GLOBAL STABILITY AND PERSISTENCE OF THREE SPECIES FOOD WEB INVOLVING OMNIVORY

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Abstract:

In this paper, the dynamics of a three species food web model consisting of producers, primary consumers and omnivory is studied analytically as well as numeri-cally. The existence of equilibrium points and local stability analysis for this model is carried out together with a bifurcation analysis. The occurrence of hopf bifurcation is also investigated. The persistence conditions of the food web model are established by using average Lyapunov function. The global stability analysis of the food web model is also presented with help of Lyapunov method. Finally, in order to confirm our analytical results, numerical simulation is carried out for suitable choices of parameters values. It is observed that, the existence of omnivory in a food web plays a vital role in the stability of the dynamical behavior of the system.

Key words:Food web, Omnivory,Sability,Persistence, Bifurcation.

الاستقرارية الشاملة والاصرار للشبكة الغذائية ثلاثية الاجناس والمتضمنة القوارت

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الخلاصة

في هذا البحث قمنا بدراسة ديناميكية الشبكة الغذائية ثلاثية الاجناس والمتكونة من المنتجين، المستهلكين و القوارت تحليليا وعدديا. وجود نقاط التوازن وتحليل الاستقرارية المحلية لها مع تحليل التفرع اجري. كذلك ناقشنا حدوث تفرع – هوبف ايضا. شروط الاصرار للشبكة الغذائية وضعت بالاعتماد على متوسط دالة ليابانوف. كذلك درسنا الاستقرارية الشاملة للشبكة الغذائية بمساعدة طريقة ليابانوف. واخيرا، من اجل تأكيد النتائج التحليلية التي توصلنا لها، اجرينا محاكاة عددية للشبكة عند قيم مناسبة للمعلمات. لوحظ بأن وجود القوارت في الشبكة الغذائية يلعب دور حيوي في استقرار السلوك الديناميكي للنظام

Introduction:

It is well known that every organism needs to obtain energy in order to live. For example, plants get energy from the sun and people eat food. A food chain is the sequence of who eats whom in a biological community (an ecosystem) to obtain nutrition. A network of many food chains is called a food web. The food chain starts with plants or other autotrophs such as bacteria (organisms that make their own food from light and/or chemical energy) these organisms are called primary producers. The primary producers are eaten by herbivores (plant-eaters) called primary consumers. The herbivores are eaten by carnivores (meat-eaters) and omnivores (animals that eat both animals and plants at different trophic levels) these organisms are called secondary consumers. Secondary consumers may be eaten by other carnivores called tertiary consumers. When any organism dies, it is eaten by tiny microbes (detrivores) and the exchange of energy continues.

It is well known that, ecological models provide a way to understand the dynamical behavior of ecosystem. The time evolution of interacting species can be governed by mathematical equations. These governing equations together represent a model which dynamical behavior can be studied using mathematical methods analytically as well as numerically. Variety of mathematical models for food web or food chain, consisting of three or more species, incorporating different factors to suit the varied requirements is available in literature; see for example [1-6].

On the other hand omnivory, defined as the feeding on nonadjacent trophic levels and found to be widespread in nature [7], is a relevant topic of this paper. It has been studied with respect to conditions for coexistence, nutrient enrichment, top-down and bottom-up effects amongst others [8-14]. Earlier empirical research led to mixed opinions on whether omnivory is ubiquitous or rare in natural ecosystems. Additionally, theoretical studies suggested that the occurrence of omnivory destabilizes certain food chains as compared to linear food chain models [7]. This fitted well with the general idea that complex ecosystems tend to be unstable and would imply that omnivory is rare in nature. For these reasons, omnivory has long been a relatively neglected subject of research. However, McCann and Hastings [9] proposed a three-species omnivory food web model with a fixed preference term, and they concluding that intermediate omnivory levels tend to stabilize the food web dynamics. In fact, there are numerous examples of omnivory in natural ecosystems explained that omnivory is widespread; see [15] and the references their in.

Keeping the above in view, in this paper consideration is given to analyze and study the dynamical behavior and persistence of a three species omnivory food web model consisting of resource – primary consumer - secondary consumer.

Omnivory food web model

Consider a three species food web model consisting of primary producers population or resources population at the first level, primary consumers population or preys at the second level these eat the primary producers at the first level and secondary consumers population or predators at the third level, which in turn eat both the primary producers at the first level and primary consumers at the second level and hence they called omnivores. The dynamics of such simple food web model may be represented by the following set of equations;

$$\begin{aligned}\frac{dX}{dT} &= rX\left(1-\frac{X}{K}\right) - aXY - bXZ \\ \frac{dY}{dT} &= e_1 aXY - cYZ - d_1 Y \qquad (1) \\ \frac{dZ}{dT} &= e_2 bXZ + e_3 cYZ - d_2 Z\end{aligned}$$

where X, Y and Z represent the densities of primary producers, primary consumers and secondary consumers or omnivores at time T respectively. It is assumed that the primary producers grow logistically in the absence of other consumers with intrinsic growth rate $r > 0$ and carrying capacity $K > 0$. The primary and secondary consumers consume their food according to Lotka-Volterra type of functional response, where $a > 0$ and $b > 0$ are the predation rates on the primary producers for the primary consumers and secondary consumers respectively; $c > 0$ is the predation rate on the primary consumers for the secondary consumers; $e_i > 0$ for $i = 1,2,3$ are the conversion rates of predation into higher level species and finally $d_1 > 0$ and $d_2 > 0$ represent the natural death rates for the primary consumers and secondary consumers respectively. Clearly system (1) defined on the space $R_+^3 = \{(X,Y,Z) \in R^3 : X \geq 0, Y \geq 0, \quad Z \geq 0\}$ and has ten parameters in all which make the analysis of system (1) difficult. Therefore, in order to simplify the system and specify which set of parameters control the dynamics of the system, the following set of dimensionless variables and parameters are used:

$$t = rT, x = \frac{X}{K}, y = \frac{a}{r}Y, z = \frac{b}{r}Z$$
$$\alpha = \frac{e_1 aK}{r}, \beta = \frac{c}{b}, \theta = \frac{d_1}{r}, \qquad (2)$$
$$\sigma = \frac{e_2 bK}{r}, \delta = \frac{e_3 c}{a}, \gamma = \frac{d_2}{r}$$

then we will obtain the following dimen-sionless system:

$$\frac{dx}{dt} = x[1 - x - y - z] = f_1(x,y,z)$$
$$\frac{dy}{dt} = y[\alpha x - \beta z - \theta] = f_2(x,y,z) \qquad (3)$$
$$\frac{dz}{dt} = z[\sigma x + \delta y - \gamma] = f_3(x,y,z)$$

Here we have $x \geq 0, y \geq 0$ and $z \geq 0$. Also the interaction functions on the right hand side of system (3) are continuous and have continuously differentiable functions on the domain $R_+^3 = \{(x,y,z) \in R^3 : x \geq 0, y \geq 0, z \geq 0\}$. Therefore they are globally Lipschitzian functions and hence for any given initial condition $x(0) \geq 0, y(0) \geq 0$ and $z(0) \geq 0$ system (3) has a unique nonnegative solution. Further more, system (3) is a dissipative system as shown in the following theorem.

Theorem 1. System (3) is dissipative system on R_+^3.

Proof. It is well known that the dynamical system is dissipative if and only if it is uniformly bounded. Now according to the first equation of system (3) we have

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

So, by solving this differential inequality we get that

$$\lim_{t\to\infty} Sup.\, x(t) \leq 1 \Rightarrow x(t) \leq 1 \;\; \forall\, t > 0$$

Consider the following function

$$U = x + y + z\,.$$

Then

$$\frac{dU}{dt} = x - x^2 - (1-\alpha)xy - (1-\sigma)xz$$
$$- (\beta - \delta)yz - \theta y - \gamma z$$

Since for any biologically feasible system the conversion rates from a specific triphic level to the higher triphic levels can not be accede the corresponding attack rates, then $\alpha \leq 1$, $\sigma \leq 1$ and $\delta \leq \beta$. Therefore we obtain that

$$\frac{dU}{dt} \leq 2 - \pi U$$

Where $\pi = \min.\{1, \theta, \gamma\}$. Therefore, by solving the last differential inequality it is observed that

$$\lim_{t\to\infty} Sup.\, U(t) \leq \frac{2}{\pi} \Rightarrow U(t) \leq \frac{2}{\pi} \;\; \forall\, t > 0$$

Thus all solutions of system (3) are uniformly bounded, and hence the system is dissipative. ■

Stability analysis and bifurcation

In this section, the existence and locally stability analysis of all possible equilibrium points of system (3) are carried out. System (3) has at most five nonnegative equilibrium points. The vanishing equilibrium point $E_0 = (0,0,0)$ and the free consumers equilib-rium point $E_1 = (1,0,0)$ are always exist. The secondary consumer free equilibrium point $E_2 = (\frac{\theta}{\alpha}, \frac{\alpha-\theta}{\alpha}, 0)$ exists in the interior of xy-plane if and only if the following condition holds

$$\alpha > \theta \qquad (4)$$

The primary consumer free equilibrium point $E_3 = (\frac{\gamma}{\sigma}, 0, \frac{\sigma-\gamma}{\sigma})$ exists in the interior of xz-plane if and only if the following condition holds

$$\sigma > \gamma \qquad (5)$$

Finally, the coexistence equilibrium point $E_4 = (x^*, y^*, z^*)$ exists in the interior of positive octant (i.e $Int.R_+^3$), where

$$x^* = \frac{\delta(\beta+\theta) - \gamma\beta}{\delta(\beta+\alpha) - \sigma\beta}$$
$$y^* = \frac{\gamma(\beta+\alpha) - \sigma(\beta+\theta)}{\delta(\beta+\alpha) - \sigma\beta} \qquad (6)$$
$$z^* = \frac{\alpha\delta + \theta\sigma - (\alpha\gamma + \theta\delta)}{\delta(\beta+\alpha) - \sigma\beta}$$

Provided that, one set of the following sets of conditions is satisfied

$$\left.\begin{array}{l} \sigma\beta < \dfrac{\sigma\delta}{\gamma}(\beta+\theta) < \delta(\beta+\alpha) \\ \alpha\delta + \theta\sigma > \alpha\gamma + \theta\delta \end{array}\right\} \qquad (7)$$

or

$$\left.\begin{aligned}\delta(\beta+\alpha) < \frac{\sigma\delta}{\gamma}(\beta+\theta) < \sigma\beta \\ \alpha\delta+\theta\sigma < \alpha\gamma+\theta\delta\end{aligned}\right\} \quad (8)$$

Now, the local stability analyses near each of the above equilibrium points are carried out by using the linearization technique and the following results are obtained

The eigenvalues of the Jacobian matrix of system (3) at the vanishing equilibrium point $E_0 = (0,0,0)$ are $\lambda_{0x} = 1$, $\lambda_{0y} = -\theta$ and $\lambda_{0z} = -\gamma$, and hence E_0 is a saddle point with locally stable manifold in the yz-plane and with locally unstable manifold in the x-direction.

