

The effect of conspecific support on the asymptotic properties of competing species

by

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Declaration

I, Avulundiah Edwin Phiri declare that the dissertation, which I hereby submit for the degree Magister Scientiae at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

Signature:

Date: November, 2018

Dedication

This thesis is dedicated to my ever supportive mom (Gledith) and my late dad (Edwin)

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Abstract

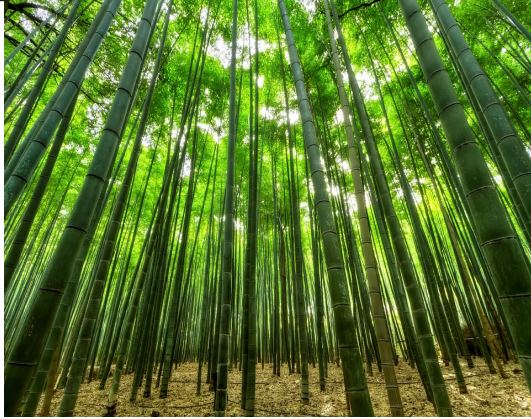
The long term properties, like coexistence and extinction, are usually determined by the demographics of the competing species or other competitive advantages. In this dissertation we consider the effect of conspecific support on the coexistence of species. We show that, even if the competing species have the same demographics and interaction, their coexistence can be destabilized by sufficient level of conspecific support. When considering large number of species the conspecific support destabilizes the coexistence equilibrium, thus producing a pattern of extinction and varied levels of existence. Up-scaling the model to continuous space variable leads to a model of pattern formation via local self-activation and lateral inhibition.

Introduction

1.1 General Overview

Competition among living organisms in an ecosystem is inevitable. We are all familiar with competition for we face it every day in our lives. Competition is a biological interaction of living organisms of either the same or different species in which one of them is affected. This occurs when there is a high demand of resources by the organisms than what the environment can actually supply. The term resource may include water, food, a space to grow, shelter, etc. If a particular resource is not enough and hence, it limits the size of the population, then we call it a limiting resource. Competition as a result of limiting resource was first described by Darwin [2] in his famous book published in 1859, "The origin of species by means of natural selection". He described competition for a limiting resource as a "struggle for existence and survival of fittest"[23]. There are different types of competitions. They can be classified into two general concepts, *intra-specific* competition, which is shown in Figure 1.1 (a)-(b), and *inter-specific* competition shown, Figure 1.1 (c)-(d). Intra-specific competition occurs within the population with the same characteristics whereas inter-specific competition occurs between populations with the different characteristics. It should be mentioned that intra-specific competition is stronger at high population density because individuals of the same species require identical resource and this can result in a process called *self-thinning*.

1.1. GENERAL OVERVIEW



(a) intra-specific competition in plants



(b) intra-specific competition in animals



(c) Inter-specific competition



(d) inter-specific competition in animals

Figure 1.1: Classification of competitions

Furthermore, competition has different forms. The competition that happens when a number of species share the resource which is limited whereby one species affects the other negatively is called *exploitation*. This form of competition is also known as *scramble* competition. In addition, when one species physically excludes another species from using a particular resource is referred to as *interference* competition. *Overgrowth* competition occurs mainly in plants when one species physically grows on top of another species and as result, limit the other species to access the resource. An example is the brown algae commonly known as Lobophora which overgrows on healthy reefs thereby which, in most cases, drive the corals of Lobophora into extinction. *Density-dependent* growth is a self-regulatory form of competition that limits the population size in nature. This happens either by slowing down the growth of the population when a population increases or reduces a decrease in population size when it is too low. This can be illustrated by two or more predators competing for a common prey. An increase in preys causes an increase in predators to control the population. On the other

hand, a decrease in preys population leads to a decrease in predators population.

Several ecologists have shown the impacts of competition by means of experiments. One of the notable experiments was carried out by a Russian ecologist, G.F Gause in 1934 [39]. He grew *Paramecium aurelia* and *P. caudatum* on the same territory competing for the same resource. He observed that one of the species did not survive and it was driven to extinction. In his "Principle of competitive exclusion", he concluded that the two species sharing the same resource cannot coexist [36]. Gause's principle of competitive exclusion was supported by Grover, Levins and Schreiber and his colleagues [42, 77, 79]. However, 33 years later, Robert and Levins [72] showed that species coexistence is possible if species have a different niche in a natural setting. In most cases, the outcome of the competition is determined by the dynamics of competing species. If on the one hand, one species is competitive superior, then the other species will eventually be driven to extinction. On the other hand, if both species have the same competitive powers, the result of the competition depends on their initial conditions. Further, if both species compete weakly, both species coexist in the same environment indefinitely. The concept of weak competition, which will be defined precisely later essentially means that the growth of one species limits its own further growth more than it limits the growth of the other.

1.2 Modelling Competition

The consequence of Gause's experiment discussed in the preceding section ignited the interest of many researchers from different fields such as biology, epidemiology, mathematics, etc. Since then, different mathematical models have been formulated trying to model coexistence of two or more species sharing a common resource. Most of these models are based on a famous classical model pioneered by Alfred J. Lotka and Vito Volterra commonly known as *Lotka-volterra* model [36]. This model makes use of the competition coefficient to determine the effect of each species on the other. The general Lotka-Volterra model takes the following

1.2. MODELLING COMPETITION

form [35]:

$$\frac{dv_i}{dt} = \frac{r_i v_i}{k_i} (k_i - v_i - \sum_{i \neq j} \alpha_{ij} v_j), \quad i = 1, \dots, n, \quad (1.2.1)$$

where n is the number of species, v_i is the species density/population size of i th species, r_i is the intrinsic growth rate, α_{ij} is a coefficient representing the effect of species j on species i and k_i is the carrying capacity for species i . Equation (1.2.1) has many applications in epidemiological modelling. For example, Ayala, et.al [35] used this form of a model to determine the conditions which can allow species in a competition to coexist. It is noteworthy that in the above model, if α_{ij} is non-negative, it means that we have a competitive interaction and if α_{ij} is negative, the interaction is described as mutualism or predation, accordingly as $\alpha_{ji} < 0$ or $\alpha_{ji} > 0$.

Furthermore, the model has extensively been used to describe a long-term dynamics of two or more species. The analysis of the model shows that coexistence of competing species is only possible if intra-specific competition is stronger than inter-specific competition. Competition in nature is assumably more complicated than we may think it is. Thus, the question, "is it reasonable to use the Lotka-Volterra model in the modelling of species coexistence in nature"? In answer to the raised question, Michael [35] among others designed the experiment to test the validity of the Lotka-Volterra model. Using experimental data, the author proved that the model is indeed valid and can reliably depict competition in a natural setting. Building on this work, Mark and his colleagues in [53] used (1.2.1) to study population invasiveness. In their model, they were able to derive the conditions that can explicitly slow or stop the spread of invading species from invading the territory of its counterpart. This study was a breakthrough to agriculturalists in pests control.

Recall a common hypothesis in the study of competitive models stated earlier, that is, in order for competing species to coexist, intra-specific competition should be stronger than inter-specific competition. However, there are several examples in literature that show the coexistence of both a weaker and a stronger species. One of many examples is presented by Amarasekare [8]. Moreover, following the given principle of competitive exclusion presented in the previous section, Hutchinson [49], proposed that fluctuating environmental conditions could lead to species coexistence and avoidance of species exclusion. His argument was that

fluctuating the environmental conditions such as regularly changing the location of resource frequently enough can alter the species ability of dominance which can result in extinction avoidance. Supported by Chesson and Warner [20, 13] although later, Chesson and Huntly stated that this might depend on the histories of competing species and on a relationship between environment and competition [13, 19]. It was shown in [14] that species in a fluctuating environment can coexist and that coexistence is facilitated by trade-offs in species' ability to manoeuvre under different environmental conditions.

In prospect of studying species competition and coexistence, the major concern of many ecologists and epidemiologists is whether there is a maximum number of species that can coexist indefinitely. Well, this concern has been addressed in the literature such as [22, 59, 72]. The authors have discussed the conditions that can give rise to the coexistence of multi-species. For example, a very recent article [56], considers the coexistence of multi-species of competitive systems with a crowding effect. The authors showed that it is possible for multi-species to coexist under the stated condition.

1.3 Competitive Systems and Pattern Formation

The study of the processes that generate spatial patterns in ecological systems has a long extensive history. Researchers have sought to explain pattern formation by connecting observed patterns to ecological processes. As a result, most of them have turned to the competitive systems as the cornerstone of the study of pattern formation [65, 82, 84]. In view of this, different mathematical models have been proposed in the quest to explain the phenomenon behind pattern formation [86]. Therefore, to get a better understanding of the underlying processes and mechanisms that generate patterns, some researchers have modified Lotka-Volterra model to come up with models that generate patterns that are identical to biological non-random patterns. Nevertheless, it is still unclear whether such theoretical models can really predict biological patterns because of the complex nature of some of the patterns. There are several known factors that influence pattern formation in nature that many researchers neglect such as environmental factors [11, 64, 69, 76]. However, it is explained in [87] that some of these factors have less influence, hence, can be neglected. For example, Werner, Franck and

1.4. SPECIES PERSISTENCE

Nicholas [87] are among other researchers who have explored the subject extensively. One of the fundamental result that they discovered is that in the absence of environmental factors, competition (intra-specific and inter-specific) alone is capable of generating regular patterns. They concluded that spatial pattern formation depends merely on the type of interactions species have and the strength of their dispersal. Nevertheless, they admitted the fact that co-occurrence analysis alone cannot explain the underlying mechanisms that generates the patterns in nature. Moreover, it is now widely accepted that competition is one of the major mechanisms underlying pattern formation and distribution of biodiversity. For example, it has been demonstrated by Jia, G, et al that plants in a community compete for light more than any other growth need such as soil nutrients [43] and this affects the plant distribution.

The pattern formation in both the discrete and the continuous model represents the mechanism given in the “Theory of Biological Pattern” by Gierer and Meinhardt [3]. However, it is not represented via systems of partial differential equations as considered by Allen Turing in 1952 in his paper, “The chemical basis of morphogenesis” [9] and also used by Gierer and Meinhardt [3, 29].

1.4 Species Persistence

Numerous theoretical studies have modelled species’ coexistence via persistence [26, 27, 50, 52, 89]. Researchers use the term persistence [89] to mean the long-term survival of species. The question (that this study also seeks to address) of whether multi-species in a competition obeying differential equations can persist indefinitely remains crucial in theoretical ecology. While there have been a number of models proposed to model persistence of multi-species, the major concern is how to obtain suitable conditions that guarantee indefinite species persistence. Often times, researchers have used a classical method of local stability analysis which can fairly be worked out to explain the asymptotic behaviour of competing species while others have gone further by using global stability analysis which has proved to be more difficult, except in cases where there are more constraint assumptions. In this dissertation, we will employ local stability analysis, especially when considering a system in three dimensions to explain the long-term behaviour of populations. We will use the concept of persistence in

doing so. There are various definitions of persistence [79]. However, in this dissertation, we adopt the one outlined by Hutson [89] because it has the following properties:

- (i) persistence must be global. This means that the criteria used should be independent of initial values of the system. This is important in ensuring that even for any trajectory starting close to an asymptotically stable coexistent equilibrium should remain close to the equilibrium even under a sudden change in the population. In other words, the population should not move (for whatever reason) into a basin of attraction of stable extinction equilibria.
- (ii) The presence of stable limit cycle should not be ignored: persistent species are mostly associated with cyclic behaviour provided the cycle remains away from the boundary. In fact, even those situations associated with strange attractors [79] should be considered as long as the attractor lies at a distance away from the boundary.
- (iii) The trajectory should not remain close to the boundary for all positive time. If it could, then there is a possibility of some species going to extinct (e.g due to epidemic or randomness in the environment). If that occurs, then we cannot consider such a system to model persistence.

With regards to the third property, Hutson [89] admitted that its formulation is somewhat vague. Thus a question of preciseness of persistence merits further attention. One possible view for persistence is that there should be a constant $\epsilon > 0$ such that once the trajectory of the system enters the region separated by ϵ from the boundary it should remain in that region for all time. We provide mathematical definitions of persistence in Section 2.4.1.

1.5 Conspecific Support

Conspecific support is when individuals of one species support their own, but not the other species. It is a common survival strategy used by living organisms. It is typically local and is manifested differently for different species, e.g. biofilms of bacteria, packs of dogs, herds of grazers, patches of grass in arid areas, patches of forest in savanna, etc. The basic mechanisms for conspecific support are joint defence, joint acquisition and retention of resources, better

1.6. RESEARCH QUESTIONS

mating opportunities, etc. The conspecific support usually results in the so called Allee Effect - positive correlation between the per capita growth rate and the population density when the population density is sufficiently small [68]. When conspecific support is essential for survival at low population density, we have a strong Allee Effect, characterised by the existence of minimum survival level, below which the species goes extinct.

1.6 Research Questions

This dissertation seeks to address the following questions;

- (i) What is the importance of conspecific support and what impact does it have on the persistence/coexistence equilibrium of two competing species (under qualified competition) and of n competing species?
- (ii) what conditions guarantee uniform persistence of a model of 3 competing species as well as a model of n competing species?
- (iii) what effect does conspecific support have on destabilising the coexistence of species and on pattern formation in discrete and continuous space models?

1.7 Aims and Objectives of this Dissertation

Aims: In this dissertation, we aim to formulate a mathematical model for modelling n species in a competition for a resource. Furthermore, will extend this model to include the term that represents conspecific support. Additionally, we aim to find mechanisms through which patterns are formed in ecosystems taking into account the competition for resources/space. The analyses of the respective models is expected to provide conditions for coexistence of species as well as the generations of patterns.

The **Objectives** of this dissertation are as follows:

- (i) to show the importance of conspecific support for competing species or sub-population groups. More precisely, we want to determine the impact of conspecific support on the

persistent/coexistent equilibrium in the case of two competing species as well as on n competing species.

- (ii) to determine the conditions for uniform persistence of a model of 3 competing species and the model of n competing species.
- (iii) to determine the effect of conspecific support on both discrete and continuous space models.

In order to address the first objective, we use the standard stability analysis technique to determine the linear stability of the boundary equilibria in \mathbb{R}_+^2 (for the case of two competing species) and computer simulations using matlab software (for the case of n competing species). For the second objective, we will use uniform persistence theory to determine the conditions for persistence of n species. Finally, we address the third objective by using a mathematical representation of the Gierer-Meinhardt theory of pattern formation via local self-activation and lateral inhibition [3, 29]. The obtained model is already discussed in [71, 70]. This will be achieved by using non-local integral operator. It is interesting to establish a link with discrete space models with conspecific support.

1.8 Organisation of the Dissertation

This dissertation has five chapters. In Chapter 2, we provide some basic mathematical principles used for analysis and proving theorems. In Chapter 3, we present the two dimensional model of competing species and discuss the conditions for coexistence of species. We will later consider the model that incorporates conspecific support and examine dynamics of the model on the stable qualified equilibrium. In Chapter 4, we present a model of Kolmogorov type. Here, we discuss the conditions that allow 3 competing species to persist uniformly. Additionally, we present a main theorem which shows that species uniformly persist. We analyse the impact of conspecific support and show that it may destabilise the coexistence of the species. Furthermore, we present numerical simulations obtained by using matlab software to observe the patterns formed due to competition. The last section of Chapter 4 deals with up-scaling of the discrete model to continuous space variable. We will observe some similarities and

1.8. ORGANISATION OF THE DISSERTATION

differences between these two models by comparing the patterns formed. The dissertation is concluded by Chapter 5, gives a summary of what is represented in Chapters 2 through to 4. The future work is presented in this chapter too.

Mathematical Tools

2.1 Mathematical Preliminaries

In this chapter, we provide some relevant definitions, concepts and mathematical theories used in the model formation and proof of results in the succeeding sections. Throughout this chapter, we denote by \mathbb{R}^n , for any $n \in \mathbb{N}$, the Euclidean space of dimension n .

Differential equations are relations involving derivatives of functions. If the function depends on a single variable only, it is said to be an *ordinary* differential equation, abbreviated as ODE, otherwise, it is called a *partial* differential equations, abbreviated as PDE. A system of differential equations is said to be *autonomous* if the right-hand side does not explicitly depend on time.

2.1.1 Equilibria of linear and non-linear autonomous system

Consider autonomous system of ordinary differential equations in the general form,

$$\dot{x} = f(x), \tag{2.1.1}$$

where $x = x(t) \in \mathbb{R}^n$ denotes a vector-valued function of $t \in \mathbb{R}$. We assume that $f \in C(\mathbb{R}^n, \mathbb{R}^n)$ and the initial condition is given at $t = 0$. The over dot in (2.1.1) represents differentiation with respect to time t and can also be written as $\frac{dx}{dt}$. Equation (2.1.1) is an example of an autonomous system of the ordinary differential equations and the function $f(x)$ is referred to as a vector field. A solution of Equation (2.1.1) is a continuously differentiable function $x : I \rightarrow \mathbb{R}^n$ satisfying (2.1.1), where I is the time interval of existence of the solution. The interval I is called a maximum interval of existence of a solution $x(t)$ if this solution cannot be extended beyond I . Note that we may also refer to $x(t, x_0)$ as a trajectory

2.1. MATHEMATICAL PRELIMINARIES

or phase curve through the point x_0 at $t = 0$. The space of dependent variables x_1, x_2, \dots, x_n in system (2.1.1) is called the phase space.

Definition 1. [85] An orbit through a point x_0 in the phase space $E \subset \mathbb{R}^n$ of (2.1.1), denoted by $\mathcal{O}(x_0)$, is a set of points in E that lie on a trajectory passing through x_0 . That is

$$\mathcal{O}(x_0) = \{x(t) \in \mathbb{R}^n : x(t_0) = x_0, t \in \mathbb{R}\}.$$

Definition 2. [33] A flow $\phi(t, x)$, denoted $(\phi_t(x))$, is a one parameter, differentiable mapping $\phi_t : \mathbb{R}^n \rightarrow \mathbb{R}^n$, such that

- (i) $\phi_0(x) = x$, and
- (ii) for all t and $s \in \mathbb{R}$, $\phi_t \circ \phi_s \equiv \phi_{t+s}$.

Thus, the vector field $f(x)$ in (2.1.1) is said to generate a flow $\phi : \mathbb{R}^n \rightarrow \mathbb{R}^n$, which transforms an initial state x_0 into some state $x(t) \in \mathbb{R}^n$ at time $t \in \mathbb{R}$, that is

$$\phi_t(x_0) = x(t).$$

The function $f(x)$ is said to be locally Lipschitz on an open set E if for every point $z \in E$, there is a neighbourhood N such that f is Lipschitz on N . That is, there exists $K_N \in \mathbb{R}$ such that

$$|f(x) - f(y)| \leq K_N |x - y| \text{ for } x, y \in N. \quad (2.1.2)$$

The function $f(x)$ is said to be globally Lipschitz or simply Lipschitz on E if (2.1.2) holds with a constant K which is independent of z and N .

Theorem 1 (Fundamental Existence-Uniqueness Theorem [33, 46]). *Let $E \subset \mathbb{R}^n$ be an open subset of real Euclidean space, let $f : E \rightarrow \mathbb{R}^n$ be locally Lipschitz at a point $x \in E$. Then, for any $x_0 \in E$, there exists a real interval I containing 0 such that (2.1.1) has a unique solution $x = x(t)$ which is defined on I and $x(0) = x_0$.*

Theorem 1 above implies that the solution of (2.1.1) can be found in an open interval I containing 0 when $f(x)$ is locally Lipschitz at a point x_0 . The solution typically exists over

a larger interval since the estimated interval I is not optimal. The largest such interval is known as the maximal interval of existence. This maximal interval of existence is the largest interval of time containing t_0 for which the solution, $x(t)$, of (2.1.1) exists.

