HARVARD UNIVERSITY

AM205: Advanced Scientific Computing, Numerical Methods

A Comparison of Three Differential Models for Predicting Population Growth

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Abstract

Predicting population growth is a complex and important task that has numerous applications in fields such as resource management, conservation, and public health. In this study, we compare three differential equation-based models that are commonly used to describe population growth: the logistic model, the geometric model, and the Lotka-Volterra model. The logistic model assumes that population growth is limited by carrying capacity, the geometric model assumes exponential growth without any limiting factors, and the Lotka-Volterra model is a predator-prey model that describes the interactions between two species in an ecosystem.

Problem formulation: Differential equation-based models are a powerful tool for predicting population growth, but it is not always clear which model is the most accurate or appropriate for a given situation. There are many different factors that can influence population growth, including environmental conditions, resource availability, and interactions with other species, and different models may make different assumptions about these factors. This study aims to compare the performance of three popular differential equation-based models for predicting population growth and to identify the strengths and limitations of each model.

Research goals: The main goals of this study are to:

1. Compare the accuracy of the Logistic, Geometric, and Lotka-Volterra models in predicting population growth under different conditions.
2. Identify the key assumptions and parameters of each model and how they influence the predictions.
3. Determine the suitability of each model for different types of population dynamics and applications.
4. Propose guidelines for selecting the appropriate model for a given situation.

To achieve these goals, we will use a combination of analytical methods, numerical simulations, and real-world data to test the performance of each model. We will also consider the implications of our findings for resource management, conservation, and public health.

Overall, this study will provide valuable insights into the strengths and limitations of different differential equation-based models for predicting population growth and help researchers and practitioners to choose the most appropriate model for a given situation.

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Chapter 1

Introduction

Scientists have often been interested in the question of how populations grow. Charles Darwin, in his theory of natural selection (Darwin, 1859), was greatly influenced by the English clergyman T.R. Malthus, who published a book in 1798 stating that populations with unlimited natural resources grow very rapidly (Malthus, 1798). However, Malthus also argued that once the population size exceeds the available resources, population growth decreases dramatically (Bowler, 2003). In 1838, P. F. Verhulst proposed the logistic model for population growth, which revisits Malthus' theory of limited resources and incorporates the idea of a carrying capacity, or the maximum population size that a given environment can sustain (Bacaër, 2011).

Differential equations are a special type of equation that involves an unknown function and its derivatives. They are useful for modeling population growth because they can describe how a population changes over time in response to various factors such as birth rates, death rates, and immigration. Prior research in this field includes Winkel's 2011 paper: "Parameter Estimates in Differential Equation Models for Population Growth", which "estimates the parameters present in several differential equation models of population growth". Differential equations are a powerful tool because they can capture complex interactions between different factors that affect population size and provide insight into how these factors may change over time.

We will consider various differential equations that model population growth. Among these models is the aforementioned logistic equation, which is widely used in ecology and biology. It is based on the idea that the growth of a population is limited by the carrying capacity of the environment in which the population is living (i.e., the maximum number of individuals that an environment can support). This model takes into account the fact that the growth of a population slows as it approaches the carrying capacity of its environment. This leads to a sigmoidal curve in the population growth data, which is often seen in real-world population data. Hence, the logistic model can be used to fit this curve and make predictions about future population growth.

The Logistic model differs from the Geometric model, which is based on the idea that the growth of a population is exponential (i.e., population increases at a constant rate over time). This leads to different shapes of the population growth curve, with the Geometric model predicting a steady exponential increase in population size, while the Logistic model predicts a sigmoidal curve (Weisstein, 2010).

Finally, we also consider the Lotka-Volterra model which is worth including in our analysis as it describes the interaction between multiple species (such as predators and preys), while the Logistic and Geometric models describe the growth of a single population. It is based on the idea that different populations influence each other through interactions such as predation and competition for resources. In this sense, it can be used to make predictions about how changes in the environment, such as changes in resource availability or climate, can affect these populations. This can be useful for understanding how ecosystems may respond to external changes and for developing strategies to manage and conserve species populations. Hence, it can provide insight into the complex dynamics that can occur in an ecosystem when multiple species interact.

From this, it is easy to see why we would need to compare different models of population growth: different models can make different predictions about how a population will grow over time, and it is important to determine which model is the most accurate and realistic. Comparing different models will allow us to assess the relative strengths and limitations of each model and to determine which model provides the best fit to the data.

Chapter 2

Geometric Model

2.1 Theory

The first model that we analyze due to its simplicity is the geometric model. The geometric model describes population growth as *exponential*, meaning that the population grows at a constant rate over time. This model is often used to model populations that are growing rapidly and without any limiting factors, such as certain types of bacteria or algae (Cuddington et al., 2015). Studying this model will pave the way and the method for later analysis and create a better insight into population dynamics.

In the *geometric model*, population grows in discrete reproductive periods between intervals of abstinence, as opposed to populations which grow without designated periods for reproduction. Let $\mathcal{P}_t$ denote the number of individuals at time t. Then the dynamics are as follow:

$$N_{t+1} = N_t + B_t - d_t \tag{2.1}$$

where B_t is birth rate and D_t is the mortality rate.

Now, let us suppose that B_t and D_t are constants and that $B_t - d_t = R$. Hence, the population dynamics can be rewritten as:

$$\mathcal{P}_{t+1} = (1 + R)\mathcal{P}_t = \lambda \mathcal{P}_t \tag{2.2}$$

Solving this equation at time t gives us a closed form solution for the population:

$$\mathcal{P}_t = \lambda^t \mathcal{P}_0 \tag{2.3}$$

This model is quite simple and gives a first intuitive discrete approximation of a population growth based on a unique parameter λ. Indeed, varying λ changes completely the population growth with a phase change for $\lambda = 1$.

One meaningful parameter of this model is the *doubling time* or *half-life time* depending on if $\lambda > 1$ or $\lambda < 1$.

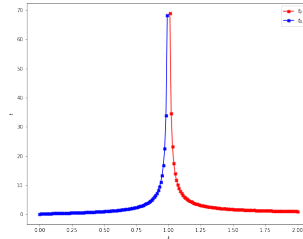| half-life time	doubling time
$\lambda < 1$	$\lambda > 1$
$t_{1/2} = -log_2(\lambda)^{-1}$	$t_2 = log_2(\lambda)^{-1}$

Figure 2.1: Half and Doubling Time

Intuitively, the *doubling time* t_2 is the time required for the population to grow to twice its size. Similarly, the *half-life time* is the time taken for the population to divide to half its size.

2.2   Numerical Resolution

Numerical simulations and resolutions are truly helpful when it comes to dynamics of population. Combining this with visualization and plots provides us a clear insight into the underlying mechanics of what is happening.
As this section requires simple differential equations resolution we decided to use *Forward Euler*. Indeed, Euler's method is known to be simple and efficient. Below is an explanation of the *Forward Euler* algorithm.

