

# A Commensal Consumer-Induced Mediation Effects on Resource–Consumer Interactions

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**Abstract** A general view of resource–consumer interactions is that resource intake by the consumers reduces the growth rate of resource population but it leads to an increase of consumer population. This view is proficiently interpreted with the classic Lotka–Volterra model that successfully describes the effects of changes in consumption rates due to changes in resource and consumer population densities. These effects are resulted in perpetual oscillatory dynamics of both the population densities, and the extent of the effects for given initial densities is measured by the oscillating frequency determined by the model parameters. But in many ecosystems, it has often observed a steep decline and delayed recovery in resource population that cannot be explained by the traditional Lotka–Volterra

model. Foraging habits and behaviors of a consumer population may facilitate others, those usually do not affect them directly, to feed on the same resource and then to reproduce successfully. Such commensal consumers (facilitated population) can heavily influence the rate of resource exploitation and thereby affect the usual resource–consumer cycles. While involving such commensal consumer-induced effects, called here commensal mediation, into the Lotka–Volterra type models, it shows that the commensal mediation can have stabilizing or destabilizing effects on resource dynamics depending on the strength of interactions and the conditions in which the interactions occur. In the natural ecosystems where the growth rate of resource population depends on its own density even in absence of consumers, the commensal mediation provides a destabilizing effect on resource dynamics; increasing commensal population density increases the amplitude of resource fluctuations and the time lags from one peak to the next. On the other hand, in the managed ecosystems where the growth rate of resource population is expected to be maintained at a constant level in absence of consumers, the commensal mediation provides stabilizing effect at a certain condition; with a given restriction on the consumer population, decreasing mortality of the commensal population can stabilize the resource population dynamics at a stable, steady-state. Moreover, while the resource population experiences saturation effect, resource–consumer interactions with the commensal mediation exhibit a range of dynamical behaviours starting from stable equilibrium, then damped oscillation, to limit cycles as the resource carrying capacity increases from a critical level. In addition, commensal mediations with both controlling facilitator consumer population and resource harvesting are analyzed separately and the results are discussed for some exemplified managed and natural ecosystems.

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## Introduction

The interactions between two species can often be affected by a population of separate species [1, 2]. This third species or mediator species commonly interacts with both the participants in a number of ways that allows it to persist in a three-cornered interaction system. These kinds of interactions were usually studied by involving a mediator species as a predator, parasite, or pathogen that favors one participant over the other [2–11]. The mediator species can act as a stabilizer or destabilizer of the system. For instance, a common predator of two competing prey species can play a stabilizing role by promoting prey coexistence either through ‘predator switching’ to attack preferentially the most abundant prey species [3, 4] or through attacking the dominant competitor prey species [6, 12, 13]. Predation also provides destabilizing effects when the predator’s functional response to prey densities causes the population cycles [14, 15]. Parasites or pathogens can play similar role [16]. In this respect, one classic example is the results of the laboratory experiment of Bouletreau et al. [17]. *Drosophila melanogaster* and *D. simulans* are morphologically similar but genetically isolated species of fruit-flies. Both the species and a parasitoid wasp (cynipid), *Leptopilina bouvardi*, coexist in natural sites, for instance in various Tunisian oases. Field observations show that the more abundant the wasp the greater the reduction in the proportion of *D. melanogaster* relative to *D. simulans* species. While in a laboratory setup two species are put together in equal numbers at a temperature of 25 °C, *D. Melanogaster* eliminates *D. simulans* in approximately 8 weeks. When the wasp, *L. bouvardi* is added to the system, a dynamic equilibrium has established at which they coexist. A more dramatic result is obtained while the temperature is lowered at 22 °C; the results are similar to those obtained in absence of *L. bouvardi*. But in presence of *L. bouvardi*, *D. simulans* eliminates *D. melanogaster*. This specific example suggests that a mediator species can play stabilizing or destabilizing roles depending upon the nature of species interactions and the conditions in which the interactions occur.

A mediator species may favor neither of the participants, rather can make use of feeding habits or behaviors of one participant species without affecting it directly, and exerts direct negative effect on the other. For example, wood-feeding beetles in the genus *Monochamus* carry a pinewood nematode, *Bursaphelenchus xylophilus* [18], a mediator species, which enters into the feeding-wounds made by the beetles and negatively affects live pine trees by feeding and

reproducing rapidly. Although such commensal consumer species are common in nature, mediation by the commensal has not been regarded as one of the major types of interactions in ecological systems comparable in importance to predator, parasite, or pathogen mediation. In many ecosystems, it has often been observed that such commensal-induced mediation has profound impact on population dynamics and thereby on the stability of the interaction system. For instance, in the previous example, the huge population of *B. xylophilus* can jam the vessels of trees to transport water and cause a severe damage to healthy pine trees, which is known as pine wilt disease. In 1979, 650 kha, 25 % of the total pine forest area in Japan had been affected by the disease, and the annual loss of timber reached the heaviest record of  $2.4 \times 10^6 \text{ m}^3$  [19]. In particular, usual resource–consumer cycles can be strongly disrupted by a population of that commensal consumer species. In the paper, this issue has been addressed, and general impacts of such mediation on the stability of resource–consumer interactions are studied with the use of a Lotka–Volterra type model. With an increasing trend of overexploitation of scarce resources due to a variety of consumer activities and functionalities, this work may help to improve the ongoing efforts towards efficient resource conservation and management for sustainable future. In particular, for example, increasing human activities such as agricultural land conversion may increase the population of common human commensals such as rats, mice, those consume or contaminate large quantities of agricultural outputs; this work can provide a threshold on such activities for regulating the commensal pest populations at a low density while maintaining the stability of the interaction system.

## Model and Methods

The models are constructed based on the fundamental assumptions of Lotka–Volterra resource–consumer equations. Here the terms consumer and resource are used broadly to encompass systems such as predators feeding on herbivores, or herbivores feeding on plants. The traditional Lotka–Volterra model relied on eminent hypothesis that growth rates of both resource and consumer populations are affected simultaneously by their own density and the density of the other. The resource population grows exponentially when there is no consumer, or the consumer population decays exponentially in absence of resource. The model was described by a pair of differential equations:

$$\begin{aligned} \frac{dx}{dt} &= (a - by)x, \\ \frac{dy}{dt} &= (-c + dx)y, \end{aligned} \quad (1)$$

where  $x$  denotes the resource population density and  $y$  denotes the consumer population density; ‘ $a$ ’ is the rate of increase of resource population in absence of consumer;  $b$  is the death rate of resource population due to consumption by individual consumer;  $c$  is the death rate of consumer population in absence of resource;  $d$  is the per capita rate at which consumed resource is converted to consumer’s offspring. There are two dynamic equilibrium points: the trivial one is  $(0,0)$  where both resource and consumer populations disappear, and another one is the feasible equilibrium point,  $(c/d, a/b)$ . Stability analysis reveals that the trivial equilibrium is a saddle point and the feasible equilibrium is a neutrally stable center with purely imaginary eigenvalues,  $\pm i\sqrt{ac}$ . As a result, trajectories of the system show oscillations around the center point with a frequency of  $\sqrt{ac}$ .

A commensal consumer species that feeds on the same resource can directly affect the dynamics of resource population by taking advantages of forging habits and behaviors of a consumer species without affecting it significantly (Fig. 1). Such commensals can strongly act as a mediator or arbitrator species while they cannot persist into a three-species interaction system in the absence of either of the resource or facilitator consumer species. These species interactions also involve indirect negative effects via the common resource that depress consumer population by decreasing resource population density. Particularly, to understand the commensal consumer-induced mediatory effects, called here ‘commensal mediation’, on the stability of interaction system, two different models are constructed. The first one is that for the ‘managed ecosystems’ in which resource population is manipulated in such a way that there is no density effect on the growth rate in absence of consumers (e.g., crop systems). This means that in absence of consumers, changes in resource population density occur only through the artificial introduction or removal of resource individuals (e.g., through plantation) but not through natural birth or death processes. Another model is designed for the ‘natural ecosystems’ in which changes in

resource population density occur through the natural birth and death processes in the absence of consumers. For both the ecosystems, the basic framework of two-species Lotka–Volterra model (Eq. 1) is considered to construct a three-species model by involving a commensal consumer species. The basic modeling assumption is that a commensal species persist in a one resource-two consumers system if and only if both the resource and the facilitator consumer species are present (i.e.,  $z(t) > 0$  if  $x(t) > 0$  and  $y(t) > 0$ ). Thus, the commensal population density cannot be zero as long as there are resource–consumer interactions in the model systems. Let  $x(t)$ ,  $y(t)$ , and  $z(t)$  be the population density of resource, consumer, and commensal species at time  $t$  respectively. For the resource species, the population growth equation in the managed ecosystem is

$$\frac{dx}{dt} = a - b_1x \quad \text{for } x > 0, \text{ and } \frac{dx}{dt} = 0 \quad \text{for } x = 0,$$

and the population growth equation in the natural ecosystem is

$$\frac{dx}{dt} = (a - b_1)x.$$

Here  $b_1$  is the death rate due to consumption,  $a$  is reinterpreted as introduction rate for the managed ecosystems, and for the natural ecosystems  $a$  is the per capita rate of increase of resource population in absence of consumers (or the per capita birth rate). The resource population density is reduced by the consumer and its commensal species that feeds on the same resource. Suppose that this reduction rate is proportional to the population density of the consumer and its commensal species, i.e.,  $b_1 = byz$ , where  $b$  can be reinterpreted as the per capita death rate of resource due to joint foraging activities of both the consumer individuals. Then the growth equation of the resource population in the managed ecosystem becomes

$$\frac{dx}{dt} = a - bxyz \quad \text{for } x > 0,$$

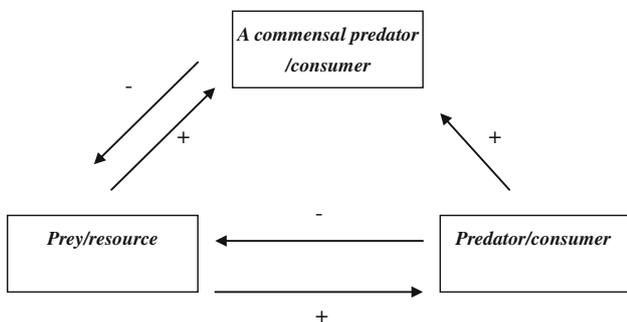
and the growth equation in the natural ecosystem becomes

$$\frac{dx}{dt} = ax - bxyz$$

For the consumer species, the population growth equations in both the ecosystems have an identical form,

$$\frac{dy}{dt} = (-c + d_1)y$$

where  $d_1$  denotes the birth rate of the consumer population. According to the Lotka–Volterra model,  $d_1$  is proportional to the density of resource population, i.e.,  $d_1 = dx$ , where  $d$  is the proportional coefficient, and has the same meaning as stated previously. Therefore, the population growth equation for the consumer species is,



**Fig. 1** A three-species interaction system showing mediation by a commensal consumer species. The effect of each interaction is indicated by plus and minus signs indicating direct positive or negative impact of one on the other

$$\frac{dy}{dt} = -cy + dxy$$

For the commensal consumer species, the population growth equation in both the ecosystems also has an identical form

$$\frac{dz}{dt} = (-m + n_1)z.$$

Here  $m$  denotes the natural death rate, and  $n_1$  denotes the birth rate of the commensal individuals. Since the changes in commensal population density exclusively depend on both the resource and the facilitator consumer populations, it is assumed that the birth rate of commensal population is proportional to the population density of the consumer and the resource species, i.e.,  $n_1 = nxy$ , where  $n$  refers to the per capita rate at which the combined benefits provided by both the resource and consumer individuals is converted to commensal's offspring. Therefore, the population growth equation is given by,

$$\frac{dz}{dt} = -mz + nxyz.$$

Combining these dynamics, population growth equations for the managed ecosystem are formulated as follows:

$$\begin{aligned} dx/dt &= a - bxyz \quad \text{for } x > 0, \text{ and } dx/dt = 0 \quad \text{for } x = 0, \\ dy/dt &= -cy + dxy, dz/dt = -mz + nxyz. \end{aligned} \quad (2)$$

And the growth equations for the natural ecosystem are,

$$\begin{aligned} dx/dt &= ax - bxyz, \\ dy/dt &= -cy + dxy, \\ dz/dt &= -mz + nxyz. \end{aligned} \quad (3)$$

Here  $a, b, c, d, m$  and  $n$  are all positive real numbers.

