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Mathematical modelling of intraguild predation and its dynamics of resource harvesting

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Abstract

The contemporary theoretical inquest concerns itself with an updated mathematical model involving intraguild (IG) predation in which the IG predator acts as a generalist predator with the inclusion of harvesting in the resource population. Due attention is paid to the positivity and boundedness of the outcomes of the system under consideration. All the conceivable ecologically feasible equilibria are explored for their existence and stability under certain conditions. Special emphasis is put forward on the consequence of harvesting for the present model system. The occurrences of Hopf-bifurcation with respect to harvesting parameters involved in the harvesting effort of the model system are captured. The subsistence of the possible bionomic equilibria is, however, not ruled out from the present pursuit. The optimal harvesting policy is initiated and duly carried out with Pontryagin's maximum principle. Numerical simulations are performed towards the end to comply with the objectives of the agreement of the numerical outcomes with their analytical counterparts and the applicability of the model is validated thereby.

Keywords: Asymmetric intraguild predation, Resource harvesting, Generalist predator, Optimal harvesting, Hopf-bifurcation
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1 Introduction

Towards the beginning of twentieth century, the fundamental predator-prey interacting species model was put forward by eminent researchers Lotka and Volterra with the employment of a pair of coupled nonlinear ordinary differential equations. Since then quite a good number of interacting species models of diverse categories have been proposed and explored ceaselessly [1]. Way back in 1997, Holt and Polis [3] characterized intraguild predation (IGP) [4, 11] as a type of interaction representing a combination of both predation and competition, because both species rely on the same prey resources and also benefit from preying upon one another. When two species compete for shared limited resources and eat each other as well, the system is often called symmetric IGP. However, for asymmetric IGP both the species compete for shared resources and either of them (designated by IG predator) eats the other (called IG prey).The system under contemplation takes into account an asymmetric IGP where IG predator is treated as a generalist predator that has an alternative food source. There are many well-established examples of intraguild predation in ecological community (cf. Table 1). It is exclaimed that there are quite a few IGP models where the

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shared resource is of economic importance and the resource is continuously harvested. Interested readers may go through the work undertaken by Bampfyled and Lewis [5] for many more instances of such IGP representations. The present article concerns itself with a three-species food chain model by means of intraguild predation and the inclusion of prey harvesting as conducted by Yun Kang and Lauren Wedekin [2]. One may refer to the topics and modus operandi of the dynamical systems [7, 8, 9] to carry out mathematical analysis of the proposed model.

In the wake of rising demand of economic gain and human exigency, the management of renewable / biological resources alongwith the harvesting of interacting species are well known to humans in fishery, forestry and wildlife management [14]. Consequently, the growing need for sustainable expansion of policy for propitious management of renewable resources is experienced in diverse perspectives of human activities to conserve the ecosystem. As a result, quite a good number of eminent ecologists and economists focused their attention to the scientific management of the resources (harvesting) exploitation. In recent times, the interactive predator-prey system is being projected to carry out these important perceptions having relevance to the management of biological resources [15, 16]. Despite the ecological reasoning behind exploring such IGP models, there are justifications in reality like many people harvest members of ecological community for food, business etc. Of all these species which are harvested by humans are members of ecological community exhibiting intraguild predation. The harvesting of interacting species possesses a strong impact on the dynamics of predator-prey system which sensibly depends on the characteristics of applied harvesting strategy.

It is an well established fact that the existence of every species is ecologically significant in a natural environment. In the widespread ecological phenomenon of intraguild predation, the predation process involves the two consumer species that share a regular resource. In an intraguild predation system, the economically significant resources may be destroyed either by IG prey or by IG predator but both of them are ecologically significant in some way or other [17, 18, 19, 20, 21, 22]. In view of this, one should be aware of the effect of prey harvesting on ecological community before some actions are taken as harvesting species at one level can have unnecessary consequences on another. One may refer to Table 1 for cotton, apples etc. as of economic concern. An attempt is made at this juncture to investigate firstly how the harvesting of these resources influences the ensuing IG prey and IG predator and secondly to explore the possibility of having bionomic equilibria together with the interior optimal solution in order to optimize the earnings through harvesting using Pontryagin's maximum principle.

The present exploration is organized sequentially as follows. The formulation of the mathematical model for the problem undertaken together with the basic preliminaries are discussed in Section 2. Section 3 concerns with the local stability analysis of the equilibria together with the dynamical attributes of the system. The influence of harvesting on the interacting species of the model system is investigated analytically in Section 4. Section 5 includes the existence of feasible bionomic equilibria while the optimal harvesting policy for the proposed system is incorporated in Section 6. Section 7 deals with the numerical simulation based on the set of model parameter values for the purpose of demonstrating the outcomes so as to validate the theoretical findings. Finally, the present article ends with concluding remarks mentioning salient observations made out of the proposed system together with their ecological relevance presented in Section 8.

2 The mathematical model formulation and its basic preliminaries

To investigate the qualitative dynamics of intraguild predator-prey system, the proposed model is an extension of the model offered by Yun Kang and Lauren Wedekin [2]. Special attention is focused on harvesting strategy as a possible extension for new findings. In the present study, the following three-dimensional ($3D$) continuous time intraguild predation model with linear prey harvesting is taken into account as

$$\frac{dP}{dT} = r_p P\big(1 - \frac{P}{K_p}\big) - a_g GP - a_m PM - a_h P, \tag{2.1a}$$

$$\frac{dG}{dT} = G\big(e_g a_g P - \frac{aMG}{G^2 + b^2} - d_g\big), \tag{2.1b}$$

$$\frac{dM}{dT} = M\big(r_m\big(1 - \frac{M}{k_m}\big) + e_m a_m P + \frac{e_m a G^2}{G^2 + b^2}\big), \tag{2.1c}$$

where $P(t)$, $G(t)$ and $M(t)$ signify the shared prey, IG prey, and generalist IG predator population size respectively at time t. All the ecological parameters r_p, K_p, a_g, a_m, a_h, e_g, d_g, a, b, r_m, K_m and e_m of the system (2.1), assume

IG predator	IG prey	Shared resource	Location
Bigeyed bugs (Geocoris punctipes, G. pallens,G.bullatus, G. uligosus)	Lepidopteran pests of cotton: whiteflies, mites, bollworm	Cotton	Southern U.S
Minute pirate bug (Orius tristicolor), insidious flower bug (O. insidiosus)	Thrips, spider mites, small caterpillars	Agricultural crops, cotton	Southern U.S
Green lacewings (Chrysoperla carnea, C.rufilabris)	Aphids, spider mites, whiteflies, moths	Cotton, sugar beet and vineyards	North America, Russia, Germany, Europe
Zetzellia mali (predaceous mites)	Apple rust mite, European red mite, two-spotted spider mite	Apples	Apple orchards
Euseius tularensis (predaceous mites)	Citrus red mite, citrus thrips, scale insects, whiteflies	Citrus fruit	Citrus plantations
Neoseiulus californicus, Phytoseiulus persimilis (predaceous mites)	Red spider mites (Tetranychus spp.)	Vegetables and greenhouse crops	Spain
Decollate snail (Rumina decollata)	Brown gardensnail (Helix aspersa)	Citrus crops and seedlings	California
Epistrophe balteata, Paragus qudrifasciatus, Syrphus corollae	Cotton aphid (Aphis gossypii)	Cotton,alfalfa	China
Syrphid fly larvae (hoverfly larvae)	Russian wheat aphid (Diuraphis noxia)	Spring barley (Hordem vulgare)	Ethiopia
Episyrphus balteatus (hoverflies, syrphid family)	Winter wheat aphid (Metopolophium dirhodium)	Winter wheat	Germany
Pseudodorus clavatus (hoverflies, syrphid family)	Brown citrus aphid (Toxoptera citridia)	Citrus fruit	North America
Pipiza festiva	Gall forming aphids	Fruit trees	Southeastern Spain

Table 1: Examples of intraguild predation in natural environment.

only positive values and will be treated as constants throughout the investigation process. The parameters r_p and r_m characterize the maximum rate of growth of the resource (shared prey) and IG predator, respectively. K_p and K_m are the carrying capacities of the resource and IG predator respectively. a_g and a_m are the predation rates of IG prey and IG predator for resource, respectively. The biological meaning of a is maximum population of IG prey killed by IG predator. b represents the IG prey density at which the population killed by IG predator reached half of its maximum. e_g and e_m are the efficiency of biomass conversion between the respective trophic levels. d_g is the natural death rate of IG prey. In this investigation, we believe that the shared prey (resource) species in the model (2.1) is of commercial / economical importance. The prey species is continuously being harvested with a constant rate a_h. Now, the system (2.1) is simplified by letting $x = \frac{p}{K_p}$, $y = \frac{a_g G}{r_p}$, $z = \frac{a_m M}{r_p}$, $t = r_p T$.

The non-dimensional form of the system (2.1) is given by,

$$\frac{dx}{dt} = x\big(1 - x - y - z - k\big), \tag{2.2a}$$

$$\frac{dy}{dt} = \gamma_1 y\big(x - \frac{a_1 yz}{y^2 + \beta^2} - d_1\big), \tag{2.2b}$$

$$\frac{dz}{dt} = \gamma_2 z\big(a_3 - a_4 z + x + \frac{a_2 y^2}{y^2 + \beta^2}\big), \tag{2.2c}$$

where $k = \frac{a_h}{r_p}$, $\gamma_1 = \frac{e_g a_g K_p}{r_p}$, $a_1 = \frac{a}{a_m e_g K_p}$, $\beta = \frac{b a_g}{r_p}$, $d_1 = \frac{d_g}{K_p e_g a_g}$, $\gamma_2 = \frac{e_m a_m K_p}{r_p}$, $a_3 = \frac{a_m e_m K_p}{r_p}$, $a_4 = \frac{r_p r_m}{K_p K_m e_m a_m^2}$, $a_2 = \frac{a}{a_m K_p}$.

