A THREE-SPECIES MODEL WITH

PREDATOR-PREY, COMPETITION, AND MUTUALISTIC INTERACTIONS

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A three-species model with predator-prey, competition, and mutualistic interactions

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Abstract

This research is inspired by Brown, Bruder and Kummel's research project on the predator-prey interaction of aphids and ladybugs on yucca plants. An important feature of this study system is that it contains ants as a third species. Therefore, this ecological system is composed of a predator-prey relationship between the ladybugs and aphids, a competitive relationship between the ladybugs and ants, and a mutualistic relationship between the aphids and ants.

Most existing mathematical models study one type of interaction or they focus on three species and study a tri-trophic food chain. We develop and analyze a new mathematical model that includes the predator-prey interaction as well as the competitive and mutualistic aspects of the system. The predator-prey interaction is described by a Rosenzweig-MacArthur model, which assumes logistic growth of the predator. To build a mathematical model for the competitive and mutualistic relationships, we use a modified Lotka-Volterra model and include terms representing competition and mutualism.

Since the three-species model is substantially harder to analyze, we first study the three submodels, i.e. the predator-prey, competition, and mutualism model. Then we use the submodel results to explore the three-species model and the significance of its parameter values. With the help of Mathematica and MATLAB, we construct phase planes and time series plots, find the equilibria of the systems, and determine the stability of each equilibrium.

1 Introduction

Population biology is the study of ecological communities with numerous species and their interactions. To understand a complex ecological community, researchers focus on the population biology of a simpler system with two or three species first. By studying the dynamics of the system, researchers can understand, explain, and predict population size changes from someone's back garden to a national forest or a much bigger community. In addition, studying a specific system may provide insights to other similar ecological systems [7].

Most existing mathematical models study one type of interaction, or they focus on three species and study a tri-trophic food chain [3]. We will develop and analyze a new mathematical model that includes the predator-prey interaction

as well as the competitive and mutualistic aspects of the system. This will provide a systematic extension of the existing theory of predator-prey dynamics, competition, and mutualism.

A previous research project by Kummel and et al [1][2] studied the population dynamics of a predator-prey system of ladybugs and aphids on yucca plants in a high prairie ecosystem along the Front Range of the Rocky Mountains [1][2]. An important feature of this system is that it contains ants as a third species. While the ladybugs prey on aphids, the ants tend to the aphid colonies and feed off the aphids' feces (honeydew). They protect the aphids from being eaten by the ladybugs by pushing the ladybugs off the plant. This is called a protection mutualism. The ant-ladybug interaction may be viewed as competitive in nature. The three-species relationship is shown in Figure 1. Our goal in this research project is to model these primary types of interaction between the three species. Through analyses of the submodels, our estimates will enable us to better understand the dynamics between three species and the factors that influence the dynamics.
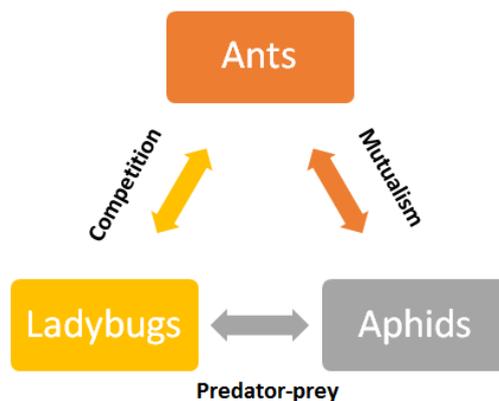

Figure 1: The nature of the interactions between the three species

2 Literature Review

Predator-prey interaction, competition and mutualism are three important interactions in ecology. Each depicts the interactions between pairs of species [7]. Historically, there have been numerous studies on predator-prey dynamics and competition, but not as many on mutualism.

Predator-prey interaction involves the action of predation. One species consumes the other species. For example, it could be an animal eating another animal, or an animal eating a plant [7]. The most well-known model is the Lotka-Volterra model. Lotka first developed the equations for the theory of chemical periodic reactions, and later used it to analyze predator-prey interactions [8] [9]. With assumptions, the simplest version of Lotka-Volterra model is adaptable to a predator-prey model. Furthermore, the system of equations can be altered to be population density dependent and correspond to different types of functional responses. By analyzing the stability of equilibria in the

predator-prey system, we can predict the behavior of the two species and if the two species will coexist or become extinct.

The Rosenzweig-MacArthur predator-prey model uses population density as the unit of variables and makes model assumptions about logistic growth, death rate and conversion rate from prey to predator [10] [11]. The model is shown below [11]:

$$x' = rx(1 - \frac{x}{K}) - \frac{sxy}{1 + s\tau x}$$

$$y' = -cy + d\frac{sxy}{1 + s\tau x} \ ,$$

where x denotes prey density, and y denotes predator density. r is the growth rate for the prey, K is the carrying capacity for the prey, c is the death rate for the predator, d is the conversion rate from prey to predator, and $\frac{sx}{1+s\tau x}$ is the per predator kill rate. Therefore,

$$x' = \text{intrinsic growth rate adjusted for logistic growth} - \text{kill rate due to y}$$

$$y' = -\text{death rate} + \text{reproduction rate} \ .$$

The stability of the equilibria is solely dependent on the isoclines in the phase planes, implying that the equilibria could be stable or unstable with different parameter combinations [10] [11].

Competition and mutualism are also two common interactions between two species. If each species has a negative effect on the other because both species eat the same animal or plant, the interaction is called competition. If each species has a postive effect on the other, i.e. they benefit from each other, the interaction is called mutualism [7].

Gause extensively studied the Lotka-Volterra model and modified it to model competition [7] [12]. By adding a coefficient representing the negative effect of one species on the other, the modified Lotka-Volterra model can depict the behavior of competition. The model is shown below [7]:

$$\frac{dN_1}{dt} = r_1 N_1 (1 - \frac{N_1}{K_1}) - \alpha_{12} N_1 N_2$$

$$\frac{dN_2}{dt} = r_2 N_2 (1 - \frac{N_2}{K_2}) - \alpha_{21} N_1 N_2 \ ,$$

where N_1, N_2 are the densities of the two species, r_1, r_2 are the intrinsic growth rates, K_1 and K_2 are the carrying capacities, and α represents the effect between two species. Furthermore, there have been extensions of the competition models built for more specific scenarios, like competition for space and competition for two resources [13] [7]. Similarly, mutualism can be modeled by adding a coefficient representing the positive effect of one species on the other [14]. However, there is not much literature on further research on the mutualistic model. So far, mutualism is the least studied interaction compared to predator-prey interaction and competition.

After many studies on 2-species interactions, researchers started to take interest in 3-species interaction modeling. Building on the work of Rosenzweig [15], various researchers have extensively studied the behavior of such systems, for example, Freedman and Waltman [16], Mccann and Yodzis [18]. Moreover, there also have been studies on three interacting predator-prey populations, with

3

two-predator-one-prey system or one-predator-two-prey system by Freedman and Waltman [17], and Pang and Wang [19]. However, Morales, Morris and Wilson pointed out that most of the previous work did not take protection mutualism into consideration [20]. In presence of a protection mutualism, the impact of the predator species on the prey species is reduced, which can lead to a larger range of dynamical outcomes of all the species [20].

Our search has not turned up any 3-species models combining predator-prey interaction, competition and mutualism in one system. Our research presents a model for the 3-species system with all three interactions, analyzes the stability of the possible equilibria, and interprets its biological implications.

3 Model derivation

In the previous field research, Kummel, Bruder and Brown studied the interaction between ladybugs and aphids on yucca plants in Colorado Springs.[1] They conducted a field survey on the population sizes of aphids, *Aphis helianthi*, and two species of ladybugs, *Coccinella septempunctata* and *Hippodamia convergens*. In addition, they conducted ladybug-free studies that allow ants and aphids to be in the same environment without the presence of ladybugs [1].

Our research is based on the three-species interaction between the aphids, ladybugs and ants exhibited in their previous study. However, our model uses a theoretical approach instead of a field approach.

3.1 The 3-species model

Our 3-species model is based on the basic Lotka-Volterra predator-prey model and the Rosenzweig-MacArthur predator-prey model. We add the third species into the system and incorporate competition and mutualistic relationships into the model. Let $x(t), y(t), z(t)$ be the density of aphids, ladybugs and ants at time t, respectively. We propose the following model:

$$Aphids: x' = r_1 x(1 - \frac{x}{k_1}) - \frac{sxy}{(1 + s\tau x)(1 + \frac{z}{k_4})} + m_1 xz$$

$$Ladybugs: y' = r_2 y(1 - \frac{y}{k_2}) + c \cdot \frac{sxy}{(1 + s\tau x)(1 + \frac{z}{k_4})} - d_1 yz \quad (1)$$

$$Ants: z' = r_3 z(1 - \frac{z}{k_3}) + m_2 xz - d_2 yz \ ,$$

where r_1, r_2, r_3 are the maximum possible birth rates (accounts for natural birth and death) of aphids, ladybugs, and ants; k_1, k_2, k_3 represent the carrying capacities of aphids, ladybugs, and ants; $\frac{sx}{(1+s\tau x)(1+\frac{z}{k_4})}$ is the predation rate of aphids due to ladybugs; the term $(1 + \frac{z}{k_4})$ represents protection mutualism of ants for aphids; c is the conversion rate from aphids to ladybugs; d_1 and d_2 represents the ladybugs' and ants' cost from competing with one another; m_1 represents the benefit aphids receive from the ants' removal of the honeydew; m_2 represents the benefit ants receive from aphids, which is honeydew as a food source. All parameters above are positive numbers, with units as in Table 1.