The eigenvalues of the Jacobian matrix of system (3) at the consumers free equilibrium point $E_1 = (1,0,0)$ are $\lambda_{1x} = -1$, $\lambda_{1y} = \alpha - \theta$ and $\lambda_{1z} = \sigma - \gamma$, and hence E_1 is locally asymptotically stable point if and only if the following conditions are satisfied.

$$\alpha < \theta \text{ and } \sigma < \gamma \quad (9)$$

However if at least one of the boundary equilibrium points E_2 and E_3 exists (that is mean at least one of the conditions 4 and 5 hold) then E_1 is saddle point.

Keeping the above in view, the occurrence of bifurcation in system (3) near E_1 is studied in the following theorem.

Theorem 2. At $\sigma = \gamma :(= \sigma_1)$ the consumers free equilibrium point E_1 transforms into a nonhyperbolic equilibrium point and if $\alpha < \theta$ then system (3) possesses transcritical bifurcation, but no saddle-node bifurcation nor pitch-fork bifurcation can occur.

Proof. Clearly, at σ_1 the eigenvalue $\lambda_{1z} = 0$ in the Jacobian matrix of system (3) at E_1, say $J_1 = DF(E_1, \sigma_1)$, with $F = (f_1, f_2, f_3)^t$. However the other two eigenvalues $\lambda_{1x} = -1 < 0$, $\lambda_{1y} = \alpha - \theta < 0$. Thus E_1 is a nonhyperbolic equilibrium point for system (3).

Now, it is easy to verify that $V = (-v, 0, v)^t$ and $W = (0,0,w)^t$ are the eigenvectors corresponding to the eigenvalue $\lambda_{1z} = 0$ of the matrices J_1 and J_1^t respectively. Here v and w are any two non-zero real numbers. So, according to Sotomayor theorem [16], it is observed that;

Since $W^t[F_\sigma(E_1, \sigma_1)] = 0$ the system does not possesses any saddle-node bifurcation.

Also since $W^t[DF_\sigma(E_1, \sigma_1)V] = vw \neq 0$ and $W^t[D^2F(E_1, \sigma_1)(V,V)] = -2\sigma_1 v^2 w \neq 0$ where $DF_\sigma(E_1, \sigma_1) = (\pi_{ij})_{3\times3}$ with $\pi_{33} = 1$; $\pi_{ij} = 0$ otherwise and $D^2F(E_1, \sigma_1)$ is a $3\times3\times3$ tensor, then system (3) possesses a transcritical bifurcation. Finally since $W^t[D^2F(E_1, \sigma_1)(V,V)] = -2\sigma_1 v^2 w \neq 0$ the system does not attain pitch-fork bifurcations. ■

Similarly, it is easy to prove that system (3) possesses transcritical bifurcation near E_1 when $\alpha = \theta$ and $\sigma < \gamma$.

The eigenvalues of the Jacobian matrix of system (3) at the secondary consumers free equilibrium point $E_2 = (\frac{\theta}{\alpha}, \frac{\alpha-\theta}{\alpha}, 0)$ are given by

$$\left.\begin{aligned}\lambda_{2x}, \lambda_{2y} &= \frac{-\theta \pm \sqrt{\theta^2 - 4\theta\alpha(\alpha-\theta)}}{2\alpha} \\ \lambda_{2z} &= \frac{\sigma\theta + \delta(\alpha-\theta) - \alpha\gamma}{\alpha}\end{aligned}\right. \quad (10)$$

Consequently, due to the existence condition (4) the eigenvalues, which describe the dynamic in the x and y directions (i.e. $\lambda_{2x}, \lambda_{2y}$) have negative real parts. Further, if the following condition holds

$$\sigma\theta + \delta(\alpha-\theta) < \alpha\gamma \quad (11)$$

Then E_2 is locally asymptotically stable in the R_+^3. However it is saddle point with locally stable manifold in xy-plane and with locally unstable manifold in the z-direction provided that

$$\sigma\theta + \delta(\alpha-\theta) > \alpha\gamma \quad (12)$$

Moreover, the occurrence of bifurcation in system (3) near E_2 is studied in the following theorem.

Theorem 3. At $\gamma = \frac{\sigma\theta}{\alpha} + \frac{\delta(\alpha-\theta)}{\alpha} :(= \gamma_2)$ the secondary consumers free equilibrium point E_2 transforms into a nonhyperbolic equilib-rium and if $\frac{\sigma\beta}{\alpha} \neq \frac{\delta\beta}{\alpha} + \delta$ system (3) possesses transcritical bifurcation, but no saddle-node bifurcation nor pitch-fork bifurcation can occur.

Proof. Clearly, at γ_2 the eigenvalue $\lambda_{2z} = 0$ in the Jacobian matrix of system (3) at E_2, say $J_2 = DF(E_2, \gamma_2)$, with $F = (f_1, f_2, f_3)^t$. However the other two eigenvalues are given in Eq. (10). Clearly λ_{2x} and λ_{2y} have negative real parts. Thus E_1 is a nonhyperbolic equilibrium point for system (3).

Now, it is easy to verify that $\overline{V}=(\frac{\beta}{\alpha}v,-(\frac{\beta}{\alpha}+1)v,v)^t$ and $\overline{W}=(0,0,w)^t$ are the eigenvectors corresponding to the eigenvalue $\lambda_{2z}=0$ of the matrices J_2 and $J_2^{\,t}$ respectively. Here v and w are any two non-zero real numbers. So, according to Sotomayor theorem [16], it is observed that;

Since $\overline{W}^t[F_\gamma(E_2,\gamma_2)]=0$ the system does not possesses any saddle-node bifurcation.

