

## Dynamics of Defensive Volatile of Plant Modeling Tritrophic Interactions

Debasis Mukherjee \*

Department of Mathematics, Vivekananda College, Thakurpukur, Kolkata-700063, India

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**Abstract:** This paper analyzes the tritrophic interactions among plants, herbivores and their natural enemies (carnivores) which are attracted by defensive volatile of plants. The functional response of herbivore and their predator is taken as Holling type II. Local stability condition of positive equilibrium point is derived. Transcritical bifurcation around the boundary equilibrium point is shown. When the predation rate of herbivore crosses a critical value, the positive equilibrium point enters into Hopf bifurcation. Persistence criterion is found out. Using Bendixson's criterion for high-dimensional ordinary differential equations due to Li and Muldowney, we show that positive equilibrium point is globally stable under certain conditions. Finally numerical examples are provided to support our results.

**Keywords:** Plant defence; Stability; Bifurcation; Persistence; Global stability

### 1 Introduction

The interaction between plants and herbivores is complex in nature. In the evolutionary process, both have developed strategies to avoid each other's defence systems. The interactions between plants and herbivores has resulted in the advancement of sophisticated defence mechanism in plants for anticipating signals from damaged cells. To avoid the herbivore attack, many plants interact with carnivores as an indirect defence against herbivores. Plants can defend themselves from herbivore attack by releasing volatile organic compounds (VOCs) that attract natural enemies of herbivores and / or providing food (e.g., extra floral nectar ) and shelter to promote the effectiveness of the natural enemies [6, 16]. Although VOCs mainly attract predatory mites and parasitic wasps. For example, lima bean and apple plants which release volatile that attract predatory mites when damaged by spider mites (Takabayashi and Dicke [19]). Other examples include cucumber, corn, cotton etc. release volatile when they are attacked by herbivores. This herbivore-induced plant volatile (HIPV) can cause benefits to the environment which are affected by the use of chemical artificial pesticides. HIPVs are the lipophilic liquids with high vapor pressures which are emitted from the different parts of the plant body namely leaves, flowers fruits etc.[7]. Furthermore, emission of volatile by plants may contribute to sustainability of forestry and agriculture. It is now widely accepted that VOCs can attract predatory arthropods and / or repel herbivores and thus serve as a plant resistance (Dicke [5], Tumilson et al. [20], Arimura et al. [1]). Though volatile of any kind have attractive effect on natural enemies, this effect is stronger for damaged plants than for undamaged plants (Price [15]).

Liu et al.[13] studied the model consisting plants, herbivores and natural enemies of herbivores in the form of tritrophic interactions. They showed that increase in attraction of strength of plant-induced volatile to the natural enemy leads to high fluctuation amplitude of plant biomass and herbivore population. Further it is noted that when the attack strength of natural enemies reaches a certain level, fluctuation amplitude of plant biomass and herbivore population decrease and plant biomass will approach to its environmental carrying capacity. Fergola and Wang [9] modified the model of Liu et al. [13] and incorporated time delay. They proved that for Volterra type interaction, the threshold value for persistence of herbivore and carnivore populations is not affected by the chemical attractions. It is found that, the attraction to carnivores is beneficial to reduce the density of herbivores and increases the density of plants. When the interaction between plants and herbivores is of Leslie type, the model exhibits the fold bifurcation. Behavioral pattern of species and the habitat where they are living, the predation process are of different forms where the amount of food consumed by predator is a

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\*Email address. mukherjee1961@gmail.com

function of prey density only (e.g., Holling type, I, II and III, see[21]). From literature, it is found that in predator-prey models, the predator functional response to prey density is monotonic increasing and has saturation effect, justification of the assumption being that as there is more prey in the environment, it is better for the predator [11]. In the previous studies [9,13], the authors did not consider the commonly used functional response such as Holling type II for predation process. Actually the standard functional response for a specialist is the Holling type II function. The majority of herbivore arthropods are specialists, limited to feeding on a single or a low number of plant population [22].

Keeping in view with the ecological relevant questions of species survival and the long term behavior of the system, we consider Holling type II response function for herbivore and its natural enemies in the form of tritrophic interactions. Our assumption on predation process signifies that when herbivore relies exclusively on a single plant population for food. Also here it is assumed that carnivore predate a particular herbivore species.

This paper is structured as follows. In Section 2, we present our model. Positivity and boundedness of solutions of system are given in Section 3. Dynamical behavior of the system are investigated in Section 4. In Section 5, we discuss global stability of the positive equilibrium point. Numerical examples are given in Section 6. We conclude our paper in Section 7.

## 2 Model

Let  $x(t)$  be the plant biomass,  $y(t)$  and  $z(t)$  be the population sizes of herbivores and their natural enemies respectively. Predation by herbivores and their natural enemies follow Holling type II response function. The model is described by :

$$\begin{cases} \frac{dx}{dt} = x\{r(1 - \frac{x}{k}) - \frac{by}{a+x}\} \\ \frac{dy}{dt} = y(-c + \frac{mbx}{a+x} - \frac{ez}{h+y} - py) \\ \frac{dz}{dt} = -dz + \frac{neyz}{h+y} + \mu xy - qz^2 \end{cases} \quad (1)$$

with initial conditions given by  $x(0) = x_0 > 0, y(0) = y_0 > 0$  and  $z(0) = z_0 > 0$ .

Here  $r$  is the intrinsic growth rate of plants,  $k$  is the environmental carrying capacity of plants,  $b$  and  $e$  are the predation rates for plant-herbivore and herbivore-natural enemies respectively,  $m$  and  $n$  are the corresponding conversion rates,  $c$  is the death rate of herbivores, and  $d$  is the sum of death rate and emigration rate of carnivorous enemies. The term  $\mu xy$  is the immigration rate of natural enemies of herbivores due to the attraction of defensive chemical from plants.  $p$  and  $q$  represent the density-dependent death coefficients for herbivores and carnivores respectively. Biological justification of the above model can be found in [3]. For example, lima bean plants (*Phaseolus lunatus* L. cv Sieva ) emit volatile when attacked by spider mites (*Tetranychus urticae*) and attract predatory mite (*Phytoseiulus persimilis*), a specialized natural enemy of spider mites.

