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# Modelling Dynamics of Competing Bacterial Populations

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# 1 Biological Problems

## 1.1 Introduction

Of the millions of different biological mechanisms constantly at work in nature, bacteria are in control of a large number. They can perform a wide array of tasks from decomposition of organic matter to preservation of healthy digestion in animal immune systems.

Scientists have modelled these activities using dynamical functions to simulate and in turn replicate their behaviour, understanding such characteristics as a population's rate of growth; both in isolation, and in environments containing multiple microbial species.

All bacteria reproduce asexually by undergoing binary fission, whereby the chromosome of each bacterial cell is replicated and the whole cell divides to accommodate, producing two identical cells from one after a single iteration [1]. This type of growth, which we will explore in the mathematical background chapter, is exponential and can be used to calculate the growth rate of the increasing population; determining the relative power of a bacterial species to gain abundance in a certain space.

When a population grows either in isolation of any other species or in co-habitation, it will typically undergo a slow lag phase, followed by a log phase where its size increases exponentially, before becoming stationary – where the number of new cells is equal to the number dying - and ultimately reaches the death phase where its size decreases after time.

Most commonly, bacteria grow amongst other species and strains, subtypes of species, so competition for resources becomes another contributing factor towards its ultimate decline, along with its own ability to reproduce before its cells start to die.

However, defence mechanisms such as venom injection can be used to increase chances of survival in competitive circumstances, as with many species of animal operating on the macro scale; and are as well utilized in the form of poisonous substances called toxins by micro-organisms like bacteria [2]. Some strains of bacterial species are able to release, or inhibit, toxins from either inside or from the surface of their cell walls, classifying them as gram negative or gram positive strains respectively; and as a result can slow the rate of cell division of competing species in the same environment, bettering their chances of long term survival. Such biological inspection has allowed for an understanding of the attributes a population of bacteria must have in order to withstand certain situations: whether its rate of cell division alone is enough for it to survive in the same environment as a strain that produces deadly toxins, for example [3].

If a particular bacterial strain causes its competitors to go extinct over time, it is known by researchers to what degree of toxicity another strain should possess such that, when introduced, can successfully maintain an abundance in the environment.

Growth interference caused by competing populations in spatially homogeneous situations - an environment occupied by two competing populations - can be categorised by identifying the different outcomes after both strains of bacteria have been fully integrated.

First referring to a pre-defined biological grouping to illustrate [1]: a competition interaction is where both populations reproduce at a rate lower to that in isolation, due to their inability to share local resources effectively; yet a mutualism interaction, otherwise known as symbiosis, defines a space where the initial resident population in the environment grows sustainably without significant fluctuation caused by resource competition when an invading population is introduced.

Commensalism and amensalism describe respectively the scenarios where one population grows whilst the other remains stationary; referring to extreme cases of interaction such that one species of bacteria is dominant enough to cause the decline and eventual stagnation of the other.

Our ability over the years to create drugs to fight bacterial diseases has led to a complete drop in their mortality rate, however their ability to mutate and regain control of the resident micro-biome requires the development of a new antibiotic to boost the size of the resident population under invasion. This is exemplified in the successful treatment of the antibiotic resistant “*Clostridium difficile*” bacteria, which was stunted in growth when the host patient received a transplant from a healthy donor, restoring the beneficial resident bacteria by re-establishing its abundance in the infected microbiome [4].

Ideally, when applying discussed population interactions, both bacteria strains want to exist in symbiosis such that they can transition through all phases of their intended growth before eventual decline, with minimal disturbance. When a resident species of bacteria is functioning in its own environment in isolation - referred to in biological nomenclature as intra-specific competition - it would like to maintain growth to the same degree despite any invading pathogens; and if preyed upon as a result, should have the necessary attributes – whether they’re the ability to inhibit toxins or the help of a new antibiotic – to re-establish and maintain its size.

We shall explore the possibilities of this by qualitatively defining such microbial interactions.

## 1.2 Bacterial Experiments

To gain more insight into the behaviour of bacterial populations growing in co-habitation, we shall evaluate an experiment conducted to observe the resulting interactions of a series of resident species of bacteria when under a degree of imposition from an introduced invading species [5].

In this experiment, each bacteria strain was individually incubated in a sterile Petri dish of constant size at 37°C, and its number of cells were recorded every 30 minutes so that its growth rate and doubling time could be determined. *Staphylococcus epidermidis* and *Staphylococcus aureus* - both gram positive bacterial species - were the chosen bacterial species, as they both possess strains that inhibit toxins as well as strains that do not, when growing under competitive circumstances.

3 strains of the former species: *S. epidermidis* B180, B155 and TU3298 were then treated in turn as the resident species of the incubated biome, and were exposed to the introduction of strain *S. aureus* SH1000 at an abundance 0.01 times that of the resident *S. Epidermidis*.

All 3 experiments were then repeated with the resident to invader roles reversed, such that the epidermis species was now the invading species with an 0.01:1 ratio abundance with the resident aureus bacteria strain.

All experiments involving 2 competing strains were carried out until both were no longer changing in size. In using multiple different strains of the *S. epidermidis* species, it was to be expected that each strain would behave differently despite all being up against the same competitor *S. aureus* SH1000. It could be assumed that if a resident strain grows more than other resident strains in the same time period, it may possess the ability to inhibit toxic substances such that it becomes less imposed by the invading strain. The observations made and the conclusions drawn from each of the 3 experiments where *S. aureus* played the role of the invader, are displayed in Table 1:

Table 1: S. Epidermis versus S. Aureus Experiments in Structured Environment.

Invader : Resident	Observations	Conclusions Drawn
SH1000 : B180	Aureus strain enters log phase with minimal imposition.	Epidermis strain not likely to inhibit toxins.
SH1000 : B155	Epidermis strain competes with aureus causing both their sizes to fluctuate, however epidermis size shortly starts to decline.	B155 more adept at surviving than B180, so may produce toxic substances.
SH1000 : TU3298	Epidermis strain maintains size for much longer, only starts to decline around the time SH1000 reaches its stationary phase.	TU3298 is more adept at competing though still declines over time, but is more likely to inhibit toxins.

From these results, the researchers concluded that S. epidermis strains B155 and TU3298 are able to inhibit some special characteristic, if not a toxic substance, such that they can compete for a time with the S. aureus invader before depleting; something that B180 could not do successfully.

In consideration of the fact that every S. epidermis strain eventually fell in size when in contact with the S. aureus strain, it is to be expected that the results would be even less favourable for the epidermis strains in the remaining 3 experiments where they occupy the role of the invader. Whether or not the S. epidermis strain is toxin producing, it will assuredly be no better at regaining control of its micro-biome when introduced at an abundance 0.01 times smaller than the size of the resident S. aureus population.

As observed from the experiments carried out, no S. epidermis strains were able to grow in symbiosis with the S. aureus SH1000; or even exceed its size to maintain the majority of the micro-biome. In concurrence with our prediction, the remaining experiments in which the S. epidermis strains were introduced at a much smaller abundance resulted in them attaining negligible growth before falling to 0 in size.

It is clear from these outlined experiments, that all epidermis strains when acting as the resident species were incapable of sustaining an abundance over long periods of time; even despite the ability of one of the strains to inhibit toxins to slow the growth of the invader.

In deriving a suitable set of formula to map the behaviour of 2 populations growing in co-habitation, we shall include variables attributed to the growth of each strain, as well as values defining the level of toxicity they are capable of inhibiting; such that when we simulate these functions we can run them for a wide range of initial values to observe numerous interactions. In doing so, we may potentially uncover ranges of such variables for which resident species can in fact sustain a positive abundance over time against a particularly toxic invading bacterial population, such as S. aureus.

## 2 Mathematical Background

### 2.1 Logistic Growth Model

In this chapter, we will outline the derivation required to produce a suitable function to map the dynamics of 2 competing, spatially homogeneous species. Thus far we have observed the resulting outcomes of competition whereby the involved micro-organisms possess vastly different initial abundances; and from this set out to adapt a model in the form of a system of functions, that when given appropriate values can simulate interactions that end in outcomes other than extinction for the resident population.

However to understand these populations to the extent where we can run more complex simulations, such as to determine numerical population sizes of competing bacteria after discrete iterations, and further deduce their relative stability over time; we must start at the beginning.

Models of growing and decaying populations in mathematics, such as the Verhulst equation and the Richards growth law, can be applied to species both macro and microscopic; and are as well initially derived from the logistic model, which is itself derived from modelling exponential behaviour. To create a linear increase of a population size, would be to multiply it by some constant after every time step:  $P_{n+1} = rP_n$  where we can define  $r$  as the growth rate of that population, and  $n$  as the number of time steps [6]. An exponential increase though, would follow multiplying the growth rate by itself after every time step, such that  $P_n = P_0 r^n$ .

If we differentiate this function of  $P_n = P(t)$ , then separate its variables and integrate, we will yield the curve of solutions  $P(t)$  of the population size, but with added respect to input parameters  $r$ ; calculating a size after any number of iterations for any chosen growth rate and of the bacteria.

The separation of variables for equation  $P(t)$  is as follows:

$$\frac{dP}{dt} = rP \Rightarrow \int \frac{dP}{P} = \int r dt \Rightarrow \ln|P| = rt + C \Rightarrow P = e^C e^{rt} \Rightarrow P = A e^{rt},$$

where  $A$  is a constant.

We can see that when  $t = 0$ , i.e before the first iteration of the function,  $P_0 = A e^{r \cdot 0} = A$ , so this extra constant accounted for during integration acts as a numerical representation of any features of the population that might affect its upcoming growth.

Because of  $A$ 's equality to  $P_0$  - the starting size of the population, one further change can be made to produce the curve of solutions to values to our dynamic differential with respect :

$$\Rightarrow P(t) = P_0 e^{rt}.$$

Re-introducing the starting differential model, we can add one final component to simulate negative growth in both linear and exponential fashion, creating a more completed growth model:

$$\frac{dP}{dt} = rP \left(1 - \frac{P}{K}\right) \quad (1)$$

where  $P$  is the population size, otherwise written as  $N$ , and  $K$  is the largest possible size (capacity) of a population.

As  $P$  divided by  $K \in (0, 1)$ , the gradient of the changing population  $\frac{dP}{dt} \in (0, rP)$ , meaning that the population size will increase when  $rP > \frac{dP}{dt} > 1$  and conversely decrease when  $0 < \frac{dP}{dt} < 1$ .

Through a procedure called non-dimensionalisation, which we will implement here and with more complex models after further study, substitutions of variables are introduced to modify a

function such that it reduces its dimensions - producing the same results but requiring fewer changing inputs.

Equation (1) can be reduced in this way by making the appropriate substitutions, giving us another more simplified model of calculating continuous logistic growth - both increasing and decreasing.

Introducing variable  $u = \frac{P}{K}$ , and expressing  $\frac{du}{dt} = \frac{dP}{dt} \times \frac{1}{K}$  as  $\frac{dP}{dt} = \frac{du}{dt} \times K$  ; we can write equation (1) as

$$\begin{aligned} \frac{dP}{dt} = ruK(1 - u) &\Rightarrow \frac{du}{dT} K = ruK(1 - u) \\ &\Rightarrow \dot{u} = ru(1 - u) \end{aligned} \tag{2}$$

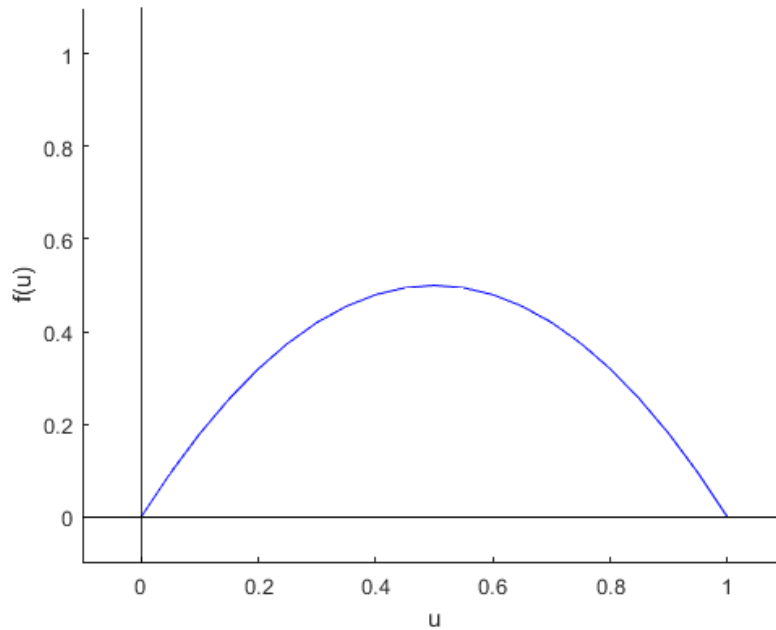


Figure 1: The Logistic Growth Parabola  $\dot{u}$  as a function of  $u$ , where the derivative  $\dot{u} = f(u)$  is plotted against its corresponding point  $u$ , for  $r = 2$ .

