

Ecology and Evolution Homework (2021-2022)
ICTP Quantitative Life Sciences Diploma
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1 More realistic model of fishery

The equation

$$\frac{dn(t)}{dt} = rn(t) \left(1 - \frac{n(t)}{K}\right) - p(n(t)) = f(n(t)), \quad (1.1)$$

describes the population dynamics of some species of fish. The (analytic) function $p(n(t))$ is the rate of fishing as a function of the population abundance $n(t)$. We are assuming

$$\begin{aligned} \lim_{n \rightarrow \infty} p(n(t)) &= p_{\infty} > 0, \\ p(0) &= 0, \\ p'(0) &= p_0 > 0, \\ p'(n) &> 0, \forall n \geq 0. \end{aligned} \quad (1.2)$$

1.1 Description of the ecological implications of the assumptions

1.

$$\lim_{n \rightarrow \infty} p(n(t)) = p_{\infty} > 0$$

This first assumption is about the dynamics of this particular fish for large populations. For large n , the predation rate $p(n) = p_{\infty}$ is constant. There is a limit in how much fishing is possible to do.

2.

$$\begin{aligned} p(0) &= 0, \\ p'(0) &= p_0 > 0, \\ p'(n) &> 0, \forall n \geq 0. \end{aligned}$$

These last three conditions describe the dependence of p on n . For no fishes, the predation is zero. From there, the predation is a strictly increasing function, with an asymptotic behavior tending to p_{∞} .

Ecological behavior

The fixed points are characterised by the equation

$$rn(t) \left(1 - \frac{n(t)}{K} \right) = p(n(t)), \quad (1.3)$$

for which there are three different situations. First, when there is no fixed point apart from zero (as shown in Figure 1.1), then regardless of the initial condition, the system always goes to extinction. Second, when there is one fixed point (as shown in Figure 1.2), which is a stable fixed point, then the system always goes to that fixed point. Lastly, when there is more than one fixed point (as shown Figure 1.3), then there is also more than one stable fixed point, and, the final state of the system depends on the initial number of fishes. Something to notice is that for a very large number of fishes, the system tends to go to the largest fixed point.

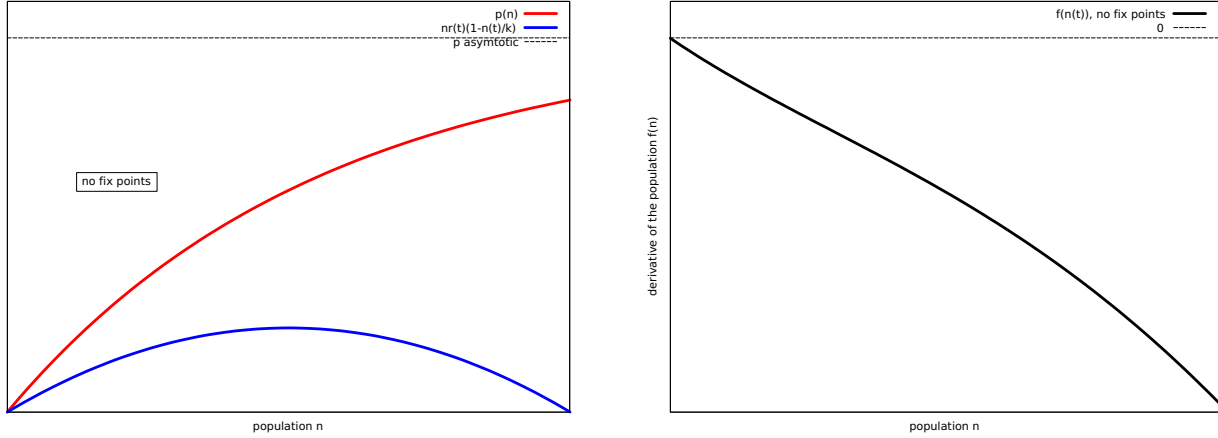


Figure 1.1: Analysis of the qualitative behavior of the derivative of the population $dn(t)/dt$ when there are no fixed points. The left graph shows a superposition of both terms of the Equation (1.3) and the right graph shows the function $f(n(t))$. The red line is the function $rn(t)(1 - n(t)/k)$, the blue line is the function $p(t)$. The dashed line in the left graph is the asymptotic behavior of $p(n)$, and in the right is the line $y = 0$. The function used is $f(n) = x(1 - x/9) - 10(1 - \exp(-x/5))$.

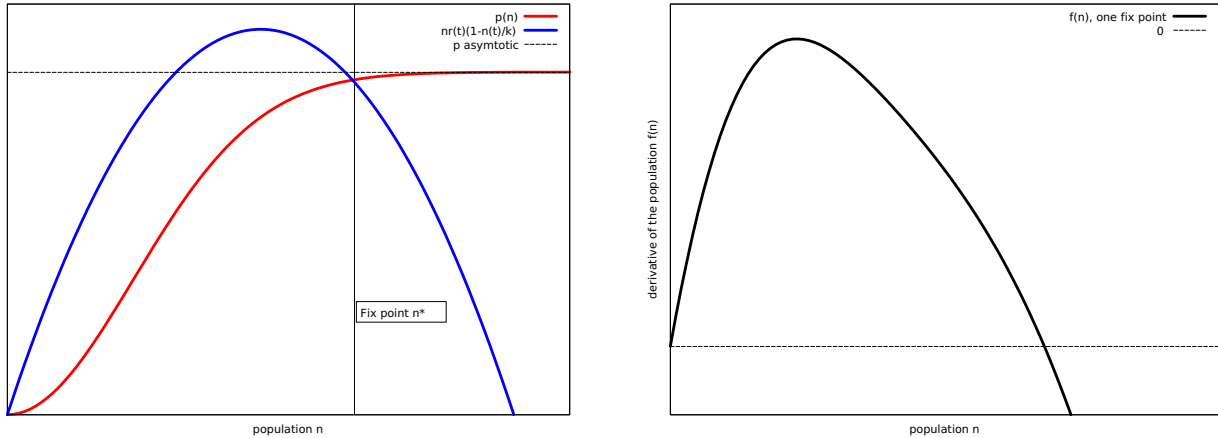


Figure 1.2: Analysis of the qualitative behavior of the derivative of the population $dn(t)/dt$ when there is one fixed point. The left graph shows a superposition of both terms of the Equation (1.3) and the right graph shows the function $f(n(t))$. The red line is the function $rn(t)(1 - n(t)/k)$, the blue line is the function $p(t)$. The dashed line in the left graph is the asymptotic behavior of $p(n)$, and in the right is the line $y = 0$. The function used is $f(n) = 5x(1 - x/9) - 10(1 - \exp(-x^2/10))$.

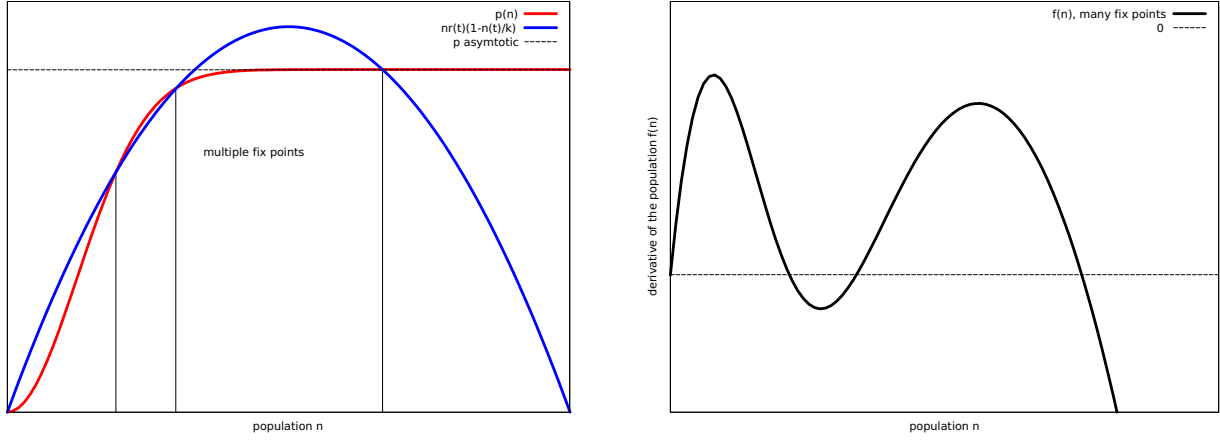


Figure 1.3: Analysis of the qualitative behavior of the derivative of the population $dn(t)/dt$ when there are many fixed points. The left graph shows a superposition of both terms of the Equation (1.3) and the right graph shows function $f(n(t))$. The red line is the function $rn(t)(1 - n(t)/k)$, the blue line is the function $p(t)$. The dashed line in the left graph is the asymptotic behavior of $p(n)$, and in the right is the line $y = 0$. The function used is $f(n) = 2.5x(1 - x/18) - 10(1 - \exp(-x^2/10))$.

Meaning of the predation term

Defining

$$\phi(n) = \frac{p(n)}{n},$$

we could say that $\phi(n)$ is the rate of fishing per number of fishes. When there are zero fishes, then $\phi(n) = p_0$, whereas, for infinite fishes, then $\phi(n) = 0$.

1.2 Fixed points and the bifurcations for a specific example

Using

$$p(n) = \frac{p_\infty p_0 n}{p_\infty + p_0 n}, \quad (1.4)$$

defining the new adimensional variables

$$u = \frac{p_0}{p_\infty} n, \quad \tau = rt,$$

and the new parameters

$$a = \frac{p_0 K}{p_\infty}, \quad b = \frac{p_0}{r}$$

then Equation (1.4) becomes

$$\frac{du}{d\tau} = u \left(1 - \frac{u}{a} \right) - b \left(\frac{u}{1 + u} \right). \quad (1.5)$$

Fixed points and stability

The fixed points are obtained solving the equation

$$f(u) = u \left(1 - \frac{u}{a} \right) - b \left(\frac{u}{1 + u} \right) = 0 \quad (1.6)$$

which has three solutions. Analyzing the stability of these points and its dependence on the parameters a and b , the stability of the fixed points can be obtained with the equation

$$\left. \frac{df}{du} \right|_{u=u^*} \quad (1.7)$$

where u^* are the fixed points. If $\left. \frac{df}{du} \right|_{u=u^*} > 0$, then the fixed points are unstable. If $\left. \frac{df}{du} \right|_{u=u^*} < 0$, then the fixed points are stable.

1. $u_1 = 0$

Using Equation (1.7),

$$\left. \frac{df}{du} \right|_{u=0} = 1 - b \quad (1.8)$$

then the fixed point is unstable for $b < 1$, and stable for $b > 1$.

2. $u_2 = \frac{(a-1) + \sqrt{(a-1)^2 + 4a(1-b)}}{2}$ and $u_3 = \frac{(a-1) - \sqrt{(a-1)^2 + 4a(1-b)}}{2}$

For $b < 1$, there is always one solution which is u_2 , because u_3 is negative as shown in Figure 1.4a. This is a stable solution (see Figure 1.4b).

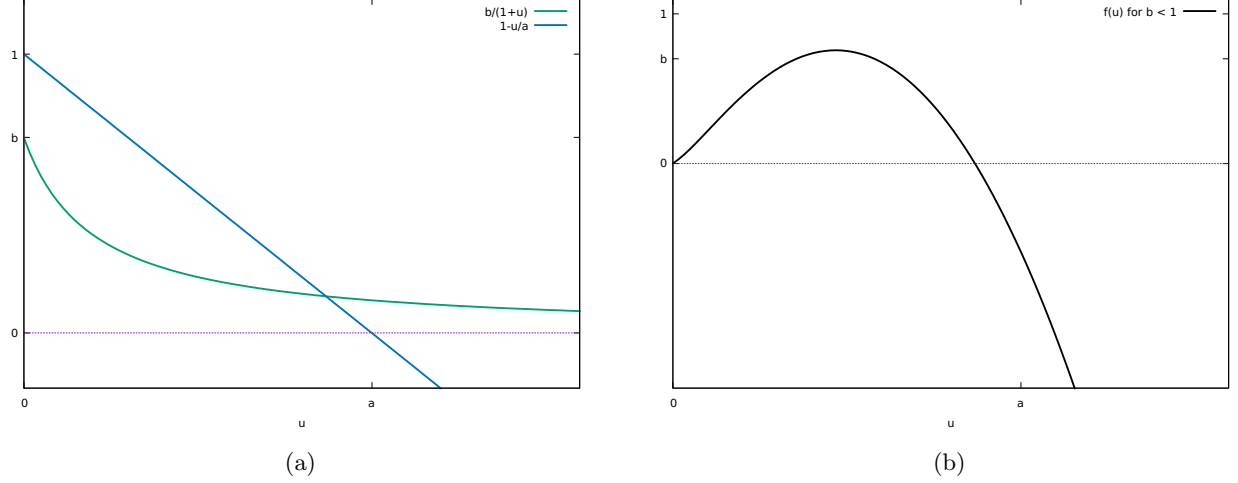


Figure 1.4: Analysis of the fixed points for the Equation (1.5) for $b < 1$. (a) Plots of the function $b/(1-u)$ in green and of the function $1-u/a$ in blue. (b) Plot of the function $f(u)$. Here, we used $b = 0.7$ and $a = 5$.

For $b > 1$, fixing the value of b , the value of $a = a_c$ for which the transition between zero and the two solutions passes is given by the critical point when the tangent of $1-u/a$ and $b/(1+u)$ is the same as shown in Figure 1.5a.

$$\frac{d}{du} \left(1 - \frac{u}{a} \right) = \frac{d}{du} \left(\frac{b}{1+u} \right)$$

with solution $u = \sqrt{ba} - 1$. Using the critical value for $u^* = (a-1)/2$, which is the value that u has when there is only one solution, we found that

$$a_c = (2b-1) + \sqrt{(2b-1)^2 - 1} \quad (1.9)$$

Figure 1.5b shows that u_2 is a stable solution and u_3 is unstable solution. The bifurcation occurring at a_c is a saddle node bifurcation, as shown in Figure 1.6.