2.1 Positive invariance and boundedness of the system (2.2)

One is well aware of the fact that an ecologically meaningful system should be positively invariant and bounded in $\mathbf{R}_+^3$. Here these properties of the system will be shown. Clearly, system (2.2) is positively invariant in $\mathbf{R}_+^3$ (see, e.g. [23, Theorem 5.2.1]). Then it follows from the first equation of system (2.2) that

$$\frac{dx}{dt} = x\big(1 - x - y - z - k\big).$$

This implies,

$$\frac{dx}{dt} \le x\big(1 - x\big).$$

By the comparison principle of ODE, we have

$$\limsup_{t\to\infty} x(t) \le 1.$$

Similarly,

$$\begin{aligned}\frac{dz}{dt} &= \gamma_2 z\big(a_3 - a_4 z + x + \frac{a_2 y^2}{y^2 + \beta^2}\big)\\ &\ge \gamma_2 z\big(a_3 - a_4 z\big).\end{aligned}$$

This implies that

$$\liminf_{t\to\infty} z(t) \ge \frac{a_3}{a_4}.$$

On the other hand,

$$\begin{aligned}\frac{dz}{dt} &= \gamma_2 z\big(a_3 - a_4 z + x + \frac{a_2 y^2}{y^2 + \beta^2}\big)\\ &\le \gamma_2 z\big(a_3 - a_4 z + 1 + a_2\big)\end{aligned}$$

implies that

$$\limsup_{t\to\infty} z(t) \le \frac{a_3 + a_2 + 1}{a_4}.$$

To show y is bounded, consider the function $v = \gamma_1 x + y$.

Now,

$$\begin{aligned}\frac{dv}{dt} &= \gamma_1 x\big(1 - x - z - k\big) + \gamma_1 y\big(- \frac{a_1 yz}{y^2+\beta^2} - d_1\big)\\ &\le \gamma_1\big(1 - d_1 y\big)\\ &= \gamma_1\big(1 - vd_1 + d_1\gamma_1 x\big)\\ &\le \gamma_1\big(1 + d_1\gamma_1 - vd_1\big).\end{aligned}$$

This implies that

$$\limsup_{t\to\infty} v(t) \le \frac{1+d_1\gamma_1}{d_1}.$$

This shows that y is bounded and consequently the system (2.2) is bounded. Moreover the species z is persistent in the system (2.2).

2.2 Existence of equilibria of the model system (2.2)

One may now study the existence of equilibrium points of the system (2.2). Particular interest is paid on the interior equilibrium point. The following are all possible feasible equilibrium points:

(i) The trivial equilibrium point $E_0(0,0,0)$;

(ii) The equilibrium point in the absence of IG prey and IG predator $E_1(1-k,0,0)$ if $k<1$;

(iii) The equilibrium point in the absence of resource and IG prey $E_2(0,0,\frac{a_3}{a_4})$;

(iv) The equilibrium point in the absence of only IG predator $E_3(d_1, 1-d_1-k, 0)$ if $d_1+k<1$;

(v) The equilibrium point in the absence of IG prey only $E_4\big(\frac{a_4(1-k)-a_3}{1+a_4}, 0, \frac{1+a_3-k}{1+a_4}\big)$ if $k < min\big\{1+a_3, 1-\frac{a_3}{a_4}\big\}$.

The interior equilibrium point can be obtained by solving the system of equations given by

$$1 - x - y - z - k = 0, \tag{2.3a}$$

$$x - \frac{a_1 yz}{y^2+\beta^2} - d_1 = 0, \tag{2.3b}$$

$$a_3 - a_4 z + x + \frac{a_2 y^2}{y^2+\beta^2} = 0. \tag{2.3c}$$

Now putting the value of x from the first equation in the third equation we get,

$$z = \frac{a_3 + 1 - k - y}{1+a_4} + \frac{a_2 y^2}{(1+a_4)(y^2+\beta^2)}.$$

Putting this value of z in the second equation, one may obtain a polynomial equation in y of degree 5 given by,

$$\begin{aligned}&a_4 y^5 + \big(a_4 k + a_2 + a_4 d_1 - a_4 - a_1 + d_1 + a_3\big)y^4 + \big(a_1 + a_1 a_3 + a_2 a_1 - a_1 k + 2a_4\beta^2\big)y^3 +\\ &\big(2a_3\beta^2 - \beta^2 a_1 + 2a_4\beta^2 k - 2a_4\beta^2 + a_2\beta^2 + 2d_1\beta^2 + 2a_4\beta^2 d_1\big)y^2 +\\ &\big(\beta^2 a_1 + a_3\beta^2 a_1 + a_4\beta^4 - \beta^2 a_1 k\big)y + \beta^4\big(a_3 - a_4 + a_4 d_1 + d_1 + a_4 k\big)\\ &= 0.\end{aligned}$$

This equation can be written as

$$A_0 y^5 + A_1 y^4 + A_2 y^3 + A_3 y^2 + A_4 y + A_5 = 0, \tag{2.4}$$

where,

$$\begin{aligned}A_0 &= a_4\ ,\\ A_1 &= a_4 k + a_2 + a_4 d_1 - a_4 - a_1 + d_1 + a_3,\\ A_2 &= a_1 + a_1 a_3 + a_1 a_2 - a_1 k + 2a_4\beta^2,\\ A_3 &= 2a_3\beta^2 - a_1\beta^2 + 2a_4\beta^2 k - 2a_4\beta^2 + a_2\beta^2 + 2d_1\beta^2 + 2d_1 a_4\beta^2,\\ A_4 &= a_1\beta^2 + a_1 a_3\beta^2 + a_4\beta^4 - k a_1\beta^2,\\ A_5 &= \big(a_3 - a_4 + a_4 d_1 + d_1 + a_4 k\big)\beta^4.\end{aligned}$$

Also, after some manipulations one may obtain the expressions of x and z in terms of y given by

$$x = \frac{d_1\beta^2 + a_1 y - a_1 k y - a_1 y^2 + d_1 y^2}{y^2 + \beta^2 + a_1 y}, \tag{2.5}$$

and

$$z = \frac{\big(y^2 + \beta^2\big)\big(1 - k - d_1 - y\big)}{y^2 + \beta^2 + a_1 y}. \tag{2.6}$$

Hence one obtains the value of y from (2.4), the values of x and z can also be found out. Now, for the existence and uniqueness of the interior equilibrium point we have the following theorem.

Theorem 1. Assume that all parameters $a_1, a_2, a_3, a_4, k, d_1, \beta, \gamma_1, \gamma_2$ are positive. Let

$$\underline{k} = \max\left\{\frac{a_1 + a_4 - a_2 - a_4 d_1 - d_1 - a_3}{a_4}, \frac{2a_4 - a_2 - 2d_1 - 2a_4 d_1 - 2a_3 + a_1}{2a_4}\right\}$$
$$\overline{k} = \min\left\{\frac{a_1 + a_1 a_3 + a_1 a_2 + 2a_4\beta^2}{a_1}, \frac{a_1 + a_1 a_3 + a_4\beta^2}{a_1}, \frac{a_4 - a_3 - d_1 a_4 - d_1}{a_4}\right\}.$$

If

$$(\mathbf{H_1}): \ \underline{k} < k < \overline{k}$$

is satisfied, then Eq. (2.4) has a unique positive real root, denote by $\bar{y}$. Furthermore, assume that

$$(\mathbf{H_2}): \ \bar{y} < 1 - k - d_1$$

holds. Then system (2.2) has a unique positive equilibrium $\bar{E} = (\bar{x}, \bar{y}, \bar{z})$ which is given by

$$\begin{aligned} \bar{x} &= \frac{d_1\beta^2 + a_1\bar{y} - a_1 k\bar{y} - a_1\bar{y}^2 + d_1\bar{y}^2}{\bar{y}^2 + \beta^2 + a_1\bar{y}}, \\ \bar{z} &= \frac{\big(\bar{y}^2 + \beta^2\big)\big(1 - k - d_1 - \bar{y}\big)}{\bar{y}^2 + \beta^2 + a_1\bar{y}}. \end{aligned} \tag{2.7}$$

Proof . Using the assumption $(\mathbf{H_1})$ we have $A_0 > 0$, $A_1 > 0$, $A_2 > 0$, $A_3 > 0$, $A_4 > 0$, $A_5 < 0$. Hence using Descartes' rule of signs, the equation (2.4) has a unique positive solution $y = \bar{y}$. Now using the condition $(\mathbf{H_2})$ along with (2.6) we obtain

$$z(= \bar{z}) = \frac{\big(\bar{y}^2 + \beta^2\big)\big(1 - k - d_1 - \bar{y}\big)}{\bar{y}^2 + \beta^2 + a_1\bar{y}} > 0. \tag{2.8}$$

Then it follows from (2.3b) that

$$x(= \bar{x}) = \frac{a_1\bar{y}\bar{z}}{\bar{y}^2 + \beta^2} + d_1 > 0.$$

Hence, the interior equilibrium $\bar{E} = (\bar{x}, \bar{y}, \bar{z})$ exists uniquely. □

3 Local stability analysis of the system (2.2)

In this section, one may discuss the local stability behaviour of the equilibrium points. At a general equilibrium point (x, y, z) the Jacobian matrix of the system is given by

$$J = \begin{bmatrix} 1 - 2x - y - z - k & -x & -x \\ \gamma_1 y & \frac{\gamma_1(x-d_1)(y^2+\beta^2-a_1 yz)}{y^2+\beta^2} - \frac{a_1\gamma_1 yz(\beta^2-y^2)}{(y^2+\beta^2)^2} & -\frac{\gamma_1 a_1 y^2}{y^2+\beta^2} \\ \gamma_2 z & \frac{2a_2\gamma_2\beta_2 yz}{(y^2+\beta^2)^2} & -2\gamma_2 a_4 z \end{bmatrix}.$$

3.1 Dynamics around E_0

Theorem 2. E_0 is unstable.

Proof . Since the Jacobian matrix at E_0 has a zero eigenvalue, one can not use the linear stability analysis method. To show that E_0 is unstable it is sufficient to show that not all trajectories starting in a small ball of radius $r > 0$ approaches E_0. For that one may take the starting point as $x(0) = x_0$ (such that $x_0 < 1 - k$), $y(0) = 0$ and $z(0) = 0$. Then $y(t) = 0$ and $z(t) = 0$ for all t. Now,

$$\frac{dx}{dt} = x(1 - x - k).$$

Then one gets

$$\frac{dx}{x(1 - x - k)} = dt.$$

On integration,

$$\frac{x}{1 - x - k} = Ce^{(1-k)t},$$

and thus one gets

$$x = \frac{1 - k}{1 + \frac{1}{C}e^{-(1-k)t}}.$$

where, C is a constant and it can be obtained by using the initial condition $x = x_0$ at $t = 0$. Using this condition we have $x_0 = \frac{1-k}{1+\frac{1}{C}}$ and $C = \frac{x_0}{1-k-x_0} > 0$ (assuming $k < 1$ always). Thus $x \geq \frac{1-k}{1+\frac{1}{C}}$ for all t. Thus $x(t)$ does not converge to 0 as $t \longrightarrow \infty$, which implies the proof of the theorem is complete. □

3.2 Dynamics around E_1

Theorem 3. E_1 is unstable.