This modified differential equation represents a logistic parabolic model of growth, plotted here, and defined as such because of its ability to log exponentially increasing and decreasing population sizes. It is defined for values  $\epsilon (0, 1)$ , where each decimal result produced after a single iteration of the function represents the decimal ratio of the population's percentage abundance:capacity in the inhabited space.

When the growth rate for a population  $r > 1$ , its rate of change in size will increase after one iteration, which is also true for  $0 < r < 1$ , though the closer to 0  $r$  is set to, the slower its increase will be. For this model,  $r < 0$  is undefined as the a population should never voluntarily act to decrease its size in nature, unless affected by its environment or a co-inhabiting species.

To determine the integrated curve of population size solutions to the logistic parabola, currently outputting the rate of change after any given number of iterations; we must perform the same steps as used with equation (1) wherein its variables are separated.

Finite difference approximation is one alternative mathematical technique that can be applied to a differential equation to find its integrated solutions, assuming a constant length of time for the duration between iterations rather than producing a continuous function over every

conceivable time. This method will be applied to later more complex formula whose variables cannot be separated as easily, but for the purposes of the simpler logistic parabola alone we will apply variable separation to derive a set of population size solutions.

As the logistic parabolic model is a rate equation:

$$\dot{u} = \frac{du}{dt} = ru(1-u) \Rightarrow \int \frac{du}{u(1-u)} = \int r dt.$$

Constructing partial fractions on the LHS gives

$$\Rightarrow \int \frac{du}{u(1-u)} = \int \left( \frac{1}{u} - \frac{1}{u-1} \right) du \Rightarrow \int \frac{du}{u(1-u)} = \ln|u| - \ln|u-1| = \ln \left| \frac{u}{u-1} \right|.$$

We now have the overall integral, which can be further modified:

$$\Rightarrow \int \frac{du}{u(1-u)} = \int r dt \Rightarrow \ln \left| \frac{u}{u-1} \right| = rt + C \Rightarrow \left| \frac{u}{u-1} \right| = e^{rt+C} \Rightarrow \frac{u}{u-1} = Ae^{rt}$$

$$\Rightarrow u = Ae^{rt}(u-1) \Rightarrow u = Axe^{rt} - Ae^{rt} \Rightarrow u(1 - Ae^{rt}) = -Ae^{rt}$$

$$u = \frac{Ae^{rt}}{Ae^{rt} - 1} = \frac{1}{1 - \frac{1}{Ae^{rt}}} = \frac{1}{1 - \frac{e^{-rt}}{A}} = \frac{1}{1 - ke^{-rt}},$$

where  $k = 1/A$ .

Setting again the value of our population  $u$  before its first iteration equal to 0, we yield:

$$u_0 = \frac{1}{1 - ke^{-r \cdot 0}} = \frac{1}{1 - k}$$

$$\Rightarrow u_0(1 - k) = 1 \Rightarrow k = \frac{u_0 - 1}{u_0},$$

allowing us to finally complete the curve of solutions to the logistic parabola, constructed by the parameter separation:

$$u(t) = \frac{1}{1 - \frac{u_0 - 1}{u_0} e^{-rt}}. \quad (3)$$

We should expect from this derivation that all initial inputs of relative population size in the occupied space  $\epsilon (0, 1)$ , should all converge to 1 after multiple iterations. This is because the logistic growth parabola has two equilibria which will always remain at the same points despite variable altercations such as a larger growth rate  $r$ .

These coordinates are  $(u, f(u)) = (0, 0), (1, 0)$ , obtained by setting the logistic growth equation differential equal to 0, and rearranging for  $u$  to find the coordinates for such point with no rate of change. This particular flow differential gives us  $0 = ru - ru^2$ , which is satisfied for the fixed points  $u^* = 0, 1$ .

The intuition behind an equilibrium, or fixed point, in a dynamical system, is that it causes local coordinate values to be either more attracted or repelled to change after iteration, than they would otherwise be in any other location.

This therefore offers a region of stability, otherwise known as a basin of attraction, for nearby points to converge to; that is if the equilibrium in question proves after experimentation to significantly decrease the rate of change of approaching size values. For instance in our logistic model, as the growing population starts to reach its size capacity, its rate of change will overtime more gradually decrease to 0 as the species is incapable of growing any further. From our derived fixed points  $(0, 0)$  and  $(1, 0)$ , it is evident that the latter refers to the population's point of capacity where the value of  $\dot{u} = f(u)$  when  $u$  is at 100% size capacity; and the former represents



the point of no change where the species is extinct. The growth rate  $r$  cannot be negative, and always gives a positive rate of change for any value, therefore we should expect that a population growing in isolation, or with intra-specific competition, should diverge from the fixed point  $(0, 0)$ , and thus ultimately converge to its capacity  $(1, 0)$ , regardless of its growth rate.

Choosing say 30%, or 0.3, as the abundance:capacity ratio of a population's initial size before iteration using the logistic parabola; we can surmise that it would take more time to ultimately converge to the point  $(0, 1)$  than a starting size of 0.7 would, if we continue to keep the growth rate at  $r = 2$ .

We can see that from our curved solution function (3) that  $e^{-rt} \rightarrow 0$  as  $t \rightarrow \infty$  and so  $u(t) \rightarrow 1$ , therefore confirming that successive points will eventually converge to 1 for any growth rate. A larger value of  $r$  would produce a smaller value of  $e^{-rt}$ , and thus a smaller denominator of (3) therefore an array of solutions closer to 1 compared with values computed with smaller growth rates.

Figure 2 plots equation (3) - the size values with respect to time  $u(t)$  to the logistic parabola - for a starting size of 30% capacity, but this time with a growth rate of  $r = 1$ . As a result its behaviour illustrates a very slight hesitation to enter its log phase after its initial lag phase with its now lessened ability to increase in size, in contrast with using  $r = 2$ .

Running any simulation of this solution function with a growth rate less than 1 for any initial abundance  $\epsilon \in (0, 1)$ , will produce values converging to capacity but over many more iterations of the function (3).

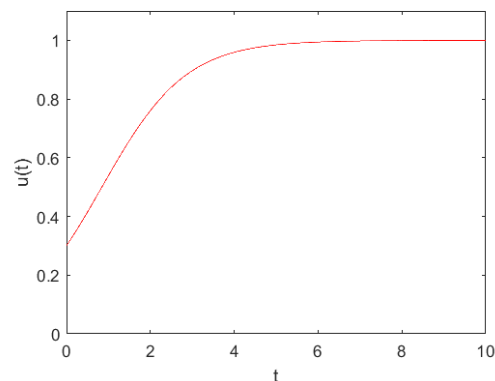


Figure 2: Plot of equation (3) for  $u(t = 0) = 0.3$ ,  $r = 1$ .

With a higher growth rate however, it should take less time for the initial population size to enter its exponential growth phase and converge to the second equilibria where the population reaches capacity.

From this analysis, it is clear that the smaller the growth rate of the species, the more difficulty it has beginning to converge to its capacity; though we cannot state its efficiency in stabilising to new cyclic equilibria appearing at higher growth rates, as with such initial conditions the system quickly becomes more chaotic in its behaviour.

To study the more chaotic outcomes of a population growing in intra-specific competition when given a larger growth rate, further emerging fixed points - still residing at coordinates with 0 rate of change - must be determined. We know from earlier deduction, that there can only be 2 fixed points for this specific parabolic differential:  $u_{1,2}^* = 0, 1$ , though the stable states that arise with populations more adept at growing are not just single coordinates, but a pairing or even a small collection of values that the function repeatedly cycles through when iterating.

These periodic solutions are found by substituting the function into itself to produce a composite formula that calculates values after every second iteration; or every third if the same substitution were to be applied a second time. Such sudden duplications of available equilibria are known as bifurcations - and calculating points of stability in this way has been a grossly powerful tool in approximating the behaviour of quickly growing populations.

For our analysis, we shall continue to decipher only fixed points that remain at the same value after each iteration, for as we now explore the qualitative effects of introducing a secondary species into the same environment, we shall discover that a population can face many more challenges in expanding even before it reaches the capability to display periodic behaviour.

## 2.2 Competition Model

In analysing the logistic growth of a population in intra-specific competition within an environment, we can now introduce new variables to our multi parameter equation (1), defining attributes of a species when in competitive circumstances. Both interacting populations will be modelled by their own, almost identical, differential formula adapted from (1) - computing their rates of change with respect to time.

From these logarithmic equations, we shall introduce further variables to produce a competitive model system - predicting instead inter-specific competition [6] : where 2 different populations interact and grow in the same immediate environment, thus directly affecting each other's rate of change in size.

Defining variables to measure how each of their respective rates of growth are qualitatively affected by each other, will be done such that they qualitatively influence the differential equations governing the behaviour of the 2 populations. These components shall be subtracted from the exponential multiplier  $rN$  of each rate equation, yielding an interference with each population's size when they are increased in magnitude, thus mimicking the effects of the inhibition of toxins:

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1} - a_1 \frac{N_2}{K_1}\right) \quad (4)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2} - a_2 \frac{N_1}{K_2}\right) \quad (5)$$

- where  $N_1$  and  $N_2$  are the sizes of each population respectively;
- $K_1$  and  $K_2$  are their largest possible size (carrying capacity);
- $a_1$  and  $a_2$  are each population's competition coefficients.

The terms  $-a_1 \frac{N_2}{K_1}$  and  $-a_2 \frac{N_1}{K_2}$  have been introduced to give each population equation in the system a component interoperating attributes of its competitor - where the prior is the growth of the first species in direct relation to the second, and the latter is the growth of the second species in presence of the first; as they both include the numerical parameters  $N$  and  $K$  of each others' populations.

Clearly for any size value of either population,  $N/k$  will multiply each competition coefficient  $a_{1,2}$  by a fraction  $\epsilon (0, 1)$ , with larger population sizes yielding values closer to 1 thus having less effect on their population's  $a$  value.

As each component is negative and detracts from its differential as it increases, we can think of  $a_1$  as the qualitative influence of the second population  $N_2$  governed by equation (5) on the first, and  $a_2$  as the competitive influence of  $N_1$  on  $N_2$ . If for example,  $a_1 > a_2$ , the second population  $N_2$  will have the competitive advantage over  $N_1$  as it more significantly interferes with its rate of growth over time.

Coefficients  $a_1$  and  $a_2$  are only defined for values  $\epsilon (0, \infty)$ , as negative values would result in a positive increase in the rate of change of each population, which isn't within the scope of a parameter meant to measure competition imposed, not help provided. Such a scenario is a rare occurrence amongst competing bacterial populations, as compared with the usual competitive outcome for survival, the integration of both populations that enable each other's growth is very unlikely in nature.

This is even evidenced by the observation made by the conductors of the bacterial experiments, simulating the behaviour of *S. epidermis* strains against an invading *SH1000 aureus*; because

of the fact that all of the strains, regardless of their abilities to compete, ultimately suffering an uninterrupted period of decline after interaction therefore clearly received no help from the invading strain.

We must make sure when constructing our system, that the left and right hand sides of each of our equations possess variables with exactly the same physical dimensions. This is more obvious with simpler formula, where it is clear for say distance over time  $d/t$  that it corresponds to the variable speed, equal to the same physical dimension  $d$  over  $t$ .

Observing equations (4) and (5), their left hand sides have a physical dimension of population size  $N$  over  $t$ , therefore their right hand sides must also have this physical dimension overall.

The inside of the bracket of each differential equation is dimensionless, as they both start with the constant 1, and overall equal either a positive or negative constant.

This means that both  $N/K$  and competition coefficient  $-aN/K$  components are also dimensionless, which is evident from the fact that both  $N$  and  $K$  describe the same variable population size, and therefore when divided by each other give a non-dimensional parameter. Values of  $a$  are only pre-determined constants, and not variable parameters, therefore when multiplied by non-dimensional fractions  $N_2/K_1$  and  $N_1/K_2$ , retain that the whole bracket of each equation is dimensionless.

So far, we have that the right hand side of each of (4) and (5) is overall dimensionless, however their left hand sides are equal to  $N/t$ , meaning that the  $rN$  component of each equation must have this dimension.  $N$  already defines the population size dimension, making  $1/t$  the physical dimension that  $r_1$  and  $r_2$  must have.

The importance of the physical dimensions of our system, is that when each equation is later extrapolated when simulated, it will want to include as few variables as possible to allow for a faster computation. The dimensions of each variable within equations (4) and (5) can be substituted by another parameter with the same physical dimensions, to reduce the number of variables in each function. This modification is known mathematically as non-dimensionalization, and is synonymous of how equation (2) in 2.1 was altered to become the logistic growth model (1).

