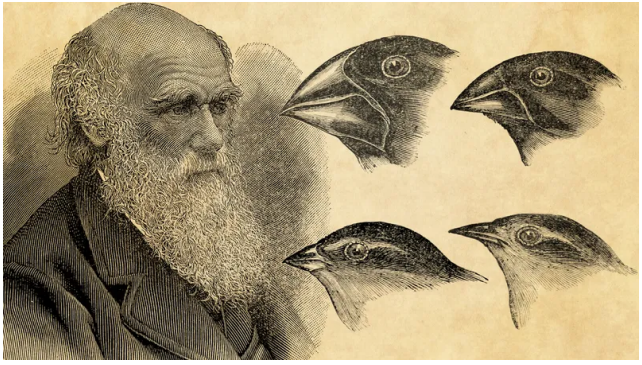
Inferring gradual evolution from invasion analyses

Darwinian evolution and the process of adaptation

A related question : can a population become uninvadable through gradual adaptive evolution, i.e. when mutations arise continuously with small effect on trait expression ?

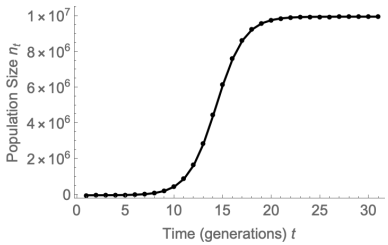


Adaptive dynamics : a formal approach to gradualism

The main assumptions behind the approach :

- populations are large – large enough so we can ignore genetic drift once the mutant has established ;
- adaptive mutations are rare – rare enough so that a population has time to reach its ecological equilibrium between the appearance of different relevant mutations.
- adaptive mutations have small effects on trait expression.

Demographics of a population with max. replication rate of 2



Waiting time for a beneficial mutation to establish $\mathbb{E}[T] = \frac{1}{2sN\mu}\left[1 + \mathcal{O}(s)\right] = 250\left[1 + \mathcal{O}(s)\right]$ generations. [1]

Invasion fitness under small mutational effects

If mutations have weak phenotypic effect (i.e. $y - x$ is small), we can Taylor expand invasion fitness in y around $y = x$ to determine the fate of mutant y :

$$\rho(y, x) = 1 + \epsilon\, S(x) + \mathcal{O}(\epsilon^2), \tag{6}$$

where $\epsilon = y - x$ and

$$S(x) = \left.\frac{\partial \rho(y, x)}{\partial y}\right|_{y=x} \tag{7}$$

is the selection gradient, which can be used to characterise gradual evolution.

Directional selection is captured by the selection gradient

Provided $S(x) \neq 0$, whether or not $\rho(y, x) > 1$ is determined by $\epsilon\, S(x)$ since

$$\rho(y, x) = 1 + \epsilon\, S(x) + \mathcal{O}(\epsilon^2) \tag{8}$$

where $\epsilon = y - x$. Specifically:

- When $S(x) > 0$, selection favours the invasion of mutants that increase trait value ($y > x$).
- When $S(x) < 0$ selection favours the invasion of those that decrease trait value ($y < x$).

Substitution and ecological changes under directional selection

For a large class of models, it has been shown that [2]:

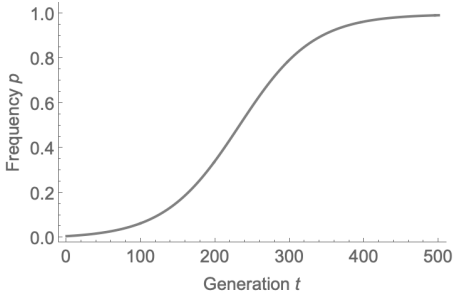
Invasion implies substitution under directional selection

When selection is weak (i.e. ϵ small), a mutant that invades fixes.

In fact, the change in mutant frequency p once it has established is given by

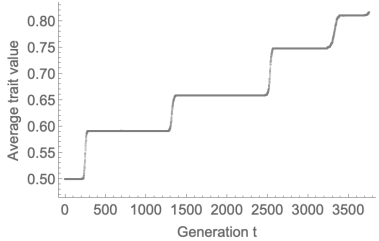
$$\Delta p = p(1-p)\epsilon S(x) + \mathcal{O}(\epsilon^2), \qquad (9)$$

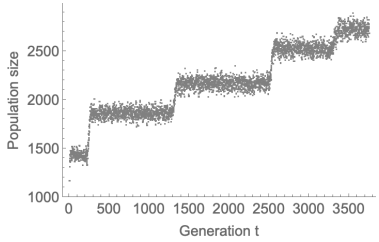
i.e. the direction of selection is frequency-independent to first order.



The trait substitution sequence under directional selection

These results mean that over time, trait evolution proceeds in a sequence of substitutions whereby under the constant influx of mutations, positively selected mutants that manage to invade rapidly sweep to fixation, so that the population effectively "jumps" from one trait value to another, interspersed by periods of stasis during which the population is essentially monomorphic.