Also since $\overline{W}^t[DF_\gamma(E_2,\gamma_2)\overline{V}]=-vw\neq 0$ and $\overline{W}^t[D^2F(E_2,\gamma_2)(\overline{V},\overline{V})]=2(\frac{\sigma\beta}{\alpha}-\frac{\delta\beta}{\alpha}-\delta)v^2w\neq 0$ provided that the given condition holds, where $DF_\gamma(E_2,\gamma_2)=(\pi_{ij})_{3\times 3}$ with $\pi_{33}=-1$; $\pi_{ij}=0$ otherwise and $D^2F(E_2,\gamma_2)$ is a $3\times 3\times 3$ tensor, then system (3) possesses a transcritical bifurcation. Finally since $\overline{W}^t[D^2F(E_2,\gamma_2)(\overline{V},\overline{V})]\neq 0$ the system does not attain pitch-fork bifurcations. ■

The eigenvalues of the Jacobian matrix of system (3) at the primary consumer free equilibrium point $E_3=(\frac{\gamma}{\sigma},0,\frac{\sigma-\gamma}{\sigma})$ are given by

$$\lambda_{3x},\lambda_{3z}=\frac{-\gamma\pm\sqrt{\gamma^2-4\gamma\sigma(\sigma-\gamma)}}{2\sigma}$$
$$\lambda_{3y}=\frac{\alpha\gamma-\beta(\sigma-\gamma)-\sigma\theta}{\sigma} \quad (13)$$

Consequently, due to the existence condition (5) the eigenvalues, which describe the dynamic in the x and z directions (i.e. $\lambda_{3x},\lambda_{3z}$) have negative real parts. Further, if the following condition holds

$$\alpha\gamma<\beta(\sigma-\gamma)+\sigma\theta \quad (14)$$

Then E_3 is locally asymptotically stable in the R_+^3. However it is saddle point with locally stable manifold in xz-plane and with locally unstable manifold in the y-direction provided that

$$\alpha\gamma>\beta(\sigma-\gamma)+\sigma\theta \quad (15)$$

Similarly as shown in theorem (3), the following theorem that presents the occurrence of bifurcation in system (3) near E_3 can be proved easily.

Theorem 4. At $\theta=\frac{\alpha\gamma}{\sigma}-\frac{\beta(\sigma-\gamma)}{\sigma}:(=\theta_3)$ the primary consumer free equilibrium point E_3 transforms into a nonhyperbolic equilibrium and if $\frac{\alpha\delta}{\sigma}+\frac{\beta\delta}{\sigma}\neq 1$ system (3) possesses transcritical bifurcation, but no saddle-node bifurcation nor pitch-fork bifurcation can occur.

Note that, according to the forms of eigenvalues of the Jacobiam matrix of system (3) near each of the above equilibrium points, there is no possibility to have pure imaginary eigenvalues. Therefore system (3) can not have hopf bifurcation near them.

Finally the eigenvalues of the Jacobian matrix of system (3) at the coexistence equilibrium point $E_4=(x^*,y^*,z^*)$ are the roots of the following characteristic equation.

$$\lambda^3+A_1\lambda^2+A_2\lambda+A_3=0 \quad (16)$$

Here

$$A_1=x^*$$
$$A_2=\alpha x^*y^*+\sigma x^*z^*+\beta\delta y^*z^*$$
$$A_3=x^*y^*z^*(\alpha\delta+\beta\delta-\beta\sigma)$$

Moreover

$$\Delta=A_1A_2-A_3$$
$$=x^*\left(\alpha x^*y^*+\sigma x^*z^*+(\sigma\beta-\alpha\delta)y^*z^*\right)$$

According to the Routh-Hurwitz criterion, all the eigenvalues of the Jacobian matrix at E_4 have negative real parts and hence E_4 is locally asymptotically stable in the $Int.R_+^3$ if and only if $A_i>0$ for $i=1,3$ and $\Delta>0$. Consequently, it is easy to verify that E_4 is locally asymptotically stable in the $Int.R_+^3$ provided that the set of existence conditions (7) with the following condition are hold

$$x^*(\alpha y^*+\sigma z^*)>(\alpha\delta-\sigma\beta)y^*z^* \quad (17)$$

Otherwise it is unstable point.

Recall that, the necessary and sufficient conditions for a hopf bifurcation to occur is that, there exists a value of a certain bifurcation parameter δ, namely δ_*, such that [17]

$$\Delta(\delta_*)=A_1(\delta_*)A_2(\delta_*)-A_3(\delta_*)=0 \quad (18)$$
$$\frac{d}{d\delta}\left(\mathrm{Re}(\lambda(\delta))\right)\Big|_{\delta=\delta_*}\neq 0 \quad (19)$$

Here $\lambda(.)$ is a root of the characteristic equation (16).

Consequently, according to condition (17) it is clear that condition (18) holds if and only if

$$\delta_*=\frac{1}{\alpha y^*z^*}(\alpha x^*y^*+\sigma x^*z^*+\sigma\beta y^*z^*) \quad (20)$$

Therefore for $\delta=\delta_*$, which may or may not be a hopf bifurcation parameter, Eq. (16) can be written as

$$P_3(\lambda)=(\lambda+A_2)(\lambda+A_1)=0 \quad (21)$$

Note that Eq. (21) has the three roots $\lambda_{41}=+i\sqrt{A_2}$, $\lambda_{42}=-i\sqrt{A_2}$, and $\lambda_{43}=-A_1$.

