



# Qualitative analysis of additional food provided predator–prey system with anti-predator behaviour in prey

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**Abstract** Predator–prey interactions are the most common phenomena in the natural population, which are widely exploited for control of economically damaging pest species in an eco-friendly manner. It is proven that the pest adopts several mechanisms for overcoming the predation pressure. Two such techniques which are not well studied in the literature are group defence, anti-predator behaviour in prey. Anti-predator behaviour of prey is a counterattacking technique, in which adult prey attacks the juvenile predators to reduce the future predation pressure. From the existing experimental studies, it is observed that the anti-predator behaviour of the pest can have adverse effects on the biological control programmes. One of the ways to overcome the loss due to anti-predator behaviour is to cater the predators with some alternative food. In this current work, we have investigated this aspect in a dynamical system framework. This study uncovers many fascinating phenomena. It is found that the considered system displays rich dynamics and demonstrates various bifurcations such as saddle-node bifurcation, (supercritical and subcritical) Hopf bifurcation, homoclinic bifurcation and a Bogdanov–Takens bifurcation of co-dimension 2 are studied. Treating the anti-predator behaviour in prey as one of the control param-

eters, and by characterising the additional food supplied to the predators, the strategies for achieving the successful biological control are derived.

**Keywords** Biological control · Pest · Predator · Additional food · Anti-predator behaviour · Hopf bifurcation · Homoclinic orbit · Bogdanov–Takens bifurcation

## 1 Introduction

Controlling of economically damaging agricultural weeds and insect pests is attracting much attention from many researchers across several disciplines from the last few decades. It is well established that the use of pesticides and insecticides has long-lasting adverse effects on the environment as well as on humankind [13, 14, 19, 64]. Consequently, research on bioremediation, biocontrol programmes and their implementation have gained a lot of momentum in the last few decades [10, 18, 47, 48]. The primary aim of these programmes is to develop techniques to identify the appropriate natural enemies and their time of release for the success of pest control programmes. A vast amount of experimental/theoretical works done in this direction [5, 15, 36, 43, 44, 77, 81, 84, 85]. Many of these studies conclude that a majority of natural enemies in nature are generalists, whose diet choices include a portion of non-prey food items derived from plants, viz., nectar, pollen, etc. The availability of these non-prey food

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sources influences the pest control efficiency of predators.

The theoretical work by Srinivasu et al. [65] carried out in the direction of accessing the impact of non-prey food sources on the biocontrol efficiency of predators, establishes that the ability of a natural enemy to control the pest is affected by the (nutritional) quality and quantity of additional food supplied. Further, it is highlighted that an arbitrary choice can lead to pest outbreaks and can even drive the predator population to extinct, a contra-intuitive result which deviates the outcomes of the biological programmes. The review work by Wade et al. [86], highlighting the role of quality and quantity of supplemental food on the success of biological control programmes supports the findings in the study of Srinivasu et al. [65].

Some of the other factors that can influence the biological control efficiency of predators are intraspecific competition, cannibalism etc. [23,24]. The effect of intraspecific competition on the prey–predator interactions and its outcome on biological control is well established in the literature [1,6,62]. Investigation by Prasad et al. [52] discusses the impact of providing additional food on the biocontrol efficiency of mutually interfering predators. A noteworthy finding of their study is that, at low mutual interference, the presence of high (nutritive) quality non-prey food sources can lead to a stable prey–predator coexistence with low prey biomass. The intraspecific interactions can sometimes lead to cannibalistic nature, especially when the resources become scarce. Many natural enemies in nature found to adopt cannibalism as a “life-boat strategy” [23,58–60,72,79]. One of the ways, to reduce the cannibalistic behaviour in predators and increase their population, is by providing the predators with some additional/alternative food [24]. A recent theoretical investigation carried out in this direction by Prasad and Prasad [53] quantifies the additional food supply with respect to quantity, quality along with the strength of cannibalism for the success of biological control programmes. This study also provides the control strategies for driving the prey population to extinct by varying quality, quantity.

Two other important phenomena linked to predator–prey interactions, which have not attracted much attention from scientists, are group defence and anti-predator behaviour in prey. The anti-predator behaviour in prey is a tactical strategy adopted by the prey, in which the adult prey species kill the juvenile preda-

tor, to avoid the future predation pressure and protect their future offsprings [8,22,27,35,40,45]. In doing so, prey may not always admit immediate benefit [7,20,27,40,55,63]. In many situations, prey adopts anti-predator behaviour as a counterattacking technique only, viz., the works of Vangansbeke et al. [76] document the counterattacking strategy of thrips in destroying the eggs of *Amblydromalus limonicus* and thus reducing their growth. In some other situations, the prey uses the anti-predator behaviour as a nutritive source for their growth. An example of this behaviour is found in the works of [33,34,75] in which it is reported that western flowers thrips, *Frankliniella occidentalis*, a cosmopolitan pest adopts anti-predator behaviour by the feedings the eggs of phytoseiid mites. A similar type of anti-predator behaviour wherein adult prey kill and consume the juvenile predators is reported in [55,56].

The predator–prey interactions exhibit complex dynamics when the prey species adopt anti-predator behaviour. As the anti-predator behaviour depends on various life history parameters of prey as well as predators, identifying the suitable natural enemies to control the pest adopting anti-predator behaviour remains a challenging task. A few theoretical models studied this effect [32,70] and concluded that the anti-predator effect of prey species is beneficial to prey population and detrimental to predator population, resulting in increasing the density of prey community and in turn the pest outbreaks.

In a recent experimental work, Vangansbeke et al. [75] investigated the influence of food supplementation on the anti-predator behaviour of prey species. This study reports a mixed results. Although the food supplementations lead to a decrease in the predation rate, the numerical response of the predators increased in the presence of right kind of food supplementation, yielding a better pest suppression. The study highlights the role of quality of food supplements in altering the counterattacking behaviour of prey. The study also documents that the knowledge on the quantification of additional food for successful biological control when prey adopts anti-predator behaviour is limited. Finally, it is concluded that further investigations are necessary to elucidate the significance of providing various additional food sources on enhancing the biocontrol efficiency of natural enemies. This observation motivated us to undertake a theoretical study to investigate the circumstances under which, the supply of additional food (characterised by quantity and quality) leads to suc-

successful biological control when the prey species adopt group defence and exhibit anti-predator behaviour. We strongly feel that this type of theoretical studies can provide valuable insights into the biological phenomena that are responsible for achieving the required target and bridge the gap between the experimental and theoretical works.

The model presented here assumes no dynamics for the additional food. It is assumed that the additional food supply is controlled by either eco-mangers or nature. Further, we assume that the group defence in prey influences the uptake of prey by predators and that the predation pressure decreases monotonically with an increase in the prey density, resulting in a Holling type IV functional response. We further assume that the prey adopts anti-predator behaviour as a counterattacking strategy only and does not benefit from the killing of the juvenile predator. Thus, the reduction in predator population as a consequence of the anti-predator behaviour by prey is modelled using mass action law.

At first, the dynamics of this model analysed systematically to identify the various equilibria that the system exhibits and their dependency on the system parameters. Subsequently, the global behaviour exemplified with the help of multiple bifurcations that are occurring in the system (treating quantity and anti-predator behaviour as control parameters). The conditions leading to the existence of complex dynamics such as the appearance of homoclinic orbit, saddle-node bifurcation, Bogdanov–Takens bifurcation, etc., are established. The results presented in this study, highlight the vital role of anti-predator behaviour, additional food quality and quantity in controlling the economically damaging pest using biological control agents.

The article is structured as follows: Sect. 2 introduces the prey–predator model with anti-predator behaviour in prey and provision of additional food to predators. Section 3 investigates the conditions for the existence of various equilibria and their stability. The mathematical analysis for various bifurcations (viz., transcritical, saddle-node, Hopf bifurcation and mainly Bogdanov–Takens) exhibited by the system are presented in Sect. 4. The global dynamics of the system treating quantity of the food that is supplied and anti-predator behaviour in prey as control parameters are presented in Sect. 5. Section 6 discusses the consequences of the provision of additional food and its util-

ity in biological control. The key finding of the analysis illustrated through numerical simulations in Sect. 7. Finally, Sect. 8 presents the discussions and conclusions.

## 2 The model

The present section is devoted to the assumptions and formulation of the mathematical model for studying the consequences of providing additional food to the predator–prey interactions that are influenced by the anti-predator behaviour in prey.

In the present study, the prey growth in the absence of predators is modelled using logistic equation. Further, it is assumed that the prey species exhibit group defence mechanism and anti-predator behaviour to escape the predation pressure. Accordingly, the functional and numerical responses of predators are considered to follow Holling type IV functional response. The anti-predator behaviour in prey, which causes a decline in the predator population by killing the predator's egg/juvenile, is modelled using mass action law. In general, the anti-predator behaviour in prey calls for a stage structure in predators. However, the present model ignores the stage structure in predators and treats both the juvenile and adult predators into a single group. This relaxation serves two purposes. This assumption enables us to investigate the effect of anti-predator behaviour in prey in combination with the additional food provided to predators, keeping predators as a single functional group [70], which is the first and foremost principal goal. The second use is reducing the system dynamics from three dimension to two dimension and enabling us to carry out the phase plane techniques to achieve the first goal.

Given the above assumptions, denoting the prey, predator population by  $N$ ,  $P$ , respectively, the following system [70] describes the prey–predator dynamics with anti-predator behaviour in prey.

$$\frac{dN}{dT} = rN \left( 1 - \frac{N}{K} \right) - \frac{cNP}{qaN^2 + a}, \quad (1)$$

$$\frac{dP}{dT} = \frac{bNP}{qaN^2 + a} - mP - \bar{\eta}NP. \quad (2)$$

For a complete analysis of model (1, 2), the reader is referred to Tang and Xiao [70]. It is established that the anti-predator behaviour in prey has a positive effect on

the growth of prey and has a detrimental effect on the predator population. This damaging effect is caused only when the predators are specialists. However, in reality many of natural enemies are generalists and depend on the other food resources. Hence, it is interesting to investigate the impact of the provision of additional food on the system dynamics and to establish the conditions under which the predators can overcome the detrimental effect caused by group defence and anti-predator behaviour of prey.

Accordingly, we now assume that predators are supplemented with an additional food of biomass  $A$ , which is distributed uniformly in the habitat. Addition of this food biomass into the system brings in qualitative changes to the functional/numerical response of predators. Accordingly, system (1, 2) gets transformed to the following system.

$$\frac{dN}{dT} = rN \left( 1 - \frac{N}{K} \right) - \frac{cNP}{(qN^2 + 1)(a + \alpha\eta_1 A)}, \tag{3}$$

$$\frac{dP}{dT} = \frac{b(N + (qN^2 + 1)\eta_1 A)P}{(qN^2 + 1)(a + \alpha\eta_1 A)} - mP - \bar{\eta}NP. \tag{4}$$

The biological description of the various parameters of models (1, 2) and (3, 4) is presented in Table 1.

Before analysing model (3, 4) for the existence of various equilibria and their stability, multiple bifurcations that the considered system admits, we first non-dimensionalise the model by using the transformations,

$$x = \frac{N}{a}, \quad y = \frac{cP}{ar}, \quad t = rT,$$

to obtain the following non-dimensionalised system:

$$\frac{dx}{dt} = x \left( 1 - \frac{x}{\gamma} \right) - \frac{xy}{(wx^2 + 1)(1 + \alpha\xi)}, \tag{5}$$

$$\frac{dy}{dt} = \frac{\beta(x + (wx^2 + 1)\xi)y}{(wx^2 + 1)(1 + \alpha\xi)} - \delta y - \eta xy, \tag{6}$$

where

$$\begin{aligned} \gamma &= \frac{K}{a}, & \eta &= \frac{\bar{\eta}a}{r}, & \xi &= \frac{\eta_1 A}{a}, \\ \beta &= \frac{b}{r}, & \delta &= \frac{m}{r}, & w &= qa^2. \end{aligned} \tag{7}$$

### 3 The model analysis

In the present section, we investigate the existence of various equilibria that system (5, 6) admits and study their stability nature.

**Table 1** Descriptions of variables and parameters present in systems (3, 4) and (5, 6)

| Parameter    | Dimension                                | Definition                                                                                                      | Non-dimensionalised representation |
|--------------|------------------------------------------|-----------------------------------------------------------------------------------------------------------------|------------------------------------|
| $T$          | time                                     | Time                                                                                                            | $t = rT$                           |
| $N$          | biomass                                  | Prey density                                                                                                    | $x = \frac{N}{a}$                  |
| $P$          | biomass                                  | Predator density                                                                                                | $y = \frac{cP}{ar}$                |
| $r$          | time <sup>-1</sup>                       | Prey intrinsic growth rate                                                                                      |                                    |
| $K$          | biomass                                  | Prey carrying capacity                                                                                          | $\gamma = \frac{K}{a}$             |
| $c$          | time <sup>-1</sup>                       | Maximum rate of predation                                                                                       |                                    |
| $b$          | time <sup>-1</sup>                       | Maximum growth rate of predator                                                                                 | $\beta = \frac{b}{r}$              |
| $m$          | time <sup>-1</sup>                       | Predator mortality rate                                                                                         | $\delta = \frac{m}{r}$             |
| $q$          | biomass <sup>-2</sup>                    | Group defence in prey                                                                                           | $\omega = a^2q$                    |
| $\bar{\eta}$ | time <sup>-1</sup> biomass <sup>-1</sup> | Rate of anti-predator behaviour                                                                                 | $\eta = \bar{\eta} \frac{a}{r}$    |
| $a$          | biomass                                  | Normalisation coefficient relating the densities of prey and predator to the environment in which they interact |                                    |
| $\alpha$     |                                          | Ratio between the handling times towards the additional food and the prey                                       | $\alpha$                           |
| $\eta_1$     |                                          | Effectual ability of the predators to detect additional food relative to the prey                               |                                    |
| $A$          | biomass                                  | Quantity of additional food provided to the predators                                                           | $\xi = \frac{\eta_1 A}{a}$         |

Before, proceeding to this, we first discuss the nature of nullcline of the considered system. One can observe that, the trivial predator and prey nullclines of system (5, 6) are  $x$ -axis and  $y$ -axis, respectively. The non-trivial prey and predator nullclines are given by, respectively,

$$\left(1 - \frac{x}{\gamma}\right) - \frac{y}{(wx^2 + 1)(1 + \alpha\xi)} = 0, \tag{8}$$

$$\frac{\beta(x + (wx^2 + 1)\xi)}{(wx^2 + 1)(1 + \alpha\xi)} - \delta - \eta x = 0. \tag{9}$$

Observe that the non-trivial prey nullcline (8) of system (5, 6) is a cubic equation which is a smooth curve joining the points  $(\gamma, 0)$  and  $(0, 1 + \alpha\xi)$  in the positive quadrant of  $xy$ -plane. Following the theory of equations [74], it can be established that the prey nullcline attains zero at  $x = \gamma$  and no other point in the positive quadrant. Now, the slope of the prey nullcline is given by

$$\frac{dy}{dx} = 2\omega x(1 + \alpha\xi) - \frac{3\omega x^2}{\gamma}(1 + \alpha\xi) - \frac{(1 + \alpha\xi)}{\gamma}.$$

A straightforward calculation shows that the prey nullcline has a negative slope at  $x = 0$  and  $x = \gamma$ . Also, from the second derivative test, we observe that the prey nullcline attains both maximum and minimum in  $(0, \gamma)$  when  $\omega\gamma^2 - 3 \geq 0$  and monotonically decreasing in  $(0, \gamma)$  for  $\omega\gamma^2 - 3 < 0$ . Figure 1 depicts these two scenarios.

Re-arranging the terms in the non-trivial predator nullcline (9), we obtain the following cubic equation concerning  $x$ , given by

$$f(x) \equiv \eta w(1 + \alpha\xi)x^3 - [\beta\xi - \delta(1 + \alpha\xi)]wx^2 - [\beta - \eta(1 + \alpha\xi)]x - [\beta\xi - \delta(1 + \alpha\xi)] = 0. \tag{10}$$

Thus, the non-trivial predator nullcline(s) of system (5, 6) are nothing but the straight lines, occurring at the roots of (10). The admission of positive coexistence equilibrium for model (5, 6) (which is nothing but the intersection of the non-trivial prey and predator nullclines) is equivalent to admitting of a positive root by Eq. (10), which is less than  $\gamma$ . Below, we establish the conditions for the existence of positive roots of Eq. (10), which are less than  $\gamma$  using the qualitative theory of cubic equations. For this, we first compute the first and second derivatives of Eq. (10), which are given by:

$$f'(x) = 3\eta w(1 + \alpha\xi)x^2 - 2w[\beta\xi - \delta(1 + \alpha\xi)]x - [\beta - \eta(1 + \alpha\xi)], \tag{11}$$

$$f''(x) = 6\eta w(1 + \alpha\xi)x - 2w[\beta\xi - \delta(1 + \alpha\xi)]. \tag{12}$$

We now have the following cases describing the existence of at least one positive root for Eq. (10).