Theorem 2 (Maximal Interval of Existence [46]). *Let $E \subset \mathbb{R}^n$ be an open subset of real Euclidean space and $f : E \rightarrow \mathbb{R}^n$ be locally Lipschitz. Then there is a maximal, open interval $I = (a, b)$ containing 0 such that (2.1.1) has a unique solution, $x = x(t)$ satisfying $x(0) = x_0$.*

It is worth noting that the existence of solutions as provided by Theorem 1 and Theorem 2 does not imply existence for $t \in [0, +\infty)$ or $t \in (-\infty, +\infty)$. Such existence of solutions of (2.1.1) is covered by the concept of *dynamical system*. Generally speaking, dynamical system is an evolution rule that defines a trajectory as function of time on a set of states.

Definition 3. [78] System (2.1.1) defines a (positive) dynamical system on a subset $E \subset \mathbb{R}^n$ if, for every $x_0 \in E$, there exists a unique solution of (2.1.1) defined for all $t \in \mathbb{R}_+$ satisfying $x(0) = x_0$ and remaining in E for for all $t \in \mathbb{R}_+$.

Theorem 3. [85] *Let $f : \mathbb{R}^n \rightarrow \mathbb{R}^n$ be globally Lipschitz on \mathbb{R}^n . Then there exists a unique solution $x = x(t)$ to (2.1.1) for all $t \in \mathbb{R}$. Hence (2.1.1) defines a dynamical system on \mathbb{R}^n .*

Theorem 4 (Existence and uniqueness for locally Lipschitz). *Let $f : \mathbb{R}^n \rightarrow \mathbb{R}^n$ be Lipschitz on a neighbourhood N of E , where E is bounded. If it may be shown that for any $z \in E$, the solution $x(t)$ of (2.1.1) satisfies $x(t) \in E$ for each $t \geq 0$ such that the solution exists, then (2.1.1) defines a dynamical system on E [78].*

Remark. It follows from Theorem 4 that to show the existence of solution for infinite time, it is enough to show that the solution is bounded on its maximal interval of existence.

Definition 4. [85] An equilibrium (fixed) point of system (2.1.1) is a point $x = \bar{x}(t) \in \mathbb{R}^n$ satisfying the condition,

$$f(\bar{x}(t)) = 0.$$

Certainly, the constant function $x(t) \equiv \bar{x}(t)$, $t \in \mathbb{R}$ is a solution of (2.1.1) and by uniqueness of solution, no other solution curve intersects it. If U is the state space of some biological systems with dynamics described by (2.1.1), then \bar{x} is an equilibrium state if when the system starts at \bar{x} it always stays at \bar{x} .

2.1. MATHEMATICAL PRELIMINARIES

Theorem 5 (Gronwall Lemma). [78] Let $x(t)$ satisfy

$$\frac{dx}{dt} \leq px + q, \quad x(0) = x_0,$$

for constants p, q . Then for $t \geq 0$,

$$x(t) \leq e^{pt}x_0 + \frac{q}{p}(e^{pt} - 1), \quad p \neq 0$$

and

$$x(t) \leq x_0 + qt, \quad p = 0.$$

2.1.2 Eigenvalues and eigenvectors

Consider an $n \times n$ matrix given by

$$A = \begin{pmatrix} a_{11} & a_{12} & \cdots & a_{1n} \\ a_{21} & a_{22} & \cdots & a_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ a_{an1} & a_{n2} & \cdots & a_{nn} \end{pmatrix}$$

which can also be represented as $A = [a_{ij}]$.

Definition 5. [60] A vector v is an eigenvector of an $n \times n$ matrix A if v is a non-zero solution to the system of linear equations

$$(A - \lambda I)v = 0.$$

The number (real or complex) λ is called an eigenvalue of A , and v is an eigenvector associated to λ . Using the invertibility criterion, it follows that λ is an eigenvalue of A if and only if λ is a root of the characteristic equation

$$\det(A - \lambda I) = 0. \tag{2.1.3}$$

2.1.3 Stability of Solutions

Generally speaking, an equilibrium point $\bar{x}(t)$ of system (2.1.1) is said to be *stable* if all solutions starting close to this equilibrium $\bar{x}(t)$ at a given time stay close to $\bar{x}(t)$ for all times. We say it is *asymptotically stable* if it is stable and in addition, all solutions starting close to $\bar{x}(t)$ tend to $\bar{x}(t)$ as $t \rightarrow \infty$. Below, we provide formal definitions.

Definition 6. Let $\bar{x}(t) \in \mathbb{R}^n$ be an equilibrium point of a dynamical system on E defined by (2.1.1). Then $\bar{x}(t)$ is said to be

(i) stable if for any $\epsilon > 0$, there exists $\delta = \delta(\epsilon) > 0$ such that

$$\text{if } \|\bar{x}(0) - y(0)\| < \delta, \text{ then } \|\bar{x}(t) - y(t)\| < \epsilon, \text{ for all } t > 0;$$

(ii) unstable if (i) above does not hold;

(iii) attractive if there exists $\epsilon > 0$ such that

$$\|\bar{x}(t) - y(t)\| \rightarrow 0 \text{ as } t \rightarrow \infty \text{ for all } \|\bar{x}(0) - y(0)\| < \epsilon.$$

small enough.

(iv) asymptotically stable if $\bar{x}(t)$ is stable and attractive. If an equilibrium point $\bar{x}(t)$ of (2.1.1) is asymptotically stable, then the set of all initial points x_0 such that

$$\lim_{t \rightarrow \infty} x(t, x_0) = \bar{x}(t),$$

is called a basin of attraction.

(v) globally attractive on E if (iii) holds for any $x_0 \in E$, that is, the basin of attraction of $\bar{x}(t)$ is E and

(vi) globally asymptotically stable on E if (iv)–(v) hold.

2.1.4 Classification of the origin in two dimensional-system

In the case of a two-dimensional linear system, the origin can be classified as: *node*, *spiral*, *saddle* or *center*. The classification largely depends on the nature of eigenvalues, that is, whether eigenvalues are [78]:

- real or complex,
- real with positive or negative sign, and
- complex with positive or negative real parts
- **Node**: we say the origin is a node if all eigenvalues are real and have the same sign. A node is stable if both eigenvalues are negative and unstable if both eigenvalues are positive. A node is called *degenerate* if both eigenvalues are real and equal. The degenerate node is known as proper if two linearly independent eigenvectors correspond to the double eigenvalue. However, the degenerate node is known as improper if only one eigenvector corresponds to the double eigenvalue.
- **Saddle**: the origin is called a saddle if both eigenvalues are real and have opposite signs. A saddle is unstable always.
- **Spiral**: we say the origin is a spiral or focus if both eigenvalues are complex and have non-zero real part. A focus is said to be stable if the real part is negative and unstable otherwise.
- **Center**: the origin is said to be a center if both eigenvalues are complex and the real part is zero. If this is the case, then every orbit is periodic. The center is stable though not asymptotically stable.

2.1.5 Hartman-Grobman Theorem

Definition 7. The Jacobian matrix of a function $f : \mathbb{R}^n \rightarrow \mathbb{R}^n$ of $x \in \mathbb{R}^n$ is the matrix of point

$$Df(x) = \begin{pmatrix} \frac{\partial f_1}{\partial x_1}(x) & \dots & \frac{\partial f_1}{\partial x_n}(x) \\ \vdots & \ddots & \vdots \\ \frac{\partial f_n}{\partial x_1}(x) & \dots & \frac{\partial f_n}{\partial x_n}(x) \end{pmatrix} \quad (2.1.4)$$

of partial derivatives evaluated at x .

In the setting of model (3.1.1)-(3.1.2), matrix (2.1.4) illustrates the impact of the size of each species on the growth rate of itself and the other species.

Definition 8. [85] Let $x = \bar{x}$ be an equilibrium point of (2.1.1). Then \bar{x} is called hyperbolic if $Df(\bar{x})$ has no eigenvalues with zero real part. An equilibrium point that is not hyperbolic is called nonhyperbolic.

Let X_1 and X_2 be any two topological spaces.

Definition 9. [33] A function $f : X_1 \rightarrow X_2$ is homeomorphism if it is continuous and bijective with a continuous inverse.

Definition 10. [33] A function $g : X_1 \rightarrow X_2$ is a C^1 diffeomorphism if it is invertible and both h and its inverse h^{-1} are C^1 maps.

Consider two functions $f_1 : \mathbb{R}^n \rightarrow \mathbb{R}^n$ and $f_2 : \mathbb{R}^n \rightarrow \mathbb{R}^n$.

Definition 11. [33] f_1 and f_2 are said to be conjugate if there exists a homeomorphism $h : \mathbb{R}^n \rightarrow \mathbb{R}^n$ such that $f_2 \circ g = g \circ f_1$, which can also be written as $f_2(g(x)) = g(f_1(x))$, $x \in \mathbb{R}^n$.

Proposition 1. If f_1 and f_2 are C^r conjugate, then the orbits of f_1 maps to the orbits of f_2 under g .

Proposition 2. If f_1 and f_2 are C^r conjugate, $r \geq 1$, and x_0 is an equilibrium of f_1 , then the eigenvalues of $Df_1(x_0) = Df_2(g(x_0))$.

Theorem 6 (Hartman and Grobman). [85] Consider a C^r ($r > 1$) vector field f and the

2.1. MATHEMATICAL PRELIMINARIES

system

$$\dot{x} = f(x), \quad x \in \mathbb{R}^n \quad (2.1.5)$$

with f defined on an open subset of \mathbb{R}^n . Suppose that system (2.1.5) has hyperbolic equilibrium point $x = \bar{x}$ and $Df(\bar{x})$ has no eigenvalues on the imaginary axis. Consider the associated linear ODE system

$$\dot{\epsilon} = Df(\bar{x})\epsilon, \quad \epsilon \in \mathbb{R}^n. \quad (2.1.6)$$

Then the flow generated by (2.1.5) is C^0 conjugate to the flow generated by the linearised system (2.1.6) in a neighbourhood of the equilibrium point of \bar{x} .

The application of Hartman-Grobman theorem is that an orbit structure close to a hyperbolic equilibrium point and the orbit structure given by the associated linearised dynamical systems around the origin are the same. Hence, the stability properties of the of the equilibrium \bar{x} of (2.1.1) are the same as the stability property of the origin for (2.1.6).

Theorem 7. *If all of eigenvalues of (2.1.4) evaluated at equilibrium $x = \bar{x}$ have negative real parts, then, the equilibrium solution $x = \bar{x}$ of the non linear vector field (2.1.1) is asymptotically stable [6, 36]. Otherwise, \bar{x} is unstable.*

Below, we discuss **Routh-Hurwitz criterion** which gives the necessary and sufficient conditions for the roots of polynomials to have negative real parts.

Theorem 8 (Routh-Hurwitz criterion [55]). *Let (2.1.3) be the characteristic equation of (2.1.4). Then we obtain the following polynomial for λ of degree k :*

$$P(\lambda) = \lambda^k + a_1\lambda^{k-1} + \dots + a_{k-1}\lambda + a_k, \quad a_i \in \mathbb{R}, \quad i = 1, \dots, k. \quad (2.1.7)$$

Construct the Hurwitz k matrices using the coefficients a_i of (2.1.7) as follows:

$$H_1 := (a_1), \quad H_2 := \begin{pmatrix} a_1 & 1 \\ a_3 & a_2 \end{pmatrix}, \quad H_3 := \begin{pmatrix} a_1 & 1 & 0 \\ a_3 & a_2 & a_1 \\ a_5 & a_4 & a_3 \end{pmatrix}, \quad \text{and}$$

$$H_k := \begin{pmatrix} a_1 & 1 & 0 & 0 & \cdots & 0 \\ a_3 & a_2 & a_1 & 1 & \cdots & 0 \\ a_5 & a_4 & a_3 & a_2 & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots & \cdots & \vdots \\ 0 & 0 & 0 & 0 & \cdots & a_k \end{pmatrix} \quad (2.1.8)$$

where $a_j = 0$ if $j > k$. The roots of (2.1.7) have negative real parts if and only if the determinant of all the matrices in (2.1.8) are positive, that is,

$$\det(H_j) > 0, \quad j = 1, \dots, k.$$

For the case when $k = 2$, the Routh-Hurwitz criterion simplifies to $a_1 > 0$ and $a_1 a_2 > 0$. Observe that $a_3 = 0$ in H_2 . This is equivalently to $a_1 > 0$ and $a_2 > 0$ and these conditions correspond to those stated in Theorem 2.1.4. Table 2.1 below provides a summary for Routh-Hurwitz criterion.

2.2. ω -LIMIT SETS, INVARIANT SETS AND ABSORBING SETS

Table 2.1: Routh-Hurwitz Criterion

k	Coefficients Signs	Additional Conditions
2	$a_1 > 0, a_2 > 0$	—
3	$a_1 > 0, a_2 > 0, a_3 > 0$	$a_1 a_2 > a_3$
4	$a_1 > 0, a_2 > 0, a_3 > 0, a_4 > 0$	$a_1 a_2 a_3 > a_3^2 + a_1^2 a_4$
5	$a_1 > 0, a_2 > 0, a_3 > 0, a_4 > 0,$ $a_5 > 0$	$a_1 a_2 a_3 > a_3^2 + a_1^2 a_4,$ $(a_1 a_4 - a_5)(a_1 a_2 a_3 - a_3^2 - a_1^2 a_4) > a_5(a_1 a_2 - a_3)^2 + a_1 a_5^2$

For the roots of a Polynomial (2.1.7) to have negative real parts, all its coefficients must strictly be positive.

2.2 ω -Limit Sets, Invariant Sets and Absorbing Sets

One of the fundamental objectives of the dynamical systems theory is to predict the asymptotic behaviour of the solutions of the system. In order to make such predictions meaningfully, we need to determine the invariant sets or ω -limit sets and the basins of attraction of the system. Our prediction of the future behaviour of the solution of the system depends with initial states depends largely on the nature of the ω -limits and their basins of attraction.

Generally, epidemiological models monitor populations (living organisms) such as humans, animals, cells, vectors and many more whose population sizes are always nonnegative. Therefore, such models ought to be considered in the regions where the nonnegativity property is preserved.

Let ϕ be the flow defined for (2.1.1).

Definition 12. [85] A point $x_0 \in \mathbb{R}^n$ is called

- i) an ω -limit point of $x \in \mathbb{R}^n$, if there exists a sequence $\{t_n\}, t_n \rightarrow \infty$ such that,

$$\phi(t_n, x) \rightarrow x_0.$$

ii) an α -limit point of $x \in \mathbb{R}^n$, if there exists a sequence $\{t_n\}$, $t_n \rightarrow -\infty$ such that,

$$\phi(t_n, x) \rightarrow x_0.$$

Definition 13. [85] The set of all ω -limit points of a flow is called ω -limit set, while the set of all α -limit points of a flow is called the α -limit set.

Definition 14 (Invariant set). [81] Let ϕ be the flow of (2.1.1). A set M is said to be an invariant set with respect to the autonomous ordinary differential equation (2.1.1) if,

$$x(0) \in M \rightarrow x(t) \in M, \forall t \in \mathbb{R}.$$

Definition 14 means that if any trajectory begins in M , it remains in M for all time. If we consider non-negative time, that is, $t \geq 0$ in Definition 14, then M is said to be positively invariant. Particularly, solutions in a positively invariant set remain there for all positive time.

Definition 15. [12] System (2.1.1) has an absorbing set \mathcal{A} if for every bounded set $\mathcal{U} \subset \mathbb{R}^n$, there exists a time $\mathcal{T}(\mathcal{U})$ such that if $x(0) \in \mathcal{U}$ then

$$t \geq \mathcal{T}(\mathcal{U}) \implies x(t) \in \mathcal{A}.$$

Definition 15 implies that all orbits of the system are eventually absorbed by \mathcal{A} .

Theorem 9 (LaSalle's Invariance Principle [46]). *Suppose U is a Lyapunov function on an open set $E \subset \mathbb{R}^n$. Let*

$$S = \{x \in \bar{E} : \dot{U} = 0\},$$

where \bar{E} is the closure of E and let M be the largest invariant set of (2.1.1) in S . If $\gamma^+(x_0)$ is a bounded orbit of (2.1.1) which lies in E , then the ω -limit set of γ^+ belongs to M ; that is,

$$x(t, x_0) \rightarrow M \text{ as } t \rightarrow \infty.$$

Corollary 1. [46] *If $U(x) \rightarrow \infty$ as $|x| \rightarrow \infty$ and $U \leq 0$ on \mathbb{R}^n , then every solution $x(t)$*

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of (2.1.1) is bounded and approaches the largest invariant set M of (2.1.1) in the set S . In particular, if $M = \{\bar{x}\}$, then the equilibrium point \bar{x} is globally-asymptotically stable.

2.3 Periodic Solutions and Limit Cycles

One of the fundamental parts in the analysis of models of differential equations is the description of behaviour of solutions near the equilibrium point, discussed in Section 2.1.5. Although linearisation is an important tool, it has limitations. For example, it can only give us information about the behaviour of solutions close to an equilibrium point. In this Section, we study different types of invariant sets, namely periodic orbits.

Definition 16. [24] A closed orbit \mathcal{O} , is said to be a limit cycle if \mathcal{O} is subset of $L_\alpha(x)$ or $L_\omega(x)$ for some x that does not lie in \mathcal{O} , where x is a point in the phase portrait of a flow ϕ_t , $L_\alpha(x)$ and $L_\omega(x)$ are α -limit set and ω -limit set respectively.

We can observe from Definition 16 that we do not require the trajectories to approach the limit cycle from both sides as it is the case with Example 3.8.1 of [24]. The limit cycle in the above mentioned example has the property that the trajectory of all points, x (where $|x| \neq 0$ or 1) are attracted to it as time increases [24].

Note that, while it is true that every attracting set is a limit set, the converse is false. Note further that a closed orbit around a center is not a limit cycle since it contains limit points of points itself only.

Below we provide a criterion that shows that there cannot be a periodic orbit in a particular region. Such results are fundamental in situations where we know that there is an asymptotically stable equilibrium and we want to make a conclusion that all solutions tend to it. Let S be a simple connected region and let $P(x_1, x_2)$ and $Q(x_1, x_2)$ be continuously differentiable in the closure of S . Here, a simply connected region is a region of the plane without holes in it. This follows from Green's Theorem [24].

Consider a system [36]

$$\begin{aligned}\dot{x}_1 &= f_1(x_1, x_2), \\ \dot{x}_2 &= f_2(x_1, x_2).\end{aligned}\tag{2.3.1}$$

Theorem 10. *Suppose that*

$$\frac{\partial f_1}{\partial x_1}(x) + \frac{\partial f_2}{\partial x_2}(x)$$

is either strictly positive or strictly negative in a simply connected region S . Then there is no periodic orbit of (2.3.1) in S .

Theorem 11. *Let $\beta(x_1, x_2)$ be continuously differentiable and suppose that*

$$\frac{\partial}{\partial x_1}(\beta(x_1, x_2)f_1(x_1, x_2)) + \frac{\partial}{\partial x_2}(\beta(x_1, x_2)f_2(x_1, x_2))$$

is either strictly positive or strictly negative in a simply connected region S . Then, there is no periodic orbit of (2.3.1) in S [36].