By reducing the number of variables in our system we can simulate its contained equations (4) and (5) more efficiently, because as they stand currently, the differentials of each function will produce values greater than 1 due to the multiplication of  $N_1$  by  $r_1$  and  $N_2$  by  $r_2$ .

Another aim when applying non-dimensionalization, is to ensure that population sizes  $N_1$  and  $N_2$  remain  $\epsilon (0, 1)$  such that they are normalized.

We can first substitute the competition coefficients with parameters that are also dimensionless:

$b_1 = a_1 \frac{K_2}{K_1}$ ,  $b_2 = a_2 \frac{K_1}{K_2}$ , and we can equate further variables to the following parameters:

$$u = \frac{N_1}{K_1}, \quad v = \frac{N_2}{K_2}, \quad T = r_1 t.$$

Further applying non-dimensionalization substitution, we can derive dimensionless equations capable of calculating changing population sizes with fewer required inputs and less memory needed for computation.

Using equation (4), we yield

$$\frac{dN_1}{dt} = r_1 N_1 \left( 1 - \frac{N_1}{K_1} - a_1 \frac{N_2}{K_1} \right)$$

$$\begin{aligned}
&\Rightarrow r_1 K_1 \frac{du}{dT} = ur_1 K_1 (1 - u - a_1 \times \frac{K_2}{K_1} v) \\
&\Rightarrow r_1 K_1 \frac{du}{dT} = ur_1 K_1 (1 - u - b_1 \frac{K_1}{K_2} \times \frac{K_2}{K_1} v) \\
&\Rightarrow \frac{du}{dT} = u(1 - u - b_1 v) = f_1(u, v).
\end{aligned} \tag{6}$$

Similarly, with equation (5), substitution of variables is as follows:

$$\begin{aligned}
&\frac{dN_2}{dt} = r_2 N_2 (1 - \frac{N_2}{K_2} - a_2 \frac{N_1}{K_2}) \\
&\Rightarrow r_1 K_2 \frac{dv}{dT} = vr_2 K_2 (1 - v - a_2 \times \frac{K_1}{K_2} u) \\
&\Rightarrow r_1 K_2 \frac{dv}{dT} = vr_2 K_2 (1 - v - b_2 \frac{K_2}{K_1} \times \frac{K_1}{K_2} u) \\
&\Rightarrow \frac{dv}{dT} = \frac{r_2}{r_1} v(1 - v - b_2 u) = f_2(u, v).
\end{aligned} \tag{7}$$

A system with once 5 variables to an equation: time  $t$ , growth rate  $r$ , population size  $N$ , carrying capacity  $K$  and competition coefficient  $a$ , covering 4 physical dimensions time  $t$  and size  $N$ ; is now only dependent on its size, growth rate and competition substitution  $b$ .

Equations (6) and (7) are dimensionless on either side due to the substitutions made prior, both computing the rate of change of non-dimensional parameter  $T$ ; and both population sizes  $u$  and  $v$  are now normalized as their values now fall between 0 and 1, thus can again represent their abundance:capacity ratio of size at any given time.

Making one final substitution to equation (7):  $r = r_2/r_1$  where we equate dimensionless parameter  $r$  to  $r_2/r_1$  with physical dimension  $1/t \times 1/t$  - cancelling with each other making the parameter non-dimensional; we can now define the growth rate  $r$  by the growth rate of population  $v$  over the growth rate of  $u$ . As  $r$  only appears in equation (7), we have added further simplicity towards the computation of both functions, through reducing their dimensions.

It can now be said with respect to the new reduced formula, that  $b_1$  and  $b_2$  are the competition coefficients of the system, as they still represent the same change to the system - belonging to the same domain  $(0, \infty)$  as their  $a$  parameters that they replaced.

If  $b_1 > b_2$ , population  $v$  will have a greater competitive influence over  $u$  in a competing interaction, and if  $b_2 > b_1$ ,  $u$  will have a competitive advantage in the space.

Clearly, if both populations' coefficient of competition  $b_1$  and  $b_2$  are positive integers, they will each have a significant effect on the other's ability to sustain its size. Yet it does not guarantee that they will grow without interference if both coefficients are set to 0; only that the 2 species would become completely independent of each other.

The previously derived logistic parabola from the reduction of equation (1), though only modelling a dynamic population growing in isolation, still produces a rate of change dependent on its growth rate and initial population size.

Now that we possess a set of reduced formula for computing changing population sizes, we can more easily discretize the functions such that, after a set number of iterations, they produce results for the populations' size over time. We will model all previously mentioned bacterial experiments by calculating the size values for each competing population after every time step, equal to 30 minutes, and conclude for which ranges of the competition coefficients the interactions stay within different categorisations of behavioural outcomes.

## 2.3 Numerical Schemes

Thus far we have derived a system of dimensionless differential equations with respect to 2 size variables, requiring only starting population abundances and competition coefficients as its initial conditions; though we are yet to turn these into functions producing actual answers for the changes in size of each interacting species, dictated by the derived rate of change equations (6) and (7).

As previously discussed in this chapter, the variables of a more simple function compared with our competition model, such as the logistic parabola, can be separated and integrated to calculate exact values of its magnitude. However our further derived model is inter-specific where the influence of each population's opposer is considered; so the equation for the rate of change of each of the competing species in our system no longer has either variable  $u$  or  $v$  as its subject, but both simultaneously making them multi-variable equations.

Defined mathematically, our system has changed from a set of 2 ODEs - ordinary differential equations - to a system of partial differential equations, where derivatives of each equation are calculated by finding all partial derivatives within the function with respect to each variable in turn.

Even though the subject of each of the 2 differential equations (6) and (7) in our system has changed to account for the influence of each other, both functions are still changing with respect to time  $t$ , and are both first order differential equations as they represent the first derivative of change of their respective populations. As they are multi-variable in nature and cannot be as easily separated and subsequently integrated to give solutions as with the single-variable Logistic Model (2), we shall return to the idea of finite difference approximation, where we shall instead compute approximations to the changing sizes of our species over specified finite time intervals.

The Runge-Kutta family of iterative procedures, is a set of different methods that when applied to a function can return its solutions through numerical integration. They operate by first defining a time step value that dictates the constant amount of time difference between the points, at which each next result is calculated.

One of the more basic methods within this set is the forward Euler method, or the explicit Euler method, which derives an iterative function of solutions to an ODE by defining a time interval between calculations, thus discretising the function, and requires an initial starting population size at time  $t = 0$ .

To solve our system of ODEs with the forward Euler method, we first make the following approximation of the first derivative:

$$\frac{dx(t)}{dt} \approx \frac{x(t + \Delta t) - x(t)}{\Delta t} = f(x(t))$$

where  $\Delta t$  is the amount of finite difference between solutions.

Changing the subject of the formula yields

$$x(t + \Delta t) \approx x(t) + \Delta t \times f(x(t)).$$

We can now solve this definition explicitly, computing the solutions to a differential function after a set time interval, and applying the forward method to our system of equations (6) and (7), we derive the following:

$$\begin{aligned}
 u(t + \Delta t) &\approx u(t) + \Delta t \times f(u(t)) \\
 \Rightarrow u(t + \Delta t) &\approx u(t) + \Delta t \times u(t)(1 - u(t) - b_1 v(t)) , \tag{8}
 \end{aligned}$$

$$\begin{aligned}
 v(t + \Delta t) &\approx v(t) + \Delta t \times f(v(t)) \\
 \Rightarrow v(t + \Delta t) &\approx v(t) + \Delta t \times rv(t)(1 - v(t) - b_2 u(t)) . \tag{9}
 \end{aligned}$$

The local error for (8) and (9) - their qualitative difference between their solutions and the exact solutions of the differential equations (6) and (7), is of 2nd order accuracy; small enough that they only deviate from the exact solutions by a difference of the second derivative of the exact functions - proven by finding its Taylor Series expansion.

Throughout our modification of the discrete approximation definition, we have kept the formulas explicit so that we can follow the forward Euler scheme of numerical integration; a more easily implemented form of numerical integration. This was done by keeping all  $u + \Delta u$  or  $v + \Delta v$  terms on separate sides of the formulas to the  $u$  or  $v$  terms, thus ensuring that the iterative functions only have to integrate explicitly rather than implicitly - where we would have to equate the variables of population size and then integrate.

The dimensionless time parameter  $T$  of equations (6) and (7) is represented here by  $t$ , only used for the sake of displaying more general notation, and not representative of the  $t = T/r_1$  used in applying non-dimensionalisation to the inter-specific set of equations. Later, when simulating functions (8) and (9) to determine all size values of each population, we will define  $T$  as the amount of computational time the system runs for; where  $\Delta t$  determines the magnitude of the differential of each reduced equation for every value of  $T$ , thus the total number of times each function is iterated is equal to  $T/\Delta t$ .

What we shall aim to discover from these tests, is in which behavioural domain, in regards to the level of competition of the interacting species, each of a variety of simulations with different initial inputs fall into; defining the subsets of characteristics for which certain species will be able to survive when in cohabitation with certain others.

### 3 Study of Competition Model

It has become apparent from mathematical studies published in the past decade concerned with modelling bacteria, that derived differential systems are only appropriate in certain situations; and fail to capture for example situations where the mediator of the interaction - the occupied micro-biome - is itself changing with time.

Of course, a logistic overview of a changing population merely intends to forecast its size in a space with fixed conditions, and cannot account for the influence of a stochastic environment - one that simultaneously changes with its containing populations, in what it offers in terms of resources and shelter.

Although our inter-specific system of differentials can't predict resulting population size changes in a domain with varying conditions, it is capable of simulating any kind of interaction between 2 species co-inhabiting the same space; including scenarios where both populations converge to a stable state overtime. Our model of microbial interactions only seeks to glean a range of values for which the attributes of each population involved lead to their eventual stabilisation of size, and is independent of the environment in which its simulated populations operate.

Practically, logistic growth formula, such as the Lotka-Volterra equations, have been used to model populations that typically interact in a predator-prey fashion - where one competing species is restricted in how it grows by the more powerful species. They can successfully track the long-term behaviour of populations of animals in their natural habitat on the macro scale, and can as well predict brief microbial interactions of bacteria [7] ; though these results are derived by the change in a population based on how it would grow in intra-specific environmental conditions. If interfering populations are wished to be studied in certain micro-biomes, whether they are under constant change or not, they must each be incubated separately in biomes with the specified conditions, without the presence of any other species, such that their key attributes can first be defined before simulating their behaviour in competition.

With this in mind, we can use our system of equations to predict the outcomes of competing populations when they are programmed by values representing their highest ability to grow when in isolation, thus ensuring that both species will only be influenced by each other and not by any other factors, such as their pertaining environment.

Ideally our populations would want to converge to a single value, excluding periodic stabilisation, after enough time competing such that their survival is guaranteed; and will do so if given the appropriate starting conditions like a satisfactory rate of growth. With our current analysis we can understand whether or not a population will grow, decline or stagnate over time, but we can also further construct from our derivations, a method of producing ranges of values for which the trajectory of a species' changing size starts to point towards a stable state.

Observing the ability of a species to maintain its size in the presence of another growing organism will uncover how adept it is at stabilising against different competitors with a variety of starting inputs.

### 3.1 Analytical Studies

Now that we possess 2 reduced differential equations for 2 competing species, dependent on initial factors like size capacity and competitive influence, we must again deduce the fixed points of the system as we did with our earlier logistic parabola model, to learn where the coordinates that each population could converge to or diverge from are.

From equations (6) and (7), setting  $\frac{du}{dt}$  and  $\frac{dv}{dt} = 0$  will give the population sizes of each competing species at the points where there is no rate of population change:

$$\begin{aligned}
 u(1 - u - b_1v) &= 0 & rv(1 - v - b_2u) &= 0 \\
 \Rightarrow 1 - u - b_1v &= 0 & \Rightarrow 1 - v - b_2u &= 0, \\
 \Rightarrow u &= 1 - b_1v & \Rightarrow v &= 1 - b_2u \\
 u &= 0 & v &= 0.
 \end{aligned}$$

Therefore,  $(u^*, v^*) = (0, 0)$  is a fixed point of the system, where  $u$  and  $v$  represent the array of population sizes of the first and second species respectively.

Substituting  $v = 0$  into  $u = 1 - b_1v$  gives  $(1, 0)$  as a fixed point, and conversely yields  $(0, 1)$  as our third fixed point from substituting  $u = 0$  into  $v = 1 - b_2v$ .

