University of Nevada, Reno

Modeling Mutualism and Competition in Interactive Population Dynamics:

How Ants and Aphids Affect Lycaenid Butterfly Ecology

A thesis submitted in partial fulfillment of
the requirements for the degree of

Bachelor of Science in Mathematics and the Honors Program

by

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Abstract

Modeling population dynamics that include mutualistic interactions is an important and complex problem in theoretical biology and quantitative ecology. Mutualistic interactions, which are generally considered relationships in which two or more species benefit from each other's presence, play a significant role in determining population dyanmics, and are essential to fully understanding the dynamics of interacting species. However, mutualistic interactions are a historically understudied topic in ecology; accurately describing populations in multi-species interactions is inherently challenging (Hastings & Powell, 1991), and models describing these populations increase greatly in complexity as the intricacy and interdependence of the relationship increases. As such, there have been relatively few attempts within the field to fully account for the particulars of these relationships. Through numerical simulation of lycaenid butterfly and aphid populations together with deterministic and stochastic mathematical models, this research aims to more thoroughly explore the facets of mutualistic and competitive interactions in population dynamics. By refining a previous model for lycaenid butterfly populations (Forister, Gompert, Nice, & Fordyce, 2010) and by adapting the models to include the dynamics of two interactive species, ants and aphids, we hope to generate a model which simultaneously predicts the fluctuation in the focal species while providing insight to the rich and complex interplay of mutualistic and competitive interactions in theoretical ecology. By using this model to examine the population dynamics of these species, we hope to generate a method which will be useful in explaining endangered lycaenid butterfly populations as well as understanding the role of mutualism in the context of quantitative and theoretical ecology.

Acknowledgements

First and foremost, I would like to sincerely thank both of my thesis advisors, Dr. Anna Panorska and Dr. Matthew Forister. As my advisor and one of my most effective teachers, Dr. Panorska aided me greatly with her consul and was responsible for guiding me into starting this research. I could never have gotten as far as I did in this work without her extensive knowledge of mathematics and her dedicated support, and for that I'm very grateful. Dr. Forister has also been invaluably helpful to me in guiding me through past research and helping me understand the scope of the ecology we were studying. From educating me on the biology of the species at hand to helping me debug our code for hours, Dr. Forister has been an incredible professor to work with, and I couldn't have wished for a better professor to introduce me to this field of research. Additionally, my thanks goes out to the Nevada System of Higher Education and the National Science Foundation for making me a recipient of the Honors Undergraduate Research Award, which funded the research I conducted. Lastly, I would also like to thank the Honors Program for making this opportunity to conduct research available to me, and helping me work towards completion of my degree. In particular, I give my thanks to Dr. Tamara Valentine for navigating me through my honors degree and making the path interesting and educating. Her assistance towards my degree was irreplaceable, and I'm very grateful for it.

<u>Table of Contents</u>

List of Figures

Introduction:

Mutualism exists when two or more species benefit from interacting with one another, and there is a growing field of research suggesting that it plays a much larger role in shaping population dynamics than previously thought (Boucher, 1988). Butterflies in the family Lycaenidae provide an excellent example for studying mutualism, since the caterpillars of this species are known to interact with ants in a way that benefits both species- caterpillars provide nectar secretions for ants in return for protection from certain predators. Furthermore, ants are known to maintain a similar relationship with certain aphids (Breton & Addicott, 1992). This research aims to improve upon previous work on lycaenid butterfly life cycles (Forister, *et al*, 2010) by extending previous models to the mutualisms between these populations, as well as modeling the competition which exists between aphids and lycaenid butterflies for food and other resources. By studying previous research and utilizing both deterministic and stochastic mathematical techniques that model changes in the populations of the interactive species, we have developed a framework that simultaneously predicts the fluctuation in the focal species while providing insight to the rich and complex interplay of mutualistic interactions in theoretical ecology.

The model constructed for this research focused on simulating populations of butterflies and caterpillars, and reproduced interactions between the two species. Using the R statistical language, we simulate many instances of aphid and butterfly populations over multiple generations and monitor the rise and decline of these populations. To ensure that the code accurately predicted these dynamics, we incorporated various parameters to represent biological factors that increased or decreased the survival factor and fecundity of both species. Both species were assumed to develop on a native host plant, *Astraglus candensis*, as well as a non-native, novel host plant, alfalfa (*Medicago sativa*), which is less beneficial to aphids and lycaneid caterpillars; representing both plants within the model allowed us to facilitate a competition factor between the two species for these resources. Additionally, we were able to numerically simulate the proportion of each

population that was tended by ants, as well as the relative degree of benefit that each species yielded from interacting with ants. These factors for resources and ant interaction, along with parameters which accounted for various other biological aspects, were used to determine the productivity of both species for a certain generation. Structurally, the model began with a generation of an initial aphid and caterpillar population. One generation of an aphid population consisted of juveniles progressing to adulthood, with their progress dependent on the ecological parameters as well as on the number of butterflies from the previous generation. Similarly, each caterpillar went through the process of moving from eggs to larvae, larvae to pupae, and pupae to adults; the number which survives this progression depended upon the ecological factors incorporated through parameters, such as interaction with ants and the abundance of resources, and the number of aphids in the previous generation. The model thus simulated populations of aphids and butterflies over multiple generations and multiple replicate (independent) populations. We observed changes in the population dynamics over each of these cycles; changing parameters of the model for a simulation meant we could investigate the conditions under which butterflies would thrive and aphids would go extinct, for example. To account for the benefit of mutualism between these species and the disadvantages of competition, we included four linear equations that incorporated certain ecological parameters as well as the number of aphids and caterpillars for a given generation. Each of the four equations that modeled mutualistic and competitive interactions included a scaling factor specific to them which we varied across a range of possible values to determine where stable populations of aphids and butterflies coexisted. The final results from this work came from the analysis of these four scaling factors. By investigating the stability of these populations with respect to the degree that these parameters bolstered or weakened the populations of both species, we determined the relative strength of the mutualism between ants and lycaneid butterflies to the mutualism between ants and aphids, as well as the competition between aphids

and butterflies. The analysis of these exchanges is what led to the conclusions regarding the interactions between these species.