It should be noted that resource population dynamics in the managed ecosystem (Eq. 2) are not uniquely defined; there is a discontinuity at  $x = 0$ . The system contains two specific regions  $\{(x, y, z): x > 0\}$  and  $\{(x, y, z): x \leq 0\}$ . In the later region both the consumer population densities decay exponentially with time, irrespective of the model parameters and initial population densities, whereas in the former region there is a feasible equilibrium point that could be stable or unstable depending on the model parameters and initial population densities. Therefore, in the three-dimensional state-space,  $x = 0$  exhibits as a boundary of discontinuity. This kind of systems, known as Filippov system, has solutions in Filippov sense, that is, the solutions that can be constructed by concatenating standard solutions in both the regions and the solutions on the discontinuity boundary obtained with the Filippov convex rule [20, 21]. As the population dynamics for  $x \leq 0$  are not biologically significant, the model analyses focus only on the population dynamics for  $x > 0$  in the following sections.

## Stability of the Interaction System

With commensal mediation, population dynamics in both the managed and natural ecosystems (Eqs. 2, 3) exhibit feasible equilibrium points  $(\frac{c}{d}, \frac{dm}{cn}, \frac{am}{bm})$  and  $(\frac{c}{d}, \frac{dm}{cn}, \frac{acn}{bdm})$ , respectively. Standard linear analysis shows that the equilibrium point,  $(\frac{c}{d}, \frac{dm}{cn}, \frac{am}{bm})$ , is stable if  $a > c^2m/(dc + dm)$ , and is unstable if  $a < c^2m/(dc + dm)$  (Appendix 1). Figure 2 depicts the population dynamics near to the stable equilibrium point. Population dynamics of the unstable managed ecosystem display oscillations, depicted in Fig. 3, for a particular set of parameter values. It has shown that a family of oscillatory solutions arises from hopf bifurcation in the Eq. (2). The phase space analysis has revealed that limit cycles arise when the parameter  $a$  drops below a critical value,  $a_{\text{hopf}} = c^2m/(dc + dm)$ , a hopf bifurcation point at which a family of limit cycles originates. With the use of a software package AUTO, the eigenvalues for the Eq. (2) are computed, with a given set of parameters and  $(x, y, z) = (\frac{c}{d}, \frac{dm}{cn}, \frac{am}{bm})$  for  $a$  increasing through  $a_{\text{hopf}}$  identifying the position of the hopf bifurcation. A typical bifurcation diagram and associated time series are illustrated in Fig. 4. Figure 4a illustrates that for small values of  $a$ , changes in stability occur via hopf bifurcation. Figure 4b is an example of these changes which clearly shows that the limit cycle grows as 'a' moves downward along the bifurcation curve starting from the hopf bifurcation point. While picking a value of 'a' just a bit above the  $a_{\text{hopf}}$ , a stable steady-state (Fig. 2) is reached. In contrast, trajectories for the values of  $a$  just below the hopf bifurcation point display a small limit cycle (Fig. 3). On the other hand, similar linear analysis for the natural ecosystem (Eq. 3) shows that the feasible equilibrium point,  $(\frac{c}{d}, \frac{dm}{cn}, \frac{acn}{bdm})$ , is unstable (Appendix 2). The population dynamics of the unstable natural ecosystem display oscillations (Fig. 5) with amplitudes depend on the initial population densities.

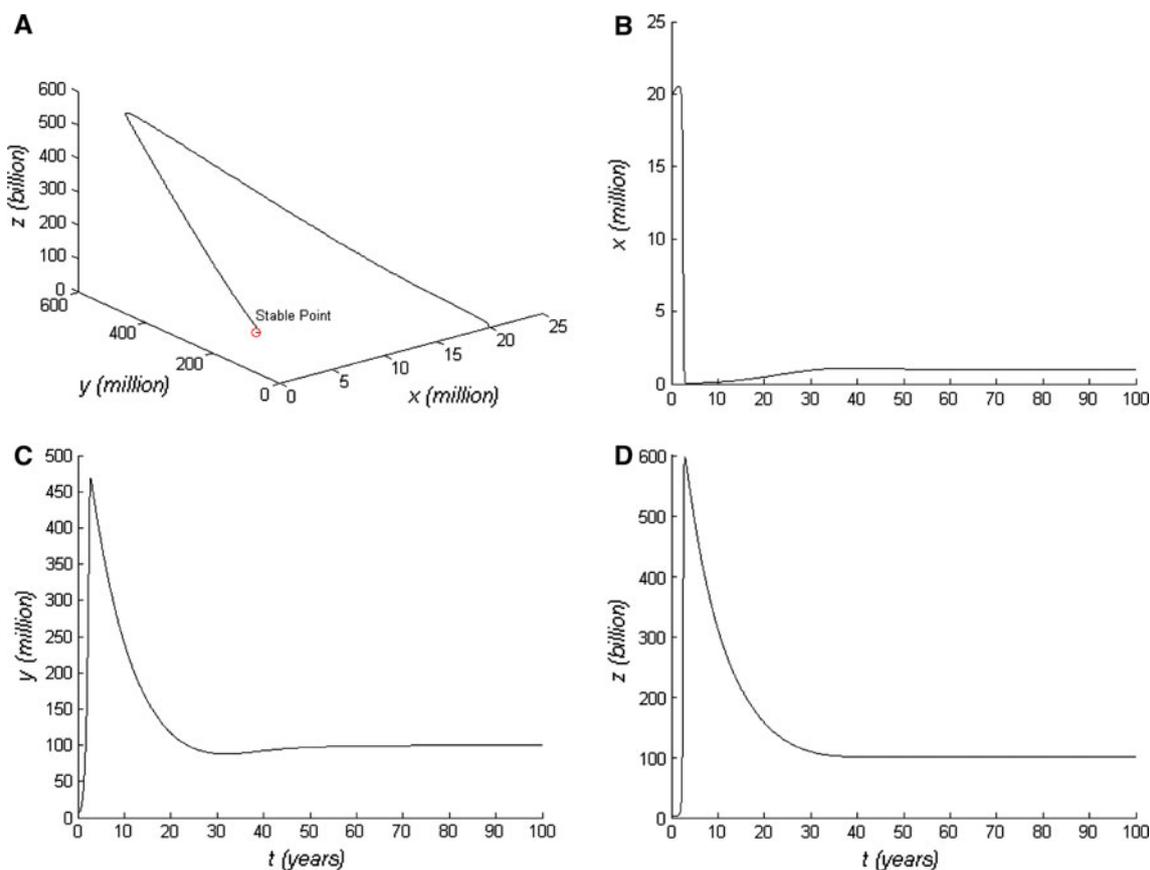
## Controlling Consumer Population

In this section, model results show how the regulation of consumer population affects resource dynamics and thereby the stability of the systems. Suppose that the consumer population is controlled so perfectly that its growth is zero, then the Eqs. (2, 3) become

$$\frac{dx}{dt} = a - bxyz, \quad \frac{dy}{dt} = 0, \quad \frac{dz}{dt} = -mz + nxyz; \quad (4)$$

$$\frac{dx}{dt} = ax - bxyz, \quad \frac{dy}{dt} = 0, \quad \frac{dz}{dt} = -mz + nxyz. \quad (5)$$

Equation (4) describe population dynamics in the managed ecosystem; Eq. (5) describe population dynamics in the



**Fig. 2** Population dynamics around a stable steady-state. **a** The trajectory of Eq. (2) in the phase space. There is a stable steady-state (1, 100, 100). **b** The dynamics of resource population. **c** The dynamics of the consumer population. **d** The dynamics of the commensal

population. Here  $a = 0.4$ ,  $b = 0.4 \times 10^{-4}$ ,  $c = 0.1$ ,  $d = 0.1$ ,  $m = 0.12$ ,  $n = 1.2 \times 10^{-3}$ .  $x(0) = 20$  (million),  $y(0) = 4$  (million),  $z(0) = 2$  (billion)

natural ecosystem. It is obvious that  $y(t)$  is a constant,  $y(0)$ , due to the zero growth, therefore, it is just needs to examine the dynamic interactions between the resource and the commensal populations. In absence of consumer i.e.,  $y(0) = 0$ , the system (4) shows that the resource population grows at a constant rate,  $a$ , and the commensal population decays exponentially with the coefficient  $m$ . In the natural ecosystem (5), resource population grows exponentially but the population dynamics of the commensal species remain the same as in the system (4). If  $y(0)$  is positive ( $>0$ ), both the systems (4) and (5) contain feasible equilibrium points,  $(\frac{m}{ny(0)}, y(0), \frac{a}{bm})$  and  $(\frac{m}{ny(0)}, y(0), \frac{a}{by(0)})$ , respectively. Stability analysis reveals that the equilibrium point,  $(\frac{m}{ny(0)}, y(0), \frac{a}{bm})$ , is locally stable (Appendix 3); Fig. 6 depicts damped oscillatory dynamics near to the stable equilibrium point. If  $y_0 < \frac{4m^2}{an}$ , the equilibrium is a stable spiral point; if  $y_0 > \frac{4m^2}{an}$ , the equilibrium is a stable node; and if  $y_0 = \frac{4m^2}{an}$ , the equilibrium may be either stable spiral point, a stable node, or a degenerate stable node depending on the parameter values (Appendix 3). For the natural ecosystem (5), the feasible equilibrium point,

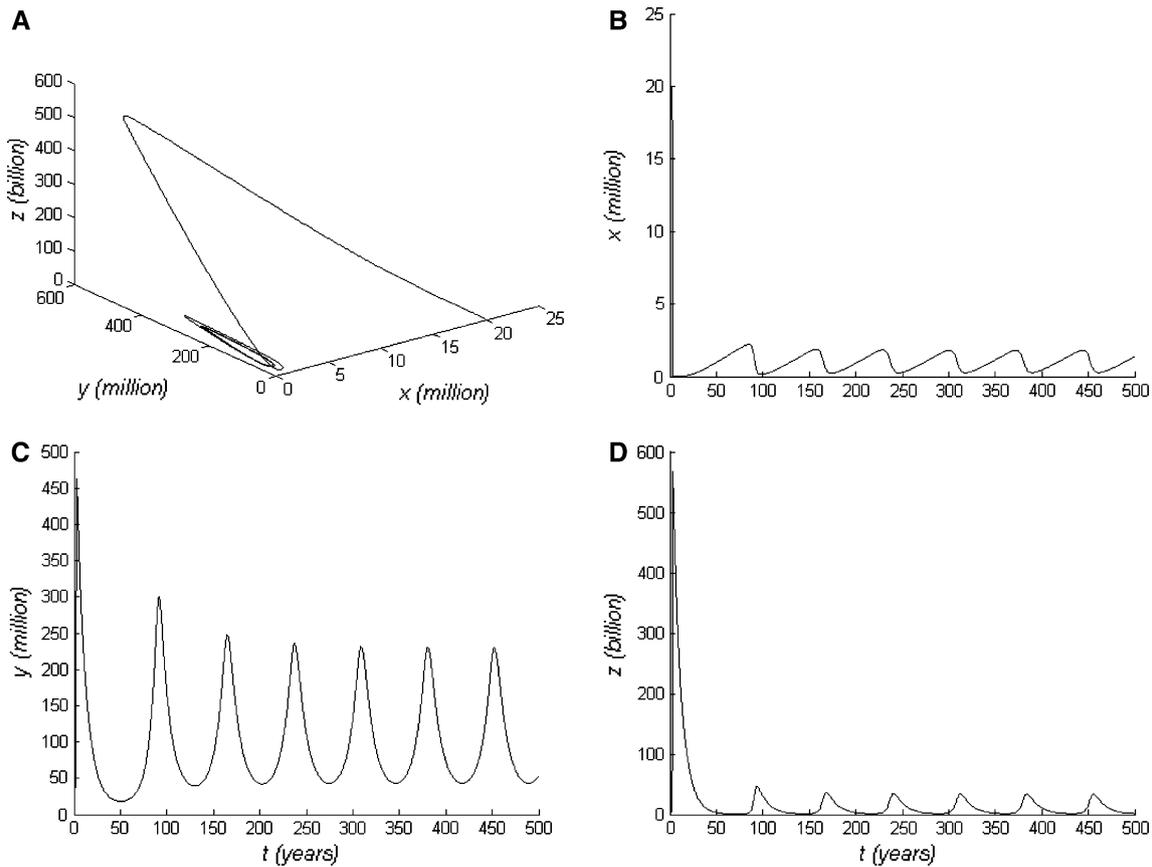
$(\frac{m}{ny(0)}, y(0), \frac{a}{by(0)})$ , is unstable (Appendix 4). The unstable natural system display oscillatory dynamics (Fig. 7).