The fourth and final fixed point comes from substituting  $v = 1 - b_2v$  into  $u = 1 - b_1v$ , and the other way round:

$$\begin{aligned}
 u &= 1 - b_1(1 - b_2u) & v &= 1 - b_2(1 - b_1v) \\
 \Rightarrow u &= 1 - b_1 - b_1b_2u & \Rightarrow u &= 1 - b_2 - b_1b_2v \\
 \Rightarrow u(1 - b_1b_2) &= 1 - b_1 & \Rightarrow v(1 - b_1b_2) &= 1 - b_2 \\
 u &= \frac{1 - b_1}{1 - b_1b_2} & v &= \frac{1 - b_2}{1 - b_1b_2}
 \end{aligned}$$

Our four fixed points - every coordinate in the system with a rate of change for either population = 0, are:  $(u^*, v^*) = (0, 0), (1, 0), (0, 1), (\frac{1 - b_1}{1 - b_1b_2}, \frac{1 - b_2}{1 - b_1b_2})$ .

The first fixed point represents an interaction where both species end up extinct, at 0% of their capacity, after many iterations, though the likelihood of this happening should be negligible if even possible compared to the remaining equilibria.  $(1, 0)$  and  $(0, 1)$  define solutions where one population stabilises to its capacity while the other stabilises to extinction; and the final fixed point shows a situation where both species can ultimately sustain themselves at positive percentages between 0 and 1.

For the purposes of categorising each outcome of the involved species based on their growth behaviour when in close proximity of each fixed point, we shall define the following subsets of input value combinations based on their ability to stabilise the rate of change of the population they represent:

A stable node in the mathematical study of 2-dimensional flows, defines a fixed equilibrium point that both competing populations converge towards over time; i.e. where the difference in these values become smaller as the fixed point is approached.

A saddle node refers to an equilibrium, again a point in 2-D space with no rate of change, that is only stable for values of one of the input population variables  $u$  or  $v$  in close proximity to it; and has local sizes of the other input parameter diverging from it at a rate deemed unstable.



For example, if we knew that a certain interaction caused both populations to stabilise to a positive size percentage - our fourth found fixed point, we would also know that the fixed point solution  $(1, 0)$  would be a saddle node as it dictates that only one population can converge to capacity while the other must converge to extinction; finding its local size values diverging from a positive equilibrium.

Finally, we shall define an unstable node as a fixed point that both populations diverge from when in close proximity of its coordinate; where as we inspect points starting at the equilibrium and beyond in both directions of size, their derivatives are likely to be high.

To now computationally observe the growth rate at points local to the fixed coordinates with 0 derivative, we must analyse the partial differentials of equations (6) and (7) with respect to both populations. The Jacobian is used to linearise a 2 variable system of equations such as our derived inter-specific model, by taking partial differentials of rate equations:

$$\mathbf{J}_{u^*,v^*} = \begin{bmatrix} \frac{\partial f_1}{\partial u} & \frac{\partial f_1}{\partial v} \\ \frac{\partial f_2}{\partial u} & \frac{\partial f_2}{\partial v} \end{bmatrix}$$

$$\Rightarrow \mathbf{J}_{u^*,v^*} = \begin{bmatrix} 1 - 2u - b_1v & -b_1u \\ -rb_2v & r(1 - 2v - b_2u) \end{bmatrix}$$

The eigenvalues  $\lambda_i$  of the system at each fixed point represent the magnitude of overall linear change to the system at a specific coordinate of both population's size, and are found for all equilibria of the system into the Jacobian, then calculating the determinant  $\det(J - \lambda I)$ , where  $I$  is the identity matrix, and solving for  $\lambda$ .

To demonstrate for our first equilibrium point:

$$J_{0,0} = \begin{bmatrix} 1 - \lambda & 0 \\ 0 & -\lambda + r \end{bmatrix}$$

$$= (1 - \lambda)(-\lambda + r) = 0.$$

Therefore the roots  $\lambda_{1,2}$ , for  $(u^*, v^*) = (0, 0)$ , are 1 and  $r$ , which will both always be positive as there cannot exist a growth rate less than 0. Positive eigenvalues show that the system at a fixed point has an overall rate of growth changing too quickly to be considered stable; as its derivative is greater than 1 therefore is incapable of quickly lowering to a level of convergence. This confirms our earlier assumption that populations will always want to build up their size - never converging to 0 abundance by choice.

$$J_{1,0} = \begin{bmatrix} -1 & -b_1 \\ 0 & r(1 - b_2) \end{bmatrix}$$

The second equilibrium point  $(1, 0)$  has eigenvalues  $\lambda_1 = -1$ ,  $\lambda_2 = r(1 - b_2)$  therefore whether or not the system is stable at this coordinate - requiring that its eigenvalues be negative - will depend on the value of parameters  $b_2$  and  $r$ .

$$(1, 0) \text{ is } \begin{cases} \text{stable,} & \text{if } b_2 > 1 \\ \text{unstable,} & \text{otherwise} \end{cases}$$

$$J_{0,1} = \begin{bmatrix} 1 - b_1 & 0 \\ -rb_2 & -r \end{bmatrix}$$

Our third fixed point  $(0, 1)$  has eigenvalues  $\lambda_1 = -r$ ,  $\lambda_2 = 1 - b_1$  therefore its stability will change depending on the value of parameters  $b_1$  and  $r$ .

$$(0, 1) \text{ is } \begin{cases} \text{stable,} & \text{if } b_1 > 1 \\ \text{unstable,} & \text{otherwise} \end{cases}$$

$$J\left(\frac{1-b_1}{1-b_1b_2}, \frac{1-b_2}{1-b_1b_2}\right) = \frac{1}{1-b_1b_2} \begin{bmatrix} b_1-1 & b_1(b_1-1) \\ rb_2(b_2-1) & r(b_2-1) \end{bmatrix},$$

Finally, fixed point  $(u^*, v^*) = \left(\frac{1-b_1}{1-b_1b_2}, \frac{1-b_2}{1-b_1b_2}\right)$  as above is substituted into the Jacobian; and after the determinant of the matrix is found - obtaining its characteristic polynomial - the formula can be rearranged to give the eigenvalues of the system at the equilibrium as:

$$\lambda_{1,2} = \frac{(b_1-1) + r(b_2-1) \pm \sqrt{((b_1-1) + r(b_2-1))^2 - 4r(1-b_1b_2)(b_1-1)(b_2-1)}}{2(1-b_1b_2)}$$

Setting this polynomial to be equal to values strictly less than 0, we can find the ranges of  $b_1$  and  $b_2$  for which this equilibrium is stable:

$$0 > \frac{(b_1-1) + r(b_2-1) \pm \sqrt{((b_1-1) + r(b_2-1))^2 - 4r(1-b_1b_2)(b_1-1)(b_2-1)}}{2(1-b_1b_2)}$$

When  $0 \leq b_1 \leq 1$  and  $0 \leq b_2 \leq 1$ , the denominator of the resulting inequality will be a negative value, hence its numerator should expectedly be overall positive to yield negative eigenvalues such that the equilibrium is stable for competition coefficients less than or equal to 1.

However, when both competition coefficients are both set to 1, the LHS and RHS of the polynomial are equal, therefore the point of stability of both populations is the same as there is no qualitative competition to affect their rate of change; thus the interacting bacteria stabilise to the same value, and as a result the fourth fixed point is neither stable nor unstable.

This inequality should be untrue for at least 1 of the 2 eigenvalues at the fixed point, for interactions where both  $b_{1,2} > 1$ ; and for situations where

$0 \leq b_1 \leq 1$  while  $b_2 > 1$ , and vice versa. The reason being is that in any interaction using these coefficients will ultimately lead to the maximum possible growth of one and the extinction of the other, thus the population with the competitive advantage has a stable growth rate as it reaches its capacity while the weaker species is more unstable hence divergent around positive sizes as it converges to 0 abundance.

Choosing for example  $b_1 = 0.9$  and  $b_2 = 1.1$  to substitute into the polynomial derived from the determinant of the Jacobian at this fixed point, we have eigenvalues:

$$\begin{aligned} \lambda_{1,2} &= \frac{(-0.1) + r(0.1) \pm \sqrt{((-0.1) + r(0.1))^2 - 4r(0.01)(-0.1)(0.1)}}{0.02} \\ \Rightarrow \lambda_{1,2} &= \frac{-0.1 + 0.1r \pm \sqrt{(-0.1 + 0.1r)^2 + 4r \times 10^{-4}}}{0.02}; \end{aligned}$$

and we see that when  $r = 1$ , the terms outside of the square root sum to 0, leaving the stability of each eigenvalue to be decided by what remains of the numerator.

Therefore the fourth and final fixed point at these competition coefficient values make a saddle node, with one stable and one unstable eigenvalue, which is to say in context, that population  $u$  with the competitive advantage is somewhat stable around size values it would otherwise converge to if both  $0 \leq b_{1,2} \leq 1$ , as it stabilises to its capacity; while  $v$  diverges from positive size values as it converges to extinction.

Generally speaking we can say that the final fixed point of the system is: completely stable when competition coefficients are between 0 and 1, completely unstable when both coefficients are greater than 1, redundant to observe if both are equal to 1, and partially stable - possessing

a positive and a negative eigenvalue - for capacity against extinction reactions where one coefficient is greater than 1 whilst the other resides between 0 and 1.

The characteristic polynomial of the fourth equilibrium of the system is also dependent on  $r$ , though in the case of the extinction interaction illustrated by the above inequality, there is no value of  $r$  that will make  $\lambda_1$  negative and thus allow both populations to stabilise at positive values, due to the magnitude of the 4 positive terms on the numerator when expanded compared with the negative term.

A huge increase in the growth rate can lead to periods of cyclic stabilisation around an array of sizes, though as observed with the fourth equilibrium acting as a saddle node when both of its eigenvalues weren't otherwise stable, no amount of periodicity will result in both of its  $\lambda$  being unstable. Even though populations will not be stabilising to the exact values they would be if competing with  $0 \leq b_{1,2} \ll 1$ , their rates of change when cycling through values can still be stable if  $\leq 1$ , therefore the resulting stability of the fourth fixed point tells us that one of the interacting populations will always be periodic with stable rates of change between values, while the rate that the other cycles between values is unstable with rates of change  $> 1$ .

Clearly, from the way we constructed the inter-specific system of equations that we then linearised, there are no whole or decimal values greater than 1 for both containing coefficients  $b_1$  and  $b_2$  that give 2 negative  $\lambda$ , leading to the stabilisation of both populations.

As in accordance with the simulations run in the 2019 published journal on toxin-mediated competition [4], using a very similar multi-variable model of differentials, the diagram below defines each equilibrium of the system as a possible interaction outcome that both populations converge to over time; in which at least one participant's ultimate stabilisation to a non 0 size, i.e. first fixed point (0,0) is guaranteed. These domains describing different outcomes in stability are only dependent on  $b_1$  and  $b_2$ :

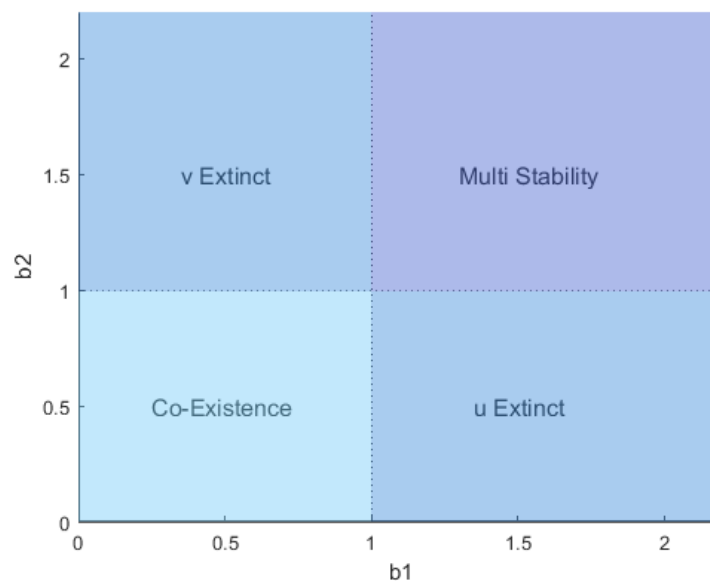


Figure 3: Discrete categorisations of the stability of equilibria, dependent on competition coefficients  $b_1$  and  $b_2$ .

As discussed in Chapter 2, an interaction of 2 species undergoing significant levels of interference in their respective growth rates, when inhabiting the same space, can be classified as competitive; though with the new information that the size values at which they ultimately converge towards are separated by strict ranges of competition coefficients  $b_1$  and  $b_2$  that define such qualitative obtrusion, we can now identify sub-categorisations of competitive situations.

