Dynamics of Amensalism, Mutualism, and Predation in a Three Species Complex Ecosystem

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ABSTRACT
Understanding the intricate interactions within ecosystems is vital for comprehending the delicate balance that sustains life on our planet. This paper is concerned with modeling an ecosystem characterized by the simultaneous occurrence of amensalism, mutualism, and predation, exploring the interplay between these ecological relationships and their impact on species diversity and community stability. The model formulated is shown to admit only positive solutions that are also bounded. We determine the equilibrium points, conduct a comprehensive analysis of their stability and numerical computations of the proposed model are provided. Further, numerical simulations that demonstrated the existence of a Hopf bifurcation about the interior equilibrium point for several parameter values are also provided.

KEYWORDS
Mutualism; Amensalism; Non-Linear Competition; Holling-Type II Response; Refuge; Hopf Bifurcation

1. Introduction

The natural world is a complex web of interactions between organisms, where the survival and prosperity of one species often depend on its relationship with others. In a dynamic ecosystem, like the one under consideration, the intricate dance of mutualism, amensalism, and predation shapes the delicate balance of life. Mutualism, the symbiotic relationship in which two species benefit from each other's presence, plays a pivotal role in maintaining stability and promoting biodiversity in the ecosystem under scrutiny. In contrast, amensalism, an asymmetrical relationship wherein one species is harmed while the other remains unaffected, introduces a contrasting dynamic. Furthermore, the presence of predation, a fundamental aspect of natural selection, adds a layer of complexity to this ecosystem's interplay. The interaction between predator and prey dictates population dynamics, influencing not only the abundance of species but also regulating trophic cascades and maintaining ecological equilibrium.

Modeling an ecosystem that incorporates mutualism, amensalism, and predation is a multifaceted endeavor, demanding a comprehensive understanding of the intricate relationships and interactions between species. The process involves constructing mathematical equations and simulations to represent the dynamics of these ecological associations. To model mutualism, factors such as resource exchange and fitness benefits must be quantified for the participating species. Incorporating amensalism entails accounting for the interaction effects of competing organisms. Predation modeling necessitates defining predator-prey interactions, predator foraging behavior, and prey population dynamics. By integrating these elements into a cohesive model, we can gain invaluable insights into the stability, resilience, and overall functioning of the ecosystem. Such models are crucial for predicting the consequences of disturbances or perturbations, as well as for formulating effective conservation strategies to safeguard these vital ecological processes.

There have been a plethora of models created to analyze the dynamics of such ecosystems. There are models which considers two species [2–4, 6–8, 13, 14, 17, 18, 28, 32, 34], three species [1, 5, 9–12, 16, 19–27] and four species [15]. Some of these models incorporate a functional response in their model, which include the Beddington–DeAngelis functional response [3], the Crowley–Martin type functional response [20], the Holling-type I functional response [5, 15, 21], the Holling-type II functional response [2, 5, 8, 10–16, 21–23, 26, 27, 34], the Holling-type III functional response [5], the Leslie-Gower functional response [2, 26, 34], the Monod-Haldane type functional response [1], and the Ratio-dependent functional response [3, 19, 28, 32]. Some models consider prey refuge [6–8, 10, 13, 14, 16, 17, 19, 21, 22, 27], harvesting [18, 24, 32], and the Allee effect [28].

In this paper, we will consider a biological system that involves three species with each pairing of species have a unique interaction. In particular, we will study an ecosystem which involves predation, non-linear mutualism, and amensalism. The pairing of species that are in a predation interaction incorporates the Holling type II functional response and refuge into consideration. An example of the ecosystem under consideration is the relationship between the drongo (a bird), the meerkat (a small mongoose) found in southern Africa, and predators (such as jackals). The drongo and the meerkat are mostly in a mutualistic relationship, where the bird helps the mammal by giving a warning cry whenever a predator is near. The meerkat often drops its food when running into its burrow for refuge to avoid the predator and the drongo swoops down to get the food, a win-win for all. In this example, the relationship between the predator and the drongo is amensalism in that the bird is not its source of food. The overpresence of the predator will keep scaring the meerkats into hiding and thus less time for foraging which in turn negatively affects the drongo.

2. Proposed Model

In this section, we will briefly introduce the desired problem to model and make some assumptions. Then we will construct a non-dimensionalized model from the assumptions. Finally, we will show some important properties the model has.

2.1. Problem Statement and Assumptions

Consider an ecosystem which involves three species, $X,\ Y,\ Z$. Species $X,\ Y,\ Z$ grows logistically at their respective intrinsic growth rate $r_x > 0,\ r_y > 0,\ r_z > 0$ with their respective carrying capacity $K_x > 0,\ K_y > 0,\ K_z > 0$ and species Z dies at a rate of e. We will also assume that each pairing of species has a unique interaction with one another. In particular, we will model an ecosystem where mutualism, predation, and amensalism are present.

We will assume that species $X,\ Y$ are in a non-linear mutualism relationship. Members from both species will interact with one another that will help both species in some way. As a result, each species will be affected by one another in some way. To illustrate this, we will let $\alpha_{xy} > 0$ be the interspecies mutualism coefficient where species X is being affected by species Y and $\alpha_{yx} > 0$ be the interspecies mutualism coefficient where species Y is being affected by species X.

We will assume that species Y, Z are in a predation relationship where species Z preys on species Y with the Holling type II response and with an attack rate of $a > 0$. As a result of this, a proportion $0 \leq p \leq 1$ of species Y will take refuge into species Z with a conservation rate of $c > 0$.

We will assume that species X, Z are in an amensalism relationship where species X is the species being negatively affected and species Z will remain unaffected. In this relationship, species X is being negatively affected at a rate of $\delta_{xz} > 0$, which we will call the amensalism coefficient.

2.2. Building the Model of this Ecosystem

With these assumptions, the governing system of equations that accurately describes this type of ecosystem are:

$$\frac{\mathrm{d}X}{\mathrm{d}T} = r_x X\left(1 - \frac{X}{K_x} + \frac{\alpha_{xy}Y^2}{K_x}\right) - \delta_{xz}XZ \tag{2.1a}$$

$$\frac{\mathrm{d}Y}{\mathrm{d}T} = r_y Y\left(1 - \frac{Y}{K_y} + \frac{\alpha_{yx}X^2}{K_y}\right) - \frac{a\,(1-p)\,YZ}{b + (1-p)\,Y} \tag{2.1b}$$

$$\frac{\mathrm{d}Z}{\mathrm{d}T} = r_z Z\left(1 - \frac{Z}{K_z}\right) + Z\left(\frac{ac\,(1-p)\,Y}{b + (1-p)\,Y} - e\right) \tag{2.1c}$$

with the initial conditions $X(0) \geq 0,\ Y(0) \geq 0,\ Z(0) \geq 0$. Then using the following substitutions $X = K_x x,\ Y = K_y y,\ Z = K_z z,\ T = \frac{1}{r_x}t,\ r_{yx} = \frac{r_y}{r_x},\ r_{zx} = \frac{r_z}{r_x},\ \varphi_{xy} = \frac{\alpha_{xy}K_y^2}{K_x},\ \varphi_{yx} = \frac{\alpha_{yx}K_x^2}{K_y},\ \varphi_{xz} = \frac{\delta_{xz}K_z}{r_x},\ u_1 = \frac{aK_z}{r_xK_y},\ u_2 = \frac{b}{K_y},\ u_3 = \frac{ac}{r_x},\ u_4 = \frac{e}{r_x}$, we can simplify and non-dimensionalize Model (2.1). This gives us the following model we will work on throughout this paper:

$$\frac{\mathrm{d}x}{\mathrm{d}t} = x\left(1 - x + \varphi_{xy}y^2\right) - \varphi_{xz}xz \tag{2.2a}$$

$$\frac{\mathrm{d}y}{\mathrm{d}t} = r_{yx}y\left(1 - y + \varphi_{yx}x^2\right) - \frac{u_1\,(1-p)\,yz}{u_2 + (1-p)\,y} \tag{2.2b}$$

$$\frac{\mathrm{d}z}{\mathrm{d}t} = r_{zx}z\,(1 - z) + z\left(\frac{u_3\,(1-p)\,y}{u_2 + (1-p)\,y} - u_4\right) \tag{2.2c}$$

with the initial conditions $x(0) \geq 0,\ y(0) \geq 0,\ z(0) \geq 0$.

2.3. Unique Properties of the Proposed Model

When creating a model that encapsulates an ecosystem, we need to make sure that it makes sense. In biology, a negative population does not make sense. To show that Model (2.2) makes sense, we will need to show that for any non-negative starting populations, Model (2.2) will provide a non-negative solution. This is shown in Theorem (2.1).

Theorem 2.1. *For any set of initial conditions $x(0) = x_0,\ y(0) = y_0,\ z(0) = z_0$ where $x_0 > 0,\ y_0 > 0,\ z_0 > 0$, Model (2.2) only has non-negative solutions.*

Proof. Starting with Equation (2.2a), we can factor out an x:

$$\frac{\mathrm{d}x}{\mathrm{d}t} = x\left(1 - x + \varphi_{xy}y^2 - \varphi_{xz}z\right)$$

From here, we can perform separation of variables:

$$\frac{1}{x}\ \mathrm{d}x = \left(1 - x + \varphi_{xy}y^2 - \varphi_{xz}z\right)\ \mathrm{d}t$$

We can then integrate both sides from $t = 0$ to $t = \tau$ for some time $\tau > 0$:

$$\int_0^\tau \frac{1}{x}\ \mathrm{d}x = \int_0^\tau \left(1 - x + \varphi_{xy}y^2 - \varphi_{xz}z\right)\ \mathrm{d}t$$

The left hand side evaluates to:

$$\ln|x(\tau)| - \ln|x(0)| = \int_0^\tau \left(1 - x + \varphi_{xy}y^2 - \varphi_{xz}z\right)\ \mathrm{d}t$$

Solving for $x(\tau)$ yields:

$$x(\tau) = x(0)\ \exp\left(\int_0^\tau \left(1 - x + \varphi_{xy}y^2 - \varphi_{xz}z\right)\ \mathrm{d}t\right)$$

Note that we have an exponential function on the right hand side. Since $x(0) > 0$, this means that the exponential function will always be positive. Thus, we can conclude that $x(\tau) \geq 0$. We can factor out an y in Equation (2.2b):

$$\frac{\mathrm{d}y}{\mathrm{d}t} = y\left(r_{yx}\left(1 - y + \varphi_{yx}x^2\right) - \frac{u_1\left(1-p\right)z}{u_2 + \left(1-p\right)y}\right)$$

From here, we can perform separation of variables:

$$\frac{1}{y}\ \mathrm{d}y = \left(r_{yx}\left(1 - y + \varphi_{yx}x^2\right) - \frac{u_1\left(1-p\right)z}{u_2 + \left(1-p\right)y}\right)\ \mathrm{d}t$$

We can then integrate both sides from 0 to τ:

$$\int_0^\tau \frac{1}{y}\ \mathrm{d}y = \int_0^\tau \left(r_{yx}\left(1 - y + \varphi_{yx}x^2\right) - \frac{u_1\left(1-p\right)z}{u_2 + \left(1-p\right)y}\right)\ \mathrm{d}t$$

The left hand side evaluates to:

$$\ln|y(\tau)| - \ln|y(0)| = \int_0^\tau \left(r_{yx}\left(1 - y + \varphi_{yx}x^2\right) - \frac{u_1\left(1-p\right)z}{u_2 + \left(1-p\right)y}\right)\ \mathrm{d}t$$

Solving for $x(\tau)$ yields:

$$y(\tau) = y(0)\,\exp\left(\int_0^\tau \left(r_{yx}\left(1-y+\varphi_{yx}x^2\right) - \frac{u_1\,(1-p)\,z}{u_2+(1-p)\,y}\right)\,\mathrm{d}t\right)$$

