

Study of a detritus-based ecosystem model for generalized functional responses

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Abstract

We have considered a detritus-based ecosystem in Sunderban Mangrove area. The ecosystem is rich with detritus, detritivores and predators of detritivores. We have formulated a three-dimensional model by general functional responses. Several dynamical properties, namely, equilibria, boundedness, persistence and stability are analyzed in terms of general functional responses. The system is then analyzed for the same dynamical characteristic using Holling type-II and ivlev-type functional responses. The analytical results are verified by numerical results.

Keywords : Functional response, nonlinear differential equations, local stability analysis.

1 Introduction

Mathematical modelling of ecological systems has very vast literatures. The mathematical biology is now very important subject of study. The study calls for interdisciplinary research of mathematical sciences as well as biological sciences. Many biological phenomena are modelled by using set of nonlinear differential equations. There are numerous species in the ecosystem. They are somehow interlinked among themselves. The species may be divided into different tropic levels. The energy in the system flows among the tropic species. The mathematical modelling of the interaction among the species is difficult to formulate. The modelling of the interaction among the species is far from reality. The Sunderban mangrove ecosystem is complex due to several land and marine species. It has several many biotic and abiotic components interlinked among themselves. The detritus-based ecosystem has components like detritus which are dead

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leaves from mangrove plants. For the mangrove trees, energy and nutrients are assimilated in leaves and also stored in the leaves of the tree [1]. The leaf litter from the trees provides the basis for adjacent marine and terrestrial food webs. Thus the primary producers are the mangrove trees. The enrichment of the nutrient affects plant growth, metabolism, and tissue quality. This affects the primary consumption.

Research is ongoing to determine the effects of nutrient over-enrichment on mangrove plant growth and interactions with other organisms. It is evident that accumulated increased nutrient availability of the primary producers results in increased insect populations and increased damage to mangroves by insect herbivores. The spruce budworm is a very famous example of the damage of the forest ecosystem in US and Canada. The nutrients as accumulated is consumed by the small animals namely, microarthropods, oligochaetes, and micro-organisms like protozoa, fungi, actinomycetes, bacteria etc. Detritivore are the above small animals who feed on the nutrient. They governs abundance and persistence of invertebrates like certain insect larvae, nematodes and unicellular animals [2, 3]. The invertebrates constitute the predators of the detritivores of the system. This kind of food chain is available in every ecosystem. This is also important as the movement of energy among the species. The detritus is generated by the acts of the organisms which are responsible for the decomposition of the dead organic matters. There are some literatures on the detritus-based ecosystems of different parts of the world which are well-studied [4, 5]. Many literatures establish that the main source of detritus in the supralittoral zone of mangrove ecosystem in Sunderban is not algae, which is mainly formed by the excessive mortality rate of insect intruders, particularly, in the larval and pupal stages due to high salinity of the trapped water in the supralittoral zone [6]. Detritivores depend upon the detritus for food, which, in turn, becomes energy. Detritivores are then become the food source for fish, insect intruders the supralittoral zones. Ecologist are very much interested in studying the various ecosystems found within the supralittoral zones of the Sunderban Mangrove area in India. It is famous for its deltaic zone and wide range of mangrove vegetation. With this, we want to model further the detritus-based mangrove ecosystem with different modelling aspect.

Thus we propose a detritus-based ecosystem model with three species. The dynamics of the system is studied with respect to general functional response of the predator and the super predator. In Section 2, we formulate the model system. Section 3 describes some basic characteristics of the model system. The equilibrium and stability properties are carried out in Section 4. In the next section the analysis takes place for specific functional responses namely, Holling type-II and Ivlev-type functional response. Section 6 describes the general discussion and conclusion.

