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Modeling Dynamics of Mutualism in Prey-Prey System with Variable Carrying Capacity in the Presence of Predator

Randy Lee, Kening Wang, and Mohammad Mahbubur Rahman

***Abstract*—We developed and analyzed two mathematical models considering indirect and direct mutualism of two prey species in the presence of predator species. The mutualism dynamics are represented by taking into account a fixed and a produced carrying capacities corresponding to different mutual interactions between symbionts. As the death rate of the predator increases, the indirect mutualism model goes through a trans-critical bifurcation, whereas, in the direct mutualism model shows a trans-critical bifurcation as well as a Hopf bifurcation.**

***Index Terms*—Mutualism, Variable carrying capacity, Stability, Limit cycle, Bifurcation**

I. INTRODUCTION

Mathematical models for symbiosis have been developed in several studies [1], [2], [3], [4], [5], [6]. The global stability of mutualistic dynamics between two species with harvesting is studied in [2]. A commensal symbiosis model with a non-monotonic functional response is investigated in [3]. Yukalov and his co-workers [1] introduced a prey-prey model featuring distinct types of symbiotic interactions and provided a detailed classification of possible dynamical regimes. In this paper, we extend the prey-prey mutualism model presented in [1] to a prey-prey-predator model and explore the stability and bifurcation behavior. While predator-prey interactions are considered in many ecological models, predation is generally not classified as a form of symbiosis. This is because symbiosis is defined by the persistence of interactions [7].

The Lotka-Volterra system was the first to model the dynamic interactions between predator and prey, analyzing how each affects the other [8], [9], [10], [11]. The standard two species model has since been modified to account for more specific factors influencing predator-prey interactions, such as handling rate and herding behavior [12], [13]. Numerous studies have also explored the dynamics of modified prey-prey-predator models [14], [15], [16]. Inspired by the work of [1], we investigate the dynamics of two mutualistic prey species by incorporating the effects of a predator species. One example of this is the multi-species herd consistes of zebras and wildebeests, both of which are prey to lions and provide mutual protection against them. Coblentz and his colleagues [22] examined how non-interaction and competition between prey species affect predator populations. Camacho et al. [23] demonstrated a shift between mutualism and predation in the relationship between predator ants and prey hemipterans. Feeney et al. [24] argued that predation is a driving factor in the recurrent convergent evolution of fish-anemone mutualism. Most recently, Lopez and colleagues [25] analyzed a system of two mutualistic prey species and one predator, incorporating a Crowley-Martin-type functional response.

The paper is organized as follows. In Section II, we introduce the mathematical formulation of variable carrying capacities consisting of a fixed and a variable term produced by two symbiotic species. In Section III, we develop the model using variable carrying capacity representing the livelihood that are influenced without direct interaction between both prey populations in the presence of a predator. We analyze the stability and bifurcation behavior after re-scaling. We further develop a model using carrying capacity representing the livelihood that are influenced with direct interaction between both prey species in the presence of a predator species in section IV and again analyze the stability and bifurcation behavior after re-scaling. In Section V, we give the concluding remark emphasizing ecological significance of the two models and discuss the possible future research.

II. INDIRECT AND DIRECT MUTUALISM

Mutualism refers to a relationship in which two or more species gain from interacting with each other. To construct our mutualism model, we start with the Lotka-Volterra framework [13] and modify it to include two prey species that influence each other through mutualistic interactions, as explored in [1]. So we start with :

$$\frac{dX_i}{dt} = A_iX_i - \frac{\mu_iX_i^2}{N_i}, \tag{1}$$

where $X_i = X_i(t)$ are functions of time $t \geq 0$. Here, the parameters $A_i > 0$ are the logistic growth rates of i-th species. The parameters $\mu_i > 0$ are the intensity of the mutual competition between the agents of the i-th species. The important difference from standard logistic equation is that the carrying capacity in mutualism is considered to be a function

$$N_i = K_i + \mu_iN_i(X_1, X_2, ...) \tag{2}$$

of the quantities X_i, for co-existing symbiotic species. The first term K_i is the carrying capacity of the given surrounding livelihood. The second term characterizes the carrying capacity produced by the other species through symbiotic

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influence. The parameter K_i is supposed to be nonzero, which implies that the species could exist without their symbionts. The symbiotic coefficient μ_i defines the positive intensity of producing, or destroying, the carrying capacity in the process of symbiosis relations. Thus we can assume $\mu_i > 0$ and the symbiosis function $N_i(X_1, X_2, ...)$ to be nonnegative. If the carrying capacity of the $i-$th species is influenced by the $j-$th species without direct interactions (the livelihood of each species is influenced by the presence of another species without involving their direct interactions), the carrying capacity can be described as

$$N_i = K_i + N_i X_j, i, j = 1, 2; i \neq j. \tag{3}$$

If the carrying capacity of the $i-th$ species is influenced by the $j-th$ species involving direct interactions (the symbiotic species influence the livelihood of each other by means of mutual interactions), the carrying capacity can be described as

$$N_i = K_i + N_i X_i X_j, i = 1, 2; i \neq j. \tag{4}$$

In Sections III and IV, we extend this idea of symbiotic relations using the carrying capacities described in (3) and (4) for two species in the presence of a predator. This allows us to investigate the dynamics of mutualism by considering both indirect and direct interactions between the prey species.

III. A MATHEMATICAL MODEL OF INDIRECT SYMBIOSIS

Consider a model of symbiosis involving three different species, where the carrying capacity of the $X(t)$ depends on the $Y(t)$ and vice versa, along with the influence of the $Z(t)$. As discussed in Section II, if the carrying capacity of the $X(t)$ is influenced solely by $Y(t)$ without direct interaction, the model can be expressed, after appropriate scaling and normalization, as

$$\begin{aligned}
\frac{dX}{dt} &= AX(1 - \frac{X}{1 + \mu Y}) - BXZ, \\
\frac{dY}{dt} &= CY(1 - \frac{Y}{1 + \nu X}) - DYZ. \\
\frac{dZ}{dt} &= -EZ + FXZ + GYZ,
\end{aligned} \tag{5}$$

The parameters A and C represent the logistic growth rates of the respective prey species. The parameters B and D denote the predation death rates. The parameter E is the natural death rate of the predator. The parameters F and G correspond the growth rates of the predator resulting from interactions with the respective prey species. The parameters $\mu > 0$ and $\nu > 0$ represent the extent to which symbiosis affects the carrying capacity of the respective species.

Before advancing with the analysis of the steady state and stability, it is necessary to perform some re-scaling to better understand how the parameters influence the dynamics. To this end, the variables are scaled as follows: $x = X, y = Y, z = \frac{B}{A}Z, t_{new} = \frac{t_{old}}{A}$ and other parameters are dimensionless as: $a = \frac{C}{A}, b = \frac{D}{B}, c = \frac{E}{A}, d = \frac{F}{A}, e = \frac{G}{A}, \mu = \alpha, \nu = \beta$. With these changes system (5) becomes

$$\begin{aligned}
\frac{dx}{dt} &= x(1 - \frac{x}{1 + \alpha y}) - xz, \\
\frac{dy}{dt} &= ay(1 - \frac{y}{1 + \beta x}) - byz, \\
\frac{dz}{dt} &= -cz + dxz + eyz,
\end{aligned} \tag{6}$$

which are still difficult to analyze qualitatively as it has seven parameters. So we make the following three assumptions to simplify the model.

Assumption 1: Both x and y species experience the same predation death rates, which results in the parameter b being equal 1.

Assumption 2: Both prey species exert the same positive effects on the predator z, leading to $d = e$.

Assumption 3: Both prey have the same symbiotic effects on each other, meaning $\alpha = \beta$.