Note that we have an exponential function on the right hand side. Since $y(0) > 0$, this means that the exponential function will always be positive. Thus, we can conclude that $y(\tau) \geq 0$. We can factor out an z in Equation (2.2c):

$$\frac{\mathrm{d}z}{\mathrm{d}t} = z\left(r_{zx}\,(1-z) + \left(\frac{u_3\,(1-p)\,y}{u_2+(1-p)\,y} - u_4\right)\right)$$

From here, we can perform separation of variables:

$$\frac{1}{z}\,\mathrm{d}z = \left(r_{zx}\,(1-z) + \left(\frac{u_3\,(1-p)\,y}{u_2+(1-p)\,y} - u_4\right)\right)\,\mathrm{d}t$$

We can then integrate both sides from 0 to τ:

$$\int_0^\tau \frac{1}{z}\,\mathrm{d}z = \int_0^\tau \left(r_{zx}\,(1-z) + \left(\frac{u_3\,(1-p)\,y}{u_2+(1-p)\,y} - u_4\right)\right)\,\mathrm{d}t$$

The left hand side evaluates to:

$$\ln|z(\tau)| - \ln|z(0)| = \int_0^\tau \left(r_{zx}\,(1-z) + \left(\frac{u_3\,(1-p)\,y}{u_2+(1-p)\,y} - u_4\right)\right)\,\mathrm{d}t$$

Solving for $x(\tau)$ yields:

$$z(\tau) = z(0)\,\exp\left(\int_0^\tau \left(r_{zx}\,(1-z) + \left(\frac{u_3\,(1-p)\,y}{u_2+(1-p)\,y} - u_4\right)\right)\,\mathrm{d}t\right)$$

Note that we have an exponential function on the right hand side. Since $z(0) > 0$, this means that the exponential function will always be positive. Thus, we can conclude that $z(\tau) \geq 0$. Since we have shown that $x(\tau) \geq 0,\ y(\tau) \geq 0,\ z(\tau) \geq 0$ for some time $\tau > 0$, this implies that Model (2.2) will always have non-negative solutions for non-negative initial conditions. □

Even though we have shown that Model (2.2) will always be non-negative for any set of non-negative initial conditions though Theorem (2.1), that is not enough to show that Model (2.2) makes sense. Populations not only exist, but they also have an upper limit. A population cannot just grow infinitely in size. After some time, a population will stop growing in size. Thus, we will need to show that our model is uniformly bounded. This is shown in Theorem (2.2).

Theorem 2.2. *For any set of initial conditions $x(0) = x_0,\ y(0) = y_0,\ z(0) = z_0$ where $x_0 > 0,\ y_0 > 0,\ z_0 > 0$, Model (2.2) is uniformly bounded above.*

Proof. We will start by placing an upper bound for Equation (2.2c):

$$\frac{\mathrm{d}z}{\mathrm{d}t} \leq r_{zx}z\,(1-z) + z\,(u_3 - u_4)$$

From here, we can perform separation of variables:

$$\frac{1}{z\left(u_3 - u_4 + r_{zx} - r_{zx} z\right)}\,\mathrm{d}z \leq \mathrm{d}t$$

Integrating both sides, we can solve for $z(t)$ to obtain the following inequality:

$$z(t) < \frac{\left(u_3 - u_4 + r_{zx}\right) z_0}{\left(u_3 - u_4 + r_{zx} - r_{zx} z_0\right) e^{-\left(u_3 - u_4 + r_{zx}\right)t} + r_{zx} z_0}$$

from which we can conclude that:

$$\lim_{t\to\infty} \frac{\left(u_3 - u_4 + r_{zx}\right) z_0}{\left(u_3 - u_4 + r_{zx} - r_{zx} z_0\right) e^{-\left(u_3 - u_4 + r_{zx}\right)t} + r_{zx} z_0} = 1 + \frac{u_3 - u_4}{r_{zx}}$$

thus proving that z is bounded above. With this, we can place an upper bound for Equation (2.2b):

$$\begin{aligned}
\frac{\mathrm{d}y}{\mathrm{d}t} &< r_{yx} y \left(1 - y + \varphi_{yx} x^2\right) - \frac{u_1 (1-p)\, y}{u_2 + (1-p)\, y}\left(1 + \frac{u_3 - u_4}{r_{zx}}\right) \\
\frac{\mathrm{d}y}{\mathrm{d}t} &< r_{yx} y \left(1 - y + \varphi_{yx} x^2\right)
\end{aligned}$$

Suppose x is bounded with a maximum value of P. Then we have:

$$\frac{\mathrm{d}y}{\mathrm{d}t} < r_{yx} y \left(1 - y + \varphi_{yx} P^2\right)$$

Solving for $y(t)$ yields:

$$y(t) < \frac{\left(1 + \varphi_{yx} P^2\right)}{1 + \left(\frac{1+\varphi_{yx}P^2}{y_0} - 1\right) \exp\left(-r_{yx}\left(1 + \varphi_{yx} P^2\right) t\right)}$$

from which we can conclude that:

$$\lim_{t\to\infty} \frac{\left(1 + \varphi_{yx} P^2\right)}{1 + \left(\frac{1+\varphi_{yx}P^2}{y_0} - 1\right) \exp\left(-r_{yx}\left(1 + \varphi_{yx} P^2\right) t\right)} = 1 + \varphi_{yx} P^2$$

thus proving that y is bounded above if x is bounded above with a maximum value of P. Suppose y is bounded with a maximum value of Q. Then we can place an upper bound for Equation (2.2a):

$$\frac{\mathrm{d}x}{\mathrm{d}t} < x\left(1 - x + \varphi_{xy} Q^2\right)$$

where the solution to this inequality is:

$$x(t) < \frac{1 + \varphi_{xy} Q^2}{1 + \left(\frac{1+\varphi_{xy}Q^2}{x_0} - 1\right) e^{-\left(1+\varphi_{xy}Q^2\right)t}}$$

from which we can conclude that:

$$\lim_{t\to\infty} \frac{1+\varphi_{xy}Q^2}{1+\left(\frac{1+\varphi_{xy}Q^2}{x_0}-1\right)e^{-(1+\varphi_{xy}Q^2)t}} = 1+\varphi_{xy}Q^2$$

thus proving that x is bounded above if y is bounded above with a maximum value of Q. With this, we have shown that for any set of initial conditions $x(0) = x_0,\ y(0) = y_0,\ z(0) = z_0$ where $x_0 > 0,\ y_0 > 0,\ z_0 > 0$, Model (2.2) is uniformly bounded above. □

3. Equilibria analysis

In Section 2, we have constructed Model (2.2) based on our initial assumptions. In addition, we have proved that Model (2.2) only has non-negative solutions for any set of non-negative initial conditions via Theorem (2.1) and is bounded via Theorem (2.2). In this section, we will identify all the equilibrium points that exists and determine the conditions for stability in Model (2.2).

3.1. Identifying Equilibria

We will start by identifying all the equilibria of Model (2.2), which is done by setting all the equations equal to 0 and solving for each variable [30]. Thus, we have to solve for $x^*,\ y^*,\ z^*$ in the following system of equations:

$$0 = x^*\left(1 - x^* + \varphi_{xy}\left(y^*\right)^2\right) - \varphi_{xz}x^*z^* \tag{3.1a}$$

$$0 = r_{yx}y^*\left(1 - y^* + \varphi_{yx}\left(x^*\right)^2\right) - \frac{u_1\left(1-p\right)y^*z^*}{u_2+\left(1-p\right)y^*} \tag{3.1b}$$

$$0 = r_{zx}z^*\left(1 - z^*\right) + z^*\left(\frac{u_3\left(1-p\right)y^*}{u_2+\left(1-p\right)y^*} - u_4\right) \tag{3.1c}$$

Theorem 3.1. *The trivial equilibrium point* $E_0 = (0,\ 0,\ 0)$ *always exist.*

Proof. The trivial equilibrium point is an equilibrium point $E = (x^*,\ y^*,\ z^*)$ where $x^* = y^* = z^* = 0$. Plugging in $x^* = 0,\ y^* = 0,\ z^* = 0$ into System (3.1), we can see that each equation reduces to $0 = 0$. Thus, we have proved that the trivial equilibrium point $E_0 = (0,\ 0,\ 0)$ always exist. □

Theorem 3.2. *The x-axial equilibrium* $E_x = (1,\ 0,\ 0)$ *always exist.*

Proof. The x-axial equilibrium point is an equilibrium point $E = (x^*,\ y^*,\ z^*)$ where $x^* \neq 0$ and $y^* = z^* = 0$. Since we are dealing with populations, we should not consider values where $x^* < 0$. Thus, a more appropriate constraint is $x^* > 0$. Plugging in $y^* = 0,\ z^* = 0$ into System (3.1), we can see that both Equation (3.1b) and Equation (3.1c) reduces to $0 = 0$ while Equation (3.1a) reduces to $x^*\left(1 - x^*\right) = 0$ which has solutions $x^* = \{0, 1\}$. With the constraint $x^* > 0$, we have proved that the x-axial equilibrium point $E_x = (1,\ 0,\ 0)$ always exist. □

Theorem 3.3. *The y-axial equilibrium* $E_y = (0,\ 1,\ 0)$ *always exist.*

Proof. The y-axial equilibrium point is an equilibrium point $E = (x^*,\ y^*,\ z^*)$ where $y^* > 0$ and $x^* = z^* = 0$. Plugging in $x^* = 0,\ z^* = 0$ into System (3.1), we can see that both Equation (3.1a) and Equation (3.1c) reduces to $0 = 0$ while Equation (3.1b) reduces to $r_{yx}y^*(1 - y^*) = 0$ which has solutions $y^* = \{0, 1\}$. With the constraint $y^* > 0$, we have proved that the y-axial equilibrium point $E_y = (0,\ 1,\ 0)$ always exist. □

Theorem 3.4. *The z-axial equilibrium $E_z = (0,\ 0,\ z^*)$ exist where $z^* = 1 - \frac{u_4}{r_{zx}}$ provided that the condition $r_{zx} > u_4$ is satisfied.*

Proof. The z-axial equilibrium point is an equilibrium point $E = (x^*,\ y^*,\ z^*)$ where $z^* > 0$ and $x^* = y^* = 0$. Plugging in $x^* = 0,\ y^* = 0$ into System (3.1), we can see that both Equation (3.1a) and Equation (3.1b) reduces to $0 = 0$ while Equation (3.1c) reduces to $r_{zx}z^*(1 - z^*) - u_4z^* = 0$ which has solutions $z^* = \left\{0, 1 - \frac{u_4}{r_{zx}}\right\}$. With the constraint $z^* > 0$, we have proved that the z-axial equilibrium point $E_z = (0,\ 0,\ z^*)$ exist where $z^* = 1 - \frac{u_4}{r_{zx}}$ provided that the condition $r_{zx} > u_4$ is satisfied. □

Theorem 3.5. *The xy-boundary equilibrium $E_{xy} = (x^*,\ y^*,\ 0)$ exist where $x^* = 1 + \varphi_{xy}(y^*)^2$ and y^* is a positive solution to $\varphi_{xy}^2\varphi_{yx}(y^*)^4 + 2\varphi_{xy}\varphi_{yx}(y^*)^2 - y^* + \varphi_{yx} + 1 = 0$ which can be achieved under the condition $\varphi_{yx} < \frac{\beta - 1}{(\varphi_{xy}\beta^2 + 1)^2}$ for some $\beta \in (1, \infty)$.*