We assume that both ladybugs and ants are generalists. In the absence of aphids, they survive on other food sources. Note that a specialist would not

survive in the absence of its only food source. We assume logistic growth for all three species.

Table 1: Variables, Parameters and Their Units

Variables and Parameters	Meaning	Unit
x	aphid density	$\frac{number}{area}$
y	ladybug density	$\frac{number}{area}$
z	ant density	$\frac{number}{area}$
r_1	maximum possible birth rates of aphids	$\frac{1}{time}$
r_2	maximum possible birth rates of ladybugs	$\frac{1}{time}$
r_3	maximum possible birth rates of ants	$\frac{1}{time}$
k_1	carrying capacity of aphids	$\frac{number}{area}$
k_2	carrying capacity of ladybugs	$\frac{number}{area}$
k_3	carrying capacity of ants	$\frac{number}{area}$
k_4	scaling parameter for protection mutualism	$\frac{number}{area}$
c	conversion rate from aphids to ladybugs	$dimensionless$
s	predator search rate	$\frac{area}{time}$
τ	the time for each predator to search a prey	$time$
m_1	the net effect of ants on aphids by mutualism	$\frac{area}{number \cdot time}$
m_2	the net effect of aphids on ants by mutualism	$\frac{area}{number \cdot time}$
d_1	the negative effect of ants on ladybugs by competition	$\frac{area}{number \cdot time}$
d_2	the negative effect of ladybugs on ants by competition	$\frac{area}{number \cdot time}$

3.1.1 Nondimensionalization

In order to reduce the number of parameters, we nondimensionalize the system, by making the following substitutions.

Let

$$u = \frac{x}{X}, \quad v = \frac{y}{Y}, \quad w = \frac{z}{Z}, \quad X, Y, Z > 0 \,,$$

5

where X, Y, Z are to be determined. Then

$$u' = \frac{x'}{X} = r_1 u(1 - \frac{uX}{k_1}) - \frac{suvY}{(1 + s\tau uX)(1 + \frac{wZ}{k_4})} + m_1 uwZ$$

$$v' = \frac{y'}{Y} = r_2 v(1 - \frac{vY}{k_2}) + \frac{csuXv}{(1 + s\tau uX)(1 + \frac{wZ}{k_4})} - d_1 vwZ$$

$$w' = \frac{z}{Z} = r_3 w(1 - \frac{wZ}{k_3}) + m_2 uXw - d_2 Yvw \ .$$

Let

$$K_1 = \frac{k_1}{X}, \ K2 = \frac{k_2}{Y}, \ K_3 = \frac{k_3}{Z}, \ s\tau X = 1, \ cX = Y, \ sY = \mu, \ Y = \frac{\mu}{s}, \ K_4 = \frac{k_4}{Z} \ ,$$

$$M = m_1 z, \ C = d_1 Z, \ m_2 X = m_1 Z, \ d_2 Y = d_1 Z \ ,$$

then

$$u' = r_1 u(1 - \frac{u}{K_1}) - \frac{\mu uv}{(1 + u)(1 + \frac{w}{K_4})} + Muw$$

$$v' = r_2 v(1 - \frac{v}{K_2}) + \frac{\mu uv}{(1 + u)(1 + \frac{w}{K_4})} - Cvw$$

$$w' = r_3 w(1 - \frac{w}{K_3}) + Muw - Cvw \ .$$

Let

$$T = r_1 t \ ,$$

so that

$$\frac{du}{dT} = \frac{du}{dt}\frac{dt}{dT} = \frac{1}{r_1}\frac{du}{dt} \ .$$

Then

$$\frac{du}{dT} = u(1 - \frac{u}{K_1}) - \frac{\frac{\mu}{r_1}uv}{(1 + u)(1 + \frac{w}{K_4})} + \frac{M}{r_1}uw$$

$$\frac{dv}{dT} = v(1 - \frac{v}{K_2}) + \frac{\frac{\mu}{r_1}uv}{(1 + u)(1 + \frac{w}{K_4})} - \frac{C}{r_1}vw$$

$$\frac{dw}{dT} = \frac{r_3}{r_1}w(1 - \frac{w}{K_3}) + \frac{M}{r_1}uw - \frac{C}{r_1}vw \ .$$

After combining parameters and renaming them, the nondimensionalized 3-species model is given by,

$$x' = x(1 - \frac{x}{K_1}) - \frac{\mu xy}{(1 + x)(1 + \frac{z}{K_4})} + Mxz$$

$$y' = r_2 y(1 - \frac{y}{K_2}) + \frac{\mu xy}{(1 + x)(1 + \frac{z}{K_4})} - Cyz \qquad (2)$$

$$z' = r_3 z(1 - \frac{z}{K_3}) + Mxz - Cyz \ .$$

Variables and Parameters	Meaning
x	aphid density after nondimensionalization
y	ladybug density after nondimensionalization
z	ant density after nondimensionalization
r_2	modified birth rates of ladybugs
r_3	modified birth rates of ants
K_1	modified carrying capacity of aphids
K_2	modified carrying capacity of ladybugs
K_3	modified carrying capacity of ants
K_4	modified scaling parameter for protection mutualism
μ	modified encounter/killing rate of predator and prey
M	modified net effect of ants on aphids by mutualism
C	modified negative effect of ants on ladybugs by competition

Table 2: Variables and Parameters after Nondimensionalization

From the 3-species model, three submodels can be derived as we set x, y, z to be zero respectively. When we set $z = 0$, there are no ants in the system, implying that aphids and ladybugs are the only active species in the system. Thus, we have a predator-prey submodel. Similarly, when we set $x = 0$, there are no aphids in the system, implying that ladybugs and ants are the only active species in the system. Thus, we have a competition submodel. Last, when we set $y = 0$, there are no ladybugs in the system, implying that aphids and ants are the only active species in the system. Thus, we have a mutualistic submodel.

The three cases are given below. We will discuss the basic dynamical properties and the equilibria of each submodel before returning to our analysis of the 3-species model.

4 Mathematical Definitions

To study the three-species model and its submodels, we use the following properties.

4.1 Positivity of x, y and z

By our assumptions, x, y, z are the densities of aphids, ladybugs and ants. Their values can only be non-negative numbers since the population density would not make sense if it was negative.

4.2 Equilibrium

An equilibrium is the solution of the system as we set the rates of change, x', y', and z', equal to zero. Equilibria are also called steady-state solutions in other applied mathematical fields. For example, if we set $x'(t) = 0$, at an equilibrium point, the rate of change for $x(t)$ is zero.

Definition 4.1. *Consider a system of ordinary differential equations*

$$x' = F(x) \tag{3}$$

with $x(t) \in \mathbb{R}^n$ and $F : \mathbb{R} \to \mathbb{R}^n$. F is continuous.
  $x^* \in \mathbb{R}^n$ is called an equilibrium of equation (3), x' if

$$F(x^*) = 0$$

[6].

4.2.1 Stability

Equilibria may be classified as either stable or unstable. For the stable equilibrium, the neighboring states are attracted to it. Once x reaches the equilibrium, it stays there for all time. Even if the system is pushed away from the equilibrium by a little, x will come back to the stable equilibrium point. For the unstable equilibrium, the equilibrium displays a repelling nature. Once x reaches the equilibrium, it will stay there. However, if x is pushed away from the unstable equilibrium, x will not come back to the unstable equilibrium point [5].

Locally stable equilibrium

Definition 4.2. *An equilibrium x^* of x' is called locally stable if and only if the following holds:*
  For any $\epsilon > 0$ there exists some $\delta > 0$ such that $||x(t) - x^*|| < \epsilon$ for $t > 0$ whenever x is a solution to x' and $||x(0) - x^*|| < \delta$.

Locally asymptotically stable equilibrium

Definition 4.3. *A locally stable equilibrium x^* is called locally asymptotically stable if and only if there exists some $\delta > 0$ such that $x(t) \to x^*$ for $t \to \infty$ whenever x is a solution to x' and $||x(0) - x^*|| < \delta$.*

Unstable equilibrium

Definition 4.4. *An equilibrium is unstable if and only if it is not locally stable, i.e., if and only if the following holds.*
  There exists some $\epsilon > 0$ and a sequence x_n of solution to x' and a sequence $t_n > 0$ such that $||x_n(0) - x^*|| \to 0, n \to \infty$, but $||x(t_n) - x^*|| > \epsilon$ for all $n \in \mathbb{N}$.