## 3 Positivity and boundedness of solutions

In this section, we shall first show positivity and boundedness of solutions of system (1). These are very important so far as the validity of the model is related. We first study the positivity.

**Lemma 1** All solutions  $(x(t), y(t), z(t))$  of system (1) with initial value  $(x_0, y_0, z_0) \in R_+^3$ , remains positive for all  $t > 0$ .

**Proof.** The positivity of  $x(t)$  and  $y(t)$  can be verified by the equations

$$x(t) = x_0 \exp\left\{ \int_0^t \left[ r\left(1 - \frac{x(s)}{k}\right) - \frac{by(s)}{a+x(s)} \right] ds \right\}, y(t) = y_0 \exp\left\{ \int_0^t \left[ -c + \frac{mbx(s)}{a+x(s)} - \frac{ez(s)}{h+y(s)} - py(s) \right] ds \right\}$$

with  $x_0, y_0 > 0$ . The positivity of  $z(t)$  can be easily deduced from the third equation of system (1). We observe that

$$\frac{dz}{dt} \geq z\left(-d + \frac{ney}{h+y} - qz\right) \Rightarrow z(t) \geq z_0 \exp\left\{ \int_0^t \left[ -d + \frac{ney(s)}{h+y(s)} - qz(s) \right] ds \right\}.$$

Also if  $x(0) = x_0 > 0$ , then  $x(t) > 0$  for all  $t > 0$ . The same argument is valid for component  $y(t)$  and  $z(t)$ . Hence the interior of  $R_+^3$  is an invariant set of system (1). ■

**Lemma 2** All the solutions of system (1) will lie in the region  $B = \{(x, y, z) \in R_+^3 : 0 \leq (\frac{\mu a}{nb} + \frac{k\mu}{nb} + m)x + y + \frac{z}{n} \leq \frac{M}{\lambda}\}$  as  $t \rightarrow \infty$  for all positive initial values  $(x(0), y(0), z(0)) \in R_+^3$  where  $\lambda = \min\{1, c, d\}$  and  $M = \frac{k(1+r)^2}{4r}(\frac{\mu a}{nb} + \frac{k\mu}{nb} + m)$ .

**Proof.** Let us consider the function

$$W(t) = (\frac{\mu a}{nb} + \frac{k\mu}{nb} + m)x + y + \frac{z}{n}.$$

The time derivative along a solution of (1) is

$$\frac{dW(t)}{dt} = x(\frac{\mu a}{nb} + \frac{k\mu}{nb} + m)\{r(1 - \frac{x}{k}) - \frac{by}{a+x}\} + y(-c + \frac{mbx}{a+x} - \frac{ez}{h+y} - py) - \frac{dz}{n} + \frac{eyz}{h+y} + \frac{\mu xy}{n} - \frac{qz^2}{n}.$$

For each  $\lambda > 0$  the following inequality is satisfied :

$$\frac{dW}{dt} + \lambda W \leq M + (\lambda - 1)(\frac{\mu a}{nb} + \frac{k\mu}{nb} + m)x + (\lambda - c)y + (\lambda - d)\frac{z}{n}. \quad (2)$$

Now choose  $\lambda$  such that  $0 < \lambda = \min\{1, c, d\}$ . Then (2) can be written as

$$\frac{dW}{dt} + \lambda W < M$$

By using the Comparison Theorem [2] we obtain

$$0 \leq W(x(t), y(t), z(t)) \leq \frac{M}{\lambda} + W(x(0), y(0), z(0))/e^{\lambda t}.$$

Taking limit when  $t \rightarrow \infty$ , we have,  $0 < W(t) \leq \frac{M}{\lambda}$ . Hence system (1) is bounded. ■

## 4 Dynamical behavior

Evidently, system (1) has a non-negative equilibrium point  $E_0 = (0, 0, 0)$  and  $E_1 = (k, 0, 0)$  which exists for all parametric values. First we give the following stability results.

**Theorem 3** i)  $E_0$  is always unstable.

ii)  $E_1$  is locally stable if  $c > \frac{mbk}{a+k}$ .

**Proof.** i)The characteristic equation at  $E_0$  is

$$(\lambda - r)(\lambda + c)(\lambda + d) = 0.$$

Since one of the roots of the above equation is positive,  $E_0$  is unstable.

ii)The characteristic equation at  $E_1$  is

$$(\lambda + r)(\lambda + d)(\lambda + c - \frac{mbk}{a+k}) = 0.$$

If  $c > \frac{mbk}{a+k}$  then all the roots of the above equation are negative and hence  $E_1$  is locally asymptotically stable.

Our next result shows that if the death rate of herbivore remains a certain threshold value then all the populations can survive in future time. ■

**Theorem 4** Suppose  $c < \frac{mbk}{a+k}$  then system (1) is uniformly persistent.

**Proof.** Suppose  $\alpha$  is a point in the positive octant and  $o(\alpha)$  is the orbit through  $\alpha$  and  $\Omega$  is the omega limit set of the orbit through  $\alpha$ . Note that  $\Omega(\alpha)$  is bounded. We claim that  $E_0 \notin \Omega(\alpha)$ . If  $E_0 \in \Omega(\alpha)$ , then by Butler- McGehee lemma [10], there exists a point  $P$  in  $\Omega(\alpha) \cap W^s(E_0)$  (which denotes stable manifold of  $E_0$ ). Since  $o(P)$  lies in  $\Omega(\alpha)$  and  $W^s(E_0)$  is the  $y - z$  plane hence unbounded orbit lies in  $\Omega(\alpha)$  a contradiction. Next, we show that  $E_1 \notin \Omega(\alpha)$ . Since  $c < \frac{mbk}{a+k}$ ,  $E_1$  is a saddle point.  $W^s(E_1)$  is the  $x - z$  plane and hence orbits in the plane emanate from either  $E_0$  or an unbounded orbit lies in  $\Omega(\alpha)$ , once more a contradiction. There does not exist any equilibria in the two dimensional plane. Thus,  $\Omega(\alpha)$  does not intersect any of the coordinate planes and hence system (1) is persistent. Since (1) is bounded, by main theorem in Butler et al. [4], this implies that the system is uniformly persistent (permanent).