Theorem 12. *Let*

$$\frac{\partial f_1}{\partial x_1}(x) < 0, \quad \frac{\partial f_2}{\partial x_2}(x) < 0$$

for $x_1 > 0, x_2 > 0$. Then, there is no periodic orbit of the system (2.3.1) in the interior of \mathbb{R}_+^2 [36].

2.4 Persistence and Stable Coexistence

A basic and a paramount concern in the study of population dynamics is the long term coexistence of the interacting populations involved. Mathematically, this corresponds to persistence of the populations. The concept of *persistence* has played a major role in analysis of mathematical models. As a result, many definitions have been developed in the quest of analysing and understanding asymptotic behaviour of such models.

The question of whether or not competing species will persist, that is, remain away from

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the extinction, is crucial in theoretical ecology. One way of addressing this question is by formulating a mathematical model and by means of a persistence function of the form

$$\rho : X \longrightarrow \mathbb{R}_+.$$

Here, we provide various forms of definitions of persistence and coexistence and the relationship between these two concepts that will help us describe the long-term behaviour of competing species in question.

2.4.1 Concepts of Persistence

Let X be any non-empty set and let $\rho : X \longrightarrow \mathbb{R}_+$.

Definition 17. [34] A semi flow $\Phi : T \times X \longrightarrow X$ is known as a:

i) *weakly ρ -persistent* on X if for every $x \in X$

$$\limsup_{t \rightarrow \infty} \rho(\Phi(t, x)) > 0, \quad \forall x \in X, \quad \rho(x) > 0,$$

ii) *strongly ρ -persistent* on X if for every $x \in X$

$$\liminf_{t \rightarrow \infty} \rho(\Phi(t, x)) > 0, \quad \forall x \in X, \quad \rho(x) > 0,$$

iii) *uniformly weakly ρ -persistent* on X if for every $x \in X$

$$\limsup_{t \rightarrow \infty} \rho(\Phi(t, x)) > \epsilon, \quad \forall x \in X, \quad \rho(x) > 0,$$

iv) *uniformly (strongly) ρ -persistent* if there exists $\epsilon > 0$ such that

$$\liminf_{t \rightarrow \infty} \rho(\Phi(t, x)) > \epsilon, \quad \forall x \in X, \quad \rho(x) > 0.$$

Definition 18. [34] A semi flow $\Phi : T \times X \longrightarrow X$ is known as

i ρ -dissipative if there exists $r > 0$ such that

$$\limsup_{t \rightarrow \infty} \rho(\Phi(t, x)) < r, \quad \forall x \in X,$$

ii weakly ρ -dissipative if there exists $r > 0$ such that

$$\liminf_{t \rightarrow \infty} \rho(\Phi(t, x)) < r, \quad \forall x \in X \text{ and}$$

iii ρ -permanent, if Φ is both uniformly ρ -persistent and ρ -dissipative.

Note. Uniform persistence implies weak uniform persistence, which in turn, implies weak persistence. Uniform persistence implies persistence, which implies weak persistence. If the flow is dissipative, then, weakly uniform persistence implies uniform persistence, that is, uniform persistence and weakly uniform persistence are equivalent. However, persistence does not imply uniform persistence and weak persistence does not imply persistence.

The definitions that follow provides the relationship that exists between persistence and co-existence of species.

2.4.2 Stable Coexistence

Definition 19. The species of the model (2.1.1) are said to coexist if the respective flow is ρ -permanent with the persistence function

$$\rho(x_1, \dots, x_n) = \min\{x_1, \dots, x_n\}, \quad (2.4.1)$$

or equivalently, there exist $\epsilon > 0$ and $r > 0$ such that if $x_i(0) > 0$, $i = 1, \dots, n$ then

$$\epsilon < \liminf_{t \rightarrow \infty} x_i(t) < \limsup_{t \rightarrow \infty} x_i(t) < r, \quad i = 1, \dots, n.$$

It is easy to see that if the species in (2.1.1) coexist in terms of Definition 17, then the n -dimensional interval $[\epsilon, r]$ is a compact absorbing set of the flow defined by (2.1.1). This type of coexistence is also called *stable coexistence* [1]. Below is the precise definition of the stable

coexistence.

Definition 20 (Stable coexistence). There exists a compact positively invariant set $M \subset \text{interior}(\mathbb{R}_+^n)$ which is stable and attracting with basin of attraction $\text{interior}(\mathbb{R}_+^n)$.

In the sequel, we consider the concepts of persistence and permanence only with the persistence function ρ given in (2.4.1). Hence, ρ will not be explicitly mentioned.

2.5 Qualified and Unqualified Competition

The two species are in a competition when an increase in the size of one species decreases the growth rate of all other species. Competition can either be *qualified* (or *weak*) or unqualified.

Definition 21. The competition is called *qualified* if the impact of the increase of the population size of one species impacts negatively on its own growth rate stronger than it impacts on the growth rate of the species it competes with.

The converse of Definition 21 is called unqualified competition.

Models of two Competing Species and Conspecific Support

In competitive system, the long term dynamics, e.g coexistence, extinction, are usually determined by the demographics of the competing species as well as the effect of their interaction on each one. In this chapter, we consider the effect of conspecific support on the coexistence of species.

3.1 A general system of two competing species

Consider a general system of two competing species of Kolmogorov-type [62]

$$\frac{dx}{dt} = xg_1(x, y), \quad (3.1.1)$$

$$\frac{dy}{dt} = yg_2(x, y), \quad (3.1.2)$$

where g_1 and g_2 are smooth real functions defined on \mathbb{R}_+^2 . Our main interest is in the coexistence or the extinction of any of the species.

Assumptions. *Every population in the absence of the other has a unique positive stable equilibrium. More precisely, the functions g_1 and g_2 are such that*

$$(i) \quad g_1(0, 0) > 0, \quad g_2(0, 0) > 0,$$

(ii) g_1 and g_2 are decreasing in both x and in y and are unbounded below.

3.1. A GENERAL SYSTEM OF TWO COMPETING SPECIES

Clearly, each of the equations

$$g_1(x, 0) = 0,$$

$$g_2(0, y) = 0$$

has a unique solution. We denote them by p and q , respectively. Then,

(i) $g_1(x, 0) > 0, x \in (0, p),$

(ii) $g_1(x, 0) < 0, x > p,$

(iii) $g_2(0, y) > 0, y \in (0, q),$

(iv) $g_2(0, y) < 0, y > q.$

It is easy to see that under assumptions (3.1)–(3.1), the equation

$$\frac{dx}{dt} = xg_1(x, 0) \tag{3.1.3}$$

defines a one dimensional dynamical system on $x \in [0, +\infty)$, with the equilibrium

$$x = p \tag{3.1.4}$$

being globally asymptotically stable (GAS) on $(0, +\infty)$. Similarly,

$$\frac{dy}{dt} = yg_2(0, y) \tag{3.1.5}$$

defines a one dimensional dynamical system on $y \in [0, +\infty)$, with the equilibrium

$$y = q \tag{3.1.6}$$

being GAS on $(0, +\infty)$.

Remark. Further, the functions can be considered as limiting growth due to limited resources because g_1 is decreasing in x and g_2 is decreasing in y .

3.2 Basic Properties of the Model

In this section, we explore some of the basic dynamical properties of system (3.1.1)–(3.1.2).

3.2.1 Existence, Positivity and Boundedness of the solution

Theorem 13. *The solutions $x(t)$ and $y(t)$ for system (3.1.1)–(3.1.2) with non-negative initial conditions exist for all $t \geq 0$ and it is unique. Furthermore, system (3.1.1)–(3.1.2) defines a dynamical system on \mathbb{R}_+^2 .*

Proof. Let $(x(t), y(t))$ be the solution of system (3.1.1) and (3.1.2) with $(x(0), y(0)) = (x_0, y_0) \in \mathbb{R}_+^2$. One can easily see that each of the right hand side of (3.1.1)–(3.1.2) exists and is continuous, by Theorem 2 and Theorem 4, the solution to the initial value problem (3.1.1)–(3.1.2) exists and it is locally unique. Moreover, the fact that g_1 and g_2 have continuous derivatives on \mathbb{R}_+^2 implies uniqueness and local existence of solution of (3.1.1)–(3.1.2) initiated at $(x_0, y_0) \in \mathbb{R}_+^2$ by Theorem 4. Considering the remark to Theorem 4, it is enough to show that the solution is bounded in its maximal interval of existence.

It is easy to see that the solution of (3.1.1)–(3.1.2) is non-negative. One way of showing this directly is by integrating

$$\frac{1}{x} \frac{dx}{dt} = g_1(x, y),$$

which yields

$$x(t) = x_0 \exp\left(\int_0^t g_1(x(s), y(s)) ds\right) \geq 0.$$

In order to prove that the solution is bounded above, we make use of equations (3.1.3) and (3.1.5). Let $\hat{x}(t)$ be the solution of (3.1.3) with $x(0) = x_0$ and let $\hat{y}(t)$ be the solution of (3.1.5) with $y(0) = y_0$. Due to assumption (3.1)–(3.1), we have

$$\hat{x}(t) \leq \max\{x_0, p\}. \quad (3.2.1)$$

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Similarly, for the solution $\hat{y}(t)$, we have

$$\hat{y}(t) \leq \max\{y_0, q\}. \quad (3.2.2)$$

Using (3.2.1)–(3.2.2) and assumption (3.1), we have

$$\begin{aligned} \frac{dx}{dt} &= xg_1(x, y) \leq xg_1(x, 0), \\ \frac{dy}{dt} &= yg_2(x, y) \leq yg_2(0, y). \end{aligned}$$

Hence,

$$x(t) \leq \hat{x}(t) \text{ and } y(t) \leq \hat{y}(t), \quad t \geq 0.$$

As a consequence, all solutions of the model with initial conditions in \mathbb{R}_+^2 remains in \mathbb{R}_+^2 . Therefore, by Theorem 4 and Corollary 2.1.1, the solution exists for all $t \in [0, +\infty)$. Thus, the system (3.1.1) and (3.1.2) defines a dynamical system on \mathbb{R}_+^2 . \square

Theorem 13 implies that system (3.1.1)–(3.1.2) is well-posed epidemiologically and mathematically in \mathbb{R}_+^2 [48], hence, it is sufficient to study qualitatively the dynamics of this system. The Jacobian of the right hand side of (3.1.1)–(3.1.2) is

$$J(x, y) = \begin{pmatrix} g_1(x, y) + x \frac{\partial}{\partial x} g_1(x, y) & x \frac{\partial}{\partial y} g_1(x, y) \\ y \frac{\partial}{\partial x} g_2(x, y) & g_2(x, y) + y \frac{\partial}{\partial y} g_2(x, y) \end{pmatrix}. \quad (3.2.3)$$

It is easy to investigate the stability properties of the equilibria $(0, 0)$, $(p, 0)$, $(0, q)$.

Indeed, at $(0, 0)$, we have

$$J(0, 0) = \begin{pmatrix} g_1(0, 0) & 0 \\ 0 & g_2(0, 0) \end{pmatrix}. \quad (3.2.4)$$

Hence, $(0, 0)$ is a repelling node.

At $(p, 0)$, we have

$$J(p, 0) = \begin{pmatrix} p \frac{\partial}{\partial x} g_1(p, 0) & p \frac{\partial}{\partial y} g_1(p, 0) \\ 0 & g_2(p, 0) \end{pmatrix} \quad (3.2.5)$$

Since $p \frac{\partial}{\partial x} g_1(p, 0)$ is negative, stability of $(p, 0)$ depends on $g_2(p, 0)$. We may have either attractive node if $g_2(p, 0) < 0$ or saddle point if $g_2(p, 0) > 0$. Similarly, one can consider $(0, q)$.

The next theorem shows that when $(p, 0)$ and $(0, q)$ are both saddle points, we have uniform strong persistence of both species.

Theorem 14. *If g_1 and g_2 are such that $g_1(0, q) > 0$ and $g_2(p, 0) > 0$, then the dynamical system defined in (3.1.1)–(3.1.2) is permanent.*

Proof. To prove the statement of the theorem, we will show that there exists ϵ such that the set $\Omega_\epsilon = [\epsilon, p + \epsilon] \times [\epsilon, q + \epsilon]$ is absorbing. Indeed, if such ϵ exists, it is easy to see that Definition 21 holds. Hence, we have permanence of both species. We will prove the existence of ϵ with the stated property in three steps.

Step 1: For every $\epsilon > 0$, the set $[0, p + \epsilon] \times [0, q + \epsilon]$ is absorbing. Let $(x_0, y_0) \in \mathbb{R}_+^2$. The statement trivially holds when $x_0 = 0, y_0 = 0$. Let $x_0 > 0, y_0 > 0$. Denote by \hat{x} and \hat{y} the solutions of (3.1.3) with $x(0) = x_0$ and the solutions of (3.1.5) with $y(0) = y_0$ respectively. Due to (3.1)–(3.1), we have

$$\lim_{t \rightarrow \infty} \hat{x} = p, \quad \lim_{t \rightarrow \infty} \hat{y} = q. \quad (3.2.6)$$

Using equations

$$\begin{aligned} \frac{dx}{dt} &= xg_1(x, y) \leq xg_1(x, 0), \\ \frac{dy}{dt} &= yg_2(x, y) \leq yg_2(0, y) \end{aligned}$$

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we have

$$\begin{aligned}x(t) &\leq \hat{x}(t), \\y(t) &\leq \hat{y}(t).\end{aligned}$$

Taking into account (3.2.6) we obtain that there exists \bar{t} such that $x(t) < p + \epsilon$, $y(t) < q + \epsilon$ for $t > \bar{t}$. Hence, $[0, p + \epsilon] \times [0, q + \epsilon]$ is absorbing.

Step 2: There exists ϵ such that $\Omega_\epsilon = [\epsilon, p + \epsilon] \times [\epsilon, q + \epsilon]$ is positively invariant. Let $\eta_1 = \min_{y \in [\epsilon, q + \epsilon]} g_1(0, y) = g_1(0, q)$. By the assumption in the theorem, it is clear that $\eta_1 > 0$. Since $[0] \times [0, q]$ is compact, there exists $\epsilon_1 > 0$ such that $g_1(x, y) > \frac{\eta_1}{2}$ for $y \in [0, q + \epsilon_1]$, $x \in [0, \epsilon_1]$. Similarly, there exists $\epsilon_2 > 0$ such that $g_2(x, y) > \frac{\eta_2}{2}$ for $x \in [0, p + \epsilon_2]$, $y \in [0, \epsilon_2]$, where $\eta_2 = \min_{x \in [\epsilon, p + \epsilon]} g_2(x, 0) = g_2(p, 0)$. Let $\epsilon = \min\{\epsilon_1, \epsilon_2\}$. Consider the vector field of (3.1.1)–(3.1.2) on the line $x = \epsilon$. The dot product of the normal vector is

$$\left[\begin{pmatrix} xg_1(x, y) \\ yg_2(x, y) \end{pmatrix} \cdot \begin{pmatrix} -1 \\ 0 \end{pmatrix} \right] = -xg_1(x, y) < -\frac{\eta_1}{2}\epsilon < 0 \text{ for } y \in (\epsilon, q + \epsilon). \quad (3.2.7)$$

Considering the dot product of the normal vector on the line $y = \epsilon$, $x \in (\epsilon, p + \epsilon)$, we have

$$\left[\begin{pmatrix} xg_1(x, y) \\ yg_2(x, y) \end{pmatrix} \cdot \begin{pmatrix} 0 \\ -1 \end{pmatrix} \right] = -yg_2(x, y) < -\frac{\eta_2}{2}\epsilon < 0. \quad (3.2.8)$$

The inequalities (3.2.7)–(3.2.8) and *step 1* imply that Ω_ϵ is positively invariant.

Step 3: The set Ω_ϵ , for ϵ as defined in step 2, is an absorbing set. Taking into account step 1, it is enough to consider $(x_0, y_0) \in (0, \epsilon) \times (0, q + \epsilon)$ and $(x_0, y_0) \in (0, p + \epsilon) \times (0, \epsilon)$. Let $x_0 \in (0, \epsilon)$ and $y_0 \in (0, q + \epsilon)$. If $x_0 < \epsilon$, we have $\frac{dx}{dt} = xg_1(x, y) > x\frac{\eta_1}{2}$. Then, the solution of (3.1.1) is such that $x(t) > x_0 e^{\frac{\eta_1}{2}t}$. Therefore, there exists $t > 0$ such that $x(t) > \epsilon$. Similarly, if $y_0 < \epsilon$, we have that $y(t) > \epsilon$ for some $t > 0$. This together with step 2 proves that Ω_ϵ is absorbing. This completes the proof of the theorem. \square

3.3 The system with linear per capita growth rate

In this section, we consider the specific model with linear per capita growth rate of two competing species. Our interest is whether or not the system of two competing species is permanent when we have a qualified competition. The system of two competing species is represented [36] as

$$\frac{dx}{dt} = x(1 - ax - by), \quad (3.3.1)$$

$$\frac{dy}{dt} = y(1 - cx - dy), \quad (3.3.2)$$

where $a, b, c,$ and d are positive constants. Equivalently, (4.5.4)–(4.5.5) can be expressed as

$$\begin{aligned} \frac{dx}{dt} &= xg_1(x, y), \\ \frac{dy}{dt} &= yg_2(x, y), \end{aligned}$$

where

$$g_1(x, y) = 1 - ax - by,$$

$$g_2(x, y) = 1 - cx - dy.$$

One can observe that this is also a Lotka-Volterra system (1.2.1) in two dimensions. In this setting, qualified or weak competition as discussed in Section 21 means

$$a > c, \quad b < d. \quad (3.3.3)$$

System (3.3.1)–(3.3.2), has the following equilibria;

$$(0, 0), \quad \left(\frac{1}{a}, 0\right), \quad \left(0, \frac{1}{d}\right), \quad (x^*, y^*),$$

where $x^* = \frac{d-b}{ad-bc}$, $y^* = \frac{a-c}{ad-bc}$.

Theorem 15. Under the assumption of qualified competition given in (3.3.3), system (3.3.1)–

3.3. THE SYSTEM WITH LINEAR PER CAPITA GROWTH RATE

(3.3.2) is permanent and the endemic equilibrium (x^*, y^*) is GAS on $(0, +\infty) \times (0, +\infty)$.

Proof. The permanence is easy to obtain by using Theorem 14. Indeed, (3.3.1)–(3.3.2) is of the form (3.1.1)–(3.1.2) with $g_1(x, y) = 1 - ax - by$, $g_2(x, y) = 1 - cx - dy$. Then, it is enough to observe that $g_1(0, q) > 0$ and $g_2(p, 0) > 0$, where $p = \frac{1}{a}$ and $q = \frac{1}{d}$. Indeed, $g_1(0, q) = 1 - \frac{b}{d} > 0$ due to Definition 21. Similarly, $g_2(p, 0) = 1 - \frac{c}{a} > 0$ due to Definition 21.