Proof. The xy-boundary equilibrium point is an equilibrium point $E = (x^*,\ y^*,\ z^*)$ where $x^* > 0,\ y^* > 0$ and $z^* = 0$. Plugging in $z^* = 0$ into System (3.1), we can see that Equation (3.1c) reduces to $0 = 0$ which leaves us with the following system to solve:

$$0 = 1 - x^* + \varphi_{xy}(y^*)^2 \tag{3.2a}$$

$$0 = 1 - y^* + \varphi_{yx}(x^*)^2 \tag{3.2b}$$

Solving for x^* in Equation (3.2a) we obtain $x^* = 1 + \varphi_{xy}(y^*)^2$. We can plug this into Equation (3.2b) to obtain the following equation in terms of y^*:

$$\varphi_{xy}^2\varphi_{yx}(y^*)^4 + 2\varphi_{xy}\varphi_{yx}(y^*)^2 - y^* + \varphi_{yx} + 1 = 0$$

There is no nice, closed-form solution for y^*, but it is sufficient to show that a positive solution $y^* > 0$ exists. First, lets treat the equation above as a function of y^*:

$$f(y^*) = \varphi_{xy}^2\varphi_{yx}(y^*)^4 + 2\varphi_{xy}\varphi_{yx}(y^*)^2 - y^* + \varphi_{yx} + 1$$

Note that $f(y^*)$ is continuous for all $y^* > 0$ and $f(0) = \varphi_{yx} + 1 > 0$. By the Intermediate Value Theorem [29], we can say that there exist a value $\beta \in (0, \infty)$ such that $f(\beta) = 0$. Thus, a solution to $f(y^*) = 0$ exists if for some $\beta \in (0, \infty)$, $f(\beta) < 0$, or:

$$\varphi_{yx} < \frac{\beta - 1}{(\varphi_{xy}\beta^2 + 1)^2} \tag{3.3}$$

Note that if $\beta \in (0, 1]$, then the right hand side of Equation (3.3) will be negative implying that $\varphi_{yx} < 0$. However, since all parameters are positive, we cannot have β fall in this range. Therefore, we know that $\beta \in (1, \infty)$. This concludes the proof. □

Theorem 3.6. *The xz-boundary equilibrium $E_{xz} = (x^*,\ 0,\ z^*)$ exist where*

$$x^* = 1 - \varphi_{xz}\left(1 - \frac{u_4}{r_{zx}}\right), \quad z^* = 1 - \frac{u_4}{r_{zx}}$$

provided that the conditions $\frac{u_4}{r_{zx}} + \frac{1}{\varphi_{xz}} > 1$ and $r_{zx} > u_4$ are satisfied.

Proof. The xz-boundary equilibrium point is an equilibrium point $E = (x^*,\ y^*,\ z^*)$ where $x^* > 0,\ z^* > 0$ and $y^* = 0$. Plugging in $y^* = 0$ into System (3.1), we can see that Equation (3.1b) reduces to $0 = 0$ which leaves us with the following system to solve:

$$0 = 1 - x^* - \varphi_{xz} z^* \tag{3.4a}$$

$$0 = r_{zx}\left(1 - z^*\right) - u_4 \tag{3.4b}$$

Solving for z^* in Equation (3.4b) we obtain $z^* = 1 - \frac{u_4}{r_{zx}}$. Here, we know that $z^* > 0$ so this solution we found implies $r_{zx} > u_4$. We can plug this solution of z^* into Equation (3.4a) and solve for x^*, which yields $x^* = 1 - \varphi_{xz}\left(1 - \frac{u_4}{r_{zx}}\right)$. Since $x^* > 0$, this implies that $\frac{u_4}{r_{zx}} + \frac{1}{\varphi_{xz}} > 1$. This concludes the proof. □

Theorem 3.7. *The yz-boundary equilibrium $E_{yz} = (0,\ y^*,\ z^*)$ exists where*

$$z^* = 1 + \frac{1}{r_{zx}}\left(\frac{u_3\left(1-p\right)y^*}{u_2 + \left(1-p\right)y^*} - u_4\right)$$

and y^* is a positive solution to

$$\frac{Y_3\left(y^*\right)^3 + Y_2\left(y^*\right)^2 + Y_1 y^* + Y_0}{r_{zx}\left(u_2 + \left(1-p\right)y^*\right)^2} = 0 \tag{3.5}$$

where:

$$\begin{aligned}
Y_3 &= -r_{yx} r_{zx}\left(1-p\right)^2 \\
Y_2 &= r_{yx} r_{zx}\left(1-p\right)\left(\left(1-p\right) - 2u_2\right) \\
Y_1 &= u_1\left(u_4 - u_3 - r_{zx}\right)\left(1-p\right)^2 + r_{yx} r_{zx} u_2\left(2\left(1-p\right) - u_2\right) \\
Y_0 &= u_2\left(r_{yx} r_{zx} u_2 + u_1\left(u_4 - r_2\right)\left(1-p\right)\right)
\end{aligned}$$

provided that the following conditions are satisfied:

$$y^* > \frac{u_2\left(u_4 - r_{zx}\right)}{\left(u_3 - u_4 + r_{zx}\right)\left(1-p\right)}, \quad \text{and} \quad 1 > \frac{u_1\left(r_2 - u_4\right)\left(1-p\right)}{r_{yx} r_{zx} u_2}$$

Proof. The yz-boundary equilibrium point is an equilibrium point $E = (x^*,\ y^*,\ z^*)$ where $y^* > 0,\ z^* > 0$ and $x^* = 0$. Plugging in $x^* = 0$ into System (3.1), we can see that Equation (3.1a) reduces to $0 = 0$ which leaves us with the following system to solve:

$$0 = r_{yx}\left(1 - y^*\right) - \frac{u_1\left(1-p\right)z^*}{u_2 + \left(1-p\right)y^*} \tag{3.6a}$$

$$0 = r_{zx}\left(1 - z^*\right) + \frac{u_3\left(1-p\right)y^*}{u_2 + \left(1-p\right)y^*} - u_4 \tag{3.6b}$$

Solving for z^* in Equation (3.6b), we get

$$z^* = 1 + \frac{1}{r_{zx}}\left(\frac{u_3\left(1-p\right)y^*}{u_2 + \left(1-p\right)y^*} - u_4\right).$$

The value of z^* is positive when

$$y^* > \frac{u_2\left(u_4 - r_{zx}\right)}{\left(u_3 - u_4 + r_{zx}\right)\left(1-p\right)}.$$

We can then substitute this value of z^* into Equation (3.6a) to obtain Equation (3.5) in y^*. It will be difficult to find an analytical solution for y^* in terms of the parameters. Instead, we will show that there exist a $y^* > 0$ that satisfies Equation (3.5). Since all the coefficients of Equation (3.5) are non-zero, then we can use Descartes' rule of signs [31]. By Descartes' rule of signs, we can say that Equation (3.5) will have at least one positive solution if $Y_0 > 0$, or $1 > \frac{u_1(r_2-u_4)(1-p)}{r_{yx}r_{zx}u_2}$. Thus, we have proved that the yz-boundary equilibrium point $E_{yz} = (0,\ y^*,\ z^*)$ exists. $\square$

Theorem 3.8. *The interior equilibrium $E_{xyz} = (x^*,\ y^*,\ z^*)$ exists where*

$$x^* = 1 + \varphi_{xy}\left(y^*\right)^2 - \varphi_{xz}z^*, \quad z^* = 1 + \frac{1}{r_{zx}}\left(\frac{u_3\left(1-p\right)y^*}{u_2 + \left(1-p\right)y^*} - u_4\right)$$

and y^* is a positive solution to

$$\frac{Y_6\left(y^*\right)^6 + Y_5\left(y^*\right)^5 + Y_4\left(y^*\right)^4 + Y_3\left(y^*\right)^3 + Y_2\left(y^*\right)^2 + Y_1 y^* + Y_0}{r_{zx}^2\left(u_2 + \left(1-p\right)y^*\right)^3} = 0 \tag{3.7}$$

where:

$$\begin{aligned}
Y_6 &= r_{yx}r_{zx}^2\varphi_{xy}^2\varphi_{yx}\left(1-p\right)^2\\
Y_5 &= 2r_{yx}r_{zx}^2u_2\varphi_{xy}^2\varphi_{yx}\left(1-p\right)\\
Y_4 &= r_{yx}r_{zx}\varphi_{xy}\varphi_{yx}\left(2\left(r_{zx}\left(1-\varphi_{xz}\right) + \varphi_{xz}\left(u_4 - u_3\right)\right)\left(1-p\right)^2 + r_{zx}u_2^2\varphi_{xy}\right)\\
Y_3 &= r_{yx}r_{zx}\left(1-p\right)\left(-r_{zx}\left(1-p\right) + 2u_2\varphi_{xy}\varphi_{yx}\left(2r_{zx}\left(1-\varphi_{xz}\right) + \varphi_{xz}\left(2u_4 - u_3\right)\right)\right)\\
Y_2 &= r_{yx}\left(\left(\left(\varphi_{yx}\left(r_{zx}\left(1-\varphi_{xz}\right) + \varphi_{xz}\left(u_4 - u_3\right)\right)\right)^2 + r_{zx}^2\right)\left(1-p\right)^2 - 2r_{zx}^2u_2\left(1-p\right)\right.\\
&\quad \left. + 2r_{zx}\varphi_{xy}\varphi_{yx}u_2^2\left(r_{zx}\left(1-\varphi_{xz}\right) + u_4\varphi_{xz}\right)\right)\\
Y_1 &= r_{zx}u_1\left(u_4 - u_3 - r_{zx}\right)\left(1-p\right)^2 + 2r_{yx}u_2\left(r_{zx}^2\left(\varphi_{yx}\left(\varphi_{xz} - 1\right)^2 + 1\right)\right.\\
&\quad \left. + \varphi_{xz}\varphi_{yx}\left(-u_4\left(2r_{zx}\left(\varphi_{xz} - 1\right) + \varphi_{xz}u_3\right) + r_{zx}u_3\left(\varphi_{xz} - 1\right) + \varphi_{xz}u_4^2\right)\right)\left(1-p\right)\\
&\quad - r_{yx}r_{zx}^2u_2^2\\
Y_0 &= u_2\left(r_{zx}u_1\left(u_4 - r_{zx}\right)\left(1-p\right) + r_{yx}u_2\left(\varphi_{yx}\left(\varphi_{xz}\left(r_{zx} - u_4\right) - r_{zx}\right)^2 + r_{zx}^2\right)\right)
\end{aligned}$$

provided that the following conditions are satisfied:

$$\frac{1+\varphi_{xy}\left(y^*\right)^2}{\varphi_{xz}} > z^*, \quad y^* > \frac{u_2\left(u_4-r_{zx}\right)}{\left(u_3-\left(u_4-r_{zx}\right)\right)(1-p)}, \quad Y_0 < 0$$

Proof. The interior equilibrium point is an equilibrium point $E=(x^*,\ y^*,\ z^*)$ where $x^*>0,\ y^*>0,\ z^*>0$. Essentially, we are solving Model (2.2) for non-trivial solutions. We can reduce the model to:

$$0 = 1 - x^* + \varphi_{xy}\left(y^*\right)^2 - \varphi_{xz}z^* \tag{3.8a}$$

$$0 = r_{yx}\left(1 - y^* + \varphi_{yx}\left(x^*\right)^2\right) - \frac{u_1\left(1-p\right)z^*}{u_2+\left(1-p\right)y^*} \tag{3.8b}$$

$$0 = r_{zx}\left(1-z^*\right) + \frac{u_3\left(1-p\right)y^*}{u_2+\left(1-p\right)y^*} - u_4 \tag{3.8c}$$