After interpreting the results about the ranges in which these competitive and mutualistic interactions render stable populations for each of these species, we attempt to generalize our results to discuss potential effects of mutualism in various species. As mentioned above, although mutualism is a critical form of interaction within biology and ecology, it is critically understudied and there is much to understand about its variant instances throughout nature. Furthermore, there is growing evidence within ecology to suggest that the positive effects of mutualism of a species are critical to the population dynamics of that species, and that competition between rivals does not dictate these dynamics as much as was previously believed (Boucher, 1988). The desire to fully understand the scale of mutualistic interactions between species was the motivation for this project. Additionally, the direction this research would take into the future would be to elaborate on these results to create a model for mutualism which we can use to explain these interactions for a multitude of species; the power to explain these interactions for the populations dynamics of any one species population dynamics would greatly expand the modeling power for biologists and ecologists. Although this aspect is not currently present in the work described here, creating such a model for mutualism in lycaenid butterflies alone is a great asset to the field, as this family is very often studied within ecology (Agrawal & Fordyce, 2000). This family of butterflies is relatively young evolutionarily, and thus is particularly interesting ecologically to see how they adapt and what developments occur in the biology of the family. Furthermore, a fair number of lycaenid butterflies are endangered, due in particular to habitat desctuction. Thus having a model that aims to reproduce simulations of such a species is invaluable as a tool of conservation. This allows the model developed within this thesis to be realized as a tool to aid the conservation of this family of butterflies. Finally, this model is unique in that it incorporates <u>two</u> mutualisms and the interaction between them: one for ants and caterpillars, and one for ants and aphids. The latter is perhaps one

of the most studied beneficial interactions in ecology, because it is common and easily observed (MacMahon, Mull, & Christ, 2000. Setting the mutualism of butterflies and ants within this context changes the perspective on how ecologists might better understand these interactions. These all contribute to the justification of our research within the field of theoretical ecology.

Literature Review:

This work draws insights on deterministic approaches, yet the models we produce have a strong stochastic component previously developed that is specific to lycaenid butterfly ecology (Forister, *et al*., 2010). We use the statistical model created by Forister, *et al*., (2010), as a framework for the model we create to simulate both aphids and butterfly populations. While a classical approach to dealing with mutualisms is using some deterministic system of equations, which are common for ecological models for interacting species (Otto & Day, 2007), the present approach we used in this research sacrificed the analytical benefits from such a system for a more realistic interpretation of the semi-random, stochastic flux of these populations. Additionally, because of the complexities of the life histories of these species, our model requires a larger number of ecological parameters used for predicting survival rates for aphids and caterpillar populations. These demographic models put forth by Forister, *et al*., (2010) previously focused mainly on the role ants play on facilitating diet breadth, or the range of host plants lycaenid caterpillar populations are able to live on. Studying diet breadth is important as this ecological factor plays a role in determining whether a species is able to adapt to changing environments and habitats, and the model constructed by Forister *et al.,* (2010) looked into studying mutualisms within host-range evolution. This model provided a basis for our work in modeling mutualistic interactions and allowing caterpillars to exist on an optimal host (*A. canadensis*) and a sub-optimal host (*M. sativa*), focusing primarily on the ratio of species on one plant to another. The research done here deviates from this focus by incorporating aphids and having ants play a stronger role in the success or failure of the populations of these two species,

to shift the focus of the model to the indirect mutualism and competition between these species. As such, we are potentially able to account many of the critical aspects of the ecology of these species, such as diet breadth and host-range evolution, while keeping the critical analysis on the mutualistic interactions.

Although our research is specific to butterflies from the lycaenid family and ants, and is extensive in the parameters it incorporates, research done in modeling multi-species mutualism dictates some of the aspects of the interactions between organisms. In particular, it is essential to understand the stability in ecological models for interacting species (Goh, 1979), for the stability of solutions over an unbounded or even finite parameter region implies that it is possible for these interactions to exist naturally. This research provides for a more rigorous mathematical treatment of the model and potentially gives insight into stability in a biological setting. Using nonlinear models for populations, Goh (1979) discusses the global stability of settings where any numbers of species are interacting. More importantly, Goh (1979) also discusses the general case of two species and draws the conclusion that the population densities of each species are dependent upon one another, and thus maintain a balance for mutualism to be possible. This research is essential in drawing characteristics for the model we employ towards ants and lycaenid butterflies; furthermore, development of the model we create in this research generates a concrete example of the stability discussed in Goh (1979) at work, and demonstrates how to expand on the ecological model equations with two species.