2 Model formulation

The mangrove ecosystem is very rich in detritus. The leaves of the mangrove trees are the main source of the nutrient. The dead leaves on the ground are decomposed into detritus which are food for the species which unicellular organisms. The unicellular organisms then become food for higher trophic level species present in the mangrove. In absence of the organisms and higher trophic level predators, the growth of the detritus is exponential except. Some of the population of the detritus always flow away. So, mathematically, the evolution equation of organisms when there is no other species is given by

$$\frac{dx}{dt} = S - \alpha x, \tag{2.1}$$

where $x = x(t)$ represents density of biomass of the plant litter of the mangroves plants after decomposition which we call detritus. Some unicellular organisms feed on the nutrient and the growth of such population together with that of the detritus is given as

$$\begin{cases} \frac{dx}{dt} = S - \alpha x - u(x)y, \\ \frac{dy}{dt} = -\beta y + du(x)y, \end{cases} \tag{2.2}$$

where $y = y(t)$ represents the density of biomass of micro-organisms and uni-cellular organisms, namely, detritivores. $u(x)$ is the nutrient uptake rate of detritivores. β is the rate of removal of the detritivores due to death. $du(x)y$ is the numerical response for the detritivores. The other species which are present in the system are in higher level. They consume all detritivores as the food. These species are considered as the predators of detritivores. The evolution equation of the whole system is given by the nonlinear ordinary differential equations

$$\begin{cases} \frac{dx}{dt} = S - \alpha x - u(x)y + c\gamma z, \\ \frac{dy}{dt} = -\beta y + du(x)y - v(y)z, \\ \frac{dz}{dt} = z[-\gamma + ev(y)], \end{cases} \tag{2.3}$$

with the non-negative initial conditions $x(0) = x_0 > 0$, $y(0) = y_0 > 0$, $z(0) = z_0 > 0$. So, it has become a two predator-prey model system. Here $z(t)$ is the density of the biomass of the predator of detritivores. Here γ is the death rate of the predator of detritivores. $c\gamma$ is detritus recycle rate after the death of predator of detritivores; $v(y)$ is the general nutrient uptake rate of the predator of detritivores. d, e are the conversion efficiencies of detritus into detritivores and of detritivores into predator of detritivores respectively. Here, all the parameters are positive and $c, d, e \in (0, 1)$.

The terms $u(x)y$ and $v(y)z$ are respectively functional response for detritivores and that of predators of detritivores response. $u(x)$ is the number of prey consumed per detritivore in unit time; $v(y)$ is the number of detritivores consumed per predator of detritivore in unit time. The term $du(x)y$ and $ev(y)z$ are respectively detritivores numerical response and predator of detriti-

vores numerical response. In view of the fact that as prey population increases the consumption rate of prey per predator increases but the fraction of the total prey population consumed per predator decreases. So, $u(x)$ and $v(y)$ have the important properties of continuity and both the functions are bounded. The functions also satisfy

$$u(x) \geq 0, \quad u_x(x) \geq 0 \quad \text{and} \quad v(y) \geq 0, \quad v_y(y) \geq 0 \tag{2.4}$$

with $u(0) = 0$ and $v(0) = 0$. The above type of model was proposed by [8].

3 Equilibria and boundedness

So, we consider the model system (2.3) presenting two predators and one prey species. Two predators are in different trophic level. The system equations are continuous and admits the existence and uniqueness of the solution in some positive octant. We find the equilibria of the system with generalized functional response $u(x)$ and $v(y)$. We assume that $u, v \in C^1[0, \infty)$. The several equilibria are given by the following zero isoclines:

$$\begin{cases} S - \alpha x - u(x)y + c\gamma z & = 0, \\ -\beta y + du(x)y - v(y)z & = 0, \\ z[-\gamma + ev(y)] & = 0. \end{cases} \tag{3.1}$$

Solving the above three equations, we get the following equilibria:

