

Summer school in Modelling for Evolutionary Biology

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Course objectives

1. Learn fundamentals of modelling for evolutionary biology using invasion analyses
2. Learn conceptual bases of adaptation
3. Learn formalisation of a biological scenario
4. Learn to communicate modelling research to other biologists

Course organisation and material

- **Lectures** : learn the basics of modelling and to interpret natural selection in ecologically relevant scenarios
- **Guided exercise sessions** : apply these basics to problems in evolutionary ecology and gain practice
- **Group work and presentations** : see what a (short) theory project might look like and learn how to communicate modelling results
- **Research seminars** : get an idea of some research programs built or guided by theory in evolutionary biology and ecology
- For lecture slides and exercise sheets, visit :
<https://lab-mullon.github.io/MEB>

Schedule

Period	Monday	Tuesday	Wednesday	Thursday	Firday	Saturday
09h00 - 10h30	Welcome and Research seminar (Sara Mitrí)	Modelling heterogeneous populations	Modelling group-structure	Group formation	Group work	Group Presentations
10h30 - 11h00	Coffee					
11h00 - 12h30	Introduction to Invasion analyses	Evolution in age - structured populations	Social Evolution	Group work	Group work	Group Presentations
12h30 - 14h00	Lunch					
14h00 - 15h30	Evolution in homogeneous populations	Guided exercises	Guided exercises	Group work	Group work	Research seminar (Laurent Lehmann)
15h30 - 16h00	Coffee					
16h00 - 17h30	Guided exercises	Guided exercises	Guided exercises	Group work	Group work	Roundtable discussion
17h30 - 18h30	Guided exercises	Free	Workshop on best practices	Group work	Group work	
18h30	Welcome drinks		Dinner	Dinner	Dinner	Closing dinner

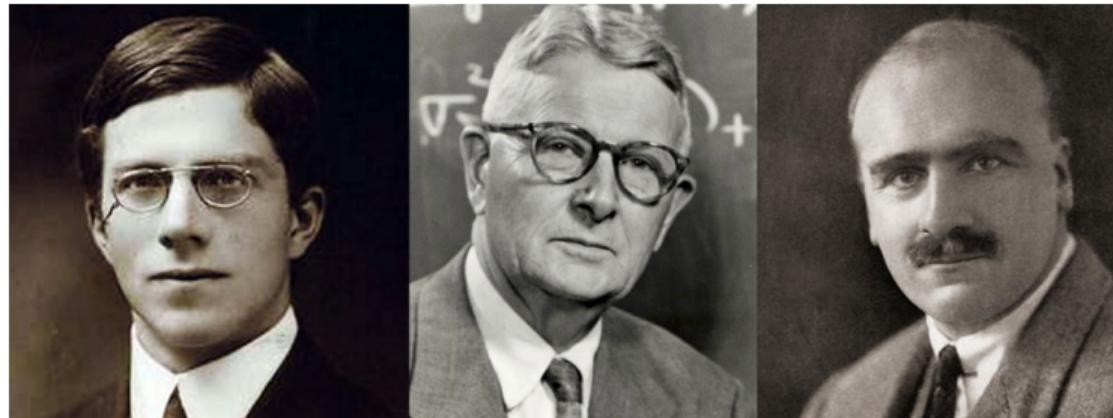
People



Modelling for evolutionary biology

Mathematical models in evolutionary biology

Modelling and mathematical formalisation have been integral to the theory of evolution.



Three main formalisms

- Population genetics : model allele frequency change – useful for molecular evolution (mutation, selection, genetic drift, recombination)
- Quantitative genetics : model changes in phenotypic distribution – useful for trait evolution (heritability, selection gradient)
- Invasion analyses : model long term trait evolution – useful for understanding adaptation (ESS, adaptive dynamics)