*Case I*  $\beta\xi - \delta(1 + \alpha\xi) \leq 0$ : In this case, we have that  $f''(x) > 0$  for all  $x > 0$  and  $f(0) > 0$ . Thus, we have that  $f(x)$  is concave up in  $(0, +\infty)$  with  $f(0) > 0$  for  $x > 0$ . Now, the existence of a positive root of Eq. (10), depends on the existence of critical/inflection point of  $f(x)$ . Consequently, we have the two sub-cases.

*Sub case I*  $\beta - \eta(1 + \alpha\xi) \leq 0$ : In this case, we have that  $f'(x) \geq 0$  for all  $x$ . This along with the fact that  $f(0) > 0$  in  $(0, +\infty)$ , implies that  $f(x)$  has no positive root in the interval  $(0, +\infty)$ , and subsequently system (5, 6) does not admit any positive coexisting equilibrium in this case.

*Sub case II*  $\beta - \eta(1 + \alpha\xi) > 0$ : In this case,  $f(x) = 0$  has a minimum at

$$x_c = \frac{a_2 + \sqrt{a_2^2 + 3a_1a_3}}{3a_1}. \tag{13}$$

Thus, the function  $f(x)$  is concave up, decreasing in the interval  $(0, x_c)$  and is concave up, increasing in the interval  $(x_c, \infty)$ . Now,

1. If  $f(x_c) > 0$  then  $f(x)$  has no positive root in  $[0, \infty)$ .
2. If  $f(x_c) = 0$ , then  $x_c$  is the only positive root of  $f(x) = 0$ .
3. If  $f(x_c) < 0$  then the  $f(x)$  admits two positive roots, denoted by  $x_1, x_2$ , given by

$$x_1 = \frac{-1}{3a_1} \left( a_2 + u_1C + \frac{D_0}{u_1C} \right), \tag{14}$$

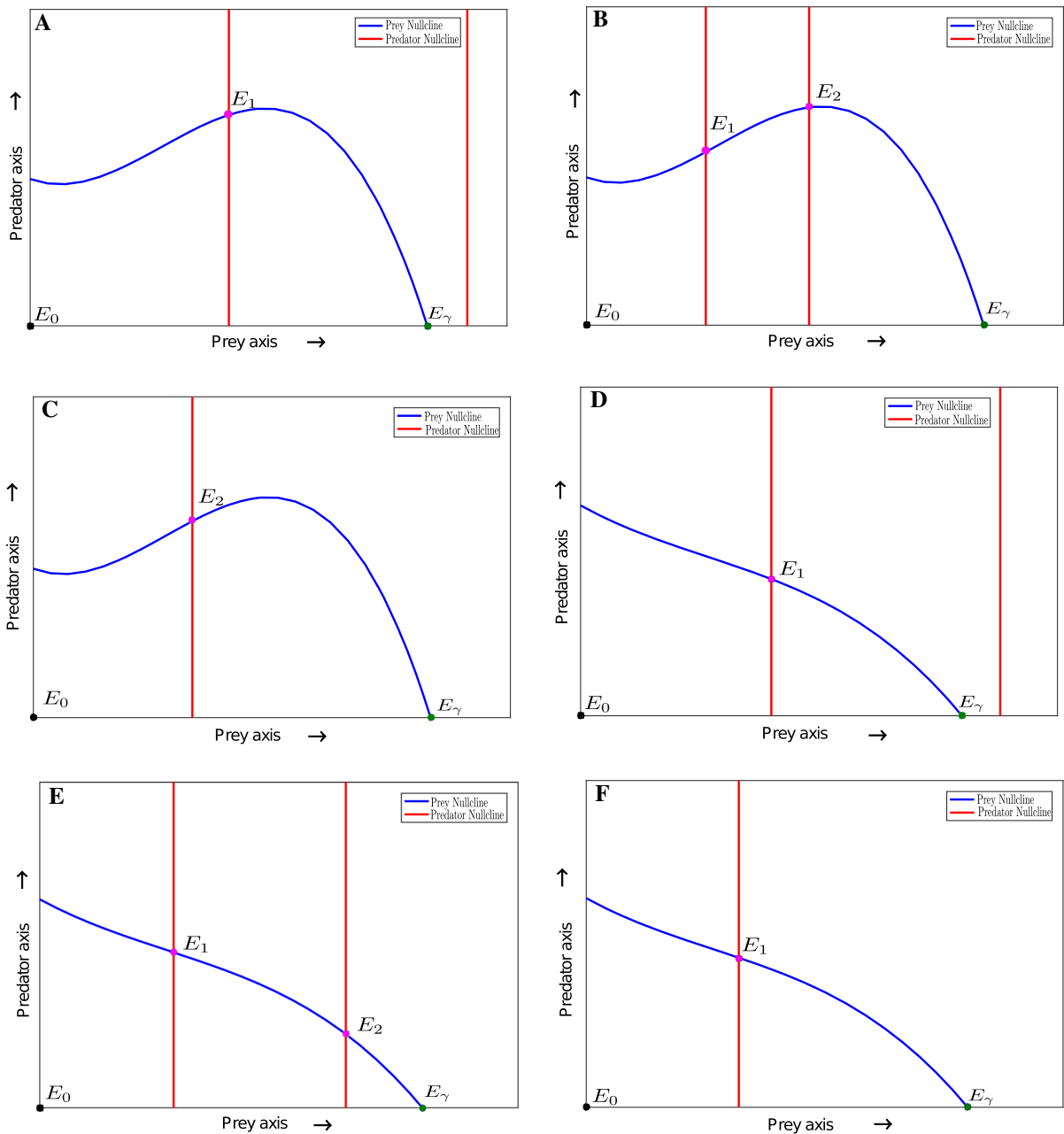
$$x_2 = \frac{-1}{3a_1} \left( a_2 + u_2C + \frac{D_0}{u_2C} \right), \tag{15}$$

with  $x_1 < x_c < x_2$ , where

$$a_1 = \eta\omega(1 + \alpha\xi), \quad a_2 = -\omega(\beta\xi - \delta(1 + \alpha\xi)),$$

$$a_3 = -(\beta - \eta(1 + \alpha\xi)),$$

$$a_4 = -(\beta\xi - \delta(1 + \alpha\xi)), \quad D_0 = a_2^2 - 3a_1a_3,$$



**Fig. 1** Graphical illustration of the qualitative behaviour of nullclines (as described in the text) and the various equilibria that the system exhibits. Frames A, B and C present the nullclines struc-

ture in the case  $\omega\gamma^2 - 3 > 0$  and the Frames D, E and F depicts the situation in the case of  $\omega\gamma^2 - 3 < 0$

$$\begin{aligned}
 D_1 &= 2a_2^3 - 9a_1a_2a_3 + 27a_1^2a_4, \\
 C &= \left( \frac{D_1 + \sqrt{D_1^2 - 4D_0^3}}{2} \right)^{1/3}, \\
 u_1 &= \frac{-1 - i\sqrt{3}}{2}, \quad u_2 = \frac{-1 + i\sqrt{3}}{2}. \tag{16}
 \end{aligned}$$

*Case II*  $\beta\xi - \delta(1 + \alpha\xi) > 0$ : In this case, we have that  $f''(x) = 0$  admits a positive real root denoted by  $x_{cc}$ . It can easily verified that  $f''(x) < 0$  for  $x \in [0, x_{cc})$  and  $f''(x) > 0$  for  $x \in (x_{cc}, +\infty)$ . Thus,  $x_{cc}$  is an inflection point for  $f(x) = 0$  and that  $f(x)$  is concave down in  $(0, x_{cc})$  and concave up in

$(x_{cc}, +\infty)$  with  $f(0) < 0$ . Now, the existence of a positive root of Eq. (10), depends on the existence of critical/inflection point and discriminate of  $f(x)$ . We now have the following two sub-cases.

*Sub case I*  $\beta - \eta(1 + \alpha\xi) > 0$ : In this case, we have that  $f'(0) < 0$ . From the theory of cubic equations, we observe that the discriminant of Eq. (10) is either negative or positive. Consequently, Eq. (10) admits one positive real root,  $x_2$ .

*Sub case II*  $\beta - \eta(1 + \alpha\xi) \leq 0$ : In this case, we observe that  $f'(0) > 0$ ,  $f(0) < 0$  and the discriminant of Eq. (10) is always negative. Thus, Eq. (10) has a pair of complex conjugate roots and one positive real root,  $x_2$ .

Denoting the positive interior equilibrium of system (5, 6) as  $E_1 = (x_1, y_1)$ , and  $E_2 = (x_2, y_2)$ , where  $0 < x_1 < x_2 < \gamma$ , and  $y_1, y_2$  are given by

(iii) *an instantaneous equilibrium,*

$$E_c = (x_c, y_c) = \left( x_c, \left( 1 - \frac{x_c}{\gamma} \right) (\omega x_c^2 + 1)(1 + \alpha\xi) \right), \tag{19}$$

when the system satisfies  $\beta\xi - \delta(1 + \alpha\xi) \leq 0$ ,  $\beta - \eta(1 + \alpha\xi) > 0$  and  $f(x_c) = 0$ ,  $x_c < \gamma$ .

(iv) *only one interior equilibrium,  $E_2$ , when  $\beta\xi - \delta(1 + \alpha\xi) > 0$  and  $x_2 < \gamma$ .*

### 3.1 Stability analysis

In this section, we investigate the conditions for stability/instability of the various equilibria that the system exhibits. The community matrix for system (5, 6) is given by:

$$J = \begin{bmatrix} J_{11} & J_{12} \\ J_{21} & J_{22} \end{bmatrix},$$

where

$$J_{11} = 1 - \frac{2x}{\gamma} - \frac{(\omega x^2 + 1)(1 + \alpha\xi)y - 2\omega y x^2(1 + \alpha\xi)}{[(\omega x^2 + 1)(1 + \alpha\xi)]^2},$$

$$J_{12} = -\frac{x}{(\omega x^2 + 1)(1 + \alpha\xi)},$$

$$J_{21} = \frac{(\omega x^2 + 1)(1 + \alpha\xi)[\beta y + 2\beta\xi\omega xy] - 2\beta(x + (\omega x^2 + 1)\xi)y\omega x(1 + \alpha\xi)}{[(\omega x^2 + 1)(1 + \alpha\xi)]^2} - \eta y,$$

$$J_{22} = \frac{\beta[x + (\omega x^2 + 1)\xi]}{(\omega x^2 + 1)(1 + \alpha\xi)} - \delta - \eta x.$$

$$y_1 = \left( 1 - \frac{x_1}{\gamma} \right) (\omega x_1^2 + 1)(1 + \alpha\xi), \tag{17}$$

$$y_2 = \left( 1 - \frac{x_2}{\gamma} \right) (\omega x_2^2 + 1)(1 + \alpha\xi). \tag{18}$$

The following theorem summarises the above findings regarding the existence of positive equilibria of the system.

**Theorem 1** *System (5, 6) exhibits*

- (i) *an unique interior equilibrium  $E_1$ , when  $\beta\xi - \delta(1 + \alpha\xi) \leq 0$ ,  $\beta - \eta(1 + \alpha\xi) > 0$  and  $f(x_c) < 0$ ,  $x_1 < \gamma < x_2$ .*
- (ii) *two interior equilibria  $E_1$  and  $E_2$ , when  $\beta\xi - \delta(1 + \alpha\xi) \leq 0$ ,  $\beta - \eta(1 + \alpha\xi) > 0$  and  $f(x_c) < 0$ ,  $x_1 < x_2 < \gamma$ .*

We now have the following theorem, establishing the stability of the trivial and axial equilibria. The proof of which follows from the evaluation of the eigenvalues of the community matrix at the respective equilibria.

**Theorem 2** (i) *The trivial equilibrium  $E_0 = (0, 0)$  is saddle whenever  $-\delta + \xi(\beta - \delta\alpha) < 0$  and unstable otherwise.*

(ii) *The axial equilibrium  $E_1 = (\gamma, 0)$  is stable for  $\frac{\beta(\gamma + (\omega\gamma^2 + 1)\xi)}{(\omega\gamma^2 + 1)(1 + \alpha\xi)} - \delta - \eta\gamma < 0$  and saddle otherwise.*

**Theorem 3** (i) *The interior equilibrium  $E_2$  (if exists) is always a saddle point.*

(ii) *The interior equilibrium  $E_1$  is stable whenever  $tr_{J_{E_1}} < 0$  and unstable otherwise.*

*Proof* Evaluating the community matrix at the interior equilibrium  $E_i, i = 1, 2$ , we have

$$J_{E_i} = \begin{bmatrix} J_{11_i} & J_{12_i} \\ J_{21_i} & J_{22_i} \end{bmatrix},$$

where

$$\begin{aligned} J_{11_i} &= -\frac{x_i}{\gamma} + \frac{2\omega x_i^2 \left(1 - \frac{x_i}{\gamma}\right)}{\omega x_i^2 + 1}, \\ J_{12_i} &= -\frac{x_i}{(\omega x_i^2 + 1)(1 + \alpha\xi)} \\ J_{21_i} &= \beta \left(1 - \frac{x_i}{\gamma}\right) (1 + 2\omega\xi x_i) \\ &\quad - (\delta + \eta x_i) 2\omega x_i (1 + \alpha\xi) \left(1 - \frac{x_i}{\gamma}\right) \\ &\quad - \eta y_i, \quad J_{22_i} = 0. \end{aligned}$$

The characteristic equation is given by:

$$\lambda^2 - \text{tr } J_{E_i} \lambda + \det J_{E_i} = 0,$$

where

$$\begin{aligned} \text{tr } J_{E_i} &= -\frac{x_i}{\gamma} + \frac{2\omega x_i^2 \left(1 - \frac{x_i}{\gamma}\right)}{\omega x_i^2 + 1}, \\ \det J_{E_i} &= \frac{x_i}{(\omega x_i^2 + 1)(1 + \alpha\xi)} \\ &\quad \left\{ \beta \left(1 - \frac{x_i}{\gamma}\right) (1 + 2\omega\xi x_i) \right. \\ &\quad \left. - (\delta + \eta x_i) 2\omega x_i (1 + \alpha\xi) \left(1 - \frac{x_i}{\gamma}\right) - \eta y_i \right\}, \\ &= \frac{x_i}{(\omega x_i^2 + 1)(1 + \alpha\xi)} \\ &\quad \left\{ -3\eta w(1 + \alpha\xi)x_i^2 + 2w[\beta\xi - \delta(1 + \alpha\xi)] \right. \\ &\quad \left. x_i + [\beta - \eta(1 + \alpha\xi)] \right\}. \end{aligned}$$

- (i) From the condition of existence for  $E_2$ , we have that  $-3\eta w(1 + \alpha\xi)x_2^2 + 2w[\beta\xi - \delta(1 + \alpha\xi)]x_2 + [\beta - \eta(1 + \alpha\xi)] < 0$ . Therefore,  $\det J_{E_2} < 0$  and that  $E_2$  (if exists) is saddle in nature.
- (ii) Similarly, from the fact that  $x_1 > 0$  and from the condition for the existence of  $E_1$ , it is to verify that  $-3\eta w(1 + \alpha\xi)x_1^2 + 2w[\beta\xi - \delta(1 + \alpha\xi)]x_1 + [\beta - \eta(1 + \alpha\xi)] > 0$ , implying  $\det J_{E_1} > 0$ . Therefore, the stability of the interior equilibrium  $E_1$  depends

on the sign of  $\text{tr } J_{E_1}$ . So,  $E_1$  is stable for  $-\frac{x_1}{\gamma} + \frac{2\omega x_1^2 \left(1 - \frac{x_1}{\gamma}\right)}{\omega x_1^2 + 1} < 0$  and unstable otherwise. □

One can easily observe that the expression for  $\text{tr } J_{E_1}$  is nothing but the slope of the prey nullcline at  $E_1$ . From the concavity properties of the prey nullcline, we have that prey nullcline is concave down, decreasing function for  $\omega\gamma^2 - 3 < 0$ . We now have the following Corollary establishing the asymptotical stability of  $E_1$ .

**Corollary 1** *The interior equilibrium  $E_1$  (if exists), is asymptotically stable whenever  $\omega\gamma^2 - 3 < 0$ .*

Figure 2 numerically depicts the stability nature of the various equilibria that the system exhibits.

