JOINT EFFECTS OF DISTINCT BIOTIC INTERACTIONS AND DISPERSAL ON A MULTI-SPECIES ECOLOGICAL SYSTEM

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JOINT EFFECTS OF DISTINCT BIOTIC INTERACTIONS AND DISPERSAL ON A MULTI-SPECIES ECOLOGICAL SYSTEM

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LIST OF ABBREVIATIONS

BP	Transcritical bifurcation
FR	Functional response
HB	Hopf bifurcation
ODE	Ordinary differential equation
PD	Period-doubling bifurcation
PDE	Partial differential equation
SNBC	Saddle-node bifurcation of cycle
1D	1-Dimensional
2D	2-Dimensional

LIST OF SYMBOLS

a Capture rate

d Death rate of the exploiter species

g Conversion efficiency

h_X Half saturation constant of the hyperbolic functional response

h_Z Half saturation constant of the hyperbolic functional response

r_X Intrinsic growth rate of the resource species

r_W Intrinsic growth rate of the competitor species

r_Z Intrinsic growth rate of the mutualist species

u Maximum benefit of the mutualist interaction

v Maximum benefit of the mutualist interaction

α Competition strength

β Competition strength

D Dispersal strength

D_X Dispersal strength of the resource species

D_W Dispersal strength of the competitor species

D_Y Dispersal strength of the exploiter species

D_Z Dispersal strength of the mutualist species

KESAN GABUNGAN INTERAKSI BIOTIK YANG BERBEZA DAN PENYEBARAN KE ATAS SISTEM EKOLOGI BERBILANG SPESIES

ABSTRAK

Salah satu persoalan utama dalam ekologi adalah bagaimana kita memelihara kestabilan komuniti dan mekanisme kewujudan bersama antara spesies dalam komuniti ekologi yang kompleks. Terdapat arus pemikiran yang mengatakan bahawa hubungan antara kesalingan, persaingan, pemangsaan dan penyebaran tempatan dapat menyokong kewujudan bersama pelbagai spesies. Dalam tesis ini, kami merumuskan semula model empat spesies merangkumi sistem interaksi pelbagai spesies (contohnya, spesies sumber-pesaing- pengeksploit-penyaling) dengan menggabungkan sebutan penyebaran ruang untuk memodelkan proses sebaran tempatan. Kami kemudian menggunakan model ini untuk menilai bagaimana dinamik proses penyebaran, kesalingan dan persaingan membentuk mekanisme kewujudan bersama dan kestabilan komuniti dalam sistem ekologi ini. Hasil dapatan kami menunjukkan bahawa interaksi kesalingan dan persaingan mempengaruhi kekompleksan dinamik ekologi dalam sistem interaksi pelbagai spesies ini dengan adanya proses penyebaran tempatan. Dengan menggunakan simulasi berangka, kami menunjukkan betapa proses kesalingan yang kuat dapat menstabilkan dinamik komuniti pelbagai spesies ini. Melalui analisis dwicabangan, kami juga mendapati bahawa kesalingan pada dasarnya dapat mengubah gerak balas komuniti ekologi ini terhadap peningkatan tekanan persaingan terhadap spesies sumber. Pemahaman ini dapat dilihat dalam penemuan kami melalui kemunculan dinamik yang menarik serta pelbagai proses dwicabangan (misalnya, dwicabangan subkritikal dan superkritikal Hopf, transkritikal, nod-pelana, transkritikal-Hopf dan homoklin). Kami memerhatikan kitaran had stabil bergantian dengan yang tak stabil apabila magnitud

persaingan berubah. Walaupun keadaan alternatif adalah biasa dalam sistem ekologi dengan interaksi kesalingan, keadaan ini seringkali stabil, sedangkan, dalam kajian kami, didapati bahawa keadaan alternatif ini boleh menjadi stabil atau tak stabil jika dimensi ruang dipertimbangkan melalui penggabungan dengan komponen penyebaran. Akibatnya, dinamik jangka panjang tertumpu kepada kewujudan bersama pelbagai spesies sama ada melalui keadaan mantap yang stabil atau kitaran had dan hal ini bergantung pada komposisi spesies pada awalnya. Juga diperhatikan bahawa kekompleksan dinamik ini terhenti berkuat kuasa apabila proses kesalingan menjadi cukup kuat. Selain itu, fenomena ketidakstabilan biodiversiti melalui kejadian kitaran had dengan amplitud ayunan yang meningkat telah dilemahkan dengan adanya proses kesalingan yang kuat dan penyebaran tempatan. Selanjutnya, hasil kajian kami menunjukkan bahawa tindak balas fungsian pemangsa mempengaruhi dinamik kewujudan bersama dalam sistem pelbagai spesies ini. Sebagai contoh, kami memerhatikan bahawa kekuatan pemangsa yang semakin lemah dalam model tindak balas fungsian jenis kedua menyebabkan ketidakstabilan komuniti apabila kepupusan spesies boleh berlaku, sedangkan model tindak balas fungsian jenis pertama dapat menyokong proses kestabilan komuniti ekologi.

