Modelling Competing Bacterial Species

MATH552

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2020

Contents

1 Summary

The aim of this paper is to understand the dynamics of a system involving two interacting species, to eventually model the outcomes of interaction where the two populations compete against each other. Several mathematical concepts will be explored, including matrix analysis and numerical integration of equations.

First, a brief outline of some feautres of bacterial cells will be presented, to develop a basic understanding of the way they grow. Moving forward, the concepts of one and two species systems will be detailed along with methods to solve them, before introducing an existing model of which the equilibria can be calculated and analysed.

By extending the previously mentioned model to include the competitive factor of each species, we will again calculate and analyse the stable equilibria of this system. The process of nondimensionalisation will be detailed and applied to the system, before using the newly dimensionless equations to model each potential outcome of the system, dependent on changing parameters. This will allow us to produce evidence of how each parameter can affect the resultant equilibrium of the system.

2 Biological Background

How different species are able to coexist in nature is one of the fundamental questions posed in ecology. While there is evidence suggesting that many environments possess a carrying capacity at a level that allows coexistence of species, as well as evidence supporting the idea of cooperative interaction between them, the consequences of special interaction remains relatively unknown [3]. With regard to bacterial cells, modelling allows us to widen our understanding of their growth and the way in which they interact. Modelling the interaction of bacterial species has a diverse range of real world applications, including safe food production and medicinal uses. For example, decades of antibiotic misuse has led to increasing levels of bacterial resistance, resulting in a continuing need to find alternate solutions [9]. Since bacterial interaction within and between species can hinder and prevent the colonisation of the other populations, mathematical modelling of their interactions allows scientists to generate an understanding of the conditions and circumstances required for preventing and eliminating the colonisation of opportunistic pathogens.

2.1 Bacterial Properties

There are many features specific to bacteria that make them unique and complex organisms. These characteristics provide bacterial species with an ability to survive and thrive in even the most hostile environments, making them one of the most abundant life forms on Earth. Binary fission, a form of asexual reproduction, is the process by which bacterial cells divide to reproduce and grow its population. Similar to mitosis, this begins with the cell replicating its DNA and elongating to twice its size, as the two sets of DNA move to opposite ends of the cell. A septum then begins to form in the centre of the cell, creating a division that allows it to divide into two genetically identical daughter cells. These cells can then separate entirely to exist and divide as independent cells, or remain joined and undergo further replication to form a cluster of cells.

Furthermore, even from a very low initial value, bacterial species can vastly grow their population. This stems from each bacterial cell possessing the ability to divide into two daughter cells, meaning each stage of binary fission doubles the size of the population. Over time, this creates a population whose growth increases exponentially. Therefore, we can calculate the number of cells that arise through binary fission starting from a single cell as;

$$\text{Number of cells at } n = \text{Initial number of cells x } 2^n$$

where n is the number of stages of replication [9].

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A key characteristic of bacterial cells is their generation time, which refers to the period of time it takes for the population of cells to double its density [9]. While the variation in generation time between species can differ significantly, most bacterial cells have a relatively short generation time of 1-3 hours. Combined with an exponential growth ability, this means mass populations of bacteria can form from minimal cells in a short space of time. Generation time is affected by several factors, with an optimal rate achieved in an abundance of resources and physical space, as well as appropriate environmental conditions being required.

2.2   Bacterial Growth

Over time, the growth of a bacterial population can be visualised as a curve, which describes the four distinct phases the population experiences during its lifecycle. These are;

Lag Phase: Upon introduction to a fresh medium, initial growth rate is low, producing a relatively flat initial gradient. Despite being metabolically active, the cells undergo a period of adjustment to acclimatise before replication. The duration of this lag phase varies between species, as well as being affected by the environmental conditions, for example availability of resources and temperature, plus any potential interaction with additional species.

Log Phase: As previously discussed, in ideal conditions a population of bacteria can achieve its maximum growth rate and reproduce exponentially. This creates a steep gradient in the graph due to high rate of division over a short period.

Stationary Phase: Despite the ability to reproduce exponentially, environmental factors create a maximum stable capacity the population can reach, for example resource availability and physical space. When reached, this limit means the population doesn't have the ability to continue its growth, resulting in the reproduction rate equalling the death rate of cells. This plateau in population size creates a flat section of the graph, where the bacteria have essentially entered survival mode.

Death Phase: Eventually, the depletion of resources in an environment, coupled with the accumulation of waste products, causes the death rate of cells to increase above the rate of replication. Thus, the population size begins to decrease, producing a negative gradient along the growth curve. Over time, the population will tend to extinction as all resources are exhausted [7].
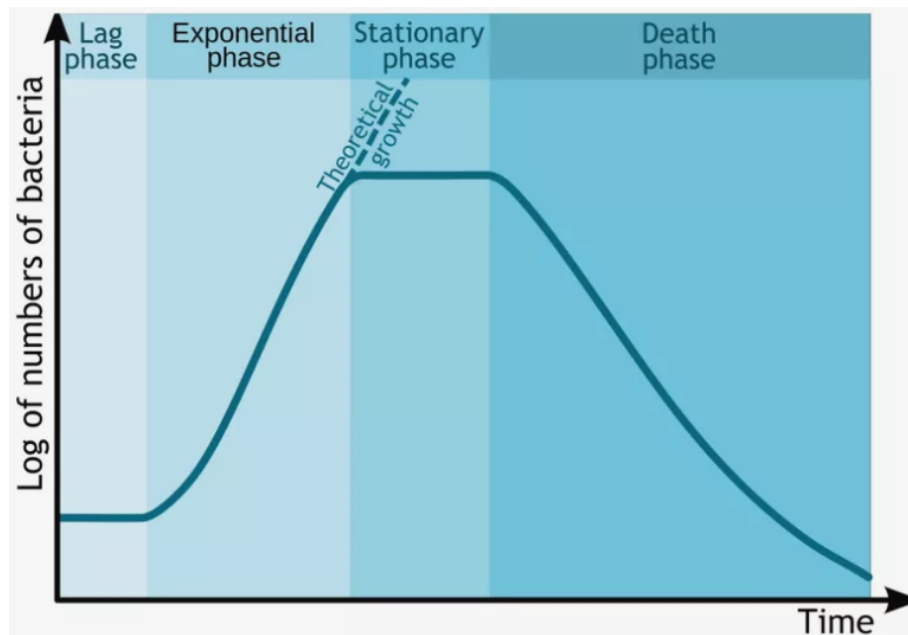
Figure 1: The general growth curve of a population of bacteria: four phases in growth dynamics are indicated.