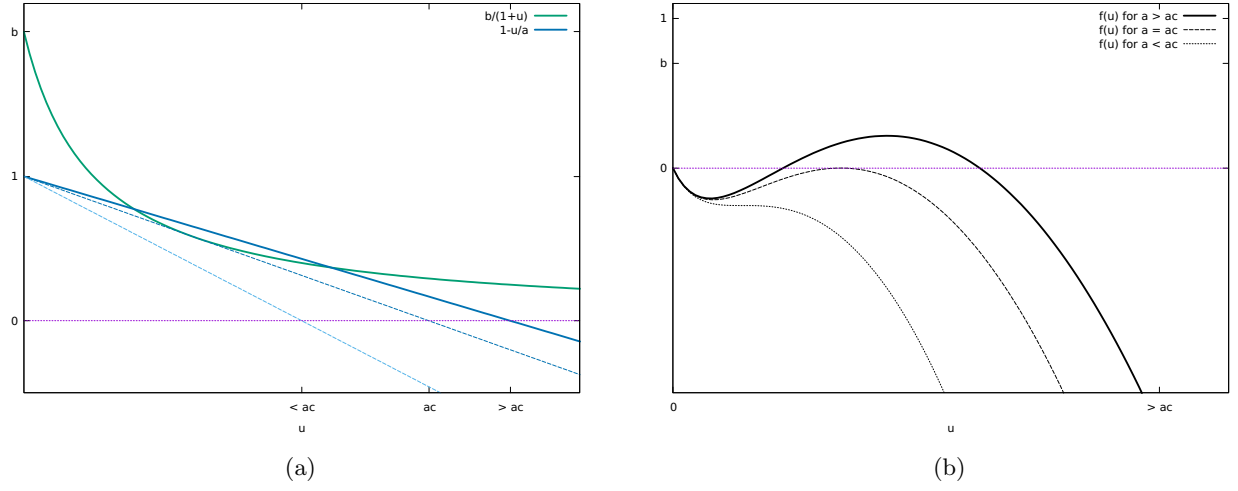


Figure 1.5: Analysis of the fixed points for the Equation (1.5), for $b > 1$. (a) Plots of the function $b/(1-u)$ in green and of the function $1-u/a$ in blue. (b) Plots of the function $f(u)$ for various values of a with $b = 2$, $< a_c = 4$, $> a_c = 7$, $a_c = 5.8$

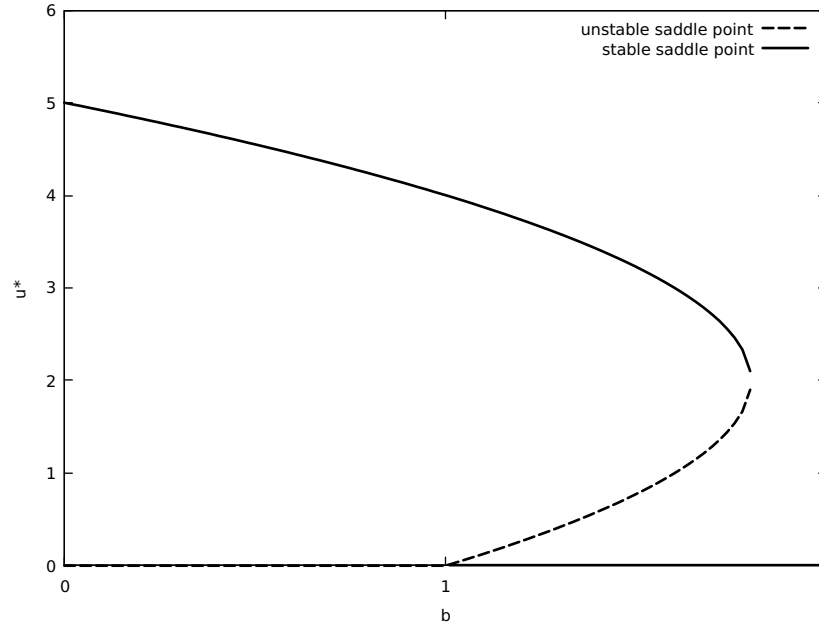


Figure 1.6: Saddle node bifurcation of the system for $a = 5$. When $b < 1$, zero is unstable fixed point.

1.3 Generalization of the previous result

The ecological behavior is determined by the interaction between the function $\phi(u) = p(u)/u$, and the linear function $(1 - n/a)$. By the definition of concavity, the necessary condition for the same behavior to be achieved is for the function $\phi(u)$ to have a positive concavity in the region of interest. So the conditions are:

$$\begin{aligned}
 \lim_{u \rightarrow \infty} \phi(u) &= 0 \\
 \phi(0) &= b \\
 \frac{d\phi(u)}{du} &< 0, \forall u \geq 0 \\
 \frac{d^2\phi(u)}{du^2} &> 0, \forall u \geq 0.
 \end{aligned} \tag{1.10}$$

1.4 Choosing another function

An example of another function that satisfies Equation (1.10) is

$$\phi(u) = be^{-u} \quad (1.11)$$

In this case, again, the fixed points would be determined by Equation (1.3),

$$1 - \frac{u}{a} - be^{-u} = 0 \quad (1.12)$$

The bifurcation is found when the tangents are the same,

$$\frac{d\left(1 - \frac{u}{a}\right)}{du} = \frac{d\left(be^{-u}\right)}{du} \quad (1.13)$$

using this condition together with Equation (1.3), given a value of a , the bifurcation is found to be

$$b_c = \frac{e^{a-1}}{a} \quad (1.14)$$

So, summarizing, zero is an unstable fixed point for $b < 1$ and stable for $b > 1$. For $b > 1$, there is always a fixed point, found by solving Equation (1.3). For $b < 1$, for a given value of a , the critical point when there is a jump between no other fixed point and two fixed points is given by b_c .

2 Large linear systems

Consider the linear system of equations

$$\frac{dx_i(t)}{dt} = \sum_{j=1}^N A_{ij}x_j \text{ for } i = 1, 2, \dots, N \quad (2.1)$$

where $A_{ii} = -1$ and the off-diagonal elements A_{ij} are independent random variables with mean 0 and variance σ^2/N , drawn from your favourite distribution (provided that it has finite moments). Describe the stability of the fixed point x^* at different values of σ . Use $N = 547$ and your favourite distribution.

2.1 Fixed Points

We want to analyze the stability of the system - because A_{ij} are independent random variables, we could expect that the system would behave in a different way for each run of the experiment. But typically we expect that the matrix A has a non zero determinant.

Because the determinant is different from zero, the solution of the equation

$$\sum_{j=1}^N A_{ij}x_j = 0, \text{ for } i = 1, 2, \dots, N \quad (2.2)$$

which is the equation that we need to solve in order to find the fixed points, will have a unique solution. Noticing that $x_i^* = 0$ is a solution for the system, we conclude that this is the only fixed point.

2.2 Analysis of the stability

For a particular set of values A_{ij} , the stability of the fixed point can be found by finding the eigenvalue of the Jacobian evaluated at the fixed point with the biggest real part. If it is positive, the fixed point is unstable and if it is negative, the fixed point is stable. For any linear system, the elements of the Jacobian are the elements of the matrix A .

$$J_{ij} = A_{ij} \quad (2.3)$$

The strategy that we used for analyzing the stability of the system is by using a sample of N systems with a given value of the variance σ^2/N , for which (see appendix A) we found the eigenvalue with the biggest real part $\text{Re}(\lambda_{Max})$. Then we plot the mean value of the biggest real part of the eigenvalue $\text{Re}(\lambda_{Max})$ as a function of σ .

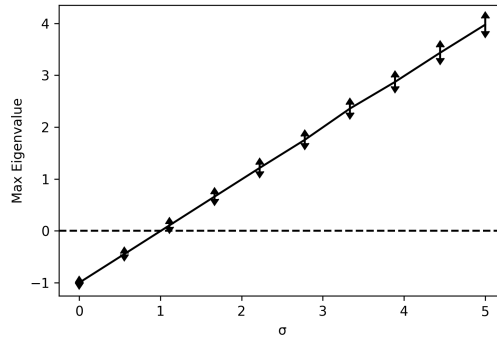


Figure 2.1: Using $N = 547$ and a Normal distribution with mean 0 and variance σ^2/N , where σ ranges from 0 to 5 having 10 equidistant data points. This is performed for 30 realizations, and the mean and standard deviation is plotted.

2.2.1 Results

Using a normal distribution, and a system of $N = 547$ equations, we found that when $\sigma < 1$, the fixed point is stable and when $\sigma > 1$, the fixed point is unstable, as it can be shown in Figure 2.1. We can interpret this result by noticing that the system has two parts, (a) a deterministic part ($A_{ii} = -1$), which tends to move towards the fixed point, and (b) a noise that drives the system away from the fixed point. When the noise is small, the deterministic part is stronger, and the system is stable. But when the noise is large enough, the system tends to go in random directions away from the fixed point.

3 More than two trophic levels

Consider the following 4 species:

- Species 1 grows logistically (in absence of other species) and is consumed by species 2 and 3.
- Species 2 and 3 go to extinction in absence of species 1 .
- Species 4 consumes both species 2 and 3 and goes to extinction if species 2 and 3 are both absent.

3.1 Model formulation and assumptions

In this model as introduced above, we have four species with different interactions with each other. We consider species 1 (X) as preys for both species 2 (Y_1) and 3 (Y_2), and on the other hand, species 4 (W) as predators for 2 and 3 .

$$\begin{aligned}
 \frac{dX}{dt} &= \underbrace{rX \left(1 - \frac{X}{k}\right)}_{\text{Logistic growth}} - \underbrace{(\beta_1 XY_1 + \beta_2 XY_2)}_{\text{predation terms by species 2 and 3}} \\
 \frac{dY_1}{dt} &= \underbrace{\alpha_1 \beta_1 XY_1}_{\text{Prey consumption}} - \underbrace{\gamma_1 Y_1 W}_{\text{Predation term by Species 4}} - \underbrace{\delta_1 Y_1}_{\text{Death}} \\
 \frac{dY_2}{dt} &= \underbrace{\alpha_2 \beta_2 XY_2}_{\text{Prey consumption}} - \underbrace{\gamma_2 Y_2 W}_{\text{Predation term by Species 4}} - \underbrace{\delta_2 Y_2}_{\text{Death}} \\
 \frac{dW}{dt} &= \underbrace{W(\sigma_1 \gamma_1 Y_1 + \sigma_2 \gamma_2 Y_2)}_{\text{Consumption of prey 2 and 3}} - \underbrace{\phi W}_{\text{Death}}
 \end{aligned}$$

with initial conditions:

$$X(0) > 0, Y_1(0) > 0, Y_2(0) > 0, W(0) > 0.$$

The assumptions we have are as follows:

- Species 1(preys) grow logistically in absence of their predators 2 and 3, with growth rate r and carrying capacity k .
- Predators 2 and 3 have different capturing rates β_1 and β_2 , respectively. The interaction between them has been ignored (in case of them being either predators or preys).
- The coefficients of conversion of preys 1 to either predators 2 or 3 are denoted as α_1 and α_2 , respectively.
- The capturing rates of species 2 and 3 by their predators 4 are γ_1 and γ_2 , respectively.
- Death rates of species 2, 3, and 4 are δ_1 , δ_2 and ϕ , respectively.
- The conversion coefficients for species 4 are σ_1 (species 2) and σ_2 (species 3).
- All the parameters are positive.

3.2 Re-scaling

The model can be written in non-dimensional form choosing

$$\begin{aligned}
 \bar{X} &= \frac{X}{k} \\
 \bar{Y}_1 &= \frac{\beta_1}{r} Y_1 \\
 \bar{Y}_2 &= \frac{\beta_2}{r} Y_2 \\
 \bar{W} &= \frac{\gamma_1}{r} W \\
 \tau &= rt
 \end{aligned}$$

and the new parameters

$$\bar{\alpha}_1 = \frac{\alpha_1 \beta_1 k}{r}, \bar{\alpha}_2 = \frac{\alpha_2 \beta_2 k}{r}, \bar{\delta}_1 = \frac{\delta_1}{r}, \bar{\delta}_2 = \frac{\delta_2}{r}, \bar{\gamma}_1 = \frac{\sigma_1 \gamma_1}{\beta_1}, \bar{\gamma}_2 = \frac{\sigma_2 \gamma_1}{\beta_2}, \bar{\phi} = \phi k.$$

The model becomes,

$$\begin{aligned} \frac{d\bar{X}}{d\tau} &= \bar{X}(1 - \bar{X}) - \bar{X}(\bar{Y}_1 + \bar{Y}_2) \\ \frac{d\bar{Y}_1}{d\tau} &= \bar{\alpha}_1 \bar{X} \bar{Y}_1 - \bar{Y}_1 \bar{W} - \bar{\delta}_1 \bar{Y}_1 \\ \frac{d\bar{Y}_2}{d\tau} &= \bar{\alpha}_2 \bar{X} \bar{Y}_2 - \bar{Y}_2 \bar{W} - \bar{\delta}_2 \bar{Y}_2 \\ \frac{d\bar{W}}{d\tau} &= \bar{\gamma}_1 \bar{Y}_1 \bar{W} + \bar{\gamma}_2 \bar{Y}_2 \bar{W} - \bar{\phi} \bar{W} \end{aligned} \tag{3.1}$$

3.3 Fixed Points

The fixed points can be found by solving $\frac{d\bar{X}}{d\tau} = 0$, $\frac{d\bar{Y}_1}{d\tau} = 0$, $\frac{d\bar{Y}_2}{d\tau} = 0$, and $\frac{d\bar{W}}{d\tau} = 0$.