JOINT EFFECTS OF DISTINCT BIOTIC INTERACTIONS AND DISPERSAL ON A MULTI-SPECIES ECOLOGICAL SYSTEM

ABSTRACT

One of the central questions in ecology is how do we maintain community stability and species coexistence mechanisms in a complex ecological community. It is thought that the interplay between mutualism, competition, predation and local dispersal support multi-species coexistence. In this thesis, we re-formulate a four-species multiple interactions type (e.g., resource-competitor-exploiter-mutualist) system by incorporating a spatial diffusion term to model local dispersal process. We then employ this model to assess how the dynamics of dispersal, mutualism and competition shape species coexistence and community stability in this ecological system. Our findings show that the interplay of mutualism and competition affects the complexity of ecological dynamics in this multiple interactions type system with local dispersal. Using numerical simulation, we demonstrate how strong mutualism could stabilize the dynamics of this multi-species community. Employing bifurcation analysis, we also discover that mutualism essentially modifies this ecological community's response to increasing competitive pressure on the resource species. These insights are evident in our findings through the emergence of intriguing dynamics and various bifurcations (e.g., subcritical and supercritical Hopfs, transcritical, saddle-node, transcritical-Hopf and homoclinic bifurcations). We observe that stable limit cycles alternate with unstable ones as competitive pressure varies. While alternative states are common in different ecological systems with mutualistic interactions, they are often stable, whereas, in our studies, we realize that there can be alternative stable or unstable states if the spatial dimension is considered through the incorporation of the diffusion component. Con-

sequently, the long-term dynamics converge to multi-species coexistence outcomes either via a stable steady state or a limit cycle depending on species' initial abundances. It is also observed that this complexity stops when mutualism becomes strong enough. Additionally, the destabilization of species biodiversity phenomenon through the occurrence of limit cycles increasing in the amplitude of oscillations is weakened in the presence of strong mutualistic strength and local dispersal. Furthermore, our result shows that the predator functional response influences the coexistence dynamics of this multi-species system. For instance, we observe that weak predation strength in Type II functional response model destabilises the community as extinction occur, whereas the Type I functional response model can support the stabilisation of the ecological community.

CHAPTER 1

ECOLOGICAL BACKGROUND AND PROBLEM DESCRIPTION

1.1 Introduction

An ecosystem comprises species of different kinds that interact through diverse types of interspecific interactions, e.g., competition, prey-predator interaction, and mutualism. Multi-species interactions are in diverse forms, and ecologists often face the question of what allows multiple species to coexist and persist in a complex ecological system. Based on previous findings, it has been shown that interspecific interactions determine population dynamics and coexistence mechanisms of multiple species (Huisman and Weissing, 1999; Kondoh, 2003; MacArthur, 1970). Several studies also demonstrate the comparative roles of diverse interaction types, and it is found that the stability for prey-predator systems can be affected by the strength of interactions between these interacting species (Allesina and Tang, 2012; May, 1972). It should be noted that the combined effects of diverse interactions type (Mitani and Mougi, 2017) and species dispersal process (Mohd et al., 2017; Mohd, 2016) on multi-species communities as well as the problem of how these different forces of species interaction affect community dynamics (Fontaine et al., 2011; Kar, 2004; Křivan and Eisner, 2006) have not been well-explored, and that is the main focus of this thesis.

Different species coexist in an ecological system, which is referred to as a community, and often species interactions affect each other directly or indirectly within the natural ecosystems (Agrawal et al., 2007; Brooker et al., 2009; Ricklefs, 2008). Several studies on simple ecological communities have tried to incorporate different

interaction modules into multi-species community ecosystem (Kondoh, 2008; Mougi, 2016; Mougi and Kondoh, 2012) and show that mixed interaction types are more realistic in modelling natural ecosystems. Some studies suggested that there has being a synergistic relationship between interaction types and species diversity in ecological communities (Kondoh and Mougi, 2015; Mougi, 2016; Mougi and Kondoh, 2012). Seymour and Altermatt (2014) reports that species interactions in multi-species communities influence the system coexistence dynamics as time progresses. Also, Field et al. (2009); Pearson and Dawson (2003); Wisz et al. (2013) report that multiple interactions shape the distribution of species in the ecosystem. The effects of diverse interactions in multi-species systems can influence the community structures across various trophic levels in the ecosystems (Estes et al., 2011; Hagen et al., 2012; Zarnetske et al., 2012).

The dynamics of multiple interactions in ecological communities influence species coexistence and diversity (Fordham et al., 2013; Gilman et al., 2010; Jetz et al., 2009; Kissling et al., 2012; Lurgi et al., 2012; McInnes et al., 2013; Sandom et al., 2013; Tylianakis et al., 2008; Wisz et al., 2013). These interactions in the ecological systems determine the properties and structures of such ecological assemblies (Estes et al., 2011; Hagen et al., 2012; Zarnetske et al., 2012). Consequently, the interactions in ecological systems between single and multiple species are rather challenging to study and analyse as they mostly depend on the context and strength of interactions in the ecosystem (Brooker et al., 2009; Harrison and Cornell, 2008; Ricklefs, 2008). Furthermore, several kinds of interactions exist among species throughout the ecosystem, and these interactions sustain the ecosystem functioning (Seymour and Altermatt, 2014). Relying on these interactions when formulating models of species interactions allows

ecologists to predict occurrences that exist in nature (Fordham et al., 2013; Gilman et al., 2010; Lurgi et al., 2012).

The interactions in ecological communities can be described as inter-specific or intra-specific (Imperio et al., 2012; Powers and McKee, 1994). Inter-specific interactions occur among species of different kinds in an ecological community, while intra-specific interactions occur between species of the same kinds (Imperio et al., 2012; Powers and McKee, 1994). Moreover, since species live within the ecological community, these interactions can influence their coexistence and community stability (Fukami, 2010). The interactions that would be discussed in this thesis are competition, prey-predator interaction, and mutualism. These three interactions are the most studied and form the basis of the complex relationships in natural ecosystems. There is a scarcity of work on the combined influences of these multiple interactions and local dispersal. In the following sections, these interactions will be discussed in detail.