For interactions with  $0 \leq b_1 \leq 1$  and  $b_2 > 1$ , population  $u$  grows with less competitive influence from  $v$  than it inflicts on  $u$  and so converges to its capacity, while  $v$  is too heavily affected by the competition to maintain abundance, and converges to extinction. This outcome describes the ranges of competition coefficients for which the second fixed point  $(1, 0)$  is a stable node. Likewise, the category named *u Extinct*, refers to outcomes in which the third equilibrium point  $(0, 1)$  possesses a stable eigenvalue for each population and is hence a stable node; as in these situations  $0 \leq b_2 \leq 1$  and  $b_1 > 1$ , therefore the first population  $u$  ultimately goes extinct as it experiences a much greater growth rate interference in comparison to  $v$ .

Competitive interactions in which both  $b_{1,2} > 1$  result in an increased interaction time before each population stabilises; however from our substitution of competition coefficients at values resulting in a convergence to both capacity and extinction into the characteristic polynomial of the fourth equilibrium point, we could see that it produced a positive and a negative eigenvalue: therefore  $(1, 0)$  is a stable node when  $b_2 > b_1$ , and  $(0, 1)$  is completely stable for  $b_1 > b_2$ .

These interactions shall be classified under *Multi Stability*, as although each population ultimately stabilises to either capacity or extinction at values of  $b_1$  and  $b_2$  both greater than 1, they will still each experience brief moments of stability as their sizes fluctuate during their interaction. Many local coordinates to these points of stability will be likely to have a rate of change  $< |1|$ , though will not decrease to 0 for more than a few iterations if any; only ultimately stabilising at one of the 2 possible equilibria resulting in their convergence to capacity of extinction.

If both communities of bacteria continue to survive and ultimately both stabilise at positive sizes, they shall be deemed in our stabilisation categorisation as interacting in *co-existence*; which would require a minimal competitive influence such that  $0 \leq b_{1,2} \leq 1$ , as evidenced from our derived ranges for which the fourth equilibrium where both populations can stabilise is itself stable.

For competition coefficient values such as these, the fourth equilibrium point of the system will be a stable node, while  $(1, 0)$  and  $(0, 1)$  will be saddle nodes as neither coordinate goes extinct, and the fixed point  $(0, 0)$  as always will be unstable.

All together we have derived ranges of parameters  $b_1$  and  $b_2$  of our inter-specific system of population size equations, for which its fixed points become stable for local values to converge towards; concluding as a result that changes in input variable  $r$ , lower than a threshold value causing periodic equilibria to emerge, only affect the longevity of interaction and not the sizes that each population will stabilise at.

This leaves us with one final set of input parameters with respect to the dimensionless rate equations (6) and (7): the starting size of each population  $u$  and  $v$ , for us to change and observe the resulting behavioural outcomes. In order to validate our conclusions made as to the magnitude of competing population sizes when they reach fixed and stable points, we will first simulate our models with both involved parties using our adapted iterative equations (8) and (9), being equal in their starting population size, such that neither party begin colonising with a spacial advantage, allowing the set of functions to operate as estimated.

Before we iterate each formula over time we can observe each fixed point's expected stability for different input values to gain an understanding of when populations should saturate in size from the values we initially assign to them.

To illustrate the behaviour of nearby coordinate values to a fixed point, we shall plot the directional derivatives at every close location to all possible equilibria  $u^*$  and  $v^*$  of populations  $u$  and  $v$ . We can express the output values of our differential equations (8) and (9) at every value  $u$  and  $v$  could be, as an arrow defined by 2 parameters: the magnitude of difference it will change after iteration due to its distance from nearby equilibria illustrated by its length, and its direction assigned by the 2-dimensional value of the partial derivatives of the system at that point - again dependent on its position in relation to stable and unstable equilibria.

In mathematical nomenclature, the magnitude of change of a differential derivative after iteration is known as its *divergence*, and its change in rotation in a 2-D space is referred to as its *curl*.

For example if a particular size percentage of a population's capacity is in close range of the first iteration its rate of change is likely to be high due to the repulsion from fixed point  $(0, 0)$ ; therefore its arrow will be longer in size and point away from this equilibrium.

If a size is close to the saturation point of a competing species, the rate of change of the equation simulating its behaviour will be low relative to other points as it is converging to either its capacity at a saddle node equilibrium, or a positive decimal value of its capacity towards the coexistence equilibrium.

In order to determine the curl of the rate of change of a size coordinate of equations (6) and (7) governing the behaviour of populations  $u$  and  $v$  respectively, we must find the partial differential at such values of each function: with respect to  $u$  for the first population and  $v$  for the second, as given by

$$\frac{\partial f_1}{\partial u} = 1 - 2u - b_1v, \quad \frac{\partial f_2}{\partial v} = r(1 - 2v - b_2u).$$

The divergence of each point's rate of change was not successfully computed by MATLAB as it was unable to determine varying lengths of each directional derivative, as displayed by arrows, given 2 separate input functions  $f_1(u, v)$  and  $f_2(u, v)$ . This meant that it could only determine a directional field of rate changes, where only the rotational attraction of each point towards equilibria was expressed and not its rate of convergence towards them. The *Slope and Directional Fields* program [8] has instead been used to calculate the directional field of all directional derivatives but to a normalised length whereby their sizes are identical, as MATLAB also fails to compute the curl as well as the divergence of all possible coordinates when given certain values of  $b_1$  and  $b_2$ .

Arrows have been artificially shortened once computed, turning the directional field calculated by the Directional Fields program [8] into a vector field, where the divergence of each coordinate is also displayed; and darker colour arrows have been added to the axes to highlight the direction of rate of change towards equilibria along them in the 2-D plot of all  $u$  and  $v$  coordinates.

Adding nullclines to our plot of directional derivatives in a 2-D plane of  $v$  against  $u$ , we derive a phase portrait of the system dependent on the initial conditions of each population. These represent the linear tangents to all equilibria, derived by setting our differentials to 0 and obtaining the resulting equations:

$$\begin{aligned} \frac{du}{dt} = u(1 - u - b_1v) = 0 & & \frac{dv}{dt} = rv(1 - v - b_2u) = 0 \\ \Rightarrow 1 - u - b_1v = 0 \text{ and } u = 0 & & \Rightarrow 1 - v - b_2u = 0 \text{ and } v = 0 \end{aligned}$$

All points of intersection of these 4 nullclines are the coordinates of all 4 equilibria of the system, circled in the phase portraits, where the the equilibrium not resting on either the  $u$  or  $v$  axis is the fourth fixed point - only completely stable for competition coefficients less than 1.

The directional field used for each phase portrait, as computed by the Directional Fields program [8], plots an arrow at all possible size values of each population - calculated using the same finite approximation as was used in the derivation of (8) and (9), with the same time step  $\Delta t = 0.1$  - where they represent the divergence and curl of the rate of change of  $u$  and  $v$  at each corresponding size:

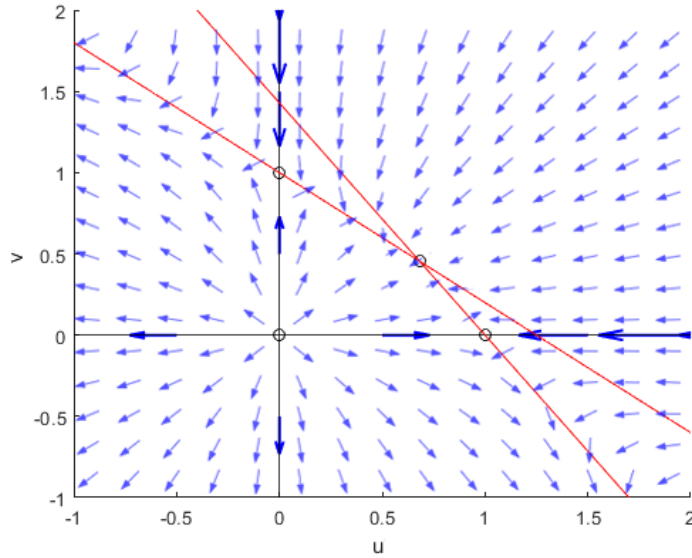


Figure 4: Phase Portrait of the system of equations (6) and (7) governing populations  $u$  and  $v$ , and calculated using equations (8) and (9); along with nullclines in red. The functions were run for  $r = 1, b_1 = 0.7, b_2 = 0.8$ , therefore simulate a coexistence interaction.

For a coexisting outcome that ends in the saturation of both species at sizes greater than 0,  $b_{1,2} < 0$ ,

and the fourth equilibrium point  $(u^*, v^*) = \left( \frac{1 - b_1}{1 - b_1 b_2}, \frac{1 - b_2}{1 - b_1 b_2} \right)$ , circled in both figures, is stable.

Local arrows to this equilibrium point towards it, and are shorter due to their successive rates of change decreasing as they converge towards the fixed point. All remaining equilibria, also circled, are unstable, as when the involved populations possess coefficients of competitions between 0 and 1 they are capable of not ultimately stabilising to extinction. We are only considering coordinates of  $u$  and  $v$  between 0 and 1, as this is the decimal percentage of their capacity; however it makes sense that derivatives of the function where  $u$  and  $v$  inputs are greater than 1 point towards their local equilibria, as they have no capacity to diverge and thus grow to exceed their population's maximum size. Likewise derivatives at negative values diverge from  $(0, 0)$  as they lack the capability to regrow in size, being non-existent coordinates.

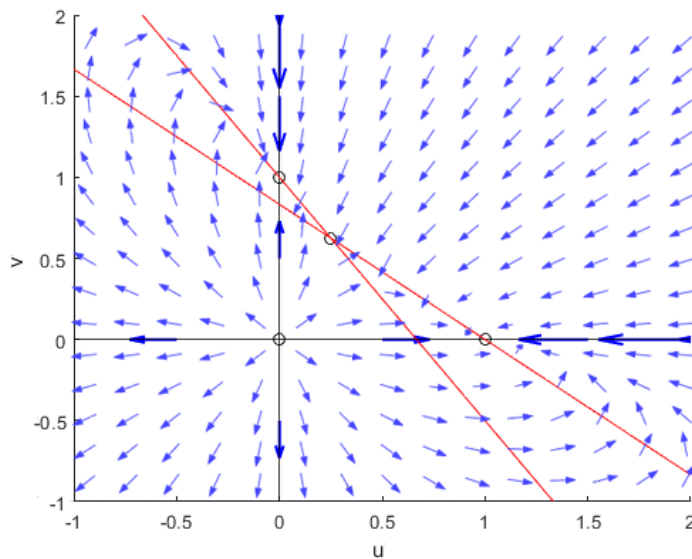


Figure 5: Phase Portrait of the system of (6) and (7), calculated using (8) and (9); also including nullclines. in red. For Figure 5, the system was run for  $r = 1, b_1 = 1.2, b_2 = 1.5$ , so illustrate a multi-stability interaction.

This phase portrait represents a multi-stability interaction, where both  $(u^*, v^*) = (0, 0)$  and the coexistence equilibrium  $(u^*, v^*) = \left(\frac{1 - b_1}{1 - b_1 b_2}, \frac{1 - b_2}{1 - b_1 b_2}\right)$  are unstable; the former always being so, and the latter because  $b_{1,2} > 1$ . Local arrows to these fixed points do not converge - pointing past the coexistence equilibrium and away from  $(0, 0)$ .

The directional derivatives inside the vector field local to the 2 remaining fixed points residing on the  $u$  and  $v$  axes, do in fact converge towards them; as the second population will likely go extinct because of its greater competition coefficient therefore making the equilibria  $(1, 0)$  and  $(0, 1)$  viable outcomes.

Arrows around fixed point  $(1, 0)$  are shorter than that of those surrounding  $(0, 1)$ , as  $b_2 > b_1$  so it is more likely that the second population will saturate at 0 abundance than the first; therefore nearby coordinates to  $(1, 0)$  will more rapidly converge.

The above phase portraits each had growth rate  $r$  set to 1, thus to ensure that the reduced rate equations (6) and (7) could run at a default setting - where neither population had an advantage in growth capability with respect to their own in isolation when their growth rates were also equal to 1.

Theoretically, a larger growth rate would cause a species to saturate to a stable state using fewer iterations, as we know from the eigenvalues of the system that no value of  $r$  can change the stability of any of the 4 equilibria therefore can only affect the time in which the populations will converge to the domain decided by  $b_1$  and  $b_2$ .

However, there could exist a pairing of initial sizes that leads to a coexistence of 2 interacting populations in significant competition with each other - having  $b$  coefficients greater than 1.

From the ranges derived from the Jacobian of rate equations (6) and (7) at each of their equilibria, for which each of their eigenvalues held stability, none were dependent on initial input sizes of each population; however the specification of these parameters is required when outputting the functions (8) and (9) giving their integrated solutions. We will run a variety of simulations in the next section of using functions (8) and (9) to produce a curve of integrated solutions: first observing stabilisation, or saturation values, with different competition coefficients and growth rates while keeping the starting size of each population constant and equal to each other; then seeing if there is any leniency in our outcome categorisations when the initial sizes of each population are changed.