We get eight fixed points with the help of Python programming language:

1. The trivial fixed point corresponding to all species equal to zero (extinction): $a_1 = (0, 0, 0, 0)$
2. Fixed point corresponding to when only species 1 exist: $a_2 = (1, 0, 0, 0)$
3. Fixed point corresponding to the extinction of species 2: $a_3 = \left(\frac{\bar{\gamma}_2 - \bar{\phi}}{\bar{\gamma}_2}, 0, \frac{\bar{\phi}}{\bar{\gamma}_2}, \frac{\bar{\alpha}_2 \bar{\gamma}_2 - \bar{\alpha}_2 \bar{\phi} - \bar{\delta}_2 \bar{\gamma}_2}{\bar{\gamma}_2} \right)$
4. Fixed point corresponding to the extinction of species 4: $a_4 = \left(\frac{\bar{\delta}_1}{\bar{\alpha}_1}, \frac{\bar{\delta}_1}{\bar{\alpha}_1} - 1 - Y_2, Y_2, 0 \right)$
5. Fixed point corresponding to the extinction of species 2 and 4: $a_5 = \left(\frac{\bar{\delta}_2}{\bar{\alpha}_2}, 0, \frac{\bar{\alpha}_2 - \bar{\delta}_2}{\bar{\alpha}_2}, 0 \right)$
6. Fixed point corresponding to the extinction of species 3: $a_6 = \left(\frac{\bar{\gamma}_1 - \bar{\phi}}{\bar{\gamma}_1}, \frac{\bar{\phi}}{\bar{\gamma}_1}, 0, \frac{\alpha_1 \gamma_1 - \bar{\alpha}_1 \bar{\phi} - \delta_1 \gamma_1}{\bar{\gamma}_1} \right)$
7. Fixed point corresponding to the extinction of species 3 and 4: $a_7 = \left(\frac{\bar{\delta}_1}{\bar{\alpha}_1}, \frac{\bar{\alpha}_1 - \bar{\delta}_1}{\bar{\alpha}_1}, 0, 0 \right)$
8. When all species coexist:

$$a_8 = \left(\frac{\bar{\delta}_1 - \bar{\delta}_2}{\bar{\alpha}_1 - \bar{\alpha}_2}, \frac{-\bar{\alpha}_1 \bar{\gamma}_2 + \bar{\alpha}_1 \bar{\phi} + \bar{\alpha}_2 \bar{\gamma}_2 - \bar{\alpha}_2 \bar{\phi} + \bar{\delta}_1 \bar{\gamma}_2 - \bar{\delta}_2 \bar{\gamma}_2}{\bar{\alpha}_1 \bar{\gamma}_1 - \bar{\alpha}_1 \bar{\gamma}_2 - \bar{\alpha}_2 \bar{\gamma}_1 + \bar{\alpha}_2 \bar{\gamma}_2}, \frac{\bar{\alpha}_1 \bar{\gamma}_1 - \bar{\alpha}_1 \bar{\phi} - \bar{\alpha}_2 \bar{\gamma}_1 + \bar{\alpha}_2 \bar{\phi} - \bar{\delta}_1 \bar{\gamma}_1 + \bar{\delta}_2 \bar{\gamma}_1}{\bar{\alpha}_1 \bar{\gamma}_1 - \bar{\alpha}_1 \bar{\gamma}_2 - \bar{\alpha}_2 \bar{\gamma}_1 + \bar{\alpha}_2 \bar{\gamma}_2}, \frac{-\bar{\alpha}_1 \bar{\delta}_2 + \bar{\alpha}_2 \bar{\delta}_1}{\bar{\alpha}_1 - \bar{\alpha}_2} \right)$$

3.4 Stability

The stability of each fixed point is analyzed by calculating the Jacobian matrix and finding the eigenvalues assessed at each fixed point. The real parts of the eigenvalues of the Jacobian matrix must be negative for the stability of the fixed points. In this work we are going to focus on the fixed points that describe the most interesting states of the system.

The system in Equation (3.1) is nonlinear. The stability can be obtained by linearizing the system with the Jacobian matrix

$$J(\bar{X}^*, \bar{Y}_1^*, \bar{Y}_2^*, \bar{W}^*) = \begin{bmatrix} -2\bar{X} - \bar{Y}_1 - \bar{Y}_2 + 1 & -\bar{X} & -\bar{X} & 0 \\ \bar{\alpha}_1 \bar{Y}_1 & \bar{\alpha}_1 \bar{X} - \bar{\delta}_1 - \bar{W} & 0 & -\bar{Y}_1 \\ \bar{\alpha}_2 \bar{Y}_2 & 0 & \bar{\alpha}_2 \bar{X} - \bar{\delta}_2 - \bar{W} & -\bar{Y}_2 \\ 0 & \bar{\gamma}_1 \bar{W} & \bar{\gamma}_2 \bar{W} & \bar{\gamma}_1 \bar{Y}_1 + \bar{\gamma}_2 \bar{Y}_2 - \bar{\phi} \end{bmatrix}$$

- The fixed point $a_1 = (0, 0, 0, 0)$ is **unstable**; one of the eigenvalues is positive $\lambda_1 = 1$ and the others are negative $\lambda_2 = -\bar{\delta}_1$, $\lambda_3 = -\bar{\delta}_2$ and $\lambda_4 = -\bar{\phi}$.
- For a_2 , the Jacobian is as follows:

$$J = \begin{pmatrix} -1 & -1 & -1 & 0 \\ 0 & \bar{\alpha}_1 - \bar{\delta}_1 & 0 & 0 \\ 0 & 0 & \bar{\alpha}_2 - \bar{\delta}_2 & 0 \\ 0 & 0 & 0 & -\bar{\phi} \end{pmatrix}$$

And the eigenvalues are : $\lambda_1 = -1$, $\lambda_2 = -\bar{\phi}$, $\lambda_3 = \bar{\alpha}_1 - \bar{\delta}_1$ and $\lambda_4 = \bar{\alpha}_2 - \bar{\delta}_2$
This point is stable with two conditions: $\bar{\alpha}_1 < \bar{\delta}_1$ and $\bar{\alpha}_2 < \bar{\delta}_2$

- The fixed point a_4 only exists when the condition $Y_1 = \frac{\bar{\delta}_1}{\bar{\alpha}_1} - 1 - Y_2$ is satisfied. In section 3.5 the stability of this fixed point is studied.
- For the fixed point a_5 , in order to facilitate the analysis, we use $\bar{\gamma}_1 = \bar{\gamma}_2 = \bar{\gamma}$. With this, the eigenvalues are:

$$\begin{aligned} \lambda_1 &= \frac{\bar{\alpha}_2 \bar{\delta}_1 - \bar{\alpha}_1 \bar{\delta}_2}{\bar{\alpha}_2} \\ \lambda_2 &= \frac{-\sqrt{\bar{\delta}_1} \sqrt{-4\bar{\alpha}_1^2 + 4\bar{\alpha}_1 \bar{\delta}_1 + \bar{\delta}_1} - \bar{\delta}_1}{2\bar{\alpha}_1} \\ \lambda_3 &= \frac{\sqrt{\bar{\delta}_1} \sqrt{-4\bar{\alpha}_1^2 + 4\bar{\alpha}_1 \bar{\delta}_1 + \bar{\delta}_1} - \bar{\delta}_1}{2\bar{\alpha}_1} \\ \lambda_4 &= \frac{\bar{\alpha}_1 \bar{\gamma} - \bar{\alpha}_1 \bar{\phi} - \bar{\delta}_1 \bar{\gamma}}{\bar{\alpha}_1} \end{aligned}$$

For λ_1 and λ_4 , the condition for stability are: $\bar{\alpha}_2 \bar{\delta}_1 < \bar{\alpha}_1 \bar{\delta}_2$ and $(\bar{\gamma} - \bar{\phi})\bar{\alpha}_1 < \bar{\delta}_1 \bar{\gamma}$.
For λ_2 and λ_3 , we need to satisfy the following inequalities simultaneously:

$$\begin{aligned} \frac{-\sqrt{\bar{\delta}_1} \sqrt{-4\bar{\alpha}_1^2 + 4\bar{\alpha}_1 \bar{\delta}_1 + \bar{\delta}_1} - \bar{\delta}_1}{2\bar{\alpha}_1} &< 0 \\ \frac{\sqrt{\bar{\delta}_1} \sqrt{-4\bar{\alpha}_1^2 + 4\bar{\alpha}_1 \bar{\delta}_1 + \bar{\delta}_1} - \bar{\delta}_1}{2\bar{\alpha}_1} &< 0 \end{aligned}$$

This is,

$$\begin{aligned} -\sqrt{\bar{\delta}_1} \sqrt{-4\bar{\alpha}_1^2 + 4\bar{\alpha}_1 \bar{\delta}_1 + \bar{\delta}_1} - \bar{\delta}_1 &< \sqrt{\bar{\delta}_1} \sqrt{-4\bar{\alpha}_1^2 + 4\bar{\alpha}_1 \bar{\delta}_1 + \bar{\delta}_1} - \bar{\delta}_1 < 0 \\ -\sqrt{\bar{\delta}_1} \sqrt{-4\bar{\alpha}_1^2 + 4\bar{\alpha}_1 \bar{\delta}_1 + \bar{\delta}_1} &< \sqrt{\bar{\delta}_1} \sqrt{-4\bar{\alpha}_1^2 + 4\bar{\alpha}_1 \bar{\delta}_1 + \bar{\delta}_1} < \frac{\bar{\delta}_1}{\sqrt{\bar{\delta}_1}} \end{aligned}$$

The first inequality is always satisfied and we can just focus on the last one

$$\begin{aligned} \sqrt{-4\bar{\alpha}_1^2 + 4\bar{\alpha}_1 \bar{\delta}_1 + \bar{\delta}_1} &< \frac{\bar{\delta}_1}{\sqrt{\bar{\delta}_1}} \\ \sqrt{-4\bar{\alpha}_1^2 + 4\bar{\alpha}_1 \bar{\delta}_1 + \bar{\delta}_1} &< \sqrt{\bar{\delta}_1} \\ -4\bar{\alpha}_1^2 + 4\bar{\alpha}_1 \bar{\delta}_1 + \bar{\delta}_1 &< \bar{\delta}_1 \\ -4\bar{\alpha}_1^2 &< -4\bar{\alpha}_1 \bar{\delta}_1 \\ \bar{\alpha}_1 &> \bar{\delta}_1 \end{aligned}$$

So, this fixed point is stable in the region in which

$$\begin{aligned}\frac{\bar{\alpha}_1}{\bar{\alpha}_2} &> \frac{\bar{\delta}_1}{\bar{\delta}_2} \\ (\bar{\gamma} - \bar{\phi})\bar{\alpha}_1 &< \bar{\delta}_1\bar{\gamma} \\ \bar{\delta}_1 &< \bar{\alpha}_1\end{aligned}$$

is satisfied.

- For solving the fixed point a_7 , we use almost the same algebraic treatment that we used in solving a_5 , i.e., we use $\bar{\gamma}_1 = \bar{\gamma}_2 = \bar{\gamma}$ and we get the eigenvalues:

$$\begin{aligned}\lambda_1 &= \frac{\bar{\alpha}_1\bar{\delta}_2 - \bar{\alpha}_2\bar{\delta}_1}{\bar{\alpha}_2} \\ \lambda_2 &= \frac{-\sqrt{\bar{\delta}_2}\sqrt{-4\bar{\alpha}_2^2 + 4\bar{\alpha}_2\bar{\delta}_2 + \bar{\delta}_2} - \bar{\delta}_2}{2\bar{\alpha}_2} \\ \lambda_3 &= \frac{\sqrt{\bar{\delta}_2}\sqrt{-4\bar{\alpha}_2^2 + 4\bar{\alpha}_2\bar{\delta}_2 + \bar{\delta}_2} - \bar{\delta}_2}{2\bar{\alpha}_2} \\ \lambda_4 &= \frac{\bar{\alpha}_2\bar{\gamma} - \bar{\alpha}_2\bar{\phi} - \bar{\delta}_2\bar{\gamma}}{\bar{\alpha}_2}\end{aligned}$$

For λ_1 and λ_4 , the condition for stability are: $\frac{\bar{\alpha}_1}{\bar{\alpha}_2} < \frac{\bar{\delta}_1}{\bar{\delta}_2}$ and $(\bar{\gamma} - \bar{\phi})\bar{\alpha}_2 < \bar{\delta}_2\bar{\gamma}$. For λ_2 and λ_3 , we need to satisfy the following inequalities simultaneously:

$$\begin{aligned}\frac{-\sqrt{\bar{\delta}_2}\sqrt{-4\bar{\alpha}_2^2 + 4\bar{\alpha}_2\bar{\delta}_2 + \bar{\delta}_2} - \bar{\delta}_2}{2\bar{\alpha}_2} &< 0 \\ \frac{\sqrt{\bar{\delta}_2}\sqrt{-4\bar{\alpha}_2^2 + 4\bar{\alpha}_2\bar{\delta}_2 + \bar{\delta}_2} - \bar{\delta}_2}{2\bar{\alpha}_2} &< 0\end{aligned}$$

This is,

$$\begin{aligned}-\sqrt{\bar{\delta}_2}\sqrt{-4\bar{\alpha}_2^2 + 4\bar{\alpha}_2\bar{\delta}_2 + \bar{\delta}_2} - \bar{\delta}_2 &< \sqrt{\bar{\delta}_2}\sqrt{-4\bar{\alpha}_2^2 + 4\bar{\alpha}_2\bar{\delta}_2 + \bar{\delta}_2} - \bar{\delta}_2 < 0 \\ -\sqrt{\bar{\delta}_2}\sqrt{-4\bar{\alpha}_2^2 + 4\bar{\alpha}_2\bar{\delta}_2 + \bar{\delta}_2} &< \sqrt{\bar{\delta}_2}\sqrt{-4\bar{\alpha}_2^2 + 4\bar{\alpha}_2\bar{\delta}_2 + \bar{\delta}_2} < \frac{\bar{\delta}_2}{\sqrt{\bar{\delta}_2}}\end{aligned}$$

The first inequality is always satisfied and we can just focus on the last one

$$\begin{aligned}\sqrt{-4\bar{\alpha}_2^2 + 4\bar{\alpha}_2\bar{\delta}_2 + \bar{\delta}_2} &< \frac{\bar{\delta}_2}{\sqrt{\bar{\delta}_2}} \\ \sqrt{-4\bar{\alpha}_2^2 + 4\bar{\alpha}_2\bar{\delta}_2 + \bar{\delta}_2} &< \sqrt{\bar{\delta}_2} \\ -4\bar{\alpha}_2^2 + 4\bar{\alpha}_2\bar{\delta}_2 + \bar{\delta}_2 &< \bar{\delta}_2 \\ -4\bar{\alpha}_2^2 &< -4\bar{\alpha}_2\bar{\delta}_2 \\ \bar{\alpha}_2 &> \bar{\delta}_2\end{aligned}$$