**Effects of Resource Harvesting**

While including the effects of resource harvesting into the classic Lotka–Volterra model (Eq. 1) by adding a linear loss term with harvesting rate  $h$  for resource population, the model becomes,

$$\frac{dx}{dt} = ax - bxy - hx, \quad \frac{dy}{dt} = -cy + dxy.$$

The per capita birth rate of resource population is reduced to  $(a-h)$  due to the harvesting. With the inclusion of resource harvesting, the feasible equilibrium,  $(c/d, a/b)$ , has changed to  $(c/d, a/b - h/b)$ . Thus, at the equilibrium point, the resource population has remained unaffected, but the consumer population has reduced due to the effects of harvesting. Although this result holds only for the equilibrium value as the typical model dynamics are



**Fig. 3** An unstable managed ecosystem with a loop. **a** The trajectory of Eq. (2) in the phase space. **b** The dynamics of resource population. **c** The dynamics of the consumer population. **d** The dynamics of the

commensal population. Here  $a = 0.04$ ,  $b = 0.4 \times 10^{-4}$ ,  $c = 0.1$ ,  $d = 0.1$ ,  $m = 0.12$ ,  $n = 1.2 \times 10^{-3}$ .  $x(0) = 20$  (million),  $y(0) = 4$  (million),  $z(0) = 2$  (billion)

oscillatory, however, by separation of variables one can easily show that the equilibrium value equals the time average over one period, i.e.,  $(1/T \int_{\tau}^{\tau+T} x(t)dt, 1/T \int_{\tau}^{\tau+T} y(t)dt)$ . This result is known as Volterra’s principle: whenever the population densities of resource and consumer determine each other, a reduction of the growth rate of resource population (e.g., by harvesting) leads to a decrease of the consumer population density that eventually results in an unaffected, equilibrium density of resource population around which the resource population oscillates perpetually. Here, the results show how and to what extent this principle works for the managed and natural ecosystems (Eqs. 2, 3).

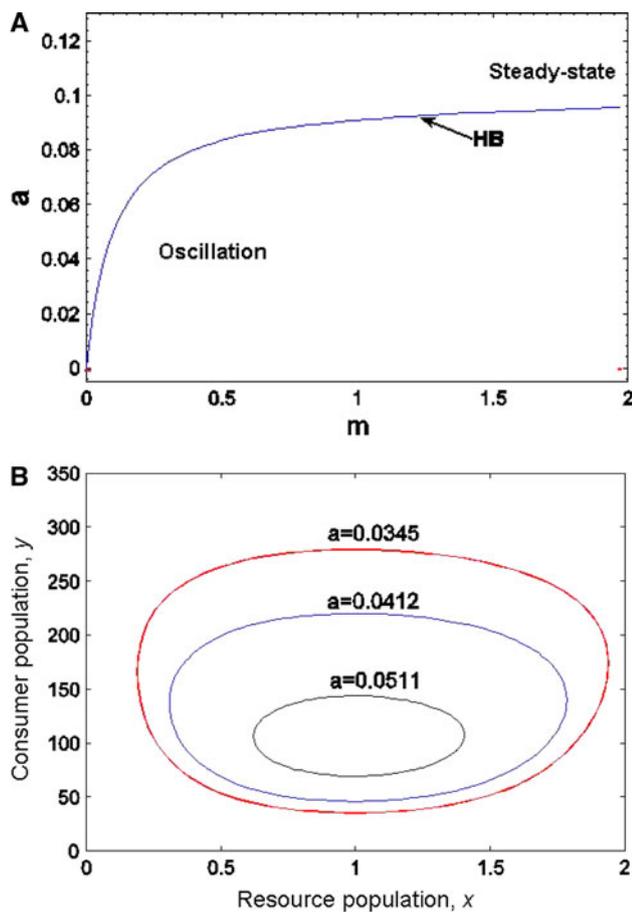
With the inclusion of a linear loss term of resource population, the system (2) becomes,

$$\begin{aligned} \frac{dx}{dt} &= a - bxyz - hx \quad \text{for } x > 0, & \frac{dy}{dt} &= -cy + dxy, \\ \frac{dz}{dt} &= -mz + nxyz. \end{aligned} \tag{6}$$

And the system (3) becomes,

$$\begin{aligned} \frac{dx}{dt} &= ax - bxyz - hx, & \frac{dy}{dt} &= -cy + dxy, \\ \frac{dz}{dt} &= -mz + nxyz. \end{aligned} \tag{7}$$

The system (6) contains two equilibrium points:  $(a/h, 0, 0)$  and  $(c/d, dm/cn, n(ad - ch)/bdm)$ . Stability analysis reveals that the equilibrium point,  $(a/h, 0, 0)$ , is locally stable if  $h > ad/c$  (Fig. 8a) and is unstable if  $h < ad/c$ . Another equilibrium point,  $(c/d, dm/cn, n(ad - ch)/bdm)$ , is stable if  $h < ad/c$  and  $a > c^2m/(cd + md)$  (Fig. 8b), and is unstable if  $h > ad/c$  and  $a < c^2m/(cd + md)$  (Fig. 8c) (see details in Appendix 5). If  $h = ad/c$ , the trajectories of the system (6) are represented in the Fig. 8d for a range of initial values of resource population density. In the natural ecosystem (Eq. 7), the model dynamics contains two equilibrium points: the trivial equilibrium point  $(0,0,0)$  and the feasible equilibrium point  $(c/d, dm/cn, (acn - hcn)/bdm)$ . The trivial equilibrium is stable if  $a < h$  (Fig. 9) and is unstable if  $a > h$ . The feasible equilibrium point is unstable for  $a \neq h$  (Appendix 6). While  $a = h$ , Fig. 10 portrays the trajectories for different initial values



**Fig. 4** An illustration of the bifurcation and the limit cycle. **a** The phase shifts in the  $m$ – $a$  parameter space. **b** The limit cycles are obtained for different introduction rate of resource population. Here  $b = 0.4 \times 10^{-4}$ ,  $c = 0.1$ ,  $d = 0.1$ ,  $m = 0.12$ ,  $n = 1.2 \times 10^{-3}$

of resource population density. It is interesting to note that for both the ecosystems, at the feasible equilibrium, the commensal population is reduced due to resource harvesting, whereas the equilibrium resource and consumer population densities are remained unaffected.

## Results and Discussion

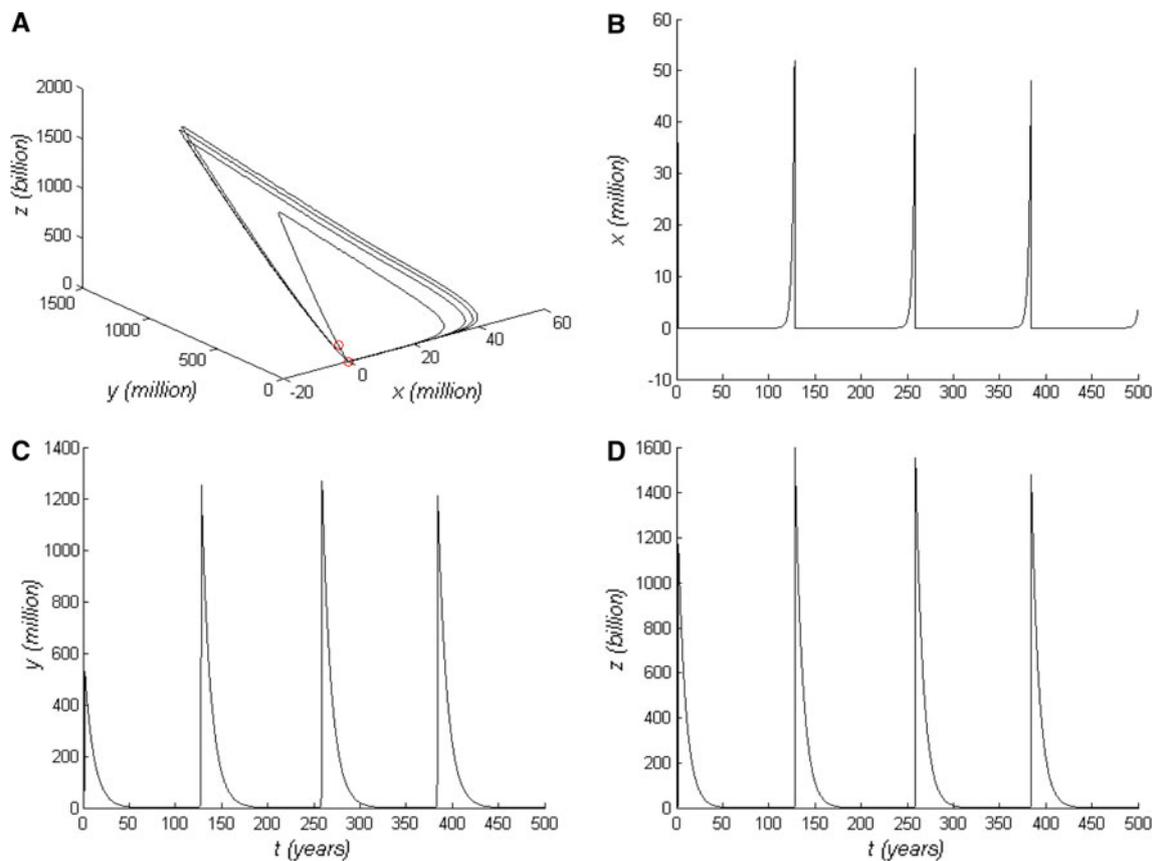
### Commensal Mediation in Managed and Natural Ecosystems

Many but not the most of consumer species' forging habits and behaviors facilitate other consumers those usually do not affect them directly to feed on the same resource and then to reproduce successfully. While those commensal consumers cannot survive in the absence of any of the resource or facilitator consumer population, their presence strongly affects resource–consumer interactions as they exert a direct negative effect on resource population. Such

intervention by a commensal consumer species, called here as 'commensal mediation', can be observed in many ecosystems. For example in the crop systems, crop density has often steeply decreased by the activities of those detrimental nematodes that are usually commensals of common herbivore insects [22]. Owing to the commensal consumer-induced strong added effects on the rate of resource exploitation, one potential consequence of the commensal mediation could be the rapid decline of resource population. In particular, the models predict that usual resource–consumer cycles can be severely disrupted by the population of a commensal consumer species. The results show that commensal mediation can specifically result in sharp periodic decline with delayed recovery in resource population density (Figs. 5b, 13).

Occurrences of resource–consumer or prey–predator interactions are common in both the managed and natural ecosystems. Although the managed and natural ecosystems differ in a number of ways, involved resource–consumer interactions in both the systems can be disrupted by a population of commensal consumer in similar or dissimilar fashions depending on a variety of conditions related to the nature and associated rates of population interactions. In the managed ecosystems such as agroecosystems or crop systems, basic management practices are concerned about minimizing the density-dependent control on growth rate of resource population, whereas in the natural ecosystems such practices are uncommon. While incorporating this particular difference into the Lotka–Volterra type models, the model results showed that when the introduction rate of resource population exceeds a characteristic level,  $a_{\text{hopf}}$ , the resource–consumer- and the commensal interactions in the managed ecosystems can reach at a stable, feasible equilibrium point at which the equilibrium resource density is solely determined by the consumer population but not by its own population; when the rate is below that level, the population dynamics are oscillatory. In contrast, the population dynamics in the natural ecosystems always display population cycles, where the amplitude of the oscillation depends on the initial population densities. For given parameter values, the qualitative analysis shows that the resource population dynamics in natural ecosystems are relatively more affected, in terms of time laps from one peak to the next, with the positive population density of the commensal consumer (Figs. 3b, 5b).