### 4 Bifurcation analysis

In this section, we investigate the various bifurcations that are occurring in the system. From the model analysis, it follows that the system dynamics depend on three crucial parameters  $\alpha, \xi$ , and  $\eta$  representing the (nutritional) quality, quantity of the additional food and strength of the anti-predator behaviour in prey, respectively. In this present study, we are mainly interested in studying the consequence of anti-predator behaviour in prey and provision of additional food; accordingly, we treat  $\eta$  and  $\xi$  as bifurcation parameters, and  $\alpha$  is a fixed parameter (maintained by the eco-manager). This assumption of treating  $\xi$  as a bifurcation parameter with fixed  $\alpha$  is justified as variations in the quantity of additional food are more convenient than changing quality; moreover, it is more economically viable [2, 3, 61, 78].

#### 4.1 Hopf bifurcation around interior equilibrium $E_1$

System (5, 6) can be represented in the form,

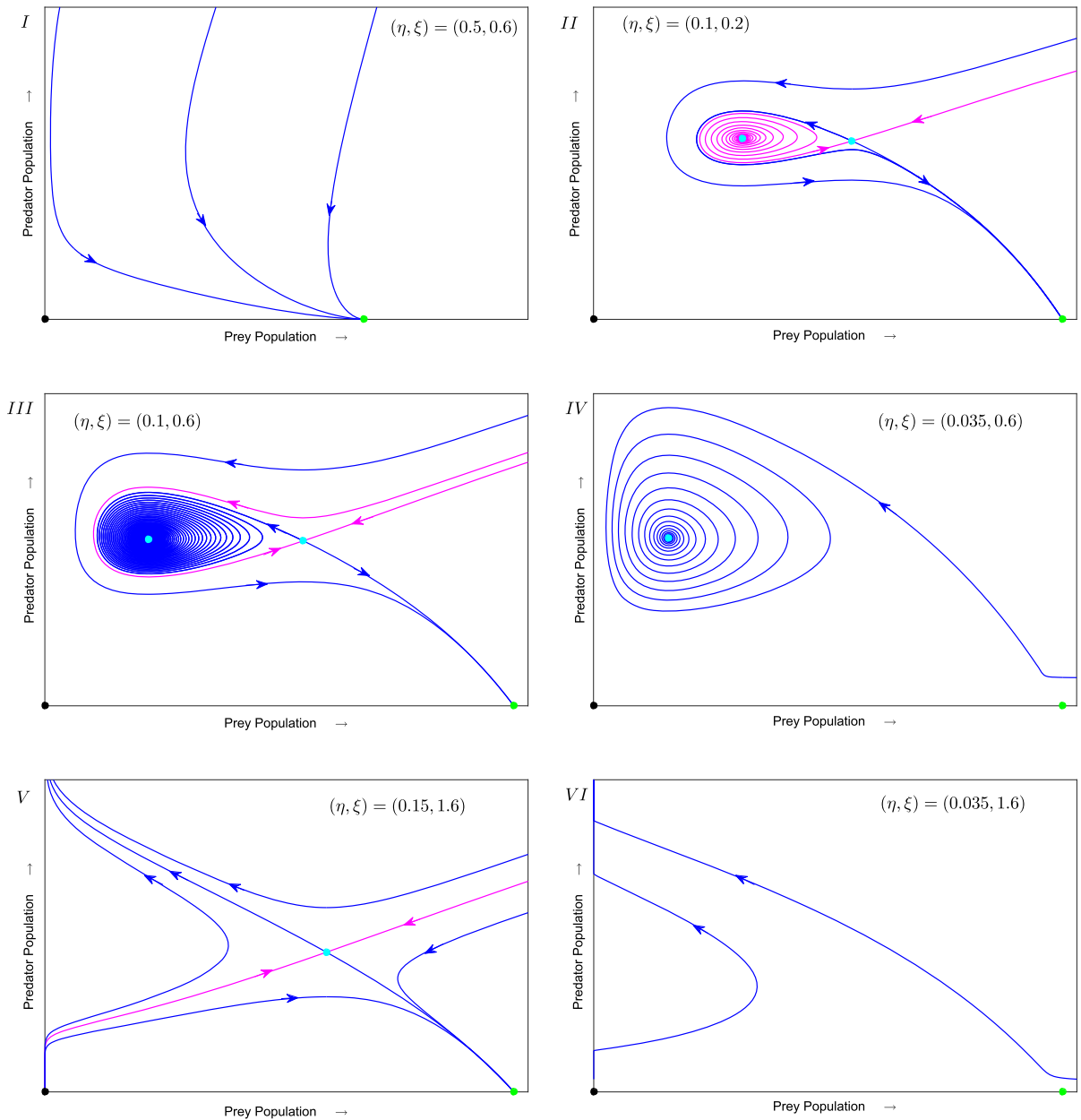
$$\frac{dx}{dt} = P(x)(F(x) - y), \tag{20}$$

$$\frac{dy}{dt} = y(-d_1 + Q(x)), \tag{21}$$

where

$$P(x) = \frac{x}{(\omega x^2 + 1)(1 + \alpha\xi)},$$





**Fig. 2** Figure depicting the stability nature of various equilibria that the system exhibits as described in Sect. 3. The ecosystem parameter values chosen are:  $\gamma = 3.3, \beta = 0.5, \delta = 0.4, \omega = 0.3$  and  $\alpha = 0.5$ . Frame I presents the global stability of  $(\gamma, 0)$  in the absence of interior equilibria. Frames II and III depict the existence of two interior equilibria with equilibrium with lower prey

population unstable (stable) in Frame II (Frame III). Frames IV and V present the scenario wherein the unique coexistence state is stable and unstable, respectively. Finally, frame VI represents case where predators experience the unbounded growth in the absence of prey

$$F(x) = \left(1 - \frac{x}{\gamma}\right) (\omega x^2 + 1)(1 + \alpha \xi),$$

$$d_1 = \frac{\delta(1 + \alpha \xi) - \xi}{1 + \alpha \xi}, \quad Q(x) = \beta P(x) - \eta x.$$

Now, the Jacobian matrix is given by

$$J = \begin{pmatrix} P'(x)[F(x) - y] + P(x)F'(x) & -P(x) \\ Q'(x)y & -d_1 + Q(x) \end{pmatrix}. \tag{22}$$

Evaluating the Jacobian matrix at  $E_1$ , we obtain

$$\det E_1 = P(x_1)Q'(x_1)y_1. \tag{23}$$

From the existence condition of  $E_1$ , it is easy to verify that  $\det E_1$  is positive. Now, the trace of Jacobian matrix at  $E_1$  is

$$\text{tr } J_{E_1} = P(x_1)F'(x_1). \tag{24}$$

Clearly, the stability of  $E_1$  depends on the  $F'(x_1)$  and the considered system exhibits Hopf bifurcation around the interior equilibrium  $E_1$  when  $\text{tr } J_{E_1} = 0$  i.e.,  $F'(x_1) = 0$ . From Corollary 1, we observe that  $F'(x_1) < 0$  whenever  $\omega\gamma^2 - 3 < 0$ . Thus, for existence of Hopf bifurcation we must have  $\omega\gamma^2 - 3 > 0$ . So, in what follows we assume  $\omega$  and  $\gamma$  are chosen so that they satisfy  $\omega\gamma^2 - 3 > 0$ . Simplifying the expression  $F'(x_1) = 0$ , leads to the quadratic equation in  $x_1$ ,

$$S(x_1) \equiv -3\omega x_1^2 + 2\omega\gamma x_1 - 1 = 0. \tag{25}$$

As  $x_1$  is a function of  $(\eta, \xi)$ , for a fixed  $\beta, \delta, \alpha$  and  $\omega, \gamma$  satisfying the condition  $\omega\gamma^2 - 3 > 0$ , we have  $S(x_1(\eta, \xi))$ , represents the Hopf bifurcation surface in  $(\eta, \xi)$  space. Equation (25) has two positive roots,

$$x_{L,H} = \frac{\gamma \mp \sqrt{\frac{\omega\gamma^2 - 3}{\omega}}}{3}. \tag{26}$$

Thus when  $\omega\gamma^2 - 3 > 0$ , the model undergoes Hopf bifurcation whenever  $x_1 = x_L$  or  $x_1 = x_H$ . The interior equilibrium  $(x_1, y_1)$  is unstable for  $x_L < x_1 < x_H$  and stable otherwise. Now, we verify the transversality condition at  $E_{x_1}$  with  $x_1 = x_L$  or  $x_1 = x_H$  and with respect to the bifurcation parameter  $\eta$ . Let  $\Gamma$  be the real part of the eigenvalue, then a straightforward computation from (22) and (24) gives

$$\begin{aligned} \Gamma &= \frac{1}{2}P(x_1)F'(x_1) \\ &\equiv \frac{x_1}{2(1 + \alpha\xi)(\omega x_1^2 + 1)}(-3\omega x_1^2 + 2\omega\gamma x_1 - 1). \end{aligned}$$

Now,

$$\frac{\partial \Gamma}{\partial \eta} = \frac{\omega x_1 \frac{\partial x_1}{\partial \eta}}{(1 + \alpha\xi)(\omega x_1^2 + 1)}(-3x_1 + \gamma).$$

From the expression for  $f(x)$  (cf. Eq. 10), establishing the existence of equilibrium prey component and it is verify that

$$\frac{\partial f}{\partial \eta} = \omega(1 + \alpha\xi)x_1^3 + (1 + \alpha\xi)x_1 > 0.$$

Further, we have that  $f(x)$  is monotonically decreasing for  $0 < x_1 < x_c$ . Thus,  $\frac{\partial x_1}{\partial \eta} = \frac{\partial f}{\partial \eta} / \frac{\partial f}{\partial x_1} < 0$  in  $[0, x_c)$ .

Therefore,  $\frac{\partial \Gamma}{\partial \eta} = 0$  if and only if  $\omega\gamma^2 - 3 = 0$  and this occurs only when  $x_L = x_H = \frac{\gamma}{3}$ . This verifies the transversality condition for Hopf bifurcation treating  $\eta$  as a bifurcation parameter.

Proceeding in a similar manner, we observe that

$$\frac{\partial \Gamma}{\partial \xi} = \frac{\omega x_1 \frac{\partial x_1}{\partial \xi}}{(1 + \alpha\xi)(\omega x_1^2 + 1)}(-3x_1 + \gamma).$$

Now,

$$\begin{aligned} \frac{\partial x_1}{\partial \xi} &= \frac{1}{\frac{\partial f}{\partial x_1}} \times \frac{\partial f}{\partial \xi} = \frac{1}{\frac{\partial f}{\partial x_1}} \\ &\times \left\{ (1 + \omega x_1^2)[\eta\alpha x_1 - (\beta - \delta\alpha)] \right\}. \end{aligned}$$

From the existence of  $x_1, x_c$  and from the qualitative properties of  $f(x)$ , we found that  $\eta\alpha x_1 - (\beta - \delta\alpha) \neq 0$  and that  $\frac{\partial \Gamma}{\partial \xi} = 0$  if and only if  $x_L = x_H = \frac{\gamma}{3}$ . This verifies the transversality condition for Hopf bifurcation treating  $\xi$  as control parameter.

Now, at the Hopf bifurcation instant, the first by Lya-punov coefficient is calculated using the formula given by Hastings [30], Wolkowicz [87], Xiao and Zhu [89], Zhu et al. [92] and is given by

$$\begin{aligned} \sigma(x_1) &= \frac{-P(x_1)F''(x_1)Q''(x_1)}{Q'(x_1)} \\ &+ P(x_1)F'''(x_1) + 2P'(x_1)F''(x_1). \end{aligned} \tag{27}$$

The Hopf bifurcation is non-degenerate in nature for  $\sigma(x_1) < 0$  and has degenerate nature for  $\sigma(x_1) > 0$ . A computationally intensive calculation with the help of scientific computing tool such as MATLAB [46], it is found that for Hopf bifurcation occurring at  $x_1 = x_H$ , we have  $\sigma(x_1)$  is negative always. Thus, the system undergoes non-degenerate Hopf bifurcation at  $x_1 = x_H$ . At  $x_1 = x_L$ , the sign of  $\sigma(x_1)$  is either negative or positive depending on the parameter values  $\gamma, \eta$  and  $\xi$ . One can establish the nature of Hopf bifurcation at  $x_1 = x_L$  numerically by identifying suitable set of parameter values  $\gamma, \eta$  and  $\xi$ . Further, it is important to

note that at the instance of degenerate nature of Hopf bifurcation occurring at  $x_1 = x_L$ , the system produces two limit cycles surrounding the locally asymptotically stable equilibrium  $E_1$ . The two cycles surrounding the equilibrium will disappear through saddle-node bifurcation of limit cycles, the normal form computation of which is tedious, and we provided here a numerical example by identifying the proper set of parameter range for which this phenomenon occurs.

Summarising the above findings, we have the following theorem establishing the existence of Hopf bifurcation.

**Theorem 4** *For a choice of  $\eta$  and/or  $\xi$  satisfying  $-3\omega x_1^2 + 2\omega\gamma x_1 - 1 = 0$ , the system always undergoes non-degenerate Hopf bifurcation at  $x_1 = x_H$ . At  $x_1 = x_L$ , the system undergoes either non-degenerate (degenerate) Hopf bifurcation for  $\sigma(x_1) < 0(> 0)$ .*

### 4.2 Saddle-node bifurcation around interior equilibrium

As seen from the model analysis, when  $\beta\xi - \delta(1 + \alpha\xi) \leq 0$ ,  $\beta - \eta(1 + \alpha\xi) > 0$  and  $f(x_c) < 0$ , the considered system exhibits utmost two interior equilibrium points  $E_1, E_2$ . Further, for  $f(x_c) = 0$ , the system admits a unique instantaneous equilibrium  $E_c = (x_c, y_c)$ , formed by the collision of  $E_1, E_2$ . This instantaneous equilibrium ceases to exist when  $f(x_c) > 0$  through saddle-node bifurcation. The following theorem establishes the conditions for the existence of saddle-node bifurcation around the instantaneous equilibrium  $E_c$ .

**Theorem 5** *System (5, 6) undergoes saddle-node bifurcation at  $E_c = (x_c, y_c)$  with respect to bifurcation parameter  $\eta$  if*

$$\det J_{E_c} = \beta \left(1 - \frac{x_c}{\gamma}\right) (1 + 2\omega\xi x_c) - (\delta + \eta x) 2\omega x_c (1 + \alpha\xi) \left(1 - \frac{x_c}{\gamma}\right) - \eta y_c = 0$$

and

$$\text{tr } J_{E_c} = -\frac{x_c}{\gamma} + \frac{2\omega x_c^2 (1 - \frac{x_c}{\gamma})}{(\omega x_c^2 + 1)} \neq 0.$$

*Proof* The community matrix evaluated at  $E_c$

$$J_{E_c} = \begin{bmatrix} a_1 & a_2 \\ a_3 & a_4 \end{bmatrix},$$

where

$$\begin{aligned} a_1 &= -\frac{x_c}{\gamma} + \frac{2\omega x_c^2 (1 - \frac{x_c}{\gamma})}{(\omega x_c^2 + 1)}, \\ a_2 &= -\frac{x_c}{(\omega x_c^2 + 1)(1 + \alpha\xi)} < 0, \\ a_3 &= \beta \left(1 - \frac{x_c}{\gamma}\right) (1 + 2\omega\xi x_c) - (\delta + \eta x) 2\omega x_c (1 + \alpha\xi) \left(1 - \frac{x_c}{\gamma}\right) \\ &\quad - \eta y_c, \quad a_4 = 0. \end{aligned}$$

Now,  $\det J_{E_c} = 0$  and  $\text{tr } J_{E_c} \neq 0$ ; thus, the community matrix  $J_{E_c}$  has a zero eigenvalue. The eigenvectors corresponding to zero eigenvalue of  $J_{(x_c, y_c)}$  and  $J_{(x_c, y_c)}^T$  are given by  $V = (1, -\frac{a_1}{a_2})^T$  and  $W = (0, 1)^T$ , respectively.

