

Mutualistic Interactions Leading to Coexistence in Competitive Ecological Communities: Mathematical Approach and Simulation Studies

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Abstract: The emerging industrial advancement and unlimited need of humans of our planet have created the problem of the ecological imbalance. The capacity to utilize the resource, which enabled the primitive man to survive, gradually attains multiple dimensions, tends to threaten the life support systems. In this article, we are concerned with the contemporary ecological issue, of coexistence in a competitive ecological community. In addition to usual dynamical behaviors, the simulation studied has also been made to support the mathematical results. A threshold value, depending upon conversion efficiency and the competition intensity of rivals have been calculated to ensure the coexistence of the system.

Key words: Mutualism, Theoretical ecology, Coexistence, permanence, Competition, Predation,

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1. Introduction

The emerging industrial advancement and unlimited need of humans of our planet have created the problem of the ecological imbalance. The analysis and control of this situation require the qualitative as well as quantitative understanding of the subject. The mathematical ecology helps

in getting an insight into the qualitative aspects of these problems, with the help of the mathematical models, using various mathematical techniques and computer simulation. Ecology, the study of organisms in relation to one another and to their surroundings, is the comprehensive study of various ecosystems. These ecosystems are very complicated and their dynamical behavior is not governed by single rule like those in physical or chemical dynamical systems. The prediction of existence, stability, persistence, and validity etc., of these ecosystems and the exploration of ecological information they contain are very difficult. Hence, it is desirable to divide these systems into several subsystems which can be studied comparatively easily. Here, in the present article, we have chosen to consider the ecosystems governed by mutualistic interactions only.

Mathematical models in population dynamics, like those in other branches of science, are extremely useful, as they both answer and raise questions. Historically, research in this area started with the works of Lotka¹ and Volterra², independently to enrich the mathematical ecology up to the conceptual and analytical sophistication level prior to Second World War A. J. Lotka, following a series of notes on the action of human parasites, carried out his mathematical analysis by constructing a system of first order differential equations and displaying the nature of their solutions. The contribution of V. Volterra in mathematical ecology was due to the need of military technology during the first World War, but they mostly deal with the models of negative interactions like predation and competition. Since then there is an unending list of mathematical ecologists including some eminent personalities e.g. Kolmogorov³; Pearl⁴; Smit⁵; Rosenweig⁶; MacArthur⁷; Lawlor⁸; May⁹ etc. The above fact together with the literature available in this field such as Darwin¹⁰ and Gauss¹¹, were enough to dominate the way of thinking of the scientists working in these areas. The result was an emphasis on the struggle for existence. Another side of nature namely mutualistic interactions was ignored¹², where there are a variety of cooperative associations, even between two completely different types of organisms. This pattern continues today, as cooperative associations have historically attracted lesser attention than other interactions such as predation, parasitism and competition¹³.

Sometimes the presence of a third species is required before the mutualism between two species can be apparent. For example, in the aphid-ant system, the association seems to be commensal, but when we consider that predators may prey upon aphids in the absence of ants, the association is clearly mutualistic. Mutualism is further divided into obligate and non-

obligate (facultative). If the interaction is crucial for the survival of one or both of the species, then it is termed as obligate, otherwise non-obligate. We will present here an example of each. A fascinating facultative mutualism involves the Boran people of Africa, and a bird known as the honey guide.

According to rock paintings, humans have been collecting honey in Africa for 20,000 years. Human hunting parties are often joined by the greater honey guide, which leads them to bee colonies. In unfamiliar areas, the average search time is approximately 8.9 hrs., when unguided, but only 3.2 hrs when guided by the bird. Borans use fire and smoke to drive off the bees, break open the nest and remove the honey, but leave larvae and wax behind. The bird gains access to larvae and wax. The use of fire and smoke reduces the bird's risk of being stung, and humans increase accessibility of nests. According to the Borans, the honey guide informs them of direction, from the compass bearing of bird flight; distance, from the duration of the bird's disappearance and height of perch; and arrival, by the "indicator call". Birds and Borans can survive without the other, but each benefit from this facultative mutualism. A mutualism between certain ants and a small tree, the acacia, provides an excellent example of an obligate mutualism. This particular system has been extensively studied in Costa Rica. The acacia provides a number of benefits to the ants, including shelter (hollow thorns), protein (beltian bodies at tip of leaflets) and nectar (secreted near base of leaves). The ant (*Pseudomyrmex*) provides several forms of protection. It attacks and removes herbivorous insects, it also removes vines that might overgrow the acacia, and kills the growing shoots of nearby plants that might become competitors. It clears away leaf litter from near the plant, and since the acacia grows in a seasonally dry environment where it occasionally is threatened by fire, the ant's activities protect the tree from fire damage as well ¹⁴.

During last three decades mutualism has received more attention ¹⁵⁻²³ as an important factor, governing the populations of the interacting species. However the mathematical theory needed to analyze such models is not yet developed. In spite of being most fertile and having a one to one correspondence with real world applications, research in the field of mathematical ecology, was accelerated after publication of a unified book by H.I. Freedman ²⁴, on deterministic mathematical models in ecology. In this book, the author has made an effort, not only to provide basic insight into the subject, but also presented a brief contemporary literature.

Initially, mathematical models, incorporating mutualism as a key factor, were two dimensional²⁵⁻²⁷. Three dimensional mutualistic models, where the

mutualism arises due to presence of a third population, were first analyzed in Rai et. al.,²⁸. Since then, until recently, there has been a fair amount of work, on three dimensional mutualistic models²⁹⁻³². Another aspect of dynamical systems namely time delay in mutualistic interactions was investigated in Rai and Singh³³, and established some useful results for the long and short time delays. In³³ the authors have derived that the introduction of the time delay in the system destabilizes the asymptotic stable equilibria, in general, but not always. In³⁴ a mathematical model, in which the mutualist helps its partner up to a certain level and then it starts harvesting the same has been analyzed. There is a very little work on four dimensional mutualistic models. Freedman and Rais³⁵ analyze four dimensional mutualistic model, throwing some light into the complex mutualistic interactions. In Freedman and Rai,³⁵ a four dimensional mathematical model arising due to interaction of two competitors each with a mutualist has been modeled and it has been shown that, in the absence of one of the mutualists the corresponding three dimensional subspace has no interior equilibrium but if the mutualist is allowed to interact, then interior equilibrium exists, establishing the reversal of outcome. Different types of mutualistic interactions have different stability properties Addicott³⁶.

