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Complex Dynamics of a Three Species Ecosystem

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Contents

Abstract

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Chapter 1

Introduction

In the vast realm of biological sciences, understanding the complex interplay of various phenomena is a formidable challenge. Nature's intricacies often defy direct observation and experimentation, necessitating the development of powerful tools that can unravel its hidden patterns. Enter mathematical models, a transformative approach that harnesses the language of mathematics to dissect, analyze, and predict the behavior of biological systems. These models serve as indispensable bridges between theoretical abstractions and empirical realities, enabling scientists to gain deeper insights into the fundamental principles that govern living organisms. By quantifying and formalizing biological processes, mathematical models offer a systematic framework to study intricate dynamics, investigate the consequences of different hypotheses, and guide experimental design.

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In this paper, we will consider a biological system that involves three species with each pairing of species have an 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 incorporrates the Holling type II functional response and refuge into consideration.

Chapter 2

Proposed Model

In this chapter, 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:

$$X = K_x x,\ Y = K_y y,\ Z = K_z z,\ T = \frac{1}{r_x}t,\ r_{yx} = \frac{r_y}{r_x},\ r_{zx} = \frac{r_z}{r_x}$$

$$\varphi_{xy} = \frac{\alpha_{xy} K_y^2}{K_x},\ \varphi_{yx} = \frac{\alpha_{yx} K_x^2}{K_y},\ \varphi_{xz} = \frac{\delta_{xz} K_z}{r_x},\ u_1 = \frac{a K_z}{r_x K_y},\ u_2 = \frac{b}{K_y},\ u_3 = \frac{ac}{r_x},\ u_4 = \frac{e}{r_x}$$

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):

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

From here, we can perform separation of variables:

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

We can then integrate both sides from 0 to τ:

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

The left hand side evaluates to:

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

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:

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

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

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

from which we can conclude that:

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

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:

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

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. $\square$

Chapter 3

Equilibria analysis

In Chapter 2, we have modified some of the assumptions the previous authors have made to create Model (2.2). 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). In this chapter, we will identify, classify, and determine the stability of all the equilibria points that exists 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 [2]. 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

$$r_{yx} y^* \left(1 - y^*\right) = 0$$

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 following condition is satisfied:

$$r_{zx} > u_4$$

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

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

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 following condition is satisfied:

$$r_{zx} > u_4$$

□

Theorem 3.5. *The xy-boundary equilibrium $E_{xy} = (x^*,\ y^*,\ 0)$ exist where $x^* = 1 + \varphi_{xy}\left(y^*\right)^2$ and y^* is a positive solution to*

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

which can be achieved under the following condition

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

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:

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

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

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

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 [1], 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 $\beta \in (1, \infty)$. With this, we have proved that the xy-boundary equilibrium point $E_{xy} = (x^*,\ y^*,\ 0)$ 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 following condition

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

for some $\beta \in (1, \infty)$. □

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 have been satisfied.

$$\frac{u_4}{r_{zx}} + \frac{1}{\varphi_{xz}} > 1, \quad r_{zx} > u_4$$

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:

$$0 = 1 - x^* - \varphi_{xz} z^* \tag{3.4a}$$
$$0 = r_{zx}(1 - z^*) - u_4 \tag{3.4b}$$

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

$$\frac{u_4}{r_{zx}} + \frac{1}{\varphi_{xz}} > 1$$

Therefore, we have proved that the xz-boundary equilibrium point $E_{xz} = (x^*,\ 0,\ z^*)$ 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 have been satisfied.

$$\frac{u_4}{r_{zx}} + \frac{1}{\varphi_{xz}} > 1, \quad r_{zx} > u_4$$

□

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

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

and y^* is a positive solution to

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

where:

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

provided that the following conditions are satisfied:

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

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:

$$0 = r_{yx} (1 - y^*) - \frac{u_1 (1-p) z^*}{u_2 + (1-p) y^*} \tag{3.5a}$$

$$0 = r_{zx} (1 - z^*) + \frac{u_3 (1-p) y^*}{u_2 + (1-p) y^*} - u_4 \tag{3.5b}$$

Solving for z^* in Equation (3.5b), we get

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

z^* is positive when

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

We can then substitute this value of z^* into Equation (3.5a) to obtain the following equation in y^*:

$$\frac{Y_3 (y^*)^3 + Y_2 (y^*)^2 + Y_1 y^* + Y_0}{r_{zx} (u_2 + (1-p) y^*)^2} = 0 \tag{3.6}$$

where:

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

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 (3.6). Since all of the coefficients of Equation (3.6) are non-zero, then we can use Descartes' rule of signs [3]. By Descartes' rule of signs, we can say that Equation (3.6) 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 where

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

and y^* is a positive solution to

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

where:

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

provided that the following conditions are satisfied:

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

□

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

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

and y^* is a positive solution to

$$\frac{Y_7\,(y^*)^7 + Y_6\,(y^*)^6 + Y_5\,(y^*)^5 + Y_4\,(y^*)^4 + Y_3\,(y^*)^3 + Y_2\,(y^*)^2 + Y_1 y^* + Y_0}{r_{zx}^2\,(u_2 + (1-p)\,y^*)^3} = 0$$

where:

$$\begin{aligned}
Y_7 &= r_{yx}r_{zx}^2\varphi_{xy}^2\varphi_{yx}\,(1-p)^3 \\
Y_6 &= 3r_{yx}r_{zx}^2\varphi_{xy}^2\varphi_{yx}u_2\,(1-p)^2 \\
Y_5 &= -r_{yx}r_{zx}\varphi_{xy}\varphi_{yx}\left(2\,(\varphi_{xz}\,(r_{zx} + u_3 - u_4) - r_{zx})\,(1-p)^2 - 3r_{zx}u_2^2\varphi_{xy}\right)(1-p) \\
Y_4 &= r_{yx}r_{zx}\left(-r_{zx}\,(1-p)^3 - 2\varphi_{xy}\varphi_{yx}u_2\,(\varphi_{xz}\,(3\,(r_{zx} - u_4) + 2u_3) - 3r_{zx})\,(1-p)^2 + r_{zx}u_2^3\varphi_{xy}^2\varphi_{yx}\right) \\
Y_3 &= r_{yx}\,(1-p)\left(\left(\varphi_{yx}\,(\varphi_{xz}\,(r_{zx} + u_3 - u_4) - r_{zx})^2 + r_{zx}^2\right)(1-p)^2 - 3r_{zx}^2u_2\,(1-p)\right. \\
&\quad \left. -2r_{zx}\varphi_{xy}\varphi_{yx}u_2^2\,(\varphi_{xz}\,(3\,(r_{zx} - u_4) + u_3) - 3r_{zx})\right) \\
Y_2 &= r_{zx}u_1\,(u_4 - r_{zx} - u_3)\,(1-p)^3 + r_{yx}u_2\left(\varphi_{yx}\varphi_{xz}^2\left(3r_{zx}^2 + 2r_{zx}\,(2u_3 - 3u_4) + u_3^2 + 3u_4^2 - 4u_3u_4\right)\right. \\
&\quad \left. -2r_{zx}\varphi_{yx}\varphi_{xz}\,(3\,(r_{zx} - u_4) + 2u_3) + 3r_{zx}^2\,(\varphi_{yx} + 1)\right)(1-p)^2 - 3r_{yx}r_{zx}^2u_2^2\,(1-p) \\
&\quad + 2r_{yx}r_{zx}\varphi_{xy}\varphi_{yx}u_2^3\,(r_{zx} - \varphi_{xz}\,(r_{zx} - u_4)) \\
Y_1 &= -u_2\left(r_{zx}u_1\,(2\,(r_{zx} - u_4) + u_3)\,(1-p)^2 + r_{yx}u_2\left(-3\varphi_{yx}\varphi_{xz}^2u_4^2 - 3r_{zx}^2\left((1-\varphi_{xz})^2\,\varphi_{yx} + 1\right)\right.\right. \\
&\quad \left.\left. +6r_{zx}\varphi_{yx}\varphi_{xz}u_4\,(\varphi_{xz} - 1) + 2\varphi_{xz}\varphi_{yx}u_3\,(\varphi_{xz}\,(u_4 - r_{zx}) + r_{zx})\right)(1-p) + r_{yx}r_{zx}^2u_2^2\right) \\
Y_0 &= u_2^2\left(r_{zx}u_1\,(u_4 - r_{zx})\,(1-p) + r_{yx}u_2\left(\varphi_{yx}\,(\varphi_{xz}\,(r_{zx} - u_4) - r_{zx})^2 + r_{zx}^2\right)\right)
\end{aligned}$$

provided that the following conditions are satisfied:

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

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:

$$0 = 1 - x^* + \varphi_{xy}\left(y^*\right)^2 - \varphi_{xz} z^* \tag{3.7a}$$

$$0 = r_{yx}\left(1 - y^* + \varphi_{yx}\left(x^*\right)^2\right) - \frac{u_1\left(1-p\right)z^*}{u_2 + \left(1-p\right)y^*} \tag{3.7b}$$

$$0 = r_{zx}\left(1 - z^*\right) + \frac{u_3\left(1-p\right)y^*}{u_2 + \left(1-p\right)y^*} - u_4 \tag{3.7c}$$

Solving for x^* in Equation (3.7a) yields:

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

and x^* is positive when:

$$\frac{1 + \varphi_{xy}\left(y^*\right)^2}{\varphi_{xz}} > z^*$$

Solving for z^* in Equation (3.7c) yields:

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

and z^* is positive when

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

We can then plug in our equations for x^* and z^* into Equation (3.7b) to get the following equation in y^*:

$$\frac{Y_7\left(y^*\right)^7 + Y_6\left(y^*\right)^6 + Y_5\left(y^*\right)^5 + Y_4\left(y^*\right)^4 + Y_3\left(y^*\right)^3 + Y_2\left(y^*\right)^2 + Y_1 y^* + Y_0}{r_{zx}^2\left(u_2 + \left(1-p\right)y^*\right)^3} = 0 \tag{3.8}$$

where

$$\begin{aligned}
Y_7 &= r_{yx} r_{zx}^2 \varphi_{xy}^2 \varphi_{yx}\left(1-p\right)^3 \\
Y_6 &= 3 r_{yx} r_{zx}^2 \varphi_{xy}^2 \varphi_{yx} u_2\left(1-p\right)^2 \\
Y_5 &= -r_{yx} r_{zx} \varphi_{xy} \varphi_{yx}\left(2\left(\varphi_{xz}\left(r_{zx} + u_3 - u_4\right) - r_{zx}\right)\left(1-p\right)^2 - 3 r_{zx} u_2^2 \varphi_{xy}\right)\left(1-p\right) \\
Y_4 &= r_{yx} r_{zx}\left(-r_{zx}\left(1-p\right)^3 - 2\varphi_{xy}\varphi_{yx} u_2\left(\varphi_{xz}\left(3\left(r_{zx} - u_4\right) + 2u_3\right) - 3 r_{zx}\right)\left(1-p\right)^2 + r_{zx} u_2^3 \varphi_{xy}^2 \varphi_{yx}\right) \\
Y_3 &= r_{yx}\left(1-p\right)\left(\left(\left(\varphi_{yx}\left(\varphi_{xz}\left(r_{zx} + u_3 - u_4\right) - r_{zx}\right)^2 + r_{zx}^2\right)\left(1-p\right)^2 - 3 r_{zx}^2 u_2\left(1-p\right)\right. \\
&\quad \left. -2 r_{zx} \varphi_{xy} \varphi_{yx} u_2^2\left(\varphi_{xz}\left(3\left(r_{zx} - u_4\right) + u_3\right) - 3 r_{zx}\right)\right) \\
Y_2 &= r_{zx} u_1\left(u_4 - r_{zx} - u_3\right)\left(1-p\right)^3 + r_{yx} u_2\left(\varphi_{yx}\varphi_{xz}^2\left(3 r_{zx}^2 + 2 r_{zx}\left(2u_3 - 3u_4\right) + u_3^2 + 3u_4^2 - 4u_3 u_4\right)\right. \\
&\quad \left. -2 r_{zx}\varphi_{yx}\varphi_{xz}\left(3\left(r_{zx} - u_4\right) + 2u_3\right) + 3 r_{zx}^2\left(\varphi_{yx} + 1\right)\right)\left(1-p\right)^2 - 3 r_{yx} r_{zx}^2 u_2^2\left(1-p\right) \\
&\quad + 2 r_{yx} r_{zx} \varphi_{xy} \varphi_{yx} u_2^3\left(r_{zx} - \varphi_{xz}\left(r_{zx} - u_4\right)\right) \\
Y_1 &= -u_2\left(r_{zx} u_1\left(2\left(r_{zx} - u_4\right) + u_3\right)\left(1-p\right)^2 + r_{yx} u_2\left(-3\varphi_{yx}\varphi_{xz}^2 u_4^2 - 3 r_{zx}^2\left(\left(1 - \varphi_{xz}\right)^2 \varphi_{yx} + 1\right)\right.\right. \\
&\quad \left.\left. +6 r_{zx}\varphi_{yx}\varphi_{xz} u_4\left(\varphi_{xz} - 1\right) + 2\varphi_{xz}\varphi_{yx} u_3\left(\varphi_{xz}\left(u_4 - r_{zx}\right) + r_{zx}\right)\right)\left(1-p\right) + r_{yx} r_{zx}^2 u_2^2\right) \\
Y_0 &= u_2^2\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}$$