In our Geometric problem we have an ODE of the form,

$$\frac{dX}{dt} = F(X, t)$$

At each timestep dt the algorithm computes an estimate for $X_{n+1} = X(t_n + dt)$ with the following discrete expression,

$$X_{n+1} = X(t_{n+1}) = X(t_n + dt) = X(t_n) + F(X_n, t_n)dt \tag{2.4}$$

We decided to run various experiments during which we could very distinctively observe the 2 regimes ($\lambda < 1$, $\lambda > 1$). From the plots below, we could compare the different increasing geometric speeds for $\lambda > 1$, and decreasing for $\lambda < 1$. One last thing we can appreciate is how sensitive this evolution is to λ.
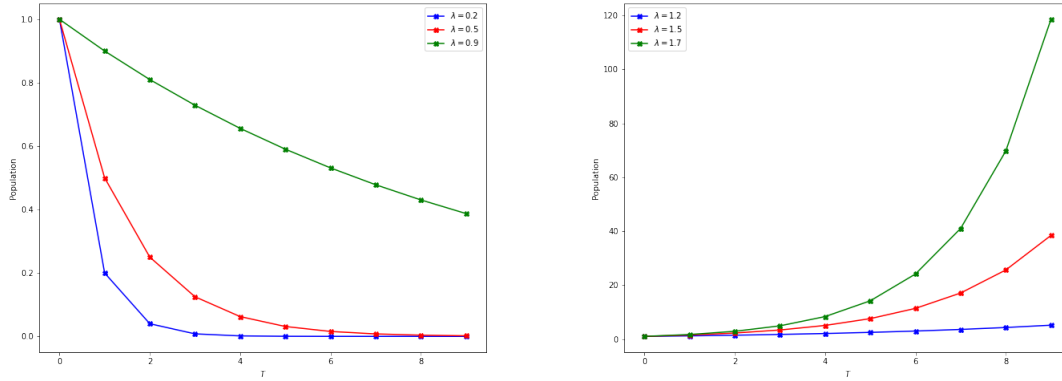

Figure 2.2: Dynamic Evolutions of the Geometric Model for $\lambda < 1$ (left) and $\lambda > 1$ (right)

2.3   Results

The most studied real-life case of geometric growth is not for humans nor animals, but for radioactive component decay! When the nucleus of a radioactive element decays, it emits one or more α, β or γ particles and becomes stable (i.e., non-radioactive). This decay process is characteristic of the particular element undergoing decay, and depends only on *time*. Therefore, for each radioactive element e we can assign a λ_e caracteristic of its decay. In this case, the most interesting parameter is the half-life of an element that can be computed as above by $t_{1/2} = -\frac{1}{log_2(\lambda_e)}$

This half-time is crucial: it depicts the decay rate of an element and must be known in case of nuclear waste or nuclear disaster. This would be for example to compute how much time it will take for a certain area to be contaminated (Lelieveld, 2012).

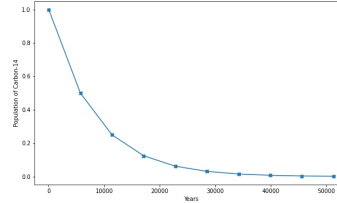| Element	Half-life
Uranium-238	4.47 billion years
Potassium-40	1.28 billion years
Carbon-14	5,700 years
Hydrogen-3	12.3 years
Radon-222	3.82 days
Polonium-214	0.00016 seconds

Figure 2.3: Half-life of radioactive elements

Also, one may stress that elements with large half-life times may be utilized to date ancient rocks, minerals, skeletons etc. This may be evidenced in Bentley's 2006 paper, "Strontium Isotopes from the Earth to the Archaeological Skeleton: A Review", which "covers the biogeochemical background, including the origin of strontium isotope compositions in rocks,weathering and hydrologic cycles that transport strontium, and biopurification ofstrontium from to soils, to plants, to animals and finally into the human skele-ton, which is subject to diagenesis after burial".

Chapter 3

Logistic model for constrained dynamics

3.1 Theory

3.1.1 Logistic Growth

The logistic model is a common model of population growth originally attributed to Pierre-François Verhulst in 1838. In this model the rate of reproduction is proportional to both the existing population and the amount of available resources, and is hence a model for a *limited ressources environment*. This equation was rediscovered multiple time throughout history. First in 1911 by A. G. McKendrick for the growth of bacteria, then by Raymond Pearl in 1920 and finally by Alfred J. Lotka (the author of our next model!) in 1925, that named it the law of population growth (Wikipedia, 2019).

Let $\mathcal{P}$ represent the population size and t represent the time, the differential evolution equation of the Logistic model is,

$$\frac{d\mathcal{P}}{dt} = r\mathcal{P}\left(1 - \frac{\mathcal{P}}{K}\right) \tag{3.1}$$

where r defines the growth rate and K is the carrying capacity.

This rather simple model has an analytical solution, whose proof may be evidenced in Appendix 7.1:

$$\mathcal{P}(t) = \frac{K}{\frac{K-P_0}{P_0}e^{-rt} + 1} \tag{3.2}$$

Here, we observe that the model converges to a limit independently of P_0 and r:

$$\lim_{t \to \infty} \mathcal{P}(t) = K$$

Another variant exists where K is not a constant but a function of t as the carrying capacity might change over time, depending of the environement and the seasonality (periodic $K(t)$). This model has no closed-form analytical solution. Hence, we will need to explore it numerically.

3.1.2 Generalized Logistic Growth

Altough very useful, logistic regression is only a simple version of a more general family of growth functions, the *generalized logistic functions*. Originally developed for growth modelling, this set of functions allows for more flexible S-shaped curves and are given by the below expression.

$$\mathcal{P}(t) = A + \frac{K - A}{(C + Qe^{-rt})^{\frac{1}{\nu}}} \tag{3.3}$$

where A is the lower left asymptot, K the upper right asymptot (previously *carrying capacity*), r the growth rate, $\nu > 0$, C typically takes value 1.

For the case $A = 0$, without loss of generality we can suppose $C = 1$, hence the dynamic equation for those curves is given by:

$$\frac{d\mathcal{P}}{dt} = r\mathcal{P}\left(1 - \left(\frac{\mathcal{P}}{K}\right)^{\nu}\right) \tag{3.4}$$

This ODE models many growth phenomena, arising in fields such as oncology and epidemiology (Devidas, 1993). We can easily remark that (3.4) is similar to the simple logistic growth (3.1) when $\nu = 1$.

One other interesting sub-family is the *Grompetz functions*, occuring when $\nu \longrightarrow 0$. In this case we can approximate equation (3.4) by,

$$\frac{d\mathcal{P}}{dt} \approx r\mathcal{P}ln\left(\frac{\mathcal{P}}{K}\right) \tag{3.5}$$

3.2 Numerical Resolution

In this section, we solve the above ODE using the *Forward Euler* method (2.4) in order analyze the form of the solution along with the dependence to parameters r, K.
From this first set of experiments below we can clearly see how r and K respectively influence the dynamics. Indeed, K is the maximum population number and represents the limited supply for this population to grow. On the other hand, r is the growth factor. A higher r is equivalent to a higher growth rate until it reaches K.
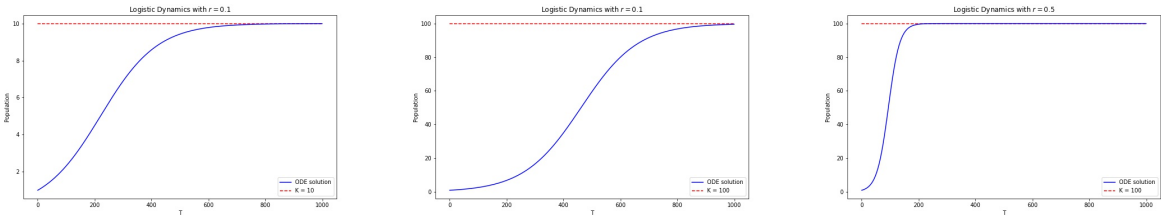

Figure 3.1: Solutions of the logistic ODE for differents parameters of r and K

We then add some sinusoidal variations in K. To this end, we set $K_1(t) = 50 \cdot \left(1.1 + \sin(\frac{t}{2\pi})\right)$,
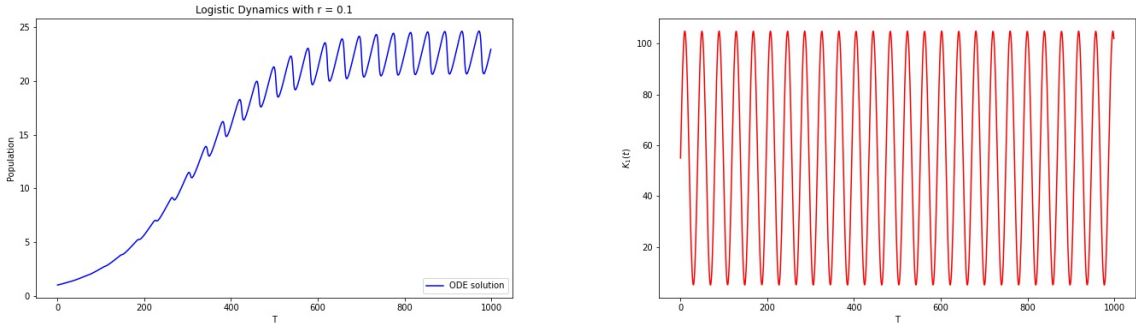