Taking into account the uniform persistence, all solutions tend to (x^*, y^*) as it is the only equilibrium in the interior of \mathbb{R}_+^2 . By step 2 of the proof of Theorem 14, all solutions are eventually absorbed in the compact set $[0, p + \epsilon] \times [0, q + \epsilon]$ for an $\epsilon > 0$. Hence, by Poincaré-Bendixson theorem, every orbit tends to either an equilibrium or a limit cycle. We show that there are no periodic orbits by using the Dulac's criterion. Indeed, we have

$$\frac{\partial}{\partial x} \left(\frac{1 - ax - by}{y} \right) + \frac{\partial}{\partial y} \left(\frac{1 - cx - dy}{x} \right) = -\frac{a}{y} - \frac{d}{x} < 0.$$

Thus, by [36, Theorem 4.8, Theorem 4.9, p. 154], the system has no periodic solutions. This means that every solution tends to an equilibrium. Therefore, since (x^*, y^*) is the only stable equilibrium, by [55, Section 3.5], (x^*, y^*) is globally asymptotically stable. Hence, the theorem is proved. \square

We show by an example that under qualified competition, system (3.3.1)–(3.3.2) has a stable equilibrium in the interior of \mathbb{R}_+^2 . Taking $a = \frac{14}{5}$, $b = \frac{9}{5}$, $c = \frac{8}{5}$, $d = \frac{13}{5}$, (3.3.1)–(3.3.2) becomes

$$\begin{aligned} \frac{dx}{dt} &= x \left(1 - \frac{14}{5}x - \frac{9}{5}y \right), \\ \frac{dy}{dt} &= y \left(1 - \frac{8}{5}x - \frac{13}{5}y \right). \end{aligned} \tag{3.3.4}$$

The equilibrium equations are

$$\begin{aligned} 0 &= x \left(1 - \frac{14}{5}x - \frac{9}{5}y \right), \\ 0 &= y \left(1 - \frac{8}{5}x - \frac{13}{5}y \right). \end{aligned}$$

This leads to the equilibria;

$$(0, 0), \left(\frac{5}{14}, 0\right), \left(0, \frac{5}{13}\right), \left(\frac{2}{11}, \frac{3}{11}\right).$$

The Jacobian matrix for system (3.3.4) is

$$\begin{pmatrix} 1 - \frac{2}{5}x - \frac{9}{5}y & -\frac{9}{5}x \\ -\frac{8}{5}y & 1 - \frac{8}{5}x - \frac{26}{5}y \end{pmatrix}.$$

The Jacobian matrix computed at $(0, 0)$ is

$$\begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix},$$

so that by Theorem 7, $(0, 0)$ is clearly unstable. The Jacobian matrix evaluated at $(\frac{5}{14}, 0)$ is

$$\begin{pmatrix} -1 & -\frac{9}{14} \\ 0 & \frac{3}{7} \end{pmatrix}.$$

Since we have a lower triangular matrix, the following are the eigenvalues; $\lambda_1 = -1$, $\lambda_2 = \frac{3}{7}$.

Since the eigenvalues have opposite signs, by Theorem 7, $(\frac{5}{14}, 0)$ is unstable. For $(0, \frac{5}{13})$, one

can easily compute the following eigenvalues; $\lambda_1 = \frac{4}{13}$, $\lambda_2 = -1$. Similarly, since eigenvalues

have opposite signs, by Theorem 7 this equilibrium is unstable too. Next, we determine the

linear stability of endemic equilibrium. The Jacobian matrix computed at $(\frac{2}{11}, \frac{3}{11})$ is

$$\begin{pmatrix} -\frac{27}{55} & -\frac{18}{55} \\ -\frac{24}{55} & -\frac{39}{55} \end{pmatrix},$$

3.4. MODEL OF TWO COMPETING SPECIES WITH CONSPECIFIC SUPPORT

and the associated eigenvalues are;

$$\lambda_1 = \frac{3(2\sqrt{13} - 11)}{55}, \quad \lambda_2 = -\frac{3(2\sqrt{13} + 11)}{55}.$$

Since all eigenvalues are negative, then we conclude by Theorem 7 that the coexistent equilibrium is stable. Figure 3.1 illustrates the numerical simulation for system (3.3.4). Observe that all trajectories in \mathbb{R}_+^2 converge to this coexistent equilibrium which means this equilibrium is globally asymptotically stable, [36].

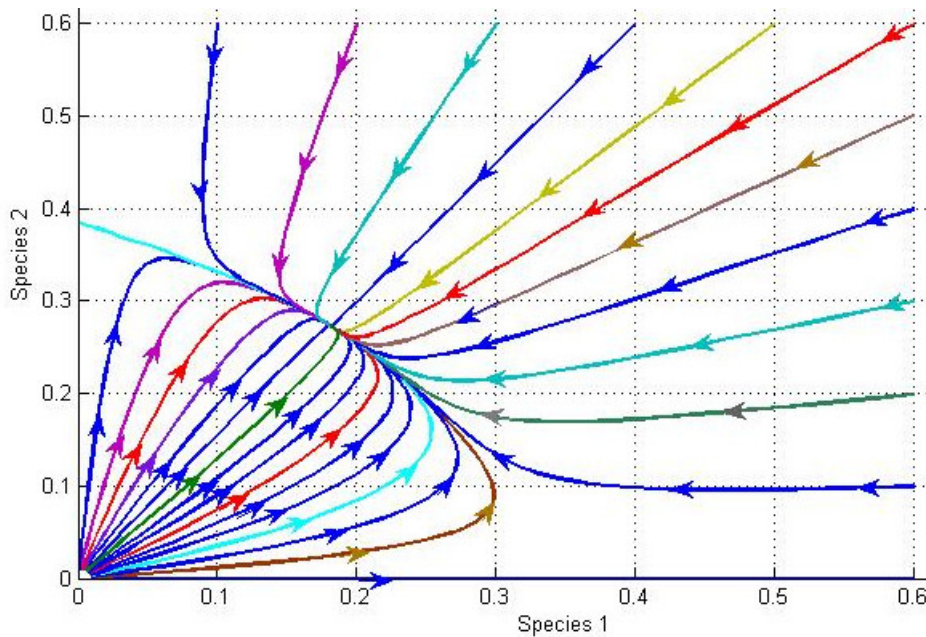


Figure 3.1: A typical trajectories

It is easy to show that if the competition is unqualified, the system (3.3.1)–(3.3.2) will not persist.

3.4 Model of two competing species with Conspecific Support

We model the conspecific support multiplying the per capita growth rate by a linear factor. We exclude from this operation the density independent mortality rate, which reflects the maximum life-span of the species and is independent of condition or support. In this way we

obtain from (3.1.1)–(3.1.2) the following system

$$\frac{dx}{dt} = x(1 + \beta_1 x)(g_1(x, y) + \mu_1) - \mu_1 x, \quad (3.4.1)$$

$$\frac{dy}{dt} = y(1 + \beta_2 y)(g_2(x, y) + \mu_2) - \mu_2 y, \quad (3.4.2)$$

where β_1, β_2 are coefficients in the respective linear factors and μ_1, μ_2 are the density independent death rates of the two species. For $\beta_1 = \beta_2 = 0$ the system (3.4.1)–(3.4.2) is exactly (3.1.1)–(3.1.2). For positive values of β_1 and/or β_2 the model (3.4.1)–(3.4.2) is of the same form as (3.1.1)–(3.1.2) with right-hand side

$$\begin{aligned} \frac{dx}{dt} &= x\tilde{g}_1(x, y), \\ \frac{dy}{dt} &= y\tilde{g}_2(x, y), \end{aligned}$$

where

$$\tilde{g}_1(x, y) = (1 + \beta_1 x)g_1(x, y) + \mu_1\beta_1 x, \quad (3.4.3)$$

$$\tilde{g}_2(x, y) = (1 + \beta_2 y)g_2(x, y) + \mu_2\beta_2 y. \quad (3.4.4)$$

Note. The fact that system (3.4.1)–(3.4.2) is of the same form as (3.1.1)–(3.1.2), the introduction of the parameters β and μ does not affect the dynamics of system (3.4.1)–(3.5.2). It can be shown that the solution of system (3.4.1)–(3.4.2) preserves existence and uniqueness properties and that it is bounded for all time.

It is easy to see that if β_1 is sufficiently large then for small population the per-capita growth rate of the first species increases as x increases. This is the so called Allee Effect. More precisely, due to the specific form chosen for representing the conspecific support, we have a weak Allee Effect, since there is no additional positive equilibrium generated by the conspecific support. Similar argument holds for the second species. Let us note that in the strong Allee Effect we have an unstable positive equilibrium referred to as a minimum survival density. We show that a type of conspecific support resulting only in weak Allee Effect may destabilize the co-existence of the species. Indeed, $\tilde{g}_1(x, 0)$ has a root $\tilde{p}(\beta_1, \mu_1) > p$.

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We show the existence of a root of $\tilde{g}_1(x, 0)$ by taking $y = 0$ in (3.4.3), which yields

$$\tilde{g}_1(x, 0) = (1 + \beta_1 x)g_1(x, 0) + \beta_1 \mu_1 x = (1 + \beta_1 x)\psi(x),$$

where

$$\psi(x) := g_1(x, 0) + \mu_1 \left(1 - \frac{1}{1 + \beta_1 x}\right). \quad (3.4.5)$$

The function ψ has the following properties;

(a) $\lim_{x \rightarrow \infty} \psi(x) = -\infty$,

(b) $\psi(p) > 0$. We can see this when we set $x = p$ in (3.4.5) to have

$$\psi(p) = \mu_1 \left(1 - \frac{1}{1 + \beta_1 p}\right) > 0, \text{ as } g_1(p, 0) = 0.$$

Thus, there exists $\tilde{p}(\beta_1, \mu_1) > p$ such that ψ changes sign from positive to negative at \tilde{p} . Equivalently, $\tilde{g}_1(x, 0)$ changes sign from positive to negative at \tilde{p} . Similarly, there exists $\tilde{q}(\beta_2, \mu_2) > q$ such that $\tilde{g}_2(0, y)$ changes sign from positive to negative at $\tilde{p} = \tilde{q}$. Then, if g_2 is unbounded below and $\tilde{p}(\beta_1, \mu_1)$ is sufficiently large, we have

$$\tilde{g}_2(\tilde{p}, 0) = g_2(\tilde{p}, 0) < 0. \quad (3.4.6)$$

It is easy to see that the Jacobian of (3.4.3)–(3.4.4) at $(\tilde{p}, 0)$ is

$$J(\tilde{p}, 0) = \begin{pmatrix} \tilde{p} \frac{\partial}{\partial x} \tilde{g}_1(\tilde{p}, 0) & \tilde{p} \frac{\partial}{\partial y} \tilde{g}_1(\tilde{p}, 0) \\ 0 & \tilde{g}_2(\tilde{p}, 0) \end{pmatrix}.$$

Since $g_1(x, 0)$ is decreasing on x , we have $\frac{\partial}{\partial x} \tilde{g}_1(\tilde{p}, 0) < 0$. Then $\tilde{g}_2(\tilde{p}, 0) < 0$ implies that $(\tilde{p}, 0)$ is stable and attractive, that is, the second species does not uniformly persist. Similarly, it is possible through the conspecific support to have an attractive equilibrium $(0, \tilde{q})$ implying that the first species does not uniformly persist. Hence, the system is not persistent.

Remark. If a root $\tilde{p}(\beta_1, \mu_1)$ of (3.4.5) with the properties (3.4.6) exists, then it is not necessarily unique. Nevertheless, the existence of such a root is sufficient to imply uniform persistence of the second species.

3.5 Destabilising the Qualified Competition Equilibrium

In this section, we consider an example of a system of two competing species with conspecific support where the qualified competition equilibrium is destabilised. The model (3.4.1)–(3.4.2) in the case of model (3.3.1)–(3.3.2) has the form

$$\frac{dx}{dt} = x(1 + \beta x)(1 + \mu - ax - by) - \mu x, \quad (3.5.1)$$

$$\frac{dy}{dt} = y(1 + \beta y)(1 + \mu - cx - dy) - \mu y \quad (3.5.2)$$

where a, b, c and d are positive constants. Clearly, system (3.5.1)–(3.5.2) is a particular case of (3.4.1)–(3.4.2). Just like system (3.1.1)–(3.1.2), the above system has four equilibria. We will determine and discuss the nature of each equilibrium.

The equilibrium \tilde{p} of the first species in the absence of the second is the positive root of

$$(1 + \beta x)(1 + \mu - ax) - \mu = 0 \quad (3.5.3)$$

or equivalently,

$$a\beta x^2 - (\mu\beta + \beta - a)x - 1 = 0.$$

Hence,

$$\tilde{p} = \frac{1}{2a\beta}(\mu\beta + \beta - a) + \sqrt{(\mu\beta + \beta - a)^2 + 4a\beta}.$$

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Considering μ fixed, we have \tilde{p} as a function of β in the form

$$\tilde{p}(\beta) = \frac{\mu+1}{2a} - \frac{1}{2\beta} + \sqrt{\left(\frac{\mu+1}{2a} - \frac{1}{2\beta}\right)^2 + \frac{1}{a\beta}}. \quad (3.5.4)$$

Similarly, the positive equilibrium of the second species in the absence of the first is

$$\tilde{q}(\beta) = \frac{\mu+1}{2d} - \frac{1}{2\beta} + \sqrt{\left(\frac{\mu+1}{2d} - \frac{1}{2\beta}\right)^2 + \frac{1}{d\beta}}.$$

Thus, for system (4.5.4)–(4.5.5) we have the following boundary equilibria;

$$(0, 0), \quad (\tilde{p}(\beta), 0), \quad (0, \tilde{q}(\beta)).$$

Lemma 1. *Properties of $\tilde{p}(\beta)$*

(i) $\tilde{p}(\beta)$ is an increasing function of β , and

(ii) $\lim_{\beta \rightarrow \infty} \tilde{p}(\beta) = \frac{\mu+1}{a} > \frac{1}{a}$.

Proof. (i) To show that $\tilde{p}(\beta)$ is an increasing function, consider the derivative of $\tilde{p}(\beta)$ wrt β , that is,

$$\begin{aligned} \frac{d\tilde{p}}{d\beta} &= \frac{1}{2\beta^2} + \frac{2\left(\frac{\mu+1}{2a} - \frac{1}{2\beta}\right)\left(\frac{1}{2\beta^2}\right) - \frac{1}{a\beta^2}}{2\sqrt{\left(\frac{\mu+1}{2a} - \frac{1}{2\beta}\right)^2 + \frac{1}{a\beta}}}, \\ &= \frac{1}{2\beta^2} + \frac{1}{\beta^2} \frac{\left(\frac{\mu+1}{2a} - \frac{1}{2\beta}\right) - \frac{1}{a}}{2\sqrt{\left(\frac{\mu+1}{2a} - \frac{1}{2\beta}\right)^2 + \frac{1}{a\beta}}}, \\ &= \frac{1}{2\beta^2} \left(1 + \frac{\left(\frac{\mu-1}{2a} - \frac{1}{2\beta}\right) - \frac{1}{a}}{2\sqrt{\left(\frac{\mu-1}{2a} - \frac{1}{2\beta}\right)^2 + \frac{1}{a^2}}}\right). \end{aligned}$$

If $\frac{\mu+1}{2a} - \frac{1}{2\beta} > 0$, then $\frac{d\tilde{p}}{d\beta} > 0$. Let $\frac{\mu+1}{2a} - \frac{1}{2\beta} < 0$. Then

$$\begin{aligned} \frac{d\tilde{p}}{d\beta} &= \frac{1}{2\beta^2} \left(1 + \frac{\frac{\mu-1}{2a} - \frac{1}{2\beta}}{2\sqrt{\left(\frac{\mu-1}{2a} - \frac{1}{2\beta}\right)^2 + \frac{\mu}{4a^2}}} \right), \\ &> \frac{1}{2\beta^2} \left(1 + \frac{\frac{\mu-1}{2a} - \frac{1}{2\beta}}{2\sqrt{\left(\frac{\mu-1}{2a} - \frac{1}{2\beta}\right)^2}} \right), \\ &= \frac{1}{2\beta^2} \left(1 + \frac{\frac{\mu-1}{2a} - \frac{1}{2\beta}}{2\left|\frac{\mu-1}{2a} - \frac{1}{2\beta}\right|} \right), \\ &= \frac{1}{2\beta^2} \left(1 + \left(-\frac{1}{2}\right) \right) > 0 \end{aligned}$$

Thus, $\tilde{p}(\beta)$ is increasing.

(ii)

$$\begin{aligned} \lim_{\beta \rightarrow \infty} \tilde{p}(\beta) &= \lim_{\beta \rightarrow \infty} \left(\frac{\mu+1}{2a} - \frac{1}{2\beta} + \sqrt{\left(\frac{\mu+1}{2a} - \frac{1}{2\beta}\right)^2 + \frac{1}{a\beta}} \right), \\ &= \frac{\mu+1}{2a} + \sqrt{\left(\frac{\mu+1}{2a}\right)^2} = \frac{\mu+1}{a} \end{aligned}$$

□

From Equation (3.5.2), we have

$$\tilde{g}_2(\tilde{p}, 0) = 1 - c\tilde{p} \xrightarrow{\beta \rightarrow \infty} 1 - c \frac{(\mu+1)}{a} = \frac{c}{a} \left(\frac{a}{c} - 1 - \mu \right). \quad (3.5.5)$$

Therefore, $\mu > \frac{a}{c} - 1$ is a necessary condition for $(\tilde{p}, 0)$ becoming attractive.

Theorem 16. *If $\mu > \frac{a}{c} - 1 > 0$, there exists β_{crit} such that for the model (3.5.1)–(3.5.2), we have $\tilde{g}_2(\tilde{p}(\beta), 0) < 0$ and $\tilde{g}_1(0, \tilde{q}(\beta)) < 0$ for $\beta > \beta_{crit}$.*

Proof. Let $\mu > \frac{a}{c} - 1 > 0$, be fixed. Taking into account Lemma 1 (i.e $\tilde{p}(\beta)$ is an increasing

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function), we have

$$\lim_{\beta \rightarrow \infty} \tilde{p}(\beta) = \frac{1}{a} = p, \quad \lim_{\beta \rightarrow 0} \tilde{p}(\beta) = \frac{\mu + 1}{a}.$$

Taking in account (3.5.5), the function

$$\tilde{g}_2(\tilde{p}(\beta), 0) = 1 - c\tilde{p}(\beta),$$

considered as a function of β , decreases from $1 - \frac{c}{a} > 0$ to $\frac{c}{a} \left(\frac{a}{c} - 1 - \mu \right) < 0$. Therefore, there exists $\beta_{crit}^{(1)} \in (0, +\infty)$ such that $\tilde{g}_2(\tilde{p}(\beta_{crit}^{(1)}), 0) = 0$ and $\tilde{g}_2(\tilde{p}(\beta), 0) < 0$ for $\beta > \beta_{crit}^{(1)}$. Similarly, there exists $\beta_{crit}^{(2)}$ such that $\tilde{g}_1(0, \tilde{q}(\beta)) < 0$ for $\beta > \beta_{crit}^{(2)}$. Then $\beta_{crit} = \max\{\beta_{crit}^{(1)}, \beta_{crit}^{(2)}\}$ is the threshold value of β required in the statement of the theorem.