Now,

$$\Delta_1 = W^T [F_\eta(x_c, y_c)] = -x_c y_c \neq 0$$

and

$$\begin{aligned} \Delta_3 &= W^T [D^2 F(x_c, y_c), \eta, (V, V)] \\ &= W_2 \left( \frac{\partial^2 G}{\partial x^2} + 2 \frac{\partial^2 G}{\partial x \partial y} V_2 \right) \\ &= \frac{-x_c}{(\omega x_c^2 + 1)(1 + \alpha\xi)} \\ &\quad \frac{2\omega\beta x_c y_c (1 + \alpha\xi)^2}{((\omega x_c^2 + 1)(1 + \alpha\xi))^2} (\omega x_c^2 - 3) \neq 0. \\ &\quad \times (\omega x_c^2 - 3 < 0 \text{ at the instance of saddle-node bifurcation}) \end{aligned}$$

Hence, by Sotomayor’s theorem [50] the system exhibits saddle-node bifurcation around the instantaneous equilibrium  $E_c$  when the system of parameters satisfies  $\det J_{E_c} = 0$  and  $\text{tr } J_{E_c} \neq 0$ .  $\square$

### 4.3 Bogdanov–Takens bifurcation

When the system exhibits the unique instantaneous equilibrium  $E_c$ , we can fine tune the parameter set  $(\eta, \xi)$  such that  $\det J_{E_c} = 0$  and  $\text{tr } J_{E_c} = 0$ . In this situation, the system can undergo Bogdanov–Takens bifurcation of co-dimension 2. Now, fixing  $(\beta, \delta, \gamma, \omega, \alpha) \in \mathbb{R}_+^5$  and choosing  $(\eta, \xi)$  such that  $\det J_{E_c} = 0$  and  $\text{tr } J_{E_c} = 0$  we demonstrate the existence of Bogdanov–Taken bifurcation. Now,  $\text{tr } J_{E_c} = 0$  implies  $-3\omega x_c^2 + 2\omega\gamma x_c - 1 = 0$  and that there exist two critical  $x'_c$ ’s and accordingly, we obtain pair of  $(\eta, \xi)$  for which  $\text{tr } J_{E_c} = 0$ . We denote these points

by  $BT_1, BT_2$ . Now,  $\det J_{BT_1} = 0$  and/or  $\det J_{BT_2} = 0$  results in a double zero eigenvalues at  $BT_1$  and/or  $BT_2$ . In this case, the Jordan form of the community matrix of  $J_{E_c}$  at  $BT_1$  and/or  $BT_2$  will be similar to  $\begin{pmatrix} 0 & 1 \\ 0 & 0 \end{pmatrix}$ . From the normal form theory [38], the equilibrium  $E_{BT_i} = (x_{BT_i}, y_{BT_i}), i = 1, 2$  is a cusp of co-dimension 2 under certain non-degeneracy conditions. For an appropriate pair of bifurcation parameters, system (5, 6) undergoes a Bogdanov–Takens bifurcation around the instantaneous equilibrium point  $E_{BT_i} (i = 1, 2)$ . The following theorem establishes the conditions for Bogdanov–Takens bifurcation.

**Theorem 6** *If we choose  $\eta$  and  $\xi$  as two bifurcation parameters then system (5, 6) undergoes a Bogdanov–Takens bifurcation around the instantaneous equilibrium point  $E_{BT_i} (i = 1, 2)$  whenever*

$$tr J_{BT_i} = 0 \text{ implies } -3\omega x_{BT_i}^2 + 2\omega\gamma x_{BT_i} - 1 = 0$$

and

$$\det J_{BT_i} = 0 \text{ implies } \beta \left(1 - \frac{x_{BT_i}}{\gamma}\right) (1 + 2\omega\xi x_{BT_i}) - (\delta + \eta x_{BT_i}) 2\omega x_{BT_i} (1 + \alpha\xi) \left(1 - \frac{x_{BT_i}}{\gamma}\right) - \eta y_{BT_i} = 0.$$

*Proof* Let us consider the neighbourhood of the bifurcation parameters  $\eta$  and  $\xi$  around their B-T point  $(\eta + \lambda_1, \xi + \lambda_2)$  with  $\lambda_i, i = 1, 2$  sufficiently small, substituting these into system (5, 6) is given by

$$\begin{aligned} \frac{dx}{dt} &= x \left(1 - \frac{x}{\gamma}\right) - \frac{xy}{(\omega x^2 + 1)(1 + \alpha(\xi + \lambda_2))} \\ &\equiv F(x, y, \lambda_1, \lambda_2), \\ \frac{dy}{dt} &= \frac{\beta(x + (\omega x^2 + 1)(\xi + \lambda_2))y}{(\omega x^2 + 1)(1 + \alpha(\xi + \lambda_2))} - \delta y - (\eta + \lambda_1)xy \\ &\equiv G(x, y, \lambda_1, \lambda_2), \end{aligned} \tag{28}$$

Substituting  $m_1 = x - x_c$ , and  $m_2 = y - y_c$ , we get

$$\begin{aligned} \frac{dm_1}{dt} &= F_0 + am_1 + bm_2 + p_{11}m_1^2 \\ &\quad + p_{12}m_1m_2 + H_1(m_1, m_2), \\ \frac{dm_2}{dt} &= G_0 + cm_1 + dm_2 + q_{11}m_1^2 \\ &\quad + q_{12}m_1m_2 + H_2(m_1, m_2), \end{aligned} \tag{29}$$

where

$$F_0 = x_c \left(1 - \frac{x_c}{\gamma}\right) - \frac{x_c y_c}{(\omega x_c^2 + 1)(1 + \alpha(\xi + \lambda_2))},$$

$$\begin{aligned} a &= 1 - \frac{2x_c}{\gamma} - \frac{y_c}{(\omega x_c^2 + 1)(1 + \alpha(\xi + \lambda_2))} \\ &\quad + \frac{2x_c^2 y_c \omega (1 + \alpha(\xi + \lambda_2))}{(\omega x_c^2 + 1)(1 + \alpha(\xi + \lambda_2))^2}, \\ b &= - \left\{ \frac{x_c}{(\omega x_c^2 + 1)(1 + \alpha(\xi + \lambda_2))} \right\}, \\ p_{11} &= \left\{ -\frac{2}{\gamma} + \frac{6\omega x_c y_c (1 + \alpha(\xi + \lambda_2))}{[(\omega x_c^2 + 1)(1 + \alpha(\xi + \lambda_2))]^2} \right. \\ &\quad \left. - \frac{8\omega^2 x_c^3 y_c (1 + \alpha(\xi + \lambda_2))^2}{[(\omega x_c^2 + 1)(1 + \alpha(\xi + \lambda_2))]^3} \right\}, \\ p_{12} &= \left\{ -\frac{1}{(\omega x_c^2 + 1)(1 + \alpha(\xi + \lambda_2))} \right. \\ &\quad \left. + \frac{2\omega x_c^2 (1 + \alpha(\xi + \lambda_2))}{[(\omega x_c^2 + 1)(1 + \alpha(\xi + \lambda_2))]^2} \right\}, \\ G_0 &= \frac{\beta x_c y_c}{(\omega x_c^2 + 1)(1 + \alpha(\xi + \lambda_2))} \\ &\quad + \frac{\beta(\xi + \lambda_2)y_c}{(1 + \alpha(\xi + \lambda_2))} - (\eta + \lambda_1)x_c y_c - \delta y_c, \\ c &= \left\{ \frac{\beta y_c}{(\omega x_c^2 + 1)(1 + \alpha(\xi + \lambda_2))} \right. \\ &\quad \left. - \frac{2\omega\beta x_c^2 y_c (1 + \alpha(\xi + \lambda_2))}{[(\omega x_c^2 + 1)(1 + \alpha(\xi + \lambda_2))]^2} - (\eta + \lambda_1)y_c \right\}, \\ d &= \frac{\beta x_c}{(\omega x_c^2 + 1)(1 + \alpha(\xi + \lambda_2))} \\ &\quad + \frac{\beta(\xi + \lambda_2)}{(1 + \alpha(\xi + \lambda_2))} - (\eta + \lambda_1)x_c - \delta, \\ q_{11} &= - \left\{ \frac{6\beta\omega x_c y_c (1 + \alpha(\xi + \lambda_2))}{[(\omega x_c^2 + 1)(1 + \alpha(\xi + \lambda_2))]^2} \right. \\ &\quad \left. - \frac{8\beta\omega^2 x_c^3 y_c (1 + \alpha(\xi + \lambda_2))^2}{[(\omega x_c^2 + 1)(1 + \alpha(\xi + \lambda_2))]^3} \right\}, \\ q_{12} &= \left\{ \frac{\beta}{(\omega x_c^2 + 1)(1 + \alpha(\xi + \lambda_2))} \right. \\ &\quad \left. - \frac{2\omega\beta x_c^2 (1 + \alpha(\xi + \lambda_2))}{[(\omega x_c^2 + 1)(1 + \alpha(\xi + \lambda_2))]^2} - (\eta + \lambda_1) \right\}, \end{aligned}$$

and  $H_1, H_2$  are power series in  $m_1, m_2$  with terms  $m_1^i m_2^j$  satisfying  $i + j \geq 3$ . Now using the affine transformation  $u_1 = m_1$  and  $u_2 = am_1 + bm_2$ , then system (29) gets converted to

$$\begin{aligned} \frac{du_1}{dt} &= F_0 + u_2 + l_{20}u_1^2 + l_{11}u_1u_2 + \bar{H}_1(u_1, u_2), \\ \frac{du_2}{dt} &= k_0 + k_{10}u_1 + k_{01}u_2 + k_{20}u_1^2 \\ &\quad + k_{11}u_1u_2 + \bar{H}_2(u_1, u_2), \end{aligned} \tag{30}$$

where

$$\begin{aligned}
 l_{20} &= \left( p_{11} - \frac{ap_{12}}{b} \right), & l_{11} &= \frac{p_{12}}{b}, \\
 k_o &= aF_0 + bG_0, & k_{10} &= bc - ad, \\
 k_{01} &= a + d, \\
 k_{20} &= \left( ap_{11} - \frac{a^2p_{12}}{b} + bq_{11} - aq_{12} \right), \\
 k_{11} &= \left( \frac{ap_{12}}{b} + q_{12} \right),
 \end{aligned}$$

and  $\bar{H}_1, \bar{H}_2$  are power series in  $u_1, u_2$  with terms  $u_1^i u_2^j$  satisfying  $i + j \geq 3$ . Now using the  $C^\infty$  change of coordinates in the neighbourhood of  $(0, 0)$ : given by

$$v_1 = u_1 - \frac{p_{12}}{2b} u_1^2, \quad v_2 = u_2 + \left( p_{11} - \frac{ap_{12}}{b} \right) u_1^2,$$

system (30) gets modified to

$$\begin{aligned}
 \frac{dv_1}{dt} &= F_0 + s_{10}v_1 + s_{20}v_1^2 + v_2 + R_1(v_1, v_2), \\
 \frac{dv_2}{dt} &= t_0 + t_{10}v_1 + t_{01}v_2 \\
 &\quad + t_{20}v_1^2 + t_{11}v_1v_2 + R_2(v_1, v_2),
 \end{aligned} \tag{31}$$

where

$$\begin{aligned}
 s_{10} &= -\frac{p_{12}}{b} F_0, & t_0 &= k_0, \\
 t_{10} &= k_{10} + 2 \left( p_{11} - \frac{ap_{12}}{b} \right) F_0, \\
 s_{20} &= \frac{-p_{12}^2}{2b^2} F_0, & t_{01} &= k_{01}, \\
 t_{20} &= (bc - ad) \frac{p_{12}}{2b} - \left( p_{11} - \frac{ap_{12}}{b} \right) (a + d) \\
 &\quad + ap_{11} - \frac{a^2p_{11}}{b} + bq_{11} - aq_{12} \\
 &\quad + \left( p_{11} - \frac{ap_{12}}{b} \right) \frac{p_{12}}{b} F_0, \\
 t_{11} &= 2p_{11} - \frac{ap_{12}}{b} + q_{12},
 \end{aligned}$$

and  $R_1(v_1, v_2), R_2(v_1, v_2)$  are power series with the terms  $v_1^i v_2^j, i + j \geq 3$ . Now, again using  $c^\infty$  change of coordinates in the neighbourhood of  $(0, 0)$

$$z_1 = v_1 \quad \text{and} \quad z_2 = F_0 + s_{10}v_1 + s_{20}v_1^2 + v_2,$$

System (31) gets transformed to:

$$\frac{dz_1}{dt} = z_2 + \bar{R}_1(z_1, z_2),$$

$$\begin{aligned}
 \frac{dz_2}{dt} &= w_{00} + w_{10}z_1 + w_{01}z_2 \\
 &\quad + w_{20}z_1^2 + w_{11}z_1z_2 + \bar{R}_2(z_1, z_2),
 \end{aligned} \tag{32}$$

where

$$\begin{aligned}
 w_{00} &= t_0 - t_{01}F_0, & w_{10} &= t_{10} - t_{01}s_{10} - t_{11}F_0, \\
 w_{01} &= s_{10} + t_{01}, & w_{20} &= t_{20} - t_{01}s_{20} - t_{11}s_{10}, & w_{11} &= t_{11} + 2s_{20},
 \end{aligned}$$

and  $\bar{R}_1(z_1, z_2), \bar{R}_2(z_1, z_2)$  are the power series in  $(z_1, z_2)$  having terms  $z_1^i z_2^j, i + j \geq 3$ . Finally, applying the following  $C^\infty$  change of coordinates in the neighbourhood of  $(0, 0)$ :

$$n_1 = z_1 \quad \text{and} \quad n_2 = z_2 + \bar{R}_1(z_1, z_2),$$

system (32) gets modified to

$$\begin{aligned}
 \frac{dn_1}{dt} &= n_2, \\
 \frac{dn_2}{dt} &= P_1(n_1, \lambda_1, \lambda_2) \\
 &\quad + n_2\phi_1(n_1, \lambda_1, \lambda_2) + n_2^2\psi_1(n_1, \lambda_1, \lambda_2),
 \end{aligned} \tag{33}$$

where  $P_1, \phi_1, \psi_1 \in C^\infty$  and

$$\begin{aligned}
 P_1(n_1, \lambda_1, \lambda_2) &= w_{00} + w_{10}n_1 + w_{20}n_1^2 + E_1(n_1), \\
 \phi_1(n_1, \lambda_1, \lambda_2) &= w_{01} + w_{11}n_1 + E_2(n_1), \\
 \psi_1(n_1, \lambda_1, \lambda_2) &= E_3(n_1, n_2).
 \end{aligned}$$

Here,  $E_1$  is the power series in the terms  $n_1^i, i \geq 3$  and  $E_2$  is the power series in the terms  $n_2^j, j \geq 2$ .  $E_3$  is a power series in the terms  $(n_1, n_2)$  with powers  $n_1^{k_1} n_2^{k_2}, k_1 + k_2 \geq 1$ .

Applying the Malgrange Preparation Theorem [9] to the function  $P_1(n_1, \lambda_1, \lambda_2)$ , we have

$$P_1(n_1, \lambda_1, \lambda_2) = \left( n_1^2 + \frac{w_{10}}{w_{20}} n_1 + \frac{w_{00}}{w_{20}} \right) B(n_1, \lambda_1, \lambda_2),$$

where  $B(0, \lambda_1, \lambda_2) = w_{20}$  and  $B$  is a power series in  $n_1$ . Now let  $\hat{u}_1 = n_1, \hat{u}_2 = \frac{n_2}{\sqrt{B(n_1, \lambda_1, \lambda_2)}}$  and  $T = \int_0^t \sqrt{B(n_1(s), \lambda_1, \lambda_2)} ds$ . Then, system (33) transforms to

$$\begin{aligned}
 \frac{d\hat{u}_1}{dT} &= \hat{u}_2 \\
 \frac{d\hat{u}_2}{dT} &= \frac{w_{00}}{w_{20}} + \frac{w_{10}}{w_{20}} \hat{u}_1 + \frac{w_{01}}{\sqrt{w_{20}}} \hat{u}_2 + \hat{u}_1^2 \\
 &\quad + \frac{w_{11}}{\sqrt{w_{20}}} \hat{u}_1 \hat{u}_2 + Q_1(\hat{u}_1, \hat{u}_2, \lambda_1, \lambda_2),
 \end{aligned} \tag{34}$$

where  $Q_1(\hat{u}_1, \hat{u}_2, \lambda_1, \lambda_2)$  is a power series in  $(\hat{u}_1, \hat{u}_2)$  with powers  $\hat{u}_1^i \hat{u}_2^j$  satisfying  $i + j \geq 3$  and  $j \geq 2$ . Applying the transformation

$$y_1 = \hat{u}_1 + \frac{w_{10}}{2w_{20}}, \quad y_2 = \hat{u}_2,$$

system (34) transforms to

$$\begin{aligned} \frac{dy_1}{dT} &= y_2, \\ \frac{dy_2}{dT} &= \mu_1(\lambda_1, \lambda_2) + \mu_2(\lambda_1, \lambda_2)y_2 + y_1^2 \\ &\quad + \frac{w_{11}}{\sqrt{w_{20}}}y_1y_2 + Q_2(y_1, y_2, \lambda_1, \lambda_2), \end{aligned} \tag{35}$$

where

$$\begin{aligned} \mu_1(\lambda_1, \lambda_2) &= \frac{w_{00}}{w_{20}} - \left(\frac{w_{10}}{2w_{20}}\right)^2, \\ \mu_2(\lambda_1, \lambda_2) &= \frac{w_{01}}{\sqrt{w_{20}}} - \frac{w_{10}w_{11}}{2(w_{20})^{\frac{3}{2}}}, \end{aligned}$$

and  $Q_2(y_1, y_2, \lambda_1, \lambda_2)$  is a power series in  $y_1$  and  $y_2$  with powers  $y_1^i y_2^j$  satisfying  $i + j \geq 3$ . System (35) is topologically equivalent to the normal form of the Bogdanov–Takens bifurcation [38] given by

$$\begin{aligned} \frac{dX_1}{dT} &= X_2, \\ \frac{dX_2}{dT} &= \mu_1 + \mu_2 X_2 + X_1^2 + X_1 X_2, \end{aligned} \tag{36}$$

Now, we establish the non-degeneracy condition for Bogdanov–Takens bifurcation around  $E_{BT_i}$ ,  $i = 1, 2$  at  $\lambda_1 = 0$  and  $\lambda_2 = 0$ .

