

The Effects of Varying Predator Dispersal Strength on Prey-Predator Dynamics with Refuge Process

Zati Iwani Abdul Manaf^{a,b*}, Mohd Hafiz Mohd^b

^aMathematical Science Studies, College of Computing, Informatics and Mathematics, Universiti Teknologi MARA (UiTM) Kelantan Branch, Machang Campus, 18500 Machang, Kelantan Darul Naim, Malaysia; ^bSchool of Mathematical Sciences, Universiti Sains Malaysia, 11800 USM Penang, Malaysia

Abstract The combined effects of (symmetric or asymmetric) dispersal and refuge mechanisms can have a significant impact on prey-predator dynamics. However, there remains a knowledge gap in concerning the incorporation of asymmetrical dispersal in the presence of prey refuges. Therefore, this paper aims to examine the influence of varying levels of asymmetrical (i.e., predator) dispersal on the interactions between prey and predators, as well as the role of prey refuges in facilitating species coexistence. The investigation begins by introducing an ordinary differential equation (ODE) model for the prey-predator system, which is subsequently extended to a partial differential equation (PDE) model. By conducting one-parameter bifurcation analysis on both models, the presence of transcritical and Hopf bifurcation points is established. Furthermore, the research delves into the spatio-temporal dynamics of the PDE model, capturing the intricate interactions between a specialized prey species and its predator. The focus is on examining the effects of different strengths of predator dispersal on the dynamics of the prey-predator system. The aim is to gain a comprehensive understanding of how predator dispersal influences the stability and persistence of the system, and to investigate the ecological implications of these dynamics in terms of prey-predator coexistence. Hence, the main findings of the research suggest that the increased levels of predator dispersal led to a wider range of prey refuges, supporting species coexistence. In conclusion, this study emphasises the critical importance of predator and prey dispersal dynamics in determining the key mechanisms that can promote species coexistence.

Keywords: Partial differential equations, dispersal, prey refuges, numerical bifurcation analysis.

Introduction

The interactions between predators and prey are crucial in shaping ecological communities. It is very important to fully understand the factors that affect these interactions in order to study population dynamics and maintain ecosystem stability. Dispersal, which refers to the movement of individuals or populations from one area to another plays a critical role in influencing prey predator systems. Additionally, the existence of prey refuges, which are separate areas or resources that provide safety and protection for prey species. Can greatly impact interactions between prey and predators.

Numerous scholarly investigations have been conducted to examine the dynamics of prey-predator systems, with particular emphasis on the mechanisms of dispersal. In a study conducted by Kim and Choi [1], the researchers investigated the impact of directional dispersal of predators. Their findings revealed that predators who moved towards regions with high predation rates experienced enhanced survival probabilities and fitness levels. In contrast, Kang *et al.* [2] studied a two-patch model where predators moved towards prey-rich patches, and they observed that dispersal could either stabilize or destabilize the system, generating multiple equilibria or leading to predator extinction. In a different

***For correspondence:**

zati431@uitm.edu.my

Received: 11 July 2023

Accepted: 21 Sept. 2023

©Copyright Abdul Manaf.

This article is distributed under the terms of the

[Creative Commons](#)

[Attribution License](#), which permits unrestricted use and redistribution provided that the original author and source are credited.

approach, Li [3] analysed a nonlocal prey-predator model with a free boundary and showed that if the habitat size and spreading coefficient were small, predators would eventually vanish and fail to establish. Lastly, Mohd *et al.* [4] explored different dispersal patterns in multi-species communities and discovered that very long-range dispersal could cause species extinctions, while intermediate-range dispersal promoted higher chances of coexistence compared to short-range dispersal.

Further research has contributed to our understanding of prey-predator dispersal. Mohd *et al.* [5] investigated the joint impact of dispersal and stochasticity on priority effects, which determine the presence or absence of multiple species. The study found that the inclusion of dispersal initially reduces the prevalence of priority effects but ultimately increases their occurrence, while also enhancing species range overlap. Mohd and Noorani [6] focused on local dispersal and predator handling times, discovering that higher levels of generalist predation, without dispersal, require shorter specialist predator handling times to maintain biodiversity through coexistence and oscillatory dynamics. Conversely, lower generalist predation forces result in longer specialist predator handling times, destabilizing species biodiversity. Aliyu and Mohd [7] extended a four-species interaction model with local dispersal, emphasizing the interplay between mutualism and competition. They found that mutualism modifies the response of the ecological community to increasing competition on resource species. Xiao *et al.* [8] explored the effects of prey diffusion in two-patch predator-prey systems, demonstrating that different diffusion scenarios can drive predator extinction while maximizing prey abundance. Additionally, sink-to-source diffusion and diffusion asymmetry can reverse outcomes observed without diffusion.

The dynamics of prey-predator systems with refuge have been extensively studied, shedding light on the intricate interplay between species and the effects of refuge on population dynamics. Ghosh *et al.* [9] found that the presence of refuge stabilized both predator and prey populations, contrary to expectations. Ma *et al.* [10] highlighted the role of prey refuge in promoting coexistence between predators and prey. Zhang *et al.* [11] incorporated fear as a driving factor in prey-predator systems with refuge, demonstrating that prey behavioural responses influenced population dynamics and stability. Das and Samanta [12] investigated a model with refuge and additional food for predators in a fluctuating environment, revealing the complex interactions between refuge availability, predator foraging behaviour, and environmental fluctuations. Manaf and Mohd [13] considered not only prey refuge but also herd behaviours in prey species, uncovering the stability and bifurcational change in dynamics of these systems.

One crucial factor that can significantly impact prey-predator dynamics is the dispersal behaviours. Symmetric dispersal and asymmetric dispersal are two distinct patterns of movement and distribution observed among individuals within a population. The concept of symmetric dispersal pertains to the phenomenon wherein individuals within a given population demonstrate a propensity to disperse or distribute themselves in a manner that is characterised by a relatively equal and uniform distribution across the available habitat. In simpler terms, there is an absence of visible bias or preference towards particular regions or directions of movement. This phenomenon has the potential to result in an increased level of homogeneity in the spatial distribution of individuals within the population. In contrast, asymmetric dispersal is a term used to describe the occurrence in which individuals within a population display an unequal or unbalanced spatial arrangement throughout the habitat during the process of dispersal. In the present context, there is an observed tendency or a tendency towards certain geographical areas. This phenomenon can lead to a spatial distribution that is characterised by heterogeneity, where certain regions display a higher concentration of individuals while others maintain a relatively lower population density.