Therefore, a diverse set of models of mutualism should be retained because conclusions based upon one type of mutualism need not apply to others. Rai and Singh³⁷⁻³⁹ analyzed four dimensional prey mutualistic models, considering different aspects of mutualistic dynamics and established that coexistence could be attained if the death rates of the predators is less than a certain threshold value depending upon conversion efficiency and the competition by the rivals, making mathematical analysis one step close to reality. Compared to previous two and three-species models of mutualism, our model represents a more realistic and reasonable view of the structure of mutualistic systems, the mechanisms by which one species benefits another, and the effect of this beneficial interaction on competitive outcome of the system under consideration. Derivation of the model by basic principles of biology and the results obtained provide an important link between mathematical models and the eventual understanding of the dynamics of the real world systems, moving one step close to the theory of competition for survival of species in nature. In particular, mutualistic interactions are seen as being conceptually different from other type of interactions like predation and competition. In any mutualistic system there may be more species involved in the interaction, because a mutualist could simultaneously benefit its partners in more than one ways. Fritz⁴⁰ observed that ants as mutualist decrease predation on treehoppers.

Apart from symbiotic associations, mutualism may arise indirectly where there is no contact between the species. For example⁴¹, have discussed a four species system in which mutualism may arise indirectly between two of them. Vance⁴², documented mutualistic systems based upon large number of species such as those in mullerian mimicry, convergence of flower types which attract pollinators. Some systems may involve interactions of at least five species in order for there to be mutualism between two of them. For example, consider a plant harboring aphids which attract ants, which in turn deter both the herbivores of the plant and the predators of the aphids. Other types of mutualisms involving beneficial interactions among two-species may still be very complex if there is multiple form of benefit involved in the system. For example, in the acacia system described by Janzen⁴³, at least five benefits are involved in the interaction between ants and acacias, including deterring predation and competition, ameliorating a biotic mortality, providing habitat and food. Among much qualitatively different type of mutualisms, we consider just one case namely mutualism with prey. A mutualist of prey may decrease the predation of its predators, or compete with its predators. A mutualist of a prey may help it to out compete its predators by adding it directly, competing with competitors or predating on its predators. Ecologically, this could involve a variety of different mechanisms, but all would have the effect of decreasing the rate at which prey are captured by the predators. For example mutualist might camouflage the prey making it less apparent to the predators; or the mutualist might make the prey harder to be captured: or it might directly deter the predators from feeding upon the prey.

In the present article, we are concerned with an important concept in theoretical ecology, namely, does the introduction of a mutualist into an existing community of species serve to enhance the long term persistence of the community? Here we address the question for the case in which existing community consists of two competing predators competing for the same prey and the prey is in a beneficial interaction with a mutualist. Often the consideration of a third species changes the commensal association into mutualism between the other two species. For example ants deter herbivore from feeding on plants, and ants deter predators from feeding on aphids. In the absence of herbivores and predators, the association between ants-plants and ants- aphids, respectively is surely commensal⁴⁴.

2. Basic Tools: Mathematics and Computer Simulation

Models in population dynamics often look at how variables such as population size, predation response, conservation efficiency etc change over

time. Mathematically speaking, such models may be termed as dynamical systems. In an ideal situation, one would like to compute the value of each variable at all times. However, this requires obtaining a general solution, which usually is not possible. Nonetheless, a lot can be learned by focusing on the equilibria of the system and their stability. The following summary of stability analysis is considered largely.

2.1 Equilibria and their Stability: Elementary Concepts

- A system at equilibrium does not change over time. In single-variable models, a particular value of the variable is equilibrium value if the variable, when started at this value, does not change. In multi-variables models, the equilibrium is given by a set of values (one for each variable) which, together, causes the system to remain unchanged.
- An equilibrium is locally stable (or locally attracting) if a system near the equilibrium approaches it.
- An equilibrium is globally stable if a system approaches it from all initial conditions.
- An equilibrium is unstable (or repelling) if the system near the equilibrium moves away from it.
- The set of initial conditions leading to a particular equilibrium is called its domain of attraction.

2.2 Techniques to determine local Stability

The techniques reviewed here are concerned with local stability. They are based on the fact that, close to equilibrium, any model can be approximated by a so called linear model, whose behavior can be readily analyzed. In general, performing a local stability analysis involves the following steps:

- Find all equilibria of the system, by noting that non-linear models can have more than one equilibrium.
- Check under what conditions the equilibria are biologically relevant (e.g., population sizes must be non-negative).
- Determine the local stability of each equilibrium. This is done by calculating eigenvalues of the system under consideration. In one-variable models, eigenvalue is simply, the derivative of the update,

rule evaluated at the equilibrium. In multi-variable models, it is calculated from the Jacobian matrix, which collects all possible derivatives of the update rules for each variable.

Case 1: One variable, Continuous time

A continuous -time one variable model is given by a differential equation

$$\frac{dx}{dt} = f(x)$$

Stability analysis requires the following steps:

- Find the equilibria by replacing x with $\hat{x}$ and setting $\frac{dx}{dt} = f(\hat{x}) = 0$ and solving for $\hat{x}$.
- Check whether and when the equilibria are biologically meaningful.
- Differentiate $f(x)$ with respect to x .
- Evaluate the derivative at equilibrium $\hat{x}$, that is, replace x by $\hat{x}$. The resulting value is the "eigenvalue" λ for this equilibrium, i.e.,

$$\lambda = f'(\hat{x}) = \left(\frac{df}{dx} \right)_{x=\hat{x}}$$

- Evaluate the stability of the equilibrium according to the following rules:
 1. $\lambda < 0$, $\hat{x}$ is stable.
 2. $\lambda > 0$, $\hat{x}$ is unstable.
- Repeat the previous two steps for each equilibrium of interest.

Case 2: Multiple variables, Continuous time

A general non-linear, continuous-time model with n dynamic variables $x_1, x_2, \dots, x_n$ is a system of differential equations

$$\frac{dx_1}{dt} = f_1(x_1, x_2, x_3, \dots, x_n),$$

$$\frac{dx_2}{dt} = f_2(x_1, x_2, x_3, \dots, x_n),$$

.....

$$\frac{dx_n}{dt} = f_n(x_1, x_2, x_3, \dots, x_n).$$

Equilibria are obtained by determining the values of the variables that cause all of the variables to remain constant, i.e.

$$\frac{dx_1}{dt} = \frac{dx_2}{dt} = \dots = \frac{dx_n}{dt} = 0.$$

Again, there may be multiple equilibria, and finding them may be difficult. Stability analysis requires the following steps:

- Find all equilibria.
- Determine whether and when they are biologically meaningful.
- Calculate the jacobian matrix.

$$J = \begin{bmatrix} \frac{\partial f_1}{\partial x_1} & \frac{\partial f_1}{\partial x_2} & \dots & \frac{\partial f_1}{\partial x_n} \\ \frac{\partial f_2}{\partial x_1} & \dots & \dots & \frac{\partial f_2}{\partial x_n} \\ \frac{\partial f_n}{\partial x_1} & \frac{\partial f_n}{\partial x_2} & \dots & \frac{\partial f_n}{\partial x_n} \end{bmatrix}$$

where $\frac{\partial f_i(x_1, x_2, \dots, x_n)}{\partial x_j}$ is the partial derivative of $f_i(x_1, x_2, \dots, x_n)$ with respect to x_j , $i, j=1, 2, \dots, n$.