Solving for x^* in Equation (3.8a) yields $x^* = 1+\varphi_{xy}\left(y^*\right)^2 - \varphi_{xz}z^*$ which is positive when $\frac{1+\varphi_{xy}(y^*)^2}{\varphi_{xz}} > z^*$. Next, solving for z^* in Equation (3.8c) yields:

$$z^* = 1+\frac{1}{r_{zx}}\left(\frac{u_3\left(1-p\right)y^*}{u_2+\left(1-p\right)y^*} - u_4\right) \text{ which is positive if } y^* > \frac{u_2\left(u_4-r_{zx}\right)}{\left(u_3-\left(u_4-r_{zx}\right)\right)(1-p)}.$$

We can then plug in our equations for x^* and z^* into Equation (3.8b) to get Equation (3.7) in y^*. It will be difficult to find an analytical solution for y^* in terms of the parameters. Instead, we will show that there exist a $y^*>0$ that satisfies Equation (3.7). Since all the coefficients of Equation (3.7) are non-zero, then we can use Descartes' rule of signs [31]. By Descartes' rule of signs, we can say that Equation (3.7) will have at least one positive solution if $Y_0<0$. Thus, we have proved that the interior equilibrium point $E_{xyz}=(x^*,\ y^*,\ z^*)$ exists. □

3.2. Stability Analysis

In order to compute the stability of these equilibrium points, we will use linear stability analysis [30] and the Routh-Hurwitz stability criterion [33]. Both methods require the Jacobian of Model (2.2), which is:

$$\mathbf{J}\left(E\right) = \begin{bmatrix} j_{11} & j_{12} & j_{13} \\ j_{21} & j_{22} & j_{23} \\ 0 & j_{32} & j_{33} \end{bmatrix} \tag{3.9}$$

where

$$\begin{aligned}
j_{11} &= 1-2x+\varphi_{xy}y^2-\varphi_{xz}z \\
j_{12} &= 2\varphi_{xy}xy \\
j_{13} &= -\varphi_{xz}x \\
j_{21} &= 2r_{yx}\varphi_{yx}xy \\
j_{22} &= r_{yx}\left(1-2y+\varphi_{yx}x^2\right) - \frac{u_1u_2\left(1-p\right)z}{\left(u_2+\left(1-p\right)y\right)^2}
\end{aligned}$$

$$j_{23} = -\frac{u_1 (1-p) y}{u_2 + (1-p) y}$$
$$j_{32} = \frac{u_2 u_3 (1-p) z}{(u_2 + (1-p) y)^2}$$
$$j_{33} = r_{zx} (1-2z) + \frac{u_3 (1-p) y}{u_2 + (1-p) y} - u_4$$

Theorem 3.9. *The trivial equilibrium E_0 is unstable.*

Proof. The jacobian at the trivial equilibrium is:

$$\mathbf{J}(E_0) = \begin{bmatrix} 1 & 0 & 0 \\ 0 & r_{yx} & 0 \\ 0 & 0 & r_{xz} - u_4 \end{bmatrix} \tag{3.10}$$

The eigenvalues of Matrix (3.10) are $\lambda = \{1,\ r_{yx},\ r_{xz} - u_4\}$. Here we can see that the eigenvalue $\lambda_1 = 1$ is positive, thus proving that the trivial equilibrium E_0 is unstable. □

Theorem 3.10. *The x-axial equilibrium E_x is unstable.*

Proof. The jacobian at the x-axial equilibrium is:

$$\mathbf{J}(E_x) = \begin{bmatrix} -1 & 0 & -\varphi_{xz} \\ 0 & r_{yx}(\varphi_{yx}+1) & 0 \\ 0 & 0 & r_{xz} - u_4 \end{bmatrix} \tag{3.11}$$

The eigenvalues of Matrix (3.11) are $\lambda = \{-1,\ r_{yx}(\varphi_{yx}+1),\ r_{xz} - u_4\}$. Here we can see that the eigenvalue $\lambda_2 = r_{yx}(\varphi_{yx}+1)$ is positive, thus proving that the x-axial equilibrium E_x is unstable. □

Theorem 3.11. *The y-axial equilibrium E_y is unstable.*

Proof. The jacobian at the y-axial equilibrium is:

$$\mathbf{J}(E_y) = \begin{bmatrix} 1+\varphi_{xy} & 0 & 0 \\ 0 & -r_{yx} & -\frac{u_1(1-p)}{u_2+(1-p)} \\ 0 & 0 & r_{zx} + \frac{u_3(1-p)}{u_2+(1-p)} - u_4 \end{bmatrix} \tag{3.12}$$

The eigenvalues of Matrix (3.12) are:

$$\lambda = \left\{1+\varphi_{xy},\ -r_{yx},\ r_{zx} + \frac{u_3(1-p)}{u_2+(1-p)} - u_4\right\}$$

Here we can see that the eigenvalue $\lambda_1 = 1 + \varphi_{xy} y^2$ is positive, thus proving that the y-axial equilibrium E_y is unstable. □

Theorem 3.12. *The z-axial equilibrium E_z is locally stable when:*

$$\frac{u_4}{r_{zx}} < 1 - \frac{1}{\varphi_{xz}}, \quad \frac{u_4}{r_{zx}} < 1 - \frac{r_{yx} u_2}{u_1 (1-p)}, \quad \frac{u_4}{r_{zx}} < \frac{1}{2}$$

Proof. The jacobian at the z-axial equilibrium is:

$$\mathbf{J}\left(E_z\right) = \begin{bmatrix} 1-\varphi_{xz}\left(1-\frac{u_4}{r_{zx}}\right) & 0 & 0 \\ 0 & r_{yx}-\frac{u_1(1-p)}{u_2}\left(1-\frac{u_4}{r_{zx}}\right) & 0 \\ 0 & \frac{u_3(1-p)}{u_2}\left(1-\frac{u_4}{r_{zx}}\right) & r_{zx}\left(1-2\left(1-\frac{u_4}{r_{zx}}\right)\right) \end{bmatrix} \tag{3.13}$$

The eigenvalues of Matrix (3.13) are:

$$\lambda = \left\{1-\varphi_{xz}\left(1-\frac{u_4}{r_{zx}}\right),\ r_{yx}-\frac{u_1\left(1-p\right)}{u_2}\left(1-\frac{u_4}{r_{zx}}\right),\ r_{zx}\left(1-2\left(1-\frac{u_4}{r_{zx}}\right)\right)\right\}$$

With these eigenvalues, this means that the z-axial equilibrium E_z is locally stable when:

$$\frac{u_4}{r_{zx}} < 1-\frac{1}{\varphi_{xz}},\quad \frac{u_4}{r_{zx}} < 1-\frac{r_{yx}u_2}{u_1\left(1-p\right)},\quad \frac{u_4}{r_{zx}} < \frac{1}{2}$$

□

Theorem 3.13. *The xy-boundary equilibrium E_{xy} is locally stable when $C_2 > 0,\ C_1 > 0,\ C_0 > 0,\ C_2C_1 > C_0$ where:*

$$\begin{aligned}
C_2 &= -j_{11}-j_{22}-j_{33} \\
C_1 &= j_{11}j_{22}+j_{11}j_{33}+j_{22}j_{33}-j_{12}j_{21} \\
C_0 &= j_{33}\left(j_{12}j_{21}-j_{11}j_{22}\right) \\
j_{11} &= 1-2x+\varphi_{xy}\left(y^*\right)^2 \\
j_{12} &= 2\varphi_{xy}x^*y^* \\
j_{21} &= 2r_{yx}\varphi_{yx}x^*y^* \\
j_{22} &= r_{yx}\left(1-2y^*+\varphi_{yx}\left(x^*\right)^2\right) \\
j_{33} &= r_{zx}+\frac{u_3\left(1-p\right)y^*}{u_2+\left(1-p\right)y^*}-u_4
\end{aligned}$$

Proof. The jacobian at the xy-boundary equilibrium in terms of x^* and y^* is:

$$\mathbf{J}\left(E_{xy}\right) = \begin{bmatrix} j_{11} & j_{12} & 0 \\ j_{21} & j_{22} & j_{23} \\ 0 & 0 & j_{33} \end{bmatrix} \tag{3.14}$$

where the elements of the matrix are as stated in the statement of the theorem. The characteristic equation to Matrix (3.14) is:

$$\lambda^3+C_2\lambda^2+C_1\lambda+C_0=0$$

where the coefficients $C_0,\ C_1$, and C_2 are as listed in the statement of theorem. By the Routh-Hurwitz stability criterion, the xy-boundary equilibrium E_{xy} is locally stable when $C_2 > 0,\ C_1 > 0,\ C_0 > 0,\ C_2C_1 > C_0$. □

Theorem 3.14. *The xz-boundary equilibrium E_{xz} is locally stable when:*

$$\frac{u_4}{r_{zx}} + \frac{1}{\varphi_{xz}} > 1, \quad \frac{u_4}{r_{zx}} + \frac{2}{\varphi_{xz}} + \frac{u_1 (r_{zx} - u_4)(1-p)}{r_{yx}\varphi_{yx}\varphi_{xz}^2 u_2 (r_{zx} - u_4)} - \frac{r_{yx} r_{zx} u_2 (\varphi_{yx} + 1)}{r_{yx}\varphi_{yx}\varphi_{xz}^2 u_2 (r_{zx} - u_4)} > 1$$

Proof. The jacobian at the xz-boundary equilibrium in terms of x^* and z^* is:

$$\mathbf{J}(E_{xz}) = \begin{bmatrix} j_{11} & 0 & j_{13} \\ 0 & j_{22} & 0 \\ 0 & j_{32} & j_{33} \end{bmatrix} \tag{3.15}$$

where

$$\begin{aligned}
j_{11} &= 1 - 2x^* - \varphi_{xz} z^* \\
j_{13} &= -\varphi_{xz} x^* \\
j_{22} &= r_{yx}\left(1 + \varphi_{yx}(x^*)^2\right) - \frac{u_1 (1-p) z^*}{u_2} \\
j_{32} &= \frac{u_3 (1-p) z^*}{u_2} \\
j_{33} &= r_{zx}(1 - 2z^*) - u_4
\end{aligned}$$

The eigenvalues of Matrix (3.15) are$\lambda = \{j_{11},\ j_{22},\ j_{33}\}$. With these eigenvalues, this means that the xz-boundary equilibrium E_{xz} is locally stable when:

$$\frac{u_4}{r_{zx}} + \frac{1}{\varphi_{xz}} > 1, \quad \frac{u_4}{r_{zx}} + \frac{2}{\varphi_{xz}} + \frac{u_1 (r_{zx} - u_4)(1-p)}{r_{yx}\varphi_{yx}\varphi_{xz}^2 u_2 (r_{zx} - u_4)} - \frac{r_{yx} r_{zx} u_2 (\varphi_{yx} + 1)}{r_{yx}\varphi_{yx}\varphi_{xz}^2 u_2 (r_{zx} - u_4)} > 1$$

□

Theorem 3.15. *The yz-boundary equilibrium E_{yz} is locally stable when $C_2 > 0,\ C_1 > 0,\ C_0 > 0,\ C_2 C_1 > C_0$ where:*

$$\begin{aligned}
C_2 &= -j_{11} - j_{22} - j_{33} \\
C_1 &= j_{11} j_{22} + j_{11} j_{33} + j_{22} j_{33} - j_{23} j_{32} \\
C_0 &= j_{11}(j_{23} j_{32} - j_{22} j_{33}) \\
j_{11} &= 1 + \varphi_{xy}(y^*)^2 - \varphi_{xz} z^* \\
j_{22} &= r_{yx}(1 - 2y^*) - \frac{u_1 u_2 (1-p) z^*}{(u_2 + (1-p) y^*)^2} \\
j_{23} &= -\frac{u_1 (1-p) y^*}{u_2 + (1-p) y^*} \\
j_{32} &= \frac{u_2 u_3 (1-p) z^*}{(u_2 + (1-p) y)^2} \\
j_{33} &= r_{zx}(1 - 2z^*) + \frac{u_3 (1-p) y^*}{u_2 + (1-p) y^*} - u_4
\end{aligned}$$