1.2 Background of Study

Competition is the prevalent interaction among species that compete for the same kind of resources for survival, and these interactions between species often lead to changes in the fitness of species in an ecosystem (Holomuzki et al., 2010). The consequence of competition in the ecological communities negatively affects weaker species as they are required to compete with stronger species for the same limited resources (Wootton, 1994). The types of competition reported in the literature are interference competition and exploitation competition (Delong and Vasseur, 2013). Exploitation competition is the kind of interaction that occurs indirectly between species, while

interference competition is the interactions that exist directly between species in the same ecological system (Holomuzki et al., 2010). Moreover, the consequences of competition often lead to the elimination of inferior species by the superior species, and the process has been called the principle of competitive exclusion (Hardin, 1960). The Lotka-Volterra model (Lotka, 1925; Volterra, 1926) is a well-known two-species system for studying the consequences of competition among interacting species. This system is used to study the relationship between the competitive strength and carrying capacity of species and the resultant effects in reducing each other population densities. The possible outcomes from this competition model are: (1) species 1 competitively eliminates species 2; (2) species 2 competitively excludes species 1; (3) coexistence of species occurs; (4) alternative stable state communities that depend on initial densities. Several studies have reported that species coexistence is possible if the inter-specific competition is weaker than the intra-specific competition (Armstrong and McGehee, 1980; del Río et al., 2019). In general, interference competition is also being classified as an antagonistic interaction (Czárán et al., 2002). This interaction occurs when the gain of one species inflicts harm on another species. Antagonistic interactions can also take the form of predation or parasitism (Hembry and Weber, 2020; Laidemitt et al., 2019; Nuismer and Thompson, 2006; Schulz et al., 2019).

Predation occurs when one species (i.e., predator) captures and feeds on another species (i.e., prey) (Sih, 1994). Some examples of predation in the ecological communities are between animals and plants; for instance, different experimental studies have reported that some protozoans feed on bacteria and protozoans, while some plants feed on insects (i.e., pitcher plant) (Kneitel and Miller, 2002). Predation usually occurs between different species (i.e., inter-specific); however, it can occur between species of

the same kind (i.e., intra-specific) (Mishra et al., 2020; Nakazawa, 2020). The prey-predator interactions sometimes exhibit traits that are called "evolutionary arms race" (Ellison et al., 1996). Some of the typical traits exhibited by predators are sharp claws and teeth, poison or stingers, agile and quick body, camouflage colouration, aural or visual brilliance. Simultaneously, some examples of the prey traits are physiological, mechanical, and chemical defenses to scare the predators (Ellison et al., 1996).

Another kind of species interactions is the mutualism. A mutualistic relationship is a win-win kind of interaction where interacting species benefits from the relationship between each other (Keeler, 1982). Mutualism in multi-species interactions can be divided into two categories, namely facultative (i.e., species that can survive on their own when separated from their mutualistic partner) or obligate mutualism (i.e., species that cannot survive without a relationship with their mutualistic partner) (Ellison et al., 1996). For example, some fungi and leafcutter ants enjoy an obligate mutualistic relationship. The ant larva feeds on fungi, and the fungi cannot survive without the ant. An example of a facultative relationship exists between plant roots and mycorrhizal fungi. A study reported that most vascular plants and mycorrhizal fungi enjoy facultative mutualistic relationship (Kaaya et al., 2011). Martignoni et al. (2020a) and Martignoni et al. (2020b) reported that mutualistic interactions support the coexistence mechanisms of multi-species. Prior et al. (2020) also show that mutualistic interactions play a functional role in species fitness (i.e., "ability to survive and reproduce in the environment") and persistence. Also, Stone (2020) reported that mutualistic interactions enhance species population densities and community stability.

Apart from the interaction between each other, species also disperse across a ge-

ographical region. The term dispersal is defined as species movement from one ecological community or location to another (Duarte and Mali, 2019). The dynamics of dispersal shape species distribution (Dexter et al., 2017; Evans et al., 2020). Ecological models contribute to the study and understanding of the advancement of dispersal in mathematical ecology. Transfer, settlement, and emigration have been reported as the ecological features of dispersal (Lidicker and Stenseth, 1992). Mohd et al. (2017) reported that the effect of abiotic and biotic factors combined with dispersal can influence species ranges and that coexistence of multiple species is possible due to the interplay of species interactions and dispersal. The dispersal dynamics in multiple interactions type system affect species distribution, community structure, and stability (Baguette et al., 2013; McPeek, 2014). Moderate dispersal strength in multiple interactions type system enhances the movement of species and this, in turn, helps maintain the endangered communities (Pulliam, 1988). In another study, dispersal has been reported to alter environmental factors impacts on multiple interactions type communities (Brown et al., 2011; Winegardner et al., 2012). The strength of dispersal in multiple interactions type system also affects the relationship between different ecological communities (Brown and Swan, 2010; Ng et al., 2009; Winegardner et al., 2012). In general, dispersal in an ecological system is divided into two: local dispersal (i.e., between adjacent spatial locations) and non-local dispersal (i.e., between larger spatial locations). In this thesis, we will focus our analysis using a local dispersal model to gain insight on the coexistence dynamics of distinct interactions between small adjacent spatial locations; for non-local dispersal mechanisms, interested readers are referred to Mohd et al. (2018) for further reading.

