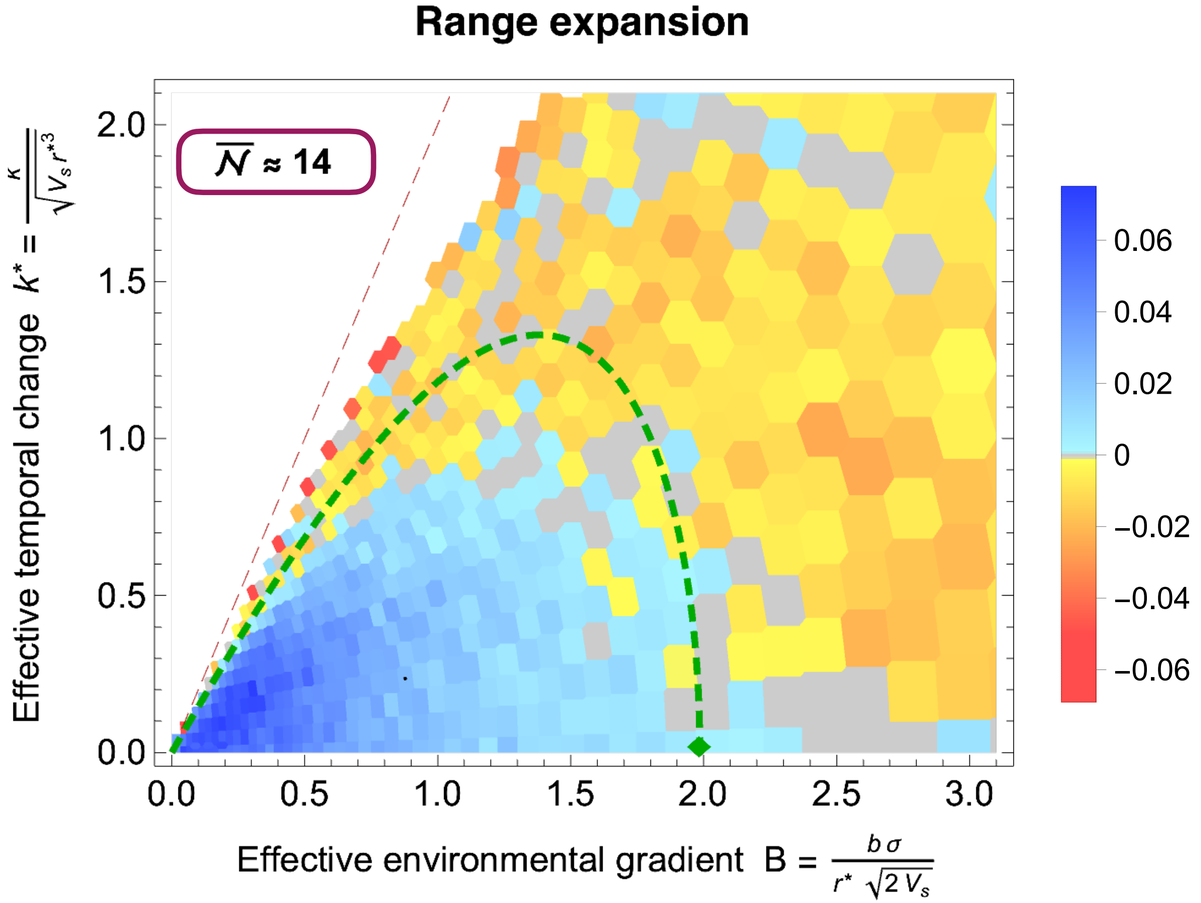


- - - expansion threshold corrected for lag load, assuming reduction of genetic variance due to genetic drift

$$k^*_{exp} = 2B\,(1 - 8/\mathcal{N})\sqrt{1 - (6.3B + 0.56)/\left(\mathcal{N}(1 - \sqrt{2}B/(\sqrt{2}B + 2h^2)\right)}$$