Figure 3.2: Plot of $K_1(t)$ along with the associated solution of the logistic ODE

Adding sinusoidal variations in K means that the limiting factor for the population growth is changing as a sinusoidal function. This could for example be a limiting food supply that has seasonal variation (e.g., increased scarcity of food in winter). In this case, the shape of the growth is quite similar of that with K constant with small oscillations. Also, it is interesting to determine the infinite regime of the population $\mathcal{P}^{\infty}$ with the non-constant parameter K_1. By looking at the figure, one may argue that the population oscillates at the same pace as the input oscillation,

$$\mathcal{P}^{\infty}(t) = A_1 \sin\left(\frac{t}{2\pi}\right) + B_1$$

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We now use a logarithmic function for K. To this end, we set $K_2(t) = 10log(t)$,
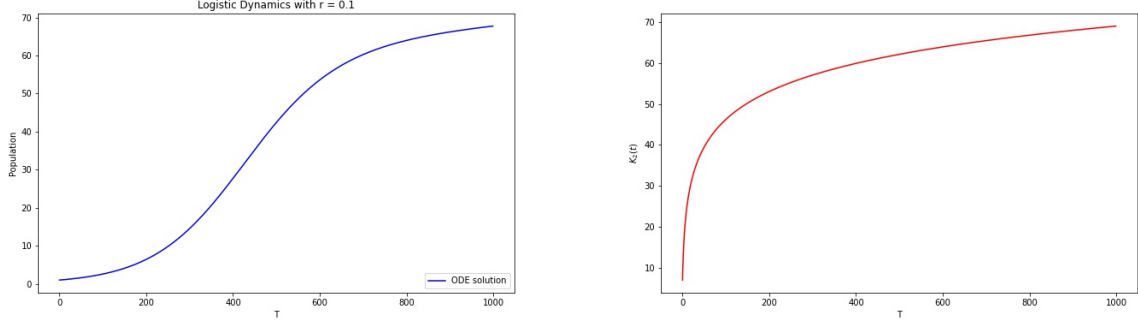

Figure 3.3: Plot of $K_2(t)$ along with the associated solution of the logistic ODE

This setup could represent the hypothetical growth of a population for which more individuals is beneficial at first and then the marginal benefit of adding a new individual converge to 0 at the rate of $\frac{1}{\mathcal{P}}$. Also, it is interesting to determine the infinite regime of the population $\mathcal{P}^\infty$ with the non-constant parameter K_2. By using the ODE and setting $\frac{d\mathcal{P}}{dt} \xrightarrow[t\to\infty]{} 0$, one may intuitively argue that:

$$\mathcal{P}^\infty(t) = K_2(t)$$

We know focus on numerical resolution of the generalized logistic model. It seems that the crucial parameters that separate the different regimes (*grompetz* , *simple logisitic*, *generalized logistic*) is ν. This led us to plot curves for different values of ν. In the left plot we set $r = 0.1$ and $K = 100$ to observe the different growths dynamics depending on ν in the constant *carrying capacity* setting. In the right plot we set $r = 0.1$ and the time-dependent *carrying capacity* $K_1(t) = 50 \cdot (1.1 + \sin\left(\frac{t}{2\pi}\right))$.
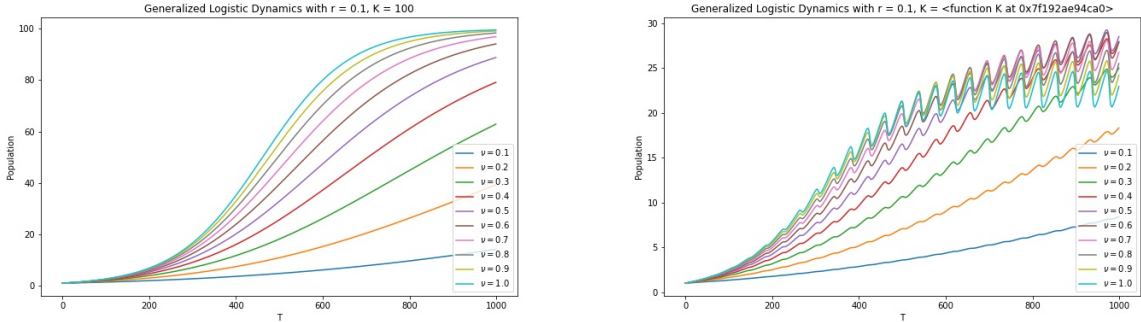
Figure 3.4: Solutions of (3.4) for different values of ν

3.3 Results

As we have seen, population dynamics under finite resources constraints can be modeled by a logistic process with different (constant or not) values of K. More interestingly, this behavior can be observed in real life like for example the dynamics of microscopic fungus in a tube (Groth et al., 2021) and of harbor seal population in the San Juan Islands (Ashley et al., 2020).

Figure 3.5: Seals population growth

Figure 3.6: Microscopic fungus population growth

Chapter 4

Extending Lotka-Volterra to an n-species ecosystem

4.1 Theory

4.1.1 2-Species Lotka-Volterra System

The Lotka-Volterra model is a set of mathematical equations used to describe the dynamics of a predator-prey system. The equations are named after their creators, Alfred J. Lotka and Vito Volterra, who independently developed them in the early 1900s.
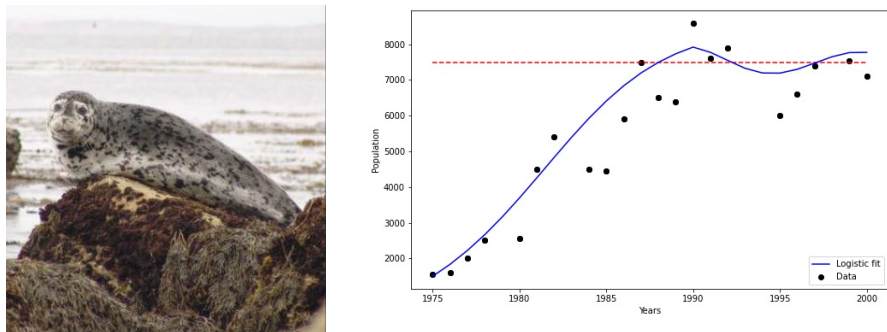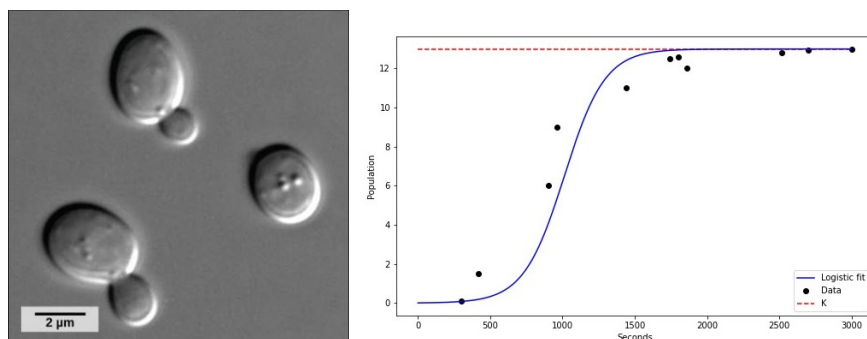
The Lotka-Volterra equations can be used to model the populations of two species that interact with each other, such as predators and their prey. The equations take into account various factors that can affect the populations of the two species, such as the growth rate of each species, the rate at which the predators catch their prey, and the rate at which the prey can reproduce.