In this section, we proved that system (1) exhibits uniform persistence provided that the conditions in Theorem 2 are satisfied. Further, it is proved in [4] uniform persistence implies the existence of an interior equilibrium point. Hence  $E_3(x^*, y^*, z^*)$  exists, that is, in effect, Theorem 2 implies that  $E_3$  exists. ■

**Theorem 5** Suppose the condition of Theorem 2 be satisfied. Further suppose that  $\frac{r}{k} \geq \frac{by^*}{(a+x^*)^2}, p \geq \frac{ez^*}{(h+y^*)^2}$  and  $(\frac{\mu x^* y^*}{z^*} + qz^*) > \frac{ey^*(a+x^*)^2 \mu}{mab(h+y^*)}$ . Then  $E_3(x^*, y^*, z^*)$  is locally asymptotically stable.

**Proof.** The Jacobian matrix of system (1) at the equilibrium point  $E_3$  is given by

$$J(E_3) = \begin{pmatrix} -x^* \left( \frac{r}{k} - \frac{by^*}{(a+x^*)^2} \right) & -\frac{bx^*}{a+x^*} & 0 \\ \frac{maby^*}{(a+x^*)^2} & y^* \left( \frac{ez^*}{(h+y^*)^2} - p \right) & -\frac{ey^*}{h+y^*} \\ \mu y^* & \mu x^* + \frac{hnez^*}{(h+y^*)^2} & -\frac{\mu x^* y^*}{z^*} - qz^* \end{pmatrix}.$$

The characteristic equation about  $E_3$  is given by

$$\lambda^3 + a_1 \lambda^2 + a_2 \lambda + a_3 = 0,$$

where

$$a_1 = x^* \left( \frac{r}{k} - \frac{by^*}{(a+x^*)^2} \right) + y^* \left( p - \frac{ez^*}{(h+y^*)^2} \right) + \frac{\mu x^* y^*}{z^*} + qz^*,$$

$$a_2 = x^* \left( \frac{r}{k} - \frac{by^*}{(a+x^*)^2} \right) \left\{ y^* \left( p - \frac{ez^*}{(h+y^*)^2} \right) + \left( \frac{\mu x^* y^*}{z^*} + qz^* \right) \right\} + y^* \left( p - \frac{ez^*}{(h+y^*)^2} \right) \left( \frac{\mu x^* y^*}{z^*} + qz^* \right) + \frac{ne^2 hy^* z^*}{(h+y^*)^3} + \frac{b^2 amx^* y^*}{(a+x^*)^3},$$

$$a_3 = x^* \left( \frac{r}{k} - \frac{by^*}{(a+x^*)^2} \right) \left\{ y^* \left( p - \frac{ez^*}{(h+y^*)^2} \right) \left( \frac{\mu x^* y^*}{z^*} + qz^* \right) + \frac{ne^2 hy^* z^*}{(h+y^*)^3} \right\} + \frac{mx^* y^* ab^2}{(a+x^*)^3} \left( \frac{\mu x^* y^*}{z^*} + qz^* \right) - \frac{eb\mu x^* y^{*2}}{(a+x^*)(h+y^*)}.$$

Clearly  $a_i > 0$  for  $i = 1, 2, 3$  by the assumption of the theorem. Again

$$a_1 a_2 - a_3 = x^{*2} \left( \frac{r}{k} - \frac{by^*}{(a+x^*)^2} \right)^2 \left\{ y^* \left( p - \frac{ez^*}{(h+y^*)^2} \right) + \frac{\mu x^* y^*}{z^*} + qz^* \right\} + b^2 x^{*2} \left( \frac{r}{k} - \frac{by^*}{(a+x^*)^2} \right) \frac{amy^*}{(a+x^*)^3} + y^* y^* \left( p - \frac{ez^*}{(h+y^*)^2} \right) \left[ x^* \left( \frac{r}{k} - \frac{by^*}{(a+x^*)^2} \right) \right\} \left\{ y^* \left( p - \frac{ez^*}{(h+y^*)^2} \right) + \left( \frac{\mu x^* y^*}{z^*} + qz^* \right) \right\} + y^* \left( p - \frac{ez^*}{(h+y^*)^2} \right) \left( \frac{\mu x^* y^*}{z^*} + qz^* \right) + \frac{ne^2 hy^* z^*}{(h+y^*)^3} + \frac{b^2 amx^* y^*}{(a+x^*)^3} \right] + x^* \left( \frac{\mu x^* y^*}{z^*} + qz^* \right) \left( \frac{r}{k} - \frac{by^*}{(a+x^*)^2} \right) \left\{ y^* \left( p - \frac{ez^*}{(h+y^*)^2} \right) + \frac{\mu x^* y^*}{z^*} + qz^* \right\} + y^* \left( p - \frac{ez^*}{(h+y^*)^2} \right) \left( \frac{\mu x^* y^*}{z^*} + qz^* \right)^2 + \left( \frac{\mu x^* y^*}{z^*} + qz^* \right) \left( \frac{ne^2 hy^* z^*}{(h+y^*)^3} \right) + \frac{eb\mu x^* y^{*2}}{(a+x^*)(h+y^*)}.$$

So positivity of  $a_1 a_2 - a_3$  follows from the assumption of the theorem. The conclusion of the result is immediate by the application of Routh-Hurwitz criterion. ■