Proof . To show that E_1 is unstable one may consider the trajectory with initial condition as $x(0) = 1 - k$, $y(0) = 0$ and $z(0) = z_0 > 0$. Then $y(t) = 0$ for all t. Now,

$$\begin{aligned} \frac{dz}{dt} &= \gamma_2 z(a_3 - a_4 z + x) \\ &\geq \gamma_2 z(a_3 - a_4 z), \end{aligned}$$

or,

$$\frac{dz}{z(a_3 - a_4 z)} \geq \gamma_2 dt.$$

On integration we get,

$$\frac{z}{a_3 - a_4 z} \geq \hat{C}e^{a_3\gamma_2 t}.$$

Hence we have

$$\begin{aligned} z \geq &\frac{a_3}{a_4 + \frac{1}{\hat{C}e^{a_3\gamma_2 t}}} \\ \geq &\frac{a_3}{a_4 + \frac{1}{\hat{C}}}, \end{aligned}$$

where $\hat{C}$ is an arbitrary positive constant. This implies that $z(t)$ does not converge to 0 as $t \longrightarrow \infty$. Hence $E_1 = (1 - k, 0, 0)$ is locally unstable in nature and the proof is finished. □

3.3 Dynamics around E_2

Theorem 4. E_2 is locally asymptotically stable if $\frac{a_3}{a_4} + k > 1$ and unstable if $\frac{a_3}{a_4} + k < 1$.

Proof . At the equilibrium $E_2 = (0, 0, \frac{a_3}{a_4})$ the Jacobian matrix is

$$J_2 = \begin{bmatrix} \left(1 - \frac{a_3}{a_4} - k\right) & 0 & 0 \\ 0 & -d_1\gamma_1 & 0 \\ \gamma_2\frac{a_3}{a_4} & 0 & -2\gamma_2 a_3 \end{bmatrix}.$$

The eigenvalues of J_2 are given by $\left(1 - \frac{a_3}{a_4} - k\right)$, $-d_1\gamma_1$ and $-2\gamma_2 a_3$. Then, by Routh-Hurwitz criteria E_2 is stable if $\frac{a_3}{a_4} + k > 1$ and unstable if $\frac{a_3}{a_4} + k < 1$. □

3.4 Dynamics around E_3

Theorem 5. E_3 is unstable.

Proof . The persistence of the species z implies that $E_3 = (d_1, 1 - k - d_1, 0)$ is locally unstable. □

3.5 Dynamics around E_4

At the equilibrium $E_4 = \left(\frac{a_4(1-k)-a_3}{1+a_4}, 0, \frac{(1+a_3)-k}{1+a_4}\right)$ the Jacobian matrix is

$$J_4 = \begin{bmatrix} -\frac{a_4(1-k)-a_3}{1+a_4} & -\frac{a_4(1-k)-a_3}{1+a_4} & -\frac{a_4(1-k)-a_3}{1+a_4} \\ 0 & \gamma_1\left(\frac{a_4(1-k)-a_3}{1+a_4} - d_1\right) & 0 \\ \gamma_2\left(\frac{(1+a_3)-k}{1+a_4}\right) & 0 & -2\gamma_2 a_4\left(\frac{(1+a_3)-k}{1+a_4}\right) \end{bmatrix} = \begin{bmatrix} J_{11} & J_{12} & J_{13} \\ J_{21} & J_{22} & J_{23} \\ J_{31} & J_{32} & J_{33} \end{bmatrix}.$$

Clearly, $J_{11} < 0$, $J_{12} < 0$, $J_{13} < 0$, $J_{21} = 0$, $J_{23} = 0$, $J_{31} > 0$, $J_{32} = 0$, $J_{33} < 0$.

Theorem 6. The feasible equilibrium point E_4 is locally asymptotically stable if $k > 1 - \frac{d_1(1+a_4)+a_3}{a_4}$ and unstable if $k < 1 - \frac{d_1(1+a_4)+a_3}{a_4}$.

Proof . The characteristic equation of J_4 is given as follows

$$\lambda^3 + A_1\lambda^2 + A_2\lambda + A_3 = 0, \tag{3.1}$$

where,

$$\begin{aligned} A_1 &= -(J_{11} + J_{22} + J_{33}), \\ A_2 &= J_{11}J_{22} + J_{11}J_{33} + J_{33}J_{22} - J_{12}J_{21} - J_{13}J_{31} - J_{23}J_{32}, \\ A_3 &= J_{11}J_{23}J_{32} + J_{12}J_{21}J_{33} + J_{13}J_{22}J_{31} - J_{11}J_{22}J_{33} - J_{12}J_{23}J_{31} - J_{13}J_{21}J_{32}. \end{aligned}$$

One may assume the feasibility conditions of E_4. Suppose $J_{22} < 0$, i.e., $\frac{a_4(1-k)-a_3}{1+a_4} < d_1$ or $k > 1 - \frac{d_1(1+a_4)+a_3}{a_4}$. Then $A_1 > 0$ and $A_3 > 0$. Now the expression for $A_1A_2 - A_3$ is given by

$$\begin{aligned} A_1A_2 - A_3 = &- J_{11}^2J_{22} - J_{11}^2J_{33} - J_{22}^2J_{33} - J_{22}^2J_{11} - J_{33}^2J_{11} - J_{33}^2J_{22} - 2J_{11}J_{22}J_{33} + \\ &J_{11}J_{13}J_{31} + J_{11}J_{12}J_{21} + J_{22}J_{12}J_{21} + J_{22}J_{23}J_{32} + J_{33}J_{23}J_{32} + J_{33}J_{13}J_{31} + \\ &J_{12}J_{23}J_{31} + J_{13}J_{21}J_{32}. \end{aligned}$$

In view of the signs of the Jacobian entries one gets $A_1A_2 - A_3 > 0$. Thus all the Routh-Hurwitz conditions hold. Hence, E_4 is locally asymptotically stable. If $k < 1 - \frac{d_1(1+a_4)+a_3}{a_4}$ then $J_{22} > 0$. So one obtains $A_3 < 0$, which implies that the characteristic Eq. (3.1) has at least a positive real root and thus E_4 is unstable. This completes the proof of the theorem.

□

3.6 Dynamics around the interior equilibrium point $\bar{E} = (\bar{x}, \bar{y}, \bar{z})$

At the equilibrium $\bar{E} = (\bar{x}, \bar{y}, \bar{z})$ the Jacobian matrix is

$$\bar{J} = \begin{bmatrix} -\bar{x} & -\bar{x} & -\bar{x} \\ \gamma_1\bar{y} & -\frac{a_1\gamma_1\bar{y}\bar{z}(\beta^2-\bar{y}^2)}{(\bar{y}^2+\beta^2)^2} & -\frac{\gamma_1 a_1\bar{y}^2}{\bar{y}^2+\beta^2} \\ \gamma_2\bar{z} & \frac{2a_2\gamma_2\beta^2\bar{y}\bar{z}}{(\bar{y}^2+\beta^2)^2} & -2\gamma_2 a_4\bar{z} \end{bmatrix} = \begin{bmatrix} J_{11} & J_{12} & J_{13} \\ J_{21} & J_{22} & J_{23} \\ J_{31} & J_{32} & J_{33} \end{bmatrix}.$$

Theorem 7. The interior equilibrium point $\bar{E} = (\bar{x}, \bar{y}, \bar{z})$ is locally asymptotically stable if $\beta > \bar{y}\sqrt{1 + \frac{2a_2\gamma 2\beta^2}{a_1\gamma_1\bar{y}^2}}$ and $a_4 > \frac{a_1}{2}$.

Proof . It is clear from the Jacobian matrix that $J_{11} < 0$, $J_{12} < 0$, $J_{13} < 0$, $J_{21} > 0$, $J_{23} < 0$, $J_{31} > 0$, $J_{32} > 0$, $J_{33} < 0$. Now suppose $\beta > \bar{y}\sqrt{1 + \frac{2a_2\gamma 2\beta^2}{a_1\gamma_1\bar{y}^2}}$ which implies that $\beta > \bar{y}$. Consequently, we have $J_{22} < 0$. Now

$$\begin{aligned} A_1 &= -(J_{11} + J_{22} + J_{33}), \\ A_2 &= J_{11}J_{22} + J_{11}J_{33} + J_{33}J_{22} - J_{12}J_{21} - J_{13}J_{31} - J_{23}J_{32}, \\ A_3 &= J_{11}J_{23}J_{32} + J_{12}J_{21}J_{33} + J_{13}J_{22}J_{31} - J_{11}J_{22}J_{33} - J_{12}J_{23}J_{31} - J_{13}J_{21}J_{32}, \end{aligned}$$

Clearly $A_1 > 0$. Also, $A_3 > 0$ provided that $J_{21}J_{33} - J_{31}J_{23} < 0$ which is true if $a_4 > \frac{a_1}{2}$. Now the expression for $A_1A_2 - A_3$ is given by $-J_{11}^2J_{22} - J_{11}^2J_{33} - J_{22}^2J_{33} - J_{22}^2J_{11} - J_{33}^2J_{11} - J_{33}^2J_{22} - 2J_{11}J_{22}J_{33} + J_{11}J_{13}J_{31} + J_{11}J_{12}J_{21} + J_{22}J_{12}J_{21} + J_{22}J_{23}J_{32} + J_{33}J_{23}J_{32} + J_{33}J_{13}J_{31} + J_{12}J_{23}J_{31} + J_{13}J_{21}J_{32}$.

In this expression all terms except $J_{13}J_{21}J_{32}$ are positive in sign. We see

$$J_{13}J_{21}J_{32} + J_{12}J_{21}J_{22} > 0 \text{ if } J_{13}J_{32} + J_{12}J_{22} > 0.$$

Now,

$$J_{13}J_{32} + J_{12}J_{22} > 0$$

implies that,

$$\frac{a_1\gamma_1\bar{x}\ \bar{y}\ \bar{z}(\beta^2 - \bar{y}^2)}{(\bar{y}^2 + \beta^2)^2} - \frac{2a_2\gamma_2\beta^2\bar{x}\ \bar{y}\ \bar{z}}{(\bar{y}^2 + \beta^2)^2} > 0$$

or,

$$a_1\gamma_1(\beta^2 - \bar{y}^2) - 2a_2\gamma_2\beta^2 > 0$$

or,

$$\beta > \bar{y}\sqrt{1 + \frac{2a_2\gamma 2\beta^2}{a_1\gamma_1\bar{y}^2}}.$$

Hence the proof is finished. □

3.7 Hopf-bifurcation around $\bar{E}$

In the subject of bifurcation one may investigate the topological change of behaviour of a dynamical system by reason of a small change in the system parameter. As $\bar{E}$ is the most important biological state of an interacting species ecosystem and the central focus of this model system lies on the linear prey harvesting term kx on the resource, one prefers k as the bifurcating parameter of the system around the interior equilibrium point $\bar{E}$.