4.3 Forward Invariance

Definition 4.5. *Let $v' = F(v), v = (x, y, z)$. A set $U \in \mathbb{R}^3$ is said to be forward invariant under F if for any initial condition $(x_0, y_0, z_0) \in U$, we have $(x(t), y(t), z(t)) \in U$ for all $t > 0$.*

If an initial point in the system starts as non-negative and it cannot become negative over time, then the system is forward invariant. This is essential in our model since the population densities of aphids, ladybugs and ants have to be non-negative numbers, otherwise the solution of the system would not make biological sense.

5 The Predator-Prey Submodel - Aphids, Ladybugs

The nondimensionalized predator-prey model is given by

$$
\begin{aligned}
x' &= x(1 - \frac{x}{K_1}) - \frac{\mu xy}{1+x} \\
y' &= r_2 y(1 - \frac{y}{K_2}) + \frac{\mu xy}{1+x} \quad .
\end{aligned}
\tag{4}
$$

By setting $z = 0$, we get the predator-prey submodel, which depicts the predator-prey interaction between ladybugs and aphids, as seen in Figure 1. By studying this submodel, we will investigate how the system behaves without ants.

5.1 Basic dynamical properties

Theorem 5.1. Forward invariance. *If $x(0), y(0) \geq 0$ in (4), $\mathbb{R}^2_+$ is forward invariant.*

Proof. When $x = 0$, $x' = x(1 - \frac{x}{K_1}) - \frac{\mu xy}{1+x} = 0$, implying that the rate of change for $x(t)$ is zero when $x(t) = 0$. Thus, when $x(t) = 0$, the value of $x(t)$ cannot become negative. Since $x' = \frac{dx}{dt} = x(1 - \frac{x}{K_1}) - \frac{\mu xy}{1+x}$, x is differentiable with respect to time. Then $x(t)$ must be continuous. Therefore, when $x(t)$ is positive, it has to go through $x(t) = 0$ to become negative. But once $x(t) = 0$, it can not become negative.

Similarly, when $y = 0$, $y' = r_2 y(1 - \frac{y}{K_2}) + \frac{\mu xy}{1+x} = 0$, implying that the rate of change for $y(t)$ is zero when $y(t) = 0$. Thus, when $y(t) = 0$, the value of $y(t)$ cannot become negative. Since $y' = \frac{dy}{dt} = r_2 y(1 - \frac{y}{K_2}) + \frac{\mu xy}{1+x}$, y is differentiable with respect to time. Then $y(t)$ must be continuous. Therefore, when $y(t)$ is positive, it has to go through $y(t) = 0$ to become negative. But once $y(t) = 0$, it can not become negative. □

Theorem 5.2. Boundedness of solutions [11]. *There exists $R_0 > 0$ such that for all $R \geq R_0$, the right triangle $T(R)$ with sides $x = 0$, $y = 0$ and $x + y = R$ is positively invariant.*

Proof. Since every initial point of the system $(x(0), y(0))$ is in the first quadrant, it satisfies that $(x(0), y(0)) \in Q$ where $Q = \{(x,y) : x, y \geq 0\}$. Furthermore, every initial point satisfies that $(x(0), y(0)) \in T(R)$ for some $R \geq R_0$. The following shows that all solution starting in the first quadrant are bounded for $t \geq 0$ since $(x(t), y(t)) \in T(R), t \geq 0$.

We need to show that solutions starting inside the right triangle $T(R)$ cannot go through the hypotenuse of $T(R)$, which is $x + y = R$. Thus we have to show that the rate of change of $x + y$ is negative, i.e. that $\frac{d}{dt}(x(t) + y(t)) = x'(t) + y'(t) < 0$, given that $x + y = R$.

We have

$$x' + y' = x(1 - \frac{x}{K_1}) - \frac{\mu xy}{1+x} + r_2 y(1 - \frac{y}{K_2}) + \frac{\mu xy}{1+x} = x(1 - \frac{x}{K_1}) + r_2 y(1 - \frac{y}{K_2}) \ .$$

Subsituting $y = R - x$,

$$x' + y' = x(1 - \frac{x}{K_1}) + r_2(R - x)(1 - \frac{R - x}{K_2})$$

$$= -(\frac{1}{K_1} + \frac{r_2}{K_2})x^2 + (1 - r_2 + \frac{2Rr_2}{K_2})x + (Rr_2 - \frac{R^2 r_2}{K_2}) = F(x)$$

The second derivative of the function $F(x)$ is $-\frac{2}{K_1} - \frac{2r_2}{K_2}$, which is always negative since K_1 and K_2 are positive. Thus the parabola of $F(x)$ is concave down and has a maximum.

Setting the first derivative of $F(x)$, we get $\bar{x} = -\frac{K_1(-K_2 + K_2 r_2 - 2r_2 R)}{2(K_2 + K_1 r_2)}$.

Thus

$$F(\bar{x}) = \frac{K_1 K_2 (r_2 - 1)^2 + 4r_2 R(K_1 + K_2 - R)}{4(K_2 + K_1 r_2)} < 0$$

if R is chosen large enough, implying that $\frac{d}{dt}(x(t) + y(t)) < 0$ when $x + y = R$. $\qquad \square$

5.2 Equilibria and their stability

To find the equilibria of system (4), set $x' = y' = 0$.

$$x' = x(1 - \frac{x}{K_1}) - \frac{\mu xy}{1+x} = 0$$

$$y' = r_2 y(1 - \frac{y}{K_2}) + \frac{\mu xy}{1+x} = 0$$

Using Mathematica to solve the equations, we obtain the following equilibria:

$$(K_1, 0), \ (0, K_2), \ (0, 0),$$

and at least one interior equilibrium $(\bar{x}, \bar{y})$.

Table 3: Equilibria of the predator-prey submodel

Equilibria	Eigenvalues	Stability
(0,0)	1 and r_2	always unstable
$(K_1,0)$	-1 and $\frac{r_2 + K_1(\mu + r_2)}{1 + K_1}$	always unstable
$(0,K_2)$	$1 - K_2 \mu$ and $-r_2$	stable if $\frac{1}{\mu} < K_2$
$(\bar{x}, \bar{y})$	see part(d)	see part(d)

The Jacobian Matrix of (4) is given by

$$J = \begin{bmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} \end{bmatrix} = \begin{bmatrix} 1 - \frac{2x}{K_1} + \frac{\mu xy}{(1+x)^2} - \frac{\mu y}{1+x} & -\frac{\mu x}{1+x} \\ -\frac{\mu xy}{(1+x)^2} + \frac{\mu y}{1+x} & \frac{\mu x}{1+x} - \frac{r_2 y}{K_2} + r_2(1 - \frac{y}{K_2}) \end{bmatrix} \ .$$

Substituting the equilibria into the Jacobian Matrix, we get the following results.

10

(a) $E_1 = (0,0)$

Substituting (0,0) into the Jacobian matrix, we get

$$J_{(0,0)} = \begin{bmatrix} 1 & 0 \\ 0 & r_2 \end{bmatrix}$$

The eigenvalues of the Jacobian matrix are 1 and r_2. Since r_2 is always positive, both of the eigenvalues are positive. Thus, E_1 is unstable.

(b) $E_2 = (K_1, 0)$

Substituting $(K_1, 0)$ into the Jacobian matrix, we get

$$J_{(K_1,0)} = \begin{bmatrix} -1 & -\frac{K_1\mu}{1+K_1} \\ 0 & \frac{K_1\mu}{1+K_1} + r_2 \end{bmatrix}$$

The eigenvalues of the Jacobian matrix are -1 and $\frac{r_2 + K_1(\mu + r_2)}{1+K_1}$. Since K_1, μ, r_2 are always positive, both eigenvalues are positive. Thus, E_2 is unstable.

(c) $E_3 = (0, K_2)$

Substituting $(0, K_2)$ into the Jacobian matrix, we get

$$J_{(0,K_2)} = \begin{bmatrix} 1 - K_2\mu & 0 \\ K_2\mu & -r_2 \end{bmatrix}$$

The eigenvalues of the Jacobian matrix are $1 - K_2\mu$ and $-r_2$. Since r_2 is positive, $-r_2$ is negative. For this equilibrium to be stable, we must have

$$1 - K_2\mu < 0.$$

Thus, it has to be the case that

$$\frac{1}{\mu} < K_2$$

for E_3 to be locally asymptotically stable.

(d) $E_4 = (\bar{x}, \bar{y})$

By way of numerical simulations, we see that E_4 may be unstable. We give the following two examples.

Stable Equilibrium (by MATLAB)

Let
$$K_1 = 50, \ K_2 = 40, \ \mu = 0.02, \ r_2 = 0.25.$$

Substituting $(\bar{x}, \bar{y})$ into the Jacobian matrix, we get

$$J_{(\bar{x},\bar{y})} = \begin{bmatrix} -0.965931169 & -0.019601114486 \\ 0.00034317 & -0.2696013855 \end{bmatrix}$$

The eigenvalues for this Jacobian matrix are -0.96592150 and -0.269611045583. Thus the equiblibrium is stable.