Polechová (2026), PNAS

Expansion threshold with spatial gradient and temporal change

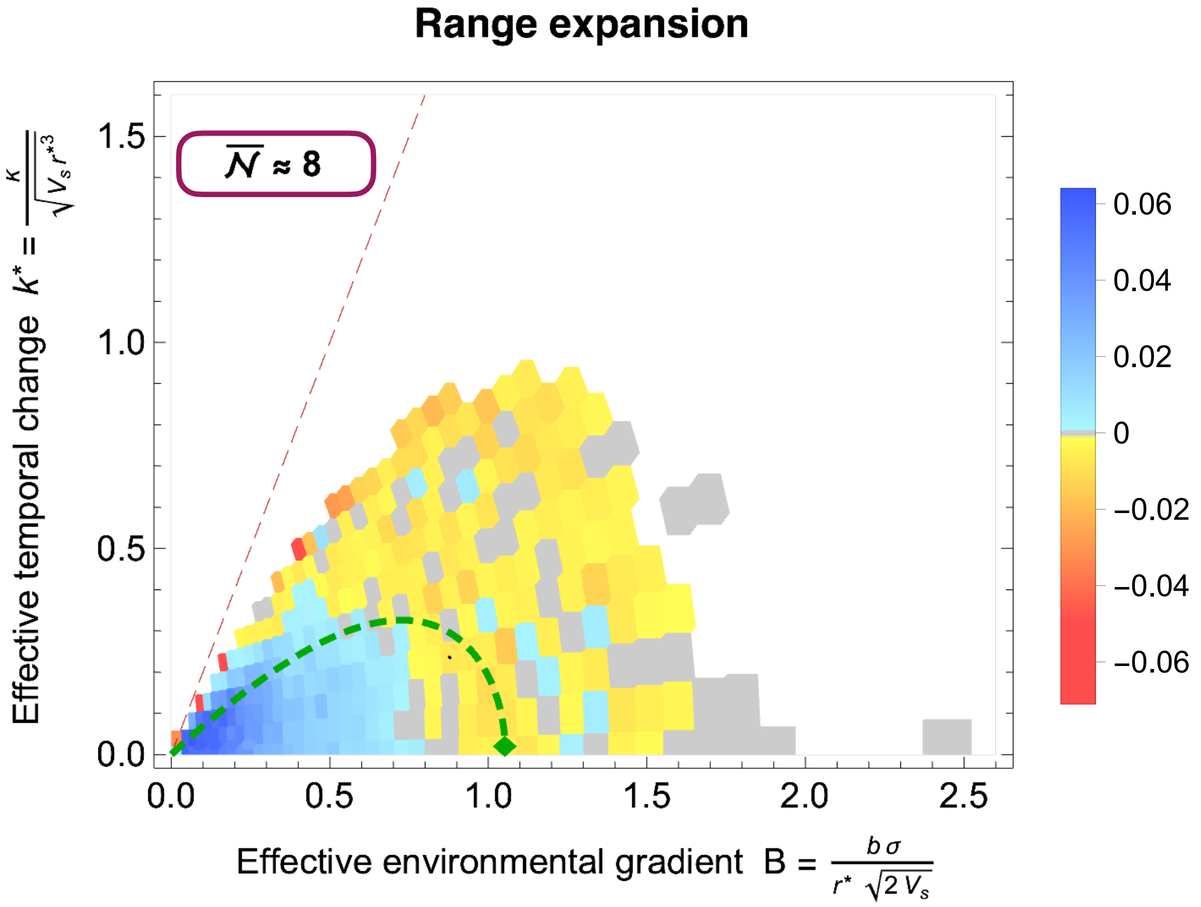


- - - expansion threshold corrected for lag load, assuming reduction of genetic variance due to genetic drift

$$k^*_{exp} = 2B\,(1 - 8/\mathcal{N})\sqrt{1 - (6.3B + 0.56)/\left(\mathcal{N}(1 - \sqrt{2}B/(\sqrt{2}B + 2h^2)\right)}$$