Then, the system becomes:

$$\begin{aligned}
\frac{dx}{dt} &= x(1 - \frac{x}{1 + \alpha y}) - xz, \\
\frac{dy}{dt} &= ay(1 - \frac{y}{1 + \alpha x}) - yz, \\
\frac{dz}{dt} &= -cz + dz(x + y).
\end{aligned} \tag{7}$$

It is important to note that the parameters a, c, d, and α always remain positive. Furthermore, for ecological analysis, the region of interest in $\mathcal{R}^3$ is confined to $H = \{(x, y, z) \in \mathcal{R}^3 | \; x \geq 0, y \geq 0, z \geq 0\}$.

A. Steady states and stability

The model system (7) has seven steady states :

(i) complete extinction $(0, 0, 0)$,
(ii) the prey x only (1,0,0),
(iii) the prey y only (0,1,0),
(iv) the prey x and predator z only ($\frac{c}{d}$, 0, $\frac{d-c}{d}$),
(v) the prey y and predator z only (0, $\frac{c}{d}$, $\frac{a(d-c)}{d}$),
(vi) the prey-prey only ($\frac{1}{1-\alpha}$,$\frac{1}{1-\alpha}$,0), and
(vii) coexistence, ($\bar{x}$,$\bar{y}$,$\bar{z}$), which is the solution to the system of equations:

$$\begin{aligned}
1 - \frac{\bar{x}}{1 + \alpha \bar{y}} &= \bar{z}, \\
a(1 - \frac{\bar{y}}{1 + \alpha \bar{x}}) &= \bar{z}, \\
\frac{c - d\bar{x}}{d} &= \bar{y}.
\end{aligned} \tag{8}$$

More specifically, when $a \neq 1$ the solutions are:

$$\begin{aligned}
\bar{x}_{\pm} &= \frac{d(a + 1) + c\alpha(2a + \alpha(a - 1)) \pm q}{2d\alpha(\alpha + 1)(a - 1)}, \\
\bar{y}_{\pm} &= \frac{d(a + 1) + c\alpha(2 + \alpha(1 - a)) \pm q}{2d\alpha(\alpha + 1)(1 - a)}, \\
\bar{z}_{\pm} &= \frac{(a + 1)(d + 2d\alpha + c\alpha^2) \pm q}{2\alpha(2d + c\alpha)},
\end{aligned} \tag{9}$$

where

$$q = \sqrt{d^2(a + 1)^2 + 4ac\alpha(2d + c\alpha) + \alpha m(a - 1)^2}, \tag{10}$$

with $m = 4d^2(\alpha+1) + 2\alpha cd + 4cd\alpha^2 + c^2\alpha^3$. We represent the steady states (vii) as $(\bar{x}_+, \bar{y}_+, \bar{z}_+)$ and $(\bar{x}_-, \bar{y}_-, \bar{z}_-)$, corresponding to the respective signs in front of q in (9) . When $a = 1$, the coexistence steady state is given by $(\frac{c}{2d}, \frac{c}{2d}, \frac{2d+c\alpha-c}{2d+c\alpha})$, which holds ecological significance when $\frac{2d}{c} + \alpha > 1$. For $a \neq 1$, we address the feasibility of these steady states in the following lemma.

Lemma 1: For system (7) with positive parameters α, a, c, d and $a \neq 1$, the coexistence steady states

(a) $(\bar{x}_+, \bar{y}_+, \bar{z}_+)$ is infeasible; and
(b) $(\bar{x}_-, \bar{y}_-, \bar{z}_-)$ is feasible if and only if one of the following set of conditions are satisfied:
  i. $a \neq 1$ and $d < c < 2d$;
  ii. $a \neq 1$, $c > 2d$, and $2d + c\alpha > c$;
  iii. $a < 1$, $a + \frac{c}{d} > 1$ and $c < d$;
  iv. $1 < a < \frac{d}{d-c}$ and $c < d$.

Proof: First of all, let us prove $(\bar{x}_+, \bar{y}_+, \bar{z}_+)$ is always infeasible.

When $a > 1$, it is obvious that both numerator and denominator of $\bar{x}_+$ are positive, and thus $\bar{x}_+ > 0$.

Let $r = d(a+1) + c\alpha(2 + \alpha(1-a))$. If $r \geq 0$, then $r + q$, which is the numerator of $\bar{y}_+$, is positive. If $r < 0$, then $q - r > 0$ and $q^2 - r^2 = q^2 - (d(a+1) + c\alpha(2 + \alpha(1-a)))^2 = 4\alpha(a-1)(c + d(a-1))(\alpha+1)(d + c\alpha) > 0$. Hence $q + r > 0$, which implies the numerator of $\bar{y}_+$ is positive. However, when $a > 1$, the denominator of $\bar{y}_+$ is negative. Thus $\bar{y}_+ < 0$.

Therefore, if $a > 1$, $(\bar{x}_+, \bar{y}_+, \bar{z}_+)$ is infeasible.

Similarly, we can prove that $(\bar{x}_+, \bar{y}_+, \bar{z}_+)$ is infeasible if $a < 1$.

Now we prove part (b).

($\Longleftarrow$) is trivial.

($\Longrightarrow$) We first discuss $\bar{z}_-$. Since both the denominator and the conjugate of the numerator of $\bar{z}_-$ are always positive, we can multiply both the numerator and denominator of $\bar{z}_-$ by the conjugate of its numerator without changing the sign of the numerator. As a result, the numerator becomes $4a\alpha(\alpha+1)(2d+c\alpha)(2d+c\alpha-c)$, which indicates that the numerator is positive when $2d + c\alpha > c$.

Next, because the conjugates of the numerators of $\bar{x}_-$ and $\bar{y}_-$ are always positive, we can determine the conditions under which $\bar{x}_-$ and $\bar{y}_-$ are positive.

The numerator of $\bar{x}_-$ multiplied by its conjugate is $4\alpha(\alpha+1)(d+c\alpha)(a-1)(a(c-d)+d)$, with the relevant part being $(a-1)(a(c-d)+d)$. The numerator of $\bar{y}_-$ multiplied by its conjugate is $-4\alpha(\alpha+1)(d+c\alpha)(a-1)(c+d(a-1))$, with the relevant part being $-(a-1)(c+d(a-1))$.

For $\bar{x}_- > 0$, we require $ac + d > ad$. For $\bar{y}_- > 0$, we need $c + ad > d$. Moreover, for $\bar{z}_- > 0$, the condition $2d + c\alpha > c$ must hold. Thus, to make the steady state exist, parameters should satisfy all three conditions.

If $a < 1$, $\bar{x}_-$ is positive. Also, if $d < c < 2d$, $\bar{y}_-$ and $\bar{z}_-$ are positive. However, when $c > 2d$, $\bar{y}_-$ is still positive, but we also need $2d + c\alpha > c$ for $\bar{z}_-$ to be positive. If $c < d$, then $\bar{z}_-$ is now positive, but $c + ad > d$ is necessary for $\bar{y}_-$ to be positive.

If $a > 1$, $\bar{y}_-$ is always positive. Like above, if $d < c < 2d$, $\bar{x}_-$ and $\bar{z}_-$ are positive. However, when $c > 2d$, $\bar{x}_-$ is still positive, but we also need $2d + c\alpha > c$ for $\bar{z}_-$ to be positive. If $c < d$, then $\bar{z}_-$ becomes positive, but we also need $a < \frac{d}{d-c}$ for $\bar{x}_-$ to be positive.

Thus we have shown the conditions for which $(\bar{x}_-, \bar{y}_-, \bar{z}_-)$ is feasible. ■

Now, let us discuss the linear stability of these steady states which is determined by considering the eigenvalues of the Jacobian matrix,

$$\begin{aligned} & J(x,y,z) \\ = & \begin{bmatrix} 1 - \frac{2x}{1+\alpha y} - z & \frac{\alpha x^2}{(1+\alpha y)^2} & -x \\ \frac{a\alpha y^2}{(1+\alpha x)^2} & a - \frac{2ay}{1+\alpha x} - z & -y \\ dz & dz & -c + d(x+y) \end{bmatrix}, \end{aligned} \tag{11}$$

evaluated at each of these steady states.