The phenomenon of asymmetrical dispersal in predator-prey systems provides valuable insights into the dynamics of populations. Huang *et al.* [14] emphasizes that intermediate dispersal levels are beneficial to predator abundance, whereas excessive levels can result in predator extinction. Furthermore, the study demonstrates how changing dispersal asymmetry can change the effect of dispersal from beneficial to detrimental, even leading to predator extinction in both patches. Fang *et al.* [15] demonstrates that asymmetric diffusion rates can result in higher equilibrium population abundances than in non-diffusion environments, challenging intuitive expectations. Similarly, Arditi *et al.* [16] highlights that dispersal asymmetry influences dispersal's effect on total population abundance quantitatively while qualitatively maintaining similar patterns as symmetric dispersal.

The combined effects of dispersal and refuge in influencing the dynamics between prey and predators has been underscored by numerous studies. In their study, Chakraborty and Bairagi [17] investigated the impact of prey refuge and diffusion on the dynamics of a system. They observed a range of spatiotemporal patterns and found that the availability of refuge for prey and the rate of species diffusion were significant factors influencing these patterns. They found that when the predator was mobile and

the prey sedentary, the dynamic complexity increased, especially with varying refuge availability. On the other hand, Xie *et al.* [18] concentrated on the stability analysis of a fractional-order prey-predator model incorporating prey refuges. They proposed conditions ensuring the uniform asymptotic stability of the positive equilibrium point. In the investigation by Bhattacharyya and Chattopadhyay [19], the focus was on the non-smooth dynamics resulting from predator-driven prey dispersal and the behaviour of prey refuge. The research highlighted that highly apprehensive prey preferred longer refuge stays, while hypervigilant prey frequently changed habitats. The study also revealed that bold but less vigilant prey remained in the open habitat at the expense of their stock, while more apprehensive and less vigilant prey chose the refuge, compromising their foraging and mating opportunities.

Some prior studies, [20-22] examined different aspects of prey-predator dynamics incorporating various factors such as time delay, refuge, harvesting, and prey dispersal. Alidousti and Ghahfarokhi [20] focused on a time-delay fractional predator-prey system with prey dispersal and demonstrated that the fractional system exhibited periodic solutions with shorter periods compared to the classical case, expanding the stability domain under the fractional order. In contrast, Hare and Rebaza [21] investigated the dynamics of a predator-prey system with refuge, harvesting, and dispersal. They introduced two patches in a three-dimensional model to represent unavailable prey habitat and a classical predator-prey relationship, including refuge and harvesting. This approach facilitated a more precise representation of the issue at hand. Yang and Wei [22] investigated a diffuse prey-predator system that includes a refuge for the prey population. They discovered Hopf bifurcation at positive equilibrium and highlighted the importance of prey refuge on both stability and bifurcation patterns.

Despite the importance of spatially explicit models of prey-predator interactions, there has been little discussion of asymmetric dispersal that incorporates prey refuge mechanisms. Thus, the concept of asymmetrical dispersal is used in this study to investigate the impact of varying predator dispersal on the dynamics between prey and predator interactions with refuge process. This study will provide valuable insights into the complex dynamics of species coexistence, which can promote the stability of population dynamics. To do this, the ordinary differential equation model was expanded into a partial differential equation to capture the spatiotemporal dynamics of prey-predator interactions. To solve the partial differential equation model, the numerical method of lines is used. This procedure entails partitioning the spatial domain of the partial differential equation into a set of discrete grid points and converting the partial differential equation with respect to time into a set of ordinary differential equations. When using the method of lines, the partial differential equation is typically discretized using finite difference or finite element techniques.

Furthermore, a one-parameter bifurcation analysis was utilised to investigate the range of parameter values that result in distinct dynamical phenomena in both models. The incorporation of these analytical methodologies yielded valuable insights into the intricate dynamics of the prey-predator system involving predator dispersal and prey refuges. The study's results have enhanced comprehension regarding the complex dynamics among predator dispersal, prey refuges, and prey-predator interactions. These findings have significant implications for the development of conservation and management strategies that seek to safeguard biodiversity and promote harmonious coexistence between predator and prey species within natural ecosystems.

The paper was structured as follows: Section 2 introduces the ordinary differential equation model as well as the partial differential models, and a stability analysis is performed. In Section 3, ODE and PDE frameworks were employed to investigate the bifurcation analysis of prey and predator populations. In particular, the effect of prey refuge was investigated. The spatio-temporal dynamics of a PDE model that captured the interactions between a specialised prey and a predator were also studied in this section. Finally, Section 4 concluded the study by summarising the key findings, discussing their ecological significance, and proposing future directions for research in the field of prey-predator interactions.

Materials and Methods

In this section, we introduce an ordinary differential equation model that incorporates the concept of prey refuge. Subsequently, we proceed to expand this ODE model into a spatio-temporal framework through the development of a PDE model. This extension enables us to investigate the spatial distribution and dynamics of both prey and predators. Ultimately, a stability analysis is conducted on the constructed model in order to examine its dynamic characteristics and evaluate its stability properties.

A Prey-predator System of Ordinary Differential Equation (ODE)

The incorporation of ODE models in the context of prey-predator systems featuring prey refuge offers a significant mathematical instrument for understanding the dynamics of populations engaged in interactions. ODE models have been extensively utilised in the field of ecological research due to their capacity to effectively represent the fundamental dynamics of species interactions throughout their temporal progression. Kar [23] carried out a study with the purpose of analysing a prey-predator model of the Lotka-Volterra type, which incorporates a prey refuge. This model allows for the quantitative description and analysis of the population dynamics of the two species involved. The mathematical formulation represented as follows:

$$\begin{aligned} \frac{du}{dt} &= hu\left(1 - \frac{u}{k}\right) - \frac{b(1-m)uv}{1+a(1-m)u}, \\ \frac{dv}{dt} &= -dv + \frac{cb(1-m)uv}{1+a(1-m)u}. \end{aligned} \tag{1}$$

The variables u and v in the model represent the densities of prey and predator populations at a given time t , respectively. All parameters h, k, a, b, c, d is considered positive constants. The parameter h represents the natural growth rate of the prey population, indicating how quickly the prey population can increase in the absence of predators and other limiting factors. Carrying capacity, denoted by k , reflects the maximum population size that the environment can sustain based on available resources. Parameter a signifies the amount of time predators spend handling a single prey, influencing their feeding efficiency and overall predation rate. The predation rate, governed by parameter b , quantifies how frequently predators encounter and capture prey. Parameter c denotes the conversion rate at which each consumed prey is transformed into a newborn predator, highlighting the efficiency of converting prey biomass into predator population growth. Predator death rate, represented by d , accounts for various factors leading to predator mortality. The parameter m , which represents the proportion of prey species employing refuge, has a notable impact on the model as it affects the vulnerability of prey to predation and influences the spatial arrangement of both prey and predators. In this case, the term $(1-m)$ represents the fraction of the prey that is not seeking refuge and prone to predation.