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 (3.8). Since all of the coefficients of Equation (3.8) are non-zero, then we can use Descartes' rule of signs [3]. By Descartes' rule of signs, we can say that Equation (3.8) 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 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

$$\frac{Y_7 (y^*)^7 + Y_6 (y^*)^6 + Y_5 (y^*)^5 + Y_4 (y^*)^4 + Y_3 (y^*)^3 + Y_2 (y^*)^2 + Y_1 y^* + Y_0}{r_{zx}^2 (u_2 + (1-p) y^*)^3} = 0$$

where:

$$\begin{aligned}
Y_7 &= r_{yx} r_{zx}^2 \varphi_{xy}^2 \varphi_{yx} (1-p)^3 \\
Y_6 &= 3 r_{yx} r_{zx}^2 \varphi_{xy}^2 \varphi_{yx} u_2 (1-p)^2 \\
Y_5 &= -r_{yx} r_{zx} \varphi_{xy} \varphi_{yx} \left(2 (\varphi_{xz} (r_{zx} + u_3 - u_4) - r_{zx}) (1-p)^2 - 3 r_{zx} u_2^2 \varphi_{xy}\right) (1-p) \\
Y_4 &= r_{yx} r_{zx} \left(-r_{zx} (1-p)^3 - 2 \varphi_{xy} \varphi_{yx} u_2 (\varphi_{xz} (3 (r_{zx} - u_4) + 2u_3) - 3 r_{zx}) (1-p)^2 + r_{zx} u_2^3 \varphi_{xy}^2 \varphi_{yx}\right) \\
Y_3 &= r_{yx} (1-p) \left(\left(\varphi_{yx} (\varphi_{xz} (r_{zx} + u_3 - u_4) - r_{zx})^2 + r_{zx}^2\right) (1-p)^2 - 3 r_{zx}^2 u_2 (1-p)\right. \\
&\quad \left. - 2 r_{zx} \varphi_{xy} \varphi_{yx} u_2^2 (\varphi_{xz} (3 (r_{zx} - u_4) + u_3) - 3 r_{zx})\right) \\
Y_2 &= r_{zx} u_1 (u_4 - r_{zx} - u_3) (1-p)^3 + r_{yx} u_2 \left(\varphi_{yx} \varphi_{xz}^2 \left(3 r_{zx}^2 + 2 r_{zx} (2u_3 - 3u_4) + u_3^2 + 3u_4^2 - 4 u_3 u_4\right)\right. \\
&\quad \left. - 2 r_{zx} \varphi_{yx} \varphi_{xz} (3 (r_{zx} - u_4) + 2u_3) + 3 r_{zx}^2 (\varphi_{yx} + 1)\right) (1-p)^2 - 3 r_{yx} r_{zx}^2 u_2^2 (1-p) \\
&\quad + 2 r_{yx} r_{zx} \varphi_{xy} \varphi_{yx} u_2^3 (r_{zx} - \varphi_{xz} (r_{zx} - u_4)) \\
Y_1 &= -u_2 \left(r_{zx} u_1 (2 (r_{zx} - u_4) + u_3) (1-p)^2 + r_{yx} u_2 \left(-3 \varphi_{yx} \varphi_{xz}^2 u_4^2 - 3 r_{zx}^2 \left((1 - \varphi_{xz})^2 \varphi_{yx} + 1\right)\right.\right. \\
&\quad \left.\left. + 6 r_{zx} \varphi_{yx} \varphi_{xz} u_4 (\varphi_{xz} - 1) + 2 \varphi_{xz} \varphi_{yx} u_3 (\varphi_{xz} (u_4 - r_{zx}) + r_{zx})\right) (1-p) + r_{yx} r_{zx}^2 u_2^2\right) \\
Y_0 &= u_2^2 \left(r_{zx} u_1 (u_4 - r_{zx}) (1-p) + r_{yx} u_2 \left(\varphi_{yx} (\varphi_{xz} (r_{zx} - u_4) - r_{zx})^2 + r_{zx}^2\right)\right)
\end{aligned}$$

