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INTERACTIONS BETWEEN LEAF-CUTTER ANTS AND FUNGUS GARDEN: EFFECTS OF DIVISION OF LABOR, AGE POLYETHISM, AND EGG CANNIBALISM

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Abstract. Division of labor (DOL), age polyethism, and egg cannibalism all play roles in shaping colony-level population dynamics in social insect colonies. The ways in which these mechanisms interact with one another to shape population dynamics is not currently understood. In this study, we examine how these mechanisms influence population dynamics in colonies of fungus-gardening leaf-cutter ants by developing and studying two sets of models: (1) We study age polyethism contribution to the dynamics of this multi-species interaction model which incorporates mechanisms of DOL; (2) We explore effects of egg cannibalism in colony dynamics and understand how to model such social conflict behavior realistically using different functional responses. Our results suggest that: (a) Age polyethism is important to keep stable population dynamics. (b) Large maturation rate and mortality rate of inside workers induce colony death. (c) Small enough egg cannibalism rate benefits adult worker ant's growth and (or) development, large proportion of ants performing a given task can promote colony survival, and too large egg cannibalism rate can lead to colony's death. (d) Increasing energy invested on brood care and (or) the conversion rate between fungus and ants could induce oscillatory dynamics in models with cannibalism.

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1. Introduction

Eusocial insects represent some of the most advanced social systems and are characterized by having cooperative brood care, an overlap of at least two generations in the same colony, and coexistence of reproductive and non-reproductive members [15]. Leaf-cutter ants are considered by many to represent one of the pinnacles of social evolution. They live in colonies that can reach population sizes in the millions, have a number of morphologically distinct subclasses, build nests over 30m wide, and are the greatest agricultural pest of the neotropics, with mature colonies devouring hundreds of pounds of leaves every year. The huge size of the colonies and success of the species is facilitated by their symbiosis with a fungus that they grow as their primary food source.

Keywords and phrases: Leaf-cutter Ants, fungus garden, mutualism, social insects, egg cannibalism, age polyethism, division of labor.

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The ants do not eat the pieces of fresh vegetation that they collect from the plants surrounding the colony, but instead provide them to their fungal symbiont which they consume in turn. They exhibit a complex system of division of labor by which task allocation depends on the age of the individual or on physical features, or on both [15]. Division of labor (DOL) in social insects, as defined by [11], "describes a process in which one individual repeatedly performs a task while another individual repeatedly performs another".

Mechanisms of DOL include size polymorphism, age polyethism, variation in response thresholds, and learning [1]. Some of the tasks performed by non-reproductive individuals include caring for the queen and brood, nest construction, foraging for resources, and cleaning and defending the nest, which have the overall purpose of increasing the colony's success [15, 42]. Age polyethism plays an important role in shaping division of labor in leaf-cutter ant colonies [4, 38]. This phenomenon is observed in many social insects in which individuals perform different tasks as they grow older [25, 39]. For example, workers in the smallest physical class take care of brood and the fungus inside the nest when they are young [4, 36], and can be seen riding on pieces of leaves being carried back to the nest by foragers when they are older, where they both protect the forager carrying the leaf from parasitic phorid flies and begin cleaning and processing the leaf fragment [4, 10, 12, 20, 36, 37]. Older workers from all size classes are also more likely to participate in the dangerous behavior of defending the nest [15]. Therefore, for social insect colonies with age polyethism, the tasks performed by individuals within a colony changes as they mature [5]. One of the interesting questions is how age polyethism in a social insect colony contributes to population dynamic's including the distribution of workers performing different tasks.

Egg cannibalism behavior has been regularly observed in social insect colonies, including leaf-cutter ants and honeybees [22, 29, 41], and is suggested to be a selfish behavior influenced by environmental factors such as shortage of food resources [21, 27, 29], and individual traits such as sex [34]. Recent studies have shown that egg cannibalism is an adaptive life strategy that can increase growth and developmental rates [19, 23, 28, 33], adult body size [24, 33], improve colony survival [19, 28, 33], and reduce competition within the colony [28, 33, 40]. There is a fair amount of literature devoted to the study of cannibalism behavior in both ecological and evolutionary settings (see [7–9, 19]).

In leaf-cutter ants, egg cannibalism behavior plays an important role during the incipient stage of the leaf-cutter colony life cycle. When the first workers eclose in the new colony started by a recently-mated queen, the queen produces large malformed trophic eggs, formed by fusing multiple eggs in the ovariole, and the workers feed them to developing larvae to reduce consumption of the still-small fungus garden. The production of these trophic eggs is crucial to the survival of the colony until it reaches the size required for stable colony growth [18]. One interesting question is whether the benefit of cannibalism behavior is reflected in a linear energy transfer from victim to consumer or in a nonlinear fashion.

A number of experimental studies have examined the respective roles of egg cannibalism [19, 23, 24, 28, 33, 40], division of labor [1], and age polyethism [4, 25, 38, 39] in shaping population dynamics of social insects. However, it has been difficult to study how these factors interact with one another to shape overall colony-level population dynamics. Increasing our understanding of how these factors individually shape population dynamics, how the effects of the factors modulate the influence of one another, and their cumulative effects will be of great value to social insect scientists. In this paper we will use a mathematical modeling approach to facilitate study of the effects of these potentially interacting variables on colony-level population dynamics.

Mathematical models have been used to understand population dynamics observed in natural environments. For instance, [16] developed a simple model to describe the colony dynamics from regulatory effects of feedback mechanisms such as brood production in eusocial paper wasps. Other models [17, 31, 32] have studied different mechanisms of division of labor. In [17, 31], they focused on studying the regulation of task partitioning of hunting behavior in a Ponerine ant colony and in construction behavior in social wasps, respectively. Both [17, 31] used a Stock and Flow modeling framework to develop a system of first-order ODEs explaining that task partitioning of hunting behavior and nest construction, can be done by regulation. In [32], an ODE model approach was used to study the task regulation of collective behavior in honeybees predicting an adaptive strategy for both bees and plants. Also, [30] proposed a model to study the population and resource dynamics of a honeybee colony emphasizing pollen supply and brood cannibalism. However, few models that could be applied to the interactions between leaf-cutter ants and their fungus garden have been produced (but see [18]).

The model proposed by [18] describes the mutualism interactions of leaf-cutter ants and their fungus with an implicit division of labor, which provides global dynamics suggesting that division of labor among worker ants is an important factor which determines survival and growth, or death of leaf-cutter ants colonies and their fungus garden. We adopt the modeling approach of [18] to investigate the effects of age polyethism and egg cannibalism on colony population dynamics. More specifically, the main purpose of this paper is to learn the possible colony dynamic outcomes by studying the effects of the explicit division of labor through the subdivision of the worker ants into two task groups that perform tasks according to their age such as tending the fungus garden and collecting leaves. We also explore how the colony may benefit from egg cannibalism behavior in linear or nonlinear fashions.

2. Derivations of models

Kang *et al.* [18] proposed the following model (2.1) to study an incipient colony growth model for leaf-cutter ants and their fungus garden based on simple density-dependent growth and death rates coupled with a fungus growth model which can be described by a generalized Michaelis-Menten equation of enzyme kinetics [18]:

$$\begin{aligned} F'(t) &= \frac{r_f a A^2}{b + aA^2} F - d_f F^2 - r_c AF \\ A'(t) &= r_a AF - d_a A^2, \end{aligned} \tag{2.1}$$

where r_f is the maximum growth rate of the fungus; $r_a = cr_f$ with c being the conversion rate between fungus and ants; b is the half-saturation constant; and d_a, d_f is the mortality rate of ants and the fungus, respectively. The parameter $a = p^2 q(1-q)$ measures implicit division of labor with p being the portion of the worker biomass of $A(t)$ performing an inside colony task such as brood care, and q being the portion of energy of each worker performing an outside colony task such as foraging. The ecological assumptions of (2.1) are listed as follows:

1. The numerical response function for ants is the Holling Type I function, *i.e.*, fungus biomass F multiplied by a constant number r_a. In addition, we assume that ants suffer from density-dependent mortality due to energy consumed by foraging for leaves and taking care of the larvae and fungus garden, which will modify population growth through density-dependent self-limitation [14].
2. The numerical response of fungus to ants is a Holling Type III function $\frac{aA^2}{b+aA^2}$ by applying the concept of the kinetics of functional response [26]. Moreover, the fungus suffers from density-dependent mortality due to self-limiting [14].

In the following subsections, we provide detailed model derivations and assumptions of the following two sets of models based on the modeling approach of (2.1) [18]:

1. We derive two models with division of labor: Leaf-cutter ants and their fungus garden interaction models with *versus* without age polyethism.
2. We derive two models with egg cannibalism behavior in the interactions of leaf-cutter ants and their fungus garden: (1) Consumption of eggs leads to the energy increasing linearly for consumer; and (2) Consumption of eggs decreases the mortality of the consumer in a nonlinear fashion.

2.1. Leaf-cutter ants and fungus garden interaction models with division of labor

Let $F(t)$ represent the biomass of fungus, and $A(t) = A_i(t) + A_o(t)$ be the total biomass of workers in a colony where $A_i(t)$ is the biomass of ants working inside the colony, and $A_o(t)$ is the biomass of ants working outside the colony at any time t, respectively. We propose the following system of nonlinear differential equations describing the biomass rate of change of two task groups of leaf-cutter ants and their fungus with their related age polyethism effect as model (2.2). We assume that ants working inside the colony A_i will age into A_o to perform more risky tasks outside of the colony with maturation rate β.

$$\begin{aligned} F'(t) &= \left[\frac{r_f A_i A_o}{b + A_i A_o} - d_f F - r_i A_i - r_o A_o\right] F \\ A_i'(t) &= c_i r_i A_i F - \beta A_i - d_i A_i (A_i + A_o) \\ A_o'(t) &= c_o r_o A_o F + \beta A_i - d_o A_o (A_i + A_o) \end{aligned} \tag{2.2}$$

The ecological assumptions of the leaf-cutter ants colony's dynamics of (2.2) are listed as follow:

1. *Biomass of fungus* $F(t)$:
   - $F(t)$ can only increase if there are ants tending the garden inside the colony and ants collecting leaves outside the colony, hence its growth will be a product thereof, taking into account the maximum growth rate of the fungus, r_f. By the kinetics of functional response, we can describe the response of the fungus as a Holling type III functional response, $\frac{r_f A_i A_o}{b + A_i A_o}$ where b is the half saturation constant.
   - $F(t)$ decreases due to natural mortality and consumption by ants, with d_f as the death rate of fungus, and r_i and r_o as the rate of consumption by ants working inside and outside, respectively.

   Thus, the dynamics of the fungus biomass $F(t)$ is described by the following equation:

$$F'(t) = \left[\frac{r_f A_i A_o}{b + A_i A_o} - d_f F - r_i A_i - r_o A_o\right] F.$$

2. *Biomass of ants working inside and outside the colony,* $A_i(t)$ *and* $A_o(t)$*:*
   - $A_i(t)$ and $A_o(t)$ increase in proportion to the biomass of fungus and their own biomass according to the rate of consumption (r_i, r_o respectively) and the rate at which they can convert the biomass of consumed fungus to their own biomass (c_i, c_o respectively).
   - $A_i(t)$ and $A_o(t)$ decreases due to density dependent mortality, *i.e.* the death rate of each of the task groups increases when the total population is too large and individuals are competing for space or resources.
   - We consider a maturation rate of ants working inside the colony βA_i. We assume that ants working inside the colony leave this task group at a per-capita rate β.

In summary, model (2.2) has explicit division of labor that is measured by the population of inside colony workers A_i and outside colony workers A_o. In our model we assume that age polyethism is an additional DOL mechanism which includes the fact that younger workers A_i performing inside colony task will age into older workers A_o performing outside colony task at a rate of β. We aim to compare the dynamical outcomes of model (2.2) for $\beta = 0$ and $\beta > 0$ in order to explore the impacts of age polyethism described by the term βA_i. We also compare dynamics of the original model (2.1) to model (2.2) to study the effects of explicit DOL.

2.2. Derivation of models with egg cannibalism in leaf-cutter ants.

Let $F(t)$ be the total biomass of fungus as time t, and $E(t)+A(t)$ denote the total biomass of a focal colony of leaf-cutter ants at time t, where $E(t)$ represents the egg population biomass that can be cannibalized by $A(t)$ at time t, and $A(t)$ represents the population biomass of larvae and adult workers that may have cannibalistic behavior at time t. We propose the following sets of nonlinear equations describing a two-stage population model of leaf-cutter ants with egg cannibalism behavior and implicit DOL:

$$\begin{aligned} F'(t) &= F\left[\frac{r_f a A^2}{b + a A^2} - d_f F - r_c A\right] \\ E'(t) &= p_1 r_a A F - \alpha A E - \beta E \\ A'(t) &= (1 - p_1) r_a A F + \beta E + c_1 \alpha A E - d_a A^2 \end{aligned} \tag{2.3}$$

$$
\begin{aligned}
F'(t) &= F\left[\frac{r_f a A^2}{b + aA^2} - d_f F - r_c A\right] \\
E'(t) &= p_1 r_a AF - \alpha AE - \beta E \\
A'(t) &= (1 - p_1) r_a AF + \beta E \ - \frac{d_a A^2}{1 + c_2 \alpha E}
\end{aligned}
\tag{2.4}
$$

Model (2.3) describes the utilization of egg cannibalism leading to the growth benefit of A due to the linear energy transformation, while the model (2.4) describes the utilization of egg cannibalism resulting in reduced mortality rate of A, and thus increase the lifespan of A. The benefits of egg cannibalism are modeled as nonlinear effects in the model (2.4). The detailed ecological assumptions for these models are described below.

First, the derivations of the biomass fungus F in both model (2.3) and (2.4) follow the same assumptions in the original model (2.1) studied in [18]. We also assume that the reproductive division of labor results in the ratio of energy gained through consuming fungus being $p_1 \in [0, 1]$ for the colony reproduction investment, *i.e.*, the colony invests $p_1 r_a AF$ in reproduction and $(1 - p_1) r_a AF$ in the growth of A-class. We also assume that egg population $E(t)$ has no natural death but can only die through cannibalism by the A-class or mature into A-class. Egg cannibalism is modeled with the Holling Type I functional response αAE, where α is the cannibalism rate; $E(t)$ matures into the A-class at the rate of βE. Thus, the population dynamics of E is described with the following equation:

$$E'(t) = p_1 r_a AF - \alpha AE - \beta E.$$

Regarding the population of A-class, this increases through the energy gained by consuming fungus $(1 - p_1) r_a AF$ and the maturation from E-class βE.

- In model (2.3), $A(t)$ can increase linearly its population/biomass by cannibalizing the egg population at a rate $c_1 \alpha AE$, where $c_1 \in (0, 1)$ is the conversion efficiency between ants and eggs.
- In model (2.4), consuming eggs at a rate αAE, $A(t)$ mortality rate $d_a A^2$ is decreased with the functional response $\frac{1}{1+c_2 \alpha E}$, which represents the benefit obtained from cannibalism. The parameter c_2 is a coefficient describing the functional response of survivability to an increasing presence of eggs which increases the number of individuals cannibalized.