Controlling consumer population has proved to be a useful management practice for sustainable resource use. Some implications of such practice for the stability of the resource–consumer- and the commensal interactions in both the managed and natural ecosystems have been derived from the models. In the managed ecosystem, controlling the consumer population can stabilize the system at a feasible equilibrium point, where the equilibrium resource

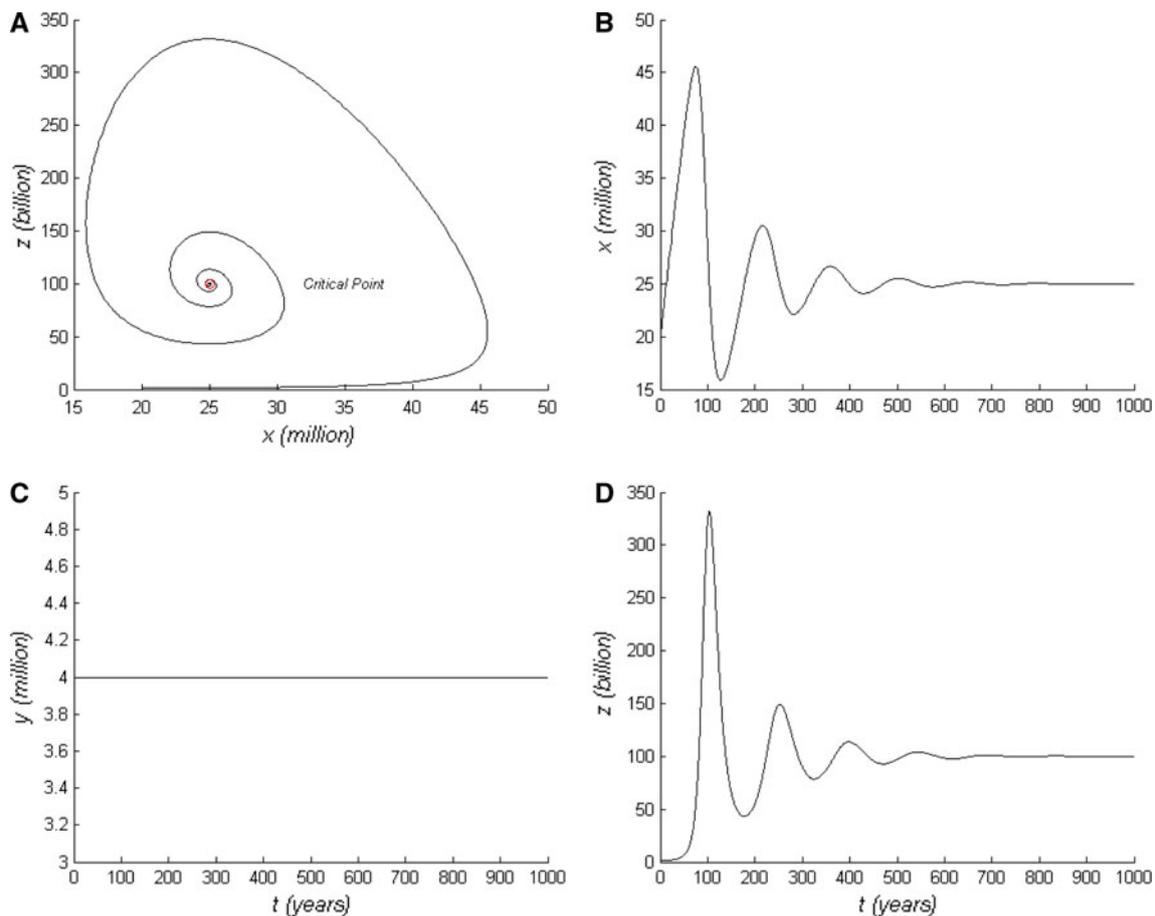


**Fig. 5** An unstable natural ecosystem, exhibiting limit cycle behavior. **a** The trajectory of Eq. (3) in the phase space. **b** The dynamics of the resource population. **c** The dynamics of the consumer population.

**d** The dynamics of the commensal population. Here  $a = 0.4$ ,  $b = 0.4 \times 10^{-4}$ ,  $c = 0.1$ ,  $d = 0.1$ ,  $m = 0.12$ ,  $n = 1.2 \times 10^{-3}$ .  $x(0) = 20$  (million),  $y(0) = 4$  (million),  $z(0) = 2$  (billion)

density is asserted by the birth and mortality rates of commensal population and the controlled density of facilitator consumer population. Special characteristics of the stable equilibrium point, such as a stable spiral point or a stable node, are exclusively determined by the constraints on the controlled level of consumer population density. On the other hand, in the natural ecosystems, controlling consumer population cannot stabilize the system; in fact the population dynamics in the natural ecosystems exhibit limit cycle behavior. It can be noted that although such interactions in the natural ecosystems are in the state of oscillation, the density of resource population can be large at a certain time, e.g. the time when the density of resource population is near to the peaks as shown in Fig. 7b. In comparison to the managed ecosystem, the natural ecosystem can reflect higher resource density at peak periods while the consumer population in both the systems is perfectly controlled (Figs. 6b, 7b). Relative to the resource population density in the natural ecosystems without a control on the consumer population, the density of resource in the natural ecosystems with a control on consumer population can have larger peaks (Figs. 5b, 7b).

Controlling the rate of anthropogenic resource exploitation is crucial for sustaining resource–consumer interactions in both the managed and natural ecosystems. According to the Volterra's principle, resource harvesting is likely to be resulted in decreased consumer population that eventually leads to an unaffected equilibrium resource density around which resource population would oscillate perpetually. However, with the commensal mediation, whether resource harvesting stabilizes or destabilizes the resource–consumer and the commensal interactions depend on the strength of population interactions and the rates and forms of resource harvesting. The present study showed that in the managed ecosystem if the harvesting rate,  $h$ , is higher than the value  $ad/c$ , it establishes a stable equilibrium resource density,  $a/h$ , which fails to support persistence of both the consumer populations. This means that a high, constant rate of resource harvesting fixes the resource density at a stable equilibrium level that cannot allow persistence of both the consumer populations via the commensalistic type facilitative interactions. On the other hand, if the harvesting rate is below the threshold  $ad/c$  and the introduction rate of resource population,  $a$ , is above the



**Fig. 6** A stable managed ecosystem while the population density of consumer species has kept at a constant level. **a** The trajectory of Eq. (4) in the phase plain. There is a stable critical point (25, 100). **b** The dynamics of the resource population. **c** The dynamics of the

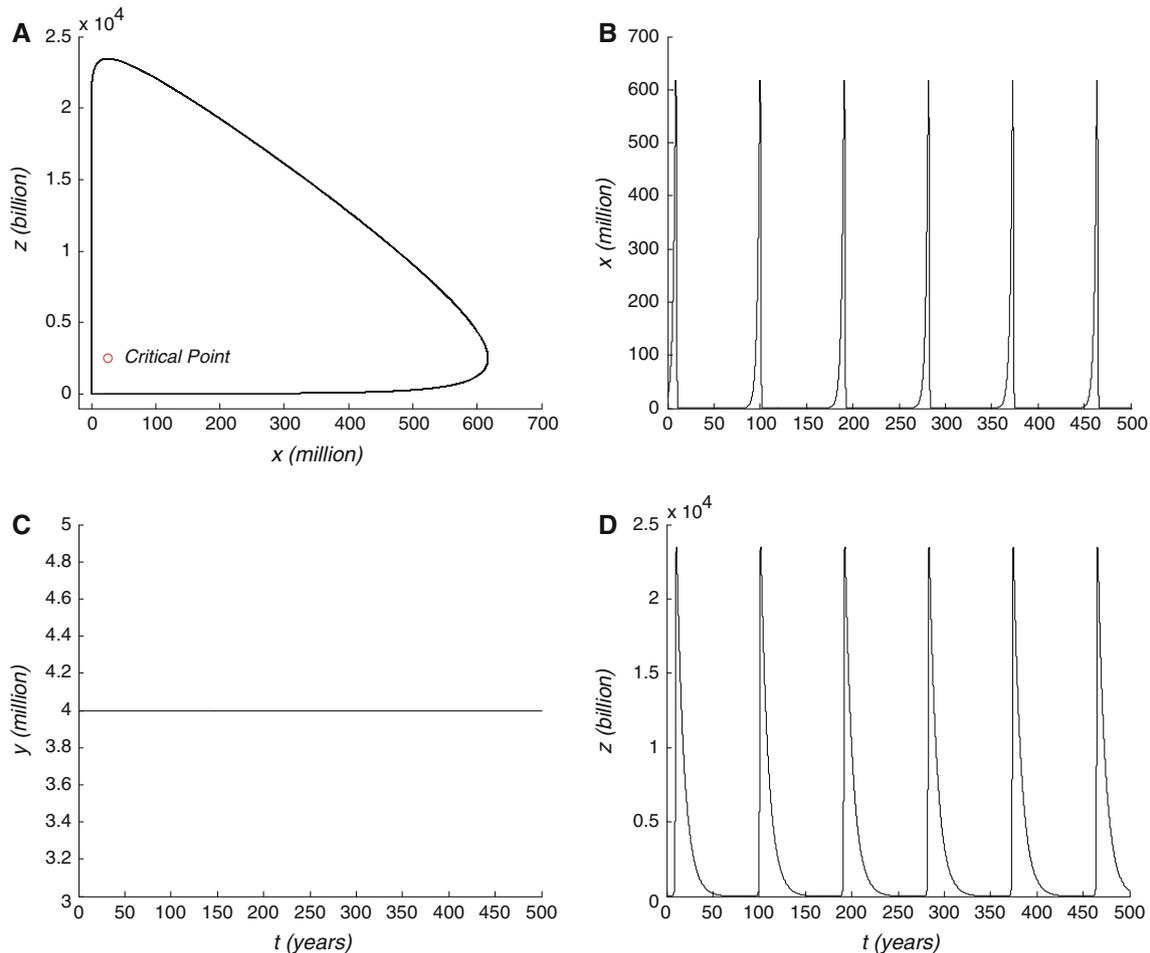
consumer population. **d** The dynamics of the commensal population. Here  $a = 0.4$ ,  $b = 0.4 \times 10^{-4}$ ,  $c = 0.1$ ,  $d = 0.1$ ,  $m = 0.12$ ,  $n = 1.2 \times 10^{-3}$ .  $x(0) = 20$  (million),  $y(0) = 4$  (million),  $z(0) = 2$  (billion)

characteristic level  $a_{\text{hopf}}$ , the resource dynamics can reach at a feasible, stable equilibrium point at which both the consumer populations can maintain their equilibrium densities. However, without that control on the introduction rate of resource population, a lower resource harvesting rate below the threshold  $ad/c$  can lead to a unstable equilibrium point at which the populations oscillate around the critical points. Furthermore, the harvesting rate,  $h$ , can heavily affect the stabilization period of resource dynamics: relatively a higher rate of resource harvesting allows the resource population to reach at a stable equilibrium point faster than in the managed ecosystems with a lower rate of resource harvesting (Fig. 11). While in the natural ecosystems the resource harvesting rate,  $h$ , is greater than the birth rate of resource population, the model dynamics collapse at a critical point in which all the interacting populations disappear, and continuing resource harvesting with this rate cannot allow the resource population to recover and then to provide necessary support to consumer populations for their future survival. However, lowering

the harvesting rate,  $h$ , below the birth rate of resource population may allow the resource population to recover from low density. Relatively a moderate resource harvesting rate allows oscillation of interacting populations around a feasible equilibrium point; this, thereby, promotes recovery of harvested resource population in the natural ecosystems.

