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Phenotypic Noise and the Cost of Complexity

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• **BACKGROUND**
Theory predicts that **phenotypic noise** is positively selected under **directional selection** because it increases the mean fitness value, and counter-selected under **stabilizing selection (1)**.

It has been suggested that under directional selection, the fitness gain provided by phenotypic noise also **promotes adaptive evolution (2)**, while the link is unclear. Evolution on multiple phenotypic characters suffers from the **cost of complexity (3)**. The impact of phenotypic noise in multidimensional phenotypes is less understood.

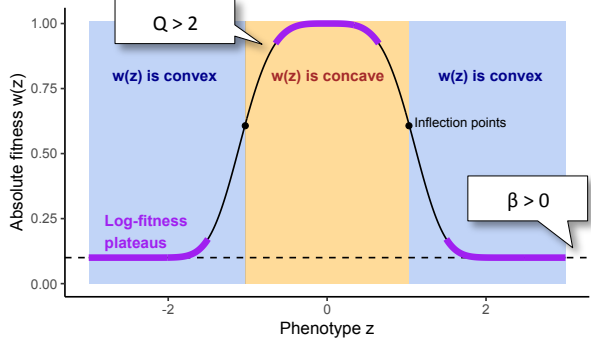
• **METHODS**
We used a quantitative model to study the adaptive evolution of organisms with multiple phenotypic traits under selection and evolvable phenotypic noise (4) in a generalized fitness landscape.

• **RESULTS**
Phenotypic noise promotes adaptive evolution under directional and/or stabilizing selection if the **logarithmic fitness plateaus**.
For multiple phenotypic characters under selection, the phenotypic noise evolves to a one-dimensional noise aligned with the direction of the fitness optimum.

• **CONCLUSION**
Phenotypic noise can **decrease the cost of complexity** and **promotes adaptive evolution in flat regions of the fitness landscape**.

1. PHENOTYPIC NOISE EFFECT ON FITNESS DEPENDS ON THE SHAPE OF THE FITNESS LANDSCAPE (SINGLE CHARACTER)

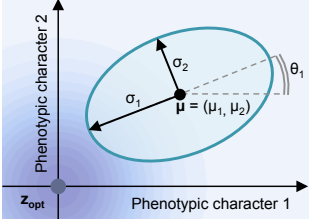
Generalized fitness function: $w(z) = (1-\beta)\exp[-\alpha z^Q] + \beta$ (5)



Parameters	Stabilizing selection (close to the fitness optimum)		Directional selection (far from the fitness optimum)	
	Q = 2	Q > 2	β = 0	β > 0
Shape of the absolute fitness function	concave (curvature < 0)	concave (curvature < 0)	convex (curvature > 0)	convex (curvature > 0)
Shape of the log-fitness function	does not plateau	plateaus	does not plateau	plateaus
Does noise increase mean absolute fitness?	No	No	Yes	Yes
Does noise promote evolution?	No	Yes	No	Yes

2. A MODEL FOR PHENOTYPIC NOISE EVOLUTION

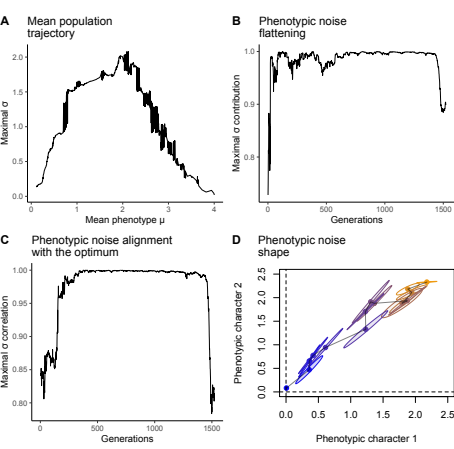
Evolvable phenotypic noise for two phenotypic characters



Multi-dimensional phenotypic noise is built from the mutable genotype {μ, σ, Θ}:

- Mean phenotype μ (mutable),
- Variances σ² (mutable),
- Rotation angles Θ (mutable),
- Covariance Σ built from σ² and Θ.
- Phenotype z ~ N_n(μ, Σ)

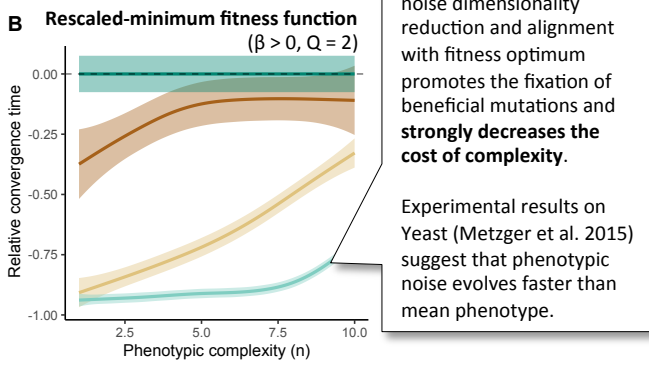
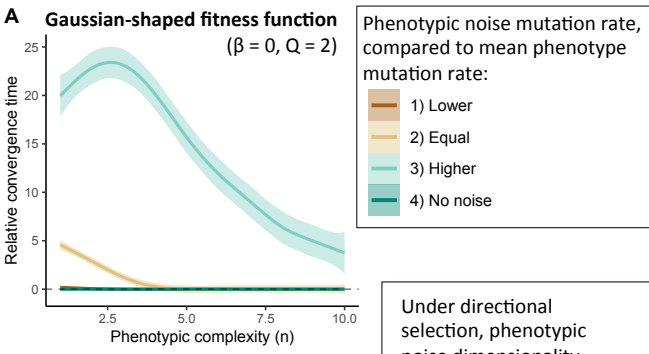
3. PHENOTYPIC NOISE DIMENSIONALITY REDUCTION



For multiple phenotypic characters under directional selection, we demonstrate that the best phenotypic noise configuration is **aligned and fully correlated with the direction of the fitness optimum**.

Example:
Simulation for two phenotypic characters:
• Initial distance: 4 units,
• Population size: 1,000,
• Mutation rate: 1e-3,
• mutation size: 0.01.

4. PHENOTYPIC NOISE PROMOTES ADAPTIVE EVOLUTION AND DECREASES THE COST OF COMPLEXITY



Under directional selection, phenotypic noise dimensionality reduction and alignment with fitness optimum promotes the fixation of beneficial mutations and **strongly decreases the cost of complexity**.

Experimental results on Yeast (Metzger et al. 2015) suggest that phenotypic noise evolves faster than mean phenotype.

- **Phenotypic noise:** variability in phenotypes of isogenic organisms in constant environment, aka developmental noise, phenotypic heterogeneity, cellular noise, biological noise, intra-genotypic variability, ...
- **Directional selection:** selection far from fitness optimum characterized by a convex (positive second derivative) fitness landscape.
- **Stabilizing selection:** selection close to fitness optimum characterized by a concave fitness landscape.
- **Adaptive evolution:** capacity of increasing mean population fitness as measured by the rate of increase of the log-fitness with respect to the mean phenotype.
- **Cost of complexity:** Reduction of the fraction of beneficial mutations when the number of phenotypic characters under selection increases.

Selected references:

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 (5) Zhang et al (2009) Mol Sys Biol 5:299; Draghi et al (2019);