So, this fixed point is stable in the region in which

$$\begin{aligned}\frac{\bar{\alpha}_1}{\bar{\alpha}_2} &< \frac{\bar{\delta}_1}{\bar{\delta}_2} \\ (\bar{\gamma} - \bar{\phi})\bar{\alpha}_2 &< \bar{\delta}_2\bar{\gamma} \\ \bar{\delta}_2 &< \bar{\alpha}_2\end{aligned}$$

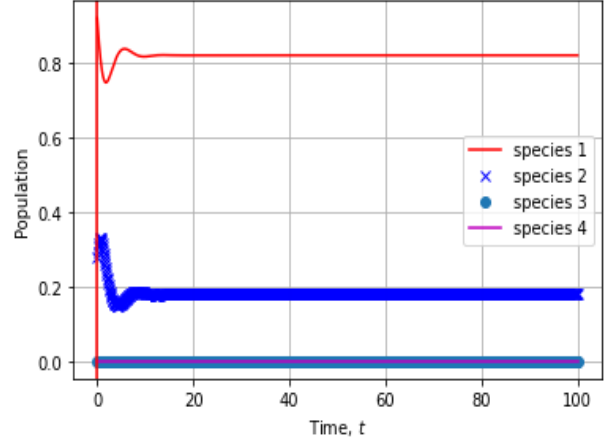
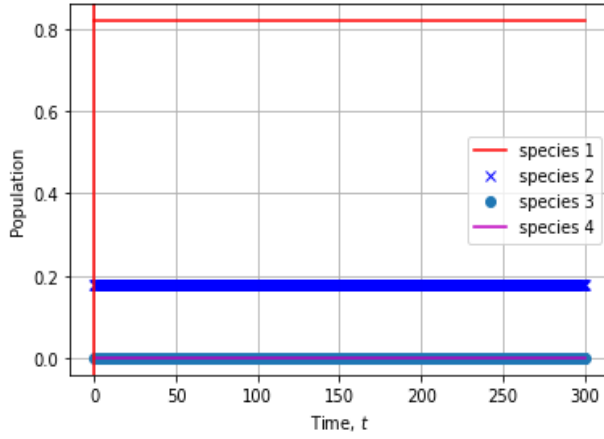
is satisfied.

- The fixed point a_8 describes the coexistence of the three species, which is going to be analyzed in the section 3.6.

3.5 Simulations for a_7 , a_4 , a_5

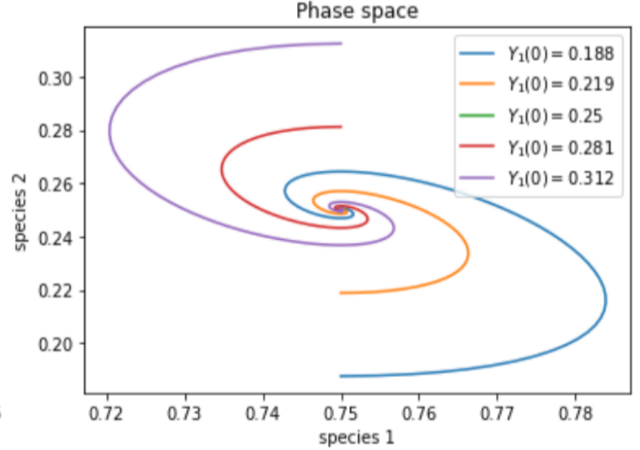
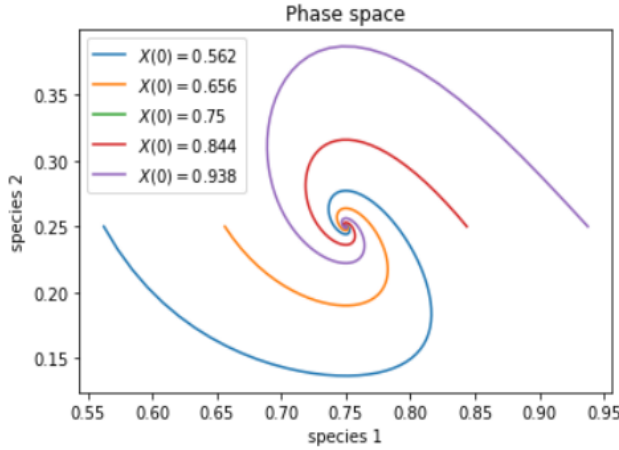
We performed the simulations to study the stability of the fixed points a_7 , a_4 , a_5 . We did this by plotting the dynamics of the population.

1. For the analysis of fixed point a_7 , the simulations are in agreement with the result that we obtained from the calculations of the stability (from section 3.4). In Figure 3.1a, we observed the usual constant behavior when the initial condition for the populations are exactly the values of the fixed point. In Figure 3.1b, the initial conditions are values above the fixed points. We observed that the final state tends to the fixed point. This behavior also happens when the initial conditions are below the fixed point. Thus, we can conclude that this fixed point is stable. In Figure 3.1c and Figure 3.1d, the dynamics of the phase space for a few values around a_7 are shown.



(a) System for initial conditions with the values of fixed point $a_7 = (\bar{X}^*, \bar{Y}_1^*, \bar{Y}_2^*, \bar{W}^*) = (0.75, 0.25, 0, 0)$ and parameters $\bar{\alpha}_1 = 4$, $\bar{\alpha}_2 = 5$, $\bar{\delta}_1 = 3$, $\bar{\delta}_2 = 4.1$, $\bar{\gamma} = 1.5$, $\bar{\phi} = 0.5$

(b) Population dynamics with initial conditions $(\bar{X}, \bar{Y}_1, \bar{Y}_2, \bar{W}) = (\bar{X}^* + 0.1, \bar{Y}_1^* + 0.1, \bar{Y}_2^* + 0.01, \bar{W}^* + 0.1)$

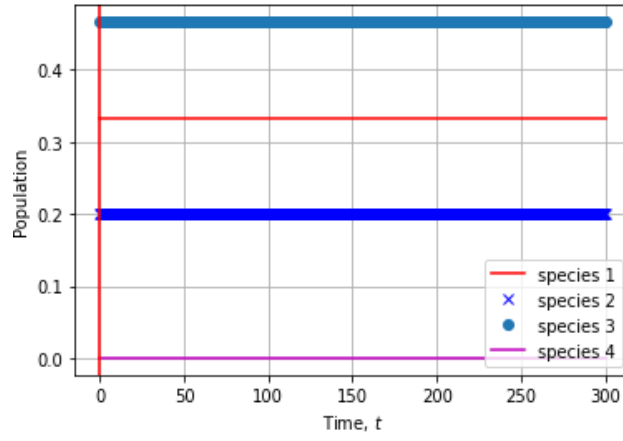


(c) Phase space with initial conditions with values around $X_0 = 0.75$ of fixed point a_7

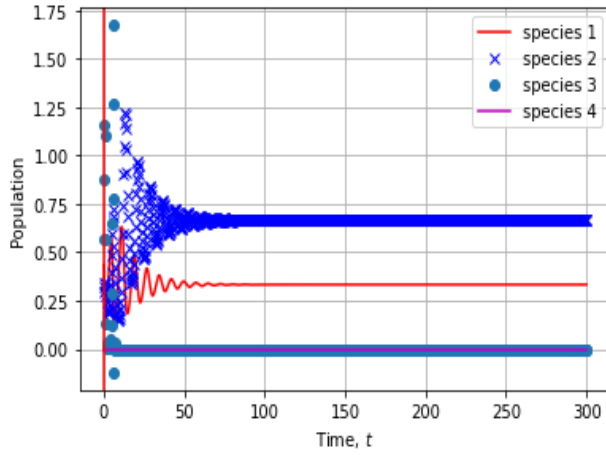
(d) Phase space with initial conditions with values around $Y_1(0)$ of fixed point a_7

Figure 3.1: Analysis of the behavior of the populations with initial conditions with values around the equilibrium state a_7

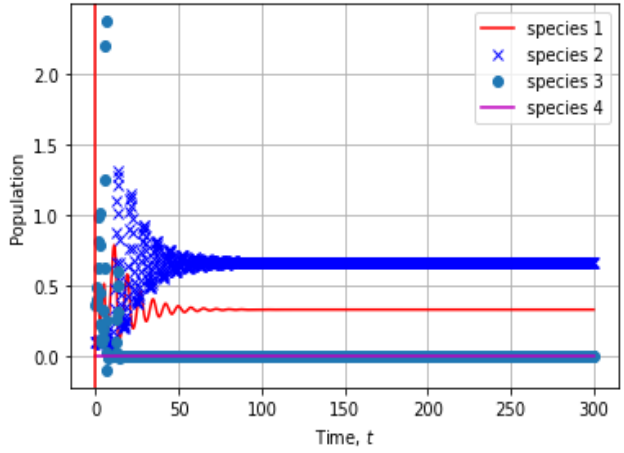
2. For the analysis of the fixed point a_4 , the fixed points are unstable because for values of the initial conditions below and above the fixed point, the final dynamical state goes towards the equilibrium point a_7 as shown in Figure 3.2.



(a) Static behavior for initial conditions with values equal to the fixed point, this is,
 $(\bar{X}, \bar{Y}_1, \bar{Y}_2, \bar{W}) = (\bar{X}^*, \bar{Y}_1^*, \bar{Y}_2^*, \bar{W}^*)$



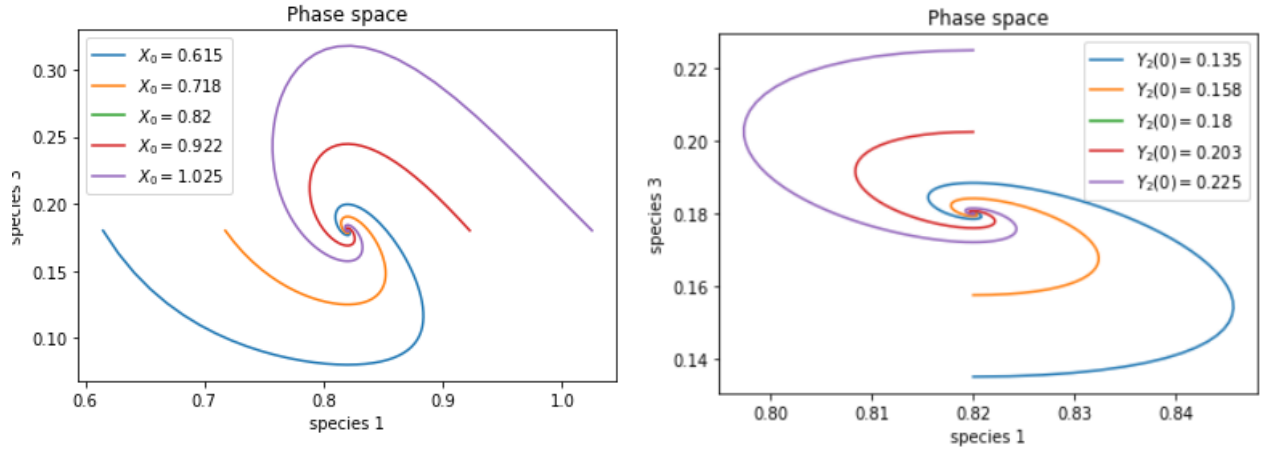
(b) Population dynamic with initial condition
 $(\bar{X}, \bar{Y}_1, \bar{Y}_2, \bar{W}) = (\bar{X}^* + 0.1, \bar{Y}_1^* + 0.1, \bar{Y}_2^* + 0.01, \bar{W}^* + 0.1)$



(c) Populations dynamic for initial condition
 $(\bar{X}, \bar{Y}_1, \bar{Y}_2, \bar{W}) = (\bar{X}^* - 0.1, \bar{Y}_1^* - 0.1, \bar{Y}_2^* - 0.01, \bar{W}^* - 0.1)$

Figure 3.2: Analysis of the behavior of the populations with initial conditions around the equilibrium state
 $a_4(\bar{X}^*, \bar{Y}_1^*, \bar{Y}_2^*, \bar{W}^*) = (0.3333, 0.200, 0.4666, 0)$

3. For the analysis of the fixed point a_5 , we get a similar behavior for the dynamic population as in a_7 . Figure 3.3 shows the phase space for some initial conditions with values around the corresponding fixed point. We can observe that the behavior of the population is around a point, thus, we can conclude it is a stable fixed point.



(a) Phase space for initial conditions with values around $X^* = 0.82$ of fixed point a_5 (b) Phase space for initial conditions with values around $Y_2^* = 0.18$ of fixed point a_5

Figure 3.3: Analysis of the behavior of the populations with initial conditions around the equilibrium state $a_5 = (\bar{X}^*, \bar{Y}_1^*, \bar{Y}_2^*, \bar{W}^*) = (0.820, 0, 0.181, 0)$

3.6 Coexistence

We can analyze this coexistence differently, but for simplification we assume that species 4 catch species 2 in such a way that $\gamma_1 = \gamma_2 = \gamma$.