Unstable equilibrium

Let

$$K_1 = 50, \ K_2 = 50, \ r_2 = 0.01, \ \mu = 0.90 \ .$$

Substituting $(\bar{x}, \bar{y})$ into the Jacobian matrix, we get

$$J_{(\bar{x},\bar{y})} = \begin{bmatrix} -0.0106541 & 0.00978012 \\ 1.01108 & -0.000219881 \end{bmatrix}$$

The eigenvalues for this Jacobian matrix are -0.105015 and 0.0941408. Thus the equiblibrium is unstable.

Unstable equilibrium

Let

$$K_1 = 100, \ K_2 = 100, \ r = 0.25, \ m = 0.35 \ .$$

Substituting $(\bar{x}, \bar{y})$ into the Jacobian matrix, we get

$$J_{(\bar{x},\bar{y})} = \begin{bmatrix} -0.701019 & 0.245787 \\ 1.70927 & -0.00421344 \end{bmatrix}$$

The eigenvalues for this Jacobian matrix are -1.08848 and 0.383251. Thus the equiblibrium is unstable.

A stable equilibrium where ladybugs and aphids could coexist is illustrated in Figure 2.
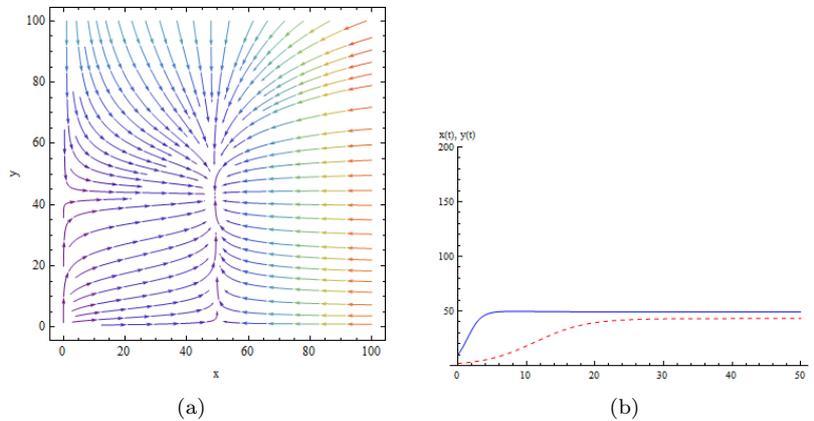

(a)   (b)

Figure 2: The parameters used in the graphs above are $K_1 = 50, K_2 = 40, \mu = 0.02, r_2 = 0.25$. The initial values are $x = 10, y = 2$. (a) shows the phase plane for the specified parameters. The x-axis represents aphids and the y-axis represents ladybugs in the phase plane graph. (b) shows the time series graph for the specified parameters. The solid line represents aphids, and the dashed line represents ladybugs in the time series plot.

A stable equilibrium where only ladybugs survive is illustrated in Figure 3.
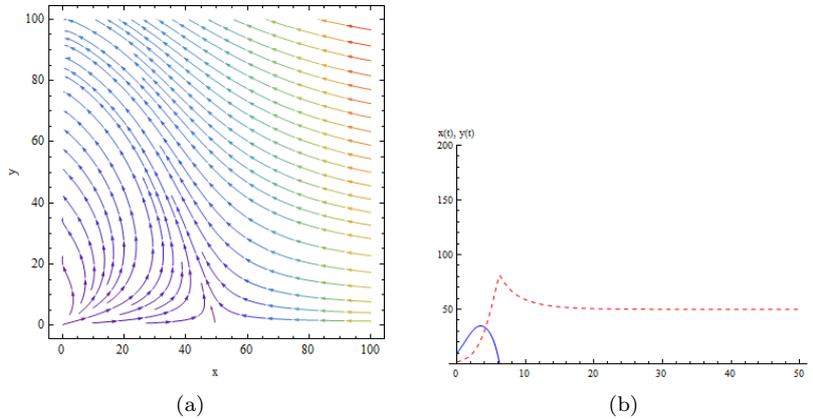
12

<p style="text-align:center;">(a)   (b)</p>

Figure 3: The parameters used in the graphs above are $K_1 = 50, K_2 = 50, \mu = 0.5, r_2 = 0.25$. The initial values are $x = 10, y = 2$. (a) shows the phase plane for the specified parameters. The x-axis represents aphids and the y-axis represents ladybugs in the phase plane graph. (b) shows the time series graph for the specified parameters. The solid line represents aphids, and the dashed line represents ladybugs in the time series plot.

By varying the predation rate, μ, we see two different behaviors of system. In Figure 2, with a relatively low predation rate, aphids and ladybugs grow to their carrying capacities over time. In Figure 3, with a relatively high predation rate, the aphid population grows initially, then goes extinct. The ladybug population grows past its carrying capacity then decreases to the carrying capacity over time.

6   Competition Submodel - Ladybugs, Ants

Let $x = 0$, then

$$
\begin{aligned}
y' &= r_2 y (1 - \frac{y}{K_2}) - Cyz \\
z' &= r_3 z (1 - \frac{z}{K_3}) - Cyz .
\end{aligned}
\tag{5}
$$

Assuming the ants are generalists (as opposed to specialists), they may survive on other food sources if there is no honey dew produced by the aphids. Thus, in the absence of aphids, the ants can still have logistic growth.

Our model tests how aphids and ladybugs would interact in absence of the protection mutualism. Naturally, they have a competitive relationship because they are competing for resources and space. By setting $x = 0$, we obtain the competition submodel, which depicts the competitive interaction between ladybugs and ants in system (5). By studying this submodel, we will investigate how the system behaves without aphids.

6.1   Basic dynamical properties

Theorem 6.1. *Forward invariance If $y(0), z(0) \geq 0$ in (5), $\mathbb{R}_+^2$ is forward invariant.*

Proof. When $y = 0$, $y' = r_2y(1 - \frac{y}{K_2}) - Cyz = 0$, implying that the rate of change for $y(t)$ is zero when $y(t) = 0$. Thus, when $y(t) = 0$, the value of $y(t)$ cannot become negative. Since $y' = \frac{dy}{dt} = r_2y(1 - \frac{y}{K_2}) - Cyz$, y is differentiable with respect to time. Then $x(t)$ must be continuous. Therefore, when $y(t)$ is positive, it has to go through $y(t) = 0$ to become negative. But once $y(t) = 0$, it can not become negative.

Similarly, when $z = 0$, $z' = r_3z(1 - \frac{z}{K_3}) - Cyz = 0$, implying that the rate of change for $z(t)$ is zero when $z(t) = 0$. Thus, when $z(t) = 0$, the value of $z(t)$ cannot become negative. Since $z' = \frac{dz}{dt} = r_3z(1 - \frac{z}{K_3}) - Cyz$, z is differentiable with respect to time. Then $z(t)$ must be continuous. Therefore, when $z(t)$ is positive, it has to go through $z(t) = 0$ to become negative. But once $z(t) = 0$, it can not become negative. □

Theorem 6.2. *Boundedness of solutions.* *Consider $y' = y \cdot g(y, z)$. Since $g_y < 0, g_z < 0$, and $g(K_2, 0) = 0$, we see that $y' < y \cdot g(y, 0) = r_2y(1 - \frac{y}{K_2})$. The last expression is logistic growth. This imply that $y(t) \leq \max\{y_0, K_2\}$. Thus this would show boundedness of y.*

Consider $z' = z \cdot h(y, z)$. Since $h_y < 0, h_z < 0$, and $h(0, K_3) = 0$, we see that $z' < z \cdot h(0, z) = zr_3(1 - \frac{z}{K_3})$. The last expression is logistic growth. This imply that $z(t) \leq \max\{z_0, K_3\}$. Thus this would show boundedness of z.

Proof. Since $y' = r_2y(1 - \frac{y}{K_2}) - Cyz = y(r_2(1 - \frac{y}{K_2}) - Cz)$, then

$$g(K_2, 0) = r_2(1 - 1) - C \cdot 0 = 0,$$

$$g_y = -\frac{r_2}{K_2} < 0,$$

$$g_z = -C < 0.$$

Therefore, we see that

$$y' < y \cdot g(y, 0) = yr_2(1 - \frac{y}{K_2}),$$

which is logistic growth with a carrying capacity. Thus $y(t) \leq \max\{y_0, K_2\}$, y_0 represents the initial condition of y. Hence, this shows boundedness of y.