## 3.2 Numerical Solutions

We have thus far defined multiple behavioural categorisations according to the derivatives of a reduced 2-variable system of equations, resembling an inter-specific model of competition: simulating 2 competing species of bacteria given that their attributes can be successfully paralleled to our specified inputs like their rate of growth and qualitative competitiveness.

To validate our predictions made based on input value ranges, we shall run a variety of tests in MATLAB - using equations (8) and (9) derived from finite difference approximation to gather the changing population sizes of each species - and display the trends in the data produced.

We will simulate our size solution equations derived from the inter-specific model for competition coefficients  $b_1$  and  $b_2$  such that each of the defined outcomes of stability occur: coexistence, and competition of different longevities leading to extinction versus capacity. We will set our growth rate  $r$  input variable, for our first set of computations, equal to 1 - where if in isolation, each species would grow at its minimum rate capable.

As well as with  $r$  we need to set the initial percentage abundance values of each population in the space, which for this first analysis, will equal  $u(0) = v(0) = 0.5$ ; where both species begin competition at half their size capacity ensuring that the only significant change to each population's size will be their competition coefficients.

Each function shall be iterated between 500 and 1500 units of time  $T$  depending on how long it takes for the populations to stabilise - where our  $\Delta t = 0.1$ , such that they are computed 10 times between each whole value of computational time  $T$ . This is because our time step  $\Delta t$  multiplies the differential of each function by 0.1 for every iteration - as shown algebraically in our reduced iterative formula (8) and (9); and  $50 < T < 150$  units of time was chosen as this is the point at which there are clearly identifiable saturation values for all interactions.

A time step less than 0.1 would iterate the function more than 10 times between each whole integer value of  $T$ , and would thus produce solutions with even smaller successive differences - potentially too minute to even display population size changes graphically. Each iteration of the equations represents one unit of discrete time  $t$  such that both populations can be expressed as functions with respect to time:  $u(t)$  and  $v(t)$ .

As predicted for a coexistence interaction where  $0 \leq b_{1,2} \leq 1$ , both populations saturate in size to a positive abundance after enough time. Here we can see that population  $u$  stabilises at approximately 0.3 and  $v$  comes to a stop at roughly 0.8; the red curve illustrating the behaviour of  $u$  resting at a lower value due to its greater competition coefficient  $b_1$ .

As the drop in abundance of  $u$  from 0.5 is significant there may be a lower initial size of  $u$  that leads to its convergence to extinction; and conversely a higher starting size of  $v$  that could lead to its stabilisation to capacity due to its increase. Either of these situations would cause the coexistence equilibrium to become unstable, and fixed point  $(u^*, v^*) = (0, 1)$  to become stable as a result.

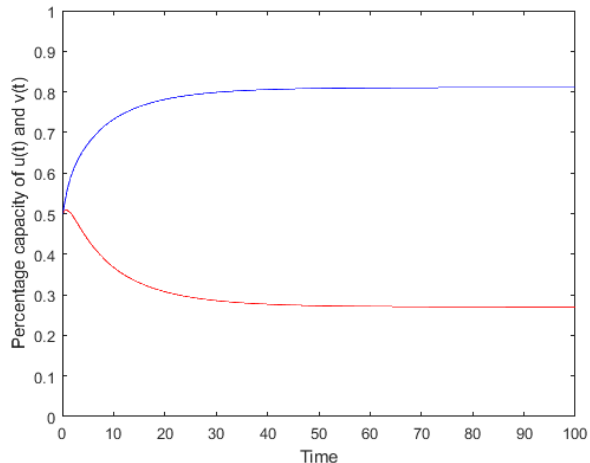


Figure 6: Coexistence interaction of system of equations (6) and (7), and calculated by solution equations (8) and (9) governing populations  $u$  and  $v$  respectively. Population  $u$  is illustrated in red, while  $v$  is in blue, and the equations were run for  $T = 100$  units of time with  $\Delta t = 0.1$ . The system was run for:  $b_1 = 0.9$ ,  $b_2 = 0.7$ ,  $r_1 = 1$  and  $r_2 = 1$  meaning  $r = 1$ , and  $(u(t = 0), v(t = 0)) = (0.5, 0.5)$ .

As it is clear however from this simulation that the coexistence equilibrium has 2 stable eigenvalues, as both populations converge to a positive size; we can substitute the competition coefficient values  $b_1 = 0.9$  and  $b_2 = 0.7$  into the derived formula dictating their exact point of convergence:  $(u^*, v^*) = \left( \frac{1 - b_1}{1 - b_1 b_2}, \frac{1 - b_2}{1 - b_1 b_2} \right)$ , and see how accurate our approximated functions (8) and (9) are in comparison.

$$(u^*, v^*) = \left( \frac{1 - 0.9}{1 - (0.9 \times 0.7)}, \frac{1 - 0.7}{1 - (0.9 \times 0.7)} \right) = \frac{0.1}{0.37}, \frac{0.3}{0.37} = 0.2703, 0.8108$$

correct to 4 decimal places, which is validated in Figure 6 by our simulated function (8) calculating the ultimate convergence of population  $u$  to 27% capacity, and equation (9) as well accurately computing the stabilisation of population  $v$  at 81% of its capacity.

After observing a coexistence interaction between 2 co-inhabiting populations of bacteria, we shall now change the input parameters  $b_1$  and  $b_2$  again, while keeping  $r$  and  $(u(t = 0), v(t = 0))$  at the same values; to produce a simulation with more significant competition, such that equilibria  $(1, 0)$  or  $(0, 1)$  will become stable.



Both Figures 7 and 8 illustrate such interactions, each with different competition coefficients such that coexistence is unstable, where one population instead stabilises to its capacity whilst the other goes extinct.

The former simulates a situation where  $b_1 > 1$  while  $0 \leq b_2 \ll 1$  meaning  $v$  reaches capacity while  $u$  converges to extinction; and the latter runs the reverse scenario where  $b_2 > b_1$  such that  $u$  has the competitive advantage, allowing it to ultimately take complete control of the environment - also disallowing its opposer to sustain a positive size due to the level of interference that  $v$  inflicts upon its rate of change.

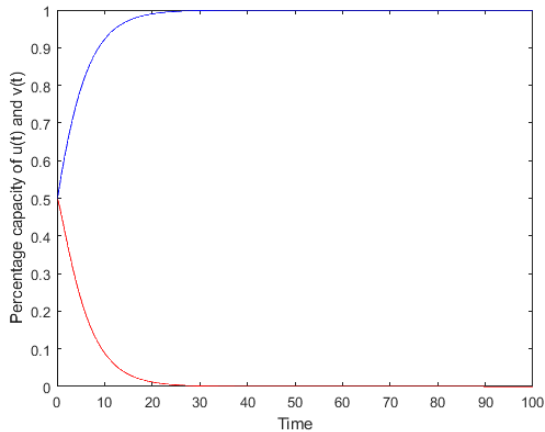


Figure 7: Extinction of population  $u(t)$  within system of equations (6) and (7), calculated by solution equations (8) and (9) governing populations  $u$  and  $v$  respectively. Population  $u$  is illustrated in red, while  $v$  is in blue, and both were simulated for  $T = 100$ , with  $\Delta t = 0.1$ . The system was run for:  $b_1 = 1.2, b_2 = 0.7, r = 1$  and  $(u(t = 0), v(t = 0)) = (0.5, 0.5)$ .

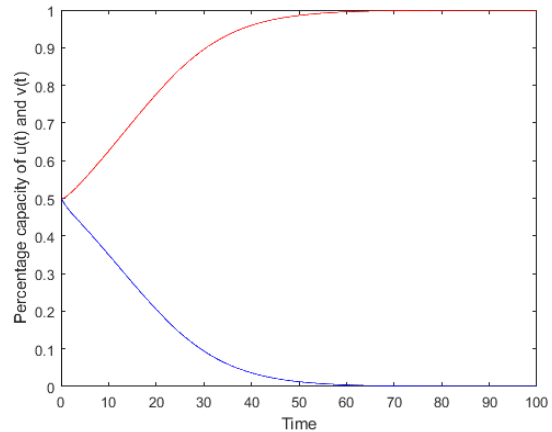


Figure 8: Extinction of population  $v(t)$  within system of equations (6) and (7), calculated by solution equations (8) and (9) determining population sizes for  $u$  and  $v$ . Population  $u$  is illustrated in red, while  $v$  is in blue, and  $T = 100$ , with  $\Delta t$  set to 0.1. The system has values:  $b_1 = 1.0, b_2 = 1.1, r = 1$  and  $(u(t = 0), v(t = 0)) = (0.5, 0.5)$ .

Figure 7 shows both populations saturating to the fixed point  $(0, 1)$  after approximately a quarter of the allowed iterations of each function, whereas Figure 8 displays an interaction involving more competition before ultimate stabilisation to fixed point  $(1, 0)$ . The first of the 2 figures has competition coefficient values such that  $b_1 > b_2$ , therefore equation (8) containing  $b_1$  undergoes more competitive influence from population  $v$  governed by equation (9), than it itself inflicts on the rate of change of  $v$ ; causing  $u$  to converge to extinction as a result.

Figure 7 illustrates a simulation of the two equations for  $b_1 < b_2$ , thus population  $u$ , illustrated again in red, instead converges to capacity while  $v$  goes extinct after iteration.

From our earlier substitution of competition coefficients with values also pertaining to the ranges declared here for convergences to extinction and capacity to occur, into the characteristic polynomial of the coexistence equilibrium; we saw that it produced a positive and a negative eigenvalue  $\lambda$  as a result, making it a saddle node under these conditions.

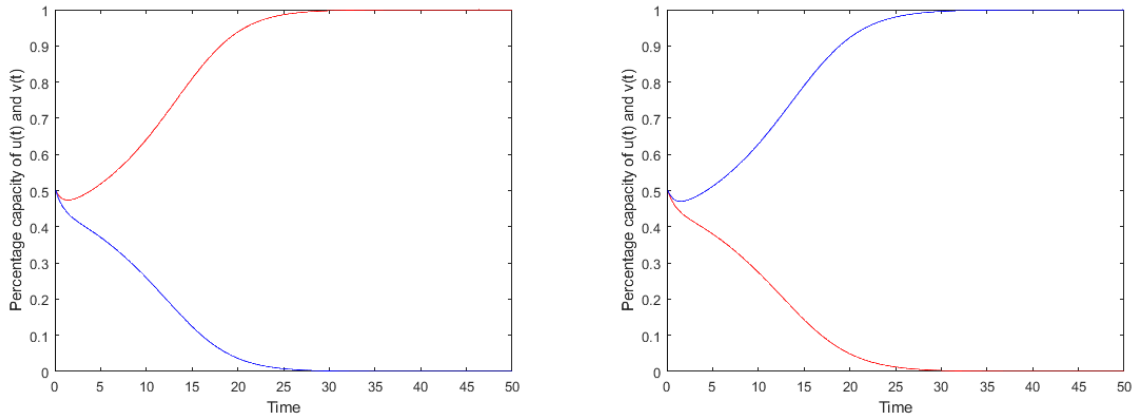
The qualitative difference between the values chosen for  $b_1$  and  $b_2$  in Figure 7, is significantly larger compared with the data used for Figure 8; therefore the competition imposed upon population  $u$  with less ability to compete is more devastating than that inflicted on  $v$  in Figure 7, causing it to converge to extinction in fewer iterations.

The lesser difference in competition coefficients used for the simulation shown by Figure 8, means that each population possesses a more similar  $b_1$  competitive ability, therefore can sustain their initial abundances in the environment for longer until population  $v$ , suffering the most competitive influence, can no longer compete to the same extent. As illustrated by the diagram, the period of divergence of both parties from their initial sizes before their gradual stabilisation

is extended compared with Figure 7, because of this more minute difference in competition coefficients.

The ranges of initial inputs for which each fixed point is stable determined from the Jacobian of the system, state that populations stabilise to fixed point  $(1, 0)$  if  $b_2 > 1$  and to  $(0, 1)$  if  $b_1 > 1$ ; which we now understand is the case for competitive interactions possessing remaining coefficient values  $\epsilon(0, 1)$ . Though by observing the same ranges for these 2 equilibria we see that each one is only dependent on the magnitude of competition inflicted upon the population it will cause to converge to extinction. In other words, the stability of fixed point  $(1, 0)$  is only changed by the value of coefficient  $b_2$ , such that if it is greater than 1 at least one of its eigenvalues will be negative and therefore stable; which is also true of the stability of  $(0, 1)$  being dependent on  $b_1$ .

For the sake of observing the the resulting interactions under all possible ranges of competition coefficients  $b_1$  and  $b_2$ , we shall also analyse the effects of setting both  $b_{1,2} > 1$ ; though we are aware that in this case, either fixed point  $(1, 0)$  or  $(0, 1)$  will be stable, and the coexistence equilibrium will still be a saddle node in either scenario.