Polechová (2026), PNAS

Expansion threshold with spatial gradient and temporal change

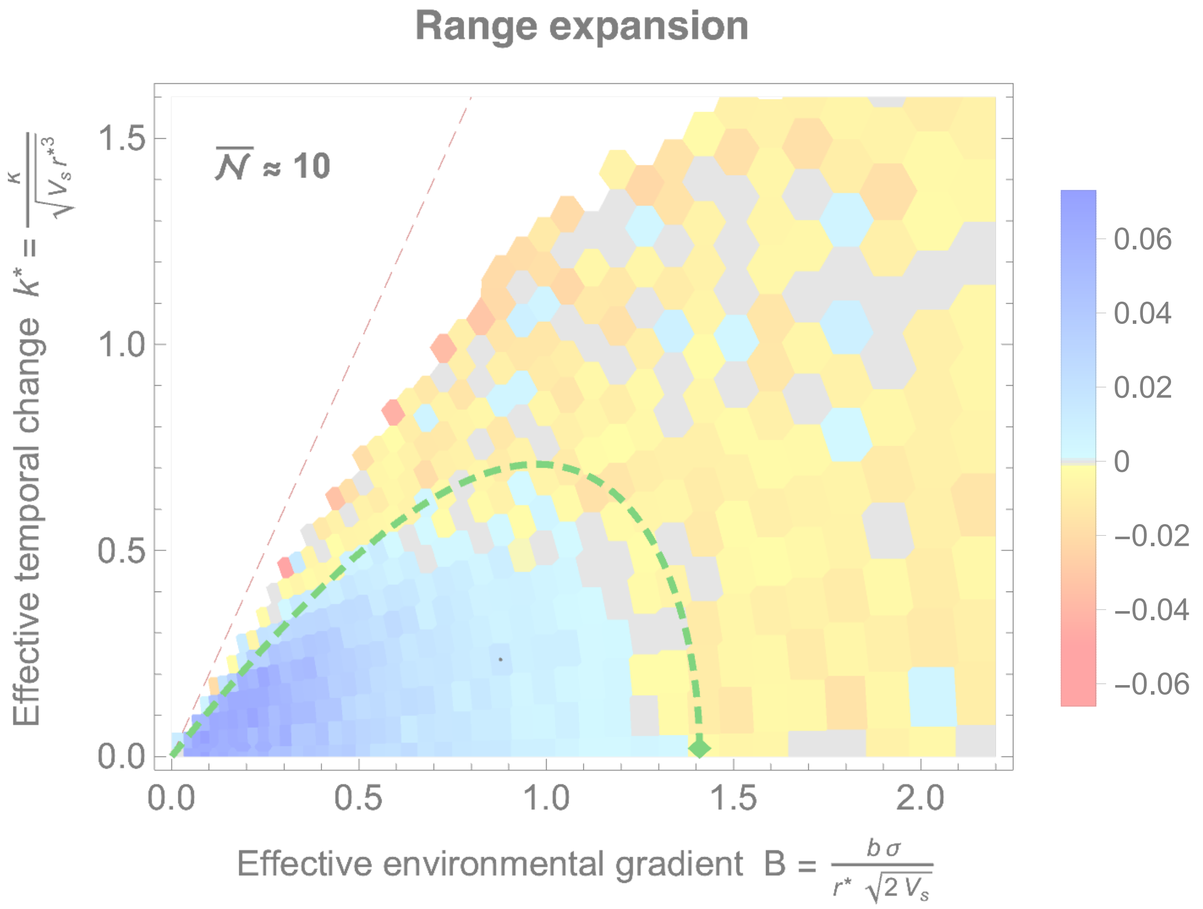


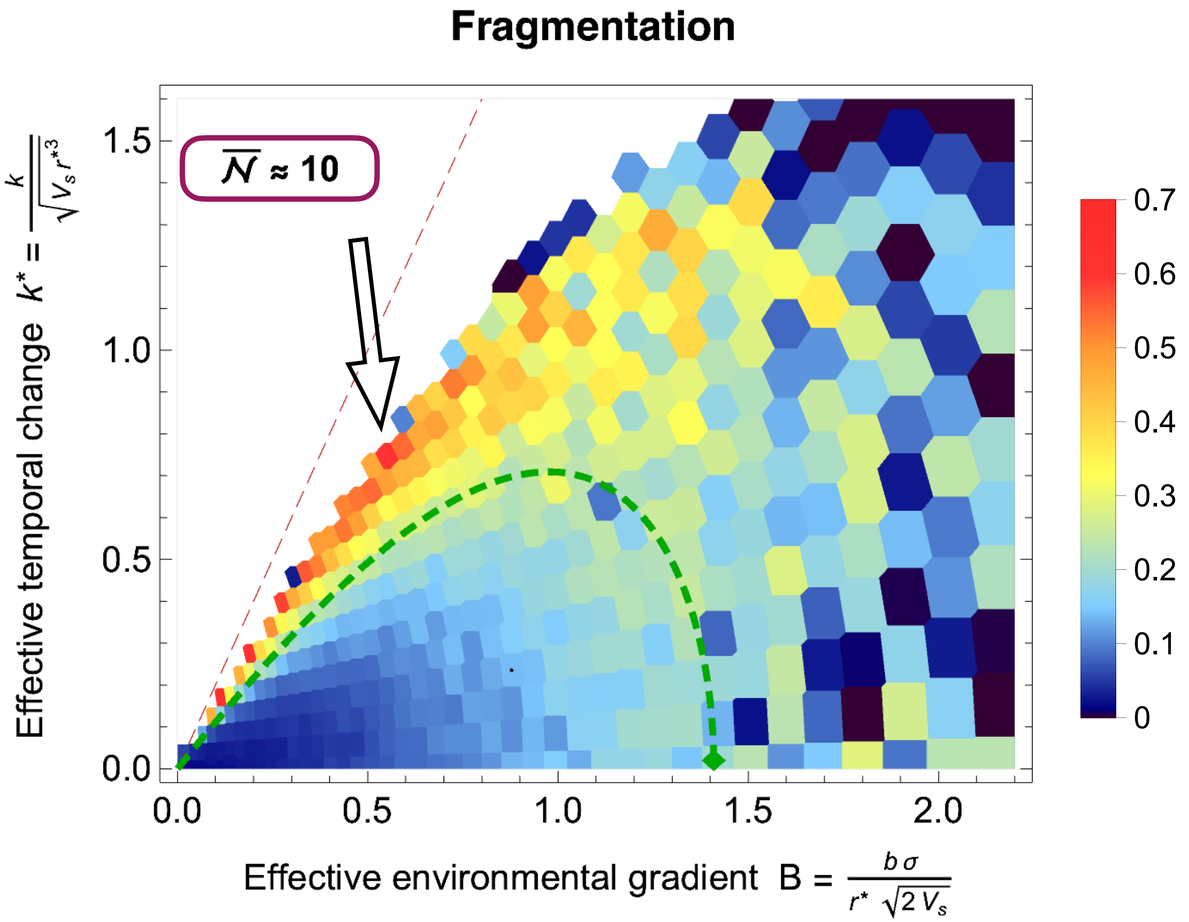
- - - expansion threshold corrected for lag load, assuming reduction of genetic variance due to genetic drift

$$k^*_{exp} = 2B\,(1 - 8/\mathcal{N})\sqrt{1 - (6.3B + 0.56)/\left(\mathcal{N}(1 - \sqrt{2}B/(\sqrt{2}B + 2h^2)\right)}$$