#### Stabilizing and Destabilizing Roles of the Commensal Consumer Population

Since the mediation by a commensal consumer species increases the mortality of resource population, it may provide a density-dependent negative feedback which is essential for the stabilization of resource dynamics [23]. The study here demonstrated that at a certain condition, commensal mediation can provide a strong stabilizing effect on the resource dynamics. In particular, the stabilizing effect is prominent in the managed ecosystems. While the birth rate related parameter of consumer



**Fig. 7** An unstable natural ecosystem while the population density of consumer species has kept at a constant level. **a** The trajectory of Eq. (5) in the phase plain. **b** The dynamics of the resource population. **c** The dynamics of the consumer population. **d** The dynamics of the

commensal population. Here  $a = 0.4$ ,  $b = 0.4 \times 10^{-4}$ ,  $c = 0.1$ ,  $d = 0.1$ ,  $m = 0.12$ ,  $n = 1.2 \times 10^{-3}$ .  $x(0) = 20$  (million),  $y(0) = 4$  (million),  $z(0) = 2$  (billion)

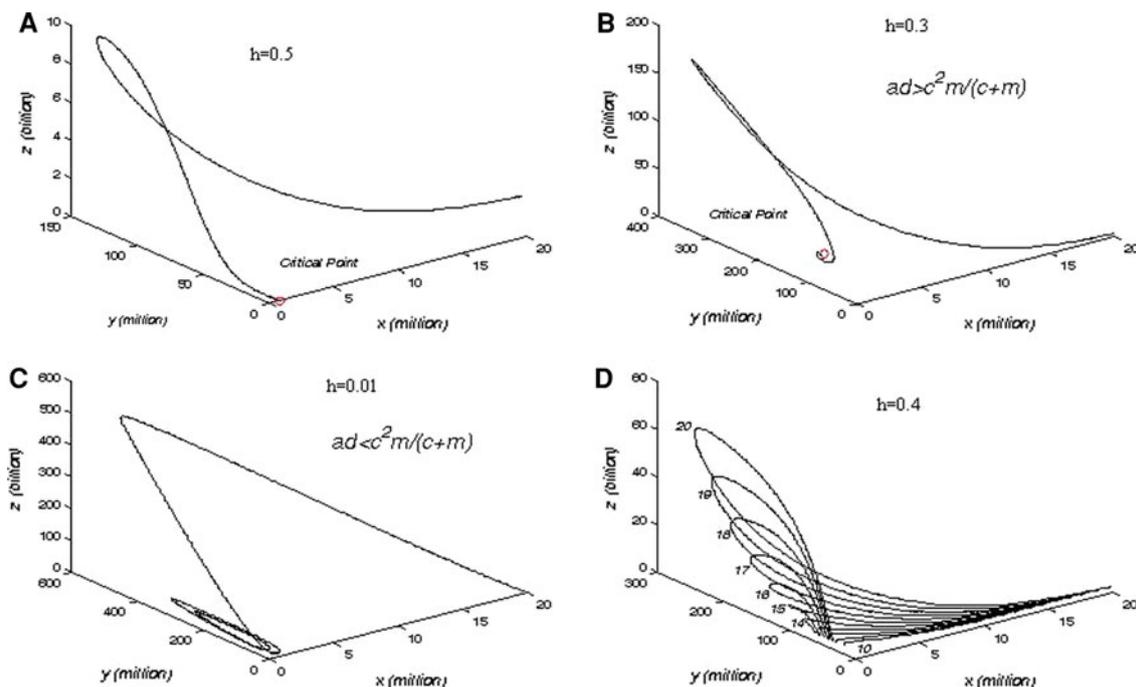
population,  $d$ , is remained below the numerical value of  $c^2/a$ , it determines an upper threshold on the mortality of the commensal population (i.e.,  $adc/(c^2 - ad) > m$ ) which eventually stabilizes the resource dynamics. With this condition, decreasing mortality rate of the commensal quickly diminishes damped oscillations into a stable steady-state. Figure 12 illustrates this phenomenon.

In the natural ecosystems, the commensal mediation provides a destabilizing effect on resource population dynamics. Numerical simulation showed that as the population density of the commensal species increases, the amplitude of the resource population cycle also increases over time with increasing delay in the recovery of resource population density (Fig. 13). In addition, the commensal mediation can further result in a sharp decline of resource population density from the peak which may not happen in the absence of commensal population. Figure 13 illustrates such destabilizing effects of the commensal mediation with the increasing birth rate of the commensal population.

In the managed ecosystems, commensal mediation provides the similar destabilizing effect on resource dynamics when the introduction rate of resource population,  $a$ , is restricted below the characteristic level,  $a_{\text{hopf}}$ , a hopf-bifurcation point. Whereas in the natural ecosystems, the model dynamics (Eq. 3) do not exhibit such hopf-bifurcation characteristic, however, replacement of the density-dependent birth rate of resource population by logistic growth emerges a suit of resource–consumer dynamics for changing carrying capacity of the resource population (Fig. 14).

#### Non-Additive Effects Of Consumers

As all species are consumers and all are in some forms consumed by other species, resource–consumer interaction is one of the most fundamental ecological processes underlying the observed community structure and biodiversity patterns [24]. While the effect of consumption



**Fig. 8** Population dynamics in the managed ecosystem with the effects of resource harvesting. **a** The trajectory of Eq. (6) in the phase space when  $h > ad/c$ . **b** The trajectory of Eq. (6) in the phase space when  $h < ad/c$  and  $a > c^2m/(cd + md)$ . **c** The trajectory of Eq. (6) in the phase space when  $h < ad/c$  and  $a < c^2m/(cd + md)$ . **d** The trajectory of Eq. (6) in the phase space when  $h = ad/c$ .  $a = 0.4$

[except for (c), in which  $a = 0.04$ ],  $b = 0.4 \times 10^{-4}$ ,  $c = 0.1$ ,  $d = 0.1$ ,  $m = 0.12$ ,  $n = 1.2 \times 10^{-3}$ .  $x(0) = 20$  (million) [except for (d), in which the initial values of  $x(0)$  ranges from 10 million to 20 million with a increasing step 1 million],  $y(0) = 4$  (million),  $z(0) = 2$  (billion). The values of  $h$  are directly shown in the figures

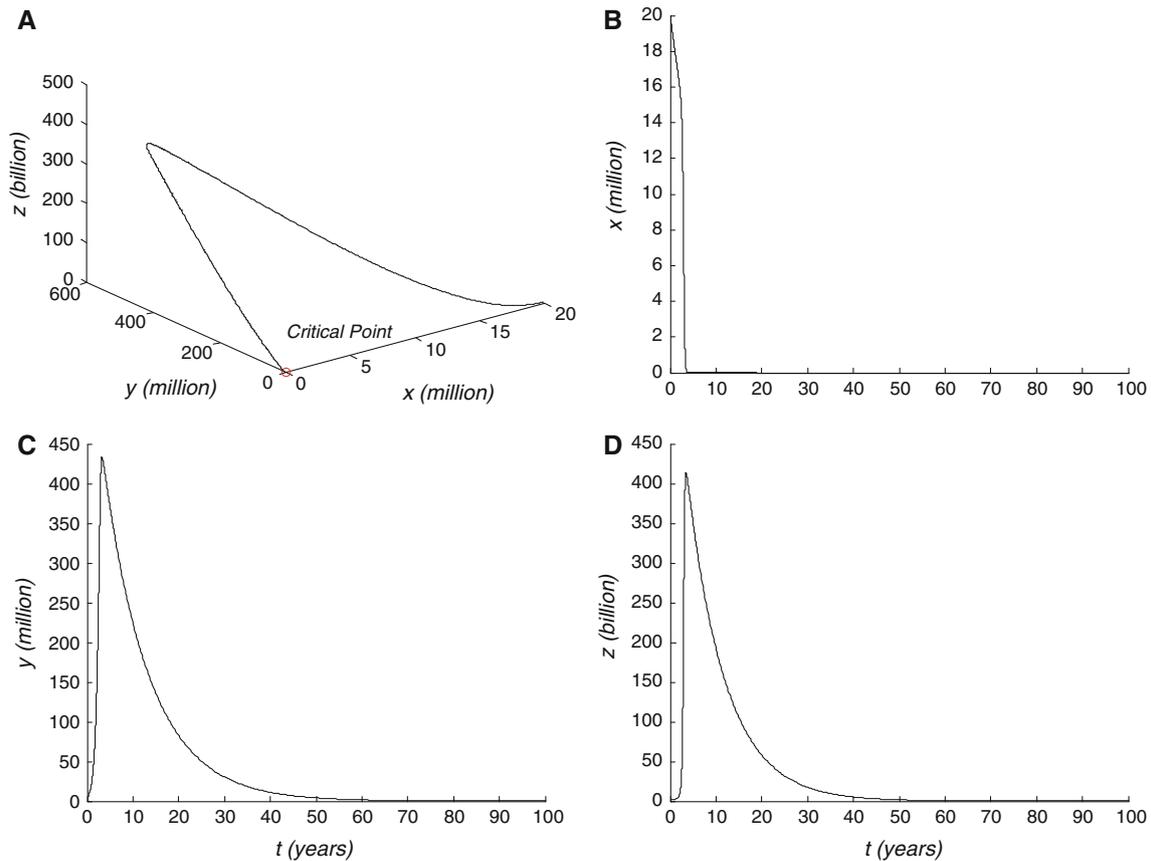
cascades downward along the trophic levels, which is known as top-down control over resource population, bottom-up control over the trophic structure arises as the availability of resources constrains the consumption rate [25]. Thus, the simple mathematical models of resource–consumer interactions that often involve both the forms of controls provide fundamental understandings of factors determining community structure and dynamics. Numerous theoretical and empirical studies have revealed the role of consumers for shaping resource dynamics, considering mostly two- or three-trophic level systems [26–28]. Many forms of complex interactions among consumers occur in nature; however, modeling studies have commonly considered multitrophic interactions where consumers belong to different trophic levels or investigated intraguild interactions among consumers. Commensalistic form of interaction in which one consumer species derives benefits from the interactions of two consumer species is the most overlooked interaction that can produce non-additive effects (synergism) on resource dynamics.

In the models of commensal mediation (Eqs. 2, 3), non-additive effects on resource population are resulted from consumers facilitating consumption of other consumer species. In managed ecosystems where resource dynamics are independent of resource density in absence of

consumers, the non-additive effect is linked to the constant introduction rate of resource population. The model results revealed that a lower introduction rate (i.e.,  $a < a_{hopf}$ ) weakens the commensalistic relationship, leading to a reduced non-additive effect resulting in perpetual oscillatory dynamics of interacting populations. With a higher introduction rate, enhanced non-additive effects allow interacting populations to reach at a stable steady state. Notably, such emergent phenomenon are absent in natural ecosystems where growth rate of resource population depends on its own density in the absence of consumers. Moreover, it has been shown that with logistic growth of resource population, the non-additive effects emerge as “the paradox of enrichment” in which increasing carrying capacity of resource population destroys stable state into unstable state and then into limit cycles.

The Paradox of Enrichment

Paradoxical effect of resource enrichment, which goes against the usual perception that the enrichment facilitates the growth of populations, has elegantly been illuminated based on Lotka–Volterra-derived model of MacArthur and Rosenzweig [29]. It states that enrichment can destroy stable steady-state of prey–predator systems and lead to



**Fig. 9** A stable natural ecosystem with the effects of overexploitation of resource. **a** The trajectory of Eq. (7) in the phase space. **b** The dynamics of the resource population. **c** The dynamics of the consumer population. **d** The dynamics of the commensal population. Here

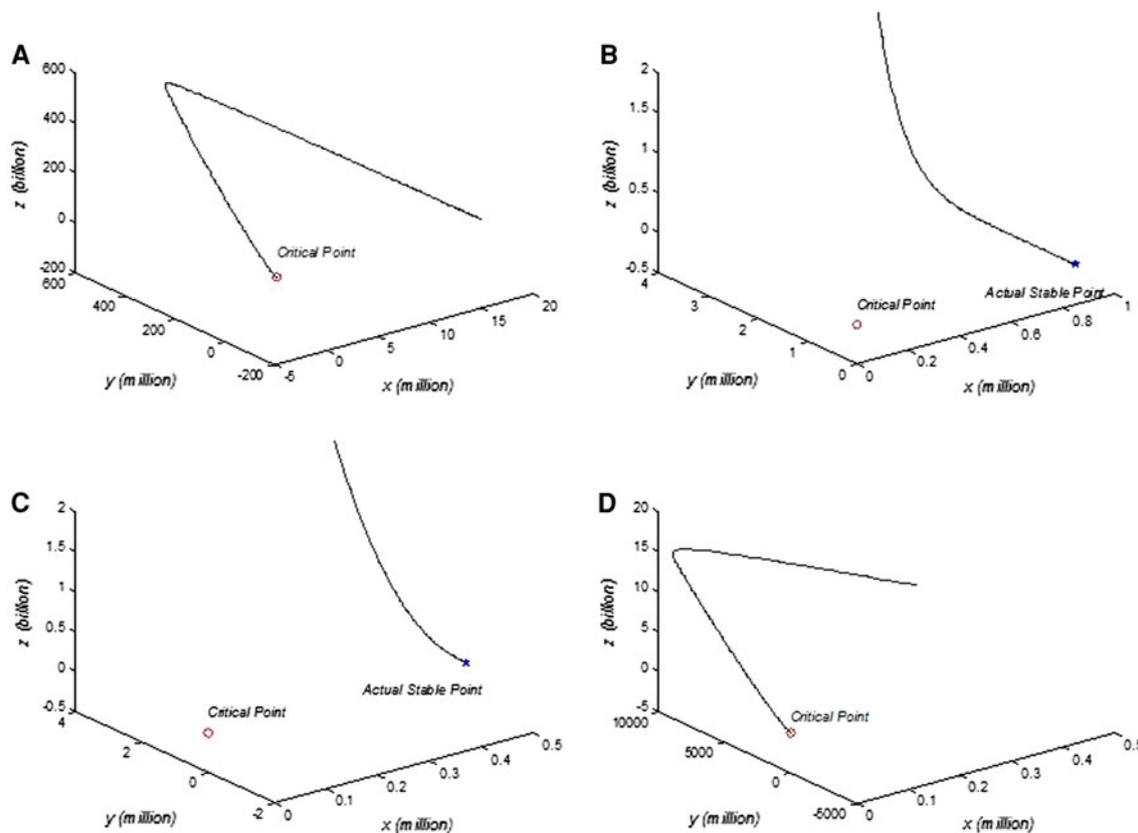
$$a = 0.4, \quad b = 0.4 \times 10^{-4}, \quad c = 0.1, \quad d = 0.1, \quad m = 0.12, \\ n = 1.2 \times 10^{-3}, \quad h = 0.5. \quad x(0) = 20 \text{ (million)}, \quad y(0) = 4 \text{ (million)}, \\ z(0) = 2 \text{ (billion)}$$

emergence of population cycle; as enrichment proceeds, this cycle brings populations closer and closer to zero [30]. Mathematically speaking, enrichment distorts stable equilibrium into limit cycle oscillations with increasing amplitude as the enrichment continues to increase [30–32]. In most theoretical models, the effects of enrichment were studied by changing the prey carrying capacity rather than the intrinsic growth rate mainly because the numerical simulations showed that increase in the intrinsic growth rate had little effect on the amplitude of the population oscillation in contrast to an increase in the carrying capacity [33]. Although the ‘paradox of enrichment’ has often been reexamined experimentally, laboratory or field data provide little support for that enrichment effect (e.g., [34, 35]). One potential reason for this failure can be the underlying difficulties in measuring functional response of predator population in the field or in the laboratory setup [36].