2.3   Special Interaction

As mentioned, the interaction of different species is an ever present occurance in nature. Within this domain, there exist several contrasting types of interaction that can arise, each of which entails different effects on the associated populations.

Competition: Here, numerous populations exist in an environment containing the same limited resources and space. Over time, interspecific (between species) and intraspecific (within a species) competition arises due to the contention for these resources, as each population aims to maintain itself. While competition aims to eliminate one of the populations, differing factors can mean coexistence is a possibility.

Predation: This involves one of the present species, the predator, requiring the consumption of the prey species to maintain its population. This type of interaction is beneficial to the predator population, while negatively impacting the other. Such interaction can create an oscillatory effect on the respective populations. In a system with a low number of predators, the prey population thrives and begins to grow, in turn creating a greater abundance of food for the predator population to consume. This causes the number of predators to grow, meaning a greater consumption of prey species, therefore decreasing the prey population. Less prey means less resources for the predators, meaning they fight to survive and their growth rate declines.

Repititions of these effects create the ever-oscillating population levels of each respective species. This also highlights how the different species can coexist, since the extinction of prey would result in the extinction of the predator species.

Symbiosis: Generally the most common cooperative interaction in microbial systems, this occurs when the interaction of species results in the maintenance of each population. Within this exist 3 types of symbiosis; mutualism, which benefits all involved populations, commensalism, where the benefit to one species has zero impact on the other, and parasitism, which negatively benefits one species while leaving the other unaffected [9].

3 Mathematical Background

Throughout the last century, the use of mathematical modelling in various branches of biology has grown significantly in popularity. With regard to bacterial species, modelling has become an important tool that opens up the ability to understand the intricacies of their growth, transmission and so on. Furthermore, mathematical models make it possible to investigate mechanisms of interaction between species, as well as predict their strength and probabilites. This type of data can be utilised in many aspects of life, for example when trying to understand the impacts infectious diseases will have on populations.

3.1 One Species System

In theory, the absence of a predatory population would result in the unbounded exponential growth of the prey population. This is where the population's per capita growth rate is maintained regardless of population size, meaning the larger the size of the population, the faster it grows.

Exponential growth can be mathematically represented by:

$$\frac{dN}{dt} = rN, \tag{1}$$

where r represents the constant per capita growth rate, which means how quickly the population grows per individual already in the population, while N represents population size.

However, physical limitations, for example resource availability, means there exists a limit on the maximum stable capacity of the population, known as the population's carrying capacity. This results in the population undergoing logistic growth, where its per capita growth rate declines as the overall size tends to the carrying capacity. Under exponential growth, initial growth rate is slow in a small population, but this increases rapidly meaning a plot of population size over time produces a 'J-shaped' curve with no limit. Meanwhile, under logistic growth, the population will experience a brief period of exponential growth based on the abundance of resources and a lack of competition. However, as the size approaches its physical limit, the growth rate slows and begins to tend to zero. This creates an 'S-shaped' curve, with a steep exponential section that flattens off at the carrying capacity. The main determining factor of a species carrying capacity stems from resource availability, which in turn creates intraspecific competition (competition within a species). While this has little impact at low population size where resources are plentiful, the strain of a large population intensifies competition.

As Verhulst derived in 1838, logistic growth can be mathematically represented [8] by the equation:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right), \tag{2}$$

where K represents the species carrying capacity, r is a measure of the rate at which K is reached and $r\left(1 - \frac{N}{K}\right)$ represents the per capita birth rate, which is dependent on N. Within this equation exist two stable points, at $N = 0$ and $N = K$. Clearly, the trivial solution $N = 0$ can be ignored since that would represent a population size of zero. Furthermore, substituting $\frac{N}{K}$ with x creates a nondimensionalised system, a process that will be described further in Section 2, meaning all physical parameters have been removed. Nondimensionalisation would create an ability to more accurately compare the logistic growth of different species, with different population sizes etc.

However, to solve the dimensional logistic equation, separation of variables is used:

$$\int \frac{dN}{N\left(1 - \frac{N}{K}\right)} = \int r \, dt$$

To evaluate the left hand side, we must separate it using partial fractions to give:

$$\frac{1}{N\left(1 - \frac{N}{K}\right)} = \frac{K}{N(K - N)} = \frac{1}{N} + \frac{1}{K - N},$$

hence;

$$\int \frac{dN}{N} + \int \frac{dN}{K - N} = \int r \, dt,$$

$$\ln|N| - \ln|K - N| = rt + C,$$

$$\ln\left|\frac{K - N}{N}\right| = -rt - C,$$

$$\left|\frac{K - N}{N}\right| = e^{-rt - C}$$

$$\frac{K - N}{N} = Ae^{-rt},$$

where $A = \pm e^{-C}$. From this, we get:

$$N(t) = \frac{K}{1 + Ae^{-rt}}$$

where $A = \frac{K - N_0}{N_0}$. Now, $e^{-rt} \to 0$ as $t \to \infty$, therefore $N \to K$ as $t \to \infty$ for any N_0, showing how a population will always tend to its carrying capacity over time.

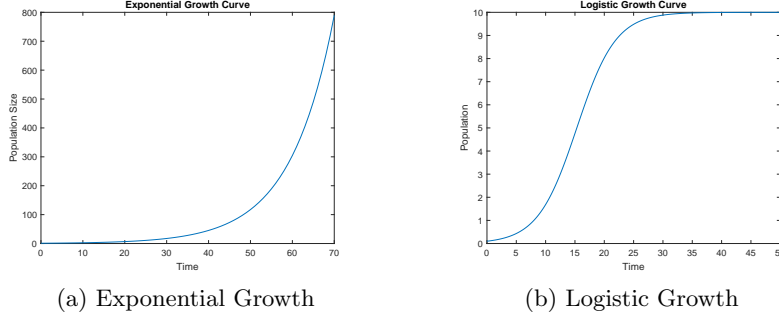(a) Exponential Growth   (b) Logistic Growth

Figure 2: Figure (a) shows the exponential growth of a population starting from $N = 1$ with a rate $r = 0.1$. Figure (b) displays a population experiencing logistic growth starting from $N = 0.3$, with rate $r = 0.1$ and the carrying capacity $K = 10$.