The assumptions above imply that, if there is no egg cannibalism (*i.e.* $\alpha = 0$), model (2.3) and (2.4) are reduced to the following system:

$$
\begin{aligned}
F'(t) &= F\left[\frac{r_f a A^2}{b + aA^2} - d_f F - r_c A\right] \\
E'(t) &= p_1 r_a AF - \beta E \\
A'(t) &= (1 - p_1) r_a AF + \beta E - d_a A^2.
\end{aligned}
\tag{2.5}
$$

We aim to compare the dynamical outcomes of model (2.5) without egg cannibalism to models (2.3) and (2.4) with cannibalism to explore how may cannibalism behavior alter the colony dynamics; and compare equilibria dynamics of model (2.3) to (2.4) to investigate how different modeling approaches of cannibalism's benefits could result in different outcomes.

3. MATHEMATICAL ANALYSIS

First, we provide the following theorem regarding the basic dynamic properties of the proposed models (2.2), (2.3) and (2.4) as follows:

Theorem 3.1 (Positive invariance and boundedness)**.** *The systems* (2.2)*–*(2.4) *are all positive invariant in* $\mathbb{R}^3_+$*. More specifically, every trajectory of model* (2.2) *is attracted to a compact set* $C = \left[0, \frac{r_f}{d_f}\right] \times \left[0, \frac{c\,r_f}{d\,d_f}\right]$*; and every trajectory of models* (2.3) *and* (2.4) *is attracted to a compact set* $D = \left[0, \frac{r_f}{d_f}\right] \times [0, M_3]$.

Models (2.2)–(2.4) are biologically well-defined, *i.e.* the populations' biomass is always positive and bounded. In addition, the extinction equilibrium $E_0 = (0,0,0)$ always exists for all models.

3.1. Effects of age polyethism

To determine the effects of age polyethism, we identify the conditions by which the colony of leaf-cutter ants can survive or perish. We do this by analyzing interior equilibria for the system (2.2) when $\beta = 0$ and $\beta > 0$. We define an interior equilibria in our model as a fix-point of the form (F^*, E^*, A^*) where $F^*, E^*, A^* > 0$. Let

$$\kappa = \frac{c_o r_o}{c_i r_i}$$

be the relative growth rate of workers performing inside colony tasks to workers performing inside colony tasks.

Let

$$A_i^* = A_o^* \left[\frac{(d_o - d_i\kappa)A_o^* - \beta\kappa}{\beta - (d_o - d_i\kappa)A_o^*} \right],$$

which depends on the positive solutions of the following nullcline equation:

$$g_2(A_o) = a_4 A_o^4 + a_3 A_o^3 + a_2 A_o^2 + a_1 A_o + a_0. \tag{3.1}$$

The complete expression for the constants a_i, for $i = 0, ..., 4$ are in the appendix.

The following theorem provides conditions for existence of interior equilibria for both considered cases of (2.2) (*i.e.*, $\beta = 0$ and $\beta > 0$).

Theorem 3.2 (Existence of equilibria)**.** *Model* (2.2) *always have the extinction equilibrium* $\mathbf{E_0} = (0,0,0)$ *which is always locally asymptotically stable. In addition, model* (2.2) *with* $\beta = 0$ *has interior equilibria if and only if* $\kappa = \frac{d_o}{d_i}$*. On the other hand, model* (2.2) *with* $\beta > 0$ *has an interior equilibrium if* $\frac{d_o}{d_i} > \kappa$ *and does not have an interior equilibria if* $\frac{d_o}{d_i} < \kappa$*.*

3.1.1. Numerical simulations

According to Theorem 3.2 and numerical simulations displayed in Figure 1, when $\kappa = \frac{d_o}{d_i}$, Model (2.2) without age polyethism (*i.e.* $\beta = 0$) has an attractor that consists of a line of equilibria where initial condition plays an important role in determining which equilibrium converges to. When the condition does not satisfy, Model (2.2) with $\beta = 0$ has only the extinction equilibrium.

The inclusion of age polyethism (*i.e.* $\beta > 0$) in model (2.2), gives us unique solutions as opposed to when $\beta = 0$ with either infinitely many solutions or non-existent positive solutions. Figure 2, shows the possible number of interior equilibria that model (2.2) with $\beta > 0$ can have and their stability. Fixing parameters $r_f = 0.7; b = 0.002; c_i = 0.5; c_o = 0.3; d_f = 0.2; d_i = 0.1; d_o = 0.2; r_i = 0.15; r_o = 0.2$ and varying β, which denotes the transition and maturation rate from inside worker to outside worker, we can see the effect of this parameter in the biomass of fungus, inside the colony workers, and outside the colony workers. Figure 2a shows

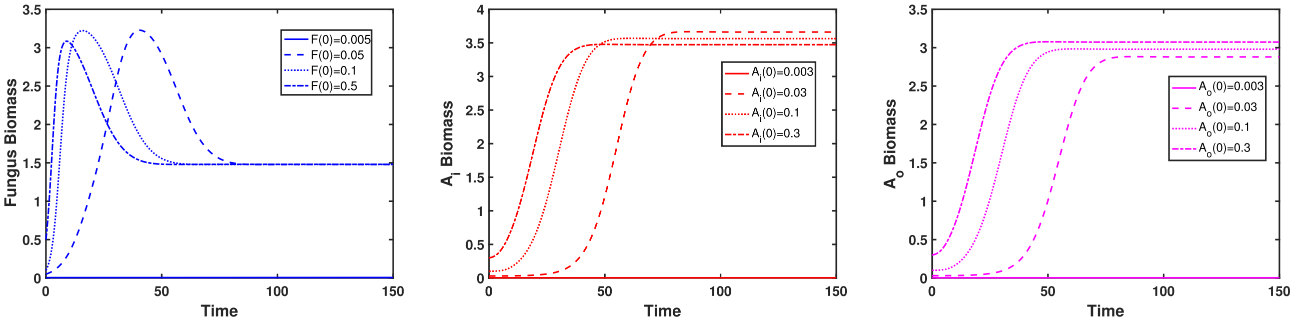
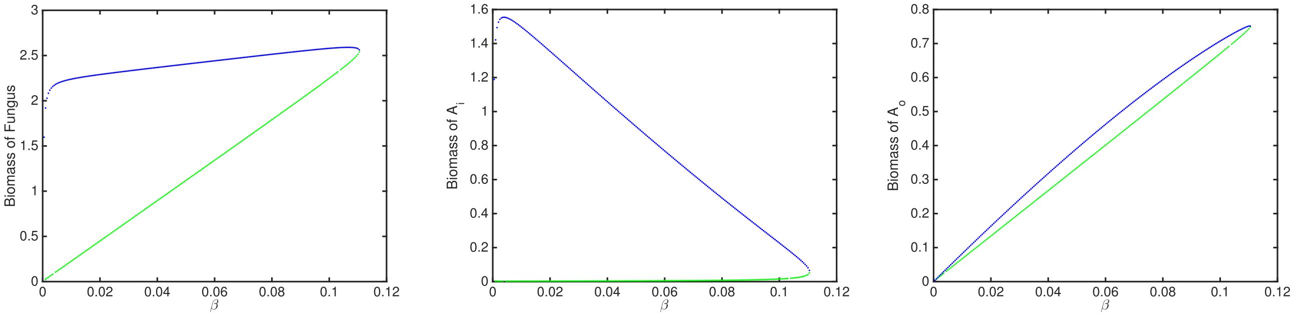


FIGURE 1. Time series solution for model (2.2) with parameters $r_f = 0.7, b = 0.002, d_f = 0.2, d_i = 0.01, d_o = 0.0095, c_i = c_o = 0.7, r_o = 0.06$ with $\mathbf{r_i} = \frac{\mathbf{d_i c_o r_o}}{\mathbf{d_o c_i}}$, choosing different initial conditions.



(a) (b) (c)

FIGURE 2. 1D bifurcation diagrams for model (2.2) studying the effect of β on biomass of fungus and worker ants where $r_f = 0.7; b = 0.002; c_i = 0.5; c_o = 0.3; d_f = 0.2; d_i = 0.1; d_o = 0.2; r_i = 0.15; r_o = 0.2$. (*Blue*: stable and *green*: unstable interior equilibria.)

that as β increases, the total biomass of fungus is benefited by its increase. This could imply that as more inside worker ants transition into outside workers (*i.e.* workers which cut, collect, and bring back leaves to the colony), the biomass of fungus increases and benefits from A_o effort. Also, as β increases, the biomass of the population of ants working inside the colony decreases (see Fig. 2b), while the biomass of the population of ants working outside increases (see Fig. 2c). However, too high of a maturation rate could affect the whole colony and both species (fungus and ants) by inducing colony's death. *An explanation of this effect is that when inside the colony workers transition very quickly to outside workers, they are now exposed to greater risks outside the nest, resulting in increased mortality. At the same time, inside the nest, the production of new workers may not be fast enough to maintain a satisfactory number of inside workers need to contribute to the efforts to keep their fungus cultivar alive.*

Figure 3 is a one-dimensional bifurcation of the death rate of outside workers to inside workers ratio showing coexistence and stability when $\frac{d_o}{d_i} > \kappa$. We also notice that as $\frac{d_o}{d_i}$ increases, the biomass of fungus and the task group of ants working outside the colony decreases, while the biomass of the task group of ants working inside the colony increases.

Figure 4 is a two-dimensional bifurcation diagram of $d_o \in (0, 1)$ and $d_i \in (0, 1)$ with different levels of maturation rate β by setting $c_i = c_o = 0.4; r_i = r_o = 0.2$, *i.e.* both task groups have the same consumption rate of fungus and conversion rate of fungus into their own biomass. *When the maturation rate is small, too large d_i can make the colony extinct. If the maturation rate is larger (e.g. $\beta = 0.1$), then the colony can go extinct if d_i is not large enough. In general if $d_i > d_o$ the colony of leaf-cutter ants can go extinct, otherwise it persists.*

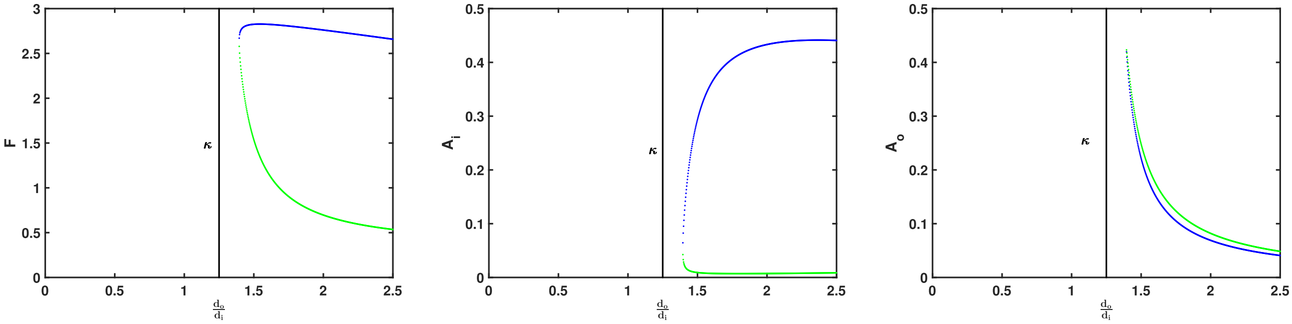
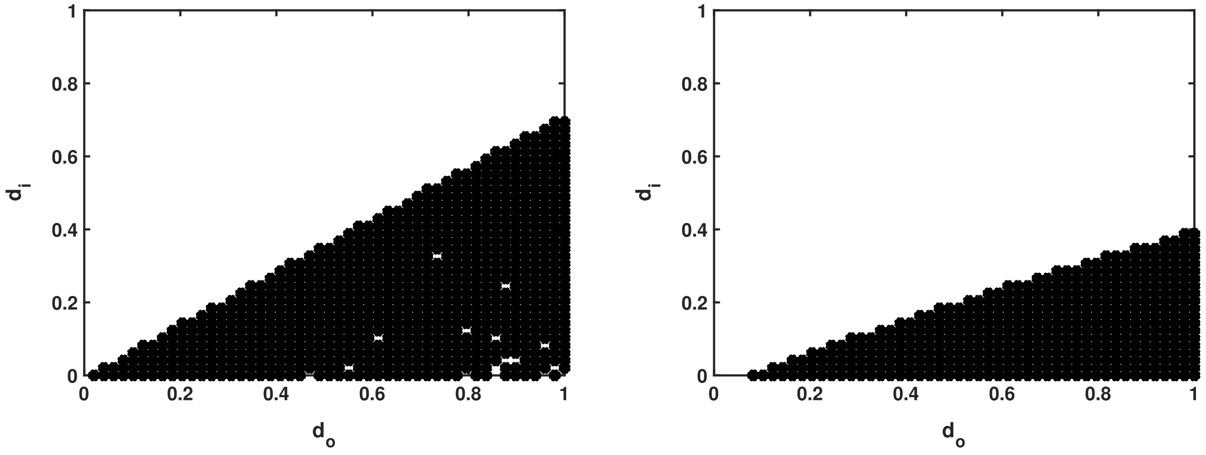


FIGURE 3. 1D bifurcation of the ratio $\frac{d_o}{d_i}$ with parameters $r_f = 0.7, b = 0.002, d_f = 0.2, c_i = c_o = 0.4, r_o = 0.25, r_i = 0.2$.



(a) $\beta = 0.02$

(b) $\beta = 0.1$

FIGURE 4. 2D bifurcation to study the effect of d_i and d_o on the existence of interior equilibria for model (2.2). $c_i = c_o = 0.4; r_i = 0.2; r_o = 0.25$. (Area in black denotes existence of interior equilibria and white represents no interior.)

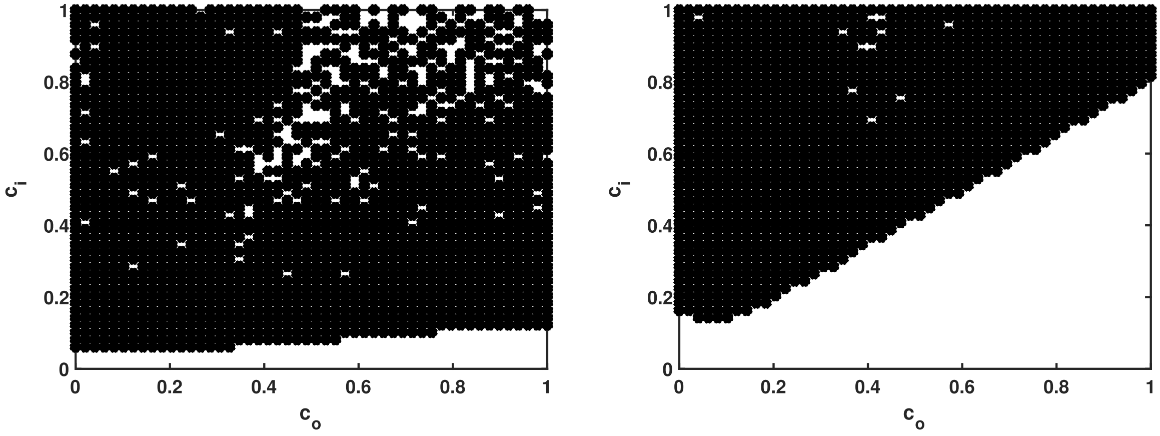
Figure 5 shows the effects of the conversion rate of fungus into the biomass of worker ants. Here, we have $c_o \in (0, 1)$ *versus* $c_i \in (0, 1)$ by setting $\beta = 0.02$, $r_i = 0.2, r_o = 0.25$ and varying the death rate of each of the task groups of worker ants. Consider $d_i < d_o$, when d_i is really small (see Fig. 5a), then when the conversion rate c_i of the worker ants belonging to the task group A_i is really small and for any value of c_o (white area in Fig. 5a), the colony cannot survive. *Now, if d_i increases but still less than d_o, the colony cannot survive for large c_o and small to medium c_i (see Fig. 5b). However, small c_o and large c_1 can promote coexistence of the two task groups and fungus.*

3.2. Egg cannibalism

Next we investigate the effects of egg cannibalism α in both models (2.3) and (2.4). If there is no egg cannibalism (*i.e.* $\alpha = 0$), system (2.3) and (2.4) reduces to system (2.5).