Theorem 8. The system (2.2) exhibits a Hopf-bifurcation at $\bar{E} = (\bar{x}, \bar{y}, \bar{z})$ for a suitable value of $k = k^{[hb]}$ assuming the parametric restrictions for the local stability of $\bar{E}$.

Proof . By Routh-Hurwitz conditions, the necessary and sufficient conditions for all roots of the characteristic equation to have negative real part is $A_1 > 0$, $A_3 > 0$ and $A_1A_2 - A_3 > 0$ which is proved in the previous theorem. To have Hopf-bifurcation, one needs $A_1A_2 - A_3 = 0$ for some values of k say $k = k^{[hb]}$. Since $A_2 > 0$ at $k = k^{[hb]}$, for some $k > \epsilon > 0$ there is an interval $(k^{[hb]} - \epsilon, k^{[hb]} + \epsilon)$ in which $A_2 > 0$. Thus, for $k \in (k^{[hb]} - \epsilon, k^{[hb]} + \epsilon)$ the characteristic equation can not have real positive roots. Now $k = k^{[hb]}$, the characteristic equation becomes $(\lambda^2 + A_2)(\lambda + A_1) = 0$ which has three roots $\lambda_1 = i\sqrt{A_2}$, $\lambda_2 = -i\sqrt{A_2}$, $\lambda_3 = -A_1$. For $k \in (k^{[hb]} - \epsilon, k^{[hb]} + \epsilon)$, the roots can be written in general form as:

$$\begin{aligned}
\lambda_1 &= \alpha(k) + i\beta(k), \\
\lambda_2 &= \alpha(k) - i\beta(k), \\
\lambda_3 &= -A_1(k).
\end{aligned}$$

Now one may verify the transversality condition

$$Re\big(\frac{d\lambda_i}{dk}\big)_{k=k^{[hb]}} \neq 0 \qquad\qquad i = 1, 2.$$

Substituting $\lambda_j = \alpha(k) \pm i\beta(k)$, $j = 1, 2$ into the characteristic equation and differentiating with respect to k we obtain

$$\begin{aligned}
\omega(k)\dot{\alpha}(k) - \phi(k)\dot{\beta}(k) + \eta(k) = 0, \\
\phi(k)\dot{\alpha}(k) + \omega(k)\dot{\beta}(k) + \mu(k) = 0,
\end{aligned}$$

where,

$$\begin{aligned}
\omega(k) &= 3\alpha^2(k) + 2A_1(k)\alpha(k) + A_2(k) - 3\beta^2(k), \\
\phi(k) &= 6\alpha(k)\beta(k) + A_1(k)\beta(k), \\
\eta(k) &= \alpha^2(k)\dot{A}_1(k) + \dot{A}_2(k)\alpha(k) + \dot{A}_3(k) - \dot{A}_1(k)\beta^2(k), \\
\mu(k) &= 2\alpha(k)\beta(k)\dot{A}_1(k) + \dot{A}_2(k)\beta(k).
\end{aligned}$$

Since $\phi(k)\mu(k) + \omega(k)\eta(k) \neq 0$ we have,

$$\begin{aligned}
Re\big[\frac{d\lambda_j}{dk}\big]_{k=k^{[hb]}} &= -\frac{\phi\mu + \omega\eta}{\phi^2 + \omega^2} \\
&\neq 0, \qquad\qquad j = 1, 2,
\end{aligned}$$

and $\lambda_3(k) = -A_1(k) \neq 0$. Hence the proof is complete. □

4 Effect of the harvesting parameter k on species x, y and z

4.1 Effect on the species x

We have,

$$\frac{dx}{dt} = x\big(1 - x - y - z - k\big).$$

This implies,

$$\frac{dx}{dt} \leq x\big(1 - k - x\big)$$

or,

$$\big(\frac{1}{x} + \frac{1}{1 - k - x}\big)dx \leq (1 - k)dt.$$

On integration one gets

$$\begin{aligned}
x &\leq \frac{1 - k}{1 + Ae^{-(1-k)t}} \\
&\leq 1 - k
\end{aligned}$$

where A is a positive constant. Also, $\frac{1-k}{1+Ae^{-(1-k)t}} \to 1 - k$ as $t \to \infty$. Now if we take $k \to 1$, then the species $x(t)$ will extinct as $t \to \infty$.

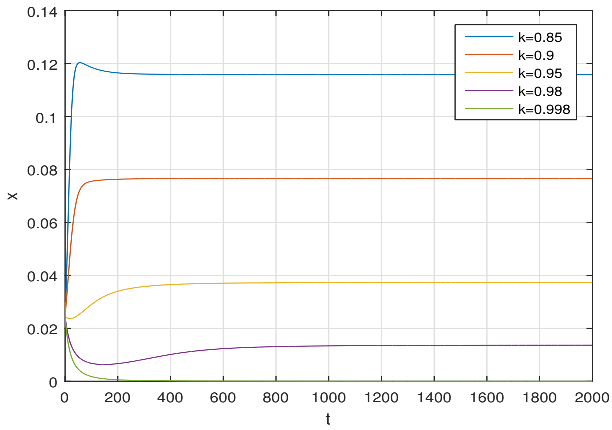


Figure 1: Time series plot of x for different values of k corresponding to the parameter values $a_1 = 1.1$, $a_2 = 0.01$, $a_3 = 0.01$, $a_4 = 3.7$, $d_1 = 0.15$, $\gamma_1 = 11$, $\gamma_2 = 0.1$, $\beta = 0.21$ and $x(0) = 0.03$, $y(0) = 0.4$, $z(0) = 0.03$.

4.2 Effect on the species z

As in the previous result we have seen that, $\liminf_{t\to\infty} z(t) \geq \frac{a_3}{a_4}$, for any value of k, $z(t)$ will not extinct i.e. as $t \to \infty$ the species z will exist in the system. This is biologically meaningful because z species is the generalist predator.

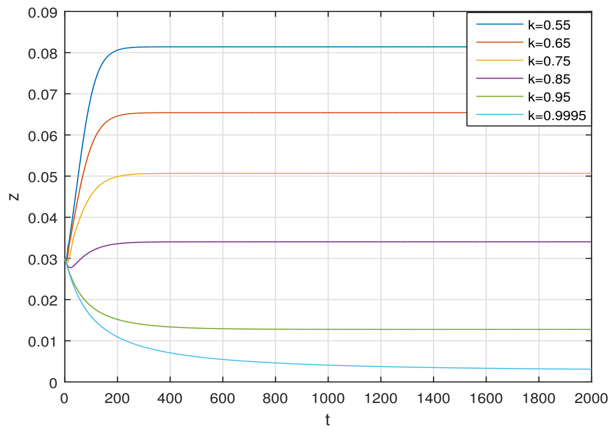


Figure 2: Time series plot of z for different values of k corresponding to the parameter values $a_1 = 1.1$, $a_2 = 0.01$, $a_3 = 0.01$, $a_4 = 3.7$, $d_1 = 0.15$, $\gamma_1 = 11$, $\gamma_2 = 0.1$, $\beta = 0.21$ and $x(0) = 0.03$, $y(0) = 0.4$, $z(0) = 0.03$.

4.3 Effect on the species y

We have

$$\frac{dy}{dt} = \gamma_1 y\big(x - \frac{a_1 yz}{y^2 + \beta^2} - d_1\big).$$

Since all the species x, y, z are shown to be bounded, $\exists M > 0$ such that $y^2 + \beta^2 \leq M$. Also we have $z(t) \geq \frac{a_3}{a_4}$ for all t and $x(t) \leq 1 - k$ for all t. Combining all these we have

$$\begin{aligned}\frac{dy}{dt} &\leq \gamma_1 y\big(1 - k - \frac{a_1 a_3}{M a_4} y\big)\\ &\leq \gamma_1 y\big(1 - k - Ny\big),\end{aligned}$$

where $N = \frac{a_1 a_3}{M a_4}$,
or,

$$(\frac{1}{y} + \frac{N}{1-k-Ny})dy \leq \gamma_1(1-k)dt.$$

On integration one gets,

$$y \leq \frac{1-k}{N + Ae^{-\gamma_1(1-k)t}}$$

where, $A > 0$ is a constant of integration. This shows that $y(t) \to 0$ as $t \to \infty$ and $k \to 1$. This implies that if k approaches to 1, then $y(t)$ goes to extinction as $t \to \infty$.

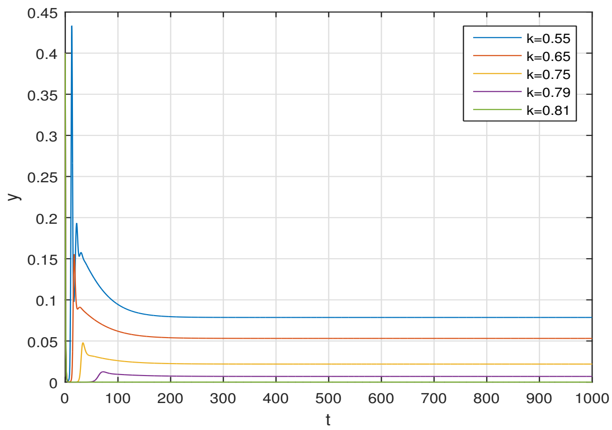


Figure 3: Time series plot of y for different values of k corresponding to the parameter values $a_1 = 1.1$, $a_2 = 0.01$, $a_3 = 0.01$, $a_4 = 3.7$, $d_1 = 0.15$, $\gamma_1 = 11$, $\gamma_2 = 0.1$, $\beta = 0.21$ and $x(0) = 0.03$, $y(0) = 0.4$, $z(0) = 0.03$.

5 Bionomic equilibrium

The term bionomic equilibrium [12] is developed from the concept of biological equilibrium and economic equilibrium. The economic equilibrium occurs when TR (total revenue obtained by selling the harvested thing) equals TC (the total cost for effort devoted to harvesting).
Let p_1 = price per unit biomass of x;
q_1 = harvesting cost per unit effort of x.
The economic rent $N = TR - TC = (p_1 x - q_1)k$.