By conducting an analysis of the ODE model, valuable insights regarding the dynamics and stability of prey and predator populations can be derived in the context of refuge presence. This model shows how refuge affects population sizes, oscillations, and system stability. It also allows researchers to study prey-predator coexistence. However, ODE models have constraints that must be considered. These models assume population homogeneity and ignore spatial variations and interactions. Thus, prey refuge analysis requires spatially explicit models, particularly PDEs. This method accurately depicts prey, predator, and refuge locations and interactions.

A Prey-predator System of Partial Differential Equations (PDE)

In this section, we incorporate self-diffusion into the existing ordinary differential equation system (1) and investigate a new system of coupled nonlinear partial differential equations. The aim is to examine the dynamics of specialist prey species $u(x, t)$ and specialist predator species $v(x, t)$ along a one-dimensional gradient. The spatial domain is defined as $0 < x < 1$. To achieve this, we utilize a PDE model that allows us to examine the intricate interactions between these species in a spatial context. Thus, the following PDE model represented as:

$$\begin{aligned} \frac{\partial u}{\partial t} &= hu\left(1 - \frac{u}{k}\right) - \frac{b(1-m)uv}{1+a(1-m)u} + D_u \frac{\partial^2 u}{\partial x^2}, \\ \frac{\partial v}{\partial t} &= -dv + \frac{cb(1-m)uv}{1+a(1-m)u} + D_v \frac{\partial^2 v}{\partial x^2}, \end{aligned} \tag{2}$$

The reaction terms in the proposed system (2) are influenced by a Holling type-II functional response [24, 25]. In the presence of refuge process, the Holling type-II functional response is defined by $\frac{b(1-m)u}{1+a(1-m)u}$, which is a fundamental concept in ecological studies, capturing the realistic dynamics of predator-prey interactions. It exhibits a non-linear relationship where the predation rate initially increases with increasing prey density but eventually plateauing as the rate reaches its maximum value. This saturation effect signifies that predators become more efficient in capturing prey up to a certain point,

after which their consumption rate stabilizes, even with further increases in prey density. This response is influenced by various factors, including the time required for handling prey, the efficiency of prey handling, and the ability of prey to evade predation. Ecologists widely accept the Holling type-II functional response because it acknowledges the limitations of predators' feeding capacity. It recognizes that predators cannot sustain an infinitely increasing consumption rate in the presence of an unlimited supply of prey. Instead, the response curve reflects the predator's ability to balance its feeding efficiency with the prey's ability to avoid being captured, particularly at high population densities. Incorporating the Holling type-II functional response into the system (2) enhances the model's accuracy in representing the dynamics of predator-prey interactions. By accounting for the saturation effect and the non-linear relationship between predation rate and prey density, the model captures the complexities of these interactions and provides valuable insights into population regulation mechanisms.

Spatial dynamics were introduced into the system by extending the model (2) along an environmental gradient. This extension involved incorporating spatial diffusion terms into the model, resulting in a system of PDEs. The PDE system enabled the capture of prey and predator dispersal across different locations or environments. In this model, it was assumed that the prey-predator interaction was localized, meaning that species only interacted when they coexisted in the same environment or location along the

gradient. The diffusion terms, represented by $\frac{\partial^2 u}{\partial x^2}$ and $\frac{\partial^2 v}{\partial x^2}$, characterise the dispersal of the prey and predator species, respectively. These terms account for the movement and migration of individuals among different locations within the spatial domain. The parameters D_u and D_v in the diffusion terms determine the magnitude of dispersal for the prey and predator species, respectively. These parameters quantify the strength or effectiveness of the dispersal process, indicating how readily individuals of each species can move or migrate through the environment. Higher values of D_u or D_v indicate greater dispersal ability for the corresponding species, enabling them to move more efficiently through the environment.

Consistent with previous ecological research [4, 26, 27], zero-flux boundary conditions were imposed for each species in order to replicate a scenario where species migration was restricted across the boundaries:

$$D_u \left. \frac{\partial u}{\partial x} \right|_{x=0,1} = D_v \left. \frac{\partial v}{\partial x} \right|_{x=0,1} = 0 \quad (3)$$

These boundary conditions ensure that there is no net transfer of individuals into or out of the system at the spatial boundaries, thus representing a closed and isolated population within the specified spatial domain. This approach allows us to focus on the internal dynamics of the system without external influences from immigration or emigration.

In this study, the parameter values in Table 1 were selected based on previous ecological studies conducted by [23]. Meanwhile, the prey refuge proportion m is varied between the range of 0.7 and 1 for this analysis due to its ecological relevance. Based on the stability analysis performed, this range represents scenarios in which a significant portion of the habitat is designated as prey refuge, thereby facilitating the stable co-existence of species while supporting the survival of ecosystems. The range of $m < 0.7$ is excluded from our analysis due to the presence of unstable dynamics regions. Interested readers are referred to previous work [13] on these unstable dynamics for further detail.

Finally, by utilizing these specific parameter values, a range of ecological dynamics, including scenarios involving both generalist and specialist predator-prey species across heterogeneous environments were explored. The goal was to capture and analyze the intricate interactions between species in a manner that aligned with ecological realism. Through this approach, valuable insights into the system dynamics were gained, contributing to our understanding of ecological processes.

Table 1. Parameter values

Parameter	Description	Value
h	Prey growth rate	5
k	Prey's carrying capacity	60
m	Prey refuge proportion	Varied between 0.7 and 1
a	Predator's handling time	0.24
b	Predator's attack rate	1.2
c	Conversion rate of prey to predator biomass	0.4
d	Predator's death rate	1

The Stability Analysis

When there is no dispersal present ($D_u = D_v = 0$), the model (2) can be simplified to an ordinary differential equation system (1). In this simplified scenario, the dynamics at a specific environment x are not influenced by the dynamics at other environments. The steady states of the system (u^*, v^*) were identified by analytically solving the equations and setting the time derivatives to zero. This enabled us to determine the equilibrium points where the population densities of the prey and predator species remained constant over time. Within the system (1), three distinct steady states were observed:

(i) The trivial steady state $E_0(0,0)$ represents the extinction of both the prey and predator populations, where no individuals of either species are present.