- (a) Axial equilibrium: $E_1(S/\alpha, 0, 0)$,
- (b) Boundary equilibrium: $E_2(x_2, y_2, 0)$, where $x_2 = u^{-1}(\beta/d)$ and $y_2 = \frac{d}{\beta}[S - \alpha u^{-1}(\beta/d)]$,
- (c) Interior equilibrium: $E_*(x_*, y_*, z_*)$, where $y_* = v^{-1}(\gamma/e)$, x_* and z_* are given by

$$\alpha x_* + (1 - cde)v^{-1}(\gamma/e)u(x_*) = S - ce\beta v^{-1}(\gamma/e), \quad z_* = [-\beta + du(x_*)](e/\gamma)v^{-1}(\gamma/e). \tag{3.2}$$

The above equilibrium E_1 always exists. Boundary equilibrium E_2 is biologically meaningful if

$$u^{-1}(\beta/d) > 0 \quad \text{and} \quad S > \alpha u^{-1}(\beta/d). \tag{3.3}$$

The interior equilibrium E_* is biologically meaningful if $x_* > 0$, $y_* > 0$ and $z_* > 0$. $y_* > 0$ gives $v^{-1}(\gamma/e) > 0$. From (3.2), $z_* > 0$ implies $u(x_*) > \beta/d$. Making use of (3.2) and $x_* > u^{-1}(\beta/d)$, the above reduces to

$$S > \alpha u^{-1}(\beta/d) + (\beta/d)v^{-1}(\gamma/e). \tag{3.4}$$

Before proceeding to analyze the stability of model system (2.3) we will prove that the system has bounded solution.

Theorem 3.1 All solutions of model system (2.3) with the positive initial conditions are uniformly bounded within the region \mathbf{B} , where $\mathbf{B} = \{(x, y, z) \in \mathbf{R}_+^3 : 0 \leq x \leq S/\alpha, 0 \leq x + y + z \leq S/\nu + \epsilon\}$, for any $\epsilon > 0$.

Proof. We assume that the right-hand sides of system of equations (2.3) are smooth functions of $(x(t), y(t), z(t))$ of t ($t \in \mathbf{R}_+$). Let $x(t)$, $y(t)$ and $z(t)$ be any solution with positive initial condition (x_0, y_0, z_0) .

Since $\frac{dx}{dt} \leq S - \alpha x$, as c is small, by a standard comparison theorem, we have $\limsup_{t \rightarrow +\infty} x(t) \leq M$, where $M = \max\{S, x(0)\}$. We consider a time-dependent function $W(t) = x(t) + y(t) + z(t)$. The time derivative of $W(t)$ along the solution of model system (2.3) is

$$\frac{dW}{dt} = S - \alpha x - \beta y - (1 - c)\gamma z - (1 - d)u(x)y - (1 - e)v(y)z.$$

Since $c, d, e \in (0, 1)$, the above expression reduces to

$$\frac{dW}{dt} < S - \nu W,$$

where $\nu = \min\{\alpha, \beta, (1 - c)\gamma\}$. Applying a theorem in differential inequalities [7], we obtain

$$0 \leq W(x, y, z) \leq S/\nu + W(x_0, y_0, z_0)e^{-\nu t} \tag{3.5}$$

and for $t \rightarrow +\infty, 0 \leq W(x, y, z) \leq S/\nu$. Therefore, all solutions of system (2.3) initiated at (x_0, y_0, z_0) enter into the region $\mathbf{B} = \{(x, y, z) \in \mathbf{R}_+^3 : 0 \leq x \leq S/\alpha, 0 \leq x + y + z \leq S/\nu + \epsilon, \text{ for any } \epsilon > 0\}$. Thus, all solutions of system (2.3) are uniformly bounded initiated at (x_0, y_0, z_0) .

This completes the proof.