Theorem 3.3 (No egg cannibalism). *Let $\gamma = \frac{4b(d_a d_f + r_a r_c)}{(r_a r_f)^2}$. System (2.5) always have the extinction equilibrium and has the following equilibria scenarios:*

(1) No interior equilibria: when $a < \gamma$.



(a) $d_i = 0.03$ (b) $d_i = 0.3$

FIGURE 5. 2D bifurcation to study the effect of c_i and c_o on the existence of interior equilibria for model (2.2). $d_o = 0.5; \beta = 0.02; r_i = 0.2; r_o = 0.25$. (Area in black denotes existence of interior equilibria and white represents no interior.)

(2) *One interior equilibria: when* $a = \gamma$.
(3) *Two interior equilibria: when* $a > \gamma$.

The equilibrium dynamics of model (2.5) when the colony does not have egg cannibalism are similar to those in the model of [18], *i.e.* $(0,0,0)$ is globally stable when it is the only equilibrium and (F_2^*, E_2^*, A_2^*) can be locally asymptotically stable when it exists.

Biological implications: Theorem 3.3 and equilibrium dynamics shown in [18] for a similar case implies that division of labor plays an important role in determining whether a colony of leaf cutter ants can survive in the absence of egg cannibalism. When a is too small, the proportion of adult ants performing certain tasks is too small, therefore they are not investing enough energy to a given task. This leads to the extinction of the colony. However, if the proportion of adult ants performing given tasks is large enough, then the colony can survive.

Theorem 3.4. *If model* (2.5) *without cannibalism has no interior equilibria, then model* (2.3) *with cannibalism cannot have interior equilibria, i.e., the colony cannot survive. Moreover, model* (2.4) *with cannibalism can have the following dynamics:*

(1) *Model* (2.4) *always have the extinction equilibrium and can have maximum two interior equilibria:* $E_i = (F_i^*, E_i^*, A_i^*)$, $i = 1, 2$.
(2) *If* $f_{\max} = \frac{r_f\sqrt{ab}-2br_c}{2bd_f} < 0$, *then model* (2.4) *has no interior equilibrium.*
(3) *If* $f_{\max} > \frac{\frac{d_a}{r_a}}{1-p_1} > \frac{d_a}{r_a}$, *then model* (2.4) *definitely has interior equilibria.*

Biological implications: Theorem 3.4 supported by Figure 6 suggests that systems such as (2.5) and (2.3), *i.e.* without cannibalism and with cannibalism used for growth benefit of A biomass, respectively, cannot fully describe the positive mechanism that egg cannibalism represents in a colony of social insects. Under critical conditions when division of labor implicitly described by a is too small, both systems only have the extinction equilibrium. However, model (2.4) with cannibalism used to increase A lifespan improves the outcomes of model (2.3) and model (2.5) by providing two existent interior equilibrium where one of them can be stable (see Theorem 3.5). This suggests that the dynamics of model (2.4) provide survival of the colony when model (2.5)

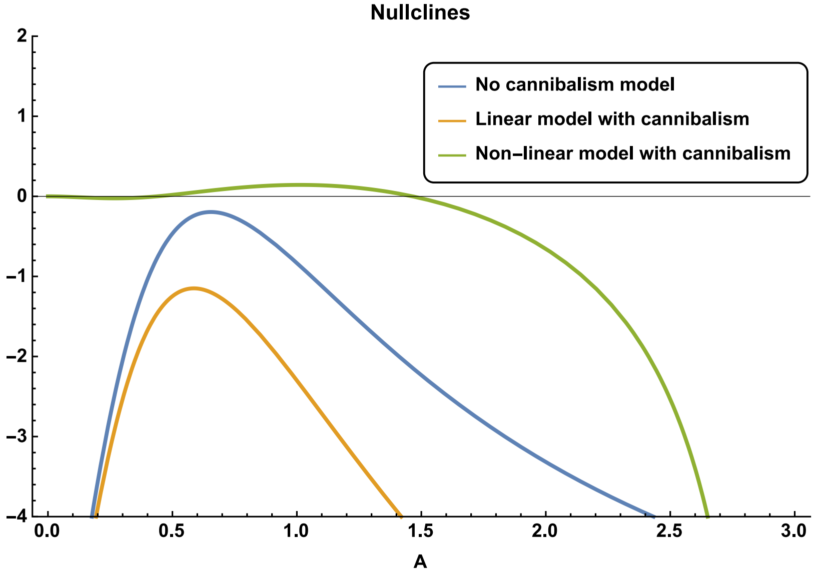


FIGURE 6. Nullclines of system (2.5) with no egg cannibalism and systems (2.3) and (2.4) with egg cannibalism.

and (2.3) cannot. Further analytical and graphical implications regarding the existence of interior equilibria of model (2.4) can be found in Appendix C.

The following theorem summarizes the conditions for existence of interior equilibria (F^*, E^*, A^*) for models (2.3) and (2.4), *i.e.* coexistence of fungus, eggs, and adult workers in a colony where egg cannibalism contributes to the growth of adult workers and increases adult worker lifespan, respectively.

Theorem 3.5 (Extinction and survival conditions)**.** *Let $a, b, c_1, d_a, d_f, p_1, r_a, r_c$ be positive parameters. We define*

$$K_1 = \frac{a\beta r_a r_f}{b(d_a d_f + r_a r_c(1-p_1(1-c_1)))} \qquad \text{and} \qquad K_2 = \frac{\alpha b(d_a d_f + r_a r_c(1-p_1(1-c_1))}{\beta r_a r_f}.$$

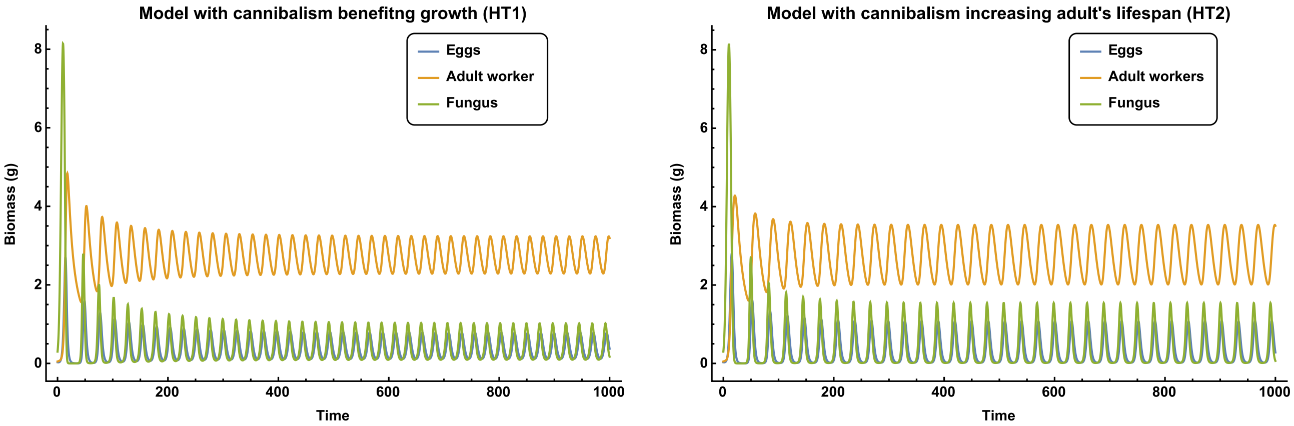
Model (2.3) and model (2.4) always have the extinction equilibrium which is always asymptotically stable. In addition, given the following conditions, both models can have maximum two interior equilibria: $\mathbf{E_i} = (F_i^*, E_i^*, A_i^*)$, $i = 1, 2$, such that all the components of $\mathbf{E_2}$ are larger than the components of $\mathbf{E_1}$ (i.e. $\mathbf{E_2} > \mathbf{E_1}$). For model (2.3):

1. *Colony dies out (zero and one interior equilibrium): If $\alpha > K_1$ or $a < K_2$, then the equilibrium $(0, 0, 0)$ is the only equilibrium of the system and it is global stability. On the other hand, when $\alpha = K_1$ or $a = K_2$, there is only one interior equilibrium which is saddle.*
2. *Colony survives (two interior equilibria): if $\alpha < K_1$ or $a > K_2$, $\mathbf{E_2}$ is locally asymptotically stable when*

$$r_a(1-p_1)F_2^* + c_1\alpha E_2^* < 2d_a A_2^*.$$

Similarly, for model (2.4), when $(0, 0, 0)$ is the only equilibrium, it is globally stable, while if two interior equilibria exists under condition 3 in Theorem 3.4, then $\mathbf{E_2}$ is locally asymptotically stable when

$$r_a(1-p_1)F_2^* < \frac{2d_a A_2^*}{1 + c_2\alpha E_2^*}.$$



Solution to model (3) with $c_1 = 0.85$

Solution to model (4) with $c_2 = 85$.

FIGURE 7. $p_1 = 0.85; \alpha = 0.08; r_c = 0.7; r_f = 2; b = 0.002; d_f = 0.2; a = 0.3; r_a = 0.15; d_a = 0.02; \beta = 0.15.$

Biological implication: Theorem 3.5 suggests that both egg cannibalism and division of labor are important factors for the survival of a colony of leaf cutter ants. For instance, if egg cannibalism rate is too large and the proportion of ants performing a given task is too small, then the colony will die out. However, for a small egg cannibalism rate and large proportion of ants performing a given task, *i.e.*, there are more ants investing energy on different tasks while using egg cannibalism as a way to regulate their growth, then the colony of leaf-cutter ants with fungus can survive. (See supplementary material in Appendix B.1).

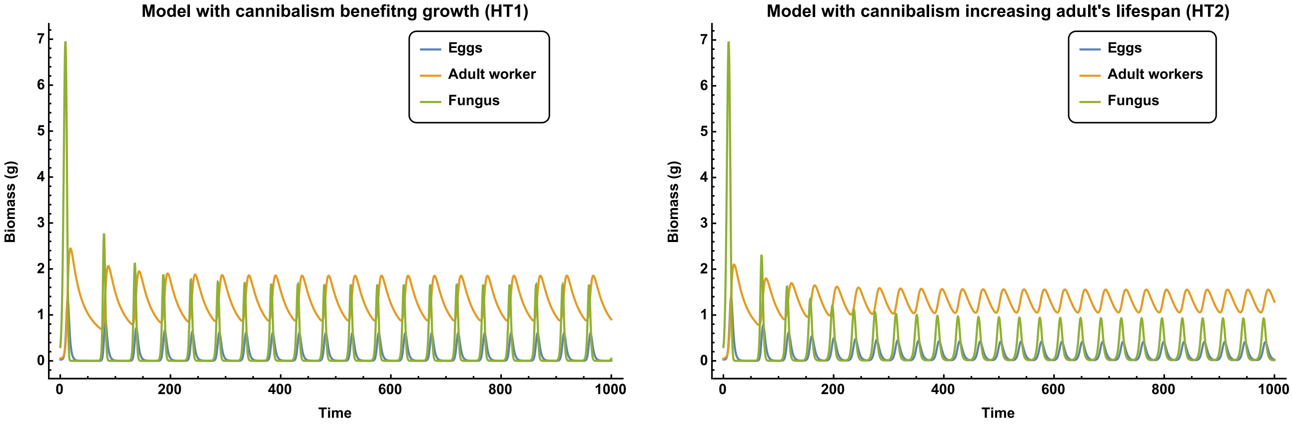
The following numerical simulations will aid to understand the different dynamics of models (2.3) and (2.4). *We investigate the effects of egg cannibalism rate* α*, the parameter measuring the division of labor among the workers* a*, and the energy spent on brood care* p_1 *on the biomass of eggs* E*, adult workers* A*, and fungus* F*.*

We compare the dynamics of model (2.3) *and model* (2.4) *with egg cannibalism used as energy for growth of the adult population described with the Holling Type I functional response* $c_1\alpha AE$ *and for energy to decrease death rate (increase lifespan) of adult workers* $\frac{d_a A^2}{1+c_2\alpha E}$.

3.2.1. Numerical simulations

The time series solutions for model (2.3) and model (2.4) when testing the increase of p_1 and r_c, respectively, are shown in Figure 7 and Figure 8. Supplementary bifurcation diagrams in Appendix B.2 show the destabilizing effects produced by the increase of parameters describing the energy gained through the consumption of fungus by the adult worker invested on brood care, p_1, and the conversion rate between fungus and ants, r_c. For high energy invested on brood care p_1 by adult workers, and (or) high conversion rate between fungus and ants r_c, both model (2.3) and model (2.4) can have oscillatory solutions. Both of these systems models egg cannibalism and its benefits in two different fashions as previously described in our model derivation. Comparing the model (2.5) with no egg cannibalism, we observe that these fluctuation in populations dynamics emerge with the presence of egg cannibalism and other mechanisms related to brood care and nutrient consumption. Also, we want to point out that when r_c is too large, *e.g.* close to or greater than 2, the system goes through catastrophic event such that all solutions go to the extinction state.