1.3 Motivating Biological Examples

Multiple species interactions (e.g., mutualist-resource-competitor-exploiter interactions) type models are known to exhibit oscillatory behaviour due to their complexity (Mitani and Mougi, 2017; Mougi and Kondoh, 2012). This large-amplitude oscillation often de-stabilises multi-species communities and increases species chances to go extinct (Mitani and Mougi, 2017; Mougi and Kondoh, 2012). Thus, the vital question is how to maintain the stabilisation of communities and species coexistence in multiple interactions type systems. One possible way to do this is to use multiple interactions type modelling framework and the incorporation of spatial diffusion mechanism into such a system to model the effects of local dispersal on multiple species interactions. This notion is in parallel with the ecological studies in Mitani and Mougi (2017) and Mohd et al. (2017); Mohd (2016), Mohd et al. (2018); using the modelling approaches, we seek to gain valuable insights into the dynamics of distinct interactions type system with local dispersal and some ecological implications related to these issues.

The maintenance of species coexistence and community stability has attracted much attention in ecology in recent times (Knowlton and Rohwer, 2003; Kondoh, 2008; Kondoh and Mougi, 2015; Mougi and Kondoh, 2012). Several theoretical studies have hypothesised that complex ecological communities (i.e., multiple interactions type system) are structurally unstable, and this is despite the positive evidence of species coexistence in nature (Gardner and Ashby, 1970; May, 1972; Pimm and Lawton, 1978). This paradoxical viewpoint has motivated ecologists to investigate what mechanisms maintain multi-species coexistence in ecological systems (Bascompte et al., 2006; Brose et al., 2006; Neutel et al., 2002). Some studies have traced this lack of con-

sistency to some unrealistic assumptions (i.e., complex ecosystem leads to ecosystem stability) made to prior ecological models (Lawlor, 1978; Pimm, 1979). However, little attention has been given to multiple interactions type system (Fontaine et al., 2011; Pocock et al., 2012). Recent studies on the complex ecological systems have demonstrated that species interaction strength are the determinants of community compositions (Emmerson and Raffaelli, 2004; Neutel et al., 2002). Also, some studies on the stability of complex systems have compared the coexistence and stability dynamics of several communities having multiple interactions (Allesina and Tang, 2012; Hender et al., 2007). The results from these studies shed some light on how antagonistic interactions shape the stability of competitive and mutualistic interactions type system, and that community destabilisation is associated with these complex ecological interactions (Allesina and Tang, 2012).

In a similar study, Mougi and Kondoh (2014c) have illustrated that diversity in the interaction type system promotes species coexistence and community stability. In this study, it is further observed that antagonistic interaction plays an essential role in the stability of multiple interactions type system (Mougi and Kondoh, 2014c). This study also illustrates that systems with either mutualism, competition, or antagonism exhibit different population dynamics and stability properties compared to a multiple interactions type system (Mougi and Kondoh, 2014c). The stability of the system follows the order of antagonistic, competitive, and mutualistic interaction. Similarly, the combination of interactions (i.e., two- or three-species interactions) type promotes species coexistence and community stability in the complex ecological system (Mougi and Kondoh, 2014c). Furthermore, the stable coexistence region is broader as the ecological system complexity increased, and vice versa (Mougi and Kondoh, 2014c).

1.4 Problem Statement

The dynamics of three-species models (i.e., mutualist, resource, and exploiter) have contributed significantly to understanding multiple interactions type system (Mougi and Kondoh, 2014b). The community dynamics observed in this three-species ecological system (Mougi and Kondoh, 2014b) motivated a further study by incorporating another interaction (i.e., competition), making the system more complex and yet realistic (Mitani and Mougi, 2017), as a result of increasing interactions. The result from this multiple interactions type system (i.e., mutualist-resource-exploiter-competitor) shows the emergence of population cycle, despite using simple ordinary differential equations and spatial dispersal phenomenon is neglected. The findings illustrated in the study of Mitani and Mougi (2017) also contradict certain real-life phenomena as multiple species can be seen to coexist in nature. To address these problems and investigate the joint effects of dispersal on multiple interactions type model, we formulate a partial differential equation (PDE) model. We have the following open questions arising from this study:

1. Under what conditions coexistence of species can occur in the multiple interactions type system with the incorporation of local dispersal process?

2. What effects do mutualistic strength and the intrinsic growth rate of competitor species have on the stabilization of community and species coexistence outcomes?

3. What effects does the interplay between local dispersal and competition have on the general dynamics of this ecological system?

4. What effects do change in predator functional response (i.e., Type I & II) have on the bifurcation dynamics in this multiple interactions type system?

Motivated by these knowledge gaps, we hypothesized the following: (1) species coexistence is possible in this multiple interactions type system for some threshold values of parameters, (2) the combined influences of mutualism and competition with local dispersal may enhance the overall species coexistence outcomes and community stability in this multiple interactions type system; and (3) predator functional response affects the species coexistence and community stability in this multiple interactions type system. In the following section, we discuss the aim and objectives of this thesis.

1.5 Aim and Objectives

This thesis aims to demonstrate how mathematical techniques can be employed to better understand the dynamical behaviour of multiple interactions type system with local dispersal. We achieve these aims by incorporating local dispersal and distinct biotic interactions (i.e., predation-mutualism-competition-resource) in the modelling frameworks. The main objectives of this thesis are listed as follows:

1. to extend the mathematical model of multiple interactions type system by incorporating a local dispersal mechanism and distinct functional responses.

2. to analyze the effects of mutualism, competition, and other biotic factors on multi-species coexistence and community stability using an ODE model.

3. to determine the effects of local dispersal and other biotic factors on the multiple species ecological systems using a PDE model.