Polechová (2026), PNAS

Expansion threshold with spatial gradient and temporal change

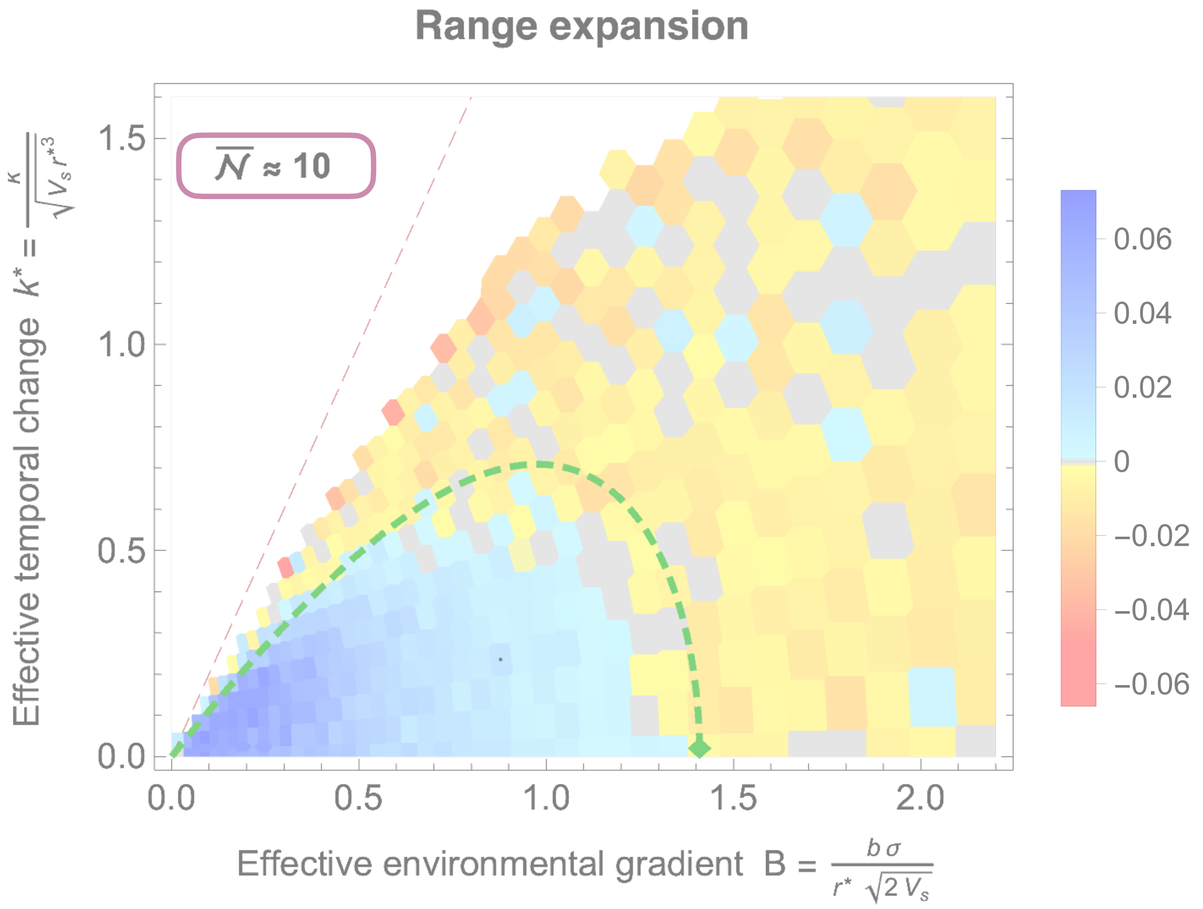


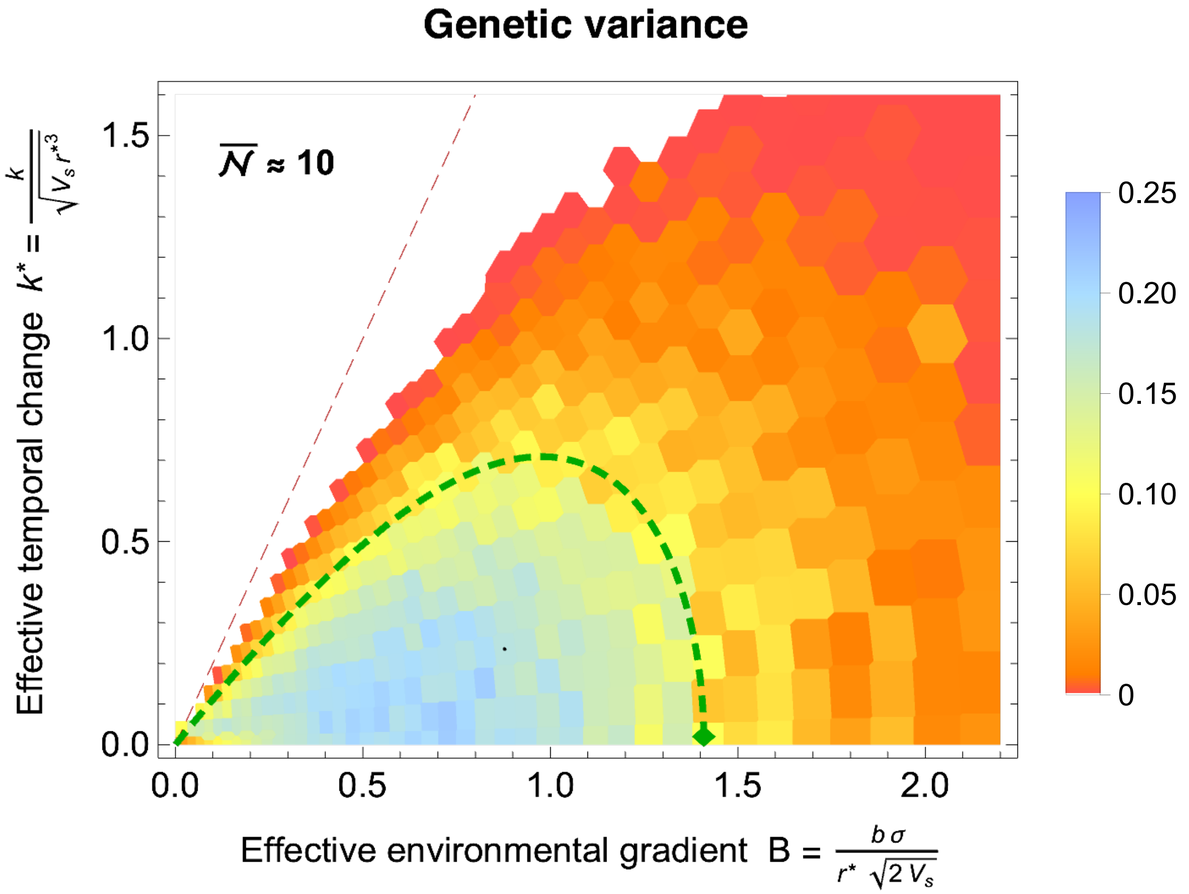


- - - expansion threshold corrected for demographic load and reduction of genetic variance due to genetic drift