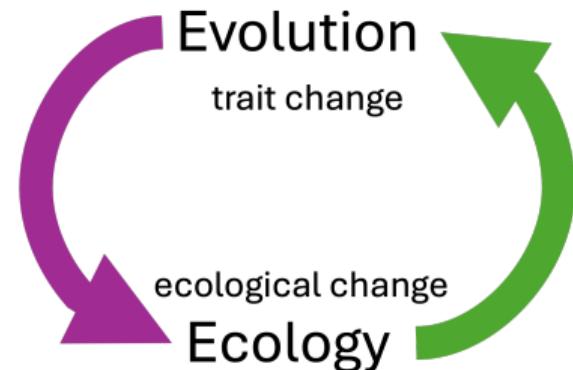
Invasion analysis for evolutionary ecology problems

Evolutionary ecology is concerned with questions at the intersection of ecology and evolution. Broadly, how interactions among individuals and their environments shape traits through selection and the consequences of the resulting evolutionary change.

The role of adaptation in shaping :

- Life-history
- Social behaviour
- Interspecific interactions

e.g. change in fecundity, boldness, dispersal, virulence



e.g. change in density, predator behaviour, prey distribution, host resistance

Goal of these lectures and exercises

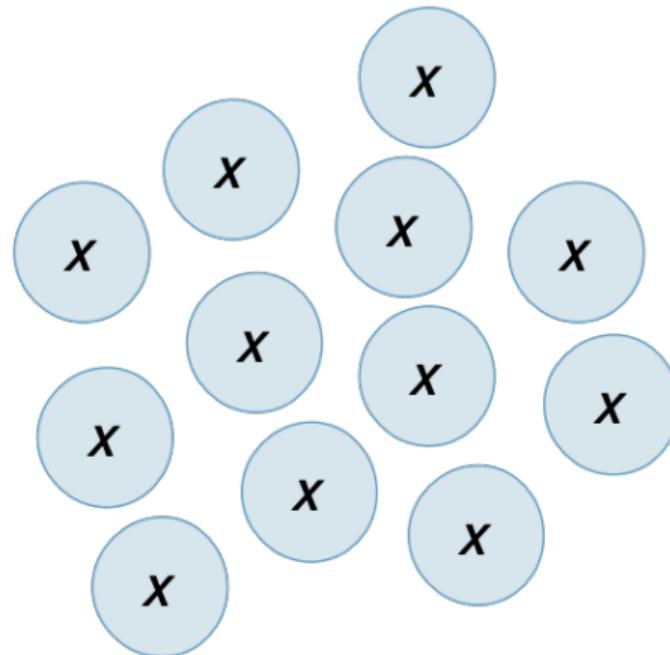
- Go over the bases in formalising and analysing these problems
- Derive the main equations describing how selection operates in ecologically relevant situations to see where they come from and help us interpret adaptation
- Apply these equations to specific scenarios during exercise sessions

Please interrupt me, ask questions, and come to the white board ! This is supposed to be interactive. And don't hesitate to try to relate this to your own research with me or the assistants.

Invasion analyses : the very basics

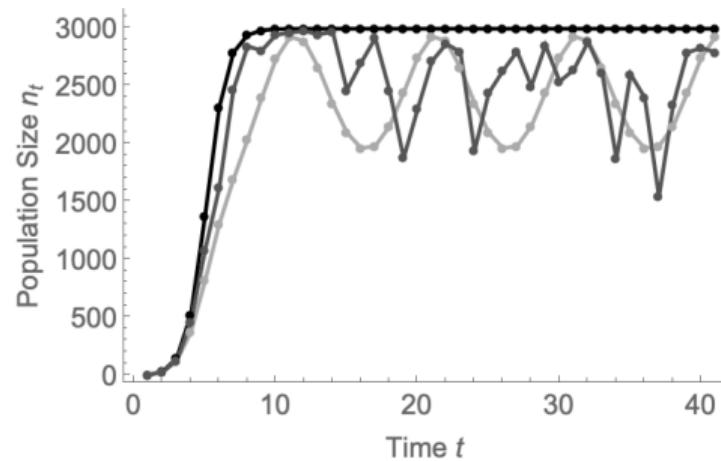
A resident population

Suppose we are interested in the evolution of a continuous trait, i.e. whose value belong to the real numbers (e.g. attack rate on a prey, investment into parental care, or proclivity to disperse). Assume that the individuals of a large asexual population of haploids all express the same genetic value $x \in X$ for this trait (where $X \subseteq \mathbb{R}$ is the space of all strategies).