Similarly, since $z' = r_3z(1 - \frac{z}{K_3}) - Cyz = z(r_3(1 - \frac{z}{K_3}) - Cy)$, then

$$h(0, K_3) = r_3(1 - 1) - C \cdot 0 = 0,$$

$$h_y = -C < 0,$$

$$h_z = -\frac{r_3}{K_3} < 0.$$

Therefore, we see that

$$z' < z \cdot h(0, z) = zr_3(1 - \frac{z}{K_3}),$$

which is logistic growth with a carrying capacity. Thus $z(t) \leq \max\{z_0, K_3\}$, z_0 represents the initial condition of z. Hence, this shows boundedness of z. □

6.2 Equilibria and their stability

To find the equilibria of system (5), set $y' = z' = 0$.

$$y' = r_2 y(1 - \frac{y}{K_2}) - Cyz = 0$$

$$z' = r_3 z(1 - \frac{z}{K_3}) - Cyz = 0$$

Using Mathematica to solve the equations, we obtain the following equilibria:

$$(0,0),\ (0, K_3),\ (K_2, 0),\ (\frac{K_2 r_3(CK_3 - r_2)}{C^2 K_2 K_3 - r_2 r_3}, \frac{K_3 r_2(CK_2 - r_3)}{C^2 K_2 K_3 - r_2 r_3})$$

In order to keep the point $(\frac{K_2 r_3(CK_3 - r_2)}{C^2 K_2 K_3 - r_2 r_3}, \frac{K_3 r_2(CK_2 - r_3)}{C^2 K_2 K_3 - r_2 r_3})$ in the first quadrant, we have to have

$$\frac{K_2 r_3(CK_3 - r_2)}{C^2 K_2 K_3 - r_2 r_3} > 0,\ \frac{K_3 r_2(CK_2 - r_3)}{C^2 K_2 K_3 - r_2 r_3} > 0.$$

There are two cases that could possibly make this happen:

1) $C^2 K_2 K_3 - r_2 r_3 > 0$,
   $CK_3 - r_2 > 0$ and $CK_2 - r_3 > 0$

   Then we have $C^2 K_2 K_3 - r_2 r_3 > 0$, $r_2 < CK_3$ and $r_3 < CK_2$.

2) $C^2 K_2 K_3 - r_2 r_3 < 0$,
   $CK_3 - r_2 < 0$ and $CK_2 - r_3 < 0$

   Then we have $C^2 K_2 K_3 - r_2 r_3 < 0$, $r_2 > CK_3$ and $r_3 > CK_2$.

Table 4: Equilibria for the competition model

Equilibria	Eigenvalues	Stability
(0,0)	1 and ϵ	always unstable
$(0, K_3)$	$-CK_3 + r_2$ and $-r_3$	stable if $r_2 < CK_3$
$(K_2, 0)$	$-r_2$ and $-CK_2 + r_3$	stable if $r_3 < CK_2$
$(\frac{K_2 r_3(CK_3 - r_2)}{C^2 K_2 K_3 - r_2 r_3}, \frac{K_3 r_2(CK_2 - r_3)}{C^2 K_2 K_3 - r_2 r_3})$	see part(d)	always stable if the equilibrium is in the first quadrant

The Jacobian Matrix of (5) is given by

$$J = \begin{bmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} \end{bmatrix} = \begin{bmatrix} 1 - \frac{2r_2 y}{K_2} - Cz & -Cy \\ -Cz & r_3 - Cy - \frac{2r_3 z}{K_3} \end{bmatrix}.$$

Substituting the equilibria into the Jacobian Matrix, we get the following results.

(a) $E_5 = (0,0)$

Substituting (0,0) into the Jacobian matrix, we get

$$J_{(0,0)} = \begin{bmatrix} r_2 & 0 \\ 0 & r_3 \end{bmatrix}$$

The eigenvalues of the Jacobian matrix are r_2 and r_3. Since r_2 and r_3 are always positive, both eigenvalues are positive. Thus, E_5 is unstable.

(b) $E_6 = (0, K_3)$

Substituting $(0, K_3)$ into the Jacobian matrix, we get

$$J_{(0,K_3)} = \begin{bmatrix} -CK_3 + r_2 & 0 \\ -CK_3 & -r_3 \end{bmatrix}$$

The eigenvalues of the Jacobian matrix are $-CK_3 + r_2$ and $-r_3$. Since r_3 is positive, $-r_3$ is always negative. For this equilibrium to be stable, we must have

$$-CK_3 + r_2 < 0.$$

Thus, it has to be the case that

$$r_2 < CK_3$$

for E_6 to be locally asymptotically stable.

(c) $E_7 = (K_2, 0)$

Substituting $(K_2, 0)$ into the Jacobian matrix, we get

$$J_{(K_2,0)} = \begin{bmatrix} -r_2 & -CK_2 \\ 0 & -CK_2 + r_3 \end{bmatrix}$$

The eigenvalues of the Jacobian matrix are $-r_2$ and $-CK_2 + r_3$. Since r_2 is positive, $-r_2$ is always negative. For this equilibrium to be stable, we must have

$$-CK_2 + r_3 < 0.$$

Thus, it has to be the case that

$$r_3 < CK_2$$

for E_7 to be locally asymptotically stable.

(d) $E_8 = \left(\frac{K_2 r_3 (CK_3 - r_2)}{C^2 K_2 K_3 - r_2 r_3}, \frac{K_3 r_2 (CK_2 - r_3)}{C^2 K_2 K_3 - r_2 r_3} \right)$

Substituting $\left(\frac{K_2 r_3 (CK_3 - r_2)}{C^2 K_2 K_3 - r_2 r_3}, \frac{K_3 r_2 (CK_2 - r_3)}{C^2 K_2 K_3 - r_2 r_3} \right)$ into the Jacobian matrix, we get

$$J_{\left(\frac{K_2 r_3 (CK_3 - r_2)}{C^2 K_2 K_3 - r_2 r_3}, \frac{K_3 r_2 (CK_2 - r_3)}{C^2 K_2 K_3 - r_2 r_3} \right)} = \begin{bmatrix} -\frac{r_2 r_3 (CK_3 - r_2)}{C^2 K_2 K_3 - r_2 r_3} & \frac{CK_2 r_3 (-CK_3 + r_2)}{C^2 K_2 K_3 - r_2 r_3} \\ -\frac{CK_3 r_2 (CK_2 - r_3)}{C^2 K_2 K_3 - r_2 r_3} & -\frac{r_2 r_3 (CK_2 - r_3)}{C^2 K_2 K_3 - r_2 r_3} \end{bmatrix}$$

The eigenvalues for this Jacobian matrix are a huge mess. Although the eigenvalues are a mess, the trace and determinants are can be computed.

The trace is given by

$$tr = \frac{r_2 r_3 (-C(K_2 + K_3) + r_2 + r_3))}{C^2 K_2 K_3 - r_2 r_3} = -\frac{r_2 r_3 ((CK_2 - r_3) + (CK_3 - r_2))}{C^2 K_2 K_3 - r_2 r_3}.$$

The determinant is given by

$$det = -\frac{r_2 r_3 (CK_3 - r_2)(CK_2 - r_3)}{C^2 K_2 K_3 - r_2 r_3}.$$

16

For the equilibrium to be stable, it has to be the case that the trace is less than 0 and the determinant is greater than 0.

As shown above, there are two cases that could make the equilibrium in the first quadrant. However, the trace is less than zero and the determinant is greater than zero only when case (2) is true. Thus the interior equilibrium is stable if it is in the first quadrant and satisfies case (2), $C^2 K_2 K_3 - r_2 r_3 < 0$, $CK_3 - r_2 < 0$, and $CK_2 - r_3 < 0$.

A stable equilibrium where only ladybugs would survive is illustrated in Figure 4.
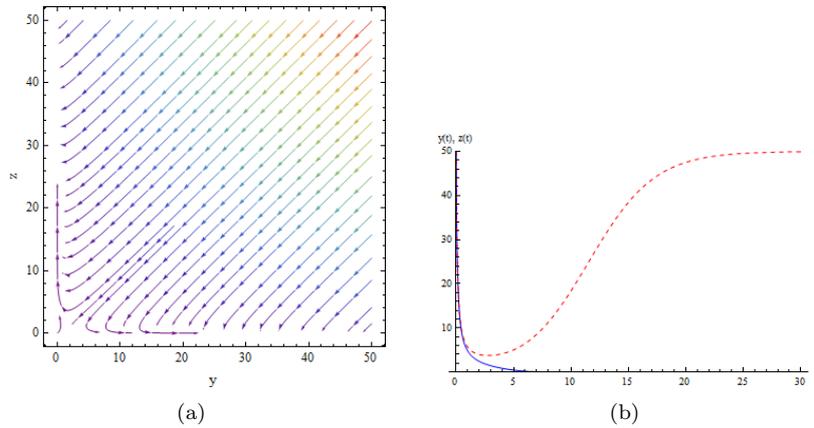

(a)   (b)

Figure 4: The parameters used in the graphs above are $r_2 = .25, r_3 = .35, K_2 = 50, K_3 = 50, C = .2$, The initial values are $y = 50, z = 50$. (a) shows the phase plane for the specified parameters. The y-axis represents ladybugs and the z-axis represents ants in the phase plane graph. (b) shows the time series graph for the specified parameters. The solid line represents ladybugs, and the dashed line represents ants in the time series plot.