**Remark 6** One directly verify that  $E_3$  is stable if  $a_1 a_2 - a_3 > 0$  and  $a_2, a_3 > 0$ .

In this section, we shall develop local bifurcation near the equilibrium points of system (1) with the help of Sotomayor's theorem [18]. System (1) can be rewritten as

$$\frac{dX}{dt} = F(X) \text{ where } X = (x, y, z)^T \text{ and } F = (F_1, F_2, F_3) \text{ with } F_i, i = 1, 2, 3 \text{ are as follow } F_1 = x \left\{ r \left( 1 - \frac{x}{k} \right) - \frac{by}{a+x} \right\}, F_2 = y \left( -c + \frac{mbx}{a+x} - \frac{ez}{h+y} - py \right), F_3 = -dz + \frac{neyz}{h+y} + \mu xy - qz^2.$$

**Theorem 7** System (1) undergoes a transcritical bifurcation around  $E_1$  when the parameter  $c$  crosses the critical value  $c = \frac{mbk}{a+k}$

**Proof.** Since  $c = \frac{mbk}{a+k} = c^*$ , one of the eigenvalue of the Jacobian matrix of system (1) at  $E_1$  is zero. Now the Jacobian matrix of system (1) at  $E_1$  with zero eigenvalue is given by

$$J(E_1) = \begin{pmatrix} -r & -\frac{bk}{a+k} & 0 \\ 0 & 0 & 0 \\ 0 & \mu k & -d \end{pmatrix}.$$

Clearly, two of the eigenvalues of  $J(E_1)$  is negative. Let  $v = (v_1, v_2, v_3)^T$  and  $w = (w_1, w_2, w_3)^T$  denotes the eigenvectors corresponding to the eigenvalue zero of the matrix  $J(E_1)$  and  $J(E_1)^T$  respectively, a simple calculation yields  $v = \theta(1, -\frac{r(a+k)}{bk}, -\mu r \frac{(a+k)}{bd})^T$  and  $w = (0, \xi, 0)^T$  where  $\theta$  and  $\xi$  are any nonzero real numbers.

Note that  $w^T [F_c(E_1, c^*)] = 0$ .

Hence system (1) does not attain any saddle-node bifurcation around  $E_1$  (see Sotomayor [18]).

Again  $w^T [DF_c(E_1, c^*)v] = -\xi v_2 \neq 0$ .

Further  $w^T [D^2F(E_1, c^*)(v, v)] = -2\xi \frac{\theta^2 r}{k} \{ \frac{ma}{(a+k)} + \frac{pr(a+k)^2}{kb^2} + \frac{er\mu(a+k)^2}{hdb^2} \} \neq 0$ , where  $DF_c(E_1, c^*) = (m_{ij})_{3 \times 3}$  and  $m_{11} = m_{12} = m_{13} = 0, m_{21} = 0, m_{22} = -1, m_{23} = 0, m_{31} = m_{32} = m_{33} = 0$  and

$$D^2F(X, c) = \begin{pmatrix} \nabla \frac{\partial F_1}{\partial x} & \nabla \frac{\partial F_2}{\partial x} & \nabla \frac{\partial F_3}{\partial x} \\ \nabla \frac{\partial F_1}{\partial y} & \nabla \frac{\partial F_2}{\partial y} & \nabla \frac{\partial F_3}{\partial y} \\ \nabla \frac{\partial F_1}{\partial z} & \nabla \frac{\partial F_2}{\partial z} & \nabla \frac{\partial F_3}{\partial z} \end{pmatrix} \in R^{3 \times 3 \times 3},$$

$\nabla \frac{\partial F_i}{\partial x} = (\frac{\partial^2 F_i}{\partial x^2}, \frac{\partial^2 F_i}{\partial y \partial x}, \frac{\partial^2 F_i}{\partial z \partial x})^T, \nabla \frac{\partial F_i}{\partial y} = (\frac{\partial^2 F_i}{\partial x \partial y}, \frac{\partial^2 F_i}{\partial y^2}, \frac{\partial^2 F_i}{\partial z \partial y})^T, \nabla \frac{\partial F_i}{\partial z} = (\frac{\partial^2 F_i}{\partial x \partial z}, \frac{\partial^2 F_i}{\partial y \partial z}, \frac{\partial^2 F_i}{\partial z^2})^T$ , for  $i = 1, 2, 3$ .

The expression for  $DF(U), D^2F(U, U)$  and  $D^3F(U, U, U)$  can be obtained analytically (see [17]). So, according to Sotomayor's theorem [18], system (1) has a transcritical bifurcation at  $E_1$  with respect to the parameter  $c$ . ■

We now present Hopf bifurcation of nontrivial periodic solution for system (1). Next we investigate whether Hopf bifurcation occurs or not for system (1). Choosing  $b$  as a bifurcation parameter, in the following we will show Hopf bifurcation occurs for system (1) at a critical value  $b_c$ .

Define  $g(b) = a_1(b)a_2(b) - a_3(b)$ .

**Theorem 8** *If there exists  $b = b_c$  such that  $g(b_c) = 0$ , and  $g'(b_c) > 0$ , then the positive equilibrium point  $E_3(x^*(b), y^*(b), z^*(b))$  is locally stable if  $b < b_c$  but it is unstable for  $b > b_c$  and a Hopf bifurcation of periodic solution occurs at  $b = b_c$ .*

**Proof.** We assume that  $E_3$  is locally asymptotically stable, we would like to know if  $E_3$  will lose its stability when one of the parameters changes. We choose  $b$ , as the bifurcation parameter, we can see that if there exist a critical value  $b_c$  such that (i)  $a_1(b_c) > 0$ , (ii)  $g(b_c) = 0$ , (iii)  $g'(b_c) > 0$ .