So the bionomic equilibrium is obtained from the solution of the system

$$x\big(1 - x - y - z - k\big) = 0, \tag{5.1a}$$

$$\gamma_1 y\big(x - \frac{a_1 y z}{y^2 + \beta^2} - d_1\big) = 0, \tag{5.1b}$$

$$\gamma_2 z\big(a_3 - a_4 z + x + \frac{a_2 y^2}{y^2 + \beta^2}\big) = 0, \tag{5.1c}$$

$$(p_1 x - q_1)k = 0. \tag{5.1d}$$

We have no interest in the case $k = 0$, so we assume $k \neq 0$. Then, from the fourth equation $x = \frac{q_1}{p_1}$.
Now if $y = 0$, then from the third equation $z = 0$ or $z = \frac{1}{a_4}\big(a_3 + \frac{q_1}{p_1}\big)$.
If $z = 0$ then $y = 0$. Now $x = \frac{q_1}{p_1}$, $y = 0$, $z = 0$ implies that $k = \frac{p_1 - q_1}{p_1}$.
If $x = \frac{q_1}{p_1}$, $y = 0$, $z = \frac{1}{a_4}\big(a_3 + \frac{q_1}{p_1}\big)$ then $k = \frac{p_1 a_4 - q_1 a_4 - p_1 a_3 - q_1}{p_1 a_4}$.
Thus we have the following bionomic equilibrium points (x, y, z, k)
(i) $\big(\frac{q_1}{p_1}, 0, 0, \frac{p_1 - q_1}{p_1}\big)$ provided $p_1 > q_1$.

(ii) $\left(\frac{q_1}{p_1}, 0, \frac{1}{a_4}\left(a_3 + \frac{q_1}{p_1}\right), \frac{p_1a_4 - q_1a_4 - p_1a_3 - q_1}{p_1a_4}\right)$ provided $p_1a_4 - q_1a_4 - p_1a_3 - q_1 > 0$;
and the interior equilibrium which can be obtained by solving the following system,

$$\big(1 - x - y - z - k\big) = 0, \tag{5.2a}$$

$$\big(x - \frac{a_1yz}{y^2 + \beta^2} - d_1\big) = 0, \tag{5.2b}$$

$$\big(a_3 - a_4z + x + \frac{a_2y^2}{y^2 + \beta^2}\big) = 0, \tag{5.2c}$$

$$(p_1x - q_1) = 0. \tag{5.2d}$$

We then have $x_\infty = \frac{q_1}{p_1}$ and $z_\infty = \frac{x_\infty - d_1}{a_1y_\infty}(y_\infty^2 + \beta^2)$ provided $d_1 < \frac{q_1}{p_1}$, where y_∞ is a positive root of

$$a_1a_3y - a_4(x_\infty - d_1)(y^2 + \beta^2) + a_1x_\infty y + \frac{a_1a_2y^3}{y^2 + \beta^2} = 0,$$

which can be written in the form

$$ay^4 + by^3 + cy^2 + dy + e = 0, \tag{5.3}$$

where

$$\begin{aligned}
a &= -a_4(x_\infty - d_1) < 0,\\
b &= a_1a_3 + a_1x_\infty + a_1a_2 > 0,\\
c &= -2\beta^2a_4(x_\infty - d_1) < 0,\\
d &= a_1a_3\beta^2 + a_1x_\infty\beta^2 > 0,\\
e &= -a_4\beta^2(x_\infty - d_1) < 0.
\end{aligned}$$

Multiplying both site of (5.3) by a we get,

$$a^2y^4 + aby^3 + acy^2 + ady + ae = 0.$$

Let the left hand expression be expressed as the difference of two squares of the form $(ay^2 + 2by + \lambda)^2 - (my + n)^2$. Comparing with the left hand expression of (5.3) one gets,

$$\begin{aligned}
6ac &= 4b^2 + 2a\lambda - m^2,\\
4ad &= 4b\lambda - 2mn,\\
ae &= \lambda^2 - n^2.
\end{aligned}$$

Eliminating m, n we get,

$$4(b\lambda - ad)^2 = (2a\lambda + 4b^2 - 6ac)(\lambda^2 - ae),$$

which gives

$$2a\lambda^3 - 6ac\lambda^2 + (8abd - 2a^2e)\lambda + (6a^2ce - 4ab^2e - 4a^2d^2) = 0. \tag{5.4}$$

Now,

$$\begin{aligned}
4abd - a^2e &= (x_\infty - d_1)a_4\beta^2\left[a_4^2(x_\infty - d_1)^2\beta^2 - 4a_1^2(a_3 + x_\infty + a_2)(a_3 + x_\infty)\right]\\
&> 0,
\end{aligned}$$

if

$$a_4^2(x_\infty - d_1)^2\beta^2 > 4a_1^2(a_3 + x_\infty + a_2)(a_3 + x_\infty),$$

or,

$$a_4^2(\frac{q_1}{p_1} - d_1)^2\beta^2 > 4a_1^2(a_3 + \frac{q_1}{p_1} + a_2)(a_3 + \frac{q_1}{p_1}).$$

Also,

$$\begin{aligned}6a^2ce - 4ab^2e - 4a^2d = 2(x_\infty - d_1)^2\beta^2a_4^2\big[&6a_4^2\beta^4(x_\infty - d_1)^2 - 2a_1^2(a_3 + x_\infty + a_2)^2\beta^2 - \\ &2a_1^2\beta^2(x_\infty + a_3)^2\big] \\ > &0,\end{aligned}$$

provided,

$$3a_4^2\beta^2(x_\infty - d_1)^2 > \big[a_1^2(a_3 + x_\infty + a_2)^2 - (x_\infty + a_3)^2\big].$$

Then (5.4) has at least one negative root say $\lambda = -\lambda^*$. The relation $n^2 = \lambda^2 - ae$ implies that $|n| < |\lambda^*|$. So the solution of (5.3) is given by the roots of the quadratic equations

$$\begin{aligned} ay^2 + (2b + m)y + (-\lambda^* + n) = 0, \\ and \;\; ay^2 + (2b - m)y + (-\lambda^* - n) = 0.\end{aligned}$$

Here, both the equations have either two positive solutions or no solution. The first quadratic equation has two positive solutions if

$$(2b + m) > 2\sqrt{a(-\lambda^* + n)} > 0,$$

and the second equation has two positive solutions if

$$(2b - m) > 2\sqrt{a(-\lambda^* - n)},$$

or,

$$(2b + m) > 2\big[\sqrt{a(-\lambda^* - n)} + m\big].$$

Hence we have the following theorem:

Theorem 9. The interior bionomic equilibrium points are $(x, y, z, k) = \big(x_\infty, y_\infty^i, z_\infty^i, 1 - x_\infty - y_\infty^i - z_\infty^i\big)$ provided $\big(1 - x_\infty - y_\infty^i - z_\infty^i > 0\big)$ for $i = 1, 2, 3, 4$ if the following conditions hold:

$$\begin{aligned} (i)\;\; & q_1 > p_1d_1 \\ (ii)\;\; & a_4^2(\frac{q_1}{p_1} - d_1)^2\beta^2 > 4a_1^2(a_3 + \frac{q_1}{p_1} + a_2)(a_3 + \frac{q_1}{p_1}) \\ (iii)\;\; & 3a_4^2\beta^2(x_\infty - d_1)^2 > \big[a_1^2(a_3 + x_\infty + a_2)^2 - (x_\infty + a_3)^2\big] \\ (iv)\;\; & (2b + m) > max\big[2\sqrt{a(-\lambda^* + n)}, 2(\sqrt{a(-\lambda^* - n)} + m)\big] \end{aligned}$$

where $x_\infty = \frac{q_1}{p_1}$, y_∞^i are the positive roots of (5.3) and $z_\infty^i = \frac{x_\infty - d_1}{a_1y_\infty^i}\big((y_\infty^i)^2 + \beta^2\big)$.

6 Optimal harvesting policy

To obtain optimal harvesting policy [6, 10], one may consider the present value J of a continuous time-stream of revenue

$$J = \int_0^\infty e^{-\delta t}\big((p_1x - q_1)k\big)(t)dt,$$

where δ denotes the instantaneous annual rate of discount and k is the control variable. The objective is to maximize J subject to the state equations

$$\begin{aligned} \frac{dx}{dt} &= x\big(1 - x - y - z - k\big), \\ \frac{dy}{dt} &= \gamma_1y\big(x - \frac{a_1yz}{y^2 + \beta^2} - d_1\big), \\ \frac{dz}{dt} &= \gamma_2z\big(a_3 - a_4z + x + \frac{a_2y^2}{y^2 + \beta^2}\big), \end{aligned}$$

by invoking Pontryagin's maximum principle. The Hamiltonian of the corresponding problem is

$$\begin{aligned}H =&e^{-\delta t}(p_1x-q_1)k+\lambda_1 x\big(1-x-y-z-k\big)+\lambda_2\gamma_1 y\big(x-\frac{a_1yz}{y^2+\beta^2}-d_1\big)+\\&\lambda_3\gamma_2 z\big(a_3-a_4z+x+\frac{a_2y^2}{y^2+\beta^2}\big),\end{aligned}$$

where λ_1, λ_2, λ_3 are adjoint variables. For optimality the necessary condition is

$$\frac{\partial H}{\partial k}=0,$$

i.e.,

$$e^{-\delta t}\big(p_1x-q_1\big)-\lambda_1 x=0. \tag{6.1}$$

The corresponding adjoint equations are

$$\begin{aligned}\frac{d\lambda_1}{dt}&=-\frac{\partial H}{\partial x}=\lambda_1(-1+2x+y+z+k)+e^{-\delta t}p_1k+\lambda_2\gamma_1 y+\lambda_3\gamma_2 z,\\ \frac{d\lambda_2}{dt}&=-\frac{\partial H}{\partial y}=-\lambda_1 x-\lambda_2\gamma_1\big[y\frac{\beta^2-y^2}{y^2+\beta^2}(-a_1z)+(x-\frac{a_1yz}{y^2+\beta^2}-d_1)\big]-\lambda_3\gamma_2 z a_2\frac{\beta^2-y^2}{y^2+\beta^2},\\ \frac{d\lambda_3}{dt}&=-\frac{\partial H}{\partial z}=-\lambda_1 x-\lambda_2\frac{\gamma_1 y^2 a_1}{y^2+\beta^2}-\lambda_3\gamma_2\big[-a_4z+(a_3-a_4z+x+\frac{a_2y^2}{y^2+\beta^2})\big],\end{aligned} \tag{6.2}$$

that is,

$$\begin{bmatrix}\dot\lambda_1\\ \dot\lambda_2\\ \dot\lambda_3\end{bmatrix}=\begin{bmatrix}a_{11}&a_{12}&a_{13}\\ a_{21}&a_{22}&a_{23}\\ a_{31}&a_{32}&a_{33}\end{bmatrix}\begin{bmatrix}\lambda_1\\ \lambda_2\\ \lambda_3\end{bmatrix}+\begin{bmatrix}e^{-\delta t}p_1k\\ 0\\ 0\end{bmatrix}, \tag{6.3}$$

where
$a_{11}=(-1+2x+y+z+k)$, $a_{12}=\gamma_1 y$, $a_{13}=\gamma_2 z$, $a_{21}=-x$, $a_{22}=-\gamma_1\big[y\frac{\beta^2-y^2}{y^2+\beta^2}(-a_1z)+(x-\frac{a_1yz}{y^2+\beta^2}-d_1)\big]$, $a_{23}=-\gamma_2 z a_2\frac{\beta^2-y^2}{y^2+\beta^2}$, $a_{31}=-x$, $a_{32}=-\frac{\gamma_1y^2a_1}{y^2+\beta^2}$, $a_{33}=-\gamma_2\big[-a_4z+(a_3-a_4z+x+\frac{a_2y^2}{y^2+\beta^2})\big]$. Now we assume that the solution of (6.3) is of the form:

$$\lambda_1=e^{-\delta t}M_1(x,y,z,t),\ \lambda_2=e^{-\delta t}M_2(x,y,z,t),\ \lambda_3=e^{-\delta t}M_3(x,y,z,t),$$

where M_1, M_2, M_3 be continuously differentiable functions. Then we have

$$\begin{aligned}-\delta M_1&=a_{11}M_1+a_{12}M_2+a_{13}M_3+p_1k,\\ -\delta M_2&=a_{21}M_1+a_{22}M_2+a_{23}M_3,\\ -\delta M_3&=a_{31}M_1+a_{32}M_2+a_{33}M_3.\end{aligned}$$

