13. Selection: How do populations *stop* growing?

Modelling replication

We have seen that populations grow through replication represented by the model:

$$\dot{x} = r\,x$$

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

$$x(t) = x_0\, e^{rt}, \text{ with doubling time } T_2 = \ln(2)/r.$$

- **?** A bacteria population has $r = 0.035\ \mathrm{min}^{-1}$. 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:

$$\dot{x} = rx\,(1 - x/K)$$

Here, r is the specific replication rate of the population only when x is much smaller than the resource limitation (carrying capacity) K. If $x \to 0$, or if $x \to K$, $\dot{x} \to 0$, so the population has an *unstable* fixed point at $x^* = 0$, but grows from any initial value $x_0 > 0$ towards the *stable* fixed point at $x^* = K$. (A superscript asterisk denotes a fixed-point value.)

Modelling selection

Suppose we have two exponential populations x and y that reproduce at different rates r and s. Suppose they have initial conditions $x(0) = x_0$, $y(0) = y_0$, then:

$$\left.\begin{aligned}\dot{x} &= r\,x\\ \dot{y} &= s\,y\end{aligned}\right\} \quad\Longrightarrow\quad \left\{\begin{aligned}x(t) &= x_0\, e^{r\,t}\\ y(t) &= y_0\, e^{s\,t}\end{aligned}\right.$$

Both x and y grow exponentially. x has doubling time $\ln 2/r$ and y has doubling time $\ln 2/s$, so if $r > s$, x will grow faster than y. Eventually, there will be more x's than y's.

- **?** Define $\rho(t) \equiv \frac{x(t)}{y(t)}$. Use the quotient rule to prove that $\dot{\rho} = (r - s)\rho$.

The solution of this equation is $\rho(t) = \rho_0\, e^{(r-s)\,t}$, so if $r > s$, ρ will grow toward infinity, and x *outcompetes* y. If in addition we assume resource are limited, the total population $x + y$ will remain constant, so if x gets infinitely bigger than y, this must mean that $y \to 0$.

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

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

- We think of x and y not as populations, but as *frequencies*. That is, we assume the sum of both population types is 1 ($x + y = 1$), so that x describes *what proportion* of the combined population are x-individuals, and y describes what proportion are y.
- In addition, we think of the growth rates r and s as *fitness* values: r describes how fit the type x is, in terms of how effectively it grows by comparison with y.
- **?** We want to make sure that the sum $x + y = 1$ of the two frequencies stays constant. To do this, we reduce the growth rates of x and y by equal amounts R in the selection

equations: $\dot{x} = (r - R)x$ and $\dot{y} = (s - R)y$. Prove that this is only possible if R is the average fitness of the two population types: $R = rx + sy$.

? One advantage of this selection model is that y depends upon x: $y = 1 - x$. Show how we can eliminate y from the two selection equations, so that we only need to solve the single equation: $\dot{x} = (r - s)x(1 - x)$.

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

- If $r > s$, $x \to 1$, so $y \to 0$, and type x is selected over type y;
- If $s > r$, $x \to 0$, so $y \to 1$, and type y is selected over type x;

Martin Nowak calls this situation "*Survival of the Fitter*".

Survival of the fittest

We can extend this 2-type model to selection between n different types in a population. If we name the individual type frequencies $x_i(t)$ (where $i = 1, \dots, n$), the structure describing all n types is a vector: $\boldsymbol{x} \equiv (x_1, x_2, \dots, x_n)$. Now define $r_i \geq 0$ as the fitness of type i, then the average fitness of the entire population of n types is:

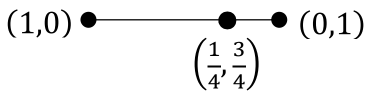
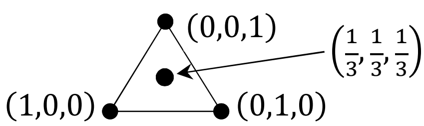
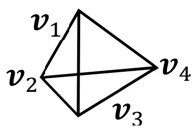
$$R = \sum_{i=1}^{n} x_i r_i = \boldsymbol{x} \cdot \boldsymbol{r}$$

We can then write the selection dynamics model as:

$$\dot{x}_i = x_i(r_i - R) \qquad \textbf{(Linear selection model)}$$

The frequency x_i of type i *increases* if its fitness r_i is higher than the population average R; otherwise x_i *decreases*. However, the total population stays constant: $\sum_{i=1}^{n} x_i = 1$ and $\sum_{i=1}^{n} \dot{x}_i = 0$. This is useful if we want to study the rise and fall of types within a population.