Figures 9 and 10 (from left to right): Multi-Stability interaction produced by system of equations (6) and (7), calculated by solution equations (8) and (9) governing populations  $u$  and  $v$  respectively. Population  $u$  is illustrated in red, while  $v$  is in blue, and both were simulated for  $T = 50$ , with  $\Delta t = 0.1$ . For Figure 9 the system was run for:  $b_1 = 1.2, b_2 = 1.3, r = 1$  and  $(u(t = 0), v(t = 0)) = (0.5, 0.5)$ . Figure 10 has the values:  $b_1 = 1.3, b_2 = 1.2, r = 1$  and  $(u(t = 0), v(t = 0)) = (0.5, 0.5)$ .

As expected, both Figures 9 and 10, running simulations with both competition coefficients greater than 1, again illustrate that under these conditions, one of our iterative equations (8) and (9) will produce solutions converging to 0 whilst the other converges to 1.

The evidence that the coexistence equilibrium is still a saddle node for competition coefficients greater than 1, is also established by substituting  $b_1$  and  $b_2$  with such values into its characteristic polynomial - giving 1 positive and 1 negative eigenvalue as it also does for coefficient pairings where one  $\epsilon(0, 1)$  while the other  $\epsilon[1, \infty)$ .

It has been identified by the ranges of stability for each of  $(1, 0)$  and  $(0, 1)$ , that both fixed points possess an eigenvalue that is always stable for all possible initial conditions, while the stability of their remaining  $\lambda$  is dependent on the competitive imposition on the weaker population.

Speaking literally,  $(1, 0)$  is stable if  $b_2$ , belonging to equation (9) governing population  $v$ , is greater than 1; and  $(0, 1)$  is a stable node if  $b_1$ , found within equation (8) calculating  $u$ , is also more than 1. In the simulations displayed by Figures 9 and 10,  $b_1$  and  $b_2$  are  $> 1$ , meaning that both  $(1, 0)$  and  $(0, 1)$  will yield 2 negative eigenvalues and therefore both be stable.

Although both fixed points  $(1, 0)$  and  $(0, 1)$  are stable for any simulation run with  $b_1$  and  $b_2$  greater than 1, one of them will always have eigenvalues with much greater magnitude, therefore possessing size values with much lower rates of change in its basin of attraction. As well as this,

the exact values of the chosen competition coefficients ultimately decide which equilibrium is the most stable, with equations (8) and (9) always correctly computing which of the populations should grow and which should decline. Therefore, only 1 of the 2 equilibria will dictate the overall outcome of a competitive interaction with  $b_1$  and  $b_2$  greater than 1.

Taking Figure 9 for example, population  $u$  ultimately converges to its capacity, as  $b_1 < b_2$ , therefore it possesses the competitive advantage. However, as the competition inflicted upon  $u$  by population  $u$  is as well greater than 1, its magnitude of competitive imposition is great enough that initially, equation (8) produces solutions with rates of change less convergent to its capacity as would be the case in Figure 8.

Such prolonged competition before saturation is also the case in Figure 10, where population  $v$  possesses the smaller competition coefficient  $b_2 = 1.2$  and thus converges to its capacity, though is significantly slowed in its period of growth by the level of interference imposed by population  $u$ , so also shows a small convergence towards extinction within the first 25 iterations before ultimately winning out - meaning that the fixed point requiring its extinction can also be classified as stable.

Referring back to our discrete categorisations of stability made in Figure 3, we can say that interactions with  $b_1$  and  $b_2$  greater than 1 will fall into the Multi-Stability domain, as they will always cause the rate of change of both populations to fluctuate in the domain  $\epsilon [-1, 1]$  for a certain number of iterations before ultimate divergence from each other in size; therefore each population manages to sustain a brief moment of stability regardless of the size value of their ultimate saturation. Despite the fact that we have defined our competition coefficients up to infinity, any values greater than 3 will not be tested by our model for the reason that they will produce differential values too steep to graphically observe any competition before saturation; however their difference from each other is important to observe.

The longevity of significant interference of each population's rate of growth before diverging to their point of saturation, is determined by the difference between  $b_1$  and  $b_2$ : as the smaller it is, the more similar the results calculated by equations (8) and (9) will be. If competition coefficients are equal, as well as each population's starting size, then they will each possess no rate of change and hence remain at their starting sizes; though there could exist an optimal pairing of competition coefficients, starting sizes and growth rates that would allow for a maximum stabilisation time of both parties close to their starting sizes, before diverging to their values of saturation.

We have already determined ranges of initial inputs  $b_1$ ,  $b_2$  and  $r$  for which a system of 2 interacting bacterial populations will mutually stabilise after multiple iterations: both to values of size greater than 0 and up to 100% of their respective capacities if they coexist with minimal competitive influence; as well calculating situations where more significant competition causes the stronger population to always ultimately stabilise to its capacity, giving the weaker party no grounds to sustain itself thus converging to extinction.

As the linearisation of our system of equations (6) and (7) at all equilibria qualitatively showed that their ability to stabilise local points is dependent only on initial conditions  $b_1$  and  $b_2$ , any combination of remaining initial inputs only seek to change the time in which populations will converge to their pre-determined saturation levels; though if both competition coefficients are less than 1 and each party can saturate at a size other than 0 or 1 they could influence the value between them in which they do stabilise at.

For all simulations modelled so far with equations (8) and (9), we have set both growth rates  $r_1$  and  $r_2$  to 1, which after non-dimensionalisation was applied is now encoded by iterative equation (9) as  $r = r_2/r_1$ , meaning that  $r = 1$ . We have as well set the starting population sizes to 50% of their maximum size, predictably causing both populations to converge to their respective points of stabilisation within the same number of iterations. This could be because our reduced iterative equations, before and after non-dimensionalisation was applied, being identical functions calculating the exact same rate of change for each interacting bacterial

population; and are both only altered by their variable imposition of growth - either  $b_1$  or  $b_2$  - by their opposer, and their own growth abilities  $r_1$  and  $r_2$ , as well as their starting sizes in the space. However, running the same simulations but with pairings of starting sizes and growth rates for each population that are not equal to each other, could yield more asymmetric values of rate of change from equations (8) and (9).

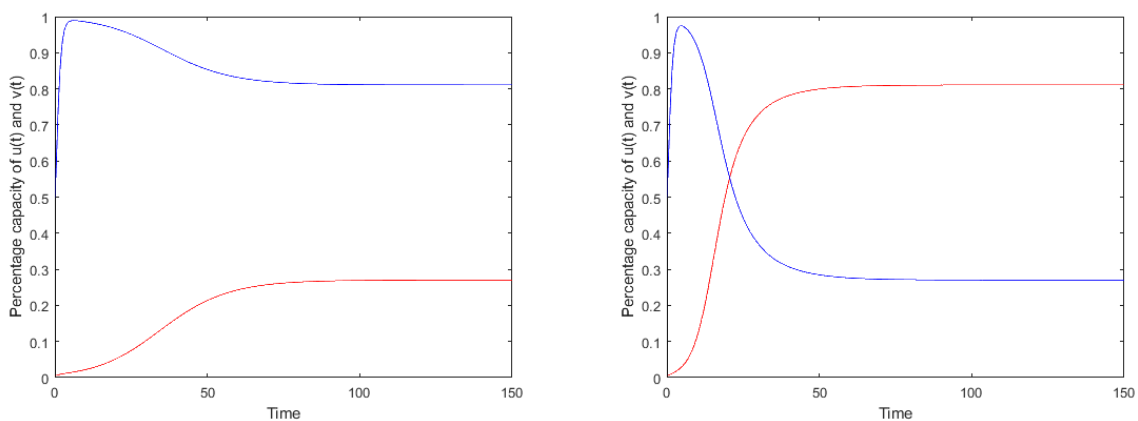
We shall observe the effects of changing the starting sizes of each population on their respective rates of change after iteration, by using as a template the bacterial experiments outlined in Chapter 1 [5], of the invasion of a secondary population to a micro-biome housing a resident species with an initial size 100 times greater.

In nature, a bacterial population colonising in an unfamiliar space is likely to start growing with a lower spacial abundance than the resident bacteria already present in the environment; regardless of whether such an invading species is more adept at competing, therefore having a lower  $b$  coefficient when modelled by our system.

Running again the same simulations with the same competition coefficients  $b_1$  and  $b_2$  of each species, and the same growth rate  $r$  for control, we shall now set the starting sizes such that:

$$u(t = 0) = 0.01 \times v(t = 0)$$

where  $u$  is the invading population and  $v$  is the resident population with the greater special advantage.



Figures 11 and 12: Coexistence interaction within system of equations (6) and (7), calculated by solution equations (8) and (9) governing populations  $u$  and  $v$ . The invading population  $u$  is illustrated in red, while resident population  $v$  is in blue, and both were simulated for  $T = 150$ , with  $\Delta t = 0.1$ . For Figure 11 the system has values:  $b_1 = 0.9, b_2 = 0.7, r = 1$  and  $(u(t = 0), v(t = 0)) = (0.005, 0.5)$ . For Figure 12, the system was run with values:  $b_1 = 0.7, b_2 = 0.9, r = 1$  and  $(u(t = 0), v(t = 0)) = (0.005, 0.5)$ .

The coexistence scenario with  $b_1 = 0.9$  and  $b_2 = 0.7$  has been simulated twice here, where for the second simulation the values have been swapped, such that we can observe the resulting array of size solutions when each the resident and invading population, in turn, have the competitive advantage.

For the purposes of these simulations, population  $u$  will act as the invading bacterial species to a biome occupied by resident population  $v$  in reference to the conducted epidermis versus aureus strain experiments [5], with an abundance 100 times greater than  $u$  at the time of its introduction.

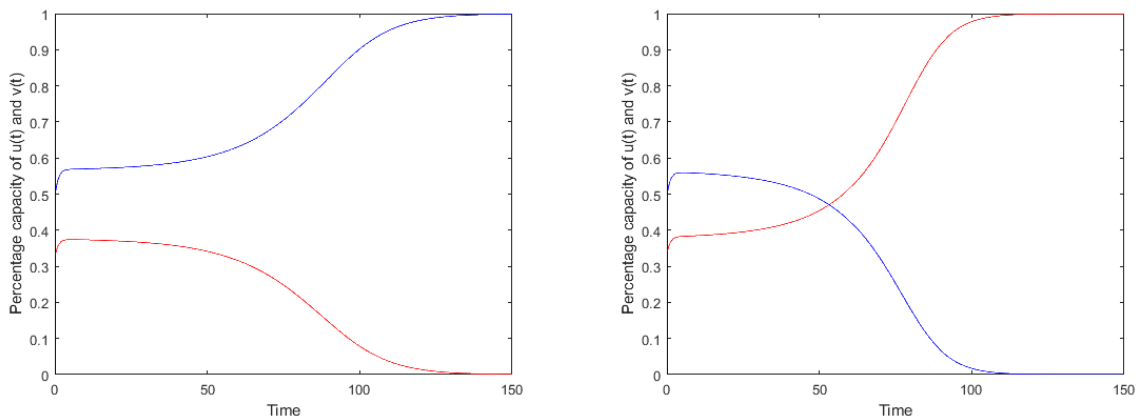
Figure 11 illustrates the transient solutions of invading population  $u$  growing under a greater competitive imposition by  $v$  than it itself inflicts upon it, where  $b_1 > b_2$ ; therefore lacks the ability to stabilise at a value equal to or greater than its opposer. However in Figure 12, population  $u$  still acts as the size inferior invading species, though here possesses a smaller competition coefficient so is able to outgrow  $v$ , saturating at a larger abundance.

Once again in these interactions, the size of saturation is dictated only by the competition coefficients of the system, as evidenced by the above graphical illustrations showing the exact same saturation values as in Figure 6, portraying coexistence with equal starting sizes. The formula for calculating the values that populations will converge to when the coexistence equilibrium is stable, are only dependent on the coefficients of competition, so their starting sizes and growth rates will have no effect on their saturation levels, though have clearly made a difference in the array of population solutions leading to these values.

When substituting the competition coefficient values of Figure 11, along with its starting sizes for each population, into the characteristic polynomial of the coexistence equilibrium rearranged for its  $\lambda$ ; both computations still give 2 negative answers. Therefore, despite the interference undergone by both populations in reaching their points of saturation, it was never such that either party sustained a rate of change  $< |1|$  during this time; in doing so causing multi-stability early on in the iterative process. It seems the occurrence of this may strictly be bound to interactions with competition coefficients greater than 1, though it is unnecessary to try to achieve in these situations, as from the fact that each  $\lambda$  is still negative, both populations are ensured a saturation at a positive size anyway due to coexistence being stable.