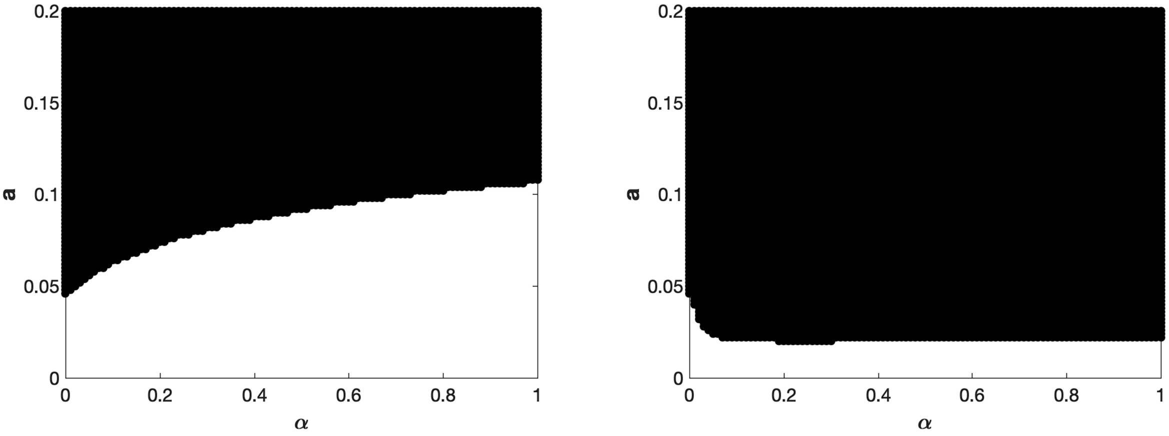
Next, we present 2-dimensional bifurcation diagrams in Figure 9, which shows the effects of egg cannibalism rate α with the parameter measuring the division of labor among the workers a in both models. In Figure 9a, we choose $c_1 = 0.1$ for model (2.3) showing that with no egg cannibalism and with small or no division of labor, the colony can die out, while large egg cannibalism rate together with a higher response of division labor the



Solution to model (3) with $c_1 = 0.8$

Solution to model (4) with $c_2 = 10$.

FIGURE 8. $\underline{r_c = 1.5}; \alpha = 0.08; p_1 = 0.8; r_f = 2; b = 0.002; d_f = 0.2; a = 0.3; r_a = 0.15; d_a = 0.02; \beta = 0.15$.



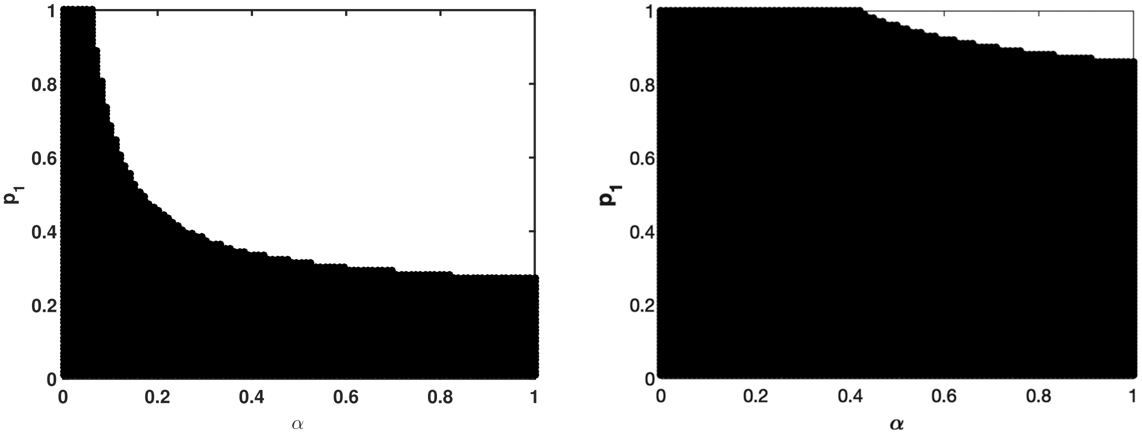
(a) Linear model. $c_1 = 0.1$

(b) Non-linear model. $c_2 = 10$

FIGURE 9. 2D bifurcation showing the effects of egg cannibalism rate with respect to the parameter measuring division of labor. $r_f = 1; b = 0.5; r_a = 0.07; d_f = 0.1; r_c = .007; d_a = 0.1; \beta = 0.5; p_1 = 0.5$. (Area in black denotes existence of interior equilibria and white represents no interior.)

colony can survive. Similarly, in Figure 9b, we choose $c_2 = 10$ for model (2.4) showing that for very small a the colony can die out, but larger a and any value of α the colony can survive. In this case, both of the models present similar results to those of model (2.1) and in [18], in which division of labor plays a role on the survival of the colony.

In Figure 10 we can see the effects that energy spent on brood care p_1 and the egg cannibalism rate α have on the existence of interior equilibria for models (2.3) and (2.4). For model (2.3), we can see in Figure 10a that the colony can survive with low energy spent on brood care p_1 or low egg cannibalism rate α. For model (2.4), we can see in Figure 10b that the colony can survive almost under any value of p_1 and α. *However, with a high egg cannibalism rate and the majority of energy being spent on brood care and not on adult's growth, the colony will not survive.* Next, we provide 1-dimensional bifurcation diagrams in Figures 11–14, which show



(a) Linear model ($c_1 = 0.1$) (b) Nonlinear model ($c_2 = 10$)

FIGURE 10. 2D bifurcation showing the effects of egg cannibalism rate with respect to the energy spent on brood care. $a = 0.05; r_f = 1; b = 0.5; r_a = 0.07; d_f = 0.1; r_c = .007; d_a = 0.1; \beta = 0.5$. (Area in black denotes existence of interior equilibria and white represents no interior.)

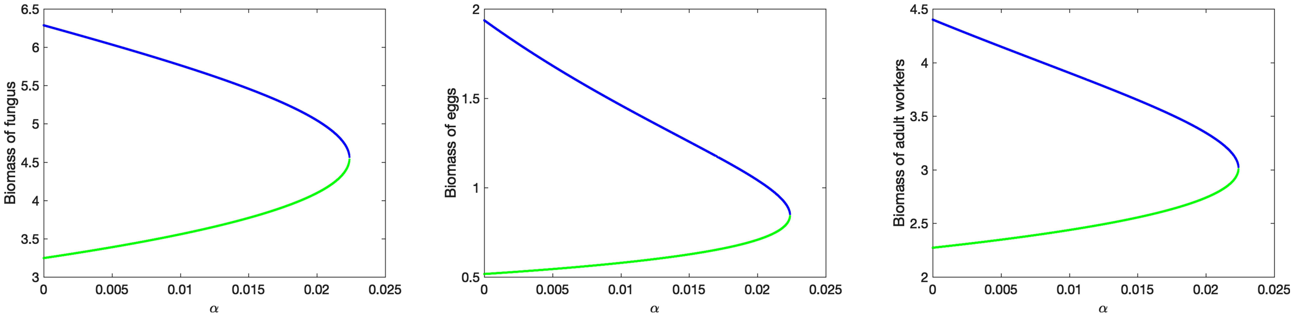


FIGURE 11. 1D bifurcation disgram of the linear model (2.3) $c_1 = 0.1; a = 0.05; r_f = 1; b = 0.5; r_a = 0.07; d_f = 0.1; r_c = .007; d_a = 0.1; \beta = 0.5; p_1 = 0.5$. (*Blue*: stable and *green*: unstable interior equilibria.)

that both models can have two interior equilibria where one of them is stable and the other one is unstable. In Figures 11 and 12, we vary the parameter describing the egg cannibalism rate α with different c_1. In both figures, we notice that as α increases, the biomass of fungus, eggs, and adult workers decreases and eventually disappears. *However, increasing* c_1 *the conversion rate between ants and eggs, allows a higher cannibalism rate between adult workers and eggs. This suggests that if egg cannibalism is utilized to maximize adult growth, then the colony can survive under difficult conditions.*

Figures 13 and 14 show the effects of egg cannibalism α and survival rate of adult workers due to cannibalism c_2 in model (2.4). The results in Figure 13 suggest that for small cannibalism rate the biomass in the colony can increase, but if the egg cannibalism is too large the colony dies out. However, for large c_2, the colony can survive even with very high egg cannibalism rate (see Fig. 14). In this case, because the energy obtained from the eggs cannibalized is been used to decrease mortality rate of adult workers, these have the highest biomass in the colony.

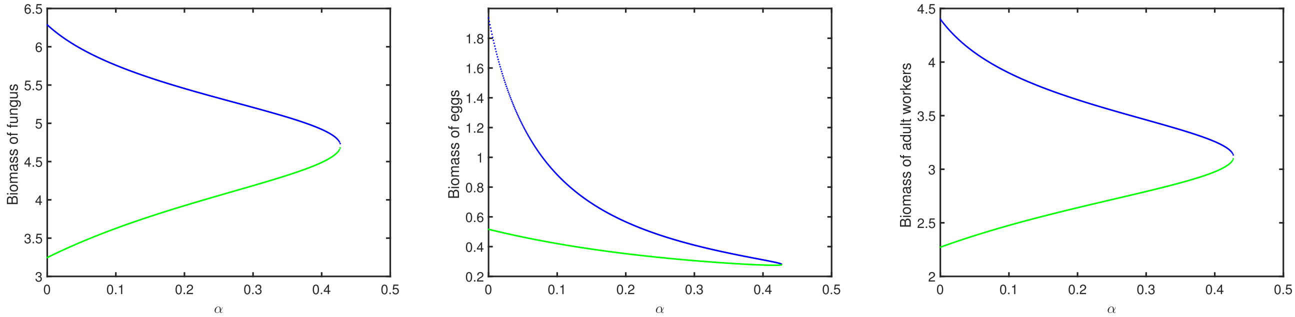


FIGURE 12. 1D bifurcation diagram of the linear model (2.3) $\underline{c_1 = 0.85}; a = 0.05; r_f = 1; b = 0.5; r_a = 0.07; d_f = 0.1; r_c = .007; d_a = 0.1; \beta = 0.5; p_1 = 0.5$. (*Blue*: stable and *green*: unstable interior equilibria.)

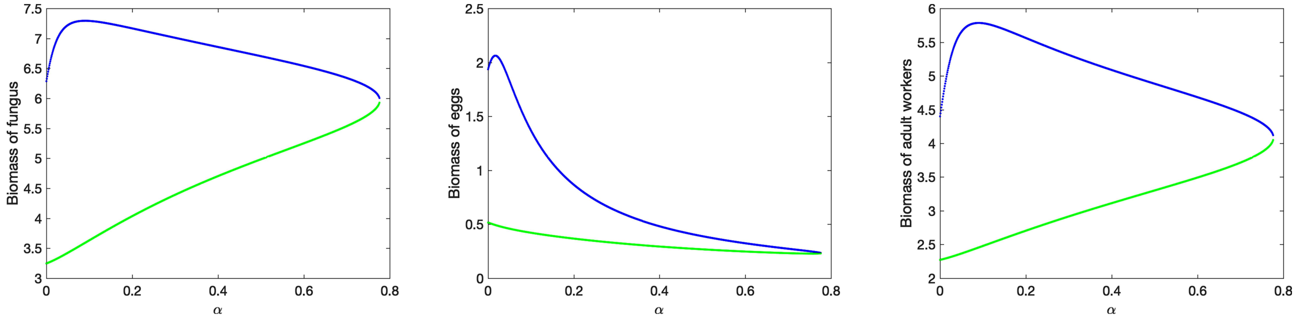


FIGURE 13. 1D bifurcation diagram of the non-linear model (2.4) $\underline{c_2 = 4}; a = 0.05; r_f = 1; b = 0.5; r_a = 0.07; d_f = 0.1; r_c = .007; d_a = 0.1; \beta = 0.5; p_1 = 0.5$. (*Blue*: stable and *green*: unstable interior equilibria.)

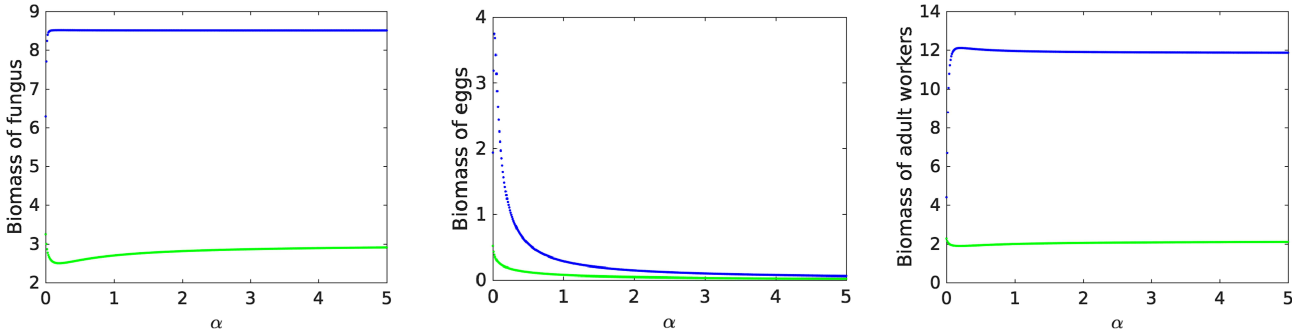


FIGURE 14. 1D bifurcation diagrams of the non-linear model (2.4) $\underline{c_2 = 10}; a = 0.05; r_f = 1; b = 0.5; r_a = 0.07; d_f = 0.1; r_c = .007; d_a = 0.1; \beta = 0.5; p_1 = 0.5$. (*Blue*: stable and *green*: unstable interior equilibria.)

4. DISCUSSION

Modeling social insect biology has helped study the complex phenomena simple mechanisms can produce. Models proposed in [16], for instance, provide some advances on understanding the dynamics of brood production and colony development of paper wasps by considering oophagy in the models. In the work of Schmickl *et al.* [29], through empirical study, they were able to determine that shortage of pollen can induce cannibalism of young honeybee larvae, and that cannibalism serves to recycle nutrients, mainly protein, to convert back into worker jelly. In [31], showed that task partitioning can lead to self-regulation mechanisms.

In this work, we presented three different models to study the effects of age polyethism and egg cannibalism on the population dynamics of a leaf-cutter ant colony. System (2.2) models the explicit division of labor of (adult) worker ants in a leaf-cutter ant colony where we subdivided the total worker population $A(t)$ in two groups: worker ants in charge of processing and cultivating the fungus garden (inside workers) $A_i(t)$ and worker ants in charge of collecting leaves to grow the fungus garden (outside/forager workers) $A_o(t)$. This system models the work done by each of these groups of ants, the consumption rate of fungus for growth/development of workers, and respective natural death rates. We considered the case when $\beta = 0$ in model (2.2) to study the effects of their age-based division of labor (*i.e.* age-polyethism) within the colony dynamics.

Our analytical and numerical results show that without age-polyethism (*i.e.* $\beta = 0$), the system (2.2) can have infinitely many solutions (*i.e.* infinitely many interior equilibria) under the condition $\frac{d_i}{c_i r_i} = \frac{d_o}{c_o r_o}$, which represents the ratio of mortality to growth in both task groups A_i and A_o. Including age-polyethism (*i.e.*, $\beta > 0$), model (2.2) has a maximum of two interior equilibria. The effects of β (*i.e.* maturation rate) on the biomass of fungus, inside and outside workers are considered to be beneficial for certain ranges, *i.e.*, a very high maturation rate could terminate the colony. An explanation of this situation could be that when inside workers begin to mature faster and switch to performing riskier tasks, this leads to an increase of mortality. Also, the production of new workers to perform inside tasks is not fast enough.Therefore, the colony experiences negative effects causing its collapse. Also, with the subdivision of workers into two task groups, we were able to capture in model (2.2) and Figure 2 that if one of the task groups decreases (in this case, A_i decreases as β increases) while the other task group A_o increases, then the fungus receives a greater contribution from the ants working outside the colony. Model (2.2) with $\beta > 0$ suggests that increasing the outside worker population has greater benefits for colony growth and development than increasing the inside worker population, as long as a certain necessary number of inside colony workers exist to care for the fungus and the brood. The evolutionary implications of this finding, and the role it plays in the life history of leaf-cutter ants, should be investigated in future studies.

