Phenotypic Noise and the Cost of Complexity

Charles Rocabert, Guillaume Beslon, Carole Knibbe, Samuel Bernard

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Charles Rocabert[1,2], Guillaume Beslon[1,3], Carole Knibbe[1,4], Samuel Bernard[1,5]
1. Inria, France
2. Synthetic and Systems Biology Unit, BRC, Szeged, Hungary
3. CNRS UMR5205 LIRIS, INSA Lyon, France
4. INSERM U1060 CarMeN, INSA Lyon, France
5. CNRS UMR5208 Institut Camille Jordan, Univ Lyon 1, France

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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 adaptative evolution under directional and/or stabilizing selection if the **logarithmic fitness plateaus**.

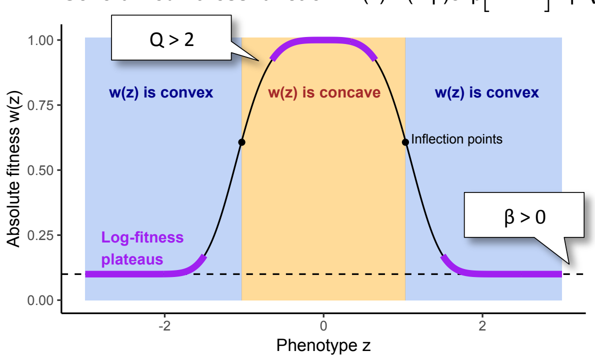
For multiple phenotypic characters under selection, the phenotypic noise evolves to a one- dimensional noise aligned with the direction of the fitness optimum.

• 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 landcape (single character)

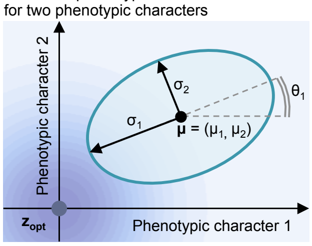
Generalized fitness function: $w(z) = (1-\beta)\exp\left[-\alpha z^Q\right] + \beta$ **(5)**



	Stabilizing selection (close to the fitness optimum)		Directional selection (far from the fitness optimum)	
Parameters	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

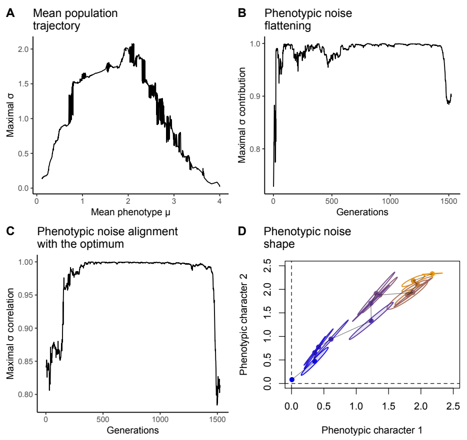
Evolvable phenotypic noise for two phenotypic characters



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 $z \sim N_n(\boldsymbol{\mu}, \boldsymbol{\Sigma})$

3. Phenotypic noise dimensionality reduction

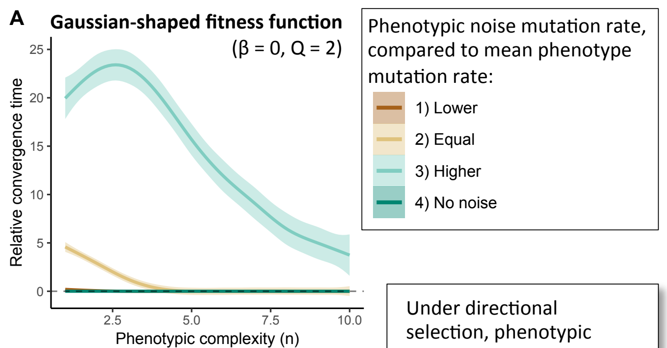


For multiple phenotypic characters under directional selection, we demonstrate that the best phenotypic noise configuration is **aligned and fully correlated with the direction of the fitness optimum.**

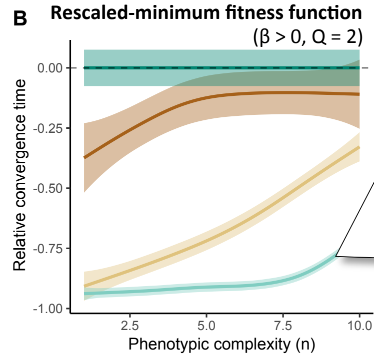
Example:
Simulation for two phenotypic characters:
- Initial distance: 4 units,
- Population size: 1,000,
- Mutation rate: 1^e-3,
- mutation size: 0.01.

4. Phenotypic noise promotes adaptive evolution and decreases the cost of complexity

A **Gaussian-shaped fitness function** (β = 0, Q = 2)



B **Rescaled-minimum fitness function** (β > 0, Q = 2)



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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