As multi-stability can occur for certain durations in competitive interactions with  $b_1$  and  $b_2$  greater than 1, where each population starts at the same size; both populations should also have this potential when starting sizes are changed. As the stability of fixed points  $(1, 0)$  and  $(0, 1)$  is only dependent on the competition coefficients of the system, both will still remain stable for any pairing of starting sizes.

However, as we know that their starting sizes and growth rates can affect the array of solutions leading to saturation; giving the invading population an initial abundance 100 times less than that of the resident species will result in it failing to diverge from near extinction even if it is less influenced competitively than the stress it imposes, in other words where  $b_1$  belonging to  $u(t)$  is smaller than  $b_2$  contained by  $v(t)$ .



Figures 13 and 14: Multi-Stability interaction in system of equations (6) and (7), calculated by solution equations (8) and (9) governing populations  $u$  and  $v$ . The invading population  $u$  is illustrated in red, while resident population  $v$  is in blue. Both equations (8) and (9) were simulated for  $T = 150$ , with  $\Delta t = 0.1$ . Figure 13 has the values:  $b_1 = 1.1, b_2 = 1.15, r = 1$  and  $(u(t = 0), v(t = 0)) = (0.33, 0.5)$ . For Figure 14, the system was run with values:  $b_1 = 1.1, b_2 = 1.15, r = 1$  and  $(u(t = 0), v(t = 0)) = (0.34, 0.5)$ .

This is evidenced by Figure 13, simulating a competitive interaction where  $b_1$  is less than  $b_2$ , yet the invading species fails to stabilise to capacity and instead stabilises to extinction. Figure 14 illustrates an interaction in which the invading population  $u(t)$  has a starting size large enough to ultimately saturate to its capacity.

This is because it is able to sustain a rate of change  $< |1|$  for enough iterations that its direction of solutions starts to converge towards the equilibrium  $(1, 0)$ . The number of initial

iterations, categorised within the domain of multi-stability, that the invading population will produce stable rates of change for under significant competition, is therefore proportional to the negative of  $r$ , and the negative of the difference between the resident and invader's starting population sizes.

As  $r = r_2/r_1$ , it enlarges when the growth rate  $r_2$  of the resident population  $v(t)$  is increased, strengthening its ability to compete thus making it harder for the invading species to sustain rates of change leading to capacity. It is clear as well from Figures 13 and 14, that the closer the starting sizes of each species are together, the longer the invader will increase in size after the simulation has started.

Figure 14 illustrates an identical simulation to Figure 13, other than that the starting size given to population  $u$  has been increased by 0.01% of its capacity, to 0.34. It is obvious from the diagrams that the transient solutions of populations  $u$  and  $v$  contrast, most notably in that a different population converges to its capacity in each of the simulations.

It is evident that the 0.01 increase in initial starting size given to the invading population  $u$ , was all it required to sustain a stable rate of change long enough to ultimately converge to its capacity instead of extinction, as in Figure 13.

This builds on our earlier assumptions as to the outcomes of bacterial interactions, in that we now understand that in situations where competition is high, whether or not a population will sustain its size in a spatially homogeneous environment is also dependent on its starting size, as well as its ability to inhibit substances toxic to its opposer's rate of growth.

In-keeping with our discrete classifications of stability that subjugate interactions simulated by our system according to their competition coefficients alone: coexistence, competition leading to extinction and multi-stable competition also ending in extinction for one population; we can say that the optimal initial values for each situation are dependent on the desired outcomes within each category.

For coexisting populations, each only require with respect to our system, that their competitions of coefficient be less than 1. With this precondition met, both populations will always saturate to positive abundances, regardless of their starting sizes or growth rates; as the coexistence will be stable as a result of each participant's relatively low competitive influence.

During microbial interactions that lead to the extinction of one population - specifically those pertaining to interactions with one coefficient having a value greater than 1 while the other is less - the population suffering the greater imposition offers little to no defence before converging to 0 abundance as the magnitude between their competitive influences is so great.

The resident population of bacteria, assumed in our numerical assessment to possess an initial abundance 100 times that of the invader, will want to at least withhold a period of multi stability if it possesses the greater competition coefficient and therefore the most imposition of growth.

We know from our linearisation of the system of equations, that interactions with at least one competition coefficient having a value greater than 1 will result in an outcome where at least one population will stabilise to extinction. However from our numerical analysis in this chapter, we understand that the population that this will apply to is also dependent on the starting sizes of each competitor; therefore the party undergoing the most competitive influence will not necessarily converge to extinction, given the right initial starting abundance.

This is evidenced in Figure 13, from the resident species in blue stabilising at its capacity despite having a larger coefficient of competition than the invading species. When granted a larger starting size such as in Figure 14, the invading population was able to converge instead to its capacity, when both parties were given the same competition coefficient values; though for the majority of iterations the resident population still managed to sustain a stable rate of change with the invading population before both diverged from each other in size.

## 4 Conclusions

After initially setting out to show through mathematical derivation the qualitative behaviour of competing populations of bacteria, fixed size coordinates and rates of growth were determined for populations growing in isolation. Through further modifications to the exponential function derived to produce the transient set of sizes of a bacterial strain, equilibria were found for inter-specific interactions involving 2 different populations; and the ultimate saturation points of each were determined by analysing the stability of their rates of change.

I learned from completing this project that the models I created had to be discretised to be simulated - where increasing the number of iterations between time steps allowed for a less piece-wise and more continuous function of solutions - and as well needed to undergo non-dimensionalisation to reduce its number of contained variables and thus run more efficiently. Through linearising my system of population equations by implementing the Jacobian and finding its determinant, I improved my understanding of using eigenvalues by observing the stability of the equilibria when changing the initial variables; achieving desired outcomes of convergence when displaying the transient solutions of each population.

I ultimately discovered that modelling a competitive interaction of bacterial populations in a static environment, one that would allow each inhabitant to grow to its capacity if undergoing no imposition from its competitor, successfully replicated the outcomes produced from the experiments involving gram positive strains of bacteria, that we informed our initial predictions of potential interactions on; and even allowed for further discoveries and hence postulates surrounding the nature of their saturation, when starting abundances were altered.

In creating a model of bacterial populations using the knowledge that they grow and decline exponentially with respect to time, and can be capable to a qualitative extent of reducing their competitor's abundance by releasing toxins; I conclude that this derived system of equations did indeed give reproducible answers to a high accuracy for the transient solutions of abundance, calculating valid outcomes under varying degrees of competitive influence in a spatially homogeneous environment of 2 populations, up to and including their saturation values.

## 5 Appendix

Here I present my MATLAB code used to generate Figures 1-14 in the document, containing 5 different sections over multiple files used within the software: each outlining the code used to create certain figures.

The first section programs Figure 1: the logistic curve, and is shown along with pseudo-code in green below.

```
%Define the intervals between iterations of the logistic function.
a = -0:0.0005:1;
%Input the logistic function with respect to dependent variable x.
b = 2*x.*(1 - x);
%Calculate and plot the function at the specified intervals.
plot(a,b,'b');

%Specify the domain and range of the graph.
xlim([-0.1 1.1]);
ylim([-0.1 1.1]);
xlabel('u')
ylabel('f(u)')

%Define and plot the diff(u) and u axes.
hold on
t=-10:0.1:10;
c = -3:10;
d = e*0;
plot(c, d, 'k')
plot(d, c, 'k')
```

The next section of code creates Figure 2: the curve of equation (3) in the document.

```
%Define an array to contain the transient solutions to the
%logistic function.
u = zeros(1,10);

%Set the growth rate and the initial size as required by the derived
%iterative formula in the project essay.
u(1) = 0.3;
r = 1;

%Set the number of iterations between values of time to a
%small fraction, and calculate the solution over a large value
%of time.
figure;
for i = 1:4001
    u(i) = 1./(1 - ((u(1)-1)/u(1))*exp(-r*0.0025*i));
end

%Plot the transient solutions with the specified interval between
%iterations, and specify the domain and range of the plotted function.
e = 0:0.0025:10;
plot(e, u, 'r')
xlabel('t')
ylabel('u(t)')
set(gca,'FontSize',13)
xlim([0 10]);
ylim([0 1.1]);
```



The third paragraph of code programs Figure 3: the categorisation of domain of values based on their stability; and was colourised after the code was executed.

```

%Define the coefficients of competition.
b1 = 0.7;
b2 = 0.8;

%Specify the domain and range of the stability categorisations graph.
figure;
xlabel('b1')
ylabel('b2')
xlim([0 2.2]);
ylim([0 2.2]);
grid off

%Plot the b1 and b2 axes.
hold on
t=-10:0.1:10;
e = -3:10;
f = e*0;
plot(h, e, ':k')
plot(e, g, ':k')
plot(e, f, 'k')
plot(f, e, 'k')

%Label each section of the diagram.
text(0.25, 0.5, 'Co-Existence', 'FontSize', 12, 'color', 'k');
text(0.35, 1.5, 'v Extinct', 'FontSize', 12, 'color', 'k');
text(1.35, 0.5, 'u Extinct', 'FontSize', 12, 'color', 'k');
text(1.3, 1.5, 'Multi Stability', 'FontSize', 12, 'color', 'k');

```

The section of code below produces Figures 6-14, illustrating the curve of equations (8) and (9) under different initial conditions, which are defined in the program and changed appropriately for each simulation.  $T$ ,  $\Delta t$  and the number of iterations are also defined in this program, as well as the starting size of each population, which were also changed accordingly though  $\Delta t$  was always kept at 0.1.

```

function population_growth

%Define the competition coefficients of the system.
b1 = 0.7;
b2 = 1.1;

%Set the interval length between iterations within one unit of time, and the total amount of time the
%function will be iterated for.
dt = 0.1;
T = 150;

% Define the number of iterations (time steps).
nt = T/dt;

%Define r: equal to the resident population's growth rate divided by the invader's rate of growth,
%where the r of v is over the r of u.
r = 1.1;

%Next define then plot the function itself.
u = zeros(1,nt);
v = zeros(1,nt);
u(1) = 0.005;
v(1) = 0.5;

```

```

%Calculate the reduced function of solutions of each population for the specified number of timesteps.
for i = 2:nt
    u(i) = u(i-1)+dt*u(i-1)*(1 - u(i-1) - b1*v(i-1));
    v(i) = v(i-1)+dt*r*v(i-1)*(1 - v(i-1) - b2*u(i-1));
end

%Plot the solutions over time for the specified number of intervals, and define the domain
%and range of the function.
E = 0:dt:T;
plot(E(2:end),u,'r',E(2:end),v,'b');
xlabel('Time')
ylabel('Percentage capacity of u(t) and v(t)')

%Plot the axes of size over time.
hold on
e = 0:0.01:1;
f = e*0;
plot(f, e, 'k');

```

The final section of code below computes Figures 4 and 5: the phase portraits of equations (6) and (7). The program computes a 2-D axes and a directional field situated at the same coordinates, however the directional field of arrows at all other locations was computed by an external program [8]. Competition coefficients  $b_1$  and  $b_2$  are also defined in this code, and were changed to fit each of the 2 desired phase portraits.

```

%Define the competition coefficients of the system.
b1 = 0.9;
b2 = 0.7;

%Specify the coordinates at which the directional derivatives of the system
%will be plotted, specifically along the u and v axes.
figure;
[a,b]=meshgrid(-2:0.5:0.5,0:1:0);
[c,d]=meshgrid(0:1:0,-2:0.5:0.5);
[e,f]=meshgrid(1.5:0.5:3,0:1:0);
[g,h]=meshgrid(0:1:0,1.5:0.5:3);

%Set the direction (curl) of the arrows to constant values.
a1 = 50*a;
a2 = 3*b;
c1 = a1';
c2 = a2';
e1 = 5*e;
e2 = 3*f;
g1 = e1';
g2 = e2';

```

```

%Plot the directional derivatives on the axes with the appropriate curl.
hold on
quiver(a,b,a1,a2, 'linewidth', 1.5, 'color', 'b')
quiver(c,d,c2,c1, 'linewidth', 1.5, 'color', 'b')
quiver(e,f,-e1,-e2, 'linewidth', 1.5, 'color', 'b')
quiver(g,h,-g2,-g1, 'linewidth', 1.5, 'color', 'b')

%Specify the domain and range of the phase portrait.
xlabel('u*')
ylabel('v*')
xlim([-1 2]);
ylim([-1 2]);
grid off

%Plot the u and v axes.
hold on
t=-10:0.1:10;
e = -3:10;
f = e*0;
g = e - e + 1/b1;
h = e - e + 1/b2;
plot(e, f, 'k')
plot(f, e, 'k')

%Plot the fixed points and the nullclines of the system.
plot(0,0,'ko')
plot(1,0,'ko')
plot(0,1,'ko')

plot((1-b1)/(1-b1*b2), (1-b2)/(1-b1*b2), 'ko')
plot(t, -t/b1 + 1/b1, 'r')
plot(t, 1-b2*t, 'r')

end

```

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