At the point  $E_{BT_1}$ , we have

$$\begin{aligned} k_{20} &= ap_{11} - \frac{ap_{12}}{b} + bq_{11} - aq_{12} \\ &= \frac{-x_{BT_1}}{(\omega x_{BT_1}^2 + 1)(1 + \alpha\xi)} \\ &\quad \frac{2\beta\omega x_{BT_1}y_{BT_1}(1 + \alpha\xi)^2}{[(\omega x_{BT_1}^2 + 1)(1 + \alpha\xi)]^2}(\omega x_{BT_1}^2 - 3) > 0, \\ l_{20} &= p_{11} - \frac{ap_{12}}{b} = \frac{-2}{\gamma} \\ &\quad + \frac{2\omega x_{BT_1}y_{BT_1}(1 + \alpha\xi)^2}{[(\omega x_{BT_1}^2 + 1)(1 + \alpha\xi)]^3}(3 - \omega x_{BT_1}^2) < 0 \\ k_{11} &= \frac{ap_{12}}{b} + q_{12} = 0. \end{aligned}$$

Thus,  $l_{20} + k_{11} \neq 0$  and  $k_{20} \neq 0$  and  $\text{sign}(k_{20}(l_{20} + k_{11})) = -1$ . So, the system undergoes supercritical Bogdanov–Takens bifurcation at  $E_{BT_1}$ .

At the point  $E_{BT_2}$ , we have

$$\begin{aligned} k_{20} &= ap_{11} - \frac{ap_{12}}{b} + bq_{11} - aq_{12} \\ &= \frac{-x_{BT_2}}{(\omega x_{BT_2}^2 + 1)(1 + \alpha\xi)} \\ &\quad \frac{2\beta\omega x_{BT_2}y_{BT_2}(1 + \alpha\xi)^2}{[(\omega x_{BT_2}^2 + 1)(1 + \alpha\xi)]^2}(\omega x_{BT_2}^2 - 3) > 0, \\ l_{20} &= p_{11} - \frac{ap_{12}}{b} = \frac{-2}{\gamma} \\ &\quad + \frac{2\omega x_{BT_2}y_{BT_2}(1 + \alpha\xi)^2}{[(\omega x_{BT_2}^2 + 1)(1 + \alpha\xi)]^3}(3 - \omega x_{BT_2}^2) > 0 \\ k_{11} &= \frac{ap_{12}}{b} + q_{12} = 0. \end{aligned}$$

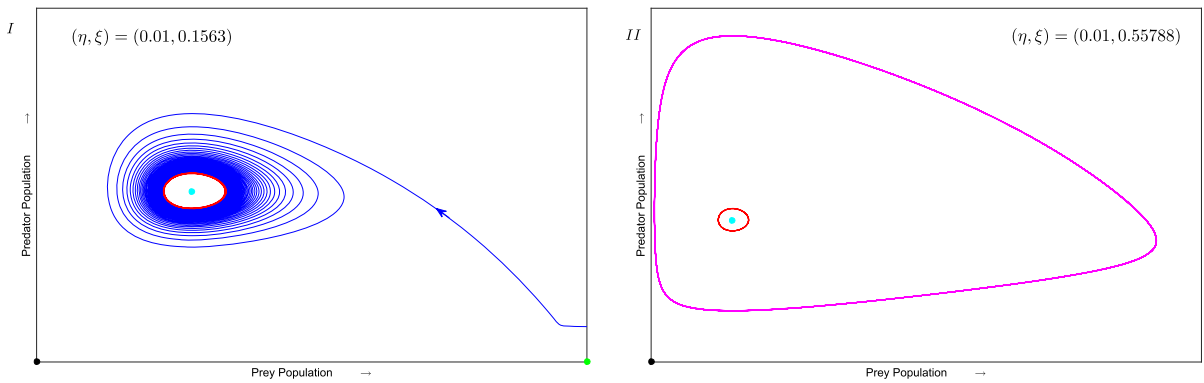
Now,  $l_{20} + k_{11} \neq 0$  and  $k_{20} \neq 0$  and  $\text{sign}(k_{20}(l_{20} + k_{11})) = +1$ . So, the system undergoes subcritical Bogdanov–Takens bifurcation at  $E_{BT_2}$ .  $\square$

#### 4.4 Numerical simulations for local and global bifurcation analysis

Here, we illustrate the existence of Hopf bifurcation (both degenerate and non-degenerate) at the interior equilibrium  $E_1$ , as well as Saddle-node bifurcation, Bogdanov–Takens bifurcations occurring at the instantaneous equilibrium  $E_c$  numerically.

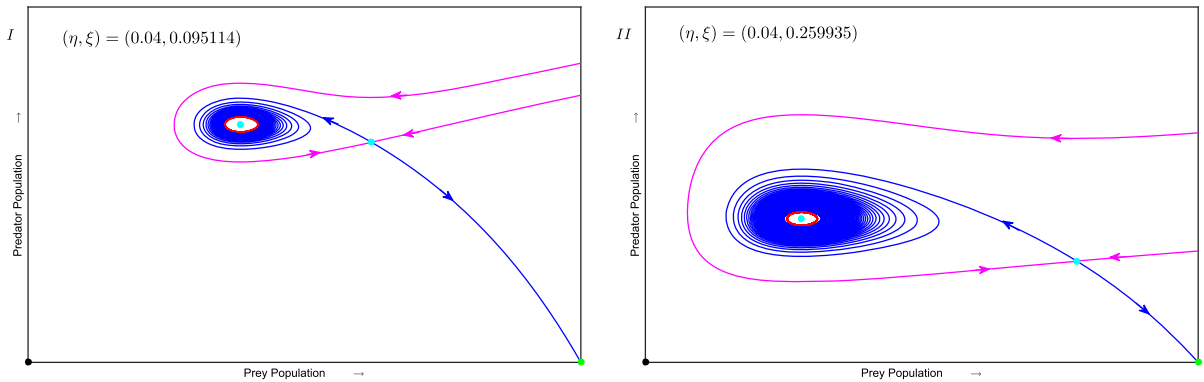
##### 4.4.1 Numerical illustration for existence of degenerate and non-degenerate Hopf bifurcation

*Example #1* We first demonstrate the existence of non-degenerate and degenerate Hopf bifurcation in the case of system exhibiting unique interior equilibrium  $E_1$ . For this, we fix the parameter set as  $\beta = 0.5, \delta = 0.4, \omega = 0.3, \alpha = 0.5, \eta = 0.01$ . Now, fixing  $\gamma = 3.2$ , we have  $x_L = 0.9034$  and  $x_H = 1.23$ . Now, choosing  $\xi = 0.1563$  we obtain  $E_1 = (0.9034, 0.9632)$  and  $\sigma(x_L) = -0.7240 < 0$ . Thus, the system undergoes non-degenerate Hopf bifurcation around  $E_1$  which is pictured in frame I of Fig. 3. For  $\gamma = 4$ , we obtain  $(x_L, x_H) = (0.5168, 2.1498)$  and  $\sigma(x_L) = 0.1868 > 0$ . For this set of parameter values, the system undergoes degenerate Hopf bifurcation around  $E_1 = (0.5168, 1.2028)$  for  $\xi = 0.55788$ . This scenario is presented in Frame II of Fig. 3.



**Fig. 3** Numerical simulations depicting the existence of non-degenerate and degenerate Hopf bifurcation when the system exhibits unique interior equilibrium. The parameter values chosen for this example are  $\beta = 0.5, \delta = 0.4, \omega = 0.3, \alpha = 0.5$

and  $\eta = 0.01$ . Frame I presents the situation where the system exhibits non-degenerate Hopf bifurcation for  $\gamma = 3.2$  and  $\xi = 0.1563$ . Frame II depicts the degenerate Hopf bifurcation scenario when  $\gamma = 4$  and  $\xi = 0.55788$



**Fig. 4** Numerical simulation depicting the existence of non-degenerate Hopf bifurcation in the case where the system admits two coexistence states. The ecosystem parameters chosen in this case are:  $\gamma = 3.2, \beta = 0.5, \delta = 0.4, \omega = 0.3, \eta = 0.04$

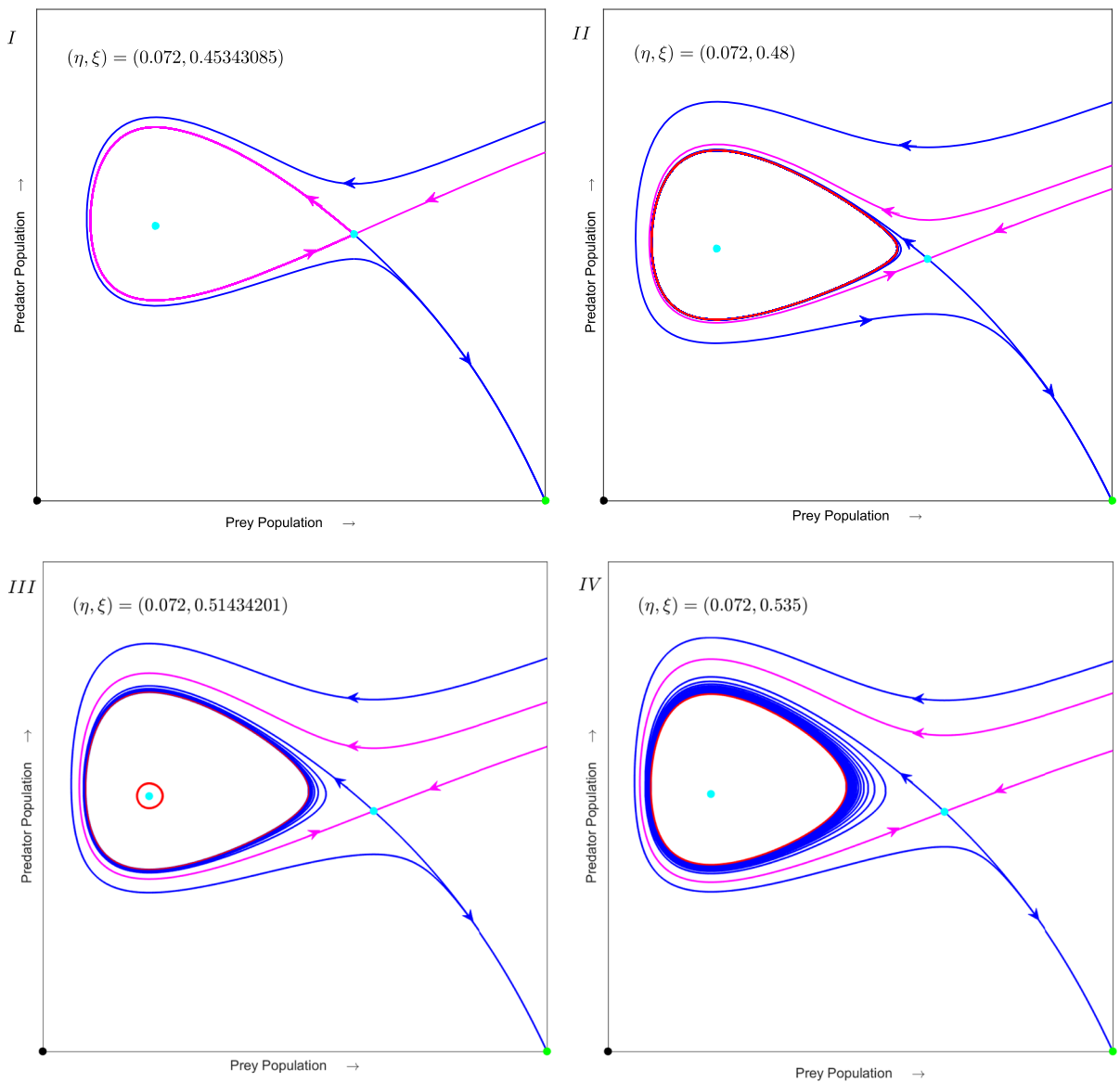
and  $\alpha = 0.5$ . Frame I presents the existence of non-degenerate bifurcation at  $x_1 = x_H$  for  $\xi = 0.095114$ . Frame II depicts the occurrence of non-degenerate Hopf bifurcation at  $x_1 = x_L$  for  $\xi = 0.259935$

*Example #2* We now demonstrate the existence of Hopf bifurcation (both non-degenerate and degenerate) in the case of existence of two equilibria  $E_1 = (x_1, y_1)$  and  $E_2 = (x_2, y_2)$  with  $E_2$  being the saddle. This situation is more interesting than the previous one as in this case the system exhibits complex dynamics in the form of homoclinic orbit existence.

At first, we fix the ecosystem parameters as  $\beta = 0.5, \delta = 0.4, \omega = 0.3, \alpha = 0.5$ . Choosing  $\gamma = 3.2$  and for a fixed  $\eta = 0.04$ , the system exhibits two interior equilibria for  $\xi \in (0, 1.3333)$ . For this choice of parameters, we have  $(x_L, x_H) = (0.9034, 1.23)$ . Now, for the critical value of  $\xi =$

$0.095114$ , we get  $E_1 = (1.23, 0.9376)$  with  $x_1 = x_H$  and  $\sigma(x_H) = -0.7955 < 0$ . Thus, the system undergoes non-degenerate Hopf bifurcation at  $E_1$ . This scenario is depicted in the frame I of Fig. 4. Now, varying  $\xi$  and choosing  $\xi = 0.259935$ , we get  $E_1 = (0.9034, 1.0095)$  with  $x_1 = x_L$  and  $\sigma(x_1) = -0.8062 < 0$ , establishing the existence of non-degenerate Hopf bifurcation at  $E_1$ . This case is presented in Frame II of Fig. 4.

Now, choosing  $\gamma = 3.4$  and for a fixed  $\eta = 0.072$ , the system exhibits two interior equilibria for  $\xi \in (0.2404, 1.3333)$ . For this choice of parameters, we have  $(x_L, x_H) = (0.7170, 1.5497)$ . Now, for the crit-



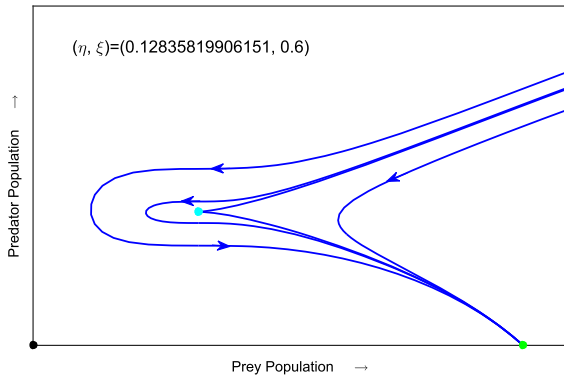
**Fig. 5** Numerical simulation illustrating the existence of degenerate Hopf bifurcation and homoclinic orbit when the system exhibits two coexistence states. Fixing,  $\beta = 0.5$ ,  $\delta = 0.4$ ,  $\omega = 0.3$ ,  $\gamma = 3.4$ ,  $\alpha = 0.5$  and  $\eta = 0.072$  and, increasing  $\xi$  from zero, the system at first exhibits homoclinic orbit, which is later shrinks to a stable limit cycle around for further increase in  $\xi$ . Frames I and II, respectively, present these two scenarios. Fur-

ical value of  $\xi = 0.45343085$ , the unstable manifold of  $E_2$  meets the stable manifold of  $E_2$ , thus forming a homoclinic loop surrounding  $E_1 = (0.7952, 1.1180)$ . Increasing  $\xi$  to 0.48, the interior equilibrium  $E_1 = (0.7598, 1.1296)$  turns into unstable and surrounded by

ther, increase in  $\xi$  system exhibits a degenerate Hopf bifurcation because of which interior equilibrium is surrounded by two limit cycles. The inner limit cycle being unstable, and outer being stable in nature. This case is presented in Frame III. Further, increase in  $\xi$  results in a semi-stable limit cycle around  $E_1$ , which is formed by the collision of both the above stable and unstable limit cycles. Frame IV depicts this scenario

a limit cycle. Further, increasing  $\xi$ ,  $\xi = 0.51434201$ , the lower prey coexistence  $E_1 = (0.7170, 1.1450)$  turns into stable through degenerate Hopf bifurcation. Here, the system exhibits multiple limit cycles around the equilibrium  $E_1$ , due to degenerate Hopf bifurca-





**Fig. 6** Graphical illustration of the case where the system undergoes saddle-node bifurcation around the instantaneous equilibrium. The system parameters are:  $\beta = 0.5, \omega = 0.3, \alpha = 0.5, \delta = 0.4, \gamma = 3.3, \xi = 0.6$  and  $\eta = 0.12835819906151$

tion at  $x_1 = x_L$ . For  $\xi = 0.5355$  the interior equilibrium  $E_1 = (0.6924, 1.1545)$  surrounded by semi-stable limit cycle arises through saddle-node bifurcation for limit cycle. This is illustrated graphically in Frames I–IV of Fig. 5.

