Adaptive dynamics
(part 1: uninvadable strategies)

Summary so far

We investigated the building blocks of ecology and evolution: population dynamics, natural selection, mutation, and random genetic-drift.

- Mutation introduces randomly variation into a population.

- Natural selection favors non-randomly certain alleles.

- Genetic-drift slows down the efficacy of selection in small populations and can lead to survival of the luckiest.

We can now use these evolutionary forces to understand the process by which organism acquire the appearance of purposefulness (or functionality). In so doing we move from short-term to long-term evolution.

Appearance of purposefulness of organisms

From physiological structures within individuals to behavioral interactions between them, organisms have the appearance of purposefulness (functionality, design, or agency).
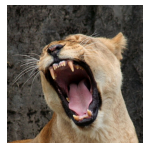
wings are built to fly

eyes are built to see

carapaces are built to protect

jaws are built to tear appart

Appearance of purposefulness of organisms

Bush crickets exhibit mimicry and camouflage by displaying colour of fresh vegetation.

Sharks have electroreceptor cells (located on skin pores) allowing them to sense electric fields with a sensitivity of up to 5×10^{-9} volt. They can detect buried preys and use the earth magnetic field for orientation.

Hence organisms "fit the demands of their environment".

Adaptation

The appearance of purposefulness (or functionality) of organisms is captured by the term adaptation in biology.

"A phenotypic variant that results in the highest fitness among a specified set of variants in a given environment"
(Reeve and Sherman 1993)

Hence, the concept of adaptation really relies on comparing different organic forms and subsumes an idea of "optimality".

Adaptation

The term adaptation is often used interchangeably in two different ways in evolutionary biology.

1. Adaptation as a phenotypic trait with a functional role that has evolved.

2. Adaptation as the process by which organisms acquire functionality over evolutionary time ("fit the environment").

Adaptation

- Random mutation plus non-random natural selection are the drivers of (organic) adaptation. This is what is meant by Darwinian evolution.

- No other linkage than that between fitness and functionality has been found (there are no documented case where functionality arises out of genetic drift).[1]

We now investigate in more details the process of adaptation for quantitative traits, which are more ubiquitous that dichotomous traits and subtend complex phenotypes.

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[1]In humans purpose can also be attributed to cultural evolution.

Phenotypic variation in natural populations is sometimes discrete (Mendelian traits)

Red morph of the beetle *Adalia bipunctata*

Black morph of the beetle *Adalia bipunctata*

Phenotypic variation in natural populations is more generally quantitative

Many phenotypes of organisms grade nearly imperceptibly from one category to the other and can be measured on a quantitative scale.


Skin colour variation in a single family.

Most traits are quantitative (or continuous)

- Weight.
- Size.
- Hair color.
- Flowering time.
- Age at first reproduction.
- Amount of resources consumed.
- Levels of parental care.
- Levels of aggression.

- Blood pressure.
- Level of hormones.
- Strength.
- Bone resistance to fractures.
- Facial features.
- Reaction time.
- Social capital.
- IQ.

Many genes usually affect quantitative phenotypes

- Generically we will denote by x a quantitative trait under scrutiny and take it as a real valued variable ($x \in \mathbb{R}$).

- The quantitative nature of such a trait is the result of many factors affecting it.
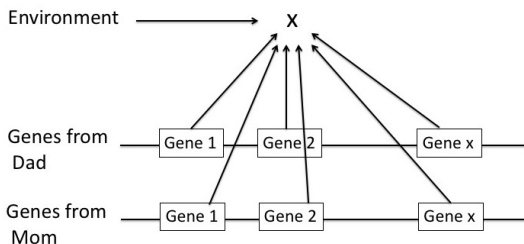
In diploid such as humans, individuals have two homologous copies of a gene, one inherited from Mom and one from Dad.

