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

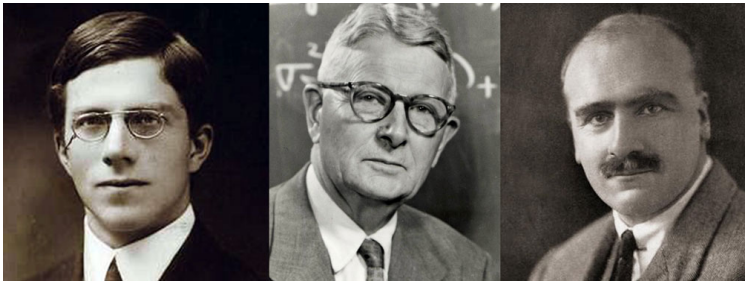
	Monday 31.08.2026	Tuesday 01.09.2026	Wednesday 02.09.2026	Thursday 03.09.2026	Friday 04.09.2026	Saturday 05.09.2027
08h30	Welcome coffee					
09h00						
09h30	Invasion analyses	Polymorphism	Social evolution	Group formation	Group work	Group presentation
10h00						
10h30	Coffee	Coffee	Coffee	Coffee	Coffee	Coffee
11h00						
11h30	Guided exercices	Guided exercices	Guided exercices	Group work	Group work	Group presentation
12h00						
12h30						
13h00	Lunch	Lunch	Lunch	Lunch	Lunch	Lunch
13h30						
14h00			Seminar S Lehtinen			Seminar L Lehmann
14h30	Gradual evolution	Class strcuture		Group work	Group work	
15h00			Coffee			Conclusion
15h30	Coffee	Coffee		Coffee	Coffee	Coffee
16h00	Seminar S Mitri					
16h30		Guided exercices	Free time	Group work	Group work	
17h00						
17h30	Guided exercices					
18h00						
18h30	Apéritif			Dinner	Dinner	Dinner in town

People

Modelling for evolutionary biology

Mathematical models in evolutionary biology

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



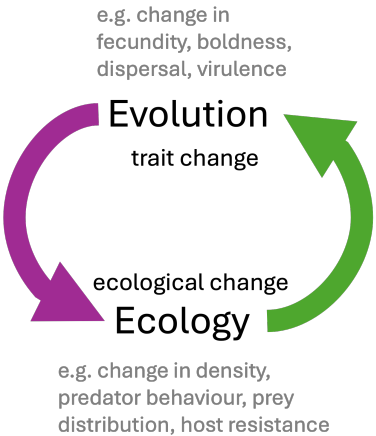
Three main formalisms

- Population genetics : model allele frequency change – useful for molecular evolution (mutation, selection, genetic drift, recombination)
- Quantitative genetics : model short term 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



Goal of these lectures and exercises

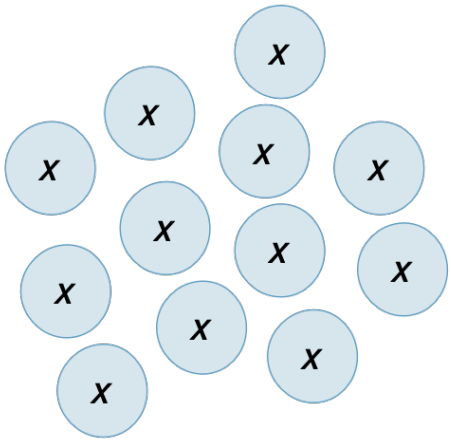
- Go over the bases in formalising and analysing these problems
- Derive the main equations describing how selection operates in ecologically relevant situations to see where they come from and help us interpret adaptation
- Apply these equations to specific scenarios during exercise sessions

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

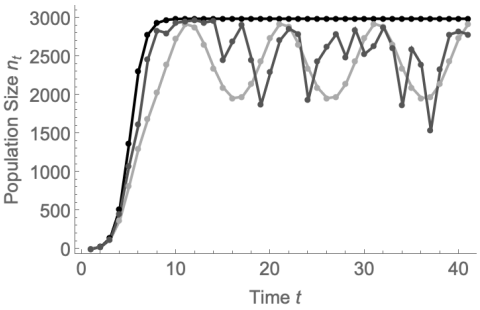
A resident population

Suppose we're interested in the evolution of a continuous trait, i.e. whose value belongs to the reals (e.g. attack rate on a prey, investment into parental care, or beak morphology). 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). We can discuss sex and diploidy during the exercise session.