For Hopf bifurcation to occur at  $b = b_c$ , the characteristic equation must be of the form

$$(\lambda^2(b_c) + a_2(b_c))(\lambda(b_c) + a_1(b_c)) = 0, \quad (3)$$

which has three roots  $\lambda_1(b_c) = i\sqrt{a_2(b_c)}, \lambda_2(b_c) = -i\sqrt{a_2(b_c)}, \lambda_3(b_c) = -a_1(b_c) < 0$ . To see if Hopf bifurcation occurs at  $b = b_c$ , we need to verify the transversality condition

$$[\frac{dRe(\lambda(b))}{db}]_{b=b_c} \neq 0$$

For all  $b$ , the roots are in general of the form

$$\begin{aligned} \lambda_1(b) &= \mu(b) + i\nu(b), \\ \lambda_2(b) &= \mu(b) - i\nu(b), \\ \lambda_3(b) &= -a_1(b), \end{aligned} \quad (4)$$

Now, we will verify the transversality condition

$$[\frac{dRe(\lambda_j(b))}{db}]_{b=b_c} \neq 0, j = 1, 2.$$

Substituting  $\lambda_j(b) = \mu(b) \pm i\nu(b)$  into (3) and calculating the derivative, we have

$$\begin{aligned} K(b)\mu'(b) - L(b)\nu'(b) + M(b) &= 0, \\ K(b)\mu'(b) + L(b)\nu'(b) + N(b) &= 0, \end{aligned} \quad (5)$$

where

$$\begin{aligned} K(b) &= 3\mu^2(b) + 2a_1(b)\mu(b) + a_2(b) - 3\nu^2(b), \\ L(b) &= 6\mu(b)\nu(b) + 2a_1(b)\nu(b), \\ M(b) &= \mu^2(b)a'_1(b) + a'_2(b)\mu(b) + a'_3(b) - a'_1(b)\nu^2(b), \\ N(b) &= 2\mu(b)\nu(b)a'_1(b) + a'_2(b)\nu(b). \end{aligned} \tag{6}$$

Noticing that  $\mu(b_c) = 0, \nu(b_c) = \sqrt{a_2(b_c)}$ , we have  $K(b_c) = -2a_2(b_c), L(b_c) = 2a_1(b_c)\sqrt{a_2(b_c)}, M(b_c) = a'_3(b_c) - a'_1(b_c)a_2(b_c), N(b_c) = a'_2(b_c)\sqrt{a_2(b_c)}$ . Solving for  $\mu'(b_c)$  from system (5) we have

$$\left[\frac{dRe(\lambda_j(b))}{db}\right]_{b=b_c} = \mu'(b_c) = -\frac{L(b_c)N(b_c) + K(b_c)M(b_c)}{K^2(b_c) + L^2(b_c)} = \frac{a'_3(b_c) - a'_1(b_c)a_2(b_c) - a_1(b_c)a'_2(b_c)}{a_1^2(b_c) + a_2(b_c)} > 0$$

if  $g'(b_c) < 0$  and  $\lambda_3(b_c) = -a_1(b_c) < 0$ . This completes the proof. ■

Define  $f(\mu) = a_1(\mu)a_2(\mu) - a_3(\mu)$ .

**Theorem 9** *If there exists  $\mu = \mu_c$  such that  $f(\mu_c) = 0$ , and  $f'(\mu_c) > 0$ , then the positive equilibrium point  $E_3(x^*(b), y^*(b), z^*(b))$  is locally stable if  $\mu > \mu_c$  but it is unstable for  $\mu < \mu_c$  and a Hopf bifurcation of periodic solution occurs at  $\mu = \mu_c$ .*

**Proof.** Proof of Theorem 6 is similar to the proof of Theorem 5 and hence omitted. ■

## 5 Global stability of positive equilibrium point

In Theorem 3, it is shown that the positive equilibrium point  $E_3(x^*, y^*, z^*)$  is locally asymptotically stable under certain restrictions. So natural question arises under what additional conditions it becomes globally asymptotically stable. To derive global stability condition it is sometimes difficult to find out a Lyapunov function. There is an alternative approach to show global stability due to Li and Muldowney [12]. Now we use a high-dimensional Bendixson's criterion of Li and Muldowney [12], which we briefly state next.

Let  $D \subset R^n$  be an open set and  $F \in C^1$ . Consider a system of differential equations

$$\frac{dX}{dt} = F(X). \tag{7}$$

According to the theory developed in [12], it is sufficient to show that the second compound equation

$$\frac{dU}{dt} = \frac{\partial F^{[2]}}{\partial X}(X(t, X_0))U(t), \tag{8}$$

with respect to a solution  $X(t, X_0)$  of system (7) is equi-uniformly asymptotically stable, namely, for each  $X_0 \in D$ , system (8) is uniformly asymptotically stable, and the exponential decay rate is uniform for  $X_0$  in each compact subset of  $D$ , where  $D \subset R^n$  is an open connected set. Here  $\partial F/\partial X^{[2]}$  is the second additive compound matrix of the Jacobian matrix  $\partial F^{[2]}/\partial X$ . It is an  $\binom{n}{2} \times \binom{n}{2}$  matrix, and thus (8) is a linear system of dimension  $\binom{n}{2}$  (see Fiedler [8] and Muldowney [14]). For a general  $3 \times 3$  matrix

$$P = \begin{pmatrix} p_{11} & p_{12} & p_{13} \\ p_{21} & p_{22} & p_{23} \\ p_{31} & p_{32} & p_{33} \end{pmatrix},$$

its second compound matrix  $P^{[2]}$  is

$$P^{[2]} = \begin{pmatrix} p_{11} + p_{22} & p_{23} & -p_{13} \\ p_{32} & p_{11} + p_{33} & p_{12} \\ -p_{31} & p_{21} & p_{22} + p_{33} \end{pmatrix}. \tag{9}$$

The equi-uniform asymptotic stability of (8) implies the exponential decay of the surface area of any compact two-dimensional surface  $D$ . If  $D$  is simply connected, this prevents the occurrence of any invariant simple closed rectifiable curve in  $D$ , including periodic orbits. The following result is proved in Li and Muldowney [12].