The Lotka-Volterra equations have been widely used in various fields, such as ecology, biology, and economics, to study the dynamics of complex systems. They are a valuable tool for understanding the interactions between different species and the effects that those interactions can have on their populations over time (Anisiu, 2014).

The populations change through time according to the following system of equations:

$$\begin{cases} \frac{dx}{dt} & = ax - bxy \\ \frac{dy}{dt} & = -cy + dxy \end{cases}$$

where x and y are the number of preys and predators respectively, and where a, b, c, and d are positive constants that represent the growth rate of the prey, the rate at which the predators catch their prey, the death rate of the predators, and the rate at which the predators can reproduce, respectively.

The first equation describes the change in the prey population over time. The term ax represents the natural growth of the prey population, while the term bxy represents the reduction in the prey population due to predation.

The second equation describes the change in the predator population over time. The term $-cy$ represents the natural death rate of the predators, while the term dxy represents the increase in the predator population due to the prey they catch.

Together, these equations provide a mathematical model of the dynamics of the predator-prey system and can be used to predict the populations of the two species over time.

The physical meaning of the equations is the following: the preys, x, find food at all time. The food supply of the predator depends directly on the population size of their preys. The food supply of preys (ex: grass) is unlimited. The rate of change of each population depends directly on their size, and on the population size of the other specie.

We assume that the predators have unlimited appetite.

The challenge behind finding an equilibrium to this system is that if the predators eat all the preys, they will not have anything to eat anymore, thus resulting in their extinction. Hence, we can intuitively guess the existence of two critical points: one when both species get extinct, another if both species cohabit eternally.

We have that the system reaches an equilibrium or critical point when the two population sizes stop changing i.e where the gradient is 0. Let us find these points analytically.

$$\begin{cases} \dfrac{dx}{dt} = x(a - by) = 0 \\[2mm] \dfrac{dy}{dt} = y(cx - d) = 0 \end{cases} \implies (x, y) = (0, 0) \text{ or } (x, y) = \left(\dfrac{d}{c}, \dfrac{a}{b} \right)$$

These two solutions confirm our previous intuition. Let us now analyze the stability of the critical points. To do so, we must compute the jacobian of f where $f_1(x, y) = x(a - by)$ and $f_2(x, y) = y(cx - d)$, and analyze its eigenvalues when evaluated at the critical points. The considered Jacobian is:

$$\mathbb{J}(x, y) = \begin{bmatrix} \dfrac{\partial \mathbf{f}(\mathbf{x})}{\partial x} & \dfrac{\partial \mathbf{f}(\mathbf{x})}{\partial y} \end{bmatrix} = \begin{bmatrix} \nabla^T f_1(\mathbf{x}) \\ \nabla^T f_2(\mathbf{x}) \end{bmatrix} = \begin{bmatrix} \dfrac{\partial f_1(\mathbf{x})}{\partial x} & \dfrac{\partial f_1(\mathbf{x})}{\partial y} \\ \dfrac{\partial f_2(\mathbf{x})}{\partial x} & \dfrac{\partial f_2(\mathbf{x})}{\partial y} \end{bmatrix} = \begin{bmatrix} a - by & -bx \\ cy & cx - d \end{bmatrix}$$

We have : $\mathbb{J}(0, 0) = \begin{bmatrix} a & 0 \\ 0 & -d \end{bmatrix}$ which has as eigenvalues : a and $-d$. Considering that both a, d are positive, the eigenvalues have opposite signs and we have that the critical point $(0, 0)$ is a saddle point. We also have that: $\mathbb{J}(\frac{d}{c}, \frac{a}{b}) = \begin{bmatrix} 0 & -bd/c \\ ca/b & 0 \end{bmatrix}$ which as eigenvalues the roots in λ of the characteristic polynomial: $\chi(\lambda) = \lambda^2 + da$, which are: $\lambda_1 = i\sqrt{da}$ and $\lambda_2 = -i\sqrt{da}$ as $da > 0$. As the eigenvalues are purely imaginary, we have that the solution is oscillatory around the considered fixed point.

Let us study further this oscillatory state. Indeed, for $T \in \mathbb{R}$, we can combine the Lotka Volterra equations at equilibrium into one as:

$$\begin{aligned} & \frac{dy}{dx} = \frac{y}{x} \frac{cx - d}{a - by} = 0 \\ & \implies \frac{dx}{x}(cx - d) + \frac{dy}{y}(by - a) = 0 \\ & \implies \int_{x_0}^{x(T)} \frac{dx}{x}(cx - d) + \int_{y_0}^{y(T)} \frac{dy}{y}(by - a) = 0 \quad \text{for } T \in \mathbb{R} \\ & \implies a(x(T) - x_0) - d \ln(\frac{x(T)}{x_0}) + a \ln(\frac{y(T)}{y_0}) - b(y(T) - y_0) = 0 \\ & \implies ax - by - d \ln(x) + a \ln(y) = V(x_0, y_0) \text{ where } x \equiv x(T), \ y \equiv y(T) \end{aligned} \quad (4.1)$$

where $V(x_0, y_0) := ax_0 - by_0 - d \ln(x_0) + a \ln(y_0)$ is a constant depending on the system's initial conditions. This contour represents the oscillating trajectory of the system around the critical points. It can be shown that the average position of x and y when they do not get extinct is $(\frac{d}{c}, \frac{a}{b})$ - see appendix.

4.1.2   3-Species Lotka-Volterra System

We now extend the Lotka Volterra equations to a three species system where species x is preyed upon by species y which is preyed upon by species z. This model is commonly referred to as the *food-chain* model. The equations become :

$$\begin{cases} \dfrac{dx}{dt} = r_1 x + c_1 xy = x(r_1 + c_1 y) \\[2mm] \dfrac{dy}{dt} = r_2 y + c_2 yz + b_1 yx = y(r_2 + b_1 x + c_2 z) \\[2mm] \dfrac{dz}{dt} = r_3 z + b_2 zy = z(r_3 + b_2 y) \end{cases}$$

Where r_i, c_i, b_i are real valued coefficients. We can see that when x or z get extinct, the three-species Lotka-Volterra equations reduce to a 2-species volterra equations that can be analyzed as in the previous part.

- The first trivial critical point is : $(0,0,0)$ reached when all species are extinct.

- If z gets extinct, then we will focus on the 2-species Lotka Volterra system between x and y which has a critical point in $(-\dfrac{r_2}{b_1}, -\dfrac{r_1}{c_1}, 0)$.

- If x gets extinct, then we will focus on the 2-species Lotka Volterra system between y and z which has a critical point in $(0, -\dfrac{r_3}{b_2}, -\dfrac{r_2}{c_2})$.

- if y gets extinct: then x and z will evolve independently. Their evolution will depend on the sign of r_1 and r_2. We will most likely have that r_1 is positive meaning that preys can proliferate and that r_3 is negative meaning that predators get extinct when none of there preys are around anymore. The equations will become: $\dot{x} = r_1 x$, $\dot{z} = r_3 z$ and the trajectories are: $(x_0 e^{r_1 t}, 0, z_0 e^{r_3 t})$ for t real.

- When no species get extinct i.e : $x, y, z \neq 0$, we have that:

$$0 = \frac{dx_i}{dt} = x_i f_i(\mathbf{x}) \quad \text{where } f : \mathbb{R}^n \to \mathbb{R}^n \ ; \ \mathbf{f} = \mathbf{r} + \mathbf{Ax}; \implies \mathbf{Ax} = -\mathbf{r} \quad \text{with } \mathbf{A} = \begin{pmatrix} 0 & b_1 & 0 \\ c_1 & 0 & b_2 \\ 0 & c_2 & 0 \end{pmatrix}$$

However, we can see that $\mathbf{A}$ is not invertible as its first and third column are linearly dependent. This means that the final solution for x and z can be expressed through a linear relation. Indeed, supposing $x, y, z \neq 0$, we have that : $y = -\dfrac{r_1}{c_1} = -\dfrac{r_3}{b_2}$ and $z(x) = -\dfrac{r_2 + b_1 x}{c_2}$. In other words, there is an infinite number of critical points that lie along a line.