1) Complete Extinction: $x = 0, y = 0, z = 0$*:* When the Jacobian matrix (11) is evaluated at $(0,0,0)$, the eigenvalues are 1, a, and $-c$. Thus, $(0,0,0)$ is unstable (saddle). This means that when populations of all three species begin with very small quantities, it is impossible for all of them go extinct simultaneously.

2) The prey x only: $x = 1, y = 0, z = 0$*:* When the Jacobian matrix (11) is evaluated at the prey x only steady state, the eigenvalues are -1, a, and $d-c$. Thus the prey x only steady state is always unstable.

3) The prey y only: $x = 0, y = 1, z = 0$*:* When the Jacobian matrix (11) is evaluated at the prey y only steady state, the eigenvalues are 1,$-a$, and $d-c$. Thus, the prey y only steady state is always unstable.

4) The prey x and predator z only: $x = \frac{c}{d}$, $y = 0$, $z = \frac{d-c}{d}$*:* When the Jacobian matrix (11) is evaluated at $(\frac{c}{d}, 0, \frac{d-c}{d})$, the eigenvalues are $\frac{c-d+ad}{d}$ and $\frac{-c \pm \sqrt{c(c+4cd-4d^2)}}{2d}$. For this steady state to be biologically feasible, we have $d > c$, which implies $4cd - 4d^2 < 0$. Moreover, if $c + 4cd - 4d^2 \geq 0$, since $4cd - 4d^2 < 0$, $c + 4cd - 4d^2 < c$, eigenvalues $\frac{-c \pm \sqrt{c(c+4cd-4d^2)}}{2d}$ are negative. If $c + 4cd - 4d^2 < 0$, then it is obvious that the real part of $\frac{-c \pm \sqrt{c(c+4cd-4d^2)}}{2d}$ is negative. In addition, $\frac{c-d+ad}{d}$ is negative if $a + \frac{c}{d} < 1$. Therefore, the steady state is stable when $d > c$ and $a + \frac{c}{d} < 1$. It does make sense since if the population of X grows much faster than Y, and if the growth rate of Z due to the interaction with X is greater than its death rate, then the prey Y will die out.

5) The prey y and predator z only: $x = 0$, $y = \frac{c}{d}$, $z = \frac{a(d-c)}{d}$*:* When the Jacobian matrix (11) is evaluated at $(x, \frac{c}{d}, \frac{a(d-c)}{d})$, the eigenvalues are $\frac{ac+d-ad}{d}$ and $\frac{-ac \pm \sqrt{ac(ac+4cd-4d^2)}}{2d}$. For this steady state to be significant, we have $d > c$, which implies $4cd - 4d^2 < 0$. With similar discussions as we did previously, either eigenvalues $\frac{-ac \pm \sqrt{ac(ac+4cd-4d^2)}}{2d}$ or their real parts are negative. Also, $\frac{ac+d-ad}{d}$ is negative if $ac + d < ad$. Hence, this steady state is stable when $a > \frac{d}{d-c} > 1$. This is similar to the previous steady state. That is, if the population of Y grows much faster than X, and if the growth rate of Z due to the interaction with Y is greater than its death rate, then the prey X will go extinct.

Note that both mathematically and logically, the "prey x and predator z only" and "prey y and predator z only" steady states cannot both be stable at the same time. That is because $a < 1$ for the former to be stable while $a > 1$ for latter.

6) The prey x and y only: $x = \frac{1}{1-\alpha}$, $y = \frac{1}{1-\alpha}$, $z = 0$: When the Jacobian matrix (11) is evaluated at this steady state, the eigenvalues are $\frac{2d+c\alpha-c}{1-\alpha}$ and $\frac{-(a+1)\pm\sqrt{(a-1)^2+4a\alpha^2}}{2}$. To be ecologically feasible, we obtain $\alpha < 1$. The conjugate eigenvalues are always negative and real. The steady state is stable if $2d < c(1-\alpha)$ and unstable otherwise. This means that if the death rate of the predator Z is greater than the growth rate of Z due to the interaction with both X and Y, then Z will go extinct.

7) The Coexistence Steady State Behavior: From Lemma 1, we know that $(\bar{x}_+, \bar{y}_+, \bar{z}_+)$ is unfeasible. The stability of $(\bar{x}_-, \bar{y}_-, \bar{z}_-)$ is presented in the following theorem.

Theorem 1: The coexistence steady state $(\bar{x}, \bar{y}, \bar{z}) = (\bar{x}_-, \bar{y}_-, \bar{z}_-)$ given in equation (9) of the model system (7) is aymptotically stable when exists.

Proof: The Jacobian matrix (11) evaluated at $(\bar{x}, \bar{y}, \bar{z})$ is given as follows:

$$\begin{aligned} & J(\bar{x},\bar{y},\bar{z}) \\ = & \begin{bmatrix} 1-\frac{2\bar{x}}{1+\alpha\bar{y}}-\bar{z} & \frac{\alpha\bar{x}^2}{(1+\alpha\bar{y})^2} & -\bar{x} \\ \frac{a\alpha\bar{y}^2}{(1+\alpha\bar{x})^2} & a-\frac{2a\bar{y}}{1+\alpha\bar{x}}-\bar{z} & -\bar{y} \\ d\bar{z} & d\bar{z} & -c+d(\bar{x}+\bar{y}) \end{bmatrix}, \end{aligned}$$

which, in turn, yields a cubic characteristic polynomial equation in λ, given by

$$P(\lambda) = \lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0, \qquad (12)$$

where the coefficients a_1, a_2, and a_3 are expressed in terms of parameters of (7) as

$$\begin{aligned} a_1 &= 2\bar{z} + \frac{2a\bar{y}}{1+\alpha\bar{x}} + \frac{2\bar{x}}{1+\alpha\bar{y}} + c - d(\bar{x}+\bar{y}) - a - 1, \\ a_2 &= a - c - ac + d(\bar{x}+\bar{y}) + ad(\bar{x}+\bar{y}) - \bar{z} - a\bar{z} \\ &\quad + 2c\bar{z} + 2d(\bar{x}+\bar{y})\bar{z} + \bar{z}^2 \\ &\quad + \frac{2ac\bar{y} + 2a\bar{y}\bar{z} - 2a\bar{y} - 2ad\bar{y}(\bar{x}+\bar{y})}{1+\alpha\bar{x}} \\ &\quad + \frac{2c\bar{x} + 2\bar{x}\bar{z} - 2a\bar{x} - 2d\bar{x}(\bar{x}+\bar{y})}{1+\alpha\bar{y}} \\ &\quad + \frac{4a\bar{x}\bar{y}}{(1+\alpha\bar{x})(1+\alpha\bar{y})} - \frac{a\bar{x}^2\bar{y}^2\alpha^2}{(1+\alpha\bar{x})^2(1+\alpha\bar{y})^2}, \\ a_3 &= ac - ad(\bar{x}+\bar{y}) - c\bar{z} - ac\bar{z} - ad\bar{x}\bar{z} - d\bar{y}\bar{z} \\ &\quad + d(\bar{x}+\bar{y})\bar{z} + ad(\bar{x}+\bar{y})\bar{z} + c\bar{z}^2 + d\bar{x}^2\bar{z}^2 + d\bar{y}\bar{z}^2 \\ &\quad - d(\bar{x}+\bar{y})\bar{z} + \frac{ad\alpha\bar{x}\bar{y}^2\bar{z}}{(1+\alpha\bar{x})^2} + \frac{d\alpha\bar{x}^2\bar{y}\bar{z}}{(1+\alpha\bar{y})^2} \\ &\quad + \frac{4ac\bar{x}\bar{y} - 4ad\bar{x}\bar{y}(\bar{x}+\bar{y})}{(1+\alpha\bar{x})(1+\alpha\bar{y})} + \frac{2a\bar{y}d(\bar{x}+\bar{y})}{1+\alpha\bar{x}} \\ &\quad + \frac{2ac\bar{y}\bar{z} + 2ad\bar{x}\bar{y}^2 - 2ac\bar{y} - 2ad(\bar{x}+\bar{y})\bar{y}\bar{z}}{1+\alpha\bar{x}} \\ &\quad + \frac{2ad(\bar{x}+\bar{y})\bar{x} + 2c\bar{x}\bar{z} + 2d\bar{x}\bar{y}\bar{z} - 2ac\bar{x}}{1+\alpha\bar{y}} \\ &\quad - \frac{2d(\bar{x}+\bar{y})\bar{x}\bar{z}}{1+\alpha\bar{y}}. \end{aligned}$$