A stable equilibrium where only ants would survive is illustrated in Figure 5.
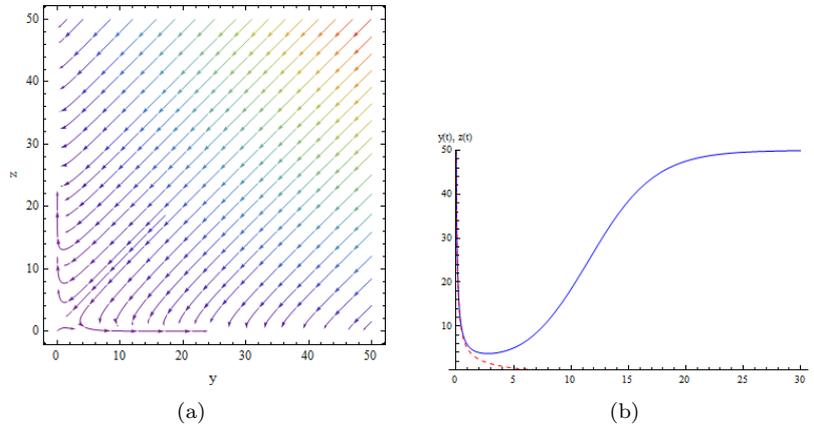
Figure 5: The parameters used in the graphs above are $r_2 = .35, r_3 = .25, K_2 = 50, K_3 = 50, C = .2$. The initial values are $y = 50, z = 50$. (a) shows the phase plane for the specified parameters. The y-axis represents ladybugs and the z-axis represents ants in the phase plane graph. (b) shows the time series graph for the specified parameters. The solid line represents ladybugs, and the dashed line represents ants in the time series plot.

By varying the growth rates of ladybugs and ants, r_2 and r_3, we see two different behaviors of the two species. In Figure 4, with a relatively high growth rate for ants, the ladybugs would slowly go extinct, and ants would slowly grow to their carrying capacity. In Figure 5, with a relatively high growth rate for ladybugs, the ants would slowly go extinct, and ladybugs would slowly grow to their carrying capacity.

7   Mutualistic Submodel - Aphids, Ants

Let $y = 0$, then

$$
\begin{aligned}
x' &= x(1 - \frac{x}{K_1}) + Mxz \\
z' &= r_3 z(1 - \frac{z}{K_3}) + Mxz \, .
\end{aligned}
\tag{6}
$$

By setting $y = 0$, we get the mutualism submodel, which depicts the mutualistic interaction between ants and aphids, as seen in (6). By studying this submodel, we will investigate how the system behaves without ladybugs, and what impact ants have on the other two species. In addition, this model can provide more understanding of mutualistic model between two species, since mutualism is the least studied interaction compared to predator-prey and competitive interaction.

7.1   Basic dynamical properties

Theorem 7.1. *Forward invariance* *If* $x(0), z(0) \geq 0$ *in (6),* $\mathbb{R}^2_+$ *is forward invariant.*

Proof. When $x = 0$, $x' = x(1 - \frac{x}{K_1}) + Mxz = 0$, implying that the rate of change for $x(t)$ is zero when $x(t) = 0$. Thus, when $x(t) = 0$, the value of $x(t)$

18

cannot become negative. Since $x' = \frac{dx}{dt} = x(1 - \frac{x}{K_1}) + Mxz$, x is differentiable with respect to time. Then $x(t)$ must be continuous. Therefore, when $x(t)$ is positive, it has to go through $x(t) = 0$ to become negative. However, $x(t)$ can never be negative because once $x(t) = 0$, it can never be negative.

Similarly, when $z = 0$, $z' = r_3 z(1 - \frac{z}{K_3}) + Mxz = 0$, implying that the rate of change for $z(t)$ is zero when $z(t) = 0$. Thus, when $z(t) = 0$, the value of $z(t)$ cannot become negative. Since $z' = \frac{dz}{dt} = r_3 z(1 - \frac{z}{K_3}) + Mxz$, z is differentiable with respect to time. Then $z(t)$ must be continuous. Therefore, when $z(t)$ is positive, it has to go through $z(t) = 0$ to become negative. But once $z(t) = 0$, it can not become negative. $\qquad\square$

Theorem 7.2. *Boundedness of solutions.*

In the literature, researchers have studied the boundedness of mutualistic models and the possibility of unbounded growth of the mutualistic model [21]. *"The first way is to declare rather arbitrarily that each species has a maximum density set by factors outside of the interaction, and that the model only applies at densities less than this maximum"* [21]. This means that it is biologically unrealistic to allow both species to grow exponentially and reach high densities. In addition, there might be other factors in nature that could limit the species' growth and they might not be included in our mutualistic model. Some studies suggest that the mutualistic model would be bounded at low densities and unbounded at high densities [21]. With the manipulate command in Mathematica, we can see that the solution could be bounded under certain conditions, such as values of a very small M and some specific parameter combinations.

The possibility of unboundedness of the solutions is a weakness of the model. We cannot prove that the solution is always bounded – it is only bounded under certain conditions. By manipulating the graphs in Mathematica, we see that the solutions may be unbounded. As we increase the values of the parameters, the population density of aphids and ants increase exponentially (sometimes within t=50, depending on the parameter). Thus the solution is only bounded under certain conditions (a very small M).

7.2 Equilibria and their stability

To find the equilibria of system (6), set $x' = z' = 0$.

$$x' = x(1 - \frac{x}{K_1}) + Mxz = 0$$

$$z' = r_3 z(1 - \frac{z}{K_3}) + Mxz = 0$$

Using Mathematica to solve the equations, we obtain the following equilibria:

$$(0,0), \ (0, K_3), \ (K1, 0), \ (\frac{K_1 r_3 + K_1 K_3 M r_3}{r_3 - K_1 K_3 M^2}, \frac{K_1 K_3 M + K_3 r_3}{r_3 - K_1 K_3 M^2})$$

In order to make the interior equilibrium point $(\frac{K_1 r_3 + K_1 K_3 M r_3}{r_3 - K_1 K_3 M^2}, \frac{K_1 K_3 M + K_3 r_3}{r_3 - K_1 K_3 M^2})$ in the first quadrant, it must be the case that

$$r_3 - K_1 K_3 M^2 > 0,$$

since both $K_1r_3 + K_1K_3Mr_3$ and $K_1K_3M + K_3r_3$ are both positive. Thus,

$$r_3 > K_1K_3M^2.$$

Table 5: Equilibria for the mutualistic model

Equilibria	Eigenvalues	Stability
(0,0)	1 and r_3	always unstable
$(0, K_3)$	$1 + K_3M$ and $-r_3$	stable if $M < -\frac{1}{K_3}$
$(K_1, 0)$	-1 and $K_1M + r_3$	stable if $M < -\frac{r_3}{K_1}$
$(\frac{K_1r_3+K_1K_3Mr_3}{r_3-K_1K_3M^2}, \frac{K_1K_3M+K_3r_3}{r_3-K_1K_3M^2})$	see part(d)	always stable if the equilibrium is in the first quadrant

The Jacobian Matrix of (6) is given by

$$J = \begin{bmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} \end{bmatrix} = \begin{bmatrix} 1 - \frac{2x}{K_1} + Mz & Mx \\ Mz & r_3 + Mx - \frac{2r_3z}{K_3} \end{bmatrix}.$$

Substituting the equilibria points into the Jacobian Matrix, we get the following results.

(a) $E_9 = (0,0)$
Substituting (0,0) into the Jacobian matrix, we get

$$J_{(0,0)} = \begin{bmatrix} 1 & 0 \\ 0 & r_3 \end{bmatrix}$$

The eigenvalues of the Jacobian matrix are 1 and r_3. Since r_3 is always positive, both eigenvalues are positive. Thus, E_9 is unstable.

(b) $E_{10} = (0, K_3)$
Substituting $(0, K_3)$ into the Jacobian matrix, we get

$$J_{(0,K_3)} = \begin{bmatrix} 1 + K_3M & 0 \\ K_3M & -r_3 \end{bmatrix}$$

The eigenvalues of the Jacobian matrix are $1 + K_3M$ and $-r_3$. Since r_3 is positive, $-r_3$ is always negative. For equilibrium to be stable, we must have

$$1 + K_3M$$

as well. Thus, it has to be the case that

$$M < -\frac{1}{K_3}$$

for E_{10} to be locally asymtotically stable.

(c) $E_{11} = (K_1, 0)$
Substituting $(K_1, 0)$ into the Jacobian matrix, we get

$$J_{(K_1,0)} = \begin{bmatrix} -1 & K_1M \\ 0 & K_1M + r_3 \end{bmatrix}$$

The eigenvalues of the Jacobian matrix are -1 and $K_1M + r_3$. For this equilibrium to be stable, we must have

$$K_1M + r_3 < 0.$$

Thus, it has to be the case that

$$M < -\frac{r_3}{K_1}$$

for E_{11} to be locally asymptotiacally stable.