We could check if the system is asymptotically stable solution by ensuring that all the real parts of the eigenvalues of the Jacobian are negative. To do so, we would have to plug in the critical points we found before in the following jacobian, determine its eigenvalues and check the sign of their real part.

$$\mathbb{J}(x,y,z) = \begin{bmatrix} \dfrac{\partial \mathbf{f}(\mathbf{x})}{\partial x} & \dfrac{\partial \mathbf{f}(\mathbf{x})}{\partial y} & \dfrac{\partial \mathbf{f}(\mathbf{x})}{\partial z} \end{bmatrix} = \begin{bmatrix} \dfrac{\partial f_1(\mathbf{x})}{\partial x} & \dfrac{\partial f_1(\mathbf{x})}{\partial y} & \dfrac{\partial f_1(\mathbf{x})}{\partial z} \\[2mm] \dfrac{\partial f_2(\mathbf{x})}{\partial x} & \dfrac{\partial f_2(\mathbf{x})}{\partial y} & \dfrac{\partial f_2(\mathbf{x})}{\partial z} \\[2mm] \dfrac{\partial f_3(\mathbf{x})}{\partial x} & \dfrac{\partial f_3(\mathbf{x})}{\partial y} & \dfrac{\partial f_3(\mathbf{x})}{\partial z} \end{bmatrix} = \begin{bmatrix} r_1 + c_1 y & c_1 x & 0 \\ b_1 y & r_2 + b_1 x + c_2 z & c_2 y \\ 0 & b_2 z & r_3 + b_2 y \end{bmatrix}$$

4.1.3 n-Species Lotka-Volterra System

We are now interested in modelling a whole ecosystem composed of n species of population size: $x_1, \cdots, x_n$. We may rewrite the Lotka-Volterra equations for n species as follows:

$$\frac{dx_i}{dt} = x_i f_i(\mathbf{x}) \quad \text{where } f : \mathbb{R}^n \to \mathbb{R}^n \ ; \ \mathbf{f} = \mathbf{r} + \mathbf{Ax}$$

where $\mathbf{r}$ represents the intrinsic nature of the species. A positive value for r_i means that species i is able to reproduce in the absence of any other species, whereas a negative value means that its population will decline unless the appropriate other species are present (e.g. a predator). We also denote by $\mathbf{A}$ the 'matrix of interaction' representing the interations between species. The value of a_{ij} represents the effect that species j has upon species

i. In our *food chain* model, we assume a hierarchical order between species: each specie is a predator while also being the prey of another, except for the 'highest' predator who is the prey of no specie, and for the 'lowest' prey which has an unlimited food supply. Our model can be illustrated as follows:

$$X_n \to X_{n-1} \to \cdots \to X_1$$

where $A \to B$ means that B is the prey of A. The Lotka-Volterra equations become:

$$
\begin{cases}
\dfrac{dx_1}{dt} = x_1(r_1 + c_1 x_2) \\
\quad \vdots \\
\dfrac{dx_i}{dt} = x_i(r_i + c_i x_{i+1} + b_{i-1} x_{i-1}) \text{ for } i \in \{2, \cdots, n-1\} \\
\quad \vdots \\
\dfrac{dx_n}{dt} = x_n(r_n + b_{n-1} x_{n-1})
\end{cases}
\qquad \text{where } \mathbf{A} =
\begin{pmatrix}
0 & b_1 & & & \\
c_1 & 0 & b_2 & & \\
& c_2 & \ddots & \ddots & \\
& & \ddots & \ddots & b_{n-1} \\
& & & c_{n-1} & 0
\end{pmatrix}
\in \mathcal{M}\left(\mathbb{R}^{n \times n}\right)
$$

where we redefined the matrix coefficients of A as b_i, c_i for simplicity. Here, we can see that the matrix A is tridiagonal with null diagonal terms. We notice that when $x_i = 0$ for $i \in \{2, \cdots, n-1\}$, then the set of differential equations becomes decoupled into two sets of $i-1$ and $n-1$ Lotka Volterra systems. Indeed the populations $x_1, \cdots x_{i-1}$ will become independent with respect to $x_{i+1}, \cdots, x_n$. This is why it is interesting to study the n-species Lotka-Volterra system when no species reach extinction.

Now when looking for an equilibrum where no species are extinct ($x_i \neq 0$ for all i), we will be looking to solve for $\mathbf{x}$ such that:

$$\frac{d\mathbf{x}}{dt} = 0 \implies \mathbf{x} = -\mathbf{A}^{-1}\mathbf{r} \text{ if } \mathbf{A} \text{ is invertible}$$

However, as shown in the 3-species case, $\mathbf{A}$ is not invertible meaning that there exists infinitely many critical points $\mathbf{x}$. This makes sense as we expect there to be infinitely many ways for a system of n species to cohabit. Similarly to previous cases, in order to analyze the stability of the fixed points $\mathbf{x}$, we would have to check the sign of the real parts of the system's jacobian evaluated at $\mathbf{x}$:

$$
\mathbb{J}(\mathbf{x}) =
\begin{bmatrix}
r_1 + c_1 x_2 & c_1 x_1 & 0 & \cdots & \cdots & 0 \\
b_1 x_2 & r_2 + c_2 x_3 + b_1 x_1 & c_2 x_2 & \cdots & \cdots & 0 \\
\vdots & \ddots & \ddots & \ddots & \cdots & \vdots \\
0 & \cdots & b_{i-1} x_{i-1} & r_i + c_i x_{i+1} + b_{i-1} x_{i-1} & c_i x_i & 0 \\
\vdots & \cdots & \ddots & \ddots & \vdots & \vdots \\
0 & \cdots & 0 & b_{n-2} x_{n-2} & r_{n-1} + c_{n-1} x_n + b_{n-2} x_{n-2} & c_{n-1} x_{n-1} \\
0 & \cdots & \cdots & 0 & b_{n-1} x_{n-1} & r_n + b_{n-1} x_{n-1}
\end{bmatrix}
$$

4.2 Numerical Resolution

4.2.1 Forward Euler

We first used the *Forward Euler* method to approximate $x_i(t)$ at time t using the first derivative of x_i. In practice, make a first order approximation of x as :

$$x_i(t+dt) \approx x_i(t) + \frac{dx_i(t)}{dt}dt = \begin{cases} = x_1(1 + r_1 + c_1 x_2)dt \text{ if } i = 1 \\ \vdots \\ = x_i(1 + r_i + c_i x_{i+1} + b_{i-1}x_{i-1})dt \text{ for } i \in \{2, \cdots, n-1\} \\ \vdots \\ = x_n(1 + r_n + b_{n-1}x_{n-1})dt \text{ if } i = n \end{cases}$$

4.2.2 Runge Kutta 4

As this section requires more advanced solver methods as the differential equations gets more tricky, we decided to shift from *Forward Euler* to *Runge-Kutta 4*. Indeed, Runge-Kutta methods are known to be more stable and have a faster convergence. Below is an explanation of the *Runge-Kutta 4* algorithm. In our Lotka-Volterra problem we have an ODE of the form,

$$\frac{dX}{dt} = F(X,t)$$

At each timestep dt the algorithm computes 4 values of F at 4 different points (hence the name of *Runge-Kutta 4*),

$$\begin{cases} k_1 = F(X_n, t_n) \\ k_2 = F(X_n + \frac{dt}{2}k_1, t_n + \frac{dt}{2}) \\ k_3 = F(X_n + \frac{dt}{2}k_2, t_n + \frac{dt}{2}) \\ k_4 = F(X_n + dt k_3, t_n + dt) \end{cases}$$

Once computed, our estimate for $X_{n+1} = X(t_n + dt) = X(t_{n+1})$ is given by,

$$X_{n+1} = X(t_{n+1}) = X(t_n) + \frac{dt}{6}(k_1 + 2k_2 + 2k_3 + k_4) \tag{4.2}$$

In the *Forward Euler* method we only took 1 point to evaluate F at each timestep dt, hence the resolution is slower, less stable and less suited to more complex resolution like this one.