- Evaluate the Jacobian matrix at equilibrium of interest. Let $E(\hat{x}_1, \hat{x}_2, \dots, \hat{x}_n)$ be an equilibrium point, then we replace $x_1, x_2, \dots, x_n$ in jacobian matrix with $\hat{x}_1, \hat{x}_2, \dots, \hat{x}_n$. This yield the local stability matrix $\hat{J} = [J]_{x_1=\hat{x}_1, x_2=\hat{x}_2, \dots, x_n=\hat{x}_n}$
- Calculate the eigenvalues of $\hat{J}$, which are the roots of the characteristic equation $\det(\hat{J} - \lambda I) = 0$, usually one has to use Mathematica (a computer software to execute tedious calculations).
- The equilibrium is locally stable if the real parts of all eigenvalues are negative. Equivalently, the real part of the leading eigenvalue (i.e. the eigenvalue with the largest real part) must be negative. If the real part of the leading eigenvalue is exactly zero, the analysis is inconclusive.
- If the eigenvalues are complex, the system will spiral around the equilibrium along some axes.

- Repeate the steps for all the equilibria of interest.

2.2.1 Routh-Hurwitz Criterion. (Coppel⁴⁵)

We will use this criterion to obtain conditions for the asymptotic stability of the equilibrium states. Consider the n^{th} order polynomial equation. Then a formal general condition can now be written, in terms of the coefficients $a_1, a_2, \dots, a_n$, which are necessary and sufficient to ensure that all the roots of the equation (2.3) have negative real parts.

In our case $n \leq 4$, so that we mention the explicit Routh-Hurwitz Criterion for $n = 2, 3, 4$

$n = 2$;

The characteristic equation takes the form $\lambda^2 + a_1\lambda + a_2 = 0$ and the condition is given by $a_1 > 0, a_2 > 0$.

$n = 3$;

The characteristic equation takes the form $\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0$ and the condition is given by $a_1 > 0, a_3 > 0, a_1a_1 - a_3 > 0$.

$n = 4$;

The characteristic equation takes the form $\lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4 = 0$ and the condition is given by 1. $a_4 > 0, a_1 > 0, a_2 > 0$, 2. $a_3[a_1a_2 - a_3] > a_1^2a_4$.

2.3 Techniques to determine Global Stability

2.3.1 Global Existence and Uniqueness. (Perko⁴⁶)

Let,

$$\dot{X} = f(X); X(t_0) = X_0,$$

and

$$f: \mathbb{R}^n \rightarrow \mathbb{R}^n \quad f: \mathbb{R}^n \rightarrow \mathbb{R}^n$$

be a given system, where $f \in C^1(\mathbb{R}^n)$. The following result gives the criterion for global existence and uniqueness of its solutions:

Theorem 2.3.1: Suppose $f \in C^1(\mathbb{R}^n)$ and $f(X)$ satisfies the global Lipschitz condition,

$$\|f(X) - f(Y)\| \leq M \|X - Y\|, \quad M > 0, \text{ for all } X, Y \in \mathbb{R}^n.$$

Then for $X_0 \in \mathbb{R}^n$, initial value problem has unique solution defined for all $t_0 \in \mathbb{R}$.

2.3.2 LaSalle's Invariance principle (Hale⁴⁷)

Consider the system of differential equations

$$\frac{dX}{dt} = f(X)$$

where $f: \Omega (\subseteq \mathbb{R}^n) \rightarrow \mathbb{R}^n$ is continuous. We call V a Liapunov function on $G \subseteq \Omega$ for the above system if $V: G \rightarrow \mathbb{R}_+$ and

1. V is continuous on G .
2. If V is not continuous at $\bar{x} \in \bar{G}$ (the closure of G) then $V(X) \rightarrow +\infty$ as $x \rightarrow \bar{x}$ for all $x \in G$, and
3. $\dot{V} = \text{grad} V \cdot f \leq 0$ on G .

Theorem 2.3.2 Assume that V is a Liapunov function for the system (2.6) on G . Define

$$S = \{x \in \bar{G} \cap \Omega : V(X) = 0\}$$

and let M be the largest invariant set in S . Then every bounded trajectory of the above system that remains in G approaches the set M eventually.

Now we mention the following results, which have been used frequently, in analyzing the models.

2. 3.4. Liapunov Function and Stability Theorem.

Consider the function $V(x_1, x_2, \dots, x_n)$ defined in the phase space of variables, $x_1, x_2, \dots, x_n$ and denote $X = (x_1, x_2, \dots, x_n)$, then $V(X)$ is positive definite in the neighborhood U of origin if $V(X) > 0$, for all $X (\neq 0) \in U$ and $V(0) = 0$.

If $V(X)$ is positive definite and has continuous partial derivatives, then for a small enough positive constant c , the following property holds.

$V(X) < c$ defines an open, bounded, connected region ϕ_c which contains the origin and has $V(X) = c$ as its boundary; the diameter of ϕ_c tends to zero as c tends to zero; and when $c_1 < c_2$ the boundary of ϕ_{c_1} is contained in that of ϕ_{c_2} .

2.3.5 Domain of Asymptotic Stability

The region $R \subseteq U$ is defined to be the domain of asymptotic stability if the Liapunov function $V(X)$, where $V'(X)$ is the derivative of $V(X)$ along the solutions of the system, $\dot{X} = AX$ have the same property as mentioned in above section .

2.4 Average Liapunov Function.

A nonnegative real valued C^1 function $\rho(X)$ defined on $\mathbb{R}^n$, is called an average Liapunov function if it satisfies the following two properties:

1. $\rho(X) > 0$ for all $X \in \mathbb{R}_+^n$ and $\rho(X) = 0$ for $X \in \partial\mathbb{R}_+^n$,
2. If we define $\psi(X) = \frac{\dot{\rho}(X)}{\rho(X)} = \frac{1}{\rho(X)} \sum_{i=1}^n \frac{\partial \rho}{\partial x_i} [X_i f_i(X)]$, then $\psi(X)$ has a continuous extension to the closure of $\mathbb{R}_+^n$, and $\psi(X) > 0$, $X \in \Omega(\partial\mathbb{R}_+^n)$.

The next result provides a sophisticated tool for proving uniform persistence of the ecological systems.