Because we are looking for coexistence, we assume that none of the species go to extinction. Rewriting the system, we have:

$$\frac{d \log \bar{X}}{dt} = (1 - \bar{X}) - (\bar{Y}_1 + \bar{Y}_2) \quad (3.2)$$

$$\frac{d \log \bar{Y}_1}{dt} = \bar{\alpha}_1 \bar{X} - \bar{W} - \bar{\delta}_1 \quad (3.3)$$

$$\frac{d \log \bar{Y}_2}{dt} = \bar{\alpha}_2 \bar{X} - \bar{W} - \bar{\delta}_2 \quad (3.4)$$

$$\frac{1}{\bar{\gamma}} \frac{d \log \bar{W}}{dt} = (\bar{Y}_1 + \bar{Y}_2) - \frac{\bar{\phi}}{\bar{\gamma}} \quad (3.5)$$

Subtracting Equation (3.4) from Equation (3.3) we get,

$$\frac{d}{dt} (\log \bar{Y}_1 - \log \bar{Y}_2) = (\bar{\alpha}_1 - \bar{\alpha}_2) \bar{X} + (\bar{\delta}_2 - \bar{\delta}_1)$$

and using Equation (3.2) and Equation (3.5),

$$\begin{aligned} \bar{X} &= 1 - \frac{d \log \bar{X}}{dt} - (\bar{Y}_1 + \bar{Y}_2) \\ (\bar{Y}_1 + \bar{Y}_2) &= \frac{1}{\bar{\gamma}} \frac{d \log \bar{W}}{dt} + \frac{\bar{\phi}}{\bar{\gamma}} \end{aligned}$$

we get the following equation :

$$\frac{d}{dt} (\log \bar{Y}_1 - \log \bar{Y}_2) = (\bar{\alpha}_1 - \bar{\alpha}_2) \left(1 - \frac{d \log \bar{X}}{dt} - \left(\frac{1}{\bar{\gamma}} \frac{d \log \bar{W}}{dt} + \frac{\bar{\phi}}{\bar{\gamma}} \right) \right) + (\bar{\delta}_2 - \bar{\delta}_1)$$

which can be rearranged as

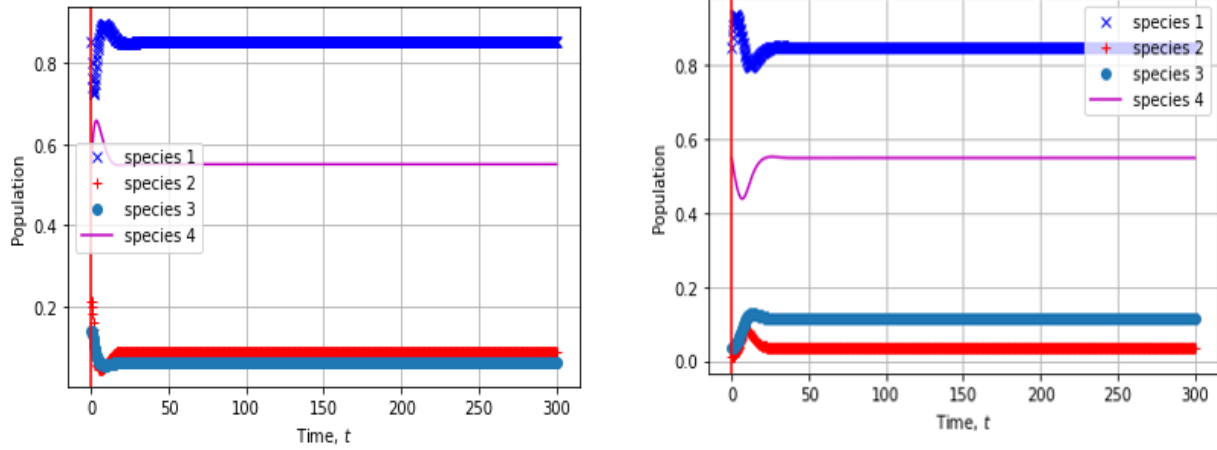
$$\frac{d}{dt} \left(\overbrace{\log \bar{Y}_1 - \log \bar{Y}_2 + (\bar{\alpha}_1 - \bar{\alpha}_2) \log \bar{X} + \frac{(\bar{\alpha}_1 - \bar{\alpha}_2)}{\bar{\gamma}} \log \bar{W}}^{L(\bar{X}, \bar{Y}_1, \bar{Y}_2, \bar{W})} \right) = \underbrace{(\bar{\alpha}_1 - \bar{\alpha}_2) - (\bar{\alpha}_1 - \bar{\alpha}_2) \frac{\bar{\phi}}{\bar{\gamma}} + (\bar{\delta}_2 - \bar{\delta}_1)}_{=C}$$

The right hand side of this equation is a constant.

Noticing that $\bar{X}, \bar{Y}_1, \bar{Y}_2$ and \bar{W} have positive finite values, and that the function L is unbounded:

1. When $C \neq 0$, the derivative of L is always different from zero and constant, and because L is unbounded, it never stops growing until it reaches infinity. This happens for at least one of the species going to extinction or reaching infinity, which is a contradiction with the original assumption. That means that there can no be coexistence for this case.
2. $C = 0$ is a necessary condition for the 4 species to coexist which restricts the problem to a 3D surface in the 4D space. The four species move maintaining L constant which cannot happen if any of the species go to extinction, which shows that for this case, there is coexistence. Because there is only one fixed point with coexistence, it would be the fixed point for $C = 0$.

To continue with the analysis of the coexistence of all species, we perform a simulation with initial conditions that are very small values above and below the corresponding fixed point a_8 , and we find that both states of the system end up in the final state of the fixed point. Therefore we can conclude that a_8 is a stable fixed point for $C = 0$, which agree with the theoretical result.



(a) Analysis of the fixed point with the initial condition $(\bar{X}, \bar{Y}_1, \bar{Y}_2, \bar{W}) = (\bar{X}^*, \bar{Y}_1^* + 0.1, \bar{Y}_2^* + 0.1, \bar{W}^*)$ (b) Analysis of the fixed point with the initial condition $(\bar{X}, \bar{Y}_1, \bar{Y}_2, \bar{W}) = (\bar{X}^*, \bar{Y}_1^* - 0.1, \bar{Y}_2^* - 0.01, \bar{W}^*)$

Figure 3.4: Analysis of the fixed point stability for coexistence of all species, with the conditions

$$\bar{\delta}_1 - \bar{\delta}_2 < \bar{\alpha}_1 - \bar{\alpha}_2, \bar{\phi} < \bar{\gamma} \text{ and } \bar{\delta}_1 < \bar{\alpha}_1 \frac{\bar{\delta}_1 - \bar{\delta}_2}{\bar{\alpha}_1 - \bar{\alpha}_2} \text{ we get the fixed point}$$

$$(\bar{X}^*, \bar{Y}_1^*, \bar{Y}_2^*, \bar{W}^*) = (0.85, 0.1125, 0.0375, 0.5499)$$

4 Density dependence

Consider the stochastic discrete-time process defined by the following transition probabilities

$$M_{n \rightarrow n+1} = \frac{N-n}{N} \frac{n}{N} \left(1 - q \frac{n}{N}\right) \quad (4.1)$$

and

$$M_{n \rightarrow n-1} = \frac{n}{N} \frac{N-n}{N} \left(1 - q \frac{N-n}{N}\right) \quad (4.2)$$

where $0 \leq q \leq 1$ and $M_{n \rightarrow n}$ is appropriately defined by the normalization condition. Study the fixation probability. You are free to use numerical simulations and/or analytic calculations, and encouraged to use both. What is the behavior in the limit $N \gg 1$? What is the interpretation of the parameter q ?

4.1 The Model

Having a finite population of N individuals, with n of species A and $(N - n)$ of species B, the transition probability from state n to state $n + 1$ is given by:

$$p(n|n+1) = \frac{n}{N} \frac{N-n}{N} \left[1 - q \frac{n}{N}\right] \quad (4.3)$$

The transition probability from state n to state $n - 1$ is given by:

$$p(n|n-1) = \frac{N-n}{N} \frac{n}{N} \left[1 - q \frac{N-n}{N}\right] \quad (4.4)$$

The probability that the number of individuals of species A does not change is given by:

$$p(n|n) = 1 - p(n|n+1) - p(n|n-1) \quad (4.5)$$

We calculate the fixation probability and based on the result, we should give a reasonable interpretation of q . Before going to the calculation, we can compare the given transition probabilities to the Moran model. In Moran model, we have a fixed total number of population, at each cycle we pick one random individual of species A and let it reproduce with probability $x = \frac{n}{N}$, then we kill another random individual from species B with probability $1 - x$. In the case of neutral Moran model without any mutation or selective advantage, the transition probabilities are given by:

$$p(n|n+1) = p(n|n-1) = x(1-x) \quad (4.6)$$

From Equation (4.6), we can have an intuition about the terms $(1 - qx)$ and $(1 - q(1 - x))$ in our model's transition probabilities which are mainly dependent on q and the fraction of each species, but we should do the calculations and see the behavior of the fixation probability with different limits in order to see how it affects by q .

4.2 The fixation probability $\pi(n)$

The fixation probability is the probability that the whole population will be of species A or species B when the other type goes to extinction. Given that we have initially n population of type A, the fixation probability $\pi(n)$ is given by:

$$\pi(n) = p(n|n+1)\pi(n+1) + p(n|n-1)\pi(n-1) + p(n|n)\pi(n) \quad (4.7)$$

4.2.1 Initial and Boundary Conditions

- Boundary Conditions: The probability to have $n = 0$ given the condition that the initial population is zero, is 1, and this is the same for an initial population of $n = N$ (assuming that we don't have any mutations).

$$p(n=0|n=0) = p(n=N|n=N) = 1 \quad (4.8)$$

$$p(n=1|n=0) = p(n=N+1|n=N) = 0 \quad (4.9)$$

- Initial Conditions: The fixation probability when we start initially with $n = N$ is 1 which means that, the probability to have finally $n = N$ given an initial population $n = N$, is 1. When we start initially with $n = 0$, the fixation probability is zero which tells us that if there is no individual of species A, then it is impossible to find the whole population being of species A (also note that there is no mutation).

$$\begin{aligned}\pi(n = N) &= 1 \\ \pi(n = 0) &= 0\end{aligned}\tag{4.10}$$

We can think about those boundaries as absorbing boundaries (once in, never out).

4.2.2 Calculating the fixation probability

By substituting from Equation (4.3), Equation (4.4) and Equation (4.5) in Equation (4.7), we get:

$$\begin{aligned}\pi(n) &= p(n|n+1)\pi(n+1) + p(n|n-1)\pi(n-1) + [1 - p(n|n+1) - p(n|n-1)]\pi(n) \\ &= p(n|n+1)\pi(n+1) + p(n|n-1)\pi(n-1) + \pi(n) - p(n|n+1)\pi(n) - p(n|n-1)\pi(n) \\ &= p(n|n+1)\pi(n+1) + p(n|n-1)\pi(n-1) - p(n|n+1)\pi(n) - p(n|n-1)\pi(n) \\ &= \pi(n+1) + \frac{p(n|n-1)}{p(n|n+1)}\pi(n-1) - \pi(n) - \frac{p(n|n-1)}{p(n|n+1)}\pi(n) \\ &= \pi(n+1) + \frac{p(n|n-1)}{p(n|n+1)}[\pi(n-1) - \pi(n)] - \pi(n) \\ \pi(n+1) - \pi(n) &= \frac{p(n|n-1)}{p(n|n+1)}[\pi(n) - \pi(n-1)] \\ &= \gamma_n[\pi(n) - \pi(n-1)]\end{aligned}\tag{4.11}$$

where,

$$\boxed{\gamma_n = \frac{p(n|n-1)}{p(n|n+1)} = \frac{N - q(N - n)}{N - qn}}\tag{4.12}$$

By applying the recursion method:

$$\begin{aligned}\pi(n+1) - \pi(n) &= \gamma_n[\pi(n) - \pi(n-1)] \\ \pi(n) - \pi(n-1) &= \gamma_{n-1}[\pi(n-1) - \pi(n-2)] \\ \pi(n-1) - \pi(n-2) &= \gamma_{n-2}[\pi(n-2) - \pi(n-3)] \\ &\vdots \\ \pi(2) - \pi(1) &= \gamma_1[\pi(1) - \pi(0)]\end{aligned}\tag{4.13}$$

we will get:

$$\pi(n+1) = \pi(n) + \pi(1) \prod_{i=1}^n \gamma_i\tag{4.14}$$

By applying the recursion method and summing:

$$\begin{aligned}\pi(n+1) &= \pi(n) + \pi(1) \prod_{i=1}^n \gamma_i + \\ \pi(n) &= \pi(n-1) + \pi(1) \prod_{i=1}^{n-1} \gamma_i + \\ \pi(n-1) &= \pi(n-2) + \pi(1) \prod_{i=1}^{n-2} \gamma_i + \\ &\vdots \\ \pi(2) &= \pi(1) + \pi(1) \prod_{i=1}^1 \gamma_i \\ \hline \pi(n+1) &= \pi(1) + \pi(1) \prod_{i=1}^n \gamma_i\end{aligned}$$

we will get:

$$\pi(n+1) = \pi(1) \left[1 + \sum_{k=1}^n \prod_{i=1}^k \gamma_i \right] \quad (4.15)$$

In order to know the value of $\pi(1)$, we should use the initial conditions, so we will let $N = n + 1$ and substitute from Equation (4.10) in Equation (4.15). We will get:

$$\begin{aligned} \pi(N) &= \pi(1) \left[1 + \sum_{k=1}^{N-1} \prod_{i=1}^k \gamma_i \right] \\ 1 &= \pi(1) \left[1 + \sum_{k=1}^{N-1} \prod_{i=1}^k \gamma_i \right] \\ \pi(1) &= \frac{1}{1 + \sum_{k=1}^{N-1} \prod_{i=1}^k \gamma_i} \end{aligned} \quad (4.16)$$

By substituting from Equation (4.16) in Equation (4.15), we get:

$$\begin{aligned} \pi(n+1) &= \frac{1 + \sum_{k=1}^n \prod_{i=1}^k \gamma_i}{1 + \sum_{k=1}^{N-1} \prod_{i=1}^k \gamma_i} \\ \pi(n) &= \frac{1 + \sum_{k=1}^{n-1} \prod_{i=1}^k \gamma_i}{1 + \sum_{k=1}^{N-1} \prod_{i=1}^k \gamma_i} \end{aligned} \quad (4.17)$$

By substituting from Equation (4.12) in Equation (4.17), we will have a general formula for the fixation probability of n individuals of species A:

$$\pi(n) = \frac{1 + \sum_{k=1}^{n-1} \prod_{i=1}^k \frac{N-q(N-i)}{N-qi}}{1 + \sum_{k=1}^{N-1} \prod_{i=1}^k \frac{N-q(N-i)}{N-qi}} \quad (4.18)$$

4.3 Studying the behavior of fixation probability

We will discuss the behavior of the fixation probabilities with different limits using analytic calculations and numerical simulations. Then, we will compare the results and based on the analysis, we will try to find reasonable interpretation for the q value.

4.3.1 The analytical method:

- For $q = 0$:

$$\begin{aligned} \pi(n) &= \frac{1 + \sum_{k=1}^{n-1} \prod_{i=1}^k \frac{N}{N}}{1 + \sum_{k=1}^{N-1} \prod_{i=1}^k \frac{N}{N}} \\ &= \frac{1 + (n-1)}{1 + (N-1)} \\ &= \frac{n}{N} \end{aligned}$$

As we see, this is the neutral Moran model without any mutation or selection advantage.