Comparing the two different cases considered in model (2.2), *i.e.* $\beta = 0$ and $\beta > 0$, we conclude that age polyethism has clear benefits for the stability of a colony, which is logically consistent with the important role it plays in the life of leaf-cutter ants [15]. However, it is interesting that the model also shows that the benefits of age polyethism are constrained by β, the maturation rate. Whether the maturation rate of leaf-cutter ants has been shaped by this restriction imposed by age polyethism should be investigated in future studies.

On the other hand, systems (2.3) and (2.4) model an implicit division of labor and egg cannibalism by including two developmental stages, *i.e.* eggs and adults, in which adults perform necessary tasks to maintain their fungus cultivar, and interact with eggs by providing brood care or cannibalizing them. Model (2.3) differs with model (2.4) by the choice of Holling Type functional response that models different ways egg cannibalism can contribute to the colony dynamics. In model (2.3), we use the Holling Type I functional response $c_1 \alpha A E$ to describe the positive input that egg cannibalism can provide to the adult class as a nutrient source for growth purposes, whereas model (2.4) has the Holling Type II functional response $\frac{d_a A}{1+c_2 \alpha A E}$ that describes the contribution of egg cannibalism as nutrient source to decrease death rate of the adult class, thus providing an increase of worker lifespan (see Figs. 11–14). This opens an opportunity to perform manipulative experimental work to determine whether egg cannibalism increase lifespan of adult workers, or if it has alternative benefits.

In the absence of egg cannibalism, *i.e.*, when $\alpha = 0$, both model (2.3) and model (2.4) reduce to model (2.5) and have simple dynamics. The dynamics of model (2.5) with no egg cannibalism suggest that division of labor plays an important factor determining whether a colony of leaf cutter ants can survive or not in the absence of egg cannibalism. In such a case, if a is too small, *i.e.*, the proportion of adult ants performing certain tasks is too small, then the energy invested to a given task is not enough to maintain a colony. This leads to colony collapse. However, if the proportion of adult ants performing given tasks is large enough, then the colony can survive. This suggests that there may be an evolutionary relationship between division of labor and egg cannibalism, which it would be interesting to explore in future work. Moreover, the dynamics of model (2.3) suggest that in addition to division of labor, egg cannibalism could also play a role in the survival of the colony. This model can show the survival of a colony when egg cannibalism is not too large and the proportion of of adult ants performing necessary tasks is large enough. Even though model (2.3) has the addition of egg cannibalism as a mechanism of survival, it is not the best model to show the positive mechanisms that egg cannibalism represent in a colony. Therefore, the functional response introduced in model (2.4) improves this model by providing survival of the colony when model (2.5) with no egg cannibalism and model (2.3) with cannibalism described in the form of Holling Type I functional response cannot.

Another interesting result of models (2.3) and (2.4) is the possibility of destabilizing effects of population dynamics, *i.e.*, fluctuations in populations size. Comparing the dynamics obtained in [18] of a model with no egg cannibalism considered and our models with egg cannibalism, we conclude that this fluctuations arise due to the egg cannibalism behavior in the colony. These fluctuations, as seen in Figures 7 and 8, are also developed by the increase of energy invested in brood care and the conversion rate of between fungus and ants. In [16], Karsai *et al.* made similar findings with respect to the fluctuations in brood dynamics in paper wasps due to egg cannibalism. Their models assumed that adults prefer to feed the larvae with the younger eggs. This will produce a huge and fast decrease of eggs, but at the same time, there is a positive feedback mechanism due to an increase of egg-laying rate, which produce the fluctuations. In [16], we can consider the adults feeding the larvae with eggs as the brood care through egg cannibalism, and therefore, our model produce similar results through this mechanisms.

Appendix A. Parameter values

These intervals are obtained from the approximations according to empirical work [3, 6, 18].

Table A.1. Intervals of parameters used in the models.

Parameter	Intervals	Reference
r_a: Maximum growth rate of ants	(0.05,0.3)	[18]
r_f: Maximum growth rate of fungus	(0.01,1)	[18]
r_c, c_i, c_o: Conversion rate between fungus and ants	(0.001,10)	[18]
d_a, d_i, d_o: Death rate of ants, inside and outside adult workers	(0.001,1)	[18]
d_f: Deterioration rate of fungus	(0.001,1)	[18]
r_i, r_o: Consumption rate of fungus	variable	
b: Half-saturation constant	(0.001,10)	[18]
a: Measurement of the division of labor	(0.0.25)	[18]
p_1: Energy invested on brood care	(0,1)	variable
α: Cannibalism rate	variable	
β: Maturation rate	(0.015, 0.25)	[2, 4]
c_1: Conversion efficiency between ants and eggs	(0,1)	variable
c_2: Regulation effect of an increase of cannibalism	arbitrary	variable

Appendix B. Supplementary material

B.1 Supplementary bifurcation diagrams comparing dynamics of egg cannibalism in models (2.3) and (2.4)

The following bifurcation diagrams compares the dynamics of egg cannibalism in models 2.3 and 2.4 explained in Theorem 3.5. The figures display dashed blue and green lines representing the stable and unstable interior equilibria, respectively, for model (2.4). The solid blue and green lines represent the stable and unstable interior equilibria, respectively, for model (2.3). Figure B.1 helps us understand better that model (2.4) provides colony survival for a larger range of α (egg cannibalism rate).

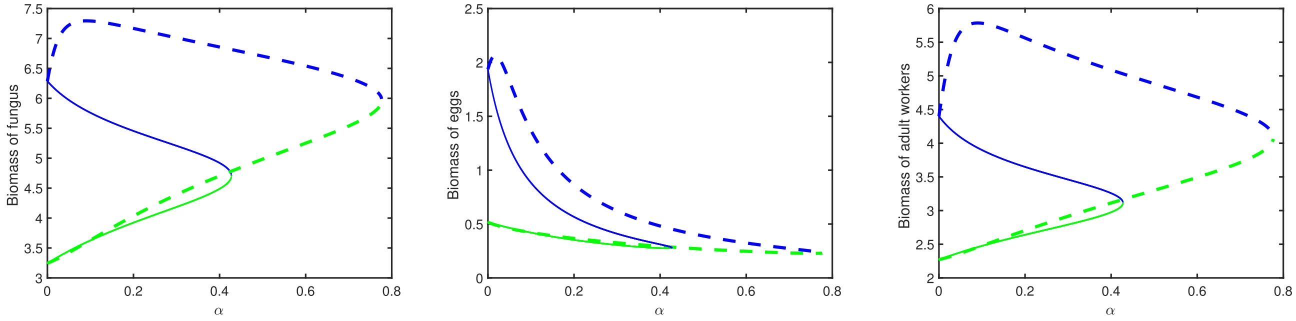


FIGURE B.1. 1D bifurcation diagrams: models comparison of egg cannibalism dynamics. $\underline{c_1 = 0.85; c_2 = 4;} a = 0.05; r_f = 1; b = 0.5; r_a = 0.07; d_f = 0.1; r_c = .007; d_a = 0.1; \beta = 0.5; p_1 = 0.5$ (*Blue*: stable and *green*: unstable interior equilibria.)

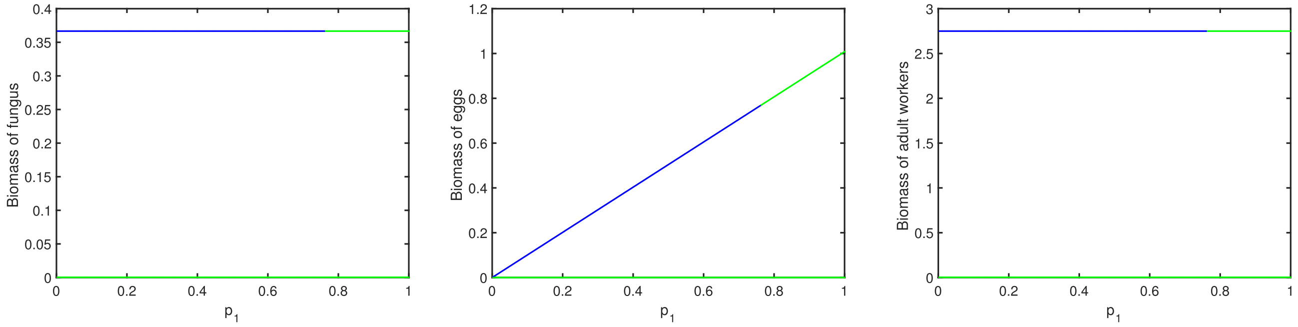


FIGURE B.2. 1D bifurcation diagrams of the model (2.5) with no cannibalism. $\underline{\alpha = 0}, \underline{r_c = 0.7}, r_f = 2, b = 0.002, d_f = 0.2, a = 0.3, r_a = 0.15, d_a = 0.02, \beta = 0.15, c_1 = 0.8$ (*Blue*: stable and *green*: unstable interior equilibria.)

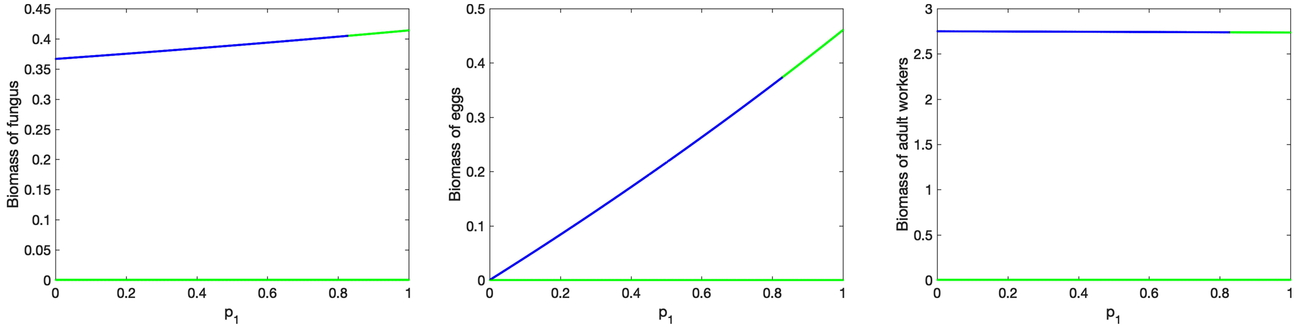


FIGURE B.3. 1D bifurcation diagrams of the model (2.3). $\underline{\alpha = 0.08}, \underline{r_c = 0.7}, c_1 = 0.8, r_f = 2, b = 0.002, d_f = 0.2, a = 0.3, r_a = 0.15, d_a = 0.02, \beta = 0.15$ (*Blue*: stable and *green*: unstable interior equilibria.)

B.2 Supplementary bifurcation diagrams for time series Figure 7 and Figure 8

In Figures B.2–B.4 we compare the effects of p_1: the energy gained through the consumption of fungus by the adult workers which is then distributed (or invested) on brood care. In Figure B.2, which represents the case when there is no egg cannibalism, the biomass of fungus, eggs, and adult workers can have oscillatory solutions if the energy invested on brood care is medium to high. In Figures B.3, we introduce cannibalism

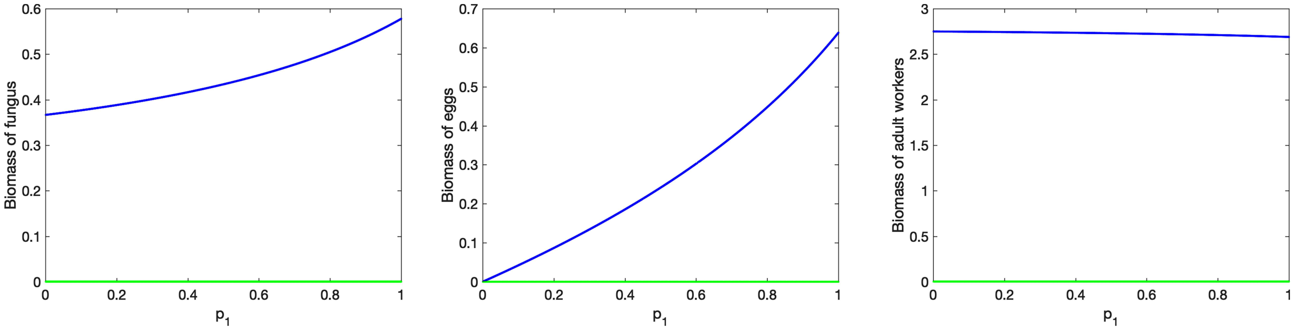


FIGURE B.4. 1D bifurcation diagrams of the model (2.4). $\underline{\alpha = 0.08}, \underline{r_c = 0.7}, c_2 = 10, r_f = 2, b = 0.002, d_f = 0.2, a = 0.3, r_a = 0.15, d_a = 0.02, \beta = 0.15$ (*Blue*: stable and *green*: unstable interior equilibria.)

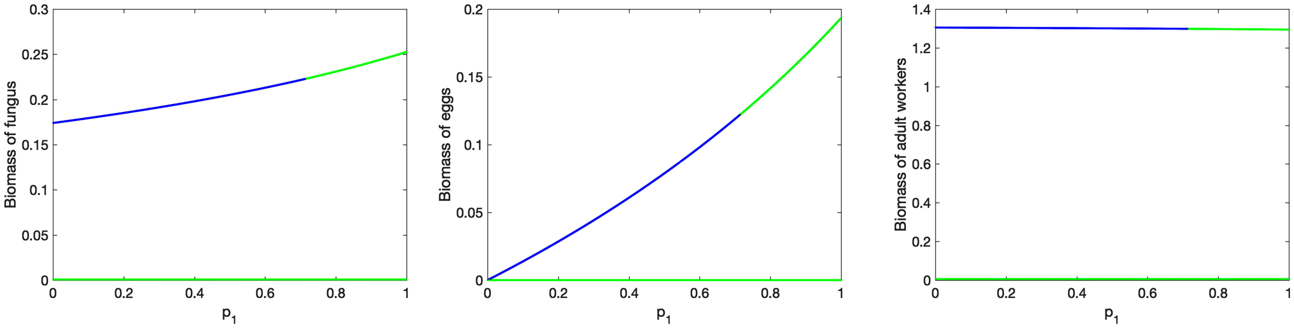


FIGURE B.5. 1D bifurcation diagrams of the model (2.4). $\underline{\alpha = 0.08}, \underline{r_c = 1.5}, c_2 = 10, r_f = 2, b = 0.002, d_f = 0.2, a = 0.3, r_a = 0.15, d_a = 0.02, \beta = 0.15$ (*Blue*: stable and *green*: unstable interior equilibria.)