Theorem 2.4.1 *If the system*

$$\frac{dx_i}{dt} = x_i f_i(X), i = 1, 2, \dots, n,$$

with $x_i(0) > 0$, is dissipative, and if a persistence function (also called average Liapunov function) $\rho(X)$ exists then the above system is uniformly persistent, and hence permanent.

4. Illustrative Example (Complete Analysis of a Model)

In this section we propose and analyze a mathematical model based on the techniques discussed in previous section.

3.1 Mathematical Model

Under the assumptions of continuous birth and death, we have modelled an ecological situation arising due to interaction of four species; two competing predators y and z , one prey x and a mutualist u to the prey species, living in the same environment, with the restriction that the mutualist deters both the predators in its interactions for the benefit of prey. Mathematically, this model can be described by the following system of autonomous differential equations:

$$\left. \begin{aligned} \dot{u} &= uh(u, x), \\ \dot{x} &= \alpha xg(x) - yp_1(u, x) - zp_2(u, x), \\ \dot{y} &= y[-s_1(y) - q_1(z) + c_1p_1(u, x)], \\ \dot{z} &= z[-s_2(z) - q_2(y) + c_2p_2(u, x)], \\ x(0) &> 0, y(0) > 0, z(0) > 0. \end{aligned} \right\}$$

Here

$$\dot{} \equiv \frac{d}{dt} \text{ and } t \text{ represents time, and}$$

$u(t)$ = population of mutualist at any time t ,

$x(t)$ = population of prey at any time t ,

$y(t)$ = population of the first predator at any time t ,

$z(t)$ = population of the second predator at any time t ; and α ,

c_1, c_2 are parameters assumed always to be positive.

Functions $h, g, q_i, p_i, s_i, ,$ for $i=1,2$; are continuous and sufficiently smooth to ensure the existence and uniqueness of solutions of initial value problem (1) with initial conditions in $\mathbb{R}_+^4$ and to allow the stability analysis of any solutions of the system (see theorem 2.3.1). We also require the solutions to be defined on some interval $[0, T)$ where $0 \leq T < \infty$. We further frame the following assumptions on the functions occurring in the model.

H1: The function $h: \mathbb{R}_+ \times \mathbb{R}_+ \rightarrow \mathbb{R}$ represents the specific growth rate of mutualist and satisfies the following assumptions:

$$(a) \quad h(0, x) > 0,$$

$$(b) \exists L: \mathbb{R}_+ \rightarrow \mathbb{R}_+ \text{ st } h(L(x), x) = 0, \text{ and } \frac{dL}{dx} \geq 0$$

$$(c) \quad \frac{\partial h(u, x)}{\partial u} < 0,$$

$$(d) \quad \frac{\partial h(u, x)}{\partial x} \geq 0.$$

Ecologically, the above assumptions impose the following restrictions on mutualist population:

1. The mutualist can grow at low densities with or without the prey (x). This indicates that mutualism is non-obligate for mutualists.
2. The population of mutualists cannot grow over a certain population size, which depends on population size of its partner prey; this implies that environment has a carrying capacity $L(x)$, for the mutualist, which is a function of prey population.
3. The population of mutualist is slowed by an increase in its own population, other populations remaining the same. This further implies that mutualist exhibits density dependent growth. Ecologically this is termed as “population effect”.
4. Population of mutualists is enhanced by an increase in the prey population for any population of the mutualist.

H2: The function $g(x)$, where $g : \mathbb{R}_+ \rightarrow \mathbb{R}$ represents the specific growth rate of prey population. We propose the following hypothesis for this function:

$$(a) \ g(0) > 0, (b) \ \frac{\partial g}{\partial x} < 0, (c) \ \exists K > 0 \text{ such that } g(K) = 0.$$

Ecologically the above assumptions impose the following restrictions on specific growth rate of the prey species:

1. The prey can grow at low densities with or without the presence of mutualists, so the mutualism is also non-obligate for the prey species.
2. The population of prey is slowed by an increase in its own numbers, for a fixed population size of mutualist. In other words the prey population exhibits density dependent growth pattern.
3. The population of prey cannot grow over a certain size in any environment. In other words the environment has a carrying capacity for the prey species.

H3: The functions $p_i : \mathbb{R}_+ \times \mathbb{R}_+ \rightarrow \mathbb{R}$ $i=1, 2$ represent predators response functions. We propose the following hypotheses on these functions:

$$(a) \ p_i(u, x) \geq 0 \text{ for } x > 0, u > 0, (b) \ p_i(u, 0) = 0, i = 1, 2,$$

$$(c) p_{ix}(u, x) \geq 0, (d) p_{iu}(u, x) \leq 0.$$

Ecologically, the above mathematical conditions impose the following restrictions on the predators response function:

1. The predator's responses to the prey densities, which refer to change in the density of preys per unit of time per predator as the prey densities changes, are assumed always to be non-negative. Also there cannot be any predation in the absence of preys.
2. For fixed population of other species, the predation is enhanced with the increase in the number of prey species.
3. The mutualist cuts down the effectiveness of predation on the prey. This may be termed as "Mutualist effect". This is the main effect incorporated in the model.

H4: The functions $q_i : \mathbb{R}_+ \rightarrow \mathbb{R}$ represent competition between predators y and z . We propose the following assumptions for these functions:

- $$(a) q_i(0) = 0, (b) q_1(z) > 0, \text{ for } z > 0, (c) q_2(y) > 0, \text{ for } y > 0, \\ (d) q'_1(z) > 0 \text{ for } z > 0, (e) q'_2(y) > 0, \text{ for } y > 0.$$

Ecologically, these hypotheses impose the following restrictions on the functions q_i , $i = 1, 2$:

1. In the absence of competing predators there is no competition.
2. Competition increases with the increase in rival densities.

H5: The functions $s_1(y)$ and $s_2(z)$ where $s_i : \mathbb{R}_+ \rightarrow \mathbb{R}$ are death rates of competing predators. We propose the following hypotheses on these functions:

$$(a) s_i(0) > 0, i = 1, 2, (b) \frac{\partial s_1(y)}{\partial y} > 0, (c) \frac{\partial s_2(z)}{\partial z} > 0,$$

Ecologically, these hypotheses impose the following restrictions on the death rates.

1. Initially death rates are positive.
2. Death remains positive for all the time.

The death rates incorporated in the model are a combination of natural deaths and harvesting of predator by other predators. Obviously our model is valid if a predator is harvested by other predators or they die a natural death.

The above assumptions are ecologically reasonable and exemplified in nature as discussed in introduction. First we shall establish that our system is well behaved in the sense that all the solutions of the system (1) remain positive and bounded, with initial positive conditions. Now, we can state the following theorem.

