Disruptive selection and evolutionary branching

What happens after convergence to a singular strategy?

Day 1 described gradual evolution under directional selection using :

$$\rho(y, x) = 1 + (y - x)S(x) + O\big((y - x)^2\big)\,. \tag{1}$$

- The sign of $S(x)$ determines the direction of gradual evolution.
- A singular strategy x^* satisfies $S(x^*) = 0$.
- If $S'(x^*) < 0$, nearby resident populations evolve towards x^*.

At x^*, the first-order term vanishes. We therefore need to examine the curvature of invasion fitness.

The Hessian characterises selection at a singular strategy

Let $\epsilon = y - x^*$. At a singular strategy,

$$\rho(y, x^*) = 1 + \epsilon \underbrace{S(x^*)}_{=0} + \frac{\epsilon^2}{2} H(x^*) + O(\epsilon^3), \qquad H(x^*) = \left. \frac{\partial^2 \rho(y, x)}{\partial y^2} \right|_{y=x=x^*}. \quad (2)$$

- $H(x^*) < 0$: any nearby mutant is disfavoured; selection is **stabilising**.
- $H(x^*) > 0$: any nearby mutant can invade; selection is **disruptive**.

Different notions of stability

Can gradual evolution reach x^*?

$$S'(x^*) < 0 \tag{3}$$

Populations with nearby resident phenotypes on either side evolve towards the singular strategy.

Can nearby mutants invade x^*?

$$H(x^*) < 0 \tag{4}$$

No. The invasion fitness $\rho(y, x^*)$ has a local maximum at $y = x^*$.

Continuously Stable Strategies

A singular strategy satisfying both $S'(x^*) < 0$ and $H(x^*) < 0$ is therefore **convergence stable and locally uninvadable**: gradual evolution takes the population there, and selection keeps it there.

This is what we expect in a maximisation problem. For example, if a trait affects only an individual's fecundity and does not change its ecological interactions, evolution can lead to the phenotype that maximises fecundity.

But there can actually be four types of singularities

$S'(x^*)$	$H(x^*)$	Local interpretation
negative	negative	x^* is convergence stable and uninvadable
negative	positive	x^* is convergence stable but invadable
positive	negative	x^* cannot be accessed gradually but is uninvadable: "Garden of Eden"
positive	positive	x^* is neither convergence stable nor uninvadable

Evolutionary branching: the emergence of polymorphism

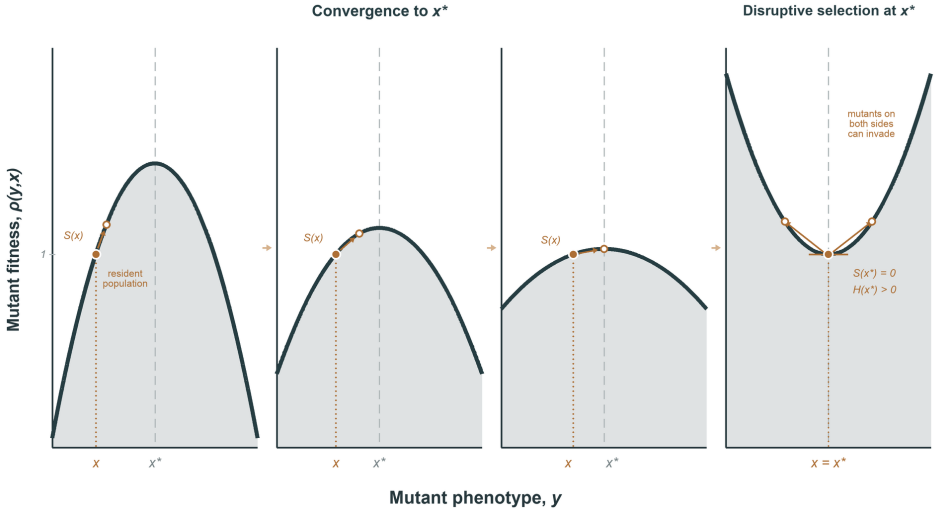
When

$$S(x^*) = 0, \qquad S'(x^*) < 0, \qquad H(x^*) > 0 \tag{5}$$

the population first evolves towards x^*. But once there, x^* is locally invadable: rare mutants on either side of the resident phenotype can invade.

In fact, they not only invade but also coexist, and this polymorphism replaces the monomorphism at x^*. Subsequent mutations then drive the two lineages apart, such that the ancestral lineage gives rise to two diverging branches. We call this **evolutionary branching**.

Evolutionary branching: the emergence of polymorphism

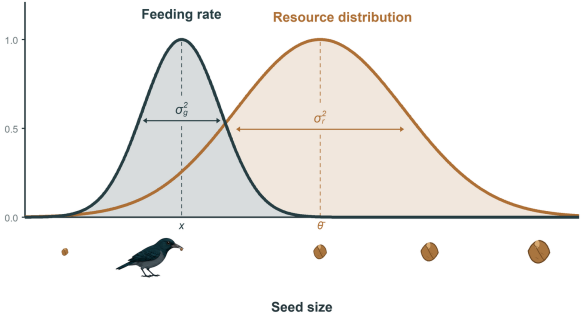


Resource specialisation through competition

Consumers exploit resources that vary in a quantitative character, such as seed size, prey speed or corolla length.