1.6 Scope of Study

In the natural ecosystem, there are different kind of species interactions, however, we are going to focus on four main interactions e.g., predation, mutualism, exploita-

tion, and competition. This is because these are the most pronounced species interactions that can affect community stability and coexistence of species in nature. We also model the effect of local dispersal using simple diffusion equation though dispersal can also be represented using non-local dispersal processes. We make this assumption in modelling dispersal because it is a major driver of species dynamics, resilience and composition. The model formulation is concentrated in 1-dimensional (1D) space habitats as opposed to 2-dimensional (2D) habitats for the ease of interpretation and simplicity of modelling results. The parametrisation employ in the numerical simulations are motivated by the ecological studies of Mitani and Mougi (2017) and Mohd et al. (2017). The ecological model employ in this thesis is assumed to be continuous in time.

1.7 Thesis Organisation

The organisation of this thesis is shown in Figure 1.1. Chapter 1 presents the introduction, problem statement, aim and objectives of the project. Chapter 2 provides an overview of some multiple interactions (i.e., mutualism-competition-predation) type models, and this chapter starts with the prey-predator model, a competition model, a mutualism model, and a diffusion model. In Chapter 3, the theoretical analysis of the multiple interactions type ODE model is presented. The analysis here includes the existence of equilibrium, local stability analysis, global stability analysis, the existence of Hopf bifurcation, the existence of a limit cycle, and the existence of transcritical bifurcation.

In Chapter 4, the analytical results of ODE model in Chapter 3 are verified for lo-

cal and global stability properties. The combined effects of mutualism and competitor species growth rate (using ODE model) on the species coexistence and community stability are investigated in this chapter. Some ecological implications of these theoretical findings are also presented. In Chapter 5, the dynamics of local dispersal, competition, and other biotic factors are demonstrated using a PDE model. The model is then analysed using numerical simulation technique and bifurcation analysis. The PDE results in this thesis is validated by comparing our findings with simpler cases, i.e., when the strength of dispersal D is relatively weak $(D \to 0)$. Further validation of result is done by comparing with previous literature (Mitani and Mougi, 2017) and comparison between numerical simulation and bifurcation analysis finding. The model results with local dispersal are also compared with no-dispersal case for an in-depth understanding of the coexistence mechanisms in this multiple interactions type system. The ecological implications of the findings are also presented. In Chapter 6, the dynamics of local dispersal, predation, mutualism, and other biotic factors are examined using PDE models with different functional responses (FR). The Holling Type II functional response (i.e., "the amount of prey consumed decreases gradually with prey density") is incorporated into the PDE model. The results of PDE models with different functional responses (Type I and Type II) are compared to enhance understanding on multiple species coexistence dynamics. The ecological implications of the results are also discussed. In Chapter 7, a summary of the thesis and the conclusion are presented. Also, the limitation of this study and recommendation for future work are presented.