Typical set of trajectories when $\beta > \beta_{crit}$ is presented on Figure 3.2 with the parameter values presented in Table 3.1

Table 3.1: Parameter values

a	b	c	d	β	μ
2.1	1	2	1.1	5	0.5

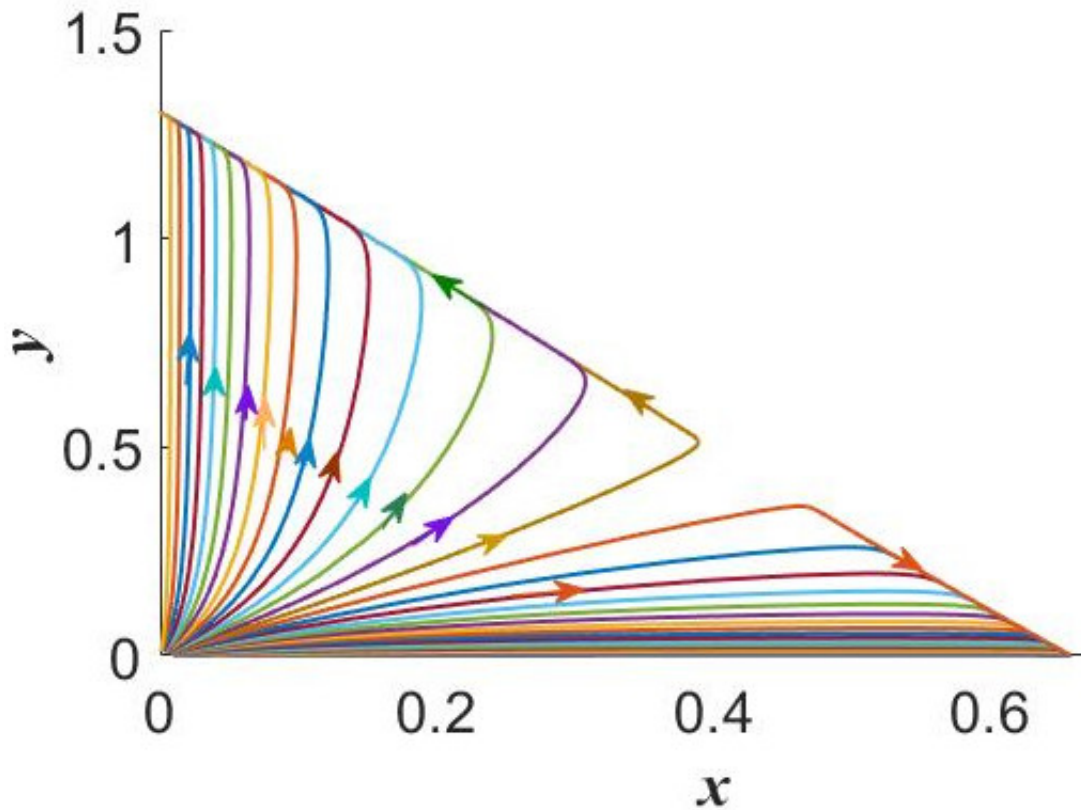


Figure 3.2: Typical trajectories of the solutions of (3.5.1)–(3.5.2) for $\beta > \beta_{crit}$

□

Corollary 2. *If $\beta > \beta_{crit}$, the system (3.5.1)–(3.5.2) is not permanent.*

In terms of Definition 19, Corollary 2 implies that the species modelled in (3.5.1)–(3.5.2) do not persist.

Model of n Competing Species

4.1 Introduction and Model Formulation

In this chapter, we show that the destabilization of coexistence due to conspecific support in the case of two species may lead to pattern formation in the case of many species. We consider n species, arranged in the order of their indexes, where every species interact competitively with its two neighbours. To avoid the influence of other factors, we consider that all species have the same vital dynamics. In fact, we can also consider them as groups of the same species, e.g. packs of dogs, prides of lions, patches of grass. Then a model with linear per capita growth rate can be written in the form;

$$\dot{x}_i = x_i(k - \alpha x_i - x_{i-1} - x_{i+1}), \quad i = 1, \dots, n, \quad (4.1.1)$$

where x_i is the size of the i th species/population of group, α represents the impact of the size/density of the i th species on its own the per capita growth rate and k is the carrying capacity. As usual, in the search for pattern formation, we use periodic boundary condition, that is,

$$x_0 = x_n \text{ and } x_{n+1} = x_1.$$

System (4.1.1) can also be written as

$$\dot{x}_i = x_i g_i(x_i), \quad i = 1, \dots, n, \quad (4.1.2)$$

where g_i is the per capita growth rate of individual species. System (4.1.2) is sometimes known as *Kolmogorov* system [66, 67]. Kolmogorov systems generally model situations where the per capita growth rate of individual species solely depends on the density vector x of

the population. The factor x_i in system (4.1.2) plays a major role, that is, ensuring that no species increases spontaneously.

4.2 Basic Properties of the System

In this section, we explore the basic properties of autonomous system of differential equations (4.1.1).

4.2.1 Existence, Uniqueness and Boundedness of Solutions

In order for system (4.1.1) to be meaningful biologically and consistent with non-negative initial populations, all state variables should remain non-negative and bounded all time.

Theorem 17. *The solution $x_i(t)$ for system (4.1.1) with non-negative initial conditions exists for all time ($t \geq 0$) and it is unique.*

Proof. Let $x_i(t)$ be the solution for system (4.1.1) with $x_i(0) = x_{i0} \in \mathbb{R}_+^n$. It is easy to see that the right hand side of system (4.1.1) is continuously differentiable in a neighbourhood of \mathbb{R}_+^n . Therefore, by existence and uniqueness theorem, the solution $x_i(t)$ of the initial value problem (4.1.1) locally exists and is unique in its maximal of existence [Theorem 2, Theorem 4].

Next, we show that the solution $x_i(t)$ satisfying $x_i(0) \geq 0$ satisfies $x_i(t) \geq 0$ for all $t \in \mathbb{R}_+$. Further, we show that the solution is bounded in the future time and hence, is defined for all $t \in \mathbb{R}_+$.

Recall that (4.1.1) can be written as (4.1.2). Then using integration factor technique, we have

$$\frac{d}{dt} \left(\exp \left(- \int_0^t g_i(x(s)) ds \right) x_i(t) \right) = 0,$$

4.2. BASIC PROPERTIES OF THE SYSTEM

which yields

$$x_i(t) = \exp\left(\int_0^t g_i(x(s))ds\right)x_i(0). \quad (4.2.1)$$

From (4.2.1), we observe that if $x_i(0) = 0$ then for all t , $x_i(t) = 0$. Further, if $x_i(0) > 0$ then $x_i(t) > 0$ for all t . Thus,

$$x_i(t) = \exp\left(\int_0^t g_i(s)ds\right) \geq 0.$$

This shows that the solution $x_i(t)$ of (4.1.1) is non-negative for all $t \geq 0$, hence it is bounded below by 0.

Furthermore, from (4.1.1), we have

$$\begin{aligned} \frac{dx_i}{dt} &= x_i(k - \alpha x_i - x_{i-1} - x_{i+1}), \\ &\leq \alpha x_i\left(\frac{k}{\alpha} - x_i\right), \\ &= kx_i\left(1 - \frac{x_i}{k/\alpha}\right). \end{aligned} \quad (4.2.2)$$

Therefore, we have

$$\begin{aligned} x_i(t) &\leq \frac{k/\alpha}{1 + \frac{k/\alpha - x_i(0)}{x_i(0)}e^{-kt}}, \\ &\leq \max\left\{\frac{k}{\alpha}, x_{i(0)}\right\}, \end{aligned}$$

which shows that $x_i(t)$ is bounded above. Therefore, since $x_i(t)$ is bounded below and above, it is bounded. \square

Theorem 18. System (4.1.1) defines a dynamical system in a biologically feasible region given by

$$\Omega = \{x \in \mathbb{R}_+^n : 0 \leq x_i \leq \frac{k}{\alpha}, i = 1, \dots, n\}. \quad (4.2.3)$$

Proof. It is clear from (4.2.2) that

$$\text{if, } x_i(0) \leq \frac{k}{\alpha} \text{ then, } x_i(t) \leq \frac{k}{\alpha}.$$

Then, taking into account that $x_i(0) \geq 0$, we obtain that $[0, \frac{k}{\alpha}]$ is positively invariant and attractive interval for x_i . Therefore,

$$\Omega = \left[0, \frac{k}{\alpha}\right] \times \left[0, \frac{k}{\alpha}\right] \times \dots \times \left[0, \frac{k}{\alpha}\right]$$

is positively invariant and attractive set for (4.1.1). Consequently, all solutions of (4.1.1) initiated in Ω remain in Ω for all $t \geq 0$. This shows that system (4.1.1) defines a dynamical system in Ω . \square

Theorem 18 shows that in order to determine the asymptotic properties of the solutions of (4.1.1) including the persistence of each species, it is enough to consider (4.1.1) on the set Ω .

4.3 Persistence/Permanence of Species

In this section, we consider the coexistence of species, that is, the permanence of the system (4.1.1). Since the system has a compact global attractor Ω , then it is dissipative. Hence, permanence/uniformly persistence. We first construct a system of (4.1.1) in three dimensions and show uniform persistence by analysing the linear stability of the boundary equilibria. We give a necessary condition under which the three species uniformly persist. Furthermore, we prove our main theorem which shows that n species persist and provide the sufficient conditions under which it is possible. We conclude the section by backing our proof with numerical simulations.

Theorem 19. *Consider system (4.1.1) in \mathbb{R}_+^3 . If $\alpha > 1$, then all 3 species uniformly persist. If $\alpha < 1$, then one or more of the species goes extinct at least for some initial positive values $x(0)$.*

4.3. PERSISTENCE/PERMANENCE OF SPECIES

Proof. For $n = 3$, system (4.1.1) can be written as a system of three differential equations:

$$\begin{aligned} \dot{x}_1 &= x_1(k - \alpha x_1 - x_3 - x_2), \\ \dot{x}_2 &= x_2(k - \alpha x_2 - x_1 - x_3), \\ \dot{x}_3 &= x_3(k - \alpha x_3 - x_2 - x_1). \end{aligned} \tag{4.3.1}$$

At equilibrium, (4.3.1) becomes,

$$\begin{aligned} x_1(k - \alpha x_1 - x_3 - x_2) &= 0, \\ x_2(k - \alpha x_2 - x_1 - x_3) &= 0, \\ x_3(k - \alpha x_3 - x_2 - x_1) &= 0. \end{aligned}$$

On the boundary where $x_3 = 0$, we have

$$\begin{aligned} x_1(k - \alpha x_1 - x_2) &= 0, \\ x_2(k - \alpha x_2 - x_1) &= 0. \end{aligned}$$

The solutions are:

$$\left\{ \begin{array}{l} x_1 = 0, x_2 = 0, \\ x_1 = 0, x_2 = \frac{k}{\alpha}, \\ x_2 = 0, x_1 = \frac{k}{\alpha}, \\ x_1 = x_2 = \frac{k}{\alpha+1}. \end{array} \right.$$

The following are equilibria for system (4.3.1) involving the situation when all species are absent (trivial equilibrium) and only one species is present (extinction equilibrium);

$$(0, 0, 0), (k/\alpha, 0, 0), (0, k/\alpha, 0), (0, 0, k/\alpha).$$

The Jacobian matrix for system (4.3.1), denoted by $J(x_1, x_2, x_3)$ is,

$$\begin{pmatrix} k - 2\alpha x_1 - x_3 - x_2 & -x_1 & -x_1 \\ -x_2 & k - 2\alpha x_2 - x_1 - x_3 & -x_2 \\ -x_3 & -x_3 & k - 2\alpha x_3 - x_2 - x_1 \end{pmatrix}.$$

The Jacobian matrix evaluated at trivial equilibrium $(0, 0, 0)$ is,

$$\begin{pmatrix} k & 0 & 0 \\ 0 & k & 0 \\ 0 & 0 & k \end{pmatrix}.$$

It follows that the eigenvalues are;

$$\lambda_1 = \lambda_2 = \lambda_3 = k > 0.$$

Since all eigenvalues have a positive real part, by Theorem 7, the equilibrium $(0, 0, 0)$ is unstable and repelling node. Further, for $(k/\alpha, 0, 0)$ we have

$$J(k/\alpha, 0, 0) = \begin{pmatrix} -k & -k/\alpha & -k/\alpha \\ 0 & \frac{k(\alpha-1)}{\alpha} & 0 \\ 0 & 0 & \frac{k(\alpha-1)}{\alpha} \end{pmatrix}.$$

Since we have a lower triangular matrix, it follows that the eigenvalues are;

$$\lambda_1 = -k < 0, \quad \lambda_2 = \frac{k(\alpha-1)}{\alpha}, \quad \lambda_3 = \frac{k(\alpha-1)}{\alpha}.$$

Observe that if $\alpha < 1$, then by Theorem 7, $(k/\alpha, 0, 0)$ is a stable node since all the eigenvalues

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are real and are negative. Therefore, species x_2 and x_3 will go to extinct for some initial values $x(0)$. However, if $\alpha > 1$, equilibrium $(k/\alpha, 0, 0)$ is a saddle point, and hence is unstable since $\lambda_2, \lambda_3 > 0$. This means that $(k/\alpha, 0, 0)$ repels towards the interior of \mathbb{R}_+^3 . Similarly, the Jacobian matrix evaluated at $(0, k/\alpha, 0)$ is

$$\begin{pmatrix} \frac{k(\alpha-1)}{\alpha} & 0 & 0 \\ -k/\alpha & -k & -k/\alpha \\ 0 & 0 & \frac{k(\alpha-1)}{\alpha} \end{pmatrix},$$

and we obtain the following eigenvalues;

$$\lambda_1 = \frac{k(\alpha-1)}{\alpha}, \lambda_2 = -k < 0, \lambda_3 = \frac{k(\alpha-1)}{\alpha}.$$

It follows from Theorem 7 that equilibrium $(0, k/\alpha, 0)$ is a stable node if $\alpha < 1$ since all eigenvalues have real parts with a negative sign. This means that for some initial values $x(0)$, species x_1 and x_3 will go to extinct. However, if $\alpha > 1$, equilibrium $(0, k/\alpha, 0)$ is a saddle point, and hence unstable since $\lambda_1, \lambda_3 > 0$. Thus, $(0, k/\alpha, 0)$ repels towards the interior of \mathbb{R}_+^3 . By symmetry, it follows that the corresponding equilibrium $(0, 0, k/\alpha)$ is asymptotically stable for $\alpha < 1$ and unstable for $\alpha > 1$.

Next, we determine the behaviour of solutions when all species are present, that is, coexistent equilibrium that we denote by

$$\mathfrak{e} = \left(\frac{k}{\alpha+2}, \frac{k}{\alpha+2}, \frac{k}{\alpha+2} \right).$$

The Jacobian matrix evaluated at \mathfrak{E} is

$$\begin{pmatrix} -\frac{ak}{a+2} & -\frac{k}{a+2} & -\frac{k}{a+2} \\ -\frac{k}{a+2} & -\frac{ak}{a+2} & -\frac{k}{a+2} \\ -\frac{k}{a+2} & -\frac{k}{a+2} & -\frac{ak}{a+2} \end{pmatrix},$$

and the corresponding eigenvalues are;

$$\lambda_1 = -\frac{(\alpha + 2)}{\alpha + 2}, \lambda_2 = \frac{(1 - \alpha)k}{\alpha + 2}, \lambda_3 = \frac{(1 - \alpha)k}{\alpha + 2}.$$

Indeed, when $\alpha < 1$, the eigenvalues λ_2 and λ_3 have positive real parts. Therefore, by Theorem 7, \mathfrak{E} is unstable node. However, observe that if $\alpha > 1$, \mathfrak{E} is asymptotically stable by Theorem 7. This means that for $\alpha > 1$, all solutions initiated at $x(0)$ close to the extinction equilibria will eventually tend to \mathfrak{E} . This completes the proof. \square

It should be noted that at $\alpha = 1$, we expect to have a bifurcation. However, we have not explored it in this research.

Corollary 3. *In a coordinate face, the equilibria in two dimension interchange between attractors and saddles. In addition, viewing the interior equilibria in the two dimensional plane, one would see that the number of saddles is less than or equal to the number of attractors.*

Below we give a geometry for system (4.3.1) in three dimension which can give rise to persistence especially the cases when there are not less than one interior equilibrium. Let h be the number of coordinate planes which contain the interior equilibrium. In this case, we have $0 \leq h \leq 3$. We assume that the interior equilibria repel side-by-side towards the plane. We denote the interior equilibria by \mathfrak{E}_{in} and the boundary equilibrium by \mathfrak{E}_{bn} where n is a plane where that particular equilibrium lies.

Case 1: $h = 1$. If we have only one equilibrium in the interior of the plane, then Corollary 3 implies that this equilibrium is an attractor. We let this equilibrium be in $x_2 - x_3$ plane. Then equilibrium \mathfrak{E}_{b_1} must repel in at least one direction and in this case, it repels towards x_2 -direction. Equilibrium \mathfrak{E}_{b_3} can either repel or attract in the x_1 -direction. Figure 4.1 illustrates

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this dynamics.

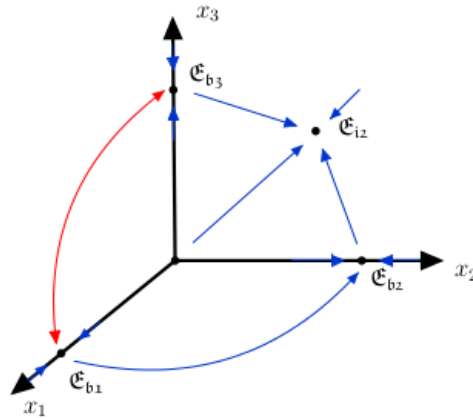
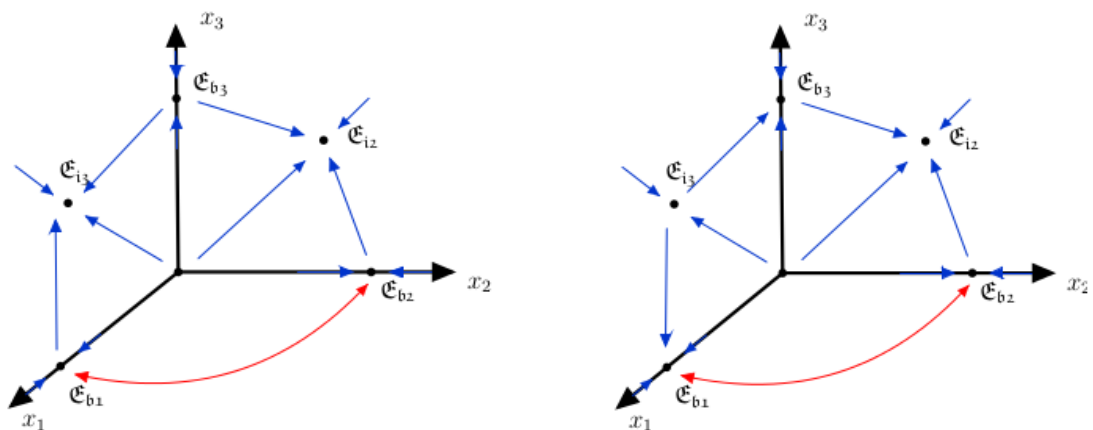


Figure 4.1: The case when we have one interior equilibrium in the plane which is attracting

Case 2: $h = 2$. In this case, we can either have one or two attracting equilibria and a saddle point according to Corollary 3. We can have either both interior equilibria are attracting or only one is attracting. Consider first that both equilibria are attracting and are lying in $x_2 - x_3$ and $x_3 - x_1$ planes. Note that E_{b1} can either attract or repel towards x_2 . Similarly, x_2 can either repel or attract towards x_1 . This is illustrated in Figure 4.2a. For the second case, one of the two interior equilibria is a saddle. Let the attracting equilibrium be in $x_2 - x_3$ plane and the saddle equilibrium be in $x_3 - x_1$ plane. This is illustrated in Figure 4.2b below.