3.2 Two Species System

The general model for two interacting populations can be described as;

$$\begin{cases} \dot{x} = f(x, y) \\ \dot{y} = g(x, y) \end{cases} \tag{3}$$

with the change of each population over time described as two different functions, both determined by the same variables x and y. The partial derivatives of this system quantify the effects of each species;

- $\frac{\partial f}{\partial x}$ represents the self-replicating effect of species x, reproduction

- $\frac{\partial g}{\partial y}$ represents the reproductive effect of species y

- $\frac{\partial f}{\partial y}$ and $\frac{\partial g}{\partial x}$ represent the effect of species y on species x, and x on y respectively.

The partial derivatives $\frac{\partial f}{\partial y}$ and $\frac{\partial g}{\partial x}$ determine the type of interaction that can take place;

- $\frac{\partial f}{\partial y} < 0$, $\frac{\partial g}{\partial x} < 0$ indicates competition between the species

- $\frac{\partial f}{\partial y} > 0$, $\frac{\partial g}{\partial x} < 0$ represents species x preying on species y

- $\frac{\partial f}{\partial y} < 0$, $\frac{\partial g}{\partial x} > 0$ represents y preying on x

- $\frac{\partial f}{\partial y} > 0$, $\frac{\partial g}{\partial x} > 0$ indicates a symbiotic system

To further analyse the two species system, the stationary points that exist can be calculated as solutions to

$$\begin{cases} f(x, y) = 0 \\ g(x, y) = 0 \end{cases} \tag{4}$$

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To calculate the exact values of x and y at which the system is at equilibrium, simultaneous equations are utilised. Having solved to find all stationary points within the system, the stability of each point can be evaluated using the system's Jacobian matrix, which is the matrix of all first order partial derivatives of a function. For the two species system, this is;

$$ J = \left[\begin{array}{cc} f_x & f_y \\ g_x & g_y \end{array} \right] $$

To determine the stability of each stationary point, the values of x and y at each point must first be inserted into the Jacobian. The eigenvalues of this matrix must then be calculated through the solution of its characteristic equation, defined as

$$ \det(J - \lambda I) = 0 $$

The real parts of the resultant values of λ_1, λ_2 deduce the stability of each point, with;

- $\lambda_1 < 0, \lambda_2 < 0$ indicating a stable node
- $\lambda_1 > 0, \lambda_2 < 0$ or $\lambda_1 < 0, \lambda_2 > 0$ signalling an unstable saddle node, or
- $\lambda_1 > 0, \lambda_2 > 0$ indicating an unstable node

3.3 Lotka-Volterra Model

Ever since the publication of the papers of Lotka [4] and Volterra [11], which focused on a predator-prey model that showed how the populations of species could permanently oscillate, there has been a great interest in studying the dynamic models of interacting populations. Since the interaction of species affects the dynamics of each population, this interest has stimulated the development of modelling approaches to analyse such effects. In real circumstances, there will generally be a large system consisting of many interacting species, called a trophic web.

Within 2-species systems there exists three main types of interaction;

- Predator-Prey Situation- In this scenario, special interaction causes the decline of one population's growth rate, whilst increasing the rate of the other population.

- Competition- Here, interaction results in the decline of both population's respective growth rates.

- Symbiosis- The result of this type of interaction is the enhancement of both population's growth rates.

To better understand the interaction of different populations, Volterra proposed the simple Predator-Prey model which mathematically describes the predation of one species by another. Letting $N(t)$ and $P(t)$ represent

the populations of prey and predators respectively at time t, then Volterra's model is;

$$\frac{dN}{dt} = N(a - bP), \qquad (5)$$

$$\frac{dP}{dt} = P(cN - d), \qquad (6)$$

where a,b,c,d are all positive constants [5].

This model is based on several assumptions. Firstly, in the absence of predation, the population of prey grows unboundedly. This is denoted by the aN term. Secondly, the effect of predation is the reduction in the prey's growth rate by a term proportional to the respective populations of prey and predator, denoted by the $-bNP$ term. Also, the absence of prey results in an exponential decay of predator population, denoted by the $-dP$ term. Finally, the cNP term describes the prey's contribution to the growth rate of the predator population, again by a term proportional to the size of the predator population and the availability of prey. In real terms, the NP terms can represent the conversion of energy through the food chain, bNP is taken from the prey and cNP accrues to the predators.

As mentioned in the two species system calculations, the stationary points of this system are calculated as solutions to

$$\frac{dN}{dt} = \frac{dP}{dt} = 0$$

which for the Lotka-Volterra model represents

$$N(a - bP) = P(cN - d) = 0$$

Rewriting as $aN = bNP$, one can see that for this to hold, $N = 0$ or $P = \frac{a}{b}$. Rearranging to give $cNP = dP$, we must have $P = 0$ when $N = 0$, or $N = \frac{d}{c}$ when $P = \frac{a}{b}$. Therefore, the stationary points for this system are $(0, 0)$ and $\left(\frac{d}{c}, \frac{a}{b}\right)$.

Through evaluation of the systems' associated Jacobian

$$J = \begin{bmatrix} a - bP & -bN \\ cP & cN - d \end{bmatrix},$$

the stability of each stationary point can be determined. The point $(0, 0)$ has the associated Jacobian

$$J = \begin{bmatrix} a & 0 \\ 0 & -d \end{bmatrix},$$

providing the eigenvalues $\lambda_1 = a$ and $\lambda_2 = -d$. In this case, the characteristic equation does not need to be solved, since the matrix is diagonal. Defined as a matrix whose only non-zero elements run from the top left to the bottom right, the eigenvalues of such a matrix are simply just the values that run along the diagonal. Since the eigenvalues at $(0,0)$ are of different signs, it can be concluded that this is an unstable saddle node. The other critical point $\left(\frac{d}{c}, \frac{a}{b}\right)$, with

$$J = \begin{bmatrix} 0 & -\frac{bd}{c} \\ \frac{ac}{b} & 0 \end{bmatrix},$$

has the imaginary eigenvalues $\lambda_{1,2} = \pm i\sqrt{ad}$. Since both values are complex, but contain real parts equal to zero, $\left(\frac{d}{c}, \frac{a}{b}\right)$ can be determined as a centre point.