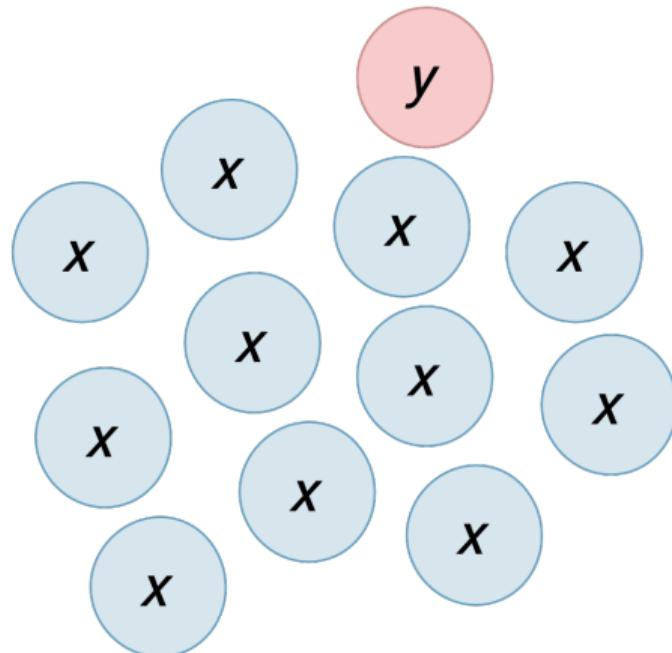
The environment or state of the resident population

Individuals can be in different states (e.g. physiology or habitats). And if the population experiences demographic or environmental fluctuations, we assume these are ergodic i.e. they explore all states over time (allows long-term averages to be well-defined and independent of initial conditions). We wait long enough for fluctuations to reach a stationary state denoted $\hat{N}(x)$ e.g. the population may settle at an equilibrium size.



A mutant type

Against this background, we introduce a mutation that causes the expression of an alternative trait value in its bearer $y \in X$. Will this mutant invade—i.e. establish, or will it be lost? For invasion to be possible, the initial mutant must give rise to a lineage whose members, on average, produce more than one other mutant. In that case, the mutant has a chance to establish and eventually fix.

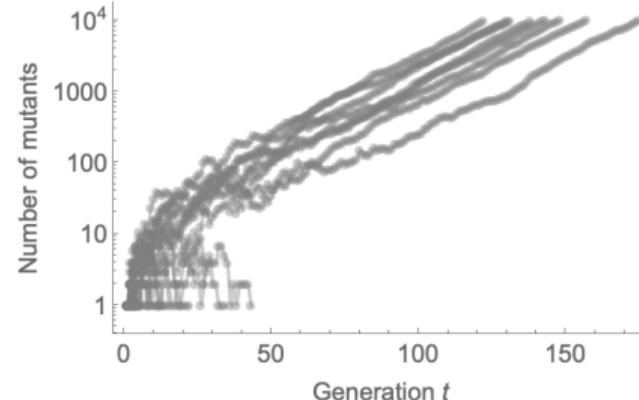
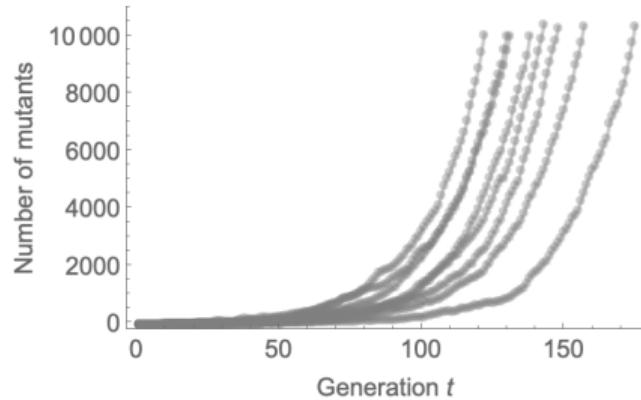