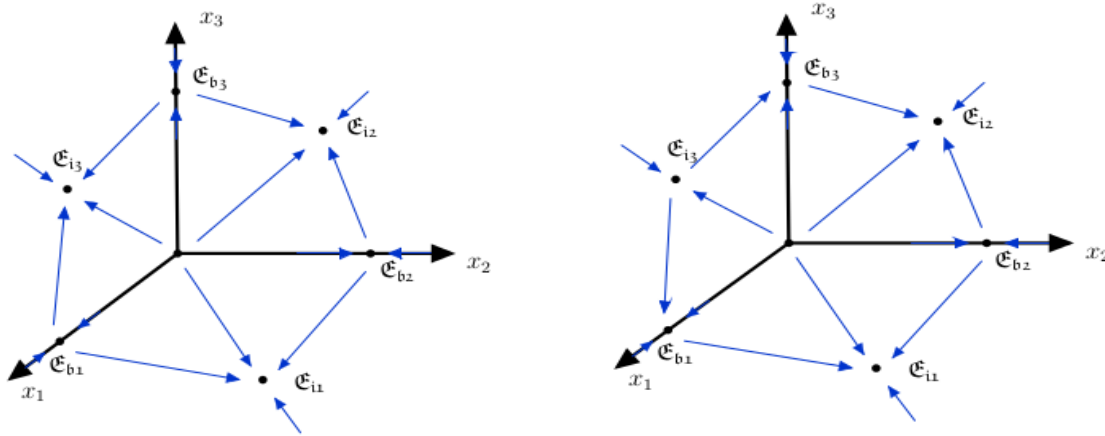


(a) When we have two equilibria E_{i2} and E_{i3} which are both attractors
 (b) When we have two interior equilibria, one is a saddle E_{i3} and another one is an attractor E_{i2}

Figure 4.2: The case when there are two interior equilibria

Case 3: $h = 3$. Corollary 3 tells us that we can have two or three attractors and one saddle

point in order to have persistence. Just like we observed above, we have two situations. In the first one, all three interior equilibria are attracting while in the second one, one of the interior equilibria is a saddle. These two situations are shown in Figure 4.3a and Figure 4.3b respectively.



(a) The case when there are three interior equilibria and all of them are attractors
 (b) The case when there are three interior equilibria where only one is a saddle point

Figure 4.3: The case when there are three interior equilibria

Special Case : $h = 0$. When there are no equilibria in the interior, Corollary 3 implies that in order to have a strong persistence, we must have at least a one dimensional manifold which is not stable. This behaviour is shown in Figure 4.4.

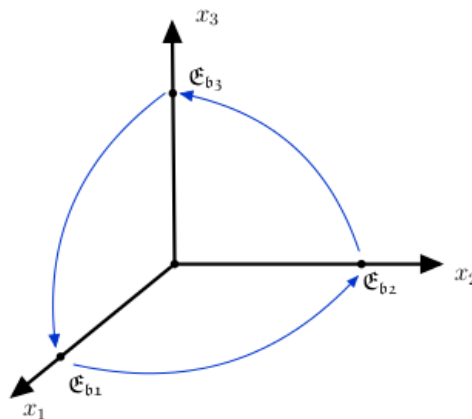


Figure 4.4: The case when we do not have any interior equilibrium in the plane

It is worthy to note that Corollary 3 applies also to n -dimensional system.

Theorem 20. *If $\alpha > 2$, then all n species uniformly persist.*

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Proof. In Theorem 18, we proved that the system (4.1.1) defines the dynamical system in a biologically feasible region given by $\Omega = \left[0, \frac{k}{\alpha}\right]^n$ and that it is positively invariant and attractive. On Ω , we have for every $i \in \{1, 2, \dots, n\}$, the following inequality;

$$\begin{aligned} \dot{x}_i &= x_i(k - \alpha x_i - x_{i-1} - x_{i+1}) \\ &\geq x_i \left(k - \alpha x_i - \frac{k}{\alpha} - \frac{k}{\alpha} \right) \\ &= x_i \left(\frac{k(\alpha - 2)}{\alpha} - \alpha x_i \right) \\ &= \alpha x_i \left(\frac{k(\alpha - 2)}{\alpha^2} - x_i \right). \end{aligned} \tag{4.3.2}$$

Let $x(t)$ be a solution of system (4.1.1) with $x(0) > 0$. Consider the equation

$$\dot{\theta} = \alpha \theta \left(\frac{k(\alpha - 2)}{\alpha} - \theta \right). \tag{4.3.3}$$

Let $i \in \{1, 2, \dots, n\}$ and let θ be the solution of (4.3.3) with initial condition

$$\theta(0) = x_i(0) > 0.$$

Taking into account inequality (4.3.2), we have

$$x_i(t) \geq \theta(t) \xrightarrow{t \rightarrow \infty} \frac{k(\alpha - 2)}{\alpha^2}.$$

Therefore,

$$\liminf_{t \rightarrow \infty} x_i(t) \geq \frac{k(\alpha - 2)}{\alpha^2} > 0, \quad i = 1, \dots, n. \tag{4.3.4}$$

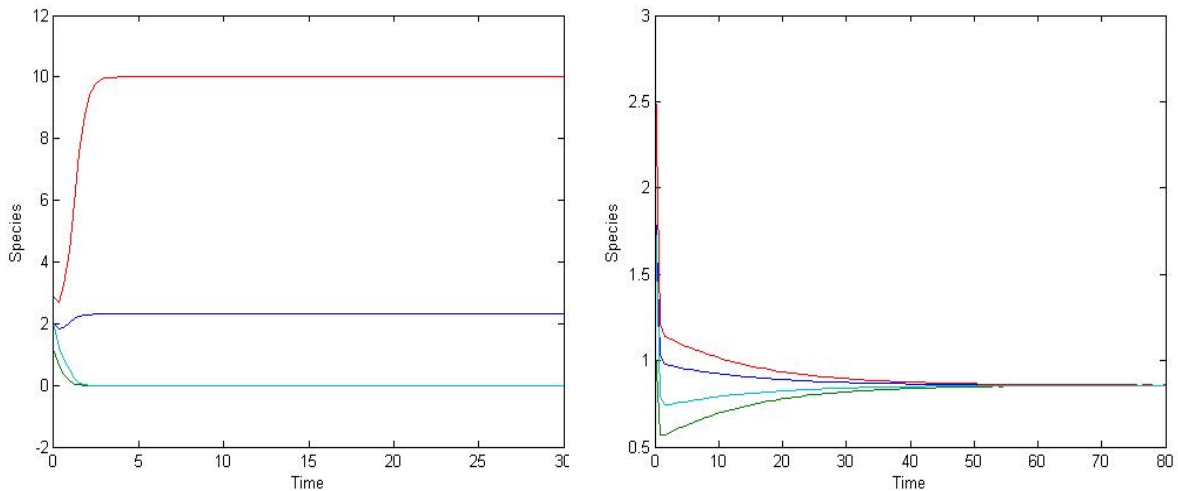
Then, the statement of the theorem follows from Definition 17. This means that all trajectories of system (4.1.1) initiated in \mathbb{R}_+^n are eventually uniformly bounded away from the boundary of \mathbb{R}_+^n when $\alpha > 2$. \square

Remark. The implication of Theorem 19 and Theorem 20 is that the solution (population) of the system (4.1.1) does not tend to a boundary equilibrium as $t \rightarrow \infty$. Biologically, this means that all species persist.

Further, for a three dimensional system, $\alpha > 1$ is a necessary condition for strongly uniformly persistence. The following numerical simulations show that $\alpha > 2$ is also a necessary condition for at least $n = 4$. Note that $\alpha > 2$ implies that the species size/density has a stronger negative impact on its own growth rate than on the growth rate of the neighbouring species.

4.3.1 Numerical Simulations

We begin the numerical simulations by considering system (4.1.1) in three dimensions. Figure 4.5a shows a long-term dynamics of 3 species when $\alpha = 0.30$ with the carrying capacity $k = 3$. Observe that not all species survive. Some fail to cope with the competition and eventually are driven to extinction by the other competitors. On the other hand, Figure 4.5b shows that all species with different initial values survive the competition and converge to a stable coexistent equilibrium in the interior of \mathbb{R}_+^3 . (Note that the extra curve on the simulations is due to noise.)

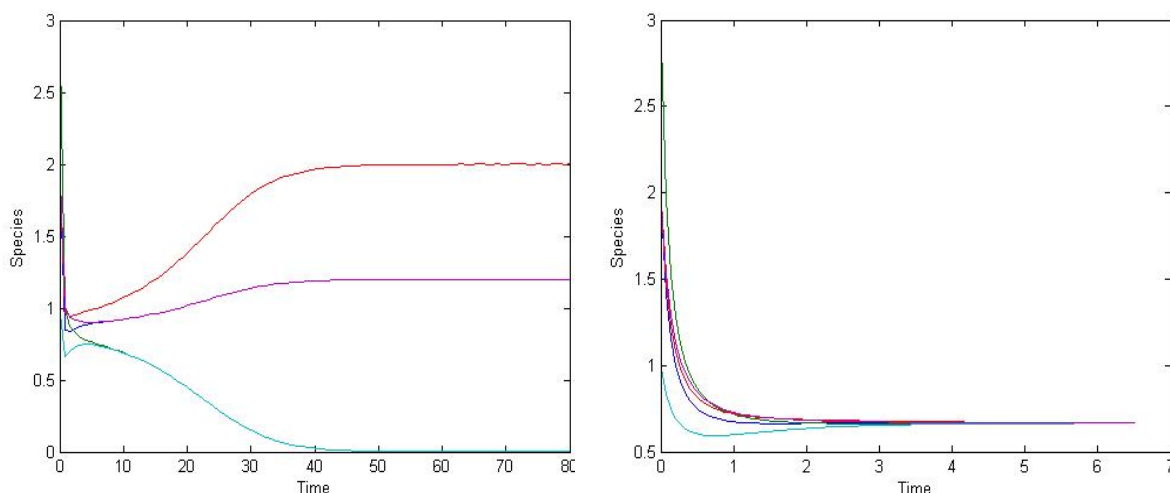


(a) No persistence of species when $\alpha < 1$ (b) Persistence of species occur when $\alpha > 1$

Figure 4.5: The case when there are three species

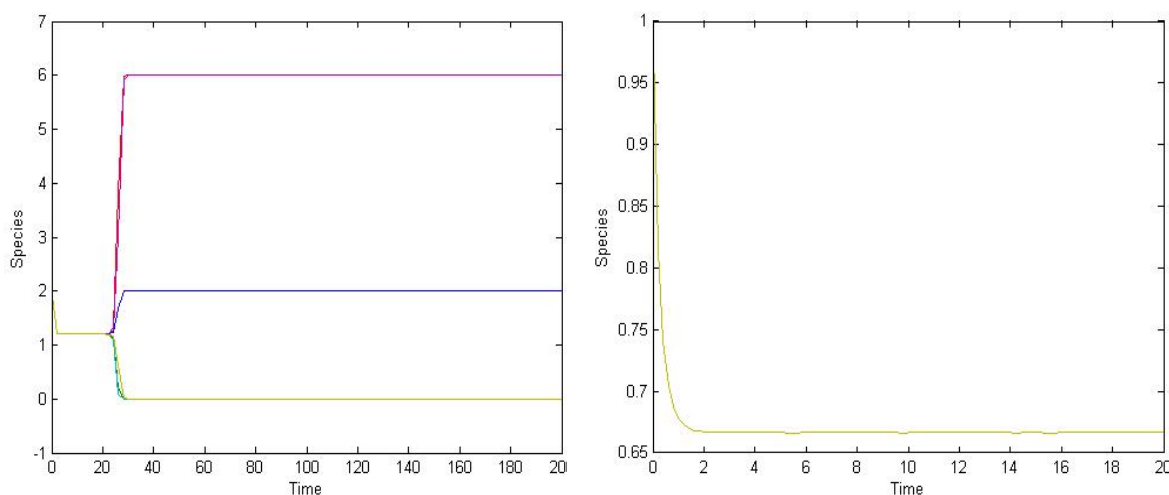
The dynamics of the species where $n = 4$ change. Indeed, $\alpha < 2$ does not satisfy the condition for persistence. Instead, $\alpha > 2$ does. Figure 4.6a illustrates for the case when $\alpha = 1.50$ and Figure 4.6b shows the simulations when $\alpha = 2.50$. Similarly, Figure 4.7a and Figure 4.7b show that persistence holds when $\alpha > 2$.

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(a) No persistence of species when $\alpha = 1.50$ (b) Persistence of species occur when $\alpha = 2.50$

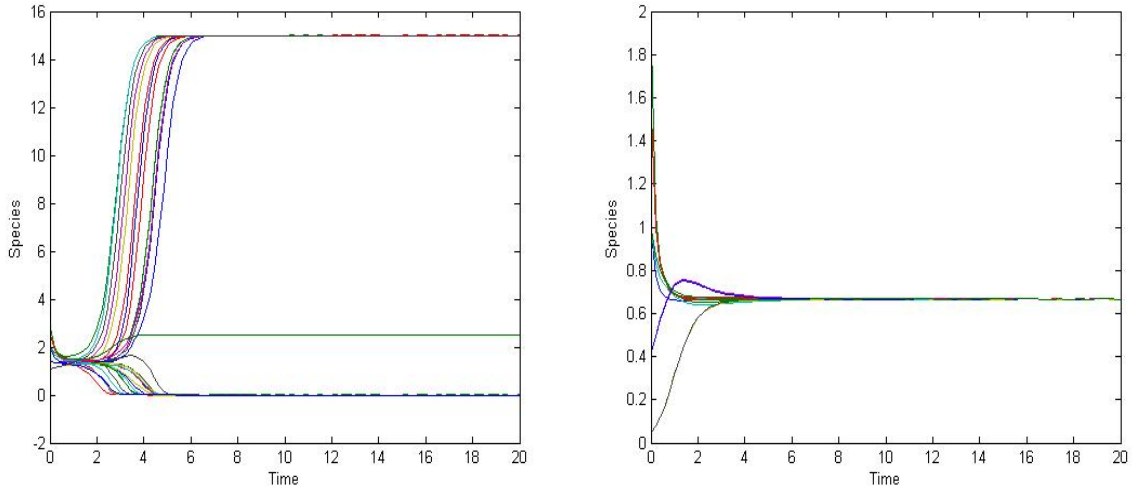
Figure 4.6: The dynamics of species when $n = 4$



(a) No persistence of species when $\alpha < 2$ (b) Persistence of species occur when $\alpha > 2$

Figure 4.7: The dynamics of species when $n = 5$

Below we increase the number of species to 50 and observe that the behaviour of solution is the same as when $n = 4$, that is, persistence occurs only when $\alpha > 2$. This is shown in Figure 4.8.



(a) No persistence of species when $\alpha = 0.20$ (b) Persistence of species occur when $\alpha = 2.50$

Figure 4.8: The dynamics of species when $n = 50$

4.4 Model of n Competing Species with Conspecific Support

A distinctive epidemiological questions such as persistence/extinction of competing species are formulated as an extension of system (4.1.1) to include conspecific support. Including conspecific support for each species or population group similar to (3.4.1)–(3.4.2) and (3.5.1)–(3.5.2) we obtain the following system

$$\dot{x}_i = x_i(1 + \beta x_i)(k + \mu - \alpha x_i - x_{i-1} - x_{i+1}) - \mu x_i, \quad i = 1, \dots, n, \quad x_{n+1} = x_1, \quad (4.4.1)$$

where $\beta > 0$ is a conspecific support parameter, and $\mu > 0$ is the density independent death rate.

4.5 Basic Properties and Persistence of the System

This section aims to explore the properties of system (4.4.1) that will enable us examine and explain the effect of conspecific support on the asymptotic properties of competing species.

4.5.1 Existence, Uniqueness and Boundedness of Solutions

Theorem 21. *The solution $x_i(t)$ for system (4.4.1) with non-negative initial conditions exists for all time ($t \geq 0$) and it is unique.*

Proof. The theorem is proved using a similar argument presented in proving Theorem 17 above. \square

Theorem 22. *The system (4.4.1) is a dynamical system in the biologically-feasible region defined by*

$$\Omega_\mu = \{x \in \mathbb{R}_+^n : 0 \leq x_i \leq \frac{k + \mu}{\alpha}, i = 1, \dots, n\}. \quad (4.5.1)$$

Proof. From (4.4.1), we have,

$$\begin{aligned} \frac{dx_i}{dt} &\leq x_i(1 + \beta x_i)(k + \mu - \alpha x_i), \\ &= x_i \alpha (1 + \beta x_i) \left(\frac{k + \mu}{\alpha} - x_i \right). \end{aligned} \quad (4.5.2)$$

Considering the above inequality (4.5.2), it is clear that if

$$x_i(0) \leq \frac{k + \mu}{\alpha} \text{ then, } x_i(t) \leq \frac{k + \mu}{\alpha}.$$

Taking into account that the solution $x_i(t)$ of (4.4.1) is non-negative, we obtain that $\left[0, \frac{k + \mu}{\alpha}\right]$ is positively invariant and attractive interval for x_i . Thus,

$$\Omega_\mu = \left[0, \frac{k + \mu}{\alpha}\right]^n$$

is positively invariant and attractive set for (4.4.1). As a consequence, all the solutions of (4.4.1) initiated in Ω_μ remain in Ω_μ for all $t \geq 0$. Hence, the theorem is proved. \square

Therefore, we consider the dynamics of system (4.4.1) in Ω_μ defined above.

4.5.2 Non-persistence of n species and Pattern Formation

In this section, we prove one of the main theorem that shows that model (4.4.1) has a stable boundary equilibria and n species will not persist. Furthermore, we will observe that the interaction of n species results in formulation of patterns.

Theorem 23. *Let $\alpha > 2$. If $\mu > (\alpha - 2)k$, there exists β_{crit} such that for $\beta > \beta_{crit}$ the system (4.4.1) has attractive boundary equilibria.*

Proof. We will give the proof in the case when n is even. The proof when n is odd is slightly more technically complicated but uses essentially the same argument.

Let

$$\varphi(\theta) = (1 + \beta\theta)(k + \mu - \alpha\theta) - \mu.$$

It is easy to see that φ has a unique positive root, which we denote by θ^* . Clearly,

$$\varphi'(\theta^*) < 0. \tag{4.5.3}$$

Further, we have

$$\varphi\left(\frac{k}{2}\right) = \left(1 + \beta\frac{k}{2}\right)\left(\mu - (\alpha - 2)\frac{k}{2}\right) - \mu.$$

Taking into account the inequality given for μ , $\varphi\left(\frac{k}{2}\right)$ is linear increasing function of β . Therefore, there exists β_{crit} such that

$$\beta > \beta_{crit} \implies \varphi\left(\frac{k}{2}\right) > 0. \tag{4.5.4}$$

Further, one can observe that since φ is a quadratic function of θ , (4.5.4) implies that

$$\beta > \beta_{crit} \implies \theta^* > \frac{k}{2}. \tag{4.5.5}$$

We will show that for $\beta > \beta_{crit}$ the system has an attractive boundary equilibrium.