**Proposition 10** *Let  $D \subset R^n$  be a simply connected region. Assume that the family of linear systems (8) is equi-uniformly asymptotically stable. Then*

- (i)  $D$  contains no simple closed invariant curves including periodic orbits, homoclinic orbits, heteroclinic cycles;
- (ii) each semi-orbit in  $D$  converges to a single equilibrium.

*In particular, if  $D$  is positively invariant and contains an unique equilibrium  $\bar{X}$ , then  $\bar{X}$  is globally asymptotically stable in  $D$ .*

One can show uniform asymptotic stability of system (8) by constructing a Lyapunov function. For example, (8) is equi-uniformly asymptotically stable if there exists a positive definite function  $V(U)$ , such that  $dV(U)/dt|_{(8)}$  is negative definite, and  $V$  and  $dV(U)/dt|_{(8)}$  are both independent of  $X_0$ .

We now require the following assumptions to prove the global stability of positive equilibrium point of system (1).

(A<sub>1</sub>) There exist positive numbers  $\alpha$ , and  $\beta$  such that  $max\{c_{11} + \frac{c_{12}\alpha}{\beta}, \frac{c_{21}\beta}{\alpha} + c_{22} + c_{23}, \frac{c_{31}}{\alpha} + \frac{c_{32}}{\beta} + c_{33}\} < 0$  and

(A<sub>2</sub>)  $c < \frac{mbk}{a+k}$ .

Assumption (A<sub>2</sub>) implies that system (1) is uniformly persistent and hence there exists a time  $T$  such that  $x(t), y(t), z(t) > \eta$  ( $0 < \eta < k$ ) for  $t > T$ .

We again denote  $X = (x, y, z)^T$  and  $F(X) = (x\{r(1 - \frac{x}{k}) - \frac{by}{a+x}\}, y\{-c + \frac{mbx}{a+x} - \frac{ez}{h+y} - py\}, -dz + \frac{neyz}{h+y} + \mu xy - qz^2)^T$ , We have

$$\frac{\partial F}{\partial X} = \begin{pmatrix} r(1 - \frac{2x}{k}) - \frac{aby}{(a+x)^2} & -\frac{bx}{a+x} & 0 \\ \frac{maby}{(a+x)^2} & -c + \frac{mbx}{a+x} - \frac{ehz}{(h+y)^2} - 2py & -\frac{ey}{h+y} \\ \mu y & \mu x + \frac{hnez}{(h+y)^2} & -d + \frac{ney}{h+y} - 2qz \end{pmatrix}$$

and by (9)

$$\frac{\partial F^{[2]}}{\partial X} = \begin{pmatrix} q_{11} & q_{12} & q_{13} \\ q_{21} & q_{22} & q_{23} \\ q_{31} & q_{32} & q_{33} \end{pmatrix}$$

where

$$q_{11} = r(1 - \frac{2x}{k}) - \frac{aby}{(a+x)^2} - c + \frac{mbx}{a+x} - \frac{ehz}{(h+y)^2} - 2py, q_{12} = -\frac{ey}{h+y}, q_{13} = 0, \\ q_{21} = \mu x + \frac{hnez}{(h+y)^2}, q_{22} = r(1 - \frac{2x}{k}) - \frac{aby}{(a+x)^2} - d + \frac{ney}{h+y} - 2qz, q_{23} = -\frac{bx}{a+x}, \\ q_{31} = -\mu y, q_{32} = \frac{maby}{(a+x)^2}, q_{33} = -c - d + \frac{mbx}{a+x} - \frac{ehz}{(h+y)^2} + \frac{ney}{h+y} - 2qz - 2py.$$

The second compound system

$$\begin{pmatrix} \dot{u}_1 \\ \dot{u}_2 \\ \dot{u}_3 \end{pmatrix} = \frac{\partial F^2}{\partial X} \begin{pmatrix} u_1 \\ u_2 \\ u_3 \end{pmatrix}$$

is

$$\begin{aligned} \dot{u}_1 &= \{r(1 - \frac{2x}{k}) - \frac{aby}{(a+x)^2} - c + \frac{mbx}{a+x} - \frac{ehz}{(h+y)^2} - 2py\}u_1 - \frac{ey}{h+y}u_2, \\ \dot{u}_2 &= (\mu x + \frac{hnez}{(h+y)^2})u_1 + \{r(1 - \frac{2x}{k}) - \frac{aby}{(a+x)^2} - d + \frac{ney}{h+y} - 2qz\}u_2 - \frac{bx}{a+x}u_3, \\ \dot{u}_3 &= -\mu yu_1 + \frac{maby}{(a+x)^2}u_2 - \{c + d - \frac{mbx}{a+x} + \frac{ehz}{(h+y)^2} - \frac{ney}{h+y} + 2qz + 2py\}u_3. \end{aligned} \tag{10}$$

where  $X(t) = (x(t), y(t), z(t))^T$  is arbitrary solution of system (1) with  $X_0(t) = (x_0(t), y_0(t), z_0(t))^T \in R_+^3$ . Set  $W(U) = max\{\alpha|u_1|, \beta|u_2|, u_3\}$  where  $\alpha, \beta > 0$  are constants.