4 Stability analysis

We want to analyze the local asymptotic stability of model system (2.3) around the equilibria. To do so, we take small perturbations X, Y and Z of the populations sizes x, y and z respectively. Then the linearized system of model system (2.3) at any equilibrium (x, y, z) is given by

$$\begin{cases} \frac{dX}{dt} = (-\alpha - u_x(x)y)X - u(x)Y + c\gamma Z, \\ \frac{dY}{dt} = du_x(x)yX + (-\beta + du(x) - v_y(y)z)Y - v(y)Z, \\ \frac{dZ}{dt} = ev_y(y)zY + (-\gamma + ev(y))Z. \end{cases} \tag{4.1}$$

The characteristic roots corresponding to the equilibrium E_1 are $\lambda_1 = -\alpha, \lambda_2 = -\beta + du(S/\alpha)$ and $\lambda_3 = -\gamma$. The equilibrium E_1 is stable if $\lambda_2 < 0$, which implies

$$S < \alpha u^{-1}(\beta/d). \tag{4.2}$$

Similarly, the characteristic equation for the equilibrium E_2 is

$$\det \begin{pmatrix} -\alpha - u_x(x_2)y_2 - \lambda & -u(x_2) & c\gamma \\ du^{-1}(x_2)y_2 & -\lambda & -v(y_2) \\ 0 & 0 & -\gamma + ev(y_2) - \lambda \end{pmatrix} = 0.$$

Two roots λ_1 and λ_2 of the equation are given by the following equation

$$\lambda^2 + [\alpha + u_x(x_2)y_2]\lambda + du(x_2)u^{-1}(x_2)y_2 = 0.$$

It is obvious that the real-parts of the roots of the equation are negative. Again, $\lambda_3 < 0$ if $-\gamma + ev(y_2) < 0$, which implies

$$S < \alpha u^{-1}(\beta/d) + (\beta/d)v^{-1}(\gamma/e). \tag{4.3}$$

Thus, the stability of the equilibrium points E_1 and E_2 are dependent on the system parameters. The constant input parameter S has role in stabilizing the system around the equilibria E_1, E_2 .

Theorem 4.1 Model system (2.3) is persistent.

Proof. From the analysis in Section 3 and above, we observe that E_1 always exists. From (4.2), it is clear that the equilibrium point E_1 is stable if $S < \alpha u^{-1}(\beta/d)$ and if the inequality reversed E_1 becomes unstable saddle along the normal to the xz -plane. Again, this is the condition ($S > \alpha u^{-1}(\beta/d)$) for existence of E_2 . Now E_2 is stable if $\alpha u^{-1}(\beta/d) < S < \alpha u^{-1}(\beta/d) + (\beta/d)v^{-1}(\gamma/e)$. If $S > \alpha u^{-1}(\beta/d) + (\beta/d)v^{-1}(\gamma/e)$, then E_2 is unstable saddle along the z -axis. But this condition ensures the existence of the interior equilibrium E_* . Thus all populations of the system persist for long time.

This completes the proof.

We now analyze the stability of the system around the co-existing equilibrium point E_* . The characteristic equation corresponding to the interior equilibrium point E_* is given by

$$\lambda^3 + L_1\lambda^2 + L_2\lambda + L_3 = 0, \tag{4.4}$$

where

$$\begin{aligned} L_1 &= \alpha + u'(x_*)y_* + (y_*v'(y_*) - v(y_*))\frac{z_*}{y_*}, \\ L_2 &= (\alpha + u'(x_*)y_*)(y_*v'(y_*) - v(y_*))\frac{z_*}{y_*} + du(x_*)u'(x_*)y_* + ev(y_*)v'(y_*)z_*, \\ L_3 &= e\alpha z_*v(y_*)v'(y_*) + [v(y_*) - cd\gamma]ey_*z_*u'(x_*)v'(y_*). \end{aligned} \tag{4.5}$$

The real-part of the roots of equation (4.4) are negative if the coefficients L_i , ($i = 1, 2, 3$) satisfy the Routh-Hurwitz criteria [8, 9], $L_1 > 0$, $L_3 > 0$, $L_1L_2 - L_3 > 0$.