Clearly for all values of δ, the roots are in general of the following roots

$$\lambda_{41}(\delta)=\omega_1(\delta)+i\omega_2(\delta)$$
$$\lambda_{42}(\delta)=\omega_1(\delta)-i\omega_2(\delta)$$
$$\lambda_{43}(\delta)=-A_1(\delta)$$

So, in order to check the occurrence of hopf bifurcation around E_4, we have to verify the trasversality condition (19), that is

$$\frac{d}{d\delta}\left(\mathrm{Re}(\lambda_{4j}(\delta))\right)\Big|_{\delta=\delta_*}\neq 0\,;\ j=1,2$$

Substituting $\lambda_{41}(\delta)=\omega_1(\delta)+i\omega_2(\delta)$ into the Eq. (21) and calculating the derivative with respect to the bifurcation parameter δ, that is $\frac{d}{d\delta}P_3(\lambda)=P_3'(\lambda)=0$, and then comparing the two sides of this equation and equating their real and imaginary parts, it is obtain that

$$\begin{aligned}\Omega(\delta)\omega_1'(\delta)-\Sigma(\delta)\omega_2'(\delta)&=-\Phi(\delta)\\ \Sigma(\delta)\omega_1'(\delta)+\Omega(\delta)\omega_2'(\delta)&=-\Psi(\delta)\end{aligned}\qquad(22)$$

where

$$\Omega(\delta)=3\omega_1^2-3\omega_2^2+A_2+2A_1\omega_1$$
$$\Sigma(\delta)=6\omega_1\omega_2+2A_1\omega_2$$
$$\Phi(\delta)=A_2'\omega_1+A_1'\omega_1^2-A_1'\omega_2^2+A_1'A_2+A_1A_2'$$
$$\Psi(\delta)=A_2'\omega_2+2A_1'\omega_1\omega_2$$

Solving the linear system (22) for the unknown $\omega_1'(\delta)$ and $\omega_2'(\delta)$ it is obtain that

$$\omega_1'(\delta)=\frac{d}{d\delta}\mathrm{Re}(\lambda_{4j}(\delta))=-\frac{\Phi\Omega+\Psi\Sigma}{\Omega^2+\Sigma^2}$$

Hence the transversality condition (19) will be reduces to verifying that

$$\Phi(\delta_*)\Omega(\delta_*)+\Psi(\delta_*)\Sigma(\delta_*)\neq 0 \qquad (23)$$

Straight forward computation shows that $A_1'(\delta_*)=0$, $A_2'(\delta_*)=\beta y^* z^*$, $\omega_1(\delta_*)=0$, $\omega_2(\delta_*)=\sqrt{A_2(\delta_*)}$, $\Omega(\delta_*)=-2A_2(\delta_*)$, $\Sigma(\delta_*)=2A_1(\delta_*)\sqrt{A_2(\delta_*)}$, $\Phi(\delta_*)=\beta x^* y^* z^*$ and $\Psi(\delta_*)=\beta y^* z^*\sqrt{A_2(\delta_*)}$.

Therefore we get that

$$\Phi(\delta_*)\Omega(\delta_*)+\Psi(\delta_*)\Sigma(\delta_*)=0$$

Hence system (3) dose not undergo a hopf bifurcation around E_4.

Persistence

In general persistence is a global property of a dynamical system; it is not dependent upon interior solution space structure but is dependent upon solution behavior near extinction boundaries (boundary planes). From the biological point of view, Persistence of a system means the survival of all population of the system in future time. However, mathematically it means that strictly positive solutions do not have omega limit set on the boundary of the non-negative cone [18]. Accordingly, if the dynamical system dose not persists then the solution have omega limit set on the boundary of the nonnegative cone, and hence the dynamical system faces extinction. Now before examine the persistence of the food web model given by system (3) by using the method of average Lyapunov function as given in [19], we need to study the global dynamics in the boundary planes xy and xz as shown bellow.

It is easy to verify that system (3) has two subsystems given by

$$\begin{aligned}\frac{dx}{dt}&=x(1-x-y)=h_1(x,y)\\ \frac{dy}{dt}&=y(\alpha x-\theta)=h_2(x,y)\end{aligned}\qquad(24)$$

And

$$\begin{aligned}\frac{dx}{dt}&=x(1-x-z)=k_1(x,z)\\ \frac{dz}{dt}&=z(\sigma x-\gamma)=k_2(x,z)\end{aligned}\qquad(25)$$

Clearly subsystem (24) is obtained in the absence of secondary consumer z, while subsystem (25) is obtained in the absence of primary consumer y. Also the subsystem (24) has three equilibrium points namely $p_0=(0,0), p_1=(1,0)$ and $p_2=(\frac{\theta}{\alpha},\frac{\alpha-\theta}{\alpha})$, while subsystem (25) has three equilibrium points given by $q_0=(0,0), q_1=(1,0)$ and $q_2=(\frac{\gamma}{\sigma},\frac{\sigma-\gamma}{\sigma})$. Moreover, these subsystems have the same local stability conditions as those of system (3) in the boundary planes xy and xz respectively.

Keeping the above in view, the following two theorems established the global dynamics in the interior of positive quadrants of each subsystem.

Theorem 5. The subsystem (24) has a globally asymptotically stable positive equilibrium point $p_2=(\frac{\theta}{\alpha},\frac{\alpha-\theta}{\alpha})$ whenever it exists.

Proof. Consider the following function $H_1(x,y)=\frac{1}{xy}$ for all $x>0, y>0$. Obviously, $H_1(x,y)>0$ is a continuously differentiable function in the interior of xy-plane.

Now, since

$$\nabla=\frac{\partial}{\partial x}(h_1H_1)+\frac{\partial}{\partial y}(h_2H_1)=-\frac{1}{y}<0$$

For all the values of $x>0, y>0$. Clearly $\nabla(x,y)$ does not change sign and is not identically zero in the positive quadrant of xy-plane. Then by using Bendixson-Dulac criterion subsystem (24) has no periodic dynamic in the interior of positive quadrant of xy-plane. Further, since p_2 is the only positive equilibrium point of subsystem (24) in the interior of positive quadrant of xy-plane. Hence according to Poincare- Bendixson theorem p_2 is a globally asymptotically stable in the interior of positive quadrant of xy-plane ■

Theorem 6. The subsystem (25) has a globally asymptotically stable positive equilibrium point $q_2 = (\frac{\gamma}{\sigma}, \frac{\sigma-\gamma}{\sigma})$ whenever it exists.