Fitness landscape

To each trait value x we can assign a fitness $w(x)$. This results in a fitness landscape:
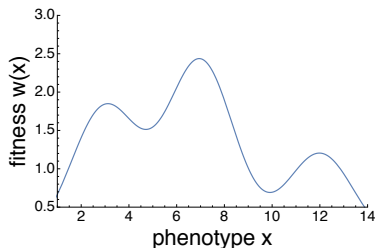
Since the distribution is peaked there is very likely to be selection on quantitative traits.[2]

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[2]An example of x could be the size of an organism: for too small x the organism is easily cached by predators and for too large x too much energy is wasted maintaining the soma. Hence, there is an intermediate value of x that maximizes fitness.

Fitness landscape example

The beak of a humming bird wing is built to maximize nectar extraction efficiency for different kinds of flowers.

humming bird

Given the constraints on size, there may be an optimal size y_{opt} for humming bird beak that maximizes nectar extraction when the bird hovers in front of flowers, i.e., the beak should neither be too long nor to small.

Fitness landscape example

A giraffe's neck is built to maximize foliage extraction for certain tree hight.
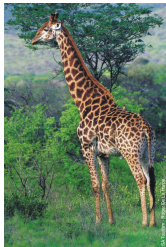
Given the constraints on bone fracture and muscle energy use, there may be an optimal neck length y_{opt} that balances the trade-off between having a too short but stable neck and a longer but unstable one.
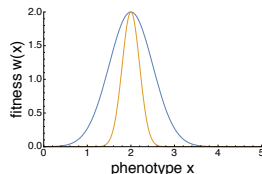
The simplest fitness landscape

Assume that the fitness of an individual with phenotype x follows a Gaussian function

$$w(x) = k \exp\left(-\frac{(x - y_{\mathrm{opt}})^2}{2\sigma_{\mathrm{w}}^2}\right)$$

thus

$$w(x) \leq w(y_{\mathrm{opt}}) \qquad \forall x \in \mathbb{R}$$

Parameters: $y_{\mathrm{opt}} = 2$, $\sigma_{\mathrm{w}} = 0.5$ (yellow) and $\sigma_{\mathrm{w}} = 1$ (blue).

Here, y_{opt} is the optimal phenotype, k is a constant of proportionality determining maximum fitness when $x = y_{\mathrm{opt}}$, and σ_{w} is the characteristic width of the fitness function.

Continuum of alleles

- Make the simplifying assumption of asexual reproduction and one gene controlling the trait.

- Each different phenotype $y \in \mathbb{R}$ is assumed to be determined by a different alleles ("continuum of alleles model").[3]


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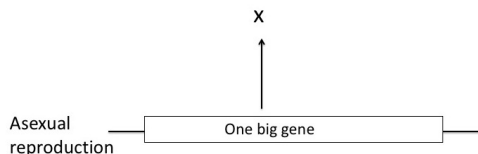
[3]Suppose the DNA sequence encoding the allele is 1000 nucleotide long, this makes 4^{1000} possible sequences, far more possible sequences than there are atoms in the observable universe (between 10^{78} and 10^{82}), and thus can encode essentially any feasible phenotype.

The metaphor of climbing up the fitness landscape

Intuitively we expect selection to push the population to climb up the slopes of the fitness landscape, with fitter alleles replacing less fit alleles, with the process eventually stoping at a peak.
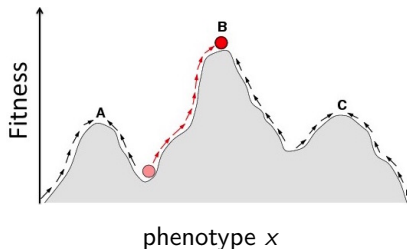
phenotype x

Darwin argued that most evolutionary change is gradual. It results in small, step-by-step transformation of the phenotype.

The central questions we address

Can we find a phenotype that is stable in the long-term and will the population converge to it?

- By stable we mean that no mutation arising in this population and having a different phenotype could invade, i.e., we cannot find an assemblage of organic forms that would result in higher fitness. This then characterizes the functionality of organism.