This can be put in the matrix form given by

$$\begin{bmatrix}a_{11}+\delta&a_{12}&a_{13}\\ a_{21}&a_{22}+\delta&a_{23}\\ a_{31}&a_{32}&a_{33}+\delta\end{bmatrix}\begin{bmatrix}M_1\\ M_2\\ M_3\end{bmatrix}=\begin{bmatrix}-p_1k\\ 0\\ 0\end{bmatrix}.$$

Let

$$A=\begin{bmatrix}a_{11}+\delta&a_{12}&a_{13}\\ a_{21}&a_{22}+\delta&a_{23}\\ a_{31}&a_{32}&a_{33}+\delta\end{bmatrix}.$$

Then

$$|A| = \delta^3 + (a_{11} + a_{22} + a_{33})\delta^2 + (a_{11}a_{33} + a_{22}a_{33} + a_{11}a_{22} - a_{13}a_{31} - a_{12}a_{21} - a_{23}a_{32})\delta \\ + (a_{11}a_{22}a_{33} - a_{11}a_{23}a_{32} - a_{12}a_{21}a_{33} + a_{12}a_{31}a_{23} + a_{13}a_{21}a_{32} - a_{13}a_{31}a_{22}).$$

which is not identically equal to 0, so $|A| \neq 0$. Hence A^{-1} exists. Now

$$adj(A) = \\ \begin{bmatrix} (a_{22}+\delta)(a_{33}+\delta) - a_{23}a_{32} & (a_{13}a_{32} - a_{12}a_{33} - a_{12}\delta) & (a_{12}a_{23} - a_{13}a_{22} - \delta a_{13}) \\ (a_{23}a_{31} - a_{21}a_{33} - \delta a_{21}) & (a_{11}+\delta)(a_{33}+\delta) - a_{13}a_{31} & (a_{13}a_{21} - a_{23}a_{11} - a_{23}\delta) \\ (a_{21}a_{32} - a_{31}a_{22} - a_{31}\delta) & (a_{12}a_{31} - a_{11}a_{32} - a_{32}\delta) & (a_{11}+\delta)(a_{22}+\delta) - a_{12}a_{21} \end{bmatrix}.$$

Hence, the solution for M_1, M_2 and M_3 is given by

$$\begin{bmatrix} M_1 \\ M_2 \\ M_3 \end{bmatrix} = \frac{adj(A)}{|A|} \begin{bmatrix} -p_1 k \\ 0 \\ 0 \end{bmatrix}. \tag{6.4}$$

Solving (6.4) yields

$$M_1 = \frac{\big((a_{22}+\delta)(a_{33}+\delta) - a_{23}a_{32}\big)(-p_1 k)}{|A|}, \\ M_2 = \frac{(a_{23}a_{31} - a_{21}a_{33} - \delta a_{21})(-p_1 k)}{|A|}, \\ M_3 = \frac{(a_{21}a_{32} - a_{31}a_{22} - a_{31}\delta)(-p_1 k)}{|A|}.$$

Then the optimality condition (6.1) takes the form

$$p_1 x - q_1 - \frac{\big((a_{22}+\delta)(a_{33}+\delta) - a_{23}a_{32}\big)(-p_1 k)}{|A|} x = 0.$$

Thus the interior optimal solution (x, y, z, k) for a given value of δ can be found by solving the system of equations given by

$$\begin{aligned} &\big(1 - x - y - z - k\big) = 0, \\ &\big(x - \frac{a_1 y z}{y^2 + \beta^2} - d_1\big) = 0, \\ &\big(a_3 - a_4 z + x + \frac{a_2 y^2}{y^2 + \beta^2}\big) = 0, \\ &p_1 x - q_1 - \frac{\big((a_{22}+\delta)(a_{33}+\delta) - a_{23}a_{32}\big)(-p_1 k)}{|A|} x = 0. \end{aligned} \tag{6.5}$$

Example: Let $a_1 = 1.1$, $a_2 = 0.01$, $a_3 = 0.01$, $a_4 = 3.7$, $d_1 = 0.15$, $\gamma_1 = 11$, $\gamma_2 = 0.1$, $\beta = 0.21$, $x(0) = 0.03$, $y(0) = 0.4$, $z(0) = 0.05$, $\delta = 0.3$, $p_1 = 2.5$, $q_1 = 0.4$. Then solving the above system using MAPLE, we get the interior optimal solutions $(0.1808, 0.0242, 0.0516, 0.7434)$ and $(0.3693, 0.4201, 0.1047, 0.1060)$.

7 Numerical study

The present numerical simulation bears the potential for the validity of the theory carried out in this investigation by way of showing a close agreement between experiment and theory. We perform numerical simulation to validate our analytical findings of the previous sections by making use of the appropriate computing software MATLAB and MAPLE. We consider three sets of parameter values provided in the following Table 2.

	a_1	a_2	a_3	a_4	d_1	γ_1	γ_2	β	k
Set I	1.1	0.01	0.01	3.7	0.15	11	0.1	0.21	0.45
Set I I	1.1	0.01	1.5	1.7	0.15	11	0.1	0.21	0.45
Set I I I	1.1	0.01	1.1	2.2	0.15	11	0.1	0.21	0.45

Table 2: A particular set of system parameter values

The unstable behaviour of E_0 is shown in the Figure 4. For the parameter values as in Set I, $E_1 = (0.55, 0, 0)$ and

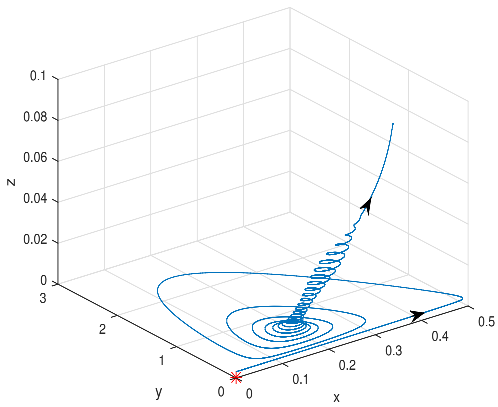


Figure 4: Unstable behaviour of the trivial equilibrium E_0 for the parameter values taken from Set I and the initial values $x(0) = 0.002$, $y(0) = 0.004$, $z(0) = 0.003$.

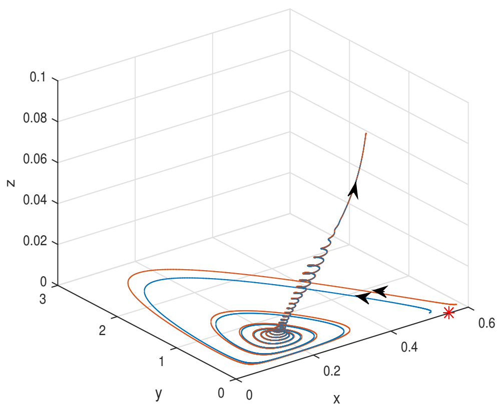


Figure 5: Unstable behaviour of the equilibrium E_1 for the parameter values taken from Set I and the initial values $x(0) = 0.5$, $y(0) = 0.004$, $z(0) = 0.003$ and $x(0) = 0.57$, $y(0) = 0.004$, $z(0) = 0.003$.

in concert with the theory it is always unstable. The unstable behaviour of E_1 is shown in the Figure 5. From the theoretical findings, E_2 is locally stable if $\frac{a_3}{a_4} + k > 1$ and unstable if $\frac{a_3}{a_4} + k < 1$. Here the parameter values in Set I satisfy the condition $\frac{a_3}{a_4} + k = 0.453 < 1$ and hence for this set of parameter values E_2 is locally unstable. On the other hand the parameter values in Set II satisfy the condition $\frac{a_3}{a_4} + k = 1.33 > 1$ and hence for this set of parameter values E_2 is locally stable. According to the theory we have E_3 is always unstable. The local unstable behaviour is shown in the Figure 8. The condition for stability of the equilibrium point E_4 is $k > 1 - \frac{d_1(1+a_4)+a_3}{a_4}$. If we choose the parameter values from the Set III, then the condition for stability holds and hence $E_4 = (0.0344, 0, 0.5156)$ is stable. The behaviour around E_4 is shown in the Figure 9.

If we choose the parameter values from Set I, then the interior equilibrium point $\bar{E} = (0.35079, 0.101193, 0.09802)$ exists uniquely. Also this set of parameter values satisfies the condition for stability $\beta > \bar{y}\sqrt{1 + \frac{2a_2\gamma_2\beta^2}{a_1\gamma_1\bar{y}^2}}$ and $a_4 > \frac{a_1}{2}$. The stability behaviour around $\bar{E}$ is shown in the Figures 10 and 11.

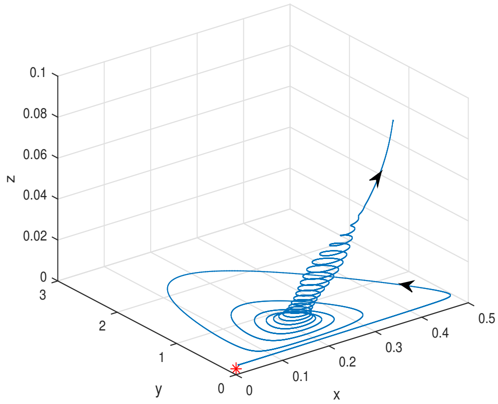


Figure 6: Unstable behaviour of the equilibrium E_2 for the parameter values taken from Set I and the initial values $x(0) = 0.005$, $y(0) = 0.006$, $z(0) = 0.44$.