The phase trajectory equation for the point $\left(\frac{d}{c}, \frac{a}{b}\right)$ is calculated through solutions to $\frac{dy}{dx}$. This is

$$\frac{g(x,y)}{f(x,y)} = \frac{y(-d+xc)}{x(a-yb)}, \tag{7}$$

where N and P have been substituted with x and y for simplicity. Now, this is a separable equation, meaning it can be integrated to give us

$$f(x,y) = -d\ln|x| + cx - a\ln|y| + by = \text{constant} \tag{8}$$

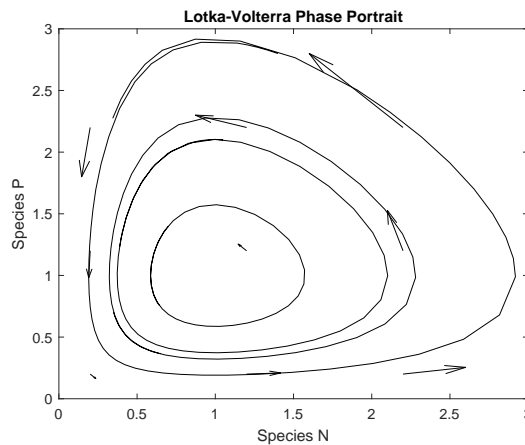Thus, we can now construct the following portrait;

Figure 3: A phase portrait is a geometric representation of the trajectories of a dynamical system. The above figure shows the change in each population of species P and N over time, representing the predatory and prey species respectively. The arrows indicate the direction of change. Taken from [1].

4 Modelling Competing Bacterial Species

This section focuses on the 2-species Lotka-Volterra model that exists, describing the competition of two bacterial species N_1 and N_2. One can analyse the system in which two species compete for resources, in turn affecting each others growth rates. Considering the competition model with species N_1 and N_2, both of whom have logistic growth in the absence of the other, we generate a new model describing the interaction of populations by

$$\frac{dN_1}{dt} = r_1 N_1 \left[1 - \frac{N_1}{K_1} - a_1 \frac{N_2}{K_1} \right] \tag{9}$$

$$\frac{dN_2}{dt} = r_2 N_2 \left[1 - \frac{N_2}{K_2} - a_2 \frac{N_1}{K_2} \right] \tag{10}$$

where r_1, r_2, K_1, K_2, a_1 and a_2 are all positive constants. The r terms represent the linear birth rates of the respective populations, while the K terms represent the maximum carrying capacity of each species. The a_1 and a_2 terms measure the competitive effect of N_2 on N_1 and N_1 on N_2 respectively. The competitve effect of each species is defined as the number of individuals of one population that are equivalent to one individual of the other species, in terms of their use of resource. For example, if 1 member of the N_1 population is equal to $\frac{1}{4}$ of an individual of the N_2 population, then $a_1 = 0.25$. If $a_1 = a_2 = 0$, the species are said to be independent of one another, since this indicates that there is no interspecific competition.

4.1 Nondimensionalisation

Nondimensionalisation involves removing the physical dimensions of an equation and replacing them with suitable variables, to help parametrise the problem by making the system unitless. One benefit of nondimensionalisation includes scaling the quantities to compare results with greater ease, relative to an appropriate unit. For example, since the values N and K are physical quantites relating to population size, using a substitution which divides N by K restricts the potential values of our new variables to between 0 and 1, with 1 indicating a population that has reached its carrying capacity. Creating a dimensionless system also reduces the number of parameters involved. Again, this creates a simpler basis for comparison of the results.

The system is nondimensionalised using the substitution of the terms;

$$u = \frac{N_1}{K_1}, v = \frac{N_2}{K_2}, \tau = r_1 t$$

The u and v terms remove the population dimension from the equations. Doing this restricts the value of u and v to between 0 and 1, meaning comparing the relative populations in proportion to their maximum capacity

is made easier. Since the system is also dependent on time, as shown by the $\frac{1}{t}$ in the left hand side of each equation, τ is used to nondimensionalise the time parameter by equating the right hand side to the same time dependency.

For equation 9, substituting in $N_1 = uK_1$, $N_2 = vK_2$, $r_1 = \frac{\tau}{t}$ and $t = \frac{\tau}{r_1}$ provides

$$\frac{d(uK_1)}{d(\frac{\tau}{r_1})} = \frac{\tau}{\frac{\tau}{r_1}} uK_1 \left[1 - \frac{uK_1}{K_1} - a_1 \frac{vK_2}{K_1}\right]$$

This system is now dimensionless, however the number of parameters is further reduced with the substitution

$$b_1 = a_1 \frac{K_2}{K_1}$$

Now, the constant K_1 in $d(uK_1)$ can be brought outside the derivative, which allows all K_1 values to be cancelled down. The τ values in the right hand side of the equation can also be removed, giving us

$$\frac{du}{d(\frac{\tau}{r_1})} = r_1 u \left[1 - u - b_1 v\right]$$

Finally, bringing the value r_1 out of the derivative allows us to remove r_1 from both sides of the equation, since

$$\frac{r_1 du}{d\tau} = r_1 u \left[1 - u - b_1 v\right]$$

Meaning we are left with

$$\frac{du}{d\tau} = u \left[1 - u - b_1 v\right]$$

For equation 10, which is

$$\frac{dN_2}{dt} = r_2 N_2 \left[1 - \frac{N_2}{K_2} - a_2 \frac{N_1}{K_2}\right]$$

the substitutions $N_1 = uK_1$, $N_2 = vK_2$ and $t = \frac{\tau}{r_1}$ create the dimensionless equation

$$\frac{d(vK_2)}{d(\frac{\tau}{r_1})} = r_2 vK_2 \left[1 - \frac{vK_2}{K_2} - a_2 \frac{uK_1}{K_2}\right]$$

Again, K_2 and r_1 can be brought out of the derivatives to give

$$\frac{r_1 K_2 dv}{d\tau} = r_2 vK_2 \left[1 - \frac{vK_2}{K_2} - a_2 \frac{uK_1}{K_2}\right]$$

Cancelling down the K_2 values and rearranging gives

$$\frac{dv}{d\tau} = \frac{r_2}{r_1} v \left[1 - v - a_2 \frac{uK_1}{K_2} \right]$$

A further reduction in parameters is again done using the substitutions

$$b_2 = a_2 \frac{K_1}{K_2}, \rho = \frac{r_2}{r_1}$$

Creating the equation

$$\frac{dv}{d\tau} = \rho v \left[1 - v - b_2 u \right]$$

This means we have created the dimensionless system

$$\frac{du}{d\tau} = u(1 - u - b_1 v) \tag{11}$$

$$\frac{dv}{d\tau} = \rho v(1 - v - b_2 u) \tag{12}$$

4.2 Analytic Study

These equations form the basis from which we can calculate the steady state equilibria and phase plane singularities, which are the solutions of $\frac{du}{d\tau} = \frac{dv}{d\tau} = 0$.