(ii) The boundary steady state $E_1(k,0)$ corresponds to the survival of the prey population while the predator population is absent. In this steady state, the prey population reaches its carrying capacity, but there are no predators preying upon them.

(iii) The interior steady state $E_2(u^*, v^*)$ where $u^* = \frac{d}{(cb - ad)(1 - m)}$ and

$$v^* = \frac{(adkm - bckm - adk + bck - d)ch}{k(m - 1)(ad - bc)(adm - bcm - ad + bc)}$$

represents the coexistence of both the prey and predator populations. This interior steady state indicates a dynamic equilibrium where the predator-prey interactions allow for the persistence of both species.

By substituting each of the steady states (i) - (iii) into the Jacobian matrix, we can calculate the corresponding eigenvalues. The stability analysis of these three steady states is thoroughly discussed in the work of [13]. The eigenvalues provide insights into the stability properties of the steady states, shedding light on whether small perturbations will dampen out or amplify over time. The analysis delves into the implications of the eigenvalues, further enhancing our understanding of the system's dynamics and its behaviour around these steady states.

In the presence of local dispersal ($D_u, D_v > 0$) in the PDE model represented by system (2), it is not possible to obtain analytical solutions for the steady states. Therefore, numerical simulations were conducted to explore the system's behaviour, and the findings are presented in subsequent sections. To numerically solve the system (2) with the boundary conditions defined in equation (3), we utilized the MATLAB *pdepe* solver until a steady state was reached. This solver applies the method of lines to discretize the PDEs into a set of ODEs. It then solves these equations by integrating them over the time span. The stability of the steady state was then assessed by verifying that all the real parts of the eigenvalues were negative. The Jacobian matrix and eigenvalues were numerically computed using the MATLAB *fsolve* and *eig* functions, respectively [28-30]. Furthermore, we utilized the numerical continuation software XPPAUT Auto [31] to systematically vary specific parameter values, track stable and unstable steady states, and identify bifurcation points. This allowed us to explore the dynamic behaviour of the system under different parameter settings.

Results and Discussion

In this section, we examined the effects of prey refuge using the bifurcation analysis of prey and predator models i.e., for both ordinary differential equations and partial differential equations frameworks. We specifically investigated how the presence of prey refuge influenced the stability and behaviour of these populations. Furthermore, we delved into the spatio-temporal dynamics of a PDE model that represents the intricate interactions between a specialist prey species and its predator. Finally, we also addressed

the consequences of distinct predator dispersal strength on the dynamics of the prey-predator system.

Numerical Bifurcation Analysis

These two research findings explore the population dynamics of prey and predator species using different modelling approaches: an ODE system (1) in Figure 1 and a PDE system (2) in Figure 2.

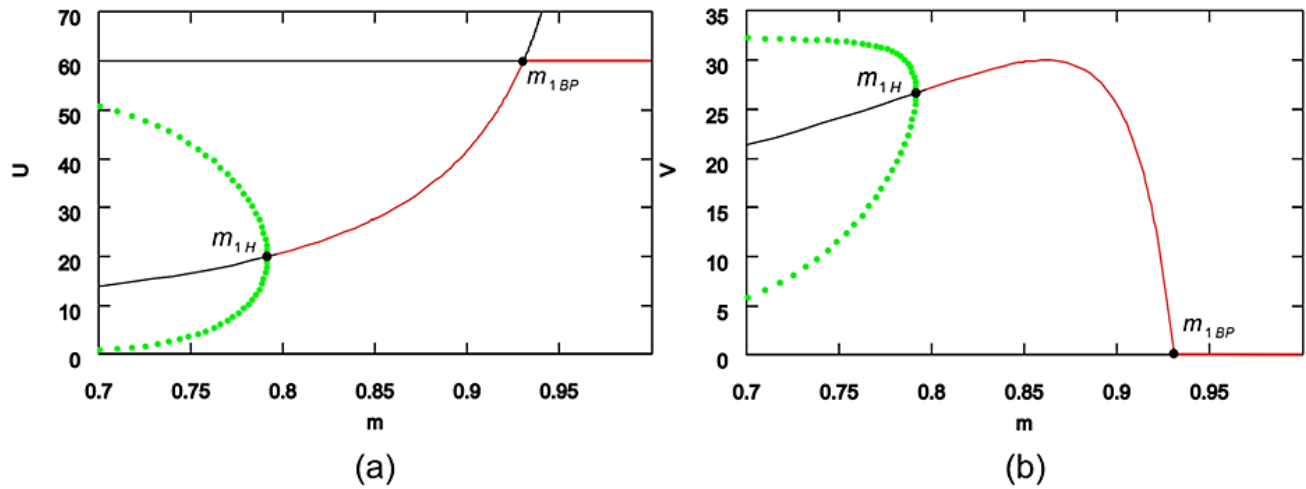


Figure 1. ODE bifurcation diagrams of prey and predator populations with respect to refuge availability parameter, m . The red and black curves (or lines) represent the stable and unstable steady states, respectively. The green-dotted curve indicates the stable limit cycle. Meanwhile, the points m_{1H} and m_{1BP} depicts the Hopf and transcritical bifurcations