4.3 Results

4.3.1 2-Species Lotka-Volterra System

The time-evolution and phase plots of the 2-species Lotka-Volterra system are shown in figure 6.2. Firstly, the phase plot clearly shows how the two populations sizes oscillate around a critical point. The second critical point $(0,0)$ is not visibile on the phase plot but does exist as proven in the theoretical section. Secondly, the time evolution plot clearly shows the interaction between the species. From a closer look at one oscillation period, we can distinguish four evolution phases.

- At a certain point, when the number of predators (x_1) is low and continuing to decrease, preys (x_2) can reproduce due to the lack of natural enemies.

- As the number of prey increases, predators have more preys to hunt and can thus survive better. The predators then reproduce, and their population increase again.

- As a result of the large number of predators, the amount of prey decreases. The number of predators continues to increase as they temporarily still have a large food supply.

- However, at some point, the decrease in number of preys makes it hard for the predators to survive and thus their population decreases. The cycle is complete and the preys can start reproducing again.
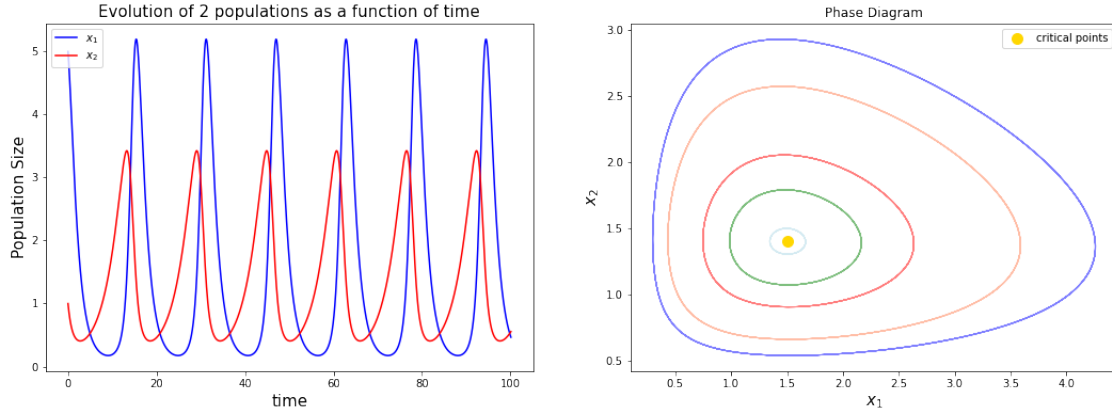
15

Figure 4.1: 2 Species Lotka Volterra Temporal Population Evolution and Phase diagrams

4.3.2   3-Species Lotka-Volterra System

In the 3-species Lotka-Volterra system, we notice three main scenarios which are shown in figures 4.2.

- The first one (leftmost), shows the evolution of the ecosystem when the 'intermediate' specie dies (x_1). By interemediate, we mean the population that is both a prey and a predator. When this population gets extinct, the predator on top of the food chain (x_2), has no more preys to feed upon, and hence enters extinction after x_1 gets extinct. However, the prey at the bottom of the food chain which has an unlimited food supply (one of our model's assumption), and no more predators threatening its existence, starts proliferating. We indeed see that the extinction of x_1 completely decouples x_0 from x_2 (and vice versa), and that the x_0 population starts increasing exponentially after both x_1 and x_2 populations enter extinctions.

- The second one (center) shows the ecosystem's evolution when either the lowest prey or upmost predator enters extinction. We can clearly see that as soon as x_0 or x_2 get extinct (x_2 in the figure), the 3-species Lotka-Volterra system switches to a 2-species system. Indeed, the resulting phase plot gets projected on a plane, and reflects the oscillating behaviour we saw in the 2-species system.

- The third one (rightmost) shows the ecosystem's evolution when no species get extinct. We can see that the preys and predators manage to cohabit. Interestingly, we see that the x_0 and x_2 population increase in average even though x_1 seems to have a constant average. The phase diagram seems to be the result of a 2-species phase diagram drifting along a third axis, oscillating around line (in gold in the plot) that compiles the system's infinitely many critical points.

4.3.3 n-Species Lotka-Volterra System

As written previously, in the case of an n species Lotka Volterra system, when species i gets extinct, for $i \in \{2, \cdots, n-1\}$, then the ecosystem can be subdivided into distinct and decoupled Lotka Volterra systems composed of $i-1$ and $n-i$ differential equations respectively. The time evolution plots shown in 4.3 clearly show this behaviour.

- In the figure displaying the temporal evolution of 4 species, we can see that as more species get extinct, the lowest prey in the food chain starts proliferating, which is what we observed in the three-species model when the two predators get extinct. Indeed, here, we can see that first x_2 gets extinct, followed by x_1, and by x_3.

- We can also see that when some species get extinct, a 2-species Lotka-Volterra system can be observed. Indeed, that is the case for the 6 and 8, 10 and 12 species ecosystems where we can see that as other species get extinct, x_1 and x_2 manage to survive and cohabit in an oscillatory way.
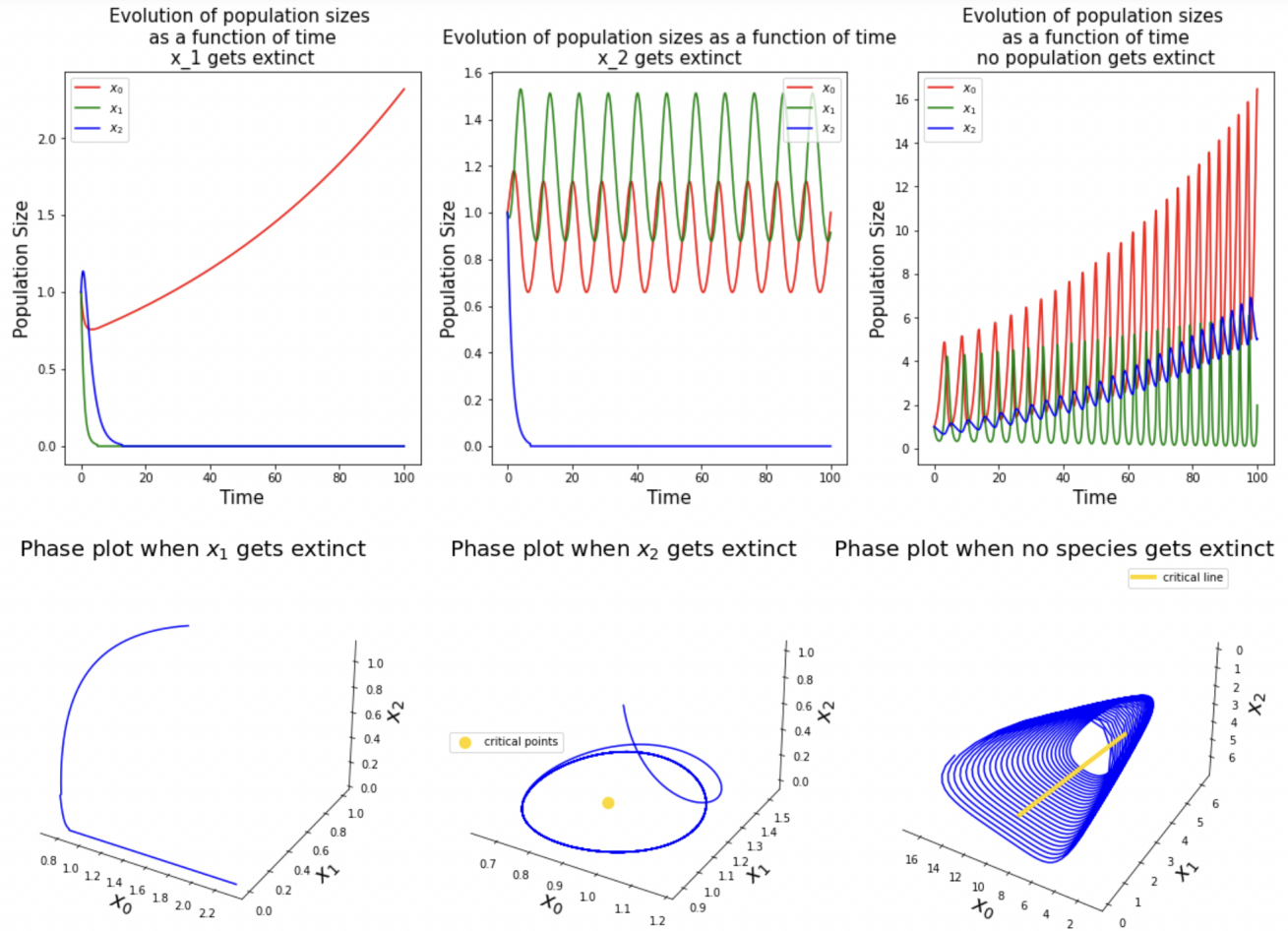
16