Invasion fitness : definition

To make this more rigorous, we define the **invasion fitness** $\rho(y, x)$ of a mutant y in a resident population x as its **geometric growth rate**: the per-capita number of mutant copies produced per time step asymptotically, i.e. as

$$\log(\rho(y, x)) = \lim_{t \rightarrow \infty} \frac{1}{t} \log \left(\lim_{N_r \rightarrow \infty} \frac{1}{N_r} \sum_{j=1}^{N_r} \frac{n_j(t)}{n_j(0)} \right) \quad (1)$$

where $n_j(t)$ is the number of mutant copies in replicate j out of N_r .



Invasion fitness determines whether the mutant can invade

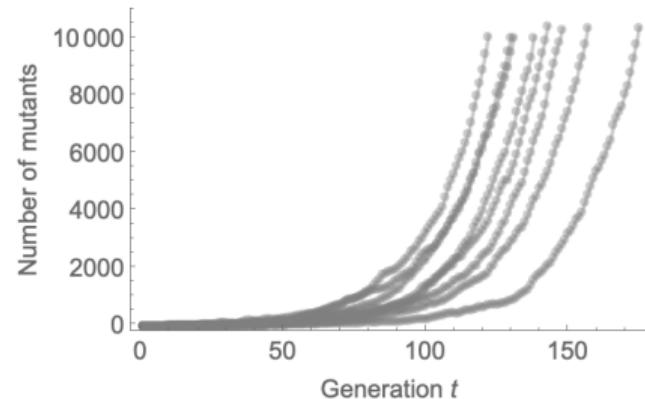
Result from branching process theory

In a branching process (where each mutant lineage reproduces independently and according to the same distribution, so offspring themselves form independent lineages at the next step):

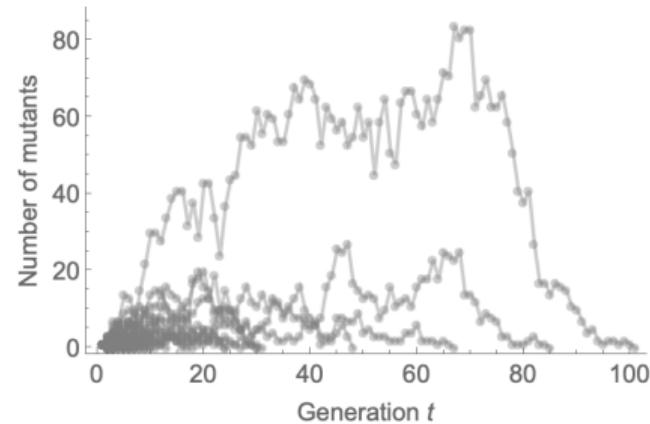
- If $\rho(y, x) \leq 1$, the mutant goes extinct with probability one.
- If $\rho(y, x) > 1$, extinction is no longer certain: the mutant lineage has a positive probability of persisting and spreading.

That is: if a mutant does not replace itself on average, it is doomed; if it does, it has a chance of establishing.

Invasion fitness determines whether the mutant can invade



Successful invasion ($\rho(y, x) > 1$)



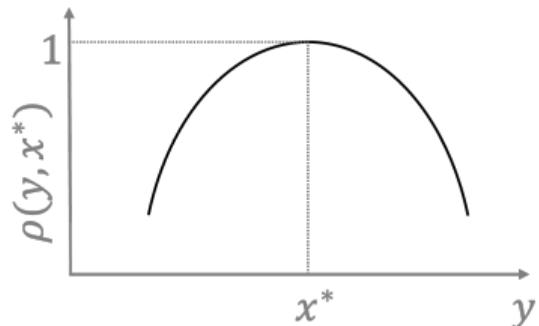
Certain extinction ($\rho(y, x) \leq 1$)