The direct calculations lead to the following inequalities :

$$\begin{cases} \frac{d^+}{dt} \alpha |u_1| \leq c_{11} \alpha |u_1| + \frac{c_{12} \alpha \beta}{\beta} |u_2| \\ \frac{d^+}{dt} \beta |u_2| \leq \frac{c_{21} \beta \alpha}{\alpha} |u_1| + c_{22} \beta |u_2| + c_{23} |u_3| \\ \frac{d^+}{dt} |u_3| \leq \frac{c_{31} \alpha}{\alpha} |u_1| + \frac{c_{32} \beta}{\beta} |u_2| + c_{33} |u_3| \end{cases}$$

where  $d^+/dt$  denotes the right-hand derivative and

$$c_{11} = r(1 - \frac{2\eta}{k}) - \frac{ab\eta}{(a+k)^2} - c + mb - \frac{eh\eta}{(h+M_1)^2} - 2p\eta, c_{12} = -\frac{e\eta}{h+M_1},$$

$$c_{21} = \mu k + \frac{hneM_2}{(h+\eta)^2}, c_{22} = r(1 - \frac{2\eta}{k}) - \frac{ab\eta}{(a+k)^2} - d + ne - 2q\eta, c_{23} = -\frac{b\eta}{a+eta},$$

$$c_{31} = -\mu\eta, c_{32} = \frac{mabM_2}{(a+\eta)^2}, c_{33} = -c - d + mb - \frac{eh\eta}{(h+M_2)^2} + ne - 2q\eta - 2p\eta, M_1 = \frac{M}{\lambda}, M_2 = \frac{Mn}{\lambda}.$$

Therefore,

$$\frac{d^+}{dt} W(U(t)) \leq LW(U(t))$$

with

$$L = \max\{c_{11} + \frac{c_{12}\alpha}{\beta}, \frac{c_{21}\beta}{\alpha} + c_{22} + c_{23}, \frac{c_{31}}{\alpha} + \frac{c_{32}}{\beta} + c_{33}\}.$$

Thus under assumptions  $(A_1)$  and  $(A_2)$  we find a positive constant  $\delta$  such that  $L \leq -\delta < 0$ , and thus

$$W(U(t)) \leq W(U(s)) \exp(-\delta(t-s)), t \geq s > 0.$$

This establishes the equi-uniform asymptotic stability of the second compound system (10), and hence the positive equilibrium point  $E_3$  of system (1) is globally stable following from Proposition 1. From above analysis, we now state the following theorem.

**Theorem 11** *If the assumptions  $(A_1)$  and  $(A_2)$  are satisfied then system (1) has no non-trivial periodic solution. Furthermore, the positive equilibrium point  $E_3$  is globally stable in  $R_+^3$ .*

## 6 Numerical examples

We now explain situations for model system (1) with examples and diagrams in the following :

**Example 12** *If  $r = 8/3, k = 4, b = 4, a = 1, c = 1/4, m = 1/2, d = 1/2, e = 1, n = 1, h = 1, \mu = 1, p = 1/4, q = 1$  then the model system (1) has an unique interior equilibrium point  $(1,1,1)$ . Conditions of Theorem 2 are satisfied, hence system (1) is uniformly persistent. Further, we have checked that  $a_1 a_2 - a_3 > 0$  and  $a_i > 0$ , for  $i = 1, 2, 3$  so the positive equilibrium point is locally asymptotically stable. We now choose  $\eta = 3$ . With the above choice of parameters we obtain  $c_{11} = -1.3133, c_{12} = -.08266, c_{21} = 5.4116, c_{22} = -7.3133, c_{23} = -3, c_{31} = -3, c_{32} = 4.4114, c_{33} = -23.25$ . The positive numbers  $\alpha = 1, \beta = 1$  such that  $\max\{-2.1399, -4.9017, -21.8386\} < 0$ . Therefore the positive equilibrium point  $E_3$  is globally stable (see Fig.1).*

**Example 13** *If we increase the value of the parameter  $b$  and keeping all other parameters value fixed, we observe that Hopf bifurcation arises when  $b = 4.65$  (see Fig.2).*

**Example 14** *If we change the value of value of the parameter  $c$  and keeping all other parameters value fixed, we observe that transcritical bifurcation arises when  $c = 1.6$  (see Fig.3).*

**Example 15** *Suppose  $r = 8/3, k = 4, b = 4, a = 1, c = 1/4, m = 1/2, d = 0.288727303, e = 1, n = 1, h = 1, \mu = 0.288727303, p = 1/4, q = 1/2$ . It is easy to see that system (1) has an equilibrium point  $(1,1,1)$ . The it follows from Theorem 6 that a Hopf bifurcation of periodic solution occurs at  $\mu = \mu_c = 0.288727303$ . (see Fig.4).*

**Example 16** *If we decrease the value of the parameter  $\mu$  and keeping all other parameters value fixed, we observe multiple limit cycles when  $\mu = 0.268727303$  (see Fig.5).*



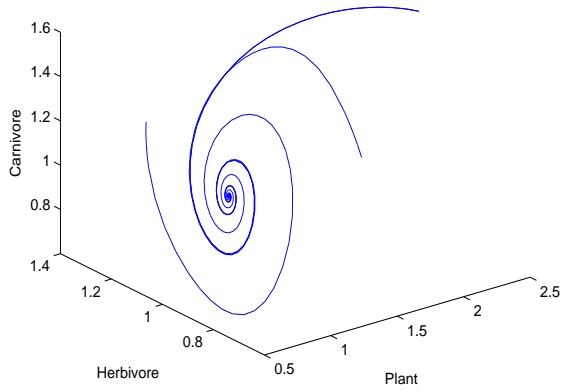


Figure 1: Phase portrait of system (1) showing global stability.

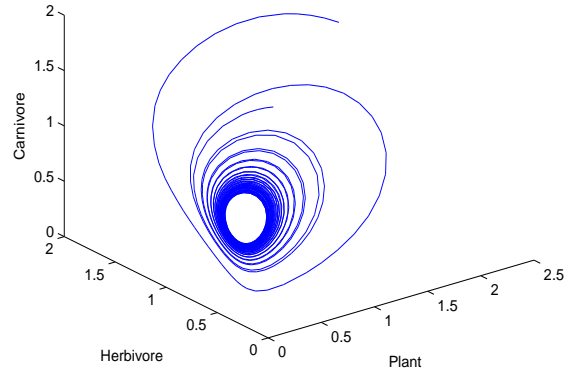


Figure 2: Periodic oscillation appears when  $b = 4.65$ .