Methodology:

DISCUSSION

We focus on the techniques put forward by Forister *et al*. (2010) in finding models for predicting lycaenid caterpillar populations on native and sub-optimal host plants, and utilize this statistical

approach to model the population data. The mathematical model developed was encoded to a numerical program using the R statistical language, which is an effective and popular choice of software in the field of ecology and statistics. The program in R simulates populations for butterflies and aphids and then monitors the life cycles of these species, and looks at the number of young and adults for each species in recurring generations. As mentioned briefly above, the model contains multiple parameters to consider a large range of ecological and biological factors that effect the lifecycle of these species, and hence there were many variables representing these parameters in its numerical implementation. Both species will be placed on the optimal *A. canadensis* and the sub-optimal alfalfa *M. sativa*, with appropriate scaling to account for the effectiveness of the plants as host species for caterpillars and aphids. Additional parameters are account for the proportion of each species tended by ants, as well as the relative benefit each species gains from interacting with ants. The values of these parameters, which express the degree of benefit or detriment of these species to one another, are ones that were derived from natural observations and literature on the subject (Pierce, Braby, Heath, Lohman, Matthew, Rand, & Travassos, 2002).

The structure of our model allows us to observe multiple generations of each species, thus the continual effect of the ecological parameters on each of the populations. For a single replicate, our model generates data for an initial aphid generation, which starts by creating some given number of live young. These young develop into adults with s given probability for survival success, which depends upon the interaction with ants and the number of butterflies in the previous generation, as well as the availability of resources within the environment. These adult aphids then reproduce to determine the number of young in the next generation. After this process is complete for aphids, the code simulates a similar process for caterpillars, first using survival probabilities to determine the number off eggs which become larvae, larvae which become pupae, and pupae which become adults. As with aphids, the success of these individual transitions depends on a number of

ecological factors, such as fecundity, rate of flowering for *M. sativa,* as well as the degree of interaction with ants and the number of aphids in the previous generation. Finally, we determine the initial number of butterfly eggs for the next generation from the reproduction of adults in the current generation. This cycle illustrates the process of our code for one generation, and this repeats multiple times cyclically for one replicate; the data we then collect for each species is then collected across multiple replicates, generating independent iterations of both interacting species. Simulating the data in this manner allows us to view entire life-cycles of both aphids and butterflies and then run statistical inferences using replications of them, to ensure and understanding of predictability and stochasticity in outcomes (see Figure 1).
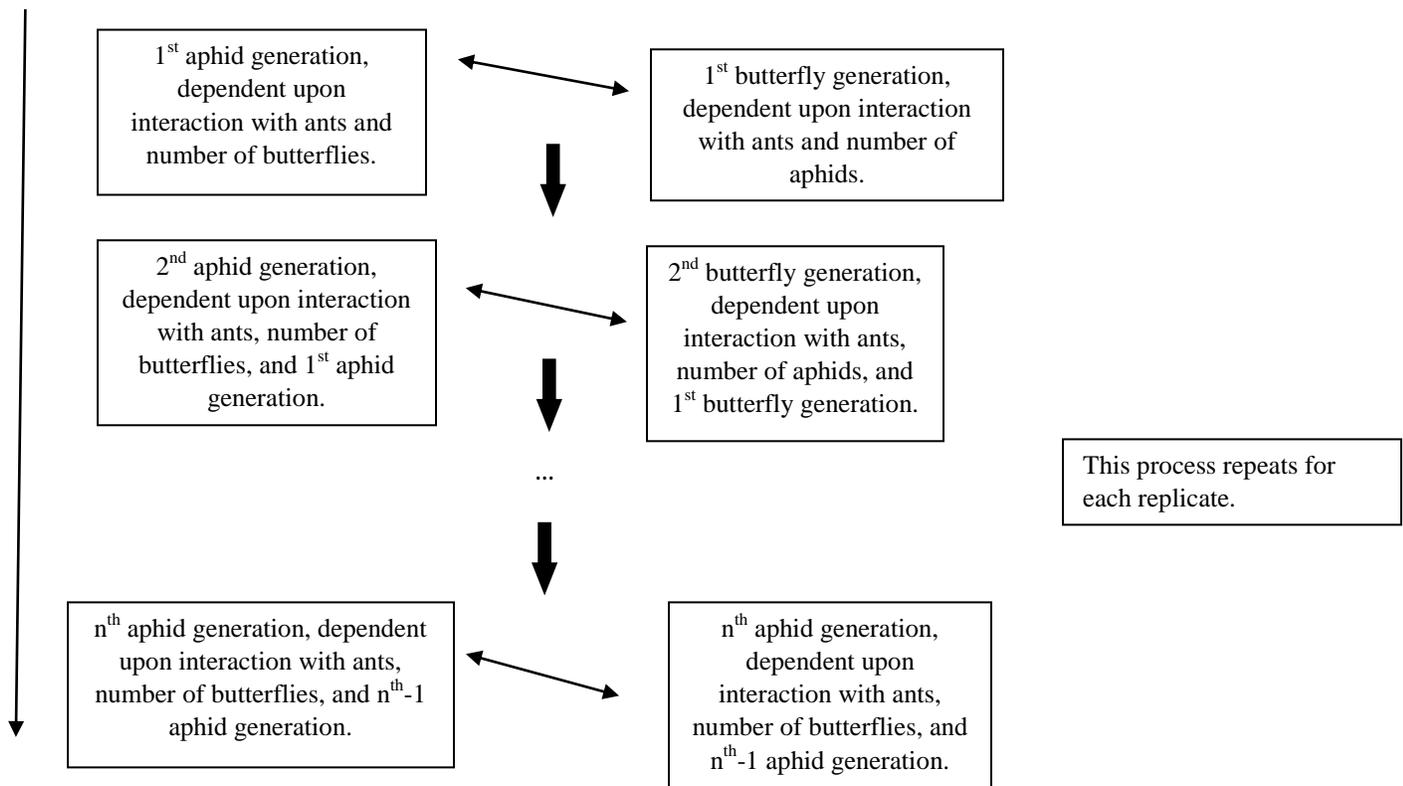