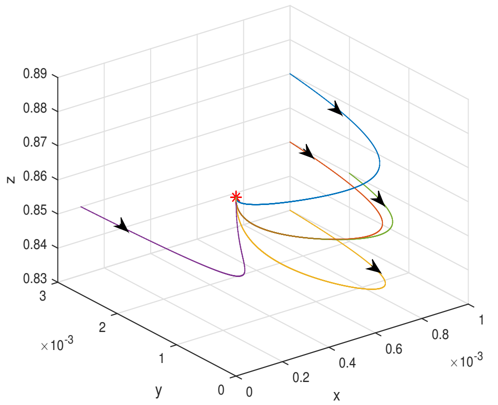


Figure 7: Stable behaviour of the equilibrium E_2 for the parameter values taken from Set II for different initial values.

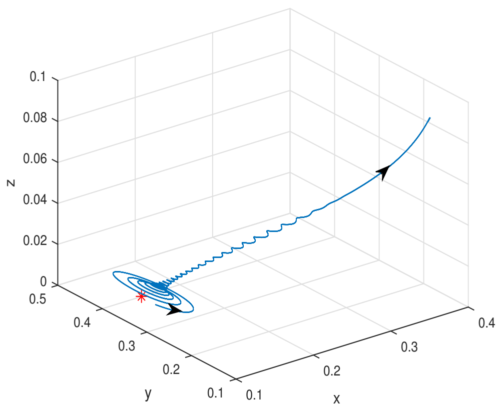


Figure 8: Unstable behaviour of the equilibrium $E_3 = (0.15, 0.4, 0)$ for the parameter values taken from Set I and the initial values $x(0) = 0.14$, $y(0) = 0.35$, $z(0) = 0.003$.

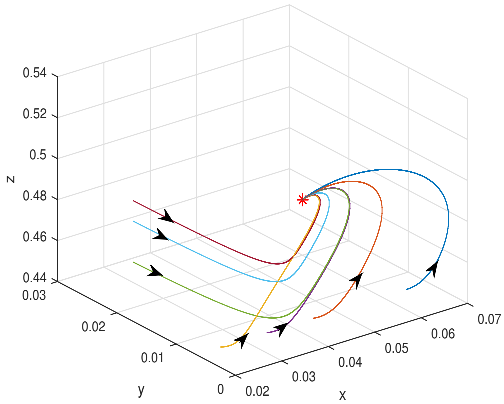


Figure 9: Stable behaviour of the equilibrium $E_4 = (0.0344, 0, 0.5156)$ for the parameter values taken from Set III and for different initial values.

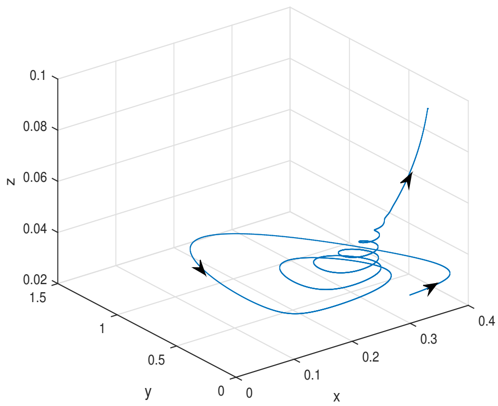
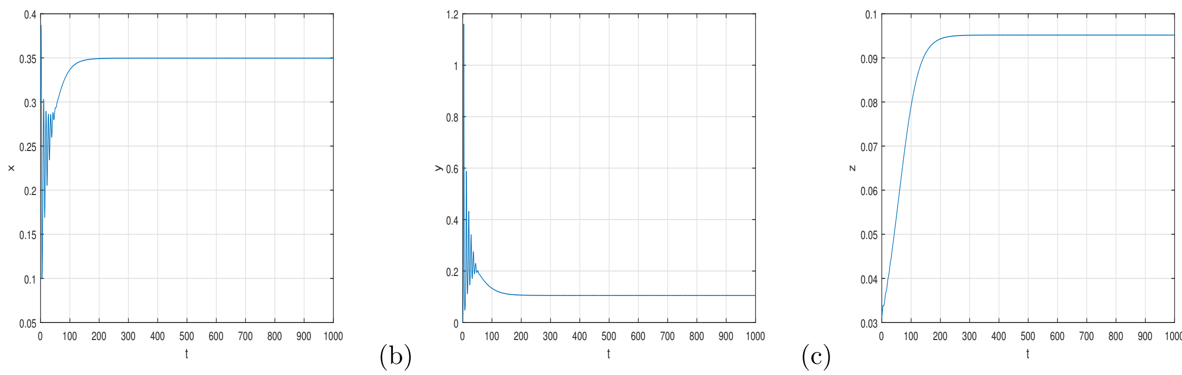


Figure 10: Stable behaviour of the equilibrium point $\bar{E}$ for the parameter values taken from Set I and the initial values $x(0) = 0.3$, $y(0) = 0.003$, $z(0) = 0.031$.



(a) (b) (c)

Figure 11: Time series plot of the system around the equilibrium point $\bar{E}$ for the parameter values taken from Set I and the initial values $x(0) = 0.3$, $y(0) = 0.003$, $z(0) = 0.031$.

One may notice the occurrence of Hopf-bifurcation around the interior equilibrium point $\bar{E}$ with respect to the bifurcating parameter k. For numerical confirmation one may keep the fixed set of parameter values other than k as in Set I. Then a Hopf-bifurcation takes place near the interior equilibrium point for the value of the bifurcation parameter $k = 0.2276$ maintaining the values of other parameters fixed. The relevant bifurcation diagram relating to the system parameter k is exposed in the Figure 12. The bifurcation diagram with respect to the significant parameter β in Figure 13 demonstrates that there is a specific interval of β where the system provides periodic solution and outside that interval the system is in the stable platform. For bifurcation diagram of the system (2.2) presented in Figure 12, the successive maxima of x, y and z in the ranges $[0.0, 1.0]$, $[0.0, 7.0]$ and $[0.02, 0.14]$ respectively as a function of k in the range $0.0 \leq k \leq 0.9$ and the other parameters are provided in the figure caption. The other bifurcation diagram is offered in Figure 13, the successive maxima of x, y and z in the ranges $[0.05, 0.7]$, $[0.0, 1.8]$ and $[0.05, 0.18]$ respectively as a function of β in the range $0.0 \leq \beta \leq 0.9$ and the other parameters are provided in the figure caption.

The oscillating behaviour of the species x, y, z and the phase diagram as well is revealed in the Figures 14 and 15. The phase diagram, as shown in Figure 15 is a limit cycle. It is observed that for the feasible Set I of parameter values, model system (2.2) have asymptotically stable behaviour with the system parameter $k = 0.24$ in the Figures 16 and 17. As a consequence taking k as control parameter it is feasible to derive the intraguild predator-prey system to required equilibrium point and to avoid the cyclic behaviour of the system. It is worth mentioning that for the system parameter values $a_1 = 0.1$, $a_2 = 0.01$, $a_3 = 0.01$, $a_4 = 0.97$, $d_1 = 0.15$, $\gamma_1 = 11$, $\gamma_2 = 0.01$, $\beta = 0.21$ and $k = 0.2$, model system (2.2) have strange limit cycle in the Figure 18. The strange attractor in xyz-view of the model system for the system parameter values $a_1 = 0.1$, $a_2 = 0.01$, $a_3 = 0.01$, $a_4 = 0.7$, $d_1 = 0.15$, $\gamma_1 = 12$, $\gamma_2 = 0.01$, $\beta = 0.21$ and $k = 0.2$ is also presented in the Figure 19.

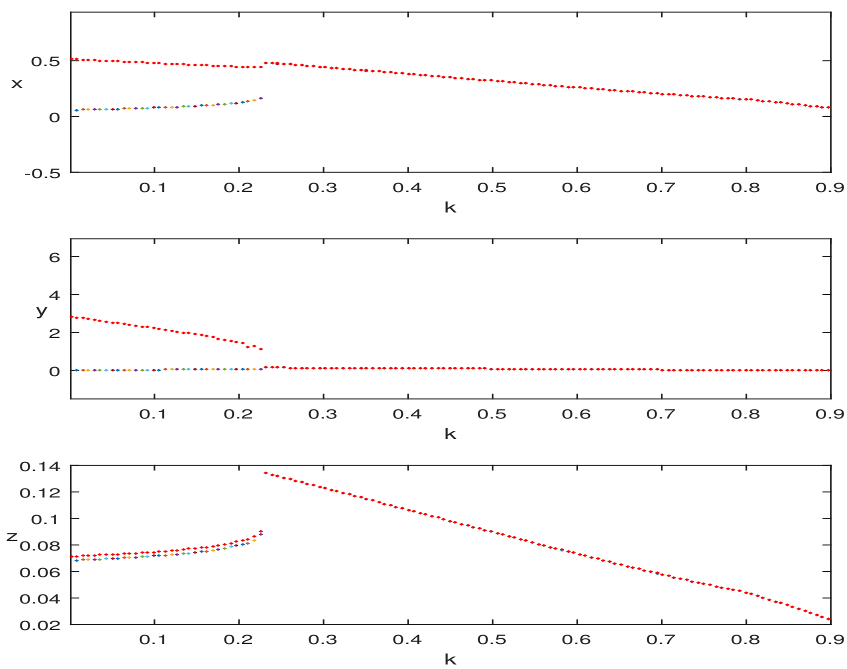


Figure 12: Bifurcation diagrams for all the interacting species with respect to k corresponding to the parameter values $a_1 = 1.1$, $a_2 = 0.01$, $a_3 = 0.01$, $a_4 = 3.7$, $d_1 = 0.15$, $\gamma_1 = 11$, $\gamma_2 = 0.1$ and $\beta = 0.21$ with initial value $x(0) = 0.03$, $y(0) = 0.4$, $z(0) = 0.05$.