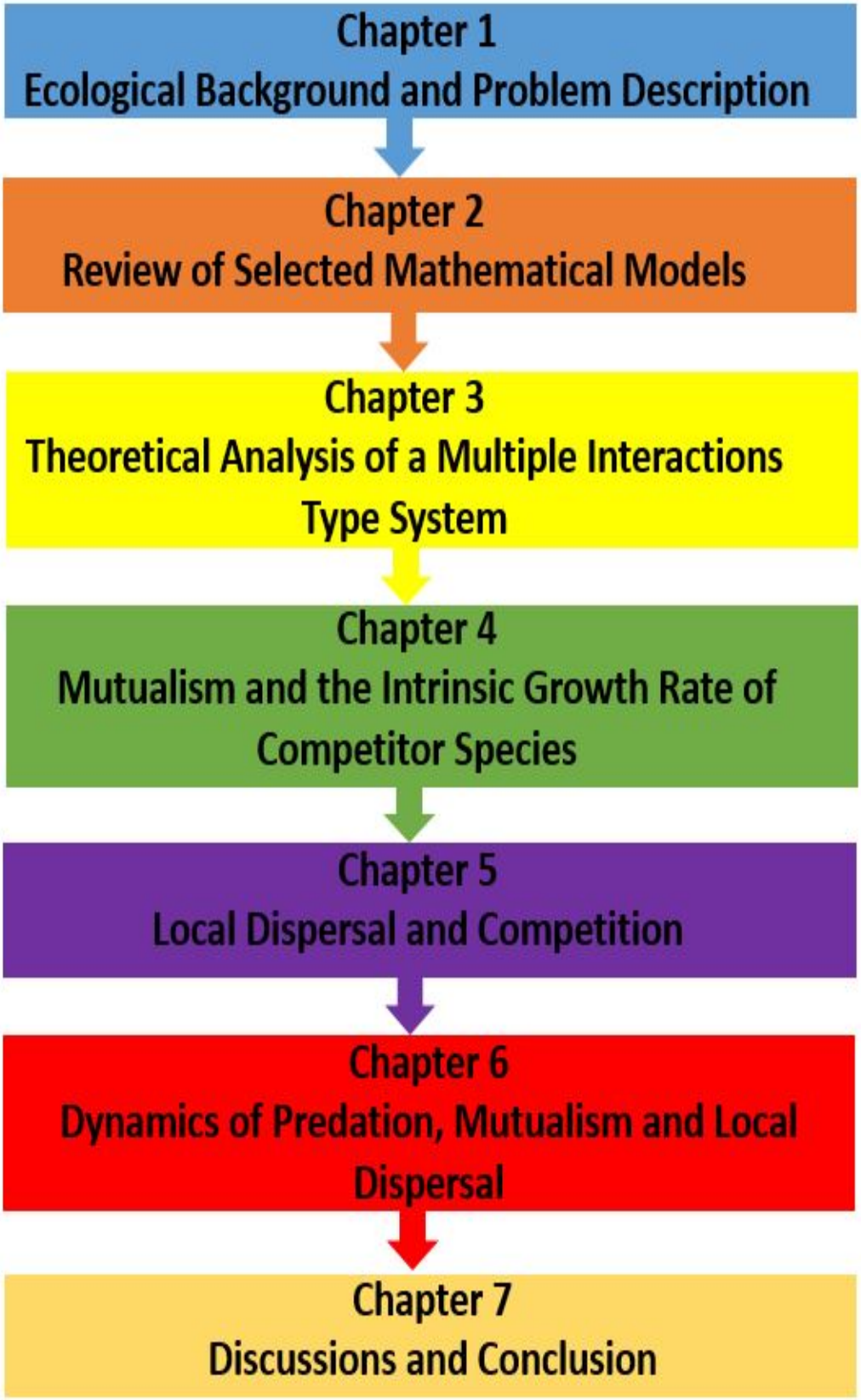

Figure 1.1: A flowchart of this thesis.

CHAPTER 2

REVIEW OF SELECTED MATHEMATICAL MODELS

2.1 Introduction

In the previous chapter, the ecological background of the study, problem statement and motivation, aim and objectives and thesis organisation has been presented. This chapter explores multiple interactions type system, and provide an overview of several multi-species models that are appropriate to this thesis. The overview from previous studies provides fundamental insights into multiple interactions type models that would be investigated throughout this thesis. In this thesis, we consider different types of multiple interactions type systems. First, we start with the predator-prey model of two-species interaction. Also, the three-species interactions type model are presented. This is followed by a diffusion model that represents species movement along an adjacent spatial location (i.e., local dispersal). The ecological applications of these models are highlighted in this chapter. Furthermore, review of previous multiple interactions type systems are discussed.

2.2 Prey-Predator Model

The first successful attempt to mathematically represent the interactions of species was achieved a century ago. Lotka (1925) and Volterra (1926) were the first to achieve this goal. Their work laid the foundation for population dynamics and mathematical ecology. Their formulated prey-predator model is a pair of non-linear first-order differential equations used to relate the interplay between two-species interaction in a

biological system. It has a simple representation as:

$$\begin{aligned} \frac{dx}{dt} &= g_1(x) + f_1(x,y), \\ \frac{dy}{dt} &= g_2(x) + kf_1(x,y), \end{aligned} \tag{2.1}$$

where g_1, g_2, f_1 and k are functions of the interaction between species. The system (2.1) represents different types of interactions. The classical type of interaction is called Lotka-Volterra competition model (Lotka, 1925), which describes the dynamic interaction between a predator population x and a prey population y. We represent the differential equations as:

$$\begin{aligned} \frac{dx}{dt} &= rx - axy, \\ \frac{dy}{dt} &= eaxy - dy, \end{aligned} \tag{2.2}$$

where systems (2.1) and (2.2) can be described as follows:

- $g_1(x) = rx$ represents the growth rate of the prey population in the absence of predators. r is the intrinsic growth rate of the prey (i.e., when the predator is absent). Therefore, the population of the prey would increase exponentially in the absence of predators as: $x(t) = x_0 e^{rt}$, where x_0 is the initial population of prey.
- $kf_1(x,y) = eaxy$ is the production/growth rate of predator offspring, where e is the conversion rate of prey into predator, where a is the capture rate and k is constant.
- $g_2(y) = -dy$ represents the predators death rate in the absence of prey and d is the mortality rate per capita of a predator when prey is not present. Therefore, predator decay exponentially in the absence of prey is: $y(t) = y_0 e^{-dt}$, where y_0 is the initial

population of predator.

More recently, there has been a renewed effort at designing sophisticated models from multiple interacting species based on the earlier works of Lotka and Volterra. The functional response (Papanikolaou et al., 2020; Spalinger and Hobbs, 1992; Wu and Huang, 2020), crowding (Diamantidis et al., 2020; Vallejos et al., 2020; Wang et al., 2020a), age structure (Bashkirtseva et al., 2020; Widayani et al., 2020), switching (Charfeddine, 2017; Jylkka et al., 2020), time delay (Barril et al., 2018; Gan et al., 2020) where the major factors considered. The hosts and parasites, parasitoid plants and herbivores and typical prey-predator relationship cover various kind of natural enemies whose interactions falls under the prey-predator relationships. Competition has also received more attention than predation despite the great feat achieved by Lotka and Volterra in their early work (Madhok, 2020; Mukherjee, 2020; Murray and Young, 2020). This attention can be attributed to the difficulties encountered in integrating biologically realistic parameter into predation models in contrast to competitive models (Arancibia-Ibarra and Flores, 2020; Ghanbari and Djilali, 2020; Hassell, 2020). The competitive effect between species or the coexistence conditions is the major results of the stability analysis of simple biological models (Bernhardt et al., 2020; Damas-Moreira et al., 2020; Luimstra et al., 2020). The dynamics of the two-species in prey-predator models are defined on the "trophic function" $f(x,y)$ which was represented in the prey equation as a functional response. In the ecological models, the more common functional responses used is classified as ratio-dependent, prey-predator and prey-dependent (Arditi et al., 1978). We discuss them in details in next subsections.