4.6. NUMERICAL SIMULATIONS AND DISCUSSIONS

Let $\beta > \beta_{crit}$ and let us consider the equilibrium

$$x^* = (\theta^*, 0, \theta^*, 0, \theta^*, \dots, \theta^*, 0).$$

Every even row of the Jacobian of the right hand side of (4.4.1) at x^* contains a single nonzero entry, which is at the diagonal and is equal to $k - 2\theta^*$. Therefore, the Jacobian has $\frac{n}{2}$ eigenvalues equal to $k - 2\theta^*$, which due to (4.5.5) are negative. After these rows and respective columns are removed, the remaining submatrix is diagonal with diagonal values equal to $\theta^* \varphi'(\theta^*)$. Therefore, the remaining $\frac{n}{2}$ eigenvalues are all equal to $\theta^* \varphi'(\theta^*)$, which is negative due to (4.5.3). Hence, the equilibrium x^* is stable and attractive. \square

Theorem 23 shows that at least for $\beta > \beta_{crit}$ there is no uniform persistence of all species. This property opens the possibility for emergence of patterns involving extinction of some species as shown in the following section.

4.6 Numerical Simulations and Discussions

We present numerical simulations of system (4.4.1). The numerical simulations were implemented with the following values of the parameters presented in Table 4.1.

Table 4.1: Parameter values

n	α	μ	β	k
100	2.1	0.5	5	3

In every figure we have time diagram (above) and a “space” diagram (below). In every figure the time diagram indicates that the equilibrium for each species is obtained. Further, it indicates that the obtained equilibrium of the model is stable with respect to small perturbations, e.g. at least of the size of the round-off error. The “space” diagram represents the sizes of each species that the obtained equilibrium in a bar-chart, where the species are arranged in the order of their indexes. The initial condition is a random vector, every coordinate uniformly

distributed in $[0.01, 1.01]$. We note that different pattern are obtained in different runs. Three pattern are given on Figures 4.9–4.11.

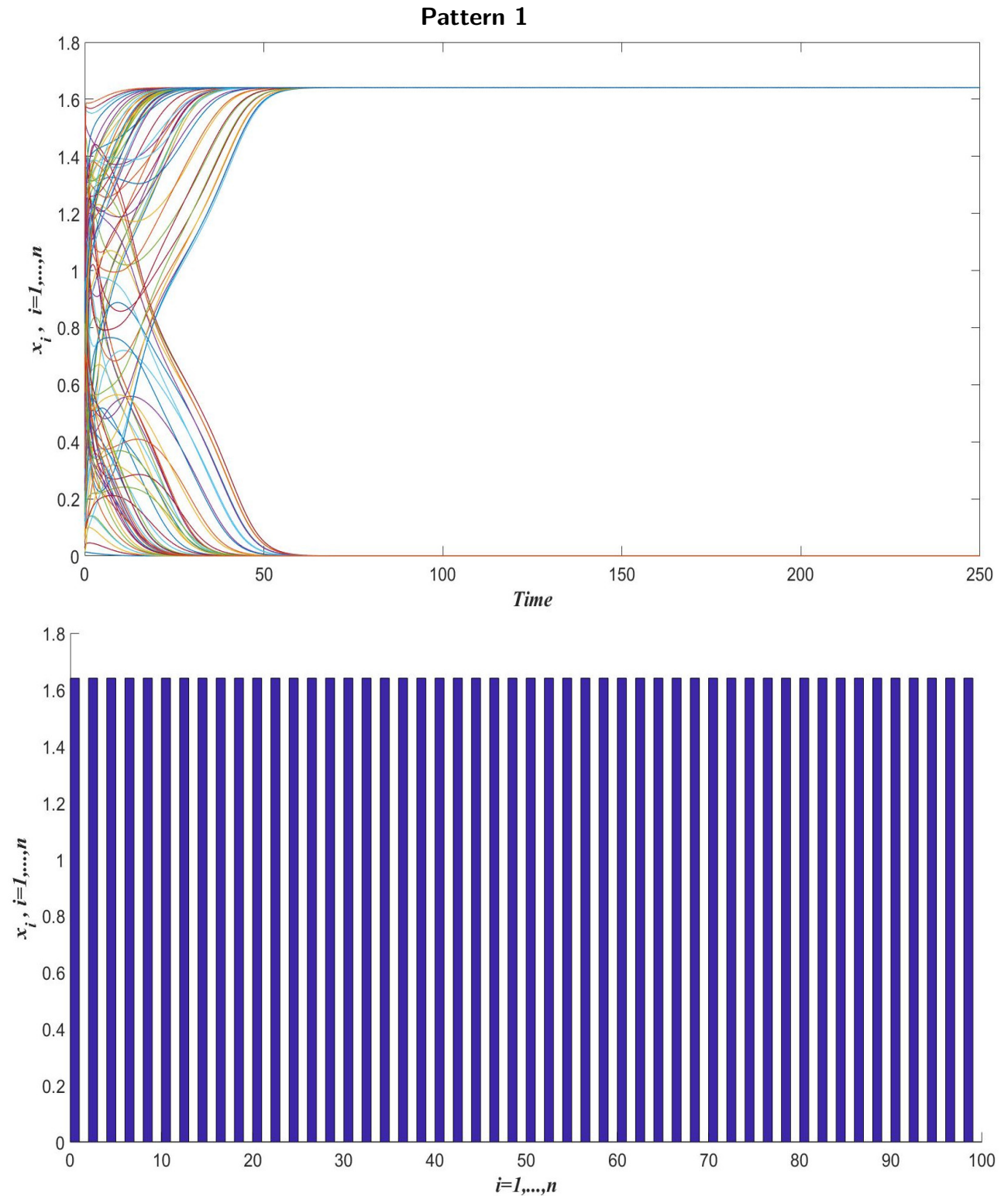


Figure 4.9: Pattern 1 of n competing species with conspecific support. Regular sequence of persistence and extinction as given in x^* .

4.6. NUMERICAL SIMULATIONS AND DISCUSSIONS

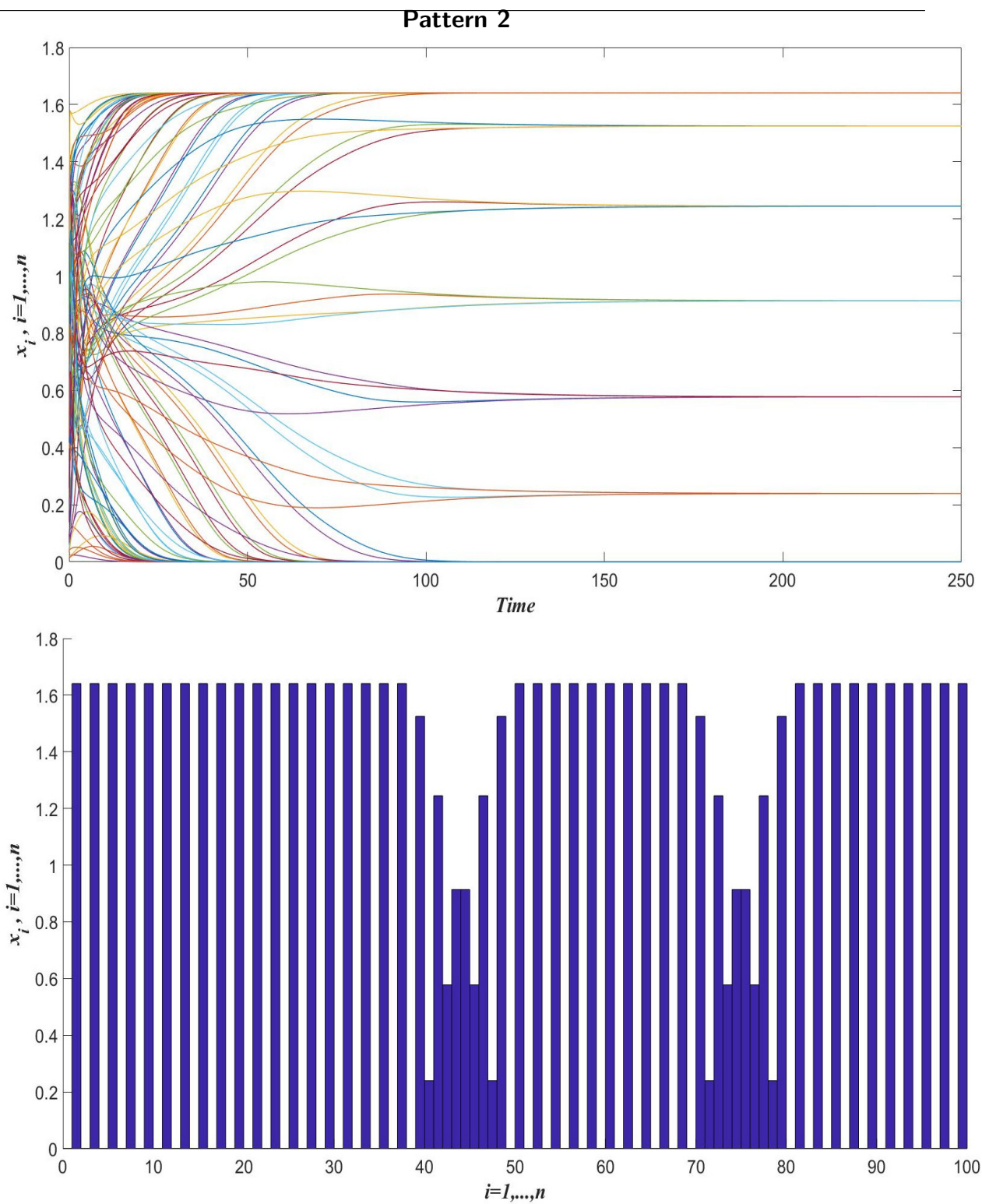


Figure 4.10: Pattern 2 of n competing species with conspecific support.

Pattern 3

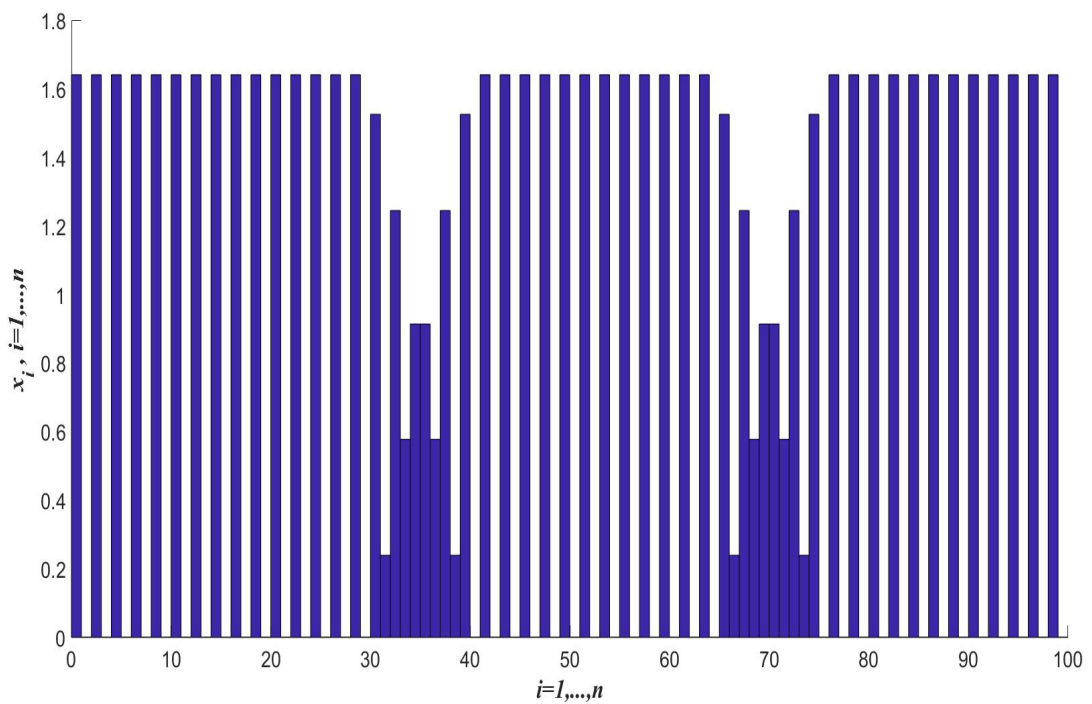
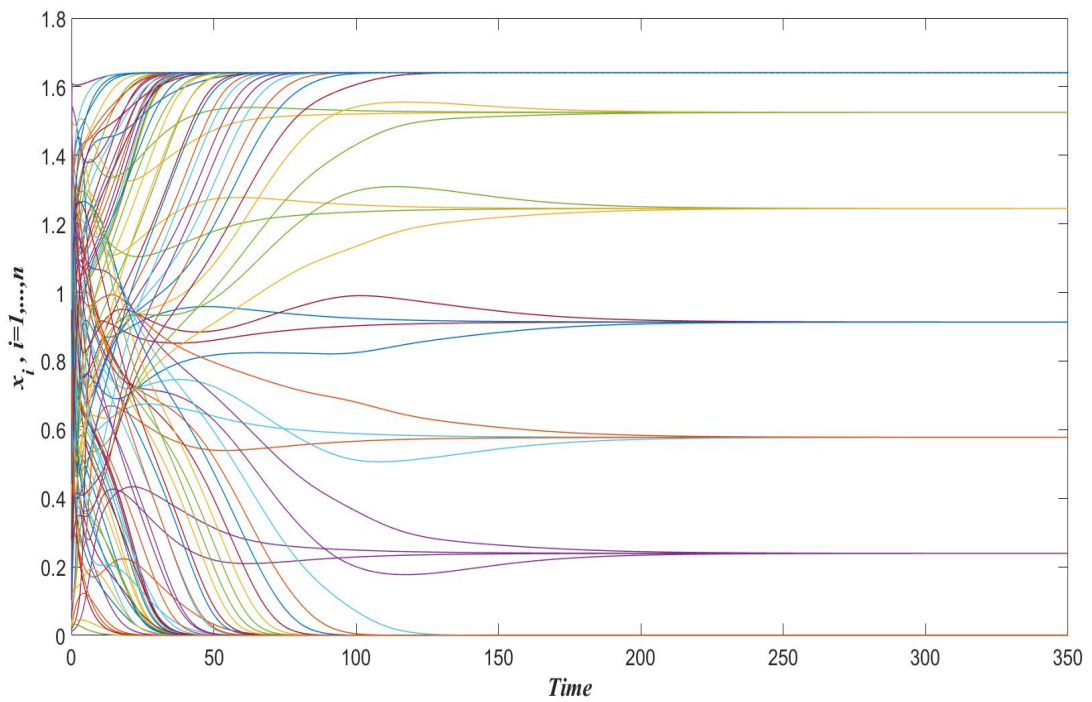


Figure 4.11: Pattern 3 of n competing species with conspecific support.

Observe that the immediate neighbour of a surviving species experience competitive exclusion (extinction), thus forming a persistence-extinction pattern over a range of n species. This

4.6. NUMERICAL SIMULATIONS AND DISCUSSIONS

is a similar case discussed before when we have unqualified competition. Observe further, especially in Figures 4.10–4.11 that a random self-organised pattern of coexisting species emerges which remains stable. This stable cluster of species persist with a density lower than the rest.

It is noteworthy that pattern formation can be caused by a small perturbation in the environment over time between activator (A) and depletion (D) [57]. The depleting factor is the carrying capacity. Thus the pattern formation in competitive system is caused by species/population using its resource and that for its immediate neighbours thereby driving them to extinction. Figure 4.12 shows examples of natural pattern formation ranging from algae (lower plants) to a bush tiger (higher animals). Observe that these patterns are similar to the ones presented in Figures 4.9–4.11.



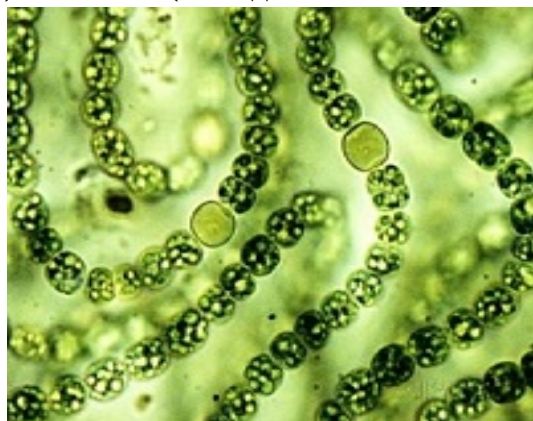
(a) Zebra (source:<https://www.google.com>)



(b) Tiger Bush (<https://www.shutterstock.com>)



(c) Succulent-Karoo of North Western Cape, SA (<https://www.google.com>)



(d) The Algae Anabaena under a microscope (<https://www.google.com>)

Figure 4.12: Pattern formation in nature

4.7 Up-scaling from Discrete to Continuous Model

4.7.1 Introduction

In this section, we propose a model of the activation-inhibitor mechanism of pattern formation by using nonlocal integral operators. This approach was first used by Lefever and Lejeune [71] in the modelling of dynamics of vegetation patterns. It turns out that the short range of the activation and the long range of the inhibition can be adequately represented by means of the supports of the kernels of the respective integrals. An advantage of using the nonlocal operator model from the point of view of its theoretical and numerical analysis is that it does not require the solution to be smooth with respect to the spatial variable.

Gierer and Meinhard [29] showed that, irrespective of the level of complexity of the system, patterns are formed via the coupling of self-activation with lateral inhibition. Therefore, it is imperative to attempt to understand this mechanism using simple systems. In this sense, the algae *Anabaena* in Figure (4.12d) serves as an example. This is because it is a single celled organism. However, the individual algae attach to form chains or filaments. Most of the cells are vegetative (propagation achieved by asexual means), focused on photosynthesis. It is estimated that in every 7-10 vegetative cells, a cell differentiates and becomes a nitrogen fixing cell called heterocyst. This simple one-dimension pattern is crucial because it spatially separates two incompatible processes: the oxygen-evolving photosynthesis (in vegetative cells) and oxygen-sensitive nitrogen fixation (in heterocysts) [21]. The control of the pattern formation is attributed to a peptide, which is produced and released by cells differentiating as heterocysts [31]. The biology of the heterocyst has been studied intensely with varied approaches [7]. However, many processes and genetic mechanisms are not yet well understood [45]. Theoretical and mathematical models have been developed using different tools, e.g. cellular automata [32].

4.7.2 Model Formulation

In most general terms we consider the spatial distribution over a domain $\Omega \subseteq \mathbb{R}^n$ of a substance, species or utility, which we denote by U . Let $u(t, x)$ denote the spatial density of

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U at time t and a space location x is a continuous variable in a real interval Ω . The forces of self-activation and the lateral inhibition of U are considered to be nonlocal in the sense that their values at given time t and space point x depends not only on the value of u at (t, x) , but on the values of u at time t at all points of the spatial domain Ω or at least of a neighbourhood of x .

For large n the vector $(u_1(t), u_2(t), \dots, u_n(t))$ is often modelled as a function $u(t, x)$. Further, we can assume interaction not only with the immediate neighbours, but with their neighbours and beyond. Then the analogy of the growth limiting factor in (4.4.1) is an integral of the form

$$I(u; t, x) = \int_{\Omega} \kappa_2(k + \mu - \alpha u(t, y)) dy,$$

where the support and the shape of the kernel κ_2 determines the span and type of interaction. Similarly, the growth with conspecific support factor in the case of a continuous variable x is modelled as

$$A(u; t, x) = \int_{\Omega} \kappa_1(y - x) u(t, y) (1 + \beta u(t, y)) dy,$$

where the support and shape of κ_1 determines the span and type of conspecific support for growth. We may assume that κ_1 and κ_2 are normalized so that

$$\int_{\Omega} \kappa_1(x) dx = \int_{\Omega} \kappa_2(x) dx = 1. \quad (4.7.1)$$

For simplicity we also assume that they have compact support. Naturally, the $\text{supp}(\kappa_1)$ is expected to be much smaller than $\text{supp}(\kappa_2)$.