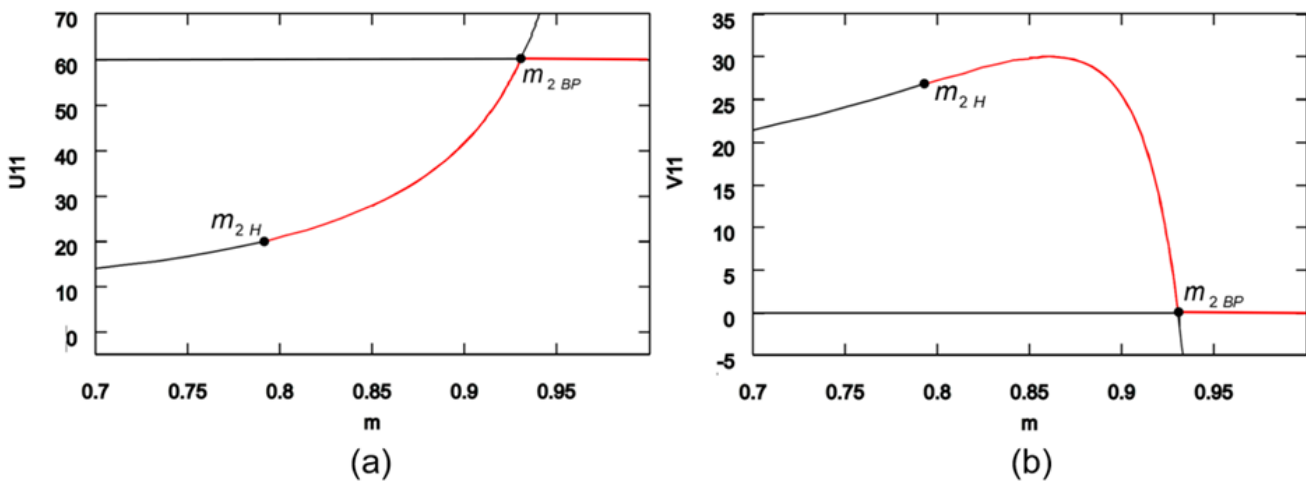


Figure 2. PDE bifurcation diagrams of prey and predator populations with respect to refuge availability parameter, m . The red and black curves (or lines) represent the stable and unstable steady states, respectively. Meanwhile, the points m_{2H} and m_{2BP} depicts the Hopf and transcritical bifurcations

Figure 1 presents bifurcation diagrams illustrating the dynamics of prey-predator interactions using an ODE system. These diagrams demonstrate how the population behaviors change as the availability of refuges, represented by the parameter (m), varies. The results indicate that the system exhibits oscillatory behavior, characterized by cyclic fluctuations in population densities, within the range of $0.7 < m < m_{1H}$. In this case, sustained oscillations occur in the populations. The presence of a stable limit cycle, represented by the green dotted curve, signifies the persistence of sustained oscillations in the system. In contrast, the black line represents unstable steady states, indicating points in the system where equilibrium cannot be maintained. At $m = m_{1H}$, a Hopf bifurcation occurs, which represents a critical point where the stability of the oscillatory dynamics undergoes a change in behaviour. Hopf bifurcations are a type of bifurcation in dynamical systems theory where stable periodic solutions emerge or disappear as a parameter is varied. In an ecological context, this can correspond to a critical transition point where a stable population cycle emerges or vanishes, leading to significant changes in ecological

dynamics. As prey refuge increases beyond m_{1H} , the system transitions into a stable state region $m_{1H} < m < m_{1BP}$. Within this region, the bifurcation diagram shows stable steady states, indicated by the red curve, representing stable population equilibria. At $m = m_{1BP}$, a transcritical bifurcation occurs. Transcritical bifurcation is a type of bifurcation where two stable states exchange stability as a parameter is varied.

Figure 2, on the other hand, presents the density of a specialist predator and prey species using a PDE system. The study investigates the effects of prey refuge availability, m , on population dynamics while considering a predator dispersal rate of $D_v = 0.4$ and a prey dispersal rate of $D_u = 0.1$. The findings indicate that within the range of $0.7 < m < m_{2H}$, the system displays unstable steady states (black curve), which represents the regions where equilibrium states are not stable. Within the range of $m_{2H} < m < m_{2BP}$, the populations transition into a stable state characterized by stable steady states (red curve) where both prey and predator populations coexist in this region. Nevertheless, if prey refuge exceeds m_{2BP} , it may result in the survival of prey species and the extinction of the predator population. Similar to Figure 1, a transcritical bifurcation ($m = m_{2BP}$) and Hopf bifurcation ($m = m_{2H}$) points occur in the reverse direction. However, the presence of a stable limit cycle does not appear in Figure 2. This happens due to the inherent complexity introduced by spatial discretization, which makes computing the limit cycle in partial differential equation models difficult. The process of discretization, which is essential for the numerical computation of partial differential equations, gives rise to errors and limitations that can pose challenges in accurately representing the dynamics of limit cycles.

Comparing the two findings, both models predict similar patterns in the oscillatory dynamics and steady states of the prey and predator populations. The presence of Hopf and transcritical bifurcations and the potential extinction of the predator population are consistent in both the ODE system (Figure 1) and the PDE model (Figure 2). However, there is a difference in the representation of stable limit cycles, with Figure 1 showing a green dotted curve indicating a stable limit cycle, while Figure 2 acknowledges the limitations in accurately depicting these cycles. Overall, these findings contribute to our understanding of the complex dynamics of prey-predator interactions and highlight the importance of refuge availability in shaping population stability. The comparison between the ODE system and PDE model offers complementary insights into the behaviour of prey and predator populations under different modelling frameworks, enhancing our ecological understanding of refuge effects on population dynamics.

Dynamics of PDE Model

Figure 3 presents the spatio-temporal dynamics of a PDE model depicting the interactions between a specialist predator $v(x, t)$ and prey species $u(x, t)$. The model considers asymmetrical dispersal scenario with predator disperses at faster rate (e.g., $D_v = 0.4$) compared to prey population (e.g., $D_u = 0.1$). Subsequently, an analysis was conducted to analyse the behaviour of the system across different levels of prey refuge. The colour intensity represents the density of prey and predators in an ecological system. Lighter shades (e.g., yellow) generally correspond to higher population densities, whereas darker shades (e.g., deep blue) imply lower population densities at a specified location (x) and time (t).

As shown in Figure 3(a), when the prey refuge levels are relatively low (e.g., $m = 0.77$), both the prey and predator populations exhibit oscillatory behaviour. In situations where there is a scarcity of areas providing shelter for prey, a significant proportion of the prey population remains vulnerable to predation. This situation allows predators to easily locate and select their targets. As a consequence, this causes significant predation pressure on the prey population. Our finding also suggests that the relatively high predator dispersal rate relative to the prey dispersal rate enables predators to locate and prey upon oscillating prey populations. The oscillations in both populations indicate a dynamical behaviour where the predator and prey populations cyclically interact, with the predator population responding to the changes in prey abundance.