A consumer performs best when its trait matches the resource character. Consumers using the same resource compete with one another.

Let's formalise this on the white board.



The population first evolves towards the average resource

Doing the maths, we get

$$S(x) = \frac{\bar{\theta} - x}{\sigma_g^2}. \tag{6}$$

So directional selection leads to

$$x^* = \bar{\theta}. \tag{7}$$

Why? Because this is where food is most abundant. A mutant closer to $\bar{\theta}$ is better matched to the available resources, gets more food and can invade.

At the average resource, rare variants can do better

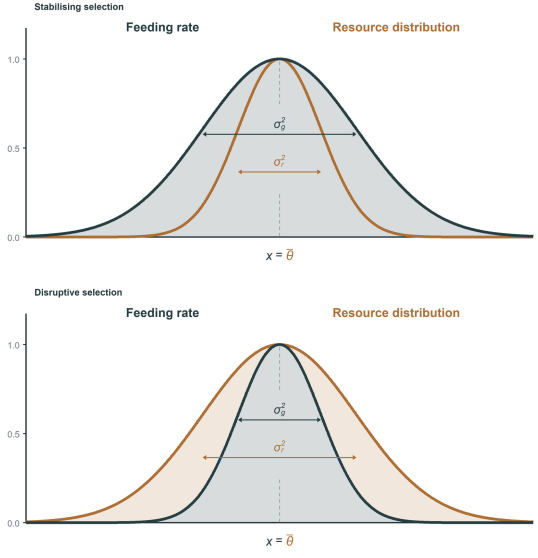
Now continuing the calculation, we get the Hessian at x^*:

$$H(x^*) = \frac{\sigma_r^2 - \sigma_g^2}{\sigma_g^4}. \qquad (8)$$

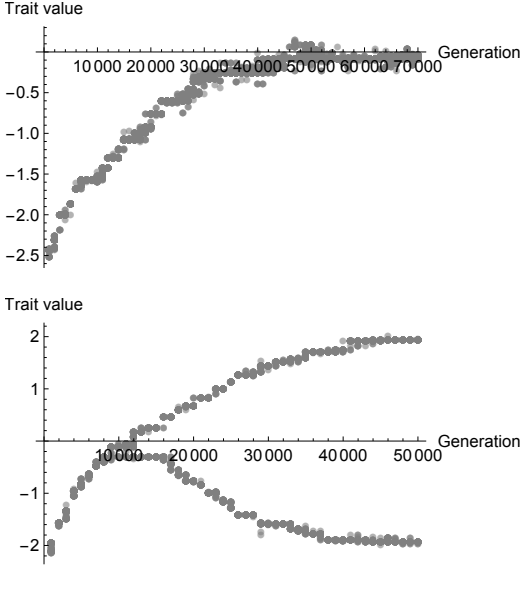
So selection is disruptive when

$$\sigma_r^2 > \sigma_g^2. \qquad (9)$$

In other words, the resource distribution must be wider than the range of resources that each consumer can efficiently exploit.



Simulations help see where branches go



Branching requires a negative feedback

At a candidate evolutionary branching point, $S'(x^*) < 0$ and $H(x^*) > 0$. Together, these imply

$$\left.\frac{\partial^2 \rho(y,x)}{\partial y\, \partial x}\right|_{y=x=x^*} < 0. \tag{10}$$

i.e. when the population trait increases, selection favours mutants with a lower trait, and vice versa. Rare individuals therefore gain an advantage by differing from the common phenotype.

This is a feedback because the common phenotype changes its ecological, social or genetic context, and this context changes which phenotype is favoured. As a mutant spreads, it changes that context again.

Near x^*, this allows two nearby phenotypes to invade one another when rare, coexist and then diverge.

Branching may be a common source of diversity

Competition and other negative population feedbacks are widespread in nature. Opportunities for evolutionary branching may therefore also be common.

- Repeated branching may contribute to ecological diversification and adaptive radiation.
- Branching also occurs in sexual diploids, but mating between divergent types continually produces intermediate heterozygotes.
- Selection can then modify the genetic architecture of the trait to reduce this genetic load.
- Branching leads to speciation only when ecological divergence becomes coupled to assortative mating and reproductive isolation. Otherwise, diversity remains within a single species.

Steps in Good Modelling Practice

We can now go back to the good-practice steps from yesterday:

1. Specify a clear, individual-based life cycle
2. Identify the evolving trait and the genetic system
3. Characterise the resident equilibrium and invasion fitness $\rho(y, x)$; check that $\rho(x, x) = 1$
4. Analyse invasion fitness: use the selection gradient $S(x)$ to locate singular strategies x^* and assess their convergence stability
5. **At a singular strategy, use the Hessian $H(x^*)$ to determine whether selection is stabilising or disruptive**
6. **Check what happens after invasion: can the phenotypes coexist, and where do the branches go? This may require an individual-based simulation or some extra maths (a story for another time!)**