Using (8), we can simplify the terms into

$$a_1 = \frac{\bar{x}(1+\alpha\bar{x}) + a\bar{y}(1+\alpha\bar{y})}{(1+\alpha\bar{x})(1+\alpha\bar{y})},$$

$$\begin{aligned} a_2 &= \frac{d\bar{x}\bar{z} + d\bar{y}\bar{z}(1+\alpha\bar{x})^2(1+\alpha\bar{y})^2 + a\bar{x}\bar{y}}{(1+\alpha\bar{x})^2(1+\alpha\bar{y})^2} \\ &\quad + \frac{a\alpha\bar{x}^2\bar{y} + a\alpha\bar{x}\bar{y}^2}{(1+\alpha\bar{x})^2(1+\alpha\bar{y})^2}, \\ a_3 &= \frac{d\bar{x}\bar{y}\bar{z}(a\alpha\bar{y}(1+\alpha\bar{y})^2 + a(1+\alpha\bar{x})(1+\alpha\bar{y})^2}{(1+\alpha\bar{x})^2(1+\alpha\bar{y})^2} \\ &\quad + \frac{\alpha\bar{x}(1+\alpha\bar{x})^2 + (1+\alpha\bar{y})(1+\alpha\bar{x})^2}{(1+\alpha\bar{x})^2(1+\alpha\bar{y})^2}. \end{aligned}$$

Applying the Routh-Hurwitz conditions, the coexistence steady state $(\bar{x}, \bar{y}, \bar{z})$ is stable if $a_1 > 0$, $a_3 > 0$, and $a_1a_2 > a_3$. Since $\bar{x}, \bar{y}, \bar{z}$, and all parameters are positive, it is evident that $a_1 > 0$ and $a_3 > 0$. The final condition, $a_1a_2 - a_3 = d\bar{x}^2\bar{z}(1+\alpha\bar{x})^3(1+\alpha\bar{y}) + a^2\bar{x}\bar{y}^2(1+\alpha\bar{y})(1+\alpha\bar{x}+\alpha\bar{y}) + a\bar{y}(1+\alpha\bar{x})(\alpha\bar{x}^3+\bar{x}^2(1+\alpha\bar{y}+d\bar{y}\bar{z}(1+\alpha\bar{y})^3) > 0$ ensures that $a_1a_2 > a_3$. Thus $(\bar{x}, \bar{y}, \bar{z})$ is stable, provided it is ecologically feasible. ■

To better understand the coexistence, Fig. 1 depicts the time series plot for x, y, z versus t.

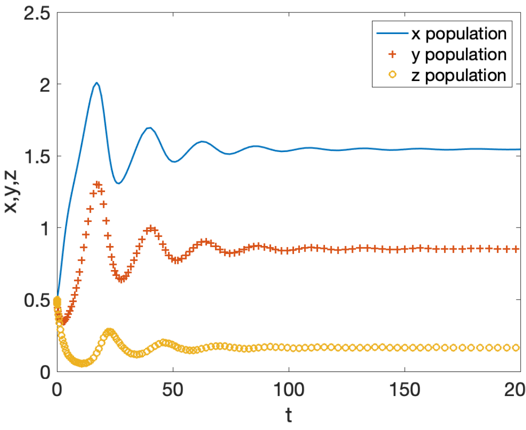

Fig. 1: The time series plot of the coexistence steady state using parameters $a = d = 0.25$, $\alpha = 1$ and $c = 0.6$ with initial conditions $(0.5, 0.5, 0.5)$

Moreover, Fig. 2 shows the phase diagram of z versus x and z versus y. It depicts that if the predator death rate is sufficiently large, there are less prey that will be killed. In this case all three species will stay around. However, the prey populations will not explode in growth due to the continual presence of the predator.

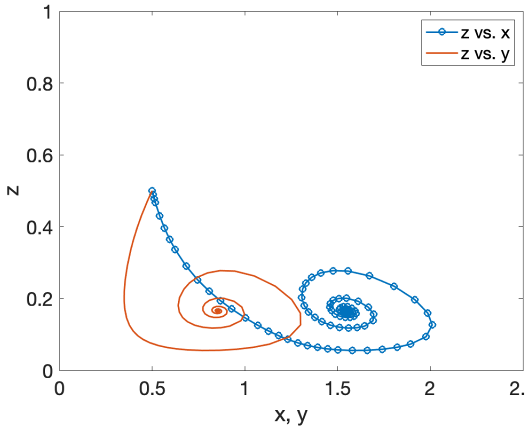

Fig. 2: The phase portraits of z vs x and z vs y of the coexistence steady state using parameters $a = d = 0.25$, $\alpha = 1$, and $c = 0.6$ with initial conditions $(0.5, 0.5, 0.5)$

B. *Bifurcations*

We now look at the stability of the system (7). Since we can not explicitly compute the eigenvalues of the Jacobian matrix (11), analytical techniques can not be used and numerical computation techniques typically must be adopted to follow the stable and unstable manifold. Using AUTO in XPPAUT (ref. [17]) is helpful in this regard. In Fig. 3, a bifurcation diagram is presented with the predator death rate c as the bifurcation parameter. The vertical axis displays, from bottom to top, the starting positions of the prey x and predator z only steady state, the coexistence steady state, and the prey x only steady state. From the diagram, we observe that the system (7) shows transcritical bifurcation at $c = 0.1875$. Ecologically, we can say that with some critical value of parameter c, when the predator population is large enough, it can cause one of the prey species to go extinct from over hunting. In this case, the prey y goes extinct. Once this happens, there is no longer an abundance of food for the predator and its population stabilizes with the remaining prey population.

IV. Mathematical Model of Direct Symbiosis

Now, consider a second model of symbiosis between three different species, where the carrying capacity of the $X(t)$ populations depend on both a fixed factor and a variable factor involving $X(t)$ and $Y(t)$, reflecting the direct symbiotic influence between them. Similarly, the carrying capacity of $Y(t)$ species in the presence of the predator $Z(t)$. Thus, as argued in Section III, using appropriate scaling and normalization of symbiotic carrying capacities the modified model system can be expressed as

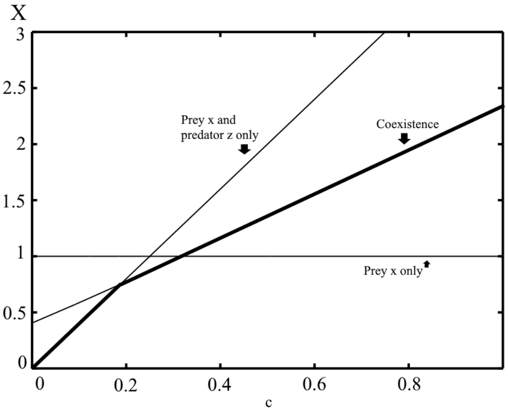

Fig. 3: The bifurcation diagram of the x population vs the predator death rate parameter c. The other parameters are $a = d = 0.25$, $\alpha = 1$. The thick curve corresponds to stable steady states while the thin curve corresponds to unstable steady states. The system shows the existence of trans-critical bifurcation at $c = c* = 0.1875$.

$$\begin{aligned} \frac{dX}{dt} &= AX(1 - \frac{X}{1+\mu XY}) - BXZ, \\ \frac{dY}{dt} &= CY(1 - \frac{Y}{1+\nu XY}) - DYZ, \\ \frac{dZ}{dt} &= -EZ + FXZ + GYZ, \end{aligned} \tag{13}$$

The parameters A and C represent the logistic growth rates of the respective prey species. The parameters B and D denote the predation death rates. The parameter E is the natural death rate of the predator. The parameters F and G correspond the growth rates of the predator resulting from interactions with the respective prey species. The parameters $\mu > 0$ and $\nu > 0$ show how much symbiosis affect the respective species' carrying capacity.