Proof. Similar to proof of pervious theorem except the use of the following Dulac function $H_2(x,z) = \frac{1}{xz}$ for all $x>0, z>0$. ■

Note that, since the boundary equilibrium points E_2 and E_3 of system (3) in the interior of the boundary planes xy and xz respectively are coincide with p_2 and q_2 of subsystems (24) and (25) respectively. Hence system (3) has no periodic dynamic in the interior of boundary planes. In fact E_2 and E_3 of system (3) are globally asymptotically stable with the basins of attractions $\Theta_1 = \{(x,y,0) \in R_+^3 : x>0, y>0, z=0\}$, $\Theta_2 = \{(x,0,z) \in R_+^3 : x>0, y=0, z>0\}$ respectively.

Theorem 7. Assume that the boundary equilibrium points E_2 and E_3 of system (3) exist. Then system (3) is uniformly persistent if and only if conditions (12) and (15) are hold.

Proof. Consider the following average Lyapunov function $\Psi(x,y,z) = x^{r_1} y^{r_2} z^{r_3}$, where each $r_i; i=1,2,3$ is assumed to be positive. Obviously $\Psi(x,y,z)$ is continuously differentiable positive function defined in R_+^3. Now, since

$$\begin{aligned}\Xi(x,y,z) &= \frac{\Psi'(x,y,z)}{\Psi(x,y,z)} \\ &= r_1(1-x-y-z) \\ &\quad + r_2(\alpha x - \beta z - \theta) \\ &\quad + r_3(\sigma x + \delta y - \gamma)\end{aligned}$$

Also, we have already proved that the solutions of system (3) are uniformly bounded in the R_+^3 (see theorem 1), and the vanishing equilibrium point E_0 is an unstable saddle point with locally unstable manifold in the x-direction. So to proof the uniformly persistence of system (3) it is enough to show that $\Xi(x,y,z)>0$ at the equilibrium points E_1, E_2 and E_3, which are belong to R_+^3, for any $r_i > 0$ and $i=1,2,3$. Note that, for $E_1 = (1,0,0)$ we have

$$\Xi(1,0,0) = r_2(\alpha-\theta) + r_3(\sigma-\gamma)$$

Thus $\Xi(1,0,0) > 0$ for any $r_i > 0$ and $i=2,3$ whenever E_2 and E_3 exist.

For $E_2 = (\frac{\theta}{\alpha}, \frac{\alpha-\theta}{\alpha}, 0)$ we have

$$\Xi\left(\frac{\theta}{\alpha}, \frac{\alpha-\theta}{\alpha}, 0\right) = r_3\left(\frac{\sigma\theta}{\alpha} + \frac{\delta(\alpha-\theta)}{\alpha} - \gamma\right)$$

Clearly $\Xi\left(\frac{\theta}{\alpha}, \frac{\alpha-\theta}{\alpha}, 0\right) > 0$ for any $r_3 > 0$ provided that condition (12) holds.

For $E_3 = (\frac{\gamma}{\sigma}, 0, \frac{\sigma-\gamma}{\sigma})$ we have

$$\Xi\left(\frac{\gamma}{\sigma}, 0, \frac{\sigma-\gamma}{\sigma}\right) = r_2\left(\alpha\frac{\gamma}{\sigma} - \beta\frac{\sigma-\gamma}{\sigma} - \theta\right)$$

Thus $\Xi(\frac{\gamma}{\sigma}, 0, \frac{\sigma-\gamma}{\sigma}) > 0$ for any $r_2 > 0$ provided that condition (15) holds.

Therefore, since there is no periodic dynamics in the boundary planes as shown in theorems 3-4 and E_i; $i=0,1,2,3$ is the only possible omega limit sets in the boundary planes. Hence system (3) is uniformly persists if E_2 and E_3 exist and conditions (12) with (15) hold. ■

Global stability analysis.

In this section, the global dynamics of system (3) is studied with the help of method of Lyapunov function. In the following theorems we present conditions for each of the equilibrium points E_1, E_2, E_3 and E_4 of system (3) to be globally asymptotically stable respectively.

Theorem 8. Assume that the consumers free equilibrium point $E_1 = (1,0,0)$ of system (3) is locally asymptotically stable. Then if

$$\beta\sigma \geq \delta\alpha \qquad (26)$$

E_1 is globally asymptotically stable in R_+^3.

Proof. Consider the following positive definite Lyapunov function about E_1;

$$V_1(x,y,z) = (x - 1 - \ln(x)) + \frac{y}{\alpha} + \frac{z}{\sigma}$$

Clearly, V_1 is a continuously differentiable real valued function defined on R_+^3. Further, we have

$$\frac{dV_1}{dt} = -(x-1)^2 - \left(\frac{\theta-\alpha}{\alpha}\right)y$$
$$-\left(\frac{\gamma-\sigma}{\sigma}\right)z - \left(\frac{\beta\sigma-\delta\alpha}{\alpha\sigma}\right)yz$$

Clearly, it is easy to verify that under the local stability condition (9) of E_1 and the above given condition (26) we obtain that $\frac{dV_1}{dt} < 0$ for any point in R_+^3, and hence E_1 is globally asymptotically stable in R_+^3. ■

Theorem 9. Assume that the secondary consumers free equilibrium point $E_2 = (\frac{\theta}{\alpha}, \frac{\alpha-\theta}{\alpha}, 0)$ of system (3) exists with

$$\alpha\delta \le \sigma\beta \tag{27a}$$

$$\sigma\theta + \frac{\sigma\beta}{\alpha}(\alpha-\theta) \le \alpha\gamma \tag{27b}$$

Then E_2 is globally asymptotically stable in R_+^3.