- If we find such a phenotype then this is an end-point of evolution.

We will answer these questions by performing an evolutionary invasion analysis.

Evolutionary invasion analysis: fitness of A (the mutant)

Consider the fitness of a *single* A mutant individual (expressing phenotype x) introduced into an otherwise monomorphic resident population for the B allele (expressing phenotype y) at its demographic equilibrium written as

$$w(x, y)$$

residents

mutant
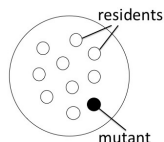
- Here, we assume that the resident population is at its demographic equilibrium (this is n^* of the chapter on population dynamics).

- Fitness $w(x, y)$ may depend on the phenotype (traits, behaviors) of all individuals in the population.[4]

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[4]This fitness is equivalent to what we denoted w_A in the previous chapters.

Evolutionary invasion analysis: fitness of B (the resident)

If the equilibrium population size in is large (say $n^* > 1000$), then the fitness of a single B individual in a population where there is a single A individual can be taken to be the fitness $w(y, y)$ of a single B individual in a monomorphic B population, which is equal to one.

$$w(y, y) = 1$$

residents

mutant
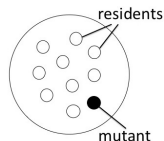
- A randomly sampled B is unlikely to interact with the (single) A individual (probability $1/n^* < 0.001$ if $n^* > 1000$).

- We will generally consider a "large" population, say at least a thousand individuals.[5]

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[5]For most of human evolution, population size was about 10^5 individuals.

Selection on the mutant

The selection coefficient[6] on allele A when introduced as a single copy is

$$s = w(x, y) - \underbrace{w(y, y)}_{1} = w(x, y) - 1$$

Allele A is not favored by selection when $s \leq 0$. That is, when

$$w(x, y) \leq 1$$

- If a A individual produces less or exactly one successful offspring in the backdrop of B it cannot invade.

- If a A individual produces more than one successful offspring in the backdrop of B it invades.

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[6]In terms of the notation of chapters 3 and 4, we have $w_A = w(x, y)$, $w_B = w(y, y)$, and the selection coefficient is $s = w_A - w_B$.

Uninvadability

We say that a trait (or phenotype) y is uninvadable (or is an uinvadable strategy) if

$$w(x, y) \leq 1 \qquad \forall x \in \mathcal{X}$$

Here, $\mathcal{X}$ is the trait (or "strategy") space, that is, the set of all feasible strategies.[7]

- A strategy is uninvadable if we cannot find any alternative strategy that would increase in frequency in the population.

- An uninvadable strategies performs well against itself. So it is robust.

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[7] The strategy space is either the entire set of real numbers ($\mathbb{R}$) or some subset of it, for instance $[0, 1]$ if x is a probability.

Uninvadability

An uninvadable strategy y satisfies

$$w(x, y) \leq 1 \qquad \forall x \in \mathcal{X}$$

- In an uninvadable population state, no assemblage of different organic forms that better fit the environmental conditions can be found given the current constraints on the organism.

- We presumed that the total rate of mutation μ at the phenotype under interest is much lower than the strength of selection s ($\mu \ll s$). This allows for the population to reach its short-term equilibrium (population dynamic and allele frequency change) before any new mutation appears[8].
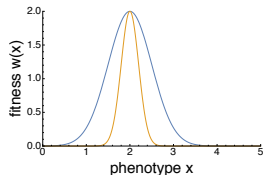
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[8]This is the separation between short-term and long-term evolution.

The simplest fitness landscape

In the above example of the Gaussian fitness function, the fitness of a mutant individual with phenotype x in a resident y population is

$$w(x, y) = k(y) \exp\left(-\frac{(x - y_{\mathrm{opt}})^2}{2\sigma_{\mathrm{w}}^2}\right)$$

- The constant of proportionality $k(y)$ absorbs density-dependent competition (since resource are limited) and thus depends on the trait of the resident population.