Figure 1 – Algorithm Flowchart: This flow chart illustrates the algorithm for our model in terms of what is occurring in the replicates and the generations for each species. In R, each species is first developed and then progresses through multiple generations, with each depending on the last. This process is then replicated for statistical inference. The interactions for mutualism and competition for this code exist entirely within the generation loop.

The part of our model of the most interest for this research is contained in four separate equations which relate the populations of aphids and butterflies. The interaction between the two is symmetric: (i) the mutualistic (positive) effect that aphids have on butterflies, (ii) the competitive (negative) effect that aphids have on butterflies, (iii) the mutualistic (positive) effect that butterflies have on aphids, and (iv) the competitive (negative) effect that butterflies have on aphids. The positive and negative effect that aphids have on butterflies and butterflies have on aphids need not be equal- that is, we can model these parameters such that butterflies derive more benefit from the presence of aphids than aphids do from the presence of caterpillars. While these modeled interactions provide a direct effect on each of these populations, the research looks at the overall indirect effect both species have on one another (see Figure 2).
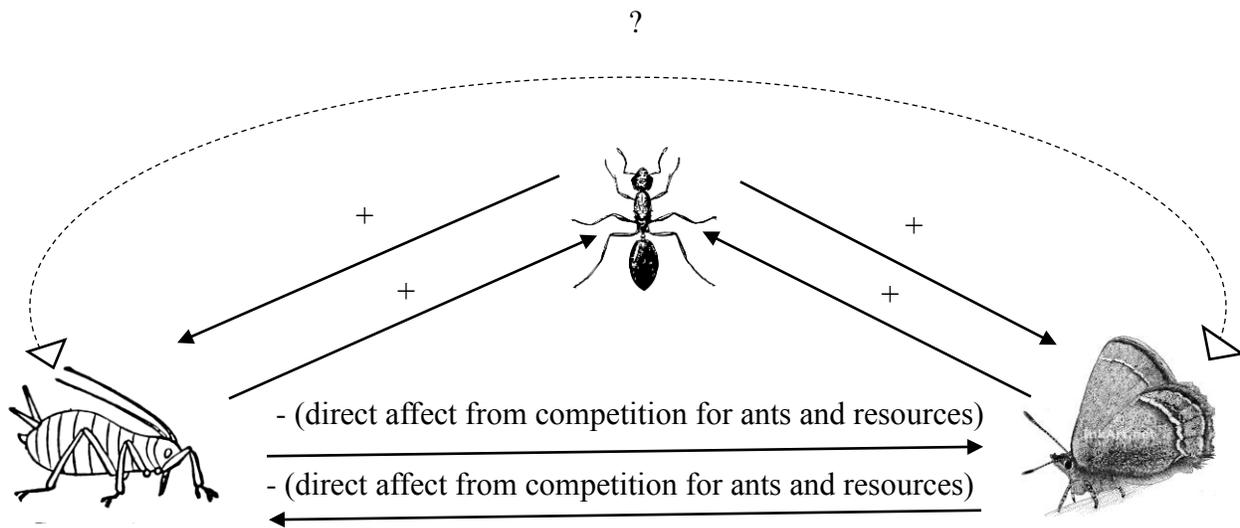

Figure 2 – Graph of Biological Interactions: Flow chart depicting kinds of interactions between aphids (bottom left), ants (top), and lycaenid butterflies (bottom right). The lines with positive feedback represent mutualisms between aphids and ants and butterflies and ants, in which both species benefit from interaction, while the interaction between aphids and butterflies is negative from competing for attention for ants and resources. The dotted line illustrates the indirect relationship between aphids and butterflies, studied in this research, which may be positive or negative.

The overall factor speaks to whether aphids and butterflies derive a net benefit or a net disadvantage from living in the same environment and coexisting as both organisms interact with ants. By viewing population growth rates for both aphids and butterflies, as well creating a heat

map illustrating the densities of aphids and caterpillars for given values of the scaling factors for the interactions mentioned above, we are able to graphically interpret the effect these interaction parameters have on the population levels of both organisms.

MATHEMATICAL MODEL

In this section, we describe in detail the mathematical model we used to conduct our research. This model was also implemented numerically in R to iteratively simulate populations of aphids and butterflies. Here we list the equations which are present within our generational loop which determine these populations. Initially, we begin with a number of butterflies on *M. sativa* (suffixed with "Med") and *A. canadensis* (suffixed with "Ast"), as well as an initial number of aphids on both of these plants:

- Initial Populations

    - For aphids

    $aphidYoung.Med = aphid.MaxPop * p_{aphid.start} * p_{aphid.Med}$

    $aphidYoung.Ast = aphid.MaxPop * p_{aphid.start} * (1 - p_{aphid.Med})$

where *aphidYoung.Med* represents the number of young aphids on *M. sativa*, *aphidYoung.Ast* represents the number of young aphids on *A. Canadensis*, *aphid.MaxPop* represents the carrying capacities for the aphid population, $p_{aphid.start}$ is the proportion of this carrying capacity present initially (that is, $0 \leq p_{aphid.start} \leq 1$), and $p_{aphid.Med}$ is the proportion of aphids that live on *M. sativa* ($0 \leq p_{aphid.Med} \leq 1$).