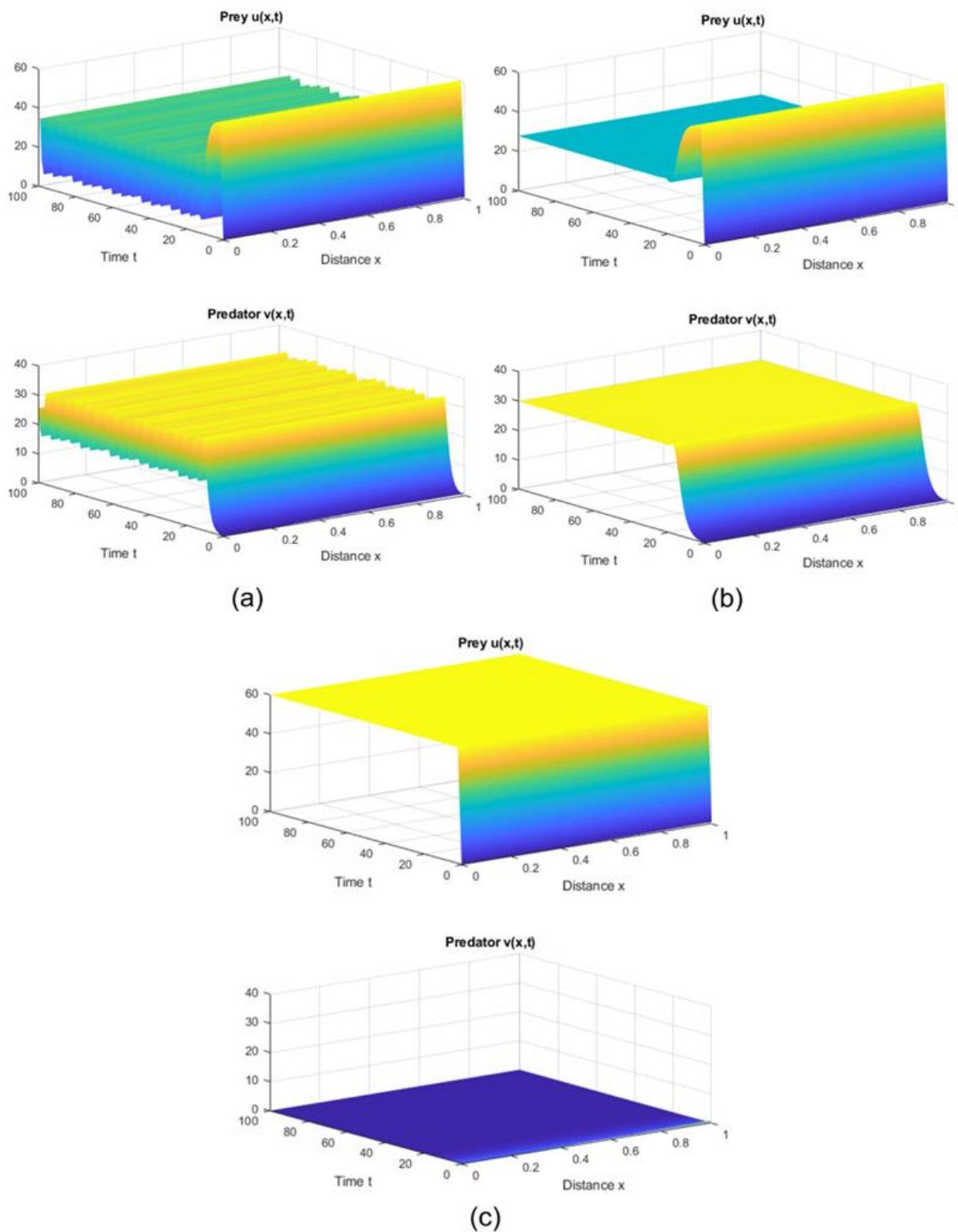


Figure 3. Spatio-temporal dynamics of a PDE model for specialist prey $u(x, t)$ and specialist predator $v(x, t)$ with predator dispersal ($D_v = 0.4$) at different prey refuge values (a) $m = 0.77$, (b) $m = 0.85$ and (c) $m = 0.95$. At the given distance (x) and time (t), lighter colours (e.g., yellow) indicate higher population densities, whereas darker colours (e.g., dark blue) indicate lower population densities

For rapid prey refuge levels (e.g., $m = 0.85$) as depicted in Figure 3(b), the system demonstrates stable steady state density, and the coexistence of both species can be observed. The previously oscillating behaviour (at $m = 0.77$) disappears in this scenario. This is because adequate refuge capacity for prey species promotes prey population growth by reducing predation pressure, allowing for the maintenance of high prey abundance while decreasing predation risk. As a result of the relatively stable prey

population within the designated refuge areas, the dynamics of predator-prey interactions exhibit a reduced cyclic pattern and stabilised at steady state. This phenomenon results in the formation of a sustainable coexistence in which both species can maintain relatively stable population levels over a long period of time. Additionally, the predator population has the ability to regulate its population size in response to the abundance of prey resources present within the refuge, allowing for multiple species coexistence.

However, when the prey refuge is very high (e.g., $m = 0.95$), as shown in Figure 3(c), the prey density reaches its carrying capacity, and the predator population becomes extinct. This indicates that high prey refuge levels, coupled with local dispersal mechanism in both prey and predator populations, hampers the predator's ability to effectively locate and capture prey. As a consequence, the predator population collapses, leading to a situation where the prey population grows to maximum levels. This scenario highlights the importance of striking a balance between the predator dispersal process and prey refuge availability to maintain the biodiversity involving predator-prey populations.

The findings of this study hold significant ecological implications. The observation of oscillatory dynamics occurring at lower prey refuge values suggests that predator-prey interactions have the potential to display cyclic patterns, characterised by periodic fluctuations in population levels. This implies that there may be periodic fluctuations in the population sizes of both predators and prey. The significance of offering appropriate refuge habitats for prey is underscored by the observation of stable coexistence occurring at intermediate prey refuge values. The presence of refuge areas facilitates the persistence of prey populations in the presence of predators, thereby fostering harmonious coexistence and mitigating the potential dominance of either species. The preservation of stable coexistence is imperative in order to uphold the proper functioning of ecosystems. Conversely, the lack of predators in environments with high levels of prey refuge highlights the pivotal function of predators in controlling prey populations. Predatory organisms serve as intrinsic regulatory agents, effectively curbing prey populations from attaining precarious thresholds and thereby upholding equilibrium within the ecological system.

These ecological implications emphasize the need for conservation efforts that consider the availability and quality of refuge habitats for prey species. Protecting and enhancing suitable refuge areas can contribute to the stability and persistence of both predator and prey populations, promoting a healthy and well-functioning ecosystem. Additionally, these findings emphasize the significance of preserving predator populations in bio-control strategies and their important role in maintaining ecological balance.

Next, we conducted numerical bifurcation analysis to examine the relationship between predator dispersal rates and the coexistence region by considering distinct refuge levels. Our analysis specifically focused on the range of m values that fell between m_{2H} and m_{2BP} , as visually represented in Figure 2. The main idea was to gain insights into how changes in predator dispersal rates impacted the extent and ranges of the coexistence region. By systematically adjusting the dispersal rates and observing the resulting changes in the coexistence region, we aimed to unravel the influence of predator mobility on the dynamics of predator-prey interactions.