- We will not model density-dependent competition explicitly for now, and often just write the constant of proportionality $k(y) = k$ as it does not affect the conclusions. We assume density-independent selection.

The selection gradient

In order to find uninvadable strategies it is useful to define

$$S(y) = \left. \frac{\partial w(x, y)}{\partial x} \right|_{x=y}$$
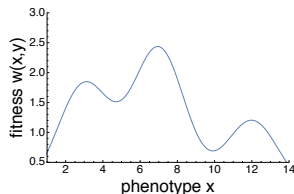
- $S(y)$ is known as the selection gradient at point y. This is the slope of the fitness landscape at point y.

- This is the marginal change in fitness at y, it is indicative of whether varying the trait increases or decreases fitness.

- All (interior) maxima satisfy $S(y) = 0$.

Necessary conditions for uninvadabiltity

An uninvadable strategy must be a maximum of fitness. Hence, necessary conditions for uninvadability are that

$$S(y^*) = 0$$

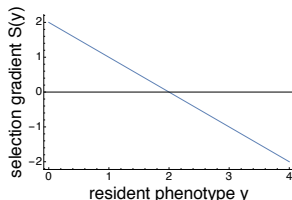$$\left.\frac{\partial^2 w(x, y)}{\partial x^2}\right|_{x=y=y^*} \leq 0$$
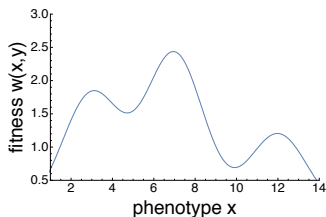
A strategy y^* satisfying the first-order condition is called a singular strategy.

Stabilizing selection: the selection gradient

The selection gradient for the above model with Gaussian fitness[9] is

$$S(y) \propto - \left(\frac{y - y_{\mathrm{opt}}}{\sigma_{\mathrm{w}}^2} \right)$$

Parameters: $\sigma_{\mathrm{w}} = 1$, $y_{\mathrm{opt}} = 2$.

- When $y < y_{\mathrm{opt}}$ increasing the trait value increases fitness.

- When $y > y_{\mathrm{opt}}$ increasing the trait value decreases fitness.

This is an example of stabilizing selection, a very ubiquitous form of selection.
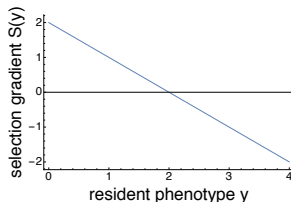
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[9] Recall that the symbol "$\propto$" means proportional to.

Stabilizing selection: the singular strategy

The single strategy (satisfying $S(y^*) = 0$) is

$$y^* = y_{\mathrm{opt}}$$

Parameters: $\sigma_{\mathrm{w}} = 1$, $y_{\mathrm{opt}} = 2$.

Since there is only a single singular strategy, i.e., the fitness landscape is single peaked and $y = y_{\mathrm{opt}}$ is also an uninvadable strategy.

This is an example of stabilizing selection.

Quality-quantity trade-off results in stabilizing selection

There is a trade-off between the quality and quantity of offspring produced, which is typical of many organisms.


Offspring of larger size are expected to have higher survival ("quality"), but producing offspring of larger size entails producing fewer number of offspring ("quantity"), since there is a constraint on the total number of resources to reproduce.

What is the optimal offspring size?

Offspring number

Let x be the size of an offspring produced (at conception) of a focal individual that has r_e units of resources to produce offspring. Let's assume that the number of offspring of size x produced by the focal individual is

$$n_J(x) = \frac{r_e}{x}$$
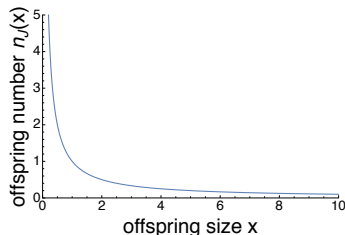
This says that the number of offspring produced is proportional to the per-capita amount of resources allocated to reproduction. The smaller the offspring, the more offspring can be produced, since each then uses up less resources.