$(\alpha > 0)$ as represented in model (2.3). In this case, the range in which oscillatory solutions can happen is decreased while the range of stable biomass is increased. This effect is produced by the way worker ants are using the converted energy from cannibalized eggs for their own growth. In Figure B.4, the energy from egg cannibalism is used to increase adult lifespan, therefore, higher levels of energy is available to invest on brood care keeping the biomasses stable. Moreover, model (2.4) shows an increase of biomass of fungus, eggs, and adult workers as p_1 increases compared to that in model (2.3), when there is no egg cannibalism. As a note, it seems that egg cannibalism can stabilize the dynamics with the nonlinear model (2.4) having better stabilizing ability. In Figure B.5, we noticed that increasing r_c, *i.e.* the conversion rate between fungus and ants, can produce oscillatory solutions as p_1 increases. This suggests that r_c can potentially destabilize the dynamics in the nonlinear model (2.4).

APPENDIX C. PROOFS

C.1 Proof for Theorem 3.1

Proof. For any $F \geq 0, A_i \geq 0$, and $A_o \geq 0$ we have for system (2.2)

$$\frac{\mathrm{d}F}{\mathrm{d}t}|_{F=0} = 0, \quad \frac{\mathrm{d}A_i}{\mathrm{d}t}|_{A_i=0} = 0, \quad \frac{\mathrm{d}A_o}{\mathrm{d}t}|_{A_o=0} = 0$$

and for system (2.2)

$$\frac{\mathrm{d}F}{\mathrm{d}t}\Big|_{F=0}=0,\quad \frac{\mathrm{d}A_i}{\mathrm{d}t}\Big|_{A_i=0}=0,\quad \frac{\mathrm{d}A_o}{\mathrm{d}t}\Big|_{A_o=0}=\beta A_i\geq 0$$

thus according to the Theorem A.24 in [35], we can conclude that for model (2.2) are positive invariant in $\mathbb{R}^3_+$. Now we show boundedness of the system. First, we have the following inequalities due to the property of positive invariance:

$$\frac{\mathrm{d}F}{\mathrm{d}t}=\left[\frac{r_fA_iA_o}{b+A_iA_0}-d_fF-r_iA_i-r_oA_o\right]F\leq(r_f-d_fF)F$$

which implies that

$$\limsup_{t\to\infty}F(t)\leq\frac{r_f}{d_f}=M. \tag{C.1}$$

This indicates that for any $\epsilon_1>0$, there exists T_1 large enough, such that

$$F(t)\leq M+\epsilon_1\quad\text{for all } t>T_1.$$

Now let $N=A_i+A_o$, then

$$\begin{aligned}N'=A_i'+A_o'&=F(c_ir_iA_i+c_or_oA_o)-N(d_iA_i+d_oA_o)\\&\leq cFN-dN^2)\\&\leq N(c(M+\epsilon_1)-dN)\qquad\text{for all } t>T_1\end{aligned}$$

which indicates

$$\limsup_{t\to\infty}N(t)\leq\frac{cr_f}{dd_f},$$

where $c=\max\{c_ir_i,c_or_o\}$ and $d=\min\{d_i,d_o\}$. Then every trajectory starting from $\mathbb{R}^3_+$ converges to the compact set $C=\left[0,\frac{r_f}{d_f}\right]\times\left[0,\frac{cr_f}{dd_f}\right]$.

In system (2.3) and (2.4), for any $F\geq0, E\geq0$, and $A\geq0$ we have that

$$\frac{\mathrm{d}F}{\mathrm{d}t}\Big|_{F=0}=0,\quad \frac{\mathrm{d}E}{\mathrm{d}t}\Big|_{E=0}=p_1r_aAF\geq0,\quad \frac{\mathrm{d}A}{\mathrm{d}t}\Big|_{A=0}=\beta E\geq0.$$

Therefore, we conclude that both model (2.3) and (2.4) are positive invariant in $\mathbb{R}^3_+$.
For the system (2.4), let $A(t),E(t),F(t)>0$ for $t\in\mathbb{R}_+$. From C.1 we have that

$$\limsup_{t\to\infty}F(t)\leq\frac{r_f}{d_f}.$$

This indicates that for any $\epsilon>0$, there exists T_1 large enough, such that

$$F(t)\leq M_1+\epsilon_1\quad\text{for all}\quad t>T_1.$$

Similarly, from the second equation of (2.4) we get

$$\frac{\mathrm{d}E}{\mathrm{d}t} = p_1 r_a AF - \alpha AE - \beta E \leq A(p_1 r_a F - \alpha E) \leq A\Big(p_1 r_a \left(\frac{r_f}{d_f} + \epsilon_1\right) - \alpha E\Big), \quad \text{for all} \quad t \geq T_1$$

which indicates

$$\limsup_{t\to\infty} E(t) \leq \frac{p_1 r_a r_f}{\alpha d_f}.$$

Therefore for any $\epsilon_2 > 0$, there exists T_2 large enough, such that

$$E(t) \leq \frac{p_1 r_a r_f}{\alpha d_f} + \epsilon_2 \quad \text{for all} \quad t \geq T_1.$$

Let $N(t) = A(t) + E(t)$, then

$$N' = A\Big(r_a F - \frac{d_a A}{1 + c_2 \alpha E} - \alpha E\Big) \leq A\Big(r_a M_1 + \frac{d_a M_2}{1 + c_2 \alpha M_2} - \frac{d_a}{1 + c_2 \alpha M_2} N\Big)$$

which implies

$$\limsup_{t\to\infty} N(t) \leq \frac{d_a M_2 + (r_a M_1 - \alpha M_2)(1 + \alpha c_2 M_2)}{d_a} = M_3$$

Then every trajectory starting from $\mathbb{R}^3_+$ converges to the compact set $D = \left[0, \frac{r_f}{b d_f}\right] \times [0, M_3]$. This implies that all three populations are bounded and this also holds for the linear system (2.3). ☐

C.2 Proof of Theorem 3.2

Proof. The interior equilibria (F^*, A_i^*, A_o^*) of model (2.2) when $\beta = 0$ is determined with $\frac{\mathrm{d}F}{\mathrm{d}t} = \frac{\mathrm{d}A_i}{\mathrm{d}t} = \frac{\mathrm{d}A_o}{\mathrm{d}t} = 0$ as follows:

$$\frac{r_f A_i^* A_o^*}{b + A_i^* A_0^*} - d_f F^* - r_i A_i^* - r_o A_o^* = 0 \qquad \Rightarrow \qquad F^* = \frac{A_i^* A_o^* r_f - (A_i^* A_o^* + b)(r_i A_i^* + r_o A_o^*)}{(b + A_i^* A_o^*) d_f} \tag{C.2}$$

$$c_i r_i A_i^* F^* - d_i A_i^* (A_i^* + A_o^*) = 0 \qquad \Rightarrow \qquad F^* = \frac{(A_i^* + A_o^*) d_i}{c_i r_i} \tag{C.3}$$

$$c_o r_o A_o^* F^* - d_o A_o^* (A_i^* + A_o^*) = 0 \qquad \Rightarrow \qquad F^* = \frac{(A_i^* + A_o^*) d_o}{c_o r_o} \tag{C.4}$$

$$\text{(C.3)} = \text{(C.4)} \Rightarrow \quad (A_i^* + A_o^*)\left(\frac{d_i}{c_i r_i} - \frac{d_o}{c_o r_o}\right) = 0 \quad \Rightarrow \quad \frac{d_i}{c_i r_i} = \frac{d_o}{c_o r_o} \quad \text{which implies} \quad A_i^* + A_o^* > 0.$$

From the equation above, we can conclude that the system has infinitely many positive solutions if and only if $\frac{d_o}{d_i} = \frac{c_o r_o}{c_i r_i}$.

We substitute (C.3) into (C.2) and we obtain

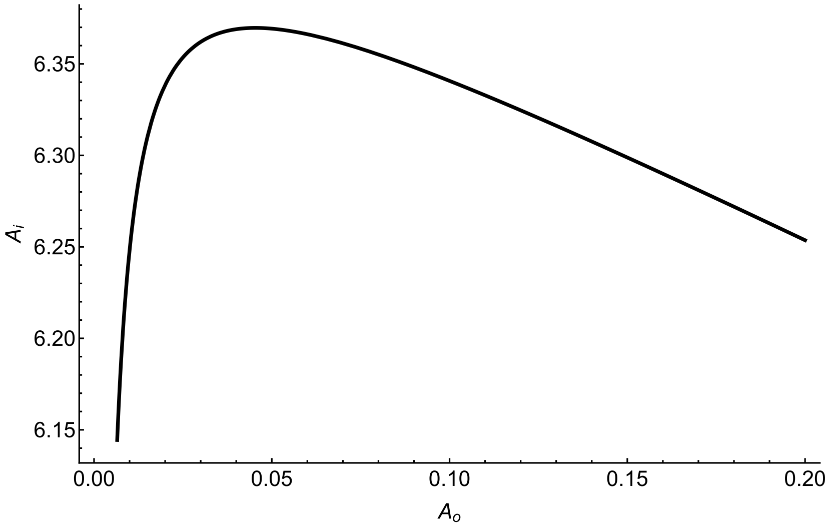


FIGURE C.1. Relation of A_i with A_o in model (2.2) when $\beta = 0$; $A_i = \frac{-c_i d_o(d_f d_o + c_o r_o^2)A_o^2 + c_i c_o d_o r_f r_o A_o - b(c_i d_f d_o^2 + c_o^2 d_i r_o^2)}{(c_i d_f d_o^2 + c_o^2 d_i r_o^2)A_o}$ with parameters $r_f = 0.7, b = 0.002, d_f = 0.2, d_i = 0.01, d_o = 0.0095, c_i = c_o = 0.7, r_o = 0.06$ with $\mathbf{r_i} = \frac{\mathbf{d_i c_o r_o}}{\mathbf{d_o c_i}}$.

$$A_i = \frac{-c_i d_o(d_f d_o + c_o r_o^2)A_o^2 + c_i c_o d_o r_f r_o A_o - b(c_i d_f d_o^2 + c_o^2 d_i r_o^2)}{(c_i d_f d_o^2 + c_o^2 d_i r_o^2)A_o}$$

The interior equilibria (F^*, A_i^*, A_o^*) of model (2.2) is determined as follows:

From $A_i'(t) = 0$, yields

$$F^* = \frac{(A_i^* + A_o^*)d_i + \beta}{c_i r_i}, \tag{C.5}$$

and from $A_o'(t) = 0$, yields

$$A_i^* = \frac{A_o^*(d_o A_o^* - c_o r_o F^*)}{\beta - d_o A_o^*} \tag{C.6}$$

Substituting equation (C.5) into (C.6) and solving for A_i, results in

$$A_i^* = A_o^*\left[\frac{(d_o - d_i\kappa)A_o^* - \beta\kappa}{\beta - (d_o - d_i\kappa)A_o^*}\right] \tag{C.7}$$

where $\kappa = \frac{c_o r_o}{c_i r_i}$.

Condition C.1: Consider $c_i, c_o \in (0,1)$, A_i^* is positive for $\kappa = \frac{c_o r_o}{c_i r_i} < 1$ whenever $\frac{\beta\kappa}{d_o - d_i\kappa} < A_o^* < \frac{\beta}{d_o - d_i\kappa}$, but also if $\kappa = \frac{c_o r_o}{c_i r_i} > 1$, then $\frac{\beta}{d_o - d_i\kappa} < A_o^* < \frac{\beta\kappa}{d_o - d_i\kappa}$, both cases satisfying $\frac{d_o}{d_i} > \kappa = \frac{c_o r_o}{c_i r_i}$.

Now substituting (C.7) into (C.2) we obtain the following nullcline:

$$g_2(A_o) = a_4 A_o^4 + a_3 A_o^3 + a_2 A_o^2 + a_1 A_o + a_0 = 0 \tag{C.8}$$

$$\begin{aligned}
a_4 &= -c_i r_i (r_i - r_o)(d_o - d_i\kappa)^2 \\
a_3 &= -(d_o - d_i\kappa)(d_o r_f + r_o\beta) - \kappa(\beta(r_o - 2r_i) - d_i r_f) \\
a_2 &= b c_i r_i (r_i - r_o)(d_o - d_i\kappa)^2 + \beta c_i r_i [d_o r_f - \kappa^2(d_i r_f + r_i\beta) + \kappa(d_o r_f + r_o\beta - d_i d_f)] \\
a_1 &= -\beta r_i (b(c_i(r_i - 2r_o) + c_o r_o)(d_o - d_i\kappa) + c_i\beta\kappa) \\
a_0 &= -b r_i r_o \beta^2 (c_i - c_o)
\end{aligned}$$

The nullcline (C.8) always have at least two positive roots. However, if a root A_o from (C.8) does not satisfy Condition A1, then model (2.2) has no interior equilibria. Additional conditions for no interior equilibria are:

$$\frac{d_o}{d_i} < \kappa, \quad r_i < r_o \qquad c_i < c_o, \qquad \beta < \frac{d_i r_f}{r_o - 2r_i}, \qquad d_o r_f(1+\kappa) + \kappa r_o \beta < \kappa^2 r_i (d_i + \beta) + \kappa d_i d_f$$

□

C.3 Proof for Theorem 3.3

Proof. The interior equilibria (F^*, E^*, A^*) of model (2.5) are determined by setting $F' = E' = A' = 0$. From the first equation of (2.5) we obtain

$$F^* = \frac{r_f a {A^*}^2}{d_f(b + a{A^*}^2)} - \frac{r_c}{d_f}A^* = \frac{A^*}{d_f}\left[\frac{r_f a A^*}{b + a{A^*}^2} - r_c\right] = A^* f(A^*) \tag{C.9}$$

By setting $E' + A' = 0$ yields

$$r_a F^* - d_a A^* = 0 \qquad \Rightarrow \qquad F^* = \frac{d_a}{r_a}A^* \qquad \Rightarrow \qquad f(A^*) = \frac{d_a}{r_a} \qquad \Rightarrow \qquad \frac{r_f a A^*}{d_f(b + a{A^*}^2)} - \frac{r_c}{d_f} - \frac{d_a}{r_a} = 0$$

Hence, by solving $f(A) = \frac{d_a}{r_a}$ for A, which is equivalent to $g(A) = -a(d_a d_f + r_a r_c)A^2 + a r_a r_f A - b(d_a d_f + r_a r_c)$, we obtain the following cases:

1. If $a > 4b(d_a d_f + r_a r_c)/(r_a r_f)^2$, then by simple algebraic calculations, we can have the following two positive solutions of $g(A)$:

$$A_1^* = \frac{r_a r_f}{2(d_a d_f + r_a r_c)} - \sqrt{\left(\frac{r_a r_f}{2(d_a d_f + r_a r_c)}\right)^2 - \frac{b}{a(d_a d_f + r_a r_c)}}$$

$$A_2^* = \frac{r_a r_f}{2(d_a d_f + r_a r_c)} + \sqrt{\left(\frac{r_a r_f}{2(d_a d_f + r_a r_c)}\right)^2 - \frac{b}{a(d_a d_f + r_a r_c)}}.$$

Thus, when there is no egg cannibalism, the two interior equilibria of model (2.5) are:

$$(F_1^*, E_1^*, A_1^*) = \left(\frac{d_a}{r_a}A_1^*, \frac{d_a p_1 {A_1^*}^2}{\beta}, A_1^*\right) \qquad \text{and} \qquad (F_2^*, E_2^*, A_2^*) = \left(\frac{d_a}{r_a}A_2^*, \frac{d_a p_1 {A_2^*}^2}{\beta}, A_2^*\right).$$