2.2.1 Prey-Dependent Functions

The rate at which the predator feeds on the prey is best to describe as prey-dependent functions. Furthermore, the prey-dependent functional response has diverse classification and has been discussed in many literature (El Bhih et al., 2020; Holling, 1959; Li and Zhao, 2020; Tripathi, 2020).

2.2.1(a) Lotka-Volterra Type

Lotka and Volterra assume in their model that the individual rate of consumption grows linearly with the population of the prey. Thus, the functional response use in their model can be written as: $f(x) = ax, x \geq 0$, where $a > 0$ represent the rate at which the predator consumes the prey. The applications of this can be found in many literature (Huang et al., 2020; Lin et al., 2020; McGee, 2020).

2.2.1(b) Holling Type I Functional Response

Holling Type I looks very much like the Lotka-Volterra type. The only difference is the maximum or upper limit (τ), which is defined as:

$$f(x) = \begin{cases} ax, & 0 < x < \alpha, \\ \\ \tau, & x \geq \alpha, \end{cases} \tag{2.3}$$

where α is the fixed amount of prey at which the predator overfeeds at τ.

Lotka-Volterra and Type I functional responses are manageably used to study ecological models despite their simple nature (Bian et al., 2017; Rosenbaum and Rall,

2018; Schröder et al., 2016).

2.2.1(c) Holling Type II Functional Response

Holling Type II assumes that the rate of consumption of each consumer rises at a reducing rate for the prey density up till when it becomes constant at saturation point. The maximum value is asymptotically approached when $a = \frac{1}{h}$. It is defined as:

$$f(x) = \frac{Ax}{1 + Ahx}, \tag{2.4}$$

where h is the time spent in consuming one prey, A is the search rate, $b = \frac{1}{Ah}$ is the half-saturation level such that $f(b) = \frac{a}{2}$, a is the rate at which the predator consumes the prey. Holling Type II is the most widely used model by mathematical ecologists. It is sometimes referred to as the "Michaelis-Menten type" because it was first used by Michaelis and Menten (Cornish-Bowden, 2013). The application of this functional response can be found in several studies (Cuthbert et al., 2019a; Fathipour et al., 2017; Pritchard et al., 2017; Sidhom and Galla, 2019).

2.2.1(d) Holling Type III Functional Response

Holling Type III assumes that the rate of consumption by the individual predator accelerates initially and thereafter reduces to the saturation point. It can be defined as:

$$f(x) = \frac{Ax^2}{1 + Ahx^2}. \tag{2.5}$$

The application of this Type III functional response can be found in several studies (Cuthbert et al., 2019b; Lazear et al., 2019; Meng and Wang, 2019; Shah et al., 2019;

Wang et al., 2020b).

2.2.2 Ratio-Dependent Functions

The abundance of the predator is not incorporated into the prey-dependent functional responses formula. Thus, Arditi and Ginzburg (1989) presented a different functional response type of model known as ratio-dependent function. Here, the prey feeding rate per predator is a function of the ratio between their respective densities and does not depend solely on the prey density. They use the ratio $\frac{x}{y}$ in place of x in the Holling Type II functional response as their functional response, and it is given below:

$$f(x,y) = \frac{A(\frac{x}{y})}{1 + Ah(\frac{x}{y})}. \tag{2.6}$$

The applications of this functional response are in several studies (Hossie and Murray, 2016; Li and Cheng, 2020; Liu and Liu, 2019; Mishra and Agarwal, 2018; Roy et al., 2020; Suryanto and Darti, 2017; Xu et al., 2018; Yang et al., 2017).

2.2.3 Predator-Dependent Functions

Here, it is assumed that the functional responses depend on both the predator and prey densities. Hassell and Varley (1969) and Beddington (1975) suggested that high predator density often causes recurrent encounter among predators population. DeAngelis et al. (1975) and Beddington (1975) were the first to use the predator-dependent functional response in their work. Their model on prey-predators is referred to as the DeAngelis-Beddington functional response. Sometimes, using mathematical analysis, the ratio-dependent functional responses and the prey-dependent functional responses

are described to be the limitation of the general case of predator-dependent functional response. Their model is represented as:

$$f(x,y) = \frac{ax}{\beta y + \alpha h x + 1}, \tag{2.7}$$

where β is a constant, and it can be defined as the product of the predator handling time and the predator encounter rate, h is the prey handling time. The applications of this functional response are found in these studies (Cai et al., 2020; El Bhih et al., 2020; Fakhry and Naji, 2020; Ghanbari et al., 2020; Hadjimichael et al., 2020; Tripathi, 2020; Tyutyunov and Titova, 2020).

2.3 Competition Model

The first successful attempt to mathematically represent the interactions of species was achieved a century ago. Lotka (1925) and Volterra (1926) were the first to achieve this goal. Their work laid the foundation for competition in two-species studies (Mittelbach and McGill, 2019). Recently, this model has been use to study $n \geq 2$ (n is the number of species in a community) competition among species (Fort and Segura, 2018; Vet et al., 2018). The basic assumption in this model is that the consequences of competition among two competing species inhibit each species in the system.

Gause (1932) employed a Lotka-Volterra competition model to forecast the consequences of competition among two paramecium species. The competition model has been reported to give a good forecast of the distribution of protozoan species (Vandermeer, 1969). Also, the Lotka-Volterra competition model has been employed to study the competition among butterfly *Melitaea cinxia* (butterfly that belongs to the family

Nymphalidae) (Lei and Hanski, 1998). From the above discussion, species coexistence is one of the consequences of this competition model when the interactions between species are weak (Jorgensen and Fath, 2014). However, species coexistence could not be observed for birds in New Guinea (Jorgensen and Fath, 2014). The ecological model is represented as follows:

$$\frac{dN_i}{dt} = \frac{r_i N_i}{k_i}\left(k_i - \sum_{j=1}^{m} \alpha_{i,j} N_i\right), \quad (i = 1,2) \tag{2.8}$$

where N_i represents the density of species i, the term r_i represents the growth rates of species i, k_i represents the carrying capacity. Also, the term α_{ij} represents the competitive impact of species j and i. For the ecological dynamics of this competition model, interested readers are referred to the works of Mohd (2016), Kot (2001), Strogatz (2001).