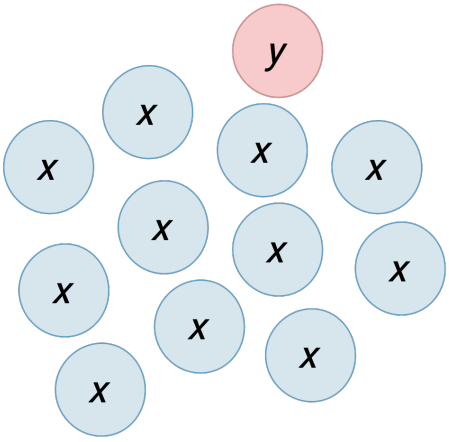
The environment or state of the resident population

For now, let's assume that the population is homogeneous (e.g. same physiology or habitats). And if the population experiences demographic, ecological 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; whether it later fixes is a separate question.



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 **asymptotic expected growth factor**: the per-capita number of mutant copies produced per time step asymptotically, i.e. such that

$$\mathrm{E}[n(t+1) \mid n(t)] = \rho(y, x)n(t), \tag{1}$$

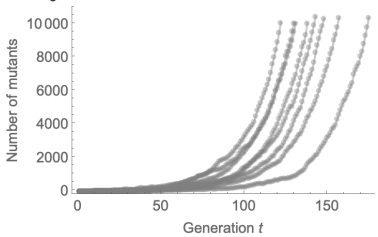
where $n(t)$ is the number of mutant copies at times t (assuming t is large).

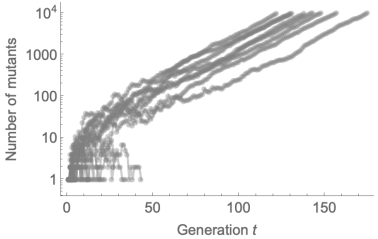
Invasion fitness : how to measure it from experiments

Invasion fitness can be quantified from

$$\log\left(\rho(y,x)\right) = \lim_{t\to\infty} \frac{1}{t} \log\left(\lim_{N_\mathrm{r}\to\infty} \frac{1}{N_\mathrm{r}} \sum_{j=1}^{N_\mathrm{r}} \frac{n_j(t)}{n_j(0)} \right) \tag{2}$$

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

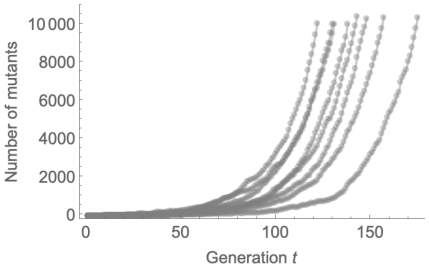
Result from branching process theory

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

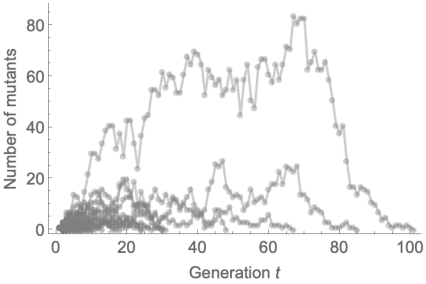
- If $\rho(y, x) \leq 1$, the mutant goes extinct with probability one.
- If $\rho(y, x) > 1$, extinction is no longer certain: the mutant lineage has a positive probability of persisting and spreading.

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



Invasion is possible ($\rho(y, x) > 1$)



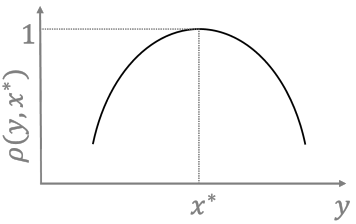
Certain extinction ($\rho(y, x) \leq 1$)

Uninvadability and the state of adaptation

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

$$\rho(y, x^*) \leq 1 \quad \text{for all} \quad y \in X, \tag{3}$$

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. (3) 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" [3].



Extra : Invasion probability depends on offspring distribution

$\rho(y, x)$ determines whether invasion is possible. It also determines the actual probability of this happening. To see this, let K be the number of mutant copies produced by one mutant, with $\mathbb{E}[K] = \rho(y, x)$, and let π be the mutant's probability of invasion. Since descendant lineages go extinct independently,

$$1 - \pi = \mathbb{E}\Big[(1 - \pi)^K\Big]. \tag{4}$$

Taylor-expanding $\mathbb{E}[(1 - \pi)^K]$ in π around $\pi = 0$ gives

$$0 = \big(\rho(y, x) - 1\big)\pi - \frac{1}{2}\mathbb{E}[K(K - 1)]\pi^2 + \mathcal{O}\big(\pi^3\big). \tag{5}$$

At neutrality, $\mathbb{E}[K] = 1$, so $\mathbb{E}[K(K - 1)] = \mathrm{Var}(K)$. The non-zero solution is therefore

$$\pi = \frac{2\big(\rho(y, x) - 1\big)}{\mathrm{Var}(K)} + \mathcal{O}\Big(\big(\rho(y, x) - 1\big)^2\Big), \qquad \rho(y, x) > 1.$$

For Poisson reproduction at neutrality, $\mathrm{Var}(K) = 1$, giving Haldane's formula.