2. If $a = 4b(d_a d_f + r_a r_c)/(r_a r_f)^2$, then the system (2.5) has only one positive equilibria:

$$(F_1^*, E_1^*, A_1^*) = \left(\frac{d_a r_f}{2(d_a d_f + r_a r_c)}, \frac{d_a p_1 (r_a r_f)^2}{4\beta(d_a d_f + r_a r_c)^2}, \frac{r_a r_f}{2(d_a d_f + r_a r_c)}\right)$$

3. If $a < 4b(d_a d_f + r_a r_c)/(r_a r_f)^2$, then there is only one trivial equilibrium: $F = 0, E = 0$, and $A = 0$.

□

C.4 Proof for Theorem 3.4

Proof. The interior equilibria (F^*, E^*, A^*) of model (2.3) can be determined as follows:
From the first equation of (2.3) we obtain

$$F^* = \frac{r_f a {A^*}^2}{d_f(b + a{A^*}^2)} - \frac{r_c}{d_f}A^* = \frac{A^*}{d_f}\left[\frac{r_f a A^*}{b + a{A^*}^2} - r_c\right] = A^* f(A^*) \tag{C.10}$$

From the second equation of (2.3) we get

$$E^* = \frac{p_1 r_a A^* F^*}{\beta + \alpha A^*} = \frac{p_1 r_a {A^*}^2}{d_f(\beta + \alpha A^*)}\left[\frac{r_f a A^*}{b + a{A^*}^2} - r_c\right] = \frac{p_1 r_a {A^*}^2 f(A^*)}{\beta + \alpha A^*} \tag{C.11}$$

Let $E' + A' = 0$, then we get

$$\begin{aligned} r_a F^* - d_a A^* - \alpha(1 - c_1)E^* = 0 \quad & \Rightarrow r_a A^* f(A^*) - d_a A^* - \alpha(1 - c_1)\frac{p_1 r_a {A^*}^2 f(A^*)}{\beta + \alpha A^*} = 0 \\ & \Rightarrow f(A^*) = \frac{d_a}{r_a}\left[\frac{\beta + \alpha A^*}{\beta + \alpha A^*[1 - p_1(1 - c_1)]}\right] \\ & \Rightarrow \frac{1}{d_f}\left[\frac{r_f a A^*}{b + a{A^*}^2} - r_c\right] = \frac{d_a}{r_a}\left[\frac{\beta + \alpha A^*}{\beta + \alpha A^*[1 - p_1(1 - c_1)]}\right] \quad \text{[from (C.10)]} \end{aligned} \tag{C.12}$$

From the above, we obtain the nullcline

$$g(A) = A^3 + q_2 A^2 + q_1 A + q_0 \tag{C.13}$$

where

$$\begin{aligned} q_2 &= \frac{\beta(d_a d_f + r_a r_c) - r_a r_f \alpha[1 - p_1(1 - c_1)]}{\alpha(d_a d_f + r_a r_c[1 - p_1(1 - c_1)])} \\ q_1 &= \frac{\alpha b[d_a d_f + r_a r_c(1 - p_1(1 - c_1))] - a r_a r_f \beta}{a\alpha(d_a d_f + r_a r_c[1 - p_1(1 - c_1)])} \\ q_0 &= \frac{b\beta(d_a d_f + r_a r_c)}{a\alpha(d_a d_f + r_a r_c[1 - p_1(1 - c_1)])} > 0 \end{aligned}$$

Let $g(A) = A^3 + q_2A^2 + q_1A + q_0$ and $g'(A) = 3A^2 + 2q_2A + q_1$.

Then $g(A)$ has the following critical points:

$$A_1^c = \frac{-q_2 - \sqrt{\Delta}}{3}, \qquad A_2^c = \frac{-q_2 + \sqrt{\Delta}}{3}$$

where $\Delta = q_2^2 - 3q_1$. Since $q_0 > 0$, the sufficient condition for $g(A)$ to have positive real solutions is $q_2^2 - 3q_1 \geq 0$, *i.e.*,

$$\alpha \leq \frac{a\beta r_a r_f}{b(d_a d_f + r_a r_c(1 - p_1(1 - c_1))},$$

otherwise, $g(A)$ has no positive real solutions. When $q_2 < 0$, *i.e.* $\alpha > \frac{\beta(d_a d_f + r_a r_c)}{r_a r_f[1-p_1(1-c_1)]}$, and $\Delta > 0$ then $g(A)$ has two positive critical points $0 < A_1^c < A_2^c$. Notice that $g''(A_1^c) = -2\sqrt{\Delta} < 0$ and $g''(A_2^c) = 2\sqrt{\Delta} > 0$, this implies that $g(A)$ has a local maximum at A_1^c and local minimum at A_2^c for $A > 0$, then $g(A)$ has two positive solutions if and only if $g(A_2^c) < 0$, otherwise it has no positive solutions, where

$$g(A_2^c) = \frac{27q_0 + 6q_1\sqrt{\Delta} - q_2(9q_1 + 2q_2\sqrt{\Delta} - 2q_2^2)}{27}$$

Therefore, $g(A_2^c) < 0$, if $q_2(9q_1 + 2q_2\sqrt{\Delta} - 2q_2^2) > 27q_0 + 6q_1\sqrt{\Delta}$.

Now, we will show that when model (2.5) has no interior equilibria, model (2.3) cannot have interior equilibria. From Proposition 3.3 and (C.3), we have that $f(A) := \frac{1}{d_f}\left[\frac{r_f aA}{b+aA^2} - r_c\right]$ and has the following properties: $f(0) = -\frac{r_c}{d_f} < 0$, $f(A)$ is an increasing function on $(0, \sqrt{b/a})$ and decreasing on $(\sqrt{b/a}, \infty)$. Therefore, $f(A)$ has a maximum $f_{\max} = \max_{A>0}\{f(A)\} = f(A^c = \sqrt{b/a}) = \frac{r_f\sqrt{ab} - 2br_c}{2bd_f}$. Hence, model (2.5) with $\alpha = 0$ can have interior equilibria if $f(A) = \frac{d_a}{r_a}$ and $f_{\max} \geq \frac{d_a}{r_a} > 0$. Therefore, if $f(A) < \frac{d_a}{r_a}$, then system (2.5) has no solutions in A, *i.e.*, when $f_{\max} < \frac{d_a}{r_a}$, but also if $f_{\max} < 0 < \frac{d_a}{r_a}$, *i.e.*, $\frac{r_f\sqrt{ab}}{2b} < r_c$, then model (2.5) can definitely not have interior equilibria, *i.e.*, colony cannot survive. Similarly, from (C.12), model (2.3) can have interior equilibria if $f(A) = \frac{d_a}{r_a}\left[\frac{\beta+\alpha A}{\beta+\alpha A[1-p_1(1-c_1)]}\right]$. Hence, since

$$\frac{d_a}{r_a} < \frac{d_a}{r_a}\left[\frac{\beta + \alpha A}{\beta + \alpha A[1 - p_1(1 - c_1)]}\right] \quad \Rightarrow \quad f_{\max} < \frac{d_a}{r_a} < \frac{d_a}{r_a}\left[\frac{\beta + \alpha A}{\beta + \alpha A[1 - p_1(1 - c_1)]}\right],$$

this implies that when model (2.5) (model representing a colony with no cannibalism) does not have interior equilibria, then model (2.3) can definitely have no interior interior equilibria.

Next, we show the dynamics of interior equilibria for model (2.4).

An interior equilibrium (F^*, E^*, A^*) of model (2.4) must satisfy the following three equations

$$\begin{aligned} 0 &= \frac{r_f aA^2}{b + aA^2} - d_f F - r_c A \\ 0 &= p_1 r_a AF - \alpha AE - \beta E \\ 0 &= (1 - p_1)r_a AF - \frac{d_a A^2}{1 + c_2\alpha E} + \beta E \end{aligned} \tag{C.14}$$

From the first and second equation of (C.14) we get (C.10) and (C.11), respectively.

If there is no egg cannibalism, then the interior solutions satisfy the equation $f(A) = \frac{d_a}{r_a}$. Complete dynamics of this case has been provided in Proposition 3.3.

Now, if there is egg cannibalism, then the interior solutions satisfy the following equation:
From (C.14), let $E' + A' = 0$, then we get

$$r_a F - \alpha E - \frac{d_a A}{1 + c_2\alpha E} = 0 \qquad \Rightarrow \quad f(A) = \frac{d_a}{r_a}\left[\frac{1}{1 + c_2\alpha E}\right] + \frac{\alpha E}{r_a A}.$$

Therefore, using (C.11)

$$f(A) = \frac{d_a}{r_a}\left[\frac{1}{1 + c_2 r_a A f(A)\frac{\alpha p_1 A}{\beta+\alpha A}}\right] + \frac{\alpha p_1 A f(A)}{\beta + \alpha A} \quad \Rightarrow \quad f(A)\left[1 - \frac{\alpha p_1 A}{\beta + \alpha A}\right] = \frac{d_a}{r_a}\left[\frac{1}{1 + c_2 r_a A f(A)\frac{\alpha p_1 A}{\beta+\alpha A}}\right]$$

$$\Rightarrow \quad f(A) = \frac{\frac{d_a}{r_a}}{\left[1 - \frac{\alpha p_1 A}{\beta+\alpha A}\right]\left[1 + c_2 r_a A f(A)\frac{\alpha p_1 A}{\beta+\alpha A}\right]} = \frac{\frac{d_a}{r_a}}{1 - \frac{\alpha p_1 A}{\beta+\alpha A}\left[1 - c_2 r_a A f(A)\left(1 - \frac{\alpha p_1 A}{\beta+\alpha A}\right)\right]}.$$

Let $h(A) = \frac{\alpha p_1 A}{\beta+\alpha A}\left[1 - c_2 r_a A f(A)\left(1 - \frac{\alpha p_1 A}{\beta+\alpha A}\right)\right]$. Thus

$$f(A) = \frac{\frac{d_a}{r_a}}{1 - h(A)} \tag{C.15}$$

From $h(A)$, we have

$$\frac{\alpha p_1 A}{\beta + \alpha A}(1 - c_2 r_a A f(A)) \le h(A) \le p_1.$$

Now, let A^* be the positive roots of the equation (C.15) subject to the condition $f(A^*) > 0$, so that the system (2.4) have interior attractors.

Therefore, we can have the following conclusions about model (2.4):

(1) If $f_{\max} < 0$, *i.e.*, $\frac{1}{d_f}\left(\frac{r_f\sqrt{ab}}{2b}\right) < r_c$, then our model has no interior equilibrium.

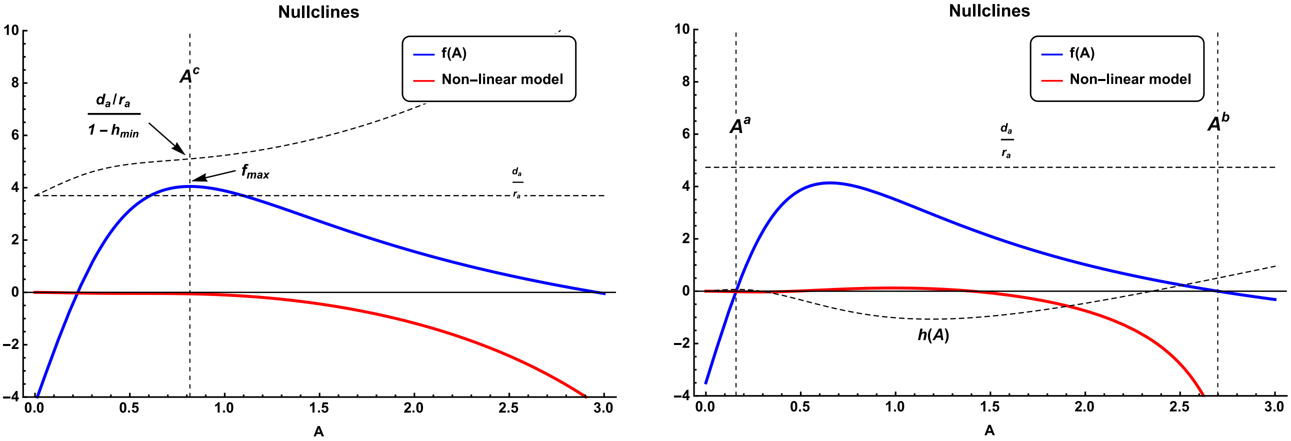
(2) If $f_{\max} > \frac{\frac{d_a}{r_a}}{1-p_1} > \frac{d_a}{r_a}$, then our model definitely has interior equilibria. This follows from the conclusion that model (2.5) can have interior equilibria when $f_{\max} > \frac{d_a}{r_a}$.

□

C.5 Supplementary material for Theorem 3.4.

Note that an interior equilibrium (F^*, E^*, A^*) of model (2.4) satisfies the equation

$$f(A) = \frac{d_a}{r_a[1 - h(A)]},$$



(a) $f_{\max} < \frac{\frac{d_a}{r_a}}{1-h_{\min}}$

(b) $f_{\max} < \frac{d_a}{r_a}$

FIGURE C.2. Two claims: $f_{\max} < \frac{\frac{d_a}{r_a}}{1-h_{\min}}$ *versus* $f_{\max} < \frac{d_a}{r_a}$

where

$$f(A) := \frac{1}{d_f}\left[\frac{r_f a A}{b + aA^2} - r_c\right] \quad \text{and} \quad h(A) := \frac{p_1 \alpha A}{\beta + \alpha A}\left[1 - c_2 r_a A f(A)\left(1 - \frac{\alpha p_1 A}{\beta + \alpha A}\right)\right].$$

Additionally to the proof and implications of Theorem 3.4, we have the following claims: If $f(A) = d_a/r_a$ has no positive solutions, then $f(A) = \frac{d_a}{r_a[1-h(A)]}$ definitely has no solutions in A if $h(A) > 0$. In general, if $f_{\max} < \frac{\frac{d_a}{r_a}}{1-h_{\min}}$ (see Fig. C.2a), where $h_{\min}$ is the minimum of $h(A)$ over $[0, A^c]$, this implies that it is possible for $f(A) = \frac{d_a}{r_a}$ to have positive solutions but $f(A) = \frac{\frac{d_a}{r_a}}{1-h(A)}$ does not have. If $f_{\max} < \frac{d_a}{r_a}$ (see Fig. C.2b), then $f(A) = \frac{\frac{d_a}{r_a}}{1-h(A)}$ can still have positive solutions in A if $h(A) < 0$ for a certain interval (A^a, A^b), where A^a and A^b are the smallest $A^a = \left((r_f/r_c) - \sqrt{(r_f/r_c)^2 - 4b/a}\right)/2$ and largest $A^b = \left((r_f/r_c) + \sqrt{(r_f/r_c)^2 - 4b/a}\right)/2$ roots of $f(A) = 0$.