8 Concluding remarks

The work undertaken in the present article copes with the response of the dynamical system comprising two prey and one generalist IG predator species. A general structure of the system is initiated with the use of different functional responses suitable for the type of interactions between the species. The stability characteristics of the proposed model system are examined in detail analytically with special attention to the boundary equilibrium points. The stability properties of the coexistence equilibrium positions of the system are also explored. It is interesting to perceive from

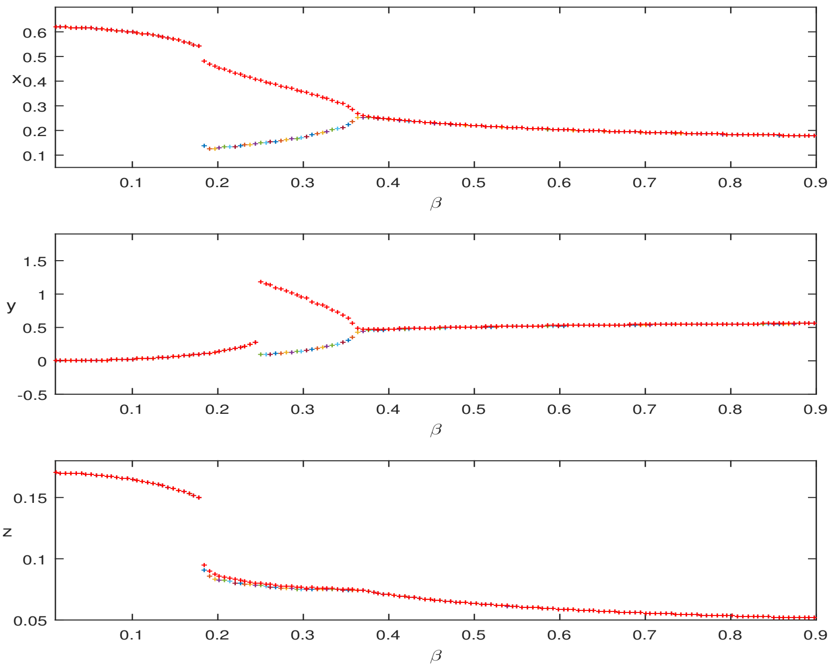


Figure 13: Bifurcation diagrams for all the interacting species with respect to β corresponding to the parameter values $a_1 = 1.1$, $a_2 = 0.01$, $a_3 = 0.01$, $a_4 = 3.7$, $d_1 = 0.15$, $\gamma_1 = 11$, $\gamma_2 = 0.1$ and $k = 0.21$.

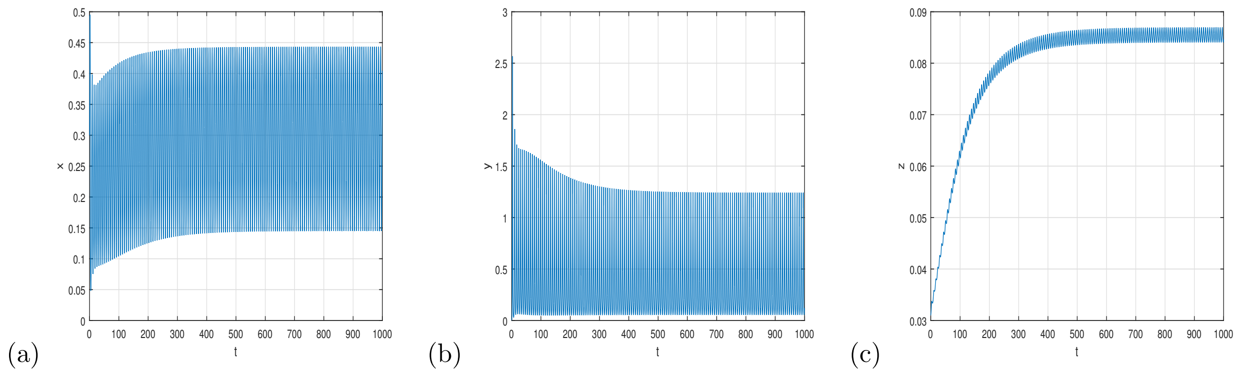


Figure 14: Oscillating behaviour of the system for $k = 0.22$ and the values of other parameters are taken from Set I with initial conditions $x(0) = 0.3$, $y(0) = 0.003$, $z(0) = 0.031$.

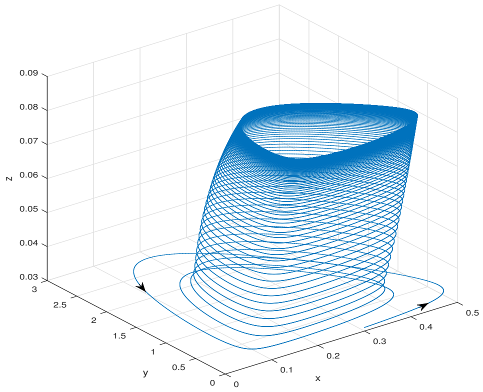
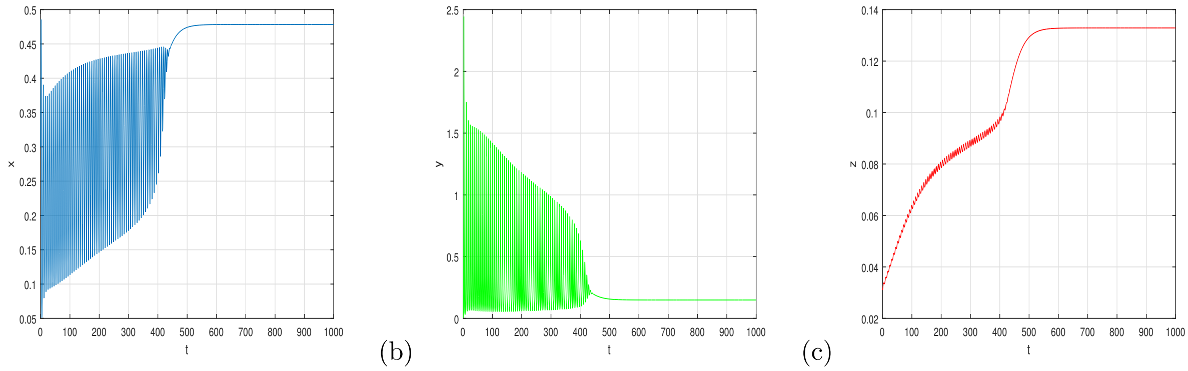


Figure 15: Phase portrait of the system for the parameter values $k = 0.22$ and the values of other parameters are taken from Set I.



(a) (b) (c)

Figure 16: Time series plot of the system for the parameter values $k = 0.24$ and the values of other parameters are taken from Set I with $x(0) = 0.3$, $y(0) = 0.003$, $z(0) = 0.031$.

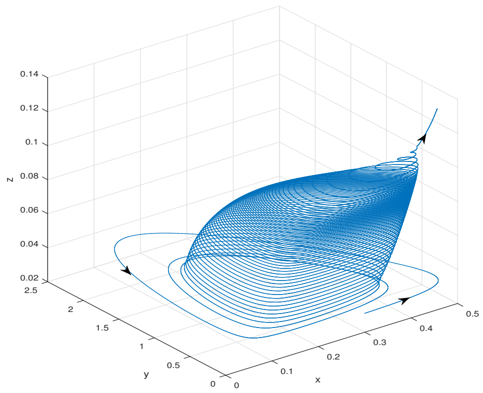


Figure 17: Phase portrait of the system for the parameter values $k = 0.24$ and the values of other parameters are taken from Set I.

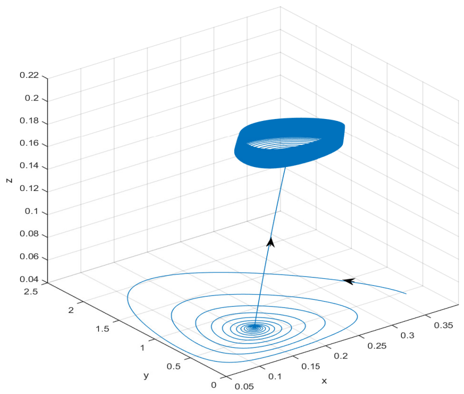


Figure 18: Strange limit cycle for the parameters $a_1 = 0.1$, $a_2 = 0.01$, $a_3 = 0.01$, $a_4 = 0.97$, $d_1 = 0.15$, $\gamma_1 = 11$, $\gamma_2 = 0.01$, $\beta = 0.21$ and $k = 0.2$ with initial value $x(0) = 0.37$, $y(0) = 0.45$, $z(0) = 0.04$.

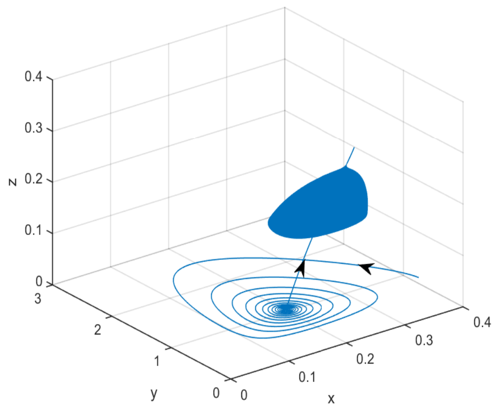


Figure 19: Strange attractor [13] of the system for the parameters $a_1 = 0.1$, $a_2 = 0.01$, $a_3 = 0.01$, $a_4 = 0.7$, $d_1 = 0.15$, $\gamma_1 = 12$, $\gamma_2 = 0.01$, $\beta = 0.21$ and $k = 0.2$ with initial value $x(0) = 0.37$, $y(0) = 0.45$, $z(0) = 0.04$.

numerical simulation that the system reveals both the stability and the bifurcation as well around the coexistence equilibrium with reference to the resource harvesting parameter. One may also note that in the event of gradual increase of resource harvesting, it contributes to extinction of the resource and the IG prey but the IG predator survives due to resource harvesting. This observation agrees well with the natural ecosystem.

The prime objective of the present three-dimensional IG predation model is to investigate the influence of harvesting on the equilibrium abundances of IG predator species. One may conclude from the contemporary study that prey harvesting can also destabilize the tri-trophic predator-prey interacting system in presence of intraguild mechanism. By and large, it may be established in the undergoing modelling framework that resource harvesting is a key survival strategy for resource (prey) in the presence of generalist IG predator. The harvesting parameter may be treated as a controlling parameter by virtue of which the system switches from stable to limit cycle around its interior equilibrium position. A sufficient condition is derived for the existence of the interior bionomic equilibrium point. The optimal solution for the optimal harvesting policy based on the derived system of equations is not ruled out, however, from the present pursuit.

In the future, one may extend this research work in several ways, e.g., the harvesting policy can be divided into two categories-linear and nonlinear groups. Constant harvesting effort could significantly impact the intraguild (IG) predation dynamics. Incorporating nonlinear harvesting effort in our model system could be another exciting research. The inclusion of self-diffusion in the proposed intraguild (IG) predation model may exhibit complex spatiotemporal pattern dynamics. Different kinds of simulated Turing patterns may be interpreted depending on the local system's ecological parameters and diffusion coefficients [24, 25, 26, 27]. One may extend or modelled this work further by considering environmental fluctuations in the ecological systems as an open system scenerio.

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