Theorem 3.1 *Under assumed mathematical conditions on the functions $h, g, q_i, p_i, s_i, ,$ for $i=1,2$; the solutions $\{u(t), x(t), y(t), z(t)\}$ of system (1) with initial positive conditions are all positive and bounded for $t \geq t_0$. Set*

$\Omega = \{(u(t), x(t), y(t), z(t)) : 0 \leq u \leq \tilde{L}; 0 \leq x \leq \tilde{K}; 0 \leq c_1 x + y \leq \tilde{M}; 0 \leq c_1 x + z \leq \tilde{N}\}$ is a positively invariant set and attracts all solutions initiating with non-negative initial conditions, where $\tilde{K} = \max\{x_0, K\}, \tilde{L} = \max\{u_0, L(\tilde{K})\},$
 $\tilde{M} = \max\{c_1 x_0 + y_0, \frac{M}{s_1}\}, \tilde{N} = \max\{c_2 x_0 + z_0, \frac{N}{s_2}\}.$

3.2 Equilibrium States (Stationary Solutions)

In this section, the criteria for existence and non-existence of various equilibria points have been discussed.

The equilibrium points of the system (1) are obtained by equating right hand side of each equation of the system equal to zero and solving them algebraically.

First we observe that trivial equilibrium $E_1(0,0,0,0)$ always exists. As well the following one-dimensional and concerned two-dimensional equilibria are obvious, $E_2(L(0),0,0,0), E_3(0,K(0),0,0), E_4(0,\hat{x},\hat{y},0,0), E_5(\tilde{u},\tilde{x},0,0), E_6(0,x_2,0,z_2).$

On ecological point of view, there must exist equilibrium in u-x plane, for otherwise one of the populations would extinct contradicting the concept of mutualism. Hence, we assume that E_5 will always exist.

There are other three other possible equilibria, which are in relative three-dimensional subspaces. If they exist, we denote them by $E_7(u_3, x_3, y_3, 0), E_8(u_4, x_4, 0, z_4), E_9(o, x_5, y_5, z_5).$ Finally, there may be a positive interior equilibrium denoted by $E_{10}(u^*, x^*, y^*, z^*).$ Later on, we will give a condition for such equilibrium to exist.

The computation of interior equilibrium in four-dimension is very complicated. We shall show the existence of the interior equilibrium, in the section of uniform persistence by the use of the theorem due to Butler⁴⁸. However, here in this section we will construct an example to demonstrate the existence of various equilibria, including the one in four-dimension.

3.2.1 Illustrative Example

In order to illustrate the above analysis we consider the following example. All coefficients and functions are taken for mathematical convenience, not exactly from a real ecological system.

$$(2) \quad \begin{cases} \dot{u} = u[1 - \frac{u}{L+x}], \\ \dot{x} = \alpha x[1 - \frac{x}{K}] - \gamma_0 \frac{xy}{1+mu} - \delta_0 xz, \\ \dot{y} = y[-s_1(1+y) - \delta_1(z) - \frac{c_1}{1+mu} \gamma_0 x], \\ \dot{z} = z[-s_2(1+z) - \delta_2(y) - c_2 \delta_0 x] \end{cases}$$

The values of the parameters specified in the system are taken as

$$L = 3, \alpha = K = 4, \gamma_0 = \delta_0 = 1, m = 4, \delta_1 = \delta_2 = 1, c_1 = 3, c_2 = 4$$

$$s_1 = \frac{1}{3}, s_2 = \frac{1}{4}.$$

With above values of parameters, the various equilibrium points of the above system are found as follows:

$$E_1(0, 0, 0, 0), E_2(3, 0, 0, 0), E_3(0, 4, 0, 0), E_4(0, \frac{1}{2}, \frac{7}{2}, 0),$$

$$E_5(7, 4, 0, 0), E_6(0, \frac{5}{17}, 0, \frac{33}{17}), E_7(4.2891, 2.1224, 17.1177, 0),$$

$$E_8(\frac{44}{13}, \frac{5}{13}, 0, \frac{47}{13}), E_9(0, \frac{7}{10}, \frac{23}{10}, 0), E^*(0.0584, 2.187, 0.4398, 0.11145).$$

Clearly our system (2) satisfies all the mathematical restrictions assumed in assumptions and also the conditions of the results are verified.

3.3 Stability Analysis

In this section we have discussed stability of the system under consideration. This section is divided into two subsections; each of which deals with a particular aspect of stability analysis namely the first subsection deals with local stability analysis while second subsection is concerned with global stability analysis.

3.3.1 Local Stability of Equilibria

Local stability analysis can be made by computing the eigen values of the variational matrix at the equilibrium points. The signs of the real parts of eigen values evaluated at given equilibrium points determine the stability.

In order to discuss stability of these equilibria, we compute the variational matrices about the various equilibria. We denote by V , the general variational matrix and use corresponding notations for the variational matrices about the corresponding equilibria. For example V_1 is the variational matrix about E_1 and so on. Local stability analysis can be made by computing the eigenvalues of the variational matrices at the various equilibrium points. The signs of the real parts of eigenvalues evaluated at given equilibrium points determine the stability.

The general variational matrix V is given by $V = (v_{ij})_{4 \times 4}$

where

$$\begin{aligned} v_{11} &= h(u, x) + u h_u(u, x), v_{12} = u h_x(u, x), v_{13} = 0, v_{14} = 0 \\ v_{21} &= -y p_{1u}(x, u) - z p_{2u}(x, u), \\ v_{22} &= \alpha [g(x) + x g_x(x)] - y p_{1x}(x, u) - z p_{2x}(x, u) \quad v_{23} = -p_1(x, u), \\ v_{24} &= -p_2(x, u), v_{31} = y c_1 p_{1u}(x, u), v_{32} = y c_1 p_{1x}(x, u), \\ v_{33} &= -s_1(y) - q_1(z) + c_1 p_1(x, u) - y s_1'(y), v_{34} = -y q_1'(z), \\ v_{41} &= z c_2 p_{2u}(x, u), v_{42} = z c_2 p_{2x}(x, u), v_{43} = -z q_2'(y), \\ v_{44} &= -s_2(z) - q_2(y) + c_2 p_2(x, u) - z s_2'(z). \end{aligned}$$

Hence the variational matrices with respect to the various equilibria have the following non-zero entries:

For V_1 ;

$$\begin{aligned} v_{11} &= h(0, 0), \quad v_{22} = \alpha g(0), \quad v_{33} = -s_1(0) - q_1(0) + c_1 p_1(0, 0), \\ v_{44} &= -s_2(0) - q_2(0) + c_2 p_2(0, 0) - z s_2'(z). \end{aligned}$$