Persistent discrepancy between the theoretical prediction and empirical observations causes controversy on the real existence of enrichment paradox. It has been argued

that quantitative forms of the rate of prey consumption by an average predator, known as predator functional response, leads to this controversial prediction [36]. A vast amount of theoretical works that are mostly derived from the classic Lotka–Volterra model and predicting the paradox have exclusively been considered prey-dependent functional response, where prey density alone determines the response. Such prey-dependence has severely been criticized, stating that the predator’s functional response depends on both predator and prey population known as ratio-dependent response; the ratio dependence refers to the functional response that depends only on the ratio of prey population density to predator population density, not on the absolute density of either populations [37].

With prey-dependent functional response, studies continue to provide models built upon MacArthur–Rosenzweig theory, which escape the paradox of enrichment by incorporating different complicating factors that can be present in natural systems. In fact, several alternative mechanisms have been proposed, but most of them have not been confirmed in the field or laboratory. The first one of these is



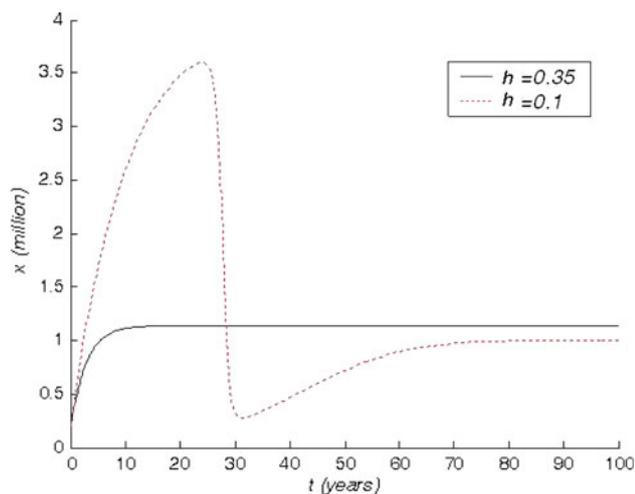
**Fig. 10** Trajectories of the model dynamics in natural ecosystem with the effects of resource harvesting and  $a = h$ . **a** The trajectory of Eq. (7) in the phase space when  $x(0) = 20$  (million),  $y(0) = 4$  (million),  $z(0) = 2$  (billion). **b** The trajectory of Eq. (7) in the phase space when  $x(0) = 0.85$  (million),  $y(0) = 4$  (million),  $z(0) = 2$  (billion). **c** The trajectory of Eq. (7) in the phase space when

$x(0) = 0.5$  (million),  $y(0) = 4$  (million),  $z(0) = 2$  (billion). **d** The trajectory of Eq. (7) in the phase space when  $x(0) = 0.5$  (million),  $y(0) = 10000$  (million),  $z(0) = 2$  (billion). Here  $a = 0.4$ ,  $b = 0.4 \times 10^{-4}$ ,  $c = 0.1$ ,  $d = 0.1$ ,  $m = 0.12$ ,  $n = 1.2 \times 10^{-3}$ ,  $h = 0.4$

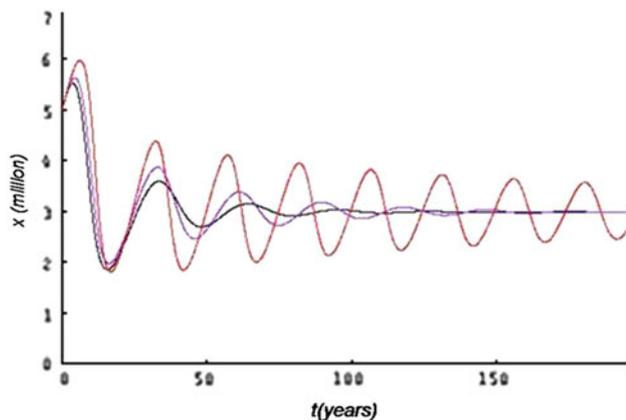
that the presence of inedible or unpalatable prey in prey–predator interactions [33, 38–40]. While the inedible prey is avoided by the predator but competes with the edible prey, destabilization via the prey enrichment always occurs as the carrying capacities of the two prey species increase. The second mechanism states that density-dependent predator mortality weakens the destabilizing effects of enrichment because addition of this factor provides strong stabilizing effects on the prey–predator interactions [41]. There are many other mechanisms that involve either the concept of prey refuge [42–46] or the spatial heterogeneity [47–50]. The presence of prey refuge or spatial heterogeneity, which usually acts as stabilizing factors, undermines the enrichment effects or depicts opposite result i.e., increasing enrichment stabilizes the population cycles [46]. In contrast to prey-dependence, the ratio-dependent models consider an extreme predator-dependence that prevents paradox of enrichment [36] and predicts extinction of both species as a result of over exploitation [51]. However, several studies have questioned the validity of ratio-dependence [52, 53]. For example, Freedman and Mathsen

[54] note that the ratios tend to infinity in the regions where the state variables are close to zero; as a result, the ratio-dependent model predicts a positive growth rate of predator even when prey densities are very low. Latest addition in this continuing debate is the book written by Arditi and Ginzburg [55], pointing out many ecologically relevant scenarios in which the fundamental assumptions of prey-dependent functional response collapses.

Instead of contributing to the debate on whether predator functional response is prey-dependent or ratio-dependent, the present study provides a snapshot that explicit considerations of resource supply mechanisms, an overlooked factor, provide better understanding of emergence or de-emergence of the enrichment paradox in a model system. It has been illustrated that while a three-species interaction system has retained the enrichment paradox with logistic growth of resource population, the paradox can be excluded under a large and constant resource supply; however, population cycles can arise when a constant resource supply rate is sufficiently small. Consequently, the present study provides a third potential explanation which underlies ‘the

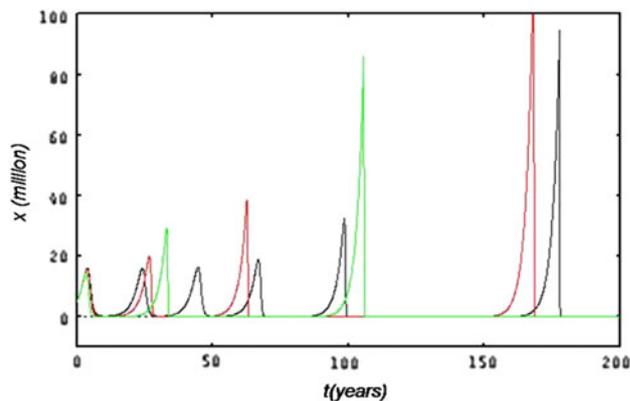


**Fig. 11** Effect of the resource harvesting rate,  $h$ , on the stabilization period while the resource dynamics approach towards a stable steady-state. Here  $a = 0.4$ ,  $b = 0.4 \times 10^{-4}$ ,  $c = 0.1$ ,  $d = 0.1$ ,  $m = 0.12$ ,  $n = 1.2 \times 10^{-3}$ .  $x(0) = 4$  (million),  $y(0) = 4$  (million),  $z(0) = 2$  (billion). The resource population dynamics with  $h = 0.1$  reaches the stable steady-state later than the resource population dynamics with  $h = 0.35$



**Fig. 12** Stabilizing effects of ‘commensal mediation’ in the managed ecosystem. Here  $a = 0.4$ ,  $b = 0.4 \times 10^{-2}$ ,  $c = 0.3$ ,  $d = 0.1$ ,  $n = 1.2 \times 10^{-3}$ ,  $m = 0.2$  (red),  $m = 0.1$  (purple),  $m = 0.05$  (black), and  $x(0) = 5$ ,  $y(0) = 4$ ,  $z(0) = 2$ . (Color figure online)

paradox of enrichment’. It has been found that in presence of commensal predator, prey enrichment (increasing carrying capacity of prey population) always destabilizes the stable equilibrium into damped oscillations and then into limited cycles with further increase in the carrying capacity (Fig. 14). Moreover, increasing density of the commensal predator largely increases the amplitude of the oscillation and the prey recovery time from one peak to the next. Notably, such enrichment effect is completely reversed in the managed ecosystem where prey (or resource) growth rate is maintained in such a way that it can provide a constant yield (expected yield) within a fixed period of time in absence of predators. In this case, enriching prey by

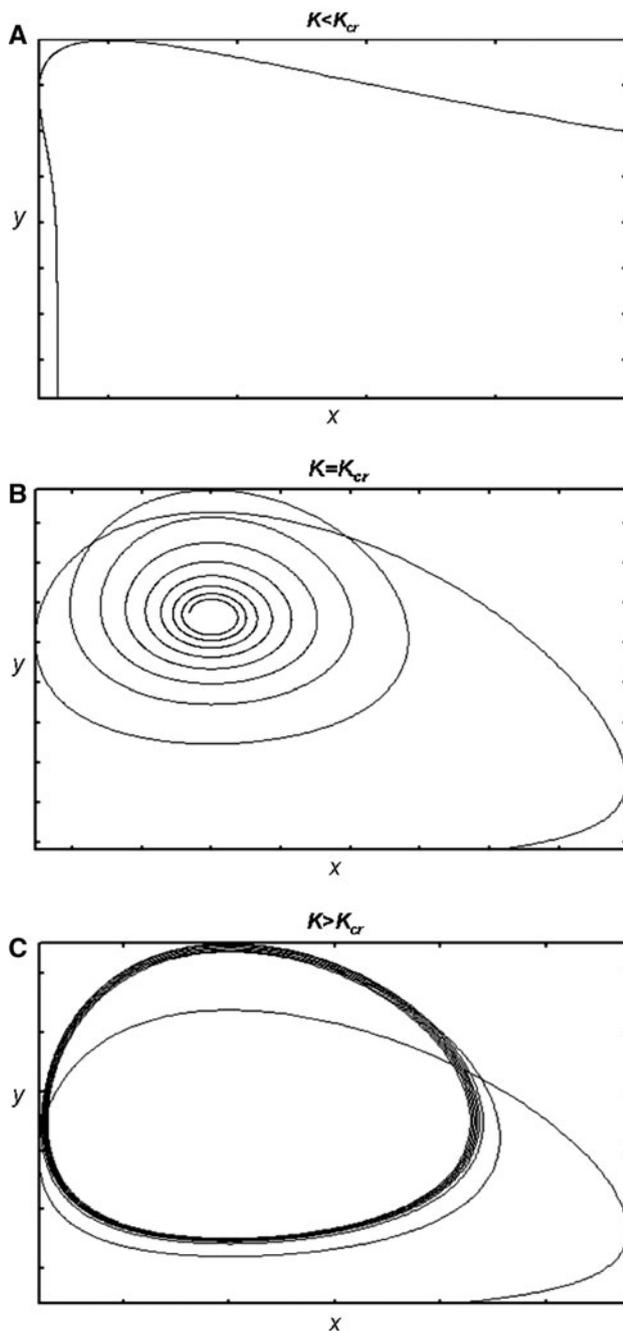


**Fig. 13** Destabilizing effects of commensal mediation for the natural ecosystem. Here  $a = 0.04$ ,  $b = 0.4 \times 10^{-2}$ ,  $c = 0.3$ ,  $d = 0.1$ ,  $m = 0.1$ ,  $n = 1.2 \times 10^{-5}$  (black),  $n = 1.2 \times 10^{-3}$  (red),  $n = 1.2 \times 10^{-2}$  (green), and  $x(0) = 5$ ,  $y(0) = 4$ ,  $z(0) = 2$ . (Color figure online)

introduction of prey individuals than a critical level,  $a_{\text{hopf}}$ , always allows the system to reach at a stable, steady-state. However, while prey enrichment remains below the critical level,  $a_{\text{hopf}}$ , the system exhibits population cycles. While comparing the models for the managed ecosystem (Eq. 2) with that for natural ecosystems, it reveals that the commensal predator-induced feedback effect on the prey birth rate is essential to exhibit destabilizing effects of prey enrichment. Enriching prey population increases the predator density which facilitates the activities of commensal predator those make use of the primary predator’s foraging habits or behaviors to feed on the same prey population. In the natural ecosystems, such enhanced activity largely depresses prey density which provides a feedback effect on the birth rate of prey population, resulting into population cycles with increasing amplitude as the prey enrichment continues to increase. In other words, prey enrichment strengthens the commensal-induced feedback effect on the prey birth rate; below a critical level of prey enrichment,  $K_{cr}$ , the commensal predator-induced feedback effect becomes so weak that it cannot destabilize the steady-state equilibrium into limit cycle oscillations with increasing amplitude. In the managed ecosystems in which prey population is managed so efficiently that in absence of predators changes in prey density can occur only through the introduction of prey individuals, the commensal predator-induced feedback effect on the prey birth rate is completely absent and so the prey enrichment provides stabilizing effects on prey–predator and its commensal interactions.