Before advancing with stability analysis, some re-scaling needs to take place so as to be better able to understand how the parameters affect the dynamics. To this end, the variables are scaled as: $x = X, y = Y, z = \frac{B}{A}Z, t_{new} = at_{old}$. We now redefine the parameters as follows: $a = \frac{C}{A}, b = \frac{D}{B}, c = \frac{E}{A}, d = \frac{F}{A}, e = \frac{G}{A}, \mu = \alpha, \nu = \beta$. Moreover, under the assumptions 1, 2, and 3 for indirect model, we have

$$\begin{aligned} \frac{dx}{dt} &= x(1 - \frac{x}{1+\alpha xy}) - xz, \\ \frac{dy}{dt} &= ay(1 - \frac{y}{1+\alpha xy}) - yz, \\ \frac{dz}{dt} &= -cz + dz(x+y). \end{aligned} \tag{14}$$

Note that our parameters a, c, d, and α are positive, and for ecological study, the region of interest in $\mathcal{R}^3$ remains in $H = \{(x, y, z) \in \mathcal{R}^3 | \; x \geq 0, y \geq 0, z \geq 0\}$.

A. *Steady states and stability Analysis*

There are eight steady states of model system (14):
(i) complete extinction $(0, 0, 0)$,
(ii) the prey x only $(1, 0, 0)$,
(iii) the prey y only $(0, 1, 0)$,

(iv) the prey x and predator z only $(\frac{c}{d}, 0, \frac{d-c}{d})$,
(v) the prey y and predator z only $(0, \frac{c}{d}, \frac{a(d-c)}{d})$,
(vi) the prey x and y only, and the two steady states are $(\frac{1+\sqrt{1-4\alpha}}{2\alpha}, \frac{1+\sqrt{1-4\alpha}}{2\alpha}, 0)$ and $(\frac{1-\sqrt{1-4\alpha}}{2\alpha}, \frac{1-\sqrt{1-4\alpha}}{2\alpha}, 0)$, and
(vii) coexistence, $(\bar{x}, \bar{y}, \bar{z})$, which is the solution to the system of equations

$$\begin{aligned} 1 - \frac{\bar{x}}{1+\alpha\bar{x}\bar{y}} &= \bar{z}, \\ a(1 - \frac{\bar{y}}{1+\alpha\bar{x}\bar{y}}) &= \bar{z}, \\ \frac{c - d\bar{x}}{d} &= \bar{y}. \end{aligned} \tag{15}$$

More specifically, when $a \neq 1$, the coexistence steady state is

$$\begin{aligned} \bar{x}_{\pm} &= \frac{d(a+1) + c\alpha(a-1) \pm q}{2d\alpha(a-1)}, \\ \bar{y}_{\pm} &= \frac{d(a+1) + c\alpha(1-a) \pm q}{2d\alpha(1-a)}, \\ \bar{z}_{\pm} &= \frac{a((4d^2 + \alpha c^2 - cd)(a+1) \pm cq)}{2(d^2(a+1)^2 + a\alpha c^2)}, \end{aligned} \tag{16}$$

where

$$q = \sqrt{(4d^2\alpha + (d - c\alpha)^2)(a-1)^2 + 4ad^2}. \tag{17}$$

We denote these coexistence steady states as $(\bar{x}_-, \bar{y}_-, \bar{z}_-)$ and $(\bar{x}_+, \bar{y}_+, \bar{z}_+)$, corresponding to the respective signs in front of q in (16). It is easy to see when $a = 1$, the coexistence steady state is $(\frac{c}{2d}, \frac{c}{2d}, \frac{4d^2+c^2\alpha-2cd}{4d^2+c^2\alpha})$, which is ecologically feasible when $\alpha > \frac{2d(c-2d)}{c^2}$. The following lemma further guarantees the existence of feasible coexistence steady state.

Lemma 2: For system (14) with positive parameters α, a, c, d and $a \neq 1$, the coexistence steady states (16)

(a) $(\bar{x}_+, \bar{y}_+, \bar{z}_+)$ is infeasible, and
(b) $(\bar{x}_-, \bar{y}_-, \bar{z}_-)$ is feasible if and only if one of the following set of conditions is met:
  i. $a \neq 1$ and $d < c < 2d$;
  ii. $a \neq 1$, $c > 2d$, and $\alpha > \frac{2d(c-2d)}{c^2}$;
  iii. $a < 1$, $c < d$, and $a + \frac{c}{d} > 1$;
  iv. $1 < a < \frac{d}{d-c}$ and $c < d$.

Proof: By the similar arguments as we did in Lemma 1, we can show that when $a < 1$, $\bar{x}_+ < 0$ and $\bar{y}_+ > 0$ and when $a > 1$, $\bar{x}_+ > 0$ and $\bar{y}_+ < 0$. Thus $(\bar{x}_+, \bar{y}_+, \bar{z}_+)$ is not biologically significant.

Now, for part (b), ($\Longleftarrow$) is trivial.

($\Longrightarrow$) Since we know the conjugates of numerators of $\bar{x}_-, \bar{y}_-$, and $\bar{z}_-$ are always positive, we can use them to find the conditions for when $(\bar{x}_-, \bar{y}_-, \bar{z}_-)$ is in positive octant.

The numerator of $\bar{x}_-$ multiplied by its conjugate gives $4d\alpha(a-1)(a(c-d)+d)$. The relevant part is $(a-1)(a(c-d)+d)$. The numerator of $\bar{y}_-$ multiplied by its conjugate is $4d\alpha(1-a)(c+d(a-1))$. The relevant part is $(1-a)(c+d(a-1))$. The numerator of $\bar{z}_-$ multiplied by its conjugate is $4a^2(-2cd+4d^2+c^2\alpha)((a+1)^2d^2+ac^2\alpha)$. The relevant part is $(-2cd+4d^2+c^2\alpha)$. The component $\bar{z}_-$ is positive when $4d^2+c^2\alpha > 2cd$, which is the same as $\alpha > \frac{2d(c-2d)}{c^2}$. This condition is guaranteed if $c < 2d$.

If $a < 1$, the numerator of $\bar{x}_-$ needs to be negative and the numerator of $\bar{y}_-$ needs to be positive. Thus we need $ac+d(1-a) > 0$ and $c+ad-d > 0$, and the second inequality requires additional conditions. If $c < d$, then $c+ad > d$. If $d < c < 2d$, no other conditions are necessary. If $c > 2d$, then $\alpha > \frac{2d(c-2d)}{c^2}$ is needed to make $\bar{z}_-$ positive.

If $a > 1$, the numerator of $\bar{x}_-$ needs to be positive and the numerator of $\bar{y}_-$ needs to be negative. Thus we need $ac+d-ad > 0$ and $c+d(a-1) > 0$, while the first inequality requires additional conditions. If $c < d$, then $a(c-d)+d > 0$, which is the same as $a(d-c) < d$. If $d < c < 2d$, no other conditions are necessary. If $c > 2d$, then $\alpha > \frac{2d(c-2d)}{c^2}$ is needed to make $\bar{z}_-$ positive.