Proof. Consider the following positive definite Lyapunov function about E_2:

$$V_2(x,y,z) = \alpha\sigma\left(x - \frac{\theta}{\alpha} - \frac{\theta}{\alpha}\ln\left(\frac{\alpha x}{\theta}\right)\right)$$
$$+\sigma\left(y - \frac{\alpha-\theta}{\alpha} - \frac{\alpha-\theta}{\alpha}\ln\left(\frac{\alpha y}{\alpha-\theta}\right)\right) + \alpha z$$

Clearly, V_2 is a continuously differentiable real valued function defined on R_+^3. Further, we have

$$\frac{dV_2}{dt} = -\alpha\sigma\left(x - \frac{\theta}{\alpha}\right)^2 - (\sigma\beta - \alpha\delta)yz$$
$$-\left(\alpha\gamma - \sigma\theta - \sigma\beta\frac{\alpha-\theta}{\alpha}\right)z$$

According to the above, conditions (27a)-(27b) guarantee that $\frac{dV_2}{dt} < 0$ for any point in R_+^3, and hence E_2 is globally asymptoti-cally stable in R_+^3.■

Theorem 10. Assume that the primary consumers free equilibrium point $E_3 = (\frac{\gamma}{\sigma}, 0, \frac{\sigma-\gamma}{\sigma})$ of system (3) exists with

$$\alpha\delta \le \sigma\beta \tag{28a}$$

$$\alpha\gamma \le \sigma\theta + \frac{\alpha\delta}{\sigma}(\sigma-\gamma) \tag{28b}$$

Then E_3 is globally asymptotically stable in R_+^3.

Proof. Consider the following positive definite Lyapunov function about E_3:

$$V_3(x,y,z) = \alpha\sigma\left(x - \frac{\gamma}{\sigma} - \frac{\gamma}{\sigma}\ln\left(\frac{\sigma x}{\gamma}\right)\right) + \sigma y$$
$$+\alpha\left(z - \frac{\sigma-\gamma}{\sigma} - \frac{\sigma-\gamma}{\sigma}\ln\left(\frac{\sigma y}{\sigma-\gamma}\right)\right)$$

Clearly, V_3 is a continuously differentiable real valued function defined on R_+^3. Further, we have

$$\frac{dV_3}{dt} = -\alpha\sigma\left(x - \frac{\gamma}{\sigma}\right)^2 - (\sigma\beta - \alpha\delta)yz$$
$$-\left(\sigma\theta + \alpha\delta\frac{\sigma-\gamma}{\sigma} - \alpha\gamma\right)y$$

Clearly, $\frac{dV_3}{dt} < 0$ for any point in R_+^3 provided that conditions (28a)-(28b) are hold. Hence E_3 is globally asymptotically stable in R_+^3. ■

Finally the global stability of the coexistence equilibrium point of system (3) is investigated in the following theorem.

Theorem 11. Assume that the coexistence equilibrium point $E_4 = (x^*, y^*, z^*)$ of system (3) exists with

$$\sigma\beta = \alpha\delta \tag{29}$$

Then E_4 is globally asymptotically stable in R_+^3.

Proof. Consider the following positive definite Lyapunov function about E_4:

$$V_4(x,y,z) = \left(x - x^* - x^*\ln\left(\frac{x}{x^*}\right)\right)$$
$$+\frac{1}{\alpha}\left(y - y^* - y^*\ln\left(\frac{y}{y^*}\right)\right)$$
$$+\frac{1}{\sigma}\left(z - z^* - z^*\ln\left(\frac{z}{z^*}\right)\right)$$

Clearly, V_4 is a continuously differentiable real valued function defined on R_+^3. Further, we have

$$\frac{dV_4}{dt} = -(x-x^*)^2$$
$$-\left(\frac{\sigma\beta-\alpha\delta}{\alpha\sigma}\right)(y-y^*)(z-z^*)$$

Consequently, $\frac{dV_4}{dt} < 0$ for any point in R_+^3 provided that condition (29) holds. Hence the coexistence point E_4 is globally asymptotically stable in R_+^3. ■

Numerical Simulation

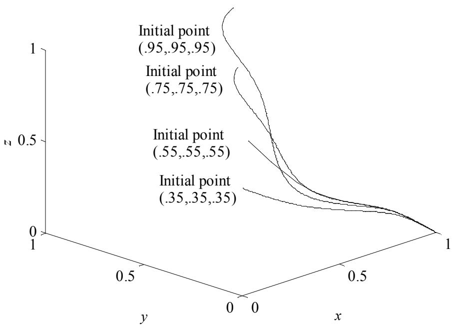
In this section the global dynamics of system (3) is investigated numerically. The system is solved numerically for different sets of parameters values and for different sets of initial conditions. The objectives are first to confirm our analytical results in the pervious sections and second understanding the effect of omnivory on the stability and coexistence of food web model.

It is observed that, for the following hypothetical set of biologically feasible parameters values

$$\alpha = 0.15, \beta = 1.0, \theta = 0.2, \quad \sigma = 0.15, \delta = 0.4, \gamma = 0.2 \qquad (30)$$

System (3) approaches asymptotically to consumers free equilibrium point E_1 as shown in the **(Figure-1)**.

Clearly at the above set of data the global stability condition (26) of E_1 is satisfied and boundary equilibrium points do not exist.