4.4.2 Numerical illustration for saddle-node bifurcation

We now numerically establish the existence of saddle-node bifurcation at the instantaneous equilibrium  $E_c$  as result of collision of  $E_1$  and  $E_2$ . For this we choose,  $\beta = 0.5, \omega = 0.3, \alpha = 0.5, \delta = 0.4, \gamma = 3.3$  and fix  $\xi = 0.6$ . For this choice of parameters from Theorem 5, we obtain  $\eta = 0.12835819906151$ . For this value of  $\eta$ , one can verify that  $\det J_{E_c} \approx 0$ . Thus, the system exhibits an instantaneous equilibrium  $E_c = (1.1134, 1.1817)$ , at which the system undergoes saddle-node bifurcation. This scenario is presented graphically in Fig. 6.

4.4.3 Numerical illustration for Bogdanov–Takens bifurcation

Here, we provide a numerical simulation for supporting the arguments presented in Theorem 6 for the establishment of Bogdanov–Takens bifurcation at  $E_c$ . Fixing the ecosystem as  $\beta = 0.5, \omega = 0.3, \delta = 0.4, \gamma = 3.3, \alpha = 0.5$ , and following the arguments presented in Theorem 6, we obtain two control parameter sets  $BT_1 = (\eta_1, \xi_1) = (0.054, 0.1280860431)$  and  $BT_2 = (\eta_2, \xi_2) = (0.1812, 0.918107668)$  at which

$\det J_{E_c} = \text{tr } J_{E_c} = 0$ . For the choice of parameters  $BT_1$ , the system exhibits instantaneous equilibrium point  $E_{BT_1} = (1.5021, 0.9721)$ . Further, at  $BT_1$  we have  $\text{sign}(k_{20}(l_{20} + k_{11})) = -1$ . Thus, the system exhibits supercritical Bogdanov–Takens bifurcation around  $E_{BT_1}$  (cf. frame I of Fig. 7). For the second control parameter set  $BT_2$ , we have  $\text{sign}(k_{20}(l_{20} + k_{11})) = 1$  and that the system undergoes subcritical Bogdanov–Takens bifurcation around  $E_{BT_2}$  (cf. frames II of Fig. 7).

5 Global dynamics

The present section deals with the global dynamics and controllability aspects of the predator–prey system with anti-predator behaviour in prey in the presence of additional food to predators. From the system analysis presented in the previous sections, it can be noted that the quality ( $\alpha$ ), quantity ( $\xi$ ) of the supplied food along with the strength of the anti-predator behaviour ( $\eta$ ) in prey influences the system dynamics. Theoretical/experimental analysis done in the direction of providing additional/alternative foods to predators reveals that the availability of fixed quality with varying quantity plays a vital role in the development, conservation and sustainability of the species [2, 3, 61, 67, 78, 82, 83, 88]. Hence, in the current study, we fix the quality and treat the quantity and anti-predatory behaviour in prey as control parameters. Accordingly, we study the global dynamics in  $(\eta, \xi)$  control parameter space treating  $\beta, \delta, \gamma, \omega$  as ecosystem parameters and  $\alpha$  as a fixed control parameter, which is maintained by the eco-managers.

From the analysis presented in Sect. 4, we infer that the global dynamics of the system are better understood by using the following bifurcation curves.

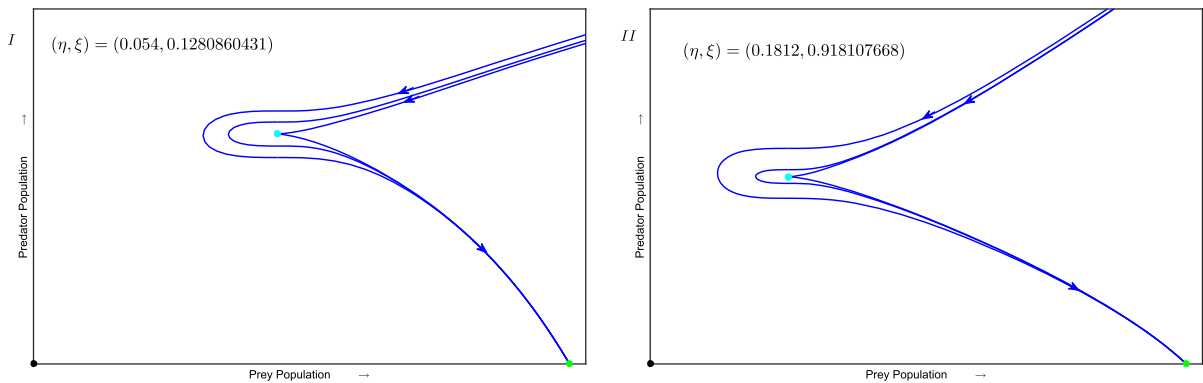
$$-\eta\omega\gamma^3(1 + \alpha\xi) + \omega\gamma^2(\beta\xi - \delta(1 + \alpha\xi)) + \gamma(\beta - \eta(1 + \alpha\xi)) + (\beta\xi - \delta(1 + \alpha\xi)) = 0, \tag{37}$$

$$\beta\xi - \delta(1 + \alpha\xi) = 0, \tag{38}$$

$$-\eta\omega x_c^3(1 + \alpha\xi) + \omega x_c^2(\beta\xi - \delta(1 + \alpha\xi)) + x_c(\beta - \eta(1 + \alpha\xi)) + (\beta\xi - \delta(1 + \alpha\xi)) = 0, \tag{39}$$

$$-3\omega x_1^2 + 2\omega\gamma x_1 - 1 = 0. \tag{40}$$

Curves (37) and (38) represent the transcritical bifurcation at  $E_\gamma$  and  $E_0$ , respectively. The saddle-node bifurcation at  $E_c$  and the Hopf bifurcation at  $E_1$  are described by curves (39) and (40), respectively.



**Fig. 7** Numerical simulation illustrating the existence of Bogdanov–Takens bifurcation. For the fixed ecosystem parameters  $\beta = 0.5, \omega = 0.3, \delta = 0.4, \gamma = 3.3, \alpha = 0.5$ , the system exhibits supercritical Bogdanov–Takens bifurcation for

$(\eta, \xi) = (0.054, 0.1280860431)$ . This scenario is depicted in Frame I. Frame II shows the existence of subcritical Bogdanov–Takens bifurcation for  $(\eta_2, \xi_2) = (0.1812, 0.918107668)$

From Eq. (38), one can observe that the system exhibits transcritical bifurcation at  $E_0$  only when  $\alpha < \frac{\beta}{\delta}$ . In this case, curves (37) and (38) intersect in the positive  $(\eta, \xi)$  space at  $(\frac{\beta - \delta\alpha}{\omega\gamma^2 + 1}, \frac{\delta}{\beta - \delta\alpha})$ . Thus, the line  $\alpha = \frac{\beta}{\delta}$  plays a crucial role in the system dynamics. Further, we have that the system exhibits Hopf bifurcation around the interior equilibrium  $E_1$  when  $\omega\gamma^2 - 3 \geq 0$ . Accordingly, we discuss the global behaviour of the trajectories of the system and its controllability by plotting the above four bifurcation curves in the  $(\eta, \xi)$  space under the following four conditions:

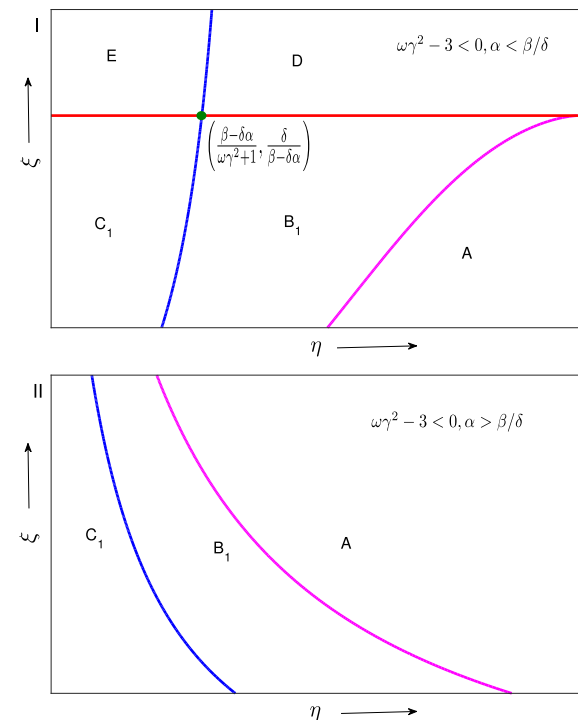
$$\omega\gamma^2 - 3 < 0 \quad \text{and} \quad \alpha < \frac{\beta}{\delta}, \tag{41}$$

$$\omega\gamma^2 - 3 < 0 \quad \text{and} \quad \alpha > \frac{\beta}{\delta}, \tag{42}$$

$$\omega\gamma^2 - 3 \geq 0 \quad \text{and} \quad \alpha < \frac{\beta}{\delta}, \tag{43}$$

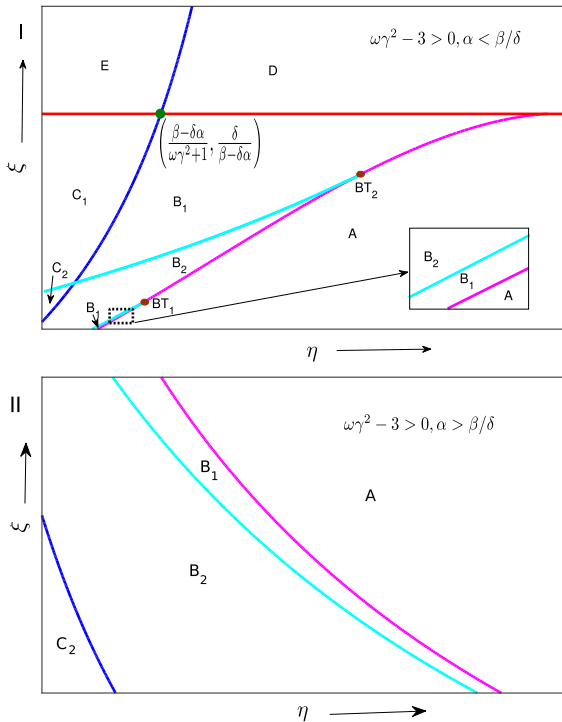
$$\omega\gamma^2 - 3 \geq 0 \quad \text{and} \quad \alpha > \frac{\beta}{\delta}. \tag{44}$$

Now, at first, we discuss the global dynamics of the system under the condition  $\omega\gamma^2 - 3 < 0$ . In this case, we have that the interior equilibrium  $E_1 = (x_1, y_1)$  with lower prey population (if it exists) is always stable. Figure 8 describes the dynamics associated in this situation. Frame I of 8 presents the dynamics in the case  $\beta - \delta\alpha > 0$ , and Frame II of 8 presents the dynamics in the case where  $\beta - \delta\alpha < 0$ . As the system undergoes transcritical bifurcation at  $(0, 0)$  along the line  $\xi = \frac{\delta}{\beta - \delta\alpha}$ , we divide the  $\xi$  limits into two: (i)



**Fig. 8** Figure presenting the various regions formed by the intersection of curves (37)–(40) when the system parameters,  $\gamma, \omega$  and  $\alpha$ , satisfy conditions (41) and (42)

$0 \leq \xi < \frac{\delta}{\beta - \delta\alpha}$  and (ii)  $\xi > \frac{\delta}{\beta - \delta\alpha}$ . In the case (i) i.e.,  $0 < \xi < \frac{\delta}{\beta - \delta\alpha}$ , for a fixed  $\eta > 0$ , we enter into the region  $C_1$ . In this region, the system admits a unique interior equilibrium  $E_1$ , which is asymptotically stable,



**Fig. 9** Figure presenting the various regions formed by the intersection of curves (37)–(40) when the system parameters,  $\gamma$ ,  $\omega$  and  $\alpha$ , satisfy conditions (43) and (44). The  $BT_1$  and  $BT_2$  points in Frame I are the Bogdanov–Takens bifurcation points, formed by the intersection points of the saddle-node bifurcation curve and Hopf bifurcation curve

which attracts all the solutions of the system. Further increase in  $\eta$ , we enter into region  $B_1$  from  $C_1$ . Due to this crossing of regions, the system undergoes transcritical bifurcation at  $(\gamma, 0)$ , which leads to the emergence of another interior equilibrium  $E_2$  with saddle in nature. As a consequence of the existence of  $E_2$ , the state space of the system is divided into two regions, of which one contains the region of attraction of  $E_1$  and another that of  $\gamma$ . In this region, the coexisting axial and trivial equilibria are, respectively, stable and saddle in nature. For further changes in  $\eta$ , we move into the region  $A$  from  $B_1$ . This passage is accompanied by the collision of the two interior equilibrium  $E_1$  and  $E_2$  and disappearance of both equilibria through the saddle-node bifurcation. Due to the vanishing of interior equilibria, all the trajectories of the system will be attracted by  $(\gamma, 0)$  making the system prey dominant. Fixing now  $\xi > \frac{\delta}{\beta - \delta\alpha}$  and choosing  $\eta$  such that  $(\eta, \xi)$  belongs to the region  $D$ , the system admits a unique interior equilibrium, which is saddle in nature.

The coexisting equilibria  $E_0 = (0, 0)$  and  $E_\gamma = (\gamma, 0)$  are unstable and stable in nature, respectively. Thus, all the solutions originating in the region of attraction of  $(\gamma, 0)$  will be driven to predator-free state. Solutions originating in the other side of this region of attraction will be driven to predator axis, eliminating prey from the ecosystem. Finally, for  $(\eta, \xi) \in E$ ,  $(\gamma, 0)$  turns into a saddle due to a transcritical bifurcation. All the solutions that are originating in this region will be driven to predator axis.

We now shift our focus on the system dynamics when the parameters of the system follow  $\omega\gamma^2 - 3 > 0$ . The division of  $(\eta, \xi)$  space in this case by the bifurcation curves (37)–(40) is presented in Fig. 9. Fixing  $\xi \in (0, \frac{\delta}{\beta - \delta\alpha})$  and choosing  $\eta > 0$  such that  $(\eta, \xi) \in C_1 \cup C_2$ , the system admits unique interior equilibrium ( $E_1$ ) along the trivial ( $E_0$ ) and axial ( $E_\gamma$ ) equilibria. The nature of trivial and axial equilibria is saddle. The interior equilibrium is stable for the  $(\eta, \xi) \in C_1$ . As we move from  $C_1$  into  $C_2$ , the system experiences Hopf bifurcation, due to which the interior equilibrium point is surrounded by a limit cycle. Now moving from  $C_1 \cup C_2$ , to  $B_1 \cup B_2$ , the system undergoes transcritical bifurcation at  $(\gamma, 0)$ , as a result there will be an emergence of second coexistence equilibrium,  $E_2$  with higher prey component, which is saddle in nature. In this region,  $E_\gamma = (\gamma, 0)$  turns into stable and the nature of  $E_0 = (0, 0)$  remains unchanged. The nature of  $E_1$  is stable (unstable) for  $(\eta, \xi) \in B_1$  ( $(\eta, \xi) \in B_2$ ). The system experiences Hopf bifurcation while crossing the regions  $B_1$  and  $B_2$ . The Hopf bifurcation experienced by the system will be either non-degenerate or degenerate depending on whether  $\sigma(x_1) < 0$  or  $\sigma(x_1) > 0$ . The system even experiences homoclinic bifurcation for a critical pair of  $(\eta, \xi) \in B_2$ . Moving into the region  $A$  from  $B_1 \cup B_2$ , the two interior equilibria collide with each other and disappear in a saddle-node bifurcation. This qualitative change in the system drives all the solutions to the prey dominated state  $(\gamma, 0)$ . At the instance of saddle-node bifurcation, the system also exhibits Bogdanov–Takens bifurcations at two decisive pairs of  $(\eta, \xi)$ . The dynamics of the system for  $(\eta, \xi)$  which belongs to the regions either  $D$  or  $E$  are similar to the dynamics described in the above case  $\omega\gamma^2 - 3 < 0$ .