- For $N \gg 1$ and $\frac{n}{N} \ll 1$, we find that:

$$\gamma_n = \frac{N-q(N-n)}{N-qn} \approx \frac{N(1-q)}{N} \approx 1 - q$$

$$\begin{aligned}
\pi(n) &= \pi(1) \left(1 + \sum_{k=1}^{n-1} \prod_{i=1}^k (1-q) \right) \\
&= \pi(1) \left(1 + \sum_{k=1}^{n-1} (1-q)^k \right) \\
&= \pi(1) \left(1 + (1-q) \frac{1 - (1-q)^{n-1}}{1 - (1-q)} \right) \\
&= \frac{\pi(1)}{q} (q + (1-q)(1 - (1-q)^{n-1}))
\end{aligned} \tag{4.19}$$

When n is close to one ($n \approx 2$) :

$$\pi(n \rightarrow 2) \approx \pi(1) (2 - q) \tag{4.20}$$

This means that for a very small n , the dominant and the only factor affecting the fixation probability is q .

When n is also large, $n \gg 1$:

$$\pi(n) \approx 1 \tag{4.21}$$

- For n close to N :

$$\begin{aligned}
\pi(n \approx N) &= \frac{1 + \sum_{k=1}^{n-1} \prod_{i=1}^k \frac{N-q(N-i)}{N-qi}}{1 + \sum_{k=1}^{N-1} \prod_{i=1}^k \frac{N-q(N-i)}{N-qi}} \\
&= \frac{1 + \sum_{k=1}^{N-1} \prod_{i=1}^k \frac{N-q(N-i)}{N-qi} - \sum_{k=n}^{N-1} \prod_{i=1}^k \frac{N}{N(1-q)}}{1 + \sum_{k=1}^{N-1} \prod_{i=1}^k \frac{N-q(N-i)}{N-qi}} \\
&= 1 - \frac{\sum_{k=n}^{N-1} \prod_{i=1}^k \frac{N-q(N-i)}{N-qi}}{1 + \sum_{k=1}^{N-1} \prod_{i=1}^k \frac{N-q(N-i)}{N-qi}}
\end{aligned} \tag{4.22}$$

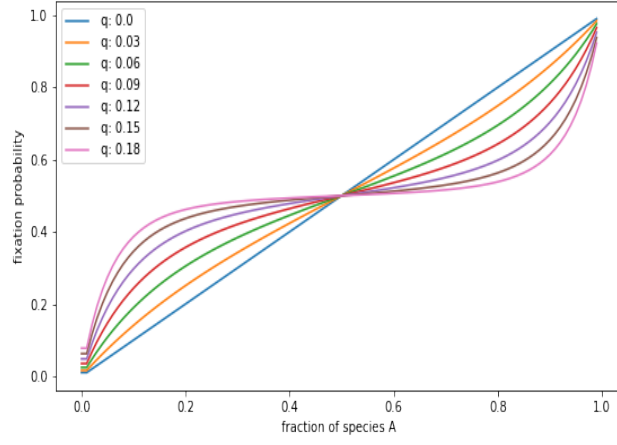
This result should be expected from the initial and boundary conditions.

4.3.2 Analysis of the different graph:

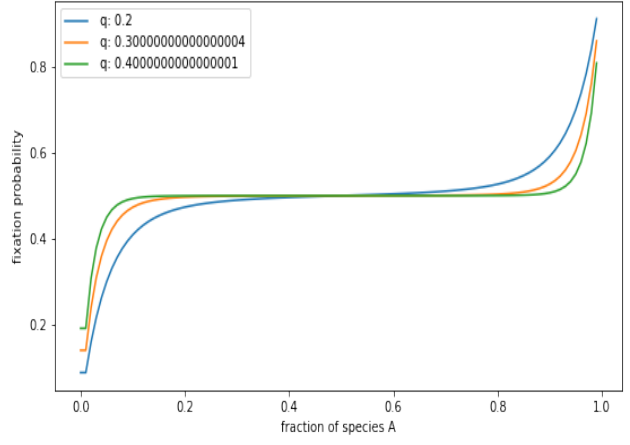
For this part we are going to give some interpretation of the graph for some specific value of n, N, q .

In (Figure 4.1) we can say that the fixation probability has three regimes:

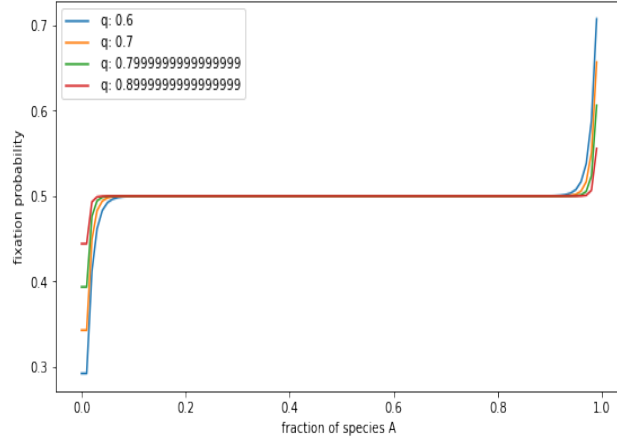
- For an initial fraction of population x slightly different from zero, the system goes to a regime where it is equiprobable to go to fixation or extinction as fast as q increases. As we said in the boundary condition, the fixation probability is zero for the fraction population equal to zero.
- For value of x far from zero and far from one, the fixation probability is more and more equal to one half as the value of q is large; which means the fixation probability is independent of x for a large value of q (close to one). For intermediate values of q , the fixation probability increases as the fraction population increases (see Figure 4.1a). For a value of q close to zero, the fixation probability is an increasing linear function with the fraction population; the slope of this function is one when we have $q = 0$ (see Figure 4.1a).
- For an initial fraction of population x slightly different from one, the system goes to a regime where it is equiprobable to go to fixation or extinction as fast as q increases. As we said in the boundary condition, the fixation probability is one for the fraction population equal to one.



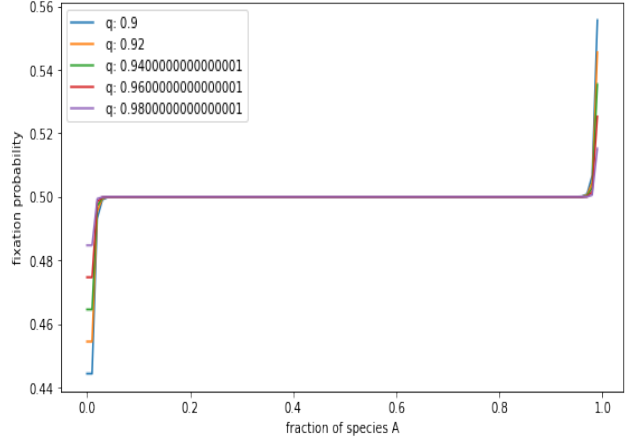
(a) Fixation probability vs fraction of species A for $q \in [0.0 : 0.1]$.



(b) Fixation probability vs fraction of species A for $q \in [0.2 : 0.4]$.



(c) Fixation probability vs fraction of species A for $q \in [0.6 : 0.9]$.



(d) Fixation probability vs fraction of species A for $q \in [0.9 : 1.0]$.

Figure 4.1: Dependence of fixation probability as a function of the fraction of species A ($x = \frac{n}{N}$) for different ranges of q and for $N = 100$.

In the next graph we give the analysis of the fixation probability with respect to q .

For n close to one ($n \approx 1$), we found that as the total population N increases, the fixation probability is becoming more and more a linear function of q . This is shown in (Figure 4.2). In addition, as the value of q increases, the fixation probability also increases.

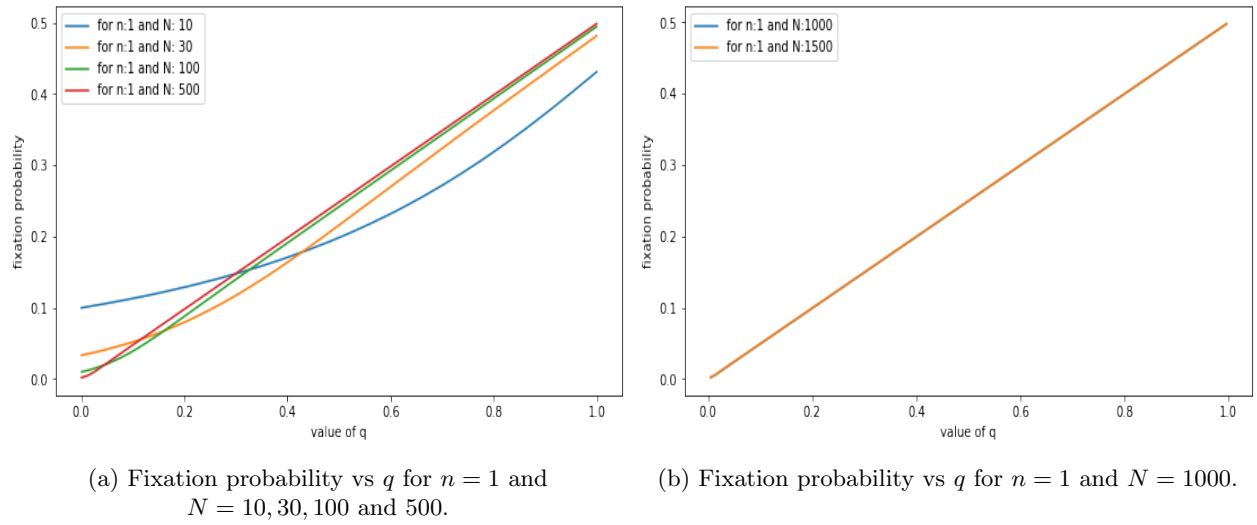


Figure 4.2: Dependence of fixation probability as a function of q for $n = 1$ and different values of population size.

For n close to two ($n \approx 2$), we found that as the total population N increases, the fixation probability is becoming more and more a quadratic function of q . This is shown in (Figure 4.3). In addition, as the value of q increases, the fixation probability also increases. And it reaches the fixation probability of 0.5 faster as the total population is larger.

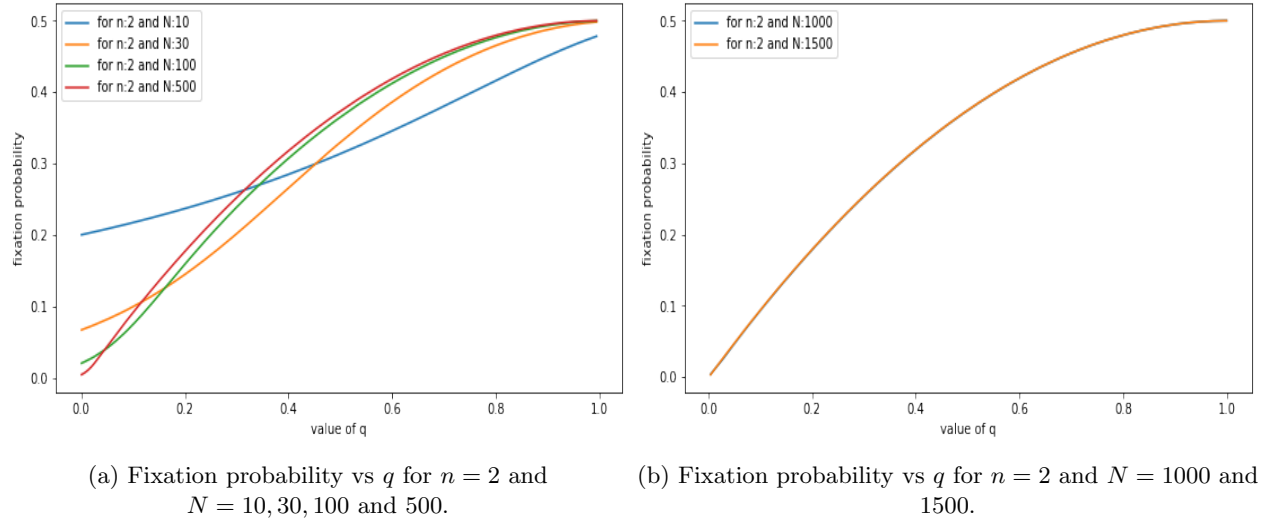


Figure 4.3: Dependence of fixation probability versus q for $n = 2$ and different values of population size.

As we saw previously, the system tends to favor the fixation probability of 0.5 as q increases. In the next plot we are looking at how the fixation probability behaves when there is half amount of population for each species initially. As we can see in (Figure 4.4), once we have half amount of species, the fixation probability is constant and this constant is one half. In this case the dependence on N disappears completely.

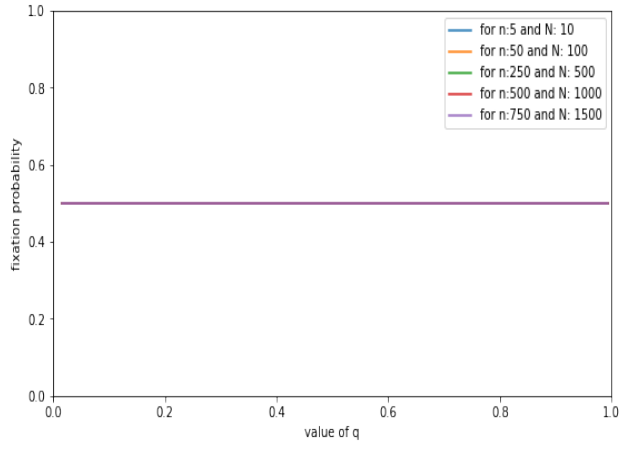


Figure 4.4: Dependence of fixation probability verses q for $n = \frac{N}{2}$ and $N = 10, 30, 100$ and 500 .

In the next plot we are looking at how the fixation probability behaves when the population of one species is very close to the total population. As we see in (Figure 4.5), the value of q increases as the disequilibrium on the fixation probability decreases. The fixation probability goes as fast to one half as the total abundance population increase as fast.