Polechová (2026), PNAS

Expansion threshold with spatial gradient and temporal change

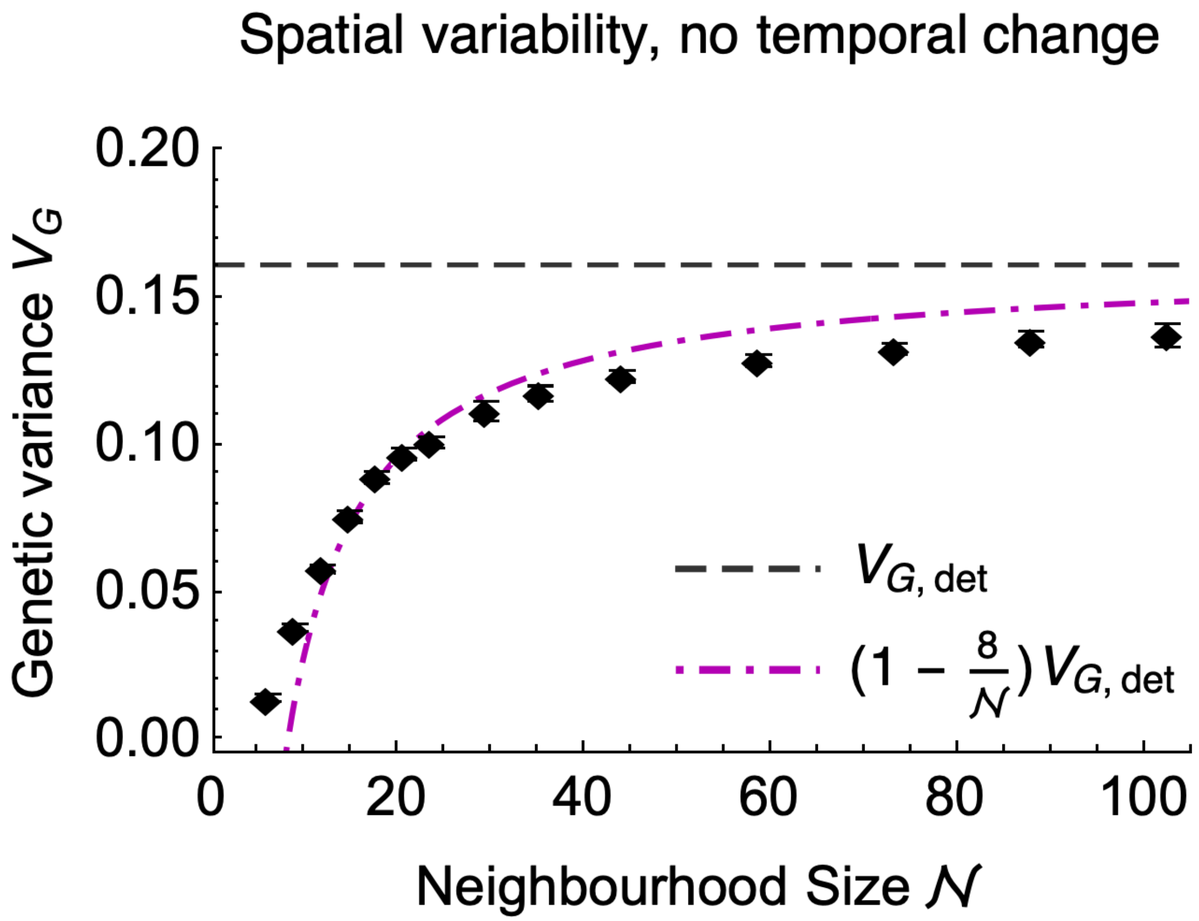




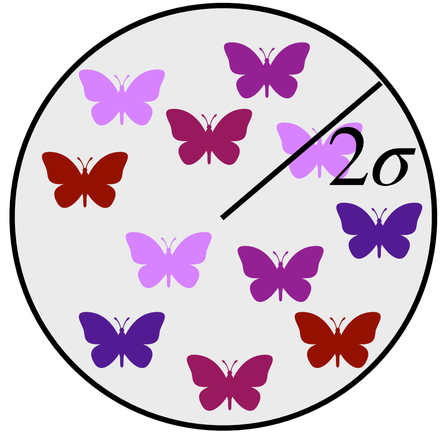
- - - expansion threshold corrected for lag load, assuming reduction of genetic variance due to genetic drift