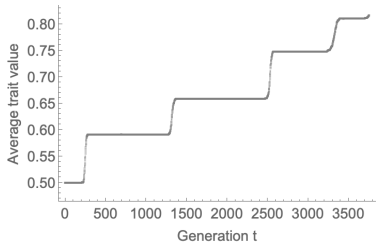


Phenotypic dynamics under directional selection

A deterministic small-step approximation to the trait substitution sequence is

$$\frac{dx}{d\tau} = k(x)S(x) \qquad (10)$$

where τ is appropriately scaled evolutionary time and $k(x) > 0$ depends on mutational input.



Fixed points and their stability

To understand the long-term behaviour of a dynamical system, we first identify its **fixed points**: values at which the system no longer changes.
Here, a fixed point x^* satisfies

$$0 = k(x^*)S(x^*). \tag{11}$$

Since $k(x^*) > 0$, an interior fixed point is therefore a singular strategy such that

$$S(x^*) = 0. \tag{12}$$

We then determine its **stability**: if the resident phenotype is slightly perturbed away from x^*, does it move back towards it or further away?
At a fixed point, the slope of trait dynamics is

$$\frac{d}{dx}\left[k(x)S(x)\right]\Big|_{x=x^*} = k(x^*)S'(x^*). \tag{13}$$

Since $k(x^*) > 0$, stability is entirely determined by the sign of $S'(x^*)$.

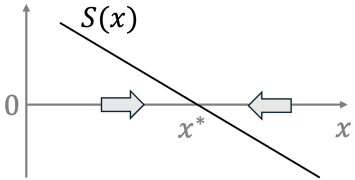
Convergence towards an evolutionary attractor

Phenotypic dynamics may thus converge to a trait value x^* such that

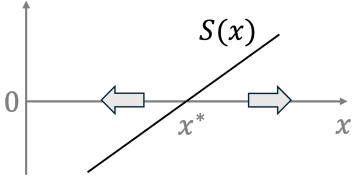
- $S(x^*) = 0$
- $S'(x^*) < 0$

Such a trait value is said to be **convergence stable**. Otherwise the population may continuously evolve larger trait values ("open ended evolution") or until it hits a minimum or maximum (the boundary of trait space).

Convergence, $S'(x^*) < 0$



Divergence, $S'(x^*) > 0$



Steps in Good Modelling Practice

A typical workflow for an invasion analysis :

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 selection gradient $S(x)$ to locate singular strategies x^* and assess their convergence stability

Summary

- Evolutionary invasion analysis offers powerful tools to study phenotypic evolution under well-defined eco–evo processes.
- It relies on a separation of timescales between fast ecological dynamics (density change, trait-mediated environment) and slower evolutionary dynamics (mutation, invasion, substitution).
- The key quantity is invasion fitness, a gene-level measure of fitness.

References

[1] Imhof, M. and Schlötterer, C. (2001). Fitness effects of advantageous mutations in evolving *Escherichia coli* populations. *PNAS* **98**, 1113–1117.

[2] Priklopil, T. and Lehmann, L. (2020). Invasion implies substitution in ecological communities with class-structured populations. *Theoretical Population Biology* **134**, 36–52.

[3] Reeve, H. K. and Sherman, P. W. (1993). Adaptation and the goals of evolutionary research. *The Quarterly Review of Biology* **68**, 1–32.

Extra : More on the trait substitution sequence

Let $\epsilon = y - x$. In a resident population of census size $\hat{N}(x)$, mutants with effects between ϵ and $\epsilon + d\epsilon$ appear at rate

$$\hat{N}(x)\mu(x)m(\epsilon \mid x)\, d\epsilon,$$

where $\mu(x)$ is the per-capita mutation rate and $m(\epsilon \mid x)$ is the distribution of mutational effects.

If invasion implies substitution, the mean trait change per generation is

$$b(x) = \hat{N}(x)\mu(x) \int \epsilon\, m(\epsilon \mid x)\pi(x + \epsilon, x)\, d\epsilon.$$

The trait substitution sequence is a random sequence of jumps; $b(x)$ is its mean rate of change:

$$\text{mutation supply} \times \text{trait change} \times \text{probability of invasion}.$$

Extra : More on the trait substitution sequence

For small mutational effects, the preceding results give

$$\rho(x+\epsilon,x)-1=\epsilon S(x)+\mathcal{O}(\epsilon^2),\qquad \pi(x+\epsilon,x)=\frac{2[\epsilon S(x)]_+}{\mathrm{Var}(K\mid x)}+\mathcal{O}(\epsilon^2),$$

where $[a]_+=\max(a,0)$ and $\mathrm{Var}(K\mid x)$ is the offspring variance of a neutral mutant in the resident environment x. For symmetric $m(\epsilon\mid x)$, with variance $\sigma^2_{\mathrm{mut}}(x)$, define

$$N_{\mathrm{e}}(x):=\frac{\hat{N}(x)}{\mathrm{Var}(K\mid x)}.$$

The leading-order mean dynamics, with τ measured in generations, are then

$$\frac{dx}{d\tau}=k(x)S(x),\qquad k(x)=N_{\mathrm{e}}(x)\mu(x)\sigma^2_{\mathrm{mut}}(x)>0.$$

Here $\hat{N}(x)\mu(x)$ is the actual mutation supply, $\mathrm{Var}(K\mid x)$ controls stochastic establishment, and $S(x)$ determines the direction of evolution.