Thus we have shown the conditions for which $(\bar{x}_-, \bar{y}_-, \bar{z}_-)$ is positive. ■

Like our first model, the linear stability of these steady states is determined by considering the eigenvalues of the Jacobian matrix of the system (14),

$$\begin{aligned} &J(x,y,z) \\ &= \begin{bmatrix} 1 - \frac{x(2+\alpha xy)}{(1+\alpha xy)^2} - z & \frac{\alpha x^3}{(1+\alpha xy)^2} & -x \\ \frac{a\alpha y^3}{(1+\alpha xy)^2} & a - \frac{ay(2+\alpha xy)}{(1+\alpha xy)^2} - z & -y \\ dz & dz & -c + d(x+y) \end{bmatrix}, \end{aligned} \tag{18}$$

evaluated at each of these steady states.
1) Complete extinction (the zero population steady state): $x = 0, y = 0, z = 0$*:* When the Jacobian matrix (18) is evaluated at this steady state, the eigenvalues are 1, a, and $-c$. For the entire system, this means that the zero population steady state is unstable.
2) The prey x only: $x = 1, y = 0, z = 0$*:* When the Jacobian matrix (18) is evaluated at $(1, 0, 0)$, the eigenvalues are -1, a, and $d - c$. This means the prey x only steady state is unstable.
3) The prey y only: $x = 0, y = 1, z = 0$*:* When the Jacobian matrix (18) is evaluated at the steady state $(0, 1, 0)$, the eigenvalues are $1, -a$, and $d - c$. This means the prey y only steady state is unstable.
4) Prey x and predator z only: $x = \frac{c}{d}$, $y = 0$, $z = \frac{d-c}{d}$*:* When the Jacobian matrix (18) is evaluated at this steady state, the eigenvalues are $\frac{c-d+ad}{d}$ and $\frac{-c\pm\sqrt{c(c+4cd-4d^2)}}{2d}$. For this steady state to be ecologically significant, we have $d > c$, which implies $4cd - 4d^2$ is negative. Following the similar discussions as before, either $\frac{-c\pm\sqrt{c(c+4d(c-d))}}{2d}$, if $c + 4d(c-d) > 0$, or the real part of $\frac{-c\pm\sqrt{c(c+4d(c-d)}}{2d}$, if $c + 4d(c-d) < 0$, is always negative. Thus the prey x and predator z only steady state is stable when $a + \frac{c}{d} < 1$. This stability behavior is the same as in the indirect interaction model. If the population of X grows much faster than Y, and if the growth rate of Z due to the interaction with X is greater than its death rate, then the prey Y will die out.
5) Prey y and predator z only: $x = 0$, $y = \frac{c}{d}$, $z = \frac{a(d-c)}{d}$*:* When the Jacobian matrix (18) is evaluated at this steady state, the eigenvalues are $\frac{ac+d-ad}{d}$ and

$\frac{-ac\pm\sqrt{ac(ac+4cd-4d^2)}}{2d}$. For this steady state to be ecologically significant, we obtain $d > c$, which implies $4cd-4d^2$ is negative. As the same as before, either $\frac{-ac\pm\sqrt{ac(ac+4cd-4d^2)}}{2d}$ or the real part of $\frac{-ac\pm\sqrt{ac(ac+4cd-4d^2)}}{2d}$ is always negative. Thus prey y and predator z only steady state is stable when $a > \frac{d}{d-c} > 1$. This means that if the population of Y grows much faster than X, and if the growth rate of Z due to the interaction with Y is greater than its death rate, then the prey X will go extinct.

Note that this and the previous steady state cannot both be stable. That is because $a < 1$ is for the previous steady state to be stable while $a > 1$ is for this steady state to be stable. The behavior of the prey y and predator z only steady states agrees with those found in the corresponding steady state of the indirect symbiosis model.

6) Prey x and prey y only: $(\frac{1+\sqrt{1-4\alpha}}{2\alpha}, \frac{1+\sqrt{1-4\alpha}}{2\alpha}, 0)$ and $(\frac{1-\sqrt{1-4\alpha}}{2\alpha}, \frac{1-\sqrt{1-4\alpha}}{2\alpha}, 0)$: We denote the two prey species only steady states as follows:

$$(\bar{x}_1, \bar{y}_1, 0) = (\tfrac{1-\sqrt{1-4\alpha}}{2\alpha}, \tfrac{1-\sqrt{1-4\alpha}}{2\alpha}, 0) \text{ and}$$
$$(\bar{x}_2, \bar{y}_2, 0) = (\tfrac{1+\sqrt{1-4\alpha}}{2\alpha}, \tfrac{1+\sqrt{1-4\alpha}}{2\alpha}, 0).$$

Note that for either steady state to be ecologically significant, we have $0 < \alpha \leq 0.25$, which indicates $1 > \sqrt{1-4\alpha}$.

When the Jacobian matrix (18) is evaluated at the steady state $(\bar{x}_1, \bar{y}_1, 0)$, the eigenvalues are $\frac{d(1-s)-c\alpha}{\alpha}$ and $\frac{\alpha(a+1)\pm r}{-(1-s)}$, where $r = \sqrt{2a(1-s) - 8a\alpha + 4a\alpha s + (a+1)^2\alpha^2}$ and $s = \sqrt{1-4\alpha}$. The second eigenvalue $\frac{\alpha(a+1)+r}{-(1-s)}$ is obviously always negative with our assumptions that the parameters a and α are positive and $1 > \sqrt{1-4\alpha}$. The third eigenvalue $\frac{\alpha(a+1)-r}{-(1-s)}$ is negative when $\alpha(a+1) > r$, that is $2a(1-s-4\alpha+2\alpha s) < 0$. Following this, we need to have $1-4\alpha < s(1-2\alpha)$. Since $1-4\alpha > 0$ and $s(1-2\alpha) > 0$, this is equivalent to $(1-4\alpha)^2 < (s(1-2\alpha))^2$, which is the same as $1-4\alpha < 1-4\alpha+4\alpha^2$. This is always true due to our assumptions $4\alpha^2 > 0$. Thus, the third eigenvalue is always negative. This means, $(\bar{x}_1, \bar{y}_1, 0)$ is stable when the first eigenvalue $\frac{d(1-s)-c\alpha}{\alpha}$ is negative, which is when $\alpha c^2 < 2d(c-2d)$.

Similarly, when the Jacobian matrix (18) is evaluated at the steady state $(\bar{x}_2, \bar{y}_2, 0)$, the eigenvalues are $\frac{d(1+s)-c\alpha}{\alpha}$ and $\frac{-\alpha(a+1)\pm u}{1+s}$, where $s = \sqrt{1-4\alpha}$ and $u = \sqrt{2a(1+s) - 8a\alpha - 4a\alpha s + (a+1)^2\alpha^2}$. In this case, we can show that the third eigenvalue, $\frac{-\alpha(a+1)+u}{1+s}$, is always positive. To do this, we need $u > \alpha(a+1)$, which is true if $2a(1+s) - 8a\alpha - 4a\alpha s = 2a(1+s-4\alpha-2\alpha s) = 2a((1-4\alpha) + (1-2\alpha)s) > 0$. It is obvious with our assumptions. Thus, $(\bar{x}_2, \bar{y}_2, 0)$ is always unstable.

Ecologically, this is reasonable because a high predator death and low growth would result in the extinction of the predator. The prey populations support each other's growth, but not to the extent that there is an excess of prey for the predator to consume.

7) Behavior of Coexistence Steady State: As demonstrated in Lemma 2, the coexistence steady state exists when specific parameter conditions are met. The following theorem establishes the stability of the coexistence steady state in our direct mutualism model (14).