Polechová (2026), PNAS

- **Genetic variance is reduced by genetic drift** $\sim 1/\mathcal{N}$

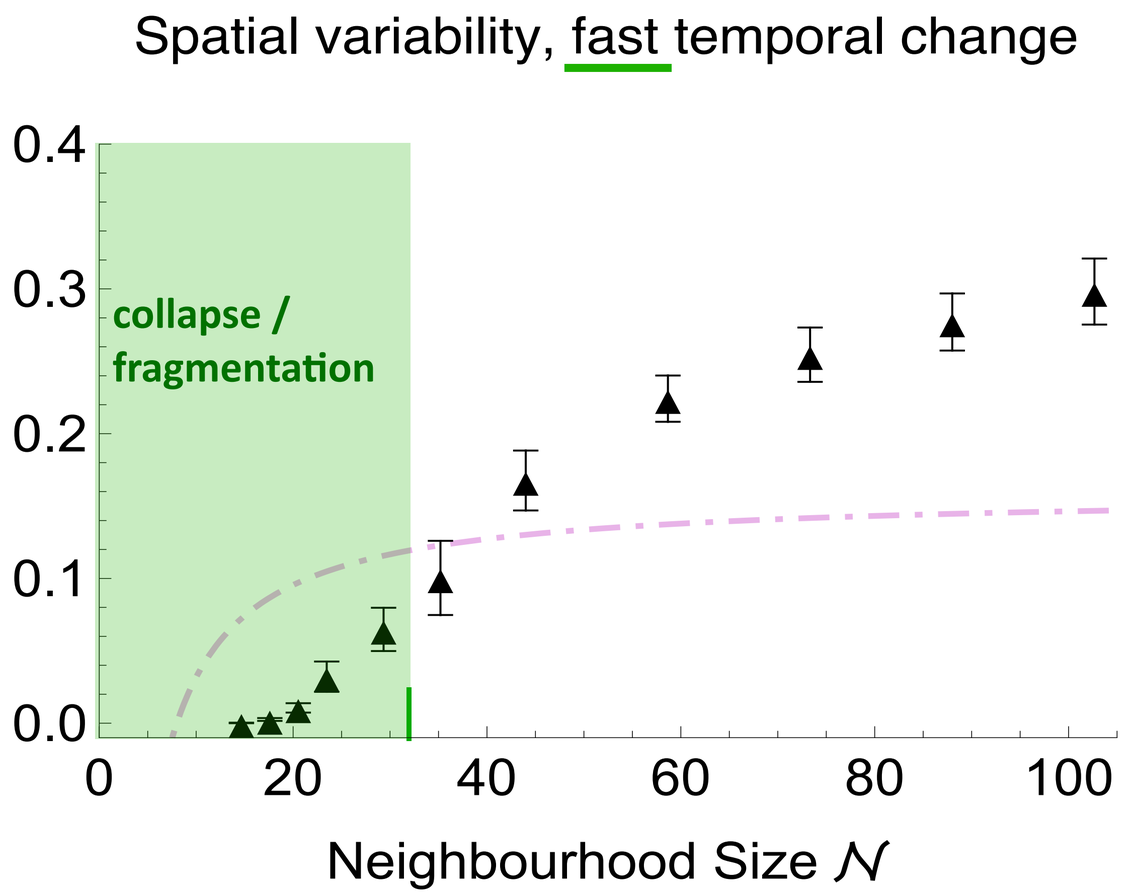


$$\mathcal{N} \sim 4\pi\sigma^2 N$$



Polechová and Barton (2011); Polechová (2026)

- **Genetic variance V_G still scales with neighbourhood size $\mathcal{N}$ <u>under temporal change</u>**

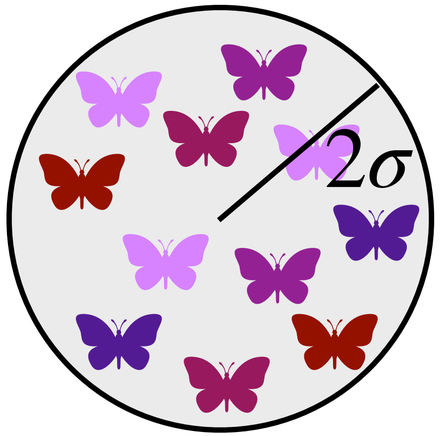


Polechová (2026)