These are;

$$u^* = 0, v^* = 0$$

$$u^* = 1, v^* = 0$$

$$u^* = 0, v^* = 1$$

$$u^* = \frac{1 - b_1}{1 - b_1 b_2}, v^* = \frac{1 - b_2}{1 - b_1 b_2}$$

where u^* and v^* represent the solutions to equations 9 and 10 respectively. The solution involving b_1, b_2 represents an equilibrium in which coexistence of species is possible, but is only stable for values of $b_1, b_2 < 1$, any other case is irrelevant.

However, the solution containing variables b_1 and b_2 are only of relevance if $u^* \geq 0$ and $v^* \geq 0$ and are such that $b_1 b_2 \neq 1$.

The stability of these steady states is determined by the community matrix, which is

$$A = \left(\begin{array}{cc} \frac{\partial f_1}{\partial u} & \frac{\partial f_1}{\partial v} \\ \frac{\partial f_2}{\partial u} & \frac{\partial f_2}{\partial v} \end{array} \right)_{u^*, v^*}$$

$$= \left(\begin{array}{cc} 1 - 2u - b_1 v & -b_1 u \\ -\rho b_2 v & \rho(1 - 2v - b_2 u) \end{array} \right)_{u*, v*}$$

We can now determine the stability of each steady point through calculating the eigenvalues λ of its community matrix, starting with $(0,0)$.

$$|A - \lambda I| = \begin{vmatrix} 1 - \lambda & 0 \\ 0 & \rho - \lambda \end{vmatrix} = 0$$

Therefore the eigenvalues are $\lambda_1 = 1, \lambda_2 = \rho$. Since these values are positive, this steady state is unstable.

For $(1,0)$, this calculation gives

$$|A - \lambda I| = \begin{vmatrix} -1 - \lambda & -b_1 \\ 0 & \rho(1 - b_2) - \lambda \end{vmatrix} = 0$$

Which generates eigenvalues of $\lambda_1 = -1, \lambda_2 = \rho(1 - b_2)$

This means that the point $(1,0)$ is

$$\begin{cases} \text{stable,} & \text{if } b_2 > 1 \\ \text{unstable,} & \text{if } b_2 < 1 \end{cases} \tag{13}$$

For the steady state $(0,1)$, the eigenvalues can be calculated as $\lambda_1 = -\rho, \lambda_2 = 1 - b_1$.

Therefore, this point is

$$\begin{cases} \text{stable,} & \text{if } b_1 > 1 \\ \text{unstable,} & \text{if } b_1 < 1 \end{cases} \tag{14}$$

Finally, for the steady state at $(\frac{1-b_1}{1-b_1 b_2}, \frac{1-b_2}{1-b_1 b_2})$, it has a matrix A when it exists in the positive quadrant. That is;

$$A = (1 - b_1 b_2)^{-1} \begin{pmatrix} b_1 - 1 & b_1(b_1 - 1) \\ \rho b_2(b_2 - 1) & \rho(b_2 - 1) \end{pmatrix}$$

The eigenvalues of this matrix are;

$$\lambda_{1,2} = \frac{(b_1 - 1) + \rho(b_2 - 1) \pm \sqrt{[(b_1 - 1) + \rho(b_2 - 1)]^2 - 4\rho(1 - b_1 b_2)(b_1 - 1)(b_2 - 1)}}{2(1 - b_1 b_2)}$$

This equilibrium point is stable for all $b_1 < 1$ and $b_2 < 1$, since such values would generate two negative eigenvalues.

To prove this, we will first look at each part of the equation individually. $(1 - b_1 b_2)$ is always positive for $b_1, b_2 < 1$, since b_1 multiplied by b_2 is a number smaller than one. Therefore, the denominator $2(1 - b_1 b_2)$ is always positive, meaning the numerator must be always negative to generate two negative eigenvalues. Since $(b_1 - 1)$ and $(b_2 - 1)$ will be negative, it follows that their sum will also be negative. For future reference, we will use

$$(b_1 - 1) + \rho(b_2 - 1) = \alpha.$$

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Now, looking at the terms under the square root, the first term

$$[(b_1 - 1) + \rho(b_2 - 1)]^2 = \alpha^2$$

and is always positive since it involves squaring a negative value. For the additional term we will use

$$4\rho(1 - b_1 b_2)(b_1 - 1)(b_2 - 1) = \beta$$

which will be strictly positive since the two negative terms $(b_1 - 1), (b_2 - 1)$ multiply to make a positive, meaning we have the positive value β being subtracted from another positive value α^2. Now there are two possibilities:

$$\beta < \alpha^2$$

$$\beta > \alpha^2$$

Looking at the first case, square rooting the value of $\alpha^2 - \beta$, where $\beta < \alpha^2$, means the resultant value will be less than $|\alpha|$, so for either case in which it is added or subtracted from our initial negative value α, the result will be negative. This means we have an always positive denominator, with an always negative numerator, resulting in two always negative eigenvalues. For the case $\beta > \alpha^2$, $\alpha^2 - \beta < 0$ meaning the resultant square root is imaginary. Therefore, we have our negative real value $\alpha \pm$ our imaginary result in the numerator. Combining this with our positive denominator means the real part of both resultant eigenvalues is negative, with the stability being determined by the real parts of the values. Since the resultant eigenvalues are always negative, we can conclude that for any values $b_1, b_2 < 1$ the equilibrium is stable.

Using the equilibrium calculations, we can now plot the schematic phase trajectories near the steady states, which gives a visual representation of how varying parameters can affect the dynamic behaviour of competing populations satisfying the above model. The nullclines for the competition model can be plotted and when combined with the stable points for each case, can be used to find the domain of attraction. Nullcines are the sets of points in the (u, v) plane at which $\frac{du}{d\tau} = \frac{dv}{d\tau} = 0$. For our system, this represents