Offspring survival

We assume that the probability that any offspring survives to adulthood is a monotonically increasing and saturating function of its size (i.e., diminishing returns in size) given by
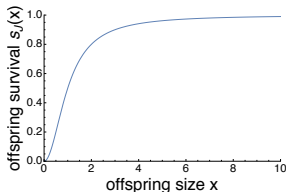
$$s_J(x) = \frac{x^2}{1 + x^2}$$
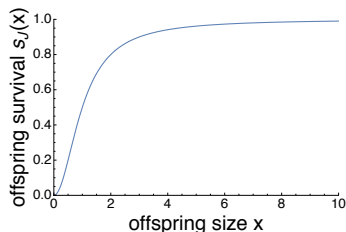
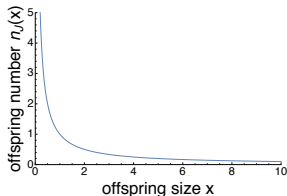The larger the offspring, the more likely it is to survive.

Quality-quantity trade-off

Because $s_J(x)$ is increasing with offspring size x and $n_J(x)$ is decreasing there is a trade-off between offspring quality and quantity.

$$\frac{\mathrm{d}s_J(x)}{\mathrm{d}x} > 0 \qquad\qquad \frac{\mathrm{d}n_J(x)}{\mathrm{d}x} < 0$$

What is the uninvadable strategy?

Fitness for the quality-quantity trade-off model

For this situation and assuming density-independent selection, we can let the fitness of a focal individual with strategy x in a resident population with strategy y be given by[10]

$$w(x, y) = kn_{\mathrm{J}}(x)s_{\mathrm{J}}(x) \quad \text{or} \quad w(x, y) \propto n_{\mathrm{J}}(x)s_{\mathrm{J}}(x)$$

The product quantifies the trade-off between number of offspring produced ("quantity") and their survival to adulthood ("quality").

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[10]The constant of proportionality k absorbs possible density-dependent competion effects on fitness.

Reproductive effort: selection gradient

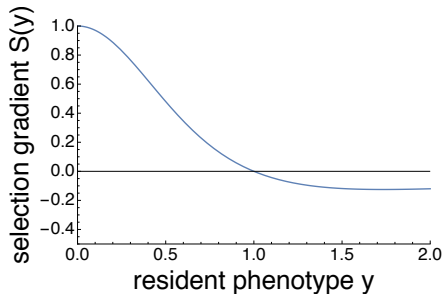The selection gradient on allocation of resources to survival is

$$S(y) \propto \underbrace{n_{\mathrm{J}}(y) \left.\frac{\mathrm{d}s_{\mathrm{J}}(x)}{\mathrm{d}x}\right|_{x=y}}_{\substack{\text{marginal benefit}\\ \frac{2r_{\mathrm{e}}}{(1+y^2)^2}}} + \underbrace{s_{\mathrm{J}}(y)\left.\frac{\mathrm{d}n_{\mathrm{J}}(x)}{\mathrm{d}x}\right|_{x=y}}_{\substack{\text{marginal cost}\\ -\frac{r_{\mathrm{e}}}{1+y^2}}}$$

- Increasing survival and increases fitness.

- Decreases offspring number decreasing fitness.

Reproductive effort: singular point

The unique biologically relevant singular strategy (satisfying $S(y^*) = 0$) is

$$y^* = 1$$

Parameters: $k = 1$, $r_{\mathrm{e}} = 1$.

- This model thus also displays stabilizing selection.

- Computing the second-order condition shows that this strategy is uninvadable.

Will an evolving population converge to the eco-evolutionary equilibrium?