(d) $E_{12} = (\frac{K_1r_3 + K_1K_3Mr_3}{r_3 - K_1K_3M^2}, \frac{K_1K_3M + K_3r_3}{r_3 - K_1K_3M^2})$

Substituting $(\frac{K_1r_3 + K_1K_3Mr_3}{r_3 - K_1K_3M^2}, \frac{K_1K_3M + K_3r_3}{r_3 - K_1K_3M^2})$ into the Jacobian matrix, we get

$$J_{(\frac{K_1r_3 + K_1K_3Mr_3}{r_3 - K_1K_3M^2}, \frac{K_1K_3M + K_3r_3}{r_3 - K_1K_3M^2})} = \begin{bmatrix} -\frac{r_3 + K_3Mr_3}{r_3 - K_1K_3M^2} & \frac{K_1Mr_3(1 + K_3M)}{r_3 - K_1K_3M^2} \\ \frac{K_3M(K_1M + r_3)}{r_3 - K_1K_3M^2} & -\frac{r_3(K_1M + r_3)}{r_3 - K_1K_3M^2} \end{bmatrix}$$

The eigenvalues of the Jacobian matrix is a huge mess. Although the eigenvalues are a mess, the trace and determinants can be computed.

The trace is given by

$$tr = -\frac{r_3(1 + K_1M + K_3M + r_3)}{r_3 - K_1K_3M^2}.$$

The determinant is given by

$$det = \frac{r_3(1 + K_3M)(K_1M + r_3)}{r_3 - K_1K_3M^2}.$$

For the equilibrium to be stable, it has to be the case that the trace is less than 0 and the determinant is greater than 0.

If the point is in the first quadrant, then the trace is always less than zero and the determinant is always greater than zero. Thus, the interior equilibrium is stable if it is in the first quadrant.

A stable equilibrium where aphids and ants coexist is illustrated in Figure 6.
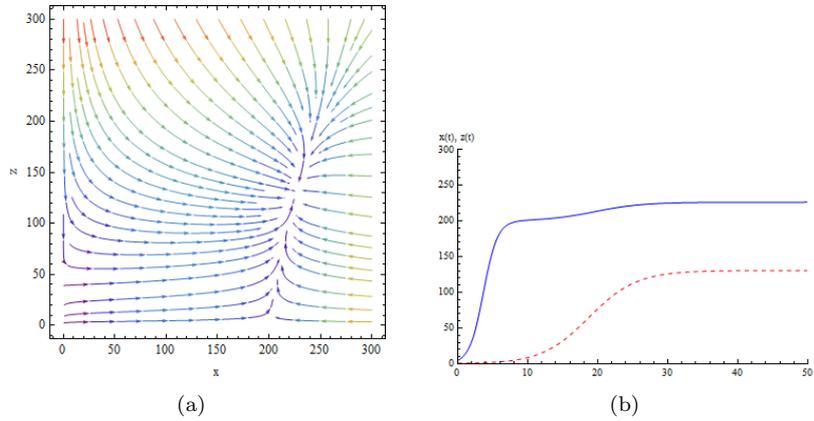
(a)   (b)

Figure 6: The parameters used in the graphs above are $r_3 = .1, K_1 = 200, K_3 = 40, M = .001$. The initial values are $x = 5, z = 1$. (a) shows the phase plane for the specified parameters. The x-axis represents aphids and the z-axis represents ants in the phase plane graph. (b) shows the time series graph for the specified parameters. The solid line represents aphids, and the dashed line represents ants in the time series plot.

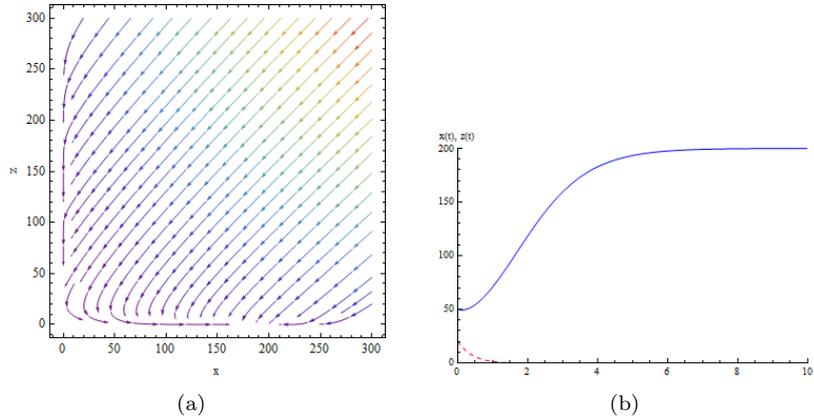A stable equilibrium where only aphids survive is illustrated in Figure 7.

(a)   (b)

Figure 7: The parameters used in the graphs above are $r_3 = .1, K_1 = 200, K_3 = 50, M = -.05$. The initial values are $x = 50, z = 20$. (a) shows the phase plane for the specified parameters. The x-axis represents aphids and the z-axis represents ants in the phase plane graph. (b) shows the time series graph for the specified parameters. The solid line represents aphids, and the dashed line represents ants in the time series plot.

By varying the value of the mutualistic coefficient, M, we see two different behaviors of the two species. In Figure 6, with a positive mutualistic coefficient, aphids and ants would grow past their carrying capacities over time. The aphid population starts growing a bit faster than the ant population. In Figure 7, with a negative mutualistic coefficient, ants would go extinct, and the aphid population would grow to carrying capacity.

22

8 Analysis of the 3-species model

After the analyses of the three submodels, we gained a basic understanding of the predator-prey, competitive, and mutualistic interactions. Now we proceed to the analysis of the 3-species model.

8.1 Equilibria and their stability

All equilibria of the subsystems, (4), (5), and (6) are boundary equilibria of the three-species model (2), meaning that at least one species is extinct at the equilibrium. For the three-species model, we note that the "phase plane" is three-dimensional, see Figure 8, 9, and 10.

Examples of Boundary Equilibria:

(1) In Figure 8, we have the predator-prey or competition $(0, K_2, 0)$ boundary equilibrium of system (2).

(a)   (b)

Figure 8: The parameters used in the graphs above are $K_1 = 3.5, K_2 = 10, K_3 = 20, K_4 = 20, \mu = .15, M = .2, C = .4, r_2 = .25, r_3 = .35$. The initial values are $x = 3.72887, y = 2.70702, z = 0.740948$. At $t = 200, x(200) = 1.6394 \cdot 10^{-19}, y(200) = 10, z(200) = -5.10835 \cdot 10^{-19}$. (a) shows the phase plane for the specified parameters. The x-axis represents aphids, the y-axis represents ladybugs and the z-axis represents ants in the phase plane graph. The big dot represents the initial condition. (b) shows the time series graph for the specified parameters. The solid line represents aphids, the dashed line represents ladybugs and the dotted line represents ants in the time series plot. The time plot is zoomed in to show the details.

With the parameters above, ladybugs grow to the carrying capacity, while the aphids and ants go extinct over time. The trajectory goes to the predator-prey or competition $(0, K_2, 0)$ boundary equilibrium.

(2) In Figure 9, we have the predator-prey interior $(\bar{x}, \bar{y}, 0)$ boundary equilibrium of system (2).
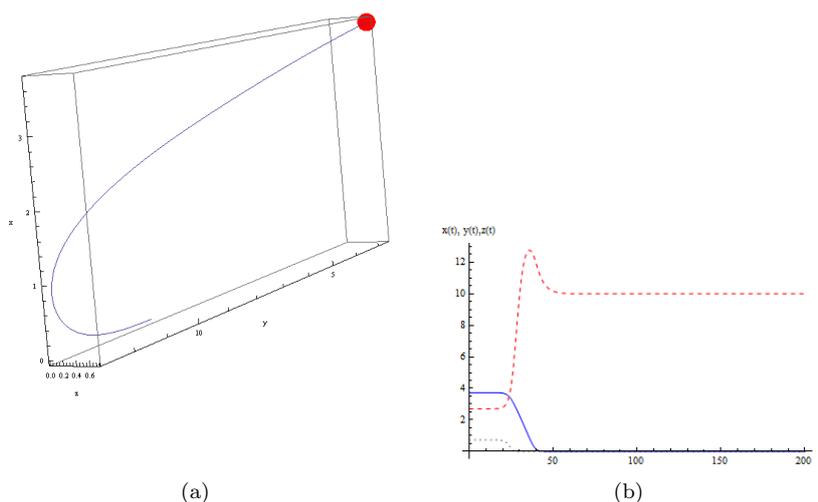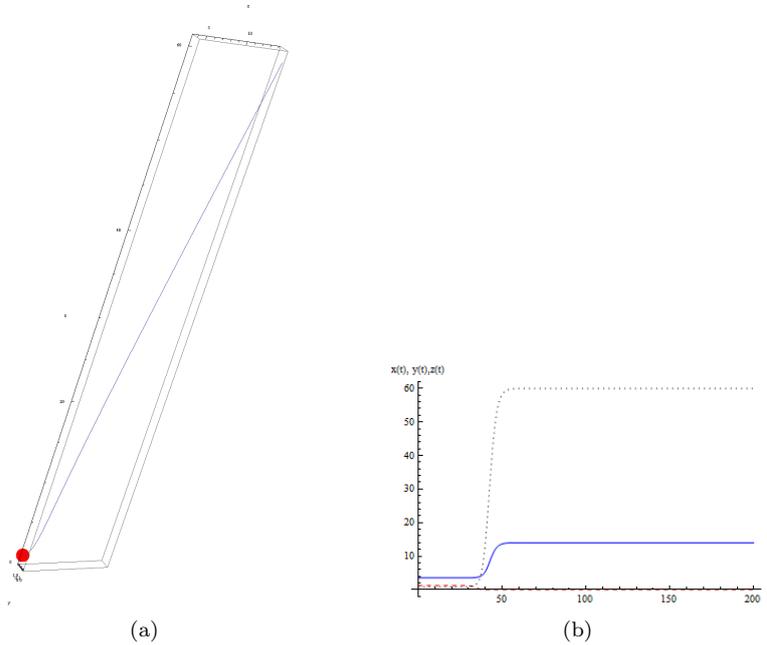