Proof. The jacobian at the yz-boundary equilibrium in terms of y^* and z^* is:

$$\mathbf{J}\left(E_{yz}\right) = \begin{bmatrix} j_{11} & 0 & 0 \\ 0 & j_{22} & j_{23} \\ 0 & j_{32} & j_{33} \end{bmatrix} \tag{3.16}$$

where the elements of the matrix are as given in the statement of the theorem. The characteristic equation to Matrix (3.14) is:

$$\lambda^3 + C_2\lambda^2 + C_1\lambda + C_0 = 0$$

where the coefficients $C_0,\ C_1$, and C_2 are as listed in the statement of theorem. By the Routh-Hurwitz stability criterion, the yz-boundary equilibrium E_{yz} is locally stable when $C_2 > 0,\ C_1 > 0,\ C_0 > 0,\ C_2C_1 > C_0$. □

Theorem 3.16. *The interior equilibrium E_{xyz} is locally stable when $C_2 > 0,\ C_1 > 0,\ C_0 > 0,\ C_2C_1 > C_0$ where:*

$$\begin{aligned}
C_2 &= -j_{11} - j_{22} - j_{33} \\
C_1 &= j_{11}j_{22} + j_{11}j_{33} + j_{22}j_{33} - j_{12}j_{21} - j_{23}j_{32} \\
C_0 &= j_{11}\left(j_{23}j_{32} - j_{22}j_{33}\right) + j_{21}\left(j_{12}j_{33} - j_{13}j_{32}\right) \\
j_{11} &= 1 - 2x^* + \varphi_{xy}\left(y^*\right)^2 - \varphi_{xz}z^* \\
j_{12} &= 2\varphi_{xy}x^*y^* \\
j_{13} &= -\varphi_{xz}x^* \\
j_{21} &= 2r_{yx}\varphi_{yx}x^*y^* \\
j_{22} &= r_{yx}\left(1 - 2y^* + \varphi_{yx}\left(x^*\right)^2\right) - \frac{u_1u_2\left(1-p\right)z^*}{\left(u_2 + \left(1-p\right)y^*\right)^2} \\
j_{23} &= -\frac{u_1\left(1-p\right)y^*}{u_2 + \left(1-p\right)y^*} \\
j_{32} &= \frac{u_2u_3\left(1-p\right)z^*}{\left(u_2 + \left(1-p\right)y^*\right)^2} \\
j_{33} &= r_{zx}\left(1 - 2z^*\right) + \frac{u_3\left(1-p\right)y^*}{u_2 + \left(1-p\right)y^*} - u_4
\end{aligned}$$

Proof. The jacobian at the interior equilibrium is:

$$\mathbf{J}\left(E_{yz}\right) = \begin{bmatrix} j_{11} & j_{12} & j_{13} \\ j_{21} & j_{22} & j_{23} \\ 0 & j_{32} & j_{33} \end{bmatrix} \tag{3.17}$$

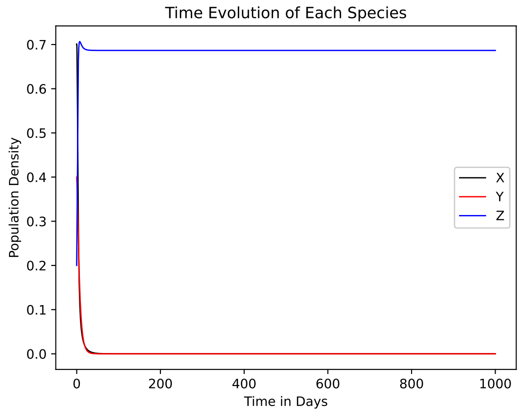
where the elements of the matrix are as given in the statement of the theorem. The characteristic equation to Matrix (3.17) is:

$$\lambda^3 + C_2\lambda^2 + C_1\lambda + C_0 = 0$$

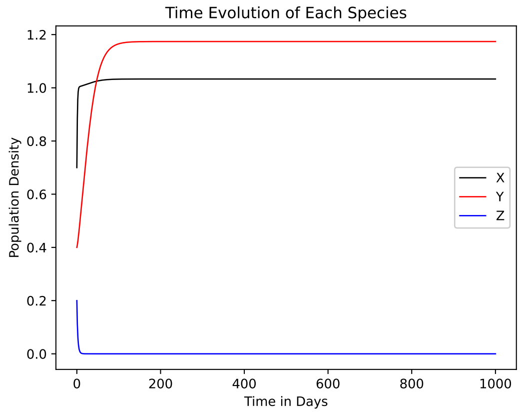
where the coefficients $C_0,\ C_1$, and C_2 are as listed in the statement of theorem. By the Routh-Hurwitz stability criterion, the interior equilibrium E_{xyz} is locally stable when $C_2 > 0,\ C_1 > 0,\ C_0 > 0,\ C_2C_1 > C_0$. □

4. Numerical Simulations

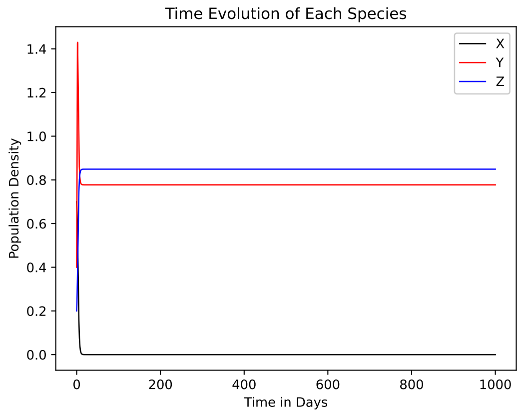
In Section 3, we used mathematical analysis to compute the equilibria that exists in Model (2.2) and determined the conditions for stability of each one. In this section, we will support and verify the stable equilibria determined in Section 3 through numerical simulations. We will also show the existence of a hopf bifurcation for the interior equilibrium through numerical simulations.



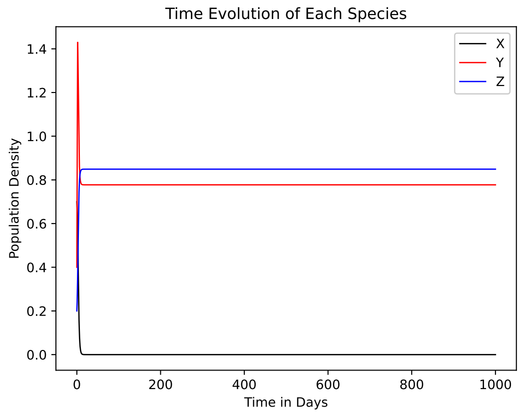
(a) z-axial equilibrium with the set of parameters (4.1)



(b) xy-boundary equilibrium with the set of parameters (4.2)



(c) xz-boundary equilibrium with the set of parameters (4.3)



(d) yz-boundary equilibrium with the set of parameters (4.4)

Figure 1. Showing the stability of non-interior equilibria for different set of parameters.

4.1. The z-axial equilibrium

By Theorem (3.4) and Theorem (3.12), we know that the z-axial equilibrium

$$E_z = \left(0, 0, \frac{r_2 - v_2}{\gamma_{31} r_2}\right)$$

exists if the condition $r_{zx} > u_4$ is satisfied and is stable if the following conditions are satisfied:

$$\frac{u_4}{r_{zx}} < 1 - \frac{1}{\varphi_{xz}}, \quad \frac{u_4}{r_{zx}} < 1 - \frac{r_{yx}u_2}{u_1\,(1-p)}, \quad \frac{u_4}{r_{zx}} < \frac{1}{2}$$

To satisfy the conditions above, lets consider the following set of parameters:

$$\begin{cases} r_{yx} = 0.007 \\ r_{zx} = 1.136 \\ p = 0.874 \end{cases}, \quad \begin{cases} \varphi_{xy} = 0.318 \\ \varphi_{yx} = 0.416 \\ \varphi_{xz} = 1.59 \end{cases}, \quad \begin{cases} u_1 = 1.655 \\ u_2 = 0.791 \\ u_3 = 0.994 \\ u_4 = 0.356 \end{cases} \tag{4.1}$$

Under this set of parameter values, the z-axial equilibrium is $E_z = (0, 0, 0.6866)$. This is further supported by Figure 1a, which is the result of numerically solving Model (2.2).

4.2. The xy-boundary equilibrium

By Theorem (3.5) we know that the xy-boundary equilibrium $E_{xy} = (x^*, y^*, 0)$ exists and Theorem (3.13) guarantees its stability under appropriate conditions. To satisfy the conditions in Theorem (3.5) and Theorem (3.13), we will let $\beta = 11$ and consider the following set of parameters:

$$\begin{cases} r_{yx} = 0.049 \\ r_{zx} = 0.467 \\ p = 0.645 \end{cases}, \quad \begin{cases} \varphi_{xy} = 0.024 \\ \varphi_{yx} = 0.163 \\ \varphi_{xz} = 0.031 \end{cases}, \quad \begin{cases} u_1 = 0.31 \\ u_2 = 0.978 \\ u_3 = 0.9 \\ u_4 = 1.004 \end{cases} \tag{4.2}$$

Under this set of parameter values, the xy-boundary equilibrium is $E_{xy} = (1.0331, 1.174, 0)$. This is further supported by Figure 1b, which is the result of numerically solving Model (2.2).

4.3. The xz-boundary equilibrium

By Theorem (3.6) and Theorem (3.14), we know that the xz-boundary equilibrium $E_{xz} = (x^*,\ 0,\ z^*)$ exist and is locally stable under certain conditions. To satisfy these conditions, lets consider the following set of parameters:

$$\begin{cases} r_{yx} = 0.199 \\ r_{zx} = 1.494 \\ p = 0.482 \end{cases}, \quad \begin{cases} \varphi_{xy} = 0.449 \\ \varphi_{yx} = 0.993 \\ \varphi_{xz} = 1.152 \end{cases}, \quad \begin{cases} u_1 = 1.671 \\ u_2 = 0.663 \\ u_3 = 1.556 \\ u_4 = 1.04 \end{cases} \tag{4.3}$$

Under this set of parameter values, the xz-boundary equilibrium is $E_{xz} = (0.6499, 0, 0.3039)$. This is further supported by Figure 1c, which is the result of numerically solving Model (2.2).

4.4. The yz-boundary equilibrium

We also established through Theorem (3.7) and Theorem (3.15) that the yz-boundary equilibrium $E_{yz} = (0,\ y^*,\ z^*)$ exists and is locally stable respectively, subject to the conditions prescribed in the theorems. To satisfy the conditions in Theorem (3.7) and Theorem (3.15), lets consider the following set of parameters:

$$\begin{cases} r_{yx} = 1.219 \\ r_{zx} = 0.452 \\ p = 0.589 \end{cases}, \quad \begin{cases} \varphi_{xy} = 0.047 \\ \varphi_{yx} = 1.587 \\ \varphi_{xz} = 1.908 \end{cases}, \quad \begin{cases} u_1 = 1.658 \\ u_2 = 1.812 \\ u_3 = 1.473 \\ u_4 = 0.289 \end{cases} \tag{4.4}$$

Under this set of parameter values, the yz-boundary equilibrium is $E_{yz} = (0, 0.7773, 0.8491)$. This is further supported by Figure 1d, which is the result of numerically solving Model (2.2).