Figure 4.2: 3 Species Lotka-Volterra Population Evolution and Phase diagrams in different scenarios

- We are also fortunate to observe an ecosystem where all populations cohabit through time in a periodic way. Indeed, this is what is illustrated by the 5-species ecosystem. Also, as the system evolves, we notice a drift where some species manage to progressively proliferate. Indeed, the x_1 population peaks increase in amplitude through time.

These results are interesting and relevant, as they show that the analysis of large systems (10-species ecosystems for example) can be analysed through the lens of smaller ecosystems. Indeed, without the knowledge accumulated in the mathematical analysis of 2-species and 3-species ecosystems evolution, we would not have been able to make an informed analaysis of the evolution of large ecosystems.
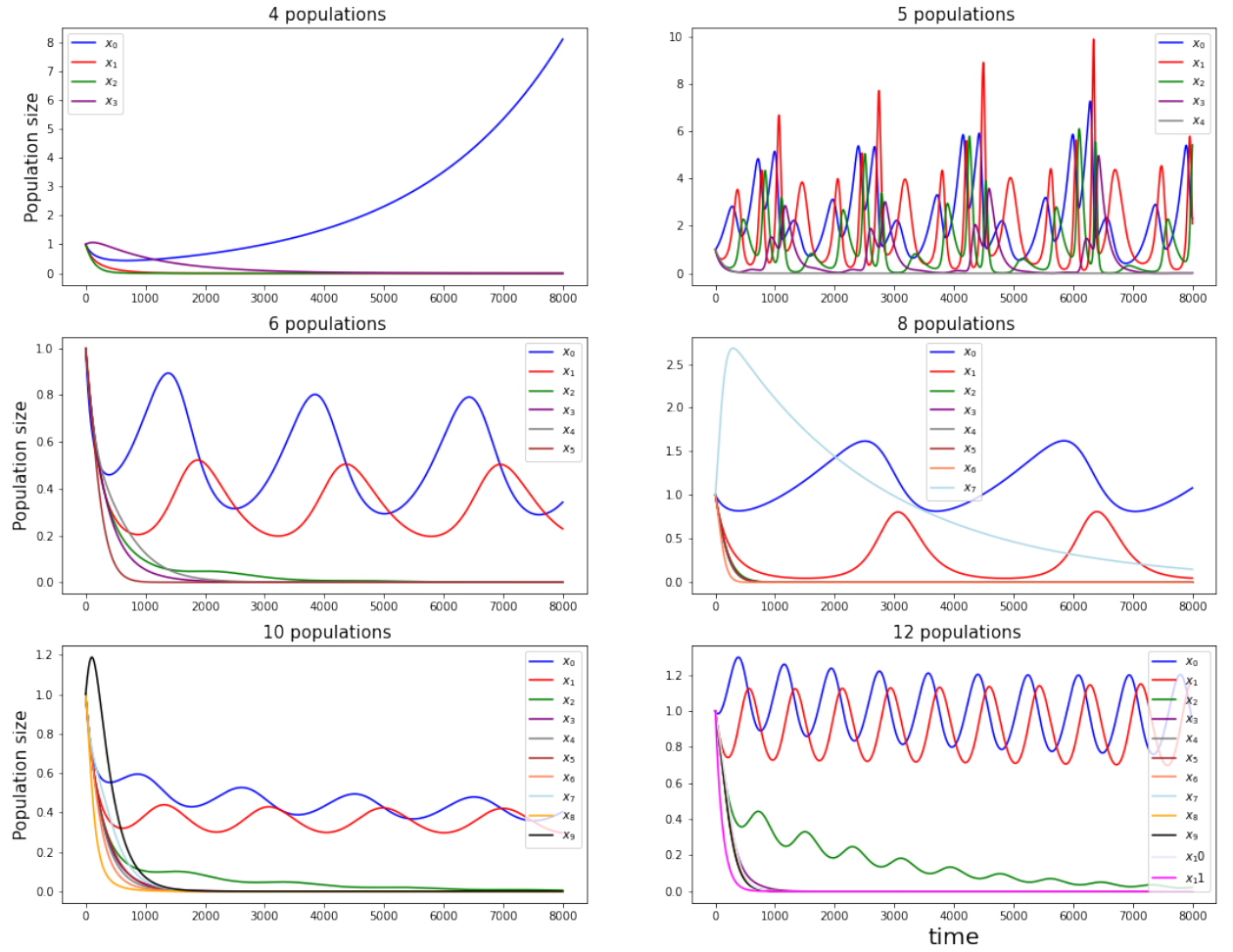
Figure 4.3: Evolution of 4, 5, 6, 7, 8, 10 and 12 species ecosystems as a function of time

Chapter 5

Conclusion

The Logistic model, the Geometric model, and the Lotka-Volterra model are all commonly used to model population growth, but they each have their own unique features and assumptions that make them more or less appropriate in different contexts.

The Logistic model hinges on the idea that population growth slows as resources become scarce. It is often used to model population growth in situations where the carrying capacity of the environment is a limiting factor. We analysed the underlying assumption that the growth rate of the population decreases as the population size approaches the carrying capacity of the environment.

The Geometric model, on the other hand, assumes that the population grows exponentially with time, with the growth rate remaining constant. This model is often used to model population growth in situations where resources are not limiting. However, for both the Geometric and Logistic models, one may cast a doubt over the assumption that the population growth rate remains constant over time. Environmental changes or the availability of new resources could also influence the growth rate of a population. For example, if the temperature or precipitation patterns change, this can affect the availability of resources and the survival rates of individuals within the population. Hence, this may not always be the case in real-world populations.

Finally, the Lotka-Volterra model is used to model the interactions between two species, and can be used to predict population growth in situations where populations are interdependent. This model takes into account both the rate at which each species reproduces and the effect that each species has on the other. However, we demonstrated that it is possible to extend the relevance of this model to a much larger ecosystem by considering it in a "n-species" setting, while using the analytical tools of the 2-species and 3-species model.

Our models mainly differ in how they incorporate the effect of limited resources on population growth. The Logistic model explicitly takes this into account, while the Geometric model assumes unlimited resources. Finally, the Lotka-Volterra model does so by modeling how species are themselves resources to other population.