The upscaling of the model (4.4.1) to continuous space variable is of the general form

$$\frac{\partial u(t, x)}{\partial t} \propto A(u; t, x) \times I(u; t, x) - \mu u(t, x). \quad (4.7.2)$$

Further, we need to take into account that the growth limiting factor $I(u; t, x)$ could be negative, while $u(t, x) = 0$ and $u(t, x)$ is nonnegative over Ω . Hence, with a modification to exclude the possibility of obtaining negative values the model is

$$\frac{\partial u(t, x)}{\partial t} = \begin{cases} rA(u; t, x) \times I(u; t, x) - \mu u(t, x) & \text{if } u(t, x) > 0, \\ \max \{rA(u; t, x) \times I(u; t, x) - \mu u(t, x), 0\} & \text{otherwise,} \end{cases} \quad (4.7.3)$$

where r is a positive constant.

The model (4.7.2) was first introduced in [71] to model patterns in tiger bush. The model (4.7.3) was used in [70] for modeling the algae *Anabaena*. It is quite interesting that these models can be linked to models like (4.4.1) of competing species with conspecific support and, in fact, can be derived through upscaling of (4.4.1) from discrete to continuous space variable.

4.7.3 Pattern Formation for the Continuous Model

Let \mathfrak{L}_1 be the size of the neighbourhood for providing self-support and let \mathfrak{L}_2 denote the size of the neighbourhood for lateral inhibition. The space independent case obtained when $\mathfrak{L}_1 \rightarrow 0$ and $\mathfrak{L}_2 \rightarrow 0$, the model is reduced to a well known cubic growth equation

$$u_t = \lambda u(1 + \beta u)(1 - u)$$

with non-negative equilibria $u = 0$ and $u = 1$. The standard linear stability analysis shows that 0 is unstable and 1 is stable. The stability of these spatially homogeneous equilibria is not preserved. For positive values of \mathfrak{L}_1 , \mathfrak{L}_2 and $\mathfrak{D} = \mathfrak{L}_2/\mathfrak{L}_1$ sufficiently large, the spatially homogeneous equilibrium is unstable and thus the stable patterns are formed.

In order to carry out numerical simulations of the dynamics of a continuous model, we first provide explicit form of the kernels κ_1 and κ_2 . We consider κ_1 and κ_2 in the following form, which is consistent with the properties discussed in the above section:

$$\kappa_1(x) = \begin{cases} (\mathfrak{L}_1 - x)\mathfrak{L}_1^{-2} & \text{if } |x| \leq \mathfrak{L}_1 \\ 0 & \text{if } |x| > \mathfrak{L}_1 \end{cases}, \quad \kappa_2(x) = \begin{cases} (\mathfrak{L}_2 - x)\mathfrak{L}_2^{-2} & \text{if } |x| \leq \mathfrak{L}_2 \\ 0 & \text{if } |x| > \mathfrak{L}_2 \end{cases},$$

where \mathfrak{L}_1 and \mathfrak{L}_2 are positive reals such that $\mathfrak{L}_1 < \mathfrak{L}_2$. The simulations are run until a stable pattern occurs. Note that for the simulations in Figures 4.14 and 4.13 we use the same values

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of the parameters as for the simulation on Figures 4.9–4.11. Figures 4.14, 4.15 and 4.16 are obtained for $\mathfrak{D} = 5$, $\mathfrak{D} = 8$ and $\mathfrak{D} = 12.5$ respectively. The pattern is very similar to the one in Figure 4.9. For smaller ratio $\mathfrak{L}_2 : \mathfrak{L}_1$ we obtained wave-like patterns not involving any local extinction as shown in Figure 4.13. The frequencies of the pulses is determined by the value of \mathfrak{D} . As \mathfrak{D} increases the pulses get more spaced as shown in Figure 4.13-4.16.

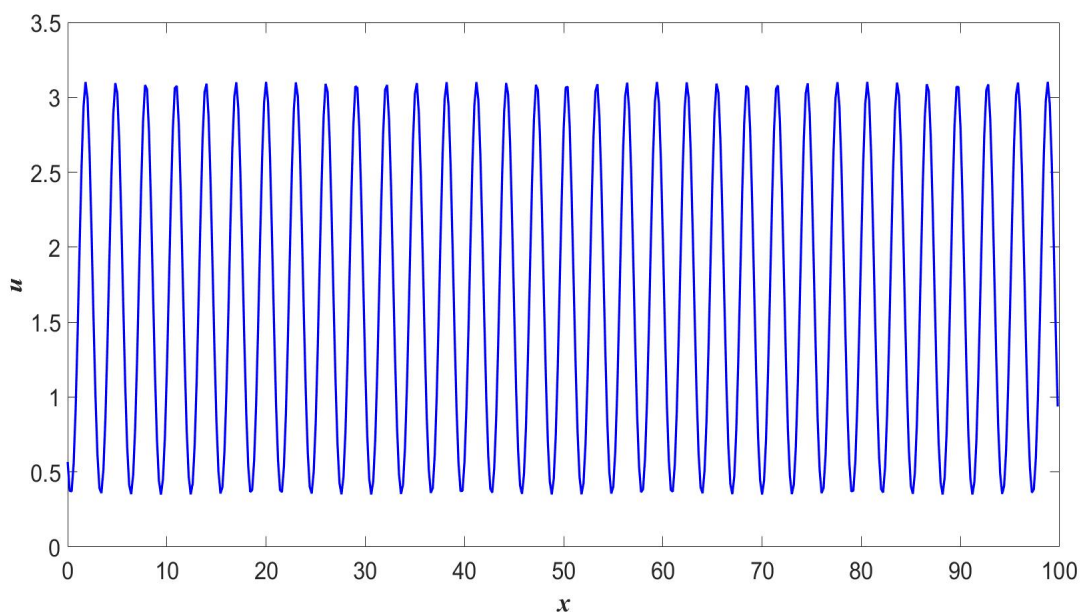


Figure 4.13: Stable pattern obtained for $\mathfrak{L}_1 = 1$ and $\mathfrak{L}_2 = 3$.

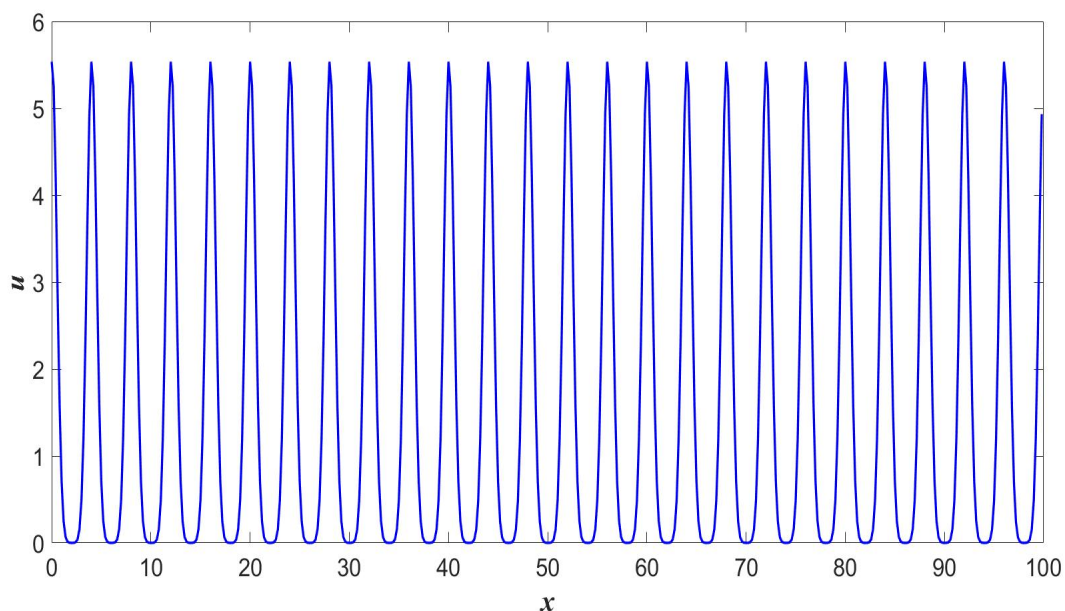
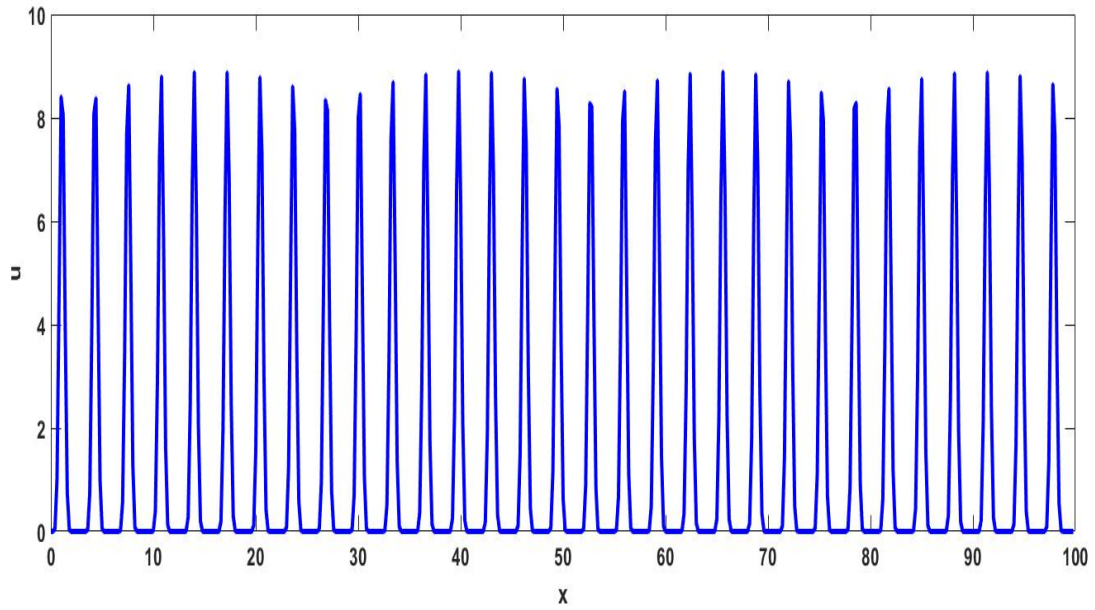
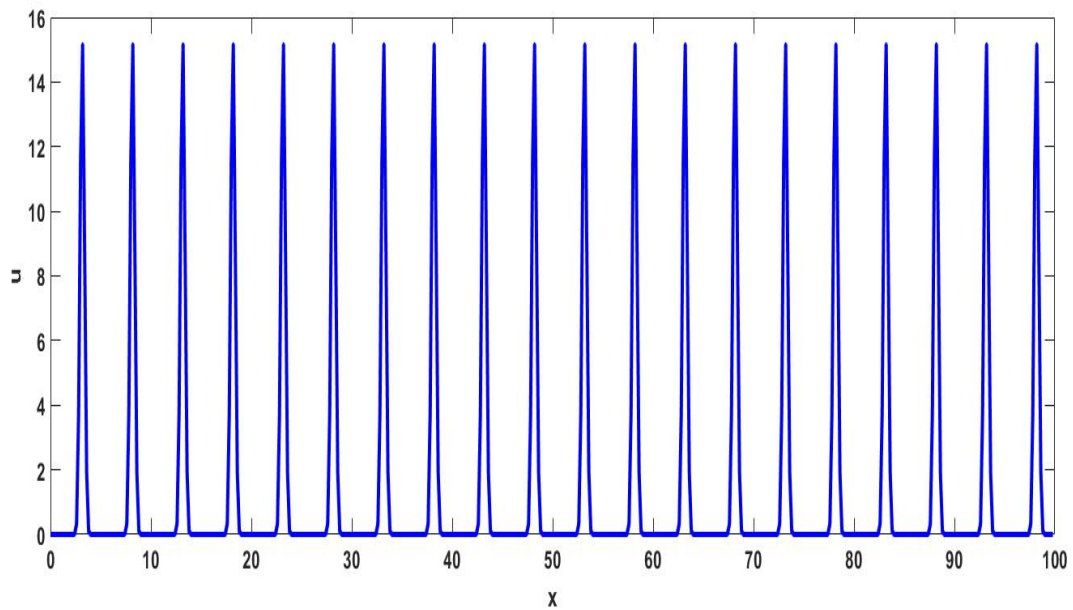


Figure 4.14: Stable pattern obtained for $\mathfrak{L}_1 = 0.8$ and $\mathfrak{L}_2 = 4$.

Figure 4.15: Stable pattern obtained for $\mathcal{L}_1 = 2$ and $\mathcal{L}_2 = 16$.Figure 4.16: Stable pattern obtained for $\mathcal{L}_1 = 2$ and $\mathcal{L}_2 = 25$.

We need to remark that these patterns are formed essentially through the Gierer-Meinhard [3] mechanism of self-activation, represented by the operator A , and lateral inhibition, represented by the operator I . Typically, this mechanism is represented mathematically via a system of reaction diffusion equations satisfying the Turing instability condition [9, 29]. Here we show, among other things, that different mathematical representations of the Gierer-Meinhard theory

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of pattern formation are possible. It is widely accepted that the Turing mechanism for systems of reaction-diffusion equations is appropriate way for modelling pattern formation, [9]. In fact, it seems that it is widely believed that it is the only way, particularly given that Gierer and Meinhardt derived independently the same model to represent their theory of biological pattern formation, [30].

Conclusion and Future Work

In this dissertation, we presented an extensive mathematical study of Lotka-Volterra competition models of the dynamics of population groups. In the first part of our study (Chapter 3), we presented the models of two competing species and demonstrated how introducing conspecific support affects the dynamics of the competition. In the last part of our study (Chapter 4), we have considered the model of n competing species and determined the future outcome of the interaction. Furthermore, we have proposed the model of the activation-inhibition mechanism of pattern formation by up-scaling the discrete model to the continuous model using nonlocal integral operators.

In Chapter 3, a general model of two competing species was presented and the model was rigorously analysed to ensure that it provides a realistic representation of the population dynamics. We observed that if $g_1(0, q)$ and $g_2(p, 0)$ are both positive, then the system is permanent, that is, the two species in the competition coexist. In the same chapter, we presented the system with linear per capita growth rate to illustrate the result obtained for the general model. In a counter distinction from the Gause's principle of competitive exclusion, we observe that two competing species coexist under the assumption of qualified competition.

In Section 3.4, we show how conspecific support can destabilise the coexistence of competing species. The conspecific support is modelled through multiplying the per capita growth rate, excluding density independent death rate, by a linear factor of the form $(1 + \beta x)$ with $\beta > 0$. We observe that in the model with conspecific support, the per capita growth rate is positively correlated with the density of population size, when it is small. Hence, the conspecific support gives rise to Alee Effect. We note that there is an increasing biological evidence that the Alee Effect is more likely to occur due to conspecific support [38, 68]. The specific form chosen here to represent the conspecific support leads to a Weak Alee Effect, since there is no additional positive equilibrium generated by the system due to the conspecific support. We discuss

the general mechanism of destabilising the permanence of the system or equivalently the coexistence of the species. In Section 3.5, we consider conspecific support in the specific case discussed in Section 3.3. We prove that under an assumption about the density independent death rate, there exists a threshold value β_{crit} such that for $\beta > \beta_{crit}$, the system is not permanent or equivalently species do not coexist.

In Chapter 4, we extended the general model introduced in Chapter 3 from two dimensions to n dimensions. While Chapter 3 basically provides the effect of conspecific support on the coexistence of two competing species, the focus of Chapter 4 is two fold:

- (i) to determine the conditions for uniform persistence of the model of three competing species as well as the model of n competing species, and
- (ii) to determine the effect of conspecific support on coexistence of all species and on the formulation of patterns of persistence and extinction.

For the first objective, investigating such condition that can allow species to coexist plays a vital role in the conservation ecology/biology for guiding management actions. This is because such information would allow ecologists/biologists to make predictions about the vulnerability of species to extinction even before they decline, thereby improving the chances of species to survive [40]. In order to achieve this objective, the model was rigorously analysed to get the insight of the asymptotic behaviour of the solutions when we have three species in the competition. The usual linear stability criterion of the boundary equilibria was used. We observe that all the boundary equilibria repel towards the interior of the \mathbb{R}_+^3 if $\alpha > 1$, and the model has an attractive boundary equilibria if $\alpha < 1$. Thus, we conclude that $\alpha > 1$ is a necessary condition for uniform persistence/permanence of three competing species since all solutions of the model are bounded away from the equilibrium in an infinite period of time. Further analysis of the model was carried out and it was shown, however, that when species are more than three, $\alpha > 2$ is the necessary condition for uniform persistence/permanence. This behaviour of the model is illustrated by numerical simulations presented in Section 4.6. The most interesting result is proved in Theorem 20 of Section 4.3, where it has been shown that n species uniformly persist in an infinite time regardless of the intensity of the competition. This result is essentially similar to what other researchers have been able to prove (the possibility

of multi-species persistence) [5, 13, 16] although these models focus on different aspects.

In Section 4.4, the model of n competing species with conspecific support has been presented as an extension of the model of n competing species in order to address the second objective of this chapter. The question of whether or not the introduction of conspecific support in the system, as observed in Section 3.5, would change the dynamics of the system is discussed. No doubt, we observe that conspecific support has a similar impact on both two and n competing species. This is demonstrated in Theorem 23 where it has been proved that if $\alpha > 2$, there exists a threshold condition β_{crit} on the model parameter such that if $\beta > \beta_{crit}$, the model of n species with conspecific support is not permanent or equivalently, some of the species go extinct.

Despite the fact that conspecific support destabilises the coexistence of species for both two and n species, it has an additional important effect on n species in competition. The theory of pattern formation is widely used to study various critical transitions which take place in biological systems, as well as in ecological systems that are believed to generate patterns [10]. Here, we show that due to conspecific support, the existence-extinction pattern will emerge. More precisely the emergence of these patterns is attributed to competition coupled with conspecific support resulting in extinction of some species. The factor behind the extinction of some of the species is due to the depletion of carrying capacity as a result of species using its own resource and that for the immediate neighbours. Since the inhibition is depletion of resources, this model of pattern formation is more appropriately referred to as *activation-depletion* rather than activation-inhibition.

In Section 4.7, we have proposed the continuous model by up-scaling the discrete model presented in Section 4.1 to model of continuous space variables. This model was first used in [71] in the modelling of dynamics of the patterns in tiger bush given in Figure 4.12b as well as vegetation patterns such as the one presented in Figure 4.12d. We find it interesting that this approach can be derived from up-scaling or analogy with the discrete model in Section 3.4. In this approach, the short range of the activation and the long range of the inhibition are modelled by the support of the kernels of the integrals as shown explicitly in (4.7.2). We demonstrate numerically that if the ratio of the size of the neighbourhood for providing self-support over the size of the neighbourhood for providing lateral inhibition is sufficiently large,

the spatially homogeneous equilibrium is unstable and the stable patterns are generated. The patterns observed in this setting are similar to those presented in Section 4.6.

The research presented in this dissertation seems to have raised more questions than it has answered. There are several lines of research arising from this work which should be pursued. For instance, there has been quite substantial recent development of the theory of equations involving non-local operators. However, there is no theory as yet on pattern formation in such equations. Here we presented mainly numerical investigation on the pattern appearing when varying the support of the respective kernels. The empirical investigation on the possible patterns and conditions under which they occur will help to acquire a broader understanding of the subject. Therefore, our future work aims at addressing the theoretical analysis of this pattern formation mechanism.

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