    - For butterflies

    $butterflyYoung.Med = butterfly.MaxPop * p_{butterfly.start} * p_{butterfly.Med}$

    $butterflyYoung.Ast = butterfly.MaxPop * p_{butterfly.start} * (1 - p_{butterfly.Med})$

where *butterflyYoung.Med* represents the number of young butterflies on *M. sativa*, b*utterflyYoung.Ast* represents the number of young butterflies on *A. Canadensis, butterfly.MaxPop*

represents the carrying capacity for the butterfly population, $p_{butterfly.start}$ is the proportions of this

carrying capacity present initially (that is, $0 \leq p_{butterfly.start} \leq 1$), and $p_{butterfly.Med}$ is the proportion of

butterflies that live on *M. sativa* ($0 \leq p_{butterfly.Med} \leq 1$).

 After establishing these initial populations, our model describes development through generations.

We begin with aphids, noting that aphids only take one step to mature into adults:

- <u>Development of generations</u>

- <u>Aphids develop into adults</u>

> *aphidAdult.Med =*
>
> *aphidYoung.Med * (aphidSurvival$_{Min}$ + Λ (aphidSurvival$_{Max}$ − aphidSurvival$_{Min}$))*
>
> *aphidAdult.Ast =*
>
> *aphidYoung.Ast * (aphidSurvival$_{Min}$ + Λ (aphidSurvival$_{Max}$ − aphidSurvival$_{Min}$))*

Here, *aphidAdult.Med* and *aphidAdult.Ast* are the number of adult aphids on *M.sativa* and *A.*

canadensis, respectively, and *aphidSurvival$_{Min/Max}$* is a proportion determining the minimum and

maximum survival rates of aphids (also on the interval [0,1]). Finally, Λ is a random variable

scaling factor coming from a beta distribution with parameters 2 and 3, that is $\Lambda \sim$ Beta(2,3), where

$$P(\Lambda = \lambda) = f_\alpha(\lambda) = \frac{\lambda(1-\lambda)^2}{B(2,3)}, where\ B(2,3) = \int_0^1 u(1-u)^2 du$$

This scaling factor adds randomness to the survival rate for aphids and makes the model used in

this research more realistic. Once this adult population of aphids has been realized, we can simulate

reproduction for the next generation of aphids.

- <u>Aphids birth next generation</u>

> *newAphidYoung.Med =*
>
> *aphidYoungBirthed$_{Min}$ + Λ_{Med}*(aphidYoungBirthed$_{Max}$ − aphidYoungBirthed$_{Min}$)*
>
> *newAphidYoung.Ast =*
>
> *aphidYoungBirthed$_{Min}$ + Λ_{Ast}*(aphidYoungBirthed$_{Max}$ − aphidYoungBirthed$_{Min}$)*

As indicated above, *newAphidYoung.Med* and *newAphidYoung.Ast* are the number of new aphids born on *M. sativa* and *A. canadensis*, respectively. These values depend upon *aphidYoungBirthed$_{Min}$* and *aphidYoungBirthed$_{Max}$*, which are ecological parameters accounting for the number of offspring produced by one individual (or pair of individuals). These values are combined with random variables Λ_{Med} and Λ_{Ast}, which are values which again are generated from a beta distribution with parameters 2 and 3 that are specific to fecundity factors of *M. sativa* and *A. canadensis*, respectively.

aphidYoungTotal = newAphidYoung.Med + newAphidYoung.Ast

*aphidYoungNext.Med = aphidYoungTotal * p$_{aphid.Med}$*

*aphidYoungNext.Ast= aphidYoungTotal * (1- p$_{aphid.Med}$)*

We then add together the number of aphids on both plants to yield *aphidYoungTotal*, which is then multiplied by $p_{aphid.Med}$ to determine the number of these young on *M. sativa*, while its complement is used to determine the number on *A. Canadensis*. These numbers are then used to determine the number of aphid young on both plants for the next generations, which concludes the development and reproduction process for aphids. We now describe the similar processes for butterflies, noting that as caterpillars go through metamorphosis, they go through 4 life-stages: eggs, larvae, pupae, and adults. We simulate the survival through these stages:

- Eggs develop into larvae

butterflyLarvae.Med = butterflyYoung.Med *

(butterflyLarvaeSurvival$_{Min}$ + Λ (butterflyLarvaeSurvival$_{Max}$ – butterflyLarvaeSurvival$_{Min}$))

butterflyLarvae.Ast = butterflyYoung.Ast *

(butterflyLarvaeSurvival$_{Min}$ + Λ (butterflyLarvaeSurvival$_{Max}$ – butterflyLarvaeSurvival$_{Min}$))

where *butterflyLarvae.Med* and *butterflyLarvae.Ast* are the number of larvae present on *M. sativa* and *A. canadensis*, respectively, *butterflyLarvaeSurvival$_{Min}$* and *butterflyLarvaeSurvival$_{Max}$* are the minimum and maximum survival rates for butterfly larvae (respectively), and Λ is again a random

variable scaling factor from the beta distribution. After the larval stage, butterflies move through pupation:

Larvae develop into pupae

$butterflyPupae.Med = butterflyLarvae.Med*$

$(butterflyPupaeSurvival_{Min} + \Lambda \, (\, butterflyPupaeSurvival_{Max} - butterflyPupaeSurvival_{Min} \,) \,)$

$butterflyPupae.Ast = butterflyLarvae.Ast*$

$(butterflyPupaeSurvival_{Min} + \Lambda \, (\, butterflyPupaeSurvival_{Max} - butterflyPupaeSurvival_{Min} \,) \,)$

where *butterflyPupae.Med* and *butterflyPupae.Ast* are the number of pupae present on *M. sativa* and *A. canadensis*, respectively, *butterflyPupaeSurvival$_{Min}$* and *butterflyPupaeSurvival$_{Max}$* are the minimum and maximum survival rates for butterfly pupae (respectively), and Λ is again a random variable scaling factor from the beta distribution. After pupation, butterflies finally develop into adults:

- Pupae develop into adults

$butterflyAdult.Med=butterflyPupae.Med*$

$(butterflyAdultSurvival_{Min} + \Lambda \, (\, butterflyAdultSurvival_{Max} - butterflyAdultSurvival_{Min} \,) \,)$

$butterflyAdult.Ast= butterflyPupae.Ast*$

$(butterflyAdultSurvival_{Min} + \Lambda \, (\, butterflyAdultSurvival_{Max} - butterflyAdultSurvival_{Min} \,) \,)$

Here, the number of adults on both *M. sativa* and *A. canadensis* is given by the values *butterflyAdult.Med* and *butterflyAdult.Ast*. These values are populated by the number of butterflies which survived through pupation, as well as survival rates for adults given by *butterflyAdultSurvival$_{Min}$* and *butterflyAdultSurvival$_{Max}$*, as well as a realization of the random variable Λ from the beta distribution. This collectively creates our estimate for the number of adult butterflies; with this, we are now able to simulate reproduction.

- Butterflies birth next generation

newButterflyEggs.Med =

butterflyYoungBirthed$_{Min}$ + Λ$_{Med}$*(butterflyYoungBirthed$_{Max}$ – aphidYoungBirthed$_{Min}$)

newButterflyEggs.Ast =

butterflyEggsBirthed$_{Min}$ + Λ$_{Ast}$*(butterflyEggsBirthed$_{Max}$ – aphidYoungBirthed$_{Min}$)

As indicated above, *newButterflyYoung.Med* and *newButterlyYoung.Ast* are the number of new

butterflies born on *M. sativa* and *A. canadensis*, respectively. These values depend upon

butterflyYoungBirthed$_{Min}$ and *butterflyYoungBirthed$_{Max}$*, which are ecological parameters

accounting for the number of offspring produced by a pair of individuals. These values are

combined with random variables Λ_{Med} and Λ_{Ast}, which are values which again are generated from a

beta distribution with parameters 2 and 3 that are specific to fecundity factors of *M. sativa* and *A.*

canadensis, respectively.

butterflyEggsTotal = newButterflyEggs.Med + newButterflyEggs.Ast

butterflyYoungNext.Med = butterflyEggsTotal * p$_{butterfly.Med}$

butterflyYoungNext.Ast = butterflyEggsTotal * (1- p$_{butterfly.Med}$)

We then add together the number of aphids on both plants to yield *butterflyYoungTotal*, which is

then multiplied by *p$_{aphid.Med}$* to determine the number of these young on *M. sativa*, while its

complement is used to determine the number on *A. canadensis*. These numbers are then used to

determine the number of aphid young on both plants for the next generations, which concludes the

development and reproduction process for aphids. Doing this ends the cycle through generations,

and so this process represents one full life-cycle of both species.

We now briefly review the linear equations which describe how aphids and butterflies interact with

one another. As mentioned previously, aphids and butterflies interact in a direct competitive sense

that harms both populations, yet also indirectly in a somewhat mutualistic sense, reinforcing the

number of ants in the environment that can aid both species. Here, we illustrate the formulas that

show the positive and negative effects butterflies have on aphids- the effect that aphids have on butterflies is completely symmetric.

To simulate the indirect positive effect that aphids have on butterflies, we use a linear model that increases the proportion of butterflies tended by ants as a function of the number of aphids present:

- <u>Mutualistic effect of butterflies on aphids</u>

$$AphidTendMod = MutFactor * ((p_{TendMax} - p_{TendMin})/ butterfly.MaxPop) * butterflyTotal$$

where *AphidTendMod* is the modification on the number of aphids tended by ants, $p_{TendMax}$ and $p_{TendMin}$ are the maximum and minimum proportion of the aphid populations tended by ants, respectively, *butterfly.maxPop* is the carrying capacity of butterflies, and *butterflyTotal* is the total number of butterflies for that specific generation. Finally, *MutFactor* is the scaling factor that determines the <u>strength</u> of this interaction. Note here that the slope of this linear equation is dependent on the change in the maximum and minimum proportion of aphids tended, as well as the number of butterflies. Thus, if we increase the scaling factor *MutFactor*, we increase the degree which the number of butterflies helps the number of aphids.