provided that the following conditions are satisfied:

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

□

3.2 Stability Analysis

In order to compute the stability of these equilibrium points, we will use linear stability analysis [2] and the Routh-Hurwitz stability criterion [4]. Both methods requires the Jacobian of Model (2.2), which is:

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

where

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

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

Proof. The jacobian at the trivial equilibrium is:

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

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 is unstable. □

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

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

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

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

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

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

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

The eigenvalues of Matrix (3.12) are:

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

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

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

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

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:

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

□

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

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

The characteristic equation to Matrix (3.14) is:

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

where

$$\begin{aligned}
C_2 &= -j_{11} - j_{22} - j_{33} \\
C_1 &= j_{11}j_{22} + j_{11}j_{33} + j_{22}j_{33} - j_{12}j_{21} \\
C_0 &= j_{33}\left(j_{12}j_{21} - j_{11}j_{22}\right)
\end{aligned}$$

By the Routh-Hurwitz stability criterion, the equilibrium will be stable if $C_2 > 0,\ C_1 > 0,\ C_0 > 0,\ C_2C_1 > C_0$. Thus, 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:

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

$$j_{33} = r_{zx} + \frac{u_3 (1-p) y^*}{u_2 + (1-p) y^*} - u_4$$

□

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

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

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 xz-boundary equilibrium in terms of x^* and z^* is:

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

where

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

The characteristic equation to Matrix (3.14) is:

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

where

$$
\begin{aligned}
C_2 &= -j_{11} - j_{22} - j_{33} \\
C_1 &= j_{11}j_{22} + j_{11}j_{33} + j_{22}j_{33} - j_{23}j_{32} \\
C_0 &= j_{11}\left(j_{23}j_{32} - j_{22}j_{33}\right)
\end{aligned}
$$

By the Routh-Hurwitz stability criterion, the equilibrium will be stable if $C_2 > 0,\ C_1 > 0,\ C_0 > 0,\ C_2C_1 > C_0$. Thus, the yz-boundary equilibrium E_{yz} is locally stable when:

$$
\begin{aligned}
0 &< -j_{11} - j_{22} - j_{33} \\
0 &< j_{11}j_{22} + j_{11}j_{33} + j_{22}j_{33} - j_{23}j_{32} \\
0 &< -j_{11}j_{22}j_{33}
\end{aligned}
$$

where

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

□

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:*

$$C_2 < -j_{11} - j_{22} - j_{33}$$

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

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

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

The characteristic equation to Matrix (3.17) is:

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

where

$$
\begin{aligned}
C_2 &= -j_{11} - j_{22} - j_{33} \\
C_1 &= j_{11}j_{22} + j_{11}j_{33} + j_{22}j_{33} - j_{12}j_{21} - j_{23}j_{32} \\
C_0 &= j_{11}\left(j_{23}j_{32} - j_{22}j_{33}\right) + j_{21}\left(j_{12}j_{33} - j_{13}j_{32}\right)
\end{aligned}
$$

By the Routh-Hurwitz stability criterion, the equilibrium will be stable if $C_2 > 0,\ C_1 > 0,\ C_0 > 0,\ C_2C_1 > C_0$. Thus, the interior equilibrium E_{xyz} is locally stable when:

$$
\begin{aligned}
0 &< -j_{11} - j_{22} - j_{33} \\
0 &< j_{11}j_{22} + j_{11}j_{33} + j_{22}j_{33} - j_{12}j_{21} - j_{23}j_{32} \\
0 &< j_{11}\left(j_{23}j_{32} - j_{22}j_{33}\right) + j_{21}\left(j_{12}j_{33} - j_{13}j_{32}\right)
\end{aligned}
$$

where

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

□

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