Table 2 presents the existence of various equilibria in each of the regions depicted in Figs. 8 and 9 along

**Table 2** Table describing the equilibrium admitted by system (5, 6) in various regions in Figs. 8 and 9

| Region(s) | Equilibria                | Nature                                                             |
|-----------|---------------------------|--------------------------------------------------------------------|
| A         | $E_0, E_\gamma$           | $E_0$ is saddle and $E_\gamma$ is stable                           |
| $B_1$     | $E_0, E_\gamma, E_1, E_2$ | $E_0, E_2$ are saddles and $E_\gamma, E_1$ are stables             |
| $B_2$     | $E_0, E_\gamma, E_1, E_2$ | $E_0, E_2$ are saddles, $E_\gamma$ is stable and $E_1$ is unstable |
| $C_1$     | $E_0, E_\gamma, E_1$      | $E_0, E_\gamma$ are saddles and $E_1$ is stable                    |
| $C_2$     | $E_0, E_\gamma, E_1$      | $E_0, E_\gamma$ are saddles and $E_1$ is unstable                  |
| D         | $E_0, E_\gamma, E_2$      | $E_0$ is unstable, $E_\gamma$ is stable and $E_2$ is saddle        |
| E         | $E_0, E_\gamma$           | $E_0$ is unstable and $E_\gamma$ is saddle                         |

with stability nature of each of these equilibria and thus summarises the global dynamics of the system.

## 6 Consequences of providing additional food to predators

In the present section, we discuss the effect of the provision of additional food to predators and its outcomes on the dynamics of the predator–prey system with anti-predator behaviour in prey. From the discussions presented in Sects. 4 and 5, we conclude that the quality of additional food plays a vital role in the system dynamics. When the system is supplemented with additional food quality satisfying  $\alpha < \beta/\delta$ , it is evident that the system exhibits very rich dynamics. On the other hand, providing an additional food of quality  $\alpha > \beta/\delta$ , we observe that the system tends to prey dominance. Accordingly, we term the additional food as high (nutritious) quality if  $\alpha < \frac{\beta}{\delta}$  and it is of low (nutritious) quality when  $\alpha > \frac{\beta}{\delta}$  similar to the arguments presented in [52, 53, 65–67].

In the absence of additional food, curves (37), (39) intersect the  $\eta$ -axis at  $\eta = \bar{\eta}_0$  and  $\eta = \bar{\eta}_1$ , respectively. Here,  $\bar{\eta}_0 = \frac{\beta\gamma - \delta(\omega\gamma^2 + 1)}{\gamma(\omega\gamma^2 + 1)}$ . The expression for  $\bar{\eta}_1$  is complex to express analytically but can be evaluated numerically using software packages such as MAPLE, MATLAB. We now discuss the consequences of provision of additional food in three distinct cases that arose due to the division of  $\eta$  line into three regions given by  $R_1 : (0, \bar{\eta}_0]$ ,  $R_2 : (\bar{\eta}_0, \bar{\eta}_1]$  and  $R_3 : \eta > \bar{\eta}_1$ .

In the case of providing low (nutritious) quality additional food, the final state of the system is dominated either completely (or) partially by prey species depending on the strength of anti-predator behaviour of prey and quantity of food that is supplied. For a fixed anti-

predator behaviour of prey,  $\eta$ , belonging to region  $R_1$ , providing the predators with additional food of quantity  $\xi \in \left(0, \frac{(\omega\gamma^2 + 1)(\eta\gamma + \delta) - \beta\gamma}{(\omega\gamma^2 + 1)[\beta - (\eta\gamma + \delta)\alpha]}\right]$ , the system exhibits stable predator–prey coexistence. Providing additional food with quantity  $\xi > \frac{(\omega\gamma^2 + 1)(\eta\gamma + \delta) - \beta\gamma}{(\omega\gamma^2 + 1)[\beta - (\eta\gamma + \delta)\alpha]}$ , the system can exhibit two coexistence states, in which the state with lower prey population is stable/unstable and the other is saddle in nature. This coexistence of multiple states divides state space of the system into two regions. The trajectories originating the region of attraction of the lower prey population state converges to this state or oscillate around it. The solutions initiating in the other region will be driven to  $E_\gamma = (\gamma, 0)$ . In this case, it can be interesting to observe that, as  $\xi$  crosses a threshold value (characterised by the system parameters), the system is entirely dominated by prey species, causing the solutions to reach the prey carrying capacity. Thus, we cannot achieve the successful biological control in this scenario. For a choice of  $\eta$  in regions,  $R_2$  or  $R_3$ , the dynamics of the system are similar to the case discussed above with only exception that the system will be attracted to the predator-free state with a small variation in the quantity.

In the case, where the predators are provided with high (nutritious) quality food, the system dynamics are much more interesting with a possibility to drive the system to the predator axis in a finite time. In this case, we observe that curves (37) and (38), intersect at  $(\eta_c, \xi_c) = \left(\frac{\beta - \delta\alpha}{\omega\gamma^2 + 1}, \frac{\delta}{\beta - \delta\alpha}\right)$ .

For  $\eta < \eta_c$ , increasing the quantity  $\xi$  from 0 to  $\frac{\delta}{\beta - \delta\alpha}$ , we observe that the system which is prey dominated initially, gets attracted to a stable state dominated by a predator as  $\xi$  reaches the critical value  $\xi_c$ . As the quantity of supplemental food crosses the threshold value  $\xi_c$ , the system becomes pest-free, and all the

solutions will be driven to predator axis. In this case, the predator population exhibit unbounded growth and are solely maintained by the additional food supply. A cut-off in the additional food supply drives the predators to extinct. The unbounded growth observed in this case is because the considered model does not account for the competition between predators.

Choosing  $\eta > \eta_c$ , and providing additional food  $\xi \in \left(0, \frac{\delta}{\beta - \delta\alpha}\right)$ , the system exhibits two coexistence states, one of which is (un)stable and other is of saddle in nature. The existence of saddle coexistence state divides the state space into two regions, of which one contains the region of attraction of coexistence state with low prey component and the other has a basin of attraction of prey carrying capacity. Now, increasing the food supply beyond the critical value  $\xi_c$ , the division of state space into two regions continues but with the exception that the basin of attraction for the first region shifts to the predator axis. All the solutions initiating in this region will be driven to a pest-free state with unlimited growth in predators. The solutions starting in the other region will converge to  $(\gamma, 0)$ . Thus, in this case, the achieving of successful biological control depends on the initial starting state. We can employ some external control strategies such as culling of the pest species to bring the state to the region of attraction of predator axis in the case, where the initial state is in the  $(\gamma, 0)$  region of attraction.

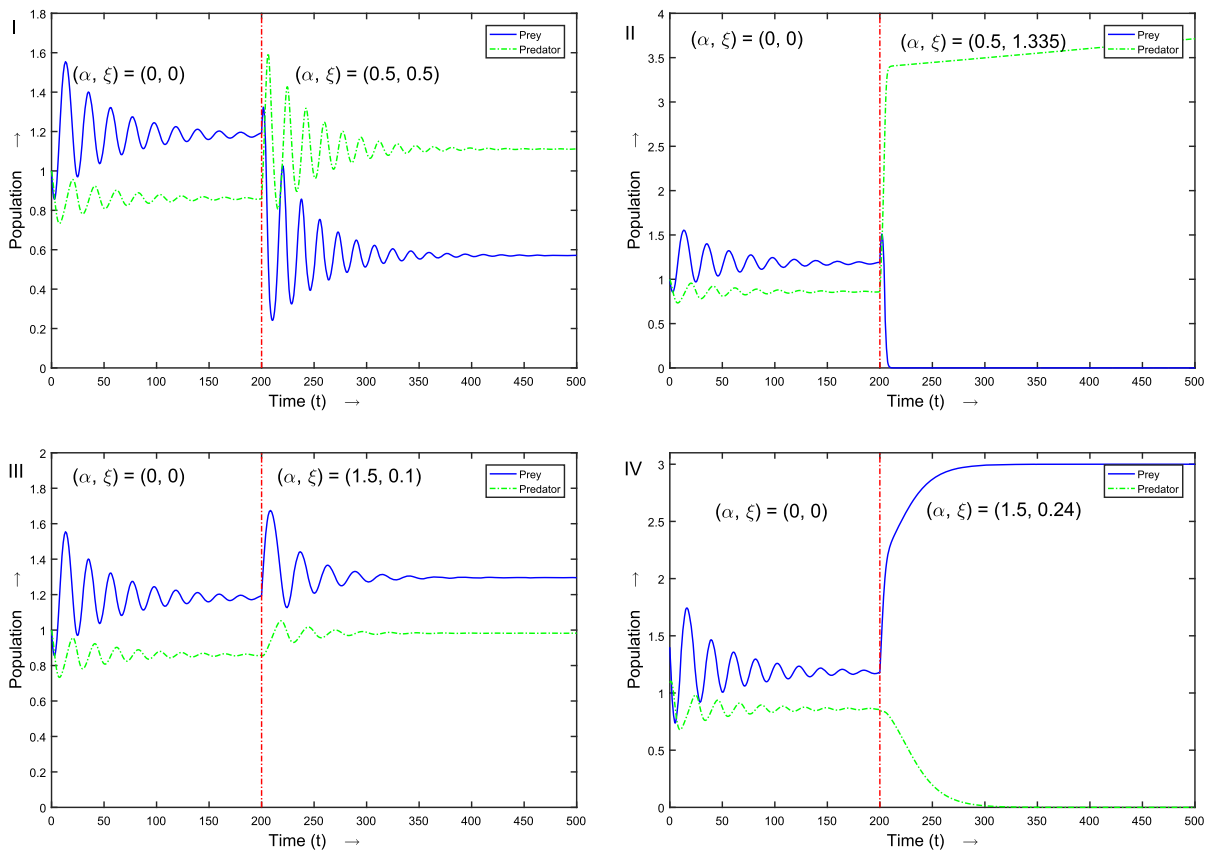
## 7 Numerical simulations for controllability

The global dynamics and stability analysis presented in the previous sections, with the help of  $(\eta, \xi)$  control parameter space division shown in Figs. 8 and 9, provide us with the control strategies to drive the system from one point to another. The key findings pertaining to the controllability of the system are illustrated through numerical simulations in this section.

At first, we demonstrate the controllability aspects of system (5, 6) in the case where in the absence of additional food admits a unique stable coexistence. For this, we fix the ecosystem parameters to be  $\beta = 0.5$ ,  $\delta = 0.4$ ,  $\omega = 0.3$ ,  $\gamma = 3$  and  $\eta = 0.014$ . With this parameter choice, the solutions of the system will be driven to  $(1.1828, 0.8600)$  asymptotically. We now provide predators with additional food of high (nutritious) quality,  $\alpha = 0.5$  after a time gap of  $t = 200$  units and investigate the controllability

aspects by varying the quantity. At first, taking quantity  $\xi = 0.5$ , we observe that the trajectories of the system will be driven asymptotically to the stable coexistence  $(0.5708, 1.1111)$ . The frame I of Fig. 10 presents this situation. Increasing quantity further and crossing the threshold value  $\xi = 1.335$ , we observe the prey gets eradicated from the system, and the predator populations will be driven to predator axis with unlimited growth. Frame II of Fig. 10 depicts this scenario. Now, providing low (nutritious) quality additional food with  $\alpha = 1.5$  and quantity  $\xi = 0.1$ , we observe that the system will be driven asymptotically to the stable coexistence  $(1.2958, 0.9827)$  with higher prey component (cf. Frame III of Fig. 10). Further increase in quantity with  $\xi = 0.24$ , crossing the threshold value  $\xi_c = 0.2317$ , the solutions will be driven to  $(\gamma, 0) = (3, 0)$ , a predator-free state making the system completely prey dominant. This scenario is pictured in Frame IV of Fig. 10.

The simulations presented in Fig. 11 depict controllability aspects of the system when the original system (in the absence of additional food) admits an unstable predator–prey coexistence. The ecosystem parameters chosen to be  $\beta = 0.5$ ,  $\delta = 0.4$ ,  $\omega = 0.25$ ,  $\gamma = 3.5$  and  $\eta = 0.0036$ . For this parameters set, the system admits an unstable coexistence  $E_1 = (1.0154, 0.8929)$ . Now the solutions originating at the initial state  $(1, 1)$  will oscillate around  $E_1$ . Let us now provide predators with some additional food after a time gap of  $t = 200$  units. Providing (high-quality) additional food with  $\alpha = 0.5$  and quantity  $\xi = 0.04$ , we observe that the system admits an interior equilibrium  $E_1 = (0.9656, 0.9108)$ , which is unstable in nature, and thus, the oscillations continue to exist, but the amplitude of the oscillations will reduce (cf. Frame I of Fig. 11). Fixing quality and increasing  $\xi$  to 0.5, the oscillations in the system are eliminated and the solutions will reach asymptotically to the equilibrium point  $(0.5419, 1.1340)$ . This situation is pictured in Frame II of Fig. 11. Further increase in  $\xi$  and crossing the threshold value  $\xi_c = 1.34$ , we observe that the prey gets eradicated from the ecosystem and the solutions will be driven to predator axis. The simulations presented in Frame III of Fig. 11 illustrate this phenomenon of complete biological control. Now, providing low-quality additional food with  $\alpha = 1.5$ , and varying quantity  $\xi$  between 0 to 0.748, we observe that, the oscillations in the system increase for  $\xi = 0.2$  and solutions get driven to prey carrying capacity for  $\xi = 0.8$ . Frames IV and V of Fig. 11 depict



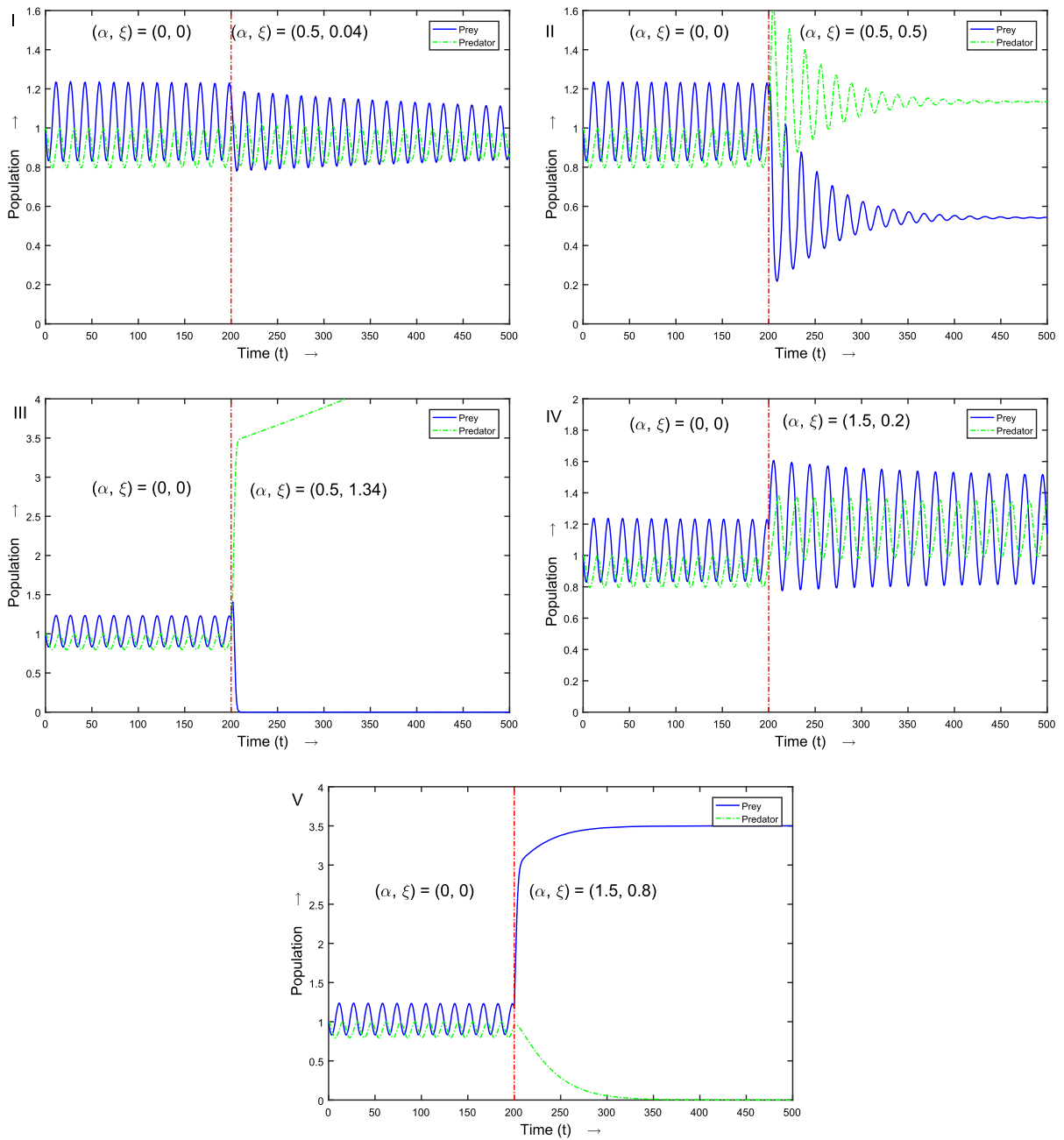
**Fig. 10** Numerical simulation illustrating the controllability aspects of system (5, 6) with provision of high-quality and low-quality additional food, when the system in the absence of addi-

tional food exhibits unique stable coexistence. The ecosystem parameters chosen for this simulation are:  $\beta = 0.5$ ,  $\delta = 0.4$ ,  $\omega = 0.3$ ,  $\gamma = 3$  and  $\eta = 0.014$

these two scenarios and illustrate the consequences of providing low-quality additional food.