For V_2 ;

$$\begin{aligned} v_{11} &= L(0)h_u(L(0), 0), \quad v_{12} = L(0)h_x(L(0), 0), \quad v_{22} = \alpha g(L(0)), \\ v_{33} &= -s_1(0), \quad v_{44} = -s_2(0). \end{aligned}$$

For V_3 ;

$$\begin{aligned} v_{11} &= h(0, K(0)), \quad v_{21} = 0, \quad v_{22} = \alpha[K(0)g_x(0, K(0))], \\ v_{23} &= -p_1(0, K(0)), \quad v_{24} = -p_2(0, K(0)), \\ v_{33} &= -s_1(0) - q_1(0) + c_1 p_1(0, K(0)), \\ v_{44} &= -s_2(0) - q_2(0) + c_2 p_2(0, K(0)). \end{aligned}$$

For V_4 ;

$$\begin{aligned} v_{11} &= h(0, x_1), \quad v_{21} = -y_1 p_{1u}(0, x_1), \\ v_{22} &= \alpha x_1 g_x(x_1) + \alpha g(x_1) - y_1 p_{1x}(0, x_1), \quad v_{23} = -p_1(0, x_1), \\ v_{24} &= -p_2(0, x_1), \\ v_{31} &= y_1[-s_1(y_1) + c_1 p_{1u}(0, x_1)], \quad v_{32} = y_1 c_1 p_{1x}(0, x_1), \\ v_{33} &= -s_1(y_1) - q_1(0) + c_1 p_1(0, x_1) + y_1 s_1'(y_1), \quad v_{34} = -y_1 q_1'(0), \\ v_{44} &= -s_2(0) - q_2(y_1) + c_2 p_2(0, x_1). \end{aligned}$$

For V_5 ;

$$v_{11} = \tilde{u}h(\tilde{u}, \tilde{x}), \quad v_{12} = \tilde{u}h_x(\tilde{u}, \tilde{x}), \quad v_{21} = 0, \quad v_{22} = \alpha \tilde{x}g_x(\tilde{x}),$$

$$\begin{aligned} v_{23} &= -p_1(\tilde{u}, \tilde{x}), v_{24} = -p_2(\tilde{u}, \tilde{x}), v_{33} = -s_1(0) - q_1(0) + c_1 p_1(\tilde{u}, \tilde{x}), \\ v_{44} &= -s_2(0) - q_2(0) + c_2 p_2(\tilde{u}, \tilde{x}). \end{aligned}$$

For V_6 ;

$$\begin{aligned} v_{11} &= h(0, x_2), v_{21} = -z_2 p_{2u}(0, x_2), \\ v_{22} &= \alpha x_2 g_x(x_2) + \alpha g(x_2) - z_2 p_{2x}(0, x_2), v_{23} = -p_1(0, x_2), \\ v_{24} &= -p_2(0, x_2), v_{33} = -s_1(0) - q_1(z_2) + c_1 p_1(0, x_2), \\ v_{41} &= z_2 c_2 p_{2u}(0, x_2), v_{42} = z_2 c_2 p_{2u}(0, x_2) \\ v_{44} &= -s_2(z_2) - q_2(0) + c_2 p_2(0, x_2). \end{aligned}$$

For V_7 ;

$$\begin{aligned} v_{11} &= u_3 h_u(u_3, x_3), v_{12} = u_3 h_x(u_3, x_3), v_{21} = 0 - y_3 p_{1u}(u_3, x_3) \\ v_{22} &= \alpha x_3 g_x(x_3) + \alpha g(x_3) - y_3 p_{1x}(u_3, x_3), \\ v_{23} &= -p_1(u_3, x_3), v_{24} = -p_2(u_3, x_3) \\ v_{31} &= y_3 [c_1 p_{1u}(u_3, x_3)], v_{32} = y_3 c_1 p_{1x}(u_3, x_3), \\ v_{33} &= -s_1(y_3) - q_1(0) + c_1 p_1(u_3, x_3) - y_3 s_1' \\ v_{34} &= -y_3 q_1'(0), v_{44} = -s_2(0) - q_2(y_3) + c_2 p_2(u_3, x_3). \end{aligned}$$

For V_8 ;

$$\begin{aligned} v_{11} &= u_4 h_u(u_4, x_4), v_{12} = u_4 h_x(u_4, x_4), v_{21} = -z_4 p_{2u}(u_4, x_4), \\ v_{22} &= \alpha x_4 g_x(x_4) + \alpha g(x_4) - z_4 p_{2x}(u_4, x_4), v_{23} = -p_1(u_4, x_4), \\ v_{24} &= -p_2(u_4, x_4), v_{33} = -s_1(0) - q_1(z_4) + c_1 p_1(u_4, x_4), \\ v_{41} &= z_4 c_2 p_{2u}(u_4, x_4), v_{42} = z_4 c_2 p_2(u_4, x_4), v_{43} = -z_4 q_2'(0), \\ v_{44} &= -s_2(z_4) - q_2(0) + c_2 p_2(u_4, x_4) - z_4 s_2'(z_4). \end{aligned}$$

For V_9 ;

$$\begin{aligned}
 v_{11} &= h(0, x_5), \quad v_{21} = -z_5 p_{2u}(0, x_5) - y_5 p_{1u}(0, x_5), \\
 v_{22} &= \alpha g(x_4) - y_5 p_{1x}(0, x_5) - z_5 p_{2x}(0, x_4), \quad v_{23} = -p_1(0, x_5), \\
 v_{24} &= -p_2(0, x_4), \quad v_{31} = y_5 c_1 p_{1u}(0, x_5), \quad v_{32} = y_5 c_1 p_{1x}(0, x_5), \\
 v_{33} &= -s_1(y_5) - q_1(z_5) - y_5 s_1'(y_5) - c_1 p_1(0, x_5), \\
 v_{41} &= z_5 c_2 p_{2u}(0, x_5), \quad v_{42} = z_5 c_2 p_{2x}(0, x_5), \quad v_{43} = -z_5 q_2'(y_5), \\
 v_{44} &= -s_2(z_5) - q_2(y_5) + c_2 p_2(0, x_5) - z_5 s_2'(z_5).
 \end{aligned}$$

It is obvious to note that V_{10} is nothing but the general variational matrix V evaluated at $E_{10}(u^*, x^*, y^*, z^*)$. From the determination of eigenvalues of the above matrices, we can make the following statements about the local stability of the equilibrium points. V_1 having positive eigenvalues in u and x -directions and negative in y and z -directions is unstable. Near E_1 , mutualist and prey populations grow while populations of both the predators decline. V_2 have positive eigenvalue in x -direction and negative in u , y , and z -directions, so unstable. Here we may conclude that E_2 attract in u , y and z -directions and repels in x -direction.