Table 2 provides insights into the relationship between predator and prey dispersal rates and their impact on the range of refuge levels (m) that supporting species coexistence in this model. In this analysis, we conduct the one-parameter bifurcation analysis for the PDE system (2) using the numerical continuation package, Auto. In all cases, the dispersal rate of prey remains constant at 0.1, while the dispersal rate of predators, D_v , is chosen at random: 0.09, 0.1, 0.4 and 0.95. This value represents the range of predator dispersals, spanning from the lowest to the highest levels of dispersal. Predator dispersal here refers to the mechanism through which predators actively seek out and locate prey within a given habitat. Based on our bifurcation analysis findings, we identify the ranges of prey refuge, which can mediate coexistence of species for distinct predator dispersal scenarios.

Table 2. Numerical simulations of different predator dispersal scenarios as prey dispersal is fixed at $D_U = 0.1$

Predator dispersal (D_V)	Region $m_{2H} < m < m_{2BP}$ (species coexistence range)
$D_V = 0.09$	$0.7917 < m < 0.9307$
$D_V = 0.1$	$0.7908 < m < 0.9307$
$D_V = 0.4$	$0.7879 < m < 0.9307$
$D_V = 0.95$	$0.7822 < m < 0.9307$

When the predator dispersal is slower than the prey, e.g., $D_V = 0.09$, the range of m , which species supports coexistence is relatively narrow ($0.7917 < m < 0.9307$). This implies that when predators have less ability to move around compared to their prey, the productivity of prey to seek refuges decrease. Conversely, in instances where the dispersion pattern of predators aligns with the prey, i.e., symmetrical dispersal levels at $D_V = 0.1$, species coexistence observation remains similar $0.7908 < m < 0.9307$. When the dispersal rate of predators (e.g., $D_V = 0.04$) exceeds the dispersal rate of prey, there is a marginal expansion in the coexistence of supporting species $0.7879 < m < 0.9307$. This finding suggests that when predator dispersal is faster than prey dispersal, a wider range of prey refuge values can support both species coexistence. Furthermore, increasing the predator dispersal levels to $D_V = 0.95$ causes the range values of m supporting coexistence outcomes to increase $0.7822 < m < 0.9307$. The findings suggest that when predator dispersal increases significantly, the range of prey refuge values that can sustain coexistence expands. This raises the prospect of a larger coexistence zone for both species.

In summary, our research reveals that how fast predators and prey move around has a significant effect on the prey survival and also species coexistence mechanisms. When predators disperse at rates that are the same or lower than the rates at which prey disperse, the range in which they can coexist tends to be more restricted. This situation could arise as a result of predators' difficulties in locating and capturing their prey. The study conducted by [32] provides support for the notion that limited rates of predator dispersal can result in localised predator extinctions and perturbations in the predator-prey equilibrium. On the contrary, when predators disperse at a faster rate than the prey, there is a possibility for species coexistence range to expand. This phenomenon occurs due to the enhanced capacity of predators to observe and exploit populations of prey in various locations. According to [33], increased dispersal among predators can lead to the coexistence of diverse species and enhance the stability of predator-prey interactions.

Conclusions

In conclusion, this study contributes significant insights into the dynamics of predator-prey interactions, highlighting the critical role of prey refuge and predator dispersal. Through the investigation of ODE and PDE models, we have obtained a comprehensive understanding of population dynamics over time. Moreover, the integration of PDE models allows us to capture spatial patterns and better comprehend the complexities of ecological systems involving organism movement. By considering individual interactions and system organization, we can develop conservation strategies with broader applicability, encompassing a wide range of ecological processes and spatial scales.

Ensuring suitable habitats for prey to seek refuge and managing the movement of predators and prey between areas have profound ecological implications. These measures play a crucial role in promoting species coexistence and maintaining ecosystem health. The protection of prey habitats is paramount for the long-term survival of prey species. Refuges provide a safe haven for prey to evade predators, increasing their likelihood of survival and successful reproduction. By safeguarding these refuge areas, prey species can thrive, leading to diverse life forms and a balanced environment within the ecosystem. Additionally, maintaining a balanced dispersal rate between predators and prey is essential for fostering stable species coexistence. When predators disperse at a faster rate than prey, it expands the range of refuge values capable of supporting coexistence. This dynamic ensures that predators can access different areas, reducing the risk of decimating prey populations in specific locations. Consequently, it fosters a sustainable relationship between predators and prey, promoting a harmonious ecological balance.

These findings underscore the significance of animals' movement within their respective habitats. The dispersal of species at varying levels can have implications for their inter-species interactions and their ecological distribution. Ultimately, the coexistence of predators and prey in each area can be determined by this. The ability of predators to effectively move around and reach different areas is really important for how they live alongside prey populations. The study also emphasises the necessity of taking into

account additional variables, such as the structure of the habitat and the availability of resources, in future research endeavours in order to gain a more comprehensive understanding of the underlying mechanisms driving these dynamics.

In conclusion, the research enhances our understanding of the dynamics between prey and predator and offers significant implications for maintenance of species biodiversity. The results underscore the significance of preserving habitat connectivity, fostering equitable rates of dispersal, and considering the spatial dynamics of prey-predator systems in the planning of conservation strategies. Subsequent investigations may delve deeper into the complex mechanisms underlying these dynamics and examine the interplay between dispersal rates and other ecological processes, thereby advancing our understanding of prey-predator interactions and how it affects natural ecosystems.

Conflicts of Interest

The author(s) declare(s) that there is no conflict of interest regarding the publication of this paper.

Acknowledgment

The authors acknowledge support from the Fundamental Research Grant Scheme with Project Code: FRGS/1/2022/STG06/USM/02/1 by the Ministry of Higher Education, Malaysia (MOHE).