Uninvadability and the state of adaptation

A population monomorphic for x^* is **uninvadable** when

$$\rho(y, x^*) \leq 1 \quad \text{for all } y \in X, \quad (2)$$

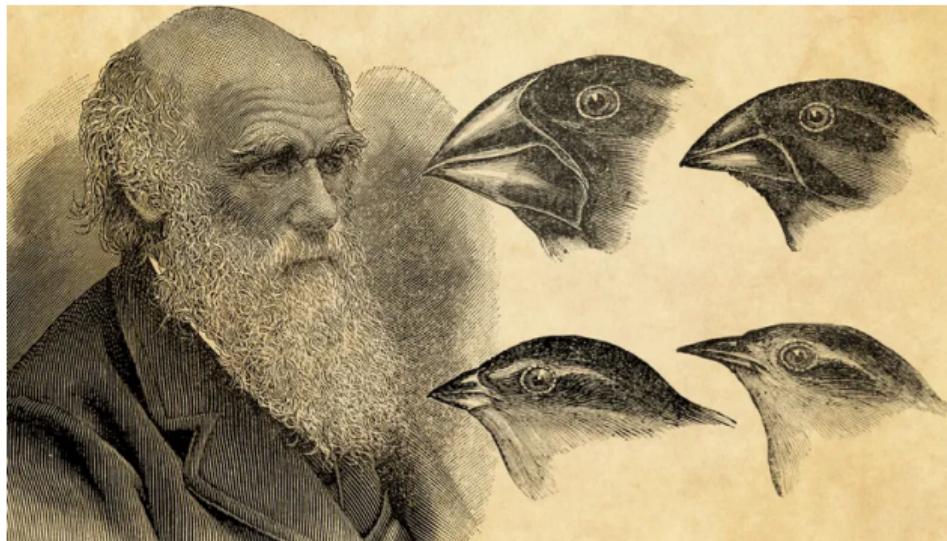
i.e. it is protected against invasion from all possible mutants. Since a neutral mutant has invasion fitness equal to one ($\rho(x, x) = 1$), eq. (2) means that x^* maximises invasion fitness. Thus, x^* satisfies the biological concept of an adaptation : “a variant that results in the highest fitness among a specified set of variants in a given environment” [1].



Inferring gradual evolution from invasion analyses

Darwinian evolution and the process of adaptation

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

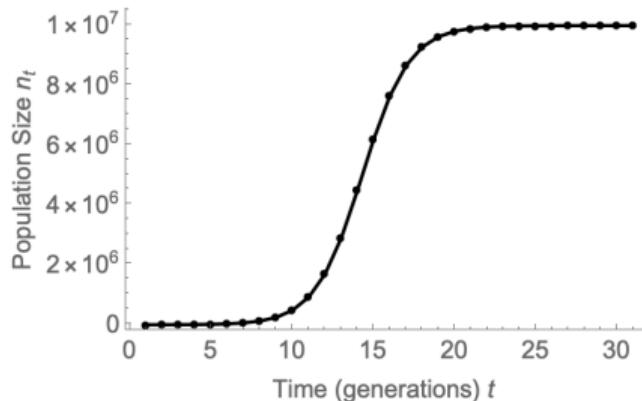


Adaptive dynamics : a formal approach to gradualism

The main assumptions behind the approach :

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

$$\approx \frac{1}{2sN\mu} = \frac{1}{2 \times 0.02 \times 10^7 \times 10^{-8}} = 250 \text{ generations. [2]}$$

Invasion fitness under small phenotypic variance

These assumptions allow us to use a Taylor expansion of invasion fitness in y around $y = x$ to determine the fate of mutant y :

$$\rho(y, x) = 1 + \epsilon S(x) + \frac{\epsilon^2}{2} H(x) + O(\epsilon^3), \quad (3)$$

where $\epsilon = y - x$ and

$$S(x) = \left. \frac{\partial \rho(y, x)}{\partial y} \right|_{y=x} \quad \text{and} \quad H(x) = \left. \frac{\partial^2 \rho(y, x)}{\partial y^2} \right|_{y=x} \quad (4)$$

are two key functions that : the selection gradient and the hessian, 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

$$\rho(y, x) = 1 + \epsilon S(x) + O(\epsilon^2) \quad (5)$$

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 :