V_3 have positive eigenvalue in u -direction and negative along x -direction. The eigenvalues in y and z -directions are positive if we assume

$$(3) \quad p_i(0, K(0)) > \frac{s_i(0)}{c_i(0)}$$

This assumption is ecologically reasonable, by noting that in the absence of mutualist and when the prey population is near its carrying capacity $K(0)$, the population of predators y and z must multiply. Thus E_3 is unstable in $\mathbb{R}_{ux}^+$.

The eigenvalue of V_4 in u-direction is $h(0, x_1)$, which is positive by (H1-a). Thus the equilibrium E_4 is unstable, population of u near E_4 increases. The eigenvalue in z-direction is given by

$$(4) \quad \lambda_z = -s_2(0) - q_2(y_1) + c_2 p_2(0, x_1)$$

E_4 is an interior equilibrium for a competitive predator-prey system, in the absence of mutualist. Freedman⁴⁹ has given the graphical analysis of this case and accordingly, we can state the following result for our system. Let us denote

$$H_1(x) = \alpha x_1 g_x(x_1) + \alpha g(x_1) - y_1 p_{1x}(0, x_1) - y_1 s_1'(y_1)$$

and

$$H_2(x) = y_1 p_{1x}(0, x_1) [\alpha x_1 g_x(0, x_1) + \alpha g(0, x_1) - y_1 p_{1x}(0, x_1) + c_1 y_1 p_1(0, x_1) p_{1x}(0, x_1)]$$

$H_2(x) > 0$ then we can state the following theorem:

Theorem 3.1. *If $H_1(x) < 0$, then E_4 is asymptotically stable and unstable if $H_1(x) > 0$.*

The eigenvalue of V_5 in y and z-directions are positive above, causing E_5 unstable, populations of predators in respective directions near E_5 increases. The eigen values in u and x-direction is given

$$\lambda_{\pm} = \frac{1}{2} [\tilde{u} h_u(\tilde{u}, \tilde{x}) + \alpha \tilde{x} g_x(\tilde{x})] \pm \frac{1}{2} [(\tilde{u} h_u(\tilde{u}, \tilde{x}) + \alpha \tilde{x} g_x(\tilde{x}))^2 - 4\alpha \tilde{u} \tilde{x} h_u(\tilde{x}) g_x(\tilde{x})]^{\frac{1}{2}}$$

Now if we denote $H_3(x) = h_u(\tilde{u}, \tilde{x}) g_x(\tilde{u}, \tilde{x})$, then we have the following result:

Theorem 3.2. *If $H_3(x) > 0$, then the eigen values $\lambda_{\pm}$ have negative real parts and E_5 is asymptotically stable in positive u-x plane.*

Eigen value of V_6 in u-direction is given by $h(0, x_2)$, which is positive (by H1-a). This implies that E_6 is unstable in u-direction, hence the population of mutualist increases near E_6 . The eigen value in y-direction is given by

$$(5) \quad \lambda_y = -s_1(0) + c_1 p_1(0, x_2) - q_1(z_2)$$

The eigen values in x and z-direction have negative real part.

$$\text{If } H_4(x) = \alpha x_2 g_x(x_2) + \alpha g(0, x_2) - z_2 p_{2x}(0, x_2) - s_2'(z_2) < 0$$

and

$$H_5(x) = s_2'[\alpha x_2 g_x(x_2) + \alpha g(x_2) - z_2 p_{2x}(0, x_2)] - z_2 c_2 p_2(0, x_2) p_{2x}(0, x_2) < 0.$$

Therefore, if the above two conditions are satisfied, then E_6 is asymptotically stable in x-z plane, but unstable in u-direction i.e., population of mutualist increases, while that of x and y decreases near point E_6 .

$E_7(u_3, x_3, y_3, 0)$, $E_8(u_4, x_4, 0, z_4)$, $E_9(0, x_5, y_5, z_5)$ are interior equilibria in respective planes, in the absence of fourth species, namely predator z in E_7 , predator y in E_8 , and the mutualist u in E_9 . A detail analysis of these equilibria including the interior equilibrium $E_{10}(u^*, x^*, y^*, z^*)$, applying Rough-Hurwitz criteria. In this technique, the computations are very complicated and the results could not be interpreted ecologically. Therefore, we choose not to repeat them in this paper. Not much can be said about $E_{10}(u^*, x^*, y^*, z^*)$, of course, stability of interior equilibrium is not clear at this point.

3.3.2 Global stability of the interior equilibrium

In this section we will discuss the conditions for the global stability of the equilibrium point $E_{10}(u^*, x^*, y^*, z^*)$.

For mathematical convenience, we denote E_{10} as E^* . Here we assume that E^* , as defined earlier, exists. It is the purpose of this section is to derive criterion for E^* to be globally stable i.e. E^* to be asymptotically stable with domain of attraction the positive cone. For this, our technique will be to construct a Liapunov function⁵⁰, whose domain of validity is the positive

cone. We have the following theorem, for the stability of interior equilibrium:

Theorem 3.11 Let $M(u, x, y, z)$ be a positive definite matrix for all points in the set $\Omega \cap \mathbb{R}_+^4$, where Ω is the region of attraction as discussed in theorem (1). Then the interior equilibrium E^* is a globally asymptotically stable equilibrium of the system with respect to solutions initiating in the $\text{int } \mathbb{R}_+^4$.

Proof. Let $X = \{u(t), x(t), y(t), z(t)\}$ be any solution of (1) and $X \in \Omega \cap \text{int } \mathbb{R}_+^4$. Since M is positive definite, $\dot{V}(X) \leq 0$, the function V defines a Liapunov function. The set $\{X \in \Omega \cap \text{Int } \mathbb{R}_+^4 : \dot{V}(X) = 0\}$ is precisely E^* .

Therefore the largest invariant set in Ω is the equilibrium point E^* , and hence by LaSalle's invariance principle, E^* globally asymptotically stable. Note. A necessary condition for the matrix $M(u, x, y, z)$ to be positive definite is that $b_{ii} = 0$, for all i , except at equilibrium values.

3.4 Uniform Persistence

In this section, we shall obtain the criteria for our system to be uniformly persistence. Followed by Rai and Singh⁵¹, the sufficient conditions for the permanent co-existence or extinction of species of system (1) are obtained by the knowledge of various equilibria and by constructing average Liapunov function. Followed by Rai and Singh, we can state the following theorem for our system:

Theorem 3.12. *Let the following conditions hold, in addition to those mentioned in the assumptions:*

1. $s_i(0) < c_i p_i(K, 0)$, $i=1, 2$, 2. $s_2(0) < c_2 p_2(x_1, 0)$
 3. $s_1(0) < c_1 p_1(x_2, 0) - q_1(z_2)$ 4. $s_2(0) < c_2 p_2(x_3, 0) - q_2(y_3)$,
- then the system (1) is uniformly persistent.*

Now at this stage, the following corollary is obvious.