Here $L_1 > 0$ if $\alpha + u'(x_*)y_* + (y_*v'(y_*) - v(y_*))\frac{z_*}{y_*} > 0$. One of the conditions that $L_1 > 0$ is

$y_*v'(y_*) - v(y_*) > 0$. Then L_2 is automatically positive. Now, $L_3 > 0$ if $cd\gamma < v(y_*)$. Again,

$$\begin{aligned}
 L_1L_2 - L_3 &= \left(\alpha + u'(x_*)y_* + (y_*v'(y_*) - v(y_*))\frac{z_*}{y_*} \right) \\
 &\times \left((\alpha + u'(x_*)y_*)(y_*v'(y_*) - v(y_*))\frac{z_*}{y_*} + du(x_*)u'(x_*)y_* \right) \\
 &+ \left((y_*v'(y_*) - v(y_*))\frac{z_*}{y_*} \right) ev(y_*)v'(y_*)z_* + cde\gamma y_* z_* u'(x_*)v'(y_*)
 \end{aligned} \tag{4.6}$$

So, $L_1L_2 - L_3 > 0$ is the sum of all positive terms, hence $L_1L_2 - L_3 > 0$. Thus the system is stable around the interior equilibrium point if $y_*v'(y_*) - v(y_*) > 0$, $cd\gamma < v(y_*)$, which implies, $y_*v'(y_*) > cd\gamma$. The system (2.3) is stable around the interior equilibrium point E_* if the above condition is satisfied.

Thus we have obtained a set of stability conditions for the given detritus-based model for any functional response $u(x)$ and $v(x)$ for the detritivores and predator of detritivores. The above conditions are general conditions and to determine the qualitative behaviour one can apply the above conditions for any particular set of functional responses. The general functional response and the implied conditions for the stability of the model system is important from the applied mathematical point of view.

To get information on the dynamical behaviour of the system (2.3) we need to choose some particular set of functional responses and analyze the qualitative behaviour of the system.

5 Equilibria and stability with $u(x) = ax/(\mu + x)$ and $v(y) = b[1 - \exp(-\rho y)]$

We considered in Section 4 the generalised functional responses. The study does not follow good information for stability of model system (2.3). We have obtained only some mathematical conditions for the generalized functional responses. The importance of the study for the ecological point of view is less significant. So, we have considered two specific functional responses for detritivores and predator of detritivores and studied to obtain some condition on the system parameter. We choose Holling type-II functional response $u(x) = ax/(\mu + x)$ for the detritivores and Ivlev-type functional response $v(y) = b[1 - \exp(-\rho y)]$ for the predator of detritivores. The choice of functional responses is very appropriate for detritus-based ecosystem. Bandyopadhyay et al. [12] studied a detritus-based model system with $u(x) = x$ and $v(y) = y$. For our choice of functional responses the model system takes the following form

$$\begin{aligned}
 \frac{dx}{dt} &= S - \alpha x - \frac{ax}{\mu+x}y + c\gamma z, \\
 \frac{dy}{dt} &= -\beta y + d\frac{ax}{\mu+x}y - b(1 - e^{-\rho y})z, \\
 \frac{dz}{dt} &= z[-\gamma + eb(1 - e^{-\rho y})],
 \end{aligned} \tag{5.1}$$

with the non-negative initial conditions $x(0) = x_0 > 0$, $y(0) = y_0 > 0$, $z(0) = z_0 > 0$. Here μ is the half saturation constant and a is the maximum uptake rate. ρ is the rate at which the saturation is achieved with increasing detritus population density and b is the maximum detritus consumption rate.