We have two models predicting some end-point of evolution as a result of a stabilizing selection
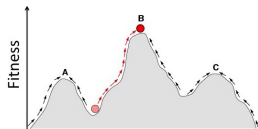
❶
$$y^* = y_{\mathrm{opt}} \qquad \text{"simple stabilizing selection"}$$

❷
$$y^* = 1 \qquad \text{"quantity-quality trade-off"}$$

In both cases, we cannot find trait values that would result in a better fit to the prevailing environmental conditions. Hence, the population is adapted. But will a population really converge to these trait values by evolution if starts far away from it?

Introducing individual-based simulations

To check convergence to the uninvadable strategy, we will carry out individual-based simulations.[11]

- The population is characterized by the array of phenotypes $\mathbf{y} = \{y_1, y_2, ..., y_n\}$ one for each individuals at the adult generation. Here, y_i is the phenotype of individual i.

- As a result of reproduction, mutation, and drift we obtain the offspring generation $\mathbf{y}' = \{y_1', y_2', ..., y_{n'}'\}$.


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[11]Individual-based simulations are sometimes also called Monte-Carlo methods. In essence, a simulation is just a computer based numerical implementation of a mathematical model that is too hard to solve "by hand"

Reproduction

Reproduction follows a Poisson distribution with mean fitness
$w_i = f(y_i)/(1 + \gamma n)$ given by a Beverton-Holt model for individual i.

$$\Pr(W_i = k) = \frac{e^{-w_i} w_i^k}{k!}$$

This is the probability that individual i produces k offspring with W_i being the random variable giving the number of offspring of i.
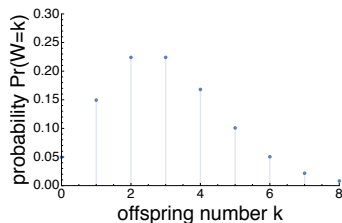

Mean $w_i = 3$

Hence, the model incorporates (real world) stochasticity and is fully individually based (hence the word individual-based simulations)

Distribution of the effect size of a mutation

When a mutation occurs (probability μ), the phenotype of an offspring of individual i is $y_i + \delta$, where δ is the step size of the mutation and is sampled from a Gaussian distribution with mean 0 and standard deviation σ_μ:
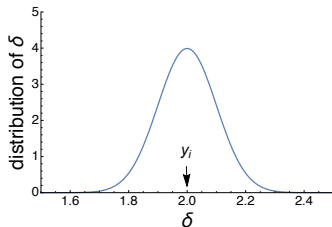
Parameter is $\sigma_\mu = 0.05$

Mutations thus introduce randomly variation into the population!

Change in mean in the population

- We have a vector of phenotypes $\mathbf{y} = \{y_1, y_2, ..., y_n\}$ in the parental generation.

- With this we can evaluate the average phenotype in the population

$$\bar{y} = \frac{1}{n} \sum_{i=1}^{n} y_i$$

With individual-based simulations we can now track the average phenotype in the population, which is subject to natural selection, mutation, and random genetic drift.

Adaptive dynamics for quality-quantity trade-off model

Running individual-based simulations with the specification of the model and recording the average phenotype $\bar{y}_t$ at time t produces
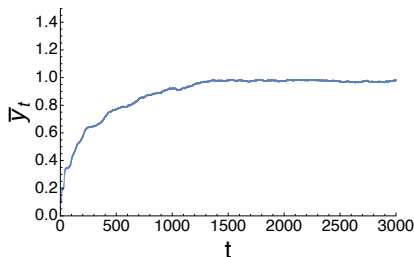
- We observe a gradual transformation of the phenotype. This is random mutation plus non-random natural selection.
- Asymptotic values are predicted by the analysis: $y^* = 1$.

Summary

- Long-term evolution can be characterized by uninvadable strategies.

- In an uninvadabe population state, organisms have the appearance of functionality (or design, agency, purposefullness).

- Example of stabilizing selection and quality-quantity trade-off predicts well the convergence to the uninvadable state in individual based simulations.

phenotype x