- **Estimation of neighbourhood size $\mathcal{N}$**

$$slope = 1/\mathcal{N}$$

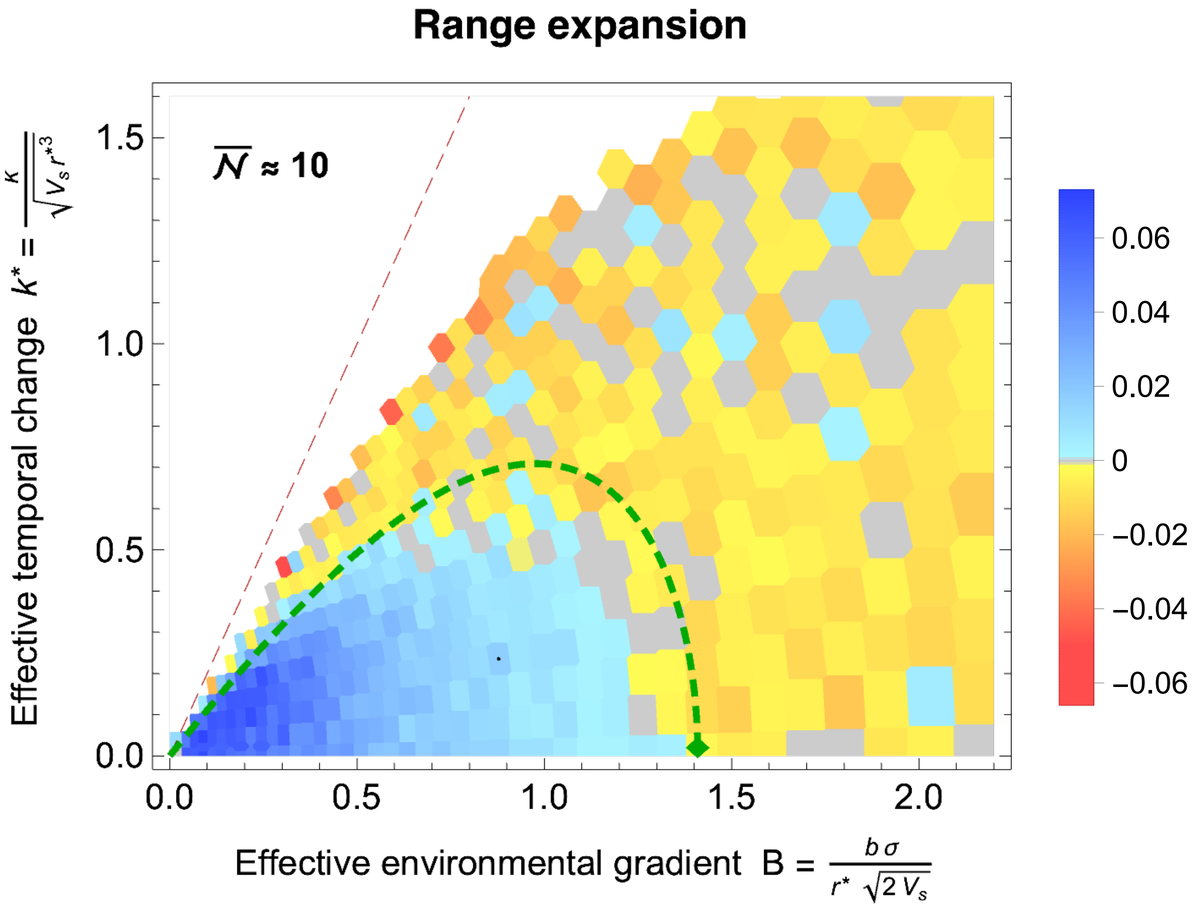
$$\mathcal{N} \sim 4\pi\sigma^2 N$$



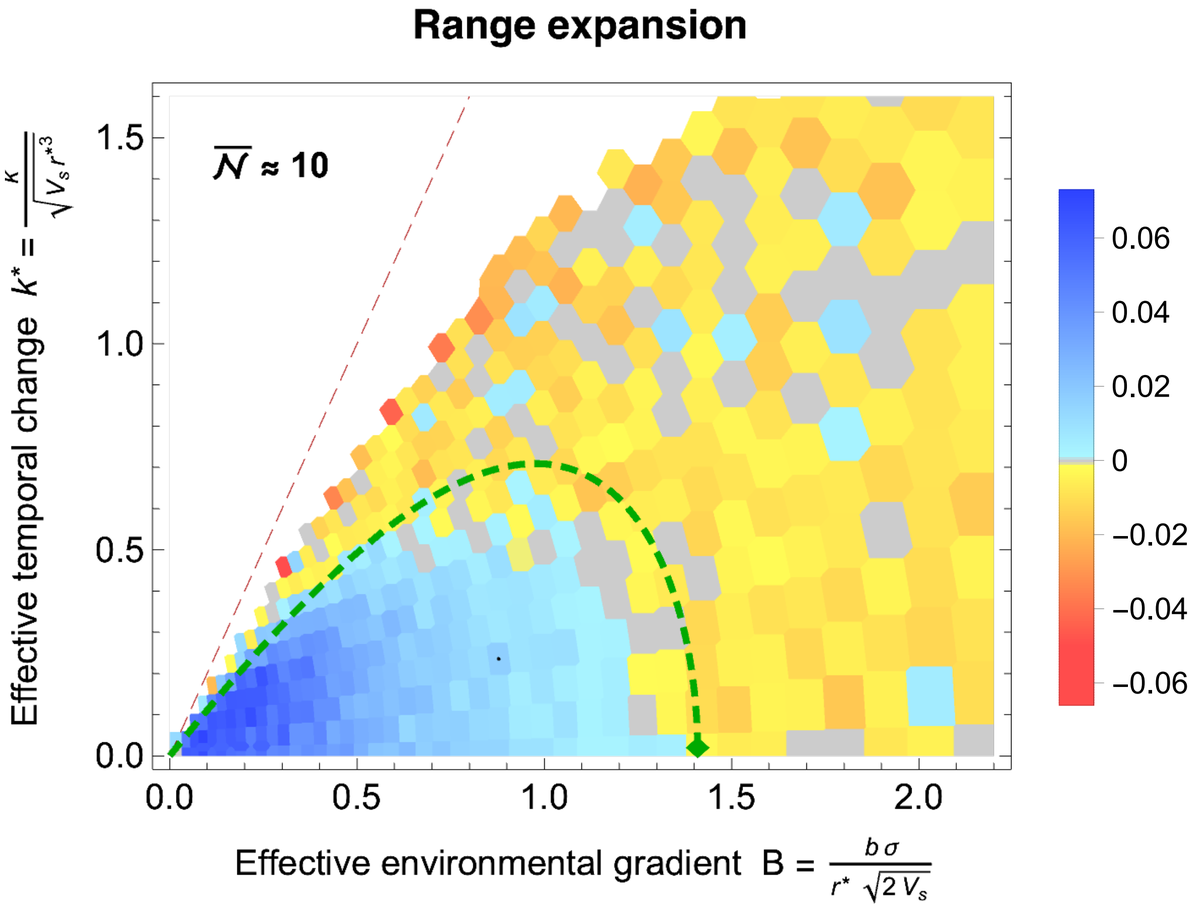
$$F_{ST} = \frac{var_{sites}(p)}{\bar{p}(1-\bar{p})}$$