4.5. The interior equilibrium

Finally, in Theorem (3.7) and Theorem (3.15), respectively, the existence and stability of the interior equilibrium $E_{xyz} = (x^*,\ y^*,\ z^*)$ were established under various sets of conditions. To ensure that the interior equilibrium exist and is stable, lets consider the following set of parameters:

$$\begin{cases} r_{yx} = 0.5 \\ r_{zx} = 0.5 \\ p = 0.6 \end{cases}, \quad \begin{cases} \varphi_{xy} = 0.6 \\ \varphi_{yx} = 0.15 \\ \varphi_{xz} = 0.4 \end{cases}, \quad \begin{cases} u_1 = 0.6 \\ u_2 = 0.08 \\ u_3 = 0.5 \\ u_4 = 0.5 \end{cases} \tag{4.5}$$

Under this set of parameter values, the interior equilibrium is $E_{xyz} = (0.9099, 0.0599, 0.2305)$. This is further supported by the four figures in Figure A1 where Figure A1a shows the time evolution of each Species, Figure A1b shows the phase portrait, and Figure A1c, Figure A1d, and Figure A1e are phase planes when numerically solving Model (2.2).

For Model (2.2), we can numerically show that a hopf bifurcation exists for each parameter. Starting with r_{zx}, we will plot the time evolution of the ecosystem at $r_{zx} = 0.35$ to show that the ecosystem expresses an oscillatory behavior as shown in Figure A3a. Then, we will generate a bifurcation diagram for Species $X,\ Y,\ Z$ over a set interval of r_{zx}, expressed in Figure A3b, Figure A3c, Figure A3d respectively. For r_{zx}, the interval is $r_{zx} \in (0.133, 0.6155)$. From the bifurcation diagrams, we can see that the ecosystem undergoes 2 changes. Denoting the stable solutions for Species $X,\ Y,\ Z$ in black, red, and blue respectively and denoting the unstable solutions in green, we can see that the ecosystem starts off in a stable state and then becomes unstable when $r_{zx} \approx 0.29$. From here, this behavior is maintained until $r_{zx} \approx 0.47$ where it transitions back to a stable state. Thus, we can say that for the set of parameters (4.5), the ecosystem maintains a stable equilibrium when $r_{zx} \in (0.29, 0.47)$ and displays an oscillatory behavior when $r_{zx} \in (0.133, 0.29)$ and $r_{zx} \in (0.47, 0.6155)$.

We can repeat this process using the same set of parameters to show that a hopf bifurcation exists for p, φ_{yx}, and u_2. For p, the ecosystem undergoes a hopf bifurcation at $p \approx 0.371$, shown in Figure A4. For φ_{yx}, the ecosystem undergoes a hopf bifurcation at $p \approx 0.387$, shown in Figure A6. For u_2, the ecosystem undergoes a hopf bifurcation at $u_2 \approx 0.051$, shown in Figure A9. For the other parameters r_{yx}, φ_{xy}, φ_{xz}, u_1, u_3, u_4, we will consider the set of parameters (4.6). Applying the above procedure to these parameters, we can conclude that the ecosystem undergoes a hopf bifurcation at $r_{yx} \approx 0.66$, $\varphi_{xy} \approx 0.125$, $\varphi_{xz} \approx \{0.402, 1.342\}$, $u_1 \approx 0.728$, $u_3 \approx \{0.511, 2.501\}$, $u_4 \approx \{0.122, 0.314\}$, depicted in Figure A2, Figure A7, Figure A8, Figure A10, Figure A11 respectively.

$$\begin{cases} r_{yx} = 0.5 \\ r_{zx} = 0.5 \\ p = 0.6 \end{cases}, \quad \begin{cases} \varphi_{xy} = 0.6 \\ \varphi_{yx} = 0.15 \\ \varphi_{xz} = 0.4 \end{cases}, \quad \begin{cases} u_1 = 0.6 \\ u_2 = 0.08 \\ u_3 = 0.5 \\ u_4 = 0.5 \end{cases} \tag{4.6}$$

5. Conclusion

In this paper, we have constructed a mathematical model that models a three species ecosystem which involves predation, non-linear mutualism, and amensalism. We have shown that the model is bounded and always yield positive solutions. We have analytically shown that eight, unique equilibrium points exist and determined the conditions of stability for each equilibrium point. To further support these results, we have done some numerical simunlations for each stable equilibrium point. For the interior equilbrium, we have shown the existence of hopf bifurcations for each parameter through numerical simulations.

References

[1] J. Alidousti and E. Ghafari, *Dynamic behavior of a fractional order prey-predator model with group defense*, Chaos, Solitons & Fractals 134 (2020), p. 109688. Available at `https://www.sciencedirect.com/science/article/pii/S0960077920300904`.

[2] M. Aziz-Alaoui and M. Daher Okiye, *Boundedness and global stability for a predator-prey model with modified leslie-gower and holling-type ii schemes*, Applied Mathematics Letters 16 (2003), pp. 1069–1075. Available at `https://www.sciencedirect.com/science/article/pii/S0893965903900966`.

[3] R.S. Cantrell and C. Cosner, *On the dynamics of predator–prey models with the beddington–deangelis functional response*, Journal of Mathematical Analysis and Applications 257 (2001), pp. 206–222. Available at `https://www.sciencedirect.com/science/article/pii/S0022247X00973438`.

[4] J. Chattopadhyay, *Effect of toxic substances on a two-species competitive system*, Ecological Modelling 84 (1996), pp. 287–289. Available at `https://www.sciencedirect.com/science/article/pii/0304380094001340`.

[5] J. Chattopadhyay and R. Sarkar, *Chaos to order: preliminary experiments with a population dynamics models of three trophic levels*, Ecological Modelling 163 (2003), pp. 45–50. Available at `https://www.sciencedirect.com/science/article/pii/S0304380002003812`.

[6] F. Chen, L. Chen, and X. Xie, *On a leslie–gower predator–prey model incorporating a prey refuge*, Nonlinear Analysis: Real World Applications 10 (2009), pp. 2905–2908. Available at `https://www.sciencedirect.com/science/article/pii/S1468121808002010`.

[7] F. Chen, Z. Ma, and H. Zhang, *Global asymptotical stability of the positive equilibrium of the lotka–volterra prey–predator model incorporating a constant number of prey refuges*, Nonlinear Analysis: Real World Applications 13 (2012), pp. 2790–2793. Available at `https://www.sciencedirect.com/science/article/pii/S1468121812000843`.

[8] L. Chen, F. Chen, and L. Chen, *Qualitative analysis of a predator–prey model with holling type ii functional response incorporating a constant prey refuge*, Nonlinear Analysis: Real World Applications 11 (2010), pp. 246–252. Available at `https://www.sciencedirect.com/science/article/pii/S1468121808002678`.

[9] M.B. Dhakne and A.B. Munde, *Stability analysis of mutualistic interactions among three species with limited resources for first species and unlimited resources for second and third species*, Differential Equations and Dynamical Systems 20 (2012), p. 405–414.

[10] S. Gakkhar and K. Gupta, *A three species dynamical system involving prey–predation, competition and commensalism*, Applied Mathematics and Computation 273 (2016), pp. 54–67. Available at `https://www.sciencedirect.com/science/article/pii/S0096300315012722`.

[11] S. Gakkhar and R.K. Naji, *Order and chaos in a food web consisting of a predator and two independent preys*, Communications in Nonlinear Science and Numerical Simulation 10 (2005), pp. 105–120. Available at `https://www.sciencedirect.com/science/article/pii/S1007570403001205`.

[12] S. Gakkhar, B. Singh, and R.K. Naji, *Dynamical behavior of two predators competing over a single prey*, Biosystems 90 (2007), pp. 808–817. Available at `https://www.sciencedirect.com/science/article/pii/S0303264707000755`.

[13] J. Ghosh, B. Sahoo, and S. Poria, *Prey-predator dynamics with prey refuge providing additional food to predator*, Chaos, Solitons & Fractals 96 (2017), pp. 110–119. Available at `https://www.sciencedirect.com/science/article/pii/S0960077917300164`.

[14] Y. Huang, F. Chen, and L. Zhong, *Stability analysis of a prey–predator model with holling type iii response function incorporating a prey refuge*, Applied Mathematics and Computation 182 (2006), pp. 672–683. Available at `https://www.sciencedirect.com/science/article/pii/S0096300306003766`.

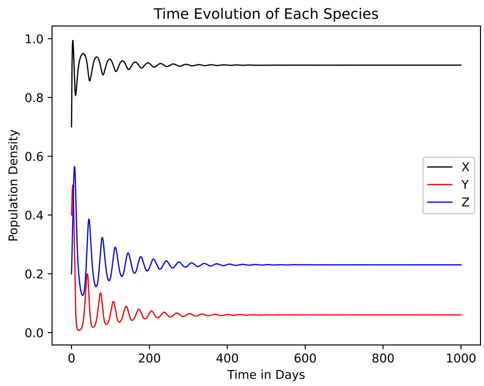
[15] A. Jana and S.K. Roy, *Behavioural analysis of two prey-two predator model*, Ecological Complexity 47 (2021), p. 100942. Available at `https://www.sciencedirect.com/`

science/article/pii/S1476945X21000350.
[16] D. Jana, A. Banerjee, and G. Samanta, *Degree of prey refuges: Control the competition among prey and foraging ability of predator*, Chaos, Solitons & Fractals 104 (2017), pp. 350–362. Available at https://www.sciencedirect.com/science/article/pii/S0960077917303624.
[17] T.K. Kar, *Stability analysis of a prey–predator model incorporating a prey refuge*, Communications in Nonlinear Science and Numerical Simulation 10 (2005), pp. 681–691. Available at https://www.sciencedirect.com/science/article/pii/S1007570404000541.
[18] T. Kar and K. Chaudhuri, *On non-selective harvesting of two competing fish species in the presence of toxicity*, Ecological Modelling 161 (2003), pp. 125–137. Available at https://www.sciencedirect.com/science/article/pii/S030438000200323X.
[19] S. Khajanchi and S. Banerjee, *Role of constant prey refuge on stage structure predator–prey model with ratio dependent functional response*, Applied Mathematics and Computation 314 (2017), pp. 193–198. Available at https://www.sciencedirect.com/science/article/pii/S009630031730468X.
[20] X.Y. Meng, H.F. Huo, H. Xiang, and Q. yu Yin, *Stability in a predator–prey model with crowley–martin function and stage structure for prey*, Applied Mathematics and Computation 232 (2014), pp. 810–819. Available at https://www.sciencedirect.com/science/article/pii/S0096300314001854.
[21] D. Mukherjee, *The effect of prey refuges on a three species food chain model*, Differential Equations and Dynamical Systems 22 (2013), p. 413–426.
[22] P. Panja, S. Gayen, T. Kar, and D.K. Jana, *Complex dynamics of a three species predator–prey model with two nonlinearly competing species*, Results in Control and Optimization 8 (2022), p. 100153. Available at https://www.sciencedirect.com/science/article/pii/S2666720722000327.
[23] P. Panja and S.K. Mondal, *Stability analysis of coexistence of three species prey–predator model*, Nonlinear Dynamics 81 (2015), p. 373–382.
[24] P. Panja, S.K. Mondal, and D.K. Jana, *Effects of toxicants on phytoplankton-zooplankton-fish dynamics and harvesting*, Chaos, Solitons & Fractals 104 (2017), pp. 389–399. Available at https://www.sciencedirect.com/science/article/pii/S0960077917303533.
[25] A.B. Peet, P.A. Deutsch, and E. Peacock-López, *Complex dynamics in a three-level trophic system with intraspecies interaction*, Journal of Theoretical Biology 232 (2005), pp. 491–503. Available at https://www.sciencedirect.com/science/article/pii/S0022519304004163.
[26] A. Priyadarshi and S. Gakkhar, *Dynamics of leslie–gower type generalist predator in a tri-trophic food web system*, Communications in Nonlinear Science and Numerical Simulation 18 (2013), pp. 3202–3218. Available at https://www.sciencedirect.com/science/article/pii/S1007570413001032.
[27] S. Sarwardi, P.K. Mandal, and S. Ray, *Analysis of a competitive prey–predator system with a prey refuge*, Biosystems 110 (2012), pp. 133–148. Available at https://www.sciencedirect.com/science/article/pii/S0303264712001529.
[28] M. Sen, M. Banerjee, and A. Morozov, *Bifurcation analysis of a ratio-dependent prey–predator model with the allee effect*, Ecological Complexity 11 (2012), pp. 12–27. Available at https://www.sciencedirect.com/science/article/pii/S1476945X12000177.
[29] J. Stewart, *Calculus: Early Transcendentals*, 9th ed., Cengage Learning, 2020.
[30] S.H. Strogatz, *Nonlinear Dynamics and Chaos: With Applications to Physics, Biology, Chemistry, and Engineering*, 2nd ed., Westview Press; CRC Press, 2015.
[31] X. Wang, *A simple proof of descartes's rule of signs*, The American Mathematical Monthly 111 (2004), pp. 525–526. Available at http://www.jstor.org/stable/4145072.
[32] D. Xiao, W. Li, and M. Han, *Dynamics in a ratio-dependent predator–prey model with predator harvesting*, Journal of Mathematical Analysis and Applications 324 (2006), pp. 14–29. Available at https://www.sciencedirect.com/science/article/pii/S0022247X05012424.

