# Selection: How do populations stop growing?

## Modelling replication

We have seen that replication is represented by the model:

where is the size of a population and is the specific growth rate of that population. This model generates the exponential growth story, for which we can formulate an exact model:

, with doubling time .

* A bacteria population has . Calculate the population’s doubling time.
* How many minutes are in a day? How many cells does 1 bacterium generate in 3 days?

This number is enormous. In fact, it is so enormous that it cannot be true! *There is no such thing as exponential growth in real life*. Rather, limited resources cause the population growth rate to drop as the population gets bigger. This is modelled by the logistic model:

Here, is the specific replication rate of the population only when is much smaller than the resource limitation (carrying capacity) . If , or if , , so the population has an *unstable* fixed point at , but grows from any initial value towards the *stable* fixed point at . (A superscript asterisk denotes a fixed-point value.)

## Modelling selection

Suppose we have two exponential populations and that reproduce at different rates and . Suppose they have initial conditions , , then:

Both and grow exponentially. has doubling time and has doubling time , so if , will grow faster than . Eventually, there will be more ’s than ’s.

* Define . Use the quotient rule to prove that .

The solution of this equation is , so if , will grow toward infinity, and *outcompetes* . If in addition we assume resource are limited, the total population will remain constant, so if gets infinitely bigger than , this must mean that .

This is *selection*: where the growth of drives to extinction. For selection to happen, we need different rates of growth of the populations and , *plus* resource limitation.

To study selection situations, we often use two simple modelling tricks:

* We think of and not as populations, but as *frequencies*. That is, we assume the sum of both population types is 1 (), so that describes *what proportion* of the combined population are -individuals, and describes what proportion are .
* In addition, we think of the growth rates and as *fitness* values: describes how fit the type is, in terms of how effectively it grows by comparison with .
* We want to make sure that the sum of the two frequencies stays constant. To do this, we reduce the growth rates of and by equal amounts in the selection equations: and . Prove that this is only possible if is the average fitness of the two population types: .
* One advantage of this selection model is that depends upon : . Show how we can eliminate from the two selection equations, so that we only need to solve the single equation: .

We know this equation: it is the logistic equation with specific growth rate and carrying capacity 1. We also know how the logistic story evolves over time – it has two equilibria at 0 and 1:

* If , , so , and type is selected over type ;
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Martin Nowak calls this situation “*Survival of the Fitter*”.

## Survival of the fittest

We can extend this 2-type model to selection between different types in a population. If we name the individual type frequencies (where ), the structure describing all types is a vector: . Now define as the fitness of type , then the average fitness of the entire population of types is:

We can then write the selection dynamics model as:

**(Linear selection model)**

The frequency of type *increases* if its fitness is higher than the population average ; otherwise *decreases*. However, the total population stays constant: and . This is useful if we want to study the rise and fall of types within a population.

The set of all values obeying the property that is called a *simplex* (denoted ). The useful thing about simplexes is that we can represent them graphically:

|  |  |  |  |
| --- | --- | --- | --- |
|  | Simplex | Geometrical visualisation | |
| 1 | Point |  | |
| 2 | Line segment |  | |
| 3 | Triangle |  | |
| 4 | Tetrahedron |  | If are four vertex position vectors, the general point of is the *convex combination*: |

For example, consider the 3-simplex (or triangle) . Here, we interpret the top point as representing the situation in which only population type 3 is present, and the other two are not. On the other hand, we interpret the centre point as the situation where all three types are present in equal quantities.

* Which point would represent the situation in which type 2 is absent, and types 1 and 3 are present in equal quantities?
* In the linear selection model above, imagine that type has greater fitness than any other type: . What does this mean for the value of the factor ? What does this mean for the growth rate of type whenever other types are present? What will be the frequency of the types after a long time? What will happen to any interior point of the simplex over time?

You have demonstrated that the exponential selection model only ever has one outcome: total competitive exclusion. This is the meaning of the phrase “*Survival of the Fittest*”.

## Exercise project (1 week)

In this project we will build a slightly more general model of selection:

**(Sublinear selection model)**

**(Superlinear selection model)**

1. Notice that when , these equations reduce to the exponentially growing linear selection model. If , the population growth is slower than exponential (*subexponential*), and if , growth is faster than exponential (*superexponential*). An extreme example of subexponential growth is immigration at a constant rate. An example of superexponential growth is sexual reproduction, where two organisms (perhaps male and female) must meet in order to replicate.
2. Let’s take the simple case . Show that in this case, if the population lies in the simplex (so ), then the rate of change of the entire population is equal to zero. What does this imply for evolution in relation to ?
3. Design a Matlab class Selection that uses RK2 to simulate the evolution of a population of three types. Your client function should use the class constructor to set the values of and the three specific growth rates, then call the method simulate([x0 y0 z0],T) to evolve the population over a time T, starting from the initial frequencies [x0 y0 z0], and plot this evolution graphically within the triangular simplex :

sel = Selection(1.2,[0.2,0.3,0.4]); sel.simulate([0.3,0.3.0.4],20);

1. Use your selection class to show that leads to *Survival of All*, while leads to *Survival of the First*, and present this work in a poster.

## Summary

* Charles Darwin and Alfred Russell Wallace realised in 1858 that all resources are   
  limited, which *necessarily* leads to selection and prevents exponential growth.
* The *linear selection* model is , where and are the *frequency* and *specific replication rate*, or *fitness*, of population type ; is the average fitness of the population; and .
* The condition means that a population in the linear selection model is represented by a point moving over time within a *simplex* whose -th vertex represents the presence of only the single population type .
* Linear selection always leads to *Survival of the Fittest*: the movement of the population from any interior point of to the vertex whose fitness is highest.
* *Sublinear* selection (, where and ) models subexponential growth such as immigration; it leads to *Survival of All*.
* *Superlinear* selection (, where and ) models superexponential growth such as sexual replication; it leads to *Survival of the First*.