The set of all values $x_i > 0$ obeying the property that $\sum_{i=1}^{n} x_i = 1$ is called a *simplex* (denoted S_n). The useful thing about simplexes is that we can represent them graphically:

n	Simplex S_n	Geometrical visualisation
1	Point	
2	Line segment	
3	Triangle	
4	Tetrahedron	 If $\boldsymbol{v}_i$ $(i = 1,2,3,4)$ are four vertex position vectors, the general point of S_4 is the *convex combination*: $\boldsymbol{x} \equiv x_1\boldsymbol{v}_1 + x_2\boldsymbol{v}_2 + x_3\boldsymbol{v}_3 + x_4\boldsymbol{v}_4$

For example, consider the 3-simplex (or triangle) S_3. Here, we interpret the top point (0,0,1) 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 $\left(\frac{1}{3}, \frac{1}{3}, \frac{1}{3}\right)$ 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 $k \in \{1,2,\dots,n\}$ has greater fitness than any other type: $r_k > r_i, \forall i \neq k$. What does this mean for the value of the factor $(r_i - R)$? What does this mean for the growth rate $\dot{x}_k$ of type k 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 S_n 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 use modelling to test a more general theory of selection:

$$\dot{x}_i = r_i {x_i}^c - R x_i; \quad R = \sum_{i=1}^{n} r_i {x_i}^c; \quad c < 1 \qquad \textbf{(Sublinear selection model)}$$

$$\dot{x}_i = r_i {x_i}^c - R x_i; \quad R = \sum_{i=1}^{n} r_i {x_i}^c; \quad c > 1 \qquad \textbf{(Superlinear selection model)}$$

1. Notice that when $c = 1$, these equations reduce to the exponentially growing linear selection model. If $c < 1$, population growth is slower (*subexponential*), and if $c > 1$, growth is faster than exponential (*superexponential*). An extreme example of subexponential growth is immigration at a constant rate. A superexponential growth example is sexual reproduction, where two organisms must meet in order to replicate.
2. Let's take the simple case $n = 3$. Show that in this case, if the population lies in the simplex S_3 (so $x_1 + x_2 + x_3 = 1$), then the rate of change $(\dot{x}_1 + \dot{x}_2 + \dot{x}_3)$ of the entire population is equal to zero. What does this imply for evolution in relation to S_3?
3. Design a type \`Selector\` (in module \`Selection\`) that uses RK2 to simulate the evolution of a population of three types. Your demo() function will use the type's constructor to set the value of c and the three specific growth rates, then call the method \`simulate!()\` to evolve the population over time `T`, starting from initial frequencies `[x0,y0,z0]`, and plot this evolution graphically in the simplex S_3. For example:

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

4. Use your Selector type to demonstrate that $c < 1$ leads to *Survival of All*, while $c > 1$ leads to *Survival of the First*.

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 $\dot{x}_i = x_i(r_i - R)$, where x_i and r_i are the *frequency* and *specific replication rate*, or *fitness*, of population type i; $R = \sum_{i=1}^{n} x_i r_i = \boldsymbol{x} \cdot \boldsymbol{r}$ is the average fitness of the population; and $\sum_{i=1}^{n} x_i = 1$.
- The condition $\sum_{i=1}^{n} x_i = 1$ means that a population in the linear selection model is represented by a point moving over time within a *simplex* S_n whose k-th vertex represents the presence of only the single population type $k \in \{1,2,\dots,n\}$.
- Linear selection always leads to *Survival of the Fittest*: the movement of the population from any interior point of S_n to the vertex k whose fitness is highest.
- *Sublinear* selection ($\dot{x}_i = r_i {x_i}^c - R x_i$, where $R = \sum_{i=1}^{n} r_i {x_i}^c$ and $c < 1$) models subexponential growth such as immigration; it leads to *Survival of All*.
- *Superlinear* selection ($\dot{x}_i = r_i {x_i}^c - R x_i$, where $R = \sum_{i=1}^{n} r_i {x_i}^c$ and $c > 1$) models superexponential growth such as sexual replication; it leads to *Survival of the First*.