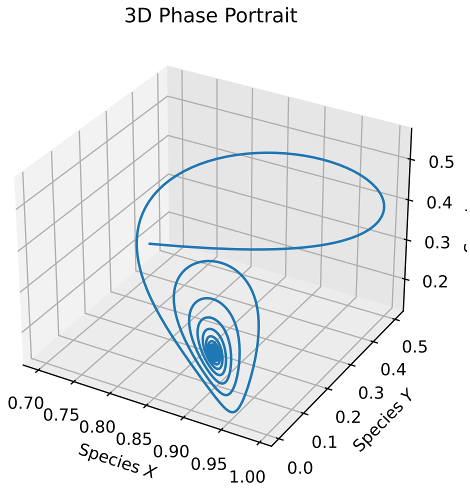
[33] X. Yang, *Generalized form of hurwitz-routh criterion and hopf bifurcation of higher order*, Applied Mathematics Letters 15 (2002), pp. 615–621. Available at https://www.sciencedirect.com/science/article/pii/S0893965902800143.

[34] S. Yu, *Global asymptotic stability of a predator-prey model with modified leslie-gower and holling-type ii schemes*, Discrete Dynamics in Nature and Society 2012 (2012), p. 1–8.

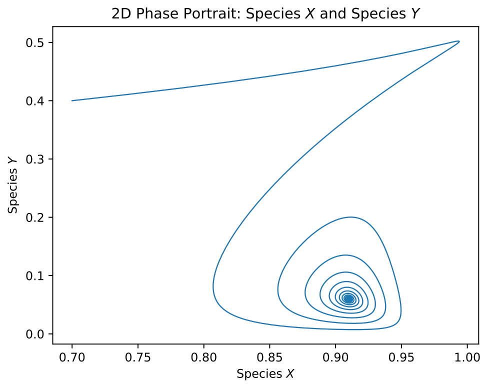
Appendix A. Figures



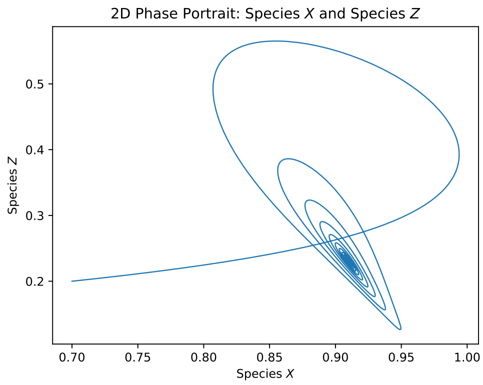
(a) Stability of the interior equilibrium.



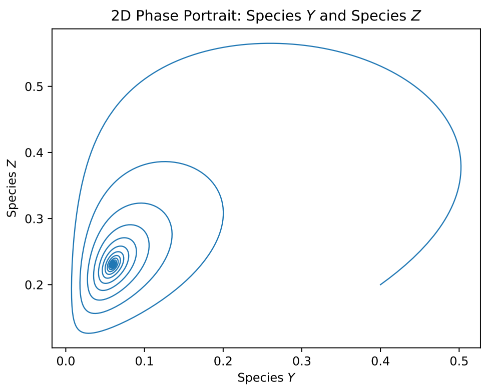
(b) 3D phase portrait.



(c) xy-phase plane.

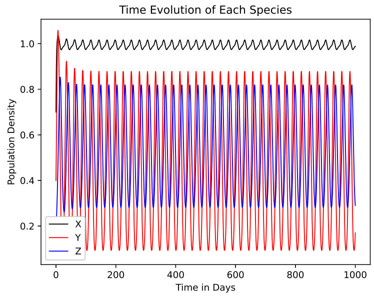


(d) xz-phase plane.

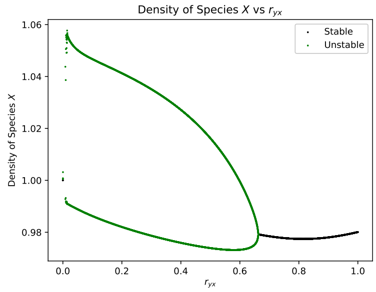


(e) yz-phase plane.

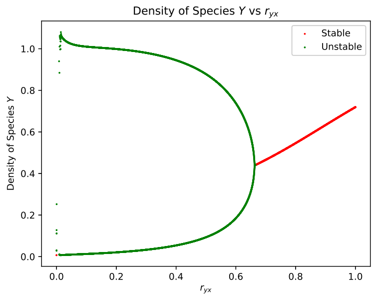
Figure A1. Different types of plots to show the behavior of Model (2.2) under the set of parameters (4.5).



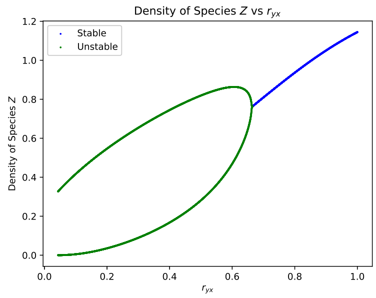
(a) Time Evolution of each species where $r_{yx} = 0.5$



(b) Bifurcation diagram of Species X

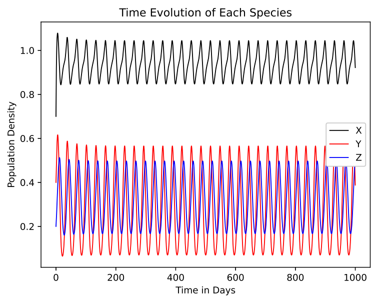


(c) Bifurcation diagram of Species Y

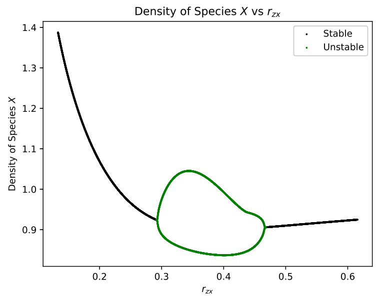


(d) Bifurcation diagram of Species Z

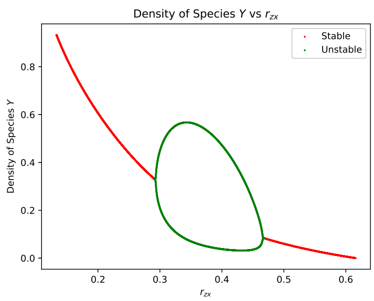
Figure A2. Time evolution of Model (2.2) at a specific value for r_{yx} under the set of parameters (4.6) and bifurcation diagrams of each species with respect to r_{yx}.



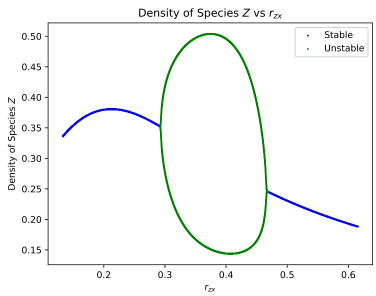
(a) Time Evolution of each species where $r_{zx} = 0.35$



(b) Bifurcation diagram of Species X

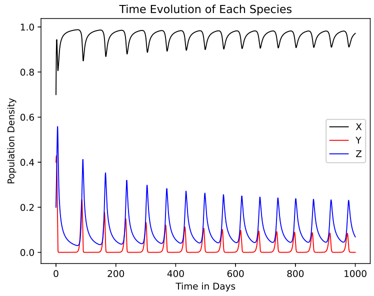


(c) Bifurcation diagram of Species Y

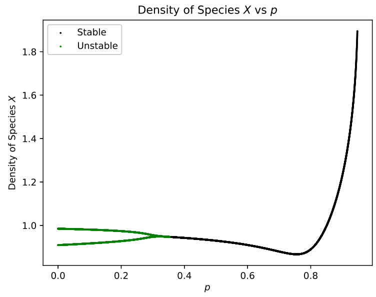


(d) Bifurcation diagram of Species Z

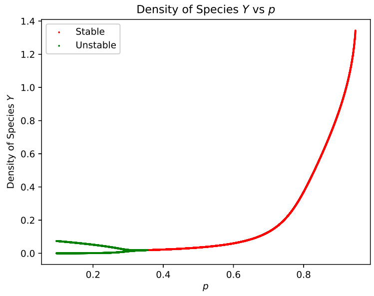
Figure A3. Time evolution of Model (2.2) at a specific value for r_{zx} under the set of parameters (4.5) and bifurcation diagrams of each species with respect to r_{zx}.



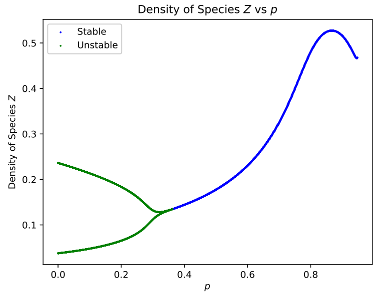
(a) Time Evolution of each species where $p = 0.1$



(b) Bifurcation diagram of Species X

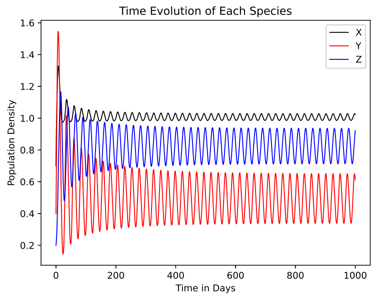


(c) Bifurcation diagram of Species Y

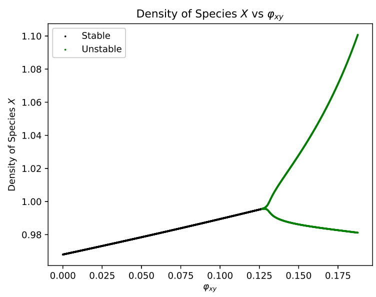


(d) Bifurcation diagram of Species Z

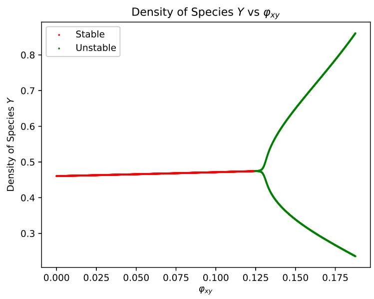
Figure A4. Time evolution of Model (2.2) at a specific value for p under the set of parameters (4.5) and bifurcation diagrams of each species with respect to p.