$$u(1 - u - b_1 v) = 0$$

$$\rho v(1 - v - b_2 u) = 0$$

meaning we have $u = 0, (1 - u - b_1 v) = 0$ from the first equation, along with $v = 0, (1 - v - b_2 u) = 0$ from the second. The points at which these nullclines meet are the stable points of the system.
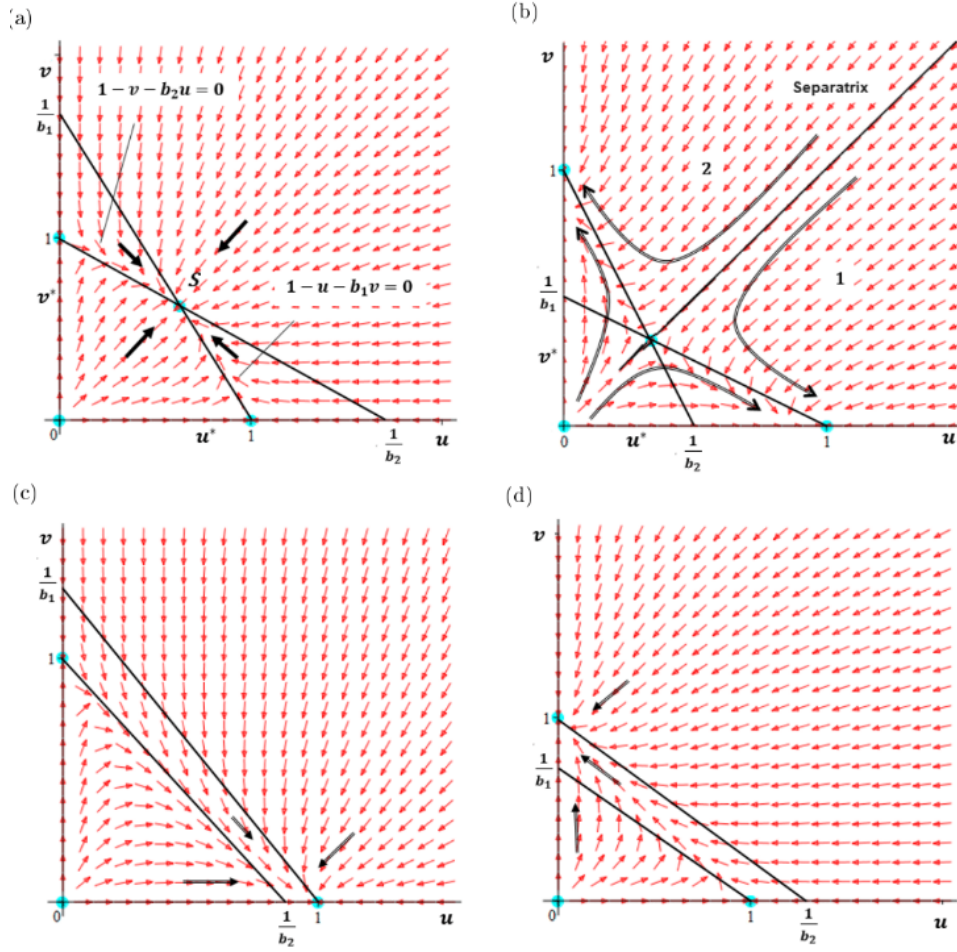
Figure 4: The nullclines and direction fields near the equilibrium points for the dynamic behaviour of the populations represented in equations 11 and 12. Taken from [9].

Figure 4 shows the phase trajectories for the four cases of dynamic behaviour of interacting populations. (a) represents $b_1 < 1, b_2 < 1$, where there exists only one steady state S at which the coexistence of the competing populations is possible. S is the only stable point in this case, with all trajectories tending toward it. (b) represents $b_1 > 1, b_2 > 1$. Here exist two stable points $(1, 0)$ and $(0, 1)$, with a separatrix passing through (u^*, v^*) splitting their domains of attraction. In this case, the initial conditions dictate which steady state is achieved. Initial conditions in domain 1 result in $u \to 1, v \to 0$, while conditions in domain 2 tend to the other steady state $(0, 1)$. This system would eventually result in the extinction of one of the competing species. (c) shows $b_1 < 1, b_2 > 1$, where there is only one stable point $(1, 0)$ and all trajectories tend toward it. The stronger competitive effect of u dominates, causing it to reach its carrying capacity, while

species v eventually becomes extinct. (d) represents $b_1 > 1, b_2 < 1$, where the only stable point is $(0, 1)$, again with all trajectories tending towards it. Similarly to (c), the higher competitive effect of v results in it achieving its carrying capacity while species u tends to extinction. Cases (b), (c) and (d) represent competitive exclusion, where one species dominates to reach its carrying capacity while the other is driven to extinction.
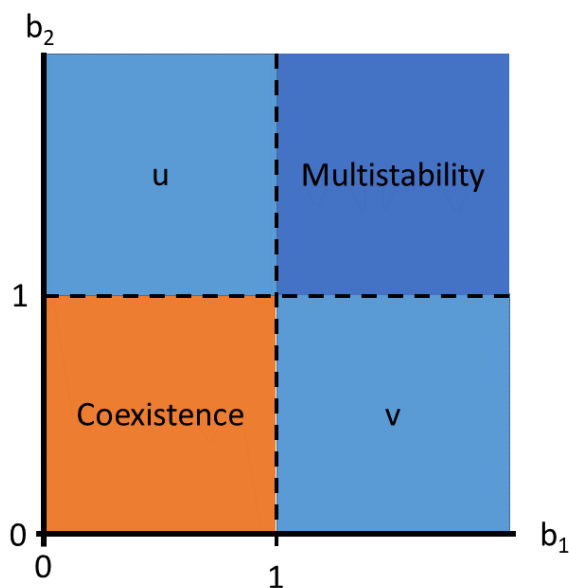

Figure 5: Visual representation of the domains of attraction for the four cases of dynamic behaviour possible between interacting populations.

Figure 5 shows another way of representing the potential equilibria that the Lotka-Volterra system can achieve. The orange panel contains the equilibria where stable coexistence is possible, relating to case (a) of figure 4. Here, $b_1 < 1$ and $b_2 < 1$. The two light blue panels indicate systems that each contain one stable equilibrium, at which one species is driven to extinction while the other reaches its carrying capacity. The top left panel is achieved when $b_1 < 1, b_2 > 1$, while values of $b_1 > 1, b_2 < 1$ would result in a point that lies in the bottom right panel. Lastly, the dark blue panel represents a system in which both $b_1, b_2 > 1$, with two stable equilibria existing within this region. This is known as multistability, where the resulting equilibrium is determined by the initial conditions of u and v, or by the relative competitive effects b_1 and b_2, as shown later in figures 7a, 7b, 8a and 8b.