Corollary 3.13 Let the assumptions (H1)-(H5) hold and conditions of the theorem (3.12) are satisfied then the interior equilibrium $E^*(u^*, x^*, y^*, z^*)$ exists.

At this point our analysis is greatly facilitated by graphical approach. We have plotted time verses interacting populations by Matlab software for different values of parameters for the system. It was found that, in the absence of mutualist and the predation is too high, then the predators may drive the prey population to zero (due to over exploitation) and as a consequence predators also go to extinction, due to non availability of prey species. Hence the entire system may collapse (Figure 1). But when the mutualist is allowed to interact in the system, there is a possibility to save the population of the prey species from going to extinction, by deterrence ($\frac{\partial p}{\partial u} \leq 0$) and the uniform persistence is possible (Figure 2).

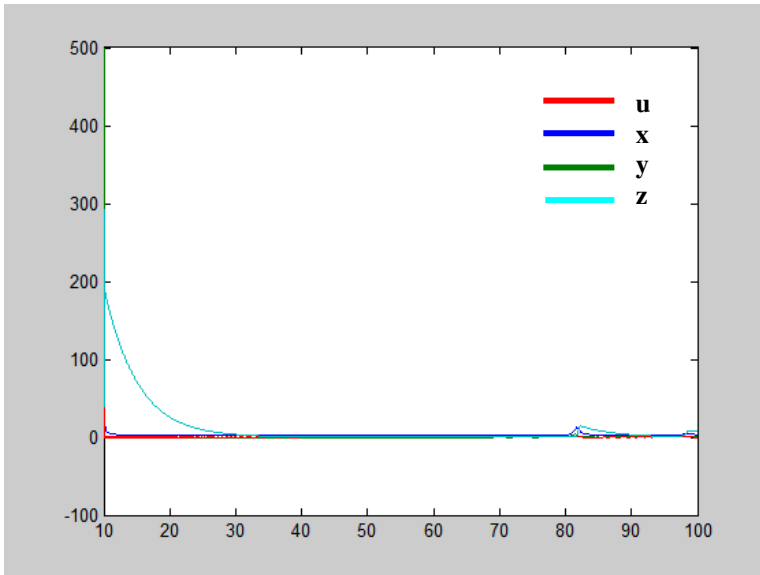


Fig. 1: Mutualist Absent

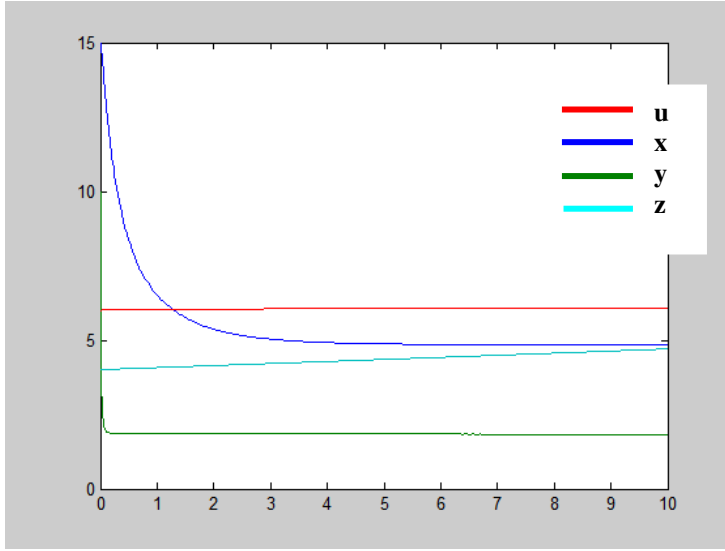


Fig. 2: Mutualist Present

3.5 An Example

In order to illustrate the above analysis we consider the following example. All coefficients and functions are taken for mathematical convenience, not exactly from a real ecological system. Mathematica (5.2), software, has been used for tedious calculations, and only approximate values have been considered.

$$(6) \quad \begin{cases} \dot{u} = u[1 - \frac{u}{L+x}], \\ \dot{x} = \alpha x[1 - \frac{x}{K}] - \gamma_0 \frac{xy}{1+mu} - \delta_0 xz, \\ \dot{y} = y[-s_1(1+y) - \delta_1(z) - \frac{c_1}{1+mu} \gamma_0 x], \\ \dot{z} = z[-s_2(1+z) - \delta_2(y) - c_2 \delta_0 x] \end{cases}$$

Specific values of the parameters are taken as:

$$L=3, \alpha=K=4, \gamma_0=\delta_0=1, m=4, \delta_1=\delta_2=1, c_1=3, c_2=4$$

$$s_1=\frac{1}{3}, s_2=\frac{1}{4}.$$

Various equilibrium points of the above system are listed as follows:

$$E_1(0,0,0,0), E_2(3,0,0,0), E_3(0,5,0,0), E_4(0, \frac{25}{49}, \frac{176}{49}, 0),$$

$$E_5(8,5,0,0), E_6(0, \frac{25}{84}, 0, \frac{316}{84}), E_7(5.18759, 4.9241, 10.2726, 0),$$

$$E_8(3.8910, 1.1132, 0.03251), E_9(0, \frac{5}{37}, \frac{269}{37}, \frac{117}{137}), E^*(28.308, 0.5251, 0.1251, 0.1254)$$

Since $s_1(0) = 0.333, s_2(0) = 0.25, c_1 = 3, c_2 = 4$.

Here in this example, we observe that conditions (H1)-(H5), framed in the assumptions are satisfied and all the conditions of the theorem (3.12) are also satisfied and hence the considered system (6) is uniformly persistent.

3.6 Summary

In this paper an ecological situation arising due to interactions of four species: two predators competing for the same prey and also in competition with each other and a mutualist to the prey species has been modelled and mathematically analyzed, where the mutualist possesses defensive mechanisms(deterrence in particular) against both the predators. After framing ecologically reasonable assumptions on the functions incorporated in the model, conditions for existence/ non-existence of equilibria were established, and the stability of these equilibria were determined. Also conditions for long term survival of all the species has been investigated in the form of uniform persistence. A specific numerical example has been discussed, in order to illustrate the results.

After analysis, it was found that by adding a mutualist to the system, the prey equilibrium value is increased. This establishes the effect in the case of a stable interaction of increasing the effective carrying capacity to the prey species. Further the carrying capacity of the mutualist is also increased, due to positive interaction with the prey. Finally, if the death rates of the predators are less than a certain threshold value, depending upon conversion efficiency and the competition by the rivals, the uniform persistence of all the four species of the system under consideration is possible.

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