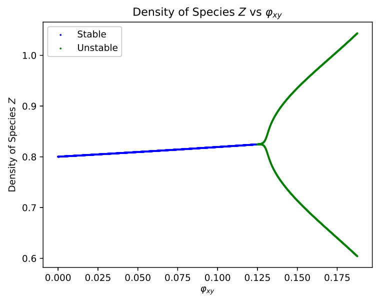
(a) Time Evolution of each species where $\varphi_{xy} = 0.15$



(b) Bifurcation diagram of Species X

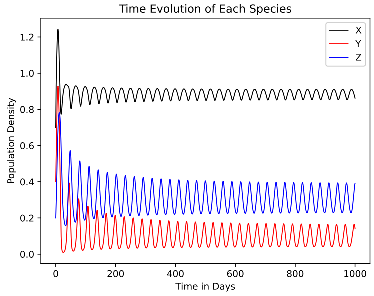


(c) Bifurcation diagram of Species Y

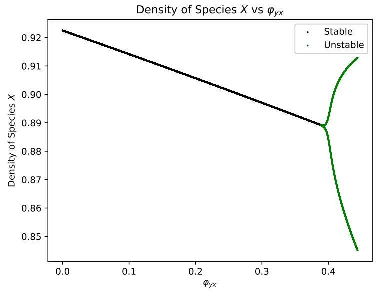


(d) Bifurcation diagram of Species Z

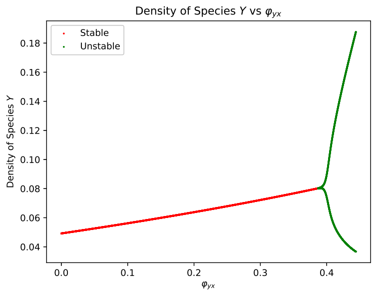
Figure A5. Time evolution of Model (2.2) at a specific value for φ_{xy} under the set of parameters (4.6) and bifurcation diagrams of each species with respect to φ_{xy}.



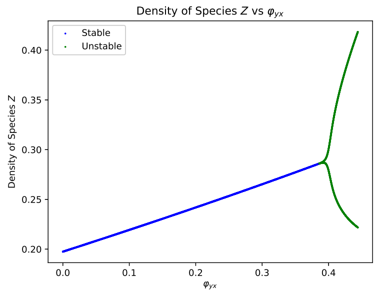
(a) Time Evolution of each species where $\varphi_{yx} = 0.43$



(b) Bifurcation diagram of Species X

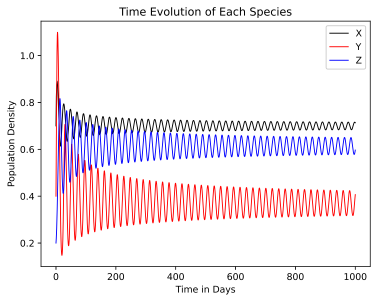


(c) Bifurcation diagram of Species Y

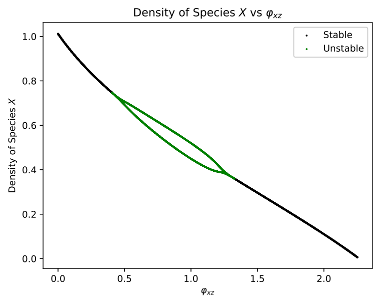


(d) Bifurcation diagram of Species Z

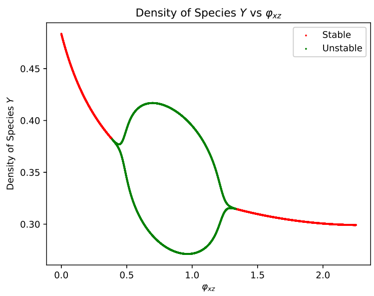
Figure A6. Time evolution of Model (2.2) at a specific value for φ_{yx} under the set of parameters (4.5) and bifurcation diagrams of each species with respect to φ_{yx}.



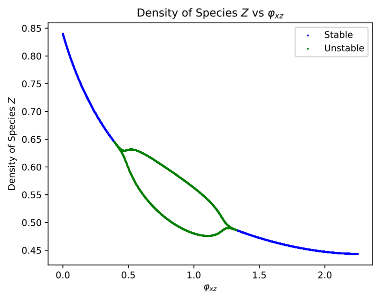
(a) Time Evolution of each species where $\varphi_{xz} = 0.5$



(b) Bifurcation diagram of Species X

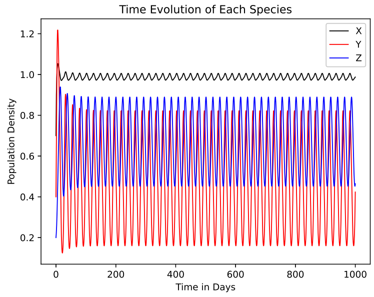


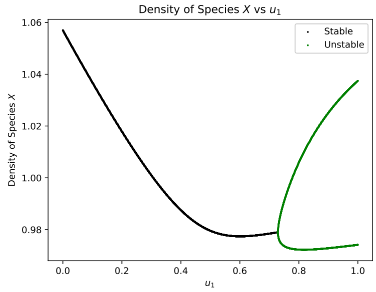
(c) Bifurcation diagram of Species Y



(d) Bifurcation diagram of Species Z

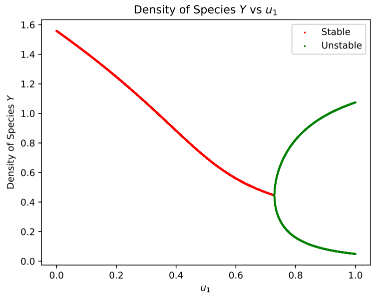
Figure A7. Time evolution of Model (2.2) at a specific value for φ_{xz} under the set of parameters (4.6) and bifurcation diagrams of each species with respect to φ_{xz}.

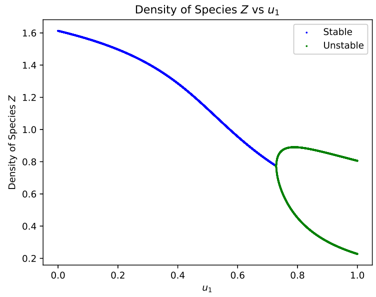




(a) Time Evolution of each species where $u_1 = 0.8$

(b) Bifurcation diagram of Species X

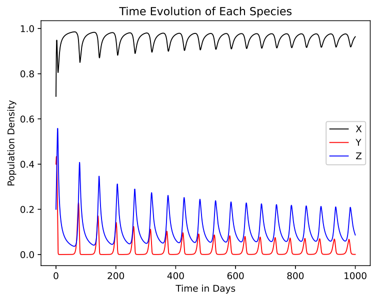


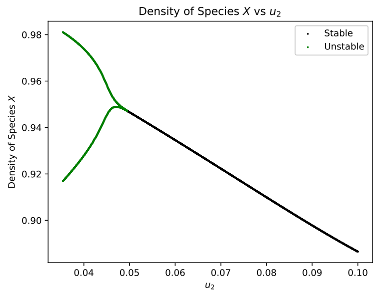


(c) Bifurcation diagram of Species Y

(d) Bifurcation diagram of Species Z

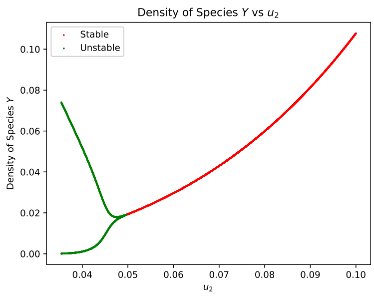
Figure A8. Time evolution of Model (2.2) at a specific value for u_1 under the set of parameters (4.6) and bifurcation diagrams of each species with respect to u_1.

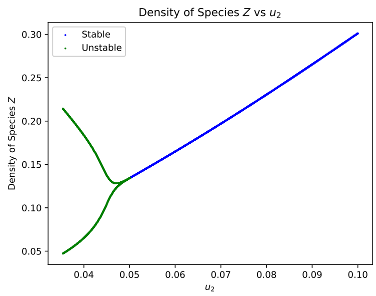




(a) Time Evolution of each species where $u_2 = 0.04$

(b) Bifurcation diagram of Species X

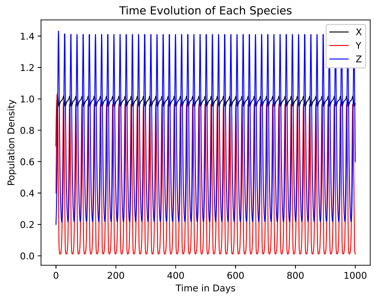


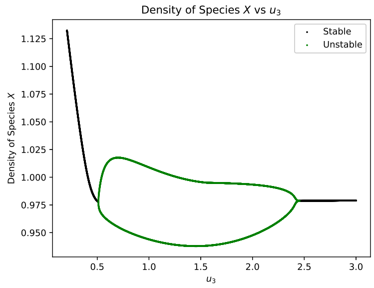


(c) Bifurcation diagram of Species Y

(d) Bifurcation diagram of Species Z

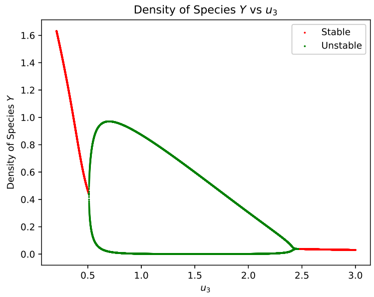
Figure A9. Time evolution of Model (2.2) at a specific value for u_2 under the set of parameters (4.5) and bifurcation diagrams of each species with respect to u_2.

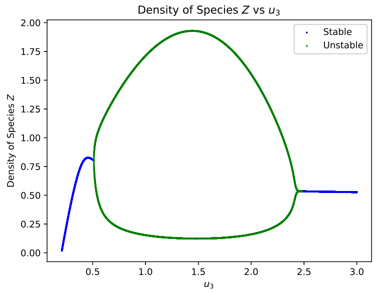




(a) Time Evolution of each species where $u_3 = 0.75$

(b) Bifurcation diagram of Species X

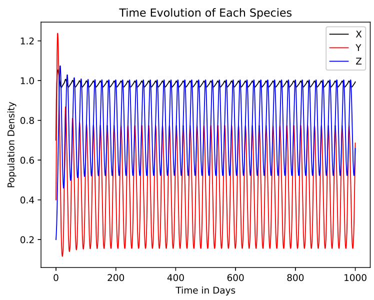


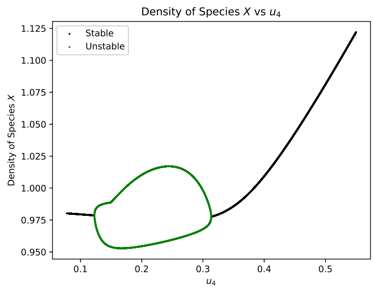


(c) Bifurcation diagram of Species Y

(d) Bifurcation diagram of Species Z

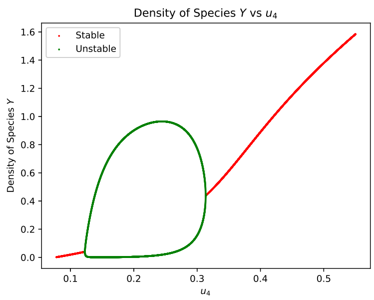
Figure A10. Time evolution of Model (2.2) at a specific value for u_3 under the set of parameters (4.6) and bifurcation diagrams of each species with respect to u_3.

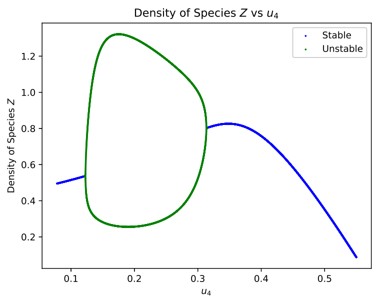




(a) Time Evolution of each species where $u_4 = 0.3$

(b) Bifurcation diagram of Species X





(c) Bifurcation diagram of Species Y

(d) Bifurcation diagram of Species Z

Figure A11. Time evolution of Model (2.2) at a specific value for u_4 under the set of parameters (4.6) and bifurcation diagrams of each species with respect to u_4.