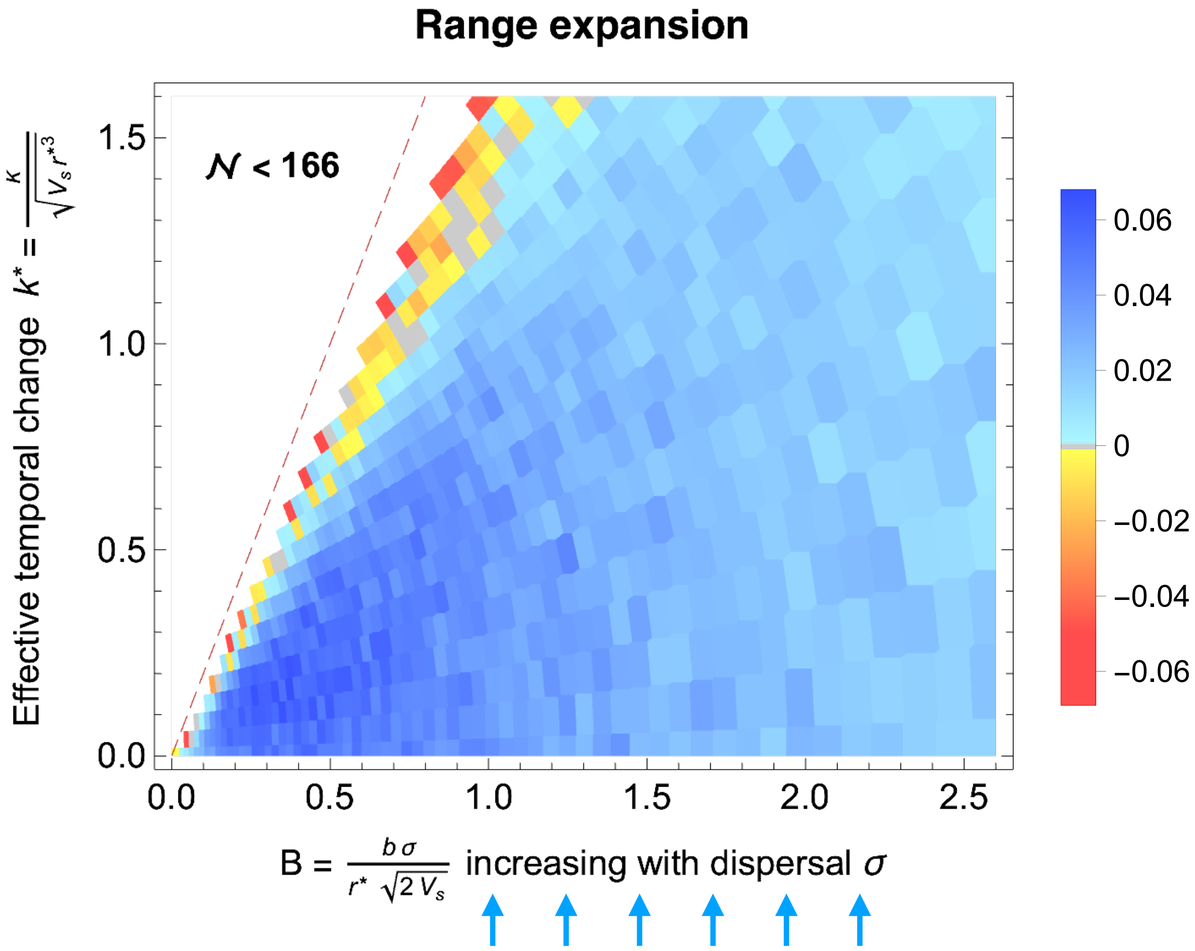
Rousset 1997, Vekemans and Hardy 2004, Watts et al. 2007

What is the effect of dispersal?



What is the effect of dispersal?





The increase of neighborhood size $\mathcal{N} = 4\pi N\sigma^2$ with dispersal^2 outweighs

the increase in the effective environmental gradient $B = b\sigma/(r^*\sqrt{2V_S})$

Summary

- **Species' range can fragment abruptly when the effective rate of temporal change k^* is too large for $\mathcal{N}, B$**

- **Neighborhood size $\mathcal{N}$ is an important parameter for eco-evo dynamics in spatially structured populations**

- **Increase of local dispersal facilitates adaptation to environmental change when genetic drift is strong**

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Hiring a PhD student!

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