References

- [1] Kim, K., & Choi, W. (2020). Local dynamics and coexistence of predator–prey model with directional dispersal of predator. *Math. Biosci. Eng.*, 17(6), 6737-6755.
- [2] Kang, Y., Sasmal, S. K., & Messan, K. (2017). A two-patch prey-predator model with predator dispersal driven by the predation strength. *Mathematical Biosciences & Engineering*, 14(4), 843.
- [3] Li, C. (2020). A nonlocal reaction–diffusion prey–predator model with free boundary. *Computers & Mathematics with Applications*, 79(2), 378-390.
- [4] Mohd, M. H., Murray, R., Plank, M. J., & Godsoe, W. (2018). Effects of different dispersal patterns on the presence-absence of multiple species. *Communications in Nonlinear Science and Numerical Simulation*, 56, 115-130.
- [5] Mohd, M. H., Murray, R., Plank, M. J., & Godsoe, W. (2016). Effects of dispersal and stochasticity on the presence–absence of multiple species. *Ecological Modelling*, 342, 49-59.
- [6] Mohd, M. H., & Noorani, M. S. M. (2021). Local dispersal, trophic interactions and handling times mediate contrasting effects in prey-predator dynamics. *Chaos, Solitons & Fractals*, 142, 110497.
- [7] Aliyu, M. B., & Mohd, M. H. (2021). The interplay between mutualism, competition and dispersal promotes species coexistence in a multiple interactions type system. *Ecological Modelling*, 452, 109595.
- [8] Xiao, S., Wang, Y., & Wang, S. (2021). Effects of prey's diffusion on predator–prey systems with two patches. *Bulletin of Mathematical Biology*, 83, 1-21.
- [9] Ghosh, J., Sahoo, B., & Poria, S. (2017). Prey-predator dynamics with prey refuge providing additional food to predator. *Chaos, Solitons & Fractals*, 96, 110-119.
- [10] Ma, Z., Wang, S., Wang, T., & Tang, H. (2017). Stability analysis of prey-predator system with Holling type functional response and prey refuge. *Advances in Difference Equations*, 2017(1), 1-12.
- [11] Zhang, H., Cai, Y., Fu, S., & Wang, W. (2019). Impact of the fear effect in a prey-predator model incorporating a prey refuge. *Applied Mathematics and Computation*, 356, 328-337.
- [12] Das, A., & Samanta, G. P. (2020). A prey–predator model with refuge for prey and additional food for predator in a fluctuating environment. *Physica A: Statistical Mechanics and its Applications*, 538, 122844.
- [13] Manaf, Z. I. A., & Mohd, M. H. (2022). Dynamical system analysis of the prey-predator interactions involving prey refuge and herd behaviors in preys. *Malaysian Journal of Fundamental and Applied Sciences*, 18(1), 105-115.
- [14] Huang, R., Wang, Y., & Wu, H. (2020). Population abundance in predator–prey systems with predator's dispersal between two patches. *Theoretical Population Biology*, 135, 1-8.
- [15] Fang, M., Wang, Y., Chen, M., & DeAngelis, D. L. (2020). Asymptotic population abundance of a two-patch system with asymmetric diffusion. *Discrete and Continuous Dynamical Systems*, 40(6), 3411-3425.
- [16] Arditi, R., Lobry, C., & Sari, T. (2018). Asymmetric dispersal in the multi-patch logistic equation. *Theoretical Population Biology*, 120, 11-15.
- [17] Chakraborty, B., & Bairagi, N. (2019). Complexity in a prey-predator model with prey refuge and diffusion. *Ecological Complexity*, 37, 11-23.
- [18] Xie, Y., Lu, J., & Wang, Z. (2019). Stability analysis of a fractional-order diffused prey–predator model with prey refuges. *Physica A: Statistical Mechanics and its Applications*, 526, 120773.
- [19] Bhattacharyya, J., & Chattopadhyay, J. (2021). Non-smooth dynamics emerging from predator-driven discontinuous prey dispersal. *Nonlinear Dynamics*, 106, 3647-3668.
- [20] Alidousti, J., & Ghahfarokhi, M. M. (2019). Stability and bifurcation for time delay fractional predator prey system by incorporating the dispersal of prey. *Applied Mathematical Modelling*, 72, 385-402.

- [21] Hare, A., & Rebaza, J. (2015). Dynamics of predator-prey models with refuge, harvesting and dispersal. *Quaestiones Mathematicae*, 38(3), 369-383.
- [22] Yang, R., & Wei, J. (2015). Stability and bifurcation analysis of a diffusive prey–predator system in Holling type III with a prey refuge. *Nonlinear Dynamics*, 79(1), 631-646.
- [23] Kar, T. K. (2005). Stability analysis of a prey–predator model incorporating a prey refuge. *Communications in Nonlinear Science and Numerical Simulation*, 10(6), 681-691.
- [24] Holling, C. S. (1959). The components of predation as revealed by a study of small-mammal predation of the European Pine Sawfly1. *The Canadian Entomologist*, 91(5), 293-320.
- [25] Holling, C. S. (1959). Some characteristics of simple types of predation and parasitism1. *The Canadian Entomologist*, 91(7), 385-398.
- [26] Mohd, M. H., Murray, R., Plank, M. J., & Godsoe, W. (2017). Effects of biotic interactions and dispersal on the presence-absence of multiple species. *Chaos, Solitons & Fractals*, 99, 185-194.
- [27] Godsoe, W., Murray, R., & Plank, M. J. (2015). Information on biotic interactions improves transferability of distribution models. *The American Naturalist*, 185(2), 281-290.
- [28] Mohd, M. H. B. (2016). Modelling the presence-absence of multiple species. Thesis PhD. University of Canterbury.
- [29] Mohd, M. H. (2019). Numerical bifurcation and stability analyses of partial differential equations with applications to competitive system in ecology. In *Dynamical Systems, Bifurcation Analysis and Applications: Penang, Malaysia, August 6–13, 2018* (pp. 117-132). Springer Singapore.
- [30] Mohd, M. H. B. (2018, June). Modelling biotic interactions, dispersal effects and the stability of multi-species community compositions. In *AIP Conference Proceedings (Vol. 1974, No. 1, p. 020079)*. AIP Publishing LLC.
- [31] Omaiye, O. J., Mohd, M. H. (2019). Computational Dynamical Systems Using XPPAUT. In: Mohd, M., Abdul Rahman, N., Abd Hamid, N., Mohd Yatim, Y. (eds). *Dynamical Systems, Bifurcation Analysis and Applications. DySBA 2018. Springer Proceedings in Mathematics & Statistics*, vol 295. Springer, Singapore. https://doi.org/10.1007/978-981-32-9832-3_10.
- [32] Amarasekare, P. (2003). Competitive coexistence in spatially structured environments: A synthesis. *Ecology letters*, 6(12), 1109-1122.
- [33] Amarasekare, P., & Nisbet, R. M. (2001). Spatial heterogeneity, source-sink dynamics, and the local coexistence of competing species. *The American Naturalist*, 158(6), 572-584.