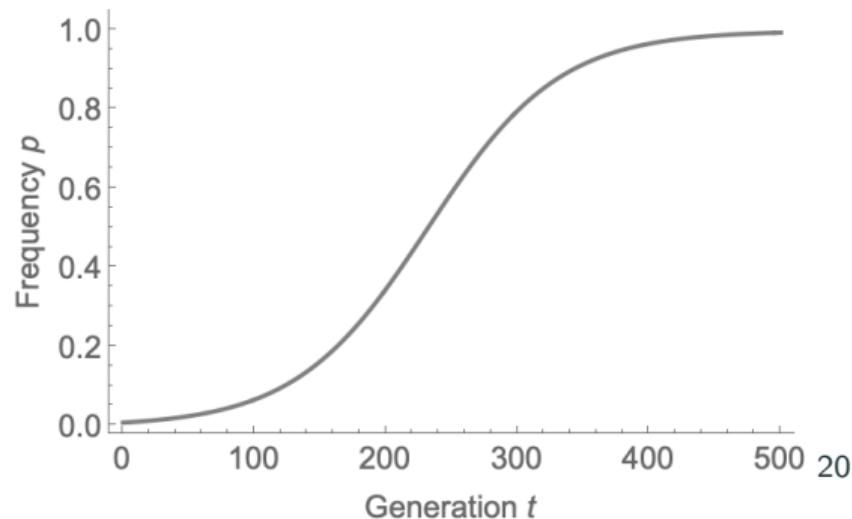
Invasion implies substitution under directional selection

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

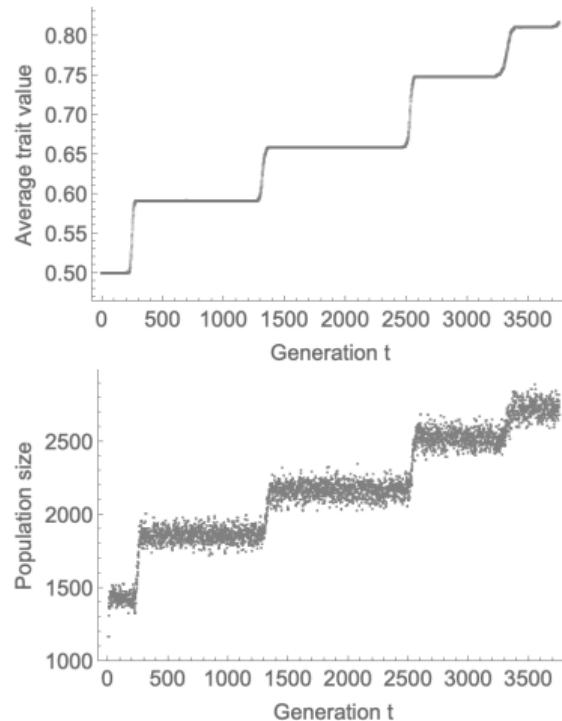
$$\Delta p = p(1 - p)\epsilon S(x) + \mathcal{O}(\epsilon^2), \quad (6)$$

i.e. the change is frequency-independent.



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.

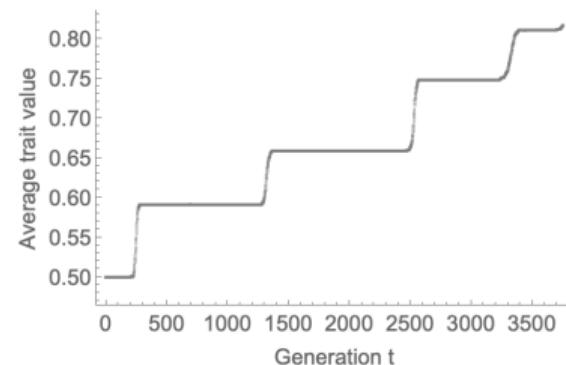


Phenotypic dynamics under directional selection

Under the trait substitution sequence,
the population evolves according to

$$\frac{dx}{d\tau} = k(x)S(x^*) \quad (7)$$

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



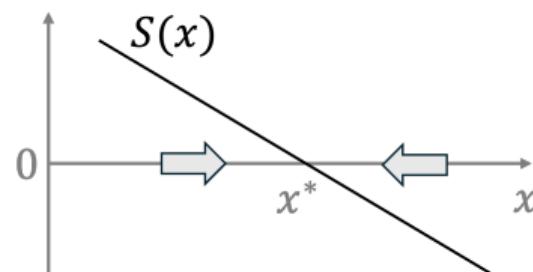
Convergence towards an evolutionary attractor