Another important difference is the time scale over which each model is applicable. The Logistic and Geometric models are best suited for modeling population growth over relatively short time periods, while the Lotka-Volterra model is more appropriate for modeling population dynamics over longer time scales.

In conclusion, the Logistic, Geometric, and the Lotka-Volterra model are all useful tools for modeling population growth in different contexts. However, there is still much room for further investigation. For example, we could explore more sophisticated models that incorporate environmental changes, disease, or migration that may influence population growth. One example of such a model could be the incorporation of a climate change factor into the logistic model, allowing researchers to better understand how rising temperatures or changing precipitation patterns may affect population growth in different species. Additionally, further research could be done to better understand the strengths and limitations of each of these models and to identify when it is most appropriate to use each one. Finally, we could also investigate how to incorporate data from real-world populations to make more accurate predictions about population growth. Overall, this research has provided valuable insights into the factors that influence population growth and the tools that can be used to model these processes, even though there is still much more to learn and discover in this field.

Chapter 6

Appendix

6.1 Derivation of the Analytical Solution to the Logistic Equation

Let $\mathcal{P}$ be the population size and t the time. From there we can obtain the differential evolution equation of the Logistic model as:

$$\frac{d\mathcal{P}}{dt} = rP\left(1 - \frac{P}{K}\right) \tag{6.1}$$

where r is the growth rate, and K is the carrying capacity. We then have:

$$\frac{d\mathcal{P}}{dt} = r\mathcal{P}\left(1 - \frac{\mathcal{P}}{K}\right)$$

$$\implies dt\frac{1}{\mathcal{P}(K-\mathcal{P})}\frac{d\mathcal{P}}{dt} = r\mathcal{P}\left(1 - \frac{\mathcal{P}}{K}\right)dt\frac{1}{\mathcal{P}(K-\mathcal{P})}$$

$$\implies \frac{d\mathcal{P}}{\mathcal{P}(K-\mathcal{P})} = \frac{r}{K}dt$$

$$\implies \frac{d\mathcal{P}}{\mathcal{P}(K-\mathcal{P})}K = \frac{r}{K}dtK$$

$$\implies \frac{K}{\mathcal{P}(K-\mathcal{P})} = rdt \implies \int \frac{K}{\mathcal{P}(K-\mathcal{P})}\,d\mathcal{P} = \int r dt$$

The L.H.S of the previous equation can be integrated using partial fraction decomposition as:

$$\frac{K}{\mathcal{P}(K-\mathcal{P})} = \frac{1}{\mathcal{P}} + \frac{1}{K-\mathcal{P}}$$

$$\implies \int \frac{1}{\mathcal{P}} + \frac{1}{K-\mathcal{P}}\,d\mathcal{P} = \int r dt \implies \ln|\mathcal{P}| - \ln|K-\mathcal{P}| = rt + C$$

$$\implies e^{\ln|\frac{\mathcal{P}}{K-\mathcal{P}}|} = e^{rt+C}$$

$$\implies \left|\frac{\mathcal{P}}{K-\mathcal{P}}\right| = e^{C}e^{rt}$$

Let $c_1 = e^C$.

$$\frac{\mathcal{P}}{K-\mathcal{P}} = c_1 e^{rt}$$

We solve this equation for $\mathcal{P}(t)$, by first multiplying both sides by $K - \mathcal{P}$, and collecting terms $\mathcal{P}$ on the L.H.S:

$$\mathcal{P} = C_1 e^{rt}(K - \mathcal{P}) \tag{6.2}$$

$$\mathcal{P} = C_1 K e^r t - C_1 \mathcal{P}e^{rt} \tag{6.3}$$

$$\mathcal{P} + C_1 \mathcal{P}e^{rt} = C_1 K e^{rt} \tag{6.4}$$

$$\mathcal{P}(1 + C_1 e^{rt}) = C_1 K e^{rt} \tag{6.5}$$

$$\mathcal{P}(t) = \frac{C_1 K e^{rt}}{1 + C_1 e^{rt}} \tag{6.6}$$

In order to determine the value of C_1, we substitute $t = 0$ and $\mathcal{P} = 0$ in lieu of $\mathcal{P}$ and solve for C_1:

$$\begin{cases} \dfrac{\mathcal{P}}{K - \mathcal{P}} = C_1 e^{rt} \\ \dfrac{\mathcal{P}_0}{K - \mathcal{P}_0} = C_1 e^{t(0)} \end{cases} \implies C_1 = \frac{\mathcal{P}_0}{K - \mathcal{P}_0}$$

We substitute this value into the previous equation:

$$\mathcal{P}(t) = \frac{C_1 K e^{rt}}{1 + C_1 e^{rt}} = \frac{\frac{\mathcal{P}_0}{K - \mathcal{P}_0} K e^{rt}}{1 + \frac{\mathcal{P}_0}{K - \mathcal{P}_0} e^{rt}}$$

Then, we have that :

$$\mathcal{P}(t) = \frac{\frac{\mathcal{P}_0}{K - \mathcal{P}_0} K e^{rt}}{1 + \frac{\mathcal{P}_0}{K - \mathcal{P}_0} e^{rt}} \frac{K - \mathcal{P}_0}{K - \mathcal{P}_0} = \frac{\mathcal{P}_0 K e^{rt}}{(K - \mathcal{P}_0) + \mathcal{P}_0 e^{rt}}$$

$$= \frac{\mathcal{P}_0 K e^{rt} \frac{1}{\mathcal{P}_0}}{[(K - \mathcal{P}_0) + \mathcal{P}_0 e^{rt}] \frac{1}{\mathcal{P}_0}} = \frac{K e^{rt}}{\frac{K - \mathcal{P}_0}{\mathcal{P}_0} + e^{rt}}$$

$$= \frac{K e^{rt} \frac{1}{e^{rt}}}{\left(\frac{K - \mathcal{P}_0}{\mathcal{P}_0} + e^{rt}\right) \frac{1}{e^{rt}}} = \frac{K e^{rt} \frac{1}{e^{rt}}}{\left(\frac{K - \mathcal{P}_0}{\mathcal{P}_0} + e^{rt}\right) \frac{1}{e^{rt}}}$$

$$\mathcal{P}(t) = \frac{K}{\frac{K - \mathcal{P}_0}{\mathcal{P}_0} e^{-rt} + 1}$$

This last equation is equivalent to equation (3.2)

6.2 Mean position of x and y in 2-Species Lotka-Volterra System

In order to determine the mean position of x and y, we wish to compute for $T \in \mathbb{R}$:

$$\bar{x} = \frac{1}{T} \int_0^T x(t) dt \qquad \text{and} \bar{y} = \qquad \frac{1}{T} \int_0^T y(t) dt$$

However, considering that:

$$\int_0^T \frac{x'(t)}{x(t)} dt = \ln \frac{x(T)}{x_0} \qquad \text{and} \qquad \int_0^T \frac{y'(t)}{y(t)} dt = \ln \frac{y(T)}{y_0}$$

and that :

$$\int_0^T \frac{x'(t)}{x(t)} dt = \int_0^T (a - by(t)) dt = aT - bT\bar{y} \qquad \text{and} \qquad \int_0^T \frac{y'(t)}{y(t)} dt = \int_0^T (cx(t) - d) dt = cT\bar{x} - dT$$

We obtain that:

$$\bar{x} = \frac{d}{c} + \frac{1}{cT} \ln \frac{y(T)}{y_0} \qquad \text{and} \qquad \bar{y} = \frac{a}{b} - \frac{1}{bT} \ln \frac{x(T)}{x_0}$$

To get the mean value of preys and predators, we have to suitably choose T. Firstly, analysing figure , one notices that number of preys and predators oscillate periodically around their respective non-zero equilibrium. It then seems natural to choose T such that : $x(T) = x_0$ and $y(T) = y_0$. This gives us that :

$$\bar{x} = \frac{d}{c} \qquad \text{and} \qquad \bar{y} = \frac{a}{b}$$

Chapter 7

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