4.3 Numerical Integration of Equations

Furthermore, we can use the nondimensionalised system of equations to generate MATLAB code that can create a graph to show how the populations of each species changes over time, dependent on varying paramaters. Using this code, we can alter the intial values of u and v, as well as assign differing values to the competitve effect each species has on each other, b_1 and b_2, to generate a group of graphs that show the different possible outcomes of the system, as shown below.
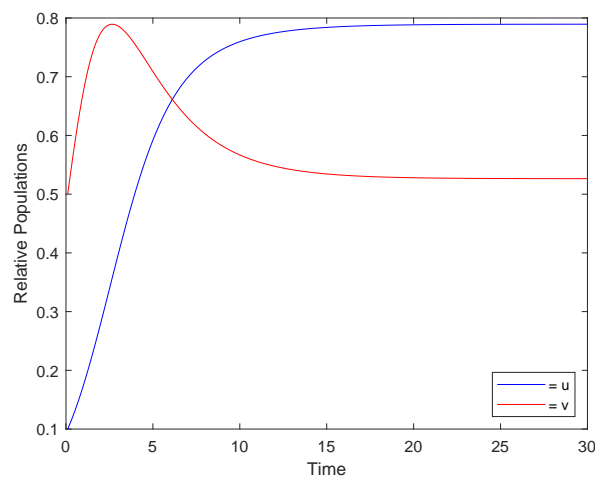

Figure 6: Numerical integration of the system of equations 11 and 12, for concentrations of populations u and v. Here, $b_1 = 0.4, b_2 = 0.6, u(0) = 0.1, v(0) = 0.5$

Figure 6 shows a system in which there exists a stable steady state where the populations can coexist, since $b_1 < 1$ and $b_2 < 1$. Both population levels reaching a steady equlibrium and all trajectories tend to this state, as highlighted by case (a) of figure 4. The level of each equilibrium is determined by the initial values of u and v, as well as the competitive effects b_1 and b_2. In this system the initial conditions are $u(0) = 0.1$ and $v(0) = 0.5$, while $b_1 = 0.4$ and $b_2 = 0.6$, indicating species u has a larger effect on v, hence u plateaus at a higher point. The higher competitive effect of u on v also explains the drop in population of v, with both populations growing initially in an abundance of resources, but the level of v declines as u grows up to its equilibrium point.

(a) $b_1 > 1, b_2 > 1, b_1 < b_2$
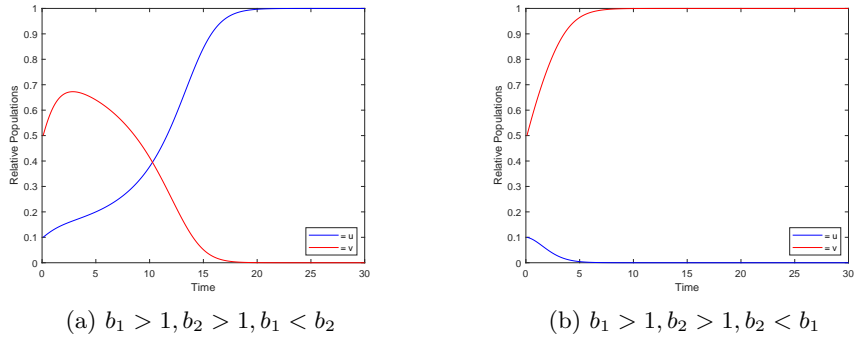

(b) $b_1 > 1, b_2 > 1, b_2 < b_1$

Figure 7: Figure 7a portrays a system where $b_1 = 1.1, b_2 = 2, u(0) = 0.1$ and $v(0) = 0.5$. Figure 7b involves the same initial conditions, however $b_1 = 2$ and $b_2 = 1.8$.

Figures 7a and 7b show systems in which both b_1 and b_2 are both greater than 1. In these systems, three non-trivial equilibria can exist, however only two stable points exist, $(0, 1)$ and $(1, 0)$. A separatrix passes through (as shown in the phase trajectories), separating the domains of attraction. The resulting equilibrium is determined by their relative competitive effects. Figure 7a shows a case where the effect of u on v is greater than the opposing effect of v on u, hence species u grows to its carrying capacity despite having a lower initial size, while the population of v tends to zero. Meanwhile, figure 7b represents the opposite case, where v has a greater impact on u, meaning species u is driven to extinction while v reaches its maximum.

(a) $b_1 > 1, b_2 > 1, b_1 = b_2, u(0) > v(0)$

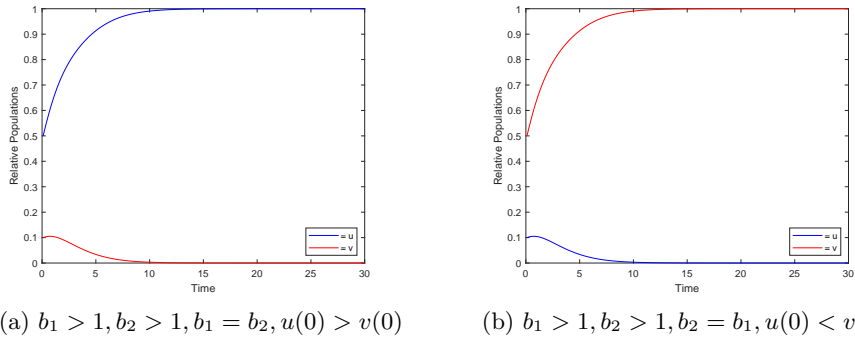(b) $b_1 > 1, b_2 > 1, b_2 = b_1, u(0) < v(0)$

Figure 8: Figures 8a and 8b show systems in which the competitive effects of each species are equal, with $b_1 = b_2 = 1.5$. However, the initial conditions for figure 8a are $u = 0.5, v = 0.1$, while for figure 8b they are $u = 0.1, v = 0.5$.

However, figures 8a and 8b show how the steady state that each of these systems achieves can also be dependent on the initial conditions, as the domain in which they lie triggers the resultant equilibrium. The figures highlight that when the competitive effects b_1 and b_2 are equal, the species

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with the greater initial population will flourish while the other one eventually dies out.