Theorem 2: For the parameter values a, c, d, and α satisfying the conditions in Lemma 2, the steady state $(\bar{x}, \bar{y}, \bar{z}) = (\bar{x}_-, \bar{y}_-, \bar{z}_-)$ is asymptotically stable if

$$\frac{(1 + \alpha\bar{x}\bar{y} - 2a\alpha\bar{y}^2)}{d(\bar{x}^2 + a\bar{y}^2)(1 + \alpha\bar{x}\bar{y})^2} > \frac{(-1 + \bar{x} + \alpha\bar{x}^2\bar{y}(\alpha\bar{y} - 1))}{\bar{x}^2(\bar{x} + a\bar{y})}. \tag{19}$$

Proof: First, we evaluate the Jacobian matrix (18) at $x = \bar{x}$, $y = \bar{y}$, and $z = \bar{z}$ and obtain

$$\begin{aligned} & J(\bar{x}, \bar{y}, \bar{z}) \\ = & \begin{bmatrix} 1 - \frac{2\bar{x}}{1+\alpha\bar{x}\bar{y}} - \bar{z} & \frac{\alpha\bar{x}^2}{(1+\alpha\bar{x}\bar{y})^2} & -x \\ \frac{a\alpha\bar{y}^2}{(1+\alpha\bar{x}\bar{y})^2} & a - \frac{2a\bar{y}}{1+\alpha\bar{x}\bar{y}} - \bar{z} & -\bar{y} \\ d\bar{z} & d\bar{z} & -c + d(\bar{x}+\bar{y}) \end{bmatrix}, \end{aligned}$$

whose characteristic equation is

$$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0, \tag{20}$$

where

$$\begin{aligned}
a_1 &= 2\bar{z} + \frac{(\bar{x} + a\bar{y})(2 + \alpha\bar{x}\bar{y})}{(1 + \alpha\bar{x}\bar{y})^2} + c - d(\bar{x} + \bar{y}) - a - 1, \\
a_2 &= a - c - ac + d(\bar{x} + \bar{y}) + ad(\bar{x} + \bar{y}) - \bar{z} - a\bar{z} \\
&\quad + 2c\bar{z} + d\bar{x}\bar{z} + d\bar{y}\bar{z} - 2d(\bar{x} + \bar{y})\bar{z} + \bar{z}^2 \\
&\quad + \frac{(2 + \alpha\bar{x}\bar{y})(-a\bar{x} + c\bar{x} - a\bar{y} + ac\bar{y} - d\bar{x}(\bar{x} + \bar{y}))}{(1 + \alpha\bar{x}\bar{y})^2} \\
&\quad + \frac{(2 + \alpha\bar{x}\bar{y})(-ad\bar{y}(\bar{x} + \bar{y}) + \bar{x}\bar{z} + a\bar{y}\bar{z})}{(1 + \alpha\bar{x}\bar{y})^2} \\
&\quad + \frac{a\bar{x}\bar{y}(2 + \alpha\bar{x}\bar{y})^2 - a\alpha^2\bar{x}^3\bar{y}^3}{(1 + \alpha\bar{x}\bar{y})^4}, \\
a_3 &= ac - ad(\bar{x} + \bar{y}) - c\bar{z} - ac\bar{z} - ad\bar{x}\bar{z} - d\bar{y}\bar{z} \\
&\quad + d(\bar{x} + \bar{y})\bar{z} + ad(\bar{x} + \bar{y})\bar{z} + c\bar{z}^2 + d\bar{x}^2\bar{z}^2 + d\bar{y}\bar{z}^2 \\
&\quad - d(\bar{x} + \bar{y})\bar{z} + \frac{2d\bar{x}\bar{y}\bar{z} + 2ad\bar{x}\bar{y}\bar{z} + d\alpha\bar{x}^3\bar{y}\bar{z}}{(1 + \alpha\bar{x}\bar{y})^2} \\
&\quad + \frac{d\alpha\bar{x}^2\bar{y}^2\bar{z} + ad\alpha\bar{x}^2\bar{y}^2\bar{z} + ad\alpha\bar{x}\bar{y}^3\bar{z}}{(1 + \alpha\bar{x}\bar{y})^2} \\
&\quad + \frac{(2 + \alpha\bar{x}\bar{y})((c - ac)(\bar{x} + \bar{y}) + (ad - d)(\bar{x} + \bar{y})^2)}{(1 + \alpha\bar{x}\bar{y})^2} \\
&\quad + \frac{ad\alpha^2\bar{x}^3\bar{y}^3(\bar{x} + \bar{y}) + ac\bar{x}\bar{y}(2 + \alpha\bar{x}\bar{y})^2}{(1 + \alpha\bar{x}\bar{y})^4} \\
&\quad - \frac{ac\alpha^2\bar{x}^3\bar{y}^3 + ad\bar{x}\bar{y}(\bar{x} + \bar{y})(2 + \alpha\bar{x}\bar{y})^2}{(1 + \alpha\bar{x}\bar{y})^4}.
\end{aligned}$$

Using (15), we can simplify the terms to

$$\begin{aligned}
a_1 &= \frac{\bar{x} + a\bar{y}}{(1 + \alpha\bar{x}\bar{y})^2}, \\
a_2 &= \frac{(d\bar{x}\bar{z} + d\bar{y}\bar{z})(1 + \alpha\bar{x}\bar{y})^3 + \bar{x}^2(1 + \alpha\bar{x}\bar{y} - 2a\alpha\bar{y})}{(1 + \alpha\bar{x}\bar{y})^3}, \\
a_3 &= \frac{d\bar{x}\bar{y}\bar{z}(1 + a + \alpha\bar{x}^2 + a\alpha\bar{y}^2}{(1 + \alpha\bar{x}\bar{y})^2}.
\end{aligned}$$

Therefore, according to the Routh-Hurwitz conditions, we can conclude that $(\bar{x}, \bar{y}, \bar{z})$ is stable if $a_1 > 0$, $a_3 > 0$, and $a_1a_2 > a_3$. Since $\bar{x}, \bar{y}, \bar{z}$, and all parameters are positive, it is evident that $a_1 > 0$ and $a_3 > 0$. Also, $a_1a_2 - a_3 = \bar{x}^2(\bar{x}+a\bar{y})(1+\alpha\bar{x}\bar{y}-2a\alpha\bar{y}^2) - d(\bar{x}^2+a\bar{y}^2)(1+\alpha\bar{x}\bar{y})^2(-1+\bar{x}+\alpha\bar{x}^2\bar{y}(\alpha\bar{y}-1)) > 0$, if the stability inequality (19) hold. ■

To better understand the solution behavior, we present the time plots and phase portraits of the solution for different values of c. Fig. 4 shows the time series plots of the stable and unstable periodic solutions for different values of c, and Fig. 5 presents the z versus x diagram and the z versus y diagram.

It is evident, from these two figures, that when the death rate parameter $c = 0.55$, the trajectory spirals in toward the coexistence steady state, and when $c = 0.60$ the trajectory spirals out from the coexistence steady state.