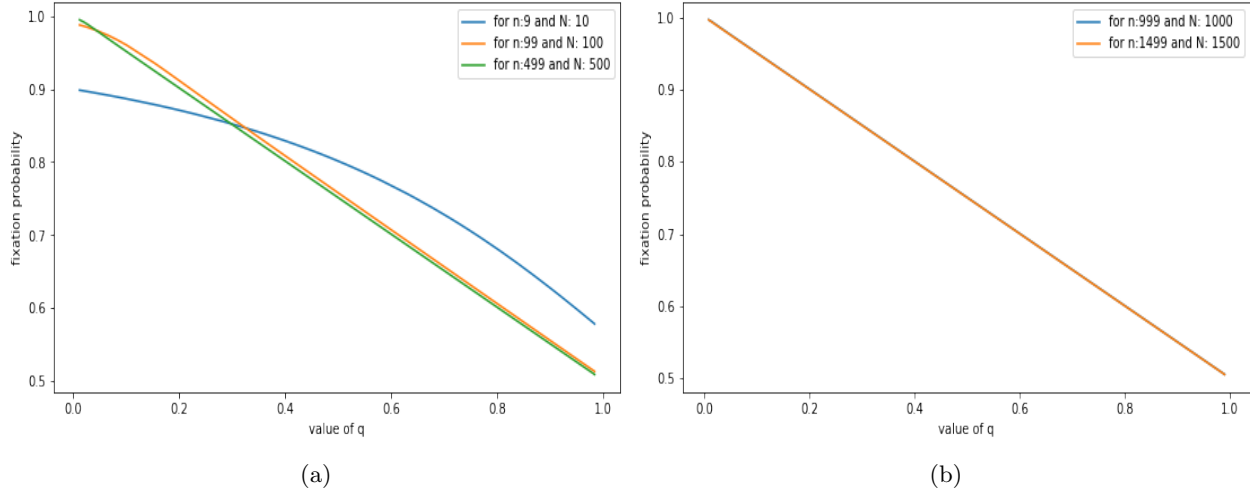


Figure 4.5: Dependence of fixation probability as a function of q , for $n \approx N$ and $N = 10, 30, 100, 500, 1000, 1500, 2000, 2500$ and 3000

4.4 Discussion

In this model, we have anti-sigmoidal shape of $\pi(n)$ when $q \neq 0$ - which is not the same as Moran model. The term $(1 - xq)$ is dependent on both q and $x = \frac{n}{N}$. It means that it's not mutation, because the mutation doesn't depend on the population size. Also, it is not a selective advantage because when $x = \frac{1}{2}$, the probability to go to extinction or fixation is the same for both species.

From the previous results, we found that the fixation probability is independent on q when $x = \frac{1}{2}$. We can imagine that for our model/system, the fixation probability is unstable when $x \neq \frac{1}{2}$, so when $n < \frac{N}{2}$, the fixation probability tends to increase until it reaches one half. Then if suddenly an unexpected event happened that changed the composition of the whole population, we can interpret this sudden event by giving a simple example for a population of two species and both were living together (growing together) and suddenly an earthquake happened that killed (by random) all population of species B, so the probability

that species A goes to fixation will be one, while if it remains only one individual of species B, this probability will tend to one half as q increase.

4.5 Conclusion

From the previous results and discussion, we can say that the behavior of our model arises from the underlying drift that tends to drive the fixation probability towards $\frac{1}{2}$. Due to a large and rare stochastic fluctuations, the population escape the effective potential well and reach fixation. The term $q \frac{n}{N}$ slows down the dynamics of the system, and generates a drift on the fixation probability, where q is a measure of the strength of these effects.

Python code:

Numerical simulation code.

Reference:

arXiv:2103.10976 [q-bio.PE]

5 Mutation asymmetry or selection?

Your friend knocks at your door asking for help. She is a yeast microbiologist working on experimental evolution. She ran an experiment on ethanol tolerance in *S. cerevisiae*, where she measured (for many replicates) the relative frequency of ethanol tolerant individuals. The molecular mechanism of ethanol tolerance is still unknown and it is not clear if the mutation from ethanol tolerance to ethanol intolerance and the reverse mutation occur equally likely. In her experiment there is no ethanol, but the ethanol tolerant phenotype might be under selection pressure for other unknown reason. She is not sure of whether her data can be explained by an asymmetry in the mutation rates or by selection on one of the two phenotypes. Can you help your friend? If no, why? If yes, what should she measure to distinguish between the two alternative scenarios?

5.1 The model

Yes, we can help our friend. We can help her by making a Moran model with selection and mutation, calculate the stationary probability distribution from this model, and then fix the parameters. One set of parameters correspond to the case where mutation asymmetry is dominant, and another set of parameters correspond to the case where selection pressure is dominant. She can then fit the model to the data, and check which set of parameters can better explain the data that she observed. Then she can conclude which of the two scenarios happened in the experiment.

The model is the following:

Having a total of N organisms, let A be the ethanol-tolerant organisms with abundance n and fitness f_A , and a the ethanol-intolerant organisms with abundance $N - n$ and fitness f_a . We define $x = \frac{n}{N}$ as the frequency of A , and $1 - x$ as the frequency of a . A can mutate to a with a rate u , whereas a can mutate to A with a rate v .

Using the Moran model with selection and mutation:

When $n_A \rightarrow n_A + 1$ or $n_a \rightarrow n_a - 1$, then we have:

$$(1 - x)x(1 - u)f_A + (1 - x)^2vf_a = b(x) \quad (5.1)$$

The first term describes the scenario when a dies with probability $1 - x$ and A reproduce with probability x , with no mutation. While the second term describes the scenario when a dies and also reproduce with the same probability of $1 - x$, and mutate to A .

When $n_A \rightarrow n_A - 1$ or $n_a \rightarrow n_a + 1$, then we have:

$$x(1 - x)(1 - v)f_a + x^2uf_A = d(x) \quad (5.2)$$

The first term describes the scenario when A dies with probability x and a reproduce with probability $1 - x$, with no mutation. While the second term describes the scenario when A dies and also reproduce with the same probability of x , and mutate to a .

5.2 Calculating Stationary Distribution

We solve for the probability distribution using the Fokker-Planck equation, and then find the stationary distribution.

$$\frac{\partial P}{\partial t} = -\frac{\partial}{\partial x}(\alpha_1 P) + \frac{1}{2} \frac{\partial^2}{\partial x^2}(\alpha_2 P) \quad (5.3)$$

Where α is:

$$\alpha_k(x) = \int dx' W(x'|x)(x' - x)^k \quad (5.4)$$

and the transition rate is:

$$W(x'|x) = b(x)\delta_{x', x + \frac{1}{N}} + d(x)\delta_{x', x - \frac{1}{N}} \quad (5.5)$$

Then

$$\alpha_k(x) = \int dx' W(x'|x)(x' - x)^k \quad (5.6)$$

$$= \int dx' (b(x)\delta_{x', x + \frac{1}{N}} + d(x)\delta_{x', x - \frac{1}{N}})(x' - x)^k \quad (5.7)$$

$$= b(x) \left(\frac{1}{N}\right)^k + d(x) \left(-\frac{1}{N}\right)^k \quad (5.8)$$

When $k = 1$

$$\alpha_1 = b(x) \frac{1}{N} - d(x) \frac{1}{N} \quad (5.9)$$

$$= (b(x) - d(x)) \frac{1}{N} \quad (5.10)$$

When $k = 2$

$$\alpha_2 = b(x) \frac{1}{N^2} + d(x) \frac{1}{N^2} \quad (5.11)$$

$$= (b(x) + d(x)) \frac{1}{N^2} \quad (5.12)$$

Solving for $b(x) - d(x)$:

$$\begin{aligned} b(x) - d(x) &= x(1-x)(1-u)f_A + (1-x)^2vf_a - x(1-x)(1-v)f_a - x^2uf_A \\ &= x(1-x)[(1-u)f_A - (1-v)f_a] + (1-x)^2vf_a - x^2uf_A \\ &= x(1-x)[f_A - uf_A - f_a + vf_a] + (1-x)^2vf_a - x^2uf_A \\ &= x(1-x)[f_A - f_a] - x(1-x)uf_A + x(1-x)vf_a + (1-x)^2vf_a - x^2uf_A \\ &= x(1-x)[f_A - f_a] - [x - x^2 + x^2]uf_A + [x - x^2 + 1 - 2x + x^2]vf_a \\ &= x(1-x)[f_A - f_a] - xuf_A + [1 - x]vf_a \end{aligned}$$

Solving for $b(x) + d(x)$:

$$\begin{aligned} b(x) + d(x) &= x(1-x)(1-u)f_A + (1-x)^2vf_a + x(1-x)(1-v)f_a + x^2uf_A \\ &= x(1-x)[(1-u)f_A + (1-v)f_a] + (1-x)^2vf_a + x^2uf_A \\ &= x(1-x)[f_A - uf_A + f_a - vf_a] + (1-x)^2vf_a + x^2uf_A \\ &= x(1-x)[f_A + f_a] - x(1-x)uf_A - x(1-x)vf_a + (1-x)^2vf_a + x^2uf_A \\ &= x(1-x)[f_A + f_a] - [x - x^2 - x^2]uf_A - [x - x^2 - 1 + 2x - x^2]vf_a \\ &= x(1-x)[f_A + f_a] - [x - 2x^2]uf_A - [-1 + 3x - 2x^2]vf_a \\ &= x(1-x)[f_A + f_a] - x(1-2x)uf_A + [1 - 3x + 2x^2]vf_a \\ &= x(1-x)[(1+s) + 1] - x(1-2x)u(1+s) + [1 - 3x + 2x^2]v \end{aligned}$$

Let $f_A - f_a = sf_a$, and set $f_a = 1$, we obtain

$$b(x) - d(x) = x(1-x)s - xu(1+s) + [1-x]v$$

and

$$b(x) + d(x) = x(1-x)[2+s] - x(1-2x)u(1+s) + [1-3x+2x^2]v$$

Finally, we have α_1 as:

$$\begin{aligned} \alpha_1 &= (b(x) - d(x)) \frac{1}{N} \\ &= \frac{1}{N} [x(1-x)s - xu(1+s) + (1-x)v] \\ \alpha_2 &= \frac{1}{N^2} [x(1-x)(2+s) - x(1-2x)u(1+s) + (1-3x+2x^2)v] \end{aligned}$$

Assuming $u \sim v \sim s \sim \frac{1}{N}$, then:

$$\begin{aligned}\alpha_1 &= \frac{1}{N} [x(1-x)s - xu + (1-x)v] \\ \alpha_2 &= 2\frac{1}{N^2} [x(1-x)]\end{aligned}$$

So, the Fokker-Planck equation becomes:

$$\frac{\partial P}{\partial t} = -\frac{\partial}{\partial x} \left(\frac{1}{N} [x(1-x)s - xu + (1-x)v] \right) P + \frac{1}{2} \frac{\partial^2}{\partial x^2} \left(\frac{2}{N^2} [x(1-x)] \right) P$$

Solving for the stationary distribution, $\frac{\partial P}{\partial t} = 0$

$$\begin{aligned}0 &= -\frac{\partial}{\partial x} \left(\frac{1}{N} [x(1-x)s - xu + (1-x)v] \right) P^* + \frac{1}{2} \frac{\partial^2}{\partial x^2} \left(\frac{2}{N^2} [x(1-x)] \right) P^* \\ 0 &= \frac{\partial}{\partial x} \left[-\left(\frac{1}{N} [x(1-x)s - xu + (1-x)v] \right) P^* + \frac{\partial}{\partial x} \left(\frac{1}{N^2} [x(1-x)] \right) P^* \right] \\ \text{cst} &= -\left(\frac{1}{N} [x(1-x)s - xu + (1-x)v] \right) P^* + \frac{\partial}{\partial x} \left(\frac{1}{N^2} [x(1-x)] \right) P^*\end{aligned}$$

Setting the constant equal to zero, the stationary distribution can be calculated as

$$\begin{aligned}P^* &= \frac{C}{x(1-x)} \exp \left[\int^x N \frac{y(1-y)s - yu + (1-y)v}{y(1-y)} dy \right] \\ &= \frac{C}{x(1-x)} \exp \left[N \left(\int^x \frac{y(1-y)s}{y(1-y)} dy - \int^x \frac{yu}{y(1-y)} dy + \int^x \frac{(1-y)v}{y(1-y)} dy \right) \right] \\ &= \frac{C}{x(1-x)} \exp \left[N \left(\int^x s dy - \int^x \frac{u}{(1-y)} dy + \int^x \frac{v}{y} dy \right) \right] \\ &= \frac{C}{x(1-x)} \exp \left[N \left(s \int^x dy - u \int^x \frac{1}{(1-y)} dy + v \int^x \frac{1}{y} dy \right) \right] \\ &= \frac{C}{x(1-x)} \exp [N (sx + u \ln (1-x) + v \ln x)] \\ &= C(1-x)^{Nu-1} x^{Nv-1} e^{Nsx}\end{aligned} \tag{5.13}$$

Equation 5.13 is the stationary distribution where C is the normalization constant. The proposal is that we could find the values of the parameters of the model (taken from the probability distribution $P^*(x; u, v, s)$) that best describes the observed data (the set of the data of the fraction of ethanol-tolerant individuals). When asymmetry mutation is dominant, $s = 0$ and $u \neq v$, then the scenario in the experiment is due to asymmetry mutation rate, and we recover the Moran Model with only mutation. On the other hand when selection pressure is dominant, $s \neq 0$ and $u = v$, then the scenario in the experiment is due to selection. If both scenarios are present, then $u \neq v$ and $s \neq 0$.

6 Fitness speed

Consider a population of size N . An individual belongs to a fitness class k with fitness e^{ks_0} . When a mutation occurs (with probability U), the fitness class of the mutant is $k + l$ where l is an integer drawn from a distribution $g(l)$. In this exercise you have to simulate the process with $g(l) = \delta_{l,-1}$ (see below on suggestions on what to simulate and how). Study the speed of adaptation, i.e. the large time behavior of the average fitness $\bar{f}(t) = \sum_k e^{ks_0} n_k(t)/N$, as a function of N (you are free to choose the values of s_0 and U , provided that $0 < s_0 \ll 1$ and $0 < U \ll 1$. Use this freedom well).