Finally, we illustrate the controllability aspects when the provision of additional food brings in two coexistence states. In this case, the system behaviour becomes very dynamic and interesting. This example illustrates the vital role played by the time of the release of additional food in controllability of the system. The ecosystem parameters are taken to be  $\beta = 0.5$ ,  $\delta = 0.3$ ,  $\omega = 0.3$ ,  $\gamma = 3.4$  and  $\eta = 0.05$ . For this choice of parameters, the original system (with out additional food) has two coexistence states given by  $E_1 = (0.8192, 0.9119)$  and  $E_2 = (2.5936, 0.7158)$  with their nature being unstable and saddle, respectively. Existence of saddle coexistence divides the state space in to two regions. The solutions initiating in the region of attraction of  $E_1$  will oscillate around the state

$E_1$ . The solutions originating outside of the regions of attraction of  $E_1$  will be driven to  $(\gamma, 0)$  (cf. Frame I of Fig. 12). Now, fixing initial population level at  $(2, 2)$  (which is in the region of attraction of  $(\gamma, 0)$ ) and providing additional food with quality  $\alpha = 0.5$  and quantity  $\xi = 0.3$  after a time gap of  $t = 20$  units. For this choice of additional food, the system admits two coexisting states  $E_1 = (0.4746, 1.0563)$  (unstable) and  $E_2 = (3.3162, 0.1219)$  (saddle). Further, at the time of release, the population level is at  $(3.08796, 0.32001)$ , which is in the region of attraction of  $E_1$ . So, the solution of the additional food provided predator-prey system converges to a limit cycle surrounding the interior equilibrium  $(0.4746, 1.0563)$  (cf. Frame II of Fig. 12). If we provide same quality and quantity of additional but after a time gap of  $t = 40$  units, the population level at this moment is  $(3.33151, 0.07952)$ , which is outside

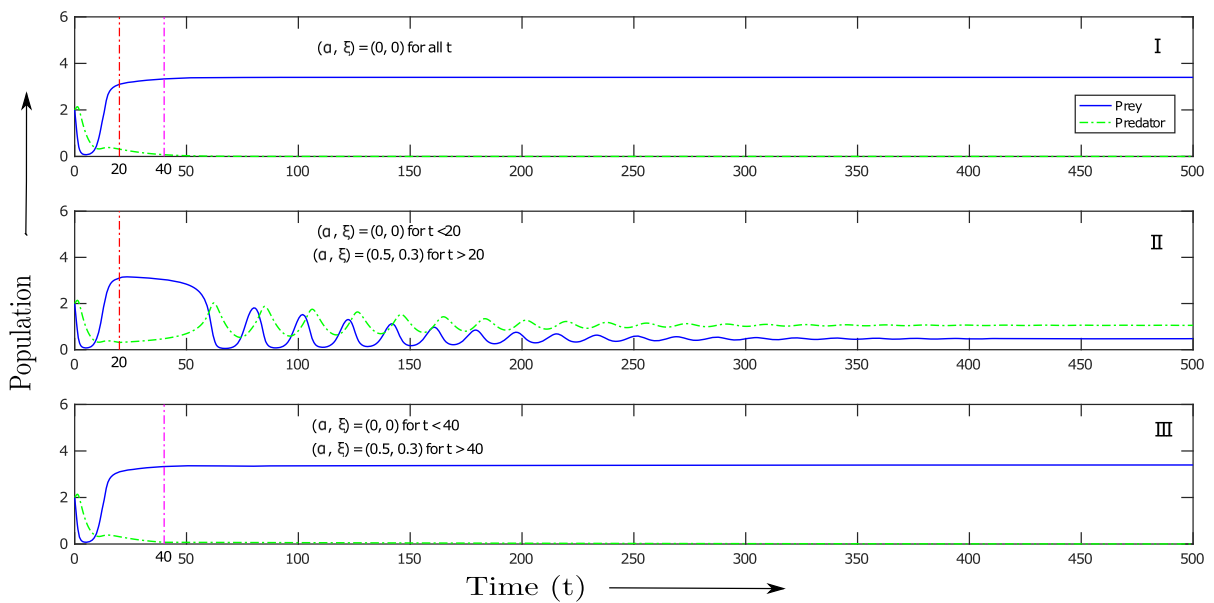


**Fig. 11** Numerical simulation illustrating the controllability aspects of system (5, 6) with provision of high-quality and low-quality additional food, when the system in the absence

of additional food exhibits unstable predator–prey coexistence. The ecosystem parameter values chosen for this simulation are:  $\beta = 0.5, \delta = 0.4, \omega = 0.25, \gamma = 3.5$  and  $\eta = 0.0036$

of the region of attraction of  $E_1$ . Thus, the solution of the system with this initial state will reach to  $(\gamma, 0)$  asymptotically (cf. Frame III of Fig. 12) deviating from the biological control target. This example cautions the

eco-managers not only about the quality and quantity of the additional food that is being supplied but also on the time of the release of additional food and the initial population levels.



**Fig. 12** Numerical simulation illustrating the importance of initial population levels and the time of the release of additional food. Frame I, depicts the scenario wherein, the trajectories of the system starting at  $(2, 2)$  in the absence of additional food will be driven to  $(\gamma, 0)$ . Now providing additional food with quality  $\alpha = 0.5$  and quantity  $\xi = 0.3$  after  $t = 20$  units of time, the

solutions of the system will be driven to a stable coexistence with low prey population. Frame II graphically illustrates this situation. When predators are provided with the same quality and quantity of additional food, but at  $t = 40$  units of time, the solutions of the system will be driven to predator-free state. Frame III presents this scenario

## 8 Discussion and conclusions

A significant portion of the theoretical modelling works done in the direction of biological control assumes pest as prey and natural enemies as predators. The relationship between these prey and predator is then modelled using differential/difference equations to study the dynamics in continuous/discrete time domain [4, 16, 37, 42, 54]. Some prominent studies carried out in modelling pest, natural enemy interactions, highlights several interesting phenomena that are responsible for the control of economically damaging agricultural insect pests and weeds [13, 14, 17, 31, 47, 68]. The empirical works in the biological control discipline establish that, many natural enemies are omnivorous in nature and depend on non-prey food sources such as pollen, nectar, etc. [5, 15, 36, 43, 44, 77, 81, 86]. These non-prey food sources many times deviate the predators from the goals of biological control. Thus, over the last few decades, the environmentalists and theoretical ecologists have been studying the consequences of providing non-pest additional food to preda-

tors to gain valuable insights for developing best biological pest control strategies [44, 47, 52, 65]. Both theoretically and empirically, it is well established that, the quality, quantity of additional food plays a crucial role in controlling the economically damaging species [52, 53, 65, 80, 81, 83, 86].

In the ecological world, the interactions between prey and predators are complex in nature, and can incorporate various phenomenon such as cannibalism [23, 24], Allee effect [29], refuge [12, 49, 73, 91], parental care [51, 71], etc. Two other important phenomena exhibited by prey to avoid predation pressure that has direct consequences for the success of biological control programmes are group defence [21, 25, 26, 28] and anti-predator behaviour (role reversals between prey and predator) [8, 22, 35, 40, 41, 45, 57]. The group defence formation by prey to overcome the predation pressure can sometimes lead to predator extinction. The adoption of anti-predator behaviour by prey as a counterattacking technique, to safeguard the young prey species from the future predation pressure, results in killing of juveniles/eggs of



predator [7,55,56]. A few experimental studies carried out in this direction reveal that in few situations the anti-predator behaviour is detrimental to the natural enemies [33,34]. In few others cases, it is found that in spite of anti-predator behaviour pest, predators when exhibit generalist nature, can achieve the targets of biological control [80,81]. This dual outcome of anti-predator behaviour calls for better understanding of the mechanisms and interactions between the prey and predator.

A very few theoretical models have studied the effect of anti-predator behaviour in prey [32,70]. It established there that, an increase in anti-predator behaviour, decreases the predator population and increases the abundance of the prey. Thus, the anti-predator behaviour of prey can have adverse effects on the successful biological control programmes. One of the ways to enhance the biological control is to overcome the diminish in the predator numbers by supplementing the predators with some additional/alternative food [11,44,81,84,86]. Theoretical works carried out in this direction establish that food supplementation can not only aid the pest control but also annihilate the predators [52,65]. The above theoretical studies do not account for the group defence and anti-predator behaviour in prey. In recent experimental research carried out by Vangansbeke et al. [75], studying the combined effects of anti-predator behaviour and additional food supply to predators, reports that the availability of nutritional food supplementation increases the efficacy of predator in controlling the pest species. This increase in the efficacy is controlled by the quality and quantity of the food supplementation. As a consequence, it is concluded that few more investigations are required to determine the type and level of food supplementation (i.e., quality and quantity) to be used for better suppression of pest species by natural enemies. These conclusions motivated us to undertake a theoretical investigation, to characterise the type and level of food supplementations that are to be provided to predators to control the prey with anti-predator behaviour. This study is taken up with an intention to bridge the gap between theoretical and experimental works, aid the experimentalists in identifying the proper food supplementation and developing the control strategies for the success of pest control programmes.

The model presented in this work assumes Holling type IV functional response from incorporating the group defence in prey in the presence of additional food. Assuming that the prey adopts anti-predator

behaviour as a counterattacking technique, the loss in predator species is modelled using mass action formula. In general, the anti-predator behaviour in prey calls for a stage structure in predators. But, in the current model, we have ignored the internal stage structure mechanism of the predators as we are primarily interested in accessing the consequence of additional food in the presence of anti-predator behaviour prey. Following the work of [65], we characterise the additional food to be *high (nutritious) quality* if the proportion of handling time between additional food and prey is less than the ratio of maximum predator growth rate and its starvation rate ( $\alpha < \beta/\delta$ ). Additional food is termed as of *low (nutritious) quality* if the above inequality reverses ( $\alpha > \beta/\delta$ ).

The model analysis reveals several interesting phenomena such as the existence of two coexistence states with one being saddle in nature. The considered system admits various bifurcations such as Hopf (degenerate, non-degenerate), homoclinic orbit, saddle-node and Bogdanov–Takens (super/subcritical) concerning the variations in the quantity and anti-predator behaviour and treating quality as a constant control parameter. Control strategies are derived for driving the system to a pest-free state. It is observed that, the presence of saddle equilibrium leading to degenerate Hopf bifurcation, saddle-node bifurcation, Bogdanov–Takens bifurcation effects the biological control outcomes. It worth noting that, the presence of degenerate Hopf bifurcation and existence of homoclinic orbit divide the entire state space into two regions. The solutions originating inside the homoclinic loop will be driven to coexistence state, whereas the solutions beginning outside of the homoclinic cycle converge to predator-free state and thus depriving targets of biological pest control. These outcomes highlight the vital role of the quantity, quality of the additional food supplied to predators and anti-predator behaviour of prey in accomplishing the biological control targets. It is even possible to drive the system trajectories to a pest-free state (with unlimited growth in predators) by providing highly nutritious additional food sufficient quantities.

Recent theoretical works investigating the prey–predator interactions guided by the anti-predator behaviour in prey [69,70] establish that the behavioural strategies of prey in adopting the anti-predator behaviour could inhibit the growth rate of predators and prove to be beneficial to prey growth rate. Our study further strengths these observations and discusses the

use of supplementary foods in overcoming the negative effects caused by prey adaption of anti-predator behaviour. We observe that supplementing predators with high nutritional food (relative to anti-predator behaviour of prey), predators can maintain the pest population below a threshold value or even annihilate the pest from the ecosystem. A critical outcome of this study that cautions eco-managers is that; it is not only relevant to provide suitable additional food of superior quality with appropriate quantity but also the time of release is vital for the success of biological control programmes. The observations of this study are in accordance with the experimental work done in this direction by Leman and Messelink [39] and Vangansbeke et al. [75], wherein the study points out that not only the providing type and quantity of additional food but also the way in which the food is distributed in the environment plays a vital role in controlling pests.

The present model can further be improved by incorporating stage structure in predator populations and even competition between predators for food resources to limit the unlimited growth in predators. Also, the model presented here does not account for the spatial variations and time delay. Inspired by the theoretical works done on the diffusive predator-prey with anti-predator behaviour and time delay [90] in biological context, it will be fascinating to investigate prey-predator dynamics in the presence of additional food by incorporating the above effects. We aim take up this study this in future.

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**Appendix A Boundedness of the solutions of the proposed system**

**Lemma A.1** *If  $\beta\xi - \delta(1 + \alpha\xi) \leq 0$ , then all the solutions of system (5, 6) initiating in the interior of the positive quadrant of the state space are bounded.*

*Proof* We define  $W = x + \frac{1}{\beta}y$ . Now, for any  $K > 0$ , we consider,

$$\begin{aligned} \frac{dW}{dt} + KW &= \frac{dx}{dt} + \frac{1}{\beta} \frac{dy}{dt} + Kx + \frac{K}{\beta}y \\ &= x \left( 1 - \frac{x}{\gamma} \right) - \frac{xy}{(wx^2 + 1)(1 + \alpha\xi)} \end{aligned}$$

$$\begin{aligned} &+ \frac{1}{\beta} \frac{\beta(x + (wx^2 + 1)\xi)y}{(wx^2 + 1)(1 + \alpha\xi)} \\ &- \frac{\delta}{\beta}y - \frac{\eta}{\beta}xy + Kx + \frac{K}{\beta}y \\ &= x \left( 1 - \frac{x}{\gamma} + K \right) + \frac{\xi y}{1 + \alpha\xi} \\ &+ \left[ -\frac{\delta}{\beta} - \frac{\eta x}{\beta} + \frac{K}{\beta} \right] y \\ &\leq \frac{\gamma(1 + K)^2}{4} \\ &+ \left( \frac{\xi}{1 + \alpha\xi} + \frac{K - \delta}{\beta} \right) y - \frac{\eta xy}{\beta} \\ &\leq \frac{\gamma(1 + K)^2}{4} \\ &+ \left( \frac{\xi}{1 + \alpha\xi} + \frac{K - \delta}{\beta} \right) y \text{ (as } x > 0). \end{aligned}$$

Choosing sufficiently small  $K (< \delta)$  and  $\beta\xi - \delta(1 + \alpha\xi) \leq 0$ , we get

$$\frac{dW}{dt} + KW \leq M \left( = \frac{\gamma(1 + K)^2}{4} \right).$$

Then, the applications of Gronwall’s inequality, we get

$$0 \leq W(t) \leq \frac{M}{K}(1 - e^{-Kt}) + W(0)e^{-Kt}.$$

Therefore,  $0 < W(t) \leq \frac{M}{K}$  as  $t \rightarrow \infty$  □

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