The zero isoclines of this three equations give the following equilibria:

(a) $E_1(S/\alpha, 0, 0)$,

(b) $E_2\left(\frac{\beta\mu}{ad-\beta}, \frac{d}{\beta}\left(S - \alpha\frac{\beta\mu}{ad-\beta}\right), 0\right)$,

(c) $E_*(x_*, y_*, z_*)$, $x_* = \frac{1}{2\alpha}\left[P \pm \sqrt{P^2 + 4\alpha Q}\right]$, $y_* = \frac{1}{\rho} \ln\left[\frac{eb}{eb-\gamma}\right]$, $z_* = \frac{e}{\gamma}\left[-\beta + d\frac{ax_*}{\mu+x_*}\right]$,
 where $P = S - ce\beta y_* - \alpha\mu - a(1 - cde)y_*$, $Q = \mu(S - \beta cey_*)$.

E_1 always exists. E_2 is biologically meaningful if $ad > \beta$ and $S > \alpha\beta\mu/(ad - \beta)$. We suppose that $S > \beta cey_*$, then x_* becomes biologically feasible and is given by $x_* = [P + \sqrt{P^2 + 4\alpha Q}]/2\alpha$. $y_* > 0$ demands $eb > \gamma$. $z_* > 0$ implies $x_* > \beta\mu/(da - \beta)$. Putting the expression for x_* we arrive at $S > \alpha\beta\mu/(da - \beta) + (\beta/d\rho) \ln[eb/(eb - \gamma)]$. This is the condition that interior equilibrium E_* is biologically feasible.

We now study the stability of the model at several equilibria. We may take small perturbation of the population sizes about the equilibria, so that, retaining only the linear terms we arrive at a linearized system of differential equations analogous to system (4.1). Then deriving the characteristic equations at different equilibria we investigate if the real-parts of the roots of the characteristic equations are negative. Then the system is stable about that equilibria.

At E_1 , the system is stable if

$$S < \alpha\frac{\beta\mu}{ad - \beta}. \tag{5.2}$$

At E_2 , the system is stable if

$$\alpha\frac{\beta\mu}{ad - \beta} < S < \alpha\frac{\beta\mu}{da - \beta} + \frac{\beta}{d\rho} \ln\left(\frac{eb}{eb - \gamma}\right). \tag{5.3}$$

About the coexisting equilibrium E_* , the characteristic equation is

$$\lambda^3 + M_1\lambda^2 + M_2\lambda + M_3 = 0, \tag{5.4}$$

where $M_1 = -(b_{11} + b_{22})$, $M_2 = b_{11}b_{22} - b_{12}b_{21} - b_{23}b_{32}$, $M_3 = (b_{11}b_{23} - b_{13}b_{21})b_{32}$. The components are $b_{11} = -\alpha - a\mu/(\mu + x_*)^2$, $b_{12} = -ax_*/(\mu + x_*)$, $b_{13} = c\gamma$, $b_{21} = da\mu y_*/(\mu + x_*)^2$, $b_{22} = -\beta + da x_*/(\mu + x_*) - \rho b \exp(-\rho y_*)z_*$, $b_{23} = -b[1 - \exp(-\rho y_*)]$, $a_{32} = e\rho b \exp(-\rho y_*)z_*$.

Using the foregoing analysis we can determine that the equilibrium point E^* is stable if $y_* \frac{d}{dy} [b(1 - e^{-\rho y})]|_{y=y_*} - b(1 - e^{-\rho y_*}) > 0$, that is, $e^{\rho y_*} (1 + \rho y_*) > 1$.

From the above analysis it is clear that the stability of the model system depends on the system parameters. We have considered the parameter S on which different restrictions are considered to analyze several dynamical behaviour.

6. Conclusion

In this paper we have considered the deterministic model of detritus-based ecosystem which is comprised of detritivores and predator of detritivores. We have stated and proved several dynamical properties and characteristics of the model system. We have different levels of the constant supply of the nutrient at which different equilibria exist and feasible. The system is persistence as there is a transition among the equilibrium points due to the increase of the value of S . The increased value of the constant input is the key to the stability properties of the equilibrium points.