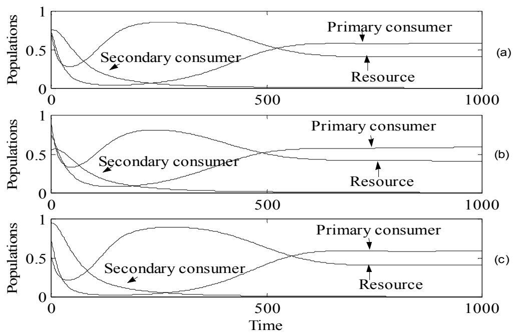


(Figure-1) System (3) approaches asymptotically to E_1 from different sets of initial points.

For the following set of parameters values

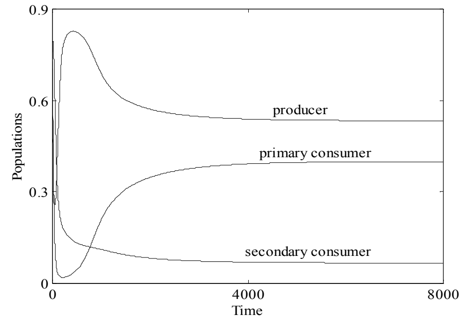
$$\alpha = 0.5, \beta = 1.0, \theta = 0.2, \quad \sigma = 0.25, \delta = 0.4, \gamma = 0.4 \qquad (31)$$

(Figure-2) shows clearly the approaching of the solutions of system (3), which started from different sets of initial points, to the secondary consumers free equilibrium point $E_2 = (0.4, 0.6, 0)$.



(Figure-2) The time series of system (3); (a) the solution approaches to E_2 from $(.75,.75,.75)$. (b) the solution approaches to E_2 from $(.95,.75,.55)$. (c) the solution approaches to E_2 from $(.55,.75,.95)$.

It is easy to verify that at the data given by (31), the global stability condition (27) of E_2 is satisfied, while E_3 do not exist. Further investigations for the dynamical behavior of system (3) show that, for the range $\sigma \leq 0.4$ with the rest of parameters as in (31), system (3) approaches to E_2, while for $0.4 < \sigma \leq 0.5$ system (3) approaches to coexistence equilibrium point E_4 as shown in **(Figure-3),** and hence the system persist. However, for the values of $\sigma > 0.5$, it is observed that system (3) approaches asymp-totically to primary consumers free equilib-rium point E_3.

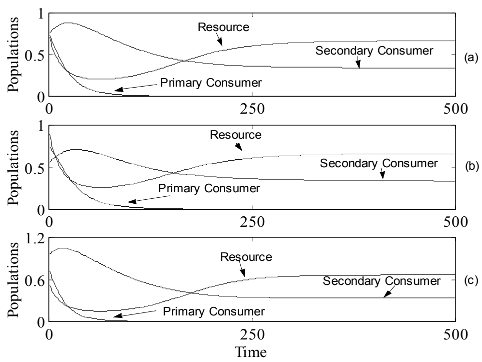


(Figure-3) System (3) approaches asymptotically to coexistence point E_4.

Moreover, for the following set of parameters:

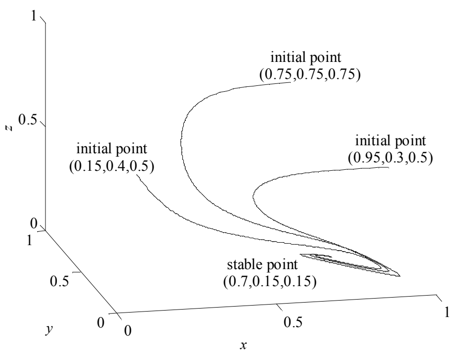
$$\alpha = 0.5, \beta = 1.0, \theta = 0.2, \quad \sigma = 0.3, \delta = 0.4, \gamma = 0.2 \qquad (32)$$

Both the equilibrium points E_2 and E_3 are exist and system (3) has a globally asymptotically stable point E_3, as shown in **(Figure-4)**.



(Figure-4) The time series of system (3); (a) the solution approaches to E_3 from $(.75,.75,.75)$. (b) the solution approaches to E_3 from $(.95,.75,.55)$. (c) the solution approaches to E_3 from $(.55,.75,.95)$.

However for the data given by (32) with $\sigma = 0.2$, system (3) has a globally asymptotically stable coexistence equilib-rium point $E_4 = (0.7, 0.15, 0.15)$ as shown in the following figure.



(Figure-5) System (3) approaches asymptotically to E_4 from different sets of initial points.

Further investigations show that, for the set of parameters given by (32) with $\sigma \le 0.25$ system (3) has a globally stable coexistence equilibrium point E_4. However system (3) has a globally asymptotically stable equilib-rium point at E_3 for $\sigma > 0.25$.

Discussion and conclusion

In this paper, the role of omnivory on the dynamical behavior and coexistence of the food web model is considered. The local as well as global stability analysis along with bifurcation analysis is carried out. The conditions at which the food web model persists are found. Finally numerical simulation for suitable sets of parameters values is used to investigate the global dynamics of the system. It is observed that existence of omnivory in a simple food web plays a vital role on the persistence and the stability of the food web model. In fact it is observed that the system has no periodic dynamics, instead of that the system approaches asymptotically to one of its equilibrium points as the control parameter varying its values, this is due to the occurrence of transcritical bifurcation. Further, when the solution of system approaches to boundary equilibrium point E_2 in the interior of $xy-$plane, then slightly increases the value of parameter σ that responsible on the omnivory in a food web model makes the system coexists and the solution approaches to positive equilibrium point. However, when the solution of system approaches to boundary equilibrium point E_3 in the interior of $xz-$plane, then slightly decreases the value of parameter σ makes the system coexists and the solution approaches to positive equilibrium point too.

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