#### Implications for the Resource Conservation and Management Practices

In the managed ecosystems such as agroecosystems or crop systems, a primary management concern is to reduce



**Fig. 14** Typical resource–consumer dynamics in the  $(x, y)$ -phase plane with commensal mediation while the birth rate of resource population follows logistic growth,  $rx(1 - x/K)$ . **a** For small values of the carrying capacity,  $K < K_{cr}$ , the equilibrium is locally stable. **b** At the critical carrying capacity,  $K_{cr}$ , the dynamics give rise to damped population cycles. **c** With sufficiently higher carrying capacity,  $K > K_{cr}$ , the population dynamics exhibit limit cycle behavior. Here  $a = r = 0.4$ ,  $b = 0.004$ ,  $c = 0.3$ ,  $d = 0.1$ ,  $m = 0.12$ ,  $n = 0.0012$ ,  $K_{cr} = 5$

fluctuations in consumer population densities through time; that less fluctuation provides a dependable, consistent high yields while a large fluctuation implies periods of heavy resource damage by the consumer populations [56].

Whereas in the natural ecosystem, the management and conservation focus is to maintain biodiversity by restricting the fluctuations of population densities that results in infrequent exclusions and thereby promote coexistence of resource and consumer populations [56]. These seemingly two different management concerns can be effectively addressed by applying the concept of stability which corresponds to the tendency of populations to exhibit restricted fluctuations. Although there are several well defined meanings of stability in ecological literatures [57], the commonly used definition in mathematical ecology, which specifically refers to dynamic tendency of population to return to equilibrium following a small perturbation, probably is associated with the idea of restricted fluctuations of population densities. This idea has been capitalized to illustrate some practical implications of the model results for some exemplified managed and natural ecosystems.

Many insects that feed on plants serve as vectors of plant diseases. All major taxa of plant pathogens, including viruses, mycoplasmas, bacteria, protozoa, fungi, and nematodes are spread by insects. Plant pathogens may be carried externally on a vector’s feet, mouthparts, or ovipositors. This mechanical transmission has been well-documented in vectors representing at least eight arthropod orders [Hemiptera (both suborders), Thysanoptera, Orthoptera, Diptera, Coleoptera, Hymenoptera, Lepidoptera, plus Acarina (mites)] [58]. These facilitator insect herbivores are the major contributors for the outbreak of pathogenic pest population particularly in crop systems. Regulating such insect facilitator population, therefore, is the common practice for eliminating crop damage by the facilitated pest. The model results and analysis, discussed in “Controlling Consumer Population” section, are relevant in this context because contemporary biological pest control practices rely on stable strategies, in the sense that their practitioners attempt to regulate the pest at a low density, rather than extirpation, by continuously present set of natural enemies. Most importantly, the results show that such control always stabilizes the facilitated population of crop pest at a low density and hence compresses the oscillation of crop density into an expected, stable steady-state. Another alternative for controlling pathogenic pest population is to harvest infected crops at a regulated rate that holds the pathogenic pest population at a low density and also maintains the stability of the system (“Effects of resource harvesting” section). This study provides a threshold on that rate, i.e.,  $h < (d/c)a_{hopf}$  which is a sufficient condition for stabilizing the population dynamics.

Populations of human commensals, such as rats, potentially increase following agricultural land conversion [59]. These populations can consume or contaminate large quantities of agricultural outputs. For example, the average

damage by the multimammate rat to maize in Tanzania has been estimated to be about 5–15 % yield loss, and for Tanzania this amounts to an average of approximately 412,500 tones per year [60]. Rather than extirpation of such commensal populations, which may cause different adverse effects on other economically and ecologically beneficial populations [61], regulating their population at a low density through the regulation of human activities such as agriculture land conversion can stabilize the interactions between human and its commensal populations. Under a crude assumption that these human commensals cannot persist without agriculture, the system represented by the Eq. (2) can describe the agriculture–human and their commensal population interactions, while the state variable  $x$  refers to agricultural production in a region or locality,  $y$  refers to the density of human population engaged in that activities, and  $z$  refers to the population density of human commensal pests. The model results show that maintaining the rate of agricultural intensification,  $a$ , above the characteristic level,  $a_{\text{hopf}}$ , stabilizes the system at a manipulated steady-state with low density of the commensal population.

The pinewood nematode (*B. xylophilus*) is a destructive pest in pine forest; it invades the stems and branches of pines causing a sudden wilting and death of the tree irrespective of its age or size. This nematode is vectored from diseased to healthy pines by certain wood boring beetles known as Cerambycids. In the diseased trees, developing beetles become contaminated with pinewood nematode. When the beetles complete development, adults emerge from the wood carrying the nematode and fly to healthy pines where they feed on succulent pine and introduce the nematode into feeding wounds. Such interactions can be described by the system represented by the Eq. (3) while the state variable  $x$  refers to the density of pine population,  $y$  refers to the density of beetle population, and  $z$  refers to the density of the nematode population. The model results show that the controlling beetle population at a low density can reduce the effects of nematode arbitration into the pine–beetle interactions; however, this control cannot stabilize the interactions at a steady-state. Alternatively, as shown in the results, immediate removal and destruction of diseased pines will help to prevent spread of the nematode to adjacent healthy pines and thereby reduce the nematode density.

## Conclusion

The resource–consumer interactions can be strongly affected by the population of commensal consumer species. In the natural ecosystems in which the growth rate of resource population depends on its own density even in

absence of consumers, the commensal mediation can distort the usual resource–consumer cycles. With positive density of commensal population, the resource population decays steeply from the peak, and there is unusual delay in resource recovery. Although controlling the facilitator consumer population at a low density cannot stabilize the system, it can reduce the extent of the negative effect of the commensal mediation on resource population. In addition, it has shown that a constant rate of resource harvesting leads to a reduction in the commensal density that eventually reduces the intensity of commensal mediation. In a managed ecosystem in which the resource population growth rate is expected to be maintained at a constant level in absence of consumers, the commensal mediation can provide a stabilizing effect on the resource–consumer interactions; it provides a density-dependent negative feedback at a certain condition that stabilizes the system at a feasible steady-state. While the condition is not maintained, the mediation provides the similar kinds of effects on the resource population dynamics as like in the natural ecosystems. However, the extent of the effect, in terms of increasing amplitude of the resource fluctuations and the time laps from one peak to the next, is less relative to the resource population dynamics with commensal mediation in the natural ecosystems. Furthermore, the study showed that prey enrichment can destabilize the stable equilibrium into damped oscillation, and then into limited cycle oscillation with the further increase in enrichment (the ‘paradox of enrichment’). It revealed that the commensal consumer-induced feedback effect on the prey birth rate increases in magnitude as enrichment increases, which eventually destabilize the stable equilibrium into limit cycle oscillation.

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## Appendix 1: Stability of the System (2)

In all the calculations, the Routh–Hurwitz criteria has been used for examining the local stability of the interaction system; if the characteristic equation of the Jacobian matrix of a system of differential equations at an equilibrium point, it is of the following form,

$$a_0\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0, \quad (8)$$

where  $a_0 > 0$ , and  $\Delta_1 = a_1$ ,  $\Delta_2 = \det \begin{pmatrix} a_1 & a_0 \\ a_3 & a_2 \end{pmatrix}$ , the equilibrium point is stable iff  $\Delta_1 > 0$ ,  $\Delta_2 > 0$  and  $a_3 > 0$ . The system (2) has a feasible equilibrium point  $(\frac{c}{d}, \frac{dm}{cn}, \frac{an}{bm})$ , and the associated Jacobian matrix is,

$$J(x, y, z) = \begin{bmatrix} -byz & -bxz & -bxy \\ dy & -c + dx & 0 \\ nyz & nxz & -m + nxy \end{bmatrix}.$$

Therefore the Jacobian matrix at the equilibrium point is,

$$A = J\left(\frac{c}{d}, \frac{dm}{cn}, \frac{an}{bm}\right) = \begin{bmatrix} -\frac{ad}{c} & -\frac{acn}{dm} & -\frac{bm}{n} \\ \frac{d^2m}{cn} & 0 & 0 \\ \frac{adn}{bc} & \frac{acn^2}{bdm} & 0 \end{bmatrix}$$

The characteristic equation,  $\det(A - \lambda I) = 0$ , is

$$\lambda^3 + ad/c\lambda^2 + (ad + adm/c)\lambda + adm = 0$$

Here,  $\Delta_1 = a_1 = ad/c > 0$  and  $a_3 = adm > 0$ ; therefore if  $\Delta_2 > 0$ ,  $(\frac{c}{d}, \frac{dm}{cn}, \frac{an}{bm})$  is a stable equilibrium point, i.e.

$$\Delta_2 = \det \begin{pmatrix} \frac{ad}{c} & 1 \\ adm & ad + \frac{adm}{c} \end{pmatrix} = \frac{a^2d^2}{c} + \frac{a^2d^2m}{c^2} - adm > 0$$

The above noted condition can be written as  $a > c^2m/(cd + md)$ . On the contrary, if  $a < c^2m/(cd + md)$ , the equilibrium point,  $(\frac{c}{d}, \frac{dm}{cn}, \frac{an}{bm})$  is unstable as  $\Delta_2 < 0$ . While  $ad = c^2m/(c + m)$ , the Routh–Hurwitz criteria do not provide any clue about stability of the equilibrium point. With this condition, the characteristic equation,  $\det(A - \lambda I) = 0$ , can be simplified to  $(\lambda^2 + cm)(\lambda + cm/(c + m)) = 0$ . Therefore, the linearized system of the Eq. (2),  $G'(t) = AG(t)$ , has a general solution

$$G(t) = c_1K_1\exp\{-\sqrt{cm}t\} + c_2K_2\exp\{\sqrt{cm}t\} + c_3K_3\exp\{-cm/(c + m)t\}$$

Here  $G(t) = (u(t), v(t), w(t))'$ ;  $c_1, c_2, c_3$  are arbitrary real numbers;  $K_1, K_2, K_3$  are the eigenvectors corresponding to the eigenvalues  $\lambda_1, \lambda_2, \lambda_3$  respectively. Using the eigenfunction in Mathematica 4.0, it obtains

$$K_1 = \left( -\frac{b(\sqrt{c} + i\sqrt{m})}{\sqrt{cn}}, -\frac{ibc^2m^{\frac{3}{2}}}{a^2n^2(\sqrt{c} - i\sqrt{m})^2(\sqrt{c} + i\sqrt{m})}, 1 \right)'$$

$$K_2 = \left( -\frac{b(\sqrt{c} + i\sqrt{m})}{\sqrt{cn}}, \frac{ibc^2m^{\frac{3}{2}}}{a^2n^2(\sqrt{c} - i\sqrt{m})^2(\sqrt{c} + i\sqrt{m})}, 1 \right)'$$

$$K_3 = \left( \frac{bm}{cn}, -\frac{bcm^3}{a^2n^2(c + m)}, 1 \right)'$$

Although  $G(t)$  is known, the stability of the equilibrium point remains undecided analytically at the condition,  $ad = c^2m/(c + m)$ .