Similarly, to simulate the direct negative effect that comes from butterflies and aphids competing for food and space resources, we use a linear model that decreases the survival rate of aphids in their progression to adulthood:

- <u>Competitive effect of butterflies on aphids</u>

$$AphidSurvivalMod =$$

$$CompFactor * ((aphidSurvival_{Max} - aphidSurvival_{Min})/butterfly.MaxPop) * butterflyTotal$$

where *AphidSurvivalMod* is the modification on the number of aphids that survive to become adults, $aphidSurvival_{Max}$ and $aphidSurvival_{Min}$ are the maximum and minimum proportions of aphids that will survive to become adults, respectively, *butterfly.maxPop* is the carrying capacity

of butterflies, and *butterflyTotal* is the total number of butterflies for that specific generation.
Finally, *CompFactor* is the scaling factor that determines the <u>strength</u> of this interaction. Notice
here that the slope of this linear equation is dependent upon the initial survival probabilities as
well as the number of butterflies. Thus, if we increase the scaling factor *CompFactor*, we increase
the degree which the number of butterflies hurts the number of aphids.

These equations illustrate the relationships established between the two species, and our research
was on the investigation of how the scaling factors in the above equations alter the population
sizes.

Results:

Analysis of the data that is produced from our model lets us understand to some effect the degree of
the key interactions between aphids and butterflies, both mutualistic and competitive. Initially, we
wanted to observe the values of the many ecological parameters that were necessary to simulate
coexistence of aphids and butterflies. In these preliminary simulations, the population sizes of
aphids and butterflies had no negative affect one on another, and simply shared a mutualistic
interaction with ants. We investigated variation in the survival rates and other factors that accounted
for the success or failure of each species. After doing so, we were able to recognize a region (in this
case, a combination of parameters) in which both species were persisting with stable populations.
Given below are histograms (sampled across replicate simulations) which describe the population
growth rate λ for both aphids and butterflies (written as lambdaA and lambdaB, respectively) for a
simulation of our code with 50 replicates and 50 generations. We note that neither species goes
towards extinction ($\lambda=1$ is a stable population, and greater values correspond to a growing
population) , implying that at this level they can coexist with one another; additionally, the growth
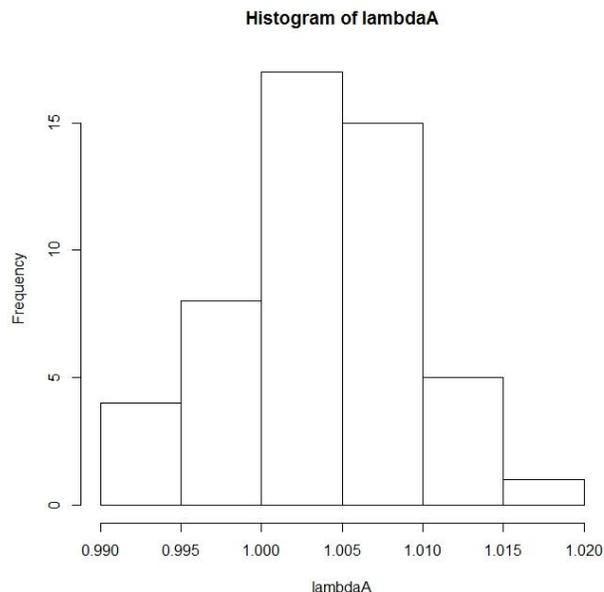rates appear to be normally distributed from the forms of the histograms (See Figure 3a, 3b).

Histogram of lambdaA

Figure 3a - **Histogram of Population Growth Rates for Aphids:** Histogram depicting the population growth rates for aphids, λ_A, produced using R. These histograms were outputs for our code when run with a realization of 50 replicates and 50 generations. We can see that they approximate the normal distribution from their form.
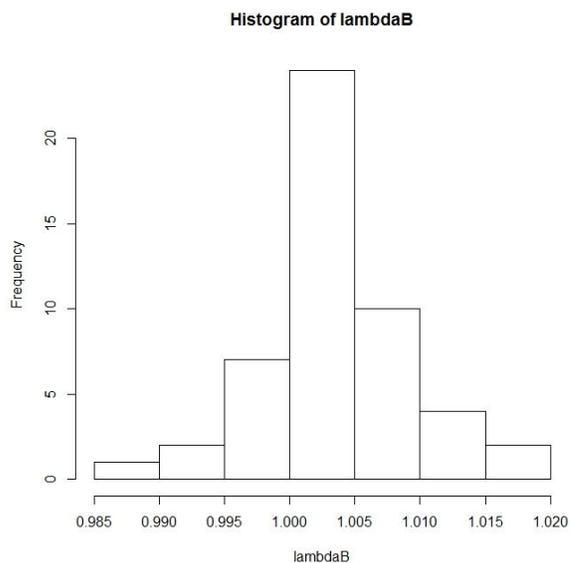
Histogram of lambdaB

Figure 3b - Histogram of Population Growth Rates for Butterflies: Histogram depicting the population growth rates for butterflies, λ_B, produced using R. These histograms were outputs for our code when run with a realization of 50 replicates and 50 generations. We can see that they approximate the normal distribution from their form.