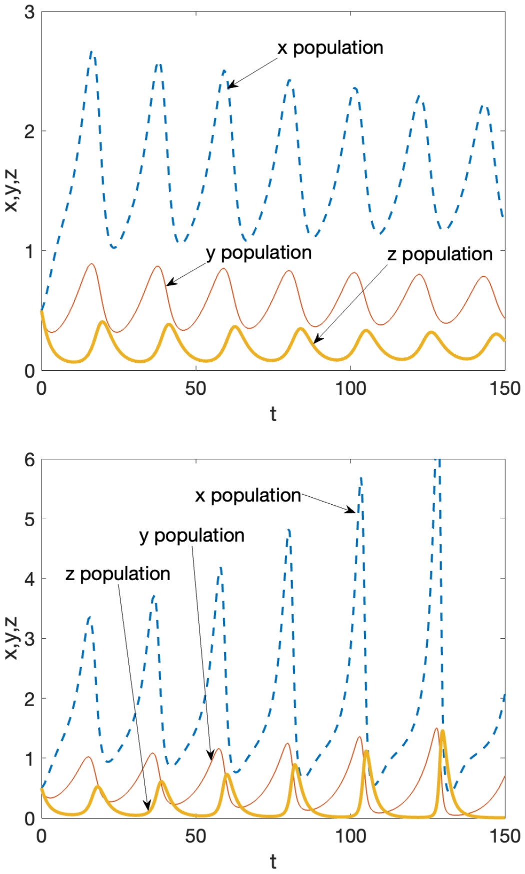

Fig. 4: The time series plots of x, y, z vs. t of coexistence steady state using parameters $a = d = 0.25$, $\alpha = 1$, and $c = 0.55$ (bottom of the left) / $c = 0.6$ (top of the right) with initial conditions are $(0.5, 0.5, 0.5)$

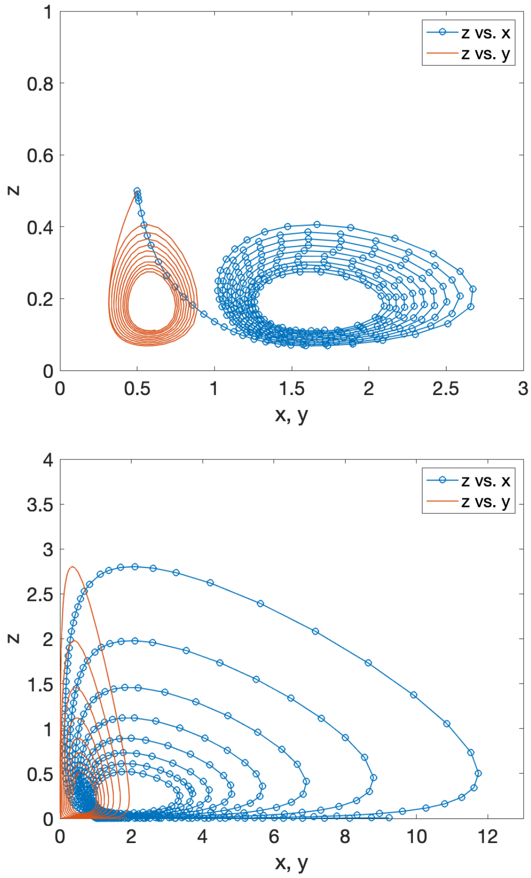

Fig. 5: The phase portraits of z vs. x and z vs. y of coexistence steady state with parameters $a = d = 0.25$, $\alpha = 1$, and $c = 0.55$ (top) / $c = 0.6$ (bottom) using initial conditions $(0.5, 0.5, 0.5)$

Moreover, using XPPAUT (see, [17]), we plot the phase diagram in Fig. 6, for the death rate parameter $c = 0.56$, which illustrates the existence of an unstable periodic solution.

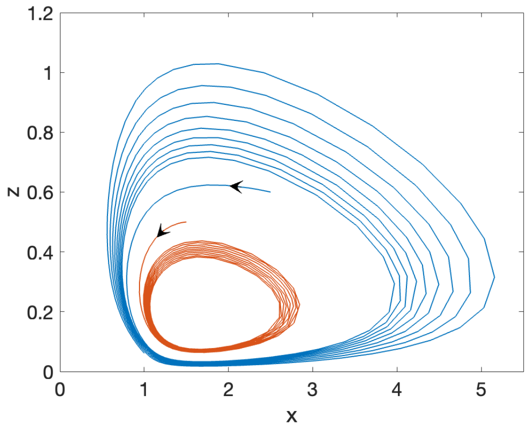

Fig. 6: The phase portrait of z vs. x with $c = 0.56, a = d = 0.25$ and $\alpha = 1$. The initial conditions are $(2.5, 0.5, 0.6)$ and $(1.5, 0.7, 0.5)$ respectively

Ecologically, this suggests that as the predator death rate increases, fewer prey are killed, allowing all three species to persist. However, after a certain point, the prey population experiences unchecked growth, leading to system instability.

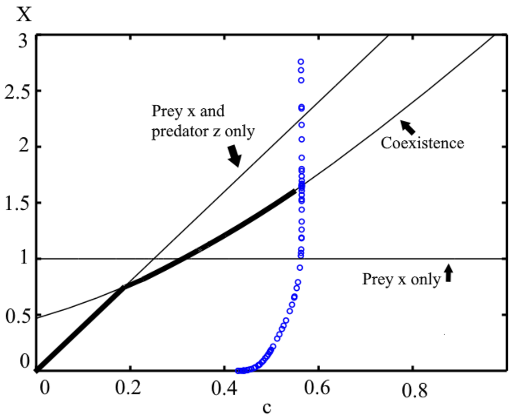

Fig. 7: The bifurcation diagram of the x population vs the predator death rate parameter c. The thick curve corresponds to stable steady states while the thin curve corresponds to unstable steady states. The open circle denotes the maximum and minimum values of the unstable periodic solution branch which begins at $c = 0.45$ and terminates at the Hopf bifurcation value $c = 0.5642$.

This is likely due to the enhanced mutualistic impact on carrying capacity when direct interactions occur between the symbiotic species.

B. Bifurcations

Now we look at the dynamics of model system (14). Because of the complexity of computing eigenvalues of the Jacobian matrix (18) explicitly, we adopt AUTO in XPPAUT [17], as we did in the indirect symbiosis model. Fig. 7 illustrates that as the death rate parameter c increases, the system undergoes both a trans-critical bifurcation and a Hopf bifurcation, with the other parameters set to $a = d = 0.25$ and $\alpha = 1$. The red curve represents a stable steady state, while the black curve indicates an unstable steady state. For the unstable periodic solutions, the maximum and minimum values of $x(t)$ are shown as blue open circles. Along the vertical axis, from bottom to top, the starting positions are the prey x and the predator z only steady state, the coexistence steady state, and the x only steady state. It is noteworthy that as c increases the system goes through a transcritical bifurcation at $c = 0.1875$, and then the periodic solution branch begins at $c = 0.45$. The open circle denotes the maximum and minimum values of the unstable periodic solution branch which begins at $c = 0.45$ and terminates at the Hopf bifurcation value $c = 0.5642$.

Ecologically, we can say that when the predator's death rate parameter is sufficiently small, the predator population is large enough to cause one of the prey species to go extinct from over-hunting. In this case, the prey x goes extinct. Once this happens, there is no longer an abundance of food for the predator and their population stabilizes with the remaining prey population.

Conversely, when the predator death rate is too large, there are not enough predators to control the prey population and they grow uncontrollably. The unstable limit cycles prior to the Hopf bifurcation represent the possibility of unstable growth for the populations given sufficiently large initial conditions.

V. CONCLUSION

In this paper, we have explored two symbiosis models that simulate the effects of indirect and symmetrically direct symbiosis in a two prey, one predator system. These models can alternatively be interpreted as two mutualistic species resisting the impact of a predator, which contrasts with previously studied models of mutualism and predation (e.g. [18], [20], [21]). In both models, at most one species will go extinct. They also share a transcritical bifurcation (exchange stability) arise as the predator death rate parameter c increases.

As anticipated, the models with different functional responses exhibit distinct behaviors. The symbiosis involving indirect interactions maintains the stability fo the coexistence steady state, similar to the classical predator-prey model with a constant carrying capacity [18], [19]. Ultimately, the coexistence steady state becomes unstable when the predator death rate increases. In contrast, the symbiosis with direct interaction can lead to unstable limit cycles as the predator death rate parameter rises. This unbounded growth is akin to other mutualism models. Future research will discuss commensalism, parasitism as well as the specific mutualistic cases, such as the multi-species herds using a square root functional response in [12], [13].

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