C.6 Proof for Theorem 3.2

Proof. The stability of the equilibrium $\mathbf{E_i}$, $i = 1, 2, 3$ of model (2.2) is determined by the eigenvalues of the following Jacobian matrix J evaluated at the extinction equilibrium:

Jacobian Matrix for model (2.2):

$$J = \begin{pmatrix} -2d_f F + \frac{r_f A_i A_o}{b + A_i A_o} - r_i A_i - r_o A_o & \left(\frac{b r_f A_o}{(b+A_i A_o)^2} - r_i\right) F & \left(\frac{b r_f A_i}{(b+A_i A_o)^2} - r_o\right) F \\ c_i r_i A_i & c_i r_i F - (2A_i + A_o) d_i - \beta & -d_i A_i \\ c_o r_o A_o & \beta - d_o A_o & c_o r_o F - (A_i + 2A_o) d_o \end{pmatrix} \tag{C.16}$$

The stability of the equilibrium $\mathbf{E_i}$, $i = 1, 2, 3$ of model (2.2) when $\beta = 0$ is determined by the eigenvalues $\lambda_i(0, 0, 0)$, $i = 1, 2, 3$ of the Jacobian matrix (C.16), *i.e.*, $J_{1(0,0,0)} = \mathbf{0}_{3\times 3}$.

Hence, we will use Center Manifold Theory to determine the stability condition of system (2.2) when $\beta = 0$ at equilibrium $\mathbf{E_0}$. First, we simplify the system using Taylor series expansion (consider only up to the second order):

$$\begin{aligned} F'(t) &= -d_f F^2 - r_i A_i - r_o A_o F \\ A_i'(t) &= c_i r_i A_i F - d_i A_i (A_i + A_o) \\ A_o'(t) &= c_o r_o A_o F - d_o A_o (A_i + A_o) \end{aligned} \tag{C.17}$$

We replace A_0 in term of a function of F and A_o. For that, consider,

$$h(F, A_o) = a_1 F^2 + a_2 F A + a_3 A_o^2 + \mathcal{O}(F^3, A_o^3)$$

By some simple calculation, we get $h(F, A_o) \equiv 0$. Thus, the flow on the center manifold is given by

$$\begin{aligned} F'(t) \ &= -d_f F^2 - r_i A_i \\ A_i'(t) &= c_i r_i A_i F - d_i A_i^2 \end{aligned} \tag{C.18}$$

Again, both eigenvalues are zero for the system (C.18) at the trivial equilibrium $(0, 0)$. Using center manifold theory for the stability at its extinction equilibrium. This system is already in the desired form to use center manifold theory. Replacing A_i in terms of a function of F, *i.e.*, $g(F) = b_1 F^2 + b_2 F^3 + \mathcal{O}(F^4)$, and by simple calculation, it can be proved that $g(F) \equiv 0$. Therefore, the flow on the center manifold is given by

$$F' = -d_f F^2, \tag{C.19}$$

i.e., model (2.2) is always locally asymptotically stable at the extinction equilibrium $\mathbf{E_0}$.

Similarly, the stability of the extinction equilibrium for system (2.2) when $\beta > 0$ can be stablished by using Center Manifold Theory. It can be concluded that the flow on the center manifold for system (2.2) is given by (C.19), *i.e.*, model (2.2) is always locally asymptotically stable at the extinction equilibrium $\mathbf{E_0}$.

□

C.7 Proof for Theorem 3.5

Proof. The stability of the equilibrium $\mathbf{E_i}$, $i = 1, 2, 3$ of models (2.3) and (2.4) is determined by the eigenvalues of the following Jacobian matrix J associated to each model, respectively, evaluated at each equilibrium:

Jacobian for model (2.3):

$$J = \begin{pmatrix} -2d_f F^* + A^* \left(\frac{a r_f A^*}{b + a A^{*2}} - r_c \right) & 0 & F^* \left(\frac{2 a b r_f A^*}{(b + a A^{*2})^2} - r_c \right) \\ p_1 r_a A^* & -(\beta + \alpha A^*) & p_1 r_a F^* - \alpha E^* \\ r_a (1 - p_1) A^* & \beta + \alpha c_1 A^* & r_a (1 - p_1) F^* - 2 d_a A^* + \alpha c_1 E \end{pmatrix} \tag{C.20}$$

Jacobian for model (2.4):

$$J = \begin{pmatrix} -2d_fF^* + A^*\left(\frac{ar_fA^*}{b+aA^{*2}} - r_c\right) & 0 & F^*\left(\frac{2abr_fA^*}{(b+aA^{*2})^2} - r_c\right) \\ p_1r_aA^* & -(\beta+\alpha A^*) & p_1r_aF^* - \alpha E^* \\ r_a(1-p_1)A^* & \beta + \frac{\alpha c_2 d_a A^{*2}}{(1+c_2\alpha E^*)^2} & r_a(1-p_1)F^* - \frac{2d_aA^*}{1+c_2\alpha E^*} \end{pmatrix} \tag{C.21}$$

1. *Stability of extinction equilibrium for model* (2.3) *and* (2.4)

The stability of the extinction equilibrium $\mathbf{E_0} = (0,0,0)$ for models (2.3) and (2.4) is determined by the eigenvalues $\lambda_i(0,0,0)$, $i = 1,2,3$ of the Jacobian matrix (C.20) and (C.21), respectively, evaluated at $\mathbf{E_0}$. *i.e.*

$$J_{(0,0,0)} = \begin{pmatrix} 0 & 0 & 0 \\ 0 & -\beta & 0 \\ 0 & \beta & 0 \end{pmatrix}$$

which gives $\lambda_1 = \lambda_2 = 0$, $\lambda_3 = -\beta$.

Now we will use Center Manifold Theory to determine the stability condition of systems (2.3) and (2.4) at equilibrium $\mathbf{E_0} = (0,0,0)$. First, we simplify systems (2.3) and (2.4) by using Taylor series expansion (consider only up to the second order). System (2.3) and (2.4) simplify as follows:

$$\begin{aligned} F'(t) &= -(d_fF^2 + r_cAF) \\ A'(t) &= (1-p_1)r_aAF + \beta E - d_aA^2 \\ E'(t) &= -\beta E + (p_1r_aF - \alpha E)A \end{aligned} \tag{C.22}$$

System (C.22) is already in the desired form with $C = \mathbf{0}_{2\times 2}$, $P = -\beta$, $x = [F, A]$, $H(x,E) = p_1r_aFA - \alpha EA$ and

$$G(x,E) = \begin{bmatrix} -d_fF^2 - r_cAF \\ (1-p_1)r_aAF - d_aA^2 + \beta E \end{bmatrix}.$$

Let

$$\begin{aligned} h(x) &= a_1F^2 + a_2FA + a_3A^2 + \mathcal{O}(F^3, A^3) \\ Dh(x) &= [2a_1F + a_2A + \cdots,\ a_2F + 2a_3A + \cdots] \\ Dh(x)[Cx + G(x,h(x))] &= [2a_1F + a_2A + \cdots,\ a_2F + 2a_3A + \cdots] \\ &\quad \begin{bmatrix} -d_fF^2 - r_cAF \\ (1-p_1)r_aAF - d_aA^2 + \beta(a_1F^2 + a_2FA + a_3A^2 + \cdots) \end{bmatrix} \\ Ph(x) + H(x,h(x)) &= -\beta(a_1F^2 + a_2FA + a_3A^2 + \cdots) + p_1r_aFA - \alpha A(a_1F^2 + a_2FA + a_3A^2 + \cdots) \end{aligned}$$

Setting $Dh(x)[Cx + G(x,h(x))] = Ph(x) + H(x,h(x))$ and collecting terms, we obtain

$$F^2 : 0 = a_1\beta \qquad \Rightarrow a_1 = 0$$

$$
\begin{aligned}
FA &: 0 = a_2\beta + p_1 r_a \qquad \Rightarrow a_2 = -\frac{p_1 r_a}{\beta} \\
A^2 &: 0 = 0
\end{aligned}
$$

Hence, $h(F, A) = -\frac{p_1 r_a}{\beta} FA + \mathcal{O}(F^3, A^3)$. Thus, the flow of the center manifold is given by

$$
\begin{aligned}
F'(t) &= -(d_f F + r_c A)F \\
A'(t) &= (1-p_1)r_a AF + \beta\Big(-\frac{p_1 r_a}{\beta} FA + \mathcal{O}(F^3, A^3)\Big) - d_a A^2 \\
&= (1-2p_1)r_a AF - d_a A^2 + \mathcal{O}(F^3, A^3) \qquad \text{(C.23)}
\end{aligned}
$$

Again, both eigenvalues are zero for system (C.23) at the trivial equilibrium $(0, 0)$. Therefore, we use center manifold theory for the stability at its extinction equilibrium. The system (C.23) is already in the desired form to use center manifold theory. Consider the function $g(F) = b_1 F^2 + b_2 F^3 + \mathcal{O}(F^4)$, then

$$
\begin{aligned}
Dg(F) &= 2b_1 F + 3b_2 F^2 + \cdots \\
Dg(F)G(F, h(F))] &= [2b_1 F + 3b_2 F^2 + \cdots][-d_f F^2 - r_c F(2b_1 F + 3b_2 F^2 + \cdots)] \\
H(x, h(x)) &= 0
\end{aligned}
$$

Similarly as before, by simple calculation and collecting terms we obtain $g(F) \equiv 0$. Therefore, the flow on the center manifold is given by the equation

$$
F' = -d_f F^2
$$

i.e. systems (2.3) and (2.4) are always asymptotically stable at the extinction equilibrium $\mathbf{E_0}$.

2. Stability of interior equilibria for model (2.3)

Let (F^*, E^*, A^*) be an interior equilibrium of model (2.3). Then its stability is determined by the eigenvalues $\lambda_i(F^*, E^*, A^*)$, $i = 1, 2, 3$ of its Jacobian matrix (C.20) at the interior equilibrium (F^*, E^*, A^*), where its characteristic equation is as follows:

$$
\lambda^3 - \left[\sum_{i=1}^{3} \lambda_i\right]\lambda^2 + \left[\sum_{i,j=1, i\neq j}^{3} \lambda_i \lambda_j\right]\lambda - \prod_{i=1}^{3} \lambda_i
$$

with $\lambda_i(F^*, E^*, A^*)$, $i = 1, 2, 3$ being the roots of the above characteristic equation:

$$
\begin{aligned}
\sum_{i=1}^{3} \lambda_i &= -\left[d_f F + 2d_a A + \alpha A + \beta - (r_a(1-p_1)F - c_1\alpha E)\right] < 0 \\
\sum_{i,j=1, i\neq j}^{3} \lambda_i \lambda_j &= -\left[F\left(\frac{2abr_f A}{(b + aA^2)^2} - r_c\right)(1-p_1)r_a A + (p_1 r_a F - \alpha E)(\beta + \alpha c_1 A) - (\beta + \alpha A)(d_f F)\right] \\
&\quad -(r_a(1-p_1)F + \alpha c_1 E - 2d_a A)(\beta + \alpha A + d_f F) > 0 \\
\prod_{i=1}^{3} \lambda_i &= F\left(\frac{2abr_f A}{(b + aA^2)^2} - r_c\right)[p_1 r_a A(\beta + c_1\alpha A) + (\beta + \alpha A)(1-p_1)r_a A] \\
&\quad + d_f F\left[(\beta + \alpha A)(r_a(1-p_1)F + \alpha c_1 E - 2d_a A) - (p_1 r_a F - \alpha E)(\beta + \alpha + \alpha c_1 A)\right] < 0
\end{aligned}
$$

According to the Routh-Hurwitz stability criterion for third-degree polynomial, the sufficient conditions for the above inequalities to be true, which provide the stability of interior equilibria are given by

$$r_a(1-p_1)F + c_1\alpha E < 2d_aA, \quad \frac{2abr_fA}{(b+aA^2)^2} < r_c, \qquad p_1r_aF > \alpha E \quad (\Rightarrow \beta > 0).$$

3. Stability of interior equilibria for (2.4)

Let (F^*, E^*, A^*) be an interior equilibrium of model (2.4). Then its stability is determined by the eigenvalues $\lambda_i(F^*, E^*, A^*)$, $i = 1, 2, 3$ of its Jacobian matrix (C.21) at the interior equilibrium (F^*, E^*, A^*), where its characteristic equation is as follows:

$$\lambda^3 - \left[\sum_{i=1}^{3}\lambda_i\right]\lambda^2 + \left[\sum_{i,j=1,i\neq j}^{3}\lambda_i\lambda_j\right]\lambda - \prod_{i=1}^{3}\lambda_i$$

with $\lambda_i(F^*, E^*, A^*)$, $i = 1, 2, 3$ being the roots of the above characteristic equation:

$$\sum_{i=1}^{3}\lambda_i = -\left[d_fF + \beta + \alpha A + \frac{2d_aA}{1+c_2\alpha E} - r_a(1-p_1)F\right] < 0$$

$$\begin{aligned}\sum_{i,j=1,i\neq j}^{3}\lambda_i\lambda_j = -\Bigg[&F\left(\frac{2abr_fA}{(b+aA^2)^2} - r_c\right)r_a(1-p_1)A + (p_1r_aF - \alpha E)\left(\beta + \frac{\alpha c_2 d_a A^2}{(1+c_2\alpha E)^2}\right)\\ &+(\beta+\alpha A)\left(r_a(1-p_1)F - \frac{2d_aA}{1+c_2\alpha E}\right) + d_fF\left(r_a(1-p_1)F - (\beta+\alpha A) - \frac{2d_aA}{1+c_2\alpha E}\right)\Bigg] > 0\end{aligned}$$

$$\begin{aligned}\prod_{i=1}^{3}\lambda_i = F\left(\frac{2abr_fA}{(b+aA^2)^2} - r_c\right)&\left[p_1r_aA\left(\beta + \frac{\alpha c_2 d_a A^2}{(1+c_2\alpha E)^2}\right) + (\beta+\alpha A)r_a(1-p_1)A\right]\\ &+ d_fF\left[\left(\frac{\beta^2E}{A} + \frac{\alpha c_2 d_a \beta E A}{(1+c_2\alpha E)^2}\right) + (\beta+\alpha A)\left(r_a(1-p_1)F - \frac{2d_aA}{1+c_2\alpha E}\right)\right] < 0\end{aligned}$$

According to the Routh-Hurwitz stability criterion for third-degree polynomial, the sufficient conditions for the above inequalities to be true, which provide the stability of interior equilibria are given by

$$r_a(1-p_1)F < \frac{2d_aA}{1+c_2\alpha E}, \quad \frac{2abr_fA}{(b+aA^2)^2} < r_c, \qquad p_1r_aF > \alpha E \quad (\Rightarrow \beta > 0).$$

The sufficient condition of the interior equilibrium is given by $\frac{r_f aA}{b+aA^2} > r_c$ for both model (2.3) and (2.4). Using this argument, it follows that the sufficient condition of the stability for interior equilibria is $A^2 > \frac{b}{a}$ or $A > \sqrt{\frac{b}{ab}}$. It can be easily verified that $A_2^* > A^c > \sqrt{\frac{b}{a}}$, thus, it can be conclude that the interior equilibrium $\mathbf{E_2}$ is always locally asymptotically stable when it exists. ☐

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