2.4 Mutualism Model

The interactions that exist between species of different kinds are mutualistic if the presence of one species increases the growth rate of the other species (Rai et al., 1983). The previous studies of two-species models of mutualism explicitly neglected the benefits derived from mutualistic interactions (Christiansen and Fenchel, 2012; Janzen, 1967; Vandermeer and Boucher, 1978; Whittaker and Likens, 1975). In some cases, two-species models of mutualism have been extended for $n \geq 3$ species without any further complexity added (Harley, 1970; Travis et al., 1979). However, in some studies, more complex models of mutualism have received significant attention (Lawlor, 1979; Vandermeer, 1980).

The concept of mutualism in ecology does not replace competition; instead, it has expanded and transformed the general perspective involving the interactions between different species. Species cooperation has enjoyed recent popularity in the study of ecology, and biological philosophers have picked tremendous interest in it (Gilbert et al., 2012). In the past, little or no importance was attached to mutualism by ecologists. Thus, Axelrod and Hamilton (1981) carried out a mathematical study on cooperation. Some years later, May (1984) documented that "mutualism has remained relatively neglected in the field of ecology, laboratory, theory and textbooks". The pioneering work of Margulis (1981) faced much resistance in promoting the understanding of mutualism as it is often regarded as symbiotic relationship and exotic, and this affects the understanding of the ecosystem functioning.

The action of mutualism can result in the production of "mutually-constituted organisms" which are intertwined, i.e., an alga and a fungus form a lichen ("a composite organism that emerges from algae or fungi in a mutually beneficial symbiotic relationship") (Spribille et al., 2016). The economic outcomes of mutualisms are great; for example, pollination is key to agriculture, and the maintenance of soil nutrients is also vital in agriculture, and all these involves a lot of mutualisms (Wall and Moore, 1999). The essential roles of "soil biota" (i.e., algae, fungi, and bacteria) in agricultural processes are too valuable (Welbaum et al., 2004). The maintenance and development of a healthy immune system and gut require the presence of bacteria (Davison, 2020). Mutualisms unlock unique ecological niches (Favareau, 2009).

The dynamics of the three-species (prey-predator-mutualist) model can be described

by (Rai et al., 1983):

$$\frac{du}{dt} = uh(u,x),$$

$$\frac{dx}{dt} = \alpha xg(u,x) - yp(u,x), \tag{2.9}$$

$$\frac{dy}{dt} = y[-s + cp(u,x)],$$

where u, x, y represents predator, prey, and mutualist species, respectively. The term $h(u,x)$ is the growth rate of the mutualist species, $p(u,x)$ is the impact of predator species on prey, $g(u,x)$ is the growth rate of prey species, x is the mutualist impact of x on u, $-s$ is the death rate of the mutualist species, and α is an arbitrary constant which will later serve as the bifurcation parameter.

Assumptions: It is assumed that the system has birth and death rates that is continuous with time. Also, $\frac{\partial h}{\partial u} < 0$, $\frac{\partial h}{\partial x} > 0$, $h(0,x) > 0$, $x \geq 0$, $u \geq 0$.

We obtain the system equilibrium by equating system (2.9) to zero.

$$uh(u,x) = 0,$$

$$\alpha xg(u,x) - yp(u,x) = 0, \tag{2.10}$$

$$y[-s + cp(u,x)] = 0.$$

The system (2.10) has six biologically-meaningful equilibria:

$E_0(0,0,0)$, $E_1(0,k(0),0)$, $E_2(0,x^*,y^*)$, $E_3(L(0),0,0)$, $E_4(u^*,x^*,0)$ and $E_5(u^*,x^*,y^*)$.

2.5 Diffusion Model

In several studies, the concept of a random walk has been used to illustrate the diffusion model. This equation represents the most notable diffusion model:

$$\frac{\partial N}{\partial t} = D\frac{\partial^2 N}{\partial x^2}, \tag{2.11}$$

where N represents species density and D denotes the diffusion strength. The model (2.11) assumes a localised dispersal pattern (i.e., dispersal takes place along adjacent spatial locations). The assumption in the system (2.11) gives a true reflection of some plant whose seeds disperses within a short distance not too far from the parents plant (Cain et al., 2000; Holmes et al., 1994; Mohd, 2016). The results from the numerical simulation of the system (2.11) demonstrate how species move from well-populated area to less populated area as time progress. It further shows that species movement is directly proportional to the dispersal strength (D).

To have a clear presentation of the effect of diffusion in an ecological system, we incorporate dispersal term into a single-species mutualist community (Rai et al., 1983) and numerically simulate the model to observe the dynamics of the system. The equation of single-species mutualist community with dispersal is as follow:

$$\frac{\partial Z}{\partial t} = Z(-s+cp) + D_z\frac{\partial^2 Z}{\partial k^2}, \tag{2.12}$$

where Z is the population density of the mutualist species, s is the death rate of the mutualist species, p is the impact of mutualist species, c is a positive constant and k represent the spatial domain. The diffusion system is numerically solved by imposition