What do you expect in the limit $N \rightarrow \infty$? Describe what is happening in your simulations.

How to simulate the process. Let $n_k(t)$ be the number of individuals in class k at time t (tip: many classes are empty, do not use your computer memory to store thousands of zeros). Let's define $x_k(t) = e^{ks_0} n_k(t)/(N\bar{f}(t))$. Generate values $\tilde{n}_k(t+1)$ from a multinomial distribution with weights $x_k(t)$, i.e.

$$P(\{\tilde{n}_k\}) = \frac{N!}{\prod_k \tilde{n}_k!} \prod_k (x_k(t))^{\tilde{n}_k} \quad (6.1)$$

By definition $\sum_k \tilde{n}_k(t+1) = N$. Some of this individuals will mutate. The number of mutant m_k in class k will be binomially distributed

$$P(m_k) = \binom{\tilde{n}_k}{m_k} U^{m_k} (1-U)^{\tilde{n}_k - m_k} \quad (6.2)$$

where U is the mutation probability. The mutated individuals will go to class $k-1$ (since $g(l) = \delta_{l,-1}$). The population at time $t+1$ will be therefore given by

$$n_k(t+1) = \tilde{n}_k(t+1) + m_{k+1} - m_k. \quad (6.3)$$

6.1 Average fitness as a function of time

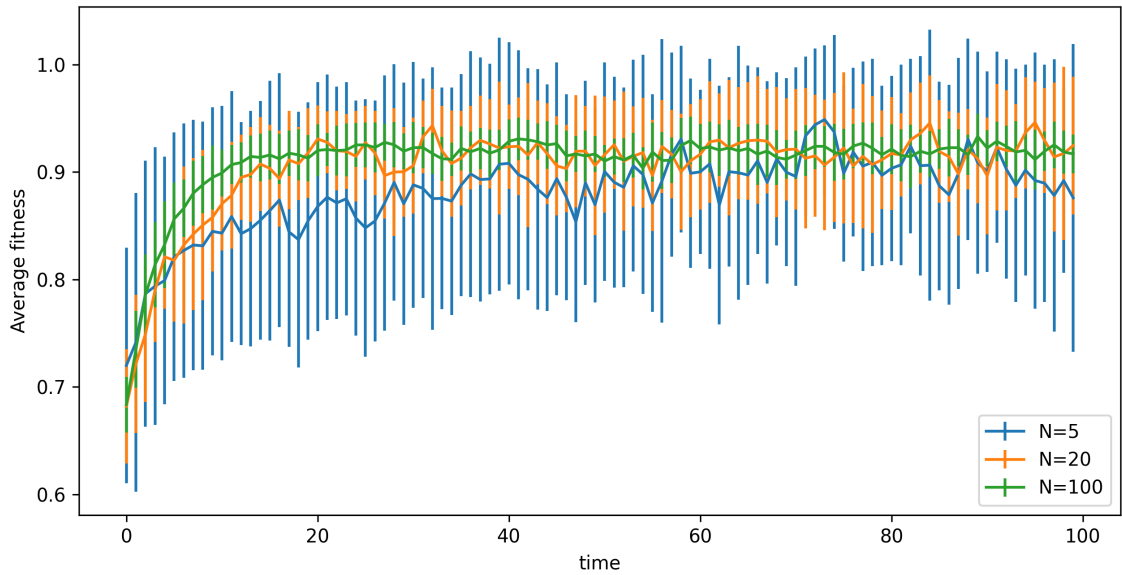


Figure 6.1: Average fitness as a function of time for $N = 5, 20, 100$ with $s_0 = 0.05$, and $u = 0.08$. For every time step, the average fitness is calculated. This is performed for 20 realizations, and the mean and standard deviation is plotted. When N is small, the variance is large, whereas as N increases, the variance decreases.

As a note: From the plot above, we considered a population with size N , an individual belongs to fitness class k , where $k = 0, -1, -2, \dots$, with fitness e^{ks_0} . When a mutation happened (with probability U), the

fitness class is $k + l$ where l is drawn from $g(l) = \delta_{l,-1}$. As an example, the population at class $k = -1$ at time $t + 1$ is the total offspring that did not mutate, plus the offspring that mutate from class $k = 0$.

The plot above shows that the average fitness increases as time increases, but plateaus after reaching a certain time. It is interesting to note that the limit behavior is not 1, but it flattens around 0.9. Because there is a competition between the two phenomena, (a) asymmetric mutation (which leads the system to move to a certain class), and (2) genetic drift (which causes randomness in the system). The equilibrium is reached around 0.9.

6.2 Average fitness as a function of N

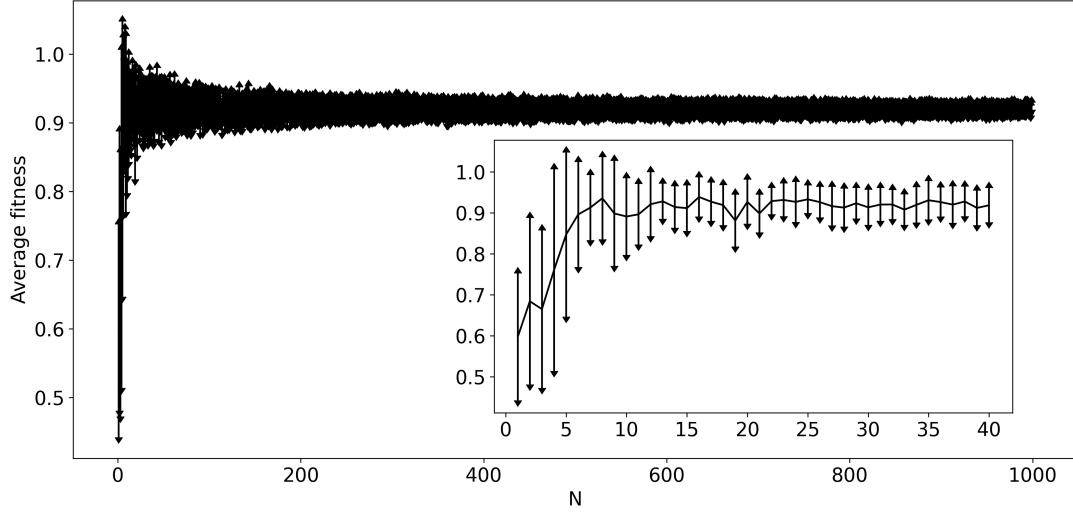


Figure 6.2: Average fitness as a function of N with class $k = 20$, time = 300, and $s_0 = 0.05$, and $u = 0.08$. N ranges from 1 to 1000 with a step of 1. This is performed for 20 realizations, and the mean and standard deviation is plotted. Inset: The inset shows the average fitness as a function of N for $1 \leq N \leq 40$.

As $N \rightarrow \infty$, the average fitness shows a stationary behavior. When $N \leq k$, the average fitness increases. This could be explained by the fact that not all classes are filled, which makes genetic drift stronger compared to mutation. But when $N > k$, the size of the population does not affect the average fitness and we see the stationary behavior. There is no dependence on N when $N > k$, this is a discontinuity of second class, which is similar to a phase transition.

Appendices

A Exercise B code

This is the code used to generate the plot of the maximum eigenvalues as a function of sigma (as shown in Figure 2.1).

```
# -*- coding: utf-8 -*-
"""Exer B.ipynb

Automatically generated by Colaboratory.

Original file is located at
    https://colab.research.google.com/drive/1coSK53BMFI2zQ3EkbsLEy5Qne504v3Qx
"""

import numpy as np
import matplotlib.pyplot as plt
from tqdm import tqdm
from google.colab import files

#calculate maximum real eigenvalue
def maxEig(N,sigma):
    A = np.random.normal(scale=sigma/np.sqrt(N),size=(N,N))
    np.fill_diagonal(A, -1)
    Eigenvalues = np.real(np.linalg.eig(A)[0])
    maxEigenvalue = np.amax(Eigenvalues)
    return maxEigenvalue

N=547
meanMaxEigs = []
errorMaxEigs = []
range_sigma=np.linspace(0,5,num=10)

#calculate max eigenvalue for different values of sigma
for j in tqdm(range_sigma):
    maxEigenvalues = []
    sigma = j
    for i in range(30):
        maxEigenvalues.append(maxEig(N, sigma))

    #take average and std
    meanMaxEigs.append(np.mean(maxEigenvalues))
    errorMaxEigs.append(np.std(maxEigenvalues))

"""Plotting maximum eigenvalues as a function of sigma"""

plt.errorbar(range_sigma,meanMaxEigs,errorMaxEigs,uplims=True, lolims=True, color='black')
plt.xlabel(' ')
plt.ylabel('Max Eigenvalue')
plt.axhline(0,color='black',ls='--')
plt.savefig('exercise_b', dpi=300)
files.download('exercise_b.png')
plt.show()
```

B Exercise F code

This is the code used to generate the plot of the average fitness as a function of time (as shown in Figure 6.1), and the average fitness as a function of N (as shown in Figure 6.2).

```
# -*- coding: utf-8 -*-
"""exer_f_no_boundary.ipynb
```

Automatically generated by Colaboratory.

```
Original file is located at
    https://colab.research.google.com/drive/1aCvENAMHwTwBmv1RIAGPWm9zQzpqghz8
"""
```

```
import numpy as np
import matplotlib.pyplot as plt
from tqdm import tqdm
from google.colab import files
```

```
"""1. Calculate  $\bar{x}_k(t)$ """
```

```
#calculate the fraction of class k
def probability(list_k, N, s):
    lst = []
    for k in range(len(list_k)):
        lst.append((np.exp(-k*s)*(list_k[k]))/N)

    return np.array(lst)/np.sum(lst)
```

```
"""2. Calculate  $P(\tilde{n})$ :"""
```

```
#calculate the number of individuals for one generation
def one_generation(list_k, N, s, u):
    #calculate the fraction of class k
    frac_class_k = probability(list_k, N, s)
```

```
#calculate the number of offspring from class k
    new_list_k = np.random.multinomial(N, frac_class_k)
```

```
#calculate the number of individuals that will mutate with prob u
    list_mutate = []
    for i in new_list_k:
        list_mutate.append(np.random.binomial(i, u))
```

```
#calculate for the number of individuals per class after mutation happened
    next_offspring_list = []
    for k in range(len(new_list_k)-1):
        next_offspring_list.append(new_list_k[k] + list_mutate[k+1] - list_mutate[k])
```

```
#the last class k is appended outside the loop, since the last class cannot have mutat
    next_offspring_list.append(new_list_k[len(new_list_k)-1] + list_mutate[0])
    return next_offspring_list
```

```
"""3. Calculate  $\bar{f}(t)$  after one generation:"""
```

```
#calculate the average fitness after one generation
#k refers to classes
def evolution_after_one_gen(time, list_N, s, u, k):
```

```

fitness_list = []

#vary the size of population
for N in list_N:
    #create the initial list for the number of individuals in each class
    list_k = np.random.multinomial(N, np.ones(k)/k)

    #let this evolve to t generations
    fitness_per_time_list = []
    for t in range(time):
        list_k = one_generation(list_k , N, s, u)

        #calculate average fitness after one generation
        ave_fitness = 0
        for j in range(len(list_k)):
            ave_fitness += (np.exp(-j*s)*list_k[j])/N

        #append the average fitness for different sizes of population
        fitness_per_time_list.append(ave_fitness)
    fitness_list.append(fitness_per_time_list)
return fitness_list

"""## Plot average fitness ( $\bar{f}(t)$ ) as a function of N"""

#number of classes
classes = 20

#value of S_0 diferent from zero and far from one
s = np.random.uniform(0.01,0.2)

#value of U diferent from zero and far from one
u = np.random.uniform(0.01,0.2)

print('value of s:', s)
print('value of u:', u)

#calculating the average fitness for each time step, for each N
realization = 20
time = 100
list_N = [5, 20, 100]

list_evo = []
for i in range(realization):
    evo = evolution_after_one_gen(time, list_N, s, u, classes)
    list_evo.append(evo)

#take the mean and standard dev for each N
list_evo_mean = np.mean(list_evo, axis=0)
list_evo_std = np.std(list_evo, axis=0)

"""Plot average fitness as a function of time for different N"""

plt.figure(figsize=(10,5))
for i in range(len(list_evo_mean)):
    plt.errorbar(np.arange(len(list_evo_mean[i])), list_evo_mean[i], yerr=list_evo_std[i], u
    #plt.ylim(0.6, 1.2)
plt.xlabel('time')
```



```

plt.ylabel('Average fitness ')
plt.legend(loc='lower right ')
plt.savefig('exercise_f_01 ', dpi=300)
files.download('exercise_f_01.png')
plt.show()

"""Plot average fitness as a function of N"""

#calculate average fitness after a lot of time/generations for different N
trials = 20
time = 300
#list of different sizes of population
list_N = np.arange(1, 1000, 1)

list_evo_N = []
for i in tqdm(range(trials)):
    evo_N = evolution_after_one_gen(time, list_N, s, u, classes)
    list_evo_N.append(evo_N)

list_evo_N_mean = np.mean(list_evo_N, axis=0)
list_evo_N_std = np.std(list_evo_N, axis=0)

#calculate mean and standard dev for each N
mean_list = []
std_list = []
for i in range(len(list_evo_N_mean)):
    mean_ = list_evo_N_mean[i][-1]
    mean_list.append(mean_)
    std_ = list_evo_N_std[i][-1]
    std_list.append(std_)

slicer=40
fig, ax1 = plt.subplots(figsize=(15,7))

#plotting inset
#these are in unitless percentages of the figure size. (0,0 is bottom left)
left, bottom, width, height = [0.45, 0.2, 0.4, 0.45]
ax2 = fig.add_axes([left, bottom, width, height])

plt.rcParams['font.size'] = '16'
ax1.errorbar(list_N, mean_list, yerr=std_list, uplims=True, lolims=True, color='black')

ax2.errorbar(list_N[:slicer], mean_list[:slicer], yerr=std_list[:slicer], uplims=True, lolims=True)

ax1.set_xlabel('N')
ax1.set_ylabel('Average fitness ')

plt.savefig('exercise_f_02 ', dpi=300)
files.download('exercise_f_02.png')
plt.show()

```