### Appendix 2: Stability of the System (3)

There are two equilibrium points of the system described by the set of Eq. (3): the trivial one is (0,0,0) and the other one is the feasible equilibrium point,  $(\frac{c}{d}, \frac{dm}{cn}, \frac{acn}{bdm})$ . The associated Jacobian matrix is,

$$J(x, y, z) = \begin{bmatrix} a - byz & -bxz & -bxy \\ dy & -c + dx & 0 \\ nyz & nxz & -m + nxy \end{bmatrix}.$$

Therefore, the Jacobian matrix at both the equilibrium points are,

$$A = J(0, 0, 0) = \begin{bmatrix} a & 0 & 0 \\ 0 & -c & 0 \\ 0 & 0 & -m \end{bmatrix} \text{ and } B = J\left(\frac{c}{d}, \frac{dm}{cn}, \frac{acn}{bdm}\right) = \begin{bmatrix} 0 & -\frac{ac^2n}{d^2m} & -\frac{bm}{n} \\ \frac{d^2m}{cn} & 0 & 0 \\ \frac{an}{b} & \frac{ac^2n^2}{bd^2m} & 0 \end{bmatrix}.$$

Obviously, (0,0,0) is unstable for  $\lambda_1 = a > 0$ . The characteristic equation,  $\det(B - \lambda I) = 0$ , is

$$\lambda^3 + a(c + m)\lambda + acm = 0$$

Therefore, the equilibrium,  $(\frac{c}{d}, \frac{dm}{cn}, \frac{acn}{bdm})$  is unstable as  $\Delta_2 = -acm < 0$ .

### Appendix 3: Stability of the System (4)

Since  $y' = 0$ , Eq. (2) can be simplified to,

$$\begin{aligned} x' &= a - by_0xz, \\ z' &= -mz + ny_0xz. \end{aligned} \tag{9}$$

When  $y_0 = y(0) = 0$ , the system becomes,

$$\begin{aligned} x' &= a, \\ z' &= -mz. \end{aligned} \tag{10}$$

The solution of the system (10) is  $(x_0 + at, z_0\exp\{-mt\})$ , where  $x_0 = x(0) \geq 0$ ,  $z_0 = z(0) \geq 0$ . While  $y_0 > 0$ , the system (9) has a feasible equilibrium point  $(\frac{m}{ny_0}, \frac{an}{bm})$  and the Jacobian matrix is

$$J(x, z) = \begin{bmatrix} -by_0z & -by_0x \\ ny_0z & -m + ny_0x \end{bmatrix}.$$

Therefore, the Jacobian matrix at the equilibrium point is,

$$A = J\left(\frac{m}{ny_0}, \frac{an}{bm}\right) = \begin{bmatrix} -\frac{any_0}{m} & -\frac{bm}{n} \\ \frac{an^2y_0}{bm} & 0 \end{bmatrix}$$

Then characteristic equation,  $\det(A - \lambda I) = 0$ , is  $\lambda^2 + any_0/m\lambda + any_0 = 0$ . Obviously  $\left(\frac{m}{ny_0}, \frac{an}{bm}\right)$  is stable, which means that  $\left(\frac{m}{ny_0}, y_0, \frac{an}{bm}\right)$  is a stable equilibrium point of the system (4). If  $y_0 < \frac{4m^2}{an}$ ,  $\left(\frac{m}{ny_0}, y_0, \frac{an}{bm}\right)$  is a stable spiral point; if  $y_0 > \frac{4m^2}{an}$ ,  $\left(\frac{m}{ny_0}, y_0, \frac{an}{bm}\right)$  is a stable node; if  $y_0 = \frac{4m^2}{an}$ ,  $\left(\frac{m}{ny_0}, y_0, \frac{an}{bm}\right)$  may be either a stable spiral point, a stable node, or a degenerate stable node depending on the parameter values (see Fig. 10.25 in Zill & Cullen’s (2001) book).

**Appendix 4: Stability of the System (5)**

Since  $y' = 0$ , Eq. (5) can be simplified to

$$x' = ax - by_0xz, \quad z' = -mz + ny_0xz. \tag{11}$$

When  $y_0 = 0$ , Eq. (11) become

$$x' = ax, \quad z' = -mz. \tag{12}$$

The solution of the system (12) is  $(x_0 \exp\{at\}, z_0 \exp\{-mt\})$ .

While  $y_0 > 0$ , the system (11) becomes the classic Lotka–Volterra model. There are two equilibrium points of the system (11): the trivial one is (0,0) and the other one is the feasible equilibrium point  $\left(\frac{m}{ny_0}, \frac{a}{by_0}\right)$ ; the Jacobian matrix is

$$J(x, y, z) = \begin{bmatrix} a - by_0z & -by_0x \\ ny_0z & -m + ny_0x \end{bmatrix}.$$

Therefore, the Jacobian matrix at the equilibrium points are:

$$A = J(0, 0) = \begin{bmatrix} a & 0 \\ 0 & -m \end{bmatrix} \text{ and } B = J\left(\frac{m}{ny_0}, \frac{a}{by_0}\right) = \begin{bmatrix} 0 & -bm/n \\ an/b & 0 \end{bmatrix}.$$

Obviously, the equilibrium point, (0,0) is unstable as  $\lambda_1 = a > 0$ . For the matrix B, it has been found that  $\lambda_1 = \lambda_2 = 0$ . Thus, the stability of the equilibrium point  $\left(\frac{m}{ny_0}, \frac{a}{by_0}\right)$  remains in doubt. Using the phase-plane method, a first-order differential equation has obtain:

$$\frac{dz}{dx} = \frac{(-m + ny_0x)z}{(a - by_0z)x}.$$

After separating variables, it becomes,

$$\int \frac{a - by_0z}{z} dz = \int \frac{-m + ny_0x}{x} dx,$$

which can be expressed as

$$\frac{z^a}{\exp\{by_0z\}} = K \frac{\exp\{ny_0x\}}{x^m}. \tag{13}$$

Here K is a constant. Let  $f(z)$  denotes  $z^a/\exp\{by_0z\}$  and  $g(x)$  denotes  $x^m/\exp\{ny_0x\}$ . It is not difficult to find that  $f'(a/(by_0)) = 0$ ,  $f''(a/(by_0)) < 0$ ,  $g'(m/(ny_0)) = 0$  and  $g''(m/(ny_0)) < 0$ , which mean that  $f(z)$  has a maximum at  $z = a/(by_0)$  and that  $g(x)$  has a maximum at  $x = m/(ny_0)$ . Let  $M_z, M_x$  represent the maximum of  $f(z)$  and  $g(x)$ , respectively. Obviously, in the case  $K > M_zM_x$ , Eq. (11) has no solutions; in the case of  $K = M_zM_x$ , Eq. (11) has a solution  $\left(\frac{m}{ny_0}, \frac{a}{by_0}\right)$ . Next, it needs to consider the case of  $K < M_zM_x$ . In Eq. (13), suppose that  $K = sM_z$ , where  $s < M_x$  is a positive real number. Here  $g(x)$  have two different solutions  $x_m$  and  $x_M$  that satisfy  $x_m < m/(ny_0) < x_M$ . Then it is easy to prove three cases. In the first case  $x < x_m$  or  $x > x_M$ , the equation also has no solutions; in the second case  $x = x_m$  or  $x = x_M$ , the equation has a solution  $z = a/(by_0)$ ; in the third case  $x_m < x < x_M$ , the equation has two solutions  $z_m$  and  $z_M$  that satisfy  $z_m < a/(by_0) < z_M$ . As  $x$  approaches  $x_m$  or  $x_M$ ,  $f(z)$  approaches  $M_z$ , i.e.  $z_m$  and  $z_M$  both approach  $a/(by_0)$ . Thus the trajectories of Eq. (11) have periodicity, which implies that the trajectories of Eq. (5) have periodicity.

**Appendix 5: Stability of the System (6)**

There are two equilibrium points of the system described by the set of equations (6): one is  $\left(\frac{a}{h}, 0, 0\right)$  and another is the feasible equilibrium point,  $\left(\frac{c}{d}, \frac{dm}{cn}, \frac{n(ad-ch)}{bdm}\right)$ ; the Jacobian matrix is

$$J(x, y, z) = \begin{bmatrix} -byz - h & -bxz & -bxy \\ dy & -c + dx & 0 \\ nyz & nxz & -m + nxy \end{bmatrix}.$$

Therefore, the Jacobian matrices at both the equilibrium points are:

$$A = J\left(\frac{a}{h}, 0, 0\right) = \begin{bmatrix} -h & 0 & 0 \\ 0 & -c + \frac{ad}{h} & 0 \\ 0 & 0 & -m \end{bmatrix}$$

and

$$B = J\left(\frac{c}{d}, \frac{dm}{cn}, \frac{ns}{bdm}\right) = \begin{bmatrix} -\frac{s}{c} - h & -\frac{cns}{d^2m} & -\frac{bm}{n} \\ \frac{d^2m}{cn} & 0 & 0 \\ \frac{ns}{bc} & \frac{cn^2s}{bd^2m} & 0 \end{bmatrix},$$

where  $s = ad - ch$  for simplicity. For the matrix A, if  $h > ad/c$ ,  $\lambda_2 = -c + ad/h < 0$ , which implies that the equilibrium point  $\left(\frac{a}{h}, 0, 0\right)$  is stable. On the contrary, if  $h < ad/c$ ,  $\lambda_2 > 0$ , which implies that the equilibrium

$(\frac{a}{h}, 0, 0)$  is unstable. For the matrix  $B$ , according to  $\det(B - \lambda I) = 0$ , the characteristic equation is

$$\lambda^3 + ad/c\lambda^2 + (c + m)s/c\lambda + ms = 0.$$

Now  $\Delta_1 = \frac{ad}{c} > 0$ . If  $\Delta_2 = \frac{s[ad(m+c)-mc^2]}{c^2} > 0$  and  $a_3 = ms > 0$ ,  $(\frac{c}{d}, \frac{dm}{cn}, \frac{n(ad-ch)}{bdm})$  will be a stable critical point. Namely, it requires that  $ad > c^2m/(c + m)$  and  $s > 0$  hold simultaneously. When  $s < 0$  or  $ad < c^2m/(c + m)$ , the critical point  $(\frac{c}{d}, \frac{dm}{cn}, \frac{n(ad-ch)}{bdm})$  is not stable.

**Appendix 6: The Stability of Eq. (7)**

There are two equilibrium points of the system described by the set of Eq (7): the trivial one is (0,0,0) and the another is the feasible equilibrium point,  $(\frac{c}{d}, \frac{dm}{cn}, \frac{(a-h)cn}{bdm})$ ; the Jacobian matrix is

$$J(x, y, z) = \begin{bmatrix} a - h - byz & -bxz & -bxy \\ dy & -c + dx & 0 \\ nyz & nxz & -m + nxy \end{bmatrix}.$$

Therefore the Jacobian matrices at both the equilibrium points are:

$$A = J(0, 0, 0) = \begin{bmatrix} a - h & 0 & 0 \\ 0 & -c & 0 \\ 0 & 0 & -m \end{bmatrix}$$

and

$$B = J\left(\frac{c}{d}, \frac{dm}{cn}, \frac{(a-h)cn}{bdm}\right) = \begin{bmatrix} 0 & -\frac{(a-h)c^2n}{d^2m} & -\frac{bm}{n} \\ \frac{d^2m}{cn} & 0 & 0 \\ \frac{(a-h)n}{b} & \frac{(a-h)c^2n^2}{bd^2m} & 0 \end{bmatrix}.$$

If  $a - h < 0$ , the characteristic equation,  $\det(A - \lambda I) = 0$ , has three negative real eigenvalues, which implies that the equilibrium point (0,0,0) is stable. If  $a - h > 0$ , the characteristic equation  $\det(A - \lambda I) = 0$  has a positive real eigenvalue, which implies that the equilibrium point (0,0,0) is unstable. The characteristic equation  $\det(B - \lambda I) = 0$  is  $\lambda^3 + (a - h)(c + m)\lambda + (a - h)cm = 0$ .  $\Delta_1 = 0$ ,  $\Delta_2 = -(a - h)cm$ ,  $a_3 = (a - h)cm$ . If  $a \neq h$ , there must be  $\Delta_2 < 0$  or  $a_3 < 0$ . That means that  $(\frac{c}{d}, \frac{dm}{cn}, \frac{(a-h)cn}{bdm})$  is an unstable equilibrium point.

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