(a)

(b)

Figure 9: The parameters used in the graphs above are $K_1 = 15, K_2 = 10, K_3 = 20, K_4 = 20, \mu = .15, M = .2, C = .4, r_2 = .25, r_3 = .35$. The initial values are $x = 15.1754, y = 8.44339, z = 0.441506$. At $t = 200$, $x(200) = 12.386, y(200) = 15.5518, z(200) = -1.31616 \cdot 10^{-23}$. (a) shows the phase plane for the specified parameters. The x-axis represents aphids, the y-axis represents ladybugs and the z-axis represents ants in the phase plane graph. The big dot represents the initial condition. (b) shows the time series graph for the specified parameters. The solid line represents aphids, the dashed line represents ladybugs and the dotted line represents ants in the time series plot. The time plot is zoomed in to show the details.

With the parameters above, the aphid and ant populations grow to their carrying capacities, while ladybugs go extinct over time. The initial condition is attracted to the predator-prey interior $(\bar{x}, \bar{y}, 0)$ boundary equilibrium.

(3) In Figure 10, we have the mutualistic interior $(\bar{x}, 0, \bar{z})$ boundary equilibrium of system (2).

(a)　　　　　　　　　　(b)

Figure 10: The parameters used in the graphs above are $K_1 = 3.5, K_2 = 10, K_3 = 20, K_4 = 20, \mu = .15, M = .05, C = .4, r_2 = .25, r_3 = .35$. The initial values are $x = 3.50145, y = 1.27657, z = 0.825347$. At $t = 200, x(200) = 14, y(200) = 6.1286 \cdot 10^{-25}, z(200) = 60$. . (a) shows the phase plane for the specified parameters. The x-axis represents aphids, the y-axis represents ladybugs and the z-axis represents ants in the phase plane graph. The big dot represents the initial condition. (b) shows the time series graph for the specified parameters. The solid line represents aphids, the dashed line represents ladybugs and the dotted line represents ants in the time series plot. The time plot is zoomed in to show the details.

With the parameters above, the ladybugs slowly go extinct; aphids and ants first stay relative the same size, then grow to the mutualistic interior equilibrium over time. The initial condition goes to the mutualistic interior $(\bar{x}, 0, \bar{z})$ boundary equilibrium.

We could not find a specific parameter combination that produce the ant equilibrium $(0, 0, K_3)$ or the competition interior equilibrium $(0, \bar{y}, \bar{z})$. Instead, we notice that as the parameter combinations change, the equilibrium switches between $(\bar{x}, 0, \bar{z})$ and $(0, K_2, 0)$.

8.2　Basic dynamic properties

Theorem 8.1. _Forward invariance._ _If $x(0), y(0), z(0) \geq 0$ in (2), $\mathbb{R}_+^3$ is forward invariant._

Proof. When $x = 0$, $x' = x(1 - \frac{x}{K_1}) - \frac{\mu xy}{(1+x)(1+\frac{z}{K_4})} + Mxz = 0$, implying that the rate of change for $x(t)$ is zero when $x(t) = 0$. Thus, when $x(t) = 0$, the value of $x(t)$ cannot become negative. Since $x' = \frac{dx}{dt} = x(1 - \frac{x}{K_1}) - \frac{\mu xy}{(1+x)(1+\frac{z}{K_4})} + Mxz$, x

25

is differentiable with respect to time. Then $x(t)$ must be continuous. Therefore, when $x(t)$ is positive, it has to go through $x(t) = 0$ to become negative. But once $x(t) = 0$, it can not become negative.

Similarly, when $y = 0$, $y' = r_2 y(1 - \frac{y}{K_2}) + \frac{\mu xy}{(1+x)(1+\frac{z}{K_4})} - Cyz = 0$, implying that the rate of change for $y(t)$ is zero when $y(t) = 0$. Thus, when $y(t) = 0$, the value of $y(t)$ cannot become negative. Since $y' = r_2 y(1 - \frac{y}{K_2}) + \frac{\mu xy}{(1+x)(1+\frac{z}{K_4})} - Cyz$, y is differentiable with respect to time. Then $y(t)$ must be continuous. Therefore, when $y(t)$ is positive, it has to go through $y(t) = 0$ to become negative. But once $y(t) = 0$, it can not become negative.

Similar for z, when $z = 0$, $z' = r_3 z(1 - \frac{z}{K_3}) + Mxz - Cyz$, implying that the rate of change for $z(t)$ is zero when $z(t) = 0$. Thus, when $z(t) = 0$, the value of $z(t)$ cannot become negative. Since $z' = r_3 z(1 - \frac{z}{K_3}) + Mxz - Cyz$, z is differentiable with respect to time. Then $z(t)$ must be continuous. Therefore, when $z(t)$ is positive, it has to go through $z(t) = 0$ to become negative. But once $z(t) = 0$, it can not become negative. $\qquad\square$

9 Discussion

9.1 The predator-prey submodel

In the predator-prey submodel, we were able to produce a stable equilibrium where ladybugs and aphids could coexist, and a stable equilibrium where only the ladybugs could survive by varying the predation rate. As we increase the predation rate, the equilibrium shifts from coexistence to aphid extinction, shown in Figure 2 and 3.

Notice that in Figure 2, both aphids and ladybugs grow to their carrying capacities over time. They never grow past their carrying capacities. However in Figure 3, the ladybugs grew past their carrying capacity at peak as the aphids slowly became extinct, then the ladybugs decreased to carrying capacity over time.

9.2 The competition submodel

In the competition submodel, we were able to produce a stable equilibrium where only one species survives by varying the rate of the ladybugs and the ants. As the ant growth rate exceeds the ladybug growth rate, the equilibrium shifts from an extinction of ants to an extinction of ladybugs. However, we could not find an equilibrium where the two species could coexist.

Notice that in both of the one-species existence equilibria, shown in Figure 4 and 5, aphids and ladybugs grow to their carrying capacities over time. They never grew past their carrying capacities.

9.3 The mutualistic submodel

In the mutualistic submodel, we were able to produce a stable equilibrium where aphids and ants could coexist, and an stable equilibrium where only aphids could survive by varying the mutualistic coefficient. As ants and aphids benefit more from each other, the equilibrium shifts from ants' extinction to coexistence, shown in Figure 6 and 7.

Notice that in the stable coexistence equilibrium, shown in Figure 6, aphids and ants grow to their carrying capacities over time. The mutualistic interaction allows them to surpass their carrying capacities in the environment. However in the stable one-species equilibrium, shown in Figure 7, neither aphids nor ants grew past their carrying capacities.

9.4 The 3-species model

In the 3-species model, we were able to produce the predator-prey or competition $(0, K_2, 0)$ boundary equilibrium, the predator-prey interior $(\bar{x}, \bar{y}, 0)$ boundary equilibrium, and the mutualistic interior $(\bar{x}, 0, \bar{z})$ boundary equilibrium. However, we did not find any specific parameter combinations that produce the 3-species coexistence equilibrium.

9.5 Strengths of the model

We simulated situations with with different parameter combinations and produced different outcomes with the submodels and the 3-species model, which would be unethical to do in nature. The different scenarios help with the understanding of predator-prey, competitive, and mutualistic interactions, as well as the three-species interaction.

In addition, the three-species model nicely reduced into submodels, especially the mutualistic model. Mutualism is the least studied interaction among the three interactions. Using specific parameters, aphids and ants grow past their carrying capacity, showing the effect of the mutualism. The two species mutually benefit from each other, and help their population grow.

9.6 Limitations of the model

One weakness of our model is that we could not prove the boundedness of the solution for the mutualistic submodel. The solution is only bounded if M is sufficiently small. The unbounded solution allows species to grow indefinitely, which is unrealistic biologically. Thus, there must be some factors in nature that we did not take into account in the model.

Another weakness of the model is that we could not find a parameter combination that produces a coexistence equilibrium for the 3-species model. This does not mean that the three species cannot coexist. A coexistence equilibrium may or may not exist. If it does, then it may only exist for a small range of parameter combinations, which could explain why we could not find a parameter combination that produces the coexistence equilibrium.

9.7 Future outlook

This 3-species model provides useful approximations for the dynamics of predator-prey, competitive and mutualistic relationship between aphids, ladybugs and ants. We must keep in mind the much more complicated nature of the realistic natural environment. It must be understood that our model is built on a series of assumptions, which may or may not be realistic. We could only approximate a natural interaction. In order to make more realistic models in future research, it is necessary to incorporate data and fit the model to field data sets.

10   Acknowledgment

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