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

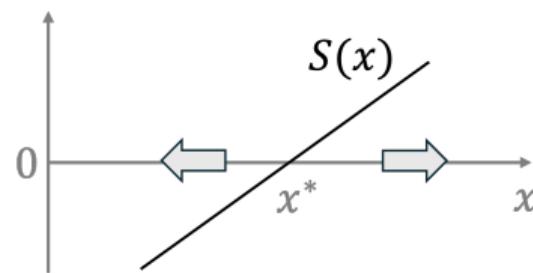
- $S(x^*) = 0$
- $S'(x^*) < 0$

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



The Hessian characterises selection once directional selection has subsided

Once the population expresses a convergence stable trait value x^* , selection is determined by $H(x^*)$:

$$\rho(y, x^*) = 1 + \epsilon \underbrace{S(x^*)}_{=0} + \frac{\epsilon^2}{2} H(x^*) + O(\epsilon^3) = 1 + \frac{\epsilon^2}{2} H(x^*) + O(\epsilon^3) \quad (8)$$

where $\epsilon = y - x^*$.

- When $H(x^*) < 0$, selection disfavours the invasion of *any* mutant, i.e. selection is **stabilising**.
- When $H(x^*) > 0$, selection favours the invasion of *any* mutant, i.e. selection is **disruptive**.

Convergence to an unininvadable trait value : convergence to an adapted monomorphic state

In a situation where there exists a trait value x^* such that

$$S(x^*) = 0 \text{ and } S'(x^*) < 0 \text{ and } H(x^*) < 0 \quad (9)$$

the population will gradually approach x^* and in the absence of extrinsic changes, remain there.

Evolutionary branching : the gradual emergence of polymorphism

In a situation where there exists a trait value x^* such that

$$S(x^*) = 0 \text{ and } S'(x^*) < 0 \text{ and } H(x^*) > 0 \quad (10)$$

the population will gradually approach x^* and then subsequently split into two lineages that will diverge and be maintained. This is due to reciprocal ecological and evolutionary changes leading the population up a peak that becomes a fitness valley.

Evolutionary branching leads to the maintenance of stable intra-specific variation and may form a basis to speciation

An example : consider a well-mixed population where individuals compete for a resource that varies in character (e.g. corolla tube lengths among flowers) and that exploitation is most efficient when individual trait (e.g. beak length in a hummingbird) matches the resource character. Say that individual with trait z exploits resource with character θ as $\alpha(z, \theta) = \exp\left(-\frac{(z-\theta)^2}{2\sigma_g^2}\right)$ and that the character is distributed according to a Normal distribution with (scaled) mean 0 and variance σ_r^2 .

Let's look into this on the white board.

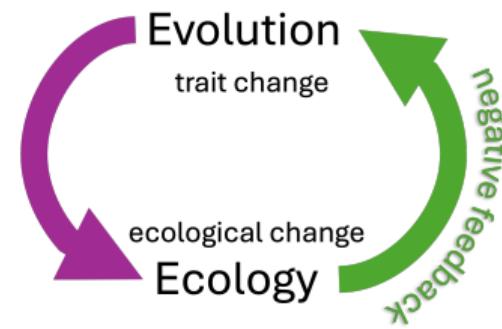
Negative trait-dependent selection is necessary for polymorphism

The two conditions for evolutionary branching

$S'(x^*) < 0$ and $H(x^*) > 0$ entail that
polymorphism requires that

$$\frac{\partial^2 \rho(y, x)}{\partial y \partial x} \Big|_{y=x=x^*} < 0 \quad (11)$$

i.e. that as mutant and resident traits diverge,
mutant fitness increase. More intuitively, there
must be a negative evolutionary feedback (via
ecology) for diversity to emerge.