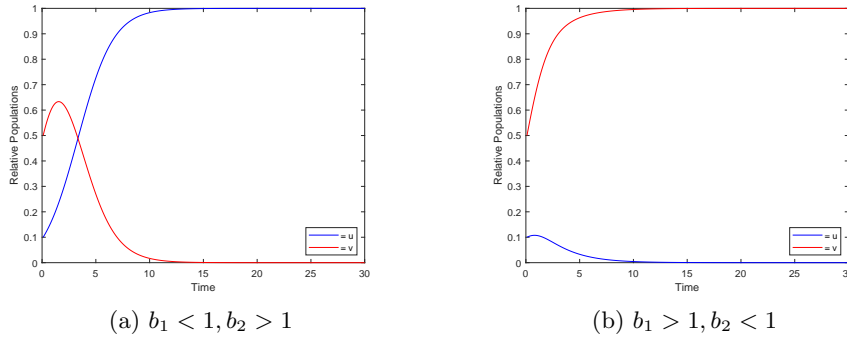(a) $b_1 < 1, b_2 > 1$ (b) $b_1 > 1, b_2 < 1$

Figure 9: Figure 9a: $b_1 = 0.4, b_2 = 1.6, u(0) = 0.1, v(0) = 0.5$. Figure 9b: $b_1 = 1.4, b_2 = 0.6, u(0) = 0.1, v(0) = 0.5$

Figures 9a and 9b display the systems in which one species has a significantly stronger competitive effect than the other. In figure 9a, the stronger competition of u causes it to dominate while species v is driven to extinction, while figure 9b shows the opposite, where species v reaches its carrying capacity while u eventually dies out. Both of these systems contain only one stable equilibrium, with all trajectories tending towards them regardless of initial conditions, as shown by the lower starting value of u in figure 9a.

To integrate the nonlinear system of equations 9 and 10, which produced the results seen above, the explicit Euler method was used. This is one of the first order numerical methods, along with the implicit Euler and other Runge-Kutta methods, that solves time-dependent ordinary differential equations that include a given initial value, by approximating the solutions at each time step. These methods are used when the differential equations cannot be solved analytically, so numerical approximation is required to understand the general trend and long term behaviour of the system.

There are several reasons for selecting to use the explicit Euler method, as opposed to implicit. For one, it is the most basic method for numerical integration, making it easier to implement, therefore also easier to code when generating the MATLAB results above. Implicit calculations are more complex due to the solution being found by solving an equation involving both the current and successive states of the system. Explicit calculations use only the current state of the system to calculate the state at each successive time step. Moreover, the explicit method tends to generate more accurate results than the implicit calculations.

5 Conclusion

The aim of this paper was to mathematically model the potential outcomes of a system involving two competing bacterial species. Initially, the growth of a single species without the external pressure of another population was successfully calculated and modelled. Here, it was shown how in theory, a population will continue to grow exponentially in the absence of a form of competition. However, as shown, limiting environmental factors create a maximum stable capacity for the population. Any point past this capacity is unsustainable, meaning the population size will always tend to this value regardless of the initial conditions. Furthermore, the interaction of two species was explored, initially focusing on the theory of how to calculate the stable points of said system. Building on this, the Lotka-Volterra model was then introduced, providing us with a predator-prey based model from which the stable points can be calculated, allowing us to then geometrically represent the dynamics of the system over time in the form of the phase portrait.

The practice from the standard Lotka-Volterra model created a basis on which we could build when modelling the competition of two competing bacterial species N_1 and N_2. Nondimensionalisation of the system first allowed us to analytically produce each equilibrium point of the system, then evaluate their respective stabilities. From these solutions, we were able to visually represent the dynamics of the system in different ways. Secondly, we were able to model each potential outcome based on the numerical integration of the equations. Using MATLAB, it was possible to create a loop code that used our parameters, b_1, b_2, u and v to generate a graph that accurately displays the resultant impact on each population, with an ability to adjust the parameters to solve for different cases. However, each of the resultant models were limited to spatially homogeneous cases, meaning the movement of each competing population was not factored into the calculations.

The produced models allowed us to highlight how the resultant equilibrium of a system involving two competing bacterial species is dependent on the relative strength of competitve effect of each species, b_1 and b_2. For the case in which $b_1, b_2 < 1$, the outcome is a stable equilibrium in which the coexistence of the two species is possible. Here, the population of the species with the higher competitive effect plateuas at a higher point. When both $b_1, b_2 > 1$, there exists two cases which determine the resultant equilbrium. If $b_1 \neq b_2$, then the species with the higher competitive effect will dominate, with the other population dying out. However, if $b_1 = b_2$, then the species with the greater initial population will dominate. Lastly, for the case in which $b_1 < 1, b_2 > 1$ or $b_1 > 1, b_2 < 1$, then the species with the significantly higher competitive effect will ultimately outcompete its rival and grow to its maximum capacity. The latter three cases highlight competitive exclusion,

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in which one species grows to its carrying capacity while the other is driven to extinction.

Finally, through completing this project, I have learned and developed many new skills and techniques relating to dynamical systems and mathematical modelling. I have enhanced my knowledge from MATH322 on how to calculate stationary points of a system, then how to evaluate their respective stability. Furthermore, I have developed an understanding of the process of nondimensionalisation, what it means and why it is necessary, as well as how to apply it to a system of equations. As seen throughout the paper, I have developed an ability to visually represent the varying dynamics of a competitive system in several ways, as well as practicing the skills relating to nullclines and domains of attraction I had also acquired in MATH322. Lastly, I have developed new MATLAB coding skills, a software I had never previously used, relating to the numerical integration of differential equations and an ability to plot the results.

Mathematical modelling holds an important place in biology due to its many benefits. The ability to test and understand systemic knowledge, as well as use this to predict future outcomes based on varying parameters, has an extensive range of real world applications. Modelling can also aid in deepening our understanding of complex problems and make them seem simpler, as well as making the analysis of anomalous results easier. Therefore, mathematical modelling will continue to grow as an ever-present part of biological studies.

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6 Appendix

The following code was used to generate the results previously seen in section 3.3.

```
clear;
t_end=30;                              % time
b1=2;                      % level of toxicity
b2=1.8;
ht=0.1;          % time step size
%inital conditions:
u=0.1;
v=0.5;
nh=t_end/ht;


%-----------------------------------------
t=0; k=0;
U1=zeros(nh,1);
V1=zeros(nh,1);
for j= 1:nh
 U1(j)=u;
 V1(j)=v;
 u0=u+ht*u*(1-u-b1*v);
 v0=v+ht*v*(1-v-b2*u);
 u=u0;
 v=v0;
 t=t+ht;
 k=k+1;
 end;
% Defining the time
   E=0:ht:t;
  % plotting the profiles

figure
 plot(E(2:end),U1,'b',E(2:end),V1,'r');
xlabel('Time')
ylabel('Relative Populations')
legend({'= u','= v'},'Location','southeast')
% Equations to quantify the success of invasions.
```

This specific code was used to generate the results seen in figure 7b. However, by simply changing the values of b1, b2, u and v seen at the top of the code, the outcome for each potential type of interaction can be produced. The code has created a loop which solves the system of equations 11 and

12 using the initial values of u and v, as well as the selected values of b_1, b_2, then continues to solve at successive time steps of 0.1 to plot the changes in respective populations over time.