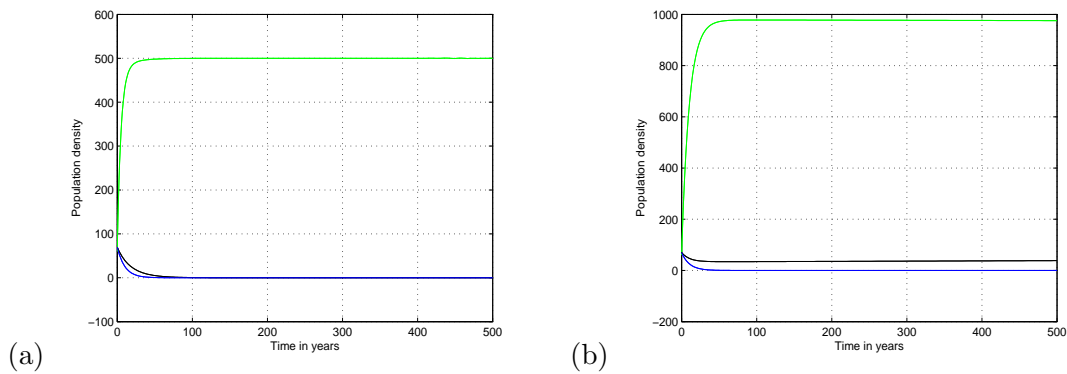


Figure 1: The system (2.3) experiences stable solutions around the axial and boundary equilibria E_1 and E_2 respectively.

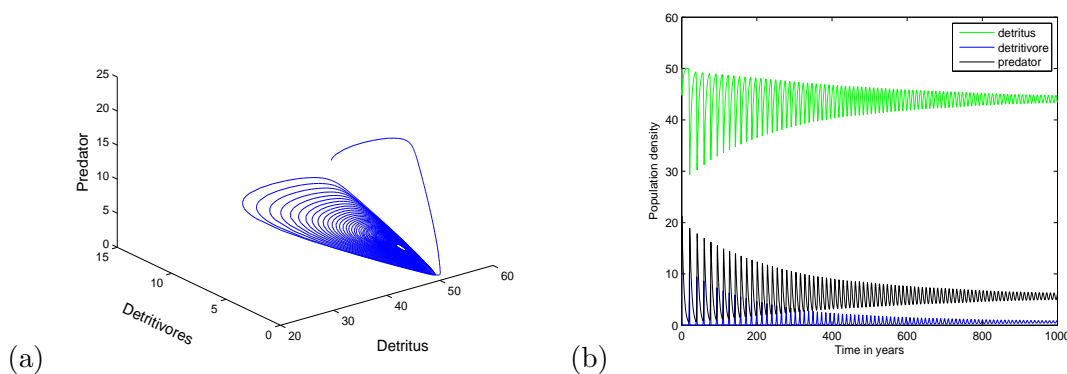


Figure 2: The system (2.3) experiences stable solution around the interior equilibrium E_* for the set of parameter values: $S = 10; \alpha = 0.20; d = 1.7; a = 2.5; c = 0.10; \gamma = 0.2; \beta = 1.5; e = 0.9; b = 70; \mu = 10; r = 0.005$.

Our numerical simulations show that the system (2.3) has stable solutions for a set of parameter values around E_1 and E_2 as shown in figure 1. For the set of parameter values $S = 10; \alpha = 2.0;$

$a = 2.5$; $d = 7$; $c = 0.010$; $\gamma = 0.02$; $\beta = 3$; $e = 0.09$; $b = 10$; $\mu = 10$; $\rho = 0.05$; and the initial population size $(10, 7, 10)$; the system has stable solution around E_* (Figure 2).

Finally, we want to remark that the input concentration of the constant supply of nutrient has very important role in shaping the dynamics of the model system. For different values of constant supply of nutrient the system may change from stable state to unstable state.

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