After we created these stable populations, we began investigating the effects of interaction between the species. By varying the scaling factors on the positive and negative effects that aphids had on butterflies and butterflies had on aphids, we were able to see how affected each species was by these particular interactions. To view the sizes of these populations over multiple values of these

scaling factors, we used the heat map function embedded within R. Initially, we designed these

graphs represented by "heatmaps" to investigate a similar range of reciprocal positive and negative

effects. We could then display the sizes of the populations (averaged across the final generation of

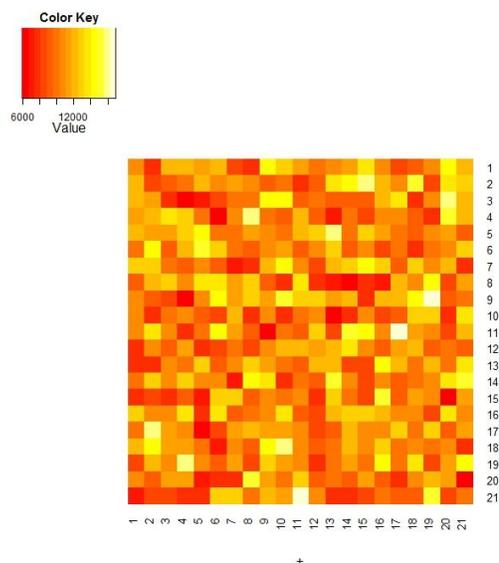replicate simulations) by the color of the heatmaps (See Figures 4a, 4b).

Figure 4a – Comparison of Positive/Negative Effects for Aphids: Graphs using the heatmap functionality in R depicting the success of aphids for varying values of the scaling factors for mutualism (horizontal axis) and competition (vertical axis). This data was generated from a realization of our code with 50 replicates and 50 generations for species. Here, each square represents one simulation of our code, and the key in the upper-left illustrates that darker shades represent lower values for the populations. We see here that for small changes in these interaction factors, aphid populations are quite robust to change.
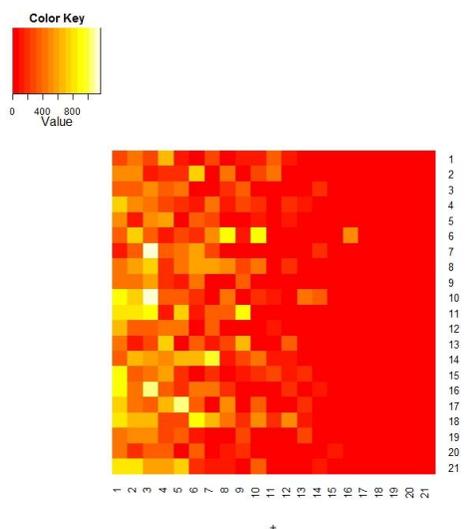

Figure 4b – Comparison of Positive/Negative Effects for Butterflies: Graphs using the heatmap functionality in R depicting the success of butterflies for varying values of the scaling factors for mutualism (horizontal axis) and competition (vertical axis). This data was generated from a realization of our code with 5 replicates and 5 generations for species. Here, each square represents one simulation of our code, and the key in the upper-left illustrates that darker shades represent lower values for the populations. Note that butterflies go extinct for various values of these factors, indicating that butterflies are more sensitive to changes in these interactions.

Analysis of these graphs allows us to infer which values of these scaling factors allow populations of both species to persist. This analysis allowed us to determine how each species depended upon one another. In particular, we could see which organism benefited more from the presence of the other, as well as which organism suffered more from the presence of the other. Doing this allows us to predict the outcome of interaction in nature.

Discussion:

As illustrated in graphs describing the positive and negative interactions of each species, we see initially that aphids are robust to changes in the scaling factors- despite what the values of these scaling factors are, aphid population sustain themselves somewhat reliably but stochastically, as we might expect them too without substantial influence from butterflies. This may be due to the rate at which aphids reproduce, which is much higher than the rate at which butterflies reproduce. This higher level of productivity implies that both the positive and negative effects butterflies have on aphids is negligible in comparison to the population sizes.

Alternatively, butterflies are highly affected by the values of these scaling factors. We can see that in particular, for large values of the scaling factor which describes the competitive effect that aphids have on butterflies, butterfly populations go extinct (apparent by the density of the graph in red, where the size of the population is 0 at the end of the simulations). Further analysis found that for butterfly populations to not go extinct, the threshold value for the scaling factor was somewhere in the range from 2-3. Similarly, although not as apparent in the graph, we can see that the indirect mutualism between aphids and butterflies can bolster butterfly populations significantly, and even enough to counteract the negative effect aphids have, depending on the sizes of these scaling factors. This implies there is in fact a range where butterflies benefit from the presence of aphids, while aphids are indifferent to the presence of butterflies. This again can be explained by the

relative prosperity of aphids compared to butterflies. Ecologically, these results are quite intriguing as they imply that butterfly populations are sensitive to the amount of aphids around, and thus could depend greatly on their interaction with aphids.

The model is contribution to the field of multi-species modeling and an extension of previously developed models of these populations, in that this simulation helps provide an approach for modeling mutualism between any two species. Lycaenid butterflies are some of the most studied subjects in ecology, and a comprehensive model for their interactions with ant populations enables ecologists to use it for a variety of different subjects or populations. Additionally, this research is a specific example of a more general framework of mutualism between species. This framework is interesting in its own right as a description of how mutualism between species appears and effects the population dynamics of the species. Finally, this model explores the mathematics that is inherent in complex multi-species interaction, and thus moves toward answering questions of how modeling can be used within the field of ecology as it matures and creates theoretical frameworks that attempt to encompass the complexity of natural systems.

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