The different time scales of ecological and evolutionary changes

The framework above gives a well-defined process of ecological and evolutionary changes experienced by a population. From fast to slow timescale :

- Ecological changes
- Mutant invasion and fixation
- Evolutionary branching

It gives us a platform to model Darwinian dynamics in a wide range of ecologically relevant situations. For the rest of the course, we'll be interested in specifying $S(x)$ and $H(x^*)$ for various scenarios to understand and model gradual evolution.

Evolution in well-mixed and homogeneous populations

Invasion fitness is a gene-level measure of reproduction

One fundamental aspect of $S(x)$ and $H(x^*)$: they are defined from invasion fitness $\rho(y, x)$. This is a measure of reproductive success at the level of the gene (more specifically its lineage) that causes the expression of y . On conceptual and empirical grounds, it is however often desirable to understand selection at the level of the individual. In populations that are homogeneous and well-mixed, this is not a problem (in the absence of genetic conflicts within individuals).

What do we mean by well-mixed and homogeneous

These are populations where individuals interact at random (“panmixia”), and the effect of the trait on individual survival and reproduction is the same on every individual. So for the purpose of invasion analyses, the *only* relevant difference among individual is whether they carry the mutant allele or not. This precludes sex-, age-, state-, generation- or habitat-specific fitness effects (i.e. no temporal, spatial or physiological heterogeneity).

Invasion fitness = Individual fitness in those populations

To see this, let n_t be the number of mutant individuals at some demographic time point t . In a homogeneous and well-mixed population invasion fitness is given by

$$E[n_{t+1}|n_t] = \rho(y, x)n_t = w(y, x)n_t, \quad (12)$$

where $w(y, x)$ is *individual* fitness: the expected number of direct descendants produced between two time points by a mutant with trait y , when the resident population expresses x .

The equivalence between invasion and individual fitness in well-mixed and homogeneous populations offers several advantages:

- *Conceptual*. Clear view on adaptation : selection leads to the expression of traits that maximise the reproductive success of its bearer (w/o conflicts).
- *Practical/Empirical*. If individual fitness increases with an intermediate quantity (e.g. fecundity, payoff) then any x^* that maximises such quantity also maximises individual fitness. This becomes a proxy, often easier to manipulate or estimate empirically.
- *Computational*. It is typically only a matter of bookkeeping to piece together an individual fitness function $w(y, x)$ for a given scenario. This makes modelling very efficient.

An example with density and frequency-dependence

Consider a well-mixed population with the following life cycle : (1) Each adult individual produces offspring with fecundity that depends on their trait and those expressed by the rest of the population (frequency-dependence). (2) Offspring survive with a probability that decreases with population size (density-dependence). (3) Adults either survive or die.

Let's study this on the white board and if we have time, go through an example of evolutionary suicide.

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 invasion fitness $\rho(y, x)$ and resident equilibrium (s.t.
 $\rho(x, x) = 1$)
4. Analyse invasion fitness: first use selection gradient $S(x)$ to locate singular
strategies x^* and assess their convergence stability, then apply the Hessian
 $H(x^*)$ to test for uninvadability or evolutionary branching
5. Validate and extend results with individual-based simulations and more
complex scenarios

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, branching).
- The key quantity is invasion fitness, a gene-level measure of fitness.
- In well-mixed, homogeneous populations and no intra-individual genetic conflict, invasion fitness aligns with individual fitness so selection tends to maximise individual fitness.
- Even so, selection maximises ecological or demographic variables only under special conditions; e.g. density can't be maximised under frequency-dependence.

References i

-  Reeve HK, Sherman PW. 1993 Adaptation and the goal of evolutionary research. *The Quarterly Review of Biology* **68**, 1–32.
-  Imhof M, Schlötterer C. 2001 Fitness effects of advantageous mutations in evolving *Escherichia coli* populations. *Proceedings of the National Academy of Sciences* **98**, 1113–1117.