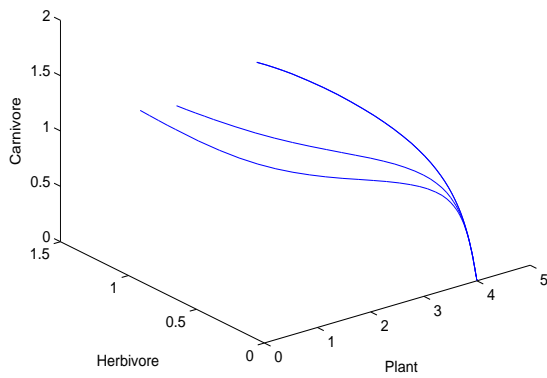


Figure 3: Solutions of (1) shows transcritical bifurcation around the equilibrium point  $(4,0,0)$  when  $c = 1.6$ .

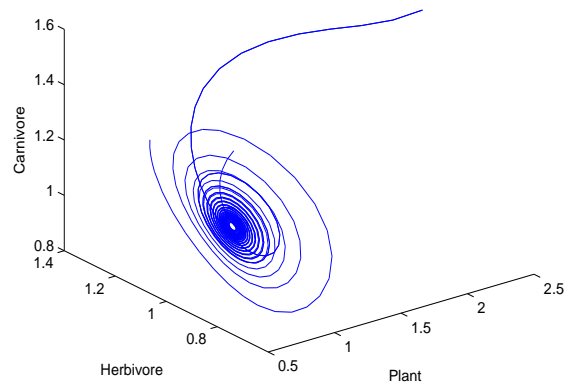


Figure 4: Hopf bifurcation occurs at  $\mu = \mu_c = 0.288727303$ .

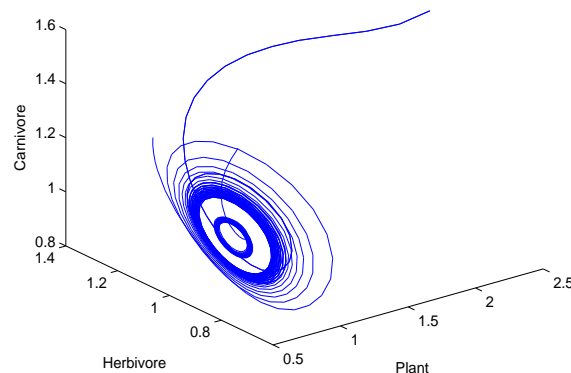


Figure 5: Multiple limit cycles appear at  $\mu = \mu_c = 0.268727303$ .

## 7 Discussion

Recent research on plant-herbivore interactions demonstrates that it is a multidisciplinary activity in plant biology and connects different fields to address chemical and ecological process affecting the plant-herbivore interactions. Furthermore, plant behaviors with their neighbors, symbionts, pathogens, herbivores and their natural enemies is even now unclear. In the past, ecological research mainly addressed plant defence against herbivores i.e., between two trophic level. The three trophic levels in insect-plant interactions was first introduced in the year 1980 (Price et al.[16]). Naturally current ecological studies consider a more holistic approach, with complex interactive studies considering the role of both plant defence and natural enemy impact on insect-plant relations. This is an fascinating area from ecological perspective and as such study of VOC-mediated tritrophic interactions is important in planning crop plants with better protection against herbivores. It is well known fact that rapid usage of pesticides and fertilizers cause major damage on farmland. So it is important to reduce the requirement for harmful pesticides for insect control. In view of above, we have considered a system where plants interact with carnivores as an indirect defence against herbivores. This work generalizes the model studied in [9]. Here we have taken the functional response of herbivore and its natural enemies (carnivores) as Holling type II as majority of herbivore arthropods are specialist.

The proposed model is shown biologically well posed in the sense that any positive solution initiates in the positive orthant remains positive and bounded. The local stability of the system in different equilibrium points are discussed. We have observed that coexistence equilibrium point is locally asymptotically stable for certain conditions and in this case all the boundary equilibrium points become unstable. We note that chemical attraction to natural enemies cannot affect the persistence of the whole system where as herbivore functional response has a positive role on persistence. Theorem 4 indicates that system admits zero eigenvalue at the equilibrium point  $E_1$ . The Sotomayor's theorem [18] is applied to ensure the existence of transcritical bifurcation. This type of bifurcation transforms a herbivore and carnivore free equilibrium point from unstable situation to a stable one and excludes the coexistence equilibrium point (see Fig.3). In this paper, we have chosen the parameter  $b$  arbitrarily for obtaining bifurcation. Qualitatively, we found the same bifurcations when varying  $\mu$  instead. In [9], it was remarked that the chemical attraction to carnivores can reduce the predation pressure from herbivores and increase the density of plants but cannot generate periodic oscillation. But we obtain periodic oscillation in our system. From Hopf bifurcation analysis we observed that increasing the predation rate of herbivores destabilizes the system, whereas the opposite holds true by the increasing the immigration rate of natural enemy of herbivores. We have established the existence of positive equilibrium point by the persistence condition. Still it is very complicated to find the coordinates of the positive equilibrium point in terms of system parameters. As it is known to us if the positive equilibrium point is globally stable it must be unique. In order to show uniqueness of the positive equilibrium point, we have discussed global stability by applying high-dimensional Bendixson's criterion due to Li and Muldowney [12].

In this work, we have investigated a system with one species of plant, herbivore and natural enemy. In natural environ-

ment, most plants are likely to be attacked by several herbivore species and pathogens. So thorough analysis is required in the study of the ecology of induced plant volatiles during multiple attack, by integrating research methodologies from molecular to ecological level, to obtain a more insight of the mechanisms involved throughout different field of biological community. In future study we will explore the dynamics of the system, when plants are faced with a multitude of attackers of which insect herbivores and plant pathogens are an important ecological component.

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